J. exp. mar. Biol. Ecol., 1976, Vol. 23, pp. 171–190; © North-Holland Publishing Company

ECOLOGICAL STUDIES OF THE SALT MARSH ECAD *SCORPIOIDES* (Hornemann) Hauck OF *ASCOPHYLLUM NODOSUM* (L.) Le Jolis[1,2]

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Abstract: The seasonal and spatial distribution of the free-living ecad *scorpioides* (Hornemann) Hauck of *Ascophyllum nodosum* (L.) Le Jolis are described from the Great Bay Estuary System of New Hampshire–Maine, U.S.A. The growth and distribution of ecad *scorpioides* show a variety of phenological and distributional relationships between *A. nodosum* and the marsh grass *Spartina alterniflora* Loiseleur-Deslongchamps. A biomass maximum of ecad *scorpioides* was found in the fall during two consecutive years; it may be attributable to an influx of source material (*i.e.*, *A. nodosum*) after storms, as well as normal seasonal growth of the ecad. *Spartina alterniflora* provides initial stability for the progenitor fragments of ecad *scorpioides* and a protective canopy during the summer. Sexual reproduction of the ecad *scorpioides* was only recorded during one of the three years of study. The morphology and reproduction of ecad *scorpioides* is compared and contrasted with the attached *A. nodosum*, as well as with several detached ecads. A gradient of morphology is evident from typical *A. nodosum* to the extreme 'marsh' ecad *scorpioides*.

INTRODUCTION

The fucoid brown alga *Ascophyllum nodosum* (L.) Le Jolis is a dominant intertidal alga of North Atlantic shores of Europe, North America and adjoining parts of the Arctic Sea (Baardseth, 1970). Typically, it grows attached to large boulders or rock outcrops in sheltered coastal and estuarine sites (Lewis, 1964). Several detached, free living populations of *A. nodosum* have also been recorded from sheltered Atlantic locations (Baker & Bohling, 1916; Gibb, 1957; Taylor, 1957; South & Hill, 1970). The detached plants are morphologically distinct from the attached ones; in addition, the former plants exhibit heterogenous morphologies that are taxonomically ill-defined.

Relatively little is known of the ecology of detached *Ascophyllum* plants. Baker & Bohling (1916) described the growth and distribution of several such populations in Great Britain. Gibb (1957) emphasized the importance of low salinities in their development. Moss (1971) compared the morphology and growth of the free-living and attached populations of *A. nodosum* in Britain, finding that the former show a loss of

[1] Published with the approval of the Director of the New Hampshire Agricultural Experiment Station as Scientific Contribution Number 814.

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apical and lateral meristems, which result in the formation of both wound-healing callus and irregular branching. Taylor (1957) described the morphology and distribution of two detached *Ascophyllum* populations from the northeastern coast of North America: *A. mackaii* (Turner) Holmes et Batters (= ecad *mackaii* (Turner) Cotton) and *A. nodosum* forma *scorpioides* (Hornemann) Reinke (= ecad *scorpioides* (Hornemann) Hauck). South & Hill (1970) summarize the distribution and abundance of ecad *mackaii* in Newfoundland. Brinkhuis (1975) has given the only previous account of seasonal growth and reproduction of North American populations of detached *A. nodosum*. Further data on detached populations of *Ascophyllum* are summarized by MacFarlane (1952), Webber & Wilce (1971) and Mathieson *et al.* (in press) for the Canadian Maritimes and New England. In general, the free-living populations of *A. nodosum* occur in sheltered coastal or estuarine sites.

Attached and free-living populations of *A. nodosum* occur in New Hampshire. The detached plants are identical to the 'marsh form' or the ecad *scorpioides* described by Baker & Bohling (1961), and are usually found in association with the marsh grass *Spartina alterniflora* Loiseleur-Deslongchamps. The present work was initiated to evaluate the interrelationships of the attached and free-living populations of *Ascophyllum nodosum*, as well as to determine what rôle, if any, *S. alterniflora* has in the ecology of ecad *scorpioides*. A combination of field and laboratory investigations were made during 1972–1974.

Materials and Methods

The variations in biomass (g dry wt/0.1 m^2) of ecad *scorpioides*, *Spartina alterniflora* and associated intertidal algae at Cedar Point, New Hampshire (Fig. 1) were determined for 15 consecutive months (August, 1972–October, 1973) by line transect-quadrat studies. Detailed data on the biomass for the associated species is not given in the present account. Three or four metered lines were established monthly at right angles to the shore and 10–12 quadrat samples were denuded per transect at 0.5 m intervals. A small quadrat frame (0.06 m^2) was used in order to minimize sampling damage and to provide adequate replication for analysis; a total of 574 samples were analysed. All of the attached plant material within the quadrats, excepting crustose forms such as *Hildenbrandia prototypus* Nardo and the roots of *Spartina alterniflora*, were removed and placed in individually labeled plastic bags. The *Spartina* samples (aerial portions) were cut off at ground level. The tidal level of each quadrat sample was determined with a transit and stadia rod. Subsequently, the elevation of each quadrat was corrected to Mean Low Water (M.L.W.) relative to a bench mark. The height of the bench mark was established by successive calibrations to predicted tide levels (Anon., 1971, 1972). The horizontal distances between transects were measured from a base line which, in this case, also served as the bench mark.

In the laboratory, the algae and marsh grass were sorted and rinsed in fresh water in order to remove mud, debris, and salt. The sorted samples were then dried for 24 h at 105 °C and subsequently weighed to the nearest 0.1 g. Temporal and tidal level biomass variations were calculated. The harvested plants of ecad *scorpioides* were also examined for the presence of fertile tips (receptacles); the density of *Spartina* stalks per quadrat was also determined.

The hydrographic conditions at Cedar Point were monitored concurrently with the monthly biomass collections, surface water temperature, salinity and nutrients being determined at high tide. Temperature was measured with a standard laboratory grade thermometer and salinity with a set of hydrometers; nitrite-N, nitrate-N, ammonia-N, and reactive phosphate concentrations were determined according to Strickland & Parsons (1968) and Solórzano (1969).

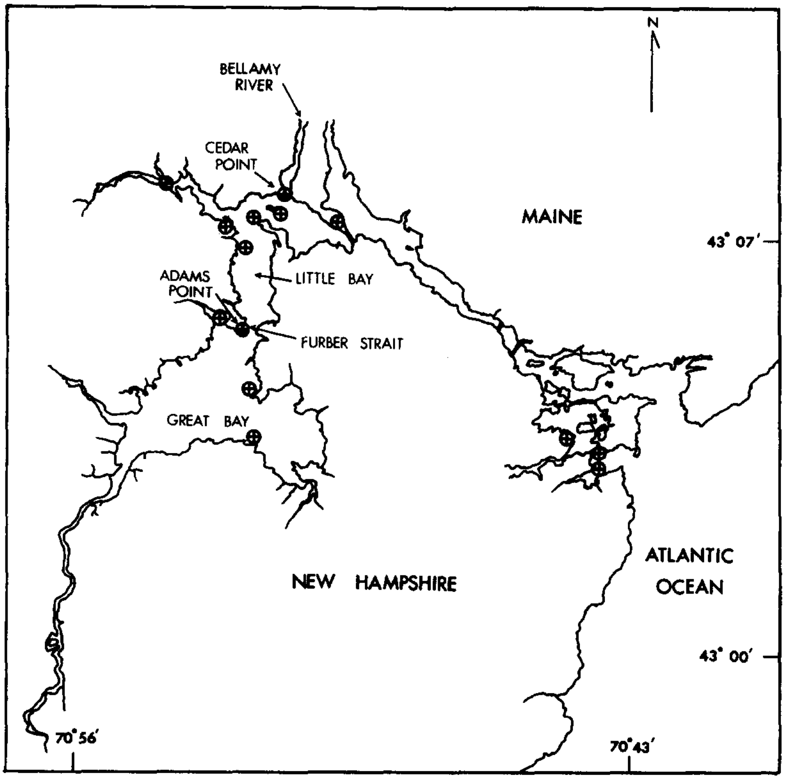

Fig. 1. Distribution of ecad *scorpioides* within the Great Bay Estuary System of New Hampshire–Maine, U.S.A.

The growth of 79 tagged plants of ecad *scorpioides* were studied at Adams Point (Fig. 1) during a ten month period between March and December, 1974. Coded plastic fish tags with braided nylon lines were attached to the main branches (Dawes, Mathieson & Cheney, 1974). The marked plants were, in turn, fastened by small wire loops spaced at one-foot intervals along a braided nylon line suspended on the shore

(Fig. 2). Removal was facilitated by using paper clips as fasteners. The levels of the suspending lines, and the attached plants, ranged from +1.0 to +1.6 m above M.L.W. Two lines were oriented perpendicular to the shore and two others approximately parallel to the shore. The lines were anchored to cement blocks which were, in turn, buried in the muddy substratum (Fig. 2). The damp-dry weights of the tagged algae were measured in the laboratory to the nearest 0.1 g. Twelve separate measurements were made during the ten month period. Deteriorating or lost plants were replaced at each measurement. The tagged plants were maintained at the same positions throughout. Epiphytes were removed by carefully brushing the plants prior to weighing. Every effort was made to maintain consistency in damp-drying the material. The percentage growth/day was calculated. The periods of submergence for the tagged algae at three different tidal heights (top, bottom, and side) were recorded during a tidal cycle at Adams Point on 19th August, 1974. A submergence curve was calculated with the average duration determined for the three positions.

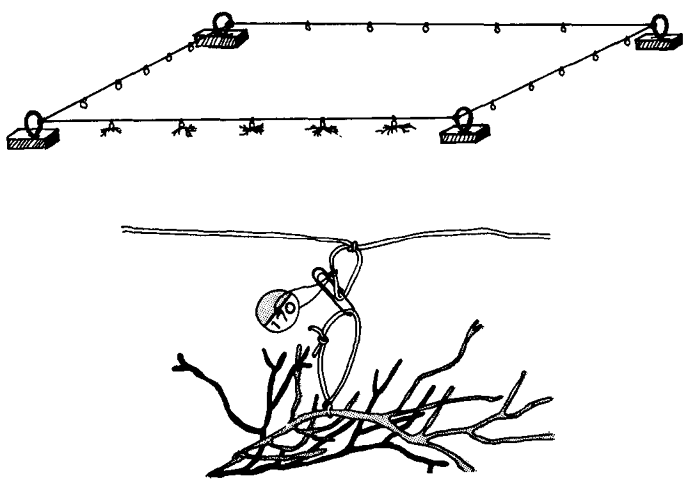

Fig. 2. Tagged plants of ecad *scorpioides* attached to nylon lines and cinder blocks at Adams Point.

Reproductive plants of ecad *scorpioides* were found for the first time during the growth study of tagged specimens at Adams Point. A sampling program was subsequently initiated during May, 1974, to determine the frequency of fertile plants using the same transect-quadrat sampling methods as at Cedar Point, except that a larger quadrat (1.0 m^2) was employed and only ecad *scorpioides* was harvested. The frequency of fertile receptacles/unit area and/dry weight of the samples were determined at different areas and tidal levels. Since the fertile receptacles were excised and preserved in 10 % formalin in sea water for further study, their weight, which was small, was excluded from the total weight.

The water temperatures and salinities at Adams Point were obtained from the Jackson Estuarine Laboratory from continuous records of the incoming sea water at the Laboratory; the mean daily values were calculated for the periods between the weight measurements.

TAXONOMY AND MORPHOLOGY OF ECAD *SCORPIOIDES*

Free-living plants of *Ascophyllum nodosum* have been variously defined taxonomically. Most frequently they have been designated as ecads (Baker & Bohling, 1916; Gibb, 1957; South & Hill, 1970; Moss, 1971) or forms (Taylor, 1957; Baardseth, 1970). For detached fucoid plants, Baker & Bohling first employed the term ecad which, according to Clements (1905), represents new variant morphologies resulting from adaptation to new habitats. Davis & Heywood (1963) give a similar definition emphasizing that the term should be used to describe the result of phenotypic plasticity. In other words, the genotype has the potential for expressing a range of phenotypes, and the mature form is determined by environmental conditions. The same authors state that the term 'form' should be used to designate transient variants differing by a single or a few linked characters; forms are also said to lack a distinct distribution. According to Davis & Heywood, genetically determined abberations may also be designated as forms. For the present, the term ecad appears to be the most appropriate one to describe free-living populations of *A. nodosum* since detached fragments of *A. nodosum* can develop into heterogenous populations (*e.g.*, ecad *scorpioides* or ecad *mackaii*), which later multiply by fragmentation and branch independently of the original fragment (see Baardseth, 1970, and the present account).

A comparison of attached and free-living populations of *A. nodosum* is given by Baardseth (1970). It is summarized below in order to demonstrate their differences, both morphologically and taxonomically. Typically the attached thallus is linear and flattened and forms vesicles at regular intervals, whereas the unattached plant develops a reduced, tufted thallus with terete branches and few, if any, randomly spaced vesicles (Fig. 3). The attached plant has primary dichotomous branching initiated by an apical cell and bilateral secondary branching originating from initials located in regular, marginal slits. On the other hand, the free-living plants have a less dichotomous habit with irregular, profuse lateral proliferations. Fertile globular receptacles occur regularly on mature attached plants (Fig. 4G). In contrast, receptacles are uncommon to rare on free-living plants; they are spindle-shaped rather than globose (Fig. 4A–F) and dichotomously divided, either wholly (Fig. 4A) or at the apex (Fig. 4B). Taylor (1957) differentiates ecad *scorpioides* on the basis of its vague axes, irregularly pinnate branching, slender, cylindrical or slightly compressed branches, entangled growth in salt marshes and tidal flats, and ovate to obovate receptacles. Ecad *mackaii* is differentiated by Taylor (1957) by its fastigiate branches which are occasionally inflated and its elongate, lanceolate receptacles which are formed on the lower parts of the plants. Gibb (1957) distinguished five different ecads of *A. nodosum*, depending on their habitats as well as their types and amount of branching. According to Gibb, the major difference between ecads *scorpioides* and *mackaii* is the proportion of apical to lateral branching; if it is "almost entirely lateral" it would be designated as ecad *scorpioides* while if it is both "apical and lateral" branching it would be designated as ecad *mackaii*. The other three plants were distinguished on the basis of their growth habitats as the beach, Baltic and turf ecads.

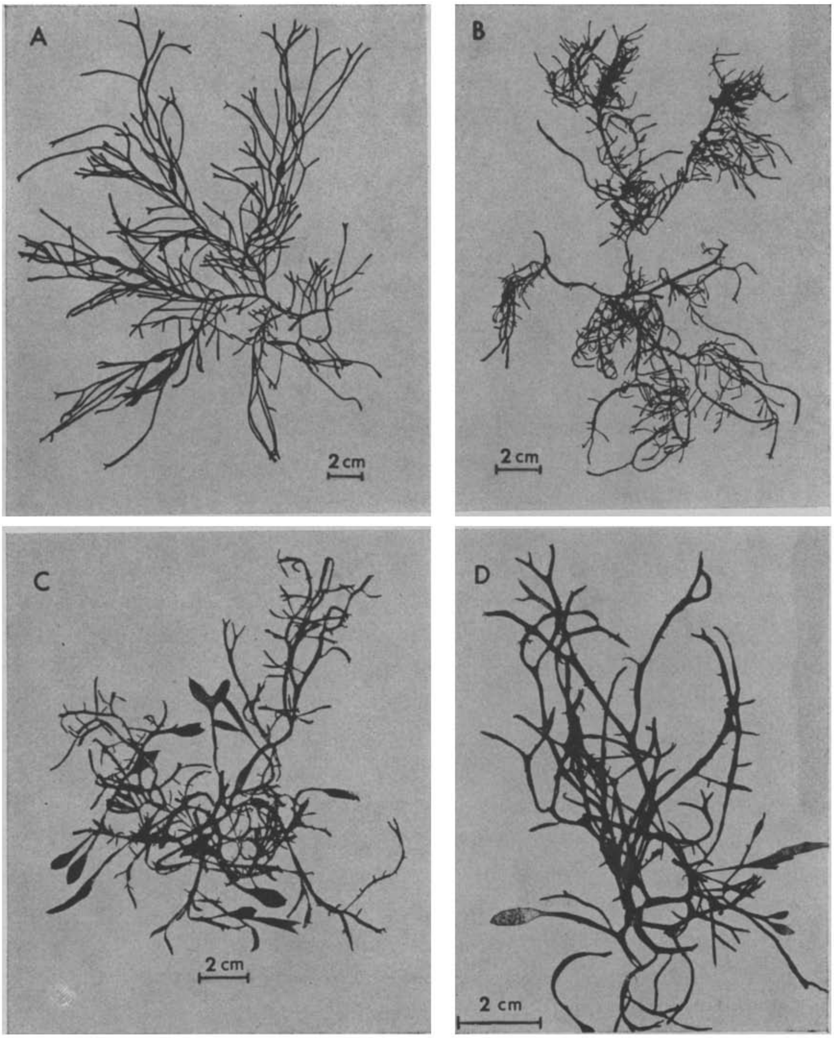

Fig. 3. Morphological variation of detached *Ascophyllum nodosum* plants: A, transitional stage similar to ecad *mackaii*; B, well developed ecad *scorpioides*; C and D, reproductive plants of ecad *scorpioides*.

A morphological gradient was observed in New Hampshire marshes between typical attached *A. nodosum* and the extreme ecad *scorpioides* (Fig. 3). All stages of develop-

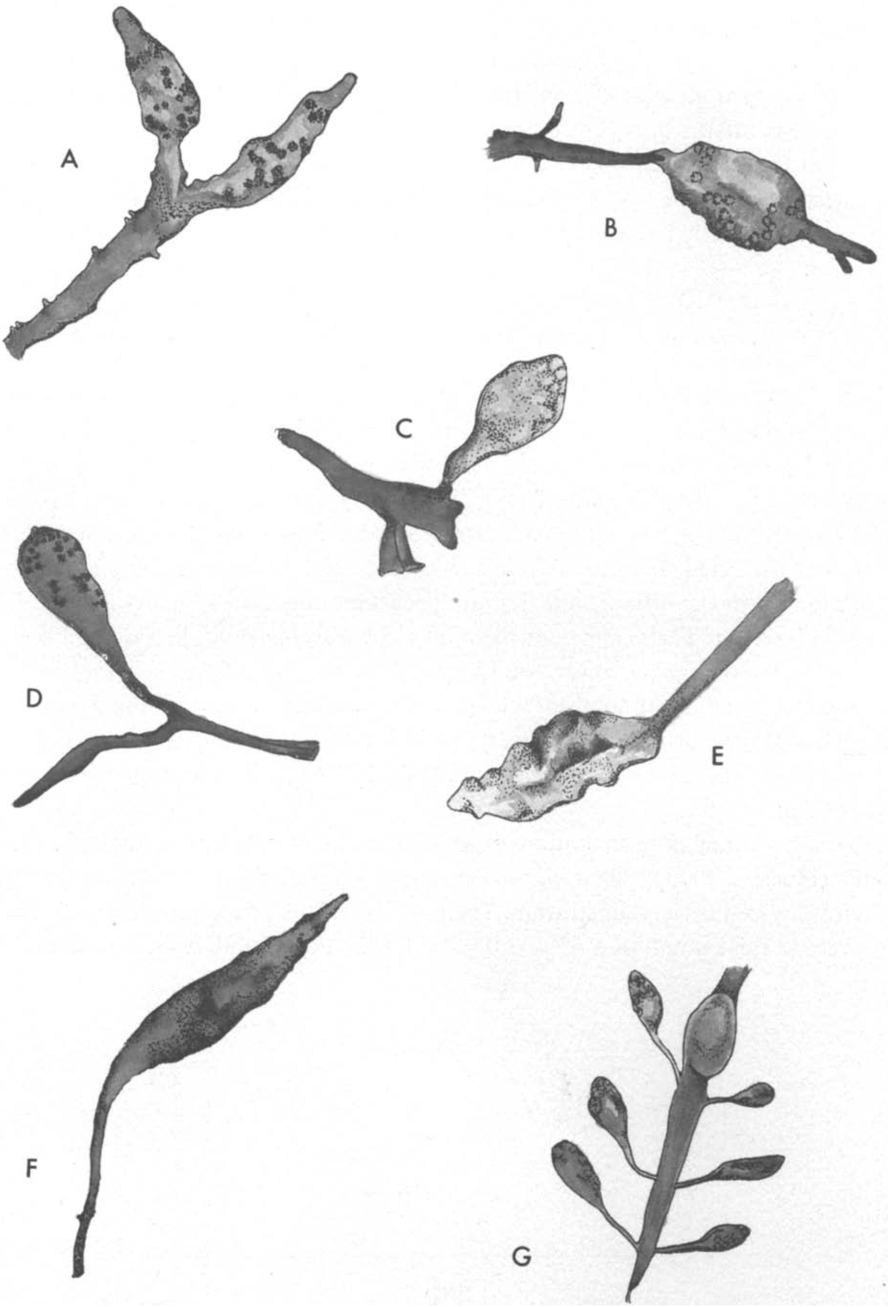

Fig. 4. Morphology of fertile receptacles on ecad *scorpioides* (A–F) and *A. nodosum* (G).

ment were observed growing within the same population, including what many would designate as ecad *mackaii*. For example, Fig. 3A shows a recently detached plant of *A. nodosum* which is very similar to ecad *mackaii.* Flattened, dichotomously divided thalli producing cylindrical lateral proliferations were also observed. Plants of the extreme type *i.e.*, ecad *scorpioides* (Fig. 3B), lack dichotomous branching and usually have dense lateral proliferations. Locally, this ecad constitutes the most abundant type. Isolated plants of the ecad *scorpioides* bear little resemblance to the parent, attached plants of *A. nodosum.* Gibb (1957), South & Hill (1970) and Moss (1971) have recorded a similar transition between attached and detached ecads of *A. nodosum.*

Description of the Areas and Environmental Factors

Attached populations of *A. nodosum* are present throughout the Great Bay Estuary System of New Hampshire and Maine where rocky substrata are not limiting; detached populations have a more restricted distribution in sheltered areas usually influenced by freshwater run-off (Fig. 1). Two typical habitats for ecad *scorpioides* were chosen for the present work, namely, Cedar Point and Adams Point (Fig. 1), these being selected because of their accessibility and limited exposure to the public. Cedar Point was the primary site; it is at the east mouth of the Bellamy River, adjacent to Little Bay. The particular population of ecad *scorpioides* studied was on the north side of the Point near the lower boundary of Royalls Cove. The second station was at Adams Point, adjacent to the Jackson Estuarine Laboratory of the University of New Hampshire. Growth studies were made at a sheltered cove at Adams Point, near a small creek due west of Furber Straits (Fig. 1). No major currents were evident at either of these sites.

The substratum at both stations is of slate bedrock overlain with clayey slit sediments (Hanson, 1973). The upper shore supports populations of *Spartina alterniflora*, which stabilize the silty substratum. The tides are of the mixed semi-diurnal type with an average tidal amplitude of $\approx$ 2.0 m at Cedar Point, and 2.2 m at Adams Point

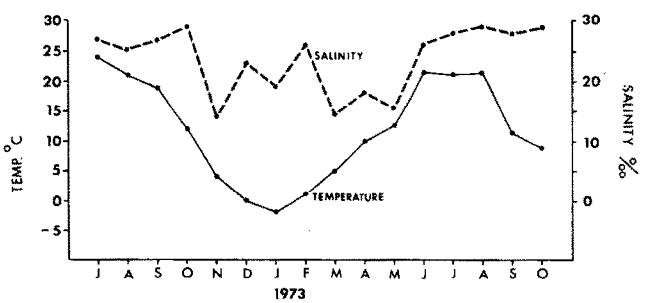

Fig. 5. Seasonal variation of surface water temperature and salinity at Cedar Point, 1972–1973.

(Anon., 1973). There are wide daily and seasonal variations of temperature and salinity. Fig. 5 summarizes the hydrographic data for Cedar Point. Surface water temperatures ranged from 23–24 °C in the summer to −2.0 °C in the winter and salinity from 29 $^0/_{00}$ to 14 $^0/_{00}$, with maximum values during the summer and early fall; salinities were at a minimum during the spring and occasionally during the fall. Fig. 6 shows the variation of nitrogenous nutrient concentrations at Cedar

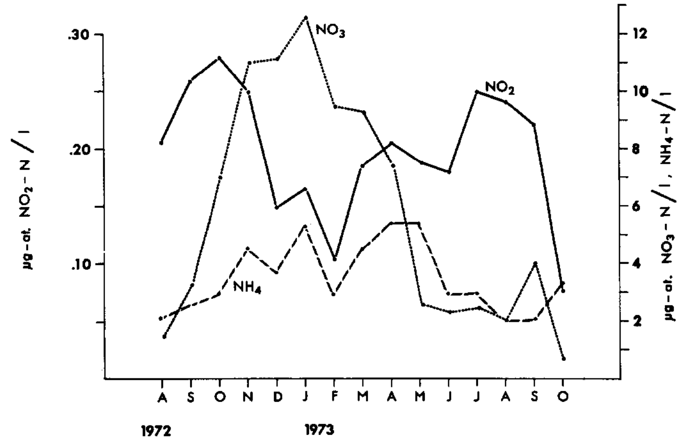

Fig. 6. Seasonal variation of nitrogenous nutrients from the surface waters at Cedar Point, 1972–1973.

Point. Nitrate-N concentrations were high (12.6–9.5 µg-at. N/l) in the fall and winter, and low (0.7–1.4 µg-at. N/l) in the summer and early fall. Nitrite-N concentrations showed an opposite variation with a February minimum of 0.105 µg-at. N/l and a summer maximum of 0.28 µg-at. N/l in October. Although ammonia concentrations were lower and more variable than nitrate-N, they showed essentially the same pattern. Reactive phosphate concentrations (Fig. 7) were high (1.86 µg-at. P/l) in the fall and

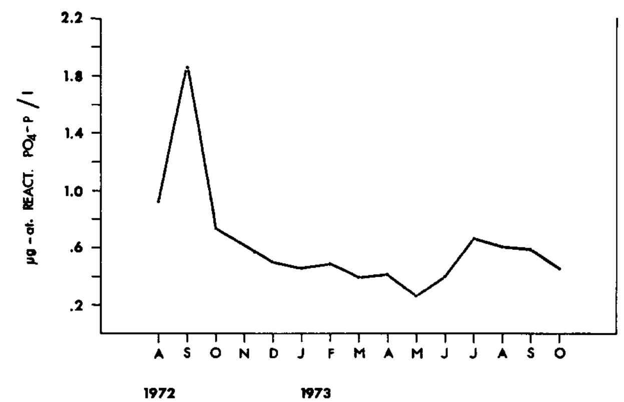

Fig. 7. Seasonal variation of reactive phosphates in the surface waters at Cedar Point, 1972–1973.

lower (0.28–0.4 µg-at. P/l) until the following summer when there were intermediate. Fig. 8 gives the mean daily temperatures and salinities at Adams Point during the growth study of tagged plants. The values represent the average calculated for the periods between the growth measurements.

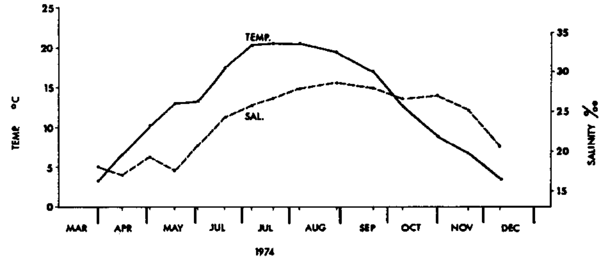

Fig. 8. Surface water temperature and salinity variations at Adams Point, March–December, 1974.

The periods of relative submergence of the tagged algae were determined during a high tide cycle in August. The lowest plants (+1.02 to +1.21 m) were submerged for a period of 30 min longer than the highest plants (+1.59 to +1.72 m) on the shore while at the intermediate heights (+1.35 to +1.58 m) the plants were submerged for 20 min longer than those highest on the shore.

Growth and Reproduction of Ecad *Scorpioides*

BIOMASS VARIATIONS

The seasonal and spatial variations of ecad *scorpioides* biomass, as g dry wt/0.1m² for a 12-month period are given in Fig. 9; the mean dry wt/0.1 m² of the plants are

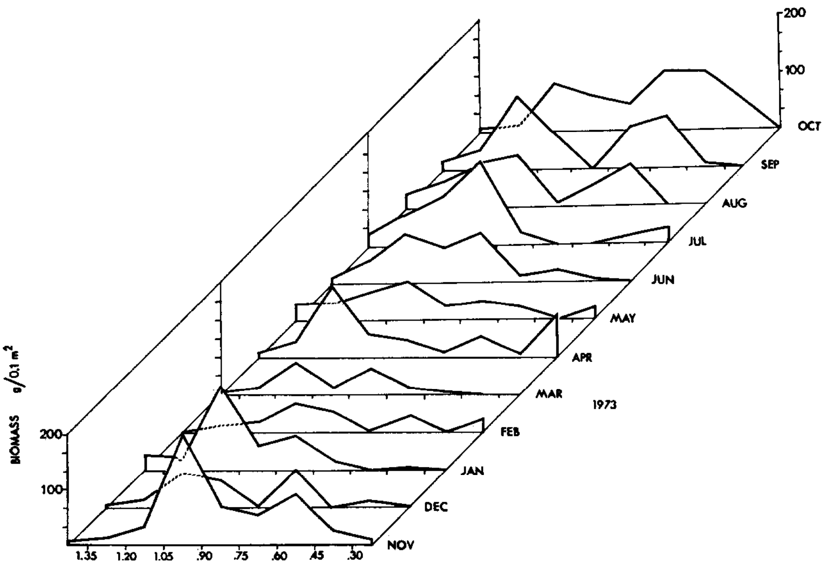

Fig. 9. Seasonal and spatial biomass variations of ecad *scorpioides* at Cedar Point, November, 1972–October, 1973.

TABLE I

Variations in biomass (g dry wt/0.1 m^2) of ecad *scorpioides* at Cedar Point, New Hampshire.

Tidal ht (m) above M.L.W.	1972					1973										Mean
	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	
1.50	4.33	8.67	18.00	7.67	3.17	26.67	0.0	3.50	5.17	28.34	8.34	21.67	17.00	13.00	6.17	11.50
1.35	41.51	11.00	14.50	11.84	13.00	21.67	11.34	11.67	27.84	31.67	41.17	54.68	46.18	33.67	15.17	25.84
1.20	70.85	72.85	66.85	35.84	61.01	144.20	18.50	54.84	124.69	49.51	88.02	84.68	77.02	124.19	81.02	77.02
1.05	2.33	74.35	155.36	192.71	47.34	43.01	48.68	20.34	42.34	69.51	62.68	144.86	89.35	59.85	59.01	74.18
0.90	35.0	32.34	49.51	67.85	0.0	58.01	35.17	45.84	28.01	27.34	86.52	23.84	8.00	0.0	44.01	36.17
0.75	1.83	–	50.34	52.18	65.01	16.50	3.50	12.50	9.67	34.34	11.00	0.83	36.84	70.85	102.02	28.51
0.60	0.0	19.17	33.34	89.52	0.0	0.67	28.67	3.50	34.67	23.34	22.50	1.00	72.01	86.85	100.19	34.34
0.45	107.35	48.51	0.0	26.51	9.50	4.17	0.0	trace	7.83	1.33	2.67	–	0.0	5.33	43.68	17.17
0.30	–	81.52	7.33	11.00	1.67	0.0	22.50	trace	76.68	20.00	–	26.84	0.33	0.0	–	16.50
0.15	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Mean	32.84	33.67	38.67	53.84	22.17	35.01	16.17	16.84	31.17	29.51	35.84	41.51	38.51	43.68	56.34	–

plotted for each 0.15 m interval from +0.15 to +1.5 m. In general, the maximum biomass occurred between +0.9 and +1.35 m (see also Table I). The low biomass between +0.75 and +0.90 m resulted from a precipituous drop in the shoreline at this elevation. The maximum biomass (193.1 g/0.1 m^2) was found during the late summer–fall, and the lowest values (0–16.7 g/0.1m^2) during the late winter. An increase in biomass was apparent on the lower shore during the fall. The January value of 144.5 g/0.1 m^2 between +1.05 and +1.20 m may have been associated with a restricted ice cover at this point relative to the adjacent areas. The highest single biomass 193.1 g/0.1 m^2 was found during November, 1972, between +0.9 and +1.05 m. In general, the largest values for all months were within the same limits of tidal height.

The seasonal and spatial patterns of biomass are given in Fig. 10, and with respect to heights for four seasonal collections (Nov., Aug., May and Feb.). The maximum biomass was at +1.0 m on each of the sampling dates. A second maximum was found at +0.5 m which corresponded to the site below the major substratum discontinuity

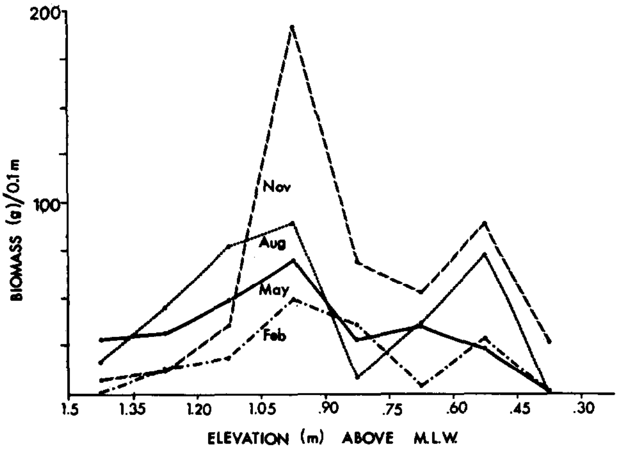

Fig. 10. Spatial biomass variations of ecad *scorpioides* during four seasons at Cedar Point.

noted earlier. Of the four months shown, the highest biomass was during November (193.1 g/0.1 m^2) and the lowest (48.7 g/0.1 m^2) during February.

A comparison of the monthly biomass variation of the ecad *scorpioides* between four height intervals at Cedar Point is shown in Fig. 11. Although there were major fluctuations at each, a summer–fall maximum and a winter minimum is apparent. Major height differences were also evident, the maximum biomass being almost always at +0.9 to +1.2 m (*i.e.*, an intermediate height) and the lowest usually between +0.3 and +0.6 m and +1.2 and +1.5 m (*i.e.*, the highest and lowest levels). The seasonal variation summed over its vertical distribution (between +0.15 and +1.35 ml) is shown in Fig. 12, which shows essentially the same pattern as Fig. 11.

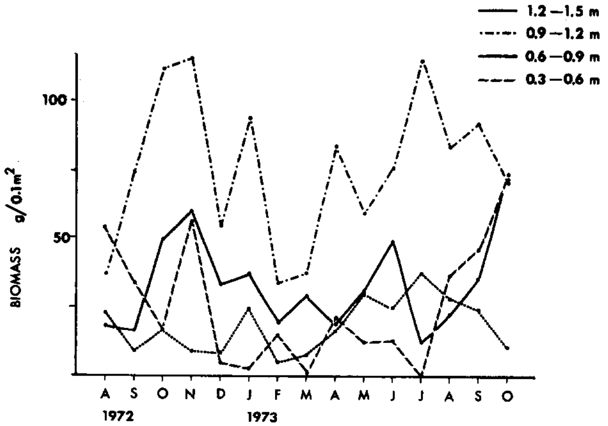

Fig. 11. Seasonal variation of ecad *scorpioides* biomass at four tidal levels, August, 1972–October, 1973.

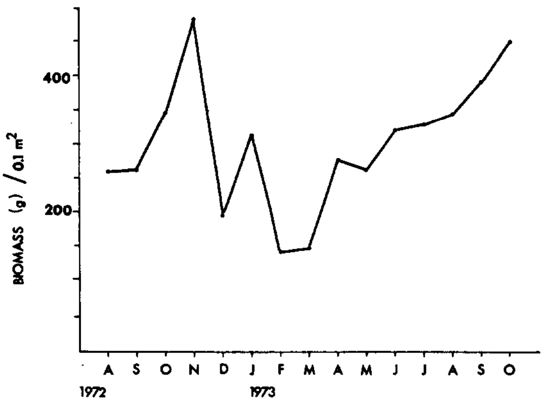

Fig. 12. Seasonal variations of ecad *scorpioides* biomass summed over its vertical distribution at Cedar Point, August, 1972–October, 1973.

GROWTH OF TAGGED PLANTS

Fig. 13 shows the seasonal growth of tagged *in situ* plants at Adams Point, expressed as the mean daily growth. Of the 79 plants, 25 were held at the highest level (+1.59 to +1.72 m), 20 at the intermediate (+1.35 to +1.58 m) and 34 at the lowest (+1.02 to +1.21 m) levels. Seasonal and spatial variations of survival were apparent. Only 28 % of the highest level plants were maintained throughout the ten-month experiment while 40 % of the intermediate and 67.6 % of the lowest plants survived. The daily growth rates shown in Fig. 13 are based on the viable plants maintained throughout the ten month study. The plants from the three levels showed their maximum growth (0.8–2.5 %/day) during the spring to early summer. Plants from the lower

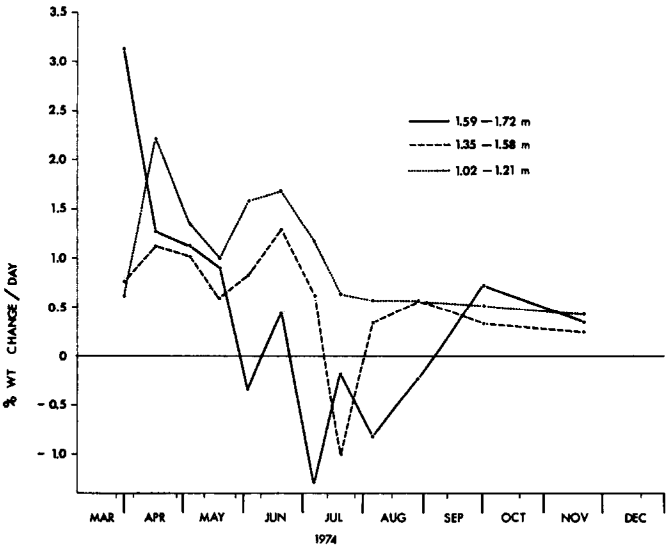

Fig. 13. Average daily growth of ecad *scorpioides* plants from three tidal levels at Adams Point, March–December, 1974.

shore showed the highest sustained growth, while those from the upper shore showed the least growth. The latter had no net growth between July and September. The plants grown at the intermediate level only suffered one period of net loss during July. The lowest level plants always showed a positive growth, with a declining growth rate from July to December.

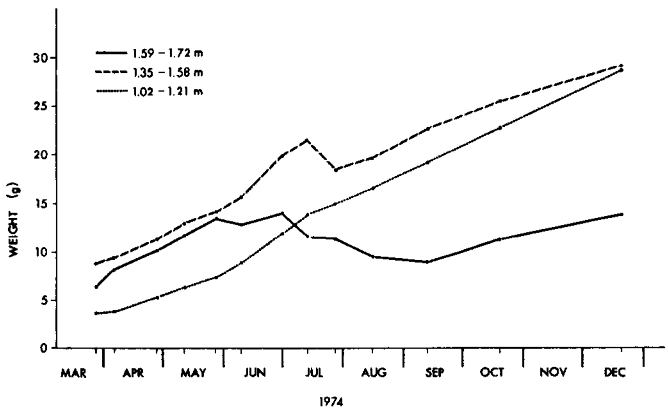

Fig. 14. Average cumulative weight of tagged ecad *scorpioides* plants from three tidal levels at Adams Point, March–December, 1974.

The seasonal growth of the surviving tagged plants, expressed relative to damp-dried weight, is shown in Fig. 14. The plants at the intermediate and lowest levels showed a similar pattern and rate of growth, except that there was a suppression of growth in the former towards the end of July. A comparison with Fig. 13 shows that plants from the intermediate level grew little during July. The plants on the upper shore showed a comparable rate of growth to those at the other two levels during

TABLE II

Summary of mean growth rates of tagged *in situ* plants of ecad *scorpioides* at Adams Point.

Tidal ht (m) above M.L.W.	Initial wt (g)	Final wt (g)	Change in wt (g)	Change (%)
1.59–1.72	6.40	13.9	+ 7.5	+117.2
1.35–1.58	8.80	29.1	+20.3	+230.7
1.02–1.21	3.60	28.6	+25.0	+694.4

March to late May. Thereafter, a relatively stable weight was maintained until late June, at which time no net growth was evident until late August (*cf.*, Fig. 13). Table II summarizes the average growth rates of the tagged plants shown in Fig. 14 during the ten month period.

SEASONAL VARIATIONS IN REPRODUCTION

As noted previously, fertile plants were first found at Adams Point during May, 1974 and subsequently at Cedar Point during the same month (Figs 15, 16). A

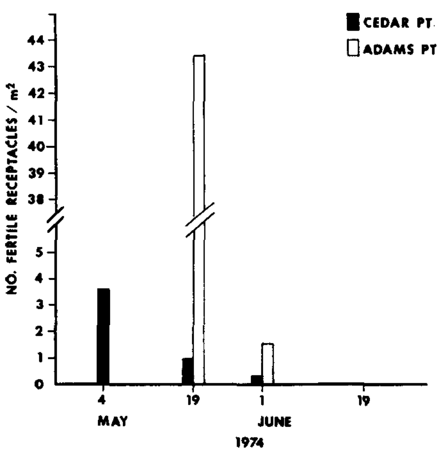

Fig. 15. Average number of receptacles/m^2 on ecad *scorpioides* plants during May–June, 1974 at Cedar and Adams Points.

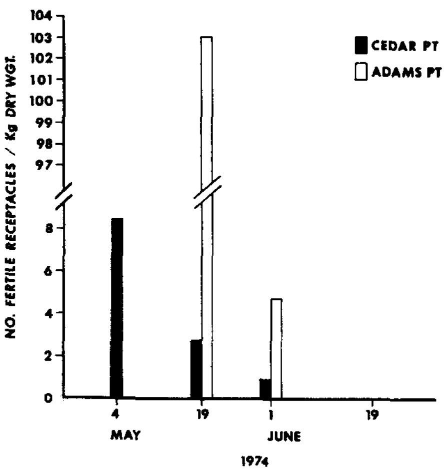

Fig. 16. Average number of receptacles/kg dry wt of ecad *scorpioides* plants during May–June, 1974 at Cedar and Adams Points.

detailed study was initiated during May, in order to determine the abundance of fertile receptacles/unit area and unit dry weight. The frequency of fertile receptacles at Cedar Point ranged from $3.5/m^2$ on 4th May to $1.0/m^2$ on the 1st of June to none at the end of June (Fig. 15). The populations at Adams Point showed a higher number of receptacles during May ($43.4/m^2$) and none in mid-June. The reproductive frequency of ecad *scorpioides*, expressed as numbers of receptacles/kg dry wt, is shown in Fig. 16; the weight of the receptacles was not included since they were preserved for anatomical studies. Essentially, the same relationship as shown in Fig. 15, is evident, *i.e.*, a late spring maximum, a mid-June absence of receptacles, and a greater abundance of receptacles at Adams Point than at Cedar Point.

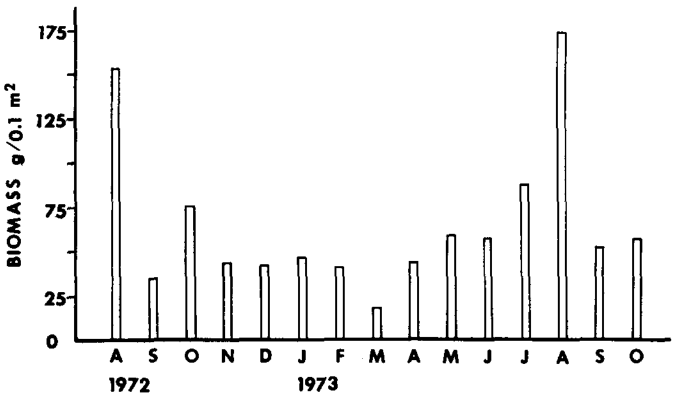

Fig. 17. Biomass variations of *Ascophyllum nodosum* populations at Cedar Point, August, 1972–October, 1973.

Comparative Biomass and Density Distributions

The seasonal variations of the biomass of attached *Ascophyllum nodosum* between +0.15 and +1.5 m are shown in Fig. 17. A gradual increase is evident from spring to summer, with maximum values in August of both years; thereafter, the biomass decreased.

The vertical distribution of *A. nodosum* and ecad *scorpioides* within the intertidal zone at Cedar Point is shown in Fig. 18. The values are based on the mean of monthly averages for a one-year period as shown in Table I. A plot of the average density of *Spartina alterniflora* stems is also given. *Ascophyllum nodosum* was broadly distributed between +0.22 and +1.42 m, with the maximum biomass between +0.22 and +0.97 m. The detached ecad *scorpioides* had a similar vertical distribution as *A. nodosum*, except that its maximum biomass lay between +0.97 and +1.12 m. The average biomass of ecad *scorpioides* was usually less than *A. nodosum*. The density of *Spartina* stalks and the biomass of ecad *scorpioides* both show maximum values at the same tidal level, namely, +1.12 m.

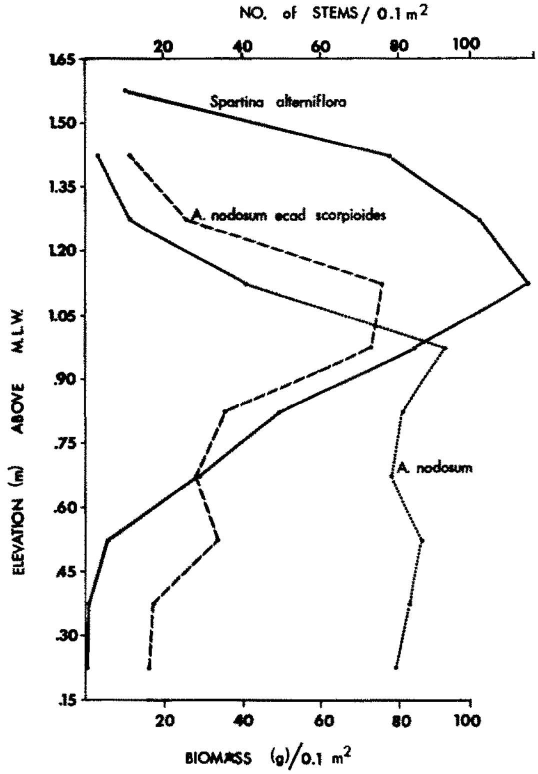

Fig. 18. Average vertical distribution of *Ascophyllum nodosum* and ecad *scorpioides* biomass at Cedar Point, as well as *Spartina alterniflora* stem density.

Discussion

The name ecad *scorpioides* has been used even though intermediate types, such as ecad *mackaii* constitute part of the population. Future studies may show that *mackaii* is the most appropriate name for all free-living ecads in various stages of development, since Turner (1808) first used the name *mackaii* for free-living plants of *Ascophyllum nodosum*. An alternative is to follow the suggestion of Baker & Bohling (1916) and designate all ecads of salt marsh fucoids as the "megecad *limicola*", with transitional entities as differential phases of development. Further studies are needed to determine the taxonomic status of detached *A. nodosum* ecads.

The field studies showed a variety of interrelationships between *A. nodosum*, ecad *scorpioides* and *Spartina alterniflora*. For example, *Ascophyllum nodosum* grows most abundantly just below *Spartina*, while the greatest biomass of ecad *scorpioides* coincided with the highest density of *S. alterniflora*. Detached fragments of *Ascophyllum nodosum* become entangled and stabilized amongst *Spartina alterniflora* and subsequently produce extensive populations of ecad *scorpioides*. During the summer, *Spartina* also provides an extensive canopy over the ecad *scorpioides* thereby decreasing light intensity and reducing water loss. The *Spartina* canopy and the associated protection for ecad *scorpioides,* is at a minimum during January to April because of extreme scouring and low winter temperatures. In contrast to the present results, where the maximum biomass of ecad *scorpioides* was found in the fall, Brinkhuis (1975) found the maximum biomass of ecads *mackaii* and *scorpioides* during the spring on Long Island, New York. There are only limited populations of attached *Ascophyllum* in Long Island Sound and this may explain the differences between the two sites.

According to Gibb (1957) the detached ecad *mackaii* shows its maximum biomass at high levels. The ecad *scorpioides* shows its maximum biomass at $\approx +1.0$ m. An interrelationship was also noted between level, longevity, and growth of ecad *scorpioides*; the highest tagged plants showed minimal growth or even a loss in weight during the summer. In contrast, tagged plants at the lowest elevations showed sustained growth during the summer. A number of workers (*e.g.*, Lewis, 1964; Zaneveld, 1969) have also emphasized that level dictates the degree to which physical conditions act upon organisms. The primary factors limiting the vertical distribution of ecad *scorpioides* are probably desiccation as well as a variety of atmospheric extremes, such as high light intensities and temperatures. Gibb (1957) has recorded the same relationships with ecad *mackaii,* for she noted that plants growing at the highest levels, with extensive desiccation and light fluctuations, exhibit "sun decay" of the terminal branches. The same discoloration and necrosis of the terminal branches of ecad *scorpioides* was also found in the highest level populations of tagged plants at Adams Point.

The daily growth rates of tagged plants of ecad *scorpioides* were maximal during the spring when temperatures ranged between 5 ° and 20 °C; the spring period of maximum growth was also associated with a major change in the light duration and intensity (Anon., 1973). The broad tolerance to light intensity and temperature (J. Chock, unpubl. data) suggests that the plant is well adapted to such fluctuations. It is suggested that growth variations with season and level of ecad *scorpioides* can be related to temperature and light variations.

The biomass of attached *A. nodosum* showed a conspicuous seasonal variation, with a major attrition during September in two successive years. A precipitous loss of *A. nodosum* in September was probably due to storm removal as found by Baardseth (1970). The data also indicate that detached fragments sustain the population of ecad *scorpioides,* since subsequent increases in biomass of ecad *scorpioides* were found during the fall months (Figs 12, 17). The influx of new fragments must contribute to this increase.

No receptacles were found on ecad *scorpioides* plants in 574 samples taken during 1972–1973 at Cedar Point; however, during the following spring of 1974, fertile receptacles bearing oogonia and antheridia, were found, first at Adams Point and subsequently at Cedar Point. The abundance of receptacles at Cedar Point was less than at Adams Point. Among others, Gibb (1957) and South & Hill (1970) have also found receptacles rare or infrequent on detached *Ascophyllum* ecads; Gibb also emphasizes that the production of receptacles varied from year to year. Observations in New Hampshire also suggest a cyclical or sporadic occurrence of receptacles. The spring period of maximum reproduction with ecad *scorpioides* (Figs 15, 16) is similar to that observed for several detached ecads of *Ascophyllum* in Great Britain (Gibb, 1957) and for attached *A. nodosum* in Europe and North America (Baardseth, 1970). It should also be emphasized that the receptacles on ecad *scorpioides* are morphologically distinct from those on *A. nodosum*; furthermore, they are usually most abundant on the largest, residual fragments of *A. nodosum*. In contrast to other fucoid algae which can show a pronounced vertical stratification of reproductive plants (Knight & Parke, 1950), no discernible stratification of reproductive plants was evident at Cedar or Adams Point.

Acknowledgements

The authors would like to thank Drs A. Baker, L. Bogel, R. Croker, and R. Kinnerson for their constructive criticism and Mr T. Norall and Miss Chris Emerich for their assistance with the nutrient analyses. The Graduate School at the University of New Hampshire is also thanked for financial support to the first author during two summers.

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