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ECAD SCORPIOIDES (HORNEMANN) HAUCK
OF ASCOPHYLLUM NODOSUM (L.) LE JOLIS.

University of New Hampshire, Ph.D.,
1976
Biological Oceanography

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ECOLOGICAL STUDY OF THE SALT MARSH ECAD
SCORPIOIDES (HORNE-MANN) HAUCK
OF
ASCOPHYLLUM NODOSUM (L.) LE JOLIS

by

JAN S. CHOCK

B.A., University of Hawaii, 1967

A THESIS

Submitted to the University of New Hampshire
In Partial Fulfillment of
The Requirements for the Degree of

Doctor of Philosophy

Graduate School

Department of Botany and Plant Pathology

September, 1975

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ACKNOWLEDGEMENTS

I wish to express my appreciation and gratitude to Dr. Arthur C. Mathieson for his inspiration and guidance throughout this study, and for his assistance and encouragement in the preparation of the manuscript. I also wish to thank Dr. Alan L. Baker, Dr. A. Linn Bogle, Dr. Robert A. Croker, and Dr. Russell S. Kinerson for their counsel and their many helpful suggestions and criticisms during the course of my research program.

I am grateful to the Graduate School of the University of New Hampshire for providing financial support for two summers through the Summer Fellowship for Graduate Teaching Assistants.

I also wish to thank Wendy Elcome for her outstanding work on many of the illustrations; Tim Norall and Chris Emerich for their assistance with the nutrient analyses and Linda Wright and Claudia Foret for typing the manuscript.

I wish to compliment my parents for their patience and support during the study which in many ways they influenced some time ago.

To my wife Connie, I express my deepest gratitude for her understanding, constant encouragement, and valuable assistance through every stage of this endeavor.

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ABSTRACT

ECOLOGICAL STUDY OF THE SALT MARSH ECAD

SCORPIOIDES (HORNEMANN) HAUCK

OF

ASCOPHYLLUM NODOSUM (L.) LE JOLIS

by

JAN S. CHOCK

The seasonal and spatial distributions of the free-living ecad scorpioides of Ascophyllum nodosum are described from the Great Bay Estuary System of New Hampshire and Maine. The growth and distribution of ecad scorpioides show a variety of phenological and distributional relationships between A. nodosum and the marsh grass Spartina alterniflora. A fall biomass maximum of ecad scorpioides was recorded during two consecutive years; it may have been attributable to an influx of source material produced by storms, as well as to normal seasonal growth. Laboratory and field growth studies suggest that S. alterniflora provides initial stability for the progenitor fragments of A. nodosum - i.e. prior to the production of the highly proliferous scorpioides morphology. The marsh grass provides a protective canopy over the ecad during the summer, but it is absent during the winter.

A variety of manometric experiments have demonstrated comparable physiological responses of A. nodosum and ecad scorpioides under varying conditions of light intensity, temperature and salinity. The ecad scorpioides exhibits a broad tolerance to temperature and salinity, which corresponds to its natural distribution within the Great Bay Estuary System.

Sexual reproduction of the ecad scorpioides was recorded during only one of three years during the study. The morphology and reproduction of ecad scorpioides is compared and contrasted with the attached A. nodosum, as well as several detached ecads. A gradient of morphology is evident from typical A. nodosum to the extreme "marsh" ecad scorpioides.

The seasonal productivity of S. alterniflora populations are assessed. No previous account of marsh grass productivity has been recorded between Rhode Island and Nova Scotia.

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 are also recorded from sheltered Atlantic locations (Baker and Bohling, 1916; Gibb, 1957; Taylor, 1957; South and Hill, 1970). The detached plants are morphologically distinct from the attached ones; in addition the former plants exhibit heterogenous morphologies that are ill-defined taxonomically. Thus, the free-living populations of A. nodosum have been variously regarded as separate species, forms, varieties or ecads of the attached species. Most recently, the detached populations of A. nodosum have been primarily designated as ecads, as defined by Clements (1905). Five ecads are currently recognized in A. nodosum (Gibb, 1957) including ecad mackaii and ecad scorpioides which are discussed here. Even so some authors (Taylor, 1957; Baardseth, 1970) do not follow this designation.

A variety of workers (see Baardseth, 1970) have conducted biological and ecological studies of the attached populations of A. nodosum. In comparison, relatively little is known about detached Ascophyllum plants. Baker and Bohling

(1916) described the growth and distribution of several detached Ascophyllum populations in Great Britain. Gibb (1957) emphasized the importance of low salinities in the development of detached Ascophyllum populations. Moss (1971) compared the morphology and growth of the free-living and attached populations of A. nodosum in Britain; she found that the detached plants exhibited a loss of apical and lateral meristems, resulting 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 (= ecad mackaii) and A. nodosum forma scorpioides (= ecad scorpioides). South and 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 descriptions and/or distributional records of detached populations of Ascophyllum are summarized by MacFarlane (1952), Webber and Wilce (1971) and Mathieson, et al. (in press) for New England and the Canadian Maritimes. 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 and Bohling (1916), and they are usually found in

association with the marsh grass Spartina alterniflora. The present study was initiated in order to evaluate the interrelationships of the attached and free-living populations of A. nodosum, as well as to determine what, if any, role S. alterniflora has in the ecology of ecad scorpioides.

Accordingly, the objectives of the present investigation were as follows: (1) to assess the seasonal growth and reproduction of in situ populations of ecad scorpioides; (2) to define quantitatively the major physical, chemical and biological factors influencing the growth and local distribution of ecad scorpioides; and (3) to evaluate the interrelationships between S. alterniflora and ecad scorpioides by comparing the autecologies of the two plants. In order to achieve these objectives a combination of field and laboratory investigations were conducted during 1972 to 1974.

MATERIALS AND METHODS

The biomass (g dry weight/0.06 m²) variations of ecad scorpioides, Spartina alterniflora and associated intertidal algae at Cedar Point, New Hampshire (Fig. 1) were determined for 15 consecutive months (August, 1972 to October, 1973) by line transect-quadrat studies. That is, three or four metered lines were established monthly at right angles to the shore and 10-12 quadrat samples (0.06 m²) were denuded per transect at 0.5 m intervals. A small quadrat frame (0.06 m²) was employed in order to minimize sampling damage and to provide adequate replication for biomass analyses. Overall a total of 574 samples were analyzed. All of the attached plant material within the quadrats, excepting crustose forms such as Hildenbrandia prototypus and the roots of S. alterniflora, were removed and placed in individually labeled plastic bags. The Spartina samples (aerial portions) were cut off at ground level. The elevation 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 elevation of the bench mark was established by successive calibrations to predicted tide levels (Anon., 1972, 1973). 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. Specimens of ecad scorpioides and S. alterniflora were examined for the presence of fertile tips (receptacles) and flowers, respectively. The sorted samples were then dried for 24 hours at 105 C, and subsequently weighed to the nearest 0.1 g.

The maximum length of each Spartina stalk/quadrat was measured (from the base to the tip) to the nearest 0.1 cm. Dead and living materials were separated. The average growth density, canopy height and flowering frequency of S. alterniflora were calculated from the quadrat data. Temporal and elevational biomass variations of the other intertidal species were calculated, as well as the average dry weights per species.

The ash-free weights of S. alterniflora and ecad scorpioides were determined from several samples from a single collection made at Cedar Point during July, 1974. Samples of both plants were rinsed with fresh water, dried for 24 hours at 105 C and then ground with a Wiley mill, using a 40 mesh seive. After redrying for another 24 hours at 100 C, the samples (approximately 1 g) were ashed in a muffle furnace (Van Waters and Rogers) for four hours at 600 C (Reiners and Reiners, 1972). Prior to ashing and after cooling, the samples were weighed to the nearest 0.1 mg.

The hydrographic conditions at Cedar Point were

monitored concurrently with the monthly biomass collections. That is, records of surface water temperature, salinity and nutrient levels were made at high tide. Temperature values were recorded with a standard laboratory grade thermometer; salinity was measured with a set of hydrometers (G.M. Mfg. Co., N.Y.). Nitrite-N, Nitrate-N, Ammonia-N, and reactive phosphate concentrations were determined according to Strickland and Parsons (1968) and Solorozano (1969).

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, et al., 1974). The marked specimens 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 heights 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, while two others were approximately parallel to the shore. The lines were anchored to cement blocks that were, in turn, buried in the muddy substrate (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 during each measurement. The tagged plants were maintained at the

same locations throughout the study. Epiphytes were removed by carefully brushing the plants prior to weighing. Every effort was made to maintain consistency in damp-drying the specimens. The percent growth/day was calculated. The submergence periods for the tagged algae at three different elevations (top, bottom and side) were recorded during a tidal cycle at Adams Point on August 19, 1974. A submergence curve was calculated with the average duration determined for the three positions.

Reproductive plants of ecad scorpioides were discovered for the first time during the spring of 1974. The plants were observed at Adams Point during the growth study of tagged specimens. A sampling program was subsequently initiated during May, 1974, in order to determine the frequency of fertile plants. The same transect-quadrat sampling methods previously used at Cedar Point were employed, except that a larger quadrat (1.0 m²) was employed and only ecad scorpioides was harvested. The frequency of fertile receptacles per unit area and per dry weight of samples was recorded at different areas and elevations. The fertile receptacles were excised and preserved in 10% formalin in sea water for further studies. Thus, their weight, which was rather negligible, was excluded from the total weight.

The water temperature and salinity values at Adams Point were obtained from the Jackson Estuarine Laboratory. The data was derived from continuous records of incoming sea

water at the Laboratory. Ambient temperatures were obtained from records of the Water Resource Research Center, in Durham, New Hampshire. The average daily values for water temperature, salinity and air temperature were calculated for the periods between weight measurements.

The rates of apparent or net photosynthesis of A. nodosum and its detached ecad scorpioides were recorded during the summer of 1974 and the winter of 1975, using manometric techniques. All of the specimens were collected from Adams Point. Healthy terminal apices, approximately 1.5 cm in length, were excised with a razor blade and immediately placed in deep petri dishes with buffered artificial sea water (Chapman, 1962). Subsequently the materials were incubated in the dark for 24 hours. Equilibration temperatures and salinities varied according to the intended experiments. The rates of net photosynthesis were evaluated under varying conditions of light intensity, temperature, and salinity with a Gilson Differential Respirometer (Model GRP 14). The respirometer was equipped with two banks of 50 watt Champion reflector bulbs. Measurements of oxygen evolution were made at ten minute intervals until at least three consecutive values were consistent; at this point it was deemed that equilibration was achieved. The rates of oxygen exchange are expressed as $\mu\text{l oxygen/g dry weight/minute}$.

The light experiments were run at ambient temperatures: 1.5 C during the winter and 15.0 C during the summer. The

light intensities ranged from 5 to 5070 foot-candles (f-c). A salinity of 34 o/oo was employed in the light and temperature experiments. The temperature studies were conducted at the "optimal" light levels previously determined. Each reaction vessel contained three apical sections (approximately 1.5 cm long) of A. nodosum or five apical tips of ecad scorpioides. Seven replicates of each plant were employed in the temperature and light studies. The July salinity test was conducted in groups of three salinities, with a minimum of three replicates for each plant. A total of 24 salinity experiments were conducted because of variable results.

One salinity-respiration study of ecad scorpioides was conducted at 0, 18 and 35 o/oo. The preparation and equilibration procedures were the same as with the previous salinity-photosynthesis experiments, except that the measurements were made in the dark. No carbon dioxide absorbant, such as KOH, was used in the center well of the vessels. Following the initial respiration measurement, the lights were turned on (1000 f-c) and the rates of net photosynthesis were then recorded after equilibration. Finally, the lights were extinguished and again the respiration rates were determined. Five replicates were used at 0 o/oo and 18 o/oo while four replicates were used at 35 o/oo.

TAXONOMY AND MORPHOLOGY OF ECAD SCORPIOIDES

Free-living plants of A. nodosum have been variously defined taxonomically. Most frequently they have been designated as ecads (Baker and Bohling, 1916; Gibb, 1957; South and Hill, 1970; Moss, 1971) or forms (Taylor, 1957; Baardseth, 1970). Baker and Bohling first employed the term ecad for detached fucoid plants, which, according to Clements, represented new variant morphologies resulting from adaptation to new habitats. Davis and Heywood (1963) give a similar definition for an ecad, 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 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. Genetically determined aberrations may also be designated as forms, according to Davis and Heywood. 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 the 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 that 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 ecads were distinguished on the basis of their growth habitats: beach, baltic and turf.

A morphological gradient was observed in New Hampshire marshes between typical attached A. nodosum and the extreme ecad scorpioides (Fig. 3). That is, all stages of development were observed growing within the same population, including what many would designate as ecad mackaii. For example, Figure 3A shows a recently detached plant of A. nodosum that 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 they usually have dense lateral proliferations. This ecad constitutes the most abundant type locally. Isolated plants of the ecad scorpioides bear little resemblance to the parent, attached plants of A. nodosum. Gibb (1957), South and Hill (1970) and Moss (1971) have recorded a similar transition between attached and detached ecads of A. nodosum.

DESCRIPTION OF STUDY AREAS AND ENVIRONMENTAL FACTORS

Attached populations of A. nodosum occur throughout the Great Bay Estuary System of New Hampshire and Maine where rocky substrate is not limiting; detached populations exhibit a more restricted distribution in sheltered areas that are usually influenced by fresh water runoff (Fig. 1). Two typical habitats for ecad scorpioides were chosen for the present study: Cedar Point and Adams Point (Fig. 1). The sites were selected because of their accessibility and limited exposure to the public. Cedar Point was the primary site; it is located at the east mouth of the Bellamy River, adjacent to Little Bay. The specific population of ecad scorpioides studied was on the north side of the Point near the lower boundary of Royalls Cove. The second station was located at Adams Point, adjacent to the Jackson Estuarine Laboratory of the University of New Hampshire. Growth studies were conducted at a sheltered cove at Adams Point, near a small creek due west of Furber Straits (Fig. 1). No major current flows were evident at either of the study sites.

The substrate at both stations is composed of slate bedrock overlain with clayey silt sediments (Hanson, 1973). The upper shore at these locations support populations of Spartina alterniflora, which stabilize the silt substrate. The tides are of the mixed semi-diurnal type with an average tidal amplitude of about 2.0 m at Cedar Point, and 2.2 m at Adams Point (Anon., 1973). Wide variations of temperature

and salinity are evident (both daily and seasonally) at both locations. Figure 5 summarizes the hydrographic data obtained at Cedar Point. Surface water temperatures ranged from 23-24 C in the summer to -2.0 C in the winter. Salinity varied from 29 o/oo to 14 o/oo, with maximum values occurring during the summer - early fall; minimum salinities were usually present during the spring and occasionally during the fall. Figure 6 shows the cyclical variation of nitrogenous nutrient concentrations at Cedar Point. Nitrate-N concentrations were high (12.6 to 9.5 ug-at/l) in the fall and winter, and low (0.7 to 1.4 ug-at/l) in the summer and early fall. Nitrite-N concentrations showed an opposite variation; a February low of .105 ug-at/l and a summer high of 0.28 ug-at/l in October. Although ammonia concentrations were lower and more variable than nitrite-N, they basically showed the same pattern. Reactive phosphate concentrations (Fig. 7) were high (1.86 ug-at/l) in the fall and lower (0.28 to 0.4 ug-at/l) until the following summer when intermediate values were present.

Figure 8 illustrates the average daily temperature and salinity values recorded at Adams Point during the growth study of tagged plants. The values represent the averages calculated for the periods between the growth measurements. The salinity cycle was similar to that of water temperature, except for an apparent lag in one month.

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 minutes longer than the highest plants (+1.59 to +1.72 m) on the shore. At the intermediate elevations (+1.35 to +1.58 m) the plants were submerged for 20 minutes longer duration than those at the highest locations on the shore.

GROWTH AND REPRODUCTION OF ECAD SCORPIOIDES

Biomass Variations

The seasonal and spatial variations of ecad scorpioides biomass, as g dry weight/0.06 m², during a 12 month period are depicted in Figure 9. Specifically, the average dry weights/0.06 m² of the plant are 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 precipitous drop in the shoreline at this elevation. The maximum biomass (115.6 g) of the plants was recorded during the late summer-fall, while the lowest values (0 to 10) occurred during the late winter. An upward shift in biomass was apparent on the lower shore during the fall. The January record of 86.5 g/0.06 m² between +1.05 and +1.20 m may have been associated with a restricted ice cover at this point versus adjoining areas. The highest individual biomass value of 115.6 g/0.06 m² was recorded during November, 1972, between +0.9 and +1.05 m. In general, the largest values for all months were observed within the same elevational limits.

A clearer picture of seasonal and spatial biomass patterns for ecad scorpioides is provided in Figure 10. Thus, the biomass of ecad scorpioides versus elevation is shown for four seasonal collections (Nov., Aug., May and Feb.). The maximum biomass was evident at +1.0 m during each of the sampling dates. A second biomass peak was found at +0.5 m,

which corresponded to the site below the major substrate discontinuity described earlier. Of the four months illustrated, the highest biomass values were recorded during November (115.6 g/0.06 m²) and the lowest (29.2 g/0.06 m²) were evident during February.

A comparison of the monthly biomass variation of ecad scorpioides between four elevational intervals at Cedar Point is shown in Figure 11. Although major fluctuations were evident at each elevation, a summer-fall maximum and a winter minimum were apparent. Major elevational differences were also evident with the maximum biomass almost always occurring at +0.9 to +1.2 m (i.e. intermediate elevation) and the lowest values usually occurred between +0.3 to +0.6 m and +1.2 to +1.5 m (i.e. highest and lowest elevations). The seasonal variation of ecad scorpioides summed over its vertical distribution (between +0.15 and +1.35 m) is shown in Figure 12. Basically, the same pattern, as shown in Figure 11, was evident.

Growth of Tagged Plants

Figure 13 shows the seasonal growth of tagged in situ plants at Adams Point, expressed as the average daily growth. Of the 79 plants employed in the study, 25 were held at the highest elevation (+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). Seasonal and spatial variations of survival were apparent. Thus, only 28% of the highest plants were maintained through-

out the ten month experiment, while 40% of the intermediate and 67.6% of the lowest plants survived. The daily growth rates shown in Figure 13 are based on the viable plants that were maintained throughout the ten month study. The plants from the three elevations showed their maximum growth (0.8 to 2.5%/day) during the spring to early summer. Plants from the lower shore showed the highest sustained growth, while those from the upper shore showed the lowest growth. The latter plants did not exhibit positive net growth between July and September. The plants grown at the intermediate level only suffered one period of net loss during July. The lowest growing plants always showed a positive growth, with a declining growth rate from July to December.

The seasonal growth of the surviving tagged plants, expressed as damp-dried weight, is shown in Figure 14. The plants at the intermediate and lowest levels showed a similar pattern and rate of growth, except that the former plants showed a suppression of growth towards the end of July. A comparison of Figure 13 shows that plants from the intermediate elevation exhibited little growth during July. The plants on the upper shore showed a comparable rate of growth to those at the other two elevations during 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 (compare Fig. 13). Table II summarizes the average growth ratio of the tagged plants shown in Fig. 14 during the 10 month period. The elevational and temporal patterns

described above are apparent.

Seasonal Variations of Reproduction

As mentioned previously, fertile plants were first noted at Adams Point during May, 1974 and they were subsequently observed at Cedar Point during the same months (Fig. 15 and 16). A detailed study was initiated during May, in order to evaluate the abundance of fertile receptacles per unit area and per unit dry weight. The frequency of fertile receptacles at Cedar Point ranged from $3.5/m^2$ on May 4, to $1.0/m^2$ on June 1 to nothing 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 no receptacles in mid-June. The reproductive frequency of ecad scorpioides, expressed as numbers of receptacles/kg dry weight, is shown in Figure 16; the weight of the receptacles was not included since they were preserved for anatomical studies. Basically the same relationship, as shown in Figure 15, was evident; that is, a late spring peak, a mid-June absence of receptacles and a greater abundance of receptacles at Adams Point than at Cedar Point.

GROWTH AND REPRODUCTION OF SPARTINA ALTERNIFLORA

Biomass, Density and Length

Figures 17 to 19 illustrate seasonal and elevational growth variations with S. alterniflora populations at Cedar Point during April to August, 1973. These five months represent the period of new growth. For the most part, S. alterniflora grows between +0.6 and +1.5 m above M.L.W. (Fig. 17). The first appearance of spring growth was evident in April and by the 23rd of May the upright shoots averaged 5 cm in length (Fig. 17). The maximum lengths were recorded in August, with shoots averaging 82.3 cm in the +0.09 to +1.20 m elevational band. The seasonal changes of biomass showed a similar pattern as shoot length (Fig. 18). Thus, the average biomass for S. alterniflora in the most productive area of its elevational range (+0.75 to +1.35 m) varied from about 0.3 to 50.1 g dry weight/0.06 m² in April and August, respectively. The largest individual biomass value of 53.7 g/0.06 m² was recorded during July between +0.9 and +1.2 m. During the same month the average standing crop of S. alterniflora between +0.6 and +1.5 m, was 37.8 g/0.06 m² or 604.8 g/m².

The shoot density of S. alterniflora at Cedar Point is shown in Figure 19. The lowest density occurred in April, the period of initial spring growth. Thereafter, a gradual increase in numbers occurred during May, followed by a decrease in density during subsequent months. During May, the maximum density of Spartina shoots occurred between +0.75 and +0.9 m. Later in the season the density distribution was

more evenly distributed between +0.45 to +1.2 m.

Figure 20 shows the average length of Spartina shoots growing between +0.9 and +1.2 m for the 15 month period from August, 1972 to October, 1973. The 1972 standing crop is represented by the light bars, while the 1973 crop is depicted by the dark bars. After September, 1972, the length values for the 1972 plants are based on dead material. The average length decreased from late summer through the winter and then increased the following spring. The longest lengths were recorded in August, 1972 (92.2 cm average) and July, 1973 (81.1 cm average). A slight increase in the average length of dead material was evident after June, 1973 because of the continued addition of dead (1973) material. The Spartina canopy averaged at least 50 cm from July to November; between December and June it averaged 25 cm. Thus, the shore and the ecad scorpioides plants are relatively exposed during the latter period because of limited Spartina canopy. A summary of the biomass variations within the same elevational band (+0.9 to +1.2 m) is given in Figure 21. Basically there is a correspondance between the length and biomass values with the largest plants and greatest biomass during the summer and the opposite situation in the winter.

Figure 22 shows the growth rates of S. alterniflora during April to September, 1973, expressed as the net daily increase in length and dry weight. The values are based on populations occurring between +0.9 and +1.2 m. The daily

rates of elongation ranged from 0.32 to 1.64 cm/day, with the fastest growth occurring during June and no net growth during July. Daily weight changes of S. alterniflora followed a similar seasonal pattern as length, with net growth of 0.2 to 1.0 g/0.06 m²/day occurring during April through June and a net loss thereafter.

Seasonal Reproduction (Flowering)

The seasonal changes of flowering with Spartina populations between +0.9 and +1.2 m are shown in Figure 21. The striped bars in Fig. 21 represent the frequency of flowering spikes. The period of maximum flowering (36.3 - 49.9%) was recorded in August of both years, with the onset of flowering occurring in July and flowers remaining until September-October. The percentage of flowering stalks also varied with elevation and time (Fig. 23). Thus, during July and August the largest number of flowering plants were evident between +1.0 and +1.5 m, while a broader distribution was apparent in September.

COMPARATIVE BIOMASS VARIATIONS

The seasonal variations of Ascophyllum nodosum biomass between +0.15 and +1.5 m are shown in Figure 24. A gradual increase was evident from the spring to summer, with maximum values occurring in August of both years. Thereafter, the biomass values decreased.

The vertical distribution of A. nodosum and ecad scorpioides within the intertidal zone at Cedar Point is shown in Figure 25. 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 illustrated in the same figure. Ascophyllum nodosum was broadly distributed between +0.22 and +1.42 m, with maximum biomass occurring between +0.22 and +0.97 m (Table III). The detached ecad scorpioides was similarly vertically distributed as A. nodosum, except that its maximum biomass occurs between +0.97 and +1.12 m. The average biomass of ecad scorpioides was usually less than A. nodosum (see also Tables I and III). The density of Spartina stalks and the biomass of ecad scorpioides both show maximum values at the same elevation, +1.12 m.

Figure 26 summarizes the vertical biomass distribution of Fucus vesiculosus var. spiralis, Pilayella littoralis, and Ulva lactuca at Cedar Point. Of the intertidal algae at Cedar Point, F. vesiculosus var. spiralis was the third most abundant species (compare Tables I, III and IV); its maximum

biomass occurred somewhat lower than that of A. nodosum in the lower intertidal (+0.45 to +0.60 m). Limited quantities of U. lactuca were recorded; it was most abundant in the lower intertidal between 0.0 to +0.37 m. The maximum biomass of Pilayella littoralis occurred in the upper intertidal between +0.82 and +1.42 m. Pilayella showed a pronounced spring growth, with maximum biomass occurring during April and May (Fig. 27). At this time it was a conspicuous epiphyte on S. alterniflora and the associated fucoids A. nodosum, ecad scorpioides and F. vesiculosus var. spiralis. A variety of other seaweeds were also recorded during the quadrat studies, but their biomass contributions were negligible. Specific details on biomass values for the latter species are summarized in Table IV.

The ash-free and dry weights for July samples of S. alterniflora and the ecad scorpioides are summarized below in order to compare the biomass values with other workers' findings. The ashed aerial portions of S. alterniflora contained 16.2% ash for an 83.8% ash-free weight. Ecad scorpioides showed a 28.15% ash or a 71.85% ash-free weight.

MANOMETRIC STUDIES

Light

Figure 28 illustrates the seasonal net photosynthesis-light responses in the laboratory of A. nodosum and the detached ecad scorpioides at 35 o/oo, 1.5 C (winter) and 15 C (summer), and under a variety of different light intensities. During the summer plants of both taxa exhibited an increase in net photosynthesis with an increase in light intensity from 185 to 850 foot-candles (f-c) but beyond 850 f-c the rates of oxygen evolution gradually decreased up to the maximum measured intensity of 5070 f-c. Thus, light intensities in excess of 850 f-c were probably saturating, while lower intensities were probably suboptimal. A differential oxygen evolution was also evident between the two plants during the summer; it ranged from 5 to 12 ul/g dry weight/minute at 1800 and 5070 f-c respectively. The same light optimum (approximately 850 f-c) was also recorded for both plants during the winter. The lower rate of oxygen evolution resulted from the lower temperature (1.5 C) employed. In contrast to the summer specimens, no consistent differences were evident between the oxygen evolution of the two plants during the winter.

Temperature

Figure 29 depicts the seasonal net photosynthesis-temperature responses of A. nodosum and ecad scorpioides at 35 o/oo, 1000 f-c and at a variety of different temperatures.

During the summer A. nodosum showed an increase in net photosynthesis with an increase in temperature to 18 C, while ecad scorpioides showed approximately the same net photosynthesis between 18 and 21 C. Both forms showed a conspicuous decrease in net photosynthesis beyond 24 C; their net photosynthesis ceased altogether at 35 C. It should also be noted that A. nodosum showed consistently higher rates of net photosynthesis than the detached ecad, except at 30 C.

In contrast to the summer, winter specimens of both plants showed a reduced oxygen evolution with a plateau of net photosynthesis between 10 and 25 C. The average net photosynthesis for both forms ranged from approximately 10 to 18 ul oxygen/g dry weight/minute, between 1.5 and 30 C. As during the summer, both plants showed no net photosynthesis at 35 C. The maximum net photosynthesis of the summer plants was 5 to 7 times that of the winter.

Salinity

The photosynthesis-salinity experiments were characterized by wide variations in values, and repeated attempts were made to achieve consistent readings. Figure 30 illustrates the rates of net photosynthesis of both Ascophyllum plants at 8 salinities, 15 C and 1000 f-c. The lowest net photosynthesis was recorded at 18 o/oo. Even so, both plants exhibited net photosynthesis between 0 - 40 o/oo. Ascophyllum nodosum showed an average net photosynthesis of 65 ul oxygen/g dry weight/minute at 0 and 40 o/oo, while the detached ecad

had rates of 32 and 52 ul oxygen/g dry weight/minute at 0 and 40 o/oo, respectively.

A single dark respiration-salinity experiment was conducted on ecad scorpioides at three salinities (0, 18 and 35 o/oo) and at 18 C (Fig. 31). The respiration values recorded immediately after 24 hours of dark equilibration (i.e. pre-illumination) were 8.0, 28.9, and 2.9 ul oxygen/g dry weight/minute, respectively for the 0, 18 and 35 o/oo salinities. The same material, when exposed to 1000 f-c for 60 minutes, evolved oxygen (i.e. net photosynthesis) at the following rates for the same salinities: 44.6, 14.4 and 32.5 ul oxygen/g dry weight/minute. Dark respiration was again monitored with the lights off (i.e. post-illumination) and the readings showed a flatter curve than the earlier respiration run.

DISCUSSION

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

The field studies showed a variety of interrelationships between Ascophyllum nodosum, ecad scorpioides and Spartina alterniflora. For example, A. nodosum grows most abundantly just below Spartina, while the greatest biomass of ecad scorpioides coincided with the highest density of S. alterniflora. Thus, detached fragments of A. nodosum become entangled and stabilized amongst S. alterniflora and they subsequently produce extensive populations of ecad scorpioides. During the summer Spartina also provides an extensive canopy over the ecad scorpioides, thereby decreasing light intensities and reducing water losses. The saturation light levels (about 850 f-c) for ecad scorpioides are relatively low, at least compared to full sunlight (i.e. approximately

10,000 f-c) and the levels would probably be an advantage during the summer in such a habitat. The Spartina canopy, and its associated protection for ecad scorpioides, is at a minimum during January to April, because of extreme ice scouring and low winter temperature - i.e. no growth of Spartina occurs and the canopy decomposes. In contrast to the present study which found the maximum biomass of ecad scorpioides to occur in the fall, Brinkhuis (1975) reported maximum biomass of ecads mackaii and scorpioides to occur in the spring.

According to Gibb (1957) the detached ecad mackaii shows its maximum biomass at high levels, even so she does not quantify its vertical biomass distribution. The ecad scorpioides shows its maximum biomass at approximately +1.0 m. An interrelationship was also noted between elevation, longevity and growth of ecad scorpioides, for the highest tagged plants showed minimal growth or a loss of weight during the summer. In contrast, tagged plants at the lowest elevations showed sustained, positive growth during the summer. A number of workers (e.g. Lewis, 1964; Zaneveld, 1969) have also emphasized that elevation 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 elevations, where extensive desiccation and light fluctuations occur, exhibit "sun decay" of the terminal branches. The same discoloration and necrosis of the terminal branches of ecad scorpioides was also noted for the highest 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. A comparison of the net photosynthesis-temperature responses of ecad scorpioides shows a good correspondance between growth and net photosynthesis, as net photosynthesis increased with an increase in temperature to approximately 18 - 20 C. As noted by Kanwisher (1966) respiration also increases with temperature, even so the differences between production and consumption results in an increasing rate of net photosynthesis and thus of growth, within the temperature range, 18 - 20 C. The spring period of maximum growth for tagged plants was also associated with a major transition in light duration and intensity (Anon., 1974). The plant's broad tolerance to light intensities suggests that it is well adapted to such fluctuations. From the above discussion it is evident that the seasonal and elevational growth variations of ecad scorpioides can be related to temperature and light variations.

The biomass of attached Ascophyllum nodosum showed a conspicuous seasonal variation, with a major attrition occur-

ring during September in two successive years. The precipitous loss of A. nodosum in September was probably due to storm removal, as reported by Baardseth (1970). The latter data also supports the fact that detached fragments sustain the population of ecad scorpioides, as subsequent biomass increases of ecad scorpioides were recorded during the fall months (Fig. 12 and 24). The influx of new fragments must contribute to the normal fall biomass increases (i.e. growth) of ecad scorpioides.

No receptacles were observed on ecad scorpioides plants in 574 samples taken during the two year period (1972-1973) at Cedar Point. However, during the following spring of 1974, fertile receptacles, bearing oogonia and antheridia, were recorded initially 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 and Hill (1970) have also described the occurrence of receptacles as 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 in ecad scorpioides. The spring period of maximum reproduction with ecad scorpioides (Fig. 15 and 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; in addition they are usually most abundant on the largest, residual fragments of A. nodosum. In contrast to other furoid algae, which can show a pronounced vertical stratification of reproductive plants (Knight and Parke, 1950; R. Niemeck, unpublished data), no discernible stratification of reproductive plants was evident at Cedar Point or Adams Point.

The manometric studies were initiated in order to compare the physiological responses of Ascophyllum nodosum and the detached ecad scorpioides under a variety of different light, temperature and salinity conditions. Of specific interest was whether or not the detached ecad scorpioides was physiologically distinct from A. nodosum, because of adaptations to a new habitat. A comparison of Figures 28 to 30 shows that no major physiological differences were evident between the two plants except for the summer photosynthesis-temperature responses of the plants. Both plants exhibited a pronounced seasonal difference in their temperature and light responses, with winter plants producing oxygen at a lower rate than the summer plants. Ascophyllum nodosum and ecad scorpioides exhibit a eurythermal response to temperature, with a more pronounced optimum occurring during the summer than the winter.

Gessner and Schramm (1971) discuss the importance of

salinity on photosynthesis of marine plants; they emphasize that no consistent relationships are apparent because of variable techniques and different species. The erratic results encountered in this study are similar to those obtained by Ogata and Schramm (1971) with Porphyra umbilicalis, for they observed a decrease in oxygen evolution with media one-half the concentration of sea water in one experiment, but not in another. Both A. nodosum and ecad scorpioides exhibited a decrease in net photosynthesis at intermediate salinities (18 o/oo), as compared to higher and lower salinities. The anomalous responses of the two furoid algae are not readily explained, and they may be attributable to a variety of factors: duration of exposure and "free space" photosynthesis. Montfort (1931) emphasized that the relationship between algal photosynthesis and salinity, as recorded by various authors, is inconsistent, because it is based upon varying periods of exposure. In the present experiments a short term incubation of 24 hours was employed, because it was thought that comparable short term variations occur in estuarine littoral habitats.

The high rate of net photosynthesis for Ascophyllum nodosum and ecad scorpioides at low salinities, may be best explained in terms of "free space photosynthesis", as outlined by Gessner and Hammer (1968), Hammer (1969) and Gessner (1969). The latter works demonstrated that chloride ions can be replaced by available bicarbonate ions in the "apparent

free space" of seaweeds and that this may account for an increased photosynthetic rate. The use of a NaHCO_3 buffer in the present studies, coupled with varying concentrations of salinity make this explanation particularly applicable for the enhanced net photosynthesis of A. nodosum and ecad scorpioides at low salinities.

Gessner and Schramm (1971) also discuss algal respiration in relation to salinity. Again, no general conclusions can be given, except that respiration tends to increase in diluted sea water. The somewhat limited results in the present study, as well as those of Hoffman (1929), Ogata (1963), and Ogata and Takada (1968) tend to substantiate this generalization. Further work on Ascophyllum is required to determine the interrelationships of respiration and photosynthesis in conjunction with salinity. Evidence from this study indicates a possible respiratory effect on photosynthetic capacity at an intermediate (18 o/oo) salinity. Similar studies should be also conducted under emergent conditions.

In summary the manometric studies suggest that A. nodosum and the ecad scorpioides are both tolerant of a wide variety of temperatures (5 to 24 C) and salinities (0 to 40 o/oo). Such physiological traits and tolerances correspond to their broad coastal and estuarine distributions where wide variations in temperature and salinity may occur (Gessner and Schramm, 1971).

Salt marshes are major contributors to coastal productivity (Mann, 1972). That is, the bulk of the material produced from the marsh grass Spartina alterniflora enters the food chain through the organic detritus cycle (Odum and de la Cruz, 1967; Mann, 1973), as minimal (approximately 5%) grazing of Spartina occurs (Teal, 1962). Many workers have recently reported on the primary productivity of marsh grass, because of its major role in estuarine-coastal productivity. Keefe (1972) gives a detailed summary on latitudinal variations of Spartina productivity, indicating that northern sites have lower rates than more southerly areas. Since then, Nixon and Oviatt (1973) have reported production rates of 840 g/m²/year in Rhode Island, while Hatcher and Mann (1975) and Martin (1974) have recorded comparable rates of about 710 g/m²/year in Nova Scotia, Canada. The results of the present study provide the only available data on S. alterniflora productivity between Rhode Island and Nova Scotia. The maximum productivity recorded at Cedar Point was 859 g/m²/year, which was higher than the rates recorded by Nixon and Oviatt (1973). Even so, the overall average productivity rate at Cedar Point was 604 g/m²/year.

It is of interest to note that the density of S. alterniflora stems at Cedar Point varied seasonally, with the highest numbers per unit areas occurring in the spring and the lower densities occurring during the remainder of the growing season. Apparently there is a pronounced competition

for light and space during the late spring-summer, causing a reduction in density. The daily growth rates of Spartina populations in New Hampshire increased with an increase in temperature, sunlight, and daylight until the end of June. In agreement with the observations of Nixon and Oviatt (1973) in Rhode Island, no resurgence of growth was evident after floral development (August) in New Hampshire. The dispersal of seeds and the dehiscence of the flowering stalk (infructescence) during the later summer-fall probably accounted for a loss in both length and weight during this period. Subsequently the stems were killed by the first frost (late September - early October), denuded by ice scouring during the winter and then entered the detritus cycle of the Estuary.

Relatively little is known about the standing crop and biomass variations of estuarine macrophytic algae. The information summarized in Table IV may be of considerable importance in the future as baseline information for estuarine production (Mann, 1973) and for future management of the Great Bay Estuary System. Of particular interest was the pronounced seasonal variations of selected species, such as Pilayella littoralis, which literally "bloomed" during the spring and then subsequently disappeared during the summer. A comparison of the monthly and average annual biomass values in Tables I, III and IV also shows the relative dominance of a variety of perennial and annual species, including the major fucoid algae Fucus vesiculosus var. spiralis, Ascophyllum nodosum and ecad scorpioides of A. nodosum.

SUMMARY

1. The seasonal and spatial distributions of the free-living ecad scorpioides of Ascophyllum nodosum are described from the Great Bay Estuary System of New Hampshire and Maine.

2. A fall biomass maximum of ecad scorpioides was recorded during two consecutive years; it may have been attributable to an influx of source material by storms, and/or to normal seasonal growth.

3. The field studies suggest that S. alterniflora provides initial stability for the progenitor fragments of A. nodosum. Subsequently the marsh grass provides a protective canopy over the ecad during the summer; a canopy is absent during the winter.

4. Comparative manometric experiments have demonstrated that A. nodosum and its free-living ecad scorpioides exhibit similar physiological responses to varying light intensities, temperatures, and salinities.

5. The ecad scorpioides exhibits a broad tolerance to temperature and salinity, which corresponds to its natural distribution within the Great Bay Estuary System.

6. Sexual reproduction of the ecad scorpioides was recorded only during one of the three years of investigation.

7. The morphology and reproduction of the ecad scorpioides is compared and contrasted with other ecads and

the attached A. nodosum. A gradient of morphology is present in New Hampshire from typical A. nodosum to the extreme ecad scorpioides.

8. The seasonal productivity of S. alterniflora populations were assessed. No previous accounts of marsh grass productivity have been recorded between Rhode Island and Nova Scotia, Canada.

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TABLE I

Biomass Variations (g dry weight/0.06m²) of ecad scorpioides at Cedar Point

ELEV. (m)	1972		1973														Mean
	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct		
1.50	2.6	5.2	10.8	4.6	1.9	16.0	0.0	2.1	3.1	17.0	5.0	13.0	10.2	7.8	3.7	6.9	
1.35	24.9	6.6	8.7	7.1	7.8	13.0	6.8	7.0	16.7	19.0	24.7	32.8	27.7	20.2	9.1	15.5	
1.20	42.5	43.7	40.1	21.5	36.6	86.5	11.1	32.9	74.8	29.7	52.8	50.8	46.2	74.5	48.6	46.2	
1.05	1.4	44.6	93.2	115.6	28.4	25.8	29.2	12.2	25.4	41.7	37.6	86.9	53.6	35.9	35.4	44.5	
0.90	21.0	19.4	29.7	40.7	0.0	34.8	21.1	27.5	16.8	16.4	51.9	14.3	4.8	0.0	26.4	21.7	
0.75	1.1		30.2	31.3	39.0	9.9	2.1	7.5	5.8	20.6	6.6	0.5	22.1	42.5	61.2	17.1	
0.60	0.0	11.5	20.0	53.7	0.0	0.4	17.2	2.1	20.8	14.0	13.5	0.6	43.2	52.1	60.1	20.6	
0.45	64.4	29.1	0.0	15.9	5.7	2.5	0.0	trace	4.7	0.8	1.6		0.0	3.2	26.2	10.3	
0.30		48.9	4.4	6.6	1.0	0.0	13.5	trace	46.0	12.0		16.1	0.2	0.0		9.9	
0.15																	
\bar{X}	19.7	20.2	23.2	32.3	13.3	21.0	9.7	10.1	18.7	17.7	21.5	24.9	23.1	26.2	33.8		

TABLE II

Summary of Average Growth Rates of
 Tagged In Situ Plants of
 ecad scorpioides at Adams Point

<u>ELEVATION (m)</u> <u>ABOVE MLW</u>	<u>AVERAGE</u> <u>INITIAL</u> <u>WT (g)</u>	<u>AVERAGE</u> <u>FINAL</u> <u>WT (g)</u>	<u>AVERAGE</u> <u>CHANGE IN</u> <u>WT (g)</u>	<u>AVERAGE</u> <u>CHANGE</u> <u>%</u>
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

TABLE III

Biomass Variations of Ascomhyllum nodosum at Cedar Point (g dry weight/0.06m²)

ELEV.	1972		1973													Mean
	(m)	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	
1.50	1.8	1.8	2.6	7.6	1.2	2.3	0.0	0.3	0.4	1.5	1.7	1.1	4.2	2.9	0.1	2.0
1.35	3.3	1.1	3.4	1.3	4.6	2.6	0.8	0.5	5.0	5.4	1.9	11.8	53.5	2.0	4.3	6.8
1.20	47.7	44.7	61.4	16.7	27.1	35.8	3.0	0.6	38.1	14.0	4.3	28.5	10.0	38.5	5.8	25.1
1.05	479.7	57.5	37.5	15.2	20.9	3.3	7.1	3.3	34.2	5.7	5.7	24.1	25.0	46.8	74.6	56.0
0.90	17.4	53.6	23.2	68.5	2.1	23.9	24.8	0.5	38.8	37.3	19.1	108.3	126.6	150.0	41.8	49.3
0.75	1.3		71.1	74.6	80.9	3.4	72.9	1.4	11.0	53.8	122.8	90.5	100.7	8.4	21.1	47.6
0.60	173.0	10.7	93.8	3.3	45.8	23.2	92.6	53.1	20.1	36.0	6.8	142.4	49.5	23.4	10.6	52.3
0.45	3.2	2.5	31.6	41.4	42.3	115.9	13.1	27.1	73.7	11.3	102.9		141.4	11.7	140.0	50.5
0.30		0.2	79.9	4.4	1.5	40.3	3.2	5.6	14.0	150.2		9.6	416.8	0.0		48.4
0.15																
X	90.9	21.5	44.9	26.2	25.3	27.9	24.2	10.3	26.1	35.0	33.2	52.0	103.1	31.5	33.5	

TABLE IV

Biomass Variations of the Selected Seaweed Populations of Cedar Point (g weight/0.06m²)*

Species	1972	1973										Mean				
	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun		Jul	Aug	Sep	Oct
<u>Fucus vesiculosus</u> var. <u>spiralis</u>	104.0	94.4	129.6	145.6	44.8	75.2	12.8	57.6	19.2	43.2	33.6	73.6	43.2	38.4	30.9	63.1
<u>Ulva lactuca</u>	2.4	6.9	13.3	5.9	1.6	1.1	2.7	0.3	0.3	1.4	1.9	0.6	0.3	0.1	0.1	2.6
<u>Enteromorpha</u> sp.	0.4	16.0	1.6	1.0		25.6		1.0	1.8	1.1	0.4	0.3		0.1	0.1	3.3
<u>Chondrus crispus</u>				1.6	0.3			0.5			0.3			0.6		0.2
<u>Petalonia fascia</u>			+					+	0.5	+						
<u>Pilayella littoralis</u>				1.0	0.3	2.4	0.6		9.6	16.0	2.5	0.3				2.2
<u>Rhizoclonium riparium</u>				0.4	0.3	3.2					1.4	+	0.3			0.4
<u>Ectocarpus</u> sp.				1.3												0.1
<u>Chaetomorpha linum</u>					0.5			0.3			0.8			+	+	0.1
<u>Gigartina stellata</u>						3.2										0.2
<u>Porphyra</u> sp.								+								
<u>Urospora</u> sp.															+	
<u>Ceramium rubrum</u>															+	
<u>Monostroma fuscum</u>									1.0	+	+				+	+
<u>Ulothrix flacca</u>									+		+					
<u>Cladophora sericeae</u>									+	+	+		+		0.3	
<u>Chorda torentosa</u>											+					
<u>Polysiphonia harveyii</u>													+	+		

* + indicates trace amounts (< 0.1g) present

Figure 1. Distribution of ecad scorpioides within the
Great Bay Estuary System of New Hampshire-Maine.

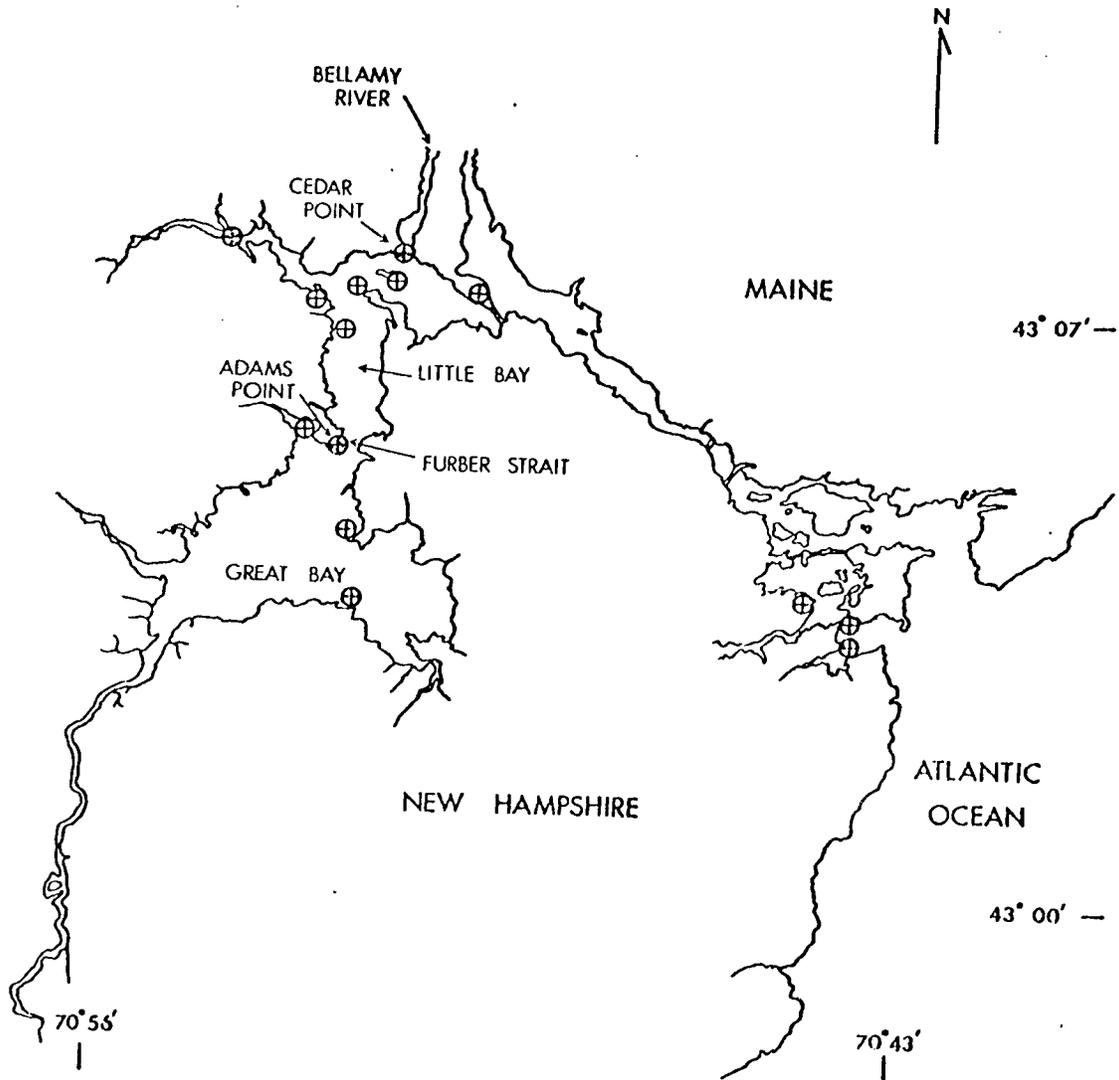


Figure 2. Tagged plants of ecad scorpioides attached to nylon lines and cinder blocks at Adams Point.

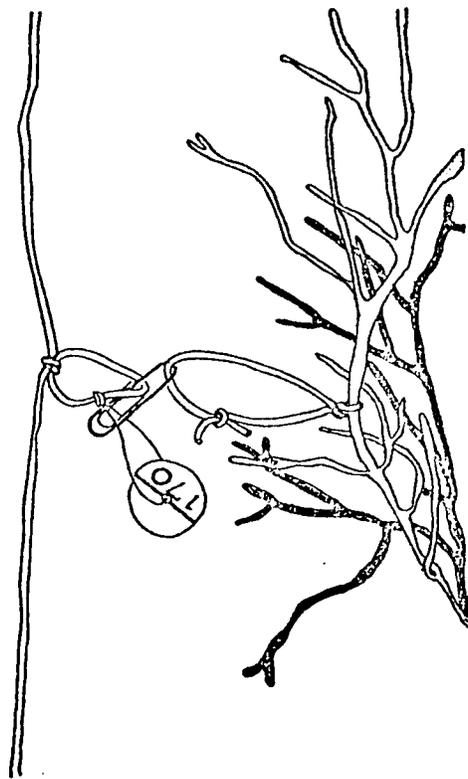
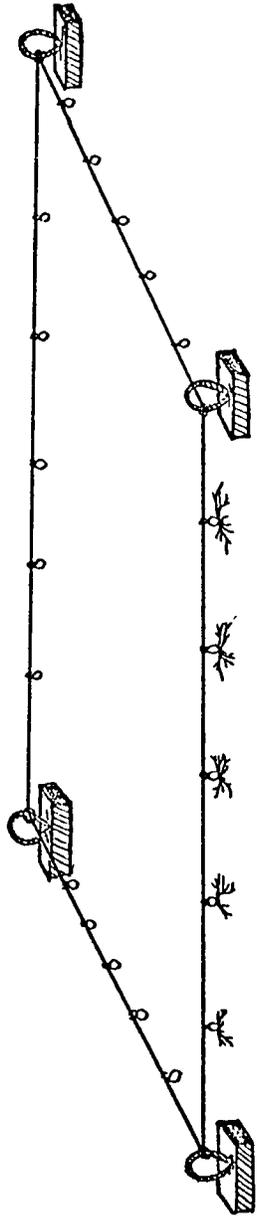


Figure 3. Morphological variation of detached Ascophyllum nodosum plants: (A) transitional stage similar to ecad mackaii; (B) well developed ecad scorpioides; (C) and (D) reproductive plants of ecad scorpioides.



Figure 4. Morphology of fertile receptacles on ecad
scorpioides (A-F) and A. nodosum (G): A, 2X;
B, 1.5X; C, 2X; D, 2.5X; E, 2.5X; F, 3X; G, 1X.

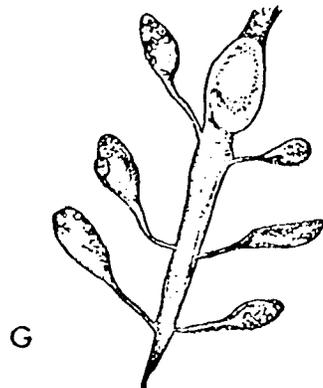
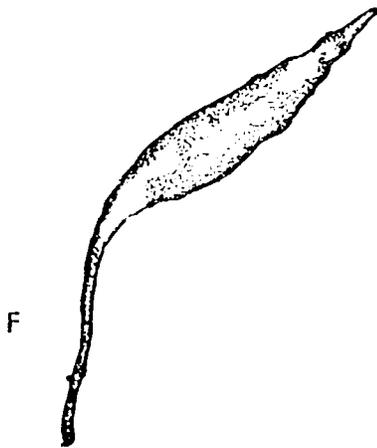
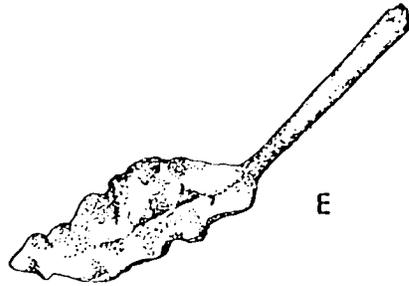
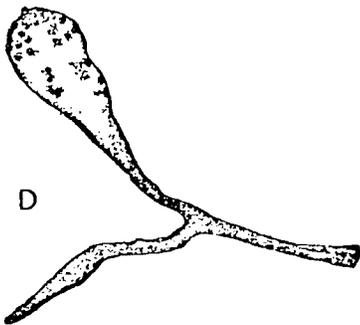
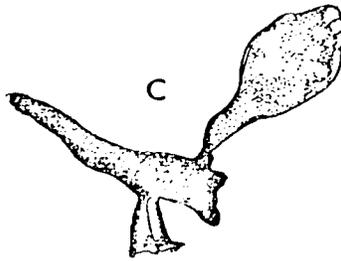
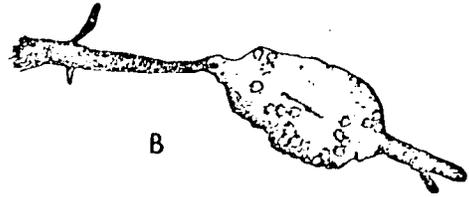
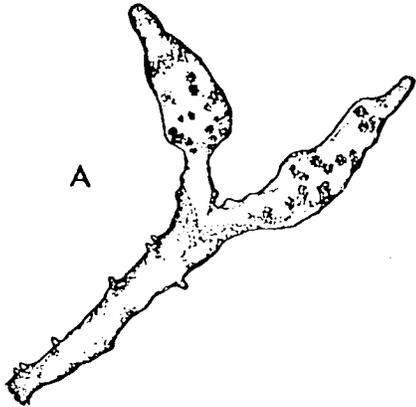


Figure 5. Seasonal variation of surface water temperature and salinity at Cedar Point, 1972 to 1973.

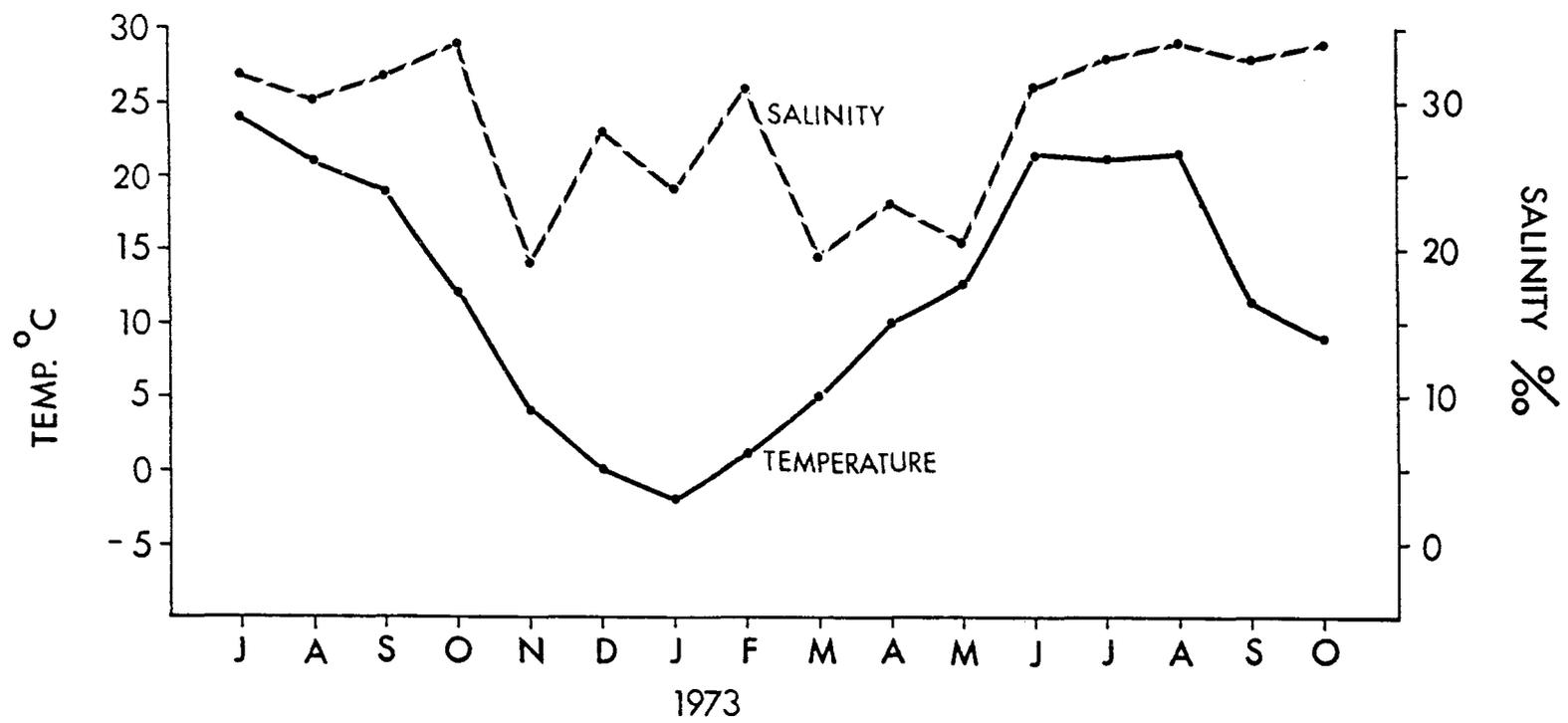


Figure 6. Seasonal variation of nitrogenous nutrients from the surface waters at Cedar Point, 1972 to 1973.

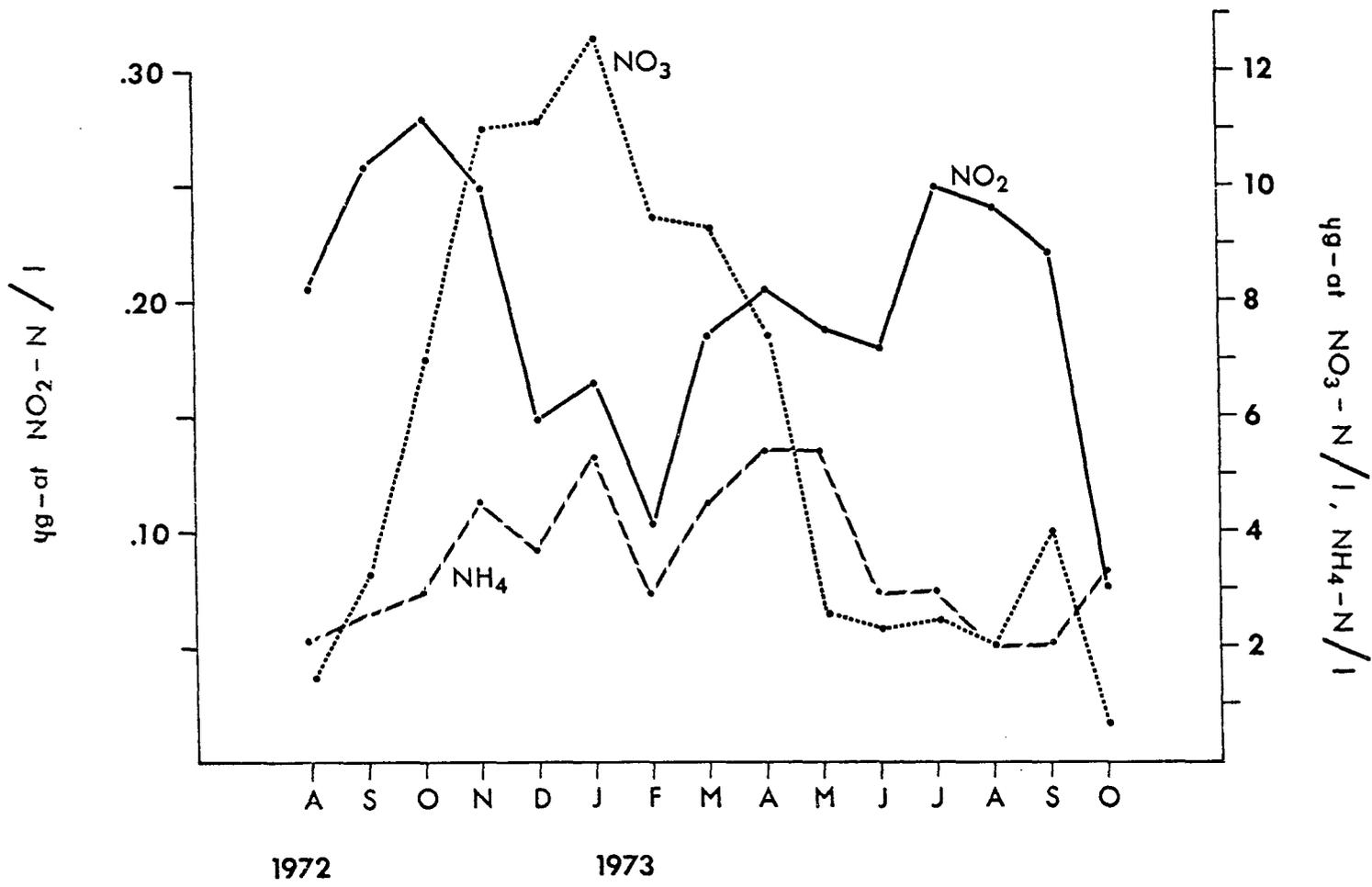


Figure 7. Seasonal variation of phosphorous nutrients
(reactive phosphates) from the surface waters
at Cedar Point, 1972 to 1973.

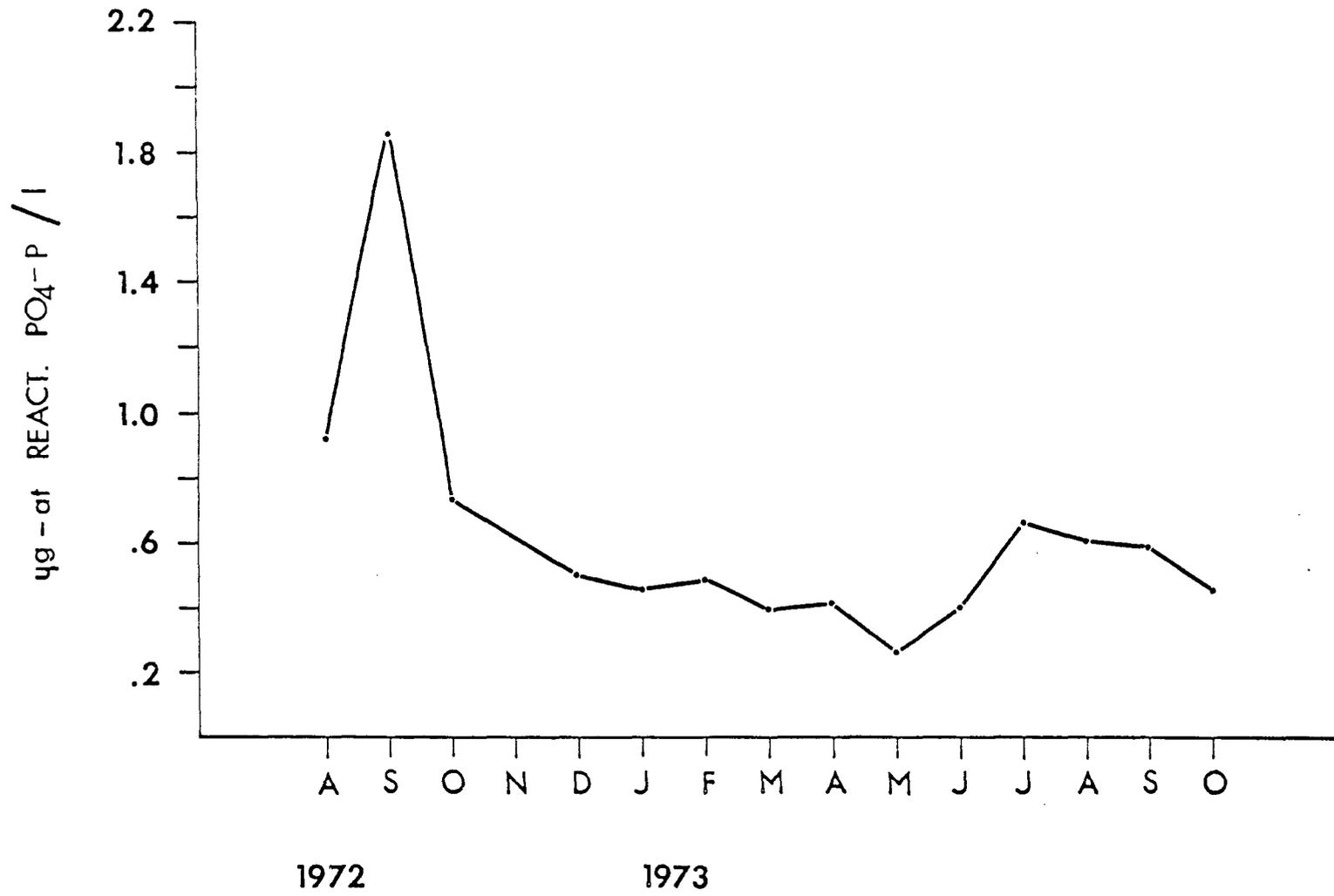


Figure 8. Surface water temperature and salinity variations at Adams Point, March to December, 1974.

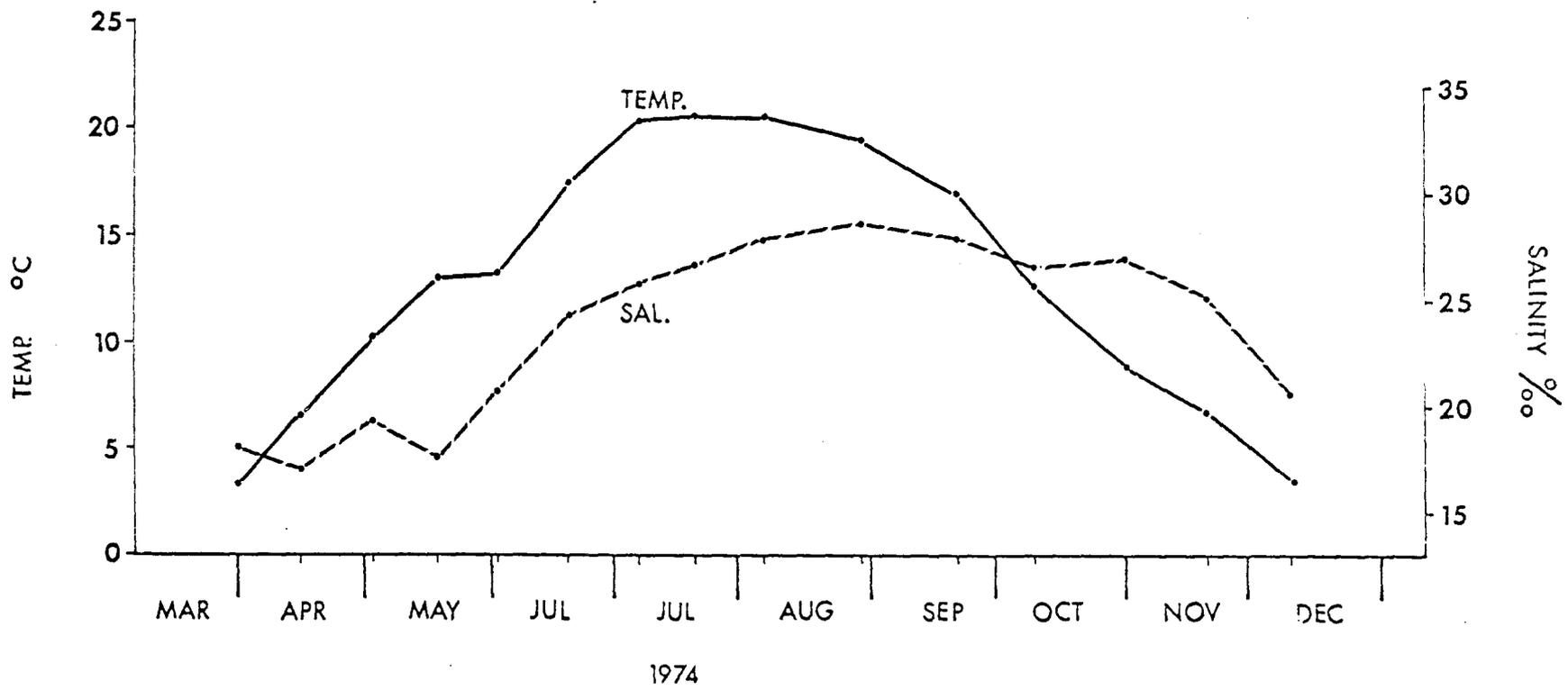


Figure 9. Seasonal and spatial biomass variations of ecad scorpioides at Cedar Point, November, 1972 to October, 1973.

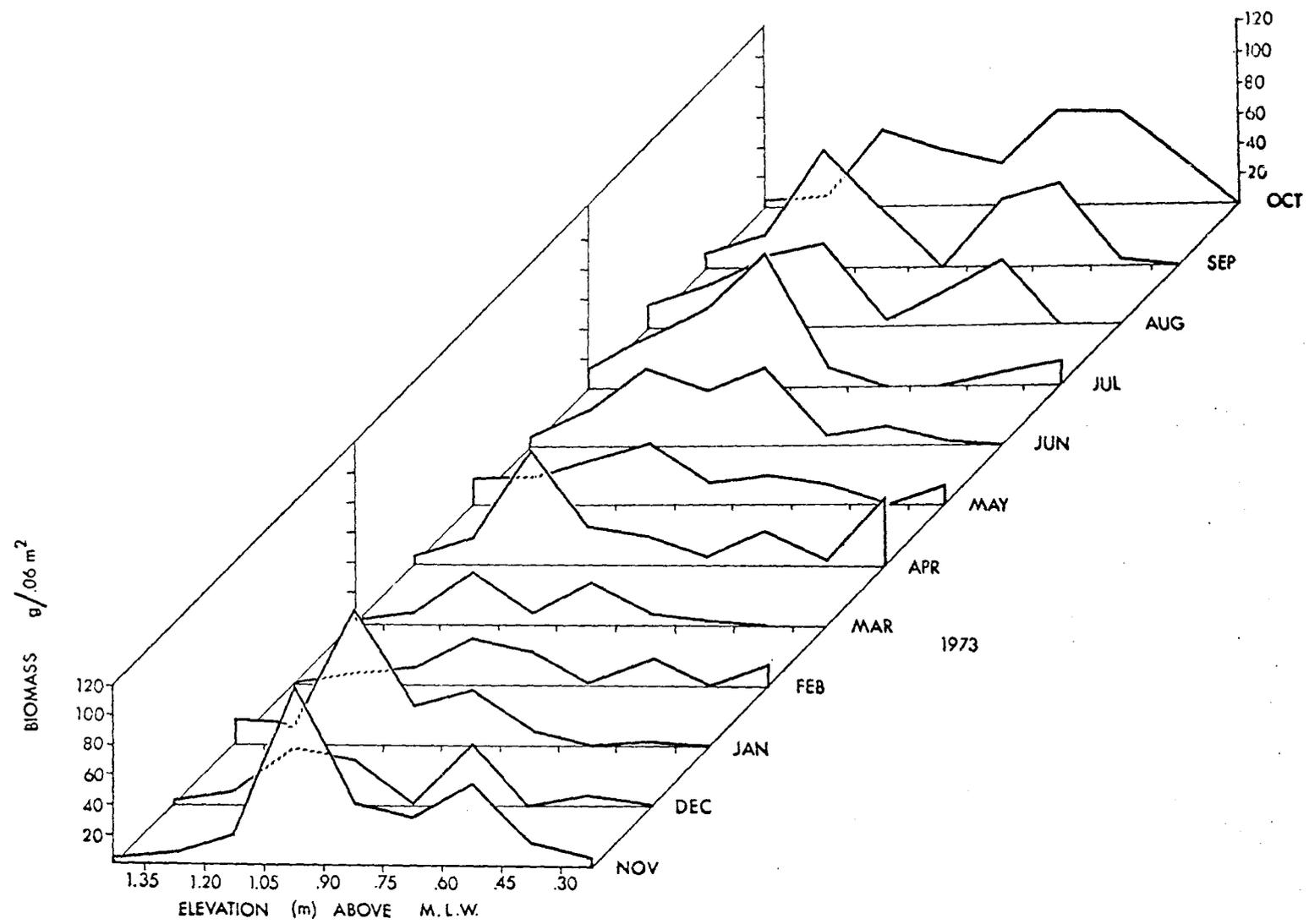


Figure 10. Spatial biomass variations of ecad scorpioides during four seasons at Cedar Point.

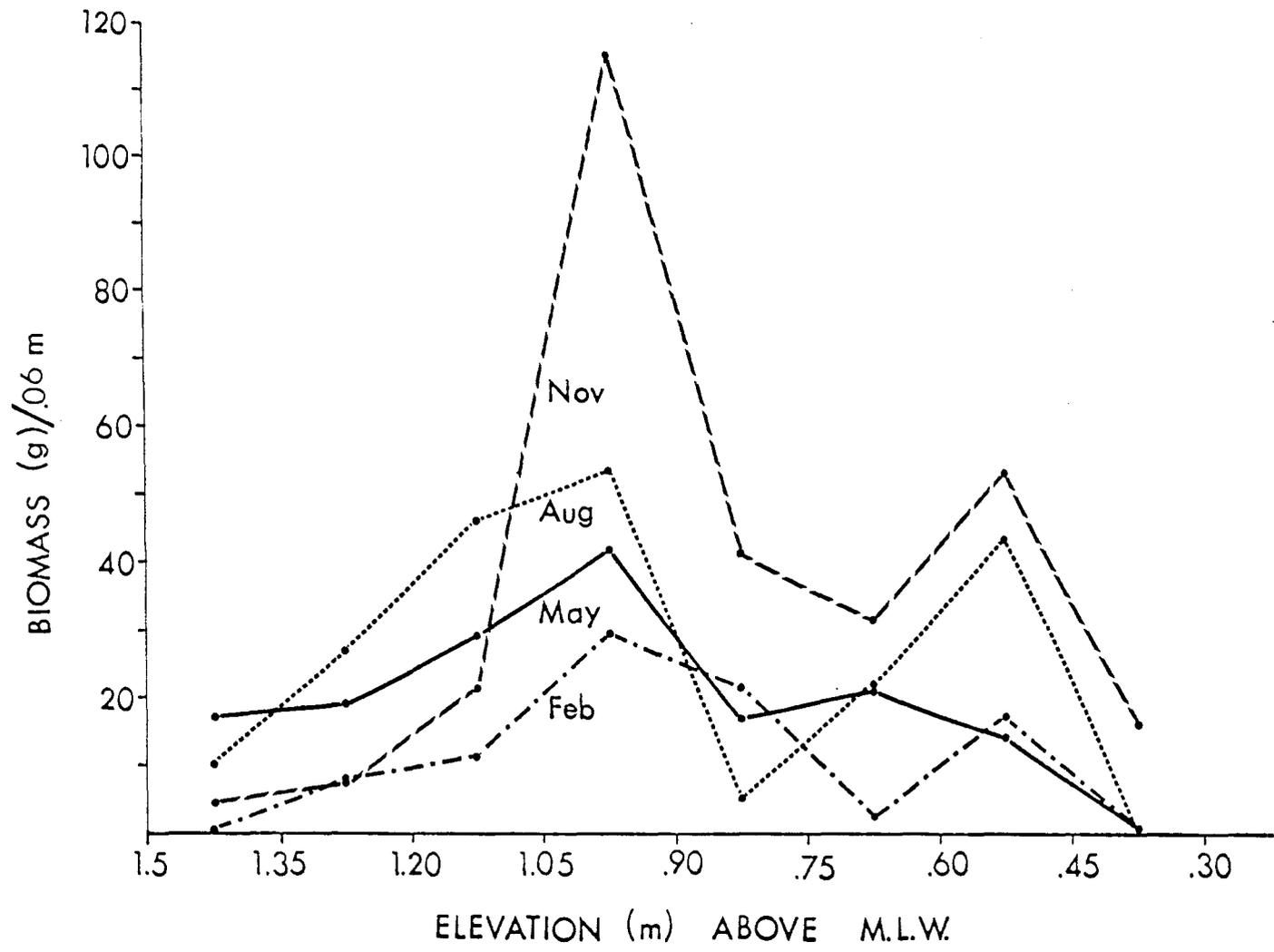


Figure 11. Seasonal variation of ecad scorpioides biomass at four elevations, August, 1972 to October, 1973.

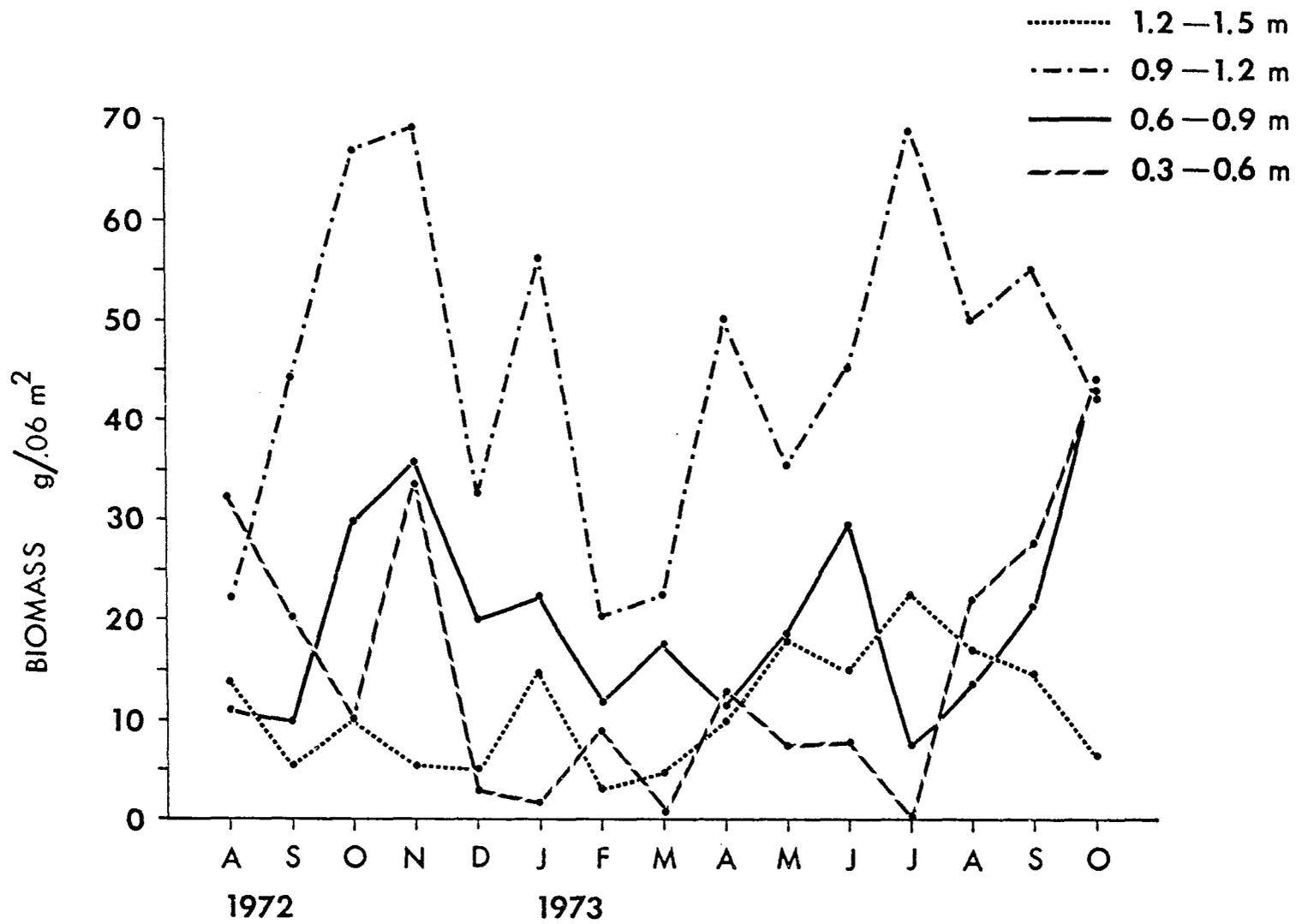


Figure 12. Seasonal variations of ecad scorpioides
biomass summed over its vertical distribution
at Cedar Point, August, 1972 to October, 1973.



Figure 13. Average daily growth of ecad scorpioides plants from three elevations at Adams Point, March to December, 1974.

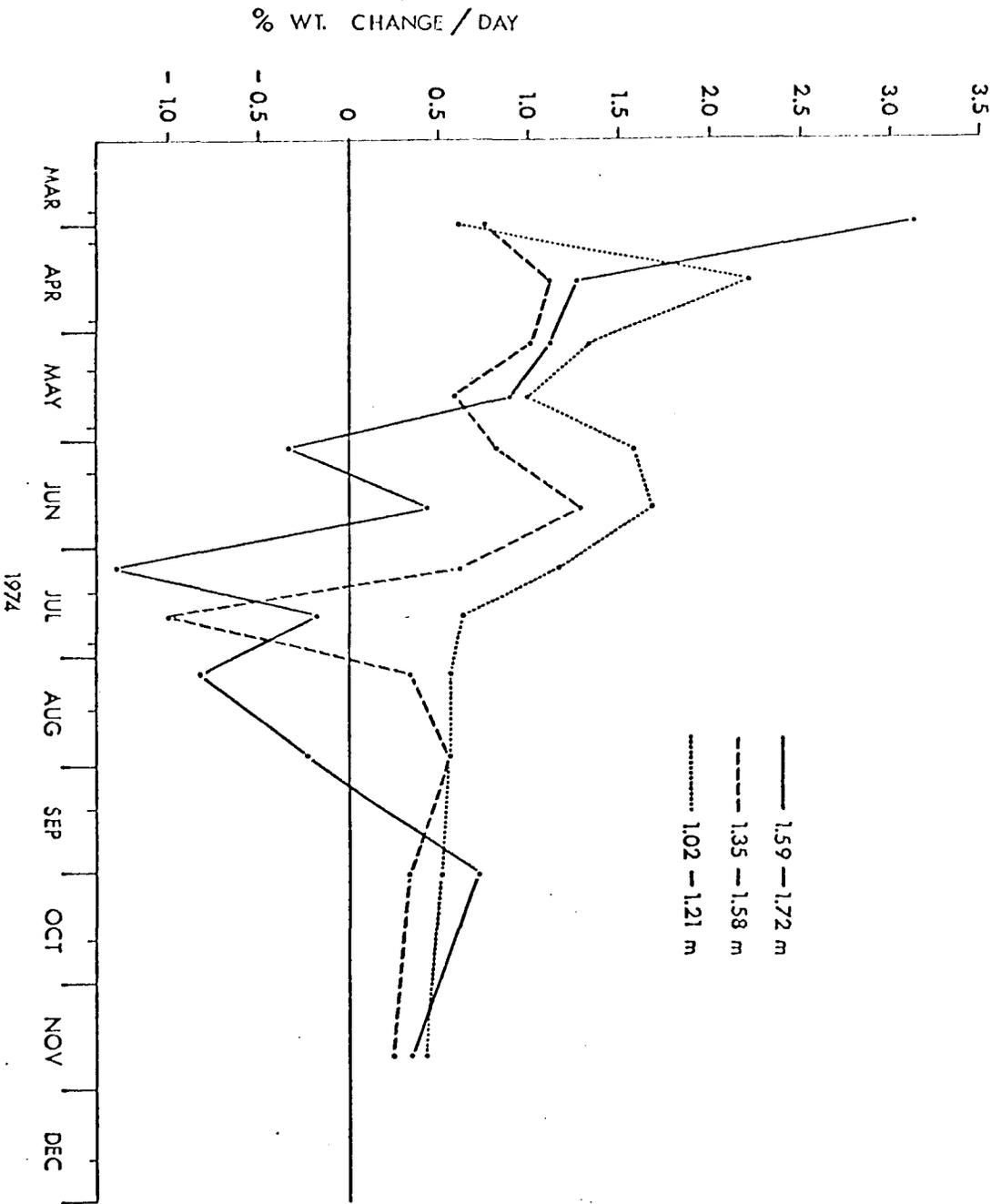


Figure 14. Average cumulative weight of tagged ecad scorpioides plants from three elevations at Adams Point, March to December, 1974.

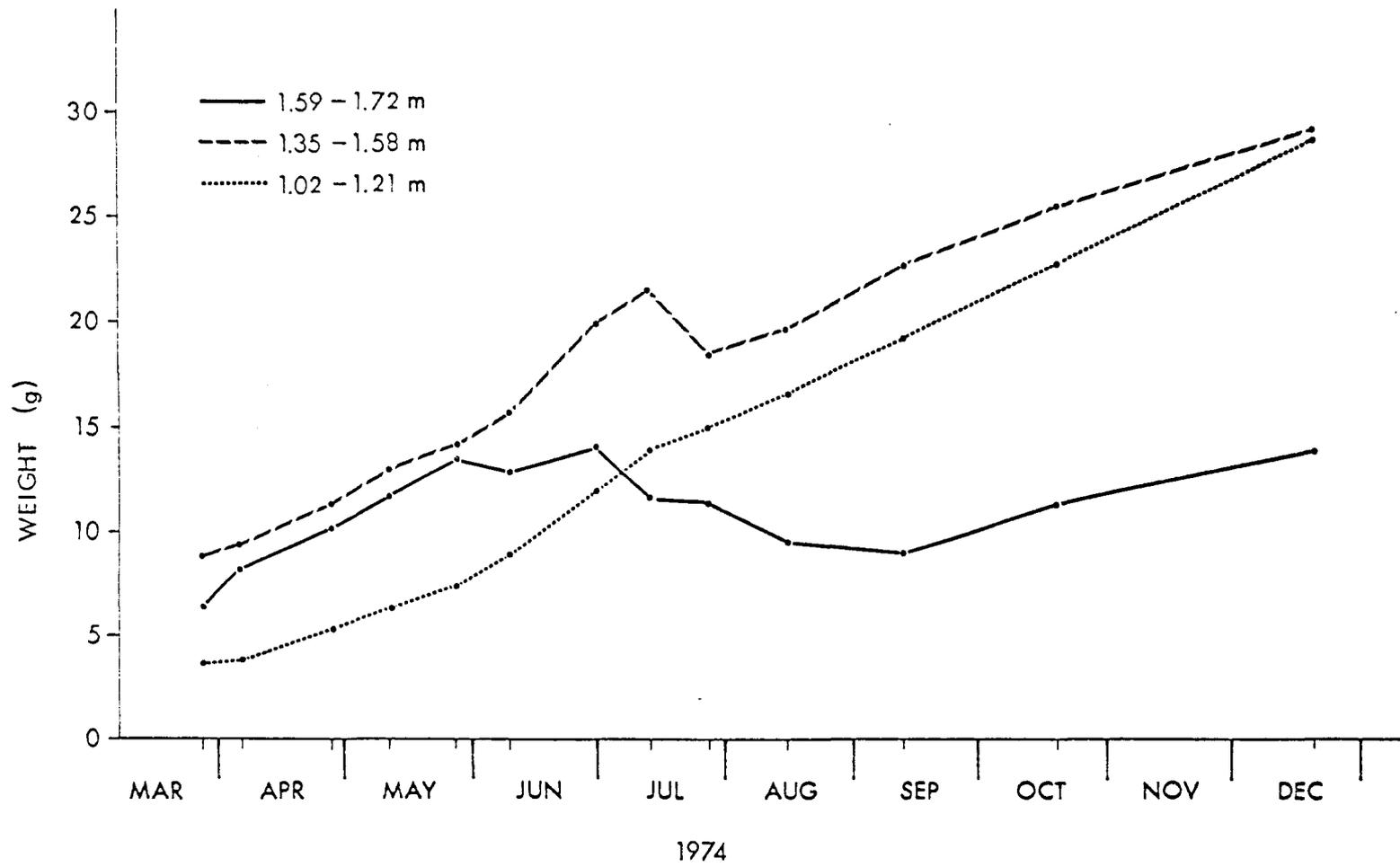


Figure 15. Average number of receptacles/m² on ecad scorpioides plants during May to June, 1974 at Cedar and Adams Point.

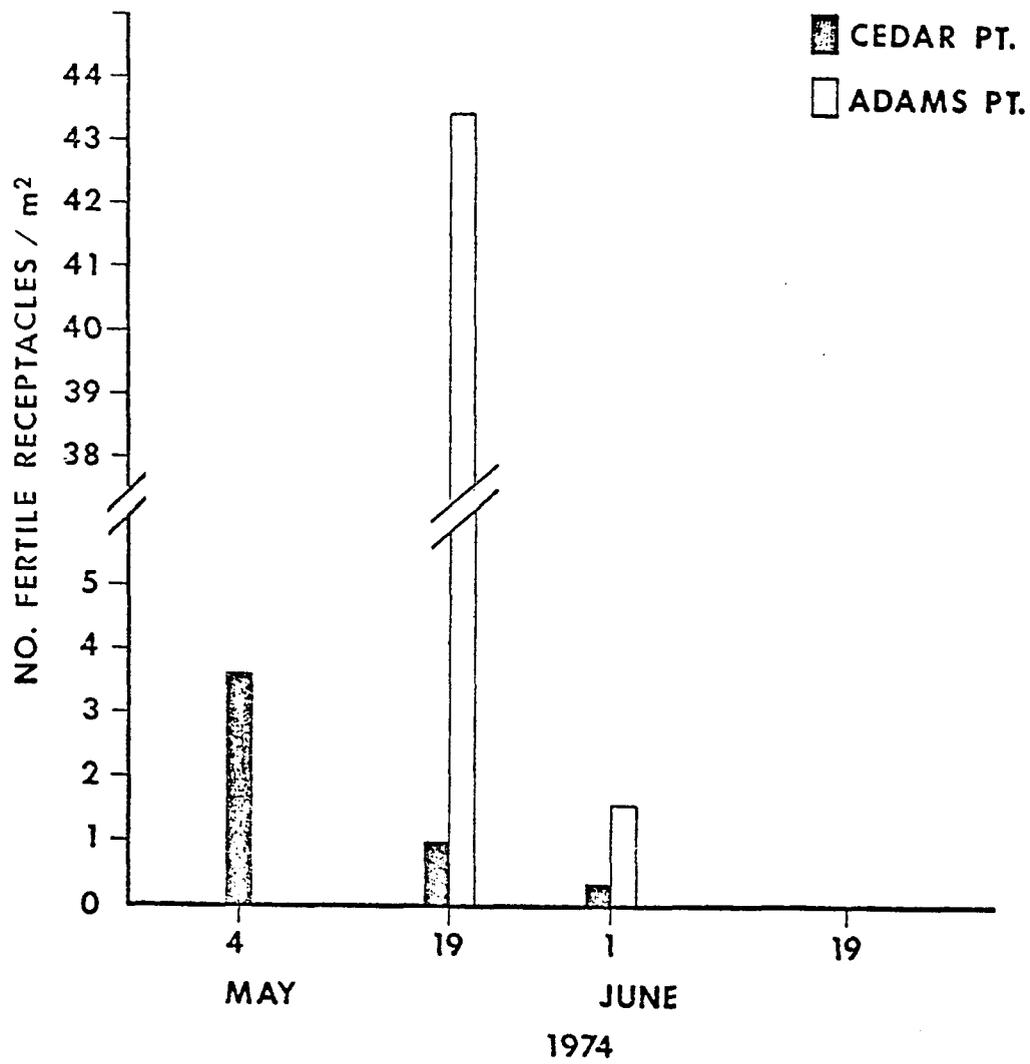


Figure 16. Average number of receptacles/kg dry weight of
ecad scorpioides plants during May to June,
1974 at Cedar and Adams Points.

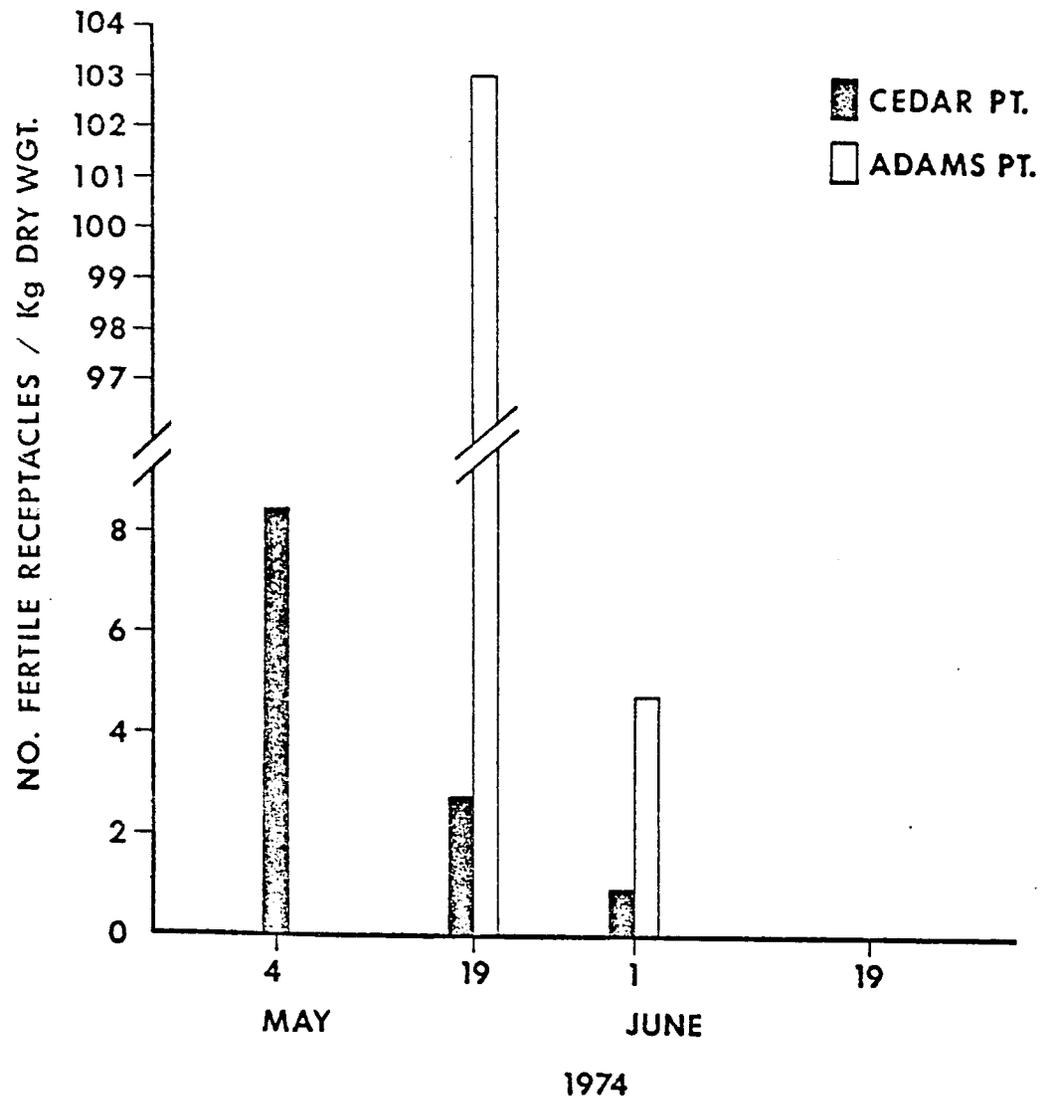


Figure 17. Average length of Spartina alterniflora stems at Cedar Point, seasonal and spatial variations during 1973.

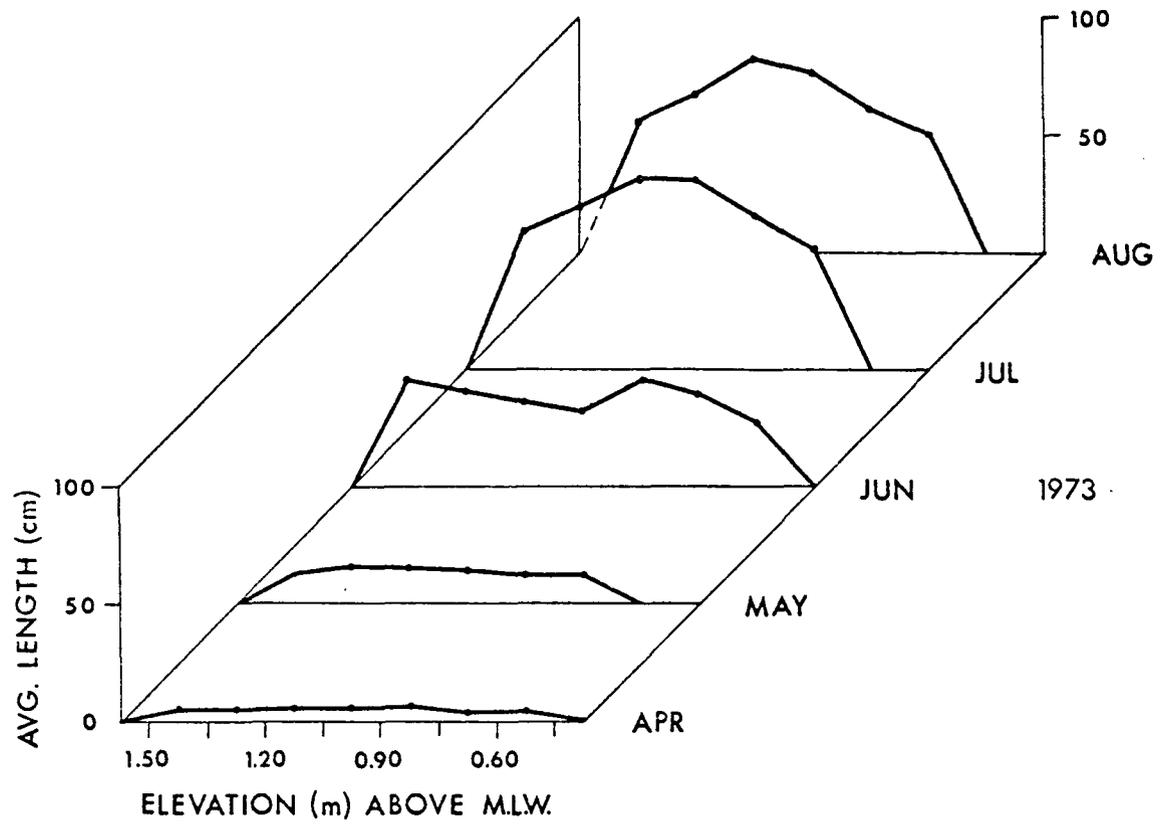


Figure 18. Seasonal and spatial variation of S. alterniflora biomass at Cedar Point during 1975.

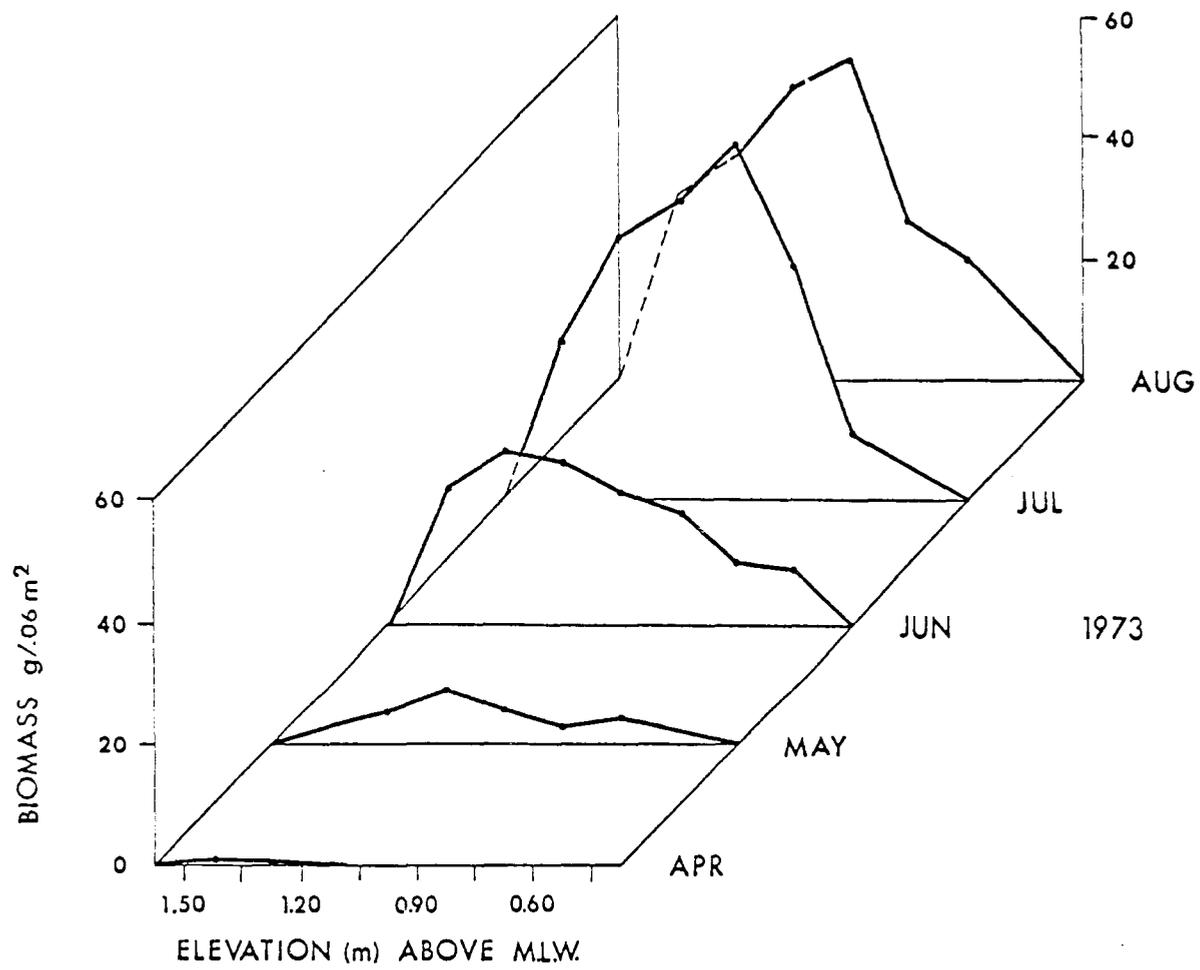


Figure 19. Average density of S. alterniflora stems at Cedar Point, seasonal and spatial variations during 1973.

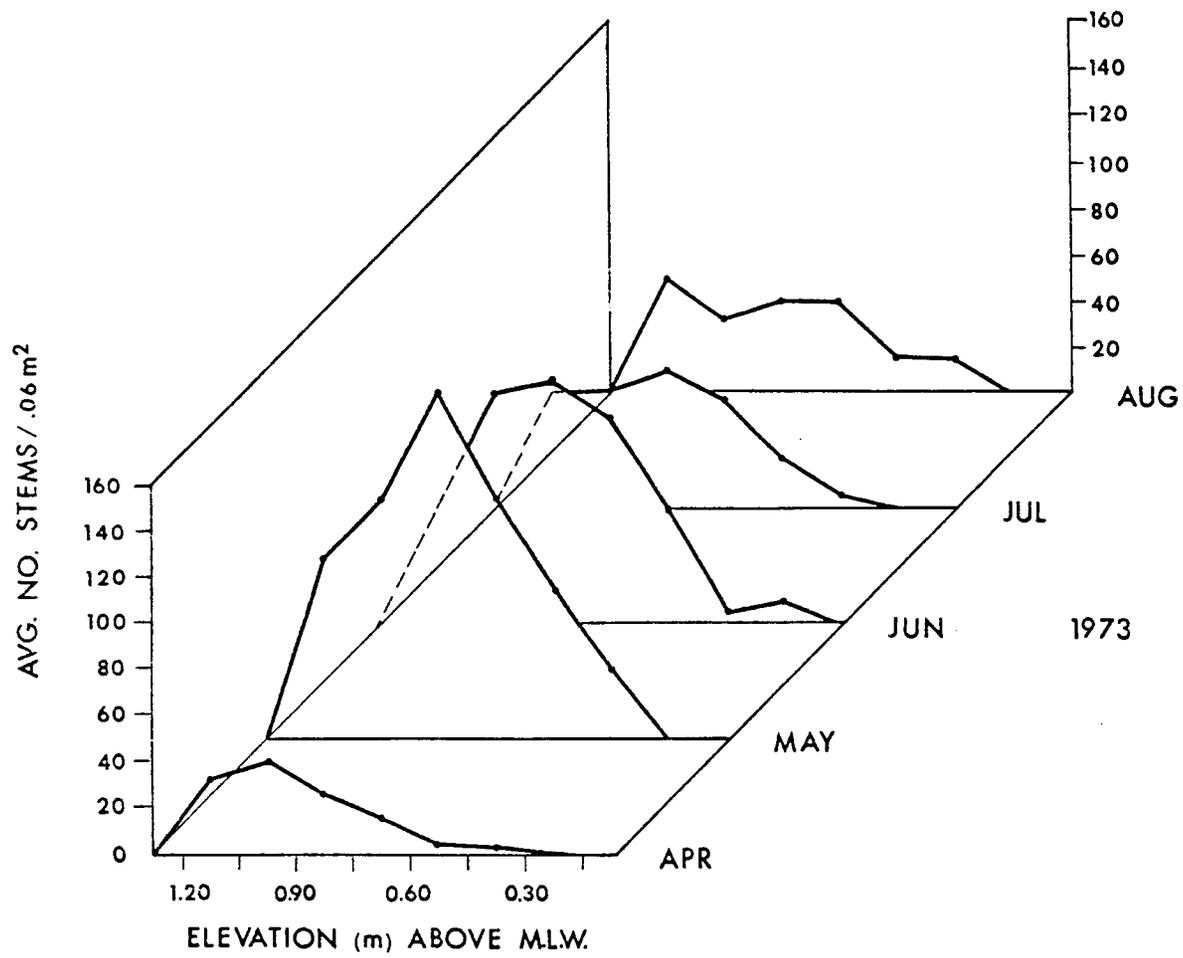


Figure 20. Average length of S. alterniflora stems at Cedar Point during 1972 and 1973.

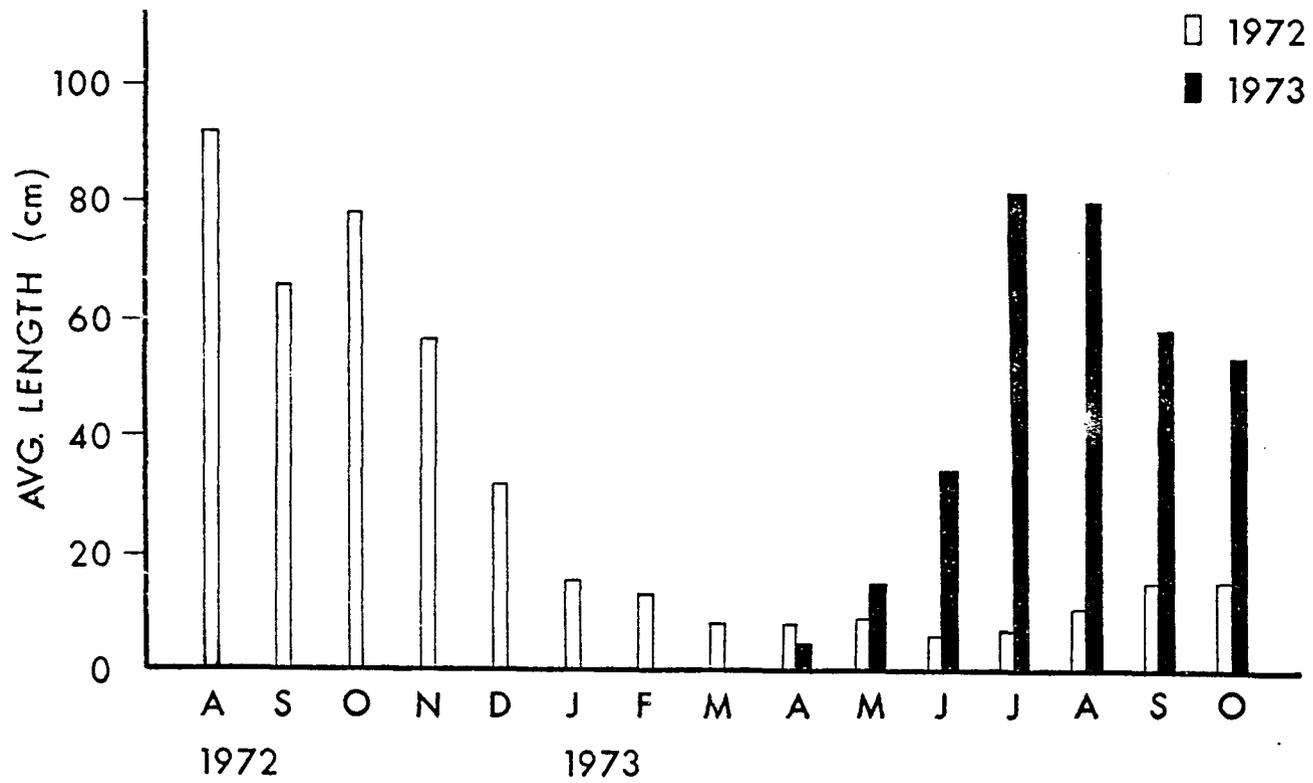


Figure 21. Variations of S. alterniflora biomass and flowering frequency at Cedar Point during 1972 and 1973.

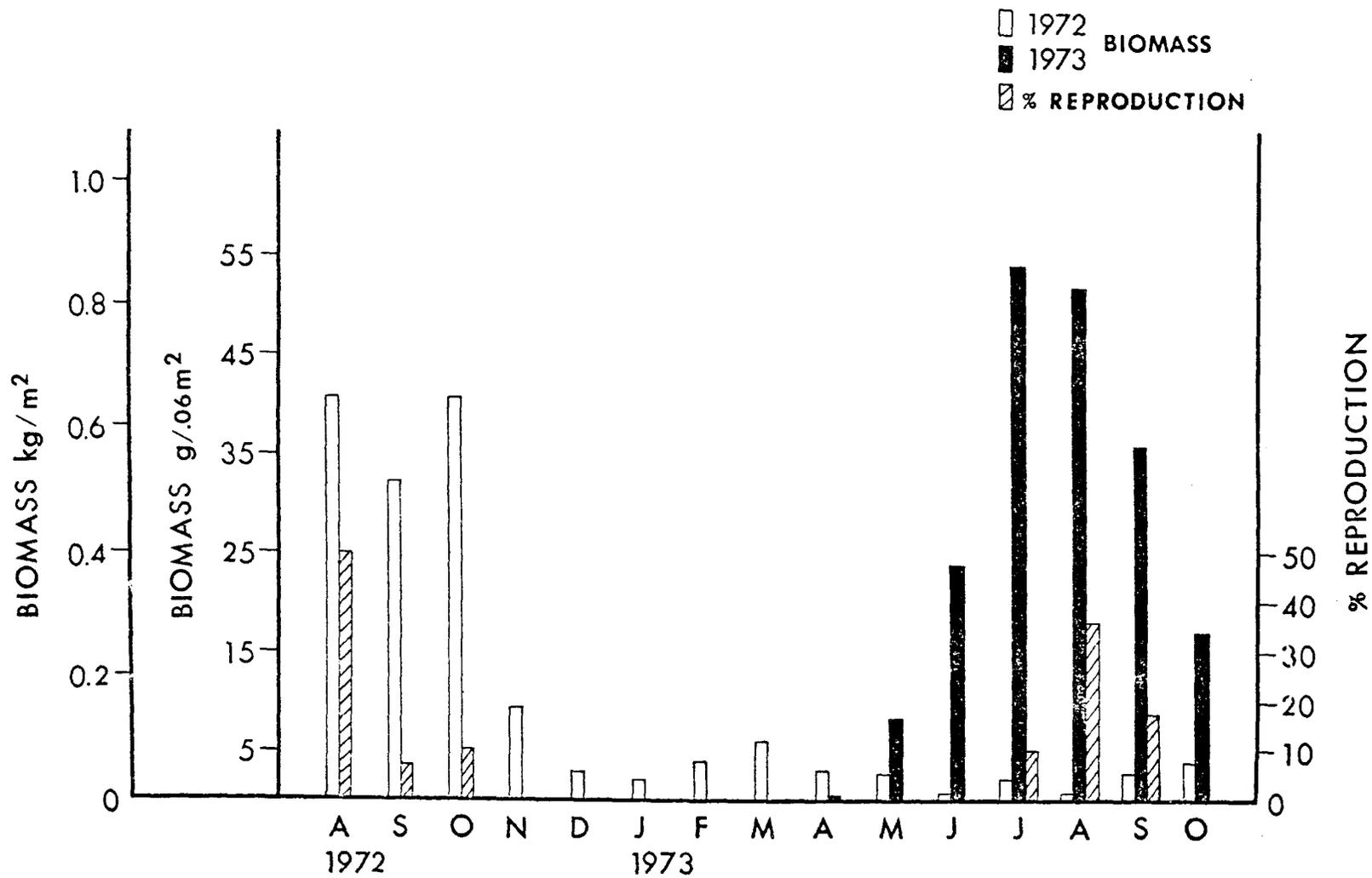


Figure 22. Average daily weight and length variations of S. alterniflora stems at Cedar Point, April to September, 1973.

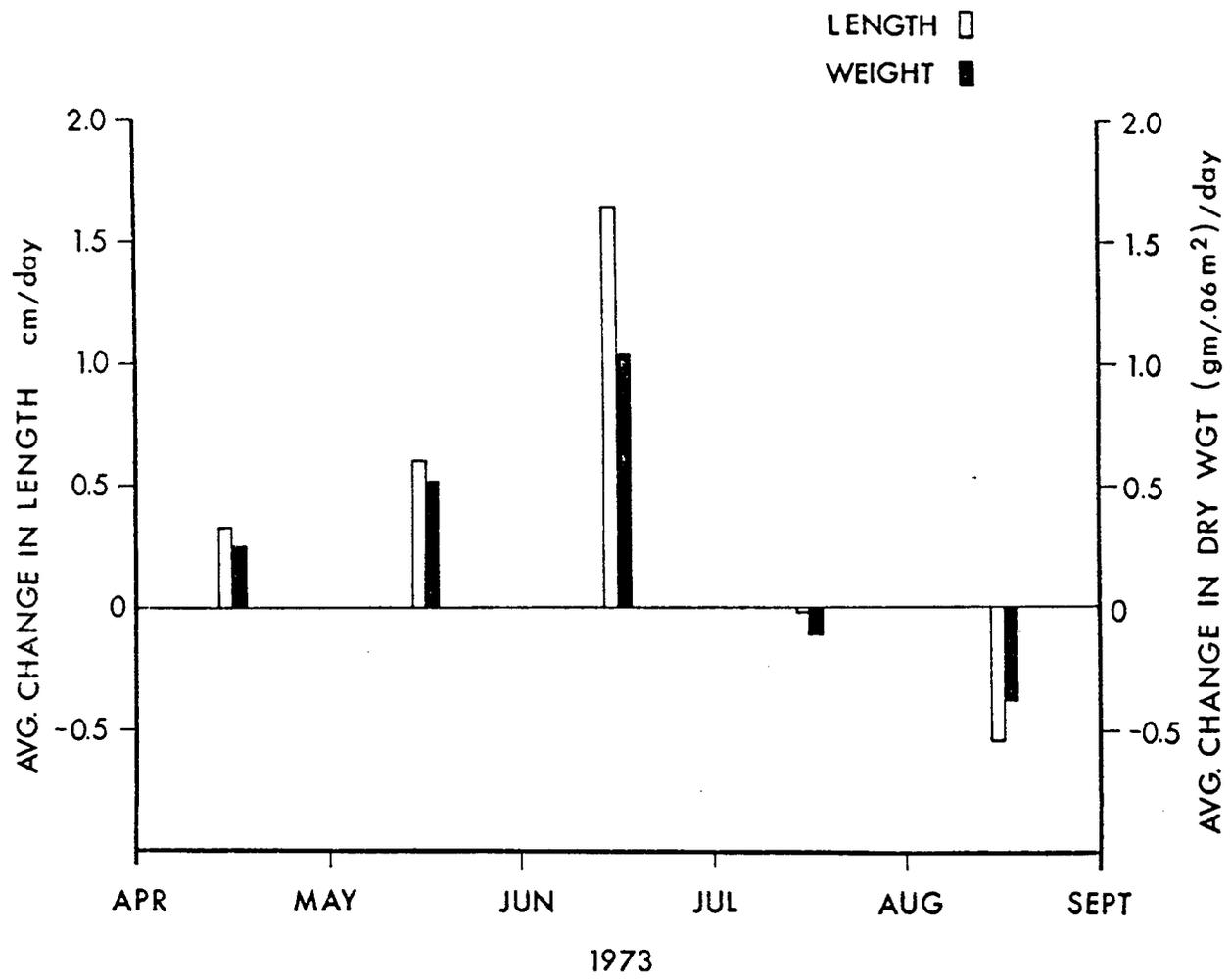


Figure 23. Flowering frequency of S. alterniflora, seasonal and spatial variations during 1973.

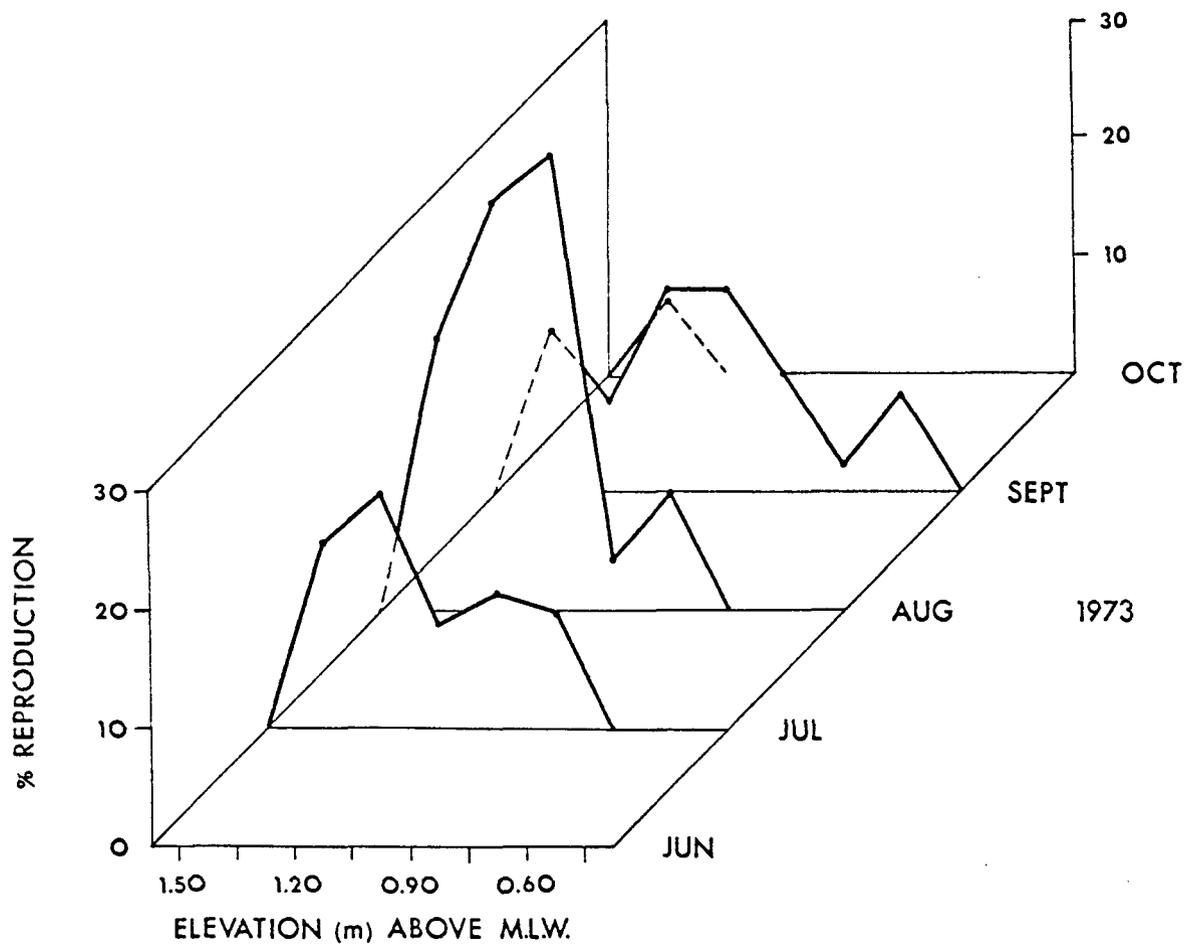


Figure 24. Biomass variations of A. nodosum populations at Cedar Point, August, 1972 to October, 1973.

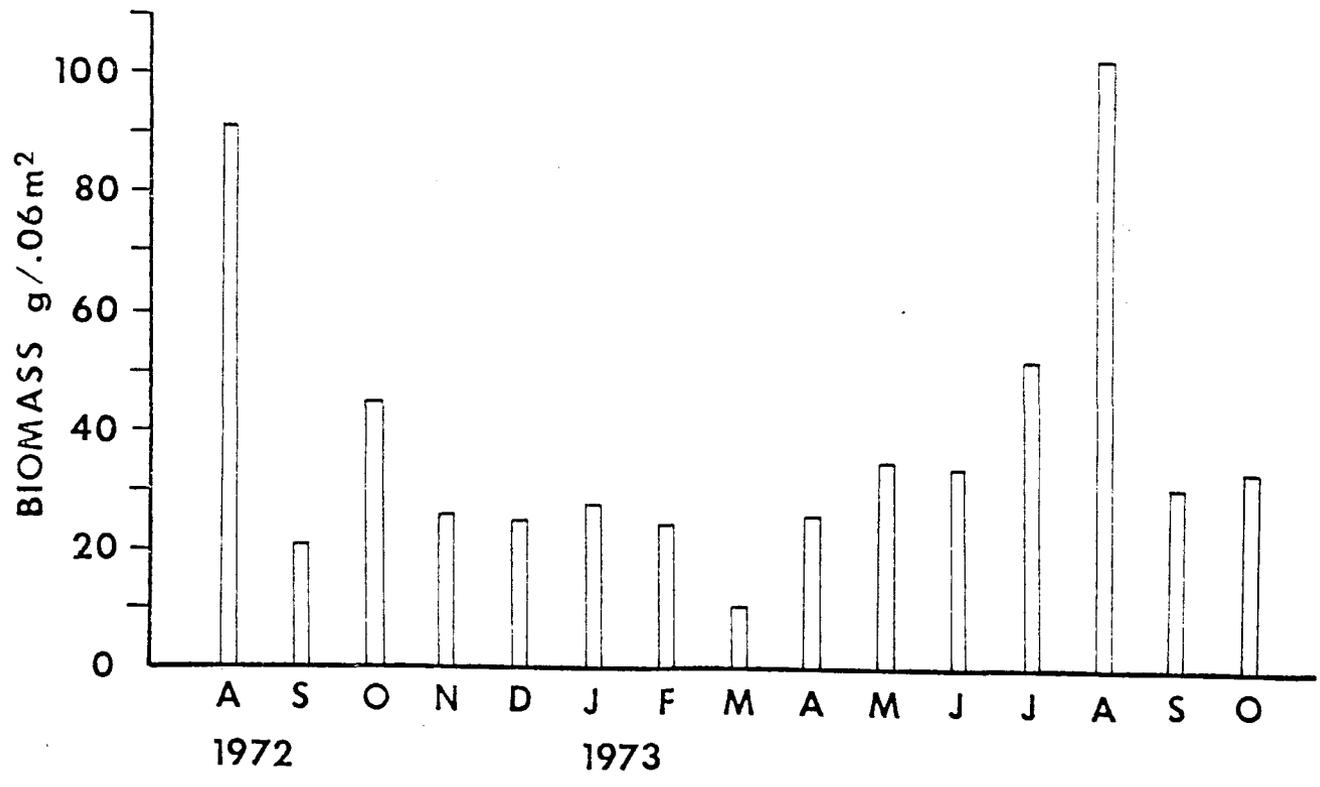


Figure 25. Average vertical distribution of A. nodosum and ecad scorpioides biomass at Cedar Point, as well as S. alterniflora stem density.

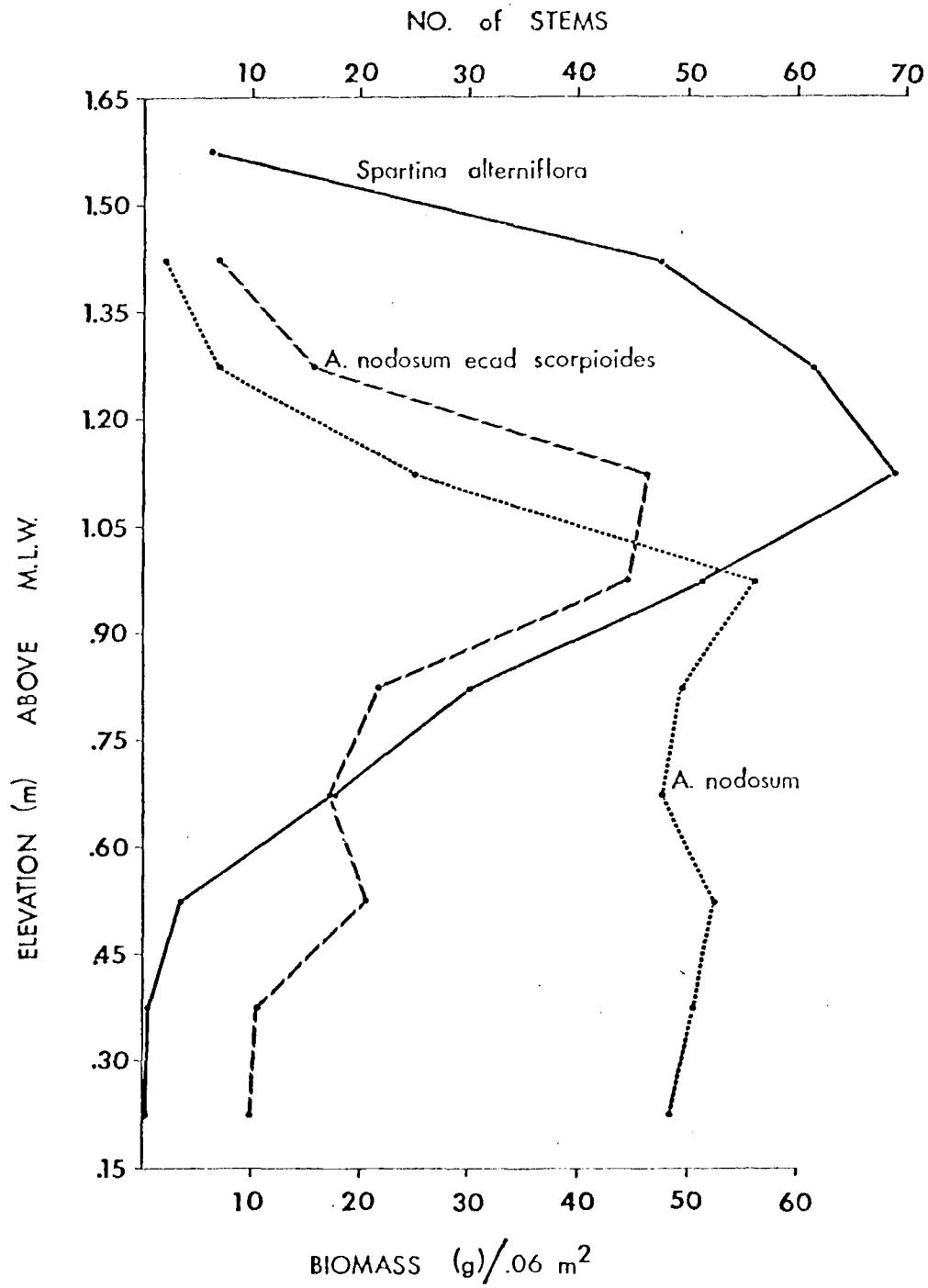


Figure 26. Average biomass distribution of Fucus vesiculosus var. spiralis, Pilayella littoralis and Ulva lactuca at Cedar Point.

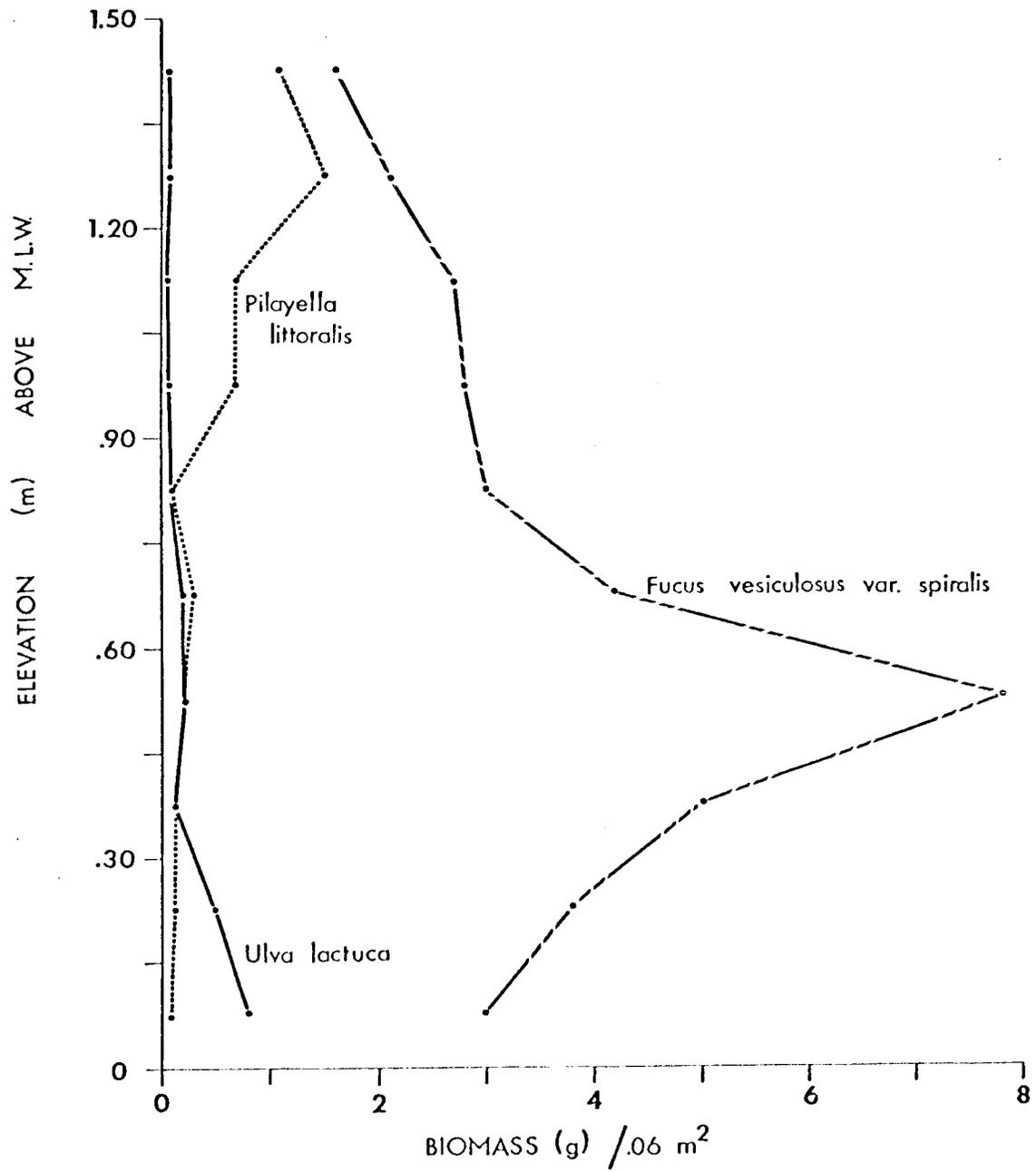


Figure 27. Seasonal variation of Pilayella littoralis biomass at Cedar Point during 1972 and 1973.

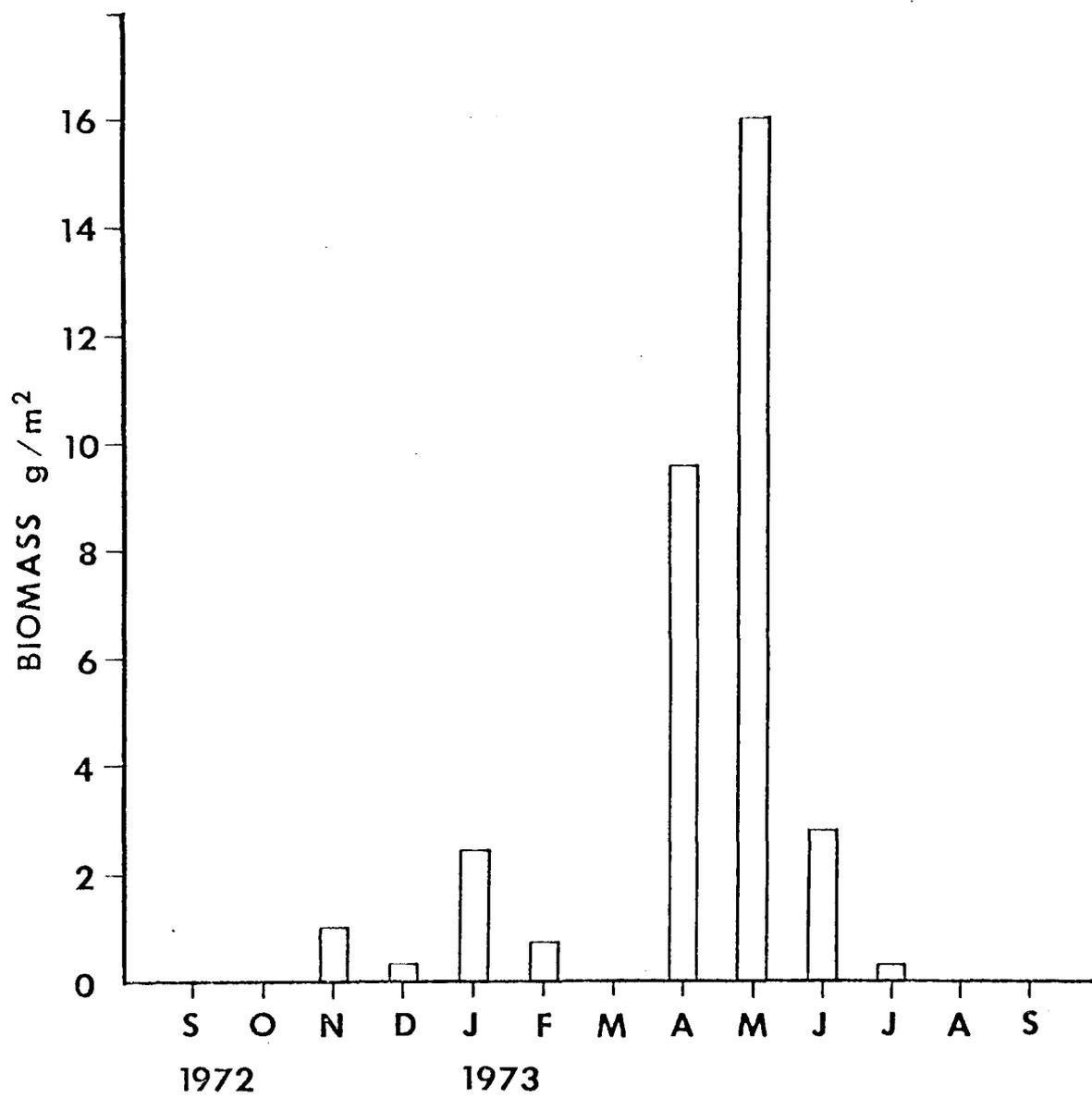


Figure 28. Net photosynthesis of A. nodosum and ecad scorpioides at various light intensities, 34 o/oo and 1.5 (winter) and 15 C (summer). Vertical lines indicate standard error of the mean.

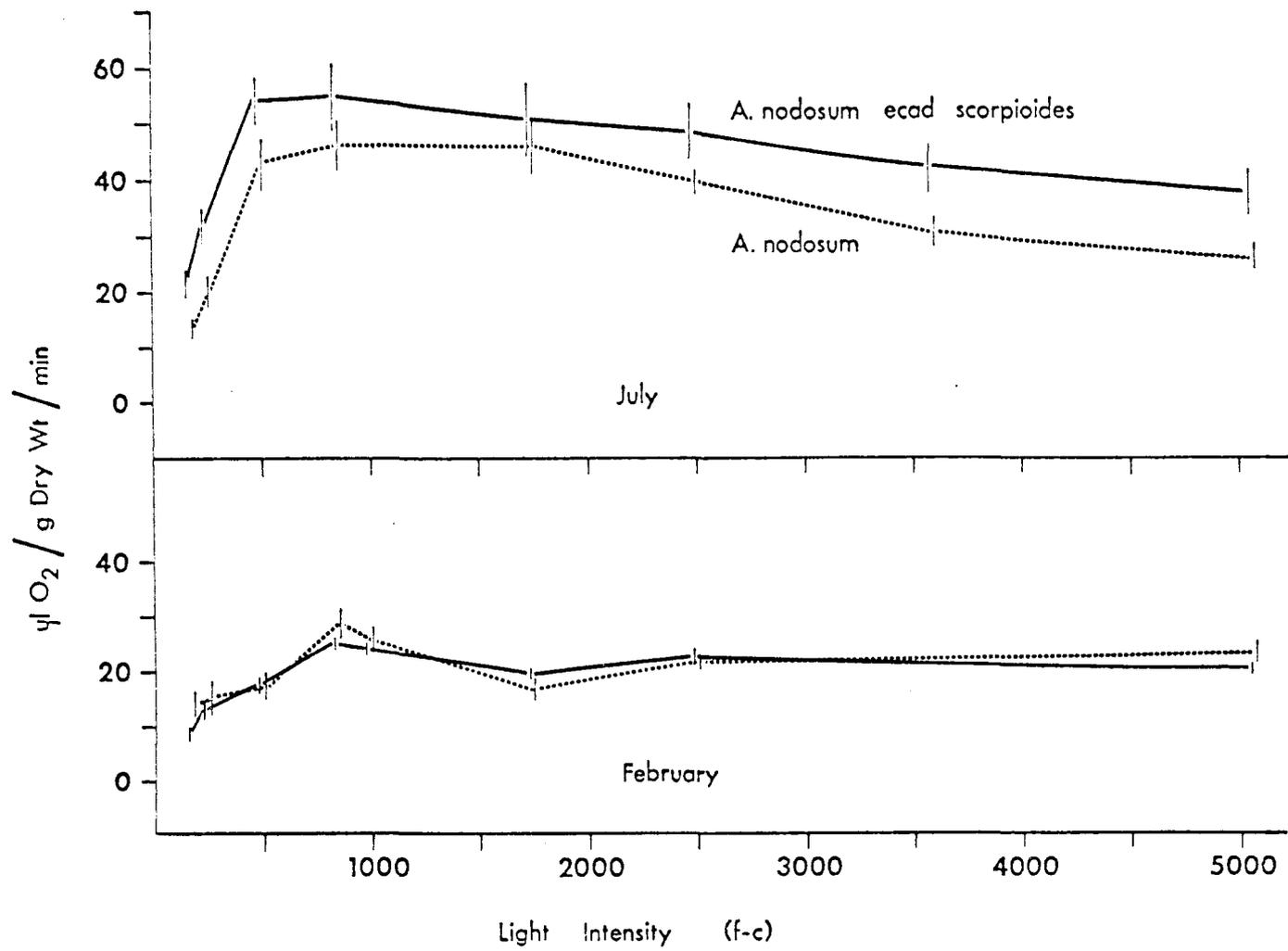


Figure 29. Net photosynthesis of A. nodosum and ecad scorpioides at various temperatures, 1000 foot-candles and 34 o/oo, during the winter and summer. Vertical lines indicate standard error of the mean.

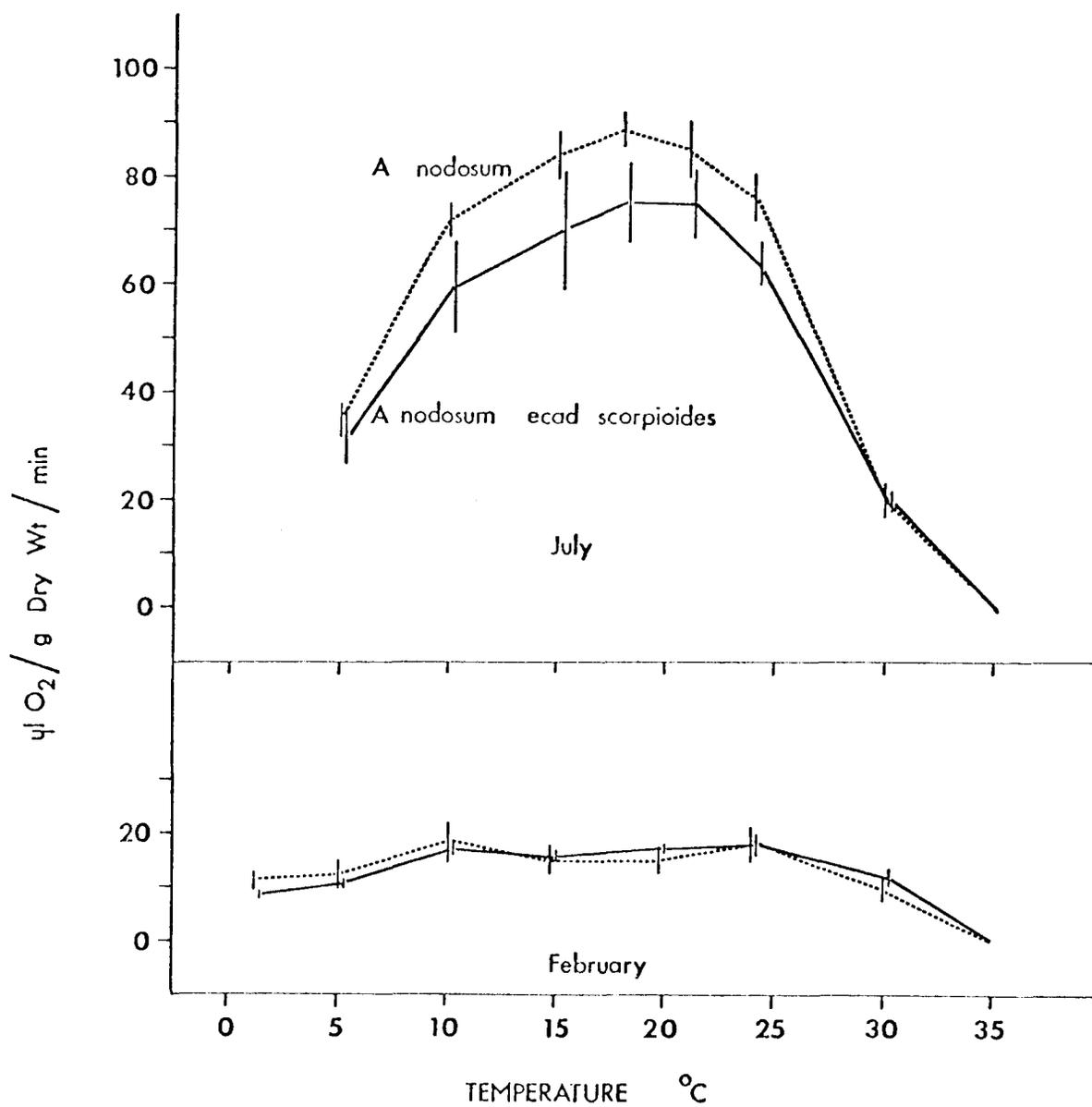


Figure 30. Net photosynthesis of A. nodosum and ecad scorpioides at various salinities, 1000 foot-candles and 15 C. Vertical lines indicate standard error of the mean.

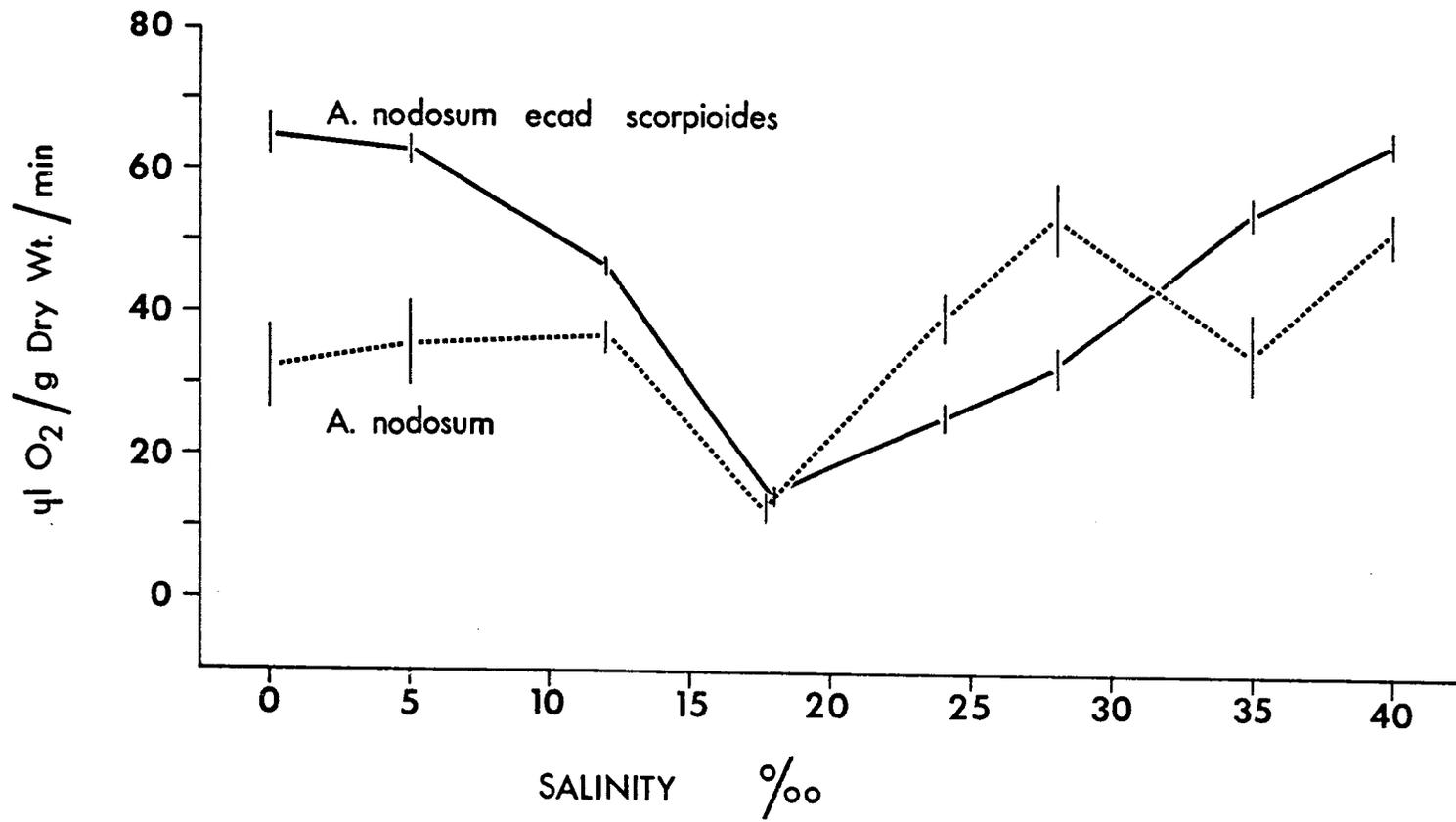


Figure 31. Dark respiration and net photosynthesis of ecad scorpioides at 18 C and 0, 18 and 35 o/oo. Vertical lines indicate standard error of the mean.

