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GRADIENTS IN SALT MARSH PRODUCTIVITY IN THE WELLS NATIONAL ESTUARINE RESEARCH RESERVE

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NOTICE

REPORT TO
NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION
U.S. DEPARTMENT OF COMMERCE

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NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION
NATIONAL OCEAN SERVICE
OFFICE OF OCEAN AND COASTAL RESOURCE MANAGEMENT
MARINE AND ESTUARINE MANAGEMENT DIVISION
WASHINGTON, D.C.

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Abstract

The WNERR contains a diverse array of habitats and species. Species diversity is high within the pristine Little River but considerably lower in the Webhannet system. Generally, plant species diversity is higher at higher tidal elevations, especially at the middle and upper estuary sites. Low and middle intertidal zones often consist of nearly monotypic stands of Spartina alterniflora and S. patens. Upper intertidal sites are usually dominated by Triglochin maritima, Plantago juncoides and Juncus spp.

Productivity was estimated by three different methods. It was estimated at all sites by measurement of standing crop in August. It was also estimated by monthly peak biomass at the low, middle and upper intertidal zones of the lower estuary of the Little River. Lastly, it was estimated by a refined paired-plot technique derived from Lomnicki et al. (1968) in the low zone of the lower Little River. The latter gave NAPP estimates of 1457 g/m^2/yr for S. alterniflora. When the peak monthly standing crop of Ascophyllum nodosum f. scorpioides and Salicornia europeae are included, the NAPP estimate for the low zone community becomes 1804 g/m^2/yr. The seasonal mortality (dead biomass) of S. alterniflora amounted to 622 g/m^2/yr, and when combined with the end of the season standing crop amounts to 1273 g/m^2/yr or 87% of NAPP. Thus the growing season turnover of S. alterniflora (biomass) contributes significantly to the annual metabolism of nearshore waters.

Productivity estimates for the lower Little River are inversely related to tidal elevation with lowest estimates occurring in the high intertidal community. Productivity in the mid and high zones peaked at 372 and 299 g/m^2/yr, respectively. Mortality estimates for the mid and high zones indicate turnover rates of one or more years respectively for these

communities. A gradient of increasing productivity, from upper to lower estuary sites, was found for low intertidal communities but not for mid or high zone stands. Productivity estimates for the Little River were 6 to 10 times greater than those for the Webhannet River, which is impacted by development and boat traffic.

Herbivores (deer and snails) produced little or no direct effects on saltmarsh plants or community structure in the WNERR. Grazer exclusion cages and covers revealed no significant effects on living biomass. Snails fed primarily on dead biomass whereas deer browsed on only a few plants early in the season. However, in places deer have compacted the peat on trails and indirectly may have influenced community structure.

The estimates of productivity for S. alterniflora are the highest reported for the Gulf of Maine and New England. By all measures, the WNERR is a highly productive marsh ranging from 300 to 1600 g/m^2/yr (standing crop estimates). Based on these studies, we conclude that the Little River is in a nearly pristine state. With its high level of productivity, it contributes significant amounts of energy to nursery areas and to fisheries in nearshore waters. Lastly, these data provide not only a baseline but also suggestions for future studies at WNERR.

Introduction

Coastal marshes of North America are among the most productive communities known to man, surpassing even intensively managed croplands (Lieth 1975). Estimates of net annual aboveground primary productivity (NAPP) in these marshes ranges from 324 to 2852 $g/m^2/yr$ (Odum 1971; Hatcher and Mann 1975). Although productivity estimates vary greatly due to the methods employed, a latitudinal gradient is evident with higher production occurring in southern marshes and lower values in northern regions (Hatcher and Mann 1975). Total production appears to be lower in New England, however, because of the smaller areas involved (but see Jacobson, et al. 1987 for revised estimates). There are fewer estimates of productivity for New England marshes, and those that exist show high variability between different sites (Nixon and Oviatt 1973; Vadas et al. 1976; Linthurst and Reimold 1978). Nonetheless some estimates approach those of southern marshes. Regardless of the variability in productivity estimates and the total area of New England marshes, these data suggest that northern marshes also contribute substantial amounts of organic carbon to estuarine and nearshore waters.

Scientific and management studies conducted in the last 30 years have revealed the importance of wetlands to fisheries, waterfowl and local environmental quality (Odum 1961; McHugh 1966; Turner 1977; DeLaune et al. 1978). Specifically, attempts to assess the economic value of marshes (Gosselink et al. 1974) indicate that they are valuable resources, serving as sources of energy for estuarine food webs, contributing to commercial fisheries and providing habitat for fish and waterfowl (McHugh 1966; Teal and Teal 1969; Turner 1977).

Despite the recognized values of undespoiled saltmarshes, human activities and developments have resulted in severe reduction in value or total destruction of large areas of estuarine wetlands. Over half of the emergent wetlands which were present in colonial times have been lost (Tiner 1984). Unfortunately the potential economic and ecologic value of many of these marshes may never be realized or even measured. This is especially true in the northern Gulf of Maine where marshes are small, isolated and frequently surrounded by small scale development. The burgeoning population in the Northeast has recently exacerbated the problem by encroaching on, despoiling or polluting many of these wetlands. Thus, opportunities to study relatively large, undisturbed and unpolluted marshes in the Northeast are rare.

Preserves, such as the Wells National Estuarine Research Reserve (WNERR), which contains extensive natural areas as well as marshland surrounded by development, provide a unique opportunity to both prevent the complete destruction of valuable marsh production and allow the concurrent study of productivity in natural and potentially impacted areas. Because of the tidal and riverine influences, WNERR also provides an opportunity to study productivity across a range of natural environmental gradients.

The WNERR also supports a large herd of protected deer that freely roam portions of the marsh. Because of the intense pressure by developers to build on the borders of wetlands, there are few natural areas with sufficient woodland continuity (critical edge) to permit even small herds to exist around most marshes. Most salmarshes, however, support only small populations of deer (Newsom 1984). The size of the WNERR herd and the fact that deer browse grasslands suggests that they may have direct or indirect impacts on plant composition, abundance and standing crop or productivity estimates in the Wells marsh system.

Rationale and Objectives

Several gradients are evident in WNERR and are utilized to establish hypotheses and a focus for our studies. The natural environmental gradients of concern or of potential importance to productivity are the period of tidal inundation, which is affected by slope, elevational differences and 3-4 m tides, and salinity which ranges from 2 to 33 ppt. Preliminary surveys and discussions with J. Lortie (Rachel Carson Wildlife Sanctuary) during fall of 1984 suggested that gradients also existed in the vegetation types that parallel the WNERR river systems.

The WNERR enables the comparison of natural and altered environments because it encompasses two dissimilar river systems; the Little and the Webhannet estuaries. The Little River estuary is in a relatively natural state having very little development abutting any of the marshlands. In contrast, the Webhannet River estuary has been ringed with houses for at least several decades (Jacobson 1987). The barrier dunes were the earliest areas to be heavily developed in the town of Wells (Figures 1 and 2). More recently condominiums have been built in Wells along the edge of the high marsh. In addition, several boat landings exist in Wells harbor. One of these was constructed on a promontory of marsh which was "developed" into upland by burial with spoils dredged from Wells harbor and the Webhannet inlet (Jacobson 1987). These areas have an increased level of boat traffic which probably results in higher levels of human disturbance than in other portions of the Webhannet or Little River systems.

As a result of preliminary observations and discussions, the absence of quantitative data on these marshes and pre-funding discussions with

Steve Meyer of WNERR and Fred Short and Tom Lee of the University of New Hampshire, we focused our studies on productivity and biomass along the various environmental and disturbance gradients (noted above). Specifically our objectives were as follows:

1. to determine productivities along gradients of salinity, tidal elevation and human impact.
2. to determine the effect of grazing on saltmarsh productivities in the various elevational zones of the Little River estuary.
3. to provide an estimate of the productivity of the WNERR saltmarsh system and to make a direct estimate of its contribution to detrital pools and thus indirectly to estuarine food webs, commercial fisheries and as export to other ecosystems.
4. to provide a baseline or reference point for assessing future impacts and year to year variability on productivity in the WNERR saltmarshes. Because of the reallocation (prior to final funding), of certain research priorities between our project and that of Dr. F. Short (aerial photography and mapping), we provide only a rough estimate of total production for the entire WNERR system. Incorporating the specific distributional and abundance patterns of the different vegetation types (mapping studies of Dr. F. Short) will allow better estimates to be made for the entire system.

Methods

Several changes from methods described in our grant proposal were necessitated by the labor-intensive nature of the productivity studies, the lack of resources to handle this overload and by features of the marsh ecosystem itself. One change that affected all of the experiments involved the sizes of quadrats. We were concerned that the proposed 20 x 20 cm quadrat size was too small, especially for the diverse stands of the high marsh system and because of the small amounts of live biomass in April. For this reason, we started the season using 50 x 50 cm quadrats until we were able to calculate species-areas curves.

To develop species-area curves, we subsampled the 50 x 50 quadrats using a nested series of quadrats. First, a 10 x 10 cm sample was harvested from a randomly selected corner of the 50 x 50 quadrat. Then a 20 x 20 cm quadrat was overlaid on the same corner and the remaining uncut area was harvested separately. This process was repeated for a 25 x 25 cm quadrat and then for the 50 x 50 cm quadrat. This yielded a series of surface areas (100, 225, 300, 325, 400, 525, 625, 1875, 1975, 2175, 2200, 2275, 2400, 2500 cm^2). For each zone, the mean number of species for each size quadrat was graphed to produce a series of curves from which the appropriate quadrat size was determined. Once the species-area results were available, we were able to determine the appropriate range of the quadrat sizes (25 cm x 25 cm to 30 cm x 30 cm); we chose the former because of logistical constraints. Other changes in design will be discussed with the descriptions of methods for the relevant experiments (below).

Productivity

The site used for intensive study of productivity was the lower estuary site, near the mouth of the Little River (hereafter termed LR/LE site). The initial design called for the use of the paired-plot technique (modified from Lomnicki et al. 1968) for all three elevational zones. However, for the middle zone (dominated by *S. patens*) and the high zone (a diverse community with no single dominant), the time and personnel required to properly conduct the paired-plot technique were simply not available. For the middle and high zones, we used the monthly harvest technique to determine the peak or maximum standing crop of the season. Because of the logistical constraints (noted above) we considered this the best available method to estimate net aboveground primary productivity (NAPP). To compare this technique with the paired-plot technique, we also extracted the maximum monthly standing crop estimates from the paired-plot data set. Monthly sampling began in April 1986 and continued through September 1986. The samples obtained each month were washed, sorted by species, dried for 48 hr at 63°C and weighed to the nearest 0.01 g.

The maximum monthly standing crop method required only calculation of descriptive statistics and comparison of monthly means. The paired-plot technique was originally described in Lomnicki et al. (1968) and involved considerably more processing both in the field and during data analysis. On each sampling date, triplicate sets of paired quadrats were chosen in a stratified random manner. In the first quadrat (A) of each pair, all aboveground biomass was clipped off, bagged and returned to the laboratory at the University of Maine for analysis of species composition and dry weight. In the second quadrat (B), dead biomass (including attached dead material) was removed, leaving the living biomass intact. This quadrat was then fenced until the next sampling date to prevent influx of dead biomass from outside the plot. The dead biomass that accumulated over the sampling interval represented the mortality of living plant tissue during that (monthly) interval.

To determine the annual net aboveground primary productivity (NAPP), we used the following equation:

$$\text{NAPP} = \sum_{n=1}^{6} \max\ \{(A_n - A_{n-1} + B_n),\ 0\}$$

where (A_n) represents the living biomass value for each monthly sample, (A_{n-1}) represents the living biomass value of the preceding month and (B_n) represents the estimate for mortality during that interval. If the resulting value was negative, the productivity value for that interval was assumed to be zero. To obtain NAPP, the monthly values were summed. Additionally, the initial dead biomass taken each month from plot B provided a rough estimate of the litter component and its flux within the estuary.

Estimates of NAPP are subject to several potential biases. The first is the amount of production that goes into belowground growth and storage. The second potential bias is the amount of production that is directly consumed by grazers. Livingstone and Patriquin (1981) reported regressions (based on density of stems) for the amount of belowground biomass present for a given amount of aerial biomass. The appropriate correction factor (1.75 X NAPP = total productivity) was used to derive an estimate of the "total" productivity from our NAPP value.

Grazing:

To estimate the impact of grazing on productivity within the WNERR saltmarshes, we used a cage-cover experimental design. The cages consisted of 1 cm X 1 cm mesh screen on 1 m X 1 m X 1 m wooden frames. The covers consisted of the same size frames, but without screening on the sides, so that they would approximate the light regime of the cages while allowing potential grazers access through the sides. The cages and covers remained in position throughout the growing season and were subsampled randomly, but non-repetively each month for living biomass. If the mean biomass of a cover treatment was less than that of the corresponding cage treatment, the difference presumably would represent the loss to grazing.

During our first sampling trip in April, evidence of herbivore (deer and periwinkles) activities led us to modify the cage-cover experiment in several ways. First, Littorina littorea (periwinkles) were found at rather high abundances in the low marsh (Spartina alterniflora zone). It was necessary, therefore, to add a fine-mesh skirt along the lower edge of each low zone cage. The original unmodified cages were used in the LR/LE high zone. Second, to broaden our monitoring of grazing by deer, we relocated the middle zone cages and covers midway up the Little River estuary (LR/ME site) where deer grazing activity was most intense (personal communication, John Lortie,) and where we observed bitten stems of green marsh plants in April. The cage-cover pairs at this site were set in three dissimilar stands to obtain preliminary information on the type of community most likely to be effected by deer grazing. This design prevents statistical comparisons but has the advantage of obtaining information on a broader range of vegetation types.

Gradients in productivity:

In addition to the estimation of NAPP, we compared late-season standing crop (in August) among sites along an estuarine-palustrine gradient within the Little River estuary and between sites on the relatively pristine Little River and on the heavily travelled Webhannet River estuary (see Figure 2).

General:

Salinity and water temperature data were taken in conjunction with the monthly biomass sampling trips. For salinities, we used a calibrated set of hydrometers. Paired, calibrated standard laboratory thermometers were used for the determination of temperatures. An aerial overflight for color infrared photography to aid in the analysis of distribution and abundance patterns of the marsh was proposed for the middle of the growing season, but prior to April was reassigned to Dr. Fred Short, University of New Hampshire. The reduction in irradiance beneath the cages and covers was determined with a LiCor pyrenometer model no. LI-2005 attached to a Campbell scientific data micrologger. One probe was positioned under a cage and another in the open. Ten paired light readings were recorded over a 3-minute period. These readings were repeated six times on two successive days under high thin clouds and sunny conditions.

Statistical analyses were performed by standard procedures using SAS and Microstat statistical packages. Analysis of Variance (ANOVA) with F-tests and comparisons among means (Duncan's or Student-Neuman-Keuls) were used to test differences between treatments or sampling patterns ($p<0.05$ is critical for significance).

Results

Descriptive information:

Over the course of the season, twenty-six plant species were encountered within the Wells National Estuarine Research Reserve (Table 1). All but two of the species are higher plants. The remaining two, Ascophyllum nodosum f. scorpioides and Fucus vesiculosus are members of the Phaeophyta (Brown Algae). These algal forms were either entwined in mud or sand or attached near the bases of Spartina alterniflora stems in the lower estuary. Drift algae of other taxa were also encountered at both the lower and the middle estuary sites, but were not included in the data.

Distinct vertical and horizontal distribution patterns were apparent for plant species along the Little River (Table 2 and Figure 3) and the Webhannet River (Table 3). Brown algae, for example, were restricted to the low zone of the lower estuary. Spartina alterniflora, Spartina patens and Salicornia europea were widely distributed, vertically and horizontally, although none of the three occurred in sample plots in the high zone of the upper Little River estuary. Several species were collected only from the high zone, and usually from only the middle or upper reaches of the Little River estuary and include: Agrostis alba, Carex paleacea, Eleocharis halophila, Scirpus paludosus and Spartina pectinata. Aster novi-belgii was found only in the upper reaches of the Little River.

Clear patterns of species diversity are also evident from these data. The fewest species occurred in the low zones of the lower Little and Webhannet Rivers. The largest number of species occurred in the high intertidal zone of the middle and upper estuary regions of the Little River. In general, diversity was greatest in the mid-estuary high marsh of the Little River at the interface between palustrine and marine habitats.

Salinities differed between sites along the estuarine gradient of the Little River (Table 4). The differences in salinity between the lower and middle estuary sites, as well as temperatures, exhibited clear seasonal trends.

Productivity:

Net aboveground primary productivity (NAPP), as determined by the Lomnicki et al. (1968) method amounted to 1457 g/m^2/yr for *Spartina alterniflora* in the low zone of the Little River lower estuary (LR/LE) site (Table 5). Living standing crop was maximal in July (1287 g/m^2 and decreased sharply between the August and September sampling dates (Figures 4 and 5). The mortality estimates (B_n) increased during each sampling interval, reaching a maximum in August (333 g/m^2). The total estimate for growing season mortality of *S. alterniflora* amounted to 622 g/m^2/yr. Adding the standing crop values for the other members of the low zone community raised the total NAPP estimate to 1804 g/m^2/yr. The decrease in living aboveground biomass between August and September was not correlated with a corresponding increase in mortality. This is consistent with the previous reports of wholesale translocation of resources into belowground storage (in rhizomes) after flowering (Hull et al. 1976).

We estimated NAPP for the other elevational zones of the lower estuary site by use of the maximum monthly standing crop method (Table 6). The maximum monthly standing crop estimate for the low zone amounted to 1634 g/m^2/yr. For the middle-zone, which was dominated by *S. patens*, the maximum monthly estimate was reached in September (Figure 6). The total NAPP estimate for this zone was 372 g/m^2/yr of which 340 g/m^2/yr was *S. patens*. The high zone contained a more diverse community, with *Triglochin* maritima as the largest component of the living biomass. The maximum monthly value for total biomass was reached in July at 299 g/m^2. Biomass estimates for Juncus gerardi and Triglochin maritima both peaked in July at 23 and 210 g/m^2, respectively (Figures 7 and 8). The biomass of Plantago juncoides peaked in July at 47 g/m^2 and maintained that value into August (Figure 9). Spartina alterniflora increased gradually throughout the season without any clear peak whereas S. patens was patchy in this sampling zone and found only in the September samples (Figures 10 and 11). The dead biomass data in Table 6 showed different patterns for the three elevation zones. In the low zone, the standing crop of dead biomass fluctuated irregularly, with no increases in response to large decreases in standing live crop. For the middle zone, dead biomass (mostly attached) is always greater than the standing live biomass. In the high zone, dead biomass declined to a minimum in July, and most of the live biomass that was attached in September apparently remained in place over the winter.

Late-season standing crop estimates of NAPP are usually made in August, or occasionally September. For the low zone, the August and September values were 1081 and 997 g/m^2, respectively. Both estimates are considerably lower than the values derived from the other two methods. For the middle-zone, the August and September values were 299 and 372 g/m^2, respectively. The latter value is the maximum monthly estimate. For the high zone, the values were 160 and 105 g/m^2, respectively. These estimates are considerably lower than those obtained for July.

Grazing:

To determine whether grazing exerted a significant impact on the estimates of NAPP, we conducted exclusion cage-cover experiments in the low zone of the lower Little River and in the high zones of the lower and middle estuary sites of the Little River. The likely grazer and the species composition within the two elevational zones differed, with deer likely to be important in the high zone and gastropods in the low zone.

In the high zone, we observed cut or bitten shoots of plants on our first visit in April. These bites were characteristic of deer grazing. The high zone is regularly frequented by deer and fresh tracks on and off trails were seen every sampling trip. Within the cage/cover experiments there were no disinct trends in dry weight for the high zone in the lower estuary. None of the dominant (by biomass) species (Triglochin maritima, Plantago maritima, and Juncus gerardi increased significantly or showed an enhancement in the cages or cover. In fact, statistical comparisons showed that the only significant differences in dry weight were opposite to those that would have been predicted by grazing (Table 7). The protected cages had significantly lower total live biomass and dead biomass than controls in the June samples. No other within-species or total biomass differences were found over the entire growing season and no differences were observed between the cages and covers.

The absence of replication for the three different vegetation types analyzed in the high zone of the middle estuary prevents statistical comparisons from being made. Nonetheless, similar to the lower estuary, control plots contained more living biomass than plots under cages or covers. However, leaves of young Triglochin maritima in control plots showed evidence of being browsed or cut at the tips. This was observed more frequently in spring and early summer, but did not result in loss or death of entire plants.

In the low zone, the potential grazer of greatest concern was the periwinkle, Littorina littorea, which was present at relatively high densities (Table 9). Snails were field sorted into four size categories and counted. Snail densities ranged from a low of $136/m^2$ in April to $768/m^2$ in July. The densities of the largest size class, and presumably the ones with the greatest impact on plants, were relatively constant (average $74/m^2$) throughout the season, except for April and September when they were lower. The maximum densities of _Littorina_ for all four size classes were found in July. Over the course of the season the size frequency pattern shifted from predominantly medium and large individuals (in April and May) to small forms (from June through August). At the end of the season there were fewer in all size classes but especially those that had recruited that year.

Because of the potential for differential impact of large and small snails we conducted regressions of shell weight on shell length (Figure 12) and body (tissue) dry weight on shell length (Figure 13). Estimates of (tissue) weight for the various size classes were derived from log transformed data points in Figure 13. These values and the mean size of each size class (Table 10) were incorporated into the following equation $\log(\text{body wt}) = -5.5394 + 3.5806 \log(\text{length})$ and presented as dry weight (Table 10). We then used correlation analysis to compare _Littorina_ numbers and living biomass to the biomass of living _S. alterniflora_, living _Ascophyllum_, total dead biomass, and drift algal biomass (Table 11). Snail abundance was a good predictor of snail biomass. Although snail abundance was significantly correlated with _S. alterniflora_ biomass snail biomass was not. Snail numbers and living snail biomass correlated best with the biomass of _Ascophyllum_ and secondly with dead biomass. All of these significant correlations could have been due to the use of _Ascophyllum_ and dead biomass for cover rather than for food.

In the low zone, some patterns were evident in the data, but none provide evidence for a grazing effect. S. alterniflora and Ascophyllum formed the dominant vegetation in these plots but neither appeared to be grazed in the living state. Standing crop estimates were highest in June and consistently higher throughout the season in control plots (Table 8). Similar to the high zone, total living biomass in the low zone was greater in the controls than in the cages and covers. Estimates of standing crop for cage and cover plots generally ranged from 30% to 60% of the controls. No differences were detected between cage and cover treatments. Considerable variability (patchiness) was encountered with both S. alterniflora and A. nodosum, and is evident from the considerable but non-significant, differences between treatments in July (Table 8).

Gradients in Productivity:

Standing crop of the saltmarsh plant community varies in species composition and in total biomass with differences in tidal elevation and with distance from the ocean. To clarify the presentation, standing crop tables are organized by elevation with the entire estuarine gradient listed on each table. For the high intertidal zone, total living biomass was greatest at the middle estuary site (Table 12). Standing crop estimates ranged from approximately 160 g/m^2 at the lower and upper estuary sites to 233 g/m^2 in the middle estuary. Although standing crop did not vary markedly across the estuarine gradient in the high zone, species composition did. Species richness, however, was greatest in the middle and high zones of the upper estuary. A similar pattern was evident for total living biomass in the middle-zone, with maximal standing crop at the middle estuary site (Table 13). However, total living biomass and species richness in the middle zone were both greater at the upper estuary site than at the lower estuary site. A distinct gradient in living biomass, however, was discovered for the low zone (Table 14). Biomass in the low zone was greatest at the lower estuary site whereas species richness was greatest in the upper estuary.

Comparison of standing crop as a function of tidal elevation and estuary location is provided in Figure 14. It is clear that an inverse relationship exists between standing crop and tidal elevation. At all of the three sites, standing crop is greatest in the low zone and least in the high zone. In fact, this pattern holds true even when the three sites are lumped together: all high zone living biomass values are lower than any of the middle-zone values which in turn, are lower than any of the low zone values. With the exception of the low zone in the lower estuary these standing crop values show a relatively uniform and linear increase with decreasing tidal elevation.

Standing crop estimates in areas potentially impacted by humans were made in the low and middle zones of the Webhannet River and Depot Brook. Samples from the middle zone of the Webhannet site had a relatively large number of species (eight) whereas samples from Depot Brook had less than half this number (Table 15). Biomass, however, was greater at Depot Brook and estimates ranged from 336 to 448 g/m^2 in the middle zones of these sites. Standing crop in the low zones of these, and one additional site in the Webhannet River (short grass area, near the landing site, Figure 2), was equivalent to the middle zone and ranged from 288 to 496 g/m^2 (Table 16). Species richness in this zone was quite low (2-4 species), and most of the biomass was incorporated into one or two species.

Discussion

The descriptive aspects of this study show that the Wells National Estuarine Research Reserve (WNERR) contains a diverse array of marsh habitats. Within the pristine Little River estuary, species diversity is high. A few species (S. alterniflora, S. patens, Salicornia europea) are ubiquitous throughout the marsh whereas five or six species are localized to the middle and upper estuary. Large variations in community species composition occur across both tidal elevation and estuarine gradients. Sampling within the Webhannet River estuary was conducted over a narrower scale and range of gradients than the Little River estuary. The Webhannet samples were concentrated near developments on or along the marsh in an attempt to determine whether productivity is affected by disturbance from human activities. The results indicate that the portion of the Webhannet estuary studied has lower diversity and significantly lower total standing crop than comparable sites along the Little River.

Interesting comparisons are also evident on a regional scale. Topographically, the WNERR marsh system is similar to the marshes found from southern New England to southern Maine. Biotically, there are interesting similarities, as well as contrasts, between the marshes of the WNERR system and tidal marshes of southern New England. The dominant plant assemblages and their distribution patterns are the same but invertebrate populations and their effects may be different. Periwinkles (Littorina littorea) are present in the low marsh areas of both WNERR and southern New England, whereas fiddler crabs (Uca pugnax) and saltmarsh mussels (Geukensia demissa) are common in southern New England (Bertness 1984a,b; Hoffman et al. 1984), but absent from WNERR.

An important difference between marshes in Maine and those further to the south is the annual (late winter) removal of aboveground biomass of S. alterniflora in Maine (Vadas et al. 1976; Keser et al. 1978). Ice action and storms remove standing dead biomass from riverbank populations in most areas of Maine, whereas much of the aboveground biomass remains intact through one or more growing seasons in southern marshes (Linthurst and Reimold 1978). The mortality of leaves during the growing season is thought to constitute a major energy export pathway from southern marshes (Teal 1962; Odum 1971). Although the extent and significance of this export has been questioned (Haines 1977), recent evidence suggests that the earlier assumptions concerning detritus export from S. alterniflora stands were valid (Peterson et al. 1980; Hughes and Sherr 1983). Long-term observations by the authors at the Harrington saltmarsh (Vadas 1981; Vadas et al. 1985) suggest that most aboveground biomass from riverbank populations of S. alterniflora is removed annually during ice-out. Thus, the export of saltmarsh detritus in Maine appears to be characterized by large pulses at the beginning of each growing season.

Productivity:

The largest single-species estimate of NAPP (1457 g/m^2/yr) was obtained for riverbank populations of Spartina alterniflora in the lower estuary of the Little River using the paired-plot technique. Expanding this into a multi-species estimate to include the entire low-zone community (347 g/m^2/yr, mostly Ascophyllum and Salicornia), the total NAPP estimate for the low-zone community becomes 1804 g/m^2/yr. This value represents NAPP for a relatively undisturbed low-zone, high salinity habitat. Productivity estimates for other low zone sites within the WNERR system, based on August standing crop comparisons, were lower and ranged from 27 to 77 percent of the corresponding August biomass value for the LR/LE site.

Comparison of the paired-plot value with the maximum monthly value (1804 $g/m^2/yr$ vs 1634 $g/m^2/yr$) shows that the measurement of growing season mortality of _Spartina alterniflora_ increased the NAPP estimate by approximately 10% or 170 $g/m^2/yr$. Thus, for stands in the low tidal zone that are dominated by _S. alterniflori_a, the maximum monthly standing crop can provide a reasonable estimate for saltmarshes in Maine. For the other two zones, further testing of the paired-plot type technique should be done.

Comparison of the maximum monthly estimates and the end-of-season sampling estimates shows that end-of-season sampling is unreliable for the low and high zones of WNERR. For the _S. patens_-dominated community the maximum live standing crop and the end-of-season estimates are identical. For both of the other zones, the phenology of the dominant species determines the timing of peak aboveground standing crop. Therefore, unless such information is already available for the community to be sampled, monthly sampling should be done to ensure obtaining at least the peak standing crop value, if not a paired-plot estimate.

The seasonal patterns of plant growth of other species also produced interesting results. _Spartina patens_ dominated the middle elevation zone in many areas of the WNERR system, often forming a nearly continuous monoculture. The growth of _S. patens_ started slowly in the spring and continued until frost. Therefore, in areas where it dominates, maximum live standing crop is found in August or September.

In contrast to the low and middle zones, which often form monocultures, the high zone of the lower Little River contains a diverse community. _Triglochin maritima_ is the most abundant species in this community, followed by *Plantago juncoides*. These two species and *Juncus gerardi* all show peak growth between June and July, and either maintain that level of standing crop or have lower values later in the season. The high zone therefore reaches its maximum monthly estimate of NAPP in July.

Previous estimates of productivity of *S. alterniflora* in Maine varied considerably although most were lower than ours. Seasonal maximum estimates of aboveground biomass derived from monthly samples in Montsweag Bay ranged from 1010 g/m^2 to 1419 g/m^2 in relatively natural areas but from 525 g/m^2 to 600 g/m^2 in areas stressed by thermal effluents (Vadas et al. 1976; Keser et al. 1978). Linthurst and Reimold (1978) also made NAPP estimates of *S. alterniflora* in Maine and reported 863 g/m^2/yr for tall *S. alterniflora*. Their estimate for *Spartina patens*, however, was 3036 g/m^2/yr, which is an order of magnitude greater than our estimate and more than 700 g/m^2/yr greater than the previous maximum estimate from Georgia. We have no explanation for the extremely high values obtained by them for *S. patens*.

Productivity estimates for the rest of New England and the Gulf of Maine are equivalent to or lower than WNERR. Comparable estimates for the low zone in the Bay of Fundy were nearly an order of magnitude lower, 272 g/m^2/yr, than for WNERR (Gordon et al. 1985). Similar estimates from the east coast of Nova Scotia were 3 to 4 times greater than the Bay of Fundy but only half the value at WNERR (Hatcher and Mann 1975). Nixon and Oviatt (1973) estimated 840 g/m^2/yr for tall and medium *S. alterniflora* in Rhode Island based on biomass at the end of the growing season. Ruber et al. (1981), using a method which accounts for mortality and decomposition, estimated 1261 g/m^2/yr for *S. alterniflora* and 935 g/m^2/yr for *S. patens* in Northeastern Massachusetts. The maximum live standing crop estimates by

Ruber et al. (1981), however, were lower, 1190 g/m^2 for S. alterniflora and 555 g/m^2 for S. patens. The estimates of NAPP for S. alterniflora at WNERR were also greater than the earlier estimates from Maine (Vadas et at. 1976; Keser et al. 1978; Linthurst and Reimold 1978; Vadas et al. 1985), but see Jacobson et al. (1987). Both of the earlier estimates for S. patens by Linthurst and Reimold (1978) and Ruber et al. (1981) are above those from WNERR.

The peak biomass value of 1287 g/m^2 for creekbank S. alterniflora in the WNERR is slightly below the range of reported biomass values from the southeastern U.S.: Virgina - 1570 g/m^2 (Mendelssohn and Marcellus 1976), North Carolina - 1752 g/m^2 (Stroud and Cooper 1968), Georgia - 1966 g/m^2 (Gallagher et al. 1972), Louisiana - 1948 g/m^2 (Kirby and Gosselink 1976). Comparison of peak standing crops, however, is subject to considerable error because of differential mortality and turnover rates (Linthurst and Reimold 1978, Shew et al. 1981). The use of more refined methods has produced considerably higher estimates of NAPP for creekbank S. alterniflora of 4251 g/m^2/yr (Wiegert 1979) and 3700 g/m^2/yr (Gallagher et al. 1980) in Georgia, 1169 g/m^2/yr in Virginia (Reidenbaugh 1983) and 803 g/m^2/yr in Nova Scotia (Livingston and Patriquin 1981). The geographic range in these values indicates that the NAPP value of 1457 g/m^2/yr for WNERR is quite realistic, and provides additional support for the notion that a distinct gradient in real NAPP occurs across the climatic gradient from Georgia to Nova Scotia.

Saltmarsh plants produce not only aboveground biomass, but also belowground organic matter. Standing crop generally is greater belowground than aboveground (Smith et al. 1979). In fact, Livingstone and Patriquin (1981) reported a ratio of 1.75:1 for belowground:aboveground biomass for the Atlantic coast of Nova Scotia, at approximately the same latitude as WNERR. Schubaüer and Hopkinson (1984) reported a ratio of 1.7:1 in Georgia for creekbank S. alterniflora. Using 1.7:1 as conservative ratio, we derive belowground and total esitmates of productivity of 2477 g/m^2/yr and 3764 g/m^2/yr (1457 + 2477) respectively, for WNERR. This compares well to previously reported values of total productivity for Nova Scotia - 1851 g/m^2/yr (Livingstone and Patriquin 1981), Massachusetts - 3920 g/m^2/yr (Valiela et al, 1976), New Jersey - 2800 g/m^2/yr (Smith et al. 1979), Georgia - 5810 g/m^2/yr (Gallagher et al. 1980), and Georgia - 7620 g/m^2/yr (Schubauer and Hopkinson 1984).

The growing season mortality of S. alterniflora (as estimated in the paired-plot study) amounted to 622 g/m^2/yr. When the total growing season mortality estimate is added to the live standing crop remaining in September, the sum (1273 g/m^2/yr) is 87% of the NAPP estimate for S. alterniflora (1457 g/m^2/yr), leaving 13% unaccounted for. It is evident that the growing season turnover of the biomass of S. alterniflora in Maine contributes significantly to the annual metabolism of nearshore ecosystems.

Fluxes and turnover rates of dead biomass apparently differ between the three elevation zones examined in this study (Table 17). In the low zone, the standing crop of dead biomass apparently fluctuates irregularly and the early season value is very low, indicating the nearly complete removal of dead biomass during the winter and early spring. These trends are consistent with the findings of Gordon et al. (1985) that due to increased flushing, leaf loss and turnover of dead biomass increased with decreasing tidal elevation.

In the middle zone, the standing crop of dead biomass was consistently higher than in the other zones and accumulated to quantities greater than the live standing crop. Adding together the live and dead September biomass values (Table 6) gives a value of 753 g/m^2 at the end of the season. Using the dead biomass value for April (536 g/m^2), we can estimate the amount (217 g/m^2) lost during the winter. Subtracting the dead biomass from September from the value in April gives 155 g/m^2 or the amount lost during the growing season. Summing these two losses yields a turnover estimate of 372 g/m^2/yr, which is very close to the NAPP estimate for this zone. Thus, biomass produced in the *S. patens*-dominated middle zone remains in situ for approximately an entire growing season.

In the high zone, there is apparently little or no biomass lost from the marsh over winter (using the same comparison as the middle zone). Due to the mid-season dead biomass minimum, decomposition during the growing season appears to be the major fate of aboveground productivity.

Grazing:

Grazing studies were initiated for three general reasons: to apply, if relevant, a correction factor to productivity estimates, to assess the fate of annual primary productivity and to begin to assess the importance of herbivores in structuring the WNERR marsh. One possible fate or pathway for NAPP is immediate consumption by herbivores. The most obvious grazers in the WNERR system were deer in the high zone marshes of the low, middle and upper estuary, and periwinkles in the lower zone of the lower estuary. If a considerable amount of the NAPP of the marsh plant community is eaten directly by herbivores, the estimates of NAPP will inevitably be low. Thus, an estimate of the direct loss to herbivory is important to understanding productivity and energy flow. In this study, we were unable to demonstrate significant losses of aboveground biomass to herbivores. This by itself does not mean that herbivores are unimportant in or to the system but only that no demonstrable negative effects occurred in our treatments.

Our inability to detect significant effects from deer or snail grazing may be real or the result of experimental design. Because of cost constraints, it was not possible to establish and sample more than three replicates of each treatment. It is also possible that our studies were initiated too late to detect the major period of impact by deer. Marshes previously studied in Maine were often covered by snow or frozen until late March and few if any plants germinated or grew until May (Vadas et al. 1976; Keser et al. 1978). In eastern Maine (Harrington Marsh) visible growth, except for a few species, was not evident until late May (Vadas 1978; Vadas, et al. 1985). Plant development at WNERR during 1986, however, began earlier, perhaps as early as late March. A preliminary visit in early April revealed the presence of green stems for several rhizomatous species including _Juncus balticus_. Furthermore it was during this period that striking evidence for deer grazing was obtained at the middle estuary site. Numerous stems of _J. balticus_ were cut off at various heights (10-20 cm) above the ground in the high marsh zone. Exclusion cages were placed at this location to assess the impact of deer. However after April there was little evidence of new or continued grazing on _J. balticus_ in this region. Feeding damage was also observed on young _Triglochin_ plants, and continued into July. Here the tips of young leaves were clearly excised. Most grazing effects were evident early in the growing season, and perhaps were related to those species that developed early. The general reduction or absence of grazing later in the spring and summer, at least for _J. balticus_, suggests that some other components of feeding behavior such as preferences may have been involved when upland species became available as food. Dietary studies on feeding habits of deer in Maine indicate that during early spring, when plants are putting out new growth, deer sample a wide variety of plant species. As the season progresses they ignore some species that they previously had browsed, and thus feed more selectively (Crawford 1982). It is also possible that the marsh species were browsed simply for salt nutrition.

A second complicating factor may have been the cages and covers themselves. Their presence may have spooked the deer, although one fresh track was observed in one of the covers in June. The trend towards higher productivity in adjacent control plots suggests that areas near the cages and covers were not subjected to grazing pressure. However there was little evidence during summer of deer grazing in areas remote from the cages, suggesting that seasonality may be important in determining feeding effects.

Another herbivore effect, however, was apparent at WNERR. Compaction by hoof and trampling disturbance was observed in areas of the upper and middle marsh, especially where deer trails regularly crossed the marsh. The specific effects of trampling have not been studied but it is likely that the peat has been compacted severely in these areas, perhaps by as much as 15-30 cm. Howell (1984) indicated that meadow voles can compact marsh peat by as much as 15 cm. Compacted areas can effect drainage patterns on the marsh which could result in altered species composition and productivity. In England trampling by sheep alters successional patterns in salt marshes and results in stands dominated by _Puccinellia_ (Daiber 1982). We made no attempt to determine if deer or other mammals were effecting the marshes at WNERR but suspect that their effects would be more important in the protected Little River. We suggest that future studies be designed to determine feeding and other disturbances, and assess the potential loss (to nearshore waters) of organic matter to terrestrial grazers.

A third point of concern is the shading effect (ca. 20 to 30% reduction in the light intensity) of the cages and covers themselves. This effect was apparent at all three grazer exclusion sites but was most obvious in the low zone of the lower estuary (Table 7 and 8). Total aboveground biomass in the high zone cages and covers averaged 83% of controls during the growing season. Even more impressive were the decreases in low zone cages and covers which averaged 60% over the season. Thus, despite their availability to grazers, plants in control areas consistently had higher growth and productivity values. Furthermore the striking (23%) differences between the two zones suggest that _S_. _alterniflora_ and _A_. _nodosum_ f. scorpioides in the cages and covers were well below light saturation intensities. In the low zone the cage effects may have been compounded by drift algae and _Spartina_ wrack that periodically was deposited on cages and covers. Conversely, plants in the high zone did not appear as light stressed, perhaps because of the shorter period of tidal innudation and less debris, both of which contributed to increased light levels beneath the structures. Nonetheless these results suggest that topless cages or corrals may be more appropriate for future exclusion experiments to reduce shading effects.

The effects of grazers on the productivity of the low marsh may be more equivocal. _Littorina littorea_ are reported to feed in the laboratory on the grass blades and rhizomes of _Spartina alterniflora_ in Rhode Island and potentially to have had a major impact on the abundance and distribution patterns of saltmarshes in New England (Bertness 1984a). Our field observations and herbivore exclusion studies do not support such an interpretation for saltmarshes in the WNERR. Our observations (immediately following high tide) reveal that an occasional *L. littorea* could be found on the stems of *S. alterniflora* but that most were feeding on *S. alterniflora* detritus. *Ascophyllum nodosum* f. scorpioides, and a variety of drift algal species were usually entwined at the bases of the stems apparently providing ample food resources. Additionally, the highest correlations of snail numbers occurred with the presence of *Ascophyllum* and of dead (mostly *S. alterniflora*) biomass. Thus despite the high densities of *Littorina* (only slightly lower than those observed by Bertness 1984a), there is no indication that snails are removing even small amounts of living biomass in the WNERR system. More refined studies on feeding behavior will be required to fully assess the impact of littorinids on the saltmarshes of WNERR and to contrast these results with those from Rhode Island.

Gradients in Productivity

Although a positive salinity or estuarine gradient was apparent for low intertidal communities (increasing productivity with higher salinity), middle and high intertidal communities had highest productivity levels at the middle estuary site. In addition, the latter communities had lowest productivities at the lower estuary (high salinity) site. These conflicting patterns indicate that salinity is not the sole factor in productivity patterns along the Little River. Similarly, aboveground production of *S. alterniflora* has been shown to be more closely related to sediment oxygen than either salinity or nitrogen (Howes et al. 1986). Other recent studies indicate that aboveground productivity of four out of five species in intertidal wetlands in Washington show an inverse relationship with increasing salinity (Ewing 1986). Individual species responses are also evident at WNERR (Table 12, 13 14) which when combined within each community tend to obscure patterns based solely on salinity.

Variations in standing crop or productivity with tidal elevation, however, are highly predictable. Both NAPP and standing crop for all Little River sites showed increasing productivity with decreasing tidal elevation (Figure 14). These data parallel earlier studies which show that both aboveground (Adams 1963; Niering and Warren 1980) and belowground biomass (Ellison et al 1986) of S. alterniflora decrease with increasing tidal elevation. However at WNERR the pattern of decreasing productivity with tidal elevation includes the entire assemblage of species and not just S. alterniflora. A similar pattern, based on standing crop estimates of the assemblage, was also evident at Harrington, Maine (Vadas et al. 1985) and may have broader generality than previously noted.

The human impact "gradient" actually is a comparison of the pristine Little River marsh with the heavily-used Webhannet and Depot Brook marshes. Total standing crop, in the middle-zone of the Webhannet (lower estuary) and Depot Brook (middle estuary) sites, is in the same range as the middle zone values for the Little River (Table 15). However, the species composition of the Webhannet middle-zone is more similar to the high zone than the middle-zone of the lower estuary of the Little River. The impact of human activities on standing crop is most evident in the Webhannet River low zone (Table 16). Standing crop of S. alterniflora at the Webhannet River lower estuary site (Web. Landing) is less than 10% of the value at the LR/LE site. Other striking differences at the Webhannet landing site include the total absence of Ascophyllum nodosum f. scorpioides, the large standing crop of Fucus vesiculosus and the paucity of attached or entwined dead biomass at the bases of *S. alterniflora* plants.

Conclusion

The WNERR encloses a highly productive marsh. Most of the marsh areas consist of middle and high tide level marshes (Jacobson et al. 1987; this report). Strips of highly productive *S. alterniflora* exist along the seaward edges of the reserve, but these are not extensive enough to dominate the total production estimates from WNERR. Thus the best estimates of total production would use the middle elevational zone dominated by *S. patens*. Nonetheless based on standing crop estimates and more refined techniques, this is a highly productive marsh ranging from 300 to 1800 g/m^2/yr. This is slightly higher than recent estimates for the Gulf of Maine (Jacobson et al. 1987).

These limited data support the contention that the Little River is in a near-pristine state at this time. These figures are even more impressive when compared to the Webhannet estuary (landing site) which is influenced by wave splash and petroleum spills from boat traffic. The estimates of standing crop for the Little River sites are 6- to 10-fold greater than for the Webhannet sites (Table 18). Although other Webhannet samples above (higher elevation) or more distant from the landing showed a 3-fold increase over the landing, they were still less than half as productive as comparable sites on the Little River. The pattern seems clear but experimental studies will be needed to accept or reject the boat traffic hypotheses. It is possible that other factors may also be involved in the reduced productivity of this site. Nonetheless it serves warning that disturbance or encroachment by humans may be directly or indirectly influencing the productivity of the marshes of the WNERR.

Although limited, our data will serve as a baseline for assessing the health of the WNERR in the future. Ideally, paired-plot productivity estimates should be generated at least once for several of the other zones or vegetation types. These will provide a better estimates of the actual productivity and contribution of these marshlands to the fishery nursery areas and nearshore waters surrounding the WNERR. Finally, a broad array of benefits results from the establishment of the Wells National Estuarine Research Reserve. Preservation of this large tract of wetlands and adjacent upland area is of value in several ways. Tidal marshes are very important to the natural economy of nearshore water. Numerous commercial and recreational fisheries depend heavily on the energy originally stored by marsh plants both above and belowground. Although most of the aboveground biomass becomes available annually, much of the belowground biomass apparently becomes available over longer periods, perhaps through the erosion of peat, which can be on the order of a few to 200 years (Kelly et al. 1987). The question as to the fate of these materials and energy remains for New England marshes. Do they perform the same or similar roles to that reported for southern marshes?

Scientific study of marshlands in the northeast will be greatly enhanced by the WNERR, not only due to the preservation of relatively pristine marsh areas such as the Little River estuary, but also to the inclusion of areas with a wider range of habitats, including those potentially altered by development. Here, altered and pristine areas can be studied comparatively to increase our knowledge of the mechanisms involved in the impacts by humans upon marshes. Finally continued scientific study at WNERR will ultimately be of importance to educational institutions in the state and Northeast, and to the increased awareness of the value of natural areas.

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Table 1. Plant species occurring at all sites in the Wells National Estuarine Research Reserve.

SCIENTIFIC NAME	COMMON NAME
Phaeophyta	
Ascophyllum nodosum f. scorpioides (Hornmann) Reinke	Wormweed
Fucus vesiculosus L.	Bladder Wrack
Angiospermae	
Agrostis alba L.	Bentgrass
Aster novi-belgii L.	Aster
Atriplex patula L.	Orach
Carex paleacea Wahlenb.	Sedge
Eleocharis halophila Fern. & Brack.	Spike-rush
Festuca ovina L.	Sheep's-fescue
Galium palustre L.	Bedstraw
Gerardia maritima Raf.	Gerardia
Glaux maritima L.	Sea-milkwort
Juncus balticus Willd.	Rush
Juncus gerardi Loisel.	Black Grass
Lathyrus japonicus Willd.	Beach-pea
Limonium nashii Small	Sea-lavender
Panicum sp.	Panic-grass
Plantago juncoides Lam.	Seaside-plantain
Puccinellia paupercula (Holm) Fern. & Weath	Alkali-grass
Salicornia europaea L.	Glasswort
Scirpus paludosus var. *atlanticus* Nels.	Bulrush
Solidago sempervirens L.	Seaside Goldenrod
Spartina alterniflora Loisel	Salt-water Cordgrass

Table 1. cont.

SCIENTIFIC NAME	COMMON NAME
Spartina patens (Ait.) Muhl.	Salt-meadow Grass
Spartina pectinata Link	Fresh-water Cordgrass
Suaeda maritima (L.) Dumort.	Sea-blite
Triglochin maritima L.	Arrow-grass

Table 2. Plant species occurring in experimental plots at three sites and three intertidal zones along the Little River (August 1986).

SPECIES	HIGH ZONE			MID ZONE			LOW ZONE		
	*LOW	MID	UP	LOW	MID	UP	LOW	MID	UP
Agrostis alba	X	X	X	X		X			X
Ascophyllum nodosum							X		
Aster novi-belgii						X			
Atriplex patula	X	X		X	X	X			
Carex paleacea		X	X			X			X
Eleocharis halophila		X	X						
Festuca ovina		X				X			
Fucus vesiculosus							X		
Gerardia maritima	X	X			X				
Glaux maritima	X	X			X				
Juncus balticus		X				X			
Juncus gerardi	X	X	X		X	X			
Juncus sp.			X						
Lathyrus japonicus		X		X					
Limonium nashii	X	X		X					
Panicum sp.		X							
Plantago juncoides	X	X		X	X				
Puccinellia paupercula	X	X		X	X				
Salicornia europaea	X	X		X	X		X		
Scirpus paludosus		X	X			X			
Solidago sempervirens	X	X							
Spartina alterniflora	X	X		X	X		X	X	X
Spartina patens	X	X		X	X	X	X	X	X
Spartina pectinata		X	X			X			
Suaeda maritima	X			X			X		
Triglochin maritima	X	X	X	X	X	X			

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* Low = Lower Estuary, Mid = Middle Estuary, Up = Upper Estuary.

Table 3. Plant species occurring in experimental plots at two sites and two intertidal zones along the Webhannet River and Depot Brook (August 1986).

SPECIES	WEBHANNET LANDING			DEPOT BROOK	
	LOW	*SHORT-CORDGRASS	MIDDLE	LOW	MIDDLE
Ascophyllum nodosum		X		X	
Fucus vesiculosus	X	X			
Glaux maritima			X		
Limonium nashii			X		
Plantago juncoides			X		
Puccinellia paupercula			X		
Salicornia europaea		X	X		X
Spartina alterniflora	X	X	X	X	X
Spartina patens			X		X
Suaeda maritima			X		

*Short-cordgrass is in the low zone.

Table 4. Salinity and temperature data for the Wells National Estuarine Research Reserve, 1986.

Date	Location[1]	Water Temperature	Corrected Mean Salinity[2]
4-2-86	LR/LE	-	32.6
5-20-86	LR/LE	15.0	31.1
	LR/ME	14.9	10.2
6-16-86	LR/LE	14.9	27.5
	LR/ME	13.8	2.5
7-16-86	LR/LE	16.9	31.3
	LR/ME	16.8	30.5
8-11-86	LR/LE	25.5	30.8
	LR/ME	25.5	13.6
	WEB	25.5	32.3
	DB	25.5	32.1
	DB/UP	-	28.0
10-21-86	LR/LE	-	33.3
	LR/ME	-	24.2

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[1] LR/LE - Little River, lower estuary
LR/ME - Little River, mid estuary
WEB - Webhannet River
DB - Depot Brook (UP - upper estuary)

[2] Corrected to 15°C

Table 5. Computation of the net aboveground primary productivity (NAPP) in g/m^2 of *Spartina alterniflora* at the Little River lower estuary site.

Month	Living biomass (A_n)	A_n	B_n	$PROD_n$
April (1)	4.56	----	---	4.56
May (2)	63.40	58.84	1.44	60.28
June (3)	397.80	329.40	14.04	343.44
July (4)	1286.92	894.12	108.84	1002.96
August (5)	1000.20	-286.72	332.56	45.84
September (6)	489.60	-510.60	165.01	0
			NAPP =	1457.08

a - NAPP = $\sum_{n-1}^{6} \max \{(A_n - A_{n-1} + B_n), 0\}$

Table 6. Monthly estimates (g/m^2) of total living and dead biomass for the Little River, lower estuary productivity site, 1986.

	MONTHLY ESTIMATES					
HIGH ZONE	APR	MAY	JUN	JUL	AUG	SEP
Juncus gerardi		6.21	16.65	22.93	0.35	0.53
Plantago	7.91	9.72	30.44	46.03	45.76	8.85
S. alterniflora	0.61	0.48	4.79	13.65	6.45	17.33
Triglochin	33.79	69.03	120.63	210.03	103.57	21.39
Total live	42.87	87.00	176.12	299.31	160.11	104.80
Dead biomass	198.20	104.40	85.35	76.27	86.77	94.67
MID ZONE						
S. patens	13.35	17.20	110.40	230.61	287.09	356.91
Total live	14.55	21.85	110.53	231.31	298.72	371.84
Dead biomass	535.53	478.77	459.23	525.12	442.45	381.33
LOW ZONE						
S. alterniflora	4.57	63.40	392.80	1286.93	1000.21	489.60
Total live	17.23	290.00	645.41	1633.87	1080.91	997.33
Dead biomass	166.49	242.51	95.95	243.31	289.44	182.67

Table 7. Comparison (ANOVA) of monthly standing crop estimates in covered, caged and control plots in the high zone at the lower estuary, Little River.

			Treatment Means (g dry wt.)[1]		
	Date	F	Control	Cage	Cover
Triglochin maritima	May	1.52	17.26	10.87	10.65
	June	2.42	30.16	23.80	16.74
	July	3.06	13.13	7.31	8.34
	Aug	0.58	6.47	9.31	6.12
	Sept	3.79	1.34	3.79	1.26
Plantago maritima	May	1.66	2.43	2.74	1.52
	June	1.58	7.61	6.66	4.05
	July	0.63	2.88	2.64	1.76
	Aug	0.23	2.86	2.42	1.87
	Sept	2.22	0.55	1.58	0.47
Spartina alterniflora	May	2.83	0.12	0.69	1.55
	June	1.06	1.20	2.31	3.00
	July	0.11	0.85	0.59	0.63
	Aug	0.34	0.40	1.15	0.96
	Sept	0.19	1.08	0.61	0.73
Limonium nashii	May	0.12	0.18	0.21	0.25
	June	0.46	0.72	0.45	0.40
	July	0.14	0.26	0.14	0.17
	Aug	1.76	0.02	0.07	0.32
	Sept	1.30	----	0.11	0.27
Total live aboveground	May	1.68	21.75	15.79	15.04
	June	5.42*	44.03a	34.93ab	25.92b
	July	4.41	18.71	10.99	11.55
	Aug	0.88	10.01	13.39	9.90
	Sept	0.83	6.55	6.35	3.64
Dead Biomass	May	0.35	26.10	26.07	22.60
	June	5.97*	21.34a	13.04b	11.88b
	July	2.16	4.77	3.76	2.78
	Aug	0.16	5.42	5.21	4.81
	Sept	1.20	5.92	7.82	5.48

---

[1] Sample plot sizes (area) were reduced by 3/4 beginning in July.

Table 8. Comparison (ANOVA) of monthly standing crop estimates in covered, caged and control plots in the low zone at the lower estuary, Little River site.

			Treatment Means (g dry wt.)[1]		
	Date	F	Control	Cage	Cover
Spartina alterniflora	May	0.12	15.85	15.72	13.34
	June	2.57	98.20	67.90	65.53
	July	4.11	80.43	32.13	34.46
	Aug	1.98	62.51	37.23	40.44
	Sept	0.04	30.60	34.75	34.95
Ascophyllum nodosum	May	1.63	56.46	31.63	7.15
	June	1.51	62.79	29.51	19.19
	July	4.63	21.68	5.48	4.56
	Aug	0.69	18.71	5.30	5.04
	Sept	3.09	31.55	5.37	1.08
Total aboveground live	May	1.20	76.37	52.76	32.06
	June	2.27	162.66	105.72	89.33
	July	4.36	103.24	38.54	44.21
	Aug	1.08	71.23	44.89	63.91
	Sept	0.56	62.34	46.08	36.68
Dead biomass	May	0.11	56.75	65.39	65.15
	June	1.93	22.67	42.43	56.95
	July	0.14	14.08	10.97	12.09
	Aug	0.59	18.09	12.07	12.83
	Sept	0.78	11.41	12.41	18.78

---

[1] sample plot sizes (area) were reduced by 3/4 beginning in July.

Table 9. Seasonal changes in size-frequency distributions and densities of *Littorina littorea* in the lower estuary of the Little River.

Month	TINY		SMALL		MEDIUM		LARGE		TOTAL	
	$\bar{X}$±sd	#/m^2	$\bar{X}$±sd	#/m^2	$\bar{X}$±sd	#/m^2	$\bar{X}$±sd	#/m^2	$\bar{X}$±sd	#/m^2
April	3±2	(12)	10±6	(40)	8±2	(32)	12±10	(48)	34±7	(136)
May	5±1	(20)	27±5	(108)	30±3	(120)	21±6	(84)	83±11	(332)
June	22±13	(88)	39±14	(156)	33±12	(132)	22±4	(88)	116±17	(464)
July*	14±9	(224)	17±6	(272)	11±3	(176)	6±1	(96)	48±1	(768)
August*	5±4	(80)	12±10	(192)	8±6	(128)	6±4	(96)	31±11	(496)
September*	1±1	(16)	5±1	(80)	3±1	(48)	2±0	(32)	11±0	(176)

*the lower (absolute) numbers for these 3 months reflect the use of a smaller quadrat (25 x 25 cm); a 50 x 50 quadrat was used for April-June (N=3).

Table 10. Mean shell length and calculated body dry weight for four size classes of *Littorina littorea*.

Size class	Size Range in mm	n	$\bar{X}$	sd	Calculated Body Dry Wt. (g)
Tiny	(<4.99)	63	4.33	0.467	0.0005
Small	(5-8.99)	167	6.44	0.998	0.0023
Medium	(9-14.99)	107	11.42	1.617	0.0177
Large	(>15)	66	19.76	2.754	0.1260

Table 11. Cross-correlation matrix for abundance of *Littorina littorea* and potential food items in the low zone of the Little River, lower estuary.

	Number	Bodywt	*Spartina*	*Ascophyllum*	Drift Algae
Number	1.0000	---	---	---	---
Bodywt	0.8443*	1.0000	---	---	---
Spartina	0.3703*	0.1745	1.0000	---	---
Ascophyllum	0.4355*	0.5550*	0.2852	1.0000	---
drift algae	0.1879	0.3055	-0.2077	-0.1093	1.0000
dead biomass	0.4102*	0.3875*	-0.2664	-0.0585	0.4137*

* critical value for the correlation coefficient ($p < 0.05$) = 0.3666

Table 12. Standing crop (g/625 cm^2) of high zone salt marsh species along an estuarine gradient in the Little River (August 1986).

SPECIES	LOW ESTUARY	MIDDLE ESTUARY	UPPER ESTUARY
Agrostis alba	0	0.12 ± 0.11	0.92 ± 1.59
Carex paleacea	0	0	0.25 ± 0.44
Eleocharis halophila	0	0	2.31 ± 2.64
Festuca sp.	0	1.25 ± 0.50	0
Gerardia maritima	0.15 ± 0.18	0.13 ± 0.12	0
Glaux maritima	0	trace	0
Juncus balticus	0	7.80 ± 3.09	0
Juncus gerardi	0.05 ± 0.09	0	0.15 ± 0.26
Juncus sp.	0	0	0.12 ± 0.20
Limonium nashii	0.02 ± 0.02	0	0
Moss	0	0	0.30 ± 0.53
Plantago juncoides	2.86 ± 1.60	0	0
Salicornia europaea	0.02 ± 0.01	0	0
Scirpus paludosus	0	2.33 ± 2.85	3.06 ± 2.03
Spartina alterniflora	0.40 ± 0.39	0	0
Spartina patens	0.03 ± 0.02	0.71 ± 0.91	0
Spartina pectinata	0	2.15 ± 2.55	0.15 ± 0.27
Triglochin maritima	6.47 ± 2.72	0.01 ± 0.01	3.45 ± 1.78
Total live	10.01 ± 1.89	14.59 ± 2.03	10.72 ± 2.79
Dead biomass	5.42 ± 1.16	46.79 ± 6.81	7.48 ± 3.02

Table 13. Standing crop (g/625 cm^2) of middle zone salt marsh species along an estuarine gradient in the Little River (August 1986).

SPECIES	LOW ESTUARY	MIDDLE ESTUARY	UPPER ESTUARY
Agrostis alba	0	0	1.31 ± 1.24
Aster novi-belgii	0	0	6.07 ± 2.27
Atriplex patula	0.01 ± 0.01	0	0
Carex paleacea	0	0	3.83 ± 3.73
Festuca ovina	0	0	3.88 ± 1.02
Juncus balticus	0	0	2.99 ± 2.98
Juncus gerardi	0	1.35 ± 2.33	0.60 ± 0.57
Limonium nashii	0.35 ± 0.60	0	0
Puccinellia paupercula	0.01 ± 0.18	0.13 ± 0.20	0
Salicornia europaea	0.26 ± 0.29	0	0
Scirpus paludosus	0	0	0.40 ± 0.69
Spartina alterniflora	0	7.40 ± 5.86	0
Spartina patens	17.94 ± 2.00	26.69 ± 10.24	1.87 ± 1.73
Spartina pectinata	0	0	0.10 ± 0.17
Suaeda maritima	0.01 ± 0.01	0	0
Triglochin maritima	0	0.01 ± 0.02	0.19 ± 0.33
Total live	18.67 ± 1.71	35.58 ± 2.13	21.22 ± 2.59
Dead biomass	27.65 ± 3.25	43.47 ± 14.77	19.93 ± 1.31

Table 14. Standing crop (g/625 cm^2) of low zone salt marsh species along an estuarine gradient in the Little River (August 1986).

SPECIES	LOW ESTUARY	MIDDLE ESTUARY	UPPER ESTUARY
Agrostis alba	0	0	0.18 ± 0.31
Ascophyllum nodosum	5.04 ± 7.55	0	0
Carex paleacea	0	0	1.19 ± 2.06
Spartina alterniflora	62.51 ± 24.06	38.21 ± 4.41	36.25 ± 0.46
Spartina patens	0	2.48 ± 3.50	0.07 ± 0.13
Total live	67.56 ± 17.32	40.68 ± 7.91	37.69 ± 2.72
Dead biomass	18.09 ± 11.13	18.44 ± 0.55	9.71 ± 5.81
Drift algae	3.67 ± 4.27	0	0

Table 15. Standing crop (g/625 cm^2) of mid zone salt marsh species at sites impacted by human activity (August 1986).

SPECIES	WEBHANNET R.	DEPOT B.
Glaux maritima	0.01 ± 0.02	0
Limonium nashii	0.06 ± 0.04	0
Plantago juncoides	1.93 ± 1.57	0
Puccinellia paupercula	2.86 ± 1.47	0
Salicornia europaea	0.29 ± 0.33	0.08 ± 0.10
Spartina alterniflora	0.38 ± 0.66	0.09 ± 0.16
Spartina patens	15.48 ± 6.84	27.87 ± 4.71
Suaeda maritima	0.12 ± 0.15	0
Total live	21.13 ± 4.75	28.05 ± 4.65
Dead biomass	9.01 ± 1.09	43.25 ± 9.22

Table 16. Standing crop (g/625 cm^2) of low zone salt marsh species at sites impacted by human activity (August 1986).

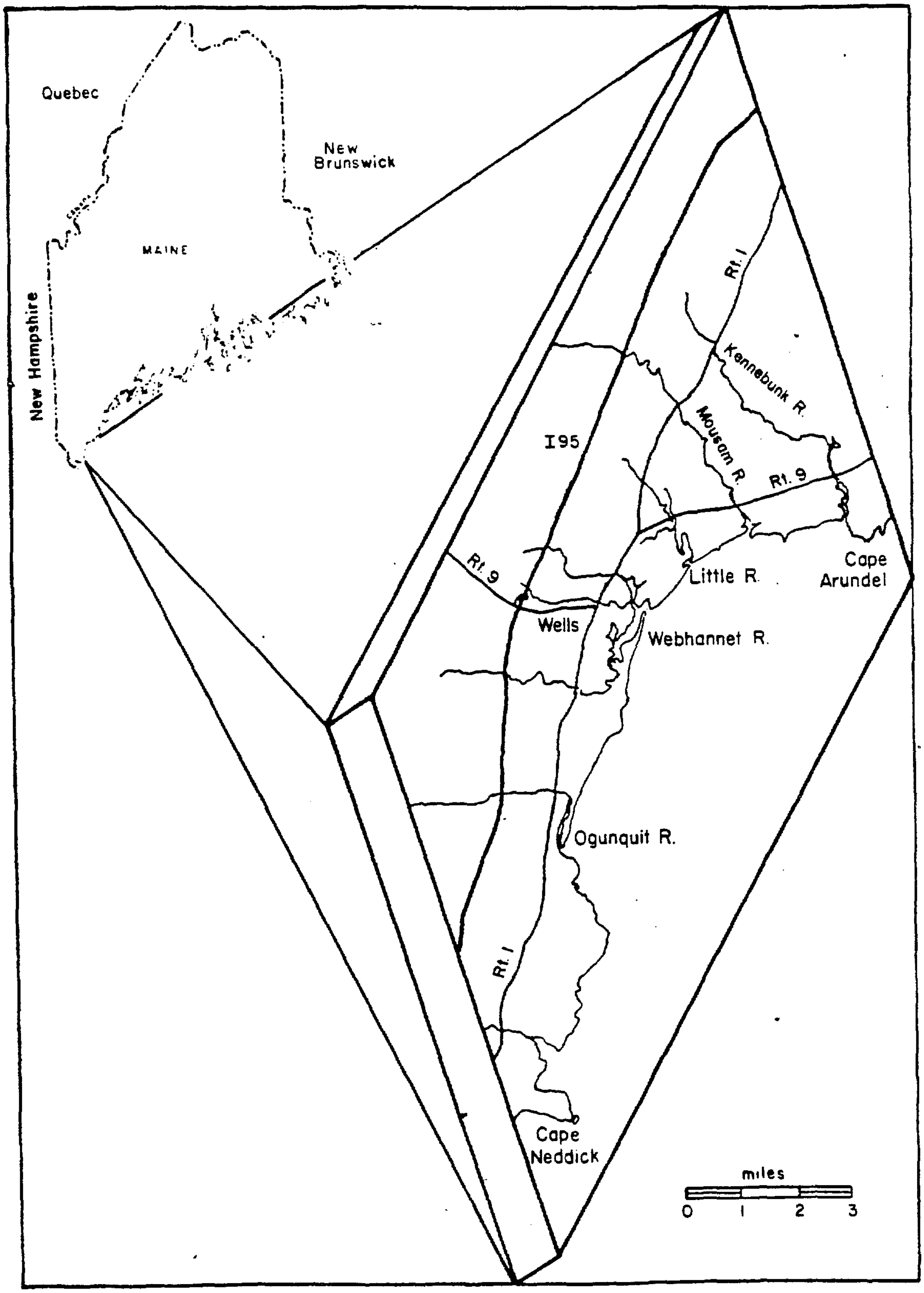
SPECIES	WEBHANNET R. LANDING	DEPOT B.	WEBHANNET R. SHORT
Ascophyllum nodosum	0	0.78 ± 1.36	1.32 ± 1.26
Fucus vesiculosus	46.40 ± 15.84	0	0.82 ± 1.05
Salicornia europaea	0	0	3.66 ± 3.18
Spartina alterniflora	5.80 ± 2.12	17.52 ± 7.41	19.87 ± 2.65
Total live	52.20 ± 15.18	18.30 ± 6.07	25.67 ± 1.89
Dead biomass	1.38 ± 0.70	4.79 ± 1.57	8.11 ± 1.27
Drift algae	0	0	0.01 ± 0.01

Table 17. Standing crop (g/m^2) of dead biomass within the Wells National Estuarine Research Reserve, summer 1986.

SITE & ZONE	MONTH					
	APR	MAY	JUN	JUL	AUG	SEP
LR/LE high	198.20	104.40	85.35	76.27	86.77	94.67
LR/LE middle	535.53	478.77	459.23	525.12	442.45	381.33
LR/LE low	166.49	242.51	95.95	243.31	289.44	182.67
LR/ME high					748.64	
LR/ME middle					695.52	
LR/ME low					295.04	
LR/UE high					119.68	
LR/UE middle					318.88	
LR/UE low					155.36	
WEB middle					144.16	
WEB short					129.76	
WEB low					22.08	
DEPOT middle					692.00	
DEPOT low					76.64	

Table 18. Standing crop, in g/m^2, for low zones or sites dominated by *Spartina alterniflora* at all sites sampled in August, 1986.

	Little River Estuary			Webhannet Estuary		
	Lower	Middle	Upper	Landing	Short-zone	Depot Br.
Agrostis alba	---	---	2.88	---	---	---
Ascophyllum nodosum	80.64	---	---	---	21.12	12.48
Carex paleacea	---	---	19.04	---	---	---
Fucus vesiculosus	---	---	---	742.35	13.12	---
Salicornia europaea	---	---	---	---	58.56	---
Spartina alterniflora	1000.16	611.36	580.00	92.80	317.92	280.32
Spartina patens	---	39.68	1.12	---	---	---
Total living biomass	1080.96	650.88	603.04	835.15	410.72	292.80
Total dead biomass	383.84	295.04	155.36	22.08	129.92	76.64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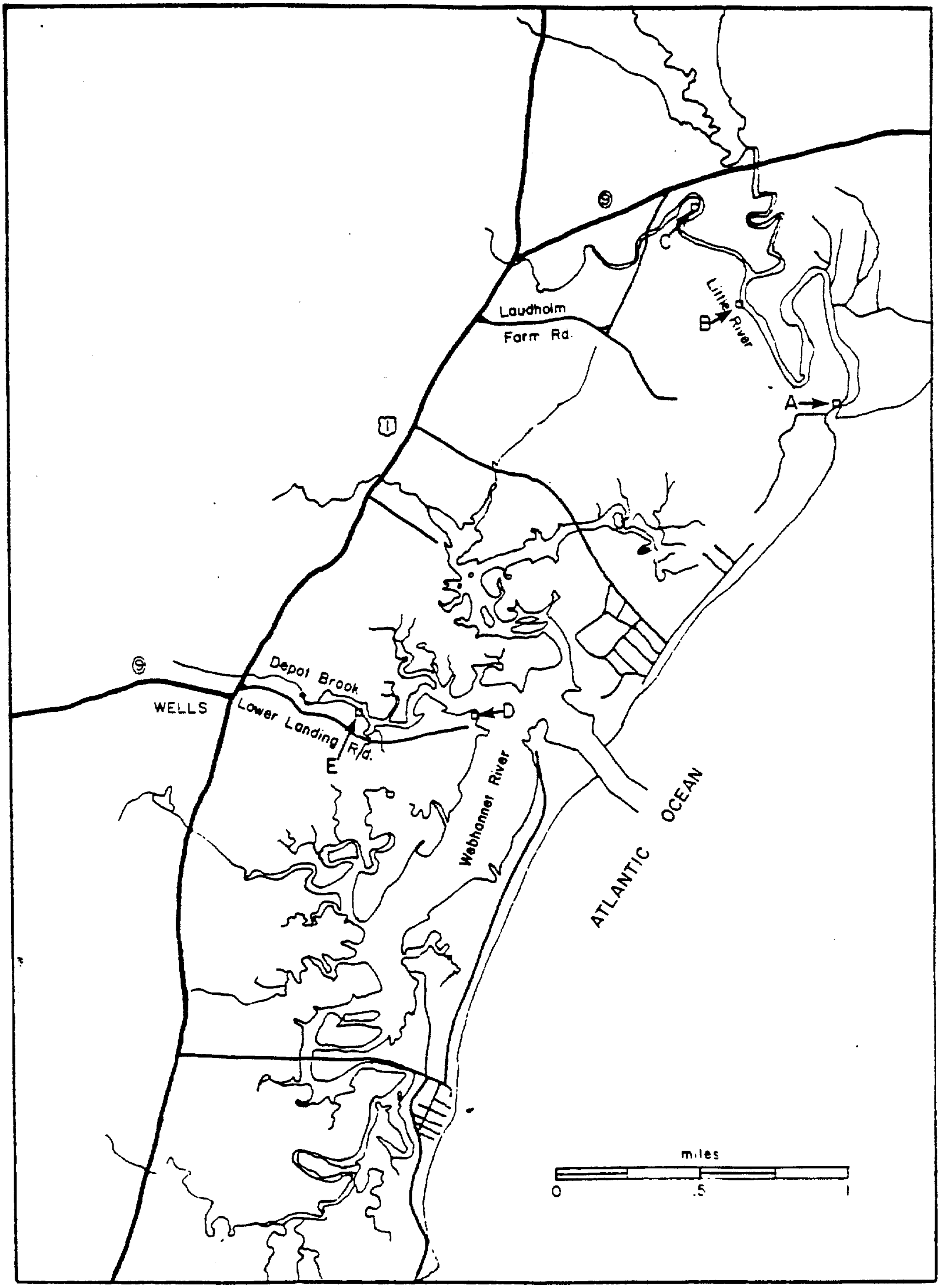
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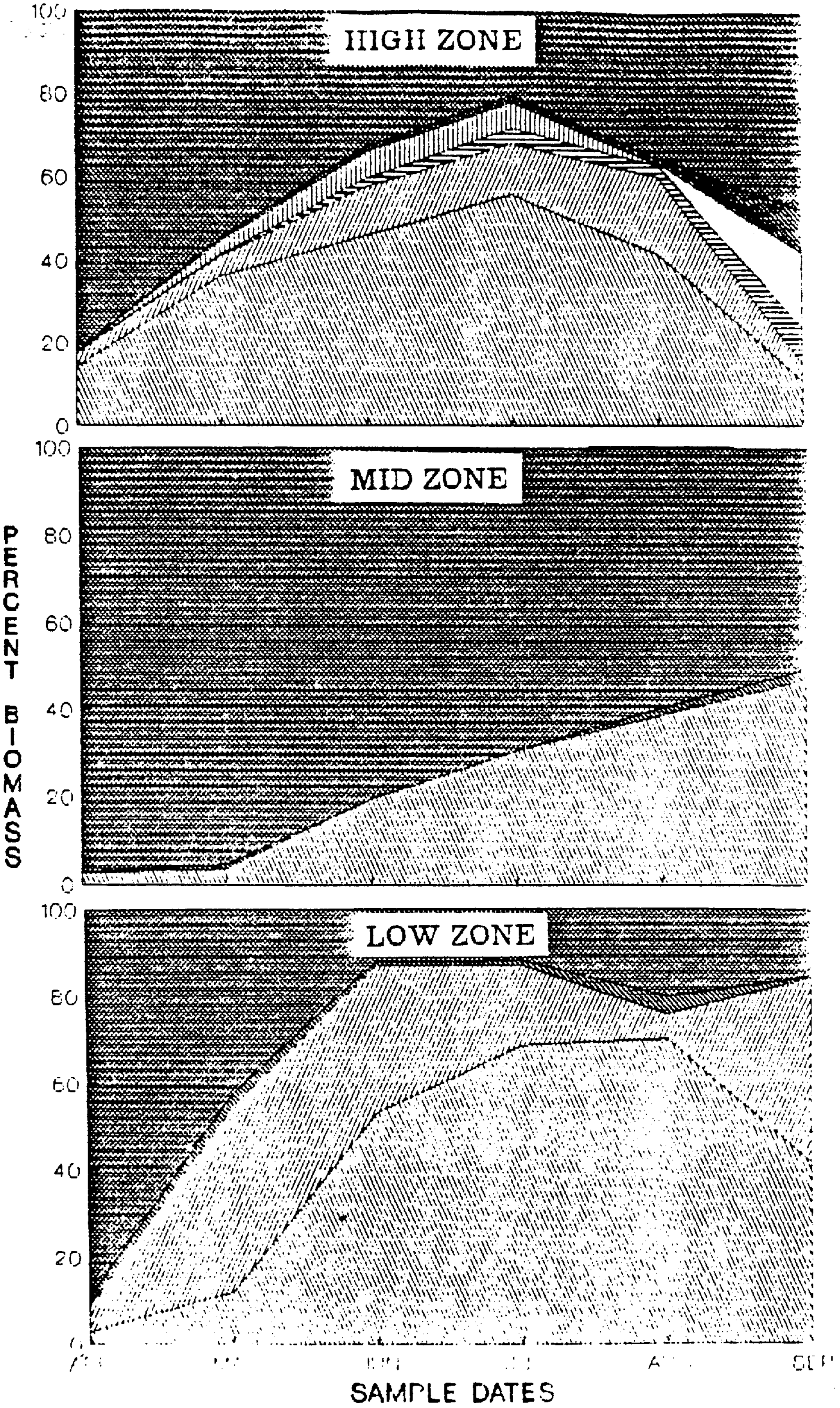
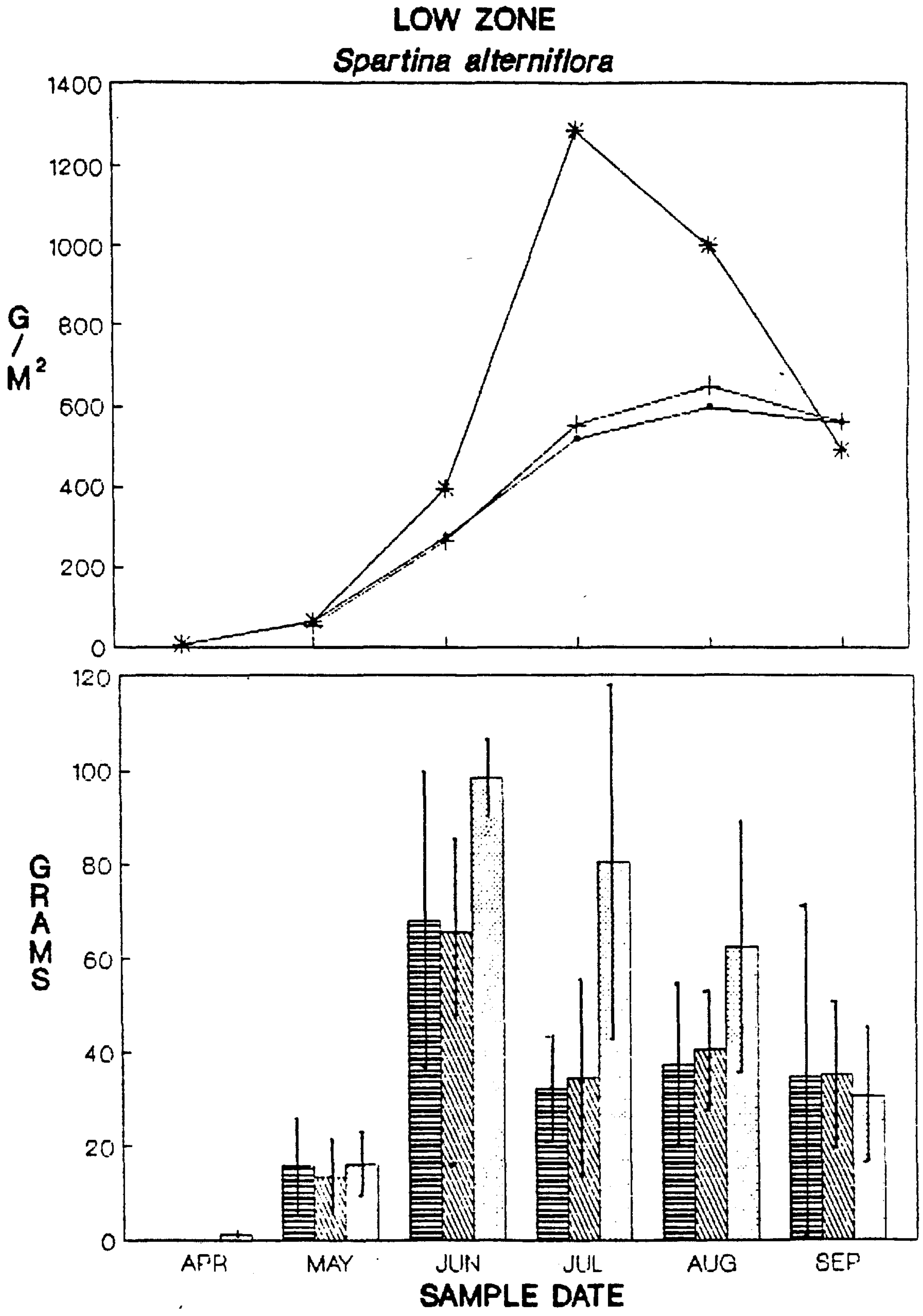
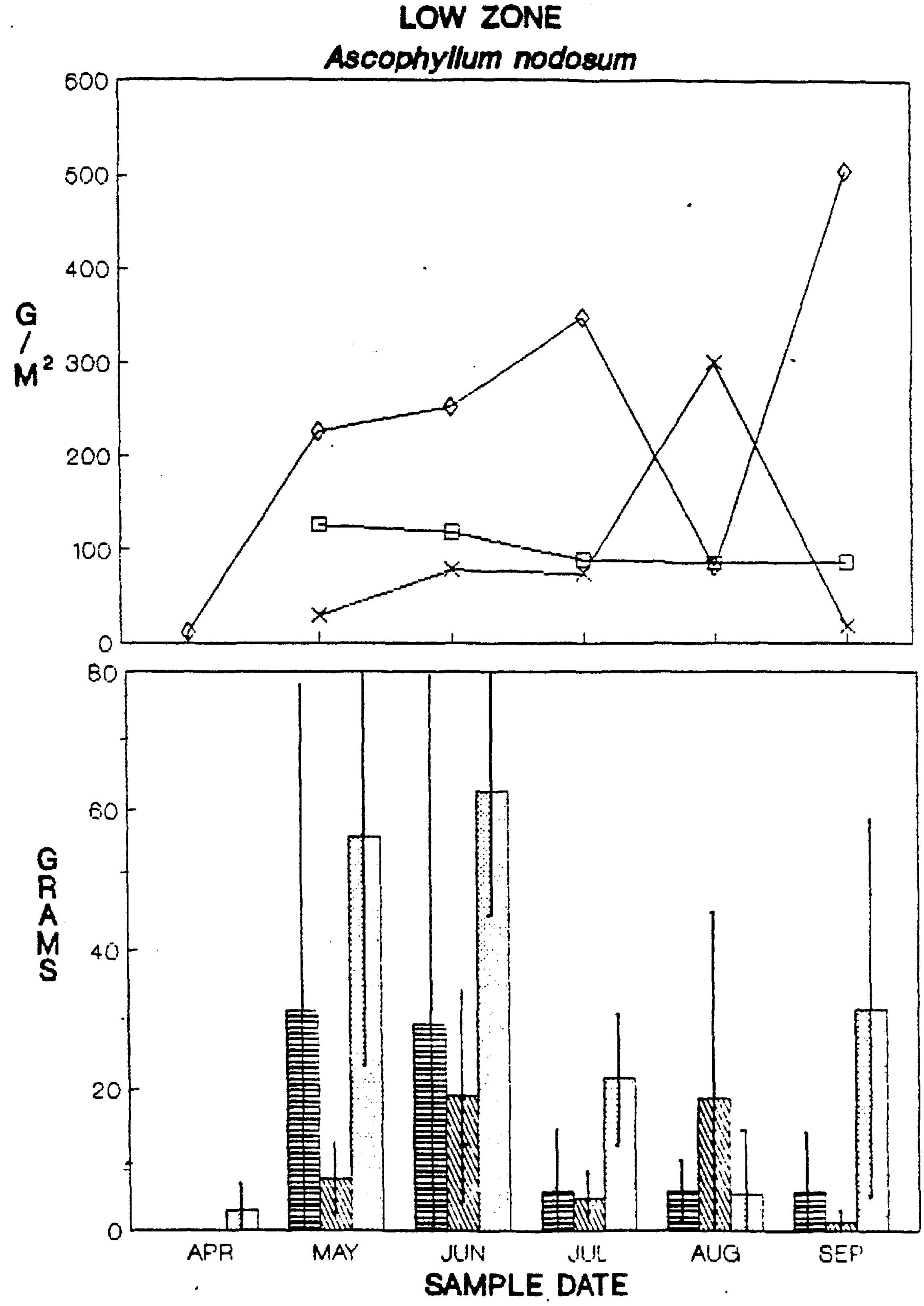
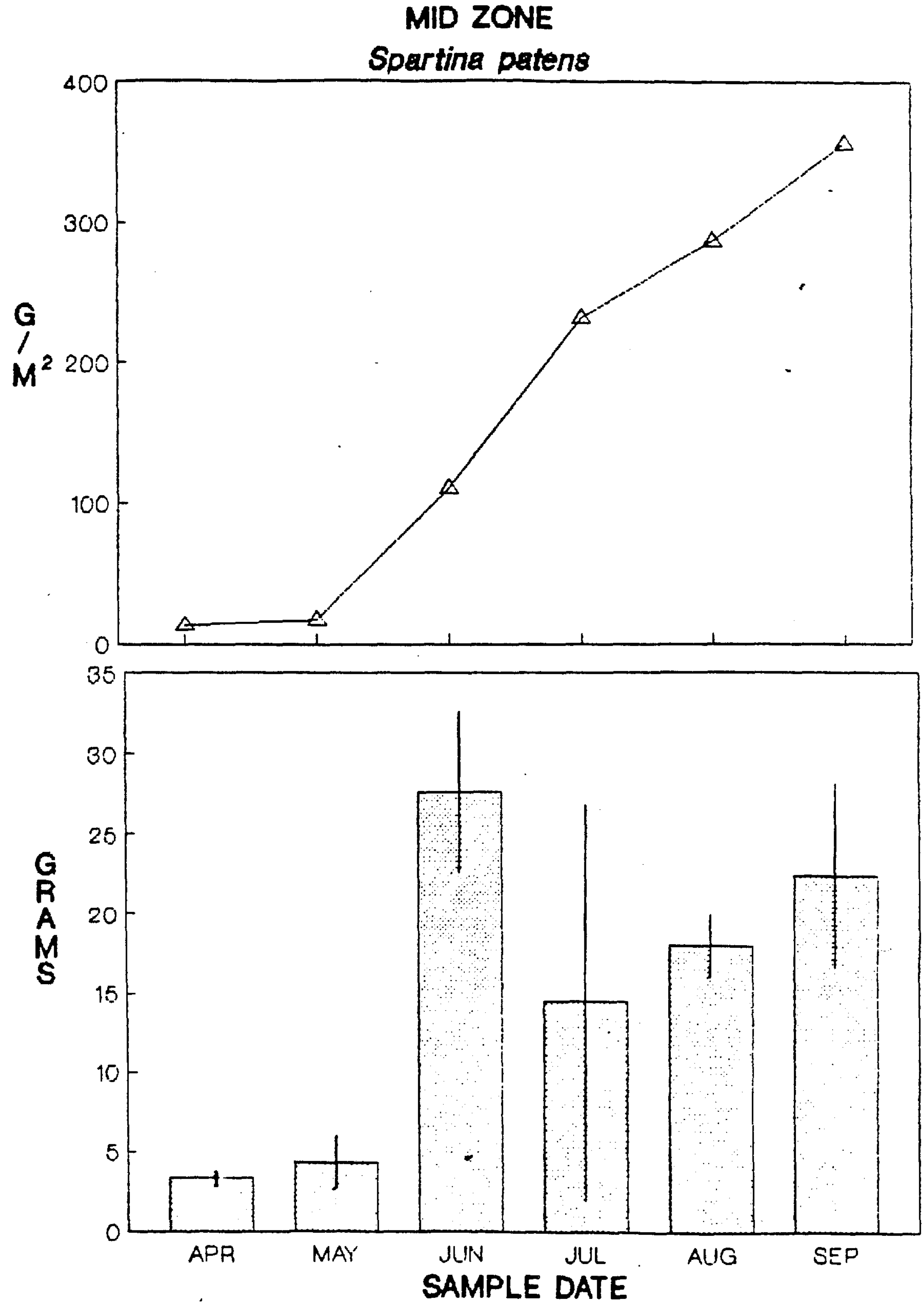
.5
1

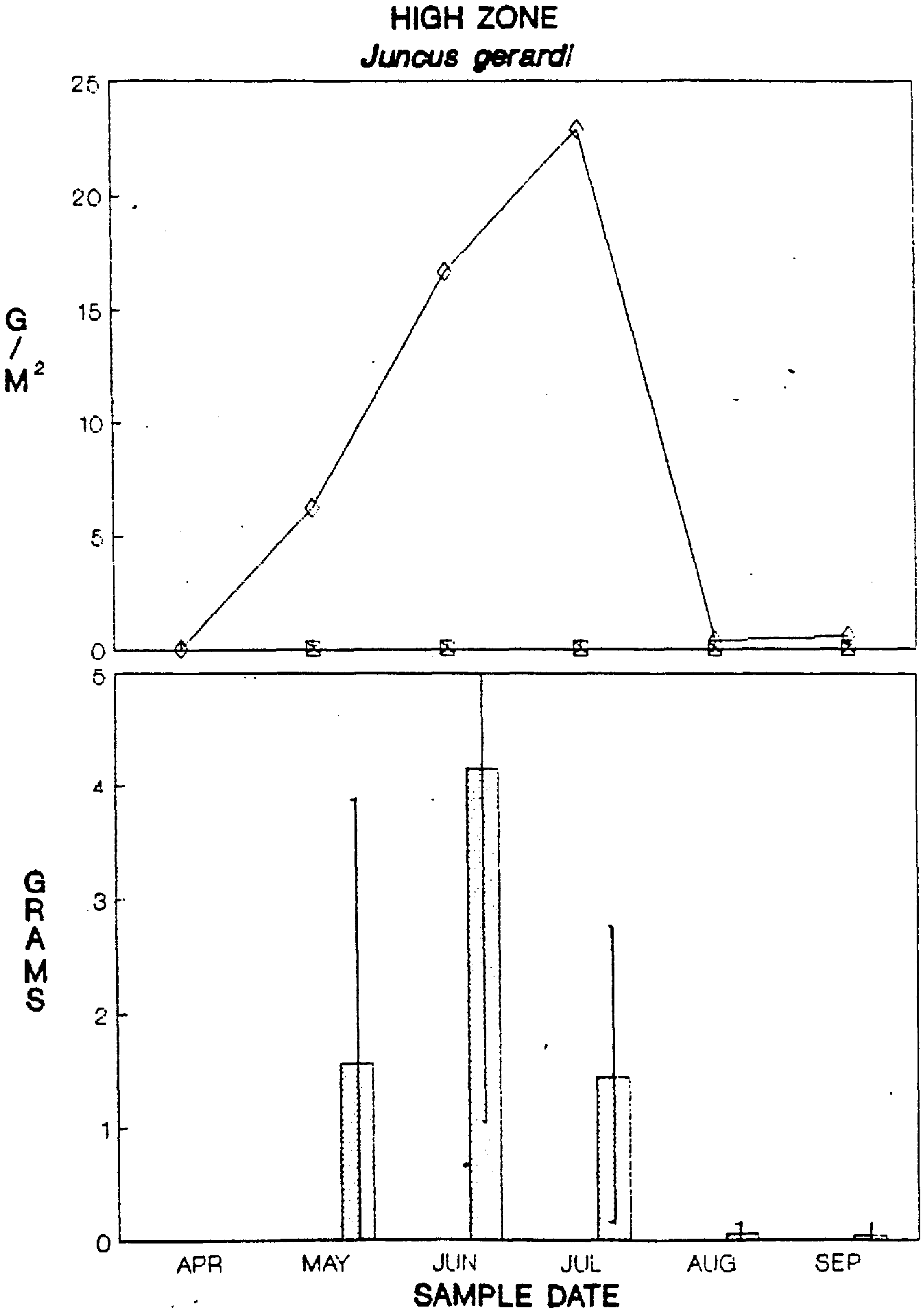

HIGH ZONE
MID ZONE
LOW ZONE
PERCENT BIOMASS
0
20
40
60
80
100
SEP
SAMPLE DATES

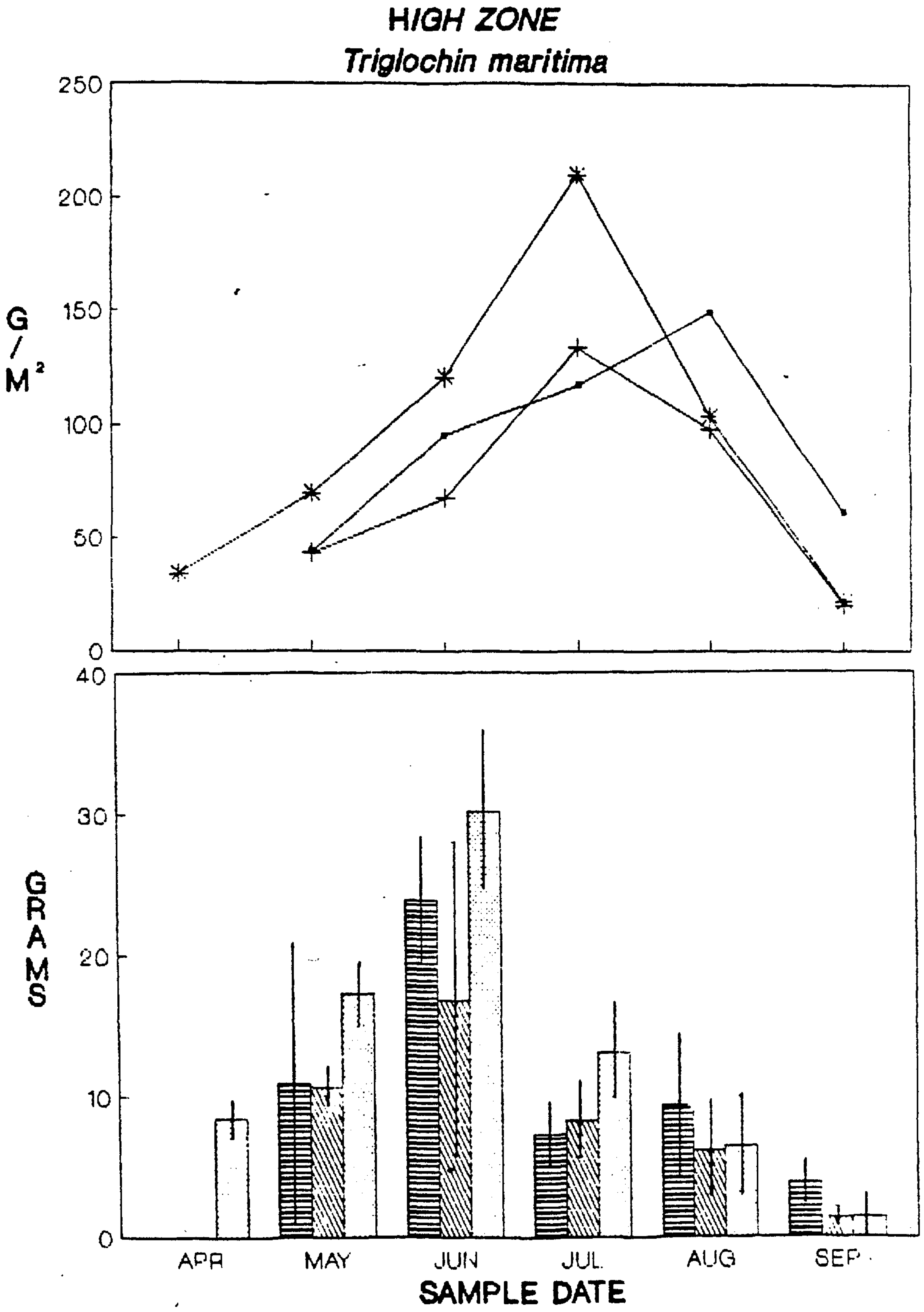

LOW ZONE

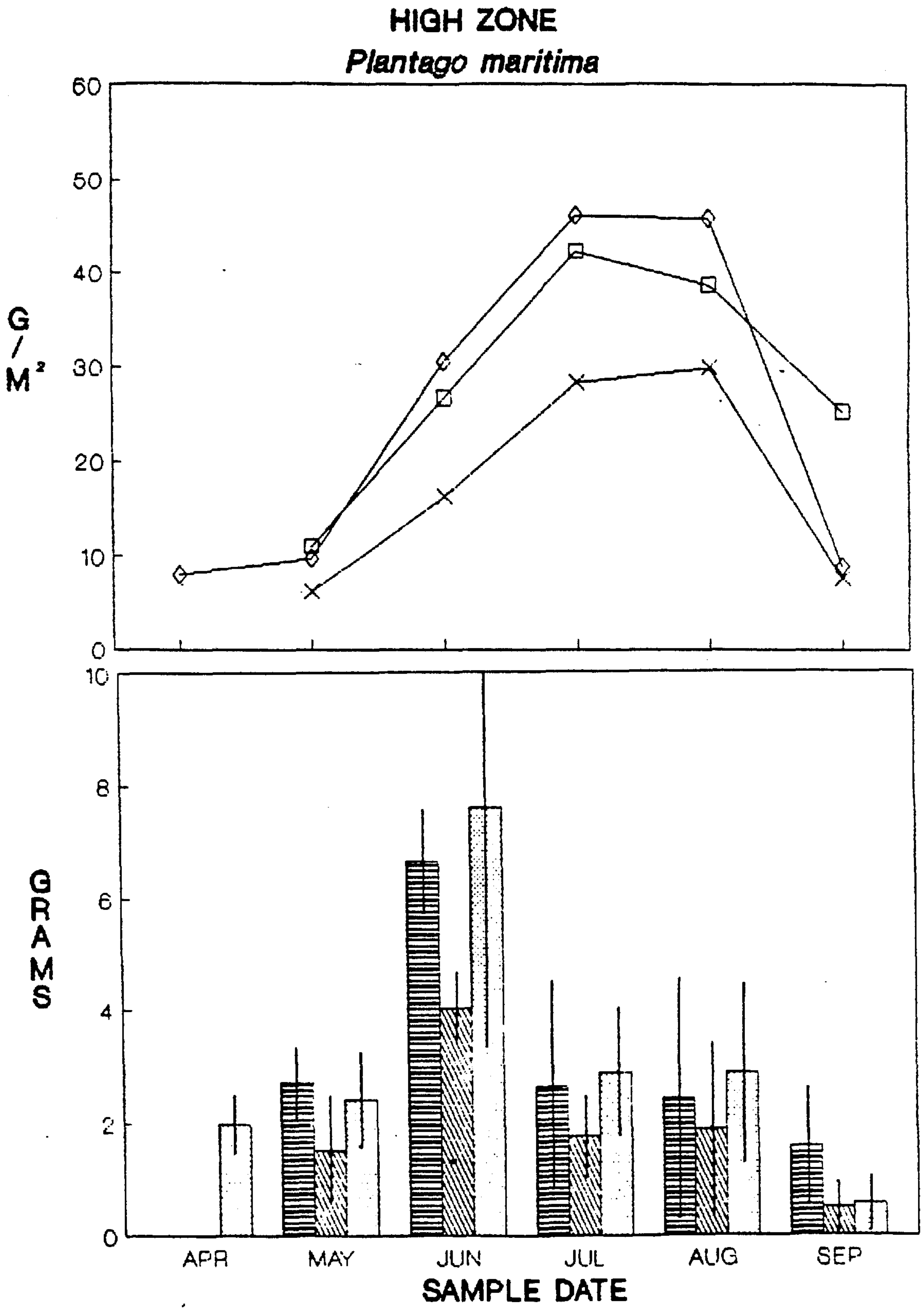
Spartina alterniflora

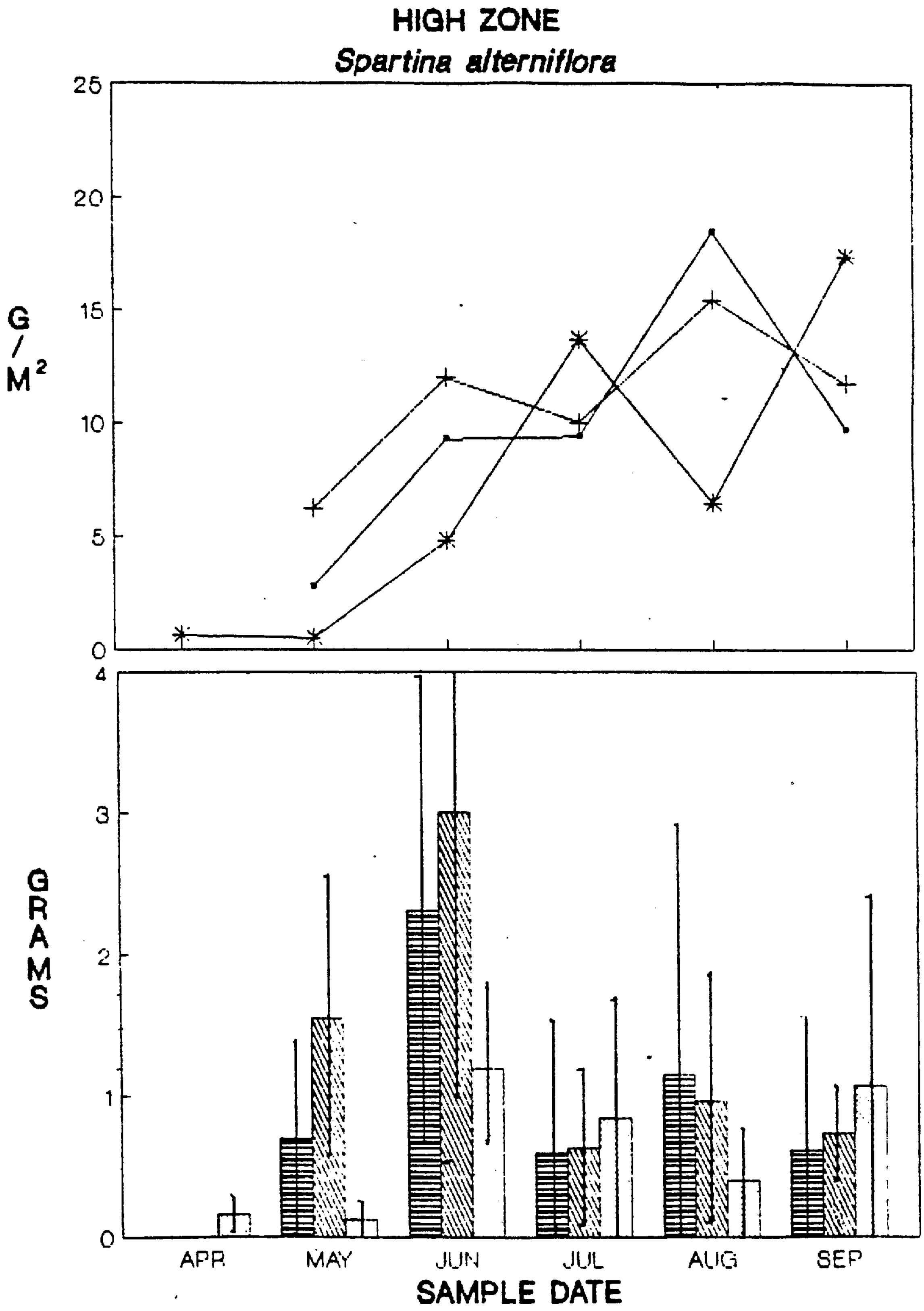

LOW ZONE
Ascophyllum nodosum
G / M²
0
100
200
300
400
500
600
GRAMS
0
20
40
60
80
APR
MAY
JUN
JUL
AUG
SEP
SAMPLE DATE


MID ZONE
Spartina patens
G / M²
400
300
200
100
0
GRAMS
35
30
25
20
15
10
5
0
APR
MAY
JUN
JUL
AUG
SEP
SAMPLE DATE

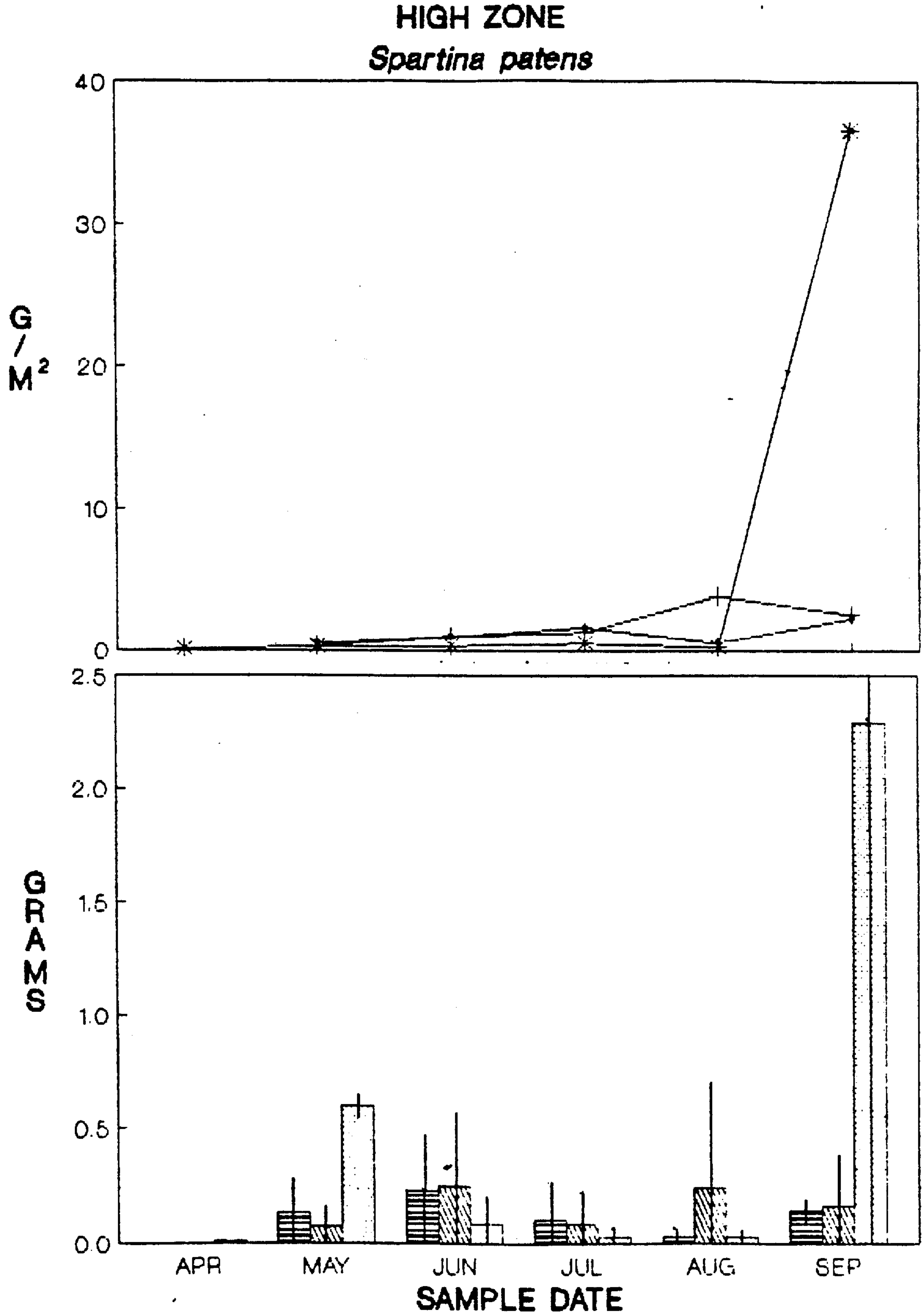

HIGH ZONE
Juncus gerardi
G / M²
25
20
15
10
5
0
GRAMS
5
4
3
2
1
0
APR
MAY
JUN
JUL
AUG
SEP
SAMPLE DATE

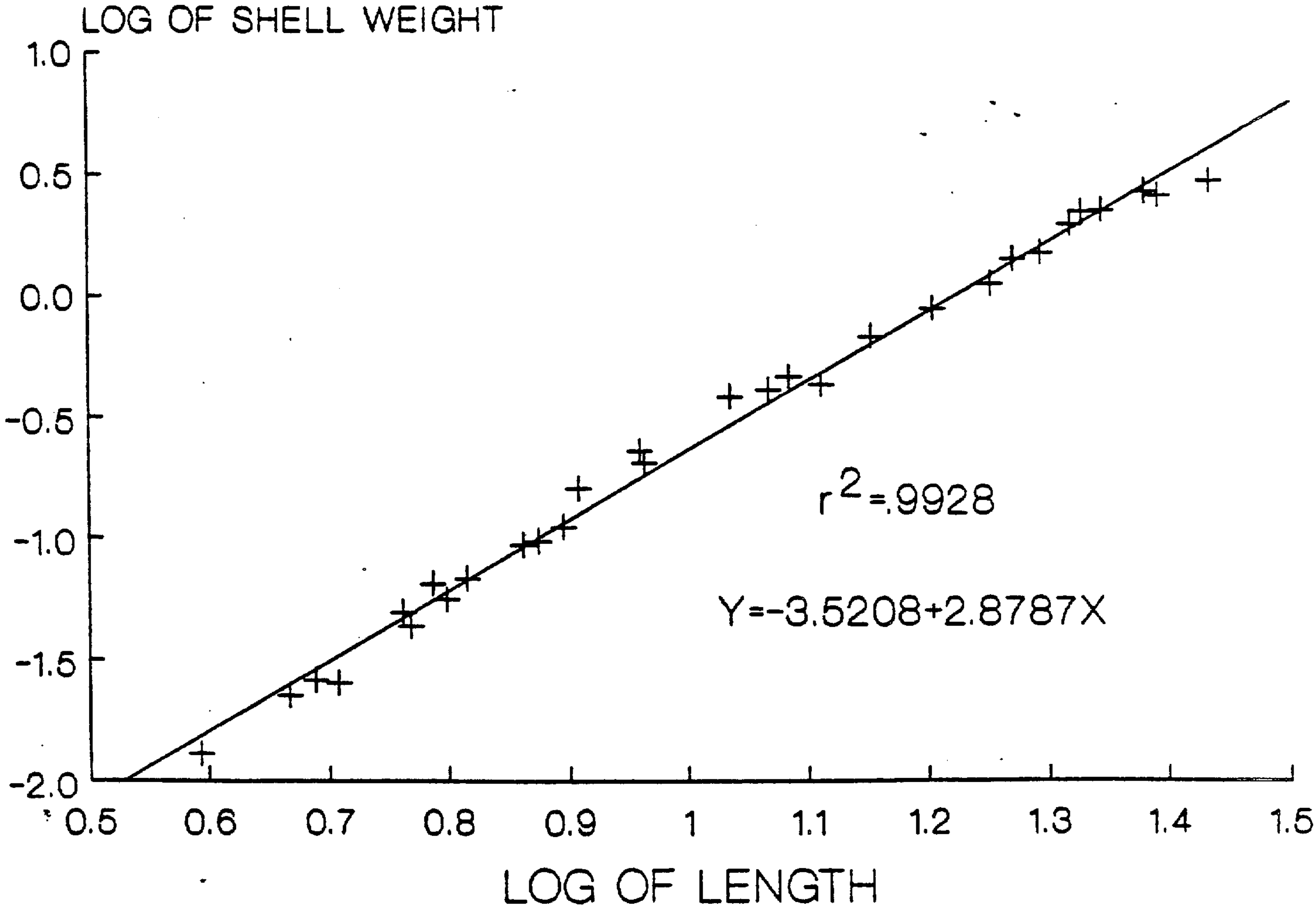

HIGH ZONE
Triglochin maritima
250
200
150
100
50
0
G / M²
40
30
20
10
0
GRAMS
APR
MAY
JUN
JUL
AUG
SEP
SAMPLE DATE

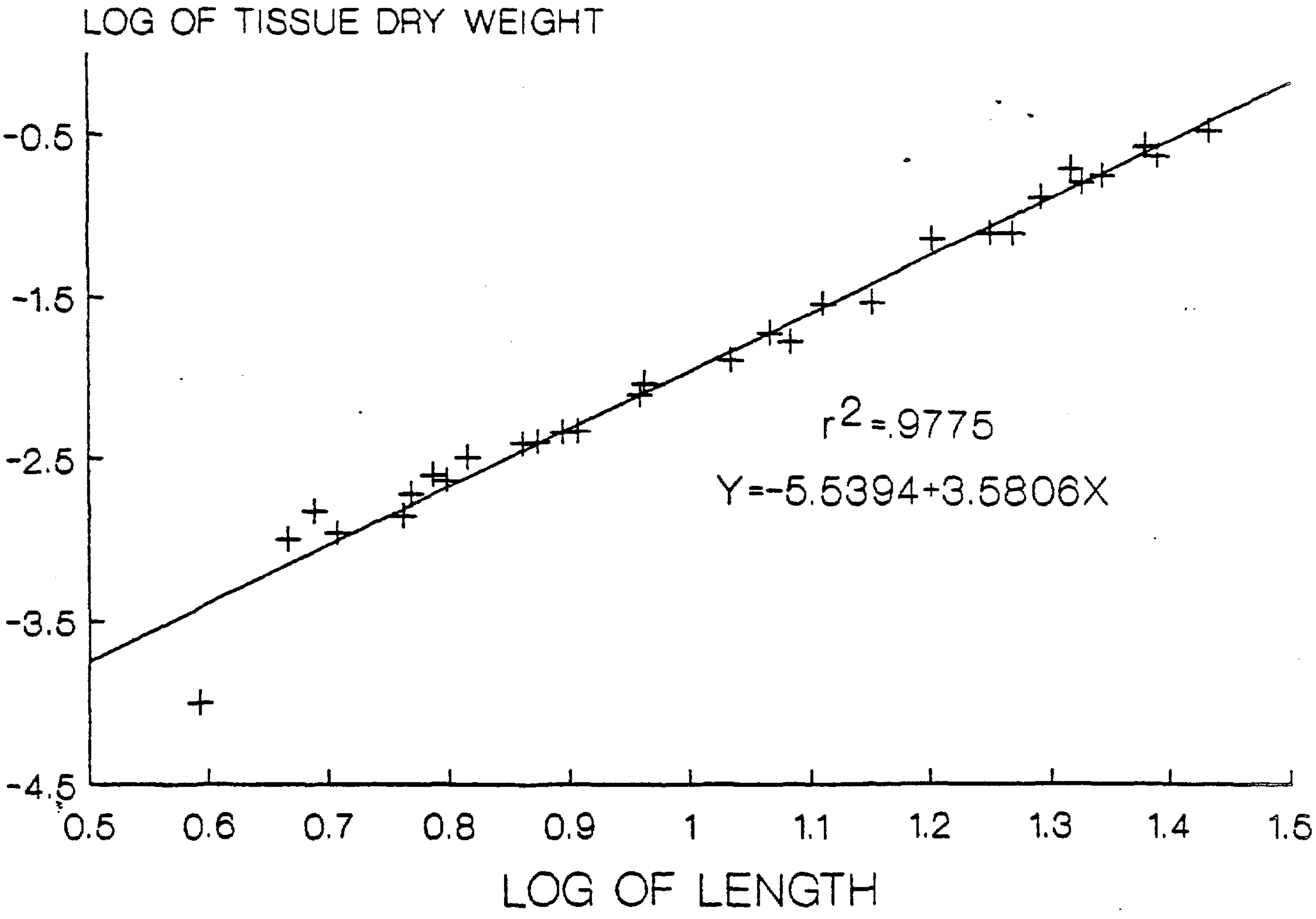

HIGH ZONE
Plantago maritima
G / M²
0
10
20
30
40
50
60
GRAMS
0
2
4
6
8
10
APR
MAY
JUN
JUL
AUG
SEP
SAMPLE DATE

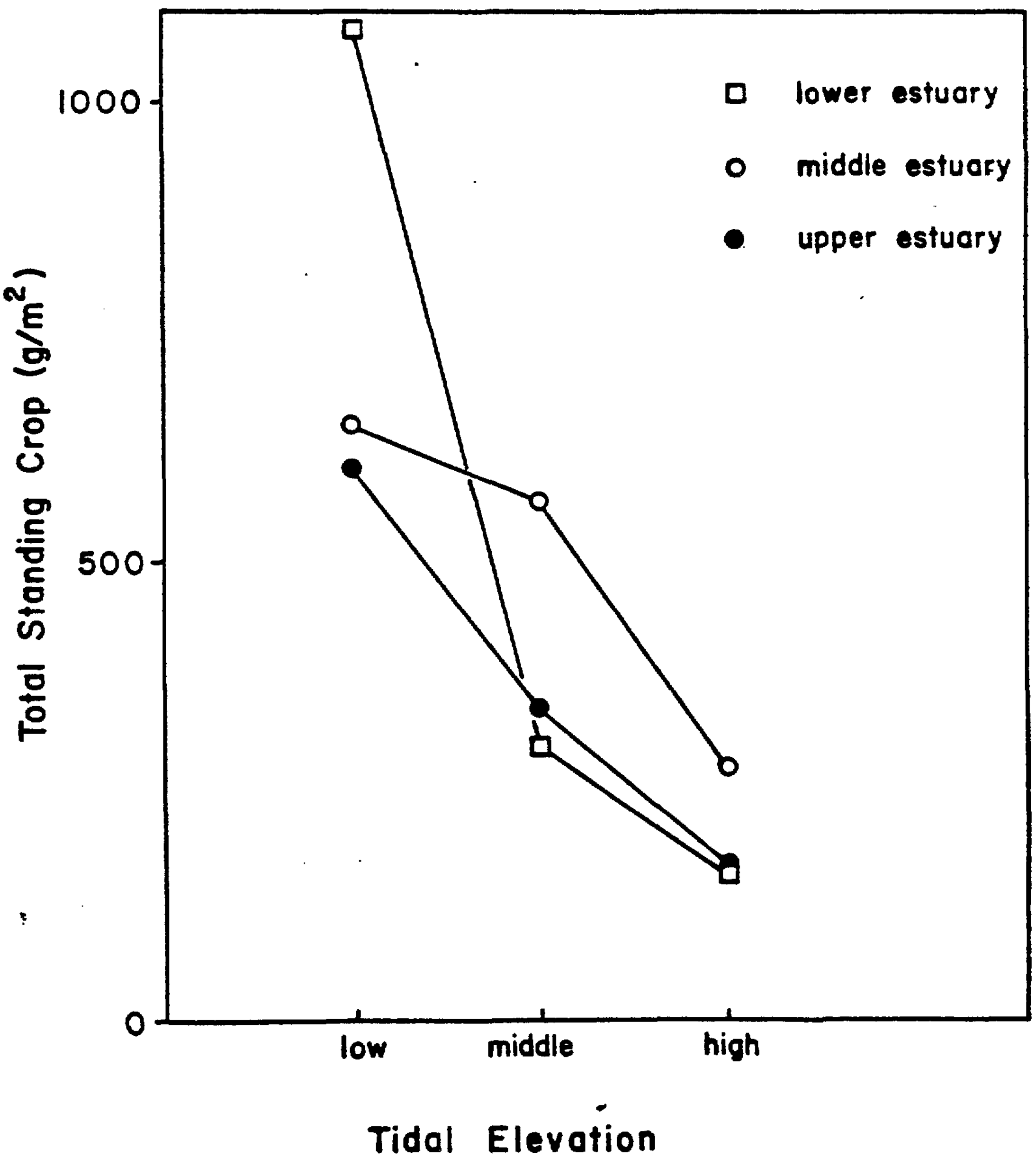


HIGH ZONE
Spartina alterniflora


HIGH ZONE
Spartina patens
G/M²
40
30
20
10
0
GRAMS
2.5
2.0
1.5
1.0
0.5
0.0
APR
MAY
JUN
JUL
AUG
SEP
SAMPLE DATE


LOG OF SHELL WEIGHT
1.0
0.5
0.0
-0.5
-1.0
-1.5
-2.0
0.5
0.6
0.7
0.8
0.9
1
1.1
1.2
1.3
1.4
1.5
LOG OF LENGTH
r2=.9928
Y=-3.5208+2.8787X


LOG OF TISSUE DRY WEIGHT
-0.5
-1.5
-2.5
-3.5
-4.5
0.5
0.6
0.7
0.8
0.9
1
1.1
1.2
1.3
1.4
1.5
LOG OF LENGTH
r2=.9775
Y=-5.5394+3.5806X



Total Standing Crop (g/m²)
1000
500
0
low
middle
high
Tidal Elevation
□ lower estuary
○ middle estuary
● upper estuary