Craig Dennis Zamuda, SEASONAL GROWTH AND DECOMPOSITION OF *Vallisneria americana* IN THE PAMLICO RIVER ESTUARY. (Under the direction of Graham J. Davis) Department of Biology, December 1976.

Seasonal rates of growth and production and of inorganic and organic matter losses were determined for *Vallisneria americana* Michx. in the Pamlico River estuary of North Carolina.

A direct marking technique was utilized to measure *in situ* changes in biomass and leaf dynamics for plants from two dissimilar locations. The upriver study site was characterized by extensive plant beds and low salinities (0-5 ^{o}/oo) while at the downriver site, plants were less dense and exposed to higher salinities (2-11 ^{o}/oo). The mean rate of leaf elongation was 5.6 mm/day for both locations, although elongation was as rapid as 9 mm/day. Plants produced a new leaf on the seasonal average of every 9.9 days, with greater rates for the downriver plants (8.2 days) as compared to those upriver (11.6 days). The seasonal mean production value was 2.3 mg ODW (organic dry weight)/plant·day, with values generally greater downriver. A July depression in growth and production coincided with peak flower and fruit production, subsequently increasing to maximum values in August. Turnover rates averaged 1.5%/day resulting in a total plant turnover of 67 days. Plant densities increased to an August maximum of 280 plants/m^2 with a seasonal mean of 200 plants/m^2. This resulted in a production estimate of 0.47 g ODW/m^2·day or a seasonal value of 115 g ODW/m^2. Total estuarine production was approximately 403 MT ODW.

Plants were harvested seasonally from the above stations and maintained submerged in nylon bags (mesh=1mm), with a littoral and midriver decay site at each station. Summer decay was rapid with as much as 70% of the organic matter lost within the first two weeks. Decay coefficients for spring and summer material (k=19.5) were greater than winter material (k=10.0). Newly harvested plants had maximum levels of inorganic nutrients in winter: N, 4.3% ODW; P, 0.6%; Ca, 0.5%; Mg, 0.4%; K, 3.7%; and Na, 2.3%. During decay N and P concentrations remained essentially constant or gradually increased on the basis of ODW remaining. Sodium and K levels fluctuated, with concentrations increasing in spring and decreasing throughout the other seasons. Calcium levels initially increased and then decreased while Mg concentrations remained constant except for a summer decline.

SEASONAL GROWTH AND DECOMPOSITION
OF *Vallisneria americana*
IN THE PAMLICO RIVER ESTUARY

A Thesis
Presented to
the Faculty of the Department of Biology

In Partial Fulfillment
of the Requirements for the Degree
Master of Science in Biology

by
Craig Dennis Zamuda
December 1976

SEASONAL GROWTH AND DECOMPOSITION
OF *Vallisneria americana*
IN THE PAMLICO RIVER ESTUARY

by

Craig Dennis Zamuda

APPROVED BY:

SUPERVISOR OF THESIS Graham J. Davis

Dr. Graham J. Davis

CHAIRPERSON OF THE DEPARTMENT OF BIOLOGY

James S. McDaniel

Dr. James S. McDaniel

DEAN OF THE GRADUATE SCHOOL

Joseph G. Boyette

Dr. Joseph G. Boyette

ACKNOWLEDGEMENTS

Grateful acknowledgement is made to Dr. Graham J. Davis. my thesis supervisor, who made this thesis possible. I would also like to thank the other members of my committee, Drs. Clifford Knight, Bernard Kane and Edward Ryan, for their support and suggestions.

Tommy Vicars, Dave Davis, Samuel Kirby, Martha Jones, Mary Strickland and my family contributed to the success of this project through their assistance both in the laboratory and the field.

This research was supported in part by funds provided by the Office of Water Research and Technology of the U.S. Department of the Interior, as authorized under the Water Resources Research Act of 1964, as amended, the Water Resources Research Institute of The University of North Carolina.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Within the littoral of shallow marine and estuarine waters, aquatic macrophytes[1] often form a productive system which supports a diversity of associated organisms.

The importance of submersed macrophytic vegetation in coastal ecosystems has been recognized for years. Petersen (1918) suggested that vascular plants were responsible for a large proportion of net primary productivity in shallow coastal waters. Boysen-Jensen (1911) indicated that organic detritus from the decay of submersed vegetation was the basic source of nutrition of animals in Danish marine waters. Blegvad (1914) stated that detritus formed the principal food of nearly all invertebrates of the Danish sea bottom, with live benthic plants of secondary importance. He concluded that live phytoplankton were virtually valueless as benthic invertebrate food.

Small fishes and invertebrates are common in submersed plant communities (Wood et al., 1967; Odum et al., 1973). Prescott (1973) has reported that certain families of fish including the Centrarchidae and Percidae, utilize the aquatic plant beds as nesting areas during the spawning seasons.

Shoots retard currents and increase sedimentation rates while the roots stabilize the sediments. Leaves may form a substrate for large numbers of epiphytic organisms which may be comparable in biomass to the leaf weight.

---

[1] The term aquatic macrophyte as used in this paper refers to the macroscopic forms of aquatic vegetation and includes macroalgae, pteridophytes and the true angiosperms.

Aquatic macrophytes may also function in cycling of inorganic nutrients between the sediment and water column. McRoy and Barsdate (1970) reported that *Zostera marina* (eelgrass) can absorb phosphorus both through the leaves and the roots. Thus phosphorus absorbed through roots may be released through leaves directly or indirectly through decay, thereby returning phosphate from the sediment to the water column. Nitrogen may also follow such pathways (McRoy and Goering 1974).

While alive submersed macrophytes are consumed by only a limited number of organisms. Although waterfowl (Martin and Uhler 1931) and other animals common to the estuarine systems such as *Mugil cephalus* (striped mullet) may feed directly on submersed macrophytes (Odum 1970), most of the primary material enters the detrital food chain. Generally less than 10% of plant production is removed by grazing. The lack of grazing has been attributed to a combination of resistant tissues, coverings of unpalatable waxes and concentrations of noxious compounds (Odum et al., 1973). With little grazing, detrital formation becomes the chief link between primary producers and consumers in the estuary (Odum and de la Cruz 1963, 1967; Teal 1962).

Various species of aquatic macrophytes have been used as feed supplements for livestock (Bauersfeld et al., 1969), as fertilizers (Van Breedveld 1966) and somewhat less successfully as indicators of water quality (Adams et al., 1973).

The detritus plus associated microbes active in the decomposition of the plant material is the basic food source of consumers (Odum et al., 1973). Extensive analyses of gut contents by Darnell (1967) and Odum (1970) provide compelling evidence of the importance of organic detritus as an estuarine food source.

In the Pamlico River estuary N.C., the main source of food is probably allochthonous organic matter (mainly from the Tar River). Although the allochthonous input of matter into the estuary is voluminous, much of it is probably refractory (humic substances, etc.) and passes through unutilized (Harrison and Hobbie 1974). Harrison and Hobbie (1974) indicated that within this estuary the detrital pathway is more important than direct feeding on phytoplankton by herbivores. Thus the submersed aquatic macrophytes may form a major food source. This contribution of organic carbon is believed more important than in many estuaries since there are few low marshes flooded and flushed by tidal currents (Copeland and Hobbie 1972).

Research by others (Harwood 1975, Reed 1976, Vicars 1976) on the submersed macrophytes of the Pamlico River estuary has dealt with diversity, biomass and temporal as well as spatial distribution of the plant beds. Their work indicates that Vallisneria americana Michx. (wild celery) was the dominant species in this estuary with the widest distribution and comprises about 90% of the total submersed rooted biomass.

The foregoing suggests several possible areas of investigation in relation to the role of submersed macrophytes in energy flow and nutrient cycling within the Pamlico River estuary. The goals of this research were to determine: 1) the dynamics of growth and production of Vallisneria in the macrophyte beds; 2) the conversion rate of living material into detritus; 3) the changes in the chemical composition (P, N, Ca, Mg, K and Na) of the plant material as it decays; 4) environmental conditions affecting the distribution of macrophyte beds.

Growth and Production

Problems have existed in obtaining reliable estimates of the primary production of aquatic macrophytes. The ideal submersed aquatic macrophyte for ecological studies would be one that begins growth each year from seeds, loses no biomass during the season to organic leaching, grazing, death, etc. and develops a well-defined maximum biomass by the end of the growing season. One would need only to determine this terminal biomass to know the net productivity of the species. Plants always vary from this ideal. Westlake (1965) discussed such variations in rooted aquatic plants.

Methods used to measure carbon assimilation by gas exchange are inadequate. Hartman and Brown (1967) have shown that this technique is unreliable since internal recycling of CO_2 and O_2 occurs in the lacunae of the plants. Zieman (1968) developed a method for measuring production of the marine angiosperm, *Thalassia testudinum*, in which he marked standing leaves at the base and later harvested the plants to determine growth, appearance of new leaves and loss of old senescent leaves which are continually sloughed throughout the growing season. Most of the growth occurred at the base of the leaves and could be measured by determining the distance between the mark's new location and the base of the plant. This direct marking technique of measuring net production has been described by an international group (McRoy 1973) as the best method available for rooted aquatic macrophytes and, with small modifications, was utilized for this study of *Vallisneria*.

Decomposition

The nylon mesh bag technique has been employed to determine conversion rates of living material into detritus by following the weight loss and nutrient change of the confined material (Burkholder and Bornside 1957, Odum and de la Cruz 1967, Kormondy 1968, Zieman 1967). Although reported as decomposition, Kormondy (1968) indicated that this nylon bag technique actually measures weight loss as a result of loss of fragments through the bag, solution of soluble substances and of enzymatic decomposition by microorganisms. However, Boyd (1970) pointed out that the weight loss does represent either true decomposition or the release of soluble organic compounds, dissolved inorganic nutrients, or small detritus and is a meaningful measure of the degradation of macrophytes. This method yields a good indication of relative rates of decomposition in different species.

The term "organic detritus" has been defined by Odum and de la Cruz (1963) as the particulate organic material originating from the dead bodies, nonliving fragments and excretions of living organisms. For simplification the term debris is used in this report to include particulate plant material such as leaves and rhizomes at various stages of decay within the decay bags. Autolysis, hydrolysis, oxidation, mechanical attrition and grazing result in the degradation of plant debris until particle size is reduced to less than 1 mm. Material of this size and its associated microorganisms is referred to as detritus within the context of this paper. The lower limit of particulate detritus herein defined is between 0.5-1 u. This size limit corresponds roughly to the size of the smallest particles visible in a light microscope and capable of being taken up by filter-feeding organisms (Jorgensen 1966).

The upper limit has been arbitrarily chosen as 1 mm because of the comparatively small number of detritus particles that exceed this dimension.

STUDY AREA

The Pamlico River estuary extends some 60 km inland from the Pamlico Sound where it joins its main tributary, the Tar River, at Washington, N.C. (Figs. 1 and 2) The Tar River arises in the Piedmont and drains southeastward across the Coastal Plain. Its watershed of around 8000 km^2 consists mostly of forest and farmland with a principally rural population. Tobacco, requiring heavy N-fertilization, is the chief agricultural commodity.

According to the functional classification of ecosystems based on energy stress (Odum et al., 1973) the Pamlico River estuary is described as a natural temperate oligohaline ecosystem with a saltwater shock zone, seasonal programming and migrating stocks. Gradients of wind and wave stress as well as turbidity and nutrients are characteristic of this estuary.

Salinity is controlled primarily by the degree of freshwater discharge from the Tar River and the Coriolis force which deflects river water to the south shore. Higher salinities are usually found on the north shore of the estuary and on occasions in bottom waters, but a well-defined salt wedge is not usually present. Salinity varies between 0-18 $^{o}/oo$ and temperature from 3-34 ^{o}C.

Turbidity is generally high in the upper reaches of the estuary but decreases downstream as the suspended sediment load from the Tar River settles out.

Estuarine phosphorus levels are high in association with sources such as urban sewage, runoff from fertilized farms and phosphate mining activities (Texasgulf, Inc.) on the south shore of the estuary. Nitrogen concentrations are controlled to some extent by the flow of the Tar River (Hobbie et al., 1972).

Fig. 1. The northern and central coastal regions of North Carolina

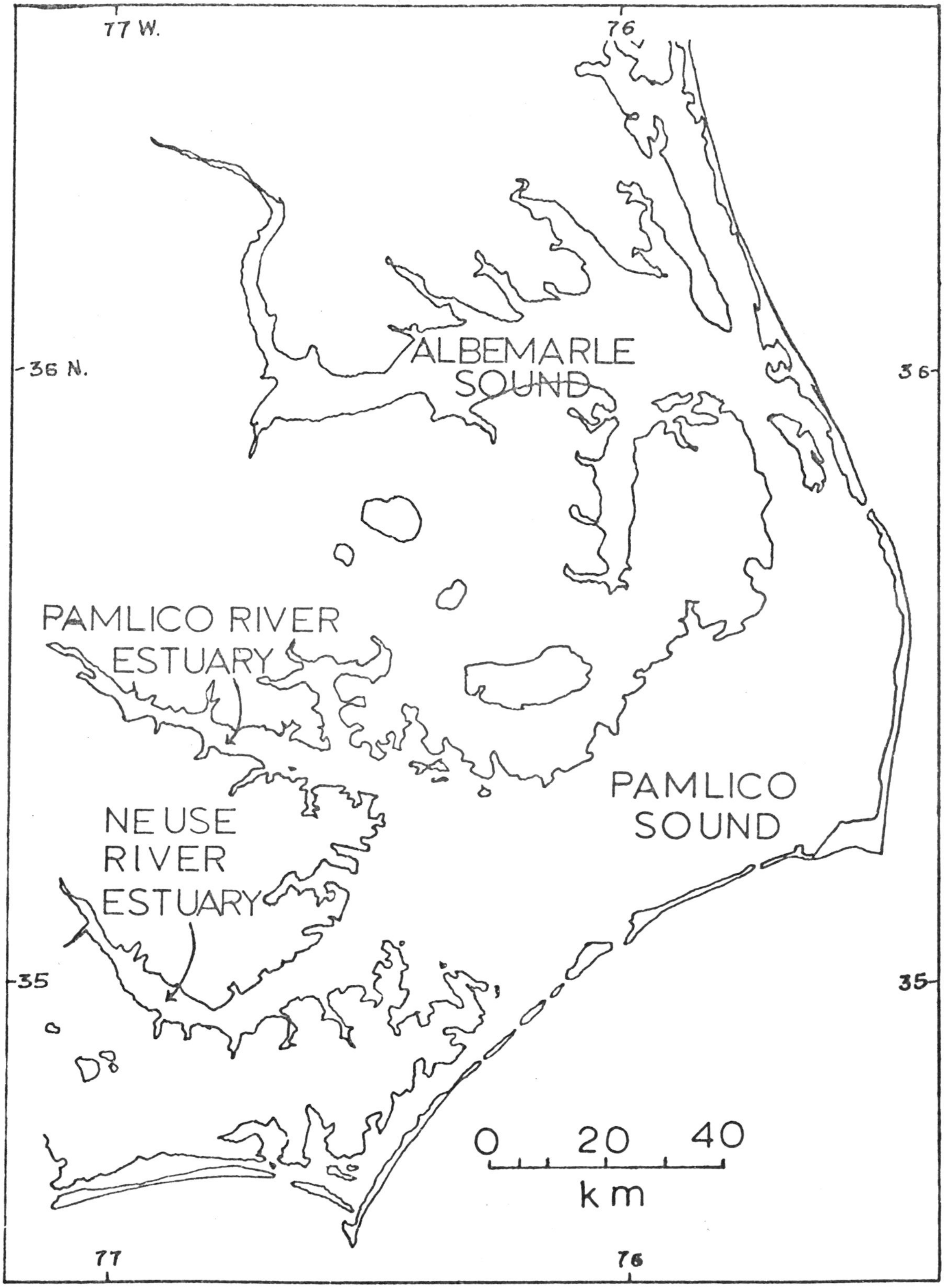
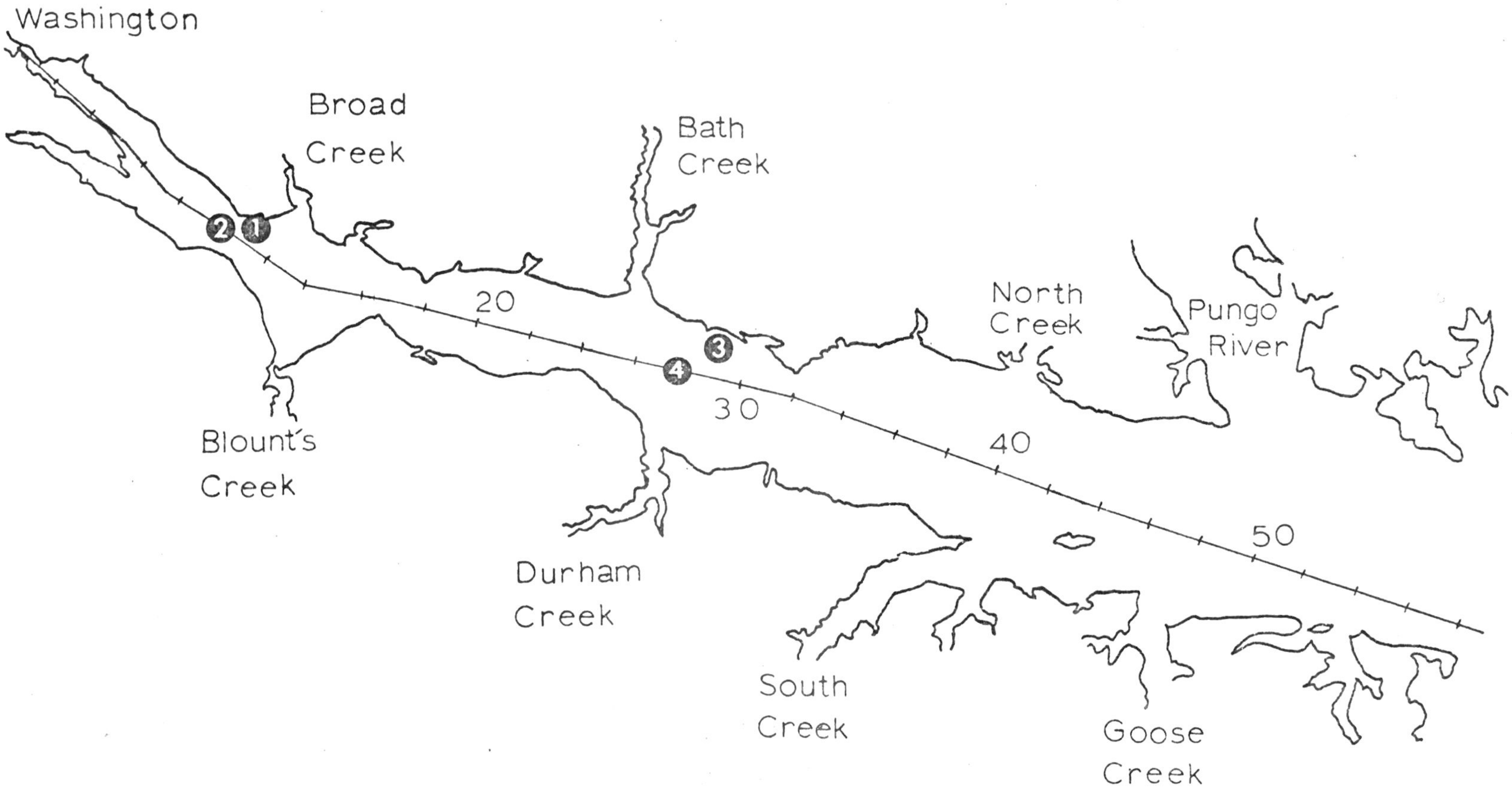

77 W.
76
36 N.
36
35
35
77
76
ALBEMARLE SOUND
PAMLICO RIVER ESTUARY
NEUSE RIVER ESTUARY
PAMLICO SOUND
0 20 40
km

Fig. 2. The Pamlico River estuary. River km as shown begin at the Pamlico River estuary-Tar River concluence and generally follow channel markers. Locations: Upriver station (1-littoral site, 2-midriver site); Downriver station (3-littoral site, 4-midriver site).


Washington
Broad Creek
Bath Creek
North Creek
Pungo River
Blount's Creek
Durham Creek
South Creek
Goose Creek
20
30
40
50
2
1
3
4

Nitrate levels within the upper parts of the estuary can exceed 100 ug-at./1 while near the mouth, levels may fall below 1 ug-at./1. Dissolved organic nitrogen is the most abundant form of nitrogen but most is not thought to be biologically available.

Phytoplankton blooms occur in the middle reaches of the estuary each winter. These blooms (mainly of the dinoflagellate, Peridinium triquetrum) appear to be associated with the higher nitrate concentrations. Phytoplankton productivity has been estimated to be 40-80 g $C/m^2 \cdot yr$. (Crawford et al., 1974).

Although there are essentially no emergent or floatin-leaved macrophytes within the estuary, submersed aquatic macrophytes are present within the upper half of the estuary and exhibited seasonal fluctuations in biomass (Harwood 1975, Reed 1976, Vicars 1976). Species present include Potamogeton perfoliatus var. bupleuroides (Fern.) Farw., Ruppia maritima L., and Najas guadalupensis (Spreng.) Magnus. The dominant rooted macrophyte was Vallisneria americana Michx. having a distribution within the littoral from just below Washington (Fig. 2, km 4 N) to the Bayview (Fig. 2, km 29 N) and Garrison Pt. (Fig. 2, km 28 S).

Textual Note: Locations in the text are cited according to the following example; (km 10 N). This notation designates a point on the shoreline of the north shore of the estuary 10 km (by channel of river) downstream from the U.S. highway bridge at Washington, North Carolina (See Fig. 2).

MATERIALS AND METHODS

Growth Dynamics and Production

Based upon observations during the previous growing season, two study areas within the Pamlico River estuary were chosen. The upriver station (km 10 N, Fig. 2) was representative of the upper regions of the estuary with extensive *Vallisneria* beds (Fig. 3) and large standing crop values of 31 g organic dry weight (ODW)/m^2. Plants here had long leaves (up to 1.7 m) and were the dominant form in this estuary. The downriver station (km 29 N, Fig. 2) represented the downstream limit of distribution of *Vallisneria* within the Pamlico River estuary. Plant beds were scattered (Fig. 4) with less standing crop (21 g ODW/m^2) and exposed to higher salinities (Fig. 5). Wave action was greater and the substrate coarser than at the upriver station. Plants had a shorter leaf form (up to 30 cm) with fragmented tips.

The beds were studied for the natural growth period (March through November 1975) on a bimonthly basis utilizing triplicate quadrats at each station. A square frame (625 cm^2) was placed within the plant bed and all of the leaves inside the quadrat were marked by punching a small hole (less than 0.5 mm in diameter) near the base of each leaf. The number of plants and leaves present was recorded. After 4 to 14 days, depending upon the rate of growth, plants within the quadrat were harvested and returned to the laboratory in water-filled buckets.

In the laboratory the total number of original and new leaves (which appeared since the time of marking) were recorded for each plant. The total length of the original leaves (those with a mark), as well as the distance from the base of the leaf to the mark, was measured. This latter measure-

Fig. 3. Aerial photograph taken from 1333 m altitude at upriver station (km 10 N).

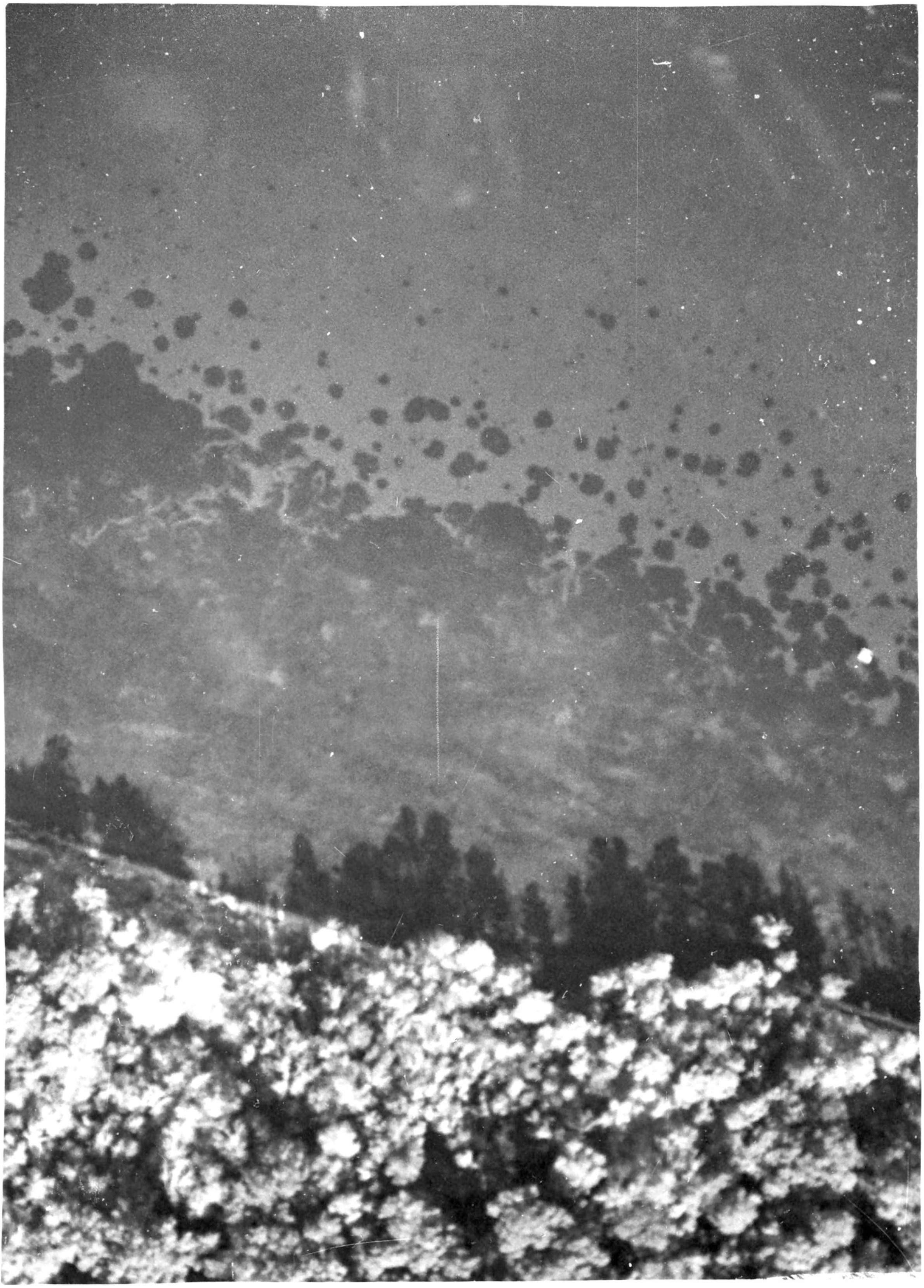


Fig. 4. Aerial photograph taken from 666 m altitude at downriver station (km 29 N).

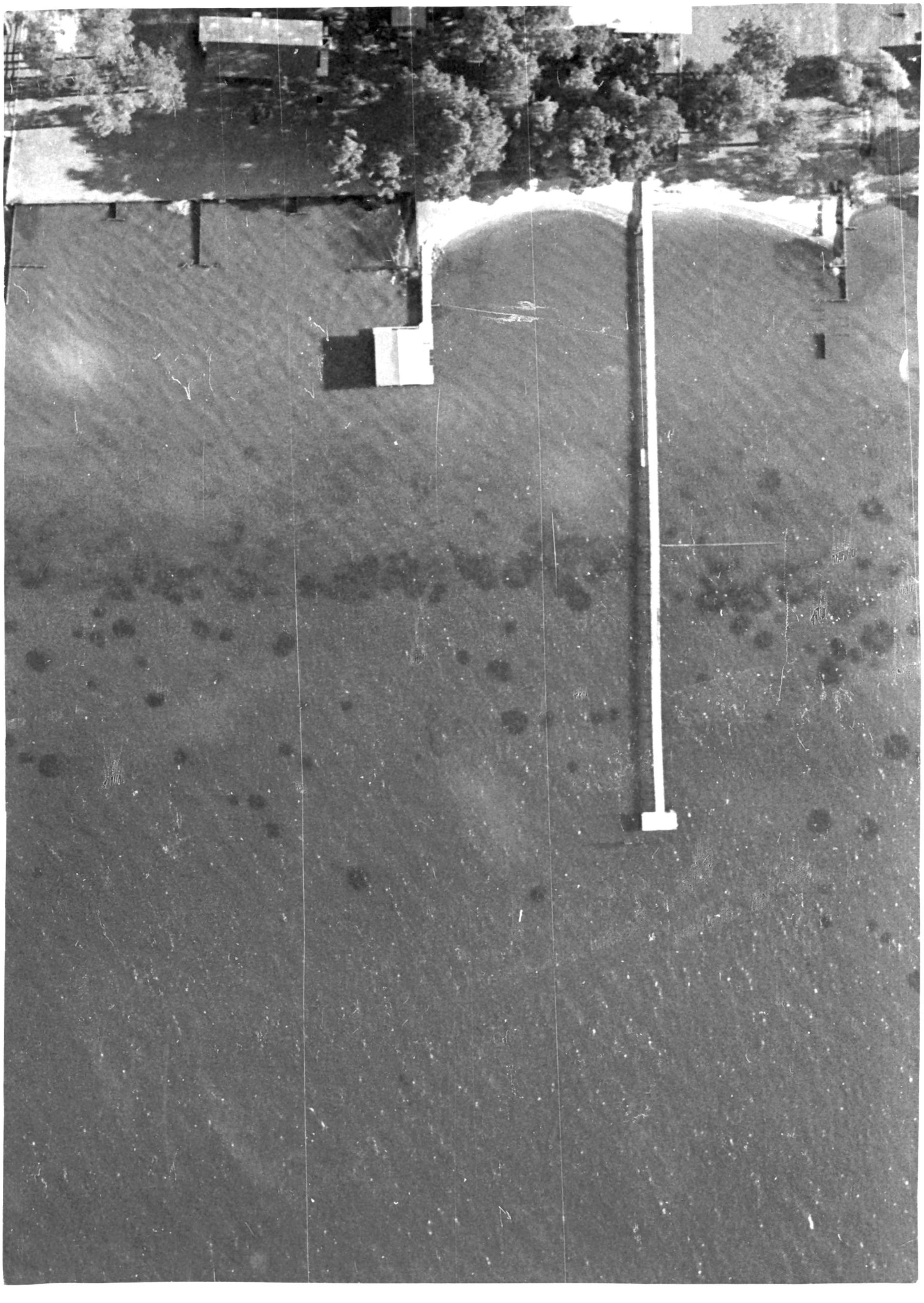
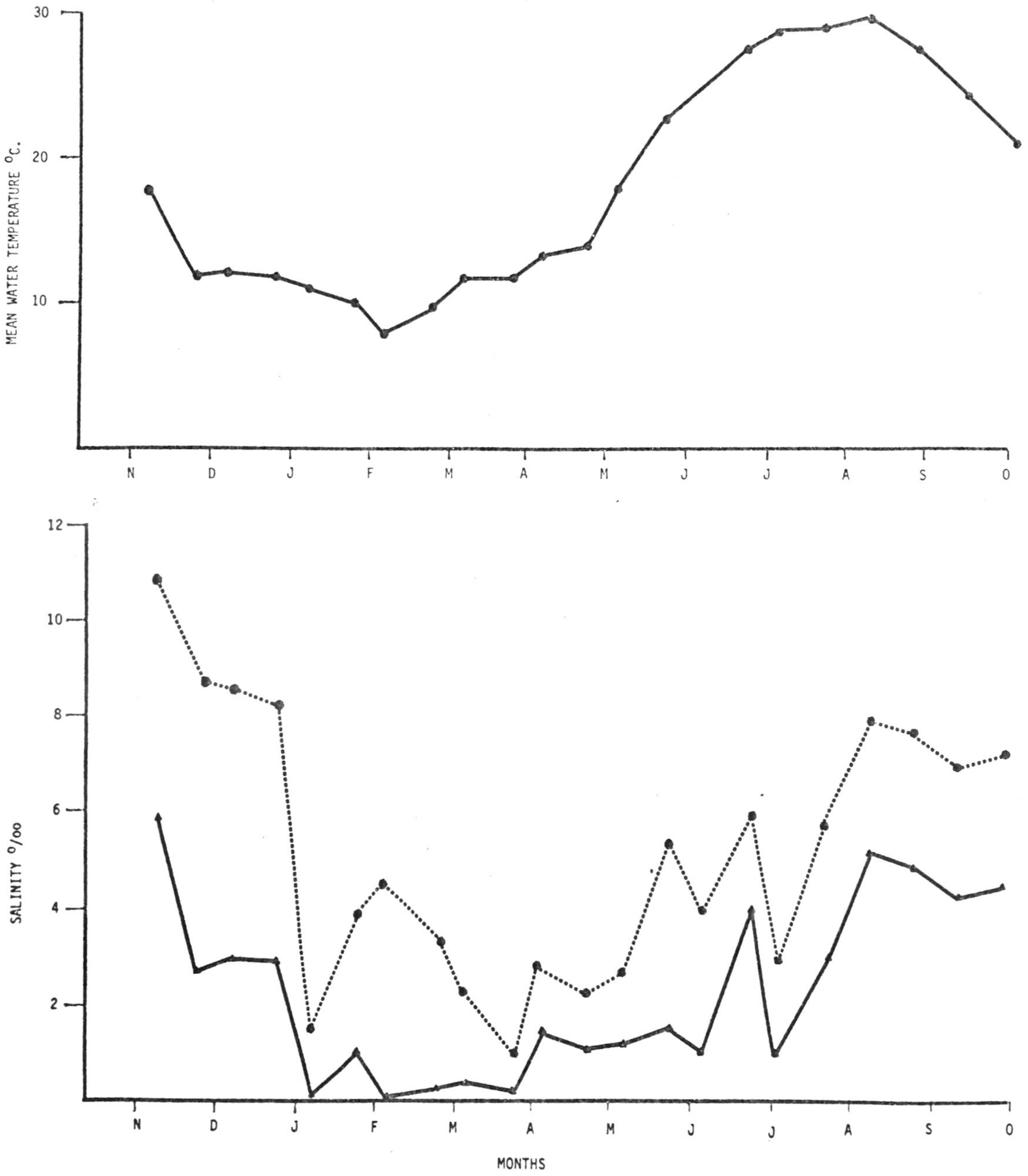


Fig. 5. Upper- Mean surface water temperatures for 7 November 1974 to 10 October 1975, in the Pamlico River estuary. Lower- Surface salinities (^{o}/oo) for 7 November 1974 to 10 October 1975, in the Pamlico River estuary. (Upriver:-▲- ; Downriver:-●--).


30
20
10
MEAN WATER TEMPERATURE °C.
N
D
J
F
M
A
M
J
J
A
S
O
12
10
8
6
4
2
SALINITY °/oo
N
D
J
F
M
A
M
J
J
A
S
O
MONTHS

ment represented new growth (elongation) of the original leaves. For new leaves (those without a mark) the entire leaf represented new growth that appeared since the time of marking and this length was recorded. Plants were then seperated into three components: 1) roots and rhizomes; 2) original leaf material; and 3) new growth of both marked and unmarked leaves. These fractions were washed thoroughly with a jet of water to remove adhering sand and loosely bound epiphytes and oven-dried at 85 °C for a constant dry weight. Samples were then ground in a Wiley mill with a #20 mesh stainless steel screen and dry ashed at 480 °C for 3 hrs in a muffle furnace to determine ODW. The weight of the new growth fraction represented new production.

Community dynamics of <u>Vallisneria</u> was associated with changing numbers of leaves and plants. If the number of leaves and plants increased between marking and harvesting, the community was increasing in density.

To determine the main region of growth of <u>Vallisneria</u> leaves, a hole was punched at the base of each leaf and successively upward at 10 cm intervals for 10 plants at each station. After a period of 1 wk the distance between each mark was measured. Any increase in length would represent growth in that region of the leaf.

Decomposition

The rate of decomposition for <u>Vallisneria</u> was determined by enclosing freshly harvested plant material within nylon mesh bags (25 X 30 cm). These bags with an aperture of 1 mm were a restraining device but water circulation occurred. The decay bag normally used were tightly closed and prohibited the entry of any organism unable to penetrate the 1 mm mesh.

To ascertain the effect of restricting the larger organisms from the plant material both open and closed bags were used in one experiment. The open bag was designed such that organisms could enter through the overlapping side flaps without loss of plant material.

Vallisneria was harvested from several spots within the beds of the upriver and downriver stations. The plants were carefully uprooted by hand with the aid of SCUBA and transported in water-filled buckets to the laboratory. Plant material was "spin-dried" (5 minute spin in a domestic washing machine) to eliminate excess water, rapidly weighed into 20 g fresh weight (FW) batches and distributed evenly and loosely within the decay bag. These bags were kept in the water-filled containers until returned to the original harvest station and tied to stakes at both the littoral and midriver sites.

Initial dry weights (DW) and concentrations of inorganic nutrients were determined from analysis of 10 aliquots (20 g FW/aliquot) of identical material for each station. Periodically (1, 2, 4, 8, 12 wks) three bags were collected from each decay site for laboratory analysis. The material was washed and dry weights obtained as described earlier. Total N was analyzed with a Coleman Nitrogen Analyzer (Model 29) utilizing approximately 15 mg samples of ground plant material. Phosphorus and cations were analyzed after dry ashing 1 g of dried and ground plant material at 480 °C. The remaining material was weighed then treated with 1N HCl and allowed to evaporate to near dryness on a hot plate. This digestate was diluted with deionized water and filtered. The filtrate was used for both cation (Ca, K, Mg, Na) and P analysis. Cations were analyzed using a Model 350B Perkin-Elmer Atomic Absorption Spectrophotometer (Perkin-Elmer 1973). Divalent cations were determined by atomic absorption and the monovalent cations by flame photometry. Phosphorus analysis was by the ascorbic acid combined reagent method to measure orthophosphate concentrations (APHA 1971).

RESULTS AND DISCUSSION

Growth and Production

Vegetative growth of Vallisneria began in March when water temperatures were approximately 10-14 ^{o}C. Growth continued during the spring with reproductive structures observed by June and maximum standing crops in August and September. This was followed by a fall die-back and virtual disappearance of Vallisneria in winter, with the exception of the winter turions (specialized buds which serve as propagules and as overwintering devices), which remained buried within the sediment.

Seed germination of Vallisneria was not observed within the estuary and is believed to be a relatively rare event. Plant growth initiating from the winter buds was the dominant mode of propagation. These buds were located within a substrate of firm muddy-sand (3-12 cm beneath the sediment surface) which exhibited an odor resembling hydrogen sulphide. This layer, as well as, the winter buds, occurred progressively deeper beneath the sediment surface further downriver. This may explain the delayed appearance of plants at the downriver locations.

New leaves originate from the bifurcation of the enclosed meristem. The ribbon-like leaves of Vallisneria are clustered at the nodes of the rhizomes and grow in rosettes. The growth of a leaf occurred primarily within the basal portion of the leaf blade (Fig. 6). Less than 9% of the total elongation of the leaf occurred beyond this segment. No observable growth was recorded beyond the initial 30 cm of leaf blade.

Vallisneria produced a new leaf on a seasonal average of every 9.9 days (Table 1). This rate of leaf output was greater downriver (8.2 days) as

Fig. 6. Relative leaf growth with increasing distances from the basal meristem for *Vallisneria* from the upriver (km 10 N) site in the Pamlico River estuary.

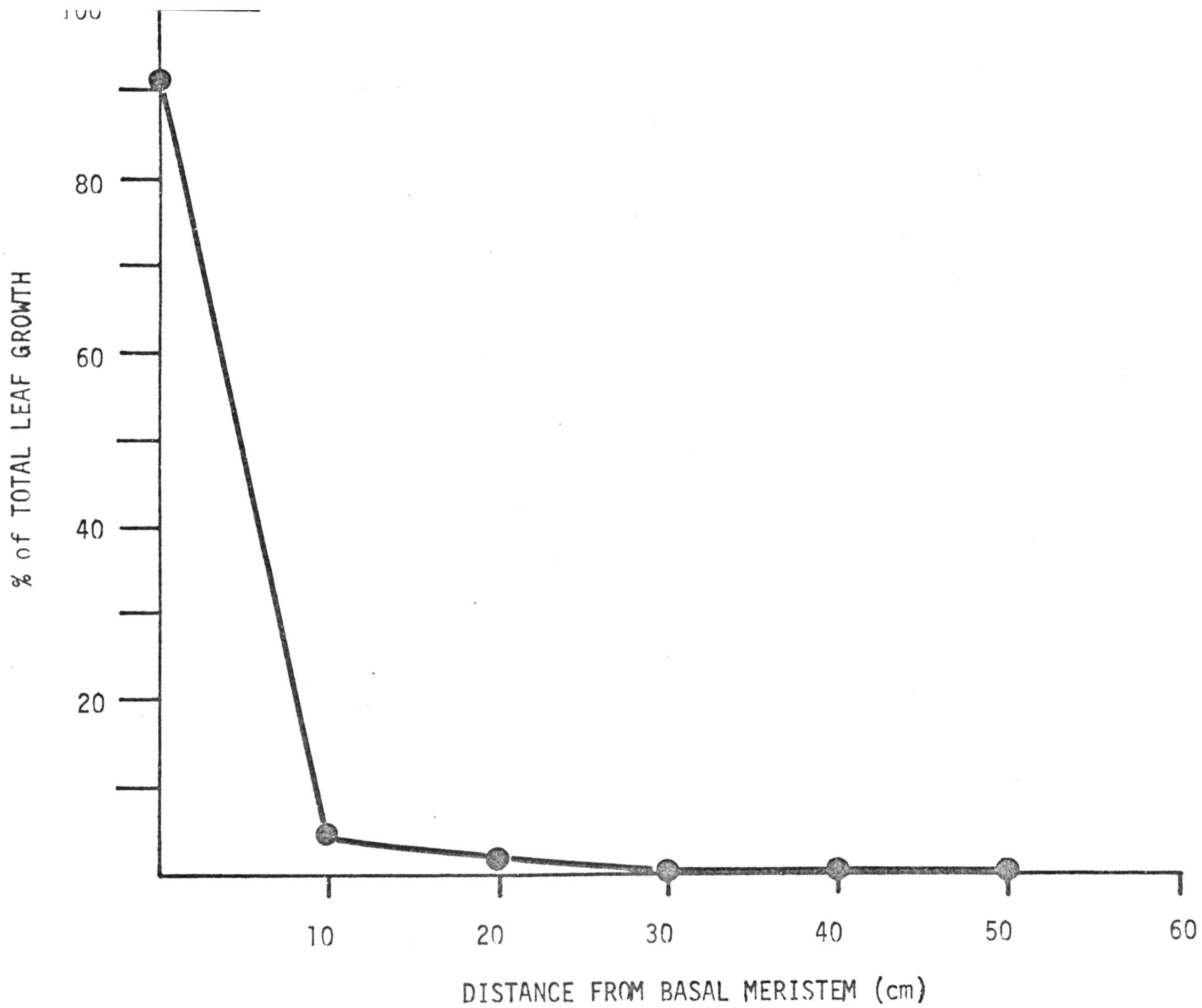

100
80
60
40
20
% of TOTAL LEAF GROWTH
10
20
30
40
50
60
DISTANCE FROM BASAL MERISTEM (cm)

Table 1. Leaf blade dynamics of *Vallisneria* from an upriver (km 10 N) and downriver (km 29 N) location in the Pamlico River estuary, May-October 1975.

Date	Leaves/plant		Leaf replacement time/plant (days)		Leaf loss time/plant (days)	
	km 10 N	km 29 N	km 10 N	km 29 N	km 10 N	km 29 N
2 May	3.8	5.4	6.3	4.8	-*	5.3
20 May	3.9	5.7	5.9	3.2	52.6	6.3
6 Jun	5.1	5.9	5.9	4.4	73.5	5.6
20 Jun	4.7	5.8	6.3	4.8	43.9	5.5
3 Jul	3.8	4.8	10.0	12.6	7.0	25.0
24 Jul	6.6	6.7	14.0	8.0	-*	13.4
8 Aug	7.6	6.5	10.1	1.8	5.7	4.9
27 Aug	6.3	7.5	8.0	3.2	9.0	2.8
13 Sep	6.2	7.3	19.2	10.4	5.4	3.1
10 Oct	5.4	5.9	30.4	28.5	3.1	2.7
Means	5.3	6.2	11.6	8.2	20.0	7.5

*No leaf loss recorded for this period of growth.

compared to upriver (11.6 days). During periods of high turnover a new leaf was produced by a plant as frequently as every 2 days (8 August marking period). In general, there was a decrease in the number of new leaves produced during July for both locations. This depression of leaf output coincided with flowering and fruiting stages of development.

<u>Vallisneria</u> is dioecious. The female flowers are carried up to the surface by the elongation of the peduncle, and when mature, lie horizontally on the water surface. The submerged male flowers when mature become detached and float to the water surface. According to Sculthorpe (1967) the male flowers are captured inside the perianth of the female flower as it closes during temporary immersion by a wave. After pollination the peduncle shortens by spiralling, thus, carrying the maturing fruit down into the water.

The development of male and female flowers was observed by early June for the upriver station, with fruits present from July through September. Although submersed male spathes were recorded for the downriver plants, female flowers and fruits never developed. This incomplete floral induction and/or development at the downriver site was associated with accelerated leaf production in late July and August as compared with the fully induced plants upriver.

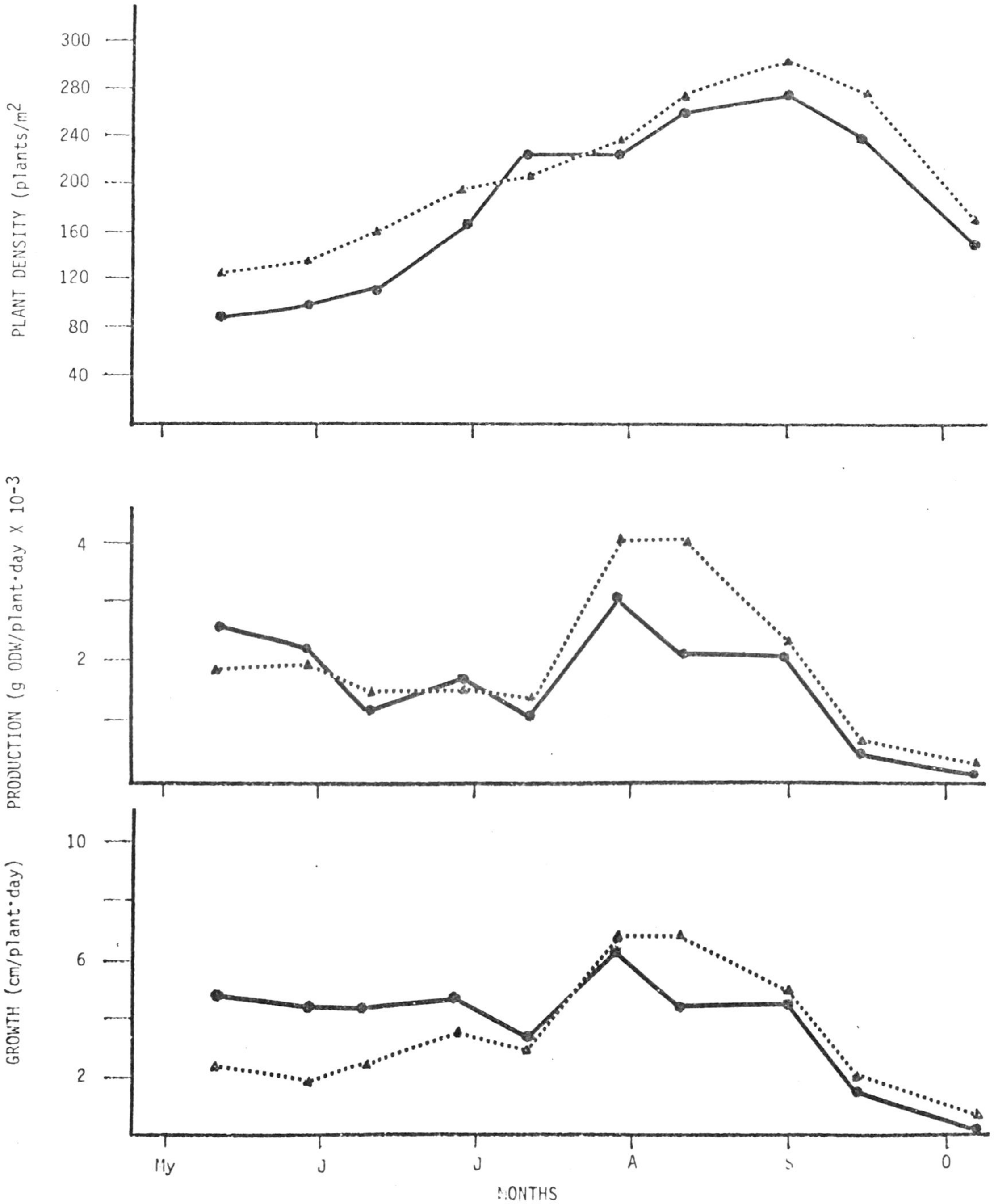
Frequency of leaf loss from <u>Vallisneria</u> is recorded in Table 1. Larger values are indicative of greater lengths of time required for the loss of leaves. Losses generally resulted from breakage due to physical forces such as water currents or wave action. Values were significantly different (p less than 0.01) for the two locations with leaves being lost more frequently for the more turbulence and wave stressed downriver plants. Leaf loss increased during the latter months of the growing season as the result of accumulation of older leaf material which through senescence becomes increasingly susceptable to breakage.

The number of leaves per plant (Table 1) fluctuated throughout the growing period. In March, usually two to three leaves per plant were observed originating from the branch primordium. This number increased to a seasonal average of approximately six leaves per plant. Values were generally higher for the plants downriver as compared to the upriver plants. The number of leaves per plant was balanced between leaf production and leaf loss.

The total leaf growth (elongation) per plant on a daily basis is represented in Fig. 7. These rates were relatively constant during the period of May-June, with greater values recorded for Vallisneria at the upriver location. Growth rates during July were initially depressed, in association with peak production of flowers and fruit. Leaf growth subsequently increased in the latter weeks of July to a seasonal maximum, with water temperatures of 30 °C. The mean rate of growth for Vallisneria leaves was 5.6 mm/day for both locations. Growth per plant averaged 5.5 cm/day. Leaf elongation was as rapid as 9 mm/day at the upriver station in spring. Following the July-August maximum there was a constant decline in elongation and net production with a virtual disappearance of above ground biomass by November.

Productivity of Vallisneria was determined from the ODW of new leaf material that appeared during the marking period. Shed leaves were usually the older senile leaves which had ceased to grow and such losses would not affect the productivity estimates. Figure 7 represents the rate of production for Vallisneria at the two locations. Productivity, expressed as mg ODW/plant·day followed the same general pattern as that for growth/plant·day. Values were greatest (3-4 mg ODW/plant·day) during the period of 24 July and 8 August for both stations. The relative higher production of the downriver plants at this time was due to increased frequency of leaf replacement, with

Fig. 7. Upper- Plant densities of *Vallisneria* in the Pamlico River estuary, 2 May 1975 to 10 October 1975.
Middle- Production rates of *Vallisneria* in the Pamlico River estuary, 2 May 1975 to 10 October 1975.
Lower- Growth rates of *Vallisneria* in the Pamlico River estuary, 2 May 1975 to 10 October 1975.
(Upriver: -●- ; Downriver: -▲-).


300
280
240
200
160
120
80
40
PLANT DENSITY (plants/m²)
4
2
PRODUCTION (g ODW/plant·day X 10-3
10
6
2
GROWTH (cm/plant·day)
My
J
J
A
S
O
MONTHS

a new leaf on the average of every five days as compared to every twelve days for the upriver plants. Growth and production decreased subsequent to this maximum. The seasonal mean production value was 2.3 mg ODW/plant·day.

Plant densities typically increased through the growing season as the community matured (Fig. 7). This information obtained from growth dynamic measurements was correlated with information obtained from aerial photography (Vicars 1976) coupled with field measurements to estimate the productivity of the estuary. Maximum plant densities of approximately 280 plants/m^2 for the upriver and downriver locations occurred in the August-September period, with a seasonal mean of 200 plants/m^2. With a production level of 2.3 mg ODW/plant·day and a density of 200 plants/m^2 the production of Vallisneria would be 0.46 g ODW/m^2 or a seasonal (March-October) production value of 115 g ODW/m^2. This results in a total estuarine leaf production for this species of approximately 403 MT ODW.

Turnover rate represents the ratio of new growth to initial biomass (expressed as percent per unit time). This rate was rapid in the spring but decreased as older plant tissue accumulated (Table 2). Rates were similar for both stations throughout the growing season. Vallisneria had a turnover rate of 1.5%/day for the months of June through October, which resulted in an average turnover time of 67 days for the Vallisneria population.

A comparison of the root-rhizome/shoot ratios of Vallisneria (Table 3) indicates a rapid establishment of the root and rhizome system associated with the initiation of seasonal growth. Subsequent to these relatively high ratios in May of 30:1 and 35:1 for the upriver and downriver sites, respectively, values decreased for both stations. Ratios were usually greater for the downriver location which implies a more rapid loss of the shoot component.

Table 2. Turnover rates of *Vallisneria* from an upriver (km 10 N) and downriver (km 29 N) location in the Pamlico River estuary, May-October 1975.

Date	Turnover rate (%/day)	
	km 10 N	km 29 N
2 May	16.0	17.9
20 May	15.1	17.5
6 Jun	1.5	2.1
20 Jun	1.9	2.3
3 Jul	1.6	3.8
24 Jul	0.6	1.2
8 Aug	0.8	2.0
27 Aug	2.2	3.6
13 Sep	1.0	1.7
10 Oct	0.2	0.4

Table 3. Seasonal comparison of the root-rhizome/shoot ratio (ODW) for *Vallisneria* from an upriver (km 10 N) and downriver (km 29 N) location in the Pamlico River estuary, May-October 1975.

Date	Location	
	km 10 N	km 29 N
2 May	29.8	35.3
20 May	8.0	10.7
6 Jun	0.6	0.7
20 Jun	0.7	0.9
3 Jul	0.8	0.4
24 Jul	0.4	1.3
8 Aug	0.3	1.0
27 Aug	0.6	1.3
13 Sep	0.7	1.5
10 Oct	1.0	2.1

Differences in values are highly dependent on variation in shoot biomass since absolute values for root and rhizome biomass were relatively constant throughout the season ($\bar{x}$ = 14.3 g ODW/m^2, SE = 0.99).

Seasonal above ground production measurements of Vallisneria indicate that estimates based only on terminal biomass measurements will be gross underestimates due to high turnover rates. A turnover time for Vallisneria of approximately 67 days results in 3.7 crops per season. Values of leaf production for this species were less than those determined for aquatic macrophytes in other systems (Table 4). Zieman (1968) utilizing a similar method of productivity measurements for Thalassia testudinum in South Florida, obtained an annual productivity value of 675 g C/m^2·yr as compared with 52 g C/m^2·yr for Vallisneria. Turnover and leaf growth rates were similar for both species, indicating that the increased level of production may be partially attributed to the greater leaf standing crops of Thalassia (average value 203 g DW/m^2) as compared with approximately 30 g DW/m^2 for Vallisneria. Compared with the annual above ground production of 294 g C/m^2 for Juncus roemerianus in a North Carolina salt marsh (Williams and Murdoch 1968) production values were considerable less although the rate of turnover and decomposition for Vallisneria was more rapid. Although the percentage areal cover of submersed communities may appear high, their DW biomass per unit area is usually small. Vallisneria may be considered an active producer when compared to annual productivity estimates of 40-80 g C/m^2 for the phytoplankton component of the Pamlico River estuary (Crawford et al., 1974). However, due to the limited coverage of the estuary by Vallisneria (1-2%) (Vicars 1976) as compared with an assumed coverage of 100% by phytoplankton,

Table 4. Annual productivity of aquatic macrophytes.

Plants	Productivity (g C/m^2.yr)	Source
Emergent:		
Juncus roemerianus	294	Williams & Murdoch 1968
Phragmites communis	1210	Harper 1918
Spartina alterniflora	256	Williams 1965
Floating Leaves:		
Eichhorina	402	Penfound & Earle 1948
Submersed:		
Myriophyllum spicatum	379	Adams & McCraken 1974
Thalassia testudinum	675	Zieman 1968
Zostera marina	346	Dillion 1971
Vallisneria americana	52	This study

the relative productivity of the rooted macrophytes was low.

Seasonal Weight Relationships and Organic Decay

The dry matter content (as percent of FW) determined for *Vallisneria* harvested from the Pamlico River estuary is presented in Table 5. Values of DW and ODW for living plants and decaying matter represent the mean of three to ten replicate analyses and 95% confidence limits were generally within 2-8% of the mean. Minimum spring levels of DW (as percent FW) were 8.0 and 7.5% for the upriver and downriver stations, respectively, and maximum levels were 8.4 and 12.7% DW for plants harvested in the fall. This increase in DW is attributed to the greater quantities of older, senescent material which accumulated during the growing season. Plants harvested from the downriver station exhibited higher dry weight percentages which result from shorter leaf form and a greater proportion of root and rhizome biomass. The dry matter content determined for *Vallisneria* was similar to that reported by Rickett (1924) and Nelson and Palmer (1938).

The ODW component was generally lower than that reported by others. Values were variable on a temporal as well as spatial basis. Plant material from the upriver station contained greater quantities of organic dry matter. The downriver plants exhibited decreasing values from spring until the termination of growth in the fall.

Rates of decomposition (Fig. 8) were determined for fresh plants in decay bags beginning on 23 Nov 74, 9 May 75 and 21 July 75. A significant difference was found in rates of breakdown on a seasonal basis. The half-life or time required for 50% of the original organic dry matter to decay was from 3-6 wks in winter but less than 2 wks in spring and summer.

Losses of dry matter progressed rapidly during the first 2 wks for all

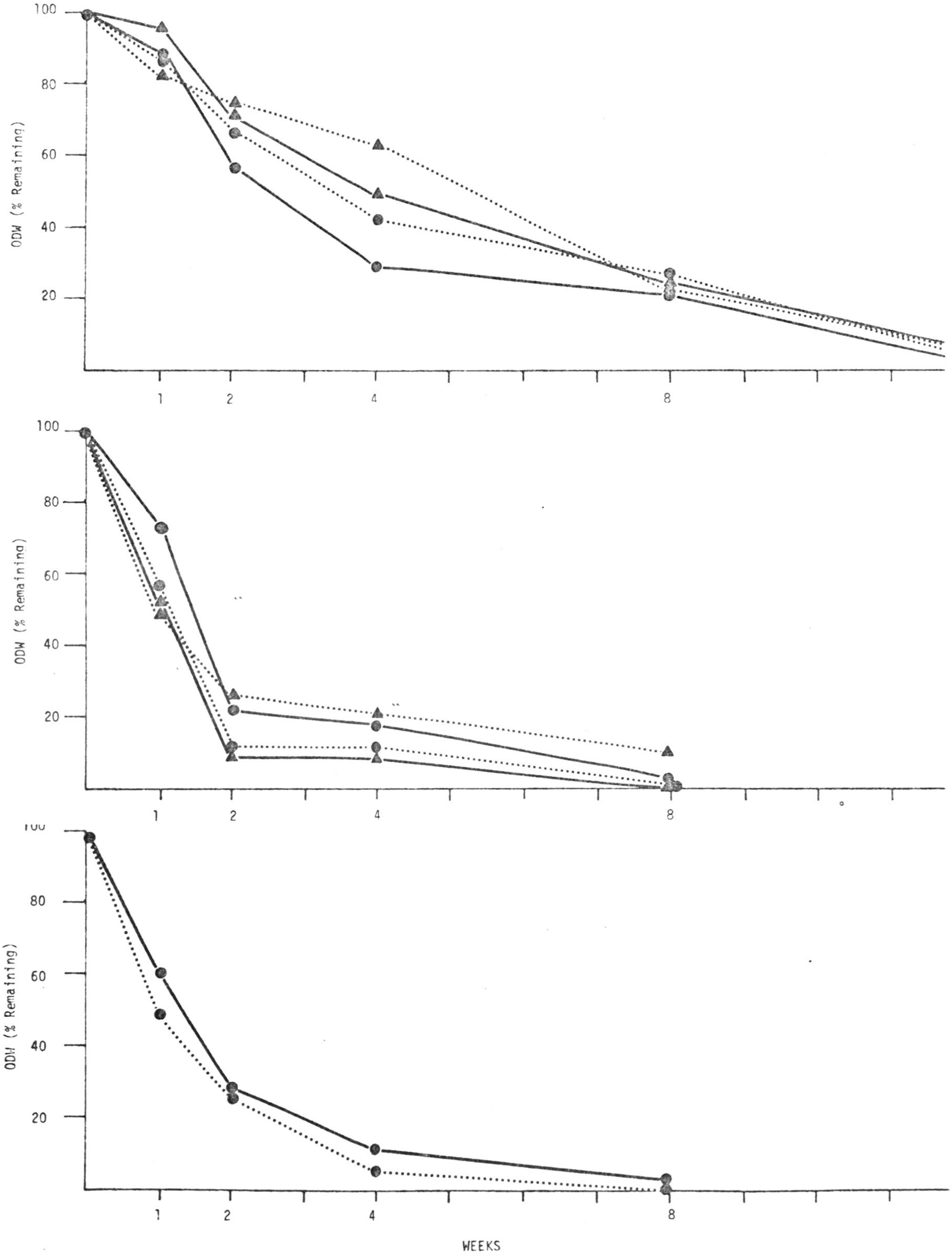
Table 5. Seasonal weight relationships of *Vallisneria* from upriver (km 10 N) and downriver (km 29 N) stations in the Pamlico River estuary.

Date Collected	Plant Source	Dry Weight (% FW)	Organic Dry Weight (% FW)	Organic Dry Weight (% DW)
23 Nov 1974				
	upriver	8.9	5.6	63
	downriver	11.2	5.5	49
9 May 1975				
	upriver	8.0	5.2	65
	downriver	7.5	5.1	68
21 Jul 1975				
	upriver	8.5	6.0	71
	downriver	10.4	6.1	59
4 Oct 1975				
	upriver	8.4	5.7	68
	downriver	12.7	5.5	43

Fig. 8. Top- Decomposition rates of *Vallisneria* during decay in the Pamlico River estuary, 23 November 1974 to 15 February 1975.

Middle- Decomposition rates of *Vallisneria* during decay in the Pamlico River estuary, 9 May 1975 to 4 July 1975. (Upriver: —●— littoral, —▲— midriver; Downriver: ··●·· littoral, ··▲·· midriver).

Bottom- Decomposition rates of *Vallisneria* during decay in the Pamlico River estuary, 21 July 1975 to 15 September 1975. (Upriver littoral; —●— closed bag, ··●·· open bag).


100
80
60
40
20
ODW (% Remaining)
1
2
4
8
100
80
60
40
20
ODW (% Remaining)
1
2
4
8
100
80
60
40
20
ODW (% Remaining)
1
2
4
8
WEEKS

locations. Decay rates calculated for Vallisneria indicated an ODW loss of as much as 50% within the first week.

Decomposition originated at the fragmented ends of leaves and progressed along the linear axis of the leaf tissue. The root and rhizome fraction was more refractory than the leaf material and persisted longer. Most of the plant material had decomposed after 4-8 wks at all locations. Less than 25% of the initial material (ODW) remained. This material left was probably composed of cellulose and lignin which are relatively resistant to microbial decomposition. Even this refractory material had disappeared from all decay bags at the end of 2-3 months.

The rapid initial rate of decay was the probable result of cellular autolysis with the subsequent loss of cytoplasmic contents. The loss of soluble organic compounds (sugars, organic acids, etc.) can result in a loss of as much as 25% of the initial dry weight of some aquatic macrophytes within the first few days (Odum et al., 1973).

Large populations of the amphipod Gammarus often appeared in decay bags after approximately two weeks of decay. Gammarus populations in association with the decay material were most abundant in the spring and rarely found at the downriver locations. The spring abundance was perhaps a contributing factor to the increased rates of decay in spring as compared to winter decay rates. Laboratory observations using Gammarus collected from decay bags indicated that Vallisneria leaves were fragmented as feeding occurred. These detritus feeders generally have low assimilation efficiences and most of the ingested material is voided as feces (Hargrave 1970).

Similar rates of decay were found utilizing both open and closed bags during the summer decay period (Fig. 8). Data on Gammarus populations associated with the decay material of this period are in Table 6. Maximum biomass occurred in the open bags after the initial two weeks of decay. Organisms smaller than one mm mesh could penetrate into the closed decay bags and were present in smaller quantities than in the open bags. Also, there is the possibility that the Gammarus could have been associated with the freshly harvested material. Further research is needed to clarify the quantitative role these crustaceans play in the decomposition of Vallisneria.

In general for any particular season, decay rates were similar between the littoral and midriver sites located both upriver and downriver. Despite the differences between sites (turbidity, salinity, bottom type, etc.) they appeared to differ little in effects on the decomposition. The maximum rates of decay which occurred during the summer months were undoubtedly linked to temperature-dependent factors such as short generation times and increased populations of microorganisms.

A comparison of decay rates of Vallisneria with other aquatic macrophytes is in Table 7. The slower rates of decay for the emergent vegetation were related to factors such as the thicker cuticle and more lignified tissue.

For terrestial studies (Gosz et al., 1973, Hodkinson 1975) the rate of dry weight loss has been described in terms of the negative exponential equation

$$W_t = W_o e^{-kt}$$

in which W_t is the dry weight at time t, W_o is the original weight, t is the time, k is a decay coefficient specific to a particular litter type and e is the base of natural logarithms. Extrapolated decay coefficients (k) half life

Table 6. *Gammarus* populations associated with *Vallisneria* in open and closed decay bags in the Pamlico River estuary, summer 1975.

Decay Period	Bag Type	*Gammarus* (Percent of Total DW)
initiation	open	0
	closed	0
1 week	open	5.3
	closed	1.2
2 weeks	open	12.2
	closed	3.0
4 weeks	open	0
	closed	0

Table 7. *In situ* decomposition rates of aquatic macrophytes.

Plants	Percent Loss of Dry Weight 1-2 wks	4	9	12	24	Source
Emergent:						
Juncus effusus	5	-	-	30	65	Boyd 1971
Typha latifolia	5	-	-	25	45	Boyd 1970
Spartina alterniflora	2	-	-	10	50	Burkholder & Bornside 1957
Floating Leaves:						
Lemnaceae	20	-	-	90	-	Laube & Wohler 1973
Nymphaea odorata	15	-	-	45	40	Kormandy 1968
Submersed:						
Potamogeton lucens	6-92	-	-	-	-	Pieczynska 1972
P. perfoliatus	6-95	-	-	-	-	
Thalassia testudinum	30	45	65	-	-	Zieman 1968
Vallisneria americana						
winter	25	38	75	-	-	This study
summer	70	80	-	-	-	

values (0.693/k) and 95% life values (3/k) for *Vallisneria* as well as litter of terrestial origin occurring in aquatic systems are given in Table 8.

The k value for *Vallisneria* in the Pamlico River estuary was greater in the spring and summer (19.5) than winter (10.0). Breakdown rates (k values) were high in comparison to those recorded for terrestial material. Decay rates for deciduous leaf litter is greater in aquatic than in terrestial systems (Thomas 1970) and may be similar to values for submersed macrophytes such as *Vallisneria*.

Table 8. Decay parameters for different litter types in aquatic systems.

Litter type	k (yearly)	Half Life (years)	95% Life (years)	Authors
Juncus tracyi Rydberg	0.41	1.70	7.33	Hodkinson 1975
Salix sp.	0.98	0.71	3.05	"
Pinus contorta Louden	0.21	3.22	13.92	"
Quercus alba L.	0.45	1.54	6.65	Kaushik & Hynes 1971
Acer rubrum L.	9.97	0.07	0.30	Thomas 1970
Vallisneria americana Michx.				
winter	10.0	0.07	0.30	This study
spring & summer	19.5	0.04	0.15	

Nitrogen Levels and Decay Dynamics

The results of chemical analyses of *Vallisneria* harvested from the Pamlico River estuary are in Table 9. Each figure represents a mean of three to 10 analyses per sample and 95% confidence levels were generally less than ± 5% of the mean. Inorganic nutrient concentrations were calculated on an ODW basis. Values for fresh material were within the range of those reported by others as indicated in Table 10. Initial N concentrations on a seasonal basis, did not fluctuate greatly from the 4100 ug-at./g ODW for the downriver plants. Nitrogen values for plants from the upriver station had a summer minimum (2750 ug-at./g ODW) with higher values recorded for the spring and winter.

The summer minimum, as well as the generally lower values for the upriver plant material, might be associated with limited available N in areas of luxuriant growth. Harrison and Hobbie (1974) recorded lower levels of N in the water of the Pamlico River estuary during the summer months. Although N is often implicated as a limiting nutrient for plant growth, values determined for *Vallisneria* exceeded the critical concentration of 1.3% (1170 ug-at./g ODW) established by Gerloff and Krombholz (1966). This critical concentration represents the minimum tissue content of N which sustains maximum growth of *Vallisneria*. Analysis of different parts of the plant indicated that the N content of the leaf material was generally higher than the root and rhizome fraction.

The initial rate of N loss from the plant material was quite rapid for winter and spring decay periods (Fig. 9). Nitrogen concentrations for summer decay material were relatively constant with only a small increase with time.

Table 9. Seasonal comparison of inorganic nutrients of *Vallisneria* from upriver (km 10 N) and downriver (km 29 N) stations in the Pamlico River estuary.

Date Collected	Plant Source	N	P	Nutrients (ug-at./g ODW) Ca	Mg	Na	K
23 Nov 1974							
	upriver	3425	302	327	470	2669	2412
	downriver	4125	605	500	617	3212	1819
9 May 1975							
	upriver	3980	245	199	162	641	1775
	downriver	4100	298	112	203	1236	1868
21 Jul 1975							
	upriver	2750	265	40	89	217	305
	downriver	-	-	-	-	-	-

Table 10. Inorganic nutrient concentrations in *Vallisneria americana*.

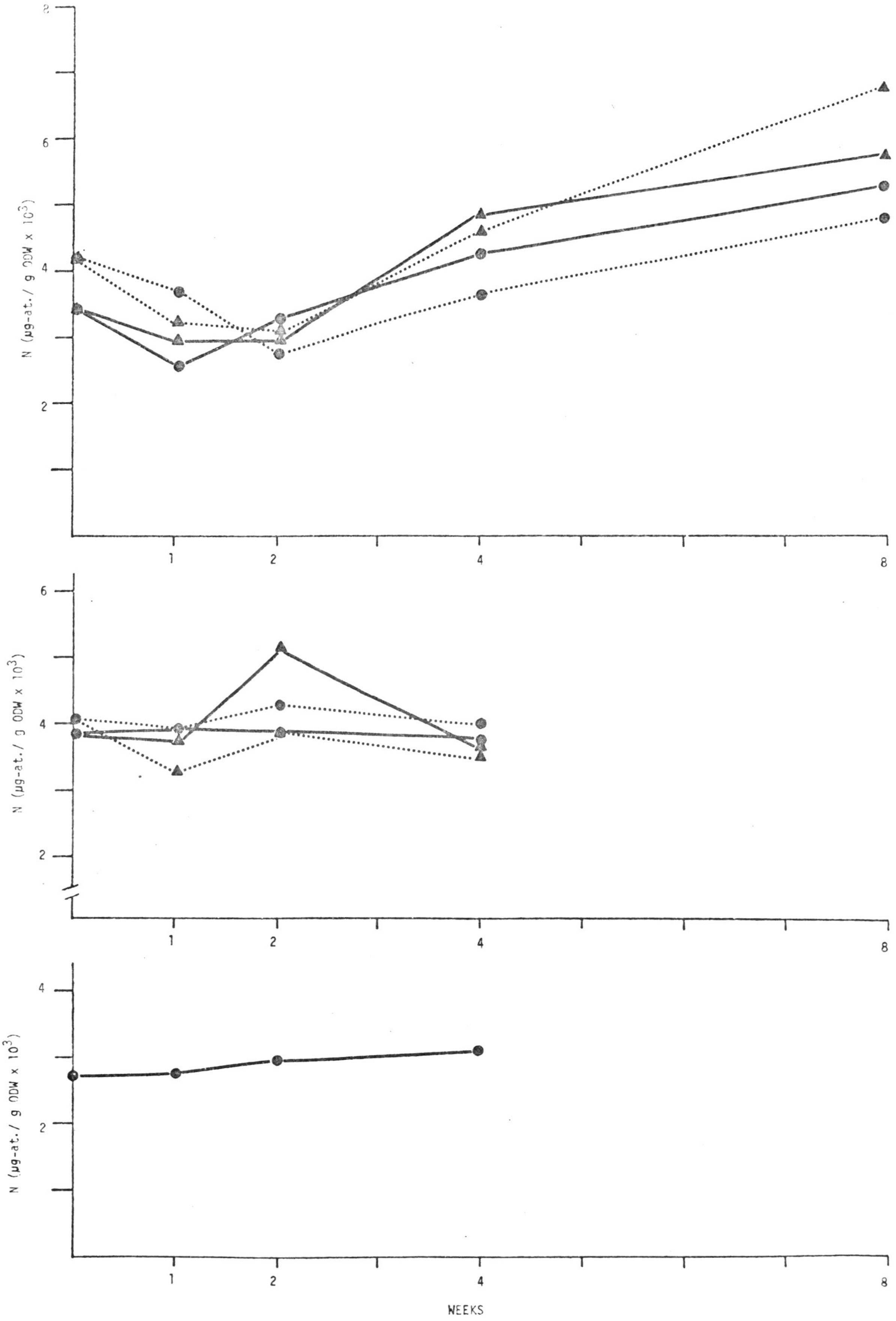
		Nutrients (Percent of Dry Weight)				
Total N	Total P	Ca	Mg	Na	K	Source
2.01	0.11	0.91	0.36	1.72	4.41	Getsinger[a]
3.6	0.43	3.2	0.28	0.18	2.2	Neal et al., 1973
2.42	0.21	1.55	0.76	2.39	6.77	Nelson and Palmer 1938
4.07	0.62	0.70	0.29	0.37	5.75	Riemer and Toth 1968
1.88	0.23	5.83	1.13	0.48	4.55	Schuette and Alder 1927
2.8	0.6	0.8	0.7	3.1	5.8	This study[b]
2.6	0.9	1.0	0.8	3.7	3.6	This study[c]

[a] Values for leaf material for *Vallisneria americana* harvested from Kitty Hawk Bay, N.C. (Unpublished data).

[b] Values for *Vallisneria americana* harvested on 23 Nov 1974 from an upriver location (km 10 N) in the Pamlico River estuary.

[c] Values for *Vallisneria americana* harvested on 23 Nov 1974 from a downriver location (km 29 N) in the Pamlico River estuary.

Fig. 9. Top- Nitrogen concentrations in *Vallisneria* decay in the Pamlico River estuary, 23 November 1974 to 18 January 1975. Middle- Nitrogen concentrations in *Vallisneria* decay in the Pamlico River estuary, 9 May 1975 to 6 June 1975. Bottom- Nitrogen concentrations in *Vallisneria* decay in the Pamlico River estuary, 21 July 1975 to 18 August 1975. (Upriver: -●- littoral, -▲- midriver; Downriver: ··●·· littoral, ··▲·· midriver).


8
6
4
2
N (µg-at./ g ODW x 10³)
1
2
4
8
6
4
2
N (µg-at./ g ODW x 10³)
1
2
4
8
4
2
N (µg-at./ g ODW x 10³)
1
2
4
8
WEEKS

Final measurements of spring decay matter gave N values (ODW basis) approximating those of the original plants. During the summer and winter decay period, N enrichment continued within plant litter and proceeded more rapidly during the winter months. Although the concentration of N may increase on a ODW basis, due to the rapid loss of ODW during decay, an increase in the absolute amount of N does not occur with *Vallisneria*, but has been reported for plant litter in terrestial habitats (Gosz 1973).

The decrease in N concentrations recorded in the initial 1-2 wk decay period is attributed to loss of N beyond that assimilated by decay organisms during cell autolysis. Increased levels of N within the decaying material occurred after this initial loss and are probably a reflection of increasing bacterial and fungal colonization. Odum and de la Cruz (1967) found that the ash-free dry material of living *Spartina* had about 10% protein. Dead leaves entering the water had about 6% while the finer detrital particles showed an increase to about 24%. Similar results have been obtained for submersed aquatic macrophytes (Boysen-Jensen 1914, Zieman 1968) as they undergo decomposition.

Final measurements of *Vallisneria* decay material for all seasons of study resulted in C:N ratios ranging in value between 5 and 12:1. This is undoubtedly a combination of an immobilization and net loss of inorganic carbon. Russell-Hunter (1970) established that most animals have adult nutritional requirements for protein which corresponds to a C:N ratio lower than 17:1. The effect of microorganisms may result in the availability of previously inaccessible stores of macrophyte energy.

Work by Thayer (1974) in shallow estuaries near Beaufort, N.C., indicates the presence of dead *Spartina* material low in N and P relative to its C content (C:N:P ratio of 383:6:1) may promote immobilization of N and P from the water column by bacterial utilization of this organic material thus decreasing the C:N:P ratio while limiting nutrient availibility to phytoplankton. This suggests the potential importance of *Vallisneria* (C:N:P ratio of 124:11:1) and its microbial populations within the estuarine ecosystem.

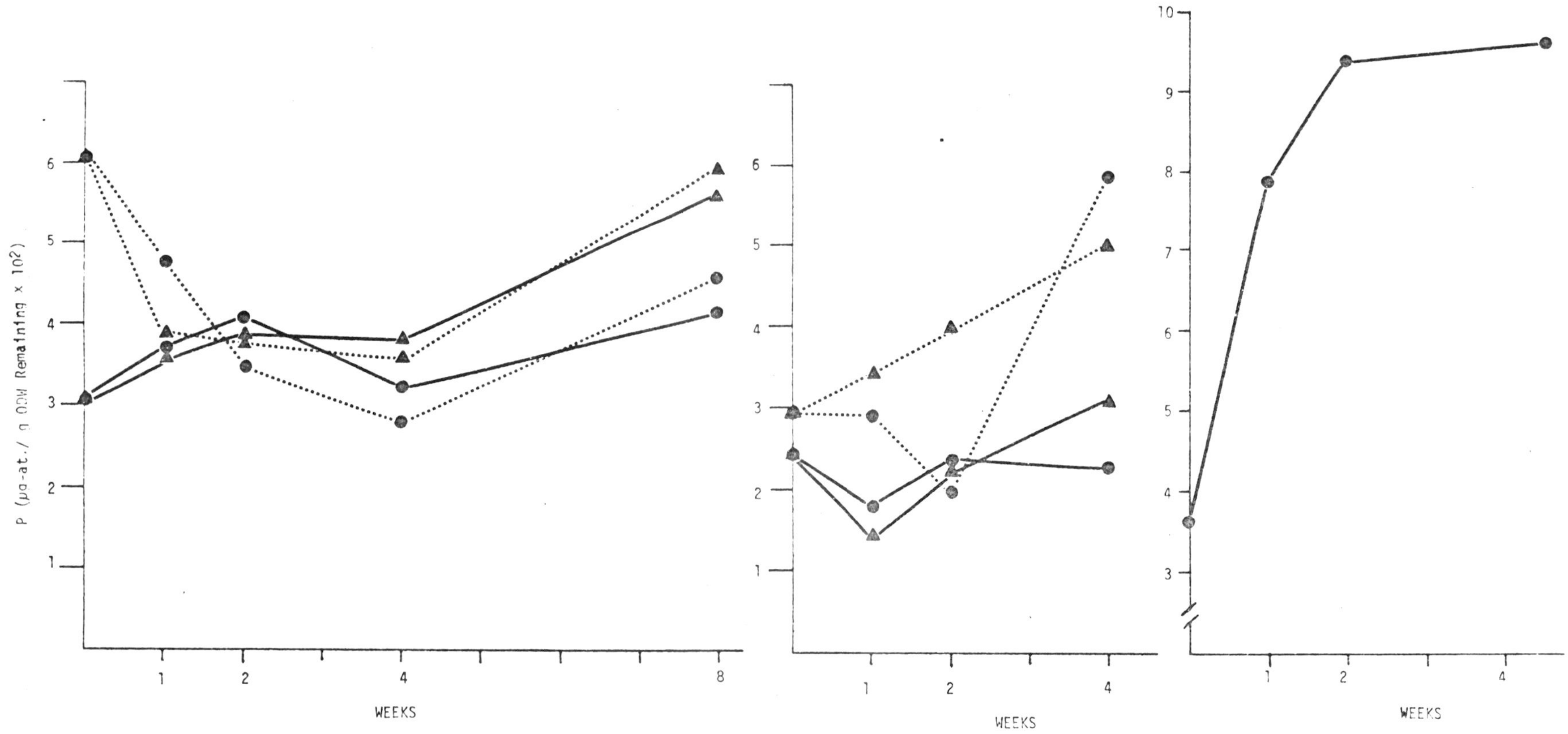
Phosphorus Levels and Decay Dynamics

Phosphorus concentrations of living *Vallisneria* are summarized in Table 9. Variations of P in freshly harvested plants from the downriver station were significant throughout the year and were consistently higher than values for the upriver plants. Phosphorus accumulation is submersed aquatic macrophytes has been shown (Wetzel 1975) to be related to ambient concentrations. Within the Pamlico River estuary higher P concentrations occur in the middle reach. No P values for harvested plants were below the critical concentration of 0.13% (52.4 ug-at./g ODW) established for *Vallisneria* (Gerloff and Krombholz 1966). Phosphorus levels for this species, harvested from the Pamlico River estuary, were generally higher than that reported for this species from other sources (Table 10). Tissue concentrations above 0.13% are attributed to luxury accumulation.

Phosphorus values showed a rapid decrease during the initial 1-2 wks of winter decay at the downriver station. The initial loss was probably associated with the leaching of soluble P from the decaying macrophyte material. The greater initial decreases recorded for this season (Fig. 10) appear to be related to the higher levels of P (605 ug-at./g ODW) in these plants. *Vallisneria* with lower initial P levels did not exhibit this rapid decrease with the onset of decomposition (Fig 10).

Decay material at all winter sites continually increased in P after four wks. This increase occurred within progressively shorter time periods for spring and summer. As suggested for N this increase in P is likely related to increasing microbial populations. This similarity is reflected

Fig. 10. Left- Phosphorus concentrations in *Vallisneria* decay in the Pamlico River estuary, 23 November 1974 to 18 January 1975. Middle- Phosphorus concentations in *Vallisneria* decay in the Pamlico River estuary, 9 May 1975 to 6 June 1975. Right- Phosphorus concentrations in *Vallisneria* decay in the Pamlico River estuary, 21 July 1975 to 18 August 1975. (Upriver: -●- littoral, -▲- midriver; Downriver: ··●·· littoral, ··▲·· midriver).


P (μg-at./ g ODW Remaining x 10²)
6
5
4
3
2
1
1
2
4
8
WEEKS
6
5
4
3
2
1
1
2
4
WEEKS
10
9
8
7
6
5
4
3
1
2
4
WEEKS

in the decay patterns during the various seasons. Apparent immobilization and incorporation of P occurred rapidly during the summer experiment with P concentrations increasing from 365 to 940 ug-at./g ODW within the first two wks of decay.

Final measurements indicated that in general the finer detrital material had higher P concentrations than the original plants. This increase was significantly greater for the summer decay material than that of winter and spring.

With respect to location, P levels during decomposition were variable. For the winter study, higher concentrations were recorded from the littoral sites of decay, while during the spring study, the downriver sites had significantly greater concentrations. The possibilities of increased physical adsorption of P within the littoral during the winter decay and increased ambient levels of P downriver during summer could explain this variation.

Cation Levels and Decay Dynamics

Ion absorption in Vallisneria occurs both from the water by foliage and from the sediment by root-rhizome systems (Sculthorpe 1967). Translocation can occur in both directions. Thus, the conceptual model of a nutrient pump results with nutrients from the sediments being accumulated during growth and subsequently lost through secretion and decomposition. Winter (1961) showed that certain cations absorbed by Vallisneria leaves can be separated into three fractions. One of these can be removed by washing leaves in distilled water, and the second by cation exchange. The third fraction, not removable by these processes, are those cations that presumably are transferred through the plasmalemma into the cytoplasm. Thus, as submersed macrophytes decompose, the quantity of cations present at any particular time will be a function of their distribution within the plants.

Calcium

Levels of Ca within harvested plant material (Table 9) were highest for the harvested winter plants and successively lower in spring and summer. Vallisneria harvested from the downriver location had higher levels of Ca in winter and lower values in spring as compared to the upriver plants.

The pattern of loss for Ca from the plant tissue is represented in Figure 11. Within the first 1-2 wks of decomposition an increase of Ca concentrations occurred. This initial increase was generally succeeded by decreasing concentrations of Ca for the decay material.

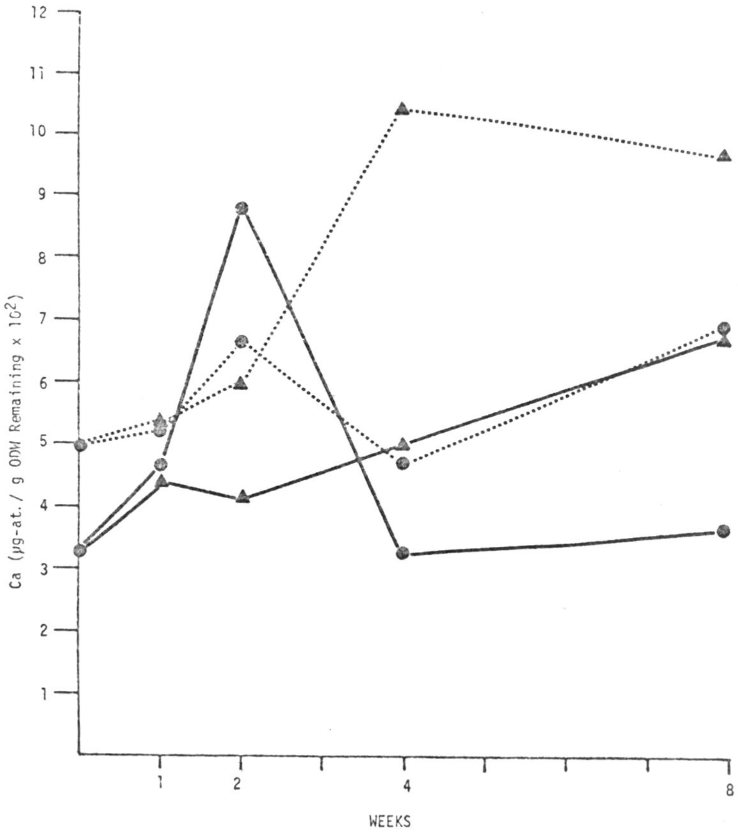
Calcium is important as a structural component of the cell walls, and its pattern of loss can be correlated with decomposition. The increase in Ca in early decay was probably associated with a relative increase in cell wall material during cellular autolysis. The decrease in later stages of decay is attributed to the digestion of cell walls and release of Ca.

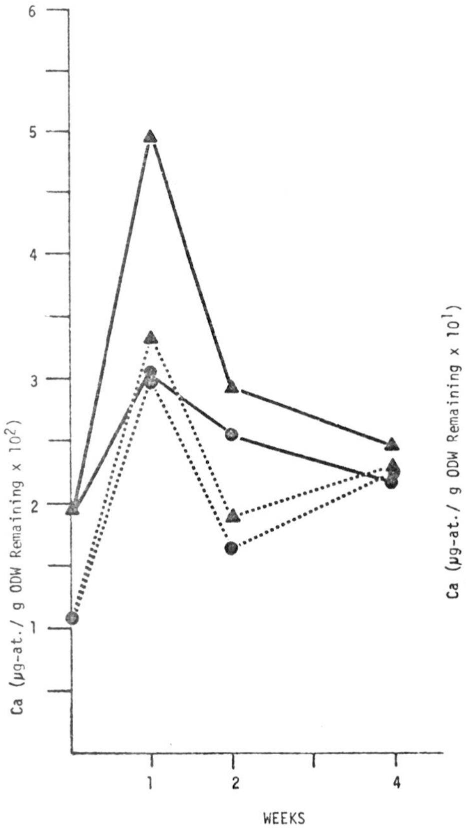
Final analysis of decay bag material for the summer study indicated a significant decrease in Ca levels. For the spring study, concentrations were generally the same as that determined for the initial plants, with the downriver material having lower final as well as initial Ca levels.

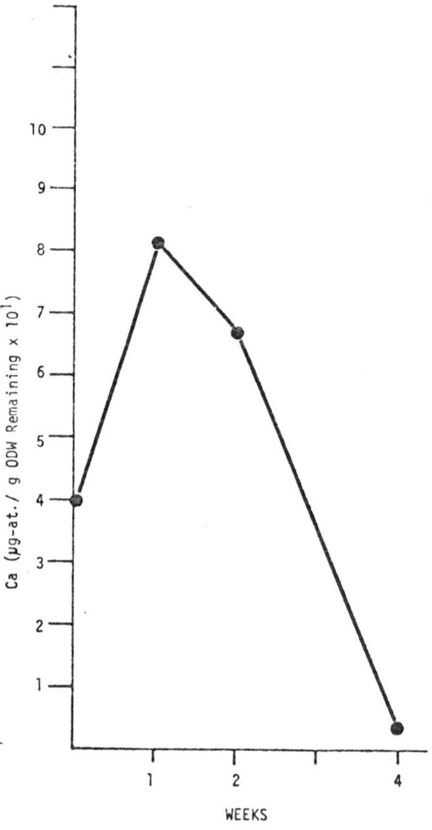
Magnesium

Levels of Mg for the living material (Table 9) had a winter maximum (616 ug-at./g ODW) and a summer minimum (89 ug-at./g ODW). Values were

Fig. 11. Left- Calcium concentrations in *Vallisneria* decay in the Pamlico River estuary, 23 November 1974 to 18 January 1975. Middle- Calcium concentrations in *Vallisneria* decay in the Pamlico River estuary, 9 May 1975 to 6 June 1975. Right- Calcium concentrations in *Vallisneria* decay in the Pamlico River estuary, 21 July 1975 to 18 August 1975. (Upriver: -●- littoral, -▲- midriver; Downriver: ··●·· littoral, ··▲·· midriver).


12
11
10
9
8
7
6
5
4
3
2
1
Ca (μg-at./ g ODW Remaining x 10^2)
1
2
4
8
WEEKS


6
5
4
3
2
1
Ca (μg-at./ g ODW Remaining x 10^2)
1
2
4
WEEKS


10
9
8
7
6
5
4
3
2
1
Ca (μg-at./ g ODW Remaining x 10^1)
1
2
4
WEEKS

relatively uniform for the upriver and downriver stations.

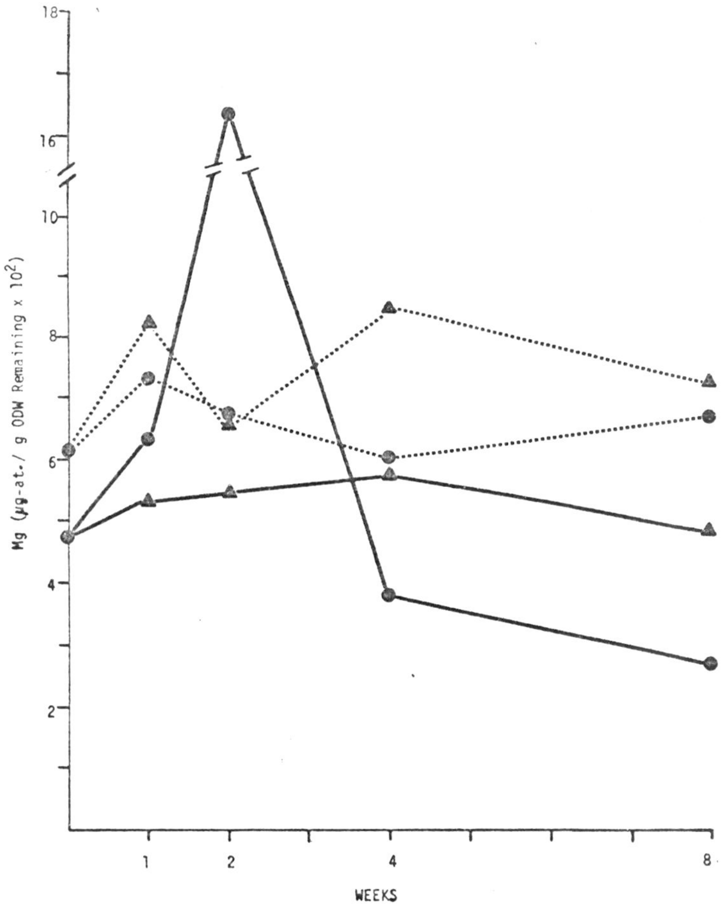
The Mg concentrations (Fig. 12) during the first wk of decay increased for the winter material to a greater extent than the spring. Concentrations for the summer material decreased insignificantly. With the exception of the continual decreasing Mg concentrations recorded in summer decomposition, values after four wks were similar to those after the first wk of decay. For the winter decay study, Mg concentrations gradually decreased during the second month od decay. Values were lowest for the upriver stations. The losses of Mg during the decay process exceeded dry matter losses and are attributed more to solubilization than to microbial uptake.

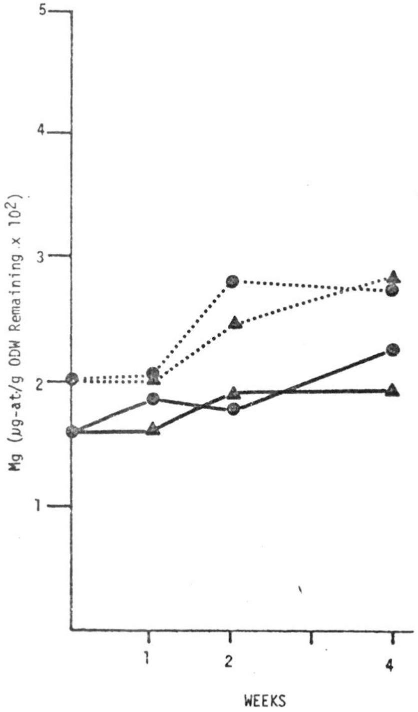
Sodium

Sodium levels for harvested Vallisneria were greater in the winter (3212 ug-at./g ODW) and lower in the summer (217 ug-at./g ODW). Values for Na (Table 9) were significantly larger than Mg and Ca. Sodium levels for Vallisneria harvested from the Pamlico River estuary were greater than those reported by other workers (Table 10) and are attributed to the increased salinity regime associated with the estuarine system. Higher levels were consistently recorded for the downriver plants. The role of Na is largely unknown although its accumulation by plants, especially under saline conditions, is a common phenomenon.

Changing Na levels as plants decay are represented in Fig. 13. The rate of release exceeded that for Ca and Mg. Values generally remained constant or decreased during the initial period of decay. As decomposition continued, values increased for the spring material but decreased for winter and summer. The initial changes are attributed to autolysis and release from the vacuoles. Subsequent changes may have resulted from absorption from

Fig. 12. Left- Magnesium concentrations in *Vallisneria* decay in the Pamlico River estuary, 23 November 1974 to 18 January 1975. Middle- Magnesium concentrations in *Vallisneria* decay in the Pamlico River estuary, 9 May 1975 to 6 June 1975. Right- Magnesium concentrations in *Vallisneria* decay in the Pamlico River estuary, 21 July 1975 to 18 August 1975. (Upriver: -●- littoral, -▲- midriver; Downriver: ··●·· littoral ··▲·· midriver).


18
16
10
8
6
4
2
Mg (µg-at./ g ODW Remaining x 10^2)
1
2
4
8
WEEKS


5
4
3
2
1
Mg (µg-at./g ODW Remaining x 10^2)
1
2
4
WEEKS

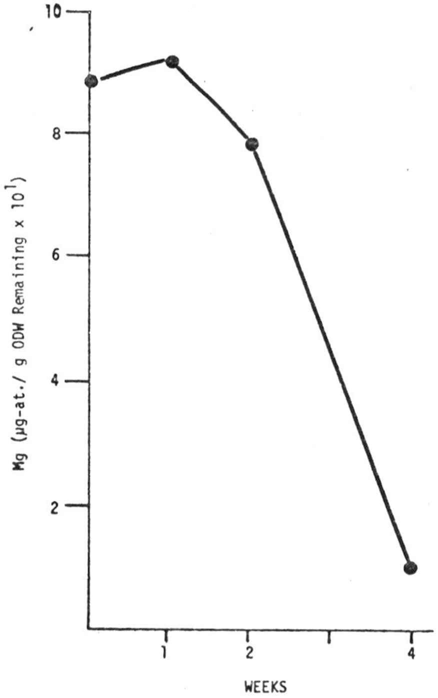
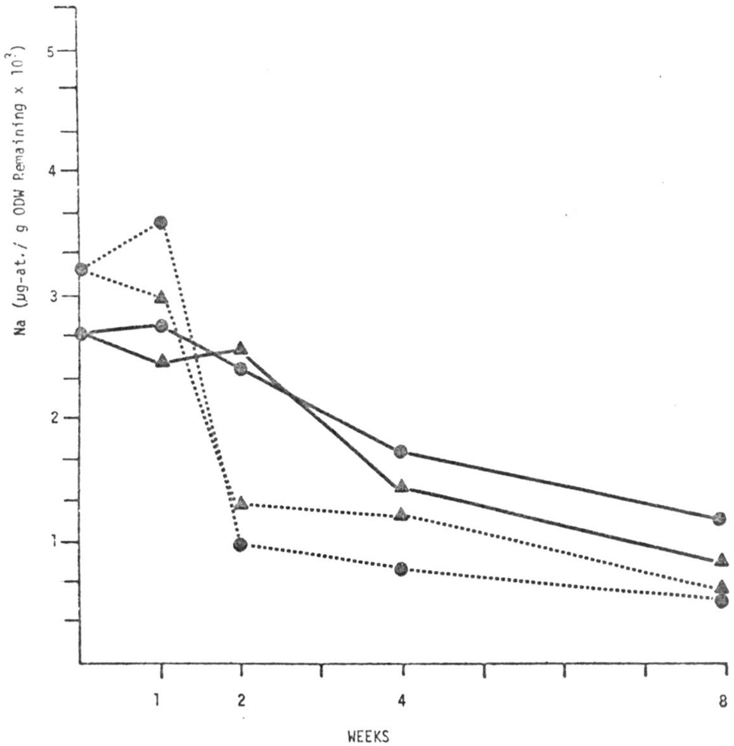
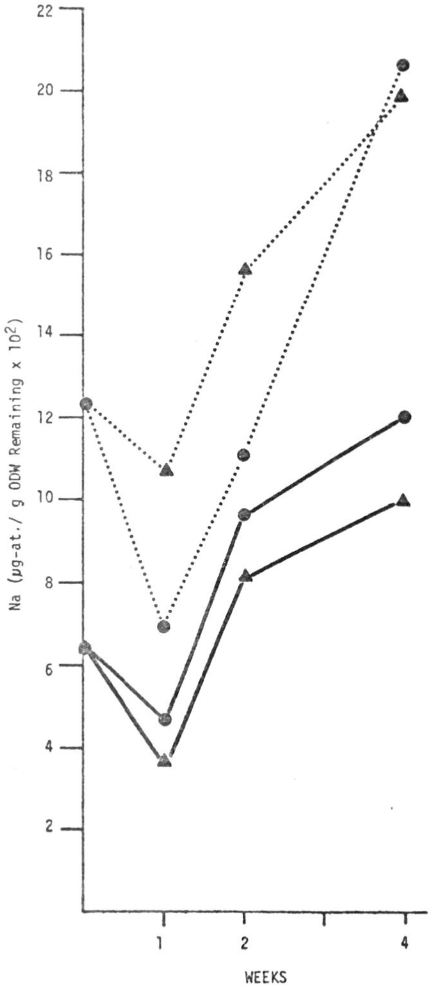
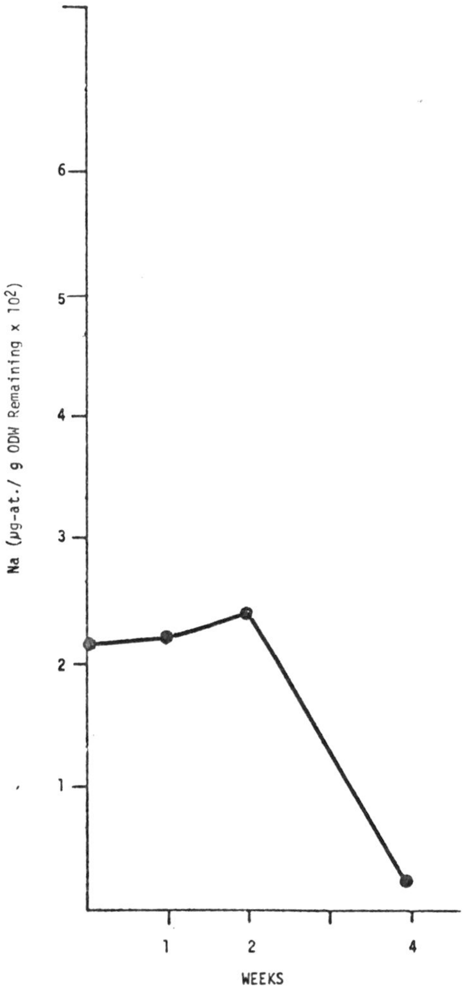

10
8
6
4
2
Mg (µg-at./ g ODW Remaining x 10^1)
1
2
4
WEEKS

Fig. 13. Left- Sodium concentrations in *Vallisneria* in the Pamlico River estuary, 23 November 1974 to 18 January 1975. Middle- Sodium concentrations in *Vallisneria* decay in the Pamlico River estuary, 9 May 1975 to 6 June 1975. Right- Sodium concentrations in *Vallisneria* decay in the Pamlico River estuary, 21 July 1975 to 18 August 1975. (Upriver: -●- littoral, -▲- midriver; Downriver: ··●·· littoral, ··▲·· midriver).


Na (μg-at./ g ODW Remaining x 10²)
5
4
3
2
1
1
2
4
8
WEEKS


Na (μg-at./ g ODW Remaining x 10²)
22
20
18
16
14
12
10
8
6
4
2
1
2
4
WEEKS


Na (μg-at./ g ODW Remaining x 10²)
6
5
4
3
2
1
1
2
4
WEEKS

ambient water, as well as, uptake by microorganisms. Decreased salinities, (Fig. 5), as a result of increased fresh water inflow from heavy July rains could have contributed to the reduced levels of Na and other cations in the summer decay material.

Potassium

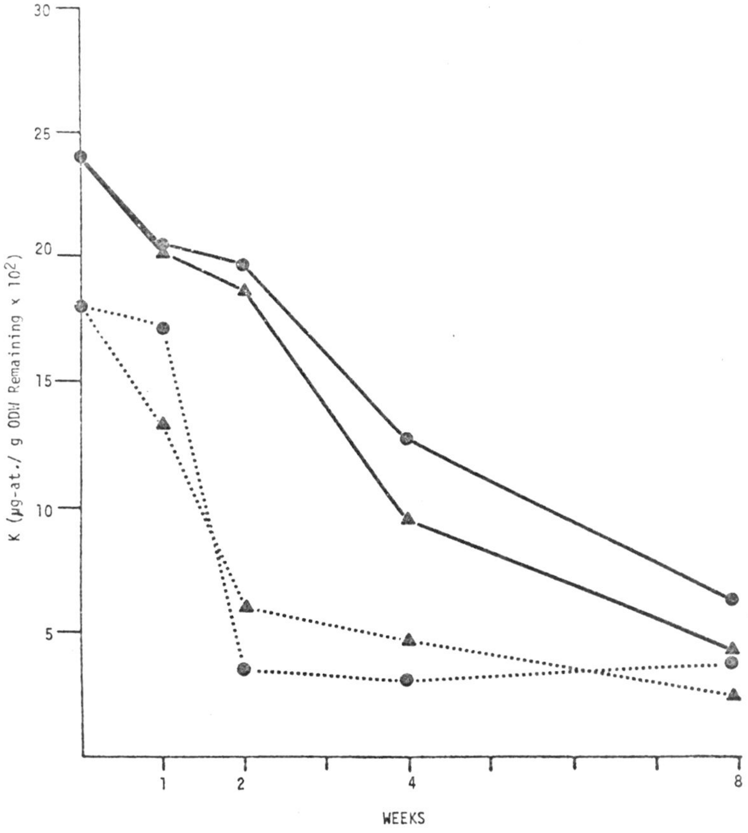
Potassium levels for harvested plants (Table 9) were minimal in summer (305 ug-at./g ODW) with winter and spring levels considerably higher. Values were approximately the same in spring for plants harvested from the upriver and downriver locations, although winter values were significantly higher upriver.

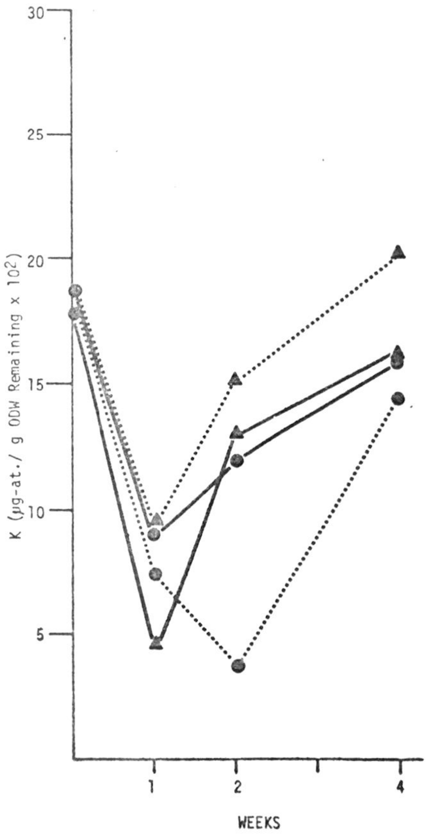
The pattern of changing levels of K during decay (Fig. 14) was similar to that for Na. Potassium is not a structural component of plant tissue and is rapidly leached from the decaying material during the winter and summer decay period. Only in the spring decay period did this decrease not continue after the initial two wks. Values instead continued to increase as decay proceeded.

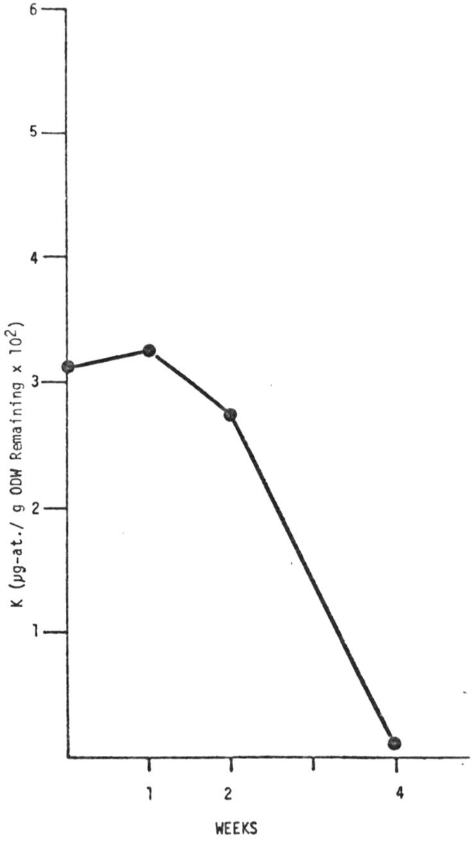
Comparisons with Other Studies

Table 10. gives a comparison of the cation levels of *Vallisneria* determined in this study and that reported by others. Despite some variability between studies, generally the Ca, Mg and K concentrations were in close agreement. Sodium levels of *Vallisneria* harvested in the Pamlico River estuary were higher than that reported by other workers. The higher Na concentrations in the plant tissue was likely associated with higher ambient levels common in the estuary as compared to fresh water study areas. Variability between studies may occur as a result of different

Fig. 14. Left- Potassium concentrations in *Vallisneria* decay in the Pamlico River estuary, 23 November 1974 to 18 January 1975. Middle- Potassium concentrations in *Vallisneria* decay in the Pamlico River estuary, 9 May 1975 to 6 June 1975. Right- Potassium concentrations in *Vallisneria* decay in the Pamlico River estuary, 21 July 1975 to 18 August 1975. (Upriver: -●- littoral, -▲- midriver; Downriver: ··●·· littoral, ··▲·· midriver).


30
25
20
15
10
5
K (µg-at./ g ODW Remaining x 10^2)
1
2
4
8
WEEKS


30
25
20
15
10
5
K (µg-at./ g ODW Remaining x 10^2)
1
2
4
WEEKS


6
5
4
3
2
1
K (µg-at./ g ODW Remaining x 10^2)
1
2
4
WEEKS

sampling periods, treatment methods and environmental levels of these elements.

SUMMARY

A direct marking technique was utilized successfully to determine the growth and production of *Vallisneria americana* Michx. at two locations within the Pamlico River estuary. Seasonal production dynamics correlated closely with temperature, as rooted plant material disappeared with the onset to winter. Plant growth initiated from the winter buds in March (water temperatures of 10-14 °C). No germination from seed was observed for this species. Leaf growth and production values were generally constant through June and increased to a seasonal maximum in August. Productivity values were lower in an upriver area of higher standing crops and extensive beds than in a downriver area of lower standing crop and scattered stands. Breakage of leaves was much greater at the wind stressed downriver site but senescing leaves were continually sloughed during the growing season at both sites. Mean seasonal values for growth and production per plant were 5.5 cm/day and 2.3 mg ODW/day, respectively. A July depression in these values coincided with peak flower and fruit production. This decrease in growth and production as a result of diversion of plant energy into sexual reproduction was not as great for the downriver plants which exhibited incomplete floral induction and/or development.

Turnover rates of 1.5% per day yield an average turnover time of 67 days or 3.7 crops per season. Thus, productivity values based only on terminal biomass estimates will grossly underestimate the net production of this species in the Pamlico River estuary.

In situ mesh bag experiments with *Vallisneria* showed that decay rates varied little when deep and shallow and upriver and downriver sites were compared. Half-life of ODW was from 3-6 wks in the winter and less than 2 wks in spring and summer. No significant difference between decay rates occurred when the open bag method was employed, although large populations of amphipods (Gammarus sp.) were apparent after 2 wks of decay in the upper reach of the estuary.

Inorganic nutrient levels of N (4100 ug-at./g ODW) and P (360 ug-at./ g ODW) were well above those reported to be limiting for Vallisneria. Concentrations of these nutrients decreased in the initial 1-2 wks of decay and was attributed to loss through cellular autolysis. Increased levels occurred after this initial loss and were probably a reflection of increasing bacterial and fungal colonization. The presence of Vallisneria material low in N and P relative to its C content (C:N:P ratio of 124:11:1) may promote immobilization of N and P from the water column by bacterial utilization of this organic matter. Thus, the result is to decrease the C:N:P ratio while limiting nutrient availability to phytoplankton. Final measurements of C:N ratios of the decay material ranged between 5 and 12 to one, indicating its potential utilization by animals that are thought to have an adult nutritional requirement for protein corresponding to a C:N ratio lower than 17:1.

The great seasonal variation in cation levels may have resulted from changing ambient levels associated with rainfall and runoff. The changing concentrations of cations, as Vallisneria undergoes decomposition, are varied and must depend on the chemical properties of the plant, the chemical properties of the elements and nutrient utilization by the biota. Calcium, which is important as a structural component of the cell wall, exhibited a long residence time as compared to K which was easily leached from living tissue.

As a result of the variety of analytical and sampling techniques utilized, comparisons of productivity values reported for aquatic macrophytes is difficult. Nonetheless it is evident that, within the Pamlico River estuary, the production of *Vallisneria* was relatively low. Its contribution to the total estuarine carbon budget is considered insignificant due to the limited coverage of the submersed macrophytes (1-2%) as compared to phytoplankton. *Vallisneria* is qualitatively significant in the support of detritus-feeding organisms in the estuary at the base of the food web and had rapid rates of turnover and decomposition.

LITERATURE CITED

Adams, F. S., H. Cole AND L. B. Massie. 1973. Element constitution of selected aquatic vascular plants from Pennsylvania: Submersed and floating leaved species and rooted emergent species. Environmental Pollution. 5: 117-147.

Adams, M. S., AND M. D. McCracken. 1974. Seasonal production of the Myriophyllum component of the littoral of Lake Wingra, Wisconsin. Journal of Ecology. 62: 457-465.

American Public Health Association. 1971. Standard methods for the examination of water and wastewater. 13th ed., 874 p.

Bauersfeld, P., R. R. Fifer AND N. W. Durrant. 1969. Nutrient content of turtle grass (Thalassia testudinum). Proceedings of the International Seaweed Symposium. 6: 637-645.

Blegvad, H. 1914. Report of the Danish Biological Station. 22: 42-78.

Boyd, C. E. 1970. Vascular aquatic plants for mineral nutrient removal from polluted waters. Economic Botany. 24: 95-103.

Boyd, C. E. 1971. The limnological role of aquatic macrophytes and their relationship to resevoir management. G. E. Hall (ed.), Resevoir Fisheries and Limnology. Special Publications No. 8, American Fisheries Society, Washington, D. C. p. 153-166.

Boysen-Jensen, P. 1914. Studies concerning the organic matter of the sea bottom. Report of the Danish Biological Station. 22: 1-39.

Burkholder, P. R., AND G. H. Bornside. 1957. Decomposition of marsh grass by aerobic marine bacteria. Bulletin of the Torrey Botanical Club. 84: 366-383.

Copeland, B. J., AND J. E. Hobbie. 1972. Phosphorus and eutrophication in the Pamlico River estuary, N. C. 1966-1969, a summary. Water Resources Research Institute, University of North Carolina. Report No. 65. 86 p.

Crawford, C. C., J. E. Hobbie AND K. L. Webb. 1974. The utilization of dissolved free amino acids by estuarine microorganisms. Ecology. 55: 551-563.

Darnell, R. M. 1967. The organic detritus problem, p. 374-375. In G. H. Lauff (ed.), Estuaries. Publication of the American Association for Advancement of Science. Publication 83.

Dillon, C. R. 1971. A comparative study of the primary productivity of estuarine phytoplankton and macrobenthic plants. Ph.D. thesis, University of North Carolina.

Gerloff, G. C. AND P. H. Krombholz. 1966. Tissue analysis as a measure of nutrient availability for the growth of angiosperm aquatic plants. Limnology and Oceanography. 11: 520-537.

Getsinger, K. 1976. Changes in a Myriophyllum spicatum L. community following 2,4-D treatment. M.S. thesis, East Carolina University.

Gosz, J. R., G. E. Likens AND F. H. Borman. 1973. Nutrient release from decomposing leaf and branch litter in the Hubbard Brook Forest New Hampshire. Ecological Monographs. 43: 173-191.

Hargrave, B. T. 1970. The effect of a deposit feeding amphipod on the metabolism of benthic micro-flora. Limnology and Oceanography. 15: 21-30.

Harper, R. M. 1918. Some dynamic studies of Long Island vegetation. Plant World. 21: 38-46.

Harrison, W. G. AND J. E. Hobbie. 1974. Nitrogen budget of a North Carolina estuary. Water Resources Research Institute of The University of North Carolina. Report No. 86. 172 p.

Hartman, R. T. AND D. Brown. 1967. Changes in the composition of submersed vascular plants in relation to photosynthesis. Ecology. 48(2): 252-258.

Harwood, J. E. 1975. Aerial multispectral sensing of aquatic macrophytes in the Pamlico River estuary, N.C. M.A. thesis, East Carolina University.

Hobbie, J. E., B. J. Copeland AND W. G. Harrison. 1972. Nutrients in the Pamlico River estuary, N.C. Water Resources Rsearch Institute of The University of North Carolina. Report No. 76. 242 p.

Hodkinson, I. D. 1975. Dry weight loss and chemical changes in vascular plant litter of terrestial origin, occurring in a beaver pond ecosystem. Journal of Ecology. 63: 131-142.

Jorgensen, C. B. 1966. Biology of suspension feeding. Oxford: Pergamon Press. 357 p.

Kaushik, N. K. AND H. B. N. Hynes. 1971. The fate of the dead leaves that fall into streams. Polski Archiwum Hydrobiologji. 68: 465-515.

Kirby, P. 1971. The annual net primary production and decomposition of the salt marsh grass *Spartina alterniflora* in the Barataria Bay estuary of Louisiana. Ph.D. thesis, Louisiana State University.

Kormondy, E. J. 1968. Weight loss of cellulose and aquatic macrophytes in a Carolina bay. Limnology and Oceanography. 13: 522-526.

Laube, H. R. AND J. R. Wohler. 1973. Studies on the decomposition of a duckweed (Lemnaceae) community. Bulletin of Torrey Botanical Club. 100: 238-240.

Martin, A. C. AND F. M. Uhler. 1939. Food of game ducks in the U.S. and Canada. USDA Tech. Bull., No. 637. Rearch Report No. 30, Fish and Wildlife. U.S. Department of Interior, Washington D.C.

McRoy, C. P. 1973. Seagrass ecosystems: Research recommendations of the international seagrass workshop. Sponsored by International Decade of Oceanic Exploration, Leiden, Netherlands. 62 p.

McRoy, C. P. AND R. J. Barsdate. 1970. Phosphate absorption in eelgrass. Limnology and Oceanography. 15: 6-13.

McRoy, C. P. AND J. J. Goering. 1974. Nutrient transfer between seagrass *Zostera marina* and its epiphytes. Nature. 248: 173-174.

Neal, J. K., S. Peterson, AND W. Smith. 1973. Weed harvest and lake nutrient dynamics. Office of Research and Development, U.S. Environmental Protection Agency. Washington, D.C.

Nelson, J. W. AND L. Palmer. 1938. Nutritive value and chemical composition of certain fresh-water plants of Minnesota. Minnesota Technical Bulletin. 1936: 3-31.

Odum, E. P. AND A. A. de la Cruz. 1963. Detritus as a major component of ecosystems. AIBS Bulletin. 13(3): 39-40.

Odum, E. P. AND A. A. de la Cruz. 1967. Particulate organic detritus in a Georgia salt marsh ecosystem. In G. H. Lauff (ed.), Estuaries. Publication of the American Association for Advancment of Science. Publication 83.

Odum, H. T. AND B. J. Copeland. 1974. A functional classification of the coastal systems of the United States. In Coastal Ecological Systems of the United States, edited by H. T. Odum, B. J. Copeland and E. A. McMahan. Volume I. Part I. Washington, D.C.: The Conservation Foundation. p. 4-84.

Odum, W. E. 1970. Utilization of the direct grazing and plant detritus food chain by the striped mullet *Mugil cephalus*. In Marine Food Chains, J. H. Steele (ed.). University of California Press. p. 224-240.

Odum, W. E., J. C. Zieman AND E. J. Heald. 1973. The importance of vascular plant detritus to estuaries. In Proceedings of the Symposium on Coastal Marsh and Estuary Management, R. H. Chabreck (ed.). Baton Rouge: Louisiana State University, Division of Continuing Education. p. 91-114.

Penfound, W. T. AND T. T. Earle. 1948. The biology of the water hyacinth. Ecological Monographs. 18: 447-472.

Perkin-Elmer Corp. 1973. Analytical methods for atomic absorption spectrophotometry. Norwalk, Conn.

Peterson, C. J. G. 1918. The sea bottom and its production of fish food. Report of the Danish Biological Station. 25: 1-82.

Pieczynska, E. 1972. Rola materii allochtanicznes w jeziorach. Wiadomosei Ekologiczne. 18: 131-140.

Prescott, G. W. 1973. How to know the aquatic plants. W. C. Brown Co., Dubuque, Iowa. p. 154.

Reed, S. 1976. Seasonal dynamics of the aquatic macrophytes of the Pamlico River estuary. M.S. thesis, East Carolina University.

Rickett, H. W. 1924. A quantitative study of the larger aquatic plants of Green Lake, Wisconsin. Transactions of the Wisconsin Academy of Science, Arts and Letters. 20: 501-527.

Riemer, D. N. AND S. J. Toth. 1968. A survey of the chemical composition of aquatic plants in Ner Jersey. New Jersey Agricultural Experimental Station, College of Agricultural and Environmental Sciences, Rutgers University. Bulletin 820. 14 p.

Russell-Hunter, W. D. 1970. Aquatic productivity and introduction to some basic aspects of biological oceanography and limnology. New York: Collier-Macmillian. 306 p.

Schuette, H. A. AND H. Alder. 1927. Notes on the chemical composition of some of the larger aquatic plants of Lake Mendota II., _Vallisneria_ and _Potamogeton_. Transactions of the Wisconsin Academy of Science, Arts and Letters. 24: 135-139.

Sculthorpe, C. D. 1967. The biology of aquatic vascular plants. New York: St. Martins Press. 610 p.

Teal, J. M. 1967. Energy flow in the salt marsh ecosystem of Georgia. Ecology. 43: 614-624.

Thayer, G. W. 1974. Identity and regulation of nutrients limiting phytoplankton production in shallow estuaries near Beaufort, N.C. Oecologia. 14: 75-92.

Thomas, W. A. 1970. Weight and calcium losses from decomposing tree leaves on land and in water. Journal of Applied Ecology. 7: 237-241.

Van Breedveld, J. F. 1966. Preliminary study of seagrasses as a potential source of fertilizer. Florida Board of Conservation. Special Science Report No. 9. 23 p.

Vicars, T. M. Jr. 1976. Remote sensing and biomass of aquatic macrophytes in the Pamlico River estuary, N. C. M.S. thesis, East Carolina University.

Westlake, D. F. 1965. Some basic data for investigation of the productivity of aquatic macrophytes. Memorie Dell' Instituto Di Idrobiologia. 18 (suppl.): 229-248.

Wetzel, R. G. 1975. Limnology. Philadelphia: W. B. Saunders Co. 743 p.

Williams, R. B. 1965. Primary production by marsh grass and eelgrass at Beaufort, N. C. Paper delivered to AERS., Hampton, Virginia.

Williams, R. B. AND M. B. Murdoch. 1968. Compartmental analysis of production and decay of <u>Juncus roemerianus</u>. Cheseapeake Science. 13: 69-79.

Winter, H. 1961. The uptake of cations by <u>Vallisneria</u> leaves. Acta Botanica Neerlandica. 10: 341-392.

Wood, E. J. F., W. E. Odum AND J. C. Zieman. 1967. Influences of sea grasses on the productivity of coastal lagoons. Symposium on Coastal Lagoons, UNAM-UNESCO, Mexico City. p. 495-502.

Zieman, J. C. 1968. A study of the growth and decomposition of the seagrass <u>Thalassia testudinum</u>. M.S. thesis, University of Miami.

Zieman, J. C. 1972. Origin of circular beds of <u>Thalassia</u> in South Biscayne Bay, Florida, and their relationship to mangrove hammocks. Bulletin of Marine Science. 22: 559-574.