1983

Metabolic and structural studies of several temperate seagrass communities, with emphasis on microalgal components (Maryland, Virginia, Chesapeake Bay)

Laura Murray
College of William and Mary - Virginia Institute of Marine Science

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METABOLIC AND STRUCTURAL STUDIES OF SEVERAL TEMPERATE SEAGRASS COMMUNITIES, WITH EMPHASIS ON MICROALGAL COMPONENTS

The College of William and Mary in Virginia PH.D. 1983

METABOLIC AND STRUCTURAL STUDIES OF SEVERAL TEMPERATE SEAGRASS COMMUNITIES, WITH EMPHASIS ON MICROALGAL COMPONENTS

A Dissertation

Submitted to

The Faculty of the School of Marine Science
The College of William and Mary in Virginia

In Partial Fulfillment
of the Requirements for the Degree of

Doctor of Philosophy

by

Laura Murray

APPROVAL SHEET

This dissertation is submitted in partial fulfillment of

the requirements for the degree of

Doctor of Philosophy

Laura Murray
Author

Approved, October 1983

Richard L. Wetzel, Ph.D.

Polly A. Penhale, Ph.D.

Kenneth L. Webb, Ph.D.

Carl H. Hershner, Ph.D.

John D. Boon, Ph.D.

Richard G. Wiegert, Ph.D.
University of Georgia

This work is dedicated to my mother, Larissa T. Murray,

for her encouragement throughout my life.

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ACKNOWLEDGEMENTS

This type of study is made possible by efforts of many individuals. I would like to express my appreciation to all those who made this study possible. Special thanks is extended to the members of my committee, Drs. Polly A. Penhale, Kenneth L. Webb, Carl H. Hershner, John D. Boon, and Richard G. Wiegert, for their guidance, efforts and time associated with the completion of this dissertation.. In addition, I would like to thank my colleagues who aided in the experimental studies, especially Rick Hoffman, Robin vanTine, Ann Evans, Damon Delistraty, William Rizzo, and Bob Middleton. I would also like to express my gratitude to the people of the computer centers at VIMS (especially Bob Lukens) and Salisbury State College and to Dawn Johnson of the SSC Biology Department for their assistance in the printing of the dissertation.

A personal thanks is extended to Michael Kemp, whose kindness and understanding helped me accomplish this work.

To Dr. Richard L. Wetzel, Chairperson of my committee, director of my research and assistant in experimental studies, I express a vary special professional and personal thanks for his dedication, patience and support. I will always carry with me the many aspects of science and ecology he has taught me.

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ABSTRACT

The relative contributions to organic matter production and the interactions between submerged vascular plants and their associated microalgae assemblages were investigated in seagrass communities characteristic of the lower Chesapeake Bay. The studies were conducted in three parts; the first compared production and respiration of the major autotrophic components in adjacent seagrass communities dominated by Zostera marina and Ruppia maritima, respectively. Annual production for the two communities differed; in the Z. marina area microalgal (i.e. phytoplankton and benthic microalgae) production dominated during the summer months, whereas in the R. maritima area, the macrophyte-epiphyte complex dominated throughout the growing season. Both areas exhibited high annual gross production rates (1580 gC m^{-2} in the Z. marina area and 1000 gC m^{-2} in the R. maritima area) of which the microalgae accounted for 45% and 36% in the two communities respectively. The ratio of net production to dark respiration (P/R) exceeded 1.0 for each of the components, suggesting export and/or burial of carbon from the system.

The second series of studies investigated specific interactions between Z. marina and its epiphytic microalgae. Two sites were examined, where pervious observations had been made of differing epiphytic colonization patterns. The two seagrass ecosystems differed markedly in epiphytic abundance, community structure, and productivity and respiration of the epiphytic complex. Based on gross morphological characteristics of the seagrass host, differences in nutrient conditions

could exist at the two sites, where the hypothetically enriched site coincided with a flourishing epiphytic community.

Effects of nutrient enrichment and light reduction on epiphytic growth were examined directly in the third phase of this study using controlled microcosm experiments. Both nutrient enrichment and light reduction led to enhanced epiphytic productivity and biomass, as well as increased light attenuation associated with epiphytic growth. Direct reduction in ambient light also stimulated epiphytic production relative to that of the seagrass host. Reduced abundance of plant leaves in the nutrient enriched systems perhaps indicated some signs of stress to *Z. marina*. This study suggests that nutrient enrichment and light reduction in the water column could increase epiphytic growth and production, possibly at the expense of the macrophyte.

Laura Murray

Department of Marine Sciences

The College of William and Mary in Virginia

METABOLIC AND STRUCTURAL STUDIES OF SEVERAL TEMPERATE SEAGRASS COMMUNITIES, WITH EMPHASIS ON MICROALGAL COMPONENTS

CHAPTER 1

GENERAL INTRODUCTION

The role and relative importance of seagrasses in shallow aquatic environments has been the subject of extensive research. Seagrass distribution and abundance has been documented on a world-wide basis by den Hartog (1970) and specifically for the Chesapeake Bay by Orth and Moore (1979). Recent work on seagrass productivity has provided annual production estimates of 200-3000 gC m^{-2} for Thalassia testudium (Jones 1968; Bittaker 1975; McRoy and McMillan 1977), 200-800 gC m^{-2} for Zostera marina (Nixon and Oviatt 1972; McRoy 1974; Nelnhuis 1980; Wetzel 1983) and 50-150 gC m^{-2} for Ruppia maritima (Verhoeven 1979; Richardson 1980; Wetzel 1983). R. maritima, which tolerates a wide range of salinities (Verhoeven 1979) is considered a seagrass in this study. These values indicate that seagrasses are major autotrophic contributers to aquatic ecosystems and on an areal basis rank second only to coastal salt marshes (Pomeroy and Wiegert 1981).

The purpose of this study is to evaluate the production and respiration of several autotrophic components of seagrass beds in the lower Chesapeake Bay. The focus is on two species of seagrasses and the microalgal components (in this system macroalgae are only present for short periods of time and are not included in this evaluation). Secondly, plant-epiphyte interactions were evaluated in relation to macrophyte growth. This portion of the study involved detemining the community structure and metabolic patterns of elphytic populations of Z. marina in two distinctly different natural systems. Thirdly, the effect of nutrient enrichment and light reduction on the plant-epiphyte complex was evaluated experimentally within micrcosms.

The approach of the study involved three separate, though integrated, investigations. In the first, field investigations of productivity and respiration of autotrophic components were conducted. In the second, estimates were made of the growth patterns and metabolic strategies of plant and epiphyte from two natural seagrass ecosystems. In the third, controlled experiments involving changes in light and nutrient conditions were performed to examine effects on seagrass-epiphyte relationships.

Seagrass communities harbor a diverse biotic assembledge containing diverse autotrophic and heterotrophic populations. Several major autotrophic components can be identified in these systems: seagrasses, benthic micro and macro algae, phytoplankton and epiphytic algae. This diversity of primary producers in a single system provides numerous pathways for autotrophic biomass utilization and leads to a greater diversity in heterotrphic organisms within the seagrass beds as opposed to surrounding bare substrates (Marsh 1975; Orth 1973; Stoner 1980). Although direct grazing on seagrasses by heterotrophs is limited (Thayer 1978; Zimmerman et al. 1979; Wilkins 1982), seagrass production does support high rates of secondary productions via detrital pathways (Zimmerman et al 1979; McConnoughey and McRoy 1979) In contrast, the microalgae populations (phytoplankton, benthic and elphytic) serve as a direct food source to many herbivorous primary consumers. In addition to the food chains associated with phytoplankton and benthic algae, epiphytic algal food chains have been demonstrated (Brasier 1975; Kekerchi and Perez 1977; Thayer et al. 1978; Harlin 1980; Ogden 1980; Morgan 1980; von Montfrans et al. 1982).

Seagrass meadows act as refuge areas for prey species. Nelson et al. (1980) and Morgan(1980) documented the use of seagrasses by small invertebrates(i.e. amphipods and mysids) to escape predation. Juvenile fish also swim into grass beds when being pursued by invertebrates(i.e. blue crabs, Heck and Orth, pers. comm.) and by larger fish (Lascara 1981).

Most studies of autotrophic production of seagrasses have involved individual measurements on the vascular plant (McRoy 1974; Zieman 1974;) or the total production of the community (Nixon and Oviatt 1972; Dillon 1971; Nelnhuis 1980; Lindeboom and DeBree 1982 Wetzel et al. 1983). The combined ecological significance of the various microalgal components has not been extensively documented. Work in freshwater lakes indicated that phytoplankton and epibentic micoralgae contribute over 50% of the total lake production (Wetzel 1964; Wetzel and Hugh 1973). Cattaneo and Kalff (1980) reported that epiphytic algae on the freshwater angiosperms Myriophyllum spicatum L. and Potamogeton richardsonii (Benn.) Rydb. contributed as much as 60% and 30%,respectively, to the total production of the plant-epiphyte complex. Comparable studies in marine ecosystems have shown similar results. Jones (1968) working in a Florida Thalassia testidinum grass bed determined that macrophyte production contributed 900 gC m^{-2} yr^{-1},the benthic microflora 200 gC m^{-2} yr^{-1}, and epiphyte production 200 gC m^{-2} yr^{-1} so that the combined microalgal contribution (excluding phytoplankton) was approximately 30% of the total. In North Carolina, Dillon (1971) estimated that the combined production of Zostera marina and Halodule beaudettei (den Hartog) production contributed approximately seven times greater organic matter input than did phytoplankton production. Bittaker (1975) reported for a T. testudinum

grass bed in Florida that the relative contribution by macrophytes and phytoplankton were approximately the same as reported by Dillon (1971). In a more detailed study, Penhale (1977) indicated that, on a dry weight basis, macrophyte and epiphyte productivity in a North Carolina Z. marina community bed were equal at certain times of the year; Borum and Wium-Andersen (1980) found similar results in Denmark.

Although the above studies studies report high rates of production by the various autotrophs in these communities, consumption (i.e. respiration) rates may also be high, especially in sediments having high faunal densities. Hargrave (1969) reported a higher benthic carbon consumption rate than could be supported by vascular plant production in a freshwater lake. Lindeboom and deBree (1982) found that both production and consumption were less for bare substrates than in nearby Z. marina areas, indicating a higher heterotrophic activity within the grass beds. Microalgae may provide more direct support of heterotrophic production in seagrass beds than the macrophytes. This is because: 1) a significant fraction of the vascular plant production may be metabolically (biochemically) unavailable to many heterotrophs; 2) some plant material is undoubtedly exported and 3) seagrass beds are generally characterized by high infaunal and epifaunal biomass, many of which directly utilize the microalgae. Thus, it is my hypothesis that significant contribution to community production by microautotrophs are characteristic of submerged grass beds in both temperate and tropical ecosystems.

A complex relationship between the seagrasses and the microalgae has been demonstrated. Studies on plant-epiphyte relations have indicated some direct transfer of materials (carbon and nutrients) between

the two (Harlin 1973, 1975; McRoy and Goering 1974; Brylinsky 1977; Penhale and Thayer 1980; Smith and Penahle 1980). Several negative interactions have also been documented, including the reduction of nutrient uptake by the macrophyte (Beer et al. 1979) and the attenuation of light by heavy epiphytic growth (Sand-Jensen 1977; Borum and Wium-Andersen 1980; Klorbe 1980), and macrophyte allelopathy to epiphytic growth (Sand-Jensen 1977; Harrison and Chan 1980; Harrison 1982). Sand-Jensen (1977) suggested that shading due to epiphytic growth on blades of the eelgrass, Z. marina, reduced photosynthetic carbon fixation by the macrophyte. Microalgal films on leaf surfaces are potentially competitors for inorganic carbon, gas diffusion barriers and light attenuating (both quantity and quality) interfaces. Most algal populations exhibit rapid and increased growth with nutrient enrichment (Welch et al. 1972; Ferguson et al. 1976) and, for eelgrass in the mid-Atlantic region, epiphytic growth consists primarily of diatoms and filimentous algae (Sieburth and Thomas 1973; van Montfrans et al. 1982), which will, hypothetically, respond in a similar manner.

The effects of increased dissolved inorganic nutrients and increased shading concomitant with epiphyte growth on leaf surfaces may potentially act as a significant control on macrophyte photosynthesis and biomass production. For example, in some freshwater systems Phillips et al. (1978) found that diatom growth on the macrophyte Najas marina increased threefold with the addition of fertilizer (N:P=10) at a rate of 2.0 g P m^{-2} yr^{-1}. Slides allowed to colonize in the same waters showed an 84% decrease in light transmission. Moss (1981) noted that freshwater lakes enriched in nitrogen exhibited higher

densities of epiphytes on the macrophyte Potamogeton pectinatus. Sand-Jensen and Sondergaard (1981) working in lakes of varying nutrient concentrations reported that epiphytic growth was 200 times greater in lakes of high ambient nutrient concentration compared to lakes of low nutrient concentration. These authors concluded that increased epiphytic growth could ultimately lead to mortality of the macrophyte due to extremely reduced light available for macrophyte photosynthesis. Sand-Jensen and Sondergaard (1981) also reported low phytoplankton concentrations corresponding to nutrient enrichment and suggested that the phytoplankton are outcompeted by attached, epiphytic algae and played a minor role in water column light attenuation. Nutrient enrichment studies involving seagrasses suggest that while some growth of vascular plants occurs with nutrient additions to the water column (Harlin and Thorne-Miller 1981), greater increases occur when they are added to the sediment (Orth 1977). Additionally, if macroalgae are present, epiphytic and planktonic microalgal growth due to nutrient enrichment is minimized (Harlin and Thorne-Miller 1981).

Light saturation of photosynthesis occurs at levels from ca 200-700 uE m^{-2} sec^{-1} for Z. marina (McRoy 1974; Penhale 1977; Wetzel and Penhale 1983). For a Z. marina bed in the lower Chesapeake Bay, mean daily in situ light intensity during the early growing season was below this range although the data are quite variable (Wetzel and Penhale 1983). If epiphyte light attenuation reduces the light available to the plant by 80% as suggested by Phillips et al. (1978) and Sand-Jensen and Sondergaard (1981), then severe limitation of plant production could occur with heavy epiphytic growth. Benthic diatoms exhibit photosynthetic light saturating intensities (20-50 uE m^{-2} hr^{-1}) much lower than

Z. marina (Taylor 1964; Ignatiades and Smayda 1970; Levin and Mackas 1972; and Admiral 1977). Assuming that the epiphytic diatoms of *Z. marina* have similar light saturation points, then their light requirements would be distinctly lower than their seagrass host and would have a competitive advantage under reduced light regimes.

In addition to the plant-epiphyte interactions described above, macrophytes may also affect benthic microalgae. Work in salt marshes has indicated that increased macrophyte growth shades the bottom, reducing benthic microflora production (Gargas 1970; Sullivan and Diaber 1975; van Ratale et al. 1976). In seagrass systems, vascular plant growth may also shade the bottom in a similar manner, decreasing available light to the benthic microalgae. However, this macrophyte growth provides a substrate for epiphytic algal growth.

This research was part of a larger project designed to assess the role of seagrass ecosystems in the lower Chesapeake Bay (Wetzel 1983). As a result of these studies, light, nutrient concentrations and perhaps temperature were determined to be the major environmental factors influencing seagrass community production. Therefore, the effect of these parameters on microalgal growth and productivity was emphasized in these studies.

CHAPTER 2
OXYGEN METABOLISM OF THE PRINCIPAL AUTOTROPHIC COMPONENTS OF A TEMPERATE SEAGRASS COMMUNITY: PLANT-EPIPHYTE, PHYTOPLANKTON, AND BENTHIC MICROALGAE

INTRODUCTION

Seagrass ecosystems are composed of several autotrophic components; macrophyte, benthic microalgae, phytoplankton and epiphytic microalgae. Evaluation of the production of the microautotrophic components is important in that it provides for a better understanding of energy available to direct secondary production within seagrass communities. Assessing the production and respiration for each of the microautotrophic components provides for an estimate of their relative contribution to the total system. An assessment of the differences in community production can be obtained by comparing the spatial and temporal values of these measurements.

The purpose of this study was to evaluate the relative productivity and respiration of the microautotrophic groups in a *Z. marina* and a *R. maritima* dominated seagrass ecosystem and to compare these measurements to those of the macrophyte. The study had the following objectives: 1) to estimate organic matter production by each of the groups relative to the total system; 2) to contrast of energy partitioning between component groups (microalgae and vascular plant) in two adjacent seagrass communities with distinctly different seasonal patterns of abundance, and 3) to assess the influence of selected environmental variables on the autotrophic groups in both communities.

STUDY SITE

This investigation was conducted in a seagrass meadow approximately 140 ha in size located on the southeastern shore of the Chesapeake Bay, Virginia, U.S.A. (37° 25' N. 75° 59' W.), locally known as Vaucluse Shores. The entire area was co-dominated by Ruppia maritima in the nearshore areas and by Zostera marina in the deeper areas with an intermediate area of mixed stands of the two species. The site was selected for its relatively pristine and stable characteristics, and because it had been previously studied, providing some background information. The area was surveyed along transects perpendicular to the shore (Figure 2.1) and a vegetative map developed by Orth and Moore (1979). The studies reported here were carried out between transects B and C and encompassed the Z. marina and R. maritima communities (Figure 2.1). The physical characteristics of the area include protection from heavy wave action by an offshore bar , a sandy sediment which is relatively low in organic content (Wetzel 1983), salinity range of 17°/oo to 25°/oo, and a temperature range of 0°C to 30°C.

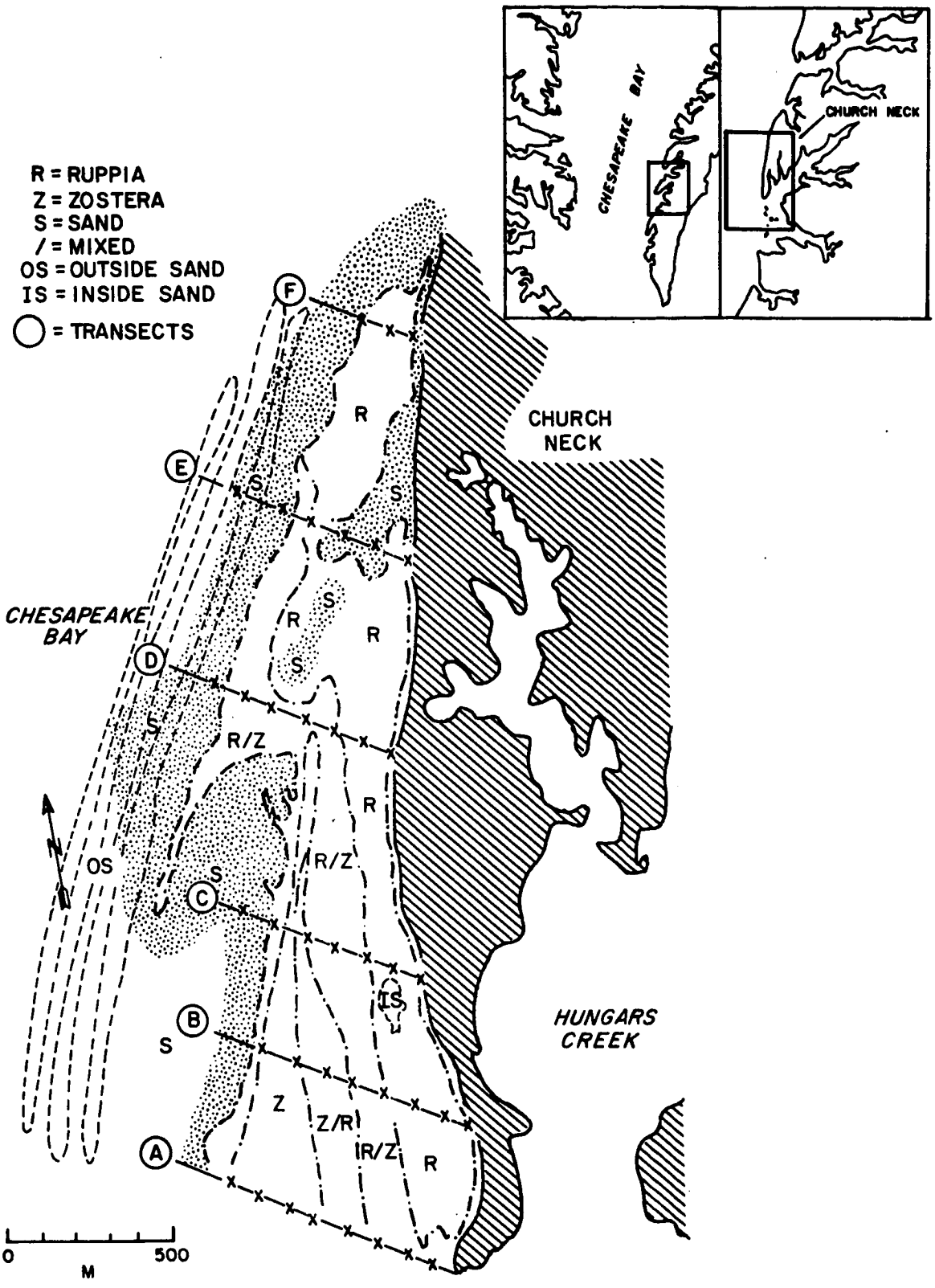

Figure 1. Geographical location of and plant community distribution at the principal study, Vaucluse Shores, Chesapeake Bay, Virginia.

MATERIALS AND METHODS

Oxygen Exchange: General Procedures

Production and respiration for each of the principal autotrophic components were estimated from the rate of evolution or consumption of dissolved oxygen various chamber designs. A multichannel, Orbisphere Oxygen Monitoring System (Model #2604) with H_2S insensitive polargraphic probes and self-contained stirrer was used to measure oxygen concentration. Light as photosynthetically active radiation (PAR: 400-700 nm) was monitored continuously using a Li-Cor Model 185A Quantum Meter equipped with surface and submarine quantum sensors. Temperature was recorded continuously from the Orbisphere which employed thermistors contained in the probe head. Area specific rates were calculated as:

$$\text{mg } O_2\ m^{-2}\ h^{-1} = [C_{I+1}-C_I]/t(t_{I+1}-t_I)\ .\ V_d\ .\ A_d^{-1}$$

where: $C_I = [O_2]$ (mg l^{-1}), I=0,1...n (hours)

t_I = time (hours) Ith interval

V_d = volume of incubation (1 liter)

A_d = bottom surface area (m^2)

Daily rates for each community were calculated by assuming that the mean, midday hourly rates were characteristic for the photo-period; respiration rates determined from dark chamber incubations were assumed constant over the 24 hr period. Photoperiod was defined as 80% of the sunrise to sunset time duration for the season. Seasonal estimates were derived by defining "season" as a function of water temperature. In the

Z. marina area the following seasonal distinctions were made: winter <10°C; spring and fall 10°to 20°C and, summer >20°C. Because the *R. maritima* area was only sampled during the growing period, seasons are defined as: spring and fall <25°C and summer >25°C. Seasonal estimates were calculated as the means between consecutive (monthly) estimates. Annual estimates are simply the sum of the seasonal estimates. For comparison to data reported elsewhere, the oxygen data were converted to carbon units assuming a PQ of 1.25 (Lindeboom and deBree 1980) for the net productivity estimates and a RQ of 1.0 for the respiration estimates.

Plankton Community O_2 Exchange

Plankton community samples were collected by a Van Doren type water sampler from just below the water surface and drained into light and dark standard BOD bottles (300 ml). Triplicate incubations for both the light and the dark bottles were made over the interval 1000 to 1400 h EST. For midday high tide studies, water depth at the *Z. marina* study site ranged from 1.0 to 1.7 m and samples from near the surface (approximately 10 cm depth) and from just above the canopy top were collected and incubated at the depth of collection. For midday low tide studies, water depth ranged from 0.5 to 0.8 m and complete mixing was assumed. At these times, only mid-depth water samples were collected and incubated. The water depth at the *R. maritima* site ranged from 0.25 to 1.25 m, therefore, only mid-depth water samples were incubated. Water column rates are reported per unit water surface area and calculated using the average water depth over the incubation interval. Oxygen concentrations in the bottles were determined at the beginning,

middle and end of the incubation period using the Orbisphere probe sealed into the BOD bottles.

Benthic O_2 Exchange

For the benthic microalgae measurements, triplicate, light and dark, cylindrical plexiglass chambers (750 ml) were placed on unvegetated sediment within the bed and incubated as for the phytoplankton samples. Duplicate clear chambers inoculated with 10 ml, 10% (v/v) buffered seawater formalin (sat. Mg CO_3) were used to estimate sediment chemical oxygen demand (COD). O_2 exchange estimates, corrected for COD, are reported as mg O_2 m^{-2}(bottom area) h^{-1}. The amount of unvegetated surface area within the Z. marina and R. maritima community were estimated from percent cover data (Orth and Moore 1982) and the areal rate estimate corrected accordingly.

Macrophyte-epiphyte O_2 Exchange

Rate estimates for the plant and epiphyte components (plant-epiphyte) were combined for the purposes of this study. Rates were calculated as the difference between total and the benthic and plankton rates estimated over the same time intervals. Total community rates were estimated by the oxygen exchange in large (260 l) plexiglass dome enclosures described in detail by Wetzel (1983). The estimates obtained in this manner were compared to other values for plant-epiphyte production from the same area. Other estimates were obtained by 1) ^{14}C radioisotope incorporation (Wetzel 1983) and 2) by oxygen production (Murray, Chapter 2) of plant leaves with epiphytes. Respiration for the plant-epiphyte component was calculated as the difference in nighttime

respiration for clear dome incubations and rates for the dark benthic chamber and dark plankton bottle incubations.

The use of dissolved oxygen evolution as a measure of primary production in seagrasses has been much criticized (e.g. Hartman and Brown 1967; Zieman and Wetzel 1980). The basis of the criticism involves the potential for O_2 storage and recycling as well as transport of O_2 to the sediments through plant roots. Recent investigations have demonstrated that the problems of O_2 storage and recycling are transient and can be minimized by stirring the water surrounding the plant (e.g. Westlake 1978; Smith and Walker 1979; Kelly et al. 1980). In addition, it appears that the amount of O_2 transport through the vascular lacunal system for most submerged vascular plants including Z. marina is small (< 5%) compared to the total O_2 produced (Iizumi et al. 1981; Sand-Jensen et al. 1982). Thus, the problems with the O_2 techniques seem to be relatively minor. Other methods such as ^{14}C-bicarbonate incorporation have similar problems (Wetzel and Penhale 1980), which may be even more serious (Sondergaard and Sand-Jensen 1980). Therefore, the O_2 method was selected for this study because it allowed simultaneous measurements of dark respiration as well. Further, the O_2 method allows for consistency of methodology for each of the autotrophic components. While the leaf-marking technique is perhaps the least ambiguous method for estimating primary production of seagrass, it gives no indication of respiration.

RESULTS

Tables 2.1A and 2.1B summarize environmental conditions for each date studies were conducted at the Z. marina and R. maritima areas. The studies covered a water temperature range of 7°C to 29°C. For these specific studies, submarine light (PAR) conditions were generally at or above photosynthetic saturation intensities for both vascular plant (Wetzel and Penhale 1983) and microalgae (Taylor 1964; Cadee and Hageman 1974; Admiraal 1977) except for Z. marina during April, early October and January studies and for R. maritima during the October study. The studies encompass the major growth and die-back periods for both vascular plant communities. Table 2.2 presents the comparison of methods for plant productivity derived by difference to those derived by ^{14}C incorporation and O_2 exchange. Method A (described by Wetzel and Penhale (1983), involved ^{14}C incubations of plants and epiphyte in 300 ml BOD bottles. Method B incorperated the same incubation design, but employed the measurement in the change of dissolved oxygen in the productivity estimates. Values in Method C were determined as the difference in total community productivity and the microalgal productivity as described in the methods section. The similarity in the values suggests agreement among the methods.

Net apparent productivity (NAP) and respiration estimates for the three, principal components of the Z. marina area are presented in Figure 2.2. The plant-epiphyte component follows the characteristic bimodal growth cycle for Z. marina in Chesapeake Bay waters (Orth et al. 1982; Wetzel 1983), which is exemplified by a summer (August) die-back period. Winter, spring and late fall are clearly dominated by the plant-epiphyte component and during mid-summer by the phytoplankton.

Table 2.1A. Experimental conditions at the Z. marina study site for in situ O_2 community metabolism studies. Data are arithmetic mean over the incubation interval.

Date	Incubation Interval (EST)	Temp °C	Par Surface	($\mu E\ m^{-2}sec^{-1}$) Bottom	Plant Biomass[1] (g dry weight m^{-2})	Plant Cover[2] (%)
3/10/81	1150-1550	8.0	-	266	n.d.	n.d.
4/09/81	1115-1345	14.0	396	104[3]	n.d.	n.d.
5/08/81	1120-1332	16.0	1860	275	95.9	93
5/22/81	1015-1430	18.0	1664	395	80.5	85
6/15/81	1030-1430	26.0	1593	323	116.	100
7/13/81	1030-1430	33.0	1183	266	61.8	70
8/04/81	1220-1525	27.0	1645	294	61.0	69
8/25/81	0950-1345	26.0	1650	285	18.7	28
10/13/81	1050-1400	20.0	1204	125[3]	24.3	33
10/22/81	1055-1455	16.0	1191	222	n.d.	n.d.
1/06/82	1020-1350	7.0	348	132[3]	n.d.	n.d.

1. Biomass data from Wetzel 1983. n.d. = not determined.
2. Estimated using Orth et al. (1979) linear regression between observed % cover and biomass ($r = 0.95$).
3. Based on Wetzel and Penhale (1982), these light intensities are suboptimal for Z. marina. All others are at or near photosynthetically saturating intensities.

Table 2.1B. Experimental conditions at the R. maritima study site for in situ O_2 community metabolism studies. Data are arithmetic means over the incubation intervals.

Date	Incubation Interval (EST)	Temp (^oC)	Par ($\mu E \cdot m^{-2}\ sec^{-1}$) Bottom	Plant Biomass[1] (g dry weight m^{-2})
6/04/81	1000-1400	23.5	627	20
6/30/81	1100-1500	25.2	-	34
7/15/81	1000-1400	29.0	720	80
8/04/81	1015-1525	27.2	355	82
8/26/81	1000-1400	24.5	469	87
9/15/81	1045-1450	26.8	371	61
10/13/81	1045-1500	20.0	125[2]	70

1. Based on Wetzel (1983).

2. Based on Wetzel and Penhale (1982), these light intensities are suboptimal for R. maritima. All others are at or near photosynthetically saturating intensities.

Table 2.2. Comparison of Methods for deriving Plant Net Productivity Estimates

A. Z. Marina - Epiphyte Complex

	$MgO_2\ m^{-2}\ hr^{-1}$		
Month	Method A(1)(4)	Method B(2)(4)	Method C(3)
Year:	1980	1982	1981
March	408	-	350
April	-	273	310
May	1106	-	-
June	-	168	395
July	-	1275	430
August	250	73	50
September	512	240	-
October	476	-	410

B. R. Maritima - Epiphyte Complex

May	191	-	-
4 August	1139	-	757
15 August	-	-	951
September	678	311	600
October	510	240	263

(1) ^{14}C radiotracer method (Wetzel & Penhale 1983).
(2) Bottle incubations of individual plants using O_2 (Ch. 2).
(3) Values obtained by difference as per this investigation.
(4) Conversion from gdw to m^{-2} based on biomass data for 1981 reported by Wetzel (1983). (gdw = grams dry weight)

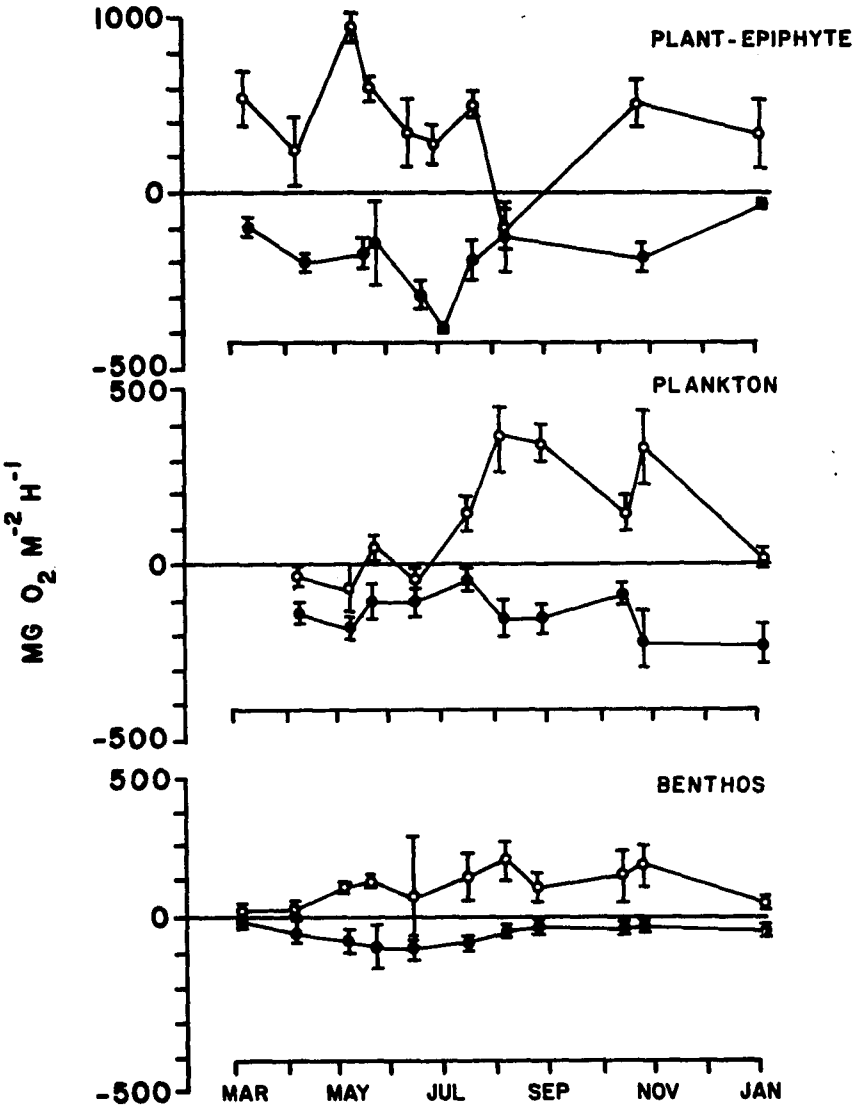

Figure 2.2. Mean (± S. D.) Net Apparent Productivity (top) and Respiration (bottom) for the three autotrophic components in the Z. marina dominated community.

Benthic algae generally had lower net apparent rates, with higher summer and lower winter values. Respiration of the plant-epiphyte component increased as plant-epiphyte NAP decreased after the highest productivity period of May, indicating a lag between the two processes. Plankton respiration showed no clear seasonal pattern but reached minimum values during the periods of peak plant-epiphyte respiration and maximum values during minimum plant-epiphyte respiration (expect in May). Benthic respiration rates were generally lower than either the plant-epiphyte or plankton components; highest rates occurred during the decline in plant productivity following the May NAP peak. Both microalgal components exhibited close coupling of NAP and respiration.

Net apparent productivity and respiration estimates for the components within the R. maritima are presented in Figure 2.3. The plant-epiphyte complex exhibit a singular peak in summer productivity, which may be a function of sampling design (e.g. measurements made from June to October). Although there are no data prior to June, Orth et al. (1979) and Wetzel (1983) report maximun biomass for R. martima during the summer months. Compared to the Z. marina community, the plant-epiphyte complex clearly dominates throughout the study period. The July peak in R. maritima-epiphyte NAP coincides with the decline in NAP of the plant-epiphyte complex for the Z. marina community. Microalgal productivity rates are considerable lower and never dominated community NAP. R. maritima plant-epiphyte respiration dominated total community respiration and tracked NAP, except for an increase with plant die-back in the fall. Generally, plankton respiration rates follow plankton NAP rates and are comparable in magnitude to those in the Z. marina phytoplankton community. Similar to the Z. marina community, the R.

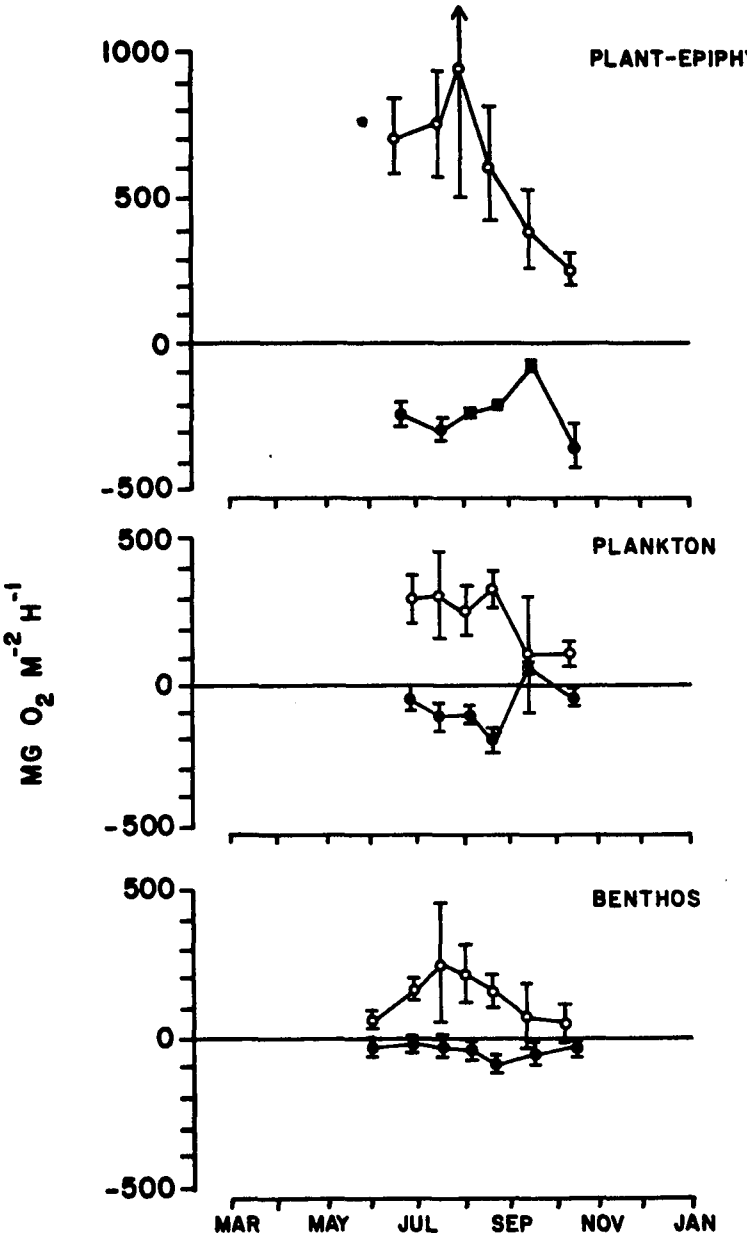

Figure 2.3. Mean (± S. D.) Net Apparent Productivity (top) and Respiration (bottom) for the three autotrophic components in the R. maritima dominated community.

maritima community benthic microalgae respiration exhibited an increase in rate following peak macrophyte NAP. Both microalgal communities followed the opposite pattern of respiration exhibited by the plant-epiphyte complex, i.e. when plant-epiphyte respiration was high, the microalgal respiration was low, and vise versa.

Tables 2.3 and 2.4 summarize the seasonal and annual estimates of gross production (calculated as the algebraic sum of NAP and respiration) and of respiration. Because of the assumption for the calculations, i.e. midday rates extrapolated to the photoperiod and constant respiration over the diel period, these estimates probably are maximized. The pattern of seasonal dominance and rates of production by the various autotrophic components indicate the potential contribution made by each to total community metabolism. Based on these calculations gross production by the plant-epiphyte component in the Z. marina community (Table 2.3) accounted for between 37% and 80% of total dependent on season. Annually the vascular plant component contributed an estimated 867 gC m^{-2} or 55% of total community gross production. Phytoplankton gross production ranged between 10% and 48% seasonally with an estimated gross annual production of 488 gC m^{-2}or 31% of total. Benthic algae contribution ranged between 10% and 25% seasonally with an estimated annual contribution of 225 gC m^{-2} or 14% of the total. Respiration by the various components in the Z. marina community varied seasonally. The plant-epiphyte respiration dominated all seasons except winter accounting for 47% to 60% of the total. In winter, the plankton component accounted for 73% of total community respiration which may be an overestimate due principally to the few measurements made, i.e. only two studies were conducted at water temperatures below 10°C. Maximum

Table 2.3. Integrated seasonal and annual estimates of gross production (P) and respiration (R) ($gC\ m^{-2}$) by the principal components and total community in the *Z. marina* area.

Component	Winter		Spring		Summer		Fall		Annual Total		
	P	R	P	R	P	R	P	R	P	R	Net
1. Plant-Epiphyte	330	53	289	105	161	140	87	117	867	415	452
% of total	55	18	80	51	41	47	37	60	55	42	76
Component P/R	6.2		2.8		1.2		0.74		2.1		
2. Plankton	205	213	36	72	134	87	113	62	488	434	54
% of total	34	73	10	35	34	30	48	32	31	44	9
Component P/R	0.96		0.50		1.5		1.8		1.1		
3. Benthos	63	25	32	30	95	68	35	15	225	138	87
% of total	11	9	10	14	25	23	15	8	14	14	15
Component P/R	2.5		1.1		1.4		2.3		1.6		
4. Total	598	291	357	207	390	295	235	194	1580	987	593
P/R	2.0		1.7		1.3		1.2		1.6		

Table 2.4. Integrated seasonal and annual estimates of gross production (P) and respiration (R) ($gC\ m^{-2}$) by the principal components and total community in the R. maritima area.

Component	25°C Spring P	R	25°C Summer P	R	25°C Fall P	R	Annual Total* P	R	Net
1. Plant-Epiphyte	306	192	259	128	142	172	707	492	215
% of total	76	76	69	80	44	46	64	62	69
Component P/R	1.6		2.0		0.8		1.4		
2. Plankton	66	54	71	27	150	190	287	291	16
% of total	16	22	19	17	46	50	26	34	5
Component P/R	1.2		2.6		0.8		1.1		
3. Benthos	30	5	45	6	31	15	106	26	80
% of total	8	2	12	3	10	4	10	4	26
Component P/R	6.0		7.5		2.1		4.1		
4. Total	402	251	375	161	323	377	1100	789	311
P/R	1.6		2.3		0.8		1.4		

* Assuming 0 in winter.

benthic respiration rates and percent contribution occurred during the summer.

Gross production by the plant-epiphyte component in the R. maritima community (Table 2.4) seasonally ranged from 44% to 76% of total, with an annual contribution of 707 gC m^{-2}, or 68% of the total community gross production. It is recognized that extrapolation on an annual basis may not represent actual values due to the lack of winter estimates. However, it is assumed that winter productivity of R. maritima is minimal compared to that of the growing season, based on personal observation of complete denudation of the R. maritima area in the winter. Clearly the microalgae components were less dominant, with annual contributions of 26% by the phytoplankton community and 10% by the benthic microalgae community. The respiration of components in the R. maritima community also varied seasonally with plant-epiphyte respiration dominating annual respiration (62%). Percent annual respiration rates of the microalgal components were similar to those of microalgal NAP.

Production to respiration ratios (P/R) indicate the autotrophic nature of each component in the two communities. Both seasonally and annually, total community metabolism was autotrophic, with the exception of fall in the R. maritima area. In terms of organic matter input to the seagrass community (ie. excess production versus respiration), within the Z. marina community the plant-epiphyte component clearly dominates in the winter and spring, the plant-epiphyte and plankton in the summer and the plankton and benthic components in fall. In the R. maritima community the plant-epiphyte and phytoplankton components are autotrophic for the spring and summer, but become heterotrophic (ie. P/R

is less that 1) in fall. The benthic community is strongly autotrophic throughout the sampling period. The lag between vascular plant production and its utilization is evident in the heterotrophic nature of the component in fall following the growing season. For the phytoplankton component, production and consumption are both spacially and temporally more closely linked. However, this pattern is not evident in the benthic component.

The productivity and respiration rate estimates were further analyzed by simple, pair-wise linear regression between selected environmental parameters (temperature and light) and vascular plant community biomass. Tables 2.5 and 2.6 summarize these results. In the Z. marina community, respiration was significantly correleated with temperature for all benthic components, while net productivity was positively correlated with temperature for the benthos. As indicated earlier, light was optimal for the majority of these experiments, which is supported by the lack of significant correlation between light and NAP. Plant biomass and Z. marina plant-epiphyte respiration was positively correlated.

There is a positive correlation between the R. maritima plant-epiphyte component and temperature, suggesting NAP-temperature by R. maritima. A stronger temperature dependence is exhibited by the benthic productivity (note the significant correlation). As with the Z. marina community, there is no significant correlation with phytoplankton productivity and temperature. Respiration was not correlated with temperature for any of the components, perhaps because temperatures were not low enough during the sampling period to limit respiratory processes. Benthic microalgal productivity was only weakly correlated

TABLE 2.5. Simple linear regression correlation coefficients for pair-wise least squares analysis of selected environmental parameters and plant community characteristics and component O_2 metabolism for the Z. marina area; NAP = Net apparent productivity; R = respiration both as mg O_2 m^{-2} h^{-1}.

	Plant-Epiphyte		Plankton		Benthos	
	NAP	R	NAP	R	NAP	R
1. Temperature (^oC)	-0.37	0.67*	0.40	0.59*	0.65*	0.57**
2. Light(μE m^{-2} sec^{-1})						
: Surface	-	-	0.22	-	-	-
: Bottom	0.20	-	0.10	-	0.40	0
3. Plant Biomass (gDW)[1]	0.13	0.81*	-	-	0.06	-0.76*

1. gdw = grams dry weight; from Wetzel (1983).

* Significant @ =0.05

** Significant @ =0.10

TABLE 2.6. Simple linear regression correlation coefficients for pair-wise least squares analysis of selected environmental parameters and plant community characteristics and component O_2 metabolism; for the R. maritima area; NAP = Net apparent productivity; R = respiration as mg O_2 m^{-2} h^{-1}.

	Plant-Epiphyte		Plankton		Benthos	
	NAP	R	NAP	R	NAP	R
1. Temperature (^oC)	0.62*	0.009	-0.47	0.001	0.61	-0.21
2. Light (μE m^{-2} sec^{-1})	0.61	-	-0.70*	-	0.62*	-
3. Plant Biomass (gDW)	-0.04	0.01	0.49	-0.40	0.43	0.54

*Significant @ the 0.10 level.

with light, due to sampling design (i.e. incubation at optimum light). Plant-epiphyte and benthic algae productivity are only weakly correlated with light, due to sampling design (ie. incubation at optimum light). Correlation of light with phytoplankton productivity is negative, perhaps due to photoinhibition (Fisher et al 1982), which would result in an underestimate in plankton production for the area.

DISCUSSION

Productivity and organic matter production in submerged aquatic macrophyte communities is partitioned among several components whose importance and contribution may vary both spatially and temporally. These are the plant and its associated epiphyte, benthic microscopic and macroscopic algae, and phytoplankton. Studies designed to investigate organic matter production, nutrient cycling and various aspects of trophic structure and/or energy-matter flux in these systems have predominately focused attention on one autotrophic component, the vascular plant. Obviously, the vascular plants structurally define the boundaries of the system. However, functional attributes of the ecosystem such as productivity, nutrient cycling and energy-matter flux with regard to the cycles of essential elements and trophic structure may be partitioned among other autotrophic components that have escaped the general attention of many studies. The studies reported here focused attention on the principle autotrophic components of a temperate seagrass ecosystem co-dominated by Z. marina and R. maritima.

The annual net production of the Z. marina plant-epiphyte was 452 gC m^{-2}, which is comparable to reported values for other temperate grass flats employing both biomass and ^{14}C radiotracer methods (Phillips 1974; Thayer et al. 1975; Penhale 1977). Maximum production for this study period at Vaucluse Shores occurred in winter, spring, and early summer and minimum rates in late summer and fall. These data support the characteristic bi-modal growth pattern reported for Z. marina existing at its southern limit (Orth and Moore 1979).

The R. maritima plant-epiphyte annual net productivity was 215 gC m^{-2}. In a Netherlands R. maritima seagrass system, Verhoeven (1980) estimated the annual production to be 150 g AFDW (ash free dry weight) m^{-2}, which relates to approximately 200 g C m^{-2} (assuming a 36.5% carbon content (Wetzel 1983)). Congdon and McComb (1979) found similar values in an Australian Ruppia dominated community (e.g. 30-180 gC m^{-2} on an annual basis, assuming the same conversion as above). These values are only slightly lower than those at the Vaucluse Shores study site, perhaps due to growing season variations.

Annual production of the benthic microalgal component in the Z. marina community totaled 225 gC m^{-2} (32-95 gC m^{-2}per season). In the R. maritima community benthic microalgal annual production was less (106 gC m^{-2}) and ranged from 30-45 gC m^{-2}seasonally. These values correspond well with annual estimates of production for a variety of sediment types which generally range between 100 and 200 gC m^{-2} (Pomeroy 1959; Grontved 1960; Pamatmat 1968; Marshall et al. 1979; Riznyk and Phinney 1972; van Raalte and Valiela 1976; Joint 1978; Zedler 1980). Comparative measures of production and respiration for different substrate types in Chesapeake Bay shoal areas have only recently been reported (Rizzo and Wetzel, unpubl. ms.). For five different but geographically close sediment types, they report an annual gross production range of 107 to 224 gC m^{-2} with a subtidal eelgrass site estimated at 187 gC m^{-2}. Considering the high degree of spatial and temporal variability associated with these measures (Rizzo and Wetzel, unpubl. ms.), the annual estimates are consistent with these data. The benthic microalgae contribute between 3% and 14% to total annual production, which brackets the 8% reported by Thayer et al. (1975).

Plankton production in the Z. marina area ranged from 36-205 gC m^{-2} and slightly lower for the R. maritima community (66-150 gC m^{-2}). Annual production was 488 and 287 gC m^{-2} for the Z. marina and R. maritima areas respectively. Considering the decrease of the water column within the R. maritima community, both areas contribute similar values. These rates are higher than those reported for other seagrass beds; e.g. I. testidinum 10-219 gC m^{-2}, (Bittaker 1975) and Z. marina 110 gC m^{-2}, (Dillon 1973). For for open Chesapeake Bay waters, phytoplankton annual production ranges from 100-200 gC m^{-2} (Patten et al. 1963; Flemer 1970; Haas 1975; McCarthy et al. 1975; Boynton et al 1982). The higher gross annual estimate for phytoplankton production in this macrophyte community agrees with the suggestion that habitats of this type have greater production than adjacent open-water areas (Takahashi and Parsons 1972). They suggest that shallower waters generally have increased production and can reach maximum levels of 1.8 gC m^{-2} da^{-1}. Thayer et al. (1975) report data that indicates the phytoplankton community contributes approximately 30% to total autotrophic production where the total was partitioned among eelgrass and epiphytes, phytoplankton and benthic microalgae. My estimates of 31% using the same principal components agrees very well with their assessment. Independent measures of phytoplankton photosynthesis from the Z. marina study site (Wetzel et al. 1979) in summer and fall using ^{14}C radiotracer techniques indicate a July average of 170 mgC $m^{-3}h^{-1}$ and an October average of 93 mgC m^{-3} h^{-1}. These agree well with the range of values for net apparent productivity (i.e. 50 mg C in July and 120 mg C in October) using oxygen.

A combination of factors might explain greater water column production within the seagrass system than adjacent open waters. Using the ^{14}C radioisotope data reported by Wetzel et al. (1979), the phytoplankton light saturate at approximately 85 uE m^{-2} sec^{-1}, which is lower than typical water column light conditions in the Z. marina area (Table 2.2). The increased in situ light conditions of the grass bed may lead to increased phytoplankton production. Water depth in this area is an average of 1.0 m, while average grass length is less than 20 cm., allowing the phytoplankton to 'take advantage' of the high remineralization rates (Nixon 1981) within the nearshore community. Therefore, it may be that the high levels of phytoplankton production in the Z. marina community are due to 1) favorable light conditions and 2) lack of macrophyte influence on phytoplankton except during peak macrophyte biomass, (i.e. note lower phytoplankton production during spring and early summer (Figure 2.2)) on phytoplankton. Although on an area basis, the phytoplankton production of the R. maritima area equaled that of the Z. marina area, there is some evidence for photoinhibition. The significant negative correlation between plankton NAP and light suggests that there is a decrease in productivity with the increase in light. If this is indeed the case, then phytoplankton production in the R. maritima area potentially could be greater than the reported values.

Carbon Production

As mentioned previously both Z. marina and R. maritima contribute similarly to the total annual gross production of the ecosystem. However, annual net production (taken as the difference in gross and respiration) in the Z. marina community exceeds that of the R. maritima

community by 282 g C m^{-2} (Tables 2.3 and 2.4). This is due to the elevated microalgal (benthic and planktonic) rates in the *Z. marina* area. Each macrophyte occupies approximately half of the 140 hectare bed, or 70 hectares. If the macrophytes occupy 50% of the area (Orth et al. 1982), it is reasonable to assume that the other 50% is occupied by benthic microalgae. Based on these calculations, the annual net carbon produced by this seagrass system is 633 metric tons (Table 2.7). (It must be realized that these values are maximized due to the high irradiance during the incubation periods (Table 2.2)). When considering that this estimate has accounted for microheterotrophic utilization, it is reasonable to assume that this maximum annual net production of carbon is available for other resident and transient consumers (e.g. macroheterotrophs) of the seagrass ecosystem. Therefore, failure to include microalgal productivity rates for seagrass systems not only underestimates total production, but ignores the perhaps more important contribution to the heterotrophic components.

Table 2.7. Annual Carbon Production for the Vaucluse Shores Seagrass Bed

Area	Component	Metric Tons Carbon		
		GPP	R	NPP
Z. marina	Plant-epiphyte	608	290	315
	Plankton	343	304	37
	Benthos	155	97	63
Area Total[1]		1106	691	415
R. maritima	Plant-epiphyte	493	342	151
	Plankton	200	187	11
	Benthos	77	22	57
Area Total[1]		770	551	219
Total for two areas		1876	1242	633

1. Assuming equal values for the *Z. marina* - *R. maritima* ecotone.

2. GPP=Gross primary production; R=Respiration; NPP=Net primary production, calculated as the difference in GPP and R.

CHAPTER 3

COMMUNITY STRUCTURE, RELATIVE ABUNDANCE AND METABOLISM OF EPIPHYTES COLONIZING *ZOSTERA MARINA* IN TWO LOWER CHESAPEAKE BAY SEAGRASS COMMUNITIES

INTRODUCTION

The epiphytic populations of macrophytes vary both structurally and functionally among naturally occurring submerged aquatic plant ecosystems. Capone et al. (1979) documented such variations in a *T. testudinum* seagrass community in Bimini. These variations may result from differences in environmental conditions, especially in nutrient concentrations and light regimes. If either of these conditions are limiting, epiphytic growth may also be limited. However, if environmental conditions become non-limiting (such as in nutrient enrichment), epiphytic growth may increase. This increase in growth could be detrimental to the macrophyte by decreasing available light to the plant and ultimately may lead to the demise of the community. The purpose of this project was to evaluate epiphytic colonization of *Zostera marina* in two lower Chesapeake Bay seagrass communities. The objectives were to determine the difference in the two areas in 1) epiphytic community structure; 2) the relative abundance of epiphyts upon the macrophytes and 3) plant and epiphyte productivity and respiration.

STUDY SITE DESCRIPTIONS

To evaluate epiphytic biomass and the productivity of macrophyte and epiphytes in natural systems, plants were collected from two seagrass beds in the lower Chesapeake Bay. The first area, located on the Eastern Shore of Virginia, at Vaucluse Shores, has been described in Chapter 1. Nutrient concentrations in the area are low, based on data from Wetzel et al. (1979). The second area, locally known as Guinea Marshes, is located on Virginia's western shore of the Chesapeake Bay at the mouth of the York River (Figure 3.1). The sampling area was located within a small embayment protected by an offshore island. The shoreline of the embayment is more populated than Vaucluse Shores; the houses are equipped with septic systems for sewage disposal. Land uses in these two areas of the Chesapeake Bay have traditionally been different. The Eastern Shore is principally agricultural and is sparsely populated. The area surrounding the study site is particularly undisturbed with only one house in the immediate vicinity. In contrast, the western shore is more densely populated and the land uses vary from agriculture to urban cities. Specifically, the area surrounding Guinea Marsh study site has some agriculture and several private residences (Figure 3.1). The two areas have similar temperature and light regimes (Orth et al. 1982; Chapter 1, this document), however, no data exists for nutrient concentrations from the embayment at the Guinea Marsh site.

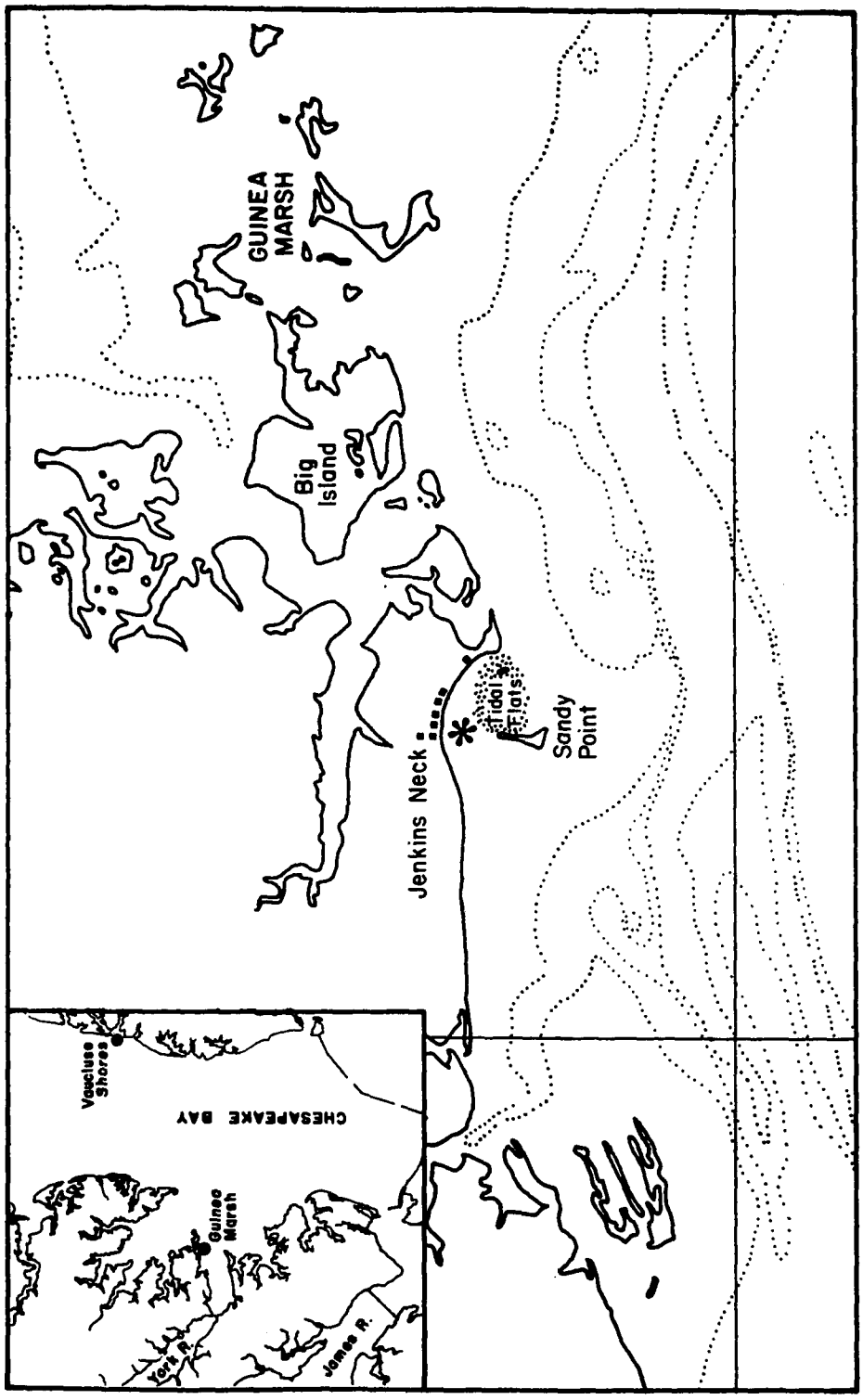

Figure 3.1. The geographical location of the Vaucluse Shores and Guinea Marsh study site with the enlargement of the Guinea Marsh site.

MATERIALS AND METHODS

Separation of Macrophyte and Epiphyte: Method Development

Cattaneo and Kalff (1977,1979) suggested that artificial substrates, i.e. plastic ribbons, develop comparable epiphytic communities to those of live freshwater submerged macrophytes. The advantage of epiphytic colonization of artificial substrates is that it allows for the determination of epiphytic biomass and productivity without disruption of the vascular plant. Beginning in April of 1980 and continuing monthly until September, polyeurythane ribbons structurally resembling Z. marina were deployed in the Vaucluse Shores seagrass bed at densities and leaf length equal to the natural vegetation (based on data from Orth and Moore, 1979). Colonization of the artificial substrates and live grasses was determined at two to three week intervals using epifloures-cent microscopy techniques. For each sampling period, slides of three separate leaf sections were prepared. A 2 cm section of leaf was placed in 3 ml sea water, stained with 20 ul proflavin (0.033%) and fixed with 200 ul 6% gluteraldehyde (Haas, pers. comm.). Ten slide grids (.024025 mm^{-2}) for each section were counted, and the mean and standard deviation for the three dominant groups are reported.

Penhale (1977) described a method for separating epiphytes from Z. marina plants from a North Carolina seagrass system. Following ^{14}C in-cubation, plants were lyophilized, after which the epiphytes were easily separated from the plant. However, epiphytic species composition and abundance of Penhale's study area differ from those at the Vaucluse Shores study site. Firmly attached diatoms of the Vaucluse Shores area were not easily removed following lyophilization (Penhale, pers. comm.),

rendering the method unacceptable to this study. Therefore, separation of the plant and epiphyte was accomplished by scraping the leaf as described below.

Production and Respiration Estimates

Plant and epiphytes were separated by gently scraping the epiphytes from the plant surface with a flat spatula. The epiphytes were scraped into filtered seawater and collected by filtration. Preliminary investigations were made to estimate the effect of the removal technique of epiphytes on plant productivity. The productivity of plants scraped clean of epiphytic material was compared with that of unscraped plants of low epiphytic densities at several light levels. Incubation of epiphytes removed from the plant resulted in very low productivity and respiration rates, perhaps indicating damage to the epiphytic cells with removal. Representative plant leaves cleaned in this fashion were checked each sampling period for removal efficiency by examining random samples using epiflorescent microscopy. Based on observation, removal efficiency was greater than 90% and for the majority of samples no epiphytes were observed on scraped leaf surface. The epiflorescent microscopy showed no observable evidence of plant tissue damage by the technique.

Productivity and respiration estimates were made by incubating plants, scraped and unscraped, in duplicate light and dark 300 ml BOD bottles. Epiphyte productivity and respiration was determined as the difference in scraped and unscraped plants. Temperature and light were controlled by placing the bottles in flow-through water baths located in full sunlight, but shaded to ambient levels by neutral density

screening. Oxygen concentration was measured at 0, 2, and 4 hours with the Orbisphere (Chapter 1) equipped with a collar designed to fit and seal into the opening of a standard BOD bottle. Productivity for both plant and epiphyte are reported as the mean mg O_2 g (dry weight plant)$^{-1}$ hr^{-1}.

Epiphyte Biomass Determination

Plants were randomly collected in the field by hand, placed in a bucket of ambient water, returned to the laboratory, and processed immediately. Epiphyte biomass was determined by scraping the leaf surfaces into filtered sea water, collected by filtration onto preweighed glass fiber filters (Whatman GF/F),and dried at 60°C and weighed to the nearest 0.01 mg. Biomass is reported as mg dry weight epiphyte.g dry weight plant^{-1}.

Enumeration of cells was made using epiflourescent microscopy to determine community structure and dominant groups. Slides of colonized live plants were prepared as described for the leaf sections. Chlorophyll *a* was determined spectrophotometerically on dimethyl sulfoxide-acetone extracts (Shoaf 1976 and Stauffer et al. 1979) of epiphytic material filtered onto glass fiber filters as above.

Plant Morphology

Plant morphology characteristics were determined on whole plants collected from the two study areas. Leaf number, length, and width was measured for eight plants from each of the sites. The means of these values and the calculated leaf area is reported.

RESULTS

Table 3.1 presents the results of the epiphytic colonization on artificial and natural macrophyte substrates field studies. The abundance and dominant groups differed between the two substrate types. Epiflourescent counts showed that the artificial substrates became colonized with bacteria within two weeks, and by eight weeks the community consisted of a varied assemblage of filamentous algae and diatoms. Colonization of the natural seagrass leaf also started with bacteria, but only one type of diatom persisted throughout the study period. This suggests that the use of artificial substrates in evaluating epiphytic communities may be erroneous, at least for Z. marina in this ecosystem.

The effect of scraping on plant photosynthesis is presented in Figure 3.2. The data indicate that the photosynthetic rate of plants with low epiphytic colonization is not inhibited at light levels greater than 200 uE m^{-2} sec^{-1} (note overlap of standard error bars). Therefore, epiphyte productivity and respiration derived as the difference in unscraped and scraped plant represents a fairly accurate estimate of epiphytic metabolism.

Figure 3.3 summarizes epiphytic biomass (Figure 3.3-A), cell abundance (Figure 3.3-B) and chlorophyll a content (Figure 3.3-C) from the two study sites. Epiphytic biomass within the two areas were equal during spring, but at the Guinea Marsh study site it increased linearly through August, while remaining relatively low at the Vaucluse Shores site. By September, no macrophytes remained at the Guinea Marsh site.

Table 3.1. Comparison of epiphytic colonization on artificial and natural macrophyte substrates. Cell abundance=number ($\bar{x}$) · m^{-2}, ±S.D.; N=30).

Date	Colonization time	Organism*	Cell Abundance artificial	Cell Abundance natural
5/9/81	2 mo.	D	ND**	0
		B	ND	345(± 15.78)
		B-G	ND	12(±1.23)
5/26	2 wks.	D	0	1
		B	114	60(±.23)
		B-G	36 (±12.16)	4
6/15/81	5 wks.	D	321 (±53.46)	2241(±30.67)
		B	solid coverage (not counted)	25(±15.52)
		B-G	0	
7/23/81	9 wks.	D	522 (±71.33)	377(±80.33)
		B	0	0
		B-G	0	0
8/4/81	11 wks.	D	518 (±11.60)	934(±8.30)
		B	0	0
		B-G	0	0
8/28/81		D	ND	69(±4.35)
		B	ND	0
		B-G	ND	0
9/17/81		D	ND	0
		B	ND	0
		B-G	ND	0

* D = Diatoms
B = Bacteria
B-G = Blue-Green Algae
** ND = Not Determined

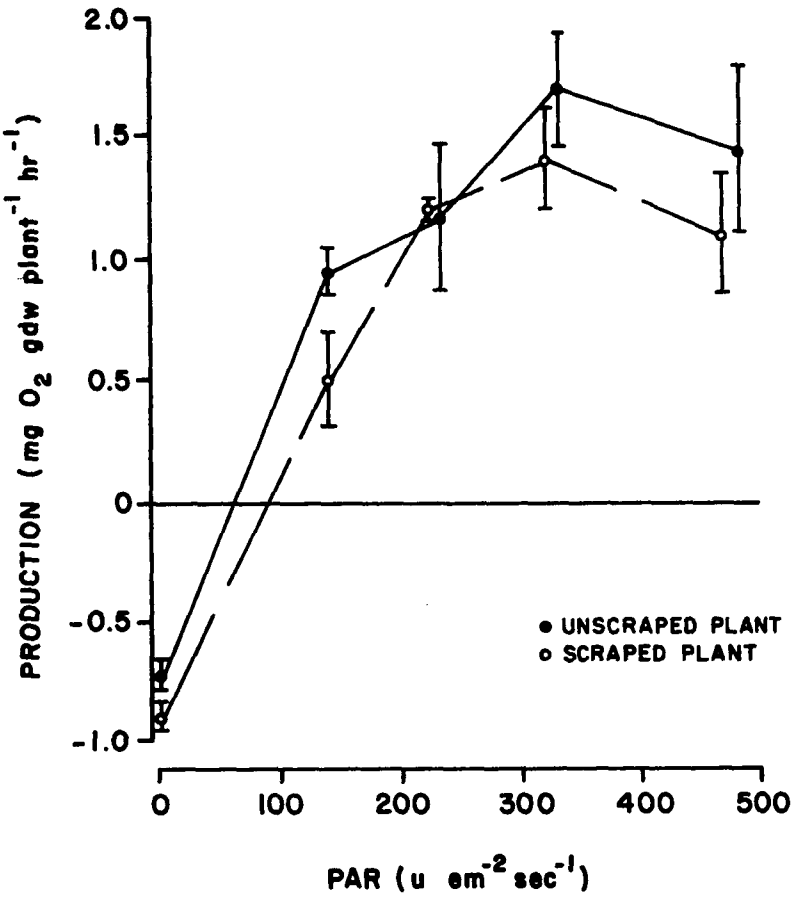

Figure 3.2. Productivity vs. Irridiance for Z. marina with and without epiphytic growth.

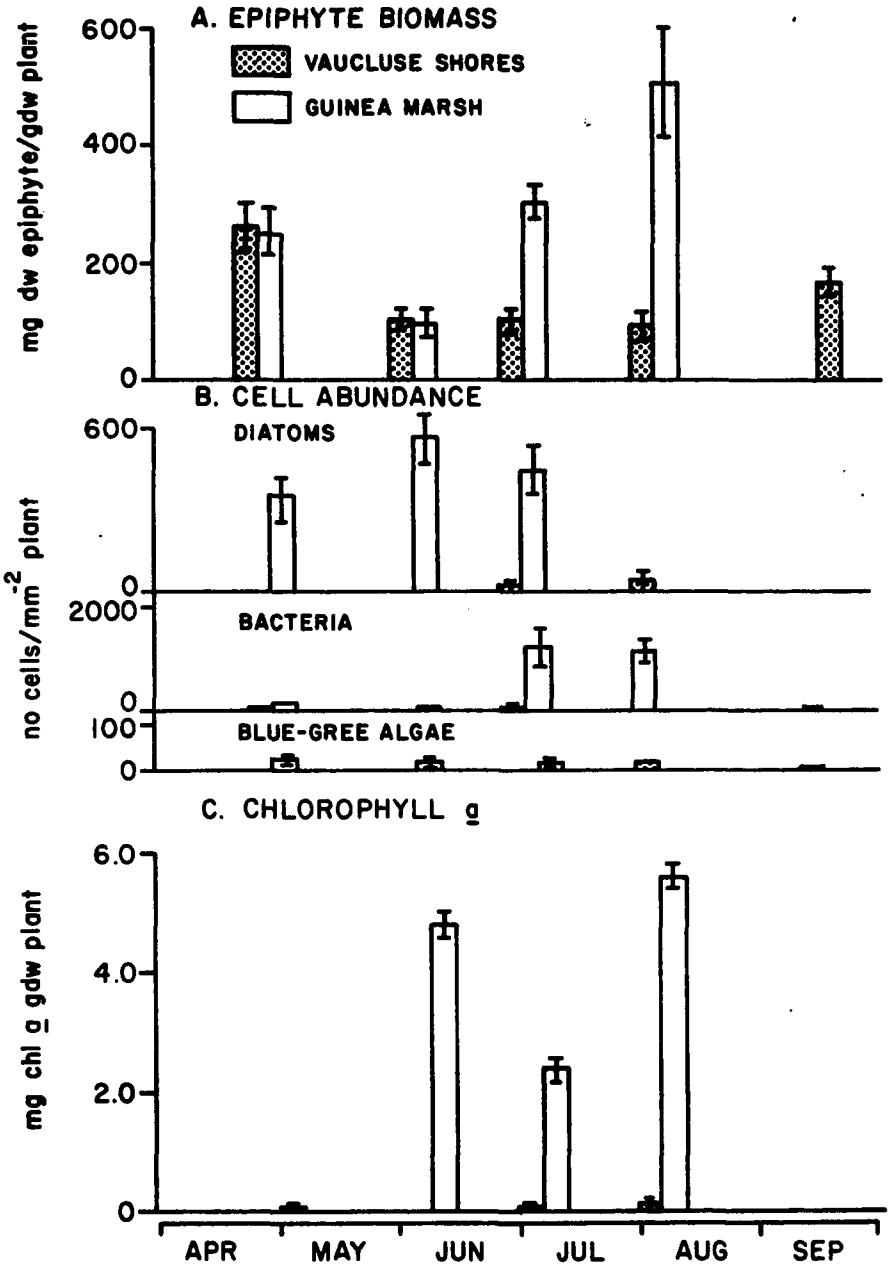

Figure 3.3 Comparison of epiphytic biomass (A), cell abundance (B), and Chlorophyll a (C) content at Vaucluse Shores and Guinea Marsh.

Community structure and cell abundance also varied between the two study sites. The three dominant components included diatoms, bacteria and blue-green algae, as described in detail by von Montfrans et al. (1982). Diatoms and bacteria were dominant for the first three months at Guinea Marsh. The August epiphytic community completely covered all plant leaf material and consisted of macroheterotrophs, including sponges, encrusting bryzoans and anemones. Due to the heavy colonization by macroheterotrophs, enumeration of individual cells by epifiourscent microscopy was not possible. Abundance at the Vaucluse Shores site remained low, with a slight increase in August in diatoms and bacteria. Although present in relatively high numbers, blue-green algae never dominated abundance in either area. Chlorophyll *a* values are consistent with the results of biomass and abundance, in that the values for the Guinea Marsh site far exceeded those of the Vaucluse Shores site. The high chlorophyll *a* values in August is due to filimentous green algae, which were not enumerated (note the lack of diatoms for this date.)

Results for plant and epiphyte metabolism studies at the Vaucluse Shores and Guinea Marsh study sites are given in Figure 3.4. Macrophyte productivity for Vaucluse Shores exhibits the same summer time depression noted in other studies for the same area (Wetzel 1983), followed by an early fall increase. Epiphyte productivity was negligible, and supports the low values of biomass and chlorophyll data. Epiphyte respiration was also low and followed epiphyte productivity. A completely different pattern is exhibited by the Guinea Marsh community. For the first three sampling periods, plant productivity increased, exhibiting an opposite pattern from Vaucluse Shores. Epiphyte productivity (while relatively high as compared to Vaucluse Shores)

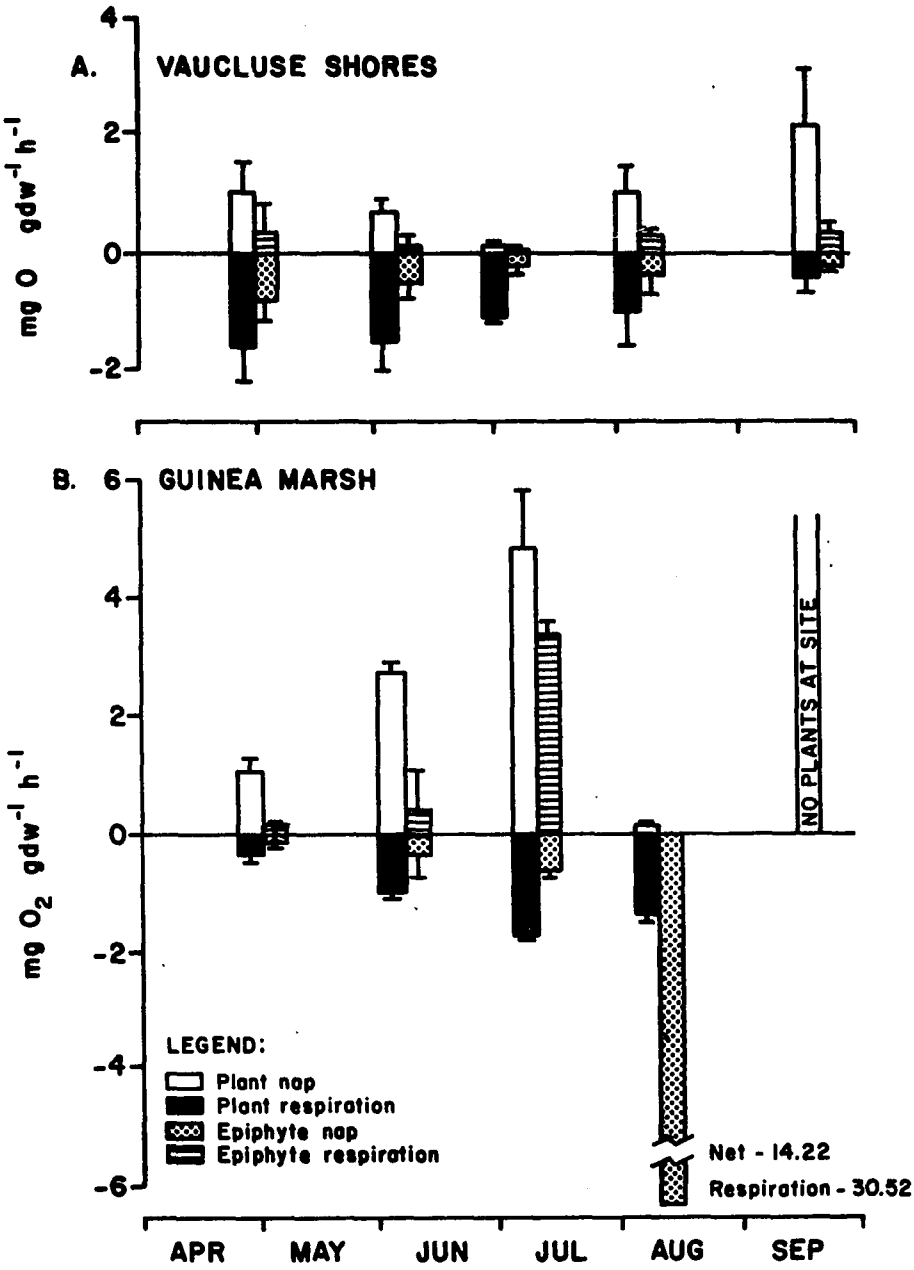

Figure 3.4. Productivity and Respiration for Plant and Epiphyte at Vaucluse Shores and Guinea Marsh

remained low until July, when it almost equaled that of the plant. In August, the epiphyte component was strongly heterotrophic, as would be expected by the heavy macrofaunal colonization. Macrophyte productivity was also greatly reduced, perhaps indicating plant stress and/or senescence. Epiphyte respiration increased as epiphytic productivity increased, which suggests a strong coupling of autotrophic and heterotrophic processes.

Plant morphology data from the two study areas are presented in Table 3.2. Significant differences in mean width and area were found for plants sampled from Vaucluse Shores and Guinea Marsh.

Table 3.2. Variations in Plant Morphology for 1981 between Vaucluse Shores (VS) and Guinea Marsh (GM) Study Sites ($\bar{x}$, I.S.D.; n=8)

Month	Leaf Number		Length (cm)		Width (cm)		Area (cm^2)	
	VS	GM	VS	GM	VS	GM	VS	GM
April	4 (±0)	4.75 (±0.97)	18.70 (±3.35)	17.60 (±3.52)	2.75* (±0.18)	3.06 (±0.49)	48.02 (±9.32)	53.56 (±12.00)
June	4 (±0)	3.88 (±0.60)	18.9* (±2.14)	27.77 (±5.16)	2.75* (±0.27)	3.63 (±0.44)	55.29* (±10.88)	105.24 (±26.79)
July	3.13 (±0.33)	3.63 (±0.48)	39.21 (±4.21)	42.75 (±5.24)	3.00* (±0.32)	3.88 (±0.35)	118.87* (±21.30)	166.55 (±29.82)
August	3.63 (±0.48)	3.25 (±0.43)	22.05* (±2.02)	32.39 (±6.79)	2.94* (±0.18)	3.50 (±0.59)	64.61 (±7.04)	122.75 (±36.42)

* Significant @ α + 0.05 level

DISCUSSION

Results of these field studies indicate differences in epiphytic community structure and abundance between the Vaucluse Shores and Guinea Marsh study sites. It is hypothesised that these differences are attributable to increased nutrient concentrations to the water column and/or reduced light at the Guinea Marsh site, perhaps due to anthropogenic nutrient loading. Iizumi et al. (1980), Phillips and Lewis (1983) and Short (1983) report that eelgrass morphology is an indicator of environmental nutrient concentrations (i.e. plants growing in areas with higher nutrient concentrations are more robust, with increased leaf width, length and area). The significant differences in the plant morphology data from these two study support the hypothesis of increased nutrient concentrations at Guinea Marsh.

Differences in the two communities are further suggested by the differences in plant productivity. The Vaucluse Shores macrophyte productivity exhibited the characteristic mid-summer decline with a late summer-early fall increase described by Wetzel (1983). However, the Guinea Marsh macrophytes followed an opposite pattern (i.e. peak in June with a steady decline thereafter). The results of the epiphytic productivity studies corroborate the assumption (made in Chapter 1) that epiphytes at Vaucluse Shores contribute little to the total community production. The values of epiphytic net production provided in Figure 3.4 are probably overestimates attributable to problems in the methodology (scraping epiphytes from plant leaves). Undoubtedly, this method causes some injury to the seagrass and its epiphytes, which can lead to

an overestimate of the relative contribution of epiphytes. Generally, the cell abundance and chlorophyll *a* data (Figure 3.3) are probably more reliable than the productivity data. Considering the fact that chlorophyll *a* levels were undetectable (by fluorometer ananlysis) in July (and therefore epiphytic production was approximately 0) the overall contribution of epiphytes to combined plant-epiphyte net production for the summer period was less than 10% at this site.

The effect of nutrient enrichment on naturally occurring *Z. marina* communities may be evident in comparing the two study sites. At the Vaucluse Shores site, which has relatively low nutrient concentrations compared to those in the lower York River (Webb, pers. comm.), epiphyte productivity remained low throughout the sampling period. At the Guinea Marsh site, where nutrient concentrations may be higher, the epiphyte productivity was low in early summer. However, in July it increased to almost equal that of the plant, while in the following months the epiphytic community became heterotrophic. Based on studies involving nutrient enrichment in a Rhode Island coastal lagoon, Harlin and Thorn-Miller (1981) hypothesized that at low water column nutrient concentrations, vascular plant growth is favored because they can draw from sediment nutrient reserves. At intermediate nutrient concentrations, macroscopic algae (i.e. *Ulva lactuca* and *Entromorpha plumosa*) become dominant, and at high nutrient concentrations, planktonic algae replace benthic autotrophs. The findings of my study are consistent with this concept if one considers that in the absence of macroalgae, epiphytic algae dominate as long as the vascular plants can persist, but under continued nutrient enrichment, the seagrass and their epiphytic community are replaced by phytoplankton (and perhaps benthic algae).

Therefore, duration of exposure as well as nutrient concentrations, may both be important in interpreting the replacement of communities at the Guinea Marsh site. First there was the initial development of a strongly autotrophic epiphyte community, which was followed by the development of a filter-feeding macroheterotrophic epiphyte community. The development of this type of community could suggest the presence of water column plankton, which serve as a food source for the filter-feeders. This hypothesis is consistent with that of Phillips et al. (1978), who suggest seagrass community replacement by plankton with continual nutrient enrichment.

CHAPTER 4

THE EFFECT OF NUTRIENT ENRICHMENT AND LIGHT REDUCTION ON *ZOSTERA MARINA* L. EPIPHYTIC GROWTH

INTRODUCTION

The variation of epiphytic growth on Zostera marina communities may be the result of variations in enviromental parameters. Nutrient enrichment to the water column of submerged aquatic macrophyte systems promotes microalgal growth, especially those epiphytic on the plant (Sand-Jensen and Sondergaard 1981). Laboratory experiments involving controlled nutrient concentrations and light regimes enable the more precise interpretation of the effects of these external parameters on the growth and metabolism of the plant-epiphyte complex.

The purpose of this study was to evaluate macrophyte- epiphyte interactions under variable nutrient and light regimes. The objectives were to: 1) investigate the effect of controlled nutrient enrichment and light reduction on epiphytic biomass of Z. marina, 2) evaluate the effect of nutrient enrichment and light reduction on plant and epiphyte productivity, 3) and estimate light reduction due to epiphytic growth on the leaf surface.

MATERIALS AND METHODS

Experimental Design

Z. marina plants were collected in mid June from the Guinea Marsh study area described in Chapter 2. Plants were returned to the laboratory and cleaned of epiphytic growth by gently scraping the leaf surfaces with a flat spatula, blotteed dry, weighed (total wet weight) and individually planted in pots containing cleaned sand. Twenty- four potted plants were placed in each of six, 10 gallon flow- through aquaria (Figure 4.1). Flow rates were maintained at approximately 350 ml $min.^{-1}$, which resulted in complete water turnover time of 1.5 hours. The aquaria were incubated on a larger, flowing sea water table to maintain ambient river water temperatures. The following experimental treatments were used: two aquaria (numbers 1 and 2) had ambient (control) nutrient levels; two aquaria (numbers 3 and 4) had nitrogen levels 30 times ambient and two aquaria (numbers 5 and 6) had nitrogen levels 70 times ambient. Nutrient amendments were added according to the Redfield ratio for nitrogen and phosphorus (NP 16:1) and concentrations were maintained using stock solution of 47 uM ammonia nitrate and 6 uM disodium phosphate by metering into the aquaria with a multi-speed transmission peristaltic pump. Metering rates were monitored daily to assure constant treatments throughout the experiment. Three of the tanks (1,3 and 5), were shaded with neutral density screens to in situ light levels (ie. light levels normally experienced by the natural community (Table 2.1)). The other three tanks (2, 4, and 6), were shaded to 50% of the in situ control levels. Water quality

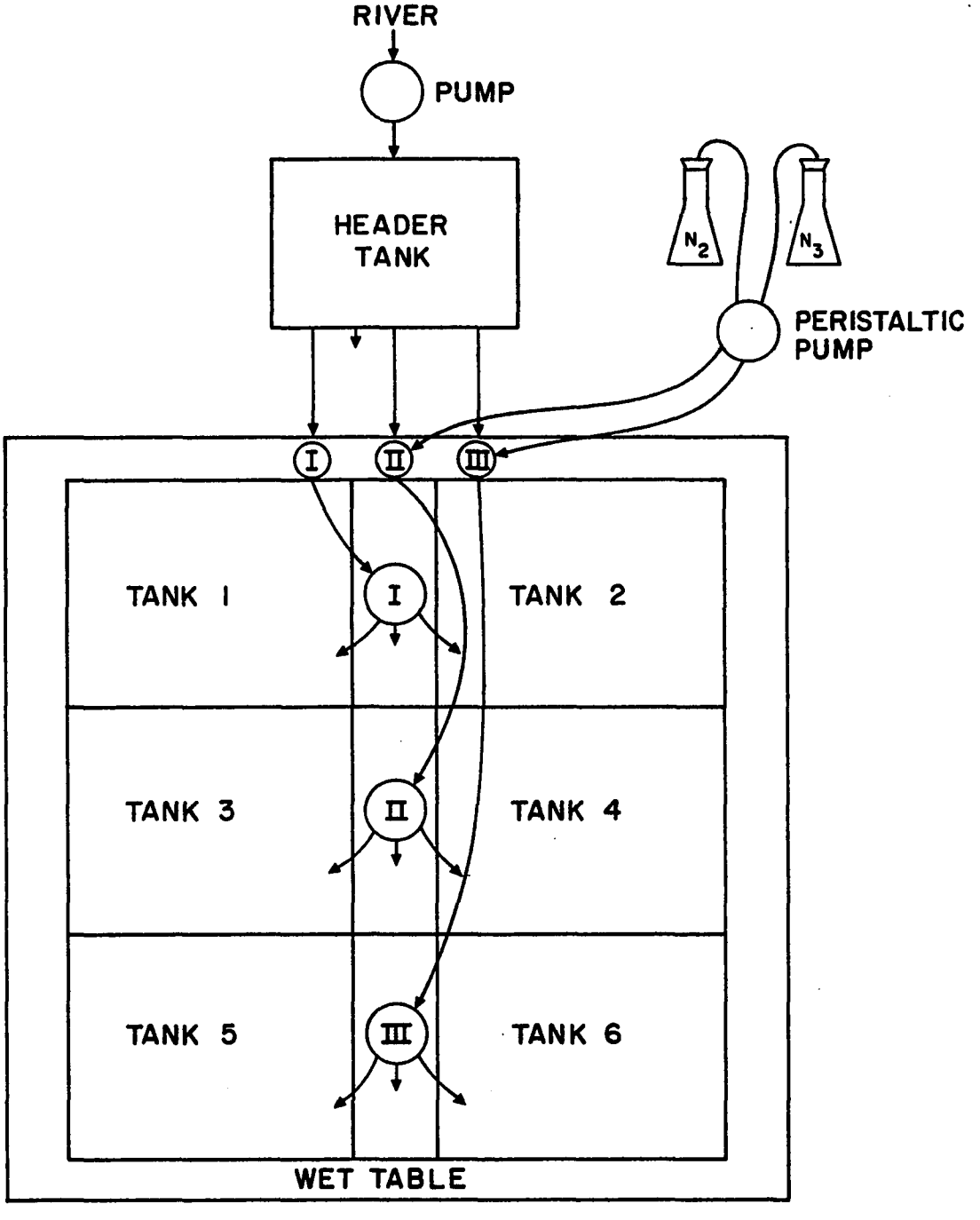

Figure 4.1. Experimental design for the nutrient enrichment and light reduction investigations.

parameters measured over the course of the study included dissolved oxygen, temperature, salinity, and light as photosynthetically active radiation (PAR). Oxygen concentration was determined with an Orbisphere Oxygen Monitor (Model #2604). Temperature and salinity were monitored daily using a max-min reversible thermometer and salinity determined using a refractometer. Light was continuously measured over the photoperiod, using a LI-COR Quantum Meter (Model #185A) at the top of the plant canopy. Concentrations of nitrate, nitrite, ammonia and orthopohsphate were determined on duplicate water samples from each tank using standard, Technicon Auto Analyzer techniques at the beginning, mid, and final dates of the experiment. The experiment was conducted for a total of two weeks to minimize enclosure effects.

Treatment effects

To determine epiphytic biomass on Z. marina leaves in these experiments eight plants were randomly sampled from each tank at the end of the two week period. The surfaces were scraped into filtered sea water, and processed as described previously (see Chapter 2) to determine epiphytic dry weight.

Light Attenuation by Epiphytic Growth

To estimate light attenuation due to epiphytic growth, two etched (sanded with rough grade sand paper) plexiglass slides were placed in each of the experimental tanks and allowed to colonize for the duration of the experiment. Light measurements were made before and after colonization by placing the slide over the quantum sensor (in water) of

the LI- Cor Quantum meter. The difference in the two values as percent was used to estimate the light reduction due to epiphytic growth.

Productivity and Respiration Estimates

Productivity and respiration estimates for *Z. marina* were made by incubating plants, scraped and unscraped, in light and dark 300 ml BOD bottles, as described in Chapter 2. Epiphyte productivity and respiration were calculated as the difference between scraped and unscraped plant. Incubations were conducted in their respective tanks to maintain ambient temperature and controlled light. Oxygen concentration was measured at 0, 2, and 4 hours with the Orbisphere (Chapter 1) using a polarographic probe equipped with a collar designed to fit and seal into the opening of a standard BOD bottle.

To estimate treatment effects on plant growth, initial and final measurements of shoot length, fresh weight and leaf number were determined on eight random plant samples from each tank. Initial plant wet weights were obtained on total plants (leaves and shoots).

RESULTS

Routine (every two days) sampling data (Table 4.1) indicated little variation among tanks for salinity (20-21o/oo) and temperature (26-31^{o}C), but relatively high midday dissolved oxygen concentrations (10-18 mg O_2). Average midday PAR measurements in the light-control tanks (1, 3 and 5) ranged from 422 to 490 uE m^{-2} sec^{-1} and in the shaded tanks (2, 4 and 6) ranged from 180 to 220 uE m^{-2} sec^{-1} or about 43% of the control light levels. Average nutrient concentrations over the experiment show that for the controls tanks (1 and 2) nitrogen:phosphorus (N:P) ratios were approximately 7:1 while in the nutrient amended tanks (3, 4, 5 and 6) were 18:1 and maintained according to intended design.

Initial and final total plant weight and final epiphyte biomass are given in Figure 4.2. There was no significant differences (α=0.05) in mean whole plant weight over the course of the experiment although all mean final values were lower than initial conditions. Epiphyte biomass at the end of the experiment was approximately equal in tanks 1 through 5. Tank 6 was higher and differed significantly from all others.

The ratio (E:P) of epiphyte biomass to plant leaf biomass was used for data reduction to and test for treatment effects. The effect of ambient light reduction and nutrient treatment on epiphytic growth is illustrated in Figure 4.3. In the shaded tanks, epiphytic growth averaged approximately 70% higher than in corresponding control treatments. In each light treatment, epiphytic growth per plant increased with increased nutrient level. In the control light tanks the

TABLE 4.1. MEAN MIDDAY DISSOLVED OXYGEN, NUTRIENT CONCENTRATIONS AND LIGHT (PAR) INTENSITY IN THE EXPERIMENTAL TANKS. ENTRIES ARE MEAN OF ALL OBSERVATIONS MADE OVER THE TWO WEEK STUDY.

Tank No.	O_2 (mg O_2 ℓ^{-1})	PO_4^{-3} (μM)	$NO_2^- + NO_3^-$ (μM)	NH_4^+ (μM)	N:P (μM)	PAR (μE m^{-2} sec^{-1})
1	11.9	0.49	1.19	3.57	7.67	470
2	9.52	0.49	0.71	2.69	6.94	180
3	16.7	7.74	72.3	59.6	17.0	422
4	10.7	7.97	68.4	67.1	17.0	188
5	18.5	13.4	128.	129.	19.2	490
6	10.5	15.1	142.	142.	19.1	220

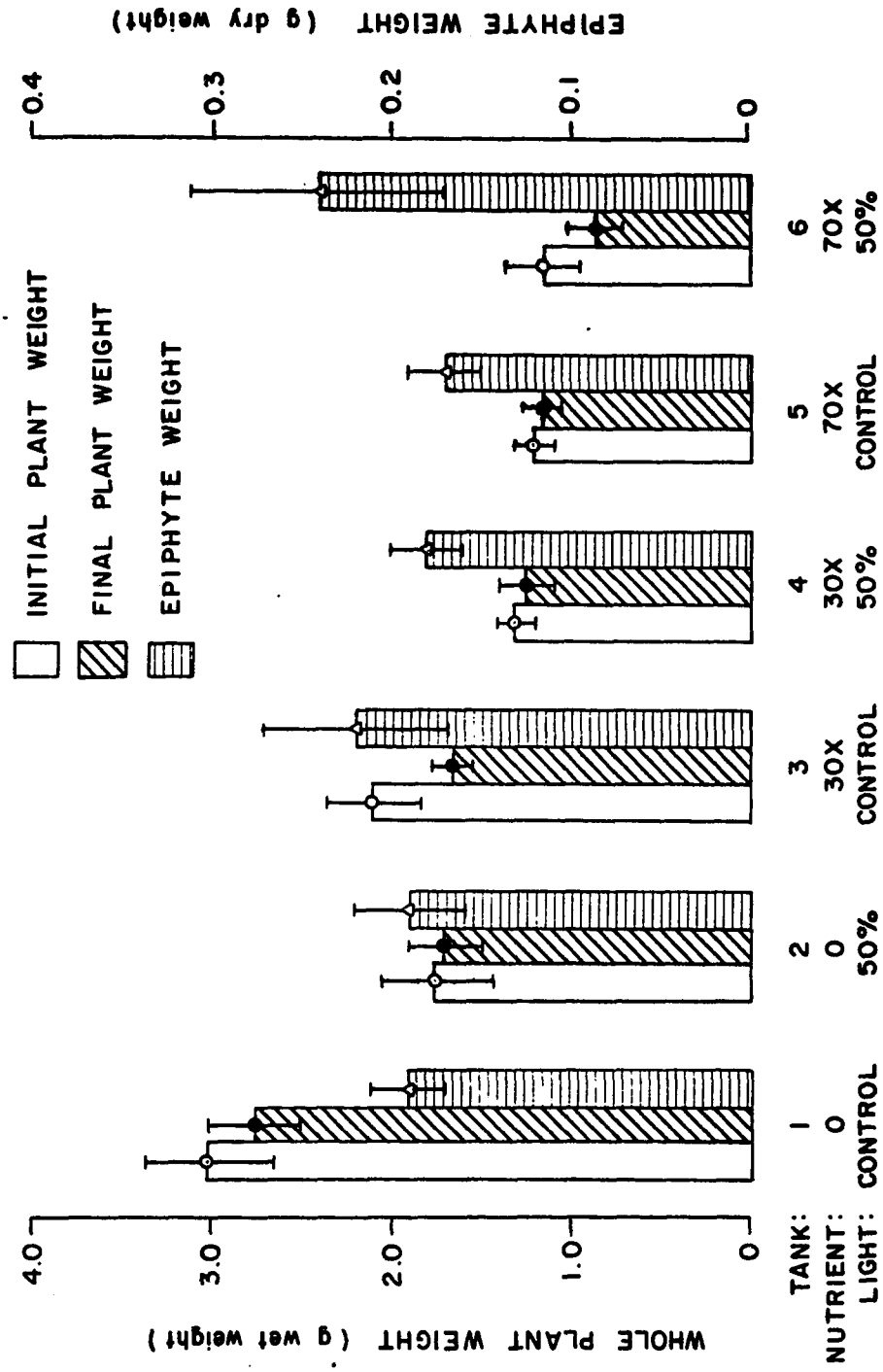

Figure 4.2. Mean (± 1 S.D.; n=8) initial and final whole plant biomass (g wet weight $plant^{-1}$) and total final epiphyte biomass (g dry weight $plant^{-1}$) following the two week experiment. Horizontal scale notes tank number, PAR regime situ; 5=50% in situ PAR) and nutrient regime (0=ambient; 30X and 70X = enrichment factor).

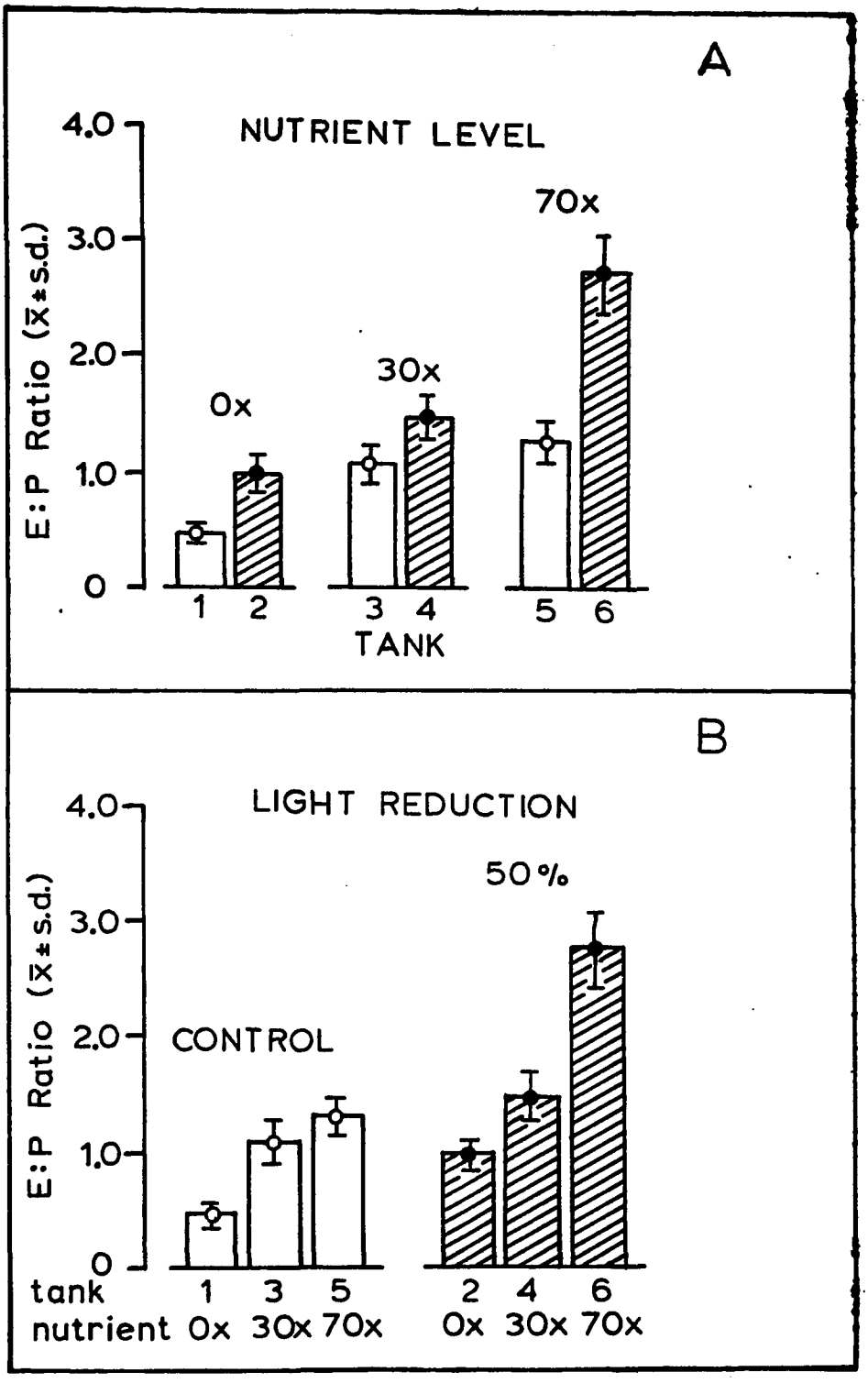

Figure 4.3. Resulting mean (± 1 S.D.; n=8) epiphyte (g dry weight to plant leaf (g dry weight) biomass ratio following the study. The upper panel is grouped by light regime and the lower panel by nutrient treatment for convenience.

greatest increase occurred between ambient and nutrient level 1. In the shaded tanks the greatest increase was between nutrient level 1 and nutrient level 2, suggesting a interactive effect between nutrient concentration and decreased light. Overall, the shaded tanks had a greater increase in epiphytic growth with increased nutrients.

Table 4.2 summarizes the results of simple pair-wise comparison of mean ratios blocked by treatment and gives the probability that the mean ratios are different. There are significant differences in mean ratios due to the light and nutrient treatments. Because the calculated t-statistics are negative for all comparisons using the blocking design illustrated, both decreased light and increased nutrient level had positive effects on the ratio and thus epiphyte growth. Table 4.3 summarizes the results of analysis of variance using an ANOVA Model I with fixed effects. As indicated, there were highly significant main effects and a lower but significant light- nutrient interactive effect.

The degree of light attentuation due to epiphyte growth, i.e. colonization on the test plates, is presented in Table 4.4. The data suggest that nutrients have a greater effect than incident light reduction (i.e. shading treatments). Figure 4.4 illustrates the relationship between epiphytic percent light reduction and the epiphytic biomass. Percent light reduction increased by an average of 58% in the nutrient enriched treatments (dotted line), while in the shaded treatments remained constant (solid line). The data suggest that percent light reduction due to epiphytic attenuation remains constant over the shading treatments but increases logarithmically with increasing nutrient levels. Overall, there is an increase in percent

TABLE 4.2. SIMPLE PAIR-WISE TESTS OF MEAN EPIPHYTE: PLANT LEAF BIOMASS RATIO DIFFERENCES BLOCKED BY LIGHT (PAR) AND NUTRIENT TREATMENTS.

Blocks	Mean Comparison Test (tanks i-j)	d.f.[1] (n)	t-statistic	P[2] ($\bar{x}_i \neq \bar{x}_j$)
a. Light	1-2	14	-3.14	>.995
	3-4	14	-1.18	>.800
	5-6	14	-2.70	>.990
b. Nutrients				
1. In situ PAR	1-3	14	-2.2	>.975
	3-5	13	-0.714	>.750
	1-5	13	-6.56	>.995
2. 50% In siut PAR	2-4	14	-1.49	>.900
	4-6	13	-2.20	>.975
	2-6	13	-3.43	>.995

1. d.f. = degrees of freedom for test statistic.

2. P = probability that the two means are significantly different.

TABLE 4.3. MODEL I ANOVA (FIXED EFFECTS) FOR NUTRIENTS, LIGHT AND INTERACTIVE EFFECTS ON EPIPHYTE: PLANT LEAF BIOMASS RATIOS.

Source	df	SS	MS	F
Nutrients	2	13.1	6.54	49.1**
Light	1	9.97	9.97	74.8**
Nutrients X Light	2	1.55	.777	5.83*
Error	40	5.33	.133	
Total	45	29.9		

* Significant @ = 0.05

** Significant @ = 0.01

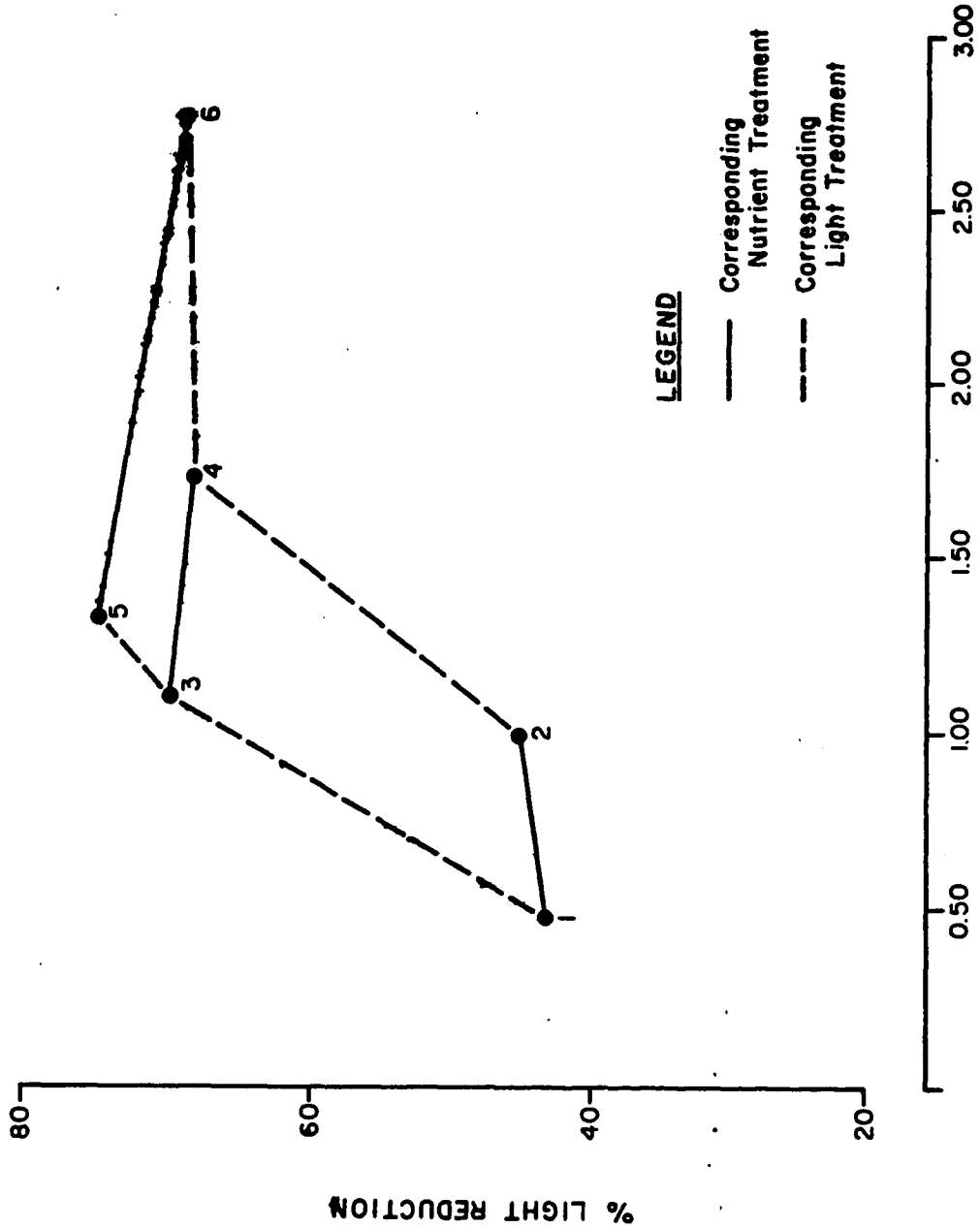

Figure 4.4. Covariant plot of % light reduction attributed to epiphytic growth (slide colonization) and mean epiphyte: plant leaf biomass ratio. The solid lines connect corresponding nutrient treatments; the dashed line, corresponding light treatments.

TABLE 4.4. TREATMENT EFFECTS ON EPIPHYTIC BIOMASS (A), $\bar{x}$ g DRY Wt. PLANT^{-1} ($\pm$ S. E.) AND LIGHT REDUCTION DUE TO EPIPHYTES (COLONIZATION OF SLIDES) (B), $\bar{x}$ PERCENT DECREASE ($\pm$ S. E.).

A.		Nutrients*		
	Light	0	1	2
	Control	47.4 (3.8)	110. (24.0)	128. (11.5)
	Shaded	91.6 (13.6)	166. (24.2	215. (58.3)

B.		Nutrients*		
	Light	0	1	2
	Control	43.6 (3.78)	70.2 (7.39)	76.3 (0.85)
	Shaded	45.1 (1.41)	67.0 (0.071)	68.3 (3.00)

* 0 = Ambient, 1 = 30X, 2 = 70X

light reduction with an increase in epiphyte biomass that appears to asymptotically approach an upper limit probably governed by leaf surface area.

Figure 4.5 summarizes the productivity estimates for macrophyte leaves and epiphytes. The first bar in each group represents total apparent net production, the second bar respiration, and the third bar gross production. The top area of each bar is epiphyte and the bottom macrophyte contribution respectively. In tanks 1, 2, 3 and 4, epiphyte and macrophyte net and gross productivity are approximately equal. Tanks with the highest nutrient concentrations (5 and 6), show a significant increase in total productivity. While there is only a slight decrease in macrophyte productivity over all treatments, epiphyte productivity accounted for approximately 90% of the total in tanks with the highest nutrient concentration under both control and shaded light regimes. Respiration remained low and relatively constant for both epiphytes and macrophytes in treatments 1 through 4 but macrophyte respiration tended to increase in tanks 5 and 6, suggesting stress.

Table 4.5 summarizes changes in various meristic characteristics for the macrophytes. All plants show a net loss in weight and shoot length following the experiment. Plants in ambient nutrient concentrations show a net gain of about one leaf per plant, while there is an average loss of appriximately one leaf and two leaves in nutrient levels 1 and 2 respectively.

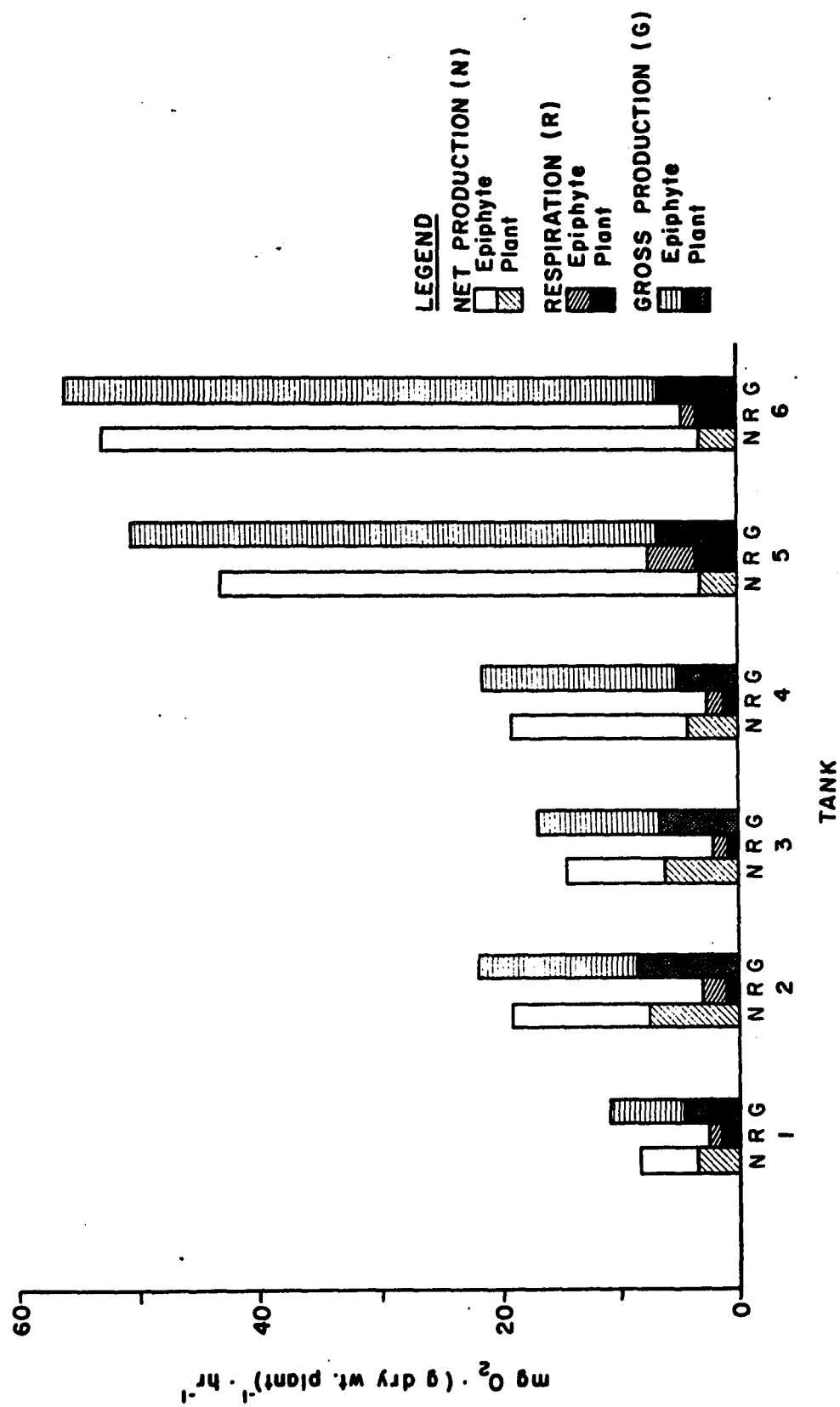

Figure 4.5. Mean estimates of gross and net apparent O_2 productivity and respiration by plant leaf and associated epiphytes. Gross apparent O_2 productivity was calculated as the algebraic sum of net and respiration estimates.

TABLE 4.5. TREATMENT EFFECTS FOLLOWING THE TWO WEEK STUDY ON VARIOUS MERISTIC PARAMETERS FOR *Z. MARINA*. ENTRIES ARE THE MEAN ±1 S.D. (n=8).

A. # g wet wt. plant $^{-1}$

	Nutrients		
Light	0	1	2
Control	-.21 (.22)	-.44 (.20)	-.04 (.08)
Shade	-.25 (.29)	-.19 (.13)	-.14 (.08)

B. #shoot length (cm)

	Nutrients		
Light	0	1	2
Control	-1.2 (0.9)	-0.3 (2.0)	0.42 (0.61)
Shade	-1.9 (1.1)	-1.8 (3.0)	-1.3 (1.1)

C. #leaf no.

	Nutrients		
Light	0	1	2
Control	+0.88 (.35)	-0.50 (.31)	-1.50 (.51)
Shade	+0.88 (.35)	-1.14 (.55)	-1.71 (.48)

DISCUSSION

The results of these microcosm studies indicate that epiphytic biomass on Z. marina increases with decreased light and increased nutrient levels, and that separately these factors have a greater effect on growth than their interactive effect. The results are consistant with data reported elsewhere, which indicate that microalgae (i.e. diatoms) photosynthetically saturate at lower light intensities than vascular plants (Taylor 1964; Ignatiades and Smayda 1970; Levin and Mackas 1972; Admiraal 1977) and assuming that epiphytic diatoms saturate at similar light intensities as benthic diatoms. From a competitive standpoint, the microalgae are at an advantage under lower estuarine light conditions. Increased nutrient concentrations in the water column also favor microalgal growth over that of the vascular plant; 1) microalgae can incorperate water column nutrients faster and easier through direct diffusion, and 2) the major source of nutrients to macrophytes is through sediment uptake, although this has not been well documented (McRoy et al. 1972; McRoy and Alexander 1975; Penhale and Thayer 1980).

Perhaps the major short term effect of increased epiphytic growth on Z. marina is in the reduction of light to the plant. The control light levels of approximately 460 uE m^{-2} sec^{-1} (Table 4.1) are well above saturating for both epiphyte (assuming a diatom population) and vascular plant. However, light available for Z. marina photosynthesis was probably in the range 115-250 uE m^{-2} sec^{-1} if the colonized slides accurately estimate percent light reduction due to epiphytic growth.

These PAR levels are suboptimal, particularly for the nutrient enriched treatments. The shaded-treatment light levels of ca. 200 uE m^{-2} sec^{-1} (Table 4.2) are above saturation for the microalgae but are at or below saturation intensities for the vascular plant. Light available under the shaded treatments for Z. marina was probably in the range 60-110 uE m^{-2} sec^{-1}, well below saturating photosynthesis, and very near the reported range for compensating light intensities of 50 to 100 uE m^{-2} sec^{-1} (Wetzel 1983). The mean percent light reduction of 45% due to epiphytic growth under ambient light and nutrient conditions suggests that for naturally occurring communities, in situ light regimes must be near 400 uE m^{-2} sec^{-1} reaching the plant canopy for maximum rates of vascular plant photosynthesis to be realized.

The effects of controled pertubation on the productivity of the plant and epiphytes are evident from the results of these laboratory experiments. Productivity of the plant-epiphyte complex in the experimental studies remained fairly constant with ambient and lower level nutrient treatment in both control and shaded light regimes (Figure 4.4, tanks 1-4). Productivity doubled in the high nutrient treatments (tanks 5 and 6) and greater than 90% of gross and net apparent productivity was attributable to the epiphyte component. These data suggest that short-term nutrient enrichment changes the community productivity strategies and becomes dominated by the epiphytic microalgae. If these results can be extrapolated to natural seagrass systems in the Chesapeake Bay, then I would suggest that continued nutrient enrichment and/or light reduction within the water column could change the productivity structure from seagrass dominnated to epiphyte cominated, perhaps eventually at the expense of the macrophyte.

CHAPTER 5

GENERAL DISCUSSION AND CONCLUSIONS

The results of the first section of this study support the hypothesis that seagrass systems are highly productive. The two seagrass communities investigated (dominated, respectively, by Zostera marina and Ruppia maritima) exhibited annual net production of about 300 to 600 g C m^{-2}. These values correspond well with values reported for similar seagrass systems (Dillon 1972; McRoy 1974; Verhoeven 1979; Nelnhuis 1980). However, the macrophytes are only partially responsible for these high production values. Other autotrophs (i.e. phytoplankton, benthic algae and epiphytic algae) contribute significantly to this high production rate. In this temperate seagrass system, the plant-epiphyte complex contributed 55% of the annual carbon produced in the Z. marina community and 64% in the R. maritima community. The remaining portion of the annual carbon budget was produced by the microautotrophic components, specifically the benthic microalgae and the phytoplankton (45% and 36% in the Z. marina and R. maritima areas, respectively.) These values compare well to other studies, which have reported microautotrophic contributions between 30% and 50% of total community production (Jones 1968; Dillon 1971; Bittaker 1975; Penhale 1977; Borum and Wium Andersen 1980). Therefore, the exclusion of microalgae in estimates of seagrass community production may result in underestimates of those values.

Evidence for heterotrophic utilization of the macrophytes via the detrital pathway lies in the increase in plant-epiphyte and benthic respiration in both communities during plant die-back periods. These data support previous findings that submerged macrophytes are most readily utilized through decomposition processes (Hargrave 1969;

Lindeboom and deBree 1982; Wetzel 1983). The annual production/respiration values of greater than one indicate the generally autotrophic nature of the components and an annual net excess of primary production. This excess production is either exported from and/or buried in the system. Orth (1977) reports higher organic content in the sediments of grassbeds compared to unvegetated areas, which suggests burial of at least part of the excess autotrophic production.

Although production values for the two communities are similar, their strategies in attaining these rates are quiet different. Z. marina exhibits a negative response to increasing temperature, causing a summer decline in macrophyte production. However, the autotrophic nature of the community is maintained by microalgae replacing the seagrass as the dominant producer (community P/R ratio = 1.10). Macrophyte production in the R. maritima community is positively correlated with increasing temperature, generating a summer peak production followed by a decline in fall. Here microalgae never dominates community production, so that reductions in seagrass production result in reductions of the community production.

In Chapter 1 the plant and epiphytes were combined into one component because gross observations indicated low epiphytic growth at the Vaucluse Shores study site. However, other studies have shown that epiphytic growth in Z. marina seagrass systems is high, and indeed the epiphytic productivity can equal that of the plant at certain times of the year. Therefore, in communities with high epiphytic growth, the potential for microautotrophic contributions to total productivity is even greater than shown in Chapter 1. Studies (Chapter 2) were undertaken to evaluate the differences in epiphytic productivity in two Z.

marina communities of the lower Chesapeake Bay; one with low epiphytic colonization (Vaucluse Shores) the other with high epiphytic colonization (Guinea Marsh).

Epiphytic productivity during the growing season at the Vaucluse Shores site remained low (less than 0.5 mg O_2 gdw $plant^{-1}$ hr^{-1}). On the other hand, the epiphytic productivity at the Guinea Marsh site reached a peak of 3 mg O_2 gdw $plant^{-1}$ hr^{-1} in July, which was comparable to the plant productivity. Further differences in the epiphytic colonizations were evident in the seasonal pattern of both productivity and respiration and in community structure (i.e. abundance and type of organisms). Both communities were similar at the beginning of the growing season and community structure remained relatively unchanged throughout the study period. However, at Guinea Marsh both productivity and respiration rose to their peaks in July, which was followed by the development of strongly heterotrophic community in August. The community structure at Guinea Marsh also changed from a bacteria-diatom community to a macroheterotrophic one, consisting of sessile filter-feeding organisms.

Clearly, the two epiphytic communities differed in structure and function. The causes of these variations may be differences in the environmental conditions of the areas. Based on the significant differences of the plant morphology from the two areas, it was assumed that nutrient enrichment at the Guinea Marsh area may be responsible for increased epiphytic growth. Additionally, decreased light caused by increased water column turbidity and epiphytic growth could lead to plant stress and/or mortality. The studies in the final section were designed

to investigate the effect of controlled nutrient enrichment and light reduction on epiphytic growth and productivity.

The results of the experiments in Chapter 3 show that both increased nutrients and decreased light caused an increase in epiphytic growth on Z. marina. This increase in epiphytic growth also causes a decrease in light available to the plant, which results in plant stress, as is evident by a decrease in the total number of leaves with nutrient enrichment. Productivity of the epiphytic component increased significantly with nutrient enrichment, and accounted for as much as 90% of the total productivity (plant and epiphyte) in the high nutrient/shaded tanks. Although these experiments were conducted for a short period (2weeks), the dramatic changes in epiphytic growth and productivity suggest that nutrient enrichment and/or associated light reduction may be in part responsible for the differences in the epiphytic communities of Z. marina.

The conclusions of these studies are as follows: 1. The high rate of production of this seagrass community is generated by at least four autotrohpic components; the vascular plant, the phytoplankton, the benthic microalgae and the epiphytic microalgae. 2. The microalgae contribute significantly to total community production and failure to include their productivity could lead to gross underestimates of seagrass ecosystem production. 3. The relative contribution to total production by the plant and epiphyte components is due to a balance in competition for available nutrients and light. 4. Changes in the nutrient and/or light regimes within a seagrass ecosystem causes a shift in this production balance from vascular plant dominated to epiphyte dominated, possibly at the expense of the macrophyte.

LITERATURE CITED

Admiraal, W. 1977. Influence of light and temperature on the growth rate of estuarine benthic diatoms in cluture. Mar. Bio. 39: 1-9.

Beer, S., A. Eshel, Y. Waisel. 1980. Carbon metabolism in seagrasses. J. Exp. Bio. 31 (123): 1027-1033.

Benedict, C. R. and J. R. Scott. 1976. Photosynthetic carbon metabolism of a marine grass. Plant Physiol. 57: 876-880.

Bittaker, H. F. 1975. A comparative study of the phytoplankton and benthic macrophyte primary productivity in a polluted versus an unpolluted coastal area. M.S. Thesis, Florida State Univ., 167pp.

Black, C. C., J. E. Burris, and R. G. Everson. 1976. Influence of oxygen concentration on photosynthesis in marine plants. Aust. J. Plant Physiol., 3: 81-86.

Borum, J. and S. Wium-Andersen. 1980. Biomass and production of epiphytes on eelgrass (Zostera marina L.) in the Oresund, Denmark. Ophelia (Suppl.),1: 57-64.

Boynton, W. R., W. M. Kemp, and C. W. Keefe. 1982. A comparative analysis of nutrients and other factors influencing estuarine phytoplankton production. pp. 209-230. In: V. S. Kennedy (ed.), Estuarine Comparisons. Academic Press, New York.

Brasier, M. D. 1975. An outline of seagrass communities. Paleontology, 18: 681-702.

Brylinsky, M. 1977. Release of dissolved organic matter by some marine macrophytes. Mar. Biol. 39: 213-220.

Cadee, G. C. and J. Hegman. 1974. Primary production of the benthic microflora living on tidal flats in the Dutch Wadden Sea. Netherlands J. Sea Res. 8: 260-291.

Cadee, G. C. and J. Hegman. 1977. Distribution of primary production of the benthic microflore and accumulation of organic matter on a tidal flat area, Belgzand, Dutch Wadden Sea. Netherlands J. Sea Res. 11: 24-41.

Capone, D. G., P. A. Penhale, R. S. Oremland, and B. F. Taylor. 1979. Relationship between productivity and N_2 (C_2H_2)fixation in a Thalassia testudinum community. Limnol. Oceanogr. 24: 117-125.

Cattaneo, A. and J. Kalff. 1978. Seasonal changes in the

epiphytic community of natural and artificial macrophytes in Lake Memphremagog (Que. and Vt.). Hydrobiologia. 60(2): 135-144.

Cattaneo, A. and J. Kalff. 1979. Primary production of algae growing on natural and artificial aquatic plants: A study of interactions between epiphytes and their substrates. Limnol. Oceanogr. 24(6): 1031-1037.

Cattaneo, A. and J. Kalff. 1980. The relative contribution of aquatic macrophyte and their epiphytes to the production of macrophyte beds. Limnol. Oceanogr. 25: 280-289.

Congdon, R. A. and A. J. McComb. 1979. The vegetation of the Blackwood River Estuary, South-West Australia. J. of Ecol. 69: 1-16.

den Hartog, C. 1970. The Sea-Grasses of the World. North Holland, Amsterdam. 275pp.

Dillon, C. R. 1971. A comparative study of the primary productivity of estuarine phytoplankton and macrobenthic plants. Ph. D. Thesis. Univ. North Carolina, 108pp.

Downtown, W. J. S., D. G. Bishop, A. W. D. Larkum, C. B. Osmond. 1976. Oxygen inhibition of photosynthetic oxygen evolution in marine plants. Aust. J. Plant Physio., 3: 73-79.

Furguson, R. L. , A. Collier and D. E. Meeter. 1976. Growth response of Thalassiusia pseudonana Hasle and Helmdal Clone 3H to illumination, temperature and nitrogen source. Ches. Sci. 17(3): 148-158.

Fisher, T. R., P. R. Carlson and R. T. Barber. 1982. Carbon and nitrogen primary productivity in three North Carolina estuaries. Estuarine, Coastal and Shelf Sci. 15: 621-644.

Flemer, D. A. 1970. Primary production in the Chesapeake Bay. Ches. Sci. 11:117-129.

Gargas, Eivind. 1971. "Sun-shade" adaptation in microbenthic algae from the Oresumd. Ophelia 9: 107-112.

Grontved, J. 1960. On the productivity of microbenthos and phytoplankton in some Danish fjords. Medd. Dan. Fish. Havunders 3: 55-92.

Haas, L. W. 1975. Plankton dynamics in a temperate estuary with observations on a variable hydrographic condition.

Ph. D. Thesis, College of William and Mary, 202pp.

Hargrave, B. T. 1969. Epibenthic algae production and community respiration in the sediments of Marion Lake. J. Fish. Res. Bd. Canada. 26: 2003-2026.

Harlin, Marilyn M. 1973. Transfer of products between epiphytic marine algae and host plants. J. Phycol. 9: 243-248.

Harlin, M. M. 1975. Epiphytic host relations in seagrass communities. Aquatic Bot. 1: 125-131.

Harlin, M. M. and B. Thorne-Miller. 1981. Nutrient enrichment of seagrass beds in a Rhode Island coastal lagoon. Mar. Bio. 65: 221-229.

Harrison, P. G. 1982. Control of microbial growth and of Amphipod grazing by water-soluble compounds from leaves of Zostera marina. Mar. Bio. 67: 225-230.

Harrison, P. G. and A. T. Chan. 1980. Inhibition of the growth of microalgae and bacteria by extracts of eelgrass (Zostera marina) leaves. Mar. Biol. 61: 21-26.

Hartman, R. T. and D. L. Brown. 1967. Changes in internal atmosphere of submersed vascular hydrophytes in ralation to photosynthesis. Ecology. 48: 252-258.

Ignatiades, L. and T. J. Smayda. 1970. Autoecological studies on the marine diatom Rhizosolinia fragilissima Bergon. I. The influence of light, temperature and salinity. J. Phycol. 6: 332-339.

Iizumi, H., A. Hattori and C. P. McRoy. 1980. Nitrate and nitrite in interstitial waters of eelgrass beds in relation to the rhizosphere. J. Exp. Mar. Biol. Ecol. 47: 191-201.

Joint, I. R. 1978. Microbial production of an estuarine mudflat. Est. Coastal Mar. Sci. 7: 185-195.

Jones, J. A. 1968. Primary productivity by trophical marine turtle grass, Thalassia testudinum Konig and its epiphytes. Ph. D. Thesis, Univ. Miami, 196pp.

Kikuchi, T. and J. M. Peres. 1977. Consumer ecology of seagrass beds. In. C. P. McRoy and C. Helfferich (eds.), Seagrass Ecosystems, A Scientific Prespective. Marine Science, Vol. 4, Marchel Dekker, Inc., New York and Basel, pp. 147-193.

Kelly, M. G., B Moselumd and N. Thysen. 1981. Productivity measurements and the storage of oxygen in the arenchyma

of aquatic macrophytes. Arch. Hydrobiol. 92: 1-10.

Kemp, W. M., M. R. Lewis, T. W. Jones, J. J. Cummingham, J. C. Stevenson, W. R. Boynton. 1981. Measuring productivity of submerged aquatic macrophytes, a comparison of methodologies. In: W. M. Kemp, et al. Sumberged aquatic vegetation in upper Chesapeake Bay. Report to U. S. Env. Protiection Agency. Horn Point Env. Lab., Cambridge, Md., Cont. no. HPEL 81-68.

Klorbe, T. 1980. Distribution and production of submerged macrophytes in Tipper Griend (Ringkobing Fjord, Denmark), and the impact of waterfowl grazing. J. of Appl. Ecol. 17: 675-687.

Lascara, V. J. 1981. Fish preditor-prey interactions in areas of eelgrass (Zostera marina). M.A. Thesis. College of William and Mary, Marine Science Institute, Gloucester Pt., Virginia. 81pp.

Lewin, J. and D. Mackas. 1972. Blooms of surf-zone diatoms along the coast of the Olympic Peninsula, Washington. I. Physiological investigations of Chaetoceros armatum and Asterionella in laboratory culture. Mar.Biol. 16: 171-181.

Lindeboom, H. J. and B. H. deBree. 1982. Daily production and comsumption in an eelgrass (Zostera marina) community in saline Lake Grevelingon: discrepancies between the O2 and 14C method. Report to Delta Institure of Hydrobiological Research,Yerseke, The Netherlands. 24pp.

Marsh, G. A. 1976. Ecology of the gastropod epifauna of eelgrass in a Virginia estuary. Ches. Sci. 17(3): 182-187.

Marshall, N., C. A. Oviatt, and D. M. Skauen. 1971. Productivity of the benthic microflora of shoal estuarine environments in southern New England. Int. Revue ges. Hydrobiol. 56: 947-956.

McCarthy, J. J., W. R. Taylor, and M. E. Loftus. 1975. Significance of nanoplankton in the Chesapeake Bay estuary and problems associated with measurement of nanoplankton productivity. Mar. Biol. 24: 7-16.

McConnaughey, T. and E. P. McRoy. 1979. 13C label identifies eelgrass (Zostera marina) carbon in an Alaskan estuarine food web. Mar. Biol. 53: 271-280.

McRoy, C. Peter. 1974. Seagrass productivity, carbon uptake experiments in eelgrass, Zostera marina. Aquaculture 4: 131-137.

McRoy, C. P., R. J. Barsdate and M Nebert. 1972. Phosphorus

cycling in an eelgrass (Zostera marina L.) ecosystem. Limnol. Oceanogr. 18 (6): 998-1002.

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

McRoy, C. P., and V. Alexander. 1975. Nitrogen kinetics in aquatic plants in Artic Alaska. Aquatic Bot. 1: 3-10.

McRoy, C. P., and C. McMillian. 1977. Production ecology and physiology of seagrasses, pp.53-87. In: C. P. McRoy and C. Helfferish (eds.). Seagrass Ecosystems: A Scientific Prespective, Marcel Dekker, Inc., New York.

Morgan, M. D. 1980. Grazing and predation of the grass shrimp Palaemonetes pugio. Limnol. Oceanogr. 25 (5): 896-902.

Moss, B. 1981. The composition and ecology of periphyton communities in freshwaters. II. Inter-relationships between water chemistry, phytoplankton populations and experimental reserviors (Lund Tubes). Br. Phycol. J. 16: 59-76.

Nelnhuis, P. H. 1980. The eelgrass (Zostera marina L.) subsystem in brackish Lake Grevelingen: Production and decomposition of organic matter. Ophelia (Suppl.) 1: 113-116.

Nelson, W. G. 1980. The biology of eelgrass (Zostera marina L.) amphipods. Crustaceana, 39 (1): 59-89.

Nixon, S. W. and C. A. Oviatt. 1972. Preliminary measurements of midsummer metabolism in beds of eelgrass, Zostera marina. Ecology 53: 150-153.

Nixon, S. W. 1981. Remineralization and nutrient cycling in coastal marine ecosystems, pp. 111-138. IN: B. Nellson and L. E. Cronin (eds.), Nutrient Cycling in Estuaries, Humana Press, Clifton, N. J.

Ogden, J. C. 1980. Faunal relationships in Caribbean seagrass beds, pp. 173-198. IN: R. C. Phillips and C. P. McRoy (eds.), Handbook of Seagrass Biology: An Ecosystem Perspective. Garland STPM Press, New York and London.

Oremland, R. S. and B. F. Taylor. 1977. Diurnal fluctuations of O2, N2, and CH4 in the rhizoshpere of Thalassia testudinum. Limnol. Oceanogr. 22: 566-570.

Orth, R. J. 1973. Benthic infauna of eelgrass, Zostera marina, beds. Ches. Sci. 14: 258-259.

Orth, R. J., K. A. Moore and H. H. Gordon. 1979. Distribution

and abundance of submerged aquatic vegetation in the lower Chesapeake Bay. U. S. Environemtnal Protection Agency, Report no. 600/8-79-029/SAV1, Chesapeake Bay Program, Annapolis, Md.

Orth R. J., K. A. Moore, and J. von Montfrans. 1982. Submerged aquatic vegetation: Distribution and abundance in the lower Chesapeake Bay and the interactive effects of light, epiphytes and grazers. Draft final report. U. S. Environmental Protection Agency, Chesapeake Bay Program, Annapolis, Md. 325pp.

Orth, R. J. and K. A. Moore. 1982. The biology and propagation of eelgrass, Zostera marina, in the Chesapeake Bay, Virginia. Final Grant Report, Grant no. R805953, U. S. Environmental Protection Agency, Chesapeake Bay Program, Annapolis, Md. 195 pp.

Pamatmat, M. M. 1968. Ecology and metabolims of a benthic community on an intertidal sandflat. Int. Revue ges. Hydrobiol. 53: 211-298.

Patriquin, D. G. 1973. Estimation of growth rate, production and age of the marine angiosperm, Thalassia testudinum Konig. Carib. J. Sci. 13: 111-123.

Patten, B. C., R. A. Mulfore, and J. E. Warriner. 1963. An annuual phytoplankton cycle in the lower Chesapeake Bay. Ches. Sci. 4: 1-20.

Penhale, P. A. 1977. Macrophyte-epiphyte biomass and productivity in an eelgrass (Zostera marina L.) community. J. exp. Mar. Biol. Ecol. 26: 211-224.

Penhale, P. A. and W. O. Smith. 1977. Excretion of dissolved organic carbon by eelgrass (Zostera marina) and its epiphytes. Limnol. Oceanogr. 22: 400-407.

Phillips, G. L., D. Eminson and B. Moss. 1978. A mechanism to account for macrophyte decline in progressively eutrophication freshwaters. Aquatic Bot. 4: 103-126.

Phillips, R. C. 1974. Temperate grass plots. pp. 244-299. IN: H. T. Odum, B. J. Copeland and E. A. Mahan (eds.) Coastal Ecological Systems of the United States, Vol. 2., The Conservation Foundation, Washington, D. C., U.S.A.

Phillips, R. G. and R. L. Lewis. 1983. Influence of environmental gradients on variations in leaf widths and transplants success in North American seagrasses. Mar. Tech. Soc. J. 17 (2): 59-68.

Pomeroy, L. R. 1959. Algal productivity in salt marshes of Georgia. Limnol. Oceanogr. 4: 386-397.

Poneroy, L. R. and R. G. Wiegert. 1981. The ecology of a salt marsh. Springer-Verlag Inc. New York. 271 pp.

Richardson, R. D. 1980. Ecology of Ruppia maritima L. in New Hampshire (U.S.A.) tidal marshes. Rhodora 82 (831): 403-439.

Riznyk, R. Z. and H. K. Phinney. 1972. Nanometric assessment of interstitial microalgae production in two estuarien sediments. Oecologia 10: 193-203.

Sand-Jensen, K. 1977. Effect of epiphytes on eelgrass photosynthesis. Aquatic Bot. (3): 55-63.

Sand-Jensen, K. and M. Sondergaard. 1981. Phytoplankton and epiphyte development and their shading effect on submerged macrophyte in lakes of different nutrient status. Int. Revue ges. Hydrobiol. 66 (4): 529-552.

Sand-Jensen, K., C. Prahel and H. Stokholm. 1982. Oxygen release from roots of submerged aquatic macrophytes. Oikos 38: 349-354.

Shoaf, W. T., and V. M. Lium. 1976. Improved extractions of chlorophyll a and b from algae using dimethyl sulfozide. Limnol. Oceanogr. 21: 926-928.

Short, F. T. 1983. The seagrass Zostera marina L.: Plant morphology and bed structure in relation to sediment ammonium in Izenbeck Lagoon, Alaska. Aquatic Bot. 16: 149-161.

Sieburth, John McN., and Cynthia D. Thomas. 1073. Fouling on eelgrass (Zostera marina L.). J. Phycol. 9: 46-50.

Smith, F. A. and N. A. Walker. 1980. Photosynthesis by aquatic plants: Effects of unstirred layers in relation to assimulation of CO2 and HCO3 and to carbon isotopic discrimination. New Phytol. 86: 245-259.

Stauffer, R. E., G. F. Lee and D. E. Armstrong. 1979. Estimating chlorophyll on an extraction basis. J. Fish. Res. Bd. Canada. 36: 152-157.

Stoner, A. W. 1980. Feeding ecology of Lagodon rhomboides (Pisces: Sparidea): Variation and functional responses. Fishery Bull. 78 (2): 337-352.

Sullivan, M. J. and F. C. Diaber. 1975. Light, nitrogen and phospohrus limitations of edaphic algae in a Delaware salt marsh. J. Exp. Mar. Biol. Ecol. 18: 79-88.

Sullivan, M. J. 1977. Structural characteristics of a diatom community epiphytic on Ruppia maritima.

Poneroy, L. R. and R. G. Wiegert. 1981. The ecology of a salt marsh. Springer-Verlag Inc. New York. 271 pp.

Richardson, R. D. 1980. Ecology of Ruppia maritima L. in New Hampshire (U.S.A.) tidal marshes. Rhodora 82 (831): 403-439.

Riznyk, R. Z. and H. K. Phinney. 1972. Nanometric assessment of interstitial microalgae production in two estuarien sediments. Oecologia 10: 193-203.

Sand-Jensen, K. 1977. Effect of epiphytes on eelgrass photosynthesis. Aquatic Bot. (3): 55-63.

Sand-Jensen, K. and M. Sondergaard. 1981. Phytoplankton and epiphyte development and their shading effect on submerged macrophyte in lakes of different nutrient status. Int. Revue ges. Hydrobiol. 66 (4): 529-552.

Sand-Jensen, K., C. Prahel and H. Stokholm. 1982. Oxygen release from roots of submerged aquatic macrophytes. Oikos 38: 349-354.

Shoaf, W. T., and V. M. Lium. 1976. Improved extractions of chlorophyll a and b from algae using dimethyl sulfozide. Limnol. Oceanogr. 21: 926-928.

Short, F. T. 1983. The seagrass Zostera marina L.: Plant morphology and bed structure in relation to sediment ammonium in Izenbeck Lagoon, Alaska. Aquatic Bot. 16: 149-161.

Sieburth, John McN., and Cynthia D. Thomas. 1073. Fouling on eelgrass (Zostera marina L.). J. Phycol. 9: 46-50.

Smith, F. A. and N. A. Walker. 1980. Photosynthesis by aquatic plants: Effects of unstirred layers in relation to assimulation of CO2 and HCO3 and to carbon isotopic discrimination. New Phytol. 86: 245-259.

Stauffer, R. E., G. F. Lee and D. E. Armstrong. 1979. Estimating chlorophyll on an extraction basis. J. Fish. Res. Bd. Canada. 36: 152-157.

Stoner, A. W. 1980. Feeding ecology of Lagodon rhomboides (Pisces: Sparidea): Variation and functional responses. Fishery Bull. 78 (2): 337-352.

Sullivan, M. J. and F. C. Diaber. 1975. Light, nitrogen and phospohrus limitations of edaphic algae in a Delaware salt marsh. J. Exp. Mar. Biol. Ecol. 18: 79-88.

Sullivan, M. J. 1977. Structural characteristics of a diatom community epiphytic on Ruppia maritima.

Hydrobiologia 53(1): 81-86.

Szczepanski, Andrzej J. 1977. Allelopathy as a measure of biological control of water weeds. Aquatic Bot. 3: 193-197.

Takahashi, M. and T. R. Parsons. 1972. Maximization of the standing stock and primary productivity of marine phytoplankton under natural conditions. Indian J. of Mar. Sci. 1: 61-62.

Taylor, W. Rowland. 1964. Light and photosunthesis in intertidal benthic diatoms. Helgol. Wiss. Meeresuntes. 10: 29-37.

Thayer, G. W.,S. M. Adams, and M. W. LaCroix. 1975. Strudtural and functional aspects of a recently established Zostera marina community, pp. 518-546 IN: L. E. Cronin (ed), Estuarine Research, Vol. 1, Academic Press, New York.

Thayer, G. W., P. L. Parker, M. W. LaCroix, B. Fry. 1978. The stable carbon isotope ratio of some components of an eelgrass, Zostera marina, bed. Oceologia (Berl.) 35: 1-12.

Verhoeven, J. J. A. 1979. The ecology of Ruppia dominated communities in Western Europe. III. Aspects of production comsumption and decomposition. Aquatic Bot. 8: 209-253.

vanRaalte, C. D. and I. Valiela. 1976. Production of epibenthic salt marsh algae: Light and nutrient limitation. Limnol. Oceanogr. 21: 862-872.

von Montfranz, J. R., R. J. Orth and S. A. Vay. 1982. Preliminary studies of grazing by Bittium varium on eelgrass periphyton. Aquatic Bot. 14: 75-89.

Welch, E. B, R. M. Emery, R. I Malsuda and W. A. Dawson. 1972. The relation of periphytic and planktonic algae growth in an estuary to hydrographic factors. Limnol. Oceanogr. 17: 731-737.

Wetzel, R. G. 1964. A comparative study of the primary productivity of higher aquatic plants, periphyton and phytoplankton in a large shallow lake. Int. Revue ges. Hydrobiol. 49: 1-61.

Wetzel, R. G. and P. A. Penhale. 1979. Transport of carbon and exretion of dissolved organic carbon by leaves and root/ rhizomes in seagrass and their epiphytes. Aquatic Bot. 6: 149-158.

Wetzel, R. L. 1983. Structural and functional aspects of the

ecology of submerged aquatic macrophyte communities in the lower Chesapeake Bay. Final Report No. 267, U. S. Environmental Protection Agency, Chesapeake Bay Program, Annapolis, Md. 187pp.

Wetzel, R. L. and P. A. Penhale. 1983. Production ecology of seagrass communities in the lower Chesapeake Bay. Mar. Tech. Soc. J. 17(2): 22-31.

Wetzel, R. L., K. L. Webb, P. A. Penhale, R. J. Orth, D. F. Boesch, G. W. Boehlert, and J. V. Marriner. 1979. The functional ecology of submerged aquatic vegetation in the lower Chesapeake Bay. Annual Grant Report, Grant no. R805974, U. S. Environmental Protection Agency, Chesapeake Bay Program, Annapolis, Md. 152pp.

Wium-Andersen, S. and W. Andersen. 1972. The influence of vegetation on the redox profile of the sediment of Grane Langso, a Danish Lobelia lake. Limnol. Oceanogr. 17 (6): 948-952.

Zelder, J. B. 1980. Algal mat productivity: Comparisons in a salt marsh. Estuaries 3: 122-131.

Zieman, J. C. 1974. Methods for the study of the growth and production of turtle grass, Thalassia testudinum Konig. Aquaculture 4: 139-143.

Zieman, J. C. and R. G. Wetzel. 1980. Productivity in seagrasses: Methods and rates, pp.87-118. IN: R. C. Phillips and C.P. McRoy (eds.) Handbook of seagrass biology: An Ecosystem Prespective. Garland STPM Press. New York.

Zimmerman, R., R. Gibson and J. Harrington. 1979. Herbivory and detritivory among gammaridean amphipods from a Florida seagrass community. Mar. Biol. 54: 41-47.

VITA

LAURA MURRAY

Born January 8, 1950 in Washington, D. C. Graduated Pass Christian High School, Pass Christian, Mississippi in 1967. Received Bachelor of Science in Marine Science from University of West Florida, Pensacola, Florida, in 1971 and a Master of Science/Education from the same University in 1973. Worked as a high school teacher in Portsmouth, Virginia from 1975-1977 and as a laboratory specialist at the Virginia Institute of Marine Science from 1977 to 1979. Entered School of Marine Science of the College of William and Mary in 1979. Joined the Faculty of Biology, Salisbury State College, Salisbury, Maryland in 1982.