PB89-134548

Structural and Functional Aspects of the Ecology of Submerged Aquatic Macrophyte Communities in the Lower Chesapeake Bay Volume 1. Studies on Structure and Function of a Temperate, Estuarine Seagrass Community: Vaucluse Shores Lower Chesapeake Bay, Virginia, USA

Virginia Inst. of Marine Science
Gloucester Point

Prepared for

Environmental Protection Agency, Annapolis, MD

Aug 82

TECHNICAL REPORT DATA *(Please read Instructions on the reverse before completing)*		
1 REPORT NO. EPA/600/3-88/051a	2	3 RECIPIENT'S ACCESSION NO PB89 134548/AS
4 TITLE AND SUBTITLE STRUCTUAL & FUNCTIONAL ASPECTS OF THE ECOLOGY OF SUBMERGED AQUATIC MACROPHYTE COMMUNITIES IN THE LOWER CHESAPEAKE BAY. Vol. I: Studies on Structure & Function of a Temperate, Estuarine Seagrass Community:		5 REPORT DATE August 1982 6 PERFORMING ORGANIZATION CODE
7 AUTHOR(S) Vanc'use Shores, Lower Chesapeake Bay, Virginia, USA Robert F. Tine and Richard L. Wetzel, Eds.		8. PERFORMING ORGANIZATION REPORT NO
9 PERFORMING ORGANIZATION NAME AND ADDRESS Virginia Institute of Marine Science and School of Marine Science, College of William and Mary, Gloucester Point, VA 23062		10. PROGRAM ELEMENT NO. 11. CONTRACT/GRANT NO. R805974 and X003245-01
12. SPONSORING AGENCY NAME AND ADDRESS EPA, Chesapeake Bay Program 2083 West Street Annapolis, MD 21401		13. TYPE OF REPORT AND PERIOD COVERED 14. SPONSORING AGENCY CODE EPA/600/05
15 SUPPLEMENTARY NOTES		

16. ABSTRACT

There is increasing evidence which suggests that primary production in both marine and estuarine systems is generally nitrogen limited. Orth (1977) demonstrated a positive growth response in Zostera marina communities in the Bay to added commercial fertilizer treatments. These data together with the consistent and predictable pattern for the depth distribution of seagrasses in the Lower Chesapeake Bay suggests that light (and/or factors influencing the quality and quantity of the light regime) and nutrients are principal factors governing the distribution and metabolism of the submerged aquatic plant communities.

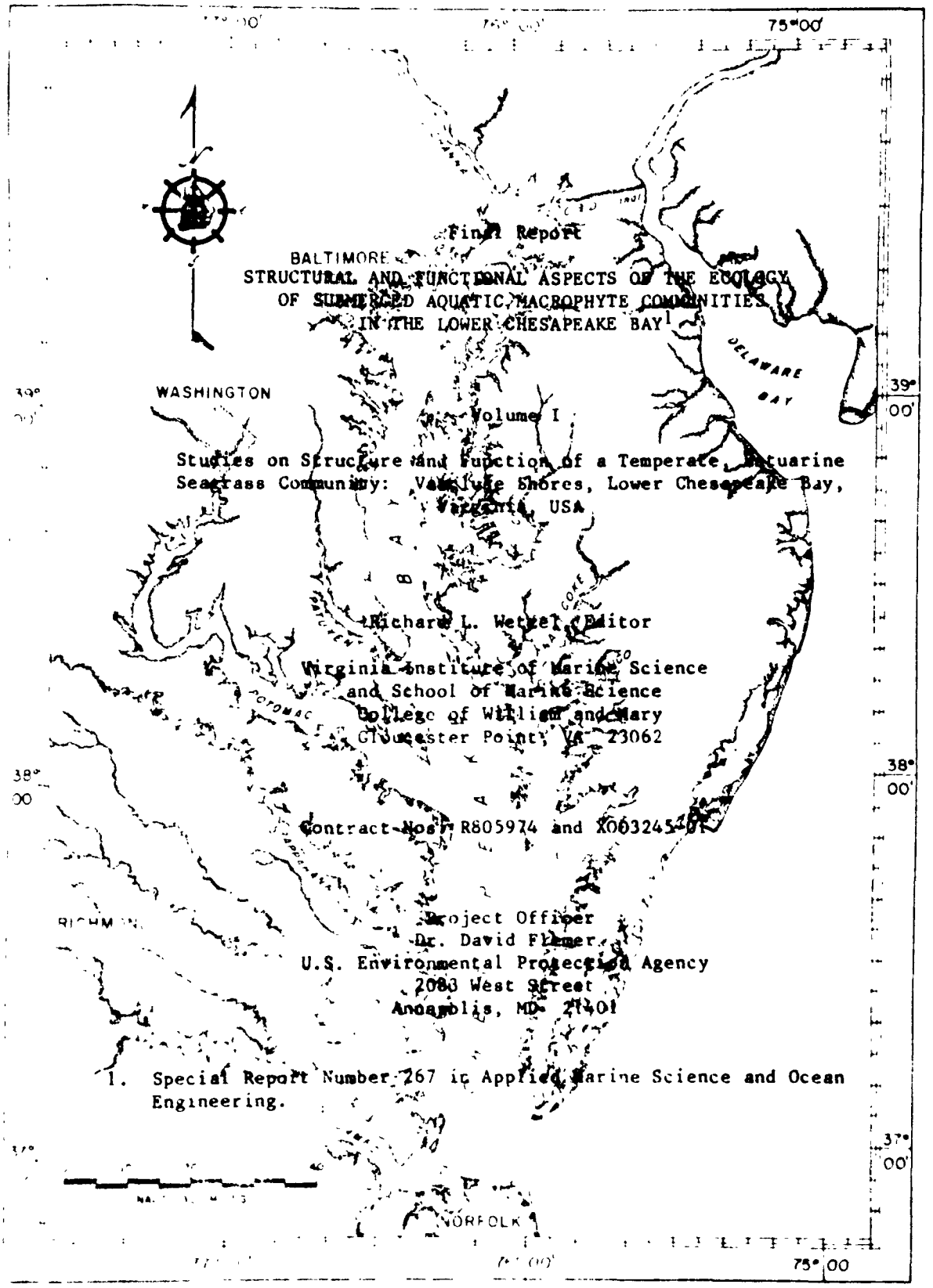
The overall objectives of the studies reported in the following chapters of this volume were: 1) to describe structural chracteristics of the plant community and environmental regimes of a natural, unperturbed SAV community in the Lower Chesapeake Bay, 2) to derive estimates of community productivity and metabolism for diel, seasonal and annual periods, and 3) to evaluate potential mechanisms controlling productiviity and community dynamics. Various studies and experimental designs were initiated and completed during the period July, 1978 through November, 1981 to accomplish these overall objectives.

17. KEY WORDS AND DOCUMENT ANALYSIS		
a. DESCRIPTORS	b. IDENTIFIERS/OPEN ENDED TERMS	c. COSATI Field/Group
18. DISTRIBUTION STATEMENT RELEASE TO PUBLIC	19. SECURITY CLASS (This Report) UNCLASSIFIED 20 SECURITY CLASS (This page) UNCLASSIFIED	21. NO. OF PAGES 192 22. PRICE

EPA Form 2220-1 (Rev. 4-77) PREVIOUS EDITION IS OBSOLETE

PB89-134548

EPA/600/3-88/051a
August 1982



Final Report

STRUCTURAL AND FUNCTIONAL ASPECTS OF THE ECOLOGY OF SUBMERGED AQUATIC MACROPHYTE COMMUNITIES IN THE LOWER CHESAPEAKE BAY[1]

Volume I

Studies on Structure and Function of a Temperate Estuarine Seagrass Community: Vaucluse Shores, Lower Chesapeake Bay, Virginia, USA

Richard L. Wetzel, Editor

Virginia Institute of Marine Science
and School of Marine Science
College of William and Mary
Gloucester Point, VA 23062

Contract Nos. R805974 and X063245-01

Project Officer
Dr. David Flemer
U.S. Environmental Protection Agency
2083 West Street
Annapolis, MD 21401

1. Special Report Number 267 in Applied Marine Science and Ocean Engineering.

NOTICE

This document has been reviewed in accordance with U.S. Environmental Protection Agency policy and approved for publication. Mention of trade names or commercial products does not constitute endorsement or recommendation for use.

Final Report

STRUCTURAL AND FUNCTIONAL ASPECTS OF THE ECOLOGY OF SUBMERGED AQUATIC MACROPHYTE COMMUNITIES IN THE LOWER CHESAPEAKE BAY[1]

Volume I

Studies on Structure and Function of a Temperate, Estuarine Seagrass Community: Vaucluse Shores, Lower Chesapeake Bay, Virginia, USA

Richard L. Wetzel, Editor

Virginia Institute of Marine Science
and School of Marine Science
College of William and Mary
Gloucester Point, VA 23062

Contract Nos. R805974 and X003245-01

Project Officer
Dr. David Flemer
U.S. Environmental Protection Agency
2083 West Street
Annapolis, MD 21401

1. Special Report Number 267 in Applied Marine Science and Ocean Engineering.

TABLE OF CONTENTS

TABLE OF CONTENTS (continued)

ACKNOWLEDGEMENTS

For a research program of this size, duration and scope it would be impossible to acknowledge the individual support of all persons associated at various times with the project. Collectively, I wish to thank the many colleagues, graduate students and technical staff of the Institute who have contributed to the studies and the overall success of the program. Specific thanks are due our Eastern Shore colleagues, Michael Castagna, John Kraeuter and Jim Moore, without whose efforts and active involvement, the program would not have succeeded. Also, without the local support of many Eastern Shore residents, particularly Lloyd and Buddy Otten, Jack Watts, Donald Hammon and Harold Rehm who contributed both the use of personal property and their time, we would certainly have fallen short in accomplishing many of our goals.

At various times throughout the program, we have used and relied on outside program reviews and visiting scientists. Especial thanks are due Richard G. Wiegert and Steven Y. Newell, University of Georgia, Robert R. Christian, East Carolina University, Douglas G. Capone, State University of New York at Stony Brook and Steven Smith and John Harrison, University of Hawaii, for their participation in the research program. To Gordon Thayer, National Marine Fisheries Service-Beaufort, John W. Day, III, Louisiana State University, Scott W. Nixon, University of Rhode Island and, again, Doug Capone, SUNY at Stony Brook, we offer our thanks for interim program reviews and constructive criticisms. I also wish to express my thanks and appreciation to Mr. William Cook, U.S. E.P.A. and former project officer of this program, for his many efforts to see the program successfully completed and effectively reducing administrative burdens. His support and enthusiasm certainly made management of the program much easier.

From a more personal standpoint, I want to acknowledge the unfailing support and dedication of my graduate students, Laura Murray, Robin van Tine, and Rick Hoffman in these efforts. To Bob Middleton and Bill Rizzo, thanks for allowing yourselves to be pressed into service at critical times. Also, to my colleagues of the "other" Chesapeake Bay, Michael Kemp, Walt Boynton and J. Court Stevenson, University of Maryland, thanks for the many stimulating discussions, comparison of results and reviews.

Especial thanks are due Ms. Carole Knox and Nancy White for their secretarial and editorial skills. Their concerted effort in typing, compiling and editing many drafts of the manuscripts contained herein while maintaining some sense of organization as well as humor is greatly appreciated. Also, to our Photographic, Graphic Arts and Word Processing Service Center, thanks to all for your excellent and quality work.

R. L. Wetzel
Program Manager

PREFACE

Richard L. Wetzel

Virginia Institute of Marine Science
and School of Marine Science
College of William and Mary
Gloucester, Point, VA 23062

Program Overview

Various autotrophic populations contribute to total primary production in estuarine and coastal marine environments. The distribution, abundance and relative contribution of each is determined in large part by geomorphology and physical-chemical regimes of a particular area (Mann, 1975). In open water, phytoplankton dominate the autotrophic input of organic matter while in shoal-benthic habitats, algae, seagrasses and marshes contribute to primary production as well. Unit area comparison of annual biomass production generally results in the ordering: salt marshes > seagrasses > macro-algae > phytoplankton for many Gulf of Mexico and U.S. Atlantic Coast estuaries. However, areal comparisons and ranking vary considerably from system to system. Coastal, temperate estuaries along the U.S. Atlantic Coast are generally characterized by inputs from all. The Chesapeake Bay is a good example.

Partitioning primary production among these various components in the Chesapeake Bay for comparative purposes is difficult due in large part to the extreme biological complexity and physical characteristics of the Bay. At least three major subdivisions of the Bay can be identified based on hydrodynamic regime. These are; 1) bay stem, the major open water area, 2) shoal-benthic areas within the major water body and grossly delineated by the basin shoreline and extending to a mean subtidal depth of 2 to 3 meters, and 3) sub-estuarine water bodies consisting of the principal tributaries entering the Chesapeake Bay. The bay stem is a major open water area and is dominated by phytoplankton production. Shoal-benthic areas and the tributaries however, make up a significant part of the estuary and are autotrophically dominated by benthic microalgae and macroalgae, submerged aquatic vegetation, and the wetland, tidal marshes. Based on gross areal approximations for the Virginia portion of Chesapeake Bay and estimates of annual net primary production for each of these components, the shoal-benthic habitat and the tidal marshes contribute 30-40% of the annual net primary production for the lower Chesapeake Bay (R. L. Wetzel, unpublished data).

On a smaller spatial scale within shoal-benthic areas, the relative contribution of submerged aquatic vegetation (SAV) primary production varies considerably. Orth et al. (1979) has estimated that Virginia SAV occupied a bottom area of approximately 85.4 km^2 in 1978. Using their figure of a 5300 km shoreline length and assuming an average lateral extent of 300m, the shoal-benthic habitat area would be approximately 1600 km^2 or approximately 5% of the bottom area. However, their figures included shoreline areas of the major tributaries where the major portion of the habitat is oligohaline or tidal freshwater and the two dominant species of SAV for the lower Bay, Zostera marina and Ruppia maritima do not exist. Using the present relative abundance and distribution data for these two species (Orth et al., 1979) and limiting the estimated shoal-benthic habitats to brackish water and mesohaline areas, the percentage of shoal-benthic habitat occupied by Zostera-Ruppia communities would significantly increase.

The productivity of SAV communities in temperate, U.S. Atlantic coast estuaries is high (Dillon 1971; Thayer et al. 1975; Penhale 1977). Within SAV communities typical of the lower Chesapeake Bay, total autotrophic production is partitioned among several autotrophs: Zostera marina, Ruppia maritima, epiphytic algae (those attached to seagrass leaves), benthic microscopic and macroscopic algae, and phytoplankton. A comparison of the productivity estimates for the major primary producers in an estuarine system near Beaufort, North Carolina, indicates the importance of seagrasses in shallow coastal systems and the relative contribution made by other autotrophs. For this system net annual production (g C m^{-2} yr^{-1}) were; 66 for phytoplankton (Thayer 1971), 249 for Spartina alterniflora (Williams 1973), 330 for Zostera marina and 73 for epiphytes of Zostera (Penhale 1977). Therefore, at least at the local level, SAV production is comparatively high and for some systems may dominate total estuarine autotrophic production (Thayer et al. 1975; Mann 1975). For certain areas of the Lower Chesapeake Bay, e.g. Bayside Eastern Shore, Mobjack Bay and shoal benthic areas in and around the York River mouth, SAV primary production is a significant source of fixed energy and organic matter available to either directly or indirectly support heterotrophic, secondary production of ecologically and/or economically important species.

Nevertheless, simply comparing production of the various estuarine primary producers oversimplifies and perhaps underestimates the role and value of SAV communities in the Lower Chesapeake Bay system as a whole. The SAV communities add structural complexity and diversity to the shoal-benthic environment creating habitat for epifaunal, infaunal and motile species and refuge areas for prey species. In addition to these non-trophic characteristics, SAV also function in the stabilization of sub-tidal sediments and probably influence shoreline erosion processes by dissipating both tidal and wind generated wave energy. SAV communities in the Lower Chesapeake Bay therefore have both trophic and non-trophic significance for the ecology of the overall system.

Historical studies of seagrass distribution and relative abundance of SAV communities in the Lower Chesapeake Bay show periods of major decline followed by periods of recovery. Eelgrass (Zostera marina) has undergone major changes in abundance in 1854 and during the period 1889-1894 (Cottam 1935 a,b). More recently, major declines in Chesapeake Bay SAV were observed during the wasting disease of the 1930's (Cottam and Munro 1954) and during a decline which began in 1973 and continued until 1978. This recent decline resulted in the lowest population levels in 40 years (Orth et al. 1979). Despite documentation of these events, these fluctuations in distribution and abundance remain largely unexplained.

Geographically, the dominant lower Bay species, Zostera marina, has a world wide distribution in temperate and subartic regions of the Northern Hemisphere (den Hartog 1970). The southern range limit along the U.S. East Coast is North Carolina. This limit is ascribed to high temperature stress effects. Thus, Z. marina in the lower Chesapeake Bay exists very near its geographical distribution limit.

Ruppia maritima has broader temperature and salinity tolerances (Richardson 1980 and references therein) which is reflected in the

geographical distribution of the species. Within Chesapeake Bay, Zostera marina and Ruppia maritima are limited to shoal benthic habitats less than two meters mean depth (Orth et al. 1979).

Factors which regulate productivity of seagrasses have been ascribed to various environmental parameters. The influence of light, temperature and salinity have received the major research effort (Biebl and McRoy 1971; Bachman and Barilotti 1976; Penhale 1977; Congdon and McComb 1979; and references therein). It is generally accepted that the local light regime limits the subtidal distribution of Zostera, while light, temperature and nutrient regimes (primarily nitrogen) interact to control specific rates of productivity over an annual cycle.

There is increasing evidence which suggests that primary production in both marine and estuarine systems is generally nitrogen limited (Postgate 1971; Ryther and Dunstan 1971; Valiela et al. 1973; Gallagher 1975; Pomeroy 1975; Orth 1977; Nixon 1980). Orth (1977) recently demonstrated a positive growth response in Zostera marina communities in the Bay to added commercial fertilizer treatments. These data together with the consistent and predictable pattern for the depth distribution of seagrasses in the Lower Chesapeake Bay suggests that light (and/or factors influencing the quality and quantity of the light regime) and nutrients are principal factors governing the distribution and metabolism of the submerged aquatic plant communities.

The overall objectives of the studies reported in the following chapters of this volume were: 1) to describe structural characteristics of the plant community and environmental regimes of a natural, unperturbed SAV community in the Lower Chesapeake Bay, 2) to derive estimates of community productivity and metabolism for diel, seasonal and annual periods, and 3) to evaluate potential mechanisms controlling productivity and community dynamics. Various studies and experimental designs were initiated and completd during the period July, 1978 through November, 1981 to accomplish these overall objectives.

Study Site

Selection of the principal study site was decided by consensus of the five original principal investigators which was composed of members associated with different aspects of SAV research within the overall program. A seagrass bed approximately 140 hectares in size located on the southeastern shore of Chesapeake Bay was chosen as the principal study area. This area is known locally as Vaucluse Shores and is situated north of Hungar's Creek at approximately 37°25'N latitude, 75°59'W longitude. Criteria used for site selection were:

1. the site had been previously studied and some background information was available,

2. the bed is well established and historically stable,

3. the area is relatively remote and unperturbed,

4. vegetationally, the bed contained the two dominant lower Bay species, Zostera marina and Ruppia maritima, and,

5. the bed was large enough to simultaneously accomodate varied studies and sampling regimes.

The bed is roughly triangular in shape with the apex to the north and bordered on the east by the Vaucluse Shoreline, to the south by the Hungar's Creek channel and to the west by an off-shore sandbar (Figure 1). The area was a site for an intensive vegetational mapping program that was completed by the initiation of our studies in July 1978. During this study permanent transects were established and are represented in Figure 1 as transect lines labeled A through F proceeding south to north. These were used in our studies for selection and identification of within-site sampling stations. The figure also illustrates the submerged plant distribution and zonal dominance by species. From these data, five habitat types were indicated and have subsequently been used for within habitat sample site selection. These areas are:

1. Ruppia maritima dominated community
2. Mixed vegetation areas
3. Sand Patches or Unvegetated bottom within the bed
4. Zostera marina dominated community, and
5. Sand Bar.

Sampling sites were selected for each of the areas between transects B and C and permanently marked with buoys to identify stations for routine sampling and experimental studies.

The contents of this volume are divided into six chapters. Each is presented separately with regard to introduction, methods, results and discussion. The format was adopted to more closely align with our previously stated overall objectives. The final chapter presents the results of studies in a tropical, Thalassia testudinum seagrass community that was in part funded through the SAV Chesapeake Bay Program and paralleled in many respects our studies in the Chesapeake Bay. Techniques and experimental designs used in the study were developed in the Chesapeake Bay seagrass research program. This volume constitutes one of three major efforts on the functional ecology of SAV in the lower Chesapeake Bay (see Brooks, et al., 1981 and Orth, et al., 1982).

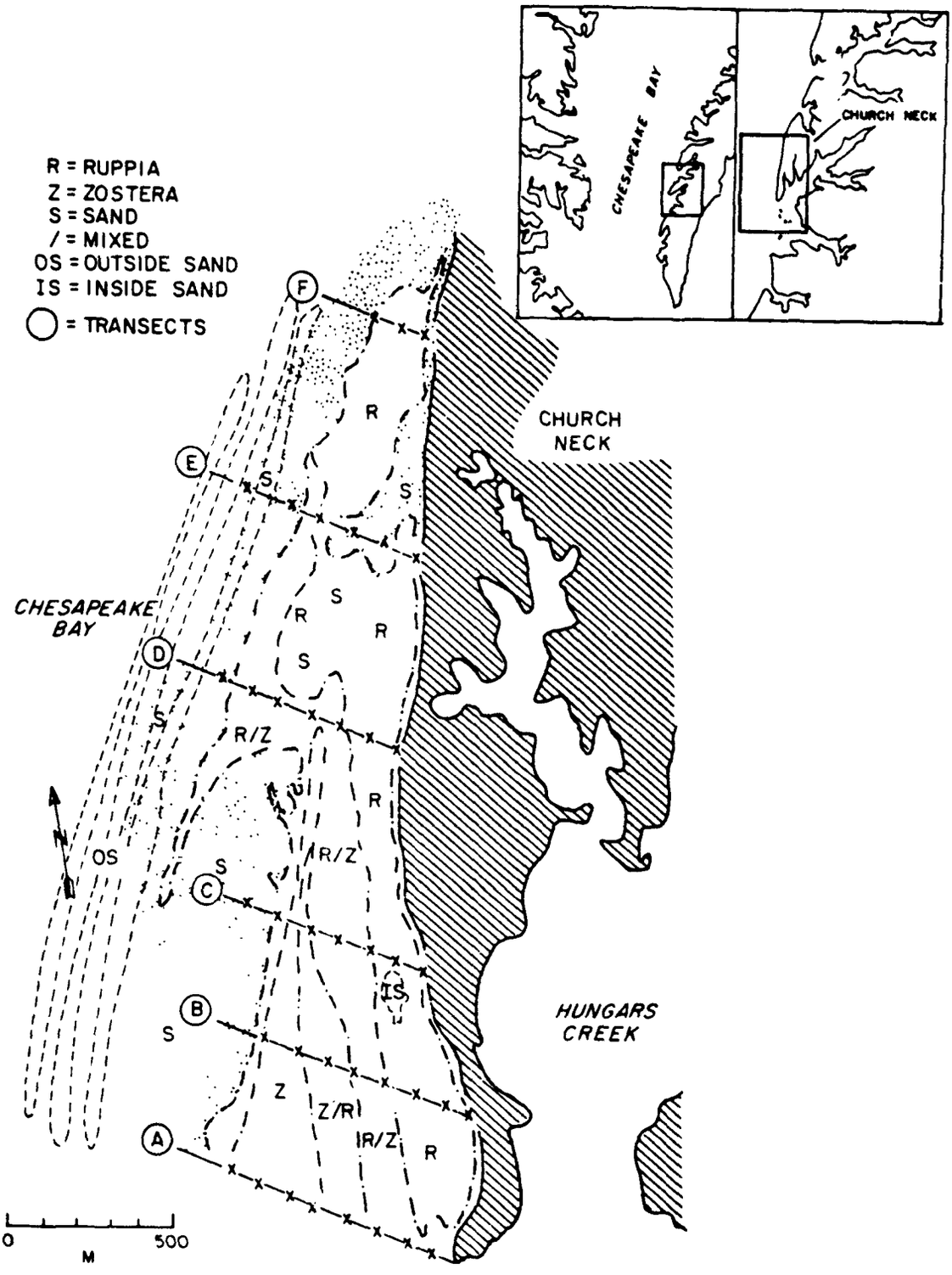


Figure 1. Geographical location of and plant community distribution at the principal study, Vaucluse Shores, Chesapeake Bay, Virginia.

LITERATURE CITED

Backman, R. W. and D. C. Barilotti. 1976. Irradiance reduction: effects on crops of the eelgrass Zostera marina in a coastal lagoon. Mar. Biol. 34:33-40.

Biebl, R. and C. P. McRoy. 1971. Plasmatic resistance and rate of respiration and photosynthesis of Zostera marina at different salinities and temperatures. Mar. Biol. 8:48-56.

Brooks, H. A. et al. 1981. Higher level consumer interactions. Draft final report, grant no. R805974, U.S. Environmental Protection Agency, Chesapeake Bay Program, Annapolis, MD. 196 pp.

Congdom, R. A. and A. J. McComb. 1979. Productivity of Ruppia: seasonal changes and dependence on light in an Australian estuary. Aquatic Bot. 6:121-132.

Cottam, C. 1935a. Further notes on past periods of eelgrass scarity. Rhodora 37:269-271.

Cottam, C. 1935b. Wasting disease of Zostera marina. Nature 135:306.

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

Dillon, C. R. 1971. A comparative study of the primary productivity of estuarine phytoplankton and macrobenthic plants. Ph.D Dissertation, University of North Carolina, Chapel Hill. 112 pp.

Gallagher, J. L. 1975. Effect of an ammonium nitrate pulse on the growth and elemental composition of natural stands of Spartina alterniflora and Juncus roemerianus in a Gerogia salt marsh. Amer. J. Bot. 62:644-648.

Mann, K. H. 1975. Relationship between morphometry and biological functioning in three coastal inlets of Nova Scotia. pp. 634-644. In, L. E. Cronin (ed), Estuarine Research, V.I, Academic Press, N.Y. 738 pp.

Nixon, S. W. 1980. Between coastal marshes and coastal waters; a review of twenty years of speculation and research on the role of salt marshes in estuarine productivity and water chemistry, pp. 437-525. In, P. Hamilton and K. B. MacDonald (eds.), Estuarine and Wetland Processes, Plenum Publ. Co., N.Y.

Orth, R. J. 1977. Effect of nutrient enrichment on growth of the eelgrass Zostera marina in Chesapeake Bay, Virginia. Mar. Biol. 44:187-194.

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. Environmental Protection Agency, Report no. 600/8-79-029/SAV1, Chesapeake Bay Program, Annapolis, MD.

Orth, R. J. and K. A. Moore. 1982. The biology and propagation of eelgrass, Zostera marina, in the Chesapeake Bay, Virginia. Final Grant Report, U.S. Environmental Protection Agency, Grant no. R805953, Chesapeake Bay Program, Annapolis, MD. and VIMS SRAMSOE 265, Gloucester Point, VA. 187 pp.

Penhale, P. A. 1977. Macrophyte-epiphtye biomass and productivity in an eelgrass (Zostera marina L.) community. J. exp. mar. biol. Ecol. 426:211-234.

Pomeroy, L. R. 1975. Mineral cycling in marine ecosystems, pp. 209-223. In, F. G. Howell, J. B. Gentry and M. H. Smith (eds.), Mineral Cycling in Southeastern Ecosystems, NTIS, Conf-74013, Springfield, VA.

Postgate, J. R. 1971. Relevant aspects of the physiological chemistry of nitrogen fixation, pp. 287-307. In, D. E. Hughes and A. H. Rose (eds.), Microbes and Biological Productivity, Symp. Soc. Gen. Microbiol., V. 21, Cambridge Univ. Press, London.

Ryther, J. H. and W. M. Dunstan. 1971. Nitrogen, phosphorus and eutrophication in the coastal marine environment. Science 171:1008-1012.

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

Thayer, G. W. 1971. Phytoplankton production and the distribution of nutrients in a shallow unstratified estuarine system near Beaufort, N.C. Chesapeake Sci. 12:240-253.

Thayer, G. W., S. M. Adams, and M. W. LaCroix. 1975. Structural and functional aspects of a recently established Zostera marina community, pp. 518-546. In, L. E. Cronin (ed.), Estuarine Research, V. 1, Academic Press, N.Y. 738 pp.

Valiela, I., J. M. Teal, and W. Sass. 1973. Nutrient retention in salt marsh plots experimentally fertilized with sewage sludge. Est. Coastal Mar. Sci. 1:261-269.

Williams, R. B. 1973. Nutrient levels and phytoplankton productivity in the estuary, pp. 59-89. In, R. H. Chabreck (ed.), Proc. 2nd Symp., Coastal Marsh and Estuary Management, Louisiana State University, Baton Rouge.

Chapter 1

PLANT COMMUNITY STRUCTURE, ELEMENTAL COMPOSITION AND SEDIMENT CHARACTERISTICS OF A TEMPERATE, ESTUARINE SEAGRASS ECOSYSTEM; VAUCLUSE SHORES, LOWER CHESAPEAKE BAY, VIRGINIA

Richard L. Wetzel, Polly A. Penhale and
Kenneth L. Webb

Virginia Institute of Marine Science
and School of Marine Science
College of William and Mary
Gloucester Point, Virginia 23062

INTRODUCTION

In order to determine structural properties of the SAV community and physical-chemical regimes characteristic of the study area, routine studies were carried out to investigate plant species distribution and relative abundance, plant canopy structure and chemical characteristics, and various sediment, chemical properties. All sampling was carried out at the Vaucluse study site between transects B and C (see Figure 1, Preface).

METHODS AND MATERIALS

Plant Distribution, Relative Abundance and Biomass

Plant distribution and relative abundance was determined along transects A, B, and C in July, 1979 and along transect B in May, July and August, 1980 to determine areal coverage by species and distribtion with water depth. A line-intersect method was employed using two divers and is described in detail by Orth, et al. (1979). Briefly, the transects illustrated in Figure 1 (Preface) were followed from the offshore sandbar beginning at low tide and progressing toward the shore. A 100 m line marked at 10 m intervals was employed along the transect line to locate point-intersections for determining species composition and estimating percent cover. At each 10 m intersection, a $0.5m^2$ frame was randomly dropped and species composition determined and percent coverage estimated by a diver. This procedure was repeated twice at each sampling point. During each transect study, time and water depth were recorded at each station and later compared to a continuous, relative tide height record kept near-shore. These data were used to calculate bottom depth relative to mean low water at each sampling point following the methods of Orth, et al, (1979). These data also provided direct comparisons with the previous intensive mapping effort (July, 1978) by Orth, et al. (1979) for identifying any major differences in distribution between years and providing relative abundance and distribution information for the bed as a whole.

Plant biomass was determined at monthly intervals for the period April, 1979 to April, 1980 in the R. maritima, mixed, and Z. marina dominated communities. These data were collected by Orth and details of sample collection and processing are given elsewhere (Orth, et al. 1981). However, for comparison to information given in this section, the results of these studies are presented for continuity.

Plant canopy structure was determined in each vegetation zone at approximately monthly intervals beginning in April, 1979 and continued through August, 1980. Canopy structure was investigated by estimating leaf area index (LAI), the ratio of leaf area to substrate area (Evans 1972). Plant samples of each species from the R. maritima Z.marina and mixed vegetation area were collected by hand, returned to the laboratory and rinsed free of sediment. Leaves were then removed and 3 replicate samples of 10 shoots each were sectioned at 5 cm intervals from the base to apex of the leaves. Leaf area (one-sided) was determined using a LI-COR Model LI13100/1+1 Leaf Area Meter.

LAI results are reported as m^2 leaf surface (one-sided) per m^2 sediment surface for 5 cm intervals for each species at each site as well as on a site basis.

Rooting depth was determined during July 1979 in the three major vegetation areas by hand coring using a 10.2 cm diameter (0.033 m^2 surface area) acrylic corer. Four replicate cores were taken per area and sectioned into 0-2, 2-5, 5-10 and 10-15 cm horizontal sections. Each section was washed free of sediment through a 1.0 mm screen and roots and rhizomes sorted by hand. The replicate samples were dried at 60°C to constant weight (48 hours) and percent contribution to total weight determined for each section.

Chemical analyses of plant tissue consisted of wet weight:dry weight, organic matter (OM) and carbon:nitrogen (C:N) determinations. Samples were collected by hand with the corer (described above) and separated by species into above and belowground fractions at the R. maritima and Z. marina site. At the mixed vegetation area, belowground tissue was not separated by species. Leaf litter (aboveground dead, unattached material) was also collected. Methods of analyses are as described in the following section.

Chemical Characteristics of Plant Tissue and Sediments

Routine samples for sediment analyses in the five habitat types were taken in July and October 1978, April, 1979 and monthly for the period June through October, 1979 and February through May, 1980. Analyses performed in relation to habitat type were, adenosine triphosphate (ATP), water content (WC) organic matter (OM), particulate organic carbon and nitrogen (POC and PON). Replicate sediment samples were taken by hand-coring to a depth of approximately 30 cm using a 5 cm diameter acrylic core tube. The cores were capped underwater and sealed with tape for transport to the laboratory. The cores were then extruded, divided vertically and horizontally sectioned into 0-2, 2-5, 5-10, 10-15, 15-20 and 20-30 cm intervals. For each core, processing consisted of: duplicate 1 cc plugs extracted using boiling, 0.1 M sodium bicarbonate for ATP analysis (Bancroft, et al. 1974); the remaining sediment fraction was frozen for later water content, organic matter and POC-PON analyses.

Water content and organic matter content was determined gravimeterically on frozen sediments by drying at 60°C to constant weight for water content and by weight loss or ignition at 550°C for organic matter determination. Wet weight:dry weight and organic matter content for plant tissue samples were determined in a similar manner. All weights were determined to the nearest 0.01 mg. POC and PON analyses for both plant tissue and sediments were performed using a Perkin-Elmer Model 240B Elemental Analyzer.

RESULTS AND DISCUSSION

Sampling and analyses to characterize plant community structure and general physical and chemical characteristics at the Vaucluse study site were conducted over various intervals beginning in July 1978 and ending in July 1980. The sampling was scheduled in such a manner to evaluate both seasonal and annual cycles of the various parameters and to create a data base for

longer term monitoring efforts. More specifically, these data have been used for designing studies around documented temporal events as well as for designing sampling strategies and experimental approaches. These data have been used to partition other data sets for both spatial and temporal correlation with other measurements.

The results and discussion of these efforts are divided into two principal areas; 1) Plant Community Structural Characteristics and Dynamics, and 2) Chemical Characteristics of Vegetated and Non-vegetated Sediments.

Plant Community Structural Characteristics and Dynamics

Relative Abundance and Distribution

Plant distribution and percent cover (as an estimate of species relative abundance) was determined along transects A, B, and C in July, 1979. Figure 1 illustrates the distribution and percent cover by species relative to bottom depth at mean low water (MLW) along the transects. In terms of areal coverage and relative abundance, the most significant stands of Z. marina are located south of transect C and occupy the deeper (>50 cm below MLW) areas of the grass bed extending shoreward of the sand bar. Significant stands of R. maritima are located along all transects but are confined to the shallow (<50 cm below MLW) areas at this time of year. There is a major zone of overlap for the two species on all the transects that ranges laterally from ca. 250 m on transects A and B to 100 m on transect C. The depth range of the overlap or mixed vegetation areas is ca. 60 to 100 cm below MLW bottom depth on transects A and B. The mixed area on transect C is confined to below 60 cm and the only monospecific Z. marina stands are adjacent to the sand bar. These results for both relative abundance and distribution follow closely the results obtained by Orth, et al. (1979) in July, 1978 for the same transects. This general pattern of depth distribution and relative abundance is characteristic of SAV communities in the lower Chesapeake Bay (Orth et al. 1979). R. maritima is the dominant species in shoal benthic habitats less than 50 cm deep (MLW) while monospecific stands of Z. marina are found in habitats >100 cm deep. The mixed Ruppia-Zostera vegetation zones are also characteristic; the depth ranges (ca. 60-90 cm below MLW) observed at the Vaucluse site are typical of the lower Bay.

The generalized distribution pattern for lower Bay seagrasses raises important questions and suggests hypotheses relative to factors governing plant distribution and abundance. Apparent among these are the physiological characteristics of each species and their response the environmental factors light, temperature, nutrients and desiccation. Direct competition between species for available substrate does not appear a natural determinate; however, few data exist to evaluate the role this potential interaction might play.

The dynamic nature of the distribution and abundance of the plant community was investigated by repeating the relative abundance and distribution surveys along transect B in May and August, 1980 (Figure 2). Based on the results of plant biomass studies (Orth and Moore 1982) these sampling times represented months of maximum growth (May through July) and

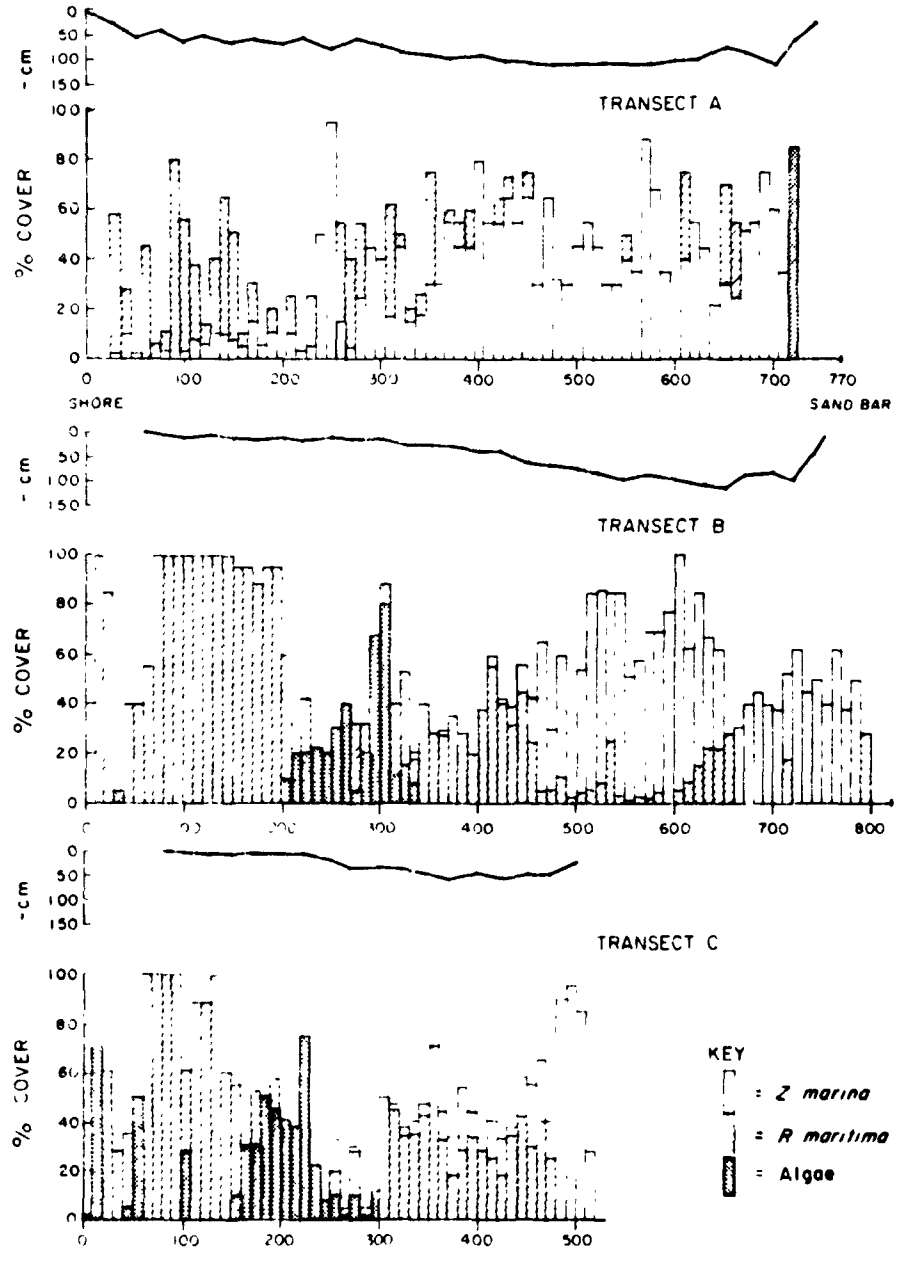


Figure 1. Submerged macrophyte distribution and relative abundance along transects A, B, and C, in July 1979, at Vaucluse Shores, Chesapeake Bay, Virginia, illustrating the depth-dependent zonation pattern typical of lower Chesapeake Bay beds. The horizontal axis is in meters from shore.

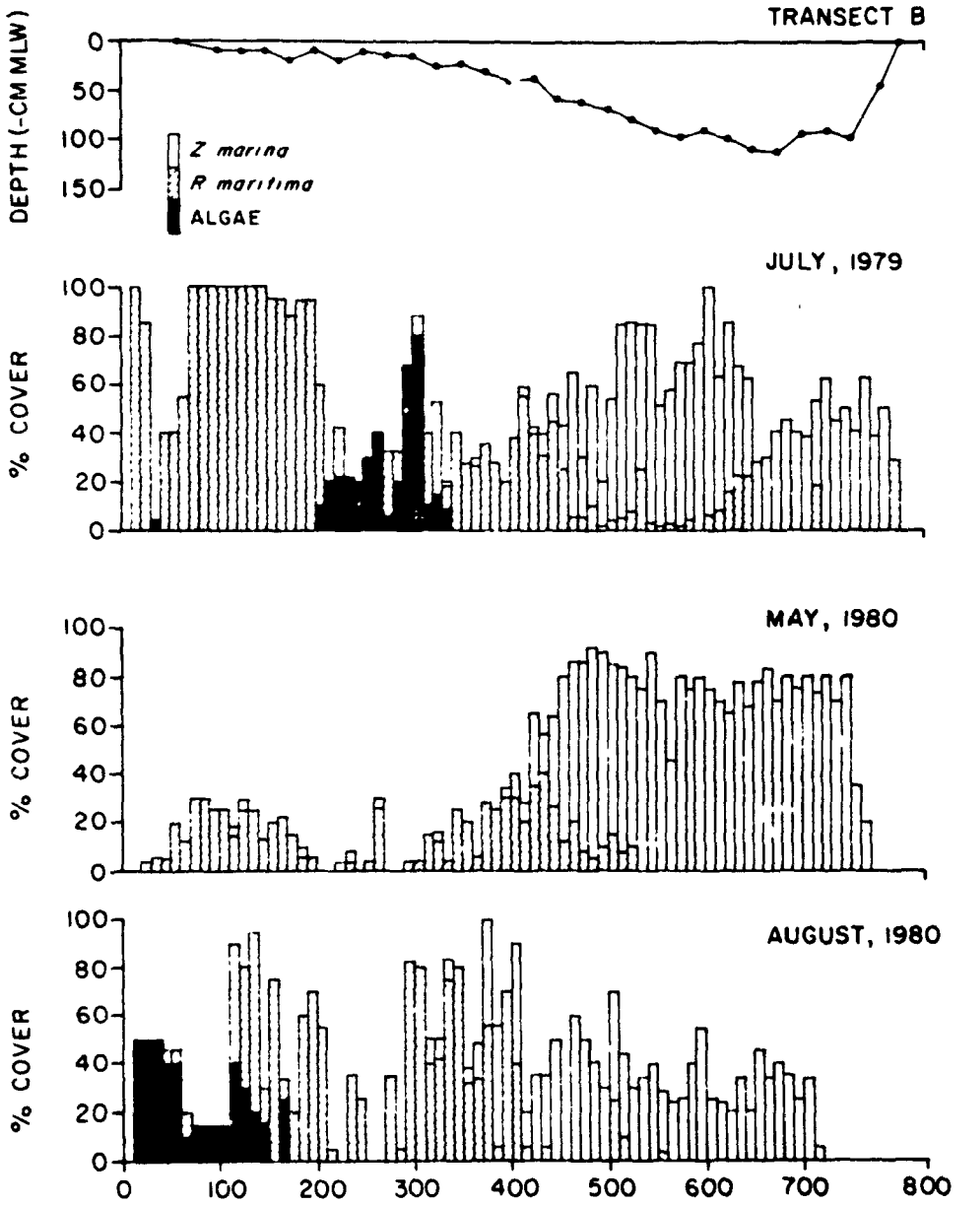


Figure 2. Submerged macrophyte distribution and relative abundance along transect B, for various times of year illustrating the dynamic nature of te vegetated zones. Horizontal scale is in meters from shore.

die-back (August) for Z. marina and R. maritima at the mixed site. R. maritima in the shallow area exhibits a late summer-fall period of maximum growth.

Species distribution along the depth gradient is similar for the three sampling periods; however, the relative abundance (% cover) is dramatically different (Figure 2). During the late spring (May) Z. marina is uniformly distributed in the deeper areas of the grass bed and has maximum relative abundance. By mid-summer (July), both species are relatively uniformly distributed within their zonal limits although Z. marina is reduced in relative abundance. There is some indication that R. maritima has invaded the deeper, Zostera-dominated areas of the bed during this period but confirmation of this must await longer term monitoring and more detailed studies. During the later part of the summer (August), Z. marina is significantly reduced in relative abundance at the deeper stations indicating natural plant mortality, and R. maritima is more patchily distributed and generally occupies the deeper areas within its range. These results suggest not only the dynamic nature of the bed as a whole, but, also the complementary nature of the growth and dynamics of the two species. We observed that species dominance and abundance shift during the growing season and these parameters are out of phase for the two seagrass species. This indicates that, as suggested previously, physiological and morphological differences between species rather than direct competitive interactions control species distribution. Consequently, from an applied standpoint, criteria developed for management of lower Bay seagrases may not apply universally to all species and for all locations.

Biomass Relationships and Rooting Depth

Above-ground plant biomass (vegetative shoots) in the three vegetated zones was also determined to provide information on growth, production and community dynamics. A summary of these data (from Orth, et al. 1981) are provided in Figure 3. Over an annual period, R. maritima exhibits a unimodal cycle in aboveground biomass. At the monospecific R. maritima site, peak biomass is in the Fall (September-October) while peak biomass occurs earlier (July-August) at the mixed site. Z. marina exhibits a bimodal cycle of annual growth with periods of maximum biomass occurring both in the spring to early summer and in the fall to early winter; these periods of maximum biomass are followed by periods of shoot die-back. The re-growth of Z. marina is not as pronounced at the mixed site as in the monospecific Z. marina site. The data also indicate to some extent the year to year variation in standing stock. For example, there was approximately a 50-60% increase in peak above-ground biomass for R. maritima between 1979 and 1980 and a corresponding 20-25% increase for Z. marina. Unfortunately, the data are not extensive enough to assign level of significance to the apparent differences.

The above-ground biomass pattern observed for Z. marina is similar to that observed in other temperate climates and probably reflects a negative growth response to increased summer water temperatures. In North Carolina, Penhale (1977) reported peak Z. marina shoot biomass in March followed by a general biomass decline throughout the rest of the year; the decline occurred as the water temperatures increased during the summer. Also in North Carolina, Thayer et al. (1975) observed a dramatic biomass decline following

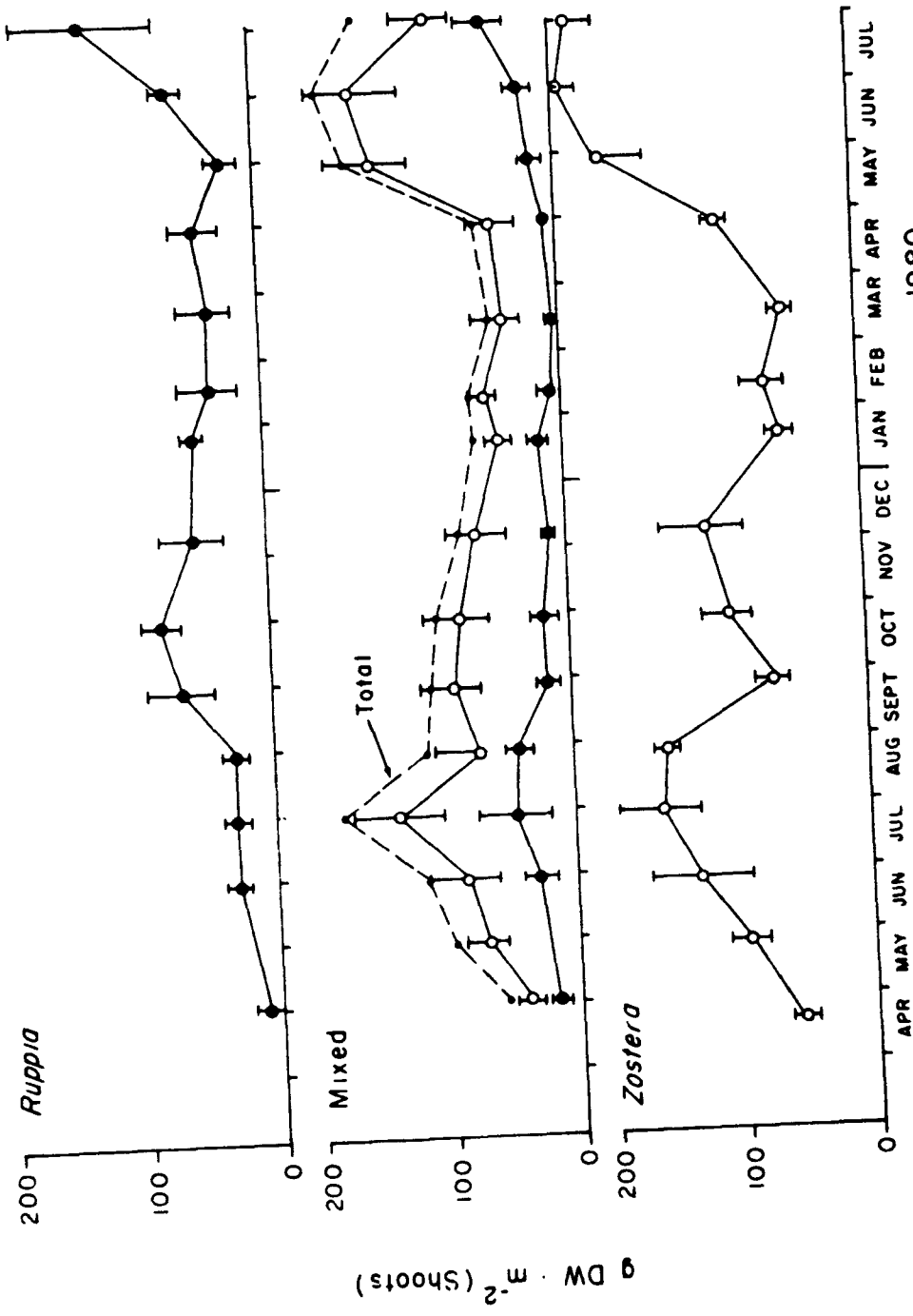


Figure 3. Mean shoot biomass (± 1 S.D.) of R. maritima (●) and Z. marina (○) at Vaucluse Shores for the three principal vegetated sites studied. (Data from Orth and Moore, 1982).

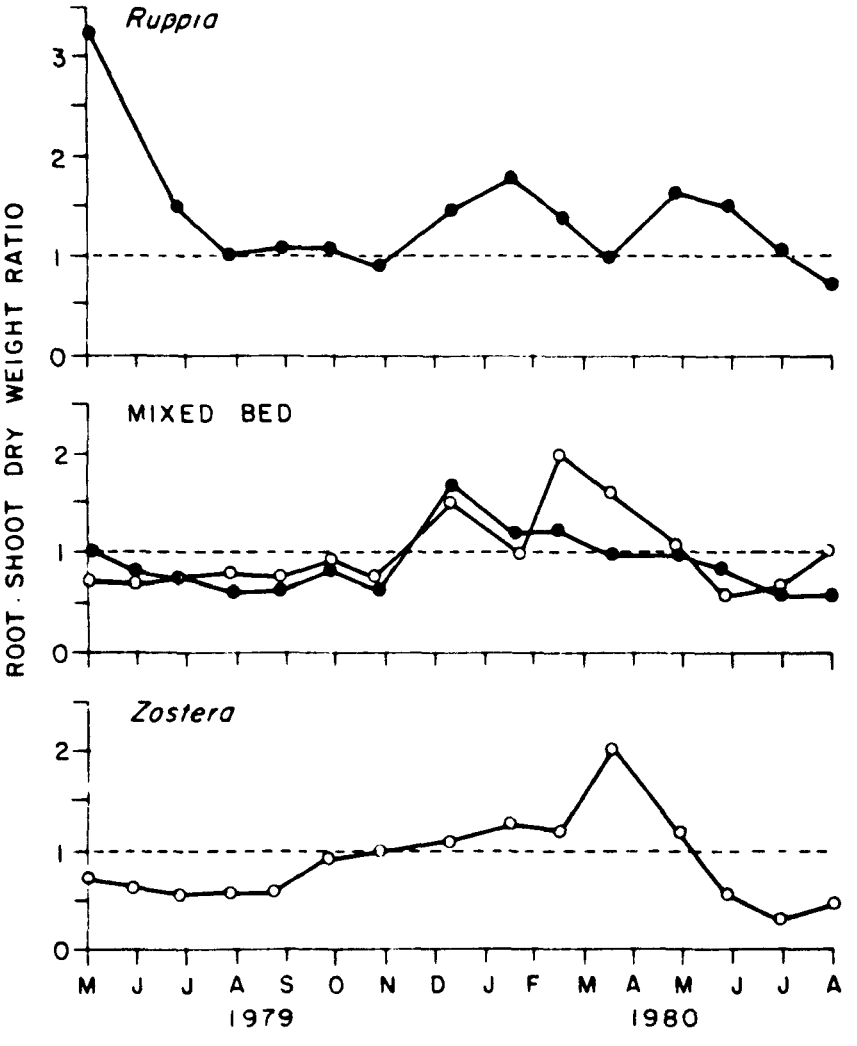


Figure 4. Mean root:shoot dry weight ratio of R. maritima (●) and Z. marina (○) at the three vegetated study sites. Calculated from the data of Orth and Moore, 1982.

peak summer water temperatures in August. Biebl and McRoy (1971) suggested that prolonged or frequent temperatures rises above 30°C could result in Z. marina mortality. A temperature response threshold is also reflected in the geographical distribution of Z. marina which reaches its southernmost limit on the eastern U.S. coast at Cape Fear, North Carolina (Thayer et al. 1975).

In general, R. maritima appears more tolerant of higher temperatures than Z. marina (Richardson, 1980 and references therein). The geographic range of R. maritima extends south to the Gulf Coast of the United States. Nevertheless, the annual growth cycle of R. maritima at Vaucluse Shores may involve a negative response to high summer temperatures as well as to other parameters characteristic of the habitat. At the monospecific R. maritima site, the shallow water allows for greater light penetration than in the mixed site; in fact, R. maritima at the shallower habitat may be photo-inhibited at times. In addition, plants in this zone are frequently exposed during extreme low tides. The low July-August biomass of R. maritima here may be due to the combination of high temperatures, high light, and desiccation damage; a more favorable light and temperature regime is probably present during its fall biomass peak. At the deeper, mixed site where the light and temperature regime is less extreme, R. maritima biomass exhibits a peak in July followed by a decline during the warm August period. R. maritima at the mixed site is shaded to some extent by Z. marina which has longer leaves; the lower annual R. maritima biomass here may reflect lower productivity rates due to less light.

Root:shoot dry weight ratios (root here includes rhizome biomass) were calculated from the mean biomass data of Orth and Moore (1981) and are presented in Figure 4. Root:shoot ratios reflect the plant's metabolic expenditure in terms of non-photosynthetic and photosynthetic tissue. Root:shoot ratios less than 1 were noted during much of the year for both species at the mixed site and for Z. marina at the monospecific site. In contrast, R. maritima at the monospecific site exhibited a ratio consistently above 1, which suggests a different strategy for the plants. The below-ground portion of the plant is considered an important site of nutrient uptake for submerged angiosperms (Penhale and Thayer 1980 and references therein). It is possible that lower interstitial nutrient concentrations may characterize the R. marina site; thus, the plant may expend more energy toward underground growth. At the deeper mixed and Zostera sites characterized by lower light penetration, root:shoot ratios less than 1 may reflect an additional expenditure toward more photosynthetic tissue.

Rooting depth analyses of the seagrasses in the three vegetated habitats indicate that greater than 98% of the root-rhizome system is located in the upper 10 cm of the sediment (Table 1). At the R. maritima site, a greater proportion of below-ground biomass was located in the upper 2 cm than at the other two sites. The mean total root-rhizome biomass was highest at the mixed site, with considerably lower values at the Z. marina site and lowest values at the R. maritima site.

The rhizosphere is the portion of the sediment under the immediate influence of the plant roots (Rovira and Davey 1974). Seagrass roots may release oxygen to the sediments (Oremland and Taylor 1977; Iizumi, et al.

TABLE 1. TOTAL AND DEPTH DISTRIBUTION OF ROOT-RHIZOME BIOMASS AT THE THREE VEGETATED ZONES AT VAUCLUSE SHORES. ALL WEIGHTS ARE REPORTED AS MG DRY WEIGHT PER CORE (0.033 m^2) ± S.D.

Site	Depth (cm)	Total Root & Rhizome Dry weight (mg)	% Total Wt.	%0-5 cm	%0-10 cm
R. maritima (n=4)	0-2	2803 ± 876	76 ± 9.7	89 ± 3.0	[illegible] ± 1.0
	2-5		22 ± 10.0		
	5-10		9 ± 3.3		
	10-15		2 ± 1.0		
Mixed Bed (n=3)	0-2	9750 ± 2273	55 ± 4.6	83 ± 11	98 ± 0.6
	2-5		28 ± 15.2		
	5-10		15 ± 10.1		
	10-15		2 ± 2		
Z. marina (n=3)	0-2	4540 ± 908	51 ± 14	93 ± 3.2	99 ± 0.6
	2-5		42 ± 15.9		
	5-10		6 ± 2.6		
	10-15		0.7 ± 0.58		

1980). Also, dissolved organic carbon compounds may be released by seagrass roots (Wetzel and Penhale 1980; Wood and Hayasaka 1981). In the highly anaerobic sediments of plant communities with submerged roots such as seagrass systems, plant activity results in a profound influence on physical, chemcal, and biological characteristics of this zone. In the Vaucluse Shores system, the rooting depth data suggest that this dynamic zone of activity is concentrated in the upper 5 cm of the sediment. In addition, plant influence on sediment processes may be greatest at the mixed site due to its greater biomass of root-rhizome material.

Canopy Structure

Plant community growth involves the response of individual plants to the environment as well as to other individuals in the community. LAI is a fundamental parameter in community analysis since community growth is not simply determined by the photosynthetic capacity of individual leaves. That is, community growth is the product of the net assimilation per leaf area and the LAI. An increase in plant density affords a greater potential for community production but mutual shading reduces the available light to a point where net production decrases. Many factors such as light intensity, leaf morphology, and leaf orientation (i.e., as influenced by tides and currents for seagrasses), play a role in determining the optimal LAI of a community.

The results of our leaf area index (LAI) studies showed differences among vegetated sites (Figure 5). Analysis of variance of one-sided LAI by date and site indicated significant differences among sites ($p = 0.016$). The maximum one-sided LAI values for the three sites in this study (R. maritima = 3.4, mixed = 4.2, Z. marina = 3.2) were within the range of maximum values reported for other seagrasses communities. For example, maximum one-sided LAI values reported for seagrass systems include 16.8 (Dennison 1979); 9 (Jacobs 1979), and 3.3 (Aioi 1980) for Z. marina; 9.3 for Thalassia testudinum (Gessner 1971), and 8.3 and 1.4 for Posidonia oceanica and Cymodocea nodosa, respectively (Drew 1978). Few data exist for canopy structure in submerged angiosperm communities compared to terrestrial communities. LAI values for terrestrial communities generally range from 1 to 12 and high LAI values tend to be positively correlated with high annual productivity (Leopold and Kreideman 1975).

In a detailed community structure analysis of a monospecific Z. marina community across a depth gradient, Dennison (1979) concluded that changing leaf area was a major adaptive mechanism to decreasing light regimes. He observed that the LAI increased with increasing depth to the deepest portion of the bed where the LAI decreased. At these stations with the lowest light penetration, further increases in LAI probably could not be maintained due to the lowered net photosynthesis with less available light. This is similar to the results obtained in this study in which LAI values generally increase from the Ruppia to the mixed site and then decline at the deep Z. marina site.

The seasonal pattern of LAI reflects various trends within the three sites (Figure 5). At the R. maritima site, the decrease in LAI during fall-winter, 1979 paralleled a decrease in shoot density, leaf length and shoot biomass data. The summer increase in LAI corresponded to increasing

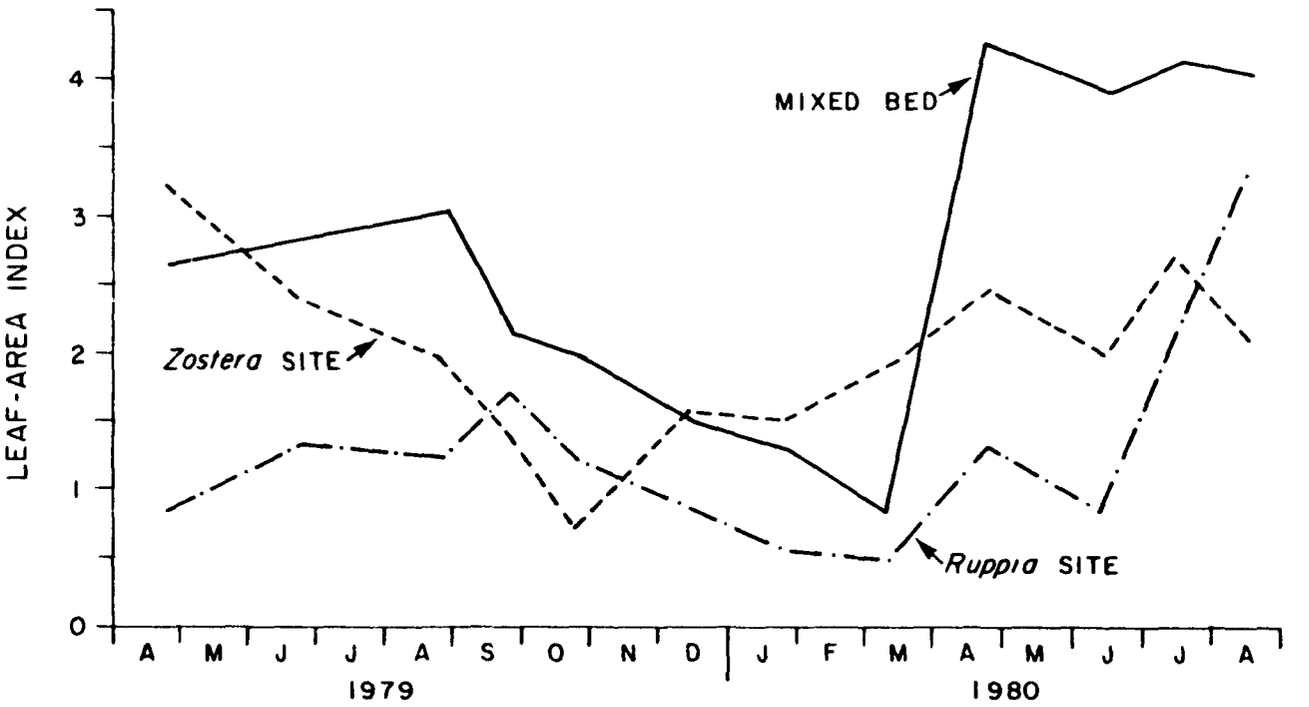


Figure 5. Monthly mean estimates of one-sided Leaf Area Index (LAI) for the three vegetated sites at Vaucluse Shores for the period 1979-1980.

insolation and increasing density, biomass and leaf length. At the mixed site, which generally exhibited the highest LAI values, the steady decrease in LAI from August, 1979 to February, 1980 was a result of decreasing biomass, length and density of R. maritima. Although the density of Z. marina increased during this period of new shoot growth, leaf length and biomass decreased. The rapid LAI increase in spring, 1980 reflected rapid increases in biomass and length of Z. marina and in density, length and biomass of R. maritima. At the Z. marina site, the steady LAI decline from April to October paralleled a decrease in leaf length. The sharp decline in LAI at all three sites from April to June, 1980 reflected an unexplained decrease in shoot density.

Interrelationships of these community parameters have been reported in other studies. In a Z. marina community in France, Jacobs (1979) observed a seasonal trend in which increases in LAI paralleled increases in shoot density and the number of leaves per shoot. Aioi (1980) observed that both the LAI and shoot biomass exhibited a similar unimodal seasonal pattern with a maximum in May; he related this pattern to day length. Center (1981) observed a continuous trend toward maximum LAI of a freshwater Eichhornia crassipes community in which inceases in plant density in response to available space were followed by increases in plant size in response to competition for light.

The results of our canopy structure studies also showed differences in LAI between species. Using Duncan's multiple range test, the analysis indicated that the mean LAI values of R. maritima and Z. marina were significantly different ($p=0.05$). The data were further analysed using a least squares test for differences among means by species for the various sites (Table 2). For Z. marina, the mean LAI was not significantly different than the mixed site. The mean LAI for R. maritima was significantly different than the mixed sites; both of these were significantly different from Z. marina.

One-sided LAI values were calculated for 5 cm vertical sections of leaf material in order to obtain information on the vertical stratification of leaf area at the three vegetated sites (Figures 6, 7, 8, 9). Scatter plots of the data collected over the 17-month study show that for both R. maritima and Z. marina, maximum leaf area was concentrated in the lower portion of the canopy. The R. maritima canopy exhibited the greatest concentration of leaf area from 0 to 5 cm above the substrate. Analysis of variance of the vertical distribution of LAI showed highly significant differences between species ($p = 0.0001$).

Examples of the vertical stratification of leaf area of R. maritima and Z. marina at the three sites are presented in Figures 10, 11, and 12. Although the LAI changes during the year, the relative distribution of leaf area does not change. Over the yearly cycle, the LAI for R. maritima and for Z. marina in the monospecific stands was generally higher than that for each species at the mixed site. The three examples illustrate a period of major biomass decline of Z. marina (August, 1979; Fig. 10), a period of low biomass of both species (January, 1980; Fig. 11), and a period of generally high biomass and long leaf length of both species (July, 1980; Fig. 12).

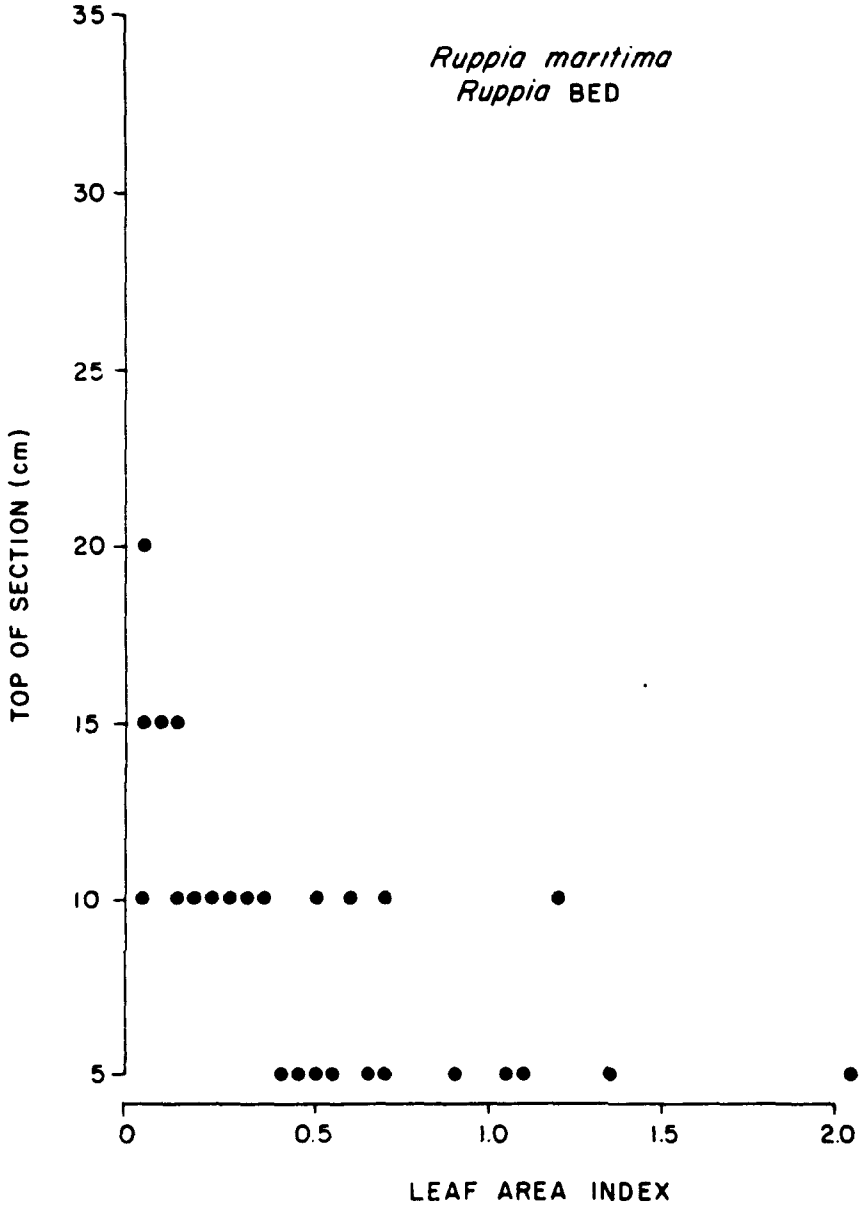


Figure 6. Scatter plot of the vertical distribution of LAI for R. maritima at the monospecific site at Vaucluse Shores.

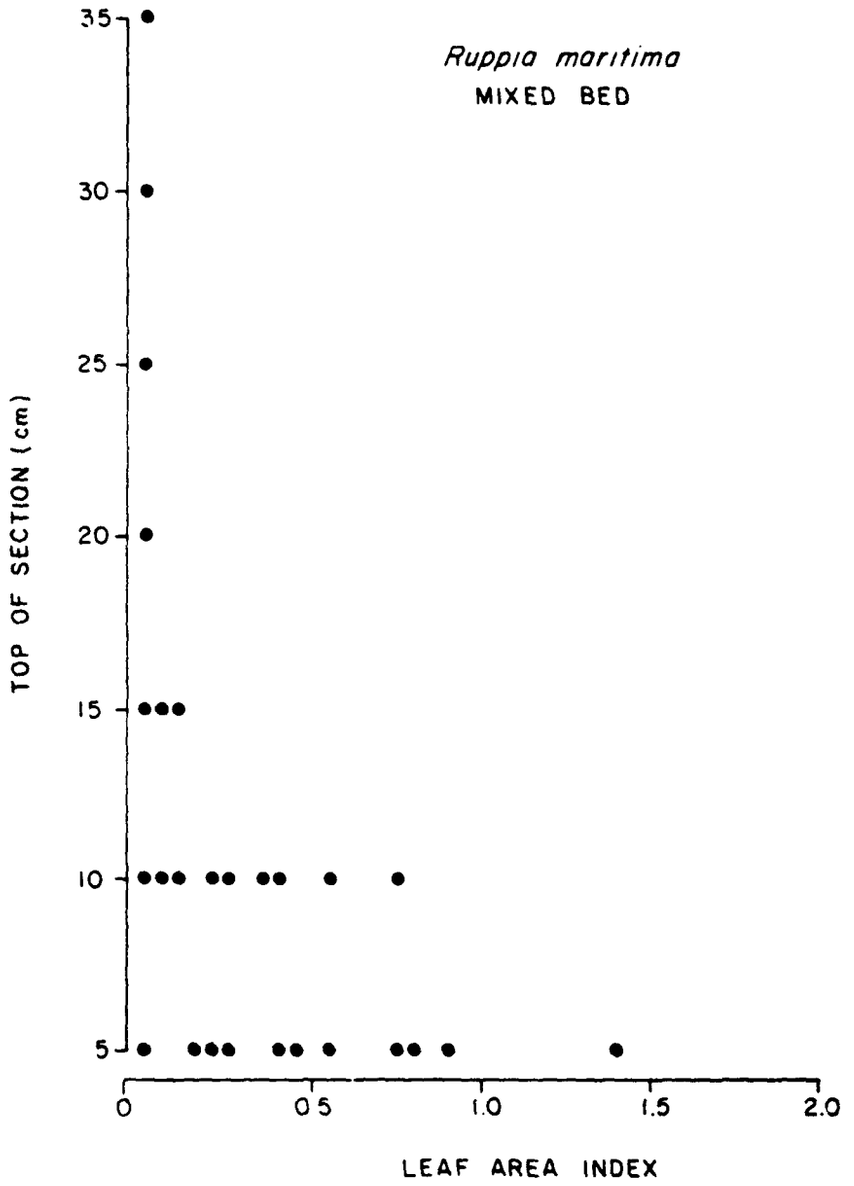


Figure 7. Scatter plot of the vertical distribution of LAI for R. maritima the mixed bed site, at Vaucluse Shores.

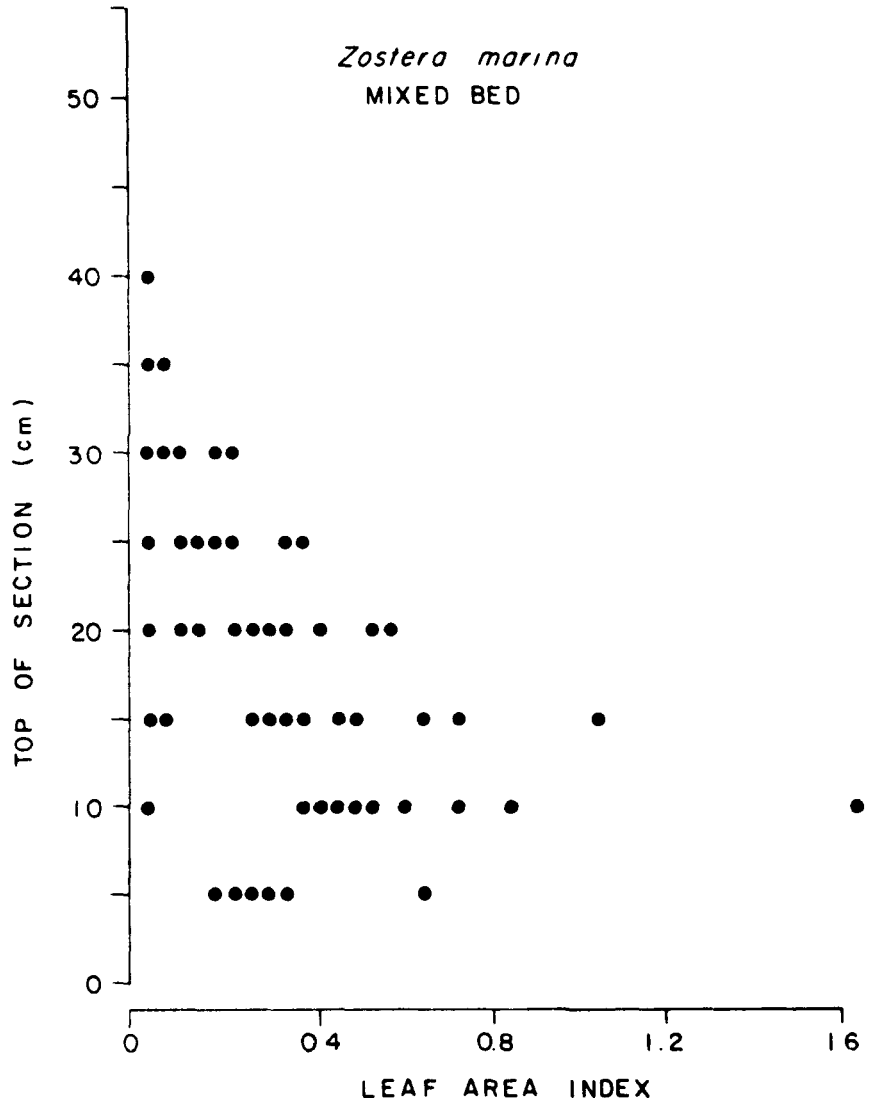


Figure 8. Scatter plot of the vertical distribution of LAI for Z. marina at the mixed bed site, at Vaucluse Shores.

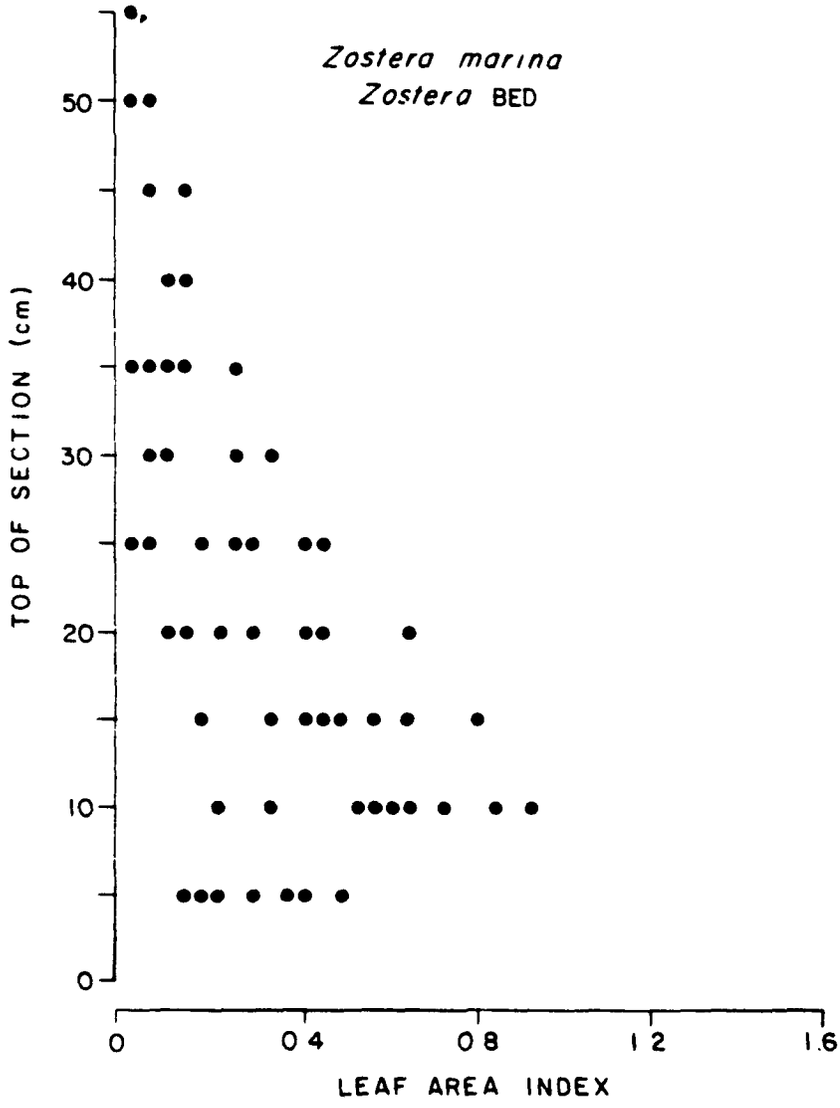


Figure 9. Scatter plot of the vertical distribution of LAI for Z. marina at the monospecific site, at Vaucluse Shores.

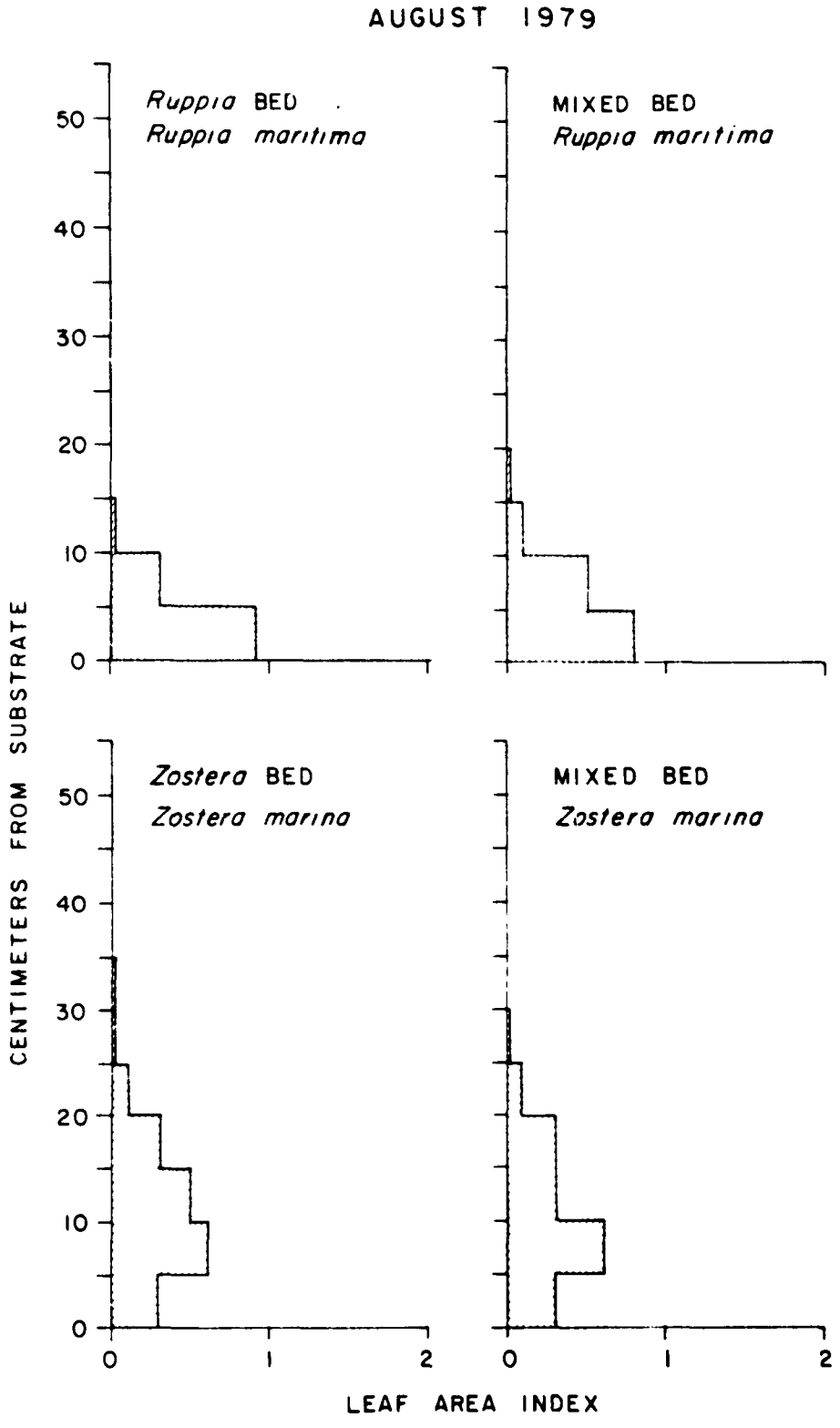


Figure 10. Vertical distribution of LAI for R. maritima and Z. marina at the three vegetated sites for August, 1979 at Vaucluse Shores.

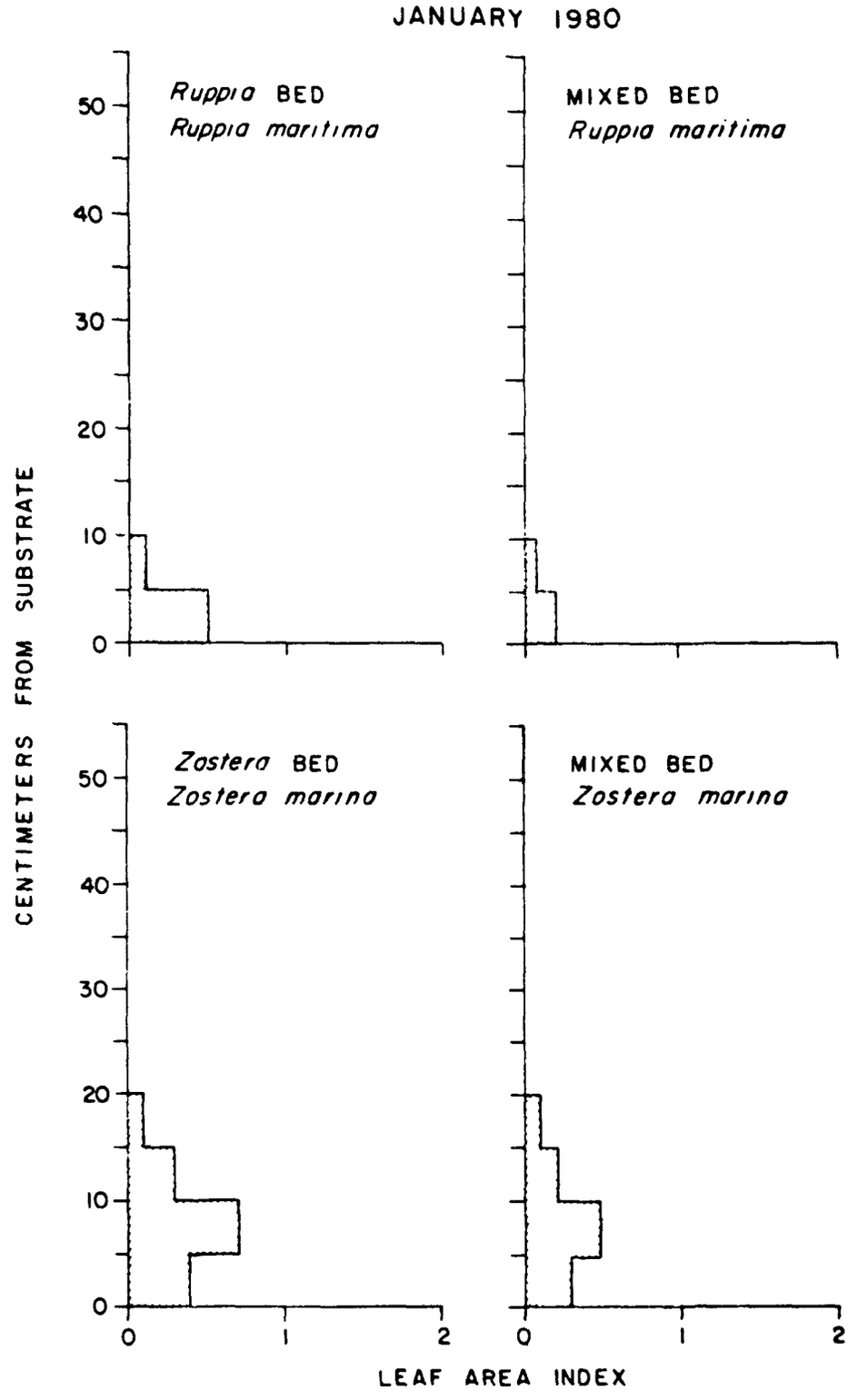


Figure 11. Vertical distribution of LAI for R. maritima and Z. marina at the three vegetated sites for January, 1980 at Vaucluse Shores.

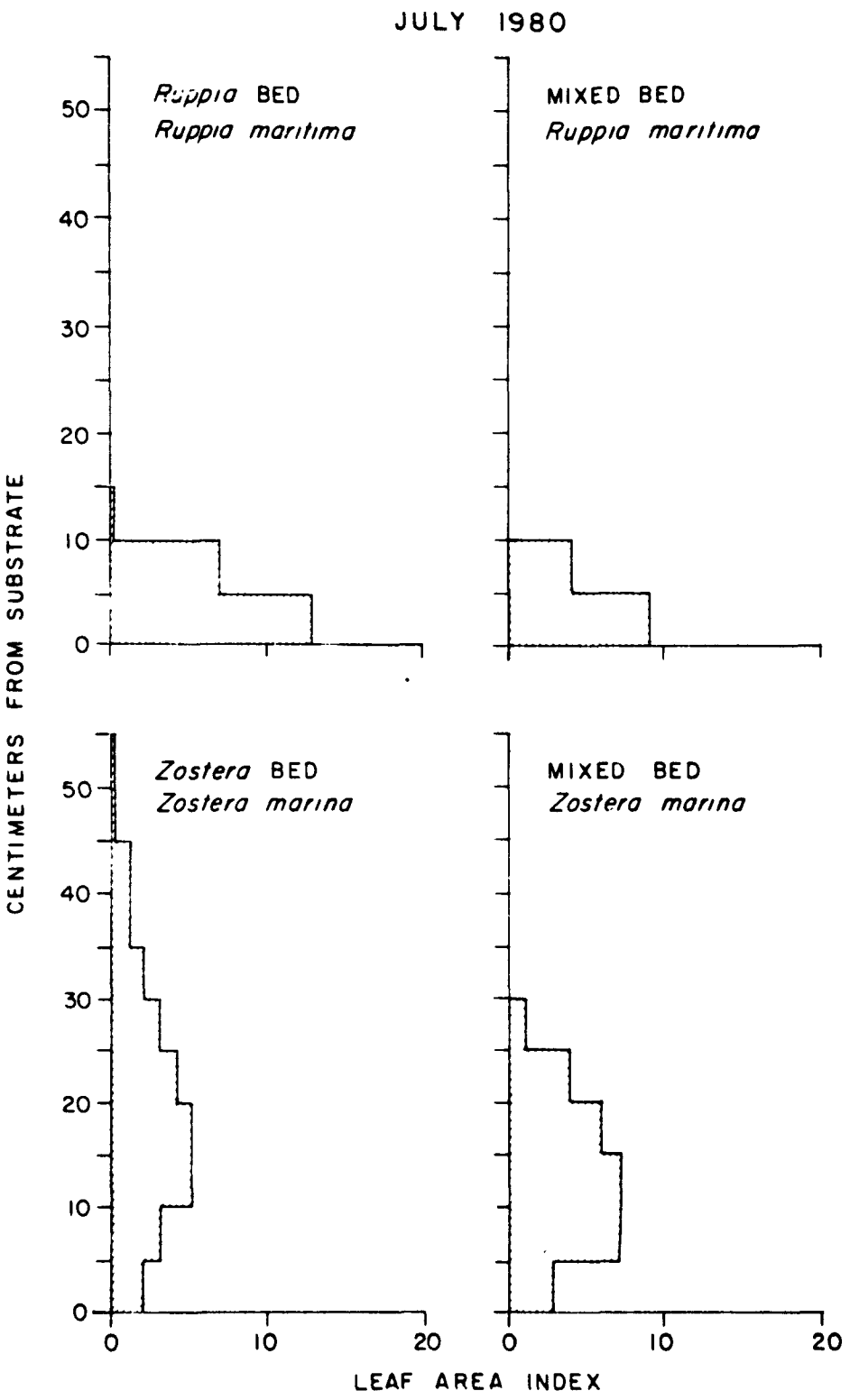


Figure 12. Vertical distribution of LAI for R. maritima and Z. marina at the three vegetated sites for July, 1980 at Vaucluse Shores.

TABLE 2. LEAST SQUARES TEST FOR DIFFERENCES AMONG MEAN LAI BY SPECIES FOR THE THREE VEGETATED STUDY SITES AT VAUCLUSE SHORES.

Group	Species	Site	I/J	Group Number 1	2	3	4
1	Ruppia	Mixed		*	0.001	0.0031	0.0001
2	Zostera	Mixed		0.0001	*	0.0288	0.2412
3	Ruppia	Ruppia		0.0031	0.0288	*	0.001
4	Zostera	Zostera		0.001	0.2412	0.001	*

Prob>|T| HO: $\bar{x}(I) = \bar{x}(J)$

The canopy structure at the three sites reflects adaptations to the specific light regimes. In the shallow, high light environment at the R. maritima site, the upper portion of the canopy may be photoinhibited during portions of the year; a greater leaf area near the substrate where light is reduced may allow for a greater net canopy photosynthetic rate. For both species at the mixed site and for Z. marina at the monospecific site, concentration of photosynthetic area in the lower canopy would compensate for the decreased light with increasing mean depth. Species differences in the vertical stratification of leaf area would be particularly important at the mixed site where R. maritima is shaded by Z. marina; these differences probably contribute to successful co-existence.

Although other factors are involved, competition for light in submerged communities is probably the most important factor in determining community structure. Haller and Sutton (1975) characterized the community structure of Hydrilla, an introduced species which often displaces native species in Florida. They proposed that Hydrilla communities, by forming a dense canopy at the water surface (which can reduce light penetration by 95% in 0.3 m) have effectively replaced native Vallisneria americana communities which are less dense. In a study of Myriophyllum spicatum and Vallisneria americana, Titus and Adams (1979) observed that the former had 68% of its foliage within 30 cm of the surface while the latter had 62% of its foliage within 30 cm of the bottom. Like Hydrilla, Myriophyllum spicatum has been successful in establishing dominance in competitive situations.

Wet:Dry Weight Ratios of Plant Tissue

Wet:dry weight ratios of R. maritima and Z. marina were calculated for samples collected in May, 1981. Ratios for R. maritima were 6.31 ± 0.76 (n=5) for leaves and 8.72 ± 0.47 (n=5) for roots and rhizomes. Ratios Z. marina were 7.20 ± 0.65 (n=4) for leaves and 8.69 ± 0.73 (n=4) for roots and rhizomes. These values are similar to ratios reported by Neinhuis and DeBree (1977) for Zostera marina (leaves, 6.7 to 11.1; roots and rhizomes, 5.5-16.7).

Elemental carbon and nitrogen analysis

Elemental analysis of plant materials is useful for a number of purposes. Tissues analysis may provide estimates of nutrient availability for growth (Gerloff and Krombholz 1966) or give an indication of possible food quality for other organisms (Godshalk and Wetzel 1978). Carbon:nitrogen atomic ratios in plankton are considered to be about 6.6 according to the Redfield Model (Redfield 1958). Goldman et al. (1979) have suggested that phytoplankton of composition with greater ratios are deficient in nitrogen, and grow slower than maximally. Angiosperms contain more structural carbohydrates, such as cellulose, than phytoplankton (e.g. Almazan and Boyd 1978), and thus these considerations are not as straight forward as in the phytoplankton although similar analogies have been used. Carbon:nitrogen ratios seldom aproach the Redfield Model value of 6.6 in seagrasses and reported values range from 10 to 80 with values of 10 to 20 being usual for Zostera marina (Table 3).

Seasonal changes might be expected in the nitrogen and carbon content of seagrasses since these plants, at least in temperate climates, undergo

TABLE 3. SUMMARY OF THE AVAILABLE LITERATURE ON WEIGHT PERCENT C AND N AND ATOMIC C:N RATIOS IN SEAGRASSES.

Species	Plant Part	Location	%C	%N	C:N	Ref.*
Amphibolis griffithii	leaves	W. Australia	30.	1.3	26.8	1
"	stems	"	30.	0.96	36.4	1
Cymodocea nodosa	leaves	Corsica	37.	1.59	27.2	1
C. serrulata	leaves	N. Queensland			21.6	2
"	leaves	"	38.	1.25	35.4	1
"	rhizomes	"			67.1	2
Enhalus acoroides	leaves	N. Queensland			19.8	2
"	rhizomes	"			82.	2
"	leaves	"	36.	1.70	24.7	1
"	leaves	Palau	39.	2.18	20.8	1
"	rhizomes	"	35.	0.94	43.4	1
Halodule uninervis	leaves	N. Queensland			33.2	2
"	rhizomes	"			27.7	2
"	leaves	"	36.	1.21	34.6	1
Halophilia decipiens		"			24.4	2
H. hawaiiana		Hawaii	24.	1.13	24.8	1
H. ovalis		W. Australia	16.	0.63	29.8	1
"		N. Queensland			51.7	2
H. ovata		"			77.6	2
H. spinulosa		"			46.5	2
"		"	29.	1.45	23.3	1
Phyllospadix scouleri	leaves	California	36.	1.98	21.2	1
Posidonia oceanica	leaves	Corsica	33.	1.57	24.5	1
"	roots	"	38.	0.76	58.2	1
"	rhizomes	"	35.	0.93	43.7	1
P. ostenfeldic	leaves	W. Australia	33.	1.04	36.9	1
"	roots/rhizomes	"	34.	0.73	54.0	1
P. sinuosa	leaves	"	22.	0.80	32.	1
"	roots	"	21.	0.55	44.9	1
Syringodium isoetifolium	leaves	N. Queensland			25.5	2
	rhizomes	"			77.5	2
Thalassia hemprichii	leaves	"	31.	1.63	22.2	1
T. testudinum	leaves	Barbados			13.9	3
"	rhizomes	"			30.1	
Zostera capricorni	leaves	N. Queensland			20.5	2
"	rhizomes	"			58.1	2
"	leaves	"	32.	1.11	33.6	1
Zostera marina	leaves	California	38.	6.14	7.2	1
"	leaves	Rhode Island	31.	2.03	17.8	1
"	leaf-sheath	Japan	37.4	2.0	18.	4
"	leaf-blade	"	40.	2.29	18.6	4
"	rhizomes	"	38.	1.4	23.	4
"	root	"	29.	1.4	18.	4
"	dead-leaves	Wash., Alaska	29.1	1.4	18.8	5

TABLE 3. (CONTINUED)

Species	Plant Part	Location	%C	%N	C:N	Ref.*
Zostera marina	leaves-green	Denmark	33.9	2.25	12.9	6
"	leaves-brown	"	30 7	1.5	17.5	6
"	leaves	Germany	38.5	2.75	12.0	6
"	leaves	Japan	36.0	2.6	11.9	7
"	rhizomes	"	34.1	2.8	10.6	7
"	root	"	26.2	2.9	7.8	7
"	leaves	Canada	35-43	1.2-4.8	9-30	8

*References 1) Atkinson and Smith, 1981; 2) Birch, 1975; 3) Patriquin, 1972; 4) Aioi and Mukai, 1980; 5) Godshalk and Wetzel, 1978; 6) Vinogradov, 1953; 7) Seki and Yokohama, 1978; 8) Harrison and Mann, 1975.

seasonal periodicity in growth. Vinogradov (1953), reviewing earlier work, suggested a seasonal change in nitrogen content of Zostera marina, with the lowest nitrogen content occuring toward fall or during winter. Harrison and Mann (1975) report a distinct sinusoidal character with a peak leaf N percentage of 4.8 in March and a minimum of 1.2 in September. Our seasonal data set for percentage nitrogen in Zostera marina leaves (Table 5) is extensive, but, as of this writing, appears inadequate to establish good correlations with season or with biomass (Figure 3). Hopefully with expansion of the data set or more complete analysis, a meaningful interpretation will be available. However, it appears extremely unlikely that any textbook picture such as is presented by Harrison and Mann (1975) will be found. An estimated median value for percent nitrogen for Zostera marina leaves from the literature (Table 3) is 2.3% and apparently higher than the mean of 1.8 from our data. Percent organic carbon in Zostera marina leaves appear to be quite similar for our data (mean of 36%) and the literature (median 36%); thus the C:N ratio of our data (25) is almost twice the median value (13) from the literature. These data would seem consistent with the suggestion that the Vaucluse grass beds are nitrogen deficient (e.g. Orth 1977).

Roots and rhizomes of Zostera marina for Vaucluse clearly contain less carbon and nitrogen than do the leaves and show a higher C:N ratio (Table 4). This relationship seems to generally be borne out by the literature as well (Table 3) with the data set of Seki and Yokohama (1978) a possible exception. Our data are for combined root and rhizome tissue and the data of Seki and Yokohama (1978) suggest that it is specifically the root tissue that may contain lower C concentration.

Since seagrasses are consumed primarily through the detrital food chain, there has been considerable interest in decomposition of the plant material. Nitrogen and carbon percentages and atomic C:N ratios in dead Zostera marina leaf material are presented in Table 6. The means are all lower than those from fresh leaf material. Harrison and Mann (1975) reported nitrogen percentages from 1 to 1.5 in contrast to our values of 1 to 2 and carbon percentages from 26 to 32 in contrast to our values of 20 to 40 for dead leaves of Zostera marina. Although no seasonal cycle is apparent for either C or N percentages, the atomic C:N ratios show a minimum of 15 in March and a maximum of 27 in September (Harrison and Mann (1975), in contrast to our data suggesting maxima in September and February of 31 and 41 respectively and a minimum of 20 in October. The comparison of C and N pecentages of live vs dead leaves of Zostera marina is in agreement with the general idea that soluble C leaches from or is translocated from living leaves before leaf death to a greater extent than soluble N. However, consideration of changes in epibiota during senescense and death of leaves may alter this interpretation.

A consideration of N and C values from Zostera marina in comparison to Ruppia maritima from the monospecific stands as well as the mixed bed may increase our understanding of species response to environmental conditions as well as factors which influence their distribution with depth. Unfortunately, we have decided that there are technical reasons which cast doubt on the validity of the mixed bed data and thus it is not reported here. Our present small data base from Ruppia maritima is given in Table 7. Carbon content of Zostera marina and Ruppia maritima are essentially the same, especially in the

TABLE 4. PERCENTAGE CARBON AND NITROGEN OF THE TOTAL ROOT AND RHIZOME MATERIAL OF ZOSTERA MARINA AND THE ATOMIC RATIO OF CARBON: NITROGEN FROM THE PURE STAND PLANT MATERIAL. NUMBERS ARE THE MEAN, NUMBER OF OBSERVATIONS AND THE STANDARD DEVIATION.

DATE	ORGANIC CARBON PERCENTAGE	ORGANIC NITROGEN PERCENTAGE	CARBON NITROGEN ATOMIC RATIO
FEB 80	33.6 (2) 0.67	1.59 (2) 0.075	24.6 (2) 0.66
MAR 80	29.1 (1)	2.01 (1)	16.9 (1)
JUN 80	30.1 (4) 2.43	1.08 (4) 0.217	33.7 (4) 9.20
AUG 79	27.5 (5) 7.11	1.27 (5) 0.456	26.1 (5) 3.35
AUG 80	31.3 (8) 3.46	1.31 (8) 0.194	28.8 (8) 5.7
SEP 79	28.5 (3) 3.38	1.35 (3) 0.0411	24.6 (3) 3.32
OCT 79	34.8 (3) 0.435	1.18 (3) 0.0705	34.5 (3) 1.69
MEAN	30.6	1.26	28.4

TABLE 5. PERCENTAGE CARBON AND NITROGEN OF THE TOTAL LEAF MATERIAL OF ZOSTERA MARINA AND THE ATOMIC RATIO OF CARBON:NITROGEN FROM THE PURE STAND PLANT MATERIALS. NUMBERS ARE THE MEAN, NUMBER OF OBSERVATIONS AND THE STANDARD DEVIATION.

DATE	ORGANIC CARBON PERCENTAGE	ORGANIC NITROGEN PERCENTAGE	CARBON NITROGEN ATOMIC RATIO
FEB 80	35.9 (1)	3.03 (1)	13.8 (1)
JUN 80	34.1 (6) 4.22	1.54 (6) 0.417	27.0 (6) 5.09
AUG 79	37.2 (10) 1.74	2.18(10) 0.336	20.3(10) 2.49
AUG 80	37.5 (5) 0.67	1.42 (5) 0.135	31.2 (5) 3.38
SEP 79	34.5 (3) 0.242	1.50 (3) 0.129	26.9 (3) 2.38
OCT 79	38.6 (2) 3.41	2.01 (2) 0.0449	22.4 (2) 2.48
MEAN	36.4	1.81	24.9

TABLE 6. PERCENTAGE CARBON AND NITROGEN OF THE TOTAL DETRITAL LEAF MATERIAL OF ZOSTERA MARINA AND THE ATOMIC RATIO OF CARBON: NITROGEN FROM THE PURE STAND PLANT MATERIAL. NUMBERS ARE THE MEAN, NUMBER OF OBSERVATIONS AND THE STANDARD DEVIATION.

DATE	ORGANIC CARBON PERCENTAGE	ORGANIC NITROGEN PERCENTAGE	CARBON NITROGEN ATOMIC RATIO
FEB 80	36.4 (3) 1.43	1.07 (3) 0.231	40.9 (3) 9.54
JUN 80	28.3 (4) 4.06	1.39 (4) 0.233	23.8 (4) 2.08
AUG 80	28.4 (5) 3.9	1.31 (5) 0.186	25.9 (5) 5 9
SEP 80	30.8 (6) 1.57	1.20 (6) 0.207	30.7 (6) 5.7
OCT 79	35.2 (3) 1.95	2.06 (3) 0.079	20.0 (3) 1.85
MEAN	27.3	1.20	22.5

TABLE 7. PERCENTAGE CARBON AND NITROGEN OF THE TOTAL MATERIAL OF *RUPPIA MARITIMA* AND THE ATOMIC RATIO OF CARBON:NITROGEN. NUMBERS ARE THE MEAN, NUMBER OF OBSERVATIONS AND THE STANDARD DEVIATION.

DATE	ORGANIC CARBON PERCENTAGE	ORGANIC NITROGEN PERCENTAGE	CARBON NITROGEN ATOMIC RATIO
LEAF MATERIAL FROM RUPPIA SITE			
	36.5 (4) 3.53	2.48 (4) 0.118	17.2 (4) 0.876
LEAF DETRITUS			
	28.8 (1)	1.91 (1)	17.6 (1)
ROOTS/RHIZOMES FROM RUPPIA SITE			
	22.0 (2) 5.23	0.85 (2) 0.078	30.1 (2) 4.6
ROOTS/RHIZOMES FROM MIXED SITE			
	34.3 (2) 3.04	1.37 (2) 0.177	29.7 (2) 6.5

leaves. Ruppia maritima leaves appear to be richer in nitroge' than leaves of Zostera marina. Until we expand the data base, no interpretations of these data are possible.

Chemical Characteristics of Vegetated and Non-vegetated Sediments

For our studies, chemical characteristics of vegetated and non-vegetated sediment were investigated by determination of organic matter and adenosine triphosphate (ATP) concentration of sectioned 30 cm cores taken from the five study sites (habitats) at Vaucluse Shores. Orth and van Montfrans (1982) report other sediment properties.

Organic Matter Content

Overall, the organic matter content of the sediment was low at all sites; most values were less than 1% of the sediment dry weight and reflect the sandy nature of the substrate. The organic content of sectioned cores at four sites during July, 1979 is presented in Figure 13. Several factors contribute to the organic matter pool in the sediments: living and dead plant and animal tissue, microbial autotrophs and heterotrophs, dissolved organic matter, etc. The influence of the plant community is seen in the total amount and depth distribution of organic matter content at the four sites. The organic content is lowest in the non-vegetated sand patch; in addition, the depth distribution of organic content is relatively uniform in the sand patch. In contrast, the sediment organic matter content was generally higher at the three vegetated sites. Here, organic matter was concentrated in the upper 10 cm of the sediment corresponding to the zone of 98% of the root-rhizome biomass (Table 1). The organic matter content in the upper 10 cm at the R. maritima site was lower than at the mixed and Z. marina sites. At these latter two sites, root-rhizome biomass in July was 3-4 times greaer than at the R. maritima site.

ATP Content

The results of the sediment ATP analyses did not clearly reflect the influence of the seagrass rhizosphere. ATP concentrations are generally used as an estimator of microbial biomass, although the ATP from any viable cell is to some extent included in the values. Higher percentages of total ATP in the upper 5 cm of the 30 cm cores were generally observed in the vegetated sites compared to the non-vegetated sand patch (Table 8) although spatial and temporal variability masked any statistically significant differences. The vegetated sites presumably contain greater concentrations of metabolizable substrates (such as dead plant organic matter and dissolved organic matter secreted by the roots) than the non-vegetated sites to support microbial growth.

The seasonal distribution of ATP concentration with depth during 1979 is presented in Figure 14. The ATP concentration at all sites was higher in the upper portion of the sediment; this trend was generally more pronounced at the three vegetated sites. The ATP concentration tended to be greater during the summer, which corresponds to the period of highest community respiration (see Chapter 2, this report). In addition, root-rhizome biomass tended to be high

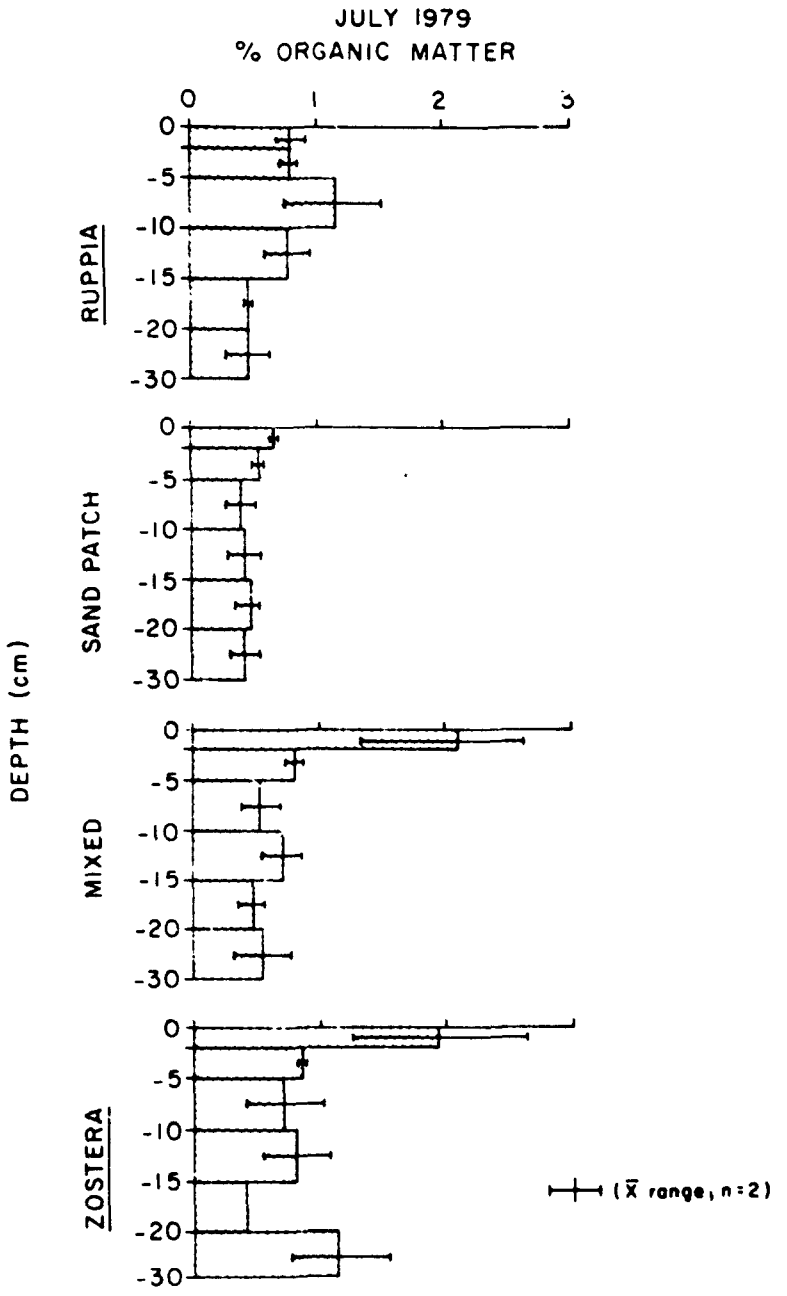


Figure 13. Vertical distribution of sediment organic matter (% of Dry Weight) during July, 1979 at the principal sampling sites within the Vaucluse Shores area. The mean and range of values (n=2) are given in the figure.

TABLE 8. PERCENT TOTAL ATP IN 0-5 CM AND 0-10 CM VERTICAL CORE SECTIONS FROM THE PRINCIPAL SAMPLING SITES WITHIN THE VAUCLUSE SHORES AREA.

Habitat	Depth (cm)	Feb	Mar	April	June	July	Aug	Sept	Oct	$\bar{x}$
Ruppia	0-5	72	44	45	44	63	36	45	23	46
	0-10	81	59	90	61	73	53	62	34	64
Mixed	0-5	69	64	51	58	49	41	37	37	51
	0-10	79	75	66	73	65	57	53	53	65
Zostera	0-5	80	59	59	60	40	-	85	36	60
	0-10	88	72	81	74	53	-	91	52	73
Sand Patch	0-5	49	-	43	65	48	-	-	34	48
	0-10	64	-	59	90	62	-	-	50	65

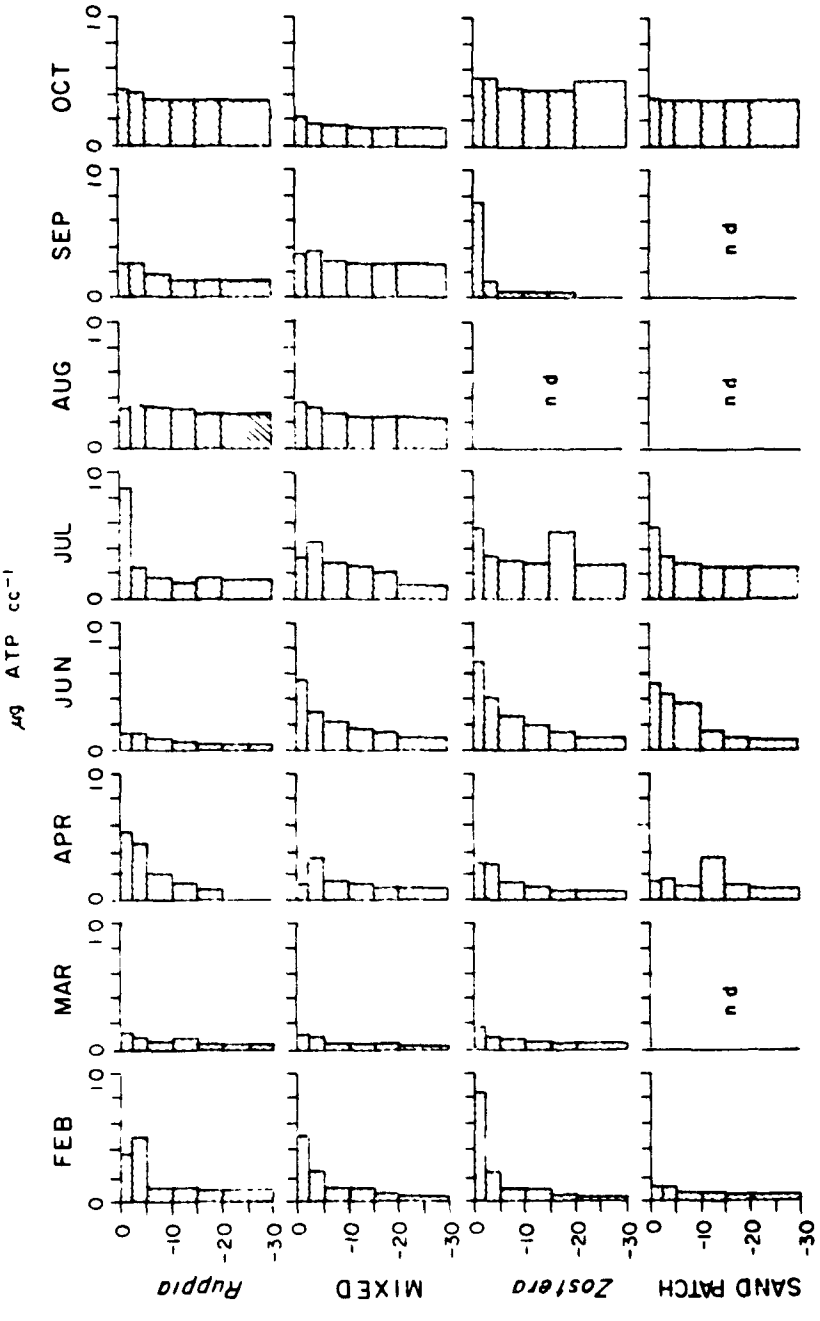


Figure 14. The depth distribution, -cm relative to the sediment surface, of ATP concentration in sediments of the principal sampling sites at Vaucluse Shores, 1979-1980.

in the summer. The seasonal behavior of ATP concentration is shown for the 0-2 cm portion of the sediment in Figure 15.

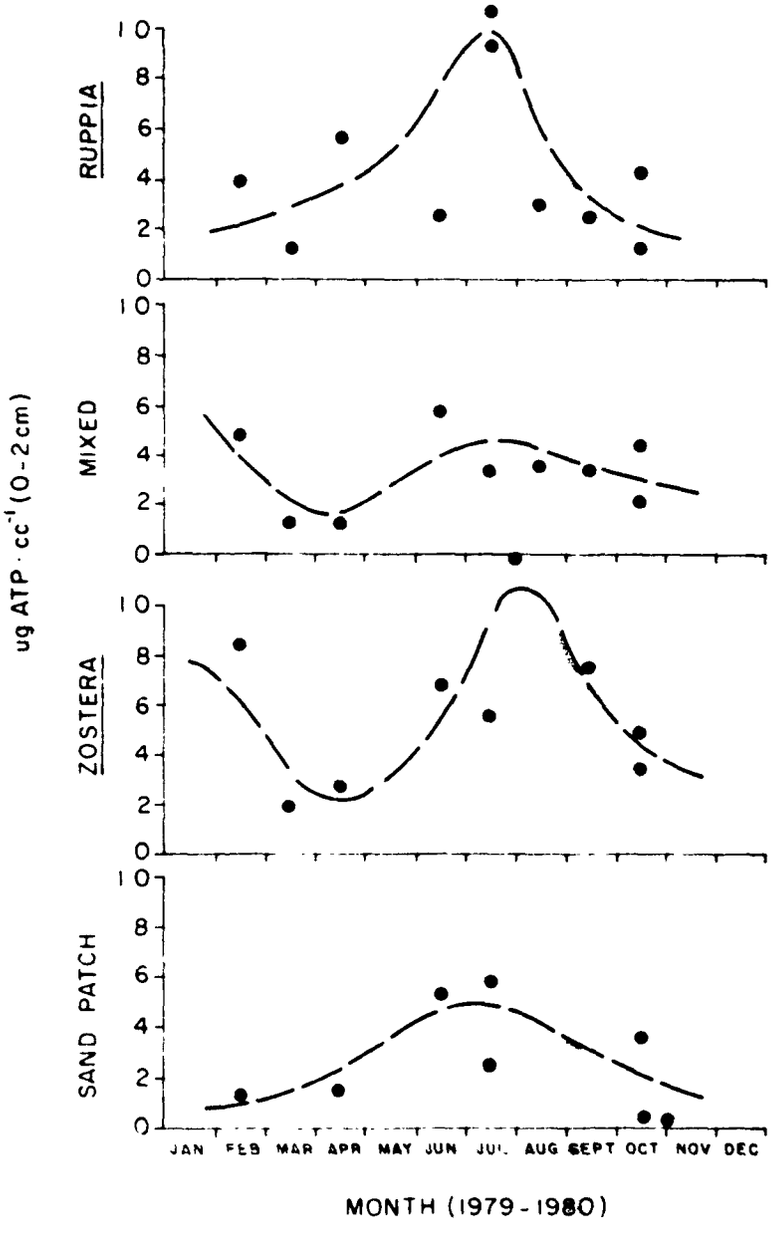


Figure 15. Mean (n=3) sediment ATP concentration in the upper 2 centimeters at the principal sampling sites at Vaucluse Shores, 1979-1980.

LITERATURE CITED

Almazan, G. and C. E. Boyd. 1978. Effects of nitrogen levels on rates of oxygen consumption during decay of aquatic plants. Aquatic Bot. 5:119-126.

Atkinson, M. and S. V. Smith. 1981. Carbon:nutrient ratios of benthic marine plants. Manuscript submitted to Nature.

Aioi, K. 1980. Seasonal change in the standing crop of eelgrass (Zostera marina L.) in Odawa Bay, Central Japan. Aquatic Bot. 8:343-354.

Aioi, K, and H. Mukai. 1980. On the distribution of organic contents in a plant of eelgrass (Zostera marina L.). Jap. J. Ecol. 30:189-192.

Backman, R. W. and D. C. Barilotti. 1976. Irradiance reduction: effects on crops of the eelgrass Zostera marina in a coastal lagoon. Mar. Biol. 34:33-40.

Bancroft, K., E. A. Paul and W. J. Wiebe. 1976. The extraction and measurement of adenosine triphosphate from marine sediments. Limnol. Oceanogr. 21:473-480.

Biebl, R. and C. P. McRoy. 1971. Plasmatic resistance and rate of respiration and photosynthesis of Zostera marina at different salinities and temperatures. Mar. Biol. 8:48-56.

Birch, W. R. 1975. Some chemical and calorific properties of tropical marine angiosperms compared with those of other plants. J. Appl. Ecol. 12:201-212.

Center, R. D. and N. R. Spencer. 1981. The phenology and growth of water hyacinth (Eichhornia crassipes (Mart.) Solms) in a eutrophic North-Central Florida Lake. Aquatic Bot. 10:1-32.

Congdon, R. A. and A. J. McComb. 1979. Productivity of Ruppia: seasonal changes and dependence on light in an Australian estuary. Aquatic Bot. 6:121-132.

Cottam, C. 1935a. Further notes on past periods of eelgrass scarcity. Rhodora 37:269-271.

Cottam, C. 1935b. Wasting disease of Zostera marina. Nature 135:306.

Cottam, C. and D. A. Munro. 1954. Eelgrass status and environmental relations J. Wildl. Mgt. 18:449-460.

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

Dennison, W. 1979. Light adaptation of plants: A model based on the seagrass Zostera marina L. M. S. Thesis, Univ. Alaska, Fairbanks. 69 pp.

Dillon, C. R. 1971. A comparative study of the primary productivity of estuarine phytoplankton and macrobenthic plants. Ph.D. Dissertation, Dept. Botany, Univ. of North Carolina, Chapel Hill. 112 pp. 112 pp.

Drew, E. A. 1978. Factors affecting photosynthesis and its seasonal variation in the seagrasses Cymodocea nodosa (Ucria) Aschers, and Posidonia oceanica (L.) Delile in the Mediterranean. J. exp. mar. biol. Ecol. 31:173-194.

Evans, G. C. 1972. The Quantitiative Analysis of Plant Growth. Univ. California Press, Berkely. 734 pp.

Gallagher, J. L. 1975. Effect of an ammonium nitrate pulse on the growth and elemental compositon of natural stands of Spartina alterniflora and Juncus roemerianus in a Georgia salt marsh. Amer. J. Bot. 62:644-648.

Gerloff, G. C. and Krombholz, P. H. 1966. Tissue analysis as a measure of nutrient availability for the growth of angiosperm aquatic plants. Limnol. Oceangr. 11:529-537.

Gessner, F. 1971. The water economy of the seagrass Thalassia testudinum. Mar. Biol. 10:258-260.

Godshalk, G. L. and R. G. Wetzel. 1978. Decomposition of aquatic angiosperms. III. Zostera marina L. and a conceptual model of decompositon. Aquatic Bot. 5:329-354.

Goldman, J. C., J. J. McCarthy and D. G. Peavey. 1979. Growth rate influence on the chemical composition of phytoplankton in oceanic water. Nature 179:210-215.

Harrison, P. G. and K. H. Mann. 1975. Chemical changes during the seasonal cycle of growth and decay in eelgrass (Zostera marina) on the Atlantic Coast of Canada. J. Fish. Res. Board Can. 32:615-621.

Haller, W. T. and D. L. Sutton. 1975. Community structure and competition between Hydrilla and Vallisneria. Hyacinth Contr. J. 13:48-50.

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.

Jacobs, R. P. W. M. 1979. Distribution and aspects of the production and biomass of eelgrass, Zostera marina L., at Roscoff, France. Aquatic Bot. 7:151-172.

Leopold, A. C. and P. E. Friedemann. 1975. Plant Growth and Development. McGraw-Hill Inc., New York. 545 pp.

Mann, K. H. 1975. Relationship between morphometry and biological functioning in three coastal inlets of Nova Scotia. pp. 634-644. In, L. E. Cronin (ed), Estuarine Research, V. I. Academic Press, N.Y. 738 pp.

Nienhuis, P. H. and B. H. H. De Bree. 1977. Production and ecology of eelgrass (Zostera marina L.) in the Grevelingen estuary: The Netherlands, before and after the closure. Hydrobiologia 52:55-66.

Nixon, S. W. 1980. Between coastal marshes and coastal waters; a review of twenty years of speculation and research on the role of salt marshes in estuarine productivity and water chemistry, pp. 437-525. In, P. Hamilton and K. B. MacDonald (eds.), Estuarine and Wetland Processes, Plenum Publ. Co., N.Y.

Oremland, R. S. and B. F. Taylor. 1977. Diurnal fluctuations of O_2, N_2, and CH_4 in the rhizosphere of Thalassia testudinum. Limnol. Oceanogr. 22:566-570.

Orth, R. J. 1977. Effect of nutrient enrichment on growth of the eelgrass Zostera marina in Chesapeake Bay, Virginia. Mar. Biol. 44:187-194.

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. Environmental Protection Agency Report No. 600/79-029/SAV1, Chesapeake Bay Program, Annapolis Maryland.

Orth, R. J. and K. A. Moore. 1982. The biology and propagation of eelgrass, Zostera marina, in the Chesapeake Bay, Virginia. Final Report, Grant no. R805953, U.S. Environmental Protection Agency. Chesapeake Bay Program, Annapolis, MD. and VIMS SRAMSOE 265, Gloucester Point, VA. 187 pp.

Orth, R. J. and J. van Montfrans. 1982. Structural and functional aspects of the ecology of submerged aquatic macrophyte communities in the lower Chesapeake Bay. *Vol. III. Interactions of resident consumers in a temperate estuarine seagrass community: Vaucluse Shores, Virginia. USA.* Final Report, Grant no. R805874, U.S. Environmental Protection Agency, Chesapeake Bay Program, Annapolis Maryland and VIMS SRAMSOE 267, Gloucester Point, VA. 232 pp.

Patriquin, D. G. 1972. The origin of nitrogen and phosphorus for growth of the marine angiosperm Thalasia testudinum. Mar. Biol. 15:35-46.

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 G. W. Thayer. 1980. Uptake and transfer of carbon and phosphorus by eelgrass (Zostera marina L.) and its epiphytes. J. exp. mar. biol. Ecol. 42:113-123.

Pomeroy, L. R. 1975. Mineral cycling in marine ecosystems. pp. 209-223. In, F. G. Howell, J. B. Gentry and M. H. Smith (eds.), Mineral Cycling in Southeastern Ecosystems, NTIS, CONF-74013, Springfield, Va.

Postgate, J. R. 1971. Relevant aspects of the physiological chemistry of nitrogen fixation, pp. 287-307. In, D. E. Hughes and A. H. Rose (eds.), Microbes and Biology productivity. Symp. Soc. Gen. Microbial., V. 21, Cambridge University Press, London.

Redfield, A. C. 1958. The biological control of chemical factors in the environment. Amer. Sci. 46:1-221.

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

Rovira, A. D. and C. B. Davey. 1974. Biology of the rhizosphere, pp. 153-204. In, E. W. Carson (ed.), The Plant Root and Its Environment. Univ. Virginia Press, Charlottesville.

Ryther, J. H. and W. M. Dunstan. 1971. Nitrogen, phosphorus and eutrophication in the coastal marine environment. Science 171:1008-1012.

Seki, H. and Y. Yokohama. 1978. Experimental decay of eelgrass (Zostera marina) into detrital particles. Arch. Hydrobiol. 84:109-119.

Thayer, G. W. 1971. Phytoplankton production and the distribution of nutrients in a shallow unstratified estuarine system near Beaufort, N.C. Chesapeake Sci. 12:240-253.

Thayer, G. W., S. M. Adams, and M. W. LaCroix. 1975. Structural and functional aspects of a recently established Zostera marina community, pp. 518-546. In, L. E. Cronin (ed.) Estuarine Research, v. 1. Academic Press, New York 738 pp.

Titus, J. E. and M. S. Adams. 1979. Coexistence and the comparative light relations of the submerged macrophytes Myriophyllum spicatum and Vallisneria americana Michx. Oecologia (Berl.) 40:273-286.

Valiela, I., J. M. Teal, and W. Sass. 1973. Nutrient retention in salt marsh plots experimentally fertilized with sewage sludge. Est. Coastal Shelf Sci. 1:261-269.

Vinogradov, A. P. 1953. The Elementary Chemical Composition of Marine Organisms. Translated from Russian by Efron, J. and J. K. Setlow, with bibliography edited and enlarged by V. W. Odum. Sears Foundation for Marine Research, New Haven, Conn. 647 pp.

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

Williams, R. B. 1973. Nutrient levels and phytoplankton productivity in the estuary, pp. 59-89. In, R. H. Chabreck (ed.), Proceedings, 2nd, symposium, Coastal Marsh and Estuary Management, July 17-18, 1972. Louisiana State Univ., Baton Rouge.

Wood, D. C. and S. S. Hayasaka. 1981. Chemotaxis of rhizoplane bacteria to amino acids comprising eelgrass (Zostera marina L.) root exudate. J. exp. mar. biol. Ecol. 50:153-161.

Chapter 2

PHOTOSYNTHESIS, LIGHT RESPONSE AND METABOLISM OF SUBMERGED MACROPHYTE COMMUNITIES IN THE LOWER CHESAPEAKE BAY, VIRGINIA

R. L. Wetzel and P. A. Penhale

Virginia Institute of Marine Science
and School of Marine Science
College of William and Mary
Gloucester Point, Virginia
23062

INTRODUCTION

The productivity and metabolism of submerged macrophyte communities is comparatively high in relation to other habitats within estuarine, shoal-benthic environments along the U. S. Atlantic east coast. In a significant portion of these shallow water areas, primary production by the submerged vascular plants Zostera marina (eelgrass) and Ruppia maritima (widgeon grass) dominates organic matter input to the habitat and provides a substrate or surface area for additional autotrophic production by an attached, microalgae dominated epiphytic community. These characteristics render the habitats metabolically active and trophically important. Because of specific diversification in autotrophic production in these communities, i.e., vascular plants, epiphytic autotrophs, benthic micro- and macroalgae, and phytoplankton, trophic structure is highly diverse and secondary production is significantly greater than in adjacent, non-vegetated habitats (Orth, et al. 1982).

Historically, studies of submerged macrophyte production in temperate and tropical seagrass communities have focused on two species; temperate eelgrass, Z. marina, and tropical turtlegrass, Thalassia testudinum. Estimates of annual biomass production reported for eelgrass range from 200 to 800 gC m^{-2} (Nixon and Oviatt 1972; McRoy 1974; Wetzel et al. 1979; Nienhuis 1980; Lindeboon et al. 1982a; 1982b). For turtlegrass, the estimates range from 200 to 3000 gC m^{-2} (Jones 1968; Bittaker 1975; McRoy and McMillan 1977). These values for seagrasses fall in the upper range reported for the more intensely studied estuarine and coastal marsh communities (Keefe 1972). Also, many of these annual values for seagrasses may prove underestimates due to the techniques employed (Zieman and Wetzel 1980). Regardless, the estimates certainly imply a correspondingly high nutrient demand met by either tightly coupled remineralization processes or new nutrient sources.

Physical, chemical and biological factors which regulate seagrass photosynthesis and organic matter production have been ascribed to temperature, salinity, hydrodynamic properties, grazing, nutrients and light. Complicating the analysis of these factors in temperature zones, estuarine seagrass communities, such as those in Chesapeake Bay, undergo wide fluctuations in all these environmental variables which have diel, seasonal and annual periodicities.

Temperature obviously has direct effects on all enzymatically mediated processes as well as on physical-chemical properties of the water environment. Together, salinity and temperature govern the geographical range and distribution of seagrasses but within the range of tolerance of a particular species in estuarine systems, these parameters are probably of secondary importance (e.g. McRoy and McMillan 1977) except to establish or interact with other factors to control the rates of specific chemical and biochemical transformations.

Hydrodynamic properties and specifically water circulation may limit plant growth for some aquatic macrophytes. In tidally dominated, estuarine systems which appear characteristically well-mixed in shallow water areas, mixing is probably sufficient to prevent establishment of strong gradients inhibiting gas diffusion and exchange (e.g. Conover 1967; Westlake 1967; 1978). However, Fonseca, et al. (1982) have suggested that current velocity within seagrass meadows may have significant influence on plant self-shading and thus plant community photosynthesis.

Direct grazing by waterfowl and larger invertebrates has been demonstrated important for some Z. marina communities (Neinhuis and van Ierland, 1978). It is considered by many, however, to be of minor overall significance and is generally regarded as episodic in character. However, any general conclusions regarding waterfowl-plant trophic interactions, especially in temperate zones, of the U. S. Atlantic east coast is highly tenuous due both to a lack of detailed review and long term study (E. W. Wilkins, personal communication, 1982).

The environmental variables considered as primary physical and chemical controls on seagrass photosynthesis and production are light and nutrients. Nutrient availability, particularily nitrogen, is generally considered, or at least has become a popular opinion, a primary control. Historic evidence supporting this view has been the general observation that estuarine and coastal waters are generally low in nutrient concentration. Needless to say, this observation may have little direct bearing on seagrass limitation from a kinetic standpoint. Kinetic relationships for seagrass nutrient utilization have only within the past decade been investigated (McRoy and Alexander 1975; Penhale and Thayer 1980; Iizumi and Hattori 1982). The relative importance of new sources (e.g. nitrogen fixation) versus recycled forms and root-rhizome versus leaf uptake are currently areas of active research (e.g. Patriquin and Knowles 1972; Goering and Parker 1972; McRoy et al. 1973; Capone et al. 1979) but there appears no consensus of opinion. For estuarine systems, particularily temperate estuaries, Nixon (1981) has presented some rather convincing agruments that nutrient remineralization in sediments dominates estuarine nutrient cycles. There are no specific arguments that would indicate seagrass communities operate any differently. For seagrass communities in the lower Chesapeake Bay, Orth (1977) has demonstrated a rapid and positive growth response by Z. marina to in situ sediment surface application of commercial fertilizer suggesting nutrient limitation. In Rhode Island, Harlin and Thorne-Miller (1981) experimenting with water column enrichments of ammonium, nitrate and phosphate demonstrated a variable response by Z. marina and R. maritima dependant on nutrient supplied, potential competitive species and current velocity.

In contrast to nutrient kinetics light-photosynthesis interactions have been extensively studied in relation to seagrass metabolism and light alone is considered the principal limiting factor in many environments (Zieman and Wetzel 1980). Seagrasses characteristically have depth-dependent distribution patterns that are explained as a species-specific response to ambient, submarine light regimes (Buesa 1975; Aioi 1980; Nienhuis and DeBree 1980; Orth et al. 1982). Williams (1977), Penhale (1977), Drew (1979), Beer and Waisel (1979) and Capone et al. (1979) have reported on the physiological response of

seagrass photosynthesis to varying light intensity. Saturating light intensities, as photosynthetically active radiation (PAR), for many seagrasses fall in the range 400-600 E m^{-2} sec^{-1}. For some coastal systems, particularily in subtropical and tropical areas, these PAR intensities are characteristic and light is considered not limiting except at extreme depth. However, in more turbid estuarine conditions, light environments of these intensities probably are not typical and submarine light regimes appear fundamentally important for growth and survival of seagrasses (Backman and Bertilotti 1976; Congdon and McComb 1979). Within limits, seagrasses can adapt both morphologically (e.g. leaf elongation and altered canopy structure) and biochemically (pigment composition) to suboptimal light regimes (Spence 1975; Bowes et al. 1977; Wiginton and McMillan 1979). However, the range of adaptation for a particular species is limited (Dennison 1979).

In terms of organic matter cycling and the trophic structure of seagrass communities, the vascular plants are generally presumed to be indirectly utilized, i.e., direct grazing or secondary, macroheterotrophic utilization of the living plant tissue is considered minor. Mortality of the plants forms the base of a detrital trophic structure (Mann 1973; Fenchel 1977; Klug 1980). Microbial decomposition of macrophyte tissue and microheterotrophic production associated with the sediments probably accounts for the principal organic matter source that goes to support secondary production indirectly from plants per se (Fenchel 1977; Klug 1980; Newell 1981).

Heterotrophic utilization of epiphytic, benthic and planktonic algae production on the other hand is probably mediated by direct grazing. In contrast to other estuarine and marine communities where either detrital or grazer pathways dominate, seagrass communities, both temperate and tropical, appear to be characterized by both. Recent studies suggest that both detrital and grazing pathways are potentially of equal importance in supporting heterotrophic metabolism and secondary production (Chapter 3, this report). Therefore, secondary production in seagrass communities results from the flux of organic matter, energy, and nutrients via two distinct, though interdependent pathways: 1) a detrital based trophic structure controlled by vascular plant production and microbial degradation, and 2) a grazing trophic structure controlled by epiphytic, benthic micro- and macroalgae, phytoplankton and, to some extent, vascular plant primary production. The degree of interdependence of the two structures remains poorly understood.

The studies reported herein focused on what we a priori assumped the principal factors controlling macrophyte production in the lower Chesapeake Bay and were directed at: 1) studies of photosynthesis by the two dominate vascular plant species in lower Chesapeake Bay seagrass communities, Z. marina and R. maritima, 2) measures of total community metabolism and, 3) evaluation of the importance of short term light (PAR) alterations and seagrass response at both specific and community levels. Total community metabolism studies were employed to estimate production and consumption by the intact community under various natural and altered light regimes as well as provide integrated rate estimates. These data were also used for more detailed studies partitioning production and consumption (see Chapter 3, this report). To the extent possible, the studies were carried out contemporaneously. All sampling and field studies were conducted in the seagrass bed at Vaucluse Shores.

Elsewhere, we have provided a detailed description of the study site (see Preface, Figure 1 and Chapter 1, this report).

MATERIALS AND METHODS

Vascular Plant Photosynthesis

Photosynthesis was estimated using ^{14}C radiotracer techniques for Z. marina and R. maritima collected from the mixed bed site following the procedures of Penhale (1977). Excised leaves of each species were collected and incubated in separate 900 ml glass jars containing seawater collected at the site. The jars were covered with neutral density screens which allowed for light penetration of 2, 4, 10, 27 and 53% of ambient light. Experiments were carried out at various times throughout the year in order to cover the range of in situ temperatures. Samples were innoculated with 10-20 μCi ^{14}C- $NaHCO_3$ and incubated under natural light from 1000 to 1400 hours in a running seawater system. Temperature was maintained about 1°C above ambient using this system. After incubation, sample processing included quick freezing in dry ice, lyophilization and combustion in a Packard Model 306 sample oxidizer. ^{14}C collected from sample combustion was assayed by liquid scintillation using a Beckman Model LS 8000 counter. All radioactivity measurements were corrected for background, recovery after combustion, and counting efficiency. Specific rates of ^{14}C-photosynthesis were calculated following the method of Penhale (1977).

Total Community Metabolism

Total community metabolism (net apparent oxygen production or consumption) within the three vegetated zones was determined using dome enclosures (acrylic hemispheres). The dome enclosures were 1 m diameter, 0.5 m in height that enclosed a water volume of 260 liters and covered a bottom area of 0.78 m^2. Vegetated areas within Z. marina, mixed, or R. maritima dominated communities were randomly selected in and around permanent station markers located between transects B and C (see Preface, Figure 1). Care was taken not to locate a specific study in an area previously used. On several occasions, dome studies were carried out in nonvegetated, sand patch areas within the seagrass bed and outside the grass bed proper on the sandbar. For all community metabolism studies, the domes were placed by diver and secured to the substrate by forcing a 10 cm vertical flange attached to the dome circumference into the sediment. The domes were equipped with ports for sampling by syringe and with standard hose fittings for attachment to an above-water pumping (recirculating) system. The pumping system was made by modifying 12 VDC bilge pumps to accept on both intake and discharge sides standard garden hose fittings for connection to the domes. The pump manifold on the discharge side of each channel was constructed of standard PVC fittings in such a manner to accept O_2 electrodes (Orbisphere Model 2705, Orbisphere Laboratories, New Jersey) and provide for both sampling of dome water and introduction of selected solutions into the recirculated water for manipulation of various parameters. A four-channel pumping system constructed in this manner could be run continuously for approximately 36 hours using three, deep-cycle, 12 VDC marine batteries connected in parallel. The rated output of the pumps was 750 gph and we determined using Rhodamine WT dye in a

simulated experiment that turnover in the domes was approximately 7 minutes. Complete replacement of enclosed water (i.e. pump-out) could be accomplished in 20 minutes. Figure 1 illustrates the dome enclosure experimental design.

In general, an experiment consisted of randomly placing four domes by diver in the selected habitat, connecting each dome to a pumping channel, and pumping out the domes for one hour following placement to insure ambient conditions of the enclosed water. We incorporated this procedure because in preliminary studies using these large domes, elevated NH_4^+ concentrations were noted which we ascribed to the effect of dome placement (sediment disturbance). Following the pump-out period, the discharge side of the pumping channel was connected to the corresponding dome and the incubation period begun.

Dissolved oxygen using Clark-type, sulfide-insensitive, polarographic electrodes (Orbisphere Laboratories, Inc.) attached to the pump manifold, temperature and dissolved oxygen in ambient water, and photosynthetically active radiation (PAR) using a LI-COR 185A Quantum Radiometer equipped with both surface and underwater PAR quantum sensors was continuously monitored in each of the four domes and ambient water. The data were continuously recorded by processing the instrument signals with a 10 channel, multiplexer (Dataplex 10, Hampshere Controls, Inc.) onto a two channel, portable strip chart recorder (Soltec, Inc.). Periodic written records were also kept during the course of an experiment as a check on recorder output and calibration. The dissolved oxygen electrodes were calibrated at the beginning of each experiment using water-saturated, air nomographs and again checked at the end of the experiment. Periodically, the probes were calibrated against the standard Winkler titrametric technique (Strickland and Parsons 1972) to insure the accuracy of the air-water calibration procedure. Factory calibrated temperature and PAR sensors were used throughout the study.

Prior to adoption of this technique using the domes, two other designs were employed and when used are noted in the results. The first design employed was placement of the domes as before but without water circulation. Sampling for dissolved oxygen was done by removing replicate, 10 ml syringe samples from each dome over various incubation intervals. Dissolved oxygen was determined using standard Winkler reagents (Strickland and Parsons 1972) and micropipet and microburet equipment (see Fraleigh 1971). The second design employed a recirculating system that was integral with the dome (i.e. all equipment was submerged) and dissolved oxygen determined by polarographic means with the electrodes fixed to the domes and all other sampling accomplished by syringe sampling through the dome ports.

The first design was abandoned because of the accumulating evidence which indicates the importance of water motion in attempting measures of exchange, whether the measures are oxygen or some other dissolved constituent (e.g. Wheeler 1980). The second design was abandoned because of inherent difficulties in sampling the enclosed water mass and recurring problems of electrical failure with the pumping system. Although we were satisfied that the pumping system maintained adequate circulation and water motion within the domes, periodic electrical failures required termination of the experiment and resulted in the loss of both data and time. Since adopting the first

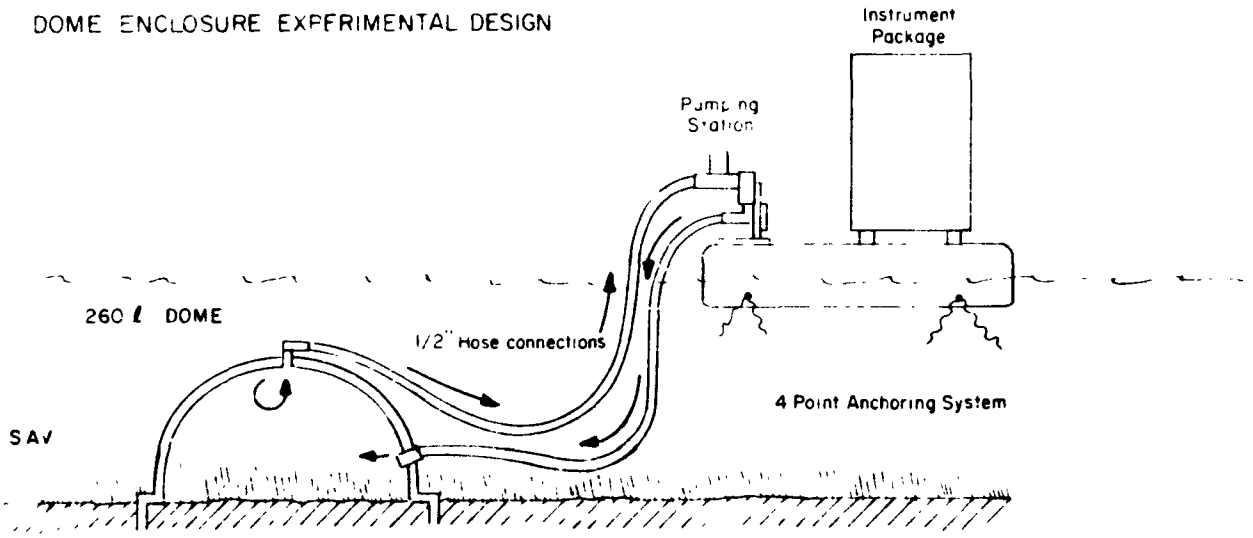


Figure 1. Schematic diagram of the dome enclosure experimental design using the surface-stationed recirculating pumps.

described technique, we have lost no experiment due to failure of the physical design and both sampling frequency and ease were significantly improved.

At certain times of the year and for specific areas, we have employed domes of different overall dimensions to accommodate studies when either plant density and/or biomass was reduced (e.g., Z. marina mid-winter) or the water depth prevented placement of the 1 m diameter domes (e.g., shallow, in shore R. maritima areas). For these specific times and/or locations, we used acrylic hemispheres of the same design and construction, except they are 0.5 m diameter, 0.25 m in height and cover a bottom area of 0.19 m^2 enclosing 32 liters of water. For studies using these smaller domes, water circulation was provided by stirrers integral to the Orbisphere oxygen probe body. Simulated experiments using Rhodamine WT as a tracer indicated that complete mixing was accomplished by the probe stirrers in a matter of a few minutes and sampling at various "depths" within the hemisphere through the syringe ports indicated no stratification of the enclosed water. The only experimental design change necessitated by using the smaller domes was that we did not have the capability of "pumping out" following placement. To reduce the potential effects of this, we placed the small domes as gently as possible when initiating a study and allowed the domes to "equilibrate" with ambient water by leaving all ports open for 30 to 60 minutes before starting the incubation. Aside from this, the designs using both large and small domes were comparable.

Total community metabolism was estimated as the net hourly rate of oxygen concentration change over various incubation intervals throughout a study and for experiments lasting 24 hours as the net rate for the diel (24 hour) period. For some comparative purposes conversion of the oxygen data to carbon equivalents was made assuming a community RQ = 1.0.

The temporal data sets were partitioned into the following intervals for calculating net apparent O_2 exchange:

Morning:	Sunrise + 1 hr. 1 min.	to 1000 hrs.
Noon:	1001 hr.	to 1400 hrs.
Afternoon:	1401 hr.	to Sunset - 1 hr.
Evening:	Sunset - 59 min.	to Sunset + 3 hr.
Night:	Sunset + 3 hr. 1 min.	to Sunrise + 1 hr.

The intervals were decided for data summary and analysis following preliminary data reduction and inspection of oxygen concentration - time curves. The actual intervals were established by setting the "noon" interval to bound the period of maximum potential solar radiation (i.e. 1000 to 1400 hrs). The "morning" and "afternoon" intervals were set according to local times for sunrise and sunset plus or minus one hour. The "evening" interval was based on initial studies that suggested during this period oxygen consumption was stimulated following the day light period and was often double the night time estimate for total community respiration.

Area specific rates were calculated as:

$$mgO_2\ m^{-2}\ hr^{-1} = \frac{[C_{i+1} - C_i]}{\Delta t\,[t_{i+1} - t_i]} \cdot V_d \cdot A_d^{-1} \qquad (1)$$

where: C_i = O_2 concentration in mg l^{-1}, i = 0,1,2...n (hours)

t = time in hours
V_d = volume of domes in liters
A_d = area of domes in m^2

Total community metabolism experiments were carried out from July 1978 through November 1980.

Light-Net Apparent Community O_2 Productivity Interactions

The effects of short term light reduction was evaluated at the community level using the dome enclosures with fitted, neutral-density screens. All studies followed the same experimental design and data reduction techniques as employed for the total community metabolism studies. Neutral density screening tailored to fit the dome surface was used to establish in situ PAR reductions of 30 to 70% of ambient light reaching the plant canopy top. Percent PAR reduction was determined from in situ measurements at or near solar noon with the domes in place. PAR reaching the plant canopy was calculated for any given level of light reduction from either 1) a continuous solar insolation record kept for the duration of the experiment, water depth and periodic (generally half-hourly) determinations of vertical water column PAR attenuation or 2) a continuous record of underwater PAR at a height above the sediment surface equivalent to the mean plant height. Light as PAR and estimates of net apparent O_2 productivity were analysed in a manner similar to the ^{14}C-photosynthesis data where possible (see Penhale 1977) or by simple linear regression statistics.

Plant biomass within the domes was determined by either harvesting a known area following the methods of van Tine (1981) or coring (0.33 m^2) within the area covered by the dome (Orth et al. 1982). Plant material was rinsed free of sediment using approximately 1 mm mesh nylon bags and stored on ice until processing could be completed in the laboratory. Laboratory processing consisted of hand sorting into aboveground live, aboveground dead, and root/rhizome fractions. Wet weights were determined on the fractions by "blotting" and dry weights determined after drying for 24 to 48 hours at 60°C. Ash free dry weights (organic matter content) were determined on subsamples of the fractions by measuring weight loss on ignition at 500°C for 24 hours.

RESULTS AND DISCUSSION

Environmental Characteristics

Figure 2 presents all water temperature data collected for 1979 through 1980 studies. Water temperatures ranged from a low of 1°C in late January early February to a high of 32.5°C in late July in the shallow R. maritima area. During the mid-summer months water temperatures could differ as much as 5°C between the off-shore Z. marina study site and the shallow, in-shore R. marina area. Maximum differences occurred during mid-day, low tides during July-August.

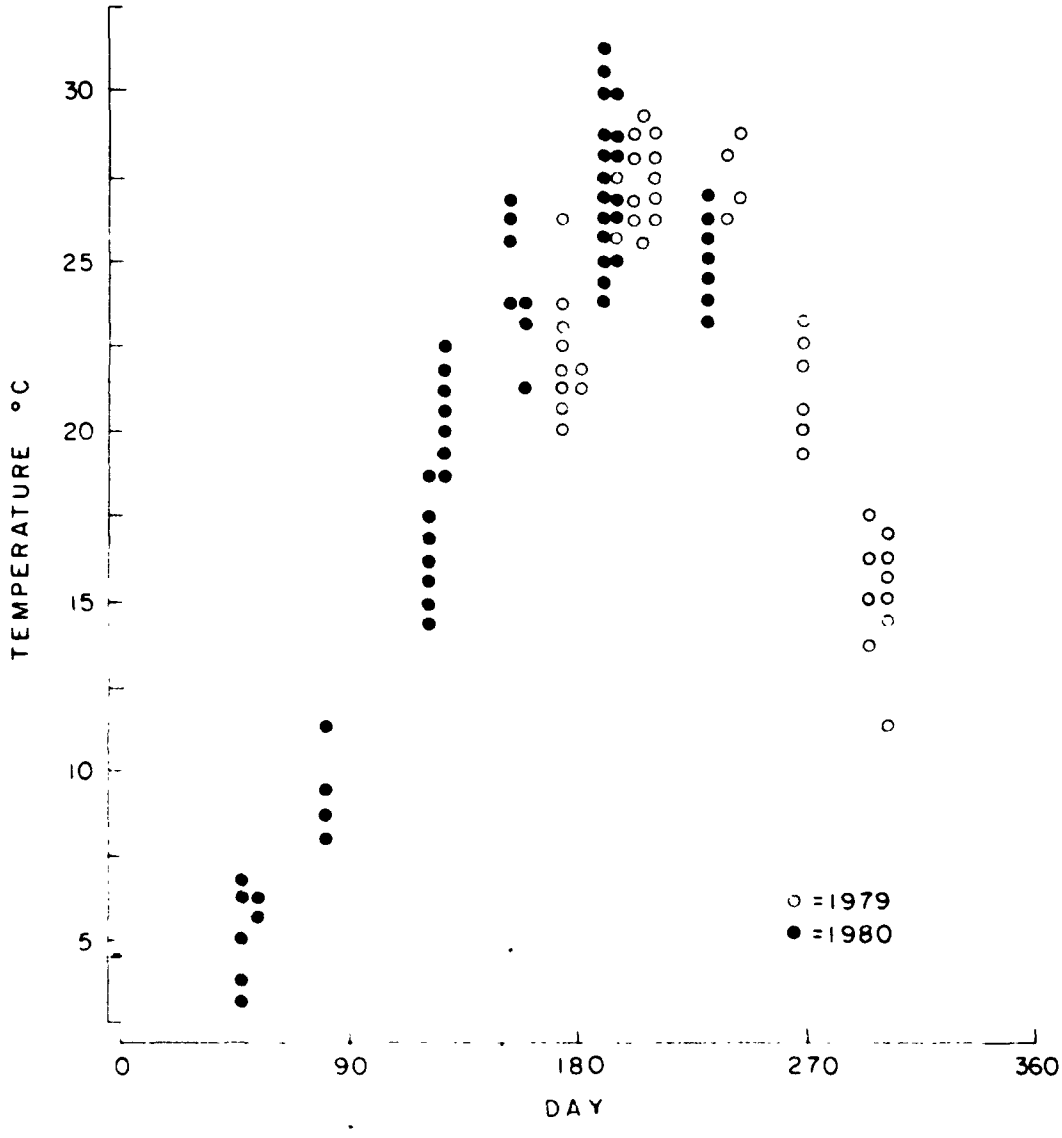


Figure 2. Daily water temperature record (all observations) at Vaucluse Shores for the period July 1979 through October, 1980.

Figure 3 illustrates the range of variation and pattern of isolation as PAR at the site during the study period. The interesting aspect of these data is the extreme range in daily isolation (ca. 10 to 60 $E \cdot m^{-2}$) during the early Z. marina growing season, i.e. spring to early summer. Climatically, this is the time of year the lower Chesapeake Bay area experiences increased rainfall and cloud cover due to the passage of slow-moving frontal systems. The theoretical maximum isolation for this latitude is illustrated by the dashed line in the figure.

Figure 4 presents the mean and standard deviation for vertical light (PAR) attenuation coefficients determined from light profiles taken in the study area. The mean range over both yesrs was -0.665 to -2.98 with extreme values of -0.225 to -8.50. Minima occurred during the winter period and maxima during the spring and early summer months. The highest attenuation coefficients and their greatest variability coincided with that for the isolation pattern (Figure 3) and is due in part to the prevailing climatic conditions during this period. The frontal systems mentioned before are characterized by persistent and at times strong southwesterly winds. Thus the study site, Vaucluse Shores, is the windward shore under these weather conditions and experiences increased wave action, resuspension, and water surface elevation. Conditions within the grassbed can become particularily severe when these weather systems are coincident with spring tides. At these times, the offshore sandbar provides minimum protection for damping wave energy. For all dates and areas within the grassbed, the annual mean attenuation coefficient and standard deviation was -1.435 ($\pm$ 0.511). There were no significant differences among vegetated zones although the Z. marina study area was consistently lower than the R. maritima area (annual means of -1.323 $\pm$ 0.327 and -1.778 $\pm$ 0.704, respectively). However, because mean water depth at the R. maritima site was approximately one-half that at the Z. marina site, PAR reaching the R. maritima plant canopy was signiiicantly greater under all conditions.

^{14}C - Photosynthesis

Figures 5 and 6 present the results of ^{14}C - photosynthesis studies with Z. marina and R. maritima collected from the mixed-bed study site. Photosynthesis-light relationships for both species generally follow the rectangular, hyperbolic function. At low PAR intensities, i.e. $\leq$ 10% of ambient, the relationship is less well defined due to both analytical and sampling variability (i.e. plant tissues in different physiological states). Thus, estimation of the light - photosynthesis parameters , I_k and I_k (see Wetzel, et al. 1982) using first order reaction kinetics was not possible for some data sets. The results indicate that maximum rates of photosynthesis (Pmax) differ between species and are temperature or at least seasonally related. Z. marina tends to have equal or higher maximum rates during the earlier, cooler months of the growing season (Figure 5) and R. maritima generally has higher maximum rates during the warmer summer and early fall periods (Figure 6).

The data were also analyzed using Caperon's model (Caperon et al. 1971) to estimate various photosynthesis-light paramters. Table 1 summarizes the results of these analyses in terms of Pmax, I_k' (equivalent to the

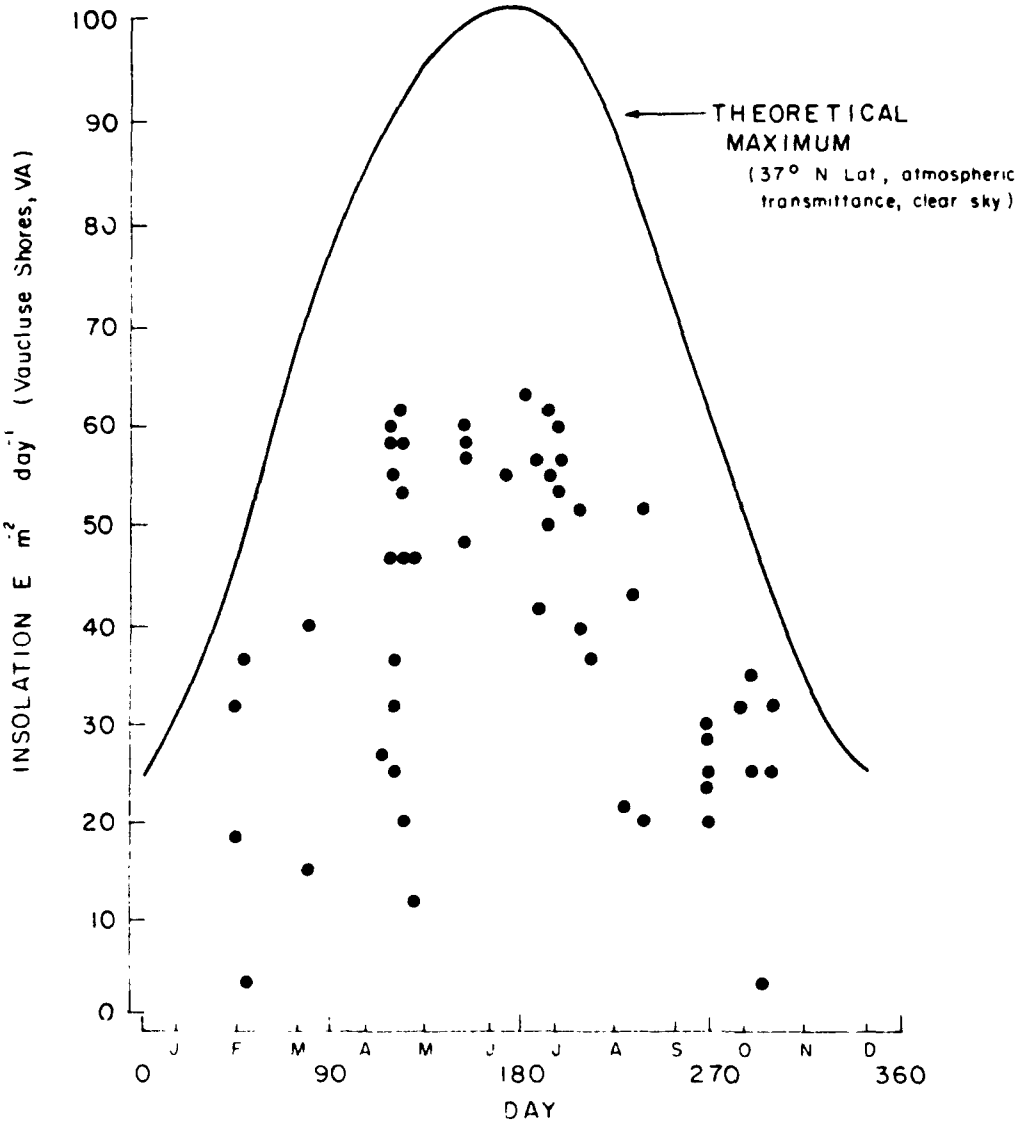


Figure 3. Daily insolation record at Vaucluse Shores for the period July 1979 through October 1980 and theoretical maximum daily insolation (solid line) at latitude 37°N. and assuming a clear sky and atmospheric transmittance of 0.70.

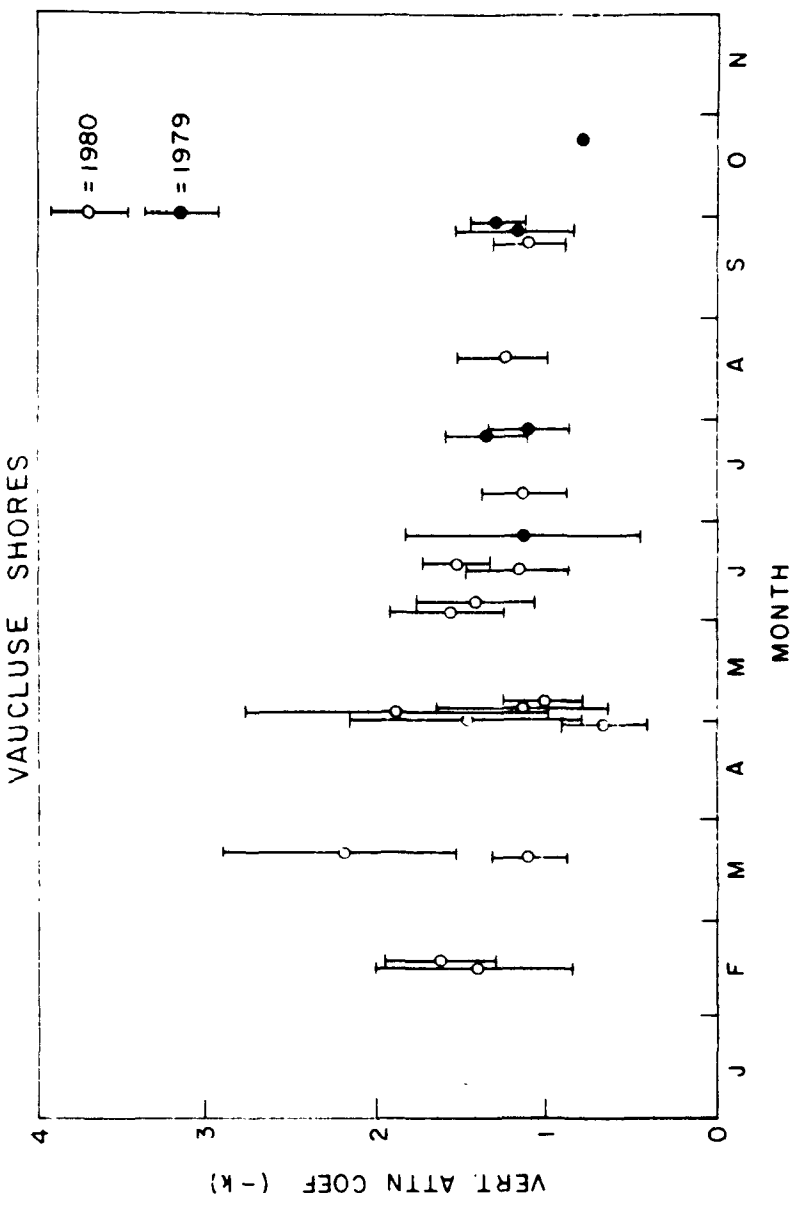


Figure 4. Mean daily vertical light (PAR) attenuation coefficients (m^{-1} ± 1 S.D.) in the Zostera marina dominated community at Vaucluse Shores.

TABLE 1. CALCULATED ^{14}C-PHOTOSYNTHESIS PARAMETERS FOR RUPPIA MARITIMA AND ZOSTERA MARINA EXPERIMENTS.

	Temp	*R. maritima* Pmax[1]	*R. maritima* I_k'[2]	α[3]	*Z. marina* Pmax	*Z. marina* I_k'	PAR[4] $\bar{x}$ (μE m^{-2} sec^{-1})
Jan	1.0	1.15	41.8	0.014	1.60	9.68	0.083	766
March	8.5	3.23	107.	0.015	3.06	18.3	0.083	1533
May	17.5	2.86	88.4	0.016	2.37	72.1	0.016	1557
May	17.5	2.87	127.	0.011	1.68	67.3	0.012	1717
Aug	28.0	4.91	152.	0.016	1.88	31.2	0.030	1827
Aug	28.0	2.81	232.	0.006	1.24	66.3	0.009	894
Sept	22.0	4.17	211.	0.010	3.84	188.	0.010	1440
Oct	10.0	3.83	220.	0.009	1.82	23.1	0.039	983
	$\bar{x}$	3.23	147.	0.012	2.19	59.5	0.035	
	S.D.	1.12	58.8	0.004	.866	57.4	0.031	

1. Pmax = mgC g(plant)$^{-1}$ h^{-1}
2. I_k' = light (μE m^{-2} sec^{-1}) @ .5 pmax
3. α = Initial Slope, $\Delta P/\Delta I$
4. PAR = $\bar{x}$ Photosynthetically Actively Radiation; 1000-1400 hrs.

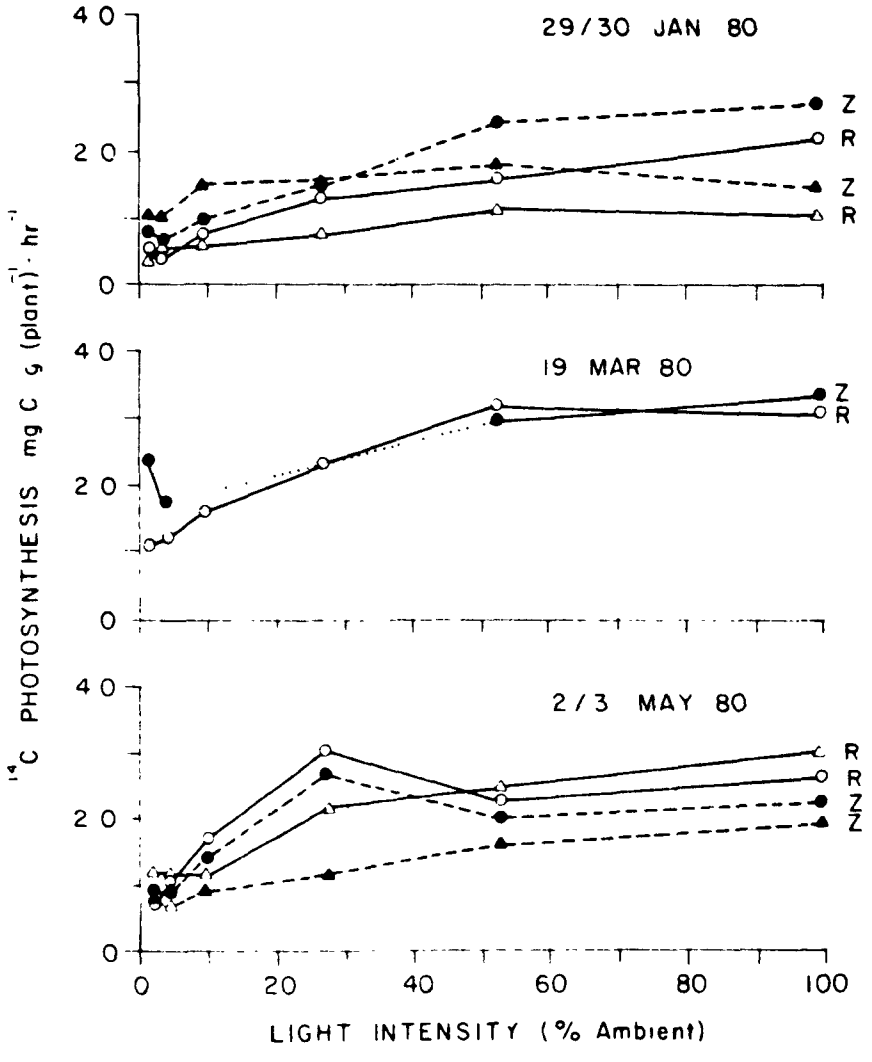


Figure 5. Z. marina (Z) and R. maritima (R) ^{14}C-photosynthesis - Light (PAR) response characteristics for the Winter-Spring period. Clear and darkened symbols are replicate experiments; solid and dashed lines connect day 1 and day 2 studies respectively.

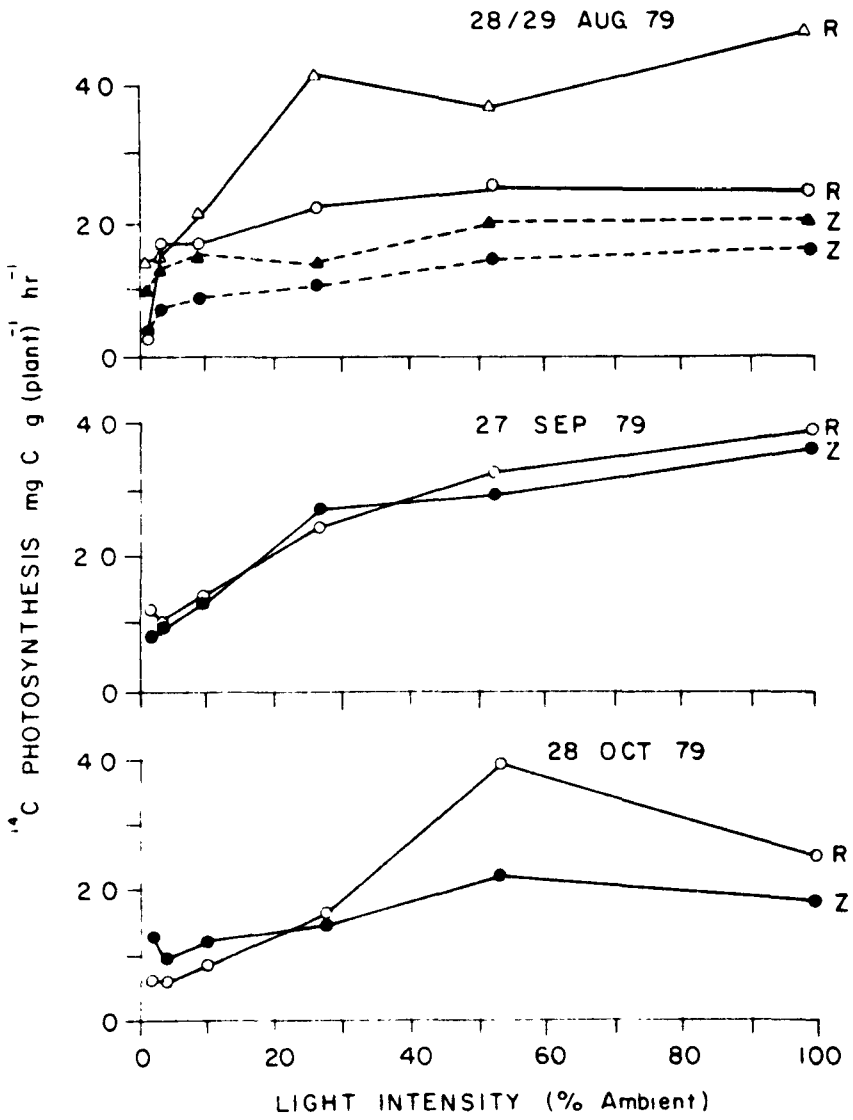


Figure 6. Z. marina (Z) and R. maritima (R) ^{14}C-photosynthesis - Light (PAR) response characteristics for the Summer - Fall period. Clear and darkened symbols are replicate experiments; solid and dashed lines connect day and day 2 studies respectively.

Michaelis-Menten half-saturation constant, K_s or I @ 0.5 Pmax), and α, the initial slope, or $\Delta P/\Delta I$ calculated for P at I_k' and assuming the line passes through the origin.

For Z. marina and R. maritima, both Pmax and I_k' are temperature related and the relationship is different for the two species. Pmax for Z. marina was generally equal to R. maritima during the early growing season at colder temperatures and declined during mid-summer to approximately one-third the maximum estimated rate (1.24 versus 3.84 mgC g(plant)$^{-1}$ hr^{-1}). Based on these data, temperature optimum for Z. marina photosynthesis is less than 28°C and probably is between 22° and 28°C. Arrhenius plots (log P versus reciprocal temperature) indicated poor correlation over all temperatures ($r = -0.25$) as well as for temperatures $\leq$ 22°C ($r = -0.49$) although the correlation obviously improved. A possible explanation for the latter result is that the data for the various temperatures at or below 22°C include two different growing seasons, i.e. Fall and Spring.

Estimated Pmax for R. maritima indicated a strong temperature-dependence with maximum rates occuring at the higher, mid-summer temperatures. Temperature optimum for R. maritima is probably at or near 30°C and obviously quite different than for Z. marina. Arrhenius plots support this conclusion with a significant correlation between log P and reciprocal temperature ($r = -0.89$). For all data, Pmax for R. maritima was approximately 1.5 x that for Z. marina but differed by as much as 4 x at 28°C (August).

Comparison of the photosynthesis - light parameters also suggests physiological differences between the species. For Z. marina, I'_k is much lower than for R. maritina and at times by as much as an order of magnitude. These data suggest a much lower light requirement and higher photosynthetic efficiency of Z. marina. This conclusion is supported by comparison of the estimated values. For all data, Z. marina light-response at low intensities is approximately 3 x that for R. maritina.

Overall, the results indicate that photosynthesis - light relationships for the two species are significantly different. Z. marina can be characterized by 1) a temperature optimum in the range 22° - 28°C, 2) high photosynthetic efficiency at low light intensity and 3) a Pmax and light-response characteristic of 'shade' or low-light plants. R. maritima can be chatacterized by 1) a temperature optimum at or near 30°C, 2) low photosynthetic efficiency at low light, and, 3) a Pmax and light-response characteristic of "sun" or high-light plants.

From these data, our best estimate for photosynthetically saturating light intensities for Z. marina and R. maritima are 200-300 μE m^{-2} sec^{-1} and 600-700 μE m^{-2} sec^{-1} respectively. From a physiological standpoint these results fit very well as a causal explanation for the characteristic depth-dependent distribution and zonation patterns of lower Chesapeake Bay grassbeds (see Chapter 1, this report; Orth et al. 1982).

Total Community Oxygen Metabolism

A total of 42 community oxygen metabolism studies were carried out at the study site during the period July 1978 through September 1980 using the dome

enclosures. Our major efforts focused on the monospecific, Z. marina and R. maritima dominated communities (31 or 74% of the total number of studies). The remainder of the studies were carried out in the mixed-bed community (five), sand patch or bare substrate areas within the grassbed (four), and on two occasions outside the grassbed on the offshore sandbar. The only studies carried out without stirring the domes (i.e. the first enclosure technique tried) were conducted in July 1978. All other studies had water circulation provided by modified bilge pumps either integral with the domes (October 1978 through July 1979) or using the surface-stationed pumps (August 1979 through September 1980).

The Zostera marina dominated community

Table 2 summarizes the net apparent rate of oxygen production or consumption in the Z. marina dominated community for various intervals over the course of the experiments. Maximum rates of net apparent oxygen production occured during the noon intervals reflecting the strong dependence on light. The noon rate estimates ranged from -18.1 to +663. $mgO_2\ m^{-1}\ h^{-1}$ with the minimum estimate occuring in late summer (August) and the maximum estimate occuring in spring (April-May). Water temperatures at these times of year average about 27°C and 16°C respectively in Z. marina dominated areas of the grassbed. These data suggest temperature dependance during all seasons except summer. Arrhenius plots (log rate vs. reciprocal temperature) and simple linear regression of the transformed data indicates that net apparent noon oxygen production is directly correlated with water temperatures $\leq$22.5°C ($r = -0.700$) (Figure 7). Inclusion of all paired temperature and rate data using this analysis indicates poor correlation ($r = -0.021$) and suggests a response threshold occurring between 22.5°C and 28°C (the maximum temperature at which community noon rates were determined). The annual mean noon rate was 230 ($\pm$ 41.0 S.E.) mg $O_2\ m^{-2}\ h^{-1}$ or approximately 86.2 mgC $m^{-2}\ h^{-1}$.

Figure 8 summarizes all noon and afternoon rate measurements by calendar day. Noon and afternoon rates were generally equal during the growing season and at temperatures at or below 20°C. During the summer periods and at temperatures ranging from 22.5 to 28°C, afternoon rates were considerably less than the noon estimates and often by a factor of 2 or 3. Our first assumption was that the depressed afternoon rates at the higher temperatures resulted from oxygen inhibition or poisoning of photosynthesis since it was at these times during the course of an experiment that oxygen concentration within the dome enclosures was generally maximum. However, combining all data, there was no significant correlation between paired rate estimates and mean oxygen concentration over the measurement intervals. Other possible explanations were: 1) lacunal storage and internal cycling of metabolic gases within the plant accounted for the apparent afternoon depression in oxygen exchange 2) some other factors in addition to light and temperature was limiting the rate, or, 3) internal metabolic pools were limiting CO_2 assimilation or photoevolution of O_2 (i.e. end product inhibition).

We tested the first hypothesis by conducting a series of measurements with repetitive dome sets; i.e. paired domes were set at 0800, 1000, 1200 and 1400 hours over the course of a day. The assumption of the experimental design was that under ambient conditions lacunal gases in the aboveground

TABLE 2. MEAN IN SITU RATES OF OXYGEN EXCHANGE (±1 S.D.) BY THE ZOSTERA MARINA DOMINATED COMMUNITY AT VAUCLUSE SHORES, LOWER CHESAPEAKE BAY, VIRGINIA.

Date	Interval (Duration)	$\bar{x}$ mg O^2 m^{-2} h^{-1} (±S.E.) Morn[1]	Noon[2]	AN[3]	E[4]	N[5]	PAR[6] (PAR @ 50cm)	$-\bar{k}_z$ (m^{-1})[7]
26 Jul 78	0845-1425	144.	316.	-	-	-	-	
	(5:40)	(-)	(93.9)	-	-	-	-	
28/29 Jul 78	1620-0815	60.0		226.	-156.	-	51.2(28.0)	-
	(15:55)	(-)		(124.)	(37.3)	-		
15/16 Oct 78	2345-1730	4.00	217.	-45.1	-103.		24.8/34.9	-
	(17:45)	(65.3)	(84.8)	(74.9)	(8.97)			
30/1 Apr-May 79	0940-1200	-	663.	207.	-583.	-163.	54.7/59.2	-
	(26:20)	-	(112.)	(148.)	(12.4)	(8.06)		
26 Jul 79	1140-1545	-	304.	-94.4	-	-	(22.7)	1.36(.24)
	(4:05)	-	(170.)	(77.2)	-	-		
29/30 Aug 79	1015-0830	320.	387.	157.		-230.	52.5/20.6	-
	(22:15)	(-)	(73.1)	(115.)		(-)		
27/28 Sep 79	1245-0910	-	402.	175.	-198.	-134.	23.6(12.5)	-1.20(.35)
	(20:25)	-	(32.6)	(38.8)	(4.94)	(25.6)	30.3(17.0)	-1.31(.16)
29/30 Oct 79	1200-1200		294.	250.	133.		-	-
	(24:00)	(24.2)	(83.3)	(-)				
14/15 Feb 80	1345-1400	-48.2	188.	208.	227.	-72.5	31.0(13.5)	-1.43(.58)
	(24:15)	(55.2)	(51.9)	(25.0)	(27.9)	(3.90)	18.4(8.12)	-1.63(.32)

TABLE 2. (CONTINUED)

Date	Interval (Duration)	$\bar{x}$ mg O_2 m^{-2} h^{-1} (±S.E.) Morn[1]	Noon[2]	AN[3]	E[3]	N[5]	PAR[6] (PAR @ 50cm)	$-\bar{k}_e$ (m^{-1})[7]
20/21 Feb 80	1705-1600 (22:55)	192. (25.0)	279. (48.0)	276. (38.7)		-70.0 (16.7)	2.96(1.83	-1.07(.58)
19/20 Mar 80	1410-1500 (24:50)	- -	192. (16.0)	225. (30.7)	0.0 0.0	-123. (-)	40.8(22.87) 15.1(5.6)	-1.11(.22) -2.22(.69)
2/3 Jun 80	1400-1820 (18:20)	- -	- -	-89.2 (33.0)	- -	-223. (19.9)	48.3(22.5)	1.59(.34)
3 Jun 80	1040-1630 (5:50)		175. (33.7)	-117. (93.4)			-	-
5/6 Jun 80	1115-1006 (22:51)	- -	176. (25.6)	-166. (43.7)		-148. (21.5)	60.7(30.6)	-1.43(.35)
16/17 Jul 80	0905-0900 (23:55)	283. (38.6)	222. (56.1)	121. (41.5)	-317. (-)	-286. (-)	59.6(31.7) 60.2(29.1)	-1.18(.30) -1.54(.20)
19/20 Aug 80	0900-0730 (22:30)	41.4 (14.7)	-18.1 (19.9)	-101. (22.3)	-241. (7.16)	-131. (39.2)	21.2(11.1) 38.5(-)	-1.27(.27)
20/21 Aug 80	1002-0547 (19:45)	-	74.9 (25.2)	-117. (33.0)	-217. (33.1)	-161. (11.2)	38.5(-) 43.6(26.2)	

TABLE 2. (CONTINUED)

Date	Interval (Duration)	$\bar{x}$ mg O^2 m^{-2} h^{-1} (±S.E.) Morn[1]	Noon[2]	AN[3]	E[4]	N[5]	PAR[6] (PAR @ 50cm)	$-\bar{k}_z$ (m^{-1})[7]
23/24 Sep 80	1139-0421	-	101.	0.07	-212.	-154.	42.3(11.6) / 17.1(3.23)	-1.12(.21)
	(16:42)	-	(60.7)	(25.1)	(14.1)	(12.2)		
	$\bar{x}$	62.3	230.	91.2	-153.	-148.		
	S.E.	39.2	41.0	35.4	63.0	19.4		
	Range	-48.2	-58.2	-166.-	-583.-	-28.1-		
		320.	663.	276.	227.	-286.		

1. Morn - Morning interval (see text)
2. Noon - Midday interval (see text)
3. AN - Afternoon interval (see text)
4. E - Evening interval (see text)
5. N - Night interval (see text
6. PAR - Photosynthetically Active Radiation, E m^{-2} day^{-1} (values separated by a "slash" or vertical line represent data for different dates covered by the experiment).
7. $-k_z$ - Vertical Light Attenuation Coefficient (mean of all profiles for the day).

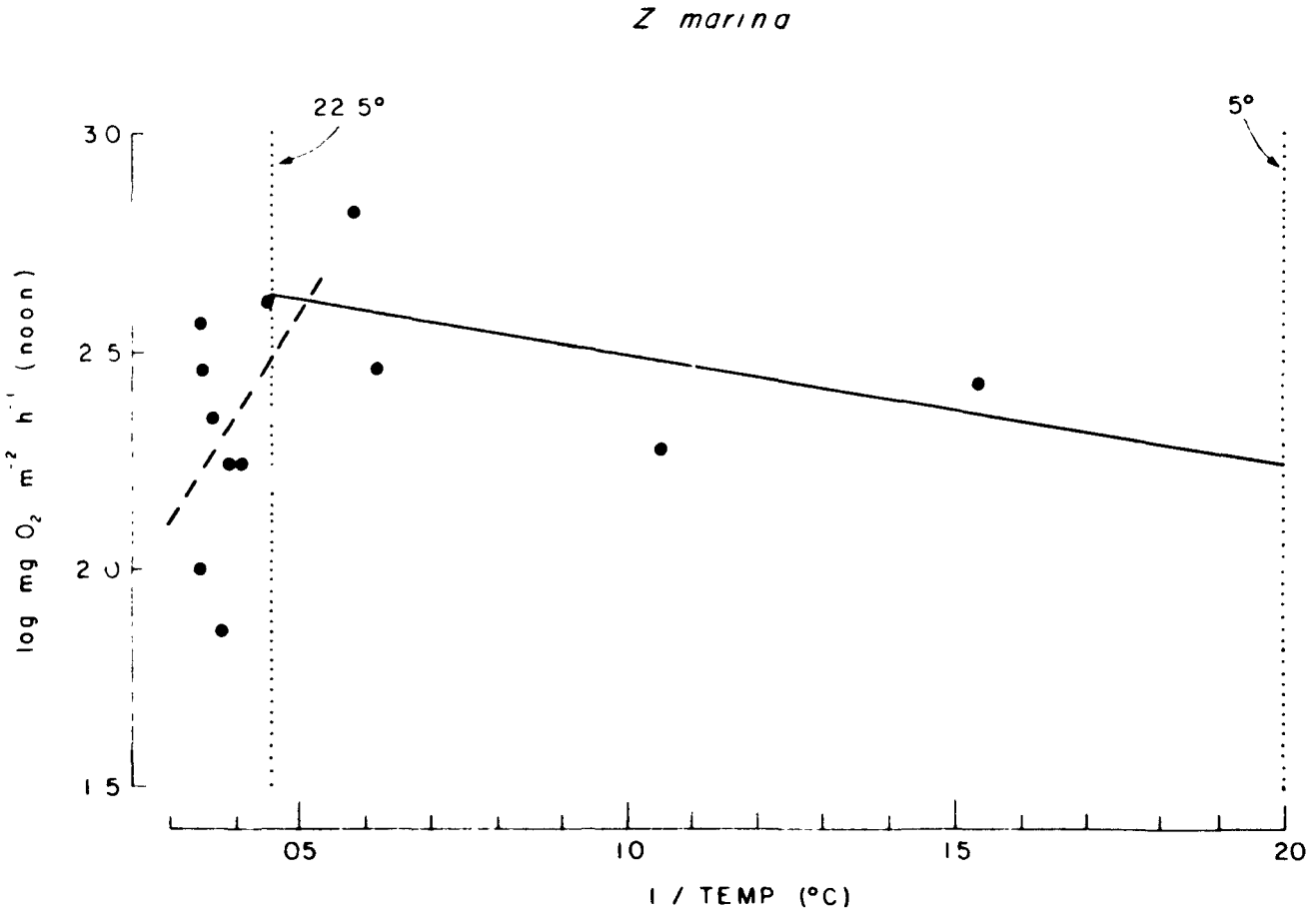


Figure 7. Arrhenius plot of net apparent O_2 productivity for noon intervals versus water temperature in the Z. marina dominated community. Solid line is simple linear lease squares line of best fit for temperatures $\leq$ 22.5°C; dashed for temperatures $\geq$ 22.5°C.

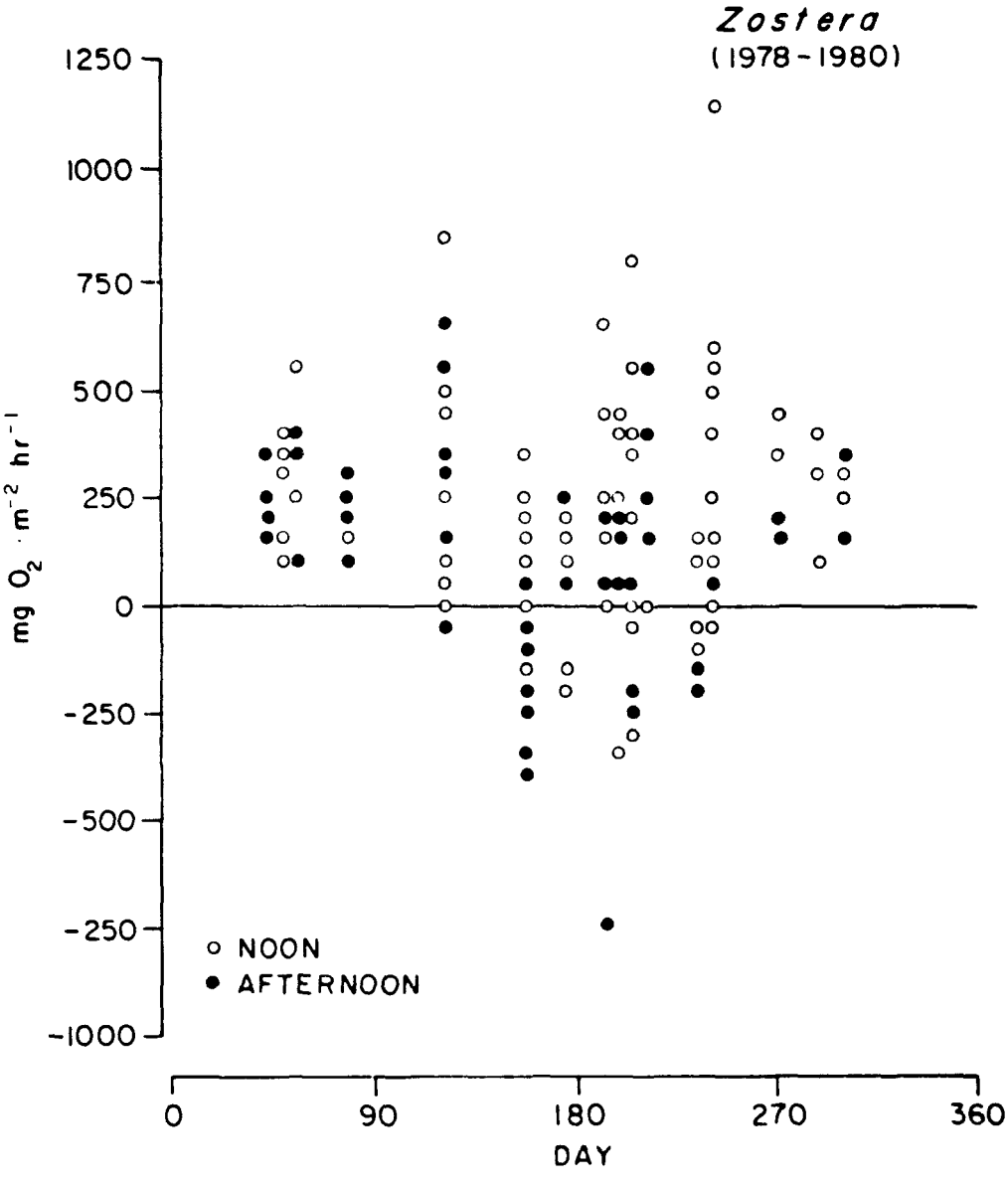


Figure 8. Scatter plot of mean daily noon and afternoon rates of net apparent O_2 productivity in the Z. marina dominated community versus calendar day.

TABLE 3. AREAL RATE OF Z. MARINA COMMUNITY O_2 PRODUCTION OR CONSUMPTION INTEGRATED OVER THE DAILY INTERVAL FOR ALL DOME ENCLOSURE EXPERIMENTS. ENTRIES ENCLOSED BY PARENTHESES WERE ESTIMATED FROM POINT MEASURES.

Date	mg O_2 m^{-2} $interval^{-1}$ Morn	Noon	AN	Even	Night	Σ
July, 1978	570.	1264.	960.	-628.	-445	1721.
Oct, 1978	12.	808.	176.	-68.	(-687)	241.
May, 1979	(2600)	2652.	824.	-2332.	-1291	2453.
June, 1979	967.	468.	838.	-840.	-1441.	-8.
July, 1979	(3383)	1228.	400.	-	-	-
Aug, 1979	1492.	1444.	781.	(-1500)	-2012.	105.
Sept, 1979	(1354)	1456.	523.	-780.	-1397	1156.
Oct, 1979	(1239)	1332.	490.	532.	-687.	2906.
Feb, 1980	242.	928.	649.	128.	-788.	1159.
Mar, 1980	(345.)	768.	702.	0.	-1240.	575.
Apr, 1980	808.	1264.	572.	-1356.	-2341.	-1053.
June, 1980	(1446)	700.	-533.	-1428.	-1337.	-577.
July, 1980	1168.	424.	421.	-1348.	-1305.	-1240.
Aug, 1980	153.	184.	-420.	-916.	-1229.	-2228.
Sept, 1980	(376.)	404.	0.	-848.	-1494.	-1562.

plant tissue would be in equilibrium with the surrounding water at the time of dome placement. If the apparent depression in the afternoon rates is a function of internal cycling which hypothetically is concentration dependant, then afternoon rates determined on the plant community having been exposed to different ambient oxygen concentrations and thus different internal storage concentrations should be different. The results of this study indicated that there was no significant difference in afternoon rate estimates dependant on time of dome placement although ambient oxygen concentrations ranged between 7.00 and 18.0 mg $^{-1}$ depending on the time of day the domes were set. If the assumption that gases rapidly equilibrate between lacunae and external water is correct, internal cycling does not appear to explain the apparent afternoon depression. For the second possibility we amended the domes in situ with various combination and concentrations of NH_4^+, NO_3^- and PO_4^{-3}. Although the data are not yet fully analysed, preliminary results suggest that the response may be nutrient-related, i.e. nutrient amendments to incubation water using NO_3^- and NH_4^+ tend to increase the estimated rates. There is no indication of what mechanism(s) may be involved as there appears to be no measurable difference in response between single treatments using either NO_3^- or NH_4^+ versus the combination. With regard to third possibility, we have not attempted any studies at this time but at least for soybean Nafziger and Koller (1976) have demonstrated the influence of leaf starch concentration on photosynthesis. Overall, the mean annual afternoon rate was 91.2 (± 35.4) mg O_2 m^{-2} h^{-1} or 34.2 mgC m^{-2} which is approximately one half the annual mean estimate for the noon rate.

Estimates of total community respiration show a typical, temperature-related response with a minimum of 28.1 mg O_2 m^{-2} h^{-1} occuring in February at 6.5°C and a maximum of 286 mg O_2 m^{-2} h^{-1} occuring in July at 27°C. Simple linear regression of Arrhenius plots supports this and indicates a strong correlation between in situ temperature and estimated night respiration ($r = -0.83$). Comparison of night and early evening estimates suggests that community respiration is stimulated at higher temperatures immediately following the photoperiod and at these times is not a good estimate for total community respiration. We attribute this response to the vascular plant rather than any diel characteristic of heterotrophic metabolism occuring in the grassbed. It would also appear that the stimulated rates are metabolically related to the vascular plant rather than physically-chemically controlled (i.e. diffusion processes). The stimulated evening rates measured at summer temperatures do not correlate with either in situ oxygen concentration or light available during the photoperiod (discussed in greater detail in the following section on light and community metabolism interaction). Mean annual estimates for evening and night respiration are -153. (±63 S.E.) and -148 (±19.4 S.E.) mg O_2 m^{-2} h^{-1} respectively and are not significantly different although the ranges are quite different. This is due to the evening estimates including rate measurements made during part of the photoperiod and the apparent stimulation occuring only at the higher, summer temperatures.

Estimates for early photoperiod or morning rates, although relatively few in comparison to the other intervals, generally tended to be lower than corresponding afternoon intervals. The effective photoperiod for the morning interval is probably less than the afternoon interval due to the approximate

north-south orientation of the grassbed and the eastern border of forrested land. The annual mean estimate for the morning interval is 62.3 (± 39.2 S.E.) $mgO_2\ m^{-2}\ h^{-1}$ or approximately 25% of the annual mean afternoon rate.

Figure 9 illustrates the annual behavior for all rate measurements by interval with the mean daily temperature over the duration of the experiments indicated. The data suggest that net apparent community O_2 productivity is bimodally distributed over the year. Productivity peaks in mid to late spring and again in fall. Water temperatures in and around 15°C appear to be near optimum. During mid-summer and at temperatures between 23° and 27°, net apparent community O_2 productivity is reduced and the Z. marina community as a whole is heterotrophic (Table 3). Temperature stress is suggested as the principal mechanism accounting for this result together with increased heterotrophic activity.

The R. maritima Dominated Community

Table 4 summarizes the net apparent rate of oxygen production or consumption in the shallow, R. maritima dominated community. As for Z. marina, maximum rates of net apparent O_2 productivity were generally associated with the noon interval throughout the growing season. Estimates ranged from a minimum of 90.6 (± 108. S.E.) $mgO_2\ m^{-2}\ h^{-1}$ in October (15.4°C) to a maximum of 536 (± 83.4 S.E.) $mgO_2\ m^{-2}\ h^{-1}$ in July (26.3°C). Arrhenius plots and simple linear regression of the transformed data (Figure 10) indicate temperature-dependance for noon estimates ($r = -0.771$). As opposed to Z. marina, the temperature-dependance appears to hold throughout the range of measured in situ temperatures (15.7 to 28.1°C). Although we have measured temperatures in the shallow areas as high as 32 to 33°C, whether R. maritima is temperature stressed at these higher temperatures is not known. These data suggest that temperature optimum for net apparent O_2 productivity and the tolerance range is higher for R. maritima than Z. marina.

Morning rate estimates were equal to or greater than noon estimates in several studies. In 1979, morning rates were equal to or greater than noon estimates only in late summer-early fall. In 1980, the situation was reversed, i.e. morning rates equalled or exceeded noon estimates during the early growing season. Morning estimates ranged from a minimum of -98.7 (± 70.3 S.E.) $mgO_2\ m^{-2}\ h^{-1}$ in April (16.4°C) to a maximum of 493 (±233 S.E.) in $mgO_2\ m^{-2}\ h^{-1}$ August (27.9°C). Combining all data, mean annual rates were 184 (± 50.0 S.E.) and 266 (± 48.9 S.E.) $mgO_2\ m^{-2}\ h^{-1}$ for morning and noor intervals respectively.

As opposed to the Z. marina community studies, afternoon rates were always depressed relative to morning and noon interval rates (Figure 11). Afternoon interval net apparent O_2 productivity estimates ranged from a minimum of -514 (± 316) in July to a maximum of 103 (±8.30) in June. The highest afternoon depression occurred during midsummer and indicated net community O_2 consumption under otherwise optimum temperatures and favorable light conditions. Testing this result in the same way as for the apparent depression in Z. marina afternoon rates during mid-summer, there was no significant correlation between rate estimates and oxygen concentration or time of dome placement. We must assume at this point that the apparent

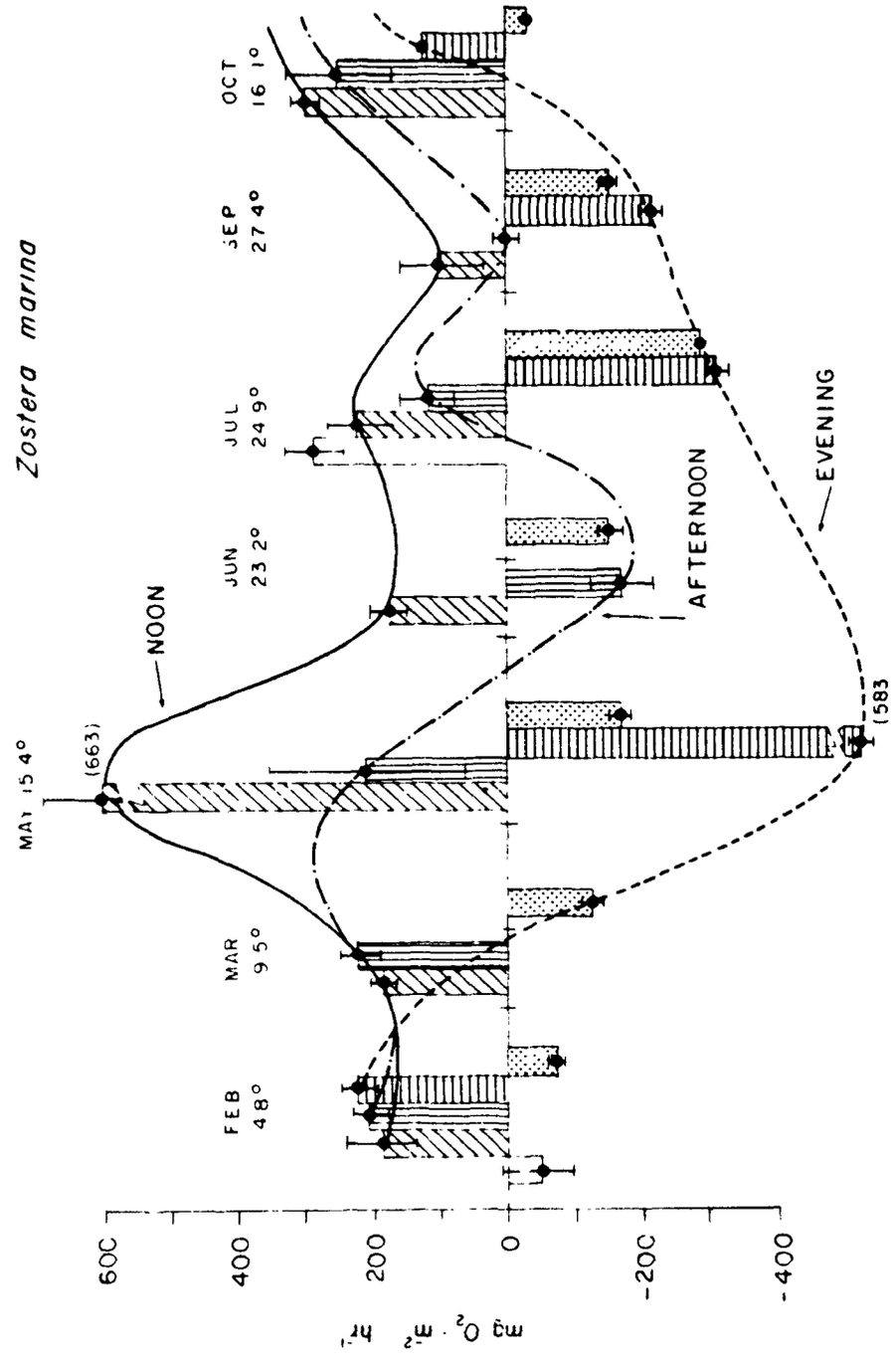


Figure 9. Annual behavior in mean net apparent rates (± 1 S.D.) of O_2 production or consumption by daily interval in the Z. marina dominated community. For any month, the order of the histogram is morning, noon, afternoon, evening and night interval. Noon, afternoon and evening intervals have been connected for convenience.

TABLE 4. MEAN IN SITU RATES OF OXYGEN EXCHANGE (± S.D.) BY THE RUPPIA MARITIMA DOMINATED COMMUNITY AT VAUCLUSE SHORES, LOWER CHESAPEAKE BAY, VIRGINIA.*

Date	Interval (Duration)	Morn	Noon	AN	E	N	PAR (PAR @ 50cm)	$-\bar{k}_z$ (m^{-1})
27/28 Apr 79	2120-1025 (13:05)	12.6 (16.3)	-	-	-	-95.6 (22.6)	26.7/25.4	
28/29 Apr 79	1225-0830 (20:25)	-98.7 (70.3)		88.9 (85.9)	-302. (99.3)	-89.9 (10.1)	25.4/46.2	
23/24 Jun 79	1100-1130 (24:30)	78.6 (10.5)	275. (20.7)	103. (8.3)	-246. (112.)	-124. (9.51)	-	-0.97/-1.14
17/18 Jul 79	0800-0800 (24:00)	285. (32.2)	536. (83.4)	-216. (63.0)	-377. (17.4)	-241. (17.6)	-	-
[illegible] Jul 79	0900-1515 (30:15)	45.0 (137.)	430. (58.0)	-514. (316.)	-306. (35.1)	-217. (16.4)	-	-
27/28 Aug 79	1330-1400 (24:15)	493. (233.)	190. (44.9)	32.6 (8.96)	- -	-142. (46.4)	-	-1.12(0.25 SD)
25/26 Sept 79	1430-1510 (24:30)	261. (62.7)	136. (57.5)	-66.5 (40.7)	- -	-91.0 (15.5)	24.7(8.74)	-2.74(1.1750)
24/25 Oct 79	1230-1330 (24:30	- -	90.6 (108.)	20.0 -	-66.7 -	-38.0 -	3.54(2.59)	(9.44)/-0.62
7/8 May 80	1330-1000 (24:32)	306. (124.)	267. (75.6)	-49.2 (34.9)	-114. (46.2)	-202. (6.36)	50.3(29.8) 55.3(34.0)	-1.28(.37) -1.10(.18)

TABLE 4. (CONCLUDED)

Date	Interval (Duration)	Morn	Noon	AN	E	N	PAR (PAR @ 50cm)	$-\bar{k}_z$ (m^{-1})
21/22 Aug 80	1135-0817 (20:25)	192. (47.8)	490. (50.2)	-224. (56.7)	-441. (49.6)	-71.8 (33.8)	43.6(26.22)	-1.10(.29)
25 Sept 80	1110-1542 (4:32)	- -	279. (49.3)	79.1 (128.)	- -	- -	20.0(10.9)	-1.28(.36)
26 Sept 80	0905-1306 (4:01)	278. (-)		- -	- -	- -	28.9(12.5)	-2.21(.57)
	$\bar{x}$	184.	26.	-65.8	-265.	-131.		
	S.E.	50.0	48.9	56.2	44.1	19.4		
	Range	-278.- 306.	-30.0- 536.	-514.- 103.	-441.- -66.7	-242.- -38.0		

*See Table 2 for an explanation of column abbreviations.

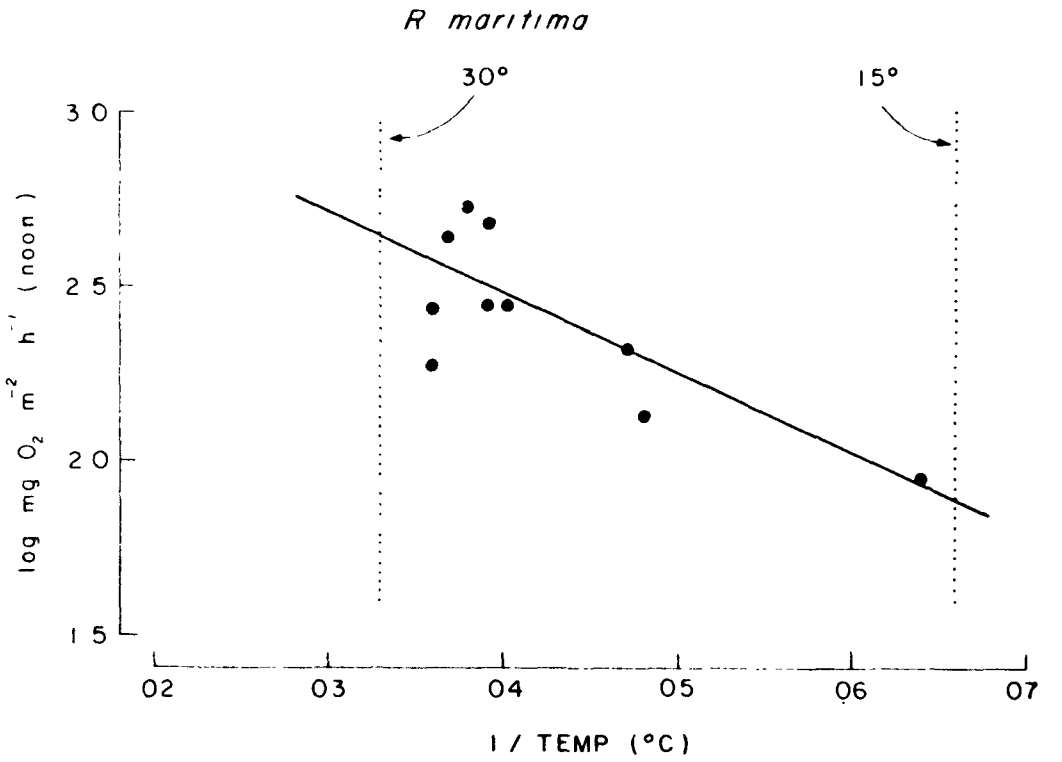


Figure 10. Arrhenius plot of net apparent O_2 productivity for noon intervals versus water temperature in the R. maritima dominated community. Solid line is simple linear least squares lines of best fit for all temperatures.

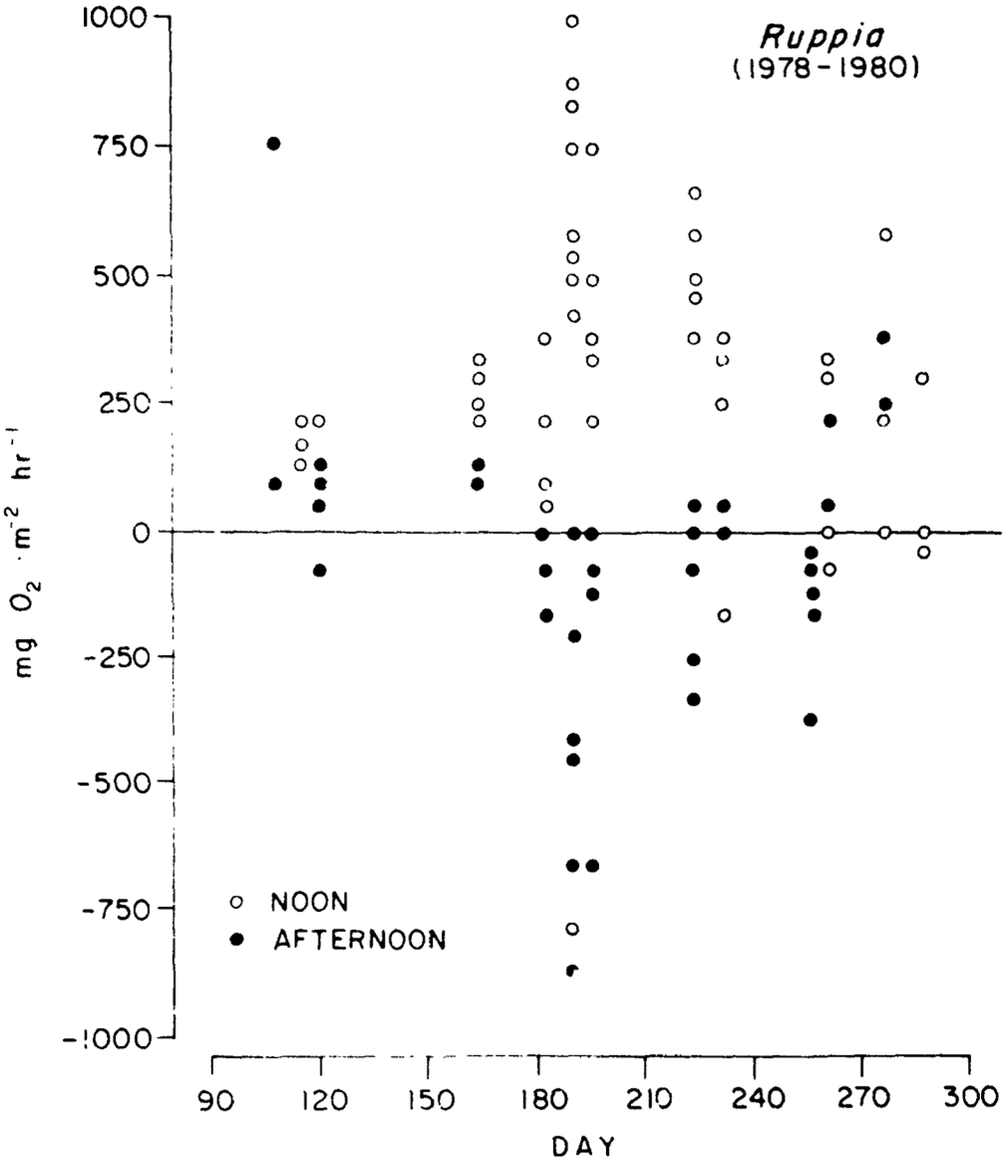


Figure 11. Scatter plot of mean daily noon and afternoon rates of net apparent O_2 productivity in the R. maritima dominated community versus calendar day.

depression which appears more characteristic for the R. maritima community results from either an internal, physiological or metabolic property of the macrophyte or limitation by factor(s) not measured or included in the experimental design. Mean annual net apparent O_2 productivity for the afternoon interval was -65.8 (± 56.2) $mgO_2\ m^{-2}\ h^{-1}$.

As for the Z. marina community study, evening interval estimates for net apparent O_2 consumption were higher on all occasions except one (July 1980) than estimated night time community respiration. The apparent stimulation of community O_2 consumption in the early evening following the photoperiod was much more pronounced in the R. maritima community and was generally double the nighttime community respiration estimate. On one occasion (August 1980), the early evening rate exceeded nighttime respiration by a factor of six. The highest rate or strongest depression tended to be associated with the highest net apparent O_2 noon productivity estimates. Simple linear regression of all paired noon and evening interval rate estimates indicate a significant inverse correlation ($r = 0.871$). As for the apparent afternoon depression in the R. maritima community, causal factors are not known although the data suggest it is coupled to plant photosynthesis and respiration and not a heterotrophic component of the community.

Total community respiration as estimated by the night interval determinations (Table 4) indicate a typical temperature-dependent response. Arrhenius plots and simple linear regression of the transformed data indicate a significant correlation ($r = -0.758$) between estimated total community respiration and temperature. Combining all data, the mean annual rate of respiration is 131 (± 19.4 S.E.) mg $O_2\ m^{-2}\ h^{-1}$ or approximately one half the overall mean rate of 265 (± 44.1) mg $)_2\ m^{-2}\ h^{-1}$ for the evening interval.

The Co-dominated R. maritima and Z. marina Community

Table 6 summaizes net apparent O_2 production or consumption at the intermediate depth, R. maritima and Z. marina co-dominated community. The studies, though fewer in comparison to the number of experiments conducted in monospecific stands of R. maritima or Z. marina, cover principal times in the growing season of both species. From the discussion and presentation of results before, it is apparent that the behavior of O_2 production or consumption in the mixed grassbed results from the combined characteristics of the two species. The data are too limited to determine correlative indices for temperature or light dependance. Maximum rates of net apparent O_2 productivity were associated with morning and noon intervals, the higher morning rates probably reflecting R. maritima influence. Depression of rates were not as clearly indicated for either afternoon or evening intervals and when a depression was indicated in the data, it was not as severe as for estimates in the R. maritima or Z. marina community alone.

Combining all data by interval, mean annual estimates of community O_2 production or consumption are summarized by vegetated community type in Table 7. The results indicate the overall response of the mixed grassbed community and suggest that in comparison to the monospecific macrophyte communities net apparent O_2 productivity extends through a longer portion of the photoperiod as a result of species specific responses, afternoon depression in apparent

rates is less severe and evening and night time interval estimates for community O_2 consumption are intermediate. From these studies, though limited in comparison, the data suggest that production-consumption relationships as estimated by O_2 exchnage maybe more evenly distributed not only over a diel period but over an annual cycle as well in these co-dominated communities.

Non-vegetated Substrates

Table 8 summarizes our relatively few studies on non-vegetated sediments both within and adjacent to the Vaucluse Shores study area. Bare sediments (i.e. sand patches) within the grassbed have rates of community O_2 production and consumption much lower (on most occassions by nearly an order of magnitude) than vegetated zones. Extremely high rates were determined on one occasion, July 1979, when an observable plankton bloom occurred in the water column. For our nearly three continuous years of study in this area, we have observed this on only one occasion and include it in the data to indicate the potential though apparently infrequent range of values possible. Bare substrates outside the grassbed (sandbar) were low and indicated net O_2 consumption at high summer temperatures and low but net O_2 production in October during the day.

Interaction between Light (PAR) and Net Apparent Community O_2 Productivity

A total of eighteen in situ plant community-light response studies were conducted during 1980 in the three principal vegetation zones at the Vaucluse Shores study site. The majority, eleven, were carried out in the Z. marina dominated community and encompassed a temperature range of 6.5°C to 28°C which covers the mid-winter to late summer period (February through September). Five studies were carried out in the R. maritima dominated community from the late spring throughout the principal summer growing season (May through September). Two studies were conducted in the co-dominated Z. marina - R. maritima community; one at 20°C (May) near the optimum temperature for Z. marina and one at 27°C (July) near the optimum temperature for R. maritima.

The Z. marina Dominated Community

Figure 12 illustrates the results for net apparent O_2 productivity (NAP) versus PAR at the plant canopy top for experiments conducted during the winter and spring seasons. NAP during these periods shows a response to increasing PAR typical of the light-photosynthesis interaction. For these data, we have assumed that the response is best described by a rectangular hyperbola and used the linearized form of the Michaelis-Menten function to estimate the various descriptive parameters for the response curve using least squares.

Net apparent community productivity light-saturates between 0.5 and 1.0 E $m^{-2}h^{-1}$ or approximately 140 and 280 μE $m^{-2}h^{-1}$ during this period of the growing season. Calculated maximum net rates for all studies generally were in the range 200 to 300 mg O_2 $m^{-2}h^{-1}$. Table 9 summarizes the descriptive parameters for the response curve in terms of the initial slope (α), light level at the estimated half-saturated rate (I_k'), and the estimated maximum net apparent rate of O_2 production (NAP_{max}). Estimated NAP_{max} is approximately 200 mg O_2 $m^{-2}h^{-1}$ for all studies and increases only slightly over the 6°C to

TABLE 6. MEAN IN SITU RATES OF OXYGEN EXCHANGE (±1 S.D.) BY THE CO-DOMINATED RUPPIA-ZOSTERA MIXED-BED COMMUNITY AT VAUCLUSE SHORES, LOWER CHESAPEAKE BAY, VIRGINIA.*

Date	Interval (Duration)	$\bar{x}$ mg O_2 m^{-2} h^{-1} (±S.E.) Morn	Noon	AN	E	N	PAR	$-\bar{k}_z$ (m^{-1})
26/27 Oct 79	1500-1410 (23:10)	191. (76.6)	62.5 (40.5)	-185. (157.)	-188. (37.8)	-64.4 (15.8)	31.9/30.8	-
18/19 Mar 80	1530-1530 (24:00)	- -	171. -	36.3 (128.)	- -	-104. -	40.8(22.9)	-1.47(-)
20 Mar 80	1120-1620 (5:00)	- -	128. (122.)	-48.6 (223.)	- -	- -	15.1(5.6)	-2.22(.69)
5/6 May 80	1135-1055 (23.20)	35.3 (110.)	63.3 (22.2)	-24.3 (35.0)	-167. (33.3)	-225. (111.)	61.9(38.3)	-1.03(0.26)
14/15 Jul 80	0810-0835 (24:25)	305. (11.4)	224. (22.3)	36.6 (3.33)	- -	-137. -	62.1(48.9)	-0.90(.23)
	$\bar{x}$	205.	128.	-37.0	-178.	-133.		
	S.E.	78.2	30.6	40.6	10.5	34.2		
	Range	35.3-305.	62.5-224.	-185. 36.6	-	-74.4--225.		

*See Table 2 for explanation of column abbreviations.

TABLE 7. MEAN ANNUAL ESTIMATES OF NET APPARENT O_2 PRODUCTION OR CONSUMPTION (mg O_2 m^{-2} h^{-1} ± S.E.) BY INTERVAL AND COMMUNITY TYPE AT VAUCLUSE SHORES.

Community	Interval				
	Morn	Noon	AN	Even	Night
Z. marina	62.3 (39.2)	230. (41.0)	91.2 (35.4)	-153. (63.0)	-148. (19.4)
R. maritima	184. (50.)	266. (48.9)	-65.8 (56.2)	-265 (44.1)	-131 (19.4)
Mixed	305. (78.2)	128. (30.6)	-37.0 (40.6)	-178 (10.5)	-133. (34.2)

TABLE 8. MEAN IN SITU RATES OF OXYGEN (±1 S.D.) BY NON-VEGETATED SUBSTRATES AT VAUCLUSE SHORE, LOWER CHESAPEAKE BAY, VIRGINIA.*

Date	Interval (Duration)	$\bar{x}$ mg O_2 m^{-2} h^{-1} (±S.E.) Morn	Noon	AN	E	N	PAR	$-\bar{k}_z$ (m^{-1})
BARE SUBSTRATES:								
29/30 Jul 78	1000-0815 (22:15)		-87.2 (-)		-34.8 (0.0)		51.2(28.0)	1.17(.09) Ret. station
29/30 Oct 79	1500-1535 (24:35)		94.8 -	11.5 -		-21.3 -	24.3	-
SAND PATCH:								
1/2 May 79	1525-1604 (24:39)	79.8 (19.1)	97.2 (10.2)	42.6 (11.0)	-68.0 (9.49)	-70.2 (19.5)	59.2/59.0	-
22/23 Jul 79	0943-0930 (23:47)	86.3 (30.6)	148. (59.3)	482. (46.0)	-366. (51.8)	-217. (13.8)	-	-
26 Sep 79	0900-1545 (6:45)	- -	16.8 (15.4)	57.4 (24.4)	-	- -	24.67	2.74(1.17)
25/26 Oct 79	1330-1420 (24:50)		26.9 (-)	46.1 (113.)	-29.0	(9.44)/31.9 (-)		-

*See Table 2 for an explanation of column abbreviations.

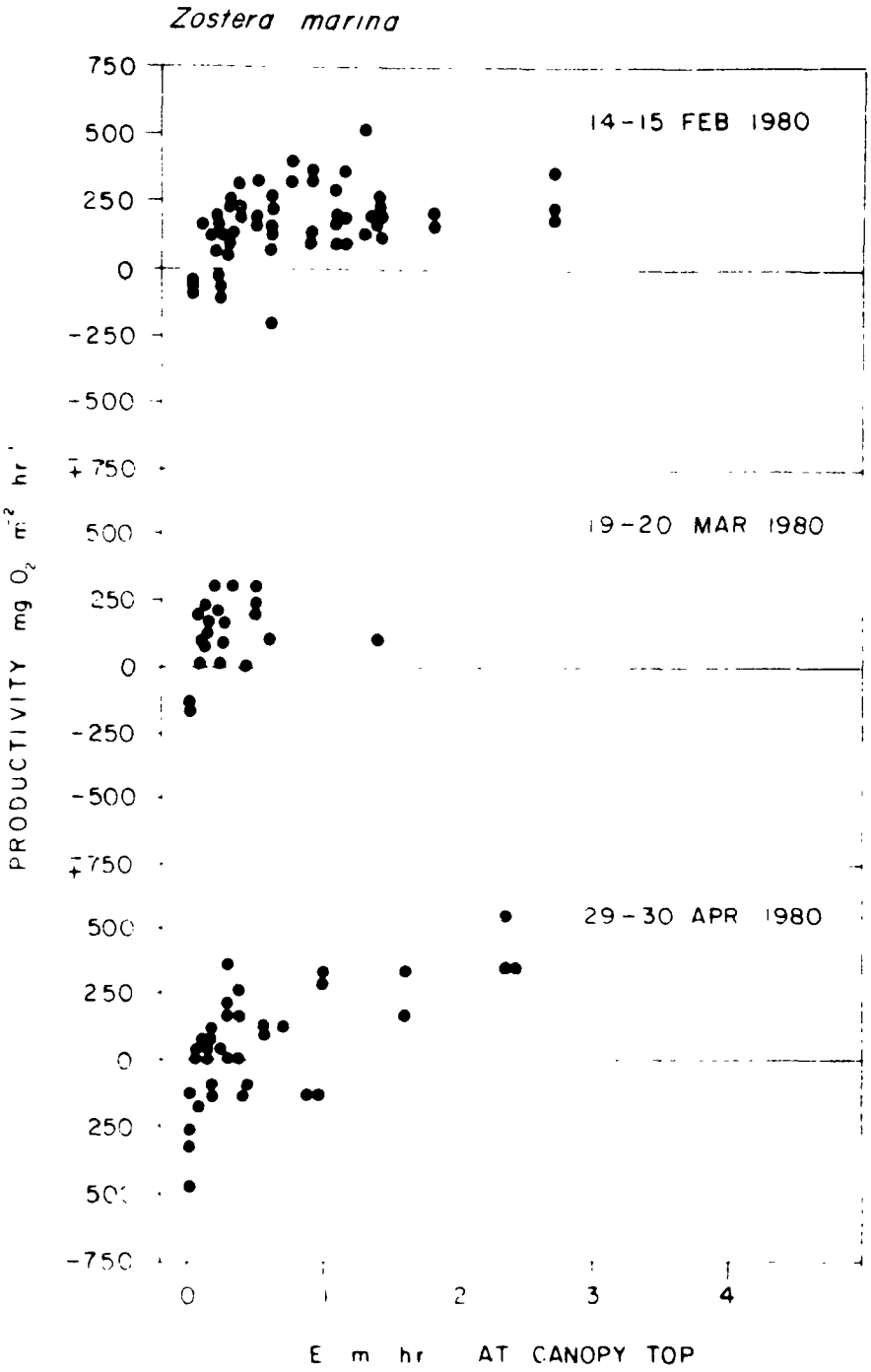


Figure 12. Scatter plot of net apparent rates of O_2 productivity versus available submarine light (PAR) reaching the plant canopy top in the Z. marina dominated community during the early growing season.

Table 9. NET APPARENT O_2 PRODUCTIVITY AND LIGHT RESPONSE CHARACTERISTICS FOR THE EARLY GROWING SEASON IN THE ZOSTERA MARINA DOMINATED COMMUNITY AT VAUCLUSE SHORES, LOWER CHESAPEAKE BAY, VIRGINIA.

Date	Temp (°C)	NAP_{max}[1]	GAP[2]	α[3] ($\Delta NAP/\Delta E$)	I_k[4]	CP[5]
20/21 Feb 1980	6.0	208	278	996.	24.8	25.0
19/20 Mar 1980	9.5	200	323	752.	35.7	35.8
29/30 May 1980	18.0	241	464	292	83.3	83.0

1. NAP_{max} = Maximum rate of estimated net apparent O_2 productivity (mg O_2 m^{-2} h^{-1}).
2. GAP = Estimated Gross Apparent O_2 Productivity (GAP = NAP_{max} + R).
3. Initial Slope or $\Delta NAP \cdot \Delta E^{-1}$.
4. Half-saturation coefficient or I @ NAP = 0.5 NAP_{max} (μE m^{-2} sec^{-1}).
5. Compensating light intensity (μE m^{-2} sec^{-1}) @ NAP = 0.

18°C temperature range encompassed by the studies. The estimated NAP_{max} values compare well with the net apparent noon rate estimates derived from the total community O_2 exchange studies (Table 2). However, gross apparent O_2 productivity (GAP), calculated as the algebraic sum of NAP_{max} and night respiration, (see Table 2) increases by a factor of 1.7 in a near linear fashion from February through May. Converting the February and May GAP estimates to specific rates using our biomass estimates and assuming a community PQ of 1.0, results in estimates of 1.10 and 1.29 $mgC \cdot g\ DW^{-1}$(plant) h^{-1} respectively which are comparable but slightly lower than the ^{14}C estimates of 1.60 and 1.68 for the same times of year (Table 1).

Light response characteristics of the community changed significantly. The estimated half-saturation light level (I_k') increases while the initial slope or low level light response characteristic (α) decreases. Both responses are probably attributable to age and growth of the community as a whole. In February, the plant community is dominated by "young" shoots (mean length = 13.5 cm) while in late May-June the plant community is dominated by "older" shoots (mean length = 24.9 cm) with obvious shoot senescence beginning. These estimated light-response parameters agree very well with those derived from the ^{14}C-photosynthesis studies (Table 1). Compensating light intensities (CP), i.e. light intensity where the net apparent rate approaches zero, track almost exactly the I_k' values and indicate the near total dominance by the macrophyte in governing O_2 production and consumption during the early growing season.

Figures 13 and 14 illustrate the net apparent rate of community O_2 productivity response to increasing light during the Z. marina summer studies. The relationship indicates a linear response for all studies with no suggestion of light saturation occuring for the levels measured. It is apparent that the community response is significantly correlated with light but cannot be described by the typical, hyperbolic, light-photosynthesis relationship. Therefore we have used simple linear regression statistics to describe the response.

Table 10 summarizes the simple linear least squares statistics for these data. Community light response decreases over the course of the summer as indicated by the change in slope of the regression equations. The change is not associated with an overall increase in community respiration and thus probably represents a photosynthetic response by the macrophyte. As discussed previously, we believe this represents a temperature-induced stress. Compensating light intensities for the community are high ($\bar{x}$ = 329 $\mu E\ m^{-2}\ sec^{-1}$) during the summer period due to, 1) the assumed photosynthetic temperature stress, 2) high community respiration and 3) the apparent simulation in afternoon respiration.

To illustrate, Figure 15 presents the results of a July study which was typical for the summer period. For this particular experiment, light levels were high or at least sufficient to attain maximum rates based on the ^{14}C studies and the early growing season results. Water temperatures were near the maximum in situ measures taken in the Z. marina community. It is apparent that the maximum calculated rates were linearly dependant only on light availability during the first part of the photoperiod. This was followed by

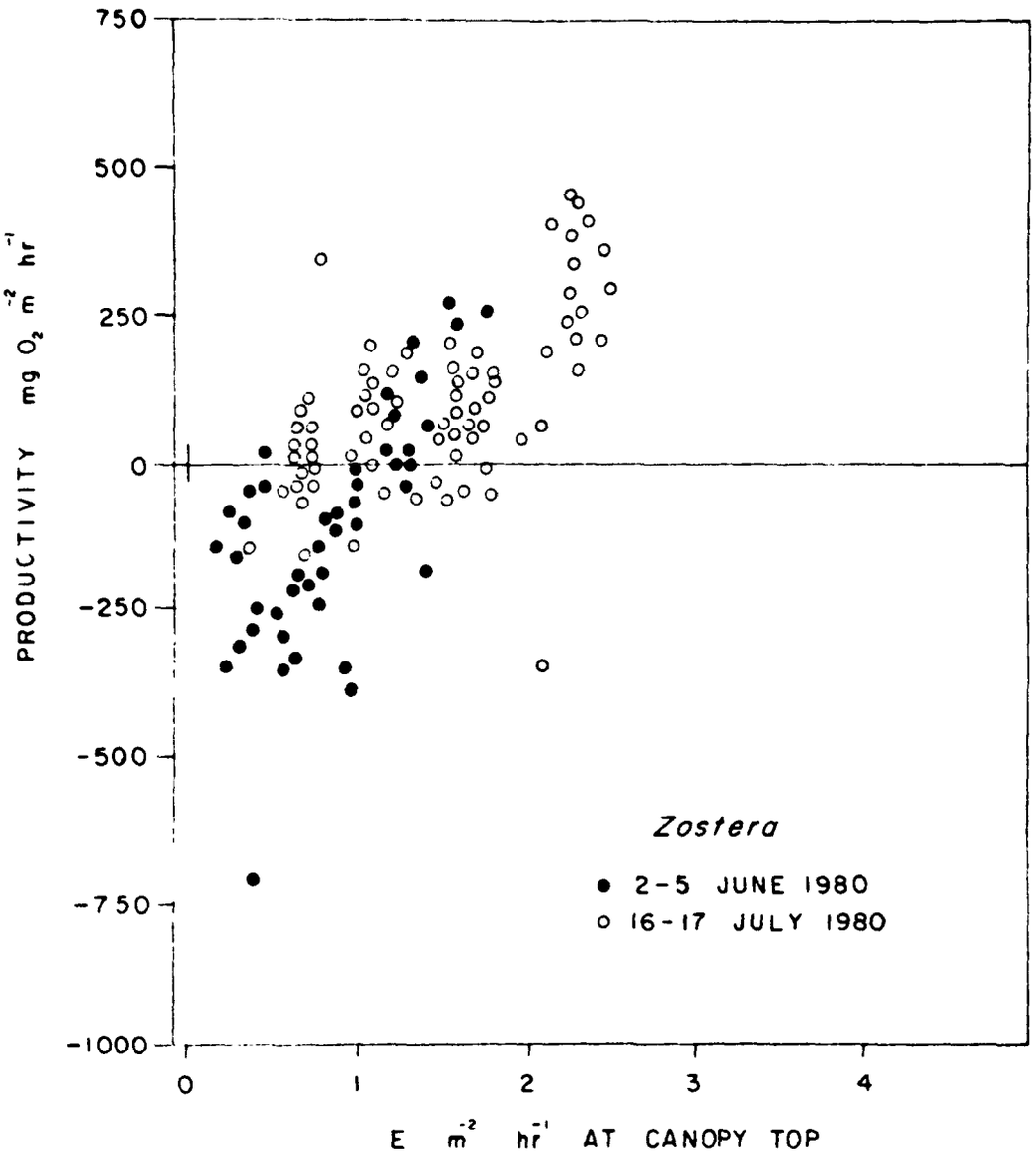


Figure 13. Scatter plot of net apparent rates of O_2 productivity versus available submarine light (PAR) reaching the plant canopy top in the Z. marina dominated community during summer.

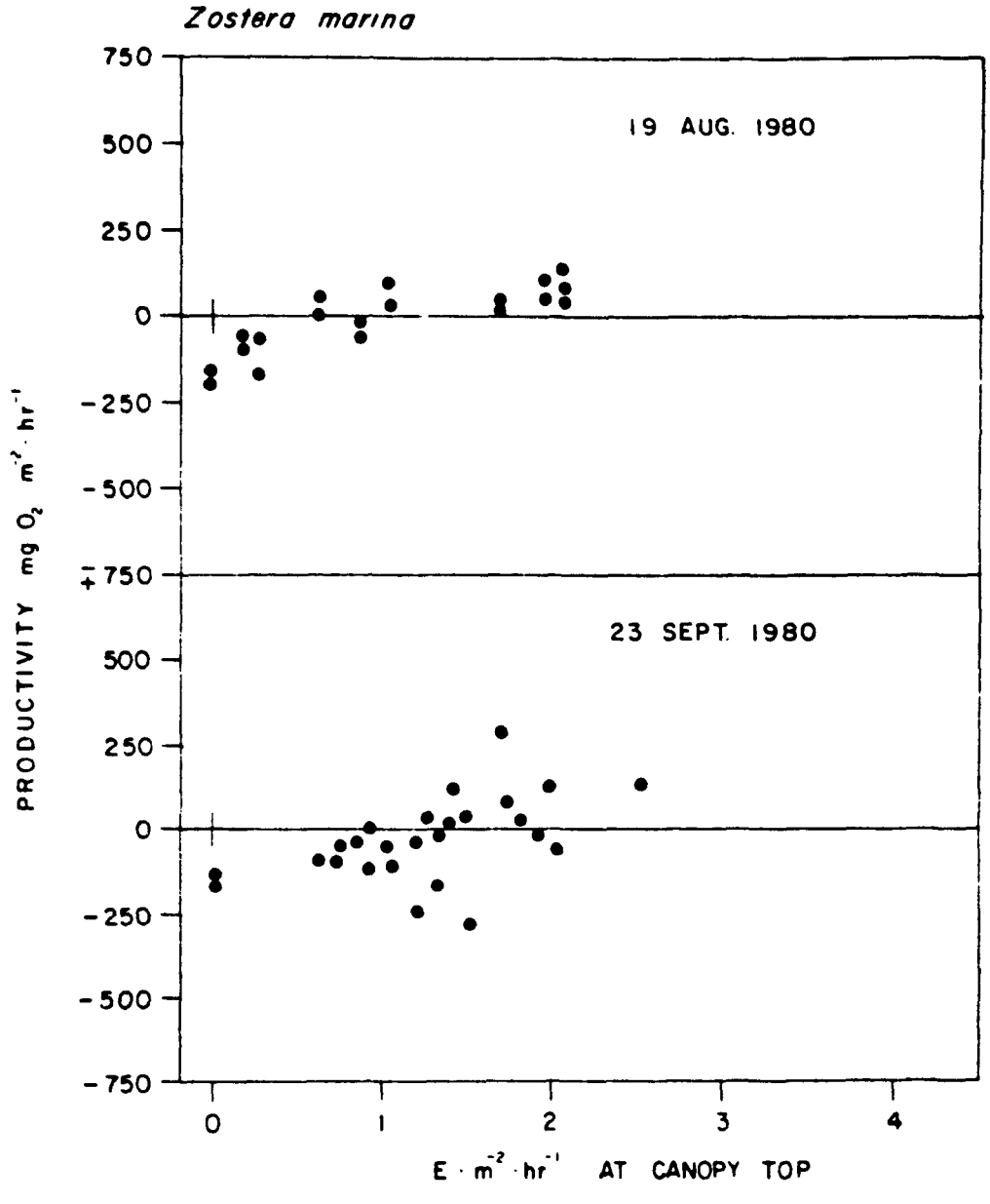


Figure 14. Scatter plot of net apparent rates of O_2 productivity versus available submarine light reaching the plant canopy top in the Z. marina dominated community during late Summer-early Fall.

Table 10. NET APPARENT O_2 PRODUCTIVITY AND LIGHT RESPONSE CHARACTERISTICS FOR THE SUMMER SEASON IN THE ZOSTERA MARINA DOMINATED COMMUNITY AT VAUCLUSE SHORES, LOWER CHESAPEAKE BAY, VIRGINIA.

Date	Temp (°C)	m[1] (ΔNAP/ΔE)	b[2] (mg O_2 $m^{-2}h^{-1}$)	CP (μE $m^{-2}sec^{-1}$)	R[3] (mg O_2 m^{-2} h^{-1})
2 June 1980	26.	307.	-472	427.	-223.
5 June 1980	26.	286.	-309	300.	-148.
9 July 1980	27.	96.5	-147	423	-
16 July 1980	27.	124	-67.1	150	-286.
19 Aug 1980	25.	89.2	-84.5	263	-131.
23 Sep 1980	28.	108.	-160.	411	-154.

1. Slope of the simple linear least squares fit equation.

2. Estimated y-intercept or R (mg O_2 m^{-2} h^{-1}) @ I = 0.

3. Estimated night time community respiration (see Table 2) (mg O_2 m^{-2} h^{-1}).

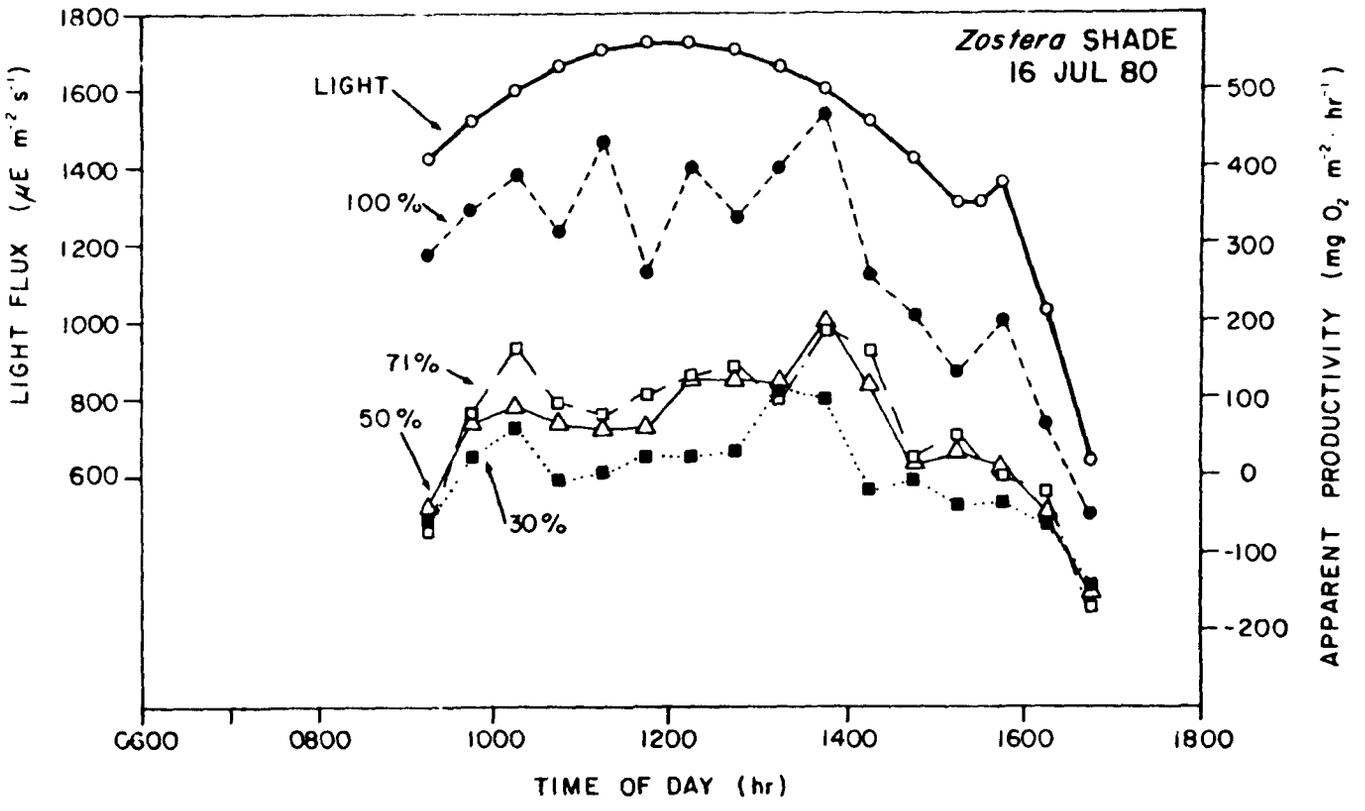


Figure 15. Net apparent rate of O_2 productivity versus PAR reduction in the Z. marina dominated community during mid-Summer using neutral density shades. Percentages given are for the percent of in situ PAR transmitted by the shades.

an afternoon depression in apparent productivity independant of light; i.e. comparison of the four light-level response curves.

Based on these data, net apparent O_2 productivity and light relationships in the Z. marina community are governed by both in situ light regimes and temperature. During the winter-spring period, submarine light regimes appear to be the principal control on net apparent community O_2 productivity. During the summer period, temperature and increased respiration due to both autotrophic (i.e. the macrophyte) and heterotrophic components controls net apparent O_2 productivity.

The R. maritima Dominated Community

Figure 16 illustrates the results typical of the light-community O_2 productivity studies conducted in the shallow, R. maritima dominated community. As discussed previously, the community characteristically had depressed afternoon rates of net apparent O_2 production and on many occasions had net rates of O_2 consumption with otherwise optimum light and temperature conditions. Earlier experiments suggested the response was independant of in situ O_2 concentration but was, over the course of an entire year of study, highly correlated with noon rates. The results of these shading studies conducted in July indicate that the response is independent of absolute light levels, at least those occuring during O_2 productivity measurement (Figure 16). All shading treatments indicate an inflection in the rate of apparent productivity near solar noon followed by depressed afternoon rates. Note that the inflection occurs prior to peak insolation regardless of treatment. We are unable to attribute any causal mechanism(s) to this response which was characteristic of both the total community O_2 exchange and shading studies.

Figures 17 and 18 illustrate the results of all community O_2 productivity and light response studies conducted in the R. maritima area. Because of the depressed afternoon rates, analyses of these data using the typical light-photosynthesis response is not possible. The majority of the low rates illustrated in the figures at otherwise high light intensities are afternoon rate determinations. The July study results come closest to approximating a typical light-photosynthesis response curve. Using only the morning and noon interval rate calculations, the plant community appears to light-saturate between 2.5 and 3 E m^{-2} h^{-1} or 694 and 833 μE m^{-2} sec^{-1} which agree well with our previous ^{14}C light saturation estimates.

As a preliminary analysis of these data, Table 11 presents the simple linear regression statistics for morning and noon intervals versus light at the plant canopy top. Using the linear regression equations, we estimated NAP_{max} at 2.34 E m^{-2} h^{-1} (650 μE m^{-2} sec^{-1}), i.e. the midpoint of the estimated ^{14}C range, and CP at zero rate of net apparent O_2 productivity. The initial slope (α) and y-intercept (b) are simply the terms of the least squares best fit equation. Based on these analyses, there is no significant change in either NAP, GAP or for the four, R. maritima light response studies summarized in the table. The experiments covered a rather limited temperature range (21°C to 28°C) but did encompass the major growth period for the macrophyte. Compared to the results from the Z. marina community shading studies (Table 9), the estimated maximum rates of NAP and GAP are higher for

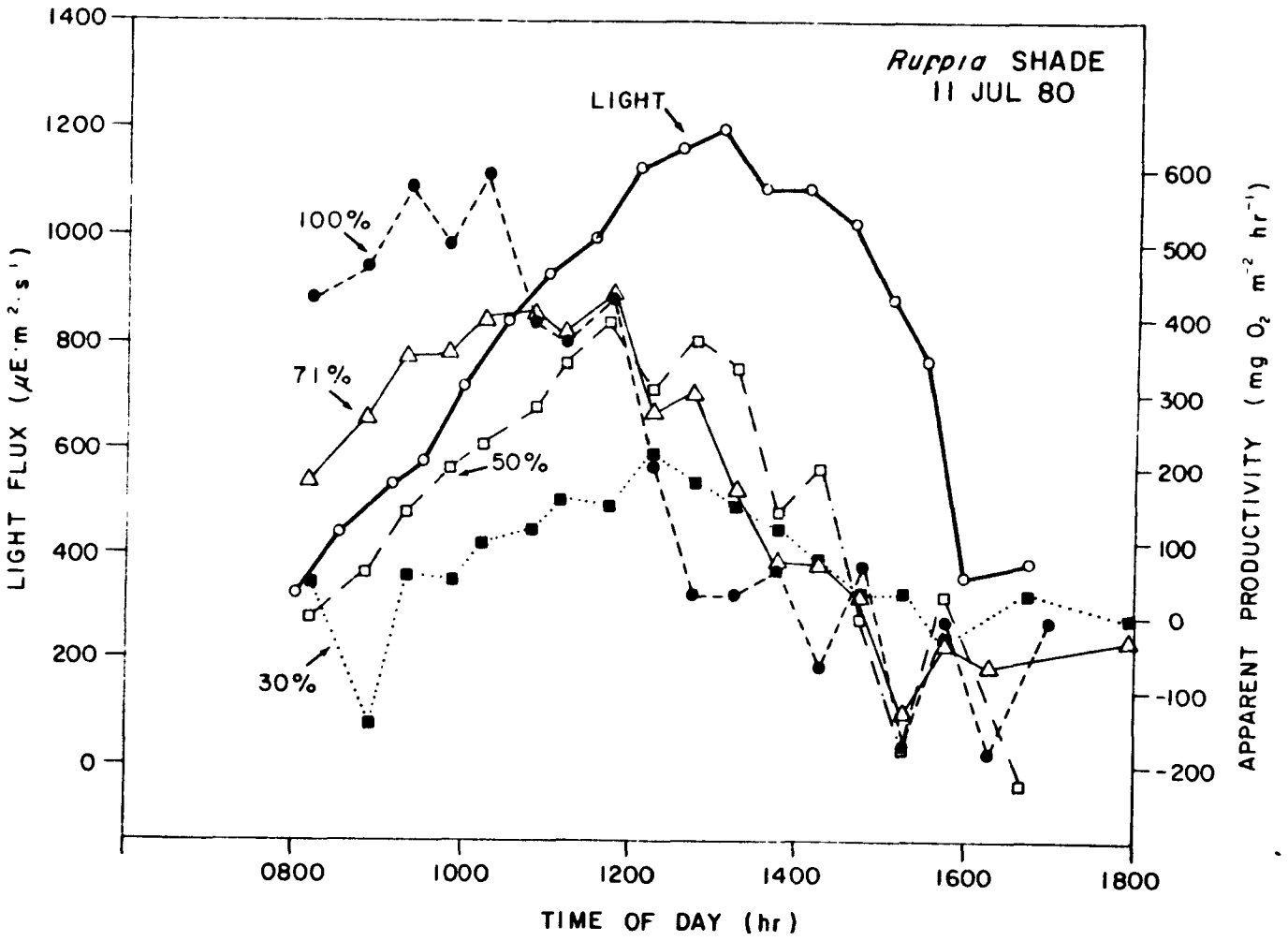


Figure 16. Net apparent rate of O_2 productivity versus PAR reduction in the R. maritima dominated community during mid-Summer using neutral density shades. Percentages given are for the percent of in situ PAR transmitted by the shades.

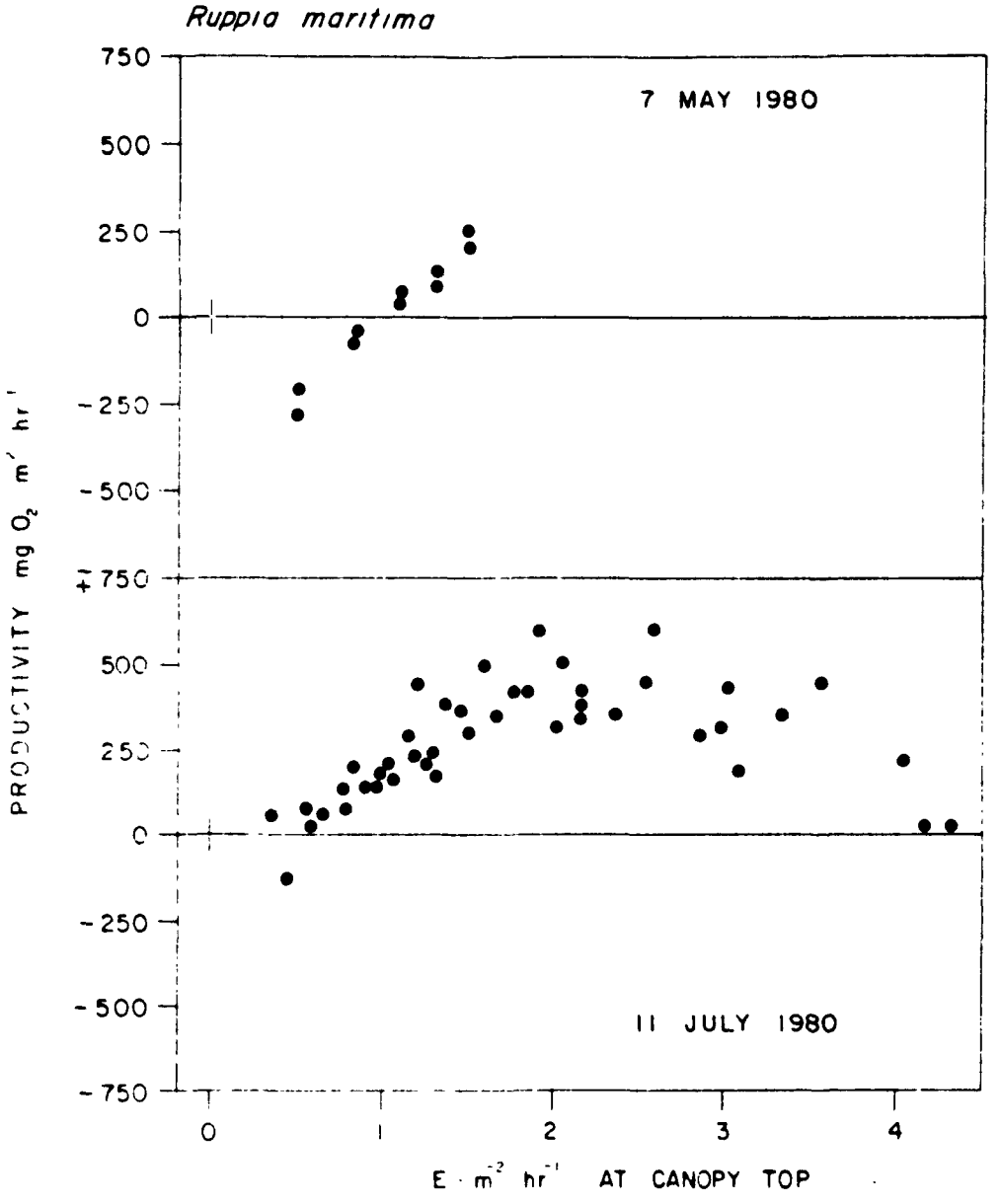


Figure 17. · Scatter plot of net aparent rates of O_2 productivity versus submarine light (PAR) reaching the plant canopy top in the R. maritima dominated community during the first half of the growing season.

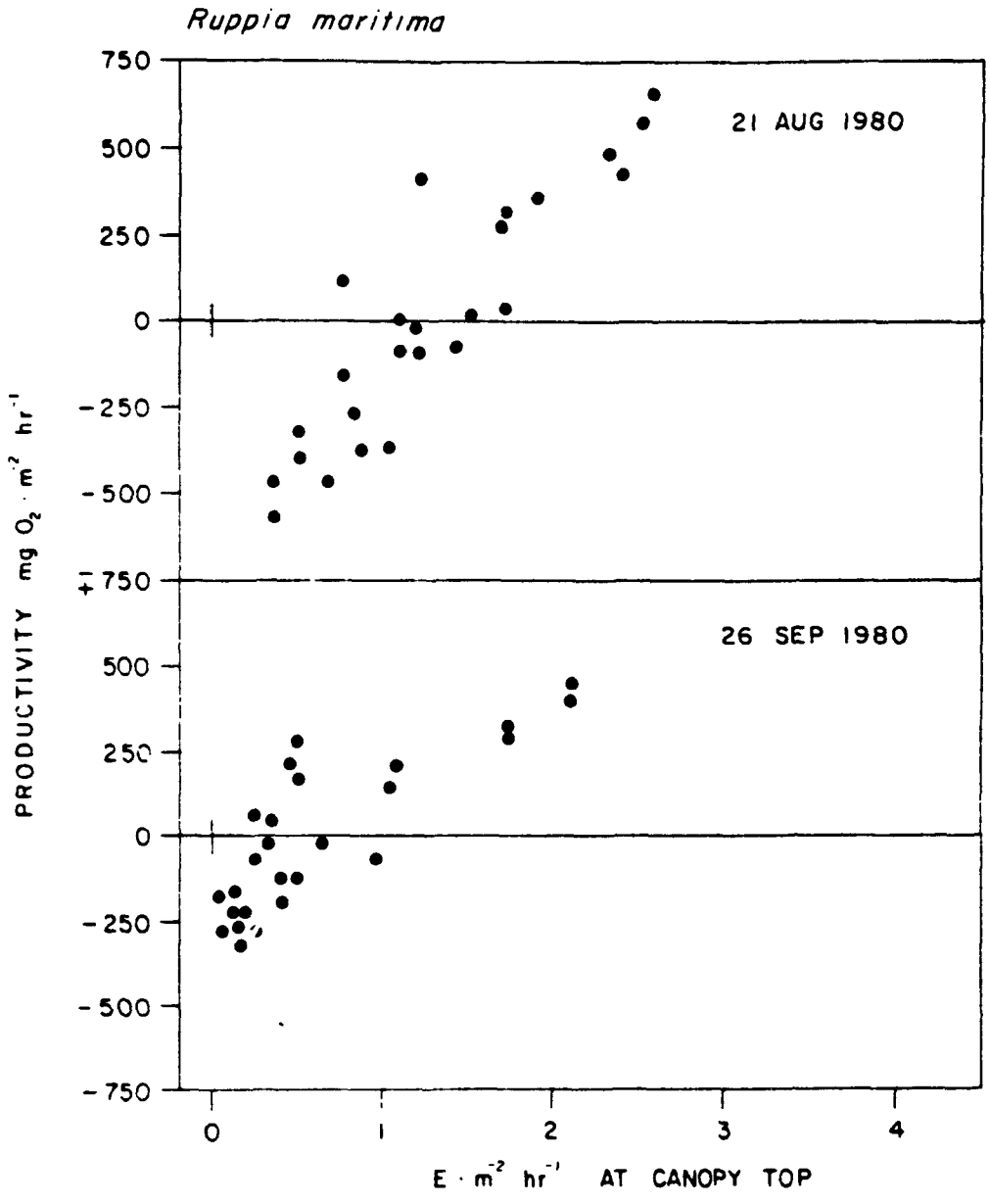


Figure 18. Scatter plots of net apparent rates of O_2 productivity versus submarine light (PAR) reaching the plant canopy top in the R. maritima dominated community during the last half of the growing season.

TABLE 11. NET APPARENT O_2 PRODUCTIVITY (MORNING AND NOON INTERVALS ONLY) AND LIGHT RESPONSE CHARACTERISTICS FOR THE R. MARITIMA DOMINATED COMMUNITY AT VAUCLUSE SHORES, LOWER CHESAPEAKE BAY, VIRGINIA.[1]

Date	Temp °C	NAPmax	GAP	α	CP	b	R^5
7 May 1980	21	613	742	487	287	-487	-129.
11 July 1980	28	665	867	346	133	-166	-202
21 Aug 1980	26	495	645	405	311	-453	-150.
25/26 Sept 1980	24.5	531	722	306	167	-183	-191.
	$\bar{x}$	576	744	386	224		

1. See Tables 9 and 10 for explanation of column headings.

R. maritima under optimum conditions and the characteristic light response (α) is lower. Compensating light intensities in R. maritima are comparatively much higher than for Z. marina. All these results are consistent with our other findings and support the conclusion that Z. marina and R. maritima are photosynthetically quite distinct having different temperature-light optimum and light response characteristics. Combining all light and productivity data for the R. maritima community since the shading studies were limited in temporal coverage, Figure 19 indicates there may be seasonal changes in light response characteristics and that the macrophyte is best adapted to high light-high temperature summer conditions in the lower Chesapeake Bay.

The Co-dominated R. maritima and Z. marina Community

The results of the two shading studies carried out in the mixed community are illustrated in Figure 20. In May, when Z. marina should have dominated the community rate of O_2 exchange, there was no obvious relationship to light and overall the net apparent rates were low. It may be that in the mixed community, the growth characteristics for the macrophyte are different than in the deeper-water, monospecific stands. For the July study, it is apparent that R. maritima dominates the community. The results follow very closely those of the study in the monospecific stand (Figure 17).

SUMMARY

Seagrass communities in both temperate and tropical environments have received increasing research attention over the past decade (e.g. McRoy and Helfferich 1977; Phillips and McRoy 1980). Studies have in large part focused in four areas; 1) macrophyte productivity including both photosynthesis and biomass production studies (e.g. Jones 1968; Zieman 1968; Dillon 1971; Patriquin 1973; McRoy 1974; Sand-Jensen 1975; Zieman 1975; Bittaker and Iverson 1976; Beer and Waisel 1977; McRoy and McMillan 1977; Penhale 1977; Zieman and Wetzel 1980), 2) nutrient relationships (e.g. Goering and Parker 1972; Patriquin and Knowles 1972; McRoy and Alexander 1975; McRoy et al. 1979; Capone et al. 1979; Penhale and Thayer 1980), 3) trophic relationships and secondary production (e.g. Zimmerman et al. 1979; Kikuchi 1980; Ogden 1980; Orth et al. 1982), and, 4) various aspects of total seagrass community metabolism (e.g. Odum and Hoskin, 1958; Odum, 1963; Nixon and Oviatt 1972; Nienhuis 1980; Lindeboom and DeBree 1982). All results point to the relative important roles these communities play in many estuarine and coastal marine ecosystems.

Comparatively, temperate seagrass communities have received far less attention than subtropical and tropical communities. In fact studies of temperate seagrasses along the U.S. Atlantic Coast prior to the mid-1970's were relatively few and focused attention almost exclusively on a single species, Zostera marina. It has only been within the past five to ten years that concerted efforts have been made to investigate the ecology of temperate, estuarine seagrass communities along the U. S. east coast. Therefore, historical data bases and comparative studies are limited and relatively few against which to specifically judge our investigations.

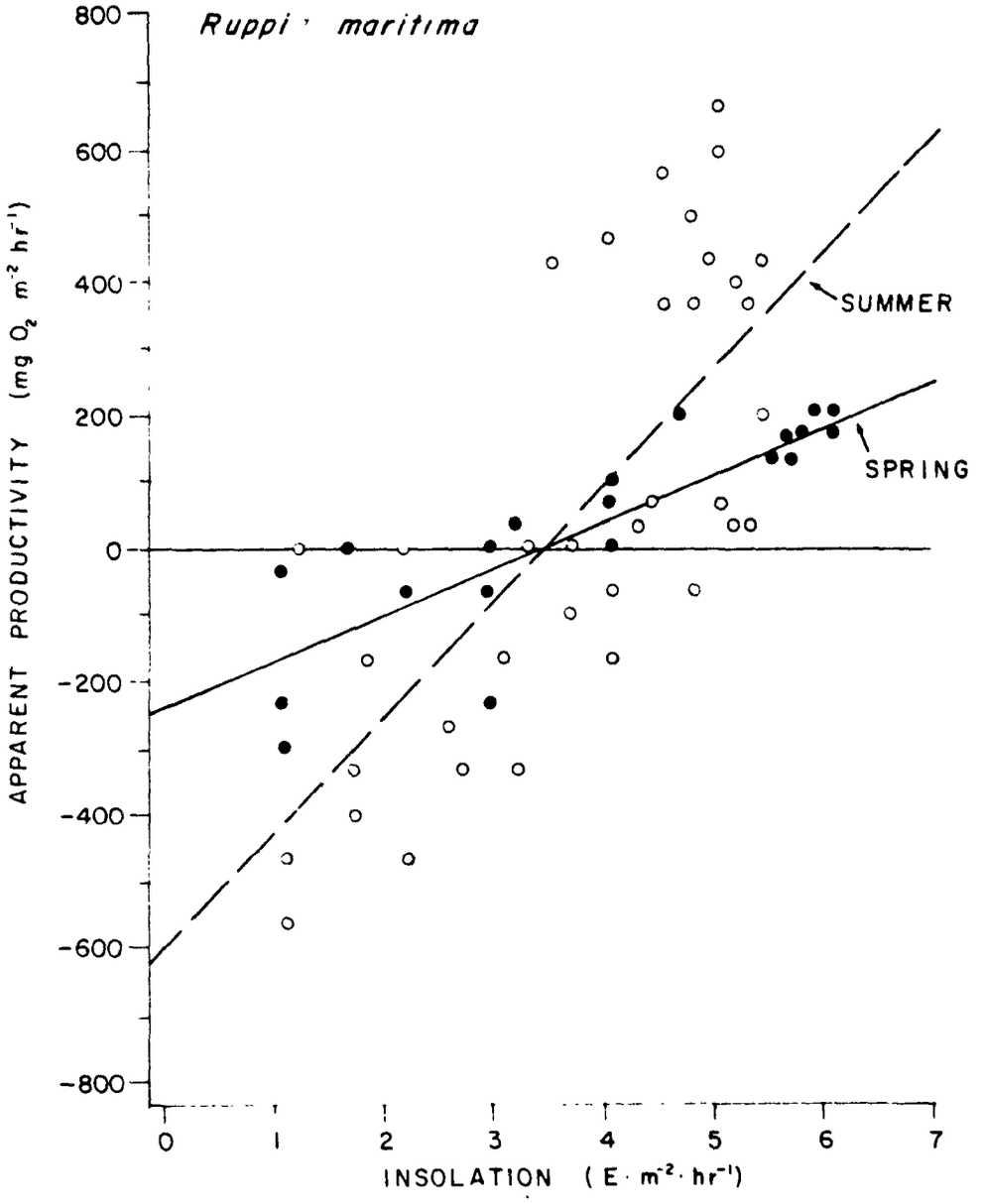


Figure 19. Scatter plots of net apparent rates of O_2 productivity in the R. maritima dominated community partitioned into Spring T°C <25) and Summer (T°C ≥) seasons. Lines illustrated in the figure are the simple, linear least squares lines of best fit.

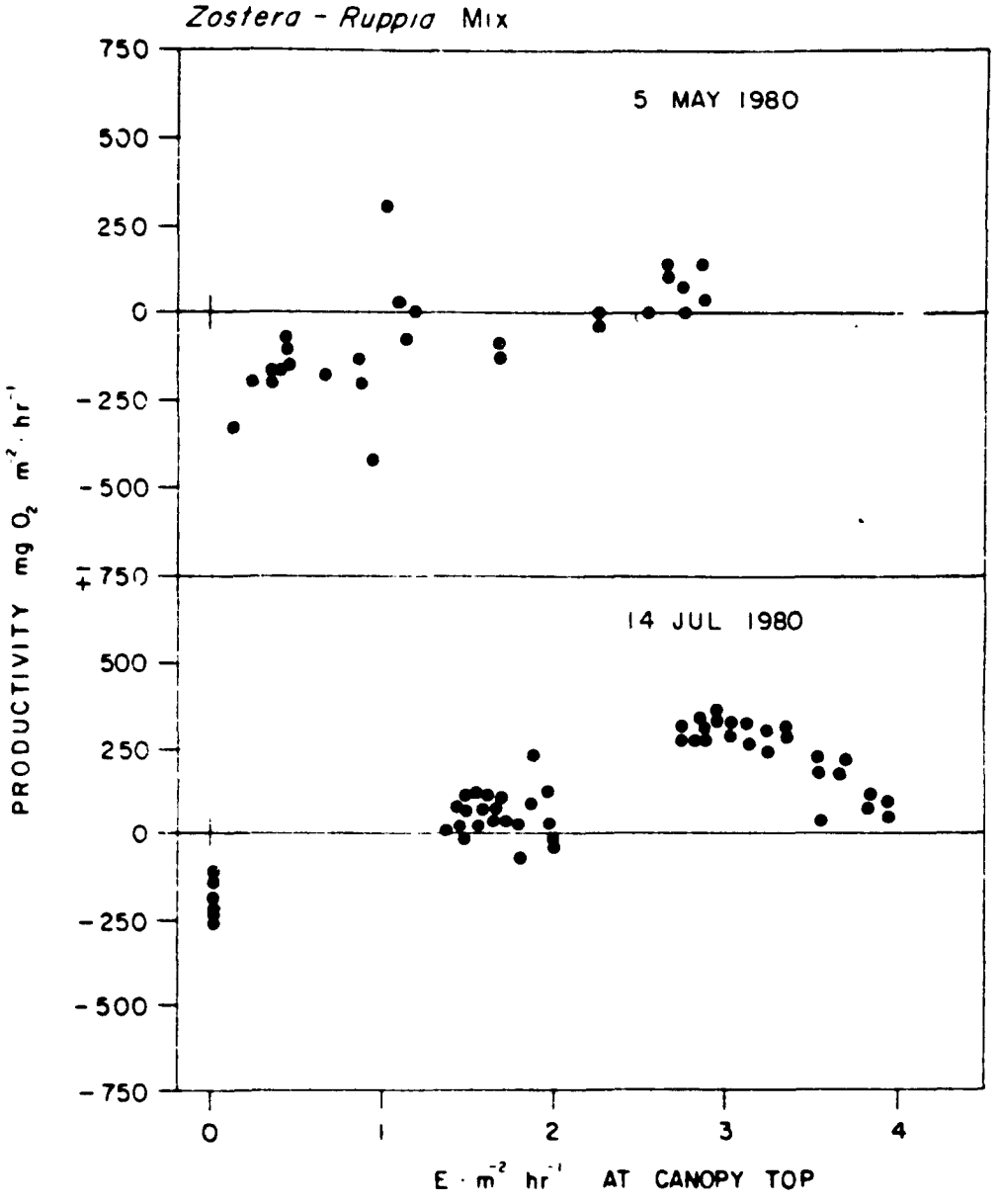


Figure 20. Scatter plot of net apparent rates of O_2 producitivity versus submarine light (PAR) reaching the plant canopy top in the co-dominated Z. marina and R. maritima community.

Orth et al. (1982) has provided a comprehensive and detailed account of the relative abundance and distribution of seagrass communities in the Lower Chesapeake Bay. The characteristic and predictable depth-dependant distribution and zonation patterns of the two dominate macrophyte species, Z. marina and R. maritima, a priori suggests significant differences in the physiological and production ecology of the two species.

The results of our studies indicate that Z. marina has a lower temperature optimum, greater photosynthetic efficiency and lower light requirements than R. maritima. At typical mid-summer water temperatures in shoal areas of the lower Chesapeake Bay (i.e. 28 to 30°C) Z. marina is temperature-stressed and in terms of total community metabolism is heterotrophic. Peak periods of productivity, spring and fall, correspond with optimum in situ light-temperature regimes. The interactive effect of increasing turbidity and water temperature in the late fall and early summer is suggested as the principal cause initiating the high summer plant mortality (die-back). In fact, the two, i.e. light regime and water temperature, may not operate in phase as controls on production and growth. For example, daily insolation and turbidity as estimated by mean vertical light (PAR) attenuation (Figures 3 and 4, respectfully) are the most variable during April and May when water temperatures are apparently near optimum. In early Summer, insolation and PAR attenuation are less variable but temperature becomes suboptimal. The interaction between these and their temporal behavior (or timing) may result in considerable year to year variation in biomass production and standing crop as indicated by Orth (personal communication, 1982). Assuming a mean daily insolation of 30 E m^{-2} day^{-1} (Figure 3) during the Spring growing season and a mean PAR attenuation coefficient of -1.50 (Figure 4) for the same period, average light intensity over a twelve hour photoperiod at a depth of 1.5 m (approximate mean depth of the Z. marina grassbed) would equal 155 μE m^{-2} sec^{-1} which is above the community compensation level but below the estimated photosynthesis light saturation intensity. These data suggest that the Z. marina community at the Vaucluse Shores study area may be light-stressed or at least growing under sub-optimal light regimes during a significant portion of the growing season. Because of the detailed similarily in structural characteristics of the Vaucluse area and other seagrass beds in the Lower Chesapeake Bay (see Chapter 1, this report; Orth et al, 1982), we assume that these conclusions are applicable to Z. marina dominated communities for the lower Bay in general. It seems apparent that Z. marina communities in terms of growth and survival in the lower Chesapeake Bay are existing under marginal environmental light and temperature conditions. This suggests that perhaps relatively small changes in either magnitude or temporal coincidence could result in significant changes in structural and/or functional aspects of their community ecology.

Compared to Z. marina, R. maritima productivity and growth response to light and temperature are nearly opposite. R. maritima photosynthesis-light response is characteristic of high-light or sun adapted species. The species is characterized by a generally higher Pmax, half-saturation light intensity, compensating light intensity and lower -value or less photosynthetic efficiency at low light intensities than Z. marina. Physiologically, R. maritima appears well-adapted to the high light-high temperature regimes characteristic of the shallow, inshore areas. Assuming a mean daily

insolation of 60 E m^{-2} day^{-1} during the summer growing season for R. maritima (Figure 3) and mean PAR attenuation coefficient of -1.25 (Figure 4) for the same period, average light intensity over a twelve hour photoperiod at a depth of 0.5 m (approximate mean depth of the R. maritima grassbed) would equal 750 μE m^{-2} sec^{-1}. This light intensity is photosynthetically saturating based on our results and suggests the R. maritima community is not generally light limited. These data coupled with the apparent high temperature tolerance of R. maritima suggests these communities in the nearshore areas are existing near optimum light and temperature conditions. However, this conclusion must remain tentative due to the apparent afternoon depression in O_2 productivity and our estimates of the various photosynthetic parameters being based only on morning and noon interval determinations. The characteristic apparent afternoon depression suggests a physiological stress either directly or indirectly related to temperature and/or light.

From the standpoint of the entire seagrass bed, production and metabolism within the dominant macrophyte communities are complimentary which tends to provide a source of organic matter production throughout the majority of the year even though the specific dynamics are very seasonal and different. In terms of production and because of these species-specific characteristics, the co-dominated communities probably represent the most trophically stable habitat.

Based on these results, light and temperature act as primary controls on seagrass photosynthesis and community metabolism. For Zostera marina, light or those factors that control submarine light regimes in the shoal benthic environment is singularly important in governing growth and survival of the species in the lower Chesapeake Bay.

Literature Cited

Aioi, K. 1980. Seasonal changes in the standing crop of eelgrass (Zostera marina L.) in Odawa Bay, Central Japan. Aquatic Bot. 8:343-354.

Backman, T. W. and D. C. Berilotti. 1976. Irradiance reduction: effects on standing crops of the eelgrass Zostera marina in a coastal lagoon. Mar. Biol. 34:33-40.

Beer, S., A. Eshel and Y. Waisel. 1977. Carbon metabolism in seagrasses. J. Exp. Bot. 106:1180-1189.

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., Tallahassee, Florida. 167 pp.

Bittaker, H. F. and R. L. Iverson. 1976. Thalassia testudinum productivity: a field comparison of measurement methods. Mar. Biol. 37:39-46.

Bowers, G., T. K. Van, L. A. Garrad and W. T. Hailer. 1977. Adaptation to low light levels by Hydrilla. J. Aquat. Plant Mgmt. 15:32-35.

Buesa, R. J. 1975. Population biomass and metabolic rates of marine angiosperms on the northwestern Cuban shelf. Aquatic Bot. 1:11-23.

Caperon, J., S. Allen Cattell and G. Krasnick. 1971. Phytoplankton kinetics in a subtropical estuary: eutrophication. Limnol. Oceanogr. 16(4):599-607.

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.

Congdon, R. A. and A. J. McComb. 1979. Production of Ruppia: Seasonal changes of dependence on light in an Australian estuary. Aquatic Bot. 6:121-132.

Conover, J. T. 1967. The importance of natural diffusion gradients and transport of substances related to benthic marine plant metabolism. Botanic Marina 11:1-9.

Dennison, W. 1979. Light adaptations of plants: A model based on the seagrass, Zostera marina L. M.S. Thesis, Univ. Alaska, Fairbanks. 70 pp.

Dillon, C. R. 1971. A comparative study of the primary productivity of estuarine phytoplankton and macrobenthic plants. Ph.D. dissertation, Univ. North Carolina, Chapel Hill, N. C. 112 pp.

Drew, E. A. 1979. Physiological aspects of primary production in seagrasses. Aquatic Bot. 7:139-150.

Fenchel, T. 1970. Studies on the decomposition of organic detritus derived from turtlegrass, Thalassia testudinum. Limnol. Oceanogr. 15:14-20.

Fenchel, T. 1977. Aspects of the decomposition of seagrasses, pp. 123-145. In: C. P. McRoy and C. Helfferich (eds.). Seagrass Ecosystems: A Scientific Perspective. Marcel Dekker, N. Y. 314.

Fonseca, M. S., J. S. Fisher, J. C. Zieman and G. W. Thayer. 1982. Influence of the seagrass Zostera marina L., on current flow. Est. Coastal Shelf Sci. 15:351-364.

Fraleigh, P. C. 1971. Ecological succession in an aquatic microcosm and a thermal spring. Ph.D. dissertation, Univ. Georgia, Athens. 128 pp.

Goering, J. J. and P. L. Parker. 1972. Nitrogen fixation by epiphytes on seagrasses. Limnol. Oceanogr. 17:320-323.

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

Iizumi, H. and A. Hattori. 1982. Growth and organic production of eelgrass (Zostera marina L.) in temperate waters of the Pacific coast of Japan. III. The kinetics of nitrogen uptake. Aquatic Bot. 12:245-256.

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

Keefe, C. W. 1972. Marsh production: a summary of the literature. Contri. Mar. Sci. 16:163-181.

Kikuchi, Taiji. 1980. Faunal relationships in temperate seagrass beds, pp. 153-172. IN: R. C. Phillips and C. P. McRoy (eds.). Handbook of Seagrass Biology: An Ecosystem Perspective, Garland STPM Press, N.Y. 353 pp.

Klug, M. J. 1980. Detritus-decomposition relationships, pp. 225-245. IN: R. C. Phillips, and C. P. McRoy (eds.), Handbook of Seagrass Biology: An Ecosystem Perspective, Garland STPM Press, N. Y. 353 pp.

Lindeboom, H. J. and B. H. H. deBree. 1982. Daily production and consumption in an eelgrass (Zostera marina) community in saline Lake Greveligen: discrepancies between O_2 and ^{14}C method. Delta Institute of Hydrobiological Research Special Report, Yerseke, The Netherlands. 24 pp.

Mann, K. H. 1972. Macrophyte production and aquatic food chains in coastal waters. Mem. 1st. Ital, Idrobiol. (Suppl.)29:353-383.

McRoy, C. P. 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. 17(1):58-67.

McRoy, C. P., J. J. Goering, and B. Chaney. 1973. Nitrogen fixation in association with seagrasses. Limnol. Oceanogr. 18(6):998-1002.

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. Helfferich (eds.). 1977. Seagrass Ecosystems: A Scientific Perspective. Marcel Dekker, N.Y 314 pp.

McRoy, C. P. and C. McMillan. 1977. Production ecology and physiology of seagrasses, pp. 53-88. IN: C. P. McRoy and C. Helfferich (eds.). Seagrass Ecosystems: A Scientific Perspective, Marcel Dekker, N.Y. 314 pp.

Nafziger, E. D. and H. R. Koller. 1976. Influence of leaf starch concentration on CO_2 assimilation in soybean. Plant Physiol. 57:560-563.

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

Neinhuis, P. H. and E. T. van Ierland. 1978. Consumption of eelgrass, Zostera marina by birds and invertebrates during the growing season in Lake Grevelingen, (SW Netherlands). Neth. J. Sea. Res. 12:180-194.

Neinhuis, P. H. and B. H. H. deBree. 1980. Production and growth dynamics of eelgrass (Zostera marina) in brackish Lake Grevelingen, (The Netherlands). Neth. J. Sea Res. 14:102-118.

Newell, S. Y. 1981. Fungi and bacteria in or on leaves of eelgrass (Zostera marina L.) from Chesapeake Bay. Appl. Environ. Microbiol. 41(5):

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

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

Odum, H. T. 1963. Productivity measurements in Texas turtle grass and the effects of dredging an intracoastal channel. Publ. Inst. Mar. Sci. Texas 9:48-58.

Odum, H. T. and G. M. Hoskin. 1958. Comparative studies on the metabolism of marine waters. Publ. Inst. Mar. Sci. Texas 5:16-46.

Ogden, J. C. 1980. Faunal relationships in Carribean seagrass beds, pp. 173-198. IN: R. C. Phillips and C. P. McRoy (eds.). Handbook of Seagrass Biology: An Ecosystem Perspective, Garland STPM Press, N. Y. 353 pp.

Orth, R. J. 1977. Effect of nutrient enrichment on growth of the eelgrass, Zostera marina in the Chesapeake Bay, Virginia, USA. Mar. Biol. 44:187-194.

Orth, R. J., K. A. Moore and Jacques van 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. EPA Chesapeake Bay Program, Annapolis, MD. 325 pp.

Patriquin, D. G. 1973. Estimation of growth rate, production and age of the marine angiosperm Thalassia testudinum. Mar. Biol. 15:35-46.

Patriquin, D. G. and R. Knowles. 1972. Nitrogen fixation in the rhizosphere of marine angiosperms. Mar. Biol. 16:49-58.

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 G. W. Thayer. 1980. Uptake and transfer of carbon and phosphorus by eelgrass (Zostera marina L.) and its epiphytes. J. exp. mar. biol. Ecol. 42:113-123.

Phillips, R. C. and C. P. McRoy (eds.). 1980. Handbook of Seagrass Biology: An Ecosystem Perspective. Garland STPM Press, N.Y. 353 pp.

Sand-Jensen, K. 1975. Biomass, net production asnd growth dynamics in an eelgrass (Zostera marina L.) population in Vellerup Vig, Denmark. Ophelia 14:185-201.

Spence, D. H. N. 1975. Light and plant response in freshwater, pp. 93-133. IN: G. C. Evans, R. Banbridge, and O. Rackhan (eds.). Light as an Ecological Factor. Blackwell Sci. Publ., Oxford 616 pp.

Strickland, J. D. H. and T. R. Parsons. 1972. A Practical Handbook of Seawater Analysis. Fish. Res. Bd. Canada Bull 167. 311 pp.

van Tine, R. F. 1981. Ecology of benthic seaweeds and seagrasses in a thermally impacted estuary of the eastern Gulf of Mexico, pp. 499-506. IN: G. E. Fogg and W. E. Jones, Proceedings of the Eighth International Seaweed Symposium. The Marine Sciences Laboratories (University of North Wales), Menai Bride, Isle of Anglesey, Gwynedd, U. K. 769 pp.

Westlake, D. F. 1967. Some effects of low velocity currents on the metabolism of aquatic macrophytes. J. Exp. Bot. 18:187-205.

Wetzel, R. L., K. L. Webb, P. A. Penhale, R. J. Orth, D. F. Boesch, G. W. Boehlert, and J. V. Merriner. 1979. The Functional Ecology of Submerged Aquatic vegetation in the Lower Chesapeake Bay. Interm Grant Report, U.S. EPA Chesapeake Bay Program, Annapolis, MD. 152 pp.

Wetzel, R. L., R. F. van Tine and P. A. Penhale. 1982. Light and Submerged macrophyte communities in the lower Chesapake Bay: A Scientific Summary. IN: R. L. Wetzel and R. F. van Tine (eds.). Structural and Functional Aspects of the Ecology of Sumberged Aquatic Macrophyte Communities in the Lower Chesapeake Bay, Vol. II, Draft Final Report, U. S. EPA Chesapeake Bay Program, Annapolis, MD.

Wheeler, W. N. 1980. Effect of boundary layer transport on the fixation of carbon by the giant kelp Macrocystis pyrifera. Mar. Biol. 56:103-110.

Wiginton, J. R. and C. McMillan. 1979. Chlorophyll composition under controlled light conditions as related to the distribution of seagrasses in Texas and the U. S. Virgin Islands. Aquatic Bot. 6:171-184.

Williams, S. L. 1977. Seagrass productivity: the effect of light on carbon uptake. M.S. Thesis. Univ. Alaska, Fairbanks. 95 pp.

Zieman, J. C. 1968. A study of the growth and decomposition of the seagrass Thalassia testudinum. MS. Thesis, Univ. Miami, Miami, Florida. 50 pp.

Zieman, J. C. 1975. Quantitative and dynamic aspects of the ecology of turtle grass, Thalassia testudinum, pp. 541-562. IN: L. E. Cronin (ed.), Estuarine Research, V. 1, Academic Press, N. Y. 738 pp.

Zieman, J. C. and R. G. Wetzel. 1980. Productivity in seagrasses: methods and rates, pp. 87-116. IN: R. C. Phillips and C. P. McRoy (eds.), Handbook of Seagrass Biology: An Ecosystem Perspective, Garland STPM Press, N. Y. 353 pp.

Zimmerman, R. J., R. Gibson and J. Harrington. 1979. Herbivory and detritivory among gammaridean amphipods from a Florida seagrass community. Mar. Biol. 54:41-48.

Chapter 3

OXYGEN METABOLISM OF A TEMPERATE SEAGRASS (*ZOSTERA MARINA* L.) COMMUNITY: PLANT-EPIPHYTE, PLANKTON AND BENTHIC MICROALGAE PRODUCTIVITY AND RESPIRATION.

L. Murray and R. L Wetzel

Virginia Institute of Marine Science
and School of Marine Science
College of William and Mary
Gloucester Point, VA 23062

ABSTRACT

Monthly studies of gross and net O_2 productivity and respiration by the principal autotrophic populations of a temperate, Zostera marina dominated seagrass community are reported. The principal components partitioned by the studies were the Z. marina-epiphyte assemblage, phytoplankton and benthic microalgae. Seasonally, the dominant autotrophic component varied. The macrophyte-epiphyte assemblage dominated when water temperatures were at or below 20°C while the plankton component dominated at higher temperatures. Benthic microalgae represented a relatively low but constant source of organic matter input. For both plankton and benthic microalgal communities, O_2 production and consumption are nearly mass balanced annually. However, approximately 40% of macrophyte-epiphyte production is available for transport. Integrated gross annual production and percent contribution to total community production are estimated at 967 gC m^{-2} y^{-1} (55%) for the macrophyte-epiphyte, 488 gC m^{-2} y^{-1} (31%) for phytoplankton, and 225 gC m^{-2} y^{-1} (14%) for benthic microalgae. Total gross autotrophic production in this temperate, Zostera marina seagrass community is estimated at 1580 gC m^{-2} y^{-1}. Of this approximately 600 gC m^{-2} y^{-1} are directly available for microheterotrophic and/or macroheterotrophic utilization and secondary production.

INTRODUCTION

The role and relative importance of seagrasses in estuarine and coastal marine environments has been the subject of recent extensive research. Seagrass meadows are generally considered valuable because they are characterized by high primary and secondary production and serve as nursery grounds and refuge areas for many marine and estuarine organisms. Most studies of autotrophic production in these communities have focused on the dominant vascular plants, Zostera marina L. in temperate zones and Thalassia testudinum Konig in the tropics, although other sources of autotrophic production can provide significant input of organic matter (Penhale 1977). Seagrass communities can have at least four other autotrophic components that directly support secondary production and are probably the least understood: benthic macroscopic and microscopic algae, phytoplankton, and epiphytic autotrophs.

Recent work on seagrass production has provided estimates ranging from 200-3000 gC m^{-2} yr^{-1} for Thalassia testudinum (Jones 1968; Bittaker 1975; McRoy & McMillan 1977) and 200-800 gC m^{-2} yr^{-1} for Zostera marina (Nixon & Oviatt 1972; McRoy 1974; Neinhuis 1980). Several methods have been employed to arrive at these estimates, including openwater flow studies (Nixon & Oviatt 1972), chamber incubations of various designs enclosing the intact community (Neinhuis 1980; Lindeboom & deBree 1982), the uptake of ^{14}C radiotracers by excised plants (McRoy 1974; Penhale 1977; Capone et al. 1979), leaf-marking techniques (Zieman 1974; Neinhuis 1980) and mathematical regression techniques using morphometric parameters (Patriquin 1973). Photosynthesis and respiration of both individual plants as well as the intact plant community have been investigated using various gas exchange methodologies (O_2 and CO_2) and ^{14}C radiotracers. Although these methods all measure something slightly different, the range of estimates among methods are surprisingly similar (Wetzel et al. 1982b).

Several investigators have demonstrated that autotrophs other than the macrophyte are responsible for a significant portion of total community production. Work in freshwater lakes indicated that phytoplankton and epibenthic algae contribute over 50% to total lake production (Wetzel 1964; Wetzel & Hough 1973). Cattaneo and Kaeff (1980) report that epiphytic algae on the freshwater angiosperms Myriophyllum spicatum L. and Potamogeton richardsonnii (Benn.) Rydb. contribute as much as 60% and 30%, respectively, to the total 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} or, combining the microalgae components, approximately 30% of the total. In North Carolina, Dillon (1971) estimated that Zostera marina and Halodule beaudettei (den Hartog) den Hartog production contributed approximetly 85% to the total organic matter input with phytoplankton making up the remainder. Bittaker (1975) reported for a Thalassia 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 macrophyte and epiphyte productivity in a North Carolina Zostera marina community bed were equal at certain times of the year and Borum & Wium-Anderson (1980) found similar results in Denmark.

Although these studies report high levels of production for the various autotrophs in these communities, consumption rates may also be high, especially in sediments having high faunal densities. Hargrave (1969) reports a higher benthic carbon consumption rate than can be supported by vascular plant production in a freshwater lake. Lindeboom & deBree (1982), found that although production is less for bare substrates than in nearby Zostera marina areas, consumption is also less, indicating a higher heterotrophic biomass within the grass beds. Considering, 1) a significant fraction of the vascular plant production may not be metabolically unavailable to many heterotrophs, 2) some plant material is undoubtedly exported and, 3) seagrass beds are generally characterized by high infaunal and epifaunal biomass, microalgal support of heterotrophic production may be greater than is generally suggested.

Based on these results and observations, it seems appropriate to hypothesize that significant contributions to community production by autotrophs other than the vascular plant are characteristic of submerged grass beds in both temperate and tropical ecosystems. The relative contribution appears to range between 20% and 50% of the total community. We report here, the results of studies designed to partition the principal autotrophic components of a temperate, Zostera marina dominated community in terms of seasonal and annual contributions to total community production and respiration. Because of a general lack of hard substrates in the Chesapeake Bay, macroalgae are not a significant portion of the autotrophic communities. Therefore we limited our studies to the plant-epiphyte, phytoplankton and benthic microalgae components.

STUDY SITE

A seagrass bed approximately 140 ha in size located on the southeastern shore of the Chesapeake Bay, Virginia, U.S.A. (37°25' N., 75°59' W.) was used as the principal study site (see Preface, Figure 1). The entire meadow is 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 studies reported here were carried out between transects B and C and confined to the Zostera marina dominated community type (See Preface, Figure 1).

MATERIALS AND METHODS

Total Community O_2 Exchange

Oxygen exchange techniques were used to estimate rates of metabolism for the various autotrophic components. Estimates of total community metabolism employed large (260 l) plexiglass domes enclosing the entire seagrass

community (see Chapter 2). Oxygen concentration was monitored continuously for all incubations. These data were used to calculate areal net apparent production (NAP), respiration (R), and gross apparent production (GAP) for the intact community.

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 employs thermistors contained in the probe head.

Area specific rates were calculated as:

$$\text{mg } O_2\ m^{-2}\ h^{-1} = \frac{[C_{i+1}-C_i]}{\Delta t(t_{i+1}-t_i)} \cdot V_d \cdot A_d^{-1}$$

where: $C_i = [O_2]$ (mg l^{-1}), i=0,1...n (hours)
t_i = time (hours) i^{th} interval
V_d = volume of incubation (l)
A_d = bottom surface area (m^2)

Daily rates were calculated by integrating the net apparent O_2 productivity hourly rates over the photo-period and respiration was assumed constant over the 24 hour period. Seasonal estimates were derived by defining "season" as a function of water temperature with winter <10°C; spring and fall 10 to 20°C and, summer >20°C. Seasonal estimates were calculated as the algebraic sum using means between consecutive (monthly) estimates. Because the relative error is directly proportional to time step (i.e. calendar days between rate estimates) for these calculations, for the data we report the winter estimates are the least reliable. Annual estimates are simply the sum of the seasonal estimates. For comparison to data reported elsewhere, we converted the oxygen data to carbon units assuming a PQ of 1.25 for the net productivity estimates and a RQ of 1.0 for the respiration estimates.

Water Column (Plankton) O_2 Exchange

Water column plankton community samples were collected by hand and incubated in triplicate, light and dark standard BOD bottles (300 ml). Incubations were for four hours over the daytime interval 1000 to 1400 h. For midday high tide studies, water depth at the 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. For these studies, only mid-depth water samples were collected and incubated. Water column rates are reported per square meter surface area and calculated using the average water depth over the incubation interval. Daily rates were estimated by assuming the mean, midday hourly rates were characteristic for the photoperiod and respiration rates determined from the dark BOD bottle incubations were constant over the

diel period. Seasonal and annual estimates were calculated as for the total community.

Benthic O_2 Exchange

For the benthic microalgae triplicate, light and dark, cylindrical plexiglass chambers (750 ml) were placed on unvegetated sediment within the bed and incubated as for the BOD bottles. Duplicate clear chambers inoculated with 10 ml, 10% (v/v) buffered seawater formalin (sat. $MgCO_3$) were used to estimate sediment, chemical oxygen demand (COD). O_2 exchange estimates, corrected for COD, are reported as $mgO_2\ m^{-2}$ (bottom area) h^{-1}. The amount of unvegetated area within the Z. marina community was estimated from percent cover data (Orth and Moore 1982) and the areal rate estimate corrected accordingly. Daily, seasonal, and annual rate estimates followed the methods and assumptions for the water column calculations.

Macrophyte-Epiphyte O_2 Exchange

Rate estimates for the plant-epiphyte component were calculated as the difference between total (dome enclosure estimates) and the benthic and plankton rates estimated over the same time intervals. Respiration for the plant-epiphyte component was calculated as the difference in nighttime respiration for the clear dome incubations and rates for the dark chamber and BOD bottle daytime incubations.

RESULTS

Table 1 summarizes environmental conditions for each date studies were conducted. The studies covered the nominal water temperature range for the area (see Chapter 2). For these specific studies, submarine light (PAR) conditions were generally at or above photosynthetically saturating intensities for both vascular plant and microalgae except for Z. marina during the April, early October and January studies. The studies encompass the major growth and die-back periods for this vascular plant community.

Net apparent productivity estimates for the three, principal components over the study period are presented in Figure 1. The Z. marina-epiphyte component follows the characteristic, bi-modal growth cycle for Zostera marina in Chesapeake Bay waters (Orth and Moore, 1982; Chapter 2). The arrows on the figure indicate rate estimates calculated from oxygen exchange studies carried out under suboptimal light conditions (i.e., less than known saturating intensities) and are therefore probably underestimates. Over the period of study, the dominant component is illustrated in the figure by diagonal line shading for the plant-epiphyte component and stippled shading for the plankton component. Winter, spring and late fall are clearly dominated by the plant-epiphyte component and during mid-summer by the phytoplankton with a possible secondary fall peak. Benthic algae generally had lower net apparent rates (note scale change in Figure 1) with no clear seasonal pattern indicated.

TABLE 1. EXPERIMENTAL CONDITIONS AT THE VAUCLUSE SHORES STUDY SITE FOR IN SITU O_2 COMMUNITY METABOLISM STUDIES ARITHEMATIC MEAN OVER THE INCUBATION INTERVAL.

Date	Incubation Interval (EST)	Temp °C	PAR ($\mu E\ m^{-2}\ sec^{-1}$) Surface	PAR ($\mu E\ m^{-2}\ sec^{-1}$) Bottom	Plant Biomass[1] (g dry weight m^{-2})	Plant Cover[2] (%)
3/10/81	1150-1550	8.0	-	266	n.d	n.d
4/9/81	1115-1345	14.	396	104[3]	n.d	n.d
5/8/81	1120-1332	16.	1860	275	95.9	93
5/22/81	1015-1430	18.	1664	395	80.5	85
6/15/81	1030-1430	26.	1593	323	116.	100
7/13/81	1030-1430	33.	1183	266	61.8	70
8/4/81	1220-1525	27.	1645	294	61.0	69
8/25/81	0950-1345	26.	1650	285	18.7	28
10/13/81	1050-1400	20.	1204	125[3]	24.3	33
10/22/81	1055-1455	16.	1191	222	n.d	n.d
1/6/82	1020-1350	7.0	348	132[3]	n.d	n.d

1. 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.

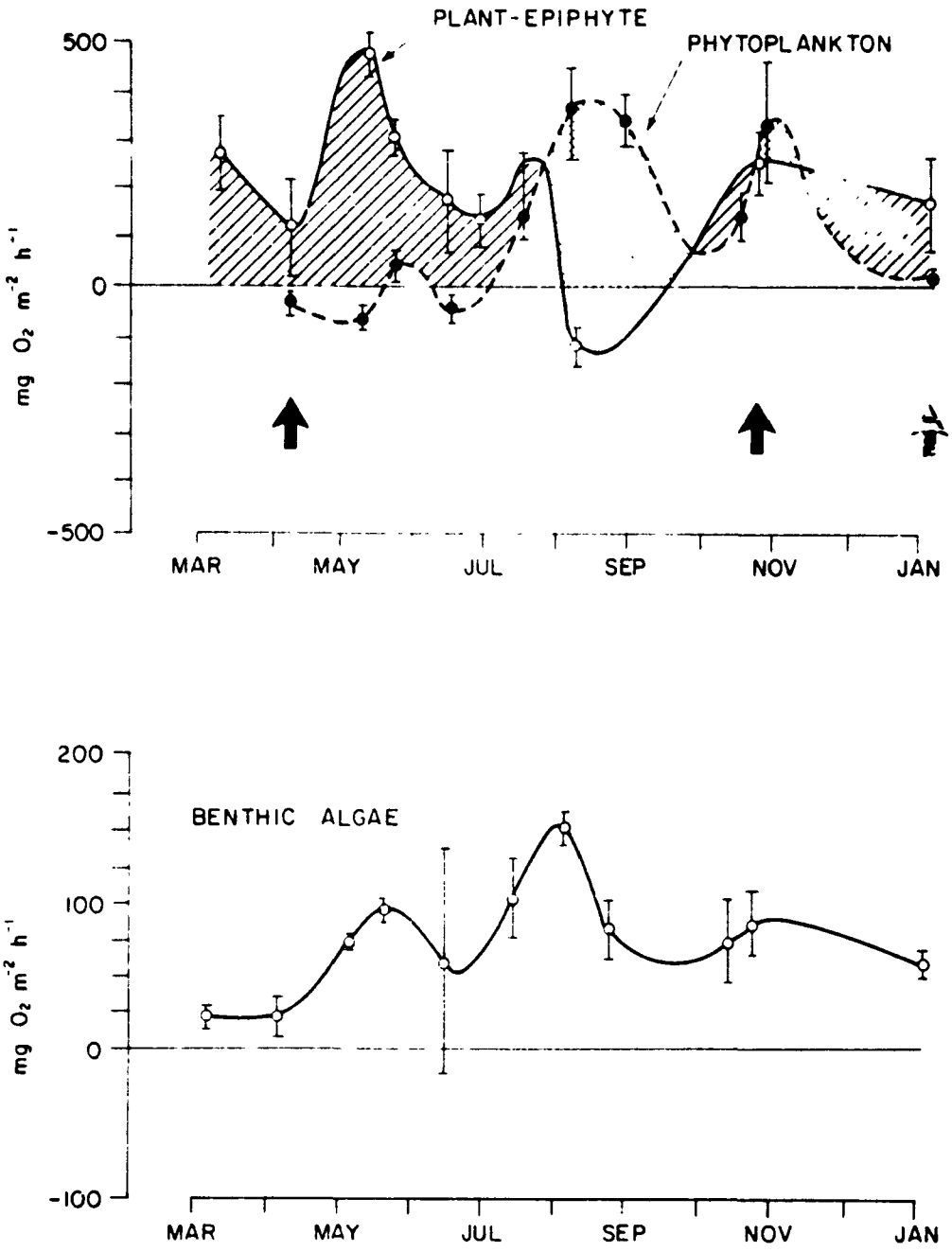


Figure 1. Mean (± S.D.) net apparent productivity for the plant-epiphyte and plankton components (top panel) and benthic component (bottom panel). Diagonal line shading and stippled shading in the top panel illustrate plant-epiphyte or plankton dominance respectively. The arrows indicate suboptimal light conditions for Z. marina.

Figure 2 presents the respiration estimates for the three components. Respiration of the plant-epiphyte component generally tracked net apparent productivity increasing with increasing water temperature. Plant-epiphyte respiration paralleled plant growth and dominated total community respiration during and following the summer die-back period and again in late fall during the secondary growth period. 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. As for net apparent productivity, benthic respiration rates were generally lower than either the plant-epiphyte or plankton components and paralleled benthic net apparent productivity estimates.

Gross apparent productivity (calculated as the algebraic sum of net apparent (Figure 1), and respiration, (Figure 2) rate estimates) is illustrated in Figure 3. The plant-epiphyte component dominates prior to late summer (August) followed by an apparent dominance by the phytoplankton in late summer and fall. Benthic gross productivity never dominated total community gross productivity but reached maximum rates during the summer.

Table 2 summarizes the seasonal and annual estimates of gross production and respiration. Because of our assumptions in the calculations, i.e. microalgae midday rates are extrapolated over the entire photoperiod and respiration is constant 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 important and potential contribution made by each to total community metabolism. Based on these calculations gross production by the plant-epiphyte component accounted for between 37% and 80% of total dependent on season. Annually the vascular plant component contributed an estimated 967 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. Similarly, benthic algae contribution ranged between 10% and 25% seasonally with an estimated annual contribution of 225 gC m^{-2} or 14% of the total. Using these estimates of annual gross production by this seagrass community is 1580 gC m^{-2}. The microautotrophic components account for approximately 45% or 713 gC m^{-2} of this.

Respiration by the various components varied seasonally. The plant-epiphyte component 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 we consider an overestimate due principally to the few estimates we have; i.e. only two studies were conducted at water temperatures below 10°C. Benthic respiration never dominated total community respiration and accounted for 9% to 23% over all seasons. Maximum rates and % contribution to total occurred during the summer.

Production to respiration ratios (P/R) indicate the generally autotrophic nature of each component. Both seasonally and annually, total community metabolism was autotrophic. P/R ratios ranged from a maximum of 6.2 for the plant-epiphyte component in winter to a minimum of 0.50 for the plankton in spring. In terms of organic matter input to the seagrass community (i.e. excess production versus respiration), the plant-epiphyte component clearly

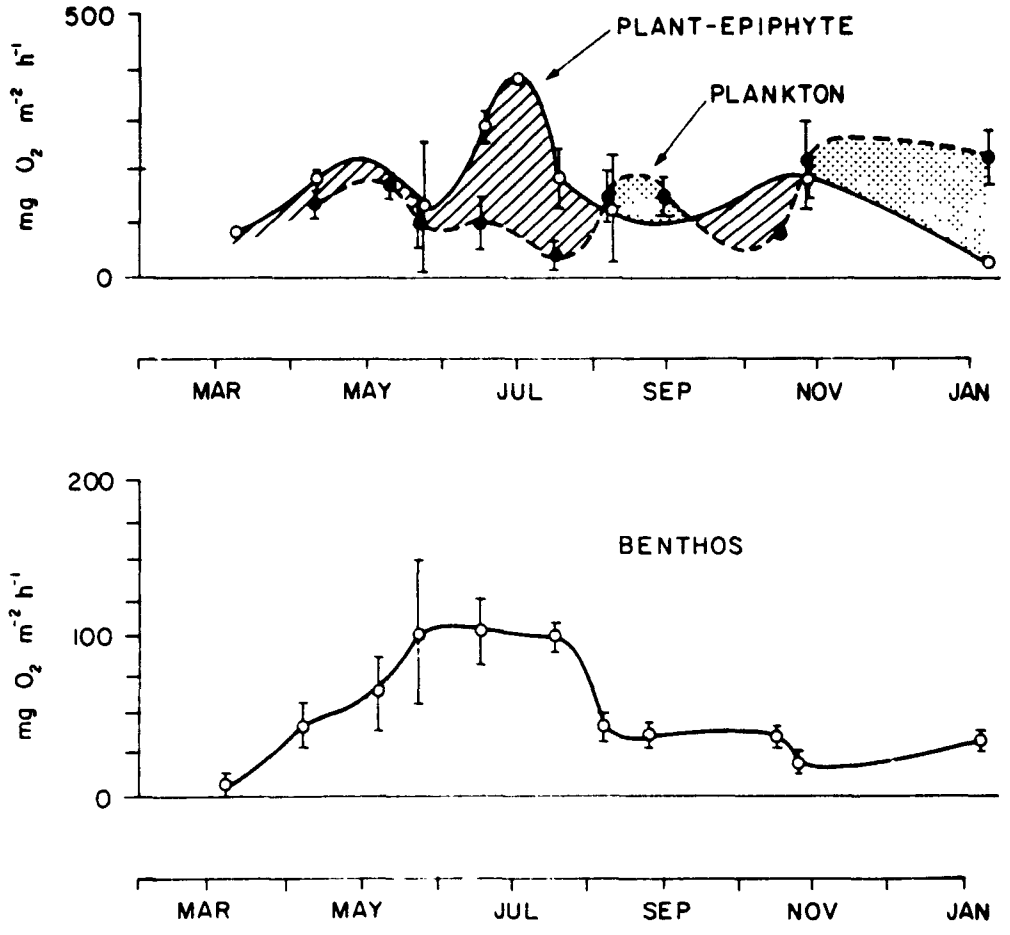


Figure 2. Mean (± S.D.) respiration for the plant-epiphyte assemblage and plankton components (top panel) and benthic component (bottom panel). Diagonal line shading stippled in the top panel illustrate plant-epiphyte or plankton dominance respectively.

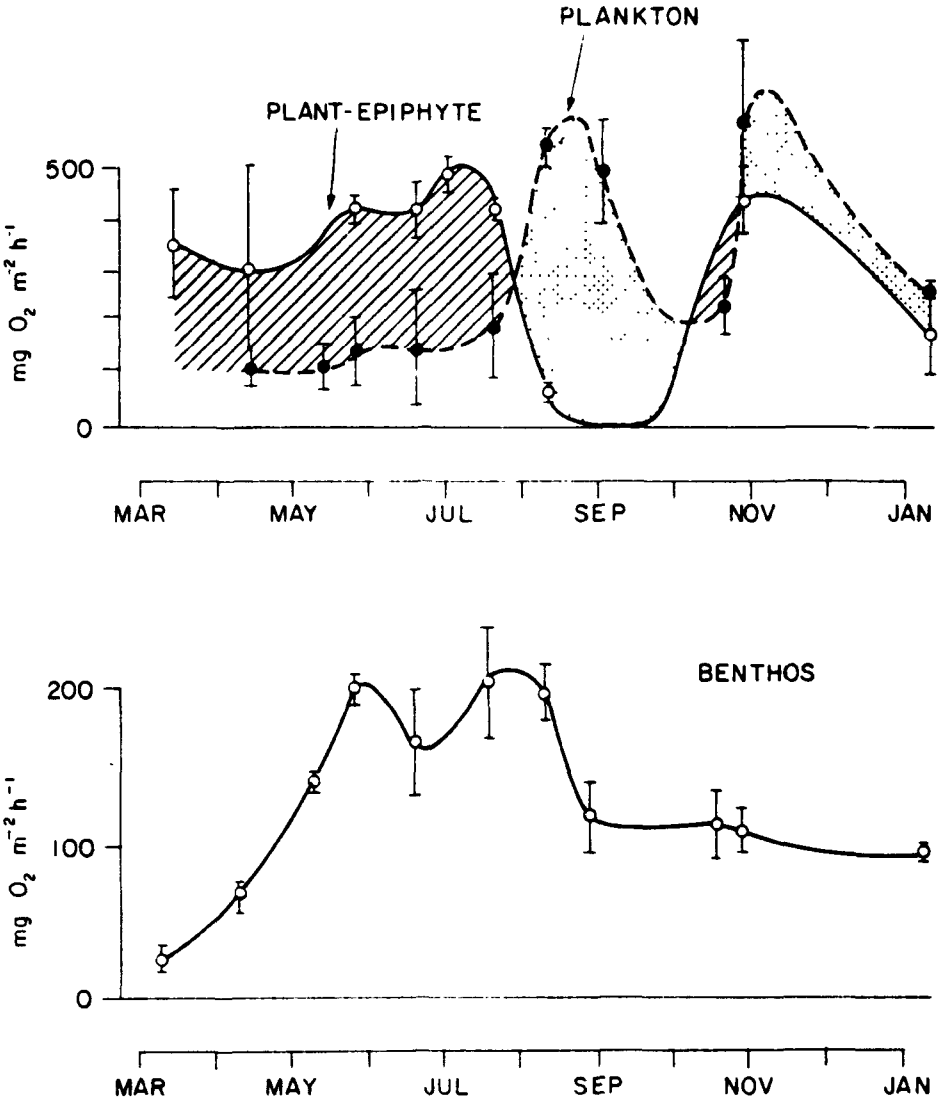


Figure 3. Mean (± S.D.) gross apparent productivity for the plant-epiphyte assemblage and plankton components (top panel) and benthic component (bottom panel). Diagonal line shading and stippled shading in the top panel illustrate plant-epiphyte or plankton dominance respectively.

TABLE 2. INTEGRATED SEASONAL AND ANNUAL ESTIMATES OF GROSS PRODUCTION (P) AND RESPIRATION (R) ($gC\ m^{-2}$) BY THE PRINCIPAL COMPONENTS AND TOTAL COMMUNITY IN A TEMPERATE, Z. MARINA DOMINATED SEAGRASS COMMUNITY.

	Component	Winter P	Winter R	Spring P	Spring R	Summer P	Summer R	Fall P	Fall R	Annual Total P	Annual Total R	Annual Total 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		

dominates in the winter and spring, the plant-epiphyte and plankton in summer and the plankton and benthic components in fall. The actual timing (i.e. availablity) however differs due to the time lag between vascular plant production and organic matter input (plant mortality). For the microalgal dominated components, production and consumption are both spatially and temporally more closely linked.

The metabolism data were further analyzed by simple, pair-wise linear regression between selected environmental parameters (temperature and light) and vascular plant community characteristics (biomass and cover). Table 3 summarizes these results in terms of the correlation coefficients for the pair-wise regressions. As expected, respiration was significantly correlated with temperature for all benthic components. Net productivity was positively correlated with temperature for both plankton and benthos but only significantly so for the latter. Net apparent productivity of the plant-epiphyte complex and temperature was negatively and weakly correlated. This result is consistent with other observations indicating that Z. marina is stressed at temperatures approaching 30°C (see Chapter 2). As indicated, earlier, light was optimum for the majority of these experiments and is supported by the lack of significant correlation between light and net apparent productivity.

Plant biomass and plant-epiphyte respiration was positively correlated as expected. Interestingly benthic respiration and plant biomass were highly correlated. This result suggests a strong interaction between vascular plant growth and sediment heterotrophic processes. There was no apparent correlation between benthic net apparent productivity and percent plant cover as might be suggested by the observation that vascular plant shading may limit benthic microalgae photosynthesis. The result may also be an artifact of the experimental design in that areas within the grass bed were chosen where obviously the benthic chambers could be placed. Also, the measured light levels are for 10 cm above the sediment surface due to the underwater sensor design and thus may not accurately measure light at the actual sediment surface.

DISCUSSION

Productivity and organic matter production in vascular plant dominated submerged aquatic communities is divisable into at least four components whose importance and contribution may vary both spatially and temporally. These are the plant-epiphyte, benthic microscopic and attached 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 and govern conditions within which other processes, both autotrophic and heterotrophic, must operate. However, functional attributes of the ecosystem such as productivity, nutrient cycing 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 Z. marina dominated habitat.

TABLE 3. SIMPLE LINEAR REGRESSION CORRELATION COEFFICIENTS FOR PAIR-WISE LEAST SQUARES ANALYSIS OF SELECTED ENVIRONMENTAL PARAMETERS AND PLANT COMMUNITY CHARACTERISTICS AND COMPONENT O_2 METABOLISM; 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 (°C)	-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)	0.13	0.81*	-	-	0.06	0.76*
4. % Cover (m^{-2})	-	-	-	-	0.04	-

* Significant @ =0.05
** Significant @ =0.10

The Plant-Epiphyte Community

Phillips (1974) reported a production range of 10 to 1200 g dry plant biomass m^{-2} y^{-1} for temperate grass flats. Assuming a mean % carbon (dry biomass) of 36.4 (see Chapter 2), the range would be approximately 3.6 to 437 gC m^{-2} y^{-1}. More recent annual estimates for temperate eelgrass communities comparable to our study area report 350 gC m^{-2} for Z. marina in a North Carolina grass bed (Thayer et al. 1975). Using Penhale's estimates (Penhale 1977) for vascular plant and epipyte productivity for the same eelgrass ecosystem, plant-epiphyte annual production would equal 402 gC m^{-2}. Penhale's estimates were based on ^{14}C uptake experiments. If, as Bittaker & Iverson (1976) report, ^{14}C estimates net carbon fixation and as Lindeboom & deBree (1982) suggest, ^{14}C may underestimate gross productivity by 50% for these seagrasses, Penhale's estimate is very similar to our plant-epiphyte annual net production estimate of 452 gC m^{-2} (Table 2). This suggests that respiratory demand by this autotrophic component is dominated by the vascular plant and would equal approximately 48% of annual gross production. Orth and Moore (1982) report data from our study area on aboveground plant standing crop over 16 consecutive months covering two yearly growing seasons. Using their aboveground biomass data and the reported mean aboveground to root/rhizome biomass ratio of 1.0 (Chapter 2), net production in the Z. marina dominated community would equal approximately 264 gC m^{-2}. If we assume that the difference between our estimate and Orth et al. (187 gC m^{-2}) represents leaf mortality, then approximately 41% is potentially available for transport out of the seagrass system. For the 70 ha Z. marina bed at our study site, export could provide approximately 130 metric tons of carbon per year to contiguous waters.

The plant-epiphyte component dominates total community metabolism in winter, spring and early summer with the highest respiratory demands occurring after the spring growing season. The significant correlations between aboveground plant biomass and respiration of the plant-epiphyte, and benthic components (Table 2) suggests a strong, direct interaction between macrophyte and sediment metabolism. Based on the work of Wetzel and Penhale (1979) the two most likely mechanisms appear to be gas transport, primarily O_2, to the rhizosphere supporting aerobic, microheterotrophic processes and/or extracellar release of dissolved compounds by the root/rhizome system during the warmer months. This tentative explanation is in part supported by sediment ATP studies reported elsewhere (see Chapter 2) which indicate that both the depth distribution (g ATP cc^{-1}; 0 to 30 cm depth) and total concentration (μg ATP m^{-2}) parallel the general bi-modal growth pattern of Z. marina at this study site. However, even if all respiratory demand of the plant-epiphyte and benthic components are supported by aerobic oxidation of vascular plant organic matter, a significant fraction of plant production must be lost to burial or exported from the system for the component to be mass balanced. Based on the comparison between harvest data (Orth and Moore, 1982 and our rate estimates, we suggest at this point that a possible major route is tidally-mediated, advective transport.

The Plankton Community

Comparative investigations of phytoplankton productivity and plankton community dynamics in shoal and shallow tidal areas of estuaries are,

surprisingly, relatively few. Most estuarine phytoplankton research has been concentrated in the deeper, openwater areas. For the Chesapeake Bay, a reasonable annual production estimate would appear to fall in the range 100 to 200 gC m^{-2} (Patten et al. 1963; Flemer 1970; Haas 1975; McCarthy et al. 1975). Our gross annual estimate of 488 gC m^{-2} in the seagrass bed (Table II) suggests that either these habitats have significantly greater phytoplankton production than adjacent open-water areas or our estimates are biased by the winter season values.

At the present we have only limited and indirect evidence to support either of the above. 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 algae. Our estimate of 31% using the same principal components agrees very well with their preliminary assessment. Independent measures of phytoplankton photosynthesis from our 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 our range of values for net apparent productivity (77 to 225 mg C m^{-2} h^{-1}) using oxygen. Also, based on the ^{14}C studies, the principal component of the phytoplankton are the nanoplankton (15 m and less) which account for 67 to 83% of ^{14}C photosynthesis and 43 to 100% of the chlorophyll a standing stock (Wetzel et al., 1979). Our tentative conclusion is that phytoplankton photosynthesis and production is generally increased in these shallow water habitats. This effect, if confirmed by further investigation, likely results from the phytoplankton residing in more favorable light conditions throughout the photoperiod, e.g. using the ^{14}C data reported by Wetzel et al. (1979), I_k = 86 μE m^{-2} sec^{-1} (SD±12, n=8) which is lower than typical ambient conditions throughout the shallow water column. The higher plankton productivity may also result from more favorable nutrient conditions due to high remineralization rates (e.g. Nixon 1981) and spatial juxtaposition between photosynthesis and nutrient regeneration in the seagrass bed.

Seasonally, plankton production compliments the plant-epiphyte component. Plankton metabolism dominates the total from mid-summer through early fall when the vascular plants are dying back. During the second fall growth period both components contribute approximately equally to total community metabolism. However, on an annual basis plankton respiration and gross production are approximately balanced; 488 versus 434 gC m^{-2}, respectively. If we assume, as a maximum, autotrophic respiration is 10% of gross production, then phytoplankton production supports a relatively large planktonic heterotrophic community. The annual P/R ratio of 1.1 suggests that production and consumption are tightly coupled over an annual cycle within the plankton component and are dynamically quite different than the plant-epiphyte component.

The Benthic Algal Community

Due to the general lack of hard substrates in Chesapeake Bay, benthic primary production is dominated by sediment microalgae. Annual estimates of production for a variety of sediment types generally range between 100 and 200 gC m^{-2} (Pomeroy 1959; Grontved 1960; Pamatmat 1968; Marshall et al. 1971;

Riznyk and Phinney 1972; Cadee and Hegemen 1974, 1977; Gallagher and Daiber 1974; 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 geographical 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), our annual estimate of 225 gC m^{-2} is consistent with these data. We estimate that the benthic microalgae contribute approximately 14% to total annual production which is approximately two fold greater than Thayer et al. (1975) estimate of 8%.

Seasonally, benthic productivity and respiration represent a relatively constant proportion of the total. As for the plankton community, respiration appears dominated by microheterotrophs. The apparent discrepancy between benthic annual gross production and respiration probably results from our respiration measures omitting macroheterotrophic contribution, i.e. amphipods, isopods and other motile, small mollusc and crustaceans probably escaped enclosure by the benthic chambers. Orth and van Montfrans (1982) report densities of individuals in these groups from 1.0×10^4 to over 1.0×10^6 m^{-2}. Therefore, benthic production and consumption are probably more closely balanced than suggested by our estimates.

SUMMARY

Total community metabolism of a temperate, Zostera marina seagrass community is both structurally (i.e., principal components involved) and temporally partitioned among the seagrass-epiphyte assemblage and the planktonic and benthic microalgae. There is a remarkably similar division in terms of percent contribution to estimated annual values for both Chesapeake Bay and North Carolina systems where the principal structural component, Z. marina, exists near its southern range limit. The data suggest that for gross annual production, the vascular plant-epiphyte complex contributes between 50 and 60% to the total, the plankton, 30% and the benthic algae 10 to 25%.

Respiration balances production for the plankton and more than likely for the benthic community. Assuming that microalgae respiration, both benthic and planktonic, is 10% or less of gross production, the data indicate that heterotrophs dominate respiratory metabolism and more than likely directly graze the autotrophic component. Therefore, coupling between production and consumption in these two subsystems is quite different than the plant-epiphyte component and probably supports secondary production to a greater extent than suggested by standing stock estimates alone.

Our results also suggest that failure to include microalgae in estimates of community productivity and respiratory processes might well result in significant underestimates of total primary production in seagrass meadows and omit components that may support heterotrophic processes equal to or perhaps greater than the direct vascular plant contribution. The generality of this conclusion awaits further and certainly more detailed study (particularly with reference to temporal scales). However, qualitatively the conclusion appears

warranted for many seagrass ecosystems and where comparative data do exist, our findings are consistent.

ACKNOWLEDGEMENTS

We would like to express our appreciation to those who aided directly in conducting these studies; Frederick Hoffman, Ann Evans, M. E. Bender and R. F. van Tine. The cooperation and land use provided by Jack Watts, Donald Hammond and Lloyd Outen is also greatly appreciated. We thank Drs. K. L. Webb, P. A. Penhale and R. J. Orth, for their reviews and insightful comments made in manuscript preparation. Especial thanks are due M. Castagna, J. Kraeuter and J. Moore of VIMS, Eastern Shore Laboratory, Wachapreague, Virginia for their many and varied contributions in support of these studies. Financial support for these studies was provided by grants to R. L. Wetzel from the U. S. Environmental Protection Agency, Chesapeake Bay Program, Grant nos. R805974 and X0003245-1 and the Virginia Institute of Marine Science, Gloucester Point, Virginia.

LITERATURE CITED

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., 167 pp.

Bittaker, H. F. and R. L. Iverson. 1976. Thalassia testudinum productivity a field comparison of measurement methods. Mar. Biol. 37:39-46.

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

Cadee, G. C. and J. Hegeman. 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. Hegeman. 1977. Distribution of primary production of the benthic microflora 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. Kaeff. 1980. The relative contribution of aquatic macrophyte and their epiphytes to the production of macrophyte beds. Limnol. Oceanogr. 25:280-289.

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

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

Gallagher, J. L. and F. C. Daiber. 1974. Primary production of edaphic algal communities in a Delaware salt marsh. Limnol. Oceanogr. 19:390-395.

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

Hass, L. W. 1975. Plankton dynamics in a temperate estuary with observations on a variable hydrographic condition. Ph.D. Thesis, College of William and Mary, 202 pp.

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

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, 196 pp.

Lindeboom, H. J. and B. H. H. deBree. 1982. Daily production and consumption in an eelgrass (Zostera marina) community in saline Lake Grevelingon: discrepancies between the O_2 and ^{14}C method. Report to Delta Institute of Hydrobiological Research, Yerseke, The Netherlands, 24 pp.

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.

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

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

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

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. Neilson and L. E. Cronin (eds.), Nutrient Cycling in Estuaries, Humana Press, Clifton, N.J.

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, M.D., U.S.A., 195 pp.

Pamatmat, M. M. 1968. Ecology and metabolism 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, G. C., R. A. Mulford, and J. E. Warriner. 1963. An annual 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.

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.

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

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

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

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

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

Wetzel, R. L., R. F. van Tine, and P. A. Penhale, 1982b. Light and submerged macrophyte communities in the Chesapeake Bay: A scientific summary. SRAMSOE 260, Virginia Institute of Marine Science, Gloucester Point, VA., U.S.A., 58 pp.

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

Wetzel, R. G. and R. A. Hough. 1973. Productivity and role of aquatic macrophytes in lakes: an assessment. Pol. Arch. Hydrobiol. 20:9-19.

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

Zedler, 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 4:39-143.

Chapter 4

PRELIMINARY OBSERVATIONS ON NUTRIENT ENRICHMENT AND LIGHT REDUCTION EFFECTS ON *ZOSTERA MARINA* L. EPIPHYTIC GROWTH

L. Murray and R. L. Wetzel

Virginia Institute of Marine Science
and School of Marine Science
College of William and Mary
Gloucester Point, VA 23062

ABSTRACT

The short-term effects (two weeks) of nutrient enrichment and ambient light (PAR) reduction on Zostera marina epiphytic growth was evaluated using a flow-through aquaria system with transplanted, epiphyte-free (scraped) plants collected from a nearby seagrass meadow in the lower Chesapeake Bay. Nutrient effects (ambient, 30 and 70 times ambient) resulted in a twofold increase in epiphyte biomass. Light reduction (ambient and ca. 50% reduction) also resulted in a positive growth response by the epiphytic community. There was a significant, positive interactive effect between nutrient enriched and light reduction treatments. Light attenuation due to epiphyte growth ranged from approximately 45% to greater than 70% for a low light-high nutrient treatment. Attenuation of this degree is sufficient to reduce light available for macrophyte photosynthesis to a range reported as compensating intensities for Zostera marina. By the end of the experiment, epiphytic microalgae accounted for greater than 90% of both gross and net apparent productivity estimates in the high-nutrient, low-light treatment. The combined effects of increased nutrients and reduced light favor epiphytic growth in the absence of other controls (i.e. grazing and alleopathy). This results in decreased macrophyte productivity and growth and overtime, would eventually lead to plant mortality.

INTRODUCTION

The interactions between submerged aquatic macrophytes and associated epiphytes range from nutrient transfer relationships (Harlin 1973, 1975; McRoy and Goering 1974; Wetzel and Penhale 1979) to epiphytic light attenuation (Sand-Jensen 1977). Sand-Jensen (1977) suggested that shading due to epiphytic growth on blades of the eelgrass, Zostera marina, inhibited 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. Algal populations generally exhibit rapid and increased growth with nutrient enrichment (Welch et al. 1972; Ferguson et al. 1976) and, for eelgrass, epiphytic growth consists primarily of diatoms and filimentous algae (Sieburth and Thomas 1973; van Montfrans et al. in press). Thus, the interactive 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. Sand-Jensen and Sondergaard (1981) working in lakes of varying nutrient levels reported that epiphytic growth increased 200 times in lakes ranging from low to high ambient nutrient concentrations. These authors concluded that increased epiphytic growth could ultimately lead to mortality of the macrophyte due to extremely reduced light availabe for macrophyte photosynthesis. The studies also reported low phytoplankton concentrations corresponding with nutrient enrichment and suggested that the phytoplankton are outcompeted by attached, epiphytic algae and played a minor role in water column light attenuation.

Photosynthetically, light saturation ranges from ca. 200-300 $\mu E\ m^{-2}\ sec^{-1}$ for Z. marina (McRoy 1974; Penhale 1977; Chapter 2). For a Z. marina bed in the lower Chesapeake Bay, mean daily in situ light intensity during the early groing season is below this range although the data are quite variable (Chapter 2). Thus, reduction in ambient light levels by 80% due to epiphyte attenuation as suggested by Phillips et al. (1978) and Sand-Jensen and Sondergaard (1981) would lead to plant mortality. Furthermore, diatoms, (the principal epiphytic component on Chesapeake Bay seagrasses (van Montfrans et al., in press; Murray, unpubl. data) exhibit photosynthetic light saturating intensities (20-50 $\mu E\ m^{-2}\ hr^{-1}$) much lower than Z. marina (Taylor 1964; Ignatiades and Smayda 1970; Levin and Mackas 1972; and Admiral 1977), indicating a significantly lower light requirement and a competitive advantage under reduced light regimes.

Although epiphytic growth may potentially decrease macrophyte photosynthesis, total community productivity may remain high. The result may be a shift from macrophyte-dominated to epiphyte-dominated productivity as

long as the macrophytes are able to survive. The interactive effects of increased nutrients and reduced light, although negative relative to macrophyte photosynthesis, may, overall, result in stimulation of autotrophic production in these communities due to increase microalgae biomass and productivity.

Based on these hypothetical and to some extent, demonstrated, interactions, our studies were undertaken to 1) investigate epiphyte growth on Zostera marina leafs under controlled nutrient and light levels, 2) estimate light attenuation due to epiphytic growth on the leaf surface, and 3) estimate the productivity of the macrophyte and epiphyte components under controlled nutrient and light regimes.

METHODS AND MATERIALS

Experimental Design

Zostera marina plants were collected from a mesohaline area of the York River subestuary of the Chesapeake Bay. Plants were returned to the laboratory and cleaned of epiphytic growth by gently scraping the leaf surfaces with a flat spatula and then individually planted in pots containing cleaned sand. Twenty-four individually potted plants were placed in each of six, 10 gallon flow-through aquaria. The aquaria were incubated on a larger, flowing sea water table to maintain ambient temperature. The following experimental treatments were used: two aquaria (numbers 1 and 2) had in situ (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 and tank concentrations were maintained by metering stock solutions of 47 mM ammonia nitrate and 6 mM disodium phosphate into the aquaria with a multi-speed transmission peristaltic pump. Metering rates were monitored daily to assure constant treatment throughout the experiment. Three of the tanks, numbers 1, 3 & 5, were shaded with neutral density screening to in situ light levels (i.e. light levels normally experienced by the natural community). The other three tanks, numbers 2, 4 & 6, were shaded to 50% of the in situ control levels. Water quality parameters measured over the course of the study included dissolved oxygen (mg l^{-1}), temperature (°C), salinity ($o/_{oo}$), and light as photosynthetically active radiation (PAR: E $m^{-2}sec^{-1}$). 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 measurements, taken continuously over the photoperiod, were made with a Li-COR Quantum Meter (Model number 185A) at the level of the plant canopy top. Concentrations of nitrate, nitrite, ammonia and orthophosphate were determined on replicate 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 2 weeks and kept relatively short to minimize enclosure effects.

Treatment Effects

To determine epiphytic biomass on Z. marina leaves, 8 plants were randomly sampled from each tank at the end of the 2 week period and the leaf

surfaces scraped into filtered sea water. Plant leaves cleaned in this fashion were periodically checked for removal efficiency by examining random samples using epiflorcsent microscopy. Based on observation, removal efficiency was greater than 90% and for the majority of samples no epiphytic growth was observed on the leaf surface following scraping. There was also no observable evidence of plant tissue damage by the technique. The epiphytes were then collected by filtration onto preweighed glass fiber filters (Whatman GF/C), dried at 60°C, and weighed to the nearest 0.01 mg.

To estimate light attenuation due to epiphytic growth, two etched plexiglass slides were placed in each of the tanks and allowed to colonize for the duration of the experiment. Light measurements before and after colonization were made by placing the slide over the quantum sensor (in water) of the Li-Cor Quantum meter. The difference in the two values (% change) was used to estimate the light reduction due to epiphytic growth.

Treatment effects on plant and epiphyte productivity was evaluated by incubating samples of unscraped and scraped plants from each tank in light and dark 300 ml BOD bottles. All samples were incubated in triplicate. The bottles were incubated in their respective tanks for a period of four hours during maximum solar insolation (1000 to 1400 hours EST). Oxygen concentration was measured at 0, 2 and 4 h with the Orbisphere using a polarographic probe equipped with a collar designed to fit and seal into the opening of a standard BOD bottle. Epiphyte productivity was calculated as the difference between colonized and cleaned leaves thus the estimates are minimum. Productivity for both plant and epiphyte are reported as the mean mgO_2 g (dry weight plant)$^{-1}$ hr^{-1}.

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.

RESULTS

Routine sampling data (Table 1) indicated little variation among tanks for temperature (26-31°C), salinity (20-21 °/oo), and midday dissolved oxygen concentrations (10-18 mg l^{-1}). Average midday PAR measurements in the light-control tanks (1, 3 and 5) ranged from 422 to 490 $\mu E\ m^{-2}\ sec^{-1}$ and in the shaded tanks (2, 4 and 6) ranged from 180 to 220 $\mu E\ m^{-2}\ sec^{-1}$ 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 (g wet weight plant^{-1}) and final epiphyte biomass (g dry weight plant^{-1}) are given in Figure 1. There was no significant differences (=0.05) in mean whole plant weight changes over the course of the experiment although all mean final values were lower than initial conditions. Epiphyte biomass (g dry weight plant^{-1}) at the end of the experiment was approximately equal in tanks 1 through 5. Tank 6 was higher and differed significantly from all others.

TABLE 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

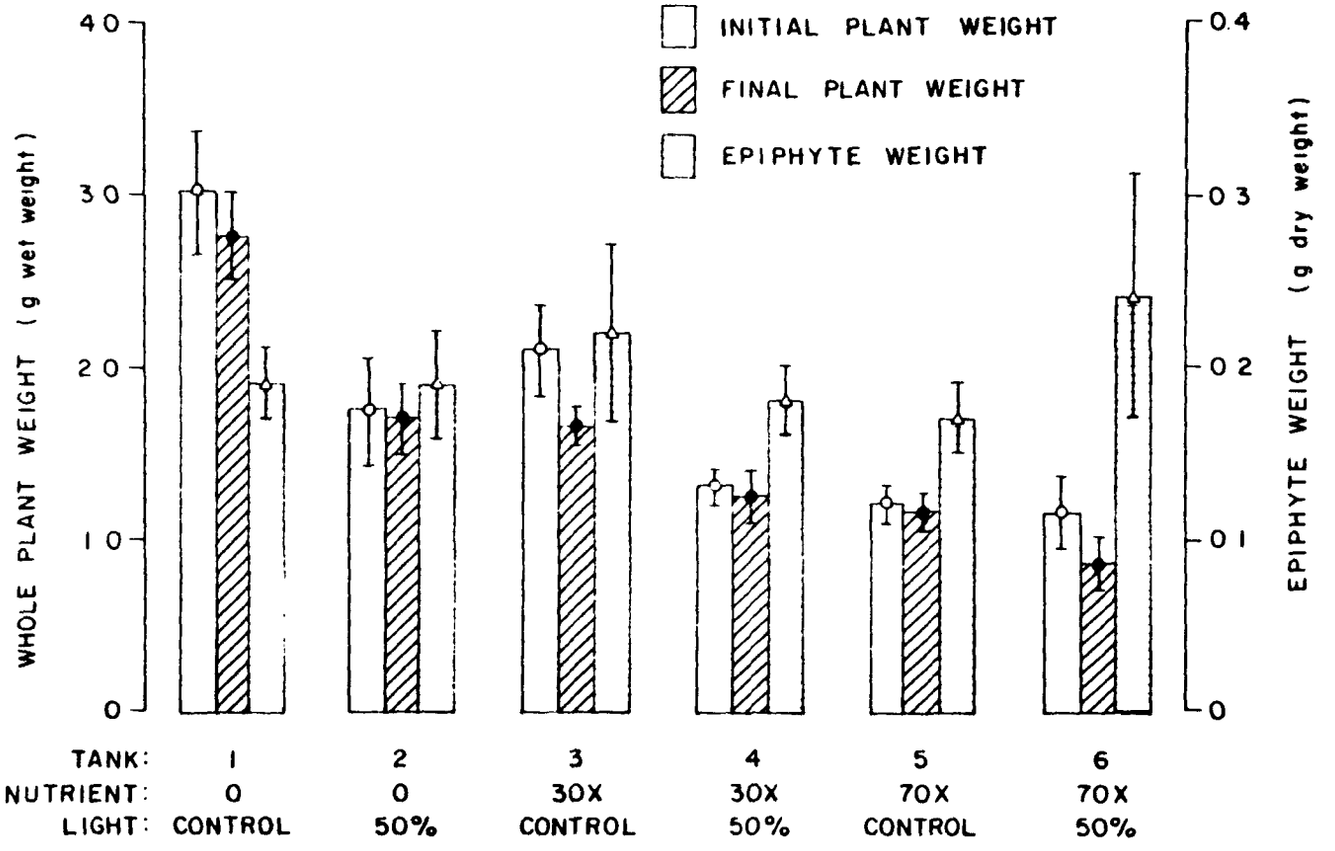


Figure 1. Mean (± 1 S.D.; n=8) initial and final whole plant biomass (g wet weight $plant^{-1}$) and total final epiphyte biomass (g dry weight $plant^{-1}$) following the two week experiment. Horizontal scale notes tank number, PAR regime situ; 5=50% in situ PAR) and nutrient regime (0=ambient; 30X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

Since epiphyte biomass is dependent on plant surface area, the ratio (E:P) of epiphyte biomass (g dry weight) to plant leaf biomass (g dry weight) was used for data reduction and test for treatment effects. The effect of ambient light reduction and nutrient treatment on epiphytic growth is illustrated in Figure 2. In the shaded tanks, epiphytic growth averaged ca. 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 greatest increase occurrred between ambient and nutrient level 1, while in the shaded tanks the greatest increase was between nutrient level 1 and nutrient level 2, suggesting a interactive effect. Overall, the shaded tanks had a greater increase in epiphytic growth with increased nutrients.

Table 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. It is obvious that there are significant differnces 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 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 epiphyte growth, i.e. colonization on the test plates, is presented in Table 4. The data suggest that nutrients have a greater effect than incident light reduction (i.e. shading treatments). Figure 3 illustrates the relationship between epiphytic % light reduction and the E:P ratio. 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 light reduction with an increase in epiphyte biomass that appears to asymptotically approach an upper limit probably governed by leaf surface area.

Figure 4 summarizes the productivity estimates for macrophyte leaves and epiphytes. The 1st bar in each group represents total apparent net production, the 2nd bar respiration, and the 3rd 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.

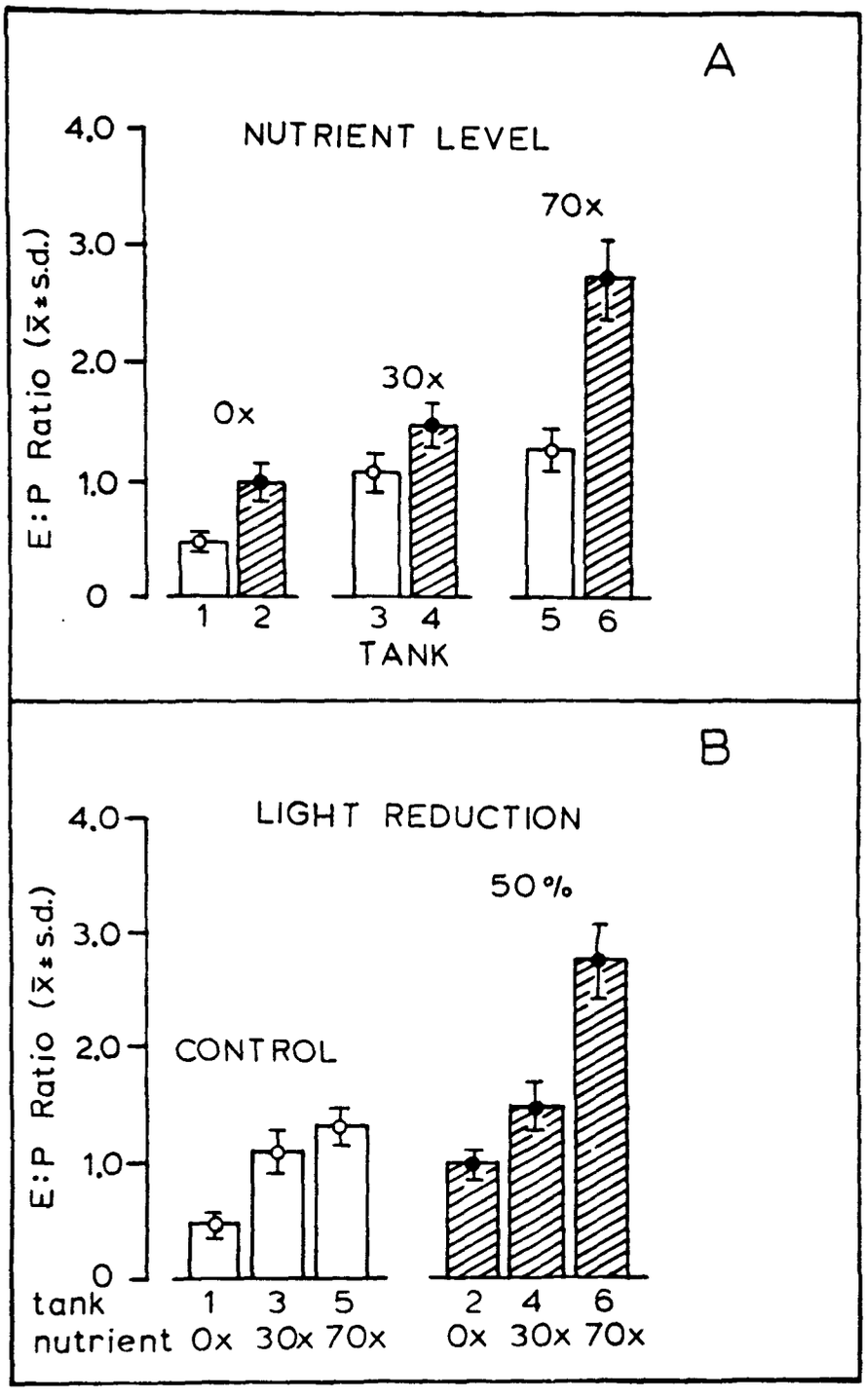


Figure 2. Resulting mean (± 1 S.D.; n=8) epiphyte (g dry weight to plant leaf (g dry weight biomass ratio following the study. The upper panel is grouped by light regime and the lower panel by nutrient treatment for convenience.

TABLE 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 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

TABLE 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

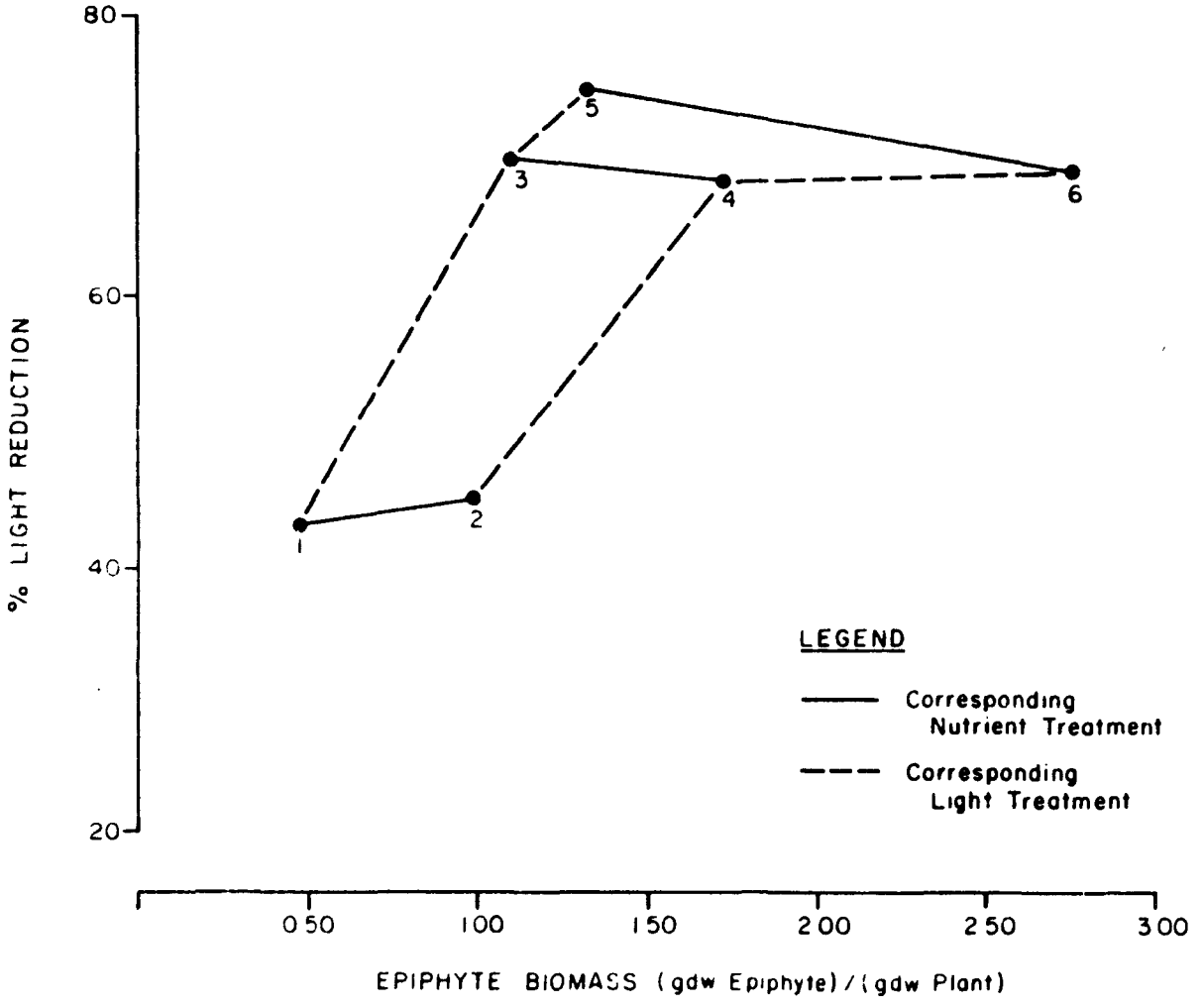


Figure 3. Covariant plot of % light reduction attributed to epiphytic growth (slide colonization) and mean epiphyte: plant leaf biomass ratio. The solid lines connect corresponding nutrient treatments; the dashed line, corresponding light treatments.

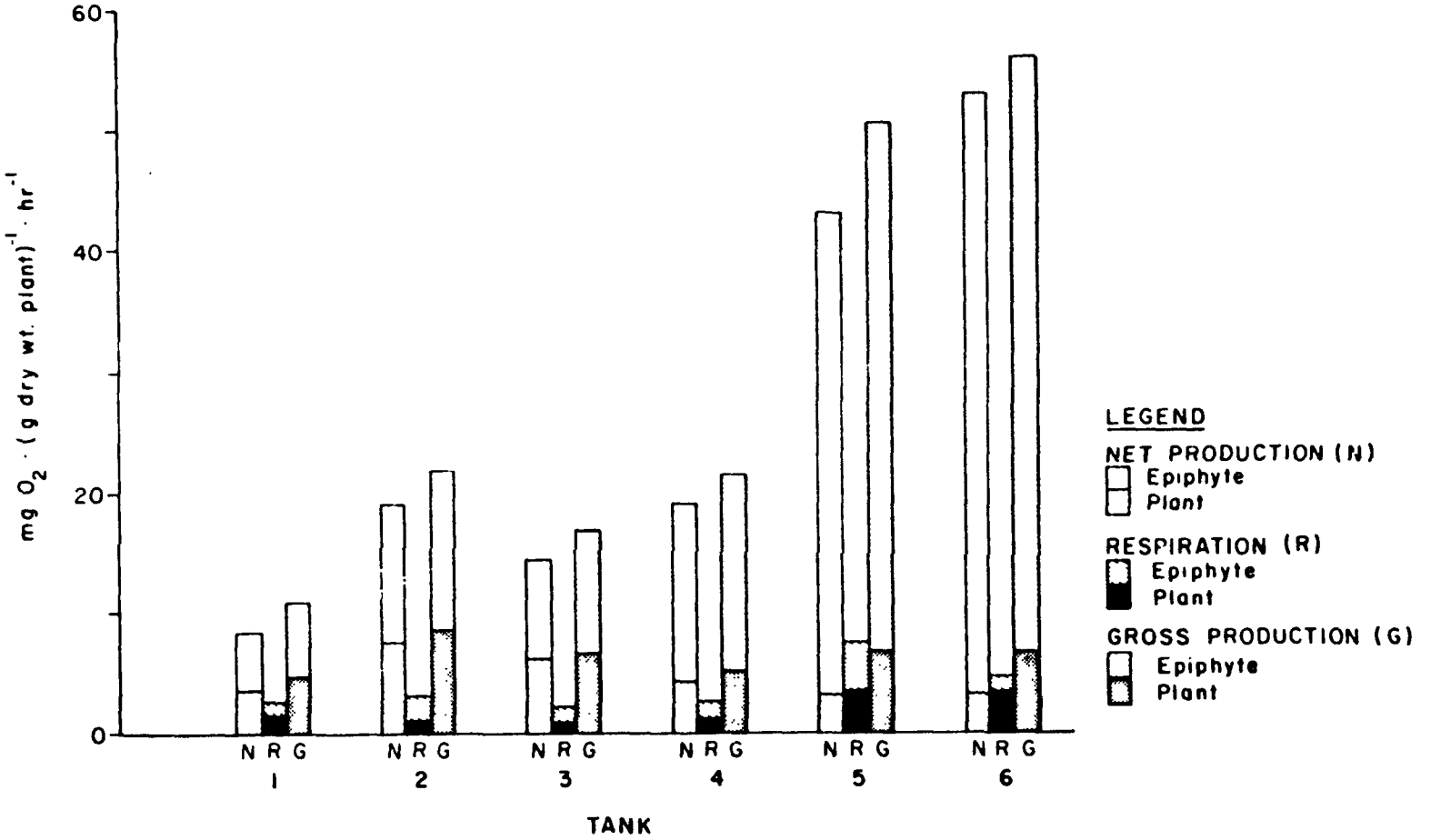


Figure 4. Mean estimates of gross and net apparent O_2 productivity and respiration by plant leaf and associated epiphytes. Gross apparent O_2 productivity was calculated as the algebraic sum of net and respiration estimates.

Table 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 ca. 1 leaf per plant, while there is an average loss of ca. 1 leaf and ca. 2 leaves in nutrient levels 1 and 2 respectively.

DISCUSSION

Submerged aquatic macrophytes are a principal autotrophic component of many freshwater, estuarine and marine ecosystems. Epiphytic growth on these living surfaces generally compliments vascular plant production and, as Penhale (1977) points out, may provide a significant autotrophic input to the resident heterotrophic community. On the otherhand, the autotrophic component of the epiphytic community also functions as a compeditor for light, inorganic carbon and dissolved inorganic nutrients as well as a physical diffusion barrier. The major controls influencing epiphytic growth on seagrasses probably result from the interactive effects of light, nutrient supply, grazing and alleopathy. In a preliminary fashion, we have tested the short term effects of the first two of these.

Photosynthesis-light relationships for microalgae and the vascular plant are quite different. Light saturating intensities for microalgae photosynthesis are much lower than for the vascular plant (Taylor 1964; Ignatiades and Smayda 1970; Levin and Mackas 1972; and Admiral 1977). Therefore, from a competitive standpoint, the microalgae are at the advantage under many estuarine light conditions. For Z. marina dominated communities in the lower Chesapeake Bay, the epiphytic microalgae are probably not light-limited while the vascular plant may be for a significant part of the year (see Chapter 2). The results of this study and the experimental conditions under which it was run indicate a significant, positive response to reduced ambient light by the epiphytic community. The control light levels of ca. 460 $\mu E\ m^{-2}\ sec^{-1}$ (Table 1) are well above saturating for both epiphyte and vascular plant, however, light available for Z. marina photosynthesis was probably in the range 115-250 $\mu E\ m^{-2}\ sec^{-1}$ if the colonized slides accurately estimate % light reduction due to epiphytic growth (Figure 3). These PAR levels are suboptimal particularily for the nutrient enriched treatments. The shaded-treatments light levels of ca. 200 $\mu E\ m^{-2}\ sec^{-1}$ (Table 1) are above saturating for the microalgae and but below saturating intensities for the vascular plant. Light available under the shaded treatments for Z. marina photosynthesis was probably in the range 60-110 $\mu E\ m^{-2}\ sec^{-1}$, well below saturating, and very near the reported range for compensating light intensities of 50 to 100 $\mu E\ m^{-2}\ sec^{-1}$ (see Chapter 2). For the control nutrient treatments, epiphyte growth increased approximately two-fold with shading. The mean % light reduction of 45% due to epiphytic growth under ambient light and nutrient conditions suggests that for the intact community, in situ light regimes must be near 400 $\mu E\ m^{-2}\ sec^{-1}$ reaching the plant canopy top for maximum rates of vascular plant photosynthesis to be realized. These light intensities are not typical at the plant canopy top for Z. marina dominated seagrass meadows in the Chesapeake Bay. Thus the plant community may be light-limited during the growing season due both to water column and epiphytic light attenuation. The

TABLE 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)

relative in situ roles of each of these sources of light attenuation remains poorly understood.

Nutrient effects and interactions are even less well understood. Nutrient dynamics in these temperate seagrass communities have been poorly investigated. Zostera marina dominated communities in the lower Chesapeake Bay generally inhabit sand-silt sediments having organic matter concentrations ranging from 2 to 4 % dry weight and pore-water nutrient concentrations of 100-125 μM $N\text{-}NH_4^+$ and $\leq$ 1.0 μM $N\text{-}NO_3$ in the top 10 cm of sediment (Wetzel et al. 1979). These data and the general observation that water column concentrations are low (K. L. Webb, personal communication, 1982) suggest that the principal route for plant uptake is via the root-rhizome system. Orth (1977) demonstrated a rapid and positive growth response by Z. marina to in situ sediment application of a commercial fertilizer indicating that lower Chesapeake Bay communities are nutrient limited. In general, the kinetic relationships of nutrient utilization by seagrasses have only been described to a limited extent (McRoy et al. 1972; McRoy and Alexander 1975; Penhale and Thayer 1980). However, the consensus seems to be that pore-water concentrations represent a source of several weeks supply while water concentrations are negligible (Patriquin 1972). Recycling and new supplies must, it appears, provide the principal nutrient sources (Capone et al. 1979).

Without knowing the kinetic properties of nitrogen and phosphorus uptake across the leaf surface, the apparent short-term response to increased dissolved inorganic nitrogen and phosphorus concentration demonstrated in our studies was attributable to the epiphytes which resulted in rapid growth. The increased nutrient supply did not result in either increased vascular plant growth (Table 5) or apparent photosynthesis (Figure 4). For all comparisons, increased nutrient supply resulted in increased epiphytic growth that asymtotically approached a maxima probably governed by leaf surface area (Figure 3). For the higher nutrient treatments, greater than 90% of gross and net apparent productivity was attributable to epiphytic microautotrophs (Figure 4). There is an obvious interactive effect between decreased light and increased nutrients both of which favor epiphytic growth and would thus negatively affect vascular plant growth and photosynthesis.

Other controls on epiphytic growth, i.e. grazing and vascular plant alleopathy which function to surpress the negative effects of epiphytic growth, have only recently been investigated for seagrasses. In subtropical Thalassia testudinum grassbeds, Zimmerman et al (1979) report data for grazing by gammaridean amphipods on various organic matter sources including epiphytic microalgae. Their reported rates for ingestion of epiphytic microalgae (ca. 1 mg (algae) mg^{-1} (amphipod) day^{-1}) are in a range which at least theoretically could control epiphyte growth although studies that have attempted to link epiphyte production and grazing (secondary utilization) are lacking. For lower Chesapeake Bay Z. marina communities, van Montfrans et al. (in press) have shown that grazing by the prosobranch gastropod, Bittium varium, can effectively remove the epiphytic community. They have suggested that this biological control may be singularily important with regard to vascular plant growth in some bay areas. Because our experimental design excluded grazing by macroheterotrophs, we can only conclude that in the

absence of grazing, the epiphytic community under both ambient and altered light-nutrient regimes exercises some degree of control over Z. marina photosynthesis and ultimately production by the community.

Alleopathy in aquatic plants has recently been reviewed by Szczepanski (1977). He concluded that for at least some aquatic species, evidence for alleopathy is strong. Two studies with Z. marina indicate that actively growing, unstressed leaf tissue produces an algal inhibitor (Sand-Jensen 1977; Harrison and Chan 1980). From our experimental design, we are not able to distinguish an alleopathic response except to note that any treatment combination which might be assumed to cause plant stress resulted in increased epiphyte growth. This may in part be explained by reduced alleopathy rather than directly attributable to light and/or nutrient treatments. At the present we are not able to distinguish the two.

In summary, these results indicate that epiphytic growth under conditions of no grazing can limit plant photosynthesis and growth. Ambient reduction in available light and/or increased dissolved inorganic nutrient supply interact to favor epiphytic growth and further limit seagrass production. Under extreme conditions this would ultimately lead to increased plant mortality and eventually demise of the entire community. For Chesapeake Bay Z. marina communities, which appear naturally light-stressed, any factor or combination of environmental perturbations that might favor enhanced epiphytic growth (i.e. reduced light, increased nutrients or relaxation of grazing pressures) would ultimately effect changes in the distribution and relative abundance of the species.

ACKNOWLEDGEMENTS

We would like to extend our appreciation to all who have contributed to this study. Our special thanks go to Mr. Damon Delistraty and Frederick Hoffman for help with maintenance and sampling of the microcosms and to Mr. J van Montfrans and R. J. Orth for the use of their seawater tables and flow-through system. Especial thanks are due Drs. R. J. Orth, P. A. Penhale and K. L. Webb for critically reviewing earlier drafts of the manuscript. For their editorial and secretarial assistance, we gratefully acknowledge the efforts of Ms. Carole Knox and Nancy White.

LITERATURE CITED

Admiral, W. 1977. Influence of light and temperature on the growth rate of estuarine benthic diatoms in culture. Mar. Biol. 39:1-9.

Capone, D. G., P. Penhale, R. S. Oremland and B. F. Taylor. 1974. Relationship between productivity and N_2 (C_2H_2) fixation in a Thalassia testudinum community. Limnol. Oceanogr. 24:117-125.

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

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

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

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.

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

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 socialis in laboratory culture. Mar. Biol. 16:171-181.

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. Peter and J. J. Goering. 1974. Nutrient transfer between the seagrass Zostera marina and its epiphytes. Nature Vol. 248:173-174.

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

Orth, R. J. 1977. Effect of nutrient enrichment on growth of the eelgrass Zostera marina in the Chesapeake Bay, Virginia, U.S.A. Mar. Biol. 44:187-194.

Patriquin, D. G. 1972. The origin of nitrogen and phosphorus for growth of the marine angiosperm Thalassia testudinum. Mar. Biol. 15:35-46.

Penhale, Polly 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 G. W. Thayer. 1980. Uptake and transfer of carbon and phosphorus by eelgrass (Zostera marina L.) and its epiphytes. J. exp. mar. biol. Ecol. 42:113-123.

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.

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.

Sieburth, John McN. and Cynthia D. Thomas. 1973. Fouling on eelgrass (Zostera marina L.). J. Phycol. 9:46-50.

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

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

Tukey, J. 1977. Exploratory Data Analysis. Addison Wesley Publ. Co., Reading, Mass.

van Montfrans, J, R. J. Orth and S. A. Vay. 1982. Preliminary studies of grazing by Bittium varium on eelgrass periphyton. Aquatic Bot. (in press).

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. and P. A. Penhale. 1979. Transport of carbon and excretion of dissolved organic carbon by leaves and roots/rhizomes in seagrasses and their epiphyton. Aquatic Bot., 6:149-158.

Wetzel, R. L., R. F. van Tine and P. A. Penhale. 1981. Light and submerged macrophyte communities in the Chesapeake Bay: A Scientific Summary. SRAMSOE 260. College of William and Mary, Va. Inst. of Mar. Sci., Gloucester Point, Va. 58 pp.

Wetzel, R. L., K. L. Webb, P. A. Penhale, R. J. Orth, D. F. Boesch, G. W. Boehlert and J. V. Merriner. 1979. The functional ecology of sumberged aquatic vegetation in the lower Chesapeake Bay. Report to EPA/CBP (R805974). U. S. Environmental Protection Agency, Philadelphia, Pa. 152 pp.

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

Chapter 5

FUNGI AND BACTERIA IN OR ON LEAVES OF EELGRASS (*ZOSTERA MARINA* L.) FROM CHESAPEAKE BAY

Steven Y. Newell

University of Georgia Marine Institute
Sapelo Island, Georgia 31327

ABSTRACT

Samples of green and brown leaves of eelgrass (Zostera marina L.) were incubated in seawater without an additional carbon source. Parallel leaf samples were used for acridine orange bacterial counting and water-soluble aniline blue estimation of fungal biovolume. The incubations produced no evidence that there is an eelgrass counterpart for the chytridialean symbiont which is very common in turtlegrass (Thalassia testudinum Konig). Sterile mycelium (i.e., living mycelium without identifiable propagules) was the most prevalent fungal form on incubated samples from submerged sites, whereas Dendryphiella salina and Sigmoidea sp. (marina?) were prevalent on brown leaves from the wrack line. Attempts to assay fungal biovolume in field samples indicated that the sterile mycelium observed after incubation represented the outgrowth of formerly dormant propagules or weakly established microcolonies. It was calculated that fungal biomass could not account for more than 0.5% of leaf mass, and it was probably much smaller than this, for no fungal structures were observed even in concentrated leaf homogenates. Bacterial densities fell within the range reported for other particulate substrates. A speculative estimate of bacterial productivity was 1.4 x the standing stock per day.

INTRODUCTION

As a part of their study of decomposition of turtlegrass (Thalassia testudinum Konig) leaves, Newell and Fell (1980) addressed the question of the magnitude of the fungal role in this process. Their findings indicate that (i) the most common active fungus of turtlegrass leaves is a rhizomycelial chytrid, apparently a symbiont of the living leaves; and (ii) hyphomycetes and ascomycetes are not major decomposers of leaves which decay in submerged sites. Newell and Fell speculated that the chytrid (Nowakowskiella or Cladochytrium sp.) might be capable of causing disease under conditions of stress to the host plant, and so might be responsible for the wasting disease of eelgrass (Zostera marina L.) if it or a related form were present in eelgrass. I report here a test of the hypotheses that (i) there is an eelgrass counterpart of the rhizomycelial chytrid of turtlegrass; and (ii) the hyphomycetes and ascomycetes reported in eelgrass (Huges 1975; Johnson and Sparrow 1961; Jones 1976; Kohlmeyer and Kohlmeyer 1979) are active decomposers of submerged eelgrass leaves, as the interpretation of Fell and Newell (in press) of the glucosamine data of Thayer et al. (1977) might suggest. The 1st hypothesis was tested by seawater incubation of leaf samples (Newell and Fell 1980). The 2nd hypothesis was tested by seawater incubation and by direct-count estimation of bacterial and fungal biovolumes (S.Y. Newell and R.E. Hicks, in press).

MATERIALS AND METHODS

Collection and Initial Processing

Collections of eelgrass leaves were made at eight stations on a 200 m transect perpendicular to the shoreline across the width of a belt of eelgrass beds on the eastern shore of Chesapeake Bay (37°25'N; 76°51'W) in July 1980. Water temperature was 29°C, and salinity was 19 to 22°/oo. Station 1 was at the outermost (bayward) edge of the bed, station 8 at the innermost (shorward) edge, where the Zostera zone graded in the Ruppia maritima L. zone. In addition, leaves were collected from two sites (9 and 10) within the wrack line on the shore at the level of the most recent high tide. At each site, leaves of two types were collected; mature, green, attached (except wrack sites) leaves, and brown, detached leaves. Leaves were not scraped or rinsed; the eelgrass leaves at this location had a much smaller epiphyte or sediment load than did the turtlegrass and cordgrass leaves, respectively, of the studies of Newell and Fell (1980) and Newell and Hicks (in press). However, the eelgrass leaves collected for the present biovolume measurements were stored in BFFSW, a bacteria-free (0.2μm filtered) 2% solution of formaldehyde in seawater 20°/oo at 4°C until processed (2 weeks later). This storage liquid was not included with the sample at the time of homogenization. Therefore, the storage BFFSW served as a rinse before the preparations, and the bacteria counted were those most firmly attached.

Frequency of Fungal Occurrence

Park (1972; 1974) and Suberkropp and Klug (1976) recommend ambient water incubation of natural samples as one means of identifying active aquatic mycoflorae. I used this method as described by Newell and Fell (1980). Briefly, *Zostera* leaves were collected in sterile bags, and duplicate subsamples (15 mm^2) were aseptically removed from each leaf and placed in dishes of filter-sterilized seawater (50 ml per dish) from sampling sites. Incubation was for 17 to 21 days in the dark at 25 to 30°C. Penicillin G (0.05%), streptomycin sulfate (0.05%), cholestrol (0.5 ppm), and $FeSO_4$ (2.0 ppm) were added to the seawater before filter-sterilization for reasons discussed by Newell and Fell (1980). Entire surfaces and peripheries of samples were searched (at a magnification of x50 to x400) for sporangia, perithecia, and conidia after incubation. Thraustochytrids were not recorded because of their similarity to protozoan cysts in unbaited natural samples, but labyrinthulids were recorded, because of their possible connection to the wasting disease of eelgrass (Johnson and Sparrow 1961; Pokorny 1967; Rasmussen 1977).

Direct-counting and Biomvolume Estimation

Leaves for biovolume estimation were processed as described for *Spartina alterniflora* leaves by Newell and Hicks (in press). Briefly, two leaf samples (one green and one brown) of measured surface area (4,800 mm^2) from each station were homogenized (rotor-stator, model BEW-5 Polytron Waring blender attachment) at low speed (15,000 rpm) for 3 min in 100 ml of BFFSW. Homogenates were filtered through a 250-m mesh screen. Filtrates were used to make acridine orange bacterial preparations (Hobbie et al. 1977; Rublee et al. 1978) or water soluble aniline blue (WSAB) fungal preparation (28; as modified by Newell and Hick, in press). These are polycarbonate membrane filtration (Nuclepore) techniques, and direct microscopic counting is performed under epifluorescence illumination. The modifications of the Paul and Johnson (1977) technique were: (i) 0.2-μm pore size Nuclepore filters were used in place of 0.4-μm filters; (ii) the 0.2-μm filters were stained in irgalan black (0.2% in 2% acetic acid) before use; (iii) the sample homogenates were stained in WSAB for 30 min before filtration; and (iv) the filters plus sample were mounted in low-fluorescence immersion oil rather than dried. Mycelium from the seawater incubation dishes was used as a control to verify the capacity of the WSAB to form fluorescent mycelial-WSAB complexes. In addition to the WSAB preparations, cleared membrane filters (Millipore Corp.) (Hannsen et al. 1974) and concentrated (settling for several hours) homogenates were prepared with WSAB and examined for funal structures by epifluorescence and phase-contact microscopy. Lengths and width of bacterial cells were measured at x2,000, and individual volumes (Baath and Soderstrom 1979) were calculated as cylinders. The coefficient of variation for bacterial counts averaged 45%. Blank filtrations gave counts which were less than 1% of sample counts. The frequency of dividing cells (FDC) was estimated as described by Hagstrom et al. (1979); cells with clear invaginations but not a clear separatory space were counted as dividing cells. Filamentous bacterial cells which were longer than the width of the microscope field projection of one subsection of the eyepiece grid used in counting (13 μm) or which consisted of chains of cells

or both were not included in total or FDC counts. They formed only a small proportion of cells counted (<1%).

Retentates (250 μm) were dried and weighed for comparison with weights of unhomogenized leaves, as an estimate of inefficiency of homogenization (Newell and Hicks, in press). Retentate weights averaged 56.3 ± 6.6% (standard error, n = 10) of original sample weights, similar to the value of 65.7% found for leaves of S. alterniflora by Newell and Hicks (in press). A small portion (<0.1%) of each 250- m retentate was suspended in 0.2μ FSW and used to estimate retention of bacterial cells. Staining (acridine orange) and filtering procedures were like those used for the filtered homogenates. Bacterial cells were counted on microscopically estimated surface areas of particles.

Statistical Analyses

The G-test of Sokal and Rohlf (1969) was used in comparison of fungal frequencies of occurrence. Mean bacterial counts were subjected to analysis of variance after transformation (X + 0.5) (Sokal and Rohlf 1969).

RESULTS

Frequency of Occurrence Fungal Species

There was no evident trend of changing frequency of occurrence of any fungal species over the transect, except between submerged sites and wrack-line sites. Therefore, data from each of these two types of site were pooled for presentation in Table 1. Only the species listed in Table 1 were recorded at greater than 10% for submerged or wrack sites for either leaf color. There was no evidence of zoosporic fungi, neither chytridiomycetes nor oomycetes, in any of the samples with the exception of Labyrinthula sp., which was recorded only one cc. Sterile mycelium (i.e., living mycelium without identifiable propagules) and Cladosporium sp. were the prevalent forms on samples from submerged sites, and they occurred at statistically equivalent frequencies on the wrack-line material. Occurrences of Sigmoidea sp., Dendryphiella salina (Sutherland) Pughet Nicot, and Varicosporina ramulosa Meyers et Kohlmeyer were largely limited to wrack-line samples, where the two former species had the highest frequencies recorded on brown leaf samples. Acremonium sp. and Lulworthia sp. were relatively rare.

Descriptive Note

The species of Sigmoidea Crane (1968) which was observed at high frequency on emersed intertidal eelgrass leaves was probably Sigmoidea marina (Haythorn et al. 1980) but in the eelgrass species, the conidia were often curved in more than one plane, as with the conidia of Anguillospora Ingold (1942). This feature was not included in the description of Z. marina. A further problem here stems from the fact that the original description of the genus Sigmoidea (Crane 1968) referes to the conidiophores as phialides or aleuriophores. There is no evidence of phialid (Kendrick 1971) conidium production in Sigmoidea sp. from eelgrass of S. marina as described by Haythorn et al. (1980). Cultures of Sigmoidea sp. from eelgrass are available upon request from the author (as culture no. SAP 9).

TABLE 1. FREQUENCY OF OCCURRENCE ON SAMPLES OF EELGRASS LEAVES AS RECORDED AFTER SEAWATER INCUBATION.

	Frequency of occurrence on:			
	Green leaves		Brown leaves	
Species or form	Submerged	Wrack	Submerged	Wrack
Sterile mycelium	75[a]	50[a]	70[a]	40[a]
Sigmoidea sp.*	0[a]	10[a]	0[a]	60[b]
D. salina*	0[a]	0[a]	3[a]	50[b]
Cladosporium sp.	38[a]	10[a]	33[a]	40[a]
Acremonium sp.	15[a]	10[a]	5[a]	20[a]
V. ramulosa*	0[a]	20[b]	0[a]	20[b]
Lulworthia sp.	10[a]	0[a]	13[a]	0[a]
Fungi absent*	10[ab]	20[a]	0[a]	0[a]

a. Asterisk after species name indicates detection of significant ($P < 0.05$) differences among frequencies for types of samples. For each species, frequencies bearing the same superscript letter were not significantly different.

b. The number of leaves from each of which two replicate samples were taken: both types of submerged, 40; both types of wrack, 10.

Bacterial Counts and Volumes

Total numbers of bacterial cells calculated for the filtered (250-μm mesh screen) eelgrass-leaf homogenates and for the 250-m retentates are presented in Table 2. Calculated values for denisty of bacterial cells per square millimeter of leaf surface are also given. Densities of bacteria on green leaves were statistically equivalent ($X = 2.0 \times 10^5$ cells per mm^2 of leaf surface) and two to three times lower than densities on brown leaves, except on brown leaves from the wrack line. There was a statistically significant gradient in bacterial density on brown leaves from bayward to shoreward edges of the bed, with the lowest value being found for wrack-line leaves. Mean bacterial cell volume did not differ significantly between green leaf and brown leaf samples; overall mean volume was $0.32 \pm 0.10 \mu m^3$ (95% confidence interval) per cell).

The 250 m retentates contained only a very small percentage of the total bacterial cells (Table 2); the range was 0.03 to 0.7% for green leaves and 0.1 to 0.6% for brown leaves. Homogenization appears to be a satisfactorily efficient means of releasing adherent bacteria from the type of leaf substrate.

Frequencies of dividing bacterial cells were 7.2% for green leaves and 7.6% for brown leaves. Decisions regarding what were and what were not dividing cells were more difficult than when counts are made of water column samples (Hagstrom et al 1979; S. Y. Newell and R. R. Christian, submitted for publication), primarily because many of the bacteria in the eelgrass samples were long rods (although mean cell length was only 1.5 μm) with indentations which may or may not have been constrictions leading to division and because the background in the eelgrass samples was not as dark as those obtainable with water column samples.

Fungal Volume

All attempts to estimate fungal biovolume produced the same result; no structures were observed which could be identified as fungal. This was true of all types of sample, green and brown, submerged and wrack line. The only fluorescent structures in WSAB preparations were clearly pieces of eelgrass (cell walls were green fluorescent) or algae (orange to red fluorescent). Under phase-contrast microscopy, no hyphae, conidia, or pieces of ascocarp were seen, even in the settled concentrates.

DISCUSSION

The complete absence of zoosporic fungi in 100 samples of green eelgrass leaves indicates that there is no counterpart in eelgrass for symbiotic rhizomycelial chytrid of turtlegrass. Since only one point in time and one geographical location were sampled, this cannot be stated definitively, but it should be noted that the chytrid symbiont of turtlegrass was recorded at high frequencies (70 to 98%, n = 79) in both winter and summer from three widely separated geographical locales (Newell and Fell 1980). Thus, the suggestion by Newell and Fell (1980) that a symbiotic chytrid might be responsible for the wasting disease of eelgrass is probably wrong.

TABLE 2. TOTAL NUMBER OF BACTERIAL CELLS IN HOMOGENATES OF EELGRASS LEAVES AND BACTERIAL CELLS PER SQUARE MILLIMETER OF LEAF SURFACE.

	Total no. of bacterial cells in:									
	Green leaves					Brown leaves				
	1+2[a]	3+4[a]	5+6[a]	7+8[a]	9+10[a]	1+2[a]	3+4[a]	5+6[a]	7+8[a]	9+10[a]
Filtrate[b]	2.6[a]	1.9[a]	2.3[a]	1.6[a]	1.4[a]	5.5[c]	6.3[c]	4.4[b]	3.8[b]	1.6[a]
Retenate[c]	0.8	0.8	0.7	0.8	0.9	8.7	7.4	8.4	7.2	9.5
Leaf surface[d]	2.7	2.0	2.4	1.7	1.4	5.9	6.5	4.5	3.9	1.7

a. Surfaces on transect. Stations 1 to 8 were submerged sites; stations 9 and 10 were wrack-line sites.

b. Undiluted homogenate after filtration through 250-μm mesh screen; data is given as the total number of cells x 10^9. Last superscript letter designates means which are not significantly different from one another ($P > 0.05$).

c. Material collected on a 250-μm mesh screen; data is given as the total number of cells x 10^6.

d. Data given as the total number of cells x 10^5 per mm^2 of leaf surface.

The pattern of occurrence of fungal species other than that for chytridiomycetes is similar for eelgrass and turtlegrass (Newell and Fell 1980). Sterile mycelium dominated samples of decaying leaves from submerged sites, and D. salina was recorded at high frequency from sandy, high intertidal sites. On eelgrass, D. salina was accompanied at high frequency by Sigmoidea sp. in the high intertidal (wrack-line) zone. For turtlegrass leaves from submerged sites, Newell and Fell (1980) found that control-validated, leaf-surface, sterilization greatly reduced recordings of mycelial fungi. This finding was taken by Newell and Fell (1980) to mean that fungi other than, perhaps, the rhizomycelial chytrid are not active decomposers of submerged turtlegrass leaves. In contrast, the high frequency of conidial fungi which Newell and Fell (25) found in intertidally decaying turtlegrass leaves, even after surface sterilization, was interpreted as an indication of a possible active role of higher fungi in the breakdown of leaves deposited on the shoreline. One could infer from the present fungal frequency data that the same situation exists for eelgrass.

My findings regarding fungal biovolume in eelgrass leaves support the inference from species occurrence data, that fungi are not active decomposers of eelgrass leaves in submerged sites. Since there is little or no fungal biomass present in these decomposing leaves, fungi cannot be converting eelgrass matter into fungal matter. Newell and Hicks (in press) estimated the volume of fungi in dead leaves of S. alterniflora, using the same sample volumes and microscopic handling as were used in the eelgrass determinations of this study. Their estimate of fungal volume in Spartina leaves was about 1/3 of the leaf volume, indicating a dry fungal biomass of 0.2 to 0.5 g/g of dry leaf. Comparison of average counts of hyphal intersections with an eyepiece grid for the Spartina samples and for eelgrass samples suggest that fungal biomass in eelgrass was less than 1% of that estimated for Spartina leaves (i.e., <0.005 g/g of dry leaf). Since no fungal structures were seen even in concentrated eelgrass leaf homogenates, the fungal fraction of eelgrass leaf mass was probably much lower than 0.5%.

Since wrack-line eelgrass biovolume samples were just as void of fungal structures as were samples from submerged sites, the implication is that there is no more fungal biomass produced in wrack-line litter than in submerged litter, in spite of the suggestion to the contrary from species occurrence data. However, both green and brown leaves of the wrack-line samples were probably from recently deposited leaf litter, since there were many green leaves within the piles of litter, and eelgrass leaves rapidly turn black under desiccating conditions (personal observations). Therefore, fungal invasion of this intertidal material may have been just getting under way. Since deposition of seagrass leaves in wrack lines may account for a major share of leaves detached (18, 36) this is a question worth pursuing.

Production of saprotrophic microbial biomass on submerged eelgrass leaves is apparently limited to bacteria. Standing stocks of adherent bacteria increased by 2 to 3 times as leaves aged from green mature to detached brown states, ranging from about 1 to 7 x 10^5 cells per mm^2 of leaf surface. This translates to 2 to 14 x 10^5 cells per g of dry leaf, using leaf area-mass data from this study and adjusting for leaching in BFFSW. Brown leaves in the recently deposited wrack show 2 to 3 times smaller bacterial standing stocks

than submerged brown leaves, perhaps another sign of a change toward an environment favoring fungal activity. Using the mean bacterial cell volume for eelgrass (0.32 m^3) and the conversion factor for biovolume to biomass given by Ferguson and Rublee (1976; 0.28 g (dry weight) per cm^3), I calculate that the standing stock of adherent bacteria is about 2 x 10^{-5} mg/mm^2 of green leaf surface and 4 to 6 x 10^{-5} mg/mm^2 of submerged brown leaf surface (= 4 x 10^{-4} mg of dry bacteria per mg (dry weight) of green leaves and 7 to 11 x 10^{-4} mg for submerged brown leaves). This represents only 0.04 to 0.11% of leaf mass, and so could account for very little of the elemental chemical content of the leaves, just as found for other marine litter (Hobbie and Lee 1980; Lee et al 1980; Rublee 1978; but see Morrison et al 1977). Apparently, the high glucosamine content of detrital Zostera leaves (about 9 mg of glucosamine per g of ash-free dry leaves) found by Thayer et al. (1977) is not in the form of living bacterial material, yet it may be a result of bacterial deposition, as discussed by Hobbie and Lee (1980).

I counted only tightly adherent bacteria on Zostera leaves; densities of bacterial cells on Spartina, Thalassia, and other types of litter and particulate detritus range up to 4 to 14 times the densities which I have recorded for Zostera (Lee et al 1980; Rublee et al. 1978; Newell and Hicks, in press; P. A. Rublee and M. R. Roman, submitted for publication). However, Harrison and Harrison (1980) reported range of bacterial concentrations of 2 x 10^4 to 1 x 10^5 cells per mm^2 of surfaces of particles of Zostera leaves in microcosms. Kirchman et al. (1980) reported that bacterial numbers on surfaces of Zostera leaves from northern temperate waters were approximately $10^7/cm^2$, and the values which I report here fall within the range (5 x 10^8 to 10^{10} cells per g of dry substrate) of bacterial densities cited by Fenchel and Jorgensen (1977) for a wide variety of substrates, including Zostera (Fenchel 1977).

The standing stocks of bacteria on eelgrass are not good indicators of bacterial productivity, if output of bacteria by predation, sloughing, etc., is substantial. Using the FDC estimated for eelgrass bacteria (about 7%) and the regression equation describing the relationship between FDC and instantaneous growth rate ( ) of marine bacteria (Newell and Christian, submitted for publication; the equation: In = 0.299 FDC - 4.961), I calculate that instantaneous generation time for bacteria on the eelgrass samles was 8.5 h. If the standing stock of bacteria was in steady state and had no diel rhythm (a tenuous assumption; see, e.g., Meyer-Reil et al 1979; Sieburth 1979), this would indicate a 24-h output of about 1.4x the standing stock. However, there remain several unanswered questions regarding the validity of the use of FDC in estimating marine bacterial productivity (Newell and Christian, submitted for publication), and use of the FDC method with homogenized litter substrates may be invalid due to the effect of homogenization on dividing cells. Therefore, the above productivity estimate is highly speculative and needs testing by alternative methods (Fuhrman and Azam 1980; Hanson 1980; Sieburth 1979).

LITERATURE CITED

Baath, E. and B. Soderstrom. 1979. The significance of hyphal diameter in calculation of fungal biovolume. Oikos 33:11-14.

Crane, J. L. 1968. Freshwater hyphomycetes of the northern Applachian highland including New England, and three coastal plain states. Am. J. Bot. 55:996-1002.

Fenchel, T. 1977. The significance of bactivorous protozoa in the microbial community of detrital particles, p. 529-544. In J. Cairns (ed.), Aquatic Microbial communities. Garland Publishing, Inc., New York.

Fenchel, T. and B. B. Jorgensen. 1977. Detritus food chains of aquatic ecosystems:the role of bacteria. Adv. Microb. Ecol. 1:1-58.

Ferguson, R. L. and P. Rublee. 1976. Contribution of bacteria to standing crop of coastal plankton. Limnol. Oceanogr. 21:141-145.

Fuhrman, J. A. and F. Azam. 1980. Bacterioplankton secondary production estimates for coastal waters of British Columbia, Antarctica, and California. Appl. Environ. Microbiol. 39:1085-1095.

Hagstrom, A., U. Larsson, P. Horstedt, and S. Normark. 1979. Frequency of dividing cells, a new approach to the determination of bacterial growth rates in aquatic environments. Appl. Environ. Microbial. 37:805-812.

Hannsen, J. F., T. F. Thingstad and J. Goksoyr. 1974. Evaluation of hyphal lengths and fungal biomass in soil by a membrane filter technique. Oikos 25:102-107.

Hanson, R. B. 1980. Measuring microbial activity to assess detritial decay and utilization, p. 347-357. In K. R. Tenore and B. C. Coull (ed.), Marine benthic dynamics. University of South Carolina Press, Columbia.

Harrison, P. G. and B. J. Harrison. 1980. Interactions of bacteria microalgae, and copepods in a detritus microcosm:through a flask darkly, p. 373-385. In K. R. Tenore and B. C. Coull (ed.), Marine benthic dynamics. University of South Carolina Press, Columbia.

Haythorn, J. M., E. B. G. Jones and J. L. Harrison. 1980. Observations on marine algicolous fungi, including the hypohomycete Sigmoidea marina sp. nov. Trans. Br. Mycol. Soc. 74:615-623.

Hobbie, J. E., R. J. Daley, and S. Jasper. 1977. Use of nuclepore filters for counting bacteria by flurorescence microscopy. Appl. Environ. Microbiol. 3:1225-1228.

Hobbie, J. E. and C. Lee. 1980. Microbial production of extracellular material:importance in benthic ecology, p. 341-346. In K. R. Tenore and B. C. Coull (ed.), Marine benthic dynamics. University of South Carolina Press, Columbia.

Hughes, G. C. 1975. Studies of fungi in oceans and estuaries since 1961. I. Lignicolous, caulicolous, and foliicolous species. Oceanogr. Mar. Biol. Ann. Rev. 13:69-180.

Ingold, C. T. 1942. Aquatic hyphomycetes of decaying alder leaves. Trans. Br. Mycol. Soc. 25:339-417.

Johnson, T. W. and F. K. Sparrow. 1961. Fungi in oceans and estuaries. J. Cramer, New York.

Jones, E. B. G. (ed.). 1976. Recent advances in aquatic mycology. Paul Elek Ltd., London.

Josselyn, M. N. and A. C. Mathieson. 1980. Seasonal influx and decomposition of autochthonous macrophyte litter in a north temperature estuary. Hydrobiologia 71:197-208.

Kendrick, B. (ed.). 1971. Taxonomy of fungi imperfecti. University of Toronto Press.

Kirchman, D. L., L. Mazella, R. Mitchell and R. S. Alberte. 1980. Bacterial epiphytes on Zostera marina surfaces. Biol. Bull. 159:461-462.

Kohlmeyer, J. and E. Kohlmeyer. 1979. Marine mycology. The higher fungi. Academic Press, Inc., New York.

Lee, C., R. W. Howarth, and B. L. Howes. 1980. Sterols in decomposing Spartina alterniflora and the use of ergosterol in estimating the contribution of fungi to detrital nitrogen. Limnol. Oceanogr. 25:290-303.

Meyer-Reil, L. A., M. Bolter, G. Liebezeit, and W. Schramm. 1979. Short-term variations in microbiological and chemical parameters. Mar. Ecol. Prog. Ser. 1:1-6.

Morrison, S. J., J. D. King, R. J. Bobbie, R. E. Benchtold and D. C. White. 1977. Evidence for microfloral succession on allochthonous plant litter in Apalachicola Bay, Florida, U.S.A. Mar. Biol. 41:229-240.

Newell, S. Y. and J. W. Fell. 1980. Mycroflora of turtlegrass (Thalassia testudinum Konig) as recorded after seawater incubation. Bot. Mar. 23:265-275.

Park, D. 1972. Methods of detecting fungi in organic detritus in water. Trans. Br. Mycol. Soc. 58:281-290.

Park, D. 1974. Accumulation of fungi by cellulose exposed in a river. Trans. Br. Mycol. Soc. 63:437-447.

Paul, E. A. and R. J. Johnson. 1977. Microscopic counting and adenosine 5'-triphosphate measurement in determining microbial growth in soils. Appl. Environ. Microbiol. 34:263-269.

Pokorny, K. S. 1967. Labyrinthula. J. Protozool. 14:697-708.

Rasmussen, E. 1977. The wasting disease of eelgrass (Zostera marina) and its effects on environmental factors and fauna, p. 1-52 In C. P. McRoy and C. Helfferich (ed.), Seagrass ecoystems. Marcel. Dekker, New York.

Rublee, P. A. L. M. Cammen, and J. E. Hobbie. 1978. Bacteria in a North Carolina salt marsh:standing crop and importance in the decomposition of Spartina alterniflora. University of North Carolina Sea Grant Publ. UNC-SG-78-11.

Sieburth, J. M. 1979. Sea microbes. Oxford University Press, New York.

Sokal, R. R. and R. J. Rohlf. 1969. Biometry. The principles and practice of statistics in biological research. W. H. Freeman and Co., San Francisco.

Suberkropp, K. and M. J. Klug. 1976. Fungi and bacteria associated with leaves during processing in a woodland stream. Ecology 57:707-719.

Thayer, G. W., D. W. Engel and M. W. Lacroix. 1977. Seasonal distribution and changes in the nitritive quality of living dead and detrital fractions of Zostera marina L. J. exp. mar. biol. Ecol. 30:109-127.

Welsh, B. L., D. Bessett, J. P. Herring and L. M. Read. 1979. Mechanisms for detrital cycling in nearshore waters at Bermuda. Bull. Mar. Sci. 29:125-139.

Chapter 6

Preliminary Studies on Community Metabolism in a Tropical Seagrass Ecosystem: Laguna de Terminos, Campeche, Mexico

R. L. Wetzel[1]
L. Murray[1]
R. F. van Tine[1]
J. W. Day, Jr.[2]
C. J. Madden[2]

1. College of William and Mary, Virginia Institute of Marine Science, Gloucester Point, VA 23062.

2. Center for Wetlands Resources, Louisiana State University, Baton Rouge, LA 70803.

ABSTRACT

Apparent O_2 productivity measures of a Thalassia testudinum seagrass community at Estero Pargo in Laguna de Terminos, Campeche, Mexico indicate that maximum areal rates are in the range 5.5 to 7.5 $gO_2\ m^{-2}\ d^{-1}$ (1.65 to 2.25 $gC\ m^{-2}\ d^{-1}$) and agree well with published data. The T. testudinum community is light-compensated ($P_a = R$) at approximately 200 $\mu E\ m^{-2}\ sec^{-1}$ and light-saturates between 700 and 800 $E\ m^{-2}sec^{-1}$. Mean above-ground biomass at the Estero Pargo site was 288 (±86) live and 285 (±147) dead $g\ m^{-2}$ (dry weight) with a mean root to total above-ground plant biomass ratio of 4.11 (±2.28). The relatively low biomass and high root/rhizome to total aboveground ratio indicates a community that is either in a die-back stage or environmentally stressed. We hypothesize that light and nutrient interactions are principal factors governing plant community production at Estero Pargo. Comparative studies within this important lagoon should help elucidate overall mechanisms controlling productivity and the role of the seagrasses in the general energy flow structure of Laguna de Terminos.

INTRODUCTION

Seagrass communities dominated by the turtlegrass, Thalassia testudinum, comprise an important and productive habitat in subtropical and tropical ecosystems. Generally, mean standing stocks range from 400 to 3000 g m^{-2} (dry weight) with daily productivity ranges of approximately 1.0 to 10.0 g m^{-2} (1.0 to 3.0 mgC g^{-1}(plant)) (McRoy and McMillian 1977). Assuming an average growing season of 250 days in these areas, the range for annual production would be 250-2500 gC m^{-2}. These values fall in the upper ranges reported for a variety of estuarine and coastal vascular plant communities (Westlake 1963; Keefe 1972) and suggest their potential importance to nutrient cycling, energy flow and trophic structure.

Most studies estimating productivity and energy flow in T. testudinum communities have been carried out in coastal waters of the United States. As Lot (1977) points out, few, if any, studies on community energetics have been done in the vast seagrass communities in both Gulf of Mexico and Caribbean waters of southern Mexico (Campeche). Nearly all studies in these areas have been surveys and descriptively oriented. These areas have vast bottom areas vegetated by T. testudinum in both lagoon (Laguna de Terminos) and coastal areas (Yucatan). Estimates of production, environmental factors regulating productivity and relative importance of seagrasses in these systems are generally lacking.

This report summarizes our preliminary findings on Thalassia testidinum community metabolism and the effects on apparent productivity of varying light regimes and dissolved inorganic nutrient conditions in Laguana de Terminos.

STUDY AREA

The study area was located in Laguna de Terminos, Campeche, Mexico. Laguna de Terminos is a large embayment (ca. 2500 km^2) bounded to the south by the mainland and to the north by Isla del Carmen. Lagoon waters communicate with the Gulf of Mexico through a net inflow channel, Puerto Real, to the east, and a new outflow channel, Carmen, to the west. The area is characterized by extensive mangrove swamps, freshwater marshes and seagrass beds dominated by Thalassia testudinum. Terminos lagoon is relatively shallow with a mean depth of 3.5 m. Figure 1 illustrates Laguna de Terminos and the location of our principal study site, Estero Pargo. The site was chosen because it is a station routinely sampled by scientist of the Centro de Ciencias del Mar Limnologia of the Universidad National Autonoma de Mexico (UNAM) investigating various chemical and biological characteristics of the lagoon. Also, the site minimized logistical problems for these initial studies. Depth of our study site averaged 1 m.

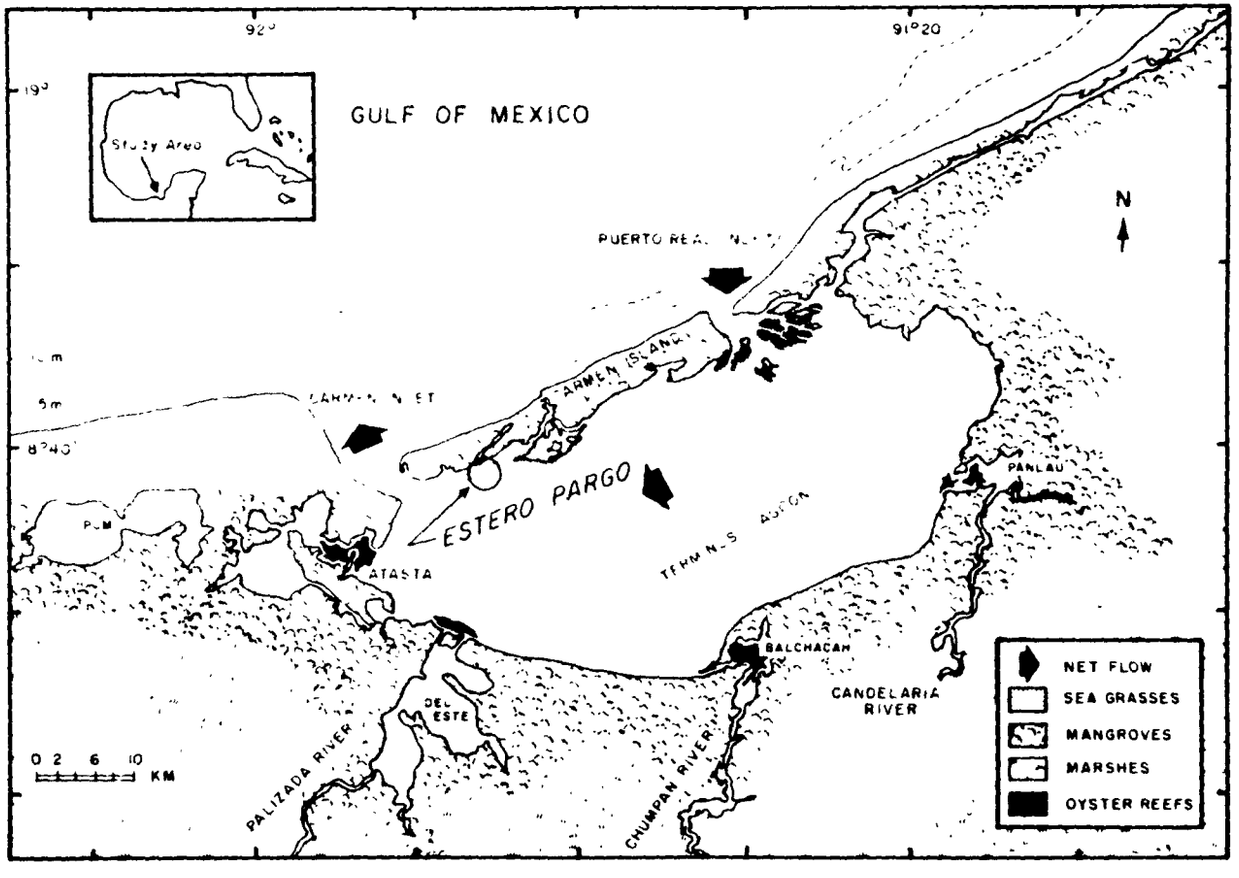


Figure 1. Geographical location of Laguna de Terminos and Estero Pargo study site. Arrows indicate the net wind-driven circulation pattern of the lagoon.

METHODS

Metabolism studies were designed and carried out to estimate; 1. net apparent community O_2 productivity (P_a), 2. community respiration (R_a), and 3. O_2 exchange by specific community components: water, non-vegetated substrate, and plant leaves. Also included in our studies were additional measures of productivity and growth to compare with the O_2 data. These included ^{14}C photosynthesis studies using individual leaves and morphological measures (leaf width and length) to estimate production according to the regression equations of Patriquin (1973) and ^{14}C productivity of the water column. Specific experiments were carried out to evaluate; 1. light intensity-apparent photosynthesis relations, and, 2. effects of short-term dissolved inorganic nutrient enrichment.

Community oxygen metabolism

Studies were conducted using 32 l acrylic hemispheres (domes) that covered a bottom area of 0.? m^2. The domes were constructed with (1) a 7.5 cm vertical flange to eliminate exchange of enclosed water, (2) equipped with ports for sampling enclosed water and (3) a collar for securing a polarographic type electrode for oxygen concentration measurements.

Net apparent community O_2 productivity and respiration was determined using clear and opaque domes respectively. During the incubation period, incubation continuous water circulation was provided by stirrers integral to the O_2 probe bodies (Orbisphere Laboratories, Inc., Geneva). According to instrument specifications, the stirrer produces a mean current velocity of 25 cm sec^{-1} at the probe head. Tests with the dome inverted and water filled indicated complete mixing within 2-3 minutes using Rhodamin WT as a tracer. O_2 measurements (mg l^{-1}) were made using temperature-compensated, H_2S insensivive sensors calibrated in water-saturated air. Calibration was carried out at the beginning of each experiment and checked at the end. For all studies, pre vs post calibration differed by no more than $\pm$ 0.2 mg l^{-1}. The domes were placed by hand with care taken to avoid disrupting the sediment surface and trapping leaves under the vertical flange. After the domes were placed, a "settling" time of 30 minutes was allowed with all ports open to ambient water before initial measures were begun. Periodic water samples were taken by syringe through the sampling ports for dissolved nutrients (NH^+_4, NO_2^-, NO_3^- and PO_4^{-3}); O_2, temperature (°C) and light (PAR μE m^{-2} sec^{-1}) at the top of the plant canopy were monitored continuously using a Dataplex Signal Scanner (Hampshire Controls) and a dual channel recorder (Soltec, Inc.). Additionally, written recorders were kept for O_2, temperature and PAR as a check against recorder performance and calibration. PAR measurements were made using a LI-COR Model 185 Quantum Meter (LICOR, Inc.) equipped with submarine and deck quantum sensors and interfaced through a switching panel with the Dataplex and recording equipment allowing semi-continuous recording surface light intensity (I_0) and light intensity at the plant canopy top (I_Z). For all studies, measurement intervals were as close as possible to the periods of peak isolation (1000 to 1400 hrs. CST).

Water column metabolism

Plankton metabolism was estimated with light-dark BOD bottles (300 ml) using both standard oxygen and ^{14}C techniques (Strickland and Parsons 1972). The oxygen bottles were suspended at mid depth (50 cm) and the ^{14}C bottles were at the surface. Incubation was four hours for the oxygen measurements and 4:45 for the ^{14}C studies.

Substrate metabolism

Metabolism of non-vegetated substrates (i.e. bare sediments within the grassbed) and adjacent sand bottoms was determined using transparent and opaque benthic chambers. The chambers measured approximately 10 cm (diameter) by 10 cm (height above sediment surface) once in place. Incubation volume in the chambers was ca. 0.8 l. All incubations for the various experiments were carried out using replicate treatments.

Light/nutrient responses

Net apparent community O_2 productivity versus light intensity was evaluated using four clear, acrylic domes and four levels of light intensity; 100%, 71%, 50% and 30% of ambient conditions. The light levels were established by using fitted, neutral density screening over the domes. Because of time constraints, we could not replicate the study but for the results reported the domes were placed in, at least observationally, a homogeneous stand of vegetation. Our experience, based on three years of study in Zostera marina dominated communities in Chesapeake Bay (see Wetzel 1983), indicate that the variance within treatments is much less than between study periods.

The short-term effect of increased concentrations in dissolved inorganic nutrients, NH_4^+, NO_3^-, and PO_4^{-3}, was evaluated by "spiking" the domes in a separate experiment to 50 μM ($NH_4^+ + NO_3^-$) and 10 μM PO_4^{-3}. Reported here are the results for changes in apparent O_2 metabolism in these treatments. Kinetic analysis of the nutrient exchange studies are reported elsewhere (Boynton et al., unpubl. ms.).

Plant Biomass

For all studies, plant biomass was determined using an acrylic hand corer (0.033 m^2). Samples were taken by hand coring to a depth of approximately 25-30 cm to include root/rhizome fractions. The samples were sorted in the field into above-ground live (AGL), above-ground dead (AGD) (defined as obvious chlorotic and/or brown-black leaf material), and below-ground root and rhizome (BG) fractions. Wet weight was determined on blotted, fresh material and dry weight determined on the samples following forced-air drying at 60°C for 48 hours.

RESULTS

Plant Biomass

Table 1 summarizes the results for all core-biomass samples taken during our the various studies. Total above ground plant biomass averaged 573 g m^{-2}

TABLE 1. ESTIMATES OF PLANT BIOMASS FOR VARIOUS FRACTIONS AT THE ESTERO PARGO STUDY SITE IN FEBRUARY, 1980.

Fraction[1]	N	$\bar{x}$ g wet weight m^{-2} ($\pm$S.D.)	$\bar{x}$ g dry weight m^{-2} ($\pm$S.D)
AGL	12	1980 (797)	288 (86)
AGD	12	2225 (1184)	285 (147)
BL	14	14783 (5467)	1979 (370)

(dry weight) and was approximately equally divided between live and dead fractions (288 and 285 g m^{-2}, respectively). Mean root (including rhizome) to shoot (live + dead fractions) ratio for all samples was 4.1 (S.D. 2.28) but varied considerable (range 1.89 to 9.71) within what we initially conceived as a relatively homogenous stand of vegetation. This high and variable root:shoot ratio probably reflects the generally nutrient poor status of the area. Biomass estimates also fall in the lower range reported for T. testudinum communities. Sediments in this area are coarse, sand-shell mixes and oxygenated to a depth of at least 15 cm (1.0 mgO_2 l^{-1}, $\pm$ 0.3).

Apparent Thalassia Community O_2 Productivity

Figure 2 illustrates the simple linear relationship between net apparent O_2 productivity and light reaching the plant canopy top. The X-intercept suggests that the community compensation point (P:R = 1) is approximately 200 μE m^{-2} sec^{-1}. The Y-intercept agrees well with measures of community respiration (200 $\pm$ 63 mgO_2 m^{-2} h^{-1}). These data suggest that plant community photosynthesis is not light saturated in the range 200-650 μE m^{-2} sec^{-1} (range of light intensity observed for these experimental conditions).

Figure 3 summarizes the specific rate determinations expressed per unit of above ground living plant material for all studies. The simple linear regression line illustrated was calculated for all measurements at light intensities equal to or less than 2.4 E m^{-2} hr^{-1} (667 μE m^{-2} sec^{-1}). The rational for this will be discussed in a following section.

Not surprisingly, both the areal and specific rates of net apparent O_2 productivity show a strong, positive correlation with in situ light flux. At the community level, it appears that light intensities above 200 μE m^{-2} hr^{-1} are required for net autotrophic production. However, if we assume a 12 hour photoperiod and a mean areal respiration rate of 200 mgO m^{-2} h^{-1}, in order to balance the community (P=R) on a daily basis (i.e. net apparent O_2 production of 400 mgO_2 m^{-2} hr^{-1}), light intensity at the canopy top must average approximately 575 μE m^{-2} sec^{-1}) over the photoperiod, or, based on a mean vertical attenuance of -1.07 (n=6), 1675 μE m^{-2} sec^{-1} insolation.

Community Response to Varying Light Regimes

Figure 4 illustrates the results of the neutral density shading studies. The four light levels are identified as: 1.0 (C), 0.71 (L), 0.50 (M) and 0.30 (H) of ambient conditions. Based on the control (1.0) and light (0.71) treatments, the autotrophic response appears to light saturate between 700 and 800 E m^{-2} sec^{-1} at the canopy top or very near solar maximum isolation (assuming $-k_z = 1.07$). The saturated, net apparent community O_2 productivity at these higher light levels is approximately 550 mgO_2 m^{-2} hr^{-1} for this time of year. Using the conversions given in McRoy and McMillan (1977), a mean standing stock of 288 gdw m^{-2}, and a mean community respiration rate of 200 mgO_2 m^{-2} hr^{-1}, maximum specific rate of production would be 0.78 mgC g (plant^{-1} h^{-1}).

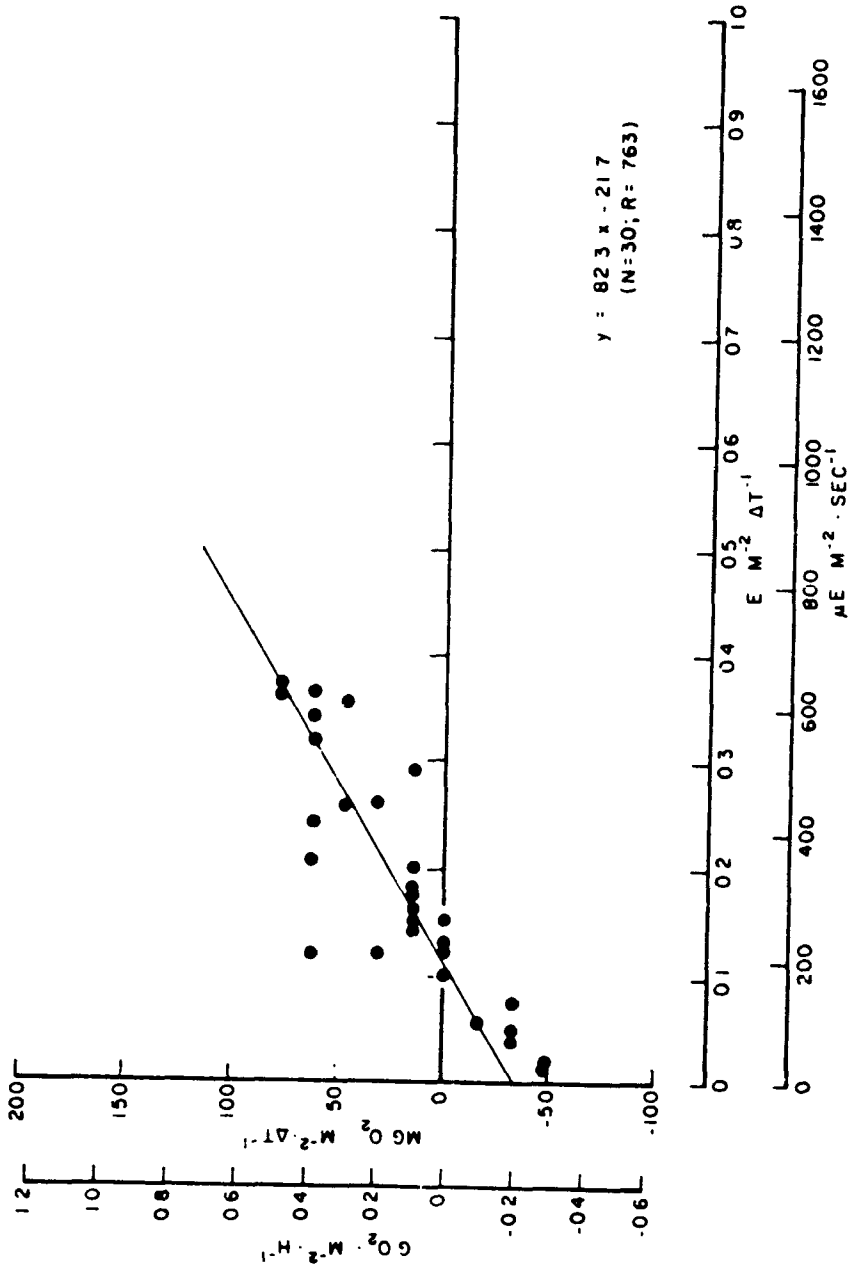


Figure 2. Net apparent O_2 productivity vs PAR at the plant canopy top; 6 Feb 1980. The line drawn is the simple linear least squares line of best fit for all data. The time interval is 15 minutes.

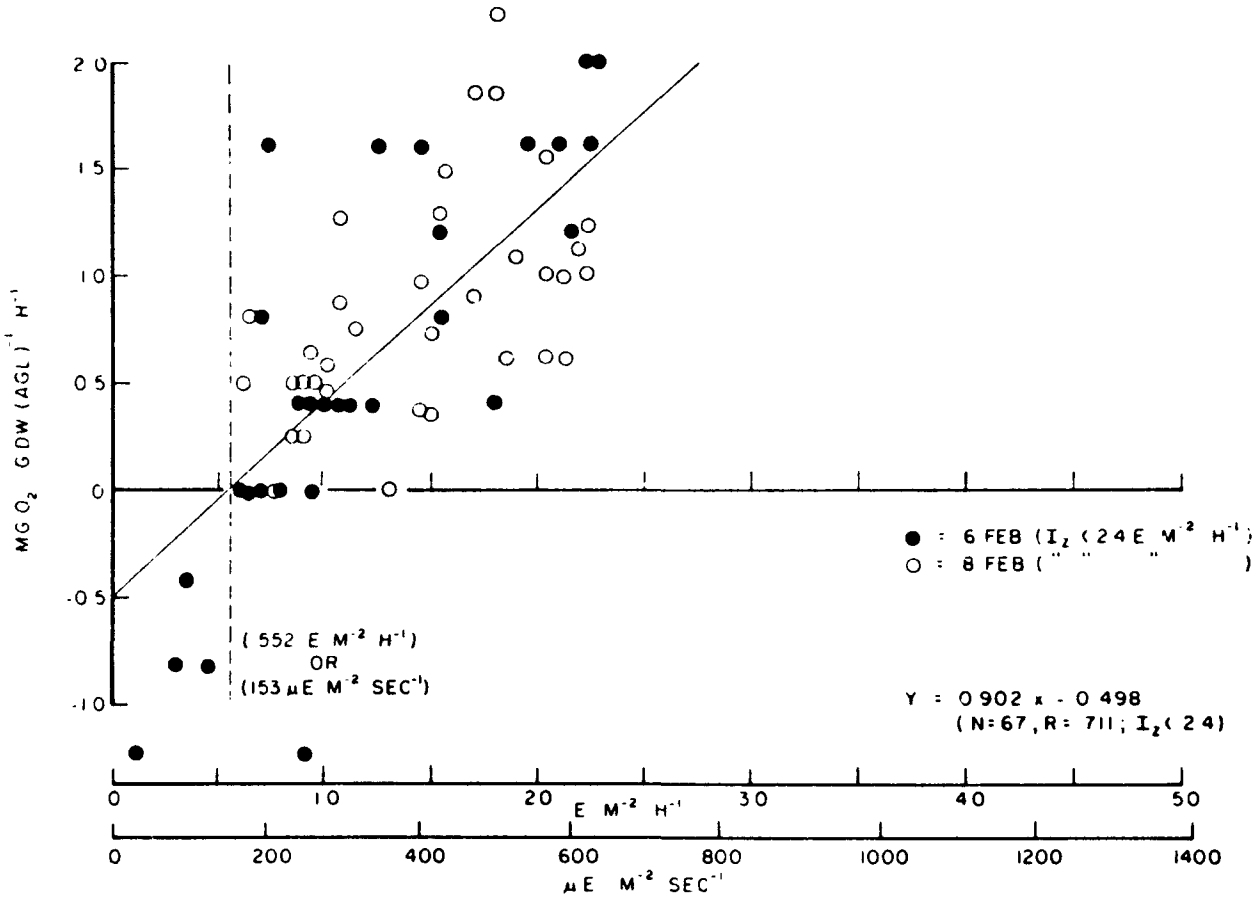


Figure 3. The specific rate of net apparent O_2 productivity vs PAR at the plant canopy top for two study dates; 6 Feb (●) and 8 Feb (○). Only data for in situ PAR (I_z) greater than 2.4 E m^{-2} s^{-1} are included due to an apparent afternoon depression (see text). The vertical dashed line marks the estimated community light compensation point (i.e., net O_2 production = respiration).

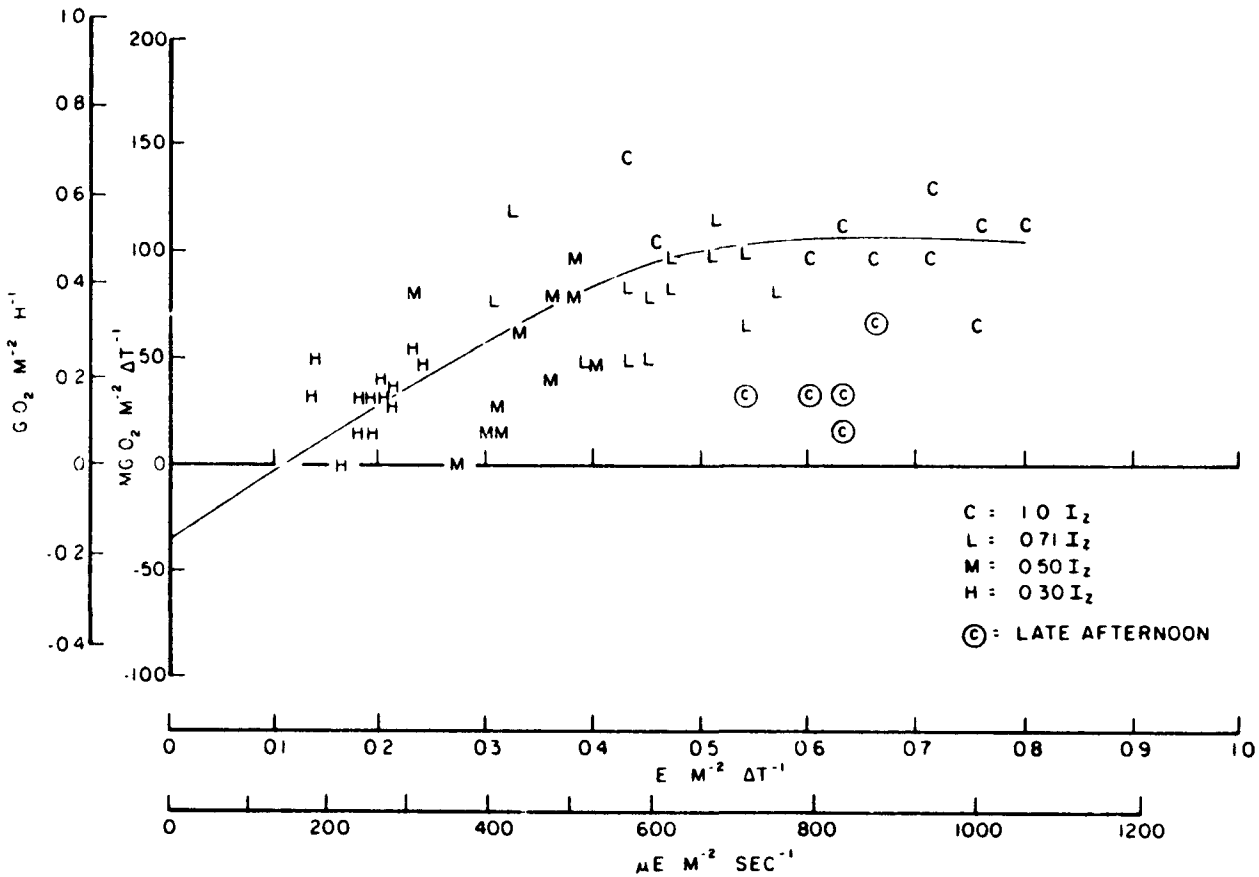


Figure 4. Net apparent O_2 productivity vs PAR using neutral density shades. PAR intensities indicated are given relative to % transmission of ambient (control). The circled points are rates determined in late afternoon. The lines were drawn by eye.

The points circled in Figure 4 identify rates determined in late afternoon (1400-1700 hr) and suggest an afternoon depression in apparent O_2 productivity under optimal light conditions. Figure 5 illustrates the response in all treatments plotted as the actual O_2 concentration versus time of day. It is apparent that the rate of change approaches zero in all treatments before there is any significant change in light regime (dashed line). Plotting the data as illustrated in Figure 6, i.e. rate of apparent O_2 productivity versus O_2 concentration, suggests that the depression in afternoon rates is not a function of in situ O_2 levels.

However, there is a strong linear relationship between apparent productivity and in situ light levels during morning and peak insolation periods. For all regression statistics given in the figures, paired observations were evaluated resulting in significant and positive correlations. As a test of light response, a significant improvement in the correlation coefficient was obtained when a time lag of 10 minutes was used for light intensity paired with rate estimates: $r = .763$ versus .913. This result suggests that for in situ studies of light:photosynthesis relations, observation intervals must be kept short, particularily in varying environments, to derive the best estimate of Pa. For the studies reported, measurement intervals of 10 to 15 minutes were used coupled with the same integration intervals for light observations.

Nutrient Response

Figure 7 illustrates the response in specific rate of apparent O_2 productivity for nutrient enriched and ambient conditions. The X-intercept's are not significantly different from previous estimates however the differences in slope suggest an enrichment effect. The data set used as a control was run in the same area two days prior to the enrichment experiment. The nutrient enrichment study was carried out under relatively low light conditions (maximum intensity approximately 280 $\mu E\ m^{-2}\ sec^{-1}$) and following a storm. We are therefore hesitant to speculate as to probable cause or even component involved. It does appear none-the-less, the community responds rapidly to increased nutrient supply. Within an hour following the spike, NH_4^+ concentrations in the domes were at ambient (pre-spiked) levels; i.e. theoretical 25 $M\text{-}NH_4^+$ to approximately 1.0 $\mu M\text{-}NH_4^+$ (Hopkinson, et al., unpubl. data).

Water Column Metabolism

Rate of surface net productivity using the ^{14}C method ranged from 0.74-1.75 $mgC\ m^{-3}\ hr^{-1}$ and averaged 1.16. This is equivalent to 4.7 $mgO_2\ m^{-3}\ hr^{-1}$ (Table 2). The results of the oxygen measurements yielded considerably higher values; 12.5 and 65 $mgO_2\ m^{-3}\ hr^{-1}$. The oxygen respiration values ranged from -37.5 to -121 $mgO_2\ m^{-3}\ hr^{-1}$.

Sediment Metabolism

Metabolism of the non-vegetated substrate communities are summarized in Table 2. The net apparent productivity of the bare substrate within the grassbed averaged 111 $mgO_2\ m^{-2}\ hr^{-1}$, while that of the sand substrate was 218

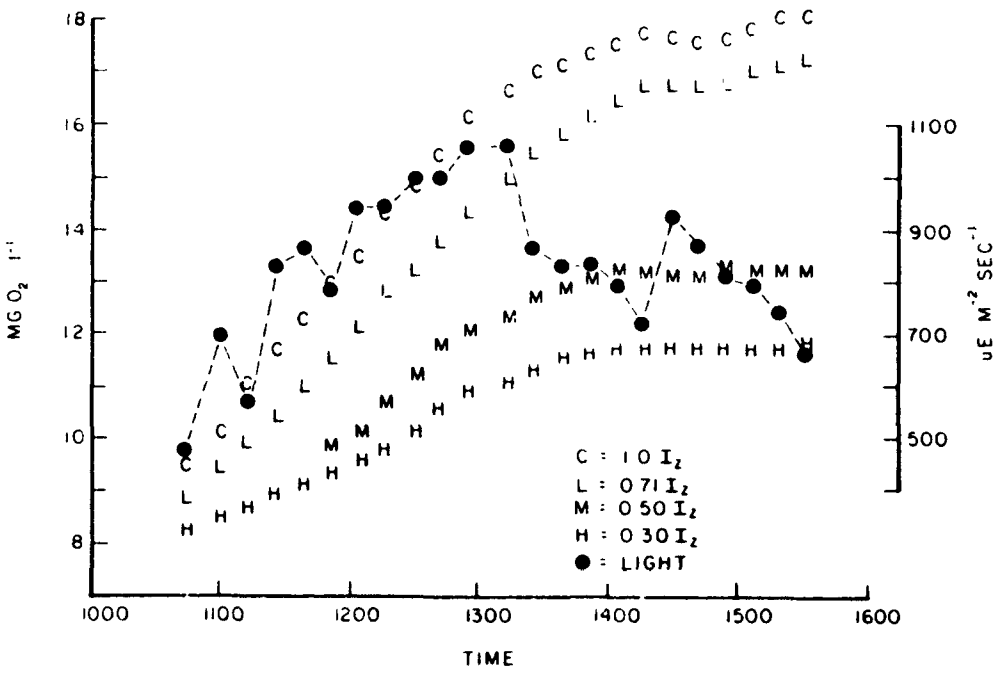


Figure 5. Continuous plot of O_2 concentration in the four dome light regimes vs time of day. PAR intensity is given at the top of the plant canopy.

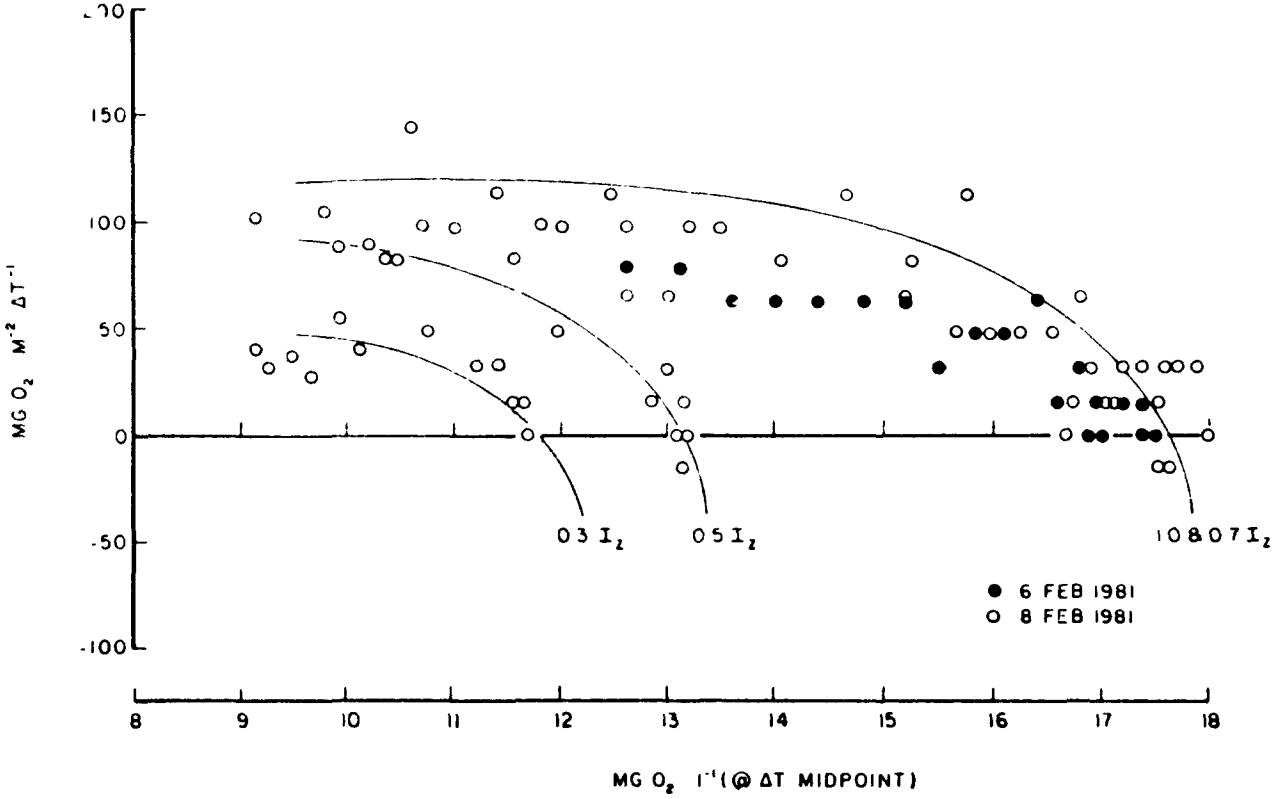


Figure 6. Covariant plot of net apparent rate of O_2 productivity in the four light treatments and O_2 concentration at the midpoint of measurement interval. The solid lines were drawn by eye. All other symbols as given before.

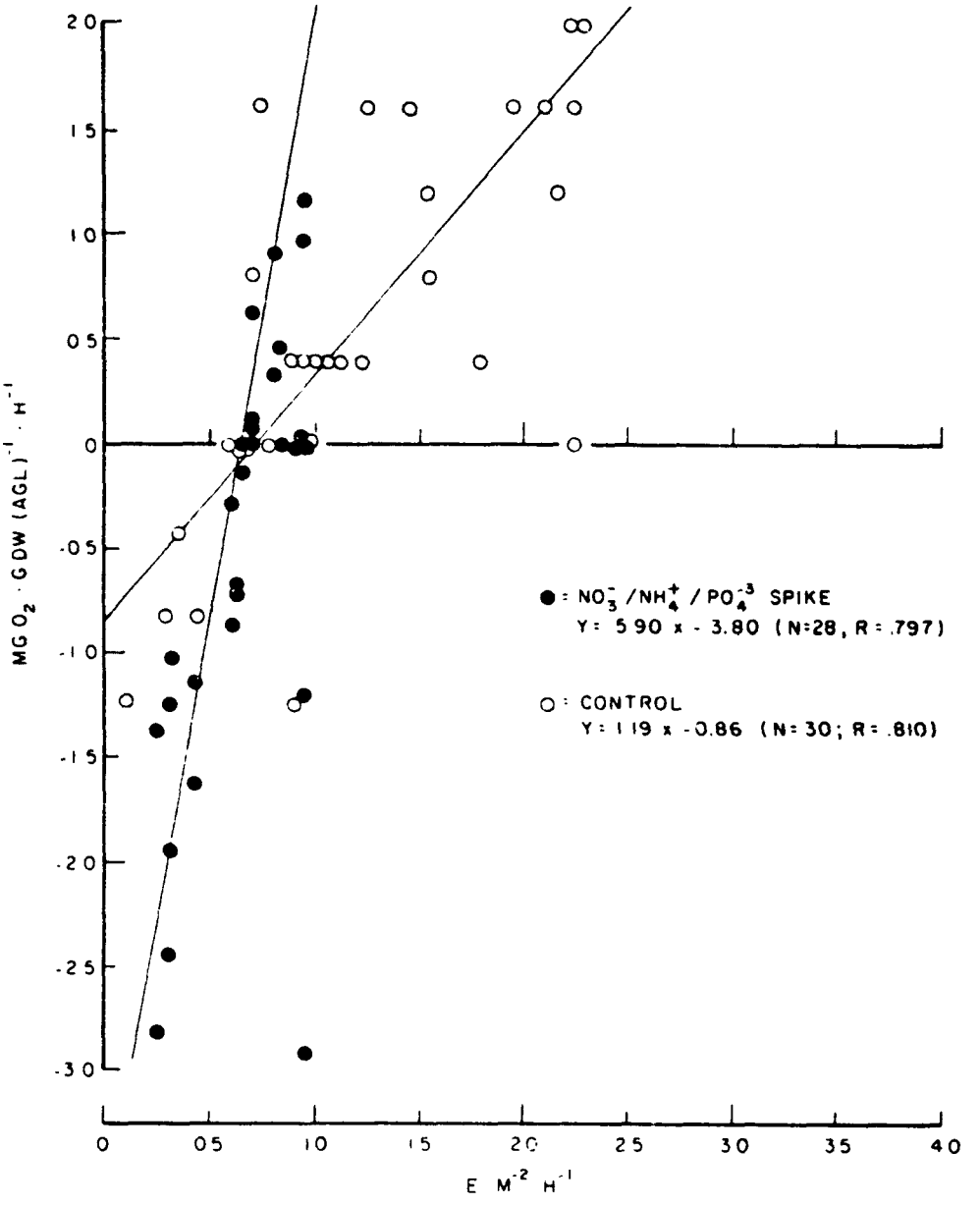


Figure 7. Scatter plot of specific rate of apparent O_2 productivity vs PAR for ambient (O) and nutrient amended domes. The line drawn are linear least squares lines of best fit for all data.

TABLE 2. SUMMARY OF COMMUNITY O_2 METABOLISM STUDIES AT ESTERO PARGO, LAGUNA DE TERMINOS, CAMPECHE, MEXICO DURING FEB. 1980; $\bar{x}$ mg O_2 m^{-2} h^{-1} ($\pm$S.D.).

Component		Net Apparent O_2 Productivity	Respiration	Gross Apparent O_2 Productivity
1. Water*	2-6-81	65. (71)	-121. (78)	186.
(mgO_2 m^{-3} h^{-1})	2-8-81	12.5 (103)	- 37.5 (25)	40.
(mgC m^{-3} hr^{-1})	2-8-81	4.7 (1.3)**		
2. Bare Substrate (w/in grassbed	2-6-81	111. (59.4)	-41.6 (15.7)	153.
3. Sand substrate	2-8-81	218. (19.8)	-63.5 (5.79)	282.
4. Total Plant Community	2-6-81	205 (145)	-200 (63.3)	405.
	2-8-81	399 (164)		599*
5. Plant + Water* (max. values)		464	-321	785

* Assuming 1.0 meter depth
** ^{14}C results were converted to oxygen using 1C = 3.33 O_2
*** Assuming respiration equals -200 mgO_2 m^{-2} h^{-1}

$mgO_2\ m^{-2}\ hr^{-1}$. Both were approximately 54% of the total plant community metabolism. The respiration of the bare substrate averaged 41.6 $mgO_2\ m^{-2}\ hr^{-1}$, and that of the sand area was -63.5 $mgO_2\ m^{-2}\ hr^{-1}$ or 20% and 30% respectively of total plant community respiration.

DISCUSSION

Standing stocks of Thalassia testudinum at the Estero Pargo site in Laguna de Terminos are in the lower range reported by McRoy and McMillian (1977): 288 g m^{-2} (dry weight) (AGL) versus a mean range of 340 to 3100 g m^{-2} (dry weight) (exclusive of Pomeroy, 1960). The site is characterized by coarse, sand and shell sediment, high root:shoot ratios, and variable light conditions (range of k_z - .56 to -2.0 for this study period). The study site is also within several hundred meters of a major inland channel draining an extensive mangrove swamp. Spectral analysis (MER 100 Spectroradiometer, Biospherical Instruments, San Diego) of light in the channel outflow and plume indicate significant changes in both subsurface light quantity and quality which may influence light-energy fields in adjacent areas (Wetzel and van Tine 1982).

Highest standing stocks of seagrasses in the lagoon are found in and around Puerto Real (net inflow channel) and progressively decrease toward Estero Pargo and Carmen (R. Roman, pers. comm.). We hypothesize, based on observations in these areas, that light quality and quantity, and sediment characteristics (implying various nutrient regimes), follow the same gradient. The conclusion seems that the area studied represents the lower range for estimates of seagrass metabolism in the lagoon system. This, coupled with the relatively large fraction of dead above-ground material, suggests that our rate measurements are probably minimum for this time of year and study site.

Table 3 summarizes the results for measurements of productivity in T. testudinum communities in Gulf and Caribbean water. In compiling this data, carbon (^{14}C) and biomass data (P and Z) were converted to O_2 equivalents using the ratios given in McRoy and McMillian (1977). There is, surprisingly, a relatively narrow range of values considering both the diverse nature of the habitats and methodologies employed. Measurements made during this study fall well within the range of values reported. Based on our previous discussion, this suggests that production by seagrass communities in Terminos (assuming this site represents minimum values), is very high. Maximum rates of apparent productivity at Estero Pargo are in the range 5.5 to 7.5 $gO_2\ m^{-2}d^{-1}$ or 1.6 to 2.2 $gCm^{-2}\ d^{-1}$. If we take McRoy and McMillan's (1977) suggestion of a 250 day growing season, this would translate to 450 to 650 $gC\ m^{-2}\ y^{-1}$; significantly higher than production by other autotrophic communities in comparable ecosystems (Beers et al. 1968).

We have used maximum rates at Estero Pargo for these comparisons. Without question, these are not realized daily rates but represent potential input of fixed organic matter to the ecosystem. Our conclusion is, assuming this area represents minimum estimates, that the seagrass communities in Laguna de Terminos represent a significant input of organic matter and nutrients to the lagoon ecosystem.

TABLE 3. SUMMARY OF PRODUCTIVITY MEASURES (Pa: $gO_2\ m^{-2}\ d^{-1}$) for THALASSIA TESTUDINUM COMMUNITIES IN GULF OF MEXICO AND CARIBBEAN AREAS.

Area	Method	Pa ($gO_2\ m^{-2}\ d^{-1}$)	Reference
1. Bahamas	p*	1.7-10.	Patriquin, 1972
	^{14}C	6.1-7.9	Capone, et al., 1979
	Z**	2.8-4.3	Capone, et al., 1979
	P	3.4-3.3	Capone, et al., 1979
2. Barbados	P	3.9	Patriquin, 1973
3. Bermuda	P	18.	Patriqein, 1973
4. Florida	Z	5.6-7.7	Zieman, 1968
	O_2	3.0-8.3	Jones, 1968
	O_2	1.2-3.8	Pomeroy, 1960
	?	9.3-47.	Thorhaug and Sterns (as cited in McRoy and McMillan 1977)
	O_2	1.9-53.	Odum, 1963
	O_2	5.6	Boynton, 1975
5. Texas	O_2	10.5	Odum, 1967
	O_2	3.0-3.0	Odum and Hoskin, 1958
6. Mexico	O_2	5.5-7.5***	This study

* See Patriquin, 1973
** See Zieman, 1968
*** Maximum rates with 10 hr. photoperiod

Controls on production of submerged aquatics have been the subject of a variety of studies (see Wetzel et al., 1981 and references cited therein). Generally, light and nutrients are the focus of attention though salinity and temperature are often included. Our preliminary studies suggest, overall, that light is singularily important in deriving the "best" estimate of productivity. The strong dependence (statistically) on predicting net productivity at the community level based on light regime indicates light, at least at Estero Pargo, as a principal factor. We remain at a loss to provide insight as to the characteristic late afternoon depression in apparent O_2 productivity, although several promising avenues of research are apparent (e.g. see Nafziger and Koller 1976).

Capone et al. (1979) provide data relative to T. testudinum light response. Their data indicate that P_{max} (light saturated rates) occur at light intensities of 800 to 1000 $\mu E\ m^{-2}\ sec^{-1}$. Their measures were derived from ^{14}C incubations on excised leaf material containing epiphytes. Considering the assumed problems in measurement using various techniques (Hartman and Brown 1967; Zieman and Wetzel 1980) our estimates are very comparable. We estimate that the T. testudinum community light-sacurates at 700 to 800 $\mu E\ m^{-2}\ sec^{-1}$. Capone et al. (1979) estimates would fall in the range 630-1050. We interpret this as support for the oxygen technique in studies of community metabolism although problems still exist in terms of recycling and translocation processes. However, the basic arguments against O_2 are applicable to $^{14}CO_2$ studies (Kemp et al. 1980).

Nutrient status, i.e. principally nitrogen, is generally presumed to limit primary production in estuarine and marine ecosystems. Patriquin (1973) and Capone et al. (1979) have reviewed and summarized contemporary data on T. testudinum dominated communities. Our data suggests a positive response to nutrient enriched conditions. We propose that Estero Pargo is a nutrient limited as well as potentially light-limited environment. Nutrient enrichment (spikes) obviously result in changes in community behavior. The levels used, however, are probably never "seen" by the community. The community does respond and available nutrients NH_4^+ and NO_3^- significantly affect community behavior as measured by net apparent O_2 productivity.

Our preliminary analyses of metabolism in a tropical T. testudinum dominated seagrass community suggests that, overall, the community is responsive to both light and nutrient regimes. In Laguna de Terminos, our studies indicate that the seagrass community is an important component of autotrophic production. For example, if we assume a three fold increase in production at the Puerto Real site (R. Roman, pers. comm.), production would approximate 1350 to 1950 $gC\ m^{-2}\ y^{-1}$ which are among the higher values reported (see McRoy and McMillan 1977; Zieman and Wetzel 1980).

The values obtained for water column productivity were very low compared to open lagoon waters. Day et al. (1982) reported an annual average value of 1.2 $gC\ m^{-2}\ day^{-1}$. The low values for the water over the grassbeds is probably a result of several factors. The shallow water and high light levels probably lead to light inhibition as indicated by the extremely low rates measured at the surface. The plankton are probably also nutrient limited. The generally low nutrient levels probably result from high uptake by the plant community.

Finally, there is almost certainly heavy predation by consumers living in and around the grassbeds. These factors combine to limit the importance of phytoplankton in the grassbed community.

The partitioning of the bare substrate metabolism suggests that the benthic microalgae contribute significantly to the overall community productivity. The areal rates of productivity for the bare substrates within the grassbed repored here are overestimates, because the ratio of non-vegetated to vegetated areas were not determined and areal estimates corrected. However, the measurements in both bare substrate areas indicate that benthic microalgae contribute significantly to the overall plant community productivity. These findings suggest that a valuable heterotrophic food source exists here in the form of benthc microalgae.

Further study is obviously needed in this important ecosystem to elucidate seasonal and annual characteristics of carbon metabolism both by autotrophic and heterotrophic components of the community and investigate the apparent major controls on production: light, nutrients and their interaction.

Finally, there is almost certainly heavy predation by consumers living in and around the grassbeds. These factors combine to limit the importance of phytoplankton in the grassbed community.

The partitioning of the bare substrate metabolism suggests that the benthic microalgae contribute significantly to the overall community productivity. The areal rates of productivity for the bare substrates within the grassbed repored here are overestimates, because the ratio of non-vegetated to vegetated areas were not determined and areal estimates corrected. However, the measurements in both bare substrate areas indicate that benthic microalgae contribute significantly to the overall plant community productivity. These findings suggest that a valuable heterotrophic food source exists here in the form of benthc microalgae.

Further study is obviously needed in this important ecosystem to elucidate seasonal and annual characteristics of carbon metabolism both by autotrophic and heterotrophic components of the community and investigate the apparent major controls on production: light, nutrients and their interaction.

ACKNOWLEDGEMENTS

A first-time study of this type was necessarily plagued with many difficulties both procedural and logistical. We want to especially extend thanks to all our Mexican colleagues who accepted and worked closely with our contingent of fourteen scientists. Ramiro Roman, Director of the Centro de Ciencias del Mar Limnologia (UNAM), provided us lodging, space, logistical support and a friendly atmosphere. Our special thanks go to Dr. Alejandro Yanez and Drs. Vivianne Solis of the Universidad National Autonoma de Mexico (UNAM) for their many contributions to the effort.

Without the help of our other American colleagues, Drs. Walter Boynton, Michael Kemp, J. Court Stevenson, University of Maryland, and Dr. C. S. Hopkinson, University of Georgia, this effort could not have been done.

We also thank Ms. Carole Knox and Nancy White for their secretarial and editorial assistance.

LITERATURE CITED

Boynton, W. R. 1976. Energy basis of a coastal region: Franklin County and Apalachicola Bay, Florida. Ph.D. Thesis, Univ. Florida, Gainesville.

Capone, D. G., P. 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(19).

Day, J., R. Day, T. Barreiro and F. Ley-Lou. 1982. Primary production in the Laguna de Terminos, a tropical estuary in the southern Gulf of Mexico. Oceanologica Acta (in press).

Jones, J. A. 1968. Primary productivity by the tropical marine turtle grass, Thalassia testudinum Konig, and its epiphytes. Ph.D. Thesis, Univ. Miami, Coral Gables. 196 p.

Keefe, C. W. 1972. Marsh production: A summary of the literature. Contrib. Mar. Sci., Univ. Texas 16:163-168.

Kemp, W. M., M. R. Lewis, T. W. Jones, J. J. Cunningham, J. C. Stevenson and W. B. Boynton. 1981. Measuring productivity of submerged aquatic macrophytes: A comparison of methodologies. Final Report, US EPA Annapolis, Md.

Lot, A. 1977. General status of research on seagrass ecosystems in Mexico, pp. 233-245. In: C. P. McRoy and Carla Helfferich (eds.) Seagrass Ecosystems: A Scientific Perspective. Marcel Dekker, Inc., N.Y. 314 pp.

McRoy, C. P. and McMillan. 1977. Production ecology and physiology of seagrasses, pp. 53-87. In: C. P. McRoy and Carla Helfferich (eds.). Seagrass Ecosystems: A Scientific Perspective. Marcel Dekker, Inc., N.Y. 314 pp.

Nafziger, E. D. and H. R. Roller. 1976. Influence of leaf starch concentration on CO_2 assimilation in soybean. Plant Physiol. 57:560-563.

Odum, H. T. 1963. Productivity measurements in Texas turtle grass and the effects of dredging an intracoastal channel. Publ. Inst. Mar. Sci. Texas. 9:45-58.

Odum, H. T. 1967. Biological circuits and the marine systems of Texas, pp. 99-157. In: T. A. Olson and F. J. Burgess (ed.) Pollution and Marine Ecology, Interscience Publishers, N.Y.

Odum, H. T. and C. M. Hoskin. 1958. Comparative studies of the metabolism of marine waters. Publ. Inst. Mar. Sci. Univ. Texas 5:16-46.

Patriquin, D. G. 1972. The origin of nitrogen and phosphorus for growth of the marine angiosperm Thalassia testudinum. Mar. Biol. 15:35-46.

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

Pomeroy, L. R. 1960. Primary productivity of Boca Ciega Bay, Florida. Bull. Mar. Sci. Gulf Carib. 10(1):1-10.

Thorhaug, A. and R. D. Sterns. An ecological study of Thalassia testudinum in unstressed and thermally stressed estuaries. Univ. Miami, unpubl. ms.

Westlake, D. F. 1974. Macrophytes, pp. 25-40. In: R. A. Collenweider (ed.). Manual on Methods for measuring primary production in aquatic environments, 2nd Ed., Int. Biol. Program Handbook 12. Blackwell Scientific Publ., Oxford.

Wetzel, R. L., R. F. van Tine, and P. A. Penhale. 1981. Light and submerged macrophyte communities in the Chesapeake Bay: A Scientific Summary. SRAMCOE 260, College of William and Mary, Virginia Institute of Marine Science, Gloucester Point, VA. 58 pp.

Wetzel, R. L. and R. F. van Tine (eds.). 1982. Submarine Light Quantity and Quality in the Lower Chesapeake Bay and Its Potential Role in the Ecology of Submerged Seagrass Communities. Final Grant Report, nos. R805974 and X003245, U.S. EPA, Chesapeake Bay Program Annapolis, Maryland.

Zieman, J. C., Jr. 1968. A study of the growth and decomposition of the seagrass, Thalassia testudinum. M.S. Thesis, Univ. Miami, Coral Gables. 50 pp.

Zieman, J. C., Jr., and R. G. Wetzel. 1980. Productivity in seagrasses: Methods and rates, pp. 87-116. In: R. C. Phillips and C. P. McRoy (eds.). Handbook of Seagrass Biology: An Ecosystem Perspective. Garland STPM Press, N.Y. 353 pp.

END
DATE
FILMED
2-23-89
NTIS