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THE FUNCTIONAL ECOLOGY OF SUBMERGED AQUATIC VEGETATION
IN THE LOWER CHESAPEAKE BAY

by

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Annual Data Report

for

EPA/CBP Grant No. R805974

to

Mr. Thomas W. Nugent
U.S. Environmental Protection Agency
Region III
6th & Walnut Street
Philadelphia, PA. 19106

Project Officer

November, 1979

Executive Summary

The research program, "The Functional Ecology of Submerged Aquatic Vegetation in the Lower Chesapeake Bay" (EPA/CBP Grant No. R805974), is an integrative effort composed of seven principal investigators. The research team has worked since July 1978 at one study site, the Vaucluse Shores area, to develop and institute a coherent research program on SAV ecological relationships.

The principal studies have focused on plant productivity, metabolism and nutrient cycling, the role of resident consumers in SAV community dynamics, the role of migratory species and efforts to develop a realistic, ecosystem simulation model of SAV communities.

The preliminary results of the first years study in these research areas are contained in the following report. Many interpretations remain preliminary at this time. We welcome comments and criticisms and in particular ideas concerning data interpretation.

Questions concerning specific aspects of the various sections should be addressed to the following:

1. Productivity, Metabolism and Nutrient Cycling; R. L. Wetzel
2. Resident Consumers; R. J. Orth
3. Migratory Consumers; J. V. Merriner
4. Ecosystem Modelling; R. L. Wetzel

The above principal investigators are all members of faculty and staff of the Virginia Institute of Marine Science and School of Marine Science, College of William and Mary, Gloucester Point, Virginia 23062.

R. L. Wetzel, Ph.D.
Program Manager

Productivity, Nutrient Cycling and Associated Microbial
Metabolic Activity in Eelgrass Communities in
the Lower Chesapeake Bay

R. L. Wetzel, K. L. Webb and P. A. Penhale

INTRODUCTION

The productivity of eelgrass communities in temperate zone estuaries along the U.S. East coast is comparatively very high (Dillion, 1971; Thayer, et al., 1975; Penhale, 1977). Primary production in submerged aquatic vegetation communities is partitioned among several components; Zostera marina, Ruppia maritima, epiphytes, benthic macro- and microscopic algae, and phytoplankton. Thayer et al., (1975) reports an annual average production for eelgrass, Zostera marina, in North Carolina of $350 \text{ gC.m}^{-2}.\text{yr}^{-1}$. Associated macrophytes in this community produce an approximately equivalent amount, $300 \text{ gC.m}^{-2}.\text{yr}^{-1}$ (Thayer et al., 1975). Partitioning of epiphytic and eelgrass production in this community was investigated by Penhale (1977). Working in a recently established Zostera community, she determined that approximately 25% of the total standing stock (epiphytes & Zostera) was epiphytic biomass and concluded that the attached epiphytes contributed 18% to productivity of the community. Assuming the same relationships hold for mature communities, production (exclusive of the phytoplankton and benthic microalgae) is on the order of $600\text{--}700 \text{ gC.m}^{-2}.\text{yr}^{-1}$. Although productivity studies per se are lacking

for the Chesapeake Bay, peak live biomass determinations, as a minimum estimate of annual production in the lower bay, suggest production is similar to the North Carolina area (Marsh, 1973; Orth, 1977).

The areal distribution of seagrass communities in mid-Atlantic estuaries is limited and generally only a few percent of total area. However, production on a unit area basis compares with salt marsh vascular plant production (Keefe, 1972). In certain estuarine areas, production by the submerged aquatic communities accounts for a significant fraction of total estuarine primary production (Thayer et al., 1975;) and can in large part be explained at the local level by basin morphology (Mann, 1975). In the lower Chesapeake, seagrass communities occupy approximately 8400 hectares in mesohaline and polyhaline regions of the Bay (Orth, Moore and Gordon, 1979).

Limitations on productivity in seagrass communities have been ascribed to several environmental and nutrient related parameters. The influence of light, temperature and salinity have received the major research effort (Bachman and Barilotti, 1976; Biebl and McRoy, 1971; Penhale, 1977; and references cited therein). It is generally accepted that the local light regime limits the subtidal distribution of Zostera; light, temperature and probably nutrient (nitrogen) regimes interact to control specific rates of productivity during the annual cycle, and geographically, temperature limits the distribution of the species.

Nutrient dynamics and specific aspects of mineral nutrient metabolism have received far less attention. For temperate zone seagrass communities along the U.S. East Coast few data are available to suggest the major routes for nutrient flux and for one of the major nitrogen production pathways, N-fixation, the reported data conflict (McRoy, et al., 1973; Patriguin and Knowles, 1972).

There is increasing evidence suggesting primary production in marine and estuarine systems is generally nitrogen limited (Postgate, 1971; Ryther and Dunstan, 1971, Valiela, et al., 1973; Gallagher, 1975; Pomeroy, 1975; Orth, 1977; and others). If temperate sea grass communities are limited by nitrogen, they may act as competitors with other estuarine components for available nutrients. With the data available, we can neither estimate the magnitude of the various nutrient interactions nor guess their functional significance within the seagrass community or the estuarine system as a whole.

Organic matter production, controls affecting the primary and annual rates of energy fixation and the mechanisms inputting energy-matter and nutrients to higher order trophic levels and supporting secondary production are thus not well-known. In this report, we present our studies focused on the above problems to investigate 1) plant distribution and relative abundance, 2) substrate-plant relations, 3) total community metabolism 4) SAV component studies and 5) nutrient exchange studies.

Study Site

Selection of the principal study site was decided by consensus of a five member research team associated with different aspects of seagrass research. An approximately 260 hectare submerged aquatic vegetation bed located in southeastern Chesapeake Bay in an area locally known as Vaucluse Shores was chosen. Geographically the area is situated approximately 37° 25' N. latitude, 76° 51' W. longitude. Criteria for site selection were;

1. The site has been previously studied and some background data exists,
2. the bed is well established and historically stable,

3. the area is relatively remote and unperturbed,
4. vegetationally, it contains the two dominant lower bay SAV species, Zostera marina and Ruppia maritima, and,
5. it is large enough to simultaneously accomodate varied studies and sampling regimes.

Also, the area was a site for intensive submerged vegetation mapping (completed July-August, 1978). During this exercise, permanent transects were established and were used for selection and identification of within-site sampling stations. Figure 1 illustrates the seagrass bed showing transects and the distribution of submerged vegetation. Figure 1 also illustrates the spatial heterogeneity and distribution of the submerged vegetation and indicates at least five distinct habitat types:

1. Ruppia maritima dominated community
2. Zostera marina dominated community
3. Mixed vegetation areas
4. Within-bed bare bottom or sand areas
5. Sand Bar

Sampling sites were selected for each of the areas between transects B and C and permanently marked (bouyed) to identify stations for routine studies.

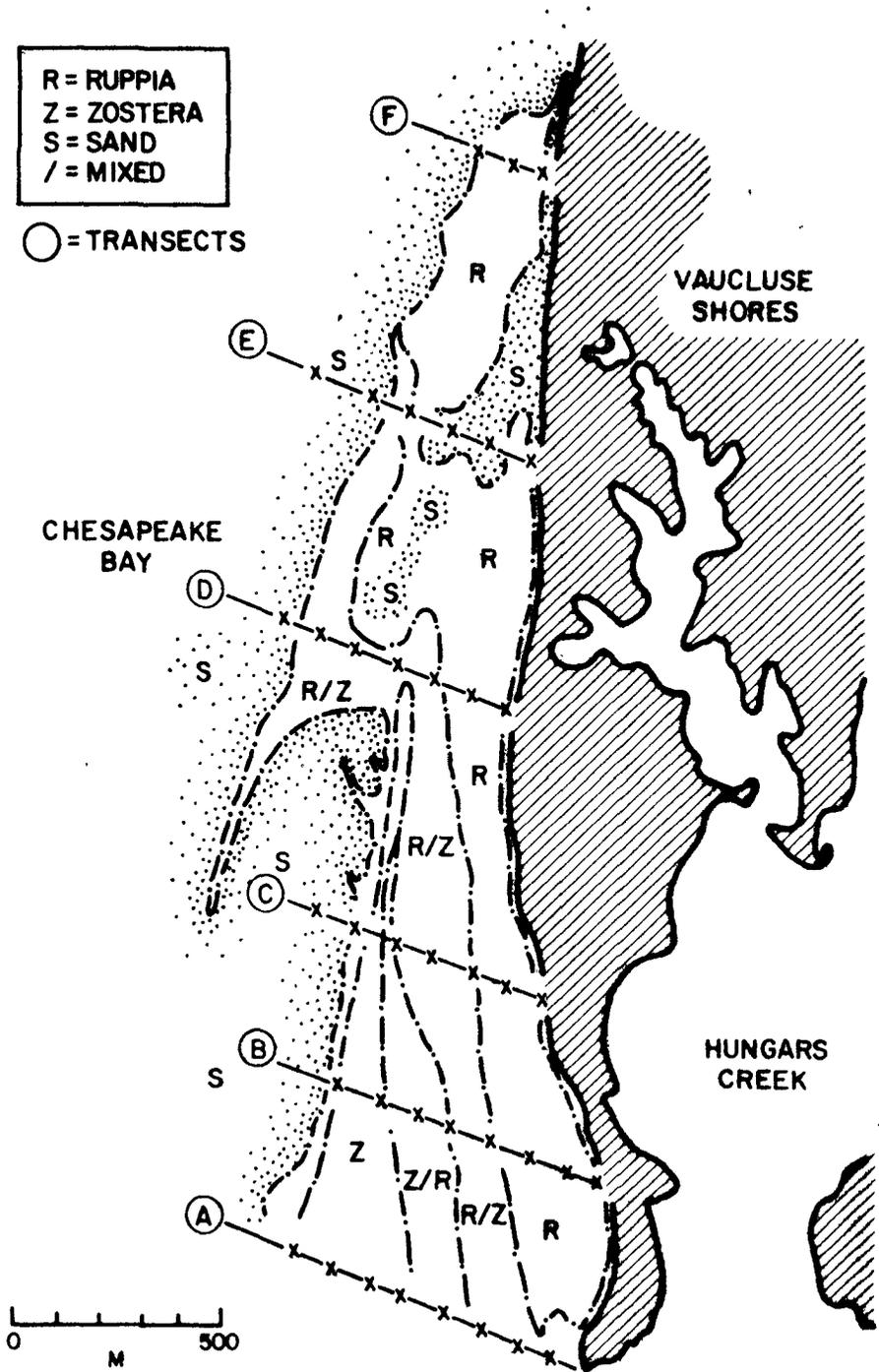
METHODS

Plant Distribution and Relative Abundance: Plant distribution and relative abundance was determined along transects A, B and C in July, 1979 to determine areal coverage by species and distribution with water depth. A line-intersect method was employed using two divers and is discussed in detail in Orth, Moore and Gordon, 1979. Briefly, the transects marked

Figure 1: Vaucluse Shores Study Site.

R = RUPPIA
Z = ZOSTERA
S = SAND
/ = MIXED

○ = TRANSECTS



in Figure 1 were followed from the sandbar beginning at low tide and progressing toward the shore. A 100 meter line marked in 10 meter intervals was employed along the transect line to locate point intersections for determining species composition and estimating percent cover. At each 10 meter intersection, a 0.5m^2 frame was randomly dropped and species composition determined and percent coverage estimated by a diver. This procedure was replicated twice at each sampling point. During each transect study, time and water depth were recorded at each station for comparison to a continuous relative tide height record kept near-shore and for calculation of bottom depth relative to mean low water (see Orth, Moore and Gordon, 1979). These data also provided direct comparisons with the previous mapping effort (July, 1978) by Orth, Moore and Gordon, (1979) for identifying any gross differences in distribution between years.

Substrate-Plant Relation: 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. Analyses performed in relation to community type were dissolved interstitial nutrients (NH_4^+ , NO_3^- , NO_2^- and PO_4^{-3}), adenosine triphosphate (ATP), water content, percent organic matter (POM), particulate organic carbon and nitrogen (POC and PON). Sediment samples were taken by hand 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. Laboratory processing consisted of decanting the top water layer, filtered, using glass fiber filters and analysed for dissolved nutrients. The cores were then extruded, split vertically and cut into 0-2, 2-5, 5-10, 10-15, 15-20 and >20 cm horizontal sections. For each core, processing consisted of: duplicate 1 cc plugs extracted using boiling 0.1 M sodium

bicarbonate for ATP analysis (Bancroft, Paul and Wiebe, 1974); the interstitial water extracted by centrifugation and glass-fiber filtered as above and the extracts analyzed either immediately or frozen (-20°C) until analysis; the remaining sediment fraction was frozen for later water content/organic matter and POC/PON analyses.

Determination of NO_3^- , NO_2^- , NH_4^+ and PO_4^{-3} utilized automated analysis techniques (EPA 1974). Modifications to these techniques include concentration of nitrate/nitrite reagents with a corresponding reduction in sampling rate to reduce volumes of reagent needed for analysis, a two reagent chemistry for phosphate determination resulting in better reagent stability and a two reagent chemistry for ammonia (Koroleff, 1970; Solórzano, 1969; Liddicoat, Tibbits and Butler, 1975; Gronutý and Gleye, 1975).

POC and PON analyses will be performed using a Perkin-Elmer Model 240B Elemental Analyzer.

Water content and organic matter content was determined on freshly frozen sediments by drying at 60°C to constant weight for water content and ashing @ 550°C for organic matter determination. All weights were determined to the nearest 0.01 mg.

Rooting depth was determined during July 1979 in the three major vegetation areas (i.e., Ruppia, Zostera and mixed areas) by hand coring using a 33 cm (diameter) acrylic corer. The cores (4 replicates per area) were taken 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.

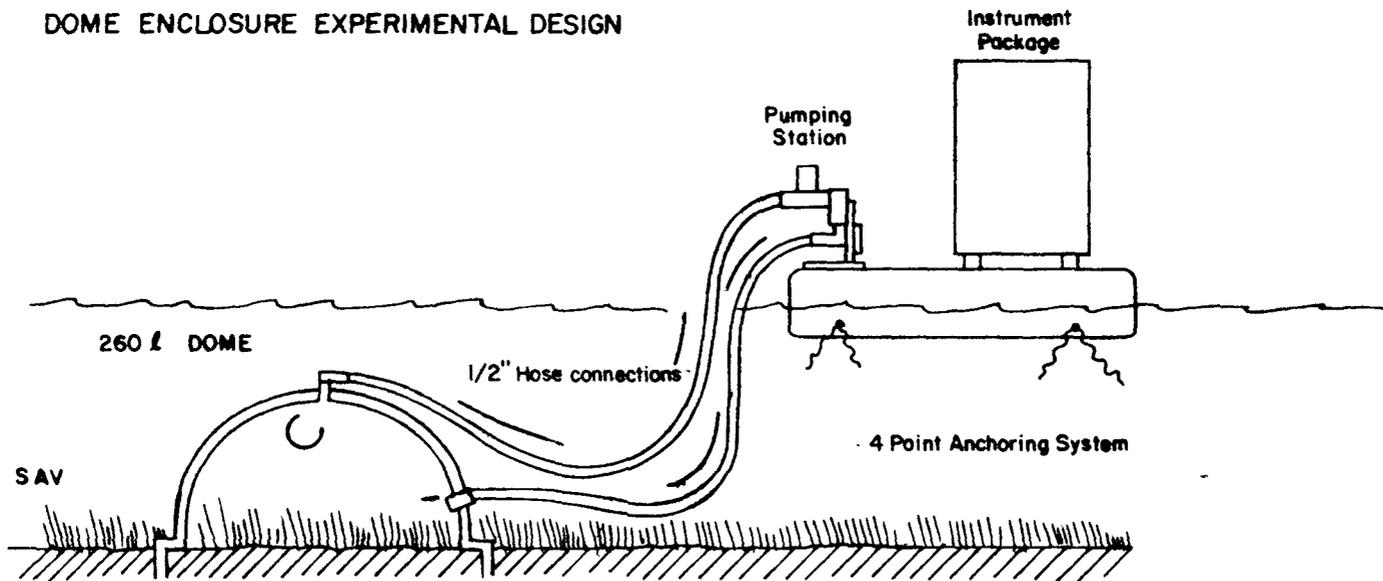
Total Community Metabolism: Total community metabolism (net community production) within the various habitats was determined using dome enclosures. The domes are hemispherical and measure approximately 1 m inside diameter by 0.5 height. Volume of the domes is ca. 260 liters and enclose a bottom area of 0.78 m². Areas within each SAV habitat type (Zostera, Ruppia, mixed vegetation, or bare bottom) were randomly selected between transects B and C for study. The domes are submerged by diver and mixed using a modified 12 VDC bilge pump in a closed loop. The domes were sampled through septums at regularly spaced time intervals for dissolved nutrients, temperature and dissolved oxygen. The dissolved inorganic nutrients (NH₄⁺, NO₂⁻, NO₃⁻ and PO₄⁻³) were determined on filtered 50 ml samples and analyzed as discussed previously. Dissolved oxygen was continuously monitored using temperature compensated polarographic (Clark-type) electrodes and calibrated using both water saturated-air nomographs and the Winkler technique (Strickland and Parsons, 1972). Experiments in each area lasted a minimum of 24 hours to bracket a complete diel cycle. The domes within each habitat and for each study were run in duplicate always and for some studies, four experimental domes were deployed. Figure 2 illustrates the general experimental design.

In addition to the parameters measured within the domes, ambient (outside water) samples were routinely taken for the same analyses. Light, as photosynthetically active radiation (PAR), was determined at the surface and routinely light profiles taken through the water column using a LI-COR 185A Quantum Meter.

At the termination of experiments conducted earlier in our program, 2 or 3 randomly placed 0.085 m² cores were taken from within the dome enclosed area to determine SAV biomass. Because of the high degree of variability in these samples, we have since harvested the entire

Figure 2: Dome Enclosure Experimental Design.

DOME ENCLOSURE EXPERIMENTAL DESIGN



dome enclosed area for biomass determination. Although very time consuming, we feel this is the only adequate way, at the present, to evaluate replicate dome variability.

SAV Component Studies: As discussed previously, the SAV community is composed of both autotrophic and heterotrophic components in addition to the dominant vascular plant species. Production and metabolism (respiration) by these components can significantly augment production and metabolism in the seagrass community. Studies of their production and metabolism have been recently initiated. We report here some preliminary findings relative to partitioning production and metabolism between components.

To date, component studies have focused on 1) the effects of light on total community metabolism and specific rates of CO₂ fixation, 2) partitioning O₂ and dissolved nutrient exchange between the above-ground plant community and the sediment substrate, 3) partitioning O₂ and dissolved nutrient exchange between the plankton, epiphytic, benthic microalgae and the SAV community.

The effect of light on total community metabolism was studied intensively during July, 1979 using the dome enclosures. Light was reduced by 53.3% and 85.7% in adjacent domes using netting and O₂ and nutrient exchange followed for 24 hours. The effects of light level on the specific rates of CO₂ fixation by intact plants has been evaluated routinely (monthly) since July, 1979 using a ¹⁴CO₂ incubation technique (Penhale, 1977) and light level modified by neutral density screening.

Partitioning O₂ and nutrient exchange between the above-ground SAV community and the sediment substrate was investigated in July, 1979 using dome enclosures. Areas in the Ruppia and Zostera dominated communities were clipped and all above-ground plant material removed in the area of dome placement. Adjacent non-clipped areas were also enclosed and

O₂ and dissolved nutrients determined over a 24 hour period.

Partitioning the major primary producer components has just begun. Production by the attached epiphytic community is being investigated using a ¹⁴CO₂ incubation technique (Penhale, 1977). Plankton community metabolism and primary production are being investigated using the standard light-dark bottle technique and ¹⁴CO₂ incubation technique respectively (Strickland and Parsons, 1972). Benthic microalgae metabolism is being studied using 1 liter in situ chamber incubations. Oxygen determinations from light and dark chambers are determined at routine sampling intervals on 10 ml fixed samples and titrated using a microliter buret (resolution = 0.1 ul). We present in this report some preliminary data to illustrate the experimental designs.

Nutrient Exchange Studies: Kinetic studies of dissolved inorganic nutrient exchange employs the same experimental design as the production/metabolism studies of plankton and SAV communities. The incubations (glass 300 ml bottles for plankton and domes for SAV habitats) are run at ambient levels and spiked (nutrient enriched) to approximately 10x ambient levels. Decay of the spiked samples is followed over time with the sampling intervals adjusted to the decay rate and continued sampling until ambient levels are reached. These studies are conducted simultaneously with the production/metabolism experiments. Analyses for NH₄⁺, NO₃⁻, NO₂⁻ and PO₄⁻³ are as previously discussed.

RESULTS

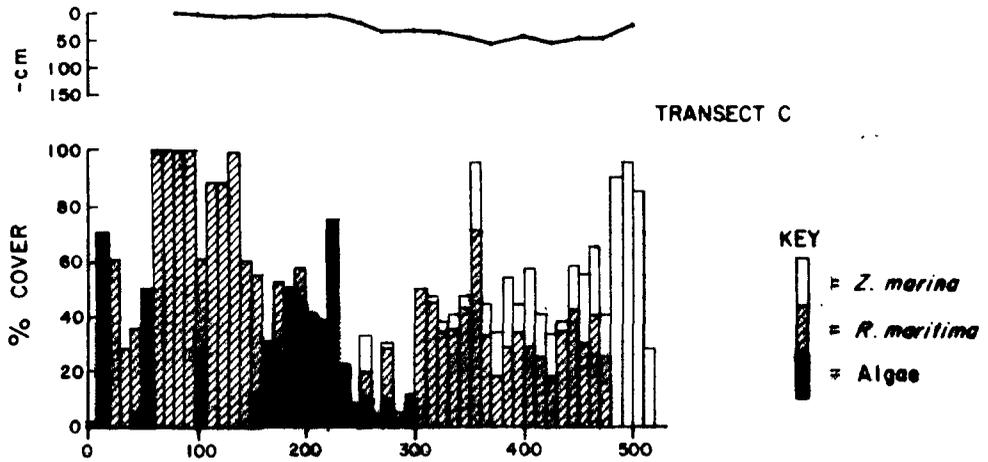
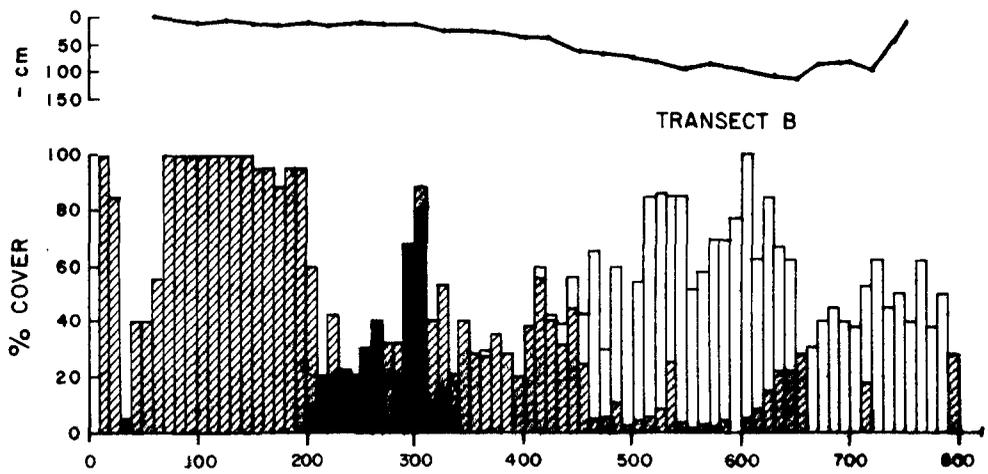
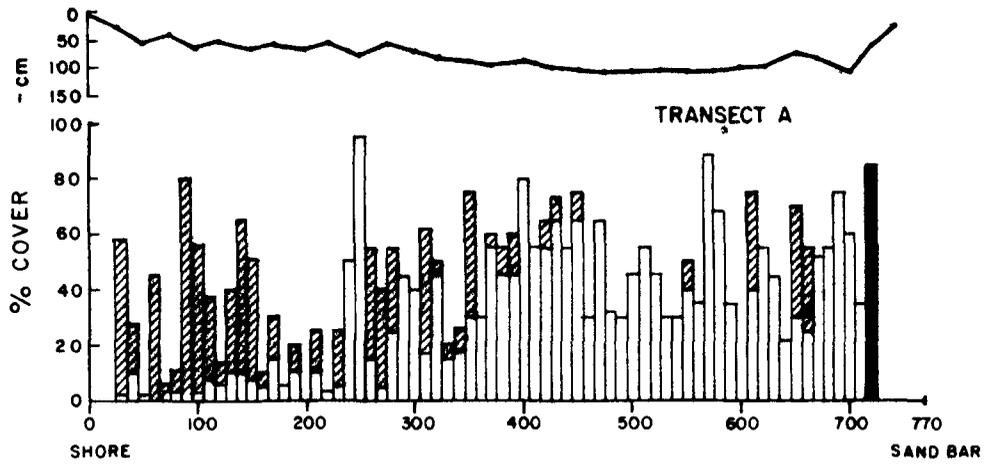
Plant Distribution and Relative Abundance: Plant distribution and percent cover, as a estimate of relative abundance, was determined along transects

A, B, and C in July, 1979. Figure 3 illustrates the distribution by species relative to water depth at mean low water and percent cover along the transects. Ruppia predominated in the shallower depths and Zostera predominated in the deeper areas (adjacent to the sand bar). In the shallower subtidal areas along transects B and C an unidentified algae contributed significantly to percent cover. These data support the general conclusions reported by Orth, Moore and Gordon (1979) of the depth dependent distribution of Ruppia - Zostera plant association but also indicate that the relationship is not a simple function of water depth alone. Ruppia occurs in the deeper areas generally dominated by Zostera (Transects A, B and C) and Zostera occurs in some shallower depths normally occupied only by Ruppia (Transect A).

Substrate - Plant Relationships: The results of the analyses for rooting depth of the dominant plant species in the three vegetated zones are presented in Table 1. The data suggest that in the Ruppia community a greater percentage of the below ground root and rhizome biomass is located in the top 5 cm and Zostera appears rooted deeper in the substrate. However, for all vegetated areas, greater than 98% of the root-rhizome system is located in the upper 10 cm of sediment.

Sediment profiles of dissolved interstitial NH_4^+ and NO_3^- and sediment ATP concentration for various times of year are presented in Figure 4 and Figure 5, respectively, for the four habitats within the seagrass bed. Table 2 summarizes the percent of total ATP (to a depth of 30 cm) contained in the top 5 and 10 cm core fractions. The data indicate both between habitat variability and suggest strong seasonal changes in all areas. The major distributional changes with depth for both NH_4^+ and ATP in the vegetated areas appears to occur at or near the maximum depth of rooting (see Table 1).

Figure 3: SAV Distribution and Relative Abundance along Transects A, B, and C, Vaucluse Shores, July 1979.



KEY
 □ = *Z. marina*
 ▨ = *R. maritima*
 ■ = Algae

TABLE 1: ROOTING DEPTH ANALYSES

SPECIES	DEPTH (CM)	$\bar{x} + S.D.$		
		% TOTAL WT.	% 0-5 CM	% 0-10 CM
<u>RUPPIA MARITIMA</u>	0-2	67 ± 9.7	89. ± 3.0	98. ± 1.0
	2-5	22 ± 10.0		
	5-10	9 ± 3.3		
	10-15	2 ± 0.96		
MIXED BED	0-2	55 ± 4.6	83 ± 11.	98 ± 0.6
	2-5	28 ± 15.2		
	5-10	15 ± 10.1		
	10-15	2 ± 2		
<u>ZOSTERA MARINA</u>	0-2	51. ± 14.	93. ± 3.2	99 ± 0.6
	2-5	42. ± 15.9		
	5-10	6. ± 2.6		
	10-15	0.7 ± 0.58		

Figure 4: Sediment Profiles of NH_4^+ and NO_3^- ; October 1978 and July 1979.

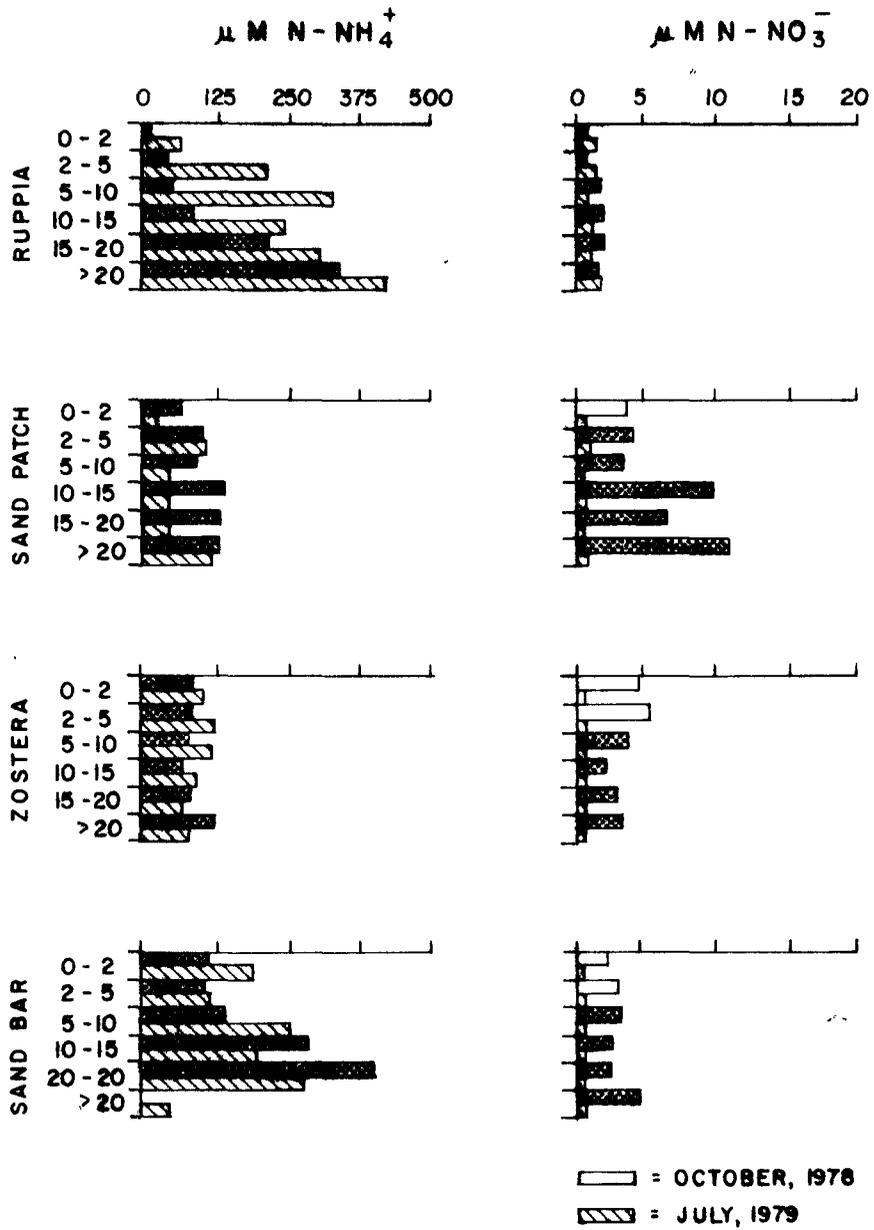
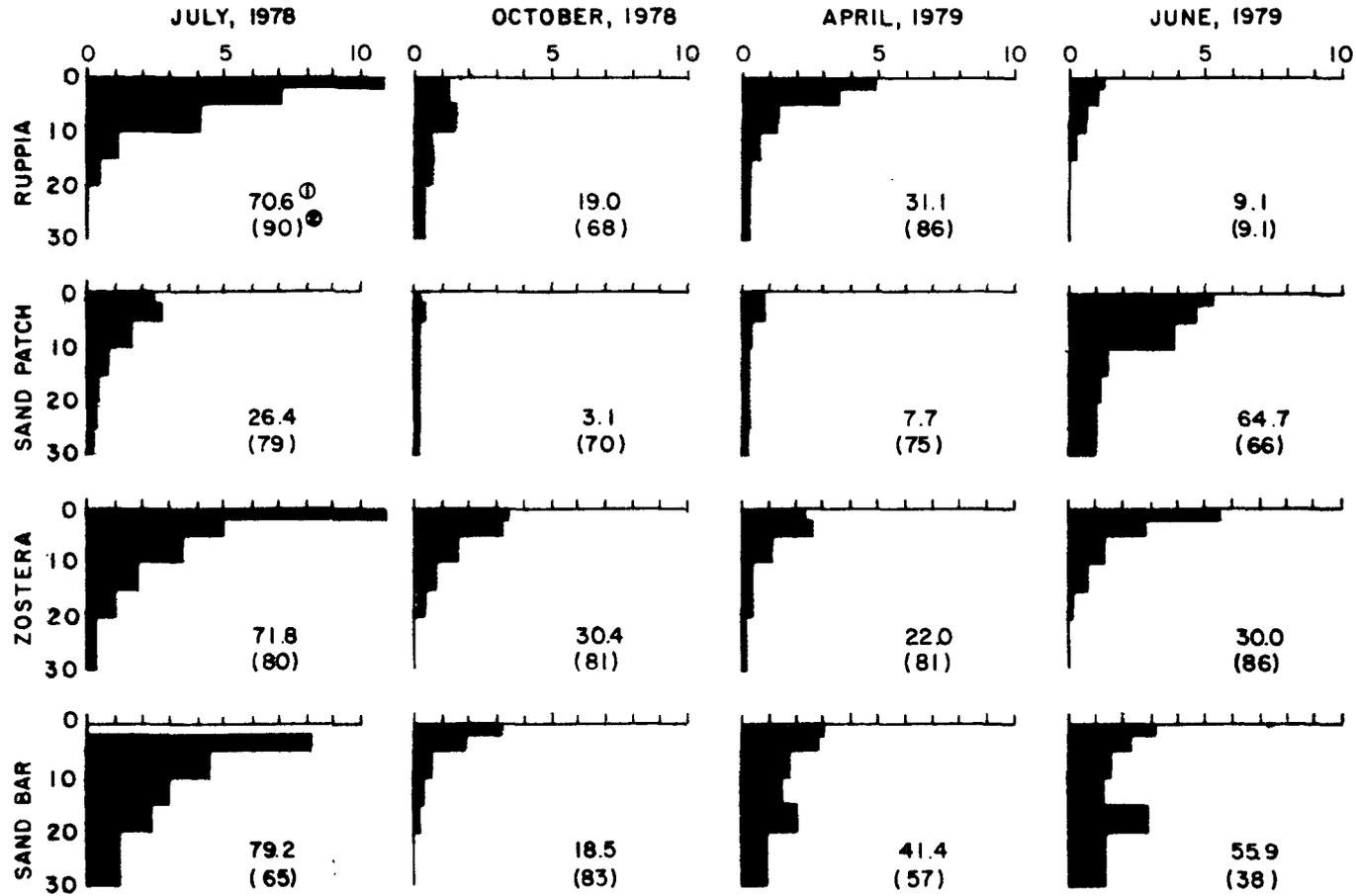


Figure 5: Sediment Profiles of ATP by habitat for various times of year.

$\mu\text{g ATP} \cdot \text{cc}^{-1} (\times 10^{-1})$



① $\Sigma \mu\text{g ATP to a depth of 30 cm}$

② % ATP in 0-10 cm depth interval

TABLE 2: PERCENT TOTAL ATP IN 0-5 AND 0-10 VERITAL CORE SECTIONS

SPECIES	DEPTH (CM)	78 JULY	78 OCT	79 APRIL	79 JUNE
<u>RUPPIA</u>	0-5	61	32	65	58
	0-10	90	68	86	91
SAND PATCH	0-5	49	43	53	37
	0-10	79	70	75	66
MIXED	0-5	N.D.	46	48	35
	0-10	N.D.	82	70	55
<u>ZOSTERA</u>	0-5	55	54	56	65
	0-10	80	80	81	86
SAND BAR	0-5	37	64	35	23
	0-10	65	83	57	38

Total Community Metabolism: Tables 3 and 4 summarize the results of the dome O_2 exchange studies. The 24 hour rate estimates net community daily production or consumption of oxygen and is the simple difference between starting and ending concentrations. The mean apparent O_2 production rates during the daylight period were determined by averaging all daytime rates from the domes. The mean apparent O_2 consumption (community respiration) rates were determined by averaging all nighttime rates from the domes.

Net Community Production (NCP) as estimated by the 24 hour difference was highly variable in both Ruppia and Zostera areas for the periods reported. In Ruppia, the highest negative values (6/79 and 7/79) for community consumption over a 24 hour period occurred when low tide coincided with the period of maximum insolation and may suggest inhibition of photosynthesis under high light regimes. (PAR = 1134 to 1323 $\mu E \cdot m^{-2} \cdot sec^{-1}$ at bottom). At other times of the year, NCP was generally positive except during the September, 1979 study. During this period high tide occurred during the middle of the day and light was reduced (PAR = 30 - 300 $\mu E \cdot m^{-2} \cdot sec^{-1}$) during the period of maximum potential photosynthetic activity. In the Zostera area, NCP was variable and for the majority of dome studies (4 of 7) was negative. Net negative values for O_2 exchange in Zostera were associated with high tides during the day coinciding with periods of maximum insolation (PAR = 350 $\mu E \cdot m^{-2} \cdot sec^{-1}$, 1330 hours at the bottom in September, 1979). However in July 1979, NCP was highly positive with high tide occurring during the middle of the day. During this period water turbidity was low, no cloud cover and maximum insolation for the dates were reported (100% maximum sunshine, Norfolk Weather Station). Light reaching the bottom during the study period ranged from 500 to 760 $\mu E \cdot m^{-2} \cdot sec^{-1}$.

TABLE 3: SUMMARY OF DOME O₂ EXCHANGE STUDIES; RUPPIA MARITIMA.

DATE (MO/DY/YR)	TIDE (TIME)	24 HR ⁻² (MG O ₂ · M ⁻²)	\bar{X} DAY ² (MG O ₂ · M ⁻² · HR ⁻¹)	\bar{X} NIGHT ² (MG O ₂ · M ⁻² · HR ⁻¹)
10/11/78		+863.	339.	-325.
10/12/78		- 99.6*	392.*	-246.*
4/27/79	0947 HT	--	--	- 84.8
4/28/79	1030 HT	+127.	86.4	-144.
5/2/79	1343 HT	- 78.5	108.	-122.
5/2/79	1435 HT	+181.*	165.*	-154.*
6/23/79	1416 LT	--	398.	--
6/23/79	1416 LT	-1760.	418.	-491.
7/17/79	0926 LT	-1089.	286.	-309.
7/18/79	1027 LT	790.*	365.*	-236.*
7/20/79	1126 LT	+332.	129.	-282.
8/27/79	1156 HT	+498.	+335.	-136.
8/27/79		+996.*	+339.*	-123.*
9/25/79	1122 HT	-108.	+116.	- 66.
9/25/79		+266.*	+359.*	-116.*
10/24/79	1056 HT	+266.	304.	- 37.2
10/24/79		+448.*	335.*	- 25.2*

* = NUTRIENT SPIKE EXPERIMENT

TABLE 4: SUMMARY OF DOME O₂ EXCHANGE STUDIES; ZOSTERA MARINA

DATE	TIDE (TIME)	$\frac{24}{\text{HR}} \frac{\text{HR}^2}{\text{M}^2}$ (MG O ₂ · M ⁻²)	\bar{X} DAY ⁻² · HR ⁻¹ (MG O ₂ · M ⁻² · HR ⁻¹)	\bar{X} NIGHT ⁻² · HR ⁻¹ (MG O ₂ · M ⁻² · HR ⁻¹)
10/16/78		--	196.	-86.3
10/17/78		+239.	193.*	-226.*
4/30/79	1202 HT	-322.	276.	-177.
6/25/79	0947 HT	-883.	212.	-99.6
6/26/79	1029 HT	- 39.8*	335.*	-26.6*
7/26/79	1040 HT		+333.	-86.2
7/27/79	1117 HT	+551.*	+307.*	-133.
7/27/79		+770.*	+385.	-133.
8/29/79	1321 HT	-2025. -1643.*	116. 178.*	-199. -206.*
9/27/79	1250 HT	-926. -1368.*	252. 219.*	-166. -173.*
10/29/79	1535 HT	+598.* +531.*	316. 261.*	-- -81.*

* = NUTRIENT SPIKE EXPERIMENT

Mean hourly O_2 production rates during the day and mean hourly O_2 consumption during the night were less variable both among and between vegetated communities. O_2 production in both communities peaked in early summer followed by a late summer depression and again increased in early fall. O_2 consumption in the Zostera community remained relatively constant during the period April to October, 1979 with values ranging from 100-200 $mgO_2 \cdot m^{-2} \cdot hr^{-1}$. O_2 consumption in the Ruppia community varied over the range of $-50 mgO_2 \cdot m^{-2} \cdot hr^{-1}$ to a late June maximum of $-570 mgO_2 \cdot m^{-2} \cdot hr^{-1}$. During this later period of maximum values (June to July) it was observed that Ruppia was highly colonized by hydrozoans.

Nutrient Exchange Studies: The experimental approach we have used to produce the kinetic parameters for relationships between nutrient uptake and rate of utilization have been in part to enrich the dome incubation chambers to elevated concentrations and follow the concentration decay with time. Uptake kinetics for inorganic nutrients and other reactive substrates are most often described by the Michaelis-Menten enzyme-substrate analogy: i.e., a rectangular hyperbola of the rate vs substrate concentration or by the hyperbola plus a linear diffusion component. The relationship is described mathematically by the equation:

$$V = \frac{V_m \cdot [S]}{[S] \cdot k_s}$$

where: V_m = maximum rate
 $[S]$ = substrate concentration
 k_s = substrate concentration at which $V = 0.5 V_m$

The equation is modified by:

$$V = \frac{V_m \cdot [S]}{[S] \cdot k_s} + d \cdot [S]$$

where d = diffusion constant

to include diffusion. The mathematical description is both useful for data reduction, understanding the system and for modelling purposes. The decay curves resemble the solid line of Fig. 6C for the hyperbola represented in Fig. 6A. The linear portion of the decay curve is representative of the maximum rate. In some experimental situations the concentration never decays to zero but comes to equilibrium at some positive concentration (dotted lines of Fig. 6C & 6D). This is interpreted as either (a) there exists a threshold concentration below which there is no uptake or (b) there are components of the system which are producing the material in question and this is the concentration at which the processes balance. If there is a diffusion component (as there often is for ammonia) the decay curve will resemble that of Fig. 6B and there will be no linear portion of the uptake curve, i.e., the rate cannot be saturated. At this point in time our data analysis has progressed only to the point of calculating V_{\max} , i.e., the saturated rate.

Figures 7A and B illustrate the decay (uptake) of NH_4^+ in replicate experiments in the Ruppia community. Uptake was extremely rapid during the photoperiod (1200 to 1600 hours) and decayed asymptotically, to ambient levels in less than 24 hours. The data suggest at least a two component system perhaps related to photoperiod. Figures 7C and D illustrate the decay (uptake) of PO_4^{3-} and NO_3^- during the same period in the Zostera area. NO_3^- uptake followed a pattern similar to NH_4^+ in the Ruppia area but appears slower from inspection of the slopes of the decay curves. Figures 8A and B illustrates the uptake of NH_4^+ and NO_3^- in a mixed spiking experiment (i.e. both NH_4^+ and NO_3^- added to the domes in combination). The initial decay rates indicate NH_4^+ is taken up faster than NO_3^- , and suggest a preference for NH_4^+ . Figure 9 illustrates the uptake of NH_4^+ in a double spiking experiment in the Zostera community

Figure 6: Michaelis-Menten Uptake vs Substrate Concentrate Curves with and without a Diffusion Component (A & B) and Typical Decay Curves for Substrate Utilization (C & D).

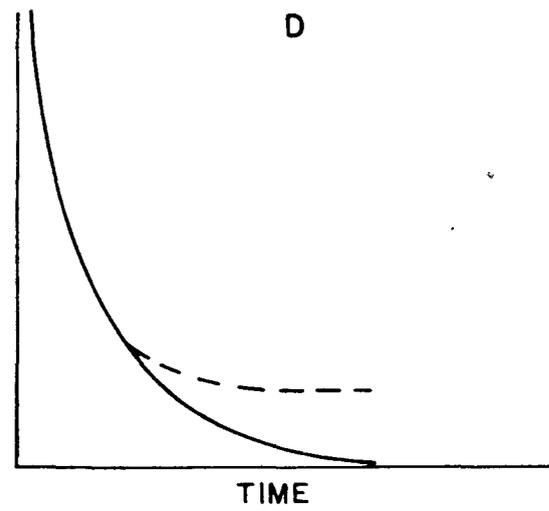
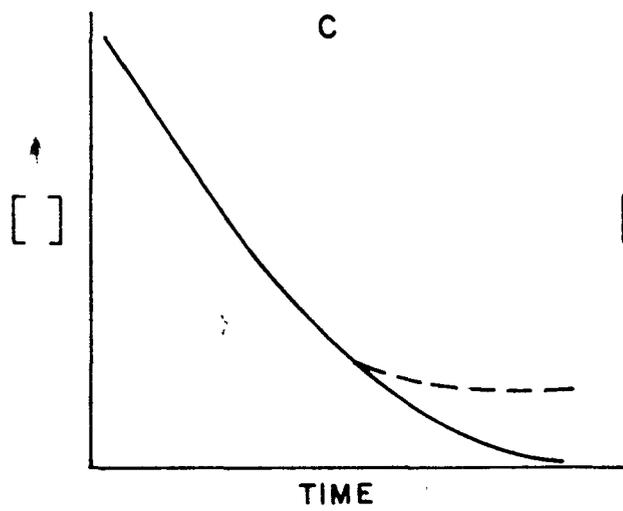
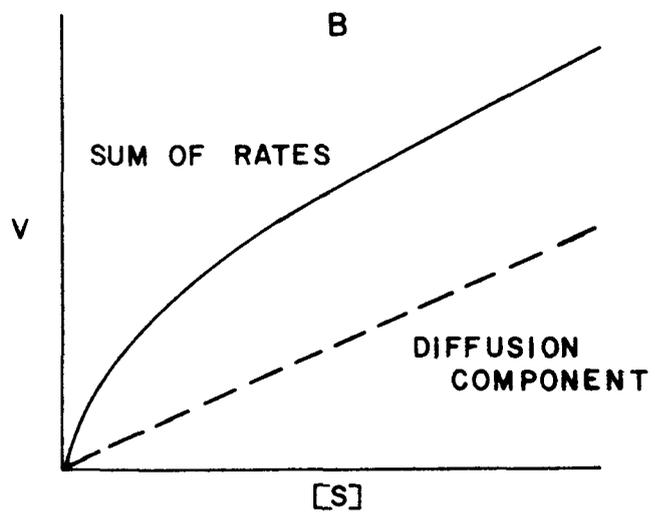
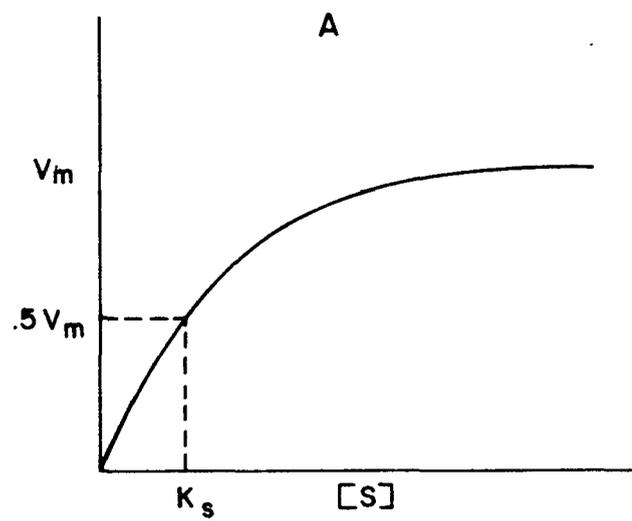


Figure 7: Decay Curves for NH_4^+ Uptake in the Ruppia Community and PO_4^{3-} and NO_3^- Uptake in the Zostera Community (October 1978).

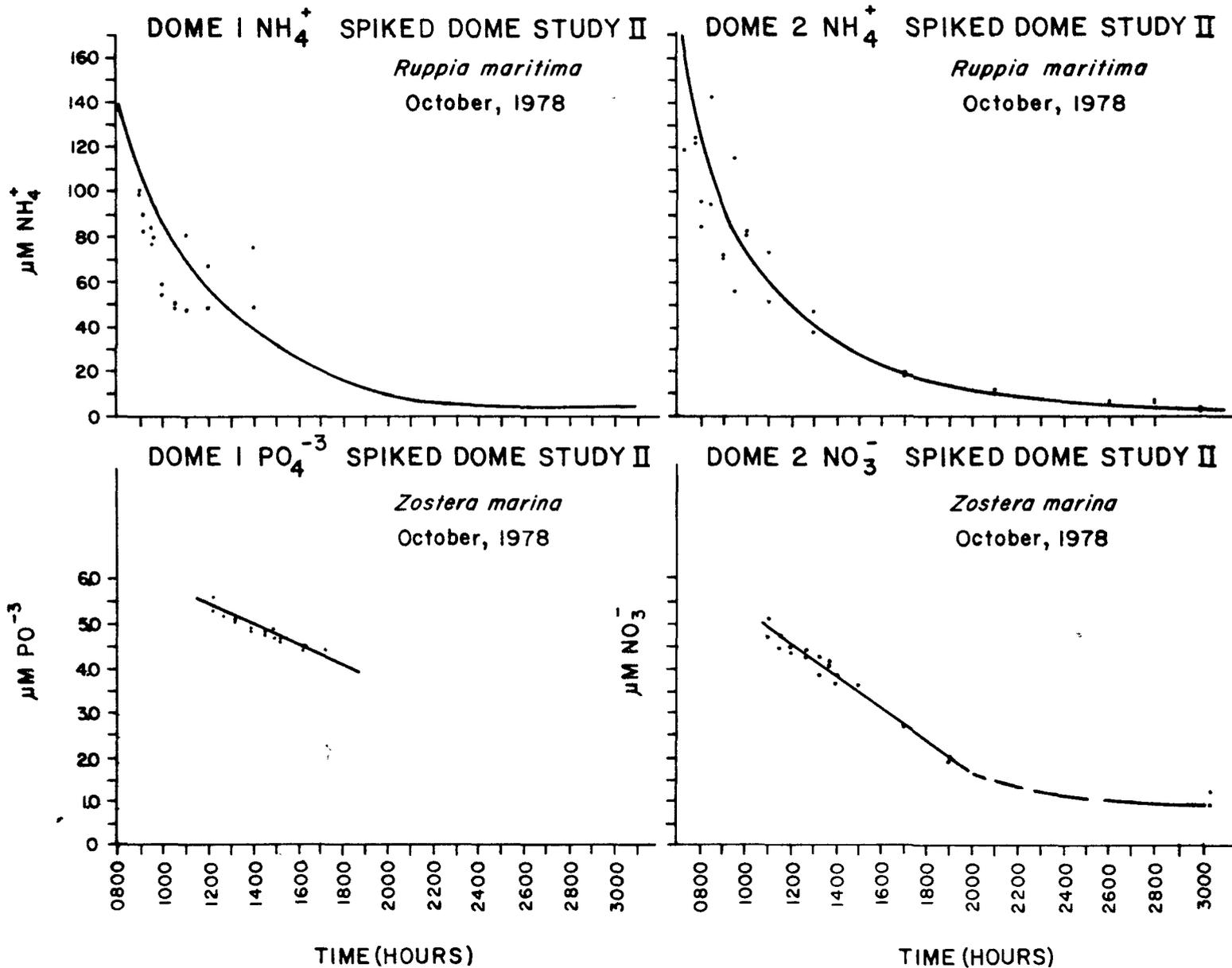


Figure 8: Decay Curves for NH_4^+ and NO_3^- Uptake in Ruppia Community (July, 1979).

$\text{NH}_4^+ - \text{NO}_3^-$ SPIKE
Ruppia maritima
 JULY 1979

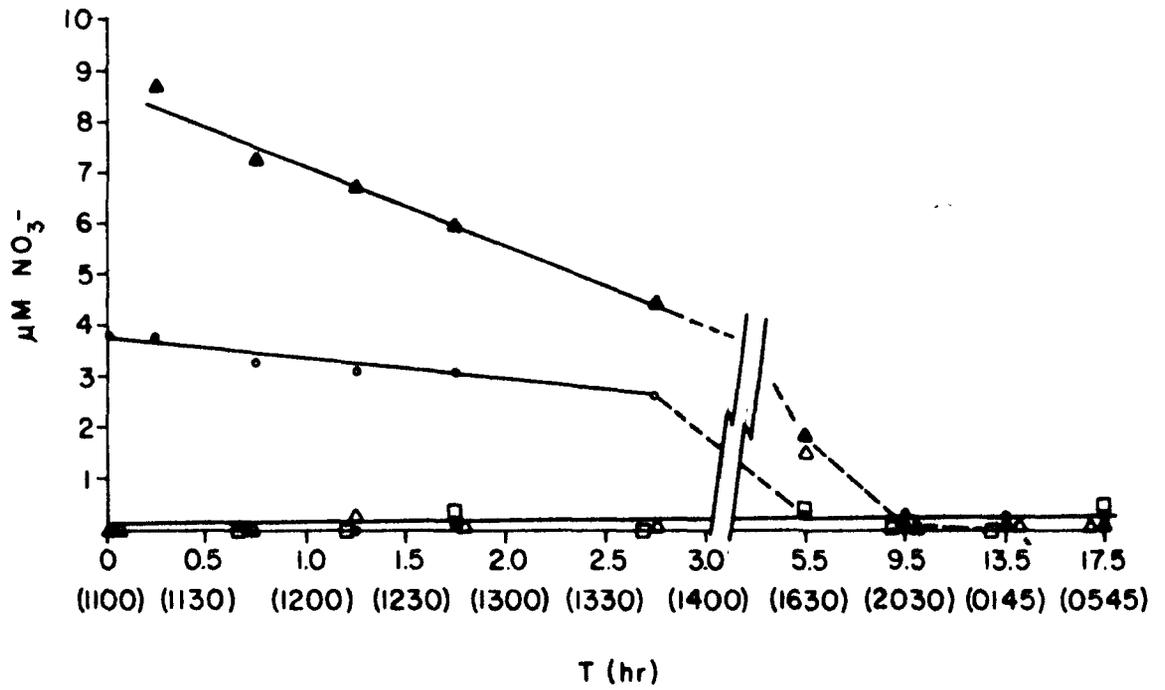
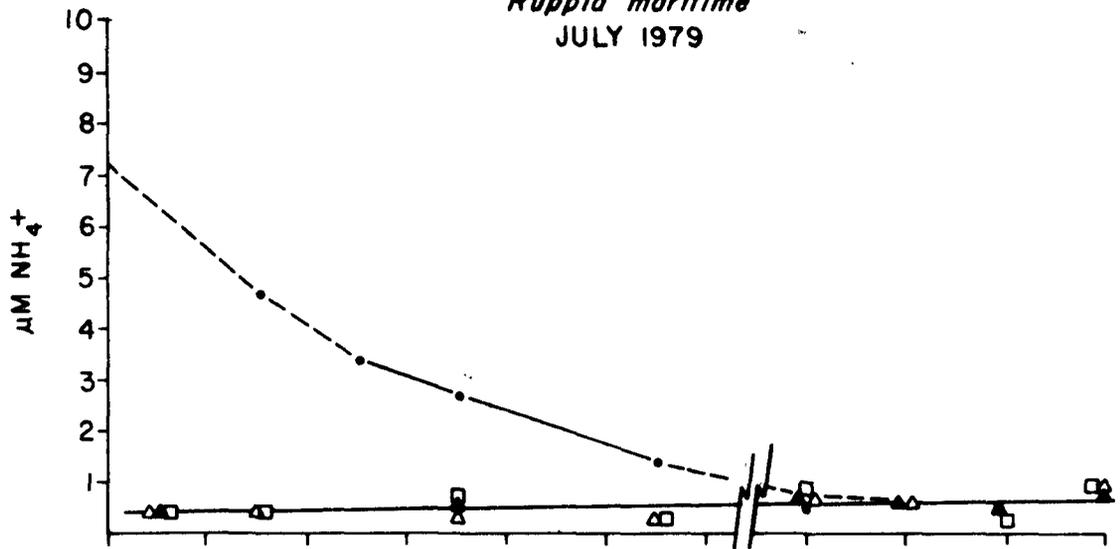
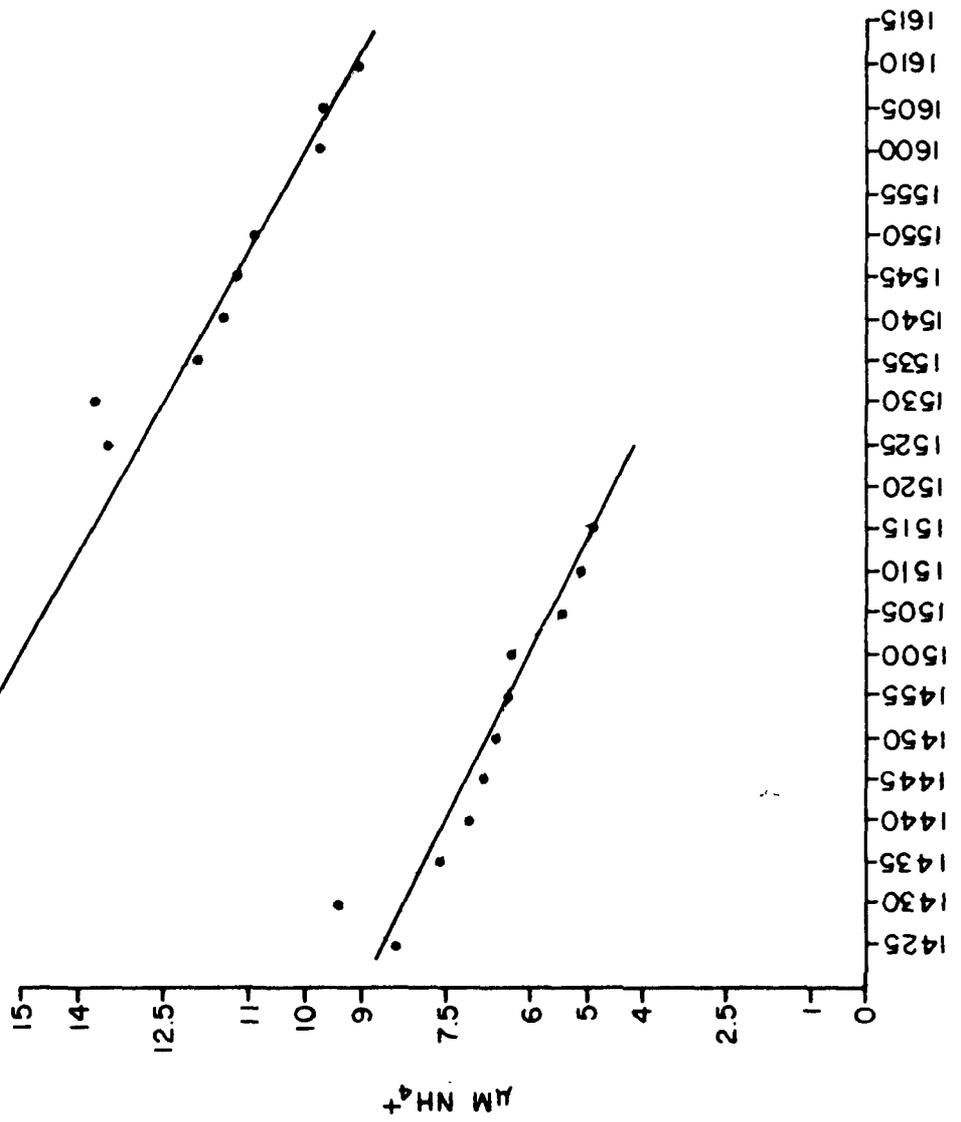


Figure 9: Decay Curves for Double NH_4^+ Spike in Zostera Community (July, 1979).

NH₄⁺ SPIKE
Zostera marina
JULY 1979



during the day. The calculated uptake rates from the two spikes are not significantly different and indicate the uptake system is saturated and operating at V_{max} .

Table 5 summarizes the summer experiments from the Ruppia and Zostera areas in terms of nitrogen uptake rates assuming saturated systems kinetics. These few data suggest that V_m is similar for NH_4^+ and NO_3^- and the rates appear higher in the Zostera community. During this sampling period, the ambient or control domes were variable in relation to NH_4^+ and NO_3^- behavior and indicated no net uptake or release of either nitrogen species except for the August, 1979 study in Zostera. In the ambient dome, a net release of $+110 \text{ ug} \cdot \text{at} \cdot \text{m}^{-2} \cdot \text{hr}^{-1}$ and NH_4^+-N was realized.

These types of experiments have been done for each study period indicated on the table's summarizing the O_2 exchange data. However, the data on nitrogen exchange has not been reduced to the point where kinetic parameters can be calculated. The above data is presented to illustrate the potential information contained in the experimental designs and data analysis technique employed with such information.

SAV Component Studies: Studies were initiated during 1978 and 1979 to partition total community metabolism and nutrient exchange into water column processes, above-ground plant community processes, sediment processes and to begin studies on the relations between light, nutrient exchange and community metabolism. These efforts are just beginning and the experiments reported herein were designed primarily to illustrate our approach and as screening experiments for designing and allocating future research effort (1980).

Photosynthesis and respiration of the plankton community was investigated using light and dark bottle incubations (300 ml BOD bottles) and the $^{14}CO_2$ incubation technique using various light regimes. Table 6

TABLE 5: SATURATED NITROGEN UPTAKE RATES.

DATE		UG·AT N·M ⁻² ·HR ⁻¹	
		NH ₄ ⁺	NO ₃ ⁻
JULY, 1979	<u>RUPPIA</u>	-441. -326.	-417. -266.
	<u>ZOSTERA</u>	-1710. -144.	--- ---
	SAND PATCH	---	-913. -365.
AUGUST, 1979	<u>RUPPIA</u>	-200. -610.	-234. -475.
	<u>ZOSTERA</u>	-249. -1410. +110.*	-112. -938.

*AMBIENT (NON-SPIKED) DOME.

TABLE 6: SUMMARY OF LIGHT-DARK BOTTLE EXPERIMENTS.

	\bar{x} GP ¹	MG C · M ⁻³ · HR ⁻¹ NP ²	R ³
JULY, 1978	39.4 (6.0)	19.9 (5.2)	23.4 (4.4)
OCTOBER, 1978	---	63.8 (+1.9)	---
APRIL, 1979	63.6 (40.8)	46.4 (39.8)	21.6 (9.0)

1. GROSS PRODUCTION
2. NET PRODUCTION
3. RESPIRATION

TABLE 7: PHYTOPLANKTON PHOTOSYNTHESIS

DATE	P_{MAX} (MG C M ⁻³ HR ⁻¹)	I_K (U E M ⁻² S ⁻¹)
JULY, 1978	180.	75.
OCT., 1978	93.	140.
JULY, 1979	160.	83.

TABLE 8A:

TIME (H)	PHOTOSYNTHESIS: PERCENT OF TOTAL IN 15 UM & LESS FRACTION.	CHLOROPHYLL A: PERCENT OF TOTAL IN 15 UM & LESS FRACTION.	
	$\text{MG C} \cdot \text{M}^{-3} \cdot \text{HR}^{-1}$	$\text{MG CHL}_A \cdot \text{L}^{-1}$	
		DRIFT STUDY	BAG ENCLOSURE
1000	67.	43.	43.
1400	82.	103.	64.
1800	71.	99.	86.
2200	75.	80.	78.
0600	83.	102.	78.

TABLE 8B:

TIME	$\text{UG CHL}_A \cdot \text{L}^{-1}$ (\pm S.D.)			
	DRIFT STUDY		BAG STUDY	
	T	F	T	F
1000	10. \pm .66	4.28 \pm .128	10. \pm .66	4.28 \pm .128
1400	2.81 .064	2.88 .192	5.61 .279	3.58 .064
1800	2.5 .36	2.48 .256	4.37 .144	3.73 .064
2200	4.11 .179	3.29 .128	4.5 .38	3.55 .111
0600	1.99 .192	2.03 .256	4.54 .111	3.55 .000

summarizes light-dark bottle studies for various seasons as measures of community metabolism. Characterization of phytoplankton photosynthesis for various seasons and light saturated rates are summarized in Table 7.

The light intensity photosynthesis relationship can be described by a hyperbola where P_{\max} is the maximum rate of photosynthesis and I_k is the light intensity at which the initial slope would intersect the P_{\max} value if it were extended. These values will be used to model phytoplankton production as well as indicate the physiological state of the phytoplankton.

The phytoplankton responsible for most of the primary production in Chesapeake Bay as well as other estuaries are usually the very small forms, i.e. less than 15 micrometers in diameter. During July 1979, we monitored both the total (T) chlorophyll a and the chlorophyll a in the size fraction less than 15 μm (F). Samples were taken both from a boat drifting with the water mass across the grass bed and from a large bag enclosure filled at the start of the "drift study" and kept suspended at the surface of the water column. Photosynthesis was measured on water samples taken from the middle of the grass bed. Table 8A and B summarize the results of these analyses. Table 8A summarizes chlorophyll a and photosynthesis distribution by phytoplankton size class. Table 8B summarizes chlorophyll a concentrations for the total (T) and less than 15 μm size fractions (F). Table 9 summarizes the values for P_{\max} and I_k of the light photosynthesis relationship for the total (T) and less than 15 μm size fraction (F) during the study. All data in the above studies is for July 28 to 29, 1979.

The effect of light reduction (shading) on total community metabolism in the Zostera area was studied in July, 1979. Shades were constructed of seine netting to reduce ambient light in the dome enclosures by approximately 50 and 85 percent. Table 10 summarizes the data for O_2

TABLE 9:

RELATIONSHIP BETWEEN P_{MAX} AND I_K FOR TOTAL (T) AND LESS THAN 15 μM FRACTION (F); JULY, 1979.

TIME	P_{MAX} (MG C M ⁻³ H ⁻¹)		P_{MAX} (MG C MG CHLA ⁻¹ H ⁻¹)		I_K (U E M ⁻² S ⁻¹)	
	T	F	T	F	T	F
1030	157.	105	15.8	24.6	83.8	94.2
1414	87.8	72.1	31.3	25.1	112.	80.5
1815	50.2	35.6	20.0	14.4	79.5	84.2
2400	63.6	47.4	15.5	14.4	78.5	78.5
0600	56.9	47.3	28.8	23.3	-	-

TABLE 10: EFFECTS OF SHADING ON ZOSTERA COMMUNITY METABOLISM.

TIME	0	$\text{MG O}_2 \cdot \text{M}^{-2} \cdot \text{HR}^{-1}$	
		53-3%	85.7%
PRE-SHADE	554.	498.	774.
SHADED (LATE AFTERNOON)	-	50.	7.
SHADED (MORNING)	-	153.	86.
POST-SHADE	-	299.	531.

exchange. The reduction in apparent O_2 production rates, as a percentage of pre-shading rates, was 69% and 89% in the 53% and 85% treatments respectively. Ambient light reaching the bottom was high (200-750 $\mu E \cdot m^{-2} \cdot sec^{-1}$) during the photoperiod and suggests that if the community does light saturate, saturation occurs above 300 $\mu E \cdot m^{-2} \cdot sec^{-1}$. Specific experiments using ^{14}C tracer techniques have been designed to address this relationship but the data have not been analyzed due to radioisotope counting equipment failure. However, experiments have been conducted since July, 1979. Nightly respiration values (rates) were not significantly different between shaded and non-shaded domes and are not included in the summary table.

Partitioning O_2 exchange and nitrogen exchange between the above-ground community and the substrate was investigated in August, 1979. Areas in both Ruppia and Zostera communities were clipped (i.e. all above-ground plant material harvested) to allow placement of the domes. Table 11A summarized O_2 exchange in clipped and non-clipped areas. Table 11B summarizes the nitrogen exchange information for the Ruppia area. For O_2 exchange, mean O_2 production was reduced during the day by 50% and the 24 hour estimate of net community production was reduced by 89% in the Ruppia dominated community. Under the conditions prevailing during the Zostera study, mean O_2 production during the day was reduced by 78% and the net negative community production rate for the 24 hour reduced by 93%. The maximum velocity (V_m) for uptake of both NH_4^+ and NO_3^- was reduced by 55% and 53% respectively in the Ruppia community by eliminating the above-ground material. Assuming that the plankton community is contributing little to the calculated rates, it would appear that in the shallower Ruppia area, photosynthesis by autotrophs associated with the sediments is high and in both areas, the major component influencing respiration is sediment related.

TABLE 11: ABOVE-GROUND AND SUBSTRATE PARTITIONING EXPERIMENT:

A. O₂ EXCHANGE

DATE	AREA	$\Delta 24 \text{ HR.}$	O ₂	
			$\bar{X} \text{ MG O}_2 \cdot \text{M}^{-2} \cdot \text{HR}^{-1}$	(DAY)
8-28-79	RUPPIA*	+854.	+195.	
	RUPPIA**	+ 93.5	+ 98.	
8-29-79	ZOSTERA*	- 20.4	+ 67.5	
	ZOSTERA**	-308.0	+ 15.7	

B. NITROGEN EXCHANGE

DATE	AREA	UG · ATN · M ⁻² · HR ⁻¹	
		NH ₄ ⁺	NO ₃ ⁻
8-28-79	RUPPIA*	610.	475.
	RUPPIA**	250.	224.

* = NON-CLIPPED

** = CLIPPED

DISCUSSION

Plant distribution and relative abundance along transects A, B, and C at the Vacluse study site closely follows the results reported by Orth, Moore and Gordon (1979). This distribution relative to water depth appears characteristic of the lower Bay mesohaline and polyhaline environments. The lower limit for Zostera marina is probably controlled by available light. However, there is some indication in the distribution data (Figure 3) that the interaction between Ruppia and Zostera is not simply explained by water depth. For both species, occurrence has been recorded at depths outside their typical ranges. At Vacluse, in the area adjacent to the sand bar occupied predominately by monospecific stands of Zostera marina, Ruppia was observed inhabiting the fringes of what appeared to be recently established bare sand areas. In addition to light, it appears that the relative distribution and abundance of Ruppia-Zostera seagrass communities is influenced by other factors; current is suggested as one possible contributing factor to the observed patterns.

Plant-substrate relations in terms of nutrient relations are difficult to interpret due to the limited amount of data reduced at this time. The depth of the rooting zone in the vegetated areas appears to correlate with the distribution of ATP and NH_4^+ ; the major inflections occurring at 5-10 cm deep. In the summer (July), NH_4^+ pore water concentrations are high in the deeper sediments (>10 cm) and NO_3^- low. In the fall (October) during the second growth period, NH_4^+ is generally reduced throughout the sediment with depth and NO_3^- increased. ATP concentrations, as an estimator of heterotrophic biomass, is highest in the warmer months and corresponds to the periods of highest community respiration measurements.

Nixon and Oviatt (1972) reported apparent O_2 production and respiration rates of $2.9 \text{ gO}_2 \cdot \text{m}^{-2} \cdot \text{day}^{-1}$ and $3.6 \text{ gO}_2 \cdot \text{m}^{-2} \cdot \text{day}^{-1}$ respectively for a pond eelgrass community and O_2 production values of $3.6 \text{ gO}_2 \cdot \text{m}^{-2} \cdot \text{day}$ for a riverine eelgrass community. These values are for the midsummer. Assuming the mean rates presented in Table 4 for June, July and August represent the mean hourly rate over the photoperiod and the respiration values are typical of the hourly rate over the diel cycle, mean hourly rate of respiration for the three month period is $-143 \text{ mgO}_2 \cdot \text{m}^{-2} \cdot \text{hr}^{-1}$. This compares favorably with the value reported for the pond eelgrass community. For the same period, the mean hourly production rate equals $+267 \text{ mgO}_2 \cdot \text{m}^{-2} \cdot \text{hr}^{-1}$. The mean daylight period at this latitude during the period June-August is 14.1 hours. If the photoperiod during which this mean production rate is realized is 80% of the daylight period, or approximately 11.5 hours, mean daily O_2 producing during the period for the Zostera area would equal $+3.07 \text{ gO}_2 \cdot \text{m}^{-2} \cdot \text{day}^{-1}$. This compares favorably with the results of Nixon and Oviatt (1972) and suggests the community is net negative with respect to daily production. Mean daylight O_2 production and night respiration values in the Ruppia community compare with the Zostera area (Table 3).

The data from the dome O_2 exchange studies suggest two potentially valuable lines of research with respect to factors controlling community metabolism, productivity and nutrient cycling. The effect of light on distribution and production has been alluded to previously. It appears from the data that available light governs the specific rate of net community production or consumption of oxygen and that the community, at least the Zostera area, is not operating in a light-saturated environment.

Small changes in available light due to either weather conditions or possibly turbidity levels have pronounced effects. The results of one study in the Ruppia dominated community also suggest that high light may inhibit apparent production by this species. The reasons for this are not clear but do suggest that available light is singularly a primary control in both communities. Tables 3 and 4 also summarize, in terms of mean hourly rates, O_2 production and respiration and the effect of nutrient (NH_4^+ and NO_3^-) additions to plant communities. In the Ruppia area, the majority of spike experiments resulted in increased apparent O_2 production during the day. The percent increase over ambient rates ranged from 1% to 210% with maximum increases occurring in early summer and fall periods. In the Zostera community the effect was not as pronounced. Increases were observed in the summer months (June through August) and averaged 30% increase in apparent hourly O_2 production rates during the day. At other times of the year either no effect was observed or the rate slightly reduced (Table 4). Whether these increases can be attributed to the vascular plants per se is not known but the community as a whole responded to the increased nitrogen supply. Based on this information more refined experiments are planned for light, nutrient and productivity studies for the following year.

Partitioning the processes of production, respiration and nutrient exchange into components of the SAV community has just begun and the data are preliminary. It appears from the light-dark bottle studies that plankton community production compared to the SAV communities is small; i.e. on the order of 10% net daytime community production. The clipping experiments (Table 11) indicate that in certain areas, benthic algal production may be significant and the major respiratory demand of the community is associated with the sediments. Our future studies will evaluate these processes in more detail with regard to energy flow and nutrient exchange.

These studies and the data gathered from the various experiments will provide the modelling effort the necessary information to realistically simulate energy flow and the effects of light and nutrients in the plant dominated communities. Unfortunately for this report much of the data has not yet been reduced and interpreted for inclusion. The data presented however is representative of our overall effort and indicative of our findings to date.

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INTERACTIONS INVOLVING RESIDENT CONSUMERS
R. J. Orth and D. F. Boesch

Introduction

One of the most notable features of SAV habitats is the characteristically high density of animals residing in the grass bed. This large standing stock of animals is thought to be fundamental to the resource value of SAV beds. The grass bed provides substrate, protection and food resources which allow maintenance of high faunal densities. The protection provided by the bed and the high prey density serve migratory utilizers of the SAV habitat, i.e. crabs, fishes and waterfowl.

The epifauna and infauna represent a diverse and complex assemblage which includes micro- and macroalgae, protozoans, polychaetes, oligochaetes, bivalves, decapods and barnacles. Many of these groups exhibit distinct seasonal pulses of abundance depending on their individual spawning periods (Stevenson and Confer, 1978).

The biotic community within grass beds is quite distinct from the communities in adjacent unvegetated areas. Because of the lack of suitable substratum, there is usually very little epifauna in bare sand or mud areas. These animals are primarily using the blades as a substratum or in the case of herbivorous gastropods, grazing on the microalgae that grow on the blades.

The fact that the epifauna may not be totally dependent on the presence of grass but rather any substrate, biotic or abiotic, for its survival, does not take away from the importance of the presence of the

grass itself. The grass is a renewable resource, unlike many other substrata, and provides a suitable substrate for growth every year. In addition, the grasses serve other functional roles that are equally important (e.g. erosion buffer, detrital source, nutrient pump), which could not be achieved with an abiotic substance.

The infaunal community is also quite distinct from that in adjacent unvegetated areas. There is a tremendous increase in numbers of species and individuals in grass areas and this may be related to increased sediment stability and/or microhabitat complexity of food supply (Orth, 1977; Thayer, Adams and La Croix, 1975). Orth (1977), working with infauna of Chesapeake Bay eelgrass, found infauna to increase in density and diversity from the edge of an eelgrass bed to the center of the bed and also with increasing size of the bed. He related this increase to the sediment stabilizing function of eelgrass and showed that decreasing the stability of sediments experimentally (removing blades of grass by clipping, simulating wave action) and naturally [cownose ray activity (Orth 1975)] decreased the density and diversity of the infauna.

The motile community is also diverse and quite distinct from surrounding unvegetated areas (Orth and Heck, unpublished; Kikuchi, 1974). Hardwick (1973) found that on the West Coast, the herring, Clupea harengus pallasii, used eelgrass leaves to lay most of their eggs on. Though Clupea spp. on the east coast do not use grass beds like the west coast species, the toadfish Opsanus tau uses the rhizomes as attachment sites for its eggs. Juveniles and adults of many species may utilize eelgrass for protection. The blue crab, Callinectes sapidus,

is found in greater abundance in eelgrass beds both as juveniles and adults (Lippson, 1970, Orth and Heck, unpublished). Changes in eelgrass abundance are thought to be a factor in variations in the commercial catch (W. A. Van Engel, personal communication). Many species use SAV habitats primarily because of the abundance of food.

One of the more complete studies of fish communities of eelgrass was done by Adams (1976a,b,c) in North Carolina. He found the highest fish biomass when temperature and eelgrass biomass were maximal. Further, food produced within the grass bed could have accounted for approximately 56% by weight of the diet of the fish community. The high fish production was due to juveniles which had higher growth efficiencies than older fishes. They accounted for 79-84% of the total annual fish production.

By simply looking at the structural complexity of SAV habitats one does not get an appreciation for the flow of energy needed to support the complex trophic structure. From analysis of feeding habits of the higher level consumers (fish and crabs) it is obvious that benthic invertebrates play a major role in the flux of energy through the seagrass system. The benthos represents the major link between primary production, detritus, and higher trophic levels.

The amount of energy or biomass produced within the system can only be estimated by a detailed look at the secondary production of the individual species inhabiting the grass bed. Secondary production estimates will provide the basis for determining the amount of energy available and the rate at which it is transferred to the higher consumers.

Although few marine organisms consume SAV directly, the SAV resource is recognized as a preferred food for many waterfowl species (Bent 1925; Cottam 1939; Cottam and Munro 1954). The availability of SAV fluctuates widely and is currently declining in the Chesapeake Bay (Stevenson & Confer 1978, Bayley et al. 1978). The impact of such a decline on waterfowl depends on the degree of dietary specificity. While the abundance of SAV is presently inadequate to totally support wintering waterfowl populations, it may be very important early in the season. The degree to which waterfowl use this resource and possibly affect the ecology of SAV is poorly understood. Birds may utilize the limited resource for conditioning and building of fat reserves to survive winter stress, when feeding is more difficult.

The general importance of seagrass beds in the marine and estuarine environment has been well documented. Although much work has been done on the structural components of eelgrass beds in the Chesapeake Bay, little information is available on the functional ecology of these beds.

Our efforts from July 1978 to the present have been directed at determining the relative importance of SAV beds and understanding the trophic role of resident consumers in such systems by: a.) determining the bases of secondary production; b.) quantifying secondary production of important consumers; c.) determining which resident consumers are trophically important to migratory consumers and d.) determining the degree to which migratory consumers control populations of resident consumers.

Methods and Materials

A. Habitat Differences:

Routine sampling was scheduled to coincide with major biological events in the grassbed and adjacent areas. These events included the arrival of major predators in the system (early spring), the partial defoliation of Zostera (mid-summer), and the major larval settling periods (spring and fall). Such timing, rather than quarterly sampling, would yield the best data on the dynamics of the grass bed and adjacent habitats.

Three habitats were sampled five times (July and October, 1978 and April, June and August, 1979) to determine quantitative and qualitative differences in their associated fauna. The habitats included an offshore sandbar system (outside sand), sandy patches within the grass bed (inside sand) and the grass bed proper (Fig. 1). Initially, 10 stations were established in each habitat. Analyses of data from the initial sampling indicated that 5 rather than 10 stations adequately represented the infauna in the two sand habitats. One sediment (3.8 cm^2) and three macroinfaunal (0.007 m^2 each) cores were taken at each station. Prior to taking infaunal and sediment cores in the grass bed an epifaunal sample was taken at each station by clipping and collecting grass from the area to be sampled. Coring was then conducted within the clipped area.

Vertical distribution of infauna was examined in July 1978. A 35 cm long plexiglass core 9.4 cm in diameter (0.007 m^2) was used to collect infaunal samples. One such core sample was taken at each station. The top 10 cm of each sample was sectioned vertically into 2

cm intervals and the remaining material was divided into 5 cm intervals. Based on these data, it was determined that a sample depth of 15 cm adequately collected the infauna.

Before sieving and preservation samples were held for at least 30 min. in labelled plastic bags containing isotonic $MgCl_2$ as a relaxant. This kept many of the smaller polychaetes and oligochaetes from crawling through the sieve. All infaunal samples were washed through 0.5 mm mesh sieves and the retained material was preserved in 10% buffered seawater formalin. A vital stain (Rose Bengal) was added to facilitate laboratory sorting.

Epifaunal samples were collected by clipping plants to within 2-3 cm of the sediment surface and easing the blades into a collecting bags with a 0.5 mm mesh bottom (Marsh 1973). Samples were kept in water and processed live by stripping all epifauna from the blades and preserving them in 10% buffered seawater formalin containing the vital stain Rose Bengal. The remaining plant material was sorted according to species (Ruppia, Zostera and algae), oven-dried at 80°C for at least 48 h and then weighed to the nearest 0.1 g.

B. Predator Exclusion Experiments:

Exclosures consisting of large circular topless pens 5 m in diameter (20 m^2) and smaller, square cages (0.25 m^2) were used in the manipulative predator exclusion experiments. One pen was constructed in a mixed Ruppia-Zostera bed and another in an adjacent inshore sandy area. The pens were made of 4.3 m long salt treated wooden pilings placed 1.5 m into the bottom. Initially, thick-wall galvanized pipes (240 cm x 2 cm) were placed between the equally spaced wooden pilings

to provide shape (Fig. 1). The pipes inadequately supported the weight of the netting during storms and were later replaced with 10 cm x 10 cm x 360 cm wooden posts. Pens were encircled by a piece of black plastic 0.63 cm mesh netting with a uv retardant (Conwed Corp. Plastic Netting #OV3010). The netting, which was 324 cm wide, was attached to the posts at a height of 240 cm above the bottom. Excess netting was stapled along the bottom with 18 cm long wire staples to form an 84 cm wide skirt which extended outward from each pen. The skirt prevented predators from burrowing into the pen. An entrance into each pen was constructed by sewing a 5 cm wide x 324 cm long strip of VELCRO to one end of the netting with the opposing piece attached to a piling.

Smaller square cages measuring 50 cm on a side and 50 cm high were constructed of reinforcing rod frames covered with the same plastic netting as used on the pens. Each cage had 30 cm long legs which were pushed into the bottom, anchoring the cage. A top attached with VELCRO strips on three sides allowed easy access into each cage. Panels simulating only the sides of cages were similarly constructed.

Triads of experimental treatments were randomly arranged in triplicate both within and outside of the pens in each of the two habitats. A triad consisted of three experimental treatments: a complete cage enclosing 0.25 m² of bottom area, and open cage with no top and parallel sides of 0.25 m², and an uncaged control area (Fig. 1). One of the three triads per experimental condition (sand; sand plus pen; grass, grass plus pen) was designed to be destructively sampled after an appropriate time interval.

Fig. 1. Design of predator exclusion experiments showing the construction of the large pen and the placement of experimental triads. Closed circles around the perimeter of the pen indicate the placement of pilings and open circles show the position of galvanized pipes which were later replaced by wooden poles.

Sampling for predator exclusion work was scheduled to take spring and fall larval sets into account. Four sample times were designated for 1979: T_0 - April; T_1 - June; T_2 - September; T_3 - November. Infauna in both the unvegetated habitat and the grass bed, and epifauna in the grass bed were collected and preserved using the same methods described for routine sampling. Ten core samples for infauna and one grass clipping (vegetated area only) were taken when each experimental area and treatment were sampled.

Pen and cage effects were examined by placing larval and sediment traps inside additional cages (sediment traps in sand area only) to assess variations in larval recruitment and sedimentation rates.

Cages and pens were cleared of fouling organisms when necessary. Crab pots and minnow traps were placed within pens to remove predators which entered as larvae on juveniles. Several blue crabs were also removed by spearing.

Two days prior to the first sampling period of 12 June, pens were breached during a severe storm. After sampling, pens were rebuilt and a backing of heavier larger mesh (13 mm) netting (Conwed Corp. Plastic Netting #OV1580) was added to the smaller mesh. After the first sampling period but prior to reconstruction of the pen, blue crabs had burrowed into all sand cages. Because of this disturbance cages were removed and replaced by new ones positioned over bottom which had been uncaged. In addition, a 24 cm wide skirt was placed around each sand area cage.

C. Secondary Production:

Eight consecutive monthly samples were taken for secondary production using a suction dredge (Fig. 2). Quantitative samples were collected from within a weighted plexiglass cylinder with a diameter of 28.6 cm (0.065 m^2) and a height of 65 cm. The cylinder was carefully placed over the grass blades and the sample was taken from within by filtering water through a clear plastic bag with a removable 0.5 mm mesh sieve bottom. Samples of larger, more motile, or widely spaced species were collected from within a weighted fiberglass cylinder 110 cm in diameter (0.95 m^2) and 30 cm high equipped with a 0.5 mm mesh screened top (Fig. 2). All samples from the larger fiberglass frame were filtered through a 1 mm x 1.5 mm mesh bag. The sampling frame was dropped from a boat over dense vegetation. Only drops over 100% vegetation cover were sampled. The majority of samples were taken from mixed Zostera-Ruppia areas where abundances of vagile epifauna appeared to be the greatest. Attached epifauna, Crepidula plana, was sampled by clipping the grass from within a 0.1 m^2 ring as close to the sediment surface as possible. Grass blades were then cleaned of all attached epifauna and saved for future processing. All samples for production estimates were preserved in 10% buffered formalin. Samples were sorted in the laboratory and up to 200 complete individuals for each species were measured, dried and weighed. Based on their trophic importance to higher level consumers 9 species were selected for production estimates:

Fig. 2. Schematic diagram of suction dredge sampler. A venturi effect in the suction head draws the sample from within the sampling frame through the collecting bag.

Decapods	Amphipods	Isopods
<u>Callinectes</u> <u>sapidus</u>	<u>Gammarus</u> <u>mucronatus</u>	<u>Erichsonella</u> <u>attenuata</u>
<u>Crangon</u> <u>septemspinosa</u>	<u>Microprotopus</u> <u>raneyi</u>	<u>Edotea</u> <u>triloba</u>
<u>Palaemonetes</u> <u>vulgaris</u>	<u>Caprella</u> <u>penantis</u>	Mysid
		<u>Neomysis</u> <u>americana</u>

Presently 4 months of data have been worked up. This report contains information on growth rate and preliminary details of life histories. Final estimates of production must wait until all the data are available. Species need to be separated into cohorts or recruit groups if possible for use of the instantaneous growth rate or removal summation methods (Water and Crawford 1973), or combined into average cohorts for production estimation by the Hynes method (Hamilton 1969).

D. Tissue Samples:

Tissue samples for the Carbon-Hydrogen-Nitrogen ratio, C^{12}/C^{13} carbon ratio ($\delta^{13}C$) and calorimetry were collected throughout the summer of 1978. Plant material was carefully checked for epiphytes or epifauna which were removed by scraping or brushing prior to drying. Benthos and fish had their guts removed or were held in screened containers in aquaria for 24 hr. to permit the voiding of gut contents. Specimens of resident consumers and predators were grouped by size. A special effort was made to examine changes in tissue chemistry with growth, especially with regard to $\delta^{13}C$ values. Shelled animals were treated with 10% HCl prior to analysis to remove shell fragments. All tissues collected were then dried, ground to a fine powder and distributed to subproject principal investigators or consultants for further analyses.

E. Stomach Analyses (Callinectes sapidus):

Eighty-three blue crab stomachs were analyzed in 1978. Individuals were collected with a 4.87 m (16 ft) otter trawl with 19 mm (3/4 in) wings and a 6.3 mm (1/4 in) cod end liner. The trawl was pulled for a period of 2 min. at a speed of 2-3 knots. Crabs collected were subsampled and those selected were immediately weighed, measured, sexed, and the molt stage noted. Stomachs were removed in the field and preserved in 10% buffered seawater formalin with the vital stain, Rose Bengal. Each stomach was carefully dissected in the laboratory and the contents enumerated and identified when possible.

F. Waterfowl Interactions:

A preliminary field effort was undertaken in 1978-1979, consisting of 34 censuses and feeding observations between 16 December and 22 March. Birds were censused during daylight hours at approximately 3-hourly intervals on 6 days. The remaining censuses were limited by poor weather or other activities at the site. Waterfowl were counted, located by transect interval, and behavior was recorded as feeding or non-feeding.

Results and Discussion

A. Habitat Differences:

Cumulative species curves for vertically sectioned cores from each habitat (Fig. 3) flattened at a depth of approximately 15 cm. Most species in each habitat were found in the top 15 cm of sediment but the composition and numbers of individuals of the dominant taxa differed from one area to the next (Table 1). A greater number of

Fig. 3. Cumulative species curves of vertically sectioned cores from three habitats.

Table 1. Vertical Distribution in Numbers Per Core (70 cm²) of Dominant Infauna by Habitat

	Grassbed Proper	Dynamic Sand Bar Area	Sand Patches Within Grassbed
Sediment Surface	<u>Polydora ligni</u> 384	<u>Gemma gemma</u> 42	<u>Gemma gemma</u> 1,931
	<u>Heteromastus filiformis</u> 204	<u>Neomysis americana</u> 11	<u>Odostomia</u> sp. 726
	<u>Nereis succinea</u> 79	<u>Scolelepis squamata</u> 6	<u>Mya arenaria</u> 7
	<u>Streblospio benedicti</u> 75		<u>Brania clavata</u> 5
	<u>Erichsonella attenuata</u> 71		<u>Glycinde solitaria</u> 5
2.0 cm	<u>Heteromastus filiformis</u> 160	<u>Scolelepis squamata</u> 7	<u>Gemma gemma</u> 30
	<u>Oligochaeta</u> 54		<u>Odostomia</u> sp. 27
	<u>Polydora ligni</u> 22		<u>Scolelepis squamata</u> 8
4.0 cm	<u>Heteromastus filiformis</u> 107	<u>Glycera dibranchiata</u> 5	<u>Heteromastus filiformis</u> 19
	<u>Oligochaeta</u> 25		<u>Chaetazone setosa</u> 9
	<u>Polydora ligni</u> 22		<u>Scolelepis squamata</u> 6
6.0 cm	<u>Heteromastus filiformis</u> 63	<u>Paraonis fulgens</u> 4	<u>Heteromastus filiformis</u> 20
	<u>Oligochaeta</u> 37	<u>Spiophanes bombyx</u> 3	<u>Chaetazone setosa</u> 4
	<u>Polydora ligni</u> 6	<u>Glycera dibranchiata</u> 2	<u>Spiophanes bombyx</u> 2
8.0 cm	<u>Oligochaeta</u> 60	<u>Spiophanes bombyx</u> 11	<u>Heteromastus filiformis</u> 11
	<u>Heteromastus filiformis</u> 28	<u>Paraonis fulgens</u> 4	<u>Glycera dibranchiata</u> 2
	<u>Glycera dibranchiata</u> 4		
10.0 cm	<u>Oligochaeta</u> 163	<u>Spiophanes bombyx</u> 3	<u>Heteromastus filiformis</u> 11
	<u>Heteromastus filiformis</u> 18	<u>Glycera dibranchiata</u> 2	<u>Glycera dibranchiata</u> 2
	<u>Pseudoeurythoe ambigua</u> 7		<u>Oligochaeta</u> 2
15.0 cm	<u>Oligochaeta</u> 16	<u>Spiophanes bombyx</u> 4	<u>Oligochaeta</u> 2
	<u>Pseudoeurythoe ambigua</u> 7	<u>Paraonis fulgens</u> 4	<u>Heteromastus filiformis</u> 1
	<u>Heteromastus filiformis</u> 5		
20.0 cm	<u>Oligochaeta</u> 9	<u>Glycera dibranchiata</u> 2	<u>Heteromastus filiformis</u> 5
	<u>Heteromastus filiformis</u> 4	<u>Eteone heteropoda</u> 1	<u>Oligochaeta</u> 3
	<u>Polydora ligni</u> 2		
25.0 cm			

individuals per section were found in the grass bed below the top 2 cm than in the other two habitats (Table 3). It is possible the grass bed afforded some degree of protection from predators or the root and rhizome mat provided a food source supporting a greater number of infauna than unvegetated habitats.

Generally twice as many infaunal species per core (0.007 m^2) were associated with the grass bed than were found in the adjacent sandy habitats (Fig. 4). An average of 21 infaunal species per core were found in SAV beds where only 9 were associated with sand patches within the grass bed and 7 were found in the offshore sand bar area.

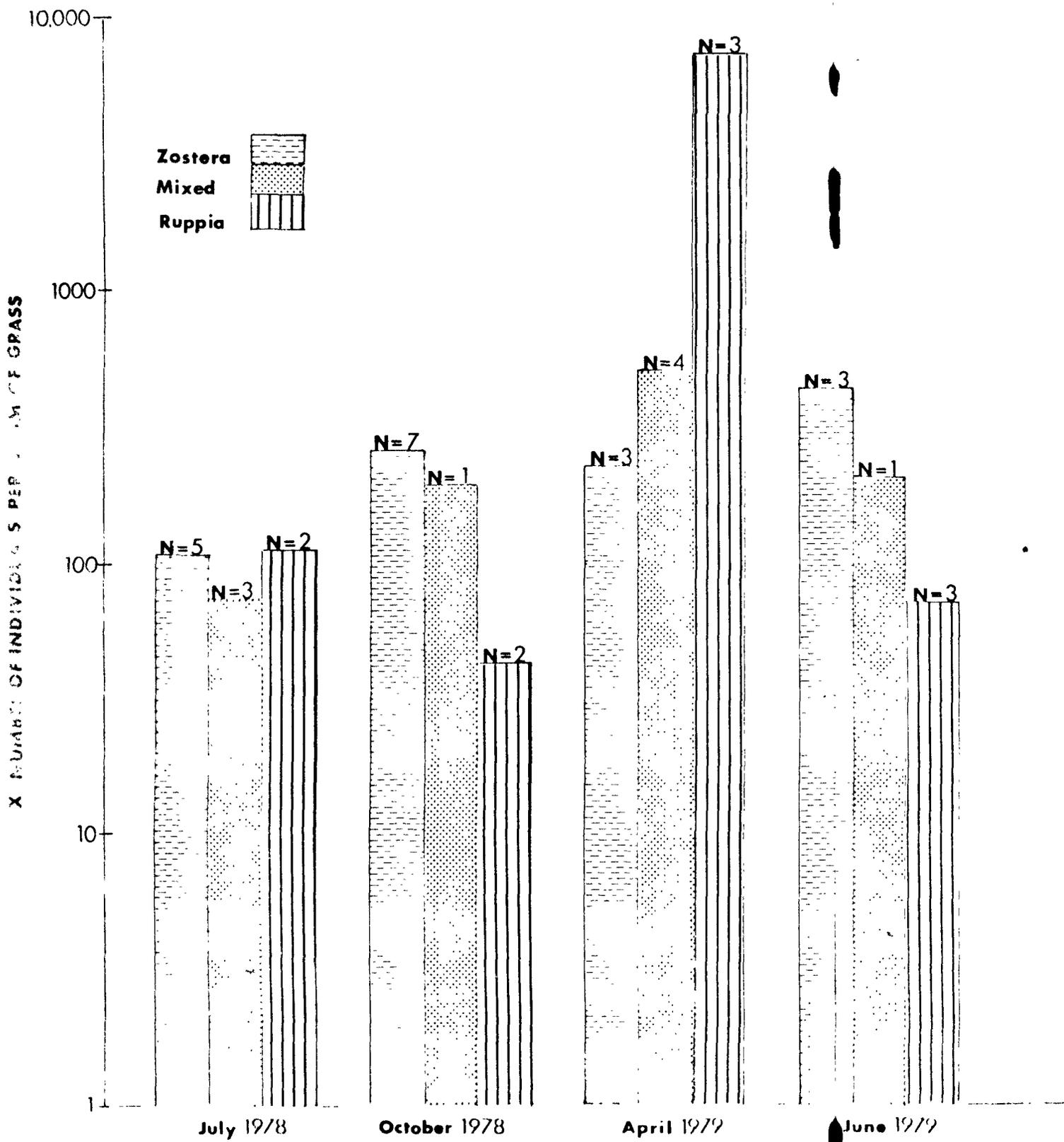
With the exception of the July (1978) sample date, there were also a greater number of individuals per m^2 in the grass bed than in either of the sand areas due in part to the relative stability of each habitat (Fig.5). The reversal in this trend during July was due to a large set of the bivalve, Gemma gemma ($32,648/\text{m}^2$). By the next sample date they had greatly declined in abundance. In addition to sediment stability, the refuge factor and structural complexity of seagrasses may be a cause for the greater abundance of grass bed fauna.

In October, 1978 and June, 1979 Zostera had a greater number of epifaunal individuals per gram of grass than either mixed Zostera-Ruppia (where both species contribute at least 15% to the sample biomass) or Ruppia (Fig.6). However, in April, 1979, Ruppia contained almost two orders of magnitude more individuals than Zostera. During July, 1978 individuals per gram of grass were more equitably distributed between the three areas of the grass bed. There is little doubt that in vegetated areas the increased habitat complexity and

Fig. 4. Mean number of infaunal species/core (0.007 m²) from the three habitats found during routine sampling.

Fig. 5. Mean number of infaunal individuals/m² from the three habitats found during routine sampling.

Fig. 6. Mean number of epifaunal individuals per gram of grass found during routine sampling.



surface area provided by the grass blades significantly enhances the number of species inhabiting the area.

From an analysis of fish gut contents, it appears that the epifauna are an important link in transferring energy from primary producers and decomposers to higher trophic levels. For example, spot (Leiostomus xanthurus) fed primarily on epifaunal organisms (amphipods, polychaetes) or those species associated with plant detritus at the sediment surface (copepods, nematodes, ostracods) (see Merriner and Boehlert, this report). Few truly infaunal species were consumed. Spot have a "vacuum cleaning" mode of feeding where an individual moves along a grass blade or the sediment surface ingesting food items and detritus and may significantly influence structure of the epifaunal community. Spot appear to have difficult foraging on the bottom in dense vegetation.

Late juvenile and early adult silver perch (Bairdiella chrysoura) feed exclusively on motile and vagile epifauna (see Merriner and Boehlert, this report) by visual cues and may also effect epifaunal community structure. Bairdiella first appears in the bed in August as juveniles and remains until water temperatures drop in the fall. The most frequent preyed upon food item, mysid shrimp, also make their appearance in the early fall. Other food sources, the majority of which are amphipods and isopods, are permanent residents in the grass bed.

Pipefish (Syngnathus fuscus) are also trophically important in grass bed ecosystems. This species forages by sight among grass blades and feeds primarily on epifauna (see Merriner and Boehlert, this report). Principal food items included calanoid copepods, mysids, and amphipods. Mysids (Neomysis americana) were more frequently consumed in October 1978, when they were more abundant in the grass bed. Capiellid amphipods were also a common food item.

B. Predator Exclusion:

Initial results of predator exclusion experiments suggested that 1) predation plays an important role in structuring the benthic communities in grass bed areas and 2) that predation may have a greater impact on community associated with unvegetated habitats than grass beds.

There were more species and individuals in the sand area cage treatments for both the penned and unpenned conditions after 2 months of caging with no consistent patterns in the vegetated area for similar treatments (Figs. 7 and 8). However, the abundance of infauna in the vegetated area was initially much higher than in unvegetated areas. In June 1979 vegetated areas contained 5 to 10 times the number of individuals found in adjacent sand patches. The abundance of individuals and numbers of species in the caged sand area was similar to the untreated vegetated areas although differences in the species composition did exist. Mya arenaria, the soft shell clam, was extremely abundant in the caged sand area (Fig. 9) but its abundances were much lower in the grass area. The caged sand community developed only after two months, primarily by recruitment from planktonic larvae, whereas the grass infaunal community represented an older, more established community which had developed from the start of the growing season.

Based on this preliminary data, we suggest that the infauna in sandy areas was more susceptible to predation. Their response to

Fig. 7. Total number of individuals per core for each treatment (S = sand area; M = mixed grass area; OC = cage with two sides only; C = complete cage; P = pen. e.g. M+P+C = complete cage treatment located inside the pen in the grass bed).

Fig. 8. Total number of species found in five cores for each treatment (see Fig. 7 for treatment designation).

Fig. 9. Total number of individuals of the soft shell clam, Mya arenaria, in five cores, for each treatment.

protection was most pronounced. The infauna of the more spatially diverse grass area are protected in part by the roots and rhizomes and respond less dramatically. This community may already be near maximum densities.

Predator exclusion studies conducted both in the Chesapeake Bay and Europe have shown similar patterns of community response (Virnstein, 1977; Reise, 1976; Orth, 1977). However, our data only represent one sampling period and definitive habitat comparisons and species response patterns will be discussed in detail following the end of the experiment.

Data for the grass bed epifauna (Table 2) are also preliminary. Uncaged treatments contained a greater abundance of individuals than caged treatments due to fewer barnacles, Balanus improvisus, in the caged areas, both within and outside the pen. Observations of barnacle set on the sediment traps placed in the sand area suggested fewer barnacles set inside than outside the cages.

C. Secondary Production:

The various methods of production estimation are sensitive to growth type (Water 1977). To accurately estimate production it is therefore necessary to know the type of growth exhibited by a species. Growth is basically the process of increasing mass in developing organisms and involves following changes in body weight or some measure proportional to weight. We have chosen to measure the lengths of various parts for the 9 species and have calculated the relationship between length and weight (Table 3). Gammarus was the only species to exhibit isometric growth (weight increased as the cube

Table 2. Numbers of epifaunal species and individuals per gram of SAV for each treatment in the predator exclusion experiment taken in June, 1979.

	M	M+OC	M+C	M+P	M+P+OC	M+P+C
<u>Balanus improvisus</u>	180.0	135.6	118.5	324.3	166.4	104.7
<u>Bittium varium</u>	2.8	4.3	6.4	3.0	3.6	0.7
<u>Polydora ligni</u>	3.7	3.9	9.4	2.2	7.4	6.4
<u>Erichsonella attenuata</u>	4.2	2.2	1.2	10.1	11.0	1.4
<u>Gammarus mucronatus</u>	4.6	2.4	0.6	1.8	5.0	1.0
<u>Crepidula convexa</u>	9.7	15.9	9.9	9.1	10.0	9.6
<u>Caprella penantis</u>			0.1	1.0	1.1	0.2
<u>Astyris lunata</u>		0.6	0.1			0.4
<u>Cymadusa compta</u>		0.2	0.4	0.8	1.5	0.1
<u>Nereis succinea</u>	0.9	0.7	1.0	1.4	2.0	1.1
<u>Styllochus ellipticus</u>	1.6	4.3	0.6	2.7	1.1	1.7
<u>Anadara transversa</u>	0.2					0.1
<u>Ilyanassa obsoleta</u>	0.7					0.4
<u>Urosalpinx cinerea</u>						0.2
<u>Mya arenaria</u>				0.2		0.2
<u>Idotea baltica</u>		1.2		0.2	1.2	0.2
<u>Mytilus edulis</u>						0.1
<u>Triphora nigrocincta</u>						0.1
<u>Heteromastus filiformis</u>	0.2			0.6		0.1
<u>Ampithoe longimana</u>	0.5		0.1	0.2	0.1	
<u>Doridella obscura</u>			0.1			
<u>Ampithoe valida</u>	0.2			0.2	0.1	
<u>Palaemonetes sp.</u>				0.2		
<u>Sabellaria vulgaris</u>				0.2		
<u>Brania clavata</u>				0.2	0.1	
Nemertean				0.2		
Nudibranch				0.2		
<u>Mitrella lunata</u>	0.9			0.3	0.4	
<u>Microprotopus raneyi</u>	0.2				2.1	
<u>Edotea triloba</u>					0.1	
<u>Paracaprella tenuis</u>					0.1	
<u>Odostomia bisuturalis</u>					0.1	
Number of Species	15	10	13	21	19	19
Number of Ind./g. SAV	210.4	170.1	148.5	359.1	213.4	128.7

Table 3. Length-weight relationships for selected crustaceans for estimation of secondary production. Weight (w) is in mg and length (l) in mm.

		n	r ²	Part measured
Decapods				
<u>Callinectes</u> <u>sapidus</u>	w = 0.0643 l ^{2.74}	71	0.96	carapace width
<u>Crangon</u> <u>septemspinosa</u>	w = 0.5999 l ^{2.41}	42	0.89	carapace length
<u>Palaemonetes</u> <u>vulgaris</u>	w = 0.5880 l ^{2.53}	43	0.92	carapace length
Amphipods				
<u>Caprella</u> <u>penantis</u>	w = 0.0610 l ^{1.77}	132	0.84	head plus 1st three segments
<u>Gammarus</u> <u>mucronatus</u>	w = 0.1272 l ^{3.00}	72	0.96	head plus 1st three segments
<u>Microprotopus</u> <u>raneyi</u>	w = 0.1333 l ^{1.66}	50	0.91	head plus 1st three segments
Isopods				
<u>Erichsonella</u> <u>attenuata</u>	w = 0.0066 l ^{2.41}	91	0.90	length head to telson
<u>Edotea</u> <u>triloba</u>	w = 0.0070 l ^{2.87}	52	0.84	length head to telson
Mysids				
<u>Neomysis</u> <u>americana</u>	w = 0.0544 l ^{3.43}	44	0.93	carapace length

of length). Allometric growth (weight did not increase as the cube of length) was exhibited by all other species. The weight of Neomysis increased faster than the cube of length whereas the opposite was true for the remaining species.

While working up the samples we noticed that species might be growing at different rates in pure Zostera, pure Ruppia or mixed Zostera and Ruppia stands. Analysis of covariance was used for determining significant differences in growth rates between these three habitats (Table 4). Significant differences were found between habitats for Erichsonella and Neomysis. Erichsonella, an isopod of limited mobility, grows larger in Zostera. Neomysis, a motile mysid shrimp, grows larger in mixed stands. Presently we are not certain what causes these growth differences but they may be related to: 1) the differential occurrence of a preferred food source in one habitat or 2) predatory cropping of larger older individuals. For Neomysis it may also be related to a refuge function since the species is very motile and may seek mixed stands to hide in since they tend to be denser than pure stands.

Life History

The life history of a species greatly influences its annual production. For marine invertebrates the number of generations/year, maximum size, life span, and time spent in the plankton as larvae are most influential. We will not know what many of these values are for our selected species until a year's data are worked up, but for the first 4 months from April to July we have some approximations (Table 5).

Table 4. Analysis of covariance of growth rates between habitats.

	df	F	Probability of >F	Habitats* compared
Decapods				
<u>Callinectes</u> <u>sapidus</u>	2	2.15	0.12	Z,M,R
<u>Crangon</u> <u>septemspinosa</u>	2	0.61	0.55	Z,M,R
<u>Palaemonetes</u> <u>vulgaris</u>	2	2.26	0.12	Z,M,R
Amphipods				
<u>Caprella</u> <u>penantis</u>	-	--	--	--
<u>Gammarus</u> <u>mucronatus</u>	2	1.29	0.28	Z,M,R
<u>Microprotopus</u> <u>raneyi</u>	1	0.72	0.40	Z,M
Isopods				
<u>Erichsonella</u> <u>attenuata</u>	1	5.90	0.02	Z,M**
<u>Edotea</u> <u>triloba</u>	1	1.26	0.27	M,R
Mysids				
<u>Neomysis</u> <u>americana</u>	2	19.82	0.0001	Z,M,R**

* Z = Zostera, R = Ruppia, M = mixed Z and R

** significant difference

Table 5. Some life history parameters for secondary production species from April to July.

	Maximum size (mg)	Minimum size (mg)	Cohort or generations to date	mobility	feeding type
Decapods					
<u>Callinectes</u> <u>sapidus</u>	6574.0	4.00	1	good	predator
<u>Crangon</u> <u>septemspinosa</u>	130.00	1.00	1	good	omnivore
<u>Palaemonetes</u> <u>vulgaris</u>	142.00	11.00	2	good	omnivore
Amphipods					
<u>Caprella</u> <u>penantis</u>	3.10	0.01	2	limited	predator
<u>Gammarus</u> <u>mucronatus</u>	6.20	0.01	2	?	herbivore
<u>Microprotopus</u> <u>raneyi</u>	0.11	0.04	2	?	herbivore
Isopods					
<u>Erichsonella</u> <u>attenuata</u>	6.90	0.10	2	limited	herbivore
<u>Edotea</u> <u>triloba</u>	3.00	0.10	2	limited	herbivore
Mysids					
<u>Neomysis</u> <u>americanus</u>	5.00	0.01	1	good	omnivore

While it is too soon to determine life span it appears that the amphipods and isopods live about 4 months. No determination for the life span of the other species can be made at this time since a complete generation or cohort has not appeared or disappeared within the 4 months of data analyzed. At least 2 cohorts have appeared for all amphipods and isopods. Only 1 cohort is present for Callinectes and Crangon. Palaemonetes is the only decapod with 2 cohorts present (Table 6). Neomysis was found only in April. Through July it had not reappeared in the secondary production samples but was taken in June from the sand bar habitat.

Production

Both the instantaneous growth method, which basically sums growth increments, and removal summation method, which sums increments of mortality, will be applied for production estimates for species with definable cohorts (Waters 1977, Crisp 1971). The Hynes method will be applied to species which cannot be separated into cohorts after analysis of 12 months of data (Hamilton 1969). To date cohorts can be recognized only for Callinectes, Palaemonetes, Microprotopus, Erichsonella and Edotea.

The most complete cohort recognized to date is cohort 1 for Erichsonella which will be used as an example to calculate production (Table 7). These production values are for one generation or cohort of Erichsonella and represent only a fraction of the annual production. The difference between the removal summation ($0.63 \text{ g dry wt/m}^2$) and instantaneous growth ($0.56 \text{ g dry wt/m}^2$) is due primarily to not having sampled the early part of the cohort in March and possibly February.

Table 6. Size frequency distribution of secondary production species (densities/m²).

	April	May	June	July		April	May	June	July
<u>E. attenuata</u>					<u>G. mucronatus</u>				
0-1.5 mm					0-.5 mm		30.8		
1.5-3.0			261.5	142.3	.5-1.0	42.8	330.8	125.3	54.9
3.0-4.5	6.6		192.3	34.6	1.0-1.5	12.5	292.3	193.4	43.9
4.5-6.0	15.4		165.4	38.5	1.5-2.0	12.5	338.5	70.3	22.0
6.0-7.5	28.6	20.5	123.1	46.1	2.0-2.5	25.1	115.4	15.4	2.2
7.5-9.0	24.2	64.1	11.5	46.1	2.5-3.0	8.1	100.0		
9.0-10.5	22.0	102.6		15.4	3.0-3.5	2.2	69.2		
10.5-12.0	8.8	161.5	19.2	19.2	3.5-4.0	1.5	30.8		
12.0-13.5	6.6	48.7	23.1	19.2	4.0-4.5				
13.5-15.0		30.8		3.8	*	104.7	1307.8	404.4	123.0
16.0-16.5		10.2							
16.5-18.0		5.1	3.8						
Cohort 1	112.2	443.5	46.1	3.8					
Cohort 2			753.8	361.4					
<u>E. triloba</u>					<u>C. penantis</u>				
0-1 mm					0-1 mm		76.7	2.2	
1-2		1.5	113.8	203.8	1-2	2.9	176.7	35.2	2.2
2-3	4.4		224.6	326.9	2-3	25.8	7.0	17.6	
3-4	17.6	6.1	181.5	146.1	3-4	29.5	41.9	6.6	
4-5	39.6	47.7	15.4	15.4	4-5	7.4	88.4	4.4	
5-6	2.2	40.0		15.4	5-6	2.9	23.2		
6-7	2.2	4.6		3.8	6-7	2.2	51.2		
7-8	2.2	3.1			7-8		20.9		
8-9					8-9				
Cohort 1	68.2	101.5			*	70.7	552.0	66.0	2.2
Cohort 2		1.5	535.3	711.4					

Table 6 (continued)

	April	May	June	July		April	May	June	July
<u>M. raneyi</u>					<u>C. septemspinosa</u>				
.3-.4 mm					0-1 mm				
.4-.5		1.0			1-2	.05	.41	.47	
.5-.6	35.9		19.8	4.4	2-3	.05	.41	7.24	5.49
.6-.7	133.3		30.8	11.0	3-4	.05	.10	3.62	2.35
.7-.8	166.7		17.6	11.0	4-5	.16	.31	.93	1.17
.8-.9	97.4	6.3	6.6		5-6	.65	.31	.23	
.9-1.0	33.3	10.5		2.2	6-7	.60	.62		
1.0-1.1		4.2			7-8		.52	.12	
Cohort 1	466.6	21.0			8-9	.05	.10		
Cohort 2		1.0	74.8	28.6	9-10		.21		
					10-11				
					*	1.61	2.99	12.61	9.01
<u>C. sapidus</u>					<u>N. americana</u>				
0-5 mm	.07	.31			0-.5 mm	.60			
5-10	2.36	1.45	.12		.5-1.0	.20			
10-15	2.51	1.45	.35		1.0-1.5	1.41			
15-20	.22	.62	.23		1.5-2.0	4.04			
20-25		.10	.23		2.0-2.5	14.93			
25-30		.21	.23		2.5-3.0	12.92			
30-35		.10	.47	.26	3.0-3.5	1.82			
35-40		.10	.47	.13	3.5-4.0				
40-45				.39	4.5-5.0				
45-50				.39					
50-55				.13					
55-60				.26					
60-65				.13					
65-70				.13					
70-75									
75-80									
80-85				.13					

Table 6 (continued)

	April	May	June	July
<u>P. vulgaris</u>				
0-1 mm				
1-2				.13
2-3				.13
3-4	.22	1.14		.13
4-5	.38	1.86	6.08	5.35
5-6	.11	1.24	.82	2.22
6-7	.11	.72	5.96	2.35
7-8		.31	7.95	2.35
8-9		.21	.82	.65
9-10				
Cohort 1	.82	5.48	21.63	10.81
Cohort 2				.39

* cohorts not distinguishable.

Table 7. Production calculation for one cohort of Erichsonella from April to July.

Removal Summation Method

	No./m ²	\bar{w}^1 (mg)	No. lost/m ² x ²	wt. at ³ loss (mg)	= Production (mg/m ²)
April	112.2	1.13	-331.3	1.66	-549.96
May	443.5	2.18	397.4	2.57	1029.27
June	46.1	2.99	42.3	3.49	147.42
July	3.8	3.98			
0.63 g dry wt/m ²				=	626.73

Instantaneous Growth Rate

	Standing Crop (mg)	\bar{w}^1 (mg)	G ⁴ x	\bar{B} (mg/m ²)	= P (mg/m ²)
April	126.50	1.13	0.66	545.59	360.09
May	964.67	2.18	0.32	551.15	176.37
June	137.63	2.99	0.29	76.38	22.15
July	15.12	3.98			
0.56 g dry wt/m ²				=	558.61

¹ \bar{w} = mean individual weight - calculated from length-weight regression and size frequency distribution

² number of individuals lost between sample dates ($t_i - t_{i+1}$)

³ weight at loss as average of \bar{w} for two consecutive sample dates

⁴ G = instantaneous growth rate as $\ln(\bar{w}_{i+1}/\bar{w}_i)$

Thus for the one cohort of Erichsonella approximately 0.56 to 0.63 g dry wt/m² of tissue were produced and available for consumption by other trophic levels, which could be either higher level consumers or lower level decomposers. Assuming this cohort of Erichsonella occurred and produced evenly over the entire grass bed (140 hectares) then 782 to 877 kg of dry tissue were available to other trophic levels. When more data become available from feeding habits studies of higher level consumers it will be possible to determine what fraction of the secondary production is utilized.

D. Tissue Samples ($\delta^{13}\text{C}$):

A preliminary analysis of $\delta^{13}\text{C}$ ratios in some floral and faunal components of the SAV habitat (Table 8) revealed similar values to those found by Thayer et al. (1978). Spyridia filamentosa, a macro-epiphyte on Zostera and Ruppia had $\delta^{13}\text{C}$ values of -17.7 which were similar to Zostera epiphytes (-16.3) in North Carolina (Thayer et al., 1979). Some of the dominant faunal components had values ranging from -13.3 (Penaeus aztecus) to -15.4 (Syngnathus fuscus). Although additional components of the grass bed await examination it appears those analyzed to date may be linked more directly to a plankton-carbon food chain than to a seagrass-carbon system. These findings are in agreement with those of Thayer et al. (1978) who examined trophic relationships in a relatively young eelgrass bed.

E. Stomach-Analyses (Callinectes sapidus):

The masticatory mode of feeding made the identification of gut contents to the species level difficult. Percent frequency of occurrence

Table 8. $\delta^{13}\text{C}$ Values in SAV Systems

	$\delta^{13}\text{C}$ Values <u>Thayer, C. W. et al., 1978</u>	<u>VIMS</u>
<u>Zostera marina (live)</u>	-10.2	-
<u>Z. marina (dead)</u>	-10.6	-
<u>Z. marina epiphytes</u>	-16.0	-
<u>Spyridia filamentosa</u>	-	-17.7
<u>Suspended particulates</u>	-20.0	-
<u>Palaemonetes vulgaris</u>	-16.3	-14.9
<u>Crangon septemspinosa</u>	-	-14.5
<u>Callinectes sapidus</u>	-	-13.8
<u>Penaeus aztecus</u>	-	-13.3
<u>Bairdiella chrysura</u>	-16.8	-15.2
<u>Leiostomus xanthurus</u>	-	-15.2
<u>Syngnathus fuscus</u>	-17.0	-15.4
<u>Syngnathus floridae</u>	-15.3	-
<u>Illyanassa obsoleta</u>	-	-14.0
<u>Nassarius vibex</u>	-15.4	-

of food item indicated that blue crabs feed on both epifaunal and infaunal species (Fig.10). Zostera was found in 70% of the stomachs analyzed. Generally, live, intact, and very uniformly cut sections of leaf material were present, indicating that crabs may ingest the blades but digest only the encrusting organisms. Epifaunal molluscs, isopods and Balanus improvisus were among the major food items in crab stomachs. Callinectes also foraged among the root and rhizome mat on infaunal molluscs. Feeding burrows and infaunal feeding were frequently observed in the field. Callinectes may be an important predator on the infauna in vegetated habitats. In addition to nutritional needs derived from the grass beds, crabs also utilize these habitats for protection from predators during the critical soft shell phase of the molt cycle.

F. Waterfowl Interactions:

The Canada goose was the most abundant waterfowl species, averaging 556 individuals per census date and exceeding 2000 individuals in one census (Table 10). Second in abundance were redheads.

present primarily at dawn and dusk. This species probably foraged in the grass beds nocturnally and were inadequately censused.

Buffleheads (Bucephala albeola) consistently utilized the area, and averaged 44 birds per day. Brant were abundant only on one census date. Whistling swans, red-breasted mergansers (Mergus serrator), and widgeons (Anas americana) were regularly encountered in low numbers.

Canada geese and redheads showed differential habitat use (Fig. 11). Canada geese, which forage by tipping up rather than diving, avoided the deeper areas (>60-80 cm). At tide levels above

Fig. 10. Percent frequency of occurrence of food items in Callinectes
sapidus stomachs.

Table 10. Mean abundances of waterfowl species at Vaucluse Shores 1978-1979

Species	Grand mean/ day	12/16	12/24	1/7	1/8	1/9	1/10	1/27	2/3	2/4	2/17	2/18	3/7	3/22
		n= 1	1	2	1	2	4	3	4	2	5	2	4	5
Canada goose	556.0*	850	1750	1647	150	24	385	613	105	719	146	840	---	---
Redhead	70.0	---	---	50	50	---	10	---	---	300	140	360	---	---
Bufflehead	43.9	---	---	33	12	11	37	24	39	57	31	173	70	83
Brant	42.4	---	---	---	---	---	---	---	---	---	550	1		
Red-breasted merganser	17.2	---	---	74	46	---	---	---	---	9	---	---	47	48
American widgeon	12.4	---	---	27	9	5	3	---	---	14	1	69	1	33
Whistling swan	4.8	13	19	5	8	---	6	---	---	---	7	3	2	---
Pintail	4.0	35	8	1	5	3	---	---	---	---	---	---	---	---
Black duck	2.6	---	---	1	---	---	---	---	1	3	---	25	1	2
Lesser scaup	1.8	---	---	---	---	---	1	---	---	---	---	23	---	---
Common goldeneye	0.4	---	---	---	---	---	1	---	---	3	---	---	---	---
Surf scoter	0.4	---	---	---	---	---	3	---	2	---	---	---	---	---
Mallard	0.2	---	---	2	---	---	---	---	---	---	---	1	---	---

* 54.9 % of this value represents feeding birds, or 305.2 birds/day.
All other species appeared to be feeding whenever censused.

Fig. 10. Distribution of dominant waterfowl species at the study site.

MLW, goose foraging is restricted to an average of 40-50% of the vegetated area throughout the grass bed. The relationship between tide level and numbers of foraging geese further emphasizes the influence of water depth (Fig.12). Redheads, which are diving ducks, were censused in deeper water, and may have utilized the same areas for nocturnal foraging. Diving buffleheads were not restricted to shallow water, and were more evenly distributed although they showed a slight preference for deeper water (Fig.12). Reduced foraging in the shallowest areas (E-F) may relate to timing of field observations. Grass in the shallows may have been depleted early in the season, when observations were not made.

Preliminary work indicated consistent utilization of the grass bed by Canada geese, redheads, buffleheads and red-breasted mergansers. However, degree of trophic support can be assessed only by comparing estimates of consumption with known dietary requirements, and the work proposed for the 1979-80 season will emphasize this approach. Several techniques including the use of exclosures, intensive censusing, gizzard content analyses, and changes in $\delta^{13}\text{C}$ values of liver tissue will be used to quantify the utilization and importance of SAV to waterfowl.

Fig. 12. Numbers of feeding vs. non-feeding Canada geese in relation to tide level.

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HIGHER LEVEL CONSUMER INTERACTIONS

J.V. Merriner and G. W. Boehlert

INTRODUCTION

The basic objectives within this subtask of the grant are to analyze the structural and functional ecology of fish communities in submerged aquatic vegetation (SAV) and to assess the importance of SAV to the production and maintenance of important commercial fish populations. Our approach has been to combine a program of field sampling with laboratory study. Areas to be addressed include the processes of recruitment and emigration from the SAV areas, the relative benefit of SAV from trophic and refuge standpoints, the effects of major predators which may frequent the SAV areas, biomass estimates of the components of the fish community, the sources of production consumed by the fish populations, and ultimately, the levels of secondary production by the fishes.

The fish community in the present study divides to three components; these are i) fish eggs, larvae, postlarvae, and pelagic juveniles, ii) resident fishes, and iii) migratory predators. Ecology of resident fish communities in eelgrass (Zostera marina) beds has been studied in the Beaufort, North Carolina area (Adams 1976a, b); species composition of the benthic fish community in the study site used in the current work has been qualitatively described (Orth and Heck, in press). The dominant resident species in the lower Chesapeake Bay eelgrass bed was spot (Leiostomus xanthurus), contrasting with the North Carolina eelgrass fish community, where pinfish (Lagodon rhomboides) and pigfish (Orthopristis chrysoptera) were the dominant species (Adams 1976a). Analysis of feeding behavior in the current study will allow determination of the trophic interrelationships and the effects on secondary producers within

the system. Mid-and late-summer gill netting also revealed certain of the migratory predators (Orth and Heck, in press), including the sandbar shark (Carcharinus milberti) and bluefish (Pomatomus saltatrix). Preliminary evidence suggested that these predators were feeding in the eelgrass area. In other parts of the lower Chesapeake Bay, the cownose ray (Rhinoptera bonasus) has been shown to feed and have dramatic effects in eelgrass beds (Orth 1975).

Previous characterizations of Chesapeake Bay ichthyoplankton assemblages (Pearson 1941; Dovel 1971; Olney 1978) have concentrated on mid-channel portions of the estuary and have neglected the generally inaccessible nearshore, shallow environments. As a result, the extent to which Chesapeake Bay fish stocks utilize these nearshore zones as spawning and/or nursery sites is unknown. This lack of data takes on added significance as a result of the recent emphasis on the importance of shallow seagrass beds as refuge and feeding grounds for many species of marine and estuarine fishes (Ried 1954; Adams 1976a, c). The greater utilization of vegetated over unvegetated habitats by juveniles and adults of many species of fishes is well documented (Briggs and O'Connor 1971; Orth and Heck, in press); the current study will document the importance of these areas to the early life history stages of fishes and will determine the time of immigration and residence for the important species. The contribution of zooplankton derived from sources outside the vegetated areas will also be analyzed in the present study.

MATERIALS AND METHODS

Field Sampling

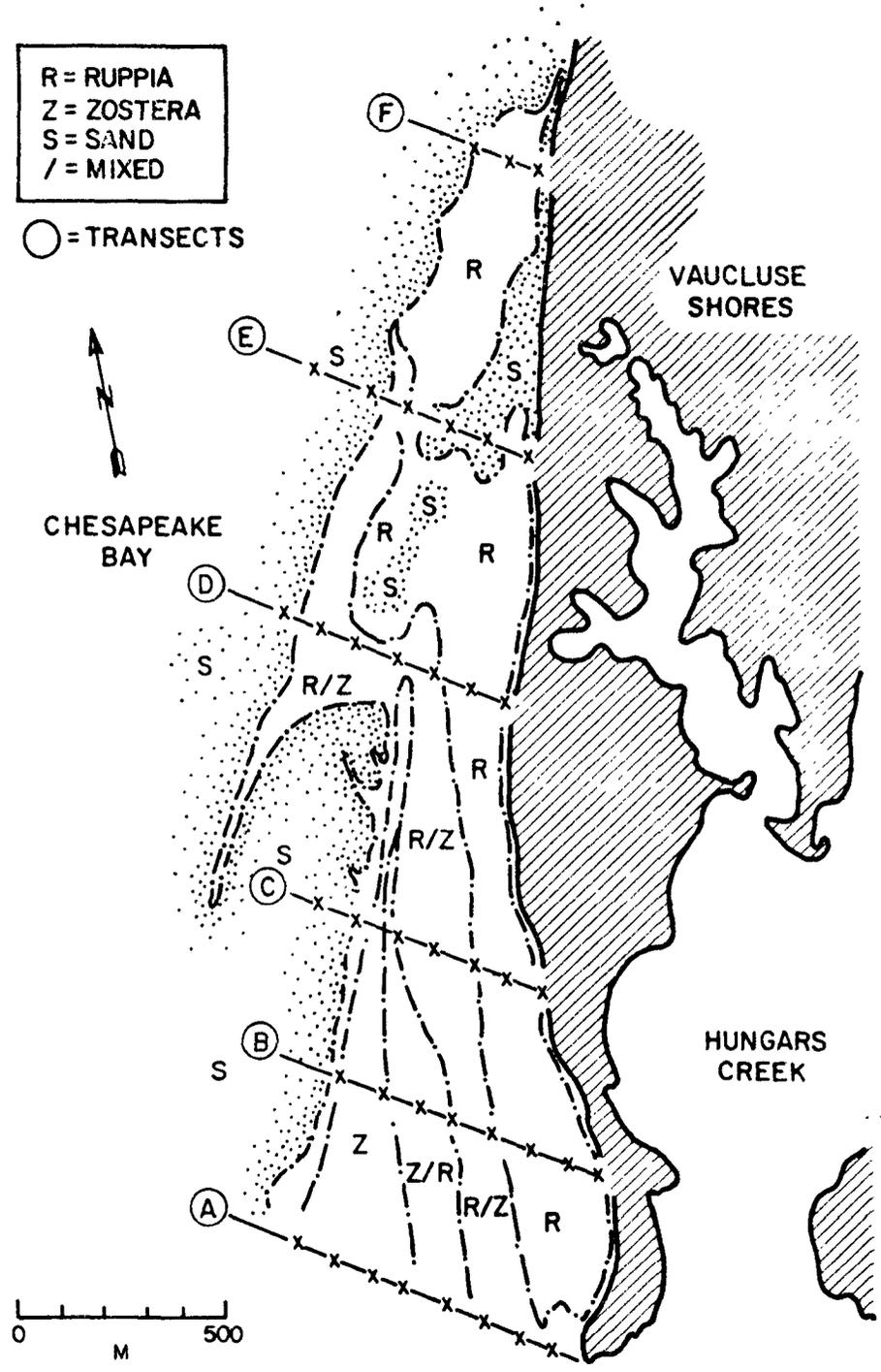
The field sampling is conducted at the Vaucluse Shores study site, north of the channel of Hungar's Creek (Figure 1). Sampling of relatively large areas is required for adequate estimations of fish densities; for this reason our sampling areas are not distinctly defined with respect to vegetation type. Sampling is divided to three areas, designated as representative of Zostera marina, Ruppia maritima, and an adjacent unvegetated area. The nominal Zostera area is located between the sandbar and land, along transect A. The nominal Ruppia area is located on and northeast of transect C. The unvegetated sampling area is on the sandbar west of transect markers B and A in depths appropriate for the particular sampling gear. As is apparent in vegetation maps of the bed, the nominal sampling areas for Ruppia and Zostera contain mixed stands as well as pure stands of the respective vegetation types (Figure 1). Differences noted between the two sampling areas may therefore represent faunal changes due to isolation from deeper water rather than differences attributable to vegetation type.

Sampling gears generally break down to those for 1) ichthyoplankton and zooplankton, 2) resident fishes, and 3) migratory predators. A variety of gears were tested for sampling these components of the fauna during the first six months of the project. Ichthyoplankton and zooplankton were initially sampled with towed, bridled nets; these were abandoned due to excessive disturbance ahead of the net from the outboard motor which resulted in avoidance by fishes and samples with excessive silt, detritus, and dislodged vegetation. Resulting samples were often impossible to

Figure 1: Vaucluse Shores study site. Location of the vegetation types are shown.

R = RUPPIA
 Z = ZOSTERA
 S = SAND
 / = MIXED

○ = TRANSECTS



preserve and sort (especially zooplankton samples with large amounts of sand). Routine sampling for ich- and zooplankton currently consists of two replicate collections in each habitat (Zostera, Ruppia, and sand) utilizing a pushnet (Figure 2) constructed of $\frac{1}{2}$ " diameter galvanized pipe and deployed over the bow of a 19 foot outboard craft. The frame is equipped with a 1 meter ichthyoplankton net (505 μm mesh) and two 18.5 cm zooplankton (202 μm mesh); the ichthyoplankton net and one zooplankton net are fitted with calibrated General Oceanics flowmeters to assess the volumes of water filtered. Nets are fished at high tide for 2-3 minutes depending on abundance of plankton. The sampling duration and boat speed allows the ichthyoplankton net to cover 74-174 m^2 of sea surface and filter from 68-117 m^3 of water. All samples are taken in the bed at high tide; routine monthly sampling is conducted at night; daylight samples are taken at high tide in selected months.

Each time the net is deployed, one ichthyoplankton and two zooplankton samples result. One of the zooplankton samples is preserved in 10% formalin for later taxonomic analysis and estimation of abundance; the other is washed with distilled water, frozen in the field on dry ice, lyophilized, weighed, and ashed in a muffle furnace (6 hours at 500°C) to determine organic biomass per unit volume. Ichthyoplankton samples are preserved in 5-10% buffered formalin. In the laboratory they are whole sorted for all fish eggs, larvae, postlarvae, juvenile, and adult stages. Specimens are later identified to the lowest taxon possible, measured, and curated.

For sampling resident fishes, a portable dropnet similar to those described in Moseley and Copeland (1969) and Adams (1976a) was built;

Figure 2: Zoo- and ichthyoplankton sampling pushnet. A. Gear array. As presently designed, the net is fished with three nets. The central net (505 μm mesh) is designed to sample ichthyoplankton and larger components of the demersal plankton. The smaller two nets, fished at a depth of approximately one meter, sample zooplankton (202 μm mesh). B. Design of the net frame. The gear is designed to fish off the bow of the boat prior to any bow wake; the nets trail under the hull of the boat. The frame pivots onto the boat to allow access to the cod ends and ease in sample processing.

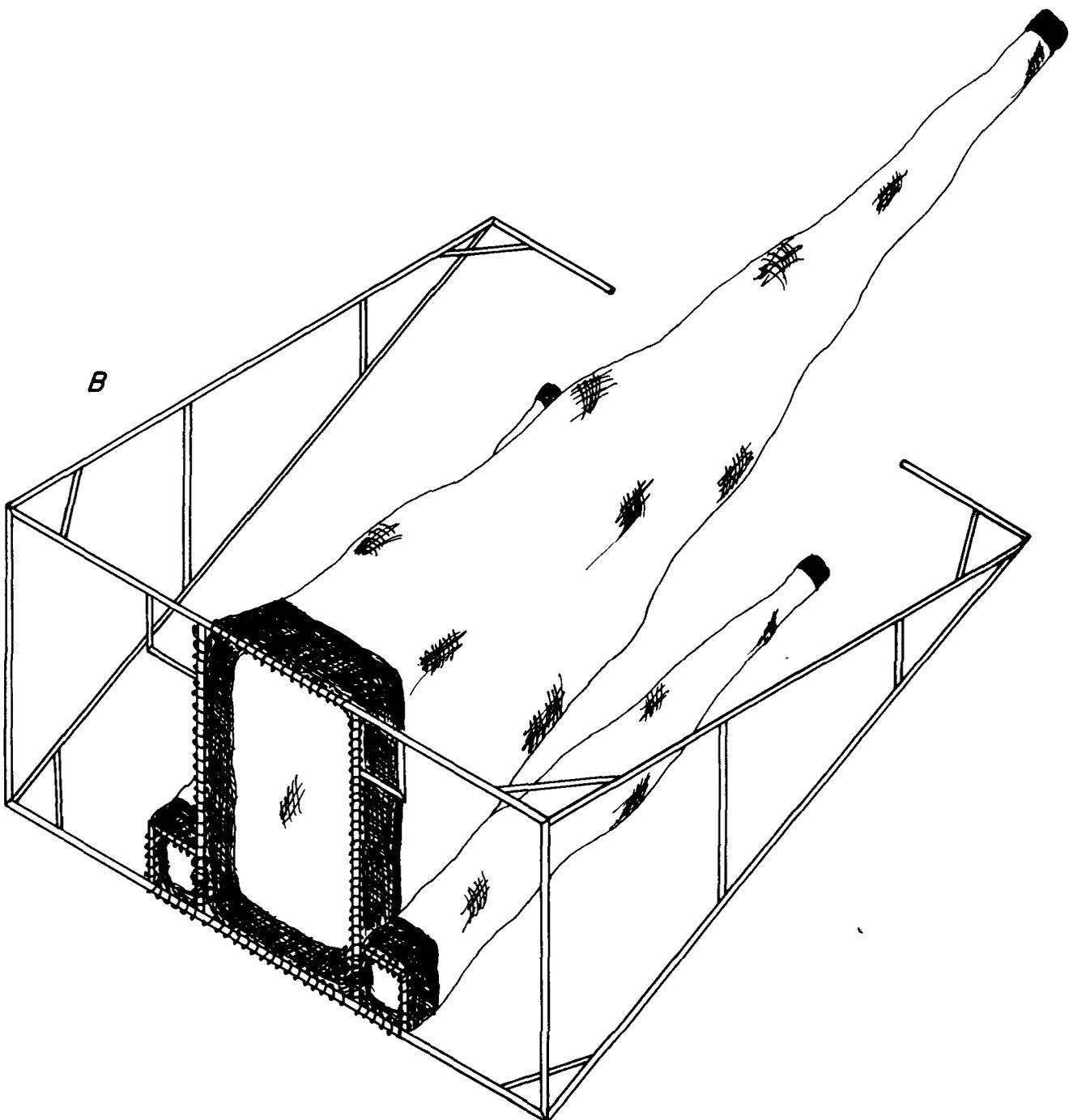
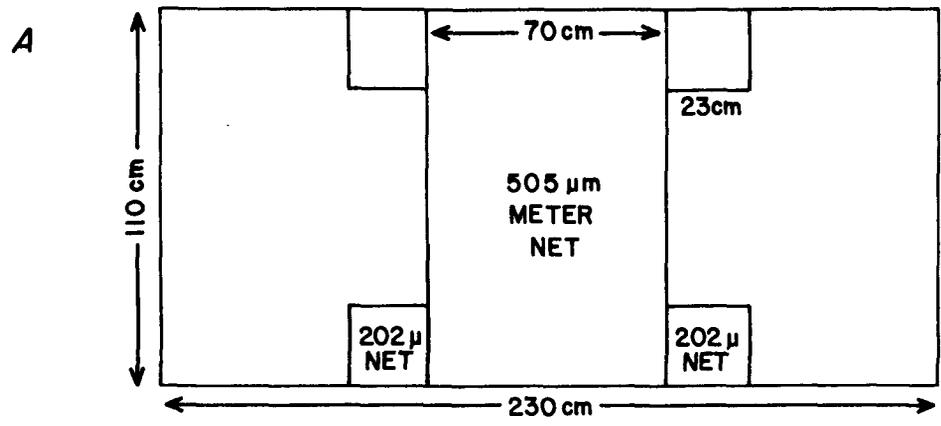


Figure 2

it covered an area of 9.3 m^2 . Our initial experiences with this gear proved it to be unsatisfactory due to the small area covered, long deployment times, and instability in rough weather. We therefore abandoned the dropnet in favor of a 40 m long, 2.4 m deep seine (Figure 3) fished in the manner described for long haul seines by Kjelson and Johnson (1974). Briefly, the seine is deployed bag end first from the bow of an outboard craft travelling in reverse. The net is set in a circle and the long wing pulled past the bag end to decrease the circumference of the circle to approximately 7.3 m, after which the bottom of the net is closed off by tightening a purse line. The catch remains in the pursed section of net and is brought on board the boat for processing. When set in an ideal circle, this gear encompasses an area of 127 m^2 . Duplicate or triplicate samples are taken monthly (from March through November) in each of the three habitats. Daylight samples are also taken in selected months for diel comparisons. Large specimens are identified, measured, and noted on the field sheets; the remainder of the catch is preserved in 10% buffered formalin for later identification in the laboratory.

Migratory predators are sampled in gill nets. Monthly sampling consists of deploying 30.5 meters each of 12.7 and 17.8 cm stretch mesh gill net perpendicular from shore in each of the three sampling habitats. These nets are fished every four hours over a 24 hour period. At each sampling time, the catch is removed, identified, measured, and weighed, and the net is reset. Observations are made on relative fullness of stomach contents and selected stomachs are removed and preserved for analysis of contents. As with other collections, additional information taken at the time of collection include date, time, habitat, tide stage, depth, water temperature, salinity, dissolved oxygen, and comments on weather.

Figure 3: Haul seine used in the collection of resident fishes; mesh size is 3.2 mm (square) throughout. The net is set from the bow of an outboard craft travelling in reverse. The short wing and bag end (a) is set first and the net paid out in a circle. After the circle is closed, the long wing end; (b) is pulled past point "a" until reaching the last 7.3 meters of net. The remaining circle is then pursed with the purse rings in this section of net and the catch brought on board the boat.

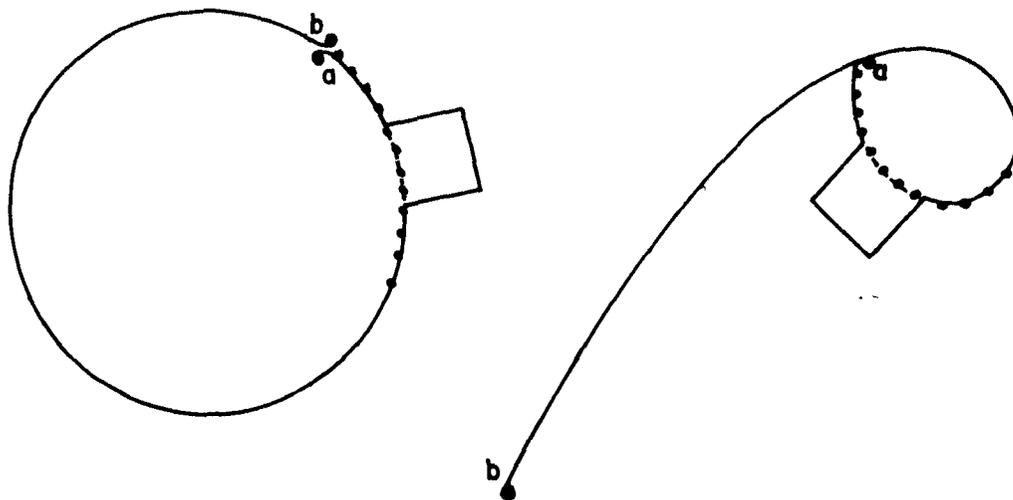
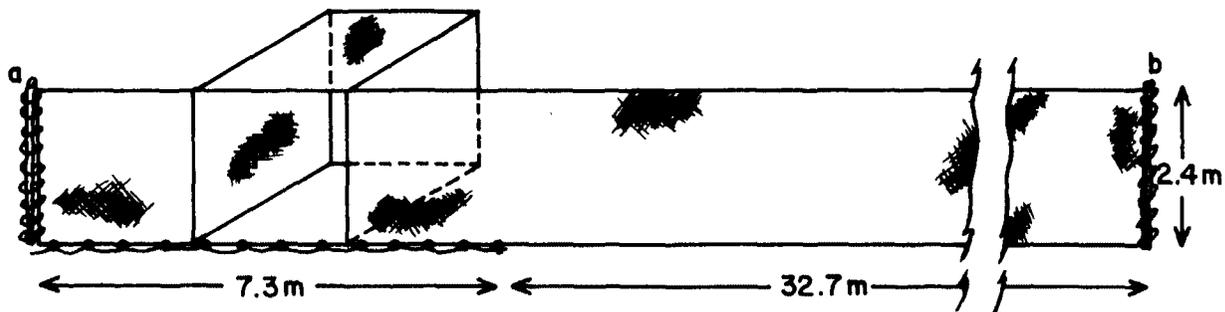


Figure 3

Laboratory Procedures

To determine the feeding behavior of the fishes and their impact upon the resident secondary producers, stomach contents and feeding periodicity studies are being conducted. The resident fishes are collected by trawl during the times of day when feeding is actively occurring for taxonomic analysis of stomach contents. For determination of feeding periodicity, trawling was conducted over 24 hour periods in May and August 1979. Stomachs from the larger, migratory predators are sampled during the monthly gill net collections.

The method of stomach collection depends upon the size of the fish. For resident fishes larger than 150 mm and for all migratory predators, stomachs are removed in the field and preserved in 10% buffered formalin immediately after capture. Tags are placed with the stomach describing fish length, species, and collection number to associate the stomach with further information available on the field data sheets. For resident fishes smaller than 150 mm, specimens are preserved whole in 20% buffered formalin; the body cavity is slit to facilitate penetration of the formalin. When stomachs are removed a qualitative index of fullness based upon the size of the specimen is assigned. Contents are transferred to 40% isopropyl alcohol prior to analysis.

Analysis of stomach contents of planktivorous and piscivorous fishes is conducted by the Higher Level Consumer Interactions group; identification of stomach contents of fishes feeding on invertebrate secondary consumers is conducted by the Resident Consumer Interactions group. When contents are removed, a second qualitative index of the state of digestion of the food items is determined. The combination of these two indices allows

preliminary analysis of feeding periodicity. After contents are identified to the lowest taxon possible, individual food items are dried to constant weight at 56°C and weighed. Certain items, such as nematodes and harpacticoid copepods are assigned weights from literature values for dry weight. Feeding of zooplanktivorous fishes will be conducted in the coming year using the technique of Carr and Adams (1972).

Feeding periodicity is being determined for spot (Leiostomus xanthurus), pipefish (Syngnathus fuscus), bay anchovy (Anchoa mitchilli), and silver perch (Bairdiella chrysoura). Collections are made by otter trawl over a 24 hour period. From each sampling period, total gut contents of up to six specimens are removed. The contents and the fish are then dried and weighed separately; the ratio of dry gut content weight to dry body weight gives an analysis of feeding periodicity which, when combined with estimates of evacuation rate at the temperature of collection, will allow analysis of daily ration. Analyses of samples taken in May and August are currently underway.

Preliminary experiments are being run in the laboratory to examine the effect of artificial Zostera marina on predator-prey relationships of migratory predators and resident fishes. The experimental setup (Figure 4) consists of two circular wading pools, (3.66 m in diameter, 0.9 meters deep) with a volume of approximately 9500 liters each. The present design utilizes a closed system with a biological filter comprised of 0.24 m³ of coarse sand, oyster shell, and gravel; circulation is provided by two 38 liter per minute pumps. Predators are captured by hook and line, prey fishes by cast net, otter trawl, and dipnet. Predators are maintained as residents in the tanks; holding tanks provide a supply of

Figure 4: Present laboratory tank setup for the predator-prey experiments. (A). 3.7 meter diameter, 0.9 m deep experimental tanks with sand substrate (B); the tank on the right consists of an unvegetated control while the tank on the left has a 1 m² artificial eelgrass mat (C); water is pumped from the tanks (F) to a biological filter (d) containing 25 cm gravel, 15 cm oyster shell, and 5 cm sand, and is gravity fed back to the tanks (G). Water depth is equalized between the two tanks (E). Predators are maintained as residents in the tanks and prey fishes are introduced to initiate the experiments.

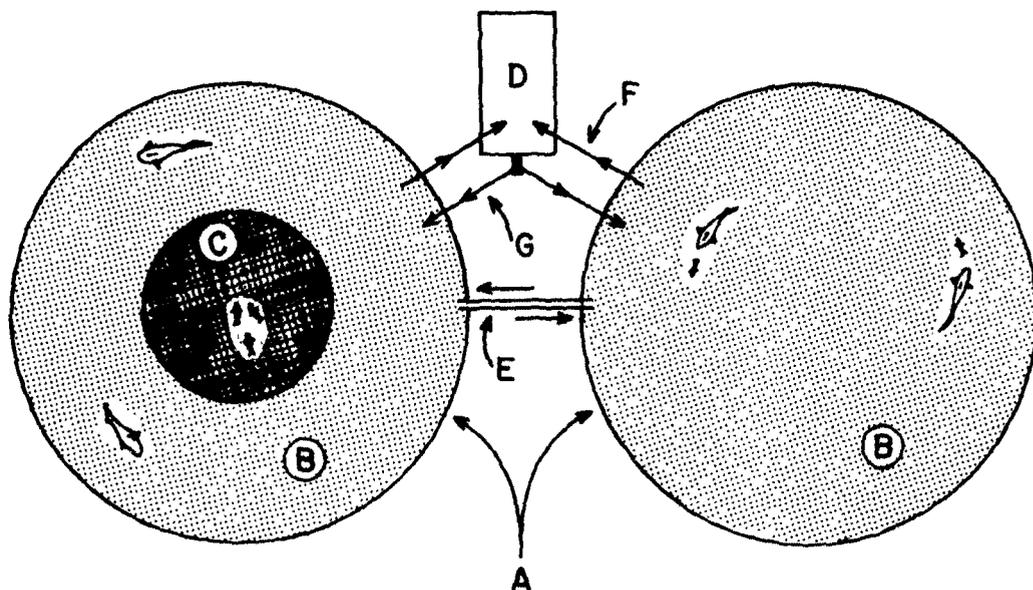


Figure 4

both predator and prey fishes. Artificial eelgrass (3/16" wide green polypropylene ribbon, 0.6 density) mats have been woven to observed field densities (dense- 1750 blades/m²; average-- 875 blades/m²). Mats (1 m²) will be placed in the center of the experimental pools to mimic an eelgrass habitat; prey will be released into the center of the tanks in both eelgrass densities and in bare bottom controls. Preliminary work has involved setting up the experimental system, determining the proper size of predators for the tank, determining appropriately sized prey for the predators, and analyzing methodological problems as necessary for determining final experimental design.

Temperature acclimation tanks have been set up in the laboratory with optional flow-through or closed system capabilities. Current acclimation temperatures are 12°, 17°, 22°, and 27°C. This will allow temperature related analysis of respiration rates and evacuation rates of Bairdiella chrysoura, the silver perch, as part of a study on the bioenergetics and physiology of this species. Evacuation rate analysis is also planned for the pipefish Syngnathus fuscus. Respiration chambers (Figure 5) have been constructed with flow-through characteristics to allow analysis of metabolic rate at different temperatures. Experiments are currently being run with B. chrysoura.

Figure 5: Flow-through respirometer. Although only two are shown, the system currently in use has five fish chambers (A), four of which contain fish and one of which is a control blank to monitor bacterial respiration. Water is pumped through chambers and tubing by a peristaltic pump (D) past oxygen probes (C) contained in special probe holders (B). Flow rates are varied between 3 and 18 m/min depending on fish size and experimental temperature and are measured (E) during each experiment.

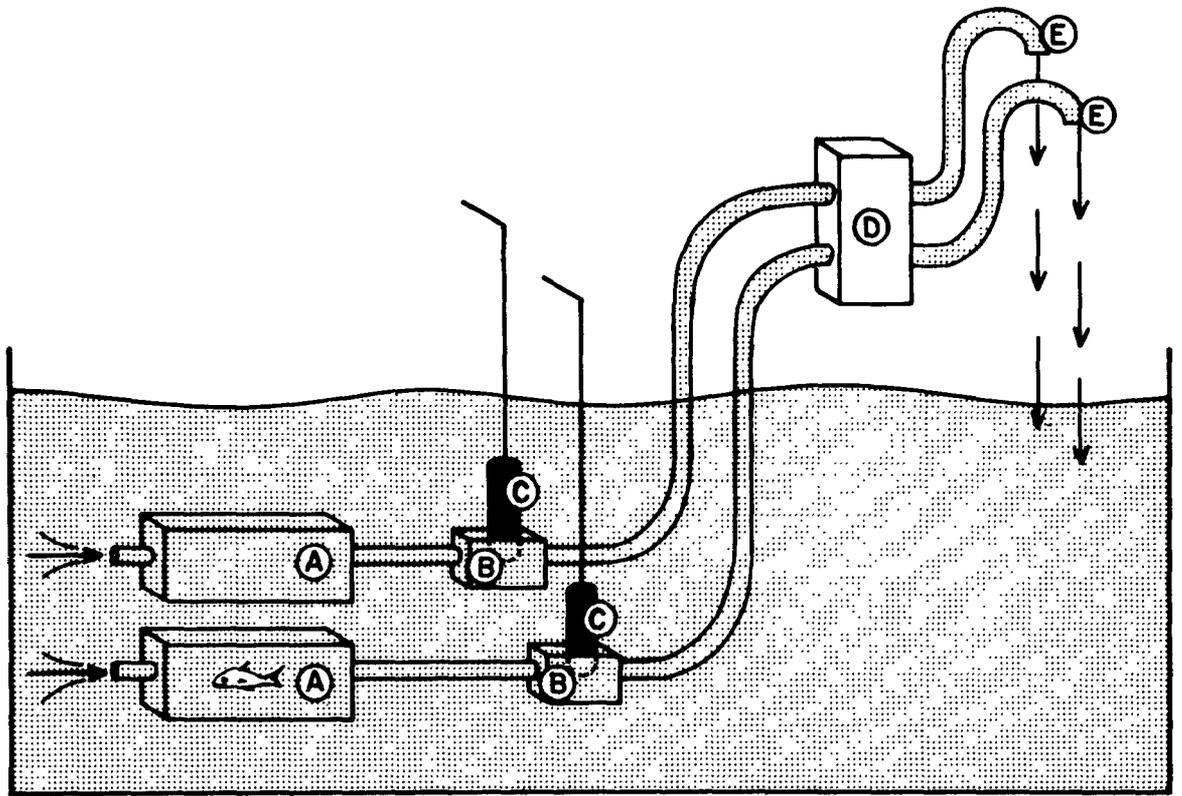


Figure 5

RESULTS

Field Program

Migratory predators sampled with the gill nets are represented by 264 specimens of twelve species in nine families. Data on catch for March through August 1979 are presented in Table 1. Catches (representing number caught over the 24 hour period with nets fished every four hours) were very low in both March and April. The April catch, represented by a single bluefish (Pomatomus saltatrix) points up the variability in catch of migratory predators. One net in the sand area fished overnight 3 days prior to sampling (a set aborted by weather) caught 45 bluefish as compared to 8 captured in the vegetated areas. In May, catch increased with movement into the bay of the teleosts Pomatomus saltatrix, Cynoscion nebulosus, C. regalis, and the elasmobranchs Rhinoptera bonasus and Dasyatis sayi. In June the sandbar shark, Carcharhinus milberti dominated the catch and has continued as the dominant through July and August (Table 1).

The greatest catch of migratory predators was made in the Zostera area (48%) followed by Ruppia and sand areas (26% each). The combined catch in the vegetated areas (representing twice the fishing effort in the sand area) provides preliminary evidence for the distribution of the species relative to vegetation type. The bluntnose stingray (Dasyatis sayi) and the cownose ray (Rhinoptera bonasus) are equally abundant in sand and vegetated areas during months with low abundance; in May, however, when the catch of the cownose ray was highest it occurred most frequently in the sand area. The sandbar shark (C. milberti) was clearly more abundant in vegetated areas. Spotted seatrout (Cynoscion nebulosus)

TABLE 1

Migratory Predators

Species	March			April			May			June			July			August		
	Z	R	S	Z	R	S	Z	R	S	Z	R	S	Z	R	S	Z	R	S
<u>Carcharhinus milberti</u>										17	9	8	44	10	4	18	21	9
<u>Dasyatis sayi</u>					2	2	2			3	1	1						
<u>Rhinoptera bonasus</u>					1	2	14			2	0	2	0	2	1	0	1	1
<u>Alosa sapidissima</u>	1																	
<u>Brevoortia tyrannus</u>	2									1								
<u>Tylosaurus acus</u>												1						
<u>Pomatomus saltatrix</u>				1			3	3	7	8	3	4	0	0	0	2	0	12
<u>Rachycentron canadum</u>																		1
<u>Cynoscion regalis</u>					4	2	1			3	4	0	0	1	0	4	1	0
<u>C. nebulosus</u>					5	1				1			1	1				1
<u>Sciaenops ocellata</u>												1						
<u>Paralichthys dentatus</u>												1						6

and weakfish (C. regalis) were captured almost exclusively in vegetated areas whereas bluefish (Pomatomus saltatrix) was dominant in the sand area in two out of three months of collection.

Two mesh sizes (12.7 and 17.8 cm square mesh) were used for migratory predators; the larger mesh size was chosen to catch the sandbar shark (Carcharinus milberti); only 12% of the catch of this species, however, was made in the 17.8 cm mesh. With the exception of Dasyatis sayi and Rhinoptera bonasus, all species were captured to a much greater extent in the 12.7 cm mesh. These two species are probably sampled poorly in gill nets; most catches occur through entanglement rather than via "gilling" due to body shape.

For most species there are insufficient captures to provide an adequate estimate of diel temporal abundance patterns. Diel pattern of catch for the most abundant species (C. milberti) is presented in Figure 6 for June, July, and August. A cursory examination of the data suggests that the highest rate of catch is in the late afternoon and dark hours. The low catch in the late afternoon of the second day in the June and August collections, however, suggests this may not be the case; in all three months, the first collection was made between 1200 and 1600. In June, an additional collection was made 24 hours after the first collection; the first collection at 1500 resulted in a catch of 20 fish while none were caught at 1500 the following day. Similarly, the catch at 1630 was high the first day in the August collection whereas only one individual was captured at 1500 the following day. This suggests that the population of C. milberti may be limited in this system and that 12 to 14 hours of fishing effectively removes them; by comparison the catches of bluefish and Cynoscion do not appear to show the same phenomenon.

Figure 6: Temporal gill net catch of Carcharhinus milberti in all three sampling areas combined. Nets are fished approximately each four hours over a 24 hour period each month; the points for the time of day represent the midpoint between setting and fishing the net. In all three months the first set was at approximately 1200 EDT.

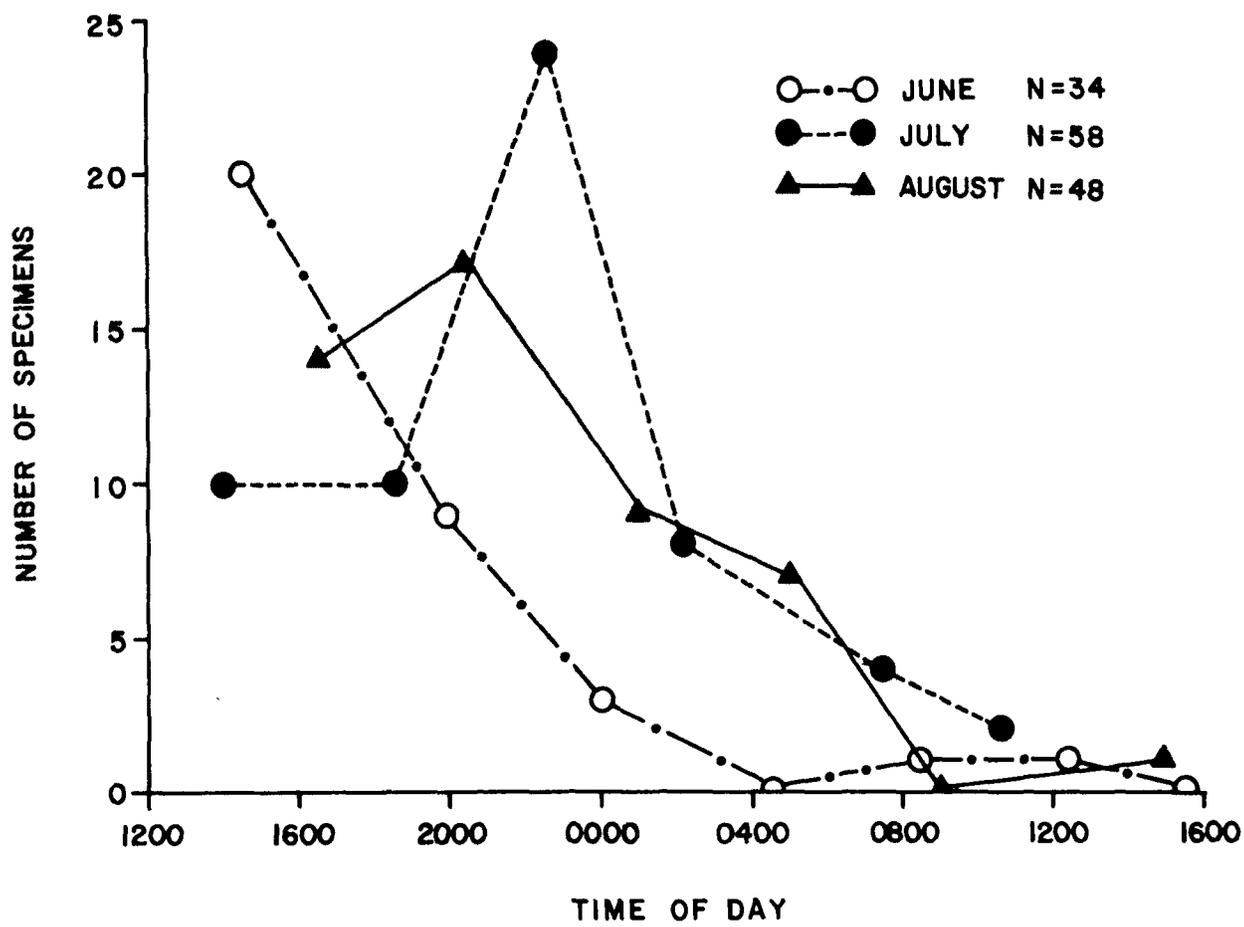


Figure 6

Resident fishes were sampled with the haul seine. Data are considered in this report from March through August 1979, which include 47 night and 9 day sets of the seine. The resulting 4856 specimens represent 30 species in 20 families. Densities of the resident species taken in the monthly night collections are presented Table 2. Generally, numbers and diversity of species were greatest in the Zostera area followed by the Ruppia and sand areas. The number of species captured and total fish density increase with temperature through April and May. Anchoa mitchilli was the most frequently and consistently captured species; it was the numerical dominant in the sand area in March and May and in all habitats during the months of June through August. The Atlantic silverside, Menidia menidia, was the dominant species in both vegetated areas in March, but decreased in abundance in April and has been largely absent from night collections since that time. Spot, Leiostomus xanthurus, recruited to the Chesapeake Bay in April and was clearly the numerically dominant species of resident fish in all habitats. Atlantic menhaden, Brevoortia tyrannus, has been present in all months since April and was the dominant species in the vegetated areas during May.

Most species captured in the haul seine are relatively uncommon and appear only sporadically. Biomass (dry weight) of seven species is presented in Table 3. The dominant species in terms of biomass differs from the numerical dominant in certain months; with few exceptions, however, Anchoa mitchilli remains the dominant species. In March, M. menidia is dominant in all habitats; L. xanthurus is the dominant species only in May in the Zostera sampling area. Although clearly the numerical dominant in April (Table 2), all specimens are newly recruited postlarvae (mean length 18.1 mm) which individually contribute little to the fish biomass.

TABLE 2

Resident Fishes
#/100 m²

	March			April			May			June			July			August		
	Z	R	S	Z	R	S	Z	R	S	Z	R	S	Z	R	S	Z	R	S
<u>Anguilla rostrata</u>							1.97											0.22
<u>Alosa aestivalis</u>				3.15	0.44	1.90												
<u>A. pseudoharengus</u>												0.58						
<u>Brevoortia tyrannus</u>					1.40	2.75	70.08	69.24	34.45		0.95	10.31	0.31	0.26		0.22	0.65	
<u>Anchoa mitchilli</u>	0.56	0.97	1.30	10.63	22.93	27.46	27.17	33.24	52.15	94.49	57.22	50.0	31.60	21.78	42.68	49.73	49.20	14.47
<u>Rissola marginata</u>				0.79	1.23		0.39	0.39						0.26	0.26			
<u>Hemiramphus brasiliensis</u>							0.79	0.66										
<u>Lucania parva</u>							8.27	1.05	0		0.95							
<u>Menidia menidia</u>	9.02	8.65	0.43	2.36	0.26	0.33												0.22
<u>Membras martinica</u>				1.18	0.96	3.28	1.97	1.71	2.88	5.51	1.54	0.35	4.72	1.57	2.53	3.31	1.95	
<u>Gasterosteus aculeatus</u>	0.43																	
<u>Syngnathus fuscus</u>							3.15	1.57		1.74	0.71		3.60	4.46	1.13	3.94	2.60	0.22
<u>Centropristis striata</u>								0.39										
<u>Orthopristis chrysoptera</u>															.29			
<u>Bairdiella chrysoura</u>																2.01	1.30	0.22
<u>Cynoscion nebulosus</u>																1.34		1.10
<u>C. regalis</u>																1.08	0.65	
<u>Leiostomus xanthurus</u>				225.2	132.48	74.67	37.80	5.39	10.49	5.80	8.39	3.51	1.74		4.61	1.95		0.66
<u>Menicirrhus americanus</u>																0.22		0.66
<u>Gobiosoma ginsburgi</u>				0.39			0.39											
<u>Peprilus sp.</u>																		0.22
<u>Paralichthys dentatus</u>								0.39		0.29	0.24	0.35						
<u>Scophthalmus aquosus</u>	0.56																	
<u>Pseudopleuronectes americanus</u>								0.66					0.31					
<u>Trinectes maculatus</u>										0.29								
<u>Sphoeroides maculatus</u>																0.22		0.22

TABLE 3

Resident Fishes
Biomass (mg dry wt/m²)

	March	April	May	June	July	August
<u>*Brevoortia tyrannus</u>						
Zostera			88.32		10.80	8.74
Ruppia		0.57	86.07	7.20	6.09	50.87
Sand		1.07	51.46	79.98		
<u>*Anchoa mitchilli</u>						
Zostera	0.94	153.19	38.88	176.95	80.80	116.07
Ruppia	3.75	70.98	42.85	95.23	47.04	121.57
Sand	2.60	102.06	72.28	80.73	97.13	38.38
<u>Membras martinica</u>						
Zostera		16.14	26.63	68.83	44.40	38.69
Ruppia		12.92	18.06	14.07	19.21	20.14
Sand		47.11	40.10	4.03	18.57	
<u>Menidia Menidia</u>						
Zostera	105.71	27.15				
Ruppia	68.08	1.12				1.80
Sand	8.96	18.24				
<u>Syngnathus fuscus</u>						
Zostera			11.62	8.19	4.71	3.53
Ruppia			5.17	0.58	6.68	5.96
Sand					1.85	0.20
<u>Bairdiella chrysoura</u>						
Zostera						2.05
Ruppia						0.94
Sand						0.31
<u>Leiostomus xanthurus</u>						
Zostera		41.08	133.38	54.59	28.41	29.06
Ruppia		22.57	15.56	43.87		
Sand		11.91	34.68	17.18	50.18	36.80

The day haul seine catches made in June included four species not taken at night in any month; these were Gobiesox strumosus, (1), Fundulus heteroclitus (1), Apeltes quadracus (3), and Pomatomus saltatrix (1). Biomass of the dominant species for day and night collections from June is presented in Table 4. Brevoortia tyrannus is dominant in the Zostera area during the day; all specimens, however, were taken in a single collection and none were taken in the other two made in daylight in Zostera. By comparison this species was common at night only in the sand area, where it was taken in all three collections. It is possible that these juveniles school in daylight and disperse at night. Anchoa mitchilli and Membras martinica occur in low densities (except for the latter species in sand) during the day and are abundant during the night; for these two species it is unlikely that the difference is an effect of enhanced avoidance during the daylight samples, since Menidia menidia is captured during the day. The increased abundance of Syngnathus fuscus during the day is probably due to increased activity during the day and better availability to the sampling gear. The lower daytime catches of Leiostomus xanthurus in vegetated areas, however, probably represents increased avoidance of the sampling gear; the ratios of night to day catch are much greater in sand, however, suggesting that some movement from the vegetated areas may occur at night for this species.

Push net sampling has been conducted monthly at night with day samples taken in May and August. Sorting and identification of catch for the ichthyoplankton samples (505 μ m mesh) have been completed for samples taken in March through July; this represents 38 total collections, including 12 collections in the Ruppia area and 13 each in Zostera and

TABLE 4

Resident Fishes
Day-Night Comparison (June)
Biomass (mg dry wt/m²)

	<u>Zostera</u>		<u>Ruppia</u>		<u>Sand</u>	
	D	N	D	N	D	N
<u>Brevoortia tyrannus</u>	573.30	0	0	7.20	0	79.98
<u>Anchoa mitchilli</u>	3.64	176.95	12.70	95.23	0	80.73
<u>Membras martinica</u>	6.91	68.83	5.90	14.07	27.53	4.03
<u>Menidia menidia</u>	37.39	0	9.64	0	6.01	0
<u>Syngnathus fuscus</u>	15.82	8.19	1.08	0.58	0	0
<u>Leiostomus xanthurus</u>	6.33	54.59	16.82	43.87	0.87	17.18

sand habitats. Volumetric and areal estimates of sampling effort (Table 5) reveal moderate monthly variability but almost equal effort (expressed as percent of total) between habitats. Push net collections yielded 2669 juvenile/adult fishes, 3243 larval/postlarval specimens and 8235 fish eggs.

Eggs of the windowpane flounder, Scophthalmus aquosus, the bay anchovy, Anchoa mitchilli, and unidentified species of the family Sciaenidae dominated push net collections (Tables 6 and 9). Additional species represented were Tautoga onitis, Trinectes maculatus, Membras martinica, Hyporhamphus sp. and an unidentified goby species. Eggs of the latter three species are demersal, being attached to vegetation by chorionic filaments (Atheriniformes) or laid in open shell nest sites (Gobiidae). As a consequence, density estimates of eggs of these species cannot be considered quantitative.

Eggs of A. mitchilli slightly outnumbered those of sciaenids (1.63:1) and density estimates (May - July) were roughly comparable in all habitats (Table 6). During each month of occurrence, peak densities of anchovy and sciaenid eggs were observed over the sand habitat and lowest densities over Ruppia beds. A. mitchilli and sciaenid egg abundance estimates ranged from 0.8 - 2018 eggs/100 m³ and 0.9 - 1159 eggs/100 m³ respectively.

Larval and postlarval stages of 14 species representing 11 families were taken in push net samples (Table 7). In addition larval atherinids (probably both Menidia menidia and Membras martinica) and Gobiosoma (probably both bosci and ginsburgi) were collected but reliable species separation was not possible.

Table 5
 Volumetric and areal estimates of sampling effort by pushnet
 at Vaucluse Shore study site.

	Zostera		Ruppia		Sand	
	m ³	m ²	m ³	m ²	m ³	m ²
March	194.37	198.50	180.66	194.60	272.19	277.96
April	269.09	274.81	246.71	265.73	271.56	277.33
May (N)	152.90	164.69	219.59	274.01	180.67	194.60
(D)	258.82	278.77	212.93	293.64	217.42	234.19
June	275.14	296.35	221.49	328.41	258.25	278.17
July	206.18	257.27	192.81	240.60	164.00	176.65
Totals	1,356.50	1,470.39	1,274.19	1,596.99	1,364.09	1,438.90
% of Total	31.9	35.4	33.9	32.6	34.2	31.9

Table 6

Monthly estimates of fish egg densities (eggs/100 m³)

from push net collections at Vacluse Shores.

Z = Zostera, R = Ruppia, S = Sand

Species	March			April			May			June			July		
	Z	R	S	Z	R	S	Z	R	S	Z	R	S	Z	R	S
<u>Scopthalmus aquosus</u>	1.5	8.3	4.0	21.2	16.2	17.3									
<u>Tautoga onitis</u>				4.4		1.5									
<u>Anchoa mitchilli</u>							139.3	10.5	491.5	16.4		130.9	11.2	0.5	2,018.3
<u>Sciaenidae</u>							12.4	11.4	29.3	11.9	0.9	127.0	322.1	7.8	1,159.2
<u>Membras martinica</u>							1.9			0.4		0.4	1.5	6.2	
<u>Hyporhamphus</u> sp.													0.5	1.0	
<u>Trinectes maculatus</u>															1.2

Table 7

Monthly estimates of larval/postlarval fish densities (fish/100 m²)

from evening push net collections at Vaucluse Shores.

Z = Zostera, R = Ruppia, S = Sand

Species	March			April			May			June			July		
	Z	R	S	Z	R	S	Z	R	S	Z	R	S	Z	R	S
<u>Ammodytes hexapterus</u>	8.6	13.9	19.4												
<u>Paralichthys dentatus</u>	3.0	1.5	2.9	0.3											
<u>Brevoortia tyrannus</u>	4.5	4.6	5.8	19.5	42.5	1.1									
<u>Pseudopleuronectes americanus</u>	0.5														
<u>Atherinidae</u>				0.2	5.3					3.7			10.5	12.9	13.0
<u>Scopthalmus aquosus</u>				4.6	0.4	0.4									
<u>Syngnathus fuscus</u>							1.8	0.7	0.5	32.7		5.4	83.2	25.4	71.9
<u>Cynoscion regalis</u>															
<u>Gobiosoma sp.</u>										116.8	2.4	385.0	1.9	4.2	4.5
<u>Anchoa mitchilli</u>										11.1		95.9	45.9	35.3	78.7
<u>Hyporhamphus sp.</u>										0.3			0.8	5.4	
<u>Hypsoblennius hentzi</u>										0.7			6.6	1.3	6.2
<u>Microgobius thalassinus</u>										0.3				0.4	0.6
<u>Chasmodes bosquianus</u>													1.9		3.4
<u>Hippocampus erectus</u>													0.4		
<u>Astroscopus guttatus</u>													0.4		

Ichthyoplankton collections were seasonally distinct. The winter-spring assemblage was dominated by postlarvae of Ammodytes hexapterus and Brevoortia tyrannus but also included postlarval Paralichthys dentatus and larvae of S. aquosus and Atherinidae species. Premetamorphic (< 30 mm SL) B. tyrannus peaked in density during April and appeared more abundant over vegetated habitats. In May, metamorphosed (juvenile) specimens (Table 8) exhibited a similar distributional patterns were apparent in other winter-spring assemblage species.

The summer was characterized by greater diversity and abundance and was dominated by larval anchovies, gobies, and pipefishes (Table 7). Young Syngnathus fuscus and larval A. mitchilli peaked in abundance in July while the largest concentrations of Gobiosoma sp. larvae appeared in June. Larval anchovies and gobies were taken in greatest densities over non-vegetated habitat. Collections of young pipefish as well as the additional 7 species making up this summer ichthyoplankton assemblage revealed no distributional patterns.

Data on juvenile and adult fishes occurring in evening push net samples are summarized in Table 8. Four species appear to be consistently available to the push net. These include juvenile/adult A. mitchilli and M. martinica and early juvenile stages of L. xanthurus and B. tyrannus. The remaining species (as well as larger size classes of B. tyrannus and L. xanthurus) are either effective avoiders of the gear, occur below the sampling depth of the push net, or are infrequent in the habitats sampled.

Day/night catch data (Table 9) for eggs and larvae was highly variable, with no trends apparent. As expected, however, catches of juvenile/adult fishes were consistently highest during evening collections.

Table 9'

Day versus night push net catch comparisons at Vauclose Shores.

31 May 1979

Species	Zostera		Ruppia		Sand	
	Day	Night	Day	Night	Day	Night
Eggs (#/100 m ³)						
<u>A. mitchilli</u>	0.8	139.3	-	10.5	55.7	491.5
<u>Sciaenidae</u>	-	12.4	-	11.4	-	29.3
<u>M. martinica</u>	1.2	1.9				
Unknown			0.9	-	1.8	-
<u>Goniidae</u>	0.4	-				
Larvae (#/100 m ²)						
<u>S. fuscus</u>	3.9	1.8	0.7	0.7	14.5	0.5
<u>C. regalis</u>					-	0.5
<u>Gobiesox strumosus</u>	4.7	-			1.3	-
<u>Atherinidae</u>	0.7	-	0.3	-	1.3	-
<u>Gobiosoma sp.</u>	0.7	-			0.4	-
<u>A. mitchilli</u>	5.7	-				
<u>H. hentizi</u>			0.3	-		
Juvenile (#/100 m ²)						
<u>M. martinica</u>	-	20.0	-	12.0	-	1.5
<u>B. tyrannus</u>	0.7	18.9	-	392.3	-	2.6
<u>A. mitchilli</u>	-	38.9	-	50.0	-	15.4
<u>L. xanthurus</u>	-	2.4			-	3.1
<u>S. fuscus</u>			-	1.1	0.9	-
<u>Hyporhamphus sp.</u>	-	0.6	-	0.4		

Table 8

Monthly estimates of juvenile/adult fish densities (#/100 m²)

from night push net collections at Vaucluse Shores.

Z = Zostera, R = Ruppia, S = Sand

	March			April			May			June			July		
	Z	R	S	Z	R	S	Z	R	S	Z	R	S	Z	R	S
<u>Alosa aestivalis</u>			0.4	0.2	0.8										
<u>A. pseudoharengus</u>															0.4
<u>Menidia menidia</u>	1.0		0.4		0.4						0.9				
<u>Membras martinica</u>				9.6	0.8	1.1	20.0	12.0	1.5		15.9	3.9	3.5	6.7	2.8
<u>Brevoortia tyrannus</u>							18.9	392.3	2.6	0.3	0.6	15.1			
<u>Anchoa mitchilli</u>	2.0		0.7	13.2	16.6	8.3	38.9	50.0	15.4	58.4	63.0	44.9	21.8	15.4	8.5
<u>Anguilla rostrata</u>	1.1	3.1	4.7												
<u>Leiostomus xanthurus</u>				26.4	38.4	19.1	2.4		3.1				1.6	1.7	
<u>Gasterosteus aculeatus</u>				0.2											
<u>Syngnathus fuscus</u>								1.1		1.0	0.6	0.4			2.8
<u>Hyporhamphus sp.</u>							0.6	0.4		1.4					

Zooplankton samples have been taken concurrently with ichthyoplankton samples. Most samples have been curated and analysis will begin in October 1979 in conjunction with the addition of personnel as requested in the amendment to EPA. In general the number of samples is double that for the ichthyoplankton sampling with half used for biomass determination and half for taxonomic analysis. Zooplankton biomass (mg ash-free dry weight/m³) has been determined for March through July 1979 and is presented in Table 10 and Figure 7. Biomass is determined as ash-free dry weight ("organic weight") due to the occurrence of sand and particulate matter in these shallow-water samples which are variable and often render dry weights alone useless. The trend shows that biomass is consistently greatest in the Ruppia area, the shallowest area sampled; Zostera and sand areas are approximately equal with fluctuations in certain months. All values are low in April and June. April samples were taken after a storm which had an effect on the fish populations; it may also have had an effect on the zooplankton biomass. It is possible, however, that the large populations of postlarval spot (Leiostomus xanthurus, see Table 2) may cause a reduction through predation. No explanation is apparent for the low values observed in June. Analysis of the taxonomic composition should help determine certain of the causative mechanisms in the low values. Day samples were taken in May; the diurnal differences in biomass are apparent (Table 10). The day samples, however, were taken after a storm had dropped approximately two inches of rain on the area. It is possible that the low biomass may be at least partially due to lowered salinity from the storm as well as vertical migration of components of the zooplankton.

TABLE 10
Zooplankton Biomass
(mg AFDW/m³)

<u>Night Samples</u>	Zostera	Ruppia	Sand
March	129.3	225.3	234.2
April	35.1	69.3	39.8
May	132.4	397.5	118.6
June	61.4	91.7	32.1
July	151.8	380.6	164.5
<u>Day Samples</u>			
May	21.5	55.7	51.2

Figure 7: Organic biomass (Ash-free dry weight per m³) of zooplankton by habitat and month. Each value represents the mean of two determinations. R: Ruppia area, Z: Zostera area, S: sand area.

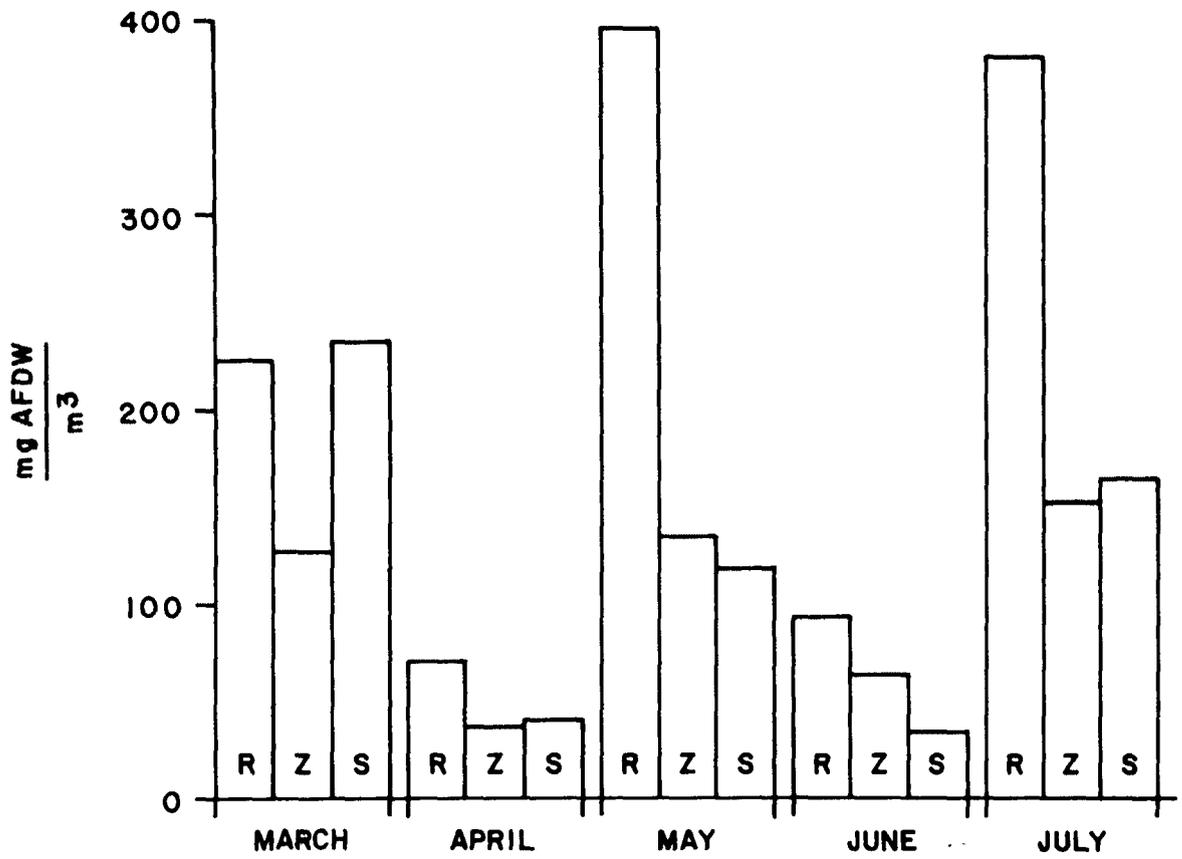


Figure 7

Non-empty stomachs from 343 resident fishes representing 10 species and 117 migratory predators representing 9 species have been collected, sorted, and contents identified. We are in the process of determining dry weights of all contents and coding the data for computer analysis. Additional specimens of these and other species have been taken to complete size ranges and seasonal sampling of the resident fishes. Stomachs from migratory predators continue to be taken as collected. The species sampled, number of stomachs, and length range are presented in Table 11. Summer flounder (Paralichthys dentatus) has been treated both as a resident fish and as a migratory predator. Specimens under 200 mm SL are considered resident fishes; prey items are almost exclusively invertebrates from within the eelgrass habitat, principally mysids and Crangon septemspinosa. Those specimens larger than 200 mm prey almost exclusively on fishes, including Syngnathus fuscus and Leiostomus xanthurus.

Gravimetric analysis of the stomach contents and coding of the data are currently underway. Preliminary analysis of the feeding behavior of three important members of the "true resident" group (based upon percent frequency of occurrence of prey items) is presented in Figures 8-11. Stomach contents of spot (L. xanthurus) collected in July 1978 and October 1978 are presented in Figures 8 and 9, respectively. Fish collected in July, when mean length was approximately 65 mm SL, fed predominantly upon benthos as is apparent from the abundance of copepods (primarily harpacticoids), nematodes, ostracods, polychaetes, and detritus (Figure 8). Epibenthic and possibly planktonic feeding also occurred as shown by the presence of amphipods, mysids, and fish eggs. In October, when mean length of the

TABLE 11
Fish Stomachs

Species	Number	Length Range
<u>Resident fishes</u>		
<u>Urophysis regius</u>	8	41-120
<u>Syngnathus fuscus</u>	84	61-160
<u>Centropristis striata</u>	3	61-160
<u>Orthopristis chrysoptera</u>	16	21-120
<u>Bairdiella chrysoura</u>	111	41-140
<u>Leiostomus xanthurus</u>	87	61-160
<u>Prionotus carolinus</u>	11	21-120
<u>Paralichthys dentatus</u>	14	121-200
<u>Pseudopleuronectes americanus</u>	8	41-100
<u>Trinectes maculatus</u>	1	121
<u>Migratory predators</u>		
<u>Carcharhinus milberti</u>	56	461-860
<u>Rhinoptera bonasus</u>	2	741-946
<u>Pomatomus saltatrix</u>	32	281-880
<u>Rachycentron canadum</u>	1	410
<u>Cynoscion regalis</u>	6	321-570
<u>C. nebulosus</u>	11	381-590
<u>Micropogon undulatus</u>	1	350
<u>Sciaenops ocellata</u>	2	381-780
<u>Paralichthys dentatus</u>	6	241-440

Figure 8: Percent frequency of occurrence of specific prey items in stomachs of resident fishes from the Vacluse Shores study site. Numbers in the figures may not equal those in Table 11 due either to inclusion of empty stomachs (in the figures) or due to sub-sampling of available stomachs; Spot, Leiostomus xanthurus collected in July, 1978.

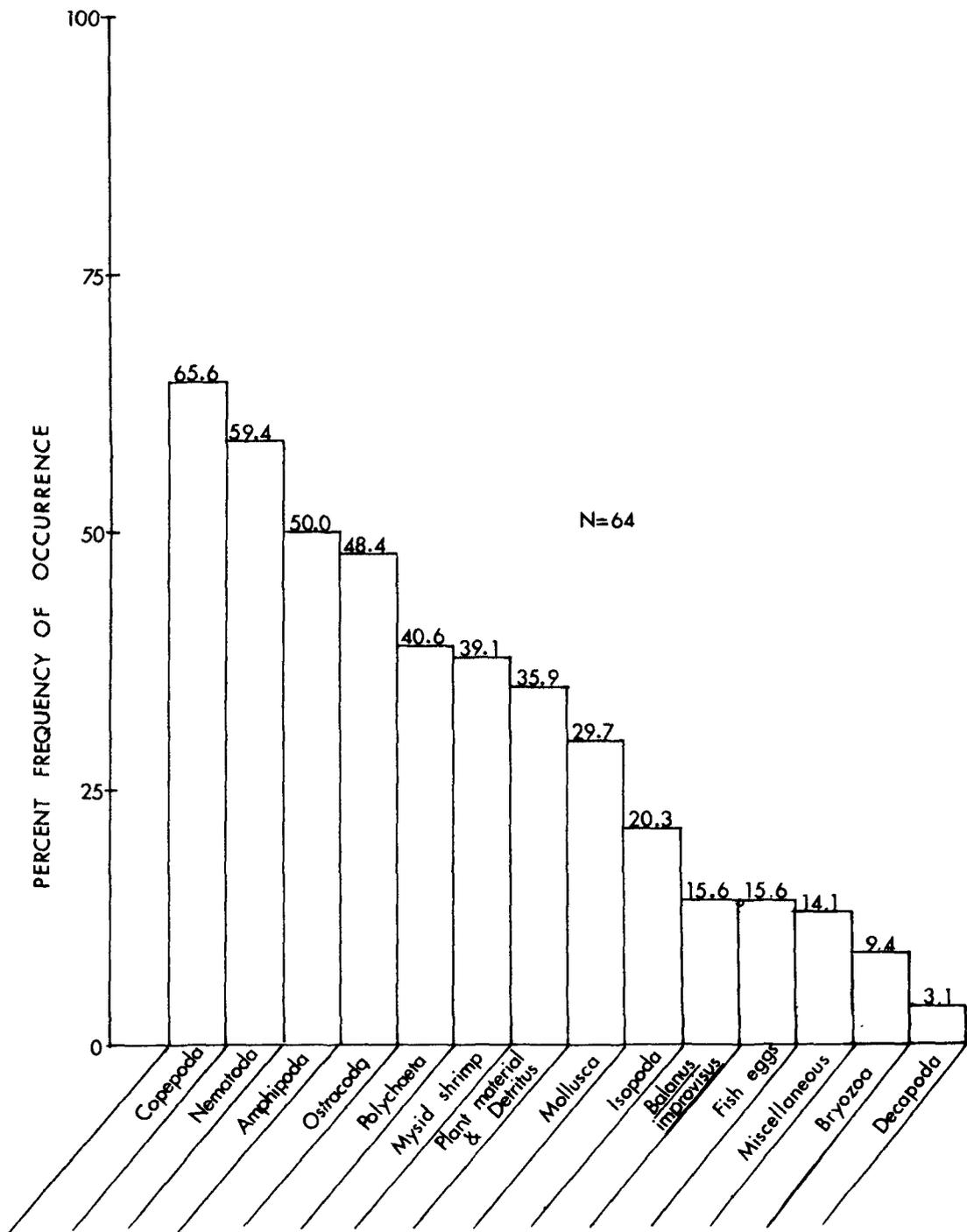


Figure 8

spot collected was 101 mm SL, mysid shrimp were more conspicuous in the diet, but benthic feeding remained important (Figure 9).

Feeding by the silver perch (B. chrysoura), all collected in the month of October, is notably different from that of spot (Figure 10). Harpacticoid copepods, nematodes, and other evidence of benthic feeding is lacking. Mysids are clearly the dominant food item, as both numerical and preliminary gravimetric analyses confirm. Planktivorous feeding is taking place as demonstrated by presence of mysids and calanoid copepods. Feeding within the vegetated areas is suggested by the abundance of amphipods and other epifauna. Pipefish (Syngnathus fuscus), captured almost exclusively in vegetated areas (Table 2), feeds on a combination of prey items from within and outside of the vegetated areas (Figure 11). Calanoid copepods occur most frequently in the fish collected in July, along with Caprella penantis and other amphipods. In the October collections, however, mysids (Neomysis americana) clearly dominate the diet; calanoids remain relatively important in the diet, but amphipods are consumed less frequently (Figure 11).

The migratory predators feed primarily on fishes and blue crab, Callinectes sapidus. Spotted seatrout (Cynoscion nebulosus) and weakfish (C. regalis) show similar feeding habits. Both species have been caught mostly in the vegetated areas (Table 1). Diet is comprised primarily of fishes (including small Brevoortia tyrannus and Leiostomus xanthurus) with lower frequencies of invertebrates (Crangon septemspinosa, Palaemonetes vulgaris and a single small Callinectes sapidus). The sizes of fish preyed upon suggest that they are captured within the vegetated areas where the fish

Figure 9: Percent frequency of occurrence of specific prey items in stomachs of resident fishes from the Vaucluse Shores study site. Numbers in the figures may not equal those in Table 11 due either to inclusion of empty stomachs (in the figures) or due to sub-sampling of available stomachs; Spot, Leiostomus xanthurus, collected in October 1978.

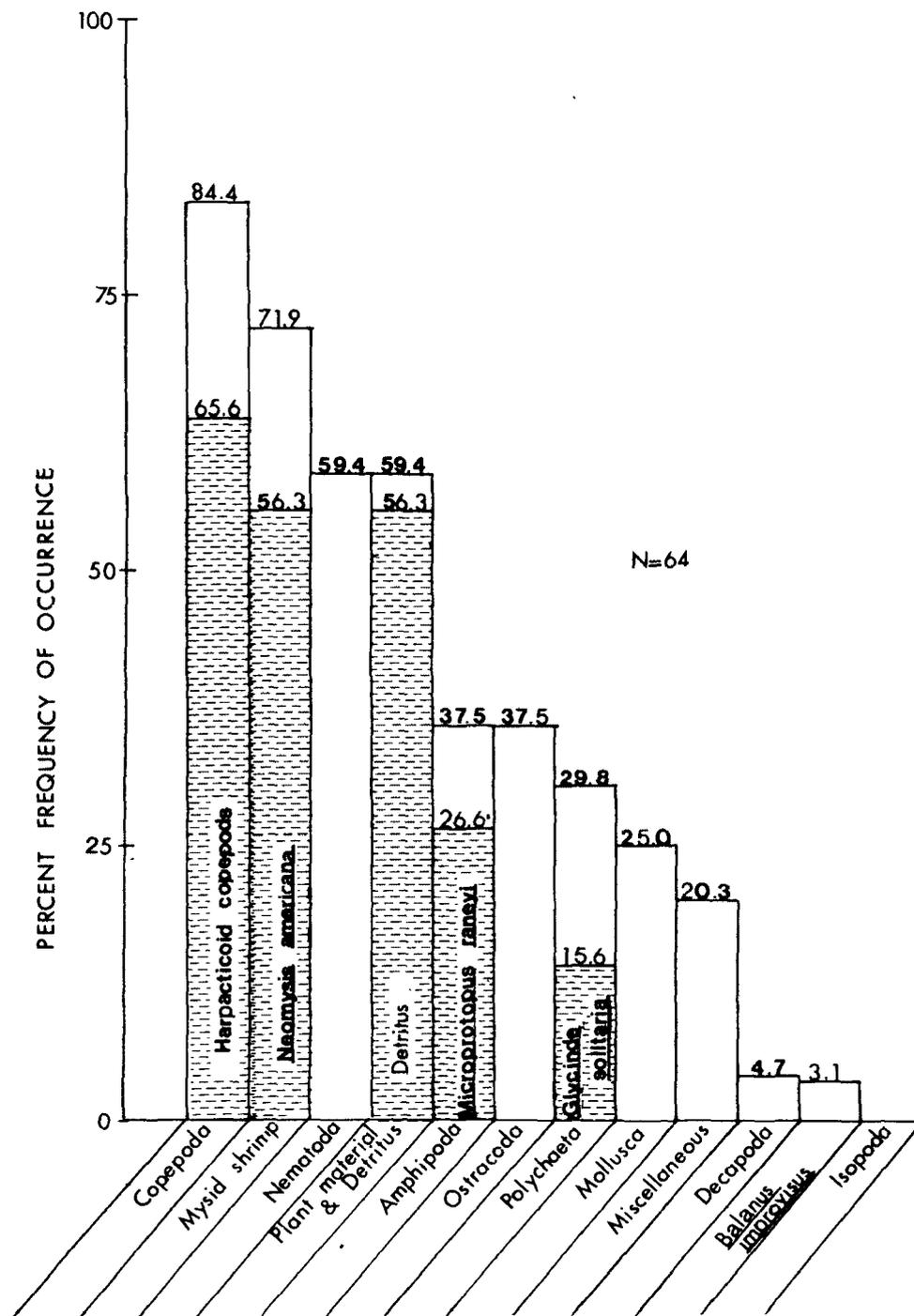


Figure 9

Figure 10: Percent frequency of occurrence of specific prey items in stomachs of resident fishes from the Vaucluse Shores study site. Numbers in the figures may not equal those in Table 11 due either to inclusion of empty stomachs (in the figures) or due to sub-sampling of available stomachs; Silver perch, Bairdiella chrysoura, collected in October 1978.

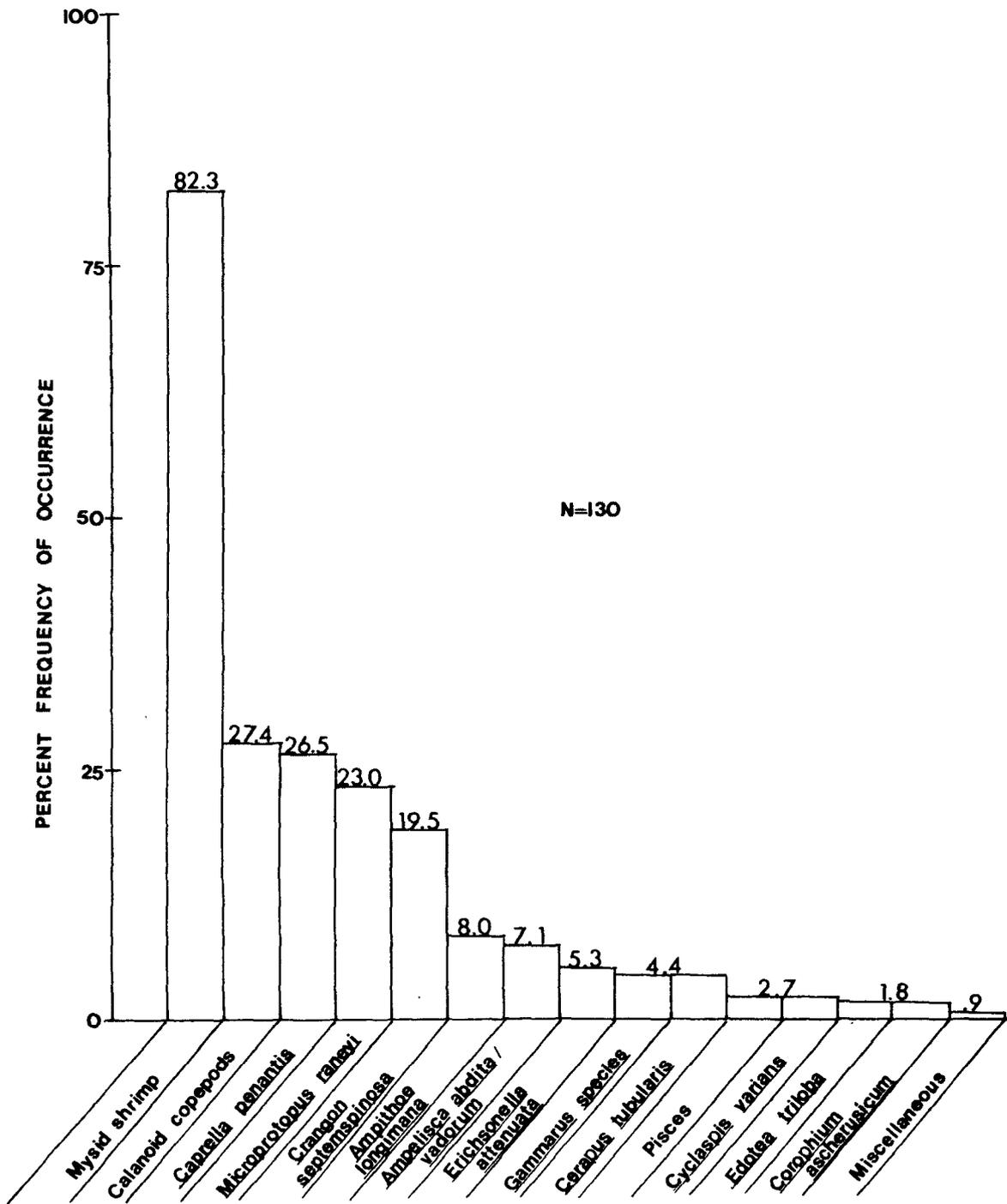
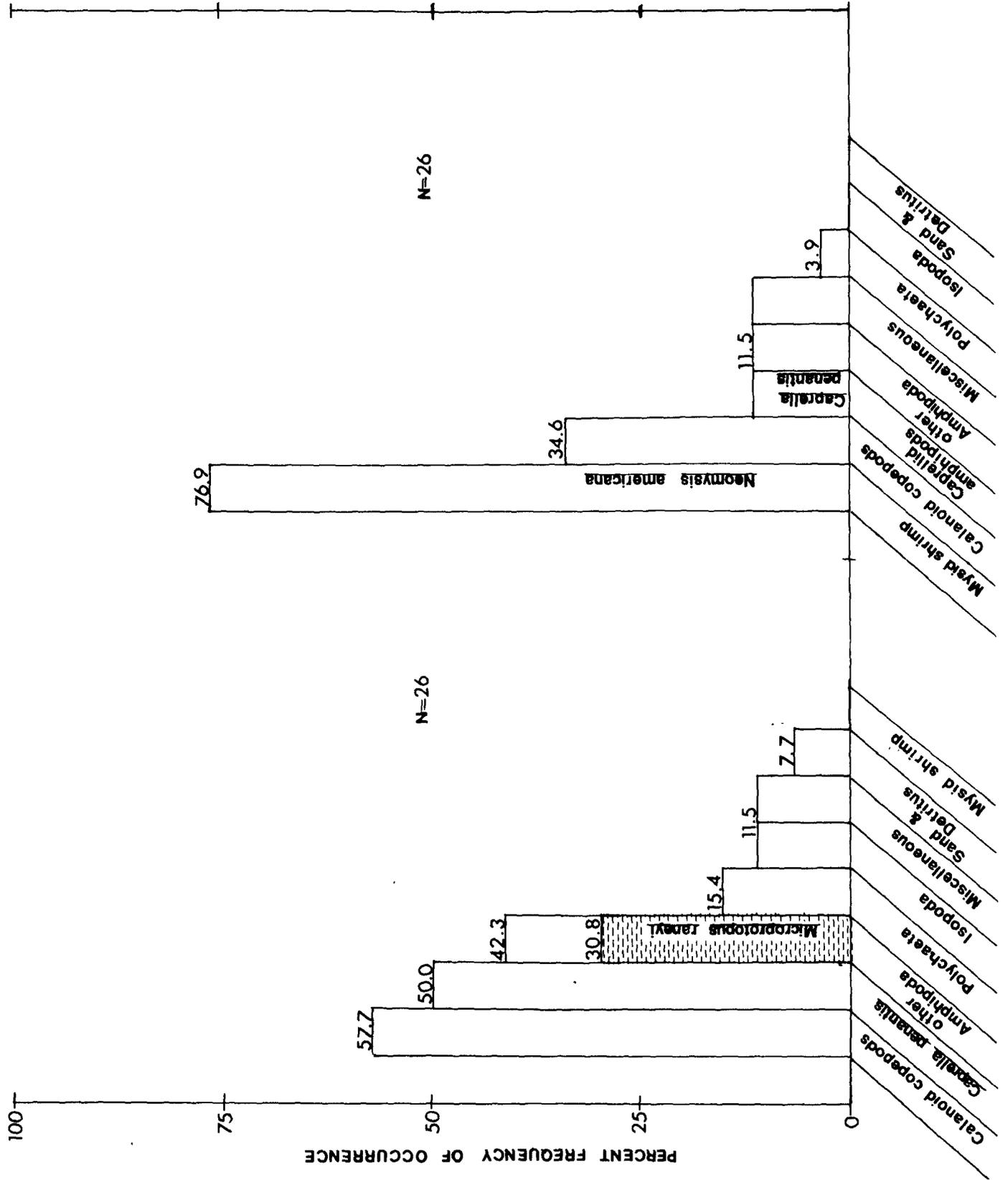


Figure 10

Figure 11: Percent frequency of occurrence of specific prey items in stomachs of resident fishes from the Vacluse Shores study site. Numbers in the figures may not equal those in Table 11 due either to inclusion of empty stomachs (in the figures) or due to subsampling of available stomachs; Pipefish, Syngnathus fuscus collected in July 1978(left) and October 1978 (right).

Figure 11



were caught. The dominant migratory predator after the May collections was the sandbar shark (Carcharhinus milberti) for which the dominant food items have clearly been fish and blue crab. Based upon frequency of occurrence, 54% have contained both fish and crab, 15% exclusively crab, and 31% exclusively fish. Of those fish which were identifiable, Brevoortia tyrannus, Leiostomus xanthurus, and Hypsoblennius hentzi were represented; all of these species are probably taken in the vegetated areas. For those stomachs where dry weight of contents has been determined, fish represents, on the average, 2.1 times the weight of crab consumed. The final species of migratory predator, Pomatomus saltatrix, feeds almost exclusively on fish with a single occurrence of blue crab. The dominant prey species have been spot (25% of identifiable fish occurrences) and menhaden (58%); in contrast to the sandbar shark and Cynoscion spp., however, the menhaden consumed by bluefish are generally larger and probably are captured outside the vegetated area.

One species included in the resident fishes is the spotted hake, Urophycis regius. This species was captured in a single trawl taken in May during a sampling effort aborted due to weather; it has not been taken prior to this time or in a series of trawls made the following week. Eight specimens have been examined for stomach contents, all of which had consumed fish. The only identifiable fish species was spot, Leiostomus xanthurus. From this consideration this species, although small (41-120 mm SL) might be defined as a migratory predator.

Adequate predators for the predator-prey laboratory experiments have been determined. Summer flounder (Paralichthys dentatus), bluefish (Pomatomus saltatrix), and weakfish (Cynoscion regalis) have been successfully maintained in both holding and experimental tanks. The size range

best suited to the size of experimental tanks is from 250 to 350 mm standard length. Summer flounder and bluefish generally commence feeding on live food after one week or less in captivity, whereas weakfish would not feed for a minimum of three weeks. All three of these species are taken in the vegetated areas at the study site; feeding behavior indicated that fish is the primary food.

Five species have been assessed as potential prey for the experiments. The mummichog (Fundulus heteroclitus) showed excessive orientation to the sides of the tanks; its availability, however, is such that it may be used for feeding predators between experiments. The pipefish (Syngnathus fuscus), although important in vegetated areas and showing proper behavior to artificial eelgrass, orients to the bottom and walls of the experimental tank such that predation is nil or low even in the unvegetated controls. The three species chosen for the experiments are spot (Leiostomus xanthurus), silver perch (Bairdiella chrysoura), and menhaden (Brevoortia tyrannus). All are important species in the vegetated areas of the study site in the diets of the three predator species. Spot remain motionless in the bottom of the tank in unvegetated controls, showing movement when confronted by a predator species. Bairdiella, by contrast, generally remains in midwater. Menhaden show schooling behavior, especially when pursued by a predator. The size ranges of all prey species are from 40 to 80 mm SL.

The predators behave differently with respect of prey pursuit. Bluefish approach the prey directly and usually slash or bite the prey to pieces, as described in Olla et al (1970). Weakfish show a more cautious pursuit and attack usually from below. Flounder stalk prey and usually approach from behind. The behavior of predators and preliminary experiments suggest that the predators will have varying success in the presence of artificial eelgrass.

DISCUSSION

Although an entire sampling season has not been completed, the trends in distribution and abundance of the migratory predators and resident fishes recorded in the present study generally show agreement with other studies in shallow-water habitats in the lower Chesapeake Bay (Orth and Heck, in press). The migratory predators (Table 1) show sporadic occurrences with the exception of the sandbar shark, C. milberti, which was consistently abundant during the last three months addressed in the present report. Although gill nets are selective (Hamley 1975), the catch in this study appears to give an estimate of relative abundance of most species with the probable exception of the rays Rhinoptera bonasus and Dasyatis sayi and probably the summer flounder Paralichthys dentatus. The rays are dorso-ventrally flattened and are captured largely due to entanglement. Although the nets foul visibly with jellyfish, large ctenophores, and drifting aquatic vegetation due to current flow, the catch is not markedly greater at night when visual detection would be less effective; this may be due to the low water clarity during most months. The temporal catch of C. milberti shows increases at night but temporal catch is difficult to analyze due to removal of an apparently resident population without replacement (Figure 6). Combining catch of both species of Cynoscion from May through September, 43% are captured during daylight hours, whereas 63% of bluefish (P. saltatrix) were captured in daylight hours. This contrasts with the data of Pristas and Trent (1977), who found 93% of the twelve most abundant species taken at night in gill nets. Thus movement to the shallow water areas is probably greatest during daylight hours when active feeding takes place.

Availability of most species arises from populations moving through the area or coming from adjacent deeper water areas. This is apparently not true for the sandbar shark (C. milberti), which appears to exist in essentially resident populations which are removed within 12-14 hours after initial setting of the gill nets (Figure 6); status as a "resident" predator is consistent with the fact that it was captured primarily in the vegetated areas with slightly greater abundance in the Zostera area (Table 1). Although captured most frequently in the vegetated areas as well, the spotted seatrout and weakfish (Cynoscion nebulosus and C. regalis) do not show a pattern of catch indicative of residence in the bed; bluefish (P. saltatrix), on the other hand, exhibits a greater variability in catch from month to month but in general is most frequently captured in the sand area. The feeding habits of these migratory predators reflect the habitat of occurrence.

Resident fishes sampled by the haul seine show the seasonal trends observed for collections made two years earlier using a trawl at the same study site (Orth and Heck, in press). In the current study, the immigration of spot (L. xanthurus) to the seagrass bed did not occur until mid to late April (Table 2), later than observed in 1977 (Orth and Heck, in press) in lower Chesapeake Bay or for most years in vegetated areas south of Cape Hatteras (Adams 1976a; Thayer et al 1974). The numerically dominant species observed by Orth and Heck was spot, whereas the numerical dominant in the current study is the bay anchovy (A. mitchilli). The increased importance of the pelagic species (B. tyrannus, A. mitchilli, M. menidia, and M. martinica) in the current study is probably due to the difference in gear type. Orth and Heck used a 16 foot otter trawl towed

behind an outboard vessel which fishes effectively only one meter off the bottom; thus both avoidance and fishing of the net below the depth of occurrence of these species suggests that their relative abundance was underestimated. Adams (1976a) showed dominance of pinfish (Lagodon rhomboides) and pigfish (Orthopristis chrysoptera) in North Carolina eelgrass beds; the former, although present in low abundance in the study by Orth and Heck, was not captured in the current study, and the latter was present only in low numbers (Table 2). Spot, however, occurred later in the year in densities similar to those observed by Adams (1976a) using a dropnet.

Within the resident fishes, two subgroups are apparent. The first is comprised of the pelagic and/or schooling group ("pelagic residents") including B. tyrannus, A. mitchilli, M. martinica, and M. menidia. Adams (1976a) did not consider these species as true residents of the bed. Although the same is probably true in the present study for all four of the above species, they are considered with the residents in terms of ecological impact upon the ecosystem due to the relatively high biomass in the vegetated areas. In the night collections these species were taken in all three habitats (Table 2) without clear trends in abundance. Comparing day and night collections for June (Table 4), no trend is apparent for B. tyrannus due to its highly contagious distribution; A. mitchilli is present in vegetated areas in the day, increasing greatly in these areas and in the sand area at night. M. martinica is taken in low abundance during the day except in the sand area; the situation reversed during the night. The other atherinid, M. menidia, however, shows an opposite pattern; none were captured at

night except in March and April while Membras densities were low. In the day collections, however, Menidia was common, especially in Zostera.

The second group of resident fishes ("true residents") is dominated by spot (L. xanthurus) and pipefish (S. fuscus) and includes the majority of other species included in Table 2. In August, silver perch (B. chrysoura) appeared and has remained important in subsequent months as observed by Orth and Heck (in press); the other sciaenids (C. nebulosus, C. regalis, M. americanus) captured in August did not remain as important components of the community. Members of this component of the resident fish group are captured most frequently in the vegetated areas with greater catches in the Zostera sampling area (Table 2). Day-night sampling conducted in June suggests that S. fuscus is more abundant in the day, but this probably reflects greater availability to the haul seine. Spot, on the other hand, appear more abundant in the night collections. Orth and Heck (in press) observed increased catch of spot in all habitats at night as observed in the present study. It remains to be determined, however, whether the increases at night are due to increased daytime avoidance or to actual movements to the bed from other areas. The relative increases are greater in unvegetated areas, however, suggesting that some movement may occur between vegetated and unvegetated areas, as suggested by Orth and Heck. In general, the biomass reported in the present study for the seven major species falls within the range of total fish biomass for Zostera marina beds in New England by Nixon and Oviatt (1972) but is less than that reported in studies to the south (North Carolina, Adams 1976a; Texas, Hoese and Jones 1963).

Ichthyoplankton collections from shallow-water vegetated habitats have not been analyzed in the lower Chesapeake Bay; qualitative comparisons,

however, of the present ichthyoplankton data with those of previous studies on Chesapeake Bay fish eggs and larvae (Pearson 1941, Dovel 1971, Olney 1978) indicate that the push net presently employed as primary ichthyoplankton gear in this study adequately samples nearshore ichthyoplankton assemblages. Species composition and seasonality of Vaucluse Shores ichthyoplankton (March-July) are in general agreement with all previous Chesapeake Bay studies. Without exception, all species encountered in the present collections have been previously recorded as eggs, larvae or juveniles in similar seasonal patterns.

Although quantitative comparisons are limited by natural variability, difference in methodology, and lack of comparative gear efficiency data, relative ichthyoplankton abundance as measured in the present study compares favorably with the most recent data on lower Bay fish eggs and larvae (Olney 1978). Differences noted may be instructive in pointing out the importance of nearshore spawning nursery habitats. Present ranges of density estimates ($\#/100\text{ m}^3$) for eggs of A. mitchilli and sciaenid fishes (0.5 - 2018.3 and 0.9 - 1159.2 respectively) are comparable to those reported by Olney (3200-14000 A. mitchilli eggs; 6.0 - 819 sciaenid eggs). Both studies found eggs of Anchoa and sciaenid fishes to dominate fish egg collections, but differences in absolute ratios of Anchoa to sciaenid eggs (1.63:1, present study; 15:1 Olney's data) suggest reduced Anchoa nearshore spawning activity and greater utilization of nearshore spawning habitat by sciaenids. Similarly, differences in abundances of goby and pipefish larvae relative to larval Anchoa point out increased utilization of shoal, vegetated habitats as spawning grounds for these species. In the present data, pipefish and goby larvae occurred

in equal and sometimes greater concentrations than anchovies. In contrast, larval concentrations of these species never surpass those of Anchoa in deeper waters (Olney 1978).

Continued examination of nearshore ichthyoplankton assemblages utilizing this gear will be instructive. In future reports, we will include length-frequency analysis, additional day-night comparisons, data on the relationship of hydrographic parameters to species occurrence, and comparative gear evaluation.

Variation between habitats for components of the ichthyoplankton differ between stages (Tables 6-8). Eggs of Scopthalmus aquosus are about equally distributed between the three habitats during the months of March and April. The more abundant eggs of Anchoa mitchilli and of sciaenids show virtually the same pattern (lowest densities in the Ruppia area, increasing in the Zostera area, and highest in the sand area). Since much of the water flow to the bed occurs up the main channel during flood tide (Figure 1), this is consistent with spawning activity either in deeper water, which communicate directly with the sand area, or possibly in the main channel or upstream in Hungar's Creek. The great density of both egg types in the sand area in July, however, favors the former explanation (Table 6). Very small larvae (Table 7) show either no difference between habitats or show a pattern similar to that of the eggs of Anchoa. With growth, however, postlarvae of some species show increased densities in the vegetated areas (Table 7). B. tyrannus and L. xanthurus, for example, are spawned off the Atlantic shelf and move into the Chesapeake Bay, arriving as postlarvae in the

shallow water habitats. Recruits of both B. tyrannus (Table 7) and L. xanthurus (Tables 2 and 8) appear to prefer vegetated habitats.

The temporal pattern of variation in zooplankton biomass is similar to that observed in a study of the plankton of the lower Chesapeake Bay (Jacobs 1978). Values observed in the sand and Zostera areas fall within the ranges observed by Jacobs, but the values for the Ruppia area greatly exceed those observed in open bay waters. The low values observed in the month of April coincide with the recruitment of large numbers of postlarval spot (L. xanthurus) and menhaden (B. tyrannus) to the lower Bay (Tables 2 and 7). These species are planktivorous in the postlarval stage; it has been suggested that immigration of large numbers of postlarval fishes may significantly reduce the standing crop of zooplankton in estuarine systems (Thayer et al 1974). In sampling deeper water, however, Jacobs (1978), although noting a decrease in zooplankton biomass in April, did not demonstrate a significant reduction in copepod density; a reduction would be expected if postlarval feeding was the causative factor since copepods make up 76-99% of the food of these fishes in this stage of the life history (Kjelson et al 1974). The diurnal differences in zooplankton biomass (Table 10) for May demonstrate a dramatic reduction in the day samples. Although Ruppia remains the highest value, the day value in vegetated areas is 15% that of the night value as compared to 43% in the sand area. Further analysis of the curated samples will elucidate the meaning of the temporal changes in zooplankton biomass.

Organic biomass of zooplankton collections shows clear differences between habitats (Table 10, Figure 7). Generally, biomass is greatest in Ruppia followed by sand and Zostera with the latter two showing similar

values. Although the importance of these differences must await analysis of the taxonomic composition of the plankton, three hypotheses are consistent with this observation, as follows: 1) obligate planktonic organisms collect in high densities in the upper end of the channel through hydrodynamic winnowing, active orientation, or swarming behavior; 2) facultative or demersal plankton are more abundant in the shallower water of the Ruppia zone; or 3) organic detritus and particulate matter retained by the 202 μm mesh is more common in the Ruppia area. Evidence against hydrodynamic winnowing is provided by the abundance pattern of fish eggs (Table 6) as discussed above, which are in lowest densities in the Ruppia area (unless high planktonic predation rates on egg stages lowers density). Swarming behavior has been observed in several shallow water habitats, including coral reefs, marine lakes, seagrass beds, and rock and sand bottoms by a variety of obligate planktonic taxa including copepods, euphausiids, and mysids (Emery 1968; Fenwick 1978; Hamner and Carleton 1979). The samples in the Ruppia area are generally taken at peak high tide (before ebb) to provide the water depth necessary for the push net. Swarming would probably be facilitated during times of slack water. The contribution of obligate or facultative plankton or of organic detritus to the high values of zooplankton biomass in the Ruppia area must await analysis of the taxonomic composition of the curated samples.

Feeding relationships of fishes within the Vacluse Shores study site are generally similar to those of the dominant species observed in other studies in vegetated habitats (Carr and Adams 1973; Adams 1976c). The lack of the dominant species from North Carolina (Lagodon rhomboides and Orthopristis chrysoptera), however, may alter the feeding behavior of

L. xanthurus in the current study through availability of other food sources. Although plant material and detritus occur frequently (Figures 9 and 10), preliminary gravimetric data suggest that they are less important in the diet than in North Carolina Zostera beds (Adams 1976c) or in Florida (Sheridan 1978). The frequency of occurrence reflects the frequency of benthic feeding rather than dietary importance. Spot are initially planktivorous, after which they switch to predominantly benthic feeding (Kjelson et al. 1974; Sheridan 1978); this will be confirmed in the current study in conjunction with zooplankton sampling in the spring of 1980. Smaller (average 65 mm SL, July data) spot exhibit predominantly benthic feeding (Figure 8). Although benthic feeding remains important in larger specimens collected in October (Figure 10), planktonic feeding represents the major food intake; analysis shows that numbers of harpacticoids and nematodes decline rapidly with size whereas the numbers of mysids per stomach increases. The data is confounded, however, by the sampling of smaller fish in July, when mysids were rare in the eelgrass bed, and larger fish in October, when mysids were abundant (see part II of this report). The increases in importance of mysids in the diet are likely evidence of high availability, since L. xanthurus has a subterminal mouth adapted primarily to feeding on infauna and benthic organisms (Chao and Musick 1976).

Bairdiella chrysoura immigrates to the vegetated areas in August (Table 2). Stomachs have been analyzed from collections in October 1978, when the fish were relatively large (mean length approximately 92 mm SL; see Table 11). This species has a terminal mouth and is adapted for pelagic feeding, although some epibenthic feeding takes place (Figure 10). Most

studies on the feeding by this species (summarized in Chao and Musick 1976) show fish, mysids, and decapod shrimp to be the predominant dietary items. Adams (1976c), by contrast, observed no mysids in the diet of this species in North Carolina eelgrass beds. The abundance of mysids in the diet is undoubtedly related to the high levels of abundance in the eelgrass habitat. The importance of availability upon feeding on mysids within the bed is stressed by the change in frequency of mysids in stomachs of pipefish (S. fuscus). Mysids were not present in stomachs of specimens taken in July but represented the major food item in October (Figure 11). The ongoing gravimetric analysis of prey items will provide more precise definition of ontogenetic and seasonal trends of feeding behavior of the fish community, their relationship to prey availability, and the impact on other components of the ecosystem.

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ECOSYSTEM MODELING

R. L. Wetzel

INTRODUCTION

The ecosystem modeling project is designed and being implemented as an integrative tool for ecosystem analysis. The modeling effort will describe the principal pathways for energy flow and evaluate those parameters associated with specific processes that control behavior. The tasks to date have centered on model conceptualization, parameterization and mathematical formulation for digital computer simulation.

METHODS

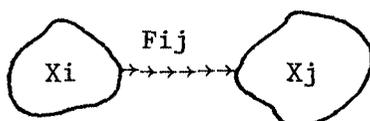
Conceptualization: Model conceptualization or compartmentalization is based on trophic interactions. The information used to decide the compartmental structure for the model came primarily from the literature and relied heavily on the expertise and experience of the several principal investigators participating in the overall research program. Following two preliminary versions, the model proposed for simulation was decided. Table 1 lists and describes the 17 compartments of the model and Figure 1 gives the interaction matrix describing compartmental exchanges. Emphasis in this model version is placed on biological organization and trophic function in response to the overall program objective to evaluate predator-prey interactions and secondary production. Evaluation of controls such as temperature, light and nutrients on primary production within the context of the model will be studied in a second model version following preliminary analysis using the current model structure.

Table 1: Model compartmentalization

<u>Symbol</u>	<u>Name</u>	<u>Description</u>
X1	CO ₂ ·H ₂ O	Carbon dioxide in water
X2	POC·H ₂ O	Particulate organic carbon in water
X3	DOC·H ₂ O	Dissolved organic carbon in water
X4	POC·Sed	Particulate organic carbon in sediments
X5	DOC·Sed	Dissolved organic carbon in sediments
X6	Phytoplankton	All autotrophic water column components
X7	Vascular Plants	<u>Zostera marina</u> , <u>Ruppia maritima</u>
X8	Epiphytes	Autotrophes associated with emergent vascular plantleaves
X9	Benthic Algae	Both macrophytic and microautotrophs assoc. with sediments.
X10	Zooplk. & Meroplankton	Heterotrophs in water column. Includes both resident and seasonally abundant larval and juvenile forms.
X11	Microheterotrophs·H ₂ O	Primarily bacteria in water
X12	Attached Epifauna	Sessile heterotrophs associated with emergent vascular plant parts
X13	Motile Epifauna	Heterotrophs that are capable of free movement within the vascular plant community.
X14	Heterotrophs·Sed	Primarily infauna
X15	Microheterotrophs·Sed	Primarily bacteria in sediments
X16	Natant residents	Large predatory, motile species
X17	Megapredators & Waterfowl	Self-explanatory

Parameterization: The parameters necessary as input data for model simulation can be grouped according to equation structure. The equational structure is based on the type of exchange in question. Generally these fall in one of four categories: 1. abiotic \rightarrow abiotic, 2. abiotic \rightarrow biotic, 3. biotic \rightarrow biotic and 4. biotic \rightarrow abiotic exchanges. Because of the high degree of biological interaction represented in the current model version, parameters associated with the last two categories of exchange dominate the data input requirements. The following summary defines these parameters and together with the next section on mathematical structure forms the basis for the computer simulation version of the model. Briefly the parameters currently being evaluated;

Given two generalized compartments and represented as:



where; X_i = donor compartment "i"
 X_j = recipient compartment "j"
 F_{ij} = flux of matter-energy from "i" to "j"

the parameters necessary to describe the various flows in the model are:

1. P_{ij} : a dimensionless number where

$$0 < P_{ij} \leq 1.0$$

that gives the preference assigned an ingestion or uptake pathway, F_{ij} .

For any biotic compartment having multiple resources (2 or greater), a preference value in the above range must be decided such that,

$$\sum_{i=1}^n P_{ij} = 1.0, \quad n = \text{number of inputs to } X_j$$

This applies, in its present form, to only biological uptake pathways.

2. τ_{ij} : The maximum specific rate of uptake or ingestion as;

$$g_C(X_i) \cdot g_C(X_j)^{-1} \cdot \Delta t^{-1}$$

Figure 1: Model Interaction Matrix

From:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	#
1. CO ₂ .H ₂ O						R	R	R	R									4
2. POC.H ₂ O				S							DR							2
3. DOC.H ₂ O					Ex						DR							2
4. POC.Sed.		RS													DR			2
5. DOC.Sed.			Ex												DR			2
6. Phytoplk.	D	M	Ec							DR		DR						5
7. Vas. Plants	D	M	Ec	M	Ec								DR	DR			DR	8
8. Epiphytes	D	M	Ec							DR			DR					5
9. Benthic Algae	D			M	Ec								DR	DR		DR		6
10. Zooplk & Meroplk	D	M/Eg	Ec									DR				DR		5
11. Microhetero H ₂ O	D		Ec							DR		DR				DR		5
12. Attached Epifauna	D	M/Eg	Ec										DR			DR		6
13. Motile Epifauna	D			M/Eg	Ec											DR	DR	5
14. Hetero.Sed.	D			M/Eg	Ec								DR			DR	DR	6
15. Microhetero Sed.					Ec								DR	DR		DR		5
16. Natant Residents		M/Eg	Ec	M/Eg	Ec												DR	6
17. Megapred. Waterfowl		M/Eg	Ec															<u>3</u>
																		<u>76</u>

D = Linear Donor controlled (LDC)
 RS = Resuspension - LDC
 M = Mortality - LDC
 Eg = Egestion - LDC
 Ec = Excretion - LDC
 S = Sedimentation
 DR = Donor-Recipient Controlled

where,

X_i and X_j as above

gC = grams of carbon

Δt = time interval

For the current model version carbon is the unit of exchange and the unit of time equals one day. For our preliminary simulation work with the model, four (4) seasonal values are assigned each ingestion or uptake pathway, i.e. winter, spring, summer and fall values.

3. AE_{ij}: The assimilation efficiency for the corresponding ingestion or uptake pathway, F_{ij} where,

$$0 < AE_{ij} \leq 1.0$$

and

$$AE_{ij} = \left\{ \frac{\tau_{ij} - (\tau_{ij} - \epsilon_{ij})}{\tau_{ij}} \right\}$$

where

ϵ_{ij} = fractional portion of τ_{ij} egested, and,

$$0 \leq \epsilon_{ij} \leq 1.0$$

4. α_{ij} : A donor determined feedback control parameter that sets the density below which a donor (resource or prey item) first becomes limiting to the recipient and reduces the flow, F_{ij} , in units $\text{gC} \cdot \text{m}^{-2}$.

5. γ_{ij} : A donor determined feedback control parameter that sets the lower limit or refuge density below which the donor (resource or prey item) is not available to the recipient. Units as above.

$$\text{At } X_i = \gamma_{ij}, F_{ij} = 0$$

6. α_{jj} : A recipient determined feedback control parameter that sets the density above which space or some space related process (i.e. crowding, competition, etc.) limits ingestion. Units as above.

7. γ_{jj} : A recipient determined feedback control parameter that sets the

maximum maintainable density for the recipient population. This is equivalent to the "carrying capacity" or K-value from other works. Units as above.

$$\Delta_t X_j = \gamma_j X_j - \sum_{i=1}^n F_{ij} = \text{maintenance costs of } X_j$$

n = no. input pathways

$$\text{and } \Delta X_j \cdot \Delta t^{-1} = 0. \quad \text{no growth}$$

The above seven parameters in equational form define the principal biological interactions for uptake or ingestion of matter-energy. The following describe the losses of matter-energy from the various populations.

8. ρ_j : Specific rate of respiration as $\text{gC} \cdot \text{gC}^{-1} \cdot \text{t}^{-1}$.
9. ξ_j : Specific rate of excretion as $\text{gC} \cdot \text{gC}^{-1} \cdot \text{t}^{-1}$.
10. μ_j : Specific rate of natural mortality exclusive of predatory mortality as $\text{gC} \cdot \text{gC}^{-1} \cdot \text{t}^{-1}$.

Mathematical Structure

The mathematical structure of the simulation model and formulation of interaction equations follows the general guides presented by Wiegert (1975, 1978). The interaction equations coupling the compartments (Table 1) are based on testable assumptions and incorporate measurable parameters; i.e. the interaction coefficients are dimensioned and have ecological meaning. The technique used for digital computer solution of the simulation model follows Wiegert and Wetzel (1974).

The current model version has 76 pathways for exchange. The equations used to describe these can be mathematically classed into one of three general categories:

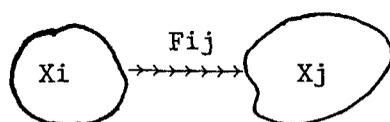
1. linear, donor controlled pathways
2. linear, recipient controlled pathways
3. non-linear, recipient controlled, donor-recipient determined pathways (feedback controlled)

Of the 76 pathways the majority (34) are classed as category three, i.e. feedback controlled ingestion or uptake fluxes. Thirty (30) pathways represent metabolic loss or natural mortality for the biotic compartments and are classed as category 1, i.e. linear, donor controlled fluxes. The remainder, 12, are abiotic \rightarrow abiotic exchanges and are either linear donor or recipient controlled fluxes.

The three mathematical categories for classifying the various exchanges can be generally represented as follows;

1. Linear, donor controlled:

Given the conceptual interaction;



where X_i = Donor compartment

X_j = Recipient compartment

F_{ij} = Flux of carbon from "i" to "j"

then $F_{ij} = C_{ij} \cdot X_i$

C_{ij} = specific rate of transfer; $gC \cdot gC^{-1} \cdot \Delta t^{-1}$

For the model, respiration, excretion, natural mortality, sedimentation and resuspension are represented in this manner with " C_{ij} " replaced with the appropriate parameter.

2. Linear, recipient controlled:

As above, except

$$F_{ij} = c_{ij} \cdot X_j,$$

the recipient compartment controlling the realized amount of transfer. At present, no flux in the model is represented with this function.

3. Non-linear, recipient controlled, donor-recipient determined:

The general form of the equation can be given as:

$$F_{ij} = \tau_{ij} \cdot X_j \{ 1 - (f_{ij} \cdot f_{ij}) \} +$$

where; F_{ij} , X_j as defined previously

τ_{ij} = maximum specific rate of ingestion or uptake; $\text{gC.gC}^{-1}.\text{day}^{-1}$

f_{ij} = resource controlled negative feedback term

f_{jj} = self or recipient controlled negative feedback term

The form of the feedback can vary depending on how a population responds to intense predation or, oppositely, to crowding or some space related limitation. Without specific information relative to the form of these feedbacks, the following general forms have been adopted;

$$F_{ij} = \left[\frac{\alpha_{ij} - X_i}{\alpha_{ij} - \gamma_{ij}} \right]_+, \text{ and,}$$

$$F_{jj} = \frac{X_j - \alpha_{jj}}{\gamma_{jj} - X_j} +$$

Wiegert (1975) discusses the various forms used in the past and Christian and Wetzel (1978) give specific examples of changes in feedback functions for microbial interactions using this modeling approach.

RESULTS AND DISCUSSION

The ecosystem modeling project during the first year of effort has;

- a. determined the compartmental model structure,
- b. formulated the mathematical structure for the interaction equations describing compartmental coupling,
- c. began data summaries for parameter estimation, and,
- d. established computer software and remote terminal communications for model simulation and analysis.

The modeling study is designed to reflect the trophic structure of submerged aquatic communities in Chesapeake Bay that are dominated by Zostera marina and Ruppia maritima. The model incorporates biologically and

ecologically realistic mathematical representations of flux pathways that are based on testable assumptions and measureable parameters. Hierarchical analysis is possible at the level of processes influencing or controlling specific fluxes as well as analysis of overall community behavior and interaction with other bay system components. The simulation model provides an organizational structure and vehicle for incorporating and evaluating the results of individual research efforts.

The overall research incorporates three other research efforts;

1. Productivity and nutrient dynamics associated with micro autotrophic and heterotrophic components of the eelgrass community including the environmental controls of light, salinity and temperature and measures of total community metabolism (KLW and RLW).
2. Within community macro-consumer dynamics (DFB and RJO).
3. SAV community interaction with bay consumer components; e.g. migratory shellfish, finfish and waterfowl (JVM).

The first model version (Fig. 1) explicitly represents these major research efforts both compartmentally and through the mathematical structure proposed, the postulated mechanisms controlling interactions and community dynamics.

The overall design is thus complimentary and highly interactive. Specific aspects of SAV community structure and function addressed by other CBP research efforts (e.g. R. J. Orth; M. Kemp, et al.,) will be incorporated to the extent that the results suggest fundamental changes in design or systems conceptualization.

The effort is approximately 30% complete to date (October, 1979). The effort for the next six months will be to have a running computer version and to have performed a sensitivity analysis with the current model. The effort will identify parameters particularly sensitive to change and aid in designing future work (see Wiegert and Wetzel, 1979).

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