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Benthic Community Responses to Hypoxic Conditions in the Lower Rappahannock River, Virginia

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Old Dominion University, 1994

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BENTHIC COMMUNITY RESPONSES TO HYPOXIC CONDITIONS IN THE LOWER RAPPAHANNOCK RIVER, VIRGINIA

by

Mary Elaine Smith
B.S. May 1992, Old Dominion University

A Thesis submitted to the Faculty of Old Dominion University in Partial
Fulfillment of the Requirement for the Degree of

MASTER OF SCIENCE

BIOLOGY

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Approved By:

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In memory of my mother, Olga B. Smith.

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ABSTRACT

BENTHIC COMMUNITY RESPONSES TO HYPOXIC CONDITIONS IN THE RAPPAHANNOCK RIVER, VIRGINIA

Mary Elaine Smith
Old Dominion University, 1994
Director: Dr. Daniel M. Dauer

The effects of seasonal low dissolved oxygen conditions upon benthic macroinvertebrate communities were studied in the lower Rappahannock River, a tributary of the Chesapeake Bay. Benthic communities were sampled during March, June, August, and September 1993 at five equidistant depths (5, 10, 15, 20, and 25 m) extending upwards from the deepwater Virginia Benthic Biological Monitoring Station LE3.4 located in the deep basin just inside the mouth of the Rappahannock River. Infaunal species diversity, richness, biomass, and density were measured along with the vertical depth distribution of organisms within the sediment. Significant sediment differences were found between the shallowest, 5 m station, and all deeper sampling depths. Benthic communities displayed a systematic response to the temporal and spatial extent of the hypoxic water mass. Following summer low dissolved oxygen conditions, infaunal communities at the shallow and intermediate depths were dominated by surface-dwelling opportunistic fauna. Several lines of

evidence indicate a continuous degradation of the communities inhabiting the two deepest sampling depths, including depressed levels of infaunal biomass and diversity preceding summer hypoxia, a year-long dominance by opportunistic fauna, and the lack of infaunal organisms inhabiting sediment depths greater than 5 cm. Comparison of these deepwater communities with an upriver station not subjected to low dissolved oxygen stress confirms this. Long-term monitoring of these deepwater communities can provide little information regarding the relative contributions of natural and anthropogenic forces to seasonal low dissolved oxygen in the lower Rappahannock River. The creation of an additional mid-water monitoring station is suggested, which in combination with the present deepwater station may be more indicative of changes in benthic community health due to Chesapeake Bay restoration efforts or changing water quality conditions.

INTRODUCTION

LOW DISSOLVED OXYGEN AND EUTROPHICATION

The occurrence of hypoxic and anoxic bottom waters in marine and estuarine systems has been reported throughout the United States (Falkowski *et al.,* 1980; Justic *et al.,* 1993; Officer *et al.,* 1984) and Europe (Friligos and Zenetos, 1988; Justic, 1987; Rosenberg and Loo, 1988) with increasing frequency in recent years. Low dissolved oxygen conditions have the potential to threaten the natural structure and functioning of benthic communities through mortality, sublethal stresses, and indirect restrictions upon habitat availability. The effects of anoxia and hypoxia can also be transferred up the food chain through trophic interactions (Pihl *et al.,* 1992) and can interfere with the biogeochemical processing of organic material and nutrients in estuarine systems (Rosenberg *et al.,* 1991).

In the Chesapeake Bay, stratigraphic evidence demonstrates an inherent long-term pattern of periodic anoxia in the deeper waters of the mainstem as benthic oxygen demands exceed bottom water reaeration processes during the summer months due to the presence of a natural pycnocline (Breitburg, 1990; Cooper and Brush, 1992; Harding *et al.,* 1992; Schaffner *et al.,* 1992). The greatly increased areal extent and volume of the anoxic water mass in the bay since the middle of this century has been attributed to the anthropogenic impacts of eutrophication (Cooper and Brush, 1993; Taft *et al.,* 1980). Excess anthropogenic nutrient loadings into the bay greatly enhance bottom water and benthic microheterotrophic oxygen demand, which stimulates earlier and more extensive occurrences of the oxygen-depleted water mass. Hypoxic and anoxic conditions presently occur in the deeper portions of the bay and its tributaries on an annual basis (Officer *et al.,* 1984). The process of nutrient enrichment intensifying summer hypoxia can be self aggravating as reducing conditions increase the release of NH_4^+ from the sediments, which stimulates the eutrophication process (Friligos and Zenetos, 1988; Rosenberg *et al.,* 1991).

In the Rappahannock River, a tributary of the Chesapeake Bay, annual summertime anoxia occurs in the deep basin located just inside the river's mouth. Although intrusion of anoxic bottom waters from the bay's mainstem can increase the severity and duration of low dissolved oxygen conditions in the lower Rappahannock River, the seasonal occurrences of hypoxia in the deep basin are independent of mainstem patterns (Kuo *et al.,* 1991). Because of a weak longitudinal salinity gradient, and thus gravitational circulation, the Rappahannock River experiences annual low dissolved oxygen conditions absent from other tributaries of the lower bay (such as the James River) that receive higher nutrient loadings but maintain stronger salinity-based circulation patterns (Kuo and Neilson, 1987). Although strong spring tides can provide sufficient mixing to break down the thermal and salinity barriers responsible for the hypoxia found in the Rappahannock River (Haas, 1977; Webb and D'Elia, 1980), the resulting uniformity of dissolved oxygen throughout the water column is seen only at the river's mouth, not within the deep basin or areas further upstream (Kuo *et al.,* 1991). Reoxygenation of these waters typically occurs in

September, when water temperatures cool below 20 °C and wind-driven mixing redistributes oxygen-saturated surface waters to greater depths (Kuo and Neilson, 1987; Kuo *et al.,* 1991).

MACROBENTHIC RESPONSES

Hypoxic conditions refer to dissolved oxygen concentrations occurring below 2.0 mg/l, a level where abrupt benthic macroinvertebrate community changes are often observed at summer temperatures above 20 °C (Harding *et al.,* 1992; Rosenberg, 1980). Mortality of macrofaunal species is generally increased when the presence of hydrogen sulphide is coupled with anoxic conditions due to its interference with aerobic electron transport chain functioning (Llanso, 1991; Miron and Kristensen, 1993; Theede *et al.,* 1969; Torrans and Clemens, 1982). Individual tolerances to both anoxic and hypoxic levels of dissolved oxygen concentration vary within a taxon, by species, and by habitat. Theede *et al.* (1969) found that muddy-bottom benthic infauna are generally more tolerant of low dissolved oxygen conditions than hard substratum or sandy-bottom inhabitants. Both behavioral and physiological mechanisms can aid in resistance to hypoxic conditions. Many taxa reduce their metabolic rates, and thus their oxygen requirements, under oxygen-stressed conditions (Theede, 1973). In addition, certain polychaetes (Magnum and Van Winkle, 1973) and bivalve and gastropod mollusks (Shumway and Scott, 1983) are capable of switching from aerobic to anaerobic metabolisms for short periods during oxygen stress.

RATIONALE BEHIND STUDY

Current benthic monitoring of macroinfaunal responses to seasonal low dissolved oxygen in the mesohaline regions of the Rappahannock River is carried out in the deepest portion of the anoxic basin. Since the deeper areas of the bay and its tributaries have a natural propensity to become anoxic due to physical factors, they are likely to experience oxygen stress regardless of anthropogenic influences. In light of this, the present benthic monitoring station in the lower Rappahannock River may be too deep to provide independent information on the expected water quality and biotic changes associated with Chesapeake Bay restoration efforts. Regardless of changing environmental quality, the benthos of this area will always experience low dissolved oxygen concentrations during the summer months.

The purpose of this study is to document intermediate levels of hypoxia and the subsequent benthic invertebrate responses along the depth gradient extending upwards from the deep water monitoring station. Shallower depths within the lower Rappahannock River basin that are presently under low dissolved oxygen stress may be more indicative of long-term changes in water quality as they are located in that area of the bottom where hypoxia is primarily dependent upon eutrophication influences. The shallowest areas along this depth gradient can serve as within-habitat reference sites to compare with the patterns observed in benthic community response to hypoxic and anoxic conditions within the deeper depths of the basin.

OBJECTIVES AND HYPOTHESES

The objectives of this study were to investigate macrobenthic community structure along the hypoxia gradient found within the Rappahannock River deep basin under summer conditions. Macrobenthic communities were described and analyzed using community biomass, species diversity, species richness, and infaunal abundance. The objectives of this research were:

1. To identify and describe the spatial and temporal distribution of macrobenthic communities along the depth gradient in the deep basin of the Rappahannock River. Hypotheses are:

Ho: Macrofaunal community structure does not differ significantly along the depth gradient on either spatial or temporal scales.

Ha$_1$: Macrofaunal community structure differs along the depth gradient in a random pattern on spatial and/or temporal scales.

Ha$_2$: Macrofaunal community structure shows a nonrandom, defined pattern of change in the biotic variables along the depth gradient on spatial and/or temporal scales.

2. To correlate any community patterns with the temporal and spatial extent of summer low dissolved oxygen events. Hypotheses are:

Ho: Any observed macrofaunal community patterns show no relationship with either the temporal or spatial extent of summer low dissolved oxygen events.

Ha: Macrofaunal communities display a defined pattern of change along the depth gradient directly relating to the spatial and/or temporal patterns of low dissolved oxygen conditions.

3. To relate these data to monitoring efforts and their attempts to demonstrate changes in water quality through measures of benthic parameters.

MATERIALS AND METHODS

SAMPLE COLLECTION

Macrobenthic communities were sampled during March, June, August, and September of 1993 at five equidistant water depths extending upwards from the Virginia Benthic Biological Monitoring Station LE3.4 (mean water depth of 21 m) located in the deep basin just inside the mouth of the Rappahannock River (Figure 1). These dates were chosen to bracket the low dissolved oxygen events that occur in the Rappahannock River and to sample during their greatest areal extent in early August when water temperatures are greatest (Kuo and Neilson, 1987). Five replicate sediment cores were collected during June, August, and September at each depth (5, 10, 15, 20, and 25 m) with a box coring device (surface area of 184 cm^2) that samples to a depth of 25 cm. March samples consisted of three replicate cores taken at each depth excluding the 5 m sampling station. Each core from the June, August, and September sampling dates was separated into 0-5 cm and 5-25 cm depth partitions to quantify macrofaunal depth distributions. After removing a standardized subsample for grain size and total organic carbon analysis, sediment samples were sieved in the field through a 0.5 mm screen to retain macroinvertebrate fauna, then relaxed in a diluted 70.0% isopropanol, and preserved in a buffered, 5.0% formalin to sea water, rose bengal solution. Hydrographic data, including temperature, salinity,

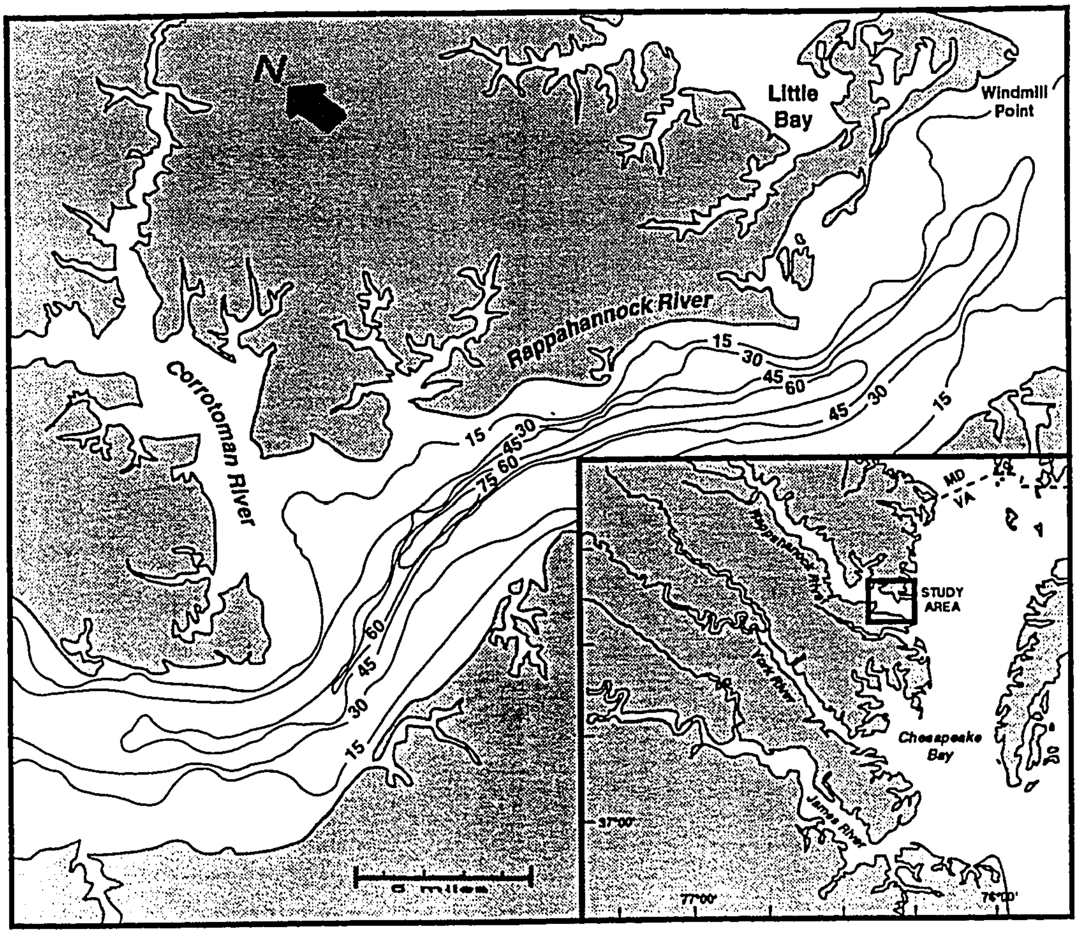


Figure 1. Map of lower Rappahannock River study area. Depth contours are in feet, which correspond roughly to 5, 10, 15, 20, and 25 m.

and dissolved oxygen were monitored throughout the water column on a bi-weekly basis from June through September using a YSI Model 33 Salinity-Conductivity-Temperature and a YSI Model 58 Dissolved Oxygen meter.

SAMPLE AND DATA ANALYSIS

Organisms retained were identified to the lowest possible taxon and enumerated. Biomass measures were expressed as ash-free dry weight (AFDW). Species diversity of each community was determined using the Shannon-Weaver index, $H' = -\sum_{S=1}^{n} P_i \log_2 P_i$, where P_i is the proportion of the *i*th species and S is the number of species (Pielou, 1966). Particle size analysis employed wet and dry techniques as described by Folk (1974).

A two-way multivariate analysis of variance (MANOVA) was performed on ranked data to test for overall temporal and depth-related effects on benthic community parameters. This procedure of using parametric statistical tests on ranked data was first proposed by Conover and Iman (1981) and is widely used in the ecological sciences (Biermann *et al.,* 1992; Carter and Rybici, 1990; Patton *et al.,* 1991). A Tukey's Studentized Range multiple comparison procedure was used in conjunction with the MANOVA to locate significant differences between biotic variables at each sampling depth and time. This test, while remaining conservative, produces results approximating the desired alpha level (i.e. is robust) with respect to the unequal sample sizes present in this study (Sokal and Rohlf, 1981). A one-way analysis of variance (ANOVA) was combined with a Tukey's Studentized multiple comparison test and performed on squared-transformed data to test for significant differences in sediment grain size between sampling depths. In order to test for the presence of a threshold value of dissolved oxygen concentration below which macrobenthic communities of the lower Rappahannock River are degraded, a graphical examination of the data was performed using benthic community data from this study combined with longterm monitoring data. Seasonal differences in scale between data sets were corrected for by standardizing all data to September values.

RESULTS

DISSOLVED OXYGEN

Hypoxic conditions were first observed in the deep basin at depths greater than 15 m in mid-May of 1993. This early event of low dissolved oxygen concentration coincided with large temperature and salinity discontinuities observed between 10 m and 15 m on May 20th (Figure 2). This intense stratification was probably related to the heavy river flow observed in the Rappahannock River in the spring of 1993. The U.S. Geological Survey (USGS) reported a spring freshet of 15,973 ft^3/sec between February and March of 1993. The long-term average (1985-1991) for this time period is 5069 ft^3/sec. The relationship between freshwater flow and dissolved oxygen concentration is poorly understood in general, however. At the shallowest, 5 m sampling depth, hypoxic conditions were observed on only one date, July 12 (Figure 3). All other oxygen concentrations at this depth remained above 3.0 mg/l throughout the summer. Hypoxic conditions below 2.0 mg/l occurred at the 10 m depth from June 24 through July 20 (Figure 4). Dissolved oxygen remained low from June 24 until August 19 at all depths greater than 15 m (Figures 5, 6, and 7). Surface values of dissolved oxygen were never recorded below 6.2 mg/l. Surface and bottom salinity values are included in Figures 3-7 to serve as indications of water column stratification.

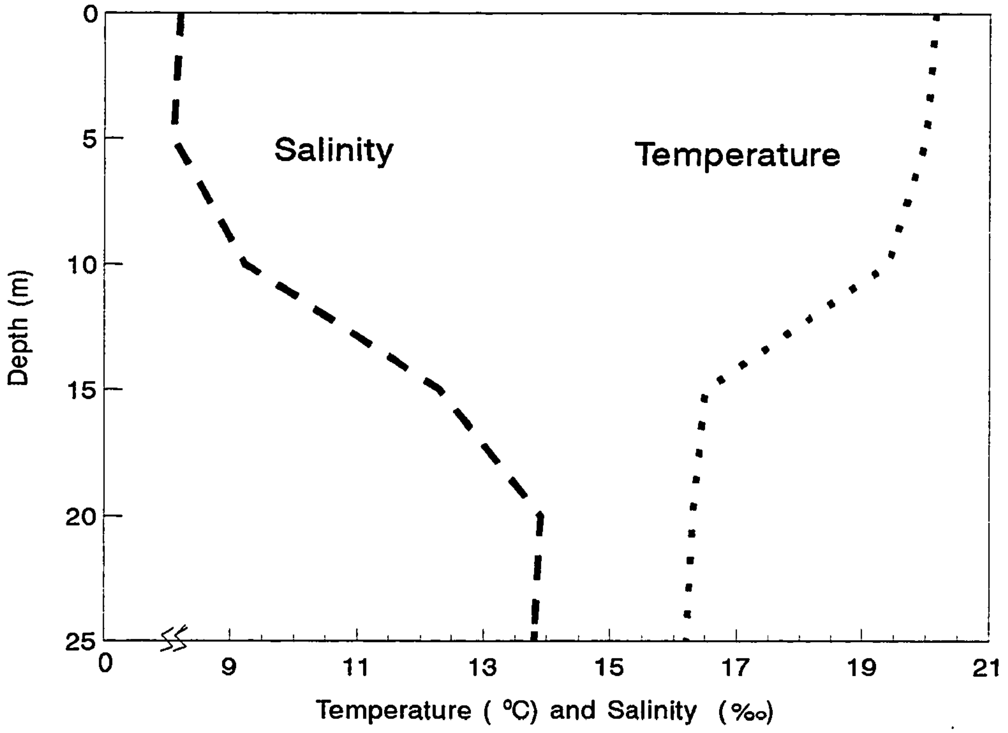


Figure 2. Temperature and salinity profiles from May 20, 1993.

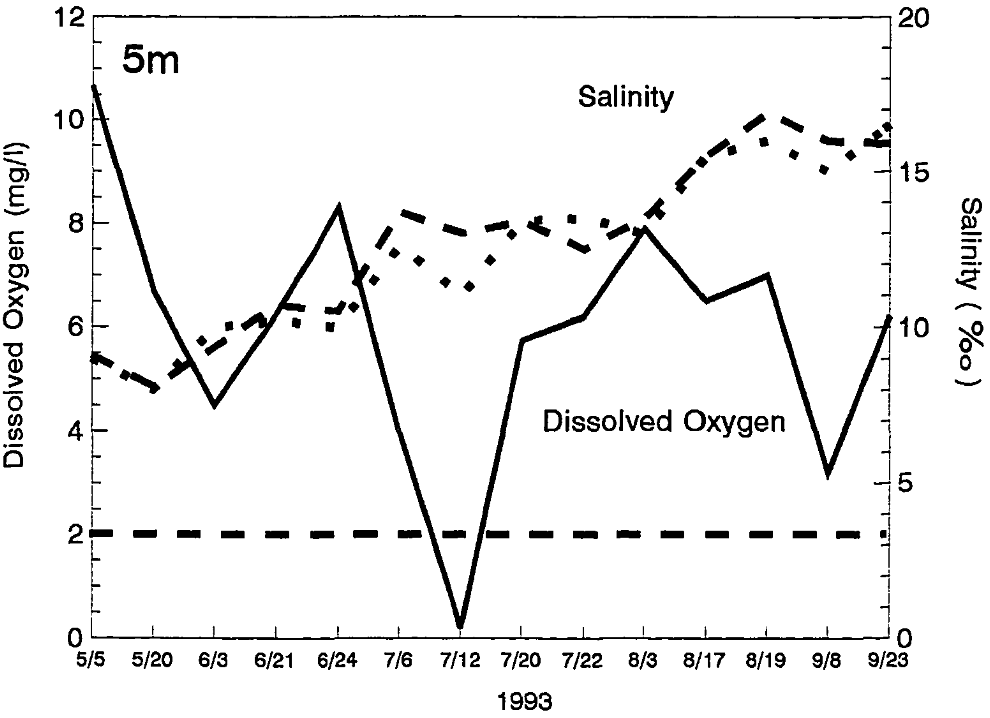


Figure 3. Salinity and dissolved oxygen concentrations from the 5m sampling depth. (• • •)= surface salinity, (– –)= bottom salinity, (——) = bottom water DO. DO values below 2mg/l are considered hypoxic.

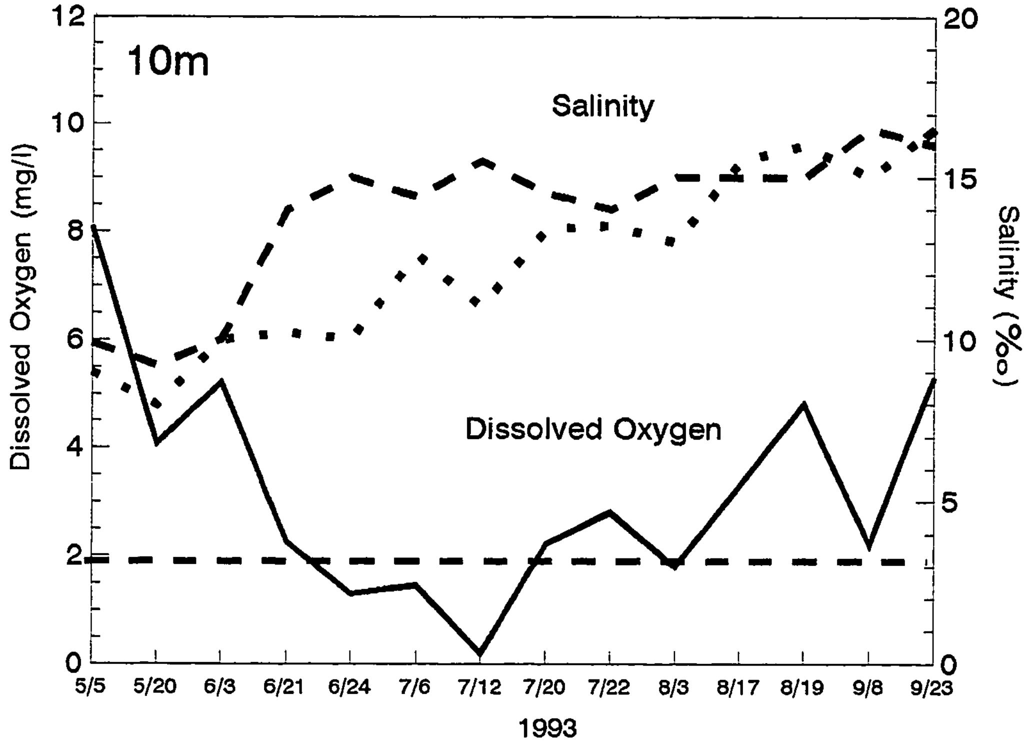


Figure 4. Salinity and dissolved oxygen concentrations from the 10m sampling depth. (· · ·)= surface salinity, (– –)= bottom salinity, (——) = bottom water DO. DO values below 2mg/l are considered hypoxic.

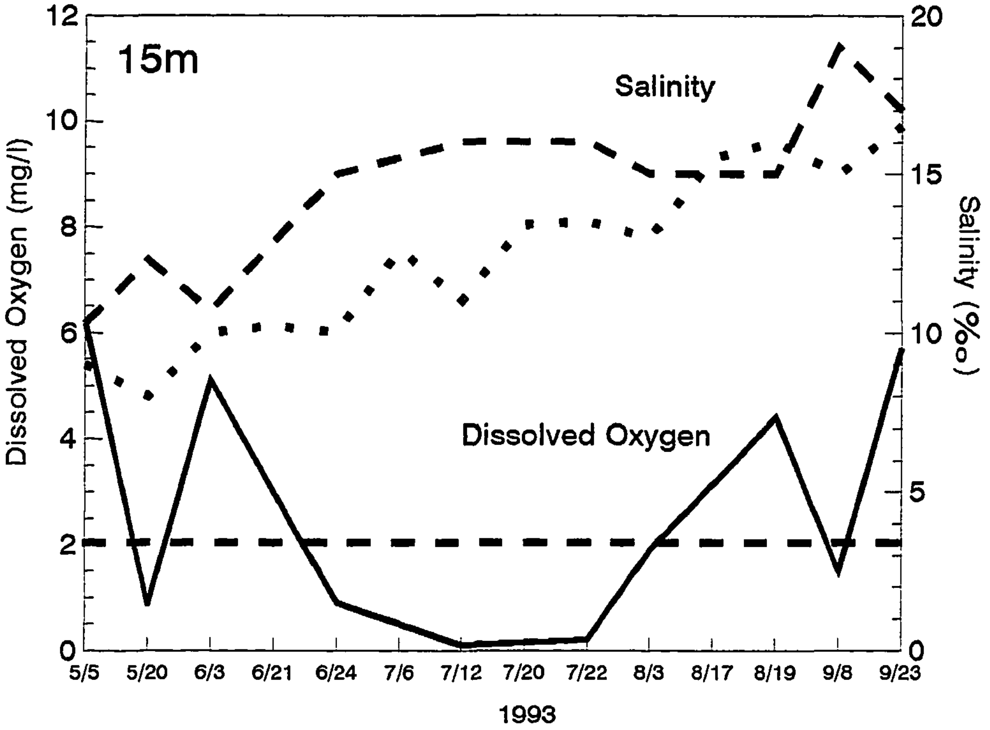


Figure 5. Salinity and dissolved oxygen concentrations from the 15m sampling depth. (• • •)= surface salinity, (– –)= bottom salinity, (—) = bottom water DO. DO values below 2mg/l are considered hypoxic.

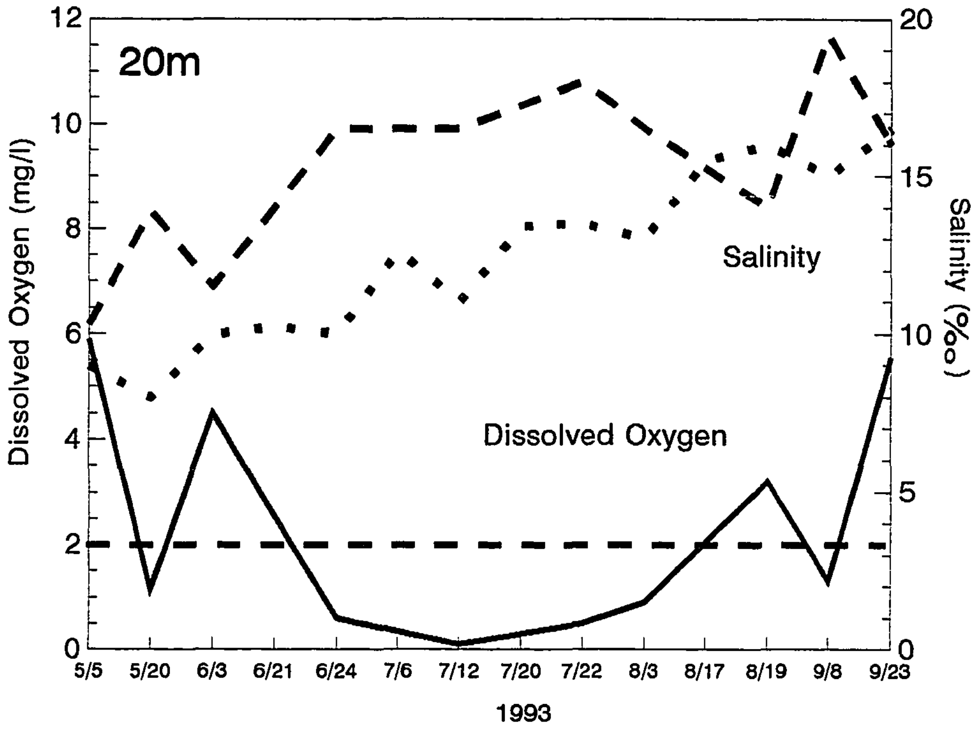


Figure 6. Salinity and dissolved oxygen concentrations from the 20m sampling depth. (• •)= surface salinity, (– –)= bottom salinity, (—) = bottom water DO. DO values below 2mg/l are considered hypoxic.

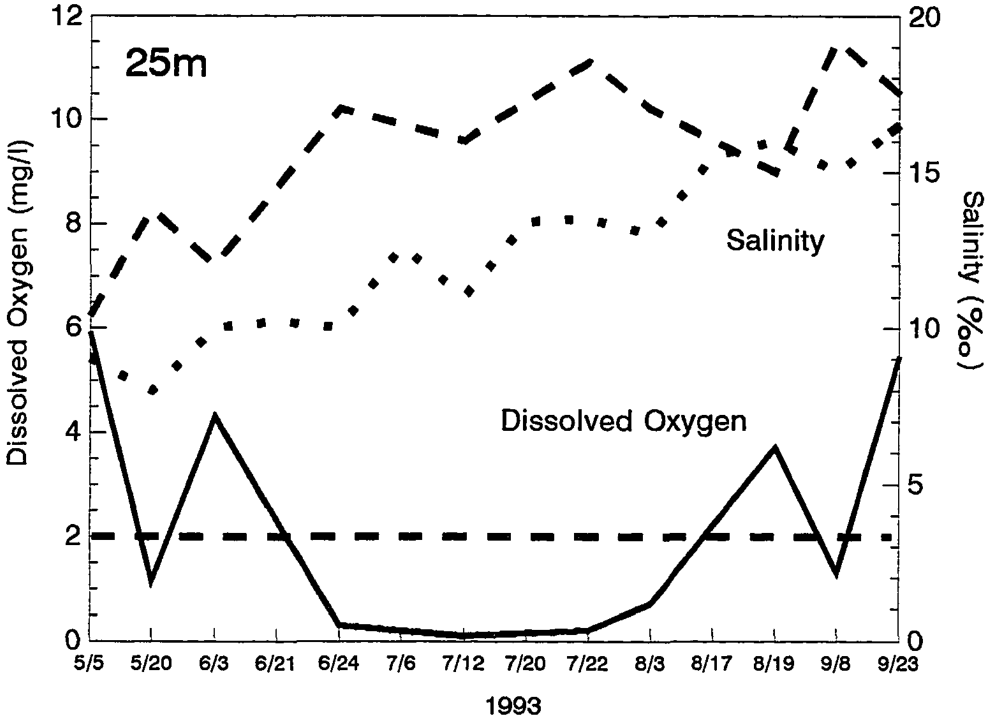


Figure 7. Salinity and dissolved oxygen concentrations from the 25m sampling depth. (• • •)= surface salinity, (— -)= bottom salinity, (——) = bottom water DO. DO values below 2mg/l are considered hypoxic.

SEDIMENTS

Sediments at the shallowest, 5 m station were significantly different from all other depths for both grain size (ANOVA, F=49.48, $p<0.0001$) and total volatiles, a measure of organic carbon (ANOVA, F= 17.34, $p<0.0001$). Silt-clay percentages at the 5 m depth varied around a mean of 36.50%, while sediments among all deeper depths ranged between 96.18% and 99.00% silt-clay. Total organic carbon averaged 3.62% at 5 m, while volatiles for all deeper sampling depths combined ranged from 8.80% to 10.66% (Table 1).

BENTHIC MACROFAUNAL RESPONSES

Community structure and composition

Over the course of the study, 45 species of benthic macroinvertebrates were collected and identified (Table 2). Of these, only three rare species, *Molgula lutlulenta, Neomysis americana,* and *Sabella microphthalma*, were excluded from analysis due to their epifaunal nature. Of the 42 infaunal species retained for further analysis, 38.10% (16 species) could be classified as either opportunistic or equilibrium taxa following Dauer *et al.*, 1992 and Ranasinghe *et al.*, 1993 (Table 3). These 16 species accounted for 81.50% of the biomass and 86.90% of the abundance of all fauna collected.

Four measures of macrobenthic community structure: species richness, biomass, abundance, and Shannon Weaver's diversity measure (H'), were all

Table 1. Sediment characterization of each sampling depth. Values are means (± 1SD) from all samples between June and September (n=15). Depths with different letters are significantly different at p=0.05 (Tukey's Studentized multiple comparison test).

DEPTH	PERCENT SILT-CLAY	TOTAL VOLATILES
5m	36.5 (27.24) A	3.62 (2.41) A
10m	98.68 (0.43) B	8.80 (1.56) B
15m	99.00 (0.58) B	9.51 (0.40) B
20m	98.73 (0.81) B	10.66 (1.14) B
25m	96.18 (6.00) B	9.78 (1.64) B

Table 2. List of species collected in lower Rappahannock River.

POLYCHAETA

Ancistrosyllis jonesi
Eteone heteropoda
Glycinde solitaria
Gyptis brevipalpa
Harmothoe extenuata
Heteromastus filiformis
Hobsonia florida
Leitoscoloplos spp.
Loimia medusa
Mediomastus ambiseta
Nereis succinea
Paraprionospio pinnata
Pectinaria gouldii
Polydora ligni
Pseudeurythoe ambigua
Sabella microphthalma
Scolecolepides viridis
Sigambra tentaculata
Streblospio benedicti

OLIGOCHAETA

Tubificoides spp. Group I

BIVALVIA

Bivalvia spp.
Ensis directus
Lyonsia hyalina
Macoma balthica
Macoma mitchelli
Mulinia lateralis
Tellina agilis

GASTROPODA

Acteocina canaliculata
Nassarius vibex
Odostomia spp.
Rictaxis punctostriatus

AMPHIPODA

Ampelisca abdita
Gammarus mucronatus
Leptocheirus plumulosus

OTHER ARTHROPODA

Chironumus spp.
Edotea triloba
Leucon americanus
Neomysis americana
Ogyrides alphaerostris
Oxyurostylis smithi

OTHER PHYLA

Hemichordata spp.
Molgula lutlulenta
Nemertea spp.
Phoronis psammophila
Turbellaria spp.

Table 3. Species collected in the lower Rappahannock River listed as opportunistic or equilibrium taxa by Dauer *et al.,* 1992 and Ranasinghe *et al.,* 1993.

OPPORTUNISTIC SPECIES

Polychaeta
- *Eteone heteropoda*
- *Gycinde solitaria*
- *Heteromastus filiformis*
- *Leitoscoloplos fragilis*
- *Mediomastus ambiseta*
- *Nereis succinea*
- *Paraprionospio pinnata*
- *Polydora ligni*
- *Streblospio benedicti*

Oligochaeta
- *Tubificoides* spp. Group I

Amphipoda
- *Ampelisca abdita*
- *Gammarus mucronatus*
- *Leptocheirus plumulosus*

Arthropoda
- *Chironomus* spp.

Bivalvia
- *Mulinia lateralis*

EQUILIBRIUM SPECIES

Bivalvia
- *Macoma balthica*

significantly different (MANOVA, $p<0.0001$) for overall time, depth, and interaction effects (Table 4) for all multivariate test criteria (Wilk's Lambda, Pillai's Trace, Hotelling-Lawley Trace, and Roy's Greatest Root). All of the benthic community measures differed significantly among months of the study. Regardless of the biotic variable measured, the 5 m sampling depth was always significantly different from the deeper stations. A summary of the Tukey's Studentized Range Test used to follow up the MANOVA results of depth effects on ranked community data is shown in Table 5. As ranked values are not readily intuitive, Table 6 reproduces this range test on raw community measures.

Benthic communities displayed a systematic response to the low dissolved oxygen conditions observed throughout the summer of 1993. The four biotic community variables measured (i.e., species abundance, biomass, richness, and diversity) all responded similarly to hypoxia throughout the summer. The pattern of infaunal abundance at each sampling depth shown in Figure 8 is representative of all the variables measured. For example, infaunal density declined at all depths deeper than 15 m from March to June in response to the deep water hypoxia event of May 20; the communities at 5 m and 10 m were unaffected. By August, communities at all other depths sampled had degraded abundance in response to the hypoxia observed throughout the water column during the preceding month. Species diversity peaked at the 5 m station in August due to an increase in evenness as the

Table 4. MANOVA tables for overall time, depth and interaction effects.

MANOVA Test Criteria for Month Effects

Statistic	Value	F	Num DF	Pr > F
Wilks' Lamda	0.2305	10.6438	12	0.0001
Pillai's Trace	0.8519	6.6432	12	0.0001
Hotelling-Lawley Trace	2.9894	15.8605	12	0.0001
Roy's Greatest Root	2.8714	48.0960	4	0.0001

MANOVA Test Criteria for Depth Effects

Statistic	Value	F	Num DF	Pr > F
Wilks' Lambda	0.2051	8.4615	16	0.0001
Pillai's Trace	1.0799	6.2866	16	0.0001
Hotelling-Lawley Trace	2.6222	10.4066	16	0.0001
Roy's Greatest Root	2.1230	36.0912	4	0.0001

MANOVA Test Criteria for Interaction Effects

Statistic	Value	F	Num DF	Pr > F
Wilks' Lambda	0.2343	2.6276	44	0.0001
Pillai's Trace	1.1684	2.5507	44	0.0001
Hotelling-Lawley Trace	1.8531	2.6743	44	0.0001
Roy's Greatest Root	0.8932	5.5215	11	0.0001

Table 5. Results of Tukey's Studentized Range test on ranked data for overall depth effects. Depths with different letters are significantly different from each other at p= 0.05 for each biotic variable.

DEPTH (m)	ABUNDANCE (ind/m^2)	BIOMASS (g/m^2)	DIVERSITY (H')	RICHNESS (spp/rep)
5	68.133 A	71.667 A	68.867 A	71.000 A
10	51.972 B	46.917 B	46.611 B	47.500 B
15	35.306 C	38.306 BC	42.972 B	38.111 BC
25	36.28 C	35.750 BC	37.361 BC	37.417 BC
20	32.083 C	31.972 C	28.333 C	30.472 C

Table 6. Range Test results reproduced with raw data for overall depth effects. Values are means (± 1SD) among months of the sampling period. Depths with different letters are significantly different from each other at p= 0.05 for each biotic variable.

DEPTH (m)	ABUNDANCE (ind/m^2)	BIOMASS (g/m^2)	DIVERSITY (H')	RICHNESS (spp/rep)
5	6807.67 (10324.95) A	5.920 (8.42) A	1.44 (0.38) A	9.87 (6.36) A
10	947.50 (818.82) B	0.387 (0.32) B	0.76 (0.55) B	4.08 (3.03) B
15	551.50 (762.76) C	0.892 (1.38) BC	0.74 (0.76) B	3.52 (3.74) BC
25	1026.50 (1699.07) C	0.360 (0.50) BC	0.65 (0.65) BC	3.97 (4.57) BC
20	670.75 (1144.15) C	0.262 (0.39) C	0.22 (0.27) C	2.05 (2.02) C

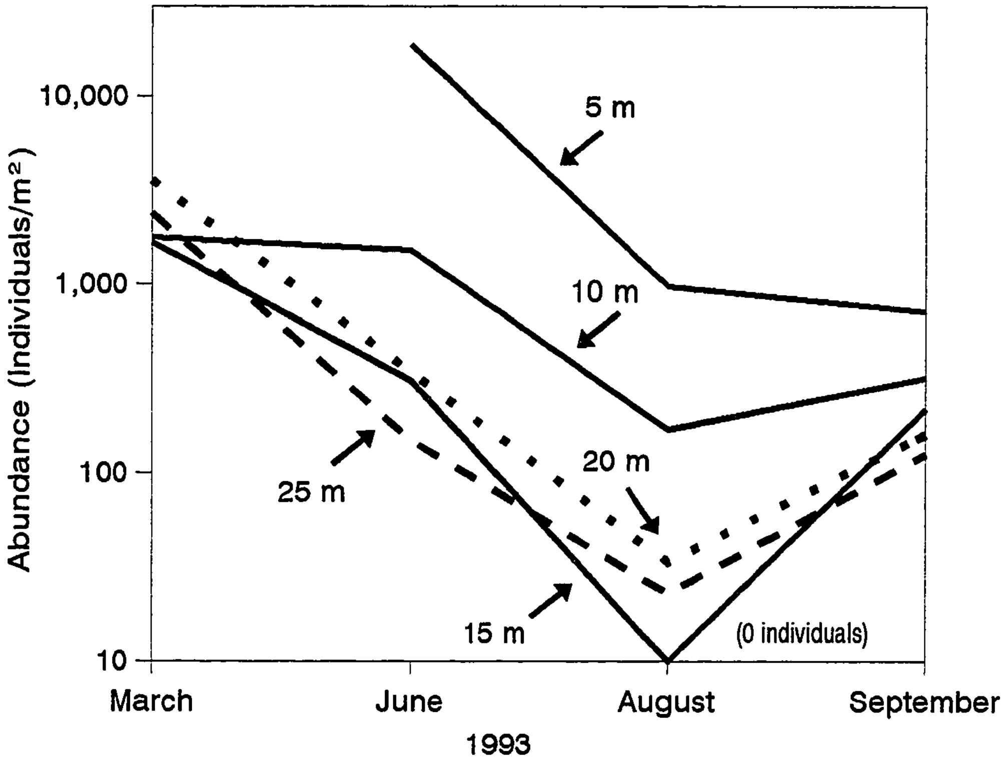


Figure 8. Mean density of macroinvertebrates at each sampling depth throughout the summer.

overwhelming dominant species in June, (the opportunistic polychaete *Streblospio benedicti*) was extremely rare in August samples. All communities except those collected from the 5 m depth recovered slightly in September samples (Figure 8).

Abundance dominants shifted at the 5 m station after the hypoxic event of July 12 (Table 7). Except where the clam *Macoma balthica* was present in large numbers, dominance by individuals also reflected biomass dominance. In June, the community at 5 m were dominated by large (5-15 mm), deep-dwelling *Macoma balthica*, the bivalve *Mulinia lateralis*, and by a dense population of *Streblospio benedicti*. By August, all of these species declined in abundance. August communities at 5 m contained a more even distribution of opportunistic polychaetes than in June, including *Glycinde solitaria, Nereis succinea,* and *Paraprionospio pinnata.* Although *Macoma balthica* dominated biomass in June samples collected at the 10 m and 15 m depths, it did not occur in dense populations. No *Macoma* were found at these intermediate depths after the June sampling date. The communities at 20 m and 25 m were dominated by opportunistic fauna both before and after the hypoxic conditions of the summer months. Species that were key in the September recovery seen at all depths greater than 5 m include *Paraprionospio pinnata, Streblospio benedicti,* and the roving gastropod *Rictaxis punctostriatus.*

Table 7. Abundance dominants from each depth throughout the sampling period. Listed are species accounting for greater than 10.00% of infaunal density at each sampling depth and time. (* = opportunistic species, # = equilibrium taxa.)

5 m DEPTH

JUNE	AUGUST	SEPTEMBER
Macoma balthica#	Glycinde solitaria*	Paraprionospio pinnata*
Streblospio benedicti*	Nemertea spp.	
	Nereis succinea*	
	Paraprionospio pinnata*	

10 m DEPTH

MARCH	JUNE
Mulinia lateralis*	Mulinia lateralis*
	Streblospio benedicti*

AUGUST	SEPTEMBER
Paraprionospio pinnata*	Paraprionospio pinnata*
Streblospio benedicti*	

15 m DEPTH

MARCH	JUNE
Mulinia lateralis*	Acteocina canaliculata
Pseudeurythoe ambigua	Macoma balthica#
	Streblospio benedicti*

AUGUST	SEPTEMBER
NO FAUNA	Paraprionospio pinnata*
	Streblospio benedicti*

Table 7 cont.

20 m DEPTH

MARCH	JUNE
Mulinia lateralis*	_Mulinia lateralis*_
AUGUST	SEPTEMBER
Sigambra tentaculata	_Rictaxis punctostriatus_ _Streblospio benedicti*_

25 m DEPTH

MARCH	JUNE
Leucon americanus _Mulinia lateralis*_	_Mediomastus ambiseta*_ _Mulinia lateralis*_ _Nereis succinea*_ _Paraprionospio pinnata*_ _Streblospio benedicti*_
AUGUST	SEPTEMBER
Pseudeurythoe ambigua _Streblospio benedicti*_	_Paraprionospio pinnata*_ _Rictaxis punctostriatus_ _Streblospio benedicti*_

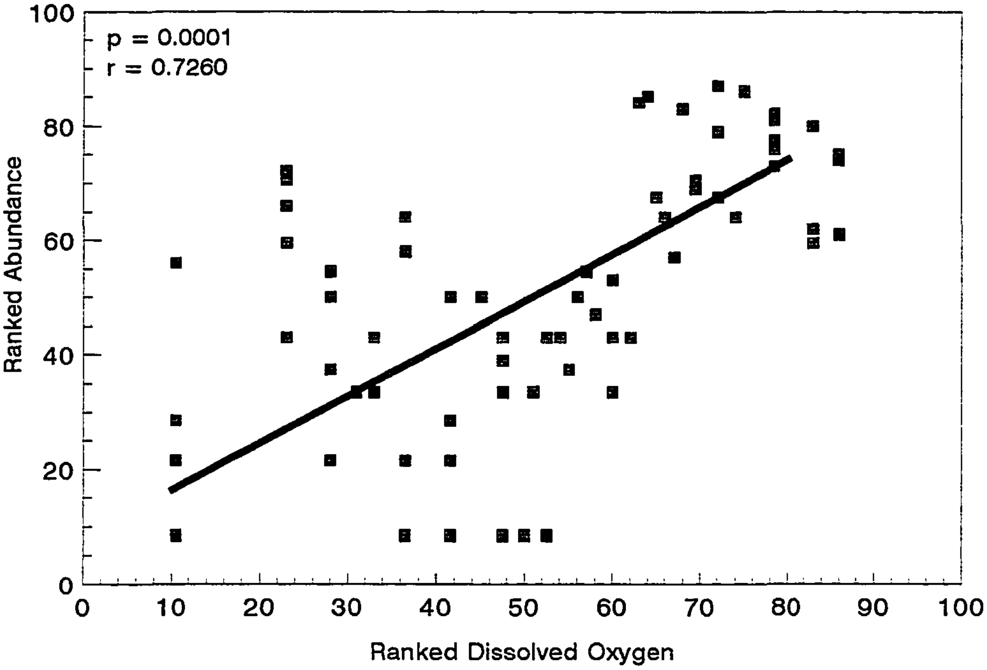
Vertical depth distributions of benthic infauna also changed in response to summer low dissolved oxygen conditions (Table 8). This table includes depth distributions both with and without *Macoma balthica* as the presence of this species can bias biomass distributions downward (Dauer *et al.,* 1987) as demonstrated during the June sampling period at the shallow and intermediate depths. From June to September, the percentage of all individuals found in the upper 5 cm of sediment increased from 91.34% to 94.44% at the 5 m depth, from 71.01% to 90.00% at 10 m, and from 94.00% to 100.00% at 15 m. In August, the lower percentage of shallow-dwelling fauna relative to June levels at the 5 m depth is due to the presence of a few deeper-dwelling predaceous species, including *Nereis succinea* and Nemertea spp. Neither the 20 m or 25 m sampling depths contained fauna inhabiting sediments deeper than 5 cm at any time during the study.

Table 8. Percentage of macrobenthic biomass and abundance found above 5 cm depth in the sediment with and without *Macoma balthica*. Values are averages of five replicates.

	PERCENT BIOMASS <5cm		PERCENT ABUNDANCE <5cm	
	With *Macoma*	W/out *Macoma*	With Macoma	W/out *Macoma*
JUNE				
5m	42.52	63.34	91.34	95.11
10m	64.14	61.51	71.01	70.14
15m	83.53	96.67	94.00	96.67
20m	100.00	100.00	100.00	100.00
25m	100.00	100.00	100.00	100.00
AUGUST				
5m	67.56	74.60	80.26	81.94
10m	100.00	100.00	100.00	100.00
15m	-	- NO FAUNA -		-
20m	100.00	100.00	100.00	100.00
25m	100.00	100.00	100.00	100.00
SEPTEMBER				
5m	90.71	89.05	94.44	94.17
10m	90.00	90.00	90.00	90.00
15m	100.00	100.00	100.00	100.00
20m	100.00	100.00	100.00	100.00
25m	100.00	100.00	100.00	100.00

Correlations between biotic variables and dissolved oxygen

A Spearman correlation analysis was performed on ranked community measures to test the second hypothesis of this study that benthic community structure can be related to dissolved oxygen conditions at specific points in time and space. Significant positive correlations were found between dissolved oxygen concentration and both benthic community biomass (p=0.0001, r=0.6549) and abundance (p=0.0001, r=0.7260) (Figure 9). Similar correlations between dissolved oxygen concentration and benthic community measures are commonly found (Friligos and Zenetos, 1988; Holland *et al.,* 1987; Hyland *et al.,* 1991). Although ranking the data was necessary to meet the assumptions of the analysis, it undoubtably increased the fit of the line by masking the magnitude of recorded values for both benthic biomass and density.



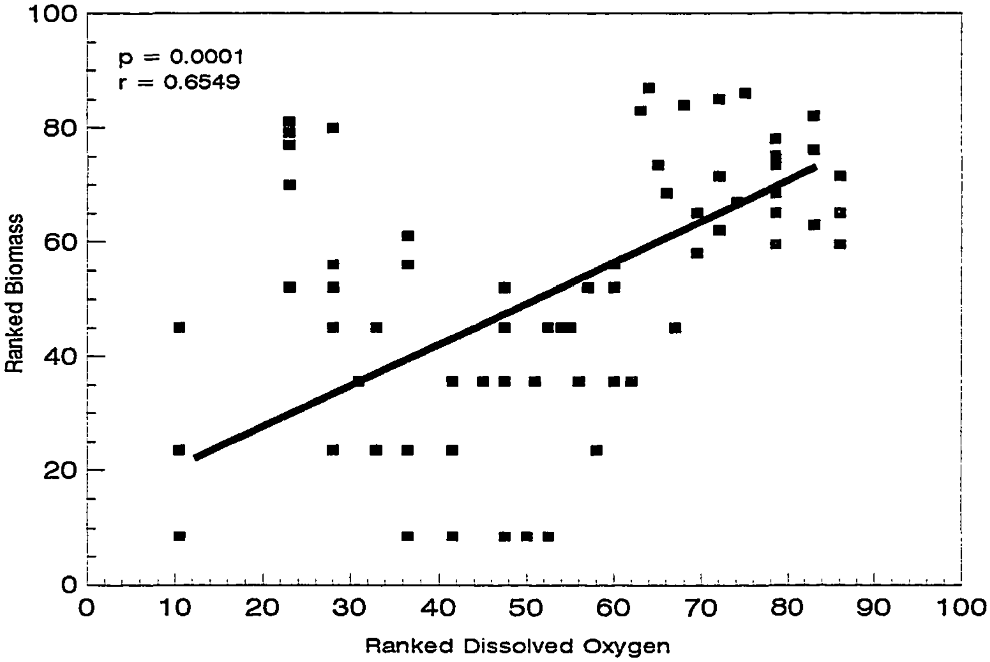


Figure 9. Ranked correlations between dissolved oxygen concentration and abundance (▨) and biomass (■).

DISCUSSION

DIFFERENCES IN SEDIMENT TYPE

Direct comparison of the 5 m station with all deeper stations was not possible. The sedimentary differences seen between the shallowest station and the deeper areas (36.5% vs. >96.0% silt-clay, respectively) precluded using the 5 m data as a within habitat reference. The impact of sedimentary differences among stations upon the benthic communities could not be accounted for statistically by an analysis of covariance (ANCOVA) due to extreme violations of the assumptions underlying the test. The influence of sediment grain size on benthic macrofaunal community composition and structure is well documented (Bloom *et al.,* 1972; Fresi *et al.,* 1983; Gaston *et al.,* 1988). The appearance of a more diverse community with denser, larger fauna at 5 m can, to some extent, be explained wholly on the basis of sediment differences. Sandier sediments often support more diverse communities than finer-grained habitats due to an increased availability of niche space for epifaunal and deposit feeding infaunal species (Boesch, 1973; Hyland *et al.,* 1991). Additionally, because of increased permeability and porosity, sandier sediments typically display deeper RPD layers than finer-grained habitats due to a larger area open to the downward diffusion of oxygen. However, anoxic and hypoxic conditions can overwhelm this benefit of high permeability found in sandy sediments (Levin *et al.,* 1991a).

IMPORTANCE OF PREDATION

Although the occurrence of hypoxic conditions during the summer of 1993 caused the degradation of deep-water benthic communities within the lower Rappahannock River, it is difficult to separate the possible effects of predation pressure at the 5 m depth. Benthic feeding vertebrate and invertebrate predators are common in the mesohaline sections of the Chesapeake Bay and its tributaries. These species include spot (*Leiostomus xanthurus*), Atlantic croaker (*Micropogon undulatus*), winter flounder (*Paralichthys dentatus*), hogchoker (*Trinectes maculatus*), blue crab (*Callinectes sapidus*), and the mud crab *Rhithropanopeus harrisii* (Holland *et al.,* 1980). Typical predation pressure by these species upon the benthic macrofauna that were dominant during June on the shallow shoals of the Rappahannock River's deep basin is greatest during the summer months and high macroinvertebrate mortalities are common (Baird and Ulanowicz, 1989; Dauer *et al.,* 1982; Virnstein, 1977).

Predation was more likely responsible for benthic mortalities at the 5 m depth than at deeper stations. The predaceous species listed above are all highly mobile, and could be driven upwards from the deeper depths of the basin by the earlier and more severe hypoxic conditions occurring there. Crabs and fish routinely migrate out of areas experiencing low dissolved oxygen conditions and onto the shallow shoals where conditions are more favorable (Breitburg, 1992; Diaz *et al.,* 1992; Officer *et al.,* 1984; Pihl *et al.,* 1992). The progressive movement shoreward of commercial crabpots placed in the lower Rappahannock River during the summer of 1993 may reflect such a migration by blue crabs (personal observation). Thus, shallow water benthic communities may experience under abnormally high predation pressure when deeper waters are under low dissolved oxygen stress.

In addition, only one dissolved oxygen level below 2.0 mg/l was recorded at the 5 m sampling depth. The duration of this hypoxic event was maximally fourteen days as normoxic conditions were measured one week before and after this value (Figure 3). Many infaunal species, including the June dominant at this depth, *Streblospio benedicti,* are known to cease activity and lie prone on the sediment surface during times of moderate oxygen stress (Diaz *et al.,* 1992; Jorgensen, 1980; Llanso, 1991; Rosenberg *et al.,* 1991). This short-term hypoxia at the 5 m depth may have imposed a sublethal stress upon the benthic infauna, which may have driven deep-dwelling forms to the surface and placed them under even greater risk of predation (Pihl *et al.,* 1992). In this study, the change in subsurface-dwelling *Macoma balthica* abundance and biomass after the July hypoxia event at 5 m is apparent (Table 8). Although Weston (1990) found that long-term variations in the depth distributions of macrobenthos are insensitive measures of chronic organic enrichment, the acute effects of hypoxia observed in this study are evident through changes in infaunal vertical distribution. Therefore, the depletion of macrobenthic infauna at the 5 m depth was likely a combination of intermediate physiological stress from low dissolved oxygen conditions and the indirect effect of greatly increased predation pressure as infauna were forced to abandon their depth refuge during a time of abnormally high predator density.

Predation was probably not responsible for the mortalities seen throughout the summer at the deeper depths sampled in this study, however. Predation pressure alone is not sufficient to cause the total habitat defaunation (Marsh and Tenore, 1990) observed at deeper stations in the Rappahannock River, and as mentioned above, mobile predators tend to abandon oxygen-stressed bottom waters. Dissolved oxygen values at the 10 m depth remained hypoxic for 27 consecutive days, while oxygen concentrations at deeper depths remained below 2.0 mg/l for at least 57 consecutive days, which is beyond the tolerance of benthic invertebrates (Rosenberg *et al.,* 1991). Finally, macrobenthic community density declined with the increasing severity and duration of hypoxia in each depth stratum, indicating that low dissolved oxygen directly affected the deeper communities directly.

At all stations located deeper than 10 m, intact, gaping bivalve shells were found during and immediately following low dissolved oxygen events, indicating that these animals did not die due to ingestion by predators, but through physiological stress directly relating to the hypoxic conditions (Jorgensen, 1980; Rosenberg, 1980). Few bivalve shells in this condition were observed at the shallowest station. Therefore, while benthos inhabiting the deeper areas of the basin probably died due to oxygen deficiency (and possible associated hydrogen sulphide toxicity, see Theede, 1973), shallow dwelling macrobenthic communities were probably defaunated due to the sublethal effects of short-term hypoxia and its indirect effect of increasing infaunal predation.

OPPORTUNISTIC SPECIES AND INDIVIDUAL TOLERANCES

The total dominance at the two deepest sampling depths (20 m and 25 m) by opportunistic fauna and the lack of any species inhabiting those sediments below 5 cm suggests that these communities are degraded not only each summer following hypoxic conditions, but all year long. Larger, more deeply dwelling equilibrium species cannot become established in these communities before the area is again subjected to summer-time hypoxia. Depauperate sediments dominated by shallow-dwelling opportunistic species are common in degraded macrobenthic communities in the Chesapeake Bay and elsewhere (Dauer, 1993; Dauer *et al.,* 1992; Gray, 1979; Pearson and Rosenberg, 1978; Weston, 1990).

Yet, the opportunistic fauna found in the deep basin of the lower Rappahannock are by no means immune to the effects of low oxygen stress (Table 9). Although their tolerances may be higher than typical equilibrium species, their adaption to environments subject to hypoxia and anoxia is often related not only to their anaerobic resistance but also to their life history characteristics (Gray, 1979). These species are able to colonize azoic or underpopulated areas quickly due to their rapid reproductive rates, their ubiquitous nature (high dispersal capabilities), and large brood size (Grassle and Grassle, 1974).

Table 9. Oxygen tolerances of some common lower Rappahannock River species. For a more complete list of Chesapeake Bay macrofaunal tolerances see Holland *et al.*, 1989. *Macoma balthica* is listed as the only equilibrium species found in this study. All other species are opportunistic. Dissolved oxygen (DO) units are mg/l. LT_{50} refers to the amount of time when 50% mortality of experimental animals is reached.

TAXA	AGE	DO	BEHAVIOR	MORTALITY	REFERENCE
Macoma balthica	Adult	0	No decrease in activity	2-3 days	Brafield, 1963
Mulinia lateralis	Juvenile	0	Maintains high levels of feeding	LT_{50} in 7 days	Shumway and Scott, 1983
	Adult	0	" "	LT_{50} in 4 days	" "
Nereis spp.	Adult	0	?	LT_{50} in 9 days	Llanso, 1991
Paraprionospio pinnata	Larvae	<1.0	?	Concentrated populations	Yokoyama, 1990
	Adult	<1.0	Growth sacrificed for gamete production	Absent from field collections	" "
Streblospio benedicti	Adult	0.5-1.0	Cease all activity, lay prone on sediment surface	LT_{50} in 14 days	Llanso, 1991
	Adult	0	" "	LT_{50} in 27 hours	" "
	Adult	0+ H_2S	" "	LT_{50} in 25 hours	" "

The polychaete *Nereis succinea* is classified by Gray (1979) as a T-strategist, where ecological success is achieved by a species through well developed individual tolerance of highly stressful environmental conditions. This species is able to survive oxygen stress due to an unusually high tolerance of hydrogen sulphide (Miron and Kristensen, 1993). However, truly opportunistic species are not characteristically adapted to withstand high disturbance conditions. For example, the opportunistic spionid polychaete *Streblospio benedicti* is not particularly tolerant of anoxic conditions (Llanso, 1991). The success of this species in oxygen-stressed benthic environments is related to its short-term adaptive characteristics, including the ability to produce either planktotrophic or lecithotrophic larvae (Levin *et al.,* 1991b). *Streblospio benedicti* larvae can reach maturity approximately one month after settlement and can thereafter reproduce multiple times in a season (Grassle and Grassle, 1974). This species is also classified as a euryhaline opportunist by Boesch (1977) and is ubiquitous over a wide range of sediment types in the mesohaline and polyhaline regions of the Chesapeake Bay (Dauer *et al.,* 1981). Thus, *S. benedicti*'s advantage in oxygen depleted areas depends not on its tolerance of anoxic conditions, but upon its ability to reinvade the area as soon as the conditions are again favorable.

Although less is known about the oxygen tolerances of another opportunistic spionid polychaete, *Paraprionospio pinnata*, this species can also colonize habitat defaunated by low dissolved oxygen conditions with large recruitment pulses of hypoxia-tolerant larvae (Yokoyama, 1990) that can settle in virtually any sediment type (Dauer *et al.,* 1981). These two resilient, if not resistant species, *S. benedicti* and

P. pinnata, were primarily responsible in the refaunation of the benthic habitat in the Rappahannock River following summer hypoxia (Table 7). Influxes of opportunistic spionid polychaetes directly following anoxia events is common in the Chesapeake Bay and other systems (Friligos and Zenetos, 1988; Holland *et al.,* 1977; Holland *et al.,* 1980). These species are both highly adapted to continual disturbance and fall into Gray's (1979) r-strategist classification, where ecological success in polluted areas is determined not by tolerance but by an inherent ability to quickly colonize and dominate new areas of the benthos.

In addition to larval recruitment, some of the fauna replenishing the deeper depths following hypoxia events may have emigrated from the shallow shoals along the basin. Adult migration to newly opened habitat has been described before for both benthic predators (Pihl *et al.,* 1992) and invertebrate macrofauna (Holland *et al.,* 1977; Llanso, 1991). Dauer and Simon (1976) found that the initial adult colonizers following a natural defaunation of benthic habitat included several opportunistic polychaetes also important in this study, including *Eteone heteropoda, Nereis succinea, Paraprionospio pinnata* and *Polydora ligni.* This emigration to deeper areas may explain the relative decrease in infaunal abundance (i.e., lack of recovery) observed at the 5 m station in September. *Macoma balthica* and *Mulinia lateralis* recruit in late-fall to early-winter; their replenishment in shallow and mid-water sediments would not have been observed unless sampling had continued past September (Boesch, 1973; Holland *et al.,* 1987).

LONGTERM DEGRADATION

A graphical comparison of macroinvertebrate biomass of communities inhabiting the deep basin with longterm data from a reference station (RET3.1) with similar sediment characteristics (although lower salinity) (Alden *et al.,* 1992) suggests and lends support to the idea that the deeper regions of the lower Rappahannock River have depressed community structure all year long (Figure 10). Except for a small number of observations, the infaunal biomass of communities inhabiting the lower Rappahannock is lower than that of the upriver reference station. If these deepwater communities were able to recover from low dissolved oxygen stress each year, then obvious breakpoint or "threshold" between communities sampled during high winter dissolved oxygen concentrations and those collected during summer hypoxic conditions should be evident (Figure 11). If so, benthic infaunal biomass could be predicted by dissolved oxygen exposure. However, deep basin communities display similar biotic measures regardless of dissolved oxygen concentration, indicating that there is either no infaunal response to summer low dissolved oxygen (which is not the case) or that benthic communities carry an annual signal of seasonal hypoxia. This pattern of hypoxia causing a community to remain suspended in a cycle of constant reestablishment has been reported previously in the ChesapeakeBay and elsewhere (Gaston and Nasci, 1988; Holland *et al.,* 1977; Tenore, 1972; Tsutsumi and Kikuchi, 1983) and has been suggested for this area of the lower Rappahannock River (Llanso, 1992). Studies where recovery from natural and experimental degradation has been demonstrated estimate reestablishment of healthy communities

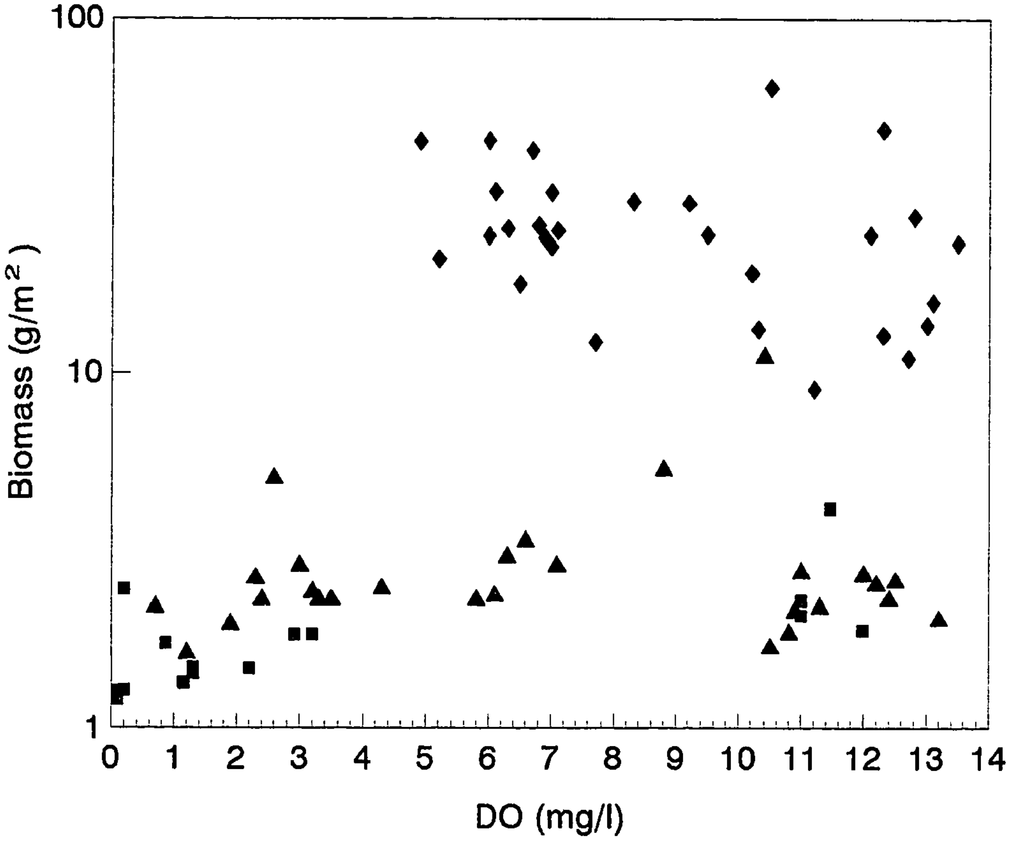


Figure 10. Plot of dissolved oxygen concentration against community biomass standardized to September values. ■ = 1993 data, ▲ = longterm data at station LE3.4, ◆ = longterm data at reference station RET3.1 See text for explanation.

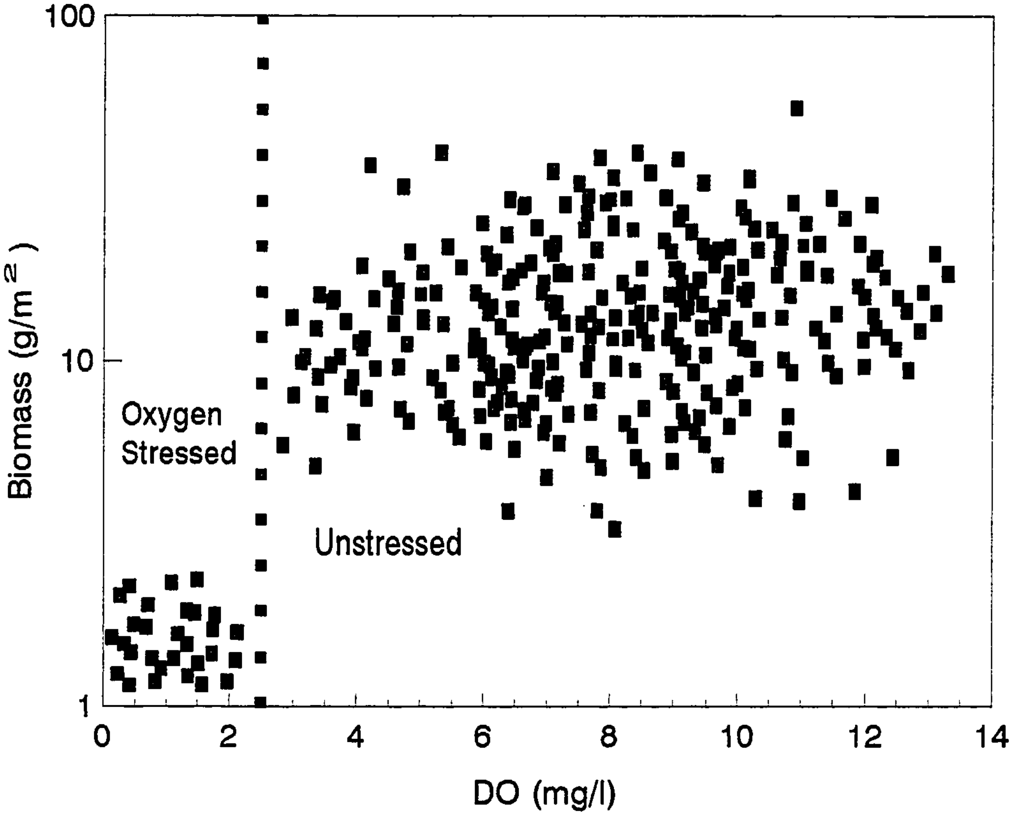


Figure 11. Theoretical plot where benthic community stress is demonstrated by a breakpoint in biomass values at some critical value of dissolved oxygen concentration.

at greater than 1.5 to 2.5 years (Boesch *et al.,* 1976; Dauer and Simon, 1976; Warwick *et al.,* 1987), a time period longer that the annual low dissolved oxygen events of the lower Rappahannock River. This indicates that within the deep basin, the current monitoring station cannot provide information relating to annual variation in community health or responses to oxygen stress.

RESTORATION GOALS

The goal of most monitoring programs is to create some useful measure of environmental and biotic integrity and change. Recently, an index of benthic community structure, the Restoration Goals Index (RGI), was developed by Ranasinghe *et al.* (1993) as a measure of benthic community health. The advantage of this index is that it is based upon longterm sampling of areas that were *a priori* determined to be of acceptable, if not pristine, environmental quality based on sediment contaminant levels and the frequency and magnitude of low dissolved oxygen events. The present data set provides an appropriate base to test the accuracy and predictability of the RGI as the deeper benthic communities in this study displayed obvious degradation through the summer of 1993.

The Restoration Goals Index for high mesohaline sands and muds is shown in Table 10. Both sediment types are shown as the sediments at the 5 m station in the present study fall into the sand range of this index (defined as <40% silt-clay) while sediments from deeper stations are classified as muds. The values presented in Table 10 represent the lower 5% and median values found for each biotic variable from reference areas. Any measure falling below the 5% value is assigned an index value of one, any between the two numbers is given a three, and all measures falling above the median are given a score of five. These scores are then averaged without weight to arrive at the RGI of community health. An RGI score of three "represents the minimum restoration goal" (Ranasinghe *et al.,* 1993) where values lower than

Table 10. Restoration Goals for benthic communities found in high mesohaline habitats. See text for explanation of values.

BIOTIC VARIABLE	SANDS	MUDS
Shannon-Weaver Diversity (H')	2.3, 2.7	2.0, 3.0
Abundance (ind/m^2)	2500, 6000	500, 1000
Biomass (g/m^2)	1.0, 2.0	0.5, 8.0
% Opportunistic Biomass	42, 16	50, 15
% Equilibrium Biomass	30, 60	-
% Taxa below 5cm	10, 40	10, 40
% Biomass below 5cm	10, 50	10, 50
% Carnivore-Omnivore Abundance	5, 15	10, 30

three are considered unacceptably stressed and those above are considered to be indicative of acceptable benthic communities.

Restoration Goals indices for the 1993 lower Rappahannock River study sites are listed in Table 11. Additional epifaunal species were discarded from the original raw data set generated from this study for this analysis following Ranasinghe *et al.* (1993) (See Appendix A for this list). The index is useful in showing the degradation of the 5 m sampling depth from an acceptable community in June to a stressed one in August and September. The singular deepwater acceptable value (3.4) found during March at the 15 m depth is driven mainly by a relatively high number of species being classified as either carnivores or omnivores (44.44%, 50.00%, and 63.64% of resident taxa in each replicate, respectively), a measure used to indicate a trophically complex community. However, the Restoration Goals Index is based upon summer-time sampling of benthic communities and interpretations of values measured outside of this time period should be treated with caution. Although the index portrays all of the deeper regions of the Rappahannock River as continuously degraded, it is still sensitive enough to detect the temporal responses of these communities to the summer low dissolved oxygen events and demonstrates the weak fall recovery at the intermediate depths. The lack of agreement between baseline community measures and the RGI regarding the September recovery at the two deepest depths of the study is probably related to the presence or absence nature of the data set. Absolute abundances were so low (1-3 individuals among 5 replicate

Table 11. Benthic Restoration Goals Index for Rappahannock River 1993 data.

DEPTH (m)	MARCH	JUNE	AUGUST	SEPTEMBER
5	-	3.75	2.25	2.0
10	2.6	2.29	1.0	1.57
15	3.4	2.43	1.0*	1.29
20	2.2	1.86	2.14	1.57
25	2.6	1.57	1.57	1.29

* No fauna

cores) that no index is necessary to demonstrate the degraded nature of these communities.

This lack of a lower limit on absolute macrofaunal densities necessary for use in the RGI should be considered using this index. Because the RGI variable are not weighted, small scale changes in community composition can result in large scale differences in the accuracy and overall usefulness of the index generated. In addition, the RGI should be used with caution when there is large variation in a data set or when few replicates are available, as in this study. More replicates may be required in order to achieve a reliable estimate that is not skewed by single large individuals, the lack of all species being classified as either opportunists or equilibrium taxa, or the appearance of mobile carnivores and omnivores, all of which become important with low absolute densities of organisms.

CONCLUSIONS

Several lines of evidence suggest that benthic communities found deeper than 20 m in the deep basin are depressed throughout the year in response to annual low dissolved oxygen stress and can therefore provide little or no information relating to overall water quality and environmental restoration goals. Support for this theory includes the observed patterns in basic community measures including infaunal density and diversity, the dominance at these depths by opportunistic fauna, the lack of any species inhabiting vertical depths greater than 5 cm, and the generally depressed community structure when compared to a reference station of similar sedimentary habitat. Additional support for this theory comes from the Benthic Restoration Goals Index developed by Ranasinghe *et al.* (1993) for the Chesapeake Bay. These communities likely reside in the area of the benthos that is under anoxia stress due to natural, not anthropogenic, forces.

Communities inhabiting the intermediate depths of this study (10 m and 15 m) should be examined more intensively and monitored on a long-term basis as they are exposed to low dissolved oxygen stress that is more likely linked to anthropogenic eutrophication. Benthic communities at both of these depths displayed characteristic changes in the depth distribution and dominance of equilibrium taxa relating to the hypoxic conditions of 1993. Long-term measures of community structure at these depths may show interannual variability that can be directly related to within-year nutrient loadings or river flow. Comparisons of benthic community structure between intermediate depths (10-15 m) and the deeper water monitoring station LE3.4 may allow assessment of the relative contributions and effects of natural physical factors and anthropogenic eutrophication to the annual summer hypoxic events of the lower Rappahannock River.

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Appendix A

Additional species listed as epifaunal taxa by the Restoration Goals Index (Ranasinghe *et al.,* 1993).

Polychaeta
  Edotea triloba
  Harmothoe extenuata

Gastropoda
  Nassarius vibex
  Odiostoma spp.

Decapoda
  Ogyrides alphaerostris

Platyhelminthes
  Turbellaria spp.