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The Relationship between Dominant Macrobenthos and Cyclical Hypoxia in the Lower York River

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THE RELATIONSHIP BETWEEN DOMINANT MACROBENTHOS AND CYCLICAL

HYPOXIA IN THE LOWER YORK RIVER

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A Thesis

Presented to

The Faculty of the School of Marine Science

The College of William and Mary in Virginia

In Partial Fulfillment

Of the Requirements for the Degree of

Master of Arts

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by

R. Joseph Neubauer

1993

APPROVAL SHEET

This thesis is submitted in partial fulfillment of the
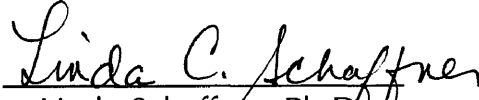requirements of the degree of
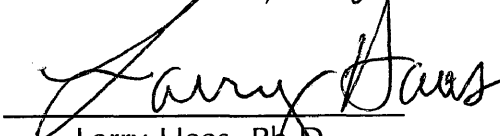
Master of Arts

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Approved, August 1993

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ABSTRACT

The low dissolved oxygen of the Chesapeake Bay is thought to be increasing in spatial extent and temporal duration. Summer hypoxia (< 2 mg l^{-1}) is now a common event in many areas of Chesapeake Bay and its tributaries. A location in 18 m depth (with sensors 1 m off-bottom) in the York River, Virginia was sampled continuously for dissolved oxygen, salinity, and temperature in the summer of 1989. The results indicate that the benthos experienced alternating periods of hypoxia coinciding with the spring-neap tidal cycle. As bottom water temperature increased throughout the summer the duration of hypoxia increased. Hypoxia was experienced for periods of up to 19 consecutive days. Faunal samples and dissolved oxygen measurements were taken at the beginning and end of normoxic and hypoxic periods from four depth strata (A: 5 to 10 m; B: 10 to 14 m; C: 14 to 20 m; D: >20 m) to estimate the sub-lethal influence of hypoxia on the growth and production of dominant benthic invertebrates. Hypoxia was most evident in the two deep strata (C and D) and decreased with decreasing depth. Stratum A never experienced hypoxia. The abundance and biomass dominants were the gastropod, *Acteocina canaliculata*, and the polychaetes, *Sigambra tentaculata*, *Paraprionospio pinnata*, *Glycinde solitaria*, and *Leitoscoloplos fragilis*. *Paraprionospio pinnata* was the dominant species overall. There was no clear relationship between abundance, daily growth, instantaneous production, or total production of these species and hypoxia. These species have been shown in the York River and other areas to be resistant to hypoxia which may explain their dominance and lack of response to hypoxia during the summer of 1989.

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INTRODUCTION

In aquatic systems dissolved oxygen is a water quality parameter used by aquatic scientists and resource managers in recent years, as a means of assessing habitat quality (Mackiernan 1987, Funderburk et al. 1991). Management decisions are being made with the intent of increasing the dissolved oxygen concentration of many aquatic systems. To make sound management decisions about the relationship between low dissolved oxygen, fauna, and ecosystem health, a better understanding of the causes and ecological implications of low dissolved oxygen is needed. This emphasis on oxygen as a regulator of ecological processes is instrumental to understanding the magnitude and extent of eutrophication (Tyson and Pearson 1991).

In Chesapeake Bay, low dissolved oxygen and its ecological impact have been the subject of recent investigations (Mackiernan 1987, Smith et al. 1992), however, low dissolved oxygen in the Bay was recorded as early as the 1930's (Newcomb 1939). Two general terms are used to describe water quality relative to oxygen. The first is hypoxia, which in this study refers to a dissolved oxygen concentration from 2.0 mg l^{-1} to 0.5 mg l^{-1}. The second term used is anoxia which describes a dissolved oxygen concentration below 0.5 mg l^{-1}. Officer et al. (1984) noted that the volume and seasonal duration of hypoxic and anoxic water have increased in Chesapeake Bay during the last century. Poorly oxygenated water is suspected to be one of the principal factors contributing to the decline in abundance of many Chesapeake Bay species. One suspected cause of the low dissolved oxygen of many aquatic

ecosystems is the degradation of excess primary production brought on by eutrophication (Rosenberg and Loo 1988).

Taft et al. (1980) cite three processes which lead to hypoxia/anoxia in the mainstem of Chesapeake Bay. First, increased freshwater flow from late winter and early spring precipitation helps establish vertical salinity stratification, which isolates bottom water from atmospheric oxygen. Strong salinity stratification requires a high energy input, such as sustained winds, to mix surface and bottom water layers. Second, with an increase in water temperature, there is an increase in water column and benthic metabolism resulting in an increased dissolved oxygen demand. The increase in temperature contributes somewhat to the establishment of a pycnocline in Chesapeake Bay but salinity is the primary controlling factor (Haas 1977, Kuo and Neilson 1987). Third, phytoplankton from the spring bloom and other organic material are deposited on the sediment surface. Aerobic decomposition of this detritus in the water column and on the bottom further depletes bottom water dissolved oxygen concentrations (Taft et al. 1980).

Low dissolved oxygen events around Chesapeake Bay vary both spatially and temporally. In Chesapeake Bay, low dissolved oxygen concentrations are primarily encountered during the summer. The deep water in the mainstem of the Bay becomes hypoxic as early as June and may be hypoxic/anoxic until September (Taft et al. 1980, Officer et al. 1984, Seliger et al. 1985). The Rappahannock River is

susceptible to hypoxia in early summer (Kuo and Neilson 1987). The York River is most susceptible to low dissolved oxygen in early to mid-summer (Haas 1977, Diaz *et al.* 1992).

A variety of mechanisms drives the frequency and duration of hypoxic/anoxic events, which are related to the density stratification of the water column and the frequency of water column mixing. Disruption of water column stratification may occur on several temporal scales, from semi-diurnal tidal mixing to seasonal fall turn-over. Shallow areas of the Bay may receive an intrusion of low oxygen water if a lateral tilting of the water column occurs as the result of an extended period of wind during the summer. Intrusions of hypoxic/anoxic water into shallow areas can cause mobile epifauna and fish to emigrate from an area or to concentrate in shallow areas (May 1973, Brietberg 1990).

In the York River, hypoxia is somewhat predictable because of the nature of the forcing mechanism driving low dissolved oxygen events. The driving force which dictates the establishment and break-up of low dissolved oxygen is the lunar spring-neap tidal cycle (Haas 1977). Because the spring-neap tidal cycle is predictable and the hypoxia in York River historically does not cause wide-scale mortality, the York River is well suited for the examination of the relationship between sub-lethal effects of hypoxia and macrobenthic energy flow.

The effects of low dissolved oxygen on benthic fauna are often described through changes in abundance of species or community composition (Holland et al. 1988, Gaston 1985, Gaston et al. 1985, Harper et al. 1981). Areas which experience anoxia have been documented to experience large scale mortality of benthic fauna (Jorgenson 1980, Gaston 1985, Seliger et al. 1985). Areas experiencing short term anoxia or hypoxia may not have large scale defaunation, however, there may be some sub-lethal responses from the benthos. Sub-lethal responses may be the emigration of fish and mobile epifauna (May 1973, Pihl et al. 1991) or the migration of infauna to the sediment surface (Jorgenson 1980, Pihl et al. 1992, Diaz et al. 1992, Schaffner et al. in review), which would make the infauna more vulnerable to predation (Pihl et al. 1992).

A change in growth or secondary production may be another sub-lethal response to low dissolved oxygen. In laboratory experiments, Forbes and Lopez (1990) have shown that low dissolved oxygen concentrations are an important factor in limiting the growth of the polychaete Capitella species 1. Macrobenthic organisms cannot tolerate hypoxic conditions for extended periods of time and should respond to hypoxic stress with reduced abundance and productivity (Holland et al. 1989). Areas that experience prolonged anoxia have low annual production (Rainer and Fithardinge 1981, Holland et al. 1988). The tolerances of fauna to low dissolved oxygen and ability to recruit and colonize an area during normoxic (non-hypoxic

dissolved oxygen concentrations) periods will affect the magnitude of secondary production (Holland et al. 1989).

Productivity estimates are the means by which the energy of a system is quantified. If different components of a system can be quantified energetically, important trophic links may be identified. Secondary production of the benthos in Chesapeake Bay is an integral part of Bay-wide energetics, providing an important link between primary production and higher trophic levels (Virnstein 1977, Baird and Ulanowicz 1989, Diaz and Schaffner 1990). An estimation of benthic secondary production and understanding the factors that influence the magnitude of this production will contribute to a better understanding of the energetics of the Chesapeake Bay ecosystem.

This study examines the growth and production of dominant benthic macrofaunal species in the field under alternating periods of hypoxia and normoxia. The species studied (the gastropod Acteocina canaliculata, and polychaetes Sigambra tentaculata, Glycinde solitaria, Paraprionospio pinnata, and Leitoscoloplos fragilis) are ubiquitous opportunists of the mesohaline to polyhaline benthos in Chesapeake Bay (Boesch et al. 1976a, Holland et al. 1989). They have been collected from both hypoxic and non-hypoxic environments and estimation of their growth and production in the York River will lend insight into the sub-lethal effects of hypoxia.

STUDY AREA

The lower York River, a sub-estuary of the Chesapeake Bay, is located in southeastern Virginia (Figure 1). The lower York River was selected because of the predictable nature of its hypoxia. The majority of low dissolved oxygen events in the York River are not anoxic but hypoxic which presents an opportunity to study potential sub-lethal effects. The neap-spring tidal cycle controls the frequency of water column mixing (Haas 1977, Hayward et al. 1986) which allows an opportunity to anticipate normoxic and hypoxic conditions. In the York River the shallow areas (<9 m) do not seem to be affected by hypoxia and may represent a refuge from low dissolved oxygen for mobile epifauna (Pihl et al. 1991, Diaz et al. 1992). The combination of predictable hypoxic events, areas subjected to hypoxia, and areas not subjected to hypoxia made the York River a prime site for a field study of the relationship between the macrobenthos and hypoxia.

Figure 1. The lower York River study area showing the location of the EPA telemetering buoy (**X**) and strata. Stratum A is 5-10 m depth, B is 10-14 m depth, C is 14-20 m depth, and D is > 20 m depth.

EPA BUOY
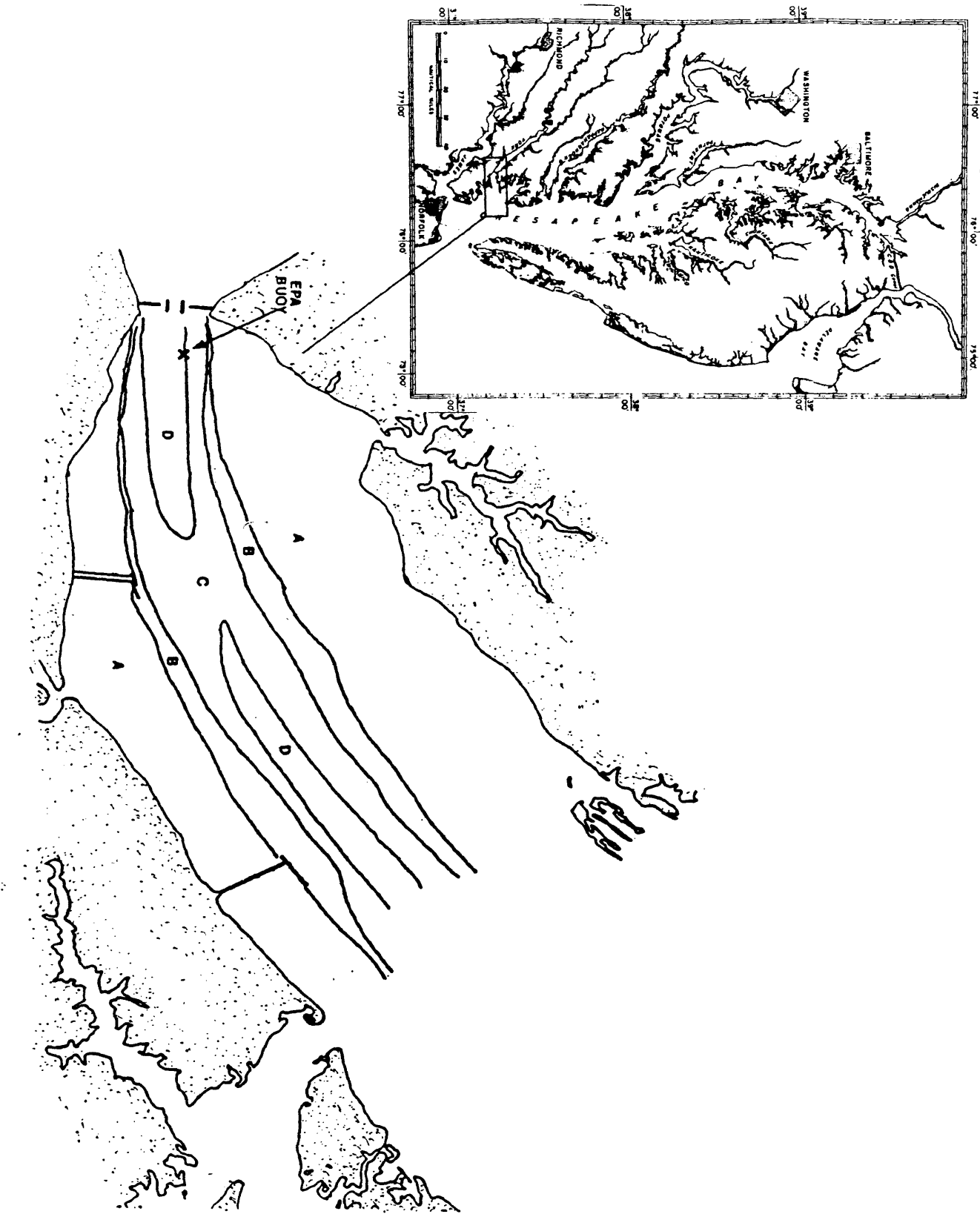
METHODS

Oxygen Measurement

To address the questions concerning the relationship between hypoxia and benthic macrofaunal growth and production, two forms of sampling were important: first, a reliable oxygen record needed to be established. Second, the collection of faunal samples needed to be over a time interval relevant to the growth and production of selected macrobenthic species and the timing of hypoxic events.

From preliminary studies conducted in 1988, dissolved oxygen measurements were obtained for every other tide at slack before ebb. This daily measurement of oxygen produced a record that only broadly characterized the oxygen environment of the benthos. To obtain a sufficiently detailed record of dissolved oxygen changes on the temporal scale of hours to minutes, which may be relevant to benthic fauna (Pihl *et al.* 1991, Diaz *et al.* 1992), a higher frequency of dissolved oxygen measurement was necessary. In 1989 a radio-telemetering environmental data buoy (Mountford *et al.* 1989) was deployed at a point approximately 500 m south of Gloucester Point, Virginia (Figure 1) and anchored in 18 m of water. The data buoy consisted of a buoy with batteries, antenna, and cable extending to a sensor package fixed 1 m off the bottom (Figure 2). The sensor package was a Seabird Seacat CTD and SBE-23 oxygen probe that monitored conductivity, temperature, and dissolved oxygen every 20 minutes and transmitted the data to a data logger in a laboratory at VIMS. The data buoy provided "real-time" dissolved oxygen data which allowed for the

optimization of faunal sampling effort. By having knowledge of the "real-time" oxygen conditions, the dates of faunal sampling could be set to span hypoxic and normoxic events. The frequency of the faunal sampling was approximately every two weeks, which was adequate to measure growth and production of species over the course of the summer as well as relevant to the timing of low dissolved oxygen events.

A Yellow Springs Instruments (YSI) oxygen meter model YSI-58 was used to obtain dissolved oxygen measurements at each station, each sampling date.

Winkler oxygen titrations were done periodically to verify the calibration of the YSI and Seabird sensors. The YSI was calibrated before each day of use. Both sensors performed well throughout the study period. The Seabird sensor was factory calibrated before deployment and after 60 days of continuous use. The factory calibration results showed that it did not vary from factory specifications.

Faunal Sampling

For faunal sampling, the river was partitioned into four strata according to depth. The strata were 5-10 m, 10-14 m, 14-20 m, and >20 m, and were designated as A, B, C, and D respectively (Figure 1). Within each stratum, five stations were randomly located and each station was sampled every fauna sampling date. The stratification based on depth allowed for a comparison between strata along depth and oxygen gradients.

Figure 2. Diagram of EPA monitoring buoy deployed in lower York River.

EPA
MONITORING
BUOY

COUNTERWEIGHT

TRANSMISSION
CABLE

SUBMERGED
BUOYS

SENSOR
PACKAGE

RAILROAD
WHEEL

1m
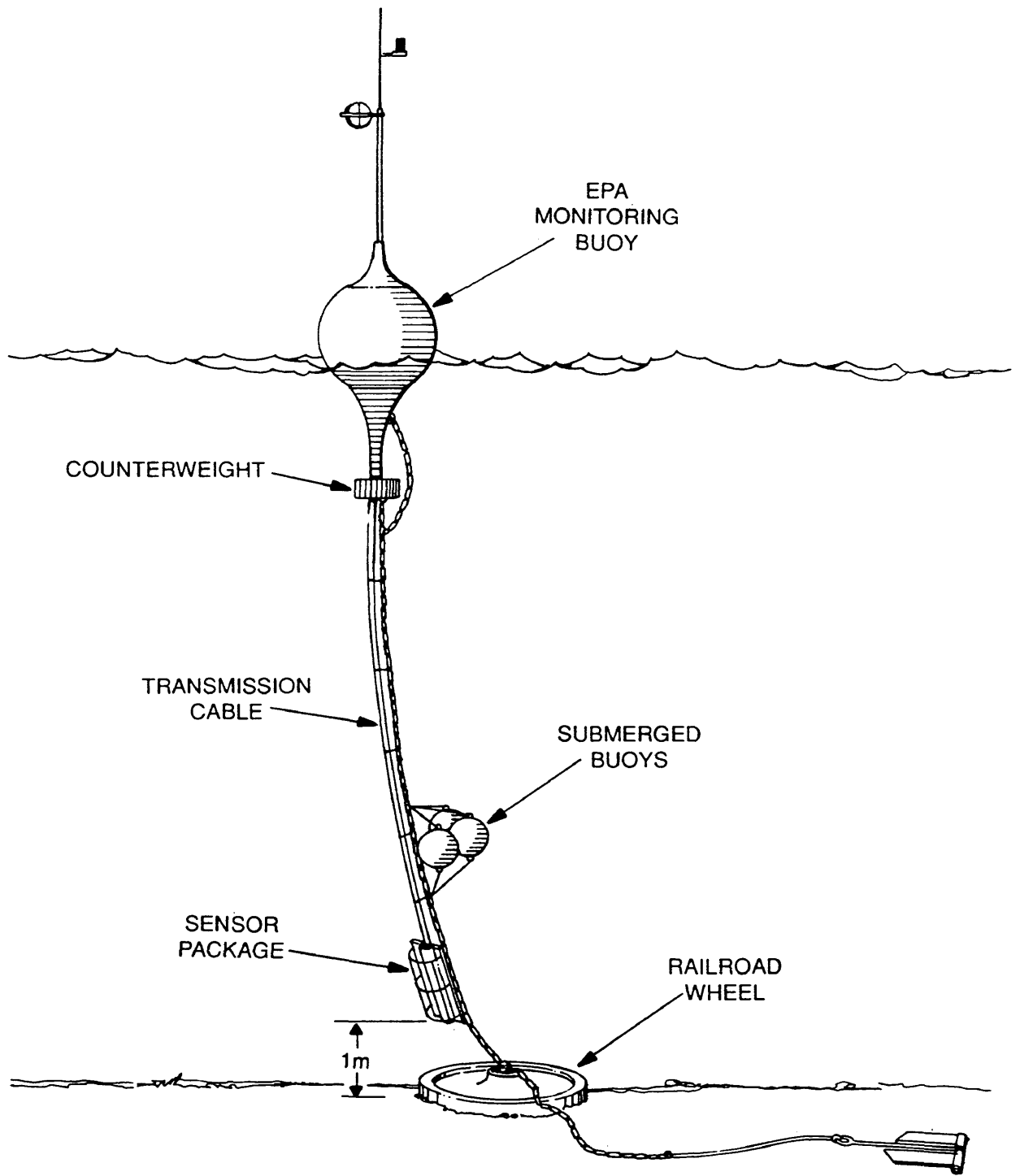
The benthos at depths < 9 m rarely experiences hypoxia (Pihl *et al.* 1991, Diaz *et al.* 1992) so stratum A acted as a reference stratum.

A Wildco 15x15x30 cm box core (225 cm^2 surface area) was used to obtain the faunal samples. On all sample dates except 23 June 1989, when several stations were missed due to weather, one core was taken at each of the five stations for a total area of 0.1125 m^2 sampled within each stratum. The dates on which faunal sampling occurred are 23 June, 7 and 21 July, 4, 15, and 31 August and 12 September. In the field, the faunal samples were divided by sediment depth into 0-2 cm and 2-10 cm fractions. The 0-2 cm fraction was sieved using stacked 250 *um* and 500 *um* sieves. The 250 *um* sieve helps prevent the loss of juveniles which occur in the surface sediments (Zobrist 1988) and are an important part of accurate growth and production estimates. The 2-10 cm fraction was sieved using a 500 *um* sieve only. All faunal samples were fixed in 10% buffered formalin with a rose bengal stain. The stain aids in location and identification of macrofauna when viewed under a microscope.

Sample Processing

In the laboratory the sediment and debris were sorted from the fauna. The fauna were then identified to the lowest taxonomic level possible and counted. Several species were then chosen for production estimates based on abundance and duration in the faunal record. The species chosen for this study were the polychaetes

Paraprionospio pinnata, Sigambra tentaculata, Glycinde solitaria, and *Leitoscoloplos fragilis,* and the gastropod, *Acteocina canaliculata.*

The individual weight of an animal was determined by drying at 60 °C for 24 hours, which for all animals gave enough time to reach a constant weight. The dry weight was determined and recorded. The animals were then put in a muffle furnace for 4 hours at 550 °C, ashed and weighed. By subtracting the ash weight from the dry weight the ash-free dry weight (AFDW) was determined.

For all selected species a regression was established that relates a linear measurement of the animal to the animal's weight. For *P. pinnata* and *S. tentaculata* the width of the first setiger was the linear measurement used. For *G. solitaria* and *L. fragilis* the width of the fifth setiger gave the best representation of the animal's weight. For *A. canaliculata* the shell length was used.

Growth and Production

Growth was estimated only for *Acteocina canaliculata* and *Sigambra tentaculata* which had distinguishable cohorts. Cohorts were defined by visual interpretation of the size frequency histograms. Both species showed more then one cohort during the study. However, in both cases one cohort dominated for the majority of the study and was chosen for growth and production estimates. Growth was calculated as specific growth:

$$G = [w_{(t)} - w_{(t-1)}]/n$$

G   =   specific growth (change in mg AFDW individual^{-1} day^{-1})

$w_{(t)}$ =   mean individual weight on sample date, t.

n   =   the number of days in the sample interval.

The mean individual weight $w_{(t)}$ was calculated from regression-derived weights by pooling all individuals of a cohort from a stratum on a given date. High and low estimates of growth were obtained by respectively adding and subtracting the standard error to the mean individual weight and then recalculating specific growth.

For *Acteocina canaliculata* and *Sigambra tentaculata* which had discernable cohorts, production was calculated using the growth increment summation method (Downing and Rigler 1984). The growth increment summation method uses the change in mean individual weight over the time period multiplied by the mean number of individuals during the time period to estimate incremental production (mg AFDW m^{-2} time interval^{-1}). The incremental production divided by the number of days of the interval gives instantaneous daily production (mg AFDW m^{-2} day^{-1}). The summation of the incremental production from all time periods, gives an estimate of total production for the study period. The general equation for the incremental summation method is:

P   = Σ {(N_i + N_{i+1} / 2} {w_{i+1} - w_i} + to n

P   =   Total Production (mg AFDW m^{-2} study period^{-1})

N_i = number of individuals m^{-2} at time i

w_i = mean individual weight (mg AFDW) at time i

n = total number of time intervals during the study

High and low estimates of production were obtained by respectively adding and subtracting the standard errors of the mean individual weight and the number of individuals m^{-2} to their mean values and then recalculating specific production.

Cohorts are often unrecognizable in natural populations, especially if recruitment is continuous. For *Paraprionospio pinnata*, *Glycinde solitaria*, and *Leitoscoloplos fragilis*, without distinguishable cohorts, the size frequency method of production estimation was employed (Downing and Rigler 1984). With the size-frequency method, all individuals for the entire study period are put into size categories. The mean number of individuals in each size group for the entire study period is then determined. The mean abundance in each size group cannot be determined until the end of the study period, therefore, only total production for the entire study period can be determined. The loss in number between successive size groups and mean biomass between successive size groups are determined. To estimate production between size groups, the change in weight is determined by multiplying the change in numbers by the mean biomass for each size group. The production from each size group has no meaning because the size groups do not represent a single time period. Summing results from all size groups gives the production estimate for the study period. The equation for the size frequency method is:

$$P = \Sigma (N_i - N_{i+1}) \{(B_i + B_{i+1}) / 2\} + \text{to } n$$

P = Total Production (mg AFDW m^{-2} study period^{-1})

N_i = total number of individuals m^{-2} that developed into a size class (i) during the study period

B_i = mean individual biomass (mg AFDW) of the size group (i)

n = the number of size classes

Statistical Analysis

A one-way analysis of variance (ANOVA) was used to tests for differences between mean abundance and mean individual weight between strata. The null hypothesis being that there is no change across strata. These statistical tests were performed following the assumptions of the individual analyses.

RESULTS

Environmental Conditions

Daily averaged dissolved oxygen measurements from the data buoy are shown in Figure 3. Over the course of a single tidal cycle the dissolved oxygen varied as much as 6 mg l^{-1} (Diaz *et al.* 1992). Over the summer the data buoy results show a trend of increasing severity and duration of the low dissolved oxygen events until a strong northeast wind event (11-15 m sec^{-1}) occurred on 3 September and lasted three days. This wind event interrupted the expected decline in oxygen concentration of the bottom water.

Hypoxia was first recorded in June with a minimum dissolved oxygen value below 2 mg l^{-1} being recorded for three consecutive days (June 27 - 29). During mid-July, the daily average dissolved oxygen fell below 2 mg l^{-1} for most of seven consecutive days (July 10 - 16), with values below 2 mg l^{-1} being recorded for two additional days (July 17, 18). A dissolved oxygen value below 2 mg l^{-1} was recorded at least once for every day in August. With the neap tides following the new moon in August the daily average dissolved oxygen remained below 2 mg l^{-1} for thirteen consecutive days.

From oxygen concentrations as measured by the YSI oxygen meter, on each faunal sampling date, at each station, general differences in dissolved oxygen along a depth gradient were observed (Figure 4). The deeper strata C and D had, overall, lower

Figure 3.   Daily mean values from the EPA continuous monitoring buoy data.

Each day is the average of 72 measurements taken at 20 minute

intervals. Relatively normoxic periods are represented by N, relatively

hypoxic periods are represented by H.   Faunal sample dates are

highlighted.

30

25

20

15

10

5

0
30 SEP

12 SEP

31 AUG

15 AUG

04 AUG

21 JUL

07 JUL

23 JUN
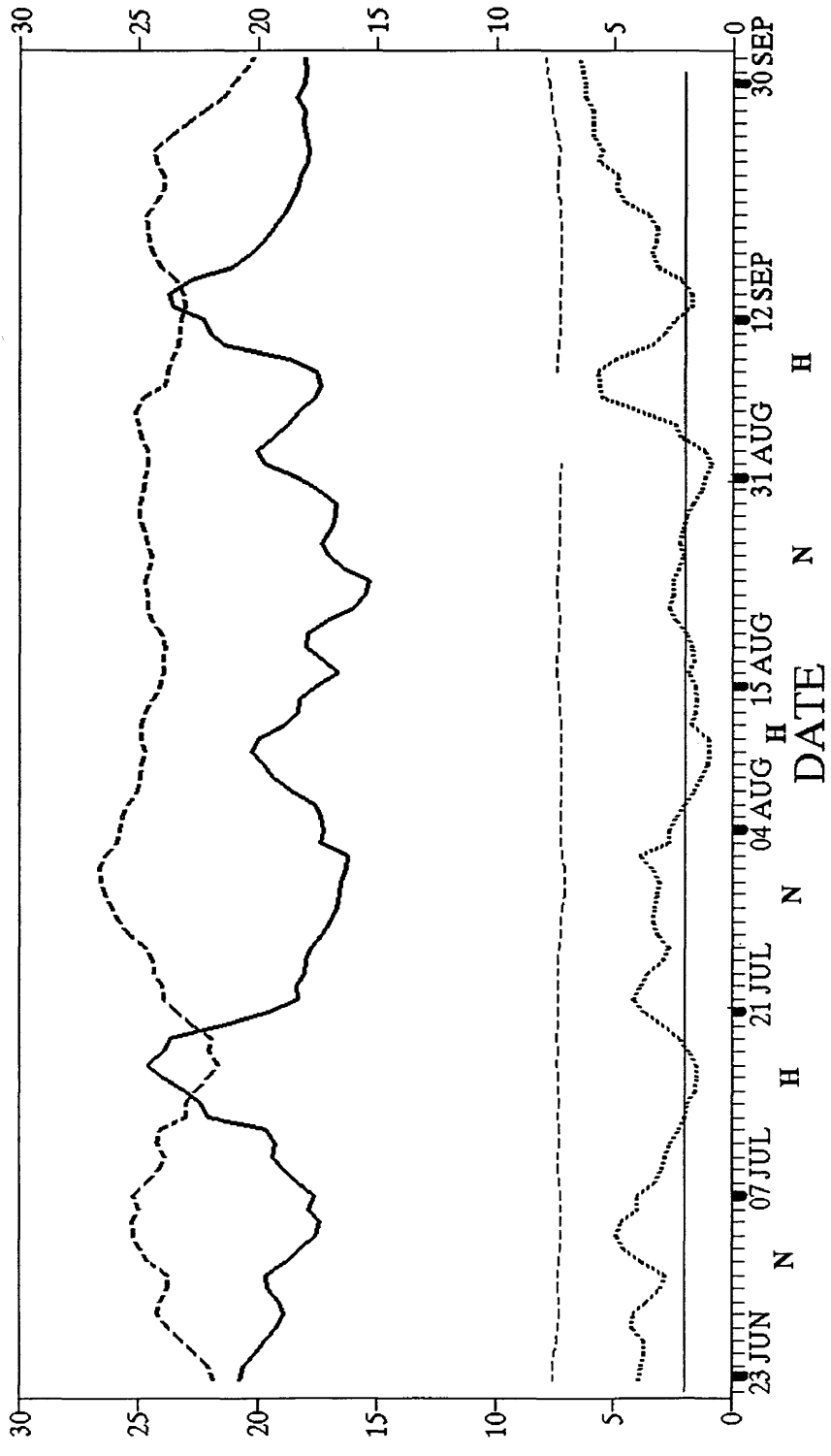
DATE

—— DO (mg/L)

········ 100% Sat.

—— Sal. (ppt.)

------ Hypoxia (2 mg/L)

------- Temp. (C)

Figure 4.   Mean dissolved oxygen concentration in each stratum (+/- SE) on each

sample date.
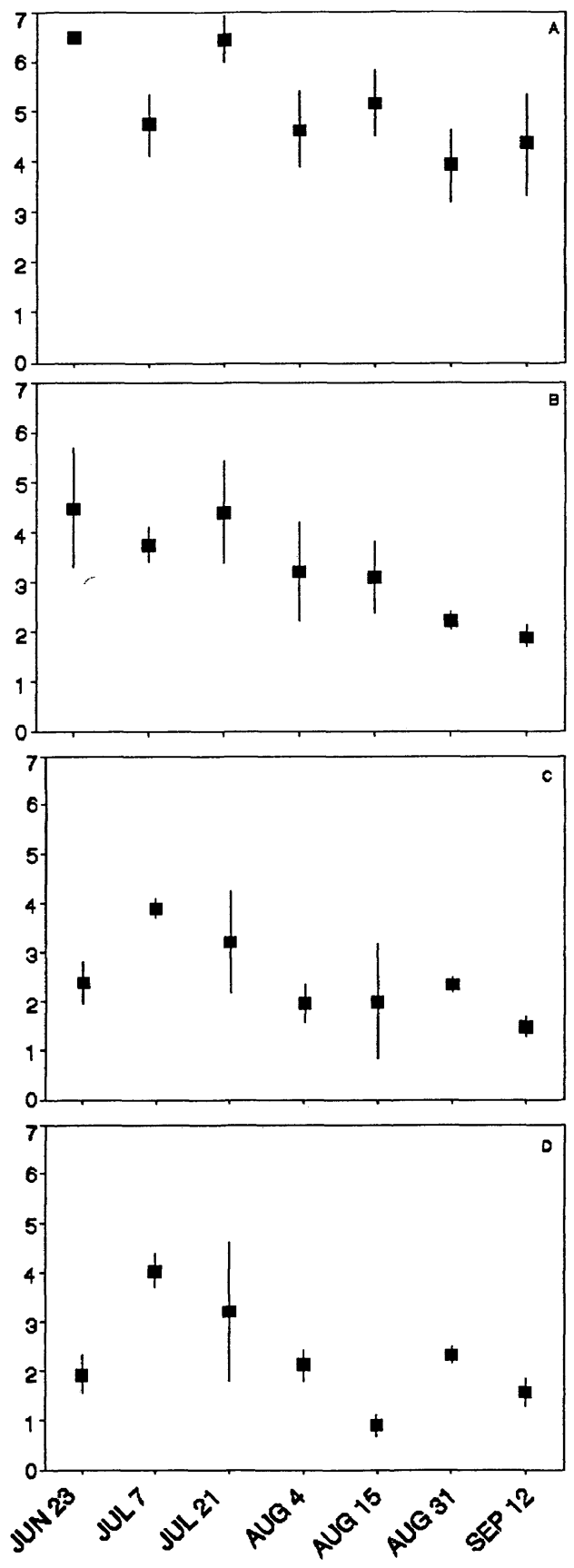
dissolved oxygen than the shallow strata (A and B). Hypoxia was recorded in all stratum except stratum A.

The sediment samples taken at each station show that the average percent silt and clay content for strata B, C, and D was between 77.5 and 92.6 percent (Table 1). The silt - clay content for stratum A was 36.4 % (Table 1).

The salinity as measured by the data buoy ranged from 17 to 25 ppt over the course of the summer (Figure 3). The bottom water temperature was between 20 and 30°C during the summer of 1989 (Figure 3).

Faunal Samples

All animals were identified to lowest possible taxonomic level and recorded. *Acteocina canaliculata*, *Sigambra tentaculata*, *Paraprionospio pinnata*, *Glycinde solitaria*, and *Leitoscoloplos fragilis* occurred in sufficient numbers throughout the study to make them suitable for production estimates. For all the target species, except for *A. canaliculata*, morphological measurements were converted to an individual ash free dry weight (AFDW) through regression equations created from individuals collected during the study (Table 2). The regression used for *A. canaliculata* was obtained from Holland et al. (1989) (Table 2). Every individual's measurement was converted to a weight by the regression equation for that species.

Table 1. Mean sediment content in each stratum.

STRATUM	% SAND	% SILT	% CLAY
A	61.7	13.6	22.8
B	19.9	33.4	46.7
C	7.3	38.0	54.5
D	22.0	28.7	48.8

Acteocina canaliculata

From the size-frequency histograms for *A. canaliculata* three cohorts were observed during the study period. This is best displayed in the size-frequency histograms for strata B and C (Figure 5). Cohort I was evident only in stratum B on June 23. Cohort II was present throughout the study at all strata and is the focus of the abundance, individual weight, growth and production estimates. Cohort III appeared first in stratum B on August 15 and later appeared in other stratum. The individuals from cohorts I and III were present in low numbers and were not used in any abundance, mean individual weight, growth or production estimates. *A. canaliculata* shell length ranged from 0.98 mm to 3.25 mm.

A. canaliculata was observed with abundances up to 631 individuals m^{-2} (Figure 6). Stratum D had the lowest overall abundance of any stratum which may have affected growth and production estimates for this stratum. Peak abundance of was recorded for strata A, B, and C on the 21 July sample date. Strata B and C consistently had higher abundance then strata A or D. Strata A and D had similar low abundance except for the 21 July peak of stratum A (Figure 6). The abundance of *A. canaliculata* did not follow the cyclical pattern observed in the dissolved oxygen record for the York River and was comparable to abundances found in other Chesapeake Bay studies (Holland *et al.* 1989). ANOVA was used to test the difference in mean *A. canaliculata* abundance, a significant difference was

Table 2.   Regression equations of the five dominant species.   AFDW is in mg

and Size is in mm.

SPECIES	EQUATION	r^2	NOTES
Acteocina canaliculata	$[\log_{10}]$ AFDW = 2.0 + 3.58 $[\log_{10}]$ Size	0.98	Holland *et al.* 1988
Sigambra tentaculata	$[\log_{10}]$ AFDW = -0.5370 + 3.23 x $[\log_{10}]$ Size	0.96	this study
Glycinde solitaria	$[\log_{10}]$ AFDW = 0.0804 + 5.43 x $[\log_{10}]$ Size	0.96	this study
Paraprionospio pinnata	$[\log_{10}]$ AFDW = -0.0762 + 4.53 x $[\log_{10}]$ Size	0.95	this study
Leitoscoloplos fragilis	$[\log_{10}]$ AFDW = 0.1380 + 4.45 x $[\log_{10}]$ Size	0.93	this study

Figure 5.   Size-frequency histograms for *Acteocina canaliculata* during the
sampling period. Midpoints (mm) of the size intervals are: 1- 1.07,
2- 1.40, 3- 1.72, 4- 2.06, 5- 2.38, 6- 2.70, 7- 3.02.   Cohorts are
labeled I, II, and III and are divided by bold vertical lines.
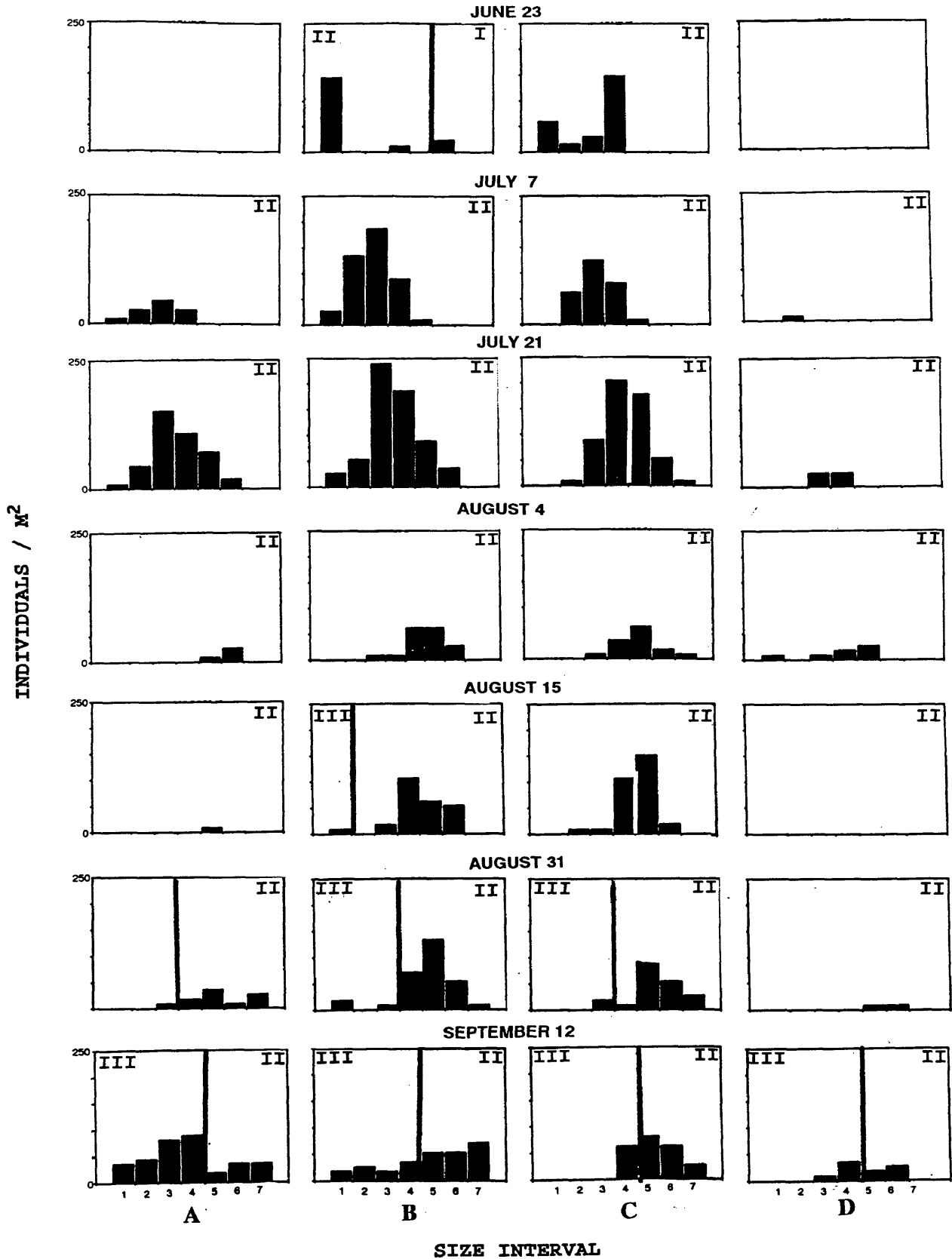
Acteocina canaliculata

JUNE 23 / JULY 7 / JULY 21 / AUGUST 4 / AUGUST 15 / AUGUST 31 / SEPTEMBER 12

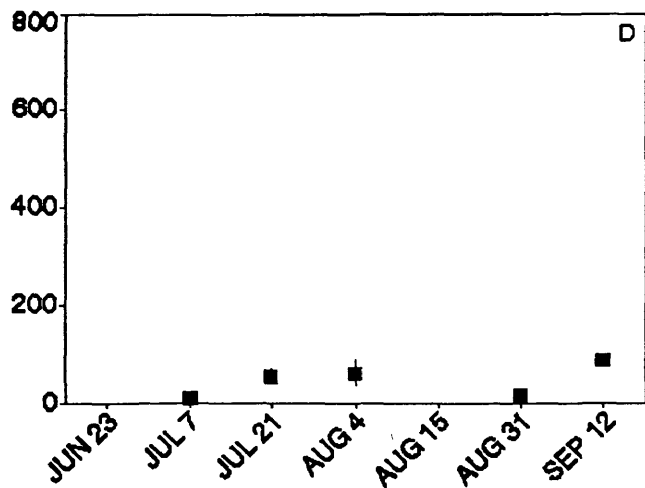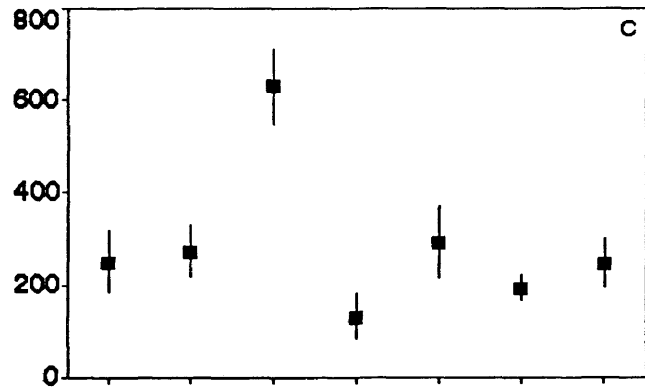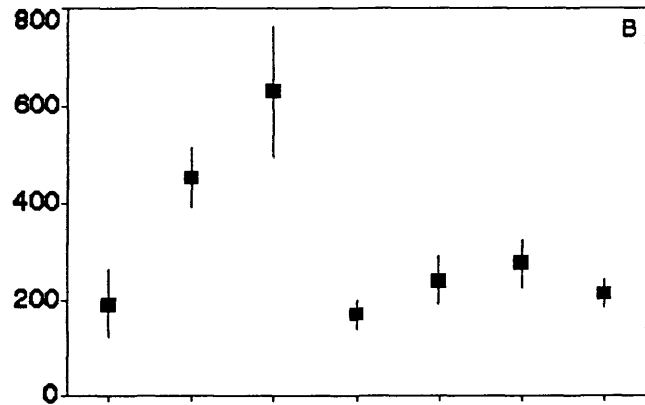INDIVIDUALS / M²

SIZE INTERVAL

A   B   C   D
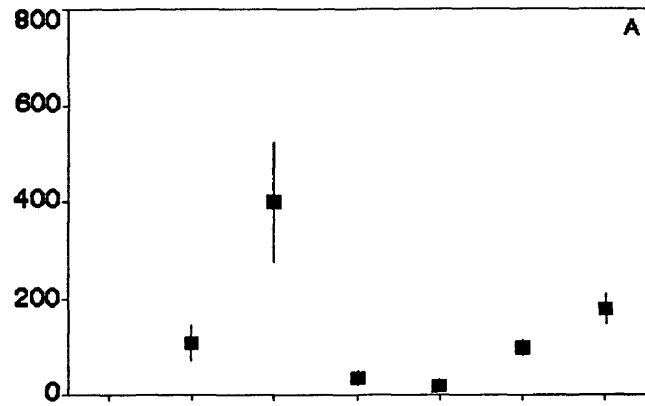
Figure 6.   Mean abundance of *Acteocina canaliculata* by stratum through time.

seen in mean abundance at p < 0.05 (Table 3). The difference was due to the consistently low abundance of stratum D.

The mean individual weight of *A. canaliculata* was similar for all strata with the exception of stratum D on the 15 August sample date when no individuals were collected (Figure 7). There is no clear relationship between the dissolved oxygen record for the York River and the mean individual weight of *A. canaliculata*. The general trend of an increase in mean weight during the course of the sample period was observed for *A. canaliculata*. The mean weight of each stratum was compared using an ANOVA. No significant difference was observed at p < 0.05 (Table 3).

Specific growth of *A. canaliculata* was determined by calculating the change in mean individual weight between two successive time intervals and dividing by the number of days during the interval (Figure 8). The unit of specific growth is mg AFDW individual^{-1}day^{-1}. *A. canaliculata* growth for stratum A was variable during the sample period and ranges from -0.0065 mg AFDW individual^{-1}day^{-1} from 4 Aug. to 15 Aug. to 0.0032 mg AFDW individual^{-1}day^{-1} during the 21 July to 4 Aug. interval. For stratum B, the specific growth ranged from 0.0007 mg AFDW individual^{-1}day^{-1} from 15-31 Aug. to 0.0099 mg AFDW individual^{-1}day^{-1} from 31 Aug. to 12 Sept. Growth of *A. canaliculata* in stratum C was variable, with three intervals showing positive growth and three intervals showing negative growth. The range in growth

Table 3. ANOVA results for *Acteocina canaliculata*

TEST	SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
ANOVA mean abundance vs. stratum	STRATUM	430241.948	3	143413.983	7.468	0.001
	ERROR	460917.362	24	19204.89		
ANOVA mean individual weight vs. stratum	STRATUM	0.079	3	0.026	4.703	0.01
	ERROR	0.134	24	0.006		

Figure 7.   Mean individual weight (+/- SE) of *Acteocina canaliculata* by stratum

through time.

Weight (mg AFDW)

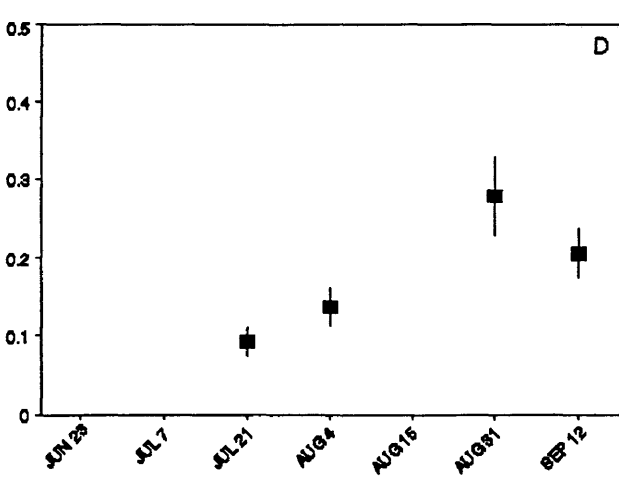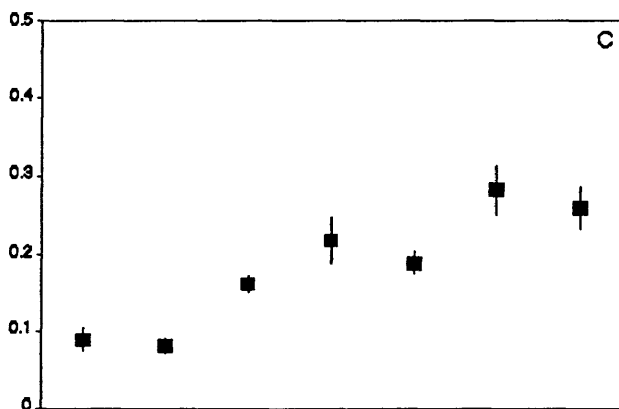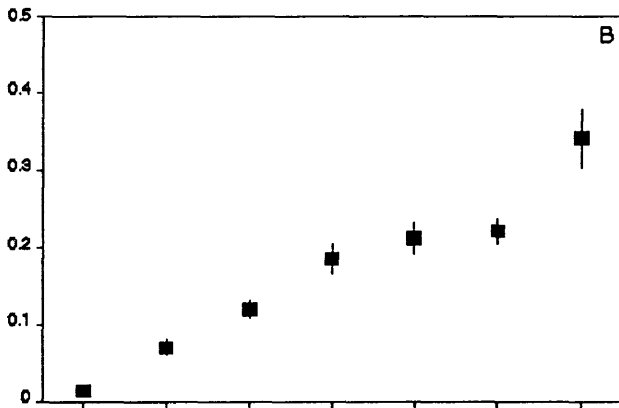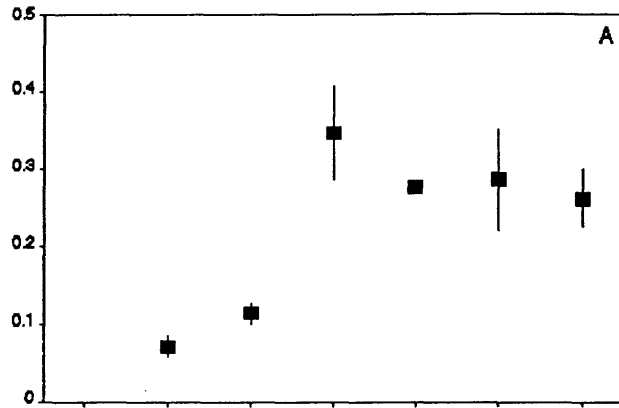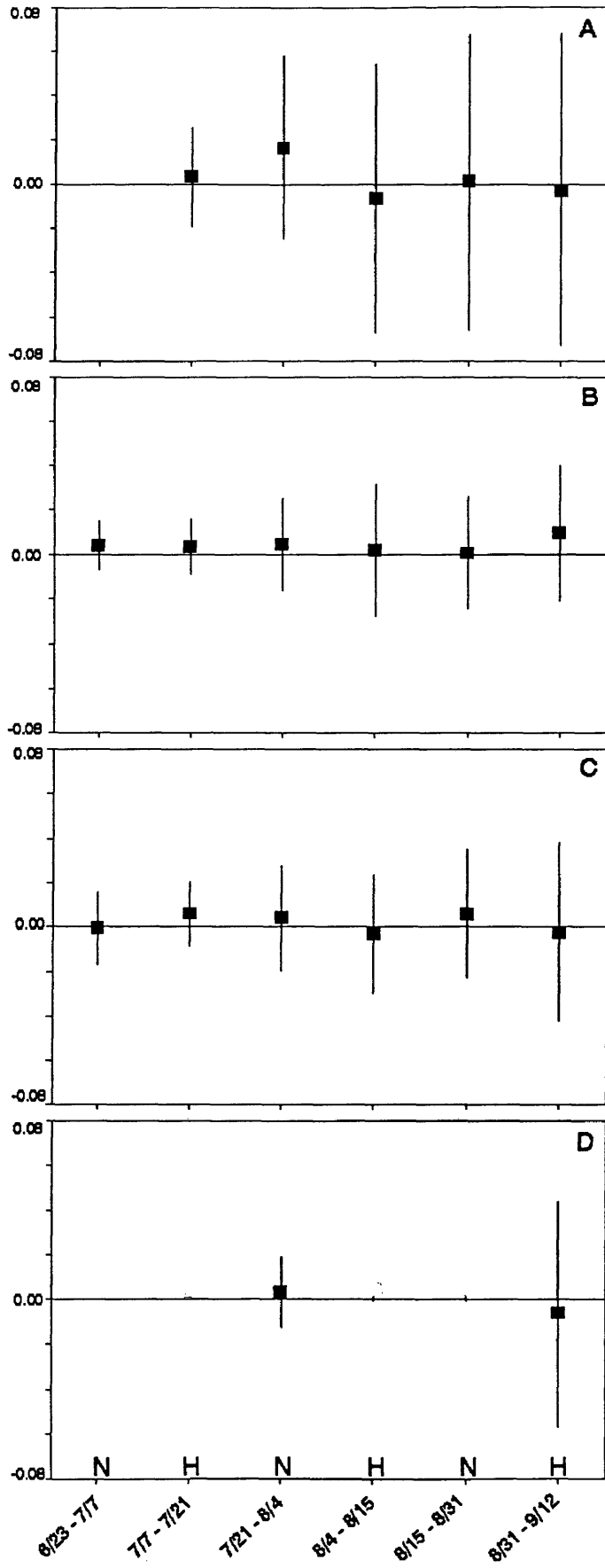Figure 8.   Specific growth of *Acteocina canaliculata* (squares) with estimated high

and low growth (vertical lines) through the sampling period. Intervals

are alternating non-hypoxic **(N)** and hypoxic **(H)** periods as shown in

Figure 3.

was from -0.0027 mg AFDW individual^{-1}day^{-1} from 4-15 Aug. interval, to 0.0059 mg AFDW individual^{-1}day^{-1} from 15 Aug. to 31 Aug. The specific growth of *A. canaliculata* in stratum D was difficult to determine because of the absence of animals on 23 June and 15 August. The growth ranged from -0.0061 mg AFDW individual^{-1}day^{-1} from 31 Aug. to Sept. 12 to 0.0053 mg AFDW individual^{-1}day^{-1} from 4-15 Aug. and 15-31 Aug. intervals.

The instantaneous (daily) production of *A. canaliculata*, measured in mg AFDW m^{-2} day^{-1} was negative for strata A, C, and D during the interval August 4-15 (Figure 9). During this interval the York River experienced hypoxia at strata C, and D (Figure 4). The decrease in instantaneous production coincides with a hypoxic event in the York River, but strata A shows a decrease in instantaneous production even though hypoxia was not recorded. The instantaneous production of *A. canaliculata* does not show a clear relationship with the cyclical nature of the hypoxia in the York River during the summer of 1989. The total production for A. canaliculata over the 82 day sampling period was lowest for stratum D at 8.0 mg AFDW m^{-2} study period^{-1}. Stratum A, B, and C total productions of 57.3, 108.6, and 66.9 mg AFDW m^{-2} study period^{-1} respectively (Figure 10). The low value for stratum D is probably due to the low abundance throughout the sampling period. The total production does not follow the trend of decreasing with increasing depth as may be expected under the observation that hypoxia severity increases with increasing depth.

Figure 9.   Instantaneous production of *Acteocina canaliculata* (squares) with

estimated high and low values (vertical lines) through the sampling

period.   Intervals show alternating non-hypoxic **(N)** and hypoxic **(H)**
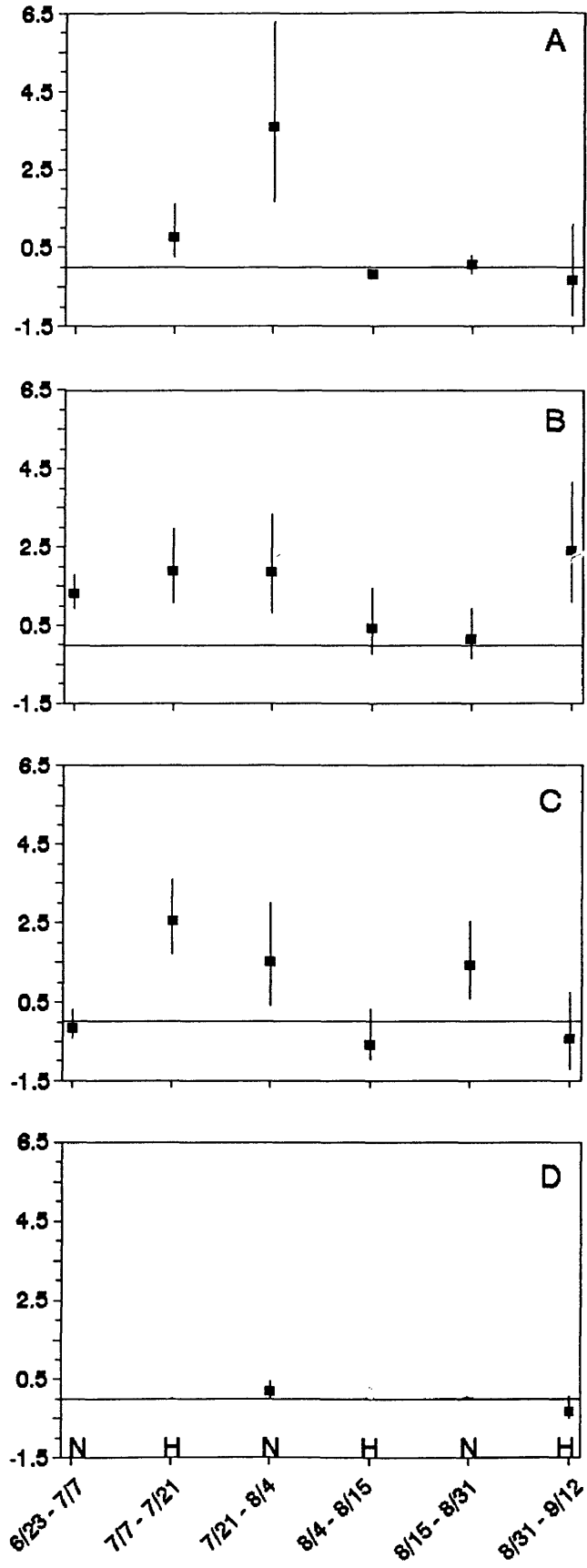
periods as shown in Figure 3.

Figure 10.   Total production (squares) with estimated high and low values (vertical

lines) for *Acteocina canaliculata* for the entire sampling period.
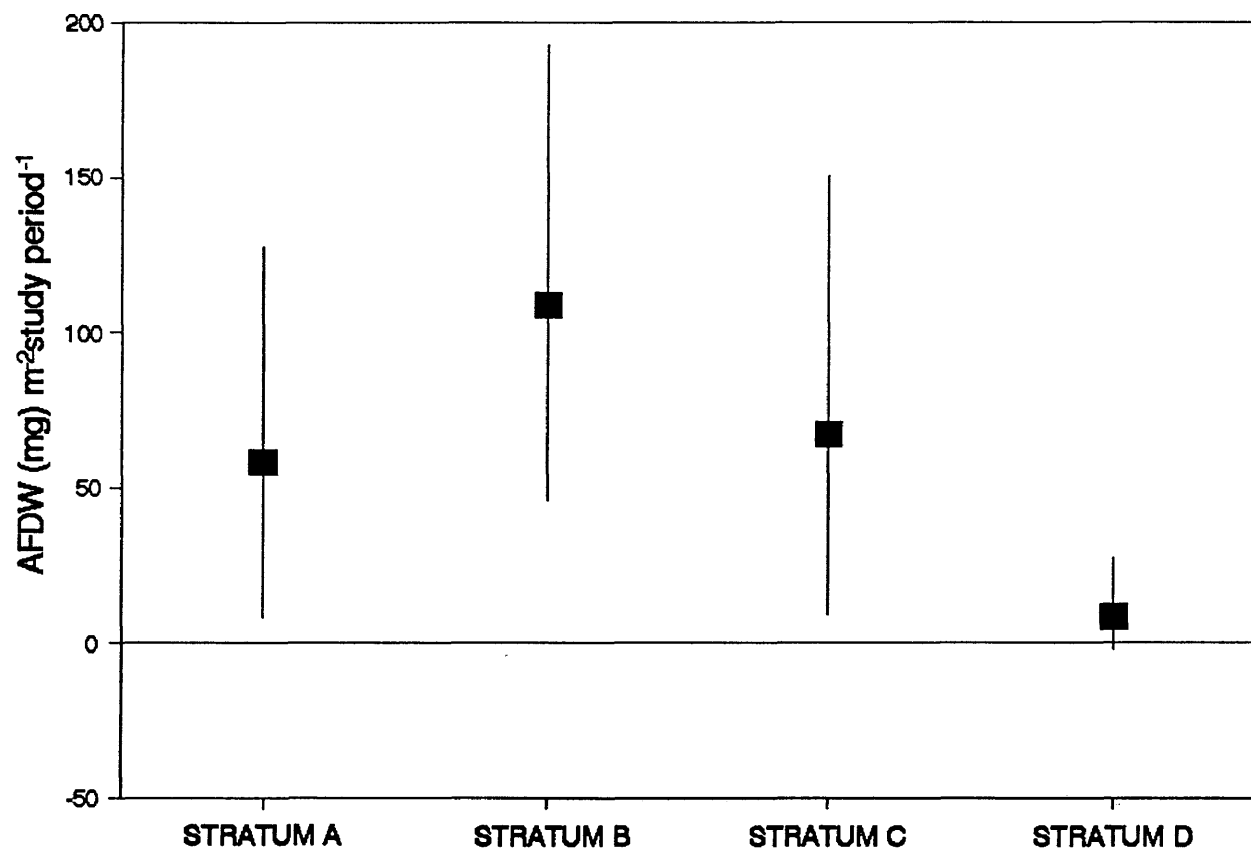
Sigambra tentaculata

In the size-frequency histogram for the pilargid polychaete *Sigambra tentaculata* two cohorts were observed (Figure 11). The first cohort ended sometime in September before the last sample period. The second cohort first appeared in mid-August, a period of low dissolved oxygen. Estimations of growth and production reported are for only the first cohort over the interval from June 23 to August 31. Growth and production of the second cohort is not reported because the cohort was present for only two sample intervals.

Sigambra tentaculata was present at all strata throughout the sampling period, but most abundant at stratum C where on June 23, 415 individuals m^{-2} were recorded (Figure 12). Stratum A had the lowest overall abundance, possibly due to the sandy sediments within that strata. Stratum A had a range in abundance from 99 individuals m^{-2} on June 23 to 27 individuals m^{-2} on August 4. Stratum B had an abundance range of 160 individuals m^{-2} on July 21 to 36 individuals m^{-2} on August 31. Stratum C had 415 individuals m^{-2} on June 23 and ranged to 98 individuals m^{-2} on August 4. Stratum D had a peak abundance of 168 individuals m^{-2} on August 15 and a low abundance of 11 individuals m^{-2} on June 23. There was no cyclic pattern of *S. tentaculata* abundance that would show a relationship between abundance and hypoxic events. The results of an ANOVA show that there was no significant difference in mean abundance between the four strata at $p < 0.05$ (Table 4).

Table 4. ANOVA results for *Sigambra tentaculata*, cohort I.

TEST	SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
ANOVA mean abundance vs. stratum	STRATUM	32962.9	3	10987.6	2.143	0.13
	ERROR	102543.3	20	5126.7		
ANOVA mean individual weight vs. stratum	STRATUM	0.004	3	0.001	0.534	0.664
	ERROR	0.055	20	0.003		

Figure 11.   Size-frequency histograms for *Sigambra tentaculata* during the

sampling period. Midpoints (mm) of the size intervals are: 1- 0.33,

2- 0.46, 3- 0.58, 4- 0.72, 5- 0.84, 6- 0.98, 7- 1.10. Cohorts are labeled

I and II and are divided by bold vertical lines.

Sigambra tentaculata
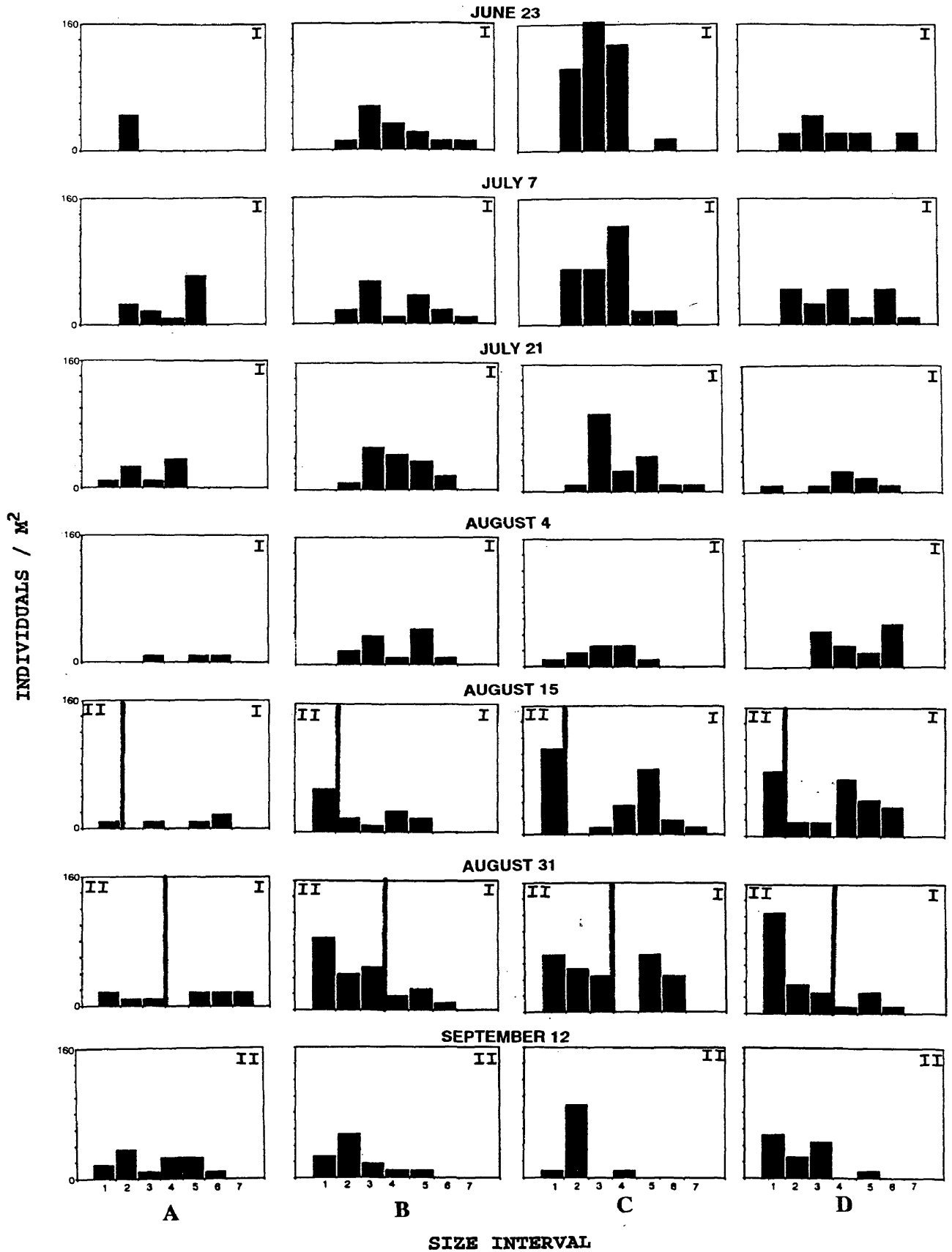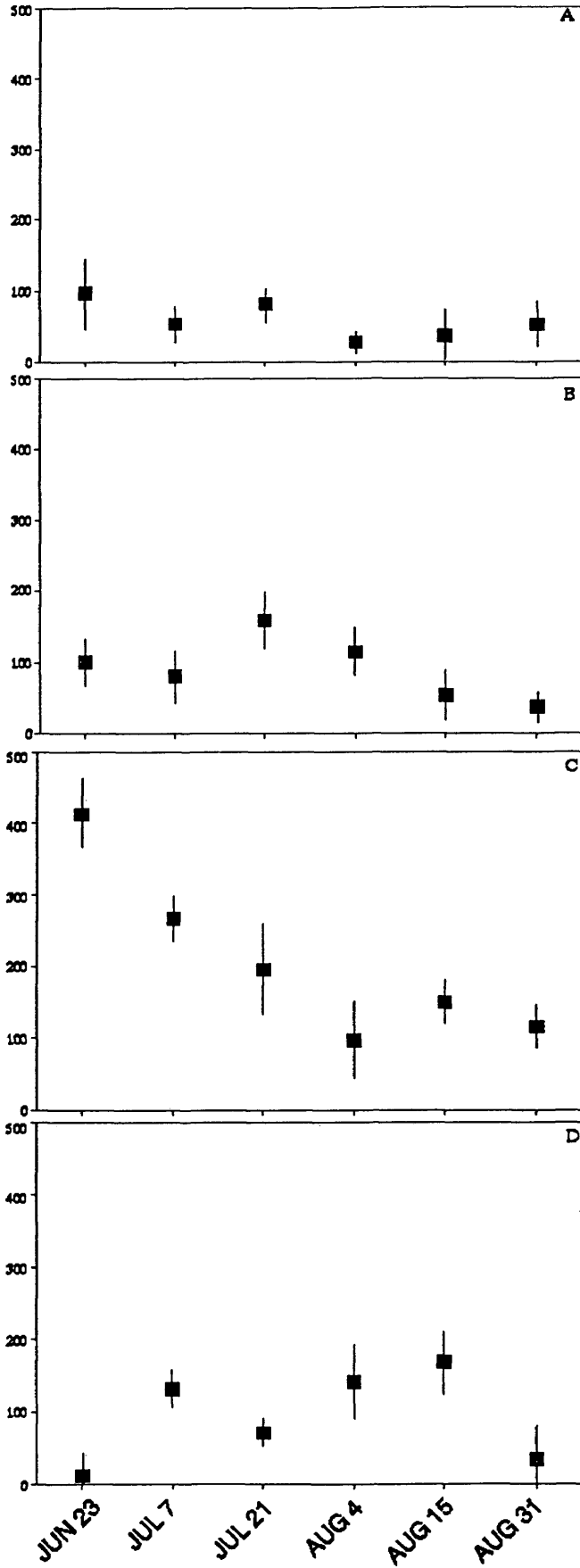
JUNE 23

JULY 7

JULY 21

AUGUST 4

AUGUST 15

AUGUST 31

SEPTEMBER 12

INDIVIDUALS / M²

SIZE INTERVAL

A   B   C   D

Figure 12.   Mean abundance of *Sigambra tentaculata* (+/- SE) by stratum through

time for cohort I.

The mean individual weight of *S. tentaculata* showed a tendency to increase slightly over time for all strata (Figure 13). The lowest mean individual weights for strata A, B, C, and D, were 0.035, 0.123, 0.090, and 0.087 mg (AFDW) respectively. The highest weights recorded for strata A, B, C, and D were 0.312, 0.207, 0.213, and 0.218 mg (AFDW) respectively. *S. tentaculata* mean individual weight did not fluctuate in a cyclic manner as did the oxygen record, there appears to be no obvious relationship between mean individual weight and hypoxia. The results of an ANOVA show that the individual weight was not significantly different at $p < 0.05$ (Table 4).

The growth of the first cohort was variable at all strata through out the sample period, and overall did not show a cyclic pattern similar to the oxygen record (Figure 14). In stratum A, specific growth of *S. tentaculata* varied from a low value of -0.0023 mg AFDW individual^{-1}day^{-1} during Aug 4 - 15 to 0.0075 mg AFDW individual^{-1}day^{-1} during July 21 - Aug. 4. Only during the Aug. 4-15 interval was specific growth of stratum A negative. Specific growth in stratum B varied over the course of the study and was negative for the first three intervals of the study (June 23 to July 7, July 7-21 and July 21 to August 4). In stratum B specific growth ranged from a low of -0.0017 during July 7-21 to a high of 0.0051 mg AFDW individual^{-1}day^{-2} from Aug. 15-31. Stratum C had negative specific growth in one of the five sample periods, the only negative interval was from July 21 to August 4. In stratum C the specific growth range was -0.0022 mg AFDW individual^{-1}day^{-2} during July 21 - August 4 to 0.0087

Figure 13.   Mean individual weight (+/- SE) of *Sigambra tentaculata* cohort I by

stratum through time.

Figure 14.   Specific growth for *Sigambra tentaculata* cohort I (squares) with estimated high and low values (vertical line) through the sampling period.   Intervals are alternating non-hypoxic **(N)** and hypoxic **(H)** periods as shown in Figure 3.

Specific Growth (mg AFDW individual⁻¹ day⁻¹)

y-axis label: Specific Growth (mg AFDW individual^{-1} day^{-1})

Panel labels: A, B, C, D

y-axis values (each panel): 0.022, 0.012, 0.002, -0.008

Treatment labels (panel D): N   H   N   H   N

x-axis labels: 6/23 - 7/7   7/7 - 7/21   7/21 - 8/4   8/4 - 8/15   8/15 - 8/31

mg AFDW individual^{-1} day^{-2} from August 4-15 (a hypoxic period). The deepest stratum, D, had variable specific growth but was comparable in magnitude to the other stratum. There were two sample periods in which negative specific growth was recorded (July 7-21 and August 4-15) both during hypoxic events. In stratum D specific growth range was -0.0015 mg AFDW individual^{-1} day^{-2} from July 7 - 21 to 0.0051 mg AFDW individual^{-1} day^{-2} from June 23 to July 7.

The instantaneous production of *S. tentaculata* was estimated for the first cohort which recruited prior to sampling and existed during the majority of the study. The overall pattern does not follow the cyclic nature of the oxygen record and is different among strata, i.e. all strata do not show decreases or increases over the same intervals (Figure 15). Stratum A instantaneous production for *S. tentaculata* ranged from a low of -0.348 mg AFDW m^{-2}day^{-1} during July 7 - 21 to a high of 0.401 mg AFDW m^{-2}day^{-1} during July 21 to Aug. 4. The instantaneous production of stratum B ranged from -0.199 mg AFDW m^{-2}day^{-1} from July 7-21 to 0.225 mg AFDW m-^{2}day^{-1} from August 15-31. In stratum C, *S. tentaculata* instantaneous production ranged from -0.330 mg AFDW m^{-2}day^{-1} from July 21 - Aug. 4 to 1.07 mg AFDW m^{-2}day^{-1} from August 4 -15. During the August 4 - 15 interval the highest *S. tentaculata* production of any strata during any interval was recorded, this was also a period of low dissolved oxygen in stratum C (Figure 4). In stratum D, the instantaneous production ranged from -0.222 mg AFDW m^{-2}day^{-1} from August 4-15 to 0.367 mg AFDW/m^{2}/day from June 23 - July 7.

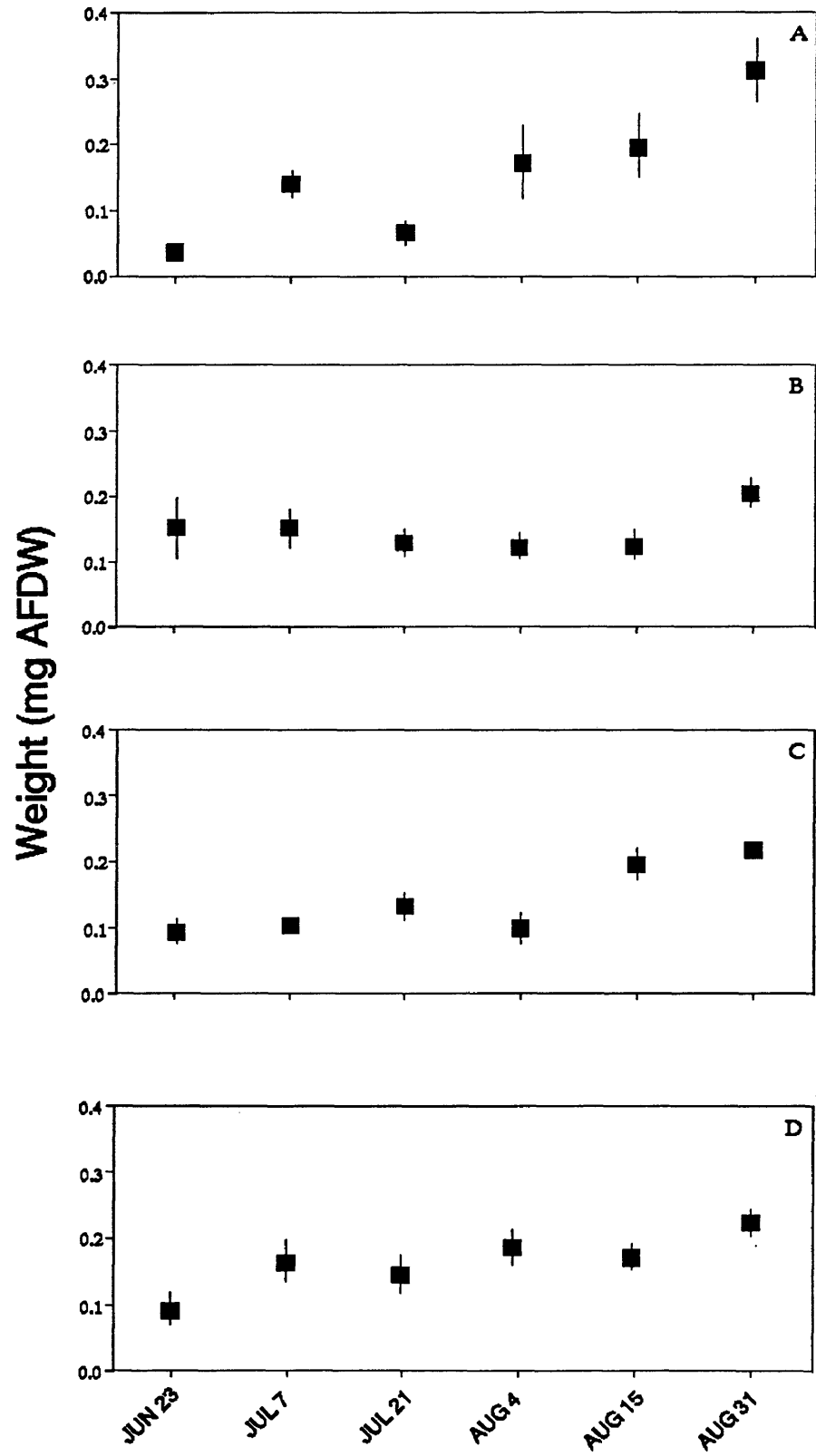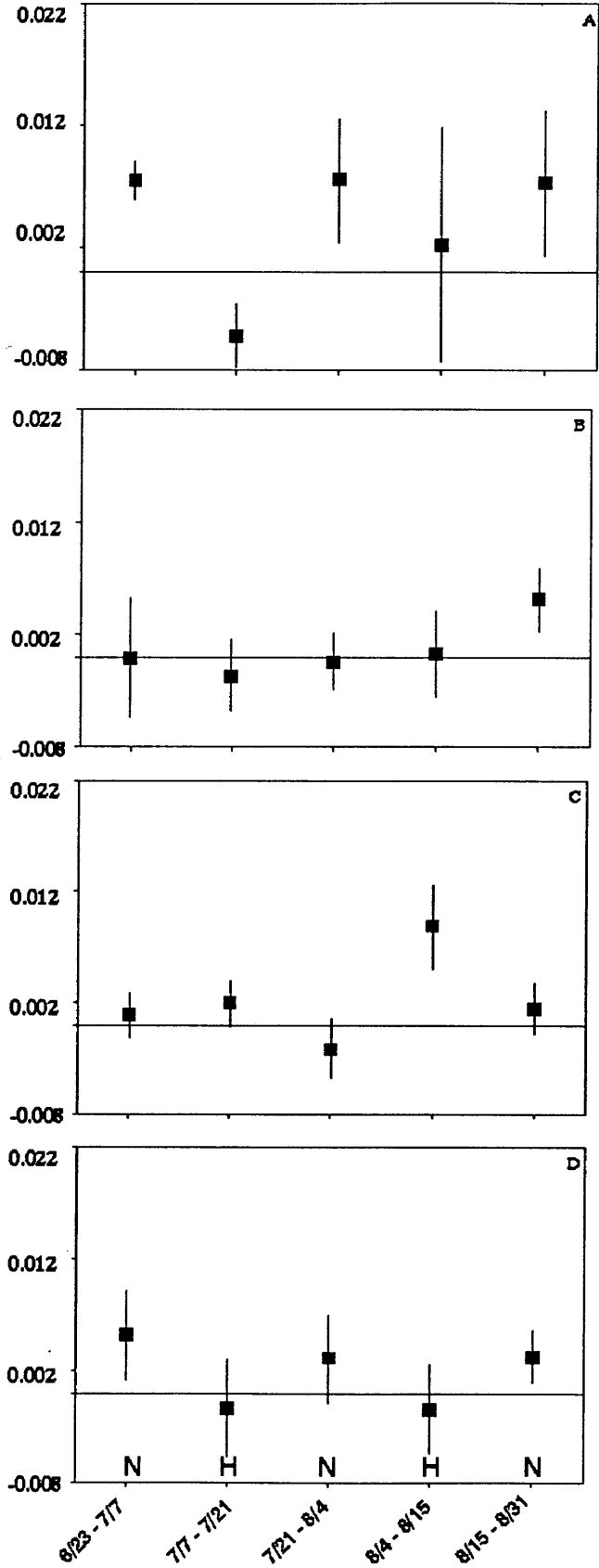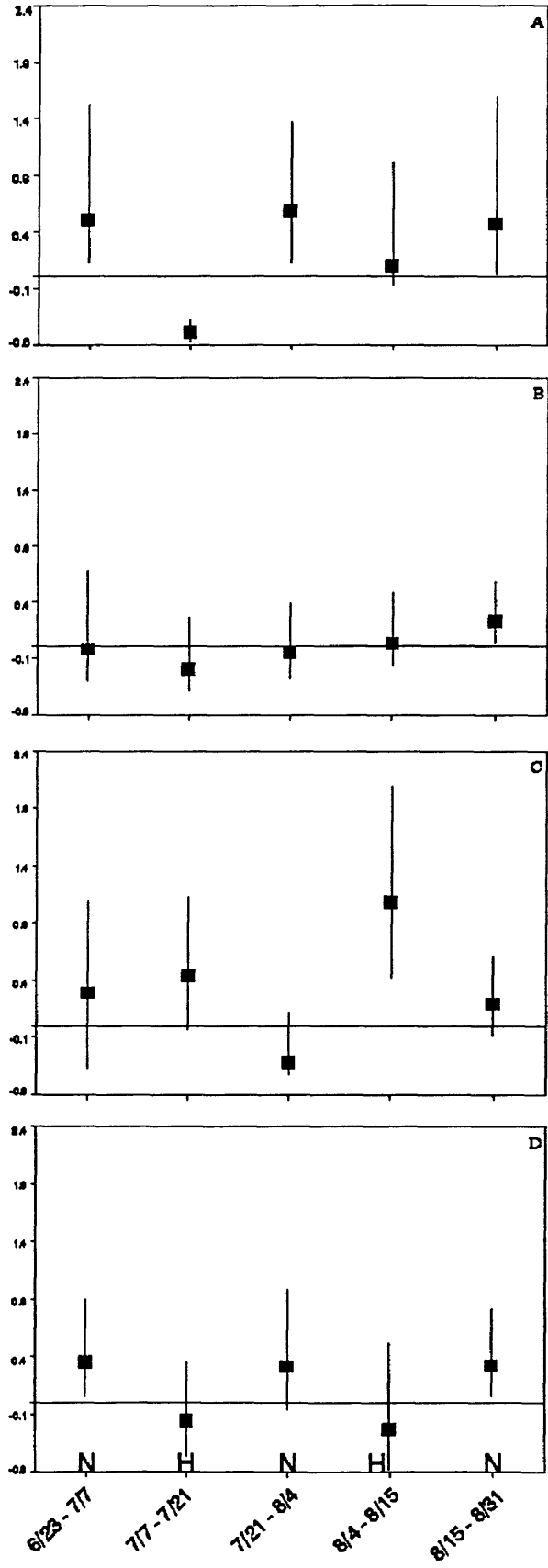Figure 15.   Instantaneous production for *Sigambra tentaculata* cohort I (squares)

with estimated high and low values (vertical lines) during the sampling

period.   Intervals show alternating non-hypoxic **(N)** and hypoxic **(H)**

periods as shown in Figure 3.

Instantaneous production (mg AFDW m⁻² day⁻¹)

The total production of *S. tentaculata* during the study was highest in stratum C at 20.2 mg AFDW m^{-2} study period^{-1} (Figure 16). Among the four strata, this was most similar in magnitude to stratum A which had a total production of 11.8 mg AFDW m^{-2} study period^{-1}. The total production at strata B was zero at 0.3 mg AFDW m^{-2} study period^{-1}. At stratum D total production was 5.3 mg AFDW m^{-2} study period^{-1}. The total production of *S. tentaculata* does not show a relationship with depth which might be expected if hypoxia were influential (i.e. decreasing production with increasing depth).

Paraprionospio pinnata

The spionid polychaete *Paraprionospio pinnata* was the most abundant polychaete over the course of the study. *P. pinnata*, a tubiculous infaunal polychaete, feeds on surface sediments with its paired palps and has also been observed feeding on suspended material by waving palps in the water column (Dauer *et al.* 1981). From observation of the size frequency histogram of *P. pinnata* (Figure 17) it was determined that cohorts were indistinguishable. A recruitment pulse, a large increase in the number of small sized individuals, was observed at strata B, C, and D on August 4 and at stratum A on August 15 (Figure 17).

The abundance of *P. pinnata* in strata B, C, and D, shows a similar pattern with peak abundance on August 15 (Figure 18). Stratum A abundance gradually increased to

Figure 16.   Total production for *Sigambra tentaculata* Cohort I (squares) with estimated high and low values for the entire sampling period.
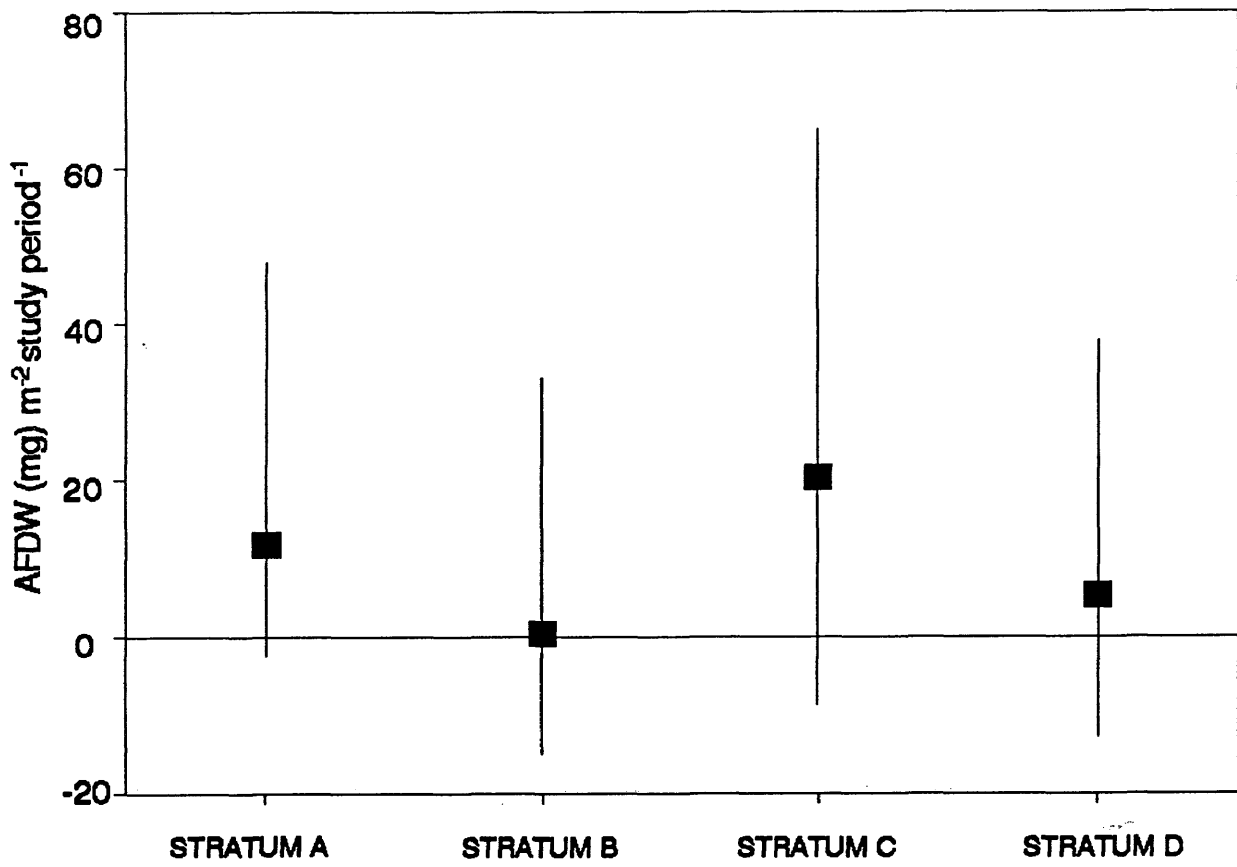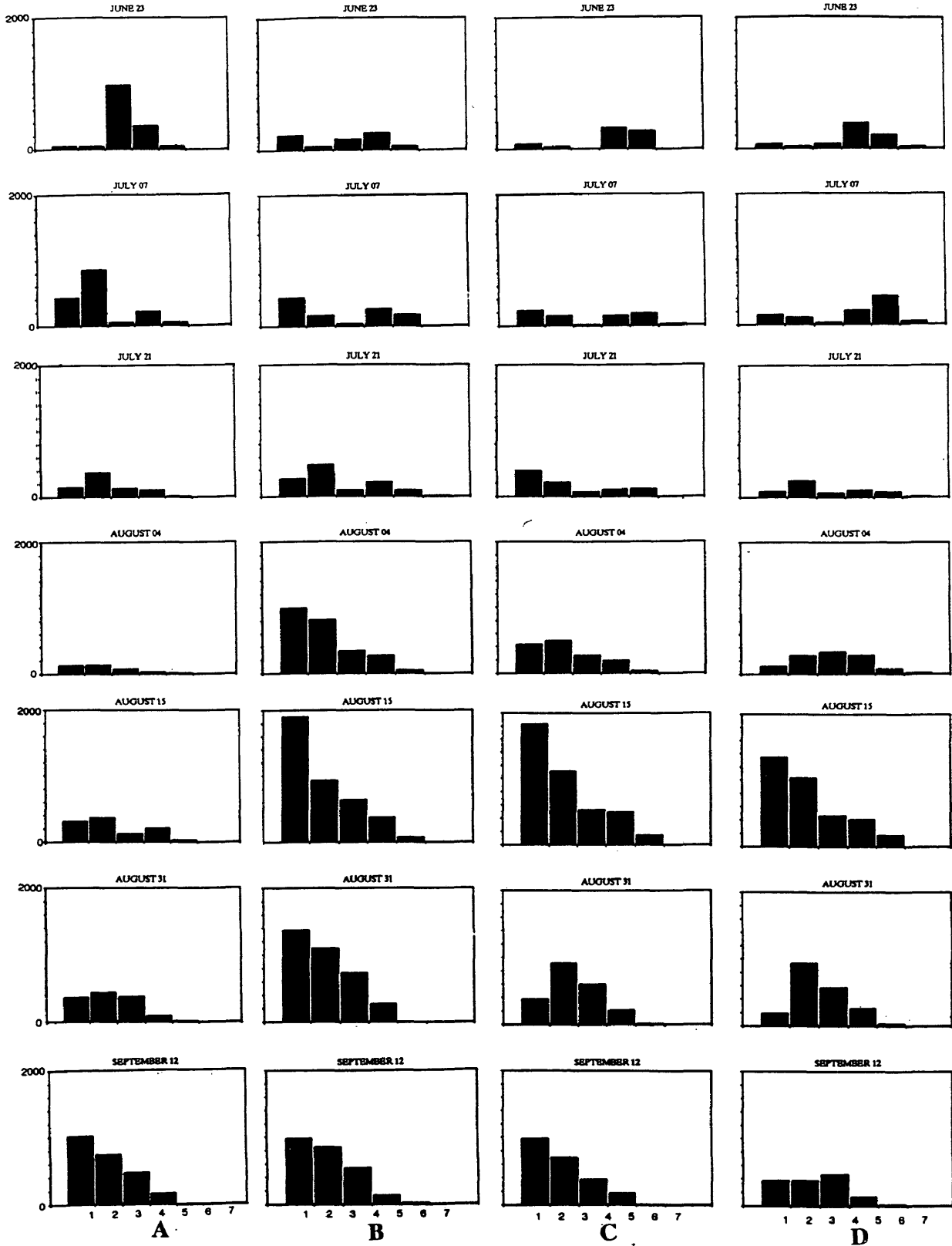
Figure 17.   Size-frequency histogram of *Paraprionospio pinnata* over the sampling

period. Midpoints (mm) of the size intervals are: 1- 0.26, 2- 0.52,

3- 0.78, 4- 1.04, 5- 1.30, 6- 1.56.
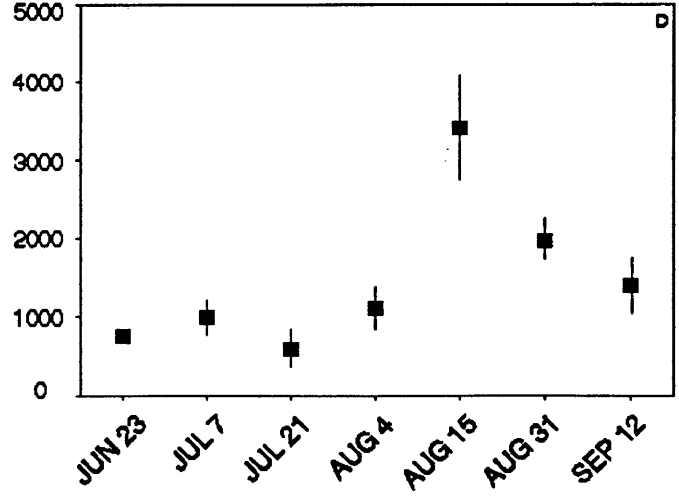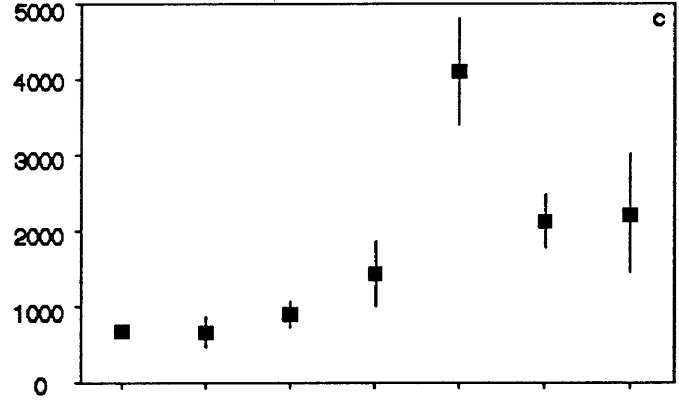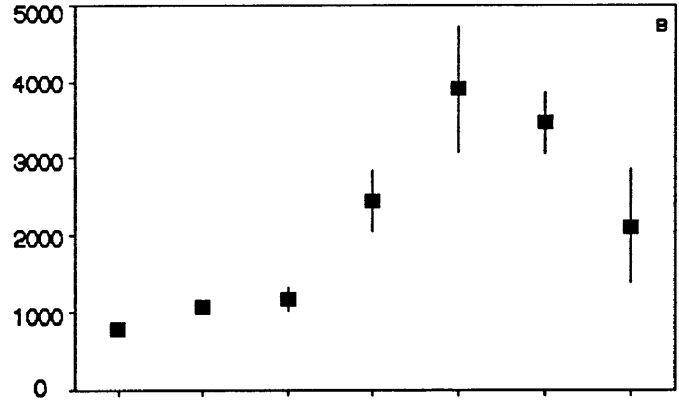
Paraprionospio pinnata

INDIVIDUALS / M²

SIZE INTERVAL

Figure 18.   Mean   abundance   (+/-   SE)   of   *Paraprionospio   pinnata*   by   stratum

through time.
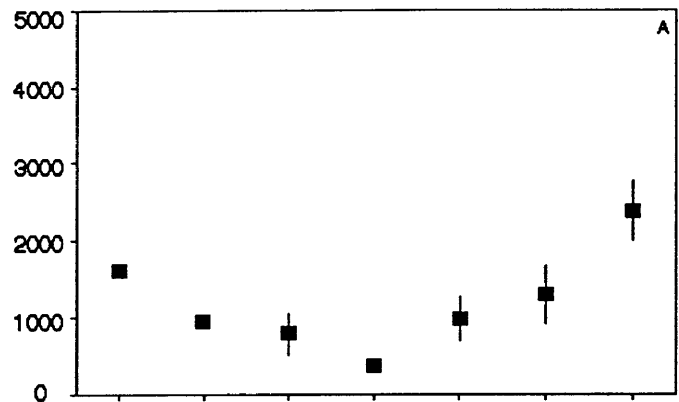
a peak on September 12 (Figure 18). The range of abundance in stratum A was from 373 individuals m^{-2} on August 4 to 2382 individuals m^{-2} on September 12. The range in abundance of stratum B was from 789 individuals m^{-2} on June 23 to 3911 individuals m^{-2} on August 15. In stratum C, *P. pinnata* abundance ranged from 640 individuals m^{-2} on July 7 to 4098 individuals m^{-2} on August 15. Stratum C had the highest abundance of all strata, which occurred during a period when low dissolved oxygen was recorded. *P. pinnata* abundance in stratum D ranged from 596 individuals m^{-2} on July 21, to 3413 individuals m^{-2} on August 15. On August 15, when the peak abundance was recorded in stratum D, hypoxia was also recorded in the stratum (Figure 4). The results of an ANOVA testing the difference in abundances of the four strata show no significant difference at $p < 0.05$ (Table 5).

Overall the mean individual weight of *P. pinnata* decreased by the end of the study at all strata (Figure 19). *P. pinnata* individual weight does not show any clear relationship with the cyclical low dissolved oxygen of the York River. The mean individual weight of stratum A ranged from a high of 0.65 mg AFDW on June 23 to a low of 0.15 mg AFDW on September 12. The range of *P. pinnata* mean individual weight of stratum B was 0.80 mg AFDW on July 7 to 0.16 mg AFDW on September 12. In stratum C the mean individual weight ranged from 1.64 mg AFDW on June 23 to 0.16 mg AFDW on September 12. In stratum D the mean individual weight peaked on July 7 at 1.83 mg AFDW and ranged to 0.27 mg AFDW on September 12.

Table 5. ANOVA results for *Paraprionospio pinnata*.

	SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO
Mean abundance vs. stratum	STRATUM	0.3645×10^7	3	0.1215×10^7	1.1010
	ERROR	0.2649×10^8	24	0.1104×10^7	
mean individual weight vs. stratum	STRATUM	1.292	3	0.431	2.156
	ERROR	4.974	24	0.20	

Figure 19.   Mean individual weight (+/- SE) for *Paraprionospio pinnata* by stratum

through time.
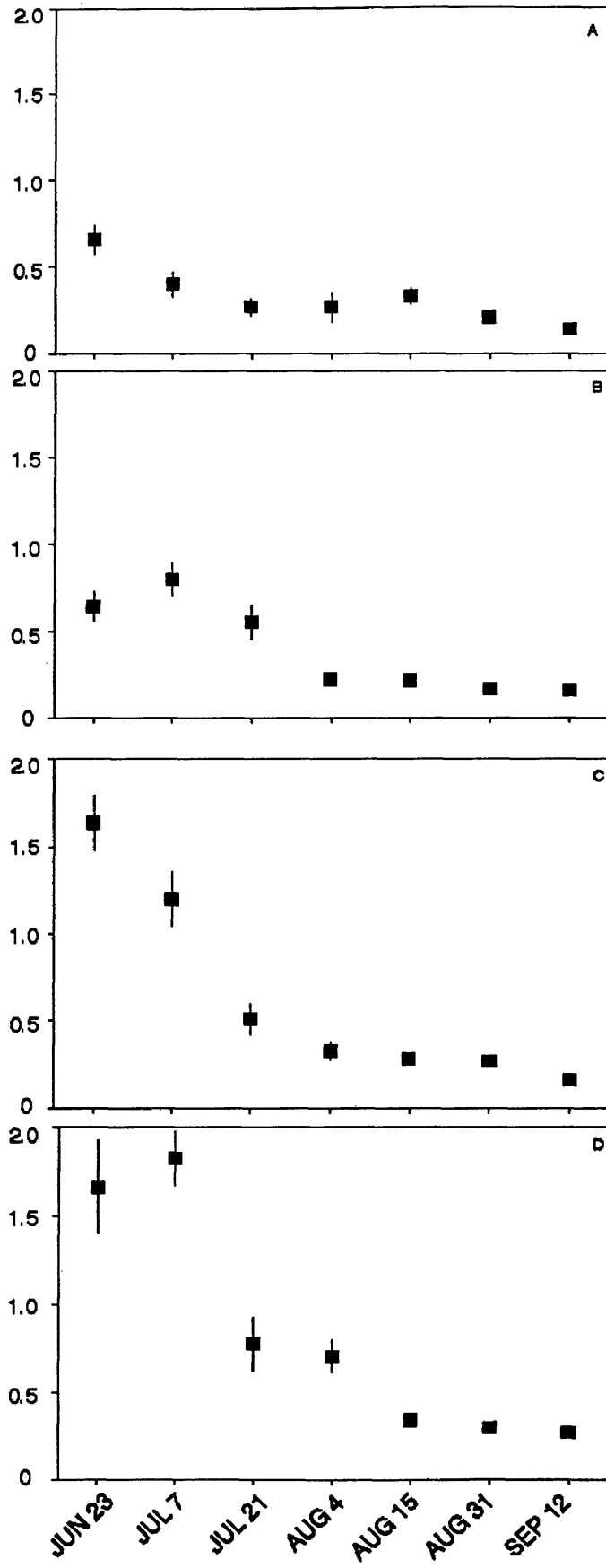
The results of an ANOVA show that there was no significant difference in the mean individual weight of the four strata, $p < 0.05$ (Table 5).

Because cohorts were not distinguishable, the size-frequency method was employed to estimate production. With the size-frequency method, all individuals collected throughout the entire study are combined to estimate production therefore an estimation of growth or instantaneous production is not possible. The total production during the entire 82 day sampling period is shown in Figure 20. The values of production at strata A, B, C, and D are 253.6, 1527.0, 480.6, and 181.9 mg AFDW m^{-2} study period^{-1}.

Glycinde solitaria

Glycinde solitaria, is an infaunal polychaete belonging to the family Goniadidae and is probably carnivorous (Fauchald and Jumars 1979). The size-frequency histograms of Glycinde solitaria do not show distinguishable cohorts (Figure 21). The abundance of G. solitaria was variable at all strata and does not show any consistent pattern across time (Figure 22). The abundance at strata A ranged from 0 individuals on June 23 to 533 individuals m^{-2} on Sept. 12. The abundance at strata B ranged from 258 individuals m^{-2} on July 21 to 778 individuals m^{-2} on June 23. The abundance of G. solitaria at stratum C ranged from 142 individuals m^{-2} on July 7 and September 12 to 373 individuals m^{-2} on August 31. At stratum D abundance ranged from 53 individuals m^{-2} on August 15 to 347 individuals m^{-2} on July 7. The results

Figure 20.   Total production for *Paraprionospio pinnata* for the entire sampling period.
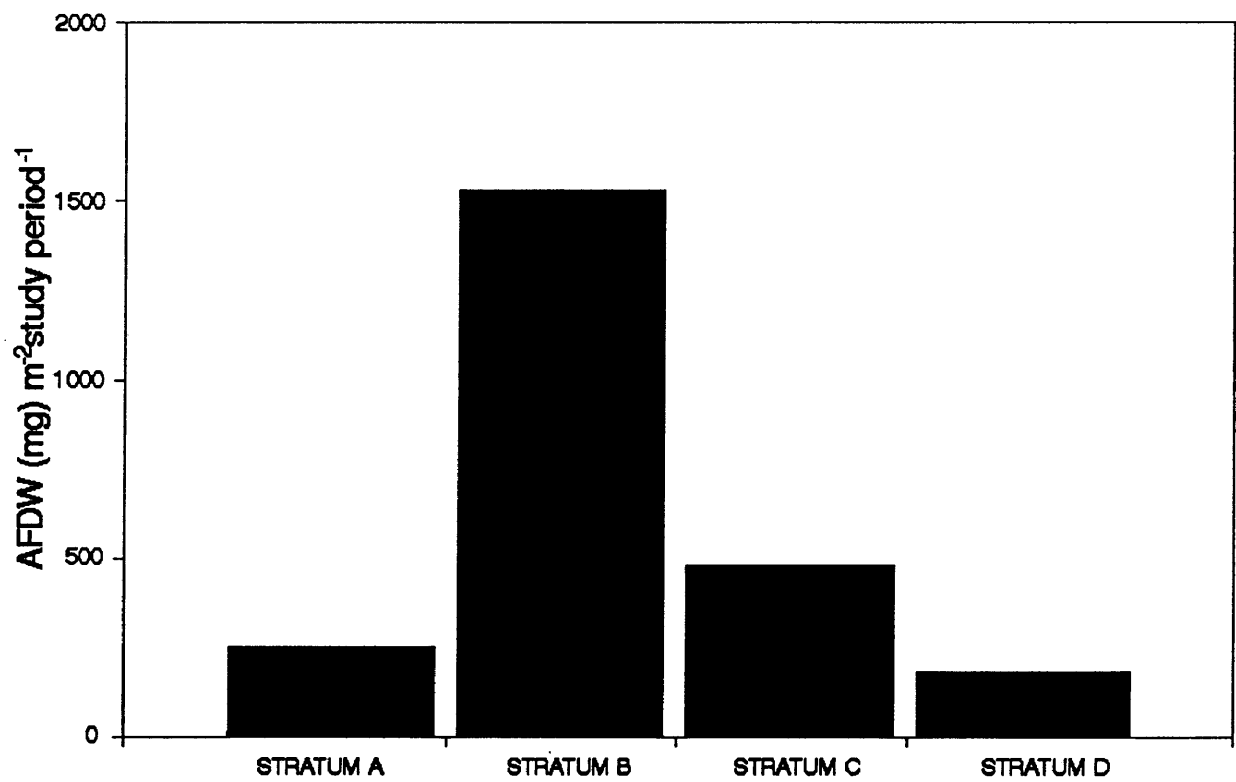
Figure 21.   Size-frequency histograms of *Glycinde solitaria* over the entire

sampling period. Midpoints (mm) of the size intervals are: 1- 0.26,

2- 0.40, 3- 0.52, 4- 0.66, 5- 0.78, 6- 0.96, 7- 1.04.

Glycinde solitaria

INDIVIDUALS /M²

SIZE INTERVAL

A   B   C   D
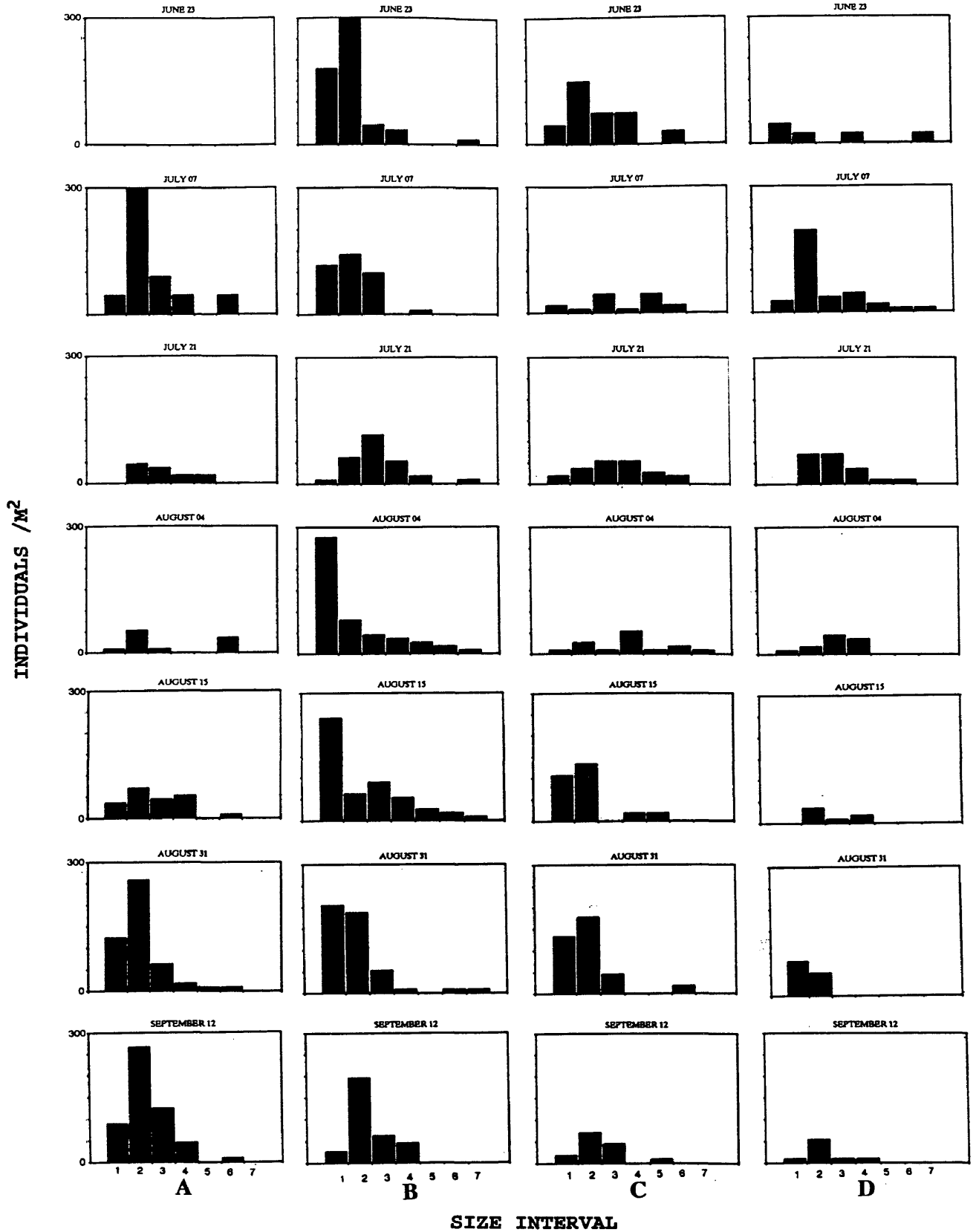
of an ANOVA comparing the abundances of each strata show no significant difference between strata at p < 0.05 (Table 6).

The mean individual weight of *G. solitaria*, like the abundance, does not show any clear pattern across time (Figure 23). At stratum A the mean individual weight ranged from a high of 0.337 mg AFDW individual[-1] on Aug. 4 to a low of 0.039 on Aug. 31. At stratum B the mean individual weight ranged from a high of 0.128 mg AFDW individual[-1] on July 21 to 0.030 mg AFDW individual[-1] on July 7. At stratum C, *G. solitaria* ranged from a high of 0.277 mg AFDW individual[-1] on Aug. 4 to a low of 0.036 mg AFDW individual[-1] on Aug. 15. The range of mean individual weight at stratum D was from 0.241 mg AFDW individual[-1] on June 23 to 0.006 mg AFDW individual[-1] on August 31. The overall pattern of mean individual weight of *G. solitaria* did not show an increase over time as would have been expected for a cohort through time. The results of an ANOVA show no significant difference in the mean weight at each strata, p < 0.05 (Table 6).

The size-frequency method was selected to estimate production. The total production for the entire 82 day sampling period was similar at strata A and D with values of 9.5 and 7.0 mg AFDW m[-2] study period[-1], respectively (Figure 24). Strata B and C had higher production estimates with 15.5 and 20.5 mg AFDW m[-2] study period[-1], respectively.

Table 6. ANOVA results for *Glycinde solitaria*.

TEST	SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO
Mean abundance vs. strata	STRATUM	386839.13	3	128946.38	3.78
	ERROR	818778.27	24	34115.76	
Mean individual weight vs. strata	STRATUM	5.366	3	1.789	0.886
	ERROR	48.471	24	2.020	

Figure 22.   Mean abundance (+/- SE) of *Glycinde solitaria* by stratum through
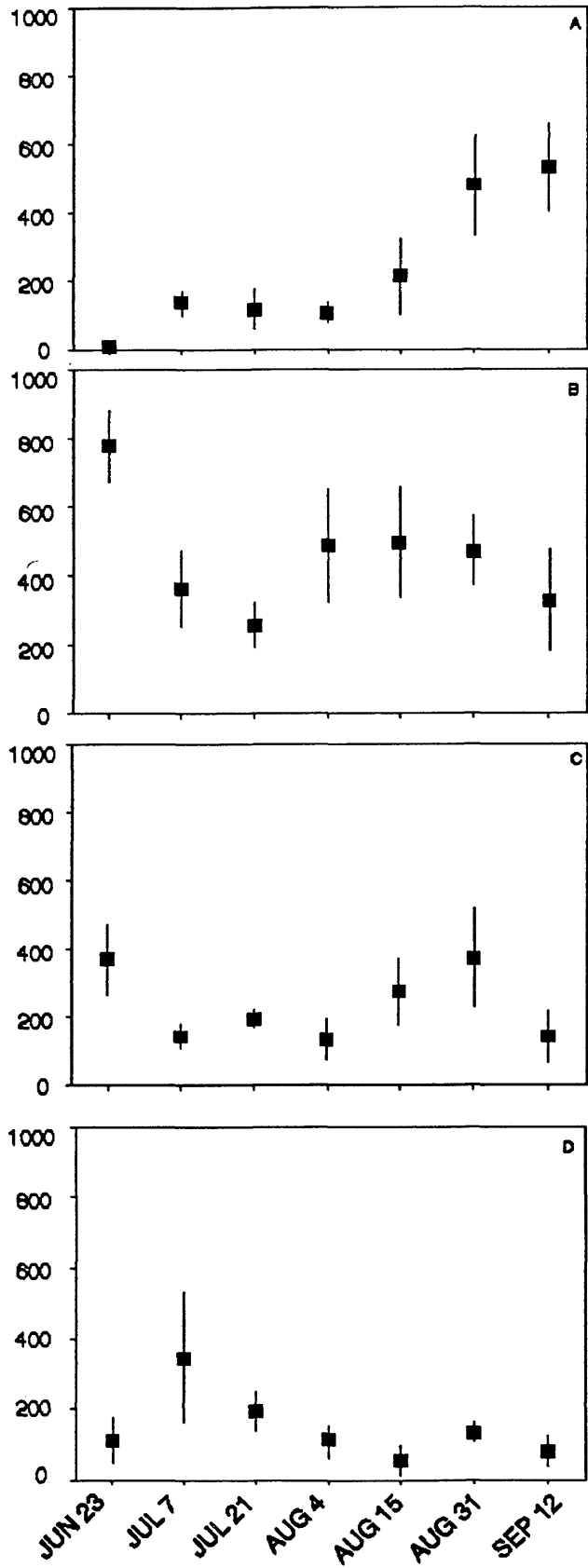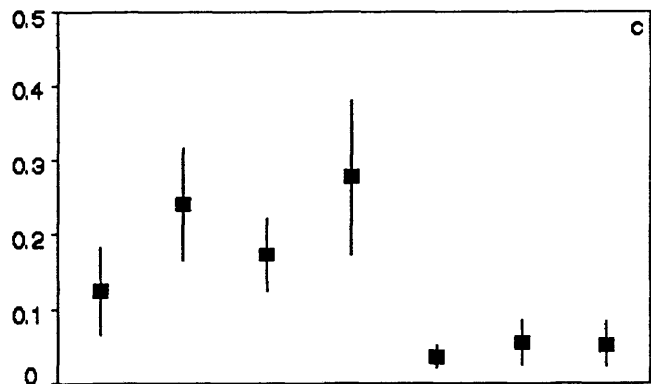
time.

Figure 23.   Mean individual weight (+/- SE) of *Glycinde solitaria* by stratum

through time.
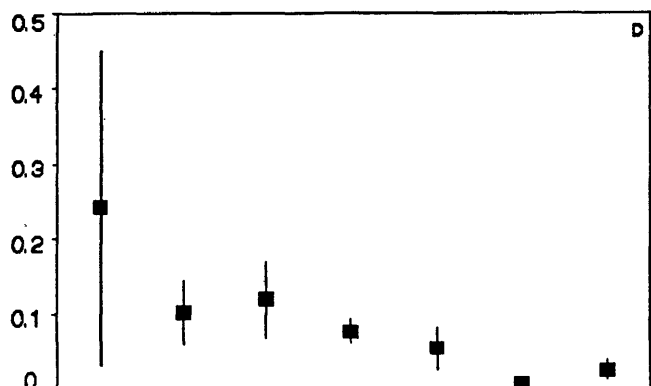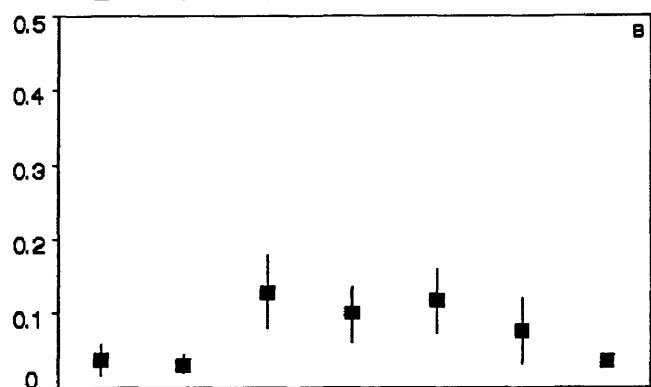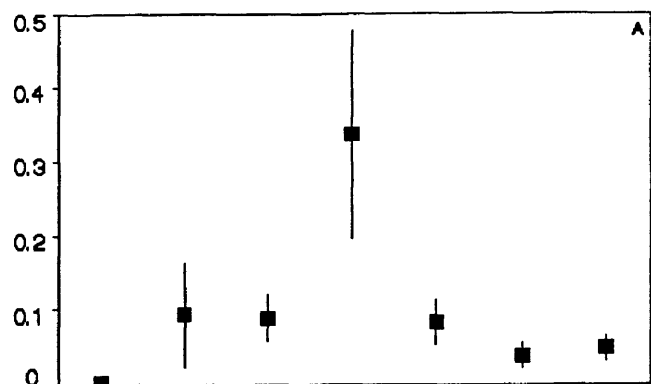
Figure 24.   Total production for *Glycinde solitaria* over the entire sampling period.
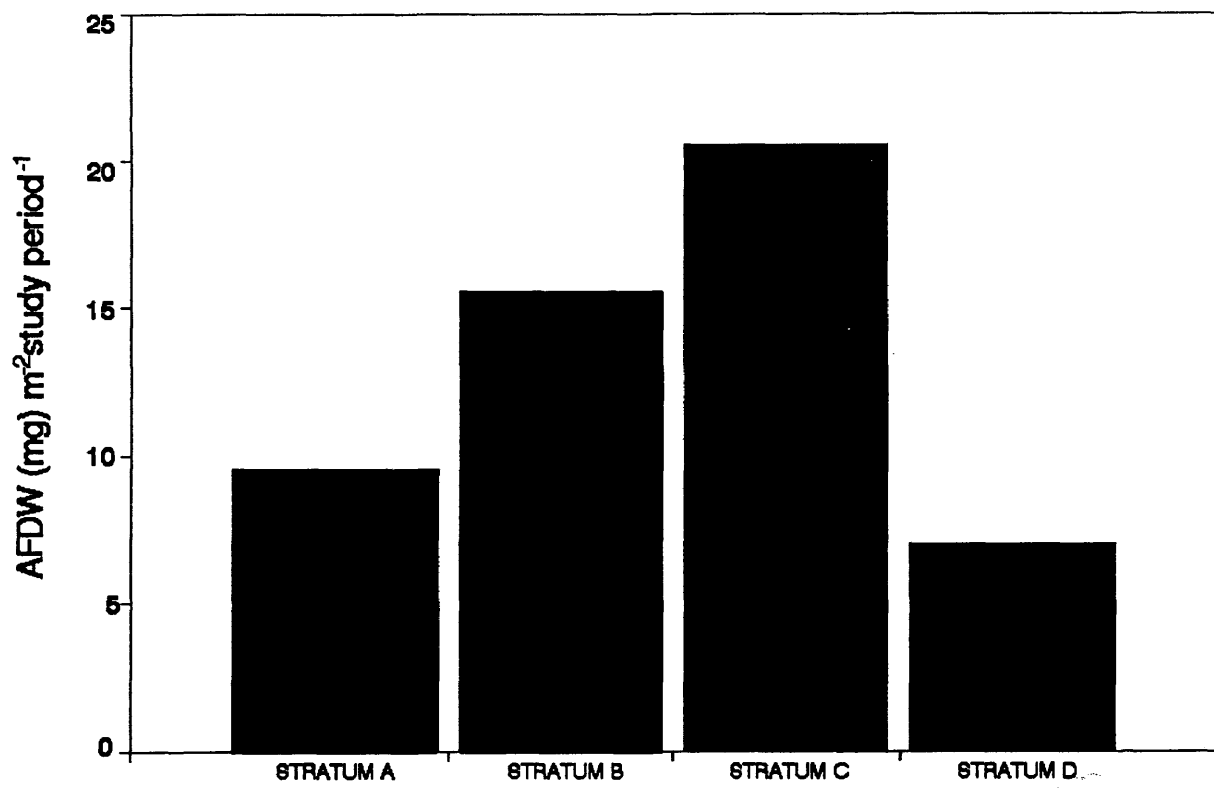
Leitoscoloplos fragilis

Leitoscoloplos fragilis is a free burrowing orbinid polychaete. It is considered a non-selective deposit feeder (Fauchald and Jumars 1979). The size-frequency histograms of *L. fragilis* do not indicate discernable cohorts, possibly because of the low occurrence of individuals in all strata after June 23 (Figure 25). The abundance showed a relative decrease over time at all strata except strata A which was relatively stable over the course of the study (Figure 26). Generally, the abundance of *L. fragilis* was lower then any other polychaete selected for estimation of production. At stratum A, *L. fragilis* had peak abundance on July 21 of 106 individuals m^{-2} and lowest abundance of 27 individuals m^{-2} on September 12. The abundance in stratum B ranged from 478 individuals m^{-2} to 27 individuals m^{-2} on June 23 and September 12 respectively. At stratum C, the abundance ranged from 204 individuals m^{-2} on July 7 to 9 individuals m^{-2} on September 12. At stratum D the abundance ranged from 511 individuals m^{-2} on June 23 to 9 individuals m^{-2} on September 12. The abundance of *L. fragilis* did not show a cyclic pattern as in the oxygen record. The results of an ANOVA show that there is no significant difference between the mean abundances of the four strata, at $p < 0.05$ (Table 7).

The mean individual weight of *L. fragilis* was relatively consistent over time except for an increase in strata A and C on August 31 (Figure 27). At stratum A the lowest weight was recorded on July 21 (0.305 mg AFDW individual^{-1}) and the highest on August 31 (1.16 mg AFDW individual^{-1}). Stratum B was relatively stable in mean

Table 7. ANOVA for *Leitoscoloplos fragilis*.

TEST	SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO
Mean abundance vs. Stratum	STRATUM	122619.7561	3	40873.2520	0.5387
	ERROR	1821080	24	75878.1910	
Mean individual weight vs. stratum	STRATUM	0.117	3	0.039	0.500
	ERROR	1.867	24	0.078	

Figure 25.   Size-frequency histograms of *Leitoscoloplos fragilis* over the entire

sampling period.   Midpoints (mm) of the size intervals are: 1- 0.22,

2- 0.42, 3- 0.62, 4- 0.82, 5- 1.02, 6- 1.22, 7- 1.42.

Leitoscoloplos fragilis

INDIVIDUALS / M²

SIZE INTERVAL

A   B   C   D
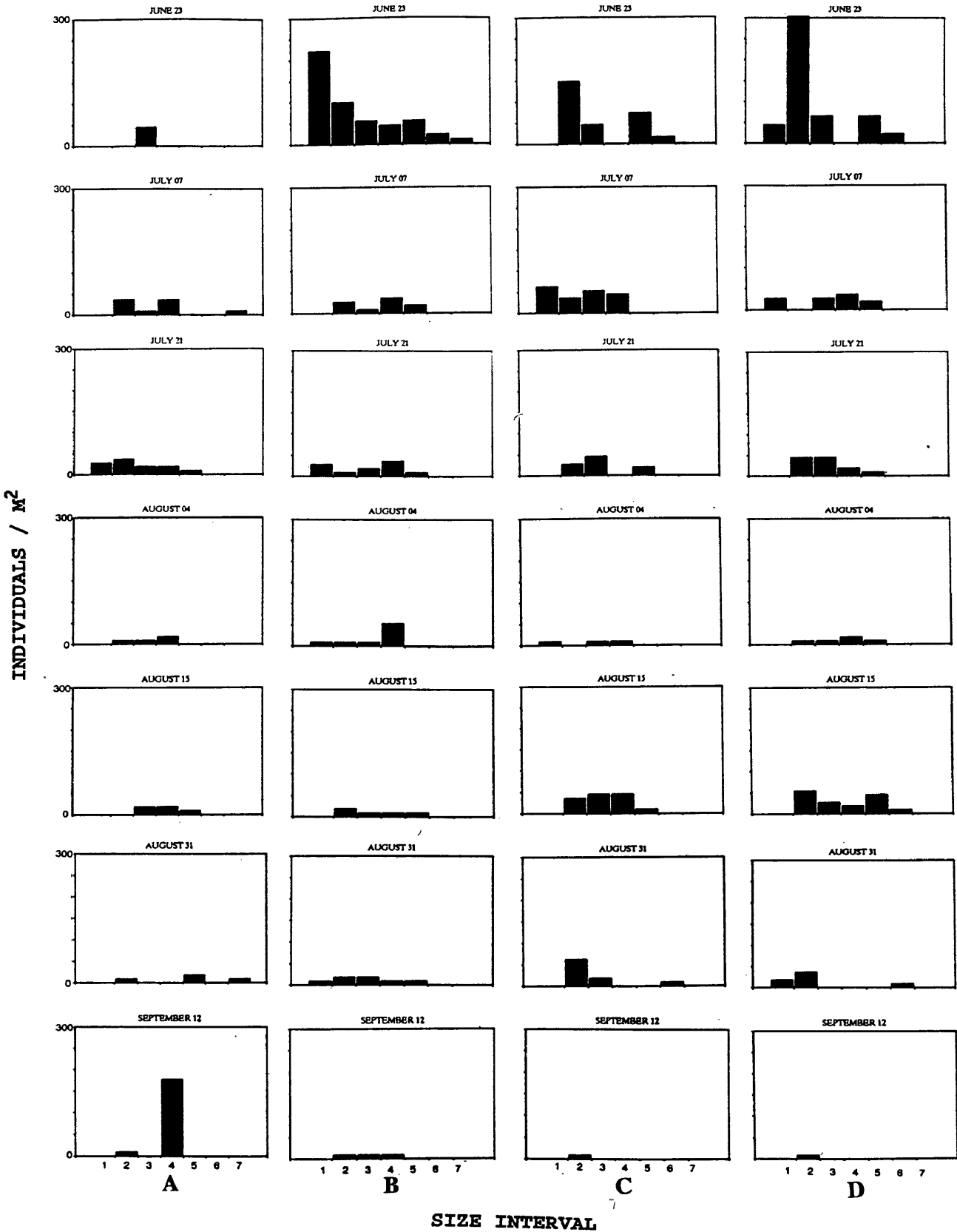
Figure 26.   Mean abundance (+/- SE) of *Leitoscoloplos fragilis* by stratum through
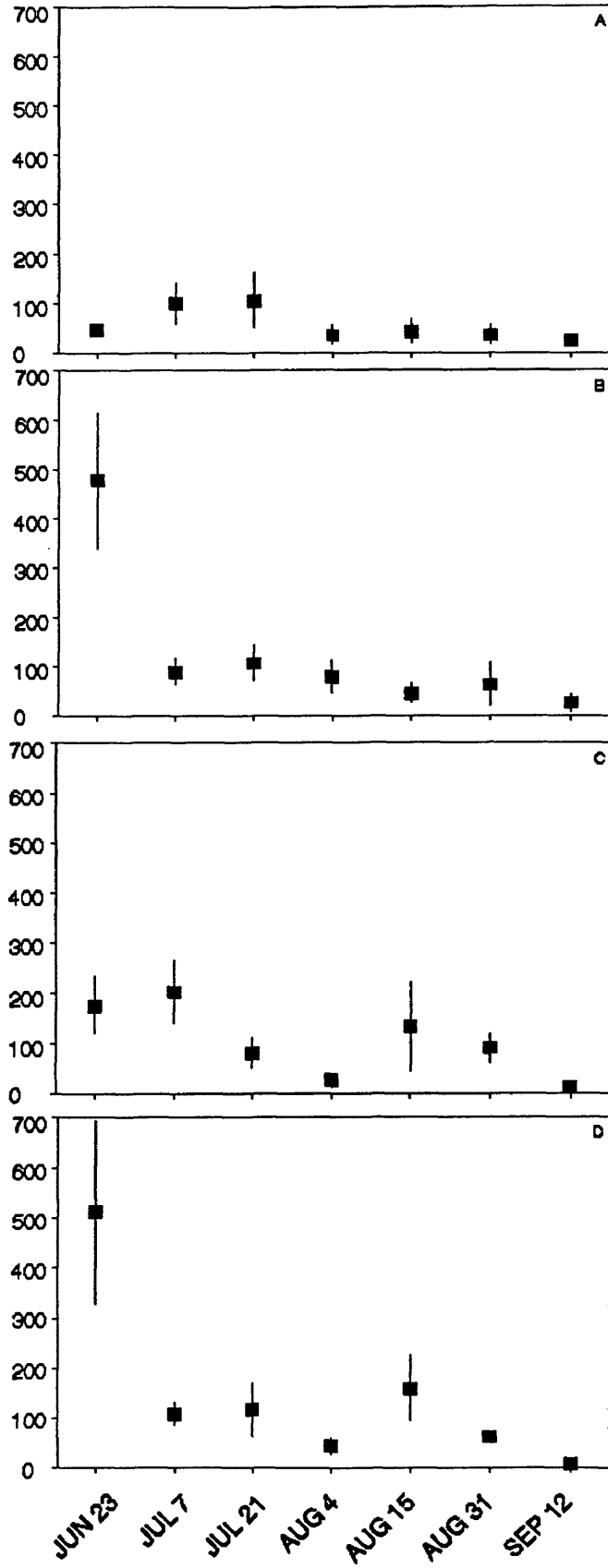
time.

Figure 27.   Mean individual weight (+/- SE) of *Leitoscoloplos fragilis* by stratum

through time.
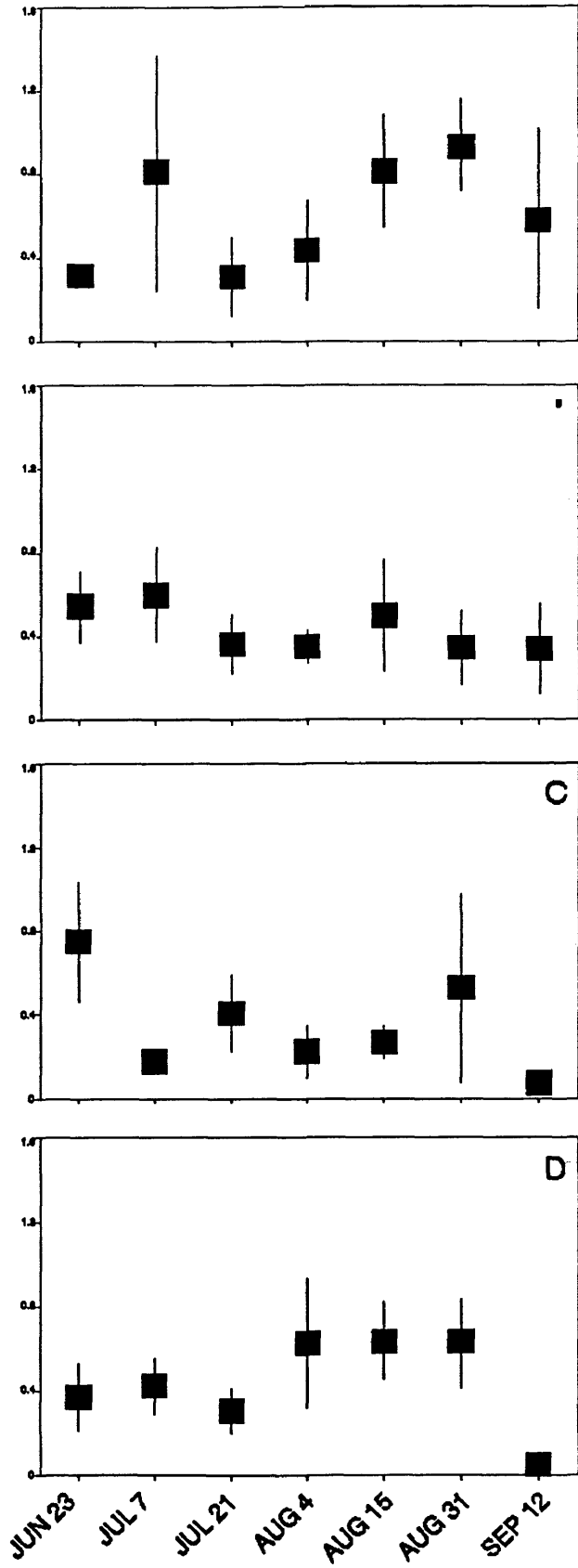
individual weight with a high of 0.600 mg AFDW individual^{-1} on July 7 to a low of 0.342 mg AFDW individual^{-1} on Sept. 12. In stratum C, *L. fragilis* mean individual weight peaked on June 23, and ranged from 0.748 mg AFDW individual^{-1} to 0.075 mg AFDW individual^{-1} on Sept. 12. At stratum D the weight ranged from a high of 0.635 mg AFDW individual^{-1} on August 15 to 0.021 mg AFDW on September 12. In this case, the low abundances found in the samples may have had an effect on the estimate of mean individual weight of *L. fragilis*. The results of an ANOVA show no significant difference in mean weight between the four strata, $p < 0.05$ (Table 7). The size-frequency method of estimating total production was chosen because of the lack of discernable cohorts. The total production of *L. fragilis* increased as depth increased. Total production of *L. fragilis* was 25.1, 45.1, 40.3, and 33.6 mg AFDW m^{-2} study period^{-1} at strata A, B, C, and D, respectively (Figure 28).

Figure 28.   Total Production of *Leitoscoloplos fragilis* over the entire sampling period.
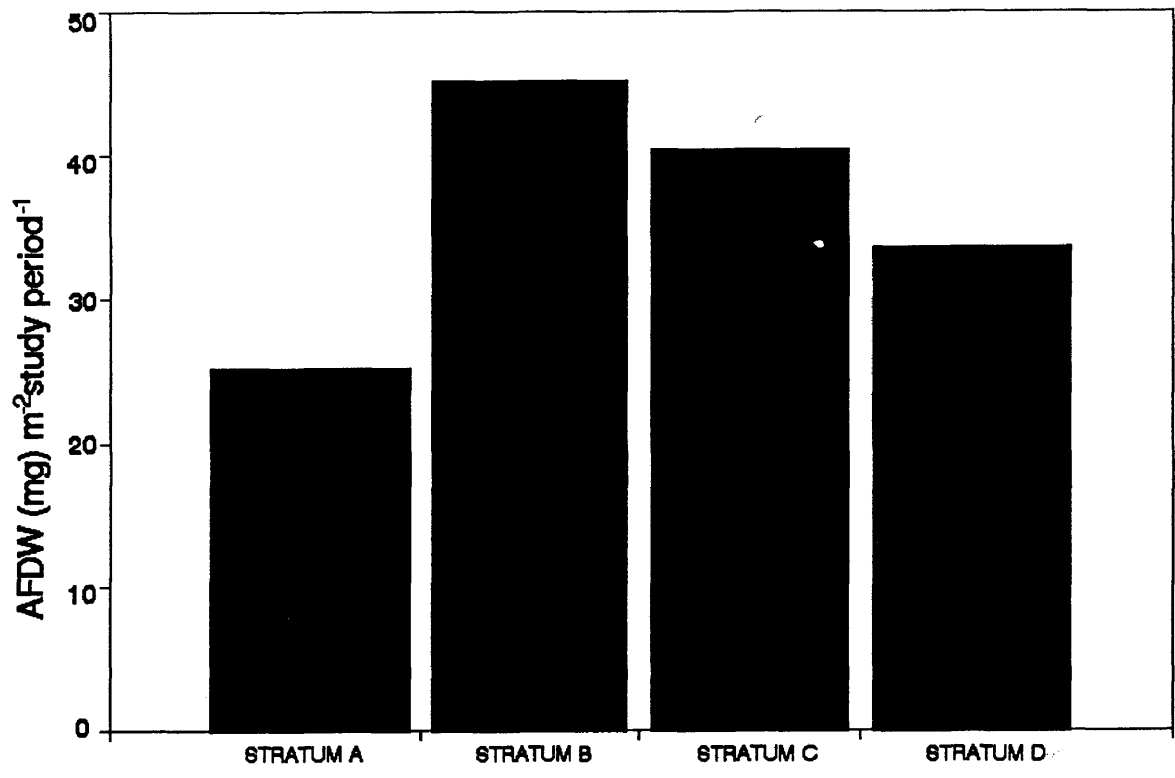
DISCUSSION

The dissolved oxygen concentration as well as salinity in the York River during the summer of 1989 varied predictably and cyclicly with the spring - neap tidal cycle. This association between dissolved oxygen and tides was first reported by Haas (1977) and appears to be a consistent feature of the York River hydrology during the summer (Kuo and Neilson 1987). The use of the continuously monitoring telemetering data buoy gave a more complete understanding of the temporal variability of the dissolved oxygen concentration, salinity and temperature. By understanding the frequency to which the benthos is exposed to low dissolved oxygen as well as the duration of low dissolved oxygen events, a realistic concept of the environmental conditions that the mesohaline benthos experience can be developed. The sensor package for this study was fixed at one meter off the bottom, the frequency and duration of low oxygen events recorded may still be an underestimate of the true conditions at the sediment-water interface. The oxygen concentration has been shown to continue to decrease within one meter off the bottom to the substrate (Rosenberg 1980).

The spatial extent and temporal duration of hypoxia in the deeper portions of Chesapeake Bay has been increasing (Officer et al. 1984, Taft et al. 1984). In addition, evidence from the sediment record suggests that periodic hypoxia has occurred in deeper portions of Chesapeake Bay since the time of European settlement

and the introduction of agriculture (Cooper and Brush 1991). The historic extent of hypoxia for the York River is unknown, however, the reported susceptibility to periodic stratification (Haas 1977) as well as recent evidence of historic periodic hypoxia elsewhere in Chesapeake Bay, indicate that the York River may have been exposed to hypoxic conditions for some time. One of the most notable hypoxic events was recorded after the rainfall from Tropical Storm Agnes (June 1972) drastically altered hydrographic conditions and initiated wide spread hypoxia that summer. The macrobenthic community composition had not recovered to pre-storm conditions for at least 2 years after the storm (Boesch et al. 1976a). The historic and recent evidence suggest that the York River benthic community may be exposed to hypoxic conditions on a seasonally regular basis.

Oxygen, salinity, and temperature of the York River, during the summer of 1989, varied over three temporal scales; seasonally (months), spring-neap tides (weeks), and semi-diurnal (hours). Of these, the most important to benthos are the seasonal and the spring-neap time scales. As temperature increases through the summer, oxygen demand also increases. The temperature increase coupled with the bi-weekly spring-neap tidal mixing of the bottom waters, set-up longer periods of hypoxia as summer progressed (Figure 3). The varying intensity of water column mixing may also cause fluctuations in primary productivity and carbon flux to the benthos (Webb et al. 1980). This changing organic quality and quantity, which has been shown to influence the growth of some polychaetes (Marsh et al. 1989, Tenore and Chesney

1985), also enhances the biological oxygen demand of the sediments. These oxygen data (from both the data buoy and YSI meter) collected during the summer of 1989 indicate that the York River benthic community did experience hypoxia. Typically, the mainstem of Chesapeake Bay experiences hypoxia earlier in the summer than the York River and the bottom water stays hypoxic for longer periods of time.

The species chosen for this study were selected primarily because of their relatively high abundance in the fauna record. If the benthic community of the York River is regularly oxygen stressed or in some other way experiences disturbance, the selection of species based upon their abundance may have precluded the observation of effects due to hypoxia. That is, if these species are abundant in the hypoxic York River, they may be adapted to that environment. In fact, the species that were examined during this study have been shown to be ubiquitous throughout the mesohaline/polyhaline Chesapeake Bay and are often numerically dominant in both hypoxic and normoxic habitats (Boesch et al. 1976a, 1976b, Holland et al. 1989). These species are often considered to be opportunistic because of their ability to colonize disturbed habitats but are not limited to stressed areas (Boesch et al. 1976a, 1976b, Gaston et al. 1985).

Many estuarine and marine invertebrates have been shown to have physiological adaptations that allow resistance to low dissolved oxygen conditions. These adaptations may exist in the form of internal oxygen reservoirs, such as gas bubbles,

or pools of high affinity hemoglobin to maintain aerobic pathways in the presence of environmentally low dissolved oxygen. In addition, some species have been shown to switch to anaerobic metabolic pathways, in some cases before environmental oxygen has been depleted (Magnum and Van Winkle 1973). Organisms possessing physiological adaptations to low oxygen conditions may not respond, even sublethally, to the periodic hypoxia of the York River.

A typical observation of the effect of hypoxia is the decrease in abundance of benthic fauna (Rosenberg 1980, Gaston 1985, Llansó 1991). Generally, the differences in abundance of each of the species examined in this study was not attributable to low dissolved oxygen in the York River. Rosenberg (1980) has observed benthic faunal reductions in environments with oxygen concentrations below 2 mg l^{-1}. Oxygen levels below 2 mg l^{-1} were observed in the deeper strata of the York River, however, wide-scale faunal reductions did not occur. The most noteworthy abundance fluctuations during this study are the recruitment pulses during periods of low dissolved oxygen observed in several of the populations examined in this study. These are best seen in the size frequency histograms for each species as an appearance of relatively large numbers of small individuals. A second cohort of *Sigambra tentaculata* began recruiting about August 15 and continued until the end of the study (Figure 11). *Paraprionospio pinnata* shows recruitment beginning August 4 at strata B, C, and D (Figure 17). *Paraprionospio pinnata* shows recruitment at all strata by August 15. This recruitment pulse occurred during the period of most

severe hypoxia indicating that juvenile *Paraprionospio pinnata* are tolerant of low dissolved oxygen. Boesch *et al.* (1976a), noted unprecedented eruptions of *Paraprionospio pinnata* after the hypoxia and freshet caused by Tropical Storm Agnes in 1972. The ability of *Paraprionospio pinnata* to quickly colonize stressed areas, coupled with the hypoxic condition of the York River, may help to explain the dominance of this species in the benthic community. *Glycinde solitaria* also shows some recruitment throughout the study period (Figure 23). The late season recruitment observed in these populations occurred during some of the most intense hypoxic events (Figure 3).

These recruitment pulses are somewhat unexpected since the larval stage of benthic fauna is typically more sensitive to low dissolved oxygen (Holland *et al.* 1989). However, Llansó (1990) has shown that the larvae of the spionid polychaete *Streblospio benedicti* can survive hypoxia for at least 4 days. The adults of several polychaete species have been shown to be tolerant to short-term hypoxia in laboratory experiments (Henriksson 1969, Warren 1977). The relative abundance of a species in a hypoxic habitat may vary. For example, in this study the abundance of *Paraprionospio pinnata* was observed to increase under hypoxic conditions in the York River, while Llansó (1990) shows depressed levels of this species under more severe hypoxic conditions in the Rappahannock River. This relative abundance of opportunistic species, such as *P. pinnata*, may indicate that the severity and duration

of the low dissolved oxygen event are critical to the degree of response from a population to low dissolved oxygen.

A decrease in abundance of a benthic species in a hypoxic or anoxic environment would be considered a lethal effect of low dissolved oxygen. However, sub-lethal responses are also possible effects of hypoxia and may be considered more subtle than lethal responses. Sub-lethal effects would be expected to be manifested in decreased growth and/or production of fauna relative to the same species in normoxic environments. Several faunal parameters, mean individual weight, specific growth, instantaneous production, and total production, were measured during this study to examine the potential sub-lethal effects of hypoxia.

The mean individual weight of the dominant species between each stratum through time was not significantly different. *Acteocina canaliculata*, which had smaller weights in the deepest stratum (D), was the only exception. However, this difference is not believed to be related to low dissolved oxygen because the highest overall individual weight was observed in stratum C which also experienced hypoxia (Figure 7). For all other species the mean individual weight showed no significant difference between stratum. In addition, there was no cyclical fluctuation of mean individual weight either in or out of phase with the normoxia-hypoxia cycles. Overall, the mean individual weight of the five species observed in the York River was not influenced by hypoxia during the summer of 1989.

Specific growth of *Acteocina canaliculata* and *Sigambra tentaculata*, the two species with distinguishable cohorts, showed fluctuations over the summer of 1989 (Figures 8 and 14), but did not vary substantially between hypoxic and non-hypoxic strata. The most obvious feature of the specific growth data is the wide range in the estimated high and low growth. The wide range is due to the high standard errors of the mean individual weight. The specific growth of both species did show relatively low or negative specific growth during some periods of hypoxia in some strata, however, the pattern of depressed specific growth did not consistently vary with the cyclical oxygen record. In stratum A, which did not experience hypoxia, both *Acteocina canaliculata* and *Sigambra tentaculata* had low or negative specific growth during periods of hypoxia. In addition, both species experienced high specific growth in hypoxic strata during the August 4 - 15 interval in which the most severe interval of hypoxia was recorded (Figures 8 and 14). These findings vary from the results of laboratory experiments that showed decreased growth in the opportunist polychaete *Capitella* species 1 held in near anoxic conditions for 48 hours (Forbes and Lopez 1991). The observed difference in the specific growth of *A. canaliculata* and *S. tentaculata* from the laboratory results of Forbes and Lopez (1991) may show the importance of the severity and duration of the hypoxic events in the manifestation of effects on the growth of benthic fauna.

The production of benthic macrofauna has been observed to be depressed in habitats experiencing more severe seasonal low dissolved oxygen then the York River (Rainer

and Fitzhardinge 1981, Holland *et al.* 1989). For the mainstem of Chesapeake Bay, the lowest total benthic production was found in seasonally oxygen deficient areas (Holland *et al.* 1989). However, the results of this study showed no clear relationship between estimated production of the five selected species and low dissolved oxygen events (either cyclical or along a depth gradient). The instantaneous production of *Acteocina canaliculata* and *Sigambra tentaculata*, like specific growth, show no variation in a cyclical manner related to the cyclical oxygen record (Figures 9 and 15). The total production of each of the five species show a variety of responses along the depth gradient. The total production of *Acteocina canaliculata*, *Paraprionospio pinnata*, and *Leitoscoloplos fragilis*, did decrease from shallow to deep strata as would be expected if the hypoxia of the York River were negatively influencing the deeper strata. However the stratum with no hypoxic events (A) had very low total production and the highest values of production for these species were observed in stratum B which experienced mild hypoxia. The total estimated production of *Glycinde solitaria* was positive for all strata over the sample period and was comparable to estimates found in non-hypoxic areas of Chesapeake Bay (Holland *et al.* 1989).

The total estimated production of *Sigambra tentaculata* was highly variable among strata, the highest values of production were observed in stratum C which experienced hypoxia and stratum A which had no hypoxia. The total production of

Paraprionospio pinnata was the highest recorded production of the species in this study.

The trends in estimates of production for *Acteocina canaliculata* and *Sigambra tentaculata* show a wide range between the high and low estimated values. This large spread is due to the high standard error associated with the mean abundance and individual weight estimates for those species. These large standard errors make it difficult to demonstrate potential sub-lethal effect of hypoxia through growth and production estimates.

CONCLUSIONS

The York River has been shown to experience hypoxic events of a cyclic nature related to the spring-neap tidal stratification/destratification (Haas 1977). The influence of these hypoxic events on the macrobenthic species chosen for this study is not clearly evident. None of the community dominants examined show a clear response to these events through changes in abundance, mean individual weight, specific growth, instantaneous production, or total production. Since these hypoxic events have been occurring for at least several years, the possibility exists that the benthos has been changed at some point in the past and that current communities are dominated by euryhaline opportunists capable of tolerating the stress imposed by the low dissolved oxygen. Boesch et al. (1976b) confirms that in the mid 1970s broad-scale changes in species composition occurred at a long-term monitoring station within the study area. At that time the macrofaunal community shifted to one dominated by euryhaline opportunists.

The species chosen have also been found to be some of the first colonizers of areas disturbed by low dissolved oxygen (Boesch et al. 1976a, Gaston et al. 1985). These first colonizers of the hypoxia affected area observed by Gaston et al. (1985) were not replaced as oxygen conditions improved and continued to be dominants of the benthic community. Perhaps the stress of hypoxia has been imposed on the York River macrobenthos and if the hypoxia increases in severity, as predicted (Officer et

al. 1984, Taft *et al*. 1984, Cooper and Brush 1991), the community composition may show differences in terms of the dominant species present. Given the broad resistance to hypoxia of these species in the York River and other hypoxic environments (Gaston *et al*. 1985), any measurable manifestation of a negative impact on their energetics will require an increase in severity and duration of hypoxia. Wide scale mortality of the estuarine benthos seems only to occur under anoxic or extended hypoxic conditions.

It is also likely that the sub-lethal parameters measured in this study were influenced by the high variability of the weight and abundance data. If subtle sub-lethal effects are occurring within the macrofaunal populations, the factors affecting the variability of the data must be considered before these populations are sampled. Another explanation for the absence of observed effects might be the natural adaptation, to hypoxia, of the abundance dominants of the macrofaunal community. Future investigators might consider attempting sub-lethal effects studies on species that are not considered opportunists but are considered representative of more stable, normoxic environments.

LITERATURE CITED

Baird, D. and R. E. Ulanowicz. 1989. The seasonal dynamics of the Chesapeake Bay ecosystem. Ecol. Monog. 59:329-364.

Boesch, D. F., R. J. Diaz and R.W. Virnstein. 1976a. Effects of Tropical Storm Agnes on soft-bottom macrobenthic communities of the James and York estuaries and the lower Chesapeake Bay. Chesapeake Sci. 17:246-259

Boesch, D. F., M. L. Wass and R.W. Virnstein. 1976b. The dynamics of estuarine benthic communities. In: Wiley, M. (ed.) Estuarine Processes. Academic Press, New York. pp. 177-196.

Breitburg, D. 1990. Near-shore hypoxia in the Chesapeake Bay: Patterns and relationships among physical factors. Est. Coast. Shelf Sci. 30:593-609.

Cooper, S.R. and G.S. Brush. 1992. Long-term history of Chesapeake Bay Anoxia. Science 254:992-996.

Dauer, D. M., C. A. Maybury and R. M. Ewing. 1981. Feeding behavior and general ecology of several spionid polychaetes from the Chesapeake Bay. J. Exp. Mar. Biol. Ecol. 54:21-38.

Diaz, R. J., R. J. Neubauer, L. C. Schaffner, L. Pihl and S. P. Baden. 1992. Continuous monitoring of dissolved oxygen in an estuary experiencing periodic hypoxia and the effect of hypoxia on the macrobenthos and fish. Science of the Total Environment. Elsevier Science Publishers B.V., Amsterdam.

Downing, J. A. and F. H. Rigler. 1984. A manual on methods for the assessment of secondary productivity in fresh waters. IBP Handbook No. 17, Second Edition. Blackwell Scientific Publications, Oxford. 501 pp.

Fauchald, K. and P. A. Jumars. 1979. The diet of worms: A study of polychaete feeding guilds. Oceanogr. Mar. Biol. Ann. Rev. 17:193-284.

Forbes, T. L. and G. R. Lopez. 1990. The effect of food concentration, body size, and environmental oxygen tension on the growth of the deposit-feeding polychaete, Capitella species 1. Limnol. Oceanogr. 35:1535-1544.

Funderburk, S. L., S. J. Jordan, J. A. Mihursky and D. Riley. 1991. Habitat requirements for Chesapeake Bay living resources, second edition. Prepared for Living Resources Subcommittee, Chesapeake Bay Program.

Gaston, G. R., P. A. Rutledge and M. L. Walther. 1985. The effects of hypoxia and brine on recolonization by macrobenthos off Cameron, Louisiana (USA). Contrib. Mar. Sci. 28:79-93.

Gaston, G. R. 1985. Effects of hypoxia on macrobenthos of the inner shelf off Cameron, Louisiana. Est. Coast. Shelf Sci. 20:603-613.

Haas, L. W. 1977. The effect of the spring-neap tidal cycle on the vertical salinity structure of the James, York, and Rappahannock Rivers, Virginia, U.S.A. Estuar. Costal Mar. Sci. 5:485-496.

Harper, D. E., L. D. McKinney, R. R. Salzer and R. J. Case. 1981. The occurrence of hypoxic bottom water off the upper Texas coast and its effects on the benthic biota. Contrib. Mar. Sci. 24:53-79.

Hayward. D., L. W. Haas, J. D. Boon, K. L. Webb and K. D. Friedland. 1986. Empirical models of stratification variation in the York River estuary, Virginia, U.S.A. In: Bowman. H. J., Yentsch, C. M. and Peterson, W. T. (eds.) Tidal mixing and plankton dynamics. Lecture notes on coastal and estuarine studies, Vol. 17. Springer-Verlag, Berlin. pp. 346-367.

Henriksson R. 1969. Influence of pollution on the bottom fauna of the Sound (Oresund). Oikos 20:507-523.

Holland, A. F., A. T. Shaughnessay, L. C. Scott, V. A. Dickens, J. A. Rnansinghe, and J. K. Summers. 1988. Progress Report: Long-term benthic monitoring and assessment program for the Maryland portion of Chesapeake Bay (July 1986 - October 1987). Prepared for Maryland Power Plant Research Program and Maryland Department of the Environment, Office of Environmental Programs by Versar, Inc. ESM Operations, Columbia , Maryland. Report No: PPRP-LTB/88-1.

Holland, A. F., A. T. Shaughnessay, L. C. Scott, V. A. Dickens, J. R. Gerritsen, and J. A. Rnansinghe. 1989. Long-term benthic monitoring and assessment program for the Maryland portion of Chesapeake Bay: Interpretive report. Maryland Dept. Nat. Res., Power Plant Prog., Annapolis MD. Report No: CBRM-LTB/EST-89-2.

Jorgenson, B. B. 1980. Seasonal oxygen depletion in the bottom waters of a Danish fjord and its effect on the benthic community. Okios 34:68-76.

Kuo, A. J. and B. J. Neilson. 1987. Hypoxia and salinity in Virginia estuaries. Estuaries 10:277-283.

Llansó, R. J. 1990. Effects of low dissolved oxygen on estuarine macrobenthos. Ph.D. dissertation, The College of William and Mary. Williamsburg, Virginia. 160 p.

Llansó, R. J. 1991. Tolerance of low dissolved oxygen and hydrogen sulfide by the polychaete *Streblospio benedicti (Webster)*. *J. Exp. Mar. Biol. Ecol. 153:165-178*.

Mackiernan, G. B. (ed.). 1987. Dissolved oxygen in Chesapeake Bay, processes and effects. Proc. Seminar Hypoxic and related processes in Chesapeake Bay. Maryland Sea Grant, College Park, Maryland. UM-SG-TS-87-03. 177 pp.

Magnum, C. and W. Van Winkle. 1973. Responses of aquatic invertebrates to declining oxygen conditions. Amer. Zoo. 43:529-541.

Marsh, A. G., A. Gremare and K. R. Tenore. 1989. Effect of food type and ration on growth of juvenile *Capitella* sp. I (Annelida: Polychaeta): macro- and micronutrients. Mar. Bio. 102:519-527.

May, E. B. 1973. Extensive oxygen depletion in Mobile Bay, Alabama. Limnol. Oceanogr. 18:353-366.

Mountford, K., R. Reynolds and N. Fisher. 1989. A telemetering environmental data buoy in Chesapeake Bay. Mar. Tech. Soc., Proc. Mar. Data Systems '89, April 1989, New Orleans. pp. 17-22.

Newcomb, C. L. , W. A. Horne and B. B. Shepard. 1939. Studies on the physics and chemistry of estuarine waters in Chesapeake Bay. J. Mar. Res. 2:87-116.

Officer, C. B., R. B. Biggs, J. L. Taft, L. E. Cronin, M. A. Tyler and W. R. Boyton. 1984. Chesapeake Bay anoxia. Origin development and significance. Science 223:22-27.

Pihl, L. 1989. Effects of oxygen depletion on demersal fish in coastal areas of the south-east Kattegat. Proc. 23rd Eur. mar. Biol. Symp., Ryland, J.S. Tyler, P.A. (eds.) Olsen & Olsen, Fredensborg, Denmark. pp. 431-439.

Pihl, L., S. B. Baden and R. J. Diaz. 1991. Effects of periodic hypoxia on distribution of demersal fish and crustaceans. Mar. Biol. 108:349-360.

Rainer, S. F. and R. C. Fithardinge. 1981. Benthic communities in an estuary with periodic deoxygenation. Aust. J. Mar. Freshwater Res. 32:227-242.

Rosenberg, R. 1980. Effect of oxygen deficiency on benthic macrofauna in fjords. In: H.J. Freeland, D.M. Farmer, and C.D. Levings (eds.), Fjord Oceanography, Plenum Publishing Corp., New York. pp. 499-514.

Rosenberg, R. and L. Loo. 1988. Marine eutrophication induced oxygen deficiency: Effects on soft bottom fauna, Western Sweden. Ophilia 29:213-225.

Seliger, H. H., J. A. Boggs and W. H. Biggley. 1985. Catastrophic anoxia in the Chesapeake Bay in 1984. Science 228:70-73.

Schaffner, L. C., R. Seitz and R. J. Diaz. in review. Effect of hypoxia and recruitment on the burrowing patterns of estuarine macrobenthos.

Smith, D. E., M. Leffer and G. MacKiernan (eds.). 1992. Oxygen dynamics in the Chesapeake Bay. Maryland Sea Grant College, Publication No. UM-SG-TS-92-01.

Taft, J. L., E. O. Hartwig and R. Loftus. 1980. Seasonal Oxygen Depletion in Chesapeake Bay. Estuaries 3:242-247.

Tenore, K. and E, Chesney. 1985. The effects of interaction of rate of food supply and population density on the bioenergetics of the opportunistic polychaete, *Capitella capitata* (Type I). Limnol. Oceanogr. 30: 1188-1195.

Tuttle, J. H., R. B. Jonas and T. C. Malone. 1987. Origin, development and significance of Chesapeake Bay anoxia. In: S.K. Majumdar, L.W. Hall, Jr., and H.M. Austin (eds.), Contaminant problems and management of living Chesapeake Bay resources. Penn. Acad. Sci. pp. 443-472.

Tyson, R. V. and T. H. Pearson (eds.) 1991. Modern and ancient continental shelf anoxia. Geol. Soc. Amer. Spec. Pub. No. 58. 470 pp.

Virnstein, R. W. 1977. The importance of predation of crabs and fish on benthic infauna in Chesapeake Bay. Ecology 58:1199-1217.

Warren, L. M. 1977. The ecology of *Capitella capitata* in British waters. J. Mar. Biol. Ass. U.K. 57:151-159.

Webb, K. L. and C. F. D'elia. 1980. Nutrient and oxygen redistribution during a spring neap tidal cycle in a temperate estuary. Science 207:983-985.

Zobrist, E. C. 1988. The influence of post-settlement mortality on recruitment patterns in a soft-bottom habitat. Masters Thesis, College of William and Mary, Williamsburg, Virginia. 78 p.