1996

Autoecology of Paraprionospio pinnata (Polychaeta: Spionide) along an Estuarine Gradient

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AUTECOLOGY OF *PARAPRIONOSPIO PINNATA* (POLYCHAETA: SPIONIDAE) ALONG AN ESTUARINE GRADIENT

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

by

Elizabeth Kathleen Hinchey

1996

APPROVAL SHEET

This thesis is submitted in partial fulfillment of
the requirements for the degree of

Master of Arts

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Approved, July 1996

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DEDICATION

To my parents, Martha and Frank

And in memory of Dr. George B. Craig Jr., a wonderful teacher, mentor, and dedicated researcher whose love of aquatic invertebrates was both contaigous and inspiring

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ACKNOWLEDGMENTS

I am grateful to my major advisor, Dr. Robert J. Diaz, who suggested this thesis topic and supported my research. I also wish to express my gratitude to the members of my thesis committee, Dr. Linda C. Schaffner, Dr. John E. Olney, Dr. Daniel M. Dauer, and Dr. L. Donelson Wright, for their time and review of this thesis.

I would wholeheartedly like to thank everyone at VIMS who assisted with my muddy and exhausting field collections. Many extraordinary crews of students and staff ensured that my long days on the York River were productive and also very fun! Special thanks to the Benthic Ecology students: Randy Cutter, Giancarlo Cicchetti, Janet Nestlerode, and Eric Wooden, who all participated above and beyond the call of duty. I would also like to recognize Tom Orrell and Sandra Brooke, two "honorary benthons" who never hesitated to help. Thanks also to the Vessels Operations staff, who willingly accommodated my needs, and Linda Meneghini, who generously guided me through sediment analyses.

I would especially like to thank my labmates, Giancarlo Cicchetti, Janet Nestlerode, and Eric Wooden, and my Maury Hall friend, Marty Cavalluzzi, for their friendship, advice, optimism, and humor throughout the last three years.

Lastly, and most importantly, I would like to thank my family for their love, encouragement, and interest in my endeavors.

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ABSTRACT

The spionid polychaete *Paraprionospio pinnata* (Ehlers) is a predominant species of the Chesapeake Bay macrobenthic community, and of macrobenthic communities throughout North and South America. This study quantifies its abundance and secondary production along an estuarine gradient in the York River, Virginia. Weekly sampling in the late summer and fall of 1994 revealed intraspecific differences in *P. pinnata* distribution and secondary production throughout the estuary. The polyhaline-high mesohaline stations in the lower York River were characterized by the highest densities and secondary production of this species, with values declining both Bayward and upriver. Continuous recruitment occurred from August through October across varying salinity and sedimentary regimes, and even during periods of low oxygen stress. Only a small percentage of animals collected were reproductive adults. Of these, the fecundity ranged from approximately 1200 to 11,100 eggs per worm. The findings of this study support the classification of *P. pinnata* as a limited euryhaline opportunist, capable of exhibiting opportunistic life history strategies over restricted ranges of environmental conditions or periods of time.

AUTECOLOGY OF *PARAPRIONOSPIO PINNATA* (POLYCHAETA: SPIONIDAE) ALONG AN ESTUARINE GRADIENT

INTRODUCTION

Many studies have examined the distribution of benthic invertebrates along estuarine gradients (Remane 1934; Boesch 1977; Dauer at al. 1987; Diaz 1989; Soetaert et al. 1994). Such estuarine-wide studies generally emphasize whole community structure and do not examine population dynamics of individual species in detail (but see Holland et al. 1987; Dauer et al. 1993). As the effects of abiotic factors on the population or species level of ecological systems can ultimately be transmitted to the community and ecosystem levels through interspecific interactions (sensu Grippo and Dunson 1991), investigation of how species population parameters vary along estuarine gradients is required for a complete understanding of estuarine community dynamics.

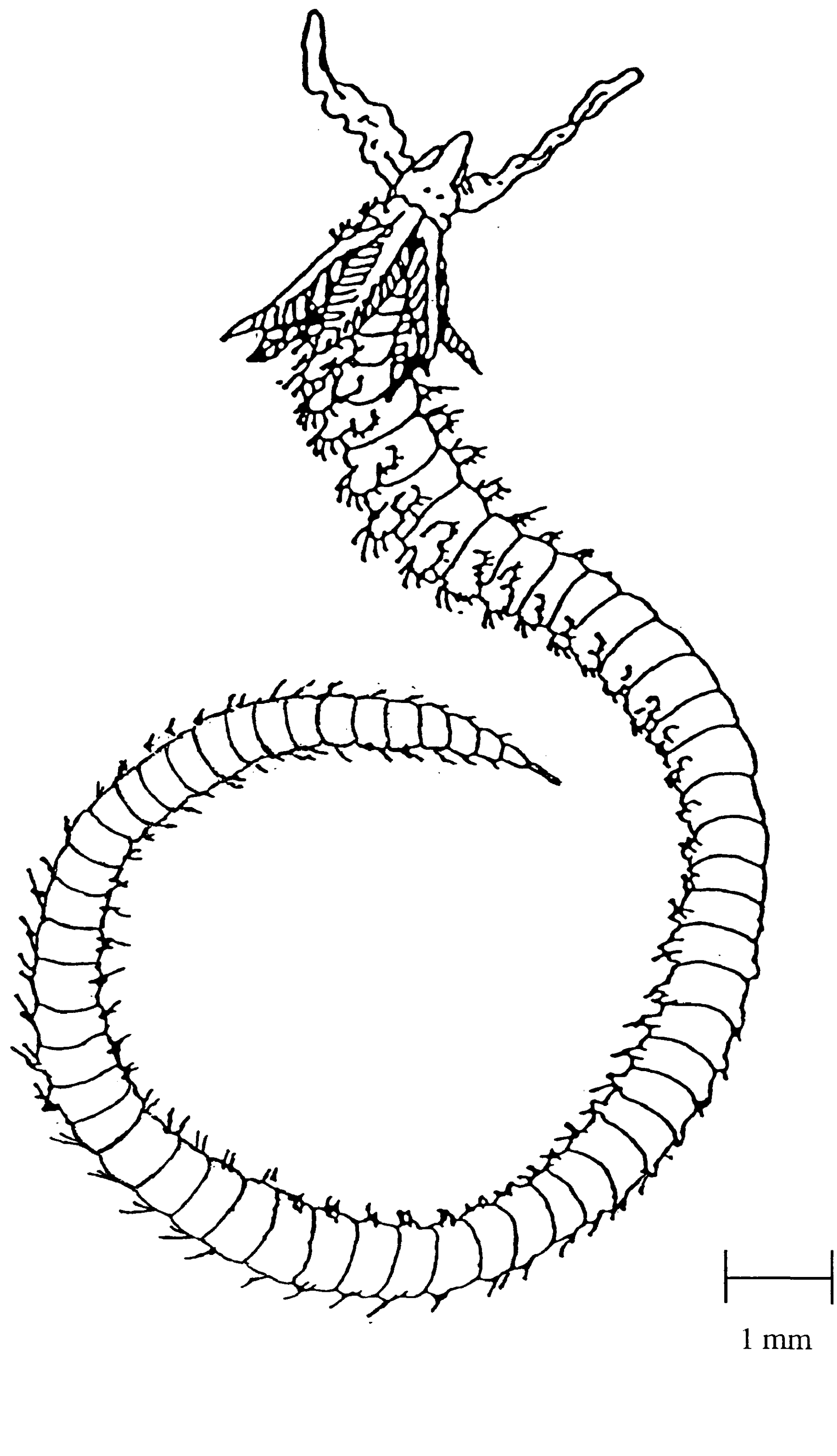
The physiological capacity for a species to survive, grow and reproduce varies with different levels of abiotic stresses (Levinton 1982; Dunson and Travis 1994). This variation results as exposure of organisms to environmental stress increases the probability of death for an individual and elicits an adaptive response which consumes energy at the expense of functions such as growth and reproduction (Levinton 1982). Therefore, at different locations along an estuarine gradient, population parameters of a species can potentially vary. These parameters include biomass (Beukema et al. 1978), reproduction (Vernberg 1983), and the processes of growth and secondary production (see Diaz and Schaffner 1990 for summary).

Small, infaunal species of polychaetes are included among the dominant inhabitants of macrobenthic estuarine communities worldwide (Day et al. 1989). Although these organisms are numerically abundant and often have important functional roles in estuarine soft-sediment benthic communities (Diaz and Schaffner 1990), the population dynamics of many species remain poorly known (Zajac 1991; Seitz and Schaffner 1995).

The spionid polychaete *Paraprionospio pinnata* (Ehlers 1901) (Fig. 1) is a numerically dominant macrobenthic inhabitant of Chesapeake Bay (Holland et al. 1977; Schaffner 1990) and of benthic communities throughout North and South America, including the Gulf of Mexico (Harper et al. 1991), the Gulf of Arauco, Chile (Carrasco and Gallardo 1983), and the Gulf of Nicoya, Costa Rica (Vargas 1988). *Paraprionospio pinnata* has been classified as a eurytopic opportunist because it typically becomes more abundant following a disturbance or in frequently disturbed or continually stressed habitats (Boesch et al. 1976; Harper et al. 1991). This species is resistant to severe hypoxia (Diaz and Rosenberg 1995), and frequently dominates community structure in hypoxia-stricken areas (Boesch and Rabalais 1991; Harper et al. 1991; Diaz et al. 1992). *Paraprionospio pinnata* also dominates communities in polluted waters (Boesch 1973). Although the dominance of *P. pinnata* in ambient and disturbed environments has been noted in the aforementioned benthic works, few studies (Mayfield 1988; Neubauer 1993) have been conducted to elucidate the details of the life history and ecology of this species. These field studies were each restricted in space to stations located in one salinity regime and thus do not shed insights regarding differences in *P. pinnata* demography along a salinity gradient.

Many aspects of *Paraprionospio pinnata* biology signify its potentially important role in the ecology of estuaries. *Paraprionospio pinnata* is a prey species for numerous benthic consumers, such as spot, *Leiostomus xanthurus* (Pihl et al. 1992), and Atlantic croaker, *Micropogonias undulatus* (Kendall et al. 1985). This polychaete also influences other estuarine processes through its feeding and burrowing activities. Newly settled juveniles and adults construct highly-branched burrow networks, with two to eight feeding locations at the surface (Dauer 1985). The worm extends a single pair of grooved, ciliated palps out of the burrow to collect both suspended (including resuspended) and deposited particles at the sediment-water interface (Dauer et al. 1981). *Paraprionospio pinnata*

Figure 1. Adult *Paraprionospio pinnata* approximately 30 mm in length (adapted from Lippson and Lippson 1984).


1 mm

deposit feeding can significantly alter local sediment grain-size distributions and therefore potentially mediate both intra- and interspecific interactions (Luckenbach et al. 1988).

This study examines population characteristics, including density, recruitment patterns, secondary production, and reproductive activity of *Paraprionospio pinnata* along an estuarine gradient. A total of seven field sites were selected in order to representatively sample along a mesohaline to polyhaline salinity gradient in the York River, Virginia. Sampling was conducted during late summer and early fall to correspond with the maximum recruitment pulse of *P. pinnata* in the York River (Neubauer 1993). This design makes it possible to evaluate how population abundance, recruitment and production are influenced by major parameters such as salinity, sediment type, and dissolved oxygen concentration. The major objective of this work is to identify the processes influencing the demography of this species along a representative estuarine gradient. This will lead to a better understanding of the processes that structure estuarine communities and the factors that regulate secondary production of this important link in the estuarine food web. Quantification of *P. pinnata* secondary production will provide important information regarding the role of this polychaete in predator-prey interactions between trophic levels (Ranier 1984). Secondary production measurements of benthic environments can also be utilized as indicators of benthic health (Waters 1977; Holland et al. 1987), used to compare ecosystems (Zaika 1973) and can provide useful information for evaluating habitat resource value (Fredette and Diaz 1986). This work will also advance our knowledge of the autecology and life history *P. pinnata*, thereby increasing our understanding of how this important species influences benthic community dynamics in estuaries.

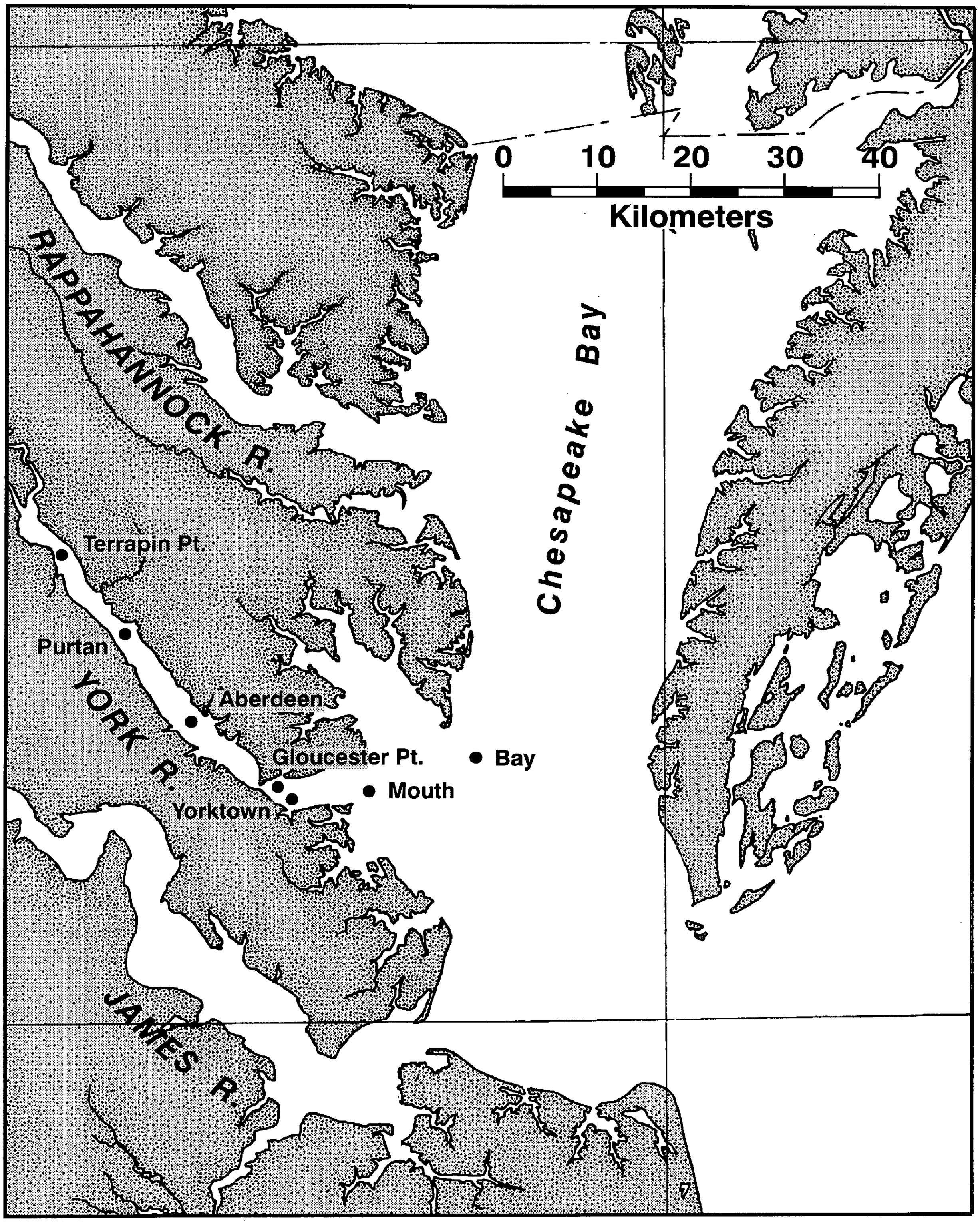
METHODS

Study area

The sampling was conducted along a transect from the lower Chesapeake Bay through the York River to Terrapin Point (Fig. 2). An estuarine gradient extends from the mouth of the Bay through the York River and into the Pamunkey River and Mattaponi River. The relatively small amount of fresh water discharge into the York system results in nearly evenly spaced isohalines in the York River (Boesch 1977). Salinity does not fluctuate widely during a tidal cycle or seasonally and is typically lowest in spring and highest in autumn (Boesch 1977). The rare passage of hurricanes or tropical storms during the summer can drastically reduce salinity (Boesch et al. 1976). Deep areas in the York River are susceptible to periodic low dissolved oxygen concentrations in early to mid-summer (Haas 1977, Kuo and Neilson 1987, Diaz et al 1992). Silts and clays are the most widely distributed sediments in the river (Boesch 1971). The sediments in the Bay are generally the sandiest, although scattered sand can also be found upriver (Boesch 1971). *Paraprionospio pinnata* has been a numerically dominant species in the lower York high mesohaline benthic community since the Fall of 1973 (Boesch et al 1976). This large, unprecedented increase in *P. pinnata* density occurred approximately one year after low salinities (12 psu) associated with a freshet created by Hurricane Agnes defaunated the benthic community (Boesch et al. 1976).

A total of seven field stations were sampled (Fig.2, Table 1). Four stations (Bay, Yorktown, Gloucester Point, Purtan) were located in areas of the York River and Chesapeake Bay which roughly corresponded with stations sampled by the Old Dominion University Benthic Biological Monitoring program. Three additional stations (Mouth,

Figure 2. York River and Chesapeake Bay study area, USA, with station locations indicated.



0
10
20
30
40
Kilometers
Chesapeake Bay
RAPPAHANNOCK R.
Terrapin Pt.
Purtan
Aberdeen
YORK R.
Gloucester Pt.
Bay
Mouth
Yorktown
JAMES R.

Table 1. Station coordinates, depths and percentages of sand, silt and clay (with SE) in sediments.

Station	Coordinates	Depth (m)	Sand (%)	Silt (%)	Clay (%)
Bay	37°14'15" N 76°12'19" W	11	68.2 ± 2.2	20.0 ± 1.5	11.8 ± 0.9
Mouth	37°14'21" N 76°21'68" W	11	30.8 ± 5.7	31.9 ± 3.8	37.5 ± 3.4
Yorktown	37°13'66" N 76°28'29" W	15	10.8 ± 2.0	32.2 ± 2.0	57.1 ± 2.3
Gloucester Point	37°14'30" N 76°29'05" W	12	16.4 ± 1.7	26.1 ± 2.9	57.5 ± 3.2
Aberdeen	37°19'93" N 76°36'76" W	4	62.8 ± 9.6	14.7 ± 4.0	22.5 ± 5.7
Purtan	37°25'12" N 76°41'39" W	9	10.4 ± 4.0	25.0 ± 2.3	64.6 ± 4.0
Terrapin Point	37°29'10" N 76°45'35" W	5	3.8 ± 1.1	28.5 ± 1.2	67.7 ± 1.4

Aberdeen, Terrapin Point) were also sampled to yield a more comprehensive representation of the estuarine gradient.

Infaunal sampling

Quantitative infaunal sampling consisted of Wildco box core samples (225 cm^2) collected on each date for each station. Two replicates were used to determine density and size of individuals. A total of three replicates were used to analyze recruitment patterns. Sampling intervals varied between some stations as a result of inclement weather conditions and logistical constraints. The Bay and Mouth stations were sampled each week from 3 August to 19 October, 1994 and again on 26 October, 1994. The Gloucester Point, Aberdeen and Purtan stations were sampled weekly from 3 August to 26 October, 1994 and again on 10 November, 1994. The Yorktown and Terrapin Point stations were sampled weekly from 10 August to 26 October, and again on 10 November, 1994.

Each box core was subsampled with a cylindrical corer of surface area 63.6 cm^2, to a 2 cm depth, for a total volume of 127.2 cm^3. This subcore was sieved on a 250 μm mesh screen and was used to determine recruitment pulses. The earliest *P. pinnata* recruits should be retained on the 250 μm screen, as Zobrist (1988) did not observe any *P. pinnata* juveniles passing through 250 μm to 125 μm screens. The remainder of the box core sample was sieved on a 500 μm mesh screen. The samples were fixed in 15% buffered formalin in the field. A sediment samples was collected on date for each station with a small corer (2.5 cm diameter) inserted vertically through the top 5 cm of the sediment in the box core. Percent sand, silt and clay composition of the sediment was determined following the sieving and pipette analysis procedures described in Folk (1980). Temperature and dissolved oxygen concentration of the bottom water at each station were measured with a Yellow Springs Instruments (YSI-58) oxygen meter deployed 1 meter above the sediment-water interface. Salinity of the bottom water collected 1 meter above the sediment-water interface was measured with a refractometer (Lecia model 10419).

Production estimates

After fixation, animals were sorted under a dissecting microscope. Numbers of *Paraprionospio pinnata* individuals were counted, and the width of the fifth setiger, excluding parapodia, was measured under a dissecting microscope fitted with an ocular micrometer. The width of the fifth setiger in formalin-fixed specimens has been shown to be a valid predictor of mean individual weight for *P. pinnata* (Maxemchuk-Daly, in progress) and for *Paraprionospio* sp. (form A) (Yokoyama 1990). Ash-free dry weights (AFDWs) were obtained for whole, unfragmented, formalin-fixed individuals from different size classes and used to generate a width-weight regression.

Fifth setiger widths were used to construct size-frequency histograms for each station. As cohorts could not be clearly defined, the size-frequency method was utilized to calculate *Paraprionospio pinnata* secondary production (Hamilton 1969; Downing and Rigler 1984). This method combines all individuals collected throughout the entire study period into an average cohort to yield an estimate of total production. The equation for the size-frequency method is:

$$P = \sum_{i=1}^{n-1} (N_i - N_{i+1})\,(B_i + B_{i+1})/2$$

P = total production (mg AFDW m^{-2} study period^{-1})

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

B_i = mean individual biomass (mg AFDW) of the size class (i) for the study period

n = total number of size classes

The accuracy of production estimates is dependent upon the accuracy of the population data. Therefore, to estimate the potential variability of production, three estimates of production (minimum, maximum, and average production) were generated. Minimum and maximum estimates of production were obtained by using the replicates with the minimum and maximum counts of individuals (with the associated size distributions) per station per date in the size-frequency method calculations. The average production values were obtained by using average counts from two replicates per station per date in the size-frequency equation. Two estimates of average production were generated. For the purpose of comparison, production estimates for each station were generated for the 57 day interval when every station was sampled (10 August to 5 October, 1994). A production estimate was also generated for the total number of days that data are available, which varied between stations.

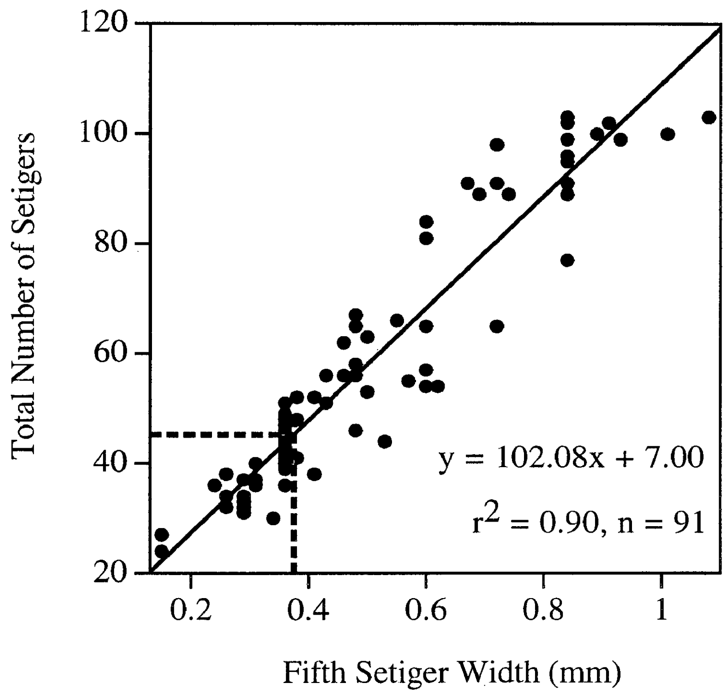
Recruitment estimates

The size-frequency histograms were used to determine when recruitment pulses of *Paraprionospio pinnta* occurred. Recruiting individuals were determined to have a fifth setiger width of 0.15 to 0.39 mm and approximately 45 setigers or less (Fig. 3).

Fecundity estimates

Paraprionospio pinnata fecundity was estimated by counting the number of oocytes in the coelom of three randomly selected reproductive segments per gravid female. The selected segments were removed from the body of the worm with dissection scissors, and then individually transferred to a slide. All oocytes in each segment were then extracted and counted. The diameter of thirty oocytes per segment was measured with an ocular micrometer. The average number of eggs per segment was multiplied by the total number of oovigerous segments to provide an estimate of fecundity.

Figure 3. *Paraprionospio pinnata*. Total number of setigers versus fifth setiger width. Measurements enclosed within box describe newly recruited individuals.


Total Number of Setigers
120
100
80
60
40
20
0.2
0.4
0.6
0.8
1
Fifth Setiger Width (mm)
y = 102.08x + 7.00
r2 = 0.90, n = 91

Statistical analyses

A multiple regression analysis was used to determine if there was a significant relationship between mean abundance of individuals and the effects of mean salinity, sediment composition (percent sand) and time. To analyze recruitment patterns, a Kolmogorov-Smirnov two-sample test was used to determine if the pattern of recruitment differed between stations. This nonparametric analysis tests the difference between two distributions. All statitical programs were performed using standard SAS System programs (SAS Instuitute Inc. 1990), following the assumptions of the individual analyses.

RESULTS

Physical conditions

Bottom-water salinity varied with location in the estuary, following a pattern of decreasing salinity as station location progressed up-river (Fig. 4). Mean salinity was highest at the Bay station (25 psu), followed by the Mouth station (22 psu), the Yorktown and Gloucester Point stations (each 21 psu), the Aberdeen station (17 psu), the Purtan station (16 psu) and the Terrapin Point station (12 psu).

Bottom-water temperatures generally increased as station location in the estuary progressed up-river (Fig. 4). Temperatures for all stations were maximum in August, followed by general declines in temperatures throughout the remainder of the study period. All six river stations experienced relatively steady temperatures throughout August, while August temperatures at the Bay station increased from a low of 18°C to a maximum of 23°C.

The Yorktown Station was the only station for which hypoxic conditions (<2 mg l^{-1}) were recorded (Fig. 3). Dissolved oxygen conditions at this station were hypoxic on three sampling occasions: 15 August (1.8 mg l^{-1}), 24 August (1.4 mg l^{-1}), and 31 August (1.3 mg l^{-1}).

Analysis of sediment samples collected at each station reveal that the average percent silt and clay content varied between stations and ranged between 31.8 and 96.2 percent (Table 1).

Patterns of abundance

Paraprionospio pinnata mean weekly density varied between the stations (Fig. 5).

Figure 4. Bottom-water salinity (psu), temperature (˚C), and dissolved oxygen concentration (mg l^{-1}) for each station and date.

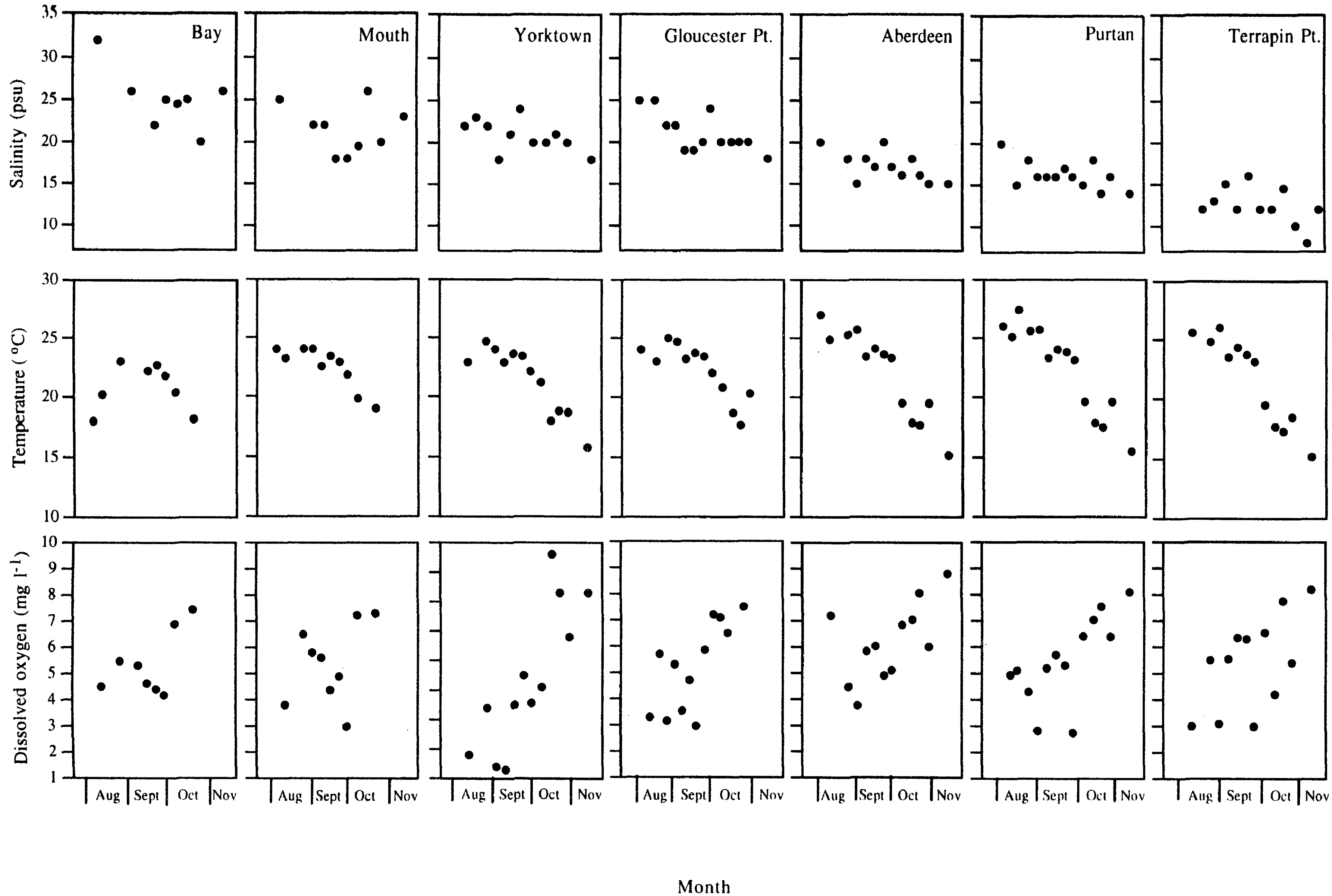
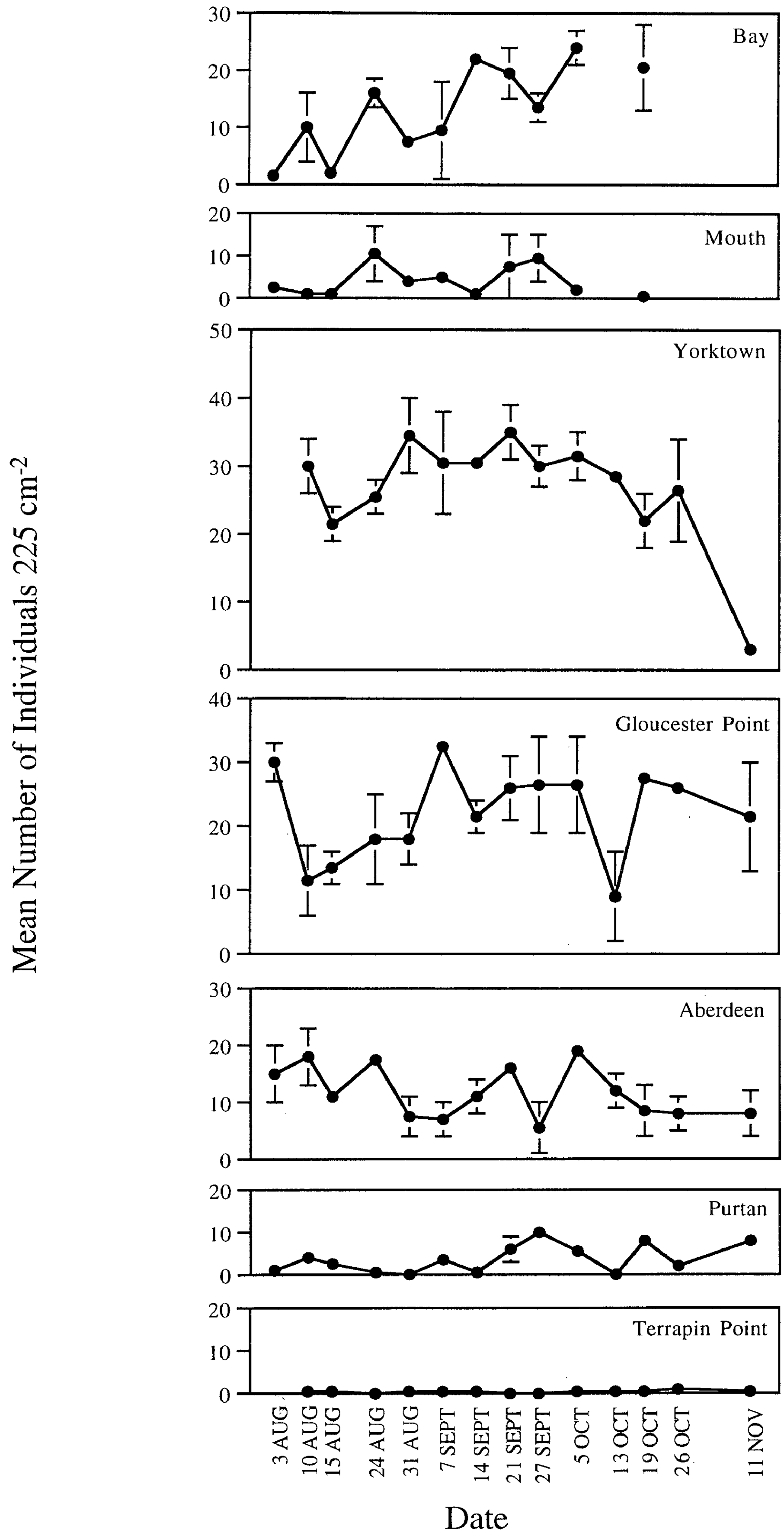

Bay
Mouth
Yorktown
Gloucester Pt.
Aberdeen
Purtan
Terrapin Pt.
Salinity (psu)
Temperature (°C)
Dissolved oxygen (mg l-1)
35
30
25
20
15
10
10
9
8
7
6
5
4
3
2
1
Aug
Sept
Oct
Nov
Month

Figure 5. *Paraprionospio pinnata*. Mean number of individuals 225 cm^{-2} (with SE) for each station and sampling date.


Bay
Mouth
Yorktown
Gloucester Point
Aberdeen
Purtan
Terrapin Point
Mean Number of Individuals 225 cm-2
3 AUG
10 AUG
15 AUG
24 AUG
31 AUG
7 SEPT
14 SEPT
21 SEPT
27 SEPT
5 OCT
13 OCT
19 OCT
26 OCT
11 NOV
Date

At the Bay station, mean density ranged from 1.5 to 24 individuals 225 cm^{-2} and tended to increase through time. At the other stations density was variable from week to week but did not exhibit consistent patterns through time. The maximum mean densities were observed at the Yorktown station (mean density ranging from 3 to 35 individuals 225 cm^{-2}) and the Gloucester Point station (mean density ranging from 9 to 32.5 individuals 225 cm^{-2}). The minimum mean density was observed at the Terrapin Point station, ranging from 0 to 1 individuals 225 cm^{-2}. A large decline in abundance occurred at the Yorktown station in November. This value of 3 individuals 225 cm^{-2} was lower than expected, based on abundance data from the long-term record of this species in this area. Abundances of overwintering *Paraprionospio pinnata* populations are usually relatively high in late fall and winter (Diaz, unpublished). Thus, it is speculated that a disturbance event or local extinction occurred at the Yorktown station somtime after the last sampling date on 26 October.

A multiple regression model was constructed to describe the relationship between mean abundance of *Paraprionospio pinnata* at the seven stations and the effects of mean salinity, mean percent sand content of sediment and time. Although the regression coefficients for mean salinity and percent sand content were significant at a probability of <0.0001, the low r^2 value (0.29) indicates that the model did not fit the data well. The regression equation generated was: mean abundance per 225 cm^{-2} = -15.88 + 1.62 (mean salinity) - 0.10 (percent sand). This equation suggests that overall abundance increased as the salinity increased but slightly decreased as sediment became sandier.

Patterns of recruitment

Paraprionospio pinnata did not exhibit cohort recruitment at any of the stations sampled (Figs. 6-12). Recruitment of new individuals (fifth setiger width <0.39 mm) to the benthic population was continuous throughout August and September and even into

Figure 6. *Paraprionospio pinnata*. Size frequency histogram for the Bay station based on width of fifth setiger. The size class interval is 0.078 mm.

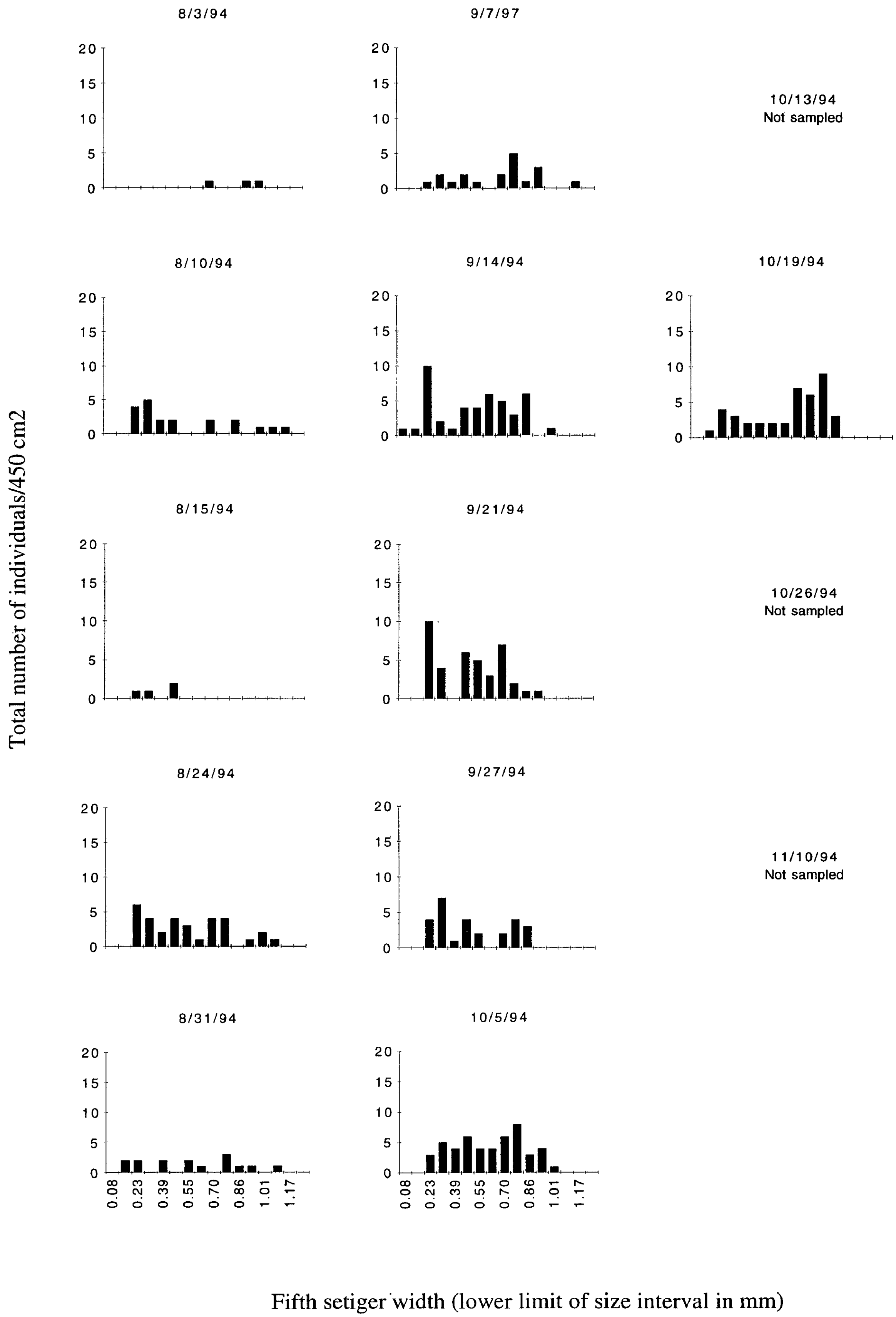

8/3/94
9/7/97
10/13/94
Not sampled
8/10/94
9/14/94
10/19/94
8/15/94
9/21/94
10/26/94
Not sampled
8/24/94
9/27/94
11/10/94
Not sampled
8/31/94
10/5/94
0
5
10
15
20
0.08
0.23
0.39
0.55
0.70
0.86
1.01
1.17
Total number of individuals/450 cm2
Fifth setiger width (lower limit of size interval in mm)

Figure 7. *Paraprionospio pinnata.* Size frequency histogram for the Mouth station based on width of fifth setiger. The size class interval is 0.078 mm.

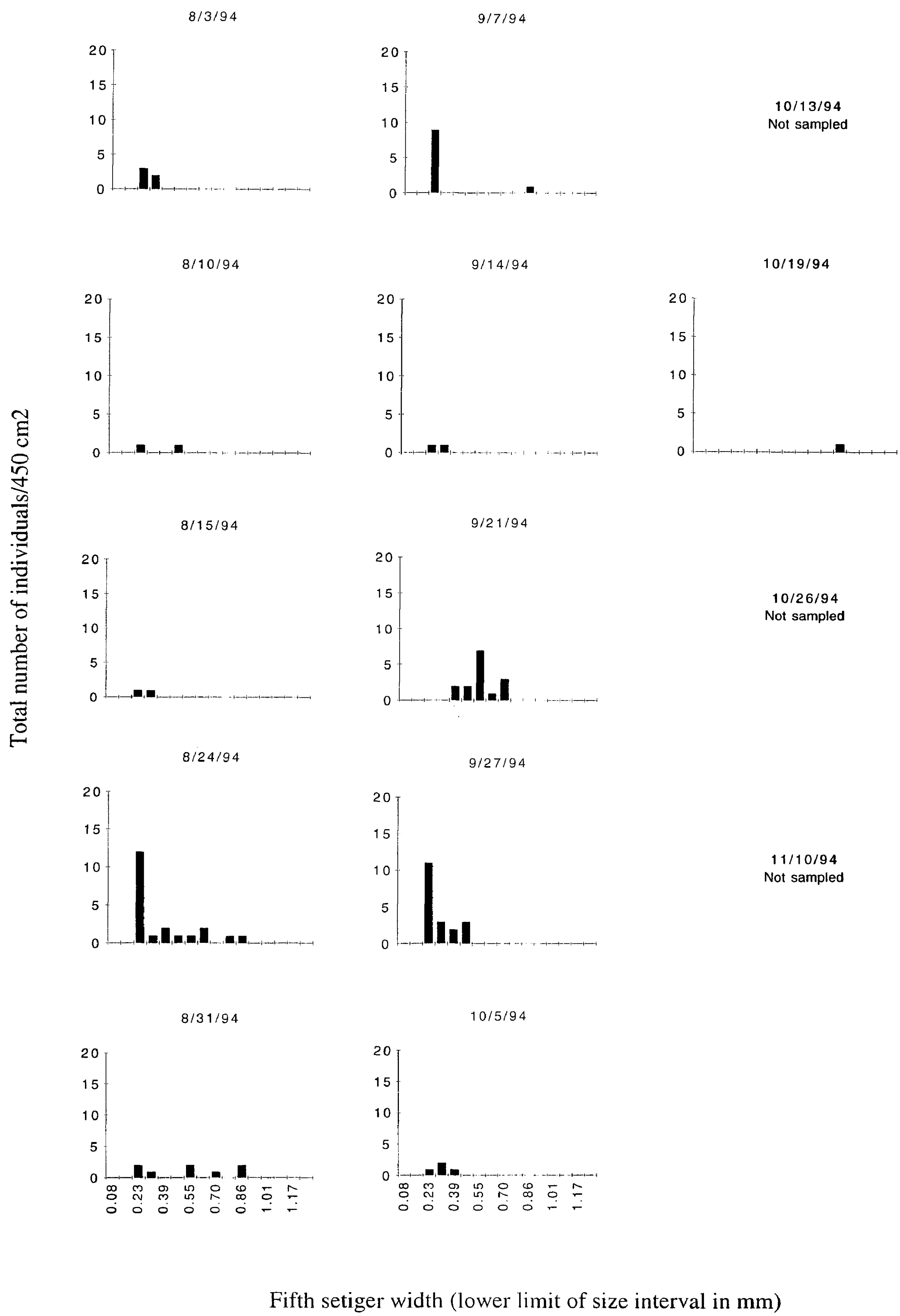

8/3/94
9/7/94
10/13/94
Not sampled
8/10/94
9/14/94
10/19/94
8/15/94
9/21/94
10/26/94
Not sampled
8/24/94
9/27/94
11/10/94
Not sampled
8/31/94
10/5/94
0
5
10
15
20
0.08
0.23
0.39
0.55
0.70
0.86
1.01
1.17
Total number of individuals/450 cm2
Fifth setiger width (lower limit of size interval in mm)

Figure 8. *Paraprionospio pinnata*. Size frequency histogram for the Yorktown station based on width of fifth setiger. The size class interval is 0.078 mm.

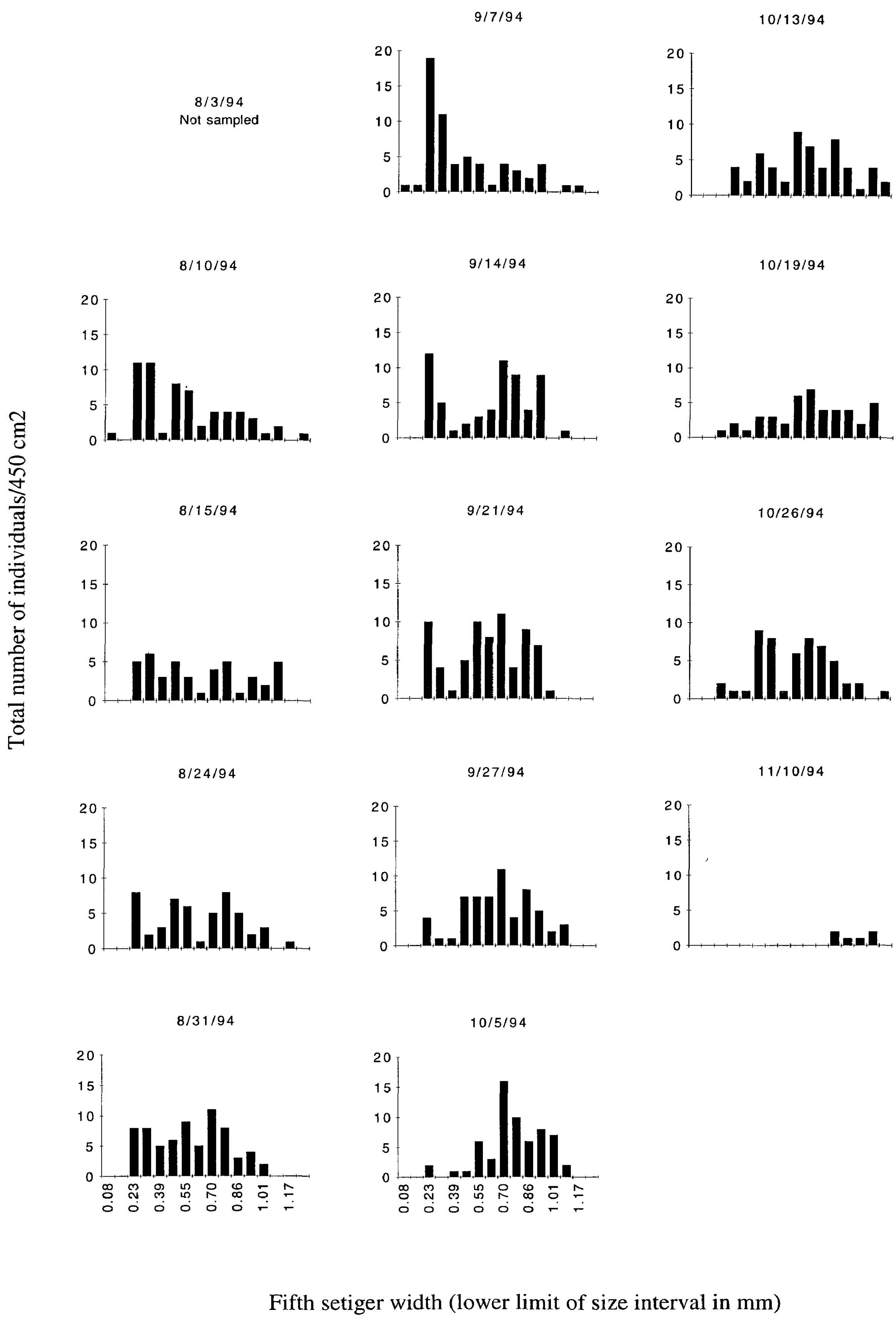

8/3/94
Not sampled
9/7/94
10/13/94
8/10/94
9/14/94
10/19/94
8/15/94
9/21/94
10/26/94
8/24/94
9/27/94
11/10/94
8/31/94
10/5/94
0
5
10
15
20
0.08
0.23
0.39
0.55
0.70
0.86
1.01
1.17
Total number of individuals/450 cm2
Fifth setiger width (lower limit of size interval in mm)

Figure 9. *Paraprionospio pinnata*. Size frequency histogram for the Gloucester Point station based on width of fifth setiger. The size class interval is 0.078 mm.

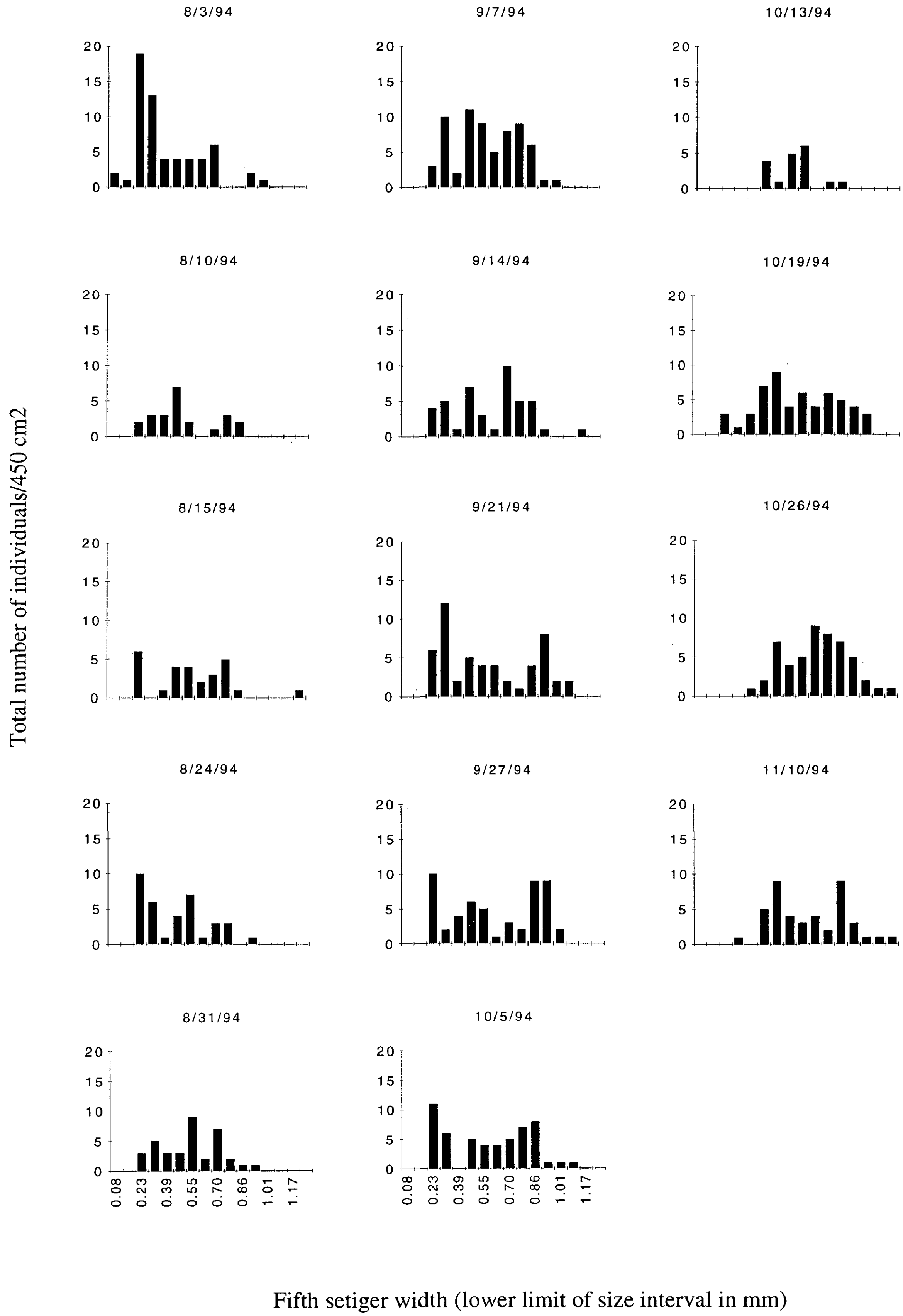
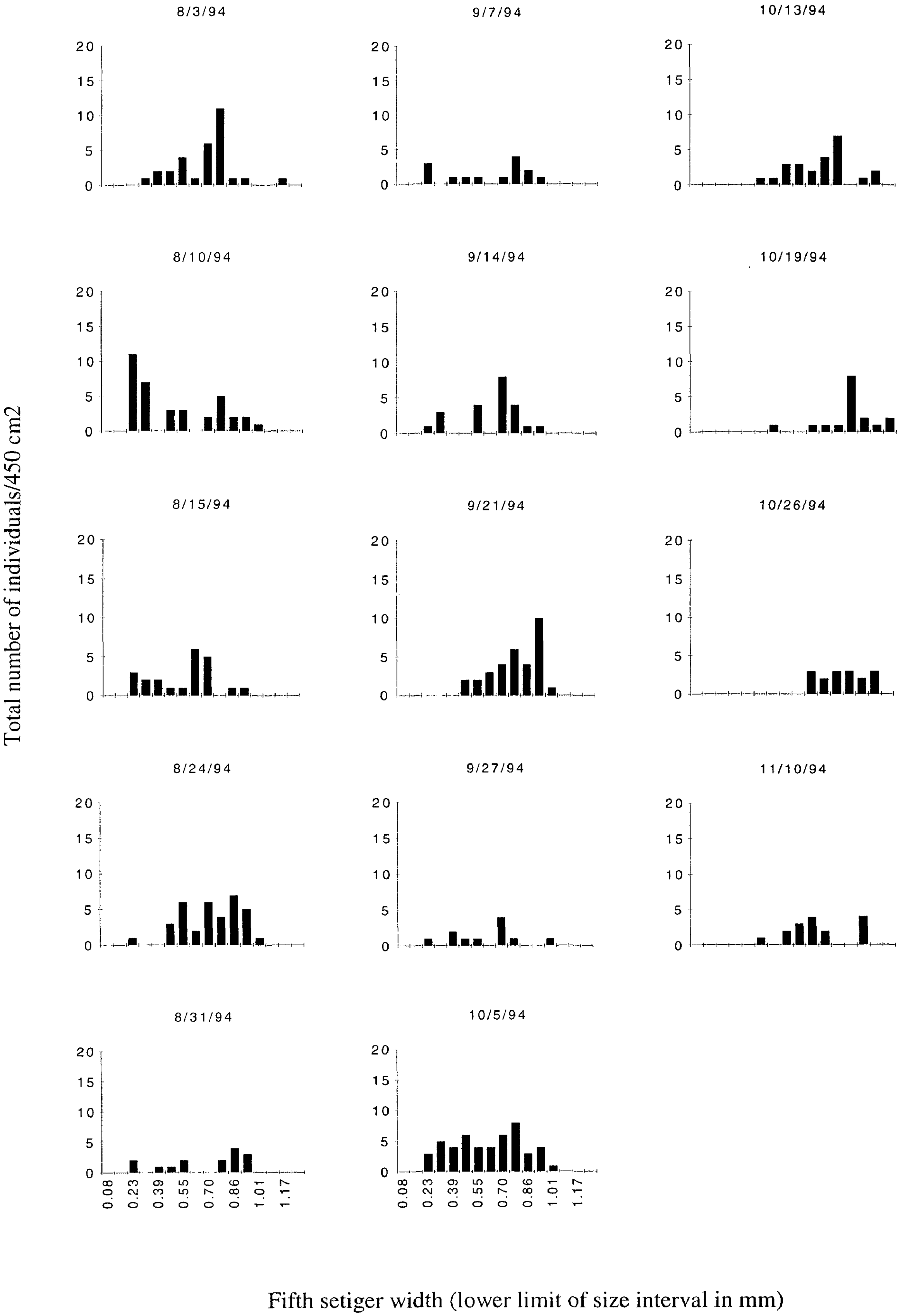
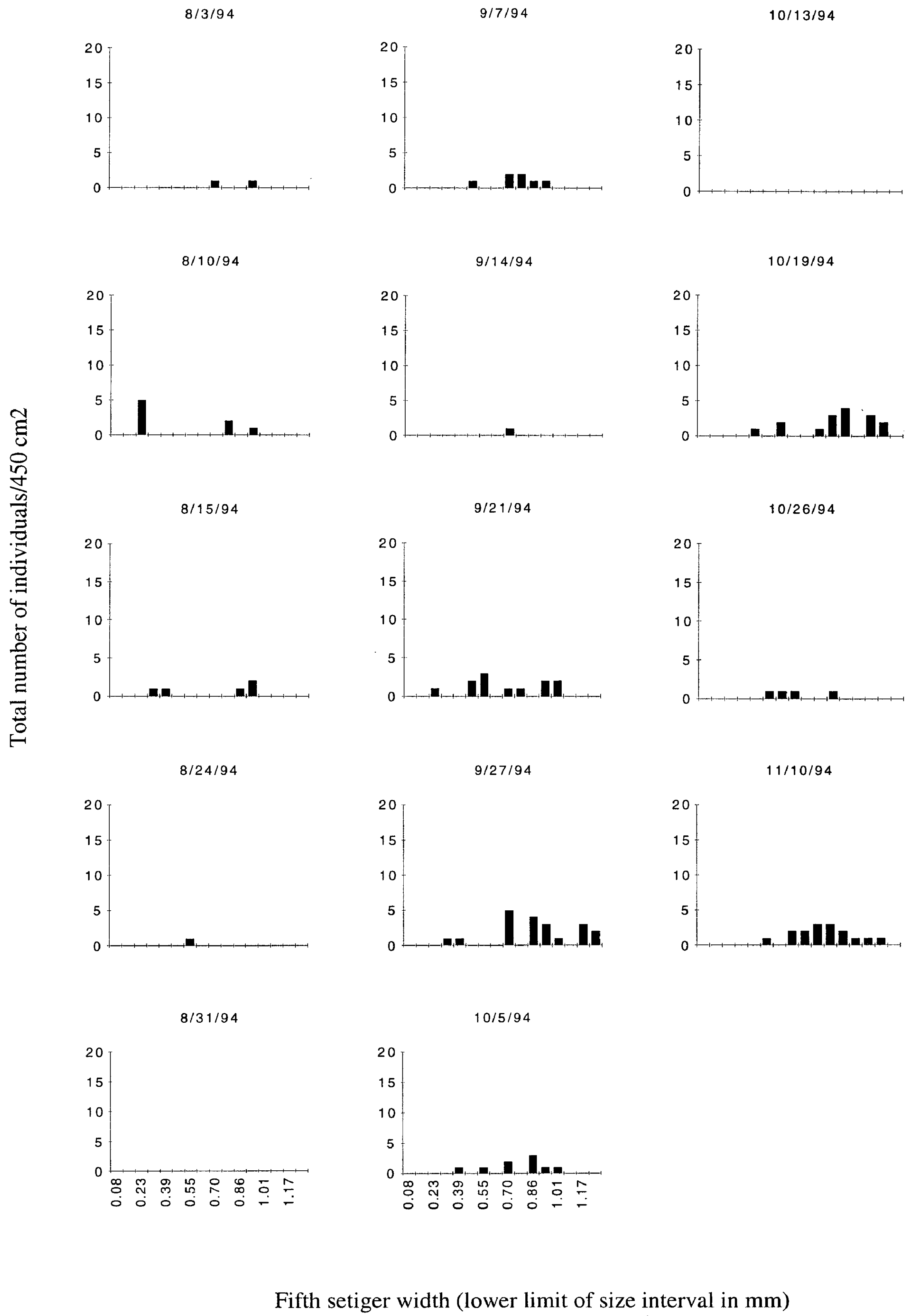

8/3/94
9/7/94
10/13/94
8/10/94
9/14/94
10/19/94
8/15/94
9/21/94
10/26/94
8/24/94
9/27/94
11/10/94
8/31/94
10/5/94
0
5
10
15
20
0.08
0.23
0.39
0.55
0.70
0.86
1.01
1.17
Total number of individuals/450 cm2
Fifth setiger width (lower limit of size interval in mm)

Figure 10. *Paraprionospio pinnata*. Size frequency histogram for the Aberdeen station based on width of fifth setiger. The size class interval is 0.078 mm.



8/3/94
9/7/94
10/13/94
8/10/94
9/14/94
10/19/94
8/15/94
9/21/94
10/26/94
8/24/94
9/27/94
11/10/94
8/31/94
10/5/94
0
5
10
15
20
0.08
0.23
0.39
0.55
0.70
0.86
1.01
1.17
Total number of individuals/450 cm2
Fifth setiger width (lower limit of size interval in mm)

Figure 11. *Paraprionospio pinnata.* Size frequency histogram for the Purtan station based on width of fifth setiger. The size class interval is 0.078 mm.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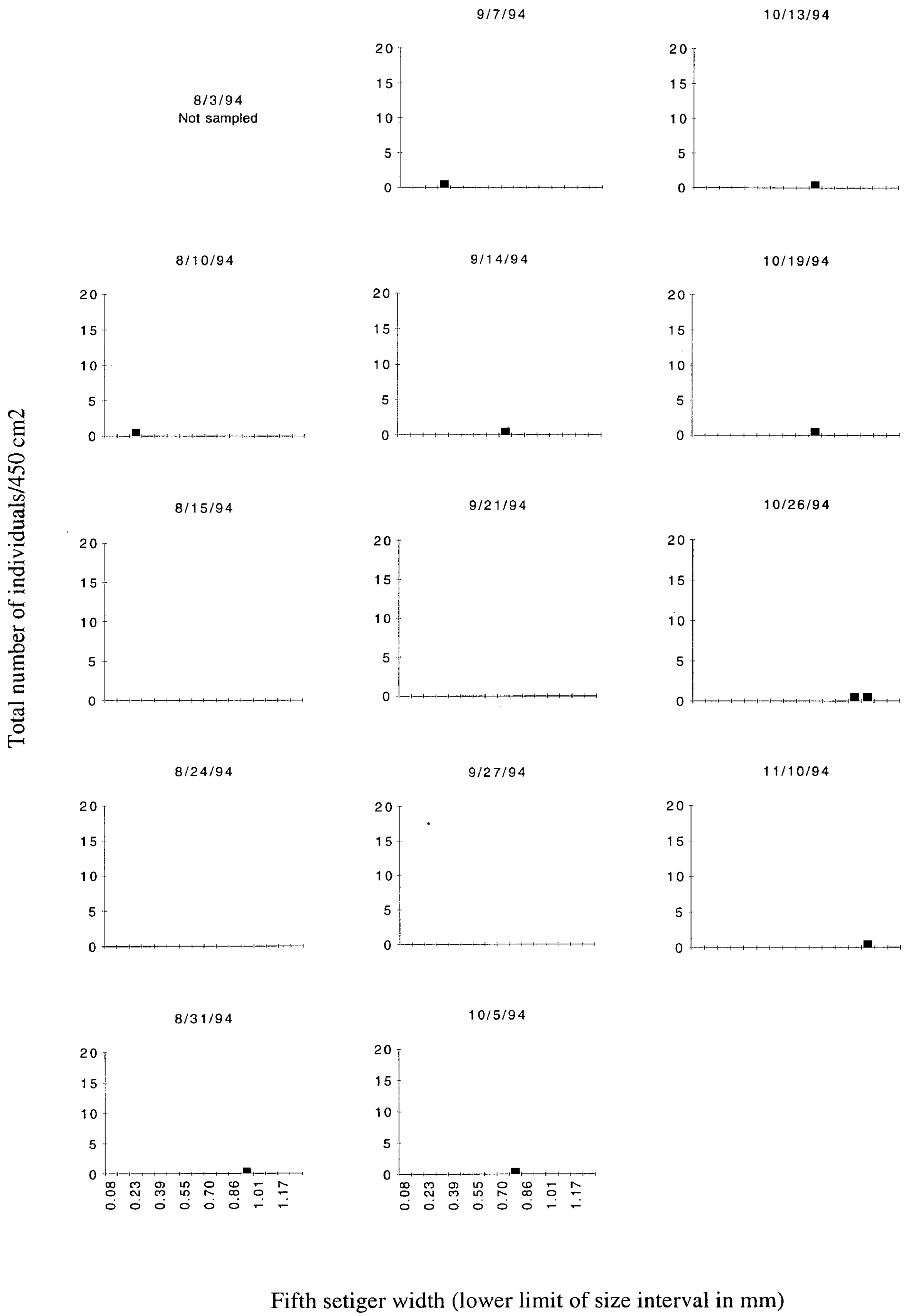
9/7/94
10/13/94
8/10/94
9/14/94
10/19/94
8/15/94
9/21/94
10/26/94
8/24/94
9/27/94
11/10/94
8/31/94
10/5/94
0
5
10
15
20
0.08
0.23
0.39
0.55
0.70
0.86
1.01
1.17
Total number of individuals/450 cm2
Fifth setiger width (lower limit of size interval in mm)

Figure 12. *Paraprionospio pinnata*. Size frequency histogram for the Terrapin Point station based on width of fifth setiger. The size class interval is 0.078 mm.



9/7/94
10/13/94
8/3/94
Not sampled
8/10/94
9/14/94
10/19/94
8/15/94
9/21/94
10/26/94
8/24/94
9/27/94
11/10/94
8/31/94
10/5/94
20
15
10
5
0
0.08
0.23
0.39
0.55
0.70
0.86
1.01
1.17
Total number of individuals/450 cm2
Fifth setiger width (lower limit of size interval in mm)

October for all stations except Purtan and Terrapin Point, which had few to no recruits, respectively (Fig. 13).

The maximum number of recruits was observed at the Yorktown and Gloucester Point stations, which experienced similar temperature and salinity regimes but different dissolved oxygen concentrations (Fig. 13). A Kolmogorov-Smirnov two-sample test indicated that the two recruitment distributions associated with the Yorktown and Gloucester Point stations were similar ($P<0.05$).

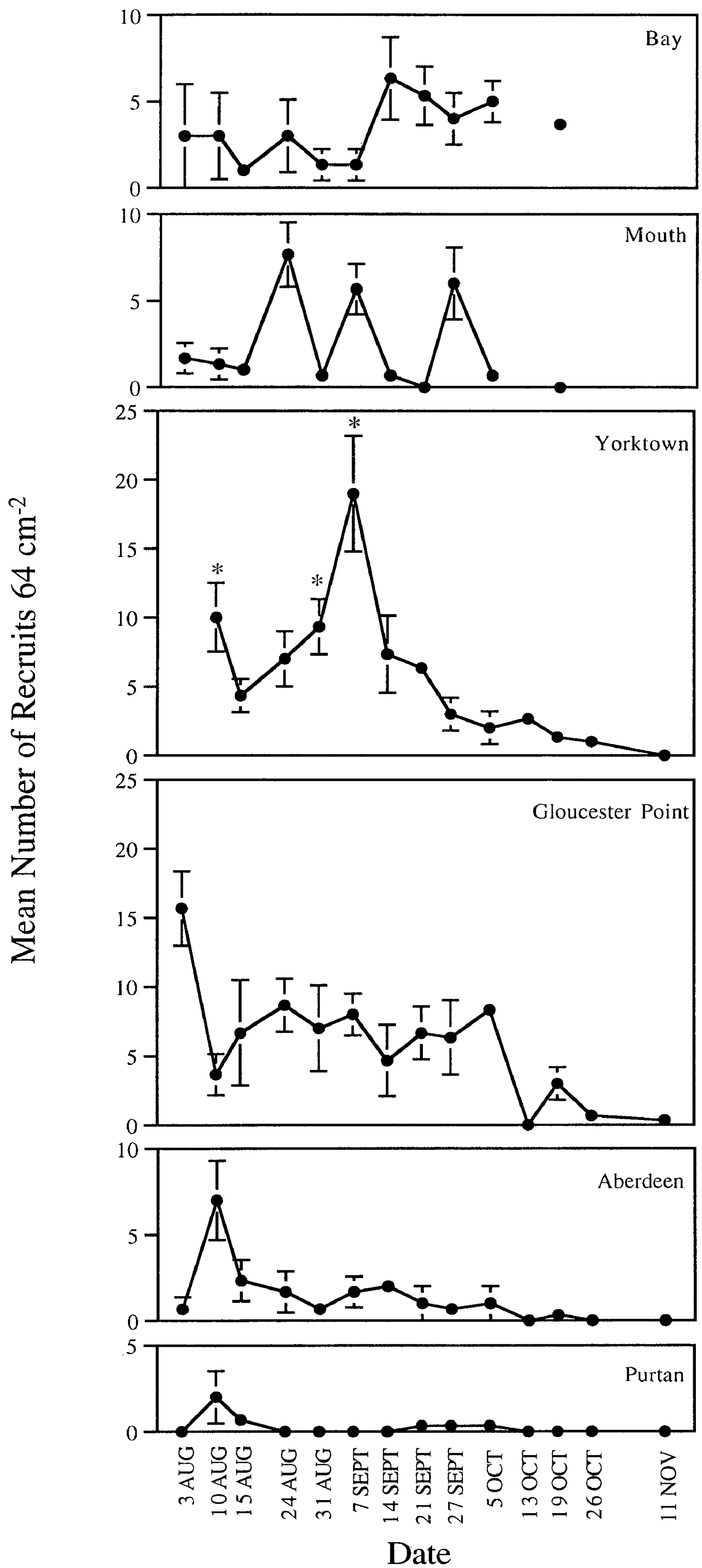
Production estimates

The relationship between fifth setiger width and mean individual weight (AFDW) was determined to be: $\ln(\mathrm{AFDW}) = 3.049 \ln(\mathrm{width}) + 0.104$ ($r^2 = 0.99$, $n = 5$). This regression did not change when calculated for worms collected from different salinities. Thus it was assumed that the worms exhibited isometric growth along the estuarine gradient, and the above equation was used to estimate *Paraprionospio pinnata* biomass for all stations.

Because cohorts were not distinguishable, the size-frequency method was utilized to estimate production. The production estimates calculated for the entire study period are given in Table 2, and the production estimates calculated for the 57 day interval when all stations were sampled are shown in Fig. 14. The secondary production for *Paraprionospio pinnata* varied among stations (Fig. 14). The average production was highest for the mid-salinity Yorktown and Gloucester Point stations (82.9 mg AFDW 225 cm^{-2} 57 d^{-1} and 50.8 mg AFDW 225 cm^{-2} 57 d^{-1}, respectively). The lowest production estimates were obtained from the high and low salinity stations.

The P/B ratios for the seven stations were relatively uniform (Table 2). The Mouth station had the highest P/B ratio (3.6), which suggests a rapid turn-over of the population.

Figure 13. *Paraprionospio pinnata.* Mean number of recruited individuals 64 cm^{-2} (with SE) for each sampling date at stations exhibiting recruitment. Asterisks indicate dates when hypoxic oxygen concentrations were observed (<2 mg l^{-1}).

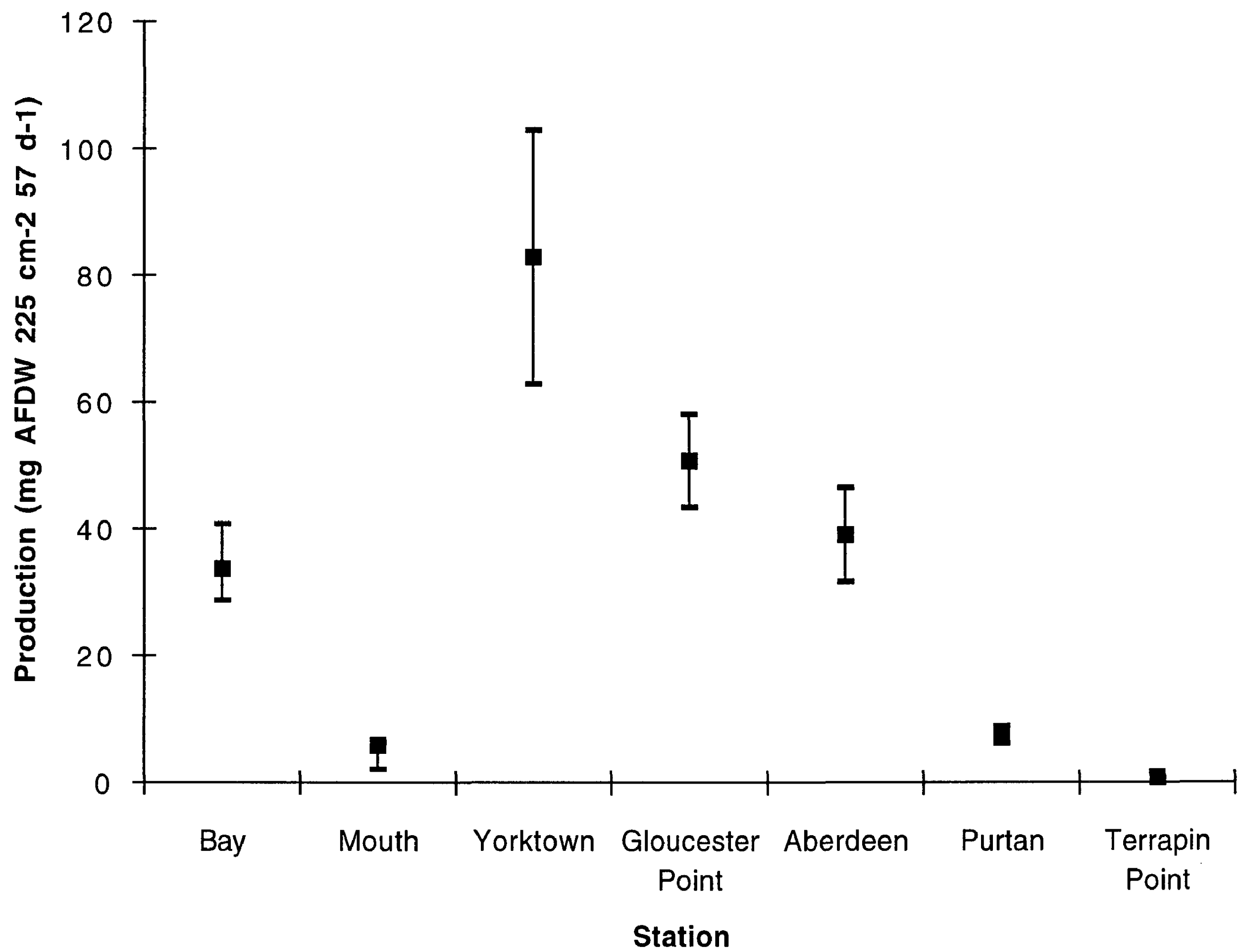


Bay
Mouth
Yorktown
Gloucester Point
Aberdeen
Purtan
Mean Number of Recruits 64 cm-2
3 AUG
10 AUG
15 AUG
24 AUG
31 AUG
7 SEPT
14 SEPT
21 SEPT
27 SEPT
5 OCT
13 OCT
19 OCT
26 OCT
11 NOV
Date

Table 2. *Paraprionispio pinnata.* Secondary production for the seven study sites. Methods used to calculate averages are described in the text.

Station	Period for which there are data	Average production (mg AFDW 225 cm^{-2} total d^{-1})	Average specific production (mg AFDW 225 cm^{-2} d^{-1})	P/B
Bay	77 d	41.8	0.6	2.7
Mouth	77 d	6.3	0.1	3.6
Yorktown	93 d	110.2	1.5	2.5
Gloucester Point	100 d	68.9	0.9	2.6
Aberdeen	100 d	50.7	0.7	2.1
Purtan	100 d	17.8	0.1	1.2
Terrapin Point	93 d	2.6	0.02	2.7

Figure 14. *Paraprionospio pinnata.* Average production estimates (mg AFDW 225 cm^{-2} 57 d^{-1}) for the seven stations. Vertical bars represent maximum and minimum estimates. Methods used to calculate averages and ranges are described in the text.


120
100
80
60
40
20
0
Production (mg AFDW 225 cm-2 57 d-1)
Bay
Mouth
Yorktown
Gloucester Point
Aberdeen
Purtan
Terrapin Point
Station

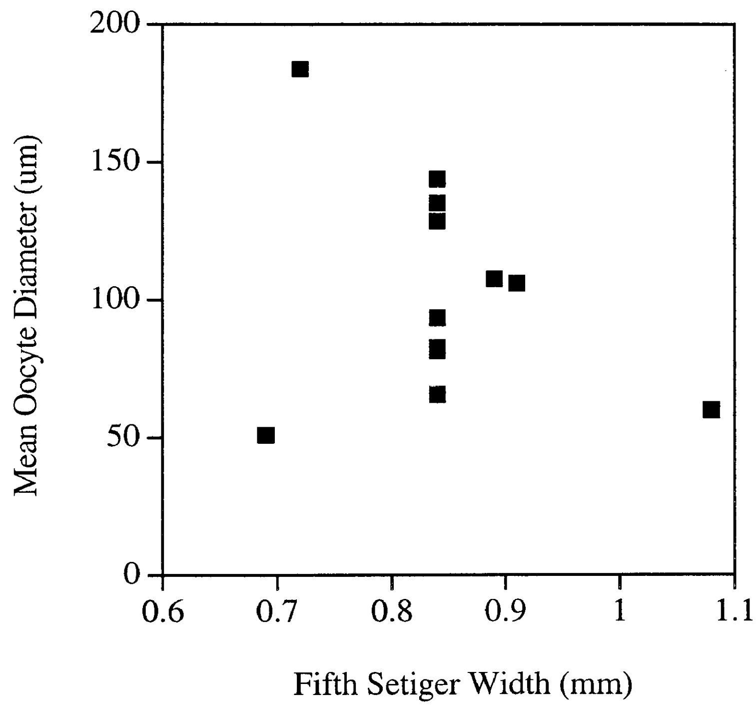
The population was dominated by small sized individuals, which resulted in a low biomass for this station. The lowest P/B ratio occurred at the Purtan station (1.2), indicating that not much excess production was observed at this station.

Fecundity estimates

Gravid females were observed in the samples from August 3 to October 13, and were collected from all stations except the Mouth and Terrapin Point. There was a surprising low numer of gravid females collected during this study. A total of 17 gravid females were collected, of which 12 were entire and had not lost oocytes as a result of worm breakage. This number represents less than 1% of all worms collected.

The smallest gravid female collected had a fifth setiger width of 0.69 mm and the largest a fifth setiger width of 1.08 mm (Fig. 15). In the worms collected, oocytes were present in the coelom from setiger 13-20 to within the last 14-40 setigers. There was no apparent relationship between mean oocyte diameter and size of gravid female (Fig. 15) or sampling date (Fig. 16). This lack of trends could have resulted from the small sample size. There was a relationship between the total number of setigers and the number of oovigerous setigers, as there are more gametic segments in a longer worm (Fig. 17).

Figure 15. *Paraprionospio pinnata.* Mean coelomic oocyte diameter versus fifth setiger width.



200
150
100
50
0
Mean Oocyte Diameter (um)
0.6
0.7
0.8
0.9
1
1.1
Fifth Setiger Width (mm)

Figure 16. *Paraprionospio pinnata*. Mean coelomic oocyte diameter per sampling date.

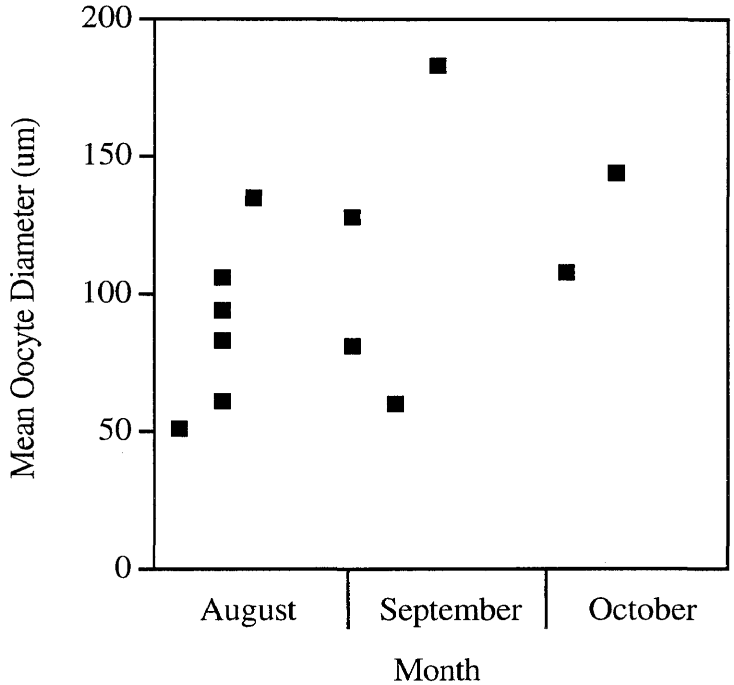
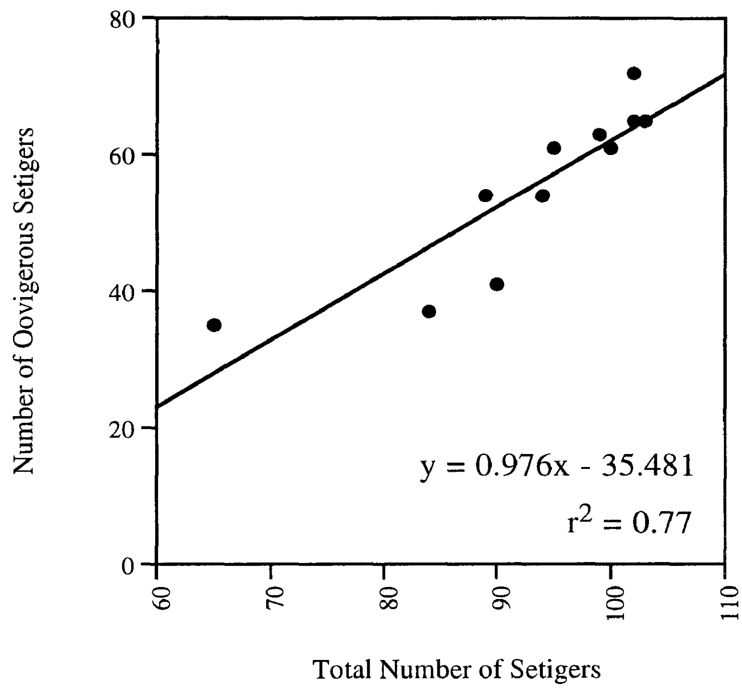

200
150
100
50
0
Mean Oocyte Diameter (um)
August
September
October
Month

Figure 17. *Paraprionospio pinnata*. Number of oovigerous setigers versus total number of setigers for gravid females.



Number of Oovigerous Setigers
Total Number of Setigers
y = 0.976x - 35.481
r2 = 0.77
0
20
40
60
80
60
70
80
90
100
110

DISCUSSION

Paraprionospio pinnata densities were highest at the lower York stations and the Bay station. The decreased density of *P. pinnata* encountered at the mouth of the York was the exception to this trend and is possibly be attributed to sediment heterogeneity. Sediments were inundated with shell fragments and dead hydroids, and could thus represent a sub-optimal habitat for *P. pinnata* settlement and colonization. Similar distribution patterns for *P. pinnata* have been observed in past studies for the same time period in the York River (Table 3). While broadly distributed in the York River during this study, *Paraprionospio pinnata* did exhibit high small-scale patchiness (on the order of meters), as evidenced by the relatively large standard errors associated with the mean abundance estimates (Fig. 5). Such population patchiness was also reported by Dauer at al. (1995).

In general, *Paraprionospio pinnata* densities were highest in the the polyhaline (18 to 25 psu) and high mesohaline (10 to 18 psu) Bay and lower York stations. The highest density of *P. pinnata* (35 individuals 225 cm^{-2}) occurred at the Yorktown station, which is located in an area of the lower York River that has historically experienced periodic recurring hypoxia (Haas 1977; Kou and Neilson 1987; Diaz et al. 1992; Neubauer 1993) and was observed to be hypoxic during this study. Neubauer (1993) observed a trend of increased *P. pinnata* abundance at stations that experienced hypoxia, but did not find a significant effect of low dissolved oxygen concentrations on abundance, mean individual weight, or total production. *Paraprionospio pinnata* dominance in this area was therefore attributed to resistance of this species to hypoxia (Neubauer 1993; Diaz and Rosenberg 1995). The observation that a *P. pinnata* population near the mouth of the Rapphannock River maintained ot increased its abundance during low dissolved oxygen events in 1987

Table 3. *Paraprionospio pinnata* . Comparison of distribution and abundance in the York River and lower Bay. H indicates station is located in an area of the of the York River that experiences hypoxia.

Location	Station code	Depth (m)	Date	Abundance (ind. m^{-2})	Salinity (psu)	Percent sand	Reference
Mainstem Bay (off York mouth)	Bay	11	8/10/94	444	--	68.2	Hinchey (present study)
Mainstem Bay (off York mouth)	Bay	11	9/14/94	978	25	68.2	Hinchey (present study)
Mainstem Bay (off York mouth)	Bay	11	10/19/94	911	26	68.2	Hinchey (present study)
Mainstem Bay (off York mouth)	CB6.4	14	9/13/94	689	15	49.3	Dauer et al. (1995)
Mainstem Bay (off York mouth)	CB6.4	10	9/8/93	471	22	51.9	Dauer et al. (1994)
Mainstem Bay (off York mouth)	CB6.4	11	10/3/89	777	22	51.9	Dauer et al. (1990)
Mainstem Bay (off York mouth)	CB6.4	11	9/15/88	652	26	59.1	Dauer et al. (1989)
Mainstem Bay (off York mouth)	CB6.4	11	10/13/87	942	23	79.1	Dauer et al. (1988)
Mainstem Bay (off York mouth)	CB6.4	11	9/26/86	362	28	29.4	Dauer et al. (1987)
Lower Bay	Wolf Trap	10-14	11/83 - 11/84	533	20-27	50-60	Schaffner (1987)
Lower Bay	Wolf Trap	10-14	11/83	450-575	20-27	50-60	Huggett (1987)
Lower Bay	Wolf Trap	10-14	8/8	200-250	20-27	50-60	Huggett (1987)

Location	Station code	Depth (m)	Date	Abundance (ind. m^{-2})	Salinity (psu)	Percent sand	Reference
Lower York	Yorktown[H]	15	8/10/94	1333	--	32.2	Hinchey (present study)
Lower York	Yorktown[H]	15	9/14/94	1356	18	32.2	Hinchey (present study)
Lower York	Yorktown[H]	15	10/19/94	978	21	32.2	Hinchey (present study)
Lower York	Yorktown[H]	15	11/10/94	133	18	32.2	Hinchey (present study)
Lower York	LE4.3B[H]	16	9/15/94	689	22	29.1	Dauer et al. (1995
Lower York	LE4.3B[H]	16	9/8/93	181	22	6.0	Dauer et al. (1994)
Lower York	LE4.3B[H]	16	10/3/89	1739	19	6.1	Dauer et al. (1990)
Lower York	B[H]	10-14	8/4-8/31/89	2500-3900	17-20	19.9	Neubauer (1993)
Lower York	B[H]	10-14	9/12/89	2100	23	19.9	Neubauer (1993)
Lower York	C[H]	14-20	8/4-8/31/89	1400-4100	17-20	7.3	Neubauer (1993)
Lower York	C[H]	14-20	9/12/89	2200	23	7.3	Neubauer (1993)
Lower York	D[H]	> 20	8/4-8/31/89	1100-3400	17-20	22.0	Neubauer (1993)
Lower York	D[H]	> 20	9/12/89	1400	23	22.0	Neubauer (1993)
Lower York	LE4.3B[H]	16	9/16/88	290	23	76.8	Dauer et al. (1989)
Lower York	Gloucest. Pt.	15	8/10/94	511	--	16.4	Hinchey (present study)
Lower York	Gloucest. Pt.	15	9/14/94	956	19	16.4	Hinchey (present study)
Lower York	Gloucest. Pt.	15	10/19/94	1222	20	16.4	Hinchey (present study)
Lower York	Gloucest. Pt.	15	11/10/94	956	18	16.4	Hinchey (present study)

Location	Station code	Depth (m)	Date	Abundance (ind. m^{-2})	Salinity (psu)	Percent sand	Reference
Lower York	LE4.3	7	9/14/94	164	17	72.5	Dauer et al. (1995)
Lower York	LE4.3	7	9/8/94	199	21	84.7	Dauer et al. (1994)
Lower York	PB	9	11/90	120	17	20-30	Diaz (unpublished)
Lower York	A	5-10	8/4-8/31/89	373-1200	17-20	61.7	Neubauer (1993)
Lower York	A	5-10	9/12/89	2382	23	61.7	Neubauer (1993)
Lower York	LE4.3	7	10/3/89	996	18	60.4	Dauer et al. (1990)
Lower York	PB	9	8/89	130	--	20-30	Diaz (unpublished)
Lower York	LE4.3	7	9/16/88	109	24	86.8	Dauer et al. (1989)
Lower York	LE4.3	7	9/28/87	308	23	91.9	Dauer et al. (1998)
Lower York	LE4.3	9	9/27/86	72	24	4.9	Dauer et al. (1987)
Lower York	PB	9	11/86	150	--	20-30	Diaz (unpublished)
Lower York	PB	9	10/85	105	--	20-30	Diaz (unpublished)
Lower York	PB	9	11/74	700	24	20-30	Boesch et al. (1976)
Lower York	PB	9	11/73	650	24	20-30	Boesch et al. (1976)
Lower York	PB	9	11/72	0	12	20-30	Boesch et al. (1976)
Middle York	Purtan	9	8/10/94	178	--	10.4	Hinchey (present study)
Middle York	Purtan	9	9/14/94	22	16	10.4	Hinchey (present study)
Middle York	Purtan	9	10/19/94	356	14	10.4	Hinchey (present study)

Location	Station code	Depth (m)	Date	Abundance (ind. m^{-2})	Salinity (psu)	Percent sand	Reference
Middle York	Purtan	9	11/10/94	356	14	10.4	Hinchey (present study)
Middle York	LE4.1	8	9/15/94	71	11	12.5	Dauer et al. (1995)
Middle York	LE4.1	8	9/9/93	0	18	61.7	Dauer et al. (1994)
Middle York	LE4.1	8	10/3/89	54	16	51.7	Dauer et al. (1990)
Middle York	LE4.1	8	9/16/88	109	19	80.4	Dauer et al. (1989)
Middle York	LE4.1	9	9/28/87	36	20	82.3	Dauer et al. (1988)
Middle York	LE4.1	9	9/27/86	72	24	74.5	Dauer et al. (1987)
Upper York	Terrapin Pt.	5	8/10/94	22	--	3.8	Hinchey (present study)
Upper York	Terrapin Pt.	5	9/14/94	22	12	3.8	Hinchey (present study)
Upper York	Terrapin Pt.	5	10/19/94	22	10	3.8	Hinchey (present study)
Upper York	Terrapin Pt.	5	11/10/94	22	12	3.8	Hinchey (present study)
Upper York	RET4.3	6	9/15/94	0	13	3.9	Dauer et al. (1995)
Upper York	RET4.3	6	9/9/93	0	13	8.0	Dauer et al. (1994)
Upper York	RET4.3	6	10/3/89	0	10	40.3	Dauer et al. (1990)
Upper York	RET4.3	7	9/16/88	18	15	13.6	Dauer et al. (1989)
Upper York	RET4.3	7	9/28/87	0	15	6.4	Dauer et al. (1988)
Upper York	RET4.3	6	9/27/86	54	17	11.5	Dauer et al. (1987)

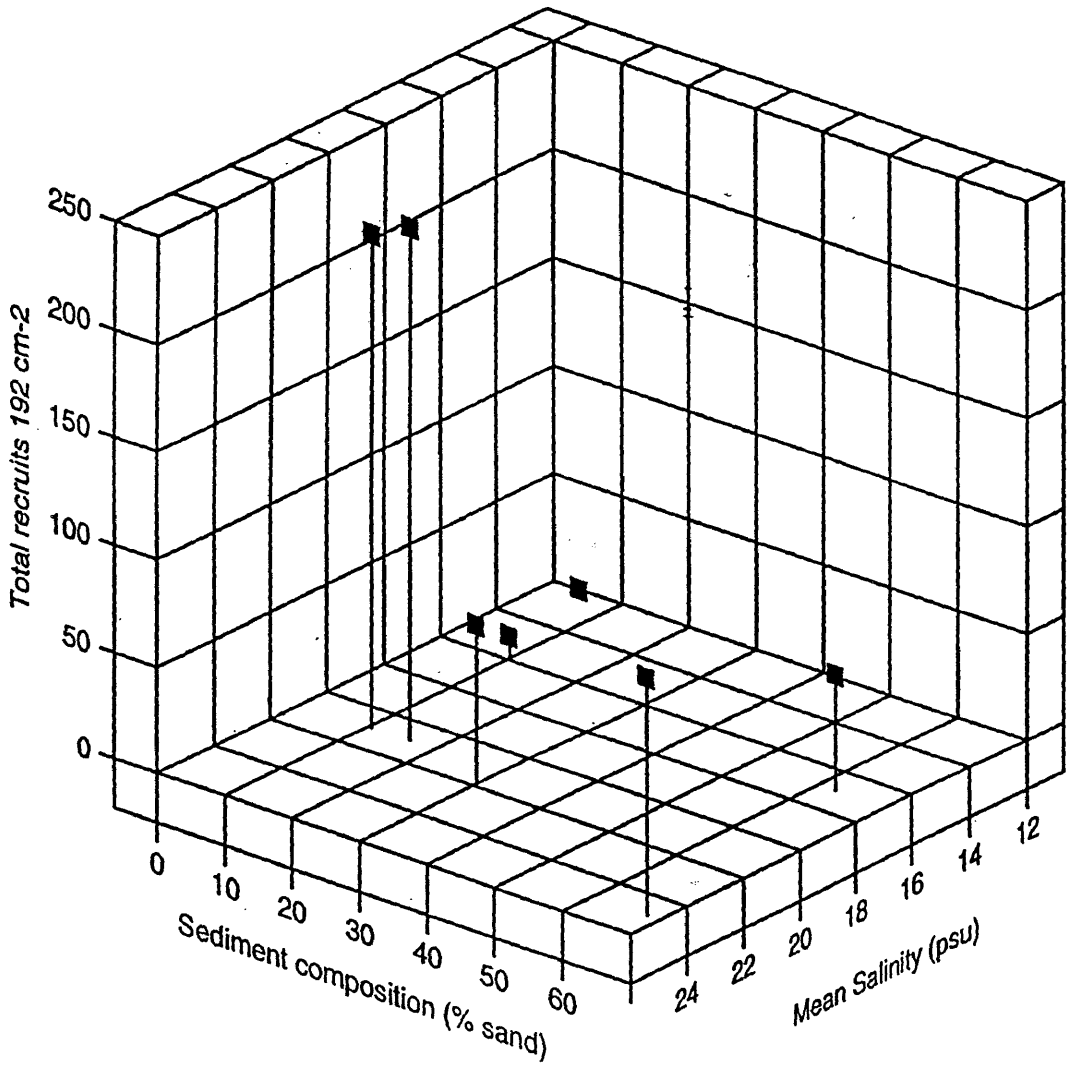
led to the conclusion that this species can survive moderate hypoxia (Llansó 1992). Although *P. pinnata* did experience reduced abundance during severe hypoxic events (<1 mg l^{-1}), it did not suffer the large mortalities experienced by other species in the afflicted area (Llansó 1992).

Paraprionospio pinnata secondary production varied along the estuarine gradient. Secondary production estimates were highest for the polyhaline-high mesohaline stations, suggesting that the greatest amount of *P. pinnata* production available for transfer to higher trophic levels is produced by populations in the lower York River. When converted to units of mg AFDW m^{-2}, the production value for the Yorktown station (64.6 mg AFDW m^{-2} d^{-1}) was higher than the production estimates calculated for the same area of the York River by Neubauer (1993). Neubauer's estimates for total production were calculated for June 23 to September 12, 1989 and ranged from 5.9 to 18.6 mg AFDW m^{-2} d^{-1}.

The continuous recruitment of new individuals into the benthic population at all stations but Terrapin Point resulted in a lack of a significant effect of time in the regression equation relating mean abundance to time, mean salinity, and percent sand composition of the sediment. Stations with the highest mean numbers of newly recruited individuals had the highest mean densities of adults, suggesting a high survival rate of settled juveniles. At the Yorktown station the two highest peaks in recruitment coincided with periods of hypoxia, but the distribution of recruits at this station was not significantly different from that of the nearby normoxic Gloucester Point station. Recruitment pulses of *P. pinnata* in the lower York River were also observed during periods of most severe hypoxia in 1989 (Neubauer 1993).

Paraprionospio pinnata recruited across a broad range of salinity, sediment composition and time, with peak recruitment at stations with a mean salinity of 21 psu and sand content of 10.8 to 16.4 percent (Fig. 18). Neither salinity nor sediment alone could be used as predictors of recruitment. For example, stations with similar salinities

Figure 18. *Paraprionospio pinnata.* Total number of recently recruited individuals 192 cm^{-2} as a function of sediment composition (percent sand content) and mean salinity (psu) for the seven stations.



Total recruits 192 cm-2
250
200
150
100
50
0
0
10
20
30
40
50
60
Sediment composition (% sand)
24
22
20
18
16
14
12
Mean Salinity (psu)

(Aberdeen and Purtan) experienced different levels of recruitment. Likewise, recruitment varied greatly at stations with similar sediment composition (Yorktown and Purtan). Adult *P. pinnata* collected in Galveston Bay, Texas, were determined to be monotelic (individuals breed once per lifetime, gametes released in one or a few large batches, Olive and Clark 1978) but due to the species' extended breeding season, multiple generations of worms were produced during the summer (Mayfield 1988). In the Texas population, spawning occurred from late April to late June, and recruitment occurred from June through December .

Few gravid females (less than 1% of all worms collected) were collected during the course of this study. It was expected that more gravid females would be observed in the samples, because spawning is believed to occur in the summer months and recruitment was observed during this study. Perhaps visual inspection of the coelom using a dissecting scope was not sensitive enough to detect developing oocytes. It is expected, however, that even if the visual inspection technique did not detect individuals with smaller, developing oocytes, any individuals which were ready to spawn and had larger oocytes in the coelom would have been easily detected.

Paraprionospio pinnata produces large numbers of small eggs, characteristic of polychaetes that produce planktotrophic larvae. Average fecundity ranged from 1204 to 11,088 oocytes per worm, depending on the size of the worm. This range was comparable to the average fecundity of 6000 oocytes per individual estimated from four gravid *P. pinnata* females in Galveston Bay (Mayfield 1988). When compared to other *Paraprionospio* species, *P. pinnata* fecundity in the York River fell within the low end of the range of 3100 to 43,000 oocytes per worm reported for *Paraprionospio* sp. (form A) in Japan (Yokoyama 1981). The average diameter of oocytes in the coelom was 51 to 184 µm, and was comparable to other ranges reported for *Paraprionospio pinnata* (100 to 150 µm, Mayfield 1988) and *Paraprionospio* sp. (form A) (10 to 110 µm, Yokoyama 1981).

Similar small oocyte diameters were reported for other species with planktotrophic development, such as *Streblospio benedicti* (70 to 90 µm, Levin 1984) and *Loimia medusa* (133-160 µm, Seitz and Schaffner 1995).

Although *Paraprionospio pinnata* is classified as a euryhaline opportunistic species characteristically abundant in salinities of 10 to 20 psu (Boesch 1977), the high degree of interspecific variation in its population parameters along the estuarine gradient indicate it only exhibits opportunistic behavior in the polyhaline-high mesohaline regions of the lower York River (Table 4). At this location in the estuary *P. pinnata* recruits in large numbers, exhibits high densities and production, and is tolerant of low dissolved oxygen concentrations, all characteristics of opportunistic species (Grassle and Grassle 1974). The differences in *P. pinnata* demography cannot be completely explained by sediment composition, dissolved oxygen concentration or salinity alone. It may be more appropriate to consider *P. pinnata* as a limited euryhaline opportunistic species, that functions as an opportunist over restricted ranges of environmental parameters.

Other studies have also shown that the opportunistic response of polychaetes can be variable. A study in a Connecticut estuary found that the well-known opportunistic species, *Streblospio benedicti* and a species of *Capitella*, actually only exhibited opportunistic responses to disturbance in one or two months out of the year (Zajac and Whitlatch 1982). Also, a recent survey by Weisberg et al. (in press) found that in Chesapeake Bay, the abundance of the *Mediomastus ambiseta* decreases at polluted sites when compared to non-polluted reference sites. This capetellid polychaete had previously been considered an opportunistic species whose presence was used as an indicator of pollution stressed areas.

These examples and the results of my study suggest that the opportunistic response of a species may depend on the time of year or on historical features of a particular habitat (sensu Zajac and Whitlatch 1982). As many opportunistic polychaetes are used as

Table 4. *Paraprionospio pinnata*. Relative density, abundance, and recruitment at different salinity regimes in the York River. H indicates region of the York River known to experience hypoxia. N indicates normoxic region of the York River.

Salinity zone	Density	Recruitment	Production
Polyhaline	Intermediate	Intermediate	Intermediate
Polyhaline- high mesohaline^{H}	Highest	Highest	Highest
Polyhaline- high mesohaline^{N}	High	High	Intermediate
High mesohaline	Intermediate	Intermediate	Intermediate
Low mesohaline	Lowest	Lowest	Lowest

indicators of pollution or disturbance, the examination of species life history characteristics for the particular habitat in question is essential.

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