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THE INFLUENCE OF POST-SETTLEMENT MORTALITY ON RECRUITMENT PATTERNS IN A SOFT-BOTTOM HABITAT

A Thesis

Presented to

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The College of William and Mary in Virginia

In Partial Fulfillment

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Master of Arts

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by

Erik Christian Zobrist

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APPROVAL SHEET

This thesis is submitted in partial fulfillment of

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DEDICATION

To my parents, B.K. and Donna Mae.

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ABSTRACT

Distributional patterns of recruiting benthic invertebrates can be determined not only by patterns of settlement but also by early post-settlement mortality. The relative importance of these two processes on early population dynamics necessitates an appropriate sampling scheme. Weekly samples were taken across a depth/sediment gradient (3, 6, 9, 12, 18 meters; 75% to 5 % sand) in the York River, Virginia, U.S.A. during spring, 1985. Sediment grain size and adult communities change along this gradient. A small-mesh sieve (125 um) was used to capture the smallest macrofauna juveniles and aid in distinguishing between settlement and early post-settlement mortality of recruits. These data reveal species-specific patterns of settlement and of early post-settlement mortality in determining recruitment along this environmental gradient.

Of the 32 species which recruited, 3 polychaetes appeared in great enough abundances to distinguish patterns across the transect. Abundances of the ampharetid *Asabellides oculata* and the phyllodicid *Eteone heteropoda* indicate that differential settlement played an important role in defining recruitment patterns while abundances of the spionid *Streblospio benedicti* suggest differential post-settlement mortality altered its recruitment patterns.

THE INFLUENCE OF POST-SETTLEMENT MORTALITY ON RECRUITMENT PATTERNS IN A SOFT-BOTTOM HABITAT

INTRODUCTION

Recruitment, the appearance of new individuals in a population, plays a key role in establishing temporal and spatial patterns of species abundance. Recruitment success is governed by two general processes: 1) arrival in the habitat and 2) survival (Thorson, 1966). The majority of benthic invertebrates produce large numbers of pelagic larvae which metamorphose and settle into the benthos (Thorson, 1946, 1950; Mileikovsky, 1971). In soft-bottom habitats, the dimensions of recently-settled juveniles are frequently smaller than 500 um (Shroeder and Hermans, 1975; Sastry, 1979), the common size division between macro- and meiofauna, and are referred to as the temporary meiofauna (McIntyre, 1969). While in this early benthic life stage following settlement, juveniles can suffer high mortality (Zajac and Whitlatch, 1982; Watzin, 1983); however, the methodology of recruitment studies frequently includes using a ≥500 um sieve and/or sampling weeks or months after settlement. When populations are finally examined the observed recruitment patterns may be a composite of settlement and early post-settlement mortality (Stimson, 1974, Luckenbach, 1984). If this distinction is not made, it can lead to erroneous conclusions about patterns of community structure (Keough and Downes, 1982) and of adaptive recruitment (Yund *et al.*, 1987). An increasing awareness of the complexity of early population dynamics has ecologists asking what the relative roles of settlement and early post-settlement mortality are in determining recruitment patterns (Underwood and Denley, 1984; Connell, 1985; Woodin, 1986; Peterson, 1986).

Settlement patterns of benthic invertebrates are affected by processes acting at different scales: 1) large-scale larval supply (Hannan, 1981; Grosberg, 1981; Gaines et al., 1986), 2) meso-scale passive deposition of larvae (Eckman, 1983; Hannan, 1984; Butman, 1986) and 3) small-scale active habitat selection by larvae (Scheltema, 1974; Woodin, 1985; Dubilier, 1988). These factors may work in concert to establish initial patterns of species distribution (Butman, 1987); however, even if competent larvae are available in the water column they do not necessarily settle (Hannan, 1981). Hannan (1984) attributed the postlarval distribution of the capitellid polychaete Mediomastus ambiseta to passive distribution of larvae, but cautioned that postlarvae may alter this pattern by choosing or rejecting microhabitats. Larval avoidance of defaunated cores containing any indication of the arenicolid polychaete Abarenicola pacifica, has been demonstrated by a spionid polychaete Pseudopolydora kempi (Woodin, 1985).

There are many sources of early mortality of newly-settled juveniles. Direct adult-larval interactions (Woodin, 1976) include ingestion of larvae from the water column (Williams, 1980; Wilson, 1980; Peterson, 1982) and of juveniles from surface sediment (Wilson, 1981; Oliver et al., 1982; Elmgren et al., 1986). Established infauna can also induce mortality indirectly by burying larvae and juveniles with sediment displaced by feeding, burrowing and defecating (Rhoads and

Young, 1970; Brenchley, 1981; Wilson, 1981). Interactions with meiofauna have also proven to decrease juvenile macrofaunal abundance (Bell and Coull, 1979; Watzin, 1983, 1986).

The ability to discern patterns of settlement and post-settlement mortality has been demonstrated on hard-bottom sessile epibenthos (Grosberg, 1981; Keough and Downes, 1982; Wethey, 1984) and for mobile epibenthos (Sarver, 1979; Cameron and Schroeter, 1980; Highsmith, 1982). Efforts to evaluate recruitment in soft-sediment habitats have historically been confounded by inadequate sampling techniques (see Butman, 1987). In the same report that Petersen (1913) declared the importance of studying populations from the "cradle to the grave", he also noted the sieves employed in his research (1.75-1.50 mm) were so coarse that "large quantities of Bivalve fry . . . pass through in such numbers that they would have been of quantitative importance." A classic European example of predator-prey interaction may only be an artifact of sample strategy. Segerstrale (1960, 1962) believed absence of the bivalve Macoma balthica from the deep waters of the Gulf of Finland to be a result of predation by the amphipod Pontoporeia sp. Unfortunately, he based his theory on annual samples sieved on a 1 mm sieve. This sample strategy could not differentiate whether M. balthica was absent because it did not settle in the deeper waters or because it did settle and experienced mortality before it grew enough to be retained on a 1 mm sieve. Recently Heffernan (1985) noted that settlement of the sigalionid Pholoe minuta went virtually undetected using a 500 um sieve. When using this sieve size in sample processing, the earliest sign of recuitment was October or November. The following year a 250 um sieve was used and it was discovered that settlement of _P. minuta_ actually starts in April.

Part of the difficulty in recruitment studies lies in the cryptic nature of settlement in soft-bottom habitats. A common approach artificially establishes T_0 with manipulated sediment (e.g. azoic defaunated treatments) in boxes or trays in or above the sediment surface; however, these treatments may not yield data pertinent to actual settlement dynamics. Sediment treatments may function as small scale disturbances attracting opportunistic species (Thistle, 1981) and structural arrays may alter flow regimes which may bias settlement abundances (Virnstein, 1977; Eckman, 1983). The alternative approach is to intensively sample the water column and/or sediment to establish settlement events in natural sediments (Muus, 1973; Williams, 1980; Bachalet, 1984; Luckenbach, 1984). These studies have employed appropriate sampling techniques to critically examine early population dynamics of benthic infauna.

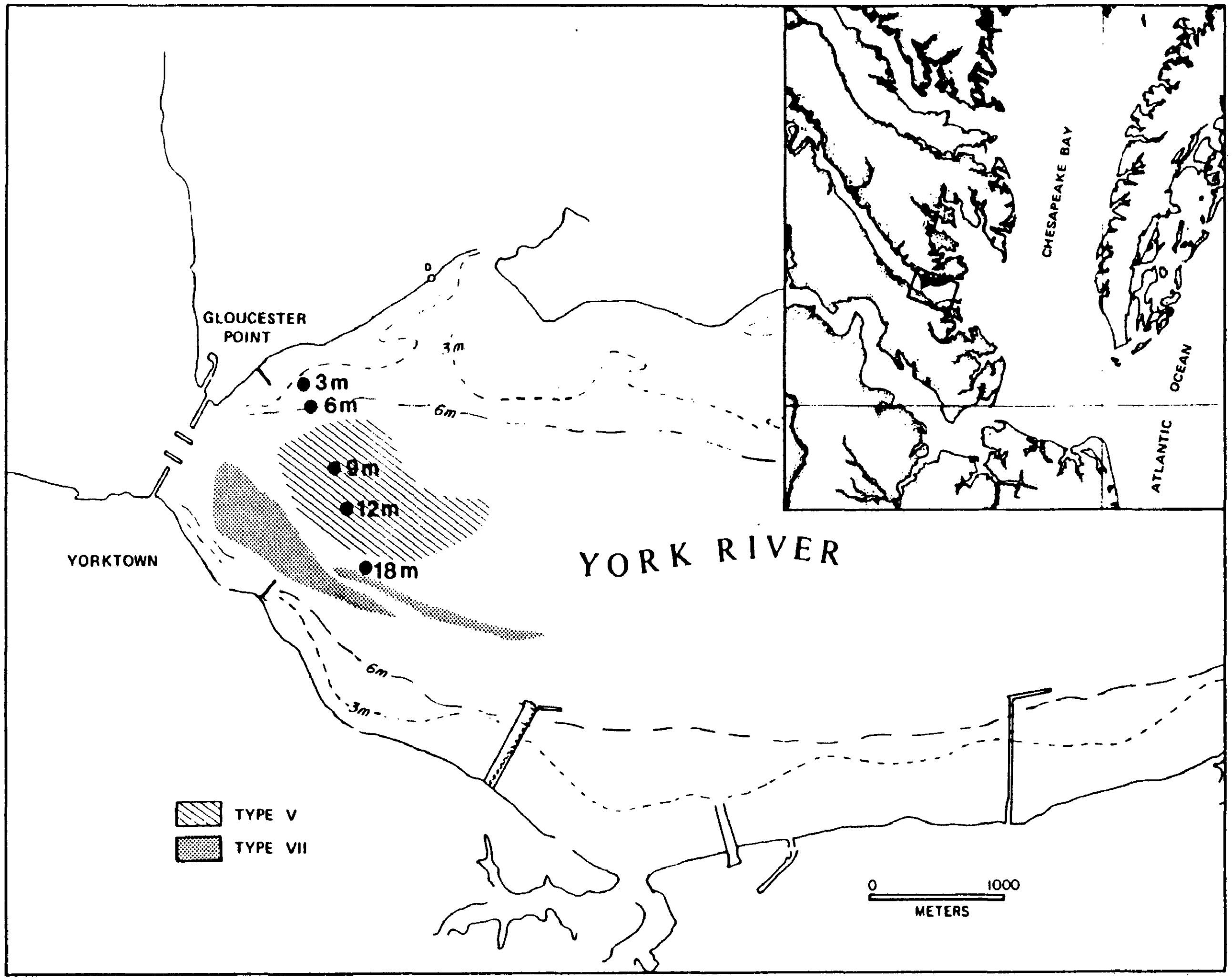
To resolve whether recruitment patterns across a depth/sediment gradient in the York River, Virginia, U.S.A. are set by differential settlement or by differential survival in an estuarine soft-sediment habitat, intensive temporal sampling with small sieve sizes was conducted. Euryhaline opportunistic polychaetes dominate this habitat (Boesch _et al_., 1976; Diaz, 1984). Five species of polychaetes dominating recruitment during this study were _Streblospio benedicti_ (Webster, 1879), _Asabellides oculata_ (Webster, 1879), _Mediomastus ambiseta_ (Hartman, 1944), _Eteone heteropoda_ (Hartman, 1951), and _Leitoscoloplos fragilis_ (Verrill, 1873). I document initial abundance patterns of newly-settled juveniles and discern the influence of early post-settlement mortality in determining patterns of faunal recruitment.

METHODS

Study Site

The study area (Fig. 1) is an unvegetated, soft-bottom habitat in the meso-polyhaline zone of the lower York River estuary, Virginia ($37^{o}15'N$, $76^{o}30'W$). Tidal amplitude is 0.7 meters and annual salinity ranges from 15 to 25 $^{o}/oo$ (Haas, 1977). A transect of five stations (3, 6, 9, 12, and 18 meters) was established along a depth gradient from near shore to the natural channel slope. Side-scan sonar mapping of the study area (Hobbs, 1986; Wright _et al_., 1987) indicates an environmental gradient of sediment type and bottom morphology (Fig. 1). The transect crosses through bottom type V to a steep slope at the channel marking the transition to bottom type VII (_sensu_ Wright _et al_., 1987). Bottom type V (9 and 12 meter stations) describes shallow muddy plains and slopes with small-scale (e.g. worm tubes) and meso-scale biogenic roughness elements. The meso-scale roughness elements punctuating the bottom are oyster shell bioherms approximately 1-1.5 m in diameter. Nikuradse roughness (a function of grain size) is very smooth (i.e. mud surface). Most of the year the sediment is covered with a thin 1-2 cm nepheloid layer of suspended material and fecal pellets. The Redox Layer Discontinuity is generally 0.5 to 2.0 cm below the sediment surface (pers. obs.). The deepest station on the transect (18 m) lies on the channel edge, a region of transition to bottom type

Figure 1. Location of sample stations and bottom morphology of the study site in the York River, Virginia (adapted from Wright *et al*., 1987).


GLOUCESTER POINT
YORKTOWN
YORK RIVER
3m
6m
9m
12m
18m
TYPE V
TYPE VII
0
1000
METERS
CHESAPEAKE BAY
ATLANTIC
OCEAN

VII. Type VII is typically characterized by tidal-current induced small-scale and meso-scale bedforms. Nikuradse roughness in this environment is medium to rough (i.e. sand).

Experimental Procedure for Assessing Population Dynamics

Weekly samples were taken at each station along the transect (3, 6, 9, 12 and 18 meters) across the York River. Stations were established with the Furuno LC90 LORAN-C System which is generally considered to have a repeatability of ± 15 meters. Sampling commenced March 15, 1985 and continued until May 16. Another set of samples were taken one month later on June 12. Three replicate 0.1 m^2 Smith-MacIntyre grabs were collected at each station. A subsample was removed from the center of each grab with an 82 cm^2 plexiglass corer. The top 2 cm of each core were carefully removed in the field and immediately fixed in 10% formalin with Rose Bengal. In the laboratory, samples were sieved through a nested series of 500, 250 and 125 um screens and identified to the lowest possible taxon (see Appendix II for taxonomic guides used in this study). The 125 um sieve ensures few if any newly-settled juveniles escape. It is then possible to identify when settlement occurred to within 7 days. These individuals will be defined as early juveniles and not settlers since some mortality may have occurred in the 7 day span between sampling. Growing recruits retained on the 250 um sieve and 500 um sieve will be categorized as late juveniles and adults, respectively.

The Smith-McIntyre grab creates only a weak, oscillatory shock wave (Wigley, 1967). This is extremely important since the goal of this sampling was to investigate the surface sediments which contain any newly-settled benthic invertebrates. Only cores which still possessed an undisturbed surface indicated by the presence of fecal pellets were retained.

Physical Measurements

Sediment samples of the top 2 cm were taken on three dates (March 15, April 18, May 16). Particle size analyses followed the procedures described in Folk (1980). After wet sieving to remove the sand fraction (particles >63 um), the silt-clay percentages were determined by time-series pipetting, a method based on particle settling velocity. The sand fraction was further broken down into phi size classes using a Rapid Sediment Analyzer (RSA). The RSA is a settling tube system that measures fall velocities of sand-size particles (Gibbs, 1974). Particle diameter was derived from the fall velocity based on an empirical equation (Gibbs _et al_., 1971).

On every sampling date, bottom temperature (C^o) and salinity ($^o/oo$) were measured at each station from Nansen bottle water samples. Salinity was estimated with a refractometer.

Data Analysis

Species were selected _a posteriori_ for data analysis. Animal abundances among stations were compared with Kruskal-Wallis non-parametric ANOVAs by ranks (Hollander and Wolfe, 1973) for each sieve size during the weeks the species appeared. A significance level of $\alpha \leq 0.05$ was chosen for all statistical comparisons. If differences were detected by the Kruskal-Wallis test, pairwise comparisons were performed using a non-parametric Kruskal-Wallis rank sum test corrected for ties

(Hollander and Wolfe, 1973). Sediment data among sampling dates was compared with a X^2 Log-likelihood ratio test.

RESULTS

Physical Conditions

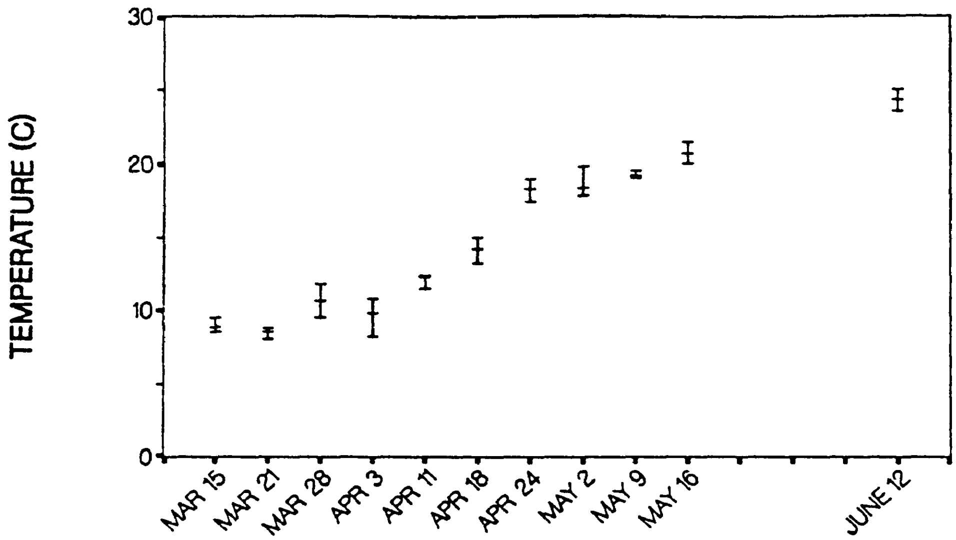
Sediments from 6m, 9m, 12m and 18m stations did not significantly differ among the three dates (Table 1). The 3m station sediments were not different between March 15 and April 18 (X^2= .533, df=2, $\underline{p}$=0.7659) but were significantly different by May 16. Although the sample size is small, it is possible the significance at 3m station reflects the physical dynamics of this inshore station. The sediment gradient along the transect is indicated by the transition from fine sand at the 3 and 6 meter stations to very fine sand at the 9, 12 and 18 meter stations. Mean sand phi was not calculated for two dates at the 18 meter station due to the small sand fraction (<5% of each sample). Sediment sizes in this study agree well with the rigorous spatial sediment analysis of the lower York River by Hobbs (1986).

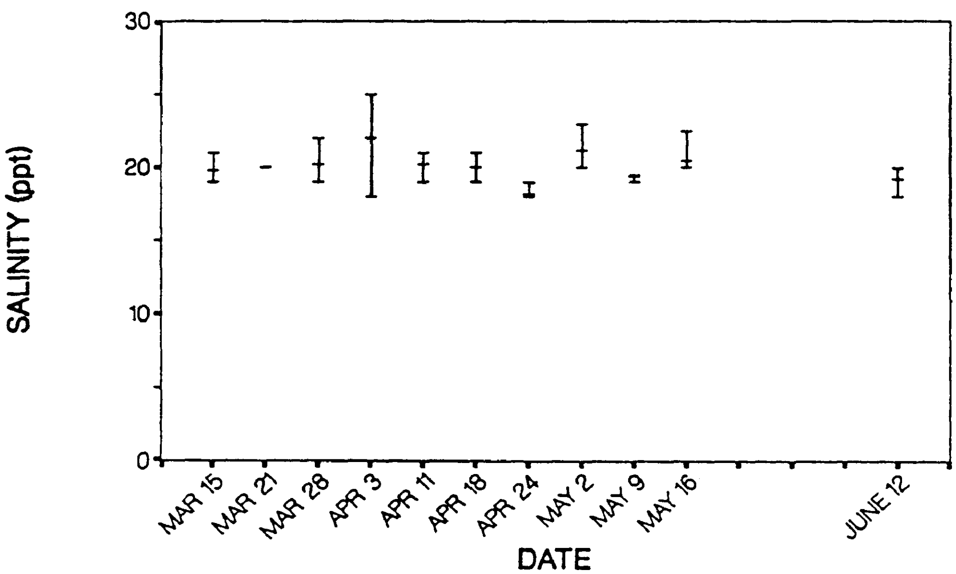
During this study, bottom salinities varied from 18 to 22 $^{o}/oo$ and did not change significantly through time (ANOVA, df=54, $\underline{p}$>.05). Bottom-water temperatures gradually increased from 8.8^{o}C on March 15 to 24.3^{o}C on June 12. Neither temperature nor salinity varied greatly among stations during a given sampling date (Fig. 2).

Table 1. Date, sediment parameters and X^2 Log-likelihood ratio for each station in transect (df=4; *, significant at $\alpha \leq .05$; NS, not significant at $\alpha > .05$).

Station	Date	Clay%	Silt%	Sand%	Mean Sand Phi	X^2
3 m	3-15	17.2	8.6	74.2	2.20	
	4-18	21.0	9.2	69.8	2.20	
	5-16	7.9	3.3	88.8	1.94	*
6 m	3-15	61.2	33.2	5.6	2.94	
	4-18	61.7	30.5	7.8	2.81	
	5-16	53.8	31.3	14.9	2.60	NS
9 m	3-15	46.3	27.4	26.3	2.89	
	4-18	49.9	28.7	21.4	3.11	
	5-16	52.5	29.8	17.7	3.10	NS
12 m	3-15	50.8	28.2	21.0	3.12	
	4-18	50.5	25.4	24.1	3.02	
	5-16	56.7	30.5	12.8	2.87	NS
18 m	3-15	67.3	30.1	2.6	----	
	4-18	59.1	34.9	6.0	3.35	
	5-16	58.7	36.3	5.0	----	NS

Figure 2. Bottom temperature (C^{o}) and salinity (ppt) mean and range for each sampling date.


TEMPERATURE (C)
30
20
10
0
MAR 15
MAR 21
MAR 28
APR 3
APR 11
APR 18
APR 24
MAY 2
MAY 9
MAY 16
JUNE 12


SALINITY (ppt)
30
20
10
0
MAR 15
MAR 21
MAR 28
APR 3
APR 11
APR 18
APR 24
MAY 2
MAY 9
MAY 16
JUNE 12
DATE

Faunal Composition

Sampling produced 165 cores from the five stations along the transect and yielded over 62,000 individuals encompassing at least 62 species (Appendix I). Polychaetes dominated the study area accounting for 86.8% (28 species) of the total individuals (Table 2). A list of the eleven most abundant species is contained in Table 3. A breakdown of total abundance by sieve size indicates the magnitude of recruitment for each species and the approximate size of early juveniles. Individuals retained on the 125 um sieve accounted for 47.1% of the total species abundance.

Five polychaetes and one oligochaete recruited in distinct peaks during the study: an ampharetid, *Asabellides oculata* (Webster, 1879); an orbinid, *Leitoscoloplos fragilis* (Verrill, 1873); a phyllodocid, *Eteone heteropoda* (Hartman, 1951); the spionids *Streblospio benedicti* (Webster, 1879) and *Polydora cornuta* (Bosc, 1802) and the naidid oligochaete *Paranais littoralis* (Muller, 1784). The bivalve *Mulinia lateralis* (Say, 1822) recruited before the study began while the capitellid polychaete *Mediomastus ambiseta* (Hartman, 1944) and the goniadid polychaete *Glycinde solitaria* (Webster, 1879) began their recruitment at the study end. Two species displayed indistinct recruitment pulses: the tubificid oligochaetes *Tubificoides* spp. and the cumacean *Leucon americanus* (Zimmer, 1943). Descriptions of the recruitment of these eleven dominant species are detailed below. Species with pelagic larvae (see Table 3) are presented first. Those species with direct development or asexual reproduction follow.

Table 2. Total abundance and number of species for major taxa collected in study.

Taxon	Abundance	% of Total	No. of Species
Polychaete	54,511	86.8	28
Oligochaete	4,254	6.8	3(?)
Bivalve	1,037	1.7	8
Gastropod	697	1.1	5
Arthropod	1,635	2.6	18
Other	620	1.0	--
TOTAL	62,804	100.0	~62

Table 3. Abundance, total and by sieve, of eleven dominants collected in the study. Asterisk indicates species with pelagic larvae. Taxon code: B-Bivalve, C-Cumacean, O-Oligochaete, P-Polychaete.

Species	Total Abundance	500 um	250 um	125 um
* Asabellides oculata (P)	23,566	1,576	4,960	17,030
* Mediomastus ambiseta (P)	14,424	3,524	4,512	6,388
* Streblospio benedicti (P)	11,450	1,970	5,115	4,365
Paranais littoralis (O)	2,841	1,338	1,399	104
* Eteone heteropoda (P)	1,640	249	636	755
Tubificoides spp. (O)	1,413	887	414	112
* Leitoscoloplos fragilis (P)	1,048	349	399	300
Leucon americanus (C)	1,045	637	407	1
* Glycinde solitaria (P)	983	282	566	135
* Mulinia lateralis (B)	790	661	128	1
* Polydora cornuta (P)	566	216	293	57

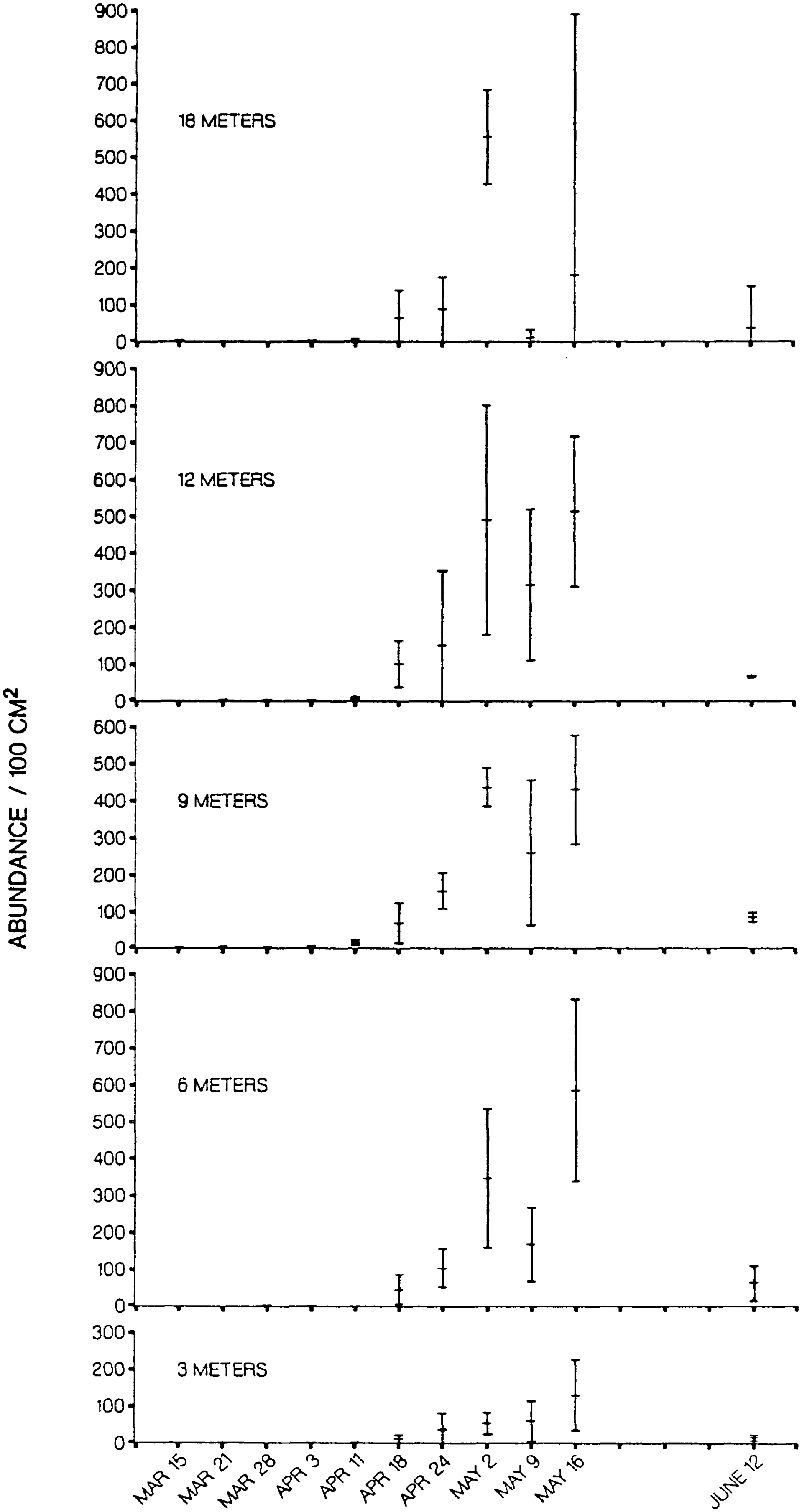
Population Dynamics

Asabellides oculata (Webster, 1879)

Recently-settled juveniles of *Asabellides oculata* were detected in seven of the eleven weeks of the study (Fig. 3). Mean early juvenile length was 791.1 $\pm$114.2 um (N=30). Larvae of *A. oculata* appeared to settle in two distinct waves peaking on May 2 and May 16. The first wave began April 11 with a few recently-settled juveniles appearing at the 9 m station. Juveniles appeared at all stations on April 18, abundances gradually increasing to a peak on May 2. Abundances fell May 9 and then increased again the following week at all stations except at the 3 m station where recruitment levels were maintained until May 16. Few juveniles were present one month later on June 12.

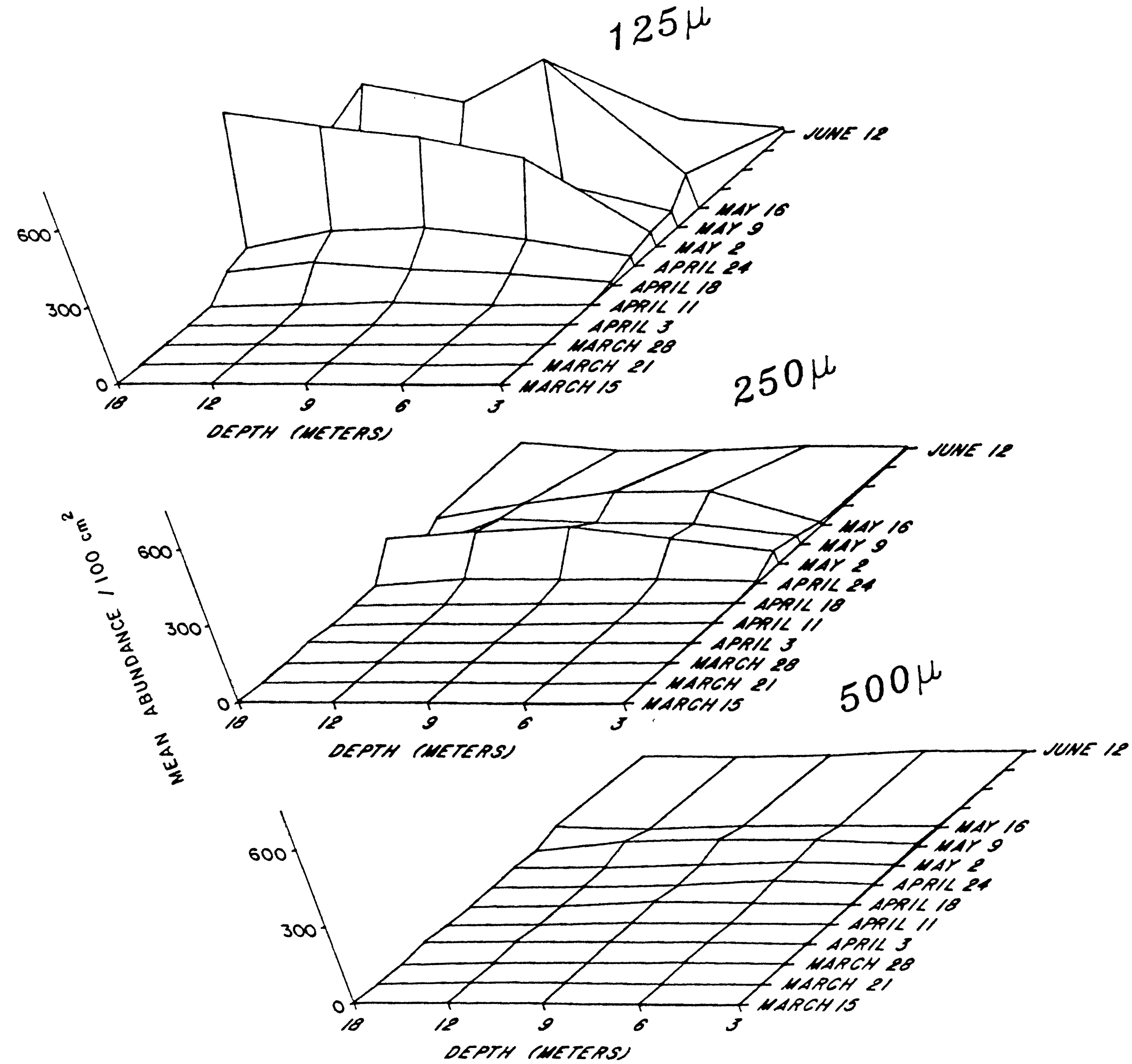
Recruitment peaks are easily seen in the three-dimensional representation of the data (Fig. 4). Approximately 72% of all individuals were captured on the 125 um sieve, 21% on the 250 um sieve and 7% on the 500 um sieve. Abundances of recently-settled juveniles, late juveniles and adults differed significantly among stations with higher abundances found at the deeper stations of the transect. Recently-settled (125 um sieve) and late (250 um sieve) juveniles appeared in significantly lower abundances at 3 m station than at the 6 m, 9 m and 12 m stations (Table 4). The 3 m and 18 m stations did not significantly differ through recently-settled and late juvenile stages. Adult abundances (500 um sieve) were significantly lower at the 3 m station.

Figure 3. *Asabellides oculata*. Weekly abundance (mean $\pm$ 95% confidence interval) of recently-settled juveniles (125 um sieve).



ABUNDANCE / 100 CM²
18 METERS
12 METERS
9 METERS
6 METERS
3 METERS
0
100
200
300
400
500
600
700
800
900
MAR 15
MAR 21
MAR 28
APR 3
APR 11
APR 18
APR 24
MAY 2
MAY 9
MAY 16
JUNE 12

Figure 4. *Asabellides oculata*. Mean abundance on each sieve (500, 250, 125 um) by station through time.



125μ
250μ
500μ
MEAN ABUNDANCE / 100 cm²
600
300
0
18
12
9
6
3
DEPTH (METERS)
JUNE 12
MAY 16
MAY 9
MAY 2
APRIL 24
APRIL 18
APRIL 11
APRIL 3
MARCH 28
MARCH 21
MARCH 15

Table 4. Results of *a posteriori* multiple comparisons of animal abundances between stations. Stations are listed in order of increasing mean rank abundance for each taxon. Stations not significantly different at $\alpha \leq 0.05$ are underlined. Total sample size (N) and probabilities listed are for *a priori* Kruskal-Wallis test. NS = no significant differences among stations detected by *a priori* testing.

Asabellides oculata							
125 um sieve	3m	18m	6m	9m	12m	N=90	$p<0.001$
250 um sieve	3m	18m	6m	12m	9m	N=75	$p<0.005$
500 um sieve	3m	12m	9m	18m	6m	N=75	$p<0.001$
Streblospio benedicti							
125 um sieve	18m	9m	6m	12m	3m	N=90	$p<0.0001$
250 um sieve	18m	9m	12m	6m	3m	N=75	$p<0.0001$
500 um sieve	18m	9m	12m	6m	3m	N=75	$p<0.005$
Eteone heteropoda							
125 um sieve	18m	12m	9m	6m	3m	N=75	$p<0.01$
250 um sieve	18m	12m	9m	6m	3m	N=75	$p<0.01$
500 um sieve	18m	9m	12m	6m	3m	N=60	$p<0.05$

Table 4. (cont.)

Leitoscoloplos fragilis							
125 um sieve			NS				
250 um sieve			NS				
500 um sieve	18m	6m	9m	12m	3m	N=165	*p*<0.001
Mediomastus ambiseta							
125 um sieve	18m	12m	9m	6m	3m	N=90	*p*<0.01
250 um sieve			NS				
500 um sieve	3m	6m	12m	9m	18m	N=90	*p*<0.05
Glycinde solitaria							
125 um sieve			NS				
250 um sieve			NS				
500 um sieve			NS				
Polydora cornuta							
250 um sieve	18m	9m	12m	6m	3m	N=90	*p*<0.01
500 um sieve	9m	18m	12m	6m	3m	N=90	*p*<0.05
Mulinia lateralis							
250 um sieve	3m	6m	12m	9m	18m	N=75	*p*<0.05
500 um sieve	3m	6m	12m	9m	18m	N=135	*p*<0.001

Table 4. (cont.)

Paranais littoralis							
250 um sieve	18m	6m	12m	9m	3m	N=120	*p*<0.001
500 um sieve	18m	12m	9m	6m	3m	N=120	*p*<0.001
Tubificoides spp.							
250 um sieve			NS				
500 um sieve	3m	6m	9m	12m	18m	N=165	*p*<0.001
Leucon americanus							
250 um sieve			NS				
500 um sieve			NS				

Streblospio benedicti (Webster, 1879)

Pelagic larvae of Streblospio benedicti settled April 11 at all stations (Fig. 5). Mean juvenile length was 563 ±80.9 um (N=24). Recently-settled juveniles continued to appear in high numbers through May 16. Over 38% of all S. benedicti recruiting during the study appeared on the 125 um sieve and nearly 45% on the 250 um sieve (Fig. 6).

Abundances of recently-settled juveniles, late juveniles and adults were significantly different among depths (Table 4). The 18 m station exhibited significantly lower abundances of recently-settled juveniles than all other stations in the transect; however, the pattern of abundance changed among the adults (Table 4). For example, the 9 m and 12 m station which differed significantly from 18 m among recently-settled and late juveniles, did not differ among adults.

Eteone heteropoda (Hartman, 1951)

Recently-settled juveniles of Eteone heteropoda appeared on April 18 at all stations, with abundances recorded through May 16 (Fig. 7). Mean juvenile length was 503.6 ±75.6 um (N=18). Over 46% of all E. heteropoda were retained on the 125 um sieve and almost 39% on the 250 um sieve (Fig. 8). Abundances of recently-settled juveniles, late juveniles and adults differed significantly among stations with highest abundances found at the shallower stations of the transect. The abundance pattern of the recently-settled juveniles and late juveniles was virtually identical (Table 4). The 3m station maintained higher abundances than the 18 m station. Adults differ with the 9 m and 18 m

Figure 5. Streblospio benedicti. Weekly abundance (mean $\pm$ 95% confidence interval) of recently-settled juveniles (125 um sieve).

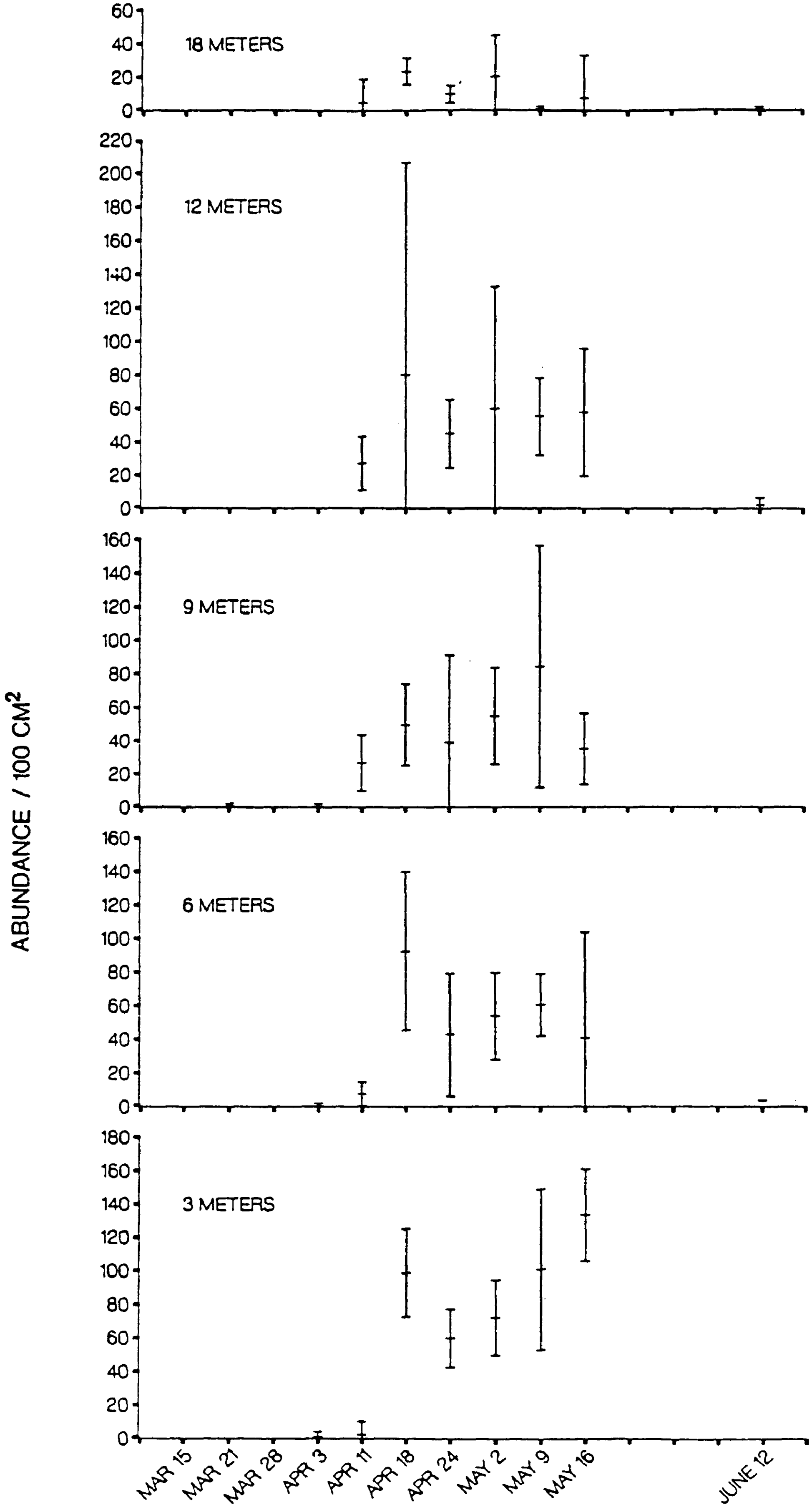

18 METERS
12 METERS
9 METERS
6 METERS
3 METERS
ABUNDANCE / 100 CM²
MAR 15
MAR 21
MAR 28
APR 3
APR 11
APR 18
APR 24
MAY 2
MAY 9
MAY 16
JUNE 12

Figure 6. Streblospio benedicti. Mean abundance on each sieve size (500, 250, 125 um) by station through time.

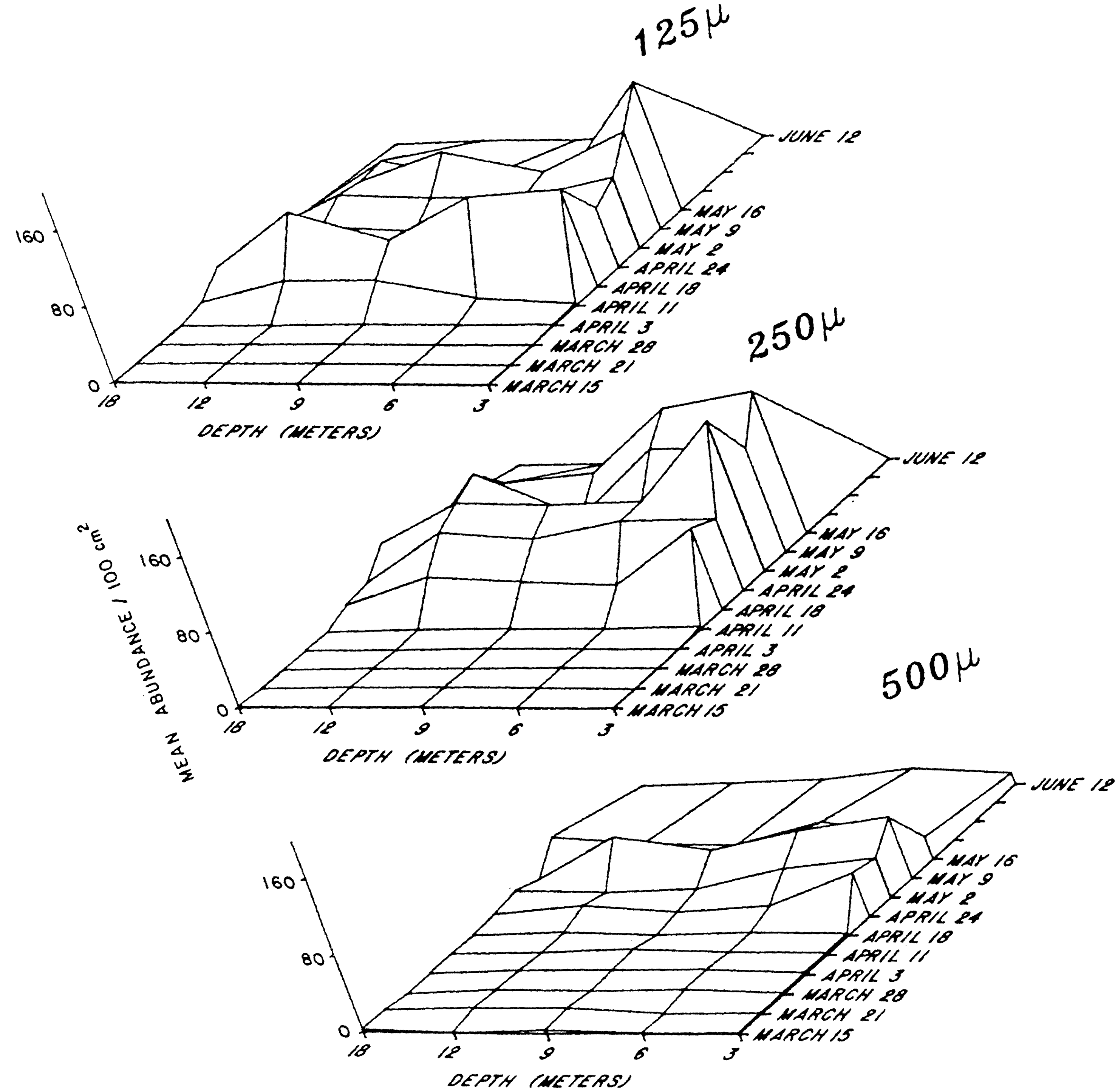

125μ
250μ
500μ
MEAN ABUNDANCE / 100 cm²
0
80
160
18
12
9
6
3
DEPTH (METERS)
JUNE 12
MAY 16
MAY 9
MAY 2
APRIL 24
APRIL 18
APRIL 11
APRIL 3
MARCH 28
MARCH 21
MARCH 15

Figure 7. *Eteone heteropoda*. Weekly abundance (mean ± 95% confidence interval) of recently-settled juveniles (125 um sieve).

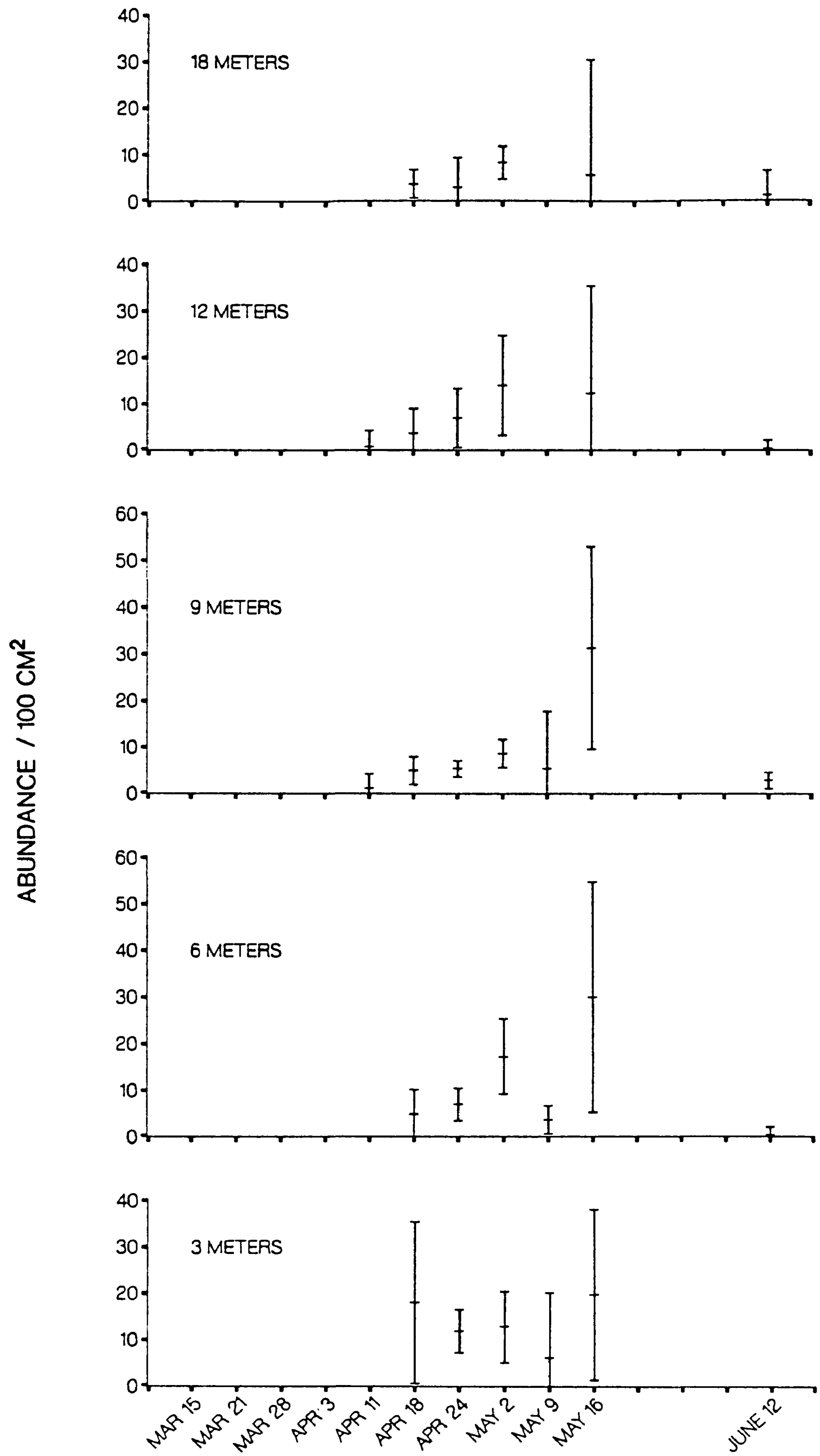
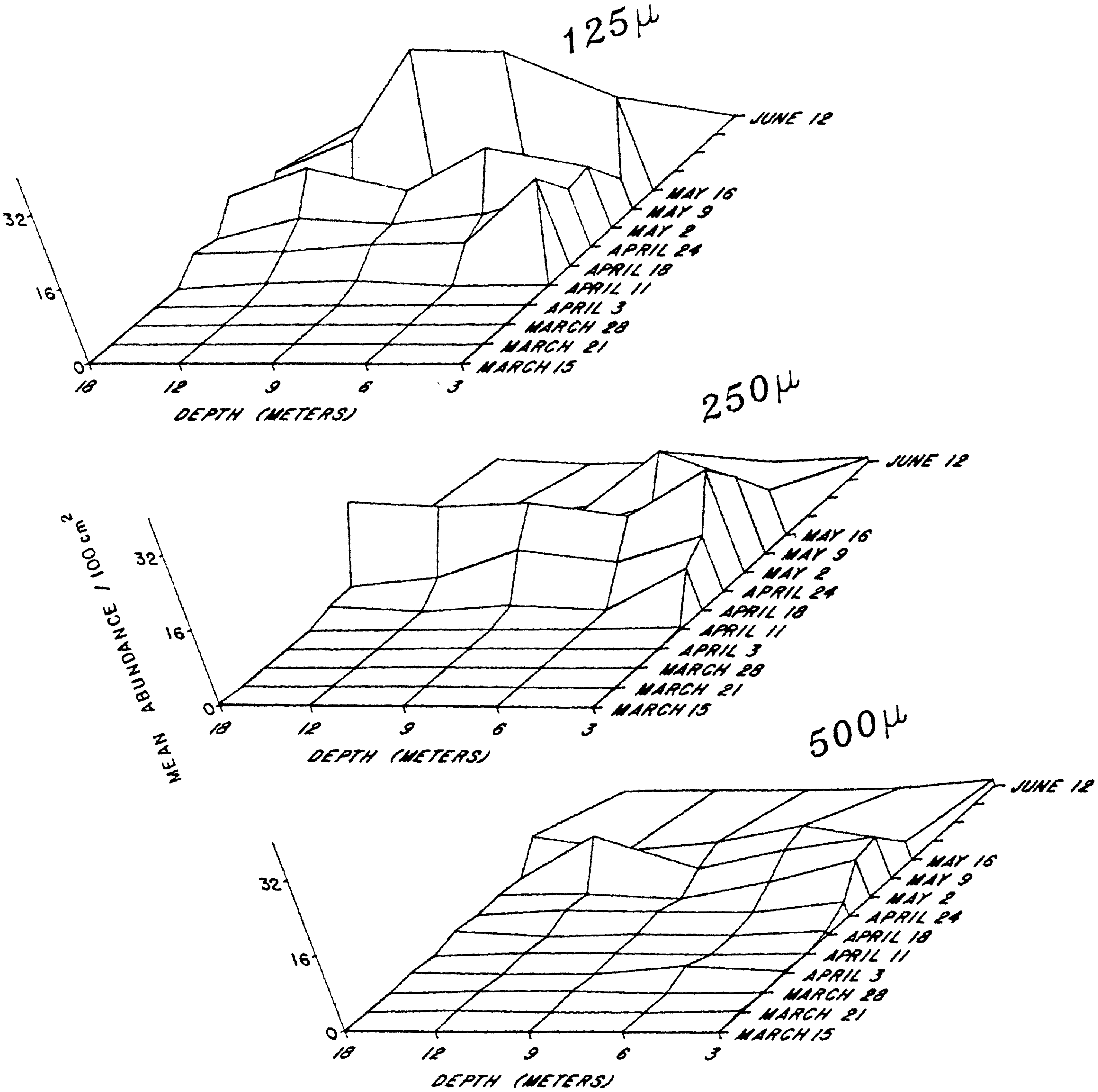

ABUNDANCE / 100 CM2
18 METERS
12 METERS
9 METERS
6 METERS
3 METERS
MAR 15
MAR 21
MAR 28
APR 3
APR 11
APR 18
APR 24
MAY 2
MAY 9
MAY 16
JUNE 12

Figure 8. Eteone heteropoda. Mean abundance on each sieve size (500, 250, 125 um) by station through time.



125μ
250μ
500μ
MEAN ABUNDANCE / 100 cm^2
32
16
0
18
12
9
6
3
DEPTH (METERS)
JUNE 12
MAY 16
MAY 9
MAY 2
APRIL 24
APRIL 18
APRIL 11
APRIL 3
MARCH 28
MARCH 21
MARCH 15

abundances significantly lower than 3 m while the 6 m and 12 m stations are not different from all other stations.

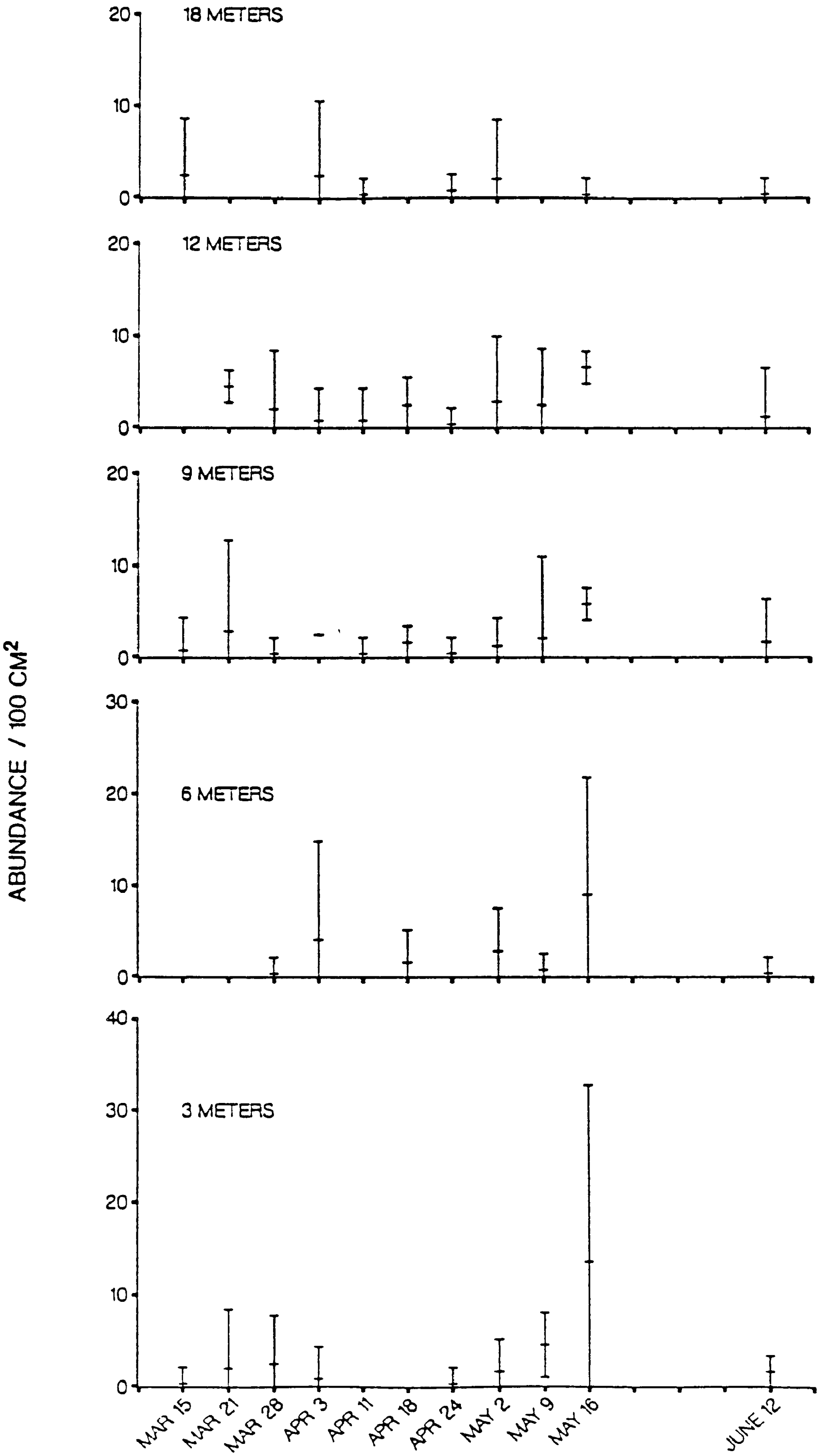
Leitoscoloplos fragilis (Verrill,1873)

Leitoscoloplos fragilis maintained fairly constant levels of recently-settled juveniles thoughout the study (Fig. 9). Mean juvenile length was 767.9 ±156.6 um (N=12). Almost equal abundances appeared on the 125, 250 and 500 um sieves (Fig. 10). No clear trend among station abundance could be distinguished among the recently-settled juveniles or late juveniles (Table 4). Adult abundances were significantly higher at 3 m than at all other stations.

Mediomastus ambiseta (Hartman, 1944)

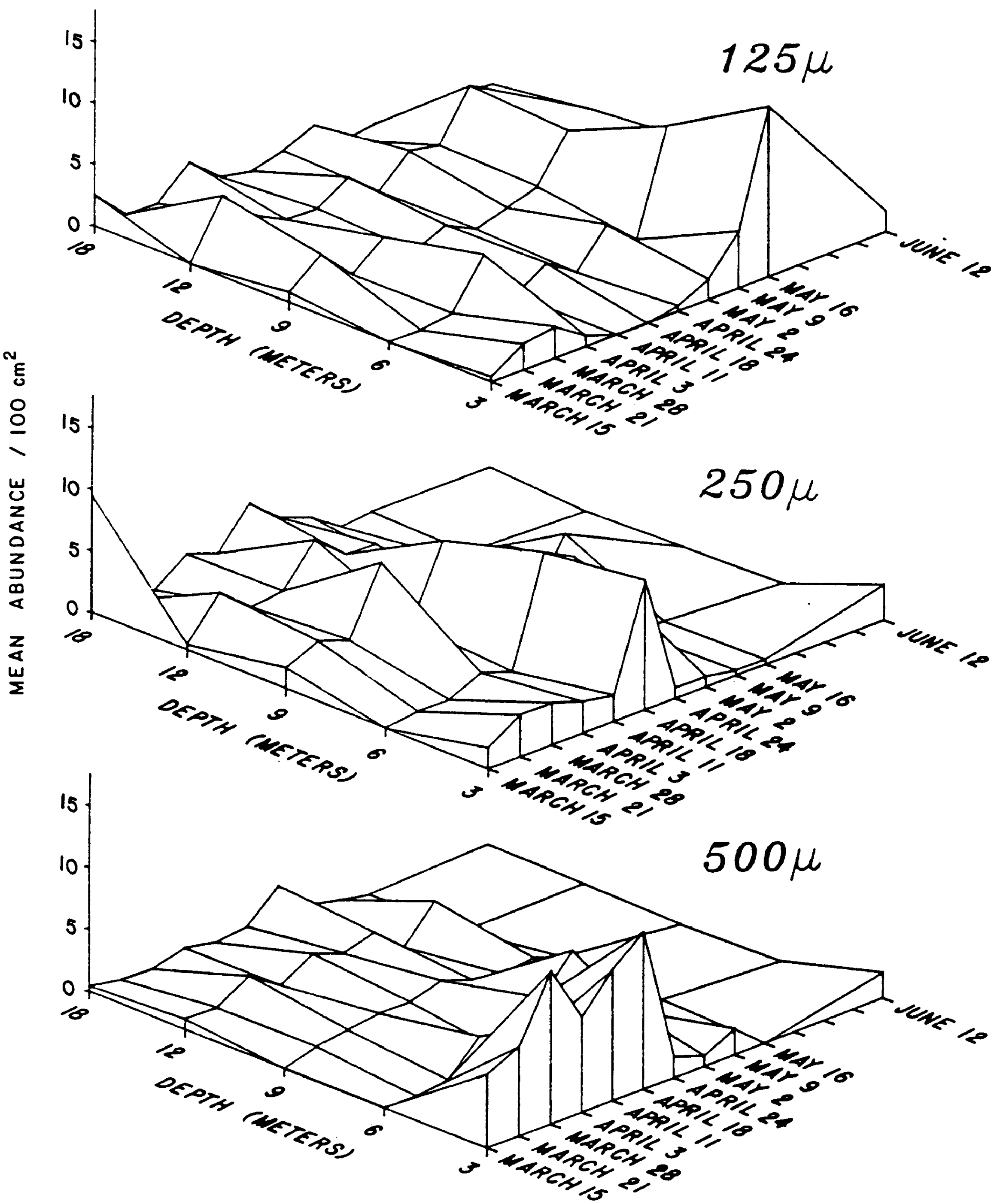
Recently-settled juveniles of Mediomastus ambiseta appeared on April 18 at all stations; however, a large settlement pulse was recorded on June 12 (Fig. 11). Mean juvenile length was 428.6 ±89.7 um (N=45). Juvenile length on the 125 um sieve in later weeks increased to as much as 3 mm. Over 44.3% of the individuals were retained on the 125 um sieve and 31.3% on the 250 um sieve (Fig. 12). Abundances of recently-settled juveniles were significantly different among stations, the 3 m station having significantly greater juveniles that the 18 m station. Late juvenile abundances indicate no clear trend. Adult abundances differed among stations, but in reverse order of recently-settled juveniles. Stations 3 m and 6 m had significantly fewer animals than the 18 m station.

Figure 9. _Leitoscoloplos_ _fragilis_. Weekly abundance (mean $\pm$ 95% confidence interval) of recently-settled juveniles (125 um sieve).



18 METERS
12 METERS
9 METERS
6 METERS
3 METERS
ABUNDANCE / 100 CM^2
MAR 15
MAR 21
MAR 28
APR 3
APR 11
APR 18
APR 24
MAY 2
MAY 9
MAY 16
JUNE 12

Figure 10. Leitoscoloplos fragilis. Mean abundance on each sieve size (500, 250, 125 um) by station through time.



MEAN ABUNDANCE / 100 cm²
125μ
250μ
500μ
0
5
10
15
18
12
9
6
3
DEPTH (METERS)
MARCH 15
MARCH 21
MARCH 28
APRIL 3
APRIL 11
APRIL 18
APRIL 24
MAY 2
MAY 9
MAY 16
JUNE 12

Figure 11. Mediomastus amibiseta. Weekly abundance (mean ± 95% confidence interval) of recently-settled juveniles (125 um sieve).

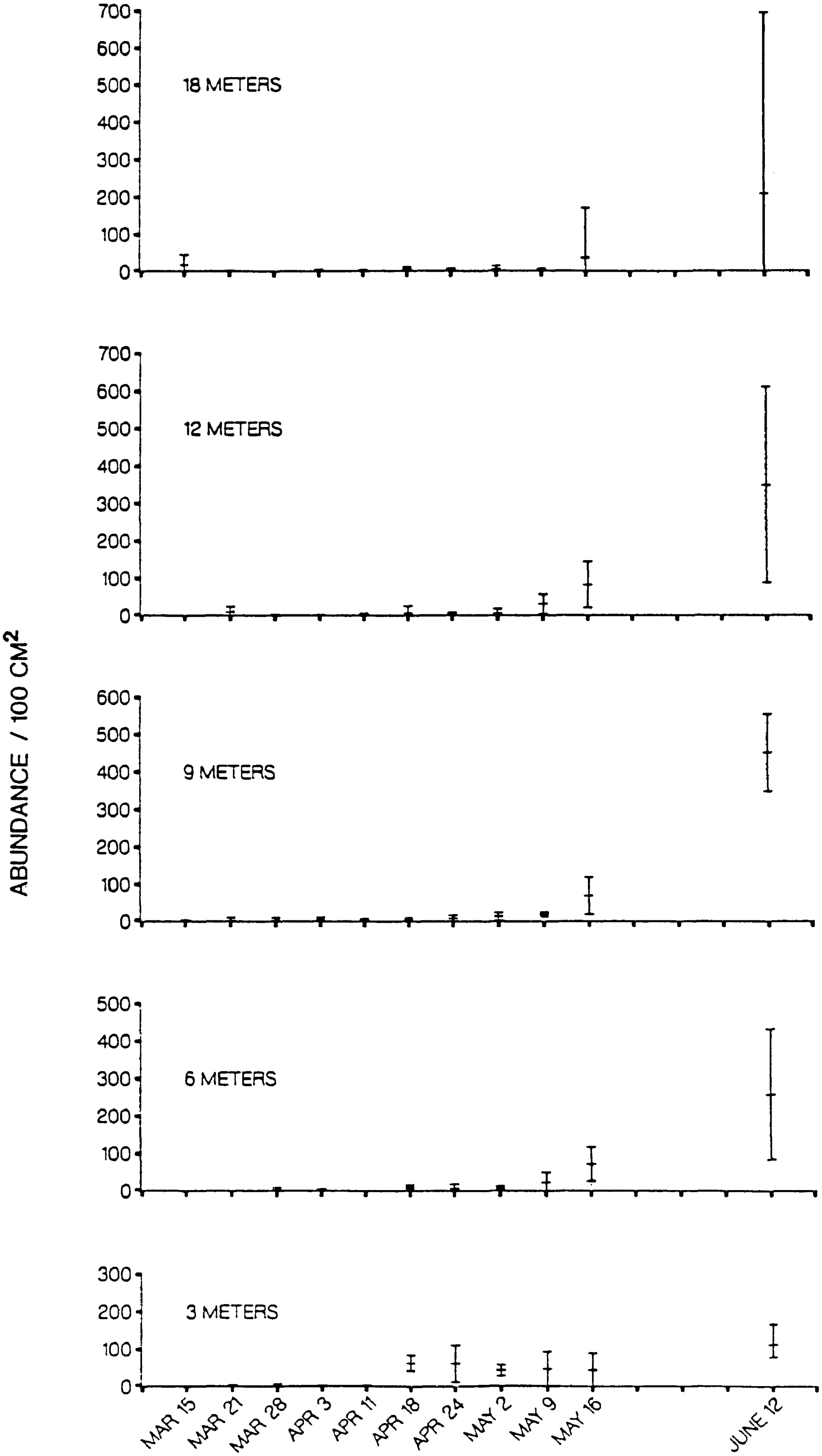
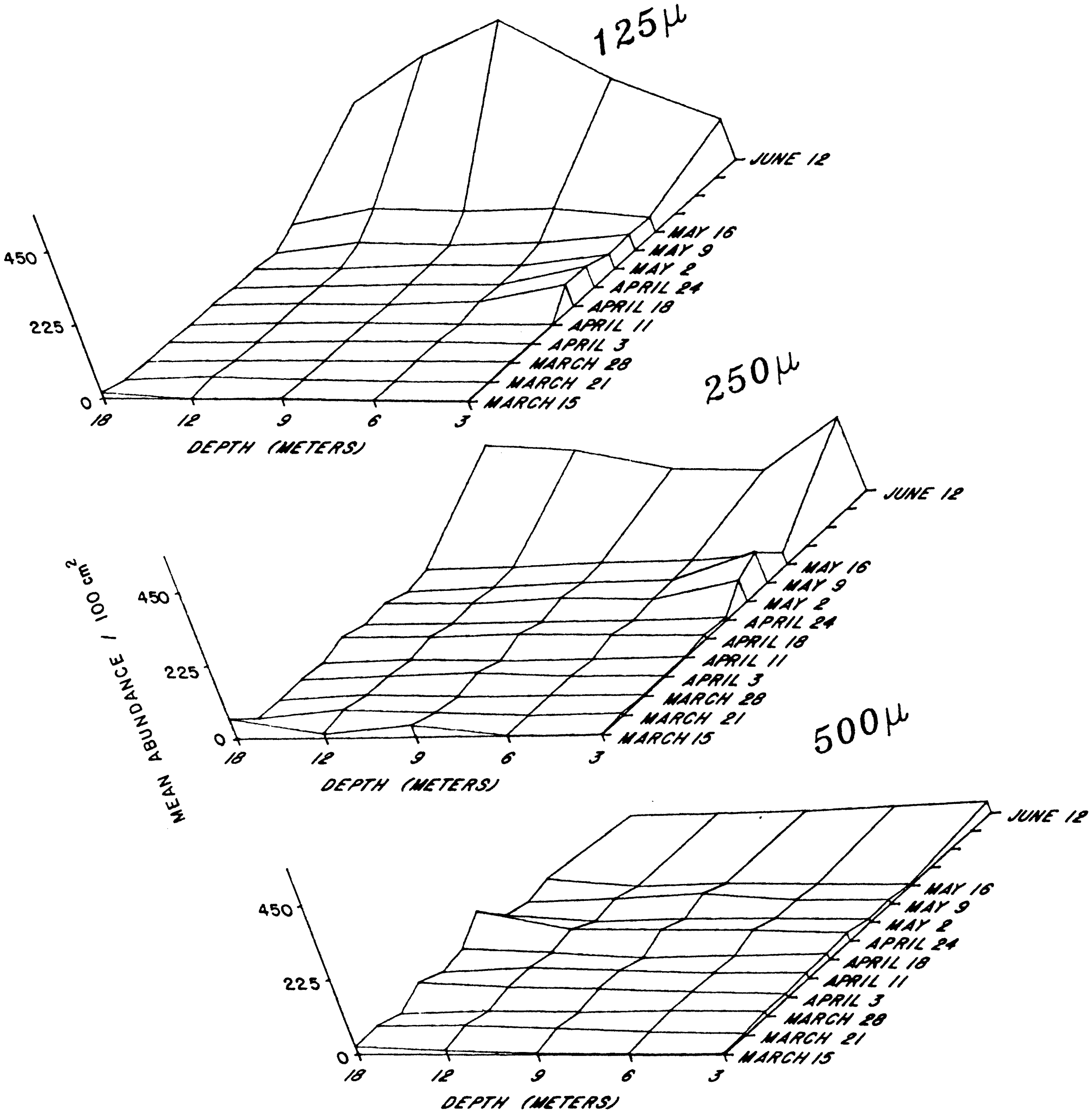

ABUNDANCE / 100 CM^2
18 METERS
12 METERS
9 METERS
6 METERS
3 METERS
0
100
200
300
400
500
600
700
MAR 15
MAR 21
MAR 28
APR 3
APR 11
APR 18
APR 24
MAY 2
MAY 9
MAY 16
JUNE 12

Figure 12. Mediomastus ambiseta. Mean abundance on each sieve size (500, 250, 125 um) by station through time.



125μ
250μ
500μ
JUNE 12
MAY 16
MAY 9
MAY 2
APRIL 24
APRIL 18
APRIL 11
APRIL 3
MARCH 28
MARCH 21
MARCH 15
450
225
0
18
12
9
6
3
DEPTH (METERS)
MEAN ABUNDANCE / 100 cm²

<u>Glycinde</u> <u>solitaria</u> (Webster, 1879)

Recently-settled juveniles first appeared May 9 with the main juvenile peak indicated on June 12 (Fig. 13). Mean juvenile length was 683.3 ±121.1 um (N=12). Approximately 13.7% of individuals were retained on the 125 um sieve, 57.6% on the 250 um sieve and 28.7% on the 500 um sieve. There was no clear trend in abundance among stations.

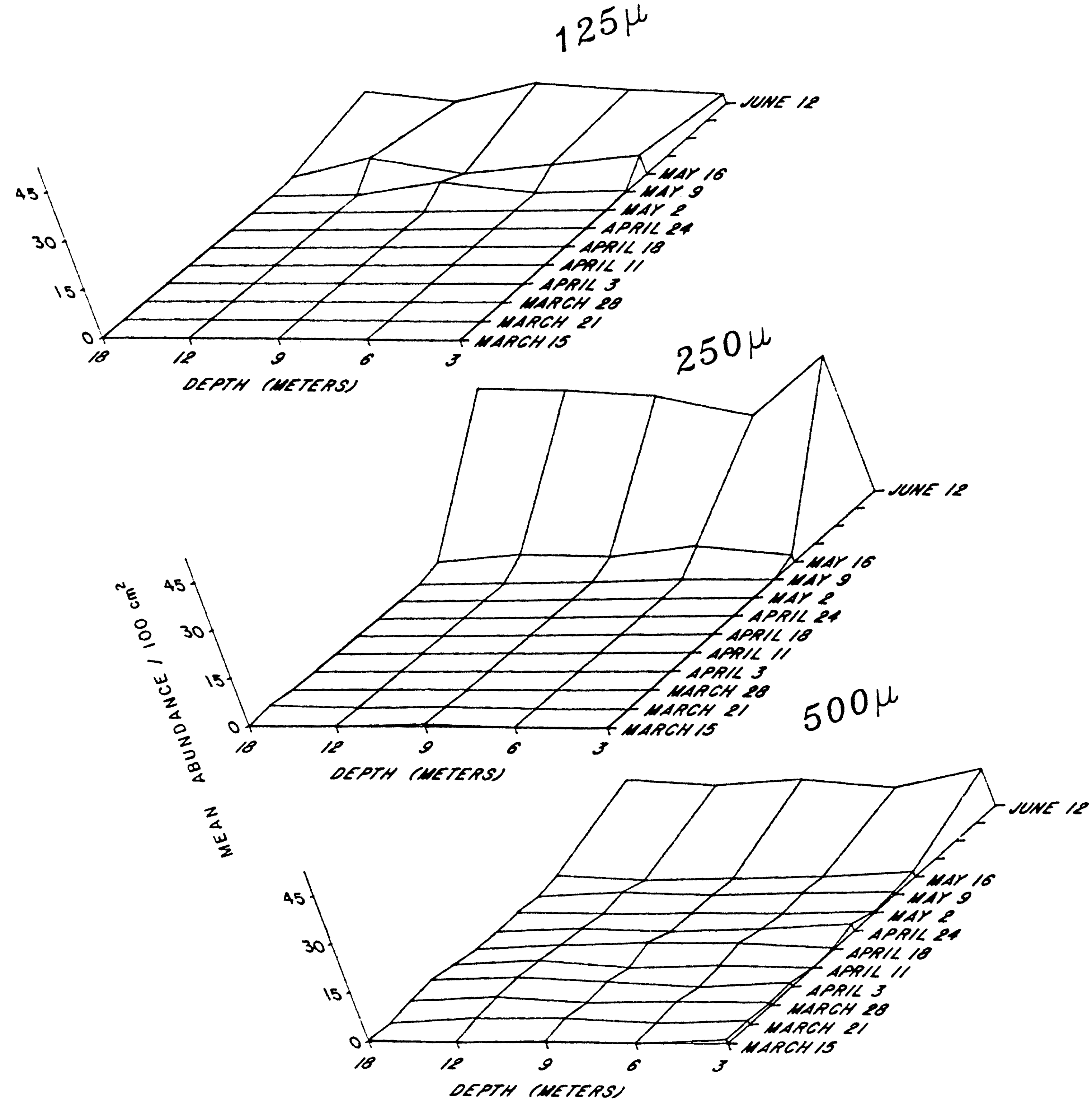
<u>Polydora</u> <u>cornuta</u> (Bosc, 1802)

Mean juvenile length was 965.6 ±108.5 um (N=16). Only 10.1% of recruits appeared on the 125 um sieve while 51.8% were on the 250 um sieve (Fig.14). Since the earliest <u>Polydora</u> <u>cornuta</u> detected were on the 250 um sieve, they will be referred to as recently-settled juveniles. Juvenile and adult abundances differed significantly among stations. Juvenile abundance was lower at 18 m than at 3 m (Table 4). Although the adult abundance was significantly different among stations (Kruskal-Wallis, <u>p</u>=0.0208), muliple comparisons could not identify which stations were different.

<u>Mulinia</u> <u>lateralis</u> (Say, 1822)

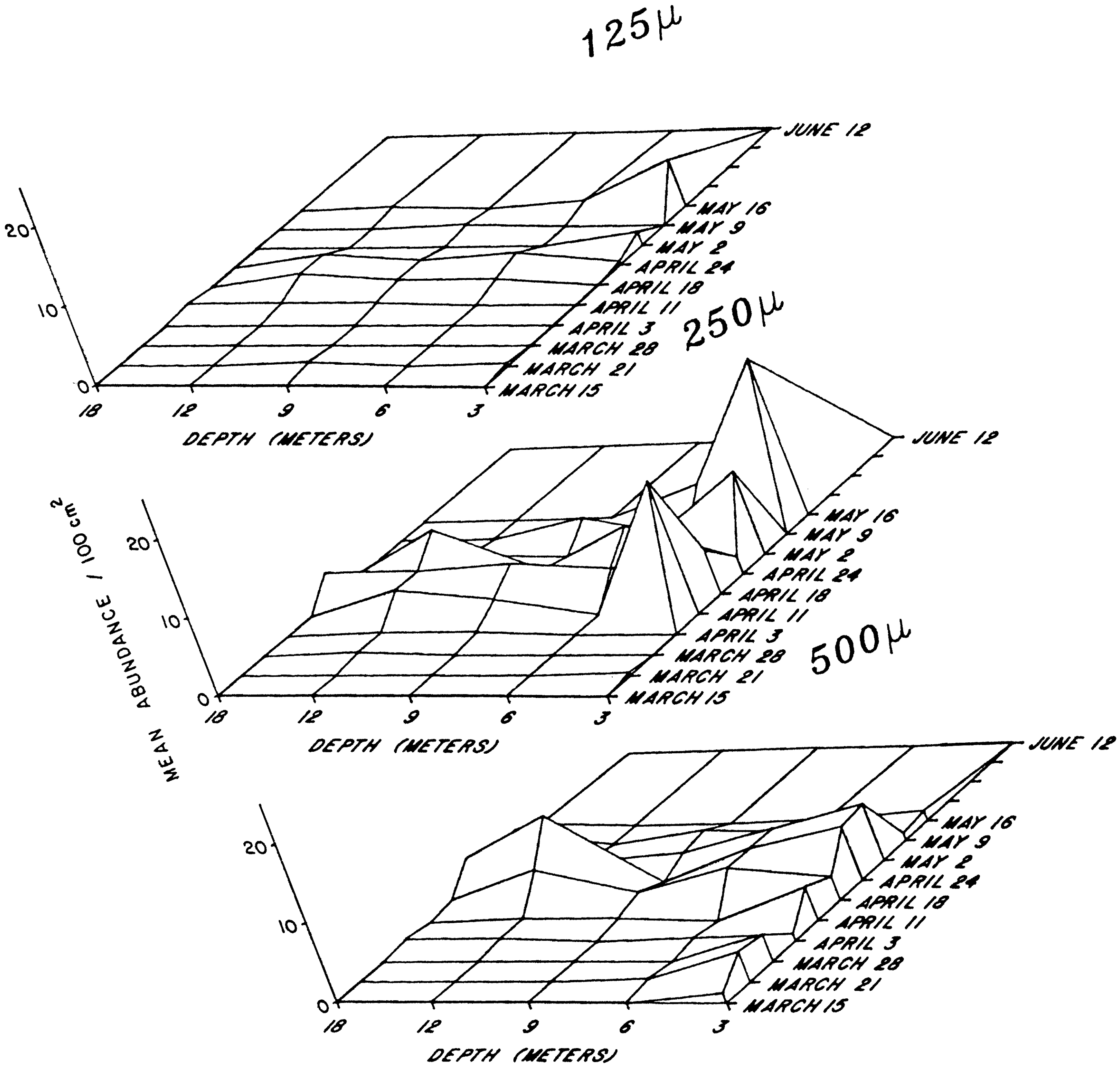
<u>Mulinia</u> <u>lateralis</u> recruited before the first sample date as indicated by only 16.2% of the individuals appearing on the 250 um sieve (Fig. 15). The majority of this species was caught on the 500 um sieve (83.7%). Juvenile and adult abundances differed significantly among stations (Table 4). Multiple comparisons could not identify which stations were different for juveniles (Kruskal-Wallis, <u>p</u>=0.0370); adults of <u>M</u>. <u>lateralis</u> were significantly fewer at the 3m station than at the 9 m, 12 m or 18 m station.

Figure 13. Glycinde solitaria. Mean abundance on each sieve size (500, 250, 125 um) by station through time.



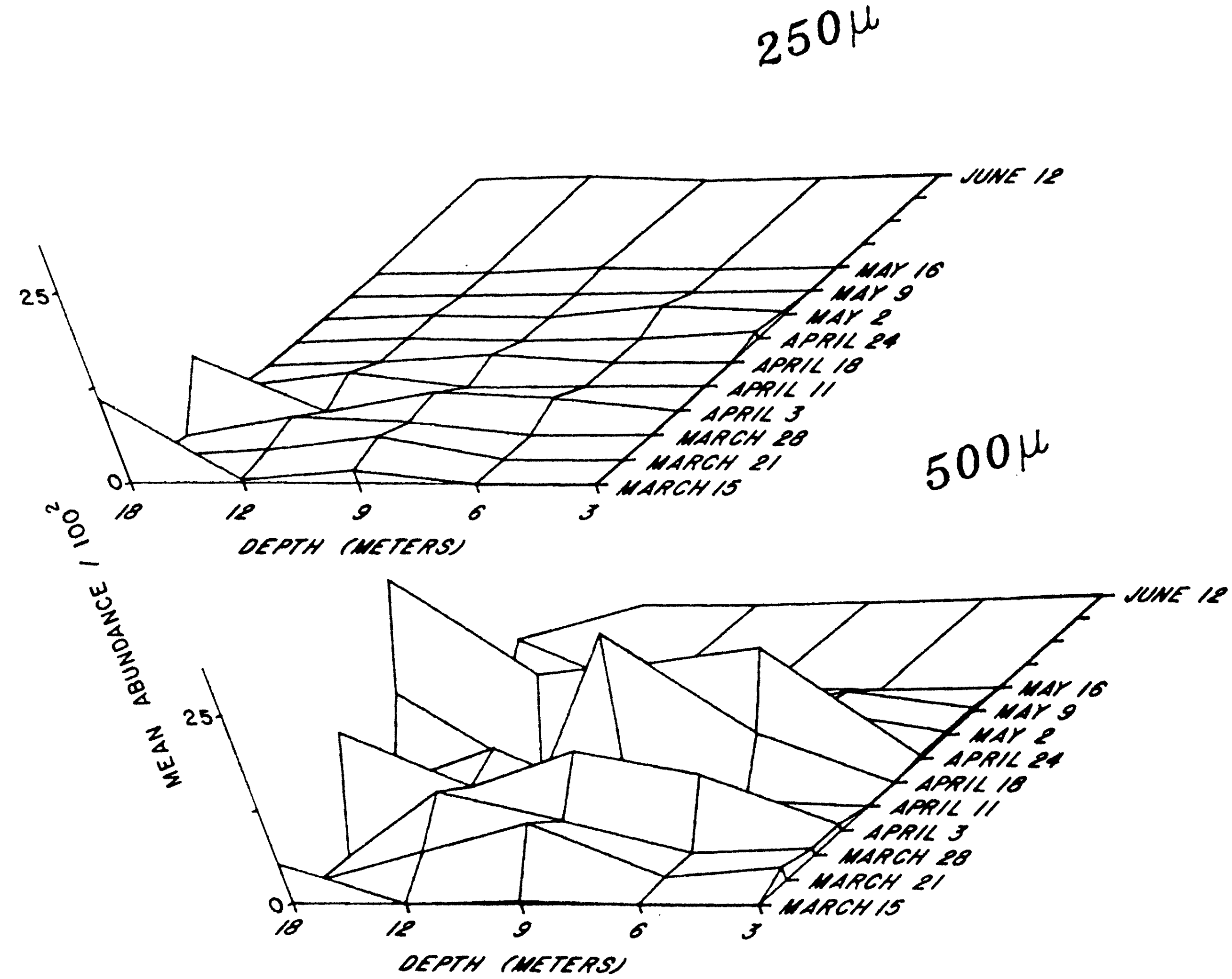
125μ
250μ
500μ
MEAN ABUNDANCE / 100 cm²
0
15
30
45
18
12
9
6
3
DEPTH (METERS)
MARCH 15
MARCH 21
MARCH 28
APRIL 3
APRIL 11
APRIL 18
APRIL 24
MAY 2
MAY 9
MAY 16
JUNE 12

Figure 14. Polydora cornuta. Mean abundance on each sieve size (500, 250, 125 um) by station through time.



125μ
250μ
500μ
JUNE 12
MAY 16
MAY 9
MAY 2
APRIL 24
APRIL 18
APRIL 11
APRIL 3
MARCH 28
MARCH 21
MARCH 15
0
10
20
18
12
9
6
3
DEPTH (METERS)
MEAN ABUNDANCE / 100 cm²

Figure 15. *Mulinia lateralis*. Mean abundance on each sieve size (500, 250 um) by station through time.


250μ
500μ
JUNE 12
MAY 16
MAY 9
MAY 2
APRIL 24
APRIL 18
APRIL 11
APRIL 3
MARCH 28
MARCH 21
MARCH 15
25
0
18
12
9
6
3
DEPTH (METERS)
MEAN ABUNDANCE / 100²

Paranais littoralis (Muller, 1784)

Most recruiting _Paranais littoralis_, which does not produce pelagic larvae, appeared at the 3m station (Fig. 16). Abundances of juveniles and adults were highly significantly different among stations (Table 4). Juvenile abundance was higher at 3 m than at 6 m or 12 m while adult abundance was higher at 3 m than at all other stations.

Tubificoides spp.

Tubificoides waselli and _Tubificoides brownae_ constitute this taxonomic complex (R. J. Diaz, pers. comm.). No attempt was made to distinguish the two since most individuals were immature and oligochaete taxonomy is based on adult genital morphology. Most individuals were retained on the 500 um sieve (Fig. 17). Abundances on the 500 um sieve were significantly different among stations; the 3 m with lower abundances than the 9 m, 12 m and 18 m.

Leucon americanus (Zimmer, 1943)

Juveniles produced via direct brooding were present April 24 through the end of sampling (Fig. 18). No clear trend of abundance could be distinguished among either the juveniles or adults.

Figure 16. Paranais littoralis. Mean abundance on each sieve size (500, 250 um) by station through time.

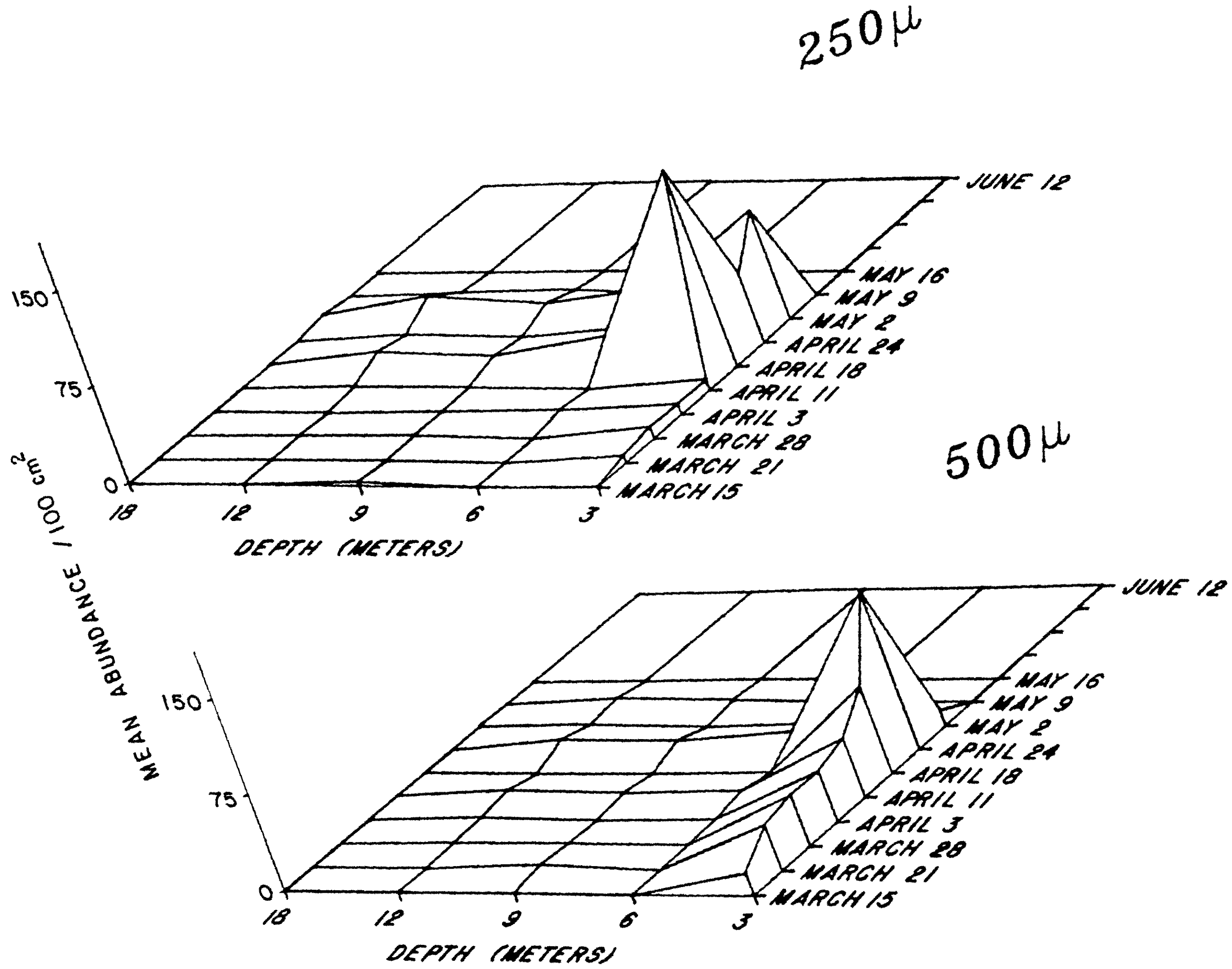
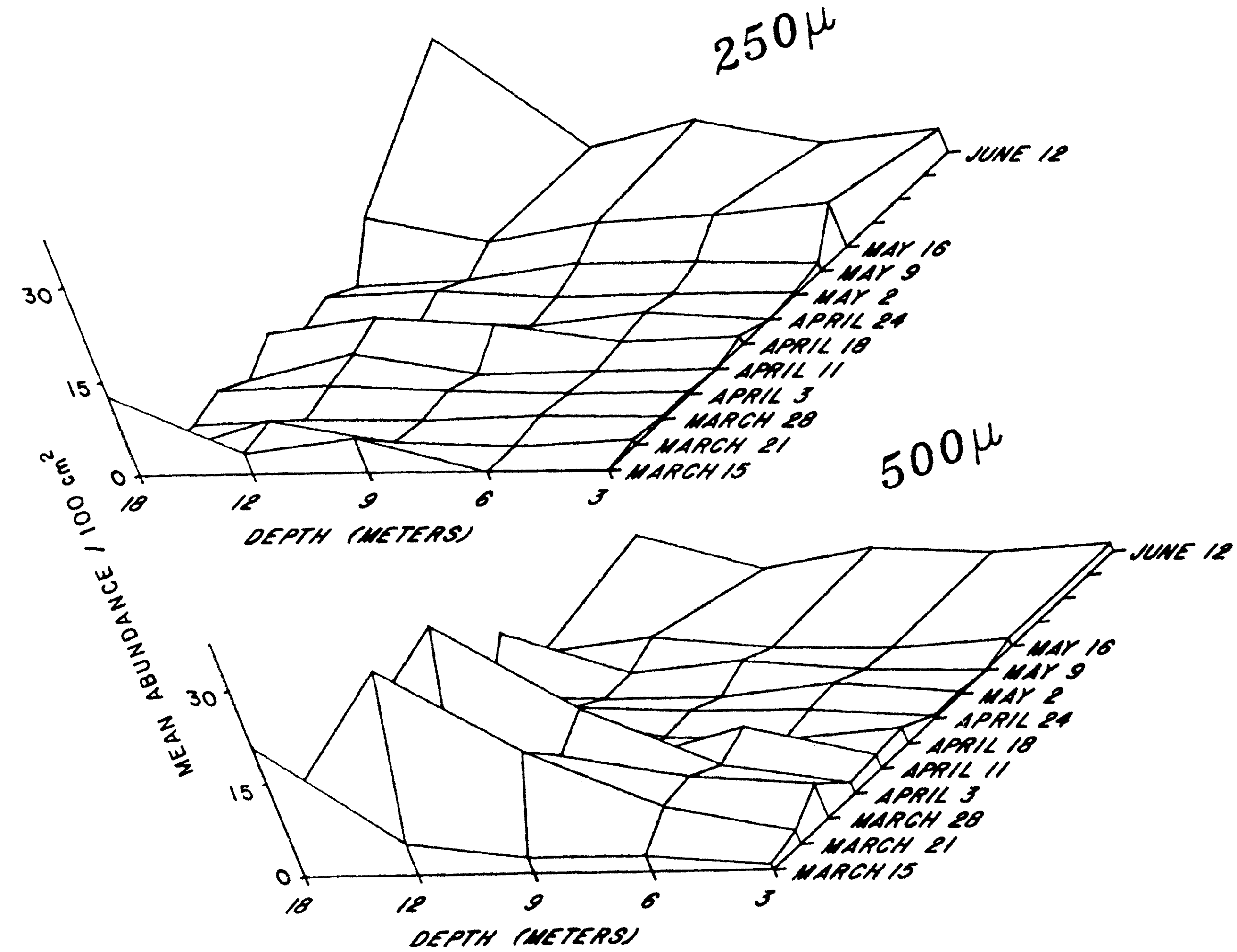
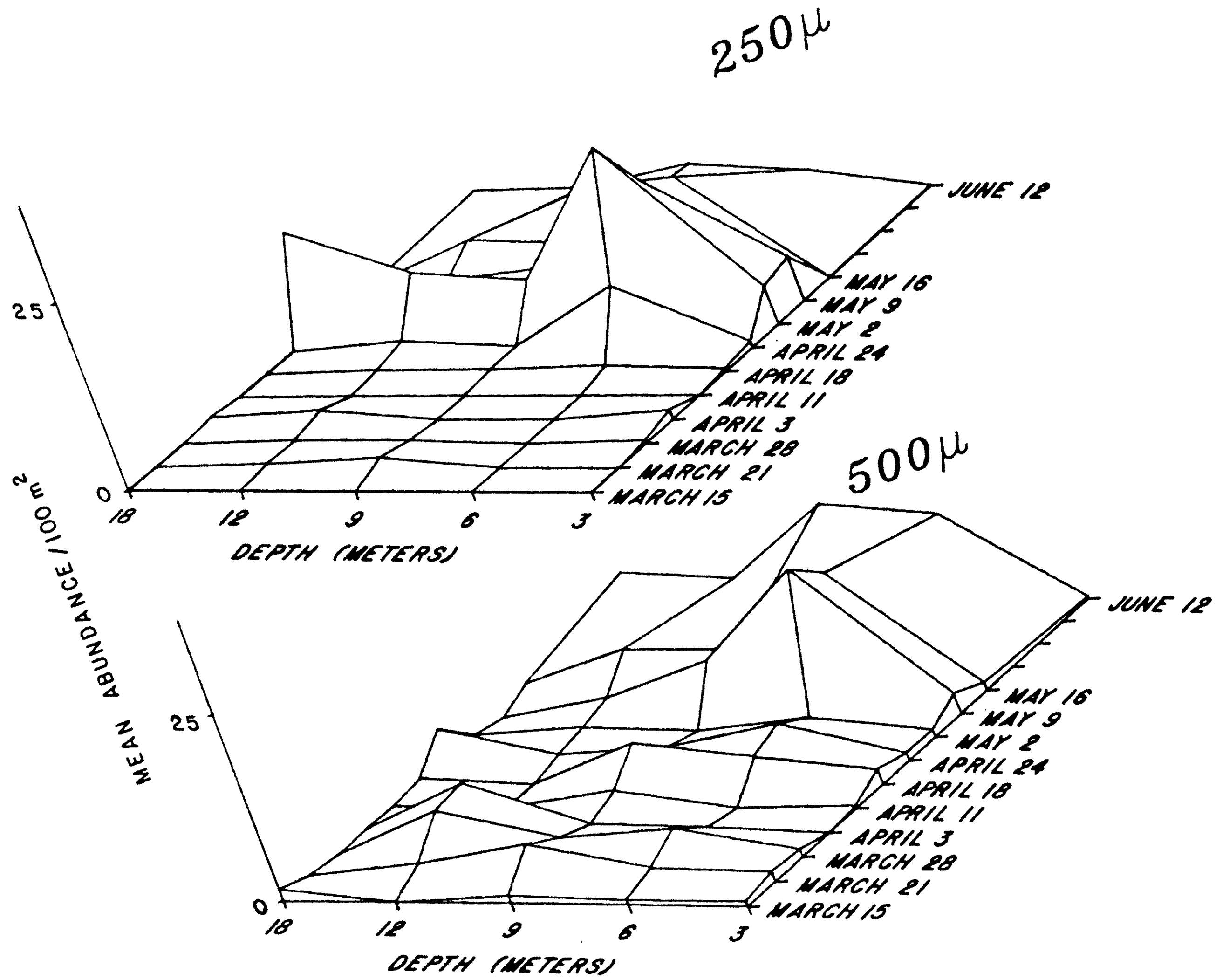

250μ
500μ
MEAN ABUNDANCE / 100 cm²
0
75
150
18
12
9
6
3
DEPTH (METERS)
JUNE 12
MAY 16
MAY 9
MAY 2
APRIL 24
APRIL 18
APRIL 11
APRIL 3
MARCH 28
MARCH 21
MARCH 15

Figure 17. Tubificoides spp. Mean abundance on each sieve size (500, 250 um) by station through time.



250μ
500μ
JUNE 12
MAY 16
MAY 9
MAY 2
APRIL 24
APRIL 18
APRIL 11
APRIL 3
MARCH 28
MARCH 21
MARCH 15
30
15
0
18
12
9
6
3
DEPTH (METERS)
MEAN ABUNDANCE / 100 cm²

Figure 18. Leucon americanus. Mean abundance on each sieve size (500, 250 um) by station through time.


250μ
500μ
MEAN ABUNDANCE / 100 m²
25
0
18
12
9
6
3
DEPTH (METERS)
JUNE 12
MAY 16
MAY 9
MAY 2
APRIL 24
APRIL 18
APRIL 11
APRIL 3
MARCH 28
MARCH 21
MARCH 15

DISCUSSION

Early post-settlement mortality can significantly reduce population abundances and alter distributions before recruitment is assessed. If the complexity of early population dynamics is not considered in a study's experimental design, inferences about settlement and population dynamics may be in error. In the present study, weekly sampling with a 125 um sieve dated settlement to within 7 days and revealed the dynamics of recently-settled populations. Length measurements of recently-settled juveniles agree well with published data for the same or similar species which produce pelagic larvae. Mean lengths of recently-settled juveniles of some species found in this study are: *Asabellides oculata*, 791 um; *Streblospio benedicti*, 563 um; *Eteone heteropoda*, 504 um; *Leitoscoloplos fragilis*, 768 um; *Mediomastus ambiseta*, 429 um; *Polydora cornuta*, 966 um. Cazaux (1982) reported early benthic juveniles of the ampharetid *Alkmaria romijni* were 550 um long. Recently settled juveniles of *Streblospio benedicti* are between 450 and 550 um or 550 and 650 um for planktotrophic or lecithotrophic larvae, respectively (Levin, 1984). Thorson (1946) reported that *Eteone longa* is about 1430 um as an early benthic juvenile. An Australian population of *Leitoscoloplos fragilis* is 659 um when it settles (Anderson, 1961). Orth (1971) found recently-settled juveniles of *Polydora cornuta* (=*P. ligni*) were about

1300 um long. Thus, it appears that the 125 um sieve retained the earliest benthic life stages of these animals.

Abundances of Asabellides oculata and Eteone heteropoda indicate differential settlement played an important role in defining recruitment patterns while abundances of Streblospio benedicti suggest differential post-settlement mortality altered its recruitment pattern. Recently-settled and late juveniles of A. oculata appeared in lesser abundances at the 3 m station than at either the 6 m, 9 m, 12 m station. The 3 m and 18 m station had similar mean abundances of juveniles, though variances at the 18 m station were high. This patchiness may have been due to physical dynamics (e.g. tidal resuspension) or small-scale differential settlement at this deep water station. Adult A. oculata (500 um sieve) had significantly lower abundances at the 3 m station than at any other station. Recently-settled juveniles of E. heteropoda displayed a pattern opposite to that of A. oculata with greater abundances at the 3 m station than the 18 m station. Nearly identical patterns were evident for late juveniles and adults. The initial distribution established by recently-settled juveniles of both A. oculata and E. heteropoda was manifested in the distributions of late juveniles and adults. This suggests that the pattern of recruitment for these species was strongly influenced by settlement.

Recently-settled Streblospio benedicti had greater abundances at 3 m, 6 m, 9 m and 12 m stations than at the 18 m station. In contrast, the adults were in similar abundance at 9 m, 12 m and 18 m. Although the stations remain in nearly identical mean rank order of abundance, post-settlement mortality at the 9 m and 12 m stations effectively altered the pattern initially established by recently-settled juveniles.

The abundance pattern for recently-settled and late juveniles of the orbinid Leitoscoloplos fragilis indicates no trend among stations; however, the adult abundances at 3 m were greater than at all other stations. Although L. fragilis recently-settled juveniles were present at all stations (Fig. 9), the abundances may indicate that this species maintains low-level recruitment through spring and summer. Data from a neighboring study site (Diaz, unpub. data) indicated the major recruitment pulse occurs during the fall and winter. It is not clear if differential settlement or differential mortality accounts for the high adult abundances of L. fragilis at 3 m. Another species in which these processes could not be readily distinguished is the capitellid Mediomastus ambiseta. Greater abundances of recently-settled juveniles appeared at the 3 m station than at 18 m while the adult pattern was exactly opposite; however, the major recruitment pulse began the last two weeks of the study and appeared to be high at all stations. Larvae of M. ambiseta may actually prefer to settle in finer sediment stations (6 m, 9 m, 12 m and 18 m). Dubilier (1988) demonstrated that organic-rich mud stimulates settlement in the confamilial species Capitella sp. I. It is possible that the main recruitment pulse of M. ambiseta results in higher abundances in the deeper stations. The adult distribution of the bivalve Mulinia lateralis is also higher at the deeper stations than at 3 m. Virnstein (1977) found predation by the blue crab Callinectes sapidus greatly reduced abundances of M. lateralis in a shallow sub-tidal exclosure. Chesapeake Bay watermen deploy crab pots from 1.8 to 18 m of water (Van Engel, 1962) suggesting blue crabs forage to that water depth; however, it is possible that deeper waters may act as a refuge from predation for M. lateralis when C. sapidus migrates to shallow water in the spring. Unfortunately, the sampling schedule did not allow a distinction between settlement and post-settlement mortality of recently-settled juveniles of L. fragilis, M. ambiseta or M. lateralis.

The oligochaete Paranais littoralis reproduces without a pelagic developmental stage. A few individuals appeared at the middle stations of the transect but most juveniles and nearly all adults were found at the 3 m station. The marked seasonal recruitment pulse observed in this study has also been noted in a European population of P. littoralis (Bagheri and McLusky, 1982). Although Tubificoides spp. abundances were not different among stations for juveniles, adult abundances were clearly greater in the deeper, finer sediment stations. Prolonged recruitment punctuated by periods of high mortality typify population dynamics of Tubificoides spp. in the lower York River (Diaz, 1984).

Settlement patterns, as indicated by recently-settled juveniles (125 um sieve), are the result of several scales of processes: 1) large-scale larval supply (Hannan, 1981; Grosberg, 1981; Gaines et al., 1986), 2) meso-scale passive deposition of larvae (Eckman, 1983; Hannan, 1984; Butman, 1986) and 3) small-scale active habitat selection by larvae (Scheltema, 1974; Woodin, 1985; Dubilier, 1988). Although no data was collected to resolve their relative contributions, all of these processes may have interacted to produce the observed settlement patterns along the study transect.

The reduction in species abundance may have been the result of mortality, emigration (passive or active) or burrowing below sampling depth. Mortality of early benthic juveniles can be high (Zajac and Whitlatch, 1982; Watzin, 1983). Direct adult-juvenile interactions

(Woodin, 1976) include ingestion of larvae from the water column (Williams, 1980; Wilson, 1980; Peterson, 1982) and of juveniles from surface sediment (Wilson, 1981; Oliver et al., 1982; Elmgren et al, 1986). Established infauna can also induce mortality indirectly by burying larvae and juveniles with sediment displaced by feeding, burrowing and defecating (Rhoads and Young, 1970; Brenchley, 1981; Wilson, 1981). Interactions with meiofauna have also proven to decrease juvenile macrofaunal abundance (Bell and Coull, 1979; Watzin, 1983, 1986). Virnstein (1977, 1979) found the blue crab Callinectes sapidus and the bottom-feeding fish Leistomus xanthurus effectively reduced abundances of shallow-dwelling infauna such as Streblospio benedicti, Polydora cornuta (=P. ligni) and Mulinia lateralis. Active emigration is possible in more motile species like S. benedicti (Dauer et al., 1981). Passive transport by waves or tidal currents (Tamaki, 1986; Luckenbach, 1986) could also account for the reduction of abundances. Benthic faunal samples in this study represent only the top 2 cm of the sediment and it could be argued that reduced abundances reflect deeper burrowing of older animals. Large decreases in abundances occurred within 2 to 3 weeks of settlement and it does not seem likely that these animals grew large enough to burrow below 2 cm, especially the surface-deposit feeders S. benedicti and A. oculata.

Efforts to evaluate recruitment in soft-bottom habitats have historically been confounded by inadequate sampling techniques. Recent studies have employed intensive spatial and temporal sampling which has revealed the complexity of early population dynamics in soft-bottom habitats (Luckenbach, 1984; Bachalet, 1984; Shaffer, 1983). Such rigorous techniques may be especially important in highly variable habitats such as estuaries (Livingston, 1987). Luckenbach (1984) found the abundance pattern initially established by recently-settled _Mulinia lateralis_ changed substantially in just 30 days. This species absence in the recent study may be the result of post-settlement mortality rather than failure to settle (Virnstein, 1977). Sampling biweekly with a 265 um sieve, Muus (1973) found settlement distribution beween two stations (18 and 27 m) coincided with later adult distributions in 10 of 11 bivalve species. The present study reveals both settlement and post-settlement mortality can significantly influence abundance patterns of estuarine polychaetes in a short time and highlights again the difficulty of inferring population dynamics from data collected long after settlement.

APPENDIX I. Abundance, total and by sieve, of benthic invertebrates collected in the study.

APPENDIX I. Abundance total and breakdown by sieve of all species collected. Taxon code: A-Amphipod, B-Bivalve, C-Cumacean, G-Gastropod, I-Isopod, N-Nemertean, O-Oligochaete, P-Polychaete, Pc-Pycnogonid, Ph-Phoronid, Po-Polyclad.

Species	Total Abundance	500 um	250 um	125 um
Asabellides oculata (P)	23,566	1,576	4,960	17,030
Mediomastus ambiseta (P)	14,424	3,524	4,512	6,388
Streblospio benedicti (P)	11,450	1,970	5,115	4,365
Paranais littoralis (O)	2,841	1,338	1,399	104
Eteone heteropoda (P)	1,640	249	636	755
Tubificoides spp. (O)	1,413	887	414	112
Leitoscoloplos fragilis (P)	1,048	349	399	300
Leucon americanus (C)	1,045	637	407	1
Glycinde solitaria (P)	983	282	566	135
Mulinia lateralis (B)	790	661	128	1
Polydora cornuta (P)	566	216	293	57
Polycladia	488	296	142	50
Ampelisca abdita (A)	345	261	84	0
Odostmia engonia (G)	256	242	15	0
Acteocina canaliculata (G)	250	212	38	0
Paraprionospio pinnata (P)	227	214	13	0
Pectinaria gouldii (P)	218	58	48	112
Corophium tuberculatum (A)	165	101	64	0
Acteon punctostriatus (G)	150	33	117	0
Cauleriella sp. (P)	123	46	69	8
Pelecypoda	110	1	29	80
Tagelus plebius (B)	55	25	25	5
Clymenella torquata (P)	42	42	0	0
Nereis succinea (P)	39	30	9	0
Lyonsia hyalina (B)	39	17	18	4
Gammarus mucronatus (A)	37	15	22	0
Gyptis sp. (P)	37	0	21	16
Scolecolepides viridis (P)	36	24	11	1
Edotea triloba (I)	32	32	0	0
Phoronis (Ph)	31	30	1	0
Amphiporus sp. (N)	28	27	1	0
Saccoglossus kowalewskii (H)	28	21	7	0
Sigambra tentaculata (P)	25	21	4	0
Gastropoda	22	0	1	21
Cirratulidae (P)	21	0	0	21
Coronadena mutabilis (Po)	16	1	14	1

APPENDIX I. (continued)

Species	Total Abundanace	500 um	250 um	125 um
Heteromastus filiformis (P)	16	15	1	0
Cyclostremiscus pentagona (G)	15	0	0	15
Ensis directus (B)	15	8	7	0
Stylochus ellipticus (N)	14	10	0	4
Tellina (B)	14	0	14	0
Caprella equilibra (A)	14	6	8	0
Glycera americana (P)	11	2	9	0
Nephtys sp. (P)	10	0	7	3
Anthozoa	10	10	0	0
Monoculodes edwardsii (A)	9	8	1	0
Sabella microphthalma (P)	9	9	0	0
Idunella clymenellae (A)	9	5	4	0
Amplisca vadorum (A)	9	9	0	0
Pinnixa sayana (D)	7	7	0	0
Phyllodoce arenae (P)	5	3	2	0
Mercenaria mercenaria (B)	5	1	4	0
Rhynchocoela	5	4	1	0
Ogyrides alphaerostris (D)	5	5	0	0
Tellina agilis (B)	4	4	0	0
Turbonilla interrupta (G)	4	4	0	0
Glyceridae (P)	4	4	0	0
Gemma gemma (B)	4	1	3	0
Harmothoe extenuata (P)	3	3	0	0
Spio setosa (P)	2	2	0	0
Melita nitida (A)	2	1	1	0
Neomysis americana (C)	1	1	0	0
Polynoidae (P)	1	0	1	0
Spiophanes bombyx (P)	1	1	0	0
Tharyx setigera (P)	1	1	0	0
Stenothoe minuta (A)	1	0	1	0
Scolelepis squamata (P)	1	1	0	0
Tanystylum orbiculare (Pc)	1	1	0	0
Anadara transversa (B)	1	1	0	0
Loimia medusa (P)	1	1	0	0
Glycera sp. (P)	1	0	0	1
Oxyurostylus smithi (C)	1	1	0	0
Idunella barnardii (A)	1	1	0	0
Mysidopsis bigelowi (A)	1	0	0	0

APPENDIX II. Taxonomic key list.

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