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The population dynamics and recruitment pattern of the phoronid, Phoronopsis viridis

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THE POPULATION DYNAMICS AND RECRUITMENT PATTERN OF THE PHORONID, *PHORONOPSIS VIRIDIS*

A Thesis
Presented to
the Faculty of the Graduate School
University of the Pacific

In Partial Fulfillment
of the Requirements for the Degree
Master of Science

by
Victoria Rolanda Starczak

May, 1979

This thesis, written and submitted by

VICTORIA ROLANDA STARCZAK

is approved for recommendation to the Graduate School, University of the Pacific.

Department Chairman or Dean:

Thesis Committee:

Steven Obrebski

Edmund H Smith

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INTRODUCTION

A dominant organism on intertidal Pacific Coast sandflats is the lophophorate *Phoronopsis viridis* Hilton. This suspension feeder builds a stiff, sandy tube, 3 mm wide and up to 20 cm long and usually lying within 6 cm of the surface (Johnson 1967a). *Phoronopsis viridis* is found over large areas and tidal ranges of sandflats in aggregate densities of over 21,000 phoronids per m^2 (Ronan 1978). On Lawson's Flat, the location of the present study, the areas of highest density of *P. viridis* have been known to persist for over 20 years (Steven Obrebski, personal communication).

The factors accounting for the persistence of these dense phoronid populations have not been studied although four hypotheses have been proposed (see Ronan 1975, 1978). These are: 1) dense clusters of adult phoronids increase the probability of successful gamete fertilization; 2) high densities of phoronids stablize the sediment, thus limiting the movement of large burrowing infauna that are potentially destructive to phoronids (Ronan 1975); 3) a dense canopy of lophophores slows currents over the sediment surface, increasing the deposition of food items; and 4) clustering limits the effects of predation. The sudden retraction of a lophophore in response to a disturbance results in withdrawl of neighboring phoronids in the area of the disturbance (Ronan 1978).

In order to evaluate the adaptive significance of population persistence it is crucial to understand the mechanism by which dense populations persist. Therefore the purpose of this study is not to assess the adaptive significance of clustering, but rather to determine what mechanisms might explain the persistence of dense phoronid populations. Consequently, this study is more applicable to an "ecological" time scale than an "evolutionary" one. In this study the population dynamics and recruitment pattern of _P_. _viridis_ is described with reference to the mechanism which enables persistence of dense phoronid areas. In addition, the effects of food abundance and the reworking activity of the surface deposit feeder, _Axiothella rubrocincta_ Johnson, a maldanid polychaete, on _P_. _viridis_ density and recruitment are measured.

STUDY AREA CHARACTERISTICS

The study was conducted on a south-facing intertidal sandflat, known locally as Lawson's Flat, and located 1.6 km south of the entrance to Tomales Bay, California ($39^{o}15'$N latitude and $123^{o}00'$W longitude). The tides are of the mixed, semidiurnal type with a mean range of 1.1 m. Throughout most of the year salinities are between 30 to 35‰. Water temperatures vary from 12 to 15°C (Johnson, 1971). The sands of the flat are well-sorted and originate from adjacent sand dunes. More complete descriptions of the area are given in Johnson (1965, 1967a, 1967b, 1970) and Daetwyler (1966).

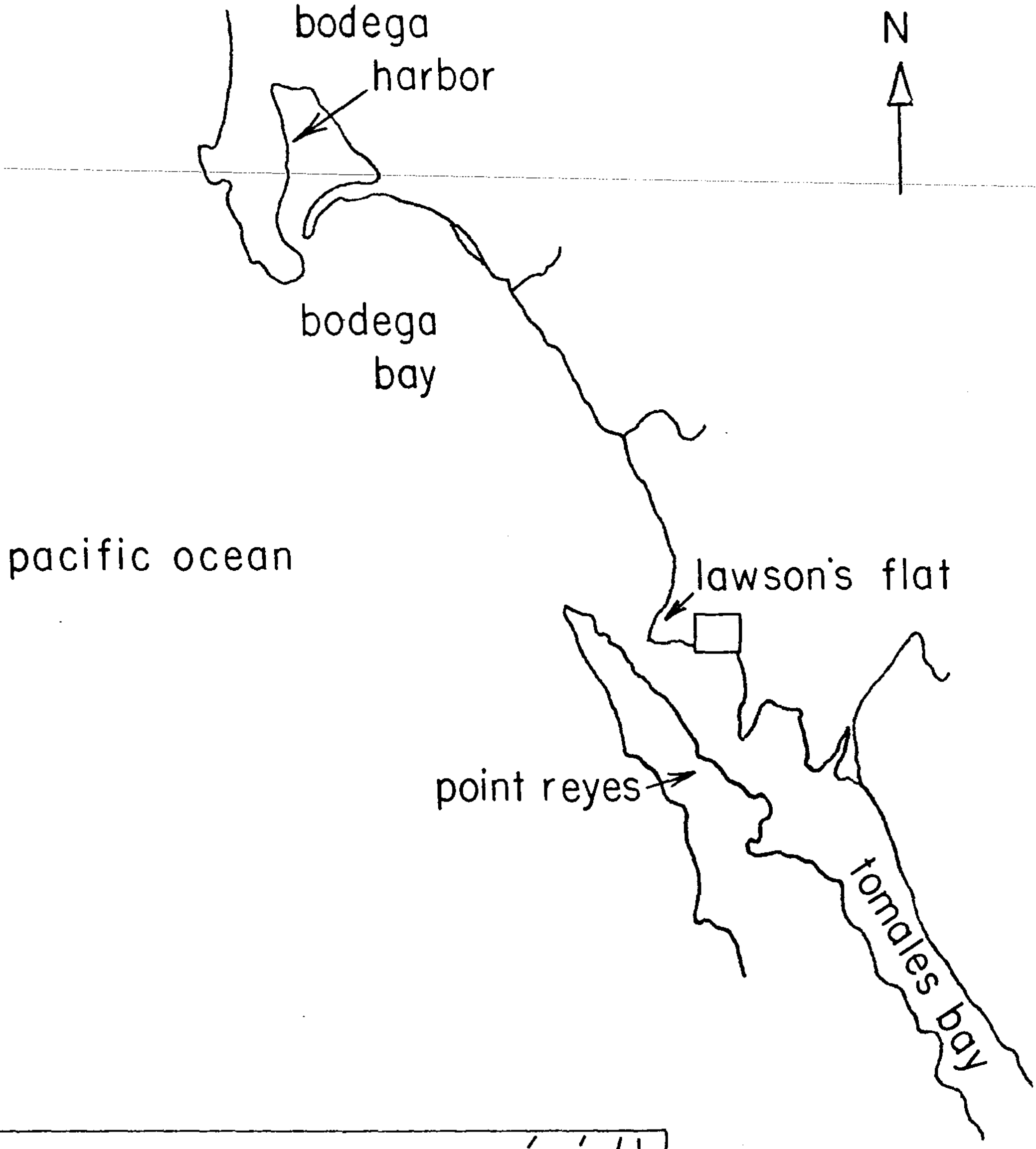
Phoronopsis viridis is found over a large portion of the intertidal sandflat at Lawson's Flat. In order to examine temporal size distribution and abundance of P. viridis, three study sites (22 m in length by 20 m in width) of different phoronid densities were chosen. The distance between Study Sites I and II is approximately 70 m; the distance between Sites II and III is 50 m. (Fig. 1) All three sites overlap in tidal height. Study Sites II and III contain sections of patches formed by individuals of the deposit-feeding polychaete, Axiothella rubrocincta.

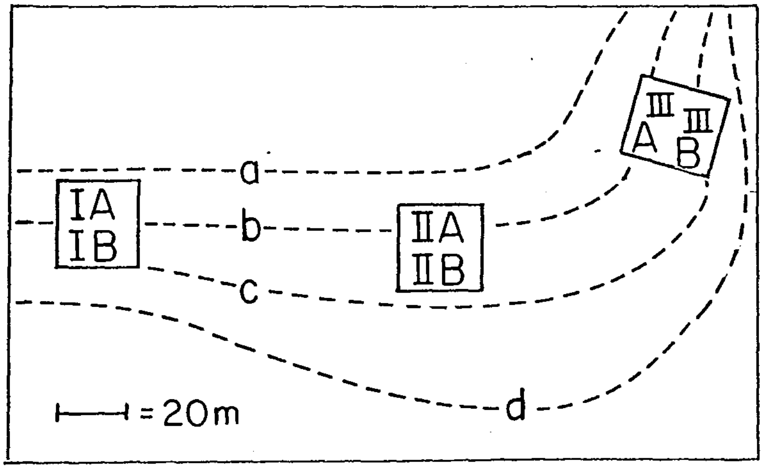
Axiothella rubrocincta inhabits U-shaped tubes composed of sand with surface openings for feeding and defecation (Kudenov, 1971). Distinctive surface structures (funnels and volcano-like mounds) are formed by the reworking activity of Axiothella rubrocincta which allows location of these patches and feeding A. rubrocincta to be monitered over time (Weinberg, 1978).

All sampling was conducted on the exposed sandflat during low tide. A stratified random sampling was performed by dividing each Study Site into an upper (A) and lower (B) half. (Fig. 1) The upper and lower half of a study site will be referred to as a study area.

Fig. 1

The location of the study sites. Insert shows the three study sites (I, II, III) with two tidal levels (A, B) on Lawson's Flat. The tidal height contours are: a=+2.5 ft, b=+2.0 ft, c=+1.35 ft, d= Tomales Bay at low tide.


bodega harbor
N
bodega bay
pacific ocean
lawson's flat
point reyes
tomales bay


III A
III B
a
IA
IB
b
IIA
IIB
c
d
=20m

METHODS

I. SEDIMENT

Sediment characteristics are beleived to be correlated with food abundance and are of primary importance in soft substrate systems. For this reason two methods were used to measure sedimet grain size and food availability in the study sites. These methods were size particle analysis and per cent total organic carbon (%TOC). The sampling design was a three-way ANOVA with treatments: study site (3), sampling time (2), and tidal level (2).

Sampling took place in October 1977 and April 1978. Three random cores (4 cm in diameter and 6 cm in length) were taken per tidal level (i.e. six cores per study site) and oven dried for 48 hours. Each sample was separated into two fractions of 100 g and 30 g each. The 100 g fractions were placed in a series of tyler sieves ($\frac{1}{2}$ Ø) shaken for 20 minutes, and the contents of each sieve weighed. Cumulative curves were plotted and the graphic median (best measure of overall mean particle size) was calculated as described by Buchanan (1974). The per cent total organic carbon (%TOC) from the 30 g fractions was measured on an Oceanography International Carbon Analyzer. Three, 0.2 g replicates were measured for each sample. Statistical analysis was performed on the %TOC results using a three-way ANOVA with nesting (replicates of the samples were the nested factor).

Statistical analysis of the data was performed on an

IBM 370 computer using the programs in the SAS statistical package (Barr et al 1976).

METHODS

II. *AXIOTHELLA RUBROCINCTA*

The sediment reworking activity of *Axiothella rubrocincta* may effect sediment and species composition. To examine possible density-dependent effects of *A. rubrocincta* on the recruitment and abundance of *P. viridis*, monthly estimates of densities of feeding *A. rubrocincta* were made (April 1977 to 1978). These estimates were made from counts of surface fecal mounds produced by the reworking activity of individual *A. rubrocincta*. This counting technique was employed because the escape response of *A. rubrocincta* made capture by direct coring difficult. Thirty replicate counts, using a 0.25 m^2 quadrat, were made within the two tidal levels in Study Site II and the upper tidal level of Study Site III (Fig. 1).

Occasionally the fecal surface mounds were washed away by wind or surface water currents, but the tube of *A.* rubrocincta remained on the surface and counts of these tubes were used for monthly density estimates (personal observation). The reliability of this counting method was tested in two ways in January, 1978. First, counts in Study Site III were compared on two consecutive days, counting tubes one day (no mounds present) and the reestablished surface mounds the next day. Secondly, the mounds in Study Site II were counted on two successive days, when mounds were present on both days.

Axiothella rubrocincta density measurements from Study Site III were not made in September 1977 due to overgrowth of algae (Entermorpha and Ulva) which covered the surface fecal mounds rendering counting impossible. Densities of feeding A. rubrocincta were measured in August and October 1977 although algae may have obscured some mounds. Quadrats in which algae occurred were not used in the calculation of mean densities.

METHODS

II. *PHORONOPSIS VIRIDIS*

A. POPULATION

To study the population dynamics of *Phoronopsis viridis*, the phoronids were sampled monthly in three study sites from April 1977 to April 1978. The sampling design was a three-way ANOVA with treatments: study site (3), tidal level (2) and time (13). Stratified random sampling was conducted by taking twenty-four cores, twelve per tidal level, in each study site. A hand held PVC core, 10 cm in diameter by 25 cm in length was used. In April 1977 cores were sieved (3.0 mm sieve) and phoronids counted in the laboratory. Thereafter, to minimize breakage of phoronids, cores were sieved in the field, phoronids were picked from the sieve and brought to the lab for counting. From September 1977 to April 1978 a 1.0 mm sieve was substituted for the 3.0 mm sieve to increase the number of *P. viridis* recruits retained. To determine if there was a significant difference in the mean number of juveniles retained in the two sieves, eight cores were randomly taken in each study site in August 1977 brought to the lab, sieved (.75 mm sieve) and phoronid recruits (less than 2.0 mm in tube width) were counted. The mean number of recruits retained in the 0.75 mm sieve was statistically compared to the mean number of recruits retained in the 3.0 sieve in the August samples.

The presence of the region of "color change" served as the criterion for including a phoronid in the mean density estimates. This region is where the red reproductive segment of a phoronid joins the opaque muscular segment and is easily observed when the phoronid is held next to a light. This technique permits accurate counts of phoronids while other methods, such as lophophore counts or counts of holes left in the sediment surface are unreliable (personal observation).

Phoronids were size classed to study the population size structure over time. The basal tube width was correlated with the phoronid dry weight (without the tube) ($R^2 = 0.871$, $N=58$, $P < .001$). Phoronids were measured only if the basal end of the tube was intact. Therefore not all _P. viridis_ counted for the mean density estimates (described in the previous paragraphs) were size classed. However, the number of phoronids size classed was correlated with the monthly mean densities to insure the population was accurately represented ($R^2=.666$, $N=65$, $P < .001$).

Size frequency graphs were plotted for every month and study area. Each graph was scaled with respect to phoronid density by multiplying each size class frequency by a scaling factor. This factor is a fraction calculated by taking the monthly maximum density for a study area and dividing by the maximum mean density for the year among all areas. This scaling factor permits a simultaneous graphical comparison of changes in phoronid density and size frequency distribution through time and space.

In one Study Area (IB), size classing was limited to the replicates in which the first 300 individuals were encountered (8-11 replicates out of the 12 taken for density measurements). In this case, the number of individuals used to estimate mean monthly density is not equal to the number of individuals (300) used for size classing. Because the scaling factor involves monthly mean densities, it was necessary to establish if the mean densities calculated from the replicates size classed (8-11) were not significantly different from the mean densities calculated with 12 replicates. These means were not significantly different for any month (t-test, $p < .05$).

METHODS

IV. PHORONOPSIS VIRIDIS

B. LARVAE

Observations on Phoronopsis viridis larval behavior, including settlement preferences were made on larvae collected in Tomales Bay from August to October 1978. Larvae were caught in a 250 μ plankton net towed by hand through the water off Lawson's dock, at Lawson's Landing. In the laboratory, the larvae were easily observed under a dissecting microscope and pipetted into finger bowls (11.5 cm in diameter) containing fresh filtered seawater. Some of the bowls contained sediment collected from phoronid areas, which had been sieved (1.0 mm sieve), dried (48 hrs at 83°C), and placed in circulating sea water for a week. All bowls containing larvae were floated in a water table with circulating sea water to keep the temperature (10°C.) as constant as possible and kept under natural lighting conditions. The seawater in the finger bowls was replaced at least every other day.

Larvae which had settled in the finger bowls were measured from the bulb to the base of the lophophore, the "peristaltic" movement of the metamorphosed larvae made measurements difficult. To be consistent, measurements were made when the larvae were most extended.

Two laboratory experiments were conducted to test the effect of the presence of adult P. viridis on larval metamorphosis. In the first experiment a live adult phoronid was carefully removed from its tube and placed in a finger bowl containing a piece of the sand tube, filtered sea water and six *P. viridis* larvae of approximately 1.0 mm in length (stage of metamorphosis). The behavior of the larvae was observed for one half hour and number and position of metamorphosed larvae after a 24 hour period was recorded. In the second experiment, fifteen adult phoronids were removed from their tubes and blended with 100 ml of filtered seawater. Approximately 3 ml of this filtered homogenate was added to a finger bowl containing 400 ml of filtered seawater. Six, 1.0 mm, *P. viridis* larvae were added to this bowl and six to a control bowl containing no extract. The number of settled individuals after 24 hours was recorded.

Larval behavior was observed with two species known to co-occur with *P. viridis* in nature, *Hermissenda crassicornis* Eschscholtz, a nudibranch and *Pseudopolydora paucibranchiata* Okuda, a spionid polychaete. These two species were chosen because they were thought to represent organisms which may prey on settling phoronid larvae. Ovservations were made when the nudibranch was placed in a finger bowl with two (1.0 mm) swimming and two recently settled larvae. The number of individuals eaten by *H. crassicornis* was noted. This nudibranch had been captured in a plankton tow and was keep in the lab previous to the observations made with the larvae. During the week the nudibranch was fed only adult phoronids removed from their tube.

Eight *Psuedopolydora paucibranchiata* in tubes were placed in a glass bowl (7 cm in diameter) with sand (treated as described above) 3 cm deep and kept in circulating sea water for three days prior to observations made with phoronid larvae. Four *P. viridis* larvae were pipetted into the sea water above the spionids and observations made under a disecting scope.

RESULTS

I. SEDIMENT

Particle size analysis of the sands from the three study sites result in a median particle size of .227 mm ± .003 (N=36). The sands are well-sorted with a silt-clay fraction ranging between 1.5 and 4.0% (Fig. 2).

The %TOC in a sediment sample is a measure of the organic carbon in the different particle types in the sediment. Organic matter is found encrusted on sand grains and in the organic matrix which binds silt and clay particles together to form aggregates. There is a significant difference in the % TOC over time, sites and tidal heights (Table 1). The % TOC was highest in October and generally increases with decreasing tidal height (Fig. 3). A Duncan's multiple range test on the mens showed that Sites I and II had the highest densities (Table 2). The significant interactions between month and site, site and tidal height, and site, month and tidal height were found. The % TOC in Site II in October was lower than the % TOC in April in Sites I and III. Within a site the lower tidal level (B) had higher % TOC except in Site II in October where tidal level A had higher % TOC than tidal level B.

Fig. 2

The particle size distribution by weight in the three study sites. Six samples were taken in each study site, three per tidal level in October 1977 and April 1978. Vertical bars are the 95% confidence intervals about the mean. Mesh opening is in microns on a logrithmic scale.

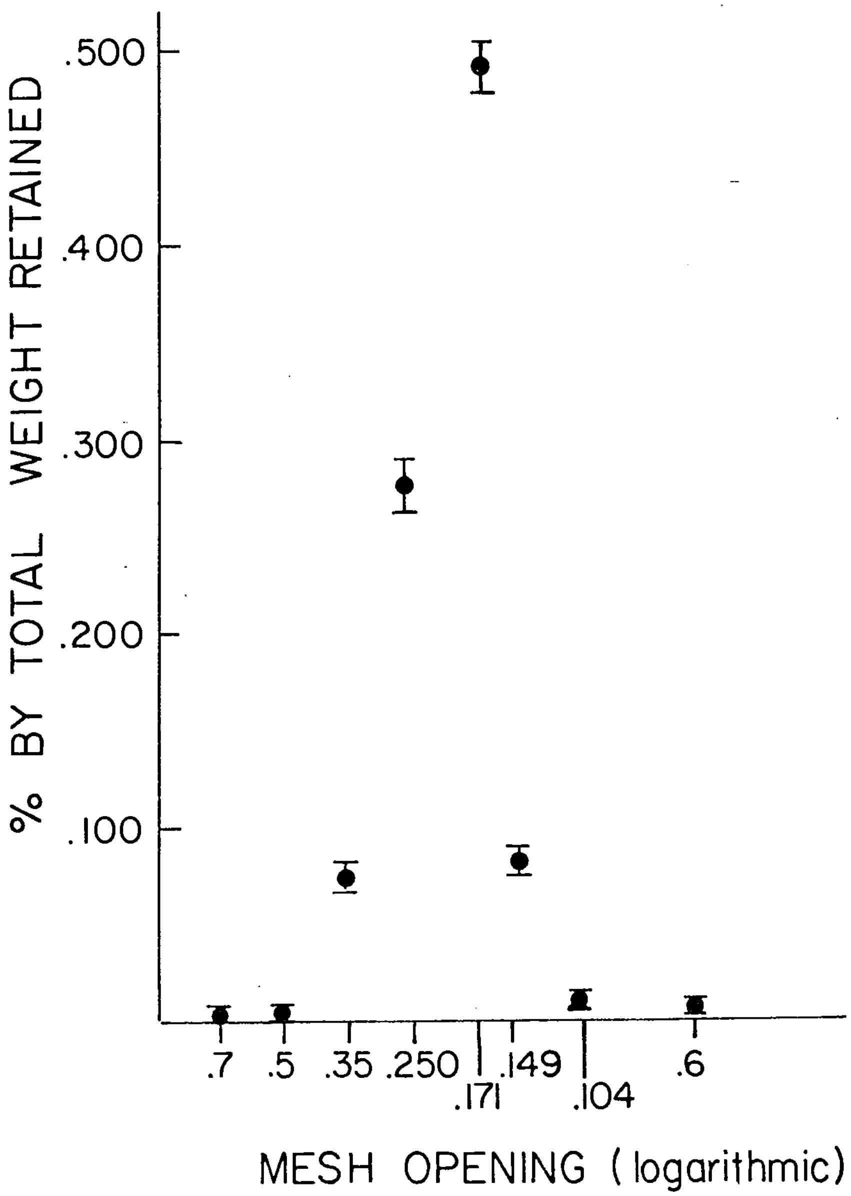

% BY TOTAL WEIGHT RETAINED
.500
.400
.300
.200
.100
.7
.5
.35
.250
.171
.149
.104
.6
MESH OPENING (logarithmic)

Fig. 3

Percentage Total Organic Carbon (%TOC) v.s. Mean Tidal Height (Feet). Each point represents a mean of three samples taken within each study area in October 1977 and April 1978. For reference the mean tidal height of each study area is listed along the y-axis. Sampling times are designated by the letters A (April 1978) and O (October 1977).

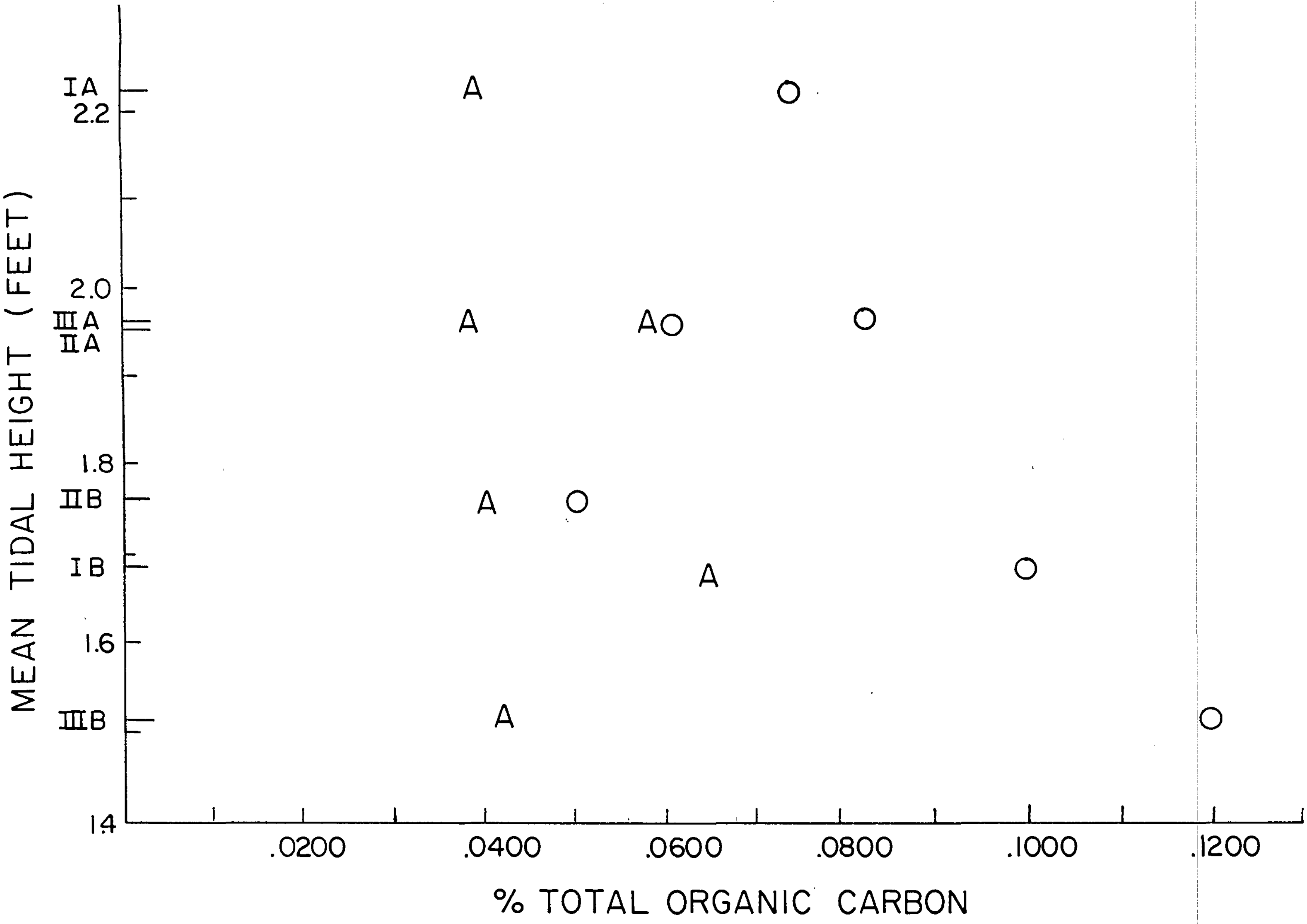

MEAN TIDAL HEIGHT (FEET)
IA
2.2
2.0
IIIA
IIA
1.8
IIB
IB
1.6
IIIB
1.4
.0200
.0400
.0600
.0800
.1000
.1200
% TOTAL ORGANIC CARBON
A
O

Table 1.

Results of a three-way ANOVA with nesting performed on the % TOC from three study sites, two tidal heights and two months. There were three samples nested within each tidal height. Three replicates were made of each sample. The data was transformed using the log+1 transformation to homogenize the variances.

SOURCE OF VARIATION	DF	F VALUE
MODEL	35	11.51 ***
ERROR	60	
CORRECTED TOTAL	95	
MONTHS	1	153.91 ***
SITES	2	39.17 ***
TIDAL HEIGHT	1	27.34 ***
MONTH*SITE	2	13.21 ***
MONTH*TIDAL HEIGHT	1	0.40 ns
SITE*TIDAL HEIGHT	2	13.20 ***
MONTH*SITE*TIDAL HEIGHT	2	3.50 *
MONTH*SITE*TIDAL HEIGHT(SAMPLES)	24	3.46 ***

Probability ranges: *= $0.05 < P < 0.01$

***= $P < 0.001$

ns= not significant

Table 2.

Duncan's Multiple Range Test of the % TOC. Month, study sites and tidal height with the same line are not significantly different. The data was transformed using a log+1 transformation. Alpha Level=.05, DF= 60.

N	MONTH	SITE	TIDE HEIGHT
8	OCTOBER	III	B
7	OCTOBER	I	B
9	OCTOBER	III	A
6	OCTOBER	I	A
9	APRIL	I	B
7	OCTOBER	II	A
7	APRIL	III	B
9	OCTOBER	II	B
7	APRIL	III	A
9	APRIL	I	A
9	APRIL	II	B
9	APRIL	II	A

RESULTS

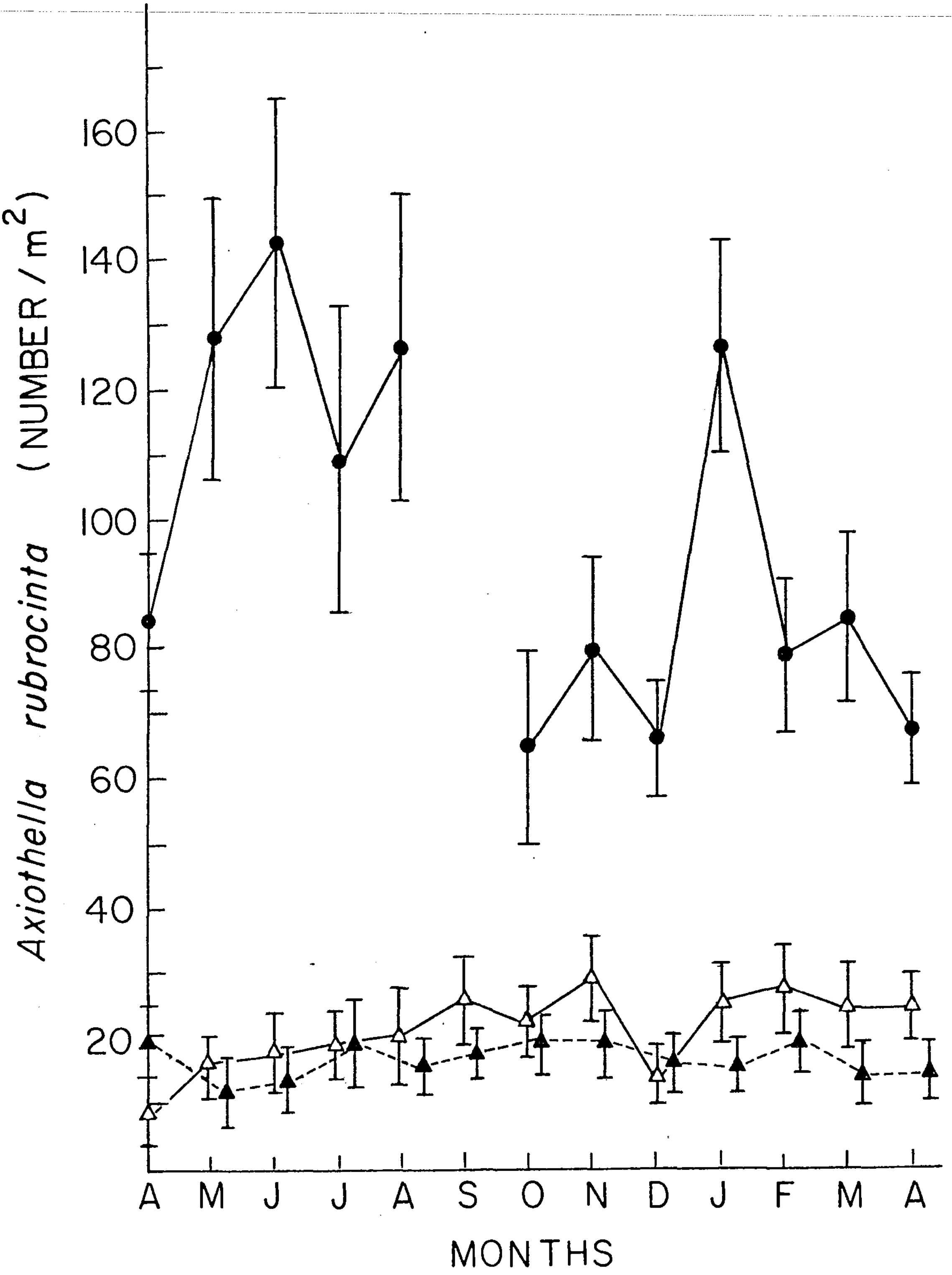
II. AXIOTHELLA RUBROCINCTA

The mean density of feeding Axiothella rubrocincta was at all times greater in Study Site II than in Study Site II (Fig. 5). In Study Site II there was a significant difference between the mean density of A. rubrocincta over the sampling period ($p<.01$). The results from a Duncan's range test on the means indicated that the highest densities in Site III occurred in the fall months and February 1978 (Table 3). A two-way ANOVA (time and tidal height as treatments) was performed on the A. rubrocincta densities in Study Site II. There was no significant difference in A. rubrocincta densities with respect to time or tidal height (Table 4). The results of a Duncan's multiple range test on the means i is presented in Table 5. A. rubrocincta densities were generally stable over time, with the upper tidal level (A) having, in general, higher densities than level B. There was a drop in densities in level A in December from a peak density in November, 1977.

The result of the comparisons of the two density estimation procedures are shown in Table 6. There was no significant difference in mean density at Site II when counts were made on A. rubrocincta tubes one day and surface fecal mounds the next day (one-way ANOVA). However the variance about the mean density using the tube counting method was significantly higher (F-max test $p<.05$) than that of the mound method in Area IIA. There was no significant difference in the mean A. *rubrocincta* density when mounds were counted on two consecutive days (Table 7) in Area IIIA. These comparisons imply that the counting method gives a temporally consistent estimate of *A. rubrocincta* feeding densty

Fig. 4

Mean density of feeding *Axiothella rubrocincta* (number/m^2) during the sampling year (April 1977-April 1978). Study Areas: IIA= —△—; IIB= --▲--, IIIA= ——●——. The vertical bars represent the 95% confidence intervals about the mean.



Axiothella rubrocinta (NUMBER / m^2)
160
140
120
100
80
60
40
20
A
M
J
J
A
S
O
N
D
J
F
M
A
MONTHS

Table 3.

Duncan's Range Test performed on the mean density of feeding Axiothella rubrocincta in Study Site III. Months with the same line are not significantly different. Alpha Level=.05, DF=327. Data was transformed using a log x+1 transformation.

N	MONTHS
30	JUNE
30	JANUARY
15	AUGUST
30	MAY
30	JULY
30	APRIL 77
30	MARCH
28	NOVEMBER
30	FEBRUARY
30	APRIL 78
30	DECEMBER
24	OCTOBER

Table 4.

Results of a two-way ANOVA performed on the density of feeding *Axiothella rubrocincta* in Study Site II. The data was transformed using the log x+1 transformation to homogenize the variances.

SOURCE OF VARIATION	DF	F VALUE
MODEL	25	2.32 ***
ERROR	717	
CORRECTED TOTAL	742	
MONTHS	12	2.58 **
TIDAL HEIGHT	1	13.94 ***
MONTHS*TIDAL HEIGHT	12	1.09 ns

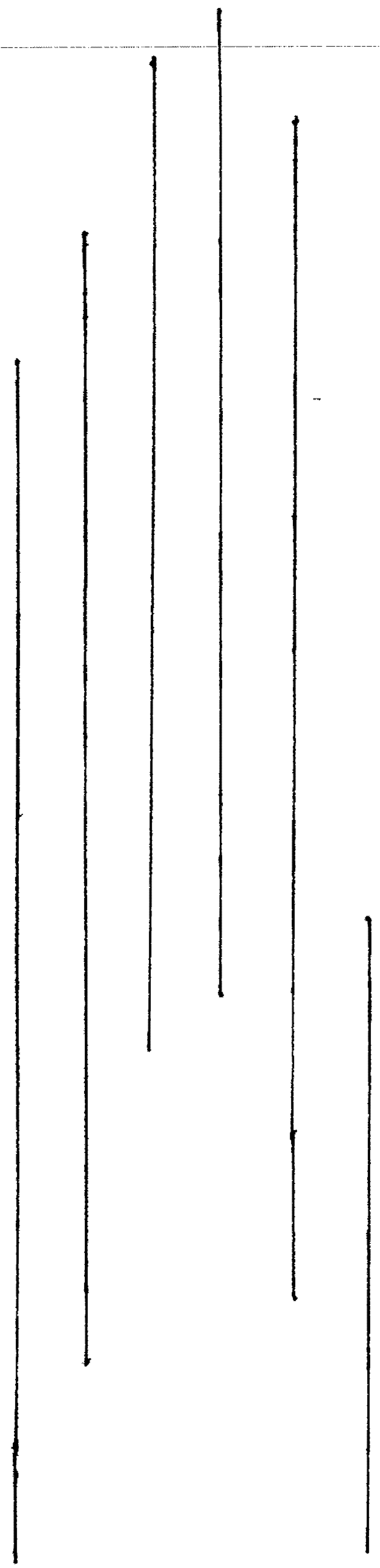
Probability ranges: **= $0.01 < P < 0.001$

***= $P < 0.001$

ns= not significant

Table 5.

Duncan's Multiple Range Test performed on the mean density of feeding Axiothella rubrocincta in Study Site II. Month and corresponding tidal height with the same line are not significantly different. Alpha Level =.05, DF=717. Data was transformed us using a log x+1 transformation.



Nº	MONTH	TIDAL HEIGHT
30	NOVEMBER	A
30	FEBRUARY	A
30	APRIL 78	A
29	JANUARY	A
30	MARCH	A
30	SEPTEMBER	A
13	APRIL 77	B
30	OCTOBER	A
30	FEBRUARY	B
30	SEPTEMBER	B
30	JULY	B
30	NOVEMBER	B
30	JULY	A
30	JUNE	A
29	AUGUST	A
30	JANUARY	B
30	OCTOBER	B
30	DECEMBER	A
29	AUGUST	B
30	DECEMBER	B
30	APRIL 78	B
30	MAY	A
30	MARCH	B
30	JUNE	B
13	APRIL 77	A
30	MAY	B

Table 6.

The means, variances and results of two one-way ANOVAs performed on the mean density of feeding A. *rubrocincta* measured on two consecutive days in Study Site II (mounds not present one day but mounds present the following day).

AREA IIA

	Day 1 (Without mounds)	Day 2 (With mounds)
Mean (*A. rubrocincta*)	16.13	26.34
Variance*	128.51	287.46
Replicates	29	29

The means are not significantly different. (F = 1.507, $P > .05$)

AREA IIB

	Day 1 (Without mounds)	Day 2 (With mounds)
Mean (*A. rubrocincta*)	12.13	16.53
Variance	122.75	99.98
Replicates	30	30

The means are not significantly different. (F = .186, $P > .05$)

* Because the variance were not homogenous the data was transformed using a log (x+1) transformation.

Table 7.

The means, variances and results of a one-way ANOVA performed on the mean density of feeding _A. rubrocincta_ measured on two consecutive days in Study Area IIIA (mounds present on both days).

AREA IIIA

	Day 1 (With mounds)	Day 2 (With mounds)
Mean (#/m^2) (*A. rubrocincta*)	120.53	127.87
Variance	1690.38	2117.12
Replicates	30	30

There is no significant difference between the means. ($F = .409$, $P > .05$).

RESULTS

III. *PHORONOPSIS VIRIDIS*

A. POPULATION DYNAMICS

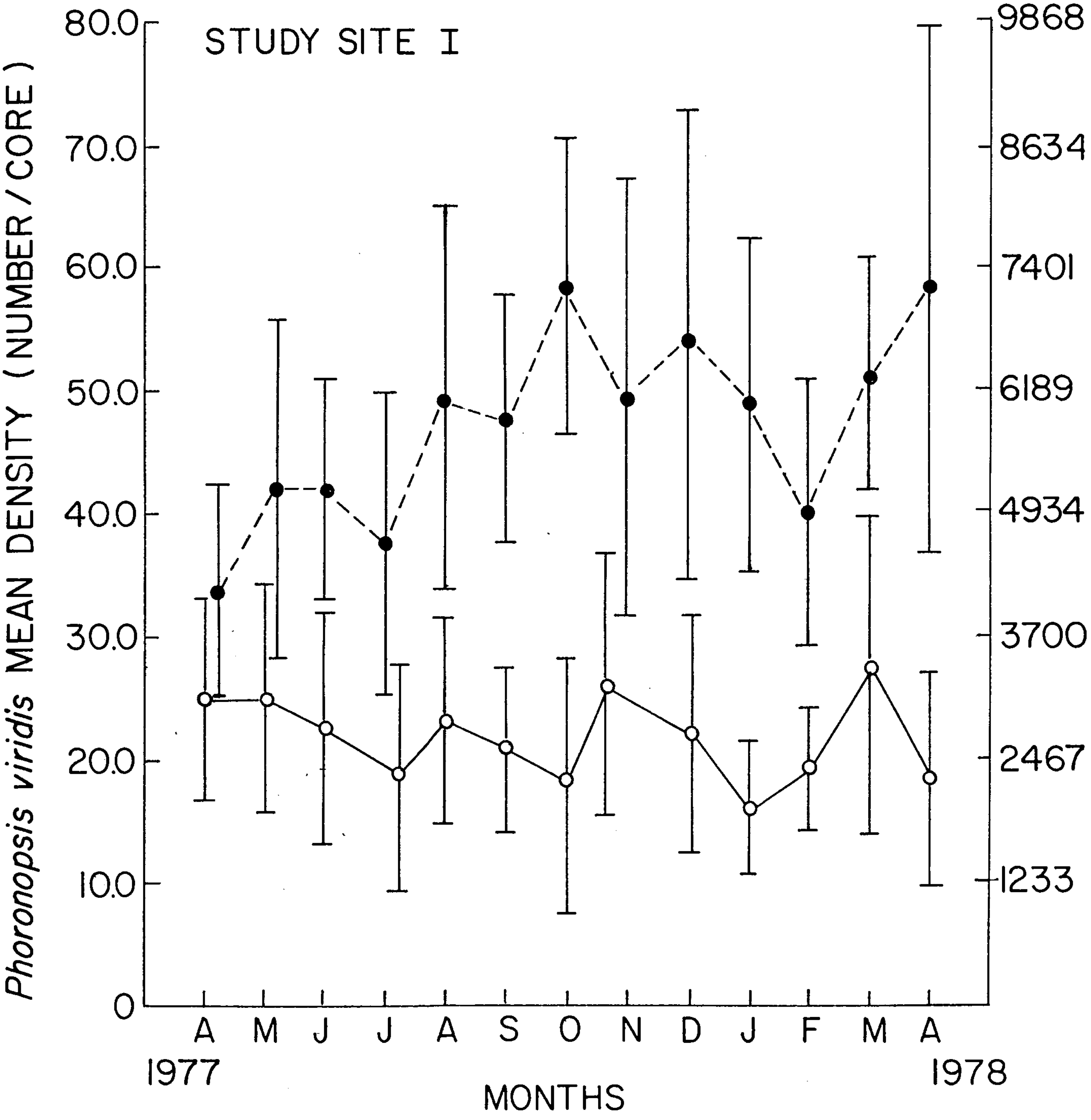
The mean density of *Phoronopsis viridis* remained relatively stable throughout the year in all of the Study Sites (Figs. 5-7). The major increase in density corresponded to the settlement of juveniles in the Fall. The results of a three-way ANOVA which tested the differences in *P. viridis* between tidal levels, sites, and sampling times are shown in Table 8. A Duncan's multiple range test was performed on all the mean *P. viridis* densities from the ANOVA (DF=854, MS=.0531, data were tansformed using a logx+l transformation to homogenize the variances). Results of the Duncan's test showed Area IB with the highest mean density over all times ($p<.05$). There was little difference between means in the two tidal levels in Site II (Fig. 6).

All sites exhibited a decrease in density from peak densities in the fall. This decrease must be the result of adult and/or juvenile mortality since *P. viridis* do not migrate. The decrease in density in Site IIIB from November to March was in part a result of the activity of fisherman attempting to capture the shrimp *Upogebia pugettensis* Dana (Eucarida: Crustacea) with slurp guns. The suction of sediment by the slurp guns leaves holes approximately 13 cm in diameter and 4 cm deep. These hole were noticed throughout Area IIIB and recently settled phoronids were observed lying horizontlly in the depressions. The effect of this disturbance on phoronid mortality was not assessed.

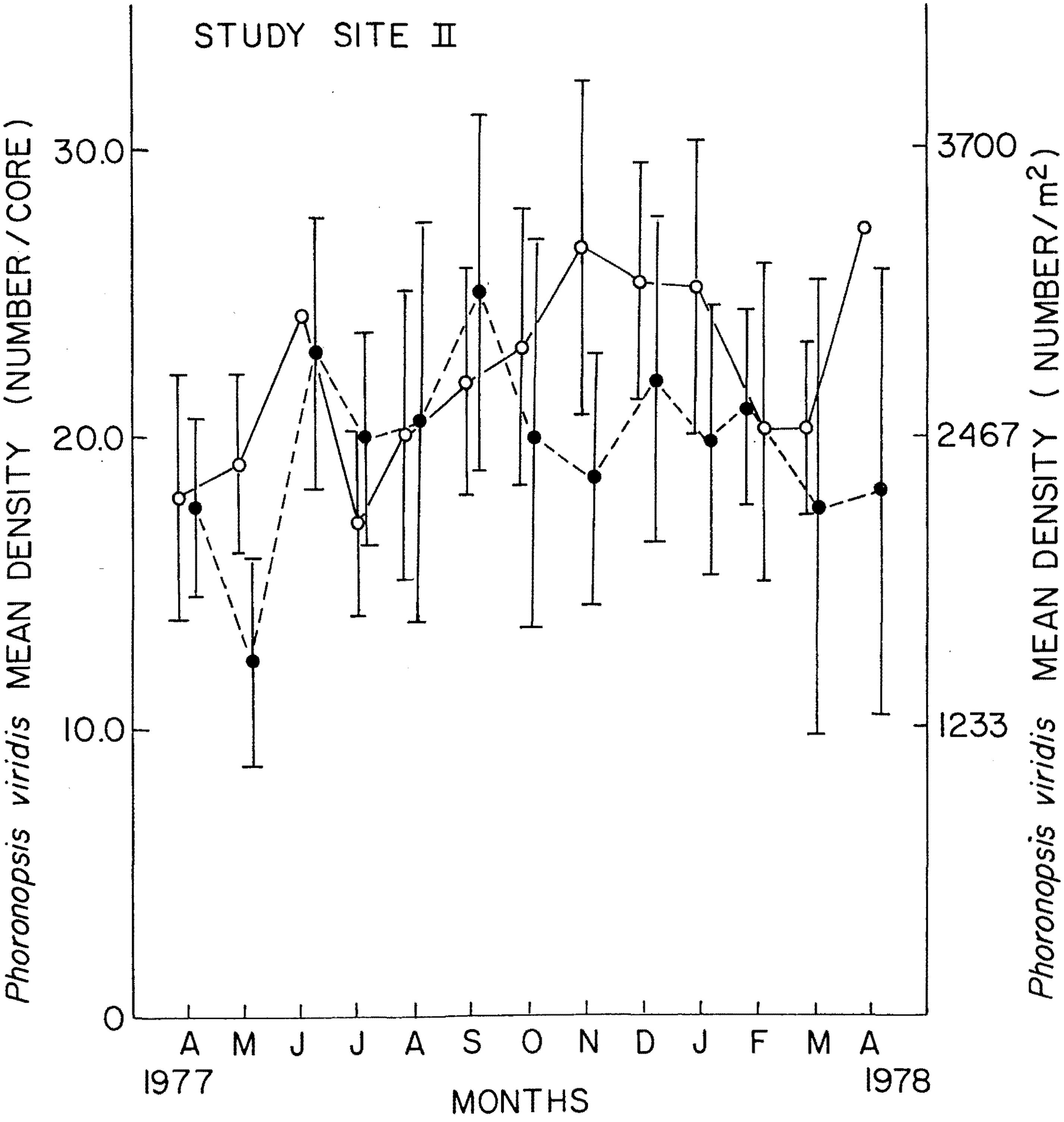
Five size classes (I-V) were created from the measured phoronids. The size classes of measured tube widths were: less than 1.4 mm (I), 1.5 to 2.0 mm (II), 2.1 to 2.6 mm (III), 2.7 to 3.2 mm (IV), and greater than 3.3 mm (V). Size classes I and II were combined and considered as the recruits throughout the text. This was based on the assumption that phoronids were at most one month old when picked from the sieve. Actual growth rates are not known but _P. viridis_ grows to adult size in four months (J. Oliver, personal communication) and grows at least one cm within the first month (T. Ronan, personal communication). The frequency histograms are shown in Figs. 8-13. The adult size (IV) persisted as the major size class throughout the year at all sites. The size frequency distributions were bimodal during the fall months when recruitment was high. Recruitment over the sampling year is best shown in Fig. 14. The proportion of recruits in all sites increased in August and September. The highest recruitment was in Site III in November and December. The lowest proportion of recruits was in Area IA. The lower tidal levels (B) of Sites I and II had higher recruitment than the upper level (A) of these sites. In contrast, higher recruitment was observed in the upper tidal level (A) of Site III than the lower (B) tidal level in this site.

Figs. 5-7

The means and 95% confidence limits of *P. viridis* density over the sampling period (April 1977 to April 1978) in Study Sites I, II, and III. Tidal Levels: A = —○—, B = —●—.



STUDY SITE I
Phoronopsis viridis MEAN DENSITY (NUMBER / CORE)
80.0
70.0
60.0
50.0
40.0
30.0
20.0
10.0
0
Phoronopsis viridis MEAN DENSITY (NUMBER / m^2)
9868
8634
7401
6189
4934
3700
2467
1233
A
M
J
J
A
S
O
N
D
J
F
M
A
1977
1978
MONTHS


STUDY SITE II
Phoronopsis viridis MEAN DENSITY (NUMBER / CORE)
30.0
20.0
10.0
0
Phoronopsis viridis MEAN DENSITY (NUMBER / m^2)
3700
2467
1233
A
M
J
J
A
S
O
N
D
J
F
M
A
1977
1978
MONTHS

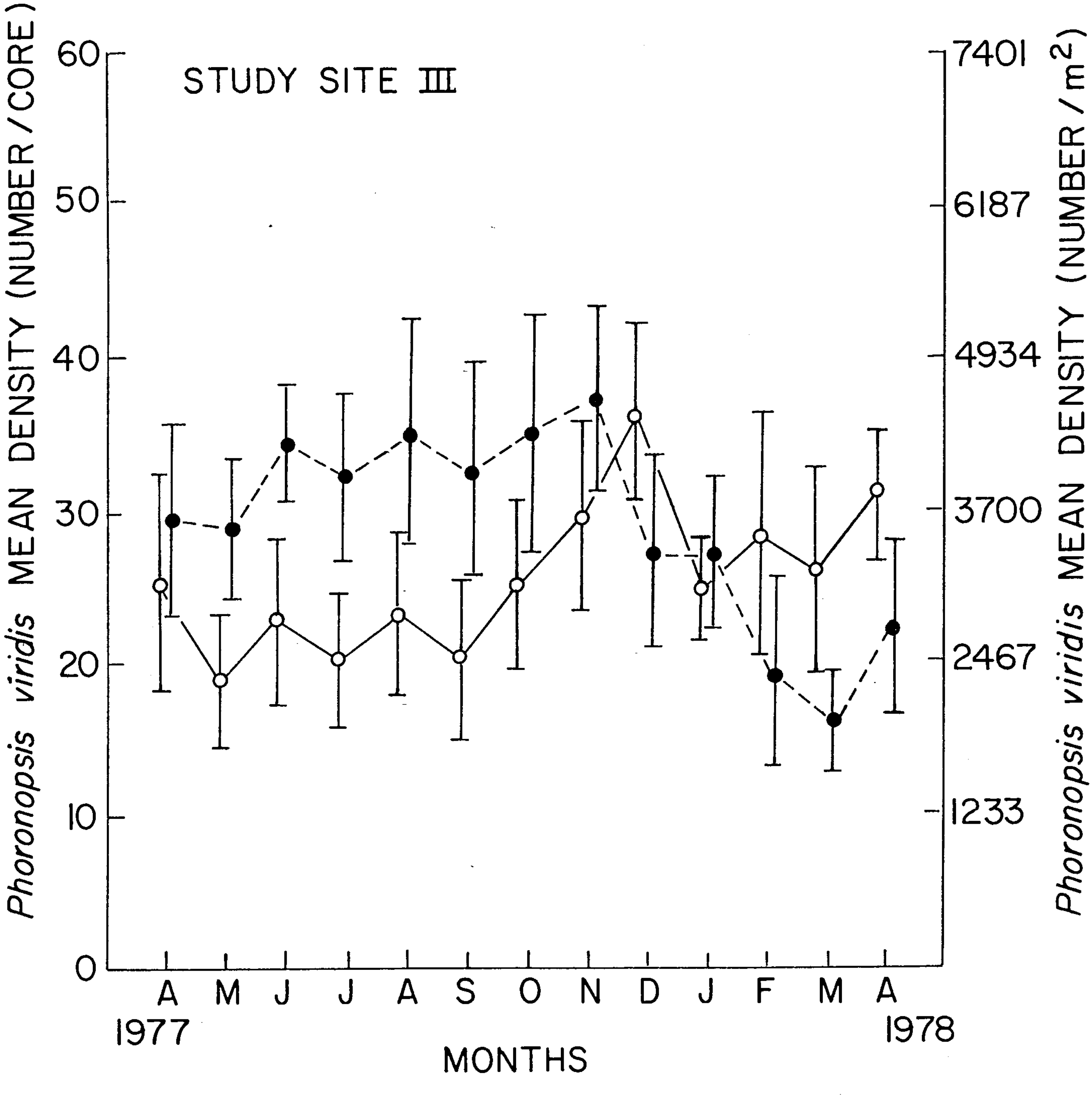

STUDY SITE III
Phoronopsis viridis MEAN DENSITY (NUMBER / CORE)
0
10
20
30
40
50
60
Phoronopsis viridis MEAN DENSITY (NUMBER / m²)
1233
2467
3700
4934
6187
7401
A
M
J
J
A
S
O
N
D
J
F
M
A
1977
1978
MONTHS

Table 8.

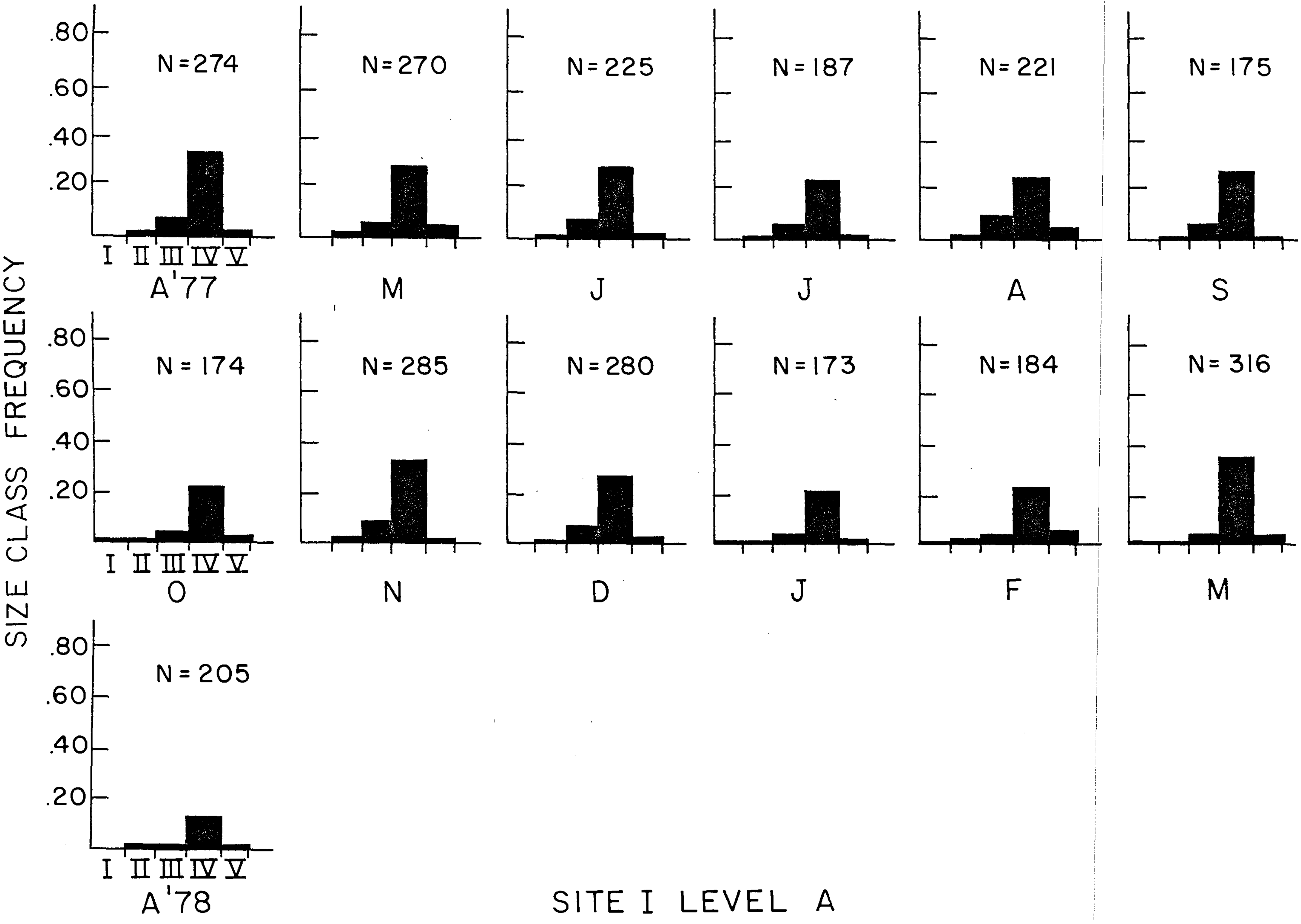
Results of a three-way ANOVA performed on the densities of <u>Phoronopsis</u> <u>viridis</u> from three study sites, two tidal heights and thirteen months. The data was transformed using the log x+1 transformation.

SOURCE OF VARIATION	DF	F VALUE	
MODEL	77	5.25	***
ERROR	851		
CORRECTED TOTAL	928		
MONTHS	12	1.86	*
SITES	2	33.78	***
TIDAL HEIGHT	1	54.94	***
MONTH*SITE	24	.87	ns
MONTH*TIDAL HEIGHT	12	1.92	*
SITE*TIDAL HEIGHT	2	82.80	***
MONTH*SITE*TIDAL HEIGHT	24	2.03	**

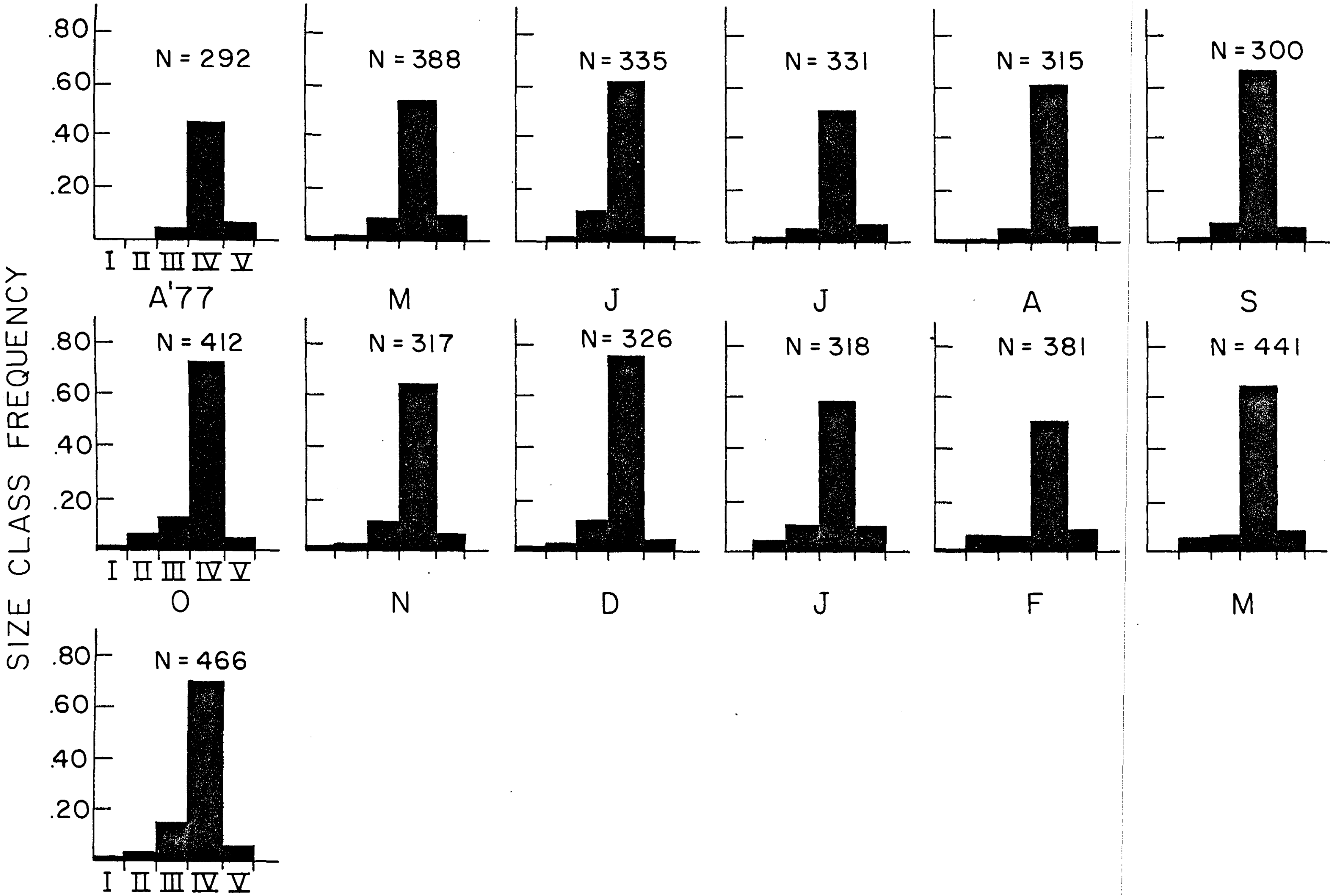
Probability ranges: * = $0.05 < P < 0.01$
** = $0.01 < P < 0.001$
*** = $P < 0.001$
ns = not significant

Figs. 8-13

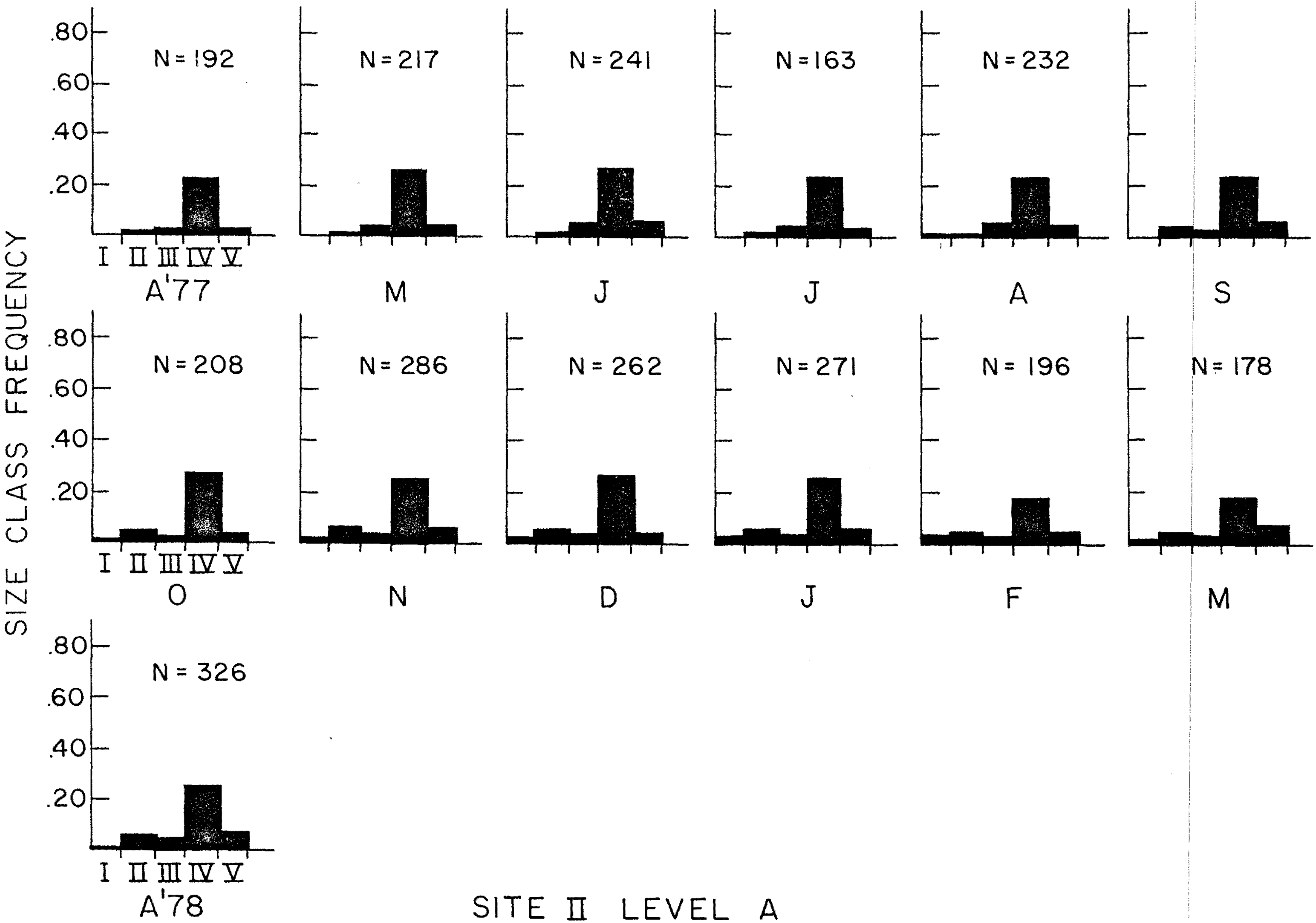
Phoronopsis viridis size frequency histograms for each study area and sampling times from April 1977 to April 1978. The size classes are: I = 1.4 mm and less, II = 1.5 to 2.0 mm, III = 2.1 to 2.6 mm, IV = 2.7 to 3.2 mm, V = 3.3 mm and greater. "N" refers to the number of individuals measured in a specific areas for a specific month.



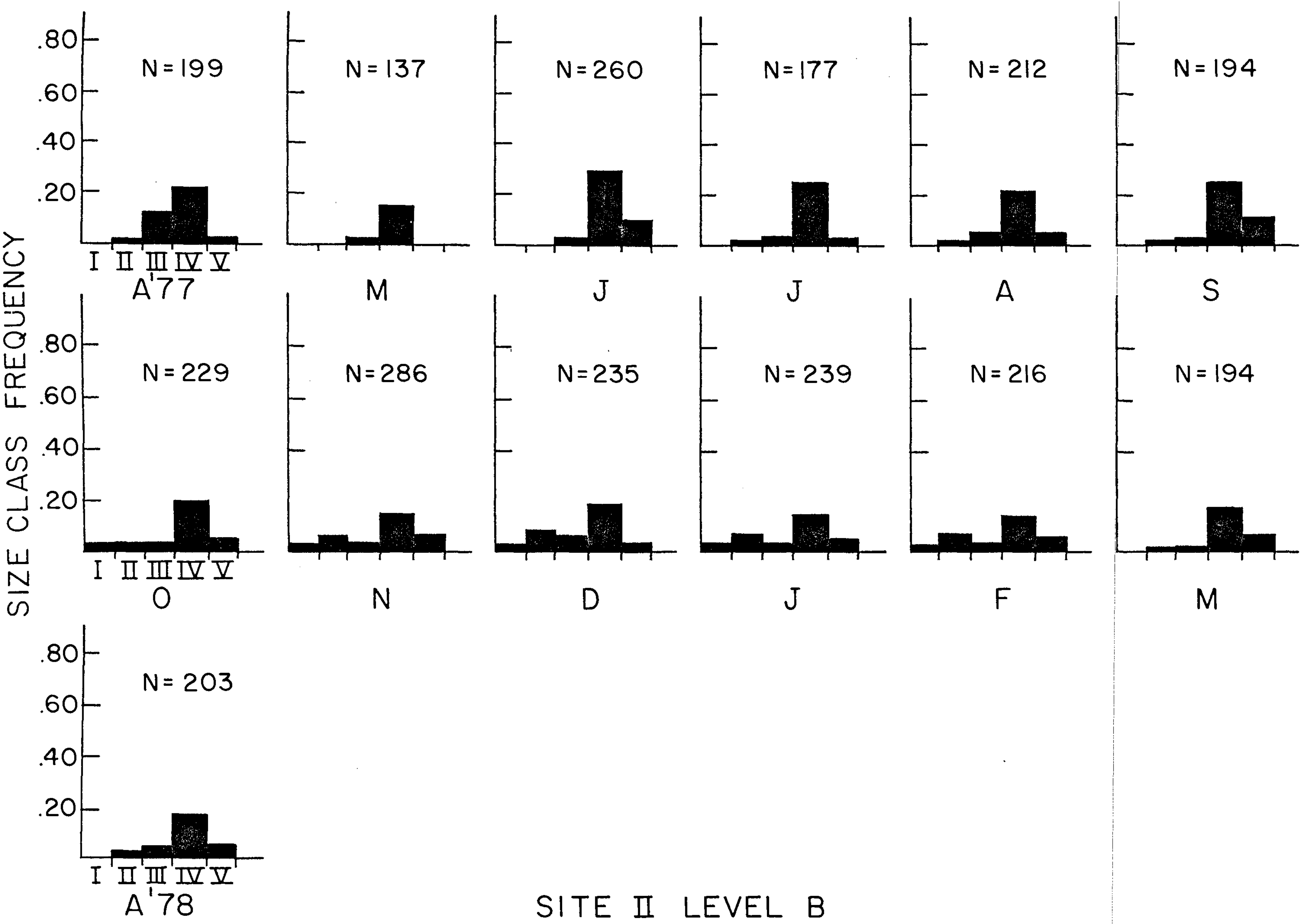
SITE I LEVEL A



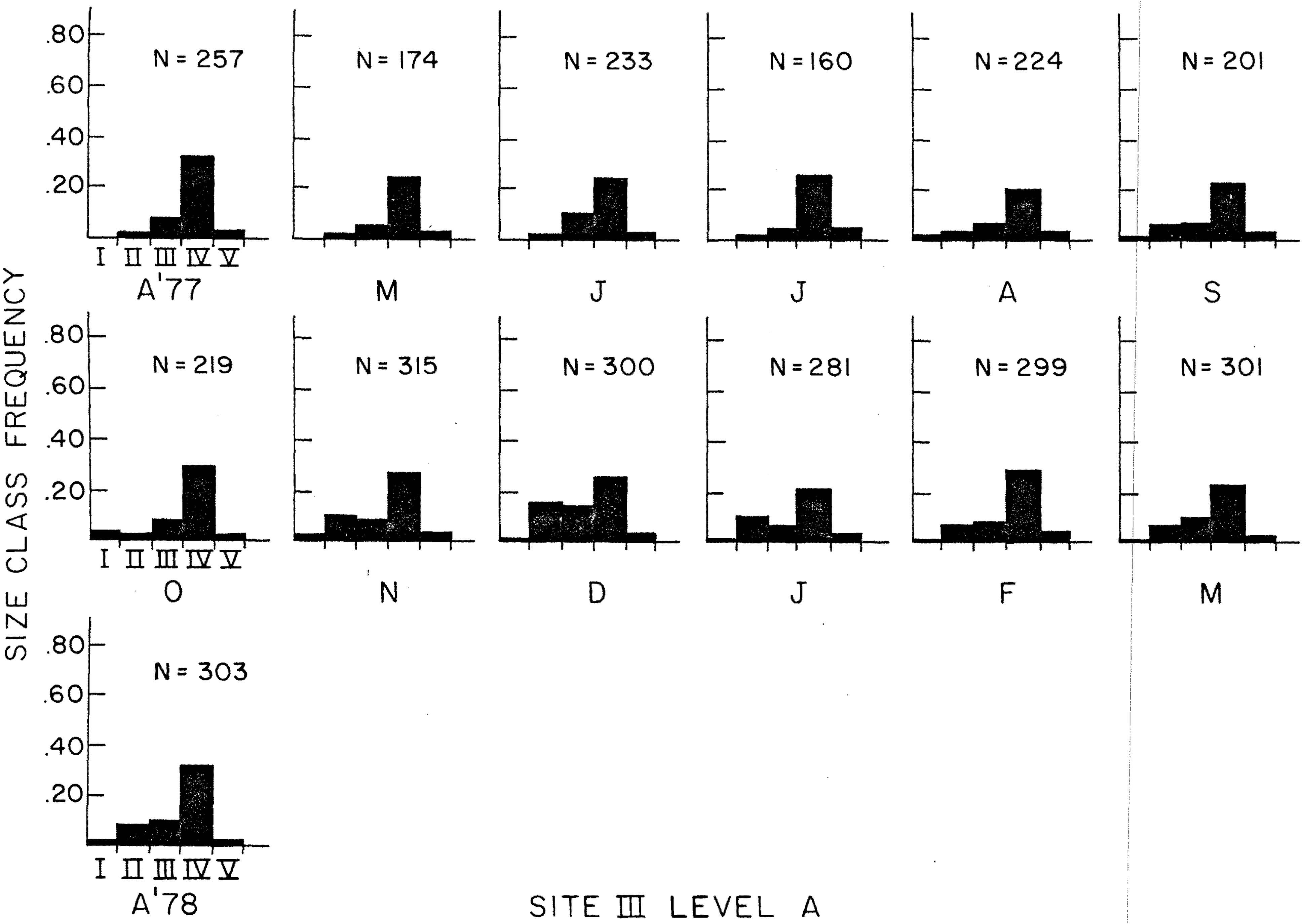
SITE I LEVEL B



SITE II LEVEL A



SITE II LEVEL B



SITE III LEVEL A

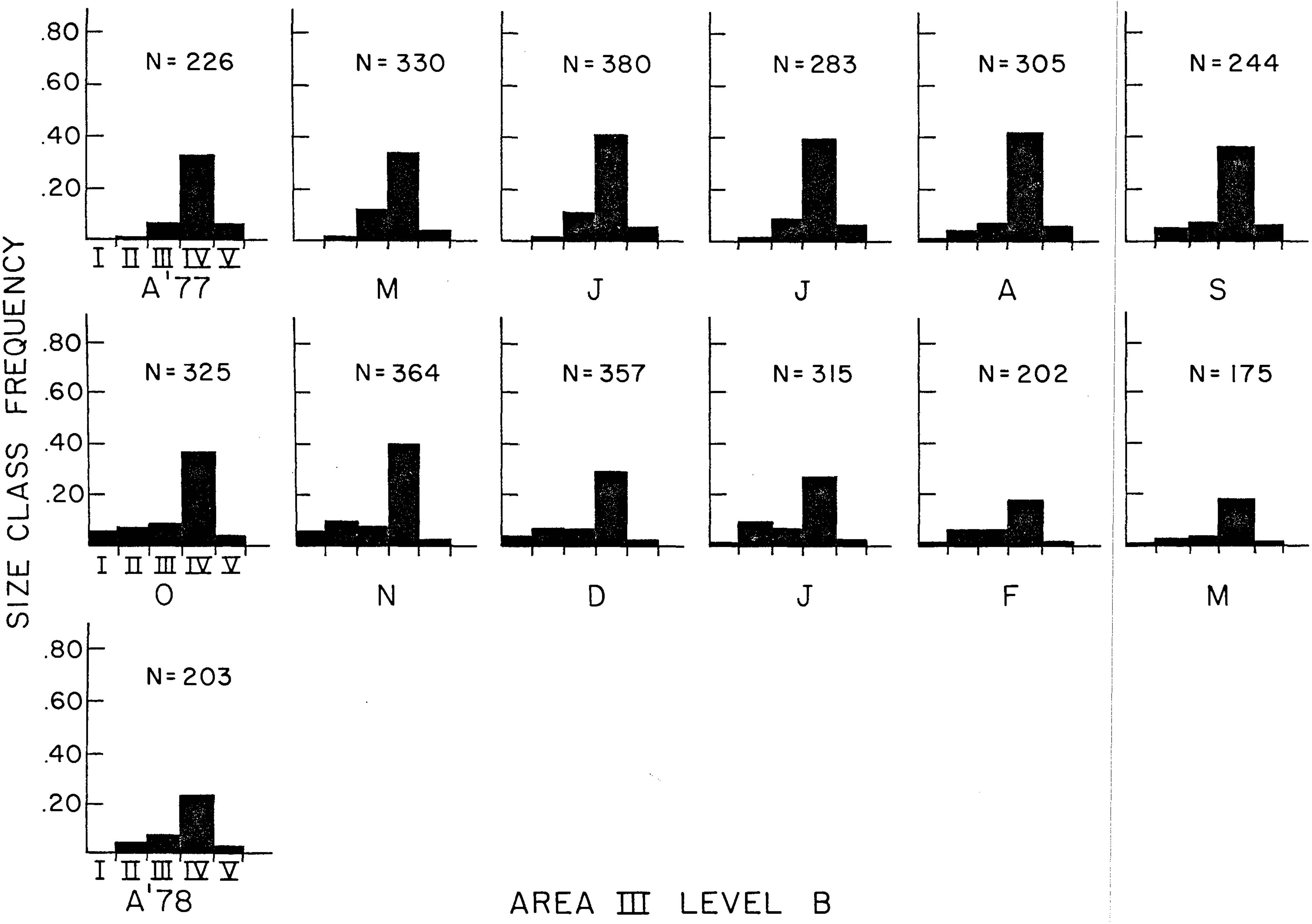
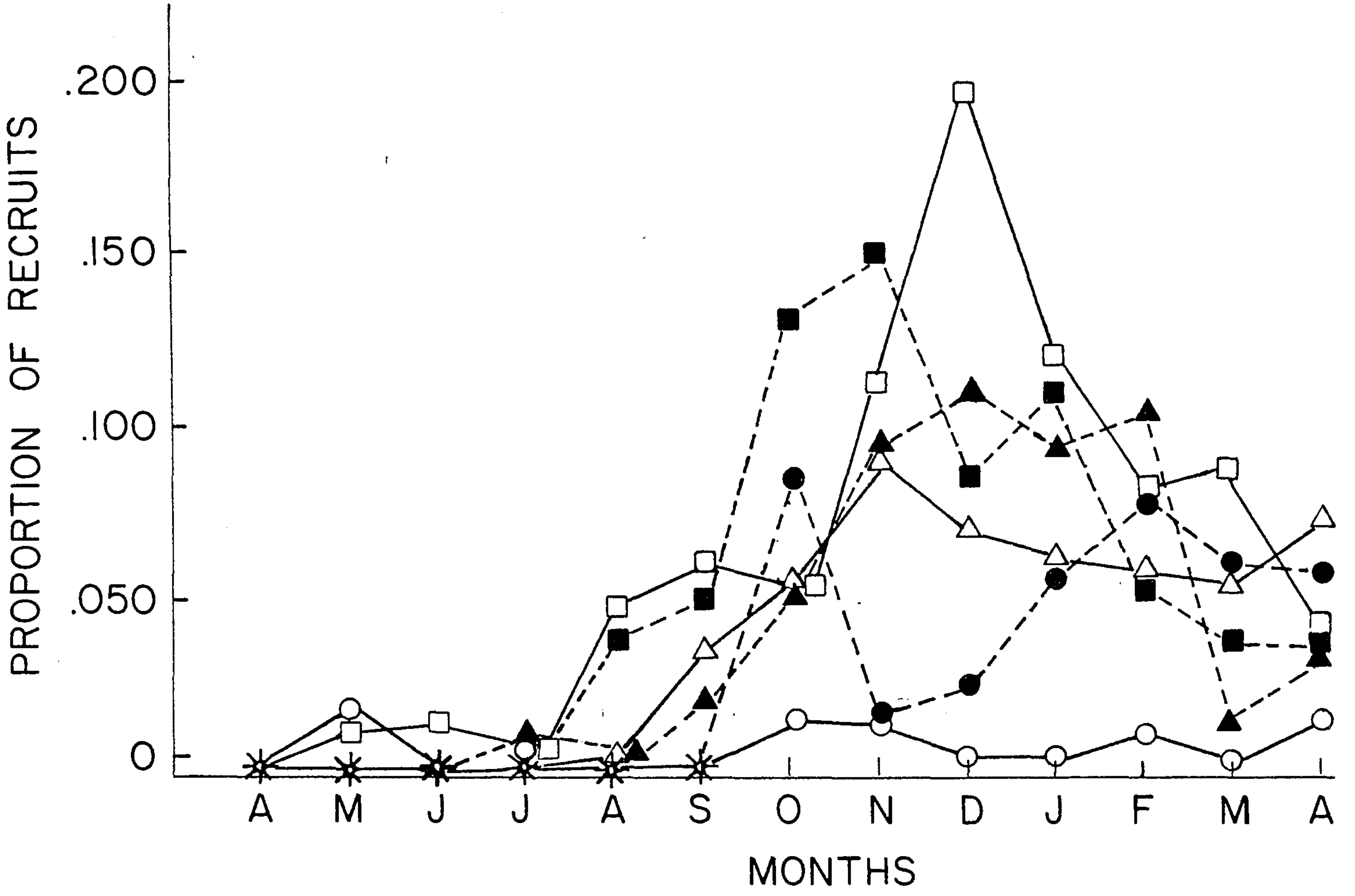

SIZE CLASS FREQUENCY
.80
.60
.40
.20
N = 226
A '77
N = 330
M
N = 380
J
N = 283
J
N = 305
A
N = 244
S
N = 325
O
N = 364
N
N = 357
D
N = 315
J
N = 202
F
N = 175
M
N = 203
A '78
I II III IV V
AREA III LEVEL B

Fig. 14

The proportion of *Phoronopsis viridis* recruits in each study area over the sampling period April 1977 to April 1978. Study Areas are represented as: IA = —○—, IB = --●--, IIA = —△—, IIB = --▲--, IIIA = —□—, IIIB = --■--. * = the proportion of recruits_ .006. For example, in May 1977 study areas IA, IIA, IIB, and IIIB had less than or equal to .006 proportion of recruits.


PROPORTION OF RECRUITS
.200
.150
.100
.050
0
A
M
J
J
A
S
O
N
D
J
F
M
A
MONTHS

sent. The length of an extended phoronid after metamorphosis was 1.8 mm ± .37 mm (N=10). The metamorphosed larvae had fourteen tenacles on the lophophore. These individuals adhered to the bottom of the bowl or to available sand grains by secreting a sticky substance.

The response of swimming P. viridis larvae to adult P. viridis was examined in two experiments. When six larvae were added to a container with the live adult phoronid, two larvae began metamorphosis within two minutes. After 24 hours, three of the larvae had settled on the adudt phoronid and one larva had settled on a piece of the adult phoronid tube. A test of the larval settlement response to the chemical presence of adult P. viridis was made by placing six larvae in a fingerbowl with 3 ml of phoronid homogenate and filtered seawater. After 24 hours 100% of the (six) larvae in the finger bowl with the phoronid homogenate had metamorphosed. By contrast, none of the six larvae in the control had metamorphosed by this time. P. viridis larval settlement is significantly greater in the presence of P. viridis homogenate (2x2 test of independence, $p < .001$).

The nudibranch, Hermissenda crassicornis consumed the P. viridis larvae (2) and the two metamorphosed P. viridis when encountered.

Observations made with P. viridis larvae and the spionid polychaete, Pseudopolydora paucibranchiata suggest that this spionid does not ingest P. viridis larvae. A P. viridis larvae was seized by the spionid palps and pulled into the spionid's tube. After approximately 15 seconds the larva "popped" out of spionid tube and continued to swim, apparently unharmed. Another *P. viridis* larva swam into a spionid tube (the spionid was withdrawn within the tube) and also "popped" out of the tube after approximately 15 seconds. The larvae, during most of the observation period inspected the sediment surface and spionid tubes. It was not determined whether larvae avoided or were attracted to the spionids.

RESULTS

IV. INTRA- AND INTERSPECIFIC INTEACTIONS

The dramatic response of *Phoronopsis viridis* larvae of adult phoronids suggested that recruitment with respect to adults should be exmained. The number of adults in a core was plotted as a function of the number of recruits for cores taken from October 1977 to April 1978 and Study Areas IB, IIA, IIB, IIIA and IIIB (Fig. 15). This time period was chosen because recruitment was highest during these months (Fig. 14). Study Area IA had an extremely low number of recruits, the lowest phoronid density, and was located highest in the intertidal zone among sites. Since the number of larvae available to settle in an area is a function of the submergence time, it was assumed Area IA was available for settlement less often than the other areas. For this reason data from Area IA is not considered in the following results involving recruitment.

The plot of recruits versus adults (Fig. 15) is a significant curvilinear regression with no significant linear component (Table 9). The inflection point corresponds to an adult density of $3700/m^2$. Density classes of adults were formed and the mean density of recruits of each density class was calculated (Fig. 16). These results imply that the recruitment of juvenile phoronids increases with increasing density of adults to a certain intermediate density beyond which recruitment decreases.

The relationship between %TOC and P. viridis density (adults and recruits) was exmained. There is no significant correlation between the mean number of adults and the % TOC in October 1977 and April 1978 (Fig. 18). However there was a highly significant positive correlation between the proportion of recruits in October and the % TOC (Fig. 17). There was no correlation between the proportion of recruits in April 1978 and the % TOC ($p > .05$, $R^2 = .016$, $N=18$). The % TOC data was not obtained for other months. These results suggest that there may have been a density dependent survival of recruits related to the % TOC in October.

Recruitment in P. viridis was compared to the density of feeding Axiothella rubrocincta. There was a significant negative correlation in Area IIIA between the mean number of recruits in any month and the mean monthly density of A. rubrocincta in the previous month (Fig. 19). It was assumed that the reworking of A. rubrocincta (or some other factor that is correlated with A. rubrocincta density) had the greatest effect on phoronids when the phoronids settle. Since the recruits were probably a month old whem picked from the sieve, the mean density of A. rubrocincta was lagged by one month in relation to the phoronid mean recruitment. In contrast to the results in Area IIIA, at Site II there was no significant correlation between mean density of recruits (time+1) and mean A. rubrocincta density (time) (Fig. 19). There was also no relationship in either site when the points were not lagged ($R^2=.201$, $p>.05$, $N=7$, Site III; $R^2=-.076$, $N=14$, p$>$.05, Site II).

There was no relationship between the density of feeding A. rubrocincta and the mean density of adult P. viridis in either Study Area IIIA or in Study Site II (Fig. 20 and 21). These results imply that the reworking activity of A. rubrocincta may negatively effect P. viridis recruitment when reworking is high. However adult P. viridis densities were not significantly effected by A. rubrocincta reworking

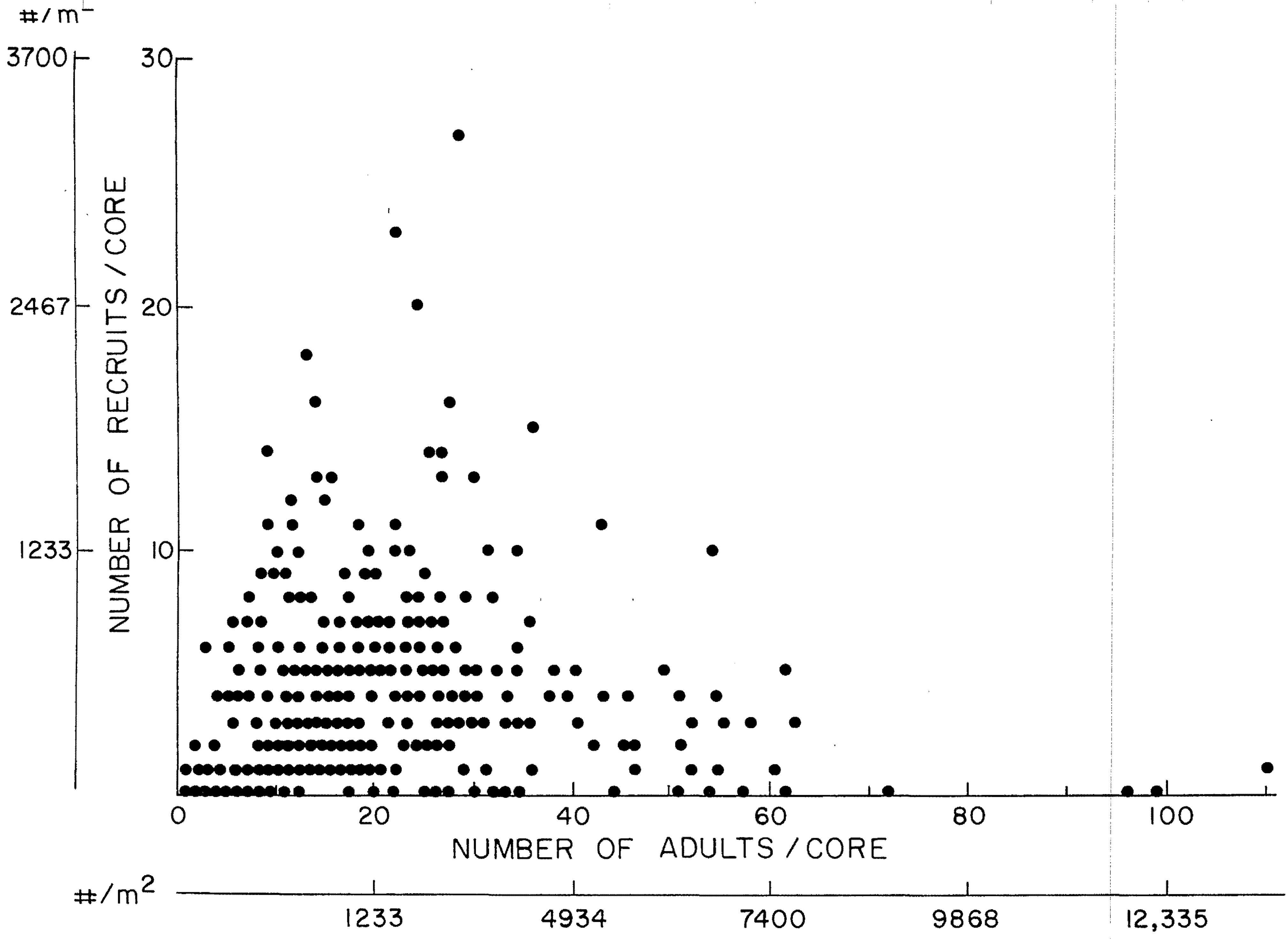

#/m²
3700
2467
1233
30
20
10
NUMBER OF RECRUITS / CORE
0
20
40
60
80
100
NUMBER OF ADULTS / CORE
#/m²
1233
4934
7400
9868
12,335

Table 9.

Curvilinear regression analysis on the density of *Phoronopsis viridis* recruits as a function of *P. viridis* adult density.

DEPENDENT VARIABLE: RECRUITS

SOURCE OF VARIATION	DF	F VALUE	
MODEL	2	21.60	***
ERROR	368		
CORRECTED TOTALS	370		
ADULTS	1	1.01	ns
ADULTS*ADULTS	1	42.19	***

REGRESSION EQUATION $Y= -0.5897 + 2.0141 X + -0.8166$

Probability ranges: *** = $P < 0.001$

ns = not significant

Fig. 16

The mean number of Phoronopsis viridis recruits as a function of adult density classes. The vertical bars represent the 95% confidence limits.

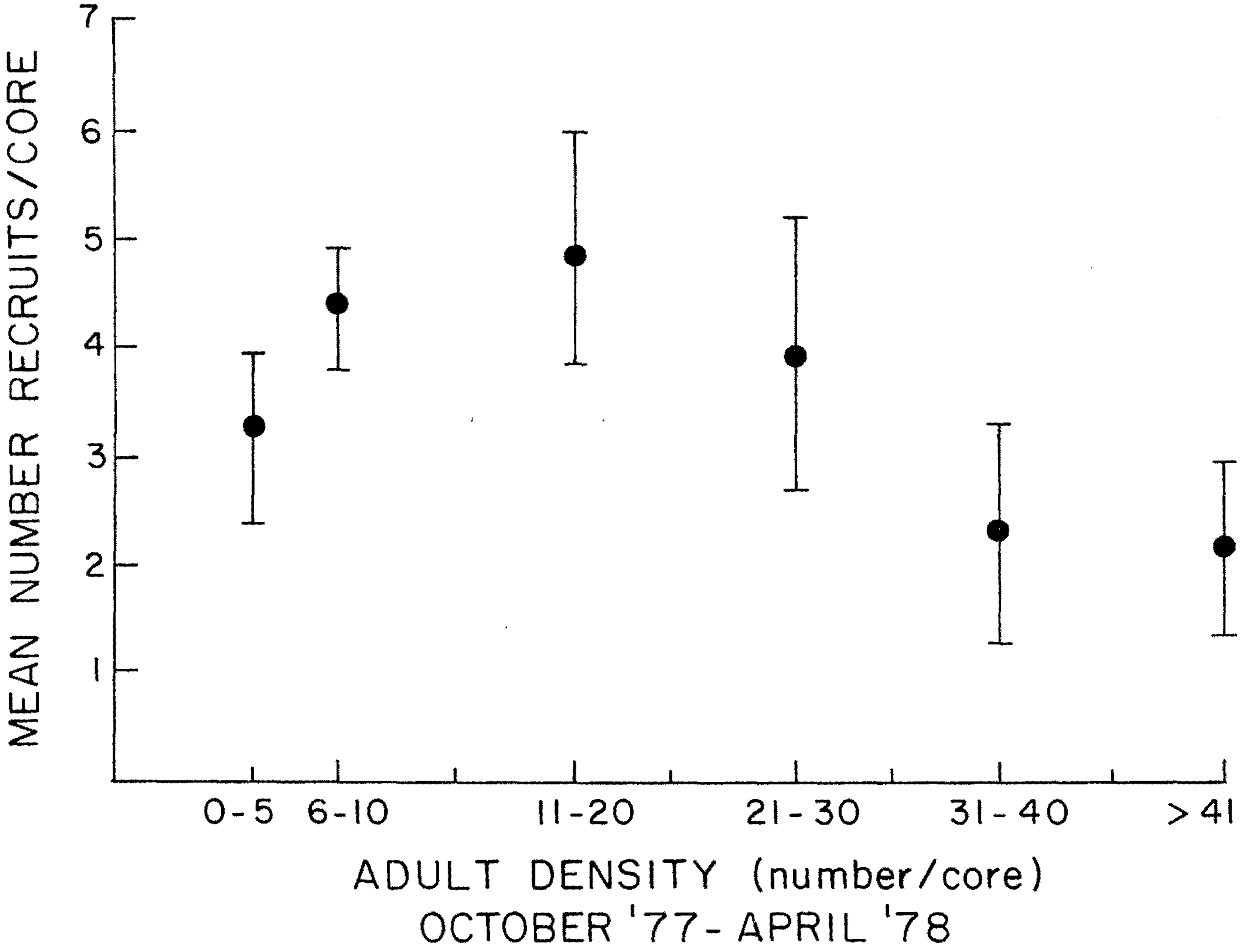

MEAN NUMBER RECRUITS/CORE
1
2
3
4
5
6
7
0-5
6-10
11-20
21-30
31-40
>41
ADULT DENSITY (number/core)
OCTOBER '77- APRIL '78

Fig. 17

The relationship between the mean % TOC and the proportion of *P. viridis* recruits in October 1977. Data is from study areas IB, IIA, IIB, IIIA, and IIIB. The horizontal bars represent the 95% confidence intervals about the mean of the three samples taken at each study area. (Pearson's Correlation Coefficient $R^2=+.8167$, $p < .01$, $N = 5$). The proportion of recruits were transformed using an arcsin x transformation to homoginize the variances.

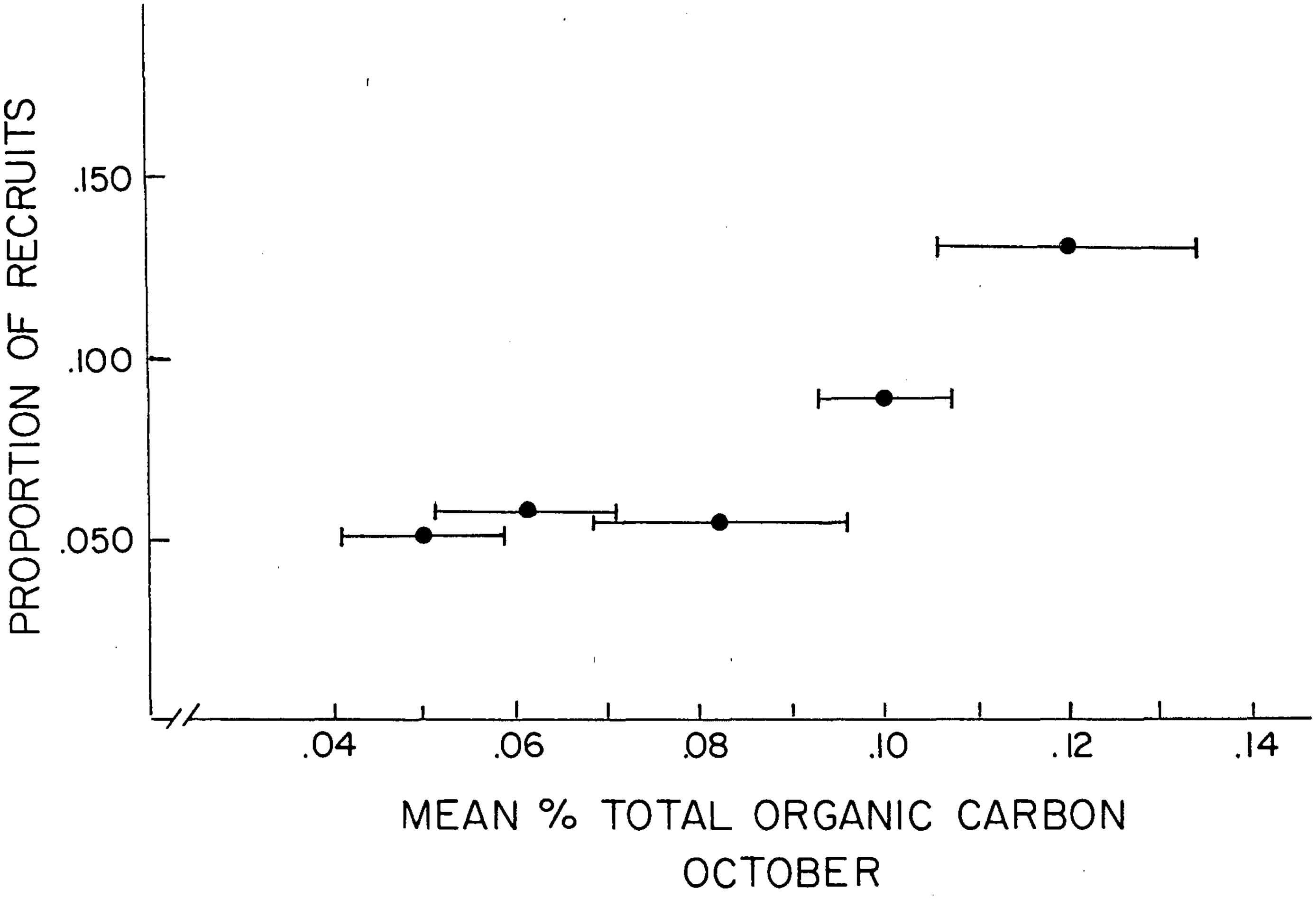

PROPORTION OF RECRUITS
.150
.100
.050
.04
.06
.08
.10
.12
.14
MEAN % TOTAL ORGANIC CARBON
OCTOBER

Fig. 18

The relationship between the mean % TOC and the mean density of adult P. viridis. The correlation is not significant ($R^2 = .108$, $N = 12$, $p < .05$). October 1977 = ●, April 1978 = △.

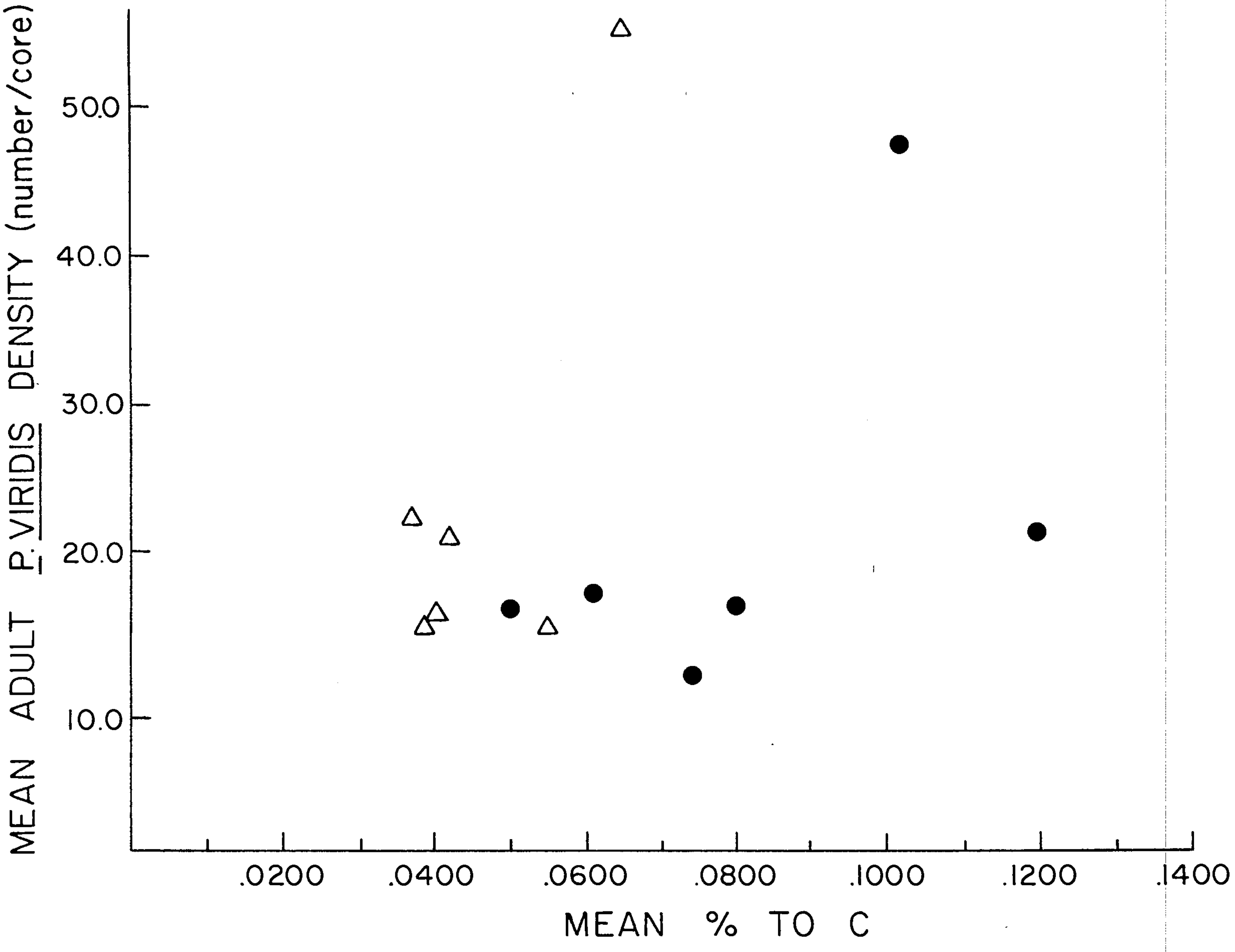
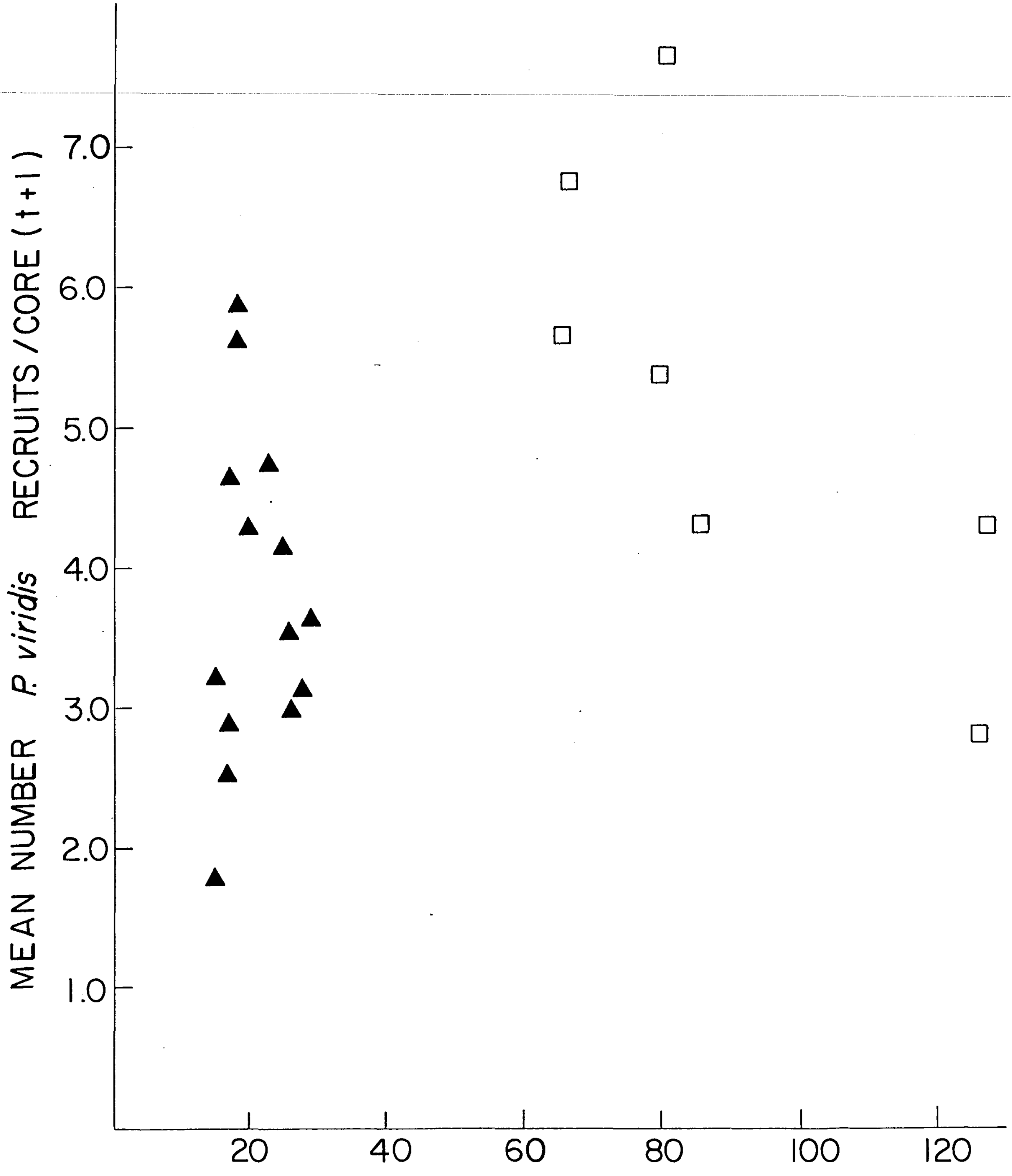

MEAN ADULT P. VIRIDIS DENSITY (number/core)
50.0
40.0
30.0
20.0
10.0
.0200
.0400
.0600
.0800
.1000
.1200
.1400
MEAN % TO C

Fig. 19

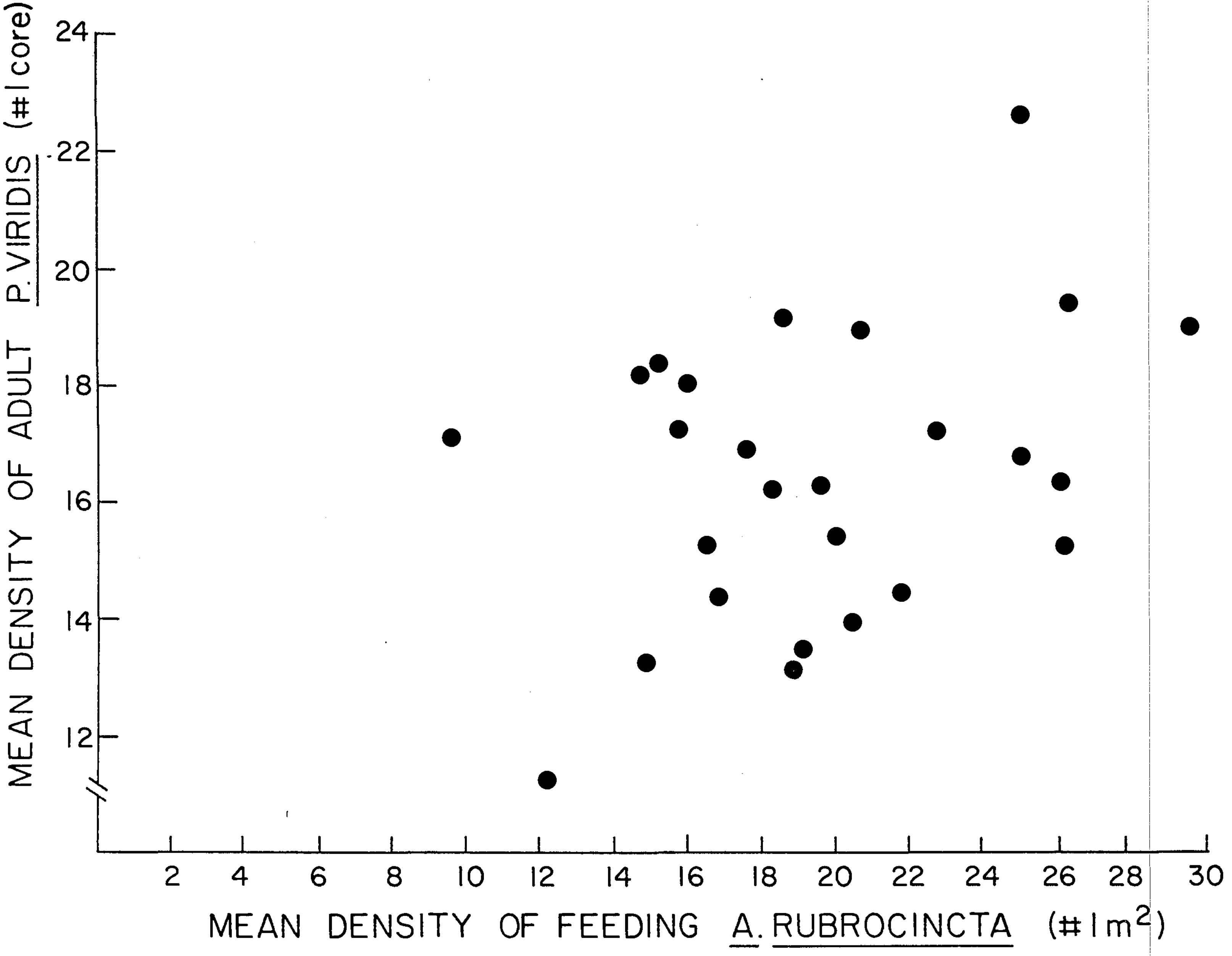
Relationship between the mean number of *P. viridis* recruits in a core and the mean feeding density of *A. rubrocincta* (number/m^2) in study sites II and III. It was assumed that sediment reworking by *A. rubrocincta* would effect phoronid settlement. Since *P. viridis* recruits are probably a month old when retained in the sieve the mean number of recruits of one month (t+1) was plotted against the mean density of *A. rubrocincta* of the previous month (t). The study sites are represented as: Study Site II=▲ and Study Area IIIA=□.



MEAN DENSITY-FEEDING *A. rubrocinta*
(NUMBER/m²) (t)

Fig. 20

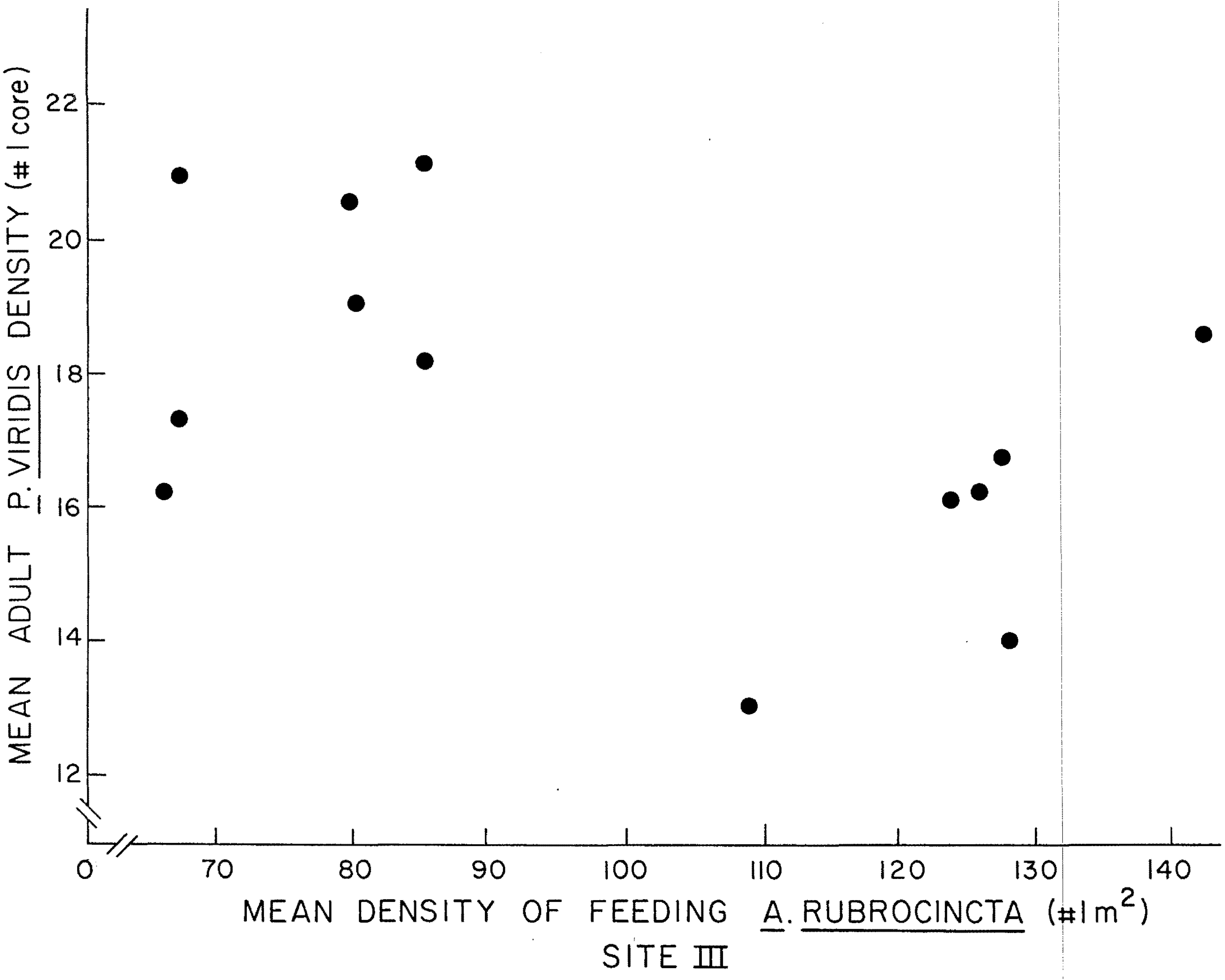
The relationship between the mean adult *P. viridis* density and the mean density of feeding *Axiothella rubrocincta* in Study Site II. Each point represents a monthly density (Pearson Correlation Coefficient $R^2 = .062$, $p > .05$, $N = 26$).


MEAN DENSITY OF ADULT P. VIRIDIS (# l core)
24
22
20
18
16
14
12
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
MEAN DENSITY OF FEEDING A. RUBROCINCTA (# l m^2)

SITE II

Fig. 21

The relationship between the mean adult <u>Phoronopsis viridis</u> density and the mean density of feeding <u>Axiothella rubrocincta</u> in Study Area IIIA. Each point represents a monthly density. (Pearson Correlation Coefficient $R^2 = -.210$, $p > .05$, $N = 12$)


MEAN ADULT P. VIRIDIS DENSITY (# l core)
22
20
18
16
14
12
0
70
80
90
100
110
120
130
140
MEAN DENSITY OF FEEDING A. RUBROCINCTA (# l m^2)
SITE III

DISCUSSION

The results indicate that Phoronopsis viridis is stable in density and age structure throughout the year, populations being dominated by older worms. This stability could be due to random larval settlement in adult colonies or to preferential larval settlement in adult areas. It was shown that the larvae respond positively to the presence of adults at the time of settlement. The response appears to be brought about by chemical recognition of adult phoronids. Chemical response by larvae to species of their own kind has also been demonstrated in Sabellaria sp. (Polychaeta) and Crassostrea viriginica (Bivalvia) (Wilson 1968, Crisp 1967, see Crisp 1974 for further examples). Moreover, no phoronid recruits were found in an area of Lawson's Flat located 200 m from the study sites reported here at the same tidal height which had no phoronids (Weinberg 1978).

The successful settlement of P. viridis is necessary for phoronids to persist in an area. The density dependent pattern (Fig. 15) suggests that the persistence of these dense phoronid areas is not the result of a simple linear recruitment of larvae into adult areas. Two types of density dependent mechanisms may limit recruitment in phoronid areas. The first mechanism results in the increase of recruitment with increasing adult density to some maximum after which another density dependent mechanism results in the decreased recruitment observed at higher densities. There are three possible explanations for the increase of recruits at low adult densities.

1) Adult Density Dependent Settlement. Larvae can track adult density and preferentially settle at higher adult densities. This would result in an increase in recruits with adult density. Phoronid larvae are thought to be in the plankton for at least one month before settlement (J. Blake personal communication). When ready to settle, larvae may choose sites by "sensing" and responding to increasing concentrations of a settlement-inducing chemical where there are more adults.

2) Food Abundance Dependent Settlement. Larvae select sites within phoronid areas on the basis of the amount of food present. The positive correlation between the proportion of recruits and the % TOC suggests that recruitment is associated with the abundance of food. Bacteria have been shown to influence settlementin polychaetes and a copepod (Day and Wilson 1934, Gray 1971, Wilson 1948, 1952, 1955, Gray 1968). If P. viridis larvae do select and settle in sites of higher food abundance, a positive relationship between adult phoronids and % TOC is also expected. This correlation was not significant (Fig. 18).

3) Density Dependent Larval and Juvenile Survival. Larvae, settling at random within adult areas, are affected by different adult density dependent factors such as a) predation, b) food abundance, or c) disturbance.

a) At low adult densities infaunal predators feed on settling and metamorphosing larvae. This would be true if predatory infauna were excluded at higher adult densitieis. However, it was shown that larvae are probably too large to be ingested by the spionid polychaete, Pseudopolydora paucibranchiata. In addition, P. viridis larvae metamorphose within 15 minutes after settling (J. Blake personal communication and personal observation). It remains to be seen what range of predators such a large (1.0 mm), rapidly metamorphosing larvae can escape.

b) Juvenile survival may be correlated with increasing food abundance.

c) Disturbance by large burrowing organisms may be greater at low phoronid dinsities and increase mortality of newly settled recruits. The movement of organisms such as Macoma secta may be restricted by the stabilized sediment associated with high phoronid density (Ronan 1975).

Of the three explantions presented to describe the increase in recruitment from low to intermediate adult densities it is tentatively concluded that the data in this study best fit the third (3). The large amount of scatter in the recruit v.s. adult density curve (Fig. 15) indicates that larvae are settling at random within adult areas and survival depends on the amount of food (% TOC) available (Fig. 17). Whether or not this is the actual explanation for the increase in recruits with adult density, another mechanism must cause the decrease in P. viridis recruitment from intermediate to high adult densities.

Density dependent predation could limit P. viridis recruitment at high densities of adults. The nudibranch, Hermissenda crassicornis consumes adult phoronids removed from their tubes and phoronid fecal pellets. The rapid escape response of phoronids into their tubes when touched by foraging nudibranchs restricts the latter to cropping only the lophophores (Ronan 1978). However, at Elkhorn Slough, California, migration of large number of H. crassicornis into a subtidal area heavily settled by phoronids (40,000/m^2) was followed by near extinction of the entire Phoronopsis viridis patch (J. Oliver personal communication) As mentioned, H. crassicornis can consume larvae and recently settled phoronids in the laboratory and may feed preferentially in high density phoronid areas. Hermissenda crassicornis occurs on Lawson's Flat during the fall but no nudibranch density estimates were made.

Fish may eat phoronids. Ronan (1978) observed bottom feeding fish cropping lophophores and on occassion pulling large phoronids from their tubes. No phoronids or phoronid larvae occurred in the gut contents of juvenile flat fish (Parophrys vetulus) collected in phoronid areas on Lawson's Flat (John Brezina, personal communication).

Space could be limiting at high adult densities. However, 7000 phoronids in a square meter, each 3 mm in width, would occupy only 5% of the area of the square meter. The same number of lophophores, 11.0 mm in width, would occupy 67% of the square meter. It seems unlikely that recruits would be limited by the amount of space available among the tubes. High densities of lophophores may limit space and therefore effect feeding. The filtering effect of high densities of lophophores on the survival of P. viridis recruits is unknown. However, predation on P. viridis larvae by adults phoronids is not important since the maximum size ingested by the phoronid is 200 u in diameter (Ronan 1978) while the larvae are much larger.

The foregoing explanations for the decrease in recruitment from intermediate to high adult densities have been, for the most part, limited to intraspecific interactions between recruits and adult phoronids. Interspecific interactions may effect recruitment. The surface deposit feeder, Axiothella rubrocincta actively reworks the sediment and when found in high densities with P. viridis may negatively effect phoronid recruitment. A significant negative correlation between phoronid recruits and A. rubrocincta occurs in Site III (Fig. 19). The trophic amensalism hypothesis suggests that surface deposit feeders reduce larval settlement by reworking the sediment (Rhoads and Young 1970). The reworking actibity of A. rubrocincta creates funnels and surface mounds approximately 5 cm in diameter each (personal observation). When A. rubrocincta occur at high density (130/m^2) 51% of the area is effected by sediment reworking. Defecation by A. rubrocincta onto the sediment surface may bury newly settled phoronid larvae. An individual

A. rubrocincta defecates on the average 9 grams of sediment during a 24-hour period (Weinberg 1978). The defecation mounds created are approximately 2 cm in height (personal observation). Most adult phoronids will emerge from burial under 2 cm of sand in 45 minutes (Ronan 1975). The survival of recruits under similar burial by sediment is not known. *Axiothella rubrocincta* may ingest *P. viridis* larvae. Gut contents of *A. rubrocincta* contain *Gemma gemma* (a small bivalve), turbellarians and algal fragments (Kudenov 1978). However the size range of particles eaten by *A. rubrocincta* was not reported. At high density, *A. rubrocincta* appears to affect phoronid recruitment.

The relationship between adult phoronids and *A. rubrocincta* is not clear. *Axiothella rubrocincta* depletes supplies of organic mineral aggregates (OMA) by sediment reworking (Weinberg 1978). OMA can occupy more than one-third of the stomach volume of the phoronid (Ronan 1978). At high densities *A. rubrocincta* and *P. viridis* may compete for OMA. This resource may be spacially partitioned between the two species since phoronids feed on suspended particles (Ronan 1978) and *A. rubrocincta* feeds on deposited particles caught in its surface feeding funnels (Kudenov 1971). Fecal pellets of phoronids may serve as a food source for *A. rubrocincta* while phoronids may consume fecal pellets (Ronan 1978) or other organic particles resuspended by the reworking activity of *A. rubrocincta*. Fecal pellets have been demonstrated by Newell (1965) and Johannes and Satomi (1966) to be an important food source. The reworking by A. rubrocincta may decrease the available time phoronids have to feed. Adult phoronids are probably able to emerge from burial by A. rubrocincta reworking. There does not appear to be a significant negative effect on adult phoronids by the sediment reworking of A. rubrocincta. Settling and juvenile phoronids are more likely to be negatively affected by the sediment reworking of A. rubrocincta.

Another factor which may have effected P. viridis density and recruitment was the presence of algae (Ulva sp. and Entromorpha sp.) during the fall recruitment period. The highest recruitment was observed in Site III (Fig. 14) which was the only site to be covered by algae when phoronid recruitment occurred. Algae may be a spatially complex refuge for phoronid larvae by reducing predation. Algal cover also raises the anoxic layer in the sediment (Woodin 1978). Adult phoronids can withstand long periods of anoxia (Johnson 1970) and are able to feed under algae (Ulva) when they become buoyed up by the tide (Ronan 1978).

The foregoing discussion suggests that several direct or higher order interactions may affect phoronid recruitment and survival. The recruitment pattern does suggest a stabilizing mechanism which allows the phoronid population to persist about a stable density. When adult density is high (greater than 40/core) (Fig. 16) recruitment is low. After natural mortality, the adult density decreases, resulting in an increase of recruitment. In this manner phoronid densities remain stable and phoronid areas persist. This stable density is probably density dependent on the carrying capacity of the environment. The dome-shaped recruitment curve is similar to observed curves for fish (Ricker 1954 and Cushing and Harris 1973). Implications of such recruitment curves have been discussed by Ricker (1954) and Beverton and Holt (1957).

In summary, the data indicates that, at least over a one year period, phoronid densities are stable and size class dominated. Phoronid areas persist over time and this persistence is a result of phoronid larvae recruiting into phoronid areas in a density dependent fashion. The curvilinear recruitment pattern is the result of two mechanisms. One mechanism accounts for the increase in recruitment to an intermediate adult density, the other mechanism accounts for the decrease in recruitment from intermediate to high adult density. Several explanations have been suggested for these mechanisms. These explanations include differential settlement by larvae and/or differential survival of larvae and juveniles. Predation, food abundance and disturbance are also possible factors effecting recruitment. The density dependent survival of phoronid recruits with respect to adult density suggests a mechanism by which dense phoronid areas may persist.

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BIBLIOGRAPHY

Barr, A. J., J. H. Goodnight, J. P. Sail and J. T. Helwig 1976. A user's guide to SAS 76. Raleigh: SAS Institute Inc. 329p.

Beverton R. J. H. and S. J. Holt 1957. On the dynamics of exploited fish populations. Fishery Investigations Lond. Ser. 2, 19, 533p.

Buchanan, J. B. 1974. Measurement of the physical and chemical environment. In: Methods for the study of the benthos, Ed. by N.A. Holme and A. D. McIntyre. Oxford: Blackwell Scientific Publications. pp. 30-50.

Crisp, D. J. 1967. Chemical factors inducing settlement in _Crassostrea_ _virginica_ Gmelin. J. Anim. Ecol. 36 329-35.

____________. 1974. Factors influencing the settlement of marine invertebrate larvae. In: Chemoreception in Marine Organisms. Ed. by P. T. Grant and A. M. Mackie. London: Academic Press. pp. 177-265.

Cushing, D. H. and J. G. K. Harris 1973. Stock and recruitment and the problem of density dependence. Rapports et Proces-Verbaux des Reunions. Conseil International pour L'exporation de la Mer, 164, pp. 142-155.

Daetwyler, C. C. 1966. Marine geology of Tomales Bay, Central California. Pacific Marine Station Res. Report, No. 6, 169p.

Kudenov, J. D. 1978. The feeding ecology of Axiothella rubrocincta (Johnson) (Polychaeta: Maldanidae). J. Exp. Mar. Biol. Ecol. 31 pp. 209-221.

Newell, R. C. 1965. The role of detritus in the nutrition of two deposit feeders, the prosobranch Hydrobia ulvae and the bivalve Macoma balthica. Proc. Zool. Soc. London. 144 pp. 25-45.

Rhoads, D. C. and D. K. Young. 1970. The influence of deposit feeding benthos on bottom sediment stability and community trophic structure. J. Mar. Res. 28, pp. 150-178.

Ricker, W. E. 1954. Stock and recruitment. J. Fish. Board of Canada. 11 pp.559-623.

Ronan, T. E. 1975. Structural and paleoecological aspects of a modern soft-sediment community: An experimental field study. Unpublished Doctoral Dissertation, Univ. of Calif. Davis, 220p.

Ronan, T. E. Jr. 1978. Food-Resources and the influence of spacial pattern on feeding in the phoronid Phoronopsis viridis. Bio. Bull. 154, pp. 472-484.

Weinberg, J. R. 1978. The synecology of dense assemblages of the deposit-feeding polychaete, Axiothella rubrocincta (Maldanidae). M. S. thesis, Univ. of the Pacific, Dillon Beach, Calif. 166p.

Wilson, D. P. 1948. The relation of the substratum to the metamorphosis of Ophelia larvae. J. Mar. Biol. Ass. U. K. 27 pp.723-60.

Wilson, D. P. 1952. The influence of the nature of the substratum on the metamorphosis of the larvae of marine animals, especially the larvae of *Ophelia bicornis* Sabigny. Annls. Inst. Oceanogr., Monaco 27, pp. 49-156.

__________. 1955. The role of micro-organisms in the settlement of *Ophelia bicornis* Sabigny. J. Mar. Biol. Ass. U. K. 34 pp. 531-543.

__________. 1968. The settlement behavior of the larvae of *Sabellaria alveolata*. J. Mar. Biol. Ass. U. K. 48 pp.387-435.

Woodin, S. A. 1977. Algal "gardening" behavior by nereid polychaetes: Effects on soft-bottom community structure. Mar. Biol. 44 pp. 39-42.