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SHORE-LEVEL SIZE GRADIENTS IN *Tegula funebralis* (A.Adams):

Seasonal changes influenced by interaction of predator preference and prey behavior.

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

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by

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May 1979

This thesis, written and submitted by

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Thesis Committee:

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James A. Blake

Dated May 1979

ABSTRACT

Aspects of the *Pisaster-Tegula* interaction are reexamined. Reproductive portions of *T. funebralis* populations are shown to be immune to seastar predation through a combination of predator preference for larger snails and a withdrawal behavior that favors the escape of smaller snails after capture by a seastar. Experimental addition of *P. ochraceus* in winter causes changes in the intertidal distribution of *T. funebralis* similar to those observed during the summer increase in seastar numbers. It is suggested that these results supplant the hypothesis that lowered prereproductive mortality influences formation and maintenance of vertical size gradients in the lower intertidal.

ACKNOWLEDGEMENTS:

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INTRODUCTION:

Many species of intertidal gastropods have a vertical size gradient in the range of their distribution. This distribution was originally thought to result from gradients in juvenile mortality in intertidal regions (Vermeij 1972), but Bertness (1977) suggested that generalizations about specific causative factors cannot adequately explain the development of size gradients since they might result from evolutionary optimization due to several interacting factors.

Larger Tegula funebralis are distributed lower in the intertidal than the more abundant smaller snails (Paine 1969). For the larger snails, Paine (1969) suggests that the advantages of increased individual fecundity due to lowered density and greater food availability outweigh the disadvantages of habitat overlap with the predatory seastar, Pisaster ochraceus (Brandt) in the lower intertidal. Paine (1969,1971) demonstrates the effects of physiological stress on larger snails in the upper intertidal but does not account for the maintenance of high densities of smaller snails in the upper area, nor does he feel T. funebralis generally has adequate escape responses against P. ochraceus predation.

Obrebski (MS) has determined that lower intertidal T. funebralis migrate upwards concurrently with seasonal increases in seastar abundance. He also records associated fluctuations in snail size and argues that lower escape velocities of smaller snails tend to substantiate Vermeij's (1972) hypothesis. The present study shows T. funebralis migration in another locality. New information on seastar feeding behavior and snail escape mechanism is reported which suggests an alternative explanation to T. funebralis size gradients. In particular, smaller snails are shown to be immune from digestion by P. ochraceus.

FIELD SAMPLING METHODS:

Field sampling was done in the Point Reyes National Seashore at the Palomarin Beach access (122°45'30" West X 37°56' North). The area was chosen because of the abundance of T. funebralis and P. ochraceus, the flat topography, the isolation from human disturbance, and the absence of significant numbers of prey other than Tegula for feeding seastars.

A transect measuring 10X50 m with the long axis perpendicular to the water's edge was established. The vertical difference between the upper and lower intertidal levels of the transect was less than 2 meters. The entire transect was exposed at a 0.0 tide except for a few shallow pools. Five 10X10 m squares were labeled X,A,B,C and D from the seaward edge upward. The lowest square (X) was only sparsely populated with T. funebralis being below their limit of distribution.

Samples were taken between March 1978 and January 1979 to determine P. ochraceus abundance and T. funebralis size and abundance. All seastars were counted at each sampling date by thoroughly examining the transect. Snails were counted in 10 randomly chosen 625 cm^2 quadrats in each of squares A,B,C and D at each sampling date. From 2 to 10 of these quadrats were also used to measure snail shell size depending upon the abundance of snails.

Shell size was measured with vernier calipers to the nearest 0.1 mm using the method of Paine (1969). All data was collected in the field and no snails or seastars were ever removed from the transect.

T. funebralis size and abundance data was collected using a nested analysis of variance (ANOVA) design. Abundance data is compared in a two level analysis with the highest treatment level as sampling dates, then squares within dates, and finally quadrats within squares as the lowest level. Snail shell size data was taken in a three level design with levels from highest to lowest: Sampling dates, squares within dates, quadrats within squares, and shell sizes of snails within quadrats. The computations were performed with the aid of a computer program adapted from Sokal and Rohlf (1969).

Pisaster ochraceus ABUNDANCE:

Seastars increase in abundance and maximum tidal level to a peak in midsummer and decline thereafter (see Figure 1).

Tegula funebralis SHELL SIZE:

The snail shell size data for the entire transect shows no significant variation between months, but highly significant variation in the lower levels of the analysis. Further analysis of the individual squares in a two level design shows a significant variation ($p < .05$) between months for sizes of snails found in the lowest square sampled (square A). Figure 2 shows that the mean size of snails in square A reaches a maximum in midsummer and declines through the fall.

The correlation between the number of seastars and the size of snails in each square was positive and significant ($r = 0.23$, $N=1230$, $p < .001$). The correlation between size of snails and tidal level (squares) was negative and significant ($r = -0.23$, $N=887$, $p < .001$).

Tegula funebralis ABUNDANCE:

Significant variation occurs at all levels in the analysis of the snail abundance data. Figure 3 shows the mean of abundance for the entire transect at each sampling date. Figure 4 shows the snail abundance means for the lowest square measured (square A). The graphs show the decline in density through the early summer months to a midsummer low and slight recovery in numbers through the fall.

The correlation between seastar numbers per square and snail abundance within squares was negative and significant ($r= -0.203$, $N=450$, $p<.001$).

EXPERIMENTAL INCREASE OF Pisaster ochraceus ABUNDANCE IN WINTER:

Two transects were established at the Palomarin site. One was the seaward 30 m of the previously described (see Field Sampling) transect (Transect 1). A second transect (Transect 2) was established in a comparable area 50 meters to the North of the first.

Both transects were sampled monthly for the two months prior to experimental manipulation in February and March. Sampling was performed as in the field sampling section. Seastars were counted in each of the three 10X10 m squares of each transect as well as in the area above the transects (There were no seastars in the higher areas at these times.). T. funebralis were subsampled for shell size and abundance in squares A and B of the transects. Ten 625 cm^2 quadrats were randomly selected and all snails found in each quadrat were counted and measured.

On February 22 another sample was taken. At this time laboratory maintained specimens of Pisaster ochraceus were brought to the field site. These seastars were added to transect 1 such that total numbers in each of the squares was comparable to peak summer abundance. Resident seastars were left in place and included in the totals. Areas adjacent to each square were also seeded with seastars to limit the effect of some lateral movement of the added animals. Transect 2 was used as a control area. Seastar abundance was checked and augmented as neccessary on the three following days. Snail size and abundance was sampled 2 and 5 days after the transplant in each transect.

On March 23 the above experiment was repeated using transect 1 as a control and adding seastars to transect 2. Snail size and abundance was sampled 2 and 4 days after the transplant.

The sampling of snail shell size was in a three level nested ANOVA design with levels: Among sample dates, between squares within dates, between quadrats wihtin squares, and snails within quadrats. Snail abundance was in a two level design with levels as above minus the lowest level.

SEASTAR ABUNDANCE DURING FIELD EXPERIMENTS:

Figure 5 shows the numbers of seastars present in square A of each transect for the duration of the two field experiments as well as data from the two previous months.

Tegula funebralis ABUNDANCE DURING FIELD EXPERIMENTS:

There was no significant change in density in either transect during the period of either experiment. Abundance was comparable in both transects.

Tegula funebralis SIZE DURING FIELD EXPERIMENTS:

The increase in size in square A of each transect after experimental manipulation (Figure 6) was significant ($p < .05$). There was no significant change in size of snails when each transect was measured as a control (Figure 6). Square B of both transects showed no significant changes.

SIZE OF Tegula funebralis PREFERRED BY Pisaster ochraceus:

The size of snail that is actually consumed by foraging seastars is a key factor in the understanding of the dynamics of the snail population. Paine (1969) estimated the numbers of T. funebralis per unit area consumed by seastars, but did not include specific data on the size range preferred by the seastar. Studies to determine the seastars preference in snail size are described below.

Snail shell held by seastars in feeding position were measured in July 1978 at the Palomarin field site. All feeding seastars encountered in a wide portion of the area were used.

In addition, six similarly sized seastars were placed, 3 in each half of a divided water table with a screened top. Twenty snails, 5 each of 4 size classes were placed in each half. At the end of each 24 hour period any consumed snails were removed measured and replaced with snails of the same size class. The design was analysed with a two level ANOVA with levels: Among replicates, size classes within replicates, and daily survival within size classes. Results were collected for 17 days.

SIZE PREFERENCE:

The data (Table 1, Figures 7 & 8) shows that seastars prefer the larger sized snails. Table 1 shows a significantly ($p < .001$) higher survivorship in the smaller size classes. The mean sizes of snails eaten in the field are compared to those found in the laboratory in figure 8. It is apparent that larger sized snails are consumed in the field. The difference between laboratory and field results is probably an artifact of the laboratory conditions. Comparison of the field data to the snail sizes found in the transect (see section 1) shows that the sizes consumed are greater than most average sizes found in the field. The field samples were taken when the seastars were spread through their peak range of tidal height and thus encountered snail populations with a lower mean size than that found in the lowest square (A) of the transect.

Visual observation of the laboratory predation experiments showed many instances of a seastar releasing small snails after capture. Also a greater proportion of small snails were found in withdrawn position indicating success of the escape response as described in the next section.

STUDIES ON NEW ASPECTS OF ESCAPE BEHAVIOR:

During laboratory observations of _Pisaster ochraceus_ predation on _Tegula funebralis_, it was discovered that the snails withdrew their entire body and operculum into the shell past the first third of the opening whorl, following capture by a seastar. This behavior was observed when snails that appeared to have been eaten during feeding experiments were subsequently found to be alive. The following experiment was performed to test the effectiveness of this escape response.

The shell opening was ground as a treatment to remove the protection of the first quarter whorl. Snails were size classed and marked before grinding and used at least a day after the operation. No difference in running speed was found in snails tested before and after grinding.

Two seastars were placed in each of four ten gallon glass aquaria with running seawater and screened tops. Seastars were randomly selected from a group of roughly equivalent wet weights and sizes. Each tank was supplied with twerty snails 5 each of 4 size classes. Two tanks held normal snails and the other two held treated snails. All tanks were checked daily for 7 days and consumed snails were scored and replaced by live snails of the same size class and type.

The experiment was designed for analysis with a three level ANOVA. The levels from highest to lowest were:

Among treatments, replicates within treatments, size classes within replicates, and survival within size classes.

EFFECTIVENESS OF WITHDRAWAL BEHAVIOR:

The data (Figure 9, Table 2) shows the decrease in survival caused by the treatment. The 10% difference in survival was significant ($p < .05$) while there was no significant difference between replicates within treatments. The difference between size classes eaten is similar to the data presented earlier and is also significant ($P < .001$).

DISCUSSION:

Limits on lower distributions of intertidal animals set by predation are widely reported (Connell 1975; Paine 1976; Bros 1978). The present study emphasizes behavioral aspects of a predator and the behavioral and morphological aspects of a mobile prey that allows the latter to extend their range into that of the former. Field data from the Pt. Reyes area agree with the observations by Obrebski (MS) indicating that a seasonal change in _T. funebralis_ distribution occurs concurrently with the upward migration of _P. ochraceus_ and a change in snail density in the lower intertidal. This correlation of the influence of seastars on turban snail migration in two localities is further supported by the field and laboratory experiments.

The field experiments demonstrate that _P. ochraceus_ has a measurable short term effect on _T. funebralis_ size distribution. The seastars prefer the larger snails. While larger snails have faster running speeds (Obrebski, MS), the smaller snails, through a combination of behavioral and morphological characteristics, escape predation by _P. ochraceus_. Previous natural history studies (Paine 1976; Landenberger 1967,1968; Dayton 1971; Jillson 1973; Mauzey 1966) generally assume that escape from predation occurs only by having a larger size or by migrating into areas inaccessible to the predators. The fact that all snails have a running response (Feder 1963; Yarnall 1964), and smaller snails may be only rarely consumed by seastars, suggests an alternative explanation for the observed gradients and migration in T. funebralis. Physiological factors (Paine 1971) cause larger snails to migrate lower where they can be better maintained due to the greater abundance of food resources. Due to increasing numbers of encounters with seastars some larger snails may be eaten and smaller snails move upward resulting in the observed increase in average snail size and the corresponding decrease in snail abundance during upward seastar migration. The reproductive characteristics of T. funebralis provide a mechanism for the maintenance of these distribution patterns despite a large snail overlap with the predator. Paine (1971) shows that T. funebralis are fully mature at sizes greater than 18 mm, well below the seastars preferred prey size of 20-23 mm. Thus, a proportion of the population that is reproductive is relatively immune from seastar predation. The tendency for smaller snails to migrate into the upper intertidal due to their escape response to seastars does not explain the selective mechanisms actually maintaining small snails in the upper intertidal, since they are able to escape digestion when caught. Other predators eat snails. Smaller Tegula are more susceptible to predation by crabs than larger ones (H. Boley, pers. communication). It is possible that the tendency for small snails to migrate upwards due to the presence of seastars is maintained because it aids in their removal from the range of activity of other predators to which they have less effective escape responses and with which seastar distributions are correlated.

Experimental manipulation of seastar populations in other localities should provide further corroborative evidence for the foregoing hypothesis and help to define the effects of other changes as possible causitive factors in *T. funebralis* migration. Further experimentation is also needed to verify assumptions about the effects of other predators.

As suggested above, a complex system of interactions results in a size gradient in the vertical distribution of *T. funebralis* intertidal populations. These facts supply further knowledge to support a detailed evolutionary explanation as suggested by Bertness (1977). The simpler explanation of lowered post-larval prereproductive mortality in higher areas suggested by Vermeij (1972) is considered insufficient. Rather, a lowered predation effect on part of the reproductive portion of the snail population provides an explanation more congruent with the new data and natural history information presented here.

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Figure 1: Numbers of _Pisaster ochraceus_ found in the 5 squares of the field transect at each sampling date. (March 1978--January 1979)

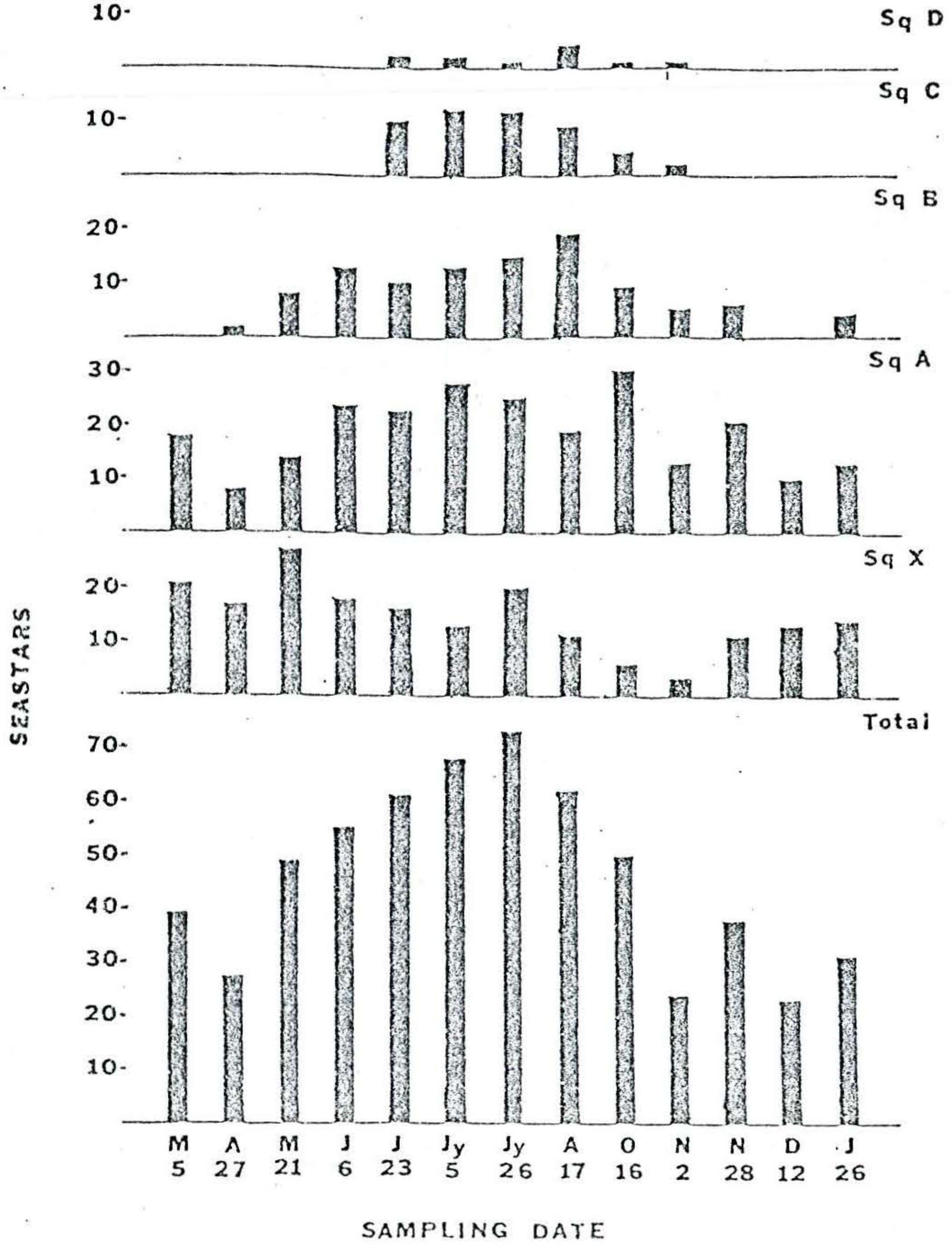
Sq D
10-
Sq C
10-
Sq B
20-
10-
Sq A
30-
20-
10-
Sq X
20-
10-
Total
70-
60-
50-
40-
30-
20-
10-
SEASTARS
M 5
A 27
M 21
J 6
J 23
Jy 5
Jy 26
A 17
O 16
N 2
N 28
D 12
J 26
SAMPLING DATE

Figure 2: Means and 95% confidence limits for size of *Tegula funebralis* sampled in Square A of the field transect at each sampling date. (March 1978-January 1979)

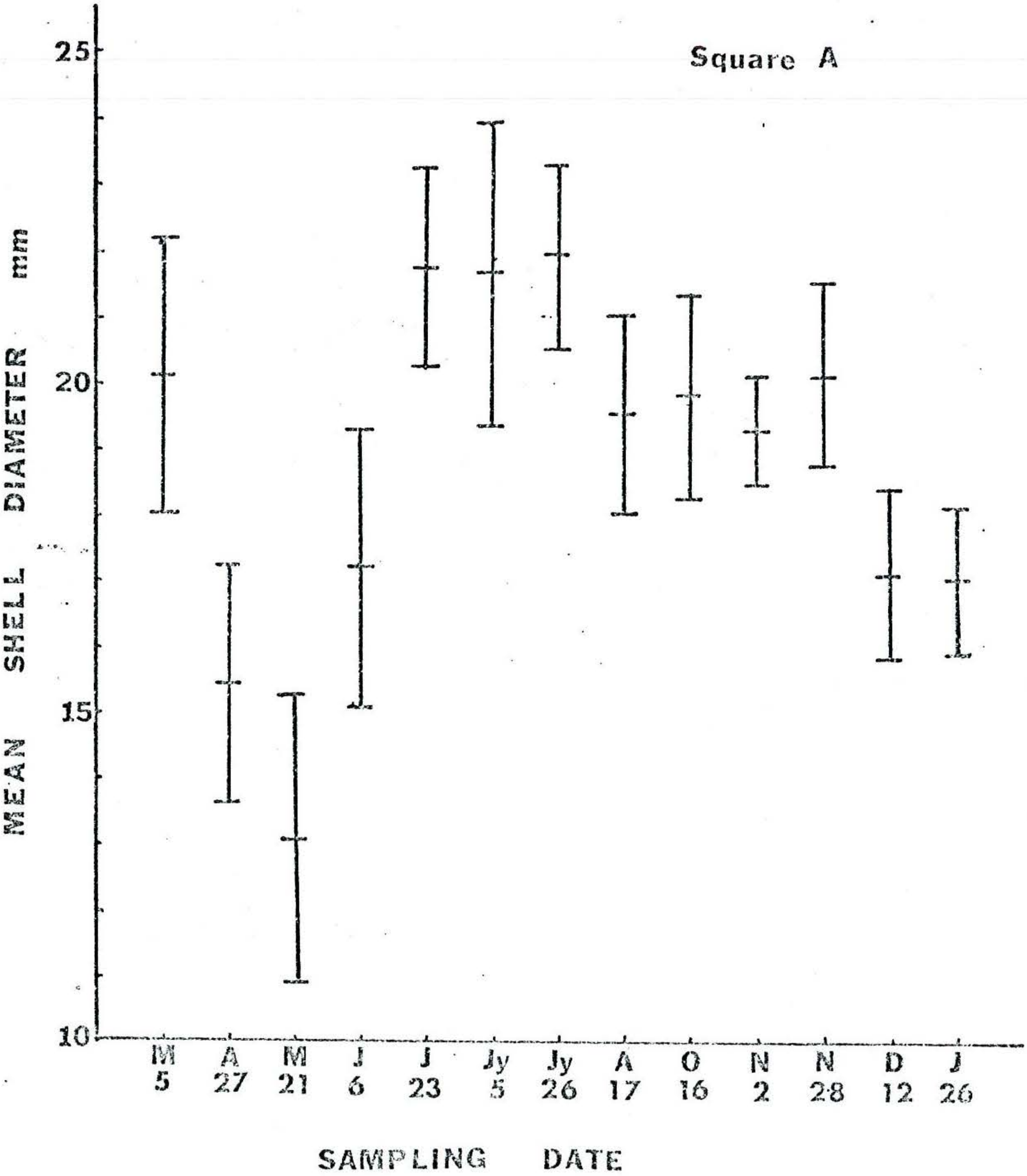
Square A
MEAN SHELL DIAMETER mm
25
20
15
10
M 5
A 27
M 21
J 6
J 23
Jy 5
Jy 26
A 17
O 16
N 2
N 28
D 12
J 26
SAMPLING DATE

Figure 3: Means and 95% confidence limits of *Tequla funebralis* abundance for the entire field transect at each sampling date. (March 1978-January 1979) Nov.28-Jan.26 samples based on squares A and B only.

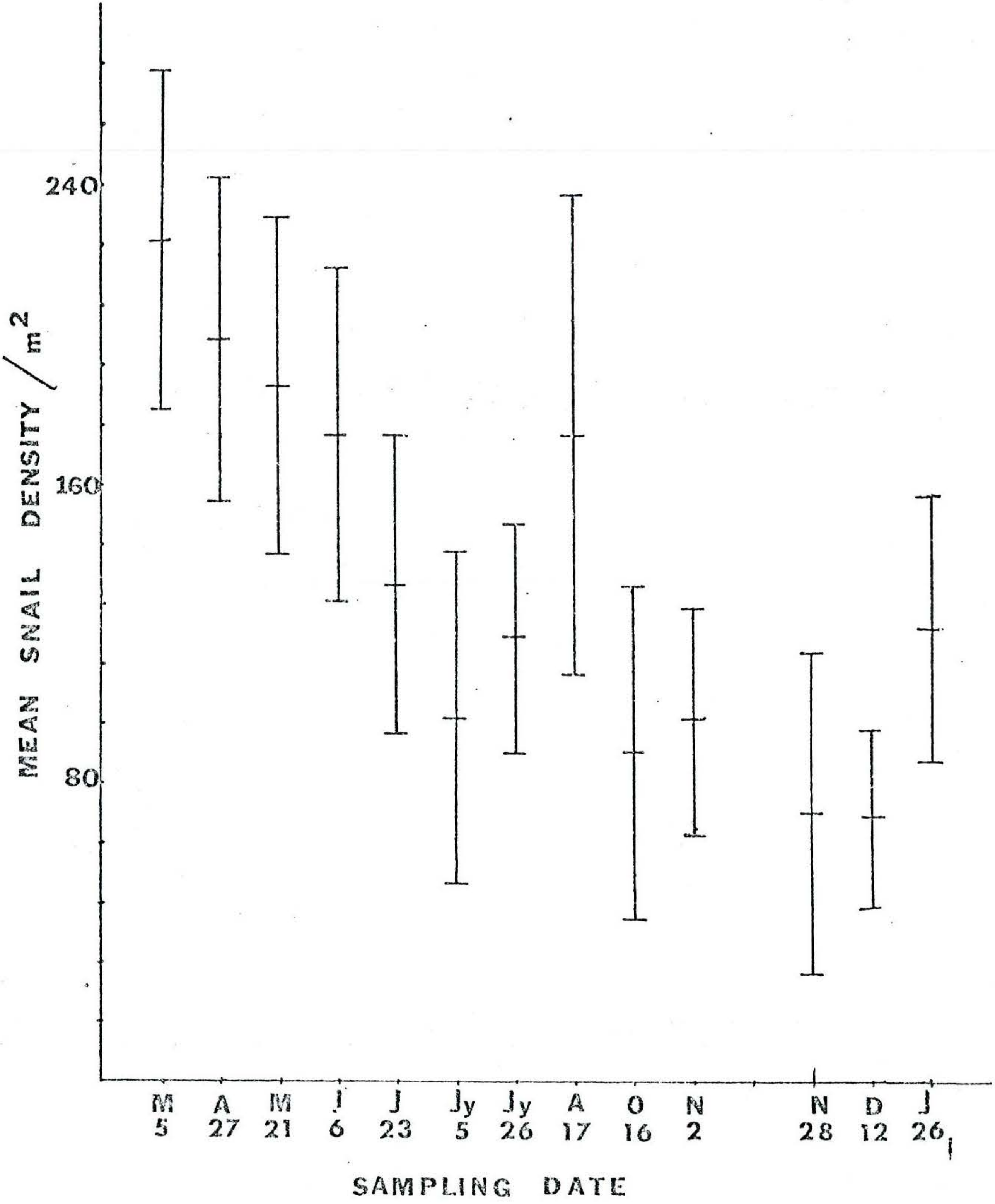
MEAN SNAIL DENSITY /m^2
240
160
80
M 5
A 27
M 21
J 6
J 23
Jy 5
Jy 26
A 17
O 16
N 2
N 28
D 12
J 26
SAMPLING DATE

Figure 4: Means and 95% confidence limits for *Tegula funebralis* abundance in square A of the transect at each sampling date. (March 1978- January 1979)

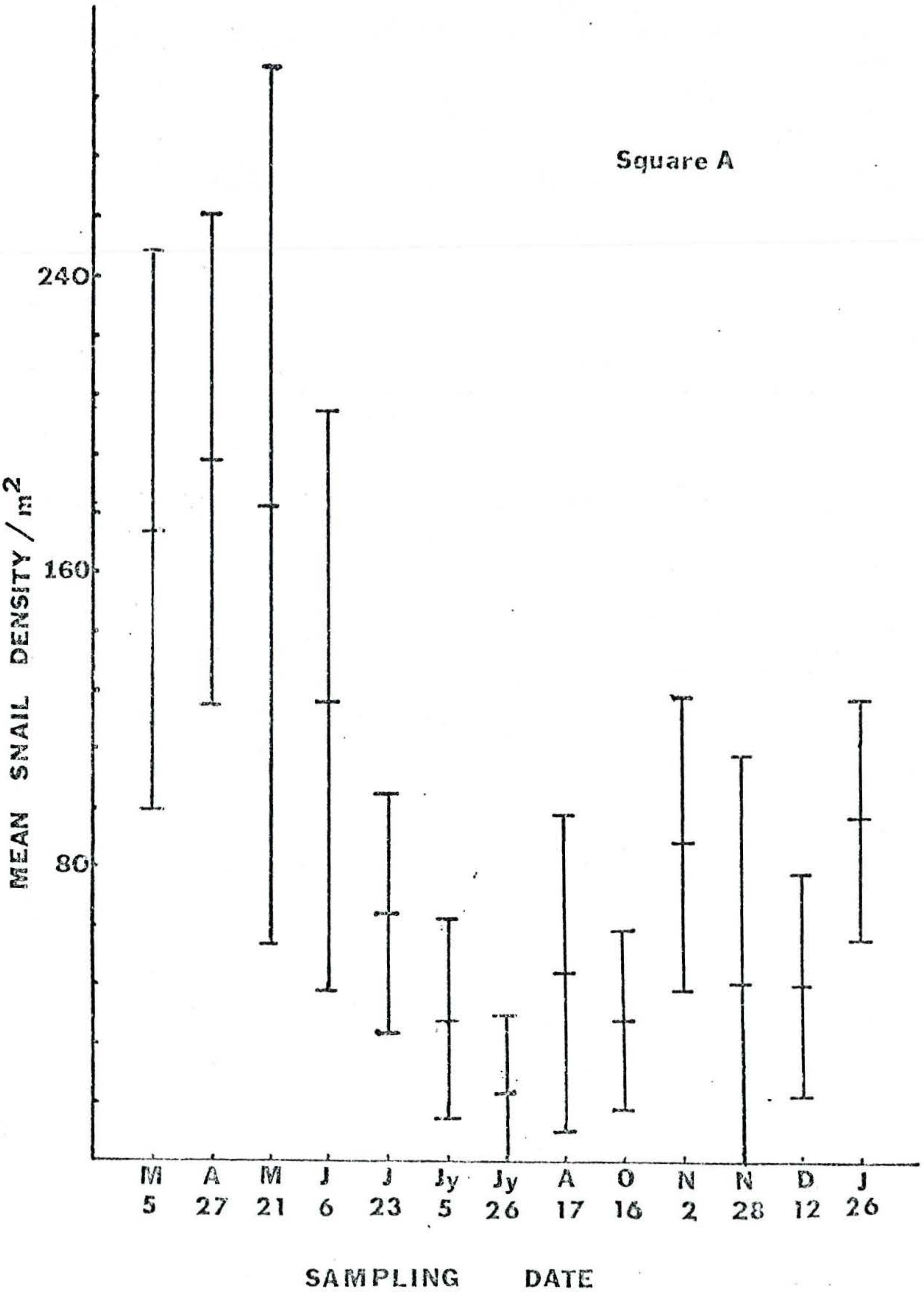
Square A
MEAN SNAIL DENSITY / m^2
240
160
80
M 5
A 27
M 21
J 6
J 23
Jy 5
Jy 26
A 17
O 16
N 2
N 28
D 12
J 26
SAMPLING DATE

Figure 5: Seastar numbers during field experiments. Solid bars indicate number present. Clear bars show those additional seastars added on that sampling date.

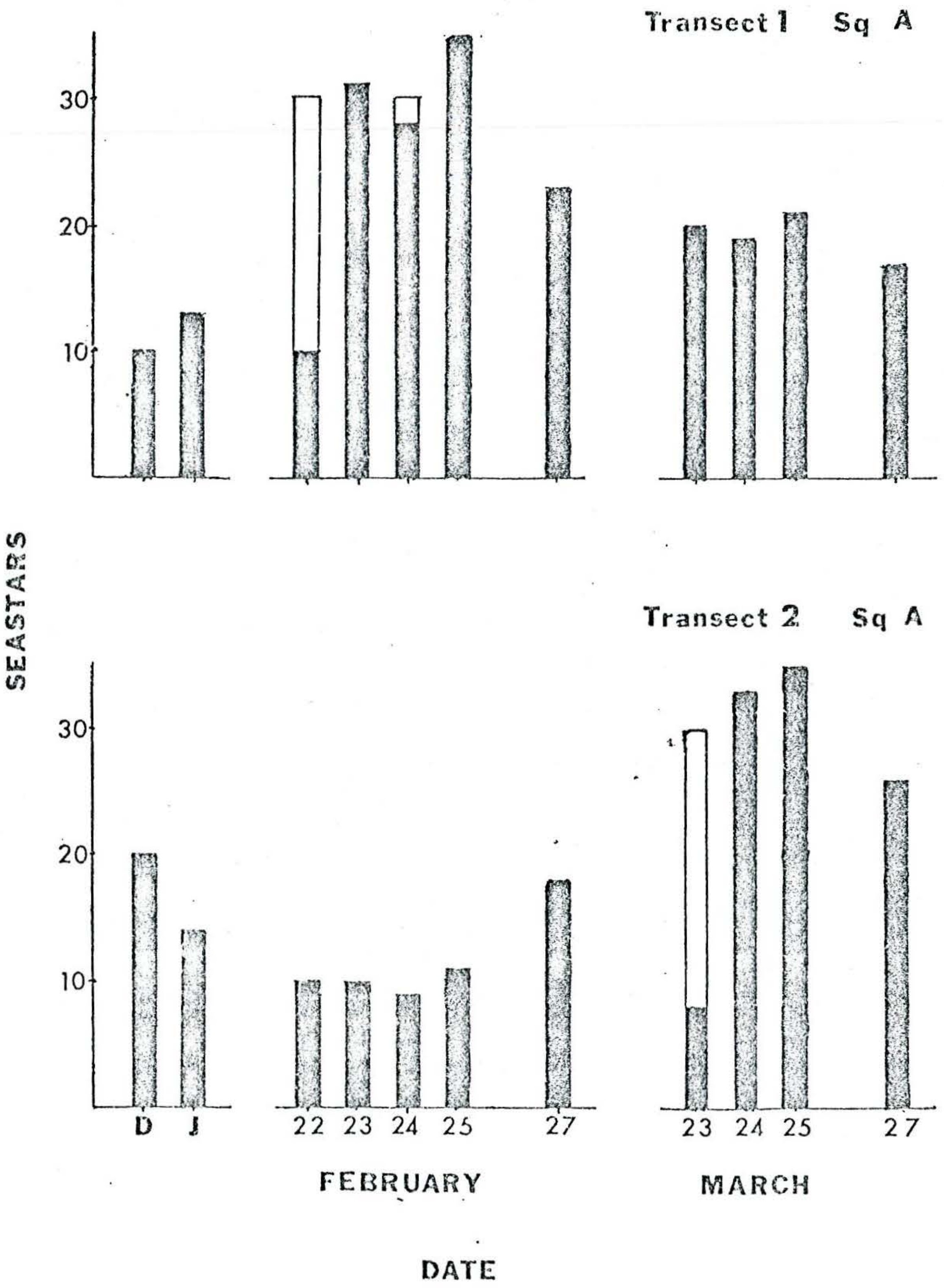
Transect 1 Sq A
Transect 2 Sq A
SEASTARS
30
20
10
D
J
22
23
24
25
27
FEBRUARY
23
24
25
27
MARCH
DATE

Figure 6: Mean and 95% confidence limits of *Tegula funebralis* shell size found in square A of the transects during the two field experiments. Dotted lines show times of experimental increase in seastar numbers.

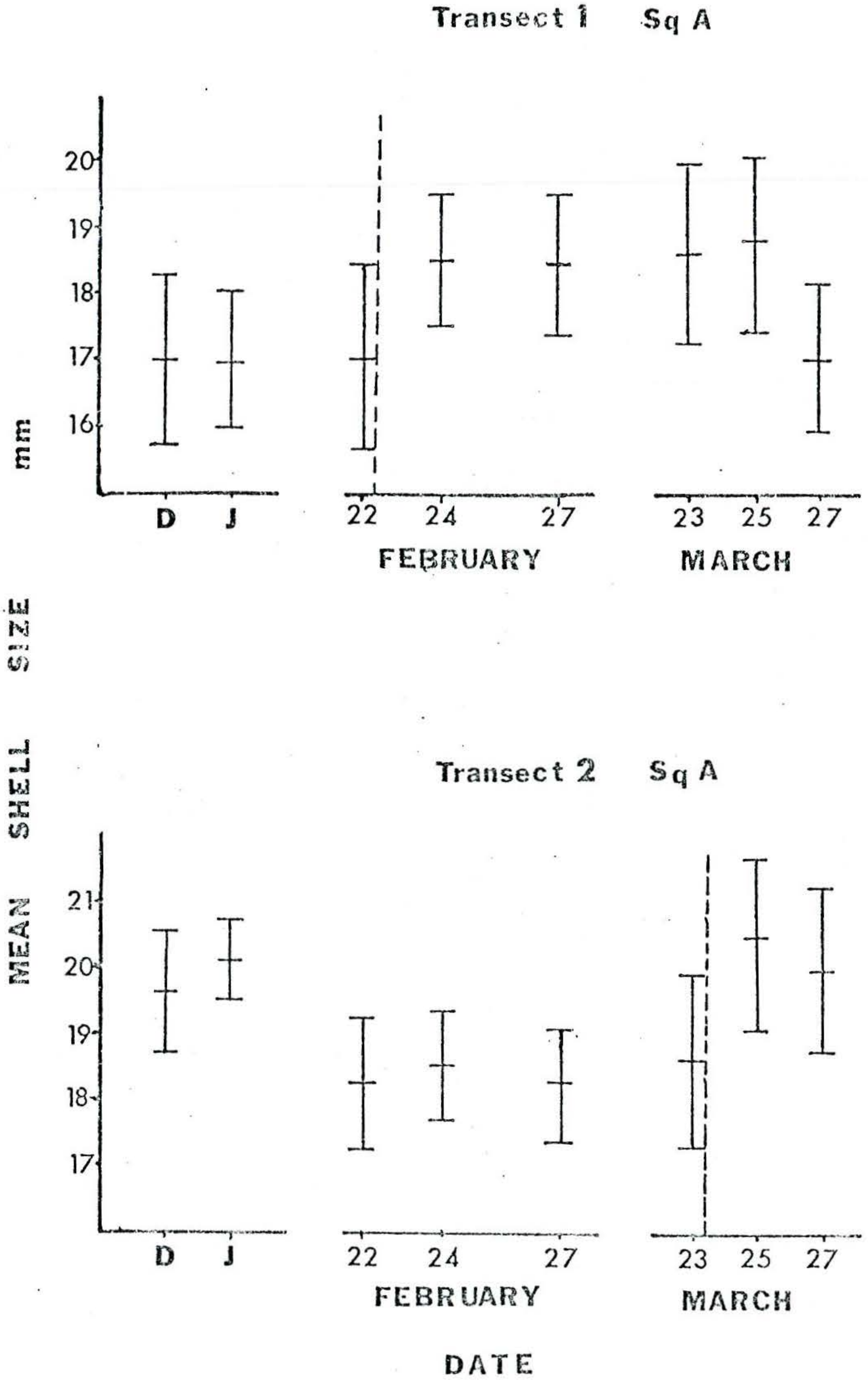
Transect 1 Sq A
20
19
18
17
16
D
J
22
24
27
FEBRUARY
23
25
27
MARCH
MEAN SHELL SIZE mm
Transect 2 Sq A
21
20
19
18
17
D
J
22
24
27
FEBRUARY
23
25
27
MARCH
DATE

Figure 7: Total numbers of *Tegula funebralis* consumed by *Pisaster ochraceus* during 17 day experiment where prey were available in 1:1:1:1 ration of each size class.

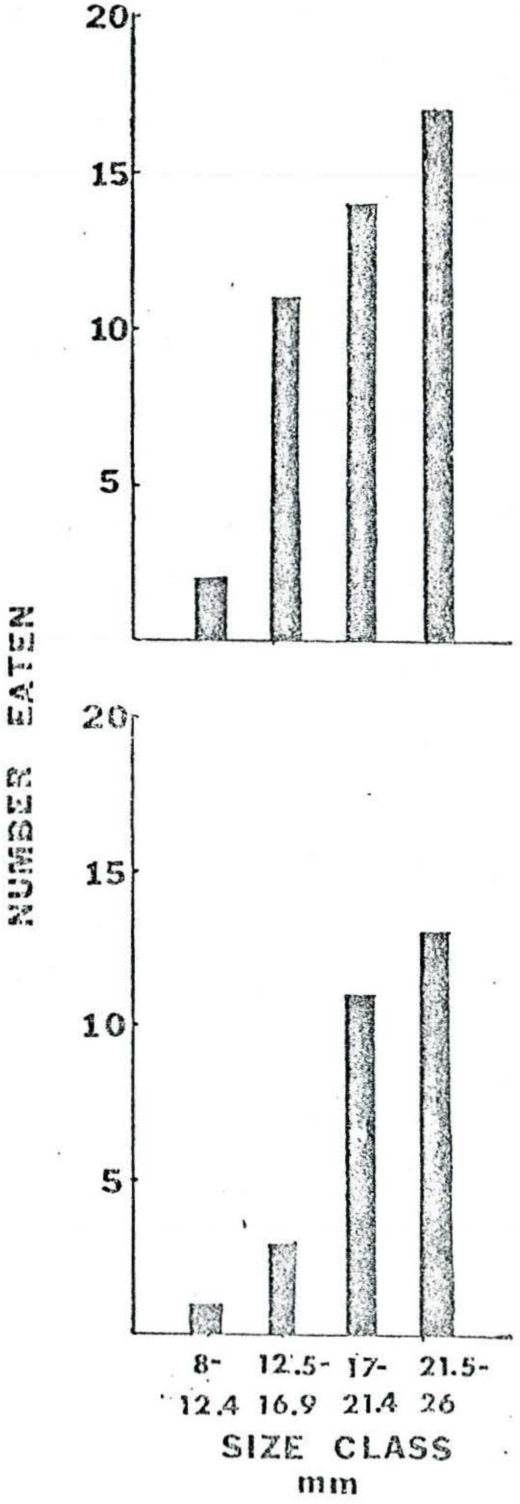
20
15
10
5
NUMBER EATEN
20
15
10
5
8-
12.4
12.5-
16.9
17-
21.4
21.5-
26
SIZE CLASS
mm

Table 1: Experimental data for <u>Tegula funebralis</u> size preferred in laboratory by feeding <u>Pisaster ochraceus</u>. Data are daily means of totals presented in Figure 7.

SHELL SIZE CLASS	1 8-12.4mm	2 12.5-16.9mm	3 17-21.4mm	4 21.5-26mm
TANK A				
Mean # eaten per day	0.12	0.65	0.82	1.0
Mean % survival per day	97.65	87.05	83.5	80
TANK B				
Mean # eaten per day	0.05	0.17	0.65	0.76
Mean % survival per day	98.8	96.5	87.05	84.7

Figure 8: Means and 95% confidence limits of snail sizes consumed by <u>Pisaster</u> <u>ochraceus</u> in 2 field and 1 lab samples. (See text)

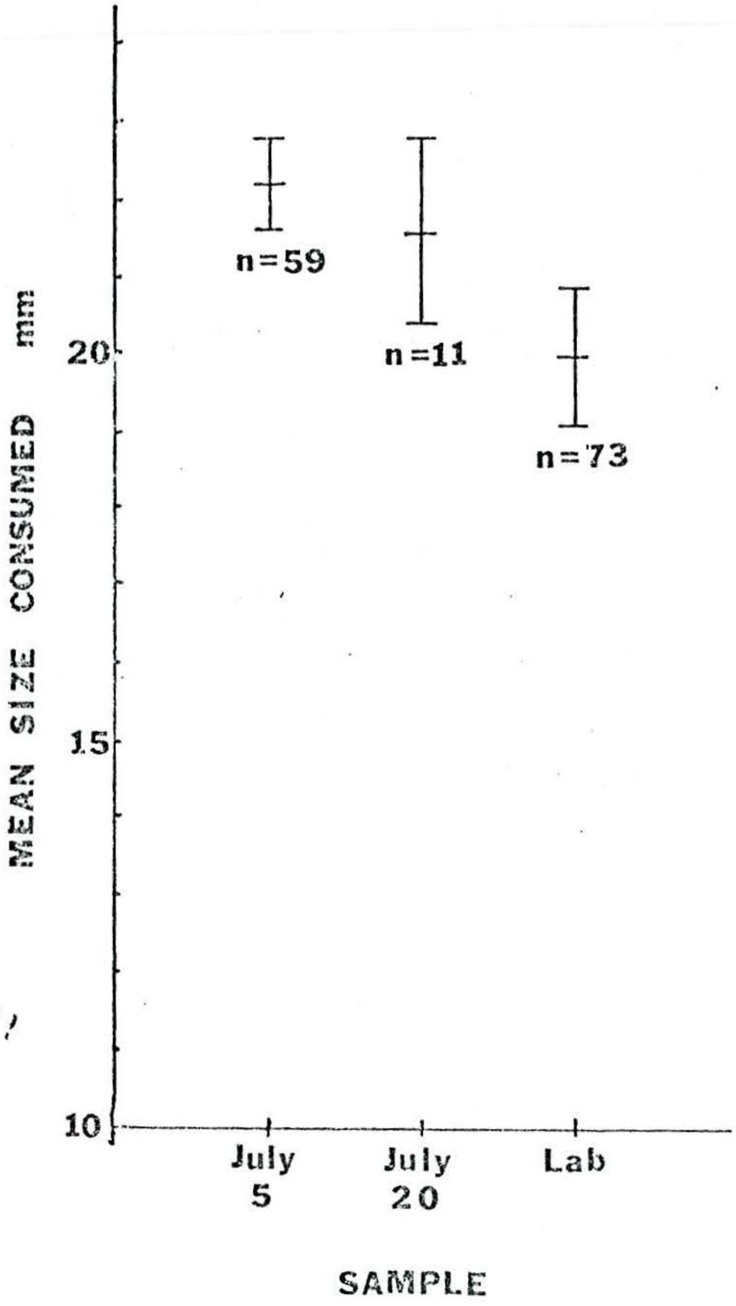
MEAN SIZE CONSUMED mm
20
15
10
n=59
n=11
n=73
July 5
July 20
Lab
SAMPLE

Figure 9: Numbers of *Tegula* *funebralis* eaten by seastars in experiment to test effectivness of withdrawal response. Size classes are the same as those listed in Table 1.

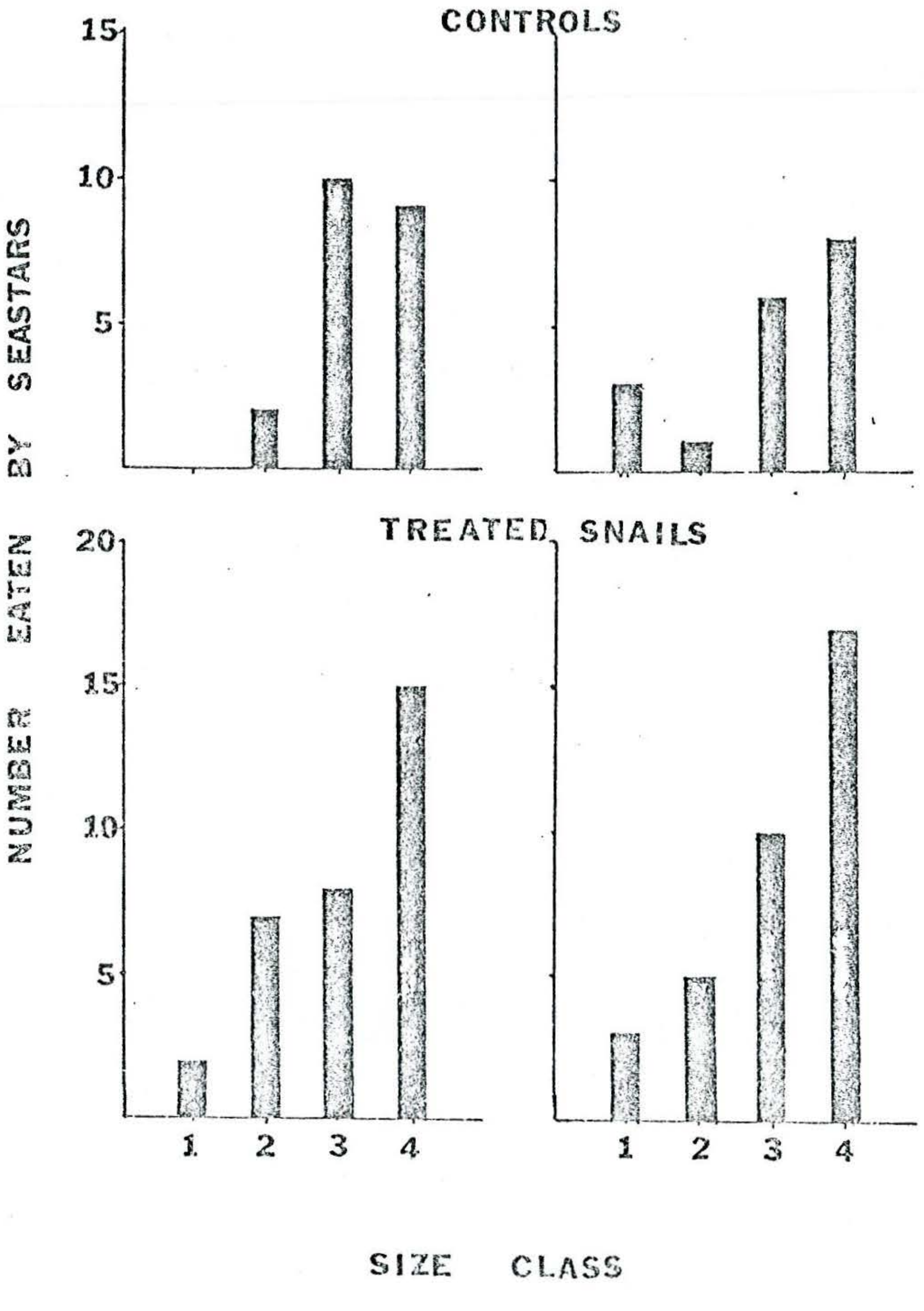
CONTROLS
TREATED SNAILS
NUMBER EATEN BY SEASTARS
15
10
5
20
15
10
5
1
2
3
4
1
2
3
4
SIZE CLASS

Table 2: Survivorship data for laboratory experiments to test withdrawal response of _Tegula funebralis_ to _P. ochraceus_ predation.

		Mean daily % survival	Mean % survival for treatment
Treated Snails	Tank 1	77.14	76.07
	Tank 3	75	
Control Snails	Tank 2	85	86.07
	Tank 4	87.14	