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FITNESS THEORY AND ASPECTS OF BEHAVIORAL ECOLOGY IN TWO SYMPATRIC PACURUS SPECIES AT DILLON BEACH, CALIFORNIA: (DECAPODA, ANOMURA)

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 in Marine Science

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by
JOHN ERICKSON WARNER, Mayor
Dillon Beach, California
March, 1974

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A very special acknowledgement goes to my parents, Mr. and Mrs. William M. Warner who in so many ways put forth the time and effort needed in publishing this work.

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INTRODUCTION

According to Levins (1968) the significance of many adaptations can be determined from observation of similar variation of different organisms in the same environment. Consequently, evolutionary laws relating size of some organisms to temperature can be deduced, or the significance of some color patterns as cryptic defense mechanisms identified. Unfortunately, many adaptations such as polymorphism, developmental homeostatisis and others cannot be shown to be adaptations to specific environments. Moreover, there must always be a lag between ideal and realized adaptations as the contribution from one generation to the next does not completely take into account added rigors of the new environment. Changing patterns in the environment require the development of strategies that optimize survival of individuals in populations. These strategies may be a change in preference and distribution between environmental types with the seasons, or the possession of a high degree of phenotypic plasticity allowing expression of different adaptations depending on which environment is encountered. The determination of the degree to which behavioral patterns are strategies maximizing individual survival in populations is an important aspect of behavioral ecology.

Hermit crabs have elaborate behavioral patterns associated with inter- and intra-specific competition. Childress (1972) has shown that hermit crabs are excellent organisms for studying the degree to which ecological pressures shape adaptive behavior patterns, using Levins (1968) concepts of fitness sets. The use of Levins (1968) concepts require that the species studied have several characteristics that are relatively easy to measure. That is, fitness is estimated from measurements of fecundity and proportions of different environments (shells) used by the species. Hermit crabs appear to fulfill these requirements.

Previous attempts to apply fitness set analysis contained several drawbacks. McNaughton (1970) used several different species of Typha to illustrate the adaptive significance of phenotypic variation. This violates the requirements of fitness set analysis that genetic variants involved in an adaptive strategy belong to the same population. Childress (1972) utilized a population of the tropical hermit crab Clibanarius albidigitus to elucidate the adaptive strategy of shell changing and related aggressive behavior. However, this study involved a one week sampling period and he observed highly variable fecundities suggesting that results could not be considered as generally representative.

In the present study, aspects of the behavior and ecology of two sympatric intertidal hermit crabs, Pagurus hirsutiusculus (Dana, 1851) and Pagurus samuelis (Stimpson, 1857) were studied with the intention of expanding the use of fitness set analysis to other species, particularly extending studies over the entire breeding season.

Fitness Set Theory

The concept of fitness, as a measure, is derived rrom the expected ultimate reproductive success for a given genotype. The genotype is conceived as receiving environmental information through receptor systems of a phenotype. This information is processed into a prediction of future environments; a best strategy for a given phenotype over a genetically predicted range of environments. Assuming all genotypes are unequal in reproductive success, selection would favor any genotype carrying genes (or gene combinations) which would increase fecundity (number of offspring produced) over time. Likewise, genotypes with genes that do not meet the average fecundity will be selected against. That is natural selection will always change gene frequency so as to increase fitness. This notion is basic to the whole theory of natural selection and offers a gauge for noting changes in adaptive strategies by measuring fitness (Levins, 1968; Emlen, 1973).

Levins (1968) noted that the sensitivity of a phenotype to an environment depends on the environmental "grain". The concept of grain is derived from the size of patches of the environment. A patch is defined to be a range of one or more environmental change(s) as it relates to a given phenotypes' utilization. These patterns of environmental change do not always follow a gradient, but may take on a mosiac or patchy form. A patch is not constant in that.it varies in time, from species to species and in relation to size and notility of a given phenotype.

Two basic examples provide a clear view of the notion of grain: (1) a bison feeding on prairie vegetation does not distinguish between a sprig of clover growing amongst grass; both are cropped. The bison consumes several patches or micro-habitats. These food differences are termed fine grained. (2) a parasite infects one of several available hosts. This is a coarse grained difference as the parasite spends its entire life in a single patch (host) (Levins, 1968; Emlen, 1973).

This concept of fine and coarse grain is expanded to include other spatial and temporal differences. A fine grained environment would exist when individuals leave an area during times of extreme environmental flucuations. In contrast, a coarse grained environment would exist when individuals are forced to remain in one place despite environmental flucuations. Moreover, enlargement of the concept treats encounters with individuals and/or objects as patches. For example, an individual may lean towards fine grained differences in feeding and coarse grained differences in distribution. That these grain differences may vary for a given individuals' utilizations suggests that some intermediate grain between the two extremes (fine and coarse) would be expected. This is shown in that grain in a spatial and temporal sense are not independent. As an example, the ability to escape times of environmental flucuations suggests a coarse grain difference between the area evacuated and the area to which an escape is made. Environments then, would appear to be neither strictly fine or coarse grained with respect to the individual (Emlen, 1973).

To understand fitness in a heterogeneous environment, it is advantageous to view grain in its two extremes. Consider each extreme patch (environment) type to include the set of all realizable genotypes in a population. A genotype reflected in a phenotype optimally constructed to withstand the rigors of one environmental type will presumably have achieved this point at the expense of fitness in another environmental type. Figures 1 & 2 translate the expense of fitness in achieving an optimum in either environmental type.

Figure 1

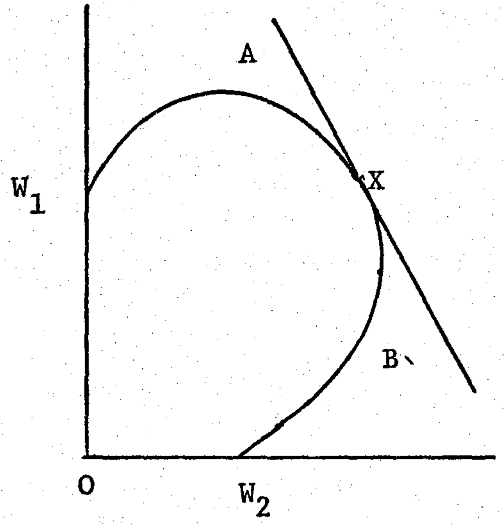
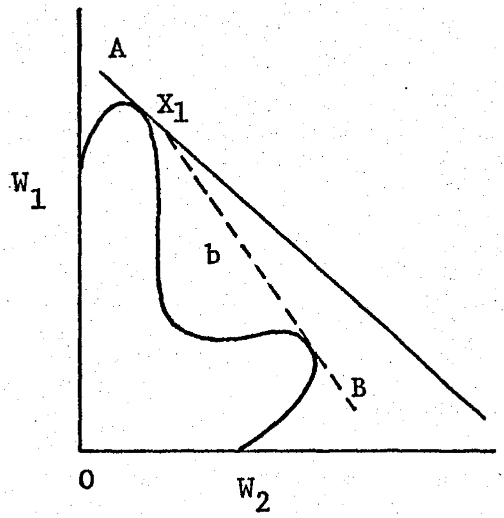


Figure 2



Here A denotes the relative fitness in one environmental type, W_1 (along the ordinate) and environmental type two, W_2 (along the abicissa) for a phenotype specialized to environment one. B denotes the same for a phenotype in environment two. In cases where the similarity between the two environmental types is great, a small genetic change improving fitness in one environment should not greatly lower fitness in the other. In Figure 1 this similarity is expressed by all the phenotypes intermediate to A and B forming a convex fitness set. In situations where environments are very dissimilar in that a slight genetic change improving fitness in one environment may result in loss of fitness in the other, the fitness set enclosed by AOB is concave (Fig. 2). The dotted line b (Fig. 2) joining A and B represents the maximum fitness relizable by a population consisiting of varying proportions of A and B favored by selection. These fitness values exceed the maximum fitness relizable by any one phenotype (Emlen, 1973). Levins (1968: p. 17) defines the difference between concavity and convexity of fitness sets as "twice the distance from the peak to the inflection point as the tolerance of the phenotype" and asserts that the fitness set is concave or convex depending on whether the environmental range is respectively greater than, or less than the tolerance of a single specie.

The use of fitness set analysis does not in itself measure an optimum strategy. Levins (1968) pointed out that overall fitness in a heterogeneous environment depends on fitness in the separate environments which is determined by the pattern of environments. The "Adaptive Function" ($A(W_1, W_2)$) is introduced as a measure of fitness in a heterogeneous environment. It is defined "to be a monotonic increasing function of its arguments" (Levins, 1968: p. 17). Emlen (1973) put the adaptive function in terms of defining a parallel set of fitness isoclines.

Consider a hypothetical case for a population in which the two environmental types (W_1, W_2) constitute a fine grained environment. A genotype traversing such a fine grained environment does not change its response to match its micro-habitat of the moment (example of feeding bison). Selection acts like the environment were a mean of all environmental types encountered. Here, a genotype spends a proportion (p) of its time in one environmental type (W_1) and a proportion (1-p) of its time in environmental type two (W_2). Selection will respond to the mean fitness ($\overline{W}$) of overall environmental types as represented by the linear function (Levins, 1968; Emlen, 1973):

$$W = A = pW_1 + (1-p)\ W_2$$

Since selection acts to increase fitness it effectively favors the genotypes with the highest fitness. A point on the fitness set which touches the curve $A(W_1,W_2) = K$ represents the favored genotype and thus, optimal strategy. Returning to Figure 1 this is represented by the point X and in Figure 2 by X_1=A.

The use of fitness set analysis assumes that all available genotypes of a population are contained within the fitness set by definition (Levins, 1968). Ideally, to meet this qualification, all members of a population making a genetic contribution to the next generation and the resulting offspring from that generation that survive and reproduce should be measured. The feasibility of such an undertaking where planktonic larvae and no direct method for testing male genetic imput are involved (as in hermit crabs) makes it impossible. Instead, clutch size is used as an independent measure of fitness being a direct function of reproductive ability (Childress, 1972). In the case of hermit crabs, a female with a large clutch is viewed as leaving more viable offspring than a female (same specie) with a smaller clutch.

With hermit crabs the fitness set theory rests on the assumption that shell size in relation to body size should play an important role in individucal fitness (Childress, 1972). Reese (1962) put this in terms of a Weight Index, an optimum shell weight/body weight ratio which confers maximum fitness to an individual. A shell too small or too large would increase the probability of succumbing to predation, dessication and eviction by a more aggressive hermit crab (Reese, 1969) thereby decreasing reproductive ability and chances of survival. Environmental grain as it relates to shell utilization also influences individual hermit crab fitness.

BEHAVIOR

Introduction

Past observation (Bellay, 1964; Orians and King, 1964; Ricketts and Calvin, 1968; Vance, 1972a) indicated that Tegula funebralis shells were preferred by P. samuelis and Thais emarginata by P. hirsutiusculus. Both P. samuelis and P. hirsutiusculus overlap in their shell utilization of the two gastropod species. Consequently, empty shells are rare, only the smallest sizes or badly damaged ones being available. This suggests that as a result of the limiting nature of useful gastropod shells there is competition among hermit crabs for suitable shells (Childress, 1972). Vance (1972a) suggested that shells of different sizes and/or species afford different degrees of protection to hermit crabs. That is, assuming that shell preference is at least partially heritable and the existence of shells of an optimum type and size would be expected to constitute the selective agents for getting and keeping optimum shells.

Methods and Materials

Shell preference and competitive behavior was studied using methods similar to those of Orians and King (1964). Crabs collected in the study area (see Ecology section) were removed from their original shells by anesthetizing them briefly in 35°C fresh water (Vance, 1972a) and then placed in 10 inch (diameter) finger bowls with fresh sea water. No noticeable ill effects resulted from the removal procedure and specimens appeared to be normal after 15 minutes.

Competitive behavior for shells was observed by: (1) placing one indifidual of two species each in a container (10 inch finger bowl with fresh sea water) with five different shell species; (2) placing two individuals of each species in one container with a single shell; (3) placing two individuals of each species in one container with one of the pairs original shell. One individual was always smaller than the other and converse tests were made. In addition, sexes were varied. After five minutes results were noted. No attempt was made to quantify behavioral data on the basis of percentage aggressive dominance, a method used by Childress (1972). This precludes the use of this behavioral data in generating behavioral fitness sets.

Results

In all cases, P. hirsutiusculus consistently preferred shells of T. emarginata leaving all other shells previously occupied even at the expense of precluding withdrawal of the carapace into the shell (preference for inadequate shell). Never did P. hirsutiusculus leave a T. emarginata shell for one of T. funebralis, L. planaxis, O. biplicata or N. obsoletus.

On the other hand, P. samuelis showed a definite preference for T. funebralis although Thais shells were occupied when no other was available. P. samuelis chose shells of a size to allow complete withdrawal of the carapace (preference for an adequate shell). P. samuelis always dominated P. hirsutiusculus by evicting the latter no matter what the size difference. In no case did _P. hirsutiusculus_ successfully evict a _P. samuelis_ even if the latter occupied a _Thais_ shell and was at a definite size disadvantage. These findings, as presented in Tables 1-3, substantiate active shell preference and prove that a dominance pattern of _P. samuelis_ over _P. hirsutiusculus_ exists.

Discussion

Information exists on behavioral patterns and related ecology for the hermit crab genus: _Pagurus_. Hazlett (1968a, 1968b, 1969a) demonstrated that hermit crabs can effect one anothers behavior (communicate) by movements of the chelipeds and ambulatory legs. Limb positions were found to be important parts of agonistic display. Also, these displays frequently involve raising up or otherwise increasing the apparent size of displaying animals. Lowering of the body position decreases the aggressive response of other crabs. Reese (1962) related submissive postures as an adaptation to aggressive behavior amongst hermit crabs. Visual displays allow hermit crabs to interact without physical damage (Hazlett, 1968b). Moreover, Hazlett (1969a) established that in conspecific agonistic displays, size was the important determinent of crab dominance (large over small). Inherent to this point is appendage size as well as position and coloration are decisive in size-dependent aggression. Reese (1961) concluded that interspecific agonistic behavior is based more on specific membership than size

Table 1: Results of Experiment 1 on Shell Preference of *P. samuelis* and *P.* hirsutiusculus involving five different shell species. (All body and shell weight indicated in grams)

Shell:	Tegula	Thais	Littorina	Nassarius	Olivella
Weight:	2.206 g.	.966 g.	.512 g.	.877 g.	1.517 g.
P. samuelis					
L. Female (egg) @ .64 g.	X				
2. Male @ 1.42 g.	X				
3. Female (no egg) @ .85 g.	X				
4. Male @ .65 g.	X				
5. Female (egg) @ 1.23 g.	X				
P. hirsutiusculus					
1. Male @ 1.08 g.		X			
2. Female (egg) @ 1.26 g.		X			
3. Female (no egg) @ .83 g.		X			
4. Female (egg) @ .96 g.		X			
5. Male @ 1.03 g.		X			

Table 2: Results of Experiment 2 on Shell Preference and Dominance Orders in *P. samuelis* and *P. hirsutiusculus* involving one introduced shell as designated. (All body and shell weights given in grams)

Introduced Shell: Weight:	Tegula 1.237 g.
1. *P. samuelis* Male @ 1.03 g. *P. hirsutiusculus* Male @ .67 g.	X
2. *P. samuelis* Female (egg) @ .97 g. *P. hirsutiusculus* Female (egg) @ .59 g.	X
3. *P. samuelis* Female (no egg) @ .81 g. *P. hirsutiusculus* Male @ .67 g.	X
4. *P. samuelis* Male @ .591 g. *P. hirsutiusculus* Male @ .91 g.	X
5. *P. samuelis* Female (egg) @ .83 g. *P. hirsutiusculus* Female (egg) @ 1.01 g.	X

	Thais .9124 g.
1. *P. samuelis* Female (egg) @ 1.12 g. *P. hirsutiusculus* Male @ .98 g.	X
2. *P. samuelis* Male @ .79 g. *P. hirsutiusculus* Female (no egg) @ .54 g.	X
3. *P. samuelis* Female (no egg) @ .72 g. *P. hirsutiusculus* Male @ .99 g.	X
4. *P. samuelis* Female (no egg) @ .66 g. *P. hirsutiusculus* Female (no egg) @ .82 g.	X
5. *P. samuelis* Male @ .98 g. *P. hirsutiusculus* Female (no egg) @ 1.13 g.	X

Table 3: Results of Experiment 3 on Shell Preference and Dominance Orders in *P. samuelis* and *P. hirsutiusculus* involving one introduced shell as designated. (All body and shell weights given in grams. Position of shell weights indicates individual occupation of shell after five minute observation period.)

Introduced Shell: *Tegula*

1.	*P. samuelis* Male @ .90 g. *P. hirsutiusculus* Female (no egg) @ .93 g.	1.88 g.
2.	*P. samuelis* Female (no egg) @ 1.15 g. *P. hirsutiusculus* Male @ 1.46 g.	2.21 g.
3.	*P. samuelis* Female (no egg) @ .89 g. *P. hirsutiusculus* Female (no egg) @ 1.13 g.	2.29 g.
4.	*P. samuelis* Female (no egg) @ .42 g. *P. hirsutiusculus* Female (no egg) @ .46 g.	.850 g.
5.	*P. samuelis* Female (egg) @ .61 g. *P. hirsutiusculus* Male @ .64 g.	1.45 g.

Introduced Shell: *Thais*

1.	*P. samuelis* Female (egg) @ .66 g. *P. hirsutiusculus* Female (egg) @ .53 g.	.682 g.
2.	*P. samuelis* Male @ .88 g. *P. hirsutiusculus* Female (no egg) @ .84 g.	.7615 g.
3.	*P. samuelis* Female (no egg) @ .62 g. *P. hirsutiusculus* Female (egg) @ .81 g.	.814 g.
4.	*P. samuelis* Male @ .96 g. *P. hirsutiusculus* Male @ 1.12 g.	.7179 g.
5.	*P. samuelis* Female (no egg) @ 1.37 g. *P. hirsutiusculus* Female (no egg) @ 1.63 g.	1.376 g.

of interesting crabs. Hazlett (1969a) suggested that interspecific agonistic behavior is probably rare in nature, owing to apparent shell type preferences and the probability of an ineffective behavioral repertoire between sympatric species.

Past literature (Bellay, 1964; Orians and King, 1964; Ricketts and Calvin, 1968; Reese, 1962a; Childress, 1972; Vance, 1972a) has shown shell preferences are common in hermit crabs. Grant (1963) demonstrated (in lab) that although hermit crabs had no visual orientation to molluse shells they had been occupying, recognition was made upon contact (71.4% of the time; taken from pooled data). Vance (1972a) found intertidal hermit crabs of the Pacific Northwest occupying shells smaller than preferred for all size classes excepting the very smallest; empty shells were absent. He concluded that the "apparent generality of the phenomenon suggests that shell inadequacy must constitute a powerful evolutionary force in hermit crab biology" (Vance, 1972a; p. 1075). Markham (1968) noted that smaller than preferred shell sizes lower hermit crab growth rates. Provanzano (1960) demonstrated that shells were a limiting resource to population growth. Vance (1972a) indicated that small shells would reduce fecundity as size and fecundity were positively correlated.

No effort was made to record behavioral displays in this experiment although aggressive movements and positions like those described by Hazlett (1968b, 1968c, 1969, 1969a, 1969b) for other species were observed. Results from the shell preference experiments (Tables 1-3) are noteworthy as they agree with Orians and Kings' (1964) findings. In both cases, *P. smauelis* dominated *P. hirsutiusculus*. The importance of banding on *P. samuelis* and *P. hirsutiusculus* (chelipeds and ambulatories) cannot be determined at this time. The results of Hazlett (1969a) suggest some significance may be attributed to them. The dominance of *P. samuelis* over *P. hirsutiusculus* appeared due to a preference for one shell type (*Tegula*) although dominance in occupying a *Thais* shell in lieu of none was observed.

P. hirsutiusculus exhibits a more aggressive behavior, but the observed failure to dominate *P. samuelis* may be a reflection of an inadequate behavioral repertoire (Hazlett, 1969a). The possibility of a chemo-tactile stimuli effecting the dominance outcome should not be ruled out (Hazlett, 1970). Hazlett (1969b) found a similar relationship between *P. cuanensis* and *P. bernhardus*. *P. cuanensis* dominated *P. bernhardus* even though the latter was more aggressive and occupied inadequate shells. Vance (1972) presented evidence indicating shell inadequacy and high levels of aggressive behavior are normal for *P. hirsutiusculus*. Vance (1972) concluded that *P. hirsutiusculus* fights whenever an opportunity arises and considers changing shells after a subordinate crabs' shell is relinquished. This strategy is considered advantageous as individuals always stand to gain by fighting in that it increases number of shell changes thereby increasing chances of obtaining a preferred shell.

ECOLOGY

Introduction

Ecological data for *P. samuelis* and *P. hirsutiusculus* was collected from March-October 1973. The sampling period was ended in October owing to the tendency of hermit crabs to bury in sand (Tomlinson, 1960). Primarily because of seasonal variation in intertidal flora and fauna, further intensive sampling would be necessary to obtain more information on ecological parameters effecting strategies. It was the objective of this sampling to provide data for fitness set analysis of ecological factors shaping adaptive strategies.

Populations of *P. samuelis* and *P. hirsutiusculus* were sampled monthly approximately 1 km. north of Dillon Beach, Marin County, California. Both species are sympatric and found in tidepools among rocky shelves or terraces partially protected from heavy wave action by rock outcroppings. Algal cover varied with seasonal flucuation and intertidal level (rich in spring-summer; poor in fall-winter). The range of both species are in agreement with Bollay (1964) and reflect specie tolerance to exposure (air, sunlight, dessication). *P. samuelis* dominates the high intertidal preferring rock-sand bottom pools while *P. hirsutiusculus* is found in upper to middle intertidal regions climbing through algea covered pools.

Methods and Materials

Hermit crabs were sampled along a 15 meter transect extending from the high (approximate level of mean high water) to middle intertidal. Sampling was accomplished using a .50 m^2 quadrat thrown into tidepools at five meter intervals descending the intertidal (high, upper middle, lower middle). Haste was made to collect all hermit crabs within the border of the quadrat before they could run away. Sampling within the quadrat was continued until all hermit crabs occupying shells greater than 4 mm (aperature length) were collected. Specimens were momentarily held in a plastic bucket for field measurements. Abundance and size distribution data was obtained from counts and measurements of all hermit crabs for most samples. Measurements of shell aperature length (of longest axis) were made with a vernier caliper. Approximately 15 hermit crabs were kept for laboratory analysis. Specimens retained were chosen by taking a hand full of individuals (without visual aid) from individual sample buckets before release of other crabs. Hermit crabs were transported to the lab in plastic buckets containing fresh sea water. Hermit crabs were kept in a large partitioned holding tank (1.5 m x 1.5 m x 15 cm) with running sea water (temperature 15-18°C) and fed *Mytilus californianus*. Three partitions within the holding tank represented intertidal levels in which appropriate samples were held. All crabs were examined within 24 hours and were removed from their shells by anesthetizing them briefly in 35°C fresh water (Vance, 1972a).

Naked hermit crabs were identified as to specie, sexed and blotted on paper to remove water before weighing on a Mettler balance, Similarly, shell species were noted and dried by shaking the remaining water out of shells then weighed. No attempt was made to sex specimens less than .35 grams (body weight) as sexual characteristics were not always fully developed. After weighing, all ovigerous females were stripped of their clutches using a fine pair of forceps. The eggs were immediately counted under a dissecting microscope (6X) for clutch size data. All clutches containing embryos with well developed eyes and legs that showed signs of life upon examination were discarded. Thus, eliminating the possibility that some of the clutch swam away before counting.

Results

Data on changes in abundance and size is summarized in Figures 3 & 4 and Tables 4 & 5. Data for March-May is not available due to experimental sampling procedure involving the addition of 50 ml. of a respiratory inhibitor, 4% Quinaldine in 95% isoprpyl alcohol into each sampled tide pool. Results were considered inconsistent as five minutes was required for the drug to act in which time some hermit crabs wandered out of the tidepool. Moreover, definite quadrat boundries were not adhered to at this time.

In the high intertidal, P. hirsutiusculus remained at a constant level of approximately 28 individuals inhabiting Tegula shells

Figure 3: Number of Shells Occupied as a Function of Months (June-October, 1973) for *P. hirsutiusculus*. Data represents .5 m^2 quadrat samples taken for Abundance Estimates. Graphs read left to right and indicate descent in tidal level.

J-June
J-July
A-August
S-September
O-October

T. funebralis - X
T. emarginata - △
L. planaxis - □
N. obsoletus - —
O. biplicata - ○

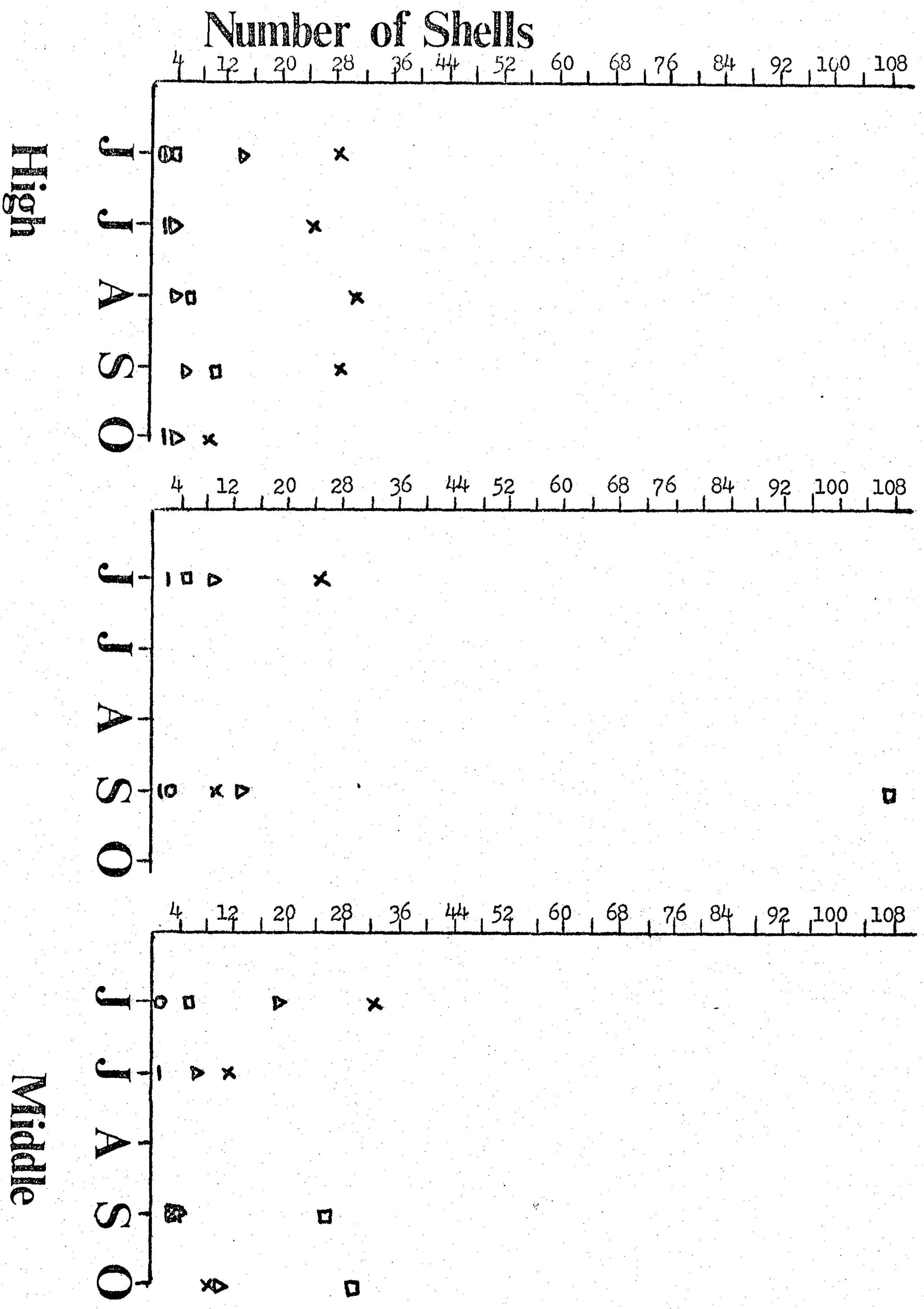

Number of Shells
4
12
20
28
36
44
52
60
68
76
84
92
100
108
High
Middle
J
J
A
S
O

Figure 4: Number of Shells Occupied as a Function of Months (June-October, 1973) for *P. samuelis*. Data represents .5 m^2 quadrat samples taken for Abundance Estimates. Graphs read left to right and indicate descent in tidal level.

J-June
J-July
A-August
S-September
O-October

T. funebralis - X
T. emarginata - △
L. planaxis - □
N. obsoletus - —
O. biplicata - ○

Table 4: Size Distribution and Shell Utilization Information gathered from June-October for Abundance Estimates of *P. hirsutiusculus*. Measurements indicate length of aperature for longest axis of designated shells in centimeters. Charts read from left to right and indicate descent in tidal level.

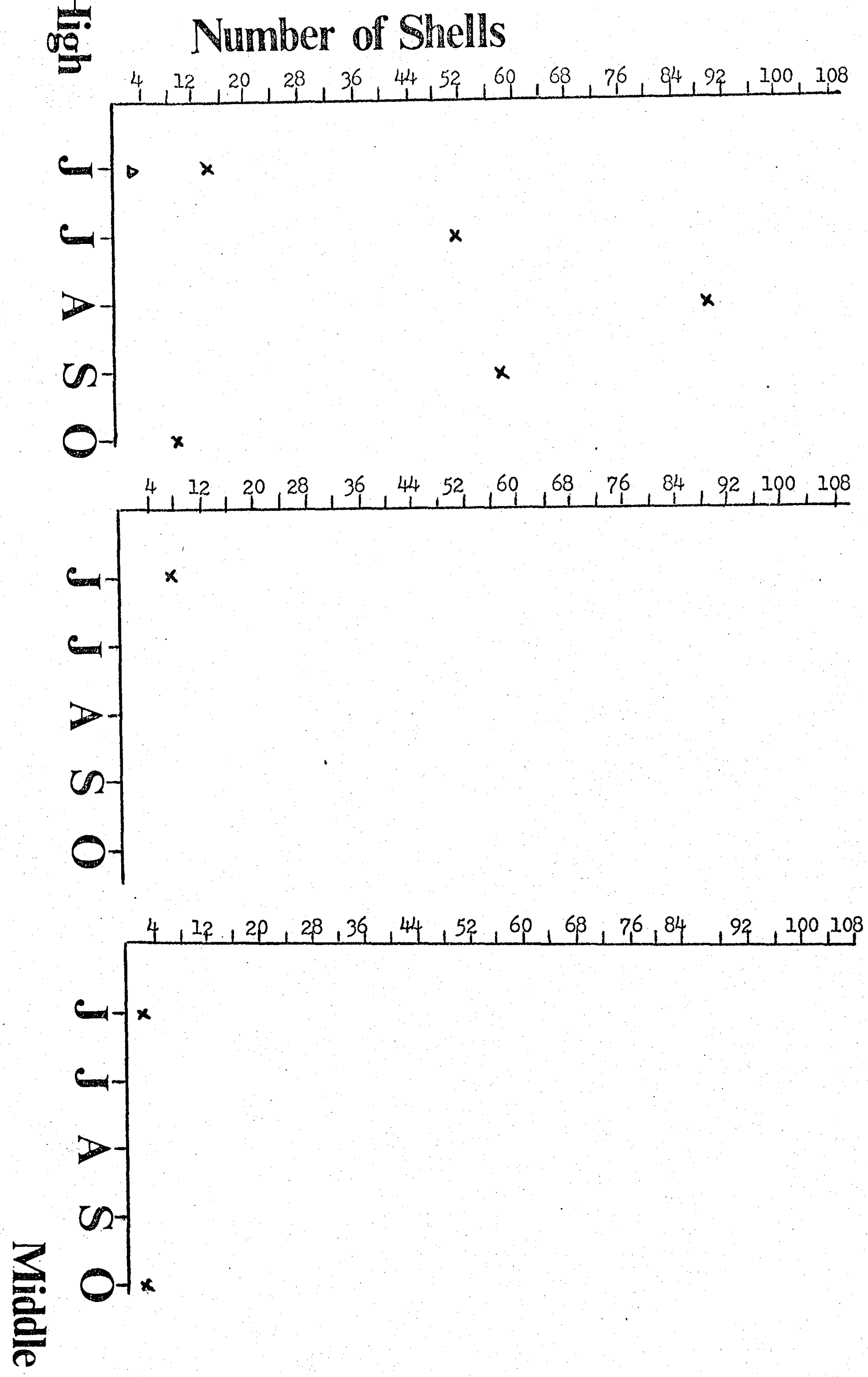
T - *T. funebralis*

Th - *T. emarginata*

L - *L. planaxis*

N - *N. obsoletus*

O - *O. biplicata*


High
Number of Shells
4 12 20 28 36 44 52 60 68 76 84 92 100 108
J
J
A
S
O
4 12 20 28 36 44 52 60 68 76 84 92 100 108
J
J
A
S
O
4 12 20 28 36 44 52 60 68 76 84 92 100 108
J
J
A
S
O
Middle

(June)

HIGH						UPPER MIDDLE					MIDDLE				
	T	Th	L	N	O	T	Th	L	N	O	T	Th	L	N	O
.2								2							
.3						2		1			2		1		
.4	4		1			2		1	1		3	1	2		1
.5	2		2	2	1	4					7		1		
.6	6	4				5					5	2	1		
.7	4	4			1	5	1				6	2			
.8	7					3	1				5	1			
.9	2	1				3	3				1	1			
1.0	2								1		2				
1.1							1					5			
1.2		2										1			
1.3		2					2					3			
1.4												1			
1.5												1			
1.6											1				
Total	27	13	3	2	2	24	8	4	2		32	18	5		1
%	57	27	7	4	4	63	21	11	5		57	32	9		2

(July)

	T	Th	L	N	O	T	Th	L	N	O	T	Th	L	N	O
.2														1	
.3															
.4	4														
.5	3			1							3	1			
.6	4			1							1				
.7	6										2	2			
.8	2	1									4	1			
.9	4	1									1	1			
1.0												1			
1.1															
1.2															
1.3		1													
1.4															
1.5															
1.6															
Total	23	3		2							11	6		1	
%	82	11		7							61	33		6	

(August)

HIGH						UPPER MIDDLE									MIDDLE
	T	Th	L	N	O	T	Th	L	N	O	T	Th	L	N	O
.2	1		1												
.3	3		1												
.4	3		2												
.5	8		1												
.6	5														
.7	3														
.8	2														
.9	4														
1.0		2													
1.1															
1.2															
1.3															
1.4		1													
1.5															
1.6															
Total	29	3	5												
%	78	8	14												

(September)

	T	Th	L	N	O	T	Th	L	N	O	T	Th	L	N	O
.2								7		1			10		
.3	2	3	7				1	26		1			1		
.4	7		2				4	67				1	13		
.5	4	1				5	2	5							
.6	2					2		1	1		1				
.7	6					1						1			
.8	3					1	2								
.9	1						1								
1.0	2					1	1				2				
1.1															
1.2		1					1								
1.3															
1.4							1								
1.5															
1.6															
Total	27	5	9			10	13	106	1	2	3	2	24		
%	66	12	22			7	10	80	1	2	10	8	82		

(October)

HIGH						UPPER MIDDLE					MIDDLE				
	T	Th	L	N	O	T	Th	L	N	O	T	Th	L	N	O
.2															
.3													6		
.4													16		
.5											1	1	6		
.6	3	1									2				
.7	3	1									1				
.8															
.9				1							2	1			
1.0		1									2				
1.1															
1.2	1											3			
1.3	1											1			
1.4															
1.5												2			
1.6												1			
Total	8	3		1							8	9	28		
%	67	25		9							18	20	62		

Table 5: Size Distribution and Shell Utilization Information gathered from June-October for Abundance Estimates of _Pagurus samuelis_. Measurements indicate length of aperature for longest axis of designated shells in centimeters. Charts read left to right and indicate descent in tidal level.

T - _T._ _funebralis_

Th - _T._ _emarginata_

L - _L._ _planaxis_

N - _N._ _obsoletus_

O - _O._ _biplicata_

(June)

HIGH						UPPER MIDDLE					MIDDLE				
	T	Th	L	N	O	T	Th	L	N	O	T	Th	L	N	O
.2															
.3															
.4															
.5															
.6															
.7	2														
.8	2					2									
.9	1					2									
1.0	3	1				1									
1.1	5	1				2									
1.2	1										1				
1.3						1									
1.4															
1.5											1				
1.6															
Total	14	2				8					2				
%	87.5	12.5				100.0					100.0				

(July)

	T	Th	L	N	O	T	Th	L	N	O	T	Th	L	N	O
.2															
.3															
.4															
.5															
.6	3														
.7	5														
.8															
.9	8														
1.0	4														
1.1	10														
1.2	8														
1.3	2														
1.4	3														
1.5															
1.6	1														
Total	51														
%	100.0														

(August)

HIGH						UPPER MIDDLE					MIDDLE				
	T	Th	L	N	O	T	Th	L	N	O	T	Th	L	N	O
.2															
.3															
.4	1														
.5	2														
.6	4														
.7	15														
.8	7														
.9	15														
1.0	13														
1.1	17														
1.2	10														
1.3	3														
1.4	1														
1.5															
1.6															
Total	89														
%	100.0														

(September)

	T	Th	L	N	O	T	Th	L	N	O	T	Th	L	N	O
.2															
.3															
.4															
.5	1														
.6															
.7	3														
.8	1														
.9	6														
1.0	16														
1.1	11														
1.2	9														
1.3	7														
1.4	3														
1.5	1														
1.6															
Total	58														
%	100.0														

(October)

HIGH						UPPER MIDDLE					MIDDLE				
	T	Th	L	N	O	T	Th	L	N	O	T	Th	L	N	O
.2															
.3															
.4															
.5															
.6															
.7															
.8															
.9															
1.0	2														
1.1	1										1				
1.2	2										1				
1.3	2														
1.4	2														
1.5															
1.6															
Total	9										2				
%	100.0										100.0				

from June-September decreasing to 8 in October (Fig. 3). *P. hirsutiusculus* inhabiting *Thais* shells were most abundant in June decreasing from 13 to 4 individuals in July-August. Hermit crabs having *Littorina* shells increased from 4 in June to 8 in September.

P. hirsutiusculus occuring in both middle intertidal regions utilized more *Thais* or *Littorina* shells than in the high intertidal. *P. hirsutiusculus* in upper middle intertidal regions occupying *Tegula* shells decreased from 25 individuals in June to 9 in September. *Thais* inhabited shells increased from 8 individuals in June to 14 in September. *P. hirsutiusculus* occupying *Littorina* shells increased from 4 individuals in June to 106 in September. *P. hirsutiusculus* utilizing *Tegula* shells in the lower middle intertidal regions dropped from 32 hermit crabs in June to 12 in July to 4 in September rising to 8 in October. *Thais* inhabited shells decreased from 18 crabs in June to 6 in July to 4 in September rising to 9 in October. *Littorina* occupied shells indicate a steady rise from 5 individuals in June to 30 in October.

P. samuelis inhabiting *Tegula* shells rose from 14 individuals in June to 84 in August decreasing to 9 in October (Fig. 4). *P. samuelis* inhabited *Tegula* shells almost exclusively. *P. samuelis* were very rare in middle intertidal regions. In June and October, numbers of *P. hirsutiusculus* exceeded numbers of *P. samuelis* in *Tegula*.

Additional data on size and shell utilization is presented in Tables 4 & 5. A consistent use of Tegula and Thais shells in the .4-.9 cm size range by P. hirsutiusculus occured in the high and mid-intertidal regions. The ratio of P. hirsutiusculus occupying Tegula shells from June-October in the high intertidal to Thais and Littorina was 4.2/1 and 7/1, respectively. In upper middle intertidal regions the ratio of P. hirsutiusculus Tegula inhabited shells from June-October to Thais and Littorina inhabited shells was respectively 1.6/1 and 1/3.2. Comparison of P. hirsutiusculus using Tegula shells to ones of Thais and Littorina in mid-intertidal regions from June-October reflect a 1.5/1 and 1/1.1 ratio. Greatest numbers of P. hirsutiusculus were found in the high intertidal regions. The mid-intertidal regions indicated increasing utilization of Thais and Littorina shells although Tegula occupancy dominated in most instants. The results did show a clear increase in the numbers of hermit crabs using Littorina shells in September and October. Chi-square analysis of the June data which provided sufficient numbers of crabs collected at the three tidal levels indicated no difference in the proportions of different types of shells used by crabs collected at different levels within their range of distribution ($p > 0.975$). In September, there is a significant difference in shell utilization between tidal levels ($p < 0.025$) due largely to the high frequencies of juvenile crabs utilizing Littorina shells in the size range .2-.5 cm predominately in the mid-intertidal regions.

P. samuelis inhabited Tegula shells in the size range .9-1.2 on aperature length (Table 5). P. samuelis found in mid-intertidal regions utilized larger Tegula shells; 1.1-1.5 cm. Data from August indicates that the largest range of shell sizes were utilized at the observed time of juvenile recruitment accounting for the presence of .4-.6 cm shell sizes found inhabited by P. samuelis.

Body weight and sex ratio data from March-October was pooled because of small monthly sample sizes (Figs. 5a-8b). Figures 5a-6b showed that P. hirsutiusculus males and females with and without clutch share the same body weights: .3-.7 grams. Juveniles ranged in body weight from .1 to .4 grams. The ratio of males to females with and without clutch and juveniles was 1/1/1/1. P. samuelis males and females (with and without clutch) ranged in body weight from .4 to .8 grams (Figs. 7a-8b). Juveniles had body weights ranging from .2 to .4 grams. The ratio of males to females was 1/4. The ratio of males to females with and without clutch and juveniles was 1/2.5 and 1/1.5 and 1/.5.

Figures 9-11 represent clutch size as a function of body weight graphed over two month intervals for both species. The March-April period (Fig. 9) is noteworthy for several reasons: (1) it represents the peak number of females with clutch for both species; (2) corresponds with the start of spring-summer algal bloom; and (3) coincides with the removal of sand accumulated over winter from the tidepools. As shown in Figure 9 females of both

Figure 5a: Number of Individual Females with no clutch as a Function of Body Weight in grams for P. *hirsutiusculus* inhabiting T. *funebralis* and T. *emarginata* shells. Information represents pooled data from March-October, 1973.

Figure 5b: Number of Individual Females with clutch as a Function of Body Weight in grams for P. *hirsutiusculus* inhabiting the above mentioned shells. Information represents pooled data from March-October, 1973.

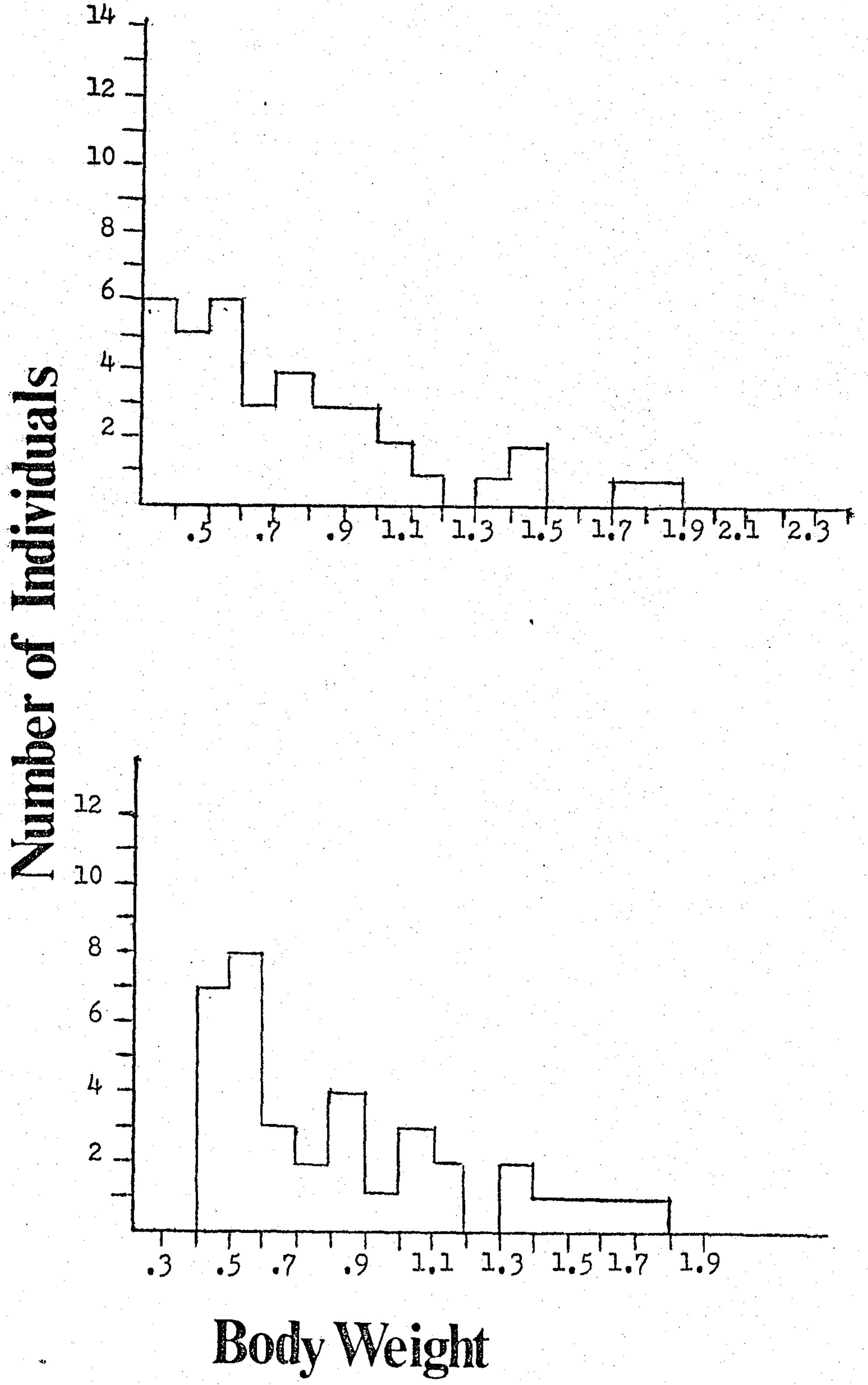

Number of Individuals
14
12
10
8
6
4
2
.5
.7
.9
1.1
1.3
1.5
1.7
1.9
2.1
2.3
12
10
8
6
4
2
.3
.5
.7
.9
1.1
1.3
1.5
1.7
1.9
Body Weight

Figure 6a: Number of Individual Juveniles as a Function of Body Weight in grams for P. hirsutiusculus inhabiting T. funebralis, T. emarginata and L. planaxis shells. Information represents pooled data from March-October, 1973.

Figure 6b.: Number of Individual Males as a Function of Body Weight in grams for P. hirsutiusculus inhabiting T. funebralis and T. emarginata shells. Information represents pooled data from March-October 1973.

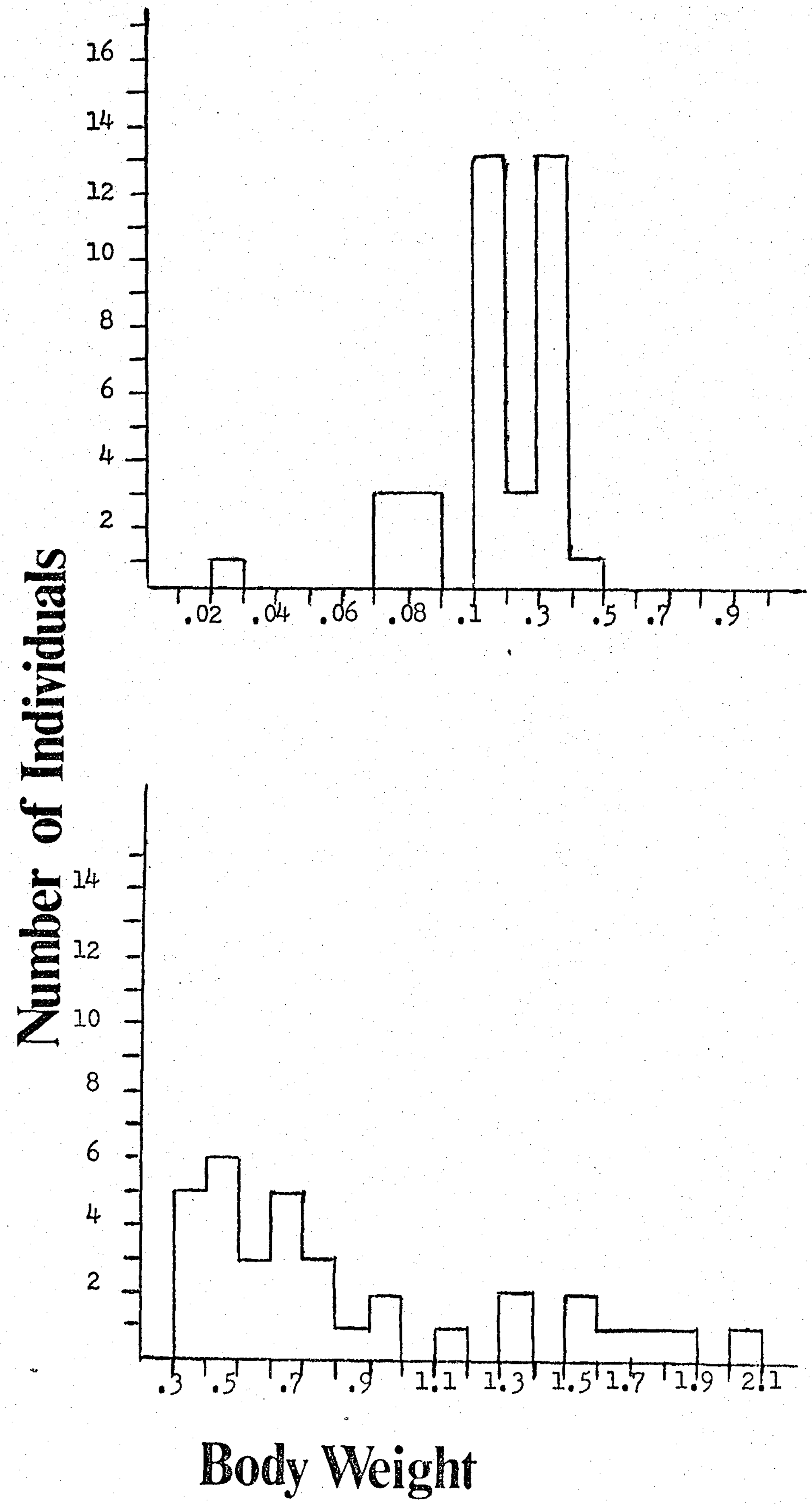

Number of Individuals
16
14
12
10
8
6
4
2
.02
.04
.06
.08
.1
.3
.5
.7
.9
14
12
10
8
6
4
2
.3
.5
.7
.9
1.1
1.3
1.5
1.7
1.9
2.1
Body Weight

Figure 7a: Number of Individual Females with clutch as a Function of Body Weight in grams for P. samuelis inhabiting T. funebralis. Information represents pooled data from March-October, 1973.

Figure 7b: Number of Individual Females with no clutch as a Function of Body Weight in grams for P. samuelis inhabiting T. funebralis. Information represents pooled data from March-October, 1973.

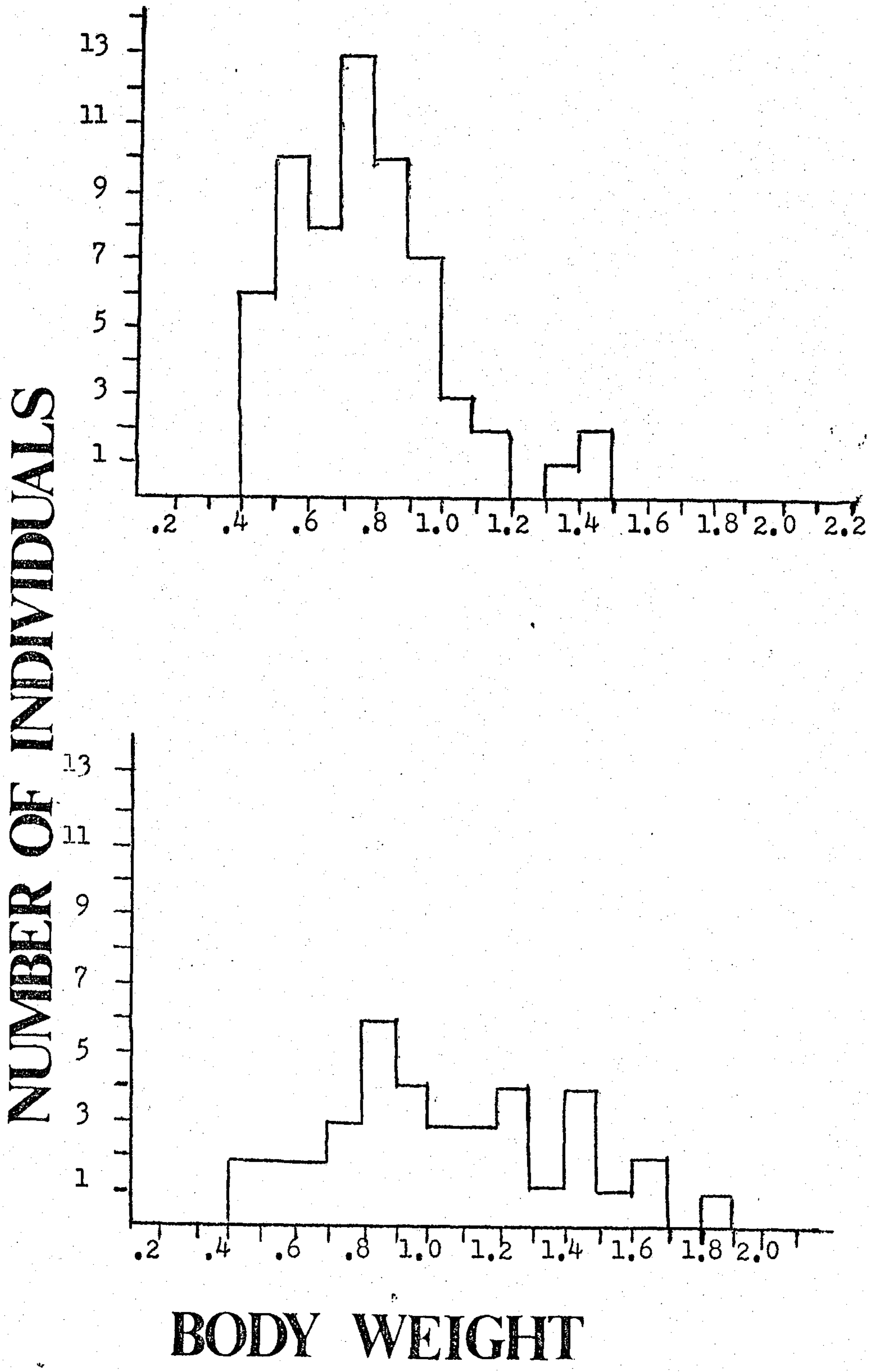

13
11
9
7
5
3
1
.2
.4
.6
.8
1.0
1.2
1.4
1.6
1.8
2.0
2.2
NUMBER OF INDIVIDUALS
13
11
9
7
5
3
1
.2
.4
.6
.8
1.0
1.2
1.4
1.6
1.8
2.0
BODY WEIGHT

Figure 8a: Number of Individual Juveniles as a Function of Body Weight in grams for P. *samuelis* inhabiting T. *funebralis*. Information represents pooled data from March-October, 1973.

Figure 8b: Number of Individual Males as a Function of Body Weight in grams for P. *samuelis* inhabiting T. *funebralis*. Information represents pooled data from March-October, 1973.

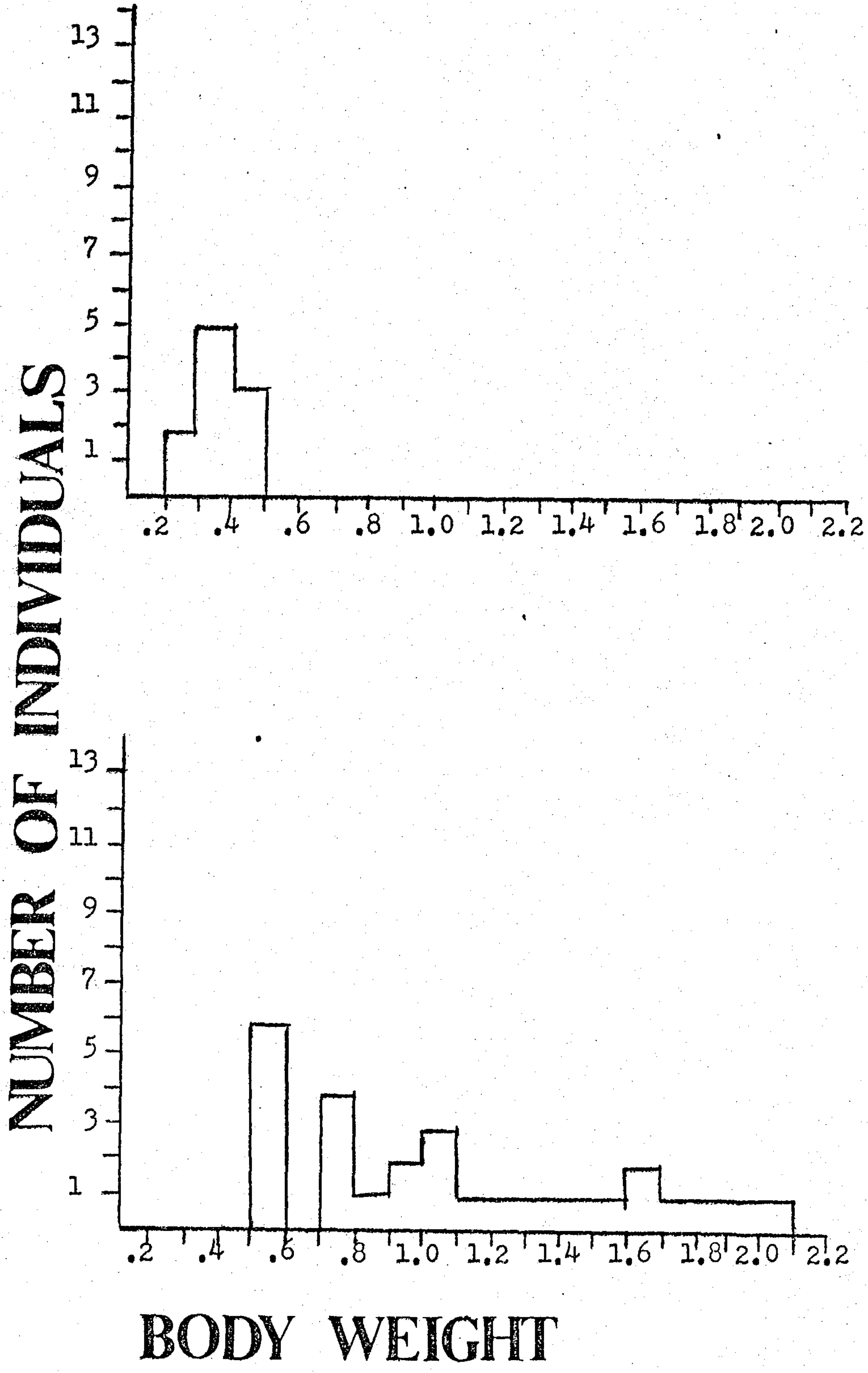

NUMBER OF INDIVIDUALS
13
11
9
7
5
3
1
.2
.4
.6
.8
1.0
1.2
1.4
1.6
1.8
2.0
2.2
13
11
9
7
5
3
1
.2
.4
.6
.8
1.0
1.2
1.4
1.6
1.8
2.0
2.2
BODY WEIGHT

Figure 9: Clutch Size as a Function of Body Weight in grams for Individual females of *P. samuelis* and *P. hirsutiusculus*. Information represents pooled data from March-April, 1973.

P. samuelis - X

P. hirsutiusculus -.

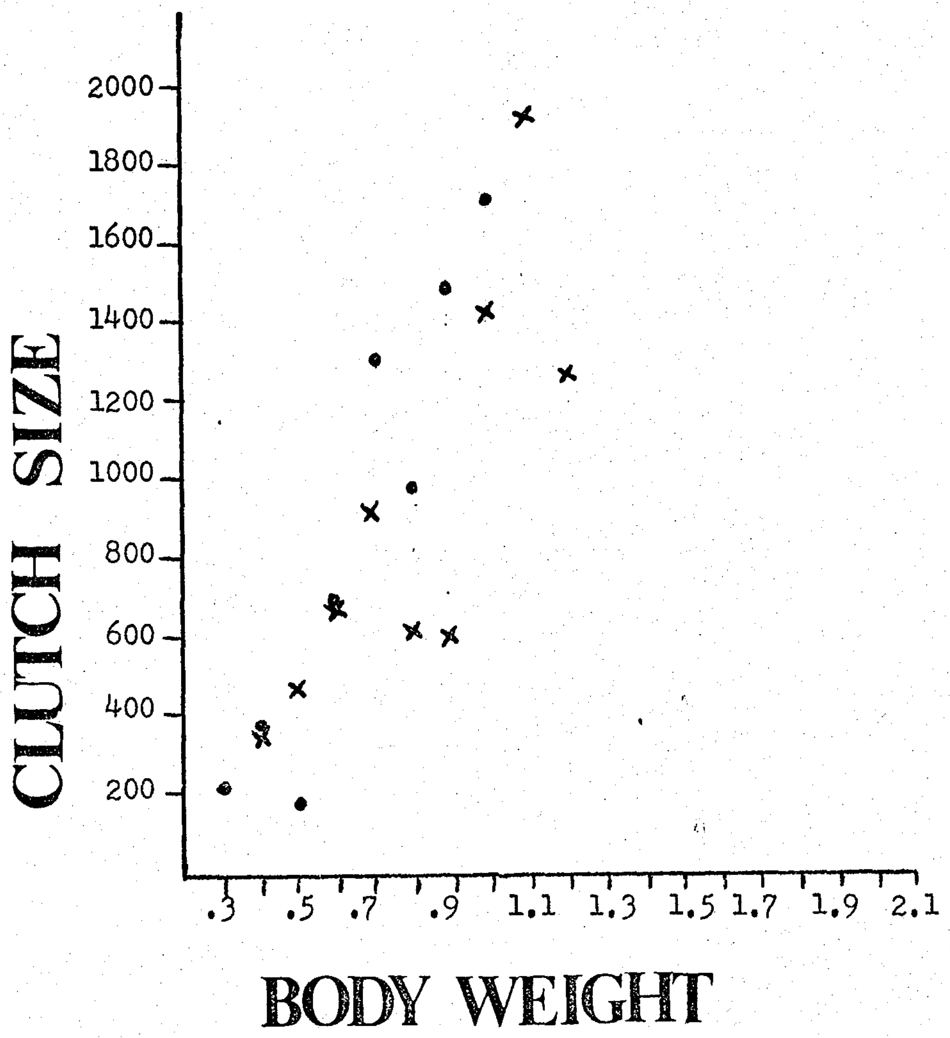

CLUTCH SIZE
2000
1800
1600
1400
1200
1000
800
600
400
200
.3
.5
.7
.9
1.1
1.3
1.5
1.7
1.9
2.1
BODY WEIGHT

Figure 10: Clutch Size as a Function of Body Weight for Individual females of *P. samuelis* and *P. hirsutiusculus*. Information represents pooled data from May-June, 1973.

P. samuelis - X

P. hirsutiusculus - •

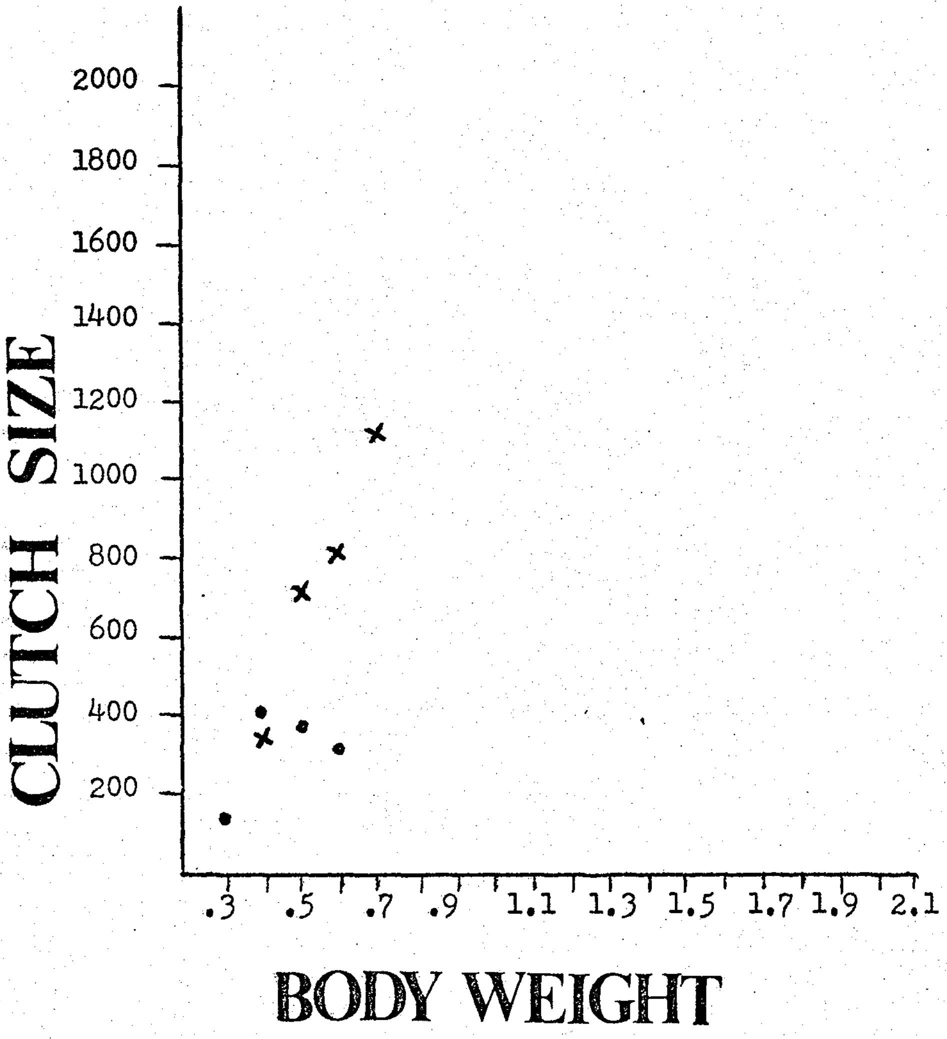
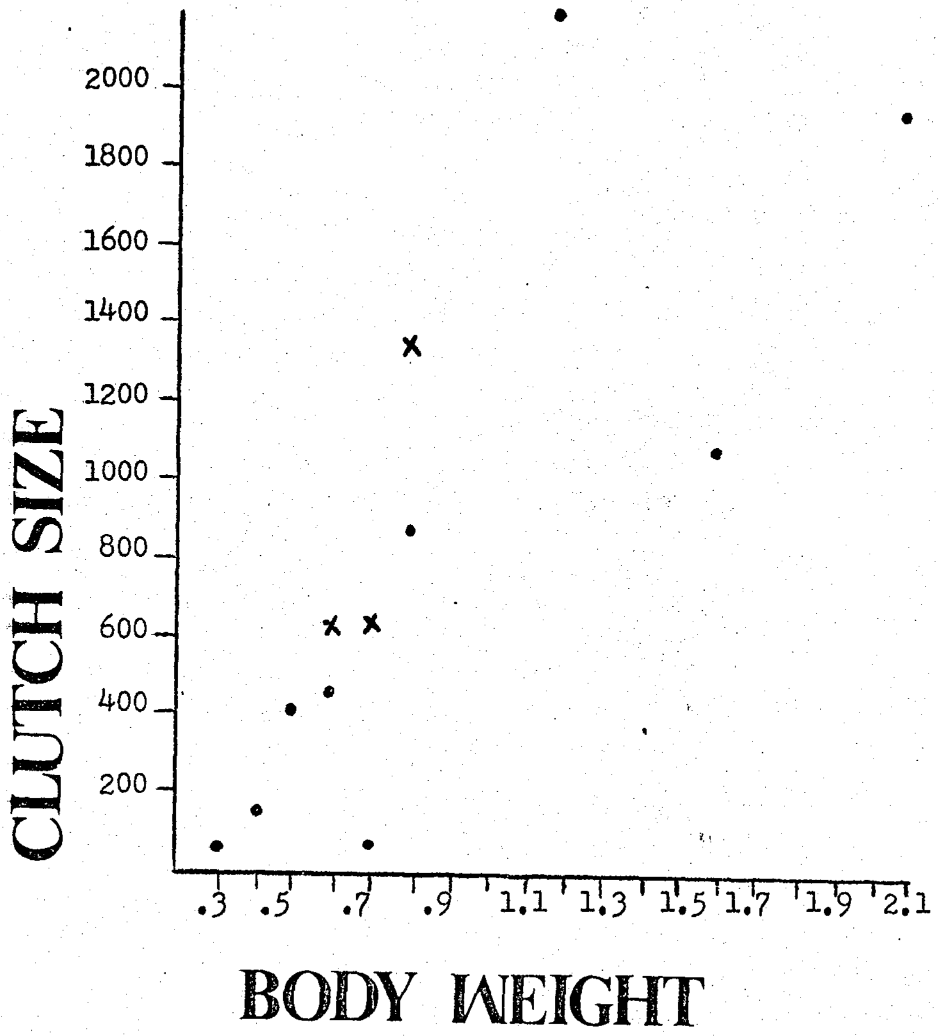

CLUTCH SIZE
2000
1800
1600
1400
1200
1000
800
600
400
200
.3
.5
.7
.9
1.1
1.3
1.5
1.7
1.9
2.1
BODY WEIGHT

Figure 11: Clutch Size as a Function of Body Weight in grams for Individual females of *P. samuelis* and *P. hirsutiusculus*. Information represents pooled data from July-August, 1973.

P. samuelis - X

P. hirsutiusculus - .


CLUTCH SIZE
2000
1800
1600
1400
1200
1000
800
600
400
200
.3
.5
.7
.9
1.1
1.3
1.5
1.7
1.9
2.1
BODY WEIGHT

species produced the same size clutch for similar body weights. Clutch size increased from 400 eggs at a body weight of .4 grams to 1,500 eggs at a body weight of 1.0 grams. The May-June period (Fig. 10) indicated the P. hirsutiusculus females producing 400 eggs at a body weight of .4 grams decreased to 300 eggs at a body weight of .6 grams while P. samuelis rose from a body weight of .7 grams producing 1,100 eggs. Figure 11 (July-August) indicated an initial even production of eggs for a given body weight before P. hirsutiusculus achieves the highest observed clutch of 2,200 eggs at a body weight of 1.1 grams. The highest observed clutch size for P. samuelis during this period was 1,300 eggs at a body weight of .8 grams.

Discussion

Size distribution and clutch size data confirm previous observations of P. samuelis and P. hirsutiusculus attaining sexual maturity at a small size (Bollay, 1964). Most females of both species were found to breed continuously from March-August although variable fecundities and females without clutch were observed. Hazlett (1970) indicated that P. bernhardus females breed continuously throughout the spring and summer months. He suggested this was not unusual for hermit crabs to breed continuously in times of environmental favorability. The clutch size data does not strongly suggest a seasonal change in clutch size for the observed six month period. Both species appear to produce similar clutch sizes for increasing body weight. More clutch size samples may have indicated a seasonality in egg production.

Considering the results of Tables 4 & 5 and Figures 5a-8b, it is reasonable to assume that P. samuelis adults (males and females with and without clutch) occupied Tegula shells in the .9-1.2 cm size range. A majority of these shells were occupied by females as suggested by the 1/4 sex ratio. Juveniles occupied smaller Tegula shells and were most abundant in August. Likewise, P. hirsutiusculus adults occupied both Tegula and Thais in the .4-.9 cm size range. Here, females inhabited twice as many shells as males. Juveniles occurred in Littorina shells and were most abundant in September. P. samuelis of the same body weight (for adults) inhabited shells larger than those occupied by P. hirsutiusculus. This last finding confirms previous behavioral observations regarding choice of adequate and inadequate shells and suggests selection for resource partioning. Vance (1972) noted that resource partitioning between sympatric species of hermit crabs minimize interspecific competition. The use of Littorina shells by juveniles of P. hirsutiusculus further suggests that resource partitioning occurs.

T. funebralis undergoes a seasonal increase in mortality due to predation by starfish in the summer, especially in August (Obrebski, 1973). This increases the seasonal availability of Tegula shells. Although previous results on clutch size did not indicate a strong seasonality in egg production, clearly there is a rise in number of Tegula shells occupied by P. samuelis from June to a peak in August.

Adequate data for testing the seasonal reoccurence of *P. samuelis* occupying increased numbers of vacant *Tegula* shells is not available. The lack of increase or peak occupancy of *Tegula* shells by *P. hirsutiusculus* is believed due to the competitive superiority of *P. samuelis* over *P. hirsutiusculus*.

FITNESS SET ANALYSIS

Fitness Set Method

The introductory remarks presented the concept of fitness set analysis. The reader is asked to return to that section for any clarification of methods presented below.

Behavioral and ecological data presented earlier indicated shell preference and shell changing behavior is common in *P. samuelis* and *P. hirsutiusculus*. That hermit crabs often change environments (shells) suggests a fine grained environment with respect to shells. Weight index data was gathered from body and shell weights of 57 *P. hirsutiusculus* occupying *Tegula* shells and 69 occupying *Thais*. This data was taken from pooled information derived from laboratory analysis of hermit crabs from March-October, 1973 (see Methods and Materials, ECOLOGY section). In turn, 137 *P. samuelis* occupying *Tegula* shells were similarly used and again represented information obtained from pooled data for March-October, 1973. *P. samuelis* having *Thais* shells were excluded as sample size was too small and reflected juvenile use. Thus, excluding *P. samuelis* from fitness set analysis. Data for fitness set analysis was taken from weight index information of 16 (41.7%) *P. hirsutiusculus* females with clutch occupying *Tegula* shells and 18 (59.3%) occupying *Thais*.

Fitness Set curves were obtained by taking the average clutch size (clutch size data reflected pooled information from March-

October, 1973) at each weight index interval and then fitting a curve through the average points. Conversion to a fitness set was achieved by plotting the fitness component (as measured by the average clutch size at a given weight index) in environment one (W_1; *Thais*) against the fitness component (as measured by the average clutch size at the same given weight index) in environment two (W_2; *Tegula*).

Results

The observed weight index for *P. hirsutiusculus* indicated two norms in the .5-1.6 range for individuals occupying *Thais* and a 1.0-2.0 range for individuals inhabiting *Tegula* shells (Fig. 12). *P. samuelis* utilizing *Tegula* shells were observed in the 2.0-2.5 weight index range (Fig. 13). As shown in Figure 14a the frequency distribution of *P. hirsutiusculus* females with clutch inhabiting *Tegula* shells appeared not to be skewed to any particular weight indexes. The average weight indexes inhabited was in the 1.9 range. In contrast, the frequency of *P. hirsutiusculus* (females with clutch) weight indexes in *Thais* were skewed towards smaller indexes (Fig. 14a). *P. samuelis* females with clutch in *Tegula* shells exhibited an overlap in weight indexes with respect to *Tegula* used by *P. hirsutiusculus* females with clutch. *P. samuelis* (females with clutch) utilized most *Tegula* shells conferring a weight index above 1.9.

Figure 15 indicated that *P. samuelis* males and females with

Figure 12: Total Number of Individuals of *P. hirsutiusculus* as a Function of Weight Index inhabiting designated shells. Information represents pooled data from March-October, 1973.

T. funebralis = – – – –

T. emarginata = ———

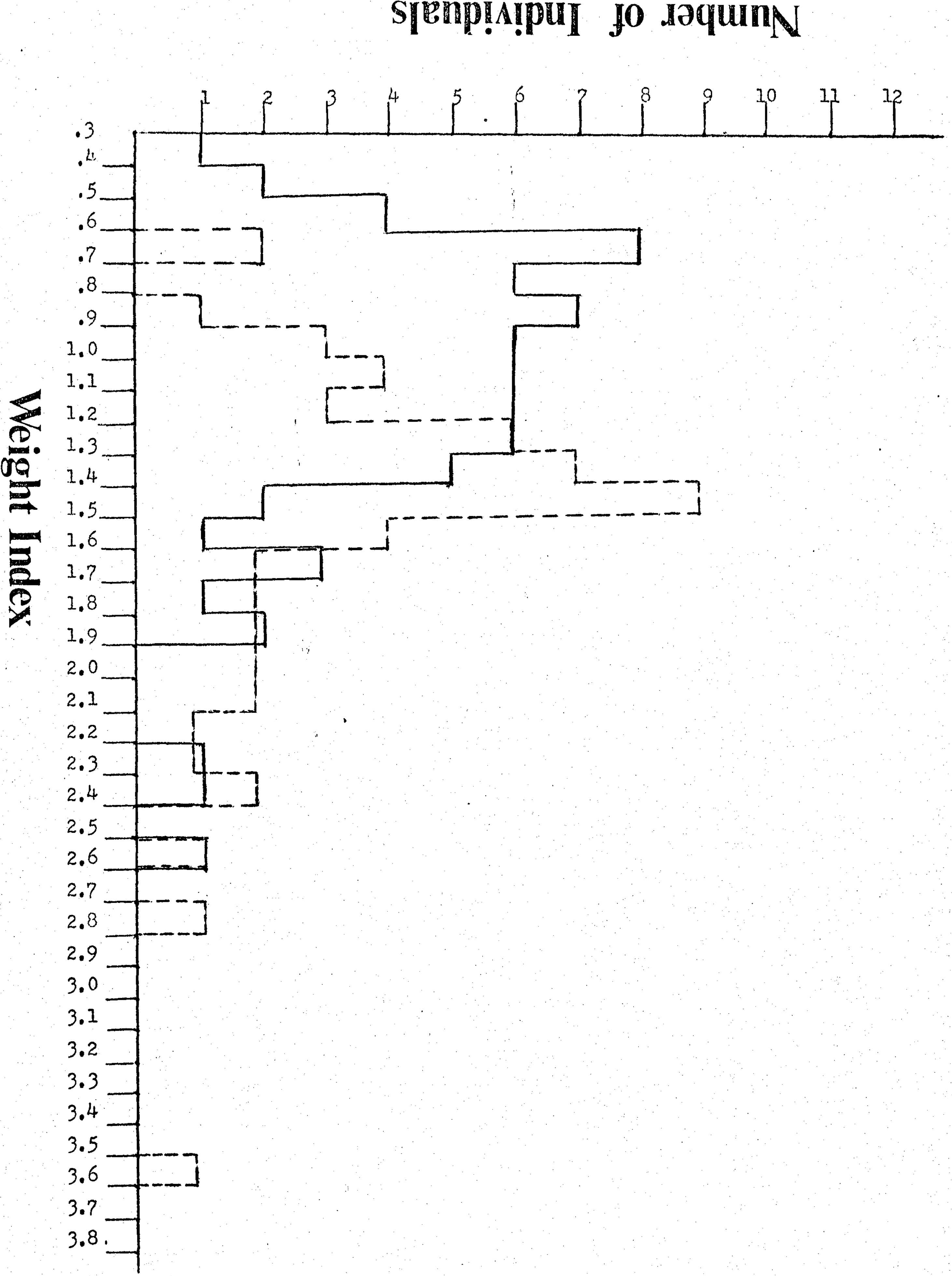

Number of Individuals
1
2
3
4
5
6
7
8
9
10
11
12
Weight Index
.3
.4
.5
.6
.7
.8
.9
1.0
1.1
1.2
1.3
1.4
1.5
1.6
1.7
1.8
1.9
2.0
2.1
2.2
2.3
2.4
2.5
2.6
2.7
2.8
2.9
3.0
3.1
3.2
3.3
3.4
3.5
3.6
3.7
3.8

Figure 13: Total Number of Individual P. samuelis as a Function of Weight Index inhabiting T. funebralis shells. Information represents pooled data from March-October, 1973.

T. funebralis = ———

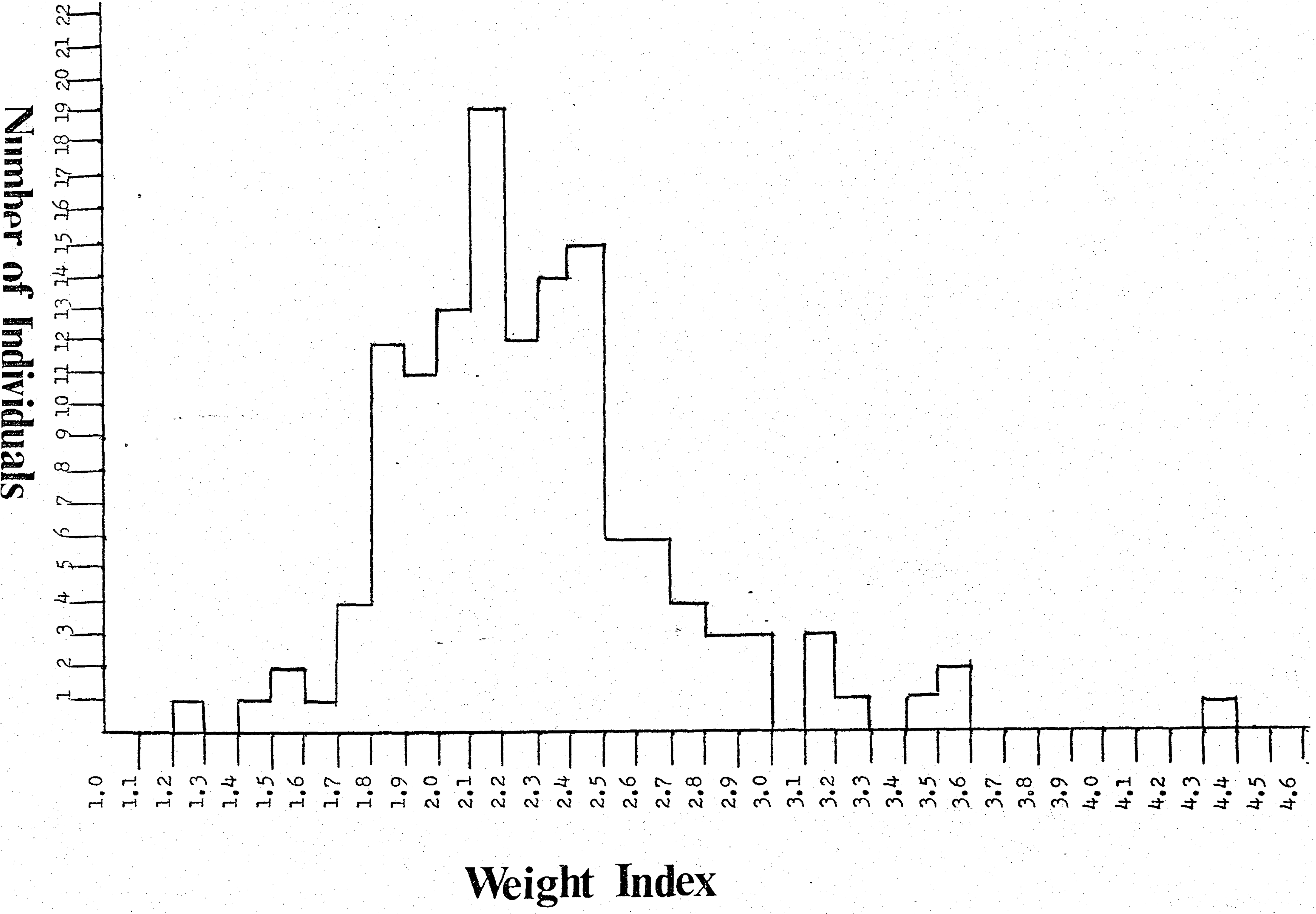

Number of Individuals
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
1.0
1.1
1.2
1.3
1.4
1.5
1.6
1.7
1.8
1.9
2.0
2.1
2.2
2.3
2.4
2.5
2.6
2.7
2.8
2.9
3.0
3.1
3.2
3.3
3.4
3.5
3.6
3.7
3.8
3.9
4.0
4.1
4.2
4.3
4.4
4.5
4.6
Weight Index

Figure 14a: Number of Individual Females with clutch of *P. hirsutiusculus* as a Function of Weight Index inhabiting designated shells. Information represents pooled data taken from Weight Index data.

T. emarginata = ————

T. funebralis = — — — —

Figure 14b: Number of Individual Females with clutch of *P. samuelis* as a Function of Weight Index inhabiting *Tegula* shells.

T. funebralis = ————

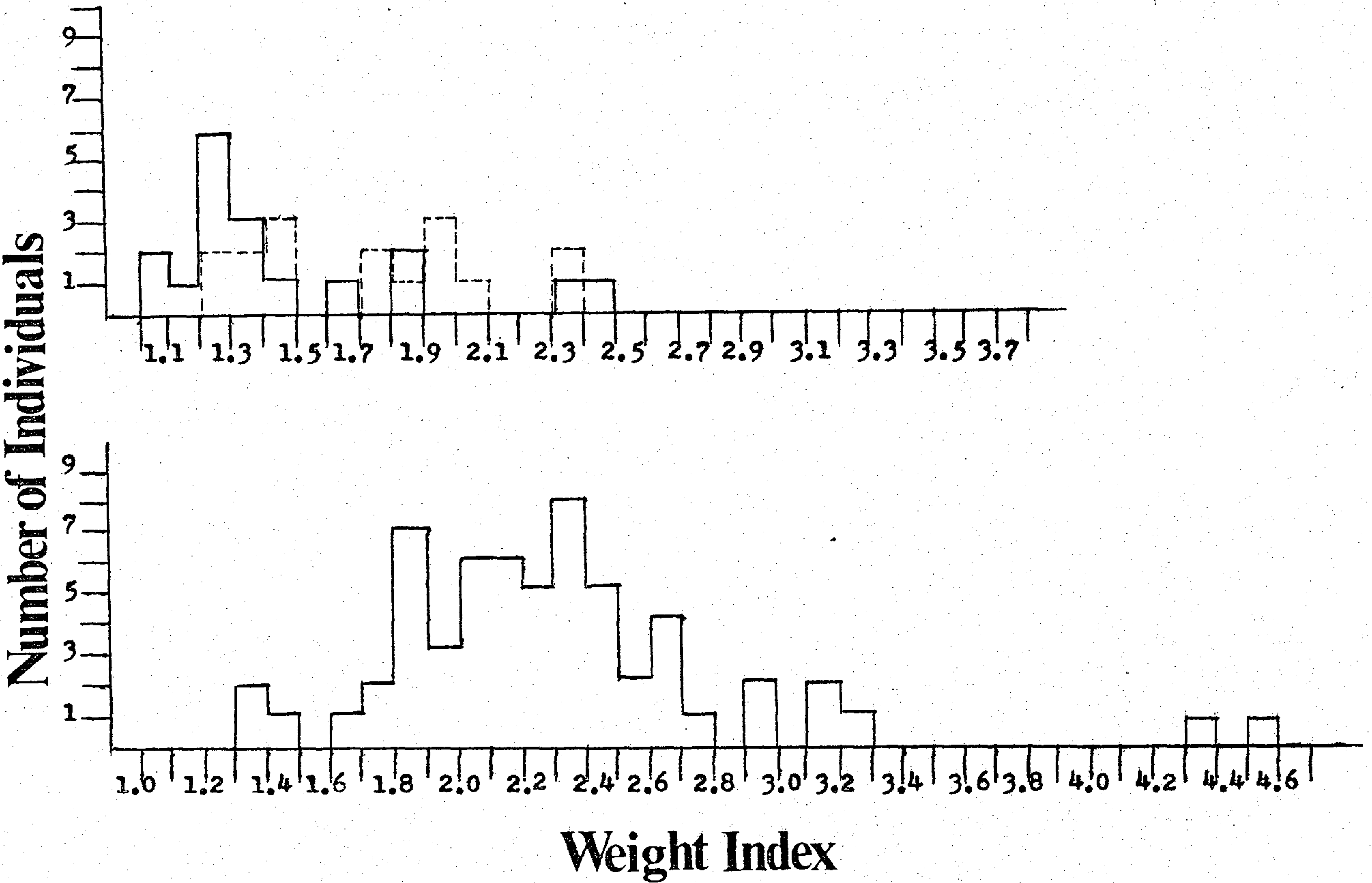

Number of Individuals
9
7
5
3
1
1.1
1.3
1.5
1.7
1.9
2.1
2.3
2.5
2.7
2.9
3.1
3.3
3.5
3.7
9
7
5
3
1
1.0
1.2
1.4
1.6
1.8
2.0
2.2
2.4
2.6
2.8
3.0
3.2
3.4
3.6
3.8
4.0
4.2
4.4
4.6
Weight Index

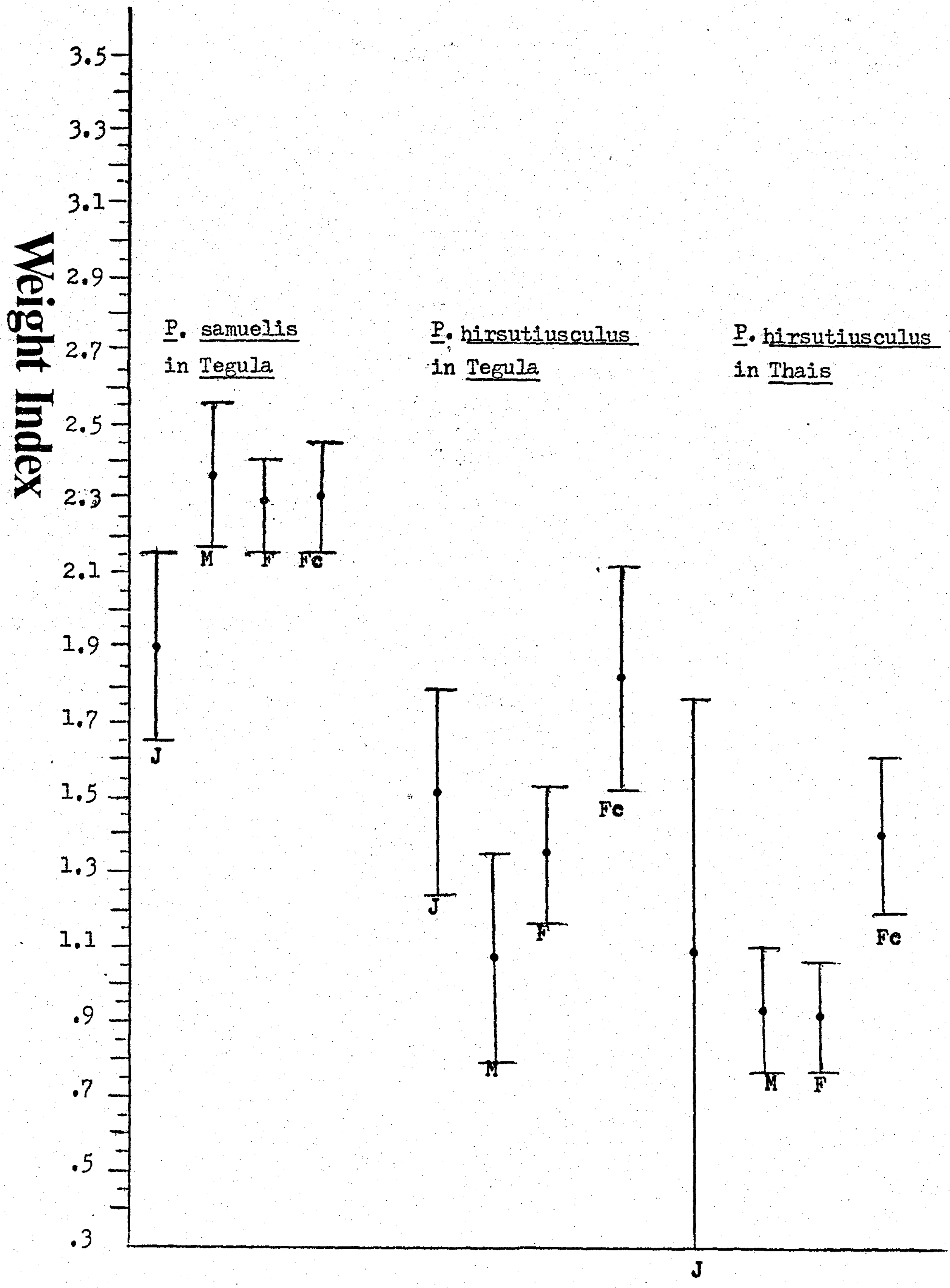
Figure 15: Mean Weight Indexes and 95% Confidence Limits for P. samuelis and P. hirsutiusculus in designated shells. Information represents pooled data for each species: March-October, 1973.

J = Juveniles

M = Males

F = Females without clutch

Fc = Females with clutch


Weight Index
3.5
3.3
3.1
2.9
2.7
2.5
2.3
2.1
1.9
1.7
1.5
1.3
1.1
.9
.7
.5
.3
P. samuelis
in Tegula
P. hirsutiusculus
in Tegula
P. hirsutiusculus
in Thais
J
M
F
Fc
J
M
F
Fc
J
M
F
Fc

and without clutch had the same mean weight index range of 2.3. Juveniles occupied a mean weight index of 1.9. P. hirsutiusculus inhabiting Tegula indicated variable mean weight indexes. Females with clutch occupied a higher mean weight index (1.8) than females without clutch at 1.35. Males and Juveniles were noted at a mean weight index of 1.1 and 1.55, respectively. P. hirsutiusculus females with clutch in Thais occupied a lower mean weight index (1.4) than in Tegula. P. hirsutiusculus females without clutch and males were found at a mean weight index of .9 in Thais. Juveniles utilized shells that gave a mean weight index of 1.1.

Figure 16 in which clutch size (the independent estimate of fitness) was plotted as a function of weight index (phenotypic expression) for P. hirsutiusculus over the two environments (Thais and Tegula shells) reflected maximum peaks occuring at 1.6 and 1.8, respectively. In turn, P. samuelis in Tegula indicated a maximum peak at 2.3 (Fig. 17). These peaks indicate the existing optimal phenotypes over each environment for both species. Figures 18-20 and 21-23 were included as they represented bimonthly breakdowns of Figures 16 & 17. In March-April (Fig. 18) for P. hirsutiusculus clutch sizes reached two peaks at 1,450 eggs for a weight index of .7 and 1,400 eggs at a weight index of 1.9. P. hirsutiusculus over the period May-June (Fig. 19) achieved maximum average clutch sizes of 1,050 eggs at a weight index of .7 and 2,000 eggs at a weight index of 1.8. The July-August period indicated one maximum peak of 2,200

Figure 16: Reproductive Fitness Curve for P. hirsutiusculus inhabiting T. funebralis and T. emarginata shells. Curves were obtained by taking the average clutch size at each weight index interval from pooled data (March-August, 1973) and fitting a curve through the average points.

T. funebralis = – – – –
T. emarginata = ———

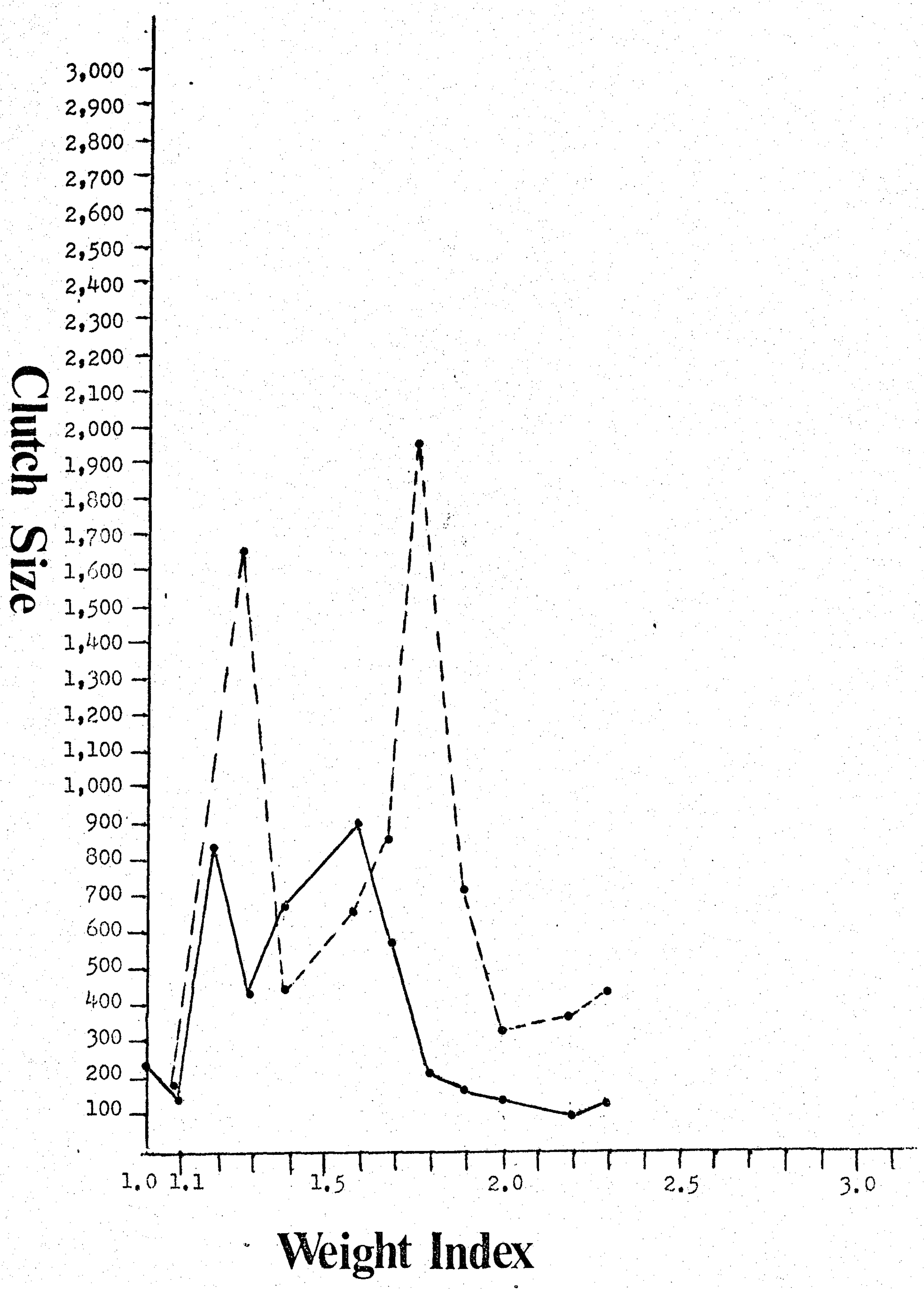

Clutch Size
3,000
2,900
2,800
2,700
2,600
2,500
2,400
2,300
2,200
2,100
2,000
1,900
1,800
1,700
1,600
1,500
1,400
1,300
1,200
1,100
1,000
900
800
700
600
500
400
300
200
100
1.0
1.1
1.5
2.0
2.5
3.0
Weight Index

Figure 17: Reproductive Fitness Curve for *P. samuelis* inhabiting *Tegula* shells. Curves were obtained by taking the average clutch size at each weight index interval from pooled data (March-August, 1973) and fitting the curve through the average points.

T. funebralis = ________

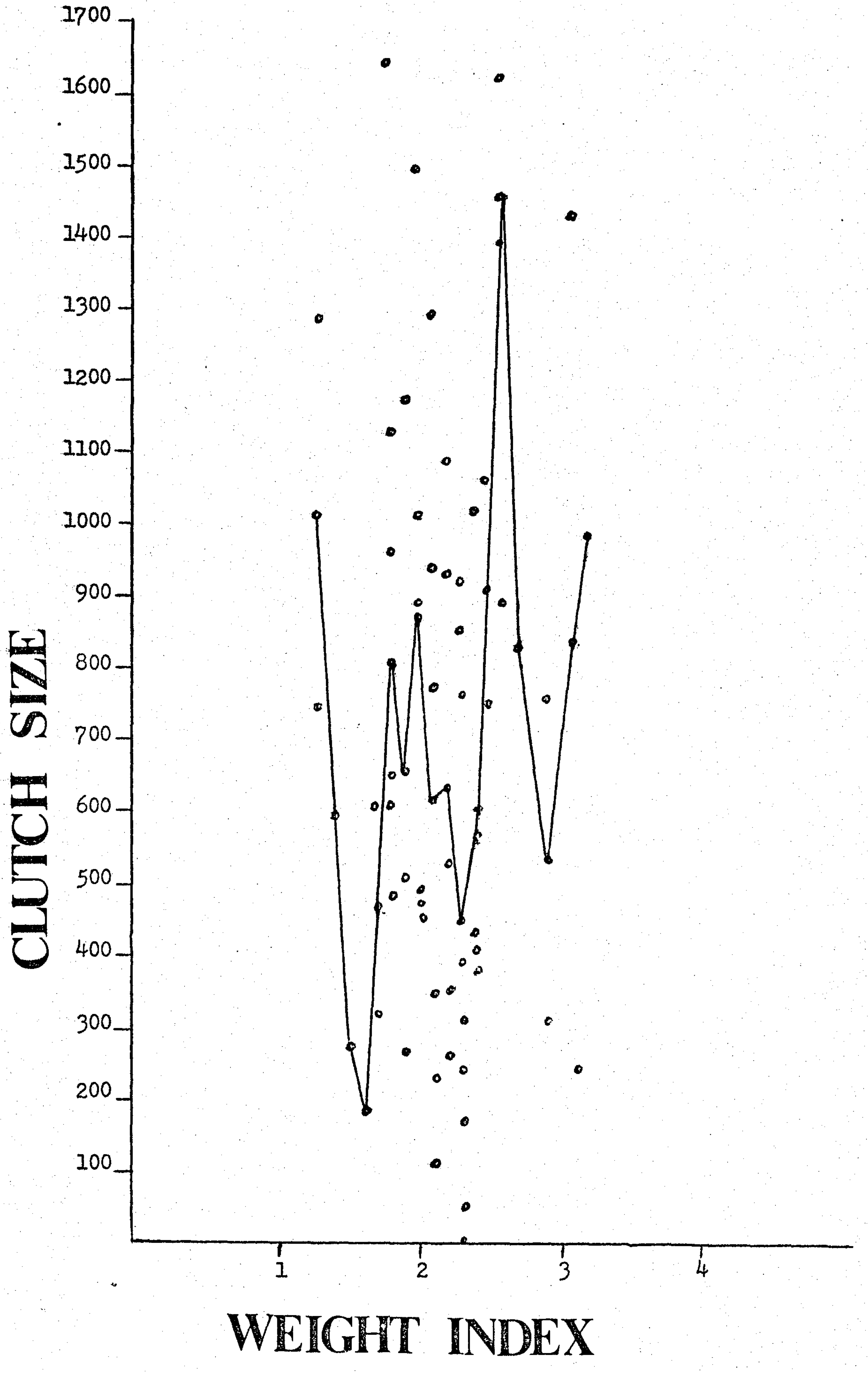

1700
1600
1500
1400
1300
1200
1100
1000
900
800
700
600
500
400
300
200
100
CLUTCH SIZE
1
2
3
4
WEIGHT INDEX

Figure 18: Reproductive Fitness Curve for *P. hirsutiusculus* inhabiting both *T. funebralis* and *T. emarginata* shells during March-April, 1973. The curve represents a bimonthly breakdown of Figure 16.

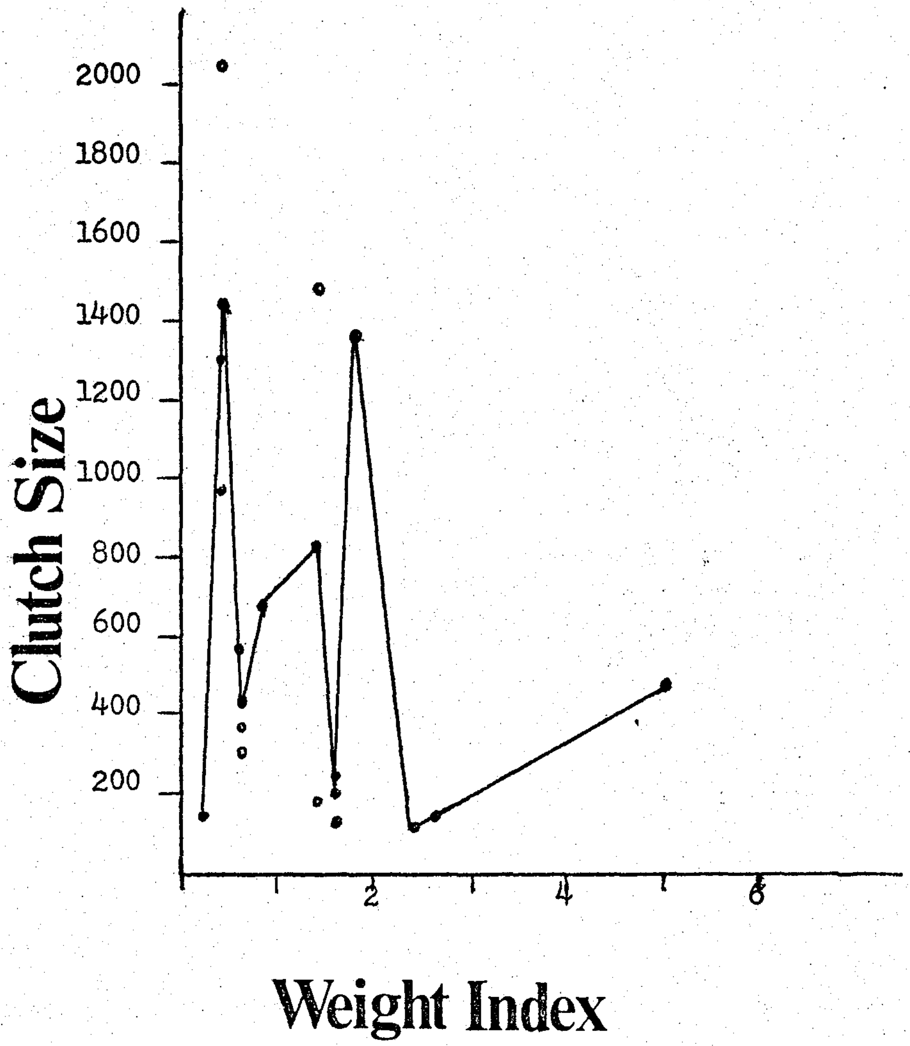

Clutch Size
2000
1800
1600
1400
1200
1000
800
600
400
200
2
4
6
Weight Index

Figure 19: Reproductive Fitness Curve for _P_. _hirsutiusculus_ inhabiting _T_. _funebralis_ and _T_. _emarginata_ shells during May-June, 1973. The curve represents a bimonthly breakdown of Figure 16.

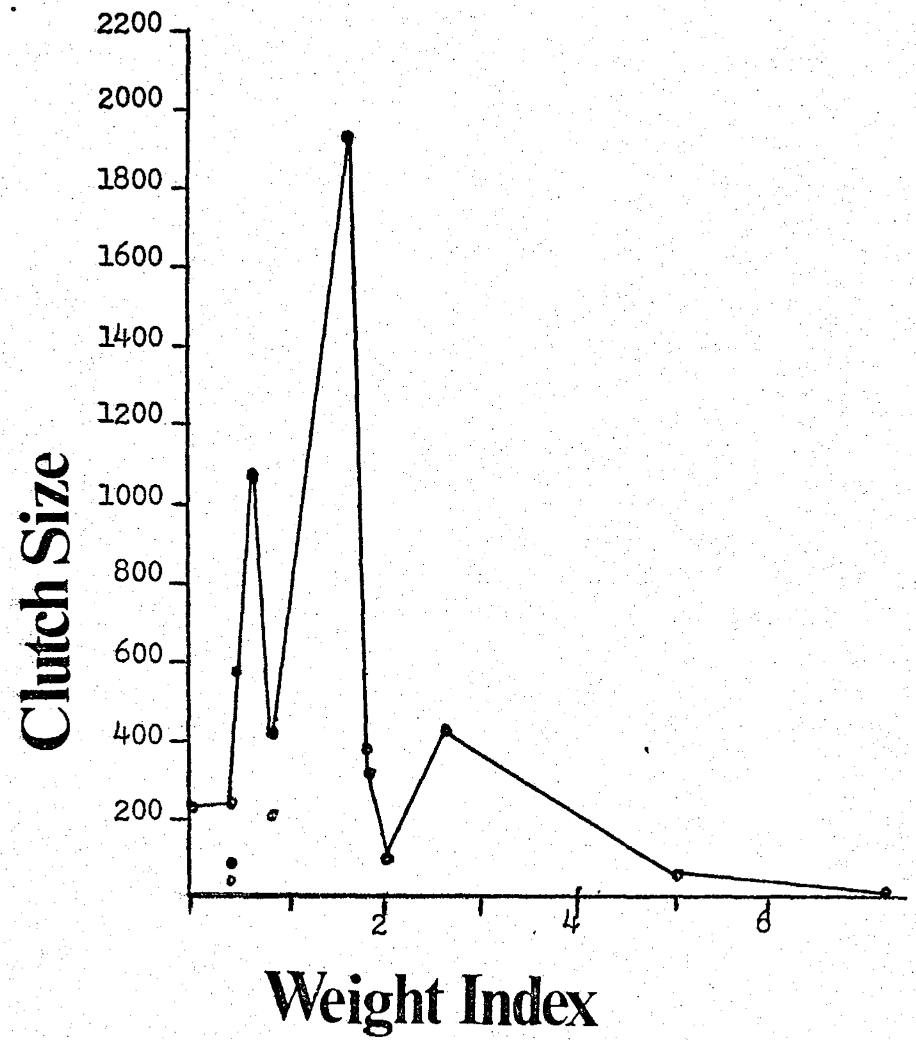

Clutch Size
2200
2000
1800
1600
1400
1200
1000
800
600
400
200
2
4
6
Weight Index

Figure 20: Reproductive Fitness Curve for *P. hirsutiusculus* inhabiting *T. funebralis* and *T. emarginata* shells during July-August, 1973. The curve represents a bimonthly breakdown of Figure 16.

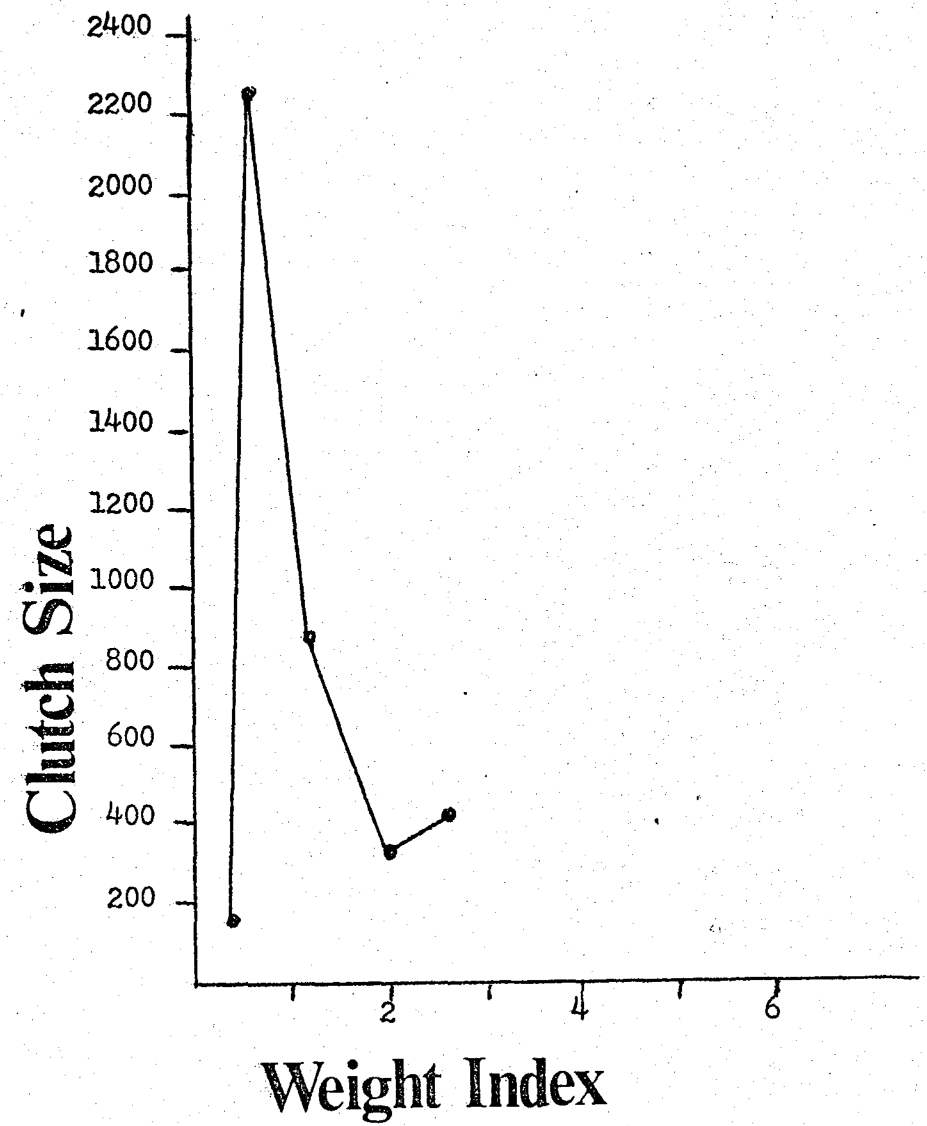

2400
2200
2000
1800
1600
1400
1200
1000
800
600
400
200
Clutch Size
2
4
6
Weight Index

Figure 21: Reproductive Fitness Curve for *P. samuelis* inhabiting *T. funebralis* shells during March-April, 1973. The curves represent a bimonthly breakdown of Figure 17.

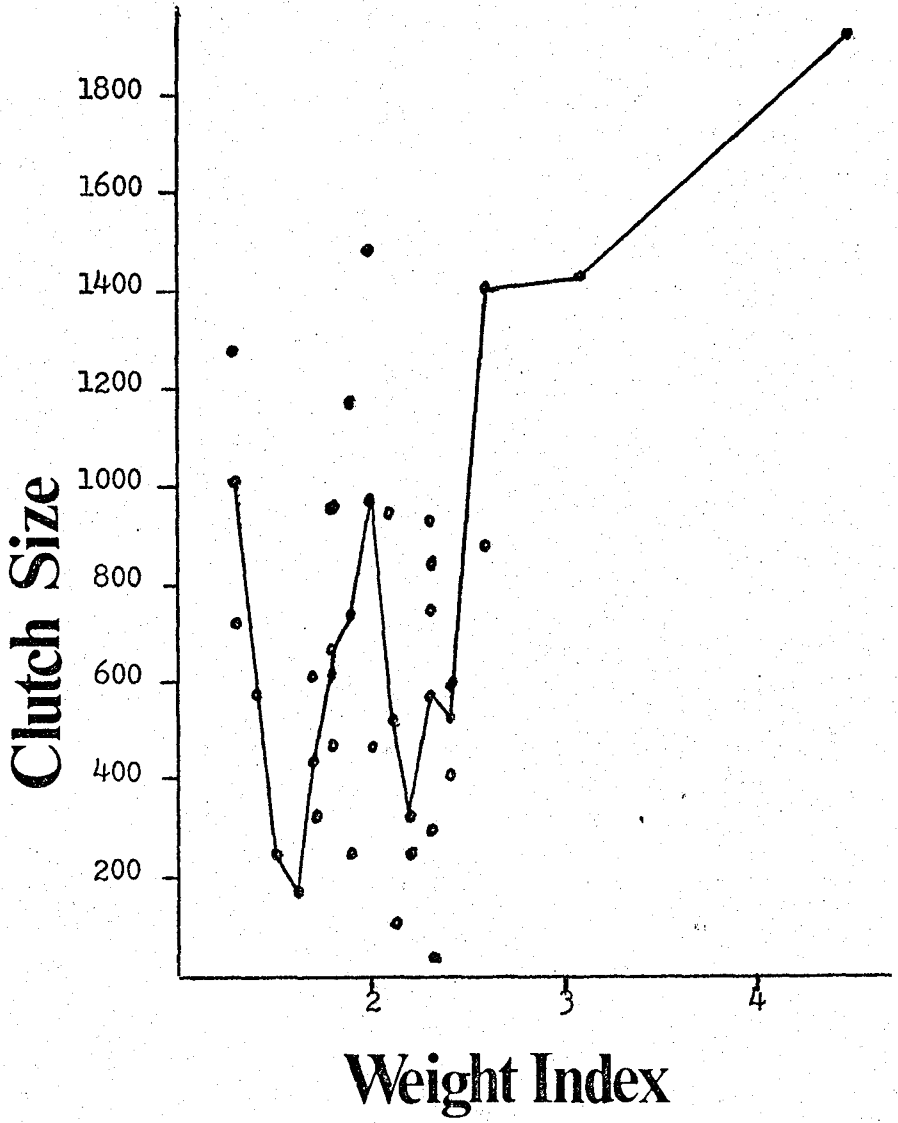

Clutch Size
1800
1600
1400
1200
1000
800
600
400
200
2
3
4
Weight Index

Figure 22: Reproductive Fitness Curve for P. samuelis inhabiting T. funebralis shells during May-June, 1973. The curve represents a bimonthly breakdown of Figure 17.

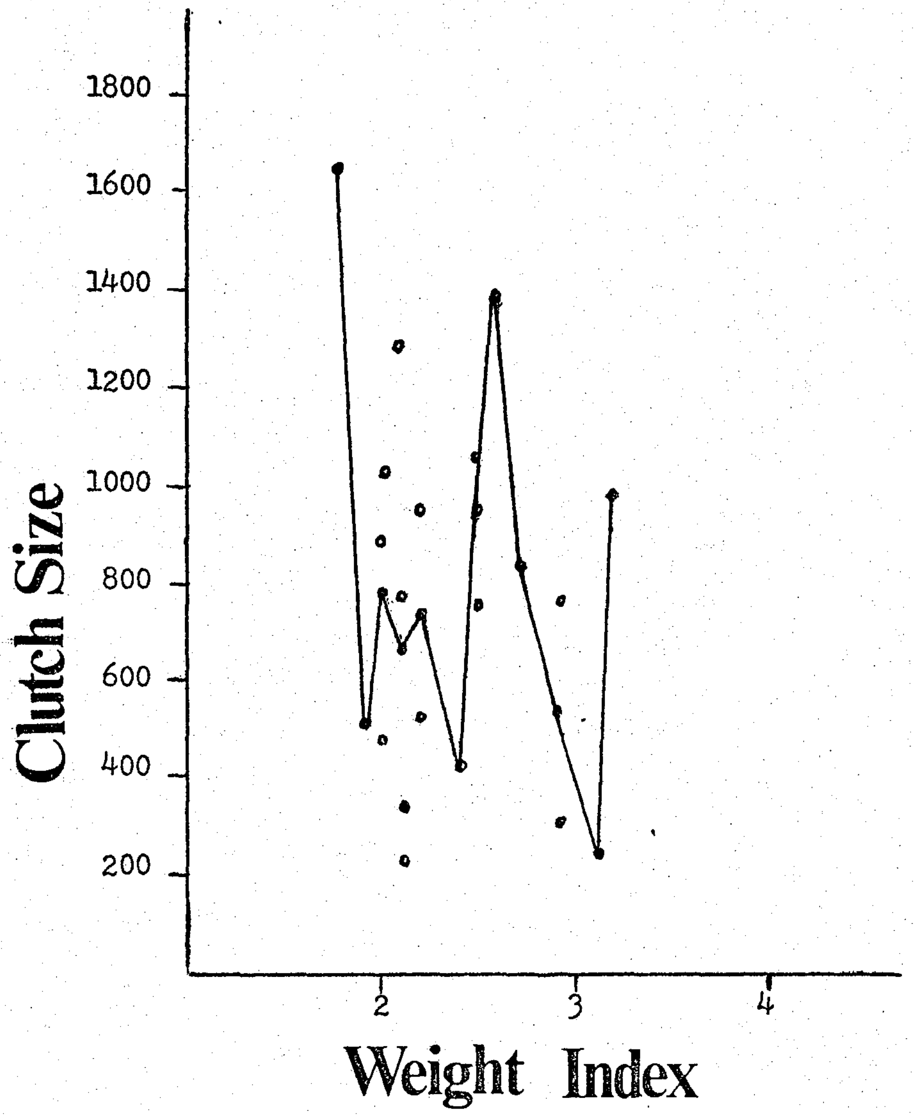
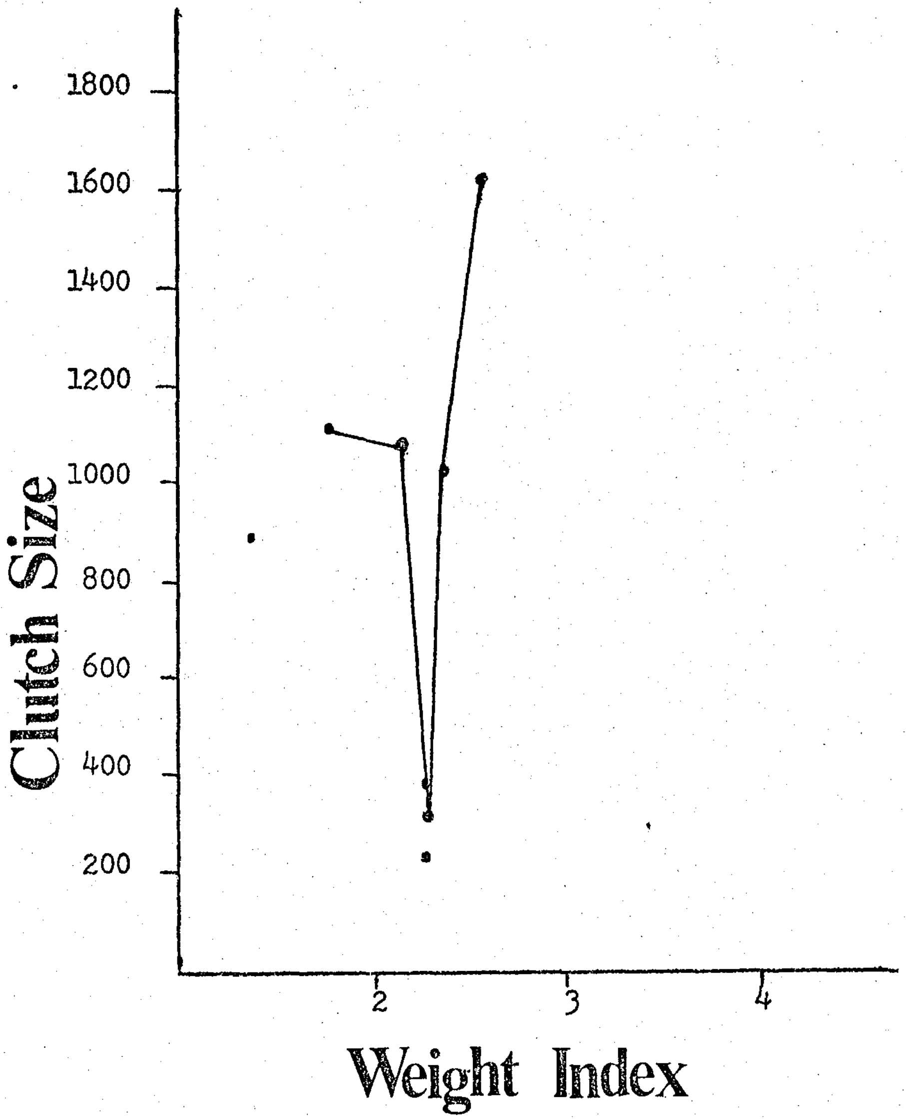

Clutch Size
1800
1600
1400
1200
1000
800
600
400
200
2
3
4
Weight Index

Figure 23: Reproductive Fitness Curve for P. samuelis inhabiting T. funebralis shells during July-August, 1973. The curve represents a bimonthly breakdown of Figure 17.

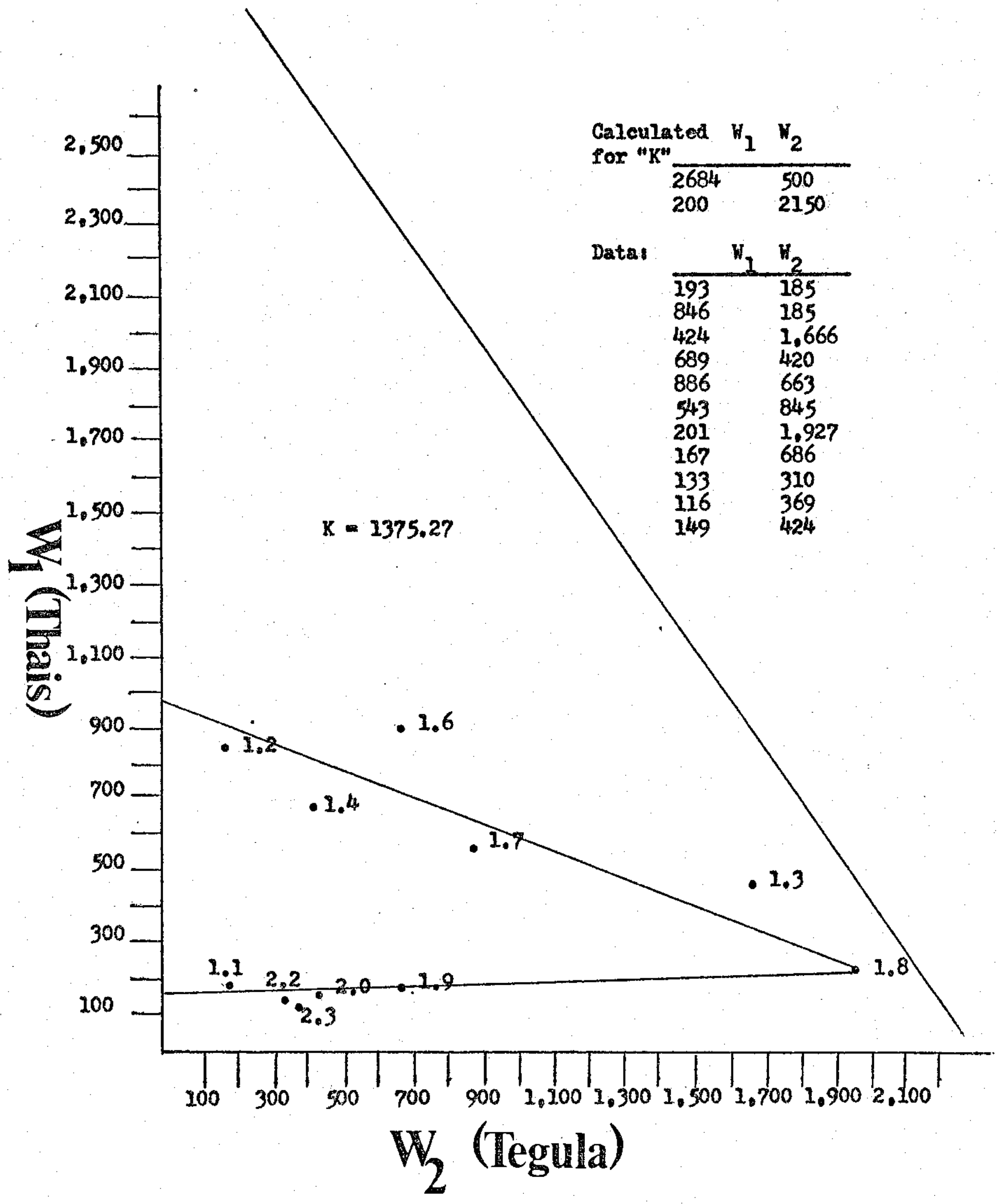

Clutch Size
1800
1600
1400
1200
1000
800
600
400
200
2
3
4
Weight Index

at a weight index of .9 for P. hirsutiusculus (Fig. 20). The period of March-April (Fig. 21) for P. samuelis reflected two peak weight indexes of 1.9 and 2.5 that produced 1,000 and 1,500 eggs, respectively. P. samuelis for May-June (Fig. 22) indicated maximum weight indexes of 1.6 and 2.6 that each yielded 1,500 eggs. In Figure 23 (July-August) two peaks of 1,100 eggs for a weight index of 1.8 and 1,600 eggs at an indexes of 2.6 were noted for P. samuelis.

Transformation to a fitness set (Fig. 24) for P. hirsutiusculus indicated the existing optimal phenotypes were those in Tegula shells and was convex. The adaptive function (expressed as a linear function) for a fine grained environment, was almost tangent to the fitness set at a weight index of 1.8 in which the observed fecundity was greatest. That the adaptive function almost touches the fitness set indicated that the carrying capacity of the environment for a given phenotype has been met. Moreover, this suggests a highly preferential optimal strategy favoring reproduction in Tegula shells by P. hirsutiusculus.

Regressions (Sokal and Rohlf, 1969) of clutch size on weight index for Tegula occupied shells over both species are represented by Figures 25 & 26. For P. hirsutiusculus the regression was not significant ($0.4 < p < 0.2$) while in the case of P. samuelis it was significant ($.01 < p < .001$). This indicated for P. samuelis that clutch size increases as weight index increases. However, there

Figure 24: Reproductive Fitness Set for P. hirsutiusculus. Points represent average clutch size at designated weight indexes in both environments. The fitness set was drawn by rendering a linear adaptation of lines connecting designated points. Information represents pooled data from March-August, 1973.



Calculated for "K"	W_1	W_2
	2684	500
	200	2150

Data:	W_1	W_2
	193	185
	846	185
	424	1,666
	689	420
	886	663
	543	845
	201	1,927
	167	686
	133	310
	116	369
	149	424

Figure 25: Regression for *P. hirsutiusculus* females with clutch occupying *Tegula* shells during March-August, 1973. Points represent individual females taken from pooled data (March-August, 1973.)

t value = 1.137

n = 9 groups; for n-2 degrees of freedom = 7

$0.4 < p < 0.2$

(.896) (1.415)

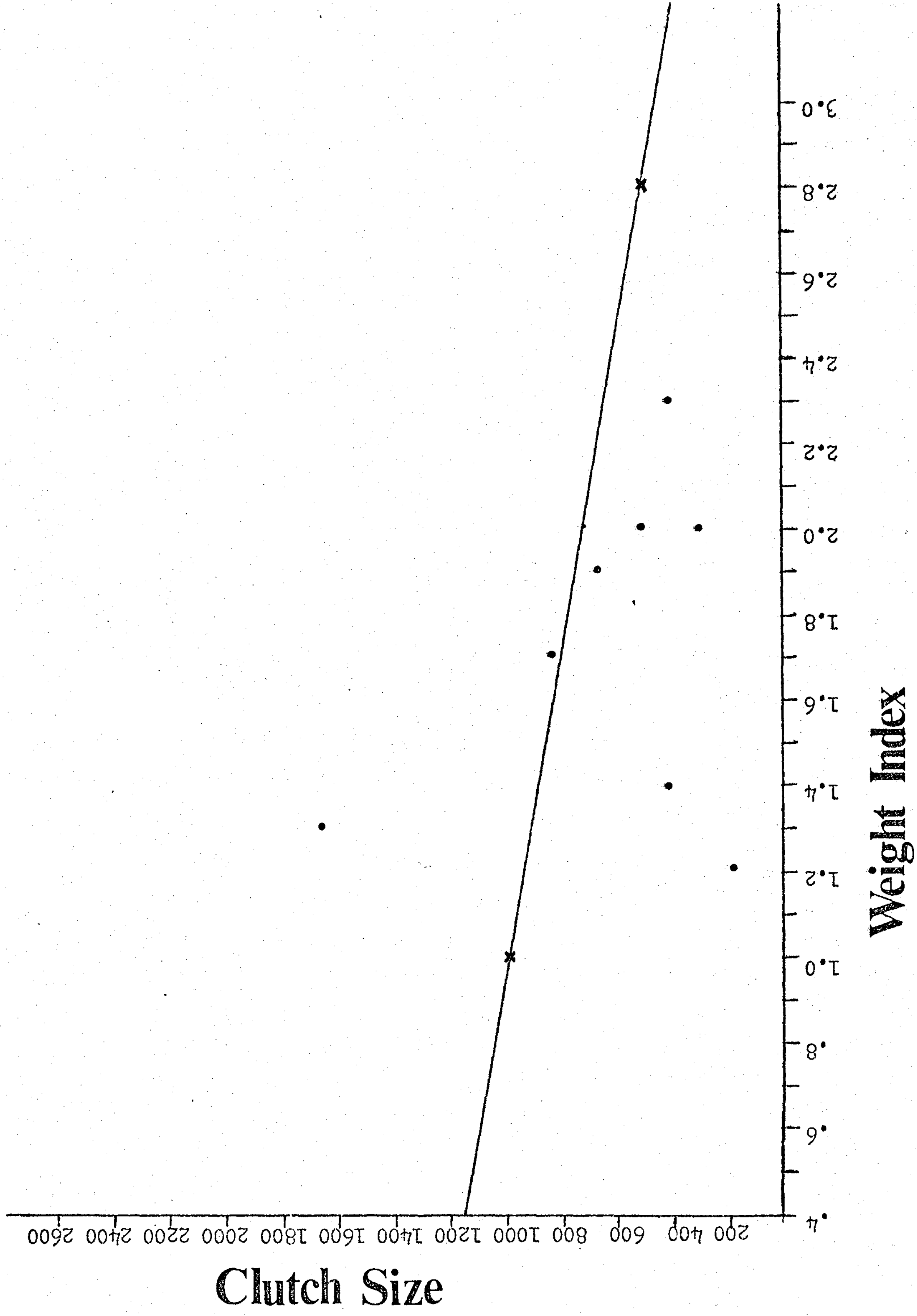

Weight Index
.4
.6
.8
1.0
1.2
1.4
1.6
1.8
2.0
2.2
2.4
2.6
2.8
3.0
Clutch Size
200
400
600
800
1000
1200
1400
1600
1800
2000
2200
2400
2600

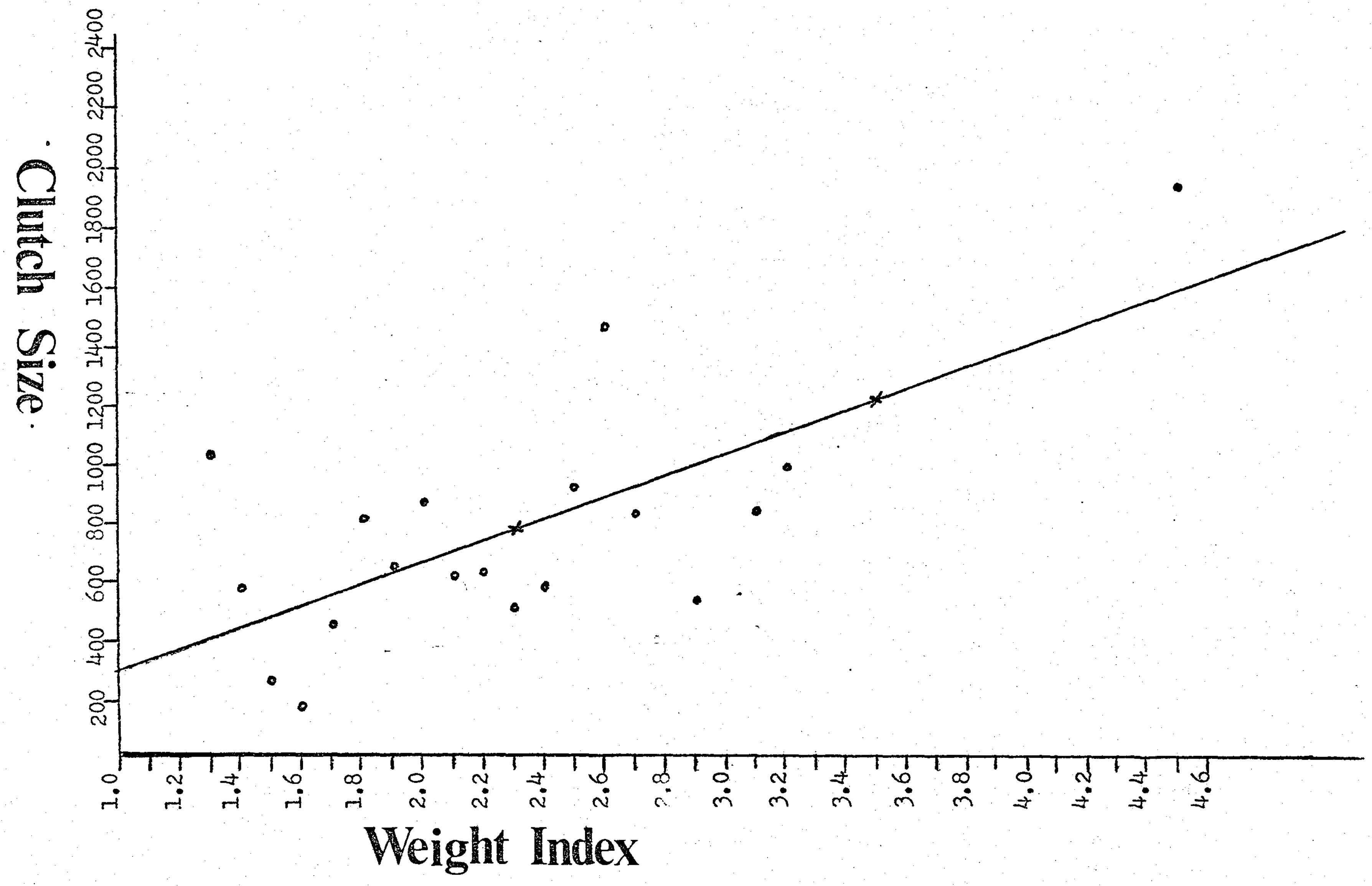
Figure 26: Regression for P. samuelis females with clutch occupying Tegula shells during March-August, 1973. Points represent individual females taken from pooled data (March-August, 1973.)

t value = 3/878

n = 8 groups; for n-2 degress of freedom = 6

$.01 < p < .001$

(3.70) (5.959)


Clutch Size
200
400
600
800
1000
1200
1400
1600
1800
2000
2200
2400
1.0
1.2
1.4
1.6
1.8
2.0
2.2
2.4
2.6
2.8
3.0
3.2
3.4
3.6
3.8
4.0
4.2
4.4
4.6
Weight Index

is no indication of increasing clutch size in relation to increasing weight index for P. hirsutiusculus, suggesting that larger Tegula shells in relation to body size do not increase fecundity. Data is not available for P. samuelis occupying shells shared by P. hirsutiusculus primarily because of P. samuelis' almost exclusive utilization of Tegula shells.

Discussion

When clutch size is used as a measure of fitness for P. hirsutiusculus the resulting fitness set predicts an optimum weight index that does not correspond with the most abundant weight indexes for that given environment (Tegula) in the natural population. These results suggest alternate interpretations: (1) that clutch size is not an accurate measure of fitness owing to highly variable fecundities, pooling of data and/or sampling error; or (2) females with clutch occupy more optimal shells than the remainder of the population. Figures 14 & 15 results favor this last proposition as P. hirsutiusculus females with clutch on an average occupied higher weight indexes. Moreover, one would expect reduced fecundity associated with occupying small shells to constitute a strong selective force promoting evolution of mechanisms for obtaining larger more optimal shells (Vance, 1972a).

Figure 24 indicated that fitness was increased for P. hirsutiusculus by occupying Tegula over Thais shells. The confered clutch size in *Tegula* being almost double for the same weight index in *Thais*. This strongly suggests that since fitness is greater in *Tegula* shells one may expect a shell preference of *Tegula* by *P. hirsutiusculus*. But, it is clearly evident that *P. samuelis* used *Tegula* shells confering a weight index of 1.9 and greater. Since *P. samuelis* is always dominant in shell changing encounters with *P. hirsutiusculus* (as shown in behavioral experiments) this suggests that the latter were limited in increasing reproductive potential by occupying larger *Tegula* shells. Indeed, as the weight index increases beyond 1.8 the fecundity of *P. hirsutiusculus* decreases very rapidly (Figs. 16 and 18-20) support this observation. In combining the above results there is an indication that any selection for larger clutches in *P. hirsutiusculus* (by virtue of occupying larger *Tegula* shells) was probably suppressed by the competitive superiority of *P. samuelis* occupying *Tegula* shells.

The strategy that emerges from the above consideration is the result of competitive interaction. Generally, any *Tegula* shell is superior and will be chosen for reproduction by *P. hirsutiusculus*. But, considering that *P. hirsutiusculus* is subordinate to *P. samuelis* immunity from eviction would only be confered when *P. hirsutiusculus* occupied a *Tegula* shell too small to confer the weight index observed for *P. samuelis*, or one (*Thais*) not utilized by the latter. That *P. samuelis* females (with clutch) overlap in

Tegula weight indexes with *P. hirsutiusculus* females (with clutches) (Figs. 14a-b) suggests an additional contributory factor to the selective premium placed on *P. hirsutiusculus* females occupying *Tegula* shells. This may account for the variable frequency distributions of *P. hirsutiusculus* females (with clutch) in *Tegula* shells and the greater proportion of reproducing females in *Thais* (Fig. 14a) although behavioral information supports *P. hirsutiusculus*' shell choice of *Thais* over *Tegula* shells. *P. hirsutiusculus* females (with clutch) found in *Thais* shells tended to use shells in the weight index range for which fitness was maximized (Fig. 24). Therefore, it seems reasonable to assume that one may have selection for shells that are not preferred by *P. samuelis* or are suboptimal to ones used by *P. samuelis* while still confering maximum fecundity. The predicted 1.8 weight index of *P. hirsutiusculus* inhabiting *Tegula* shells is considered to represent the maximum of this compromise as does the weight index of 1.6 for *Thais* shells (Fig. 24).

Comparison of fitness set results with those of *P. hirsutiusculus* observed preference of *Thais* in the laboratory were discrepant (Fig. 24 and Tables 1-3). Consideration of past literature (Bollay, 1964; Orians and King, 1964 and Vance, 1972a) allows an explanation in that generally *Tegula* occurs in restricted populations whereas *Thais* is found almost anywhere on rocky shores of the Pacific coast. It is likely then, that selection for *Thais* by *P. hirsutiusculus* may have arisen because of its relative abundance and/or lack or utilization by other hermit crab species thereby minimizing competition and allowing for species co-existence through shell resource partitioning (Vance, 1972a). Thus, the general behavioral strategy for P. hirsutiusculus would be to respond to the dominant shell environment (Thais) preferentially. P. hirsutiusculus found in Tegula shells are probably there because Thais shell abundance is limiting to population growth (Vance, 1972a). The possibility of P. hirsutiusculus having an ineffective behavioral repertoire because Tegula occupation is rare in its evolutionary history (Hazlett, 1969a) should be considered. It is suggested that the sample area studied in this work offered a unique environmental situation in that more Tegula shells were available than Thais giving rise to the duality in preferred shell types. A zoogeographical study of Thais and Tegula population with respect to P. hirsutiusculus would test the above hypothesis.

Vance (1972) noted that resource partitioning played a large role in allowing P. hirsutiusculus to coexist with other hermit crab species, although mobility and habitat diversity were important factors. Figures 12 & 13 support active shell resource partitioning between the two species as shells inhabited by P. hirsutiusculus conferred a weight index below the 2.0 index observed for P. samuelis. Moreover, Figure 15 clearly indicated the partitioning of weight indexes in shells used by both species.

Indeed, Orians and King (1964) hold it is possible to observe a relationship between the types of shells preferred and habitat utilized. *P. hirsutiusculus* which preferred smaller shells (with respect to those occupied by *P. samuelis* at the same body weight) is much more mobile than *P. samuelis* being able to climb over algal growths from tide pool to tide pool. *P. samuelis* restricts its activity to usually barren bottoms of tide pools. This suggests that along with the selective advantage incurred by occupying a *Thais* shell (minimizing interspecific competition) reinforcement of the behavioral trait may have arisen from the habitat utilized. Further, habitat heterogenity would offer spatial refuge from interspecific competition. Data on whether resource partitioning arose because of the selectional pressure placed on *P. hirsutiusculus* by *P. samuelis* competitive superiority, or was existant prior to species contact is unavailable.

Childress (1972) found *Clibanarius albidigitus* reproducing females chose a shell weight index much larger than the weight index for which maximum fecundity occured (5.9 as compared to 4.2). He explained the difference between the predicted optimum weight indexes with an "optimal ratio strategy". This strategy takes into account the chances of shell changing being infrequent due to shell rarity, severe competition for shells and the limitation of shell changing behavior (ie. the subordinate crab relinquishing its shell being smaller than the dominant crab and thus occupying a shell suboptimal to the dominant crabs). "Thus, in order to maximize the time it takes for the weight index to decrease beyond the optimum reproductive weight index, it would be to the individuals advantage to trade up to a shell that gives a weight index slightly larger than the reproductive optimum" (Childress, 1972; p. 963). This represents a compromise between shell changes and a reduction of fitness brought about by a shell too large. In this case, strong intraspecific competition accounted for the different optimal reproductive and behavioral fitness sets.

Unfortunately, Childress (1972) worked with one specie of hermit crab inhabiting two different but structurally similar environments without taking into account the effect of other sympatric species in occupying the same shells. Moreover, he did not indicate sex ratios, or hermit crab shell preferences. There was no mention of seasonality in breeding period or changes in population abundance with respect to shells. This is probably due to the shortness of the sampling period (one week) and the lack of ecological data.

The high and narrow convexity of Childress' (1972) fitness sets underscores the high degree of similarity between the shell environments encountered. This is not the case for P. hirsutiusculus where a broad and convex fitness set was observed indicating that Tegula and Thais shells offer dissimilar environments with respect to P. hirsutiusculus' utilization. Moreover, given the degree of similarity between Childress' (1972) environments, changes in proportion of either environment would alter the slope of the adaptive function but not significantly change the optimum weight indes. This indicates that the shell weight index choice of C. albidigitus is stable in the face of flucuations in shell abundance. For P. hirsutiusculus any changes in proportion of one environment while greatly altering the slope of the adaptive function would not cause a large shift in the observed weight index unless the slope was parallel and tangent to all the points on the fitness set curve for the highest fecundities thereby favoring a large range of optimum weight indexes. The evolutionary stability of P. hirsutiusculus' strategy is patent in the increased utilization of different shells that offer different weight indexes given shell abundance flucuations.

Comparable estimates of behavioral dominance to those employed by Childress (1972) were not made in this study. It is not surprising though when comparing reproductive fitness set results that weight index optima differ with species of hermit crabs. This is to be expected as hermit crabs differ in size and evolutionary history of shell availability. However, it is interesting to find two different causes for observed shell occupation strategies, that is optimal ratios strategies due alternately to intra and interspecific competition.

Levins (1968) fitness set approach appears to be a very useful gauge in determining behavioral strategies in changing environments evolved from ecological factors, especially with respect to competitor interactions for limited resources. The use of additional proofs support fitness set analysis in this study. The present results suggest they would need to be repeated in the field with more precise estimates of fitness and detailed studies of intra and interspecific behavioral dominance. Future studies would benefit from more emphasis on estimation of fecundities in hermit crabs. The high observed variability in clutch size in this work and Childress' (1972) study suggest that a variety of other environmental factors might effect this parameter. It would be especially useful to obtain sufficient data to determine if there are seasonal changes in optimum strategies in reproducing females and to determine the optimal strategies of male and juvenile crabs. It is quite likely that seasonal and age specific differences of this type exist.

SUMMARY

A study of the behavior and aspects of the seasonal ecology of *P. hirsutiusculus* and *P. samuelis* was made at Dillon Beach, Marin County, California during most of the active season for both species of hermit crabs in 1973. Observations indicated attainment of early sexual maturity and timing of continuosly breeding populations of hermit crabs with times of environmental favorability. Moreover, observations confirmed previous reports of behavioral dominance of *P. samuelis* over *P. hirsutiusculus*. *P. hirsutiusculus* were confirmed to prefer *Thais* shells in behavioral choice experiments. Data on sex ratios, fecundity and other ecological observations on *P. hirsutiusculus* and *P. samuelis* were obtained. Field observations indicated that *Tegula* shells were not only the preferred shell inhabited by adult *P. hirsutiusculus*, but that fecundity was greater for this specie in *Tegula* than in *Thais* shells for comparable weight indexes.

It was found that juvenile *P. hirsutiusculus* enter the population in the middle part of the range distribution for the specie and occupied small *Littorina* shells. Otherwise, no changes were observed in the preferential use of *Tegula* shells by older crabs at different tidal levels and in different seasons. Although *P. hirsutiusculus* and *P. samuelis* (females with clutch) overlapped somewhat in *Tegula* shell utilization, evidence is presented using fitness set analysis and other data to indicate the preferential use of *Thais* shells by *P. hirsutiusculus* is due to the competitive interactions with the superior competitor, *P. samuelis*. The use of fitness set analysis to study "optimal ratio" strategies between different species of hermit crabs id discussed.

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