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Bruce A. Menge

I studied the feeding behavior of marked individuals of the carnivorous marine snail Thais melones in a rocky shore habitat of Pacific Panama. The population of snails consume a variety of invertebrate species such as bivalves, limpets, and polychaetes. Individuals exhibited a range of diet breadth, with some specialized, but others generalized. Some individuals foraging over the same patch of habitat chose strikingly different diets. Interindividual variability in diet was not due solely to foraging by individuals in a homogeneous patch of a few prey species nor was it likely to be determined by relative abundance of prey in the environment. Shell growth was influenced by the consistency within an individual diet rather than by the identification of the prey consumed. Significantly more shell growth occured in those individuals that ate fewer prey species or ate relatively more of one species than other species represented in the diet. There was no significant relationship between type of prey species and growth.

A six-month laboratory feeding experiment showed that shell growth but not gonad development was affected significantly by previous experience with particular prey, and by species composition of the diet. Snails grouped by previous experience (diet chosen during 1 month in laboratory experiments) were fed single species and restricted mixed diets. Different combinations of diet and experience had both positive and negative influences on shell growth, depending on the specific combinations of the original and restricted diets. After feeding for 5 months on a restricted diet of a certain prey species, individuals presented with a choice of the 3 prey species usually chose prey corresponding to the species of their restricted diet.

Monthly gonad samples of 20 adult snails indicate that male gonad indices remained almost constant over a year whereas females peaked from June through October. Fertile individuals of both sexes were found throughout the year.

Thais melones females deposit their flattened, lens-shaped egg capsules inside clean, recently dead bivalve or barnacle shells. Egg capsules were deposited throughout the year with larvae hatching from capsules as swimming planktonic veligers.

Prey Selection by the Tropical Marine Snail *Thais melones*: A Study of the Effects of Interindividual Variation and Foraging Experience on Growth and Gonad Development

by

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GENERAL INTRODUCTION

Although individual differences between members of the same population have long been recognized, quantitative study of intrapopulation characteristics and interactions is infrequent (Heinrich 1976, 1979, Werner et al. 1981). Intrapopulation variation has been considered by geneticists (Dobzhansky et al. 1977, Wright 1978, Coulthart et al. 1984), behaviorists (Curio 1976, Krebs 1970) and population biologists interested in resource use (Hassell & Southwood 1978, Tabashnik et al. 1981, Jaenike & Grimaldi 1983). Van Valen (1965) explored morphological variation in bird populations and proposed that birds living in patchy environments will show inter-individual variation in feeding activities and associated morphology. Grant (1971) expanded this idea by suggesting that the members of a population can either "differ in their modes of exploitation, being either specialists or generalists" or be "similar (provided variances are small) and ... all generalists". Roughgarden (1972, 1979) treated some of these ideas theoretically when modeling components of niche width. He suggested that the degree of inter-individual specialization in a population is dependent on competition and on the productivity of the population's surroundings. As yet there are not enough empirical studies of inter-individual variability to evaluate these

ideas. The only way to distinguish between a population of generalists and a population of specialists arrayed along a resource spectrum is to examine individuals.

Studies of individuals are relevant to optimal foraging theory (Krebs 1978, Hughes 1980, Pyke 1984). Foraging behavior is usually viewed from the perspective of the average individual of the population or species, but knowledge of inter-individual variability may be essential for the construction of realistic foraging models. Hughes (1979) incorporated recognition times, probability of prey misidentification and learning into a traditional optimal foraging model and predicted that when a predator learns to handle certain prey more efficiently, that particular prey's position in the predator's preference hierarchy may change. Traits, such as prey recognition, handling, and other aspects of foraging that involve learning, can be influenced by genetic characteristics of the individual and the microhabitat in which the predator lives. Thus, these traits may vary among individuals. Although the present study was not a test of optimal foraging theory, its results are relevant to the assumptions made by that theory in its simplest forms.

The goal of this study was to examine in detail the feeding behavior of individuals in a population of tropical marine snails, and how this affects growth and reproduction. The study animal, Thais melones is a member of the order Neogastropoda, and ranges from the Gulf of Tehuantepec, Mexico to Callao, Peru and the Galapagos Islands (Keen 1971). Thais melones consumes a variety of invertebrates, commonly bivalves, gastropods, chitons, barnacles

and polychaetes (Menge & Lubchenco 1981, West pers. obs.). This snail is an important predator on the Pacific Coast of Panama (Menge & Lubchenco 1981, Menge et al. 1985), and other members of the genus have major effects on prey in rocky coastal areas of Great Britain (Connell 1961, Morgan 1972), New England (Menge 1976, 1978a & b), and the northeast Pacific (Dayton 1971, Connell 1970, Palmer 1983).

Results of the study are organized as follows: Chapter 1 describes field studies of foods selected by marked individual snails in relation to natural abundances of the surrounding prey species. Data concerning individual diets, temporal change of prey availability, and relationships of diet and growth are presented. Chapter 2 presents the results of long-term experimental studies of the effects of prey species and previous feeding experience on growth and gonad development of Thais melones. Chapter 3 describes the seasonality of gonad development and characteristics of egg case deposition and development of Thais melones.

CHAPTER 1

PREY SELECTION BY THE TROPICAL SNAIL *THAIS MELONES*: A STUDY OF INTERINDIVIDUAL VARIATION

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ABSTRACT

I studied the feeding behavior of marked individuals of the carnivorous marine snail Thais melones in a rocky shore habitat of Pacific Panama. These snails consume a variety of invertebrate species such as bivalves, limpets, and polychaetes. Thais melones is generalized in overall diet at the population level but individuals varied in degree of specialization. Of 282 marked snails, 243 were observed through two or more feeding attacks in the field. Feeding sequences divided into size classes for the 137 snails observed through five or more sequential feeding attacks illustrate three major points.

(1) Within each study site and between individuals close to the same size, the diets chosen by some individuals differ markedly. Interindividual variability in diet was not due solely to foraging by individuals in a homogeneous patch of a few prey species nor was it likely to be determined by relative abundance of prey in the environment. (2) There was a range of dietary specialization and generalization among individuals of the same size class foraging in the same habitat. (3) Some individual snails show a high degree of consistency in their diets, at least over time periods less than or equal to 3.5 months. Two individuals out of a total of five snails observed over longer periods showed consistency for 11 and 13 months until they were lost. Populations of Thais melones at sites A and B attacked 10 and 16 prey species respectively, but no individual snail was observed to eat more than 5 species at either study site throughout

the entire study.

Shell growth was influenced by the content of individual diets. Significantly more shell growth occured in those individuals that ate fewer prey species or ate relatively more of one species than other species represented in the diet. There was not a significant relationship between type of prey species and growth. Interindividual differences in diet were most likely maintained by the increased efficiency gained by repeated feeding on the same type of prey.

INTRODUCTION

Foraging patterns of individuals within a population should lie between two extremes: either all individuals eat the same diet (be it broad or narrow) or individuals eat different diets (Van Valen 1965, Grant 1971, Roughgarden 1972, 1979). Although most studies of foraging are focussed at the population level, studies may also evaluate foraging patterns at the individual level. Hence, predatory species can be characterized by individual diet breadths, degree of interindividual differences, relative numbers of individuals with specific diet breadths, and changes in these relationships through time. In particular, since evolutionary change in a species depends on the degree of interindividual variation in the population, studies of interindividual foraging patterns are necessary to understand the evolution of foraging tactics. For example, if populations of a single species have different relative proportions of foraging specialists, these populations may vary in the pressures they exert on the community. Menge (1978) suggests that future predator-prey models should include the effects of individual variation due to differences in phenotype, genotype, or in experience and learning.

Generalizations about the degree and extent of interindividual variability are not yet possible due to a small number of investigations. Most studies comparing foraging individuals within a population find high variation among individuals (see references in Hassell & Southwood 1978, Heinrich 1976, 1979, Arnold 1981, Werner et al. 1981), although a few studies report little variation

among individuals. For example, Kitting (1980) reports that individual limpets maintained similar mixed diets of algae on different rock surfaces.

In a study of a temperate population of the carnivorous marine snail Nucella (=Thais) emarginata, I found that some individuals in the same location often chose strikingly different diets (West in press). Individuals foraging in the same habitat exhibited a range of specialization and generalization, with some individuals showing a high degree of consistency in their diets. Food choices were not a simple reflection of the relative abundance of the surrounding prey species or the different prey distributions that each predator encountered in microhabitats.

The goals of the present study were (1) to examine the individual foraging patterns of a tropical carnivorous snail Thais melones in relation to relative abundances of prey species, and (2) to explore growth of individuals in relation to diet and temporal changes in relative abundance of prey. Study of the degree of interindividual variability within populations helps to distinguish the roles of the many factors that influence foraging behavior.

STUDY SITES AND BIOTA

This investigation was done at the Naos Laboratory of the Smithsonian Tropical Research Institute, Balboa, Panama, from January through March 1980, January through May 1982, and October 1982 through December 1983. Study sites were on the western shore of Naos Island (Fig. 1, site A), and the southern shore of Culebra Island (Fig. 1, site B), both of which are near the Pacific entrance to the Panama Canal (8°45'N, 79°30'W). Thais melones is the most (site A) and second-most (site B) abundant of 7 common species of relatively large carnivorous snails occurring at those sites (Table 1). [Numerous species of small snails (Spight 1983) and rarer larger-bodied species are not included in this table].

All study site surfaces were in the middle intertidal zone (Menge & Lubchenco 1981). Site A consisted of tightly wedged boulders and was protected from direct wave action. Site B consisted of shelves and deep crevices of andesite or basalt and was relatively exposed to direct wave action. A rich array of species inhabit the rocky intertidal shores of Panama Bay. In the mid-zone, encrusting algae dominate space and sessile animals are concentrated in crevices (Menge & Lubchenco 1981). For additional descriptions of the environment and biota see Glynn (1972), Reimer (1976a,b), Garrity & Levings (1981), Menge & Lubchenco (1981), Lubchenco et al. (1984), and Menge et al. (1986).

Natural History

Thais melones (order: Neogastropoda) ranges from the Gulf of Tehuantepec, Mexico to Callao, Peru and the Galapagos Islands (Keen

1971). It is an inconspicuous and heavy-shelled snail that may reach 48mm in shell length. It consumes a variety of invertebrates, commonly bivalves, gastropods, chitons, barnacles and polychaetes (Menge et al. 1986, see below). Observations made at both low and high tides indicate that the snails are most active when submerged during periods of darkness. Snails are generally inactive after exposure to air at low tide and during daylight, even when submerged. Garrity (1984) found that Thais melones reduce heat and desiccation stress by moving into crevices during low tide. If an animal is feeding during a receding tide, it may continue to grip its prey while exposed to air. Submerged or dry, snails remained with the same individual prey from hours to days, depending on the size and species of the prey (Table 2).

Thais melones use different attack techniques to penetrate different species of their invertebrate prey. They usually drill through the shell at specific locations on their morphologically diverse prey species. Drill site location also depends on the snail's ability to maintain a foothold on the substrate, especially during strong water movement and with mobile prey that do not remain attached to the substrate when injured. On two occasions I observed T. melones carry small coiled snail prey into a crevice before starting to consume them.

With the exception of large Nerita, most coiled gastropod prey (including vermetids), and polychaetes were always drilled through the operculum. Limpets and chitons were drilled at the mantle edge and/or frequently flipped over. Barnacles were drilled between the opercular plates; bore holes were usually evident. Bivalves were

attacked in diverse positions, depending on the orientation of the bivalve and the predator. Bivalves with one valve permanently attached to the substrate (e.g. oysters) were usually drilled at the mantle edge, through one valve only. Mussel-shaped bivalves, such as Brachidontes and Lithophaga, were usually drilled between the valves. Irregularly shaped byssate bivalves (Isognomon & Sphenia) that live inside cracks and dead shells of other organisms were drilled in what appeared to be the position most accessible to the snail predator.

Thais melones are strongly attracted to the chemicals of damaged prey species (L. West pers. obs.). Clusters of snails frequently surrounded particularly large prey such as oysters or chitons that had been attacked by another individual or damaged by other means (people collecting oysters for food). These clusters sometimes contained mixtures of sizes of T. melones. Smaller snails were commonly seen climbing on the shells of large snails or abandoning the area, possibly to avoid cannibalism. Cannibalism and climbing behavior are common in a number of species of carnivorous snails (Abbott and Haderlie 1980). Larger Thais melones were observed to eat smaller T. melones occasionally throughout this study.

METHODS

Thais melones feeding and activity were observed in the field. Snails and their prey were observed with minimal disturbance. When necessary I gently tilted a snail away from the substrate to detect prey; these snails rarely lost their foothold or moved away. A small mirror was used to view underneath the animal or inside crevices. When a snail was clinging to potential prey, the presence of a partially or completely drilled bore hole through the shell of the prey was considered active predation. Infrequently, prey were consumed without evidence of boring marks. In such cases I determined if predation caused death by examining the prey for partially digested prey tissue.

The movements and feeding activities of individually marked snails were followed to record their diets in relation to food availability. Although observations were made during all tidal phases, I concentrated on periods when both submergence and darkness coincided because these were the times the snails were most active. I did not snorkel during the highest point of the tide when it was dark. Most observations were made when the water depth was not more than 1.5 m, during incoming and outgoing tides.

Study sites were mapped to scale to show topography and locations of sessile species. Within each site, Thais melones were individually marked in place. Quick setting "five-minute" epoxy was used to glue numbered tags to the snail shell. Tags were made from plastic reflector tape that was roughened with fine sand paper (to prevent beading of the ink) and hand numbered with indelible

ink. Shells were dried and lightly sanded by hand in the location where a tag was to be attached to remove algal crusts and other epizoic organisms. Epoxy was also placed on top of the tag for further protection once it was attached to the snail shell. Four numbered tags were located on each snail. One was positioned on the shoulder of the spire and three were glued to the outside aperture edge. These aperture marks were used to determine shell growth at the aperture margin. At times in the field when a simpler (but short-term) marking technique was necessary, colored wax crayons provided satisfactory identification of individuals. Shell length of all marked snails (from apex to siphonal canal tip) was measured to the nearest 0.5 mm with vernier calipers.

The position of the snail, its feeding activity, the nature and size of its food (if any) and the prevailing environmental conditions (time, general surf conditions) were recorded on photocopied maps of the study site. The precise location of each marked snail was determined at each observation (e.g. on successive low tides) by measuring its position with respect to two established landmarks on the study surface. A technical divider was used to convert the substrate measurement to distance on the scale map. Snail movement paths were estimated by connecting successively mapped positions of an individual with straight lines that followed the major contours of the substrate surface.

To quantify prey abundance, clear 0.25 m^2 vinyl quadrats with 100 dots plotted on them at random were used to estimate percentage cover of prey and other species (Menge & Lubchenco 1981). Mobile and solitary sessile animals within the quadrats were also counted.

Nine permanently marked quadrats were monitored monthly at study site B, February through May 1982 and January through December 1983. On surfaces where snails were feeding, relative abundance of prey was also quantified using the quadrat technique. These data were taken within two weeks of the feeding incidents.

To obtain observations of individual snail diets in the field, intense observations were conducted during three periods: January through March 1980, February through May 1982, and June through September 1983. Starting in February of 1980, observations were made at essentially all low tides during these time periods (two incoming or outgoing low tides / day).

Probability Calculations

To determine the likelihood that random foraging through available prey produces the diet observed for each individual, the probability of a given snail eating the observed diet was calculated by computer using the multinomial distribution (Feller 1968, West in press):

$$\frac{n!}{k_1!\,k_2!\,\ldots\,k_r!}\; p_1^{k_1} p_2^{k_2} p_3^{k_3} \cdots p_r^{k_r}$$

where,

n represents the total number of observed feeding attacks made by one snail.

k_i's are the number of times the snail fed on prey species i.

p_i (i=1,...,r) represents the relative abundance of prey species i, where $p_1+\ldots+p_r = 1$. I used the density values for i (see methods above) instead of the percentage cover values, because they were larger and more conservative when used in this test.

Any specific sequence of prey is highly improbable. In other words, obtaining identical sequences of prey is extremely unlikely when multiple samples are taken from the same array of foods, even if the foods and their proportions are identical. To account for this, I used the following calculation procedure, (illustrating only one snail diet as an example).

For snail 64 (Fig. 3) the computer tabulated all possible combinations of prey for a sequence length of 12 prey taken from the prey species eaten by small snails in 1980. It then calculated the probability of each of those sequences using the proportions of prey available in the environment and the multinomial distribution. The computer then compared the probability of snail 64's diet to each probability of the possible diets, sorting out and saving those probability values that were equal or smaller than the probability of snail 64's diet. These probabilities were then added to the probability of snail 64's diet. This composite probability for snail 64 is 4.520×10^{-2} and is graphed along with the other composite probabilities calculated for each individual (Fig. 9). These probability values are conservative because they account only for the number of prey species in the diet, not the specific order in which those prey species occur.

Index of Specialization

Growth data were compared to individual diets using the following diet specialization index (SI).

$$SI = \left(\frac{\text{number of the most abundant species in an individual sequence}}{\text{total number of prey eaten in the individual sequence}} \right) + \left(\frac{\text{number of prey in the individual sequence}}{\text{number of species in the individual sequence}} \right)$$

This index yields a simplified representation of the degree of specialization of an individual's diet. A large index value indicates that the individual ate fewer different species, or predominantly one species over others.

RESULTS

The Thais melones population did not simply select prey species according to their relative abundance in the environment (Fig. 2). The snails ate at least 10 prey (including species of molluscs, barnacles, polychaete worms) at site A; at least 16 prey species in 1982 and 15 prey species in 1983 at site B. At site A, oysters, limpets and serpulid worms were eaten in proportion to their abundance, but at site B, oysters and limpets were eaten in numbers larger than would be suggested by their abundance, while fewer serpulids were eaten.

Snails ate more oysters and fewer limpets in 1982 than 1983, though measures of availability of those two species were very close for the two years. In 1983 snails took slightly more serpulids although relative abundance of that prey dropped. In all years, at both study sites, the barnacle Chthamalus was taken in low numbers compared to their abundance in the environment.

Thais melones was generalized in overall diet at the population level but individuals varied in degree of specialization. Out of 282 marked snails, 243 were observed through two or more feeding attacks in the field. Feeding sequences divided into size classes for the 137 snails observed through five or more sequential feeding attacks (Fig. 3, Table 3, Appendix) illustrate three major points.

(1) Within each study site and between individuals close to the same size, the diets chosen by some individuals differ markedly (Fig. 3). For example, snail 39 (in the fourth sequence, Fig. 3)

ate five oysters and two barnacles, while snail 60 (fifth sequence, Fig. 3) took five serpulid worms with one oyster and one limpet.

(2) There was a range of dietary specialization and generalization among individuals of the same size class foraging in the same habitat. For example, snail 65 (9th sequence, Fig. 3) ate six serpulids and one oyster, while snail 92 (11th sequence, Fig. 3) ate five different prey species (Siphonaria, vermetid, Chama, serpulid, and Ostrea) out of the six eaten.

(3) Some individual snails show a high degree of consistency in their diets, at least over periods less than or equal to 3.5 months. Out of a total of five snails observed over longer periods, two individuals showed consistency for 11 and 13 months until they were lost (Table 3). Populations of Thais melones at sites A and B attacked 10 and 16 prey species respectively (Fig. 2), but no individual snail was observed to eat more than 5 species at either study site throughout the entire study (Fig. 4). The number of prey species per individual diet does not appear to be an increasing function in the longer sequences of feeding observations (Fig. 5).

At both study sites, the data suggest that most individual diets consisted solely of molluscs (Fig. 6). At site A however, 13 individuals fed on combinations of molluscs and polychaetes. Large (>30mm), intermediate ($20 \leq \leq 30$mm) and small (<20mm) snails all had individuals specializing on molluscs.

Although apparent specialization by individuals on different prey could simply be shaped by a patchy distribution of prey and predator, patchy distributions did not cause the patterns described

here. Routes of each marked snail indicate that a variety of potential prey are encountered between successive tides (Figs. 7 & 8). Routes of snails 64, 65, (both small snails) 7, and 18 (both large) are representative of maps for all individuals. While the lines do not show the exact routes traveled, they summarize a snail's movement over rock surfaces. The maps show that sequential attacks on the same prey species are not artifacts of feeding through a prey patch consisting of a single species. These maps show ambits of individuals of the same size class feeding on the same rock surfaces and choosing different prey species. Snail 64 ate mostly Siphonaria (limpets), while snail 65 ate mostly serpulid polychaete worms. Both snails also ate oysters. Snail 18 ate a vermetid (start position) close to where snail 7 ate two oysters.

How likely is it that random foraging through available prey produces the diet observed for each individual? The probability of getting a diet consisting of the observed numbers of individuals of each prey species was calculated incorporating the relative abundance of prey available in the study areas (see methods). At site A (Fig. 9) one third of the diets were more specialized than would be predicted by chance and the relative abundance of prey (i.e. 1/3 of the diets had probability values $<.05$). Most of the diet probabilities were greater than 0.1. In contrast, at study site B in 1982 and 1983, three quarters of the diets were more specialized than would be predicted by chance and the relative abundance of prey.

Shell growth of T. melones was influenced by individual diet

composition. The effects of initial size of the snail and the number and type of prey species eaten on shell growth of T. melones were determined using multiple regression and analysis of variance. Significantly more shell growth occurred in those individuals that ate fewer prey species and/or ate relatively more of one species than other species represented in the diet (Table 4; see diet-index in methods). There was no significant relationship between prey species and growth.

Initial size had a highly significant effect on growth (Table 4). When size classes were analyzed separately, the smallest and largest size classes of snails showed no significant relationship between diet index and growth, but medium snails that ate fewer species of prey showed significantly more growth (Fig. 10 & Table 5).

Temporal shell growth was variable. Shell growth was greater in all snail size classes during the dry season, January through March 1983 (Fig. 10). Growth during the same period in 1982 was less; values were closer to 1983 monthly values other than January through March data. The individual diets analyzed with respect to specialization spanned the months of January through May 1982 and July through September 1983. The seasonality data suggest that this information is representative of the characteristics of growth and diet overall, but does not cover a peak time of growth.

DISCUSSION

Members of a population of Thais melones may choose different diets from the same array of prey species in their environment. These observations of interindividual differences in serial feeding attacks are similar to those reported for temperate snails (West in press) but in this tropical habitat, snail diets are broader, with individuals eating up to five prey species and the overall population eating at least 16 prey species (Fig. 4, also Fig. 2).

In Panama, feeding observations show that there was a range of dietary specialization and generalization among individuals of the same size class foraging in the same habitat. Within many of those individual diets prey choice was consistent, at least over time periods less than or equal to 3.5 months. Two of five snails observed over longer periods were consistent for 11 (snail R93, which ate predominantly limpets) and 13 months (snail r48, which ate predominantly oysters; Table 3).

Prey selection by both the Thais melones population and its individual members did not simply reflect the relative abundance of those prey species in the environment. At site A, oysters, limpets and serpulid worms were eaten in proportion to overall abundance but at site B, oysters and limpets were eaten in numbers greater than would be suggested by their abundance, while fewer serpulids were eaten (Fig. 2). Maps of the net movement of individuals also suggest that prey were not attacked solely on the basis of relative abundance (Fig. 7 & 8). Further, calculated probabilities of obtaining the observed individual diets based on chance and the

relative abundance of those prey were highly unlikely for site B but more likely for site A (Fig. 9).

Other studies also suggest that predatory snails do not forage randomly. Hughes and Dunkin (1984b) for example, reported that diet preferences of Nucella lapillus in laboratory choice experiments were not changed by short-term fluctuations in relative abundance of prey species. In Washington state (USA) Palmer (1984) found that Nucella emarginata and two other species, N. canaliculata and N. lamellosa did not simply eat potential prey as they encountered it, nor did snails choose prey in proportion to the relative abundance found in their surroundings. In the Malaysian snail Natica maculosa, a week of feeding on a less preferred prey species did not influence this predator's preference (Broom 1983).

In my study, individual diets were compared to available prey by calculating probabilities of obtaining those diets with regard to the relative abundance of prey species available and the prey species eaten by particular size groups. Calculations for diets at site A indicate that snails were choosing prey more closely to what would be predicted by chance (Fig. 9). At site B in both years snails were taking diets that were unlikely to be predicted by chance. In temperate Nucella emarginata, the majority of diets were even more unlikely to have been obtained by chance; all but 5 diets out of 46 had probabilities less than 0.05 (West in press).

Although overall diet choice at site B is more complex than a simple reflection of abundance, relative abundance and accessibility of prey may shape the diets of predators (Murdoch &

Oaten 1975, Hassell & Southwood 1978, Krebs 1978). For example, snails ate a greater variety of prey at site B (Fig. 2), presumably because Siphonaria and Ostrea, the overall preferred prey, were less abundant there. Overall, site B also has less surface area of prey than A.

A variety of studies have shown that experience with specific prey may act to reduce handling time of that prey (e.g. Heinrich 1976, 1979, Laverty 1980, Werner et al. 1981 and references therein). This is especially well documented in different species of carnivorous snails. Feeding experience increases both feeding rate and prey preference in carnivorous snails, Polinices duplicatus (Edwards & Huebner 1977) and Nucella lapillus (Hughes & Dunkin 1984a&b and Dunkin & Hughes 1984). Palmer (1984) demonstrated that experienced temperate snails of three species of the genus Thais chose prey that yielded them the most growth. He also found that rates of growth varied as a function of predator size, prey size and prey species (Palmer 1983). In the present study the data suggest that significantly more shell growth occurred in those individuals that ate fewer prey species and/or ate relatively more of one species than other species represented in the diet (diet specialization index, Tables 4 & 5). There was no significant relationship between type of prey species and growth (Table 4 & 5).

Some studies of the relationship between food species and growth rate have documented that certain food species or combinations of species promote more growth than alternative foods.

Ecologists have explored whether organisms grow well on the species they commonly choose. Among carnivores, spiders (Holmberg & Turnbull 1982) and marine snails (Engle 1942, Edwards & Huebner 1977, Palmer 1984), do grow faster on the species they choose; however, other carnivorous snails grow equally well on less prefered prey (Bayliss 1982, Luckens 1970). Palmer (1984) raised an interesting point. Although he found that certain prey species promote more growth than other prey species, he also found that for some predators the rank of prey species promoting growth changed with predator size. Palmer states that such rank shifts underscore the need to define prey types in units relevant to the predator, and species type may not always be relevant.

In the present study initial size but not prey species had a significant effect on growth when data were analyzed as a whole (Table 4). Further complexities of the relationships between prey species and growth in carnivorous snails are reported in Moran et al. 1984. The whelk Morula marginalba prefers oysters over barnacles and tube worms. Although snails grew rapidly on both tube worms and oysters (and slowly on barnacles), data suggest that tube-worm fed snails die at a higher rate than oyster-fed snails. Similarly, Natica maculosa fed the preferred bivalve Anadara granosa grew at the same rate as those fed the less preferred bivalve prey Pelecyora trigona, but Natica that were fed Pelecyora, reached a smaller size than those fed Anadara (Broom 1983).

Some mechanisms that may be responsible for maintaining interindividual variability in populations are: feeding experience (Heinrich 1976, 1979, Laverty 1980, Werner et al. 1981), ingestive

conditioning (Wood 1968), physiological phenomena (Kitting 1980, West Chapt. 2), and genetic variability (Arnold 1981). These topics are discussed in West (in press). Two other potential mechanisms that may be worth exploring are the following:

(1) Diet preferences may be established by prey availability at the site of settlement of the predator; i.e. lifetime diet could be established by chance events in the individual's early development. Rittschof et al. (1983) reports that naive laboratory Urosalpinx were attracted to effluents of barnacles and a mixture of bryozoans, but whether young snails will pass by and ignore other prey organisms to eat barnacles and bryozoans is not reported. If the naive hatchling eats whatever prey it runs across, the nearest prey to the settlement site might influence subsequent prey choice by ingestive conditioning. Differences in the microhabitats where young settle could result in different diet preferences between newly settled snails. Later when snails are older and have traveled throughout their normal habitat, an observer might see individuals feeding on the same rock surface yet consistently choosing different species diets. In addition variation in the timing of T. melones settlement and the seasonality and growth rates of prey could cause even more complex patterns.

(2) Heavy predation by fish, crabs, (Menge & Lubchenco 1981, Bertness et al. 1981) and octopus (West pers. obs) might select for interindividual variability in feeding behavior of some prey. If an animal often fed on a neighboring individual's prey type,

corresponding to a certain type of habitat (e.g. patch of serpulid worms), such behavior may increase the risk of higher-order predators associating that animal with that habitat, and searching more effectively for it. Thus, different foraging behavior phenotypes could be maintained much the same as different color morphs are maintained in the terrestrial snail Cepaea (Cain and Sheppard, 1950). (Shell color of Thais melones did not reflect habitat types in my study areas.)

In conclusion, the results of this study suggest that interindividual variability in diet was not due to foraging by individuals in a homogeneous patch of a few prey species nor was it likely to be determined by relative abundances of prey in the environment. For medium sized snails, individual specialization was linked to faster shell growth, but the species of prey did not have a significant effect. Interindividual differences in diet were most likely maintained by the increased efficiency gained by repeated feeding on the same type of prey.

CHAPTER 2

INDIVIDUAL FORAGING EXPERIENCE: EFFECTS ON GROWTH, GONAD DEVELOPMENT, AND PREY CHOICE IN A CARNIVOROUS MARINE SNAIL *THAIS MELONES*

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ABSTRACT

A laboratory experiment investigated the influences of foraging experience and prey species on shell growth and gonad development of the tropical marine snail Thais melones. Sequential feeding attacks made by individually marked snails from an array of equal abundances of three prey species were monitored for 1 month in the laboratory. Out of 600 snails, 476 were observed to eat at least 8 prey individuals. Of those 476 snails, 247 ate one prey species for at least 75% of the observed diet.

Snails that chose these "focussed" diets were sorted into groups based on the predominant prey species of their diet. Snails with long sequences that chose the most equally mixed diets were sorted into a fourth group. Sixty-four snails of each diet group were compartmentalized and fed one of four restricted diets for 5 months. The effects of the original diet and the restricted diet were quantified using shell growth and gonad development at the end of the experiment. At the end of the 5 month restricted diet regime, individuals were separated and tested for their choice of prey when presented with the 3 prey species simultaneously.

The results suggest: (1) Neither a mixed diet nor any diet restricted to one species can be called the best diet because foraging experience influences shell growth in Thais melones. The interaction between original diet and restricted diet was complex. Combinations of original diet groups with restricted single species and mixed restricted diets influenced shell growth both positively and negatively, depending on the specific combinations of the

original and restricted diets. These results may reflect complex interactions with digestive enzymes. (2) Thais melones maintain gonad development at the expense of shell growth. There were no significant differences in mean gonad development between treatments of the diet experiment. Further, gonad development in the lab was not significantly different from snails sampled the same month in the field. (3) After feeding for 5 months on a restricted diet of a certain prey species, individuals presented with a choice of the three prey species usually chose prey corresponding to the species of their restricted diet, suggesting that diet is influenced by ingestive conditioning.

INTRODUCTION

The degree of "foraging experience" that an organism possesses is a result of the surroundings of the consumer, the physiological characteristics of the consumer, and the changes of those interacting factors through time. In most ecological and behavioral studies the term foraging experience refers to the situation where a consumer has previously come in contact with a food species in combinations of tactile, chemical, or visual situations. Such studies report the influences this prior contact has on some specific features of the organism's subsequent foraging behavior (see refs. in Hassel & Southwood 1978, Werner et al. 1981). Foraging experience can modify a consumer's choice of prey (Werner et al. 1981, Rowell-Rahier 1984), its mobility in relation to foods (Pyke 1984), its capture techniques (Werner et al. 1981), its manipulation of food to obtain nutrients (Heinrich 1979, Laverty 1980, Hughes & Dunkin 1984b), and its digestive enzyme production (Stuart et al. 1985).

Some ecological studies have shown that an organism will process a particular food more efficiently when it has previously consumed that food repeatedly. Examples include bumblebees (Heinrich 1976, 1979, Laverty 1980), fish (Werner et al. 1981), snails (Hughes & Dunkin 1984a,b, Dunkin & Hughes 1984), and crabs (Cunningham & Hughes 1984) all of which have measured time spent and energy gain as the indicators of efficiency. Yet, a longer study measuring growth and gonad development, may provide information about the consequences of specific behaviors and also

include more physiological influences of foraging (e.g. enzyme activity).

Here I extend the approach of earlier studies and examine the relationship between repeated consumption of particular foods and growth and reproduction of the predator. Studies of characteristics of foraging in relation to reproduction give a broader view of the importance of specific behaviors with regard to natural selection. If previous experience influences a forager's choice of food and subsequent reproductive success, this factor should be incorporated into our expanding body of knowledge of population biology, community characteristics, and foraging theory (Emlen 1966, Hughes 1972, Hassell & Southwood 1978, Werner et al. 1981).

Previous field studies indicated that gastropod individuals foraging across the same rock surfaces, facing nearly identical relative abundances of prey species, frequently consumed diets that contained contrasting prey species (Chapter 1). These diets were not a simple reflection of local relative abundances of prey species. Here, I examine some of the consequences of this individual consistency of prey choice. I present the results of laboratory experiments exploring how repeated consumption of specific prey influences snail growth and gonad development and how this feeding experience influences subsequent prey choice. More specifically, the experiments addressed the following questions: (I) When individual snails are sorted into groups based on the prey species they choose in the lab and those groups are divided and restricted to experimental diets for 5 months: (A) What species

combinations of original-diet-of-choice and 5-month-restricted-diet, promote the most growth and gonad development? (B) Does the original-diet-of-choice or the 5-month-restricted-diet or another prey species different from those, dictate subsequent choice of prey from an array of available species? The results suggest that neither a mixed diet nor any diet restricted to one species can be called the best diet because foraging experience influences shell growth. Repeated consumption of one prey species also influences subsequent prey choice.

METHODS

The research reported in this paper was carried out at the Smithsonian Tropical Research Institute, Naos Laboratory, Balboa, Panama, May through December 1983. Descriptions of rocky intertidal shores and biota of the Pacific side of Panama can be found in Glynn 1976, Menge and Lubchenco 1981, Garrity and Levings 1981, Lubchenco et al. 1984, and Menge et al. 1985.

The study species is the carnivorous marine snail Thais melones (Order: Neogastropoda). This snail ranges from the Gulf of Tehuantepec, Mexico to Callao, Peru and the Galapagos Islands (Keen 1971). It consumes a variety of invertebrates, commonly bivalves, gastropods, chitons, barnacles and polychaetes (Menge et al. 1985, L. West pers. obs). T. melones drills through prey shell or gains access to soft body tissue by other means (e.g., flipping over limpets and chitons).

Snails of a size range of 17.5 to 30 mm (shell length) were collected from the middle intertidal zone on the southern shore of Culebra Island, near the Pacific entrance of the Panama Canal. Snails were maintained in the laboratory in four seawater tanks. Individuals were marked with hand-numbered tags cut from plastic reflector tape. Snail length was measured to the nearest 0.5 mm using Vernier calipers. Shells were dried and lightly sanded by hand in the location where a tag was to be attached. Five-minute epoxy was used to attach and cover the top surface of the tag. Four numbered tags were located on each snail. One was positioned on the shoulder of the spire and three were glued to the outside

aperture edge. These aperture marks were used to determine shell growth at the aperture margin.

I used three prey species in laboratory feeding experiments, the boring bivalve Lithophaga sp., the barnacle Tetraclita panamensis and the limpet Siphonaria maura, chosen because (1) they were abundant in the field, (2) could be collected without damage, and (3) provided representatives of three major prey groups of Thais melones, i.e., bivalves, barnacles and limpets. Although the barnacle Balanus was eaten in the field more often than Tetraclita, it was not possible to collect undamaged Balanus in large enough numbers to conduct the experiment. In contrast, Tetraclita settle on older barnacles that can be broken off and cleaned with no damage to the epizoic barnacle. Because chemicals released by damaged prey are a strong attractant to Thais melones (L. West pers. obs.), I rejected all prey that could not be collected without damage. If the animal to which the Tetraclita was attached had been alive, its shell was exposed to hermit crabs and other invertebrate scavengers two days before use in the diet experiments. Limpets were collected by grabbing them suddenly, when they were active. They were immediately placed on a rigid sheet of plastic and allowed to reattach. Limpets were maintained for two days in the laboratory before they were presented to snails. Less than 2% of the limpets died using this technique. Lithophaga, which bore into shell and rock, were collected by removing thick pieces of oyster shell from the rocks with hammer and chisel. The oyster shells were broken apart in the laboratory

to remove all undamaged lithophagids. Prey used in the diet experiment were of uniform size: For Siphonaria 14-16 mm in shell length; for Lithophaga 26-29 mm; for Tetraclita 14-18 mm.

To determine original diet preferences, 600 Thais melones were collected and marked during the last week of April and the first week of June, 1983. These snails were divided into 4 groups of 150, each group of which was placed with prey in a fiberglass seawater tank (1 x 1 x 0.35 m) (Fig.1). Every two days, old prey were removed and replaced with new prey in the proportion of 4 individuals of each species to one predator. Since some prey were always left over after the end of each 2-day period, I assumed that food was not limited.

Starting on June 5, 1983, I recorded individual diet sequences in the laboratory. Observations were made in darkness with a dim flashlight because the largest percentage of Thais melones feed during night (L. West, pers. obs.). The diets of snails observed eating at least eight individual prey were sorted into categories. Snails whose diets were $\geq$ 75% focussed on 1 prey species were grouped according to their chief prey species, Tetraclita (=T), Siphonaria (=S), and Lithophaga (=L). A fourth group, mixed (=M), consisted of snails with the longest laboratory feeding histories that ate similar numbers of each prey species. The diets of these four groups are termed "original diets".

Sixty-four snails of each original diet group were fed one of four restricted diets (T,L,S,M; Fig. 12) from July 1st to November 30th, 1983. Each of four seawater tanks contained four vexar-mesh compartments. Within each compartment 4 marked and numbered snails

of each of the four diet history groups (snails focussed on S,L,T and mixed snails, M) were put together for a total of 16 snails per compartment. Each of the compartments in a tank was then supplied with a different experimental diet (i.e., T,S,L,or M). This allowed the water flow to circulate chemical exudates that the prey may release during normal metabolism or when under attack. Snail shell growth was measured every month and gonad size was determined for each snail at the end of the experiment.

Handling times of prey were determined during the first month of diet choice (Table 1). When I observed a snail just beginning to attack prey, I would continue to check on the feeding at half-hour intervals until the snail was finished eating.

Concurrently, monthly gonad samples and growth rates of snails in the field were also monitored. The bulk of these field data are presented elsewhere (Chapter 3) but they are summarized here to compare growth and reproduction of snails in the lab vs. those in the wild.

At the end of the 5-month-restricted-diet experiment (Fig. 12), individuals were separated and maintained in 20cm diameter and 11cm deep plastic containers with flowing seawater and presented with 3 prey individuals from which to choose. These diet choices were then analyzed with regard to their original diet and their restricted diet. I compared each single species restricted diet group to the mixed diet group using the Log likelihood ratio test (Sokal & Rohlf, 1981).

Gonad indices were determined using the following method. The

snails were anesthetized with magnesium chloride, after which the shell was cracked open with a hammer to allow removal of the soft parts and fixation in formalin. After at least two weeks, the gonad was separated from the other soft body tissue under a dissecting microscope and both gonad and other soft tissues were dried to constant weight. A gonad index was calculated for each individual as:

$$\frac{\text{Gonad Weight}}{\text{Gonad Weight + Other Soft Tissue Weight}}$$

Results of the feeding experiment were analyzed using multivariate analysis of variance techniques. The model analyzed was:

$$G,S = \text{CONSTANT} + O + R + X + O*R + O*X + R*X + O*R*X$$

with G = gonad index (continuous variable)

S = shell growth (continuous variable)

O = 1st month diet choice (T,L,S,M)

R = restricted diet (T,L,S,M)

X = sex (male, female)

RESULTS

Original Diets

During the original diet determination, i.e., the first month of the diet experiment, Thais melones ate significantly different proportions of prey species from the equal proportions of the three prey species available (Fig. 2, $G=339.5 >> x^2 =10.59$, $p<.001$; log likelihood ratio test, Sokal & Rohlf, 1981). The observed feeding rate is only slightly less than the actual feeding rate determined by drilled and cleaned prey shells removed from the tanks (Fig. 13). Despite the problem of missed prey, the observational data are very close to the actual prey eaten.

Out of the 600 marked snails, 476 ate at least 8 prey individuals during the first month of diet choice and 16 ate 0 prey (Fig. 14). Out of the 476 diet sequences of eight or more, 247 snails were observed to eat one prey species for at least 75% of their diet.

More snails focussed on the barnacle Tetraclita than on the other two prey species, Lithophaga and Siphonaria (Fig. 15). Almost equal numbers of snails focussed on the latter two species. These data and those presented in Fig. 13 suggest that, in the laboratory Thais melones preferred the barnacle Tetraclita. This pattern was not observed in the field, (L. West, pers. obs.) because Tetraclita normally occur higher on the shore than do most Thais melones. However, Thais melones do consume Tetraclita in the field, so use of this prey should not introduce an artifact into the experiment. Further, Tetraclita become more abundant lower on

the shore when Thais (and other predators) are removed (B. Menge, pers. comm.), suggesting the scarcity of this barnacle in the habitat is due partly to predation by Thais.

Restricted Diets

I designed this laboratory feeding experiment to investigate the effects that restricted diets of selected prey species would have on the shell growth and gonad development of Thais melones. I also wanted to explore the effects of previous foraging experience and how they might interact with the effects of restricted diets.

The effects of original diet, restricted diet and sex on gonad development and shell growth of T. melones were determined using multivariate analysis of variance (MANOVA). Subsequent multiple comparisons were done using ANOVA with the critical levels adjusted with the Bonferroni approximation (Neter & Wasserman 1974).

Average shell growth in each treatment is shown in Table 7. Shell growth, but not gonad development was affected by both original and restricted diets as indicated by the significant statistical interaction between these factors (Table 8). Neither gonad development nor shell growth was affected by the sex of the snail.

Laboratory shell growth and gonad index data were then compared with shell growth from marked unrestricted snails in the field, and gonad index data that were sampled from unmarked snails during the same time periods as laboratory snails. Sample size of field growth data is small because in this comparison I used only those field snails that corresponded to size of the lab snails.

Gonad development of snails in the field was not significantly different from that in the laboratory, whereas shell growth in the field was significantly higher than it was in the laboratory (Table 9). These data suggest that snails put their energy into maintaining gonad development before investing energy in shell growth. Snails feeding in the laboratory were doing well enough to maintain a gonad index comparable to the field snails but were not doing as well overall as indicated by shell growth.

The interaction between original and restricted diets was significant both with and without the gonad index and sex variables (Table 8). The interpretation of this interaction suggested by Figure 16 is that snails with an original diet of Lithophaga and Siphonaria, both molluscan species, grew less on a restricted diet of the barnacle Tetraclita than snails from either a mixed or an original diet of Tetraclita. Snails experienced with Tetraclita did not grow less when restricted to molluscs; they grew well on Lithophaga. The details of the other interactions did not offer much insight, so I compared groups of treatments using unplanned comparisons tests, with the GT2 method (Sokal & Rohlf 1981). I asked five questions: (1) How does growth in focussed snails which were restricted to a diet of their original choice (LL, SS, TT; Table 7) compare to focussed snails which were restricted to prey different from their original choice (LS, LT, ST, SL, TL, TS; Table 7)? (2) How do mixed diet snails which were allowed to maintain a mixed diet (MM, Table 7) compare to focussed snails which were restricted to their original diet (LL, SS, TT; Table 7)? (3) How do mixed diet snails which were allowed to maintain a mixed diet

(MM, Table 7) compare to focussed snails which were forced to change to a different diet (LS, LT, ST, SL, TL, TS; Table 7)? (4) How do focussed snails which were allowed to choose prey from a mixed array (LM, SM, TM; Table 7) compare to focussed snails which were restricted to their original prey (LL, SS, TT; Table 7)? (5) How do mixed-diet snails which were restricted to single species diets (ML, MS, MT; Table 7) compare to focussed snails which were restricted to their original prey (LL, SS, TT; Table 7)? The analyses indicate that there are no significant differences between the means of any of the paired comparisons. In each comparison the $| \bar{X}$ group1 $- \bar{X}$ group2 $|$ was $<$ MSD; respective values for questions 1-5 are:.3512<.5680 $p>0.05$; .6519<1.140 $p>0.05$; 1.003<1.070 $p>0.05$; .4593<1.580 $p>0.05$; .2575<.7837 $p>0.05$.

Choice Test

Experience with the restricted diets shaped later prey choice. After 5 months on a restricted diet each snail was tested for its prey choice when presented with the three prey species simultaneously. All but two of 230 snails chose prey within a week. (The eventual choice of those two was not to be known because all snails were sacrificed to determine the gonad index). Out of 228 choices, 49% were Tetraclita, 22% were Lithophaga and 29% were Siphonaria. Despite an overall preference for the barnacle Tetraclita, prey choice was influenced by recent feeding experience, i.e., by the prey species that the snails were restricted to during the feeding experiment. For example, snails that had an original diet of T and were restricted to a diet of S

(treatment TS), most often chose S: 8 chose S, 2 chose L and 5 chose T (Fig. 6). To test the significance of this pattern within each original diet group, I compared the choices of conditioned snails (snails restricted to monospecific diets) to snails that were able to eat what they wanted from the mixed diet. For example, prey choice in the TL treatment was not significantly different from that in the TM treatment (Log likelihood ratio test, $p>.05$). In four cases snails were significantly more likely to choose the prey they had been eating most recently (for 5 months prior), treatments MS, SL, SS, and TS; $p < .01$. In the remaining cases there was a nonsignificant trend in the same direction: snails were most likely to choose the diet to which they had been restricted immediately prior to the choice test. When all the groups are combined and the LL, SS, TT and MM treatments are removed (Fig. 7), L and S conditioned snails' choices are significantly different from M ($p < .01$). The restricted diets of T appear to have a conditioning effect but due to the overall preference for T, these data were not significant.

DISCUSSION

Observations of marked individuals feeding both in the laboratory and under natural conditions (West pers. obs.) indicate that some individual Thais melones tend to focus on one prey species from an array of suitable prey. This phenomenon has also been reported in a wide range of consumers such as insects, fish, birds, etc. (see references in: Werner et al. 1981, Bayliss 1982, Hall et al. 1982). Regardless of the cause of stereotyped prey selection, the act itself gives a forager increased experience with the particular food. That experience is known to both modify foraging behavior (Werner et al. 1981) and influence physiological responses such as enzyme activity (Stuart et al. 1985).

In the present study, experimental combinations of foraging experience with particular species and restricted diets of those species had a significant influence on T. melones shell growth (Table 8). Some effects were positive, while others were negative, depending on the specific combinations of the original and subsequently restricted diets (Fig. 16). These data suggest that enzyme reactions may enhance or hamper prey processing. Snails with an original diet of molluscan prey (L and S, Fig. 16) that were restricted to a diet of the barnacle Tetraclita, grew less than snails with original diets that were either mixed, or focussed on Tetraclita. These data suggest that snails process barnacle tissue differently from molluscan tissue; however, snails experienced with Tetraclita did not grow less when restricted to molluscs; they grew well on Lithophaga.

In many organisms, feeding initiates the synthesis of digestive enzymes (Head & Conover 1983). Zooplankton change the ratios of gut enzyme activities, amylase to protease and amylase to laminarinase, in response to different foods (Stuart et al. 1985). The mudsnail Nassarius is reported to dramatically change enzymes in response to carrion if it has been previously feeding on a diet of plant tissues (Brown 1969). Enzyme activities are complex, but conditions where experience alters biochemical pathways deserve continued study.

Some researchers have investigated whether organisms grow well on the foods they choose most commonly. Sea urchins (Vadas 1977, Larson et al. 1980) and temperate carnivorous snails (Palmer 1983) grow better on diets of their most preferred foods. In contrast, the herbivorous snail Tegula pulligo grew more slowly on a pure diet of its preferred species than on a pure diet of a less preferred species (Watanabe 1984). Carnivorous snails in Australia (Bayliss 1982) and Japan (Luckens 1970) grew at the same rate whether they were fed their preferred species or an alternative, less preferred species. Luckens (1970) reports that snails grew equally well on barnacles or bivalves. Most researchers agree that there can be a complex interaction of environmental circumstances (e.g. predation, competition, physical conditions) in addition to food quality and predator condition that shape foraging preferences (e.g. Menge 1983). In the present study, there is no simple hierarchy of the rates at which prey species promote growth; rather, previous foraging experience and different species of prey

interact in subtle ways to influence growth.

Studies of the relationships between food species eaten and gonad development or other indices of reproductive condition can give clues to the reproductive effects of specific foraging patterns (Thompson 1982, Palmer 1983, Watanabe 1984, Hurd 1985, Fritz & Morse 1985). In my study, there were no significant differences in mean gonad development between treatments of the diet experiment (Table 8). Further, gonad development in the laboratory was not significantly different from snails sampled the same month in the field (Table 9). In contrast, shell growth in the laboratory was significantly less than in the field (Table 9). Thus, gonad development, but not shell growth was equal to that of field snails.

After feeding for 5 months on a restricted diet of a certain prey species, T. melones individuals presented with a choice of the original three prey species, usually chose the prey corresponding to their restricted diet. These results resemble the phenomenon of ingestive conditioning described by Wood (1968) where a snail's preference for the effluent of a species of prey could be changed by feeding it a restricted diet of another species. In my study, prey choice and ingestion were monitored instead of testing snail response to effluent.

It is puzzling that when the groups of focussed snails allowed to feed on their original prey (treatments LL SS TT) were compared to the groups of focussed snails restricted to prey different from their original choice (LS LT ST SL TL TS), mean shell growth was not significantly different (Table 9). Further comparisons between

other diet groups also failed to show significant differences (see results section). Prey choice in Thais melones was influenced by prior restricted diet. Because foraging experience in snails is known to increase mechanical feeding efficiency (Edwards & Huebner 1977, Hughes & Dunkin 1984a,b, Dunkin & Hughes 1984), I hypothesized that if I compared the means of experienced snails to the means of snails that were forced to change diet, shell growth should be faster in the former.

My results suggest that snails tended to do well or at least not poorly when they ate species with which they had previous experience (Fig. 16); however, the patterns are complex. Perhaps improved efficiency is important to field snails in a natural situation, but key foraging constraints lacking in the laboratory must be present for this efficiency to influence growth and reproduction.

Physical and biological conditions in the field may select for snails that attack and handle prey quickly. Studies of T. melones activity patterns (West pers. data) indicate snails forage predominantly in darkness, when they are submerged. Due to the cycling of the tides, the period of submergence corresponding with darkness shifts daily. Some 24 hour periods have very little foraging time before snails are exposed to dryness or daylight. Snails also reduce their foraging activity during rough water-flow (L. West pers. obs.). These factors in addition to periods of low-tide exposure with concurrent changes in temperature and desiccation stress (Garrity 1984) limit foraging time. Less

obvious factors such as attacks by crabs and octopus at night (L. West pers. obs.) may also limit foraging time.

With the exception of daylight, laboratory snails were free of the foraging constraints mentioned above. If some of the selective factors that encourage efficiency were not present in the lab, inefficient snails might do just as well eating slowly as their more efficient associates. (Satiation probably also plays a role in this scenario because even with unlimited food, individuals did not consume prey continuously).

My studies were not designed to test Optimal Foraging Theory (Pyke 1984) but they are pertinent to certain issues. Experience is recognized to be an important factor in optimal foraging studies because it can change the rank of prey in simple hierarchies of choice, based on factors such as calories, nutrients, etc. (Hughes 1979, McNair 1981). Because experience influences foraging behavior across a spectrum of qualities (e.g. species recognition: Ware 1971, Bryan & Larkin 1972, Pietrewicz & Kamil 1979; species choice: Rowell-Rahier 1984, Jaenike 1983, Derby & Atema 1981, Fauchald & Jumars 1979; choice of prey size: Palmer 1984, Dunkin & Hughes 1984a,b; search behavior: Heinrich 1976, 1979, Werner et al. 1981; capture: Ware 1971, Bryan & Larkin 1972, Laverty 1980; mechanical and chemical processing: Cunningham & Hughes 1984, Stuart et al. 1985), it raises difficulties for the simpler optimality models. Individuals in a population are not physiologically identical, and it is unlikely that they will have identical experiences even in the same habitat. Thus, predicting criteria for foraging that will satisfy the average individual of a

population may not be appropriate for many real individuals in a population. In my studies for example, no clear hierarchy of prey can be used to predict growth because of the interacting factors of predator experience and prey species.

CHAPTER 3

EGG CAPSULES AND LARVAL DEVELOPMENT OF THE MARINE SNAIL *THAIS MELONES* IN A ROCKY SHORE HABITAT OF PANAMA

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ABSTRACT

The tropical carnivorous whelk Thais melones deposits flattened, lens-shaped egg capsules inside clean, recently dead bivalve or barnacle shells. These egg masses were monitored in place, in a rocky intertidal habitat near the Pacific opening of the Panama Canal. Egg capsules were laid throughout the year, with embryo development times ranging from 20-39 days from deposition to hatching. The larvae hatch from the capsules as planktonic veligers. Bigger females laid larger capsules with more embryos per capsule, but this difference was not sufficient to lead to the production of more larvae per clutch. Numbers of capsules per clutch were not significantly related to snail size.

Monthly gonad samples of 20 adult snails indicate that male gonad indices remained almost constant over a year whereas females peaked from June through October. Fertile individuals of either sex were found throughout the year.

INTRODUCTION

In some prosobranch gastropod species, larvae are free-swimming veligers which hatch from capsules and develop pelagically. In others, young undergo complete development inside the capsule and juveniles hatch as a miniature form of the adult. These alternative developmental modes have been a focus of studies trying to understand the relationships between ecological conditions and life history traits of gastropods (Thorson 1950, Amio 1963, Mileikovsly 1971, Perron 1981).

Thorson (1950) noted that the majority of bottom dwelling gastropods in tropical areas have planktonic larvae while those inhabiting temperate and polar regions possess larvae that crawl from the capsule. He suggested that planktonic development in polar regions is limited in part by light constraints on phytoplankton blooms and the influence of cold temperatures. Yet, some planktonic gastropod larvae do survive well in polar regions (Thorson 1950, Mileikovsky 1971) and some tropical larvae undergo complete development inside egg capsules (Perron 1981) so that the complex of phylogenetic and environmental factors resulting in patterns of latitudinal distribution of developmental types is not yet understood.

Planktonic developmental stages may allow the juvenile to feed from a different source from that available to the adult while also providing a means of dispersion (Strathmann 1974). Concurrently, young are exposed to new sources of mortality. Some authors have discussed the possible costs and benefits of a planktonic form in an organism's life cycle (see refs. in Strathmann 1974). Menge

(1975, 1986) suggests that in the search for causes of reproductive patterns, it is important to link adult and larval ecology, for example, by exploring the possible consequences of high larval mortality on adult reproductive characteristics. Perron (1981) examined the energetic cost of egg capsules and shorter time spent in the plankton. In the Hawaiian snail Conus, species that lay relatively large eggs require longer faunal development times inside capsules and invest more energy into capsular material than adjacent species with planktonic larval development (Perron 1981). Studies that examine reproductive characteristics such as capsule structure, embryo development time within capsules, egg size, parent size, numbers of larvae per clutch etc., help to provide a base of empirical work to test more general explanations for observed biological patterns.

The present study describes the characteristics of Thais melones (order: Neogastropoda) egg capsules and the timing of capsular larval development in a rocky shore habitat of Panama. Thais melones ranges from the Gulf of Tehuantepec, Mexico to Callao, Peru and the Galapagos Islands (Keen 1971). The reproductive biology of this snail is hitherto undescribed. Results of this study indicate that T. melones have planktonic veliger larvae that hatch from capsules usually 3 to 4 weeks after deposition. The flat lens-shaped capsules deposited inside empty barnacle and bivalve shells sharply contrast to the stalked columnar and pouch-shaped egg capsules previously described for other species of temperate and tropical Thaidae.

METHODS

This investigation was done at the Naos Marine Laboratory of the Smithsonian Tropical Research Institute, Balboa, Panama, from October 1982 through December 1983. The study site was on the southern shore of Culebra Island, near the Pacific entrance to the Panama Canal (8°45'N, 79°30'W). The site consisted of shelves and deep crevices of andesite or basalt and was relatively exposed to direct wave action. For additional descriptions of the environment and biota see Glynn (1972), Reimer (1976a,b), Garrity & Levings (1981), Menge & Lubchenco (1981), and Lubchenco et al. (1984).

Observations were made during all phases of the tidal cyle, but I concentrated on periods when snails were most active, when submergence and darkness coincided. All observations, which were made while snails were submerged at night, were recorded when the water depth was not more than 1.5 m, during incoming and outgoing tides.

When I suspected that a snail was depositing egg cases I marked the substrate next to the snail with colored wax crayon. If the snail was not previously marked from my other studies (Chapter 1), it was marked with minimal disturbance in one of two ways: if the snail was dry, quick setting "five-minute" epoxy was used to glue a numbered tag to the shell; if the snail was wet, the shell was temporarily marked with crayon and later marked in the above more permanent fashion. Snails were measured on subsequent sitings when they moved away from the egg cases.

Since Thais melones lay egg cases in cryptic locations, I used

a medical otoscope to monitor them in the field. Known egg masses were monitored daily to determine field hatching time. To compare number of embryos per egg capsule to numbers hatching, one capsule from the edge of the mass was removed shortly after deposition and another just before hatching. After the larvae hatched, the entire egg mass was collected and the empty capsules were counted and measured. Any remaining embryos were also noted. To determine whether or not sampling the edge capsule introduced a bias, I counted the number of embryos per capsule on transects from the outer edge to the center of clutches of egg capsules whose age and parentage were unknown. Counts of these capsules in the laboratory indicate that there was not an obvious capsular pattern in embryo number (Table 10).

Monthly samples of 20 snails ranging from 30 to 35mm in length were collected to determine an index of gonad development. Snails were anesthetized with magnesium chloride, the shells cracked with a hammer, and then fixed in formalin for a minimum of two weeks. The gonad was separated from the other soft body tissue under a dissecting microscope and both gonad and other soft tissues were dried to constant weight. A gonad index was calculated for each individual as:

$$\frac{\text{Gonad Weight}}{\text{Gonad Weight + Other Soft Tissue Weight}}$$

GENERAL CHARACTERISTICS OF REPRODUCTION

In Thais melones, sexes are separate and fertilization is internal. From one to six copulating pairs were observed per month throughout the 14 month study, but a seasonal pattern was not apparent. None of the females from these pairs was observed in the act of depositing capsules in the field, so the time sequence of copulation and deposition was not revealed. Some details on reproduction are known for a congener Thais haemastoma, which lives on the Carribean side of Panama, that may be relevant to Thais melones. In T. haemastoma, oviposition may be preceded or followed by copulation (D'Asaro 1966), suggesting that females store viable sperm. D'Asaro (1966) describes the spawning process for T. haemastoma using morphological evidence from serial sections. Briefly, eggs collect in the lower oviduct at the site of the albumen gland. Fertilization takes place near this area. The capsule gland encloses eggs and albumen material in an envelope of 2 membranes. The snail passes the new capsule along a ciliated groove on the right side of the foot to the propodial region and the anterior pedal gland. This gland shapes and aids in cementing the capsule.

Neogastropod larvae may hatch as planktonic veligers, which spend time in the water column before metamorphosing into a crawling snail, or may undergo complete metamorphosis from swimming veliger to crawling snail inside the capsule. Thais melones hatch as planktonic veligers. The opercular plug at the top of each capsule dissolves and the veligers swim out through the opening.

The exodus is gradual as the diameter of the operculum (.25-.55mm) does not allow more than one or two veligers (.15-.20mm) to pass at a time. Attempts to culture these larvae were unsuccessful.

RESULTS

Females choose extremely cryptic locations to deposit their eggs. Their flattened, lens-shaped capsules line the inside of clean, recently dead bivalve or barnacle shells (Fig. 19). During oviposition the head and anterior portion of the foot are well extended and sometimes squeezed through relatively small openings to deposit the capsules. (The gonoduct is located on the right dorsolateral body wall just behind the head.) The clutch is usually deposited so that the individual capsules are attached to each other and the capsule mass takes on the overall shape of the shell in which they are encased. Capsules are deposited in the farthest reach of the shell first and overlap slightly, progressing toward the female's shell until the female withdraws from the host shell. In the field, egg capsules were never found outside of shells in crevices or other sites. Capsules were not deposited in old empty shells which had been colonized by common sessile species such as the bivalves Lasaea, Sphenia, Isognomon or spirorbid and serpulid polychaetes. This pattern was consistent, suggesting that snails may seek newly dead shell surfaces only, possibly for better capsule adhesion. Errant polychaetes, the crab Pachygrapsus and numerous small snails clambered about on top of capsules causing no apparent damage. Predation on T. melones capsules was never observed.

Females were not observed to lay egg masses communally in the field. In the laboratory however, three snails did lay their eggs together underneath a terracotta tile. In the field an

interspecific combination of clutches was discovered in a single large Ostrea angelica (oyster) shell. The clutches were in close proximity but not intermixed or fused. The shell contained egg capsules from other snails: Thais melones, T. triangularis, Opeatostoma pseudodon and Columbella sp.

Thais melones egg capsules within a clutch were uniform in shape, but capsule size within a clutch was somewhat variable. In 9 of 41 clutches examined, the last capsules deposited were .2 to .7 mm smaller in diameter than the first capsules and contained 14 to 86 fewer eggs. In at least 1 clutch these smaller capsules were not laid by a smaller snail adding capsules to those of a larger snail because I witnessed the deposition in the field. The other 8 clutches were probably also deposited by one snail each because within each of the 9 clutches the capsules were of the same developmental stage, and there was a slight gradation in capsule size in 4 clutches.

Numbers of embryos within capsules were relatively consistent within a given clutch (Table 10). Analysis of variance indicated that the degree of variation between clutches largely outweighed the variation of numbers of embryos per capsule within clutches (ANOVA, $p<.001$). Egg capsules were deposited throughout the year, with field development times from deposition to hatching ranging from 20-39 days (Table 11). Regardless of length of development time within the capsule, hatching size was very uniform. As embryos develop, they change color. The transparent capsules appear white for 5 to 7 days then take on a darker, creamy-yellow color. About 10 days after deposition, they develop to a rose

color. After around 16 days the rose color becomes grayish, probably due to development of the anal gland (D'Asaro 1966) and optic vesicles. The amount of swimming space for veligers within a capsule varies depending on the number of veligers per capsule. Crowding did not affect hatching success, however. Healthy capsules had close to 100% hatching rates. Unhealthy capsules were usually obvious early in the developmental sequence because embryos changed color to purple, and no embryos from such capsules survived. From 0 to 17 ($\bar{x}$=4) capsules per clutch died. Mortality occurred at different developmental stages and there was no obvious pattern or cause for the mortality.

There was no evidence of embryos feeding on nurse eggs (Thorson 1950, Spight 1976); embryo number per capsule immediately before hatching was equal to or just slightly less than the number soon after deposition (Table 11). Capsules within the same clutch hatched from one to five days apart. The order of hatching did not fit any simple pattern: for example, capsules deposited first did not necessarily hatch first.

Monthly gonad samples of 20 adult snails indicated that male gonad indices remained almost constant over a year, whereas females peaked from June through October (Fig. 20). Fertile individuals of either sex were found throughout the year. The sex ratio was approximately equal, and monthly samples of smaller snails suggest that snails become reproductive at a shell length of about 21mm.

There was a positive relationship between size of snail and various parameters of the snail's reproductive biology, measured in

several ways. Bigger females laid larger capsules with more embryos per capsule (regressions, $p<0.01$; $p<0.05$; Fig. 21a&b). This difference was not sufficient to lead to the production of more larvae per clutch ($p>0.05$: Fig. 22). Larger females may lay fewer capsules/clutch but the regression was not significant ($p>0.05$; Fig. 23a). Reproductive output (biomass or calories) probably did not vary with size either, since the embryos developing from larger females were not significantly larger than those from small females (regressions, $p>0.05$; Fig. 23b). Except for the few cases of declining capsule size in the later stages of capsule deposition, capsule size and number of embryos per capsule were relatively constant within a clutch of capsules.

Analysis of all clutches, including those for which parental size was unknown, indicates that larger capsules contained more embryos (regression, $p<0.001$; Fig. 24a). However, larger clutches did not contain significantly larger capsules (regression, $p>0.05$; Fig. 24b). Further, embryo size was not associated with either number of embryos per capsule (regression, $p>0.05$) or capsule size ($p>0.05$).

DISCUSSION

The flattened egg capsules deposited by Thais melones are a striking contrast to the columnar egg capsules reported for other Neogastropoda (Thorson 1950, Kohn 1961, Phillips 1969, D'Asaro 1970) and observed with Thais triangularis and T. kiosquiformis in Panama Bay (L. West unpublish. data). Thais melones capsules are also more cryptic than the capsules of many other species because individual females deposit their clutches inside clean shells of bivalves and barnacles. This cryptic location is probably less obvious to predators (Menge & Lubchenco 1981, Menge et al. 1986) and is likely to reduce heat and desiccation stress (Garrity 1984). In Panama Bay other species of snails occasionally deposit their columnar capsules inside shells, but they do not appear to be as faithfully restricted as Thais melones.

Thais melones larvae hatch from their capsules as free-swimming veligers. The opercular plug at the apex of the capsule dissolves and the veligers gradually swim through the opening. Prosobranch capsules that have been analyzed by histochemistry show they are composed of several structural layers of carbohydrate and protein (Bayne 1968, Sullivan and Maugel 1984). Pelseneer (1935) and Sullivan and Maugel (1984) suggest that the larvae may release a protease or carbohydrase that dissolves the operculum when they reach a certain developmental stage.

Deposition of capsules and hatching of larvae occur throughout the year for T. melones. The peak of female gonad development occurred from June to October when water temperatures are

seasonally higher (Lubchenco et al. 1984). Without controlled experiments the influences of temperature on spawning cannot be unravelled. The snails Dicathais, Ocenebra, and Thais canaliculata are reported to spawn in response to temperature fluctuations (Phillips 1969, Hancock 1959, Houston 1972), yet Thais emarginata does not (Houston 1972). Intertidal snails exposed to daily high variation in temperature might respond to temperature differently than a related species that lives in a subtidal, more constant temperature regime. Houston (1972) and Phillips (1969) report that, like T. melones, North-west American Thais emarginata and West Australian Dicathais aegrota deposit egg capsules throughout the year. Mileikovsky (1971) proposes that continuous annual spawning is likely to reduce the chances of recruitment failure for individuals of species with prolonged pelagic larval development.

Prosobranch species living in tropical areas tend to have planktonic larvae and species living in temperate regions tend to have larvae that crawl out of egg cases (Thorson 1950, Mileikovsky 1971). Thais melones in Pacific Panama fit this pattern but as the literature expands, contrary examples of development continue to be found (See refs in Menge 1975). Thorson (1950) also reports that the broad-ranging Atlantic species Thais haemastoma has nurse egg development in higher latitudes and planktonic development in lower latitudes. No nurse egg development was observed in the present study; numbers hatching from each capsule closely reflected initial embryo counts. Since Thais melones is also a broad-ranging species, it would be informative to have reproductive studies from higher latitudes and in areas such as the Galapagos where both cold

and warm currents influence rocky shores in relatively close proximity. Dicathais also does not have nurse eggs but commonly had leftover eggs in the capsules that may have been unfertilized (Phillips 1969). Though T. melones do not have nurse egg feeding, they might obtain additional nutrition required for early development by ingesting albuminous capsular fluid as reported in T. haemastoma (D'Asaro 1966).

Development times within capsules sometimes increase with egg size for closely related species faced with similar water temperatures (Spight 1975, Perron 1981). Perron (1981) reports that larger eggs take longer to develop in Conus in Hawaii, and that more energy is apportioned into protection in capsules that contain larvae for longer periods. Duration of pelagic larval development is inversely related to egg size in Hawaiian Conus. Although similar data are not available for Thais species it is notable that with the exception of the Indian Ocean species (Table 12), planktonically developing Thais from very different geographical locations have relatively uniform ovum size and overlapping ranges of embryo development times within capsules.

The degree of interspecific difference in capsule shape is highly variable for Neogastropods. In some genera, capsules are clearly species specific: Murex, Nassa (Thorson 1959), Thais species from Florida (D'Asaro 1970), and Thais species from Pacific Panama (L. West, unpublished data). On the other hand, intraspecific differences mask interspecific characteristics of capsules in Conus species (Kohn 1961). There is little

intraspecific variability in egg capsule morphology of Thais melones. All capsules are uniform in shape.

No communal spawning was observed in Thais melones as was seen in other Panamanian species like Thais kiosquiformis, Acanthina and Muricanthus (L. West unpublished data), and as has been reported for other species (D'Asaro 1970, and Phillips 1969). Interspecific communal spawning has been reported by D'Asaro (1966) but it is not clear if the spawning is chemically stimulated as D'Asaro proposed, or if these interspecific communal sites occur simply because there are relatively few good sites for deposition.

When embryos died, all members of one capsule died and the capsule turned a darker, purple color. No developmental stage appeared to be free from occasional mortality of a few capsules. Similar color change of dead capsules occurs in other species (Kohn 1966, Phillips 1969, Hancock 1960). In Thais melones, capsule mortality was low. In contrast, temperate Thais lamellosa lay their egg capsules in open areas that give high mortality due to physical factors but which allow the newly hatched crawl-out young ready access to a supply of small barnacle prey (Spight 1977).

Some aspects of Thais melones reproductive biology resemble those reported for other Neogastropods. Size at hatching for T. melones was consistent both within and between clutches, independent of the development times for individual clutches. Larger snails produced larger capsules that contained significantly more embryos. Thais melones and other planktonically developing Thais from very different geographical locations have relatively uniform ovum size and overlapping ranges of embryo development times within capsules.

Table 1. Densities of common carnivorous snail species summarized from daily counts of individuals on the study surfaces at low tide.

NUMBER OF SNAILS PER METER^2

Species	Site A ‡			Site B ‡					
	1980 64 days			1982 116 days			1983 122 days		
	mean	range	S.D.	Mean	Range	S.D.	Mean	Range	S.D.
Thais melones	1.35	14-58	.595	0.440	10-49	.236	.520	10-40	.198
Acanthina brevidentata	1.03	4-47	.514	1.98	16-81	.714	2.13	13-98	.685
Opeatostoma pseudodon	.14	0-8	.141	0.061	0-7	.060	.070	0-12	.077
Thais triangularis	.12	0-5	.087	0.060	0-7	.047	.064	0-9	.050
Leucozonia cerata	.05	0-3	.048	----------			----------		
Muricanthus radix	.08	0-5	.080	----------			----------		
Columbella labiosa	--------			0.048	0-11	.084	.039	0-13	.092

‡ Total surface area of study sites is 22.14m for site A and 43.57m for site B.

Table 2. Sizes and consumption times of prey species eaten by Thais melones under natural conditions in the field.

SPECIES	LARGE N	LARGE predator size(mm)	LARGE prey size(mm)	LARGE time (hrs)	MEDIUM N	MEDIUM predator size(mm)	MEDIUM prey size(mm)	MEDIUM time (hrs)	SMALL N	SMALL predator size(mm)	SMALL prey size(mm)	SMALL time (hrs)
Ostrea	11				13				4			
	mean	33.8	22.2	16.7		25.4	16.7	11.8		15.3	17.7	15.4
	range	30.5-40	13-31	3.5-33		20.5-29.5	4-27.5	2.5-21.5		12.5-17	11.5-23	9-26.5
	S.D.	3.3	6.2	8.0		2.7	6.7	5.7		1.7	4.1	6.6
Siphonaria	4				13				7			
	mean	35.4	11.0	9.1		24.0	10.3	8.9		16.9	8.8	8.2
	range	34-38.5	10-12	4.5-13.5		20.5-29	7-16	2.5-14		12-20	3-12	5-14.5
	S.D.	1.9	0.8	3.3		2.7	2.8	3.9		2.8	2.9	3.1
Balanus	0				3				1			
						20	4	6		17.5	5	4
						26.5	3	3.5				
						27	4	9				
Serpulid worms					2				3			
						23	1.5	3		10	3	6
						26	2	3		16.5	2	9.5
										17	3	8
Brachiodontes					1				2			
						29	10	4		8	6	7
										9	6.5	4.5

Table 2. continued

SPECIES	LARGE N	LARGE predator size(mm)	LARGE prey size(mm)	LARGE time (hrs)	MEDIUM N	MEDIUM predator size(mm)	MEDIUM prey size(mm)	MEDIUM time (hrs)	SMALL N	SMALL predator size(mm)	SMALL prey size(mm)	SMALL time (hrs)
Isognomon									3			
										11	11.5	6
										18.5	10	10
										19	14	7.5
Vermetids	3											
		21	8	24								
		25	10	30.5								
		31	9	22								
Anachis									2			
										11	5.5	15
										13	5	8.5
Acanthina	1											
		31	19	29								
Lithophaga					1							
						28.5	21	10				

Table 3. Longterm feeding observations of individual diets for *Thais melones*.

Individual Diet---------->	1982								1983					
	Feb. - May					June - Oct.	Nov. & Dec.				Jan. - Mar.			
						No Observations								
r48	O	Is	O			----------	O	O	O		O	Is	O	O	O	O
r64	O	Sm	X	Sm	Ser	----------	Ver	Ver	O	Sm	Sm	Ver	O			
R93	Sm	Sm	Sm	Sm		----------	Sm	O			Sm	Sm	Sm	O		
G6	Fos	Fos				----------	Ser	Mit	Ner	Mit	An					
B87	Is					----------	Brc	Sm	Is		O	Is				

KEY TO SYMBOLS

Bivalves
- O Ostrea
- Is Isognomon
- Brc Brachidontes

Limpet
- Sm Siphonaria

Sessile snail
- Ver vermetid

Coiled snails
- Fos Fossaris
- Mit Mitra
- Ner Nerita
- An Anachis

Polychate worms
- Ser serpulid

Unidentified organisms cryptically positioned
- X

Table 4. Linear regression between growth and diet specialization index, prey species, and initial predator size for *Thais melones*. Regression model is: growth = 2.795 + 0.197(diet specialization index) + 0.68(prey species code) - 0.081(initial predator size).

VARIABLE	COEFFICIENT	STD. ERROR	STD. COEF.	TOLERANCE	T	P(2 TAIL)
constant	2.795	0.492	0	0	5.68	0.000
diet index	0.197	0.079	0.0235	0.90911	2.48	0.016
species	0.068	0.043	0.152	0.90054	1.59	0.115
initial sz	-0.081	0.014	-0.541	0.98294	-5.94	0.000

ANALYSIS OF VARIANCE

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
regression	43.199	3	14.4	15.440	0.000
residual	70.877	76	0.933		

Table 5 a,b,c. Linear regressions between growth rate and diet specialization index, species and initial size for Thais melones grouped by size class: a. small < 20mm b. 20 ≤ medium ≤ 30mm c. large > 30mm.

Table 5a. REGRESSION MODEL

small snails growth = 3.33 + .078(specialization index) + .105(species) - .107(initial size)

VARIABLE	COEFFICIENT	STD. ERROR	STD. COEF.	TOLERANCE	T	P(2 TAIL)
CONSTANT	3.337	1.330	0.	.	2.51	.020
Diet index	0.078	0.204	0.075	0.97752	.38	.705
Species	0.105	0.097	0.212	0.98229	1.09	.289
Initial size	-0.107	0.069	-0.299	0.99281	-1.55	.136

ANALYSIS OF VARIANCE

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
REGRESSION	4.700	3	1.567	1.279	.305
RESIDUAL	28.167	23	1.225		

Table 5b. REGRESSION MODEL
medium snails growth = 2.09 + .359(specialization index) + .101(species) - .068(initial size)

VARIABLE	COEFFICIENT	STD. ERROR	STD. COEF.	TOLERANCE	T	P(2 TAIL)
CONSTANT	2.093	1.537	0.	.	1.36	.184
Diet index	0.359	0.123	0.501	0.85271	2.91	.007
Species	0.101	0.058	0.293	0.87354	1.72	.096
Initial size	-0.068	0.057	-0.193	0.95232	-1.19	.244

ANALYSIS OF VARIANCE

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
REGRESSION	10.908	3	3.636	3.917	.019
RESIDUAL	25.994	28	0.928		

Table 5c. REGRESSION MODEL
large snails growth = 1.078 + .119(specialization index) - .058(species) - .020(initial size)

VARIABLE	COEFFICIENT	STD. ERROR	STD. COEF.	TOLERANCE	T	P(2 TAIL)
CONSTANT	1.078	1.632	0.	.	.66	.518
Diet index	0.119	0.094	0.302	0.82269	1.26	.226
Species	-0.058	0.068	-0.200	0.87811	-.86	.401
Initial size	-0.020	0.044	-0.106	0.90703	-.46	.649

ANALYSIS OF VARIANCE

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
REGRESSION	1.770	3	0.590	1.363	.288
RESIDUAL	7.363	17	0.433		

Table 6. Sizes and consumption times of prey species supplied to *Thais melones* in the laboratory.

Species	Size				Time		
	$\bar{X}$ mm	S.D.	range	n	$\bar{X}$ hrs	S.D.	range
Siphonaria maura shell length	15.18	0.77	14-16	20	6.28	2.86	2-14
Lithophaga sp. shell length	27.78	0.94	26-29	20	12.08	5.32	1-22
Tetraclita panamensis basal diameter	16.73	1.30	14-18	20	8.78	3.31	3-17

Table 7. Means of shell growth (mm measured at the aperture lip) for the experimental treatments combining original diet and restricted diet for Thais melones. Diets consist of: L = Lithophaga (bivalve), S = Siphonaria (limpet), T = Tetraclita (barnacle), and M = mixed diet of all 3 prey species.

			RESTRICTED DIETS			
			M	L	S	T
ORIGINAL DIETS	M		MM	ML	MS	MT
		$\bar{X}$	2.298	1.210	1.094	1.662
		N	13	11	16	14
		SD	1.419	.645	.990	1.161
	L		LM	LL	LS	LT
		$\bar{X}$	1.540	1.450	2.423	.574
		N	16	16	16	14
		SD	1.305	.971	2.042	.380
	S		SM	SL	SS	ST
		$\bar{X}$	.959	1.281	1.323	.644
		N	16	12	13	16
		SD	.369	.726	1.486	.433
	T		TM	TL	TS	TT
		$\bar{X}$	1.021	1.794	1.323	.644
		N	12	15	15	14
		SD	1.375	1.331	.461	1.141

Table 8. The effect of original diet, restricted diet and sex on shell growth and gonad development using multivariate analysis of variance (MANOVA). Subsequent multiple comparisons were done using ANOVA with the critical levels adjusted with the Bonferroni approximation (Neter and Wasserman 1974). Degrees of freedom in parentheses.

	MANOVA Significant Effects on Shell Growth combined		ANOVA Significant Effects on Shell Growth univariate F tests					
	F	prob.		F	prob.		F	prob.
	5.179 (222)	.006 *		6.381	.012 *	Gonad Index	4.882 NS	.028
Original Diet = O	4.440 (2,220)	.013 *		6.748 (1,221)	.010 *		2.840 (1,221) NS	.093
Restrict Diet = R	3.828	.023 *		7.611	.006 *		.261 NS	.610
Sex = X	2.851 NS	.060		2.154 NS	.144		4.024 NS	.046

Table 8. continued

MANOVA			ANOVA					
	Significant Effects on Shell Growth				Significant Effects on Shell Growth			
	combined		univariate F tests					
	F	prob.	F	prob.	F	prob.	F	prob.
Interactions								
Original by Restricted diet	3.933	.021 *	6.004	.015 *	2.486	.116 NS	5.985	.015 *
Original diet by Sex	3.014	.051 NS	2.699	.102 NS	3.852	.051 NS		
Restricted diet by Sex	1.330	.267 NS	.531	.467 NS	2.307	.130 NS		
Original by Restricted diet by Sex	2.378	.095 NS	1.434	.232 NS	3.694	.056 NS		

Table 9. Comparison of laboratory shell growth and gonad development to field values for Thais melones from July 1st to November 30, 1983, using the Wilcoxon two-sample test; * = 0.05>P>0.02.

	Initial size		Shell growth		Final Size		Gonad Index	
	field	lab	field	lab	field	lab	field	lab
				*				NS
Mean	23.05	23.25	1.943	1.389	24.69	23.99	0.013	0.019
Standard Dev	4.76	3.96	1.128	1.205	2.94	3.64	0.012	0.016
N	47	229	47	229	8	229	8	229

Table 10. Summary of the numbers of embryos per capsule for *Thais melones* from a sample of 10 capsules per clutch, with a sample size of 10 clutches.

Clutch	Number of capsules per clutch	Number of embryos per capsule 10 sample capsules (edge) 1	2	3	4	5	6	7	8	(inside) 9	10	Number of embryos per capsule range	mean	S.D.	coefficient of variation
1	40	230	177	249	279	245	241	236	254	194	262	177-279	244.4	28.9	0.12
2	28	141	163	164	154	139	144	137	158	129	136	129-164	146.5	11.6	0.08
3	39	120	98	108	97	119	113	126	122	117	103	97-126	112.3	9.7	0.09
4	36	188	170	186	169	191	184	189	175	171	179	169-191	180.2	8.0	0.04
5	67	216	203	207	232	222	219	209	218	217	216	203-232	215.9	7.7	0.04
6	27	258	241	239	251	220	255	246	252	242	240	220-258	244.4	10.3	0.04
7	42	84	96	99	93	89	90	86	85	83	95	83-99	90.0	5.2	0.06
8	49	127	122	120	119	128	130	117	122	128	109	117-130	122.2	6.0	0.05
9	44	46	82	53	8	79	61	56	48	46	55	46-82	57.4	12.4	0.22
10	35	117	136	110	126	116	130	111	133	135	121	110-136	123.5	9.3	0.08

Table 11. Development times of Thais melones larvae in the field when female and egg capsules were observed during spawning.

Size of Female	No. of capsules	Mean size of capsules	No. of Larvae 1st observ.	No. of Larvae near hatching	Date deposited	Date hatched start/finish	A	B	C
18mm	57	2.6mm	46	48	7/28/83	8/21-8/26	24	5	0
20	40	2.3	97	103	11/10/83	11/30-12/3	20	3	0
22	26	2.3	76	66	8/9/83	9/7-9/11	29	4	6
24	24	3.1	156	142	5/24/83	7/20-7/21	27	1	2
27	37	3.4	141	198	12/18/82	1/26-1/28/83	39	2	1
28	39	2.9	143	185	7/21/83	7/17-7/18	26	1	0
30	12	3.5	155	153	6/16/83	7/16-7/18	31	2	3
34	35	3.6	120	89	9/5/83	9/29-10/1	24	3	0
41	27	4.8	258	261	8/12/83	9/15-9/19	34	4	2

A. No. of days from deposition to first hatching.
B. No. of days between 1st capsule hatching and last capsule hatching.
C. No. of capsules whose embryos died.

Table 12. Larval development of Neogastropoda species with planktonic veligers.

Species	Ova/Capsule	Ovum size(mm)	Development time in days	Hatchlings /capsule	Hatched veliger size(mm)	Location	References
Thais melones	46-258	.1-.15	20-39	46-258	.2-.25	Pacific Panama	this paper
Thais carinifera	146	.20-.25	4	-----	.417	Indian Ocean	Natarajan 1957
T. javanica	57-91	.20	4-5	-----	.367	Indian Ocean	Natarajan 1957
T. haemastoma	1500-2000	.11-.13	30	1000-2000	.21	Mediterranean	Franc 1943*
T. haemastoma	600-700	------	12-14	-----	.16	Mississippi	Moore 1961
T. haemastoma	500-900	.10	15-17		.13	Florida	D'Asaro 1966
Dicathais aegrota	730-7180	----	20-70		.24	Australia	Phillips 1969
Chicoreus ramosus	300-346	.25	35-38	18-21	1-1.1		Eisawy 1961*
Chicoreus ramosus	1000-2500	.18-.20	40-45	30-40	1.1		Eisawy 1961*
Murex trapa	163-204	0.267	20	10-26	1-1.27	Indian Ocean	Natarajan 1957
Rapana venosa	400-1000	.25	12	-----	.40	Japan	Amio 1963
Siratus ponderos	440-731	.2-.217	20	-----	-----	Indian Ocean	Natarajan 1957
Bedevina birileffi	60-90	.19	14	-----	.31	Japan	Amio 1963
Conus pennaceus	80	.46	16	-----	1200	Hawaii	Kohn 1961
C. quercinus	9700	.215	15-16	-----	285	Hawaii	Kohn 1961
C. abbreviatus	1300	.20	14	-----	270	Hawaii	Kohn 1961

* = Reference from Shuto 1983

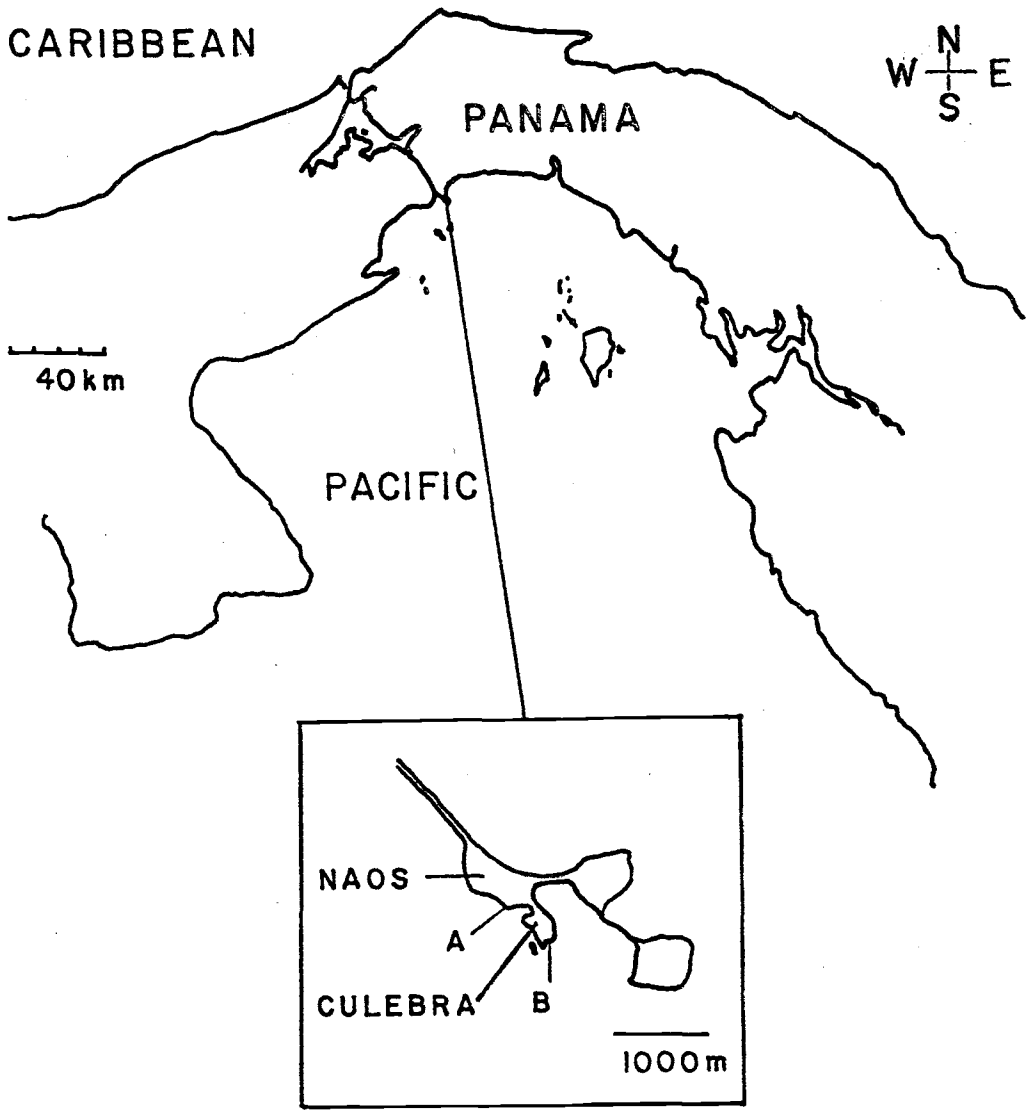

Fig. 1. Map of the study sites.

Fig. 2. Summary of observed feeding attacks by Thais melones. Solid lines indicate densities of prey changed to percentages while dotted lines indicate percentage cover estimates from 100 random points per meter^2.

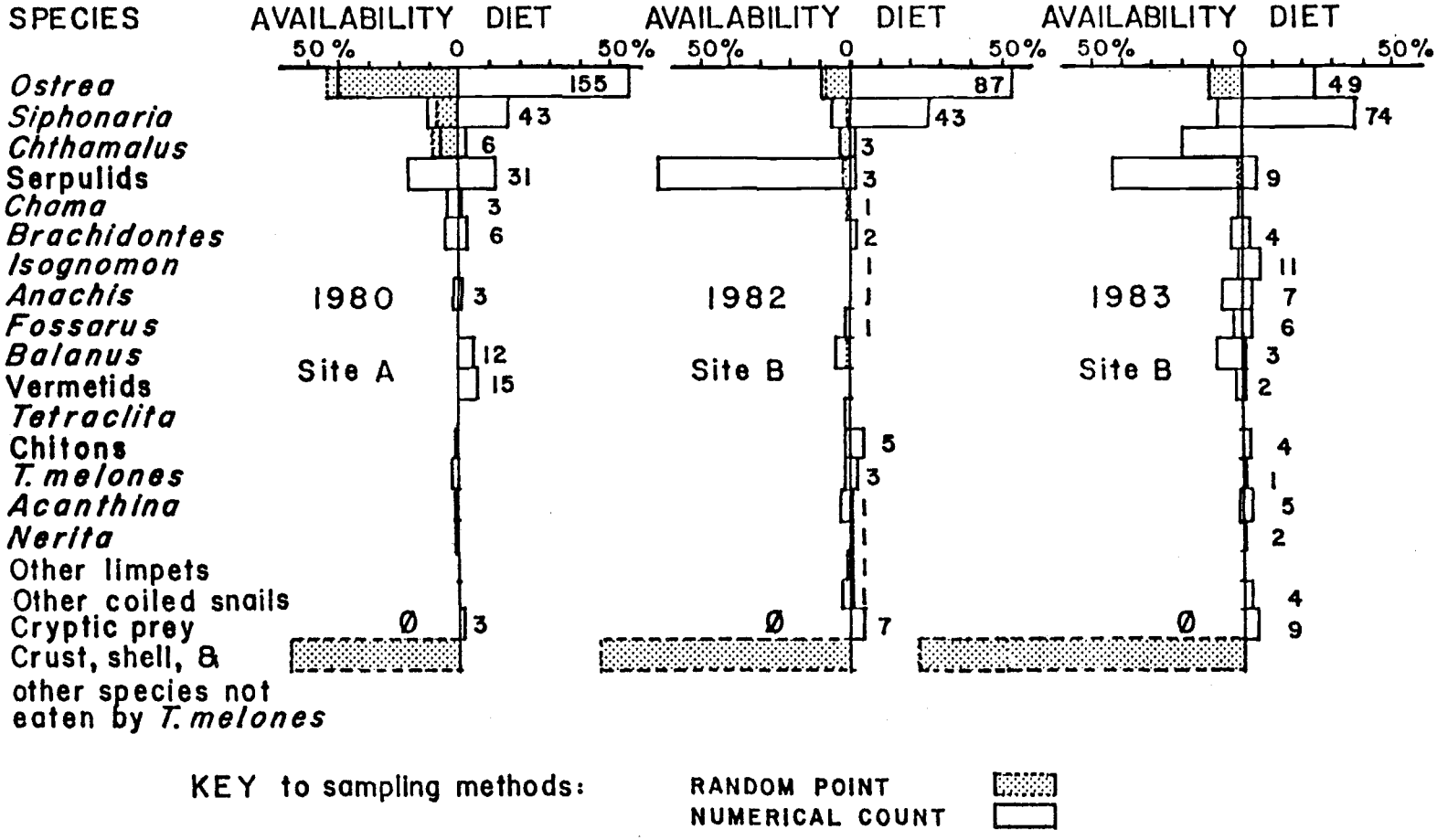
SPECIES
AVAILABILITY DIET
AVAILABILITY DIET
AVAILABILITY DIET
50% 0 50%
50% 0 50%
50% 0 50%
Ostrea
Siphonaria
Chthamalus
Serpulids
Chama
Brachidontes
Isognomon
Anachis
Fossarus
Balanus
Vermetids
Tetraclita
Chitons
T. melones
Acanthina
Nerita
Other limpets
Other coiled snails
Cryptic prey
Crust, shell, & other species not eaten by T. melones
155
43
6
31
3
6
3
12
15
3
Ø
1980
Site A
87
43
3
3
1
2
1
1
1
5
3
1
1
1
7
Ø
1982
Site B
49
74
9
4
11
7
6
3
2
4
1
5
2
4
9
Ø
1983
Site B
KEY to sampling methods:
RANDOM POINT
NUMERICAL COUNT

Fig. 2

Fig. 3. Individual diet sequences of *Thais melones* that were observed feeding five or more times. Prey species represented: *Ostrea* spp.= Os, *Brachidontes* sp.= Brc, *Chama echinata*= Chm, *Siphonaria maura*= Sm, vermetid gastropods= Ver, *Balanus* sp.= Bal, serpulid worms= Ser, and unobservable organisms located inside shell or rock= X. Data for snails <20mm shell height, 1980 only, all other diets located in appendix.

Snails <20mm in Shell Height, 1980

Individual	Diet	
64	Bal Os Os X Os Os Sm Sm Os Sm Sm Sm	4 (12)
31	Os Sm Os Os Sm Sm Sm Sm Brc	3 (9)
13	Os Ser Os Ser Ser Sm Ser Ser	3 (8)
39	Os Os Os Os Os Bal Bal	2 (7)
60	Os Sm Ser Ser Ser Ser Ser	3 (7)
107	Bal Bal Bal Brc Ser Bal Brc	3 (7)
53	Os Ser Ser Os Sm Sm Sm	3 (7)
24	Os Os Os Sm Os Sm Os	2 (7)
65	Ser Ser Ser Ser Ser Os Ser	2 (7)
21	Os Os Ser Os Os Ser Os	2 (7)
92	Sm Ver Chm Ser Ser Os	5 (6)
58	Ver Os Os Os Os X	2 (5)
69	Sm Brc Sm Sm Sm	2 (5)
20	Sm Sm Ser Sm Sm	2 (5)
36	Bal Bal Bal Bal Bal	1 (5)
25	Sm Ver Sm Os Os	3 (5)
51	Bal Sm Sm Bal Bal	2 (5)

Fig. 3

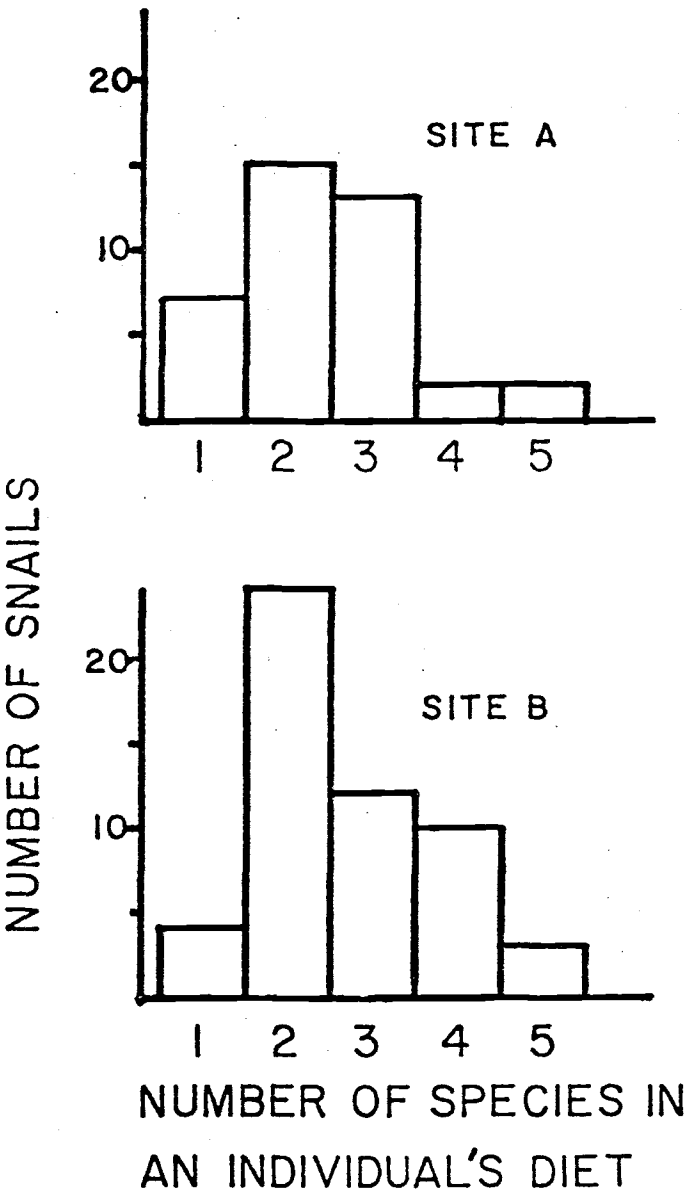

Fig. 4. Summary of individual Thais melones diets that contained from one to five prey species.

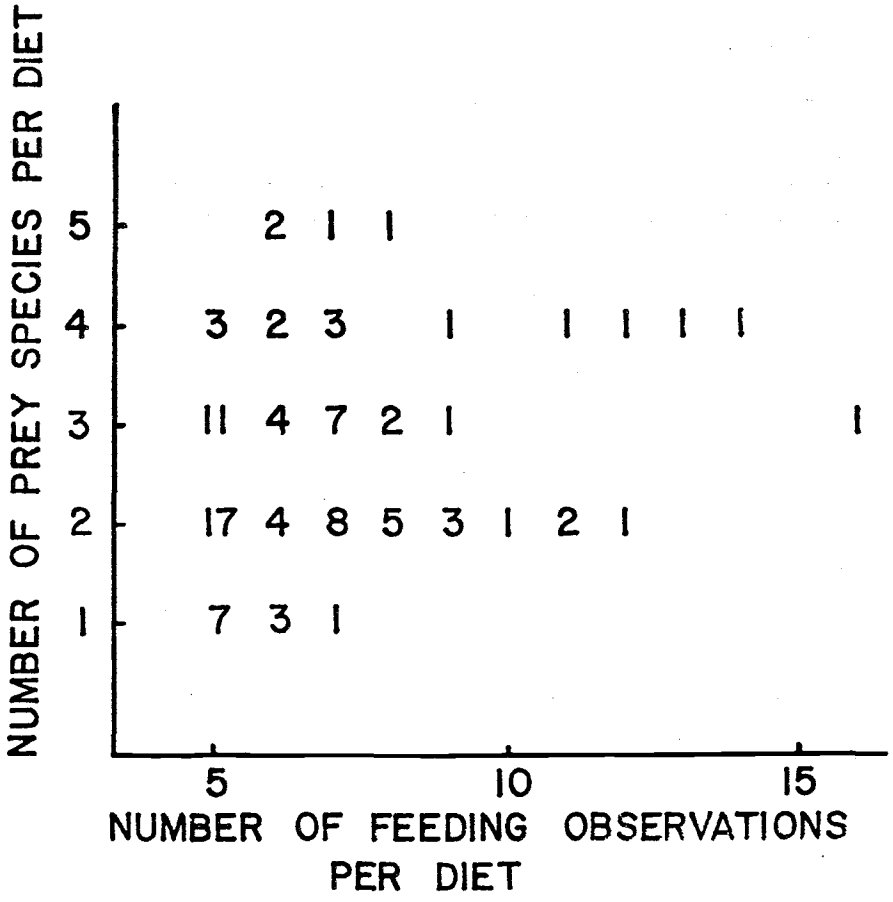

Fig. 5. Number of prey species per individual diet sequence in relation to the number of feeding observations in the individual diet sequence.

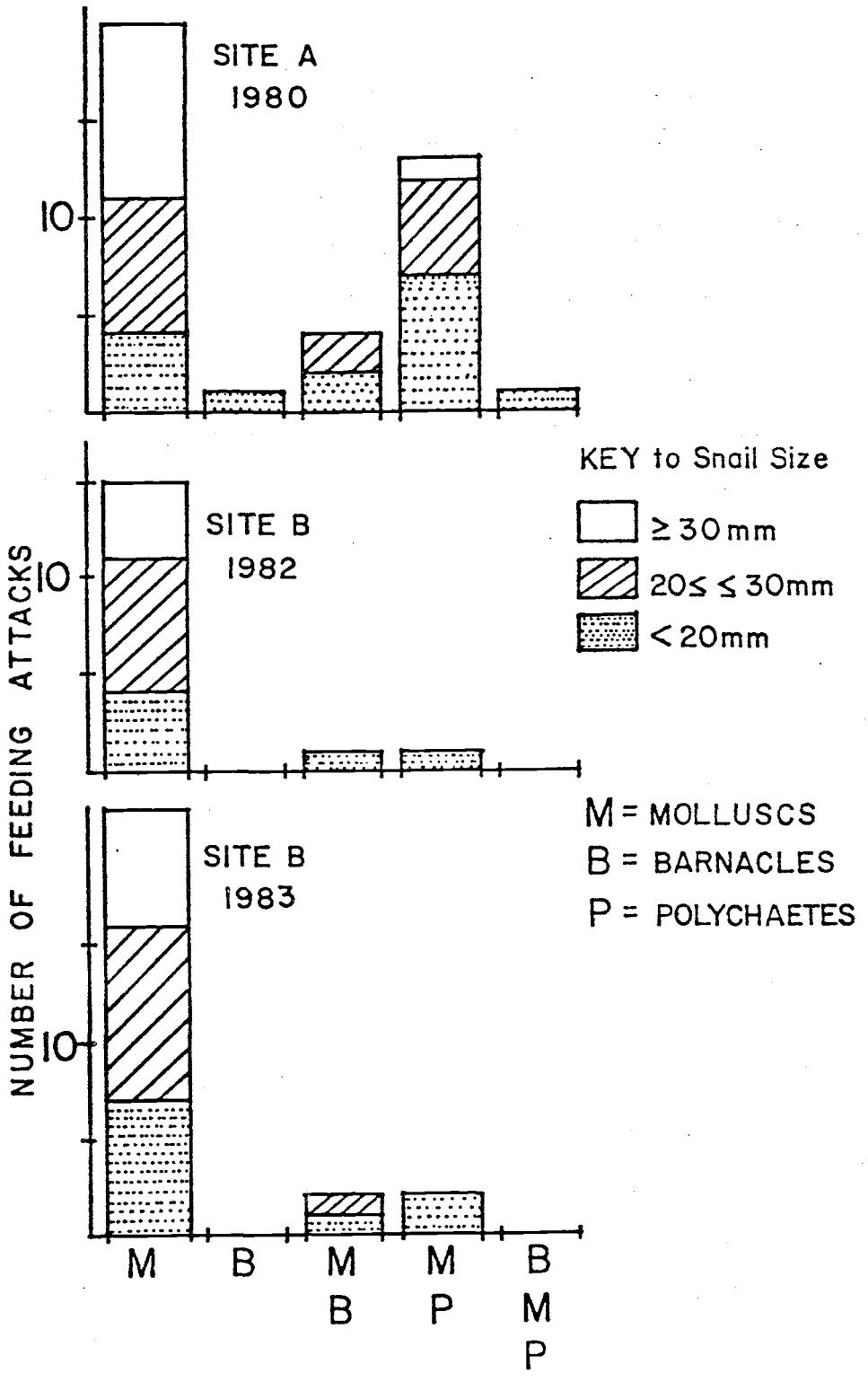

Fig. 6. Summary of observed feeding attacks by Thais melones grouped by size class and prey category.

Fig. 7. Net displacement record and sequential feeding attacks made by two Thais melones in 1980 at site A. Sequential observation periods were numbered (see numbers along the snail path). The number of observation periods that the snail remained at the specific location is also indicated by those numbers. Letters indicate prey eaten: S = Siphonaria, O = Ostrea, and Ser = serpulid polychaetes. Availability of prey species on the rock surfaces that the snail moved across are summarized at right.

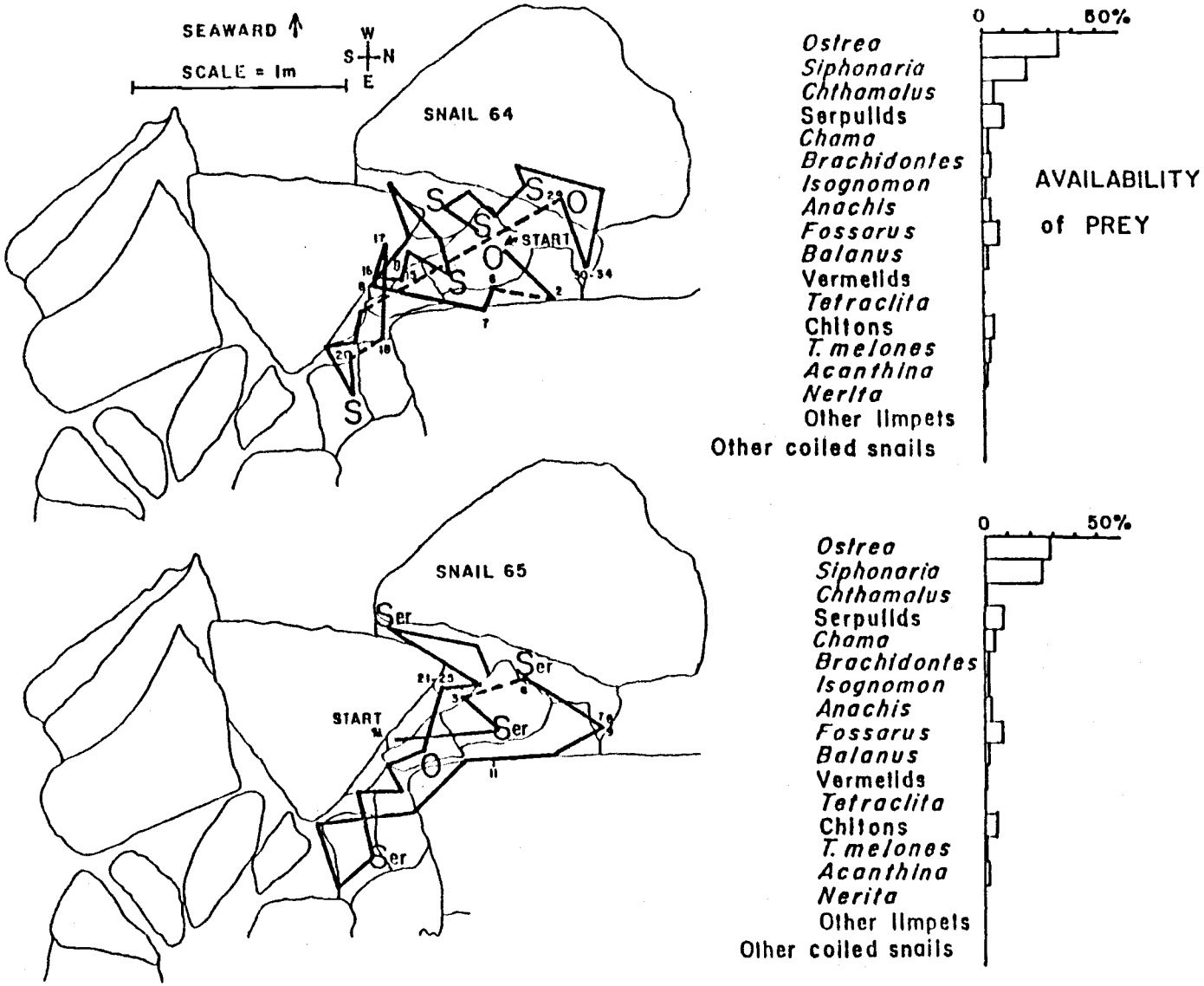
SEAWARD
SCALE = Im
W
S
N
E
SNAIL 64
START
SNAIL 65
START
Ser
0
50%
Ostrea
Siphonaria
Chthamalus
Serpulids
Chama
Brachidontes
Isognomon
Anachis
Fossarus
Balanus
Vermetids
Tetraclita
Chitons
T. melones
Acanthina
Nerita
Other limpets
Other coiled snails
AVAILABILITY
of PREY

Fig. 7

Fig. 8. Net displacement record and sequential feeding attacks made by two Thais melones in 1980 at site A, as in Fig. 7. Letters indicate prey eaten: O = Ostrea and V = vermetid gastropod.

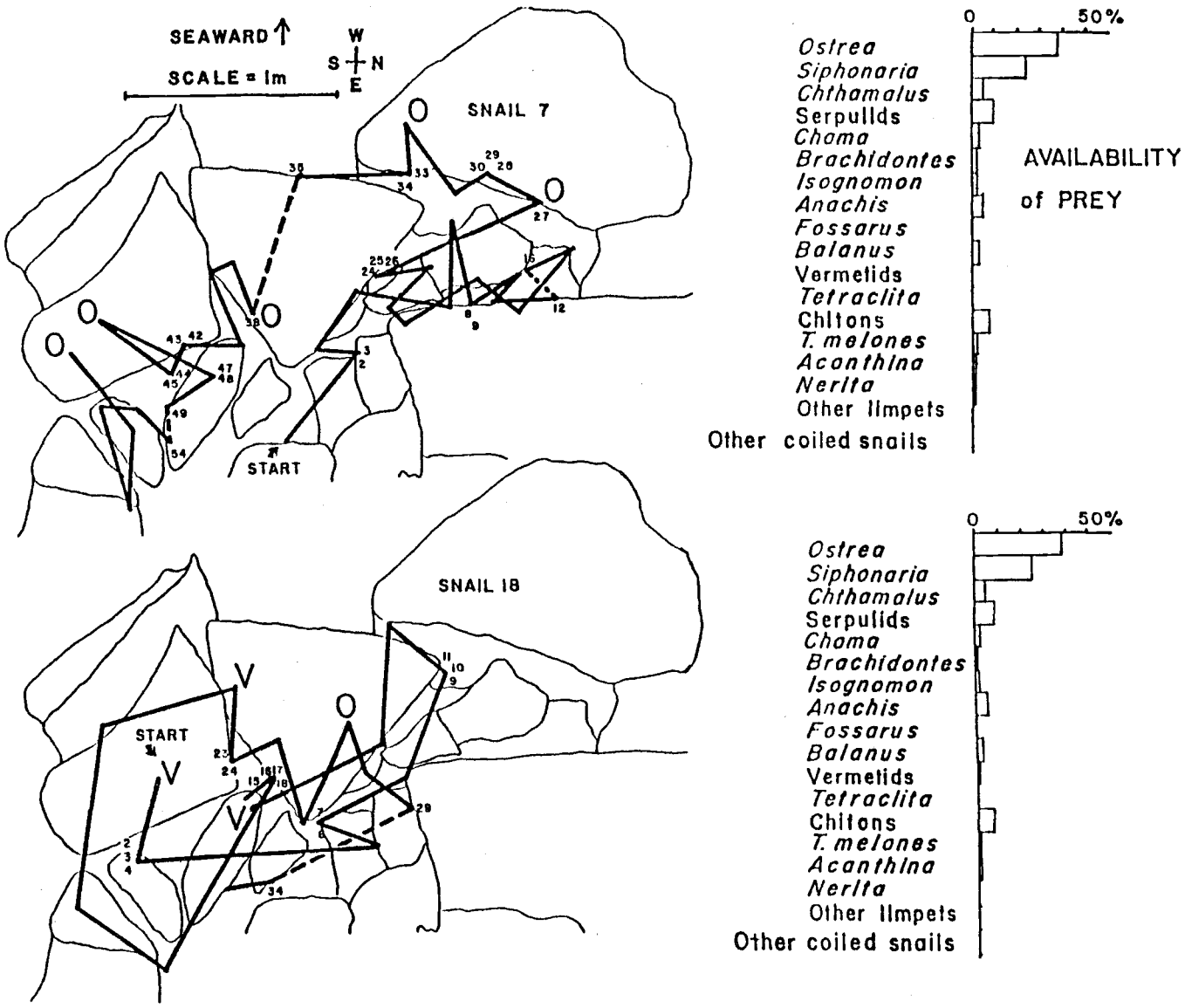
SEAWARD
SCALE = 1m
W
S
N
E
SNAIL 7
START
SNAIL 18
START
0
50%
AVAILABILITY
of PREY
Ostrea
Siphonaria
Chthamalus
Serpulids
Choma
Brachidontes
Isognomon
Anachis
Fossarus
Balanus
Vermetids
Tetraclita
Chitons
T. melones
Acanthina
Nerita
Other limpets
Other coiled snails

Fig. 8

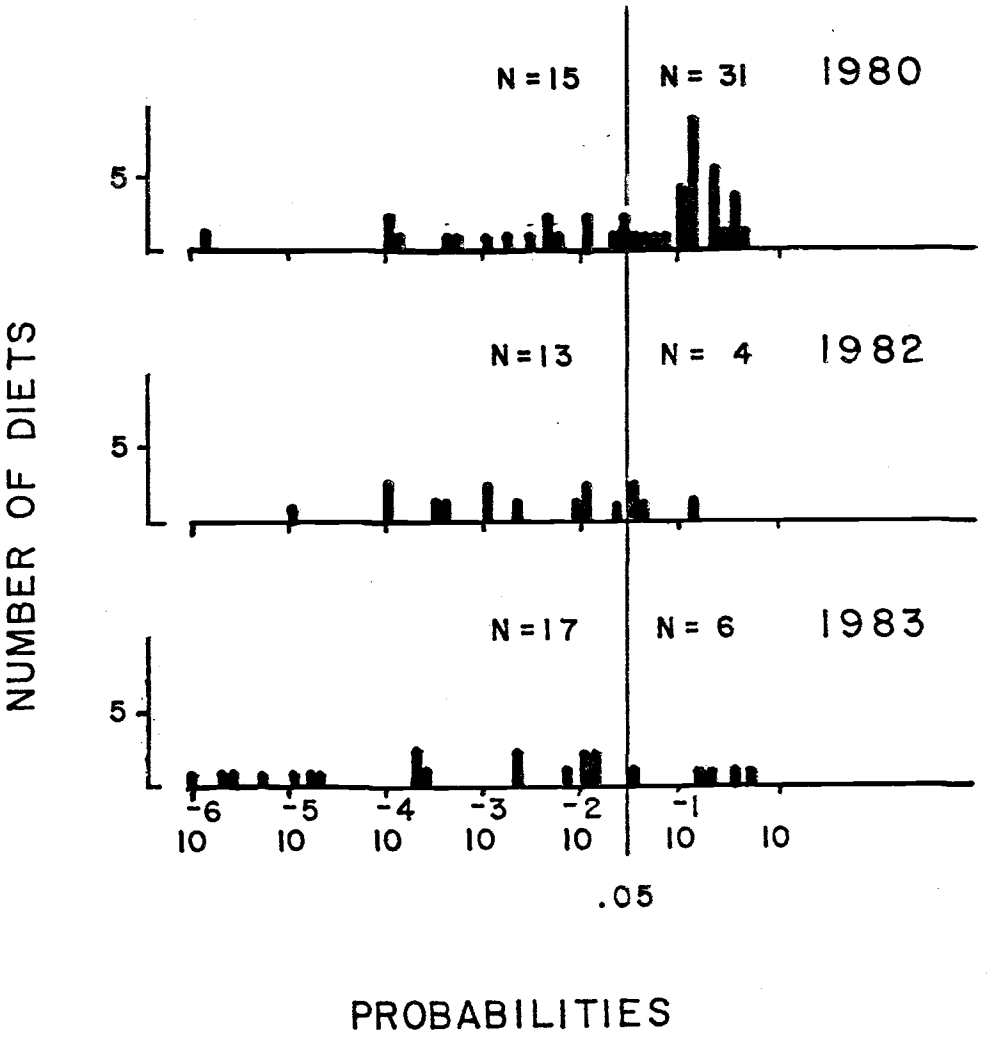

Fig. 9. Distributions of the calculated probabilities of obtaining the observed diet sequences if Thais melones were to eat what ever prey they contacted while moving about (see methods). Diet probabilities less than 0.05 indicate that it is very unlikely that those diets were obtained by chance encounter with prey.

Fig. 10. Plots of Thais melones shell growth in relation to the diet specialization index:

$$SI = \left(\frac{\text{number of the most abundant species in an individual sequence}}{\text{number of prey in the individual sequence}} \right) + \left(\frac{\text{number of prey in the individual sequence}}{\text{number of species in the individual sequence}} \right)$$

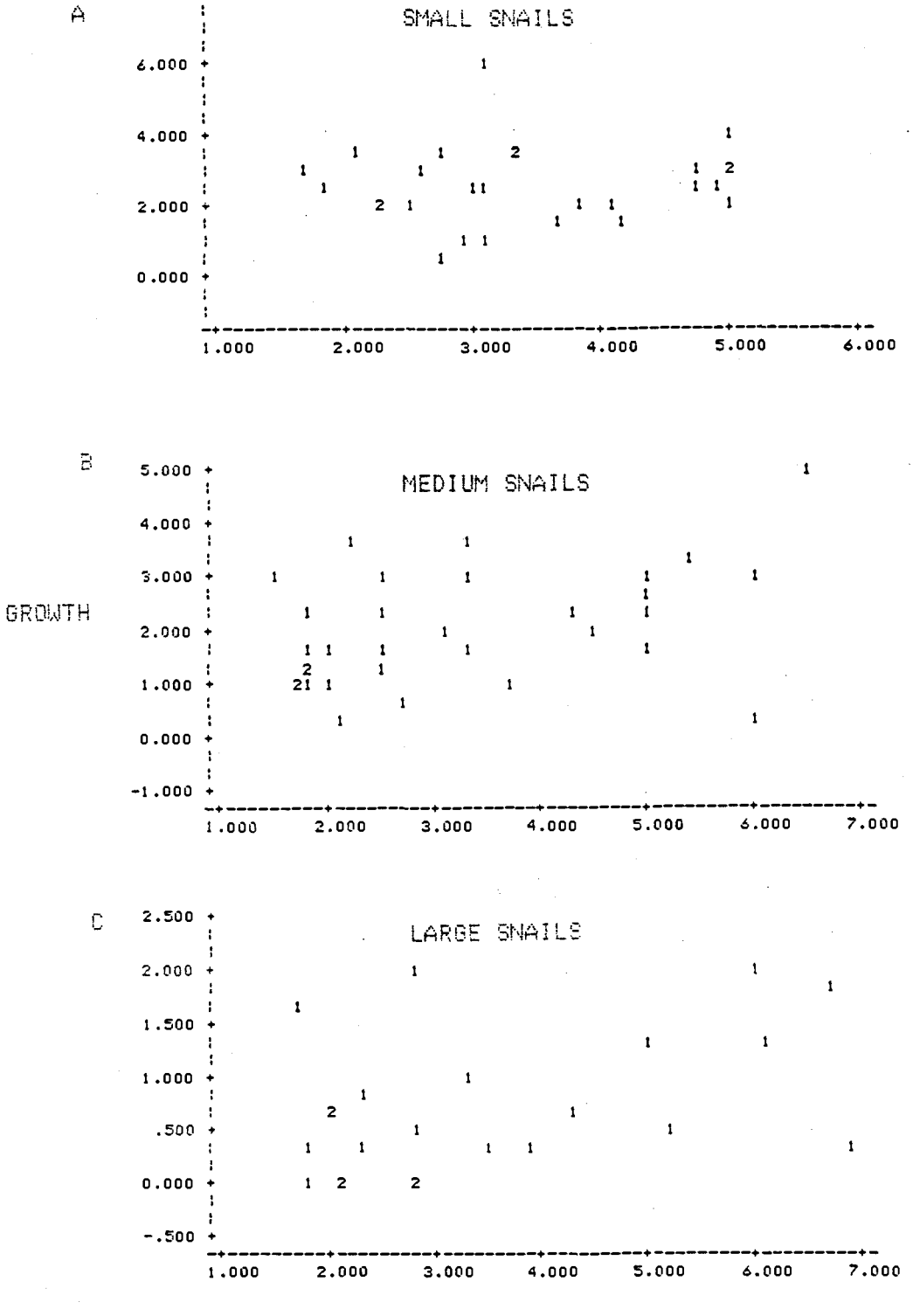
A
SMALL SNAILS
6.000
4.000
2.000
0.000
1.000
2.000
3.000
4.000
5.000
6.000
B
MEDIUM SNAILS
GROWTH
5.000
4.000
3.000
2.000
1.000
0.000
-1.000
1.000
2.000
3.000
4.000
5.000
6.000
7.000
C
LARGE SNAILS
2.500
2.000
1.500
1.000
.500
0.000
-.500
1.000
2.000
3.000
4.000
5.000
6.000
7.000
DIET SPECIALIZATION INDEX

Fig. 10

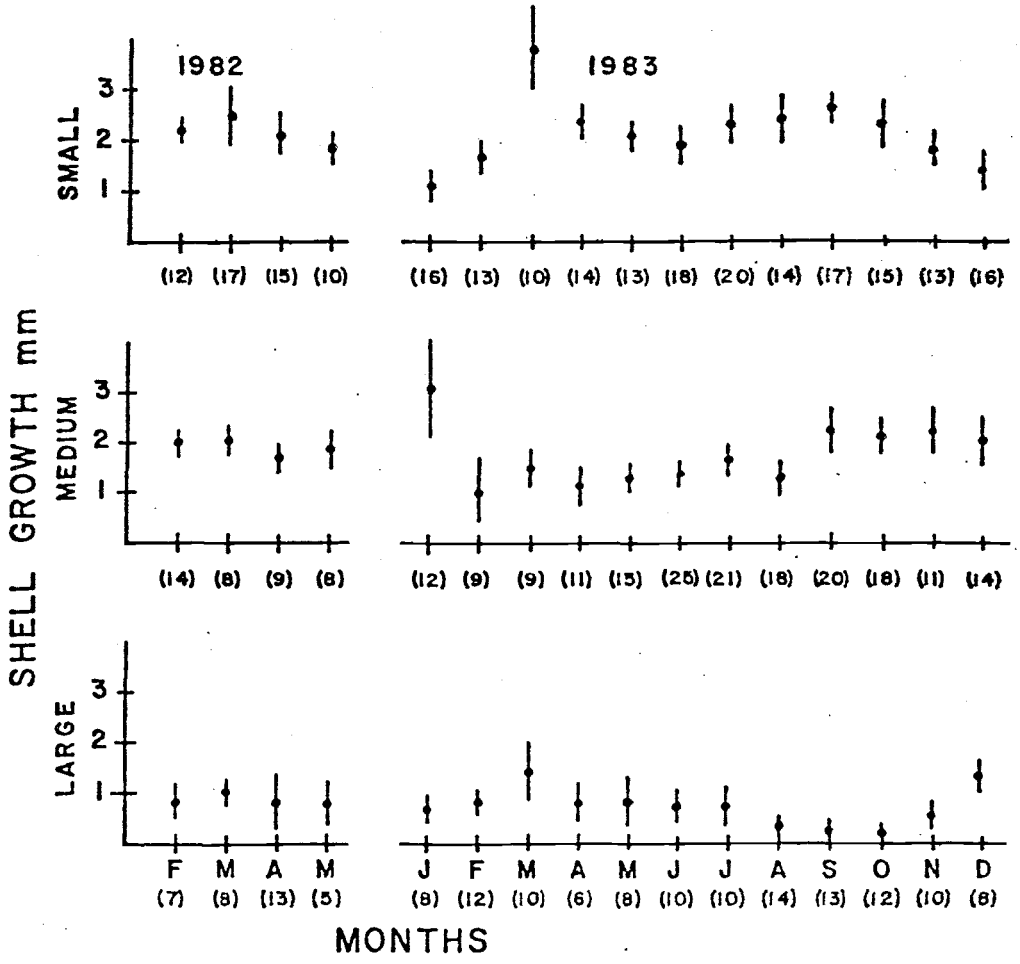

Fig. 11. Monthly means of shell growth for Thais melones grouped by size class. Bars indicate standard error. Numbers in parentheses indicate sample size (number of marked individuals found & measured each month). Small = snails < 20 mm; Medium = 20 mm ≤ snails ≤ 30 mm; Large = snails > 30 mm.

Fig. 12. Format of *Thais melones* diet experiment conducted from June 1983 to December 1983. Original Diet was determined from June 1 to June 30, 1983. Restricted Diets were maintained July 1 to Nov 30, 1983. Choice tests were conducted December 1 to December 14, 1983. See methods section for further explanation.

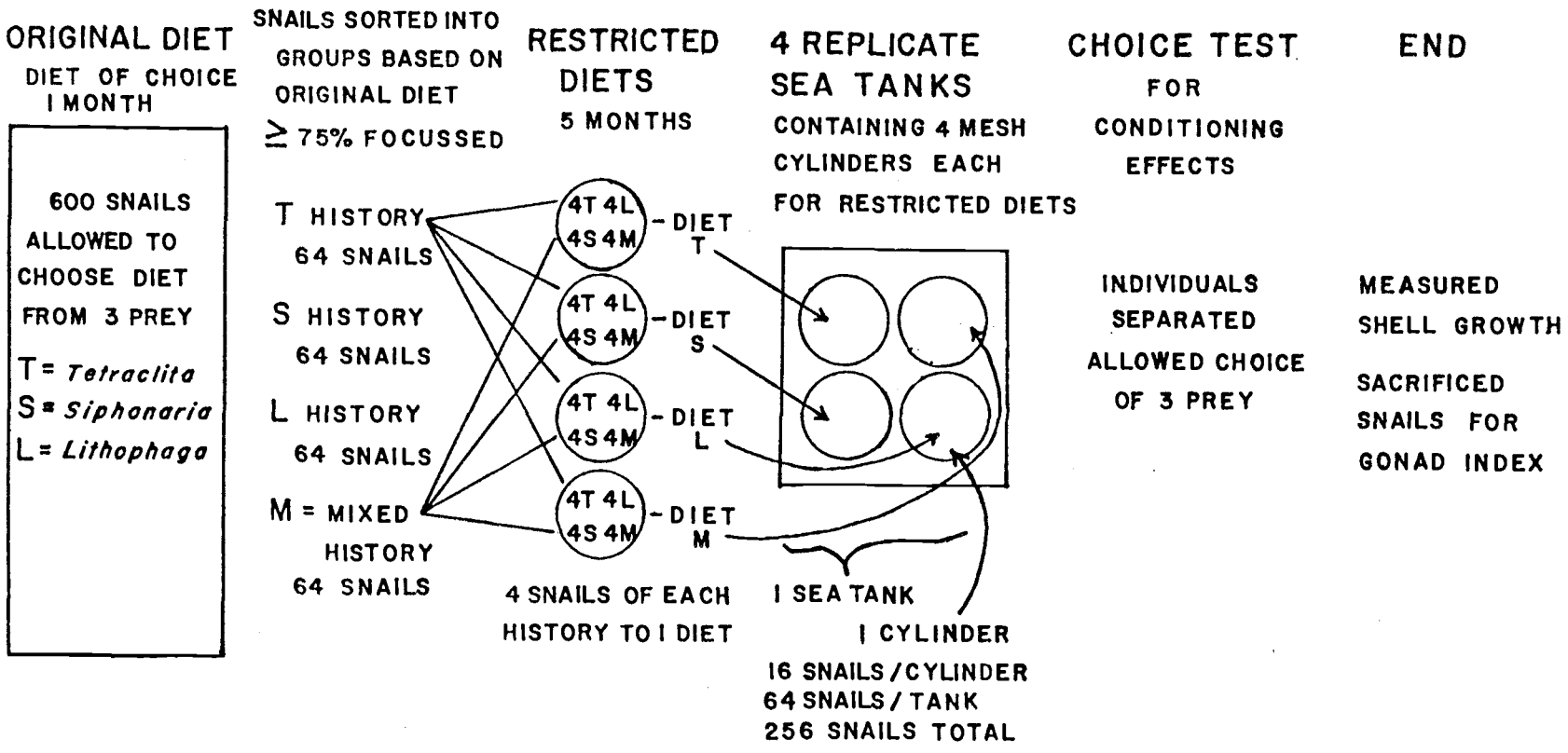
ORIGINAL DIET
DIET OF CHOICE
1 MONTH
600 SNAILS ALLOWED TO CHOOSE DIET FROM 3 PREY
T = Tetraclita
S = Siphonaria
L = Lithophaga
SNAILS SORTED INTO GROUPS BASED ON ORIGINAL DIET
≥ 75% FOCUSSED
RESTRICTED DIETS
5 MONTHS
4 REPLICATE SEA TANKS
CONTAINING 4 MESH CYLINDERS EACH
FOR RESTRICTED DIETS
CHOICE TEST
FOR
CONDITIONING
EFFECTS
END
T HISTORY
64 SNAILS
S HISTORY
64 SNAILS
L HISTORY
64 SNAILS
M = MIXED HISTORY
64 SNAILS
4T 4L 4S 4M
DIET T
DIET S
DIET L
DIET M
4 SNAILS OF EACH HISTORY TO 1 DIET
1 SEA TANK
1 CYLINDER
16 SNAILS / CYLINDER
64 SNAILS / TANK
256 SNAILS TOTAL
INDIVIDUALS SEPARATED
ALLOWED CHOICE OF 3 PREY
MEASURED SHELL GROWTH
SACRIFICED SNAILS FOR GONAD INDEX

Fig. 12

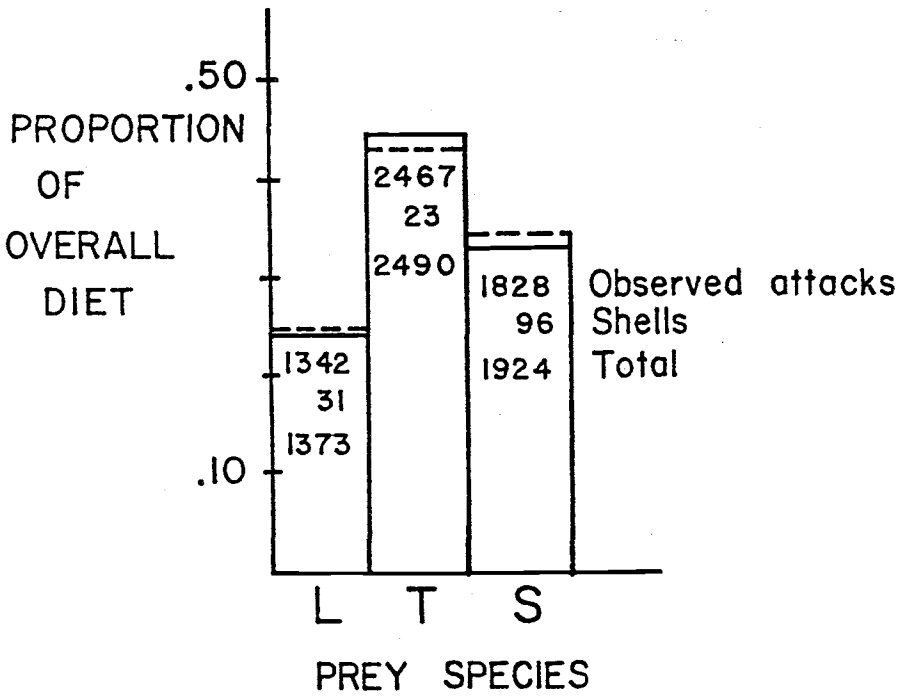

Fig. 13. Solid lines indicate proportions of observed feeding attacks made by 600 Thais melones during the first month (Original Diet section) of the feeding experiment. Snails chose food from equal abundances of 3 prey: L = Lithophaga sp. (bivalve), T = Tetraclita panamensis (barnacle), and S = Siphonaria maura (limpet). Dotted lines indicate proportions of both observed and unobserved feeding attacks determined from drilled prey shells.

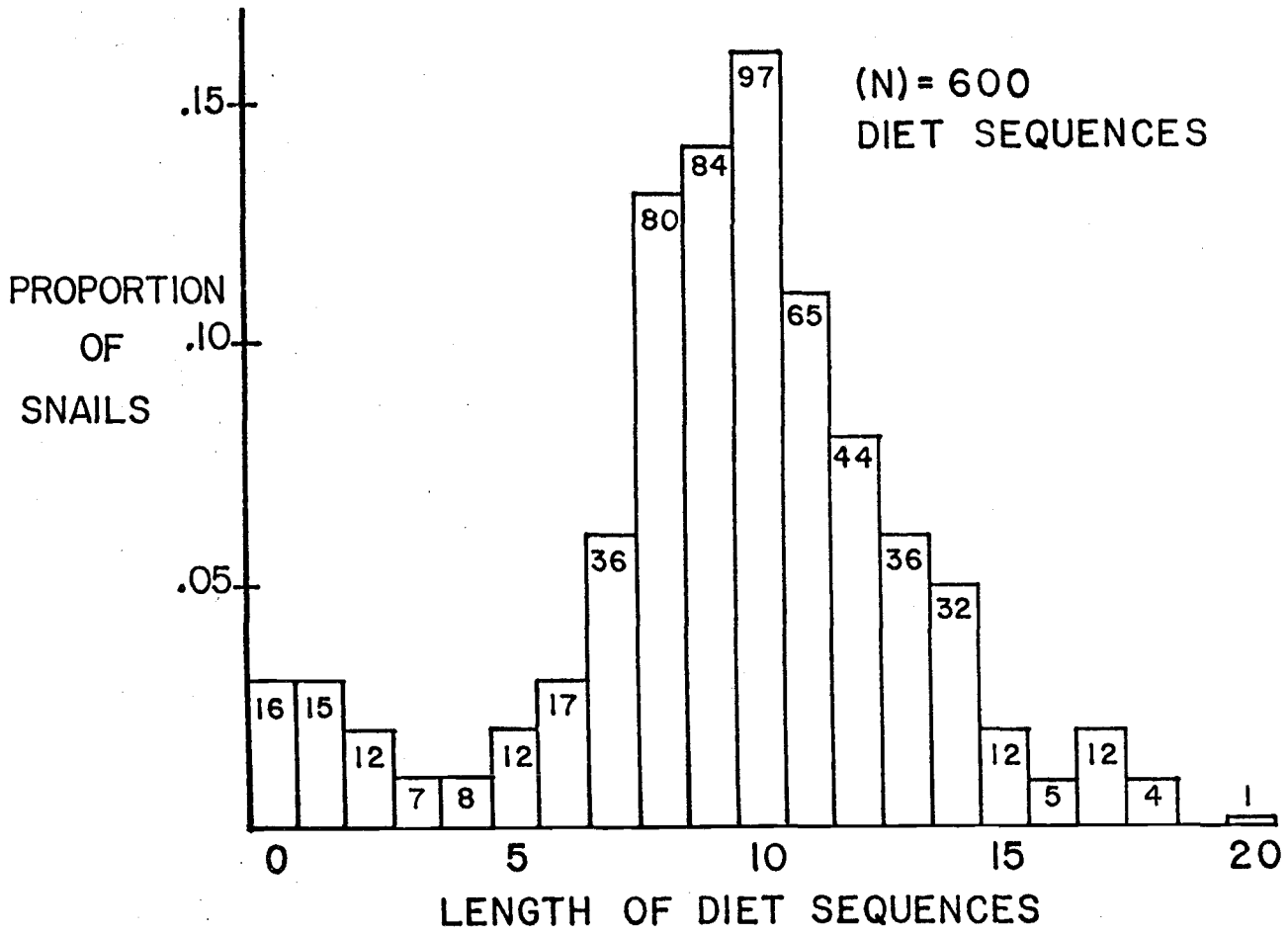

Fig. 14. Lengths of individual diets by Thais melones observed during the Original Diet section of the feeding experiment. N = 600 snails.

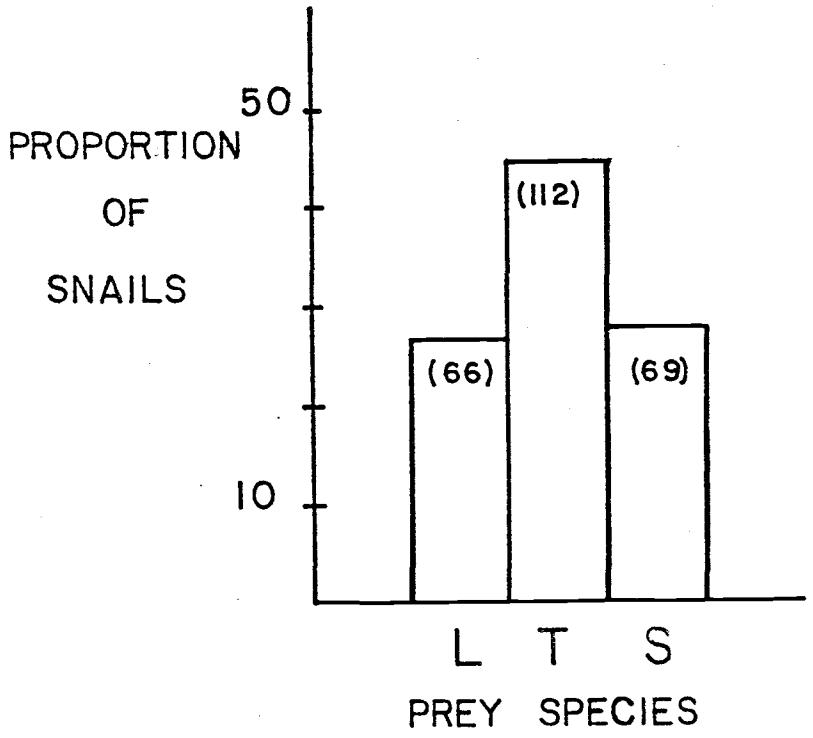

Fig. 15. Proportions of diets focussed on each species, out of a total of 247 individual diets by Thais melones that consisted of 75% or more of one prey species.

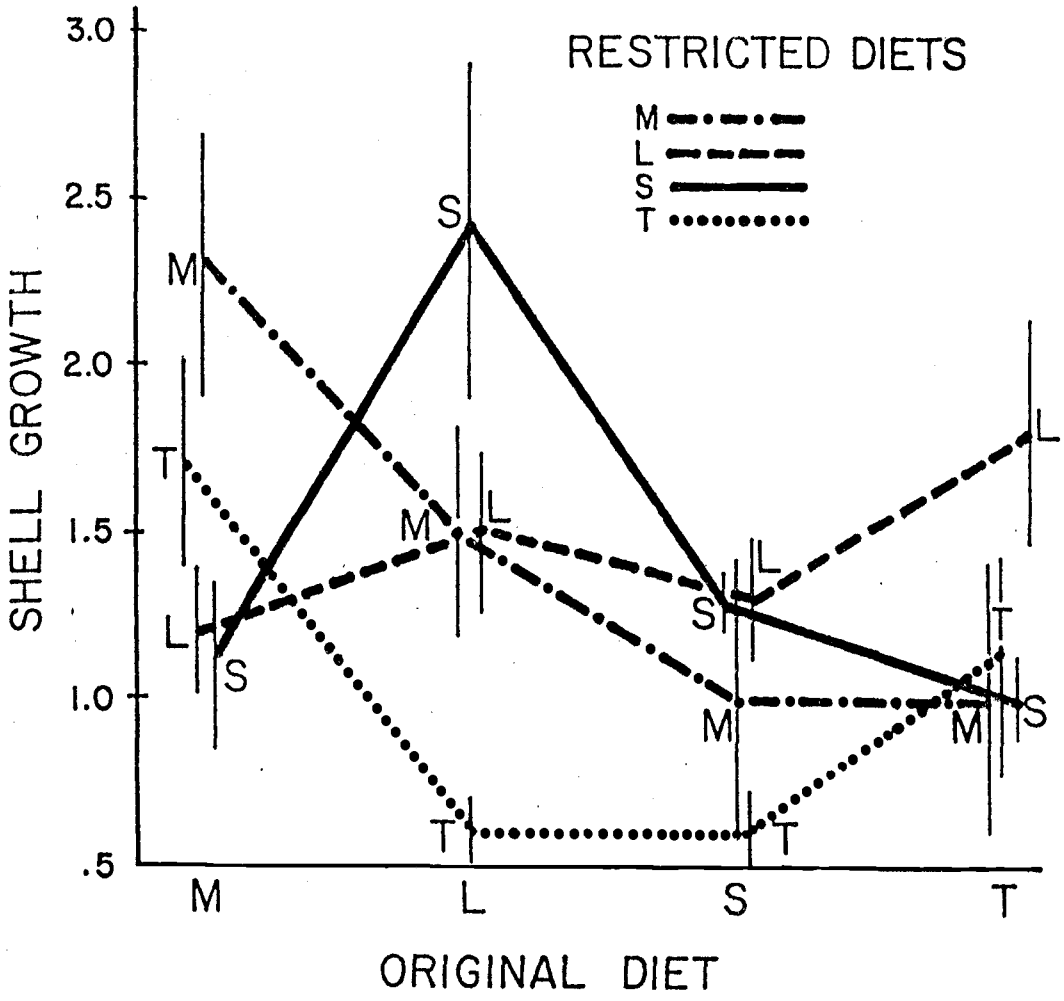

Fig. 16. Shell growth means of treatments of Thais melones diet experiment plotted with Original Diet choice and 5-month Restricted Diet. Error bars = standard error.

Fig. 17. Histograms of the final choice made by each Thais melones from a particular treatment of the diet experiment. ** = $p<0.01$; ---- = $p>0.05$.

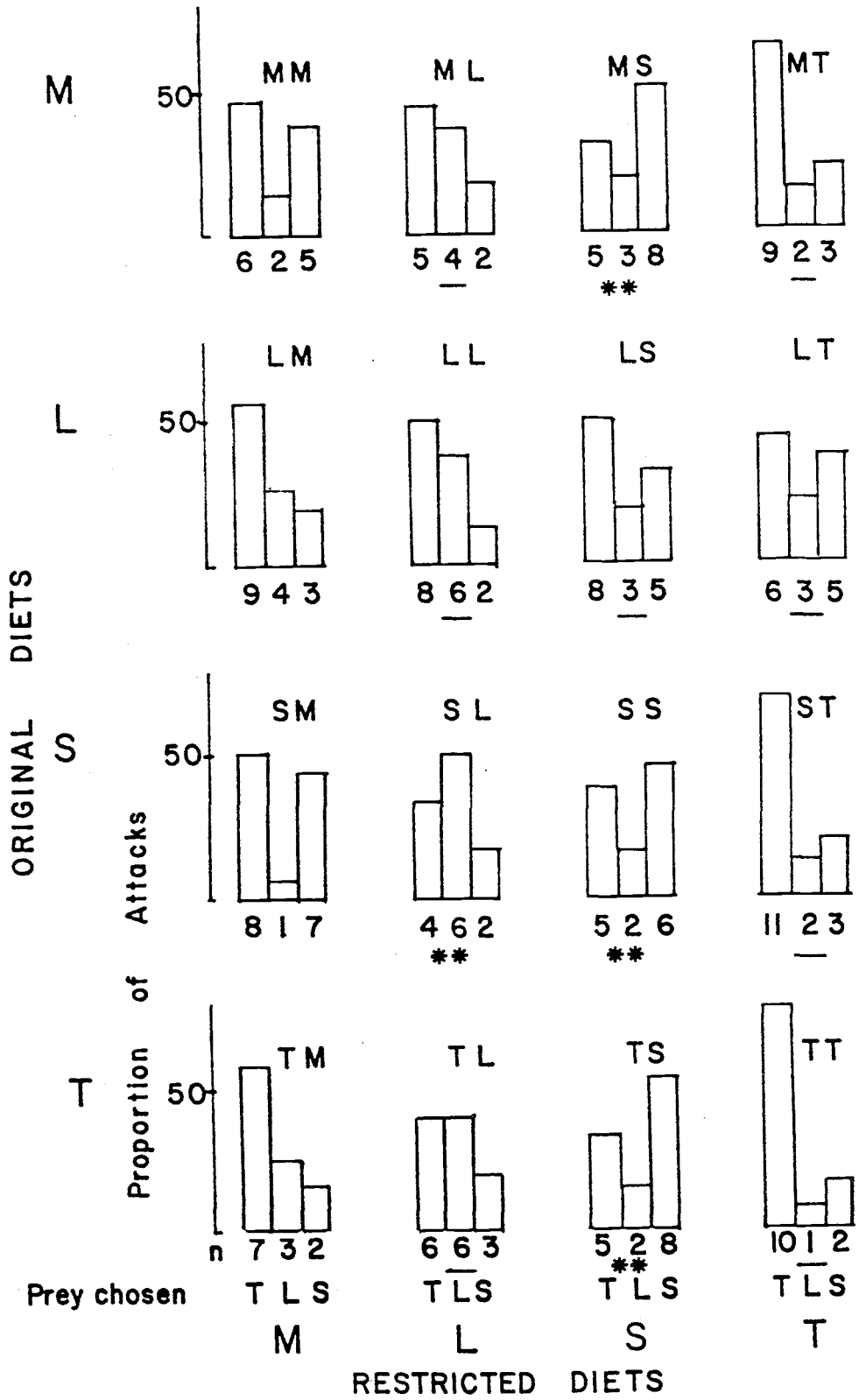
M
L
S
T
ORIGINAL DIETS
Proportion of Attacks
50
MM
ML
MS
MT
6 2 5
5 4 2
5 3 8
9 2 3
LM
LL
LS
LT
9 4 3
8 6 2
8 3 5
6 3 5
SM
SL
SS
ST
8 1 7
4 6 2
5 2 6
11 2 3
TM
TL
TS
TT
n 7 3 2
6 6 3
5 2 8
10 1 2
Prey chosen T L S
T L S
T L S
T L S
M
L
S
T
RESTRICTED DIETS

Fig. 17

Fig. 18. Histograms of the final choice made by each Thais melones with original diet groups combined and treatments MM, LL, SS, and TT removed. ** = $p<0.01$; ---- = $p>0.05$.

Fig. 19. Illustrations of Thais melones egg capsules: (A) view of top surface of capsules, (B) lateral view, (C) capsules deposited inside a shell of the barnacle Tetraclita, (D) capsules deposited inside a bivalve shell Chama, (E) position of a female depositing egg capsules into a barnacle shell.

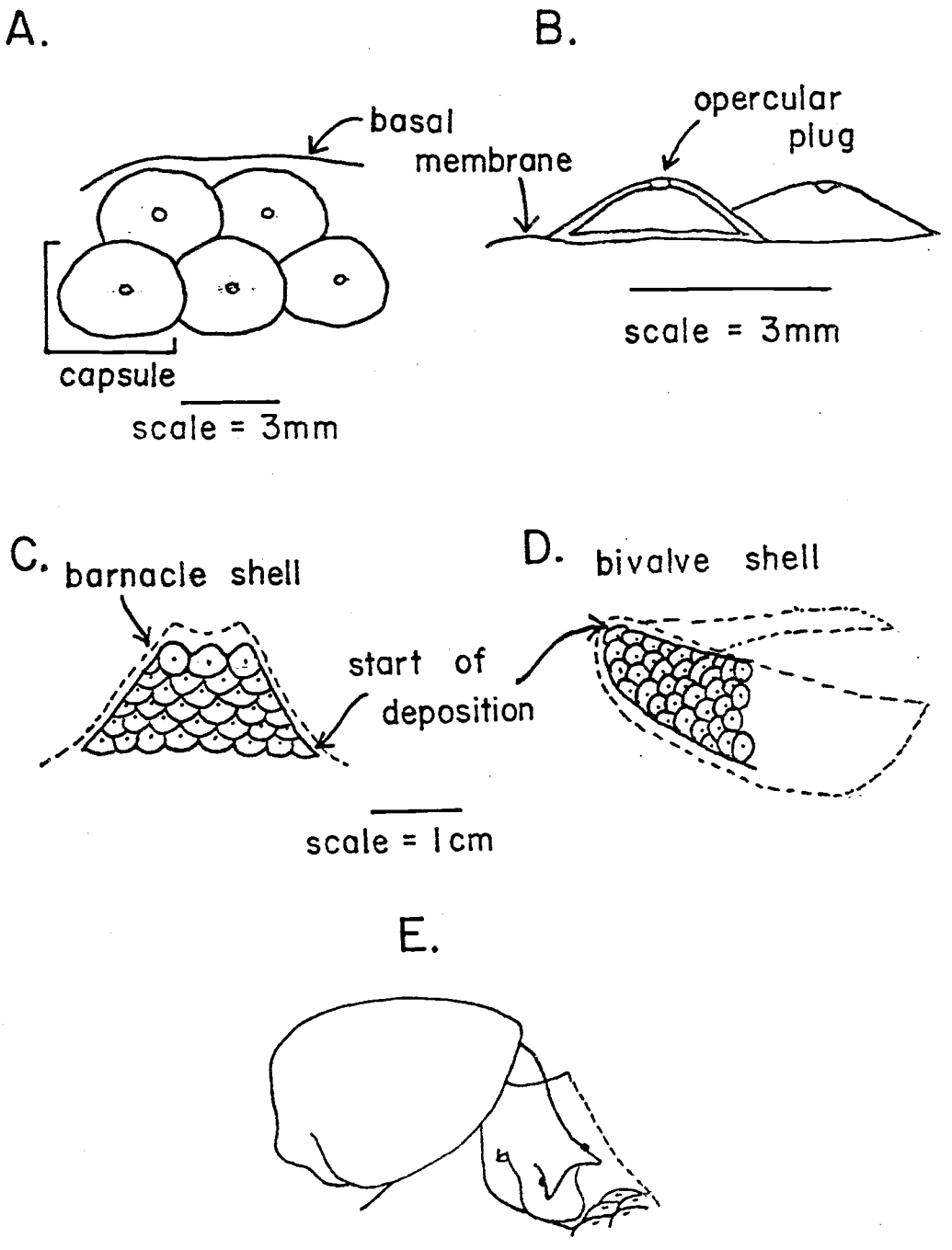
A.
basal membrane
capsule
scale = 3mm
B.
opercular plug
scale = 3mm
C.
barnacle shell
start of deposition
scale = 1cm
D.
bivalve shell
E.

Fig. 19

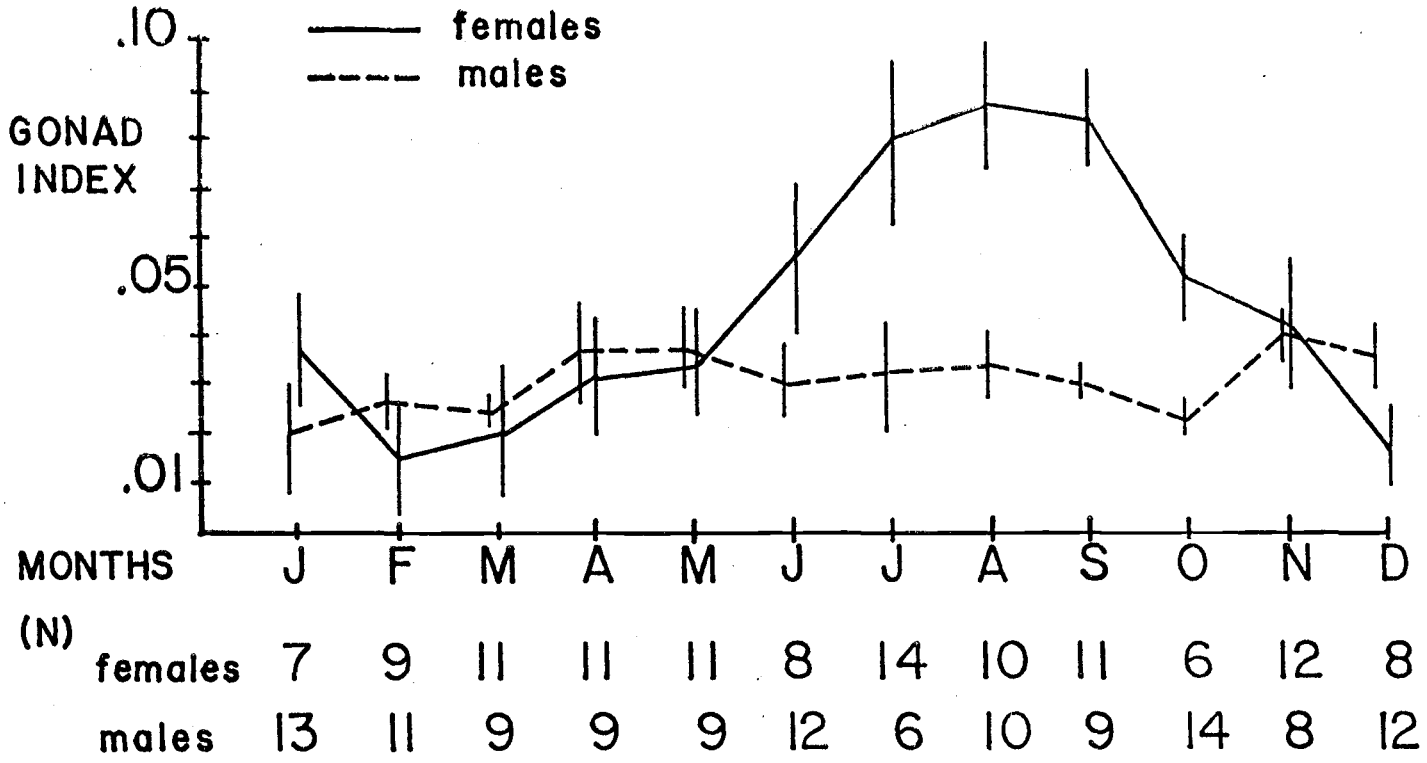

Fig. 20. Monthly gonad index of 20 Thais melones ranging in size from 30 to 35 mm in length. Error bars indicate standard error. N = numbers of males and females in sample.

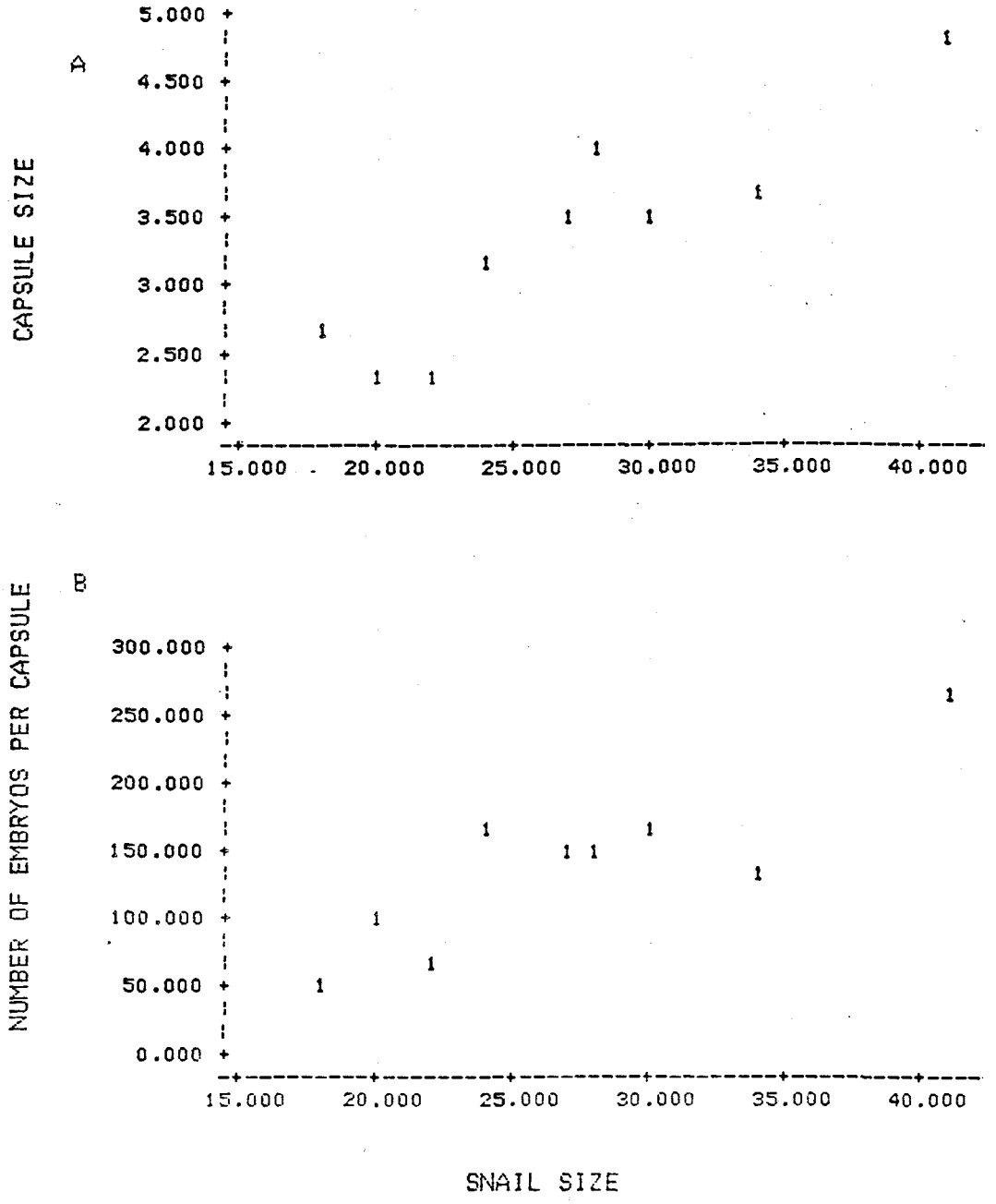

Fig. 21. Plot of Thais melones snail size against:(A) capsule size, (B) number of embryos per capsule.

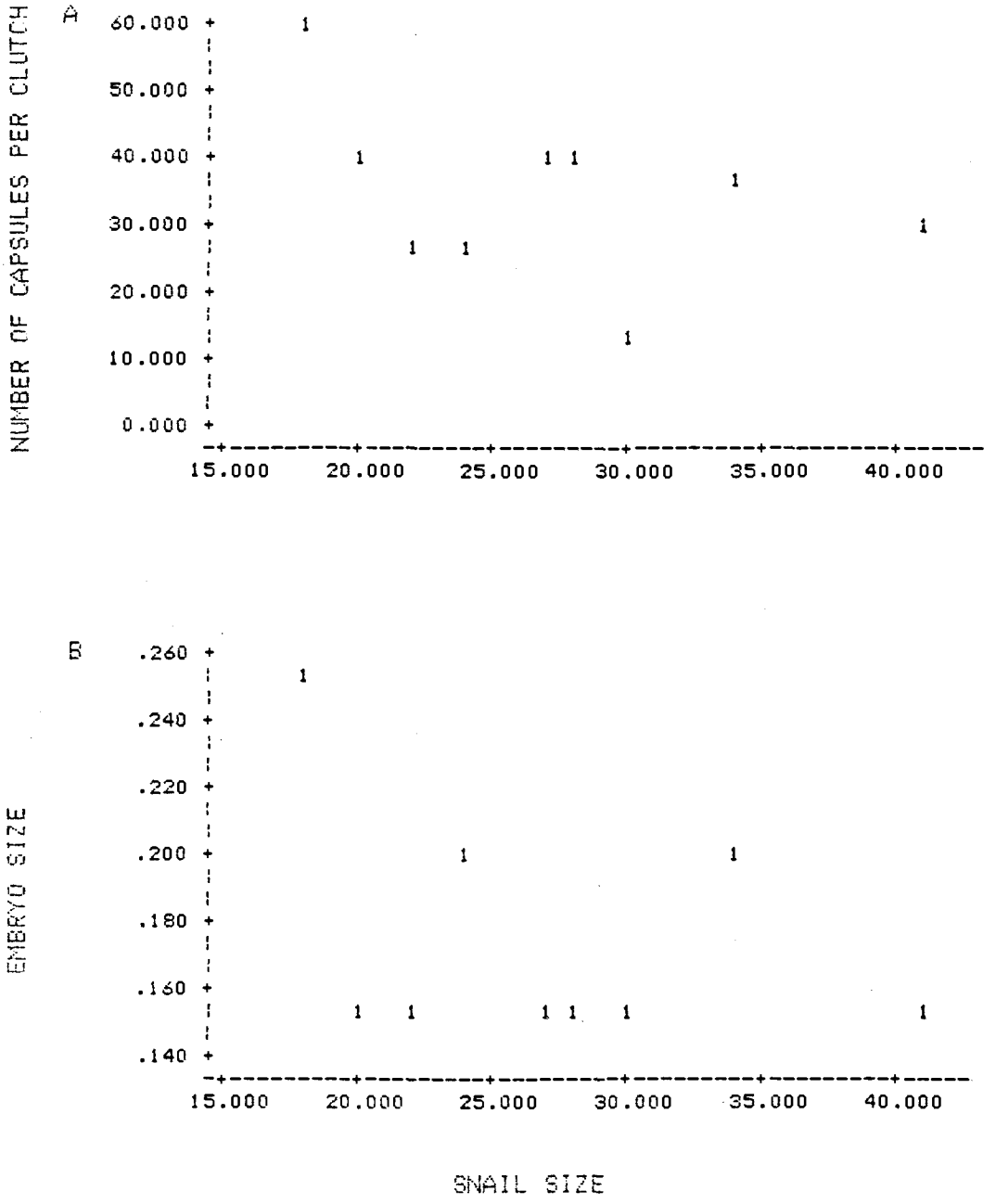

Fig. 22. Plot of Thais melones snail size against:(A) number of capsules per clutch, (B) embryo size.

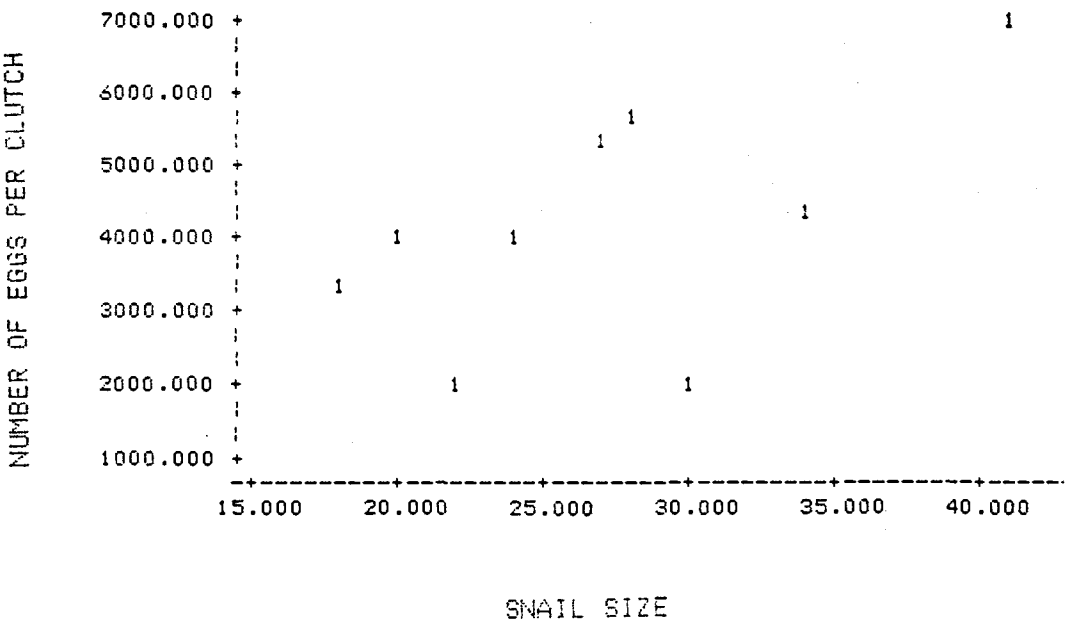

Fig. 23. Plot of Thais melones snail size against number of eggs per clutch.

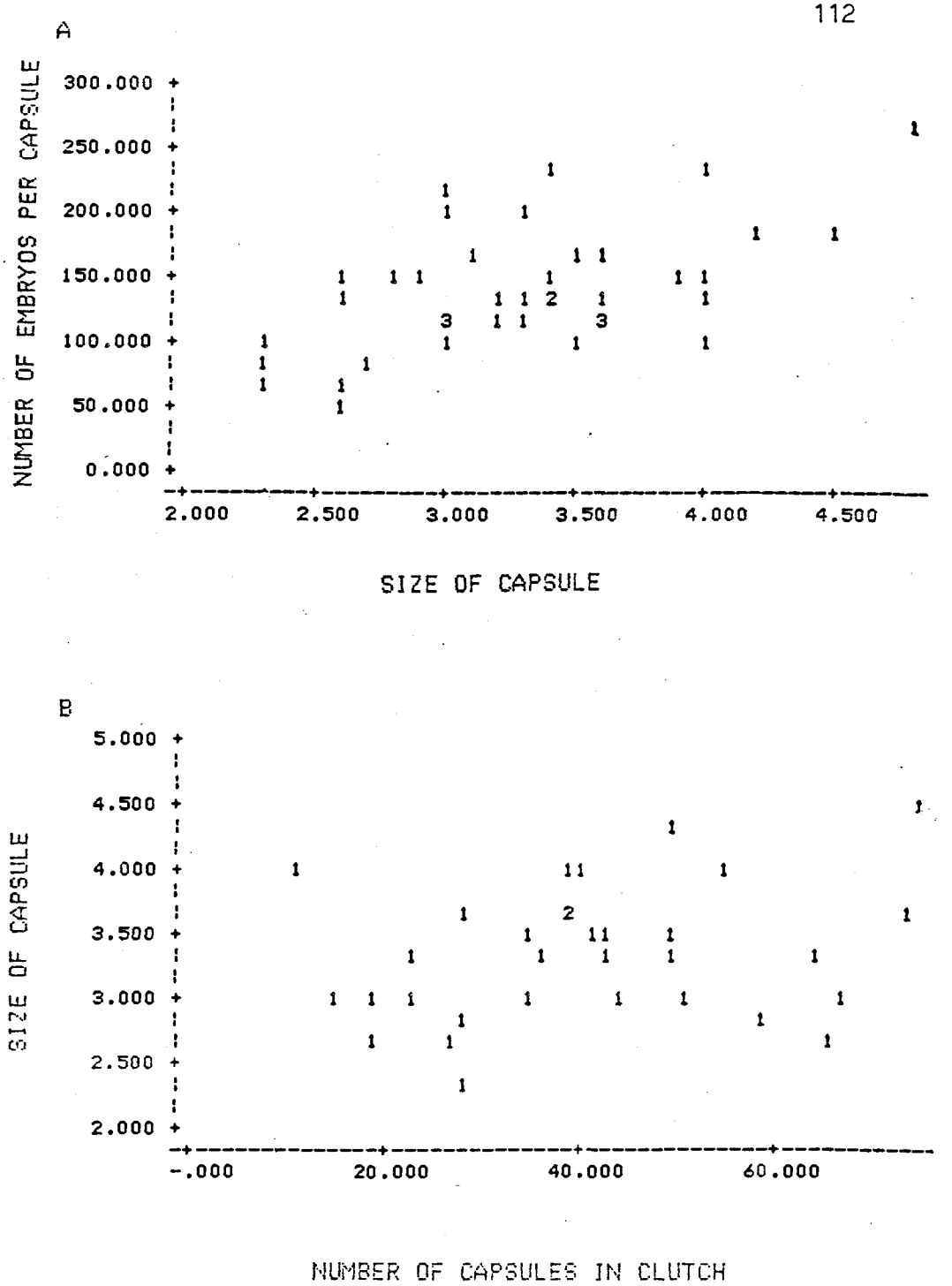

Fig. 24. (A) Plot of size of capsule against number of embryos per capsule. (B) Plot of number of capsules per clutch against size of capsule for Thais melones.

LITERATURE CITED

Abbott, D. P. and E. C. Haderlie. 1980. Prosobranchia: marine snails. Pages 230-307 in R. H. Morris, D. P. Abbott and E. C. Haderlie, editors. Intertidal invertebrates of California. Stanford University Press, Stanford, California, USA.

Amio, M. 1957. Studies on the eggs and larvae of marine gastropods. Journal Shimonoseki College of Fisheries 7: 107-127.

Arnold, S. J. 1981. Behavioral variation in natural populations. II. The inheritance of a feeding response in crosses between geographic races of the garter snake, Thamnophis elegans. Evolution 35:510-515.

Bayliss, D. E. 1982. Switching by Lepsiella vinosa (gastropoda) in south Australian mangroves. Oecologia 54:212-226.

Bayne, C. J. 1968. Histochemical studies on the egg capsules of eight gastropod molluscs. Proceedings of the Malacological Society of London 38:199-211.

Broom, M. J. 1983. A preliminary investigation into prey species preference by the tropical gastropods Natica maculosa Lamarck and Thais carinifera (Lamarck). Journal of Molluscan Studies 49:43-52.

Brown, S. C. 1969. The structure and function of the digestive system of the mud snail Nassarius obsoletus (Say). Malacologia 9:447-500.

Bryan, J. E. and P. A. Larkin. 1972. Food specialization by individual trout. Journal of the Fisheries Research Board of Canada 29:1615-1624.

Cain, A. J. and P. M. Sheppard. 1950. Selection in the polymorphic land snail Cepaea nemoralis. Heredity 4:275-294.

Connell, J. H. 1961 Effects of competition, predation by Thais lapillus and other factors on natural populations of the barnacle Balanus balanoides Ecological Monographs 31:61-104.

Cunningham, P. N. and R. N. Hughes. 1984. Learning of predatory skills by shorecrabs Carcinus maenas feeding on mussels and dogwhelks. Marine Ecology Progress series 16:21-26.

D'Asaro, C. N. 1966. The egg capsules, embryogenesis, and early organogenesis of a common oyster predator, Thais haemastoma floridana (Gastropoda: Prosobranchia). Bulletin of Marine Science 16:884-914.

D'Asaro, C. N. 1970. Egg capsules of prosobranch mollusks from south Florida and the Bahamas and notes on spawning in the laboratory. Bulletin of Marine Science 20:414-440.

Dayton, P. K. 1971. Competition, disturbance and community organization: provision and subsequent utilization of space in a rocky intertidal community. Ecological Monographs 41:351-389.

Derby, C. D. and J. Atema. 1981. Selective improvement in responses to prey odors by the lobster homarus americanus following feeding experience. Journal of Chemical Ecology 1:1073-1080.

Dunkin, S. de B. and R. N. Hughes. 1984. Behavioural components of prey-selection by dogwhelks, Nucella lapillus (L.), feeding on barnacles, Semibalanus balanoides (L.) in the laboratory. Journal of experimental Marine Biology and Ecology 79:91-103.

Edwards, D. C. and J. D. Huebner. 1977. Feeding and growth rates of Polinices duplicatus preying on Mya arenaria at Barnstable Harbor, MA, USA. Ecology 58:1218-1236.

Emlen, J. M. 1966. The role of time and energy in food preference. American Naturalist 100:611-617.

Engle, J. B., 1942. Growth of oyster drill, Urosalpinx cinerea Say, feeding on four different food animals. Anatomical Record 84:505

Fauchald and Jumars. 1979. The diet of Worms. Oceanography and Marine Biology Annual Reviews 17:193-284.

Feller, W. 1968. An introduction to probability theory and its applications. Volume 1. Third edition. J. Wiley and Sons Incorporated. New York, New York, USA.

Fritz, R. S. and D. H. Morse. 1985. Reproductive success and foraging of the crab spider Misumena vatia. Oecologia 65:194-200.

Garrity, S. D. 1984. Some adaptations of gastropods to physical stress on a tropical rocky shore. Ecology 65:559-574.

Garrity, S. D. and S. C. Levings. 1981. A predator-prey interaction between two physically and biologically constrained tropical rocky shore gastropods: direct, indirect and community effects. Ecological Monographs 51:267-286.

Glynn, P. W. 1972. Observations on the ecology of the Caribbean and Pacific coasts of Panama. Bulletin of the Biological Society of Washington 2:13-30.

Grant, P. R. 1971. Variation in the tarsus length of birds in island and mainland regions. Evolution 25:599-614.

Hall, S. J., C. D. Todd and A. D. Gordon. 1982. The influence of ingestive conditioning on prey species selection in Aeolidia papillosa (Mollusca: Nudibranchia). Journal of Animal Ecology 51:907-921.

Hancock, D. A. 1956. The structure of the capsule and the hatching process in Urosalpinx cinerea (Say). Proceedings of the Zoological Society of London 127:565-571.

Hassell, M. P. and T. R. E. Southwood. 1978. Foraging strategies of insects. Annual Review of Ecology and Systematics 9:75-98.

Head, E. J. H., and R. J. Conover. 1983. Induction of digestive enzymes in Calanus hyperboreus. Marine Biology Letters 4:219-231.

Heinrich, B. 1976. The foraging specializations of individual bumblebees. Ecological Monographs 46:105-128.

Heinrich, B. 1979. Majoring and minoring by foraging bumblebees, Bombus vagans: an experimental analysis. Ecology 60:245-255.

Holmberg, R. G. and Turnbull A. J. 1982. Selective predation in a euryphagous invertebrate predator, Pardosa vancouveri (Arachnida: Araneae). Canadian Entomology 114: 243-257.

Houston, R. S. 1971. Reproductive biology of Thais emarginata (Deshayes, 1839) and Thais canaliculata (Duclos, 1832). Veliger 13:348-357.

Hughes, R. N. 1979. Optimal diets under the energy maximization premise: the effects of recognition time and learning. American Naturalist 113:209-221.

Hughes, R. N. and S. de B. Dunkin. 1984a. Behavioural components of prey selection by dogwhelks, Nucella lapillus (L.) feeding on mussels, Mytilus edulis (L.) in the laboratory. Journal of Experimental Marine Biology and Ecology 77:45-68.

Hughes, R. N. and S. de B. Dunkin. 1984b. Effect of dietary history on selection of prey, foraging behaviour among patches of prey, by the dogwhelk Nucella lapillus (L.). Journal of Experimental Marine Biology and Ecology 79:159-172.

Hurd, L. E. 1985. On the importance of carrion to reproduction in an omnivorous estuarine neogastropod, Ilyanassa obsoleta (Say). Oecologia. 65:513-515.

Jaenike, J. 1983. Induction of host preference in Drosophila

melanogaster. Oecologia. 58:320-325.

Keen, A. M. 1971. Sea shells of tropical west America. Stanford University Press, Stanford, California.

Kitting, C. L. 1980. Herbivore-plant interactions of individual limpets maintaining a mixed diet of intertidal marine algae. Ecological Monographs 50:527-550.

Kohn, A. J. 1961. Studies on spawning behavior, egg masses, and larval development in the gastropod genus Conus, part 1: observations on nine species in Hawaii. Pacific Science 15:163-179.

Krebs, J. R. 1978. Optimal foraging: decision rules for predators. in J. R. Krebs and N. B. Davies, editors. Behavioral Ecology. Sinauer Associates, Sunderland, Massachusetts.

Larson, B. R., R. L. Vadas, and M. Keser. 1980. Feeding and nutritional ecology of the sea urchin Strongylocentrotus droebachiensis in Maine, USA. Marine Biology 59:49-62.

Laverty, T. M. 1980. The flower-visiting behaviour of bumble bees: floral complexity and learning. Canadian Journal of Zoology 58:1324-1335.

Lubchenco, J., B. A. Menge, S. D.Garrity, P. J. Lubchenco, L. R. Ashkenas, S. D. Gaines, R. Emlet, J. Lucas and S. Strauss. 1984. Structure, persistence, and role of consumers in a tropical rocky intertidal community (Taboguilla Island, Bay of Panama). Journal of Experimental Marine Biology and Ecology. 78:23-73.

Luckens, P. A. 1970. Predation and intertidal zonation at Asamushi. Bulletin of the Marine Biological Station Asamushi. 14:33-52.

McNair, J. N. 1981. A stochastic foraging model with predator training effects: II Optimal diets. Theoretical Population Biology 19:147-162.

Menge, B. A. 1975. Brood or broadcast? The adaptive significance of different reproductive strategies in the two intertidal sea stars Leptasterias hexactis and Pisaster ochraceus. Marine Biology 31:87-100.

Menge, B. A. 1976. Organization of the New England rocky intertidal community: Role of predation, competition and environmental heterogeneity. Ecological Monographs 46:355-393.

Menge, B. A. 1978a. Predation intensity in a rocky intertidal community. Relation between predator foraging activity and environmental harshness. Oecologia 34:1-16.

Menge, B. A. 1978b. Predation intensity in a rocky intertidal community. Effect of an algal canopy, wave action and desiccation on predator feeding rates. Oecologia 34:17-35.

Menge, B. A. 1983. Components of predation intensity in the low zone of the New England rocky intertidal region. Oecologia 58:141-155.

Menge, B. A., and J. Lubchenco. 1981. Community organization in temperate and tropical rocky intertidal habitats: prey refuges in relation to consumer pressure gradients. Ecological Monographs 51:429-450.

Menge, B. A., J. Lubchenco, L. R. Ashkenas, and F. Ramsey. 1986. Experimental separation of effects of consumers on sessile prey on a rocky shore in the bay of Panama: direct and indirect consequences of food web complexity. unpublished manuscript.

Menge, B. A. 1986. A preliminary study of the reproductive ecology of the seastars Asterias vulgaris and A. forbesi in New England. Bulletin of Marine Science in press.

Mileikovsky, S. A. 1971. Types of larval development in marine bottom invertebrates, their distribution and ecological significance: a re-evaluation. Marine Biology 10:193-213.

Moran, M. J., P. G. Fairweather and A. J. Underwood. 1984. Growth and mortality of the predatory intertidal whelk Morula marginalba Blainville (Muricidae): the effects of different species of prey. Journal of Experimental Marine Biology and Ecology. 75:1-17.

Murdoch, W. W. and A. Oaten. 1975. Predation and population stability. Advances in Ecological Research 9:1-131.

Neter, J., and W. Wasserman. 1974. Applied linear statistical models. Richard D. Irwin, Inc. Homewood, Illinois.

Palmer, A. R. 1983. Growth rate as a measure of food value in Thaidid gastropods: Assumptions and implications for prey morphology and distribution. Journal of Experimental Marine Biology and Ecology 73:95-124.

Palmer, A. R. 1984. Prey selection by Thaidid gastropods: some observational and experimental field tests of foraging models. Oecologia 62:162-172.

Pelseneer, P. 1936. Essai d'ethologie zoologique d'apres l'etude des mollusques, pp. 1-662 in: Moore, H. B. 1938. Marine Biological Association of the United Kingdom 23:67-74.

Perron, F. E. 1981. The partitioning of reproductive energy

between ova and protective capsules in marine gastropods of the genus Conus. American Naturalist. 118:110-118

Phillips, B. F. 1969. The population ecology of the whelk Dicathais aegrota in western Australia. Australian Journal of Marine and Freshwater Research. 20:225-265.

Pietrewicz, A. T., and A. C. Kamil. 1979. Search image formation in the blue jay (Cyanocitta cristata). Science 204:1332-1333.

Pyke, G. H. 1984. Optimal foraging theory: a critical review. Annual Review of Ecology and Systematics 15:523-575.

Reimer, A. A. 1976. Description of a Tetraclita stalactifera panamensis community on a rocky intertidal Pacific shore of Panama. Marine Biology 35:225-238.

Reimer, A. A. 1976b. Succession of invertebrates in vacant tests of Tetraclita stalactifera panamensis. Marine Biology 35:239-251.

Rittschof, D., L. G. Williams, B. Brown and M. R. Carriker. 1983. Chemical attraction of newly hatched oyster drills. Biological Bulletin 164:493-505.

Roughgarden, J. 1972. Evolution of niche width. American Naturalist 106:683-718.

Roughgarden, J. 1979. Theory of population genetics and evolutionary ecology. Macmillan Publishing Company Incorporated, New York, New York, USA. pp.512-513.

Rowell-Rahier, M. 1984. The food plant preferences of Pharatora vitellinae (Coleoptera: Chrysomelinae). B. A laboratory comparison of geographically isolated populations and experiments on conditioning. Oecologia 64:375-380.

Shuto, T. 1974. Larval ecology of prosobranch gastropods and its bearing on biogeography and paleontology. Lethaia 7: 239-256.

Shuto, T. 1983. Larval development and geographical distribution of the indo-west Pacific Murex. Bulletin of Marine Science 33: 536-544.

Spight, T. M. 1975. Factors extending gastropod embryonic development and their selective cost. Oecologia 21: 1-16.

Spight, T. M. 1976. Hatching size and the distribution of nurse eggs among prosobranch embryos. Biological Bulletin 150: 491-499.

Spight, T. M. 1977. Do intertidal snails spawn in the right places? Evolution 31:682-691.

Strathmann, R. 1974. The spread of sibling larvae of sedentary marine invertebrates. American Naturalist 108: 29-44.

Sullivan, C. H. and T. K. Maugel. 1984. Formation, organization and composition of the egg capsule of the marine gastropod, Ilyanassa obsoleta. Biological Bulletin 167:378-389.

Sokal, R. R., and F. J. Rohlf. 1980. Biometry. W. H. Freeman and Company, New York.

Stuart, V., E. J. H. Head and K. H. Mann. 1985. Seasonal changes in the digestive enzyme levels of the amphipod Corophium volutator (Pallas) in relation to diet. Journal of Experimental Marine Biology and Ecology. 88:243-256.

Thompson, R. J. 1982. The relationship between food ration and reproductive effort in the green sea urchin, Strongylocentrotus droebachiensis. Oecologia 56:50-57.

Thorson, G. 1950. Reproductive and larval ecology of marine bottom invertebrates. Biological Reviews 25:1-43.

Vadas, R. L. 1977. Preferential feeding: an optimization strategy in sea urchins. Ecological Monographs 47:337-371.

Van Valen, L. 1965. Morphological variation and width of ecological niche. American Naturalist 99:377-390.

Ware, D. M. 1971. Predation by rainbow trout (Salmo gairdneri): the effect of experience. Journal Fisheries Research Board of Canada 28:1847-1852.

Watanabe, J. M. 1984. Food preference, food quality and diets of three herbivorous gastropods (Trochidae:Tegula) in a temperate kelp forest habitat. Oecologia 62:47-52.

Werner, E. E., G. G. Mittelbach and D. J. Hall. 1981. The role of foraging profitability and experience in habitat use by the bluegill sunfish. Ecology 62:116-125.

West, L. in press. Interindividual variation in prey selection by the snail Nucella (=Thais) emarginata. Ecology

Wood, L. 1968. Physiological and ecological aspects of prey selection by the marine gastropod Urosalpinx cinerea (Prosobranchia Muricidae). Malacologia 6:267-320.

APPENDIX

LIST OF PREY SPECIES AND ABREVIATIONS USED IN APPENDIX

Oysters

Os	*Ostrea* spp.

Other bivalves

Is	*Isognomon*
Brc	*Brachidontes*
Lth	*Lithophaga*
Chm	*Chama echinata*

Gastropods

Sm	*Siphonaria maura*
Fis	*Fissurella longifissa*
Crp	*Crepidula incurva*

Whorled gastropods

Nr	*Nerita scabricosta*
Ac	*Acanthina brevidentata*
Fos	*Fossarus* sp.
An	*Anachis* sp.
Mit	*Mitra* sp.
Vit	*Vitularia* sp.
Tm	*Thais melones*
Ver	Vermetids

Chitons

Cht	*Chiton stokesii*

Barnacles

Bal	*Balanus* sp.

Polychaetes

Ser	serpulid sp.

Others

X	unobservable organisms located inside shell or rock

20mm ≤ Snails ≤ 30mm in Shell Height, 1980

Individual	Diet								
44	Os	Ver	Ser	Os	Ver	Os	Os	Os	3 (8)
122	Ver	Os	Os	Ser	Os	Os	Sm		4 (7)
131	Os	Os	Os	Os	Os	Ser	Os		2 (7)
42	Sm	Os	Bal	Sm	Os	Os	Os		3 (7)
5	Ver	Ser	Ser	Os	Os	Os	Sm		4 (7)
37	Os	Os	Os	Os	Os	Os			1 (6)
35	Os	Os	Os	Os	Ser	An			3 (6)
61	Os	Os	Ver	Brc	Os	Os			3 (6)
108	Chm	Os	Sm	Os	Sm	Os			3 (6)
132	Os	Os	Os	Os	Os	Os			1 (6)
125	Os	Os	Os	Bal	Os				2 (5)
29	Ver	Os	Os	Os	Sm				3 (5)
110	Os	Os	Os	Brc	Os				2 (5)
27	Os	Os	Bal	X	Os				3 (5)
52	Os	Os	Os	Os	Sm				2 (5)

Snails >30mm in Shell Height, 1980

Individual	Diet	
103	*Os* *Os* *Os* *Os* *Os* *Os* *Os* *Os* *Ser* *Os* *Os*	2 (11)
11	*Ver* *Ver* *Os* *Ver* *Os* *Os* *Os* *Os* *Os*	2 (9)
49	*Sm* *Os* *Os* *Os* *Os* *Os* *Os* *Os*	2 (8)
41	*Os* *Os* *Os* *Os* *Os* *Os* *Os*	1 (7)
33	*Os* *Os* *Chm* *Os* *Os* *Os*	2 (6)
10	*Ver* *Os* *Os* *Os* *Os*	2 (5)
4	*Os* *Os* *Os* *Os* *Os*	1 (5)
7	*Os* *Os* *Os* *Os* *Os*	1 (5)
3	*Os* *Os* *Os* *Os* *Os*	1 (5)
14	*Os* *Ver* *Ver* *Os* *Os*	2 (5)

Snails <20mm in Shell Height, 1982

Individual	Diet	
r16	*Cht* | *Sm* | *Os* | *Sm* | *Sm* | *Os* | *Sm* | *Sm* | *Os* | *An* | *Sm* | *Sm* | *Sm* | *Sm*	4 (14)
B2r	*Sm* | *Sm* | *Os* | *Os* | *Os* | *Os* | *Os* | *Os*	2 (8)
G94	*Os* | *Chm* | *Os* | *Os* | *Os* | *Os* | *Os* | *Os*	2 (8)
B20	X | X | *Os* | *Os* | *Os* | *Os*	2 (6)
R90	*Sm* | *Is* | *Ser* | *Fos* | *Sm*	4 (5)
B13	*Sm* | *Sm* | X | *Sm* | *Os*	3 (5)
B17	*Sm* | *Crp* | *Brc* | *Sm* | *Sm*	3 (5)

20mm ≤ Snails ≤ 30mm in Shell Height, 1982

Individual	Diet	
r 82	Os | Os | Os | Os | Os | Os | Os | Sm | Os	2 (9)
R 91	Cht | Os | Os | Sm | Os | Os | Os | Lth | Sm	4 (9)
R 85	Os | Os | Os | Sm | Sm | Sm | Sm | Os	2 (8)
R 96	Cht | Os | Ser | Os | Ser | X | Sm | Os	5 (8)
r 101	Ac | Os | Tm | Sm | Os | Sm | X	5 (7)
r 15	Brc | Os | Os | Os | Os | Os | Os	2 (7)
B 47	Sm | Sm | Sm | Sm | Sm	1 (5)
R 84	Os | Os | Sm | Sm | Sm	2 (5)

Snails >30 mm in Shell Height, 1982

Individual	Diet	
R097	Os | Os | Os | Os | X | Os | Os | Os | Os | Os | Os | Os | Os | Os | Os | Lth	3 (16)
r 3	Tm | Tm | Os | Os | Os | Os | Os | Os | Os | Os | Os | Os	2 (12)
G 12	Cht | Sm | Sm | Sm | Sm | Sm | Cht | Sm | Cht	2 (9)
r 8	Os | Os | Os | Os | Os | Os	1 (6)
r 18	Cym | Os | Os | Cht | Os	3 (5)
r 10	Os | Os | Cht | X | Os	3 (5)

Snails <20mm in Shell Height, 1983

Individual	Diet										
209	Os	Os	Os	Sm	Os	Os	Sm	Sm	Sm	Os	2 (10)
G	Sm	Sm	Sm	Sm	Sm	Sm	Is	Sm			2 (8)
i	Sm	Sm	Mit	An	Sm	Sm	Sm				3 (7)
161	Sm	Bal	Bal	Sm	Sm	X	Sm				3 (7)
x8	Os	Fos	Os	Os	Os	Os	Fos				2 (7)
58	Ser	Ser	Ser	An	Ser	Ser					2 (6)
c	Is	Is	Brc	Is	Brc						2 (5)
174	X	Is	Brc	Is	X						3 (5)
160	Brc	Ser	Ser	Ser	Ser						2 (5)
400	Sm	Is	Is	Is	Sm						2 (5)
390	Fos	Mit	Fos	Fos	Fos						2 (5)
17 Z	Sm	Os	Sm	Os	Os						2 (5)

20mm ≤ Snails ≤ 30mm in Shell Height, 1983

Individual	Diet												
125	Sm	Sm	Sm	Lth	Sm	Sm	Sm	Sm	Sm	Sm	Sm	2	(11)
146	Sm	X	X	X	Lth	Sm	Os					4	(7)
198	Sm	Sm	Bal	Sm	Sm	Os						3	(6)
242	Ac	Nr	Ac	Sm	X	Os						5	(6)
185	Os	Os	Os	Sm	Os	Sm						2	(6)
141	Sm	Sm	X	Os	Is	Is						4	(6)
177	An	An	Nr	An	Sm	Ac						4	(6)
157	Sm	Lth	Sm	Sm	Sm							2	(5)
249	Tm	Mit	Ac	Os	Os							4	(5)
147	Os	Os	Os	Os	Os							1	(5)
183	Sm	Ver	Sm	Sm	Sm							2	(5)
124	Cht	Sm	Os	Sm	Cht							3	(5)

Snails >30mm in Shell Height, 1983
Wet Season

Individual	Diet		
117	Os Os Os Os Cht Sm Os Os Ac Os Os Ac Os	4	(13)
133	Sm Sm Sm Sm Os Sm Ver Lth Sm Sm Sm	4	(11)
102	Sm Sm Lth Sm Sm Sm Sm	2	(7)
108	Lth Sm Sm X Lth Os Os	3	(7)
143	Sm Os Os Vlt Ac	4	(5)
250	Lth Lth X X Os	3	(5)
145	Os Os Os Os Cht	2	(5)
190	Sm Sm Sm Sm Sm	1	(5)