EMLEN, John Merritt, 1938-
TIME, ENERGY AND RISK IN TWO SPECIES OF
CARNIVOROUS GASTROPODS.

University of Washington, Ph.D., 1966
Zoology

University Microfilms, Inc., Ann Arbor, Michigan

TIME, ENERGY AND RISK IN TWO SPECIES OF CARNIVOROUS GASTROPODS

by

JOHN MERRITT EMLEN

A thesis submitted in partial fulfillment
of the requirements for the degree of

DOCTOR OF PHILOSOPHY

UNIVERSITY OF WASHINGTON

1966

Approved by Robert T Paine
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Date: July 15, 1966

We have carefully read the dissertation entitled Time, energy and risk in two species of carnivorous gastropods. submitted by John M. Emlen in partial fulfillment of the requirements of the degree of Doctor of Philosophy and recommend its acceptance. In support of this recommendation we present the following joint statement of evaluation to be filed with the dissertation.

This thesis represents an investigation of the biology of two species of carnivorous marine gastropods, *Thais emarginata* and *T. lamellosa*. Particular emphasis has been placed on understanding patterns of abundance and intertidal placement as the result of highly evolved behavior patterns. Emlen has based his work on the implicit assumptions that natural selection will operate both to maximize assimilated food energy intake per unit time, and to minimize the probability of death associated with certain behavior patterns.

A mathematical model was derived, based on these assumptions, that was used to predict an optimal behavior given knowledge of certain environmental features, such as spatial and size distribution of the prey and relative tolerance to such physical hazards as temperature stress and desiccation. Extensive field measurements were made on frequency of feeding, the size of the prey species, the rate of movement of marked individuals at different seasons and under different stresses, and the number and placement of egg capsules produced by the female snails. These data were supplemented by indirect observations obtained from a time-lapse movie camera, properly encased, and anchored under water. These data on how submerged snails behave provided information on rate and linearity of movement, amount of time spent moving, and the amount of time spent sitting on barnacles, presumably in the process of drilling and ingesting them.

In general the comparison between observed values and those predicted from the models were in close agreement. *T. emarginata* prefers to feed on *Balanus glandula*, and not on the larger *B. cariosus*. The upper limit to effective feeding is explained. The spatial distribution and movement pattern of both snail species is predicted accurately, and the calculated rate of feeding, not directly observed, is in close agreement with other authors' estimates for similarly sized snails.

The major contribution of this study, aside from providing fundamental life history information on four of the commonest, macroscopic local marine invertebrates, is its demonstration of the relationship between time, energy and risk. Time and energy budgets have provided a basis for many evolutionary hypotheses. Considerations of mortality (risk) are a common component of ecological study. This thesis makes an important and scholarly contribution by indicating how and why these approaches are inseparable.

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INTRODUCTION

Time, Energy and Risk in Two Species of Carnivorous Gastropods

It is a basic tenet of biology that organisms evolve anatomical, physiological and behavioral characteristics that improve their ability to survive and reproduce in their environment. This tenet, which more than any other idea in biology has become accepted as general law, offers a very convenient vehicle upon which to build further hypotheses and to make specific predictions, but can easily lead the careless scientist into dangerous pitfalls. For example, we assume that small desert mammals are adversely affected by the midday sun and that their habit of remaining in their burrows during the heat of the day is thus a behavioral adaptation to desert life. On the other hand, our primary reason for assuming the deleterious effect of the sun on these mammals is the observation that they appear to avoid it. The adaptation argument in this case is thus quite circular. Without some specific information on the relative effects on the animals of exposure and protection, small mammals who avoid the midday sun can no more be said to be behaving optimally than those mad dogs and Englishmen who don't.

The type of specific information that is needed in any argument on adaptation is easily determined. Natural selection operates through the agency of reproductive success, and such success depends first upon the amount and efficiency of an individual's expenditure of energy in reproductive activities, and second, on the survival probability of its young. The amount of energy available for, and used in, reproduction depends among other things on the net rate and efficiency with which energy is accumulated, and on the probability that the individual will live to reproduce. Anatomical, physiological and behavioral evolution, then, should follow a pattern which tends to maximize net energy intake per unit time and minimize the risk of death of both parents and offspring. The important parameters are time, energy and risk. An analysis of these parameters in a species' ecology, should enable an investigator to explain and predict aspects of the species' biology without danger of circularity.

The two predatory, marine gastropods, _Thais_ _emarginata_ and _T._ _lamellosa_ appeared to me ideal for such an analysis. They are both extremely common and easily accessible on rocky intertidal beaches. Both feed primarily (in the areas where this study was carried out) on barnacles, sessile, small food items easily counted and analyzed for energy content. And the effects of risk from predation and desiccation can be observed on beaches where each boulder offers the snails a choice of either feeding in an exposed position or fasting in a sheltered position.

Both species are active only at high tide, and thus most observations, made necessarily at low tide, showed only activities frozen in time or abandoned in progress, and clues left by unobserved behavior. An explanation and analysis of such indirect observations is not always a simple matter and a number of mathematical models have thus been constructed and used in order to interpret the incomplete data obtained. The approach used in this study, then, is a combination of direct field observations and inference based on treatment of these observations by mathematical means. Direct checks on activities were made, as far as was possible, using underwater time lapse photography.

ACKNOWLEDGEMENTS

I would like to thank the members of my committee, Dr. s R. T. Paine, G. H. Orians, E. Florey, P. L. Illg, and also Dr. A. J. Kohn, for reading the manuscript and offering many suggestions. Dr. Paine particularly deserves my thanks for his criticism of the thesis and the many hours spent in discussion with me. Dr. R. A. Cloney helped with suggestions for study areas and provided the film editor on which some analysis of data was carried out, and Mr. Ken Reuhl helped with much of the field work. My appreciation also goes to Dr. R. L. Fernald who offered much interesting information and to Mrs. Charles Ruby who kindly provided me with both food and lodging during my stays at the primary study area. Finally I would like to thank my wife who spent many hours collecting data under miserable, cold, wet conditions and many more accepting my long absences in the field without complaint.

This work was supported by a university of Washington graduate school research fund, initiative 171, in summer, 1963, a National Science Foundation summer fellowship in 1965, and a National Aeronautics and Space Administration traineeship in 1965-1966.

THE SPECIES

Thais emarginata is roughly 15 to 34 millimeters in length when adult. The shell shows one large body whorl and two or three minor whorls; the protoconch is often worn away by the time the snail reaches 20 mm. The shell color is highly variable: black, white, grey, yellow, brown, red and purple as well as striped individuals are found. Axial color striations generally occur as indistinct lines of color change, while transverse stripes are usually distinct, and usually brown on white or grey. The brown spiral stripes when present, generally alternate with a series of ten to twelve spiral cords or ridges on the body whorl, and continue onto the minor whorls. The ridges may be evenly spaced or grouped in twos.

On calm water beaches, T. emarginata is primarily of the ridged, striped variety, and minimum reproductive size (length) is about 22mm (See Reproduction-age). On the open coast, individuals are much more variable in color, and somewhat smaller, under 20mm in length. These differences in size and color between calm water and open coast individuals were mentioned by Dall (1916). They have also been described in the related T. lapillus of Britain, Europe, and the east coast of North America (Pelseneer, 1935; Colton, 1916, 1922) although Moore (1936) did not find such differences. The increase in color variety on the open coast may represent a balanced polymorphism for protective coloration. Colton (1916) finds a definite drop in the fraction of light colored T. lapillus on Mytilus beds as opposed to barnacle areas, and I have found the same to be true of T. emarginata at Archcape, Oregon (see table 1). At Port Townsend, Washington, a calm water area of scattered boulders and essentially no mussels, all T. emarginate are grey, generally with pale brown spiral stripes and ridges. To the human eye, this seems the most cryptic of the various morphs for this particular beach. At Golden Gardens Park, in Seattle, where the beach is similar to that at Port Townsend, the same morph predominates except in areas where the sand gives way to black mud. Here, T. emarginata is black.

Thais lamellosa is considerably larger than T. emarginata, the adults commonly reaching a length of 55mm or more. At Port Townsend, snails over 60mm in length are not uncommon, and one individual 112mm long was found in 1964. There is, again, one large body whorl, and three minor whorls. T. lamellosa shows much more than T. emarginata the result of abrasion, and the protoconch is seldom present in adult animals. The shell shape in T. lamellosa appears adaptive. In areas with little tidal current (Golden Gardens, Port Townsend) most individuals show a degree of longitudinal fluting and pronounced shoulders whereas those individuals occurring in rough water areas or places with strong tidal currents (Mukkaw Bay, Washington--Port Orford, Oregon, and Barview, Oregon, respectively) are more apt to be somewhat elongated, with much less ric rac, and with smaller shoulders. This species is usually a dull grey in color both in calm and rough water, although individuals with one or two broad, white spiral bands are not uncommon. Rarely, a bright yellow or orange animal may be found.

T. emarginata occurs from the Okhotsk Sea in the west, across the Bering Sea, to the american coast in the east, and south into Baja, California. T. lamellosa occurs as far north as the Bering straits, and south, in the west, to Sado island, in the Japan sea. In the east, it ranges south along the coast from the Aleution islands to Santa Barbara, California.* Keen (1937) gives the range of T. emarginata as extending from 16° N latitude to 58° N, and that of T. lamellosa from 34° N to 65° N.

STUDY AREAS

Most of the work reported here was carried out at one area, and unless otherwise stated, all data mentioned may be assumed to have been collected at Jefferson county park, Port Townsend, Washington (48° 8' North, 122° 46' West). This area is a sand-cobblestone beach with numerous scattered rocks up to about five feet in diameter and three feet in height. It faces north, stretching east-west for about 200 meters. The beach continues on beyond the study area for perhaps a mile to the east and considerably more to the west. The slope is quite uniform, with a grade of roughly three percent. During the summer sand washed in from subtidal levels covers most of the cobblestones in the mid and upper intertidal (above the zero foot level), but sand is almost entirely absent at lower inter-tidal levels and during the rest of the year.

The beach is near the town and has a small boat launching ramp. In spite of this, however, few people congregate even in the

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*Geographical range information was taken from the Minutes of the Conchological Club of Southern California, Vol. 52: 7.

summer, and the tidal flats only 100 feet from the ramp probably receive only a dozen visitors daily on summer low tides, and considerably fewer at other times. It is, therefore, quite undisturbed and offers a practical area for study.

The areas at Barview, Oregon, and Golden Gardens park in Seattle, are somewhat similar to that at Port Townsend, but with much less extensive beaches. The Golden Gardens beach is partly polluted and, being adjacent to a large city swimming beach, sustains much human interference. The Barview area is relatively undisturbed, like that at Port Townsend, but has a much steeper slope. Both areas have fewer large rocks than Port Townsend.

The Archcape, Oregon, Port Orford, Oregon, and Mukkaw Bay, Washington areas are all open coast. The Archcape beach consists of several cliff faces, withstanding heavy wave shock, joined by sheet rock. At Mukkaw Bay, there is much sheet rock, but fewer vertical rock faces than at Archcape. Port Orford is also an area with rough water, but here the terrain is more like that at Port Townsend; a cobblestone beach with scattered boulders.

FEEDING BEHAVIOR

Food and the Feeding Process

The food of *Thais* varies. In calm water areas little is eaten besides acorn barnacles (*Balanus sp.*) and mussels (*Mytilus edulis*), although in the late spring when food is scarce, *T. emarginata* has been observed to feed on limpets (*Acmaea sp.*), and on its own egg cases. On exposed coasts, *T. emarginata* utilizes goose neck barnacles (*Mitella polymerous*) and the open coast mussel (*Mytilus californianus*). *T. lamellosa* is scarce on the open coast and few feeding records have been obtained in such areas.

By far the most important foods for *Thais* both in calm and rough water areas, however, are the barnacles, *Balanus cariosus* and *B. glandula*. *B. cariosus* is a large barnacle measuring in size up to about 20mm across the operculum (maximum internal distance between lateral plates at their distal ends). The mean size is roughly 7.5mm at Port Townsend (February, 1966 data). It occurs intertidally from about -2.5' up to about +4.0', the upper level varying somewhat from rock to rock and from place to place on the beach. Its larvae settle in the spring, near the beginning of April. *B. glandula* is a smaller barnacle, usually measuring less than 3.5 or 4.0mm in opercular diameter but rarely approaching 6mm in some protected spots. The population mean at Port Townsend is about 1.6mm in late June immediately after the heaviest larval settlement, and increases to a February value of 2.25mm, where it remains until the following summer settlement. Larval settlement continues from early June, through late August or early September. B. glandula occurs in a tidal zone of roughly 0.0' to +5.0'.

Two other barnacle species occur at Port Townsend. B. nubilus is a very large barnacle which occurs subtidally and occasionally at very low intertidal levels. It may be eaten by T. lamellosa when small although no feeding records have been obtained. The large individuals are probably not eaten except by the very largest Thais due to their habit of grinding the opercular plates about with considerable force. The other species, Cthamalus dalli, occurs high in the intertidal, overlapping the upper part of the range of B. glandula. It is smaller than B. glandula and as a result of its size, probably represents a rather poor food to Thais. (The relationship of food size to diet will be discussed later). It is rarely eaten.

Thais feeds by first drilling a small hole through the plates of the barnacle. This is accomplished with the radula, probably with the periodic, alternate use of an accessory boring organ. (For experimental work on the drilling process of related snails, see Carriker, 1961). The drill-hole is usually found between the opercular plates of the barnacle, but is occasionally seen through the lateral plates (see also, Connell, 1960). The latter placement of the drill hole, however, is inefficient for the snail, which must work somewhat longer than it would have had the hole been placed, as usual, between the scuta, and is of rare occurrence. In the case of the related species, T. lapillus, it has been claimed that at this point a toxin is injected into the prey, causing it to relax (Clench, 1947). The existence of such a toxin has also been suggested for T. emarginata and T. lamellosa (Connell, 1960). Whether or not this toxin occurs, however, the barnacles, when drilled, do in fact relax. The opercular plates gape open, the snail generally perches itself stop the barnacle--if it is not already so positioned--and proceeds to rasp out the barnacle flesh. Rarely, when the barnacle has been drilled through the lateral plates, the snail will enlarge and feed through the original drill-hole.

Experimental Methods and General Considerations

In order to analyze the time and energy aspects of Thais' feeding behavior, it was necessary to approximate the time required for a snail to drill, and to feed on one barnacle. Since it soon became obvious that straightforward observations on the snails placed in aquaria would not yield the necessary information, an underwater, time-lapse camera was set up to replace the observer.

Such a set-up has the advantage that it can be anchored on the beach, and record snail activity in the field. A 16mm Bolex camera was used, and the single-frame mechanism was triggered by a solenoid controlled by a variable interval, electronic timer which was set to fire at time intervals of 1-1/2, 2, or 2-1/2 minutes. The whole apparatus--timer, firing mechanism, and camera--conveniently fit into an 8"x10"x12" case of 3/4" lucite. A flange was bolted to the bottom of the case which could thus be screwed down, and securely fastened by a lock nut, to a threaded stainless steel pipe embedded in cement on the beach. Three such pipes were embedded, at tidal levels of -2', 0', and +2', in positions such that the camera lens, when the case was in place, faced a large rock at a distance of about two feet. At this distance an area of rock roughly 12"x18" was covered in the photographic field, and with Kodachrome II daylight film, enough contrast and detail were obtained to allow for detailed analysis of the pictures.

One can easily tell whether a snail is, or has recently been ingesting a barnacle by carefully lifting it and checking to see whether the opercular plates of the barnacle directly beneath the anterior part of its foot are gaping. In most cases such snails do not exhibit the extended probescis one would expect to see if the snail were actively feeding. Only 9 of 96 (9.4%) feeding T. emarginata and 10 or 27 (37%) feeding T. lamellosa showed extended proboscids. It appears, then, that in many cases, feeding is either interrupted by tidal exposure, or, being of short duration for one barnacle, is generally finished by the time observations can be made. New drilling is probably not initiated when the snail is exposed. Such a conclusion is in keeping with the observation mentioned previously that *Thais* tends to cease activity when exposed.

Camera data indicate that *Thais emarginata* individuals begin to feed shortly after immersion (roughly one hour) and tend to eat more than one barnacle in a very small area. They then make a rather long move, roughly 15 to 90 cm, generally horizontal and in a straight line, and proceed to eat again.

The tendency to eat several barnacles in a clump was confirmed by a nested quadrat technique (Morisita, 1959). The procedure consisted of counting the number of eaten barnacles in each of 144 one inch squares arranged in a 12x12 matrix. Disjoint sets of square quadrats were then defined such that all members of each set consisted of m^2 adjacent one inch squares. A value, $I_\delta = q\sum_i \frac{n_i(n_i - 1)}{N(N-1)}$, was then calculated ($q$ = number of quadrats, n_i = number of eaten barnacles in the ith quadrat, N is the total number of eaten barnacles in all quadrats) for each set of quadrats and plotted graphically against the size of the quadrats (m^2).

Curves rising to the left, such as those calculated from data gathered at Port Townsend, indicate a clumping of the eaten barnacles (see Figure 1).

The average distance per move per snail under camera observation in August, 1965, was 38cm and since all of the snails either entered or left the field of vision still moving, the actual average distance may have been considerably more. The average distance moved per immersion period by actual marking and measuring on successive low tides (July, 1965) was 45 cm. Since the distance per move and the total distance moved per immersion period are very similar, it would appear that only one move is made by a snail on a given day. In the same month, 25 other T. emarginata were marked and for four days the distances from their origins on the first day were noted. The distances averaged 42cm after the first day, 88cm after the second, and 118cm after the third. These data from the first three days suggest linear movement not only day by day, but over a series of days until the point of maximum possible distance from the origin is reached. At this point, the snails turn and move in a new direction. The size of the rock was such that a snail could move an average distance of only about 120cm from its initial point before entering poor foraging areas. The average distance from origin on the fourth day was 109cm.

It was not possible, on the basis of the photographic data, to distinguish directly between the time required to drill a barnacle (T_d) and the time required to ingest it (T_f). However, the facts that feeding activity appears to begin shortly after immersion and ceases shortly after exposure (from photographic and low tide observations,. respectively), and that _T._ _emarginata_ individuals move once, along a straight line during immersion, make possible the use of a model which indirectly indicates feeding and drilling times (see appendix 1). Values of the average drilling and ingestion times (on the average sized barnacles appearing in the diet), $\overline{T}_d$ and $\overline{T}_f$, obtained for _T._ _emarginata_ are given in table 2.

Food Preferences--Thais emarginata

The amount of time required for a snail to drill a barnacle, T_d, should be very nearly proportional to the distance the snail must drill, i. e. the thickness of the opercular plates at the point where they meet (the drill-hole is nearly always between the scuta). As figure 2 indicates the thickness of the scuta at the point where they abut is proportional to the linear dimension of the barnacle for both barnacle species.

(1) Thickness = .07 opercular diameter.

Assuming T_d to be proportional to scutum thickness, then, the time required for a snail to drill a barnacle _x_ times the size of the average barnacle is approximately:

(2) $T_d = x\overline{T}_d$.

Similarly, the time required to ingest a barnacle should be proportional to the amount of flesh rasped out. By weighing dried barnacles before and after ashing in a muffle furnace, the amount of organic material in barnacles of different sizes was determined (see figure 3). It was discovered that the amount of organic material in *B. glandula* varies very nearly as the 1.55th power of the barnacle's opercular diameter, so that T_f can be approximated by the expression:

(3) $T_f = x^{1.55}\overline{T}_f$ (*B. glandula*).

For B. cariosus, the relationship is:

(4) $T_f = x^{3.5}\overline{T}_f$ (*B. cariosus*).

$\overline{T}_f$ for *B. glandula* and *B. cariosus* are not necessarily the same. The actual amount of organic material (ash free weight) in grams is:

(5) Ash free weight = $.029L^{1.55}$ for *B. glandula*, and

(6) Ash free weight = $.089 \times 10^{-3} L^{3.5}$ for *B. cariosus* where L is the opercular diameter of the barnacle in mm.

Now the energy spent by a snail in drilling a barnacle should be roughly proportional to the time spent drilling and may thus be approximated by $T_d E_d$ where E_d is the approporiate conversion coefficient. Similarly, the assimilated energy gained in the ingestion process should be nearly proportional to the amount of organic material removed from the barnacle--except for very small barnacles relative to snail size where the energy gain is somewhat lower than this (Connell, 1960). This, as previously mentioned, is about proportional to the time spent feeding. Thus, the assimilated energy gained in feeding may be written $T_f E$ where E is the appropriate conversion factor, and the total net energy gain per unit time to the snail, from one barnacle, is:

$$\frac{T_f E \quad T_d E_d}{T_f + T_d} \qquad \begin{cases} \dfrac{x^{1.55}\overline{T}_f E \; - \; x\overline{T}_d E_d}{x^{1.55}\overline{T}_f \; + \; x\overline{T}_d} & \text{(\textit{B. glandula})} \\[2ex] \dfrac{x^{3.5}\overline{T}_f E \; - \; x\overline{T}_d E_d}{x^{3.5}\overline{T}_f \; + \; x\overline{T}_d} & \text{(\textit{B. cariosus})} \end{cases} \tag{7}$$

The values of the above expressions increase with *x*. That is to say, the larger the barnacle, the more it is worth to its snail predator in terms of energy gain per unit time. If the snails are well adapted to their environment, then, such change in food quality should be reflected in a preference for the largest barnacles.

Size preferences for *T. emarginata* on *B. glandula* were measured by dividing *B. glandula* into three size categories (opercular diameter < 1mm, 1 to 3mm, > 3mm) and then dividing the proportions of each size category in the snails' diet by the relative abundance of that size category in the environment. When normalized, the results give a measure of food preference which I have called the "importance" value, I. It was assumed that feeding was initiated according to no set temporal pattern, and thus that the number of a given food size eaten could be expressed as proportional to the number of observed feedings divided by $\overline{T}_f+\overline{T}_d$. The method used for determining barnacle densities is shown in appendix 2. The importance values for different food size categories are shown in table 3. As expected, T. emarginata shows a marked preference for the largest B. glandula. Feeding records of T. emarginata on B. cariosus are fairly scarce and no attempt has been made to determine food size preferences for this species.

In order to predict food species preferences, actual values of energy gain per time from B. glandula and B. cariosus of several sizes must be calculated. In September, 1965, the average sized B. glandula was 2.37mm in opercular diameter and took 2.9 hours to eat. The ingestion rate of an average T. emarginata, then, is $\frac{(.029)(2.37)^{1.55}}{2.9} = .038$ grams/hour (see equation 5). The same sized barnacle took 2.0 hours to drill, implying a drilling rate of $\frac{(.07)(2.37)}{2.0} = .08$ mm/hour (see equation 1). Assuming that both barnacle species are drilled at the same rate and with the same effort, and that both yield about the same food value per gram organic weight, the gain per time to a snail from a barnacle of size L (in September, 1965) was:

$$(8)\qquad \text{Gain/time} = \frac{\frac{.029L^{1.55}}{.038}E - \frac{.07L}{.08}E_d}{\frac{.029L^{1.55}}{.038} + \frac{.07L}{.08}}$$

$$= \frac{.76L^{1.55}E - .88LE_d}{.76L^{1.55} + .88L}$$

for B. glandula, and:

$$(9)\qquad \text{Gain/time} = \frac{\frac{.089X10^{-3}L^{3.5}}{.038}E - \frac{.07L}{.08}E_d}{\frac{.089X10^{-3}L^{3.5}}{.038} + \frac{.07L}{.08}}$$

$$= \frac{.00234L^{3.5}E - .88LE_d}{.00234L^{3.5} + .88L}$$

for B. cariosus.

In order to evaluate E and E_d, it was assumed that the large number of B. glandula of size 1mm or less in the diet of T. emarginata in the early summer of 1965 (17 out of 101 feeding snails were observed on these small barnacles) indicates that the gain from these food items is positive. This being so,
Gain = $(.76)(1)^{1.55}E - (.88)(1)E_d > 0$, so $E_d < .86E$. Gain/time values for B. glandula and B. cariosus of different sizes, for September, (for $E_d = 0$, and $E_d = .86$) are given in table 4 along with values for August and January calculated by multiplying the time factors in equations 8 and 9 by the appropriate scalar values (see appendix 1).

Obviously, B. glandula is a much better food for T. emarginata than is B. cariosus. In addition, at high and mid levels (rock bases above the 1.5' tide level), the barnacles on each rock are zoned, a band of *B. cariosus* at the base, and a band of *B. glandula* above. Whether a snail eats more *B. glandula* or more *B. cariosus* with respect to what is available on the entire rock, then, would seem clearly to be affected by the zone in which the snail tended to stay. This proposition is backed up by data from September, 1965, when feeding records were kept for snails occuring both in the *B. glandula* and in the *B. cariosus* bands. The results are shown in a contingency table (table 5). By a X^2 test, the position of a snail on a rock was found to be highly correlated with its diet. From the barnacle densities given in table 6, it is clear that the *B. glandula* is superior to the *B. cariosus* band in terms of food availability above 1.5 feet and one would thus expect *T. emarginata* to preferentially inhabit the upper rock area. If so, then, both in terms of food availability and value per food item, *B. glandula* represents the better food. As expected, *T. emarginata*, when feeding, does in fact congregate in the *B. glandula* band and shows a marked preference for this species at high and mid levels. Importance values for *B. glandula* and *B. cariosus* at these levels were $I_{B.\ glandula} = .95$, $I_{B.\ cariosus} = .05$ in August and September, 1965 (based on 137 feeding records), and $I_{B.\ glandula} = .96$, $I_{B.\ cariosus} = .04$ in December, 1965 and January and February, 1966 (based on 49 feeding records).

At lower tidal levels, B. cariosus are relatively much more common (see table 6) and at levels below about 1.5', B. glandula occurs in no distinct band, but is scattered among B. cariosus on the upper portions of the rocks. Thus, one might expect the preference for B. glandula to fall off with decreasing tide level. Other factors must be taken into consideration, however. First, according to theory (Emlen, in press), a drop in the relative abundance of the preferred food may cause only a very small corresponding drop in the relative abundance of that food in the diet. Second, whereas, in summer, it takes only about three hours for a T. emarginata to ingest an average sized B. glandula, it would require about fourteen hours completely to ingest a B. cariosus 12mm in size. And, whereas there is room for only one snail atop a B. glandula, two or more can perch on a B. cariosus. The increased ingestion time means that cruising snails are more likely to come across the already drilled B. cariosus, and the available room means that they can take advantage of the already drilled food source. Observations do in fact show that such hangers-on, are quite common when snails are found feeding on B. cariosus (8 of 46 feeding records on B. cariosus equal to or larger than 5mm in size showed one hanger-on, one showed two hangers-on). Needless to say, the presence of such hangers-on will considerably lower the value of a barnacle to the snail who drilled it, and should tend to make B. cariosus a relatively less useful food than it would be were these freeloaders absent. The fact that the hangers-on benefit from their behavior is immaterial to the argument that it is selectively disadvantageous for snails to initiate drilling on these large barnacles.

The effect of hangers-on may be calculated as follows. Let n be the number of hangers-on, and suppose that all n appear immediatly after cessation of drilling. Then:

$$(10)\quad \text{Gain/Time} = \begin{cases} \dfrac{T_f E(\frac{1}{1+n}) - T_d E_d}{T_f(\frac{1}{1+n}) + T_d} & : T_d + T_f(\frac{1}{1+n}) < T, \\[2ex] \dfrac{(T - T_d)E - T_d E_d}{T} & : T_d + T_f(\frac{1}{1+n}) > T, \text{ and} \end{cases}$$

feeding interrupted by exposure is not continued upon the next submersal. These expressions represent the minimum gain per time; actual gain per time would lie somewhere between these values and those obtained for n=0. Actually, the second of the above equations shows no energy loss due to hangers-on, but the conditions for the application of this equation seldom occur. Only the first equation need be considered. It can be calculated that in the summer, a 12mm B. cariosus, for example, without hangers-on yields roughly between .57E (E_d=0) and .20E (E_d=.86E) energy units per time to a snail predator (see table 4). With only one hanger-on these values may be lowered respectively to as low as .40E and -.12E--ie somewhere between a net energy loss and about 70% of the original value.

The expected tendency for the food preferences of *T. emarginata* to gradually shift toward *B. cariosus* at low tide levels seems to be effectively offset by the superiority of *B. glandula* in terms of energy yield, and the effects of hangers-on. Importance values for levels below 1.5' show (June, 1965--based on 6 feeding records) $I_{B.\ glandula} = .83$, $I_{B.\ cariosus} = .17$, and (December, 1965--based on 33 feeding records) $I_{B.\ glandula} = .99$, $I_{B.\ cariosus} = .01$.

Food Preferences--Thais lamellosa

Due to the variability in the size of *T. lamellosa* individuals and their food, the model used to calculate drilling and feeding times for *T. emarginata* is not meaningfully applicable to *T. lamellosa*. Any analysis of the time and energy aspects of *T. lamellosa* feeding behavior, then, must be by comparison with the information presented for *T. emarginata*.

Let $T_f = Xa$, and $T_d = Ya'$, where X = organic volume--which is proportional to L^{β} ($\beta = 1.55$ for *B. glandula*, 3.5 for *B. cariosus*), Y = thickness--which is proportional to L, and *a* and *a*' are the appropriate proportionality constants. Then energy gain= $XaE=Xb$, and energy expense = $Ya'E_d = Yb'$, and the ratio of gain per unit time to a snail from two conspecific barnacles of sizes L and αL, where $\alpha < 1.0$, is given by:

$$(11) \quad \frac{Xb-Yb'}{Xa+Ya'} \div \frac{Xb\alpha^{\beta}-Yb'\alpha}{Xa\alpha^{\beta}+Ya'\alpha} = \frac{abX^2\alpha^{\beta}+a'bXY\alpha-ab'XY\alpha^{\beta}-a'b'Y^2\alpha}{ABX^2\alpha^{\beta}+a'bXY\alpha^{\beta}-ab'XY\alpha-a'b'Y}$$

Since all terms except the second and third are the same, the value of the ratio varies with

$$\frac{a'bXY\alpha - ab'XY\alpha^{\beta}}{a'bXY\alpha^{\beta} - ab'XY\alpha} = \left(\frac{\frac{a'}{a} - \frac{b'}{b}\alpha^{\beta-1}}{\frac{a'}{a} - \frac{b'}{b}\alpha^{1-\beta}} \right) \alpha^{1-\beta}.$$

Connell (1960) has shown that when a barnacle is very small relative to the size of its snail predator, a certain amount of the calcareous skeleton of the barnacle may be ingested, lowering the assimilation efficiency of the snail. It is expected, then, that as a snail becomes larger, its assimilation efficiency for a given sized barnacle--and thus the value of *b* in the above expression--slowly decreases. Since $\alpha^{1-\beta} > \alpha^{\beta-1}$ for both barnacle species, the above expression increases in size as *b* decreases and the relative value of the larger barnacle to the snail increases. Thus, snails, as they grow larger, should shift their food preferences to larger barnacles. *T. emarginata* data collected in January and February of 1966 show this to be true (see table 7). It also appears to be true for *T. lamellosa* (table 8).

Since the organic volumes of the two barnacle species vary with barnacle size in very different ways, it is impossible, without knowing $\bar{T}_f = xa$ and $\bar{T}_d = ya$ for *T. lamellosa* for at least one barnacle species, to assess the relative values of the two barnacles to the snails. However, if, as previously assumed, drilling rates are the same on both *B. glandula* and *B. cariosus*, the value of *B. cariosus* should surpass that of B. glandula (size = 2.3mm) when:

$$\frac{k_1(.089\mathrm{X}10^{-3})L^{3.5}E-k_2(.07)LE_d}{k_1(.089\mathrm{X}10^{-3})L^{3.5}+k_2(.07)L}=\frac{k_1(.029)(2.3)^{1.55}E-k_2(.07)(2.3)E_d}{k_1(.029)(2.3)^{1.55}+k_2(.07)(2.3)} \tag{12}$$

where k_1 is the feeding rate and k_2 the drilling rate. This will occur at a critical size of roughly 12mm. Now, if a large *T. lamellosa* requires less time to feed on a given sized barnacle than an average sized *T. emarginata* (which seems a reasonable assumption), there should be fewer instances of hangers-on than were found in the case of *T. emarginata*. That *T. lamellosa* is larger than *T. emarginata* and thus leaves less room over a barnacle also mitigates against hangers-on. There are, in fact, very few instances in which *T. lamellosa* hangers-on have been found. The loss in food value which is at least partly responsible for discouraging the use of *B. cariosus* by *T. emarginata*, then, has much less effect on *T. lamellosa*, and *B. cariosus* greater than the critical size of 12mm mentioned above should be of greater value to this snail species than *B. glandula*. Also, since, as shown above, a snail's energy intake per unit time increases faster with large than with small barnacles as the snail increases in size, large *B. cariosus* should be relatively more useful as food to *T. lamellosa* than they are to *T. emarginata*. Clearly, *T. lamellosa* should show a stronger tendency to use *B. cariosus* than does *T. emarginata*. In addition, while the energy per unit time gained from a small *B. glandula* is perhaps somewhat greater for a large *T. lamellosa* than for a smaller T. emarginata due to the former's faster consumption rate, the energy needs of a T. lamellosa also may be larger than those of a T. emarginata. It may be that for large enough snails, small B. glandula simply cannot supply enough energy fast enough to maintain these predators. Large T. lamellosa may well fall into this category. At any rate, large T. lamellosa should do well to eat more B. cariosus than does T. emarginata. Small T. lamellosa may be expected to feed more in the pattern of T. emarginata. Since $\overline{T}_d$ and $\overline{T}_f$ are unknown for T. lamellosa on either barnacle species, it is impossible to determine the number of each barnacle species eaten by T. lamellosa. However, if the number of observed feedings is used, it is clear that as T. lamellosa increases in size, the relative percent of B. cariosus in its diet increases as predicted (see table 9). Data taken from Connell (1960) and reworked show the same results. By actually counting barnacle mortality within enclosures, Connell has gathered information that shows small T. lamellosa eating more B. glandula while large T. lamellosa prefer B. cariosus (see table 10).

* * * * *

It has been shown that Thais shows feeding preferences that tend to maximize its energy intake per unit time. The snails appear capable of discriminating both between different barnacle species and between size classes within each species.

So far, the role of risk has not entered the picture. However, snail movements, distribution and reproduction, which depend on efficient energy intake and thus on food distribution, are strongly modified by the presence of dangers from desiccation, storm, and predation. In the following section some of the dangers and their effects on snail behavior are discussed.

THE EFFECTS OF RISK

Mortality

Direct mortality measurements on the natural population were carried out on adult and near adult T. emarginata (greater than 15mm in length) and on young of the same species (less than 15mm in length). Of the former, 109 snails were individually numbered in July of 1964, and 246 on August 7. On August 20-22 of the same year, 500 more were numbered. On subsequent months a thorough search was made of the entire study area and every marked snails found was recorded. After the drop in the observed number of marked snails between marking in August, and first "recapture" in September--due in part to dispersal and redistribution on the rocks--it was reasoned that further monthly drops would roughly indicate the actual decrease in population, i. e. the mortality. Taking the number observed in September as the "base" number--i. e. the number expected in following months, in the absence of deaths--the mortality rate during the year of 1964-1965 could be calculated. A second series of observations, based on newly numbered snails, was started in April, 1965. On the basis of the data gathered (see table 11, figure 4) yearly survivorship after the first year of age can be estimated by extrapolation at .0184 (roughly 2%). The survivorship between the ages of approximately 6 and 18 months, calculated by a similar method, is roughly .06 (6%) (see table 12, figure 5).

The effects of the weather on mortality can be examined to a point. Experimental tests in which T. emarginata were exposed in the field to the sun or in the laboratory to the rays of a heat lamp for periods of 5 hours resulted in no mortality whatsoever until the temperature reached a point between roughly 18 and 32°C (see p. 30). Death results, then, I believe, not from desiccation but from the washing ashore or, in the case of T. emarginata, out to sea of snails that have released their hold on their rock due to exposure. Detachment should be expected to be greatest in warm, dry weather, and the dangers of subsequently being washed off the rocks greatest in stormy weather.

In order to test the hypothesis that snails would be more likely to become detached as a result of higher temperatures, T. emarginata were collected and placed on a high level rock on the beach for periods of five hours. In January, 1966, at 3.9°C, all snails remained firmly attached to the rock, but in May, at 17.2°C, only two of 21 snails greater than 15mm in length remained attached. Supplementary tests at 10°C in the zoology department cold room showed two of 15 large snails becoming detached in 19-1/2 hours, indicating that about .035 of the snails would be expected to detach every five hours. At 32.2°C, under a sun lamp, 31 of 31 snails had released their hold after five hours. The effect of temperature on large snail detachment is shown, taken from the above data, in figure 6.

It was also discovered that small T. emarginata are more rapidly affected by the sun than larger individuals. At 17.2°C in May, under natural conditions on exposed rocks, after 2-1/2 hours, five of seven snails less than 20mm long, but only four of 19 larger snails were detached. This difference is significant, by a contingency table, Chi square test, at a level between .01 and .025. The experiment was repeated in the laboratory at 32.2°C with the following results. After 2-1/2 hours all snails were detached. Seven of 16 snails less that 15mm in length and none of 27 larger snails appeared dead and failed to recover after 3-1/2 hours submerged in sea water. The difference in mortality between the large and small snails is significant at a level less than .005.

Similar tests were not attempted with T. lamellosa but the presence of T. lamellosa individuals hanging limply and dropping from rocks on warm days indicates that this species is prone to the same danger as T. emarginata.

No attempt was made to determine the eventual fate of snails detached under natural circumstances, but, as previously mentioned, it is presumed that those washed ashore and those T. emarginata washed out to sea as a result probably die. Displacement to subtidal levels probably does not harm T. lamellosa since populations of this species have been dredged from depths of 6 fathoms (personal observation) and even 30 fathoms (Kohn, pers. comm.).

The extent and importance of predation on the two species is difficult to measure, but is thought to be slight (for predation on developing young, see Reproduction--and appendix 3). Crows were occasionally seen pecking at T. emarginata which had fallen to the ground, and freshly broken T. lamellosa placed neatly atop the larger rocks provided strong evidence of gull predation. Nevertheless, nearly all of the shells of dead snails found on the beach were perfectly intact. On open coast areas where mussels (Mytilus californianus) and/or Pisaster are common, death may occur either from entrapment by byssus threads (personal observation) or by starfish predation (Feder, 1959; Mauzey, in press; Paine, 1966) both of which leave intact shells. However, at Port Townsend, mussels and starfish are rare. Kibling, et al (1964) have indicated that large crabs may be a source of mortality in the related species, T. lapillus. At Port Townsend, however, I have never seen large crabs, and at any rate, such predation would leave broken shells. It appears that the greatest cause of mortality here is the washing ashore or out to sea of individuals which, because of prolonged tidal exposure, have lost their grip on their rock.

Movements I

Other authors (Ackerman, 1964; Connell, 1960; Glynn, 1965) have indicated that Thais individuals move up and down their rocks (or pilings) with the daily tides. This may be true of the snails at some localities, but is certainly not the rule at Port Townsend. The snails remain on the tops of rocks at low tide on many days and, judging from day to day measurements of movement (see discussion of distances moved, p. 41) many remain low on the rocks at high tide. An impression of vertical, tidal migration for both snail species, however, is easy to get since there are often only a few snails left on the tops of rocks at low tide, and many near the rock base. This is due not to daily movements, but is an indirect response to the long periods of tidal exposure which come for a few days every two weeks:

Let T be the time submerged per day,

T_E be the time exposed per day,

x be the detachment rate on the tops of rocks due to exposure,

y be the detachment rate on the lower parts of the rocks due to exposure,

R be the daily respiration rate in calories,

C be the calories assimilated as food per barnacle.

Now, the amount of energy that a snail can put into reproduction is the amount of accumulated energy left over after respiration and growth. Since growth is essentially negligible in snails of reproductive age (see Reproduction--Age), this factor can be ignored. The amount of energy available for reproductive purposes is thus: $\frac{T}{T_d+T_f}$ C-R when food is available. Food is always available to those individuals on top of rocks, but not to those low on the rocks in the *B. cariosus* zone. Measurements show on three days in September, 1965, 88 of 120 *T. emarginata* in the *B. glandula* band feeding, but of those lower on the rocks, only 6 of 124. "Down" *T. emarginata* thus spend only $\frac{6/124}{88/120} = .066$ as much time feeding as "up" snails, and the reproductive energy gained by the latter is $\frac{.066T}{T_d+T_f}$ C-R. *T. lamellosa* can do better than this unless it moves all the way to the rock base where sand scouring has eliminated all food items. Since those individuals that can spend the most energy on reproduction should leave the largest number of viable offspring, on the basis of the above comments it can be stated, as a very rough approximation, that the number of genes passed by an "up" animal is proportional to $\frac{T}{T_d+T_f}$ C-R, and by a "down" animal, $b\frac{T}{T_d+T_f}$ C-R, where *b* is .066 for *T. emarginata*.

The number of genes passed, however, is also proportional to the probability that the individual is alive to pass them. This probability can be written e^{-xtd} for snails on top of the rocks and e^{-ytd} for those low on the rocks, where d is the probability of death in the event of detachment from the rock and t is the time exposed. The expected number of genes passed, then, by a snail which spends N-n days near the rock base and n days on the rock top, is:

$$(N-n)\left(b\frac{T}{T_d+T_f}\,C-R\right)e^{-y(N-n)T_E d} + (n)\left(\frac{T}{T_d+T_f}\,C-R\right)e^{-xnT_E d}$$

An examination of this equation will show that for each combination of T, T_E, T_d+T_f, C, R, x, y, and d (where $x>y$) there will be a value of n/N between zero and one, for N large, for which the number of genes passed is maximum. That is to say, snails will behave optimally, in terms of natural selection, if they spend a certain proportion of their days on top of rocks, and the rest on the lower parts of rocks. The necessary condition that x be greater than y is met. On May 22, 1966, for example, the temperature on top of the rocks at 10 AM was 18.3°C, and at their shaded bases, 12.2°C. From figure 6, it is clear that the mortality at 18.3° (x) is greater than that at 12.2° (y). It can also be stated, on the basis of the equation, that a proportional rise in x and y, or a rise in d, or T_E will require a larger percent of time on lower portions of the rocks if the snails are to behave optimally.

It is reasonable to assume that the effects of exposure and desiccation increase as a snail becomes progressively warmer and dryer, and it is clear that this is, in fact, the case. In the first 2-1/2 hours of exposure in a test at 17.2°C, only four of 19 T. emarginata longer than 20mm had become detached, but in the next 2-1/2 hours, 13 more were detached. In a repeat of this experiment at 24.4°C, none of 48 snails over 15mm in length had become detached after 2 hours, but after three hours, 8 were detached. x and y, therefore, increase as continuous exposure time increases. The best strategy for a snail to follow, then, is to move to the rock base and spend its allotted "down" time there during periods when xT_Ed and yT_Ed are high or T_E is continuous and long, and to move to the rock top and spend its allotted time there when xT_Ed and yT_Ed are low and the daily exposure time is broken into two, shorter parts. One would thus expect to find snails low on their rocks following warm or stormy days, or days of low low tides. On three rocks, on April 19, 1966, for example, after several sunny days, only 11 of 87 (=.126) T. emarginata that could be found were on the tops of these particular rocks. The 20th was cold and cloudy, as were the 21st through the 24th, and as expected, the number of snails on top of the rocks increased. In addition, snails hidden in crannies and not visible on the 20th, gradually appeared, so that by the 25th, 125 of 219 (=.57) snails were perched on top of the rocks. In September, 1965, when the weather was somewhat more uniform, the fraction of T. emarginata high on particular rocks continued to decrease after several days of long, continuous tidal exposure, from 84 of 138 (=.63) on September 22, to 38 of 111 (=.21) on the 23rd, to 10 of 90 (=.11) on the 24th. Instead of one long exposure every 24 hours as on the preceding days, snails on rocks at these levels would have been exposed for two shorter periods beginning on the 24th, and on the 25th, and following days, the fraction high on the rocks should have increased again. Unfortunately this expectation was not checked. In May, 1966, the temperature remained warm (17.2° to 18.3°) on the rock tops from the 18th to the 22nd except for slightly cooler weather on the 21st. These were days of increasingly low low-tides and long, continuous exposure periods. On the 18th, 38 of 50 (=.76) T. emarginata were on the tops of their two rocks. On the 19th, the fraction had dropped to 26 of 39 (=.67)--the other 11 presumeably hidden in crannies--and by the 22nd, only 1 of 31 (=.03) remained on the rock tops.

No quantitative measurements were made on similar T. lamellosa movements, but it can be stated that this species behaves essentially like T. emarginata. The difference in vertical distribution of both T. emarginata and T. lamellosa on their rocks on hot versus cold, overcast days, and on days of long exposure versus short exposure time, is often striking.

Since small T. emarginata are more readily detached than their elders (see Effects of Risk--Mortality)--i.e. their d value is higher--they should spend a larger amount of time on the lower parts of their rocks than do the larger individuals. On three particular rocks, on the 19th and 20th of April, 1966, 52 of 89 T. emarginata larger than 20mm in length, but only 19 of 67 smaller individuals were on the tops of their rocks. By a contingency table, Chi square test, the fraction of smaller snails on the rock tops (=.28) was significantly smaller ($p < .005$) than the corresponding fraction of large snails (=.58). On smaller rocks, where shelter is under rather than down on rocks, the same is true. The average sized T. emarginata on top of such rocks in April, 1966, was 25.6mm, and under, 18.1mm. The difference is significant by a t test, with $p < .005$.

In addition to moving up and down on their rocks in response to biweekly tidal cycles and temperature and storm conditions, both snail species exhibit seasonal movements which often carry them off their rocks and onto scattered rocks. In the case of T. emarginata these movements are controlled by a balance between the advantages accruing from the food supply existing on the smaller rocks, and the risks arising from sand burial while reaching or feeding on these rocks. When the sand, which at mid and high tide levels may lie up to 1-1/2 feet deep or more, encroaches in June, T. emarginata individuals are forced into concentrated pockets on those rocks remaining exposed. Since the snails will be unable to reach one rock from another without the risk of losing their grip in the sand and being washed away, they will do best, in late spring, to migrate to the large boulders, where they will have access to large areas in the B. glandula zone, and where they will be able to move down the rocks to shelter without having to risk being trapped by sand. T. emarginata does in fact behave this way, and the last part of June and the first part of July see a great increase in snail density of the larger rocks and a drop in density on the smaller rocks (see table 13). While the snails are devouring the settling and growing barnacles on the large rocks in June through September, however, those smaller rocks which have been spared burial by sand are supporting a barnacle population relatively free from snail predation. These rocks, then, carry rich food sources, and when the sand recedes in September and October, there is a rapid decline in T. emarginata population densities on large rocks, as the snails disperse to the now available smaller rocks (table 13).

T. lamellosa also shows seasonal movements, but these are of an entirely different nature from those of T. emarginata. At the levels inhabited by T. lamellosa there is essentially no sand even in the summer. Organized movement about the beach is thus not associated with sand wash, and appears to have nothing to do with food. Rather, the movements are in the form of a fall migration, starting in late September or October, toward the spawning areas--usually very large rocks at the zero foot tide level or slightly below--and a spring migration, after spawning, back to other rocks. Troubles encountered in marking techniques made it impossible to determine whether the snails returned to the same rocks from which they had come in the fall.

Movements--II

It has already been noted that T. emarginata may feed on several barnacles in one small area and then move to another spot and repeat this behavior (see Feeding--Experimental Methods and General Considerations). In the interest of saving time and energy the snails might be expected to move a minimal distance between these feeding spots, but again, the risk factor appears to play a role in modifying behavior.

Each large rock sitting on the beach within the mid and upper part of T. emarginata's range may be thought of as a hemisphere, approximately the top quarter of which corresponds to the upper, B. glandula band. Now consider the hemisphere to be bisected by a vertical plane running east-west. One half of the hemisphere (and actually slightly more) will, by virtue of facing south, face the sun, and the other half will face the ocean to the north. Consider a snail at some point on the southern face of the rock hemisphere. If the weather is sunny, this snail will do well to move to the shady side of the rock during the next tidal submersal so that it will be sheltered from the sun on the following day. Also, unless conditions are such as to trigger movement to the lower portions of the rock (see Effects of Rist--Movements--I), the snail will do better not to move down, but to move horizontally and stay within the B. glandula band where it can feed. In order to assure its being in the shade the next day without moving down it must move at least, but not farther than, a distance $\pi r'$, where $\underline{r}'$ is the perpendicular distance to its current position from the vertical. Since $\underline{r}'$ can be expressed as $\sqrt{r^2 - z^2}$ where $\underline{r}$ is the radius of the hemisphere and $\underline{z}$ is the snail's height on the rock, the average value of $\pi r'$ for all snails in the B. glandula band, is:

$$(14) \qquad \frac{4}{r}\int_{\frac{3r}{4}}^{r} \pi r' \, dz = \frac{4}{r}\int_{\frac{3r}{4}}^{r} \pi\sqrt{r^2 - z^2} \, dz = 1.44 \, r.$$

It is hypothesized that as the temperature in which a T. emarginata finds itself increases, and as the time period over which the snails is exposed to that temperature increases, the snail's tendency to move a distance approaching 1.44r increases. Thus, in spring and summer, those individuals who, after cloudy or cool days or days of short exposure, find themselves exposed on the sunny, southern half of their rock should, during the following high tide, move a distance close to but less than 1.44r. In the winter, those individuals on the northern, seaward side of their rock on a stormy day will do likewise if the temperature or perhaps wind during exposure is enough to significantly raise the possibility of detachment. Snails on the sheltered side of their rocks or on the protected lower portions should, in view of time and energy considerations and relative lack of risk, move much shorter distances.

On one particular rock, which measured (165x132x91 cm in its maximum diameter, minimum diameter and height, respectively, the average value of r can be calculated as $\frac{165/2 + 132/2 + 91}{3} = 79.8$cm. In May, 1966, at 17.2°C those snails on the sunny side of the rock which did not move down to shelter, then, should have moved somewhat less than (1.44)(79.8) = 115cm. On May 18, several snails on this rock were numbered and their positions on the rock mapped. On the following day the distances moved were measured and found to average 67.5cm with a standard deviation of 37.5cm. Four of seven snails reached the shady northern side of the rock. Those initially on the shady side moved an average of only 21.3cm with a standard deviation of 38.4cm and for those initially on the lower part of the rock and remaining there, the average and standard deviation were, respectively, 9.6cm and 29.2cm. Thus while the distances moved by snails not exposed to the sun are somewhat greater than might have been expected, the hypothesis, so far, is supported.

Now, on a smaller rock, the optimal moving distance for snails in the sun is less than that above. On another rock measuring 122x76x51 cm, and thus with an average radius of 50cm, the snails should have moved (1.44)(50) = 72cm. On the same day measurements were made on the larger rock, the snails on this rock moved 17.5cm. The low value probably is due to the fact that, in the case of this rock, a good deal less than the top quarter was in the unsheltered B. glandula band. If equation 16 is recalculated with integration limits of r and 7/8 r, the optimal distance becomes (.88) (50) = 44cm which is in better agreement with operation.

Two additional bits of information may be sought in support of the hypothesis: First, in the winter, due to stormy weather, the seaward snails should move farther than those on the southern, shore side of their rocks. This difference should not be so pronounced as the opposite summer difference in which the snails on the southern side move farthest, though, because without detachment or at least a weakening of the snails' hold on their rocks due to daylight exposure, the effect of rough water will be small and fewer snails will respond by moving long distances. Second, because there is less tendency for snails to move the predicted long distance in cooler weather, the average distance moved by all snails should be less in the cold months than in the summer.

In February, 1966, nine T. emarginata on the northern, seaward side of their rock, moved 16.5cm with a standard deviation of 11.7cm. Fifteen T. emarginata on the other side of the rock moved 9.6cm with a standard deviation of 7.6cm. The difference, though not statistically significant, is in the expected direction with $.05<p<.10$, and indicates a trend. The change in average distance moved by all snails, measured on rocks of similar size from month to month, is also as expected (Table 14).

Distribution--Thais emarginata

Since T. emarginata can utilize B. glandula with a much higher efficiency than B. cariosus, and as a result, whenever possible, feeds almost entirely on B. glandula, one would expect T. emarginata to occur within the range of B. glandula. Counts were made of all T. emarginata found along line transects at various tidal levels on the beach. Quadrats of about 200cm^2 were placed at random intervals along the rope and the number of T. emarginata in each counted. It will be recalled that B. glandula occurs from roughly 0.0' to +5.0' (see Feeding Behavior--Food and the Feeding Process). The range of T. emarginata quite obviously coincides almost exactly with that of B. glandula (figure 7).

Most T. emarginata show a tendency toward what might loosely be called a home range. While there was some movement of snails between the large rocks during the course of this study, much of this movement may have been the result of individuals, detached by the effects of the sun--or perhaps dislodged by an over-zealous researcher--, not re-attaching firmly to their rocks before the incoming tide washed them to other points on the beach. Of 745 snails individually numbered by August 20-22, 1964, counts in subsequent months showed few leaving the boulder on which they were originally marked, or the small rocks in the immediate vicinity of that boulder (see table 15). If the rate at which these snails left the general area of their parent boulder is assumed to be independent of season (this is not quite true, since the spring dispersal may well carry individuals into other areas--see Effects of Risk--Movements--I), a simple linear relationship between the rate of leaving and time may be set up:

(15) $\frac{1}{N}\frac{dN}{dt} = -\mu$ where μ is the rate of leaving, so that:

(16) $\ln\frac{N_t}{N_o} = -\mu t.$

Plotting the data from table 15 on a graph (figure 8) and filling in the linear expression (ln of the fraction remaining vs. time) by eye, a value of $\mu = .063$ per month is obtained. Such a line can be drawn from the data because of the absolute certainty of the point at coordinates 0, 0. Only about one snail in every 16 leaves its "parent" rock area each month.

The rate of movement about the beach, even though small, however, allows for a certain amount of aggregation of snails on rocks at favorable levels and a general tendency to avoid rocks at unfavorable levels. Since the greatly preferred food is B. glandula, and since the densest population of this barnacle occurs on the top halves of rocks at fairly high levels (bases at levels above +2.0'), this aggregation should occur near the top part of the snails' range (+3' to +5'). A glance at figure 7 shows this to be the case.

In the lower parts of the range of T. emarginata, there are a few B. glandula and many B. cariosus (see table 6). For example, in September, 1965, 87% of all barnacles at high and mid levels (rock bases above 1.5') were B. glandula. At low levels (rock bases = 1.5'), B. glandula made up only 9.4% of the barnacle population. In February, 1966, the values were, respectively, 67% and 2.5%. Thus one would expect to find a general avoidance of low levels by the snails in favor of high and mid levels. Since large T. emarginata can presumably handle B. cariosus better than small T. emarginata (see p. 25), this avoidance might be somewhat less in the largest snails than in the smallest. If, in fact, this is so, the lowest level individuals should average somewhat larger than the mid level individuals. This should be true at all times of year except perhaps in the spring when the smaller snails at mid levels have left their rocks (see p. 47). Significant differences were, in fact, found in both August, 1965 (summer) and in January, 1965 and February, 1966 (winter). In October, 1965, a trend but no statistically significant difference was found. In April, 1965, no trend was found. (see table 16).

Now small snails are more prone to the dangers of desiccation than larger snails, and therefore, in warm months, spend more time in low, sheltered positions on their rocks (see Effects of Risk--Movements--I). Many of them crawl to the unobserveable, undersides of their rocks or become difficult to find among the B. cariosus and anemones. Since exposure times are greatest at high levels, this is particularly true on the highest rocks. Consequently, one should expect to observe proportionately fewer small snails on high rocks than on lower rocks. That is to say, the average sized snail should appear to be larger on high than on mid level rocks in warm months. This would probably not be true in the winter. As expected, data show observed snails to be larger on high than on mid level rocks in the summer, but not in the winter (table 17).

In fall and winter, the B. glandula population is thinning, due, in part, to snail predation, and, at mid levels, by April, will essentially reach zero. The response to this drop in food availability is, as previously mentioned, to leave the "parent" rock and to roam the smaller nearby rocks. Since small snails can use B. cariosus--which is always available--much less efficiently than their larger kin, it is reasonable to expect that they should leave the rocks first, and in the greatest numbers as B. glandula disappears. Table 18 shows the numbers of different sized snails on rocks in summer, and in winter, and it is clear that, as expected, small snails must be leaving the mid level rocks in the fall and/or winter at a greater rate than are large snails. As a result, the average snail size on mid level rocks is larger in the winter than in the summer (see table 16). At high levels, B. glandula is also thinning, but never comes close to disappearing. Consequently the gradual drift away from high level parent rocks is due largely to the freedom of motion allowed by the receding sand in the fall (see Effects of Risk--Movements--I), not food shortage, and the difference in rate of drift between large and small snails is much less marked than at mid levels. For this reason, there is no appreciable difference in average snail size between summer and winter on high rocks (see table 17).

Distribution--Thais lamellosa

That T. lamellosa can apparently live adequately on either B. glandula or B. cariosus is obvious from the fact that the species does quite well both at Port Townsend where the adults appear to eat mostly B. cariosus, and at Barview, Oregon, where B. cariosus is quite uncommon. Since B. glandula is common well above the top of the range of this snail species at both localities, it would appear that desiccation factors are important in determining the upper limit of snail distribution. On the other hand, small T. lamellosa are more susceptible to the effects of desiccation than large (of 15 T. lamellosa exposed to air at room temperature, 25.6°C, all four snails under 15mm in length and none of the larger snails were dead after 13-3/4 hours), yet small individuals are found higher on the beach than large ones at Port Townsend. It thus appears that the adult T. lamellosa remain low on the beach less because of the danger of desiccation at higher levels, than because of some other factor--probably the inferiority of the smaller food items at high levels. Table 19 shows the sizes of T. lamellosa on rocks with base levels at about +1.0' and -1.5.

Since most young T. lamellosa (less than 15mm long) are found higher on the beach than the levels where the eggs are laid, it is clear that the young migrate up the beach. Then, as they grow older, and larger, they move back down to their original lower tide levels. The reason for such movements can only be food. The young, I believe, are simply unable to use large *B. cariosus* and so many of them move up the beach and take advantage of the smaller *B. glandula*. Since the eggs appear to hatch at roughly the same time of year as the heaviest settlement of *B. cariosus* larvae, there is at least some available potential food present for the young snails at low levels, but from the information in the section on food preferences, it is clear that except for quite large individuals *B. cariosus* represent a very poor food source.

In an area such as Barview where essentially no *B. cariosus* occurs and where *B. glandula* is found commonly well down into *T. lamellosa* range, there would be no need for the young snails to migrate up the beach. Here, desiccation factors should play the key role in determining the distribution of snails. At Barview, then, one should expect the opposite from Port Townsend--that is, the highest *T. lamellosa* should be larger than the lowest. Table 20 shows that this is the case. On the pilings at Cantilever Pier, Friday Harbor, Washington, the highest *T. lamellosa* are also found to be the largest (Connell, 1960), and here, both *B. glandula* and *B. cariosus* occur. On pilings, vertical movement is relatively uninhibited, and since small snails tend to move down into sheltered areas more readily than large when the danger of desiccation exists, it is hardly surprising that on days of very low tides, the small individuals should be lower on the pilings than the large.

The lower limit of T. lamellosa's range is much harder to determine and explain than the upper limit. At Port Townsend there appears to be a break in the population below about -2.5'. This is due to the presence of clay sheets with no barnacles, replacing barnacle-encrusted boulders. Below about -3.5', however, there is apparently another, subtidal population of T. lamellosa. This observer has never seen these lower individuals in their continually submerged lairs, but a few scattered individuals were reported by a diver (D. Jamison, pers comm). Their existence becomes obvious only in late fall and winter when they move up into the low littoral to join the intertidal individuals in spawning clumps.

Since spawning takes place over the intertidal range at Port Townsend (see Reproduction--Placement of Egg Capsules), one might expect the entire spawning population to avoid time and energy loss by living intertidally themselves. A problem, then, is to find some explanation for the fact that some individual snails live at other levels, semi-isolated from the main population, during most of the year. One possible explanation is the following:

Subtidal individuals are much larger than the snails usually seen. Whereas a length of 60mm is quite large for an intertidal individual, the subtidal snails are commonly 70 to 90mm long or even more. The largest one observed measured 112mm. These snails also produce many fewer eggs than the smaller snails (see Reproduction--

Age). Since, for snails less than about 70mm in length, the number of eggs produced per individual increases with snail size, the sudden drop in reproductive ability above this size (see figure 11) might well be symptomatic of a difficulty in finding enough food both to maintain homeostasis and provide for normal reproductive activities. This is not surprising in view of the very large size of these snails and the relatively small size of even large B. cariosus. There are, however, at Port Townsend, a few B. nubilus, a very large barnacle, at very low intertidal and subtidal levels. To a huge snail, such barnacles would probably offer a much better food source than B. cariosus, and the subtidal habit of large T. lamellosa may be simply the result of a need for food--a preference for the adequate food species which occurs only at very low littoral and subtidal levels.

* * * * *

It is hypothesized that most mortality of adult snails results from the washing ashore, or occasionally out to sea, of individuals that have lost their grip on the substrate due to desiccation--or perhaps extreme temperatures or wind. On the basis of this hypothesis and on considerations of food distribution several aspects of snail size distribution and snail movements are accurately predicted.

REPRODUCTION

General Considerations

Fertilization in Thais is internal and usually takes place just prior to or during spawning. The eggs are laid in capsules. By dissecting open these capsules and counting the contents, it was found that T. emarginata lays from 300 to 1000 eggs per capsule (mean = 615, standard deviation = 221). In the case of T. lamellosa the number ranges from 20 to 150 (mean = 81, standard deviation = 27). There is no free swimming larva in either species. When hatched, T. emarginata measures roughly two or three mm in length. No newly hatched T. lamellosa were observed.

T. emarginata females begin spawning when they reach about 22mm in length (two years of age as can be extrapolated--see growth chart, figure 9), and deposit their egg capsules in groups of anywhere between one and seventy or eighty, but usually in the neighborhood of 9 to 12. Several such clumps are laid each year. In order to determine the rate at which capsules are deposited by this species, a number of spawning females were marked in the summer of 1965, and without disturbing them, the number of visible capsules beneath each was noted for each of several days. Since not all the capsules beneath each female could be seen and since the females often moved about slightly, the number of capsules counted sometimes dropped from one day to the next, but over a large enough number of counts, the increase in number of visible cases per day per snail should have closely approximated the rate of capsule deposition. The results are shown in table 21, and indicate a spawning rate of about 1.5 capsules per female per day. If the temperature factors relating to feeding rates (see appendix 1) are similar to those relating to reproductive activity, then the spawning rate in winter should be roughly 1.5/1.2 = 1.3 capsules per female per day.

By observing a large number of marked individuals over a period from July, 1964 to June, 1965, I found that .082 of all observed snails in the summer, and .064 in the winter were spawning females. The sex ratio appears to be roughly 7:4 in favor of females. Of 39 snails collected randomly at Port Townsend, 23 were females, and at Mukkaw bay, similar censuses (Paine, pers comm) showed 53 females to 30 males. It can thus be said that each female spends, on the average, $\frac{11}{7}(.082) = .129$ of her time in the summer, and $\frac{11}{7}(.064) = .101$ of her time in the winter spawning. That is to say, about $.129 \frac{365}{2} = 23.5$ days in the summer half of the year and $.101 \frac{365}{2} = 18.4$ days in the winter half of the year are spent spawning. Each female, then, produces roughly $(1.5)(23.5)+(1.3)(18.4) = 59$ capsules, implying roughly five to seven egg clumps, per year. Unmarked females and freshly spawned egg cases were observed at all times of the year. The actual number of egg clumps per snail could not be measured but the fact that nine marked females were observed spawning at two widely separated times proves the existence of multiple spawnings.

Since none of the capsules brought into the lab hatched satisfactorily, the determination of the total development time was somewhat difficult. The method used is shown in appendix 3 and the value obtained was 80 days (at spring temperatures).

An incidental fact gained in these calculations is that the total mortality on egg capsules (during the spring of 1966) was 43%. If this is a fair estimate of the average mortality rate on egg capsules over the year, then about (.57) (59) = 33.6 capsules per female make it through the development period. Since, as shown in the previous section on mortality, about .06 of all snails alive at 6 months of age survive to 18 months (this value is used as an estimate of first year survivorship) and .0184 live through their second year, (.06) (.0184) = .001104 of all snails live to reproduce. Thus, in order to maintain the population at a steady level, each female must produce at least $\frac{1 + \frac{4}{7}}{.001104} = 1423$ viable eggs. Since an estimated 33.6 capsules are successfully produced and hatched, this means that 1423/33.6 = 42.3 eggs must hatch, on the average, from each capsule. This is in agreement with the findings of Dehnel (1955) that five to fifty eggs hatch from each capsule. The remaining eggs in each capsule, several hundred of them, are eaten by the developing young and are known as "nurse eggs."

T. lamellosa first spawns at a size of about 40mm, and deposits its capsules in one large clump. It may remain in the immediate area of the clump for a period of three to five months. The number of capsules per female is somewhat difficult to determine since many females group together in a large spawning group, some appearing or leaving a month or two before or after others. However, by stripping off the snails in a spawning clump when the spawning season was about half through and the number of snails present was maximum, counting the number of cases per spawning snail and multiplying by two, one can find a lower estimate of the number of capsules per female. Using this method, half of one spawning clump was stripped and found to contain 2625 capsules. Twenty-six females were removed from this area so it appears that each female would have laid very roughly $\frac{2625}{26}$ = 202 cases per year. *T. lamellosa* females, then, apparently deposit a good many more egg capsules than do their *T. emarginata* counterparts.

A lower estimate for the rate of capsule deposition can also be calculated. The spawning period lasts very roughly five months ie 150 days, or less. If 202 capsules are deposited by each female during this period, then at least 202/150 = 1.35 capsules are deposited per female per day.

The method of determining development time was somewhat different from that employed with *T. emarginata*. First, a large spawning clump was mapped in detail on December 4, 1965. It had been previously observed that *T. lamellosa* follow a definite pattern in their spawning behavior, beginning near the middle of a rock face and working downward. On December 4, a fair area of rock was already covered with capsules and the snails had formed a large clump below and contiguous with these. Because of the gradual downward movement of the snails, it was reasoned that the uppermost capsules should hatch first and that those capsules observed immediately above the descending group of snails would hatch precisely t days after December 4, where t is the development time. The temporal sequence of hatching eggs did in fact follow the predicted downward trend, and those capsules just completed on December 4 were hatched on April 24, 1966, implying a maximum t of 140 days. Since the uppermost capsules not yet completely finished on December 4 were not yet hatched on April 24, 140 days may also be taken as an approximate lower limit for t. The longer development time of *T. lamellosa* (20 weeks as opposed to 11 or 12 for *T. emarginata*) is probably a consequence of the large amount of yolk in *T. lamellosa* eggs. While *T. emarginata* utilizes nurse eggs for food in the capsule, *T. lamellosa* apparently relies entirely on its yolk supply. There are no *T. lamellosa* nurse eggs.

Mortality of Eggs

Mortality of T. emarginata capsules is roughly 43%. This seems to result largely from exploitation by the isopod, Idothea which is often seen sitting on torn up capsules. That these arthropods are often the agent of destruction is supported by their behavior in the laboratory where they readily and voraciously destroy egg capsules placed with them. Amphipods and the marine pulmonate, Onchidiella, are often seen on torn capsules also, but show no destructive tendency in the laboratory on either intact or open capsules. Nemerteans, which are abundant at mid and low tidal levels, may also prey on snail egg capsules as reported by Glynn (1965), but no supporting observations have been made at Port Townsend. In one instance (J. Barnes, pers comm) a chiton (Mopalia sp.) was observed to have passed through a group of egg capsules, leaving them cut off near the base. Subsequent examination showed the chiton's stomach to contain particles resembling pieces of egg capsule wall. This sort of occurrence was never observed by me, however, and there is no other evidence pointing to chitons as regular predators on Thais egg capsules. Other than Idothea probably the greatest source of egg capsule mortality is Thais itself. Several observations, in the spring, were made of T. emarginata devouring T. emarginata capsules. (see also Ricketts and Calvin, 1962, pp 190). This cannibalism undoubtedly has selective value in a species, such as T. emarginata, where intraspecific competition for food in the spring is intense (Brower, 1961; Brereton, 1962; Paine, 1965).

In the case of *T. lamellosa*, there seems to be relatively little predation on egg capsules. *Idothea* occurs at the levels where *T. lamellosa* deposits its capsules (0' to -3' at Port Townsend), although in smaller numbers than somewhat higher, but have never been seen on *T. lamellosa* egg capsules. Nemerteans are extremely common and are often seen coiled about among the cases, but no instances of predation have been observed. In fact, unlike the *T. emarginata* capsules which are very commonly found with jagged rips in them, unhatched *T. lamellosa* cases seldom appear molested. The only mortality that has been definitely established is the result, direct or indirect, of burial by sand. Cases that become so covered are usually, when later re-exposed, torn open, presumably by sand dwelling organisms, or intact but dead. More will be said of the effects of sand wash in the following section.

Placement of Capsules

The spawning behavior of Thais, like all other activities, is governed by considerations of time, energy and risk. Since food appropriate for young T. emarginata is available in the normal range of this species, there seems little reason for spawning females to migrate up or down in the inter-tidal. Furthermore, such migration would require time and energy which could be otherwise used in feeding or more spawning, and would entail the risk of crossing exposed sandy areas where the chances of desiccation, burial or being washed ashore or out to sea are considerable. T. emarginata, then, should and does spawn within and throughout its normal range. T. lamellosa, on the other hand, undergoes a certain amount of pre-spawning movement. Since the young do well to move somewhat higher on the beach than their parents (see Effects of Risk--Distribution) egg capsules are best deposited toward the upper part of the snails' range, or higher. But, as with T. emarginata, moving out of the normal range would entail expenditure of energy which could be used for producing more eggs, a loss of time which could be spent feeding, and increased risks of desiccation higher on the beach. In addition, as mentioned on p. 57, there seems to be little predation on Thais egg capsules within the range occupied by T. lamellosa, and a considerable amount at higher levels. The optimal spawning level for T. lamellosa, then, would appear to be within, but in the upper portion of, the snails' range. The infrequent occurrence of very low tides makes it impossible to assess the amount of spawning in the lower portion of T. lamellosa's range, but the fact that many individuals move up from subtidal levels to the upper portion of the range to spawn implies a concentration of reproductive activity at these higher levels. The presence of mobile predators such as Pisaster and Pycnopodia in some areas may force the T. lamellosa population, and thus also their spawning activity, to somewhat higher levels than those found at Port Townsend. At Mukkaw Bay, for example, where sea stars are common, T. lamellosa occurs and spawns higher in the intertidal than at Port Townsend (Paine, pers comm). The same appears to be true at Golden Gardens Park in Seattle.

As might be expected, both species tend to place their egg cases on the lower parts of rocks in positions sheltered from the sun. Sand wash is seldom great at levels below about 0', and therefore the danger of egg case burial presents little problem to T. lamellosa (although two instances have been observed). As a result egg cases are often seen at the very base of rocks. At higher points on the beach, there is little sand during the fall, winter and early spring, but up to two feet of sand in the summer. For T. emarginata spawning in the spring and summer, then, there is a real danger of sand burial if the cases are deposited too low on the sides of the rock. T. emarginata egg capsules are always placed above the sand scoured levels of the rock, in among the B. cariosus and anemones.

It has been mentioned (Reproduction--General considerations) that T. emarginata tends to deposit its capsules in groups of about nine to twelve. Although the reason for clumping the capsules in such a way is not entirely clear, there are several factors that may interact to produce this pattern.

If, for every spawning clump, T. emarginata were to move down from the rock top to a suitable spawning area on the side of the rock, a certain amount of time and energy would be spent in so doing. Time and energy would thus be conserved if only one such move were made--that is, all cases were deposited at once in one large clump. On the other hand, if the spawner were already in a suitable position, having moved down due to desiccation dangers (see The Effects of Risk--Movements--I), the time and energy expenditure in moving down for spawning purposes may be considered zero. In this case, there is no advantage accruing from large or small egg-case clumps. If predators find and destroy cases with a probability proportional to the area or cross section of an egg case clump, then it is obviously best to make such clumps very small, but if predation occurs independently of clump size then there is, again, no criterion for predicting optimal clump size. Actually, whether a snail moves down the rock for the express purpose of spawning or not, the time and energy expense is negligible. Furthermore, mortality does not appear to increase with increased clump size, at least within the normal size range. In January, 1965, for example, 11 of 132 (=.084) capsules in clumps containing less than 15 capsules were observed destroyed. The corresponding number for clumps with more than 15 capsules was 28 of 332 (=.084). Clump size, then, cannot be simply or quantitatively explained. It seems to depend, rather, on two, more complex factors.

First, there is no great disadvantage to spreading spawning activity over the year (see Reproduction--Timing) and there would definitely be a problem of finding enough suitable spawning sites if all T. emarginata females were to spawn once, over a few months of the year. Dividing the total egg yield into several parts over the year would result in a general limitation in the number of capsules deposited each time the snail spawned. Since summer appears to be the optimal season for spawning (see Reproduction--Timing) however, there should be a tendency to deposit more cases at this time and thus to form larger egg case clumps. The average clump size in July, 1965 was 12.18 while that in December of 1965 was 9.45. The difference is significant by a t-test, with $p < .005$. Second, in the snails' more usual habitat on the open coast, one fairly obvious impetus to short bursts of spawning rather than one long session is the considerable risk of becoming entrapped and, as a result, often dying among the byssus threads of mussels if too much time is spent in one spot. At Archcape, Oregon, an area of outer coast, 58 of 1652 (=3.5%)

observed T. emarginata were caught in byssus threads and another 54 showed a few attached threads indicating that they had at one time been entwined, but had managed to break loose. Not all snails break loose, however, and quite often, entrapped, empty shells are found. The habit of avoiding long spawning sessions on the open coast may have been retained in the calm water habitat at Port Townsend.

In contrast to T. emarginata, T. lamellosa lays all its eggs at once. The reason is at least two-fold. First, since there is apparently very little predation on T. lamellosa capsules, there is no selective advantage in dispersing them. Saving in time and energy, then, --T. lamellosa must migrate to the top of its range to spawn (see Reproduction--Placement of Capsules)--is the most important consideration, and this is accomplished best by spawning only once. Second, there are environmental factors which make it adviseable to spawn at a particular time of year (see Reproduction--Timing). Since the spawning process takes a long time and since the rather long development period--roughly twenty weeks--occurs during the spring when temperatures may be quite variable, there is already a considerable spread in hatching time. If the snails were to take the time to move from one area to another to deposit a series of separate egg clumps, the spread would be even greater and the advantages of proper seasonal timing in reproduction would be greatly impaired. Synchronous spawning also simplifies the problem of males and females finding each other. Any tendency to lay in a series of separate clumps, then, should be selected against.

Gregariousness in Spawning

If, as in the case of *T. emarginata*, snails spawn at high intertidal levels where predation is heavy and where large masses of egg capsules would present local, rich and easily exploited food sources, then it would certainly not pay a female to seek out another female's capsules and deposit her own on the same spot. Unfortunately the number of really large egg capsule masses was so small that no meaningful comparisons with normal masses as to predation rate could be made. *T. emarginata* females nearly always spawn alone, accompanied occassionally by a male, often in the act of copulating with her.

T. lamellosa females, on the other hand, spawn at lower levels where egg capsule predation is much less severe (p. 58). There seems no a priori reason why several females should not spawn in the same spot. There are, in fact, two reasons why this species should form spawning aggregates. First, instead of roughly 59 capsules spread out over the year and over a vertical tidal range of about 5 feet as with *T. emarginata*. *T. lamellosa* females produce on the order of 200 capsules during a period of four or five months over a vertical tidal range of roughly 2 feet. If these capsules were spread out horizontally over many rocks, they would become an obvious feature at all points on the beach within their tidal range and might attract predators. There would be a great advantage to *Idothea*, for example, to shift more to the lower extremity of its range during these months to make use of the abundant food source. By all females spawning together in just a few large, concentrated masses, and thus highly localizing the placing of capsules, this problem is eliminated. Second, when spawning must be carried out during a certain season, a system of haphazard mating when females and males happen to come across each other is disadvantageous; there is, to snails' massing together in one place, the advantage of more easily finding a mate. Both of the above arguments are, of course, contingent upon the existence of rocks large enough to support many snails and their egg capsules, and on the absense of predators, such as *Pisaster* and *Pycnopodia* which normally occur at these levels and which, by moving about over considerable distances, might find and concentrate their attention on such a large, concentrated food cache of spawning snails. At Golden Gardens Park in Seattle, there are few, widely scattered boulders, a small population of *Pisaster* and *Pycnopodia*, and *T. lamellosa* usually spawns in small groups (10 to 30). At Port Townsend, there are many large boulders, essentially no predatory starfish, and the *T. lamellosa* spawn in huge masses (up to roughly 1000 snails).

Timing

At least two proximate factors seem to play roles in determining at what time of year *T. emarginata* deposits its egg capsules: food and temperature. When very young, due to their small size, *T. emarginata* cannot handle large barnacles or move rapidly and efficiently over large areas in search of food. As a consequence, those snails hatched in the spring when food is very scarce will have great difficulty surviving. In late May or early June, however, *B. glandula* settles in tremendous numbers and the food supply rises throughout August and into September. Survival of young snails, on the basis of considerations of food supply, then, should be greatest during the late summer when food is most abundant and when most of the food is in the form of small, newly settled *B. glandula*. If food were the only factor affecting the reproductive behavior of *T. emarginata*, one would expect to find spawning occurring primarily--or only--in the early summer, 80 days before the resulting eggs would hatch in August and September. A secondary, smaller burst of spawning might be expected in early January, somewhat more than 80 days (development time is undoubtedly somewhat longer in the winter than in the spring due to the lower temperatures) before *B. cariosus* settles in early April.

Since small snails are very susceptible to detachment and, presumably, consequent death by desiccation, the daylight summer low tides should be particularly hard on them (see Effects of Risk--Mortality). The fact that their death rate is lower than that of their elders (.06 calculated survivorship between the sixth and eighteenth month, .018 during both the second and third year--figure 5) simply implies that they seek shelter more readily. If a female is to minimize first year mortality for her young, then, she should spawn at such a time that her young will grow as large as possible before summer--that is, in the late summer and early fall.

On the basis of the preceding arguments, there are advantages to concentrating spawning behavior in the early summer and in January (based on feeding considerations) and in the late summer and early fall (based on mortality considerations). We should expect to find one peak in spawning activity through the summer and another in January. Figure 10 shows the fraction of marked snails spawning over the year, 1964-1965, and clearly, except for an unexplained low point in early summer, bears out the above prediction.

For young _T. lamellosa_, the food situation is much the same as for _T. emarginata_. The small snails require small barnacles. In response to this need, many small _T. lamellosa_ might be expected to move up the beach into the B. glandula zone (see p. 47, 48). On the rocks where _T. lamellosa_ hatch, there are never many _B. glandula_, and except in the summer, the number may be considered negligible. If young _T. lamellosa_ had to depend entirely on _B. glandula_ at their initial tidal level for food, summer would be the only feasible time to hatch. In addition, at all times of year other than summer, _B. glandula_ is sparse even at the levels where the young snails find themselves after migration, and the advantages, in terms of food, gained from moving up the beach may not be worth the risk of getting washed ashore or out to sea. Summer, then, is the most advantageous time to hatch, although the newly settling B. cariosus, a poor but abundant food source, make hatching possible as early as April.

Hatching dates of roughly April 1 to September 1, considering a development time of 140 days (see Reproduction--General Considerations) would indicate a spawning period from November 12 to April 16. Actual observations show adult T. lamellosa beginning to move across the beach toward spawning sites (that is to say, a general downward movement of those individuals highest on the beach and a general upward movement of all others) in early October of 1964, and late September of 1965. Spawning groups were formed as early as mid-October in 1965 although no egg cases were yet present. In 1964, the first capsules were noted on November 20. Capsules may have been present in November of 1965--no field trip was made that month--and were definitely present by December 10. In 1965, T. lamellosa was still spawning on March 12, and one possible instance was recorded on April 16. Spawning had apparently ceased by April 21 in 1966. Both the onset and the end of spawning behavior, then, closely fit that predicted.

Age

Reproductive activity should occur only when there is a greater selective advantage in producing young than in putting all energy in excess of metabolic needs into growth. That is, if a smaller individual, for physiological or other reasons can produce only a small fraction of the viable eggs that larger snails produce, and by spawning will retard its own growth and thus remain small the next year, then there will be a size threshold below which that individual's best strategy is to hold off on egg laying. In order to discover this size threshold, an attempt was made to determine the number of eggs that could be produced by snails of different sizes over a given period of time.

The number of eggs per T. emarginata capsule varies widely from about 300 to 1000 in capsules of all sizes, and considering the fact that only a small and perhaps variable fraction of these are viable, no definite statement can be made as to the number of viable eggs laid per capsule by a T. emarginata of a given size.

The number of egg case clumps deposited per unit time was impossible to count for any single snail and this fact further complicated the problem of evaluating the reproductive activity of the snails. Instead, an attempt to get at the number of clumps per snail per year was made by comparing the sizes of those snails actually observed spawning more than once with those seen egg laying only once. Since the chance of observing the activity more than once increases with the number of times it actually takes place, it was reasoned that a significant difference in size would indicate that large snails spawn more often than small, or vice versa. The average sizes for snails observed spawning once and more than once were 28.20 and 27.425mm respectively; there is no significant difference between these values. This suggests that different sized T. emarginata spawn an equal number of times throughout the year.

In order to determine the number of capsules deposited per clump by T. emarginata of different sizes, a number of spawning females were lifted and the number of egg cases beneath them counted. Since, on the average, one would expect the snails to have half completed their feeding when examined, the observed number of cases should be roughly one half the total number normally deposited. Figure 11 shows the average number of observed capsules plotted against the size of the spawner. Since there was no reason to believe that the fate of a group of capsules deposited by a small snail was any different from an essentially identical group deposited by a large snail, the differences in the number laid at one sitting are presumed to be at least indirectly physiologically based. That is, either the smaller snails are incapable of depositing more egg cases at one time, or else their total, yearly, productive capacity, coupled with an advantage to spreading out production in time is the cause of the small clumps. If the trend shown in figure 11 is extrapolated to the left, it is clear that, barring some totally unexpected upswing in the curve, T. emarginata of 20 or 21mm in length can produce essentially no capsules at all. Thus, in spite of the difficulties resulting from a vagueness in the number of viable eggs per case and the number of spawnings per year, it can be stated with little doubt, that *T. emarginata* females less than 20 to 22mm in length probably are sexually immature (at Port Townsend) and will certainly do better to put all excess energy into growth rather than reproductive activities. It is true that while *T. emarginata* less than 20 to 22mm grow at a fairly linear rate of about one millimeter per month (see figure 9), larger snails grow at a much reduced rate. The average changes in length of 28 marked snails initially 24 to 28mm in length and 32 snails 29mm or more in length over a nine month period from September, 1964 through June, 1965, were, respectively, -1.6mm and -0.5mm. The decrease is due to abrasion and to sampling error.

It might be expected to be selectively advantageous for individuals above the minimum reproductive size, as they become larger, to put less energy into growth and more into reproduction. Larger individuals do in fact spend a larger proportion of their time spawning, as demonstrated by marked snails (see table 22). The decline in spawning rates among very large females may be due to increased homeostasis costs or to parasites and disease. This problem was not explored.

The onset of reproductive maturity in male *T. emarginata* may be determined by the size at which the penis is large enough to reach under the female's mantle cavity and into the bursa copulatrix. Males accompanying spawning females are often smaller than the female but seldom below 22mm in length.

To examine the reproductive capacity of T. lamellosa, a large spawning clump was stripped half way through the spawning season. The total number of eggs per case was counted for several case sizes, the total number of cases of several size categories was counted, all spawning females were counted and measured, and for each spawning female, snail size was plotted against egg case size. Figure 12 shows the number of eggs per case plotted against egg case size, and figure 13 shows the size distribution of cases. Figure 14 shows snail size versus egg case size. Since there is no indication that larger or smaller snails arrive first at the spawning site or spawn first, the data mentioned above enables one to construct a table showing the relative number of eggs produced by females of different sizes (table 23). These data are plotted in figure 11. The general pattern is much the same as that shown for T. emarginata, as shown in the same figure. The size below which reproductive activity ceases coincides with the size below which the expected number of eggs produced approaches zero. The drop in egg production among very large snails may, again, be due to disease, parasites, or problems of body upkeep associated with size.

Males in the spawning clumps, as in the case of T. emarginata, may be slightly, but not much smaller than the females with whom they are copulating.

Conclusions reached in the two preceding sections on feeding behavior and risk are applied to the questions of the vertical distribution, social aspects and timing of reproductive activities. It may be concluded that time, energy and risk considerations can lead to accurate predictions and descriptions, in a qualitative sense, of *Thais* spawning behavior.

Conclusions and Summary

The concept of natural selection is extremely useful to the ecologist (Orians, 1962) although it can easily lead the careless investigator into a realm of circular reasoning. To avoid such pitfalls it is necessary to investigate the habits of those animals under study from the aspects of the parameters time, energy and risk. Such an investigation was attempted in a study of the two predatory gastropods, *Thais emarginata* and *T. lamellosa*.

Based on the implicit assumption that natural selection will operate to maximize assimilated food energy intake per unit time (Emlen, in press), a mathematical model was derived which predicted a preference, among *T. emarginata*, for the barnacle *Balanus glandula* over the congeneric *B. cariosus*--a prediction which was nicely borne out by data. In addition, it was predicted that large *B. glandula* should be preferred to small, but that the effect of "hangers-on" sharing the food from each individual *B. cariosus* made that still larger food less useful than might otherwise be expected. Again the expectations were supported by observation.

It was impossible to gather data of the sort that would allow a similar treatment for *T. lamellosa*. Nevertheless, by making qualitative comparisons of size characteristics between the two snail species, it was possible to predict that young *T. lamellosa* should behave, in in their dietary habits, much like *T. emarginata*, while adults should rely much more on B. cariosus. Observations bear out these predictions.

Considerations of time and energy in relation to diet imply a range for T. emarginata essentially the same as that of its food supply, B. glandula, while T. lamellosa should be able to occupy this same range and also spread downward into the zone of B. cariosus. In addition, time and energy considerations would lead one to expect the snails to remain constantly in favorable feeding areas and to minimize time and energy loss resulting from moving over long distances when food items are closely spaced. Predictions based on time and energy, however, must be tempered with consideration of risk. An individual cannot pass genes and thus contribute to the direction of evolution no matter how healthy it is and no matter how much energy it can put into reproduction if it dies before leaving offspring. There is always a delicate balance between behaving optimally with respect to time and energy conservation under dangerous circumstances and compromising ideal feeding and/or reproductive behavior in order to minimize risk. Qualitative calculations based on this concept of balance indicate that snails will behave optimally if they move down their rocks, away from the abundant food supply, and literally starve for a certain proportion of the days each month. Such movements should and do take place primarily on warm, dry days, very stormy days, and days of very low tides. Such calculations also indicate that snails exposed to the sun at low tide on warm days, or to rough water, should tend to move distances up to 70 or 80cm during a given submersal period in order to avoid repeated exposure the next day. Snails in more sheltered positions need not contend with the risk of exposure and thus move smaller distances in conformation with that predicted on the basis of time and energy considerations alone.

Tidal and spatial distribution also are affected by the risk factor. While young *T. lamellosa,* unable effectively to use *B. cariosus* as food, move up the beach to use *B. glandula,* adult *T. lamellosa,* more efficient with *B. cariosus* but perfectly capable of using the smaller barnacles, remain low, in the *B. cariosus* zone. Apparently the aquisition of territory with adequate but inferior food is not worth the risk entailed in moving up and remaining at higher intertidal levels. Risk affects the movements of different sized *T. emarginata* differently also, and results in larger individuals being found at high rather than mid intertidal levels in the summer, but not the winter, and in a size increase in the snails occupying mid level rocks in the fall and winter.

Reproduction also was examined with respect to time, energy and risk. Considerations of egg capsule and first year mortality and food availability at spawning and other levels indicate that *T. emarginata* should, as it in fact does, spawn throughout its normal range, depositing a number of egg capsules in several clumps spread over the year. Two spawning peaks are expected, and were observed; one in the summer, and a smaller one in the winter. _T. lamellosa_ individuals also behave according to expectation, depositing all their cases at one time, in the late fall, winter and early spring, in large spawning aggregates near the top of their range.

The largely proximate question of physiological and anatomical development and its relation to the ultimate question of minimal reproductive age was discussed with the conclusion that _T. emarginata_ will contribute more genes to future generations if it does not spawn below a size (shell length) of 20 to 22mm. _T. lamellosa_ should begin spawning at a length of roughly 40mm. Both estimates appear to be accurate.

In conclusion, I believe that circular reasoning in the application of natural selection theory to ecology can be avoided only by analyzing the biology of the organisms under investigation with respect to the parameters time, energy and risk. Such an analysis can tell an investigator much about his subjects and will, in the process, lead perhaps to a fuller understanding of what biological and environmental interactions constitute a special case, and which may lead to general ecological law.

TABLE 1

Number of _T. emarginata_ observed on

Areas Dominated by:

	Mussels	Barnacles
Number of black snails	71	24
Number of other colored snails	378	364

$\chi^2 = 18.87$ with 1 d.f.

$p < .005$

TABLE 2

Drilling ($\overline{T}_d$) and Ingestion ($\overline{T}_f$) Times for *T. emarginata* (in hours)

Month	$\overline{T}_d$	$\overline{T}_f$
August, 1965	2.0	2.9
September	2.1	3.1
December	2.4	3.4
January, 1966	2.2	3.1

TABLE 3

Normalized Importance Values, I, in the Diet of *T. emarginata*, for *B. glandula* of Different Sizes (See text for definition of I)

	April, 1965	February, 1966	
$I_{\text{small barnacles}}$	---	---*	size less than one mm
$I_{\text{medium barnacles}}$	.18	.35	size one to three mm
$I_{\text{large barnacles}}$	.82	.65	size larger than three mm
Number of feeding records	91	48	

*Methods of barnacle density estimation were considered too inaccurate for tiny barnacles to be meaningful in calculations of *I* values.

TABLE 4

Net Energy Gain to *T. emarginata* from Barnacles of Different Sizes

(E_d =0/E_d =.86E) See text for explanation of symbols

Species and size	August 1965	September 1965	January 1966
B. glandula			
1mm	.48E/0	.46E/0	.43E/0
2mm	.59E/.06E	.56E/.06E	.52E/.06E
3mm	.65E/.06E	.61E/.06E	.57E/.06E
B. cariosus			
2mm	.01E/0*	.01E.0*	.01E/0*
4mm	.08E/0*	.08E/0*	.07E/0*
6mm	.20E/0*	.19E/0*	.17E/0*
9mm	.41E/0*	.39E/0*	.36E/0*
12mm	.60E/.21E	.57E/.20E	.53E/.18E

* An asterisk after a zero implies a net energy loss

TABLE 5

Number of T. emarginata Observed Feeding on Mid Level Rocks (September, 1965)

Number observed feeding on:	in the: upper, *B. glandula* band	lower, *B. cariosus* band
B. glandula	88	3
B. cariosus	0	3

By a Fisher exact probability test, $p = .00015$

TABLE 6

Barnacle Density (number per meter^2) on

Rocks with Base level:

	3.5'		1.5'-3.5'		1.5'	
	B. glandula	cariosus	glandula	cariosus	glandula	cariosus
April 9, 1965	5,500	3.700	510	12,350	510	8,650
May 15	3,430	3,140	380	11,000	---	-----*
June 26	15,400	2,270	770	12,200	---	-----
July 27	18,600	1,550	14,850	9,600	7,130	12,500
August 23	35,600	1,980	24,000	11,000	4,470	15,800
September 21	50,000	1,340	20,800	9,200	1,350	13,050
October 11	32,030	1,340	21,100	8,700	2,470	12,950
December 10	9,450	1,460	5,100	9,900	1,370	11,650
January 4, 1966	21,900	-----	6,600	-----	-----	-----
February 4	11,000	440	6,210	7,900	245	9,700
April 21	2,240	510	120	4,350	0	5,560
June 19	9,850	544	5,722	5,365	544	6,777

* A broken line indicates no data

TABLE 7

Relation between Size of Snail Predator (*T. emarginata*) and Prey Size

T. emarginata length	Food (*B. glandula*) size					
	January, 1966			February, 1966		
	$\bar{x}$	s^2	n	$\bar{x}$	s^2	n
less than 25mm	2.320	.289	11	2.465	.419	20
greater than 25mm	2.620	.157	10	2.761	.3056	28

t = 1.435 with	t = 1.78 with
19 d.f.	46 d.f.
$.05 < p < .10$	$p < .05$

TABLE 8

Relation between Size of Snail Predator (*T. lamellosa*) and Prey Size

T. emarginata	Food (*B. cariosus*) size					
	February, 1966			June, 1966		
length	$\bar{x}$	s^2	n	$\bar{x}$	s^2	n
less than 40 mm	4.63	4.211	8	5.00	7.40	8
40mm to 50mm	7.42	13.265	12	8.64	5.18	11
over 50 mm	10.00	4.00	4	9.38	1.56	4
Difference between small and medium sized snails	$t = 1.97$ with 18 d.f. $p < .05$			$t = 2.73$ with 17 d.f. $p < .01$		
Difference between medium and large sized snails	$t = 1.33$ with 18 d.f. $p \approx .10$			No significant difference		

TABLE 9

Diet Differences between Different

Sized Individuals of T. lamellosa

Length of T. lamellosa	Number of T. lamellosa observed feeding on: B. glandula	B. cariosus	Percent on B. cariosus
12mm-20mm	1	0	--
20mm-30mm	13	0	0.0
30mm-40mm	17	9	34.6
40mm-50mm	49	90	64.8
over 50mm	5	15	75.0

TABLE 10

Predation by *T. lamellosa* on

B. glandula and *B. cariosus* (with Importance values)

at Cantilever Pier (from Connell, 1960)

	Barnacle Species	Number of barnacles available	Expected number of Survivors (From Controls)	Actual number of Survivors	Number eaten	Importance value
large *T. lamellosa*	*B. glandula*	385	270	206	64	.35
	B. cariosus	402	390	223	167	.65
small *T. lamellosa*	*B. glandula*	357	338	223	115	.71
	B. cariosus	545	529	386	143	.29

TABLE 11

Number of Marked Snails (*T. emarginata*) Recovered (of 855 marked)

Date	Number recovered	Survivorship
September 4, 1964	331 (base number-- see text)	1.00
October 4	92	.28
November 21	74	.22
December 4	36	.11
January 16, 1965	55	.17
February 15	24	.07
March 12	19	.06
April 9	34 (base number = 294*)	.12
May 2	15	
May 15	21	
June 2	12	
June 26	10	
May 2	69 (of 125 marked in April)	
May 15	53	
June 2	18	
June 26	21	
August 22	24	
April 9	Survivorship estimated from data for September through April	.08
May 15	(pooled data from above)	.07
June 2		.037
June 26		.032
August 22		.028

*Rocks representing 95 marked snails no longer are being checked, so base number is now $331 - \frac{331}{855} 95 = 294$.

TABLE 12

Number of Marked Young *T. emarginata* Recovered

Number marked in April = 101

Date	Number recovered	Survivorship (from June 25)
June 25, 1965	41 (base number)	1.00
July 12	18	.44
July 27	12	.29
August 23	17	.42
September 23	13	.32
October 12	10	.24
December 11	3	.07
January 4	3	.07
February 5	6	.15

TABLE 13

T. emarginata Population Density

Date	Number per meter^2 on large rocks with base levels ≥ 1.5'	Sand depth at levels ≥ 1.5'
July, 1965	31.3	up to roughly two feet
September	15.8	absent
October	6.3	absent
December	2.9	absent
January, 1966	5.9	absent
February	7.2	absent
April	4.7	absent
June	9.8	Beginning to wash in--perhaps 6" deep
July	16.3	roughly 12" deep

TABLE 14

Distance Moved per Immersion Period

Date	Average distance moved (in cm)	
September, 1964	74	
June, 1965	56	
August	45	summer--warm weather
September	58	
December, 1965	36	
January, 1966	23	winter--cold weather

TABLE 15

Fraction of Snails (*T. emarginata*) Marked by August, 1964, Remaining within Six feet of their "Parent" Rock

Date	Number within six feet/total number observed	
September, 1964	745 marked	
October	98/106	= .92
December	24/27	= .89
January, 1965	24/39	= .62
February	13/18	= .72
March	11/16	= .69
April	18/32	= .56
May	15/23	= .65
June	11/16	= .69

TABLE 16

Length of All T. emarginata on Rocks at Two Tidal Level

Base level of rocks	Approximate mean level of snails	January, 1965			April, 1965			August, 1965			October, 1965			February, 1965		
		$\bar{x}$	s^2	n	$\bar{x}$	s^2	n	$\bar{x}$	s^2	n	$\bar{x}$	s^2	n	$\bar{x}$	s^2	n
2.5'	4.0'	27.2	4.6	10	25.2	4.7	18	20.0	28.9	44	24.4	5.9	11	25.1	6.0	14
1.5'	3.0'	29.6	6.7	24	24.1	14.5	41	26.7	12.7	8	25.1	9.7	22	28.4	8.6	14
		$t = 28$ with 32 d.f. $p < .005$			No difference			$t = 3.42$ with 50 d.f. $p < .005$			$t = 1.15$ with 31 d.f. $p \approx .10$			$t = 3.15$ with 26 d.f. $p < .005$		

TABLE 17

Length of All *T. emarginata* On Rocks at Two tidal levels

Base level of Rocks	Approximate mean level of snails	August, 1965			February, 1966		
		$\bar{x}$	s^2	n	$\bar{x}$	s^2	n
3.5'	5.0'	24.0	13.08	54	22.53	27.15	34
2.5'	4.0'	20.0	28.93	44	25.14	5.97	14

t = 4.4 with 96
$p < .005$

t = 0.98 with 46 d. f.
Higher snails are actually smaller--but not significantly

TABLE 18

Seasonal Differences in the Number of *T. emarginata* on Two Large Rocks

	Snail length greater than 22mm	 less than 22mm
summer	17	16
winter	12	2

$X^2 = 4.969$ with 1 d.f.
$p \approx .025$

TABLE 19

T. lamellosa Length at Port Townsend (August, 1965)

Rock base level	$\bar{x}$	s^2	n
-1.5'	41.51	73.73	66
+1.0'	35.33	53.53	15

$t = 3.31$ with 79 d.f.

$p < .005$

TABLE 20

T. lamellosa Length at Barview (July, 1963)

Intertidal level	Average length
below -1.0'	40.9 mm
-1.0' to 0.0'	45.4 mm
0.0' to +1.0'	48.0 mm
above +1.0'	47.6 mm

TABLE 21

Change in the Number of Visible Egg Capsules per Snail (<u>T. emarginata</u>) per Day

Marked clump Number:	Change from previous census in the number of cases visible on day: 1	2	3	4	5	6	7	Total change in number of visible cases	Total number of snail-days
1 and 2	4	12	4	3}	0			24	9
3	0	0	0	-1	2	-1	-1	-1	7
4	-2	2	0	0	1	1	1	3	7
5	0	8	-7	5	5	-3	3	11	7
6	-7	6	2	1	0	11	-15	-2	7
7	3	3	0	4	5	2	-1	16	7
8	0	6						6	2
9	2	0	3					5	3
10	2	2	5					9	3
11	2	1	3					6	3
12	-3	0	7	1	-5	-8	10	2	7
13	0							0	1
14	10	-3	2	11				20	4
15	2	3	1	0				6	4
16	2	3	1					6	3
17	3	1						4	2
					Total			115	76

Mean number of cases/snail/day = $\frac{115}{76} = 1.5$

TABLE 22

Relation between Spawning Activity and Snail (*T. emarginata*) Size

Length of snail in mm	Number of observations spawning	Number of observations total	Relative time spent spawning
less than 22	0	31	0.000
22-24	4	42	0.096
24-26	8	63	0.127
26-28	12	43	0.279
28-30	11	31	0.355
30-32	2	14	0.143
greater than 32	0	9	0.000

TABLE 23

Number of Eggs Laid per Snail (<u>T. lamellosa</u>) per Year

Snail Size in mm	Number of snails	Number of corresponding capsules	Number of capsules per snail	Number of eggs per capsule	Number of eggs per snail
10-20	0	0	--	--	--
20-30	0	0	--	--	--
30-40	0	0	--	--	--
40-50	7	1,416	202	39	7,900
50-60	10	2,142	214	57	12,200
60-70	3	1,302	344	75	25,800
70-80	2	486	243	94	22,800
80-90	3	156	52	112	5,800
90-100	1	18	18	130	2,400

TABLE 24

Relation between Distance Moved during One Tidal Immersion and the Fraction of Snails Subsequently Feeding at Tidal Exposure

	D_m (in cm)	Fraction feeding	
September 2-3 1964	0 to 25	2/6	
	25 to 51	1/3	
	51 to 76	1/2	level = +3'
	76 to 102	1/2	
	102 to 127	0/2	T = 17.33 hours
	127 to 152	1/2	
	152 to 178	---	
	178 to 203	3/3	
September 3-4 1964	0 to 25	0/7	
	25 to 51	0/4	level = +1'
	51 to 76	0/1	
	76 to 102	0/4	T = 19.60 hours
	102 to 127	0/2	
	300	1/1	
September 4-5 1964	0 to 25	0/1	
	25 to 51	0/2	level = +4.5'
	51 to 76	0/2	
	76 to 102	---	T = 16.05 hours
	102 to 127	0/2	
	127 to 152	0/2	
	152 to 175	0/1	
	175 to 203	---	
	203 to 229	0/1	
August 21-22 1965	0 to 13	7/10	
	13 to 25	14/16	level = +4.0'
	25 to 38	7/15	
	38 to 51	8/19	T = 15.37 hours
	51 to 64	7/16	
	64 to 76	2/9	S (snail speed) = 87cm/hr
	76 to 102	1/5	
	102 to 127	0/4	
	127 to 152	---	
	152 to 178	1/1	

TABLE 24, continued

September 21-22	0 to 13	8/9	
1965	13 to 25	15/16	level = +4.0'
	25 to 38	11/13	
	38 to 51	17/19	T - 16.33 hours
	51 to 64	3/7	
	64 to 76	1/4	
	76 to 89	2/2	
	89 to 102	1/1	
September 22-23	0 to 25	6/8	level = +4.0'
1965	25 to 51	7/13	T = 16.57 hours
	51 to 76	3/9	
December 14-15	0 to 25	2/3	level = +4.0'
1965	25 to 51	3/5	T = 18.57 hours
	51 to 76	2/4	
January 5-6	0 to 13	5/6	
1966	13 to 25	3/11	level = +4.0'
	25 to 38	1/6	
	38 to 51	1/4	T = 16.21 hours
	51 to 64	0/1	

TABLE 25

Combined Data from Table 24 Corrected for Superposition on August, 1965 graph (Figure 16)

D_m (in cm)	fraction feeding
-330 to -280	0/11 = .00
-280 to -229	0/5 = .00
-229 to -178	5/10 = .50
-178 to -127	4/10 = .40
-127 to -76	8/13 = .62
-76 to -51	39/57 = .69
-51 to -25	34/55 = .62
-25 to +25	29/47 = .62
+25 to +76	27/64 = .42
+76 to +152	1/12 = .08
+152 to +203	1/2 = ---

TABLE 26

String Count Distribution and Probability Density for Different Sized *B. glandula* in the Summer

$F(r)$	$k_i = f(r)$	domain	(see text for explanation)
$1.052r + b_1$	1.052	$.50 > r > .25$	
$0.853r + b_2$	0.853	$1.2 > r > .50$	
$0.400r + b_3$	0.400	$1.4 > r > 1.2$	
$0.120r + b_4$	0.120	$1.5 > r > 1.4$	
$0.120r + b_4$	0.120	$1.6 > r > 1.5$	
$0.100r + b_5$	0.100	$1.8 > r > 1.6$	
$0.035r + b_6$	0.035	$2.0 > r > 1.8$	

where b_i is some undefined constant.

TABLE 27

Approximate Barnacle Densities on High Rocks

(Use L in centimeters and multiply
final result by 10^5 for number per meter^2)

	<1mm	1-3mmm	3-8mm	> 8mm	
June and July	$\frac{.365S}{L}$	$\frac{.407S}{L}$	$\frac{.016S}{L}$	---	*B. glandula*
August-October	$\frac{.415S}{L}$	$\frac{.486S}{L}$	$\frac{.016S}{L}$	---	
December-May	0	$\frac{.500S}{L}$	$\frac{.0225S}{L}$	---	
	0	$\frac{.0239S}{L}$	$\frac{.0387S}{L}$	$\frac{.1745S}{L}$	*B. cariosus*

TABLE 28

Destruction of *T. emarginata* Egg Capsules

Days after marking (=x)	Fraction of capsules destroyed (of those found) (= f(x))
2	.025
3	.041
4	.038
5	.056
6	.050

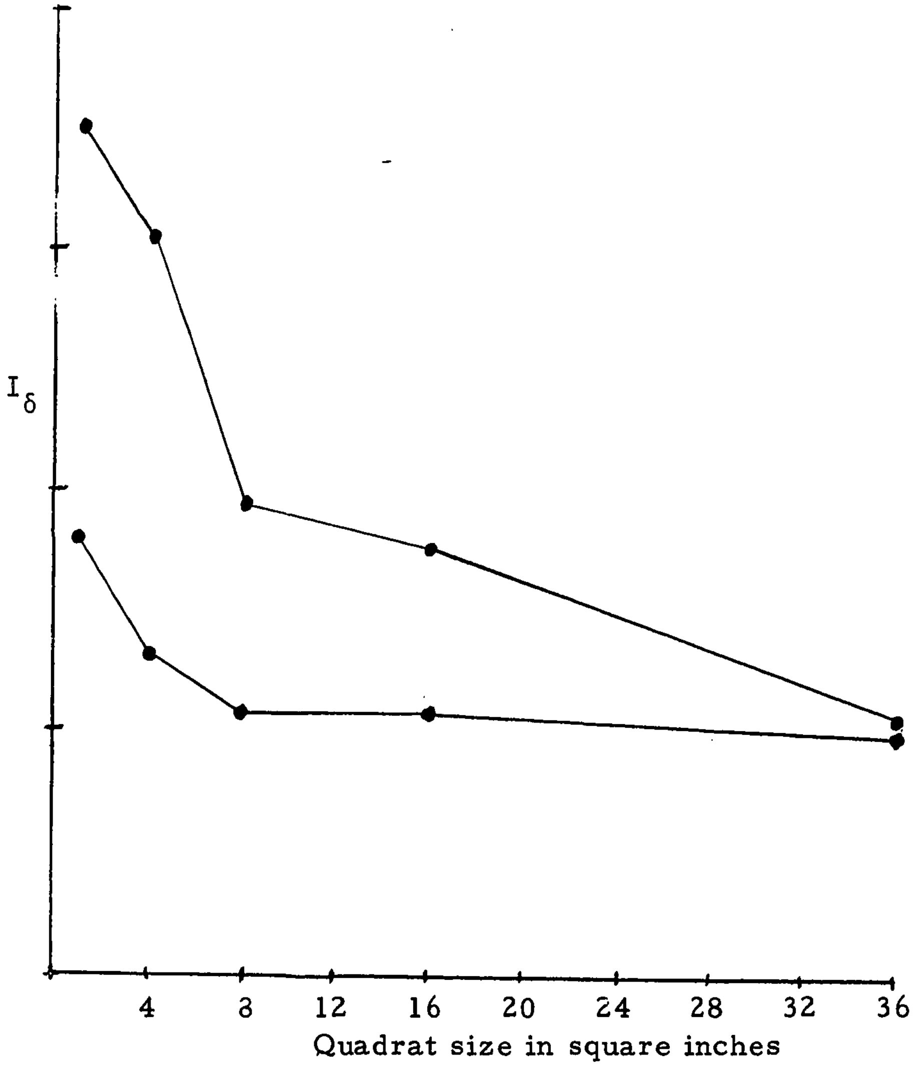


FIGURE 1

Tests for Dispersion Pattern of Freshly Eaten Barnacles on Two Rocks (See text for explanation)

FIGURE 2

Relation between Opercular Diameter and Scutum thickness in *B. glandula* and *B. cariosus*

(Curve fitted by eye)

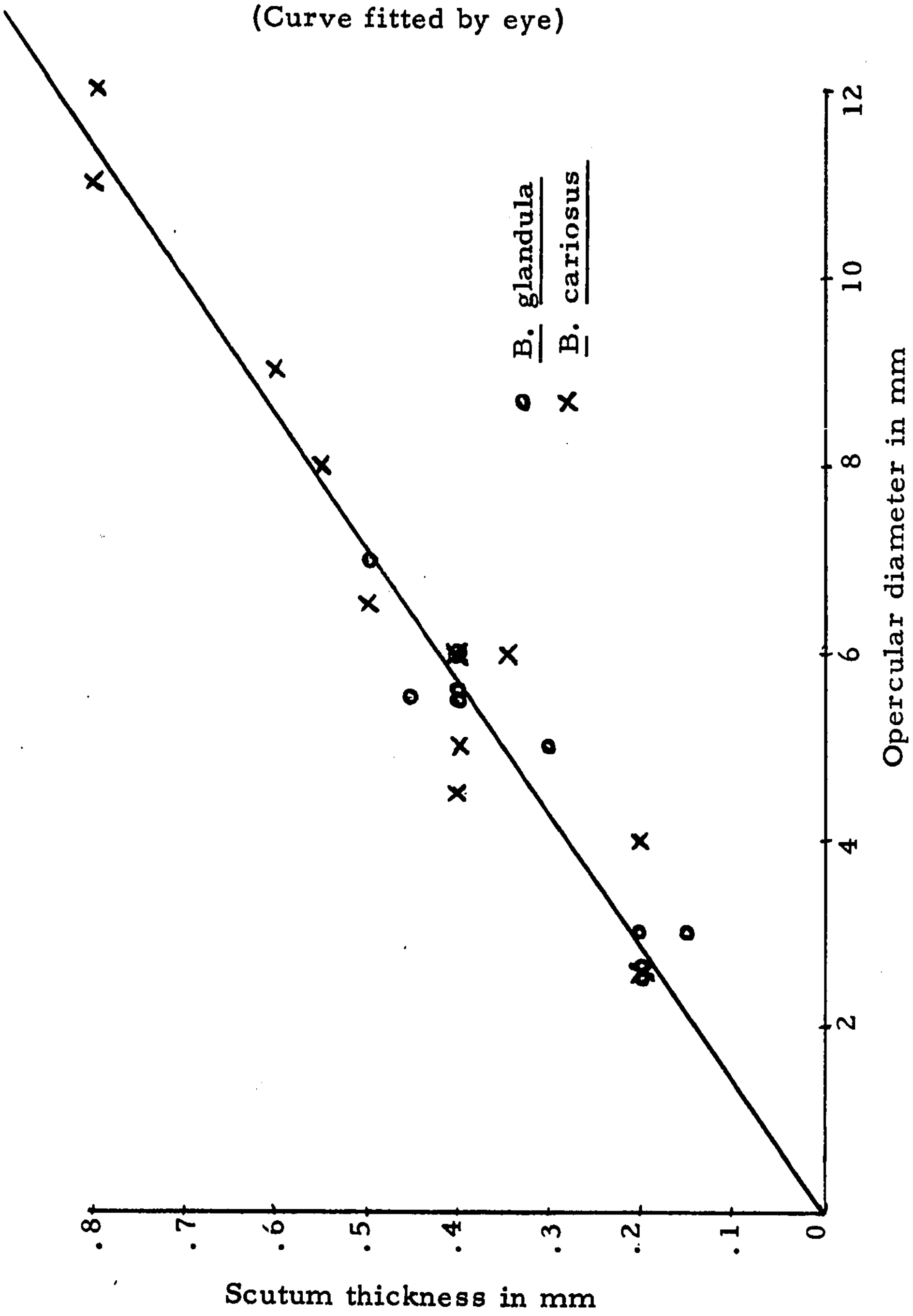


FIGURE 3

Relation between Opercular Diameter and Ash Free Weight in B. *glandula* and B. *cariosus*

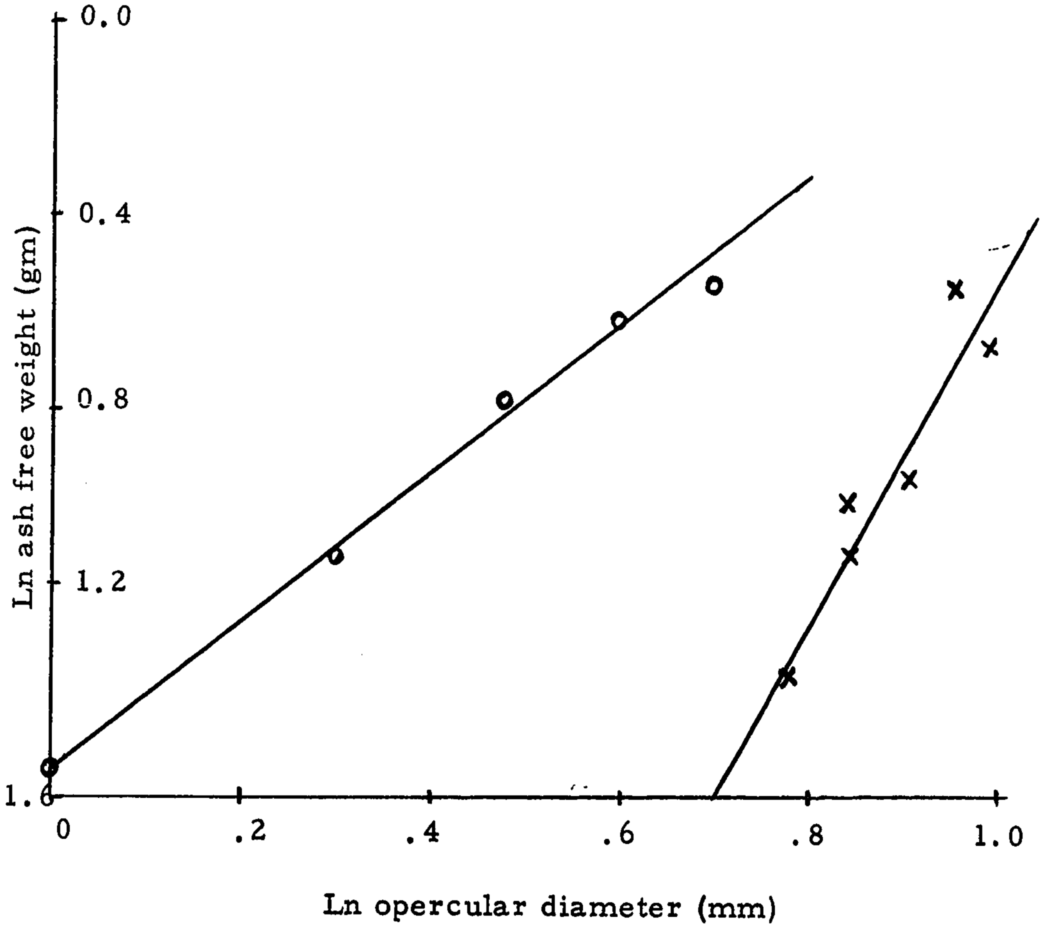
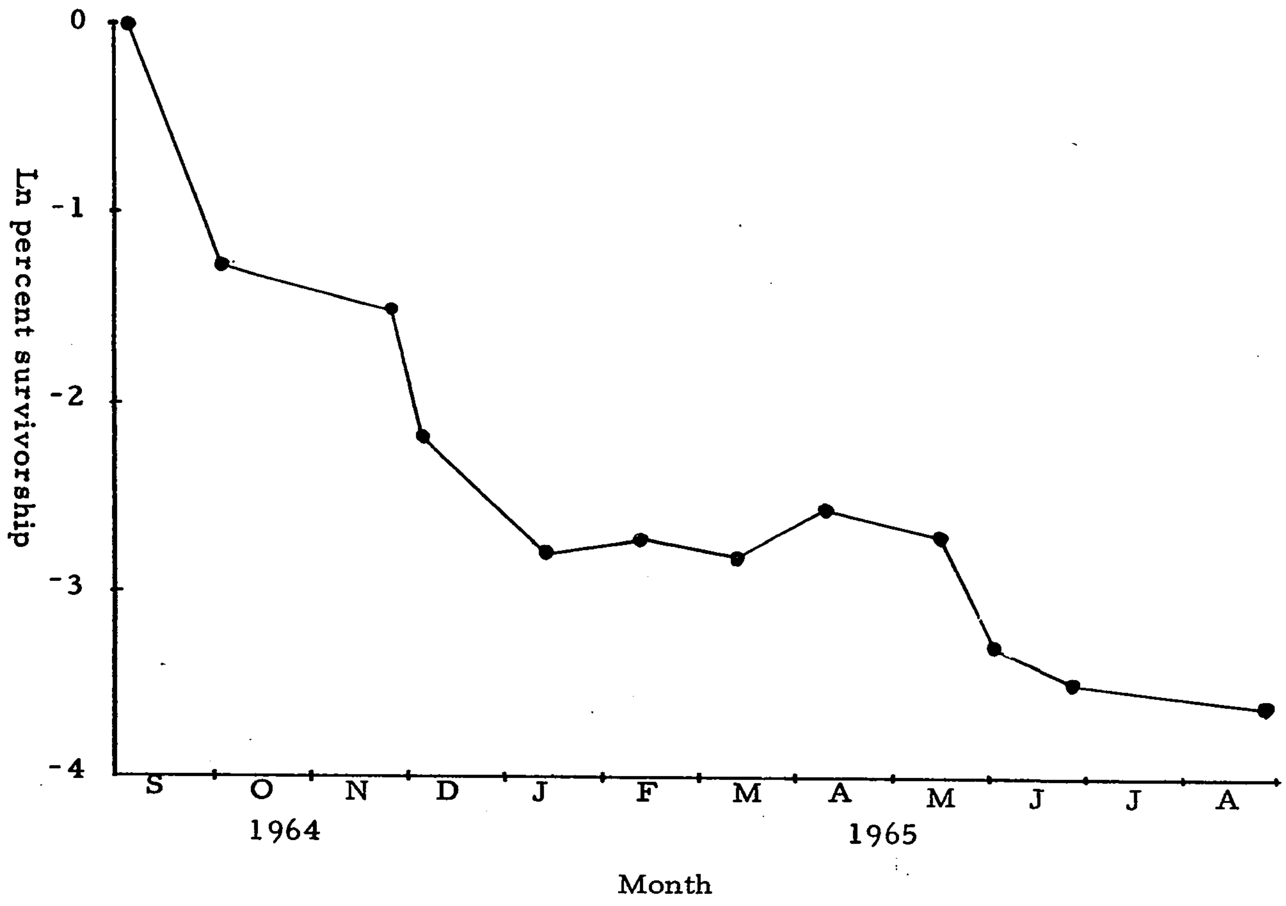


FIGURE 4

Survivorship for Adult _T._ _emarginata_



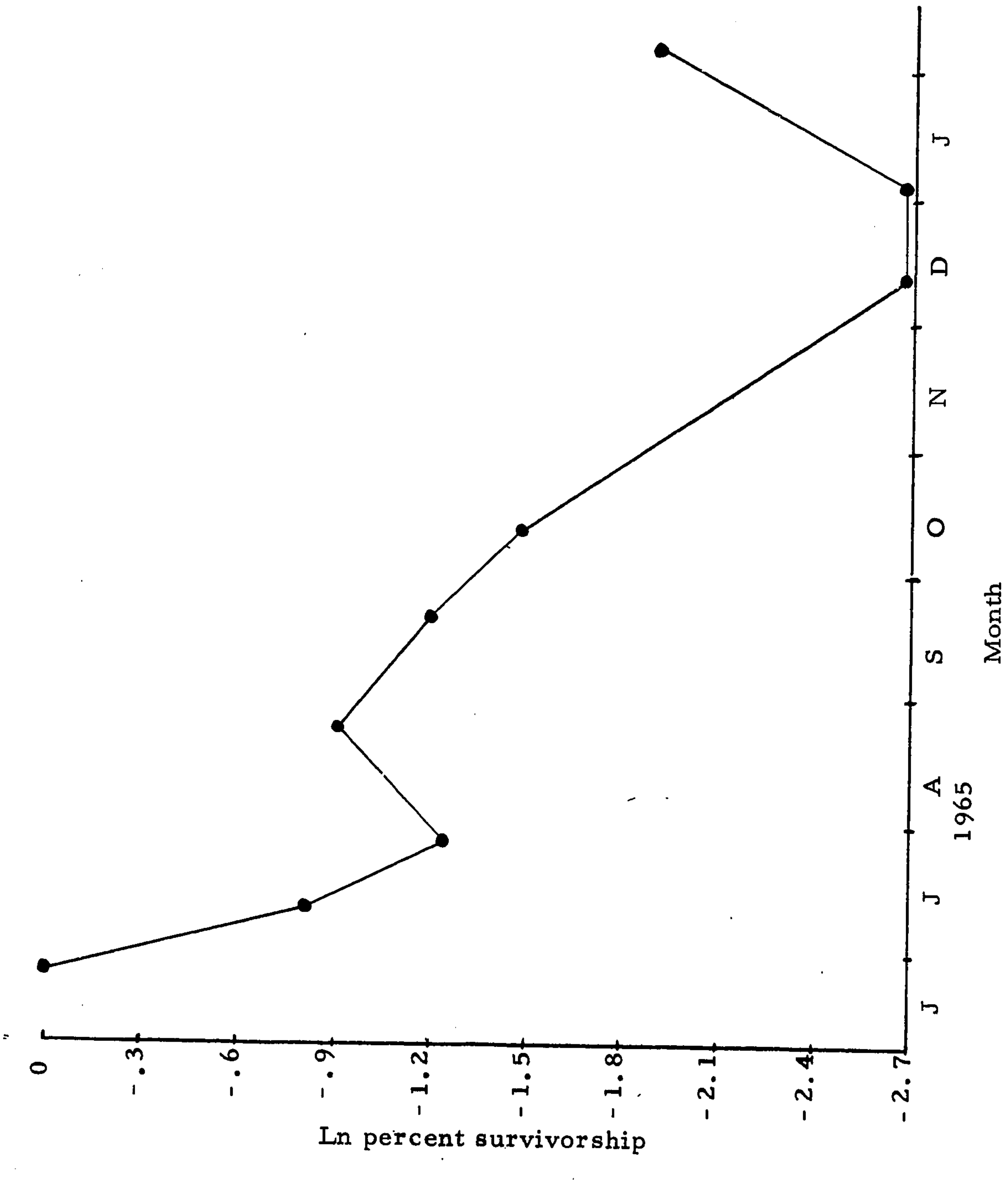


FIGURE 5

Survivorship for _T. emarginata_ between the Ages of

Six and Eighteen Months

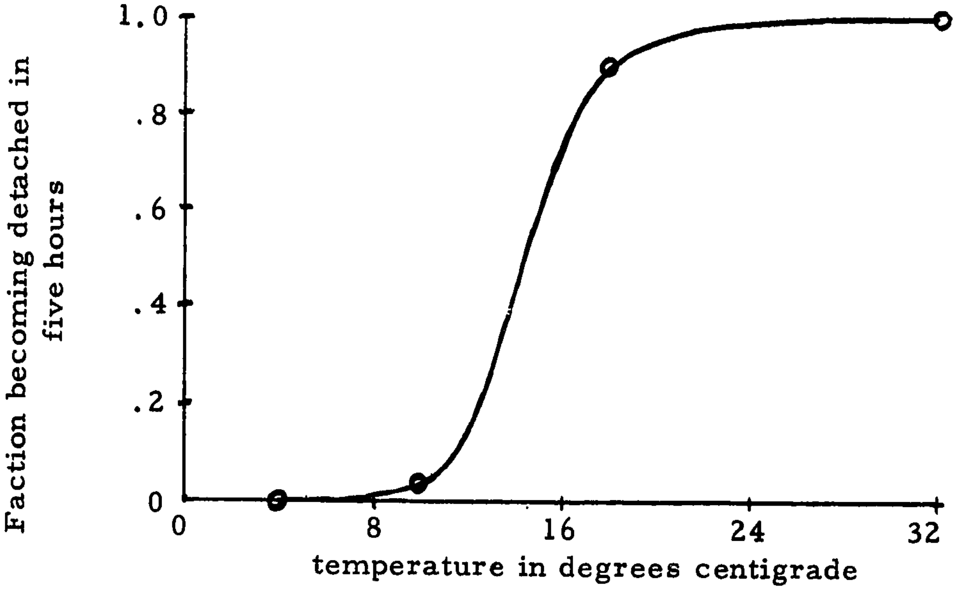


FIGURE 6

Relation between Temperature and Detachment

Rates of T. *emarginata*

(Both laboratory and field data included)

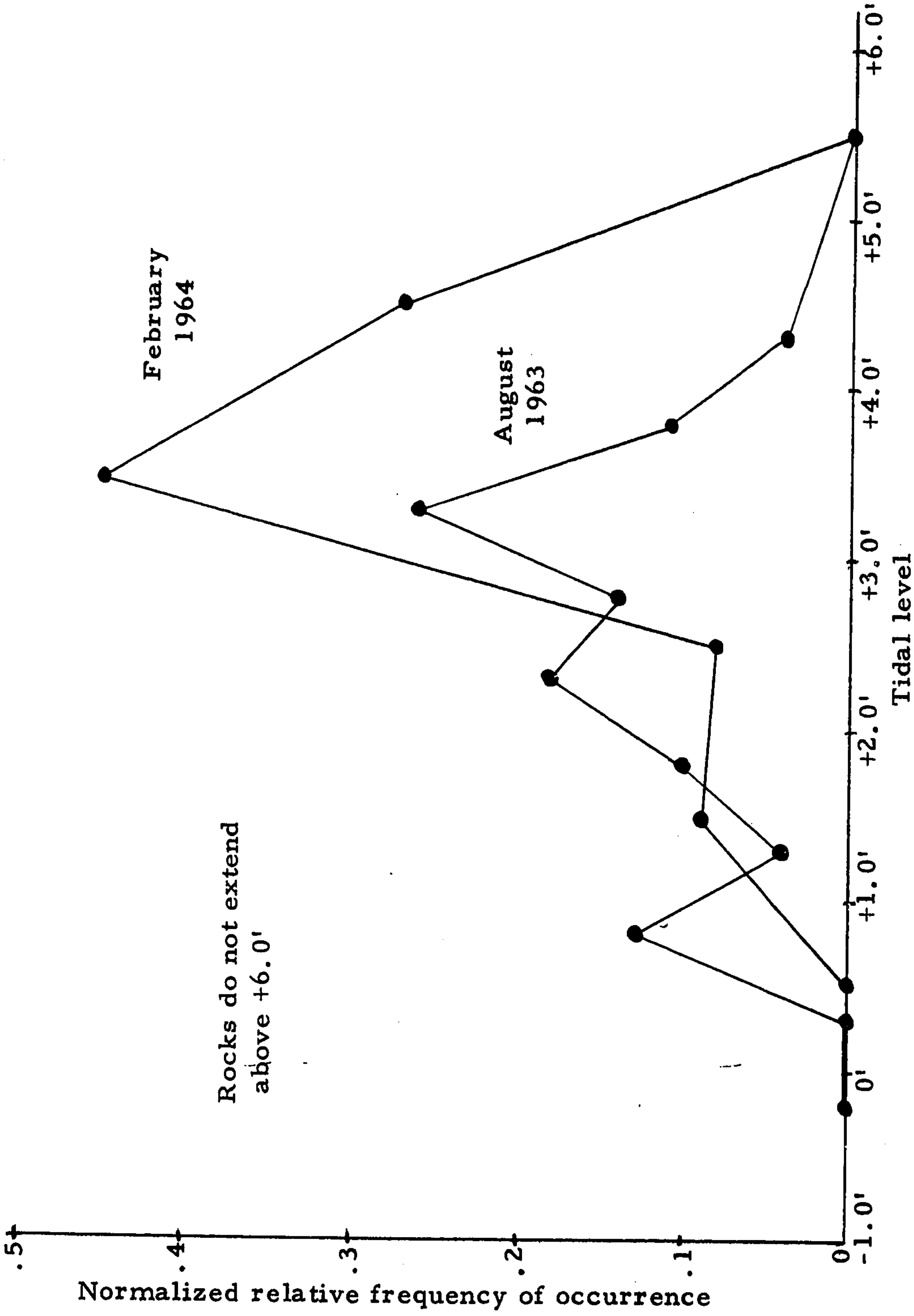


FIGURE 7

Distribution of T. *emarginata* (Normalized Relative Population Densities) With Tidal Level

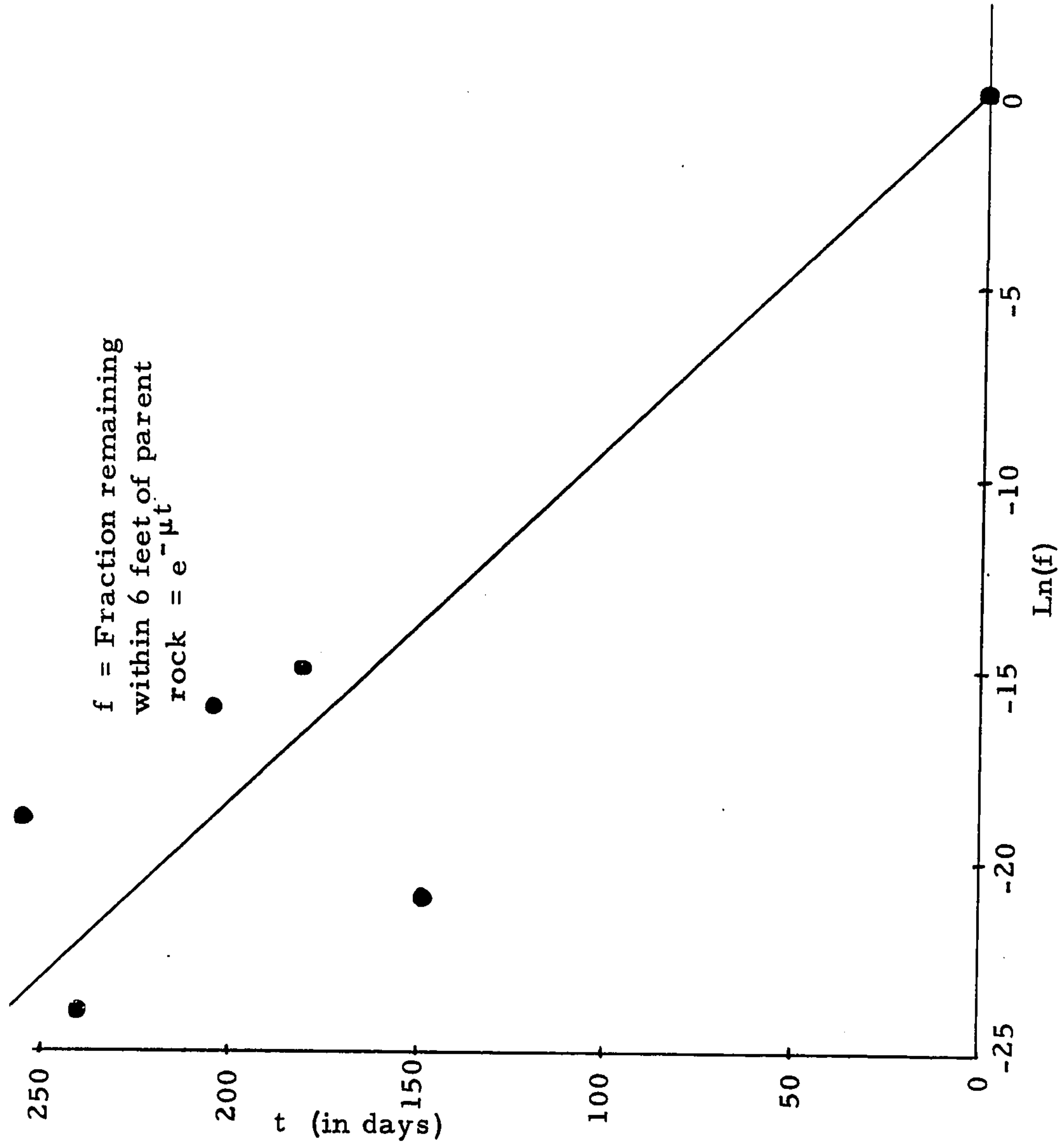


FIGURE 8

Rate at Which T. emarginata Stray from

An Area Within Six feet of their Parent Rock

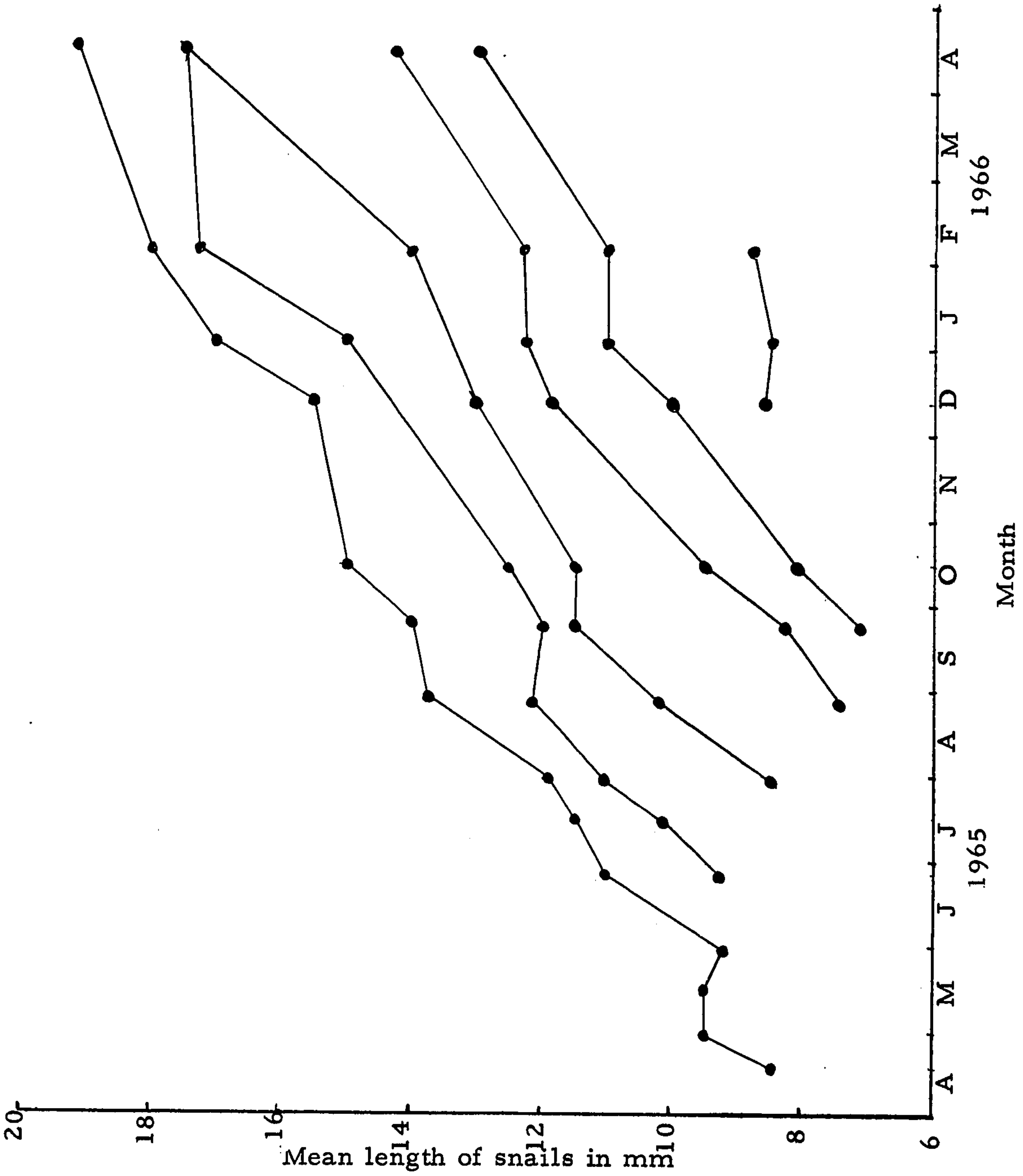


FIGURE 9

Growth of Young T. emarginata

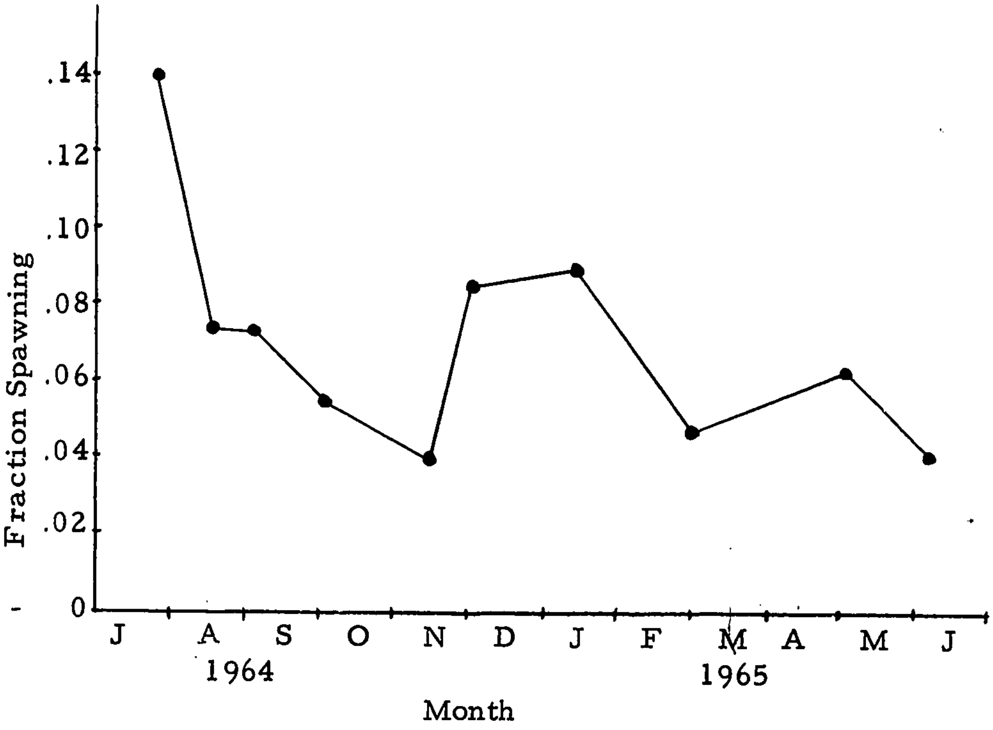


FIGURE 10

Fraction of T. emarginata Spawning

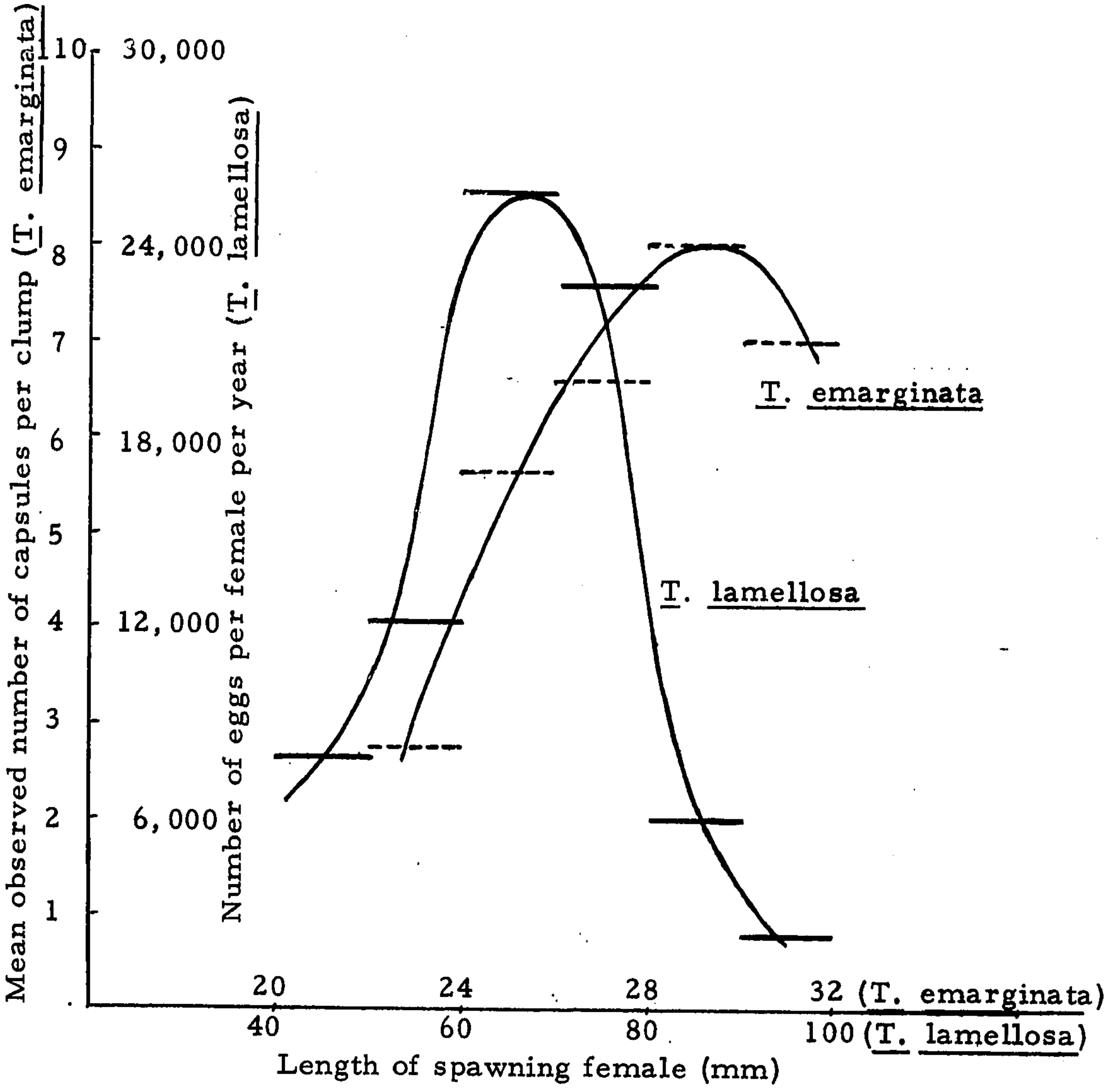


FIGURE 11

Relation between Snail Size and Spawning Activity

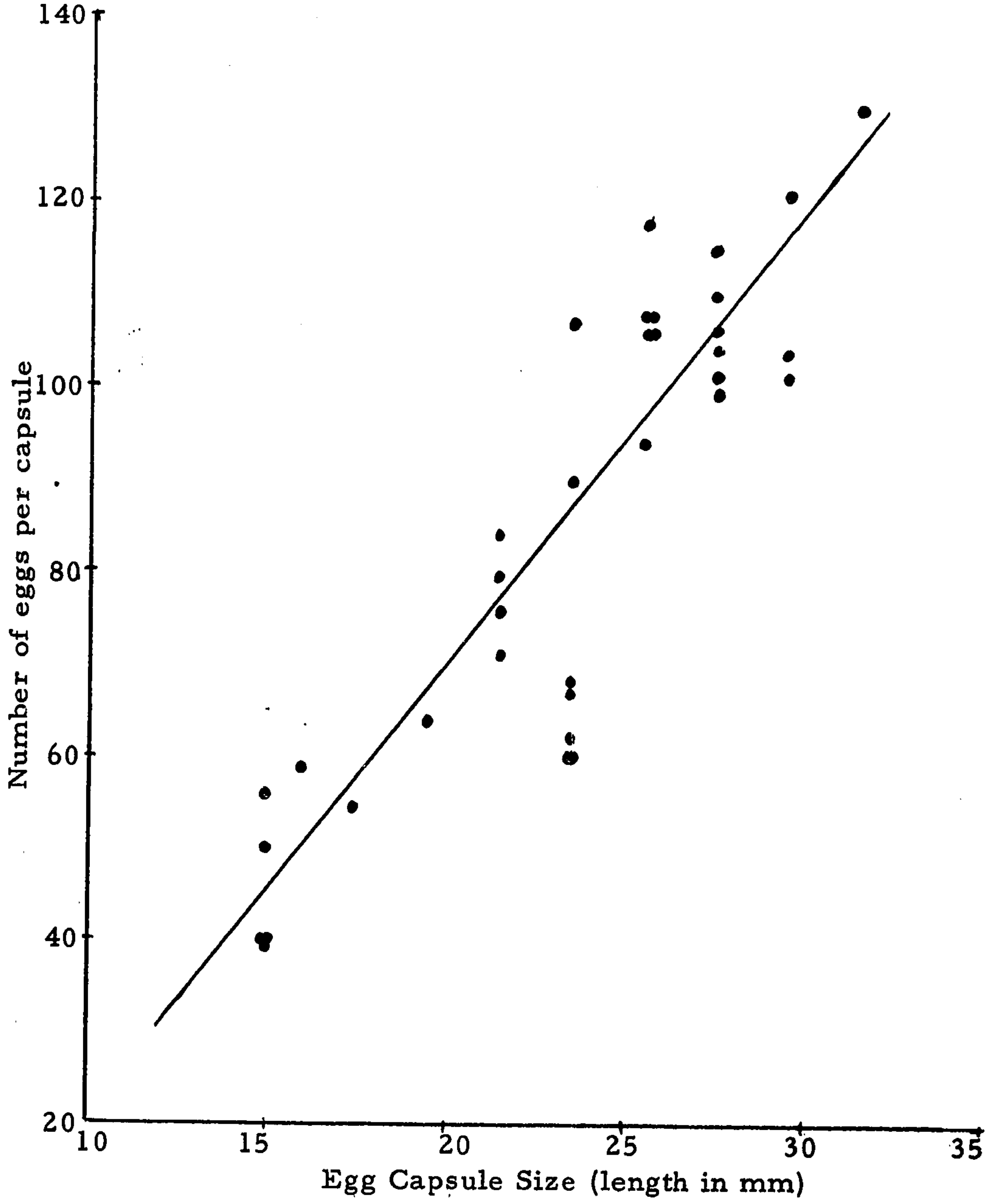


FIGURE 12

Relation between Egg Capsule Size and Number of

Eggs per Capsule for T. lamellosa

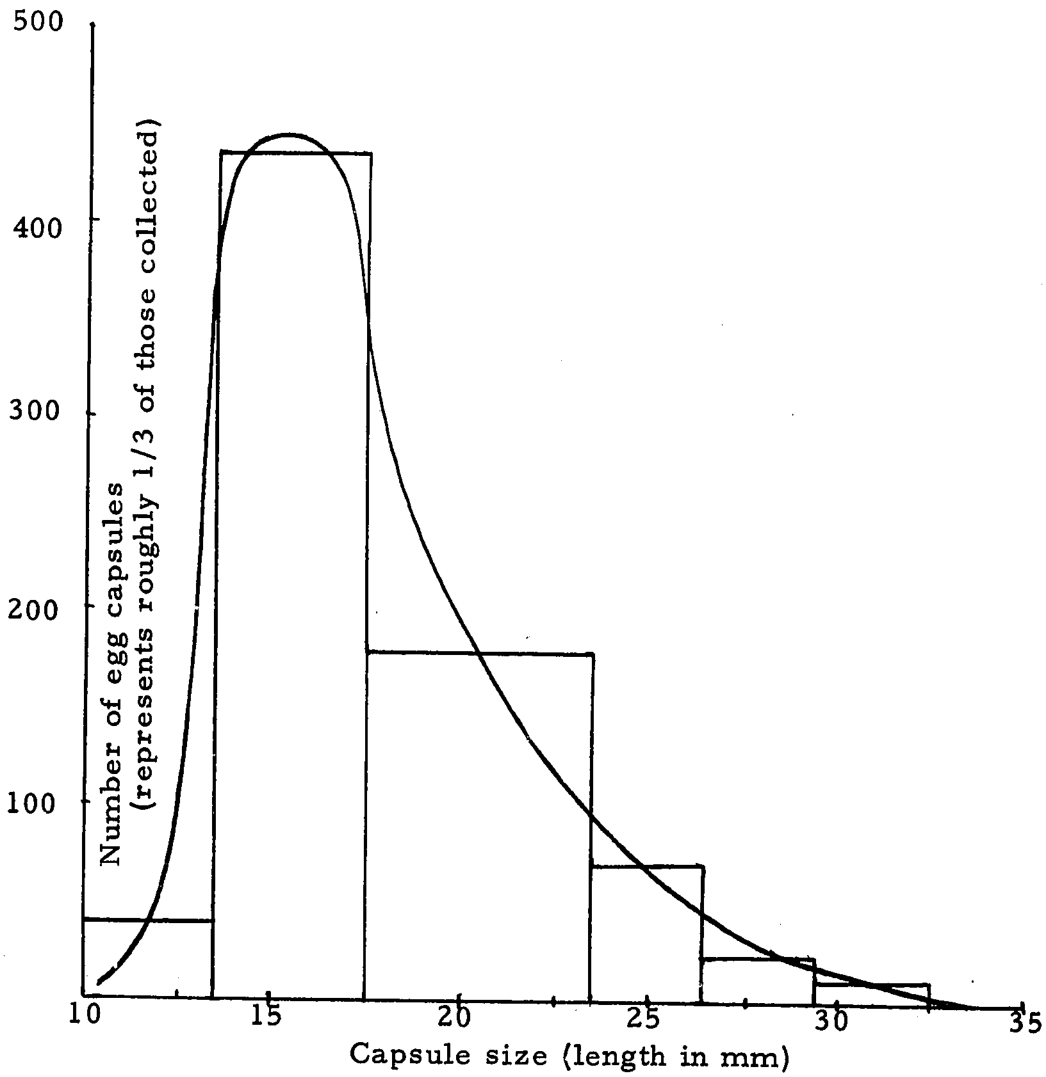


FIGURE 13

Size Distribution of T. lamellosa Egg Capsules

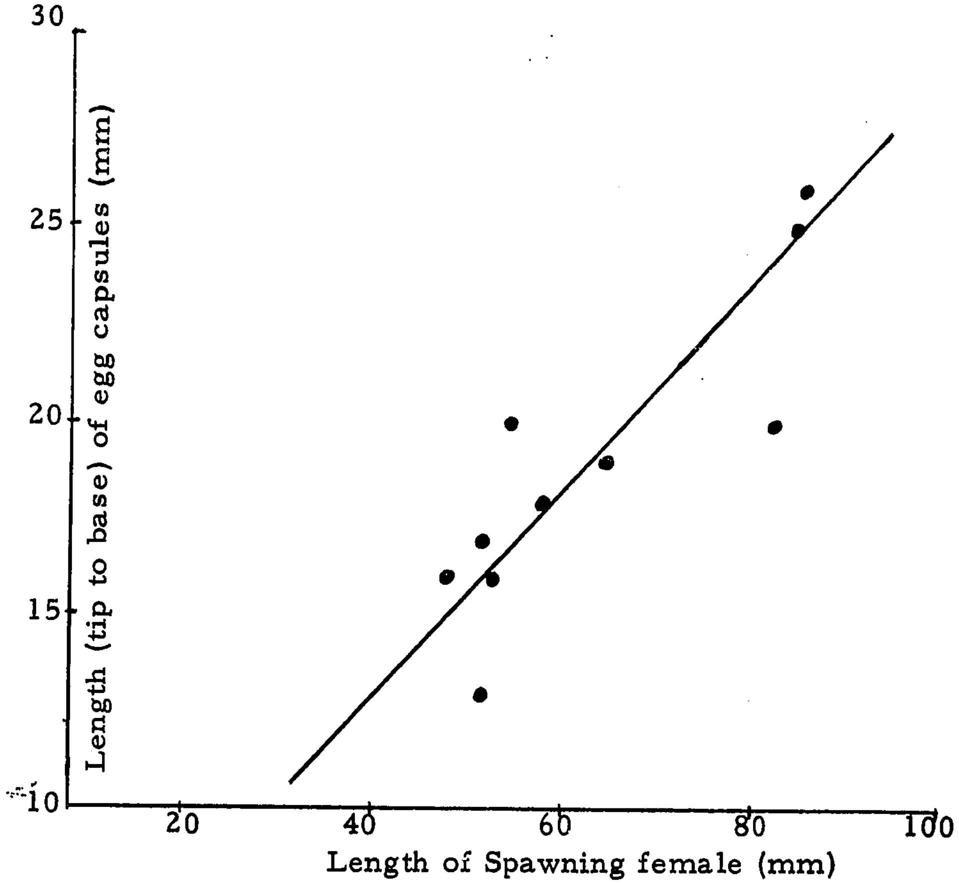


FIGURE 14

Relation between T. lamellosa Size

and Egg Capsule Size

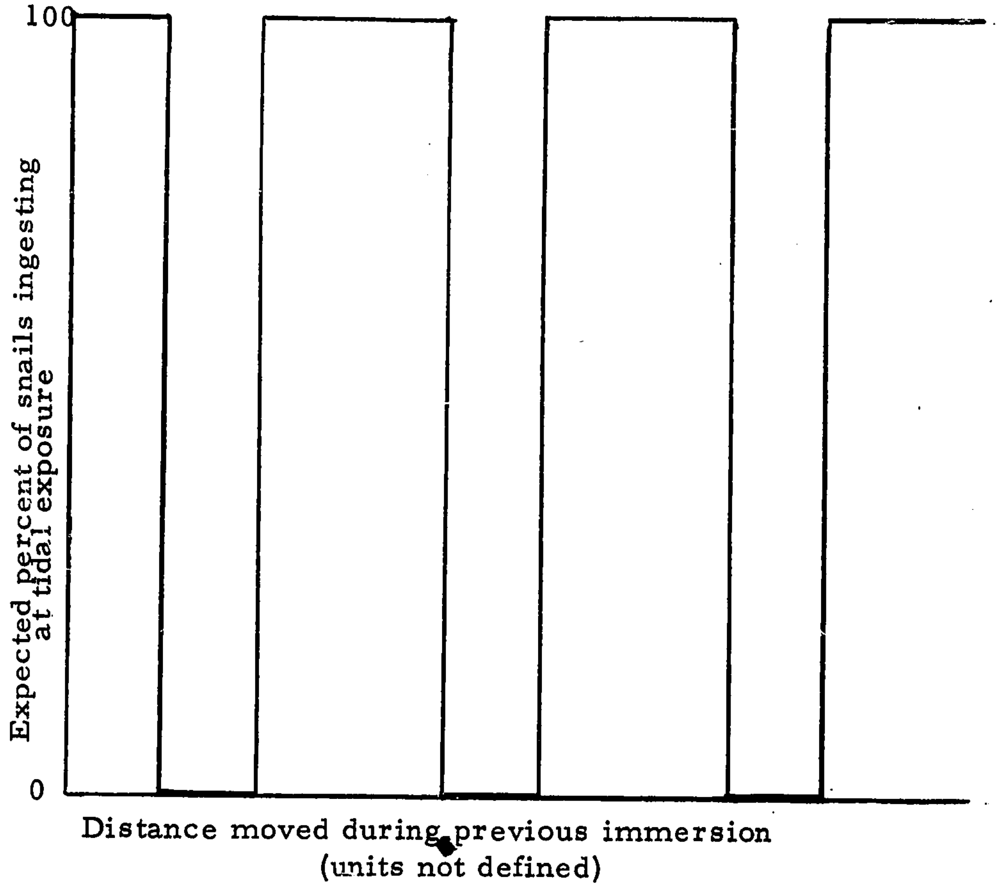


FIGURE 15

Expected Relation between Ingestion

At Tidal Exposure and Movements

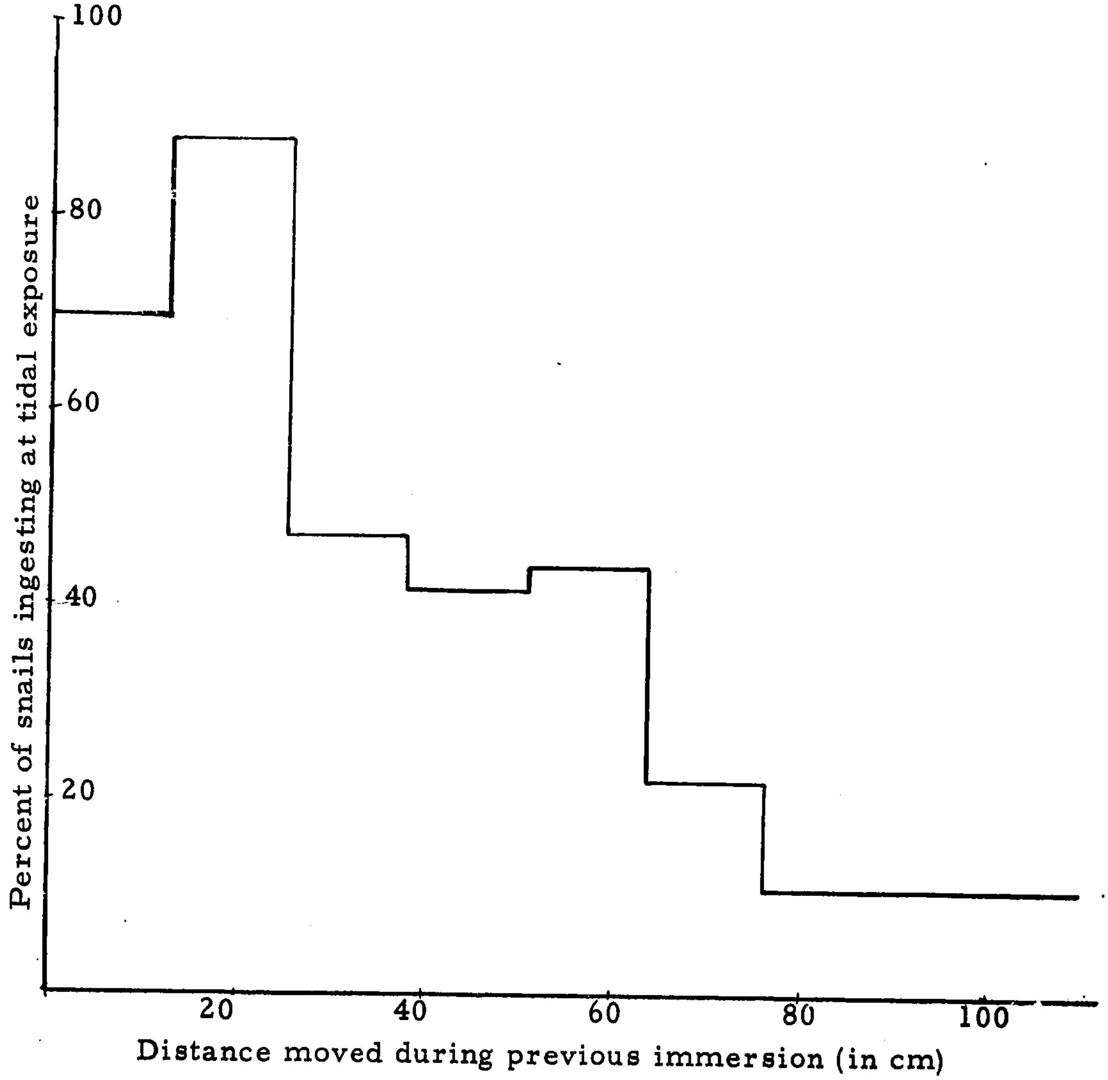


FIGURE 16

Relation Between Ingestion at Tidal Exposure

and Movements (August, 1965)

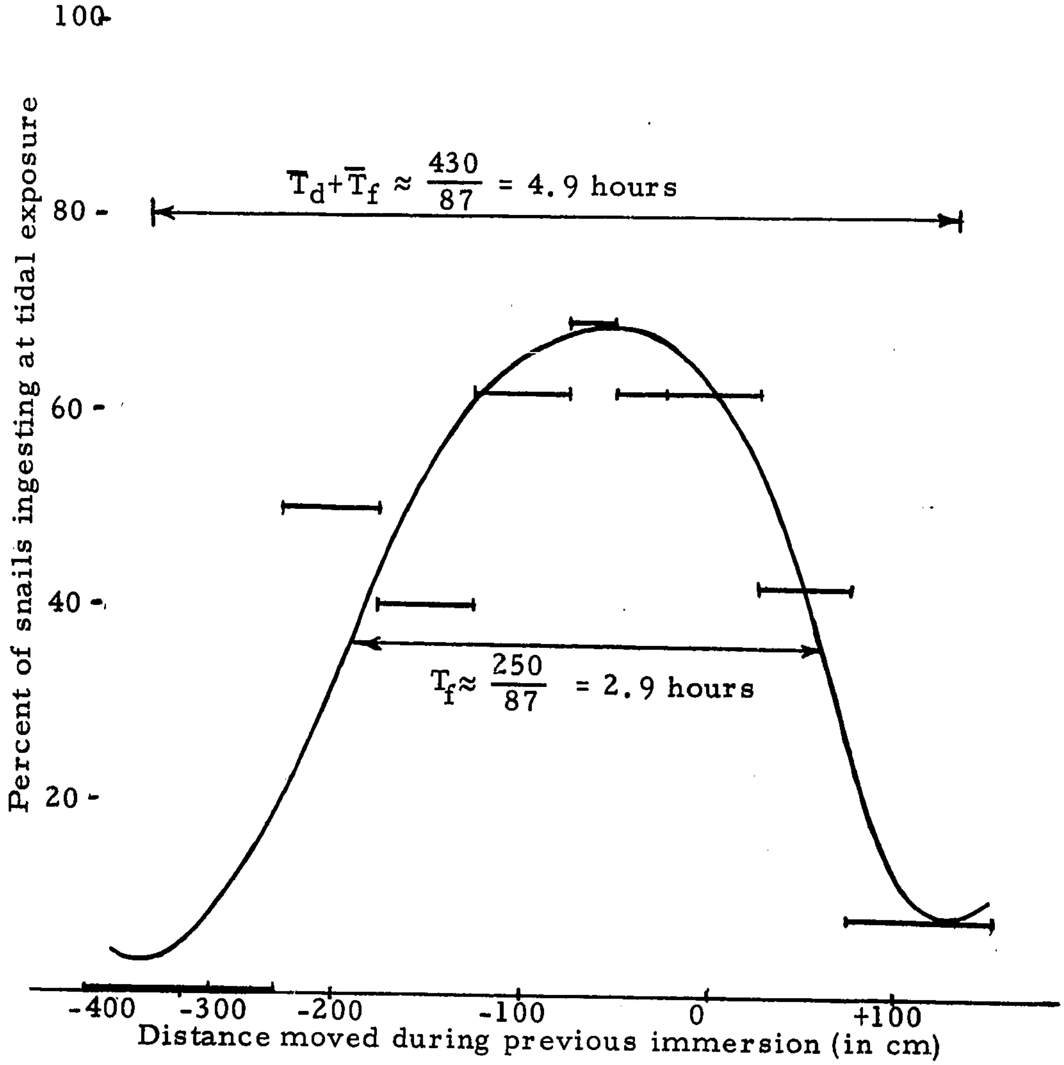


FIGURE 17

Relation between Ingestion at Tidal Exposure

and Movements (Combined Data)

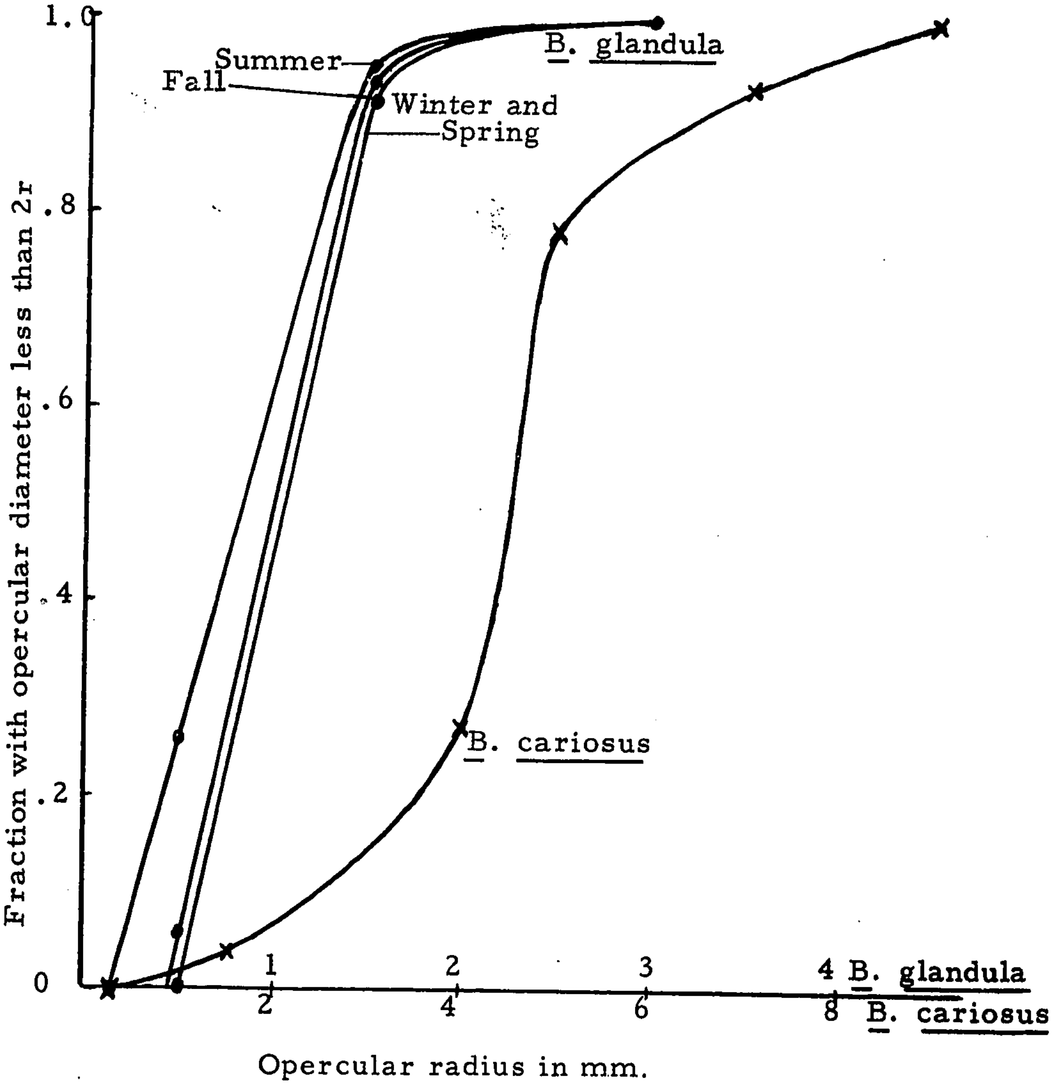


FIGURE 18

Barnacle Size Distribution Functions

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APPENDIX 1

Let T be the total submerged time per submersal period,

T_d be the time required to drill one barnacle,

T_f be the time required to ingest one barnacle,

T_m be the time spent moving in one submersal period,

n be the number of barnacles completely drilled and devoured during one submersal period,

S be the speed with which a snail moves (measured in August, 1965, at 87 cm/hour):

Then, the time left over after moving for a time, T_m, and finding, drilling and devouring n barnacles, for a given snail, is $T - [T_m + n(T_d+T_f)]$. Now since essentially all _T. emarginata_ observed in positions where their preferred food was common were either ingesting or drilling (scraped surface or pit in the scuta), it can be assumed that the snails spend nearly all their time drilling, ingesting, or moving. If the time left over, as shown above, is greater than T_d, then, the snail in question will have had time to complete drilling its next barnacle, and should have been ingesting it when exposed. If this time is less than T_d, the snail, when exposed, should still have been in the process of drilling the barnacle. On the other hand, it is clear that if the time left over after eating n+1 barnacles is less than zero, i.e., the snail has not finished its last barnacle, then in this case also, the snail will have been ingesting when exposed. Thus:

(17) $T - [T_m + n(T_d+T_f)] \gtrless T_d$ implies the snail $\left\{\begin{matrix}\text{was}\\ \text{was not}\end{matrix}\right\}$ ingesting,

and:

(18) $T - [T_m + (n+1)(T_d+T_f)] \lesseqgtr 0$ implies the snail $\left\{\begin{matrix}\text{was}\\ \text{was not}\end{matrix}\right\}$ ingesting.

Rearranging terms, it can be seen that ingestion will have been taking place at the time of exposure if and only if:

(19) $T - (n+1)(T_d+T_f) < T_m < T - T_d - n(T_d+T_f)$, and that the range of T_m over which ingestion will have been taking place is:

(20) $[T - T_d - n(T_d+T_f)] - [T - (n+1)(T_d+T_f)] = T_f$.

Similarly, the range of T_m over which ingestion will not have been taking place is:

(21) $[T - n(T_d+T_f)] - [T - T_d - n(T_d+T_f)] = T_d$.

If we now plot T_m versus the probability that a given snail will have been ingesting, we obtain a graph such as that shown in Figure 15. The position of the first peak will depend on the values of T, T_d and T_f. For calculation purposes, T_m may be related to the actual distance moved, D_m by the formula, $D_m = ST_m$. Of course T_d and T_f vary from snail to snail and from barnacle to barnacle, so the peaks obtained from actual data cannot be expected to be so clear cut as those in Figure 15.

Data was obtained by first marking a large number of snails on several rocks at the same tidal level, and mapping their positions on these rocks. At the next tidal exposure, the distance moved by each snail was measured, and the barnacle beneath that snail was examined to determine whether the snail had or had not been ingesting when first exposed. As an example of the kind of results obtained, the data for T. emarginata for August, 1965, are shown in Figure 16. The curves obtained by this method are far less informative than might be expected; the number of snails moving long distances was never sufficient to demonstrate a second peak. Nevertheless, by combining the data obtained, it was possible to estimate $\overline{T}_d$ and $\overline{T}_f$ -- that is, the average time required for a snail to drill and ingest an average sized barnacle (average of those occurring in the diet) for each of several months.

In August, 1965, the end of the feeding peak appears to have been roughly 58cm. Thus:

(22) $T - (n+1)(T_d+T_f)_{Aug.} = 58/87 = .67$ hours (see equation 19).

Substituting in the proper value for T, the equation may be rewritten:

(23) $15.37 - (n+1)(T_d+T_f)_{Aug.} - .67$, so $(T_d+T_f)_{Aug.} = \frac{14.60}{(n+1)}$.

If temperature changes are assumed to change S, T_d and T_f from month to month, similar expressions may be derived for the other months for which data were collected. Let the temperature factor relating August to September, 1965 be α_1, so that $S_{Sept., 1965} = S_{Aug.}/\alpha_1$. Similarly let the factors relating August to December, 1965 January, 1966, and September, 1964 be respectively α_2, α_3, and α_4. Then:

(24) September, 1965: $16.33 - (n+1)(T_d+T_f)_{Aug.}\alpha_1 = .70\alpha_1$, so $(T_d+T_f)_{Aug.} = \frac{16.33 - .70\alpha_1}{(n+1)\alpha_1}$, and $\alpha_1 = 1.06$ (see equation 23). Similarly $\alpha_2 = 1.19$, and $\alpha_3 = 1.09$. Data for September, 1964, were not adequate for similar treatment but since September, 1964, was colder than September, 1965, (field notes--no temperature data available), and certainly warmer than December, 1965, α_4 may be approximated as 1.1. This being so, S for the various months may be given by:

$S_{Aug.} = 87$ cm/hr

$S_{Sept., 1965} = 82$cm/hr

$S_{Dec.} = 73$ cm/hr

$S_{Jan.} = 80$ cm/hr

$S_{Sept., 1964} = 78$ cm/hr.

Thus, moving a distance, D_m of (for example) 25 cm in August, 1965, would take .29 hours, and is equivalent (in terms of the graph, Figure 15) to .29X82 = 24cm in September, 1965. By making this type of adjustment to the distance data shown in Table 24, and then properly translating the resulting D_m values (for example, $T_{Aug.} = 15.37$ hours, $T_{Sept., 1965} = 16.33$ hours, so the September curve is shifted 16.33-15.37 = .96 hours to the right of the August curve. Thus 10 cm in September, 1965, is equivalent to $10\text{x}\frac{87}{82} - .96\text{X}87 = -73$cm in August) the data for all months may be superimposed on the August, 1965, graph. The result is shown in

Table 25 and Figure 17.

From the shape of the graph in Figure 17, $(\overline{T}_d+\overline{T}_f)_{Aug.}$ can be approximated as 4.9 hours. Since the end of the peak, can be ascertained with some accuracy at about 58cm, $\overline{T}_f$ can also be estimated (see Figure 17) at 2.9 hours.

By equation 23, $(T_d+T_f)_{Aug.}$ is equal to $\frac{14.60}{n+1}$. For n=2, this expression gives $(T_d+T_f)_{Aug.} = 4.9$ hours which is identical to the estimated value of 4.9 hours shown on the graph. Thus if $\overline{T}_{f\ Aug.} = 2.9$ hours, then $\overline{T}_{d\ Aug.} = 4.9 - 2.9 = 2.0$ hours.

By way of a very rough check, camera data from August, 1965, showed total feeding times of 2.5, 3.6, > 3.2, > 3.2, > 5.8 hours, with an average of >3.7 hours.

Values of $\overline{T}_d$ and $\overline{T}_f$ for months other than August can be found by multiplying the August values, 2.0 and 2.9, by the appropriate α value. Thus, for example, $T_{f\ Dec.} = 2.9\ \alpha_3 = (2.9)(1.19) = 3.45$ hours.

APPENDIX 2

The method used to calculate barnacle density is an approximate one, sacrificing some accuracy for ease and quickness of application. This was necessary since large rock surfaces had to be considered during a short enough period of time to allow for other aspects of data collecting during low tides.

Consider a thin string (ideally of negligeable thickness) stretched across an area 2R units wide and L units long. Suppose that within this area, there are n_r barnacles of opercular diameter 2r. The probability that the string will pass over the operculum of any one of these barnacles, then, is $2r/2R = r/R$. If we assume that all barnacles are distributed independently over the area in question, then the expected number of barnacles of size 2r crossed by the string is:

(25) $m_r = \frac{r}{R} n_r$.

Actually the barnacles are not distributed independently, but since L can be thought of as a series of disjoint lengths over relatively homogeneous rock areas, and since 2R may be chosen very small (but not so small as to introduce edge effects), the assumption of independent distribution is not entirely unreasonable for the purposes of these calculations. Solving the equation for n_r:

(26) $n_r = \frac{Rm_r}{r}$, and since the density, ρ_r is equal to

n_r/area = $n_r/2RL$, it is clear that:

(27) $$\rho_r = \frac{Rm_r}{2RLr} = \frac{m_r}{2rL}.$$

Since the expected number of barnacles crossed by the string of length L can be approximated by the actual string count, m_r may be taken as the actual string count, and ρ_r as the expected barnacle density.

Equation 27 can be generalized to a situation where r ranges over a continuum, by writing:

(28) $d\rho = S\frac{f(r)dr}{2rL}$, or: $\rho_r = \frac{S}{2L}\int \frac{f(r)}{r}\,dr$, where f(r) is the probability density of barnacles of size 2r being crossed by the string, and S is the total number of barnacles crossed by the string. If one can now break up the distribution function, F(r)--which can be determined from field data--into a series of linear functions, $k_i r + c_i$, over given domains of r, $(b > r > a)$, then f(r) can be written $d/dr\ (k_i r + c_i)$, where i denotes the appropriate domain of the function, and density can be written:

(29) $$\rho_{b > r > a} = \frac{S}{2L}\int_a^b \frac{k_i}{r}\,dr = \frac{Sk_i}{2L}\ \ln(b/a).$$

The next step is to determine as closely as possible the F(r) curve so that the values of k_i and the corresponding values of <u>a</u> and <u>b</u> can be found. Upper and lower limits may be placed on barnacle sizes. <u>B</u>. <u>glandula</u> and <u>B</u>. <u>cariosus</u>, when first settled, measure about .5mm in size, and B. glandula essentially never exceeds a maximum size of 4mm when full grown. From February, 1966 data, it appears that within the largest *B. cariosus* size group, 397/561 = .71 are between 8 and 10mm, 510/561 = .91 are below 14mm in size, and none exceeds 18mm. From this information, it is possible from string count data on barnacles of several size classes (< 1mm, 1-3mm, >3mm for *B. glandula*, and < 1mm, 1-3mm, 3-8mm, > 8mm for *B. cariosus*) to draw distribution functions, F(r) for both species. The results are shown in Figure 18. From the summer curve for B. glandula, for example, it can be calculated that $\rho_{1.2 > r > .5} = .853S/2L\,(\ln 1.2/.5)$, $\rho_{1.4 > r > 1.2} = .400S/2L\,(\ln 1.4/1.2)$, and so on (see Table 26). The density of the size group, 1mm to 3mm, then, is

$$S\left[\frac{.853(\ln 1.2/.5 + .400(\ln 1.3/1.2) + .120(\ln 1.5/1.4)}{2L}\right]$$

$= .407S/L$. Densities for other size groups are similarly found. The results (based on data from high level rocks--base level 3.5') are presented in Table 27.

Since *B. glandula* larger than 3mm occurs essentially only on high rocks, size preference data were taken from these high levels and the density relations of different sized *B. glandula* used in calculating importance values were taken from Table 27. From the information in this table, it is clear that the total population density of *B. cariosus* is roughly .2372S/L, and of *B. glandula*, about .788S/L in June and July, .917S/L in August through October, the .523S/L in winter and spring. These expressions were used to derive the approximate barnacle densities listed in Table 6.

APPENDIX 3

Let the time which an egg capsule spends in the process of being deposited be T_c, and developing, be t. Then, in the absence of mortality, the ratio T_c/t should be equal to the ratio of the number of capsules observed being deposited to the total number present and unhatched--assuming that over the preceding t days, spawning rates were constant from day to day.

Now if the capsules are predated, or die of other causes, at a rate of k_2 per day, then $l_x = e^{-k_2x}$ where l_x is the survivorship. Thus the fraction present of all capsules, now age x, originally spawned, is e^{-k_2x}, and if deposition of capsules takes place at a rate, k_1, the total number of age x to x+dx capsules now present should be $k_1e^{-k_2x}dx$. The total number of unhatched capsules, then, over the number that would have been present in the absense of mortality, is:

$$(30)\qquad \frac{\int_0^t k_1 e^{-k_2x}\,dx}{\int_0^t k_1\,dx} = \frac{1-e^{-k_2t}}{k_2t}.$$

Since the number of capsules observed in the process of development was 734, the expected number that would have been present, had there been no deaths, is $(734)(\frac{k_2t}{1-e^{-k_2t}})$. The number of capsules seen in the process of being spawned was 9, and thus:

$$(31)\qquad \frac{9}{734(\frac{k_2t}{1-e^{-k_2t}})} = T_c/t \text{ (see paragraph one).}$$

Now the rate of deposition of capsules is roughly 1.5 per day, and since exposure does not seem to cancell this activity, T_c can be calculated to be 1/1.5 = .67 days per case. Thus:

(32) $\frac{9(1-e^{-k_2t})}{734k_2t} = \frac{.67}{t}$, and so

(33) $1-e^{-k2t} = 54.4k_2$.

2289 egg capsules were marked on April 19-22, 1966, and checked for several days for mortality. The results are given in Table 28. By the least squares method, where f(x)= fraction destroyed = $1-e^{-k_2x}$, the death rate, k_2, was found to be .01039. Substituting this value of k_2 into equation 33:

(34) $1-e^{-.01039t} = (54.4)(.01039) = .5652$, which is the fraction surviving through the development period, and t is found to be 80 days.

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