Studies on the Biology of the Naticid Clam Drill *Polinices lewisi* (Gould) (Gastropoda Prosobranchiata)

by F. R. Bernard

FISHERIES RESEARCH BOARD OF CANADA

TECHNICAL REPORT NO. 42

1967

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STUDIES ON THE BIOLOGY OF THE NATICID CLAM DRILL POLINICES LEWISI (GOULD) [GASTROPODA PROSOBRANCHIATA]

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F. R. Bernard

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Biological Station, Nanaimo, B. C.

December, 1967

INDEX

Introduction

Snails of the naticid genus Polinices are predators on bivalves, accounting for a considerable percentage of nonpathological mortality in the clam population in British Columbia. In 1963 a program of research in the general biology and estimates of destructive capacity was instituted under the direction of Dr. D. B. Quayle of the Fisheries Research Board, Nanaimo.

Study Areas

Small comparative collections of Polinices lewisi (Gould) were obtained intertidally and by dredging from many areas in British Columbia. Large numbers of individuals for statistical analysis and for gonad samples were collected over a four year period from three areas near the Biological Station, Nanaimo, in southeastern Vancouver Island (see Fig. 1).

Area A. A mud, sand and gravel beach opposite the Biological Station in Departure Bay. This gently sloping beach was approximately 200 meters in length. Situated within the Bay, Area A was protected from violent wave action. The western end consisted of a large bed of Zostera but the central area bore a large clam population. This locality furnished the majority of individuals used in population analysis and gonad studies. [Area A is now covered by dredged material to be used as foundations for the extension of the Biological Station.]

Area B. Situated on the tip of Stephenson's Point is a small body of sand with a substantial clam population. Only a small population of Polinices was present.

Area C. The upper range of this beach consists of large boulders and rock fragments; only a narrow area exposed at extreme low tide was suitable for clams. Collecting at Spring tides by means of SCUBA, a large number of small ($<$ 30 mm shell length) P. lewisi were obtained. There were very few large individuals.

Systematics

Polinices lewisi (Gould)

Natica lewisii Gould. 1847. Proc. Boston Soc. Nat. Hist., Vol. 2: 239.

Lunatia lewisii Gould, Carpenter. 1864. Brit. Assn. Adv. Sci. Rept. for 1863: 661.

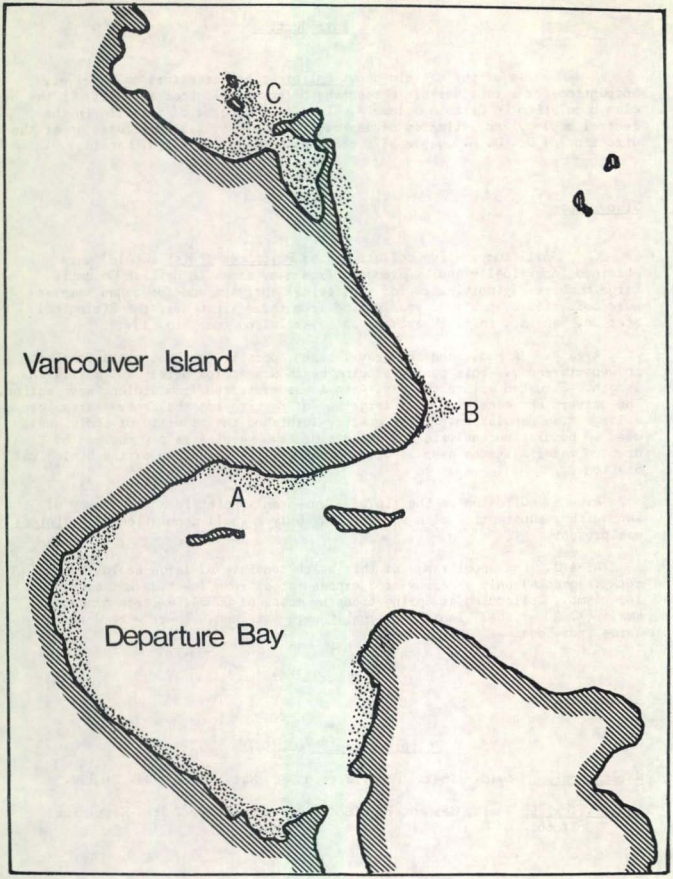


Fig. 1. Polinices study areas.

Polynices (Lunatia) lewisii Gould, Arnold. 1903. Mem. Calif. Acad. Sci. Vol. 3: 315.

Polinices lewisi Gould, Packard. 1918. Univ. Calif. Publ. Zool. Vol. 14, 325, pl. 38.

Polinices (Euspira) lewisii Gould, Dall. 1921. U.S. N. Mus. Bull. 112: 165.

Polinices (Euspira) lewisii Gould, Grant and Gale. 1931. Mem. San Diego Soc. Nat. Hist. Vol. 1: 804.

Type locality: Discovery Harbour, Puget Sound.

Geological range: Pliocene to recent.

Bathymetric range: Intertidal - 50 fathoms.

Geographical range: San Diego - Masset, Q. C. I. (31°N-54°N).

Confusion has surrounded the nomenclature of the Naticidae. The original genus was Natica; subsequently Lunatia, Neverita, Euspira, and Polinices were applied. It is now accepted that Natica comprises those species having a shell operculum and Polinices a corneous operculum; Lunatia and Neverita are of doubtful value but are sometimes employed as subgenera within Polinices. [Strictly, Natica is a tropical group and our species should be referred to Tectonatica (Sacco, 1890).]

Population

Estimates of population

In area A, P. lewisi was most abundant low down on the beach and in the central portion, the area of maximum concentrations of butter clams (S. gigánteus). A block 100 meters by 20 meters was marked off parallel to the water and random replicate plots were dug and all Polinices counted. The number fluctuated from none to five per square meter. As pointed out by Hunter and Grant (1966), population density estimations by such means are not accurate. Moonsnails are capable of deep burrowing and long periods of inactivity. An attempt at indirect estimates was made by releasing 100 snails which had been marked on the shell and operculum. Two days later another collection of snails was made and all marked individuals counted.

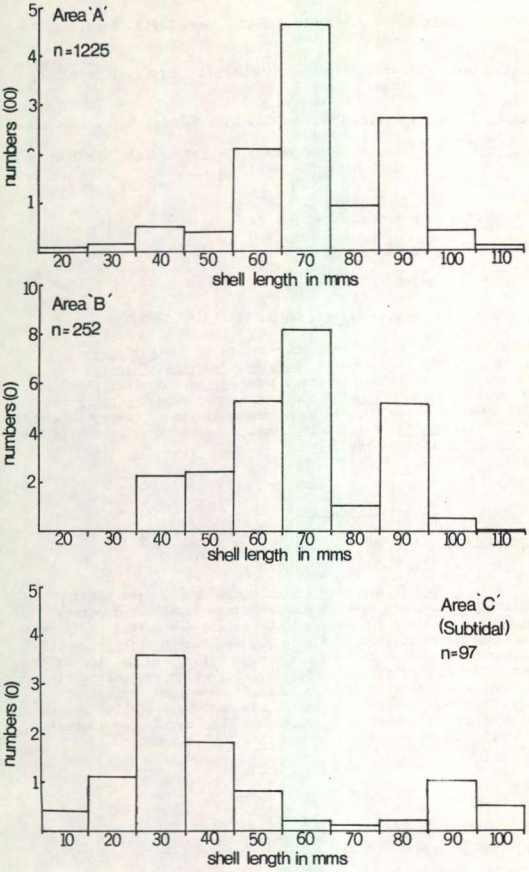


Fig. 2. Shell length/frequency histograms for study areas.

Assuming that the released marked snails become homogeneously dispersed through the general polulation, the easiest estimate of population is obtained by the formula:

$$P = \frac{TM + 1}{R + 1}$$

where P = estimate of population based on recapture

T = total numbers of individuals collected on second collection

M = number of marked individuals originally released

R = number recovered

95% confidence levels are calculated by standard binomial procedure.

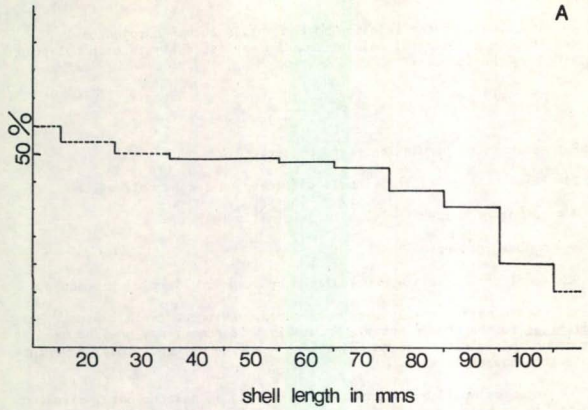
Twelve marked snails were recaptured, giving an overall density of .85 Polinices to the square meter. Naturally this number may only be used as a very rough approximation as no adjustment was made for individual movements in and out of the study area.

Accuracy would be improved by collecting at a later date, allowing marked snails to become more homogeneously distributed throughout the population. A collection made one month after release failed to include one marked snail, indicating that the population is very much greater and more mobile than first estimated.

Population structure

Studies of other species of Polinices have shown that distinct size-classes are present (Stinson, 1946; Wheatley, 1947, for P. triseriata). Medcof and Thurber (1958) suggest that the male and female of Lunatia (Polinices) heros have different growth rates. Turner (1951) proposed that food is abundant for juveniles but scarce for adults, resulting in a 'telescoping' of the size-classes.

Population studies of P. lewisi undertaken in the years 1963-1966 revealed a basic unimodal distribution with distinct year classes. The mode for the populations of areas A and B falls at the 70 mm shell length. The picture is further complicated by sexual dimorphism and an apparent second mode at about 90 mm due to poor recruitment or high mortality in the 80 mm class (see Fig. 2, A and B). The picture is different in area C, where collections were principally made by means of SCUBA. Here, the mode falls at about 30 mm with very few individuals between 50 and 80 mm, though there is a proportionate increase in very large individuals, due no doubt to offshore migration (see Fig. 2 C).



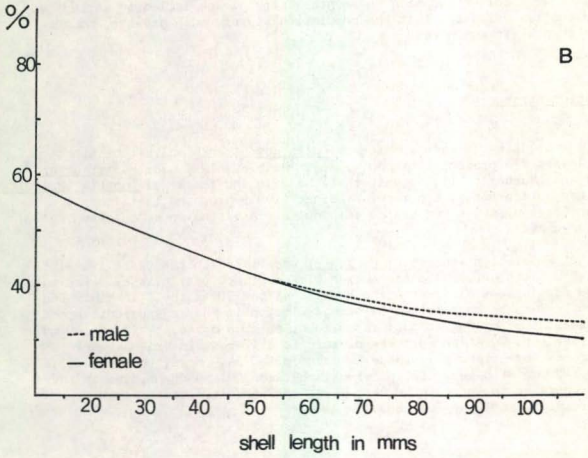


Fig. 3. A. Histogram of percentage of males in total population.
B. Graph of percentage males/females.

In the four years of study the population distribution and structure remained constant and stable. Recruitment from other areas did not alter the original year classes which moved in the same ratio with increase in size. A small collection of individuals (187) from area B, taken in September 1967, gave a mode at 80 mm with the least numbers at 90 mm. This would show that the shell length/frequency distribution is a function of year classes.

Dimorphism

In the smaller size groups there is an approximately equal distribution of the sexes. As size increases the relative abundance of males decreases. The presence of both sexes in each group, though in different proportions, would suggest that the groups represent age-classes and not different sexes of the same age-class. Examination of juveniles (2-30 mm shell length) show that when the gonad is fully developed and gametogenesis has commenced (around 30-40 mm shell length) the distribution of the sexes is equal. At 100 mm shell length, 90% of the individuals are female (see Fig. 3 A). Histological examination of large numbers of gonads from all size classes rules out the possibility of protandric hermaphroditism.

Analysis of population measurements suggests that males grow at a slower rate. Examination of mating pairs shows that the male is invariably the smaller. There is no difference between male and female shell height/width ratio, but the males possess a significantly thicker and heavier shell. In juveniles the total weight/shell weight ratios are similar in males and females but after the commencement of breeding (> 55 mm) the male shell becomes proportionately and increasingly thicker than the female. Of 1,875 individuals measured, the mean of the total weight/shell weight ratio was statistically significant, being 0.472 for males and 0.401 for females (see Fig. 3 B).

It is highly probable that not only is the differential growth rate responsible for the decrease in males as size increases, but mortality is higher in males, living on an average two thirds as long as females. Examination of collections of dead shells showed that a high proportion of them had the thicker shells associated with male Polinices.

Predation

Species preference

While it is known that P. lewisi feeds almost exclusively on bivalves, it is not known whether any species specificity is involved. The relative clam abundance in Area A was calculated by means of a series of random replicate plots. Eighteen hundred drilled shells were collected from the sand surface and the species and position of drill hole noted.

Table I. Species abundance and percentage drilled shells.

Species	% Species abundance	Drilled shells %
Clinocardium nuttalli	7	0.4
Protothaca staminea	48	46.0
Saxidomus giganteus	27	47.6
Venerupis japonica*	1*	0.4
Tresus nuttalli	14	1.0

* V. japonica is situated high up on the intertidal, normally above the P. lewisi range.

Although Clinocardium nuttalli cover most of the Polinices range, this heavy ribbed shell is avoided: this may indicate a preference for thin-shelled prey. Oysters (Crassostrea gigas) were present in several localities but in no case was one found bearing drill marks. Tresus, though present in fair numbers, was not commonly attacked by Polinices, possibly due to the relatively deep burial of this bivalve in areas consisting of fine sand and mud.

Analysis of the site of drilling showed that there is a consistent positioning of the drill hole. The greater percentage of shells are drilled a little ventral to the umbo; in only 8% did it depart from this position. Seven per cent of the valves showed partial drill marks and no account could be taken of the bivalves destroyed by Polinices without drilling at all. No evidence was found to support the suggestion of Verlain (1936) that naticids learn to position the hole so as to reach the underlying gonad.

Table II. Drill position on shell valve.

Position of drill site	% shells drilled
Left valve	61
Right valve	39
Region of umbo	92
Away from umbo	8
Partially drilled	7

The small percentage of partially drilled shells is misleading owing to the difficulty of distinguishing a shell that has died of other causes. In limited aquarium observation, over 60% of Saxidomus consumed showed no drill marks.

Rate of predation

Experiments were undertaken to establish a measure of predation. Ten each of P. staminea, S. giganteus and T. nuttalli were placed in a large tank, the bottom of which had been filled with a three-inch layer of sand and gravel. Ten Polinices which had been starved for five days were introduced. Each 24 hours the substrate was sifted and all clams accounted for. If a drill was in the process of consuming a clam, both were returned to the tank. Dead and consumed clams were removed and replaced by new ones, so that the clam population remained constant. At first the drills ate the entire clam; subsequently only the softer portions were eaten, the siphon and adductor muscles remaining within the shell.

Day	P. staminea	S. giganteus	T. nuttalli
1	3	0	1
2	0	1	0
3	2	2	1
4	0	1*	2*
5	1*	0	1
6	2*	0	0
7	3 (2*)	1	0
8	1	0	1*
9	0	0	1*
10	2	1*	0

* Denotes partial consumption.

In a ten-day period 27 clams were consumed by ten adult P. lewisi, approximately one clam per drill in a four-day period.

A better estimate of predatory activity was obtained incidental to another experiment involving the transportation of a number of marked butter clams (Saxidomus giganteus). Three hundred and eighty marked clams were buried in a 6'×6' plot in the central portion of Area A. Twenty days later, 97 dead clams were recovered, 29 of which bore full or partial drill marks. Twelve days later, another 17 drilled clams were collected. In a 32-day period, 9.4% of the planted clams were destroyed by P. lewisi. The actual number is probably greater, as in aquaria tests 25% of clams consumed by P. lewisi bore no drill marks at all.

Movement

General

A three month study made in June-August 1965 of fifty tagged individuals showed that locomotion within the clam bed was general and non-directional. No overriding movements could be detected, though individuals do tend to avoid one another. During cold weather, most drills were buried up to eight inches below the surface. More drills were visible on the surface at night than in the day. At certain times, most frequently after heavy rain, many of the drills were on the surface, lying on the shell with the foot extended. This behaviour was observed by Ziegelmeier (1953) in P. josephinus. He interpreted it as a 'swimming motion'. Likely it is an irritation syndrome evinced by overcrowding, lack of oxygen, abrupt salinity changes and other undesirable situations.

Surface movement

The movement of Polinices lewisi was further studied in glass aquaria and cement tanks. In most cases the foot was kept fully expanded and progression depended on limited pedal contractions and mostly on cilial action. Even large drills experienced no difficulty climbing the vertical sides of the aquaria, supported to some extent by the viscous pedal mucus but mostly by the sucking-cup action of the sole of the foot.

Movement through substrate

Motion of P. lewisi while buried was studied by allowing them to burrow in plastic-sided and bottomed containers with 2-3 inches of gravel in them. When buried, the snail retracts the propodium and covers with it the front part of the shell; the back and sides being covered by the metapodial folds. This gives the entire animal a wedge-shaped profile ideal for penetration. Progression consists of a combination of ciliary and hydrostatic actions.

Burying movements

Drills placed on loose gravel experienced no difficulty burying themselves in 6-8 minutes. If a more compact sand-mud mixture was offered, greater time and effort were needed. The snail remained stationary with greatly expanded mesopodium. The propodium was extended to a pointed structure some distance from the shell and forced laterally into the substrate by a downward peristaltic contraction and an up-and-down movement, digging an ever-deepening trench in which the snail travelled, obtaining added purchase with the mesopodium on the sides.

Search patterns

The behaviour of a hungry and a recently fed drill are entirely different. Having consumed a clam, the drill remains buried for a period of 8-24 hours then moves away in a straight path for a long distance. The average for five drills was 14 feet (in one case the drill travelled 22 feet). When hungry, the movements are faster with short journeys bounded by large angular turns, generally in excess of 90°. This gives the hungry drill a zig-zagging course, its path often crossing itself. This may be termed the 'search-pattern' of movement.

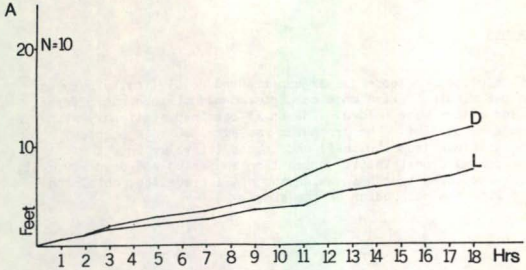
Feeding movements

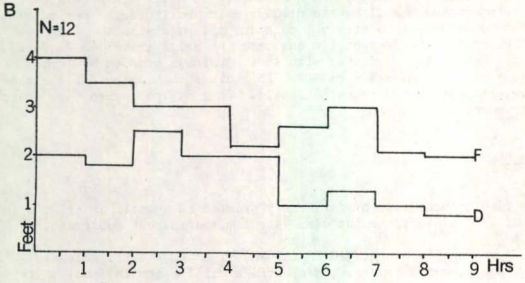
The feeding behaviour of drills was studied in a small aquarium with three inches of 1/8" glass spherules used as a semitransparent substrate.

One Mya arenaria was placed in the aquarium and a drill released. The experiment was repeated several times until a drill began to feed. After primary contact the clam was explored by the tip of the propodium; the drill then dug down parallel to the clam and with a twisting motion enveloped it in the propodium and mesopodium, returning to a position just below the surface, shell uppermost and the clam entirely enveloped in the foot complex which exuded large quantities of mucus.

Periodicity

Movements of P. lewisi in aquaria and in the natural habitat were studied to determine whether there were any patterns of rhythmic activity. These snails appear more active at night for they tend to emerge at night but, when buried, activities are equal either day or night. Ten marked drills were placed in each of two eight-foot diameter tanks provided with three inches of





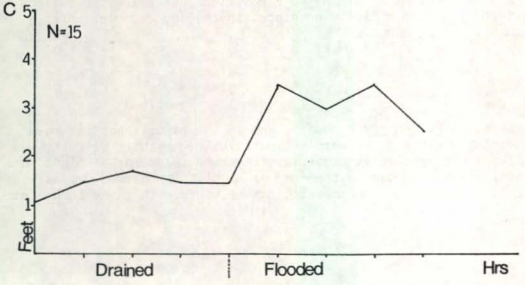


Fig. 4. Legend on facing page.

gravel and the snails' movements plotted at hourly intervals. One tank was illuminated with fluorescent lighting and the other kept dark. At the end of 18 hours the drills in the lighted tank had moved an average of seven feet and the drills in the dark tank had moved eleven feet (see Fig. 4 A). The greater activity in the dark tank was due to the tendency of the snails to emerge from the gravel and travel on the surface by means of ciliary action. If only the buried snails are considered, activity was about equal in the two tanks. Photoreceptive sites appear generalized on the edges of the foot.

If the temperature is about 5°C, activity continues after the habitat is drained. P. lewisi are often very active just below the surface of the drained beach and will actively hunt for clams, though they will seldom commence feeding until flooded by the incoming tide. The activities of twelve snails in each of two aquaria was noted. The snails in the drained tank travelled less than the snails under water but activity was probably the same as more exertion is needed to force a path through drained gravel (see Fig. 4 B). While snails are active for many days at a time, now and then they bury themselves to a depth of six to eight inches and remain for long periods (3-4 days) without movement.

While the snails remain active during low tide it is interesting to note that there is an outburst of accelerated activity just subsequent to flooding by the incoming tide. In aquarium tests the average movement rates more than doubled in the first hour after flooding, then slowly decreased (see Fig. 4 C).

Detection of prey

Experiments to determine whether there was any chemical or other taxis involved in prey detection were inconclusive. A drill must pass within six inches of an entire clam to detect its presence. The case was otherwise with minced clam meat, where definite response was observed at a distance of over six feet away.

Fig. 4. Movements of P. lewisi. A = cumulative movement (in feet) of 20 individuals in two aquaria; [D - in darkness; L - in light]. B = average hourly movement of 24 individuals in two aquaria; [D - drained; F - flooded with 14 inches of water]. C = average hourly movements of 15 individuals in a drained aquarium, flooded at the fourth hour.

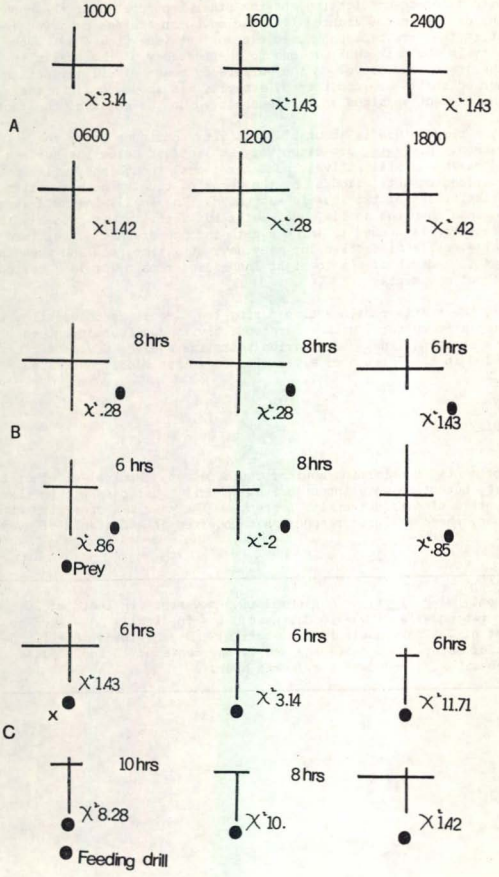


Fig. 5. Legend on facing page.

Analysis of movements

Prey location

The movements of drills within the clam bed were studied. To limit extraneous stimuli the observations were repeated in a six-foot diameter tank and analyzed statistically. Movements of snails through the substrate in search of food and other directional preferences and interreactions were studied in circular tanks six feet in diameter, containing three inches of gravel. Numbered snails were released at the centre and periodical observations on position plotted. The tank was divided into four quadrants and observations considered as quadrant scores, each quadrant having a frequency score and the sum of these frequencies being the total score for the given quadrant. To avoid mutual interferences, the maximum number of snails that could be placed in the tanks was 14. With such a number, the expected unbiased distribution will be 3.5.

$$\chi^2 = \sum_4 \frac{(obs)^2}{Exp_4} - n$$

The standard chi-square test was applied. At the 95% expectation value is 7.81. If movement is other than random, the chi-square value will be greater than the 95% expectancy.

The quadrant vectors with their χ^2 values are shown in Fig. 5.

Bias/random movement determinations

The tank containing the numbered snails was uniformly lighted in one half and the other half kept dark. Quadrant scores were made at six-hour intervals. Analysis demonstrated no bias in movements (see Fig. 5 A).

Prey location

A wire cage containing three butter and three soft-shell clams (Saxidomus giganteus and Mya arenaria) was buried near the wall of the experimental tank. Quadrant scores were noted at six- and eight-hour intervals.

Fig. 5. Circular distribution graphs of P. lewisi movements in circular aquaria. A = bias/random patterns of movement. B = prey location. Live clams buried at point ● . C = location of and taxis to, a feeding Polinices, situated at ● .

Though some of the P. lewisi approached within four inches of the buried clams, they did not attempt to reach them nor did they congregate around the cage. Analysis showed that movement still was random (see Fig. 5 B).

Location of a feeding drill

In the final experiment the clam-containing cage was removed and placed in another aquarium. A fasting drill was placed in the cage and allowed to commence to feed. The undisturbed cage with the feeding drill was returned to the experimental tank and the quadrant scores noted at six- to ten-hour intervals. Analysis showed that drills are highly sensitive to the feeding of another individual, probably a chemotaxis to the mucus exuded in great quantity by feeding P. lewisi (see Fig. 5 C).

Experiments using minced clam meats showed that although drills could detect this some distance through the water they were much more sensitive to the mucus of another feeding member of the species.

Reproduction

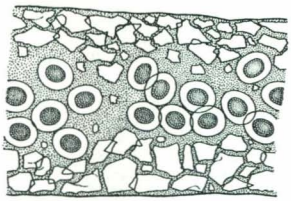
Reproductive cycle

Polinices lewisi is a long-lived prosobranch, probably attaining eleven to fourteen years for females. It is noteworthy that egg-collars which, according to Giglioli (1955), are molded on the shell curvature by the foot, are all approximately the same size. Examination of juvenile drills showed that sexual differentiation was completed and gametogenesis started at about 35 mm shell length but actual breeding did not take place until the individual was approximately 55 mm in shell length.

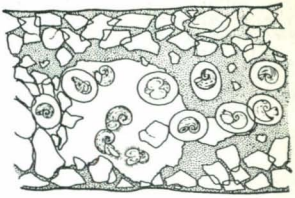
Egg collar

Giglioli (1955) gives a full description of naticid collar formation and structure. He states that in P. lewisi the egg capsules tend to occur in definite clusters, or nidi. This was not observed in the Departure Bay material. Individual egg capsules are randomly distributed in a relatively sand-free central jelly layer, bounded on either side by a thick jelly-bonded sand coat (Fig. 6 A). The eggs are small, about 250 μ in length. The intra-capsular jelly is a clear, viscid fluid.

Fig. 6. Early development of P. lewisi. A, B - vertical sections through egg collar. 1-7, stages of egg cleavage. 8, 9, early veligers. 10, separation of constituent egg cells.



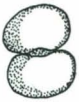
A



B

1

2



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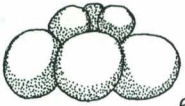

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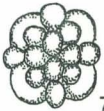

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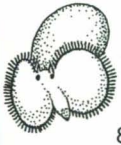


8

9

10

Fig. 6. Legend on facing page.

Collars are found from the mid-water mark to about ten fathoms, though one collar was dredged from 30 fathoms. They make their appearance in April, reach a maximum in May-June, then decline in number, becoming rare by the end of September. Collars have been observed as early as the beginning of February on the east coast of Moresby Island, Queen Charlotte Islands, and as late as November.

Gastrulation

The centrally embedded egg is a spheroid dark body which undergoes division to the four cell stage within two days of collar formation. A plate of small cells is formed on the apical surface, then division is rapid and irregular (Fig. 6, 1-7). The intracapsular veliger has a large, well-developed velum (Fig. 6, 8) but this is reduced and the foot area increased while the veliger is in the collar chamber (Fig. 6, 9). In most collars up to 10% of the eggs disintegrate into separate cells after the four cell stage, division continuing until a mass of separate cells is formed. It might be possible that these eggs serve as a food source for larvae released in the collar chamber (Fig. 6, 10).

Development

Considerable development takes place within the collar. When the veliger is fully developed within the egg capsule, the internal jelly of the collar breaks down, forming internal chambers bounded by the remaining sandy walls (Fig. 6 B). Here the veliger remains as long as ten days and when finally released by breakdown of the outer walls the foot is well developed. It is possible that the central jelly of the collar has a nutritive function.

Collars have been kept in the laboratory for more than eight days after collection before disintegrating. In nature and cold water tanks at least six weeks elapse from time of formation to the start of breakdown of the egg-collar.

In all cases, larvae were released by breakdown of the collar walls. As Polinices lewisi also lays its eggs subtidally, collars were kept submerged and examined at intervals. Breakdown was slower in this case, but disintegration could be accelerated by allowing water to reach room temperature. No analogy could be found with the method of release of deep water Naticidae which bore through the collar wall (Thorsen, 1935).

When the veligers are released in the internal space of the collar they possess about 3/4 of a shell whorl, the velum is small, the operculum fully developed and the foot is large. The larva is capable only of very weak swimming efforts. Experimentation demonstrated that at first the larva is not photo responsive but later becomes negatively phototropic. Total intra-capsular and intra-collar life is at least six weeks. The planktonic life is very short.

Nursery areas

Small P. lewisi are not generally found intertidally. Medcof and Thurber (1958) reported that they were unable to find juvenile P. heros. In Massachusetts, Turner (1951) could not locate juvenile P. duplicata and believed this was the result of rapid growth to mode size. Shuster (1951) suggested that there was an on-shore migration of young animals from a "nursery" area. The same situation existed in Departure Bay. The smallest P. lewisi found intertidally measured 25 mm from spire to lip, at least in its second and possibly third year.

A detailed search for possible environments of the young drills was undertaken. The problem was particularly perplexing as larvae were found leaving egg-collars on the flood tide but no trace of them could be found in repeated plankton tows made during and after release periods. Neither were the young found in the sand and mud surrounding the crumbling collars.

Samples of mud and sand from various beach levels were screened and examined for young. Results were negative. Dredge hauls were made in various depths; these too proved to contain no juvenile drills. On the theory that the flocculent surface layers of the bay bottom were being stirred up and not collected by the heavy naturalist dredge, a very light apparatus was constructed. In one location, in approximately 50 feet of water, a quantity of fine sand mixed with alga (Ulva sp.) was brought to the surface. The haul was washed through fine screens. The washings contained many small naticids in the 2 to 3 mm range.

Ulva and bottom layers were collected separately by means of SCUBA and examined. A host of small naticids were found browsing on the surface layers of the weed. Microscopic examination of the shell and radula confirmed that they were the juveniles of P. lewisi. Further sampling showed that though the Ulva sp. was widespread, the young drills were present only in a narrow bank parallel to shore in 35 to 40 feet of water below the low tide mark.

Ulva and young were placed in an aquarium and examined at regular intervals. At this stage the young were feeding on the diatoms on the surface of the weed. Later the weed itself was attacked. Growth is rapid, the animal doubling in size in two months. Five months later only two individuals were recovered from the aquarium. Although measuring only 5 mm and 6 mm they were carnivorous, testified by the great number of drilled minute bivalves found in the aquarium. Giglioli (1955) suggests that P. lewisi undergoes an indirect development consisting of a shore intracapsular period followed by the release of a pelagic veliger larva. This estimate was based on preserved material and made solely on the fact of the small size of the capsule and quantity of capsular jelly.

Stinson (1946) observed that the larva of P. triseriata was benthic on emergence and lacked a planktonic stage. P. heros were planktonic and bore a well-developed velum. Giglioli (1949) found the P. triseriata was "semi-planktonic". Further, Giglioli (1952) states there is no evidence to support the theory that larvae settle offshore in a "nursery" area and later move inshore. He gives no hint where the young are situated.

On release from the egg-collar the larva has a small, inadequate velum and swims weakly through the water between the substrate particles. Light response is negative. In less than 24 hours the velum is lost and the larvae settle. The dorsal portion of the propodium is prolonged to form two tentacles with pigmented "eye-spots" at their bases and pigmentation patches are also evident on the foot. The radula is well developed with individual denticles considerably longer than in the adult animal. Microscopic examination of gut contents showed that the young are at first browsers upon the diatoms epithytic on the Ulva. Later the young attack the weed itself. Transition to carnivorous behaviour takes place at the fifth or sixth month of life (5-6 mm shell length), probably precipitated by the rapid disappearance of the Ulva in late winter and early spring. when the young move to the sand substrate. Growth is rapid, the juveniles remaining in deeper waters until at least 3 cm in length, when they start moving shoreward.

When young P. lewisi are placed in a container of water that is allowed to reach room temperature, they leave the weed and bottom of the container, expand the foot and stick to the surface film of water. Shuster (1951) reports seeing great numbers of Polinices sp. behave this way just off a tidal flat. He suggests this is a means of distribution.

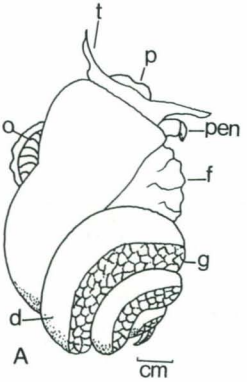
Anatomy

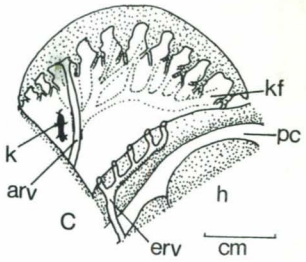
General

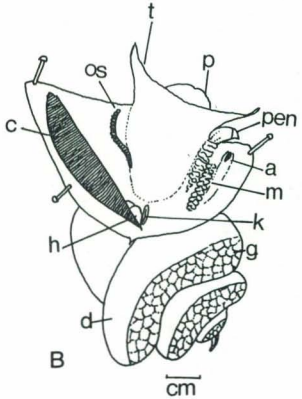
The general anatomy of Polinices lewisi is similar to other prosobranch molluscs with the exception of a modification of the circulatory and aquiferous systems connected with the specialized subterranean habitat.

The visceral hump is completely covered by the shell. The mantle cavity is large and richly supplied with cilia and mucous glands. Communication with the outside is accomplished by means of a metapodial fold which assumes the function of a siphon. The upper external covering of the mantle cavity is extremely muscular (Fig. 7 A) and the ctenidium and osphradium can only be examined by a lateral incision of the righthand portion of the mantle cavity roof.

Fig. 7. General dissections of P. lewisi. A = dorsal view of male animal removed from shell. B = mantle cavity opened by left marginal incision. C = kidney pouch opened by lateral incision. Afferent renal vein plastic injected. D = floor of mantle cavity removed to display buccal complex. a = anus; arv = afferent vein; bm = buccal mass; c = ctenidium; d = digestive gland; erv = efferent renal vein; f = foot; g = gonad; h = heart; k = kidney opening; kf = kidney folds; m = mucous gland; o = operculum; og = oesophageal gland; os = ospradium; p = proboscis; pen = penis; s = salivary gland; t = tentacles.







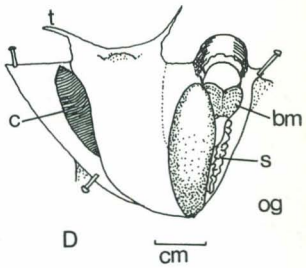


Fig. 7. Legend on facing page.

The ctenidium is very well developed and fills a great part of the mantle cavity. At the extreme posterior end is situated the kidney opening. The osphradium is a small elongated body lying on the left side and roof of the mantle cavity. The anus and sexual duct open on the anterior portion of the right side of the mantle cavity (see Fig. 7 B).

Below the floor of the mantle cavity and directly overlying the buccal mass is a large gland connecting with the posterior oesophagus (see Fig. 7 D & 8 D). The nature and function of this gland is unknown but it bears a remarkable similarity to the glandular pouch described by Fretter (1951) in Triphora perversa. Internally the glandular pouch is provided with many involutions bearing a variety of secretory cells. The supra-oesophageal gland is supplied by two large trunks of the anterior aorta.

In Polinices the kidney is a large cavity communicating directly with the pericardial cavity and opening on the posterior wall of the mantle cavity by a large elongated pore. The lamellae are elaborate and thrown into complex folds. The right portion of the kidney is much darker and larger than the left (see Fig. 7 C).

Kidney pigmentation is due to the presence of many dark granules in the cytoplasm of the kidney's epithelial cells and in the kidney cavity itself, probably representing products of catabolism. The renal epithelium consists of two cell types, one vacuolated and densely packed with dark granules and the other ciliated and free of inclusions. The left portion of the kidney contains much proteinaceous material of a crystalline nature, the function and origin of which is not known.

The kidney is not only concerned with the excretion of waste products but also with ionic regulation of the blood. In Polinices, which takes up large quantities of seawater into the podial complex, the blood separated by thin, permeable vessels, kidney osmoregulatory functions are important. Differences in concentration are probably maintained by filtration of fluid from the blood into the kidney lumen and subsequent differential ionic reabsorption.

A large penis is present in the male at all times but during the breeding season it is considerably enlarged and projects from the mantle cavity and is carried close to the right side of the head. The gonad in both sexes is large and lies on the digestive gland. In the male, tubules join on the columellar side of the visceral mass and fuse to form the testicular duct. The anterior end of the duct becomes widened and very convoluted and serves as a sperm storage area. The duct communicates via a small pore with the cavity of the kidney. The testicular duct now is thick walled and highly convoluted and forms a true vas deferens. Communication with exterior is via the penis. No trace of any openings to the mantle cavity could be detected (see Fig. 8 A).

Fig. 8. General dissections of P. lewisi. A = diagrammatic representation of male reproductive system. B = diagrammatic representation of female reproductive system. cg = capsule gland; dg = digestive gland; ko = kidney opening; o = ovary; od = oviduct; p = penis; t = testis; vd = vas deferens.

C = sagittal section of buccal mass. j = jaw; m = mouth; o = oesophagus; r = radula; rc = radular cartilage; rs = radular sheath.

D = sagittal section of suprapharyngeal gland. ant = anterior; d = duct; o = oesophagus; sg = suprapharyngeal gland.

Inset - blood supply of suprapharyngeal gland. aa = anterior aorta.

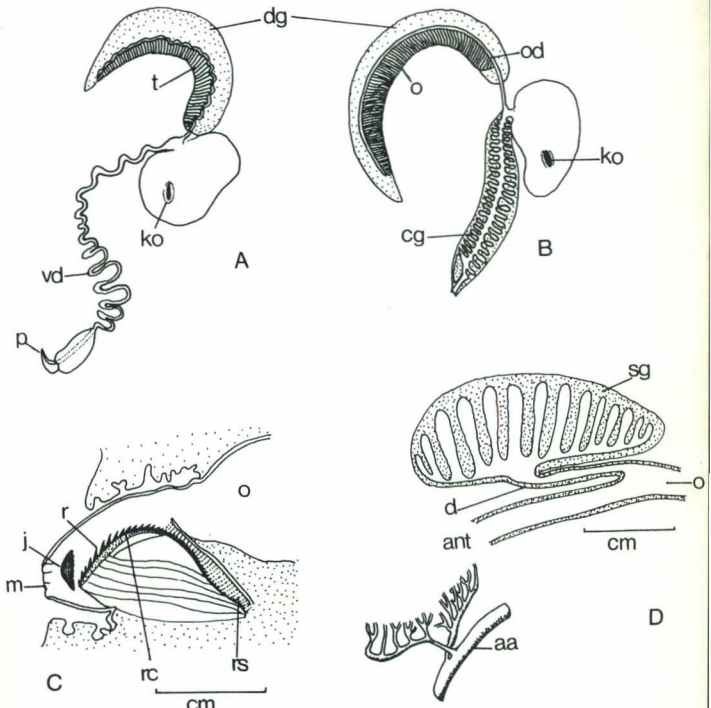


Fig. 8. Legend on facing page.

The basic structure in the female is similar but the post kidney ovarian duct is very enlarged and lined with many glandular structures. These produce the capsule membranes and the internal jelly layers of the egg-collar. There is no spermary structure such as a bursa copulatrix but there must be some mechanism of sperm storage as fertile eggs have been laid in aquaria up to six weeks after segregation of individual females (Fig. 8 B).

Feeding

The mouth is situated at the apex of the protrusible proboscis (see Fig. 8 C). When the proboscis is withdrawn, the accessory boring organ lies within a fold of the rhynchodaeum. When the proboscis is protruded the ABO lies on the anterior ventral surface of the proboscis.

The radula varies in length from a few millimetres to 40 mm by 3 mm wide in large individuals. The anterior end of the radula is situated within the buccal capsule between the two maxillae. The basal membrane of the radula diverges into two lateral odontophoral plates which serve as point of muscle attachment. Posteriorly, the radula lies in a sheath, penetrating the pharynx and buccal capsule and entering the foot cavity at the pharyngo-oesophageal commissure. The dentition is taenioglossan, the radula consisting of seven longitudinal rows of posteriorly directed teeth, the formula being: R + 2 + 1. The rachidian row consists of large teeth firmly embedded in the basal membrane. The two marginal rows are smaller and also firmly embedded. These three central rows are considered "rigid". The lateral row of teeth consists of a long claw-like crown with a small, loosely embedded root.

Circulatory system

The heart in P. lewisi is very large and lies in the pericardial cavity in the left basal part of the visceral mass. The auricle is a thin-walled chamber and is connected to the much more muscular ventricle. The aortic bulb is about twice as long as the heart and is a major organ of circulation, the walls being very muscularized and provided with several bundles of trabeculae. The aortic bulb merges posteriorly and anteriorly with the posterior and anterior aortas. The posterior portions supply the reproductive and general visceral areas. Anteriorly, the aorta makes a right-angled turn and plunges vertically, giving off a number of branches. The first two and largest are the arteries supplying the supra-oesophageal gland. Next a smaller vessel runs to the radular pouch; the last major vessel supplies the buccal mass. The anterior aorta then enters the central foot region; here it divides laterally into two portions which again divide antero-posteriorly and ramify throughout the entire tissues of the foot (see Fig. 9, 1).

Fig. 9. Circulation and aquiferous systems of P. lewisi. 1 - Diagrammatic representation of arterial system; 2 - Diagrammatic representation of venous system; 3 - Aquiferous sinus system; 4 - Arterial "capillaries"; 5 - Venous sinuses. 6 - External view of heart seen from left side. a = auricle; aa = anterior aorta; ab = aortic bulb; arv = afferent renal vessels; ba = buccal artery; ca = columellar artery; cas = cephalic aquiferous sinus; cv = cephalopedal vein; ev = efferent brachial vessel; erv = efferent renal vessels; mas = metapodial aquiferous sinus; oa = oesophageal artery; pa = pedal artery; pas = propodial aquiferous sinus; poa = posterior aorta; ps = pedal sinus; sa = suprapharyngeal gland artery; v = ventricle; vv = visceral vein.

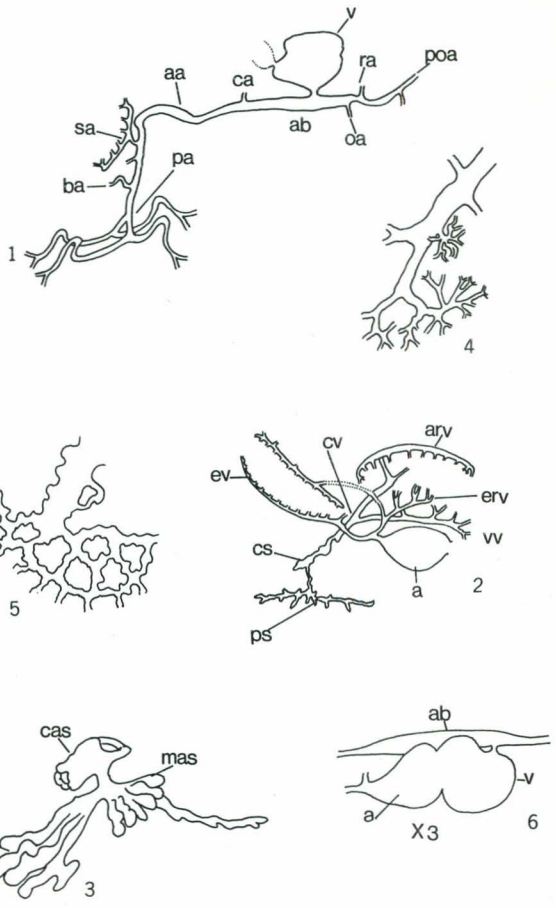


Fig. 9. Legend on facing page.

The venous return system is modified in its anterior and pedal portions. Posteriorly and in the visceral hump, blood is collected into haemal spaces and is returned via the visceral vein, as in the usual prosobranch system. The haemal sinus of the foot is reduced to a narrow, convoluted tube connected to the very small cephalic sinus. Here a muscular septum separates the cephalopedal sinus from the rest of the body. The septum bears a number of narrow apertures through which the blood flows. Muscular contraction of the septum prevents hydrostatic pressures of the foot being transmitted to the visceral area. The cephalic sinus is joined to the afferent renal vein. Venous blood returns to the auricle of the heart by two paths. The efferent renal vein picks up blood from the kidney and the efferent ctenidal vein brings blood from the ctenidium (see Fig. 9, 2).

The major modifications of the vascular system in Polinices lewisi are those vessels supplying the pedal complex. Here every nerve and muscle fibre is ensheathed in a blood-containing membrane. The pedal arteries anastomose until what can only be described as a capillary bed results (see Fig. 9, 4). The venous return system is comparable, consisting of a plexus of thin-walled vessels forming small haemal sinuses (see Fig. 9, 5).

Aquiferous system

Speculation has surrounded the mechanics of foot dilation in the Naticidae. Early theories which held that expansion was due to the uptake of water from the surrounding medium were discarded when Carriere (1882) showed that for many species foot dilation and turgescence was accomplished by the influx of large quantities of blood and hypothesized that this was the situation in all molluscs. Schiemenz (1884) described the aquiferous system in the Naticidae and stated that turgescence was the result of water uptake through small marginal slits in the foot. Because such a system is unique to the naticids, Schiemenz' work was largely ignored. Morris (1950) demonstrated that the Australian naticid Uber strangei (Reeve) takes in water for foot expansion. Ziegelmeier (1958) in his description of the pedal movements of Polinices josephinus Risso noted the exudation of water on the contraction of the foot.

Of all naticids, P. lewisi possesses the largest foot, a pale grey oedematous mass up to four times the total shell volume. On irritation, the foot contracts, exuding quantities of fluid and can be completely withdrawn into the shell. This exudable water makes up approximately 23% of the total weight of the expanded snail. Table III lists the expanded and contracted weights of twenty individuals.

Table III. Expanded and contracted weights (in grams) of 20 Polinices lewisi

	Expanded	Contracted	Difference
1	279	180	99
2	147	69	78
3	210	120	90
4	301	160	141
5	225	120	105
6	310	200	110
7	340	167	173
8	640	322	318
9	201	104	97
10	453	231	222
11	150	93	57
12	343	185	158
13	103	81	22
14	290	175	115
15	410	230	180
16	91	67	24
17	80	53	27
18	120	95	25
19	253	147	106
20	298	186	112
$\bar{X}$	262	149	113

It has been suggested by some workers that the fluid lost is blood rather than water, due to the rupture of blood sinuses and vessels, and that full withdrawal of the foot is irreversible and causes the death of the individual. Microscopic examination of the precipitate of centrifuged exudate failed to reveal any appreciable numbers of amoebocytes as would be expected if it were blood. In physical respects the characteristics of the exudant are similar to the surrounding medium in which the snail has expanded.

Repeated experiments with various individuals have clearly demonstrated the expansion/contraction cycle to be repeatable and to have no deleterious effect upon the snail. Table IV lists the weights of two individual snails subjected to five cycles of contraction and expansion.

Table IV. Weight of two P. lewisi during five contractions.

No. 1		No. 2	
Expanded	Contracted	Expanded	Contracted
240	170	95	70
210	160	100	73
200	173	91	74
230	179	103	80
205	180	110	71
$\bar{X}$ 217	172	$\bar{X}$ 100	74

Morphology

The large, spreading foot, metapodial folds covering the shell and the wedge-shaped propodium are adaptations to existence and ability to progress through mud and gravel. The external morphology of the Polinices foot is well known and need not be repeated.

Anteriorly the pedal aquiferous sinus is a large chamber provided with a meshwork of muscular cords (Fig. 10 A). Posteriorly, it flattens out and is connected to the exterior via 40-80 ostia (Fig. 10 A, O) situated on the margin

Fig. 10. Aquiferous system of Polinices lewisi.

A. Sagittal section of entire podium.

B. Corrosion model, made by injection of liquid plastic into aquiferous system.

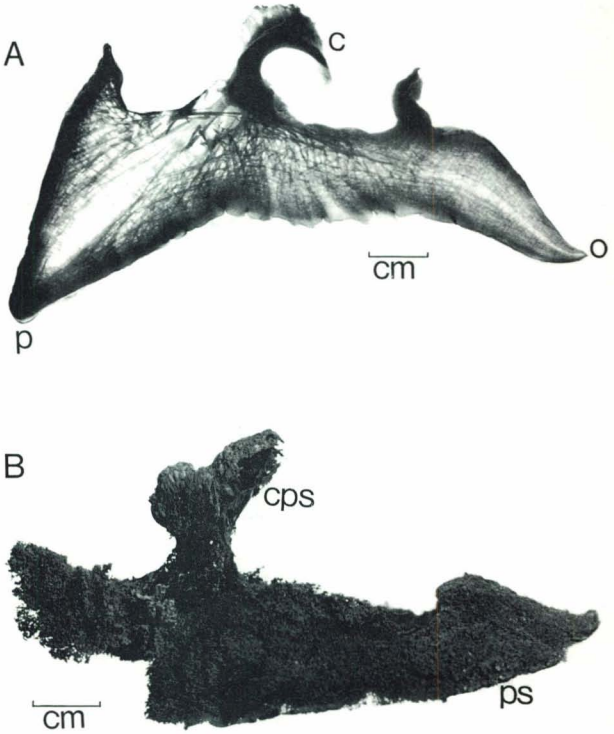


Fig. 10. Legend on facing page.

of the postpodium. When liquid plastic is injected in the pedal aquiferous sinus, the entire pedal and circumpharyngeal regions are impregnated but no blood vessels or body haemal sinuses are filled (Fig. 10 B). The aquiferous system of P. lewisi is separate from and unconnected with the blood circulatory system.

The largest aquiferous sinus is situated in the anterior portion of the propodium and consists of eight interconnected lacunae which branch out to fill the entire podial and metapodial complex. A secondary and smaller sinus surrounds the pharynx and proboscis (Fig. 10 B, cps). Posteriorly, the eight lacunae fuse and form a broad thin chamber extending to the edge of the postpodium and ostial margin.

Located on the edge of the postpodium are lateral slits approximately 40 μ in width, the marginal ostia. The edge of the postpodial sinus is supplied with many vertical and lateral muscle bundles which are capable of constriction, closing off the ostia in the manner of a sphincter (Fig. 11 A, B).

On contraction the propodium is rapidly detumesced and withdrawn into the shell, the volume of water being transferred to the postpodium which then contracts, ejecting water from the ostia with considerable force.

The influx of 'raw' seawater into the tissues of the snail poses problems. It is obvious the admixture of blood and seawater cannot be tolerated, neither can such a large mass consisting of a complex meshwork of muscular and neural fibres (Fig. 11 D) be entirely unsupplied by blood vessels. The solution has been the ensheathing of all muscular and neural structures with a collagen-reaction type of connective tissue, protecting all tissues from direct contact with the seawater in the aquiferous sinuses (Fig. 11 C).

Fig. 11. Aquiferous and haemal systems of Polinices lewisi.

A. Sagittal section of edge of postpodium, showing ostium. Harris's haematoxylin-eosin × 90.

B. Section of ostium. Harris's haematoxylin-eosin × 200.

C. Transverse section of relaxed muscle bundle, showing haemal sheaths and blood space (b). Masson's tri-chrome × 430.

D. Section of foot showing muscle bundles and aquiferous sinus (a). Masson's tri-chrome × 90.

E. Section of pedal blood sinus, Heidenhain's haematoxylin-eosin × 200.

F. Plastic model of fine arteries from propodium, tissues cleared in potassium hydroxide × 50.

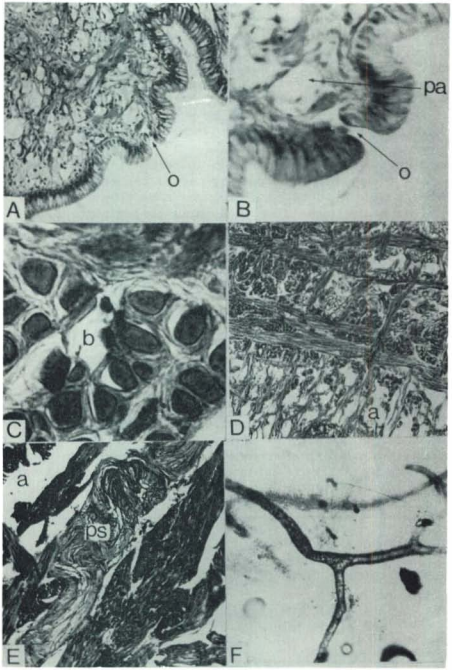


Fig. 11. Legend on facing page.

The arterial supply to the foot is in its posterior portions, homologous with other prosobranchs. Anteriorly the aorta passes below the radular pouch and divides into cephalic and pedal branches. After plunging into the foot the pedal aorta divides into posterior and anterior vessels which further divide and branch out to embrace all parts of the podial and metapodial complexes (Fig. 11 F). The capillary bed is continuous with the perimuscular sheaths, so that muscles and neural structures are bathed in blood and isolated from the seawater in the aquiferous sinuses. The sheaths are connected to isolated lacunae, the remains of the pedal venous sinus (Fig. 11 E, ps) which join with the cephalic sinus. From the cephalic sinus springs the cephalic vein, running to the kidney through a muscular septum placed anteriorly to the cephalic sinus. This muscular septum acts as a valve isolating the body organs from the hydrostatic pressure of the foot.

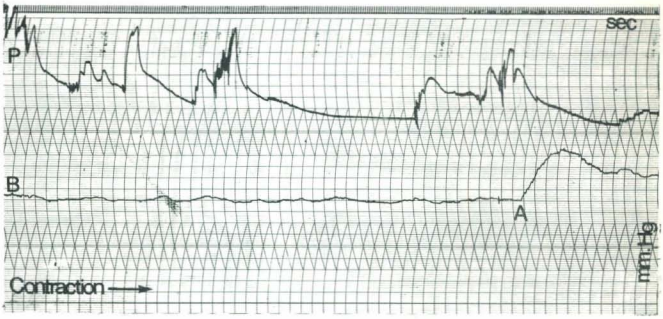
The major portion of the expansion and oedematous condition of the foot is due to the uptake of surrounding water by way of the postpodial ostia. Blood pressure within the muscle sheaths probably does have some effect, especially in early phases of expansion. A contracted snail placed on damp weed will expand to a small degree, the edge of the postpodium being extended and capable of movement. This is entirely due to blood pressure in the muscular sheaths. If, at this stage the edges of the postpodium are sealed with haemostats, the snail is unable to expand even if placed in water.

When a contracted snail is placed in water the postpodium is first extended and engorged with water, a sudden series of contractions expands the propodium and more water is now taken up by the postpodium. The water take-up is due to the relaxation of the muscles of the foot coupled with the tumescence of the perimuscular sheaths, which cause a lengthening of all muscle bundles and enlargement of the aquiferous sinuses. Contraction is the opposite action, the detumescence of the blood-containing sheaths and contraction of the muscle fibres. Figure 12 (upper) is a pressure graph of conditions in the propodium (P) and in the pericardial cavity (B). Pressure fluctuations are evident in the contracting foot, while the visceral pressure is uniform except for a rise on closure of the operculum (A on chart). This pressure differential is attributable to the muscular septum pierced by the cephalic vein.

Fig. 12. Pressure graphs of contracting Polinices lewisi.

Upper: P. pressure in propodium. B. body pressure. A. Closure of operculum.

Lower: Pr. pressure in propodium. Po. pressure in postpodium. O. ejection of water from ostia.



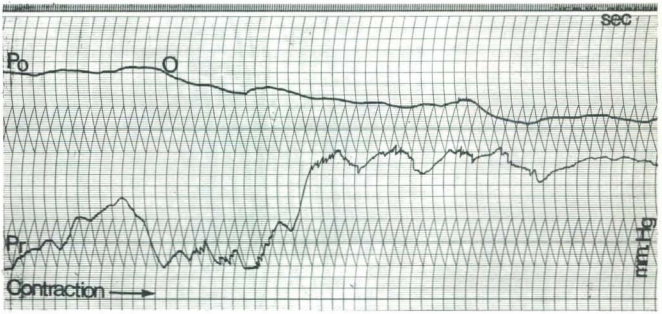


Fig. 12. Legend on facing page.

A great degree of differential pressure control can be exercised by P. lewisi. This hydrostatic system is of importance for movement through the substrate. While the snail is provided with a coating of cilia on all exposed surfaces, these are not used for progression while the snail is buried. The snail spends most of the time partially or entirely buried in sand, mud or gravel. Movement is accomplished by the thrusting forward of the propodium, then its dilation with water to push upwards and away the substrate, pulling the body and shell of the snail along. In the aquarium boulders up to four pounds have been moved by travelling snails. The mechanics of movement are different from that displayed by many bivalves, where the distal end of the projected foot is expanded to form an anchor and the body pulled along by the contraction of the retractor muscles of the extended foot. Figure 12 (lower) demonstrates the pressure differential between the propodium and postpodium. Rapid contractions and pressure rises are apparent in the anterior portion, while there is a steady pressure rise in the postpodium, water starting to pour out of the ostia ('O' on chart).

Accessory boring organ

Much debate has surrounded the way naticids perforate the shells of their prey. Reaumur (1711) suggested a chemical means; however, Schiemenz (1891) was the first to offer concrete evidence. He argued that the proboscis was not motile enough, nor the radular teeth hard enough, to produce the characteristic cylindrical hole. His theory was supported by the discovery of a pad-shaped papilla attached to the ventral side of the distal tip of the proboscis. This he identified as a 'boring organ', mainly on his assertion that secretions from this organ reddened litmus. These findings were upheld by other workers. Ankel (1937) showed that glands removed from Natica etched the surface of a Trivia. Repeating the experiment at a later date, Ankel (1938) did not obtain similar results and postulated the presence of an enzyme 'calcase' that destroyed the prey's shell. Giglioli (1949) supported this theory and Hirsch (1915) demonstrated that the diameter of the 'boring organ' and the diameter of the produced hole were identical and assumed that one was made by the other.

Fischer (1922) found the 'boring organ' of Natica to be composed mainly of muscle and connective tissue, lacking obvious gland cells. Coupled with the fact that he could get no effect on litmus, he concluded that the 'boring organ' could have no direct function with penetration of the prey. Loffens (1926) upheld this view. The most detailed description of naticid boring is given by Ziegelmeier (1954), who is of the opinion that penetration is by mechanical means alone. Ziegelmeier overcame the considerable difficulties inherent in direct observation of the boring process by Natica nitida and states that never once did the 'boring organ' enter the hole made by the rasping of the radula, though during resting periods the proboscis was removed from the hole and the 'boring organ' brought close to the site. He concluded that it might well be a tactile organ used to provide information pertaining to penetration as this action is normally carried out while the drill is buried in the substrate.

Carriker (1959) in a series of experiments and observations has shown that an alternation of chemical and mechanical means is used by muricids to effect penetration. Considering the similarity of the structure of the organ on the naticid proboscis and the muricid organ (which lies in the mid-anterior part of the foot), it is reasonable to speculate that the drilling process in the two groups of prosobranchs is fundamentally similar.

Unlike Ziegelmeier, Carriker states that when in use the accessory boring organ is distended by haemostatic pressure and is in close contact with the bottom of the hole. Further, Carriker demonstrated that the radular teeth alone are poor shell removers, as little shell is removed at the close of a rasping period. The boring organ is then re-introduced into the hole and alternate periods of chemical action and rasping maintained until perforation is completed.

The nature of the secretion of the boring organ is as yet unidentified. Experiments by Ankel (1938), Fischer (1922), and Hirsch (1915), in which fluids from the boring organ and unfinished perforations were tested with pH indicators, and homogenates of the organ were titrated with NaOH, indicated a neutral reaction. The fact that acids are not involved and the suggestion by Hirsch (1915) that a calcase is present has nurtured the hypothesis that the boring organ secretes a conchiolinase acting upon the matrix of the shell, or a calcase which would dissolve the mineral component. Since mechanical rasping is also involved, chemical secretions need not wholly destroy the shell but only render it sufficiently soft fot the radula removal.

The reporting of drilled egg capsules of the marine snail Sipho by Thorsen (1935) and the drilled egg cases of rays by Jensen (1951) showed that naticids could penetrate noncalcareous material. Jensen demonstrated that the cases were acid resistant and the edges of the holes showed minute scratches characteristic of radular action. Turner (1953) determined the ability of P. duplicata to perforate shells of Mya arenaria which had first been coated with histological paraffin wax or with plaster of paris (calcium sulphate). In either case, the drills had no difficulty boring the usual hole.

The secretory caps of a number of ABOs of Polinices were removed and tested for pH; this value was over 8.9. This high reading certainly hypothesizes the presence of a proteolytic-chelating substance such as is believed to be responsible for the formation of dental caries. Further extracts were made to investigate the possible formation of mono- and disaccharides from the hydrolysis products from the organic constituents of the prey's organic shell matrix. The measure of such hydrolytic activity was interpreted from the decrease in turbidity of a standardized suspension of colloidal chitin and conchiolin (both containing polysaccharides), measured by an electric turbidity meter. Experiments demonstrated a slight decrease in turbidity. No direct evidence could be found for the production of lower sugars. The decomposition of chitin has been investigated by Berger and Reynolds (1958) using a chitinase from Streptanyces griseus. This enzyme hydrolysies chitin to N-acetylglucosamine and N, N-diacetyl chitobiose without forming saccharides.

A brief qualitative experiment was undertaken using periostracum from the razor clam (Siliqua patula) to demonstrate the possible breakdown of the organic constituent of shell by ABO extract. A small piece of periostracum about 15 μ in thickness was placed in the manner of a dialysis membrane on a tube containing ABO extract and immersed in normal saline. The periostracum disintegrated in approximately eight hours at 30° C, demonstrating without doubt the ability of ABO products to lysolize the organic matrix and periostracum of shell.

In P. lewisi, the ABO consists of a papilla situated on the distal lower end of the proboscis. The surface is depressed centrally and covered with a plicated surface with many small apertures.

Internally the body consists of connective and muscular tissue and a large aquiferous sinus (see Fig. 13 C). The ABO is supplied with a separate artery from the buccal artery and is richly enervated. The peripheral region contains many surface and deeper mucous cells which are similar to the mantle mucous cells (see Fig. 13 B).

The central area is highly specialized and is supplied with cells differing from all others found in Polinices. In the expanded ABO these are long, narrow bodies (25 × 200 μ) with a centrally placed nucleus and many cytoplasmic inclusions. The upper surfaces are fused into a continuous plate, pierced at intervals. Ziegelmeier (1954) interpreted this surface as being cuticular. Freter and Graham (1962) interpreted it as a rodlet border (see Fig. 13 A). Ziegelmeier felt that no secretions of the underlying tall glandular cells could escape through the "cuticle". This is not the case, as many microscopic sections transversed secretory openings. Further research is being undertaken on the detailed histology of this structure.

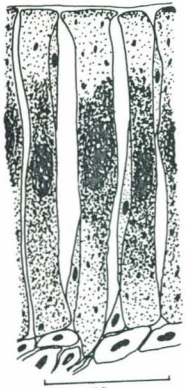
It is idle to speculate that the ABO is merely an adhesive papilla, especially because of the similarity it bears to the structure present in the mid-foot region of the muricidae.

Fig. 13. ABO of Polinices lewisi.

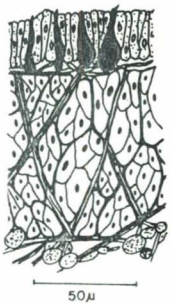
A = high power detail of central secretory cells.

B = high power detail of mucus-producing cells on periphery of ABO.

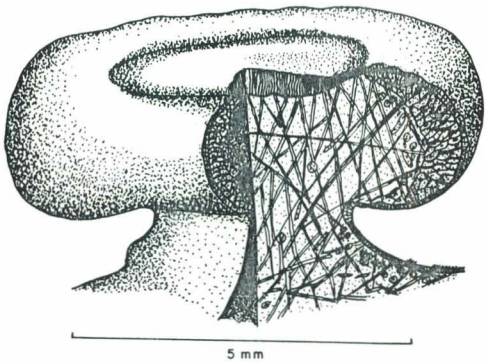
C = ABO with segment removed to show internal structure and central secretory cells.



A



B



C

Fig. 13. Legend on facing page.

Summary

Research for the past five years on the histology, predation and population of the naticid clam drill Polinices lewisi (Gould) yielded the following information:

1. Estimates of population by indirect and direct methods on a beach in Departure Bay gave a density of between .85 and 4 P. lewisi to the square meter.

2. Size frequency showed a unimodal distribution with distinct year classes (size classes) present.

3. Sexual dimorphism is present, males growing at a slower rate than females.

4. Adult P. lewisi consume approximately one clam each four days.

5. Movements are random and nondirectional. Clams are not sensed from any distance.

6. Drills are very sensitive to other feeding drills and will locate and move towards a feeding drill.

7. Drills are equally active on the surface or buried. Maximum activity takes place immediately after flood tide.

8. While P. lewisi is sexually differentiated at 20 mm, reproduction does not take place until the animal is at least 55 mm.

9. Egg-collars break down internally and retain the veligers for several days prior to freeing them.

10. Drills breed and lay their eggs on the beach but the veligers settle on sublittoral weed such as Ulva. At first the young are browsers but become carnivorous with the disappearance of the weed.

11. Profound modifications have taken place with the adaptation to a burrowing habit. A special aquiferous sinus system has been developed to expand the enormous foot.

12. To prevent contact with seawater all muscles and nerves in the foot are ensheathed in a collagenous material.

13. The accessory boring organ secretes an enzyme capable of destroying Siliqua periostracum.

Acknowledgements

I wish to express my gratitude to Dr. D. B. Quayle for all his assistance and for suggesting the problem. Grateful thanks are extended to Mrs. J. Bain for her painstaking typing of the manuscript and to Mr. C. Morley for preparation of the photographic plates.

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