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Title

Further Observations on the Biology of Whelks of the Family Naticidae including Polinices.

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Author

M. E. C. Giglioli

(Revised by J. C. Medcof)

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TABLE OF CONTENT

Page

Introduction.

Figures 75 to 107 on file at St. Andrews

INTRODUCTION

With the author's return to the Atlantic Biological Station, St. Andrews, N.B., during the 1950 summer season, it was felt that this year's report on biological observations on the whelks take the form of an appendix to the writer's 1949 report. The essential nature of the 1950 work was that of "filling in" gaps in our knowledge of these animals accumulated since the clam-drill study began in 1946. This accounts for the heterogeneous nature of the subjects treated in this report which would not ordinarily be grouped under one title and their arrangement as separate papers each with its own set of bibliographic reference. In spite of this splitting up of the report pagination has been kept sequential throughout to assist the reader in ready reference.

It is proposed to present a separate report later dealing with population studies and efforts made at population control. This would have a status equal to that of the 1949 report and its 1950 appendix combined.

I. The Radulae of Polinices heros Say (1822), Polinices duplicata Say (1822) and Polinices triseriata Say (1826) and the Possible Taxonomic Value of Radular Dentition.

Introduction

The radulae of Polinices heros and Polinices triseriata have been discussed already (Giglioli, 1949) insofar as their functional adaptations to the feeding habits of these gastropods are concerned. The objects of this paper are:

(1) The presentation of a more detailed description of this structure and the functions of its several parts in the same two Canadian species and in P. duplicata as represented by Massachusetts collections and

(2) The assessment of the value of dentition patterns in a taxonomic study of the three species.

The Radula

In all specimens of these species that have been examined, the radula presents the same basic structure. It consists of a long "toothed" ribbon varying in length from a few millimeters in small specimens to 20 millimeters in large specimens of Polinices heros. It has never been found to exceed two millimeters in width. Anteriorly, within the buccal capsule of the pleurembolic proboscis, the radula expands into two lateral wing-like Odontophoral plates which serve as points for muscle insertion and form the articulation surface on which the radula oscillates during feeding.

The backward extension of the ribbon lies in a sheath which passes through the buccal cavity and pharynx to emerge into the "foot cavity" at the pharyngo-eosophageal junction. This, ensheathed extra-pharyngeal portion of the radula can move forward or backward thus allowing for intrusion and extrusion of the proboscis.

The radular ribbon comprises a "chitinoid" basement membrane (Ankel 1938) which supports seven longitudinal rows of backwardly directed teeth (Fig. 75). This membrane is flexible and during feeding acts as a rasping and tearing instrument and as a "conveyer belt", owing to its flexibility, transporting food backwards to the pharynx.

The teeth lining this ribbon can be divided morphologically into two types which occur in separate longitudinal rows: the rigid which compose the median and sub-median rows (3 in all), and the pseudo-articulated which compose the sub-lateral and lateral rows (4 in all).

Structure of the Teeth

Each tooth is composed of two parts, the "root" or "basal plate" and the "crown".

(a) The Root or Basal Plate -- this is a horizontal plate imbedded in the basement membrane.

(b) The Crown -- is an anterior prolongation of the root's leading edge which, depending on the tooth, may stand perpendicular to the basal plate and radular membrane, or may rest parallel and flat on the latter's surface. The crown is subject to further morphological differentiation in the median and sub-median teeth, (vide infra).

This basic tooth structure has two modifications which differ in their relationships to the root of the basement membrane.

(1) The rigid tooth -- (Fig. 75) is typical of the median and sub-median rows, characterized in both by a large, flat basal plate firmly imbedded in the membrane. These teeth show the same basic structure but differ in detail.

(a) The median tooth -- the crown is formed by the fusion of three conical extensions of the basal plate and thus divisible into:

(i) "basum" formed by the fused bases of the cones.

(ii) "conicles" or "dentary cones" formed by the free apices of the cones. Typically the median conicle is the most prominent. Proportions between the conicles vary within the individual radula and between the species.

The root or basal plate of the median tooth is wide, symmetrical with its anterior leading margin bent in the vertical plane to form the forwardly-directed crown, and its posterior edge prolonged symmetrically into two latero-posterior lobes.

(b) The sub-median tooth -- this rigid structure is composed by a large and long basal plate bending mediad to form a small, spur-like crown this is simple and undifferentiated into conicles.

(2) The pseudo-articulated tooth -- characteristic of the lateral and sub-lateral longitudinal rows, shows less differentiation than the rigid tooth (Fig. 75).

It has a small disc-like root and a large recurved claw-like crown, showing little differentiation between these component parts.

(a) The root is poorly imbedded in the radular membrane and thus possesses a fair degree of articulation.

(b) The crown is long and claw-like, forming a continuous extension of the basal plate and lying, in the same plane. Owing to its length and direction it passes from the lateral field of the radula to the region of the median tooth.

Unlike the median and sub-median teeth and because of their "articulated" nature, the pseudo-articulated teeth are not erect when at rest, but lie horizontally across the basement membrane.

This type of tooth is typical for both the lateral and sub-lateral longitudinal rows of teeth, there being no structural differences between these as there was between median and sub-median.

Arrangement and Structural Relationships of Radular Teeth (See Figure 75).

(1) The unpaired median row of teeth -- The symmetrical basal plate articulates latero-anteriorly with the root of the sub-median tooth.

(2) The paired sub-median rows of teeth -- The elongated basal plate extends into the lateral fields of the radular ribbon, to articulate termino-anteriorly with the sub-lateral tooth and termino-laterally with the root of the laterals. This articulation is loose and does not lend greatly to the rigidity of the ribbon, as is the case with the articulation between the median and sub-median teeth.

(3) The paired sub-lateral rows of teeth -- These are in the marginal field of the radula, articulating caudad with the basal plate of the sub-median tooth, and termino-ectad with the root of the lateral tooth. Thus they are located anteriorly and between the sub-median and lateral teeth.

(4) The paired lateral rows of teeth -- These form the ectad row of teeth along the margins of the radular membrane, articulating with the sub-median and sub-lateral roots.

Functional Relationships of Teeth

In the Naticidae, feeding necessitates preliminary perforation of the shell of the molluscan prey. This operation is executed by chemical solution (Ankel 1938) and not, as popularly believed, through mechanical abrasion by the radular teeth.

After penetration, during the actual feeding the radula forms an oscillating rasp biting into the meats during its backsweep. This biting and tearing action is further assisted in the Naticidae by a pair of horny maxillae situated lateral to the odontophoral plates.

On the backsweep, with all teeth erect, the flattened radular membrane is opposed to the meats, thus exercising its maximum rasping surface. As the radula moves caudad, and away from the prey, the basement membrane bends to form a trough. In this action the rigid median and sub-median teeth are removed from the feeding "face" although tending to pull it into the mouth while the laterals and sub-laterals are forced into the meats of the prey, thus changing the feeding mechanism from a rasping to a pulling tearing action.

It would seem that the structural arrangement of the teeth is well adapted functionally to this method of feeding, giving maximal efficiency, as an excavating organ and as a conveyer of food from the site of feeding to the eosophagus.

Taxonomic Value of Dentition

There has been much argument among taxonomists as to the propriety of considering Polinices heros and Polinices triseriata as separate species; but most now follow Johnston (1934) and accept these as species senso proprio. However, recognizing the lack of ready means of specific identification, the author felt that a study of their dentition in comparison with that of Polinices duplicata (of more southern distribution) might add to our grounds for speciation and afford that much needed basis for quick identification of dubious specimens.

The technique adopted for studying the radula involved the removal of the proboscis and digesting this in concentrated KOH or NaOH. This allows for easy removal of the radula which may be observed in situ or mounted in Canada balsam. When balsam mounts are prepared the radulae should be thoroughly washed and dehydrated to avoid clouding of the mounts. For general study the unmounted radulae are preferable. In mounted specimens the coverslip compresses the teeth and reduces definition.

There is no significant variation in the structure of the sub-median, sub-lateral and lateral teeth of these three species. The clearly visible crowns of the median teeth exhibit the only variance of taxonomic significance.

The "crown" of the median tooth shows a degree of variation even within the individual radula. This may be caused by:

(1) Actual variation of structure at time of development.

(2) Differential wear and tear on the dentary cones in different parts of the radula.

(3) The angle of observation. Proportions are altered, depending on the angle at which the erect tooth is observed. These descriptions and diagrams have been obtained by viewing the crown with the long axes of its conicles lying in a horizontal plane.

Notwithstanding this intra-radular variation, there are differences in the shapes and arrangements of the conicles composing the crown that are characteristic for each species. The diagnostic features are found in the relative proportions of the dentary conicles, to one another, and to their fused "basum". Thus the crown, exclusive of the root, supplies the basis for differentiation when "typical" median teeth are examined.

(a) Polinices heros. (Fig. 76 I). The crown of the median tooth is composed of a broad, deep basum terminating apically in three short dentary conicles, widely separated by shallow, gently curved inter-conicular sulci. Of the three, the median conicle is slightly the largest.

The conicles are widely separated and the sulci often possesses small grooves passing from the inner edges of the conicles into the basum.

(b) Polinices duplicata. (Fig. 76 II). The basum is greatly reduced and the conicles have deep, narrow sulci between them. Contrasted with Polinices heros the conicles are longer and thinner and the difference in the length of the median and lateral conicles is greater.

(c) Polinices triseriata. (Fig. 76 III). The basum is conspicuous by being thickened and crescentic. The three conicles are distinct but the median is greatly enlarged.

Thus, within the three species there are progressive differences in the order indicated above in the relative development and proportion of the dentary conicles. This pattern grades from the widely-spaced sub-equal denticles of Polinices heros, through the long and closely-grouped conicles of Polinices duplicata, which show some reduction of the laterals, to the compact grouping of these in Polinices triseriata where the large and prominent median cone is flanked by the greatly reduced laterals.

Irrespective of structural variations of the median tooth within individual radulae, a basic pattern, typical of each species, can be demonstrated.

It is felt that like otoliths radular dentition can be used by a competent observer as a reliable diagnostic tool for species separation. However, as a taxonomic characteristic for common usage by the uninitiated, with little or no comparative material, it is not likely to be helpful.

Further Implications on the Relationship of these Species.

On the basis of this structure, and this alone, there appears to be an interesting natural relationship between these species which has been overlooked in the compilation of artificial keys based on external morphology.

Say described Polinices heros and Polinices duplicata in 1822, grouping under the former what he recognized in 1826 to be Polinices triseriata. Ever since 1826 conchiologists have debated the validity of this separation. However, recent investigation at this station of shell structure, coloration, and the egg collars of these whelks leaves no doubt as to the distinctness of these two species.

The similarities in morphology of the soft parts (visceral hump)(Giglioli 1949), in shell structure and in radular dentition, suggest a very close relationship within the genus. However, it is interesting to note that the results of the study of radular dentition implies, contrary to previous opinion, closer ties between P. heros and P. duplicata than between P. heros and P. triseriata.

Figure 75.

Figure 75. Disposition of teeth on a section of the radular membrane, showing one of the lateral teeth bent ectad.

Figure 76 Figure 77

Figure 76. Variations in the crown (basum and conicles) of the median tooth in

I Polinices heros
II Polinices duplicata
III Polinices triseriata

Figure 77. Diagramatic comparison of the crowns of three species of Polinices.

From this and previous studies (Giglioli 1949) it is clear that systematic differentiation, for these three species of very close taxonomic affinities, can be based on structure of their egg cases or differences in shell shape and coloration or radular dentition.

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II. The Mating Habits of the Whelks, Polinices heros Say (1822) and Polinices triseriata Say (1826).

Observations on the mating habits of these two species at Belliveau Cove, N.S., during the summers of 1946, 1947 and 1949 were recorded earlier (Giglioli 1949). These reports profess to describe the complete act of mating, but it is now evident that they apply only to the preliminary stage, here termed the "pre-conjugal march". During the 1950 season the complete mating process for Polinices heros was observed at Holt's Point, N.B., and this has clarified our interpretation of earlier observations on Polinices triseriata.

Apparently mating in the genus Polinices takes place in two distinct phases, a preliminary "pre-conjugal march" (Giglioli 1949) and the definitive act of copulation involving insemination. The former has already been discussed at length in previous reports on the biology of these snails (Stinson 1946, Wheatley 1947 and Giglioli 1949) but is summarized briefly below. The latter stage was apparently not observed until the summer of 1950, though some predictions as to its probable nature were made by the author in 1949.

Mating commences in late April and early May and continues until late July, reaching its peak of intensity in June. It occurs with the greatest frequency on the surface of the flat during the "night" low tides, but may also take place during the day below the surface of the flat. (Stinson 1946).

The pre-conjugal march. When the low tide follows dusk, paired snails are observed on the flat. The females of the pair are larger than the males, bearing a ratio of 1.6 to 1 (height of shell being used as size index). In this phase the couples maintain their normal crawling posture and move about constantly. The male assumes a postero-dextrad position parallel to the female, and occasionally he is partly supported by the latter's expanded foot. The male's propodium is extended anteriorly and bent sinistrad so as to partly surround the dextro-anterior face of the female's shell and may be inserted into her pallial cavity. (Fig. 78 I).

Field observations and a study of the morphology of the adult genitalia of both sexes of both species (Giglioli 1949) have established that insemination is effected by copulation which would be impossible so long as the mating pairs maintain the position observed in the pre-conjugal march.

During the march, the females frequently travel at greater speeds than the males and often lose their partners after a variable period of time without completing the act. There is some evidence (Giglioli 1949) that this is a device whereby the female may exercise some selection of her partner. This discarding appears to be more frequent in cases where the male is much smaller than the female than in cases where he more nearly approximates her size. This would appear to be a mechanism for confining mating to members of the same or closely related size or age class.

Figure 78. Diagrams of mating snails.

I - Position adopted during the pre-conjugal march.

II - Position adopted during insemination by copulation.

Copulation -- This latter phase of mating follows the pre-conjugal march.

(a) In Polinices heros. After a variable period of time the pre-conjugal march terminates and the paired snails become stationary. The female remains in the expanded condition, while the male moves from his position parallel to his mate to a position at right angles and in front of the female, (Fig. 78 II), with his propodium directly opposed to her pallial cavity. The male's propodium surrounds the distended penis which projects ventro-anteriorly. In this stance, the penis, which is normally located latero-anteriorly on the right hand side is prolonged ventrad and inserted into the vaginal papilla, which is situated on the posterior extremity of the pallial floor of the female. (For diagram of genitalia see Fig. 23 and 24, Giglioli 1949.)

The period of copulation is variable and the whole mating act may last as long as two hours.

(b) P. triseriata is unlike P. heros whose entire mating process usually occurs on the surface with copulation immediately following the pre-conjugal march. In P. triseriata the march takes place on the surface, but the pairs ordinarily burrow into the substratum prior to copulation. By digging an observer may find them a few inches below the substratum in much the same relative position as that assumed at the surface by copulating pairs of P. heros.

Summary -- Mating in the whelks of the genus Polinices is subdivided into two definite phases, the incipient or "pre-conjugal march" and the definitive act of insemination by copulation. The latter stage follows the former, though mating may be interrupted by spontaneous separation of the pairs during the march.

Copulation requires the male to assume a different position from that observed during the march.

In P. heros copulation usually occurs on the surface, while in P. triseriata the end of the march is marked by burial of the pairs prior to copulation.

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III. Some Unidentified Egg Collars of the Family Naticidae Collected Along the Canadian Atlantic Seaboard.

Introduction

During the summer of 1949, four different kinds of gastrapod egg masses were collected from deep water (18-25 fathoms) off the Canadian Atlantic seaboard. These are the typical sand-encrusted gelatinous ribbons or "collars" such as described by Ankel (1930), Hertling (1932) and Thorson (1935) as characteristic of the Naticidae and no other prosobranch family. It seems reasonable, therefore, to refer them to this family, but since the snails that formed them were not recovered it is impossible to ascribe them to any of the genera: *Natica*, *Polinices*, *Amaura*, *Amauropsis*, *Bulbus*, *Sinum*, *Eunatica*, or *Gyrodes* or to any particular species within these genera. For this reason they are referred to herein as collars A, B, C and D.

The descriptions limit themselves to the external and internal structure of the collars, with emphasis on those points of difference which appear to be of diagnostic value.

It is hoped that the following descriptions will be of some assistance in eventually assigning these collars to their proper taxonomic position.

Definition of Terms Used

In the following discussion the collars are described with reference to their axes; for clarity these sections are defined and represented diagrammatically in Fig. 79.

"X" section - This might be described as a vertical cross-section. It is prepared by flattening the collar into a ribbon form and cutting across the ribbon (Fig. 79 II and 82, 86, 93 and 97).

"Y" section - This might be described as a tangential section. It is prepared by flattening the collar into its ribbon forms and cutting through the ribbon parallel to its face (Fig. 79 III).

Dimensions discussed - a collar has a diameter, width (referred to as height in discussing erect collars) and thickness. These terms are self-explanatory and need not be defined. Length is sometimes referred to. This means the length of the ribbon produced when the collar is uncoiled and flattened out on a plane surface.

Apical and basal margins. These would be described as the upper and lower edges of collars resting in their natural position. They are composed of sand and jelly and are typically thin lamellar borders containing no egg capsules.

Egg capsule - a gelatinous sphere containing the maturing embryo, varying from spherical or oval to a spheroidal mass of three diameters.

Acapsular - a term applied to parts of the collar that are devoid of capsules, e.g. the apical and basal margins of many collars.

Slope - refers to the angle of slope of the outer wall of the collar from the horizontal when the collar is resting in the natural position on a flat surface.

In this discussion the four egg masses have been treated in two groups based on morphological similarities. Some tentative suggestions as to their taxonomic position are made.

GROUP I

Collar "A"

1) General

This type (Figs. 80 to 83) is represented by a single collar recovered from a Danish seine haul on July 21, 1949, off the Southern point of Orphan Bank (47.38.30 Lat. and 63.20.00 Long.) in 38 fathoms on a rocky bottom in the Gulf of St. Lawrence.

It was damaged in the drag and the portion recovered appears to represent 1/2 to 1/3 of the complete collar.

2) External structure

a) General features - This collar is a thick, leathery, semi-rigid, truncated cone with gently sloping sides which are bounded by wide acapsular basal and apical margins. It is grey-brown in colour with large, clearly-visible, egg capsules. Both apical and basal margins are non-plicated and form a continuous marginal lamina throughout the length of the collar.

b) Slope of walls and the apical and basal margins - The angle of slope of the basal margin lower walls is approximately 35 degrees but this gentle slope changes suddenly where the capsules end because the apical margin is vertical and forms a sort of crown or cone.

c) Appearance and arrangement of the egg capsules - The egg capsules form a single layer enclosed in the sand-imbedded gelatinous matrix. Owing to the great thickness of the collar walls (3 mm. in the capsular area) the capsules, though clearly visible, do not bulge the surface conspicuously thus giving the collar a uniformly smooth surface. The capsules are large and arranged in groups of seven - six situated at the vertices of a hexagon and the 7th in the center (heptacunx). This is the fundamental arrangement but on cursory inspection the capsular arrangement may appear to be curvi-linear (Fig. 80 and 81).

Figure 79. Diagrams illustrating terms used in collar descriptions.

I. Lateral view of an egg collar in its natural position.

A) acapsular apical margin.
B) acapsular basal margin.
C) acapsular portion of collar.

II. Vertical cross-section - "X" section in our descriptions.

III. Tangential section - "Y" section in our descriptions.

Figure 80. Collar "A" in natural position lateral view.

Figure 81. Collar "A" apical view.

3) Internal Structure

a) Vertical cross section of the collar ("X" section) - (Fig. 82). The thick walls of the egg case surrounding the large ovoidal egg capsules, are composed of very fine and closely-packed sand grains imbedded in a clear gelatinous matrix.

b) Capsular shape - (Fig. 83). The capsules in "X" section are oval; but in "Y" sections they are circular. Thus the capsules have three different diameters.

c) Capsular contents - In the single specimen of this collar that we recovered and studied the egg capsules contained only one embryo each. The degree of development of the embryos varied throughout the collar from well developed veliger larvae to primary clevage stages. This differential degree of development is not confined to any given area within the collar, having a random distribution.

(i) Early capsule with multicellular embryos - In these the gelatinous complex showed the characteristic pattern described for P. triseriata (Giglioli '49). The capsule is contained by a thin tenacious pellicle, closely associated with the "matrix" jellies of the collar. Within this, is a zone of dense colloidal fluid enclosing a large sphere of jelly with an outer hyaline "crust" and inner dense, laminated zone. This denser zone surrounds a cavity bounded by a strong hyaline membrane which loosely contains the embryo.

(ii) Old capsules with veliger larvae (Fig. 83). The gelatinous portion is greatly reduced and appears as a sediment within the capsule, bounded by a strong outer pellicle containing in addition to the gelatinous sediment an increasing amount of dense colloidal fluid surrounding the larva. The outer capsular membrane, unlike the condition encountered with the early embryo (vide supra) is in loose association with the matrix gellies of the collar.

The visceral hump of the larva is contained in a clear sack which in older veligers appears to constrict around the hump to form the prodissoconch.

The veligers of collar "A" are described later in conjunction with those of collar "B".

4) Table of measurements

Subject	Measurement (mm.)
Length of collar (incomplete)	198
Width or height	57
Thickness (on horizontal axis)	3
Width of apical margin (average)	12
Width of basal margin (average)	5 - 6
Capsule	
in "X" section	
diameter on horizontal plane	2
" " vertical plane	3
in "Y" section	
diameter	3

Figure 82. "X" section through collar "A".

Figure 83. Collar "A" capsule containing veliger larva.

5) Comparison with the collar of Polinices triseriata

Collar "A" shows close affinities with the collar of P. triseriata. It has the same straight, rigid walls, large capsules, a single embryo per capsule and lamellar acapsular basal and apical margins. It differs from it in its larger size and general proportions. The similarities of these two collars are sufficient to suggest a close taxonomic relationship of the parents though it is not suggested that they are of the same species. However it may be speculated that the mode of collar formation is the same and thus presume that the same relationship between snail height and collar width, recorded for P. triseriata holds true. (Giglioli; 1949, page 92). In which case we might assume that the parent snail of collar "A" was roughly 57 mm. in height.

Collar "B"

1) General

One collar of this type (Fig. 84-87) was recovered from a haul with a scallop drag on July 28, 1949, approximately 5 miles due North-West of Digby Gut, N.S., in 45 fathoms of water on a rocky bottom. A second specimen was recovered in the same locality on July 20, 1950 (Fig. 88).

2) External structure

(a) General features. A large truncated cone with thick rigid walls steeply sloping to a narrow acapsular apical margin. The egg case is gray-brown in colour, with capsules that are so large as to make the walls bulge conspicuously. Both apical and basal margins are non-plicated, and though they form a continuous band around the collar, they are narrow and so poorly developed that this collar lacks the vertical apical cone which characterised collar "A".

(b) Slope of walls and the basal and apical margins. The thick walls of the collar slope acutely to the apex at an angle of 60 degrees. The narrow apical and basal margins are inconspicuous and have the same slope as the collar walls.

(c) Appearance and arrangement of egg capsules. These are in a single layer in the clear sand-imbedded gelatinous matrix. Because the capsules are so large the inner and outer surfaces of the collar walls bulge conspicuously. The arrangement of the capsules is basically like that of collar "A", i.e. "heptacunx", but the general pattern appears less regular (Fig. 80 and 84).

3) Internal structure

(a) "X" section (Fig. 86). Sectioned in this plane the capsules appear oval. The thick, compact walls bulge slightly opposite the capsules.

Figure 84. Lateral view of Collar "B" collected in 1949.

Figure 85. Apical view of Collar "B", 1949 collection.

Figure 86. "X" section through collar "B" collected in 1949. Note the peripheral hyaline capsular jelly and denser matrix.

Figure 87. Excised capsule of collar "B" containing veliger larva.

Figure 88. Egg collar, similar to collar "B" collected off Digby Gut in 1950.

Figure 89.

I Larva (velum and foot) excised from collar "A".

II Larva excised from collars "A" and "B". The inter-velar structures are shown separately. They may have diagnostic value.

Figure 90. The larva from collar "A" showing shell structure and general proportions.

to induce the torsion of the shell which forms its first suture prior to becoming opposed to the visceral mass.

3) The foot.

There is slight difference in the shape of this organ in the two types of larvae recovered from collars "A" and "B". These minor differences are set forth in figure 89. Basically the foot is spatulate with a dense core and granular marginal area.

4) The velum.

The larvae figures for collars "A" and "B" were different but cannot be held as typical for each collar for the one (Fig. 89, I) was found only in collar "A" while the other (Fig. 89 II) occurred in both collars "A" and "B". In both types there are two large velar lobes, but in the more advanced form (Fig. 89, II) the velum is characterised by an enlarged portion along the anterior margin and small posterior velar depressions. In the earlier stage (Fig. 89, I) the converse holds true, this being characterised by large medio-posterior lobes at the point of junction between the velar lobes and the foot. In both specimens the velar cilia are numerous and small, suggesting poor natatorial abilities. This further corroborates the speculation that these larvae lack a planktonic stage and probably emerge from the collar as a post larval, benthic form.

5) Structures between the velar lobes. There is a composite of structures between the velar lobes, differing in form in the two types of larvae recovered. For exact diagnostic differences see figure 90.

6) Discussion. Collar "A" shows larvae only of the type portrayed in figure 89, I, while collar "B" shows both types of larvae portrayed in figure 89.

It is possible that the occurrence of similar larvae in both collars signifies their close and possibly co-specific relationship and that the external differences previously recorded for these two collars are merely within-species variation, such as have been encountered in egg cases of P. triseriata and P. heros (Giglioli '49). However the differences in collar morphology are so great that, without knowing more, to be valid we might reasonably attribute them to different species and explain the occurrence of larvae of the same type in both collars as indicating a close inter-species relationship of the parents.

This latter speculation is based on the previously-made assumption that the larvae recovered, though advanced in "larval" development, nevertheless represent an early stage of their intracapsular growth and thus cannot be considered as typical of the emergent form of larvae from these collars. If such is the case we might expect divergences of these larvae in stages of development subsequent to those described here.

A solution of this problem is possible only when more collars like these have been studied, described and possibly "hatched" and assigned to species. Tentatively, the author, for one, is inclined to consider them as from parents of different species.

GROUP II

Collar "C"

1) General.

One collar of this type (Fig. 91-94) was recovered from a Danish seine haul on August 2, 1949, off the Magdalen Islands (47° 08' 00" Lat. and 61° 45' 00" Long.) in 18 fathoms on a mixed sand and gravel bottom.

2) External structure.

(a) General features. A grey-brown, rigid, truncated cone with steeply sloping thick sides, bounded basally and apically by wide acapsular margins the former being regularly plicated.

(b) Slope of walls and the apical and basal margins. Both margins are wide and acapsular. The wider basal margin is regularly plicated to form conspicuous projections when the collar is viewed apically (Fig. 92) but owing to the continuity of the basal margin these plications are hard to distinguish when the collar is viewed laterally. (Fig. 91). The apical margin is vertical or nearly so and forms a flaring crown. The capcular parts of the collar walls slope steeply at an angle of 50 degrees.

(c) Appearance and arrangement of the egg capsules. The capsules are contained in the sand-imbedded gelatinous collar "matrix". They form a continuous single layer one capsule thick (mono-capsular layer) throughout the collar and their great size causes the collar walls to bulge conspicuously.

The geometrical arrangement of the capsules differs from the two previously described collars. In collar "C" this is in a linear series on both axes, horizontal and vertical, but the capsules in successive horizontal rows are staggered so that the successive capsules in any one vertical row occur only in alternate horizontal rows (Fig. 91 and 92).

3) Internal structure

(a) "X" section of collar: When the egg mass is viewed in "X" section (Fig. 93) the capsule appears circular and the bulging of the walls around each capsule shows clearly. The walls are compact

Figure 91. Collar "C" in natural position, lateral view.

Figure 92. Collar "C" apical view.

Figure 93. "X" section through collar "C".

Figure 94. Collar "C" capsule containing ovum.

and rigid being composed of fine sand grains tightly imbedded in a clear gelatinous matrix.

(b) Capsular shape. In "X" and "Y" sections they appear circular.

(c) Capsular contents. There is never more than one embryo per capsule. This specimen collar must have been formed immediately before collection because none of the eggs had developed beyond early clevage stages.

The egg capsules containing these early embryos were typical of their counterparts in collar "B". A pellicle bounded the capsule and contained a hyaline mass of jelly grading centrad to a denser laminated layer surrounding the peri-embryonal space.

4) Table of measurements

Subject	Measurements (mm.)
Length of collar	220
Width or height of collar	41
Thickness of collar	2.6 - 2.3
Width of apical margin	5-6
Width of basal margin	6-10
Capsules	
in "X" section	
diameter on horizontal plane	2
diameter on vertical plane	2.1
in "Y" section	
diameter	2.3

Collar "D"

1) General

A single specimen of this type (Fig. 95-98) of collar was recovered from the Gulf of St. Lawrence in a Danish seine haul on July 15, 1949, off Tignish, P.E.I. (46° 54' 30" Lat. and 63° 45' 00" Long.) in 20 fathoms on a sandy bottom.

2) External structure

(a) General features. A low flattened semi-conical structure with thin apical and basal margins. The basal margin is strongly plicated in a series of high regular arches. The compact and thick walls are brittle and grey-brown in colour with large "bulging" capsules.

Figure 95. Collar "D" in natural position, lateral view.

Figure 96. Collar "D" apical view.

(b) Slope of walls and apical and basal margins. In profile the sides are gently arched from the plicated basal margin to the flat and regular apical margin (Fig. 95). The angle of slope taken tangenially to the arched sides is 35 degrees from the horizontal plane.

The basal region of the egg case, when viewed in profile, is characterised by a series of regularly-spaced, arch-like, plications. The acapsular apical margin is narrow, regular and smooth. The basal margin is also acapsular, narrow and follows the regular plications of the basal region.

(c) Appearance and arrangement of the egg capsules. The large capsules cause the walls of the collar to bulge conspicuously. The capsular arrangement is similar to that of collars "A" and "B" showing the heptacunx pattern.

3) Internal structure.

(a) "X" section of the collar. In "X" section (Fig. 97) the capsule is oval and in "Y" section circular. The walls are rigid but brittle with thick and well defined intercapsular septa.

(b) Capsular contents. The capsule never contains more than one embryo and none of these were developed beyond early clevage stages. The egg space showed all of the characteristics described for the egg capsule at this stage of development in collars "A", "B" and "C".

The embryo is contained in a peri-embryonal space and this is surrounded by a dense laminated gelatinous mass which passes ectad into a clear hyaline jelly, which, in turn is contained within a pellicle or capsular membrane with which it is in close association.

4) Table of measurements.

Subject	Measurement (mm.)
Length of collar	180
Width or height of collar	23-21
Thickness of collar	2.3-1.8
Width of apical margin	1-2
Width of basal margin	2-6
Capsules	
In "X" section	
diameter on horizontal plane	1.4
diameter on vertical plane	2.1
In "Y" section	
diameter	2.3

Comparison of Group II Collars

No larvae of group II were available for study and the possible relationships of the parents of the two types of collar can

Figure 97. "X" section through collar "D".

Figure 98. Collar "D" capsules containing early embryos.

be judged only from a comparison of the collars themselves. The between-type differences seem to be much greater (cf. Fig. 91 and 96) than in Group I (cf. Fig. 80 and 84). For this reason the writer feels confident in assuming that their parents were of different species.

The nature of the collars is somewhat like that of <u>Polinices triseriata</u> and one might speculate on the basis of the snail-collar size relationship already referred to (Giglioli 1949) that the parent of collar "C" was 41 mm. high and of collar "D", 23 mm. high.

Discussion of the Four Unidentified Collars

From the data at hand it is impossible to ascribe these collars to individual species or, for that matter, to any one of the eight genera of the family <u>Naticidae</u> with any certainty. Indeed it is questionable that we are dealing with collars of four different species. It appears that collar "C" and "D" belong to two separate species but the relationship between "A" and "B" is doubtful; they may belong to separate species or may only represent intra-specific variation.

Thus we can say that possibly we are dealing with 4 collars of separate species, but more probably with those of 3 species.

From previous studies it was found that the ratio of the height of the maternal snail to the width of collar produced was 1:1 for <u>P. triseriata</u> and 1:1.5 for <u>P. heros</u>. Assuming this relationship to hold throughout the family we can speculate that:

a) egg cases with stiff straight sides, like <u>P. triseriata</u> follow the 1:1 ratio.

b) and those with thin flexible sides, like <u>P. heros</u>, follow the 1:1.5 ratio.

All of the unidentified collars, though they may be grouped into two divisions distinguished by the presence or absence of a plicated basal margin, are all similar in structure to the egg case of <u>P. triseriata</u>. Thus we can assume that the 1:1 ratio may hold true for these egg cases. On this assumption we have estimated the sizes of snails producing the previously described egg cases as follows: "A" - 57 mm. (2¼"): "B" - 45 mm. (1¾"): "C" - 41 mm. (1 5/8"): "D" - 23 mm. (1").

By consulting Johnson's (34) distributional list of mollusca for the Atlantic coast with reference to the <u>Naticidae</u> we obtain the following possible parent snails in Canadian waters:

List of species of Naticidae* found in Canadian Atlantic waters and their maximal recorded size and distribution (Johnson 1934).

Genus	Species	Recorded Height (inches)	Distribution
Polinices	triseriata	1½	Gulf of St. Lawrence - N. Carolina
	heros	2-3	" " " "
	groelandica	½	" " " "
	immaculata	13/40	" " " "
	nana	¾	Greenland - Block Is.
	duplicata	2-3	Gulf of Mass.
	levicula	-	Gulf of Maine
Natica	clausa clausa	12/20	Greenland - N. Carolina
	clausa vitata	<1	" "
	affinis	-	Greenland
Amanura	candida	-	Gaspe and Gulf of St. Lawrence
Amauropsis	islandica	-	Labrador - Georges Bank.
Bulbus	smithii	-	Gulf of St. Lawrence - Georges Bank.

* According to Johnson, the genera Sinum, Eunatica and Gyrodes are not represented in these northern waters.

Unfortunately it was impossible to obtain information on the maximum size of Polinices levicula, Natica affinis, Amanura candida, Amauropsis islandica and Bulbus smithii, thus no statement can be made concerning these species as possible parents of the unidentified egg collars. Of the species whose sizes are listed in the table, the only snails that would qualify as possible parents are P. heros and P. duplicata. However these two species cannot be implicated as their collars have been studied and described either here or in last year's report (Giglioli '49) and bear no similarity to the unidentified egg cases.

It is possible that the 4 unidentified egg cases belong to some of the 5 previously mentioned species, for which size data are lacking but it is the writer's opinion that the parent species of these collars are so far unrecorded in Canadian waters and possibly not yet described in the literature.

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IV. The Egg Collar of Polinices duplicata Say (1822).

1) General.

The writer is presently studying and describing several unidentified egg collars of Canadian species of the snail family Naticidae (See Part III of this report). Johnson (1934) does not list P. duplicata as occurring in Canadian waters and the writer is unaware of any such record. Nevertheless it seemed desirable to study the collar of this species to be sure that it was not one of the four unidentified types in our collections. Some difficulty was encountered in obtaining satisfactory material for this study but this was overcome through the co-operation of two American workers to whom the writer wishes to express his thanks.

Dr. M. R. Carriker of Rutgers University supplied formalin-preserved fragments of a collar formed in 1949 by a female P. duplicata held for some time in an aquarium. A study of these fragments gave no clues whatever as to the P. duplicata collar but did show that its internal structure is so strikingly different from all others examined previously that the writer felt he could confidently identify whole collars of the species if he encountered them.

An extensive August 1950 collection of collars from Massachusetts (Cape Cod) beaches was made by Mr. H. J. Turner of the Woods Hole Oceanographic Institution and kindly supplied by him. These were found to have precisely the same internal structure as the fragments supplied by Dr. Carriker and besides, showed the gross structure very well. By piecing together the information from these two sources the writer feels that there is no reasonable cause to doubt the identification he has made or the conclusion based on it, that collar of P. duplicata is not represented in our collection of unidentified Canadian collars.

Because the collars of P. duplicata have never been adequately described, such a description is attempted here following Thorson's (1946) general plan of ourlining both external and internal features. Emphasis is placed on those features that the author considers important in distinguishing this egg case from those of P. heros and P. triseriata (Giglioli '49) which, so far as the writer is aware, are the only ones of North American species that have been studied to date. In conclusion some suggestions are advanced on the taxonomic relationship of P. heros, P. triseriata and P. duplicata.

2) External features. The collar of P. duplicata is basically similar in size and shape to that of P. heros (Fig. 99 and 100 compare with Giglioli 1949 Figs. 44-46). It has wide, thin, flexible walls which curve convexly from the basal margin becoming concave as they approach the apical region where they flare to form an upright cylindrical crown. A typical P. duplicata collar from Turner's collection showed the following dimensions:

Figure 99. *P. duplicata* egg collar, lateral view.

Figure 100. *P. duplicata* egg collar, apical view.

Length of basal perimeter	345 mm.
Length of apical perimeter	125 mm.
Width or height of collar	60 mm.
Thickness	1 mm.

P. heros collars collected in Canadian areas usually show very little variation in size. Judging from Turner's collection this is also true of Massachusetts P. duplicata collars. A feature which is peculiar to and consistent for the species and therefore most useful in identification is the regular scalloping of the basal margin by well-defined arches 5-8 mm. in height. P. heros collars have straight even basal margins. The capsules, though hard to discern from the exterior extend to the very edge of the apical and basal margins.

3) Internal structure.

The internal structure of P. duplicata collars is just as strikingly characteristic as the external features and can be relied on for species identification in cases where entire collars are not available for examination. It can be readily studied from vertical cross-sections 1 mm. or less in thickness, cut with a razor blade. The following characteristics have been noted (Fig. 101).

(a) Collar jellies. It is composed of the same three basic jellies as described for the Canadian species (Giglioli '49), namely:

1. The peripheral layer forming a continuous pellicle around the collar.

2. The sand-imbedded matrix jelly forming the mass of the collar, responsible for the collar's shape and structure because of its rigidity.

3. The capsular jelly composed of a thin but dense peripheral portion containing a hyaline core surrounding the embryo.

(b) Capsular arrangement. The capsules are not regular in arrangement, but dispersed at random between the imbedded sand grains rather than in a regular "mono-capsular layer" so typical of collars of P. heros and P. triseriata. They occur right out to the edge of the collar so there is no "acapsular" margin such as is found in P. triseriata collars.

(c) Capsular structure. The capsule is small (250µ. on its widest diameter) and oval in shape and has never been noted to contain more than one egg or larva.

Figure 101. "X" section through the egg collar of *P. duplicata*. Insert diagrams show egg capsule and shell of emergent larva.

Figure 102. Egg capsules of *P. triseriata*, *P. duplicata* and *P. heros*.

There is a clearly-defined capsular wall present during the egg and early larval stages but by the time the larva has developed to advanced veliger stages this wall disappears. The larva then continues to occupy the same cavity but is in direct contact with the matrix of the collar.

4) Comparison with other collars.

The features of internal structure of this collar, which differentiate it clearly from that of P. heros are (1) the capsules are irregularly rather than regularly arranged and (2) there is a single rather than many eggs or embryos per capsule. It resembles the collar of P. heros in that the capsules are small and thus cannot be observed from the exterior by transmitted light and in that there is no acapsular margin of jelly. In both of these latter features it differs sharply from P. triseriata.

Taxonomic Relationships of P. heros, P. triseriata and P. duplicata.

In Part I of this report dealing with radulae some hypotheses were advanced concerning taxonomic relationships of P. heros, P. duplicata and P. triseriata and the reasons for the taxonomic difficulties encountered by early students of these species were discussed. The writer's opinion was that P. duplicata is closer in its affinities to P. heros than to P. triseriata. Support and amplification of this same conclusion is afforded by a comparison of collar characteristics of the three species. These are set forth in the following table.

In 7 of the more important of the 15 characteristics listed in the table (numbers 1, 2, 3, 5, 6, 7 and 13) P. heros and P. duplicata correspond closely and differ from P. triseriata. In contrast there are only two characteristics (numbers 8 and 9) and one of these is minor, in which P. duplicata seems to be closer to P. triseriata. There are three characteristics (numbers 11, 12 and 14) in which P. triseriata and P. heros seem to be more closely related than either is to P. duplicata.

The general conclusions to be drawn from this comparison are that P. duplicata,

(1) Is more closely related to P. heros than to P. triseriata

and

(2) Occupies an intermediate taxonomic position between P. triseriata and P. heros.

The radular study reported earlier supported conclusion (1) but did not suggest (2).

If there still remains any need to bolster the argument that P. triseriata is a species, sensu proprio, and not the young of P. triseriata this conclusion as to the intermediate position of P. duplicata should supply it.

Tabular comparison of characteristics of egg cases of three species of *Polinices*.

No.	Characteristics Compared	*P. heros*	*P. duplicata*	*P. triseriata*
	External Characters			
1	Collar rigid with straight sides, standing erect	no	no	yes
2	Thickness of sides	>1 mm.	usually >1 mm.	<1 mm.
3	Size of collar	large	large	small
4	Regularly scalloped lower margin	no	yes	no
5	Capsules large: clearly visible in whole collar with transmitted light	no	no	yes
6	Presence of an apical and basal acapsular margin	no	no	yes
	Internal Characters			
7	Diameter of capsule	250µ.	200µ.	900µ.
8	Shape of capsule	spherical	oval	oval
9	Number of eggs per capsule	4 - 100	1 - 3	1
10	Presence of nurse cells	no	no	no
11	Capsular pattern	regular	irregular	regular
12	Capsular arrangement	a single even layer	many jumbled layers	a single even layer
13	Shell-height of emergent veliger (approximate)	130µ.	200µ.	300-500µ.
14	Capsular jelly in old collars containing larvae	present	absent	present
15	Type of larva	planktonic	(unknown)	semi-plantonic or benthic.

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V. Adult Movement and its Effect on the Distribution of the Whelk <u>Polinices heros</u> Say (1822)

Introduction

The general problem of means of distribution in our species of Polinices was briefly outlined in the writer's report for 1949 (Giglioli '49, p. 136) where adult movement was shown to be accomplished in two different ways:

(a) by pedal locomotion.

(b) by expansion of the foot and attachment to the "surface film" of moving tidal waters. This latter mode of travel is possible only in calm and shallow waters, usually toward the definitive end of the ebb tide and practicable only by small snails because the surface tensional film is not strong enough to support much weight.

During the 1950 summer season, an attempt was made to estimate accurately the range and rate of distribution of adult whelks. Because the "surface tension flotation method" is comparatively unimportant owing to the limitations described above this study involved only distribution by pedal locomotion.

Experiments were conducted in tanks at the Atlantic Biological Station (St. Andrews, N.B.) and on the flat at Holts Point, N.B., from late June to early July.

Owing to the great abundance near St. Andrews of Polinices heros and the greater ease of "tagging" and recovering it, this larger species was selected for trials rather than P. triseriata. However the writer's extensive field experience with this species suggests that similar results would have been obtained with P. triseriata and that the same conclusions would apply.

Techniques and Working Sites.

1. "Tagging" of sample snails. Good results were obtained by marking the snails' shells with Volger's opaque black ink. In the first field experiments sample snails were indicated with an "X" sign while in the more exacting second test and in the tank experiments the animals were "numerically tagged". Each snail was assigned a serial number and this was painted on the shell with a camel's hair brush.

Owing to the nocturnal habits of the whelk, recovery on the flats was greatly aided by using a Coleman pressure gasoline lantern which was found to be superior to any form of previously tested electric battery light. The marked specimens were quickly and easily recognized among the unmarked (provided, of course, that the whelks were on the surface) and the use of numbers, rather than other marks of identification, made it possible to study individual as well as mass movement.

2. Tanks. The field work at Holts Point was limited to periods of low spring tides, because of the nature of the flat, and conducted at night because of the habits of the whelks. It was therefore decided to attempt smaller experiments in tanks where more frequent observation was possible.

The tanks available are considered to have provided approximately natural flat conditions and were so constructed as to enable the observer to alter light conditions at will from day-light intensities to almost absolute darkness. They were floating types whose depth could be regulated (Fig. 103 and 104) and moored in a tidal pool at the Atlantic Biological Station.

The tank was 16' by 10' and divided by a fixed wooden partition into two longitudinal compartments which could be further subdivided into halves (i.e. 4 compartments in all) by adjustable partitions. The tank proper rested on floats supporting a "cat walk" around its perimeter. It was filled with 4 - 6 inches of sand and submerged in water so that there was a depth of 6 inches above the sand surface.

The two longitudinal compartments were separately roofed with 6' x 3' wooden hatches lined with light-proof tarred paper. This allows for easy handling and minimal exposure of the tanks to light during diurnal observations.

3. Experimental plot at Holts Point. The purpose of this plot was to release numbered snails at one point on the flat and observe their nightly and night-to-night movement from the point of release with reference to the direction of movement.

To obtain this information a release stake was placed 50' offshore on the sandy flat some 40-60 ft. from extensive mussel (Mytilus) beds. The position of this plot was such that the snails could move through uniform soil inshore, offshore or along-shore on any point of the compass. The point of release was in proximity to a large source of food which might "attract" the whelks if they are susceptible to attraction as preliminary experiments seemed to indicate and as certain American workers have suggested.

To simplify observations 8 stakes were placed in a circle from the release stake at the 4 primary and 4 secondary points of the compass dividing the area into 8 sectors, A to H, (Fig. 105).

Movement from the point of release was graphed nightly by systematically examining successive 5-foot-wide circular bands starting from the center with the aid of a calibrated chain attached to the central stake. As marked specimens were observed on the surface, their numbers were noted and plotted on a circular graph showing their distance from the point of release and their sectoral position.

Figure 103. Floating tank at St. Andrews.

Figure 104. Tank showing removable covers and part of the longitudinal compartments.

Figure 105. Disposition of experimental plots at Holts Pt., N.B., compare with Fig. 4.

Figure 106. Panoramic view of Holts Pt., flat. Note position of plot and other notes in plate.

Tank Experiments at the Atlantic Biological Station, St. Andrews, N.B.

The purpose of the tank experiments was twofold: (1) to show the degree of movement by pedal locomotion and to compare these observations with the larger scale recordings obtained in nature at Holts Point, N.B., and (2) to obtain an estimate of the rate and manner of movement of individual snails.

To accomplish this, fifty Polinices heros were collected at random on the flats, measured and "tagged" numerically thus enabling close observation on movements of individual snails. The following table shows the size-distribution of the fifty numbered snails. Each number in the table represents one whelk.

Shell height mm.	Tag number
23	6
24	
25	
26	4,5,7
27	8
28	1,2,9,10
29	3,11,13
30	
31	12,14,16,21
32	24
33	15,17,18,19
34	28,35,49
35	20,25,26,40,46
36	22,23,29,41,47
37	33,37,42,43
38	30,34,36,38,44
39	31,39,45,48
40	27,32,50
41	
42	

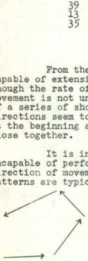
1) Rate and manner of movement.

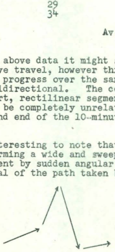
Snails when on the surface of the flat may be stationary or in movement, the former state is usually associated with drilling and feeding though occasionally snails may be observed stationary for no apparent reason. When in movement they may be in slow locomotion but more often in a rapid and apparently purposeful march over the sand. In an effort to discover their distributional capacity and efficiency the rate of movement of snails moving at a steady rate over the sand in the tanks was measured. This was determined by studying randomly selected moving, individual snails for 10-minute periods and measuring exactly the distance covered. This was done by carefully laying down pieces of twine behind the whelks as they progressed over the sand and finally measuring the length of the time. The results of 20 such observations are listed in the following table.

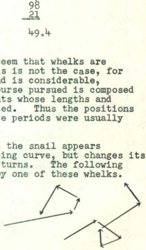
Tag Number of Snail	Height of Snail mm.	Distance covered in 10 minutes - cm.
42	37	37
16	31	23
45	39	47
42	37	64
17	33	83
20	35	96
50	40	80
7	26	12
46	35	40
15	33	38
11	29	89
10	28	53
2	28	45
8	27	60
6	23	72
9	28	8
21	31	25
39	39	47
13	29	98
35	34	21
	Av.	49.4

From the above data it might seem that whelks are capable of extensive travel, however this is not the case, for though the rate of progress over the sand is considerable, movement is not unidirectional. The course pursued is composed of a series of short, rectilinear segments whose lengths and directions seem to be completely unrelated. Thus the positions at the beginning and end of the 10-minute periods were usually close together.

It is interesting to note that the snail appears incapable of performing a wide and sweeping curve, but changes its direction of movement by sudden angular turns. The following patterns are typical of the path taken by one of these whelks.







The lack of sustained rectilinear movement apparent from these small experiments suggests that pedal locomotion is an unimportant factor in the overall distribution of the species.

2) Mass movement in tanks.

The purpose of these tests was to estimate the ability of groups of snails, under optimal conditions, to spread from one region and invade another. Thus every attempt was made to force the whelk to execute maximum rectilinear movement.

To achieve this the 50 sample snails described in the table were all placed in a 1' x 5' compartment at one end of the tank behind a partition and allowed to "rest" for a period. Then the restricting partition was removed and the positions of the snails recorded at regular intervals of time. Because the snails tend to bury themselves when exposed for any length of time to daylight the experiments were conducted either at night or with the tank hatch covers on by day.

It is assumed that the movement recorded in terms of rectilinear locomotion is somewhat greater than might be expected in nature owing to (1) the restrictions imposed by the oblong shape of the tank tending to force them more or less in one direction only, and (2) the crowded conditions present before lifting the position was probably inimical. Both these might tend to provoke more rapid dispersion. Besides this the snails were starved for 20 days before being placed in the tank and want of food probably provided an added incentive to rapid movement.

The tables following show the results obtained in two experiments, one on a cloudy day and one in the evening. Figures 107 and 108 describe the movements of several individual snails. Additional data on movement in these tanks is recorded in the report dealing with feeding rate. The light intensity was measured with a General Electric photographic exposure meter. Tha tank was marked off crosswise into 14 one-foot-wide zones and the numbers of emergent snails in each zone recorded at the times indicated.

Experiment I. Light intensity in covered tanks - 2 foot-candles.
Sky - overcast. Water temperature - 11°C.

Time of observ.	No. in compartment where released	Zone number (Distance in feet from compartment where released) 1	2	3	4	5	6	7	8	9	10	11	12	13	14	% emergence
9:30a.m.	20															40
10:30	11	6	4	2						1	4		1			58
11:30	4	3	2	1	1	2	4	3	1	2	1					48
12:30p.m.	2	3		2	3	1	2	2	1	2			1			38
1:30	3	3	2	3	1		1	3	2	4	3	1	1			54
2:30	5	3	1		1			2	2	2	1	1		2	1	42
3:30	6	3			1			1	1	2	1	1	1	2	1	40

Experiment II. Light intensity in tank (cover off) 1½ foot-candles: twilight: Water temperature - 9°C.

Time of observ.	No. in compartment where released	Zone number (Distance in feet from compartment where released) 1	2	3	4	5	6	7	8	9	10	11	12	13	14	% emergence
8:30p.m.	29															58
9	12	3	3	5												46
9:30	6	3	5			2	2	2	1	2						46
10	5	2	6	4	2		2	1	1					1	1	50
10:30	8	4	5			2		2		2			1			48

Figures 108 and 109 and the two tables must be interpreted in the light of the study reported in section (1) above. Although the movement of individual snails is erratic, the overall mass movement tends to be away from the point of release and assume the pattern of unidirectional movement. It is probable that this was conditioned by crowding and the limitations on direction of movement imposed by the size and shape of the tank.

The general importance of crowding is shown by the tendency to travel at first rapidly away from the crowded point of release and then to slow down and to become more and more erratic as the effects of crowding are reduced. The animals tend to spread out to avoid one another as much as possible and occupy what space is available.

It should be remembered that the interval between observations was large and that the lines in the figures are not intended to portray the actual paths taken by the individual snails between observations. If this were attempted figures 108 and 109 would show a far greater degree of erratic non-directional movement.

We can conclude from this study of mass movement that under normal circumstances and in the absence of such factors as crowding and other stimuli (vide infra) the movement of the individual whelk is an erratic wandering varied in rate and extent and in itself probably of little consequence as a factor in species distribution.

Flat Experiments at Holts Point, N.B.

The preliminary experiments on movement in tanks were followed up by observations of movement on a sand flat where the animals commonly occur in nature. For this purpose the flat at Holts Point, N.B., was selected and the experimental plot (see "Introduction" to Part V) established. Since this flat is accessible only at low spring tides it was decided to perform a rough preliminary experiment to ascertain the difficulties involved and follow this up with a more exacting secondary test.

Figure 107. Holt's Pt. showing experimental plot, looking offshore across the mussel beds.

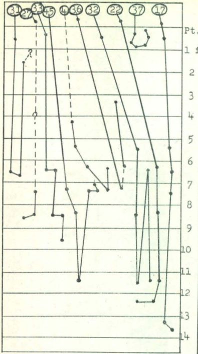


Fig. 108. Movement of numbered snails in a 6-hour period: each observation shown by dark circle: one hour lapse between consecutive observations joined by solid line. Dotted line indicates burial of snail and loss of consecutive observations. Total number of observations possible: 7.

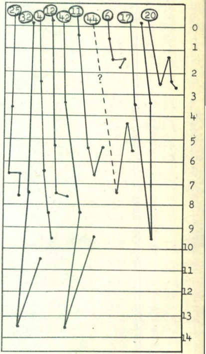


Fig. 109. Same as figure 108. Lapse between observations $\frac{1}{2}$ hour, total no. of observations possible: 5.

1) Preliminary Experiment.

In this test 200 snails were marked while in the field with a black "X" on their shell. These were released some 30 ft. from the mussel beds (Fig. 105) and observed on 4 successive nights (23-26 May). Nightly recovery never exceeded 13% and averaged only 8%.

It should be noted that the method of marking used in this experiment allowed for the estimation of mass movement but gave no indication of the individual movement. Specimens used in the second test were tagged numerically, like those used in tanks.

Movement in the primary test was judged to be greater inshore than offshore because there was a greater frequency of recoveries towards the mussel beds. This apparent attraction to food (positive "Tropho-tropism") of the whelk has been previously postulated by U.S.A. workers who speculated that this might be used to advantage by setting "bait traps" in whelk-control campaigns.

It was noted that though the greatest number of snails migrated inshore, the greatest distance of movement by any one snail was in an offshore direction. On the third night one specimen was observed 90 ft. outside the release stake. Had this animal travelled constantly in a straight line for the 72-hour period at the average rate of movement of the tagged animals in the tide pool (See table in section "Rate and manner of movement") it would have covered a distance of 75 ft.

2) Secondary Test.

This experiment was designed to accurately demonstrate movement under natural conditions and simultaneously confirm or deny the existence of the "Tropho-tropism" suggested by the preliminary experiment. To provide for the latter, the release stake was set about 50' from the extensive mussel beds (Fig. 105 and 107) so that sectors A, H, G, F and E faced a sandy flat, practically devoid of shellfish. (The few native clams in this locality were very large and deeply buried and thus outside the range of the whelks burrowing capacity.) In this position the inshore sectors B, C and D were separated by a narrow belt of barren sandy flat from the Mytilus beds.

In this test, 400 numerically tagged snails were used. These were collected at Holts Point in late May and early June and brought to St. Andrews for tagging, where they were kept in tanks until the date of release. The 400 snails were collected manually at random from surfacing snails and with certain reservations their size-frequency distribution can be considered typical of the general population present at Holts Point. The heights of 100 of these were measured. The size-frequency distribution is shown in the following table:

Size (mm.)	Frequencies	Total
31	/	1
32	//////////	10
33	/////////////////	17
34	//////////////	14
35	///////////////	15
36	/////////////	13
37	///////////	11
38	////////	8
39	///	3
40	///////	7
41	/	1
42		
43		
		100

The sample of 400 tagged snails was released on the night low tide on Saturday 24 June. Observations were made until the 5th July. During this time two methods of observation were adopted, the most common form was by examining the flat systematically at night and recording all emergent tagged snails observed, noting their distance and position with reference to release stake as described in the section "Experimental plot at Holts Point".

The other method was used only at daylight low-water periods and consisted of digging up a circular area (5 ft. radius) around the release stakes and counting the number of tagged snails in this area. The results appear in the following table. For movements of individual snails see Graphs I to V.

Counts and positions of tagged snails observed at various times.

Date	Time of obs. o'clock a.m.	p.m.	Distance moved (ft. from stake)	Number of tagged snails in sector A	B	C	D	E	F	G	H	% emergence
25 June	11		within 5 ft.	13	24	19	25	15	29	37	33	0
25 June		12	1 - 5	0	1	13	2	1	3	1	0	
			5 - 15	2	7	0	2	3	4	1	2	
			15 - 25	0	1	5	5	0	0	0	1	
			25 - 35	0	4	1	1	1	0	0	2	
			35 - 45	0	8	2	2	0	0	0	0	
			45 - 55	0	0	0	1	0	0	0	0	19

(Continued)

Date	Time of Obs. a.m. o'clock	p.m.	Distance moved (ft. from stake)	Number of tagged snails in sector A	B	C	D	E	F	G	H	% emergence
26 June	1		1 - 5	0	0	2	1	2	0	0	0	
			5 - 15	0	2	1	0	1	0	0	0	
			15 - 25	0	2	4	3	0	2	2	0	
			25 - 35	2	2	2	2	1	0	1	2	
			35 - 45	1	1	0	0	0	1	0	0	
			45 - 55	0	0	1	2	0	0	0	0	9.7
27 June		2	within 5 ft.	0	0	2	1	2	4	3	0	0
27 June	2		1 - 5	0	0	0	0	0	0	0	0	
(rain)			5 - 15	0	0	0	0	0	1	0	1	
			15 - 25	1	0	1	0	0	0	0	0	
			25 - 35	0	1	0	0	0	0	0	0	
			35 - 45	0	0	0	1	0	0	0	0	
			45 - 55	0	0	0	0	1	0	1	0	2
28 June	3		1 - 5	0	0	0	0	0	0	1	1	
			5 - 15	0	1	4	2	1	1	7	0	
			15 - 25	1	0	3	0	2	0	5	3	
			25 - 35	0	2	1	0	0	1	0	0	
			35 - 45	0	0	0	1	2	0	1	4	
			45 - 55	0	0	2	1	0	0	0	2	
			55 - 65	1	0	2	1	2	0	0	0	
			65 - 75	0	0	0	0	0	1	0	0	14
29 June		3	within 5 ft.	1	0	0	1	1	1	2	2	0
29 June	4		1 - 5	0	1	0	0	0	0	0	0	
			5 - 15	1	0	0	0	1	0	2	1	
			15 - 25	0	0	0	0	0	0	1	0	
			25 - 35	0	1	0	0	2	0	2	1	
			35 - 45	0	0	0	1	0	0	0	1	
			45 - 55	0	1	4	0	0	2	0	0	
			55 - 65	0	0	0	4	1	0	1	0	
			65 - 75	0	0	0	0	0	0	0	0	
			75 - 85	0	0	0	0	0	0	0	1	7.2
29 June		4	within 5 ft.	1	0	0	1	1	1	2	2	0
30 June	5		zero emergence - rain and fog.									
1 July	6		1 - 5	0	0	0	0	0	0	1	0	
(fog)			5 - 15	2	0	0	1	1	1	1	0	
			15 - 25	0	0	2	1	1	0	1	0	
			25 - 35	0	0	0	0	3	0	0	0	
			35 - 45	0	0	0	0	0	0	1	0	
			45 - 55	0	1	1	2	0	1	1	1	
			55 - 65	0	0	0	0	0	1	0	0	
			65 - 75	0	0	0	0	0	0	0	0	
			75 - 85	0	0	0	0	0	0	0	1	6.2

(Continued)

Date	Time of Obs. a.m. o'clock	Time of Obs. p.m. o'clock	Distance moved (ft. from stake)	Number of tagged snails in sector A	B	C	D	E	F	G	H	% emergence
1 July		6	within 5 ft.	0	0	0	0	0	0	1	1	0
2 July	7		1 - 5	0	0	0	0	0	0	0	0	
			5 - 15	0	0	1	0	0	0	0	0	
			15 - 35	0	0	0	0	0	0	0	0	
			35 - 55	0	0	0	0	0	1	1	1	
			55 - 65	0	0	0	0	0	0	0	1	
			65 - 75	0	0	0	0	0	1	1	0	17
2 July		7	1 - 5	0	0	0	0	0	0	0	0	
			5 - 15	0	0	0	0	0	1	0	0	
			15 - 25	0	0	0	0	0	0	0	0	
			25 - 35	0	0	0	0	0	1	0	1	
			35 - 45	0	0	0	0	0	0	0	0	
			45 - 65	0	0	0	0	0	1	0	0	
			65 - 85	0	0	0	0	0	1	2	0	
			85 - 105	0	0	0	0	0	0	0	0	
			105 - 125	0	0	0	0	0	0	1	1	2.2
3 July	8		1 - 45	0	0	0	0	0	0	0	0	
			45 - 65	0	0	0	2	0	1	0	0	
			65 - 75	1	0	0	0	0	0	1	0	
			75 - 95	0	0	0	0	0	0	1	0	1.5
3 July		8	1 - 5	0	0	0	0	0	0	0	0	
			5 - 15	0	0	0	0	1	1	0	0	
			15 - 25	1	0	0	0	0	0	0	0	
			25 - 45	0	1	0	0	0	1	0	0	
			45 - 65	0	1	1	2	0	0	0	0	
			65 - 95	0	0	0	0	0	0	0	0	
			95 - 105	0	0	0	0	0	0	0	1	
			105 - 115	0	0	0	0	0	0	0	0	
			115 - 125	0	0	0	0	0	0	1	0	2.7
4 July		9	1 - 5	0	1	0	0	0	0	0	0	
			5 - 25	2	0	0	1	2	0	0	0	
			25 - 45	0	1	2	0	0	1	0	0	
			45 - 65	0	0	0	2	0	0	0	0	
			65 - 85	0	0	0	0	0	1	2	0	
			85 - 115	0	0	0	0	0	0	0	0	
			115 - 125	0	0	0	0	0	0	1	1	4.2
5 July		10	1 - 5	0	0	0	0	0	0	1	0	
			15 - 35	0	0	0	0	0	0	0	0	
			35 - 55	0	0	4	10	0	1	0	0	
			55 - 75	0	0	0	1	0	0	0	0	
			75 - 95	0	0	0	1	0	0	0	0	4.5

The above table does not attempt to show the behaviour of individual snails although the data from which it was composed were records of serial numbers of individual snails. Particulars on the behaviour of individuals which showed the greatest frequency of emergence and greatest distances moved are shown in Graphs I to V and the following table lists the observations on this limited group.

Serial numbers of snails described in graphs I to V and dates on which they were observed.

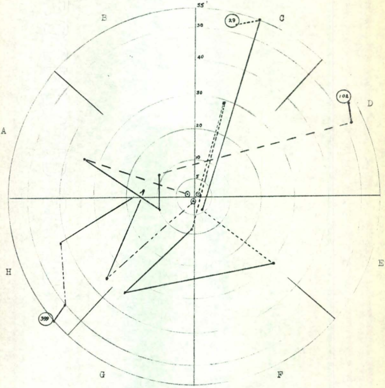
Graph No.	No. of snail	June 25	26	27	28	29	30	July 1	2	3	4	5
I	399		-	-	-			-	-			
	102		-	-				-			-	-
	29		-		-	-		-	-	-		-
II	177		-		-	-						
	341			-	-			-				
	73					-		-			-	
	94	-						-		-		
III	279	-			-							-
	301					-					-	-
	392		-		-						-	
	217	-	-									-
IV	135		-		x--	-				-		
	354	-				-						-
	16		-		-				-			
	45					-		-	-			
V	322				-			-			-	
	383					-			-			
	120							-		-		
	208 128) one observation								-		-	

x Two observations on the same date, i.e. on a.m. and p.m. tide.

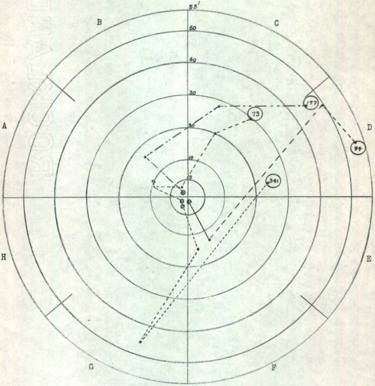
In studying Graphs I - V the following conventions should be kept in mind:

1. A dotted line connecting two observations signifies that there was at least one visit between when this animal was not seen.

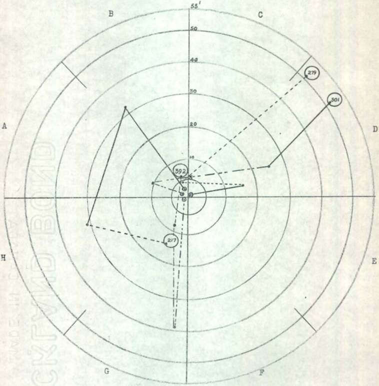
2. A continuous line indicates that observations were consecutive and that there was no "skip", i.e. the two were separated by a 24-hour interval only.



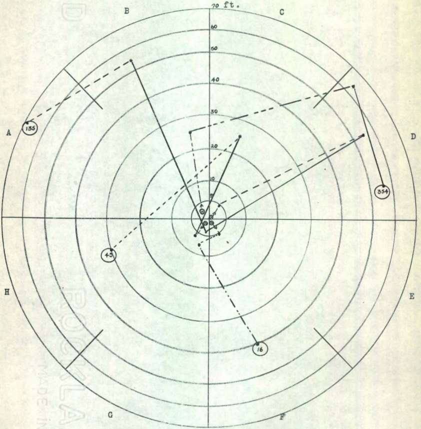
Graph I



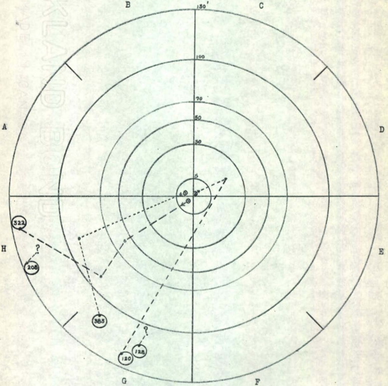
Graph II.



Graph III.



Graph IV.



Graph V.

3. As in describing movement in tanks, a line connecting two observations in chronological order does not pretend to portray the actual path followed by the snail between these two points.

The animals described in Graph I showed the greatest regularity of emergence and therefore a more complete picture of activity can be had from it than from the other four graphs.

As previously noted in experiments on movement with shorter time intervals between observations the course taken by the moving snail is most erratic. The field tests support the same conclusions as the tank experiments.

Conclusions and Discussion

1. On distribution. The animals are capable of extensive movement but owing to the lack of sustained rectilinear movement, pedal locomotion is probably of little importance in distribution of the species. Presumably the wide discrimination of veliger larvae by tidal currents makes up for this.

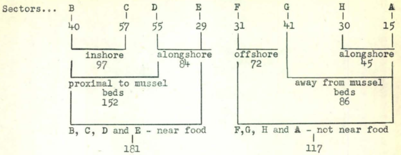
2. On tropho-tropism. It is probable that one of the most important factors instigating pedal locomotion is the need for food. Whether the reaction of whelks observed in these experiments are such as to be justly called a tropism is doubtful and debatable. The Holts Point experimental data do not deny or confirm this view but do exhibit interesting features worthy of further discussion here. Of all the sectors in the circular plot B, C and D were closest to the mussel beds and thus important in this consideration.

From the Graphs I - V two facts are apparent:

a) There is a greater tendency for the snail to become stabilized in the sectors adjacent to the source of food than in those opposite it. This is accomplished only after a period of wandering search (trial and error) during which the whelk covers much ground with its typical "zig-zag" manner. Whether this apparently erratic direction of movement is conditioned by a systematized pattern or by a random coverage of available flat is questionable.

b) The greatest movement away from the release stake was observed in offshore sectors, H and G, diagonally opposite to B and D.

The basis for these conclusions is a little clearer when the data are presented in the diagram below. This shows the total numbers of observations of tagged animals in each sector from June 25 to July 5 and the distribution of these in relation to the source of food (Fig. 105).



From the figures supplied it might be inferred that there is a positive food tropism but the writer does not favour this deduction even though he was inclined to it earlier (Giglioli 1949). There is little doubt that the "food urge" plays a very important part in stimulating pedal locomotion, and that the apparently erratic direction of movement represents a systematic search of the flat in the immediate proximity of the snail. Notwithstanding these facts and the possible attraction of snails to food when separated by small distances (a few inches), there appears to be no generalized mass movement towards food which would justify the term "tropism".

On the basis of general field observations the writer suggested in 1949 the existence of a positive tropho-tropism. This was based on the coincidence of high snail populations and abundant food. The data, now at hand clearly indicates the fallacy of the above speculation. The snail executes a "multi-directional" search until it locates food, if the supply is abundant, it then becomes stabilized and its subsequent movement is negligible. For this reason the population over sources of food, such as the mussel beds and clam relays (Thurber 1949) is cumulative and rapidly increases. This, however, is not due to attraction but to the whelk "happening" to locate the source during its wandering search for food and becoming settled there. If food is not found, then movement continues and may become extensive (See Graph V Sectors G and H).

3. <u>On Bait-traps</u>. In the light of the foregoing discussion it is felt that the use and advisability of bait traps ought to be briefly discussed at this point.

It has been suggested that baiting would be an aid to control along with manual collection of drills and that the bait proper need not be formed by shellfish, but that rotting fish et alia are efficient in attracting the whelk and simplifying collection.

Though the writer has not tested the value of baiting experimentally, two observations have been made which cast doubt on its likely value.

(a) Never has either P. heros or P. triseriata been observed feeding on carrion though opportunity is not lacking for scavenging in many abandoned weirs which have been visited regularly. At Belliveau Cove scavenging amongst the gastropod population present is undertaken solely by the ubiquitous Nassa trivitata.

(b) As previously indicated, it appears that living baits such as clam relays do not "attract" the snail but tend to stabilize the wandering whelk once this encounters the source of food.

It appears, then, that any value bait traps may have is limited and that the cheapest baits are not likely to be useful, and that bait will not "draw" snails to it in the regular sense of the word. It might aid collection but this aid would be derived from the tendency of the snail to wander and then become "quasisedentary" on reaching abundant supplies of food.

4. On Emergence. While conducting the second flat test at Holts Point and from the analysis of the data obtained an observation was made that invites speculation without suggesting a solution to the problem it presents. Some snails are more likely to emerge than others.

Recovery of tagged specimens was accomplished by a systematic search with a Coleman pressure gasoline lantern so that if the tagged snails emerged at all the chances of the observer overlooking them were very slight. Adverse weather conditions during the experiment were frequent (fog, rain and rough waters) and these have been previously noted to affect percentage emergence. The % emergence varied from 19-0, these low percentages have been observed previously and though not clearly understood they add nothing to our present concept of factors conditioning and governing the rate of emergence. The emergence in tanks (See tabulation of results of experiments I and II) was much higher. The observation, that may open new approaches to this problem, is that although the tagging operation was the same for the whole of the second sample of 400 tagged snails released at Holts Point, 191, almost 50%, were never observed during the 16 flat examinations that were made. Only two tagged specimens were found dead so that the low "recovery" cannot be attributed to tagging mortality. From this it would appear that half the sample remained buried throughout the experiment. Does this mean that emergence is affected by such factors as: age, sex, mating, collar formation and that nightly emergence is not typical of the population as a whole but only of a particular fraction of it? As a basis for speculation on the part of the reader the frequencies of observation of each of the tagged specimens is listed in the following table.

Serial numbers of the 400 "tagged" snails released at Holt's Point and the total number of times each was observed in the 16 examinations of the flat. No figure opposite the serial numbers indicates that this snail was never observed after release. "N" is the tag number and "F" is the frequency of observations.

N	F	N	F	N	F	N	F	N	F	N	F	N	F	N	F	N	F	N	F
1	1	11		21		31		41		51		61	1	71	1	81		91	
2	1	2		2		2	1	2		2	1	2	2	2		2		2	1
3	1	3	1	3	2	3		3	2	3	3	3		3	3	3		3	
4		4	2	4		4	2	4	1	4		4		4		4	1	4	3
5		5	2	5		5	3	5	3	5	1	5	1	5		5	1	5	1
6	1	6	4	6	1	6		6	1	6		6	1	6	1	6		6	
7		7		7	2	7	3	7		7		7	1	7	1	7	1	7	
8	3	8	1	8	1	8		8		8	1	8	1	8	2	8		8	1
9		9		9	7	9		9	2	9		9	2	9		9		9	
10	1	20		30	1	40	1	50		60	1	70		80		90		100	1
101	1	111	2	121	1	131		141	3	151		161		171	2	181		191	1
2	5	2	1	2		2	1	2	1	2	2	2		2		2	1	2	1
3		3	1	3		3		3	1	3		3	2	3	1	3		3	
4	2	4		4	2	4	2	4	1	4	2	4		4	1	4	2	4	
5	1	5		5	1	5	5	5	1	5	1	5	1	5		5	2	5	
6	3	6		6	2	6		6	1	6		6		6	1	6	1	6	
7	1	7		7	2	7		7		7		7	1	7	3	7		7	
8		8		8	1	8	1	8		8	2	8		8	1	8		8	
9	2	9		9	1	9	1	9		9		9	1	9	1	9	1	9	
110	1	120	2	130	1	140		150		160		170		180		190	1	200	
201		211		221	1	231		241	1	251		261	1	271		281		291	
2	1	2	1	2		2	1	2		2		2		2	1	2		2	
3	1	3		3		3	1	3	1	3	1	3	1	3	1	3	2	3	
4		4		4		4	3	4		4	1	4		4	2	4		4	
5	2	5	1	5	2	5	1	5		5	1	5		5		5			
6		6	1	6		6	2	6		6	2	6		6		6		6	
7		7	3	7		7	1	7	1	7	2	7		7		7		7	
8	1	8		8	1	8	1	8		8		8	1	8	1	8		8	1
9		9		9		9	2	9	2	9		9		9	3	9		9	
210	1	220		230		240	1	250		260	2	270		280		290	2	300	
301	3	311	1	321	2	331	1	341	3	351	2	361		371		381		391	
2		2		2	3	2	1	2		2		2		2	2	2		2	3
3		3	2	3	1	3		3	2	3	1	3	1	3	1	3	2	3	1
4	1	4		4		4	2	4		4	3	4	2	4	1	4	2	4	
5	1	5	2	5	2	5	2	5	1	5	1	5	1	5	1	5	1	5	1
6	2	6		6	1	6		6	1	6	2	6		6	2	6		6	
7	2	7		7		7	2	7	2	7	2	7	1	7		7		7	
8		8		8	2	8	2	8		8		8	1	8		8		8	
9	1	9		9		9		9	2	9	1	9		9	1	9		9	5
310		320		330	2	340	1	350		360	2	370	2	380		390	1	400	

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VI The 1950 Emergent Larvae of P. heros and P. triseriata.

Introduction

Stinson ('46) observed that theemergent larva of P. triseriata was benthic and lacking a planktonic stage. In aquaria he demonstrated that the smaller and more active larva of P. heros was truly planktonic with an active natatorial phase; however he failed to recover either of these larvae in tows notwithstanding the abundance of P. heros egg collars on the flat.

In 1949 the writer observed that P. triseriata larvae possessed a "semi-planktonic" stage and made the suggestion that this and Stinson's 1946 observations were not necessarily fundamentally discordant. The semi-planktonic condition in 1949 might possibly have been brought about by the unusually high temperatures encountered that summer. These might conceiveably have instigated an earlier-than-normal crumbling of collars and a release of premature larvae. 1950 was expected to be and turned out to be cooler than 1949 on the Acadian shore so it was planned to examine plankton catches to see if this would bring about conditions such as Stinson described for this species at Belliveau Cove.

In 1949 the writer has little success in gaining an understanding of the movements of P. heros larvae. Stinson's in vitro observations were confirmed, but it was impossible to recover it in tows at Belliveau Cove. In late September one larva of this species was recovered from a tow made at St. Andrews, N.B, and a few others were collected in shallow water in the immediate vicinity of crumbling collars during the early stages of flood tide.

This poor recovery of larvae that should have been abundant, judging from the large numbers of egg collars continued to be a mystery.

In the 1949 report a larval release at incipient flood tide and an offshore migration of larvae to deep waters was postulated as an explanation of our general failure to discover specimens of P. heros 3 mm. to 15 mm. in shell height in the intertidal zone in all localities we have explored. Offshore settlement of larvae and onshore migration of sexually mature animals from deep water seemed rather involved but some such explanation was required.

The 1950 investigation was chiefly concerned with the above problem. A search was made for offshore concentrations of larvae.

1950 Work.

In 1949 tows with a No. 18 mesh plankton net were made mainly close to the surface and within 1500 feet of shore. In 1950 ten-minute tows with the same net were made parallel to shore and at three distances from high-water mark at Belliveau Cove:

a) at 1300 ft. (inshore of the weir).

b) at 1700 ft. (immediately offshore of the weir).

c) at approx. 1½ miles offshore.

So far as possible all drags were deep rather than superficial. It was impossible to make them right on the bottom because its irregularities were a hazard to the delicate and costly net.

In several instances tidal currents were strong enough to distend the net and plankton catches were made simply by anchoring the boat and putting the net overboard. The "towing" time in such instances was the same as in regular hauls - ten minutes.

The main work was performed at Belliveau Cove but other drags were taken in New Brunswick. Seven were taken from the Pottery Bridge cove near the Biological Station. In addition to these drags which were taken mostly from motor boats at high tide, hauls were made from dinghies at Holts Point immediately over crumbling egg collars at incipient flood and definitive ebb tide in 2-3 ft. of water.

The catches were examined by taking 3 random samples composed of 3 cc. each from the suspended plankton in the original one-pint collecting jar. These samples were removed with a piston pipette and counts made in a squared petri dish under a magnification of 30 diameters. The results are listed in the following tables. For the examination and identification of larvae in Pottery Cove catches the author wishes to thank Mrs. Esther Lord of the Atlantic Biological Station who worked with him.

Table A

Larvae recovered from 9 cc. samples of ten-minute plankton catches made in deep water at Belliveau Cove, N.S., and Holts Point, N.B., 1950.

Place	Date	Position of Station	Varieties of larvae found			Bivalve larvae
			P. triseriata	*P. heros*	*Nassa* sp.	
Belliveau Cove	19 July p.m.	1300 ft.*	1	0	0	0
		1700 ft.*	7	0	0	0
		1½ mi. *	4	0	0	0
	12 July p.m.	1300 ft.	22	0	0	0
		1700	4	0	0	0
		1½ mi.	2	0	0	0
	23 July p.m.	1300 ft.	8	0	1	0
		1700	7	0	0	0
		1½ mi.	3	0	0	0

* Tow taken at anchor

(Continued)

Place	Date	Position of Station	Varieties of larvae found			Bivalve larvae
			P. triseriata	*P. heros*	*Nassa* sp.	
Belliveau Cove	24 July p.m.	1300 ft.	10	0	0	0
		1700 ft.	4	1	0	0
		1½ mi.	15	2	2	0
	25 July p.m.	1300 ft.	5	0	0	1
		1700 ft.	24	0	6	0
		1½ mi.	23	0	1	0
	26 July a.m.	1300 ft.	7	0	0	0
			0	0	0	0
			1	0	0	0
	27 July a.m.	1300 ft.	0	0	0	0
		1700 ft.	3	0	0	0
		1½ mi.	0	0	0	46
	28 July a.m.	1300 ft.	11	0	2	5
		1700 ft.	1	0	0	8
		1½ mi.	2	0	0	20
	28 July p.m.	1300 ft.	3	0	0	6
		1500 ft.	5	0	0	4
		1½ mi.	4	0	1	22
	29 July a.m.	1300 ft.	2	0	0	10
		1700 ft.	2	0	0	5
		1½ mi.	2	0	0	3
	30 July a.m.	1300 ft.	1	0	1	1
		1700 ft.	0	0	0	4
		1½ mi.	0	0	0	0
	31 July p.m.	1300 ft.	5	0	2	2
		1700 ft.	3	0	2	3
		1½ mi.	0	0	1	5
	1 Aug. p.m.	1300 ft.	4	0	2	4
		1700 ft.	0	0	0	8
		1½ mi.	0	0	0	3
	7 Aug. p.m.	1300 ft.	2	0	1	9
		1700 ft.	0	0	0	10
		1½ mi.	0	0	0	10
Holts Pt., N.B.	11 Aug. a.m.	over flat	0	0	0	97
		1½ mi.	0	0	0	13
	12 Aug. a.m.	over flat	1	0	0	114
		1½ mi.	0	0	0	159
	13 Aug.	over flat				
		(a) surface	0	0	0	2
		(b) deep	0	0	0	111
		1½ mi. offshore				
		(a) surface	0	0	0	65
		(b) deep	0	0	0	75

Table B

Larvae recovered from ten-minute Holts Point tows made in water 2-3 feet deep at definitive ebb and incipient flood tide August 13 above crumbling collars.

	Drag	P. triseriata	P. heros	Nassa sp.	Bivalve larvae
Definitive ebb	1	0	0	0	5
	2	0	0	0	20
	3	0	0	0	16
Incipient flood	1	0	0	0	4
	2	0	0	0	0
	3	0	0	0	0

Table C

Larvae recovered from three-quarter-hour tows in deep water in the main bays between St. Andrews and Holts Point, N.B., Aug. 14.

Locality	P. triseriata	P. heros	Nassa sp.	Bivalve larvae
Bocabec	0	1	0	39
McCanns Cove	0	0	0	20
Pottery Cove	4	3	0	13

Table D

P. heros larvae recovered from 10-minute drags over flats at Pottery Cove, N.B. Identification by Mrs. E. Lord of the Atlantic Biological Station.

Date	P.heros larvae no.
17 Aug.	3
19 "	2
21 "	11
22 "	1
23 "	20
24 "	3
25 "	6

Discussion of Results

Re: P. triseriata. It would appear that during the summer of 1950 semi-planktonic larvae of P. triseriata were present in just as large numbers as in 1949. There was no evidence to substantiate Stinson's conclusion that the larvae of this species are benthic. It is possible but improbable that benthic and semi-planktonic larvae of the same species may co-exist and that the writer has failed to observe the former and Stinson the latter. The writer's opinion, however, is that Stinson mistook semi-planktonic larvae for benthic and that the larvae of P. triseriata are typically semi-planktonic.

Re: P. heros. The results of study in the 1950 season have contributed little towards a satisfactory understanding of the distribution and settlement of these larvae. We can now certainly state that they are truly planktonic but little more except that there were no observed concentrations of larvae offshore.

From the tables the following questions arise:

a) Why is it possible to collect numerous P. heros larvae in one locality and not in another where adults and egg collars are equally abundant (cf. Belliveau Cove and Pottery Cove)?

b) Holts Pt. is probably the area of densest population for this species on the whole Fundy coast. Why were recoveries so low there?

c) Why is recovery over crumbling collars so low under field conditions when the very same collars release thousands of larvae if crushed in an aquarium of seawater when taken immediately to the laboratory?

d) Where do the larvae go after release from the collar?

e) What is the distribution of adults under 15 mm. in shell height?

Conclusion.

From our studies we can safely assume that the distribution of larvae of P. triseriata is mainly controlled by tidal currents which may vary with location and thus determine the extent of distribution. The relatively large size of the larva and the small size of the swimming organ (velum) suggests that the larval period is brief. It is apparently long enough, however, to offset any advantage collection of egg collars on clam flats might have in controlling the numbers of adults of these destructive snails.

The larvae of P. heros are truly planktonic and subject to the same factors regulating distribution as those of P. triseriata. The smaller size of the animal and the relatively larger size of the velum suggest that the larval period is longer and that it has accordingly a better chance for wider distribution. The inadequacy of collar collection as a means of controlling the numbers of adults of this species on our clam flats is obvious.

Considering the large numbers of larvae present in mature P. heros egg collars, and the abundance of these on certain flats it would appear that counts of them in plankton catches are a poor index to their true abundance.

There is no evidence to support the theory that the larvae concentrate and settle offshore to maintain a stock of juveniles less than 15 mm. high there that could sustain an inshore population of adults by shoreward migration.

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VII. Clam Flats and their Problems.

Introduction.

In the author's report for 1949, and in the foregoing sections of the present report, emphasis has been placed on the biology and functional anatomy of the clam drills. Little reference has been made to their environmental relationships except where they directly concerned the survival or depletion of clam stocks (Mya arenaria). In the present section more attention is directed to those aspects of the biology of these animals that are of more general ecological significance and wherever feasible tentative conclusions are drawn.

Flat Conditions Affect Chance for Study.

If we are to consider the flat as an environment, it is probably worth while to make a few general remarks on conditions observed by the writer under which the populations of Mya and Polinices co-exist in New Brunswick and Nova Scotia and how they affect the chances for their investigation.

A wide flat, such as that at Belliveau Cove, N.S., sloping gently from high- to low-water mark, composed of sand and mud to form a compact but plastic substratum, and free of freshwater influences and large beds of seaweed or rocks is probably the best locality for the study of Mya and the two species of clam drill, P. heros and P. triseriata. P. triseriata is found mainly at higher levels on intertidal flats while P. heros owing to the poor resistance of its egg collars to dessication and to its truly pelagic larvae P. heros is restricted to the lower parts of flats. The upper parts of some flats are rocky and steeply sloping, such as at Holts Point, N.B., but the lower parts almost level and therefore extensive. The upper beach is rocky and therefore unsuited to either species of drill. The lowest level is sandy and never exposed at neap tides and exposed for only brief periods at spring tides. In this area as might be expected, P. heros abounds but P. triseriata is absent.

In spite of beach level preferences, it will be noted that where the soil is sandy and compact P. heros will sometimes predominate and that P. triseriata will predominate where the soil surface is of soft mud. This latter condition is often found in weirs at low levels on the beach and the food of the drill in these cases often consists of mussels which abound there. A flat that shows a mixture of these soil conditions is considered best for a study of predator-prey relationships of the two species but need not necessarily be the best suited to the survival of vigorous stocks of clams.

Factors Affecting Survival of Clams and Drills.

1. During the Fertilization of Eggs

Because the clam is a quasi-sedentary animal and cannot seek out a member of the opposite sex and assure fertilization of its germ cells, it must produce these in enormous numbers and shed them freely into the water to ensure that some are fertilized.

The possibility of fertilization depends on two main factors:

(i) the presence in large numbers of these to overcome the probability of non-fertilization.

(ii) the simultaneous release of eggs and sperms by the mature adults.

We must take into account the factors which make fertilization difficult. That is to say, those factors which reduce the density of germ cells such as dispersion by tidal currents or those factors which reduce the chances for germ cells of opposite types (sperms and eggs) being free in the water at the same time.

The possible importance of this second factor may not be great if the principle of "mass spawning" as demonstrated by British workers in oysters, applies in the case of clams. They showed the ability of mature oysters in densely-populated habitats to simultaneously release their germ cells by a hormonal trigger mechanism. So long as the density of the parent stock remains high, the chances for successful fertilization are likely to be good but as the populations are more and more depressed by intense fishing as Canadian east coast clams now are, this factor assumes increasing importance in the maintenance of stocks.

The sedentary clam's method of reproduction contrasts sharply with the efficient internal fertilization by copulation demonstrated by mobile Polinices.

2. During Larval Development.

After fertilization, the development of the clam embryo into a truly planktonic larva, is subject to the risk of encountering unfavourable conditions of temperature, salinity, exposure and dessication, poor availability of phytoplankton as food and exposure to large numbers of enemies that are plankton-feeders. The fertilized egg of both clam drills, on the other hand, undergoes its early development in the stable and secure environment of the sand collar, which in the case of P. triseriata crumbles and releases a well developed semi-planktonic larva, with a short planktotrophic existence. The larva of P. heros has a long planktotrophic life and capable of wider tidal distribution than P. triseriata but nevertheless is protected during its earliest, most helpless stage. It does not emerge from the egg case until it is a well-formed veliger.

3. At Larval Settlement

Whether the place of settlement of mature clam larvae is determined purely by chance and by tidal agency, or whether it is "selected" to some extent by the larvae is still a controversial question. The fact that large quantities of spat clams are found in restricted areas may be taken as evidence of gregarious selection but could be explained equally well by assuming that the position of settlement on the flat is determined by chance factors such as tidal action just as tidal action determines the distribution of beach wrack in regular patterns.

After settlement, the clam's survival will depend on the availability of planktonic food, on its resistance to temperature and dessication during the intertidal phase, and on the presence or absence of such predators as gulls, flounders and clam drills.

In contrast, the pelagic life of the P. triseriata is short but still long enough to insure dissemination during the larval phase of development.

The larva life of P. heros presents an unsolved problem. Apparently, it has a long planktonic existence and, to all appearances, leaves the intertidal zone, returning only as an adult.

4. During Adult Life

From larval settlement to maturity, both clams and snails are exposed to predation by gulls, flounders, and crabs. Besides these, clams have two serious enemies -- drills and man.

Although adult clams are comparatively safe from all predators except the last two mentioned, their quest for food is laborious, and on an open tide-swept flat, often precarious. In contrast we have shown the snail to be capable of extensive movement in quest of food, and if this is not found, able to withstand long periods of starvation.

The Role of Beach Cover in Regulating Clam Populations

It is obvious that all factors which tend to disperse a population, or its germ cells when released, or to prevent settling of the spat or to reduce the availability of phytoplanktonic food, will lead to low survival, poor colonization. As previously indicated, there are many environmental factors bearing on this but of these, the writer believes there is one upon which this problem principally revolves. This is the degree of "natural cover" on the flat. In most cases, this can be stated more specifically as the degree of coverage by eel grass, Zostera marina.

This view has been questioned and has received little factual support, but the writer is convinced that this is because the problem has not yet been properly looked into. We have reports by the Massachusetts Department of Conservation of increased clam sets on flats where eddies and vortices are formed by natural or man-made obstructions on the flat, such conditions have been caused by laying thatch from marsh banks over the substratum. It is logical to expect the presence of eel grass or algal beds on a flat to have similar effects. The binding effect of eel grass roots stabalizes the flat and gives greater security to semi-sessile animals living within it because the "scouring" action of the seas is so greatly reduced. Furthermore, the blades of grass will set up disturbances in the water flow tending to form local eddies which may help in precipitating late planktonic stages and will supply these with stable holdfasts. The presence of this vegetation, by reducing the current speeds close to the bottom, especially when the water is shallow at early flood and late ebb tide, tends to concentrate and retain plankton and organic detritus, thus increasing the available source of food to sedentary animals such as the clam.

The eelgrass roots form a dense mat that presents an obstacle to animals such as the clam drill, who spend the greater part of their life burrowing in the flat. The same root mat offers clams protection from gulls and flounders whose depredations are dependent on looseness of the substratum, which must be washed aside by "puddling" or "flopping" to expose the buried food organisms.

The Role of Man - Conservation and Depletion of Clam Stocks

As long as there is a heavy commercial demand for small clams and no demand for clam drills, conservation and protection of clams will continue to be difficult. It has been clearly shown that manual collection of adult snails or their egg cases is impractical as a means of controlling the numbers of these clam enemies. The only means of insuring survival is to grow the clams where there are no drills. Transfer of clams from drill-infested grounds to drill-free grounds is a wise action but cannot be recommended as a "sure-fire" method until we develop a clear idea of what flat conditions are necessary for good clam survival. Planting a now depleted flat, which, fifteen years ago supported a large population of clams, may or may not be a wise move if there are drills in the area.

Even though drills are capable of great destruction it seems improbable that thev can have been responsible for the great drop in clam stocks which has been noted in many areas on our coast even though drill-abundance is said to have increased in recent years. The writer's belief is that the physical environmental demands of clams and drills are different and that changes in the relative abundance of the two should be taken as evidence of changes in the environment rather than as resulting from a predator-prey relationship. A more realistic approach to the problem of restoring clam stocks could be had by studying the conditions under which vigorous populations of clams still survive - e.g., in the Sissiboo River -- and trying to recreate these in the depleted areas than by pursuing a search for methods of drill control. Such efforts would probably involve experiments with obstructions which would tend to break currents and encourage algal growth on "naked" flats that are suffering from want of stability.