FISHERIES RESEARCH BOARD OF CANADA

MANUSCRIPT REPORTS OF THE BIOLOGICAL STATIONS

No. 398

Title

Some observations on the biology of the whelk, *Polynices heros* Say (1822), and *Polynices triseriata* Say (1826), at Belliveau Cove, Nova Scotia.

Author

M.E.C.Giglioli

1949.

Misleading Errata

Page	Paragraph	Line	
1	3	5	Read "Beairsto" not "Baeristo" here and throughout report.
1	3	5	Beairsto 1948 not -49.
26	6	10	See Fig. 11.
32	1	8	Read Fig. 15, 16, 17 and 18-21.
33	3	1	Read Fig. 23 not 19.
	5	6	" " " " "
	6	9	" " 24 " 20.
35	2	6	Read "possibly" not "possible".
36	6	11	Read Fig. 23 not 19.
45	5	a)	Read not 1.0/1.1 but 0.9/1
		b)	" " " " "
58	Fig. 12		Read "secretory" not "secretary".
73	4	3	Read "coarse sand" not "clay".
74	7	2	Add "as those of P. triseriata."
83	Fig. 42		Delete "laminated".
88	Fig. 50	6	Read "forty-five" not "five".
92	-	1	First entry, read Ht. of snail 2.3 not 1.3.
93	1	1	Read "review" not "revise".
100	-	-	In line 5 of "N.B." read "capsular" not "capillar".
112	Fig. 65	-	Read "infected" not "affected".
114	3	5	Delete "no".
116	8	7	Add "Both larvae are characterized by two small "eye spots" situated medio-posteriorly in the velar lobes."
127	7	3	Read "....of the various strands of wool".
130	2	1	Delete ".....it is probable", read ".....we might suggest".
136	7	2	Read "wet" not "wheat".
Appendix page 2	Section 6	8	Read "artifact" not "artifice".

ACKNOWLEDGMENT

The writer would like to express his thanks to Dr. J.S. Stanley, Chairman, Biological Sciences Group, McGill University, for allowing the author to submit this report to meet the requirements of the prescribed B.Sc. (Honours) project and for placing at his disposal the facilities of the Department of Zoology.

My thanks are due to Dr. N.J. Berrill, McGill University, for tempering my more extravagant speculations and for his kind criticisms. To Dr. M.J. Dunbar, McGill University, for his valuable held in placing at my disposal pertinent references and in obtaining microfilm copies of others.

I am in great debt to Dr. P. Bondesen, of Copenhagen, for his friendly advice, constructive criticism and welcome suggestions, papers and encouragement.

To Mr. P. Hobbsbawn I owe for the translation of Dr. W.E. Hankels' papers. I am greatly indebited to my co-worker and friend, Mr. D. Therriault of Belliveau Cove N.S. for his faithful and efficient service in the field.

Special thanks are due to Miss Margaret Davidson, of McGill University, for her valuable help and patience in the editing of the rough draft, and to Miss Betty Dunn for her neatness and efficiency in mimeographing the report.

To Mr. W. Pollock, of McGill University, goes the merit and my sincerest gratitude for many painstaking hours spent in providing the superb microphotographs and reproductions of drawings illustrating the report.

My greatest debt of gratitude goes to the staff of the Atlantic Biological Station of St. Andrews N.B. and more specifically to Dr. J.C. Medcof who supervised the field work on Polynices and made the writing of this report possible by his incessant labours and friendly support. Among other kindnesses I wish to thank him for his valuable advice, constructive criticism, for the provision of essential materials and papers and above all for allowing the writer a high degree of freedom in executing the investigation. Last but not least I wish to re-express my gratitude to Dr. J.C. Medcof and Dr. M.J. Dunbar who shared the ungrateful task of re-editing the final draft of the report and for making many constructive suggestions, which have greatly improved its manner of presentation.

March 1950

Acknowledgment of Illustrations Used In This Report

Figure	Drawn by	Photographer
1	M.E.C. Giglioli	W. Pollock
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Figure	Drawn by	Photographer
51	M.E.C. Giglioli	W. Pollock
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70	"	"
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72		M.E.C. Giglioli
73	M.E.C. Giglioli	W. Pollock
74	"	W. Pollock

Table of Contents

Report on Polynices Investigation at Belliveau's Cove, Nova Scotia, 1946-1949.

Fisheries Research Board,
Atlantic Biological Station,
St. Andrews, N.B.

I. Introduction:

A) 1949 problem as presented to the author and the attitude taken in the report.[1]

The potential threat to clam stocks presented by snails of the genus Polynices (Natica Lunatia) was first realized by investigators, along the Atlantic American seaboard, who attempted control by manual collection of egg collars and adult snails. When Polynices was shown to be an important participant in the destruction of (Mya arenaria) clam stocks in the Maritimes, it was decided that a general investigation, aimed at effective Polynices control, should be investigated. The task of surveying the Atlantic species of snail and assessing the value of mechanical control measures by manual collection of both adult and egg collar was undertaken by the Atlantic Biological Station of the Fisheries Research Board and directed by Dr. J. C. Medcof of St. Andrew's, New Brunswick.

After a critical examination of the affected areas in the Maritime Provinces Dr. J. C. Medcof, in the summer of 1945, selected Belliveau Cove, Nova Scotia, as a desirable location for the investigation. This choice was based on the abundance of the snail and on the once plentiful clam stocks there, suggesting a well balanced population of predator and prey and thus offering optimal conditions for general observation of the cockle's life history, its relation to the clam, and the feasibility of control.

Field work at Belliveau Cove was commenced in May, 1946, by R. H. Stinson, a seasonal field assistant, and was continued during the summers of 1947, 1948 and 1949 by J. M. Wheatley, A. Larocque and the author respectively; further studies were undertaken by Miss F. Baeristo, in 1949, and L. Thurber, 1949, at St. Andrew's. Prior to 1949 all possible aspects of the problem were considered, from life history, morphology, habits and flat ecology to control. At the initiation of the 1949 season the author was requested to approach the summer's work with the aim of closing the investigation; the scope of the work was thus limited to checking, enlarging and concluding previously commenced aspects rather

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1. This report is based on data compiled from the annual reports of six field assistants. Tables and observations submitted herein have been credited to the original investigators. To avoid unnecessary repetition some minor aspects which were not considered pertinent were neglected in this comprehensive review of the Polynices problem. The selection of data and manner of reviewing it was left entirely to the discretion of the writer; if further details are desired see the original manuscripts.

than developing new ones. Consequently in this report the author attempts to coordinate and draw tentative conclusions from the data compiled by the past five field workers. In order to achieve this a fair measure of liberty has been taken in suggesting and deducing possible conclusions from inadequate experimentation in the sincere hope of coordinating the many aspects treated and stimulating further investigation to prove or disprove some of the more theoretical interpretations; these speculations may eventually prove to be of practical importance in the more immediate field of control.

B) Polynices in Canadian waters - Historical.

The first recorded observation of Polynices in Canadian waters was made by Champlain (1604) in the Bay of Fundy region at the present site of Weymouth harbour, in St. Mary Bay, N.S. He described the local marine fauna as including: "Many shellfish such as mussles, cockles and sea snails." The latter were considered by Ganong (1889) to be the large whelk, Buccimium undatum and Polynices heros.

Ganong (1889) recorded the tidal distribution of P. heros from low water to 40 fathoms. Melville (1930) corroborated his observation but limited the distribution to 17 fathoms, while Pratt (1927) reported the recovery of specimens from a depth of 238 fathoms.

C) Belliveau Cove - geographical location and general description of locality.

Belliveau Cove is situated some 24 miles southwest of Digby, N.S., on the Digby-to-Yarmouth highway, on St. Mary Bay. St. Mary Bay is bounded to the northeast by the Acadian shore and to the southwest by the Digby Neck peninsula, Brier and Long Islands, these lying approximately 5 miles across the Bay from Belliveau Cove.

The Acadian shore is typified by an undulating coast dropping steeply to the sea. Belliveau Cove is situated in a depressed area between the relatively high ground of St. Bernard to the northeast and Church Point to the southwest. The Cove proper is approximately one mile long, taken from the promontory separating it from White's Cove to Mayor's Point, and about half a mile deep.

D) General review of Polynices investigations undertaken by the Atlantic Biological Station.

At the initiation of the investigation in 1946, very little was known about representatives of the genus Polynices found in Canadian waters, in spite of the fact that control measures had already been attempted in American waters. The task of identifying the local species and investigating such problems as reproduction, identification of egg collars, embryology, larval development and description, adult growth, feeding habits, and the possible role of predators and parasites in the snail's life history was commenced by R. H. Stinson in 1946. His work was continued in the summer of 1947 by J. M. Wheatley, who, in addition, commenced a study of the whelks population and distribution on the flats in connection with an attempt to estimate the value of mechanical control by collection of the adult snail.

During the 1948 season A. Larocque at Belliveau Cove inaugurated a large scale control by egg collar collection, a method suggested by the encouraging results obtained in smaller areas by Wheatley (1947). Further work on sexual dimorphism and on the feeding habits of the snail was undertaken by Miss F. Baeristo, at St. Andrew's, N.B.

In 1949 L. Thurber, operating from St. Andrew's, performed a series of very satisfactory experiments at Holt's Point, N.B. on the value of control by collection of the adult snail, and the effect of thus clearing areas for clam relaying. Meanwhile at Belliveau Cove the author attempted to complete and check the various phases of the investigation commenced by his predecessors, and to assess results of Larocque's attempted control by collar collection; this latter unfortunately proved to be of little value owing to the poor selection of the area and the inadequacy of basic data collected in 1948 for comparison with that available in 1949. Because of this insufficiency it was impossible to draw any definite conclusion from the 1948 control work and a second trial was necessary in 1949; the effects of this will have to be assessed in 1950.

E) Local views on the clam-<u>Polynices</u> relationship.

Clams were once abundant on Belliveau Cove flats but have been scarce for the past several years. According to the reports of the local inhabitants similar reports come from other localities along this shore - Gilbert Cove for instance.

The older people of Belliveau Cove recollect with nostalgia the by-gone days of wooden ships and productive fisheries. Prior to 1930 Belliveau Cove supported a prosperous clam industry; the distribution of <u>Mya</u> was universal on the flats and large clams of excellent quality were abundant. The villagers relate that it was then possible for a single digger to secure one to one and one-half barrels of high grade clams during the period of one tide, whereas today three buckets per tide is considered a good yield and these clams are reported to be of low grade compared to those of the past.

Today the clams are almost strictly limited in their distribution to three areas on the flat (see Fig. 1), the best clamming being on the high sandy soil situated around pier Number 2; the seaward limit of the clam population is defined by a line running approximately 600 to 900 feet off-shore. This present limit represents a further reduction of the population and distribution observed by Stinson in 1946.

The 1949 size-frequency distribution of the clam population had a mode at 56 mm. (i.e. 1-¾ inches), in terms of length; specimens under 42 mm. were relatively scarce, and living spat of the 1948 class were practically non-existent. However, numerous empty shells, ranging from the large three inch to the small spat size, were found on the flat and at the high water line, thus attesting to a past abundance, and current yearly depositions of spat, and emphasizing the high seasonal mortality of the latter.

The present distribution of the clam, its localized survival, and the high spat mortality are very closely related to and dependent upon the distribution of the snail. At present, as in the past, the two species of Polynices found at Belliveau Cove have a differential, but fixed, distribution on the flat: that of the larger whelk, P. heros, commences at 1300 feet from high water, while the smaller P. triseriata is located mainly from high water to 1500 feet off shore. They also show a differential burrowing ability, which is approximately directly proportional to their size. This ability has determined the present distribution of the clam, for in areas populated by the large but relatively scarce P. heros the stock of Mya arenaria has been completely exhausted, whereas the present clam population is located in the region inhabited by the plentiful, but smaller, P. triseriata. Unless depleted by man they will probably remain, but the establishment of new clam stocks are inhibited by the heavy annual destruction of the newly settled spat.

In addition to soft shell clams the flats formerly supported extensive beds of mussels, Mytilus edulis, (used locally as fertilizer) and heavy populations of bar clams, Mactra solidissima, (used locally for food). Today these stocks, too, are practically extinct and although some digging for bar clams still goes on, the stock is sufficient to support only domestic consumption and bar clams are considered a luxury. The present importance of these two genera (Mytilus and Mactra) in flat ecology is that they are a source of food for the snail, and are found mainly in areas devoid of Mya so that together with Mya they permit the snail to occupy the whole beach. Further details of this relation will be discussed later in the sections considering snail feeding habits and clam relays.

After discussing this problem with the local clam diggers and the Atlantic Biological Station's Staff, it is felt that regardless of what agents keep the present stock low now, the decrement of clam stocks cannot be attributed either entirely or to the extent previously suggested, to Polynices. The question of what instigated the apparently sudden increase of the snail population still demands satisfaction.

The fishermen of this area have often emphasized that the decline of profitable clamming and in many localities of good fishing too, followed the complete destruction of eel grass (Zostera marina) in 1930-32 by a blight disease which swept the Atlantic seaboard from Cape Hatteras to Labrador. The consensus of opinion along the shore is that those flats which supported a heavy Zostera growth were the ones of high clam productivity. The Acadians, who in the past used the whelk P. heros extensively as food, relate that the snail was most commonly found in areas devoid of eel grass. This observation agrees with that of the old clam-diggers who recollect seeing neither the snail nor its collar as frequently in the past as they do today. This circumstance may result from limited observations by the whelk-seeker who in the past probably concentrated on the bare areas of the flat and ignored those thickly overgrown by Zostera.

It may be that Zostera has no effect, either direct or indirect, on the clam or snail, but there is little doubt in the author's mind that a very vital relation does exist between the clam and its environs through the medium of soil composition and stability. This relationship will have to be investigated and clearly understood before clam relays can become a commercial reality and before we can say that Zostera is or is not significantly concerned in Mya-Polynices relationships.

II. Belliveau Cove Flats.

A) Flora and fauna on the flats.

The local flat flora is considerable. It is composed mainly of green, brown and red algae. The brown alga Ectocarpus and the green alga Enteromorpha are particularly abundant, and are conspicuous owing to their association with the egg collar of the snail; they will be discussed at length in the section on natural enemies in the life history of the snail.

Eel grass (Zostera marina), which was observed rarely and in a diseased condition by Stinson, appears to have increased and to be increasing in luxuriance and extent of its distribution. Extensive beds of Zostera are now to be found from the northeast end of the Cove to the seaward stations of series I, i.e Stations 5,6 & H and surrounding Series III, i.e. Stations C,D,E,F & G. The distribution of the grass is restricted to a loose clay substratum; this relation held true throughout the summer when the appearance of Zostera in a new location on the flat was always preceded by a change in flat composition from packed sand to loose muddy soil, a condition which usually followed periods of rough water.

The northeast end of the Cove is bounded by a rocky promontory where dense beds of rock weed (Fucus) are prevalent.

The littoral invertebrate fauna in this area was varied and plentiful. Cursory observations of local fauna apart from Polynices, Mactra, Mya, and the mussels Mytilus and Modiola, showed the presence of the bivalve Ensis and Gastropods such as Purpura, Littorina and Nassa. The latter was by far the most prevalent form of life on the flat. Nereis was a common representative of the Polychaeta errantia, and the sand tape Cerebratulus was particularly abundant.

In the beach wrack shells of Buccinium and Chrysodemus were not uncommon. Crustaceans in the form of Amphipods and Isopods were abundant, phosphorescent specimens of the former being numerous in August.

Crabs and Asteroideans were poorly represented throughout the season, but the July spring tides brought inshore masses of the jellyfish Aurelia. Exceedingly large numbers of small specimens of Littorina and the Dinoflagellate Cerantium were recovered from plankton drags using a No. 18 net. (See Fig. I - show in distribution of Mya, Mactra and Mytilus and Fig. 2 for distribution of Zostera.)

B) Position of Stations - bearings and surveyed distances.

At the commencement of the Polynices investigation at Belliveau Cove in 1946 Stinson established a series of seven stations in the northeast half of the flat extending from the high water line to 1,970 feet offshore. These have been referred to as Series I (Ser. I). Their position allowed for a comparative study of snail distribution on the various levels of the flat.

In 1947 Wheatley renewed Series I and in addition, for evaluating control by manual collection of the adult snail, established areas 'I' and 'R' (50 by 50 feet each) approximately 500 feet offshore.

Larocque, in 1948, used stations 1 to 6 of Series I, areas 'I' and 'R', and laid out six stations on the southwest half of the Cove extending from high water to 1500 feet seaward, so forming Series II (S.II).

In June, 1949, the author renewed Series I and II, and established Series III (S.III), comprised of six stations passing from 600 feet to 1700 feet offshore, and Stations A, 13, I, J, X, and Z. Stations 13 and X are situated in a weir, standing approximately in the middle of the investigational area at the 1500 foot level. (For the exact location of and distances relating these stations to fixed reference marks see Tables I, 2, 3, 4, 5, and Figs. 3, and 4.)

The reference marks were guide stakes erected along the shore line above high water mark at the end of the season to facilitate re-establishment of stations for future work. A diagramatic representation of the evolution of these stations established by the respective field workers is given in Fig. 5.

When the question of renewed control by egg collar collection arose in 1949, a cursory examination of the flat in terms of snail population indicated that the only area in the Cove showing comparatively even distribution was located east of the line running from the shore to the weir (331 degrees magnetic) and limited in this direction by a fresh-water drain emerging at low tide from the harbour proper. It is a strip approximately 1000 feet wide, extending from high to low water. This zone contains series I (S. I.) and was further subdivided on its longitudinal axis by the establishment of series III (S. III). With the division of this area by the two series of stations, the half containing S. I. was controlled by manual collection of the egg collar, while the half containing S. III. remained as a non control area for comparison with data collected from the control area. (For further details of this selection see discussion of snail population and egg collar control).

Tables I, 2, 3, 4, and 5 record data necessary for the exact location of the aforementioned stations in terms of surveyed distances and magnetic compass bearings on the guide stakes of each area, and Figures 3 and 4 which are scale drawings show these relationships graphically.

Series I contains observation areas No. 1 to No. 6; Series II areas No. 7 to No. 12. All these and Station 13 in the weir mouth, are fifty-foot-square plots staked out on the flat. They are used both for egg collar and snail population counts and are represented on the charts as black squares. The stations of Series III and Stations A, H, I, J, and Z, marked by a single stake, were used exclusively for population counts and are represented on the charts as black circular areas.

Series I and III are in a region of higher elevation than Series II, so that the ebb tide uncovers the stations on the eastern half of the Cove before it recedes from the corresponding ones on the western half. To obtain information about this relationship the waterline at dead low tide for Neap and Spring flood was surveyed. The low water mark of a Neap tide 6.8 above datum (August 17, 1949, A.M. tide) crossed Series III and I at the height of Stations D and 5 respectively, this being approximately 1100 feet from high water mark; the same tide was noted to cross Series II on the western side of the Cove at Station 9, 900 feet offshore. Similar measurements of a low Spring tide 0.6 above datum (August 26, 1949, P.M. tide) showed a maximum distance of 2800 feet from high water, measured along Series I (i.e. 1100 feet from Station H on a 321 degree magnetic bearing), and of 2400 feet measured along Series II (i.e. 900 feet from Station 12 on a 327 degree magnetic reading).

The establishment of the stations taken either individually or as series was proportional to the demands of the investigator's program. The position of these areas on the flat permitted a comprehensive study of snail population as related to its intertidal distribution, while the existence of the three series dividing the Cove on its east-west axis provided for accurate observation of the species' distribution along this component.

C) Flat composition.

A description of flat composition in terms of soil structure was deemed important when this was noted to coincide with certain aspects of the distribution of the snail and clam and the position of the Zostera beds.

On the basis of flat composition the Cove is divided into three main zones whose boundaries run north and south. The first of these, extending from the fresh water outlet to approximately 100 feet west of Series II, grades from a high, compact, sandy flat inshore to a low, loose, mud and sand composition offshore. The next zone, containing Series I, extends westward from zone I to the limit of the 1949 control area, is mainly composed throughout of mud and sand, but of a compact and stable nature. The third zone, continuing westward beyond zone 2 including Series II, was for the greater part of the 1949 season of a loose, waterlogged, sandy composition throughout, making it 'plastic' and unstable, but at the end of the summer after periods of rough water acquired a superficial layer of mud. (The flat characteristics at each of the several stations are summarized in Table 6.)

Within the three zones there are small areas which differ markedly in composition from the surrounding flat and seem to be characterized by abnormal snail population densities . One such area of discord is inside the weir, which though surrounded by a compact, dry, sandy flat, is muddy and constantly submerged. Owing to this variation three stations were established, the first (St. 13) along the weir "leader", the second (St. Z) in the weir mouth, and the third in the weir proper. Data collected from these stations showed that although they were only 50 feet apart there was a marked difference in snail population and collar production. (See Table 6, page 11.)

It is not suggested that the factor of flat composition in itself has caused the variations noted above, but that this in addition to other factors, such as food and temperature, has contributed to the abnormal populations found in the weir and at Station Z. (For further discussion see sections on population and collar production.)

TABLE I. Compass bearings (magnetic) of stations and boundaries pertinent to the investigation from fixed reference marks on the shoreline at high water mark. (See Fig. 4.)

Reference stake from which bearings were taken from; proceeding E-W.	App. distance of reference stake along shore line from Pier 3(feet)	Bearing degree (magnetic)	Bearing taken on.	Stations or boundaries indicated by this bearing.
I.	150	325	Series III	St. B,C,D,E, F & G.
II.	200	321	Series I	St. 1,2,3,4, 5,6 & H.
III.	300	320	St. A.	St. A & relay plots 1,2,3.
IV.	900	331	The axis of the weir leader	Westward limit of the 1949 control area.
V.	1700	9	Weir mouth	Westward limit of 1948 control area.
VI.	2150	327	Series II	St. 7,8,9,10, 11 & 12.

TABLE 2. Bearings and surveyed distances taken from shore reference stakes to the stations of Series I, II & III. (See Fig.4)

SERIES	Reference stake number. (See Tab. I)	Bearing degree magnetic.	Station	Distance from reference stake to each station.
I.	2	321	1	300
			2	600
			3	900
			4	1100
			5	1300
			6	1500
			H	1700
II.	6	327	Z	150
			7	300
			8	600
			9	900
			10	1100
			11	1300
			12	1500
III.	1.	325	B	600
			C	900
			D	1100
			E	1300
			F	1500
			G	1700

TABLE 3. Distances between stations of S. I. and the corresponding stations of S. III.

Stations S. I.	S. III.	Distances feet.
2	B	100
3	C	115
4	D	140
5	E	180
6	F	200
H	G	240

TABLE 4. Location of stations not contained in the series. (See Fig.4.)

Station	Bearing taken from station	Bearing magnetic	Distance feet
I.	6	280	240
13	6	263	St. 13 is along the weir leader near the weir mouth.
X	No ref.station	Station X is in the weir mouth proper.	
J	11	79	240
A	2	180	150

TABLE 5. Surveyed distances from Pier II to points of intersection of various North to South boundaries with an East to West line joining the Western corner of Pier II to Mayors Point (bearing of joining line from Pier II to Mayors point 280°)

Distance taken to.	Distance feet.
Mayors Pt.	3900
Series II	2025
West. limit of 1949 control	1150
Series I	450
Series III	150

Table 6. Tabulated sketch of each station showing its characteristic flat composition.

Series	Stat.	Mud loose	Mud-Sand loose	Mud-Sand compact	Sand loose plastic	Sand Compact	Low submer-ged	High dry	Zostera present
III.	B.			////////				/////	
	C.			////////			//////		///////
	D.		///////				//////		///////
	E.	//////					//////		///////
	F.	//////					//////		///////
	G.		///////				//////		///////
I.	I.			/////////			//////		
	2.			////////			//////		
	3.					//////		//////	V.Sparce
	4.					//////	//////		
	5.		///////				//////		///////
	6.				///////		//////		///////
	H.					//////		////	
II.	Z.	/////					//////		
	7.		///////					//////	
	8.		///////				//////		
	9.				//////			/////	V.Sparce
	10.				//////			/////	V.Sparce
	11.				///////		//////		
	12.					//////		////	
Miscell.	13.					////////		//////	
	X.	///////					///////		
	A.			////////			///////		
	I.			////////			///////		
	J.					///////		//////	
	Weir.	///////					///////		V.Sparce

D. Meteorology - Its role in the biology of Polynices (as related to the flats in particular.)

Wheatley, in 1947, suggested a possible relation between the moon phase and the nightly emergence of the snail. In 1949 the author noted that the emergence was nocturnal and seemed to be governed by sudden changes in light. The fecundity of sexually mature snails was noted to vary, and this variation appeared to be related to water and flat temperatures though other physical factors should be considered and assessed.

Owing to the possibility of meteorological factors having some effect on the biology of the snail it was decided to record air temperatures and general water conditions, during the 1949 season. No such data were collected by the past workers and thus limits the value of the 1949 records. They may be useful in any future comparison.

The summer of 1949 was exceedingly dry in this locality rain being recorded only on 11 days throughout the period of June 13 to August 30. The villagers claimed that it was an extremely hot summer, though temperatures never surpassed 87° F. and the lowest recorded was 38° F. in the shade.

Because sea water covers the flats except at low tide and because the snail burrows when the low tide occurs in daylight hours, atmospheric temperatures may be considered to have little direct effect on the snail. At low tide they determine the rate of dessication of the collars and the high temperatures may kill the few adults that get stranded at high water mark during the hottest hours of the day. Indirectly, however, atmospheric conditions by effecting water and flat temperatures, are believed to regulate: collar formation, incubation, crumbling and larval emergence and activities of the adult such as feeding and possibly mating. Because flat temperatures are regulated by tidal cycles it is reasonable to expect that these features of the snails activity will be related to tidal cycles and their interactions with meteorological phenomena.

The important ecological factors, other than temperature, which affect the snails behaviour are light and water movement and wind causing water movement. Thus true meteorological phenomena as well as air temperatures may be expected to affect the snail.

The currents of the Cove at high water, were of two types; the bottom current was stable and unidirectional throughout the summer, running in a curved sweep from West to East; while the surface flow depended on the direction of the prevailing wind.

Records of "flat" temperature were obtained from reading an ordinary laboratory thermometer whose bulb was pushed to a depth of (3") into the substratum; air temperatures were recorded from an ordinary "Sixes-type" maximum and minimum thermometer held in a shaded, ventilated wooden box 3 feet off the ground, recordings being taken in the evening (6-8 p.m. A.S.T.) water temperatures were obtained with an ordinary reversing centigrade thermometer. These records appear in Tables 7-9; in these the water and flat temperatures have been divided into A.M. and P.M. tide to give some appreciation of the differences encountered between the hottest and coldest periods of the diurnal cycle. This arrangement simplifies the table but tends to mask these differences. Under the heading of "time observation" the approximate time of the temperature recording has been entered; reference to this will offset the disadvantages previously mentioned. All water temperatures were taken at high tide and all flat temperatures were recorded during the low tide, approximately at the period of dead water, air temperatures were taken between 6-8 p.m. A.S.T..

Table 7. Meteorological Data for the Month of J

Date June	Air Temp. C. Max.	Min.	Water Temp. C. Time of observation	A.M. Tide Surface	A.M. Tide Bottom	P.M. Tide Surface	P.M. Tide Bottom
13	22.3	15.6	1400			19½	
14	21.1	15	1400			19½	
15	21.6	15.6	1430			21½	
16	21.3	16.2	1500			21½	
17	24.5	15	1600			21½	
18	22.8	15.6	1600			23	
19	22.3	15	1600			22	
20	18.9	16.7	1700			18	
21	15	11.7	800			13	
22	16.7	10.6	800 1930	12	11 2/5	13¾	13 1/5
23	19.4	11.1	900 2100	13¾	12 1/5	18½	15 1/5
24	20	11.7	900 2130	14	14	15½	15 1/5
25	18.4	13.9	1000 2130	14¾	13	15½	14 1/5
26	21.1	15	1100 2130	16	13 2/5	18	15 2/5
27	20	12.2	1130	14½	13 2/5		
28	21.1	12.2	1130	16	12 4/5		
29	15	3.9	1300			19	14
30	17.8	7.8	1300			18½	15 1/5
Average	19.9	13.0		14.4	12.9	18.6	14.6

3	23.4	16.6	1500			21½	17 2/5	1000 2300
4	25.5	17.8	1600			21½	18 2/5	1100 2400
5	23.3	16.1	1700			21½	17 2/5	1200 0030
6	23.3	10	1900			20	18	200 1400
7	22.7	7.8	2000			20½	17 4/5	330 1500
8	23.3	4.5	1100 2100	18	13 4/5	18½	14 2/5	400 1600
9	23.9	11.6	930 2130	18½	14 2/5	18½	17 3/5	430 1700
10	23.3	12.8	1000	15	14 4/5			500 1700
11	24.4	15.6	1100	19	14 3/5			1800
12	23.3	7.8	1100	20				700
13	19.5	13.3	1300			17	14 1/5	
14	25.5	15.6	1300			20	15	
15	25.0	12.2	1400			21	16 4/5	
16	25.0	12.2	1500			22	14 4/5	
17	21.6	16.6	1600			21	18 1/5	
18	23.3	17.8	1600			22	18 4/5	1100
19	23.3	17.8	1900			20	16 4/5	
20	23.9	15.6	1900			21	18 1/5	
21	23.3	16.6	1900			21	20 2/5	1400
22	24.4	8.6	2100			20	18 1/5	1500
23	23.3	17.8	2100			20	19	1600
24	22.2	16.6	2130			20	19 1/5	1600
25	22.2	8.9	2200			17	16 3/5	1700
26	18.8	15	2300			17	15 2/5	
27	23.9	16.1	100	19	17 3/5			1700
28	26.7	18.9	1300			22	17 2/5	
29	28.9	18.9	1500			23	18 1/5	
30	30.5	18.9	1530			21	18	900
31	28.9	23.0	1600			24	19 2/5	1000 2200
Average	23.7	14.1		18.2		21.9	15.4	

6	29.5	16.7	900	17	16			1600	
7	26.7	13.3	1000	19	17 4/5				
8	26.7	17.8	1100	20	18 2/5			1700	
9	30	18.9	1100	20	17 3/5				
10	28.1	11.1	1400			18	16 4/5		
11	23.3	16.7	1400			17 1/2	17	700	16
12	22.8	17.2	1500			16	16		
13	24.5	12.2	1500			16	15		
14	26.1	11.7	1600			17	16		
15	23.8	7.8	1600			20	18	800	16
16	24.5	3.3	1700			20	17		
17	20.3	11.1	1700			21	20	1200	18
18	29	15.6	1700			19	18 2/5		
19	19.5	14.5	1900			17	16		
20	18.9	12.8	1930			17	16	1400	
21	22.3	15	900	14	13 4/5				
22	21.1	11.9	930	15 3/5	15 2/5				
23	23.9	16.2	1000	15 4/5	15 1/5				
24	20	13.4	1100	15 2/5	15 1/5				
25	25.6	4.5	1200	15 2/5	15 2/5				
26	22.9	13.9	1300			15 4/5	15 2/5	1900	
27	27.8	13.4	1400			15 4/5	15 2/5		
28	26.2	17.2	1400			18 1/5	17 2/5		
29	26.2	22.9	1500			19	18 3/5		
30	24.5	15.6	1600			23 1/2	19 1/5		
Average	24.8	14.3		16.8	16	18.9	17.1		17.1

Figure 1

Distribution of Mya, Mactra and Mytilus Stocks at Belliveau Cove.

Figure 2

Distribution of _Zostera marina_ at Belliveau Cove, 1949

Figure 3

Map of Belliveau Cove showing positions of stations occupied in 1949.

Figure 4

Bearings and distances of stations occupied in 1949 from shore reference marks.

Figure 5

Development of Stations at Belliveau Cove
by various field assistants from 1946-1949

III. Local Species of Polynices

A) Polynices as described by the literature.

Polynices has been referred to in taxonomy under the generic names of Lunatia, Neverita and Natica. Borradaile and Potts (1938) classified Natica as belonging to order Prosobranchiata of the molluscan class Gastropoda, and to sub-order Monotocardia due to the presence of one auricle in the heart.

Arnold (1903) mentioned the family Naticidae and with regards to genus said: "There has been much confusion in the generic nomenclature of this family". The old name Natica once did service for all the species then included in Euspira, or Lunatia, Neverita and Polynices. These were recognized sub-divisions of Natica but all were considered to have only sub-generic, rather than the generic rank we now accredit to some of them.

The genus Natica now comprehends those forms possessing a shelly operculum, and Polynices those having a corneous operculum. Lunatia (synonimous to Euspira) and Neverita are now considered sub-genera of the genus Polynices.

Johnson (1934) lists 15 species of Polynices for the Atlantic Coast of North America. Of these the following occur in Canadian waters: P. nana Moller (1842), P. heros Say (1822), P. triseriata Say (1826), P. groelandica Moller (1842), and P. immaculata Totten (1835).

Johnson arranged P. heros and P. triseriata in sub-genus Neverita.

Pratt (1927) arranged Polynices in the following taxonomic scheme.

Class Gastropoda
- Order Prosobranchiata
  - Sub order Pectinibranchiata
    - Division Taenioglossa
      - Sub division Platypoda
        - Family Naticidae
          - a) Genus Natica
          - b) Genus Polynices.

This scheme was based on the following taxonomic characteristics:

a) Presence of a distinct head possessing 1 or 2 pairs of tentacles, shell coiled or lacking ...... Class GASTROPODA

b) Mostly acquatic snails; ctenidia anterior in position, shell well developed .... Order PROSOBRANCHIATA

c) Gills monopectinate .... Sub Order PECTINIBRANCHIATA

d) Radula long and narrow, with central tooth, one pair of laterals, and two pairs of marginal teeth .... Division TAENIOGLOSSA

e) Foot with broad sole .... Sub Division PLATYPODA

f) Aperture without siphonal canal, animal marine, foot when extended almost completely concealing the shell, which appears to be embedded in it. Shell usually globose, with a short spire, aperture round or lunar; lip sharp, umbilicus open or closed by a callus; foot very large and capable of being swollen by the absorption of water and being reflected back over the shell so as to almost cover it. Tentacles small, lanceolate and wide apart being united by a veil; eggs deposited in sand collars .... Family NATICIDAE

g) Shell with about 5 whorls, smooth and regular, gray or brown, eyes wanting; predacious animals, living in sand, where they burrow after bivalves which they envelop in their foot and penetrate by drilling a hole through the shell with the radula.

aa) If they possess a "shelly operculum" .... Genus NATICA

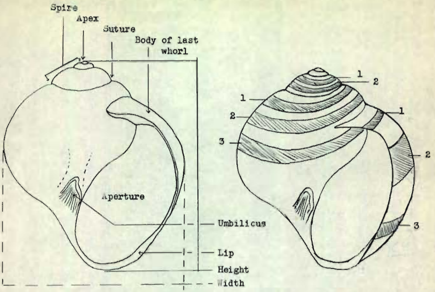
a'a') If they possess a "corneous operculum" .... Genus POLYNICES

Within the genus Polynices there has long been discord as to the specific status of P. triseriata; Arnold stated of P. triseriata: "A small shell of exactly the same shape as P. heros, but decorated with three revolving series of light blue or chestnut colored spots. It is pretty well determined that this so called species is only the young of P. heros." Belding (1930) in mentioning P. triseriata stated that it was "possibly erroneously considered to be the young P. heros" while Gould and Binney as far back as 1870 described in detail P. heros and P. triseriata considering these to be two distinct species.

Because of our present extensive knowledge of behaviour and anatomy there is now, no doubt that these snails represent two distinct species, but it is understandable that P. triseriata should have been mistaken for the young P. heros by early authors who studied only the shells of these animals.

B) Polynices - as described by the author for field identification.

Diagram illustrating terms and measurements taken in the following discussion



Stinson (1946) in describing the snail states: "After studying many specimens the writer came to the conclusion that there were on the flat two varieties of Polynices, growing at different rates, and to different ultimate sizes. One was called "A" and the other "B".

The "A" corresponds closely to the description given by Gould and Binney (1870) for P. triseriata, and the "B" to the description for P. heros; but assignment of the animals to these species should await their careful study by a systematist."

Wheatley (1947) confirmed and adopted Stinson's tentative classification of the local species of snail.

1) Polynices triseriata. This is a comparatively small snail, its shell height and width (taken as the greatest dimension from the apex to the basal lip of the aperture, and as the greatest dimension at right angles to the height measurement) were reported by Stinson not to exceed 30 by 22 mm. The largest specimen found in 1949 at Belliveau Cove was 25 by 17 mm., while Thurber recovered from Holt's Point (New Brunswick) a sample measuring 29 by 24 mm. in height and width respectively. The smallest adult snail observed in 1949 was 2 mm. in height and 3 mm. in shell width.

The shell in the younger stages varies in colour from a cream-yellow to a blue-gray. It is adorned with three rows of chestnut or dark blue-gray spots running spirally with the whorls.

In the older specimens these rows become unbroken bands and the shell looses its glossy appearance assuming an ashy-white colour.

The first of these characteristic bands is thin and borders the suture formed by the last whorl and the spire of the shell. The second is the most conspicuous and uniform commencing at the middle of the apertures lip and continues up the spire. The third commences on the lower portion of the lip circumscribing the shell (the last whorl) once and disappearing into the aperture dorso-laterally to the umbilicus. (See previous diagram for bands 1, 2, 3.)

The identity of these bands is retained for 540 degrees of rotation (1.1/2 whorls) from the aperture, on the spire they fuse and loose their definition. They are very conspicuous when the shell is held against a light and observed from the inside of the aperture.

In very young snails the shell width exceeds the height, but this relation is rapidly reversed with growth. The ratio of height/width usually remains close to 1 (one), thus giving the shell a "globose" appearance. Though all the specimens examined at Belliveau Cove were characterized by a relatively low spire, Thurber collected at Holt's Point (New Brunswick) samples with a high spire and conical shape whose classification as P. triseriata would be very doubtful if based on shell shape and not on the presence of the typical bands.

In typical P. triseriata the umbilicus is deep and narrow. The aperture is pear-shaped, being wide and oval below the umbilicus level and tapering to an acute angle above it. The lip is smooth and thin with a slight flaring and thickens below the umbilicus in older snails. Stinson relates this thickening to the termination of growth.

The shell is dextral and composed of approximately 5 (five) whorls forming a low convex spire.

The foot may be extended to twice the length of the shell and is of a glossy white or pink colour tinted with light blue.

The mantle, anteriorly, and part of the post-podium foot may be extended to cover the entire shell and operculum, this being pressed against the posterior face (wall) of the fifth whorl.

The snail moves smoothly on its extended foot without any apparent effort or movement of this organ; its two small lanceolate tentacles are projected from the aperture and directed anteriorly.

When disturbed the whelk quickly contracts by expelling water from its foot, then retracts the mantle and later the tentacles. Finally the post-podium is drawn into the aperture and closes it by virtue of the attached corneous operculum, which hinges on the foot in line with the umbilicus. In this response the foot proper does not undergo any change in colour.

2) P. heros. This species grows to a far larger size than P. triseriata. The largest specimen collected at Belliveau Cove was 80 mm. in height and 79 mm. in width. In this species the ratio of height/width remains approximately 1 (one) at all stages from the larval to the very large adult. In young specimens (20 mm.) the shell colour is usually a light gray striped with darker lines and yellow tones giving it an ash like tinge; the shell is not as highly polished as P. triseriata, and in older specimens the periostracum develops a dirty gray chalky texture and often serves as a holdfast for algae.

The inner wall of the shell as seen through the aperture is mottled with purple tones and highly glossy, reminiscent in some specimens of tortoise shell.

The last whorl is large and pronounced thus upsetting the symmetry between the shell and the spire. Owing to the width of the last whorl the aperture, unlike P. triseriata, is large and oval.

The lip in young specimens is thin, brittle and sharp. In older shells it thickens and flares below the umbilicus. The umbilicus is deep and flaring.

Like P. triseriata the shell is dextral, but composed of approximately 5.1/2 whorls forming a relatively small and convex spire. The foot can be extended until its length is three times the shell height and its width twice the shell height. The method of locomotion and other foot characteristics are similar to those of P. triseriata except in colour. In P. heros this is pink with a very fine black reticulum, particularly noticeable along the margins of the extended foot. On contraction this reticular pigmentation seems to increase and the foot appears almost black. This characteristic reaction was suggested by Stinson as a method of differentiating between the two species in the field (See Fig. 21).

The operculum of both species is corneous, amber coloured and translucent; its shape is characteristic of the shell's aperture. Arising from the opercular "nucleus" (See Fig. 6) and passing to the margin is a ridge which serves as point of insertion to the opercular retractors.

The separation of these species is simple and certain if the identifier has fresh, preferably living specimens and examines them for the following characteristics:

1) Shape of shell
2) Colour and markings on the shell
3) Size of snail
4) Colour of retracting foot

3. Schematic comparison of the two species of Polynices at Belliveau Cove.

Character	P. triseriata	P. heros
1) Shell shape	The shell is sub-globouse, with a distinct spire. The aperture is acute and narrow towards the spire and flears basally below the umbilicus to have a "tear" shape (See Fig. 7).	The spire appears low owing to the great expansion of the last whorl thus reducing the ratio between height/width and giving the shell a globose appearance. The aperture is even and oval (See Fig. 7).
2) Umbilicus	It is narrow.	It flears slightly but in general it is narrow and deep.
3) Ultimate size	Never found exceeding 25-30 mm.	Found up to 80 mm. in height and never smaller than 15 mm.
4) Lip character	The lip is blunt and thick becoming thicker after reaching heights of 16 mm. by males and 24 mm. by females.	The lip remains thin and rather brittle tending to thicken with age in the sub-umbilical region.
5) Colour	Three typical bands formed by the fusion of many small chestnut or blue-gray spots. These spiral bands pass up the shell which forms a blue-gray background in young specimens and of a yellow ash colour in older.	The shell of young snails is light gray striped by darker lines and yellow tones giving it an ash like tinge. In older whelks the periostracum is eroded and assumes a dirty amorphous grey colour.
Soft parts		
1) Foot colour	When expanded or retracted remains a clear semi-translucent pink colour.	When expanded it is characterized by a very thin black reticulum imbedded in its light pink substance, on retraction this reticulum swells and the whole foot appears black or dirty gray (See Fig. 11).
2) Penis size	16 mm. males have a large penis	16 mm. males have a small sized penis.
3) Internal anatomy	There appears to be no significant difference in the morphology of these two species.	

C) Morphology

1) The Shell. The colour and external shape have been treated previously under the heading of: "Description for identification".

The external surface of the shell, in both species, is broken by innumerable annuli arising at the whorl sutures and converging into the umbilicus; this pattern is apparent on each whorl. The annuli vary in their definition, the majority though quite definite are so closely spaced as to make counts almost impossible but at irregular intervals depending on the age of the shell, there appear annuli of greater width and definition (See Fig. 8). The same pattern holds true for the operculum of both species. The nature of these more distinct annuli suggests that they are formed during periods of arrested growth. Providing these are of a seasonal nature they may be of value in the estimation of age and growth rate.

Vertical sections of the shell made at right angles and parallel to the shell aperture are portrayed in figures 9 and 10. These give a clear picture of the internal structure of the whorls.

Soft parts. The whelks body is divisible into 3 obvious regions, the head, the foot, and the visceral hump. The last remaining at all times within the confines of the shell. (See Fig. 11).

The integument of the visceral mass is the characteristic molluscan mantle which is free from the body below the visceral mass and can be extended through the shells aperture and everted around the lip to cover the outer surface of the shell.

2) The head of the snail. Anterior to the visceral hump and dorsal to the propodium is a crescentic "flap" of tissue which by the presence of the antennae appears to fulfill the functions of the cephalic region.

It is a membrane whose leading edge has been "pinched and pulled" to form two lanceolate tentacles. Ocelli are absent.

Median and ventral to the head and partly covered by it, is the Rhynchostome or apparent mouth. This is not the true buccal cavity but the region of integumentary involution which forms the protrusable proboscis Thus the true mouth becomes apparent only when the tube like proboscis is everted. (See Figs. 11 & 12).

3) The foot. This forms the greater part of the body normally seen protruding from the shell. As already described its appearance and consistency, in life, varies greatly. In preserved specimens it becomes singularly tough and elastic assuming in P. heros a dirty brown-black colour.

The foot is muscular and capable of great extension and contraction; in the former state it is soft, viscid and translucent, while in the latter it is hard and elastic.

In composition it is muscular and glandular. Antero-dorsally it forms a cavity which contains the inverted proboscis, oesophagus and oesophageal glands.

Ventral to the cephalic fold lies the pro-podium; this forms a long fold, which is overlapped by the head, and which surrounds the anterior extremity of the foot and descends either flank to the sole, so forming a continuous deep grove. This grove is richly glandular and seems to be related to the secretion of pedal jelly, associated with collar formation and the feeding habit (See Fig. 11).

The pro-podium is prehensile and extensively used in reaching and clasping food.

Caudad, the foot, is attached to the eccentric opercular nucleus and in its expanded condition it may be seen to recurve around the edges of the operculum and in some cases cover it completely.

The postero-dorsal region of the foot is elongated dorsally to form the columellar muscle, which attaches the snail proper to the shell, having its point of insertion on the columellar wall of the 5 whorl. The expanded sole is oval in shape with smooth and pleated edges.

In ordinary locomotion wave formation can be noted on the margins of the extended foot passing antero-posteriorly along the edge of the sole. The snail is also able to move by extending the propodium and using this as a hold fast, to pull up the rest of the body.

4) The visceral hump - its contained organs.

Organs of the Pallial complex, i.e. those organs located between the mantle and the dorsal surface of the body proper.

These are outlined by Dakin (1912) in treating the welk Buccinium as: "The structures developed largely from the mantle proper: the osphradium, and the mucous gland.

Furthermore there are to be considered the Rectum and anal opening the renal and genital openings."

The former group were not considered pertinent to the study of Polynices and so omitted, the latter organs were dissected and examined.

The alimentary canal. This opens at the true mouth, situated at the apex of the long retractile proboscis, which is usually everted in specimens killed by relaxing in Epsom's salts. (See Methods).

The proboscis. (See Fig. 12) The body wall invaginates to form the false mouth or Rhynchostome in which by intussusception telescopes the proboscis, thus forming a cavity between this organ and the involuted body wall, known as the Rhynchodaeum. This type of proboscis was described by Lankester (1883) as a pleurembolic proboscis, from the fact that when withdrawn it is the base that is retracted and hence the first to disappear.

The extruded proboscis is sausage shaped with the odontophore complex situated immediately within the true mouth. (See Figs. 12 & 13.)

On the anterior mid-ventral surface of the proboscis there is a small circular plate. This plate according to the extensive investigations conducted by Ankel (1938) is the main drilling organ of the Naticidae; being composed of glandular and muscular tissue and producing a secretion which dissolves Calcium Carbonate. (See Feeding Methods.) When the proboscis is inverted this lies in the Rhynchodaeum.

The Odontophore Complex. The Radula is attached in the mouth and prolonged into a free end which passes posterior through the Pharynx and emerges into the "foot" cavity at the Pharyngo-oesophageal junction.

To expose the whelk Odontophore complex, an incision is made along the mid-dorsal line between the tentacles, prolonged into the mantle cavity and then laterally; this will allow the two flaps so formed to be pinned sideways and expose the point of junction between the foot and the visceral hump.

Immediately ventral and caudad of the head the foot forms a cavity which contains the proboscis, oesophagus and the oesophageal glands; slight muscular connections between the foot and these organs are found. Dissecting the muscle attachments from the Pharynx to the foot and cutting the Rhynchodaeum's integument at the point of involution will free the anterior part of the digestive tract. This can be removed for further study.

Cutting the Pharynx dorsally to enter the Pharyngeal cavity will allow this to be folded open and so expose the Odontophore complex.

The Odontophore consists of the Radula, the Odontophoral cartilages and their muscular attachments. The anterior part of the Radula expands into two symmetrical and curved "wings" or "plates" these representing the Odontophoral "plates". The radula proper, the toothed portion, extends anteriorly between these plates, and progresses posteriorly as a narrow and slightly tapering ribbon of symmetrically arranged teeth. (See Fig. 14 and 15.)

The Odontophoral cartilages serve as points of insertion for the muscles activating the radula and they form pivots because of their shape, position and muscular control. On and by virtue of these the radula can oscillate so assuming a function and movement similar to that of a "band saw".

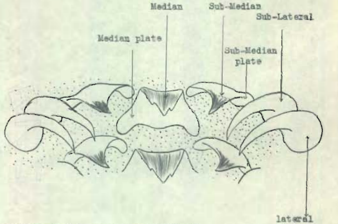
Posterior to these cartilages the "free end" of the radula proper is retained in a thin elastic and muscular sheath, which remains continuous with the terminal free end of the radula projecting into the "foot cavity". At the point where the radula emerges from the pharynx the surrounding sheath has external muscular connections with the Pharynx.

In one dissection there appeared to be two "axe" shaped horny plates situated vertically and laterally to the Odontophoral plates. These are diagrammatically illustrated in Fig. 14.

These plates according to Ankel (1938) are typical of the Naticidae and this author refers to them as "jaw plates or maxillae" recording that in this family alone in the Gastropods they aid in feeding by exercising a scissor like tearing action on the food in conjunction with the radula. (See Feeding Methods.)

The Radula. This is a long narrow ribbon expanding anteriorly into the Odontophoral plates. This "chitinoid" ribbon supports the posteriorly directed denture; according to Hankel (1938) the radular mechanism can be homologised to a band saw which oscillates on the odontophoral cartilage and "bites" into the preys tissues on the backsweep.

The teeth can be divided into two types: rigid and pseudo-articulated, the median line of teeth is composed of a row of single rigid piramidal teeth, on either side of these, postero-laterally runs a row of what may be termed "central" teeth, these are rigid short and sharp. The median and central rows are supported by small dental sclerites imbedded in the "chitinoid" ribbon. Obliquely lateral to the "centrales" are the two, paired, outer rows of teeth; these are characterized by being loosely articulated on the basal membrane and by being long, tapering and curved structures. Thus progressing from the median teeth towards the outer row the length and degree of articulation of the individual tooth increases.



Other terms used in naming Radular Teeth
1. Median, Medio-central, Central - Tooth
11. Sub Median, Centrals, Laterals - Teeth
111. Sub Lateral } Marginal Teeth
1V. Lateral }

Dakin (1912) describes the odontophoral cartilage as being concave on its dorsal surface thus forming a radular canal, which would tend to flex this organ on its lateral width, thus forming a long trough like food canal which on apposition to the preys tissues would tear off small pieces of its tissue and transport them into the oesophagus. Ankel records the horny jaw like structures, characteristic of the Naticidae as assisting by scissor like movements by biting off small portions of meat in conjunction with the radulas "rake" like action. (See Fig. 15, 16, 17.) (For clear diagram of the buccal cavity the reader is referred to Fig. 53 pp. 274 of Hankel's paper on Gastropod radulae - 1938, see bibliography.)

The Oesophagus. (See Fig. 13.) This extends from the Pharynx to the stomach and is the longest section of the Alimentary canal. From the Pharynx the Oesophagus passes posteriorly curving ventrally to accommodate the Oesophageal glands in the foot cavity; then it recurves antero-dorsally to enter the visceral mass on its left side below the Ctenidium. (i.e. assuming an "S" shape.) It proceeds along the left flank of the visceral hump to the stomach, situated on the left latero-ventral side of the digestive gland.

The Oesophageal glands are two definite structures, the smaller the salivary, lying immediately posterior to the Pharynx, the larger, believed to be the so-called gland of Leiblein is located caudad of the salivary gland along the Oesophagus. The gland of Leiblein appears to have regions with separate secretory ducts.

The Oesophagus appears to be imbedded in the salivary gland and no secretory duct could be noted connecting these organs.

The Stomach. This is a bag of considerable size lying between the digestive gland (so called Liver) and the bounding integument on the left side of the animal. The stomach is in very close association with the Liver and receives many small ducts from this organ. See Fig. 22.)

The Digestive Gland. This is the largest structure in the visceral hump. It extends from the Pericardiac region to the tip of the Spire and is limited anteriorly by the renal organ and mantle, latero-posteriorly by the stomach on the left side and dorso-posteriorly by the gonad.

It is brown-green in colour, soft in consistency and contains a well defined network of vessels. Dakin in discussing this gland states: "This large gland, which is made up of fine branching tubules, was formerely regarded as the "liver". It is now agreed that this name is unsuitable as the digestive functions are more comprehensive and unite the functions of the different digestive glands of the vertebrate gut. It is furthermore, the chief organ in the body for absorption of digested food." (See Figs. 11, 19 & 20.)

The Intestine. This is short and passes dorso-laterally down the right flank of the hump to open into the Pallial cavity, where it descends on the right side along the extreme edge of the Pallium. (See Fig. 22.)

5. Reproductive organs and the problem of sex determination.

In both species of Polynices at Belliveau Cove the sexes are separate in the adult. In external features the sexual organs are similar in both species, though differences in size and development of the penis are found.

The Male Organs. (Fig. 19.) The gonad resembles the ovary in shape, size, position and colour. It is situated dorsal to the digestive gland and covered by the common integumentary membrane. The testis is imbedded in the "liver" posterior to the Renal organ and extends to the tip of the spire. By virtue of its light yellow colour (bright yellow in formalin - preserved specimens) it stands out prominently from the darker tissue of the digestive gland.

Ventro-lateral to the gonad, on the right side and imbedded in the "liver", runs the male duct or Vas-Deferens, which is clearly defined. It is narrow and characteristically convoluted. On entering the Pallium it penetrates the penis.

The penis, in the adult of both species, is a permanent and large organ arising on the right side of the "neck" and resting in the Pallial cavity with its tip situated near the base of the right tentacle. The penis is narrow at its point of insertion, widening at the middle and then tapering to its eccentric free end. The edges of this organ are crenated so allowing for vascular extension and contraction. (See Fig. 19.)

The Female Organs. The ovary and oviduct occupy the same position in the visceral mass as their Male counterpart, though the oviduct is less convoluted than the Vas-deferens. On reaching a position ventro-lateral to the Renal organ the oviduct expands and assumes a thick muscular wall (ovd") which appears to be lined internally by many small rugae which are believed to be glandular and related to the formation of the capsular jelly of the collar. The Oviduct descends to the Pallial floor on the right extreme tapering to a small papilla which bears the vaginal opening. (See Fig. 20.)

Discussion of the problem of sex determination.

In all P. heros specimens collected the sexual organs were always well formed and the sexing of the sample could be based on the presence or absence of the penis or vaginal papilla.

In P. triseriata this method of sex determination is effective when applied to specimens over 6 mm. in height; but for snails smaller than this it is of little value as the external genitalia are lacking.

The explanation given to this problem is impirical and lacks experimental verification: a) Wheatley (1947) and Larocque (1948) suggest that snails under 6 mm. in height are all females and that after this stage of development sex reversal occurs and the male genitalia are developed.

Baeristo (48) lists the following results for a sample of P. triseriata under 10 mm. in height, received from Belliveau Cove.

Table 10. Sex ratio in different size classes of P. triseriata.

Size	3 mm.	4 mm.	6 mm.	10 mm.
Sex ♀	15	21	14	13
♂	0	4	9	5

Having accounted for the sample she states: "Because none of the 3 mm. group possessed a distinct penis, the snails were all placed in the female class; but it is very probable that snails of this size are sexually immature."

The author disagrees with the tentative statement made by this worker and believes that the lack of genitalia in these specimens under 6 mm. in height is due to sexual immaturity and does not account for the presence or absence of the vaginal papilla. In all specimens of this size examined by the author (approximately 200), sex determination was impossible owing to the complete absence of either sexes genital organs.

If sex reversal applied to this problem one would expect that the females' organs would be present in these specimens lacking a penis while the complete absence of either genitalia strongly suggests sexual immaturity.

The exact nature of this problem will be understood only after a hystological study of the mature and "immature" gonads has been conducted. (The author hopes to submit this in the appendix to this report.)

This problem does not apply to P. heros, but this may be due to the fact that no small specimen of this species has been recovered.

Wheatley (47) in discussing the relation between length of penis and snail height, submits the following table: (Table 11)

Table 11. Length of Male genitalia compared to height of shell.

	P. heros Shell height	Penis length	P. triseriata Shell height	Penis length.
	mm.	mm.	mm.	mm.
	16	2	7	1.5
	26	5	13	6.5
	28	6	17	6.0
	34	8	17	6.5
	36	12	19	7.0
Average	28	7	15	6.0

In samples of P. heros the author has noted some large snails with proportionately small penes.. This observation was never duplicated with P. triseriata. Specimens showing this abnormal condition varied in shell size from 26 mm. to 34 mm.. No explanation is offered for this phenomenon, though it should be noted that Dawes (1949) makes reference to similar observations where the growth of genitalia was inhibited by excessive damage to the gonad of the Gastropod by Redial and Cercarial Trematodes. This casual observation and possible relationship should be investigated in conjunction with investigations on the Trematode parasites of the winter flounder present in this area.

In discussing the problem of sexing, Wheatley suggests: "In some larger female specimens of Polynices, at least at certain times of the year, e.g. June and July, the ovaries may be seen packed with tiny light colored eggs, apparently hexagonal. The ovaries seem to be dark brown, while in the mature male the corresponding region appears light brown and possible contains sperms." This is accurate but of little use to solving the problem as the adult possessing mature germ plasm will naturally have well developed genitalia, thus permitting visual sexing in situ.

Baeristo investigated the possibility of sex determination based on differences in shell proportions and studied samples of both sexes of the two local species.

The following data and ratios were collected by this worker:

1) Height of shell
2) Width of shell
3) Width / Height
4) Height of aperture
5) Height of aperture / Height of shell
6) Width of aperture
7) Width of aperture / Height of shell
8) Width of aperture / Height of aperture

(For exact results see Baeristo's report 1948.)

The results failed to show any marked and significant variation between the sexes of either species which might be used in the laboratory or the field as a reliable method of sex determination in specimens lacking external genitalia.

At present for P. triseriata under 6 mm. in height, means of sex determination seems to lie in a microscopic (hystological) examination of their gonads.

D) REPRODUCTION

1) Mating Habits. In all observed mating pairs the male was consistently smaller than the female. Mating on the surface of the flat was observed at low water during the dusk to dawn period. The peak of mating activity being in the hours following dusk and in those preceeding dawn, the former period being that of greatest incidence. Stinson (1946) records the recovery of mating pairs immediately below the flat surface during the day.

In copulating on the surface both snails retain their crawling posture. The male assumes a position postero-dextrad to the female and in some cases "he" may be supported, in part, by the latters expanded foot. The propodium of the male is extended and bent sinistrad so as to surround partly the dextral face of the females shell, and then be inserted into the latters pallial cavity.

When mating takes place on the surface the copulating pairs move about constantly, the female travelling at a greater speed than the male and often loosing him in this "conjugal march". After a variable period of time the "couple" burrow into the flat, the initiative in this operation being taken by the female.

Stinson (1946) and Wheatley (1947) assumed that sperm transfer takes place during the "conjugal march". Stinson states: "The propodium of the male is extended around (the shell) as a narrow band with the penis extended, and inserted under the shell of the female. Fertilization is therefore internal." Wheatley says: "The penis, which is located at the base of the right tentacle, is extended across the breadth of the male and inserted under the female's shell." This is incorrect, for the tip of the penis, not the point of insertion, is located at the base of the right tentacle; thus to perform this act as described by Wheatley this organ would have to be bent sinistrad. The normal curvature to its axis is dextrad. (See Fig. 19.)

In the author's opinion this march is "pre-conjugal" rather than "conjugal", to be more specific the observed pairs arè not actually in copula, and that the transference of sperms takes place under the surface after burrowing.

This belief is not completely substantiated but is supported by the following observations:

a) In all pairs observed, by the writer, only the pro-podium appeared to be inserted into the pallial cavity of the female. The penis was not involved.

b) The morphology of the genitalia of both sexes leaves no doubt that insemination required copulation; yet their position and the position assumed by the "mating" pairs is such to prevent insertion of the penis into the vaginal papilla during the march. To perform this act, the penis would require a greater degree of articulation and extensibility than it possesses.

c) The only alternative method by which insemination could be carried out in this position would be by the pro-podium acting as a trough or conducting canal between the two genital openings. This seems most unlikely when the anatomy of the genitalia is considered.

d) There is no doubt that this characteristic march of the snails is connected with mating, but the animals must assume some other position for insemination of the female, and the fact that burrowing regularly follows the march might indicate that insemination takes place below the surface.

2) Height Relationship of Mating Pairs. Pairs found in what the author will henceforth refer to as the "Pre-conjugal march" were collected and measured by Stinson and the present writer (See Table 12 and 13). These records show that the mating female are larger than their male partner. We might explain this by assuming that the males were younger than the females, or that they were the same age but had differing growth rates. We have still to discover which of these assumptions is correct.

Table 12. Height relationship of male and female <u>P. triseriata</u> in mating pairs. (1946) (Stinson Table 6.)

Date of collection	Time of day	Location	Height of female mm.	Height of male mm.	Ratio F/M
June 11	2 p.m.	under sand	23	14	1.6
"	"	"	23	15	1.5
"	"	"	21	15	1.4
"	"	"	18	15	1.2
"	"	"	21	19	1.1
"	"	"	20	17	1.2
June 14	5 p.m.	"	21	16	1.3
"	"	"	19	9	2.1
July 1	8 p.m.	"	21	18	1.2
"	"	"	25	18	1.4
"	"	"	19	19	1.0
"	"	"	24	18	1.3
		Mean	21.2	16.1	1.36
July 3	9 p.m.	on surface			
"	"	"	25	13	1.9
"	"	"	18	10	1.8
"	"	"	21	13	1.6
"	"	"	22	16	1.4
"	"	"	16	17	0.9
"	"	"	23	15	1.5
"	"	"	23	14	1.7
"	"	"	24	15	1.6
"	"	"	17	16	1.1
"	"	"	22	14	1.6
"	"	"	22	14	1.6
"	"	"	19	16	1.2
"	"	"	20	13	1.5
"	"	"	21	16	1.3
August 22	"	"	25	15	1.7
		Mean	21.2	14.4	1.50
		General Mean	21.2	15.2	1.43

Table 13. Height relationship for P. triseriata found mating. (1949).

Date of collection	Time of day	Location	Height of female mm.	Height of male mm.	Ratio F/M
June 28	10 p.m.	on surface	21½	10	2.1
June 30	11 p.m.	"	18	13	1.3
"	"	"	15	12	1.2
"	"	"	14	12	1.1
"	"	"	14	10	1.4
"	"	"	15	12	1.2
July 1	"	"	15	12	1.2
"	"	"	14	12	1.1
July 3	12 p.m.	"	17	15	1.1
"	"	"	14	12	1.1
"	"	"	17	14	1.2
"	"	"	14	13	1.0
"	"	"	12	11	1.0
July 9	1 a.m.	"	13	11	1.1
July 15	11 p.m.	"	17	11	1.6
"	"	"	16	12	1.5
"	"	"	12	10	1.2
"	"	"	14	11	1.2
"	"	"	13	10	1.3
"	"	"	13	12	1.0
"	"	"	11	10	1.1
July 17	10 p.m.	"	14	12	1.1
"	"	"	16	13	1.2
"	"	"	17	14	1.2
"	"	"	14	12	1.1
"	"	"	14	10	1.4
"	"	"	11	9	1.2
"	"	"	15	12	1.2
"	"	"	17	13	1.3
		Mean	15.08	11.72	1.25

Two P. heros were recovered during the 1949 season in copula their respective heights were:

Date	Hour		Female mm.	Male	Ratio F/M
July 3	11 p.m.	under sand	38	30	1.20
"	"	"	50	39	1.28

The data compiled in Tables 12 and 13 are graphed (See Fig. 25) and these indicate some rather interesting relationships. When the 1946 and 1949 mating pairs are represented in graphical form by plotting males versus females (height) a peculiar distribution is obtained, this demonstrates a remarkable variation in size for the size of mating pairs in these two seasons. In seeking an explanation to this peculiar distribution the sex ratios collected by Stinson (August 21-22, 1946) and the present writer (August 24, 1949) are graphed in Fig. 26; these corroborate with the distribution of the mating pairs in showing that:

the maximum distribution, in terms of height, for the:

a) male population in 1946 is approximately at 16 mm. while the average figure for the male in the mating pairs is 15.2 mm.
b) the female population has its mode at 22 mm., while the average female in the mating pairs is 21.5 mm. in 1946.

In contrast to these figures the 1949 sex ratios show that:

a) the female population is bimodal with a maximum distribution at 9 mm. and a second peak at 14 mm.; while the average figure obtained from mating pairs is 15.08 mm.
b) the male population has its maximum distribution at 9 mm. and an average of 11.7 mm. for mating pairs.

Certain speculations can be made on the occurence of these distributions, but clear understanding of this problem will only be possible when more is known about the growth rate of the snails.

a) With the 1949 figures it would appear that, though the sex ratios show the female population to be bimodal in terms of size (height), it is only those females represented by the second mode (14 mm.) that are sexually mature and are thus found mating. Similarly it appears that the sexually mature male is consistently smaller than the female and that this is not restricted to the actual mating pair but to the whole population in terms of its sex ratio.

From this, one can postulate, that either the male reaches maturity before the female assuming the growth rate to be the same for both sexes, or that both members of the mating pair are of the same age but that the mature male does not reach the ultimate size of the female. This second statement seems more feasible in the light of Stinson's limited investigation on growth rate, where he states: "It seems probable that the size class with its mode at 16 mm. is composite, embracing several year classes and that the ultimate size of P. triseriata males seldom exceeds 18 mm." This assumption is strengthened by the observation that snails of this size class showed much variety in shell and body characteristics.

He proceeds in his description pointing out that within this mode he found males with new and old shells but both with well developed genitalia, thus presuming these to be mature though not of the same age.

Thus the relation between the male and the female of the mating pair appears to be due to the differences in growth rate and not to a differential sexual development.

b) This, however, does not explain the reduction in size of the mating pairs observed in 1949, neither does it explain the occurence of the decreased modes in the tables showing sex ratios for 1949. In considerating the sex ratios and the distribution of the modes for both seasons for P. heros it is noted that no comparison to the figures for P. triseriata can be made owing to the multi-modal distribution obtained in plotting the former's population in terms of height frequency distribution of sexes.

The decrement in the position of the size frequency distribution modes of each sex is probably due to the absence of one or more "year" classes; that is in 1946 the large snails found (23 mm. for females and 17 mm. for males) represent an old year class, possibly 3-5 years old, while in 1949 no such age class is found owing to the failure of one of the previous years "snail spat" to become established. Thus the population recorded in 1949, though sexually mature and actively reproducing represents a younger population than the one present at the Cove in 1946.

Dr. Medcof suggests the possibility of selection being exercised by the female in picking the male in mating, holding that this may explain the "pre-conjugal" march. This speculation is based on the constancy of the female to male ratios obtained from Table 12 & 13. From Figure 25 it would appear that some selectivity was exercised by the 1949 mating sample, but it is hard to concile this with the 1946 recordings.

Thus it would seem that some selectivity, based on size, is exercised by the mature and growing snail, as long as its size retains it in that portion of the population which can be subdivided by a height frequency distribution into year classes; but on reaching the end of growth, when the snail will be in that part of the population frequency distribution of comparatively equal size but composed of heterogeneous year classes, this selectivity appears to be lost as indicated by the 1946 results in Figure 25.

Hence it is possible that the mature but growing population tend to mate within their year group, but on the cessation of growth with age this relationship is lost and mating takes place between snails of differing year classes but of comparatively even size within the sexes.

Mating pairs of P. heros were sought by the past and the present investigators but only two were found. It may be that in this species there is no pre-conjugal march or that it is of very short duration and probably takes place under the surface as both specimens were found mating under the substratum.

3. Time and mating.

a) Season. This seems to commence early in the season for all investigators have noted the presence of egg collars on the flat at the time of their arrival in early May. The earliest recorded observation of mating was made by Stinson on June 3rd. (1946), though he observed the presence of collars in May.

The mating continues throughout the season reaching its peak in late July, but this probably varies from year to year. The latest recorded entry for observed mating was made by Stinson on August 22nd.

b) There seems to be a considerable lapse of time between insemination and egg collar formation, though on one occasion a female with a partially finished collar was found in the company of a male, suggesting that collar formation is immediately subsequent to insemination, this observation was never repeated and the two snails were not in any way attached, thus their relation probably was purely incidental.

E) Feeding Habits of Polynices.

In this locality the whelk feeds largely on the soft shelled clam (Mya), the bar clam (Mactra) and the mussels (Mytilus and Modiola). Other bivalves and numerous gastropods, including Polynices itself, are drilled. Occasionally the snails are found feeding on small fish and crustacea.

1) Methods of feeding. Polynices usually devours its molluscan prey by insertion of the proboscis into a hole it drills through the valves, though they frequently eat bivalves without drilling.

a). Drilling is probably the most common method of feeding and may be best observed on the surface of the flat when the low water period follows dusk, but it goes on beneath the surface, as well, especially during the day. Stinson found snails firmly holding clams in their folded foot at depth of 6" below the surface during the day. The method by which the whelk drills differs slightly depending on the relation of the prey to the substratum. If it is an unattached form, like a clam, the snail wraps its expanded foot around the victim and completely covers the drilling operation from view. If the animal is attached to the substratum, such as mussels are, the snail being unable to surround the prey merely attaches itself to one part of the shell without abnormal expansion of the foot. This permits more than one snail to feed on the same victim. (See Fig. 27.)

Method of drilling. On encountering the prey, such as a clam, the snail spreads its foot over the victim, this takes place on and under the surface of the flat, and then proceeds to enclose the shellfish by cupping medio-ventrally the post-podium, thus forming a pouch to retain the prey. The whole shell of the prey is usually covered, but occasionally a small ventral area is in contact with the substratum and exposed to it. The snail does not always devour the clam immediately but may wander about on the surface with the clam held in the post-podium (N.B. the longitudinal axes of the prey and predator correspond, as shown by Fig. 28) with the umbo and pallial edge clearly outlined by the stretched opalescent post-podium. The snail may proceed to burrow immediately still withholding the prey or may cease its wanderings and begin to drill the victim while still on the surface. With the clam thus held there is a copious secretion by the pedal glands, forming a thick, elastic and tenacious gelatinous envelope around the prey. This secretion was noted in all cases regardless of the nature of the food and was found in all cases where the food had been obtained by drilling or other means.

Drilling operations commence with the cessation of locomotion and an anterio-ventral folding of the post-podium which displaces the clam near the Rhynchostome. The umbo of the clam shell is usually apposed to this region. With the displacement of the clam from its position prior to drilling to the drilling position, instead of being held flatly as in the former case it is held on edge so that usually the umbo is apposed to the probosial region; this probably occurs owing to the greater expansibility of the marginal area of the foot which is better able to enclose the wide pallial edge of the clam shell (especially considering that the size ratio of prey and predator is 1/1). With the clam in this position the proboscis is evaginated and directed ventrad, seeking the clam shell and usually making contact with the umbo; simultaneously the pro-podium expands meso-ventrally so as to completely cover and obscure the feeding process. With this change in the disposition of the foot (See Fig. 29 & 30)the whelk is unable to retain its balance, owing to its now spherical shape, and characteristically rolls on its side. It remains in this position until the feeding operation is completed, though if disturbed it will rapidly retract its foot and proboscis into the shell, and release the prey (See Fig. 31).

Baeristo (1948) succeeded in obtaining some photographs of the extended proboscis by placing a shucked clam meat between two glass plates which were separated sufficiently to allow the snail to insert its proboscis between them and extend it towards the clam (See Figs. 32, 33, 34). These photographs do not portray the actual feeding method or the interesting process of drilling but they demonstrate the remarkable extensibility and manuvrability of the proboscis and give graphic proof of the snail's ability to detect prey, as reported by Ankel (1938) who showed that carnivorous gastropods detect the proximity of food by means of the osphradium and the anterior margin of the pro-podium. In similar experiments with clams and snails the author noted that the pro-podium possesses great extensibility and is prehensile being used extensively in reaching and obtaining food from otherwise unaccesible locations.

The actual drilling and mechanical penetration of the shell was thoroughly investigated by Dr. W. E. Ankel (1938) when he performed a survey on gastropod radulae. From his investigation it was clearly shown that the Naticidae and Muricidae do not use the radula in drilling the shell, and contrary to popular belief, this operation is performed by the secretions of a ventral sub-terminal proboscial gland (See Figs. 12 & 13) producing a $CaCO_3$ dissolving secretion which Dr. G. C. Hirsh tentatively called a calcase after Professor Krollpfeiffer, on Ankel's instigation, failed to show the presence of an acid in this gland's secretions. (Tested for: Sulphuric, Nitric, Phosphoric and Formic acid.)

Though there is no doubt that drilling in the Naticidae is a purely chemical operation, as yet determination of the active principle in this solvent is wanting.

Either the right or the left valve of the shell-fish may be drilled. In the soft shelled clam and the mussel, the drill hole is usually slightly posterior to the umbo and closer to it than the free margin of the shell. Stinson records that with bar clams over two inches in length, the hole is often on the umbo of either valve. Belding (1930) states that the point of perforation varies but is usually towards the siphonal end (posterior) of the valve.

Though the snail usually penetrates the shell in the region of the umbo, shells drilled near the pallial margin are not uncommon (See Fig. 35). This relation is possibly governed by the size ratio of predator and prey, as drilling appears to usually take place with the prey held at right angles to the predators longitudinal axis and thus governed by the expansibility of the marginal region of the foot. There is no reason to assume that drilling necessitates complete encapsulation of prey by the predator's foot, and thus that there should be any size limit on prey, though the writer never observed Polynices feeding without typically enveloping its prey (except with mussels) Ankel suggests that this is of common occurrence.

Once penetration of the shell has been achieved "chemically" the proboscis is inserted into the prey and feeding commences.

This feeding process consists of a mechanical rasping action by the radula which is extruded with the odontophoral complex and apposed to the food; with the backsweep of the radula the backwards directed teeth are forced into the flesh and fragments are transported posteriad to the oesophagus. During this backsweep the flexible basement membrane of the radula is bent by passing over the grooved Odontophoral cartilage thus the rigid median and sub-median teeth form the fundus of this "conveyer belt" while the recurved sides are functionally prolonged medially by virtue of the articulated marginal and sub-marginal teeth. Thus on apposition to the prey's meat during the radular backsweep this organ forms a posteriorly moving food canal which rasps off tissue and transports it to the oesophagus. The rasping stroke is further assisted in the Naticidae by the presence of two lateral "jaws" (See Fig. 14) which arch dorsally and meet medianly to the radula and assisting this, with scissor like movements, in cutting some of the larger fragments engaged by the radula.

b) Feeding without drilling. The snail can surround the prey with its foot, and in a manner not clearly understood, devour the meat without drilling the shell. (For evidence see Wheatley's report pp. 11-12.)

This alternate method of feeding is clearly manifested by the large numbers of empty, non drilled clam shells, found with gaping valves enfolded within the characteristic gelatinous secretion of the snail.

Feeding commences, as previously described, by the snail retaining the clam in its post-podium and secreting around it a thick elastic coating of pedal jelly. Much speculation has been raised as to the exact means employed by the whelk in gaining access to the clam without drilling the shell. Wheatley suggested that this gelatinous envelope may have an anesthetizing quality which would aid the snail by causing the clam to relax its adductor muscles, thus allowing the valves to be forced open. This would appear to be somewhat similar to the reported secretions of some Asteroideans and might be adopted as an explanation of the following statement by Gannong (1889) "The writer saw last summer, at Oak Bay, a large Buccinium undatum which had been attacked by a Lunatia, a little larger than itself. Though the boring had not commenced the former was completely enclosed by the foot of the latter, and had its aperture quite covered with a sticky slime. It at first seemed dead, but on being placed in water it revived and seemed none the worse for its adventure."

Though this effect may well occur it should be noted that the symptoms described by Gannong may be considered typical of an oxygen deprivation, as observed with whelks left for long periods in aquaria without adequate changes of water. Thus it should be considered that this secretion, though it may have a chemical effect, may also act mechanically on the clam, by tending to suffocate the bivalve; which in an effort to free itself from the gelatinous envelope, opens its valves. In this weakened condition it thus becomes an easy prey for the snail. Wheatley records the frequent occurence of clam shells found in an upright position in the sand with half of their shell exposed above the surface. The contents of these clams were either wholly or partially gone; the valves were gaping and in many cases the remains of the mantle was stretched across this gap. Wheatley suggested that characteristic position and occurrence of dead clams indicated that the snail was not only capable of digging after its prey but in addition it approached it from below and "chased" it towards the surface, thus the occurrence of dead partly emerged shells.

From Stinson's Table 13, one notes that the parts most frequently left uneaten by the whelk are: the end of the siphon, the mantle edge, the dark digestive gland and sometimes the adductor muscle.

Wheatley observed the snail feeding, on the surface, on clams whose shell had been damaged by gulls and other agencies. This is not uncommon, but it should be noted that the clams were still alive, there being no observation on record indicating that these snails are scavangers; this role in flat ecology, at Belliveau Cove, rests completely with the large population of Nassa trivitata.

2) Size relationship of drill and prey. Some observations have been recorded concerning this relationship in studying factors that limit the destructive capacity of the snail. Stinson (1946) by field collection of the whelk and its prey and by experimentation in vitro with the larval snail and spat clam, demonstrated a size relationship between predator and prey, giving the following ratios:

a) Adult snail to clam. 1.0/1.1
b) Larval snail to spat clam. 1.0/1.1

Wheatley, (1947) corroborates with Stinson's conclusions for adults but suggests that a truer average value for the ratio size of adult snail to clam is 1.0/1.1

Belding reports that a half inch (1/2") snail can destroy a one inch (1") clam, though Stinson's evidence indicates that this seldom happens. Belding further states that a 1.1/2 inch snail cannot operate on a clam over two inches in length. While this accords in general with Stinson's and Wheatley's findings it may not be impossible because we have evidence that whelks often drill without necessarily enveloping their prey. Thus it can be stated that snails usually attack clams that are about their own size avoiding those that are much larger or much smaller.

The peculiar feature of this relationship is that large snails seldom feed on small clams, though there are no apparent limiting factors for this feature.

Tables 14 and 15 give the size relationship of the adult predator and prey collected on the flat. Table 16 lists data for the larval snail and spat clam assembled by Stinson in laboratory experiments.

Figure 36 is a graphical representation of these tables and shows that over the whole range the size of the shellfish attacked tends to vary directly with the size of the attacking snail and that the predator generally attacks a clam whose length is 1.1 to 1.2 times its own height.

Table 14. Size relationship of *P. triseriata* and its prey in nature. (Wheatley Table 6.)

	Height of snail in mm.	Length of clam in mm.
	25	28
	24	29
	25	29
	18	9
	25	29
	15	26
	17	30
Average	21.3	25.7

Table 15. Size relationship of prey and predator in nature. An abstract of Stinson's Table 13 showing the relative sizes of predator and prey (*Mya*) for *P. triseriata* and *P. heros* recorded in 1946. (No differentiation was made between the two species in this Table by Stinson.) (Stinson Table 16.)

Height of snail in mm.	Length of clam in mm.
23	20
20	13
22	26

Continued.......

Continued -

Height of snail in mm.	Length of clam in mm.		Height of snail in mm.	Length of clam in mm.
13	20		25	20
21	21		20	19
20	24		18	18
20	18		22	23
16	23		38	37
25	24		33	35
21	20		24	31
17	19		23	28
16	19		18	25
19	22		21	19
15	18		20	21
17	24		21	21
23	26		17	16
15	19		18	23
18	23		19	26
17	19		19	25
15	23		22	20
20	27		18	18
15	17		19	22
19	20		19	24
13	21		18	25
19	21		18	24
16	21		17	23
20	24		21	20
21	22		21	21
15	24		15	15
16	21		20	19
16	20		21	20
14	20		14	17
14	18		17	20
		Average	19	22

Table 16. Relative sizes of newly-emerged P. triseriata and the clam spat they attacked in laboratory tests. (Stinson Table 16.)

	Height of Snail mm.	Length of Spat mm.	Diameter of hole mm.
	0.9	0.75	0.16
	0.9	0.85	0.2
	0.95	0.8	0.15
	0.9	1.0	0.15
	0.9	0.8	0.15
	0.9	0.85	0.16
	1.1	1.2	0.15
	0.9	0.9	0.2
	0.9	1.0	0.17
	0.9	0.95	0.15
	0.95	1.5	0.15
	0.95	1.3	0.16
	0.9	1.2	0.15
	0.9	1.0	0.18
Average	0.93	1.0	0.16

3. Destructive capacity.

a). With small (post-larval) snails: Little success has been achieved in field trials to evaluate the destructive capacity of newly emerged snails in terms of clams destroyed per snail per day; because it is difficult to make the necessary precise observations on the flats, this difficulty is greatest when working with the small post larval snail and spat sized clams.

Stinson obtained some results which cannot be regarded as typical of natural conditions because they were obtained by laboratory experiments. Nevertheless they give some indication of the destruction wrought by the young snails.

He placed newly emerged P. triseriata (under 1 mm. in height) in vials containing sand and water, to which he added clam spat. After a period of 11 days he examined the sand and recorded the numbers of drilled and undrilled spat.

From this experiment he concluded that the newly emerged snails burrow into the sand after the spat and drill their shells in a manner similar to that of the adult.

Stinson refined this experiment in an attempt to determine the number of clam spat the post-larval snail could kill per unit time. (See Table 17.)

Table 17. Summary of data on the destruction of clam spat by newly-hatched P. triseriata in vitro. (Stinson Table 17.)

Spat per vial	Snail height mm.	No. of spat bored	Time days	Length of spat mm.	Clams destroyed per day per snail
5	0.95	1	4.0	0.8	0.25
5	0.9	1	4.0	1.0	0.25
5	1.1	1	4.5	1.2	0.2
10	0.95	2	4.0	1.3 1.5	0.5
10	0.9	2	4.0	1.05 1.2	0.5
				Average	0.34

From these results Stinson calculated that a newly emerged snail destroyed 0.34 clam spat per diem which would approximate to a monthly average of 10 clams per snail.

b) With the adult snail: The present and past workers attempted an evaluation of the destructive capacity by placing clams and snails in wire cages sunken in the flat surface.

The authors experiments met with failure and the death of the caged clams could not be related to Polynices. However, Stinson and Wheatley succeeded in a minor way (Table 18, 19 & 20) and from their "inadequate" results they suggested a destructive capacity of 0.07 to 0.4 clams per day per snail.

Table 18. Feeding of 3 separately caged P. triseriata. (Stinson Table 18.)

Snail ht. mm.	Clams per cage	Days	No. of clams drilled	Length of drilled clam mm.	Clams destroyed per capita per diem (number)
20	6	3	2	18, 20	0.7
32	6	3	1	21	0.3
20	10	5	4	20, 21 21, 22	0.2
				Average	0.4

Table 19. Feeding of caged P. heros. (Wheatley's Table 52.)

Period of test days	No. of snails	No. of clams	Ht. of P. heros mm.	Length of clam mm.	No. clams drilled	Length of drilled clams. mm.	Clams destroyed per capita per diem (number)
7	3	8	20,36,45.	32,34, 36,37, 39,40, 56,63.	2	34,36.	0.10
3	2	6	36,45.	32,37, 39,40, 56,63.	1	39.	0.17
4	2	5	36,45.	32,37, 40,56, 63.	2	37,40.	0.25
4	1	4	36.	31,31, 34,36.	3	34,36, 34.	0.75
4	1	4	45.	32,40, 56,63.	1	32.	0.25
4	2	2	14,22.	28,29.	0		0.00
4	1	2	36.	31,34.	2	31,34.	0.50
1	1	1	36.	56.	0		0.00
1	1	2	38.	40.63.	0		0.00
						Average	0.224

Table 20. Feeding of P. triseriata. (Wheatley's Table 5b.)

Period of test days	No. of snails	No. of clams	Height of snail mm.	Length of clam. mm.	No. of clams drilled	Length of drilled clams mm.	Clams destroyed per capita per diem (number)
7	1	3	12.	28,29,31.	1	31	0.14
7	2	6	13,15.	30,31,31, 34,34,36.	1	31	0.07
3	1	5	13.	30,31,34, 34,36.	1	30	0.33
2	3	2	12,16,18.	28,29.	0		0.00
4	2	2	12,16.	28,29.	0		0.00
4	1	2	16.	28,29.	0		0.00
1	3	2	12,13,14.	28,29.	0		0.00
						Average	0.07

When these figures (average) are compared with Wheatley's results the adult P. heros and the previously discussed observations on post-larval feeding rate for P. triseriata it would appear that the young snail is more voracious than the adult. (Table 21.)

Table 21. Summary results of the feeding experiments including both species of snails, showing the number of clams destroyed per snail per day and per month (30 days).

	Clams per day	Clams per month	Investigator
a) with young snails	0.34	10.2	Stinson
b) with adult snails	0.40	12.0	Stinson
	0.22	6.6	Wheatley
	0.07	2.1	Wheatley
Average	0.23	7.7	

Belding in Massachusetts (1930) considers a 2" snail (presumably P. heros) to be the most destructive and estimates that they kill 26 clams per month (0.8 per day). The results obtained should not be considered critical measures of the snails destructive capacity and are submitted in this report as an acknowledgment to this phase of the investigation rather than an exact estimation of voracity. The author feels that Stinson's and Wheatley's figures are not indicative of the destructive capacity at Belliveau Cove and that any tentative conclusion would be pure speculation and thus valueless.

c) Relative importance of drills in contributing to total mortality. Stinson attempted to estimate the snails contribution to the total mortality of bivalves in this locality by counts of the numbers of living and dead bivalves in screened samples and sample of shells found in the beach wrack.

Table 22. Observations on screened soil samples. (Stinson Table 14.)

Condition of clam	Mya arenaria	Mactra	Tellina	Unidentified bivalves	TOTAL
Alive	0	4	1	3	18
Dead - not drilled	12	1	0	0	13
Dead - drilled	176	9	0	1	186
				Total	217

From these results he drew the following conclusions:

1) Drills are responsible for a high proportion of the mortality of small bivalves at Belliveau Cove (up to 90%).
2) Of the several species studied, soft shelled clams are the hardest hit in proportion to their numbers.
3) It is possible for the drills to completely eliminate Mya before turning to other prey.
4) Nevertheless, 9 out of 10 dead bar clams were killed by drills.

These conclusions were reached by Stinson on the assumption that the counts made included all living clams in the areas sampled, and that shells of all dead shellfish remain intact and buried in the sand. No observations were made to determine how long empty shells persist in the sand before disintegrating.

Stinson collected random samples from beach wrack of shells of clams and mussels, apparently of the 1945 set and whose valves were unbroken and still connected.

Table 23. Summary of observations on shells from beach wrack. (Stinson's Table 15.)

Type of shell	NUMBERS		
	Total examined	Drilled	Not Drilled
Clam	100	33	77
Mussel	50	42	8

From these records he suggests:

1) "That in clams of spat size at least one third of the mortality can be attributed to Polynices.
2) Comparing this estimate with that from the study of screened shells which were on the average much smaller, it would appear that large clams are less subject to attack by the snail than the smaller.

(This statement in the light of later investigation appears to be a misconception. This is not due to an inter-relationship between the prey and predator, but to their distribution; Stinson's samples were taken near the shore line where the population is purely composed of small P. triseriata which have easy access to the superficial spat size clam and not to the deeply burrowed large Mya. Hence in this region there is almost 100% mortality of spat and equally good survival of the adult clam. It is true that the large clam here is less subject to attack by the snail present in this region, but this is due to the poor burrowing ability of the snail of this size and not to the fact that the large clam has a degree of immunity from the snail in general, as suggested by Stinson.)

3) Of the agents that kill the mussels without destroying or removing the shell from the flats Polynices is the most important."

In conclusion it may be stated that though the data cited is inadequate and controversial in giving a precise portrayal of the snails' destructive capacity, it does give some indication of the possible degree of damage that a snail can accomplish and this is more than sufficient to explain the ubiquitous occurrence of drilled shells and to emphasize the potential danger to clam stocks once the snail becomes established on the flats.

Figure 6

P. heros operculum; Op. Nuc. - opercular nucleus.

Figure 7

Upper row - P. heros shell characters
Lower row - P. triseriata shell characters

Figure 8

P. heros shell characteristics.

Figure 9. Sectional view of *P. heros* shell. Col. - Columella; Umb. - Umbilicus; Wh. - Whorl.

Figure 10. Sp. - Spire; Sut. - Suture; Ap. - Aperture.

Figure 11

P. heros soft parts with shell removed in situ. Col. Mus. - Columella muscle; Ct. - ctenidium; Pall. edge - pallial edge; Ped. fold - pedal fold; Tent. - tentacle; Prob. - proboscis; Dg. Gl. - digestive gland; St. - stomach; Gn. - gonad; Op. - operculum; Ped. gl. - pedal gland.

Figure 12

P. heros everted proboscis; lateral, ventral and dorsal anterior view.

Tent. - tentacle; Prob. - proboscis; S. Pd. - secretary pad; Mo. "true" mouth.

Figure 13

(A) Lateral view of proboscis (inverted) and oesophageal glands dissected in situ.

(B) Diagrammatic representation of inverted proboscis (sectional).

(C) Diagrammatic representation of everted proboscis (sectional).

Rad. - pharyngeal radula; Rad." - extra-pharyngeal radula; Rhyn. - rhynchostome; Oes. - oesophagus; Sal. gl. - salivary gland; Ln. gl. - gland of Leiblein; Ph. - pharynx; Mo. - mouth; S. pd. - secretary gland.

Figure 14. Diagrammatic representation of Odontophore complex. X - Ankel's maxillae; Rad. - radula.

Figure 15. Radula in situ.
Od. Pl. - Odontophore plates.

Figure 16.

Radula - showing part of the Odontophore plates and the buccal end of radula ribbon.

Figure 17.

Radula - Vide supra.

Figure 18.

Radula - arrangement of teeth. 1. Median tooth; 2. Sub-median tooth; 3. Sub-lateral tooth; 4. Lateral tooth.

Figure 19.

Radula - arrangement of teeth in specimen mounted in balsam.

Figure 20.

Radula - teeth. Ia. Median plate. Ib. median tooth. IIb. sub-median plate. IIa. sub-median tooth.

Figure 21.

Radula - teeth. 3. sub-lateral tooth. 4. lateral or marginal tooth.

Figure 22.

Digestive tract removed and shown diagrammatically.
S. Pd. - secretary pad; Ph. - pharynx;
Oes. - oesophagus; Sal. gl. - salivary gland;
Ln. gl. - gland of Leiblein; St. - stomach;
Pall. - pallial edge; An. - anus;
Rad.* - extra pharyngeal radula.

Figure 23.

P. heros - male. Pallium partially removed to expose genitalia in situ. Ren. gl. - renal gland; Pall. - pallium; Tent. - tentacle; Pen. - penis; V. def. - vas deferens; Op. - operculum; Col. mus. - columellar muscle; Test. - testis; Dg. gl. - digestive gland.

Figure 24.

P. heros - female. Vide supra. Ovar. - ovary; Ovd. - oviduct; Ovd.' - glandular oviduct; Vg.- vagina papilla.

Figure 25. Height relationships of males and females in mating pairs collected in 1946 and 1949.

Figure 26. Height-frequency distribution of males and females in 1946 and 1949.

Figure 27.

Surface feeding at night by P. heros on the soft shelled clam at Holt's Point, N. B.

Figure 28.

P. heros transporting a clam in the postpodium.

Figure 29.

P. heros commencement of drilling, the clam is withheld in the cupped foot. The post-podium (Ps. Pod.) moves anteriorly to meet the ventrally expanding propodium (P. Pod.) while the contained clam is brought in apposition to the extruded proboscis (Prob.)

Figure 30.

Night feeding at Holt's Point, N. B. by a small whelk on a large clam. Note the greatly expanded foot partially containing the clam whose syphon extrudes towards the top of the plate.

Figure 31.

P. heros retracting foot to expose prey.

Figure 32. Figure 33.

Demonstration of feeding in vitro. A shucked clam meat is placed between two glass plates so as to prevent the snail from gaining easy entry to the prey. Note the expanded propodium forced between the glass plates in an attempt to reach the clam: the progressive extrusion of the proboscis to reach the meat. The clam syphon shows as a dark oval area.

Figure 34.

Figure 35.

Comparison of drilled specimens including Mactra, Mya and Polynices showing the variation in the location of the drill hole.

Figure 36.

Height relationships of prey and predator.

IV. Egg Collars of the Local Species

A. Description.

General. The egg case or "sand collar" as it is popularly called, has been described by many authors, but in the present writer's opinion these descriptions are general and inadequate in differentiating between the collars of different species.

Arnold (1903) records their shape as: "A basin with the bottom knocked out and broken at one side"; Verril (1875) states: "They consist of a broad ribbon of sand coiled up into a circle and shaped something like a saucer, but without a bottom"; Stinson (1946) describes the collar of P. triseriata as follows: "The collar is characteristic in form resembling an old fashioned detachable collar, lying with its widest diameter on the surface of the flat." For P. heros he states: "The egg case is constructed on the same general plan as P. triseriata. Although it has a turned up upper margin compared with the former which tends to be straight sided. It lies on the sand with the wide diameter down and is far less inclined to become buried than the collar of P. triseriata." (Figure 37.)

It is felt that a careful study of the photographs illustrating the two egg cases under consideration will provide a more adequate appreciation of their shape and structural differences than any verbal description the author can provide. (See Figures 38,39,42,44,45,47,49,51.)

1). Egg collar of P. triseriata. There is considerable variation in size and shape; collars laid at the commencement of the season are erect structures appearing at first glance like obtuse truncated cones with a slope of 30 degrees from the vertical. (Figures 38,39.) Closer inspection will show that the basal edge is not sloped but forms a vertical marginal strip about 1-2 mm. wide and tapering to a thin edge. In well formed collars a similar vertical peripheral strip is found on the apical margin of the collar. (Figure 39.) The average width of these collars varies from 22 mm. to 15 mm.

The end of the 1949 season was characterized by the appearance of very small collars (Table 27.) Their general shape is similar to the large collars but they tend to loose the vertical margins, especially the apical margin, and to lie flatter on the beach and are therefore less conspicuous. These late collars are more reduced in length rather than width, thus affecting their total area and capsular contents (See Table 27). Their width is usually under 18 mm.

The collars are composed of a gelatinous matryx with imbedded sand grains surrounding the contained egg capsules. They are a firm but pliable ribbon 8-20 mm. wide and 1-1/2 mm. thick, containing a single layer of egg capsules. Both margins and the terminal free ends are thin, clear and gelatinous, lacking egg capsules but containing a few imbedded sand grains. The end of the collar, that is the last produced, usually contains a few dispersed egg capsules suggesting that all mature eggs that are laid in the one collar pass out in continuous succession and that these represent the last "stragglers" to be evacuated and thus do not settle within the bulk of capsules.

Internal structure of the collar. If a thin strip, approximately one capsule thick, is sectioned off on the vertical axis of the collar and examined microscopically, the following structures are noted:

a) Only if the collar is new, a very thin outer layer of jelly is present. This gives the egg case its outer sheen and their smooth and viscid feeling.

b) Underlying the above mentioned layer is the gelatinous matrix which contains the egg capsules and in which are imbedded particles of fine or coarse clay, or in some cases of shell, depending on the soil composition of the flat where the collar is formed. This matrix constitutes the bulk of the egg case and is responsible for the rigidity of the collar. It surrounds the capsules forming their outer walls and the intercapsular septa. The sand grains are imbedded throughout this layer and not limited to the periphery. The outer wall of the collar, as seen in section, appears pinched at the region of intercapsular septa, and then bulged where it surrounds the capsule, thus making the capsules visible to the naked eye in situ. (See Figures 39, 41). These capsules in P. triseriata are clearly visible when the collar is held up to incident light.

c) The terminal ends of the section, that is the apical and basal margins, are devoid of capsules and taper to a sharp edge (unlike P. heros). (See Figures 42 & 51).

The egg capsule. When viewed laterally the egg capsules appear spherical but in section they are oval; they contain, when newly formed, a clear, semigelatinous matrix contained by a stout "pellicle", this complex tends to shrink, become slightly yellow and more transparent on aging (See Figure 43). In this capsule the embryo is located, usually one embryo per capsule, though two are not infrequent and Stinson records having found capsules with 3 embryos.

The capsules are 800 to 1000 u. in diameter and though closely packed they are arranged with a degree of symmetry, this being described by Rogers (1913) as quincunxial. Each capsule is separated from the other by an intercapsular lamina usually 100 to 200 u. thick but never thicker than one layer of sand grains.

When the collar is viewed in situ or held up to the light, the capsules show clearly as spherical translucent areas against the darker surroundings of the collar matrix. The egg case's surface, especially the inner one, bulge conspicuously above each individual capsule so forming a definite and symmetrical pattern. (See Figure 39 and Table 26,27,28).

2) Egg collar of P. heros. This is constructed on the same general plan as previously described, in contrast to the collar of P. triseriata it is, usually larger, thinner and never more than 1 mm. thick. The sides of this sand collar are quite high (20-30 mm.) and assume a characteristic curvature, which is like the mirror image of a sigmoid curve. It is convex around the collars' base, then flat and finally concave and flaring to a perpendicular apical margin (See Figures 44,45,46). As the collar ages there is a progressive loss of rigidity in the naturally weak walls, and the egg case tends to collapse. The base spreads and the walls lie almost parallel to the substratum, while the apical margin retains its erect and cylindrical shape. (Figure 47.)

Because of this greater flexibility of the walls there is a lesser tendency for these collars to move or become buried in the flat as is the case with those of P. triseriata.

The capsules are smaller in diameter than those of P. triseriata (See Tables 24, 25 and Figures 41,42,48) but far more numerous and less regularly arranged. Because the capsules are so small, the outer walls of the collar appear smooth with no obvious capsular bulges, neither can the position of the capsules be detected when the collar is viewed against incident light.

In section (Figure 48) under the microscope it will be noted that the capsular bulges are actually present and tend to occur between the capsules rather than around the capsules. There is a slight variation in the size of collars (Table 24,25) but this is not as pronounced as in P. triseriata. There are, however, as in P. triseriata two basic types of egg case as regards shape, and contours, but these are non seasonal. (See Figures 49-51.)

The collars of P. heros have no thin, transparent and tapering margins; they are well rounded throughout their edges and the egg capsules are distributed to the very margin which forms a rounded and truncated edge, rather than tapering to a thin lamina. (See Figure 42.)

In examining a thin strip sectioned off the vertical axis of the collar the following becomes obvious:

a) New collars have the same thin outer covering of clear jelly enveloping the collar matrix and the imbedded sand.

b) The capsules are spherical and vary from 700 to 800 u. in diameter. Unlike P. triseriata they contain large and varying numbers (10-50) of embryos. In no cases has the presence of "nurse cells" been noted at Belliveau Cove area.

c) The walls owing to the smallness of the capsules appear almost parallel and with slight bulging not around the capsule but opposite the intercapsular spaces.

d) The terminal margins do not taper but round off around the last peripheral row of capsules. (See Figure 42.)

e) The capsular jelly is greatly reduced and visible only in the new collars, it is far less tenacious than its counterpart in P. triseriata; because of this reduced amount of jelly it is believed that the collar cannot withstand dissection as well as P. triseriata, and thus its distribution on the flat is limited to the lower tidal reaches, where it is not exposed to long periods of dissection during low waters.

3). Measurements and egg counts with the collars of the two species. Considerable attention has been given to the measurement of the dimensions of collars and the estimation of their egg contents as a means of estimating the relative fecundity of the two species of drills. (Table 24-28.)

Table 24. 1946 observations on P. heros collars. (Stinson Table 9.)

No.	Date of collection	Av. ht. of collar (cm.)	Area of collar (cm^2)	Av. No. capsules per cm^2	Av. No. of eggs per cap.	No. of capsules per collar (calculated)	Eggs per collar (calculated)
1	June 18	4.5	70	90	40	6300	250,000
2	July 9	3.7	66	100	33	6600	220,000
3	" 19	3.7	41	100	21	4100	86,000
4	" 20	3.5	53	90	21	4800	100,000
5	" 22	2.8	28	80	21	2200	46,000
6	" 22	4.8	86	90	24	7700	185,000
7	" 22	3.5	40	85	19	3400	65,000
8	" 22	4.5	61	80	33	4900	160,000
9	" 22	4.5	88	100	31	8800	270,000
10	" 22	5.0	105	85	42	8900	370,000
11	" 22	4.8	93	80	47	7400	350,000
12	" 22	4.7	77	90	33	6900	230,000
AVERAGE		4.2	67	89	30	6000	194,000

Table 25. 1949 observations on P. heros collars.

No.	Date	Ht. of collar (cm.)	Basal circum-fer. (cm.)	Apical circum-fer. (cm.)	Area of collar (cm^2)	Av. No. of capsules per (cm^2)	No. of eggs per cap.	Av. No. of cap. per collar (Calcul.)	Av. no. of eggs per collar (Calcul.)
1	3 Aug.	4.8	29.3	12.6	87	112	40	9744	389,760
2	"	5.3	26.2	10.2	88	118	23	10384	238,832
3	"	3.5	20.3	10.6	52	116	32	6032	193,024
4	"	3.1	23.3	10.4	46	121	21	5546	116,466
5	"	3.3	18.9	7.3	37	100	19	3700	70,300
6	"	3.1	25.6	11.7	66	121	8	7986	63,888
7	"	2.5	20.2	9.2	32	225	48	7200	345,600
8	"	3.8	20.2	8.4	51	144	33	7244	239,052
9	"	5.6	35.4	15.3	118	100	21	11800	247,800
10	"	4.8	27.5	13.7	88	144	22	12472	274,384
11	"	5.2	33.8	15.7	119	100	29	11900	345,100
AVERAGE ...		4.1	25.5	11.4	71.3	127	27	8546	229,473

The figures supplied in the above tables for the egg collar of P. heros should be held only as an approximation to the actual figures, as far as the No. of capsules per collar, the No. of embryos per capsule and collar are concerned, for these are difficult to estimate owing to variation in the density of distribution of capsules in any one collar and from collar to collar.

The figures submitted for P. triseriata, on the other hand are more precise because of the greater size, smaller numbers and more even and symmetrical distribution of the capsules. The smaller variation in the numbers of eggs per capsule makes the estimate of number of eggs per collar more precise too.

Table 26. 1946 observations on P. triseriata collars. (Stinson Table 8)

No.	Date of collection	Av.Ht.of collar Cm.	Area of collar Cm^2	Cap. per Cm^2	Eggs per capsule	No.of caps. per collar (calculated)	No.of eggs per collar (calculated)
1	June 19	1.6	15	36	1	540	540
2		1.8	13	37	1	480	480
3		1.7	16	44	1	700	700
4		1.9	18	37	1	670	670
5		1.8	18	32	1	580	580
6		1.7	14	38	1	530	530
7		1.8	24	43	1	1030	1030
8	June 21	1.5	15	35	1	530	530
9		1.8	14	43	1	600	600
10		1.7	12	40	1	480	480
11		2.0	18	27	1	490	490
12	June 26	1.7	15	33	1	500	500
13		1.5	14	40	1	560	560
14		1.3	9	39	1	350	350
15		1.4	12	45	1	540	540
16		1.4	12	46	1	550	550
17		0.9	5.3	47	1	250	250
18		1.7	15	42	1	630	630
19		1.4	11	43	1	470	470
20		1.3	8.6	48	1	410	410
21		1.2	7.5	45	1	340	340
22		0.9	4.8	47	1	230	230
23		1.4	13	49	1	640	640
24		0.9	6.2	38	1	240	240

Table 27. 1949 observations on P. triseriata collars.

No.	Date of collect.	Ht. of collar cm.	Basal circumf. cm.	Apical circumf. cm.	Area cm^2	No. cap. per cm^2	Eggs per cap.	No. of cap per collar. (calculated)	No. of eggs per collar (calcul.)
1	July 24	1.5	13.7	7.5	18	55	1	990	990
2		1.8	11.4	5.4	15	33	1	495	495
3		2.3	16.8	8.0	31	37	1	1147	1147
4		2.3	18.3	8.3	31	52	1	1612	1612
5		2.1	18.0	8.7	23	36	1	1008	1008
6		1.9	16.1	7.2	21	44	1	924	924
7		2.0	14.0	6.2	20	36	1	720	720
8		2.1	17.9	8.8	23	45	1	1035	1035
9		1.6	9.2	4.1	8	39	1	312	312
10		1.9	15.3	7.2	20	53	1	1060	1060
11		1.8	12.3	6.4	18	41	1	738	738
12		1.6	12.5	6.7	18	42	1	756	756
13		1.7	10.6	4.9	11	36	1	396	396
14		1.4	12.5	6.1	13	33	1	429	429
15	Aug. 3	2.2	14.1	7.2	24	39	1	936	936
16		1.6	10.4	4.9	9	45	1	404	404
17		2.0	10.3	3.8	12	35	1	420	420
18		1.6	10.6	4.6	11	36	1	396	396
19		1.0	4.2	2.2	4	18	1	74	74
20		1.0	5.7	3.1	4	24	1	98	98
21		1.2	5.8	3.0	6	42	1	252	252
22		1.0	8.9	4.2	6	45	1	270	270
23		1.1	6.1	3.0	5	38	1	190	190
24		1.1	9.1	4.7	8	36	1	288	288
25		1.4	9.0	4.2	8	44	1	352	352
26		2.5	8.4	4.0	11	41	1	451	451
27		1.4	8.1	4.0	10	43	1	430	430
	AVERAGE ...	1.63	11.5	5.5	14.2	39.6	1	599	599

From the tables submitted on the egg collar of P. triseriata there appears to be no such variation in component measurements as indicated for P. heros and it can be held as a general rule that the capsule of the former species contains only one embryo, though occasionally it has been noted to contain 2 and rarely 3 embryos.

In the 1949 recordings there seems to be noticeable diminution in the size of the collar related to its occurrence in the season. The collars collected on August 3rd are considerably smaller than those recorded previous to this date, the advent of these small collars was particularly conspicuous to the casual observer on the flats; no record of this nature was made by Stinson.

Few tentative suggestions were made to explain this phenomenon which would seem to be related to atmospheric conditions and possibly more specifically to flat temperatures. It was suggested that the adult snail under certain indefinite circumstances produced two collars per summer, and that the second so formed was represented by this small egg case which appears only at the end of the collar production season. This postulation assumes that under natural conditions the snail lays one egg collar per season, there is no evidence to affirm this stipulation, but the numbers of collars produced and the numbers of adult snail found in this locality strongly suggest this.

Another explanation advanced, suggested that the immature snail under abnormal atmospheric conditions, possibly like those recorded at Belliveau Cove this summer, reached maturity one season before it would normally. The product of this precocious development may well be this "abortive" egg case.

Table 28. Comparison of the average readings recorded for both species during the 1946 and 1949 seasons.

Season	Av.Ht.of collar Cm.	Av.area of collar Cm^2	Av.No.of eggs per capsule	Av.No.of capsules per Cm^2	Av.No.of capsules per collar	Av.No.of eggs per collar
P. heros						
1946	4.2	67	30	89	6000	194,000
1949	4.0	71.2	27	127	8546	229,473
P. triseriata						
1946	1.5	13.6	1	42	540	540
1949	1.6	14.2	1	39	599	599

P. heros. Table 28 indicates that there were more capsules per square cm. of collar in 1949 than 1946. This may and probably is the result of differences between Stinson's and the author's technique which is unknown to the present writer. (For the writer's methods see "Field Technique.")

On the whole there seem to be no significant differences between the collars produced in 1946 and those of 1949.

P. triseriata. Figures supplied on the collars of this species are more precise and any significant 1946-1949 variation may be considered reliable, rather than due to differences in technique.

The 1949 season seems to be characterized by a greater size variation of the collars produced; unlike 1946 the 1949 season showed a large number of smaller collars being produced at the end of the summer so dividing this period into two, the former part from June to August typified by well shaped and normal large collars, and the latter period consisting of August which was characterized by the occurrence of large numbers of small and ill-formed collars. Whether this indicates the premature production of egg collars by next year's "mature" class, possibly due to abnormally high temperatures and prolonged breeding season is not known.

Distinguishing features of the egg collars of P. triseriata and P. heros. (This tabular summary should be used in conjunction with Figs. 50, 51 for the identification of the two types of egg collar.)

P. triseriata	P. heros
1. Small collar, with thick rigid sides keeping the egg case erect at all times.	1. Large collar with thin and pliable sides, whose lack of rigidity causes the collar to collapse on the flat, into its characteristic shape.
2. Sides of collar are sloping and straight.	2. Sides curved always flaring into the typical apical cylinder.
3. The apical, basal and terminal margins of the collar taper to form a thin transparent lamina, which is free of capsules and contains little sand.	3. Margins of the collar rounded without taper: distribution of sand and egg capsules continuous to the edge.
4. Capsules large, and clearly visible when the collar is held up to light, collar walls bulge conspicuously opposite capsules.	4. Capsules small and numerous, not apparent when the collar is held up to light, collar walls appear smooth.
5. Capsules oval in vertical section.	5. Capsules are spherical in vertical section.
6. Eggs are large and never more than 3 per capsule.	6. Eggs are small and are on an average 30 per capsule.
7. Collar shows tidal movement and becomes typically buried on the flat.	7. Collar rarely moves or becomes buried.
8. Collar distributed over the whole intertidal flat.	8. Collars distribution restricted to the lower reaches of the intertidal flat or to continuously submerged parts within the intertidal zone.

Figure 37.

Upper row - _P. heros_ collars; note on the middle and left-hand side collar egg rows of _Nassa trivittata_.
Lower row - _P. triseriata_ egg cases.

Figure 38.

Diagrammatic representation of _P. triseriata_ collar. Note the scapsular laminated basal and apical margins of the collar.

Figure 39.

P. triseriata egg collar. Note clearly visible egg capsules; straight slanted sides with vertical apical and basal margins.

Figure 40.

Top view of Figure 39. Note same characteristics.

Figure 41.

Sections of the collar walls of P. triseriata. Em. - embryo; Cap. Jel. - capsular jelly; Col. Jel. - matrix jelly; S. G., - sand grains.

Figure 42.

Comparison of margins and collar sections in the two species. Upper - P. triseriata, lower - P. heros. Note large capsules with clearly defined jelly containing one large embryo per capsule in P. triseriata. Note marginal acapsular laminated rim in P. triseriata; contrast with P. heros.

Figure 43.

Multi-cellular cleavage of P. triseriata embryo contained in capsular jelly after dissection from collar.

Figure 44.

Diagrammatic representation of P. heros collar. Note wide base, curved sides and flared appical cylinder. Note also absence of acapsular margins.

Figure 45.

P. heros - representing the large and typically flared collar which occurs throughout the season (Cp. with Figure 46 & 47.)

Figure 47.

P. heros - representing the smaller and more abundant collar found during the season.

Figure 46.

Top view of Figure 47.

Figure 48.

Section of the collar wall of *P. heros*. Note spherical capsules, small but numerous embryos.
Cap. - capsule; Em. - embryo; Cap. jel. - capsular jelly; S. G. - sand grain; Col. jel. - matrix jelly.

Figure 49.

Comparing typical collars of the two species. The six small collars to the right belong to P. triseriata. The three large collars with flared sides belong to P. heros; while the remaining collar in the first row to the extreme left, characterized by straight sloping sides, remains to be identified.

Figure 50.

Typical shapes and sizes of the two local species, P. triseriata (r.h.s.), P. heros (middle), and unidentified egg case to the left.
This unidentified collar was recovered off Digby Neck in a scallop drag in five fathoms of water.

Figure 51.

The diagrammatic representation of the main differences in external shape and internal structure for the two collars are summarized schematically and should be closely studied in conjunction with the foregoing plates.

Diagrams I - IV show the typical variations in external shape.
Diagrams V & VI show the basic similarity in that both collars are produced clock-wise.

Diagrams VII & VIII show the differences in capsular arrangement and size, the presence or absence of free margins and the typical "bulges" produced in P. triseriata by the large capsules.

B. Mechanics of Collar Formation.

For diagrammatic representation see Figures 53, 54.

1. Importance. Though the comprehension of the mechanics of collar formation and the relation of the jellies in the collar to the embryo may appear to be of theoretical importance, it is believed that a clear understanding of these may eventually lead to a practicable biological control of the snail. The basis and importance of this statement will become apparent in the following discussion.

2. General Observation. Collar formation takes place in two characteristic phases: the initial stage begins at low tide on the surface of the flat; the secondary stage, that of actual collar production, commences with the flood tide and can only take place when the flat is covered by the tide if the collar being formed is to be normal in shape and structure. This latter stage is carried out under the surface of the flat at a depth of two to four inches.

The completed collar is forced to the surface by the snail during the ebb tide following that of the initial stage. Thus collar formation is completed in 10 - 12 hours involving one high water period. Collar production is most vigorous when the moon is new or full and when low water periods occur in the twilight hours of mornings and evenings, than when the moon is in its first and third quarter when low water occur at midday and midnight.

Earlier writers have offered brief and tentative explanations of the mechanics involved in the formation of this remarkable structure, but as far as the author knows no detailed and satisfactory explanation has been advanced.

Some speculators suggest that the collar assumes its shape by being secreted and moulded inside the mantle cavity, but this seems improbable in the light of the data supplied in Table 29, (Fig. 52) which shows that the collar produced is usually wider than the aperture of the snail's shell and further this explanation would not account for the inclusion of sand in the collar matrix.

The characteristic shape assumed by the whelk's foot during the first stage of collar formation led the author at first to believe that the shape of the finished collar was due to moulding by the folded foot, but this belief was abandoned in the light of later investigation.

Rogers (1913) in "The Shell Book" (P.144) says: "The eggs are laid in a sticky mass of clear jelly which is moulded over the shell; this explains its peculiar collar shape. There is but one layer of egg capsules, arranged in regular quincunx order. A layer of fine sand covers each side of the collar, making it about the thickness of an orange peel. While this remains in the water the mucous is rubber-like and the eggs are safely concealed under the protective film of gray sand. Cast ashore, the sand collar becomes dry and brittle."

From observations made this summer the writer believes that Rogers is basically correct in this sketchy description.

3. Proposed Explanation of Collar Formation. Efforts to induce collar formation in acquaria at Belliveau Cove were fruitless and those at St. Andrews nearly so, for although some "abnormal" collars were produced, the actual process went unobserved.

It is especially difficult to piece together an account of collar formation in nature, because it takes place below the surface of the sand when the tide is in. Thus observations were necessarily restricted to the beginning and the end of the process when the flats were bare or covered by shallow water.

The features observed were as follows:

a. commencement of production taking place on the surface of the flat at low tide.

b. Position and movement assumed by the snail under the surface while making the collar, this generally occurring at high tide.

c. emergence of collar by agency of the snail at the following low water.

d. formation of collar in a clockwise direction, the snail's shell has a clockwise whorl rotation.

From these the writer attempts to piece together what appears to be the most likely method of collar formation.

Table 29. Size relation between the female P. triseriata and the collars they produced - 1949.

No.	Date of collection		Ht. of snail Cm.	Opercular aperture Cm. Height	Width	Basal circumference of collar Cm.	Ht. of collar Cm.	Area of collar Cm^2.
1	13	June	1.3	1.4	0.9	18.7	2.1	32
2	24	"	2.1	1.7	0.9	24.6	2.2	43
3	26	"	1.6	1.1	0.6	12.1	1.8	14
4	28	"	1.7	1.1	0.6	14.0	1.8	18
5	28	"	2.2	1.4	0.8	19.8	2.2	31
6	30	"	2.4	1.5	0.8	18.2	2.2	29
7	30	"	1.5	1.0	0.6	13.5	1.6	17
8	30	"	1.3	0.9	0.5	13.0	1.3	13
9	30	"	1.6	1.1	0.6	10.0	1.6	13
10	30	"	1.3	0.8	0.5	12.0	1.3	14
11	30	"	1.6	1.0	0.6	5.3	1.6	7
12	1	July	1.6	1.1	0.6	12.3	1.5	17
13	1	"	1.4	1.0	0.5	8.1	1.2	7
14	1	"	1.5	1.1	0.6	12.7	1.6	15
15	1	"	1.5	1.0	0.5	14.6	1.3	16
16	1	"	2.0	1.3	0.6	14.8	1.8	22
17	1	"	1.3	0.9	0.5	12.5	1.2	12
18	2	"	1.3	0.9	0.5	10.6	1.3	10
19	16	"	1.3	0.9	0.5	7.4	1.3	8
20	16	"	1.7	1.1	0.7	14.2	1.8	17
21	16	"	1.9	1.3	0.7	15.2	1.9	23
22	16	"	2.0	1.3	0.7	9.1	1.6	11
23	16	"	1.9	1.3	0.7	10.5	1.3	12
24	16	"	1.7	1.0	0.6	13.1	1.7	16
25	16	"	1.7	1.1	0.6	18.5	1.9	22
26	17	"	2.1	1.4	0.8	12.1	2.0	18
27	17	"	1.4	1.0	0.5	10.4	1.5	10
28	17	"	1.8	1.1	0.6	13.5	1.9	17
29	18	"	1.9	1.2	0.7	21.0	2.0	29
30	18	"	1.4	1.0	0.5	8.5	1.4	8
31	18	"	1.6	1.1	0.6	10.3	1.7	13
32	18	"	1.1	0.7	0.4	7.1	1.5	7
33	18	"	1.4	0.9	0.5	7.4	1.3	7
34	18	"	1.6	1.1	0.6	6.8	1.3	8
35	18	"	1.5	1.0	0.5	6.1	1.4	4
36	18	"	1.5	1.0	0.5	11.3	0.9	9
37	18	"	2.0	1.4	0.8	11.7	2.1	16
38	18	"	1.5	1.0	0.5	9.2	2.0	11
39	18	"	1.5	1.0	0.5	6.3	1.2	7
	Average		1.6	1.1	0.61	12.2	1.6	15.5

Before commencing actual description it would be well to revise the basic structure of the collar in terms of its component "jellies" described earlier.

a) The capsular jelly associated with the embryo, and involved in maintaining the water content of the collar and embryo so preventing their dessication during exposure at low tide.

b) The jelly forming the matrix proper of the collar. This is responsible for the collar shape, the retension of embryonal capsules and serves as a medium for the imbedded sand. This jelly seems to be neutral to water passage in or out of the collar.

c) The very thin layer of peripheral jelly applied by the snail on the completion of formation over the whole surface of the collar; this is not lasting in nature and is the first of the jellies to disintegrate.

Of these three jellies the last is secreted by the pedal gland. Whether there is a different origin for the other two could not be determined, though it seems reasonable to assume that the first originates from the female's genital apparatus. If so it possesses remarkable gelating qualities.

Hypothesis

1. Incipient stage of collar production. (See Fig. 53). This takes place on the surface of the flat when the ebb tide is nearing dead low water. In this phase the snail lies on its side as if in a stupor with its foot folded along its mid ventral line. From the foot anteriorly a mass of clear viscid jelly emerges and is distributed in long festoons by the water movement. In this there appear a few dispersed eggs. This jelly is possibly the precursor of the "Matrix" jelly and if so seems to be a pedal secretion.

As these festoons float over the sand they may collect a few grains on their surface but not in any great quantity. The author has often attempted to "mix" sand into the jelly by placing this in the palm of his hand and mixing sand grains into it with his fingers. This method, whether done gently or otherwise, has always met with failure for the sand would not mix. On every attempt the jelly tore. A certain measure of success was met with by dragging strands of jelly over the sand, though the best results were obtained by pressing the sand into the jelly.

With the commencement of the flood tide the snail seems to come out of its state of stupor and burrow under the surface and in so doing leaves most of its gelatinous festoon on the surface. Having completed this, there seems to be a pause before actual collar moulding begins. With this stage the snail becomes inaccessible owing to the incoming tide. Exposing or disturbing the whelk at any step of the formation, excepting the incipient stage, will cause it immediately to retract into its shell and cease all activity.

2. Stage of actual collar formation. The burrowed snail (3 to 4 inches deep depending on its size and species) assumes a horizontal position lying on its side with

the shell spire directed towards the surface; in this position it moves in a clockwise direction of varying radius forcing its way through the sand. If it is not loacted too deep its progress can be observed from the surface by a slight bump in the sand.

Snails performing the above movements have been noticed and on exposing them no collar could be observed but their foot was greatly expanded and in most cases it covered the whole outer surface of the shell; it is believed that the expanded lateral edges of the foot tend to meet along the fifth whorl and thus guide the apical and basal margins of the extruded gelatinous mass. This arrangement would allow the inner and outer surfaces of the collar to be moulded against the shell and the environment, respectively, and the limits of this mould basically and apically would be formed by the expanded foot.

As the snail moves in a clockwise direction it extrudes partly from the genital opening and partly from the pedal glands a jelly which is guided anteriorly by the foot to meet the genital secretion being extruded from the mantle cavity.

This mass of pedal and genital jelly containing the fertilized eggs is passed out over the pallial edge and guided by the foot along the outer surface of the fifth and sixth whorl. As the jellies are extruded against the shell the snail is progressing in its clockwise pass so that the advancing shell forces sand against the jelly and at the same time forces this mass against the surrounding sand: the jelly remains static and the moving shell acts as the moulding surface. This can only take place if the environment is denser than the jellies. There appears to be a correlation between collar formation and the occurrence of the high water period; the meaning of this relation is difficult to assess but it may be possibly due to the following factors.

Egg collar formation at Belliveau Cove coincides on the flats with the distribution of the sexually mature snails of the two species, and thus does not usually take place inshore. But in other localities the author has noted collar production in comparatively shallow areas but of long water coverage, one such condition being reported by Stinson between Pier 2 and 3 at Belliveau Cove in 1946.

Thus it may be said that collar formation necessitates either the presence of water coverage or the pressure created by this coverage. The latter seems untenible as though the pressure on the substratum would increase with the height of water above it, so would the buoyancy of the sand thus rendering the substratum less packed; and this would not explain the occurrence of collars in shallow water.

From this it would appear that the important factor is the presence of water which loosens the substratum, irrespective of water volume. The loosened sand provides an ideal medium for the external moulding surface of the collar and by its reduced density allows the snail to move freely without damaging the delicate jellies. This condition would necessitate that the snail should bury deeper than the area of surface turbulence, and this appears to be met by the whelk which is located 4-6" below the flat surface. This seems to be further substantiated by the decrease in nightly collar production which follows periods of rough water which would tend to set up excessive turbulence between substratum and water.

The necessary force to imbed sand into the collar is supplied by the pressure exerted by the advancing shell on the extruded jellies, which assume the shape of the shell and are left behind as a flattened ribbon composed of a single layer of egg capsules surrounded by imbedded sand grains.

From the above stipulations the following corollaries can be suggested:-

1. Collar production does not take place at low tide because the substratum is too dense and though the snail can progress through the "dry" sand the collar would probably be fragmented owing to the greater degree of environmental resistance.

2. A snail that is insufficiently buried would be located in the area of surface turbulence and the collar produced would be insufficiently "sanded".

At this stage some consideration should be given to certain characteristic relations: (See Fig. 54 .. Diagram VI, VII.)

a. the shell is always whorled clockwise
b. the direction of movement of the female during collar formation is in a clockwise circle
c. the collar is formed during the above movement and thus is made in a clockwise direction too.

From these facts it will be noted that presuming the collar is formed as previously described it can only be so done by the snail that follows stipulations (a) and (b) for if the snail retains the position observed while buried, to move in an anti-clockwise direction, it would have to be of an anti-clockwise whorling and hence would produce an anti-clockwise collar. This is best understood by consulting Figure 54, Diagram VI and VII, the former shows by means of arrows the direction of the snail, the collar as it is produced and left behind and the shell of a whelk with clockwise rotation, the latter shows what would have to be if the same condition held true and the snail was of an anti-clockwise whorling.

Figure 53 shows the incipient stage taking place on the flats surface, while Figure 54, Diagram I to III demonstrate the actual formation of the collar as would be observed if the whelk was exposed and studied in situ; the arrows indicate the direction of clockwise movement, and the diagrams portray various steps in the formation, showng the progressive movement of the female, the collar passing posteriorly along the shell and guided by the expanded foot which is extended to cover the shell (Diagram III).

Diagram IV and V demonstrate how by apposition against the shell the collar assumes its typical shape.

3. <u>The Terminal and Emergent Phase of Formation.</u> (Figure 54, Diagram VIII and IX) having finished the basic structure of the collar, the whelk completes the circle it has described and again circles the collar in a clockwise direction.

This third phase in collar production takes place at the low water period following the incipient phase and thus has often been noticed on the flat.

The completed collar and the snail are still two to four inches below the flat surface. The whelk commences recircling the collar, but as it does this, it passes around the width of the egg case thus performing a spiral around the collar; its foot is well expanded and acts as a "finishing" tool smoothening the exterior of the collar, adding and pressing in more sand where this is needed and simultaneously secreting a thin layer of jelly from the "pedal" glands. This very thin gelatinous deposit causes the newly formed egg case to appear glossy and makes the collar quite viscid to the touch. This external layer serves as a containing envelope to the sand grains imbedded in the gelatinous matrix and is soon lost owing to natural erosion. It probably serves to hold the sand while the matrix jelly "sets". When it wears off the collar looses its gloss and is gritty rather than smooth to the touch. Formalin preserved specimens usually loose this surface film rather quickly.

While the whelk is progressing around the collar proper, and its width in a spiralling fashion, it serves a double purpose, it secretes the aforementioned layer of jelly and simultaneously tilts and lifts the collar every time it passes beneath it. Its activity loosens the sand around the egg case, and slowly forces the collar on to the surface of the flat, so exposing it to tidal action and distribution.

This terminal phase is represented in Figure 54, Diagram VIII and IX. The former shows the spiral clockwise movement of the snail while secreting pedal jelly and the latter gives a diagrammatic representation of the modus of emergence.

With the emergence of the collar, the whelk usually burrows and travels in a straight line away from the newly formed egg case.

4. Discussion of Collar Formation. In the author's view the proposed explanation of collar formation is more apt for P. heros than for P. triseriata. In the former the size and contours of the collar conforms closely to the size and shape of the shell of the parent female. In the latter the collar width is usually greater than the shell height of the parent. (See Table 29). In spite of this difference, available evidence indicates that the methods of formation are basically alike. The fact that the margins of the collars in P. triseriata are free of eggs and lack the "finished" appearance suggests that the foot may not play such an important role in moulding the margins, as in P. heros.

5. Imperfect Egg Cases Found in Nature. Imperfect collars of P. heros were never observed in nature. This may be because of their more seaward distribution permitting longer periods of tidal coverage or they may be able to work more rapidly. Their deeper burrowing habits may be significant in this connection.

For P. triseriata Stinson records: "An occasional collar was found in which the snail had not secreted sufficient sand: the clear jelly of the capsules was visible and the egg within." It is evident that this worker did not realize the full significance of his observation and thus treated it lightly. In the light of later investigation the above statement appears to be completely erroneous. The snail does not "secrete" sand into the collar and a close study of these imperfect collars (See Figs. 55, 56, 57) gives us a clue to what may have caused their deformity.

Imperfect specimens were collected this summer by the author at Belliveau Cove, they were found near the weir at low water, partially covered by the substratum and usually still associated with the maternal snail.

The following observations were made:

a. All the collars of this nature found were newly formed and often still in close association with the maternal snail.

b. If complete, they had the characteristic shape of the normal collar.

c. Some were completely "sanded" but the distribution of sand grains was sparce and allowed clear vision through the collar, when held up to the light. Others were well supplied with sand but this was limited in its distribution, usually around the outer apical margin of the collar.

d. Others were incomplete and some mere fragments, with thick localized deposits of sand often forming ridges. In some cases, instead of the usual single layer of capsules there appeared to be two layers deep.

e. In all cases the thin layer of peripheral jelly was lacking, thus imparting a gritty feeling to the collar and making it possible to remove some of the less deeper imbedded sand grains. These observations are in complete accord among themselves and with the preceeding hypothetical description of collar formation if we make the following assumptions:

1. That the maternal snail was insufficiently buried and thus in the area of surface turbulence, where water movement rendered the substratum too unstable for complete imbedment before the collar jellies set.

2. That the female was "caught short" by the falling tide (as stated earlier submergence in water seems necessary for collar formation) and the increased density of the sand with drying forced the snail to surface and accompanied, by the setting of the jellies, resulted in poor imbedment.

Of the two assumptions the first seems more logical and applicable.

6. <u>Imperfect P. heros Collars Obtained in Acquaria at St. Andrews.</u>

Fifty <u>P. heros</u> adults were placed by the author in concrete tanks at the Biological Station at St. Andrews prior leaving for Belliveau Cove, and these were observed in his absence by Mr. L. Thurber.

The object of this experiment was to determine:

1. the mode of formation of collars
2. whether collars could be formed in the shallow (depth 3 feet) tanks
3. whether they could be formed in the absence of a loose substratum
4. what shape the collars would assume if formed.

The results obtained are very interesting, for although they did not supply answers to all of the above questions they did raise new aspects of a rather startling nature.

Although fifty snails were placed in these thanks only three collars were formed. No snails were observed in the act of collar formation. Two of the collars are very similar, appearing as thin ribbons, one capsule thick and approximately 1.½ inches long and of a semicircular shape. (See Figs. 58 to 64.) The jelly is transparent and the capsules and their contents are clearly visible. The embryos in the capsules appear normal in size, and numbers. These two collars are referred to as A and B in the following table showing counts of capsular contents.

The other collar produced in the St. Andrews tanks, collar C, is a thick shapeless mass of unequal thickness, two capsules thick in places. These collars are compared in other respects in Table 32.

The embryo counts per capsule in collars A and B are roughly the same and likewise their average capsular diameters (Table 31) compare favorably. They contrast sharply with "C" whose embryo counts and capsular diameters are far greater. The snails that produced these collars were of approximately equal size, in the same environment and the same species, namely P. heros.

Dr. J. C. Medcof in the summer 1947 collected at Pinette P.E.I. a snail of this species found extruding a clear mass of jelly and eggs very similar in structure to the masses described above; the author has examined the capsular contents of this collar referred to as "D" and has recorded his observations in Tables 30 and 31. The capsule diameter in "D" is about the same as in "C" but the embryo count are much higher. The embryos in all collars were uniform in size indicating that "nurse" cells are not present.

No explanation is advanced for these striking differences in collar characteristics. They have been recorded in the hope that further investigation will make them intelligible. As a further record photographs of the collars and their capsules are presented in Figures 58, 59, 60, 61, 62, 63, 64.

Table 30. Embryonal counts per capsule from 4 imperfect P. heros collars. (Collars A, B, C were produced at the Atlantic Biological Station while collar D was collected at Pinette, P.E.I.)[x]

	Collar A Fig. 58,59	Collar B	Collar C Fig. 60,61,62	Collar D Fig. 63,64
	38	8	28	71
	33	10	32	80
	5	8	28	52
	6	3	23	89
	8	9	37	48
	2	11	29	89
	30	9	21	98
	6	10	40	63
	12	6	35	84
	8	7	31	69
	7	12	20	85
	9	13	32	75
	10	11	28	99
	6	5	27	95
	40	6	24	84
	5	4	29	95
	8	2	34	89
	6	9	27	99
	7	5	28	90
	6	12	25	125
Average	13	8	29	84

x The counts recorded in this table unlike previous estimates are very accurate owing to the development of a simple technique. For this vide Appendix under heading 'Methods'.

Table 31. Measurements of the maximum diameter of capsules taken at random in the imperfect P. heros collars.

	Collar A	Collar B	Collar C	Collar D	Normal collar preserved in formalin
	6.8 u	8.4 u	12.2 u	15.2 u	8.7 u
	5.3	7.6	11.4	15.2	10.4
	7.6	7.6	12.9	12.9	8.7
	6.1	4.6	13.3	12.2	9.8
	4.6	6.8	14.4	11.4	9.8
	6.8	6.1	11.4	11.4	10.9
	7.6	6.8	8.1	12.2	9.2
	6.8	6.8	13.3	12.9	8.3
	6.1	7.6	13.3	12.2	7.5
	7.6	6.8	15.2	11.4	9.9
	5.3	6.8	12.9	11.4	10.4
	6.1	7.6	14.4	10.6	9.6
	6.8	6.1	10.6	12.9	8.3
	5.3	6.8	14.4	14.4	9.9
	6.1	5.3	11.4	12.9	8.8
	6.8	6.8	12.9	13.3	8.6
	6.1	6.1	11.4	13.3	10.4
	4.6	7.6	11.4	15.2	9.6
	6.1	3.8	12.9	7.6	9.6
	7.6	7.6	13.3	13.3	8.3
Average	6.3	6.7	12.6	12.6	9.4

N.B. The contrast found in the measurements supplied in this table with the sizes given for descriptions of developmental stages is justifiable when it is considered that these specimens were preserved in formalin and probably shrank as a result. This table illustrates the variation in capsular size rather than the exact capillar diameter.

From the foregoing descriptions, tables and accompanying plates it is evident that eggs can be laid in shallow water and in absence of a loose substratum. It should be noted that though these tanks are irrigated with running water the flow is slow and tends to be superficial. The tanks are three feet deep. Thus the extruded collar jelly of snails on the bottom is unlikely to be disturbed by currents. Although eggs were produced the collar shape and other collar characteristics were atypical. It is possible that the moulding, or better retention, of extruded jellies in these specimens was performed by agency of the foot. Exposure of these collars to the air showed that their resistance to dessication is low in comparison with that of the normal egg case, possibly because of their lack of sand.

7. Collar Jellies and Their Possible Significance. Certain observations have been made while working with the embryos of the two species and their collars that may be pertinent in seeking effective control measures. The suggestions advanced are poorly supported experimentally, but their importance is such as to warrant their recording.

Stinson noted in 1946 that the collars of P. triseriata (though not exclusive in this species) often contracted an algal growth that hastened their crumbling and suggested this as a possible parasite of the egg case. Regarding this alga he states: "Without doubt the most important destructive agent of the snail is the brown algae (Ectocarpus) which attacks the egg case. By invading the collar and destroying the eggs it greatly reduces the number of young that hatch." (See Fig. 65.)

In 1947 J. Wheatley sent specimens of these algae to Professor Bell of the Department of Biology at Dalhousie University for identification.

This authority identified the specimens as belonging to genus Ectocarpus and Enteromorpha, and regarding their life history he stated: "These are Epiphytes and there is no evidence of their being parasitic but they do often kill by smothering."

The author has examined numerous collars infected with these algae and describes the pathology thus:

a. External. The exterior of the collar when examined microscopically shows little effect by the alga which has grown into the gelatinous matrix forcing its filaments between the imbedded sand grains; there is little localized damage of the collar surface at the point of algal entry. The collar thus infected appears covered by a short pile and in other cases it has long green filaments attached to its surface.

b. Internal. When the infected collar is sectioned and examined little mechanical damage can be noted to the capsule but the embryo contained is completely destroyed appearing literally "blown up".

The filaments, resembling hyphal infiltrations penetrate the capsular jelly, which loses its clear transparency. It assumes a yellow colour and becomes merely translucent. The contained embryo disintegrates and its cellular components are scattered throughout the capsule.

The filament does not necessarily terminate in the capsular jelly but may penetrate the opposite wall of the collar.

It is possible that, contrary to Dr. Bell's statement, these algae are parasitic feeding on the capsular jelly, but it is felt that this damage is incidental and of a mechanical nature which will become apparent when the discussion on collar jellies is considered. Dr. Medcof (personal communication) suggests the presence of an internal mould growing in the collar in conjunction with the superficial algae.

As previously described there are 3 types of jelly involved in collars. They appear to differ both in their origin and in their physiological function. Two interesting observations have been made in the course of the summer with respect to these.

1. When young embryos of P. triseriata are removed from the collar they usually come out surrounded by a tenacious sphere of jelly (See Fig. 66), which has been termed the capsular jelly, this proved quite difficult to separate from the embryo and in most cases when this operation was effected in fresh sea water, young embryos on liberating immediately disintegrated.

This might be attributed to faulty technique, but it has been noted with such frequency that it seems feasible to assume that young embryos are not istonic with sea water and undergo di-plasmolysis.

As the embryo develops this incompatibility seems to be reduced. Simultaneously a change in the capsular jelly can be noted (See Larval Development). Unlike P. triseriata, P. heros never showed this phenomenon, but these differences are outstanding. In P. heros the capsules are considerably smaller, their embryo counts are higher and the capsular jelly small in volume, in some cases almost indetectable. By virtue of these differences the collar of P. heros cannot withstand dessication by exposure as can that of P. triseriata, and specimens of the former that were placed inshore where they do not usually occur, and where they were exposed for longer periods at low water, became completely dessicated and crumpled by wave action, within a few tides of their exposure to this treatment, thus killing the embryos.

In P. heros clear pathological symptoms are not associated with algal infection. The destruction seems to be purely mechanical. The alga weakens the thin collar walls rendering it easily broken by wave action and so liberating its capsular contents before maturity.

2. The second observation which supplies a possible indication of difference in the physiological functions of these jellies was noted accidentally when the author having found the imperfect collar portrayed in Figs. 55 to 57 preserved it in some 80% Glycerine-Alcohol because the formalin supply was exhausted. The following day it was noted that the matrix jelly was as clear and transparent as when collected, but the capsular jelly containing the embryos, had changed from a clear and transparent medium to a cream colored opaque sphere.

This test was repeated with other collars, imperfect and normal, with similar results. Control experiments with fresh water and solutions of formalin were tried but with no effect on the capsular jelly. The capsular jelly was apparently dehydrated by the hydrophillic solution which did not affect the other collar jellies.

From these observations two deductions can be made:

1. The matrix jelly, containing the imbedded sand, is "neutral". By this is meant that it can loose or gain water without suffering irrevocable change.

2. The capsular jelly seems to be of dual importance. Primarily it controls the embryos' water contents. It prevents dessication of the embryo and collar during their low water exposure, this ability being proportional to the amount of jelly present in the capsule, and it further constitutes a barrier to excessive osmosis.

This ability appears clearest in P. triseriata collars during the early development of the embryo. It is lost gradually as the embryo matures and presumably no longer needs this osmotic protection.

From the above observations it would seem that the capsular jelly is the prime factor in maintaining the water contents of the collar, and that any damage or physical change in its structure would affect its water retensive capacities. Visual changes can be discerned in the optical density of this jelly with the progressive development of the embryo, thus it is probable that with the progressive loss of its retensive properties, conditioned by embryonal growth, the collar becomes more liable to dessication during its intertidal exposure, and that this advancing defficiency culminates in the crumbling of the collar and larval release.

The actual crumbling of the egg case is conditioned by the disintegration of its walls, i.e. the matrix jelly, which will retain its gelatinous complex as long as the capsular jellies can supply it with water during its periods of exposure. But with the progressive loss of water retension by the capsular jelly, the necessary demands for water by the matrix jelly, during exposure, cannot be met so that eventually this suffers from progressive dessication during low tide periods eventually, having lost its gelatinous resiliance is easily broken by wave action so releasing its larval contents. Thus crumbling is not an accidental phenomenon but appears to be related through the medium of collar jellies to the degree of embryonal development and thus instigated when the larval form is mature and able to withstand the vicissitudes of the external environment.

To summarize, the apparent functions of the collar jellies are as follows:

1. The peripheral jelly applied on the termination of collar formation probably allows the matrix jelly to "set" and thus withold the imbedded sand. This is eroded off within a few tides after collar production but after this function is completed. Peripheral jelly seems to originate from the pedal glands.

2. The "matrix" jelly gives the necessary support to the collar and acts as a container for the capsules, protecting these from the mechanical exigencies of the outer environment; but takes no part in the maintenance of water supplies to the embryos; probably of pedal gland secretion.

3. The "capsular" jelly forms:
   - the necessary medium for the developing embryo,
   - controls the water content of the collar, thus preventing premature dessication of the capsule and collar
   - in P. triseriata it acts as a water barrier. Gradual deterioration of its effectiveness as a barrier takes place as the embryo develops its own ability to maintain its water balance
   - its deterioration with age, related to the embryonal development allows for collar crumbling to correspond to the development of the free living larva.

   Capsular jelly is probably a genital secretion.

The question may be raised as to the significance of these observations in the light of a possible biologic control. The answer is self evident, the collars of both species and more specifically that of P. triseriata are susceptible to algal attack, this algal destruction appears to be conditioned by the relation of the jellies to the embryo and to the dessication of the collars. Thus a close study of the algae and their ecology may lead to an effective control, by their culture under controlled conditions and release in nature in the early summer when the egg collars are becoming abundant. Consequent invasion of the egg collar by the algae will cause the death of embryos in their capsules and destruction of the gelatinous complex will ensure premature dessication and crumbling of the collar, thus increasing prelarval death and reducing the adult population.

Figure 52.

Comparing the snail and the size of the collar it produced. To the right P. triseriata, to the left, P. heros.

Figure 53.

Commencement of collar formation, occurring on flat surface.

Note longitudinally folded foot (Ft.) with anteriorly extruding gelatinous festons (Col. jel.)

Top - lateral view.
Bottom - ventral view.

Figure 54.

Diagrams I - III as would be seen if the whelk was exposed during period burial and looked down upon. Note the progressively extruded collar which on emergence from the pallial cavity and pedal mass is opposed to the shell.

[illegible] aspect of [illegible]ar and shell and the part the latter plays as a molding surface.

Diagrams VI & VII show the relations between direction of movement, direction of collar formation and the dextral or levo-rotatory spiraling of the parent snail.

Diagrams VIII & IX show the definitive phase of collar formation with the simultaneous application of the thin peripheral jelly by a spiral movement of the parent which forces the collar to the surface.

Figure 55.

P. trisariata 'freak' collar apical view of outer surface. Note the large capsules retained in the clear gelatinous matrix with poor sanding.

Figure 56.

Ventral view of Figure 55. Vide supra. Note almost complete absence of sand on inner surface.

Figure 57.

High power view of the capsules contained in the 'freak' collar of P. triseriata. Note the large capsules varying from 1000 - 1300 u. in diameter. The embryo proper appearing as darker central masses in the capsule. Capsular shape would appear to be conditioned by degree of crowding.

Figure 58.

'Freak' <u>P. heros</u> collar (Collar A). Note irregular shape and poor distribution of capsules.

Figure 59.

High power view of egg capsules of collar A. Note small number of embryos (average 13) and small capsular diameter (average 6.3 u.).

Figure 60.
P. heros 'freak' collar (Collar C). Note irregular shape and uneven thickness (dark patches represent areas of multicapsular thickness.)

Figure 61.
High power view of Collar C. Note large embryonal contents per capsule (Average 29) and large diameter (12.6 u.)

Figure 62.
A higher magnification than Figure 61, showing the large number of embryos and their double thickness.

Figure 63.

P. heros 'freak' collar (Collar D).

Figure 64.

Note large even capsules (Avg. diam. 12.6 u) and excessively large embryonal contents (Avg. 84).
N. B. Figures 59 and 61 are of the same magnification and Figure 62 and 64 likewise.

Figure 65.

Collars of P. triseriata. Middle and right hand collars affected with algal growth.

Figure 66.

First cleavage division of P. triseriata embryo, showing this contained in the capsular jelly with its denser peripheral pellicle.

C. Larval Life and Development.

1. The collar and its position on the flat. The egg cases of P. triseriata are distributed from high to low-water mark. At Belliveau Cove at low spring tides this is a distance of 2800 feet. The region of greatest abundance is a band parallel to and approximately 1300 ft. seaward of high-water-mark.

Unlike the former species, P. heros lays its collars seaward of the 1100 contour. The author has never recovered egg cases of this species inshore from this, though Stinson reports their occurrence in 1946 near the piers, a distance of not more than 100 to 300 feet from the high water line in the brook outlet (Figure 3).

The distribution of egg collars corresponds closely with that of adult snails. A striking departure from this rule was observed at station "Z". Abnormally high numbers of adult P. triseriata were observed feeding on the muscle beds here yet throughout the season no collars were recovered from this locality. Examination of these snails showed that their sex organs were of normal development and similar in all respects to the rest of the population which was producing large numbers of egg cases. This phenomenon cannot be explained but is possibly related to soil and water temperatures which were consistently higher at Station Z than at the other stations in the cove.

The over-all distribution of adults of the two species has already been related to their ability to withstand dessication and the premature crumbling of exposed collars of P. heros and the ability of P. triseriata collars to withstand dessication has been treated. It appears that the distribution of both the collars and the snails themselves is controlled by their ability to withstand dessication.

An average tide at Belliveau Cove exposes about 1900 feet of flat, the lowest recorded tide this summer receded 2800 feet, and the "highest" low Neap tide only 1300 feet. (Figure 3.)

Under such conditions the collars of P. heros, by virtue of their distribution, were exposed for periods varying from 1-4 hours while those of P. triseriata were exposed from 1-8 hours.

Because there is such a great variation in the period of exposure at different beach levels the incubation period, especially that of P. heros, owing to its reduced jelly contents and greater thermal reaction, might be expected to vary with the beach level. This relationship is based on generalized observation and lacks an accurate analysis.

2. Larval development. Appropriate equipment for a thorough study of pre-hatching development was lacking. However, certain aspects that were observed will be discussed at length.

In P. triseriata the egg is a spherical or slightly oval, yellow body about 350 u in diameter suspended in the clear capsular jelly. The method used to study these in situ was that suggested by Stinson dissecting off the outer collar wall thus exposing the individual capsules. This technique allows for a fair degree of visibility but clear differentiation is poor. It might be much simpler to study embryology if imperfect collars previously described were used. The developing embryo could be observed through the clear jelly without the impediment of imbedded sand and the chances of damaging delicate structures during dessication would be greatly reduced.

Shortly after collar formation the egg undergoes clevage which can can be clearly seen until the four cell stage is reached. After this the division is irregular. A multicellular structure composed of a small apical plate surmounting four to six large basal cells is distinguishable but development beyond this was too complex to follow with the equipment at hand.

The next stage that could be easily identified was the appearance of the shelled veliger larva. This when it first appears has a height of approximately 500 u. and as Stinson describes it "the velum moves constantly, the cilia beat rapidly and if removed from the capsule it will swim about in the water." During the 1949 season no intracapsular development stopped at this stage because the larvae were released by the crumbling collars. (See Larval Description). Stinson in 1946, however, described further development within the capsule, stating: "From this stage onwards the shell develops a reddish-brown colour. By this time a half whorl of shell has developed, the dextral twisting is quite clear. The operculum is now well formed so that when the foot and velum are retracted into the shell it completely fills the shell's aperture. The velum disappears when about three quarters whorl of shell has developed. By the time the larva is 1.1/3 to 1½ whorls it is ready to leave the capsule. At this stage it is 900 to 1000 u. in height and reddish brown in colour. The foot is quite active, so that when a snail that has just emerged is placed on sand, it begins to burrow at once. Apparently this variety has no free swimming phase in its life cycle."

The above statements should be borne in mind when considering the discussion on the 1949 emerged larva because there seems to be good evidence of year-to-year differences. As the embryo develops in P. triseriata the capsular jelly turned slightly opaque becoming progressively less tenacious; by the time the larva develops into the veliger stage the jelly is quite fluid thus allowing the larva to swim about actively and to be extracted quite easily.

In P. heros the egg is only 100 u. in diameter but its development is essentially like that of P. triseriata. In P. heros there is little capsular jelly; this is almost liquid in nature thus allowing the embryos to flow out if the capsule is broken. As in P. triseriata the capsular jelly changes with age, but being less in quantity and of a more fluid nature to start with, this change is not so apparent as in the latter species.

The development of the multicellular stages is very rapid and in a matter of days the capsules when viewed with a low power magnification appear to be literally "alive" with many small embryos in great activity.

At one stage the embryo is bell-shaped with two posterior bladder-like evaginations and the anterior end fringed with active cilia. This was taken to represent the Trochophore stage. It must be very brief because it was noted only in one of the collars examined throughout the summer.

Shortly after this the embryos emerge as definitely free-swimming larvae. In this respect the larvae development of the two species contrast sharply.

3. Incubation and collar crumbling. Determining the period of incubation has been so far rather unsatisfactory. Previous workers had difficulty in keeping trace of free collars on the flat, and the present writer in trying to solve this problem by wire cages found that caged collars collected the previously discussed algae and were destroyed.

The incubation period in aquaria was measured but this cannot be considered typical of conditions in nature. There is no doubt in the author's mind that water and beach temperatures are an important factor affecting the rate of maturation in both species, and possibly even within the collar proper for it is not infrequent to find embryos of one capsule in their primary clevage and those of another within the same collar in an advanced multicellular state.

This variation is particularly noticeable in comparisons of the apical and basal margins of collars. The latter are always either buried in the flat or in contact with its damp surface and probably experience less extreme temperature changes.

Stinson, in his consideration of the period of incubation, states: "In P. triseriata the total developmental period for this snail's larva is estimated as at least two month and possibly three. At no time during this period is it free swimming."

For P. heros he records: "It is probable that the incubation period averages one month to six weeks, that is only half the time required for P. triseriata." Proceeding in his observations he notes that it produced free swimming larvae in acquarial incubation, but admits his failure to recover this stage in nature by plankton drags.

Wheatley followed up Stinson's observations and agreed with his estimates.

In 1949 the author failed to get a satisfactory measure of the period but did uncover evidence of variations in the incubation period depending on the collar distribution and season. During the warm summer months this period seemed much shorter than in the cold spring months. For during August the writer got the impression from general observations that the development of P. heros was reduced to a period not exceeding one to two weeks at the warmest part of the summer.

Similarly throughout the season and especially in the hot month this effect appeared depending on the distribution of the collars; those collars occurring near the shore where exposed to longer periods of atmospheric temperatures than those occuring seawards, as maturity was based on crumbling it may be that this is not an indication of accelerated development but premature crumbling owing to excessive dessication.

Before considering the mechanics involved in collar crumbling and consequent larval release, it would be well to discuss at further length the possible functions of the capsular jelly.

As previously described this jelly in the young capsule of P. triseriata appears as a clear sphere whose outer periferal boundary or pellicle is composed of a denser material. (See Figure 66).

As the embryo develops this gelatinous sphere becomes more transparent and of a yellow color. If the jelly is ruptured and salt water comes in direct contact with the embryos they explode if they are young. With growth there appears to be a progressive loss of this incompatability finally resulting in complete tolerance of the larval stage.

Crumbling is characterized by apical disintegration of the collar which progresses basally in P. triseriata, while in P. heros the disintegration of the apical margin is usually accompanied by rupture of the collar's sides where they come in contact with the substratum, that is in the concavity at the base of the vertically flared apical cylinder. The prelude to crumbling is signified by marginal dessication during the low water period with the collar becoming a light brown-to-yellow colour along this margin. On the following low tides portions of the collar become detached by crumbling under the wave impact, this effect progresses basally until the whole egg case has disintegrated.

As dessication and the ability to withstand this appear to be conditioned by the capsular jelly, as previously discussed, it seems feasible to assume that the same changes that take place in this jelly, which allow for progressive compatability of the developing embryo to the external environment, affect the water retensive properties of the capsular jelly, thus precipitating the phenomenon of crumbling.

With the progressive loss of controlled water balance the collar becomes exposed to two extremes, dessication during the low tide exposure and complete water absorption during high tide. These extremes of water contents in conjunction to the mechanical buffeting by waves appear to exert an erosive effect on the collar resulting in the progressive disintegration accompanied by larval release.

4. 1949 Larval emergence. The 1949 larvae of P. triseriata recovered by tows with a No. 18 mesh plankton net, had a maximum length of 302u and a height of 250u and 1-1½ shell whorls. In all cases they were free swimming on emergence, exhibiting a characteristic rotatory movement. Stinson in 1946 reported a minimum height of 500u and 1 1/3 to 1½ shell whorls for the emergent larvae of this species which he observed to be non-planktonic on release from the collar.

The 1949 emergent larvae of P. heros had a maximum length of 134u, height of 125u, and a maximum width of 67u taken across the expanded velum. No figures on the dimensions of the larvae of this species were recorded by Stinson. This larva was free swimming in acquarial incubation and was recovered only once in drags at St. Andrews, N.B., though the author had some success in collecting immediately above crumbling collars at Belliveau Cove.

From the above it appears that:

1. the 1949 season was characterized by smaller larvae than recorded in 1946 for P. triseriata, (this may include premature larval release when considered with 2)

2. the 1949 observations on larval recovery, by drags, indicate that both of these species can have a free swimming, planktonic stage.

5. The 1949 larvae of the two species. The P. triseriata (See Figures 67,68,71) veliger larva has a small but well-formed velum. According to Stinson this is quite active during most of the period in the capsule, but by the time of emergence when the larvae is 900 to 1000u in height and has developed 1 1/3 to 1½ whorls, the velum is reduced and inactive. The foot is well developed meanwhile so that on release the snail burrows thus commencing its life in the substatum immediately after the collar crumbles.

The 1946 observation gave great hope for the control of this species by manual collection of collars; for the lack of a planktonic stage would seem to be a limitation to wide distribution, thus allowing control to be effective in small areas and not necessitating the uneconomical task of treating large areas. With the demonstration, during the 1949 summer, of a planktonic stage for this species, it is evident that the emergent larva of P. triseriata can vary from year to year in producing either a planktonic or a non-planktonic larva, thus further complicating the problem of effective mechanical control.

In the 1949 season the writer noted that the emergent larva was smaller than that reported by Stinson. Its shell varied from 1 to 1 1/3 whorls and was yellow brown in colour. It had a small but very active velum. On emergence this larvae did not proceed to the substratum and burrowed as in 1946 but remained natatorial.

Its movement was not unidirectional but consisted of a continuous rotary movement around the same axis. This movement in itself is of little use in distribution but it does keep the larva in suspension and permits its dispersion. It is not a truly planktonic larva and is best described by the term coined for it by Dr. P. Bondesen - "semiplanktonic".

The discordant 1946 and 1949 observations invite speculation. There is no doubt in the author's mind as to the reliability of these observations and he is confident that an explanation will someday emerge. Unfortunately no metereological observations were made by Stinson for exact comparison with those compiled in 1949, but it is generally agreed that the temperatures along the Acadian shore were abnormally high in 1949. Possibly the higher temperatures hastened embrionic development and more specifically created greater extremes during the diurnal tidal cycle thus accelerating collar crumbling and precipitating premature larval release.

Larvae of P. triseriata were recovered in abundance in planktonic drags this summer. (See Table 33).

P. heros (See Figures 69,70,71) This larva is small, being approximately 134 u in length and 125 u in height, its velum is well developed, measuring 67u at its widest diameter. The foot is small, tapered and transparent. The ubiquitous larva of Nassa trivitata resembles that of P. heros but differs in having a lobe like foot with a darker granular core and a longer "sac like" shell.

The shell of the P. heros larva may be colourless or a light yellow-brown. There is no indication of whorling except a small median notch and sulcus passing dorsal from it and in general is horn shaped.

The velum in the emerged larva is very active and large in proportion to the body, thus permitting the snail great motility and a degree of directional movement such as is found in many truly planktonic forms.

This activity and typically free swimming habit was noted in the larvae produced by acquarial incubation but neither Stinson nor the present writer were able to recover the larvae in plankton drags (No. 18 mesh net) at Belliveau Cove. However, the author has collected small numbers of larvae in bottles of water taken besides and about crumbling collars when they were still covered by a few inches of tidal water. These larvae under microscopic examination were found to be definitely free swimming and in all respects similar to the ones obtained in acquaria.

Previous to leaving St. Andrews, N.B. in September, one last attempt was made to recover this larvae in the plankton at Pottery Cove. Hauls were made in deep water beyond the low tide mark. One larva was found that could be certainly identified as P. heros.

There is little doubt that the behaviour of the larvae cultured in acquaria is similar to that of larvae occurring in nature. It is to be expected that where, the capsule is small, the embryos within numerous, and the capsular jelly reduced that the period of incubation would be short and that the larva released would be immature as compared to that of P. triseriata.

This, however, does not explain the poor larval recovery in drags. Stinson and the author in performing these hauls, reasoned that the larval distribution would be with the tide and thus best recovery would be inshore of the areas of highest collar incidence. In 1949 drags were taken at three heights on the flat, 900 feet, 1300 feet and 1500 feet offshore. Hauls at these locations yielded no P. heros larvae but gave good recovery of P. triseriata, thus showing their tidal dispersion during the 1949 season.

It should be noticed at this point that no adult specimen of P. heros were found inshore of 1100 feet and that members of this species under 10 mm. in height have never been recovered on the flats at Belliveau Cove. Possibly there is no dispersion inshore, and thus no recovery of larvae. This suggests an offshore larval migration and settlement, followed by a progressive inshore movement of the adult to regain its position at the low water mark, thus accounting for the observed peculiarities of this species distribution. It is also possible that the zero recovery of larvae in drags was due to the small population of this species in the cove.

6. Discussion. It can be stated that the larvae of P. heros irrespective of ecological conditions are always planktonic while those of P. triseriata may be non-planktonic or semiplanktonic depending on uninvestigated factors but probably on temperature which affect incubation and crumbling.

The importance of this conclusion so far as P. heros is concerned is neglegible, at Belliveau Cove, for this whelk is not common in this locality and appears to be always planktonic. But the possession of a planktonic stage permitting wide distribution of P. triseriata larvae presents a serious obstacle to control by manual collection of the egg cases. The importance of this will be fully stressed in the section "Distribution and Its Effect On The Snails' Life History".

Figure 67.

Typical P. triseriata semi-planktonic larva in 1949. Note small but active velum (Vl.) Well formed shell with clearly defined whorling (Wh.) and large foot (ft.)

Figure 68.

Semi-planktonic larva of P. triseriata, 1949.

Figure 69.

P. heros planktonic larva 1949. Note large and well developed velum (Vl.), small but active foot (ft.), small 'helmet' shaped shell containing the visceral hump (Vis. Hp.) which lacks whorling.

Figure 70.

Ventral and dorsal view of P. heros larva. Note the wide vela with long and active cilia: the pointed and hyaline foot. (Ft.) (Contrasting with N. trivitata characterized by a lobate foot with dark granular core.) Note evenly expanding shell when viewed anteriorly or posteriorly as compared with N. trivitata which is characterized by a small bulbar shell with a basal 'neck'.

Figure 71.

Comparison of emergent larval shells of the two species. Note the distinctive differences in shape, size and degree of whorling.

V. Distribution and its Effect On The Snail's Life History

A. Distribution of the Collar

1. Tidal Dispersion. The previous workers have speculated on the possibility of collar distribution by tidal agency, but unfortunately they failed to find suitable methods for marking and identifying collars on the flat and this hampered the investigation. Some attempted identification by cutting notches into the collar, others by attaching pieces of twine but in all cases their methods failed.

Wheatley and Beairsto concluded that collar dispersion by tidal agency was considerable and thus of importance in the overall problem of distribution but did not elaborate on this statement.

The author investigated this matter with respect to P. triseriata in Belliveau Cove and concluded that for this locality, movement is small and neglegible when considered as a factor in overall distribution of the whelk.

The method used to mark collars was to paint them with white enamel in a striped pattern so as to offer the best recognition and at the same time cause the least damage to the collar. In a preliminary experiment samples of such collars varying from 20 to 29 in number were placed at various positions marked with stakes on the flat. With each sample were included 10 unpainted collars forming a central core and an outer ring to the painted ones. These acted as a control to show whether the paint was affecting the collars and so jeopordizing the experimental results. On no occasion did the movements of the two types differ, thus it seems feasible to assume that the results obtained in the main experiments with marked collars alone are typical for collar movement in this locality.

Five different areas were selected for study of collar movements. These were selected as representative of the more important of the great variety of conditions to which collars are exposed in Belliveau Cove.

Site A. This area (Station 15, Fig. 4) is in the lee of the weir "lead" where the soil is clear hard packed sand. There was a heavy natural stock of collars there suggesting it to be a natural collecting area and thus representative of collar movement. Twenty-nine (29) collars were released here on June 11 and their movements observed at intervals until August 14. (Table 32 A)

Site B. This area (Station 10, Fig. 4) is exposed to the full effects of wind and waves. It seemed likely that collars would show the greatest movement here if they moved at all. Moreover this locality was crossed at low water by a steady flow of water from N.W. to S.E. draining from tide pools further up the beach. The soil is clear sand and the natural incidence of collars low. Twenty-eight (28) collars were released on June 21 and observed until July 6. (Table 32 B)

Site C. This area (Station 5, Fig. 4) is less exposed than either of the first two. The soil is muddy and there is a high incidence of collars. Twenty (20) collars were released here on July 15 and observed until August 14. (Table 32 C)

Site D. This area (Station 9, Fig. 4) is similar in most respects to site B. Twenty (20) collars were released on July 23 and observed until August 14. (Table 32 D)

Site E. This area (within Station 5, Fig. 4) was in a depressed area and therefore continually submerged. There was a luxuriant growth of eel grass (Zostera marina) which might interfere with the movement of the collars. Twenty (20) collars were released on July 21 and observed until August 14. (Table 32 E)

At each observation date the distance of the marked collars from their release stake was measured and the direction of movement recorded. In reporting these observations in Table 32 the wind direction during the two days prior to the date of observation is indicated. In some instances collars could not be located; these are recorded in the tables.

A review of the tabulated observations leads to the following conclusions:

1) As the experiment progressed the collars tended to become more and more widely scattered. This movement was greatest in the exposed sandy areas (Sites A, B & D) but in no case did it exceed 90 feet in two weeks with an average of 15-20 feet per 2 weeks.

The least movement was observed in the protected muddy area (Site C) and in the eel grass tide pool (Site E) were maximum movements from the original position in almost a month was only 20 feet.

The total movement was not great enough to be considered significant in the distribution of the species.

2) The direction of movement was with the recent prevailing wind i.e. across the beach from S.W. to N.E. in most cases. The collars at site B. behaved irregularly presumably because of the fast flowing drain water from the N.W. to S.E.

3) Losses of collars were greatest in the exposed areas (Site A & B) where they were subjected to burial by the shifting bottom, and least in the more stable and protected areas (Sites C & E).

Table 32. Observations on Collar Movements (P. triseriata).

A 29 Collars Station 13 Sandy	Date of Observation	0'	0-5'	0-10'	0-15'	0-20'	0-25'	0-30'	0-35'	0-40'	0-45'	Collars Missing No.	Gen. Direction Collar movement since last observed	Wind during last 2 days
			Distance Moved											
	12-June	29										0		S.W.
	13-(a.m.)	29										0		S.W.
	13-(p.m.)		28	1								0	N.E.	S.W.
	14-June		28		1							0	N.E.	S.W.
	15-June		28		1							0	N.E.	S.W.
	21-June		Rem		1			1		1		0	S.E.E.	S/E,S/E
	22-June		Rem	1				1		1		0	S.E.E.	S/W,N/W
	28-June			24	1		1					3	S.	N/E,N
	30-July			13	2		1					13	Generalized Undirectional	S.W.
	5-Aug.			15		1						13	NE.E	S.W.
	14-Aug.			7		1		1			1	19	SE.E	N.
	Gaps in recorded data due to burial of collars by silt usually after storms.													
B 28 Collars	22-June	26		1								0	S.E.E.	N.N.W.
	23-June	23	2		2							0	General-	S.E.

Several observations subsidiary to this experiment were conducted. These greatly help in interpreting the experimental results.

Collar movement was noted to take place at the commencement of the flood tide, but movement does not take place on every flood tide, for the collar after moving one flood tends to become buried and thus stabilized in its position during the following ebb tide.

While observing these collars the author noted that after a period of relative stability the collars would move en masse. This was rather puzzling until it was observed that whenever there was a shift in the direction of the prevailing South-Westerley wind during the incipient phases of the flood tide, the collars would move; this movement being usually in the direction of the wind prevailing during the flood. If, however, the wind shifted when the flood was well advanced no mass movement could be detected. From this generalization it was possible to foretell movement and the direction it would take from observing weather conditions at the commencement of the flood.

The generalization may be stated more particularly as follows.

a) The greatest collar movement takes place during the initial stages of the flood tide, if there is a change in the wind direction during this critical period. After such movements the collars seem to stabilize and will not change their position any further during subsequent flood tides so long as the wind continues to blow from the same quarter.

b) Little collar movement takes place during the ebb tide if the wind persists in the direction it held at the beginning of the previous flood.

c) If, however, the wind shifts during the high tide period there is likely to be collar movement during the late stages of the ebb tide and in the direction of the wind.

d) When it is perfectly calm there is no movement. Presumably it is wave action rather than steady currents that bring about collar movement. The wave action seems to be effective only when the water over the flat is shallow, i.e. at early flood and late ebb tide.

e) Collar movement is complicated and impeded by the tendency of collars to become partially buried in the soil This burial process seems to occur during the definitive stages of the ebb tide.

The burial stabilizes the position of the collar until there is a shift in wind direction during the incipient stages of subsequent flood tides.

f) Owing to the small numbers of P. heros collars to be found in the cove and to their seaward distribution it was impossible to repeat similar experiments with the egg cases of this species. However, individual collars were observed and from general observation on the flats it was noted that movement with these collars was very restricted.

This relative stability can be easily explained when one considers the morphology of this egg case. The collar remains upright but owing to its wide and thin walls it collapses so causing the lower or basal half to spread out and act as an anchor while the apical margins remain erect and perpendicular to the flat surface, similarly there is little tendency to bury, though typical peripheral fossa are formed around the collar (See Fig. 72).

2. Hypothesis on the mode of collar movement. (See Fig. 73)

Before attempting to explain the nature and mechanics involved in movement and burial it will be well to re-examine the collar as it appears on the flat. The egg case of P. triseriata stands erect on the substratum, by virtue of its low and thick walls, it offers resistance to tidal forces. Their conical shape and typical structure can be compared to the pillar of a bridge lacking in foundation.

For convenience and simplicity in the following hypothetical examples it is assumed that normal conditions are in effect, that is wind direction is S.W., wind speed is normal and all other factors are typical. The effect of unusual conditions, etc. discussed in terms of the advanced hypothesis after its presentation.

When the previously recorded observations showed that movement was coincident with the initial phases of the flood tide, the author seeking an explanation spent many a long hour watching collars during their primary stages of water coverage by the flood tide. When water coverage was considerable collars were observed from an anchored boat through a glass aquarium used in the place of a water telescope.

From these observations it was possible to advance the following hypothesis. Figure 73, Diag. 1 shows diagrammatically the typical wave formation at the incipient flood tide when this is only a few inches above the substratum.

Each "crest" can be resolved into two components of movement:

a) The horizontal component causing lateral displacement. This is superficial in distribution, having its greatest expression within the amplitude of the wave, its force decreases rapidly as one proceeds away from the crest towards the substratum.

b) The vertical component, though of superficial distribution appears to exert visible effects at greater depth than the horizontal. The vertical component does not cause lateral displacement but aids this by instigating a vertical "bobbing" movement which tends to dislodge and "suspend" the collar if this is buried.

These components were observed by attaching lengths of waxed wool at intervals on a long piece of wire (3 to 5 ft.) and placing this vertically in the water while the tide is in. The movement of the various indicates the nature of the water movements at different depths.

Conspicuous movement both vertical and horizontal were found to be superficial. They will therefore affect collars only when the water is shallow. For then obviously the direction of wave, and hence collar movement, will be conditioned by the direction of the prevailing wind at the time.

It should be noted that collar movement is not due to a continuous application of force exerted by the incoming water, for owing to its streamlined shape and relative inertia it resists this. Movement results from the continuous buffeting by a succession of waves so overcoming the inertia and destroying the equilibrium of the egg case.

Figure 73 - Diagram II. Shows the collar and the components of movement
Diagram III, I, - shows the collar being displaced and a diagrammatic representation of the decrement of the horizontal component with depth.

Diagram III, 2 & 3. Show the actual movement, when the collar after having its inertia overcome by the horizontal and vertical components is carried by the former until gravity restores it to the substratum.

Diagram IV. Shows the collar responding only to the vertical component with a "bobbing" movement. The horizontal effect being neglegible owing to the increased depth.

Diagram V. Shows the uneffected and stable collar owing to the removal of the components of movement by increased depth.

(The scales showing depth and movement are not in terms of any standard linear measurement.)

3. Hypothesis on the process of collar burial. (See Fig. 74.)

The phenomenon of burial was noted by the previous workers and after careful investigation in 1949 it appears to be characteristic of the final stages of the ebb tide, under normal conditions.

However, burial will not occur and movement will ensue if at the end of the ebb, when the water is shallow over the flat, the wind veers from the prevailing S.W. (inshore) to an offshore direction.

From this statement it would appear that the factor conditioning burial is basically the same as that instigating movement, the difference being in its degree of expression. There is little doubt in the author's mind that both conditions are due to wave action and that the key to the contrasting results lies in the wave shape and length.

Observation shows that burial takes place during the very end of the ebb, when water coverage was only a few inches. The process continues even at depths of less than one inch where draining goes on in a continuous movement without wave formation.

At Belliveau Cove, the prevailing wind is South Westerly i.e. in shore and opposite in direction to the flow of the receding waters at ebb tide thus usually causing a "rippling" of the surface.

The ebb tide wave pattern (Fig. 74, Diag. I) appears to differ considerably from that of the flood, basically it is a succession of long wave formations of low amplitude, thus exerting on the substratum a continuous force rather than the "joulting" effect as described for the quick train of crests characterizing of the flood.

This wave motion as the water depth decreases over the flat is gradually lost until the draining flat water appears as a smooth and moving film.

Thus under prevailing conditions the substratum during the late ebb, is subjected to a continuous and directional undertow, which depending on the strength of the wind, may have short "ripples" superimposed on the long waves, previously described. However, if the wind veers to an offshore direction, which is unusual, then the movement of receding water and wind coincide in direction and the effects are additive and cause collar displacement.

Under normal circumstances, the previously discussed components of movement of the long waves, do not hit the collar in rapid succession and so overcome its inertia but create a turbulence and a pattern of eddies against the face of the egg case. These are especially marked on the side facing the current.

Thus there are 3 areas involved in this process:

a) The side facing the current: here turbulence is set up and erosion of the substratum will ensue.

b) The central area contained by the collar: this is a space of dead water, into which, sand grains suspended by the afore mentioned turbulence, deposit so building up a stabalizing central core of sand.

c) The face of the collar away from the current: this is another area of turbulence and erosion.

The turbulence is greatest at the two faces mentioned though it is present and can be observed all around the basal periphery.

Burial commences with turbulence and erosion accompanied by deposition in the central space contained by the circular walls of the collar.

With the cessation of all wave motion and the steady drain of the flat water (under 1 inch deep, usually less), turbulence and erosion cease and the reduced currents tend to smooth the substratum, so causing the eroded areas to become filled in thus burying the collar.

From this it becomes apparent that the greatest degree of erosion and thus of burial take place on the same axis as the direction of the receding waters. Owing to this factor the collar is not evenly entrenched, but presents a stable axis (Fig. 74, Diag. 9, axis YY) and a weak axis of intrenchment at right angles to the previous one (Fig. 74, Diag. 9, axis AA).

At Belliveau Cove the direction of receding tidal waters is away from the land and towards the mouth of St. Mary Bay to the South West; thus direction of ebb tide in this locality coincides with the quarter of the prevailing wind. Due to this, after the collar is buried its strongest axis of intrenchment (YY) will be along the axis taken by the incoming flood; if the wind remains South Westerly; no movement will ensue. But if the wind changes on the next flood then the incoming waves will hit the entrenched collar on one of its weaker axes and probably dislodge it causing movement. When the wind remains stable, then with each succeeding ebb, the collar tends to become more and more firmly established.

Having discussed their method of burial and movement it is probable that the greatest displacement takes place immediately after collar formation, and possibly later on, depending on the stability of meteorological conditions. The above description is illustrated figuratively in the following diagrams.

Figure 74. Diagram I. Shows wave shape during late ebb tide.

Diagram II. Shows early effect of reaction. Diag. 11 shows the same only in a more diagrammatical manner.

Diagram III, IV, V, VI. Show the cumulative effect of this process which results in burial by excavation.

Diagram VII & VIII. Show the loss of wave formation, this being replaced by the steady flow of the flat drain during the last stage of the ebb.

Diagram IX. Shows the buried collar and its axes of maximum (YY) and minimum strength of entrenchment (AA).

Discussion. The hypothesis advanced is intended to apply only to the collars of *P. triseriata* at Belliveau Cove as these by virtue of their shape offer resistance to the current and show movement. The collars of *P. heros* are comparatively stable, for due to their lack of rigidity they collapse on the substratum and when subjected to the components of movement during the flood they may show a slight bobbing motion but lateral displacement was never observed. Similarly they do not tend to become buried like the egg case of *P. triseriata*, though extensive erosion around their basal margin, may occur. (See Figure 72.)

Thus it may be concluded that water movements affect the distribution of collars of *P. triseriata* to a far greater degree than those of *P. heros*, but that the extent of this distribution at Belliveau Cove is neglegible when considered as an agent of species dispersion.

Figure 72.

P. haros collars on the flat at the end of ebb-tide. Note the peripheral fossae excavated around the basal margins of the collars.

Figure 73.

Diagrammatic representation of the hypothesis of collar movement.
Diagram I - shows typical wave movement at commencement of flood.
Diagrams II and III show collar movement when this is exposed to vertical and horizontal components of motion.
Diagrams IV and V show collar stability by removal of the action of these components owing to increased water depths.

Figure 74.

Diagram I shows typical wave formation at the end of ebb-tide.
Diagram II - the turbulence established on the face of the collar meeting the current.
Diagrams III - VI - the progressive basal erosion of the margins and central building up within the collar.
Diagrams VII & VIII - the partially buried collar is consolidated by the even and continuous drain of water from tide pools.
Diagram IX - the buried collar showing its axis of maximum entrenchment (YY) and that of weakest consolidation (AA).

B. Distribution of Emergent Larvae.

1. P. triseriata. This larva has been previously described and some light has already been shed on the controversy which has arisen on the nature of the emergent stage.

Stinson (1946) by incubating collars of this species in vitro showed that the emergent larvae possessed a rudimentary velum and that on release from the crumbling collar they immediately sink to the bottom and bury themselves by means of their active foot into the substratum.

In nature he demonstrated the absence of the larvae in plankton, and rightly concluded that this species lacked a planktonic phase and thus is of limited distribution.

This being established, it was suggested that control, based on manual collection of the adult and the collar, would be effective, and economically feasible if applied to limited areas of high clam productivity menaced by the whelk.

The writer repeated Stinson's investigations and observed that the 1949 P. triseriata larva was free swimming; but by virtue of its reduced velum it performed a rapid circular movement which would keep it in suspension and so expose it to tidal distribution. This observation was corroborated in nature when plankton drags yielded good numbers of the larva. (See Table 33.)

The existence of a semiplanktonic larva in 1949 does not discredit nor contradict Stinson's observations for it is probable that this phenomenon was conditioned by the abnormally high temperatures recorded this summer. These by excessive dessication may have accelerated crumbling and thus caused premature larval release. (This is further substantiated by the smallness of the 1949 veliger . Apparently the larva of this species may be non-planktonic and semi-planktonic in the same locality, depending on metereological conditions.

Table 33. Numbers and species of larvae recovered from plankton drags performed at Belliveau Cove during the 1949 season.

The drags were made at 900, 1300 and 1500 feet offshore along the width of the cove in an East-Westerly direction.

Date	Larval recovery	900 ft. drag	1300 ft. drag	1500 ft. drag
August 10'49	P.triseriata	0	0	5
	P.heros	0	0	0
	Nassa trivitata	6	13	0
	Mya arenaria	0	0	0
August 12'49	P.triseriata	6	13	31
	P.heros	0	0	0
	Nassa trivitata	0	4	6
	Mya arenaria	0	0	0
August 13'49	P.triseriata	11	6	5
	P.heros	0	0	0
	Nassa trivitata	5	2	1
	Mya arenaria	0	0	0
August 15'49	P.triseriata	4	6	1
	P.heros	0	0	0
	Nassa trivitata	0	5	1
	Mya arenaria	9	5	1
August 18'49	P.triseriata	3	5	13
	P.heros	0	0	0
	Nassa trivitata	0	1	0
	Mya arenaria	0	5	1
August 22'49	P.triseriata	3	3	0
	P.heros	0	0	0
	Nassa trivitata	0	0	0
	Mya arenaria	0	0	0
August 23'49	P.triseriata	4	5	2
	P.heros	0	0	0
	Nassa trivitata	0	0	0
	Mya arenaria	0	0	0
August 26'49	P.triseriata	0	2	0
	P.heros	0	0	0
	Nassa trivitata	0	0	0
	Mya arenaria	0	2	0

This demonstration of two types of larvae for P. triseriata indicates that control of the species in limited areas is impractical because areas cleaned of egg collars can be seeded by larvae from other areas so nullifying the effects of control.

2. P. heros. In contrast to the previous species, the emergent larvae of P. heros, when incubated in vitro, has always yielded a truly planktonic veliger, yet it has never been recovered in hauls made at Belliveau Cove.

The author succeeded, late in the season, in recovering one such larva in deep water drags at Pottery Creek, St. Andrews, N.B. He also took some in bottles at late ebb tide directly above a crumbling collars. At Belliveau Cove microscopic examination of this sample showed the presence of six veliger larvae, similar in all respects to the in vitro specimens.

There seems to be no doubt that the larva of P. heros is truly planktonic and capable of wide distribution. Localized control of this species, based on clearance principles is therefore out of the question.

Larval Distribution - Discussion. When the distribution of the larva and the post-larval stages is considered, two opposing patterns of dispersal present themselves to the observer.

The population of P. triseriata, in terms of size distribution, progresses from the minute snail under 4 mm. along high water line to the large adult of 10-20 mm. approximately 1300-1500 feet offshore. This height frequency distribution (See adult population) indicates that the emergent larva is carried inshore and with growth migrates offshore.

To explain the observed distribution pattern one may speculate that the greatest release and distribution of larvae must take place during the flood so they may be moved inshore to the place and that collar crumbling should coincide with the flood. This appears feasible when it is considered that the mature collar at the end of the ebb is dessicated and brittle from exposure, rendering little resistance to the wave action of the incoming tide, and so crumbling. The chances of crumbling during the ebb, however, are poor, for wave action influences the egg case only when the water is shallow, and at this time, after its period of submersion the collar walls are elastic (owing to their prolonged submersion) and able to resist crumbling.

This larval release on the flood and the stable shorewards bottom currents at the Cove (See Fig. 3) made possible the demonstration of the semiplanktonic larva in nature and the data recorded in Table 33 for the drags were performed inshore of the area of greatest collar density, i.e. inshore of 1500 feet on the late flood and early ebb tide.

With the high tide and the accompanying period of slack water before ebb the larva probably becomes benthic and on reaching the substratum ceases its semiplanktonic life and burrows thereafter, so becoming of shore-line distribution.

The recorded distribution of P. heros at Belliveau Cove presents a puzzling picture. This species adult and collar are never found (1949) inshore of 1100 feet (at Belliveau Cove) and there was no larval recovery from inshore drags. Another mystery is the complete lack of specimens of this species under 15 mm. on the flats.

It is impossible to believe that the development from larva to the 15 mm. adult is so rapid as to pass unobserved on intertidal flats.

We might postulate an offshore migration of the veliger larva (which has shown experimentally to be capable of directional movement) settlement and early development in deep water and a slow inshore return of the developing adult to near low water mark on reaching maturity.

C. Distribution of the Adult

This is accomplished in two ways:

a) by pedal locomotion.
b) by expanding the foot and attaching this to the water surface film.

a & b apply to P. triseriata while (a) only is applicable to the P. heros as encountered in the Cove.

1. Pedal Locomotion. This can be easily observed at night on the surface of the flat when the snail emerges from the substratum. The movement is very smooth, the welk seems to glide effortlesly over the surface. This type of movement takes place to a lesser extent during the day under the substratum.

The extent and significance of this factor in distribution have been poorly assessed owing to the difficulty in marking the snail in experimental samples.

Metal tags and the like as a means of identification are impractical owing to the shape of the shell. Marking fluids have been used.

These qualities are necessary in an ideal marking fluid:

1) It should be applicable to the wheat shell.
2) It should be bright in color and possibly luminiscent.
3) It should dry quickly and tenaciously so as to withstand water action and sand erosion while the snail is buried.

The importance of a bright and possibly luminescent paint cannot be overemphasized as this work can only be done at night, when the whelk is on the surface and visibility poor.

The only exact available information on the degree of pedal locomotion is that collected, incidentally, by Stinson while working on growth rate this is presented in Table 34.

Table 34. Movement of marked specimens of P. triseriata (Stinson Table 4)

Specimen No.	Date of release at marker.	Date of recovery	Distance travelled feet.	No. of days required to travel same distance.
1	June 5	June 18	6	13
2	"	Aug. 22	18	78
3	"	Aug. 17	2	73
4	June 8	June 18	18	10
5	"	June 19	18	11
6	"	June 18	6	10
7	"	June 18	1	10

From the above results and general observation it appears that pedal locomotion is considerable but non directional, thus small in terms of rectilinear progress and of negligible importance in distribution of the species. However, there is good evidence that the snail is attracted to areas of high clam (or other food) incidence and migrates in their direction, so establishing regions with abnormally high populations.

2. Locomotion by tidal agency. This was first recorded by Dr. J.C. Medcof in 1948 who describes it as such: "Snails can be seen walking on the sand at any time during low water at night, but they have another and much more rapid means of locomotion. They can float. To do this they extend their foot, turn upside down and attach themselves to the surface film, Snails up to 10 mm. in height have been frequently observed going down with the tide in this way, supported by the surface tension of the water and travelling at approximately the same rate as the receding waters. As might be expected this takes place only when the water is shallow and its surface smooth, for attachment to the surface film is difficult to maintain with rippling. It is probably for this reason that snail travelling on the surface film seem less common with the rising tide which is often accompanied by rippling, even on a calm evening, than with the ebb tide."

This method of locomotion imposes a limit on the size of the snail that may use it, for the surface film will sustain only a certain size (weight), thus it has never been recorded in specimens of P. heros, though it is characteristic with the small P. triseriata and may well be their main method of migrating offshore with maturity.

This method allows for movement with the tide, which along this uneven coast dotted with coves, would ensue an inshore and offshore migration rather than coastwise dispersion, for it can only take place when the water is calm and relatively shallow (usually under 6 inches), thus it is important in the distribution within the intertidal zone, but of small value in increasing the costal distribution.

D. Discussion of distribution and control.

From the foregoing facts it is apparent that distribution in terms of successful dispersion and invasion of new areas is poor. The most successful stage in distribution appears to be the larval phase but as previously shown they hatch close to shore and the currents in this locality tend to be off or inshore but not along the shore, thus in the case of the prevalent P. triseriata the distribution tends to remain static and increase in numbers in the foci of infection. This is further manifested in the costal distribution of these species which is not ubiquitous as might be expected for an organism with a planktonic stage but is composed of densely populated pockets separated by areas which appear to render ideal conditions for the establishment to a Polynices colony. Fresh water outlets appear to be a barrier to their distribution, this being particularly conspicuous at Weimouth on the Sissiboo river seven miles from Belliveau Cove.

It was this limited distribution and apparent inertia of these species that gave hope and faith in the possiblity of applying a successful program of control based on manual collection of the adult and the egg collars. In the light of late investigation it appears that this, to be successful, would have to be a treatment of the whole of the infected area, for although the invasion of as yet uninfected areas is inefficient, the distribution within infected flats is efficient and would nullify the effects of a localized control within the populated area..

Thus for success within the area the principle of control to be followed is that of all or nothing at all, and even though the affected localities may be relatively small control aimed at complete clearance is economically impossible, the effort would cost more than the value of the clam stock that would be protected.

SUMMARY

Owing to unforeseen limitations it has been necessary to subdivide this report into two sections. The one dealing with the biology of the whelk, Polynices and the second with the attempts to control the Canadian species and with the related investigations on clam (Mya) relaying in Polynices infested areas.

The investigations which this report reviews were instigated with the object of determining an effective means of controlling this predator on clam stocks. Before the problem of control and means of treatment could be approached it was deemed necessary to undertake a detailed study of the snail, in terms of its morphology, habits, life history, ecological relationships, and distribution.

Detailed descriptions of anatomy and external morphology of the Belliveau Cove species has ensued with the identification of the local predators as P. heros and P. triseriata.

Further advance has been accomplished in understanding their mating habits and the conception of selectivity and the preconjugal march as performed by mating pairs has been introduced.

The feeding habit by drilling by chemical agency or by not well understood pedal secretions have been confirmed. Attempts to demonstrate the destructive capacity indicate that this is relatively neglegible for the individual snail but of cumulative importance when the high incidence of the predator is considered.

The egg collar has assumed a greater importance in the life history than previously supposed; the inter-relations of the component jellies and the embryo appear to be of utmost significance and may give valuable help in the field of control.

The larval incubation period appears to vary with season and location on the flats, this variation seems to be related to temperatures and the period of intertidal exposure.

Advance has been made in an understanding of collar formation which is conditioned by water coverage, loose substratum and the moulding surface of the shell.

The emergent larva of P. heros has been shown to be always planktonic in this locality, while that of P. triseriata may vary from semiplanktonic to benthic, this occurrence seems conditioned by prevailing temperatures during incubation.

Investigations on the means and efficiency of distribution has shown that dispersion of the adult and collar are negligible while distribution of the larval stage may be considerable and mainly dependent on water currents for P. triseriata.

The costal distribution of these two species along the Canadian

Atlantic seaboard is wide but tends to be localized and not continuous along the shore.

There is no doubt that penetration of either species in areas of high clam productivity has heralded the decrease of the clam stocks and that this can be largely attributed to the destructive capacity of the snail, but there is some indication that the whelk is an indicator species of ecological conditions which are unfavourable to Mya arenaria and thus hasten its destruction.

In conclusion this report attempts to review the known facts pertinent to Polynices and draw suggestions which though lacking sufficient experimental verifycation, appear to be within the scope of the investigation, thus it is hoped that this compilation of facts and hypothetical interpretions may act as a base line to future investigation on these species with effective control as an ultimate goal.

APPENDIX

"Methods and Field Techniques"

Certain techniques were used for obtaining measurements and other estimates to problems that presented themselves in the field. These had to be improvised and thus are rather rudimentary in cases. A record of these is submitted so that future workers may benefit from the experience of the present writer and it is felt that a standardization of techniques would go a long way in solving the variation in certain observations.

a) Morphological Techniques

With the adult snail:

1. Preservation of the adult. It was found that the adult snail will deteriorate rapidly if pickled in 4 or 10% formalin and similarly it tends to ferment in 70% alcohol.

2. Killing of specimens. Great difficulty was met in seeking a method of killing the snail without causing retraction of its foot. The most satisfactory method was by a progressive administration of Epsoms salts over a period of 4-5 days and sometimes longer.

3. Removal of the snail from the shell. This is best effected by heating in water practically to boiling from 5-10 minutes and then with a blunt probe separating the collumellar muscle from its point of insertion along the columnella. This technique can be used as well without heating but it is rather difficult to perform this without damaging the underlying tissue or breaking the visceral hump.

4. Extrusion of the proboscis, use Epsom salts technique.

5. The radula, dissection of this is comparatively easy if a dorsal incision is made along the proboscis; heating in KOH removes any particle of food captured under the teeth thus allowing for clear definition. Study of the dentition is best done under a dissecting microscope without mounting the radula in balsam et al.

With the egg collar.

1. For microscopic examination. It is best to cut off a section, one capsule thick, along the height of the egg case. If the collar crumbles on this treatment better results may be obtained by heating the collar in water or by immersion over night in hydrochloric acid.

2. Removal of capsules with embryo, only satisfactory technique was by simple paintaking dissection.

3. To determine area of collar. A piece of plastic sheet was ruled into square measuring $\frac{1}{2}$ by $\frac{1}{2}$ cm. this was superimposed on the collar and area was taken to the nearest whole square.

Height was measured directly with calipers and circumference by flattening the collar and using a piece of thread to gain this measurement.

4. To measure No. of capsules per $cm.^2$.:

   a) for P. triseriata a piece of plastic sheet was used with a square 1 cm. by 1 cm. cut out of it, this was apposed at random to the collar and capsules contained were counted by puncturing with a needle.

   b) for P. heros this was more difficult, especially in the lack of a dissecting microscope, an approximation was gained by cutting at random in the collar a right angle, along the sides of the angle one cm. was measured off and cut; count of capsules bisected by the line of cut on either side were counted and multiplied, the product being taken

      e.g. side (a) ..... 8 capsules
      side (b) ..... 6 capsules

      total capsules per contained square ... 48

5. Embryonal counts.

   a) in P. triseriata this is easily accomplished by dissecting out the capsular contents or by making a thin section as in (4) and counting under the microscope.

   b) in P. heros owing to the smallness of the capsules and the large number of embryos per capsule this is impossible visually or microscopically (see Fig. S. 61-63) an accurate method was devised by making a very thin micropipette with a long cannula followed by a bulbar reservoir, terminating in an aspirator of soughts, preferably a long rubber tube to the mouth. Under the microscope insert the cannula gently into the capsule and aspirate its contents, place these in a beaker and count under low power.

6. Suggestion for future studies on embryonal development in situ in the collar. Place snails in a tank with a hard substratum e.g. concrete and allow them to form a collar (Figs. 58-60) without sand, the collars allow for easy vision of embryos in the capsules through the clear jelly, they can be observed every day and placed under different conditions, e.g. being kept always submerged, or in shade etc; thus allowing for an exact study of development and possible variation in the rate of development depending on type of exposure, with the minimum of handling and artface causation.

7. Marking of collars on the flat - this is best done with white paint placed vertically, to give best visibility with minimum application.

b. Feeding and incubation experiments.

Types of cages.

1. For feeding experiments cages of ¼" wire mesh were made, they were 12" deep by 8" by 8". These were sunk into the flat surface until approximately 1" was projecting above the flat.

2. For collar incubation experiments, similar cages were made about 2 feet to 3 feet in diameter, these projected 4-5" above the flat. They were not very satisfactory as they accumulated the previously mentioned algae which soon invaded the contained egg collars and so destroyed the samples. This method might be modified by making larger cages and streamlining them with the direction of the current.

For techniques as devised in population studies see Part II of this report.

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