LITTORINA UNIFASCIATA GRAY AND *L. PRAETERMISSA* MAY (MESOGASTROPODA, LITTORINIDAE) IN SOUTH AUSTRALIA

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SUMMARY

The Gastropod Genus Littorina Ferrusac is represented in South Australia by two species L. unifasciata Gray and L. praetermissa May. These two species are sympatric in the same supralittoral fringe and have somewhat similar ecological relationship. However, the latter species tends to occupy more sheltered areas and crevices of the habitat than the former.

The shells of Littorina unifasciata and L. praetermissa are easily distinguishable, but the two species are so similar ecologically that the snails might not be regarded as valid species on their shell characteristics alone. Therefore, a study was made to determine the morphological characters which might show the snails to be two distinct species. The inner morphology of the shell was also studied by thin sectioning and differences are observed in the formation of the lamellae on the columellar axis. Differences between the two species are also found in the penile anatomy, the radula and the colour of the male and female gonads. These are the characteristics of littorinids on which specific differences are usually based.

The snails are easily maintained in the laboratory, so their breeding habits have been studied in laboratory experiments and comparisons are made with other littorinid species. Both species release planktonic egg capsules but differences between the species are observed in the structure of the egg capsules, their development time from zygote to veliger larva and in the structure and the

degree of development of the hatched veliger larva. Furthermore, Littorina unifasciata breeds throughout the year, whilst L. praetermissa breeds only for a few months in the winter.

The population of Littorina praetermissa is relatively small compared to that of L. unifasciata. A study on the distribution of the two species was made along the South Australian coast. Both species were found along the whole coastline. However, three small areas were found (Fishery Bay (Eyre Peninsula), Coobowie (Yorke Peninsula) and Cape Du Couedic (Kangaroo Island)) where some rocks or cliff faces were found to be shaded from direct sun through the whole of the day. In all three of these sites, the two species were present in more or less equal numbers and in some cases numbers of L. praetermissa slightly exceeding those of L. unifasciata. Usually however, L. unifasciata and L. praetermissa were present in numbers with ratios of about 4:1. The latter species being mostly in the more sheltered areas and crevices in the environment.

This suggests strongly that there is a difference in tolerance to desiccation between the two species, Littorina praetermissa having the lower tolerance. This was shown to be the case in the desiccation experiment; L. unifasciata surviving for much longer periods in low relative humidities and high temperatures than L. praetermissa.

DECLARATION

This thesis contains no material which has been accepted for the award of any other degree or diploma at any University, and, to the best of my knowledge contains no material previously published or written by another person, except where due reference is made in the text of the thesis.

ACKNOWLEDGEMENTS

I am most grateful to my supervisor, Mr. I.M. Thomas for his critical advice, his kindness and his encouragement given to me throughout this study. I am also grateful to Dr. H.M. Laws (former Curator of Marine Invertebrates, South Australian Museum) and Dr. A.J. Butler (Zoology Department, Adelaide University) for their valuable suggestions. Mr. P.I. Leppard gave invaluable help in writing the computer programme that was used to analyse the desiccation experiment.

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In the production of this thesis I have been helped greatly by Miss B. Holloway, who typed the manuscript, Miss S.H. Lawson, who gave invaluable suggestions and Mrs. L. Buzzell and Mrs. M. Holloway who read the proofs of this thesis. I much appreciate their willing co-operation.

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CHAPTER I. INTRODUCTION

Littorina unifasciata, Gray 1826 and L. praetermissa, May 1909 are widely distributed along the rocky coasts of South Australia inhabiting hard surfaces where microscopic algae grow in the supralittoral fringe. The name "unifasciata" is based on the single dark band around the whorls. L. praetermissa has escaped attention until recently named by May. It can be easily distinguished from L. unifasciata by its coarser spiral sculpture, colour markings and considerably more rounded whorls. Rosewater (1970) gave further information on their distribution and summarised the work to date of these two species in his revised edition on the classification of the family Littorinidae in the Indo-Pacific region.

"Representatives of the family are found in most regions of the world, occupying habitats from relatively shallow waters below the intertidal zones to situations high above the sea, when they may be wetted only ocassionally by spray" (Rosewater 1970). Most work on littorinid species has been carried out in Britain, Bermuda, Japan and Hawaii. Although Littorina unifasciata and L. praetermissa have quite a wide range of distribution in Australia, except for taxanomic studies with morphological differences, no other work has been published. They were referred to as "neglected" Australian littorinid species (Rosewater 1970, Pilkington 1971). My study on these two species is mostly on species differences, since very little is known of their biology.

The British species Littorina littorea(L) is the best exemplified "Typical" Littorina species. The anatomy of this species has been described in some detail by Fretter and Graham (1962). The anatomy of other littorinid species which have been studied is usually compared with the Littorina type species mentioned. Species differences are observed in the penile anatomy, the structure of the radular teeth and in the colour of the gonad. I have also studied the comparative anatomy of the two species of my study and compared with that of Littorina littorea.

Species characteristics are also found in their breeding habits and in the spawn. "The diversity in the type of spawn produced by species of one genus may be as great as that of species from unrelated families" (Fretter and Graham 1962, p. 386). Laboratory studies on the breeding habits of littorinid species are very rare. Of the few which have been conducted, the authors have stated that the captive snails did not mate freely (Struhsaker 1966, and Pilkington 1971). I have not found any published technique for maintaining the snails successfully in the laboratory to study the breeding habits. Therefore, I developed a technique of maintaining the snails, based on their behaviour in the field (see 3.4). With this method achieved, I found that the two species of my study could easily be maintained and they responded readily to the stimulus applied for mating and spawning. Hence, in studying the breeding habits of Littorina unifasciata and L. praetermissa, I have conducted the experiments in the laboratory (see Chapter 4).

The two species are distinctly different in their breeding habits. Littorina unifasciata breeds throughout the year and L. praetermissa has a short distinct period in winter (see 4.2.2.4). The species release planktonic egg capsules with different sculpturing. This is one of the differentiating factors of littorinid species.

I was unable to study the developmental stages from fertilized egg to metamorphosed juvenile stage in the laboratory. However, development from zygote to veliger larva took place without any problem and differences are observed in the developmental time from fertilized eggs to veliger larva between the two species and the hatched veliger larvae also differ.

The two species are sympatric, occupying the rocks of supralittoral fringe. However, the population of Littorina praetermissa is very small compared to the population of L. unifasciata and the former species tends to aggregate in sheltered areas and crevices, whilst the latter can be found in all areas in the habitat either exposed or sheltered.

Littorina praetermissa was once thought to be a morph of L. unifasciata because of its sparse distribution amongst the large population of the latter, especially in the areas much exposed to desiccation. However, the differences observed in their anatomy, their breeding habits and their spawn confirm the fact that they are indeed two different species.

The distinct and short breeding period in Littorina praetermissa may account for its smaller population compared with that of L. unifasciat

Its preference for sheltered areas and crevices in the habitat could be of a disadvantage in distribution when compared with L. unifasciata which has no special preference for either sheltered or exposed areas.

In a study on the distribution of the two species, I made a trip along the South Australian coast. In all the localities I have visited, except at Fishery Bay (Eyre Peninsula), Coobowie (Yorke Peninsula) and Cape Du Couedic (Kangaroo Island), (see Fig. 6-1 for the location of the places), Littorina praetermissa has had smaller number than L. unifasciata. The ratio is approximately 1:4 (see 6.3.2). In the three mentioned localities, the two species are one as abundantly distributed as the other. The conditions of these places are very sheltered from direct sun compared to all other localities (see 6.3.2).

Sheltered areas and crevices would have higher humidities and lower temperatures than the exposed areas. Thus the tendency of Littorina praetermissa aggregating in sheltered areas and crevices more than L. unifasciata suggests that probably, the former species has lower degree of tolerance to desiccation than the latter, or it may be to encounter higher humidities and lower temperatures. If so, this may be another explanation for the small population of L. praetermissa.

Any field observation would not be complete without some support from a laboratory experiment. Therefore, I conducted an experiment on the differences in the degree of tolerance to desiccation between the two species at various temperatures and humidities. The

result of the experiment was analysed with help from Mr. P.I. Leppard of the Statistics Department. The data obtained fitted well into the Logit Model, a standard statistical method. It shows that the death rate of the two species differs at all temperatures and humidities. Littorina praetermissa has higher death rate than L. unifasciata. Thus it seems that the latter species has higher degree of tolerance to desiccation than the former. This may further suggest why the population of L. praetermissa is smaller than L. unifasciata.

One may be able to gain more information from this experiment, if it was run for a longer period. However, as a preliminary study on these two species, I had some problems, and spent most of my time in choosing the most suitable method to conduct this experiment. Therefore, the data obtained from this experiment was not adequate enough to give all the required information (see 7.1).

In general, the main aim of my thesis is to support the two named species with their physiological differences and also to present their behaviour with field observation. Although many gaps remain, the information I have presented and the comparison made with other littorinid species, which have been studied, especially those inhabiting the hard surfaces where microscopic algae grow in the supralittoral fringe, will throw some light on Littorina unifasciata and L. praetermissa which are referred to as "neglected" littorinid species of Australia.

CHAPTER II. TAXONOMY, DESCRIPTION OF THE SHELL MORPHOLOGY AND COMPARATIVE ANATOMY OF THE TWO SPECIES

2.1 INTRODUCTION

There is little variation in general pattern of littorinid speciation. The shells are usually rounded, turbinate or some modification of this shape, and there is nothing conspicuous about their appearance. Thus the insignificant snails could be overlooked by the beachcombers. However, to Zoologists littorinids are the snails which best show the mechanisms of adaptations to the hazardous supralittoral conditions.

Although the general pattern of the snails is similar throughout the genus, differences between the species are observed in the shape and sculpture of the shells and in anatomical details. The systematists' task of classifying species and groups of species into genera has thus depended on consistent differences on the mentioned characteristics.

Rosewater (1970) has revised the classification of the family Littorinidae in the Indo-Pacific. Amongst the Indo-Pacific littorinids, very little is known of *Littorina unifasciata* and *L. praetermissa*. The snails are referred to as "neglected" littorinids.

In my study ~~with~~ of these two species, I have followed the classification of Rosewater. The structure of the shell and the

anatomy of the two species are studied, and the differences between the species are described.

The terminology used in describing the shell is based on Moore (1960). The anatomy of Littorina unifasciata and L. praetermissa is compared with that of L. littorea, which has been studied in some detail by Fretter and Graham (1962). As regards anatomy, not only the differences between the species are studied, the form of the reproductive systems of both sexes are also followed and compared with that of L. littorea, so as to guide the research into the breeding and spawning of the two species.

Figures presented on the anatomy in this chapter are mostly of Littorina unifasciata and of L. praetermissa are presented only when the differences are observed.

2.2 TAXONOMY OF LITTORINA UNIFASCIATA AND L. PRAETERMISSA

Phylum:	Mollusca	
Class:	Gastropoda	
Subclass:	Prosobranchia	
Order:	Mesogastropoda	
Family:	Littorinidae	Gray, 1840
Subfamily:	Littorininae	Gray, 1840
Genus:	Littorina	Ferussac, 1822

Subgenus:	littoraria Gray, 1834	austrolittorina Rosewater, 1970
Species:	praetermissa May, 1909	unifasciata unifasciata Gray, 1826.

Synonymy of Littorina unifasciata

1826, Littorina unifasciata Gray in P.P. King, p. 483.

1833, Littorina diemenensis Quoy and Gaimard, vol. 2, part 2, p. 479, pl. 33, Figs. 8-11.

1843, Littorina acuta Menke, p. 9, 1844, p. 57.

1847, Littorina mauritiana crassior Philippi vol. 2, p. 165, pl. 3, Fig. 17(a).

1850, Littorina diemenensis - Gray vol. 4, p. 78.

1858, Littorina laevis Reeve, vol. 10, pl. 17, Fig. 95.

1885, Littorina diemenensis pseudolaevis Nevill, part 2, p. 141.

1959, Melaraphe unifasciata - Cotton, p. 350.

1970, Littorina (austrolittorina) unifasciata unifasciata - Rosewater, p. 418, pl. 325, Figs. 17, 18, p. 468, pl. 359, Figs. 1-12, p. 469, pl. 360, Figs. 1-5.

Synonymy of Littorina praetermissa

1909, Littorina praetermissa May, 1908, p. 57, pl. 6, Fig. 3.

1959, Melaraphe unifasciata - Cotton, p. 350.

The synonyms of the two species have been checked in the references given by Rosewater (1970). The outer morphology of the two species described by Rosewater, was compared with the snails of my study. Therefore there is no reason to doubt the identification of the species.

2.3 DESCRIPTION OF THE SHELL

Over 50 snails of each species, collected from my three study areas, Glenelg, Port Willunga and Second Valley (Fig. 3-2 and 3-4, for the location of the study areas see Fig. 6-1) were studied and thin sections made of the shell to describe the morphology. Thin sections of the shell were made in the Department of Geology, University of Adelaide. The technique of thin sectioning was shown to me by Mr. J. Trevelyn (a laboratory technician) and description of the section was discussed with Mr. M. Bouniauto (Ph.D. student, fossil molluscs) of that Department. The terminology used in the text in describing the outer and inner morphology of the shell is as shown in Figs. 2-1, 2 and 4 based on Moore (1960). For the range in the size of the shell see Table 4-2.

Fig. 2-1. Directional terminology for a high spired shell (after Moore 1960)

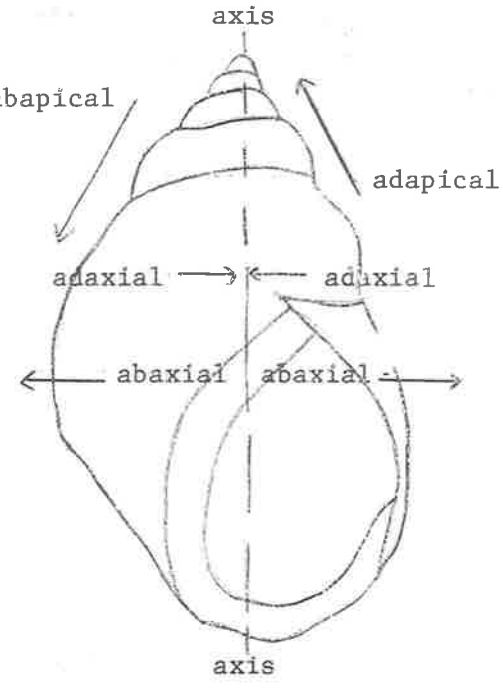


FIG.2-2 Terminology for the outer morphology of a high spired shell.

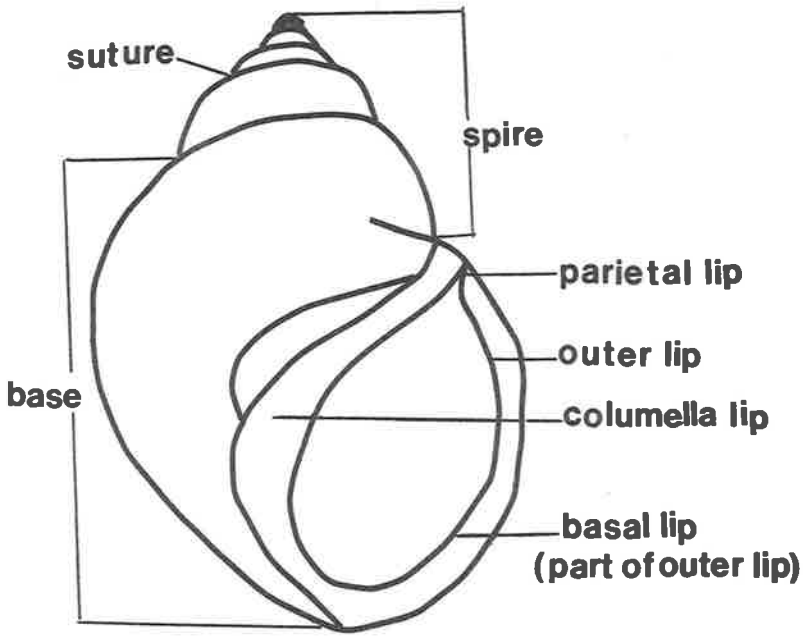
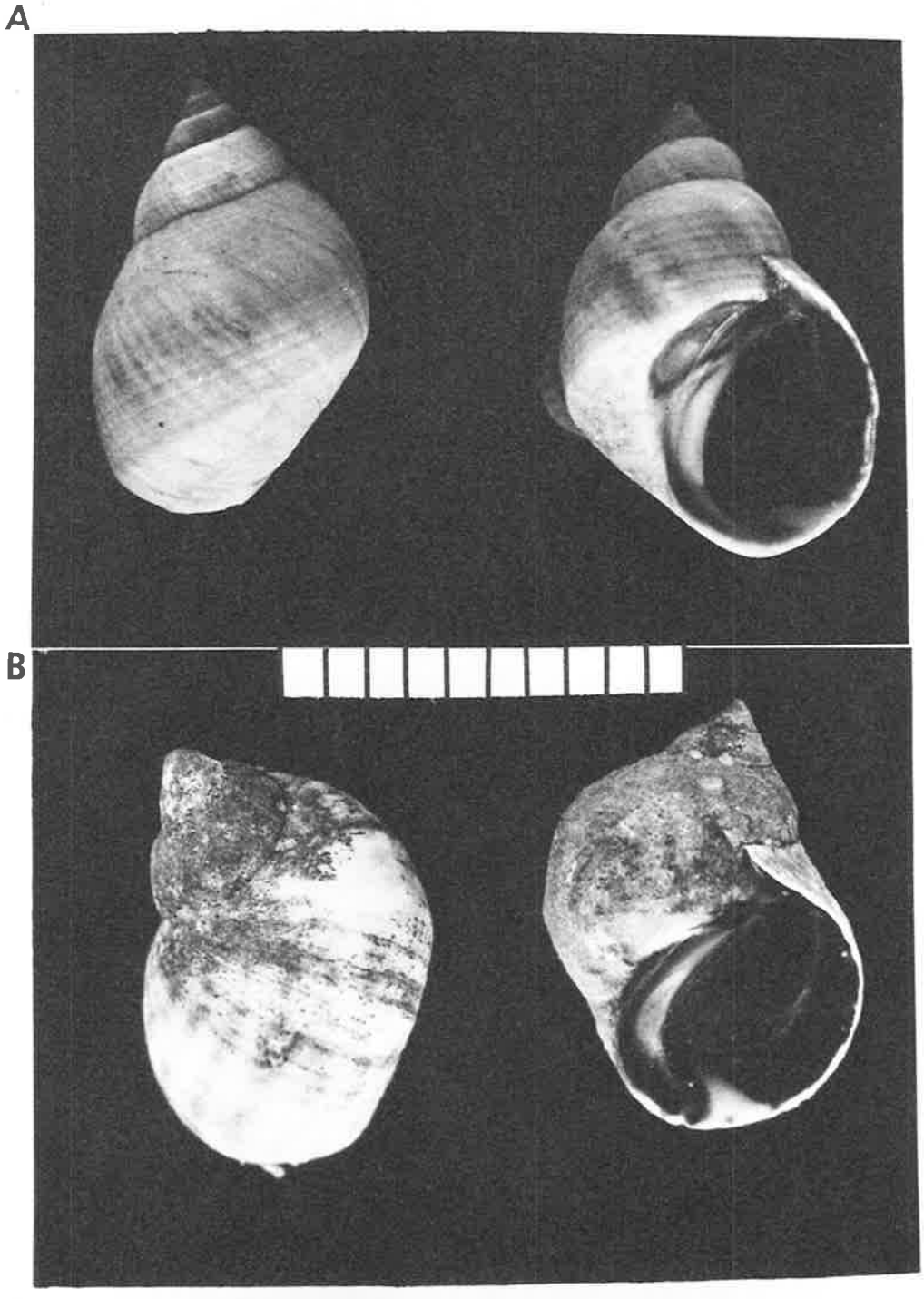


Figure 2-3 Outer morphology of the shell:-

(A) Littorina unifasciata; left, dorsal; right, ventral.

(B) Littorina praetermissa; left, dorsal; right, ventral.

FIG. 2-3



The description of the shell of the two species are described separately and differences between the species are summarised at the end of the description.

Littorina unifasciata:

Outer morphology: (Fig. 2-3A). Shell small, thick, turbiniform, high spired with whorls rather overlapping increasing more in height than in diameter; 5-7 whorls. Abutting sutures, abaxial margins of the whorls convex and steep. Base subconcave bounded by a slight round corina; peristome holostomatous oval.

Lips: parietal thin and convex; outer thick and convex; columellar base thick and convex.

Lip connections: parietal - outer deep broad gutter; outer basal slightly angular; basal columellar and parietal columellar imperceptible; the columellar lip produces abaxially a narrow adherent lobe covering the columellar body which is abaxially bounded by a broad shallow groove.

Protoconch is homeostrophic and constituted of 3 whorls with morphology similar to the teleoconch and is composed of calcareous substance.

Colour: the external ground colour of the shell is usually greyish white with a rather diffuse blue-grey band encircling the body whorl and anterior portion of spire whorls; apex light brown.

Ornaments: growth lines prosocline with adapical steepening; flat broad spiral costae separated by very fine marked grooves which become fainter towards the base.

FIG. 2-4 Terminology of the inner morphology of a gastropod shell.

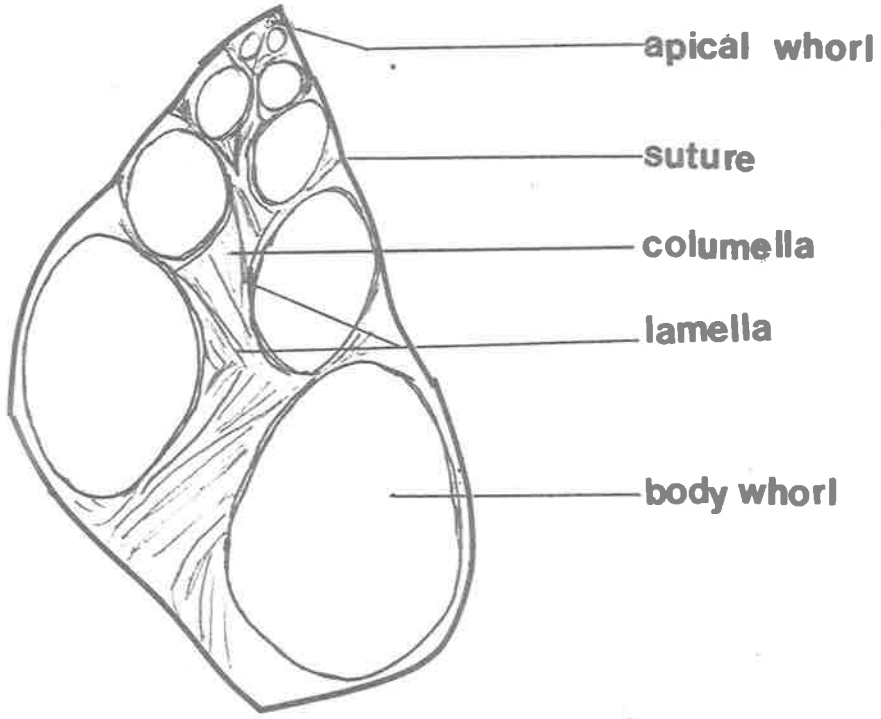
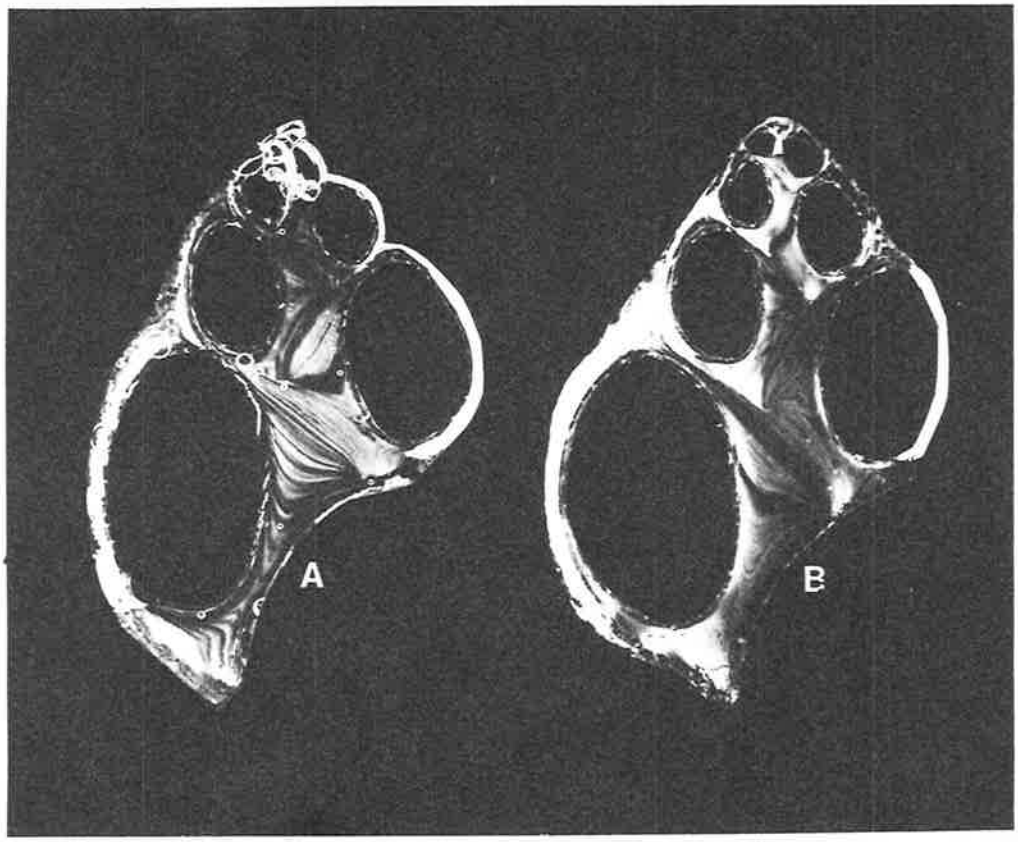


Figure 2-5 Inner morphology of the shell

(A) Littorina unifasciata

(B) Littorina praetermissa

FIG. 2-5 Inner morphology of the shell.



Inner morphology: (Fig. 2-5A). Inner shape of the body whorl regularly eliptical with height greater than the diameter. Outer shape of the whorl subtriangular with the adaxial vertex containing the coiling axis. The layers of the body whorl show an abrupt thickening at the adapical and abapical vertexes; a more regular thickness at the abaxial margin and a sharp thinning at the region in contact with the proceeding whorls. From the adaxial margin, thin spiral lamellae are produced and form a triangle-shaped columellar body. In each whorl, the lamellae are increasing in steepness in the younger part of the whorls sloping both adapically and abapically, and in the older part of the whorls dipping abapically from very steep to sub vertical.

Littorina praetermissa:

Outer morphology: (Fig. 2-3B). Shell thick, turbiniform, rather high spired. Whorls rather overlapping in relation to the coiling axis and completely overlapping in relation to the columellar axis. 4-5 whorls. Abutting suture. Adaxial margin convex.

Last whorl: convex base; semilunar peristome; columellar body depressed separated from the base by a sharp ring and partly covered by a thin lobe.

Lips: parietal very reduced, abaxial and adapical eliptical; columellar straight.

Lip connections: parietal abaxial angular producing a narrow deep gutter; abaxial imperceptable; abapical columellar angular; parietal columellar slightly angular.

Protoconch: is homeostrophic and constituted of 3 whorls and is composed of horny substance.

Colour: external ground colour of shell greyish white, with usually prominent pinkish brown zizag lines overall.

Ornaments: shell surface overall rather uneven and bumpy. Flat broad spiral ribs separated by fine grooves; growth lines prosocline. Occasional axial irregular scars produced by traumatism.

Inner morphology: (Fig. 2-5B). Inner shape of the body whorl ovoidal, rather elongated with adaxial margin slightly flattened. Outer shape of the body whorl subtriangular with the coiling axis passing through the adaxial vertex.

Margins: adapical and abapical nearly straight; abaxial eliptical; the shell thickness has its maximum at the adaxial adapical and a abaxial abapical vertices; and its minimum in the contact region with the proceeding whorl is nearly constant at the abaxial margin. The adaxial vertex is constituted by the columellar body and is produced by the adaxial middle layer of the shell. In the younger part of the whorls the adapical lamellae are steeper and adaxially reflected by the lamellar from the abapical in the middle region. In the older part of the whorls, the steepness is decreasing to be nearly normal to the axis at the abapical end. These lamellae appear to converge all to the rim outwardly bounding the columellar body.

Differences between the two species

1. Littorina praetermissa may be distinguished at once from L. unifasciata by its coarser spiral sculpture, colour markings and considerably more rounded whorls.
2. The lamellae in Littorina praetermissa decrease in steepness, whilst in L. unifasciata, they increase in steepness from the younger to the older part in the whorls.
3. The lamellae are consequently shorter in Littorina unifasciata than in L. praetermissa.
4. The distance from the coiling axis of the inner adaxial margin of the body whorl is shorter in Littorina unifasciata than in L. praetermissa.
5. The inner shape of the body whorl is more elongated and greater in height than in diameter in Littorina unifasciata, than in L. praetermissa.
6. The contact region between each adjacent whorl is narrower in Littorina unifasciata than in L. praetermissa.
7. The protoconch in Littorina unifasciata is of calcareous substance, whilst it is of horny substance in L. praetermissa.

Rosewater (1970) has placed the two species under separate subgenus; Littorina unifasciata as (austrolittorina) and L. praetermissa as (littoraria) based on the following characters:-

1) Base of shell adjacent to columellar flattened or hollowed out forming a crescent-shaped area ..... (austrolittorina).

2) Shell not thin for its size, often with subdued colouration or lacking pattern, usually rock living species ..... (littoraria).

The differences I have observed between the two species in the inner morphology of the shell may justify and support the distinction of the species at subgeneric level by Rosewater.

2.4 COMPARATIVE ANATOMY OF THE TWO SPECIES

2.4.1 GENERAL PLAN OF THE ANATOMY

When the snails are in their inactive phase, the whole animal is concealed within the shell, with the operculum acting as a shutter (see 3.2.2). The operculum is attached to the posterior part of the dorsal surface of the foot. The foot (f) and the head (hd) are the only parts extruded when the snails are active. Towards its posterior end the head bears a pair of laterally placed, mobile tapering structures, the tentacles (t).

The surfaces of the tentacles of Littorina unifasciata are darkly-pigmented, whilst that of L. praetermissa are lighter in pigmentation (Fig. 2-6).

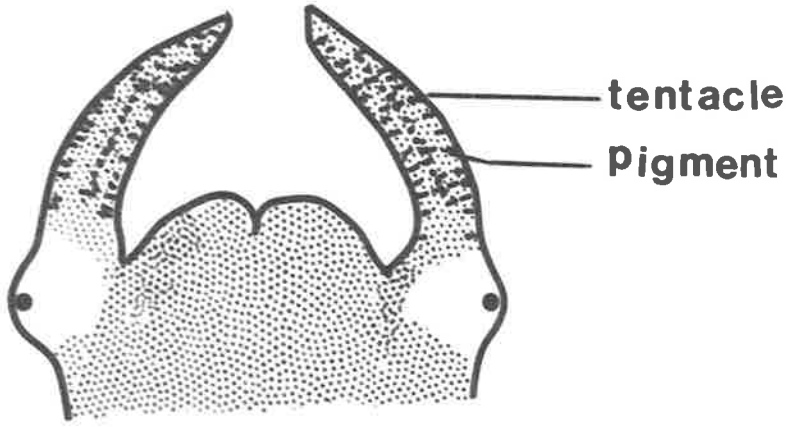
At the base of each tentacle on the outer side, is a flat, broad base, on which a dark spot with a lighter halo around it is seen. The dark spot is the eye (e). The mouth lies anteroventrally in the head.

When the animal is exposed after the removal of the shell, it can be seen to have been attached to the columellar axis by the columellar muscle.

The snails are dioecious and it is only by the presence or absence of the penis (p) that the sexes can be readily differentiated (Figs. 2-7 and 8).

FIG. 2–6 Pigmentation of the tentacles in the two species.

A. Littorina unifasciata



B. Littorina praetermissa

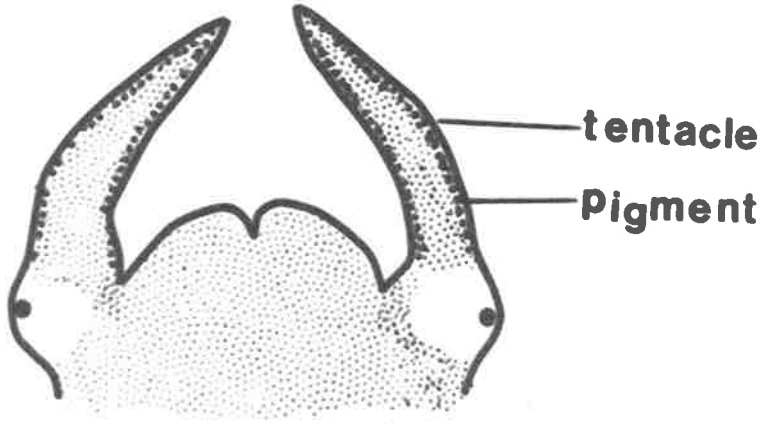


Figure 2-7 Male Littorina unifasciata after the removal of the shell

t, tentacle; f, foot; hd, head;
e, eye; p, penis; png, penial gland;
mst, mantle skirt; k, kidney;
td, testicular duct; te, testis;
dg, digestive gland.

FIG. 2–7

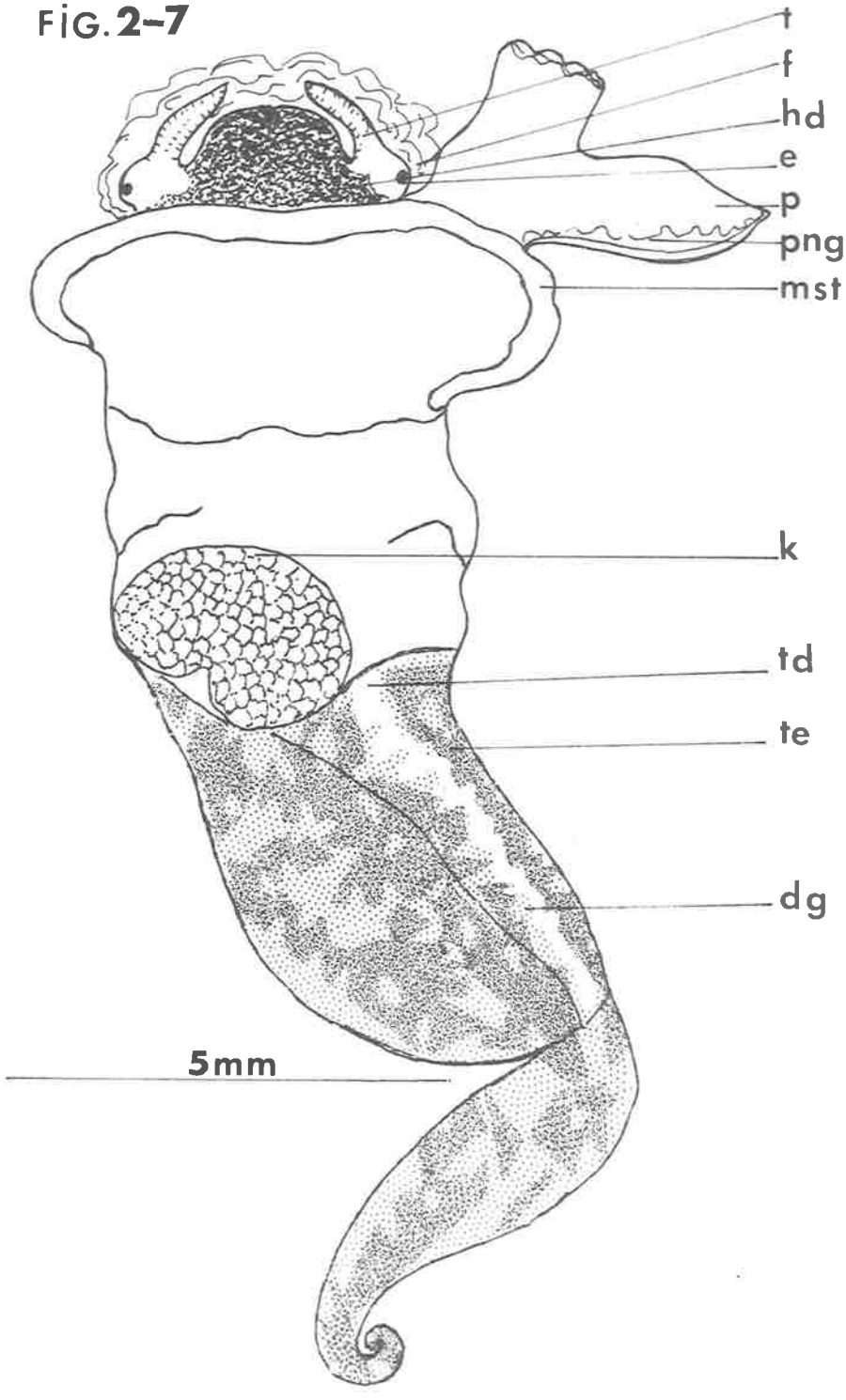
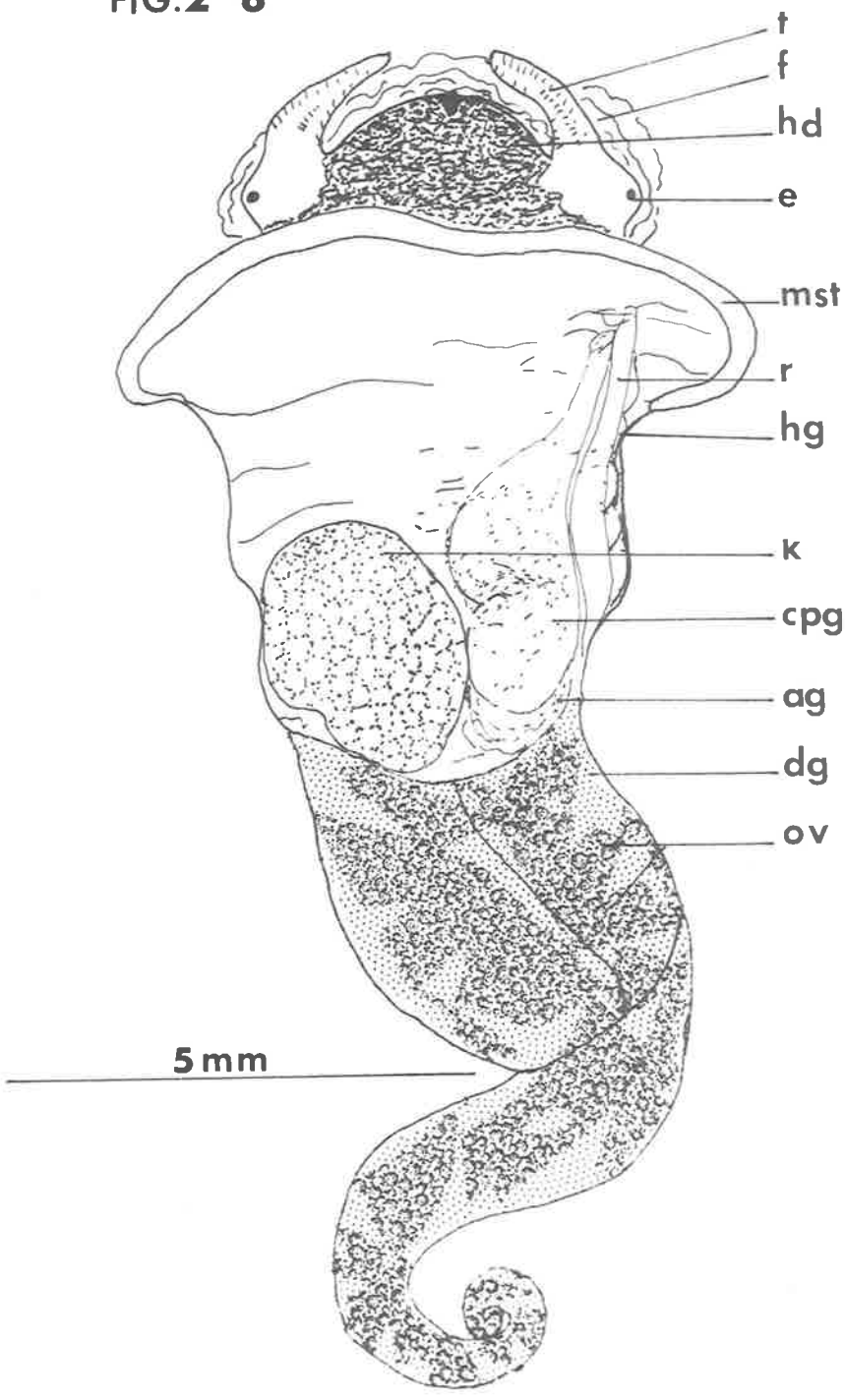


Figure 2-8 Female Littorina unifasciata after the removal of the shell

t, tentacle; f, foot; hd, head; e, eye; mst, mantle skirt; r, rectum; hg, hypobranchial gland; k, kidney; cpg, capsule gland; ag albumen gland; dg, digestive gland; ov, ovary.

FIG. 2-8



The penis is forked in both species. However, the two arms of the penis are more or less the same size in Littorina praetermissa (Fig. 2-13A), whilst it is of a longer and a shorter arm in L. unifasciata (Fig.2-7p). Reduction in the size of the penis is observed in the former species, when the snails are out of breeding condition, whilst the penis of the latter remains the same once developed (see Table 4-4).

The gonad in both sexes in both species is distributed superficially amongst the lobules of the digestive gland (Figs. 2-7(te) and 2-8(ov)). The kidney is a white or purplish structure.

The rest of the organs, such as the heart, ctenidium and part of the reproductive system, etc., lie within the mantle skirt (mst) which is opened at the anterior end. These organs are mostly visible, through the transparency of the skin, and they are exposed after the mantle skirt has been opened by a longitudinal median cut (Fig. 2-9).

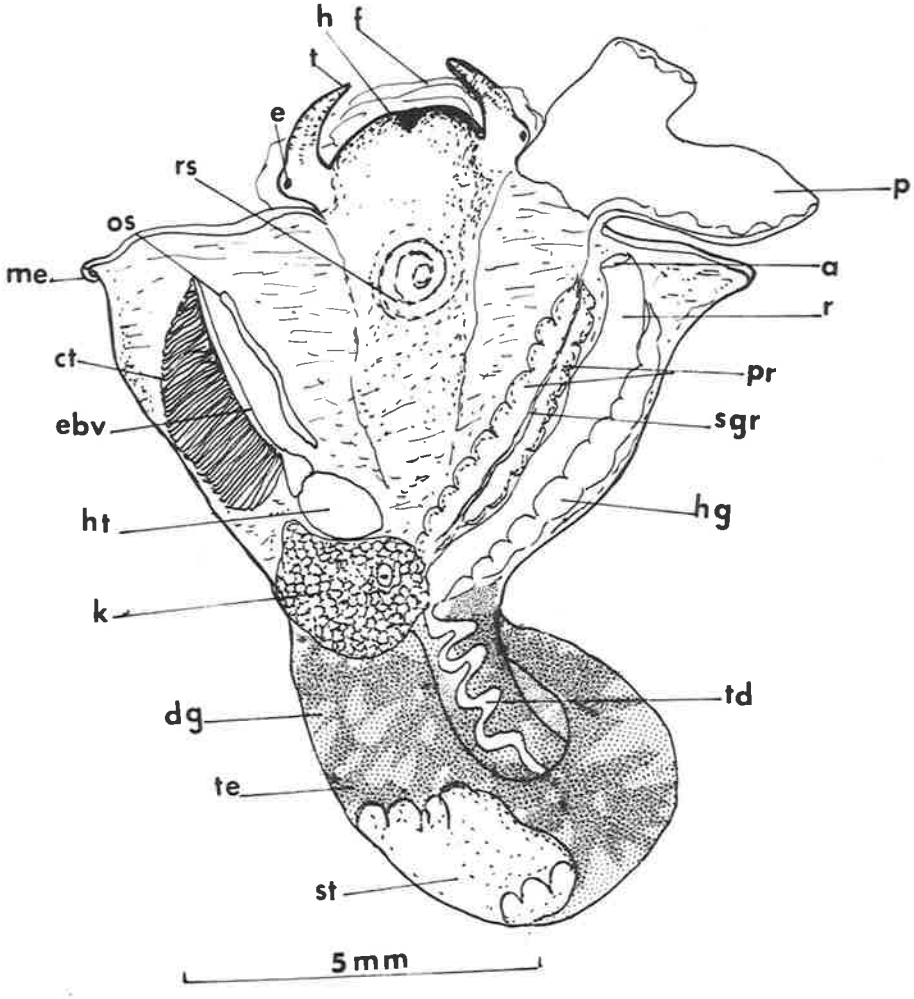
The organs described in both species, occupy similar positions to those described in Littorina littorea (Fretter and Graham 1962).

The position of the radula (r) is observed through the transparent floor of the mantle cavity, when the two halves of the mantle skirt have been pulled apart (Fig. 2-10A). The radula in both species is of typical littorinid type. It lies within its sheath, which is coiled except for the anterior portion, which runs along the mid-dorsal surface of the buccal mass to the odontophore.

Figure 2-9 Male Littorina unifasciata dissected in the longitudinal median line through the mantle skirt

a, anus; e, eye; f, foot; k, kidney; p, penis; r, rectum; t, tentacle; ct, ctenidium; dg, digestive gland; ebv, efferent branchial vessel; hd, head; hg, hypobranchial gland; ht, heart; me, mantle edge; os, osphradium; pr, prostate gland; rs, radular sac; sgt, sperm groove; st, stomach; td, testicular duct; te, testis.

FIG. 2-9



A median cut through the floor of the mantle cavity exposes the whole structure of the radula. It is a long narrow band.

Species differences in the family Littorinidae are usually observed in the forms of the radular teeth. Therefore, I have examined the radulae of my two species in detail to study the differences.

2.4.2 MATERIAL AND METHOD OF EXAMINING THE RADULAR TEETH

The specimens used for examining the radular teeth were collected from the breakwater at Glenelg (Fig. 2-4A and for the location see Fig. 6-1).

Thirty snails of selected sizes were chosen from the collected snails. Shell heights of the snails were taken as sizes. The sizes ranged from 7-12mm. Measurements of the shell height in relation with the length of the radula were taken of 5 snails of each respective size.

For the method of measuring the shell height see Section 4.2.1. The coiled radula can be straightened in a petri dish with a pair of fine needles after removal from the snail. The measurements of the radulae were taken by placing the dish with radula and seawater on a graph paper. The petri dish used is approximately 19cm. in diameter and 4cm. in height.

The radulae after recording the measurements, were boiled in concentrated potassium hydroxide to remove the soft tissue, and washed in distilled water and a series of alcohol from 30-70%.

Staining of the specimen was done in alcoholic borax carmine.

The radula, after staining, was cut into parts and temporary mounts made to study the pattern of the radular teeth. The parts from the entire length were examined as far as possible.

Detailed study on each single tooth was made by separating each tooth from its row with two fine needles. Temporary mounts of these teeth were made and the forms and the number of cusps present were studied under high power microscope. Drawings were made with a camera-lucida and measurements taken with an eyepiece micrometer.

This method gives satisfactory results to show the structural differences in the radular teeth of the two species.

2.4.2.1 OBSERVATION

TABLE 2-1 LENGTH OF THE RADULA IN RELATION TO SHELL HEIGHT IN LITTORINA UNIFASCIATA AND L. PRAETERMISSA

Species	Shell ht. in mm.	Range of Radula length in mm.											No. of snails
		35	40	45	50	55	60	65	70	75	80	85	90	
Littorina unifasciata	7	1		1		2	1							5
	8	1		2			1	1						5
	9				1			2	1				1	5
	10	1		1	1		1					1		5
	11		1		1	1		1	1					5
	12		1			1		1		1			1	5
Littorina praetermissa	7	1			1		2			1				5
	8		1	1			1		1		1			5
	9		1		1		1	1					1	5
	10	1			1	2		1						5
	11		1	1	1		1						1	5
	12	1		1		1		1			1			5

* Measurements of the radula taken to the nearest ± 2mm.

Examination of Table 2-1 shows that there is apparently no relation between the length of the radula and the shell height in both species.

"Radular teeth are formed at the inner end of the radular sac and are gradually moved forward along the sac, and on to the surface of the buccal mass, as those already there are lost or broken in use" (Fretter and Graham 1962). Feeding capacity of the snails could thus influence the radula, and it is most unlikely

that the feeding capacity would be constant in every individual snail. Hence, the length of the radula may vary even within the same size.

The narrow band is made up of a series of transverse rows of teeth, closely arranged one after the other. Each single transverse row consists of 7 teeth; 1 median, 2 laterals and 4 marginals. The formula is 2-1-1-1-2 which is the typical pattern of the littorinids.

Except for the rachidian or the median tooth, which could be observed clearly on the whole structure, in a transverse row, the rest overlap each other and are visible only in lateral view (see Fig. 2-10A and B). Lying close to the outer cusps of the rachidian on each side are the laterals. The posterior half of the laterals are overlapped by the inner marginals. Then overlapping the posterior half of the inner marginals are the two outer marginals. This description applies to both species.

The form and the number of cusps present in each tooth could be studied only after it had been separated from the transverse row. The differences between Littorina unifasciata and L. praetermissa are observed only then.

The differences between the species are observed markedly in the form and the number of cusps present. Except for the differences in measurements, the other radular teeth are very similar (Fig. 2-10 and Table 2-2).

TABLE 2-2 DIMENSIONS OF RADULA, SHAPE AND NUMBER OF CUSPS IN RADULAR TEETH OF THE TWO SPECIES

Species	No. of snails	Range Total length in mm.	Mean length in mm.	Tooth	in micron *L	W	No. of cusps	Shape of cusps
Littorina unifasciata	30	35-90	app.55	central	50	36	3	Rounded
				lateral	120	50	4	Rounded
				inner marginal	95	27	4	Rounded
				outer marginal	95	35	8	Rounded & pointed
Littorina praetermissa	30	35-90	app.57	central	50	36	3	Rounded
				lateral	123	53	3	Rounded
				inner marginal	118	50	4	Rounded
				outer marginal	125	32	12	Rounded & pointed

* L = length, W = width: the above measurements of radular teeth are averages only.

Figure 2-10 Radula

A. Position of the radula in the snail

B. Left half of the transverse row of radular teeth in Littorina praetermissa

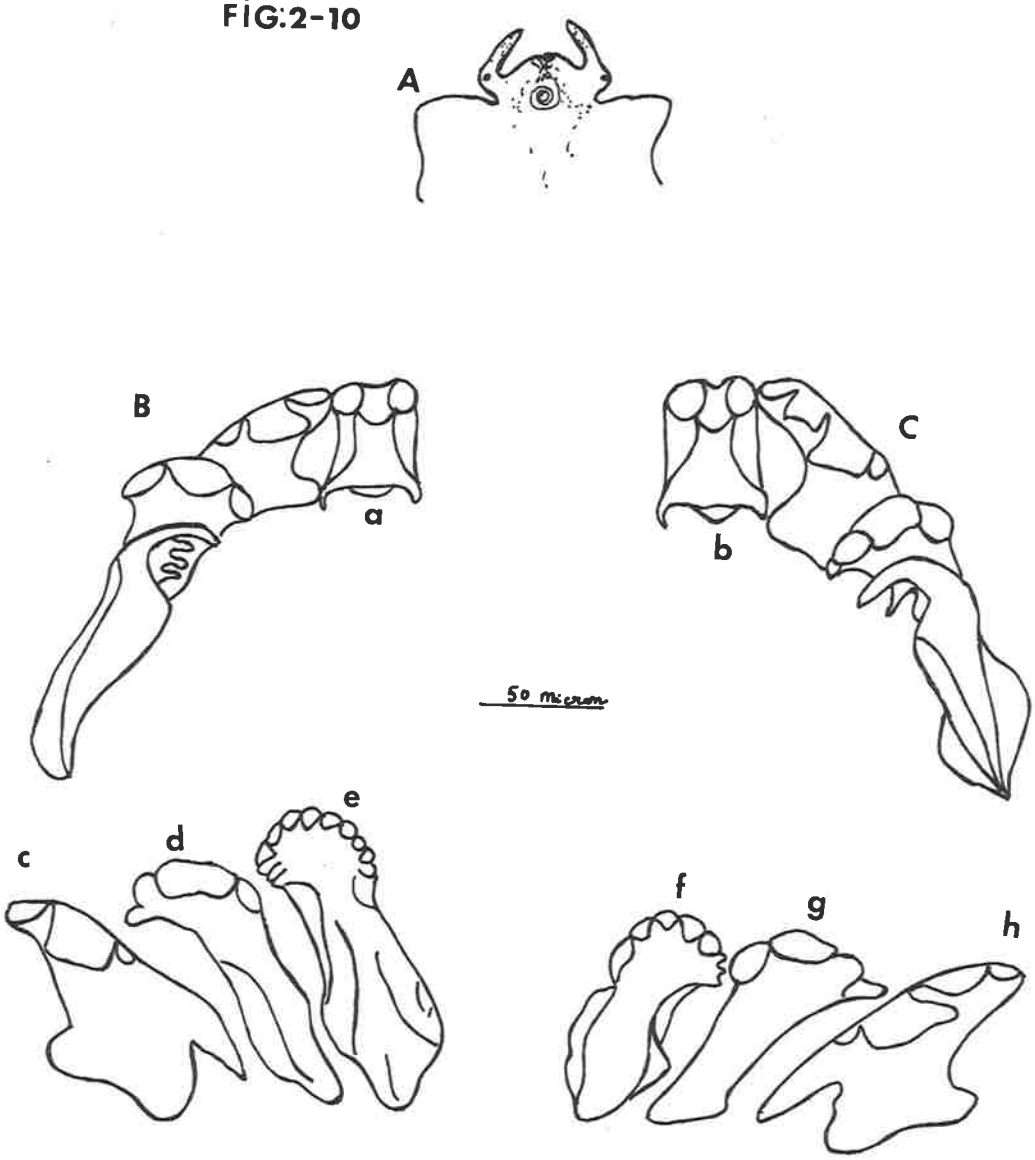
C. Right half of the transverse row of radular teeth in Littorina unifasciata

c,d,e, separated radular teeth from right half of the transverse row (Littorina praetermissa)

f,g,h, separated radular teeth from the left half of the transverse row (Littorina unifasciata)

c and h, laterals; d and g, inner marginals; e and f, outer marginals.

FIG:2-10



Each radula tooth bears a row of cusps at the anterior end. The cusps are usually rounded, except in the outer marginals, which is a mixture of rounded and pointed.

The rachidian is a short flat structure with a row of 3 cusps, distinctly located in the middle of the transverse row. (Fig. 2-10a and b). There is not much difference in the rachidian between the two species.

The laterals are markedly distinguished from the rest of the radular teeth by ~~its~~ their flat broad middle portion and the narrow posterior process. The laterals of Littorina unifasciata bear 4 cusps at the anterior end, whilst those of L. praetermissa bear only 3 cusps (Fig. 2-10c and h).

The marginals are narrower and more elongated in form when compared with the rachidian and the laterals.

The inner marginals have less cusps and are smaller in size than the outer marginals. The inner marginals of the two species are very similar (Fig. 2-10d and g).

The outer marginals have distinctive specific characters. Those of Littorina unifasciata bear 8 cusps and the tooth broadens towards the posterior end, whilst those of L. praetermissa are narrow and elongated throughout the entire length and bear 12 cusps at the anterior end (Fig. 2-10e and f).

2.4.3 MALE REPRODUCTIVE SYSTEM

The penis is a muscular, glandular structure lying close to the base of the right tentacle near the head. It is forked with two arms in both species. Differences between the species are observed in the sizes of the arms. The longer arm is approximately 3mm. and the shorter approximately 2mm. in Littorina unifasciata (Fig. 2-11p), whilst the two arms are more or less the same size and measure approximately 2mm. in L. praetermissa (Fig. 2-13(p)A). The white edges of the arms indicate the glandular portion of the penis. Once developed, the structure of the penis remains the same in L. unifasciata which breeds throughout the year, but reduction in the size is observed in L. praetermissa which has a distinct breeding season (see 4.2.2.4). The reduced penis is observed only as a muscular stub near the head when the animal is out of breeding condition (Fig. 2-13(p)B).

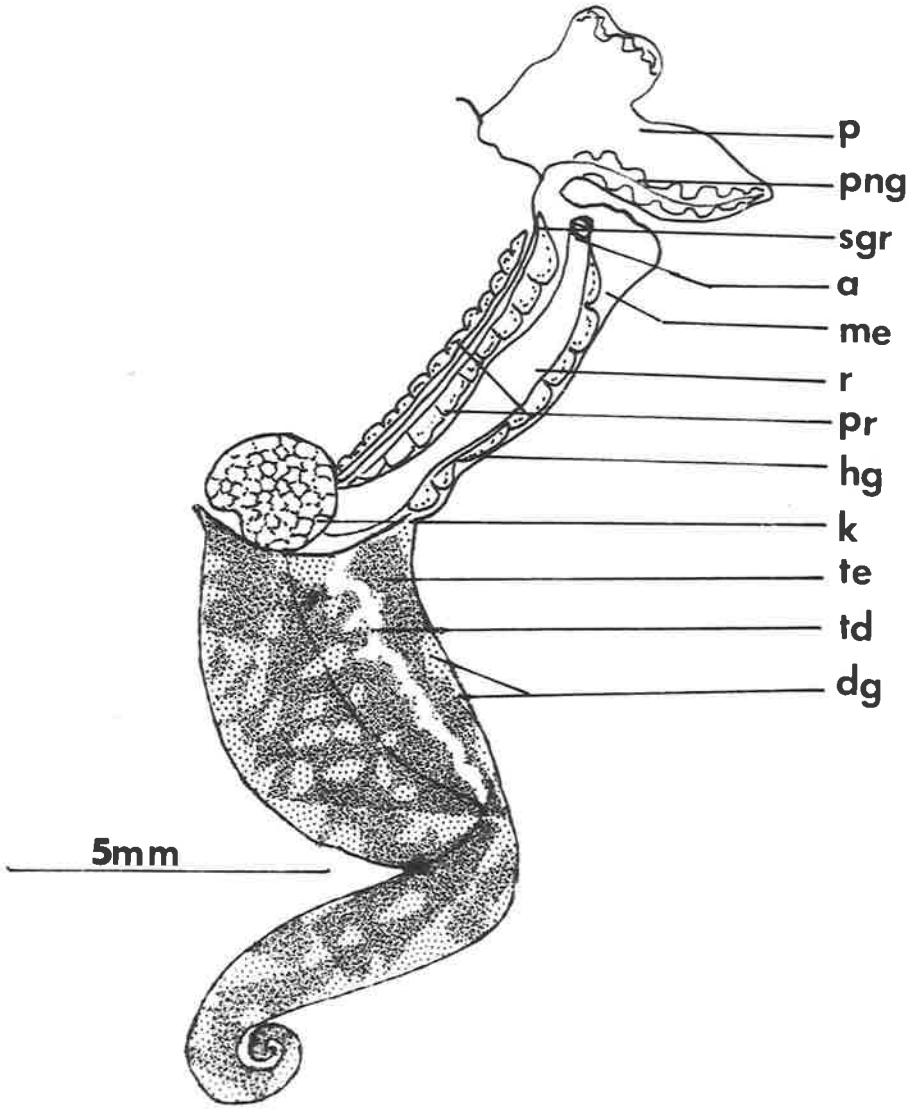
The position of the gonad and the associated glands are the same in both species though the colours differ. The systems of the species are described together below mentioning the differences between the species.

The testis (te) is a large diffuse branching organ which lies superficially over the digestive gland. As the snails approach the breeding condition, it thrusts itself between the lobules of the digestive gland and takes up space wherever available. The colour of the testis at this stage is reddish brown in Littorina unifasciata and yellowish brown in L. praetermissa.

Figure 2-11 Male reproductive system of *Littorina unifasciata*

p, penis; png, penial gland; sgr, sperm groove; a, anus; me, mantle edge; r, rectum; pr, prostate gland; hg, hypobranchial gland; k, kidney; te, testis; td, testicular duct; dg, digestive gland.

FIG. 2-11



The tubules of the testis join to form the testicular duct along the columellar side. When the duct is filled with spermatozoa, it is very distinct and swollen. The testicular duct is pink at this stage in Littorina unifasciata and white in L. praetermissa.

The course of the testicular duct is straight at first, but it becomes convoluted as it approaches the mantle cavity (Fig. 2-11td). From there a sperm groove runs forward on the floor of the mantle cavity on to the side of the head and along the edge of the outer arm of the penis (Fig. 2-7sgr). Along the pallial stretch of the sperm groove is the prostate gland (Fig. 2-11pr).

In comparison with Littorina littorea, the course is very similar except the colour of the testis and the structure of the penis. The testis of L. littorea (L) is commonly a greyish, grey-green or grey-brown and the penis is of paddle shape (Fretter and Graham 1962). Reduction of the penis is observed in this species. In this aspect L. praetermissa resembles L. littorea.

2.4.4 FEMALE REPRODUCTIVE SYSTEM

The reproductive organs of the female are more elaborate than those of the males, since not only do they provide the eggs with food but fertilization also takes place in them. Furthermore, the fertilized eggs have to be provided with protective capsules, within which the earliest developmental stages are undergone.

The ovary lies in a similar position to that occupied by the testis in the males (Fig. 2-12ov). Differences between the species can be recognised by the colour. The colour varies from green to yellow in Littorina unifasciata and from light pink to dark pink in L. praetermissa, depending on the breeding conditions of the female (see Table 4-4).

Only the course and the major parts of the reproductive system are described here. The origin of the ducts and the associated gland is not studied. However, the course and its associated glands are very similar to that of Littorina littorea. Thus, it is assumed that the origin and the connection is the same as described by Fretter and Graham (1962).

The ovarian duct runs to the inner end of the mantle cavity along a straight path. The oviduct opens at this point into a further section of the duct, which is enclosed in a tube formed by the folding of the mantle skirt. This is the pallial section of the oviduct (po) and lies along the side and to the right of the rectum. The female pore (fo) thus opens near the anus (Fig. 2-12).

The pallial section of the female genital tract is composed of a series of glands, which become extremely large and prominent at the height of breeding season and in addition chambers for the storage of spermatozoa after copulation are also present. Reduction in the size of these associated glands are observed in Littorina praetermissa during the resting period (Fig. 2-13C and D). This behaviour has been observed in littorinid species which has a distinct breeding period e.g. Littorina littorea.

Figure 2-12 (A) Female reproductive system
(B) Pallial oviduct dissected from the dorsal

me, mantle edge; a, anus; fo, female opening; hg, hypobranchial gland; r, rectum; po, pallial oviduct; cpg, capsule gland; rcs, receptaculum seminis; ag, albumen gland; k, kidney; ov, ovary; dg, digestive gland; cov, covering gland; bcp, bursa copulatrix; ms, mantle skirt.

FIG. 2-12

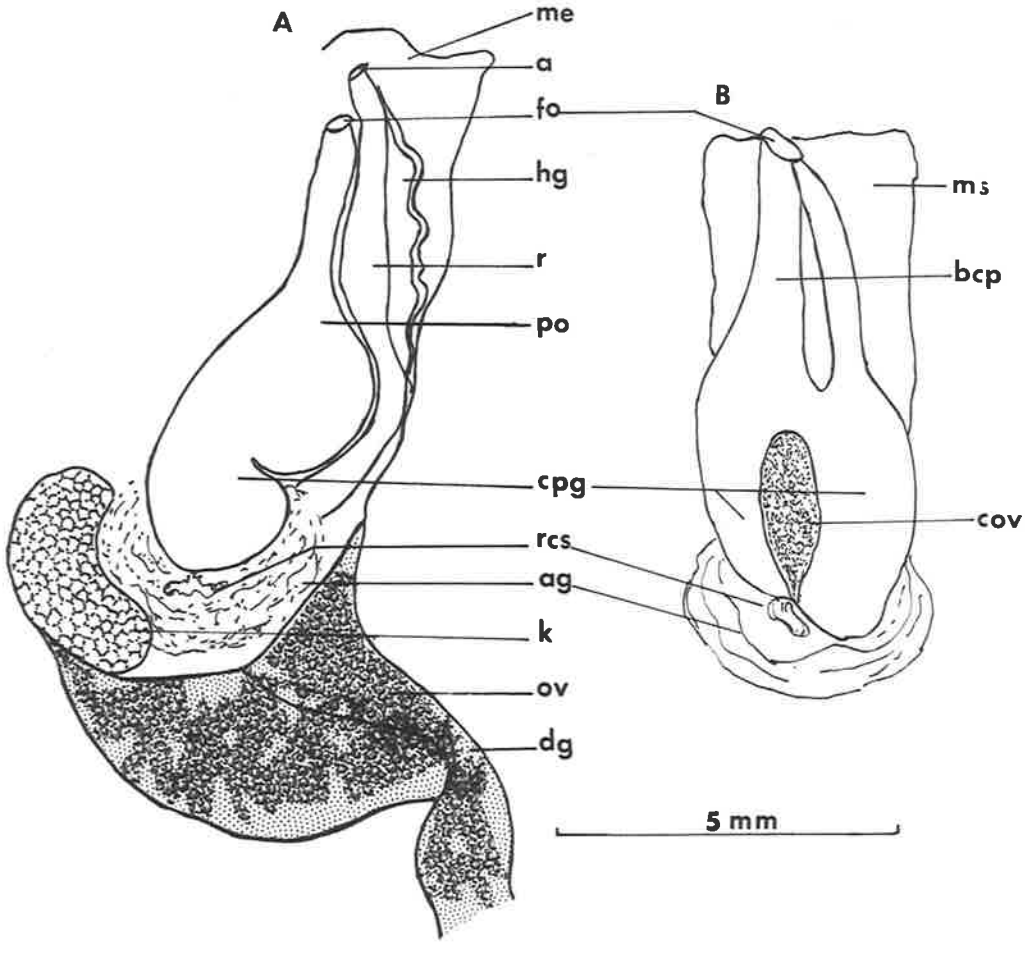
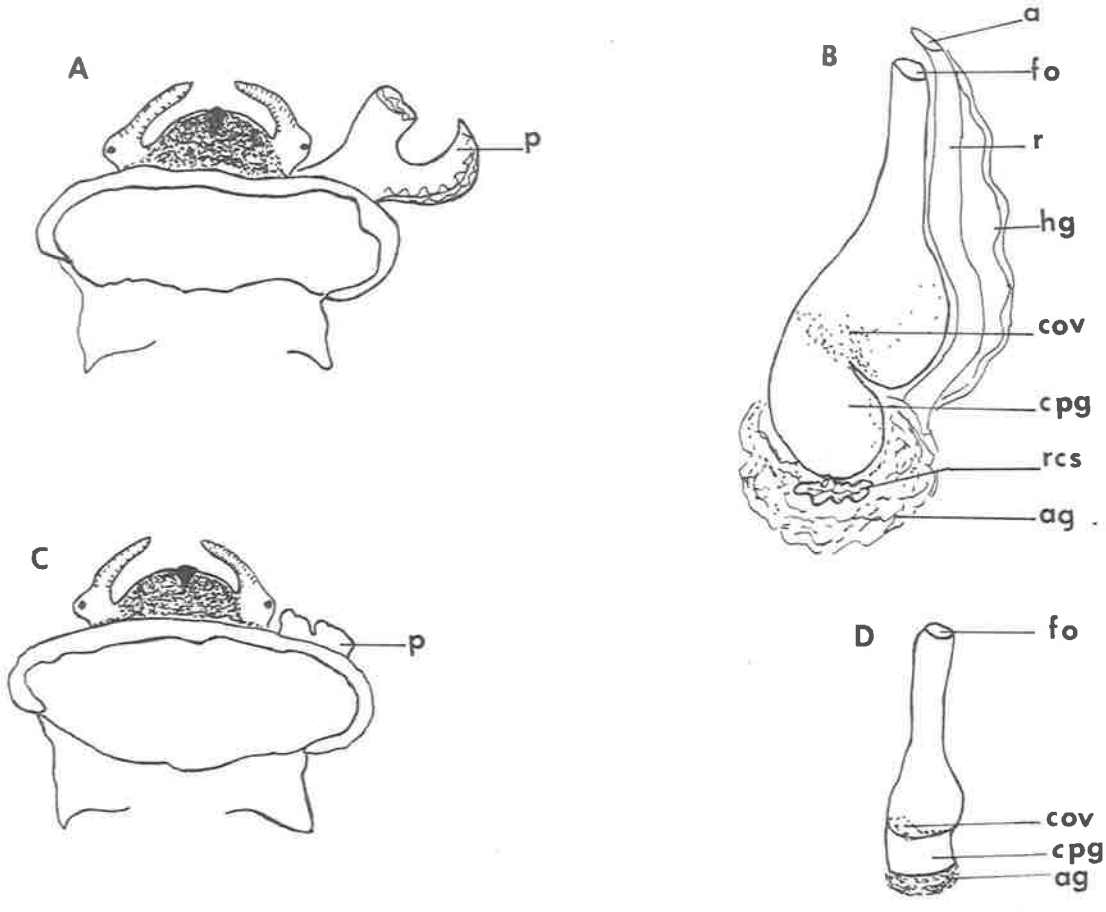


Figure 2-13 Reproductive organs of Littorina praetermissa

(A) Male in breeding condition
(B) Female in breeding condition
(C) Male out of breeding condition
(D) Female out of breeding condition

p, penis; a, anus; fo, female opening; r, rectum; hg, hypobranchial gland; cov, covering gland; cpg, capsule gland; rcs, receptaculum seminis; ag, albumen gland.

FIG.2-13



The receptaculum seminis (rcs) is visible at the upper end of the mass of glandular tissue as a refringent white streak. This becomes spherical in shape as it becomes filled with spermatozoa after copulation (see 4.4). Bursa copulatrix (bcp), albumen gland (ag) covering gland (cov) and capsule gland (cpg) are other associated organs of the female reproductive system (Fig. 2-12A and B).

In comparison with Littorina littorea, the position of the reproductive glands, and the course of the ovarian duct are similar, except in the colour of the ovary, which is yellow to pink or violet in this species (Fretter and Graham 1962).

TABLE 2-3 SUMMARY OF DISTINCTIVE ANATOMICAL CHARACTERS DISTINGUISHING LITTORINA UNIFASCIATA AND L. PRAETERMISSA

	Littorina unifasciata	Littorina praetermissa
Tentacle pigmentation	dark	light
Radula outer marginal	8 cusps, broadens at the posterior end	12 cusps, narrow and elongated throughout
Penis structure	forked, a shorter and a longer arm	forked, both arms the same in size
reduction in size	no reduction	present
Testis colour	reddish brown	yellowish brown
testicular duct filled with spermatozoa	pink	white
Ovary colour developing	green	light pink
matured	yellow	dark pink

2.5 DISCUSSION AND CONCLUSION

Littorina praetermissa though a distinct and easily recognizable species, escaped attention until named by May in 1909. This could be probably due to ~~their~~ their relatively small population size. It could be distinctly distinguished from L. unifasciata by its coarser spiral sculpture, colour markings and considerably more rounded whorls.

The two species are sympatric inhabiting the rock surfaces of the supralittoral fringe. However, the former species seeks crevices and more sheltered areas in the habitat than the latter (see 3.2.1).

Littorinid species usually differ in the morphology of the shell and the structure of radular teeth. Allen (1952) who did detailed research on the morphology of the radula of Littorina irrorata has suggested that the study of radular teeth is of taxonomic value. Whipple (1965) has used the structural differences in the radular teeth as one of the species characteristics in her study with the Hawaiian littorinid species. Rosewater (1970) has stated that:- "Species differences may be noted in penile anatomy, reproductive habits and characters of egg capsules".

In my study with the two species, I have observed the differences between the snails in the shell morphology and in details of their anatomy as I have mentioned in Sections 2-3 and 2-4. These distinguishing characters are usually observed in other littorinid species. Therefore, there is no doubt that Littorina unifasciata

and L. praetermissa are definitely two different species. Furthermore, the two species have distinct breeding habits (see 4.2.2.3).

CHAPTER III. THE BEHAVIOUR OF LITTORINA UNIFASCIATA AND L. PRAETERMISSA UNDER NATURAL CONDITIONS AND MAINTENANCE OF THE SNAILS IN THE LABORATORY

3.1 INTRODUCTION

Animals in their natural habitat are well adapted to their environmental conditions. To carry out a research on any particular animal would in most cases be impossible without field studies, since it alone gives the information on the mechanisms of adaptation of the animals to their special environmental conditions. Then from this study, the method of maintenance in the laboratory could be achieved, by applying artificial conditions similar to the natural conditions observed in the field. Therefore, in my study on the two species, field studies were first approach to understand their behaviour.

The method of maintenance was then developed with field observation as a guide and once the problem was solved, laboratory experiments were carried out with captive snails, concentrating on the aspects of differentiating the two species.

3.2 FIELD OBSERVATION

3.2.1 HABITAT

The terminology of the intertidal zones differ with the views from authors of all over the world. However, the description of the supralittoral fringe as given by Stephenson and Stephenson (1972)

fitted the area which Littorina unifasciata and L. praetermissa inhabit. "Near high-water level, there is an arid zone subject to conditions transitional between those of land and sea. It is affected by spray, but wetted by waves only in the heavy weather or at the higher spring tides, when at least its lower parts become washed or submerged. The number of species inhabiting the zone is relatively small and includes snails adapted to arid conditions and belonging to the genus Littorina and to related genera, or to genera of snails containing similar adapted species". Thus I have applied the term supralittoral fringe to the habitat of the snails.

The two species are sympatric and inhabit the rocks and wooden piers of the supralittoral fringe. Microscopic algae are the only ones growing in the habitat of the snails. Although the two species are sympatric, Littorina praetermissa shows preference for crevices and sheltered areas of the habitat, whilst L. unifasciata shows no strong preference for either sheltered or exposed areas. The [illegible] of L. praetermissa is almost absent among the large population of L. unifasciata in exposed areas.

3.2.2 ADAPTATION TO HABITAT CONDITIONS

The supralittoral fringe is dry and greatly exposed to desiccation when the tide is low. The snails inhabiting this area are immobile during this period. In the immobile stage, the animal is completely sealed inside the shell with the operculum serving as a shutter. Then the outer lip of the shell is attached to the substratum

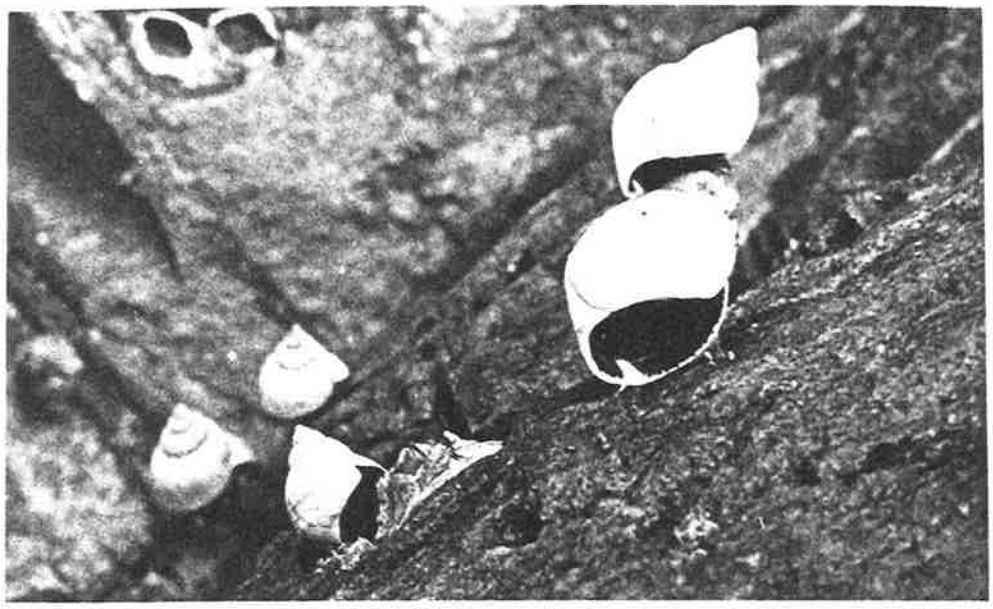
Figure 3-1 Adherence of the snails by the outer lip with a rim of mucus, when the substratum is dry.

A. On flat horizontal rock surface at Marino Rocks.

B. From the cliff at Coobowie.

FIG. 3-1

A



B

with the mucus secreted by the foot (Fig. 3.1). Thus this mechanism prevents the animals from rapid desiccation.

The snails are stimulated to activity by the splashes caused by the incoming waves at high tide. After the animal has been emerged from the shell, a great quantity of mucus is produced. This aids them in having a strong hold on the substratum, whilst they are subjected to heavy wave splashes. Once initiated, the snails remain active, until the substratum dries up, when the tide has ebbed away from the habitat.

3.2.3 BEHAVIOUR OF THE SNAILS IN THE ACTIVE PERIOD

When the supralittoral rocks have been wetted by wave splashes, the foot and the head are extruded from the shell and the creeping sole of the foot is applied to the substratum. The secreted mucus leaves a trail as the animal moves along. The tentacles which extend just beyond the shell are in almost continual movement from side to side feeling and touching obstacles on the substratum as the snails crawl along. Most of the head remains under the shell. The protrusible buccal mass moves in all directions over the rock surface and the radula can be seen scraping off material from the substratum. Thus, most of the time that the animals are moving, they are also feeding.

Mating pairs occur in great number after the snails have been wetted by wave splashes. The sexes cannot easily be differentiated externally. However, the snail which climbs on to

another snail is usually a male. It climbs on to another snail from any angle, but once on top, it moves to the right side of the snail underneath, where the female pore is situated. The extension of the penis could be observed from the dorsal side, but its actual insertion could be seen ~~took place~~ in the ventral aspect. Therefore the whole process of mating cannot be studied in the field, because of the solid opaque substratum and the snail. When the position of the male is on the right side and tightly clasped to the snail underneath, it is definite that the male has found its right partner (Fig. 3.5d). If the snail underneath should be a male, the male on top soon crawled away, soon after the extension of the penis. Male and male pairing is very rare. The mating pairs when disturbed break apart easily.

This mating behaviour applies to both Littorina unifasciata and L. praetermissa but the whole process lasted from 15-25 minutes in the former species and from 30-45 minutes in the latter. Throughout my field observations, I have never observed any interspecific mating between L. unifasciata and L. praetermissa. The snails remain active until the substratum starts to dry up. They then became quiescent and assumed their immobile stage soon after.

3.3 THE MAINTENANCE OF ZONATIONAL POSITION

3.3.1 INTRODUCTION

Animals of the supralittoral fringe move around when the substratum is wetted by the incoming waves, although they

are immobile during the dry period.

If their movements were completely at random, the constant pattern of zonation of the snails would in time be upset. Smith and Newell (1955) have given reasons to believe that on the shore at Whitstable individual winkles (Littorina littorea (L) tend to remain faithful to the particular beach level which they adopted during the first year of life after larval settlement. Gowanloch and Hayes (1926) presented evidence from observations on marked specimens that winkles migrate back to the particular level on which they dwelt after displacement to other situations whilst Moore (1937), who marked winkles (L. littorea) with cellulose paint with a view to following the growth rates of particular specimens, was able to collect many of these again, quite a considerable period of time after their replacement in roughly the same area. Newell (1958a) had found that if left undisturbed, the snails will move but will return to similar but not necessarily identical positions, and if removed from the place where they have settled, their chances of getting back home are reduced.

With these different views on the maintenance of zonational position of the snails, it is interesting to study on this aspect with the snails of my study.

The jetty wall at Second Valley is an ideal place to carry out a research with the snails on this aspect (Fig. 3-2, for the location see Fig. 6-1). Unfortunately, although Littorina unifasciata is abundantly distributed on the jetty wall, there is hardly any

Figure 3-2 A. Second Valley jetty.

B. The area of the archway of the jetty, where the field experiment on the maintenance of the zonational position of Littorina unifasciata was carried out.

FIG. 3-2

A

B

L. praetermissa present, due to the jetty wall being greatly exposed to desiccation. Hence, the experiment was carried out only with the former species.

In April 1971, when I first started my research, a few snai s were marked in an area on the jetty wall. These marked snails were observed on every fortnightly field trip till December 1972, and these snails were found in the area or in the vicinity of it. This observation of the pilot experiment is similar to behaviour of Littorina littorea as observed by Newell (1958) in that the snails tended to remain in the same locality.

However, to get proper information, I carried out a further experiment on the jetty wall in December 1972.

3.3.2 MATERIAL AND METHOD

Three areas, each of 50cm. by 50cm. were chosen on the jetty wall as follows:- (i) proximal half of the jetty wall, (ii) the adjacent wall in the archway and (iii) on the opposite wall of the archway. All areas chosen were approximately 60cm. above the ground and each area was approximately 450cm. away from the corner of the archways. The reason for choosing the areas in the mentioned positions of the jetty wall was, because, although the diurnal high tide level is unequal (Stephenson and Stephenson 1972), the water level definitely reaches the archway during high tide period. Then by choosing the plots only 160cm. above the ground, the sprays caused by the incoming waves would not miss wetting the chosen areas even when the sea is slight.

Four nails were placed at the corners of each of the three areas, so that a perspex sheet marked with a 2cm. grid could be suspended and the position of all the animals could be recorded on square graph paper each day. The number of snails marked were 25 in area I, 16 in area II and 20 in area III.

In marking of the snails, the paint was mixed with cement to prevent it from being washed away. The snails were marked with a needle in serial dots. The maximum number of dots that could be marked on a snail was five. Different colours were used so that individual snails could be identified. The marking was done when the substratum was dry and snails immobile, thus avoiding displacement of the snails from their original positions. The original positions of the snails were as in Fig. 3.3A (a,b and c).

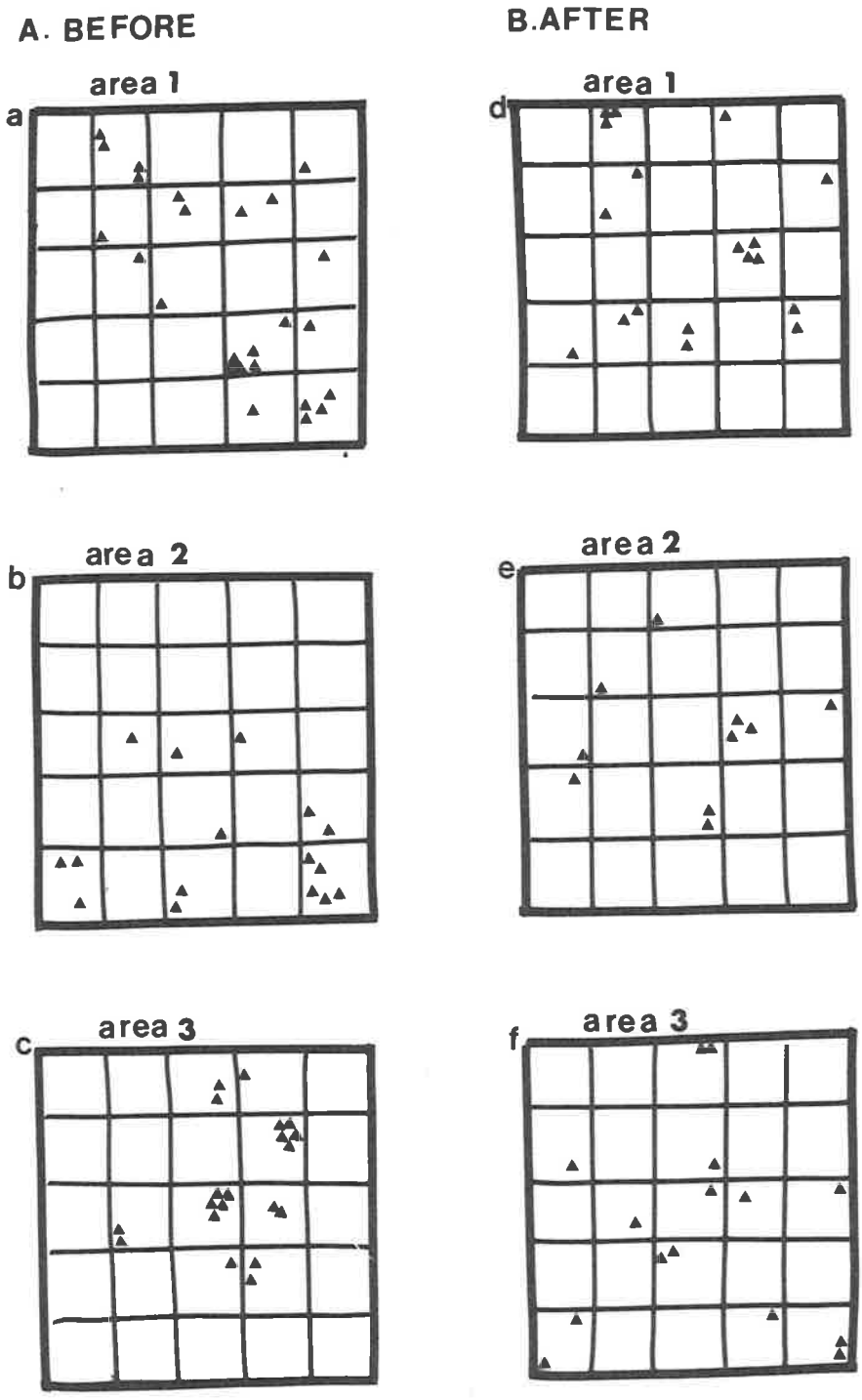
3.3.3 OBSERVATION AND DISCUSSION

The data obtained are presented in Table 3.1. At every recording, some snails were observed in their respective areas and some had moved away from them. This happened in all three areas. The snails outside the areas were usually recorded on the left and right of the square and these snails might be recorded back in the area at the next recording. The maximum distance moved by a snail during that study period was 110cm. away from the area, but those that had moved that far were recorded again in or near the area in the next recordings. Those which were observed in the square did not stay permanently in their original position. They moved around in the area. During that

TABLE 3-1 DAILY RECORDS OF THE SNAILS IN AND OUT OF THE AREA

Date	Area I		Area II		Area III	
	No. of snails		No. of snails		No. of snails	
	in the area	outside the area	in the area	outside the area	in the area	outside the area
19.12.72	25	-	16	-	20	-
20.12.72	23	2	15	1	17	3
21.12.72	17	8	14	2	10	10
22.12.72	11	14	9	7	13	7
23.12.72	11	14	6	10	4	16
24.12.72	10	15	11	5	10	10
25.12.72	13	12	14	2	12	8
26.12.72	15	10	14	2	11	9
27.12.72	17	8	12	4	10	10
28.12.72	14	11	11	5	10	10
29.12.72	12	13	8	8	13	7
30.12.72	14	11	10	6	14	6
31.12.72	17	8	11	5	12	8
1. 1.73	20	5	7	9	10	10
2. 1.73	19	6	10	6	15	5

FIG.3-3 Position of the snails in the area before recording and final positions after the experiment.



fortnight daily recording period, I observed every individually marked snail to move out and return to the area. However, I did not observe any snail back in its original position on their return. The last records of the snails I have taken in that fortnight period is as in Fig. 3.3B (d,e and f).

The snails in all three plots were observed to have moved on their respective walls, usually in a horizontal direction and movements upwards or downwards rarely took them outside the areas and then even for only short distances. If the snails should continue to move from where they have stopped after the previous active period, in their next active phase, I would at least record some snails from plot I in plot II or vice versa, since area I and area II were at right angles to each other. It was noted that for the duration of this experiment, no snails from area I passed around the corner to area II or those from area II to area I.

I kept on checking the snails on my fortnightly field trips after this. However, I was able to continue only with area III, since areas I and II were spoilt by holiday makers. Friends at Second Valley saw holiday makers pick the marked snails from areas I and II and place some of them on the piers of the jetty. I found these distrubed snails on the piers on my field trips, but the snails in the undisturbed area III were still found in or around the area till the end of my field study in November 1973.

In one experiment, I swapped 50 marked snails from the proximal end of the jetty wall with 50 marked snails inhabiting the rock surfaces at the distal end of the jetty. These swapped snails were observed in their newly placed areas. This observation conflicts with Gowanloch and Hayes (1926) who presented evidence, from observations on marked specimens, that winkles migrate back to the particular level on which they normally dwelt, after displacement to other situations.

Overall conclusion of the observation with Littorina unifasciata shows that the snails return to similar but not necessarily identical positions, and that if removed from the place where they dwelt, their chances of returning to the area is low, which is similar to the behaviour observed in L. littorea by Newell (1958a).

Wilson (1929) has noted that Littorina littorea attached to the substratum with a rim of mucus, would easily be toppled over by a puff of light wind. If so, the zonational position of the snails would be readily disturbed. This statement conflicts with the observation I have made on Littorina unifasciata.

The observation area in Second Valley is open to strong winds. During my study a strong gale with wind speed up to 60 m.p.h. occurred on the 28th of June, 1972. The bridge over the archway was blown off and some of the boat sheds in that area were wrecked. However, I still found my marked snails of 1971 after that bad weather.

Firmer adhesion results when the foot is partly extruded and makes contact with the substratum. This normally happens when the habitat is wetted. This form of attachment to the rock surface can replace the attachment of the shell lip to the substratum, which occurs when the rock is dry.

This form of firmer attachment with the foot and the mucus secreted would help the snails to maintain their zonational position during very rough weather.

3.4 MAINTENANCE OF THE SNAILS IN THE LABORATORY

3.4.1 INTRODUCTION

A technique for the maintenance of Littorina pintado was published by Chu and Edwards (1960). The technique used was a closed system which consisted of a large jar inverted over a finger bowl. This method was established because of the failure of maintaining the snails in the aquarium.

Pilkington (1971) who worked on the two New Zealand species Melarapha cincta (Quoy and Gaimard) and M. oliveri Finlay on their breeding and spawning maintained the snails in a closed system similar to the published technique and she found that snails do not spawn freely, nor did copulation occur under laboratory conditions. Only one copulating pair was seen in her study. Struhsaker (1966) did detailed comprehensive life history studies on three Hawaiian littorinid species, Littorina pintado (Wood), L. picta Philippi, and L. scabia (Linne). In her laboratory, snails copulated infrequently,

even when the substratum was moist and humidity high. She only observed two actual copulating pairs during her study. She has no explanation for this and suggested that possibly water movement is necessary.

The method I have used in maintaining the snails of my study in the laboratory is developed from field observation. It is very simple and mating and spawning of the snails occur freely in the laboratory.

3.4.2 MATERIAL AND METHOD

The snails were collected from the breakwater at Glenelg, old piers at Port Willunga or from the jetty wall and rocks at Second Valley (Figs. 3.2 and 3.4).

In testing the methods, square aquaria approximately 30cm. in each dimension were used. Different treatments were given to the snails in each aquarium. Then after achieving the suitable method of maintenance, petri dishes of approximately 20cm. in diameter and 4cm. in depth were used, instead of an aquarium, because it is easier to manage small containers than big ones in maintaining the snails. In describing the treatment, I have categorised them as Methods (a), (b) and (c). Both species, Littorina unifasciata and L. praetermissa were kept together in the same container. In Methods (a) and (b), each aquarium contained over 100 individuals of L. unifasciata and over 50 individuals of L. praetermissa.

Figure 3-4 A. Breakwater of Glenelg.

B. Old piers of Port Willunga.

FIG.3-4

A

B

Method (a)

The snails were kept in the aquarium together with pieces of wood and rocks collected from the field. Pieces of wood were kept under the rocks, in order to prevent them from floating when the sea water was added. Then sea water was filled to a depth of about 9cm. just enough to submerge the snails and pieces of wood and rocks. No water movement was caused.

Method (b)

The snails were kept in the aquarium as described in Method (a). However, water movement was caused in the water by passing air through 6 air bubblers which were held down by rocks to prevent them from floating around in the aquarium. The air passed created vigorous water movement and caused splashes over the snails present in the aquarium. This condition was applied from 1-2 hours. Then the water was completely sucked away by a suction pump, thus leaving the substratum the snails were on, just wetted.

Method (c)

Sea water was added to containers with the snails which were attached to pieces of wood and rock and the dish shaken, so as to stimulate the snails in extruding the foot and use it as means of adhering. The shaking of the petri dish with the snails and the sea water was done from 5-10 minutes. Then the water was completely sucked away with the suction pump. This treatment was repeated from 3-4 times. Then this container with the treated snails was put in an aquarium, where there was a level of sea water enough to submerge it.

The air bubblers were placed in the dish held down with pieces of rocks and caused splashes on the snails, when the air was passed. This was done from 30-60 minutes. Then the dish was taken from the aquarium together with the snails and pieces of wood and rocks. The water in the dish was completely sucked away leaving the substratum just wetted.

3.4.3 OBSERVATION AND DISCUSSION

In method (a) where the snails were kept submerged without any water movement, most of the snails crawled above the water level and crawled onto the glass wall of the aquarium or out of the aquarium and adhered themselves to the dry substratum. Others remained quiescent on rocks or wood or aggregated on the floor of the aquarium. I did not observe the snails feeding or mating using this method.

It has been noted in the field that activities of the snails began when they were splashed by waves. The habitat at supralittoral fringe is rarely submerged and if submerged the water is never still. There is always water movement caused by the wave action. The snails inhabiting the supralittoral fringe would thus be adapted to these conditions. Hence, the snails maintained as in Method (a) would not behave normally, since required conditions were not applied.

Method (b) treatment is most suitable in stimulating the snails to activity. Soon after water movement has been created, the snails extruded the foot and once the foot hold is secured, the snails

remained firmly attached to the substratum, while vigorous splashes were maintained. The snails could not be easily dislodged by the splashes or sucked up by the suction pump at this stage. However, those which did not have the strong foot hold could be readily sucked up together with the water into the bottle fitted to the suction pump system. Of those which were firmly adhered to the substratum continued to feed and mate after the water had been completely sucked away and assumed their manner of attachment with a rim of mucus when the substratum dried up.

The snails which were accidentally sucked away by the suction pump, crawled up the water level in the bottle and aggregated on the bottle wall. The snails remained attached with the foot but they were quiescent. The condition in the bottle is similar to the closed system described by Chu and Edwards (1960). From what I have observed of the snails in the bottle, it shows that the snails may survive in a closed system for quite some time, but normal behaviour such as mating and spawning would not occur, since they were not encountering normal environmental conditions. Thus it would not be appropriate to maintain the snails in a closed system in order to study their mating and spawning behaviours.

The snails behaving with the treatment given as in Method (b) shows that the snails are encountering conditions which they are well adapted to in their natural habitat.

No tidal cycle was created in the laboratory, and only artificial conditions similar to wave splashes was applied. This

stimulus was applied any time of the day and the snails responded readily.

The above fact and the snails not behaving normally when kept in still water as described in Method (a), show that the most affective stimulus, the snails responded to activity is the wave splashes. This is probably the reason, why the snails are easily maintained in the laboratory with the treatment as described in Method (b).

After achieving this method of maintenance, I have kept the snails in the manner as in Method (b). The two species were kept together in the same container. The stimulus was applied daily. Spawning in Littorina unifasciata was once observed on the 23rd of September, 1971, while maintaining process was being carried out. The female was firmly adhered onto the rock, while fertilized eggs were being released into the water in the aquarium.

Method (c) was introduced because mating pairs usually occurred on the floor of the container. The insertion of the penis can only be seen from the ventral view. Petri dishes being small and light are easier to lift up and the whole process of mating can be seen from the ventral view through the glass bottom. However, the treatment given in Method (c) is just a modification of Method (b).

Further techniques in creating splashes could be developed from this method of maintenance, but since this simple and inexpensive device of maintenance served the purpose of my study, I did not go further into the aspect.

3.5 LABORATORY STUDIES OF LITTORINA UNIFASCIATA AND L. PRAETERMISSA

This study is a supplement to field observations. Obs rvation of the activities of animals crawling on clear glass allows various living processes to be seen.

The snails were stimulated to activity by causing water movement in the container with the snails either by passing air through the water or by squirting the water with a syringe on the snails before placing them in small petri dishes of approximately 12cm. in diameter and 2cm. in depth.

3.5.1 FOOD AND FEEDING BEHAVIOUR

Microscopic algae grow on the supralittoral rocks and piles. Both species are browsers and can be observed rasping food off the substratum. The faeces examined of both Littorina unifasciata and L. praetermissa ~~consist~~ contains of minute pieces of rocks from the snails collected from breakwaters at Glenelg and Second Valley and minute pieces of wood from those collected from old piers at Port Willunga. This suggests that the snails would rasp off anything (e.g. detritus, loose part of the substratum) from the substratum together with microscopic algae. If so, impressions on the rocks or wooden piles could be caused by the snails.

In the laboratory, the snails were placed in a petri dish smeared with a culture Dunaliella sp., and these snails were observed

rasping the Dunaliella off the dish. Rasping motion of the snails can be noted by the radula protruding and retracting alternately on the floor of the petri dish. This behaviour is observed frequently as the snails crawled about.

The captive snails were fed with microscopic algae growing on the pieces of rocks and wood collected from the field and cultured Dunaliella sp. smeared on the wall of the container. The snails feed freely on the food given. This could be noted by the large quantity of faeces present in the water, while the stimulus was applied the next day.

3.5.2 MANNER OF ATTACHMENT

To observe the manner of attachment of the snails which had been stimulated into activity, some were placed in a moist and some in dry petri dishes.

The snails crawled around in both moist and dry petri dishes after placing, but they assumed the manner of attachment in dry petri dish sooner than in the moist one. This would be, because the moist condition in the dish would increase the wetness of the snails, whilst in the dry dish, except for the snails themselves being wetted by the stimulus, there was no supplement to this wetness from the substratum. However, the snails in both petri dishes became quiescent, once the conditions started to dry up and assumed the manner of mucus attachment by the outer lip. This behaviour is most likely to avoid rapid desiccation.

The snails soon after becoming quiescent, drew the head in first. After 25-30 minutes, the foot was drawn forward bringing along with it the mucus secreted. By the time the foot was drawn into the shell, the outer lip of the shell was attached to the substratum with a rim of mucus. This dried in time to give secure attachment (Fig. 3.1).

3.5.3 MATING BEHAVIOUR

Mating behaviour was studied on the aquarium wall and on the bottom of the petri dish. The stimulus was applied as described in Method (b) and (c) (see 3.4.2). The mating behaviour of the two species is described together except when differences occur.

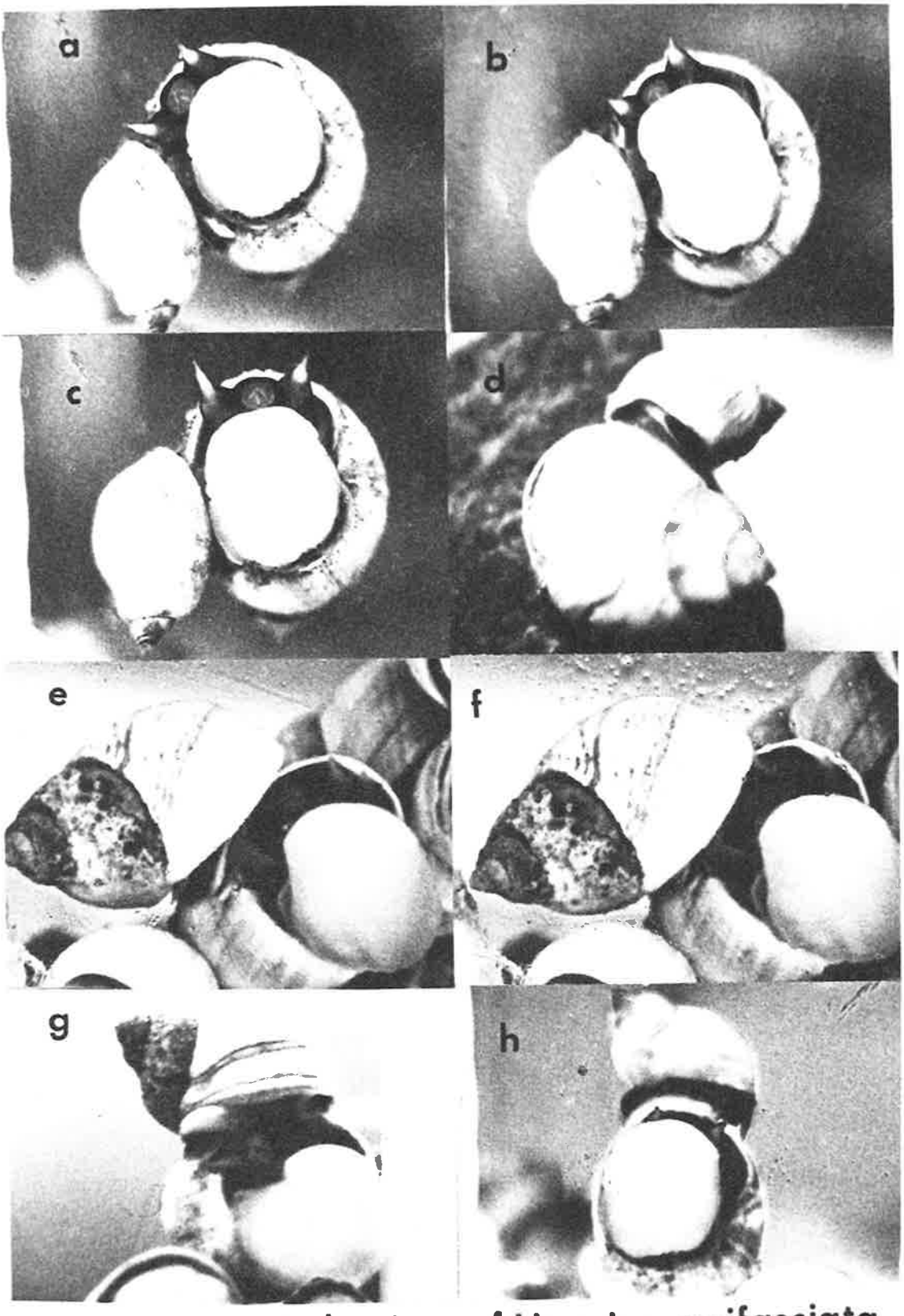
The snails have the tendency of following the path made by another snail. This behaviour could promote the chances of encountering their mating partners. The actual means by which the sexes distinguish each other is not known. It is probably by the sensitivity of the tentacles, since one of the noticeable characters in the snails is the continual movement of the tentacles from side to side as the snails move along.

The male has the tendency to climb onto another snail which it encounters while in search of a mate. Two snails on meeting stroke each other's tentacles. After this behaviour, the male climbs onto the encountered snail. There is no set pattern from which angle the male climbs onto the female. It corrects itself to the right side of the snail underneath, where the female pore is situated.

Figure 3-5

a,b; beginning of mating process
c; mating process in progress (ventral view)
d; mating process in progress (dorsal view)
e&f; nibbling of the penis by the female
g&h; after the mating process

FIG.3-5



The mating behaviour of Littorina unifasciata

When the right position is achieved extension of the penis begins. The extended penis is greatly stretched approximately three times the normal length and it becomes translucent. The longer arm, where the sperm duct runs is first inserted into the female pore and the second arm is drawn in later. The second arm of the penis probably serves as a holdfast. The foot of the male is used in clasping tightly onto the shell of the female. If the snail underneath should be another male, insertion of the penis is attempted, which may last from 2-3 minutes, but the male on top crawled away after that. However if it has found the right mating partner, the penis is properly inserted and it is completely concealed from the view (Fig. 3.5c). The position of the male is more on the side and tightly clasped, when the penis has been inserted and the mating process is in progress (Fig. 3.5d). The whole mating process lasts from 15-25 minutes in Littorina unifasciata and from 30-40 minutes in L. praetermissa.

The elongation of the penis can be observed from the dorsal aspect but the actual insertion of the base of penis can be seen only from the ventral view. However, judging by the position and clasping of the male onto the female and by the time taken, mating pairs can be easily recognised from the dorsal view.

Towards the end of the mating process, just before the withdrawal of the penis, nibbling of the penis by the female is observed in Littorina unifasciata (see Fig. 3.5f) but this behaviour is absent in L. praetermissa. When the process is over, the male

climbs down from the female and goes on his way (Fig. 3.5g and h).

During copulation, the female will feed normally, carrying the male on her shell. The male attached to the female remains immobile after the insertion of the penis. Most work during the process of copulation was carried out by the male. Except in having the penis inserted into the female pore, the process does not affect the activities of the females. However in Littorina unifasciata, the motion of the female stopped just before nibbling of the penis and the head swayed towards the penis soon after and started to nibble (Fig. 3.5e). The nibbling may last from 1-2 minutes.

In the mating pairs of Littorina praetermissa, males are always smaller than the females, whilst it could be of any size ratios in L. unifasciata. Measurements of 72 pairs of the former and 172 pairs of the latter species were recorded (see Table 3.2, Figs. 3-6 and 7).

It was observed that on encountering a mating pair, a male will try to push the mating male off. The success depended on the size and how far the mating process had proceeded. When mating was in progress, the second male had no chance, regardless of the size in dislodging the mating male off the female. However, if the mating had just begun, the male of larger size had the advantage, whether it encountered the female first or later. The male which lost the battle went on his way in search of another possible mating partner. The female was not affected by the disturbance. She had no

TABLE 3-2 SIZE RATIOS IN THE RECORDED MATED PAIRS OF LITTORINA UNIFASCIATA AND L. PRAETERMISSA

Littorina unifasciata								Littorina praetermissa		
Size ratios of mating pairs		No. of mated pairs	Size ratios of mating pairs		No. of mated pairs	Size ratios of mating pairs		No. of mated pairs	Size ratios of mating pairs		No. of mated pairs
6mm.	8mm.	2	10mm.	10mm.	1	13mm.	15mm.	1	6mm.	8mm.	1
	10mm.	1		11mm.	3	14mm.	9mm.	1		9mm.	1
	12mm.	5		12mm.	9		10mm.	2		11mm.	6
	16mm.	3		13mm.	1		11mm.	1		13mm.	9
7mm.	7mm.	2		14mm.	6		12mm.	3		16mm.	3
	9mm.	3	11mm.	8mm.	1		15mm.	2	7mm.	10mm.	1
	10mm.	6		9mm.	4	15mm.	9mm.	3		11mm.	2
	11mm.	1		10mm.	2		11mm.	2		13mm.	12
	12mm.	2		11mm.	3		12mm.	1		14mm.	10
8mm.	9mm.	3		12mm.	1		16mm.	1		15mm.	1
	11mm.	1		13mm.	7					16mm.	2
	12mm.	4		14mm.	3				8mm.	9mm.	1
	13mm.	1		15mm.	1					10mm.	1
	14mm.	4	12mm.	9mm.	2					11mm.	2
	15mm.	6		10mm.	4					12mm.	1
	16mm.	2		11mm.	2				9mm.	10mm.	1
9mm.	9mm.	7		12mm.	6					11mm.	1
	10mm.	3		13mm.	3					12mm.	1
	11mm.	2		14mm.	4					13mm.	1
	12mm.	4		15mm.	1					15mm.	5
	13mm.	2	13mm.	8mm.	2				10mm.	11mm.	1
	14mm.	3		9mm.	1					12mm.	1
	15mm.	6		10mm.	5					13mm.	1
10mm.	8mm.	2		12mm.	1					14mm.	5
	9mm.	3		13mm.	4					15mm.	1
									12mm.	16mm.	1
Total no. of mated pairs 172									Total no. of mated pairs 72		

FIG. 3-6 Shell heights of males against shell heights of females in the mating pairs of Littorina unifasciata.

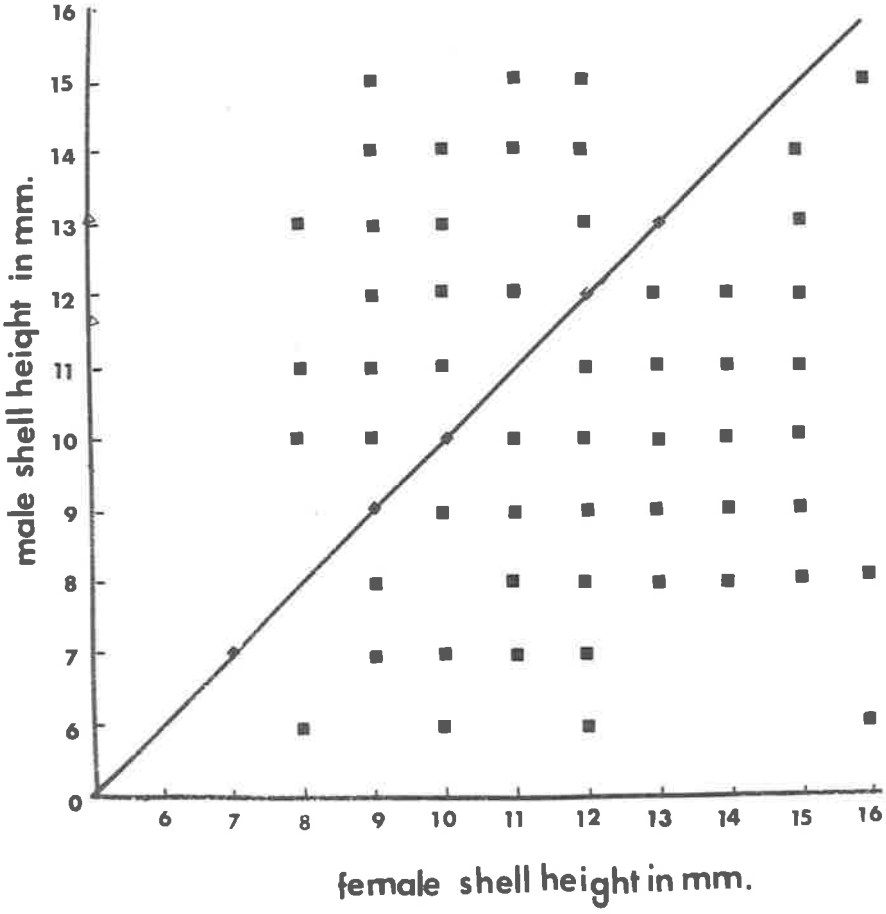
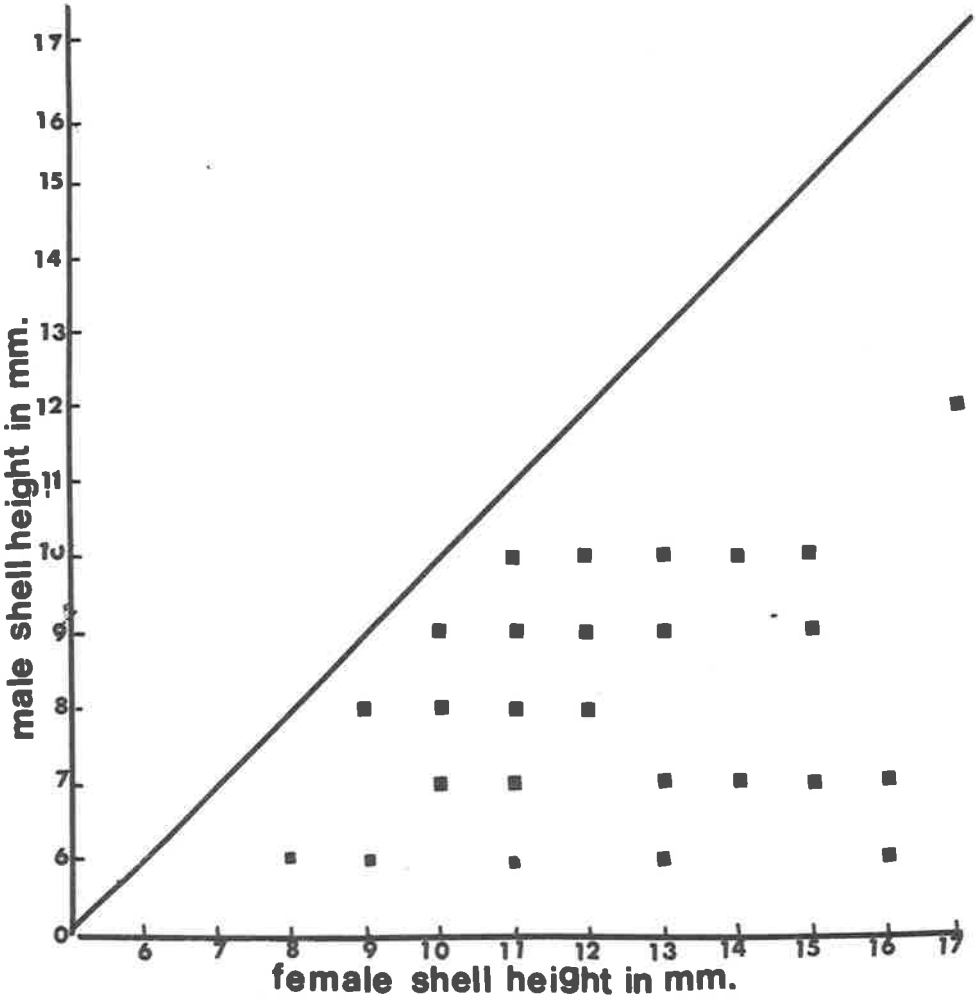


FIG. 3-7

Shell heights of males against shell heights of females in the mating pairs of Littorina praetermissa.



priority for whichever male climbed on her first or later. She contentedly carried on the mating process with the male which remained on her.

A female mating with two males at the same time was observed once in the laboratory. The mating process was observed on the wall of the aquarium. Thus the actual inserted penes of the two males in the same female pore were clearly seen.

Although Littorina unifasciata and L. praetermissa were maintained in the same container and the snails responded to the same stimulus in mating, I did not observe any interspecific mating. It has been observed that the tentacles in the snails of both species are continuously moving from side to side, which suggests to be feeling around when they are in activity. This behaviour may be a means of detecting its own species. The sculpture of the shell morphology differ distinctly between the two species. The shell of L. praetermissa is of coarser spiral sculpture compared to that of L. unifasciata (see Fig. 2-3). Thus by the sensitivity of touch, the snails would be able to recognise its own species by the shell morphology.

3.6 DISCUSSION AND CONCLUSION

Supralittoral fringe is an arid zone, subject to conditions transitional between those of land and sea. It represents the upper fringe of tidal area, the boundary strip between land and the sea (Stephenson and Stephenson 1972). This area is affected by spray,

but wetted by waves only in the heavy weather or at higher spring tide, when at least its lower parts become washed or submerged.

Animals inhabiting this area are well-adapted to the hazardous conditions of their habitat, and went through an immobile phase, while the habitat is devoid of sea water. When the substratum is dry and while in immobile phase, the snails are completely concealed inside the shell with the operculum serving as a shutter and attached themselves to the substratum by the outer lip of the shell with a rim of mucus. This is the outstanding character of littorinid species inhabiting the supralittoral fringe. "This device would be to avoid rapid desiccation" (Newell 1958a).

It is a general feature of the supralittoral fringe that the sea level reaches this area only during high tide. Thus the contact of the snails with sea water is greatly dependent on the tidal ranges. The tides are subjected to a progressive change in the amplitude of rise and fall according to the phase of the moon. It is at a maximum just after the new or full moon and at minimum at intermediate phases of the moon (neap tides). Furthermore, the actual magnitude of rise and fall during spring and neap tides varies according to more complex factors ([redacted]) which result not only in the well known equinoctial spring tides of especially large amplitude but also in large diurnal inequalities between the two tides of the day in some parts of the world. The diurnal inequality is featured principally in the tide levels in South Australia (Stephenson and Stephenson 1972).

Taking the above facts into account, the snails of supralittoral fringe will go through critical periods during mean [redacted] of neap tides. The habitat could be exposed to air for days. In studying with Littorina unifasciata and L. praetermissa, I find that the captive snails can survive without sea water for over a month period. The snails are well-adapted to the hazardous conditions. Animals living high in the intertidal zone are in general better adapted to resist the extremes of the physico-chemical environment than their encounter parts lower on the shore. Almost all intertidal animals are also found to be well-adapted for life in the particular zone which they live (Newell 1972).

Although the littorinid species of supralittoral fringe are greatly durable to extreme conditions, they were noted difficult to be maintained in the laboratory. The laboratory studies on these snails are rare. Of a few which were studied in the laboratory, it was observed that the snails did not copulate freely in the captive stage (Struhsaker 1966 and Pilkington 1971).

As far as I am aware, I have not come across any published technique to maintain the snails successfully in the laboratory. However, I have found the two species of my study feeding, copulating and spawning freely in the laboratory with the method I have achieved, and the external stimulus the snails responded shows mainly to be the water splashes.

CHAPTER IV. BREEDING AND SPAWNING OF LITTORINA UNIFASCIATA AND L. PRAETERMISSA

4.1 INTRODUCTION

A diversity of reproductive types is found within the family Littorinidae. Littorina saxatilis (Olivi) and L. angulifera Lam; are viviparous (Lebour 1937, 1945); L. littoralis lays gelatinous egg masses and fastens them on to the fronds of the fucoids amongst which it lives (Lebour 1937), but the majority release planktonic egg capsules and the young pass through a free swimming veliger stage before metamorphosis.

The breeding and egg capsules of Japanese littorinids were studied by Kojima (1960), and the spawning and egg capsules of some Bermudan species has been described by Lebour (1945). However very few studies on the breeding and spawning have been studied in the laboratory. Of the spawning experiments which are conducted in the laboratory, the maintenance of the snails has been a problem. Struhsaker (1966) has made a study on detailed comprehensive life histories of three Hawaiian littorinid species, Littorina pintado (Wood), L. picta Philippi and L. scabra (Linne) by conducting laboratory spawning experiments with collected field mated females and Pilkington (1971) of two New Zealand species Melarapha cincta (Quoy and Gaimard), and M. oliveri Finlay. Differences between the littorinid species are well marked in the breeding habits and the sculpture of the egg capsules, in those which release planktonic spawn.

Although the snails of supralittoral fringe might almost be expected to be semiterrestrial in habit, their life history is very dependent on the sea, especially those which release planktonic spawn. Previous workers on the snails occupying this area (e.g. Struhsaker (1966) and Pilkington (1971)) have mentioned that the snails did not copulate or spawn readily in the laboratory.

The two Australian species Littorina unifasciata and L. praetermissa also inhabit the supralittoral fringe. The mating and spawning of these two species have not hitherto been reported on. However, I have succeeded in stimulating the snails to mate readily in the laboratory (see 3.4.3) and have studied the factors involved in spawning in the two species. I have conducted spawning experiments with laboratory mated females and also with a few which were collected in the field.

The breeding season of the species was determined by the examination of the gonads of specimens collected regularly from the field and from their spawning period.

4.2 DEVELOPMENTAL STAGES

4.2.1 MATERIAL AND METHODS FOR EXAMINING THE DEVELOPMENTAL STAGES OF THE GONAD

The snails were collected regularly from Glenelg, Port Willunga and Second Valley on fortnightly field trips throughout this study. To avoid depleting their small population, samples of Littorina praetermissa were limited in numbers. The number of snails

collected were approximately 30 of L. unifasciata and approximately 10 snails of L. praetermissa from each locality for gonad study and maintenance.

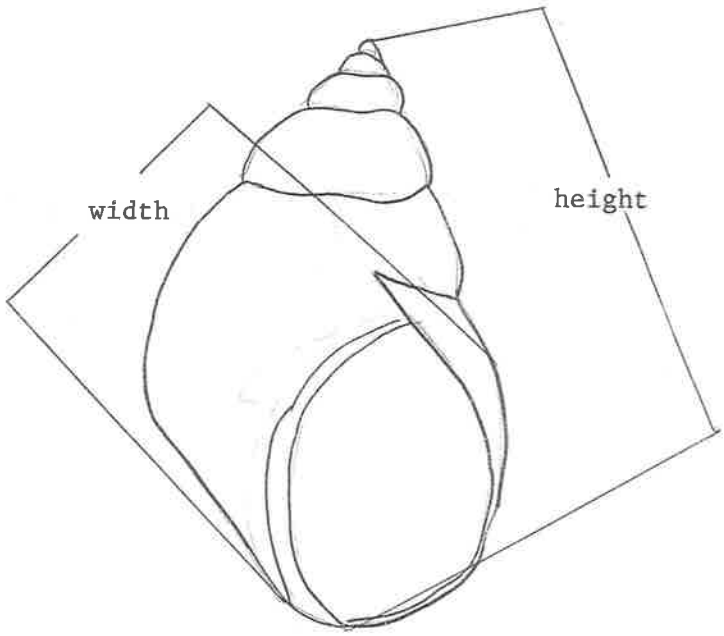
In the beginning of the study, approximately 10 snails of each sex in Littorina praetermissa and 20 of each sex in L. unifasciata were examined every fortnight. As the sexes of the snails could not be distinguished externally, I picked some snails randomly from the collected samples and induced mating by splashing the animals with sea water (see 3.4.3). The sexes could then be distinguished by their behaviour.

As the study advanced and adequate observations were obtained to show the different breeding periods of each species, the number of snails examined was reduced.

The gonad is a branching organ in both sexes of Littorina unifasciata and L. praetermissa. The way in which the branches of the gonad are distributed amongst the lobules of the digestive gland differs with different developmental stages. The ovary changes in colour as the mature eggs predominate over the immature ones. The mature eggs are spherical, whilst the immature eggs are irregular. Measurements of the mature eggs were taken with an eye-piece micrometer under a compound microscope. The testicular duct in the males becomes swollen and distinct, when filled with spermatozoa. Thus visual assessment is possible in studying the different stages. Then by studying the developmental stages with the gonad examination, the breeding season of two species can be followed.

The snails are usually found in groups in their natural habitat. Each group may consist of various sizes from the biggest to the smallest. Hence for all work on sex ratio and sexual dimorphisms, every specimen in groups of snails were collected. Measurements of the shells were taken with a vernier caliper. The maximum height and width utilized is as in the following Figure 4-1.

Fig. 4-1. Dimensions of the snail utilized



Over 200 individuals of Littorina unifasciata and over 50 of L. praetermissa from each study locality were collected as above to determine the sex ratio.

4.2.2 OBSERVATION

4.2.2.1 SEX RATIO

The sex ratios of the two species determined from the snails collected from Glenelg, Port Willunga and Second Valley were approximately 1:1 in each locality (see Table 4-1).

TABLE 4-1 SEX RATIO OF LITTORINA UNIFASCIATA AND L. PRAETERMISSA SAMPLED FROM THE THREE STUDY AREAS

Species	Locality	Total no. of snails	♂	♀	Percentage ♂	Percentage ♂	*95% confidence limits for %♂
Littorina unifasciata	Glenelg	261	132	129	50.6%	49.4%	44.90-57.08%
	Port Willunga	232	121	111	52.2%	47.8%	45.47-58.45%
	Second Valley	246	131	115	53.3%	46.7%	46.67-59.25%
	Total	738	384	355			
Littorina praetermissa	Glenelg	79	32	47	40.5%	59.5%	23.98-52.87%
	Port Willunga	87	37	50	42.5%	57.5%	32.54-53.94%
	Second Valley	101	45	56	44.6%	55.4%	35.09-57.17%
	Total	267	114	153			

* From Rohlf and Sokal (1969) p. 212.

4.2.2.2 SEXUAL DIMORPHISM

It was observed in the mating pairs of Littorina praetermissa that the male is smaller than the female, whereas in L. unifasciata, mating pairs were of varying size ratios (see Figs. 3-6 and 3-7). However, the comparison made between the shell heights and shell widths of males and females from the measurements recorded showed sexual dimorphism in both species (see Table 4-2 and 4-3).

TABLE 4-2 COMPARISON BETWEEN MEAN SHELL HEIGHTS OF MALES AND FEMALES IN LITTORINA UNIFASCIATA AND L. PRAETERMISSA

Species	Sex	No. of snails	Range shell height mm.	Mean shell height mm.	*Varn.	*Varn. ratio	*"t"	*d.f.	Probability
Littorina unifasciata	♂	384	3.2 15.7	10.28	3.23	1.08	2.65	∞	.001<P<.01
	♀	355	3.2 15.9	10.81	2.98				
Littorina praetermissa	♂	114	3.2 14.8	9.23	1.36	2.46	2.93	∞	.001<P<.01
	♀	153	3.2 15.4	10.11	3.34				

* Varn. = Variance, "t" = Invented "t", d.f. = degree of freedom.

TABLE 4-3 COMPARISON BETWEEN MEAN SHELL WIDTHS OF MALES AND FEMALES IN LITTORINA UNIFASCIATA AND L. PRAETERMISSA

Species	Sex	No. of snails	Range shell width mm.	Mean shell width mm.	*Varn.	*Varn. ratio	*"t"	*d.f.	Probability
Littorina unifasciata	♂	384	2.8 11.4	8.27	1.88	1.03	3.07	∞	.001<P<.01
	♀	355	2.8 12.4	8.70	1.94				
Littorina praetermissa	♂	114	2.8 11.4	7.73	1.85	1.47	3.27	∞	.001<P<.01
	♀	153	2.8 12.1	8.58	2.32				

* Varn. = Variance, "t" = Invented "t", d.f. = degree of freedom.

The measurements were recorded from the snails which were also used in determining the sex ratio. Although the snails were collected from three different localities, the range and the mean in shell heights and widths are similar. Therefore, I have presented them all together in the same table.

Though there is sexual dimorphism in the mean shell heights and shell widths, the ranges overlap to a large extent in both species. Hence, males and females could not be distinguished by their size. Sexes were confirmed only after examining for the presence or absence of the penis, and from mating pairs, when the actual mating process had been observed.

4.2.2.3 SEXUAL MATURITY

Sexual maturity is reached at a [redacted] height of approximately 3mm. in both sexes of Littorina unifasciata and L. praetermissa. Although mature spermatozoa and mature eggs are predominant at sexual maturity, immature stages are still present, since all spermatozoa or all eggs do not necessarily mature at the same time. At this stage the branches of the gonads thrust themselves amongst the lobules of the digestive gland and take up space wherever available and the gonad is conspicuous and lobular.

The branches of the gonad in both sexes of the two species are minute and sparsely distributed amongst the lobules of the digestive gland in the early stage of development. The colour of the testis is light pinkish brown in Littorina unifasciata and it is light yellowish brown in L. praetermissa. The colour of the ovary is green in the former and light pink in the latter at this stage.

As the developing stage proceeds, the branches get larger and take up space wherever available amongst the lobules of the digestive gland, as the mature spermatozoa in the testis and mature eggs in the ovary predominate over the immature ones, and the colour of the gonad becomes darker. The testis of Littorina unifasciata becomes darker shade of pinkish brown and that of L. praetermissa darker shade of yellowish brown. The ovary of the former is yellow and it is dark pink in L. praetermissa. The testicular ducts in the males are distinct and the eggs in the columellar part of the ovary

mature first before the rest. This could be recognised by a thick yellow or pink patch on the columellar region with each respective species.

Then in the maximum of the breeding condition, the gonad is very lobular and conspicuous superficially spread all over the digestive gland. The testicular ducts in the males are distinct and swollen with spermatozoa. The associated reproductive glands in the females, such as the capsule gland, the covering gland and the albumen gland in the females are very distinct, rigid and swollen. Immature spermatozoa and immature eggs are greatly predominated by the mature ones at this stage.

Littorina unifasciata breeds throughout the year and all developmental stages are present in the gonad of both sexes at all times of the year. Once developed, the penis in the males and the reproductive glands of both sexes remain unchanged throughout the year.

Littorina praetermissa on the other hand has a limited breeding period. Towards the end of November till the end of March the snails are in resting condition. At this stage, no trace of gonad is visible on the digestive gland. Reduction in the size of the penis in the males and capsule gland, covering gland and albumen gland in the females are observed. Therefore, the developing stages from early stage to mature breeding stage can be clearly recognised in this species.

The changes in the gonad through the breeding cycle of Littorina praetermissa are shown in Table 4-4.

TABLE 4-4 DEVELOPMENTAL STAGES IN LITTORINA PRAETERMISSA

Definition of developmental stages	Male		
	penis	gonad	testicular duct
1. Recovering spent	distinct but not very developed	minute white branches of testis sparsely distributed amongst the lobules of the digestive gland (Fig. 4-2B)	faint duct without any spermatozoa
2. Maturing	well developed and prominent	yellowish brown branches of the testes compact over digestive gland (Fig. 4-2C)	distinct with some matured spermatozoa
3. Fully mature	the two arms well developed with glandular white edges (app. 2mm.) (Fig. 2-13A)	lobular branches of the testis extensively spread amongst the lobules of the digestive gland (Fig. 4-2D)	distinct, swollen filled with matured spermatoza
4. Partially spent	prominent and glandular	except for a patch of testis on the columellar region, the rest is hardly visible	distinct with matured spermatoza
5. Spent	vestigeal (Fig. 2-13Bp)	faint branches of testis hardly visible (Fig. 4-2A)	faint duct without any spermatoza

Table 4-4 continued overleaf

Figure 4-2 Developmental stages of the testis in Littorina praetermissa

a) spent stage
b) developing stage (Recovering spent)
c) partial breeding stage (Maturing)
d) breeding stage

The condition of the partial spent stage is similar to partial breeding stage. col rgn, columellar region; te, testis; dg, digestive gland; td, testicular duct.

FIG. 4-2

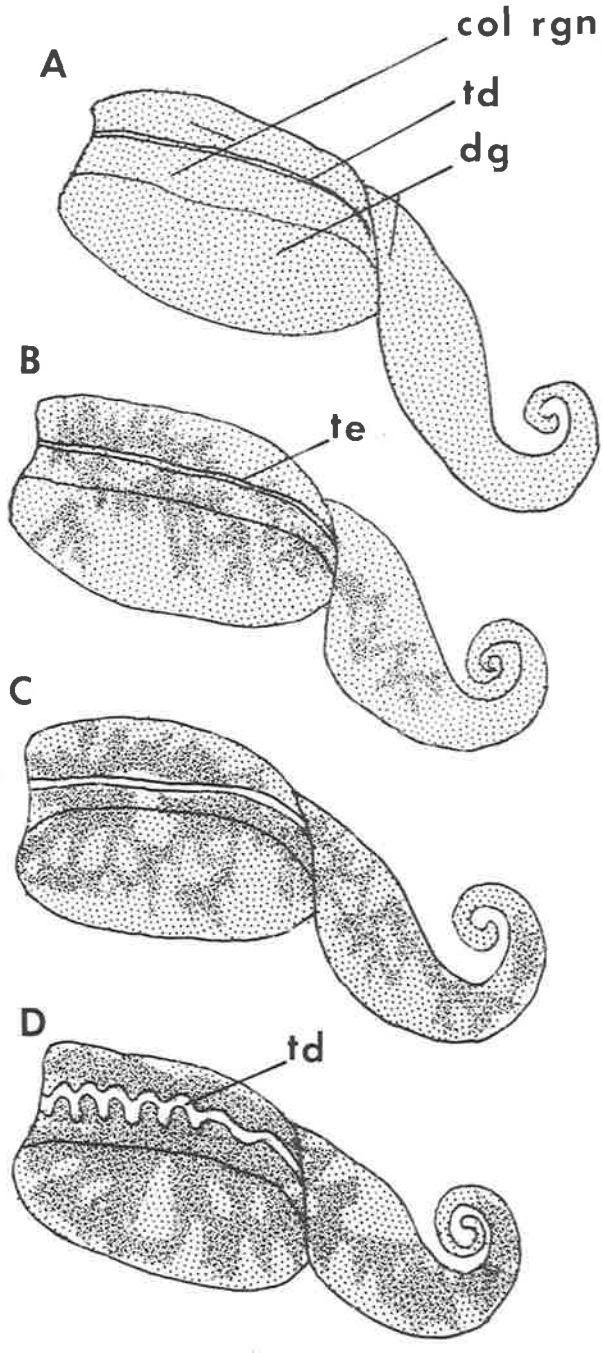


TABLE 4-4 DEVELOPMENTAL STAGES IN LITTORINA PRAETERMISSA (continued)

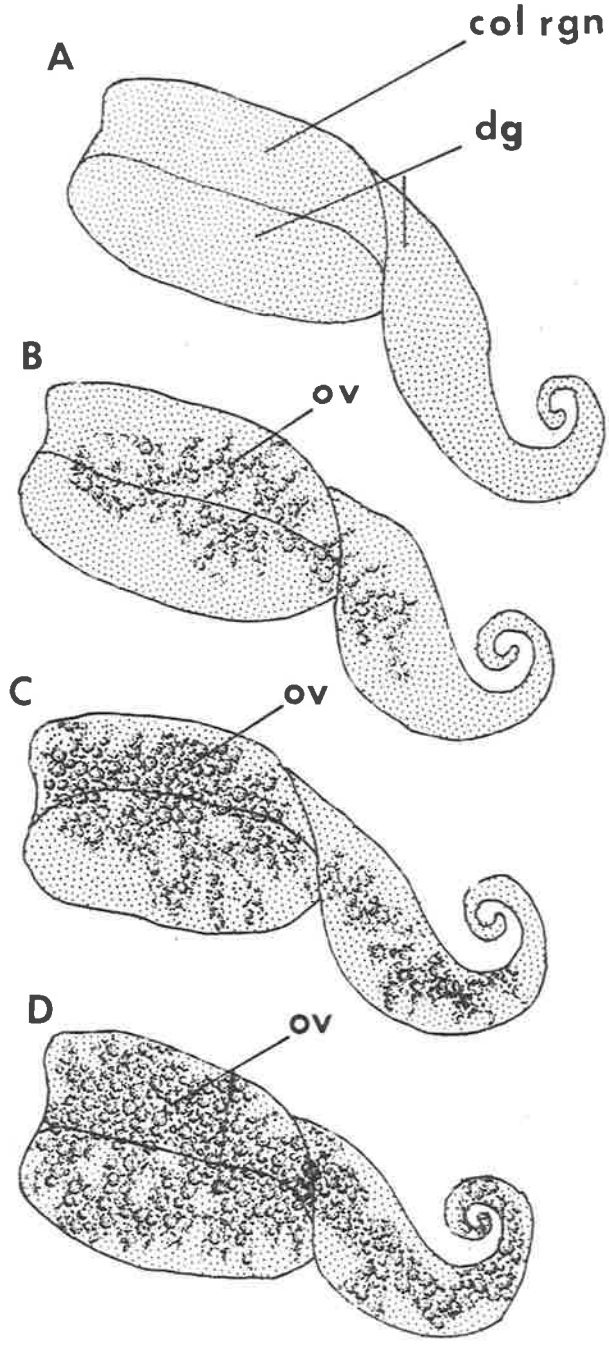
Definition of developmental stages	capsule gld, covering gld and albumen gld	Female Receptaculum seminis	gonad
1. Recovering spent	the glands distinct but not swollen	not visible	light pink minute branches of the ovary sparsely distributed amongst the lobules of the digestive gland (Fig. 4-3B)
2. Maturing	swollen distinct and white; distinct brown, distinct greyish brown	minute white streak	mature pink eggs intermingled with immature ones are present on the columellar region (Fig. 4-3C)
3. Fully mature	conspicuous, rigid and white; distinct brown; distinct greyish brown	prominent white streak	conspicuous, lobular branches of ovary mostly with pink mature eggs extensively spread amongst the lobules of the digestive gland (Fig. 4-3D)
4. Partially spent	the glands still distinct and conspicuous	white streak	except for a compact area of ovary on the columellar region with pink mature eggs, the ovary is hardly visible
5. Spent	flat creamish brown mass (Fig. 2-13D)	not visible	faint branches of ovary hardly visible amongst the lobules of the digestive gland (Fig. 4-3A)

Figure 4-3 Developmental stages of the ovary in Littorina praetermissa

a) spent stage
b) developing stage (Recovering spent)
c) partial breeding stage (Maturing)
d) breeding stage

The condition of the partial spent stage is similar to partial breeding stage.
ov, ovary; dg, digestive gland; col rgn, columellar region.

FIG. 4-3



4.2.2.4 BREEDING SEASON OF LITTORINA PRAETERMISSA

From the study of the developmental stages, the breeding season of Littorina praetermissa was determined as in Table 4-5.

TABLE 4-5 BREEDING SEASON OF LITTORINA PRAETERMISSA

Month	Males					Females				
	*1	2	3	4	5	1	2	3	4	5
January	-	-	-	-	+	-	-	-	-	+
February	-	-	-	-	+	-	-	-	-	+
March	-	-	-	-	+	-	-	-	-	+
April	+	-	-	-	+	-	-	-	-	+
May	+	+	+	-	-	+	-	-	-	+
June	-	-	+	-	-	+	+	+	-	-
July	-	-	+	-	-	-	-	+	-	-
August	-	-	+	-	-	-	-	+	-	-
September	-	-	+	-	-	-	-	+	+	-
October	-	-	+	+	-	-	-	+	+	-
November	-	-	-	+	+	-	-	-	+	+
December	-	-	-	-	+	-	-	-	-	+

* The number in the table corresponds to developmental stages in Table 4-4. - = absent, + = present.

The males of Littorina praetermissa come into breeding condition earlier than the females. Recovering spent males are observed in early April, and towards the end of May, most of them are in breeding condition, whilst the females approach breeding condition in early May and only towards the end of June are most individuals observed to be fully matured (see Table 4-5).

A few maturing females are observed in early June and copulating pairs started to occur at this stage. Once during this study I came across a mating pair of Littorina praetermissa on the 14th of June 1972. The fertilized eggs of this mated female cultured at this period did not develop successfully into veliger larvae. However, this female mated several times in the laboratory (see Table 4-10), and the spawn after later copulations developed normally into veliger larvae.

Most of the snails come into maximum breeding condition in July and by October most of the snails examined are usually in partial spent condition. Then towards the end of November they are totally in spent condition till the end of March (males) and till the end of April (females) (see Table 4-5). Hence, from this observation, it appears that the breeding period of Littorina praetermissa is rather a short one, approximately 3 months which corresponds with the cold period of the year.

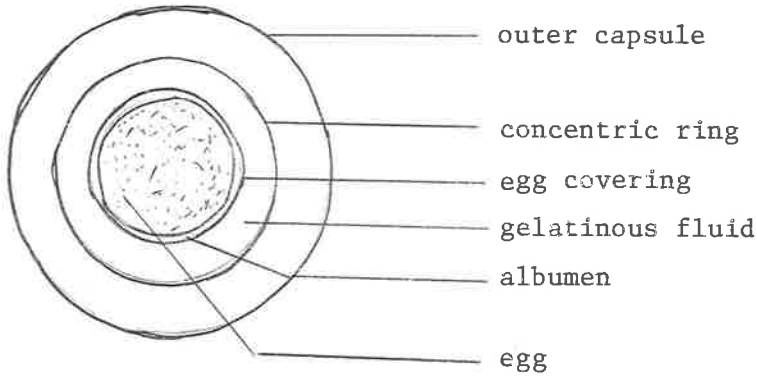
4.3 COPULATION

The copulation process has been described in 3.5.3.

4.4. FERTILIZATION

The fertilized egg of both species consists of an egg covering and an outer egg capsule. There is a gelatinous fluid between the outer capsule and the egg covering; albumen between the inner egg covering and the egg (Fig 4-4).

Fig. 4-4. Fertilized egg in egg capsule (dorsal view).



The receptaculum seminis for the storage of spermatozoa is at the end of the mass of glandular tissue. The eggs descending from the ovary would have to transverse in close proximity to the receptaculum seminis. Then it would pass through the glandular tissue to obtain the respective layers. The albumen gland is the most

posterior section of the pallial oviduct (Fig. 2-12ag), then the covering gland and the capsule gland (Fig. 2-12). Thus, the first layer the fertilized egg obtained would be the albumen, then the egg covering and finally the egg capsule. This hypothesis is logical, thus it seems likely that fertilization takes place, soon after descending from the ovary.

If this should be the case, it suggests that it is essential for the spermatozoa to reach and be stored up in the receptaculum seminis after copulation, before fertilization can take place. To study on this aspect, I dissected the females of Littorina unifasciata which mated at the same time at different intervals after mating and the changes in the structure of the receptaculum seminis were noted. The conditions observed are as presented in Table 4-6.

The change in the structure of the receptaculum seminis from a white streak to a spherical turgid condition shows that the spermatozoa transmitted by the males in copulation have reached the region of storage about four to six hours after copulation.

In studying the spawning behaviour, I have observed that the snails did not spawn readily when stimulated to spawn immediately after mating. However, when stimulated some hours or even days after copulation had taken place, they spawned within 15-30 minutes after the appropriate stimulus had been applied (see 4.5.2.1). Therefore, the storage of spermatozoa in the receptaculum seminis after copulation seems to be one of the factors in initiating eggs to descend from the ovary when the external stimulus is appropriate.

TABLE 4-6 THE STRUCTURE OF RECEPTACULUM SEMINIS RECORDED FROM THE FEMALES OF LITTORINA UNIFASCIATA

Condition of the female	Structure of receptaculum seminis	Measurement of receptaculum seminis	No. of snails examined	Remark
non mated female	white streak	-	10	The measurement of the receptaculum seminis cannot be taken 1-3 hrs. after copulation, because though distinct, it is irregular in shape. When the receptaculum seminis is spherical and turgid, measurement is taken under the compound microscope by placing a marked scale on the receptaculum seminis. The measurements range between 0.4-1.2mm. averaging .8mm. in diameter 4-6 hrs. after copulation.
1 hr. after copulation	white streak	-	10	
2 hrs. after copulation	slight swelling	-	10	
3 hrs. after copulation	distinct swelling white mass	-	10	
4-6 hrs. after copulation	spherical and turgid	approximately .8mm. (average)	20	

Furthermore, the fertilized eggs released are always in a single cell stage in both Littorina unifasciata and L. praetermissa in spite of the different intervals at which the snails are stimulated to spawn after copulation. The developmental time from one cell stage to hatched veliger larva stage is also the same in both species. This fact shows that spermatozoa can be stored in receptaculum seminis for quite some time and that fertilization would take place, only

when the essential external stimulus is encountered.

These mentioned facts have not been looked into with other littorinids. Unfortunately, I was unable to study the structure of the receptaculum seminis of Littorina praetermissa as I have done with L. unifasciata, because of their limited breeding season and their relatively small populations. However, the time taken to spawn after copulation is similar to that of L. unifasciata and I therefore assumed that storage of spermatozoa in the receptaculum seminis is one of the necessary factors in fertilization in L. praetermissa also.

4.5 SPAWNING

4.5.1 INTRODUCTION

In the initial stage of my study (May 1971), eggs with planktonic capsules were observed in the sea water in which I kept mated females of Littorina unifasciata collected from the field. In July (1971) I first came across mating pairs of L. praetermissa. This species was also found to produce planktonic eggs. Laboratory observations show that both species belong to the littorinid group which release planktonic egg capsules.

The spawning periodicity of some littorinid species which release planktonic eggs is found to correlate with fortnightly spring tide and daily high tide. Linke (1935) and Lysaught (1941) have noted in their field observation that spawning of Littorina nereitoides probably occurs during fortnightly spring tides. Tattersall (1920) observed that Littorina littorea(L) liberated capsules an hour or two

after copulation and then intermittently for a month or more, and that these capsules were usually released at night during a high tide period. Struhsaker (1966) has concluded from her laboratory spawning experiments that the two Hawaiian species L. pintado (Wood) and L. picta Philippi spawn only during high tide period. Therefore, in conducting laboratory spawning experiments, I have also looked into this aspect with the two species of my study.

4.5.2 MATERIAL AND METHOD IN TESTING THE RESPONSE OF THE MATED FEMALES TO STIMULUS IN SPAWNING

The laboratory mated females were isolated individually in sea water in petri dishes of approximately 9cm. in diameter and 2cm. in height. Different treatment was given to the isolated females as follows:-

The females used in the experiment were all mated at the same time and the method used applied to both species.

(a) The mated females were isolated immediately after copulation without stimulating them as in (b).

(b) The mated females were isolated immediately after mating but the snails were stimulated before isolation. The stimulus was applied by shaking the snails in a bowl of sea water two to three minutes. Then the water was drained away.

This procedure was repeated from four to five times, before isolating the snails in petri dishes with sea water.

The procedure has to be repeated several times, because it is necessary for the snails to encounter sufficient splashes with sea water.

(c) The mated females were isolated four to six hours after mating without stimulating them as in (b).

(d) The mated females were isolated four to six hours after mating and stimulus was applied as in (b) before isolating them.

Each experiment was repeated with ten snails and was conducted at room temperature. The temperature ranged from 12^{o}-20^{o}C in winter and from 21^{o}-35^{o}C in summer. The breeding season of Littorina praetermissa falls in winter. Thus the spawning experiments with this species were carried out only at winter temperatures. With L. unifasciata which breeds throughout the year, spawning experiments were carried out at varying temperatures of different seasons of the year.

4.5.2.1 OBSERVATION

In experiments (a), (b) and (c) the snails did not spawn readily. They kept crawling out of the dishes and when kept covered, stuck onto the lid. They took hours or days to spawn. In (d) however, the snails spawned readily within 15-30 minutes after isolation.

The snails isolated immediately after copulation did not spawn readily, either stimulated or not, but when stimulated and

isolated four to six hours after copulation, they responded to the stimulus readily.

It seems then that two distinct stimuli, one internal and one external are necessary to induce spawning. These are, firstly that the receptaculum seminis must be full or at least contain a sufficient quantity of spermatozoa, and secondly wetting and splashing with sea water needed to occur. If either of these factors is lacking, spawning may be delayed or may not happen at all.

The receptaculum seminis is full of spermatozoa four to six hours after mating (see Table 4-6) and those given the second stimulus before spermatozoa has reached the receptaculum seminis, generally do not respond readily to spawning. Similarly a female with a full receptaculum seminis will usually not spawn without the external stimulus being applied. Hence, the internal and the external stimuli are necessary for spawning.

The second stimulus applied in the laboratory apparently would be similar to the beating of waves or sprays in their natural environment.

Hence, females with full or containing sufficient quantity of spermatozoa in the receptaculum seminis, would spawn when the sea water is at the habitat, in their natural environment, which would be at high tide level.

After this experiment, in conducting the spawning experiments, the mated females were kept at least four to six hours

after copulation and treated as in (b) (see 4.5.2) before isolating them in sea water in petri dishes.

4.5.3 SPAWNING BEHAVIOUR

The snails of both species usually crawled around the petri dish after isolation and became quiescent just a few minutes before spawning took place. They can spawn with the foot stuck to the dish, but the snails usually turned over and spawned with the foot up. This behaviour may be due to the restricted area of the containers, where the snails were kept.

Once the spawning began, the difference in behaviour between the two species became apparent.

Littorina unifasciata spawned from one to three hours after the stimulus had been applied as in (b) (see 4.5.2). They then crawled out of the petri dish and assumed their normal manner of attachment with the outer lip and the mucus secreted (see 3.2.2) on the side of the petri dish or on the floor near the dish. The snails responded and spawned again, when stimulated the next time, and behaved in the same manner as above. Except when the number of eggs released was less than one hundred, the snails could respond to the stimulus from three to eight times after a single copulation.

Littorina praetermissa on the other hand, spawned intermittently for days and did not crawl out of the petri dish during the spawning period, once the spawning began, after the stimulus. The greater number of days over which the snails spawned the greater is

number of eggs produced (see Fig. 4-6) and the total differs with the different stages of the breeding conditions of the snails (see Table 4-9).

4.5.4 SPAWNING PERIODICITY

In checking the spawning periodicity, the snails were stimulated to spawn at different intervals correlating with high and low tidal periods.

TABLE 4-7 DATA ON SPAWNING PERIODICITY

Date	Time	Tide level	No. of snails		spawning female		non spawning female	
			*U	P	U	P	U	P
19.7.72	9:07 a.m.	2.5 metre (high tide)	2	1	2	1	-	-
	3:04 p.m.	1.2 metre (low tide)	2	1	2	1	-	-
	8:42 p.m.	2.1 metre (high tide)	2	1	2	1	-	-
20.7.72	9:50 a.m.	2.3 metre (high tide)	2	1	2	1	-	-
23.7.72	10:42 p.m.	0.9 metre (low tide)	2	1	2	1	-	-
25.7.72	11:04 p.m.	0.7 metre (low tide)	2	1	2	1	-	-

* U = *Littorina unifasciata*, P = *L. praetermissa*

All these snails used in this experiment spawned within 15-30 minutes after isolation, inspite of the different tide levels at which the snails were stimulated and isolated. Therefore, it can be concluded that spawning period of the two species of my study do not correlate with the tidal periodicity, except in so far as they are more likely to be wetted at a period of high tide in their natural habitat.

Then to test whether the snails are influenced by light in spawning, I conducted the experiment both at night and in the day time. Of those which were conducted at night, the snails stimulated and isolated were placed in the darker area of the laboratory and to screen out any rays from the electric light in the other part of the laboratory, the apparatus was covered with a black plastic sheet taking care that the sheet did not touch the petri dishes containing the snails. The experiment was repeated three times using five snails each time.

All the snails used in the experiment either at night or in the day time spawned within 15-30 minutes after being stimulated and isolated. Thus light does not affect in spawning in either Littorina unifasciata or L. praetermissa.

4.5.5 NUMBER OF EGGS SPAWNED AFTER COPULATION

4.5.5.1 METHOD OF COUNTING EGGS

The number of eggs spawned after copulation varies with individuals. It ranges from twenty five to thousands of eggs.

When a snail produced small numbers of eggs (i.e. between 25-100), the eggs were counted by pipetting eggs singly from the petri dish and noting the count by doing so.

When the number of eggs was large (over 100-1000s) the eggs were distributed evenly in a petri dish of known area. The dish was then placed under a dissecting microscope and the number of eggs in the field was counted in several different areas of the petri dish. Then the average number of eggs per area was determined and finally multiplied by the total area of the petri dish.

This method of counting the eggs may vary ± 100 from the number of eggs spawned. I checked this error by taking the egg count of the same female twice by two different methods. Firstly by taking the egg count as described as above and secondly by pipetting every egg from the petri dish and the number recorded. This check up was carried out on ten snails.

4.5.5.2 METHOD OF RECORDING THE EGG COUNTS

The spawning behaviour differed between Littorina unifasciata and L. praetermissa (see 4.5.3). Therefore, I have treated the species differently in this aspect and descriptions of the methods are given under separate headings.

Littorina unifasciata: From three to five mated females were stimulated to spawn after each fortnightly field trip throughout this study. This species responded several times to stimulus in spawning after a single copulation. The snails spawned from one to

three hours after each stimulus and crawled out of the petri dish. Therefore, I counted the eggs as described in 4.5.5.1 after the snails had crawled out. They were then stimulated again the next day and the egg count taken. This was repeated, until the snails no longer responded to the stimulus. The sum of egg counts after every stimulus was taken as the number of eggs a female would produce after a single copulation.

Of these snails, those which produced less than 100 eggs, and did not respond to the second stimulus were dissected and the condition of the gonad examined. In these snails immature eggs tend to predominate the mature ones. Therefore, they were discarded in the record.

The shell heights were also recorded together with the egg counts to observe the relationship between the snail's size and the number of eggs produced. The record was taken on five of each size as far as possible.

Littorina praetermissa: This species breeds during the cold period of the year only (see 4.2.2.4). Except in the first year of my study, I have recorded the egg counts of two females which mated and spawned in the laboratory every fortnight during the breeding period. This depended on the occurrence of the mating pairs. As the snails approach the end of the breeding period, occurrence of mating pairs become infrequent (see Table 4-8).

The snails used in the spawning experiment ranged between 12 and 13mm.

TABLE 4-8 THE SPAWNING FEMALES OF LITTORINA PRAETERMISSA RECORDED IN THE BREEDING PERIOD DURING THE STUDY PERIOD *

Month	1971	1972	1973
July	-	4	4
August	4	4	4
September	4	2	3
October	2	2	1
November	1	-	1

* I have excluded the snails which mated several times in the laboratory in this table.

The species once started to spawn after the stimulus, spawned intermittently for days. Therefore in taking the egg counts I transfered the snails into new petri dishes on each day and the egg counts in the old petri dishes were taken as a day's spawn. This was repeated until the snails stopped spawning, and the sum of the eggs produced daily was taken as the total number of eggs produced during the spawning period after one copulation.

During my study period, I came across five snails which mated several times in the laboratory, one in 1972 and four in 1973. The egg counts of these females during the spawning period after every mating were recorded. The sum of eggs produced in every spawning period after each mating in the females which started to mate in the early part of the breeding period, was assumed to be the number of eggs a snail would produce in the total breeding period. These

snails were dissected when I came across snails which were in the ~~breeding~~ spawning stage collected from the ~~breeding ground~~ natural habitat in my fortnightly gonad examination.

4.5.5.3 OBSERVATION

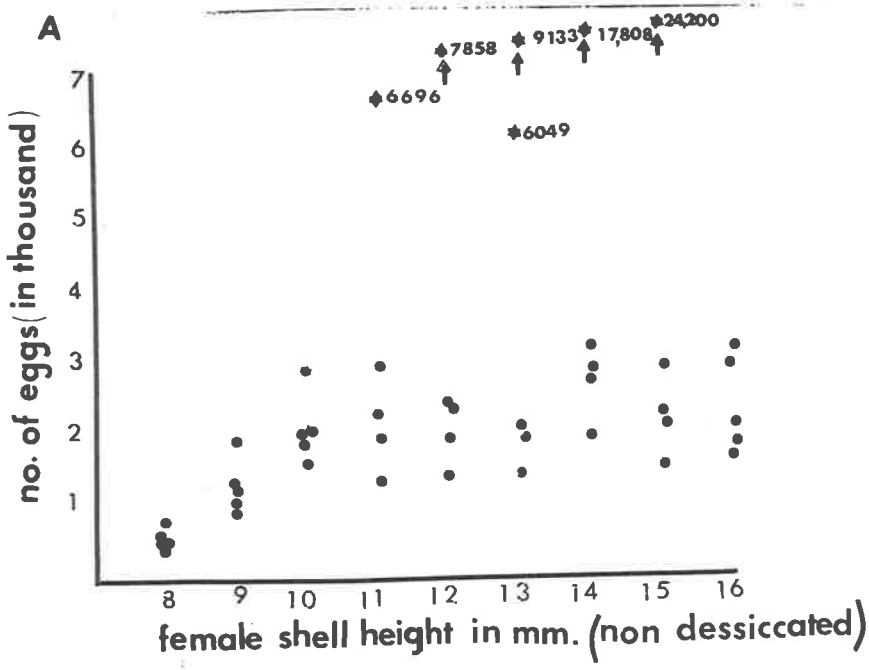
Littorina unifasciata: After a single copulation, the snails usually responded three times to the stimulus to spawning, and the number of eggs produced during that time usually ranged between 2000-4000 eggs. Of the 45 snails of various sizes recorded, 6 snails were observed to release over 6000 eggs (Fig. 4-5A), and these snails of rare cases responded eight to eleven times to the stimulus in spawning after the copulation.

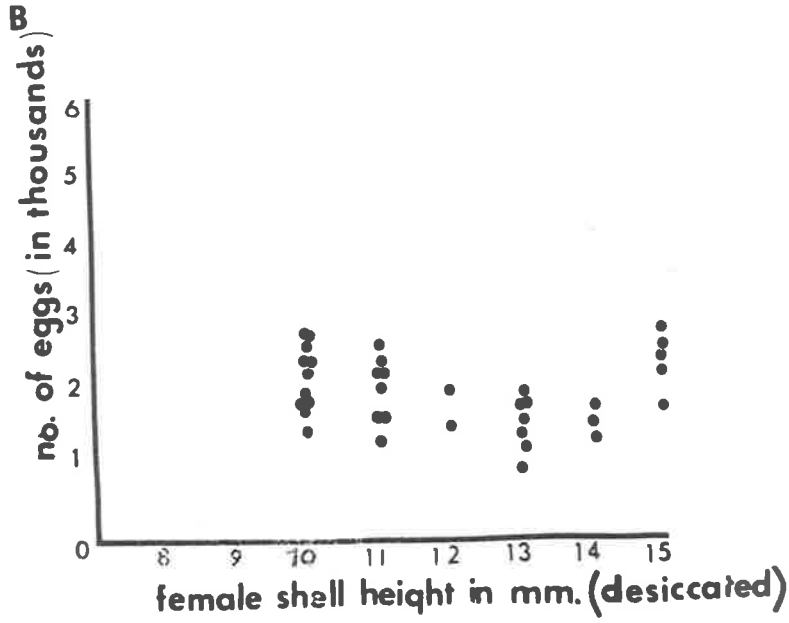
I did not observe any relationship between the snail's size and the number of eggs produced. Except for the smallest size recorded, the range in the number of eggs produced overlapped in all the sizes (Fig. 4-5A).

Struhsaker (1966) in studying the breeding habits of the Hawaiian littorinid species has stated that:- "It is possible that other factors than size and age relate to spawning readiness. These may be:- (a) number of mature eggs present when the female is fertilized (b) number of spermatozoa obtained during fertilization or (c) influence of certain physical factors, i.e. temperature and desiccation".

The above three factors mentioned by Struhsaker may also explain for the fluctuation in the number of eggs produced in the spawn after copulation in all the sizes of the snails observed

FIG. 4–5 Relationshp between shell height and number of eggs spawned in Littorina unifasciata





in Littorina unifasciata.

Littorina praetermissa: The duration of spawning of the snails after one copulation varied with different stages of the breeding condition. In the early stages of breeding period and towards its end, spawning lasted from one to two days after copulation, whilst in the full breeding condition, the snails usually spawned from three to eight days after. Of the snails recorded, two females however, spawned for a period of 15 and 17 days after copulation.

The spawning period of the snails which mated and spawned in July were never observed to be less than 6 days. Thus it could be taken that most snails reached full breeding condition in July (see Table 4-9).

The number of eggs produced early or later in the breeding period when spawning lasted only one or two days, ranged from 25-200 eggs, but in the full breeding condition when spawning continued for three to eight days, it ranged from 3000-12,000 eggs (see Table 4-10). The longer the spawning period, the larger is the number of eggs produced. Thus the precise duration spawning time and the number of eggs produced are associated. However, there is fluctuation in the number of eggs produced within the same spawning period (see Fig. 4-6). This would also depend on the three factors as mentioned in Littorina unifasciata (see p. 78).

In Table 4-9, it will be seen that Littorina praetermissa usually spawned longer in July, August and September and the duration

FIG.4-6 Relationship between number of eggs spawned and the spawning period after one copulation in Littorina praetermissa

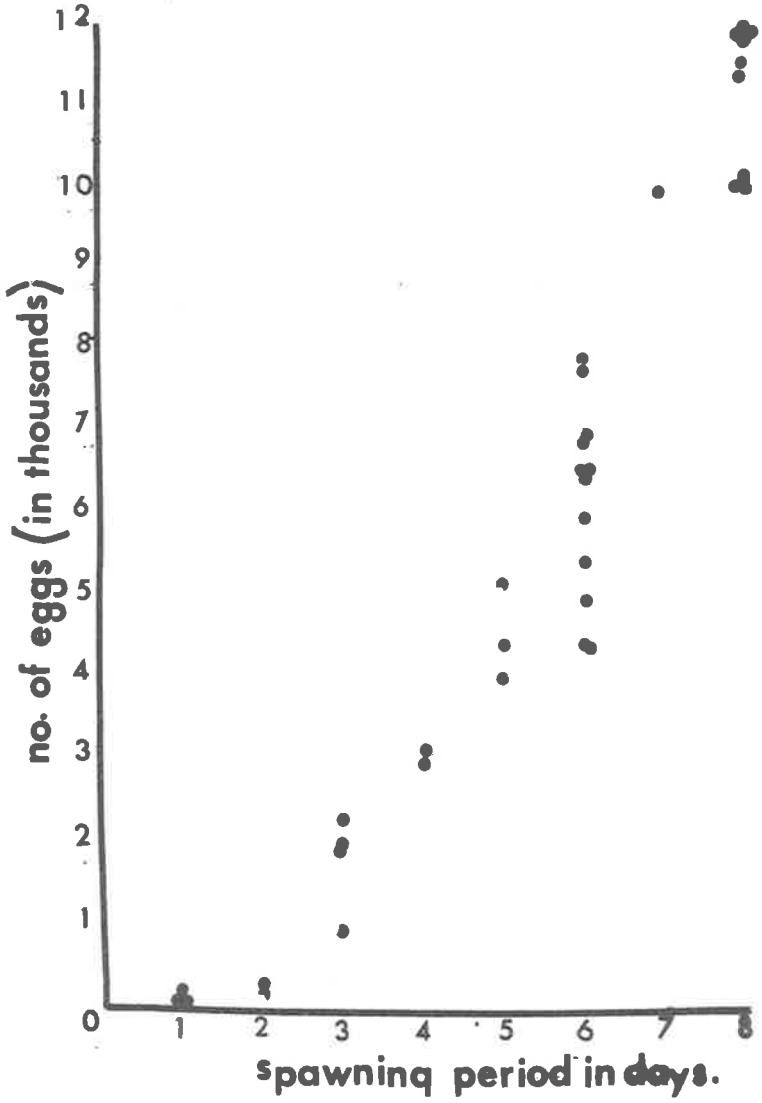


TABLE 4-9 THE LENGTH OF SPAWNING PERIOD AFTER COPULATION IN THE SNAILS RECORDED IN TABLE 4-8

Month and year		Length of spawning period in days								
		1 day	2 days	3 days	4 days	5 days	6 days	7 days	8 days	15 days
July	1971	-	-	-	-	-	-	-	-	-
	1972	-	-	-	-	-	-	-	3	1
	1973	-	-	-	-	-	1	1	2	-
Aug.	1971	-	-	1	2	-	-	-	1	-
	1972	-	-	-	-	1	2	-	1	-
	1973	-	1	-	-	1	2	-	-	-
Sept.	1971	-	-	-	-	1	2	-	1	-
	1972	-	-	1	-	-	-	-	1	-
	1973	-	-	-	-	-	3	-	-	-
Oct.	1971	1	1	-	-	-	-	-	-	-
	1972	1	-	1	-	-	-	-	-	-
	1973	1	-	-	-	-	-	-	-	-
Nov.	1971	1	-	-	-	-	-	-	-	-
	1972	-	-	-	-	-	-	-	-	-
	1973	1	-	-	-	-	-	-	-	-

of the spawning period declined towards October and November. These periods correspond to those in which I observed breeding and spent stages in the gonad examination fortnightly (see 4.2.2.4). This change is distinctly observed in the females which mated several times in the laboratory (see Table 4-10).

TABLE 4-10 NUMBER OF MATINGS AND THE NUMBER OF EGGS PRODUCED DURING THE SPAWNING PERIOD AFTER COPULATION, IN THE FEMALES WHICH MATED SEVERAL TIMES IN THE LABORATORY IN LITTORINA PRAETERMISSA

sr. no. of snails	Times mated by the female															Total no. of eggs after every mating
	1st time			2nd time			3rd time			4th time			5th time			
	*D	SP	E	D	SP	E	D	SP	E	D	SP	E	D	SP	E	
1	14.6.72 June	1	193	26.6.72 June	5	7,431	10.7.72 July	11	21,496	29.7.73 July	2	369	11.8.73 August	2	131	29,620
2	28.6.73 June	6	10,561	16.7.73 July	9	21,594	29.9.73 Sept.	7	9,653	2.10.73 October	2	521	5.10.73 October	1	56	42,385
3	15.7.73 July	17	43,775	9.8.73 August	5	4,981	28.8.73 August	3	4,081	17.9.73 Sept.	2	537	5.10.73 October	1	25	53,399
4	16.8.73 August	5	6,942	26.9.73 Sept.	1	32										6,974
5	12.9.73 Sept.	3	7,016	26.9.73 Sept.	1	139										7,155

* D = Date, SP = Spawning period, E = Number of eggs

Of the snails which mated several times in the laboratory, the mating of three snails occurred in the early part of the breeding period and these mated several times before the end of the breeding season (see Table 4-10). These snails were dissected in November and were found to have gonads in the resting condition. The gonad examined of the snails collected at this time were also observed to be in a resting condition. Thus, it is assumed that a female of this species can produce from 29,000-54,000 eggs in one breeding season if the laboratory conditions are overlooked.

To observe the gonad of the females of Littorina praetermissa which mated several times in the laboratory, to be in the resting stage in November, in agreement with the snails collected from the field, further confirmed the fact that this species has a limited breeding period.

4.5.6 DESICCATION AND SPAWNING IN LITTORINA UNIFASCIATA

Due to their limited breeding season experiments on desiccation in relation to spawning were not carried out on Littorina praetermissa but were confined to L. unifasciata.

Forty females of Littorina unifasciata mated on the same day were kept in a dry petri dish with no free moisture and at room temperature. Then five snails were stimulated as indicated in (b) Section 4.5.2, and isolated on each day of the eight succeeding days. Daily egg counts of all the snails were taken as described in Section 4.5.5.2 for L. unifasciata.

4.5.6.1 OBSERVATION

Six days of desiccation did not mar the abilities of the snails to spawn when given the usual stimulation. The eggs produced were normal in number (Fig. 4-5B) and developed normally into veliger larvae. After seven and eight days of desiccation, some (1 or 2 snails) failed to spawn after the standard stimulation. However, after feeding them for about fifteen minutes, they spawned readily and normally.

The snails were not desiccated for more than eight days, because it is unlikely that desiccation period would be longer than this time in the natural habitat.

The snails which failed to spawn, responding to the stimulus after feeding, shows that spermatozoa will remain viable in the female for at least eight days, and starvation could be the cause in the failure in spawning. However, in their natural environment, the snails are most likely to have the chances of feeding before spawning once the waves break up at their habitat.

4.5.7 DISCUSSION AND CONCLUSION

Although the breeding period of the two species overlapped, Littorina praetermissa has a break in breeding. L. unifasciata breeds throughout the year and in this regard resembles closely to the Hawaiian species, L. pintado and L. picta and the New Zealand species Melarapha cincta and M. oliveri.

Struhasker (1966) has found the spawning period of L. pintado and L. picta correlating with highest high tide level, but In L. unifasciata, spawning occurs not periodically but after suitable physical stimulation.

Littorina praetermissa with its distinct breeding period, resembles the British species L. littorea From field observations, this species is noted to spawn usually at high tide period and by night (Fretter and Graham 1962, p. 47). The spawning periodicity is absent in L. praetermissa and the stimuli it responded in spawning is similar to those of L. unifasciata.

The two species of my study never failed to respond to the stimulus as described in (b) Section 4.5.2, four to six hours after copulation and spawned within 15-30 minutes after isolation in sea water in petri dishes.

This suggests that water movement, which is similar to the wave splashes they encounter in their natural habitat, is the essential external stimulus in spawning and tidal rhythm as such is ineffective.

The internal stimulus appears to be the receptaculum seminis sufficiently filled with spermatozoa and it has been shown that the receptaculum seminis becomes turgidly filled with spermatozoa about four to six hours after copulation (see Table 4-6). It was observed that it changes from a white streak to a turgid spherical structure. Once the internal condition is right, the snails responded readily to the external stimulus.

It has been noted by Fretter and Graham (1962) that Littorina littorea spawned 2-12 hours after copulation, and it has been noted in all other littorinid species which have been studied, that the snails took hours to spawn after copulation, whether spawning periodicity has been observed in them or not. This being the common case, the influential factor of the storage of spermatozoa in the receptaculum seminis in spawning may also be true to all littorinid species.

The eggs are always in one cell stage when laid regardless of the difference in time in spawning even when egg laying has been delayed for relatively long periods after copulation by desiccation. This shows that spermatozoa stored in the receptaculum seminis of the females remain viable for quite some time. Eggs are fertilized shortly before being laid.

Snails which released planktonic eggs are in more danger of losing their offsprings than those in which development is direct. Thus littorinids of this type always produced large numbers of eggs, to compensate for the high mortality and to ensure survival of the species. The mechanisms I have observed in the breeding and spawning of Littorina unifasciata and L. praetermissa, would thus be associated with the adaptations of the snails to their environmental conditions which will promote in their survival.

CHAPTER V. DEVELOPMENT

5.1 INTRODUCTION

Littorina unifasciata and *L. praetermissa* belong to the littorinid group which produce planktonic egg capsules. The snails usually release their eggs singly, but some clusters of eggs consisting of about 80 in number, may be produced in the thousands of eggs spawned. However, these clusters soon break up in the sea water in the petri dishes. Thus it is most likely that in their natural environment, the eggs would be dispersed singly in the sea once they had been released. In the laboratory, the eggs usually sink to the bottom of the petri dishes. This could be due to the restricted area of the petri dishes and the still sea water. The turbulence of the sea is most likely to keep them afloat in their natural environment.

Littorinid species which produce planktonic egg capsules, spend a period of their life history in the plankton as a developing egg or a veliger larva. They are washed ashore to the habitat only in their metamorphosed stage. Thus their survival is very dependent on the hazardous conditions of the sea. Therefore, a large number of eggs must be produced to compensate the mortality of these stages, and to ensure survival of the species.

Developmental stages from one cell to hatched veliger larvae of the two species, were studied with the spawn collected from laboratory mated females. Rearing of the veliger larvae was not a success. However, laboratory studies of the larvae provided evidence

that the larvae of both Littorina unifasciata and L. praetermissa would spend at least 3-4 weeks in the plankton before metamorphosis.

5.2 EGG CAPSULES

In both species a normal egg capsule consists of a fertilized egg of approximately 80μ in diameter, with an egg covering and the transparent colourless egg capsule.

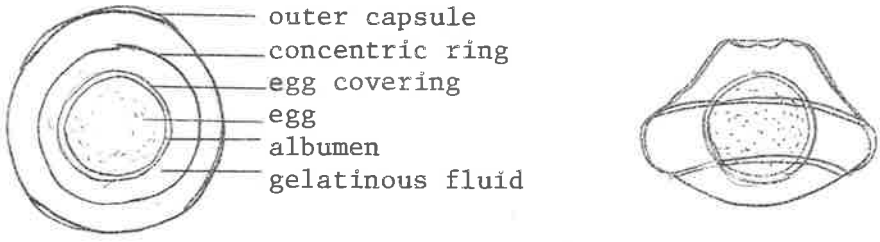
From the dorsal aspect the capsule is a disc shape in both Littorina unifasciata and L. praetermissa (Fig. 5-1A and B). However, species differences are observed in the size and the shape of the outer capsule. The measurement of the capsule in maximum diameter ranges from 100-140μ in the former species, and from 240-300μ in the latter. The concentric ring in the outer capsule is simple in L. unifasciata, but it is serrated in L. praetermissa (Fig. 5-1A and B (cr)).

The capsule is helmet-shaped in Littorina unifasciata, whilst that of L. praetermissa resembles that of a broad brimmed hat from the lateral view (Fig. 5-1C and D).

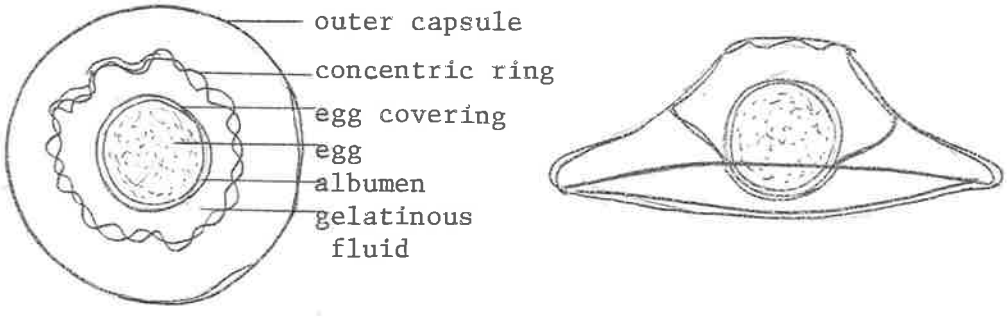
On rare occasions, a few abnormal egg capsules with more than one egg may be observed amongst the several thousands of eggs produced. The capsule is often much deformed in these cases (Fig. 5-2(b,c,d,e and f); and Fig. 5-3(e and f)).

Fig. 5-1. Egg capsules of the two species

A. Littorina unifasciata



B. Littorina praetermissa



5.3 MATERIAL AND METHOD IN STUDYING THE DEVELOPMENTAL STAGES

Freshly spawned eggs were collected from laboratory mated females. These eggs were reared in petri dishes of approximately 9cm. in diameter and 2cm. in depth with sea water which was filtered twice. The sea water had to be filtered twice, because the eggs reared in unfiltered sea water were greatly infested by protozoa and intermingled with detritus present in the sea water. The eggs were also washed several times with filtered sea water before rearing. Each petri dish contained about 500 eggs. The eggs were counted as described in Section 4.5.5.1. The water was changed daily until the larva hatched.

The hatched veliger larvae were reared in finger bowls of approximately 10cm. in diameter and 6cm. in depth, or in petri dishes of approximately 19cm. in diameter and 5cm. in depth filled with filtered sea water. The number of hatched veliger larvae in each of these containers never exceeded 500. The veliger larvae in petri dishes and finger bowls can be seen with the naked eye, so the water could be changed daily without loss of larvae. I also attempted to rear the hatched veliger larvae in an aquarium of approximately 40cm. x 22cm. x 25cm. with filtered sea water to about 12cm. in depth. Air was passed through to maintain the larvae in suspension. In a spacious container like the aquarium, the larvae cannot be seen easily. Thus renewing the water daily was not possible.

The larvae of both species were reared at room temperature which ranged from 12°-20°C in winter and from 21°-35°C in summer. With Littorina praetermissa, because of its limited breeding season, rearing of the larvae could only be achieved at winter temperatures, whilst in L. unifasciata, rearing of the larvae was achieved throughout the year.

To estimate the mortality of the veliger larvae, 500 larvae were collected soon after hatching and reared in five petri dishes. The petri dishes used were approximately 9cm. in diameter and 2cm. in depth. Each petri dish contained 100 veliger larvae. These petri dishes were examined and water renewed daily until the mortality rate could be estimated.

Developmental times were recorded by checking the stages hourly after spawning. For this study the eggs which were spawned approximately at the same time, were collected and reared in petri dishes in the same procedure as described previously. Each petri dish contained 50-100 eggs. Measurements were taken of one cell stage and the veliger larva only.

With this method, segmentation was followed up to the 8 cell stage. The trochophore and veliger larval stages were identified so that information on the time of development from one cell to the hatched veliger larval stage was gained.

5.4 OBSERVATION

5.4.1 DEVELOPMENT FROM ONE CELL STAGE TO VELIGER LARVA

Development from the one cell to the veliger larva took place within the egg covering. The period was longer in Littorina praetermissa than in L. unifasciata (see Table 5-1). The veliger larva hatched approximately 6-7 days in the former and approximately 3-4 days in the latter.

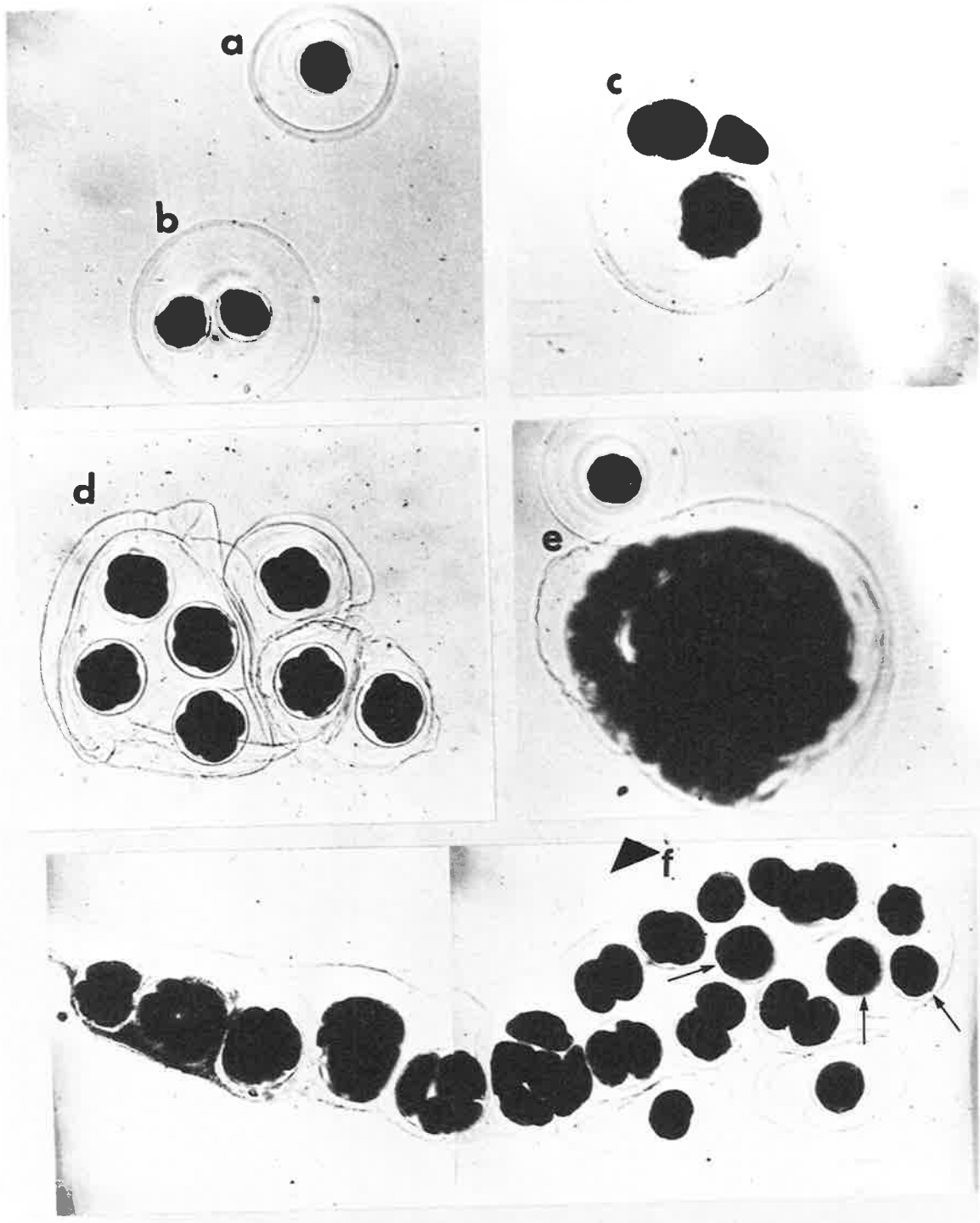
TABLE 5-1 DEVELOPMENTAL TIME FROM ONE CELL TO HATCHED VELIGER LARVA IN LITTORINA UNIFASCIATA AND L. PRAETERMISSA

	Littorina unifasciata	Littorina praetermissa
Developmental stages	app. time after spawning	app. time after spawning
1 cell	0 hr.	0 hr.
2 cell	2 hr.	4 hr.
4 cell	4 hr.	6 hr.
8 cell	6 hr.	8 hr.
later cell stages	8-20 hr.	10-24 hr.
trochophore	24-28 hr.	24-32 hr.
early veliger	45-56 hr.	49-60 hr.
hatching	75-93 hr. (app. 3½ days)	165-175hr. (app. 7 days)

Figure 5-2 a, normal egg capsule
b,c,d,e and f, abnormal egg capsules

All the fertilized eggs in (d) developed normally into veliger larvae and the eggs indicated with the arrows developed normally into veliger larvae in (f).

FIG. 5-2

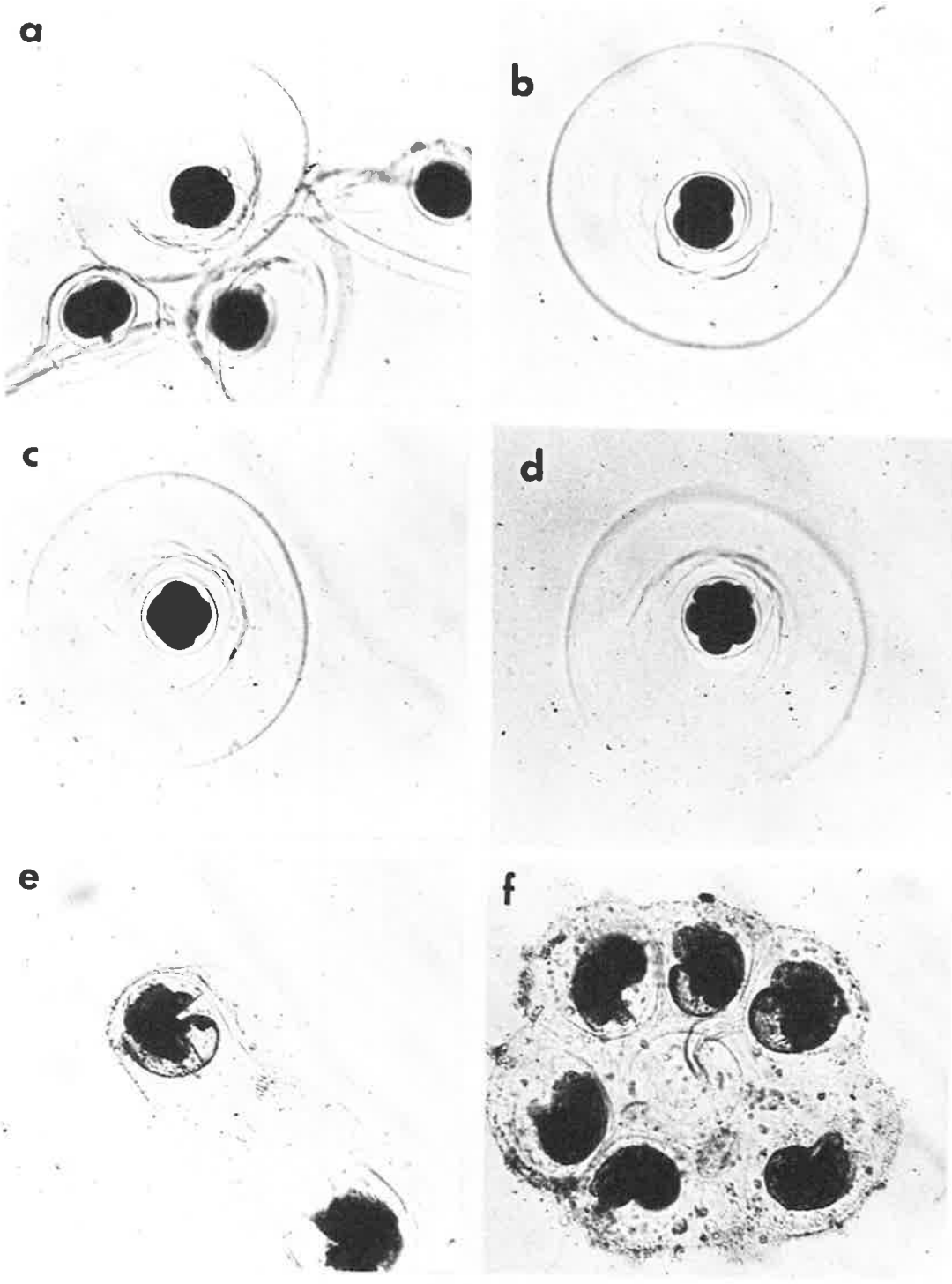


Egg capsules of Littorina unifasiata

Figure 5-3 a,b,c,d , normal egg capsules

e&f, abnormal egg capsule with developing veliger larvae.

FiG.5–3



Egg capsules of Littorina praetermissa

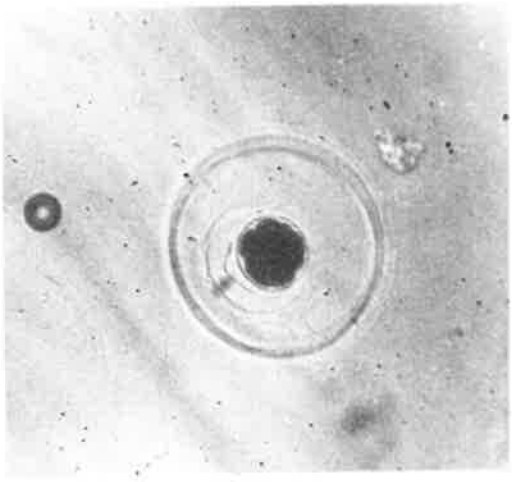
As long as the egg had its own egg covering, it never failed to develop to the veliger stage whether it was in a normal or an abnormal egg capsule [Fig. 5-2(d), some eggs in (f) shown with the arrows, and Fig. 5-3(e) and (f)]. When the eggs were in a condensed mass within the same egg covering as in Fig. 5-2(c), (e) and some in (f) without the arrows; they did not develop at all. However, the occurrence of this type is very rare. The noticeable cases I have come across during my study are all presented in Fig. 5-2.

On one occasion after laboratory mating, eggs of Littorina praetermissa failed to develop. These eggs were the first spawn of female no. 1 (1972) which was subsequently mated several times in the laboratory (see Table 4-10). This female mated for the first time in early June. From the fortnightly gonad study on other snails collected from the field at this period, showed that females of this species were still in the early breeding condition. Therefore the observed female could still be in the initial stage of breeding condition. If so, the eggs in the ovary would not be fully matured. Hence, this could cause the eggs in not developing.

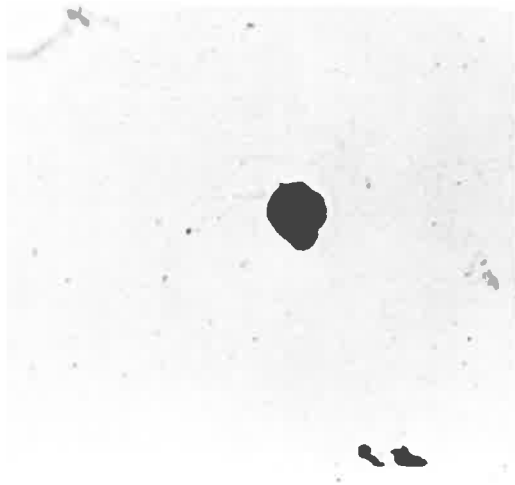
5.4.2 VELIGER LARVA

In both Littorina unifasciata and L. praetermissa, the larva hatched from the concave ventral surface of the egg capsule. Species differences are observed in the newly hatched larva. The

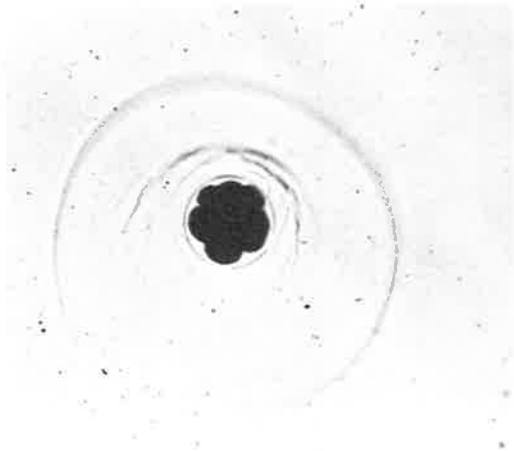
FIG.5-4



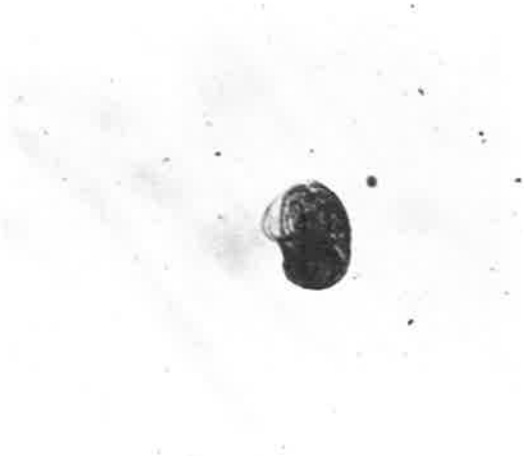
*Egg capsule of
Littorina unifasciata



veliger larva of
Littorina unifasciata



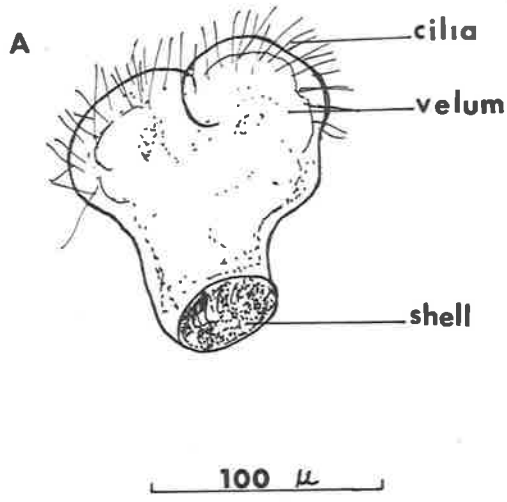
*Egg capsule of
Littorina praetermissa

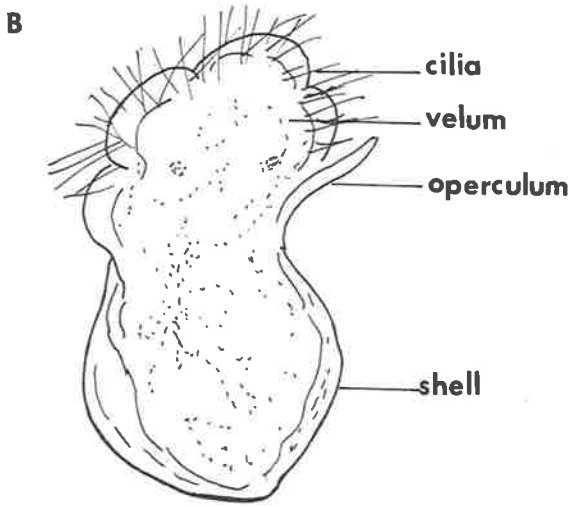


veliger larva of
Littorina praetermissa

* multicellular stage

FIG.5 – 5





Newly hatched veliger larvae. A, Littorina unifasiata; B, Littorina praetermissa.

protoconch in the former species is small and is approximately 35μ, whilst in the latter it is approximately 100μ and well formed with an operculum at this stage (Figs. 5-4 and 5-5). However, the whole animal measures approximately from 100-150μ in both species.

The velum of the larva is bilobed in both species and the velar lobes are equal in sizes. Two conspicuous pigmented spots are present on the velum.

The newly hatched larvae of Littorina unifasciata are most active and swim at the surface by means of the velar cilia. The protoconch grows approximately 100μ in size complete with an operculum two or three days after hatching and at this stage resembles the newly hatched veliger larva of L. praetermissa. The activities of the larvae slow down at this stage and they gradually sink to the bottom. This is presumably due to the increase in growth and the weight of the shell thus causes it to sink. Mortality of the larvae is very high at this period (see 5.4.3).

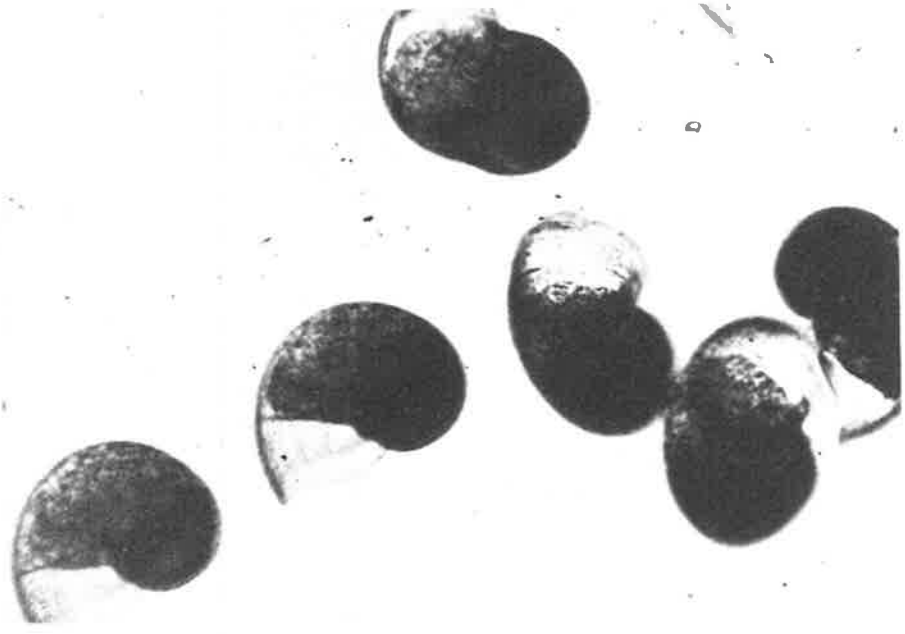
In Littorina praetermissa the newly hatched veliger larvae usually swim below the water surface and these also gradually sink to the bottom two to three days after hatching, as in L. unifasciata. By then the shell has grown approximately 125-150μ in length and shell sculpture has set in (Fig. 5-6B). The larvae usually die after that in the laboratory, except on one occasion I came across one veliger larva of this species which lived for 9 days. The measurement of the shell was approximately

FIG. 5–6

A

100 μ

B



Veliger larvae of Littorina praetermissa. A, 9 days after hatching; B, 2–3 days after hatching.

170μ and the third whorl of the shell was incompletely formed (Fig. 5-6A).

5.4.3 MORTALITY OF THE VELIGER LARVA

In both species the mortality rate of the cultured larvae is approximately 80% in the first four days after hatching. Of those which remained alive, became quiescent at the bottom, and except for a slight movement of the velar cilia, no other movement was observed. They died before reaching the crawling stage.

The failure of rearing the veliger larvae in the laboratory would be mostly due to lack of proper diet. To achieve such a method of rearing the larvae successfully in the laboratory is time consuming. However, I have observed the differences between the species from what I have achieved. Therefore no further work was carried out on this aspect.

5.4.4 DISCUSSION AND CONCLUSION

There is a wide range in the form of the capsules in those species which produce planktonic egg capsules. A summary of the classification of these capsule type is given by Kojima (1960). The capsules of *Littorina unifasciata* and *L. praetermissa* come within the "helmet" type resembling those of *L. pintado* (Wood) (Ostergaard 1950), *L. nereitoides*(L.) (Lebour 1935), *L. brevicula* (Philippi) (Kojima, 1959, 1960) and *L. littorea*(L.) (Lebour 1935).

However, there is a variation in the shape and the size of the egg capsule between the species. The egg capsule of all those mentioned species contains only one egg; except in L. littorea where the egg capsule contains from 1-5 eggs.

The two species of my study differ distinctly in the shape and the size of the egg capsule (see 5.2). They also differ in the rate of development from one cell to veliger larva stage (see 5.4.1).

The development rate from one cell to veliger larva stage in Littorina unifasciata resembles more that ~~those~~ of the Hawaiian species, L. picta and L. pintado (Struhsaker 1966) and New Zealand species, Melarapha cincta and M. oliveri (Pilkington 1971) than ~~to~~ it does L. praetermissa.

The protoconch is small approximately 35μ in the newly hatched larva of Littorina unifasciata, whilst in L. praetermissa, it is well formed with an operculum (see 5.4.2). The newly hatched larva with a well formed protoconch would survive better in the sea than the one with a small protoconch. Hence, the structure of the protoconch in the newly hatched larva may promote the chances of the existence of the species in L. praetermissa, although this species in most aspects is less tolerant to the environmental conditions than L. unifasciata (see Chapter 7).

The structure of the veliger larva is closely related in the littorinid species which pass through a free swimming larva stage. The Hawaiian species L. picta, L. pintado and L. scabra are

characterised by an asymmetry in development, which results in the right velar lobe being larger than the left (description in Struhsaker 1966). The velar lobes of L. unifasciata and L. praetermissa are equal in that they resemble the two New Zealand species, Melarapha cincta and M. oliveri more closely (description in Pilkington 1971).

The largest shell I have recorded in the larva of Littorina praetermissa on the 9th day after hatching is with incomplete formation of the third whorl. The developmental time and the structure of the shell observed is very similar to that of L. picta. This species also hatches as an early veliger stage of comparable size and has a planktonic life of 3-4 weeks (Struhsaker and Costlow 1968). Therefore it is assumed that the veligers of the two Australian species would spend at least 3-4 weeks in the plankton.

CHAPTER VI. DISTRIBUTION

6.1 INTRODUCTION

The surfaces of the rocks, jetty piles and piers in the *supralittoral fringe (*Stephenson and Stephenson 1972) along the South Australian coast are inhabited mainly by the two littorinid species Littorina unifasciata and L. praetermissa. The snails are widely distributed but the latter species could be overlooked amongst the more abundantly distributed population of the former species, especially in the exposed areas of the habitat. Many species of Littorina show a great variability in the shell (Whipple 1965). Therefore, L. praetermissa, because of its sparse distribution, and furthermore, since the two species are so similar ecologically, it could be taken as a morph of the abundantly distributed L. unifasciata. They are however, found to be different in the details of the anatomy and are distinctly different in their breeding habits.

It has been pointed out in Chapter IV that Littorina praetermissa has a short breeding period, whilst L. unifasciata breeds throughout the year. This could be an explanation for the smaller population of L. praetermissa.

In my three field study areas, namely Glenelg, Port Willunga and Second Valley, which I had chosen for the fortnightly collection of the snails, I observed reasonable numbers of Littorina praetermissa occupying crevices and sheltered areas in the

habitat, whilst L. unifasciata was observed occupying exposed and sheltered areas. Thus, the former species, because of its restriction to sheltered niches may be at a disadvantage in distribution when compared to the latter species. This was first noted at the three selected study areas, so it was decided to investigate their distribution over a variety of rocky shore lines both sheltered and exposed conditions along the South Australian coast.

6.2 SOUTH AUSTRALIAN COASTLINE

The following information on the South Australian coastline is taken largely from Womersley and Edmonds (1958).

Much of the South Australian coastline is of Recent to Pleistocene age and consists of beach sands and dunes which in many areas have become consolidated to form calcareous sand rock cliffs and reefs. The coastline is usually "supported" by capes or headlands of more resistant Palaeozoic rocks such as quartzites and schists, or of igneous rocks such as granites. Thus, by the nature of the substrates present, the coastal topography is classified into (1) steeply sloping Palaeozoic rocks, often granite, schists or quartzites, dropping fairly steeply into deep water or rough coasts, less steeply under calmer conditions (2) calcareous sand-rock cliffs of Recent or Pleistocene age which form wave cut platforms at low tide level (3) sandy beaches between calcareous platforms or areas of older rock (4) sandy or muddy tidal flats

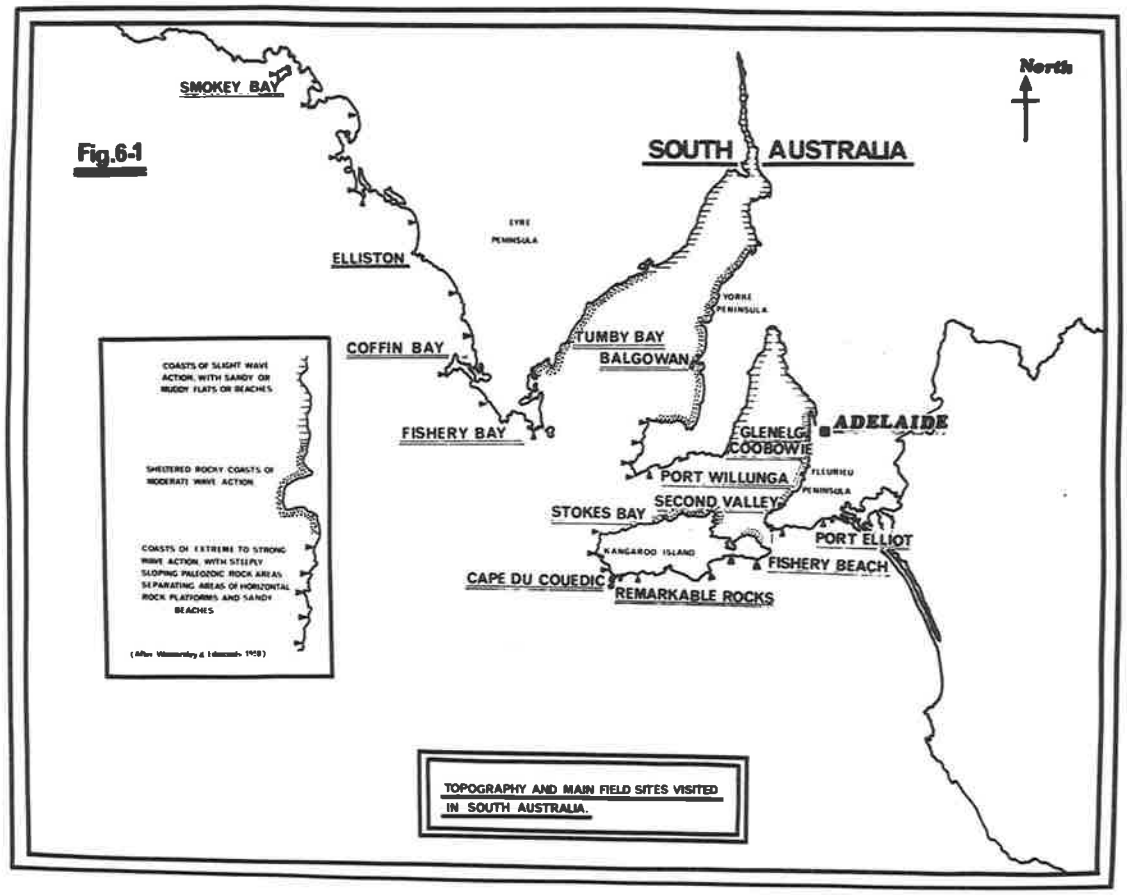


Fig.6-1
SMOKEY BAY
SOUTH AUSTRALIA
North
EYRE PENINSULA
ELLISTON
YORKE PENINSULA
COFFIN BAY
TUMBY BAY
BALGOWAN
FISHERY BAY
GLENELG
ADELAIDE
COOBOWIE
FLEURIEU PENINSULA
PORT WILLUNGA
SECOND VALLEY
STOKES BAY
KANGAROO ISLAND
PORT ELLIOT
FISHERY BEACH
CAPE DU COUEDIC
REMARKABLE ROCKS
COASTS OF SLIGHT WAVE ACTION, WITH SANDY OR MUDDY FLATS OR BEACHES
SHELTERED ROCKY COASTS OF MODERATE WAVE ACTION
COASTS OF EXTREME TO STRONG WAVE ACTION, WITH STEEPLY SLOPING PALEOZOIC ROCK AREAS SEPARATING AREAS OF HORIZONTAL ROCK PLATFORMS AND SANDY BEACHES
(After Wilmsenley & Edmonds 1978)
TOPOGRAPHY AND MAIN FIELD SITES VISITED IN SOUTH AUSTRALIA.

developed in bays or inlets or in the upper part of Spencer and St. Vincent Gulfs.

The coastal features and the areas I have visited are shown in Fig. 6-1 (after Womersley and Edmonds (1958)). The snails of my study inhabit hard, solid surfaces; thus the localities I have visited are mostly the rocky coasts.

Those parts of the coastline which are fully exposed to the south or west are subject to a heavy surge with lines of breakers up to 2 metre or more high. Only on fairly calm days with an offshore wind are conditions greatly moderated and such days occur only a few times during summer. The accompanying map (Fig. 6-1) shows that most of the South Australian coastline, except the gulf regions, the north coast of Kangaroo Island and small bays otherwise exposed coast falls into this category.

Sea temperatures just off exposed coasts are 18^{o}-20^{o}C in summer and 14^{o}-16^{o}C in winter. On the south east coast of South Australia, temperatures are lower in summer by 2-3^{o}C but only 1^{o} or so in winter.

The mean maximum daily air temperatures during summer and the seasonal variations of daily temperatures are much greater at localities along the coasts of the gulf than along the open coast. The mean minimum daily temperatures during winter along the open coast do not differ very much from those along the gulf coast. The seasonal variation of relative humidity is much greater along the gulf coasts than along the open coasts. Temperatures are lower and

humidity higher in the south east coast of South Australia than other localities.

The map Fig. 6-1 shows that the localities I have visited covers all the above mentioned conditions of South Australian coastline.

6.3 FIELD OBSERVATION

In the following sections where I have presented figures on distribution, except when otherwise mentioned, all specimens of both species were collected together from within 30cm. quadrats. At every mentioned locality the snails were collected from 5 such areas about one metre apart.

6.3.1 OCCURRENCE OF THE SNAILS ALONG THE COASTLINE

Both species are found along the coast, wherever there are hard substrates, such as rocky cliffs and rock platforms of either schists, quartzites, granite or sedimentary rocks and also jetty piles and piers. The snails usually occur in groups, consisting up to 50 or so individuals and there may be few isolated individuals. However, the occurrence of Littorina praetermissa in the areas exposed to direct sun, for example flat jetty walls or horizontal flat rock surfaces, is very rare. If present, there might just be one or two intermingled with groups of L. unifasciata, which does not seem to have any special preference for exposed or sheltered areas.

Along the coast in some localities (e.g. Fishery Beach, Fleurieu Peninsula), there are low flat horizontal rocks in the supralittoral fringe. On those rock surfaces, groups of Littorina unifasciata in large numbers are distinctly noticeable. The snails in each group are never less than 20 individuals and there is not a single L. praetermissa on these rock surfaces (Fig. 6-2). However, reasonable numbers of L. praetermissa are observed in sheltered areas and crevices in the habitat in all the localities I have visited (Fig. 6-3).

The barnacle Chamaesipho columna (Spengler) is usually found together with the snails in the habitat, and often the mussel Modiolus pulex Lamarck is often found occupying the area below the snails' habitats (Fig. 6-4). Gastropods, such as Bembicium nanum Lamarck and Melanerita melanotrogus Smith are also found in the lower area of the habitat.

Although the snails inhabit rocks of all types, I have observed them to be sparsely distributed on granite rocks when compared with other types of rocks, such as schists and quartzites. Furthermore, Littorina praetermissa tends to be larger than L. unifasciata on the rocks (Fig. 6-5). Both species were not occurring in groups. They were scattered individually.

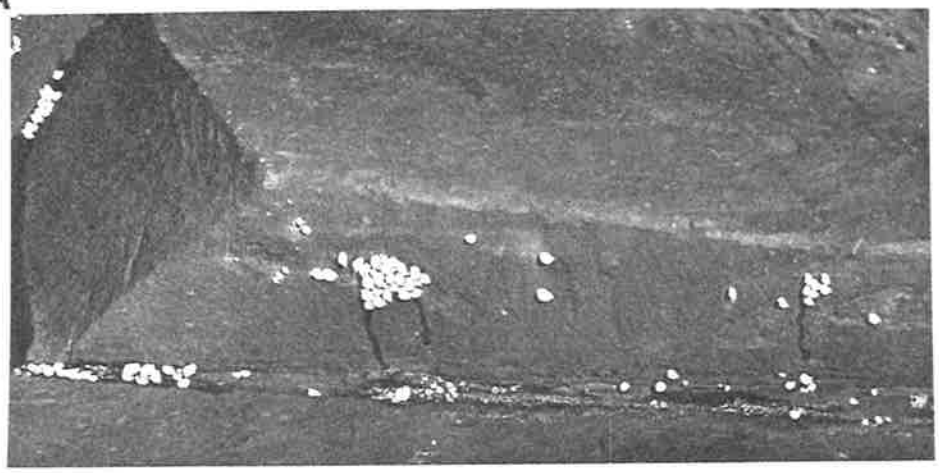
The growth of algae on granite rock is thin in comparison with that growing on other types of rock. This was recognised by the colouration of the rock. When the growth of algae is thick on rock surfaces, it is richly textured in green, whilst it is poorly

Figure 6-2 (A) Groups of Littorina unifasciata on flat exposed rock surface.

(B) A single group of Littorina unifasciata at Fishery Beach (Fleurieu Peninsula).

FIG. 6-2

A



B

Figure 6-3 Occurrence of the two species in the habitat.

Locality: A. Second Valley

B. Marino Rocks

C. Port Willunga

Littorina praetermissa occupies more in the crevices than L. unifasciata.

The area indicated with the arrow in (A) shows where L. praetermissa usually occurs.

This condition is observed in all the localities visited along the South Australian coast.

FIG. 6-3

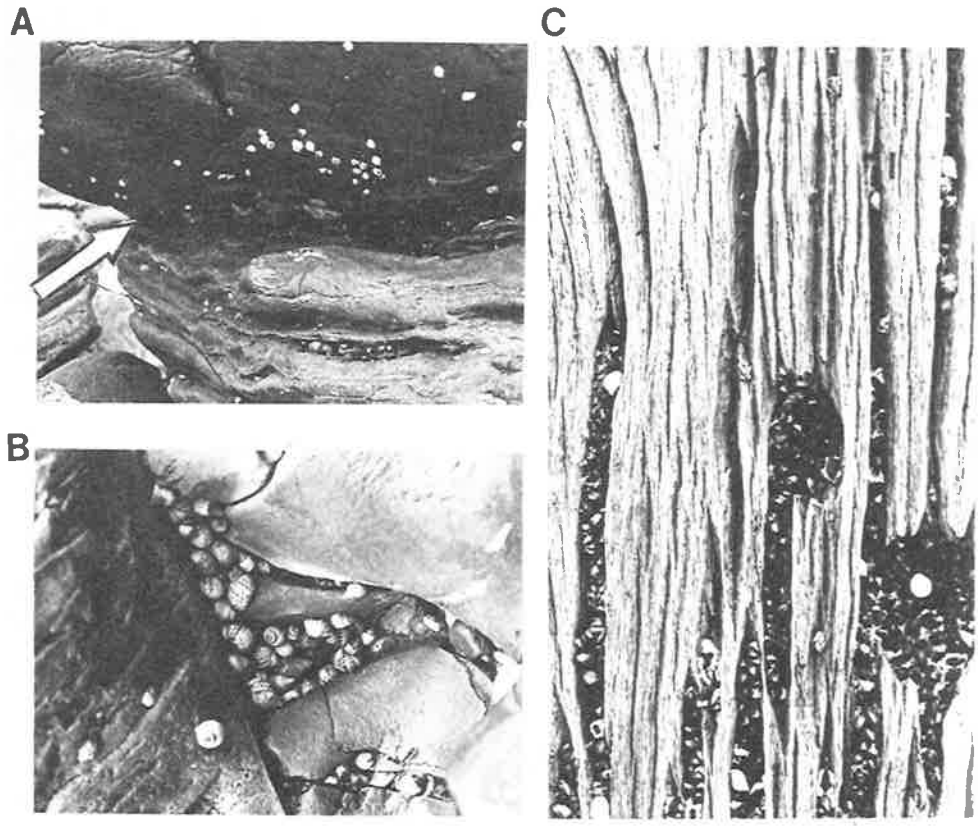
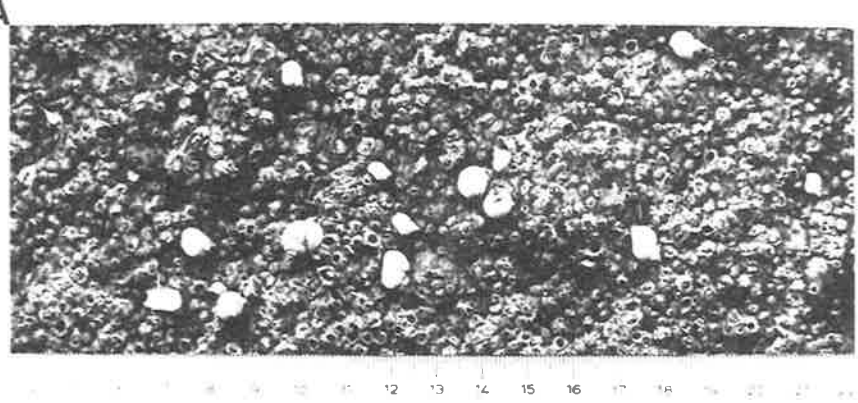


Figure 6-4 (A) The occurrence of the snails together with the barnacle Chamaesipho columna (Spenglu) and (B) with the mussel Modiolus pulex.

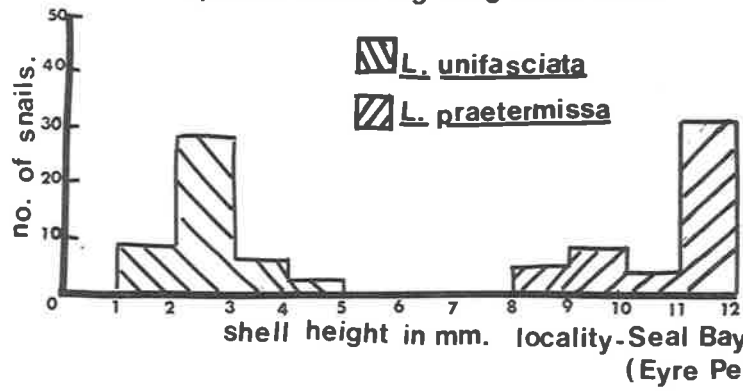
FIG.6-4

A

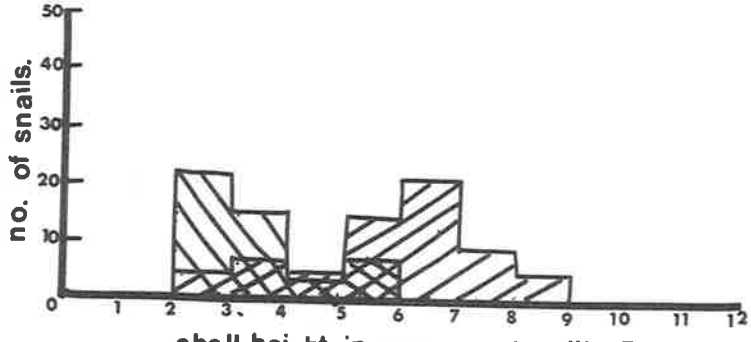


B

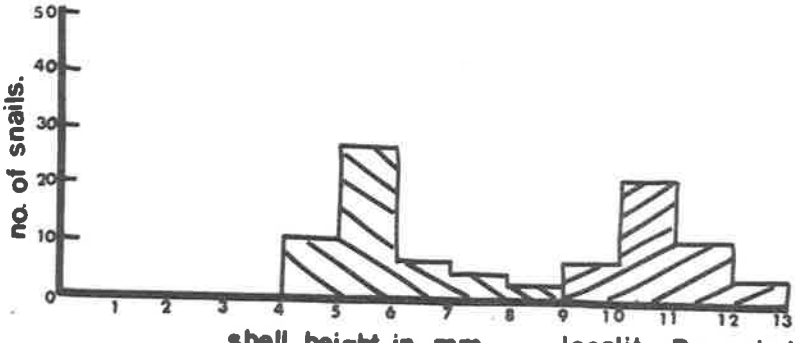
FIG. 6–5. Comparison in the sizes between the two species occurring on granite rocks.



shell height in mm. locality-Seal Bay (Eyre Peninsula)



shell height in mm. locality-Port Elliot (Fleurieu Peninsula)



shell height in mm. locality-Remarkable Rock (Kangaroo Island)

textured in green as thin patches, when the growth of algae is poor. There ~~is~~ are rarely any crevices on the surfaces of granite rock, whilst rock surfaces of schists and quartzites have many crevices.

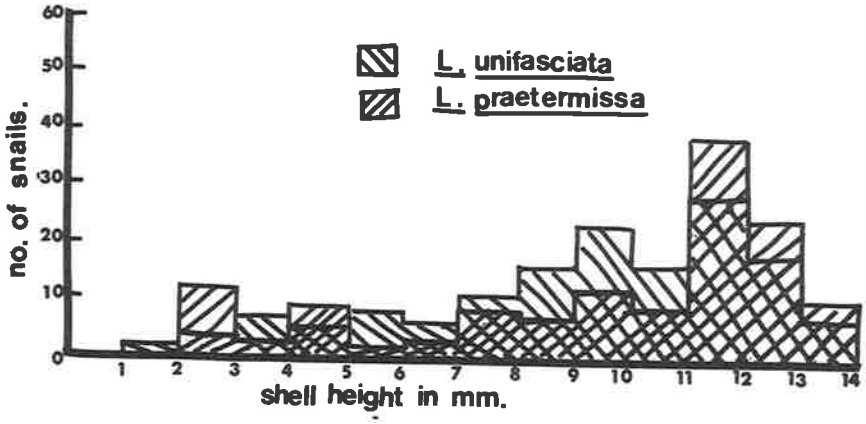
Littorina praetermissa not only seeks sheltered areas and crevices in the habitat, but it is usually found at the lowest level on the seaward faces of the rocks in the supralittoral fringe, whilst L. unifasciata is widely distributed from the uppermost to the lowest levels.

6.3.2 RELATIONSHIP BETWEEN THE DISTRIBUTION OF THE TWO SPECIES IN THE HABITAT

It has been said in the last section that Littorina praetermissa seeks sheltered areas and crevices, whilst L. unifasciata occupies both the sheltered and exposed areas of the habitat. In most of the localities I have visited where the two species are found together, usually 3-5 specimens of L. praetermissa are found with 12-17 snails of L. unifasciata within the same quadrat area. From this, the ratio of the two species could be approximately 1:4.

However, I came across three localities in my study, where Littorina praetermissa is as abundantly distributed as L. unifasciata. These localities are:- (1) Fishery Bay (Eyre Peninsula), (2) Coobowie (Yorke Peninsula) and (3) Cape Du Couedic (Kangaroo Island). Of these three localities, Cape Du Couedic is

FIG. 6-6. Distribution of Littorina unifasciata and Littorina praetermissa on a boulder approximately one metre in height at Cape Du Couedic.



in the coolest part of South Australia. The sea temperatures are lower in summer by 2-3°C but only 1°C or so in winter in this region (see Section 6.2). The one common feature of the areas where L. praetermissa is found in abundance together with L. unifasciata, is that it is very sheltered and never exposed to direct sun.

The terrains at Fishery Bay and Cape Du Couedic are similar. The rocky cliffs slope steeply into the sea with rock platforms at intertidal levels. Boulders are also present at the base of the cliffs. There is an archway shading over the boulders and part of the rock platform at Cape Du Couedic, but there is none at Fishery Bay, instead large boulders present at the base of the cliff shade over the smaller ones. The waves break frequently onto these regions.

A noticeable fact in the occurrence of the two species on the boulders in these areas is that Littorina praetermissa tends to occupy the vertical faces, whilst L. unifasciata occupies the horizontal faces. In the surfaces, where the particular species is found in abundance, there are only a few snails of the other species sparsely distributed.

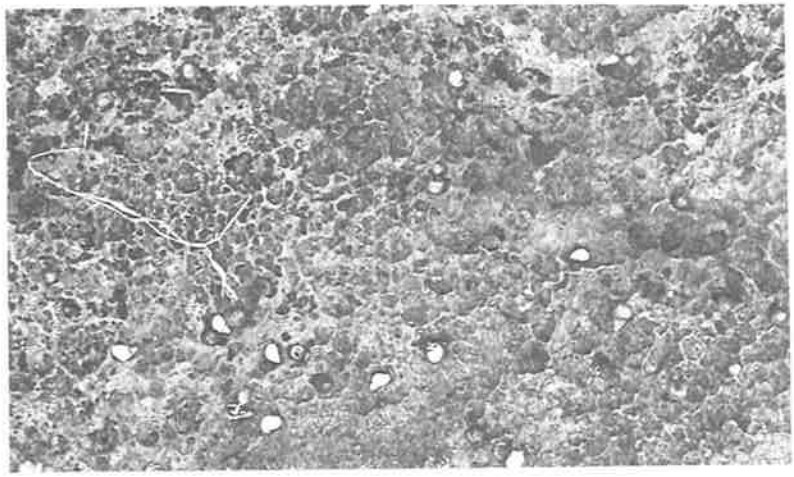
From a boulder at Cape Du Couedic, I collected all the snails present on the vertical and horizontal surfaces. The boulder was approximately one metre in height and 1½ metre in width. Of 145 snails collected from the vertical surface, there were only 17 Littorina unifasciata present together with L. praetermissa and

Figure 6-7 A. The area of the cliff at Coobowie where the snails are found.

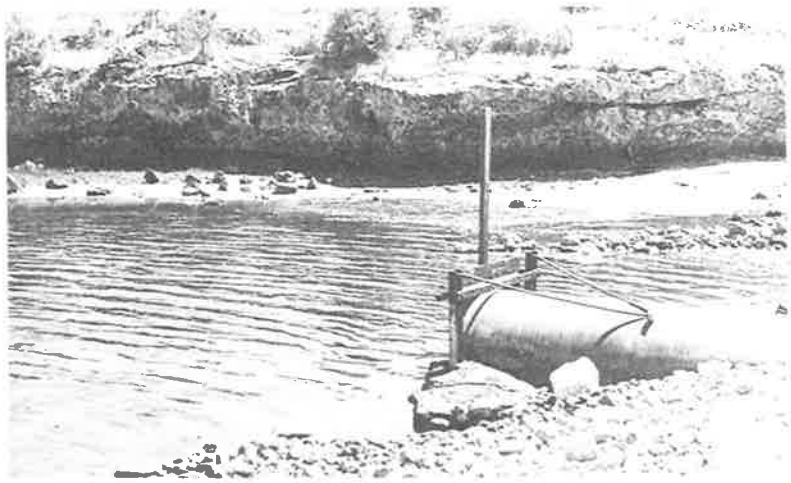
B. Condition of the Coobowie area.

FIG. 6-7

A



B



of 157 snails collected from the horizontal surface, there were only 7 of the latter species present together with the former (see Fig. 6-6). The numbers of snails present together with the other species in each respective species are excluded in the figure.

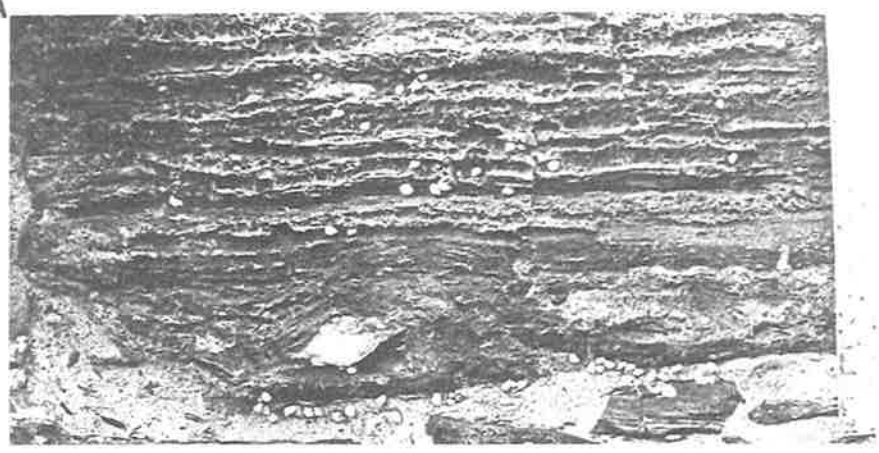
In an area at Coobowie, Littorina praetermissa is found in greater numbers than L. unifasciata. The nature of this area is very different from those at Fishery Bay and Cape Du Cauedic. A part of the sea is cut off by a causeway carrying a highway. The sea can flow through a pipe about 2 feet in diameter with a valve, which allows the tide to run in fairly freely but water flows out more slowly (Fig. 6-7B). As this passage is the only connection with the sea, the tide level in this area is never as low as it is in the sea. Only the basal part of the cliff approximately 1/3 of the height is splashed at high tide. This area of the cliff is covered with crevices and is remarkably sheltered and never exposed to direct sun. The two species are found in the splashed area of the cliff (Fig. 6-7A). From the snails collected in 30cm. quadrats, there were only 2-5 of L. unifasciata found together with 16-23 snails of L. praetermissa in each quadrat. The estimate percentage ratio would be approximately 85%:15%.

Figure 6-8 A. The average size of *Littorina unifasciata* present on the jetty wall at Second Valley.

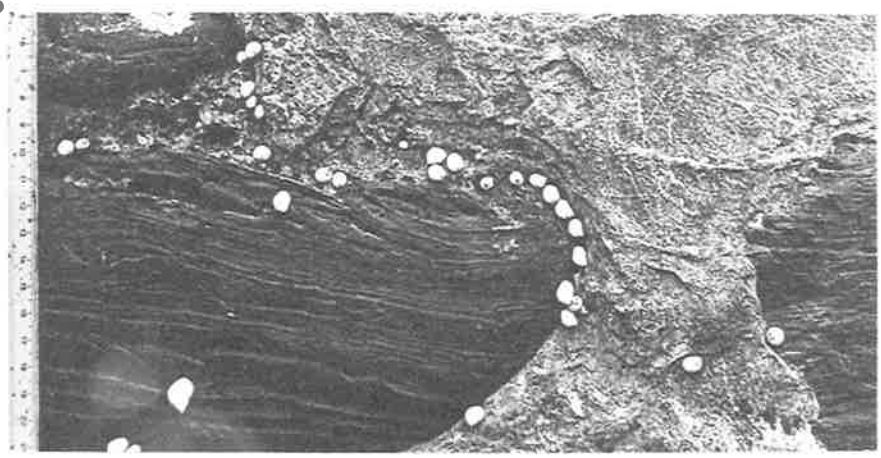
B. The average size of *Littorina unifasciata* present on the landward side of the jetty wall at Second Valley.

FIG. 6-8

A



B



6.3.3 VARIATION IN THE SIZES OF THE SNAILS IN EXPOSED AND SHELTERED COASTS

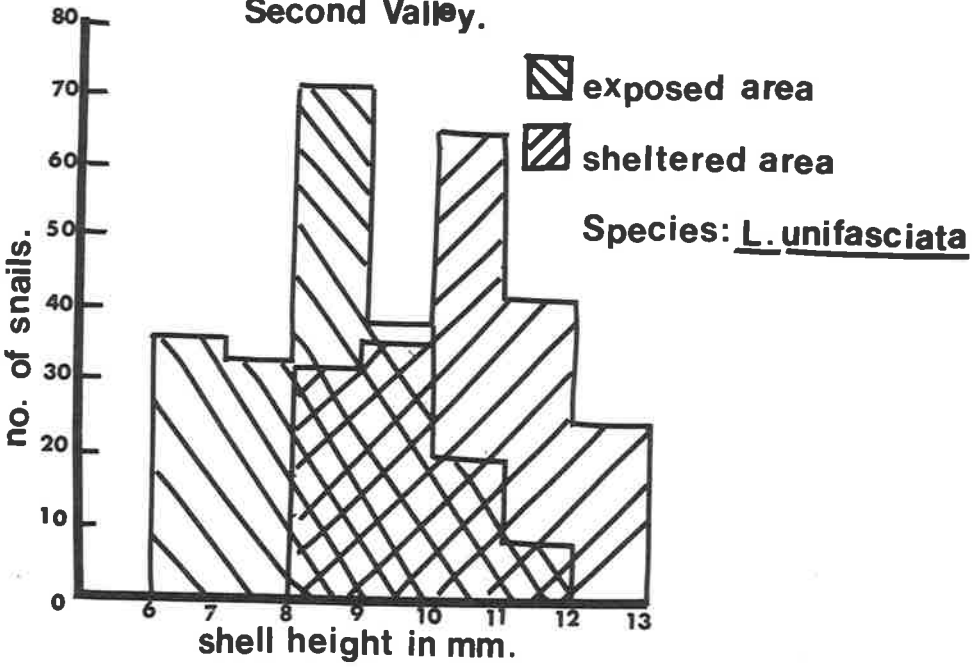
Wave action is more frequent and stronger at high tide level on the habitat of the snails in the exposed coast than it is in the sheltered coast.

Rock types of either schists or quartzites are present in both sheltered and exposed conditions. The two species of my study are found on these rocks, where microscopic algae grow, either in exposed or sheltered coasts. However, the snails inhabiting the habitats of sheltered coast tend to be larger than those of exposed coast.

The above observation was noted in all the localities I have visited along the South Australian coast. The average shell height of the snails in the exposed areas is about 9mm. and that of sheltered areas is about 11mm.

Variation in the sizes of the snails in the exposed and sheltered areas is distinctly noticeable on the jetty wall at Second Valley. The wave action at high tide is stronger and more frequent on the area of the jetty wall facing the sea than on the landward side of the archway. The sizes of the snails inhabiting the former area is considerably smaller than those of the latter area (Fig. 6-8). Unfortunately, there is hardly any *Littorina praetermissa* present on the jetty wall (see 3.3.1). Therefore, adequate numbers of this species were unable to obtain from the jetty wall to show the differences. However, *L. unifasciata*

FIG. 6–9. Comparison in the sizes between the snails collected from exposed and sheltered areas of the jetty wall at Second Valley.



collected randomly from the jetty wall shows the difference in the sizes between the exposed and the sheltered areas (see Fig. 6-9).

The largest size of the snails recorded in both species is about 16mm. and these snails were collected from Coffin Bay (Eyre Peninsula). This locality is noted to be very sheltered along the South Australian coast.

6.4 DISCUSSION AND CONCLUSION

One consistent observation I have made in all the habitats of the snails in the localities visited, is that Littorina praetermissa aggregates more in the sheltered areas and crevices than L. unifasciata which occupies, either exposed or sheltered areas in the habitat and furthermore, the latter species is usually more abundantly distributed than the former.

However, in the three areas (1) Fishery Bay (2) Coobowie and (3) Cape Du Couedic which are greatly sheltered from direct exposure to sun, especially at Coobowie in comparison with other localities, Littorina praetermissa occurs in great numbers and is as abundant as L. unifasciata or more so. Even then in these sheltered areas, the former species occurs in crevices and sheltered rock faces.

Shaded areas and crevices would have lower temperatures and higher humidities when compared with those of exposed faces of the rocks. The snails inhabiting these areas would thus be in less danger of rapid desiccation. Taking these facts into account,

the nature of the occurrence of the two species in the habitat, suggested strongly that Littorina unifasciata probably has higher degree of tolerence to desiccation than L. praetermissa (see Chapter 7). Thus, this fact may explain for the small population of the latter species.

The sparse distribution of the two species on granite rocks is most likely due to the availability of food. The snails are browsers on microscopic algae. They rasp anything off the substratum including detritus and the rock itself (see 3.5.1). The growth of algae on granite rocks is poor, and the rock structure is solid and hard when compared with other types of rocks. Furthermore, there are usually many crevices in the surfaces of quartzites and schists, but crevices are rare in the granite rock. Thus poor growth of algae and the structure of the granite rock may cause the snails to be sparsely distributed. As regards the size of Littorina praetermissa being larger than L. unifasciata on granite rocks, I have no explanation. I have not looked into the physiological conditions of the two species on this aspect.

The variation in the sizes of the snails between exposed and sheltered coasts could be influenced by the time in feeding. Wave action is stronger and more frequent in the exposed coasts than the sheltered coasts. In the laboratory I have observed that the snails when stimulated to activity, adhered firmly onto the substratum with the foot, while water movement was strong around them (see 3.4.3 para. 3). The activities of the snails such as

feeding and mating were observed only when the water had been completely sucked away and the substratum just wetted. Thus, the snails distributed along the exposed coast would have less time in feeding than those of sheltered coast, where there would be quite an interval before the next wave breaks up on to the rocks.

An examination of rock surfaces in the sheltered and exposed coasts shows that the rocks in the former area are more green than those of the latter. Therefore it is most likely that the growth of microscopic algae on sheltered rock is denser than that on exposed rock. If so the availability of food could also affect the variation of the sizes of the snails inhabiting the exposed and sheltered coast.

The overall observation in most of the localities I have visited along the South Australian coast shows that the population of Littorina praetermissa is relatively small compared with that of L. unifasciata and this observation is similar to the preliminary observation I have made in my three study areas, namely Glenelg, Port Willunga and Second Valley.

CHAPTER 7. DESICCATION EXPERIMENT OF THE TWO SPECIES AT VARIOUS TEMPERATURES AND RELATIVE HUMIDITIES

7.1 INTRODUCTION

In most of the previous chapters, I have mentioned that although the two species are sympatric, the population of Littorina praetermissa is considerably smaller when compared with that of L. unifasciata especially in the exposed areas of the habitat, where the former species is sparsely scattered amongst the large numbers of the latter.

"Animals living high in the intertidal zone are, in general, better adapted to resist the extremes of the physico-chemical environment than their counterparts lower on the shore" (Newell 1972 p. 46). The two species in my study inhabit hard surfaces in the supralittoral fringe, where microscopic algae are the only plants. This is an arid zone exposed to extreme of temperatures and desiccation.

From my field observation, I have found that Littorina unifasciata is much more abundantly distributed than L. praetermissa and the latter species occurs more in the sheltered areas and crevices than the former in most of the localities I have studied. Thus, it seems likely that L. unifasciata has a higher degree of tolerance to extreme conditions than has L. praetermissa.

In two of the localities I have visited however, namely Fishery Bay (Eyre Peninsula) and Cape Du Cauedic (Kangaroo Island), I have observed the two species are equally abundantly distributed.

These two localities are sheltered from direct sun and the waves break very frequently over the rocks on which they live (see Section 6.3.1). These areas will experience little desiccation. Therefore, Littorina praetermissa would be as compatible to the environmental conditions as would L. unifasciata.

In an area at Coobowie (southern Yorke Peninsula) which is fully sheltered from direct sun, Littorina praetermissa is more abundant than L. unifasciata (see 6.3.1). Areas which are sheltered from direct sun would have lower rock temperatures than would exposed areas. Hence, the occurrence of the former species in great numbers in fully sheltered areas, suggests that probably low temperatures and high humidities are suitable for this species.

To answer these problems, I conducted desiccation experiments at various relative humidities and temperatures.

7.2 METHODS OF CONDUCTING THE EXPERIMENT

7.2.1 TEMPERATURE AND HUMIDITY CONTROL

The chosen temperatures were 15^{o}, 20^{o} and 25^{o}C, since the snails are most likely to encounter the temperatures within this range in their natural environment. The constant temperatures were obtained by using thermostatically controlled incubators with a fan running continuously. The temperatures in the incubators were checked daily and they were found to be maintained within $\pm 1.0^{o}$C of the experimental temperatures.

I chose saturated solutions as described by Winston and Bates (1960) to maintain constant Relative Humidities (R.H.) since their chart gives a reasonable range of temperatures for one constant R.H.

Saturated solutions of the salt required for specific R.H.'s were kept in desiccators in the temperature cabinets and stabilised for over a period of 14 days. Readings of the R.H.'s were taken with a hair hygrometer for 14 days before running the experiment. These readings were each within $\pm 1\%$ of the required R.H.

A preliminary experiment was run at Relative Humidities 99%, 88%, 75% and 65%. Although some of the snails kept in 75% and 65% R.H.'s died within 4 weeks, the snails in 99% and 88% R.H. remained alive. Therefore, the data obtained was not adequate to do a full analysis. Thus, the R.H. range was changed to be approximately 76%, 70%, 65% and 60% (see Table 7-1).

The four R.H.'s were maintained at each of the experimental temperatures. The only effective way to check the death rates of the snails was to revive them in sea water and the snails were discarded after this (see 7.2.2). Therefore, a set of 4 desiccators was required to maintain each experimental R.H., since the snails were checked weekly, and the experiment was run for a period of 4 weeks.

7.2.2 METHOD OF CHECKING DEAD SNAILS

Pomeroy (1966) in a similar experiment weighed snails (Helicella virgata) and found that when weighed at intervals, at low humidities, there was a sudden fall in the weight when the snails died. The same technique proved to be unsuitable here, as weight decreased at a more or less uniform speed before and after death. A sunken operculum was not a sure sign of death. To determine whether snails were alive or dead, it was necessary to attempt to revive them by the stimulus of wetting as described in Section 3.4.2(c). If they failed to respond to this, they were presumed to be dead. It was therefore necessary to conduct the experiment with large numbers of snails as specimens once stimulated had to be discarded.

Over 900 specimens of each species were required for the experiment (see 7.2.3). Although Littorina unifasciata was available in large numbers, it was more difficult to get L. praetermissa in sufficient numbers from the same locality on local beaches. However, with help from friends, this was achieved.

7.2.3 CONDITIONS OF THE SNAILS KEPT

Twenty individuals of each species were kept together in the same desiccator with controlled R.H. Four different R.H.'s were maintained in each of the experimental temperatures and a set of 4 was necessary for each controlled R.H. (see 7.2.1). Therefore,

there were 16 desiccators with controlled R.H in each temperature cabinet.

Preserving jars of approximately 10cm. in width and 18cm. in height with air tight covers were used as desiccators. The mouth of the jars was further sealed with thin plastic sheets.

These jars accommodated plastic coated racks with five shelves. Of the 20 specimens of each species used, 5 snails of each species were kept together in petri dishes of approximately 1 x 4cm., were placed on the shelves. This condition applied in all the desiccators used. The snails in each experimental R.H. in each temperature cabinet were checked as described in Section 7.2.2 and discarded after.

7.3 RESULT

TABLE 7-1 NUMBER OF SNAILS DEAD AT VARIOUS TIMES, TEMPERATURES AND HUMIDITIES

Temp.	Relative Humidity	Initial No. of snails for each week	Number of snails dead							
			1st week		2nd week		3rd week		4th week	
			*U	P	U	P	U	P	U	P
15°C	76% (Nacl)	20	-	-	-	1	-	2	2	4
	70% (NH_4No_3)	20	-	-	-	-	-	2	3	5
	68% ($NaNo_2$)	20	-	-	-	-	-	4	4	10
	61% ($NaBr.2H_20$)	20	-	-	-	-	1	7	7	12
20°C	76% (Nacl)	20	-	-	-	-	1	3	3	5
	70% (Nacl+Kcl)	20	-	-	-	-	2	4	3	7
	65.5%($NaNo_2$)	20	-	-	1	2	2	5	4	12
	59.0%($NaBr.2H_20$)	20	-	-	1	3	4	11	7	14
25°C	75.5%(Nacl)	20	-	-	-	1	2	5	3	7
	71.5%(Nacl+Kcl)	20	-	-	-	1	3	6	5	9
	64% ($NaNo_2$)	20	-	-	-	1	4	9	7	12
	60% ($Fecl_2.2H_20$)	20	-	-	1	2	5	11	7	16

* U = *Littorina unifasciata*, P = *L. praetermissa*

7.3.1 ANALYSIS OF THE RESULT

1. The data from two species of snail consisted of the number of deaths/cell (from a possible 20) in a 4 x 3 x 4 factorial experiment.

(Species 1 ≡ Littorina unifasciata, 2 ≡ L. praetermissa). The factors were: (1) time : 1, 2, 3, 4 weeks

(2) temperature : $15^{o}C$, $20^{o}C$, $25^{o}C$

(3) humidity : 75.8%, 70.5%, 65.8%, 60%

2. The data for Weeks 1 and 2 for each species were not suitable for analysis. Only 13 deaths occurred from a possible 240.

3. The analysis consisted of fitting and comparing logit models.

4. Logit model

$$P(\underset{\sim}{x}) = \Pr\{\text{death} \mid \underset{\sim}{x}\} = \frac{e^{\underset{\sim}{\beta}^{1}\underset{\sim}{x}}}{1 + e^{\underset{\sim}{\beta}^{1}\underset{\sim}{x}}} \qquad \text{("death function")}$$

where $\underset{\sim}{x}$ = vector of known observation

$\underset{\sim}{\beta}$ = vector of coefficients (to be estimated)

5. Inspection of the data suggested that the factors (1), (2), (3) above could be used linearly, with (perhaps) one interaction term needed.

i.e. $x_1 = 1$

x_2 = temperature (t)

x_3 = humidity (h)

x_4 = t x h

x_5 = time (T)

6. A logit model with $\underset{\sim}{x}$ as in 5 was fitted by the method of maximum likelihood to <u>each</u> species, and the fit tested by chi-square. In both cases the agreement between model and data was acceptable.

<u>Species 1</u> : $\chi^2_{18} = 10.24$

<u>Species 2</u> : $\chi^2_{18} = 4.11$

7. A new model was then fitted with

$$x_1 = \begin{cases} 1 & \text{species 1} \\ 0 & \text{species 2} \end{cases}$$

$$x_2 = \begin{cases} 0 & \text{species 1} \\ 1 & \text{species 2} \end{cases}$$

$x_3 = t$

$x_4 = h$

$x_5 = t \times h$

$x_6 = T$

This model was tested against the separate models described in 6 using the likelihood ratio test. A non-significant chi-square value of 2.3 on 4 d.f. was obtained. As a further check, this new model was compared with the data by the χ^2 goodness-of-fit test, resulting in $\chi^2_{41} = 16.49$.

<u>CONCLUSION</u>: the effect of time, temperature and humidity on the probability of death is the same for both species.

8. A common model (i.e. $\underset{\sim}{x}$ as in 5) was fitted to both species, and tested against the model in 7 giving $\chi^2_1 = 61.16$ (sig. at "any" level).

CONCLUSION: the species have basically different death functions.

9. Let the probability of death be $P_1(\underset{\sim}{x})$ and $P_2(\underset{\sim}{x})$, with parameters $\underset{\sim}{\beta}_1 = \begin{bmatrix} \gamma_1 \\ \underset{\sim}{\gamma} \end{bmatrix}$ and $\underset{\sim}{\beta}_2 = \begin{bmatrix} \gamma_1 \\ \underset{\sim}{\gamma} \end{bmatrix}$ respectively. (Follows from 7.)

Then when $.05 \leqslant P_1(\underset{\sim}{x}), P_2(\underset{\sim}{x}) \leqslant .95$,

$$P_1(\underset{\sim}{x}) \doteqdot \frac{1}{2} = \frac{1}{6}(\gamma_1 + \underset{\sim}{\gamma}^1 \underset{\sim}{x}) \quad \text{and} \quad P_2(\underset{\sim}{x}) \doteqdot \frac{1}{2} + \frac{1}{6}(\gamma_2 + \underset{\sim}{\gamma}^1 \underset{\sim}{x})$$

Therefore, $P_2(\underset{\sim}{x}) - P_1(\underset{\sim}{x}) \doteqdot \frac{1}{6}(\gamma_2 - \gamma_1)$

and $V(P_2(\underset{\sim}{x}) - P_1(\underset{\sim}{x})) = \frac{1}{36}\left[V(\gamma_2) + V(\gamma_1) - 2\mathrm{Cov}(\gamma_1, \gamma_2)\right]$

Using the maximum likelihood estimates of these parameters

$$P_2(\underset{\sim}{x}) - P_1(\underset{\sim}{x}) \doteqdot \frac{1}{6}(3.58 - 2.34) = .21$$

$$V(P_2(\underset{\sim}{x}) - P_1(\underset{\sim}{x})) \doteqdot \frac{1}{36}\left[23.95 + 23.94 - 2 \times 23.93\right] = 8.3 \times 10^{-4}$$

i.e. $P_2(\underset{\sim}{x}) \doteqdot P_1(\underset{\sim}{x}) + (.21 \pm .06)$

CONCLUSION: for a given set $\underset{\sim}{x}$ of observations

Pr {death in species 2} = Pr {death in species 1} + .21

7.3.2 DISCUSSION AND CONCLUSION

The model used in the analysis of the result is a standard model. The data obtained from the experiment were rather limited. Therefore, all the information wanted, could not be analysed. However, death rate of *Littorina praetermissa* is higher than *L. unifasciata*. In other words, it shows that the latter has higher degree of tolerance to arid environmental conditions than

the former.

The species with lower tolerance to environmental conditions would be less likely to survive in areas of extreme desiccation than would the ones with higher tolerance. This could account for the sparse distribution of Littorina praetermissa in the exposed areas of the habitat. The species could however, survive in the sheltered areas and crevices. Lower tolerance in L. praetermissa might account for the smaller numbers of the species usually found.

BIBLIOGRAPHY

Allen, J.F. (1952) The morphology of the radula of Littorina irrorata (Say). Trans. Am. microsc. Soc. 71(2) : 139-145.

Anderson, D.T. (1960) The life histories of marine prosobranch molluscs. J. malacol. Soc. Aust. 4 : 16-29.

Andrewartha, H.G. (1970) Introduction to the study of animal populations. (Second edition) Methuen.

Barnes, (1964) Invertebrate Zoology Saunders.

Berry, A.J. (1961) Some factors affecting the distribution of Littorina saxatilis (Olivi). J. Anim. Ecol. 30 : 27-45.

Bingham, F.O. (1972) Several aspects of the Reproductive Biology of Littorina irrorata (Gastropoda). Nautilus 86(1) : 8-10.

Buckland, Nicks, et al. (1973) Oviposition and development of two intertidal snails Littorina sitkana and Littorina cutulata. Can. J. Zool. 51 : 359-365.

Burden, Jones C. and Charles, G.H. (1958) Light reactions of littoral gastropods. Nature 181 : 129-131.

Chestnut, A.T. (1955) The distribution of oyster drills in North Carolina. Proc. natn. Shellfish Ass. 46 : 134-139.

Chu, George W.T.C. and Edwards, P.R. (1960) A technique for maintenance of the snail Littorina pintado in the laboratory. J.Parasit. 46 : 249 (Biological abstracts).

Cole, H.A. (1942) The American whelk tingle, Urosalpinx cinerea (Say), on British oyster beds. J. mar. biol. Ass. U.K. 25 : 477-501

Colman, J. (1933) The nature of the intertidal zonation of plants and animals. J. mar. biol. Ass. U.K. 18 : 435-476.

Comfort, A. (1951) The pigmentation of molluscan shells. Biol. Rev. 26 : 285-301.

Cotton, B.C. (1959) South Australian Mollusca (Archaeegastropoda). W.L. Hawes, Government Printer, Adelaide.

Crowe, John H. (1972) Evaporative water loss by tardigrades under controlled relative humidities. Biol. Bul;. 142(3) : 407-416

Dahl, A.L. (1964) Macroscopic algal foods of Littorina planaxis Philippi and Littorina scutulata Gould (Gastropoda Prosobranchiata). The Veliger 7(2) : 139-143.

Dehnel, P.A. (1955) Rates of growth of gastropods as a function of latitude. Physiol. Zool. 29 : 115-144.

Evans, F. (1965) The effect of light on zonation of the four periwinkles, Littorina littorea(L.), L. obstusata(L.), L. saxatilis (Olivi) and Melarapha neritoides(L.) in an experimental tidal tank. Neth. J. sea. Res. 2 : 556-565.

Evans, R.G. (1948) The lethal temperatures of some common British littoral molluscs. J Anim. Ecol. 45 : 165-173.

Federighs, H. (1931a) Further observation on the size of Urosalpinx cinerea (Say). J Conch. 19 : 171-176.

Fraser, J.H. (1931) On the size of Urosalpinx cinerea (Say) with some observation on weight length relationships. Proc. malacol. Soc. Lond. 19 : 243-254.

Fretter, V. (1948) The structure and life history of some minute prosobranchs of rock pools. J. mar. biol. Ass. U.K. 27 : 597-632.

Fretter and Graham (1962) British prosobranch molluscs. Ray Society.

Fretter, V. and Shale, D. (1973) Distribution of prosobranch veligers. J. mar. biol. Ass. U.K. 53 : 471-492.

Gibson, III D.G. (1964) Mating behaviour of Littorina planaxis Philippi (Gastropoda Prosobranchiata). The Veliger 7(2) : 134-139.

Graham, A. and Fretter, V. (1947) The life history of Patina pellucida(L.). J. mar. biol. Ass. U.K. 26 : 590-601.

* GOWANLOCH, J.N & HAYES, F.R (1926) Contributions to the study of marine gastropods I. The physical factors, behaviour and intertidal life of Littorina. Contr. canad. Biol. N.S 3 pp135-165

Graham, A. (1954b) Some observations on the reproductive tract of Ianthina janthina(L.). Proc. malac. Soc. Lond. 31 : 1-6.

Gray (1826) P.P. King, Narrative of a survey of the coasts of Australia. Vol. 2, App. B. p. 483.

Gray (1850) Figures of Molluscous animals. 4 : 78.

Hancok, D.A. (1956) The structure of the capsule and the hatching process in Urosalpinx cinerea (Say). Proc. Zool. Soc. Lond. 127 : 565-571.

Haseman, J.D. (1911) The rhythmical movements of Littorina littorea synchronous with ocean tides. Biol. Bull. Woods Hole 21 : 113-121.

Hyman, L.H. (1967) The Invertebrates. Vol. VI, McGraw Hall, New York.

Krull, W.H. (1934) Life history studies on Cotyphoron cotylophoron (Fischaedei 1901) Stiles and Goldhergen 1901. J. Parasit. 20 : 173-180.

Lebour, M.V. (1931a) The larval stages of Nassarius reticulatus and Nassarius incerassatus. J. mar. biol. Ass. U.K. 17 : 797-818.

Lebour, M.V. (1931b) The larval stages of Triora europaea. J. mar. biol. Ass. U.K. 17 : 819-832.

Lebour, M.V. (1932a) The larval stages of Simnia patula. J. mar. biol. Ass. U.K. 18 : 107-115.

Lebour, M.V. (1932b) The eggs and early larval stages of two commensal gastropods, Stilifer stylifer and Odostomia eulimoides. J. mar. biol. Ass. U.K. 18 : 117-122.

Lebour, M.V. (1933b) The life histories of Cerithiopsis tuberculous (Montagu), C. larleei Jeffreys and Triphora perversa(L.). J. mar. biol. Ass. U.K. 18 : 491-498.

Lebour, M.V. (1935a) The breeding of Littorina neritoides. J. mar. biol. Ass. U.K. 20 : 373-378.

Lebour, M.V. (1936) Notes on the eggs and larvae of some Plymouth Prosobranchs. J. mar. biol. Ass. U.K. 20 : 547-565.

Lebour, M.V. (1937) The eggs and larvae of the British prosobranchs with special reference to those living in the plankton. J. mar. biol. Ass. U.K. 22 : 105-166.

Lebour, M.V. (1945) The eggs and larvae of prosobranchs from Bermuda. Proc. Zool. Soc. Lond. 114 : 462-489.

Lebour, M.V. (1947) Notes on the inshore plankton of Plymouth. J. mar. biol. Ass. U.K. 26 : 527-547.

LINKE, O. (1935) Der Laich von LITTORINA (MELARAPHE) NERITOIDES L. Zool. Anz 112 pp 57-62.

Lysaught, A.M. (1941) The biology and trematode parasites of the gastropod Littorina neritorides(L.) on the Plymouth Breakwater. J. mar. biol. Ass. U.K. 25 : 41-67.

Lysaught, A.M. (1943) The incidence of larval trematodes in males and females of the gastropod Littorina neritorides(L.) on the Plymouth Breakwater. Parasitology 35 : 17-22.

May (1908) Papers and Proceedings of the Royal Society of Tasmania for 1908, p. 57, pl. 6. fig. 3.

Menke, (1843) Molluscorum Novae Hollandiae (1844) Zeitschrift für Malakozoologie p. 57.

Moore, H.B. (1934) The relation of the shell growth to environment in Patella vulgata. Proc. malac. Soc. Lond. 21 : 217-222.

Moore, H.B. (1937a) The biology of Littorina littorea Part 1. Growth of the shell and tissues, spawning length of life and mortality. J. mar. biol. Ass. U.K. 21 : 72-742.

Moore, H.B. (1938a) The biology of Purpura lapillus Part II. Growth. J. mar. biol. Ass. U.K. 23 : 57-66.

Moore, H.B. (1938b) The biology of Purpura lapillus Part III. Life history and relation to other environmental factors. J. mar. biol. Ass. U.K. 23 : 67-74.

Moore, H.B. (1940) The biology of Littorina littorea Part II. Zonation in relation to other gastropods on stony and muddy shores. J. mar. biol. Ass. U.K. 24 : 227-237.

Moore, R.C. (1960) Treatise in Invertebrate Paleontology Part I. Mollusca I geological society of America, University of Kansas Press.

Morgan, C.L. (1894) The Homing of limpets. Nature Lond. 51 : 127.

Murray, F.V. (1964) The spawn of some Australian marine prosobranch molluscs. Aust. natn. Hist. 24 : 405-408.

Newcombe, C.L. et al. (1936) Preliminary report on respiratory studies of Littorina irrorata. Nature Lond. 137 : 33.

Needham, J.G. et al. (1937) Culture methods for Invertebrate animals. Dover Publications Inc., New York.

Nevill (1885) Hand list of Mollusca in the Indian Museum Calcutta, Part 2, p. 141.

Newell, G.E. (1958a) The behaviour of Littorina littorea under natural conditions and its relation to position on the shore. J. mar. biol. Ass. U.K. 37 : 229-239.

Newell, G.E. (1958b) An experimental analysis of the behaviour of Littorina littorea(L.) under natural conditions and in the laboratory. J. mar. biol. Ass. U.K. 37 : 241-266.

Newell, R.C. et al. (1971) Factors affecting the feeding rate of winkle Littorina littorea. Mar. Biol. 9 : 138-144.

Newell, R.C. (1972) Biology of intertidal animals (Paul Elek) (Scientific Books Limited).

North, W.J. (1954) Size distribution, erosive activities and metabolic efficiency of the marine intertidal snails, Littorina planaxis and L. scutulata. Biol. Bull. Woods Hole 106 : 185-197.

Orton, J.H. (1929a) Habitats and feeding habits of Ocenebra erinacea. Nature Lond. 124 : 370-371.

Orton, J.H. (1929b) Observations on Patella vulgata Part III. Habitat and habits. J. mar. biol. Ass. U.I. 16 : 277-288.

Orton, J.H. (1946) Biology of Patella vulgata L. Nature Lond. 158 : 173-174.

Orton, J.H. et al. (1956) Studies on the biology of limpets Part II. The breeding of Patella vulgata L. in Britain. J. mar. biol. Ass. U.K. 35 : 149-176.

Ostergaard, J.M. (1950) Spawning and development of some Hawaiian marine gastropods. Pacif. Sci. 4(2) : 75-115.

Peile, A.J. (1937) Some radula problems. J. Conch. 20 : 292-304.

Peters, R.L. (1964) Function of the cephalic tentacles in Littorina planaxis Philippi (Gastropoda Prosobranchiata). Veliger 7(2) : 143-148.

Philippi (1847) Abbildunges and Bechreibungen Conchylien. 2 : 165, Littorina pl. 3, fig. 17 (a).

Picken, L.E.R. (1937) The mechanism of urine formation in invertebrates II. The excretory mechanism of certain Mollusca. J. exp. Biol. 14 : 20-34.

Pilkington, M.C. (1971) Eggs, larvae and spawning in Melarapha cincta (Quoy and Gaimard) and M. oliveri Finlay (Littorinedae Gastropoda). Aust. J. mar. Freshwat. Res. 22 : 79-90.

Pomeroy, D.E. (1966) The ecology of Helicellar virgata and related species of snails in South Australia (Ph.D. thesis, Adelaide Uni.).

Prosser and Brown (1961) Comparative animal physiology (Second editions) Saunders.

Quoy and Gaimard (1833) Voyage de de'couvertes del' Astrolabe, 2(2) : 479 pl. 33, fig. 8-11.

Quick, H.E. (1924) Length of life of Paludestrina ulvae.

Rees, C.B. (1940) A preliminary study of the ecology of a mud-flat. J. mar. biol. Ass. U.K. 24 : 185-199.

Reeve (1858) Conchologia Iconica, Vol. 10, Littorina pl. 17. Fig. 95.

Rolf, F.J. and Sokal, R.R. (1969) Statistical tables (W.H. Freeman and Co., San Francisco).

Rosewater, J. (1970) The family Littorinidae in the Indo-Pacific. Indo-Pacifi. Mollusca 2(2) : 417-506.

Schilder, F.A. (1936) Anatomical characters of the Cypraecea which confirm the conchological classification. Proc. malac. Soc. Lond. 22 : 57-112.

Segal, E. (1956) Adaptive differences in water holding capacity in an intertidal gastropod. Ecology 37 : 174-178.

Seshappa, G. (1947) Oviparity in Littorina saxatilis (Olivi). Nature London 166 : 335.

Smith, J.C. and Newell, G.E. (1955) The dynamics of the zonation of the common periwinkle Littorina littorea(L.) on a stony beach. J. anim. Ecol. 24 : 35-36.

Smith, A.W. (1958) The resistance of animals to cooling and freezing. Biol. Revs. 33 : 35-36.

Sokal, R.R. and R.F.J. Biometry (W.H. Freeman and Co. San Francisco).

Sollas, I.B.J. (1907) The molluscan radula, its chemical composition and some points in its development. Q. Jl. microsc. Sci. 51 : 115-136.

Southward, A.J. (1958) Note on the temperature tolerances of some intertidal animals in relation to environmental temperatures and geographical distribution. J. mar. biol. Ass. U.K. 37 : 49-66.

Southward, A.J. and Orton, J.H. (1954) The effects of wave action on the distribution and numbers of the commoner animals living on the Plymouth Breakwater. J. mar. biol. Ass. U.K. 33 : 1-19.

Stephenson, T.A. and Stephenson, Anne (1949) The universal features of zonation between tide marks on rocky coasts. J. Ecol. 37 : 289-305.

Stephenson, T.A. and Stephenson, Anne (1972) Life between tide marks and rocky shore. (W.H. Freeman and Co. San Francisco).

Struhsaker, J.W. (1966) Breeding, spawning, spawning periodicity and early development in the Hawaiian Littorina: L. pintado (Wood), L. picta, Philippi and L. scabra (Linnaeus). Proc. malac. Soc. Lond. 37 : 137-166.

Struhsaker, J.W. and Costlew Jr., J.D. (1968) Larval development of Littorina picta (Prosobranchia Mesogastropoda) reared in the laboratory. Proc. malac. Soc. Lond. 38 : 153-160.

Tattersall, W.M. (1920) Notes on the breeding habits and life history of the periwinkle. Sci. Invest. Fisheries Branch, Dept. Agr. Ireland 1 : 1-11.

Thompson, D.A.W. (1942) On growth and form (Cambridge University Press).

Whipple, J.A. (1965) Systematics of the Hawaiian Littorina Ferussac (Mollusca: Gastropoda) 7 (3) : 155-166.

Wilbur, K.M. and Young, C.M. (1964) Physiology of Mollusca. (Academic Press: New York).

Wilson, D.P. (1929) A habit of the common periwinkle (Littorina littorea Linn). Nature Lond. 124 : 443.

Winston, P.W. and Bates, D.H. (1960) Saturated solutions for the control of humidity in Biological Research Ecology 42 : 232-237.

Womersley, H.B.S. and Edmonds, S.J. (1958) A general account of the intertidal ecology of South Australian coasts. Aust. J. mar. Freshwat. Res. 9(2) : 217-260.

Wrigley, A. (1934) Spiral sculpture and colour markings of the Cassididae. Proc. malac. Soc. Lond. 9(2) : 217-260.

Wrigley, A. (1948) The colour patterns and sculpture of molluscan shells. Proc. malac. Soc. Lond. 27 : 206-217.

Young, R.T. (1946) Stimulation of spawning in the mussel (Mytilus californianus). Ecology 26 : 58-69.