ASPECTS OF THE BIOLOGY OF *LUTRARIA LUTRARIA* (L.) (BIVALVIA : MACTRACEA)

Thesis

for the

Degree of Doctor of Philosophy

in the

University of Glasgow

by

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Date: November, 1981

DECLARATION

I hereby declare that this thesis describes work carried out by myself, unless otherwise cited or acknowledged, and that it is my own composition.

This dissertation has not in whole, or in any part, been previously presented for any other degree.

A.K Kerr

A.K. Kerr

Date: 12th November 1981

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SUMMARY

1. The life history of a population of Lutraria lutraria in a depth of 7m at Hunterston, Ayrshire is discussed. Much of the present population is thought to have settled in 1967.

2. The functional morphology of Lutraria is described and related to its life as a large, deep-burrowing bivalve.

3. Lutraria spawned in late spring and continued to do so through the summer in 1979 and 1980. Animals became spent in August and September.

4. Unsuccessful attempts were made to induce spawning in the laboratory. Artificial fertilization was successful but development did not proceed beyond the ciliated gastrula stage.

5. Larvae of Lutraria were not identified in plankton samples and young stages were not encountered in sieved sediment samples.

6. The biochemical cycle of the total animal and five component parts (gonad and visceral mass, digestive gland, adductor muscle, siphon and 'other' tissue) is investigated.

7. A marked increase in weight, reflected in an increase in weight of the component parts, was recorded in Autumn 1979. This is thought to be related to an exceptional increase in the phytoplankton at this time.

8. Although a relationship between the biochemical cycle and reproductive cycle remains uncertain, definite seasonal changes were recorded in the respiration rate of Lutraria. At 10°C, the maximum rate of a standard 20g animal was 0.1283mls O_2/g. dry wt./hr. in May 1980 and the minimum rate was 0.059mls O_2/g. dry wt./hr. in October 1980.

9. The effect of temperature on respiration rate was also investigated. Significant differences were recorded for five experimental temperatures (10°C, 15°C, 20°C, 25°C and 30°C) in August and October but only between two temperatures (10°C and 30°C) in April. There was a decrease in respiration rate at 30°C in August and October, but an increase in April.

10. Respiration rate is affected by a reduction in oxygen tension. A variety of responses were recorded with a small degree of regulation shown.

11. Individuals of Lutraria were able to survive 48 hours under anaerobic conditions.

12. In fully oxygenated conditions heart rate ranged from 4-15 beats per minute with an average of 8 beats per minute. Heart beat was markedly affected by changes in temperature and oxygen tension, increasing to a maximum 22 beats per minute at 25°C, and decreasing to a minimum 2 beats per minute in anaerobic conditions.

13. Heart rate is reduced (12 beats per minute to 5 beats per minute) on exposure to air.

14. Lutraria exhibits an intermittent pattern of pumping activity. Under normal conditions 35% of the time is spent pumping and this increases as oxygen is reduced ($\triangleq$3.00mls O_2/litre) to 65% of the time spent pumping.

15. Under normal conditions the respiratory flow varies between 0.382 litres per hour and 1.023 litres per hour.

16. Adult Lutraria maintain their ability to burrow, albeit slowly.

INTRODUCTION (GENERAL)

In the past, inacessibility of certain shallow sublittoral bivalve species has prohibited the investigation of their general biology. The recent development of suitable sampling techniques has now made these studies possible.

Lutraria lutraria is a deep burrowing mactrid occurring for the most part, in the sublittoral zone but is found on a few West Coast sandy shores at very low spring tides. Although of little commercial value to date, this species is of interest in terms of its adaptations to its deep burrowing mode of life in comparison to other large deep burrowing bivalves. Previous workers have dealt with some aspects of the life of Lutraria. For example, Yonge (1949) discusses cleansing mechanisms of the mantle and the fourth pallial aperture, Holme (1959) the taxonomy of the Lutraridae found in the United Kingdom and Hunt (1973) the chemical analysis of the siphon sheath.

The aim of the present work is to study the general biology of Lutraria and concentrates on four aspects. Form and function is described and its adaptations to a life permanently buried deep in the sediment are discussed. The seasonal variation in the biochemical components, (protein, lipid, carbohydrate and ash), are determined and related to the reproductive cycle. Metabolism is investigated through measurement of respiration, heart and pumping rates, and the effect of certain environmental factors on them determined. The biochemical analyses are also related to the metabolic data for the large size of the adult lends itself to physiological studies of this nature. Finally, investigations have been made on burrowing behaviour and population structure.

CHAPTER 1

SAMPLING TECHNIQUES AND ECOLOGY

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1.1. SAMPLING TECHNIQUES

Lutraria lutraria were obtained from a subtidal site at Hunterston in the Clyde Sea Area (Fig. 1.1.). A diver operated bottom sampler designed by Barnett and Hardy (1967), modified for operation from a boat (pers. comm. P. Barnett) was used to collect specimens. Barnett and Hardy (1967) discuss the need for this type of equipment which utilizes an airlift pump to force a cylinder into the sediment and how it could be of particular use in the study of the deep burrowing macrofauna, e.g. Lutraria spp. and Ensis spp. The sampler covers an area of $0.1m^2$ and can penetrate to a depth of 60cm. Plates 1.1. and 1.2. illustrate the bin in action. On two occasions only (September 1979 and December 1979) gales in the Clyde prevented the use of the suction bin, however, on these occasions it was possible to obtain animals by digging at extreme low water tide on the adjacent Fairlie Sands.

In late 1979 and early 1980 mass mortalities occurred at the original sampling site and it was necessary to move slightly inshore. In the shallower water there was an insufficient head of water to use the suction bin and an alternative method was sought. An hydraulic hose from the boat was utilized by the diver to remove individuals from the sediment. The bin was placed randomly on the sediment.

The contents were sieved through a fine mesh on the boat in an endeavour to obtain juveniles and to determine what other species of

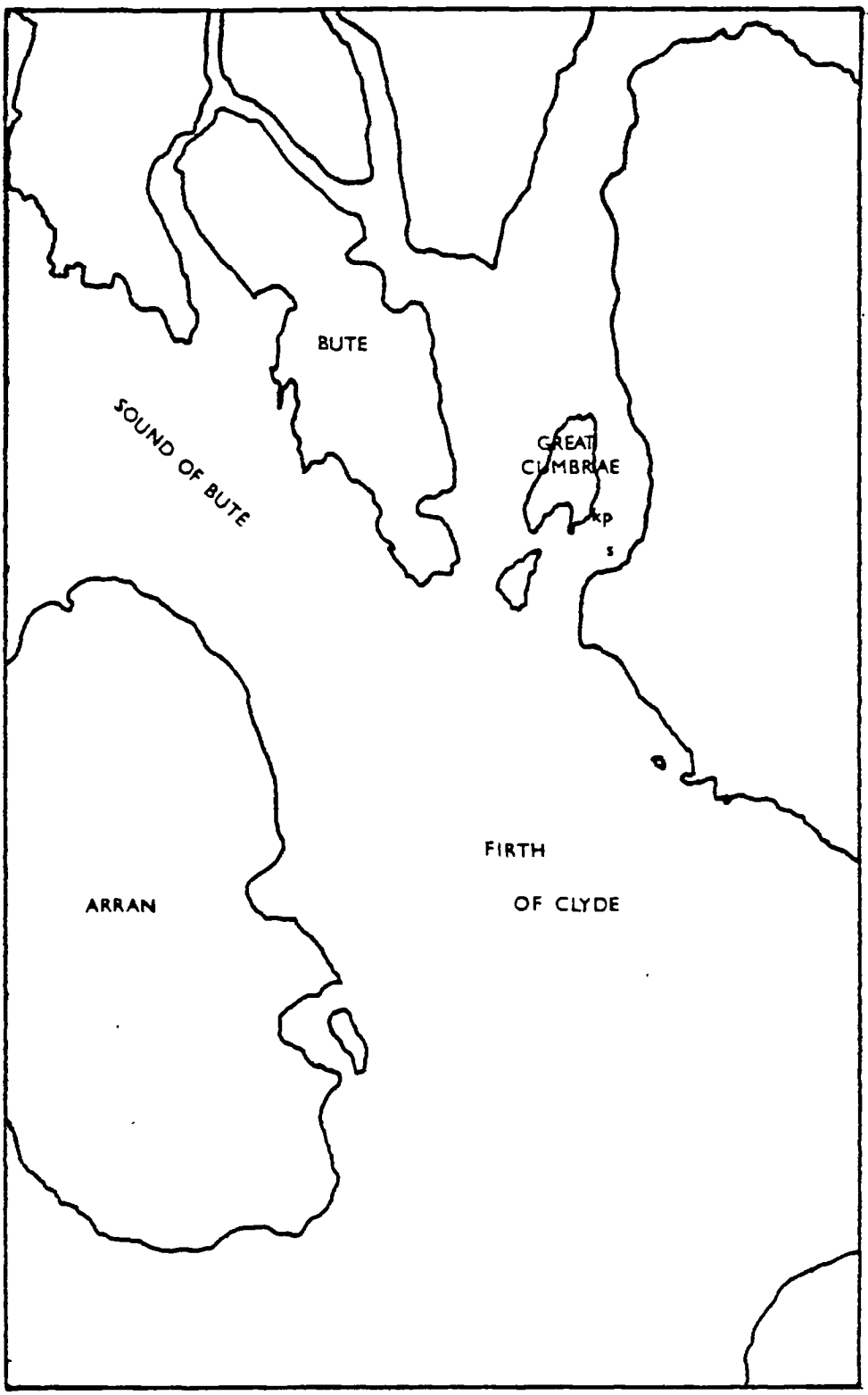
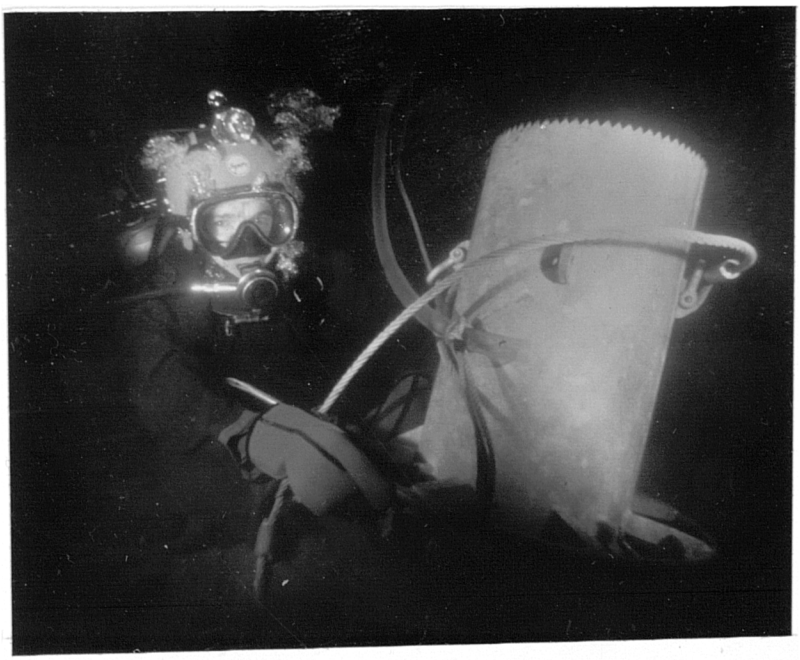


Figure 1.1. Diagrammatic sketch of the Clyde sea area showing the sample site (s) and Keppel Pier (kp).

PLATE 1.1. Suction bin in operation: embedded in sediment.

PLATE 1.2. Suction bin in operation: inverted for ascent.



bivalve were present in the Lutraria bed. These latter included Mya truncata and Ensis arcuatus, however, Lutraria dominated. No young stages were found.

The variation in the number of animals collected in each suction bin is given in Table 1.1. and discussed in the following section.

1.2. HISTORY OF THE POPULATION AND MORTALITY

Long term studies on the growth of Lutraria in the Clyde Sea Area (P. Barnett and J. Watson, pers. comm.) indicate that the majority of the present population probably settled in summer 1967. Thus, they are now approximately fourteen years old. The few juveniles collected in September and October 1979 measured between 0.8 - 0.9cm in length. Most of the individuals in the population measured between 11.00 and 12.00cm in length, with very few animals less than 11.00cm and greater than 12.00cm. A few, measuring 13.50cm, are likely to be representatives of a previous settlement in 1963 (P. Barnett and J. Watson, pers. comm.). Thus, the samples are dominated by one year class.

Comfort (1957), reviewing the duration of life in molluscs, pointed out that many are capable of surviving for many years e.g. Tivela stultorum 20 years, Scrobicularia plana 18 years, Siliqua patula 19-25 years. He further suggests that there is no acceleration in mortality rate with age in many long-living species and that the decline in numbers is gradual.

In early 1980 mass mortalities occurred in the Lutraria populations of the Clyde Sea Area. Empty shells then outnumbered live ones by three to one. Mortalities also occurred at Hunterston and Inverkip (P. Barnett and J. Watson, pers. comm.). The cause of the mortalities

TABLE 1.1. Lutraria. Variation in the number of animals in a bin sample

NO. OF HAULS	AUG. 1979		OCT. 1979		NOV. 1979		JAN. 1980		FEB. 1980	
	BIN	HOLE	BIN	HOLE	BIN	HOLE	BIN	HOLE	BIN	HOLE
1	4	1	12	4	11	7	2	0	1	1
2	4	-	10	3	4	1	3	1	2	2
3	2	2	9	-	12	5	0	1	1	-
4	17	3	8	4	16	11	3	3	0	1
5	3	-	0	-			7	0	0	-
6	11	1	0	3			4	1	2	1
7	15	3	1	3			2	2	1	-
8			9	6			3	3	4	-
9							3	2	2	-
10							1	1	1	1
11							1	0	3	-
12							2	6	2	-
13							1	6	3	-
14									0	-
15									2	-
16									4	-
17									2	1
18									1	2
AVERAGE PER HAUL	8 ± 6.25		6 ± 5		10.70±5		2.57±2		1.72±1.22	

is not known though they may be linked with the age of the population or, possibly, the very low winter temperatures of late 1979. Other possible causes include anaerobic conditions, predation, the effect of silting, the effect of changing salinity and parasitism.

1.3. THE DISTRIBUTION OF THE LUTRARIA POPULATION

Table 1.1. lists the variation in the number of animals in each random bin sample and its associated hole. The bin was moved a few feet from one sample to the next. These figures indicate that the Lutraria population is not distributed in a random fashion but occurs in patches as confirmed by the Kruskal-Wallis test. The number of animals in a patch is random (χ^2 test).

Other bivalves have also been found to exhibit various degrees of contagion. These include Scrobicularia plana (Hughes, 1970), Spisula solidissima (Flowers, 1972) and Tresus capax (Wendell, et al., 1976).

CHAPTER 2

THE FUNCTIONAL MORPHOLOGY OF LUTRARIA LUTRARIA

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2.1. INTRODUCTION

The superfamily Mactracea (Lamark) comprises two families - the Mactridae (Lamark) and the Lutraridae, (the otter shells). The commonest British species of Lutraria is the subject of this study namely Lutraria lutraria (Linné).

The Lutraridae are large lamellibranchs occurring from low water mark into shallow waters where they live permanently and deeply burrowed. Characteristically the family have an inequilateral shell, widely gaping at both ends, especially posteriorly, a somewhat irregular hinge line and non-retractile siphons covered to the tips with a rough epidermis.

Holme (1959) describes the three British species of Lutraria - as listed in Winckworth's (1932) British Marine Molluscs - Lutraria lutraria (Linné), Lutraria magna (Da Costa) and Lutraria angustior (L. elliptica var angustior Phillippi). Of the three species Lutraria lutraria is the commonest occurring in muddy sand at low water mark and offshore to a depth of 90m. Lutraria magna is more localised and inhabits muddy sediments at the mouth of estuaries. Lutraria angustior is described by Holme (1959) as the third British species and is present in muddy sand and muddy gravel.

The Lutraridae are found in temperate regions and widespread in Australia, the Phillipines, New Zealand, Britain, the Mediterranean and Africa (Adams and Adams, 1858).

The present work is based on a study of Lutraria lutraria collected from a population in the Clyde Sea Area.

Fresh animals were used to determine ciliary currents, while both fresh and preserved animals were used for general morphological studies. Sections were prepared from tissues fixed in seawater Bouin's fluid, embedded in paraffin wax and stained with Erhlrich's haematoxylin and eosin and Mallory's trichrome stain.

It was not practical to carry out serial sections of such a large animal. A whole animal was embedded in wax and then transversely subdivided into three main blocks, posterior to anterior. These were then subdivided into between three and five blocks from which sections were cut at fairly regular intervals and the slides examined.

2.2. THE SHELL

The shell of Lutraria lutraria has been well described by several authors including Forbes & Hanley (1853), Jeffreys (1863), Yonge (1948) and Holme (1959).

Briefly, the shell is broadly elliptical in outline, equivalve, inequilateral and gaping posteriorly. The shell can attain a length of 14cm and height 7cm. The external surface of the shell is covered with a layer of olive-brown periostracum, beneath which the shell colour may be white, light yellow or fawn. The beaks are in front of the midline and directed inwards.

The ligament is relatively small, triangular, partially external and slightly opisthodetic. The external ligament is short and immediately behind the beaks. The internal ligament is found in a triangular pit below and behind the beaks (Yonge, in press).

Fused periostracum extends posteriorly from the ligament to the siphons in Lutraria. There is no anterior fused periostracum.

The hinge teeth have been well described (Jeffreys, 1863; Tebble, 1966; Holme, 1959). Diagrams of the teeth of the right and left valve are seen in figures 2.1. and 2.2.

The distinguishing feature between Lutraria lutraria and Lutraria magna is the dentition of the right valve. The differences between Lutraria lutraria and Lutraria angustior are less obvious, but examination of the degree of curvature of the teeth, the periostracum and pallial scars combine to differentiate between them.

The right valve of Lutraria has two cardinal teeth anterior to the ligament and a small ridge-like lateral posterior; the ridge carrying the anterior cardinal tooth is crossed by a small lateral groove posterior to its mid point.

The left valve has two cardinal teeth joined to form a ⋀ shaped projection, and a slight ridge-like anterior lateral tooth and a similar posterior lateral. Posterior to the posterior lateral tooth and anterior to the ligamental pit is a thin leaf-like cardinal.

The inside of the shell is white and slightly glossy. The pallial sinus is very deep, extending to a position below the base of the ligamental pit. The pallial line is not confluent with the ventral line of the pallial sinus, but is well defined.

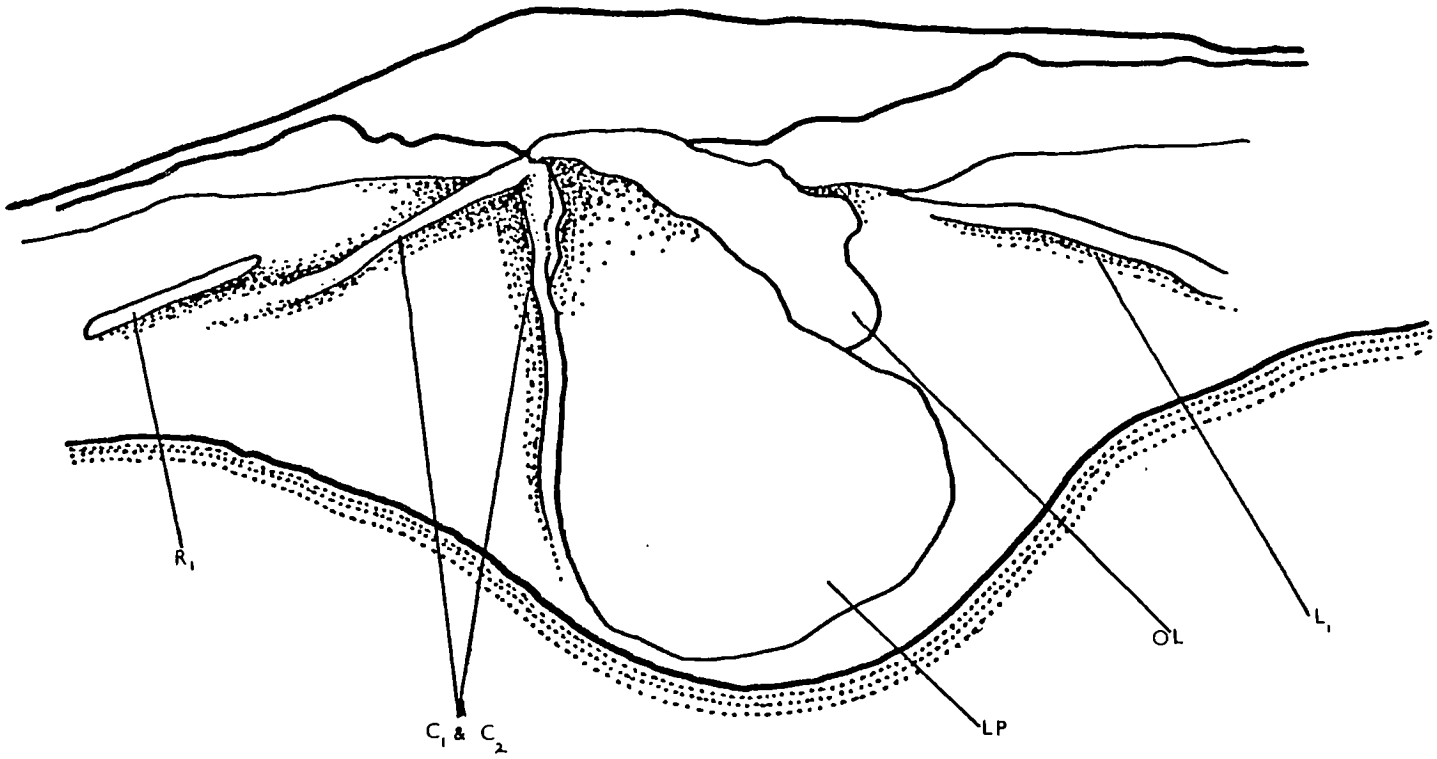
The adductor muscle scars are similar in size though differing slightly in shape. Posterior and anterior retractor muscle scars are present.

The structure of the shell layers is described by Boggild (1930).

Figure 2.1. Lutraria. View of the right hinge (actual size ¾")

Key

C_1	cardinal teeth anterior to ligament
C_2	
L_1	ridge-like lateral posterior tooth
R_1	ridge supporting the anterior cardinal tooth
OL	outer ligament
LP	ligament pit (chondrophore)

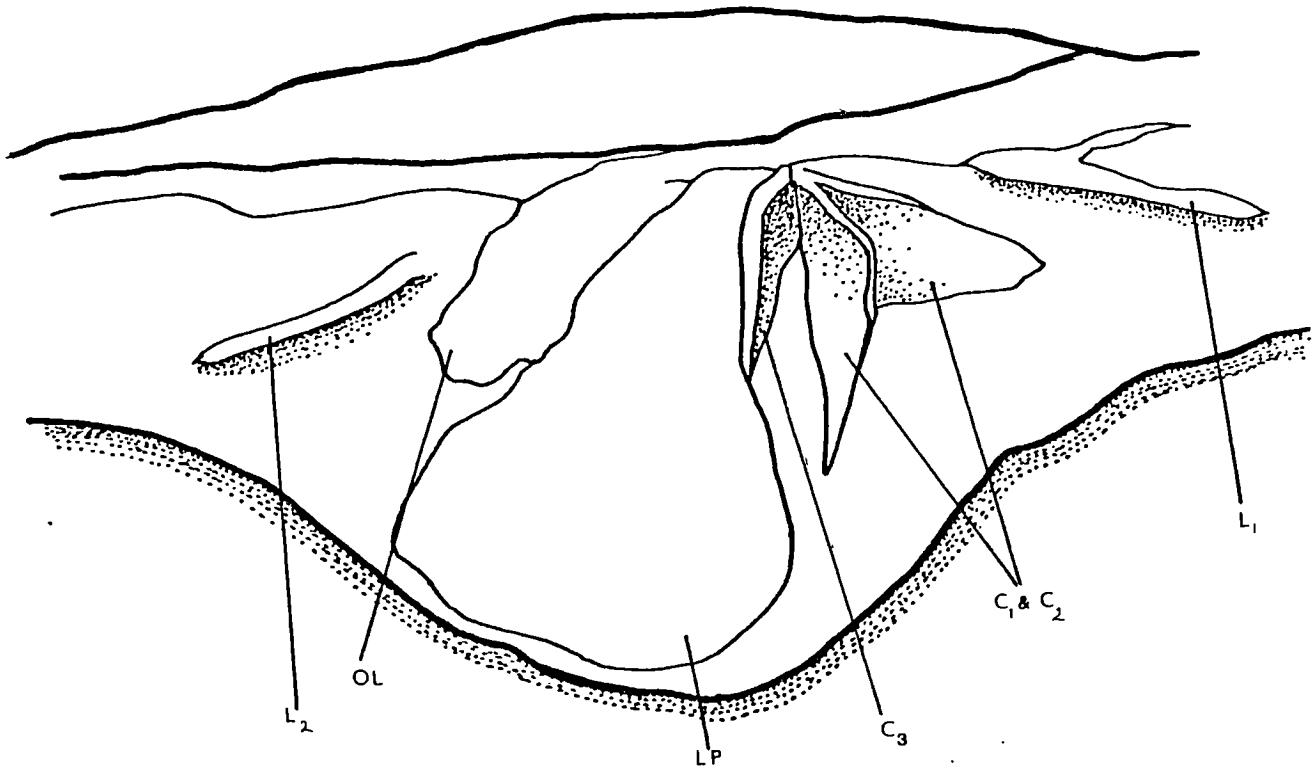


x 10

Figure 2.2. Lutraria. View of the left hinge (actual size $\frac{3}{4}$")

Key

C_1	cardinal teeth joined together forming $\wedge$ shaped projection
C_2	
C_3	leaf-like cardinal tooth, anterior to ligament pit
L_1	anterior lateral tooth
L_2	posterior lateral tooth
OL	outer ligament
LP	ligament pit (chondrophore)



×10

2.3. MANTLE EDGE, MANTLE FUSION AND THE SIPHONS

In Lutraria lutraria the mantle cavity is extensive. As in other lamellibranchs the mantle margin comprises three folds - the inner is the largest and is very muscular, the middle is sensory, and the outer secretes the outer shell layer. The mantle is attached to the shell by a line of muscle fibres of the inner lobe, internal to the shell margin. This, the pallial line, is characteristic to each species and, as previously stated, in Lutraria is very deep and well marked.

Formation of the adductor muscles involves fusion of the inner mantle folds for some distance anterior and posterior to the mantle isthmus. In Lutraria further fusion or adhesion, defines four openings in the mantle margin to the exterior - namely the exhalant, inhalant, pedal and fourth pallial apertures.

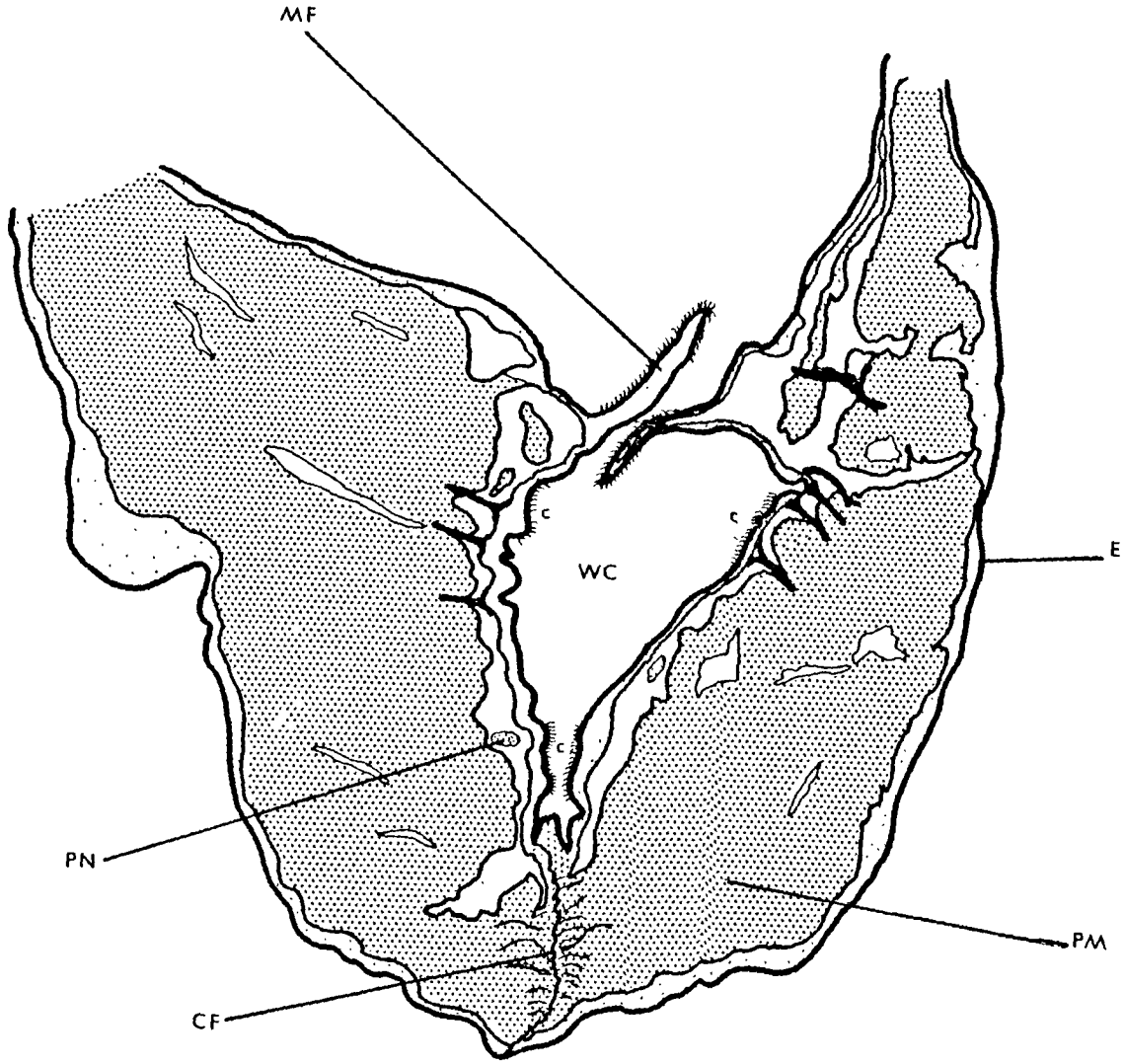
The junction of the ventral margins between the small pedal aperture and the fourth pallial aperture is type B (Yonge 1957) and involves the inner folds and the inner surface of the middle folds. The junction is cuticular i.e. adhesion between the cuticular boundaries of the opposing epithelial cells. This line of adhesion can be seen in figure 2.3. Very fine muscle fibres can be seen under high power penetrating the epithelial cells giving a fibrillar appearance. The attachment is firm and the surfaces only separate after long exposure to formalin. The cuticular surfaces are heavily folded.

Atkins (1937c) suggested that fine muscle fibres from one mantle lobe cross into the other lobe and there is an appearance of this here. Cuticular folding makes it difficult to be certain as Atkins (1937c) also found. The existence of such muscle fibres in Lutraria might explain why the surfaces do not separate easily. The ready separation of the similar line of adhesion in Ensis siliqua, Ensis arcuatus and Cultellus pellucida may be explained by the lack of these muscles.

Figure 2.3. Lutraria. Semi-diagrammatic drawing of a transverse section through the fused mantle edge and waste canal anterior to the fourth pallial aperture.

Key

MF	mantle fold
PN	pallial nerve
CF	cuticular fusion of mantle edges (line of adhesion)
PM	pallial muscle layer
c	ciliated epithelium
WC	waste canal
E	epithelium



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In Lutraria the fusion between fourth and pedal apertures involves tissue fusion (Yonge 1948). The well developed folds covering the main mantle rejection tract extend from just posterior to the fourth aperture to near the posterior margin of the foot and the visceral mass (Figs. 2.3. and 2.4.). The ciliated canal transports pseudofaeces to the fourth aperture.

Yonge (1948) has described the currents and ciliation of the waste canal and these are confirmed here. All particulate mantle waste enters the canal. There are no cilia along the midline where the cuticular surfaces are joined, but there are tracts of cilia in positions shown in figure 2.3. In these ciliated regions the epithelial cells are larger than those adjacent. There are mucous glands associated with the ciliated epithelia.

There is some evidence to suggest that there is a muscular component involved in the functioning of the waste canal. In figures 2.3. and 2.4. transverse muscles can be seen in the region of the extra mantle fold and the pallial muscles are greatly enlarged adjacent to the waste canal. Well developed pallial nerves are present.

Figure 2.5. shows a transverse section through the area of the pedal gape. The middle (sensory) fold of the mantle lobe is represented by only a very small projection. There is a pad of glandular tissue in this region (Figs. 2.5. and 2.6.) and from examination of slides it was found to extend far anterior. Yonge (1948) states that elongate areas of mucous cells on either side of the pedal opening such as those found in Mya supply mucous for the consolidation of waste particles. He also states that no such glandular areas are present in Lutraria lutraria, however this study shows that they are in fact present.

There is a functional but small (5mm x 3mm) fourth pallial aperture in Lutraria lutraria through which pseudofaeces are ejected.

Figure 2.4. Lutraria. Semi-diagrammatic drawing of a transverse section through the fused ventral mantle and waste canal anterior to Fig. 2.3.

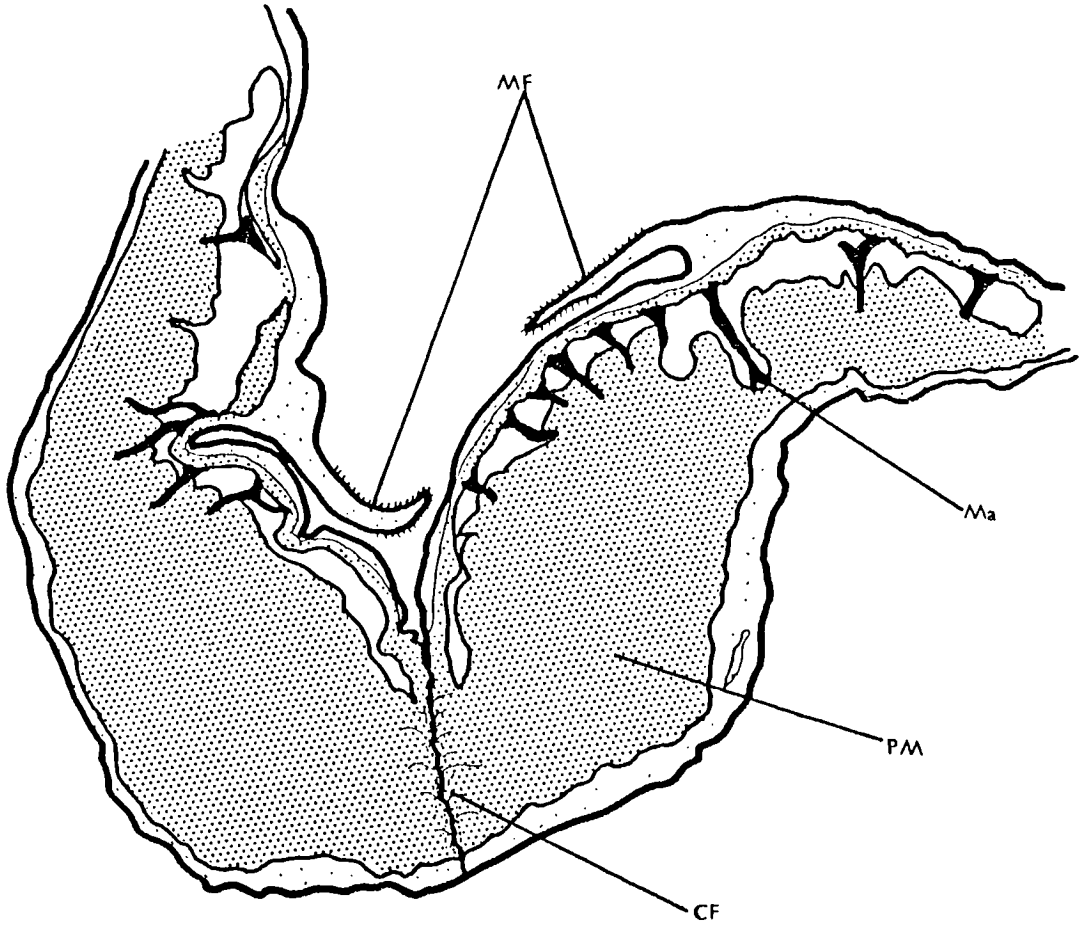
Key

MF mantle folds

Ma additional transverse muscles

PM greatly enlarged pallial muscles

CF cuticular fusion of mantle edges (line of adhesion)



× 20

Figure 2.5. Lutraria. Semi-diagrammatic drawing of a transverse section through the ventral mantle edge in the region of the pedal gape.

Key

PN pallial nerve

GP pad of glandular tissue

OF outer fold

PG periostracal groove

MdF middle fold - only slight projection

PM pallial muscles

F foot musculature

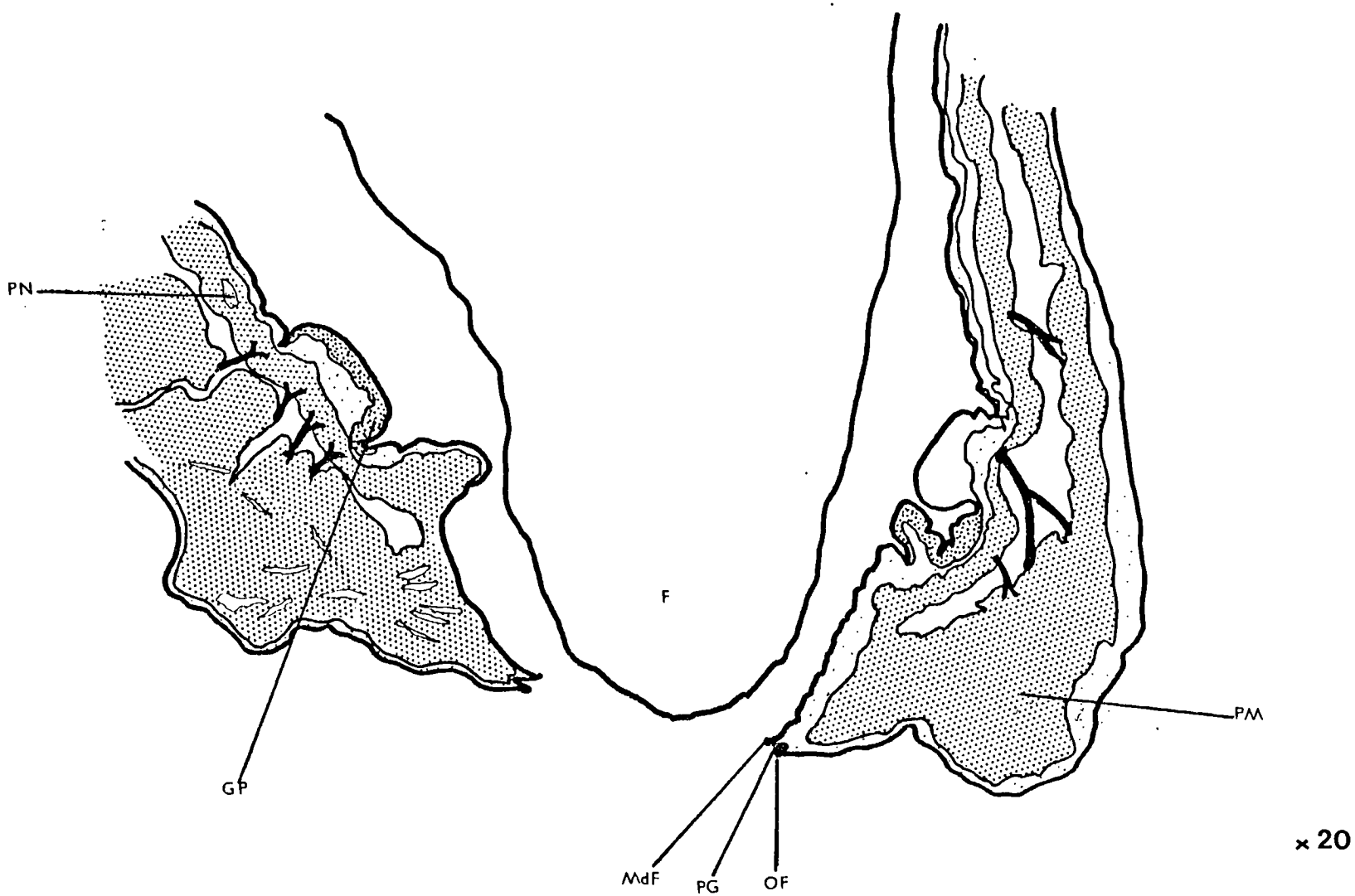
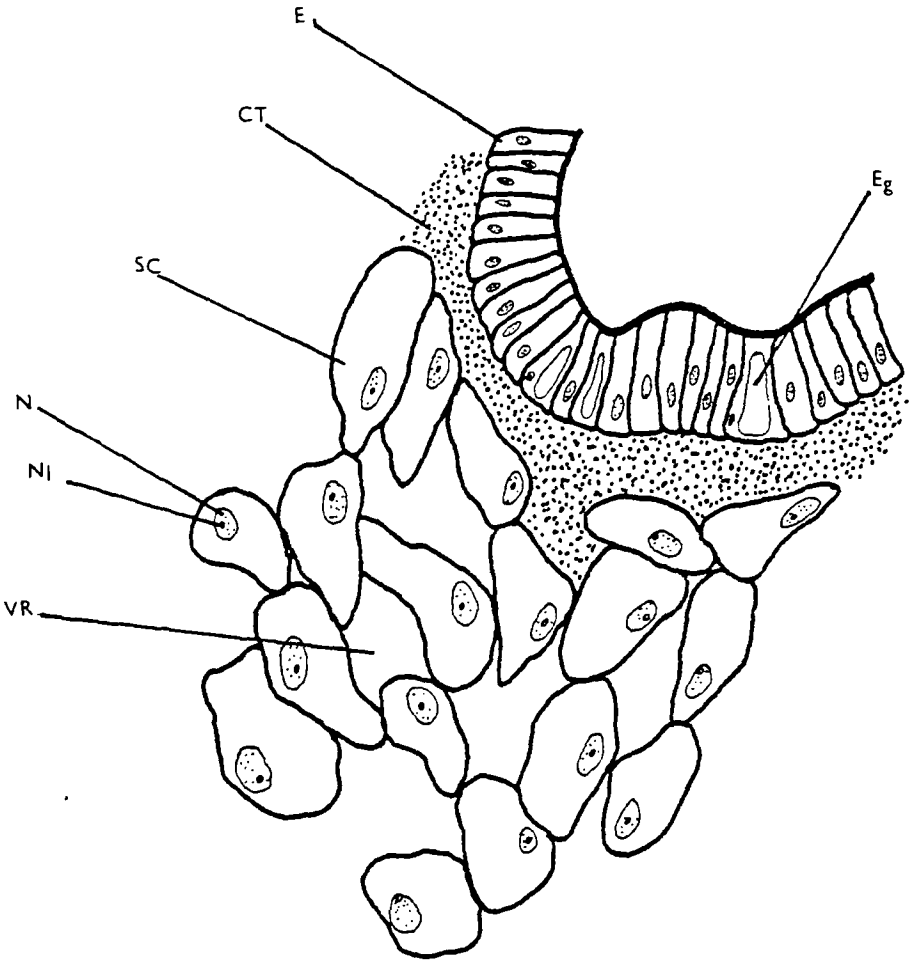

PN
GP
F
PM
MdF
PG
OF
× 20

Figure 2.6. Lutraria. High power drawing of the glandular area in the mantle edge near the pedal gape.

Key

E	columnar epithelial cell containing nucleus
Eg	glandular epithelial cell
N	nucleus
N1	nucleolus
VR	vacuolated region
SC	large secretory cells
CT	dense connective tissue



× 50

By fusion and extension of the mantle folds posterior to the fourth aperture, siphons of type C are formed (Yonge, 1957). The fusion involves the inner, middle and inner surface of the outer fold. In siphons of type C the inner surface of the outer folds extends to the tip of the siphons such that they are completely covered with periostracum. The periostracal groove extends round the outer distal rim of the siphons at the base of the ring of tentacles formed from the middle fold. In the formation of type C siphons the valves are united by periostracum posterior to the ligament. This is clearly seen in Lutraria. It is not regarded as representing secondary extension of the ligament as the periostracum is not involved in any way with valve movements.

The siphons of Lutraria species are well described by Holme (1959) and his observations are confirmed here. Hunt (1973) describes in detail the siphonal sheath. The sheath is bilayered with an inner loose gelatinous layer protected by a thin outer periostracal layer. The inner 'gelatinous' layer is very obvious in preserved specimens (Plate 2.3.).

The siphons themselves are creamy yellow in colour being marked with purple spots towards the tips. They are capable of extending up to 2-3 times the length of the shell. Plate 2.1. gives an indication of siphonal extension.

Both the inhalant and exhalant apertures are ringed with tentacles and these can only be observed well in relaxed specimens.

Plate 2.2. shows an end on view of the siphonal apertures and the interdigitation of the tentacles, while in figure 2.7. the apertures are closed.

In Lutraria the exhalant siphon is fringed with numerous small tentacles while the inhalant siphon has usually eight long tentacles with smaller tentacles interspersed between. Holme (1959) noted two circles of smaller tentacles to the outside of the opening of the inhalant siphon and this is true of the Clyde specimens. The tentacles surrounding both

Plate 2.1. Lutraria. View of an individual showing the extended siphons (x ½)

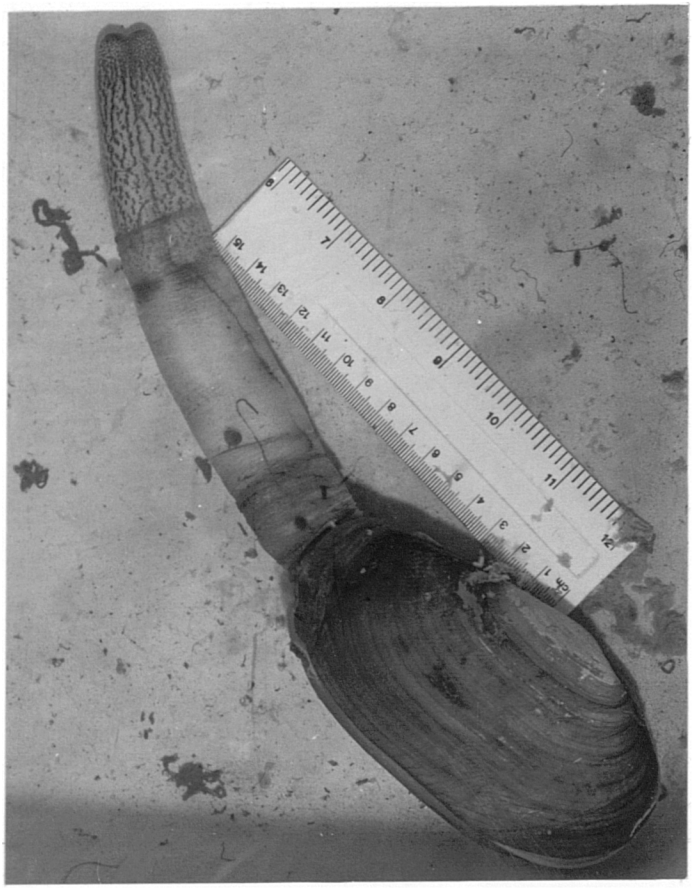


Plate 2.2. Lutraria. View of the siphonal apertures of a specimen in sediment to show the arrangement of the tentacles.

(I - inhalant siphon; E - exhalant siphon
D - distortion due to exhalant current)


D
I
E

Plate 2.3. Lutraria. View of a preserved specimen to show the large siphonal retractor muscle (SR) (x $\frac{1}{2}$) and gelatinous siphonal sheath (G)

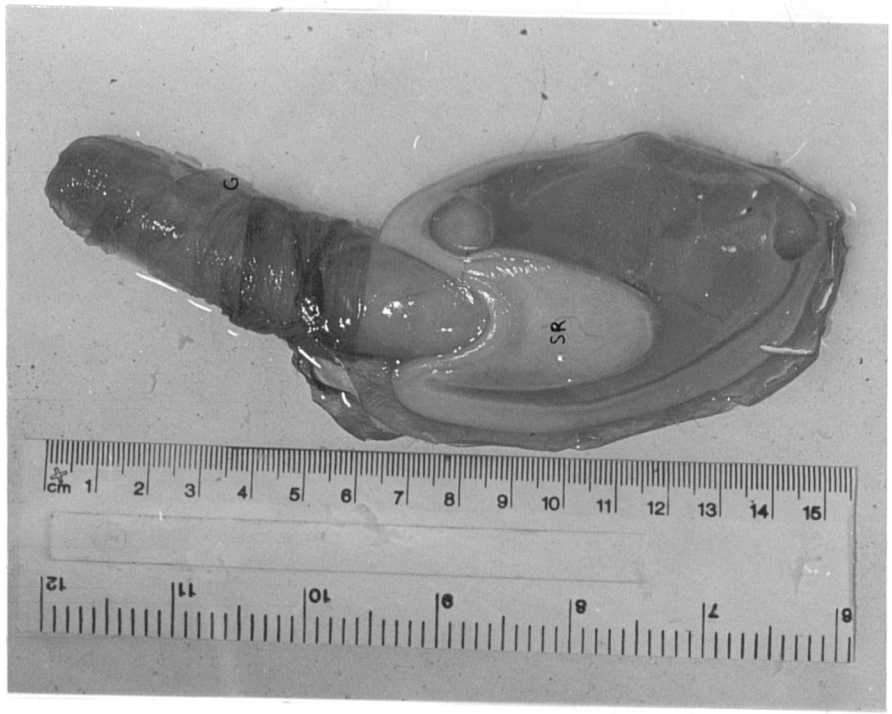
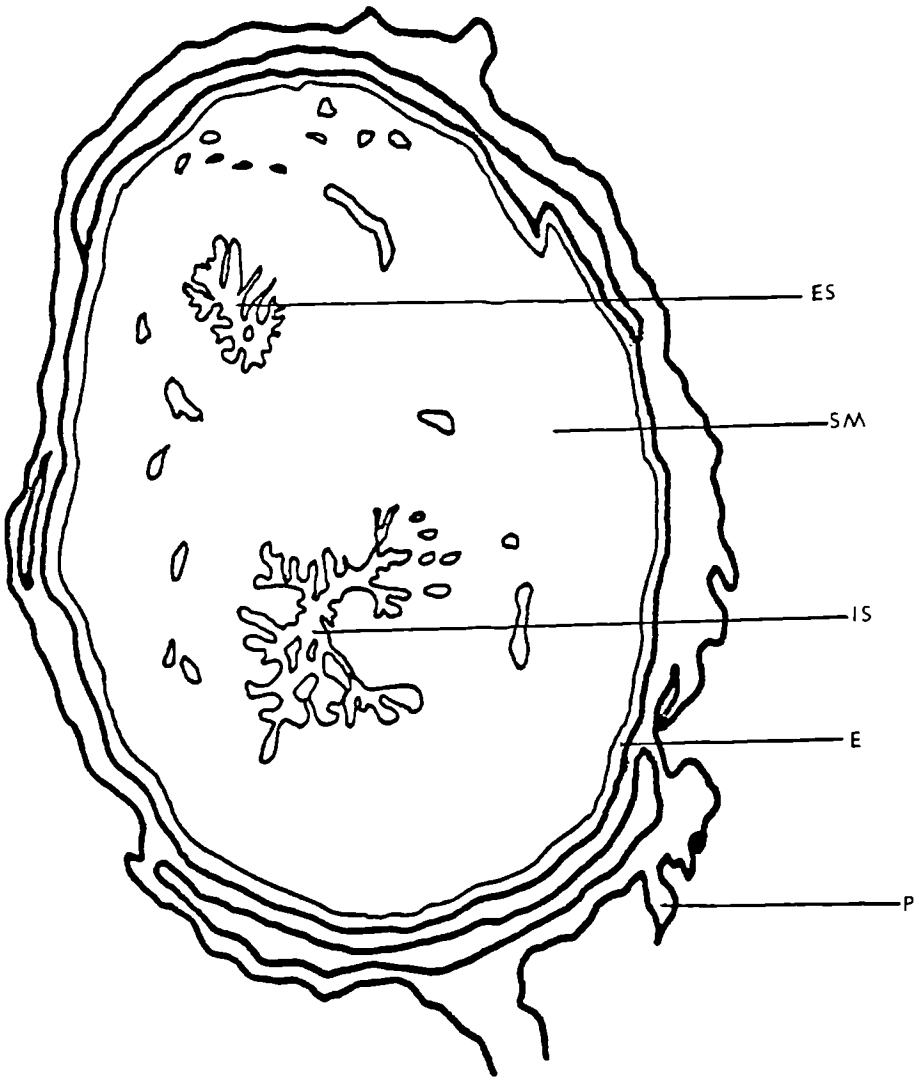

G
SR
cm 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15
12 11 10 9 8 7 6

Figure 2.7. Lutraria. Semi-diagrammatic drawing of a transverse section through the siphonal apertures.

Key

ES	exhalant siphon
SM	siphonal musculature
IS	inhalant siphon
E	epithelium
P	periostracum



× 15

the siphons is derived from the middle (sensory) fold of the mantle. The muscular rings of both apertures are derived from the inner muscular fold.

In transverse section (Fig. 2.8.) the organisation of the siphonal muscles is seen to be complex. There are two distinct layers of longitudinal muscle, the inner of which is slightly smaller than the outer.

There are 70 to 75 muscle blocks around the inhalant siphon in both muscle layers and a maximum of 55 muscle blocks around the exhalant siphon. The longitudinal layers are separated by distinct circular muscles with some radial strands. An array of siphonal nerves are present at the middle base of the longitudinal blocks. The nerves are irregular in size, shape and positioning. There are 12 nerves in the inhalant tissues, and 10 in the exhalant. The observations by Duval (1963) on siphons of Lutraria is confirmed here except that only two haemocoels were seen in the present specimens as opposed to the four reported by Duval. The sure presence of a haemocoel in section is dependent to a large extent on the condition of the animal in fixation, i.e. to what extent it is contracted, and the state of the tissue.

2.4. MUSCULATURE

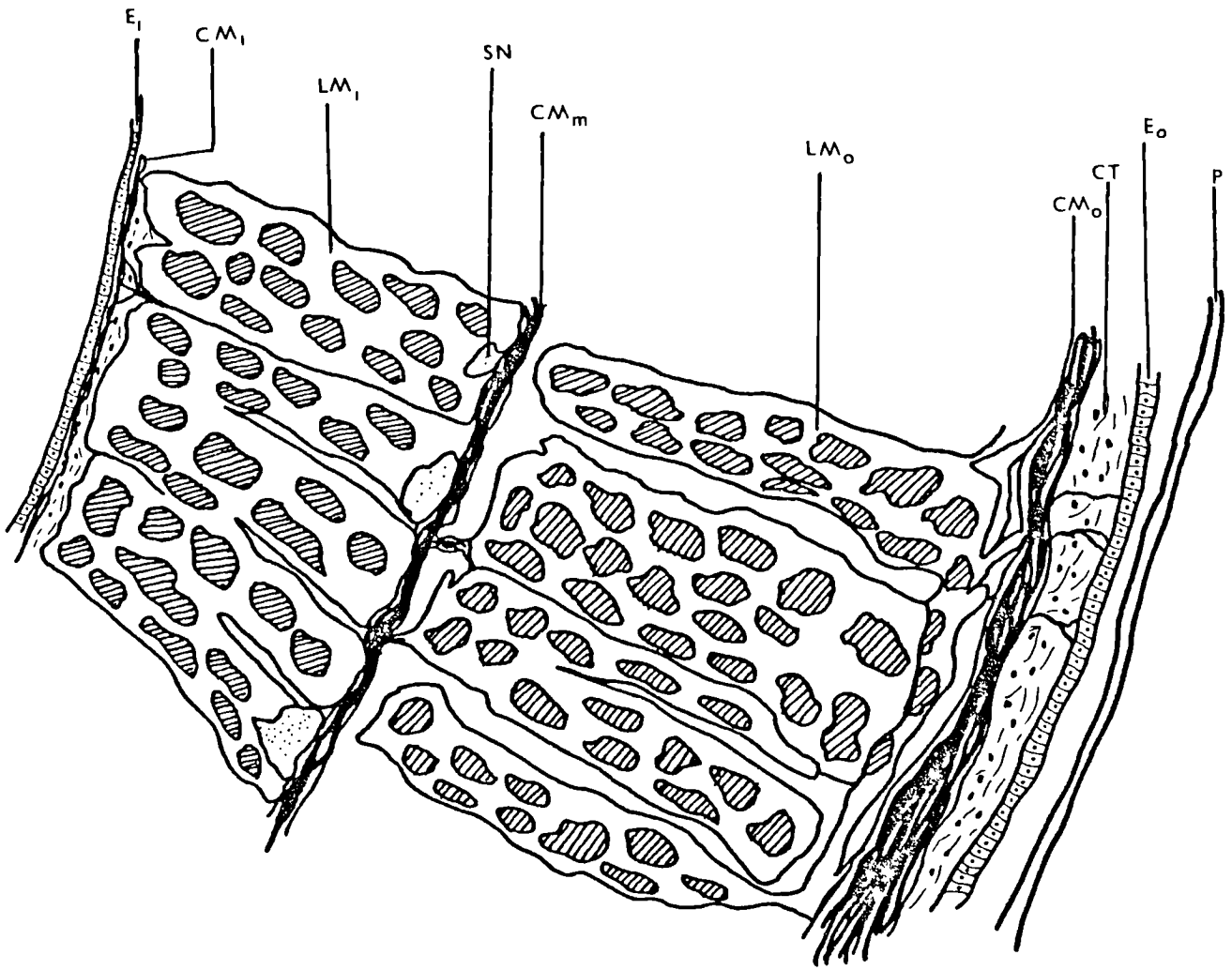
The adductor muscles in Lutraria, though they differ in shape, are isomyarian. The posterior muscle is oval, the anterior muscle is pear shaped. A sharp demarcation between the 'quick' and the 'catch' portion of the muscles can be seen.

Anterior and posterior pedal retractor muscles are present and the scars can be seen to the inside of and just above those of the adductor muscle.

Figure 2.8. Lutraria. Semi-diagrammatic drawing of a transverse section through the siphonal wall.

Key

P	periostracum
E	outer epithelium
CT	connective tissue with some radial muscle fibres
CM_o	outer circular muscle layer
LM_o	outer longitudinal muscle layer
CM_m	middle circular muscle layer
SN	siphonal nerve
LM_I	inner longitudinal muscle layer
CM_I	inner circular muscle layer
E_I	inner epithelium



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No pedal protractor muscles or byssal retractor muscles were seen, however siphonal retractor muscles are very extensive (Plate 2.3.).

2.5. ORGANS OF THE MANTLE CAVITY

The disposition of the organs in the mantle cavity can be seen in figure 2.9. and plate 2.4., a lateral view of Lutraria. Jeffreys (1863) describes the body of Lutraria lutraria as "elongated, somewhat cylindrical and compressed".

The gills are pale brown in colour, the outer demibranchs being slightly smaller than the inner. Both have ascending and descending lamellae. The anterior portion of the ascending lamellae of the inner demibranch and the upper portion of the ascending lamellae of the outer demibranch are attached, respectively, to the visceral mass and mantle. The attachment is cuticular and as described by Atkins (1937c).

The ctenidia are plicate and homorhabdic and typically eulamellibranchiate (Fig. 2.10.). The present observations on gill structure and ciliary currents confirm those of Atkins (1937b) and Ridewood (1903). The individual filaments are extremely small, approximately 25μm broad by 100μm long with interfilamental spaces 17μm. There are approximately 34 filaments per plica.

Atkins (1937a) found that in Lutraria lutraria, despite the deep plication of the gills, the lateral walls of the marginal grooves are not scalloped, the plicae tending to 'smooth out' towards the margins of the gill.

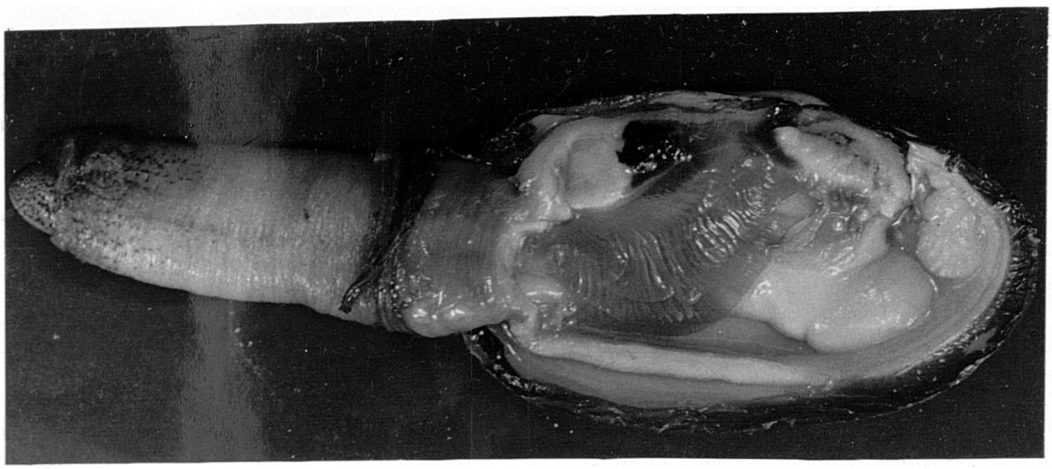
The ciliary currents can be ascribed to type C(2) (Atkins, 1937b) in which both the inner and the outer demibranch bears a ventral marginal food groove. There is also a well defined food groove along

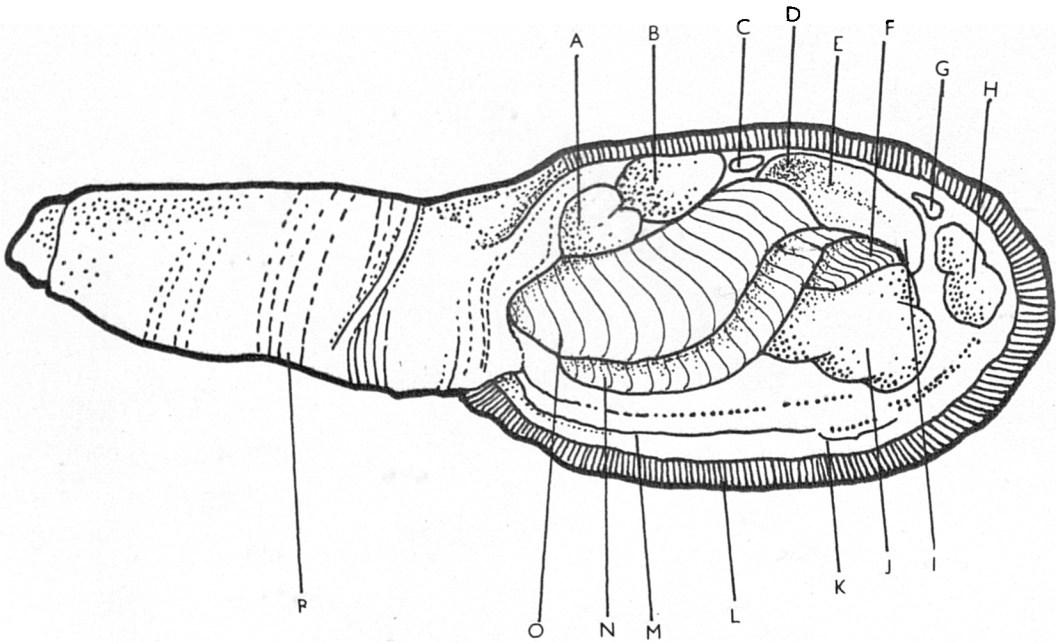
Plate 2.4. Lutraria. Lateral view showing the disposition of the organs in the mantle cavity (right mantle lobe removed) (x ½)

Figure 2.9. Lutraria. Diagram of the photographed specimen with the various organs labelled (right mantle lobe removed) (x ½).

Key

A	posterior adductor muscle
B	kidney
C	pericardium
D	region of pericardial glands
E	digestive gland
F	labial palp
G	anterior pedal retractor muscle
H	anterior adductor muscle
I	gonad
J	visceral mass and foot
K	region of pedal gape
L	periostracum
M	mantle edge (adhesion)
N	inner demibranch
O	outer demibranch
P	combined siphons




A
B
C
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the ctenidial axis. Lateral, frontal and laterofrontal cilia are present on each filament and no cilia are visible on the abfrontal surface. Except over the dorsal region of the descending lamellae of the outer demibranch, where for a short distance the cilia beat dorsally into the tract between the two demibranchs, the frontal currents on all lamellae are towards the free margins of the demibranchs.

2.5.1. The Palps

The labial palps in Lutraria lutraria are fairly large, approximately one third the size of ctenidia. They are triangular and paler in colour than the ctenidia. Their general structure is shown in figure 2.11. Except in regions of mucous secretion, cilia are present on the surface of all epithelia. Mucous cells are fairly numerous, especially on the distal edge of the palp. Muscle fibres are seen along the proximal side and beneath the furrows between the ridges on the inner surface.

The palps are selective organs passing material from the ctenidia either to the mouth or to the lip of the palp where as unwanted material it is rejected. Rejected material from the palps collects on the mantle or visceral mass and is then removed as pseudofaeces via the main rejection tract of the mantle (Yonge, 1948). The ciliary currents on the palps are similar to those of many other eulamellibranchs, eg ventral rejection, a dorsal acceptance tract and resorting currents on the upper halves of the ridges being confirmed here. The ciliation shows no significant difference from the basic eulamellibranch type and large anteriorly directed cilia are present on the summit of the palps ridges.

Figure 2.10. Lutraria. Semi-diagrammatic drawing of a transverse section through a homorhabdic tissue junction of the ctenidium.

Key

LC	lateral cilia
LFC	latero-frontal cilia
FC	frontal cilia
SR	skeletal rod
F	filament
IE	interlamellar non ciliated end

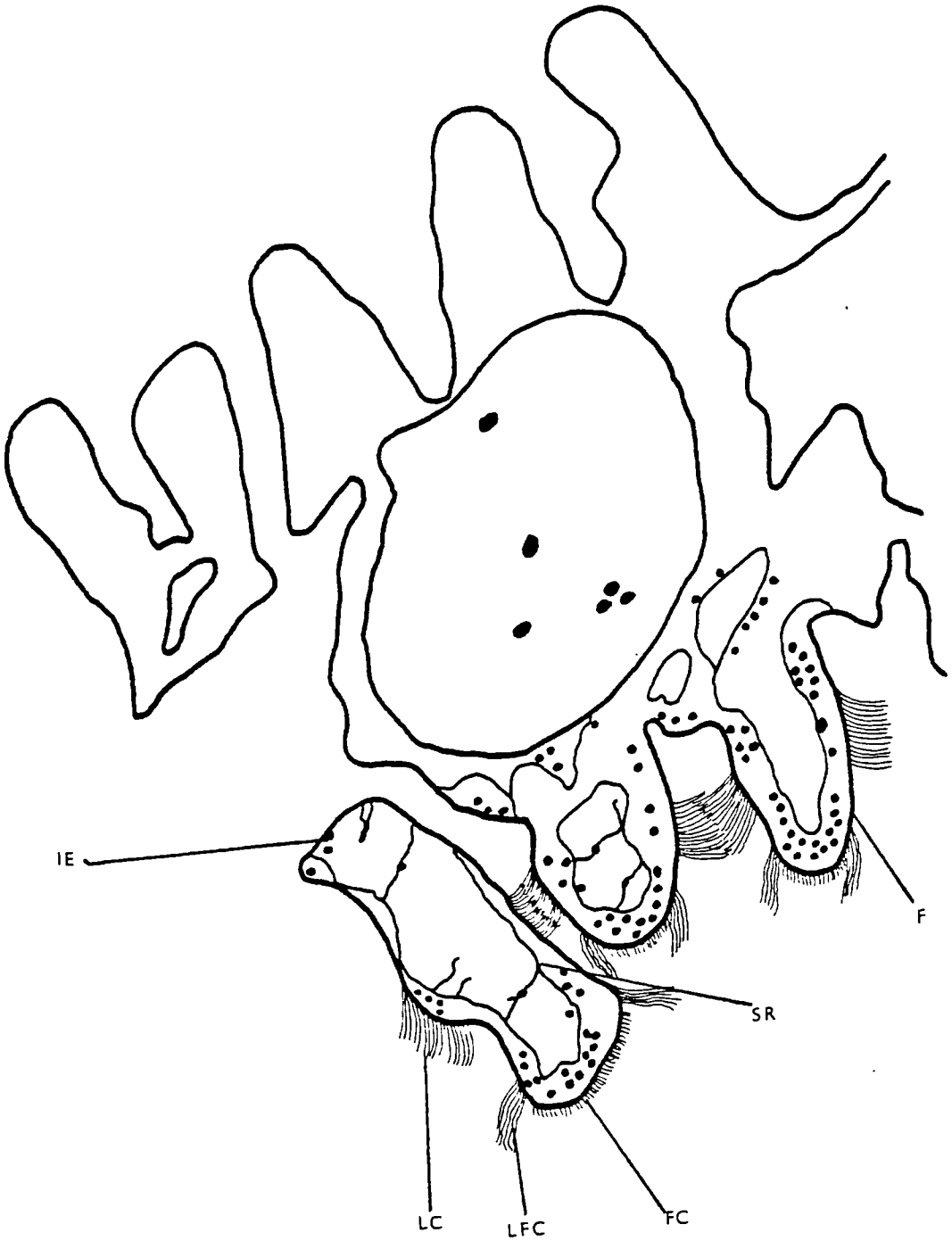

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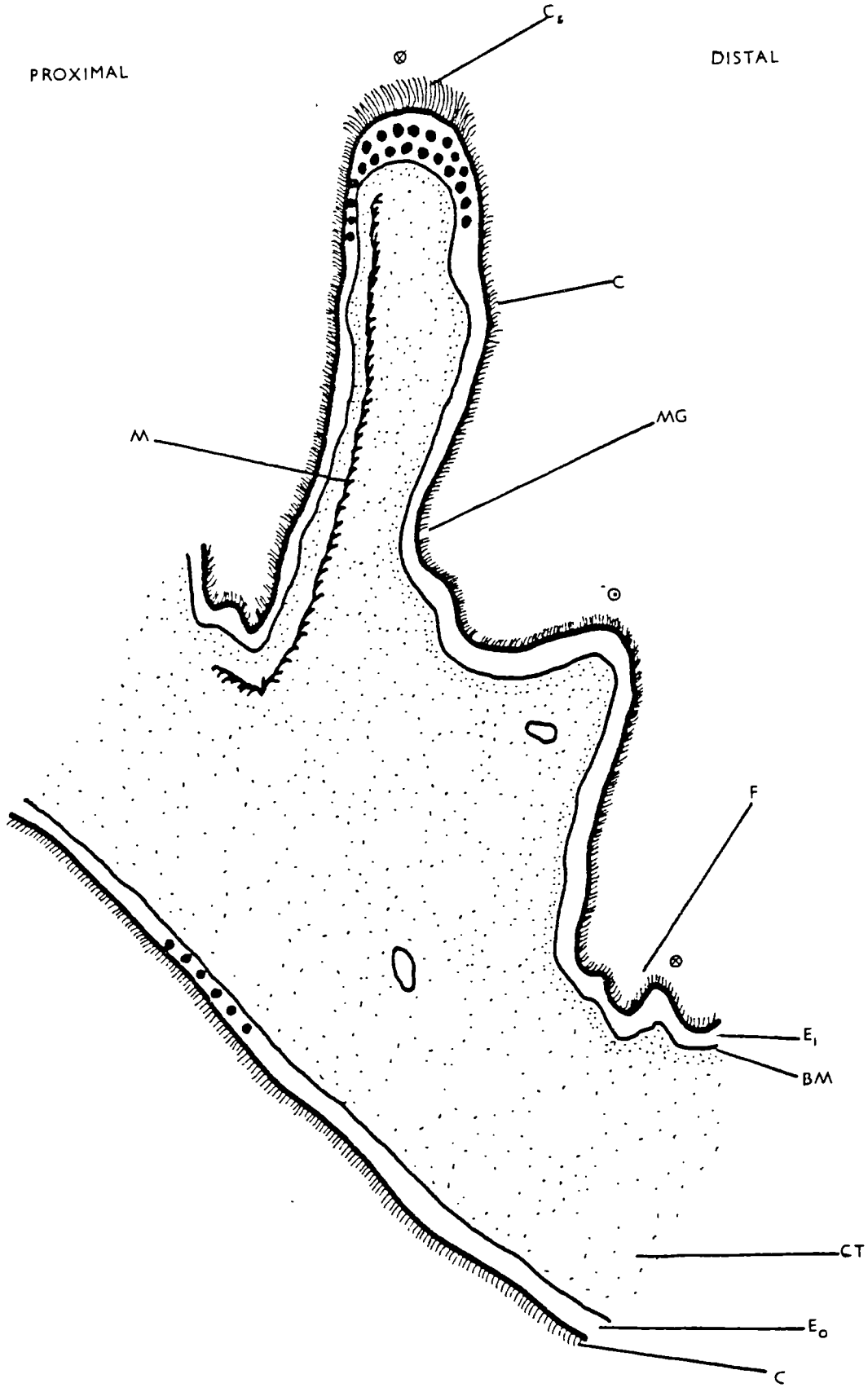
Figure 2.11. Lutraria. Semi-diagrammatic representation of a transverse section through a single fold of the labial palps.

Key

M	muscle fibres
C_s	large cilia on summit of the palp
C	cilia
MG	region of mucous glands (unciliated)
F	furrow between folds
E_I	inner epithelium
CT	connective tissue
E_o	outer epithelium
BM	basal membrane
⊗	rejection current ventrally directed
⊙	acceptance current dorsally directed



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2.5.2. Visceral Mass and Foot

The visceral mass is large, but the foot, though fairly well developed for a deep burrower, is not large. The extent to which Lutraria lutraria has retained its burrowing ability is discussed in Chapter 6. The pedal gape is not extensive and is confined to the anterior third of the ventral margin. Byssus threads are not produced in the adult.

The course of ciliary currents on the visceral mass have been described by Yonge (1948) and were confirmed in the present work. They are mainly rejectory and transport unwanted material to the waste canal. Many mucous and subepithelial gland cells are present in the foot and these are particularly associated with the heavily ciliated distal areas.

2.5.3. Reproductive system

Lutraria is dioecious. The gonads ramify throughout the visceral mass. They occupy the spaces between the alimentary canal and the body wall and extend deeply within the musculature of the foot as is shown in figure 2.12. Gonadial tissue does not extend into the mantle when mature. The gonads discharge above the inner demibranch into the epibranchial chamber through the genital duct. There is a slit like opening posterior to the body mass.

The reproductive cycle of Lutraria lutraria is described in Chapter 3.

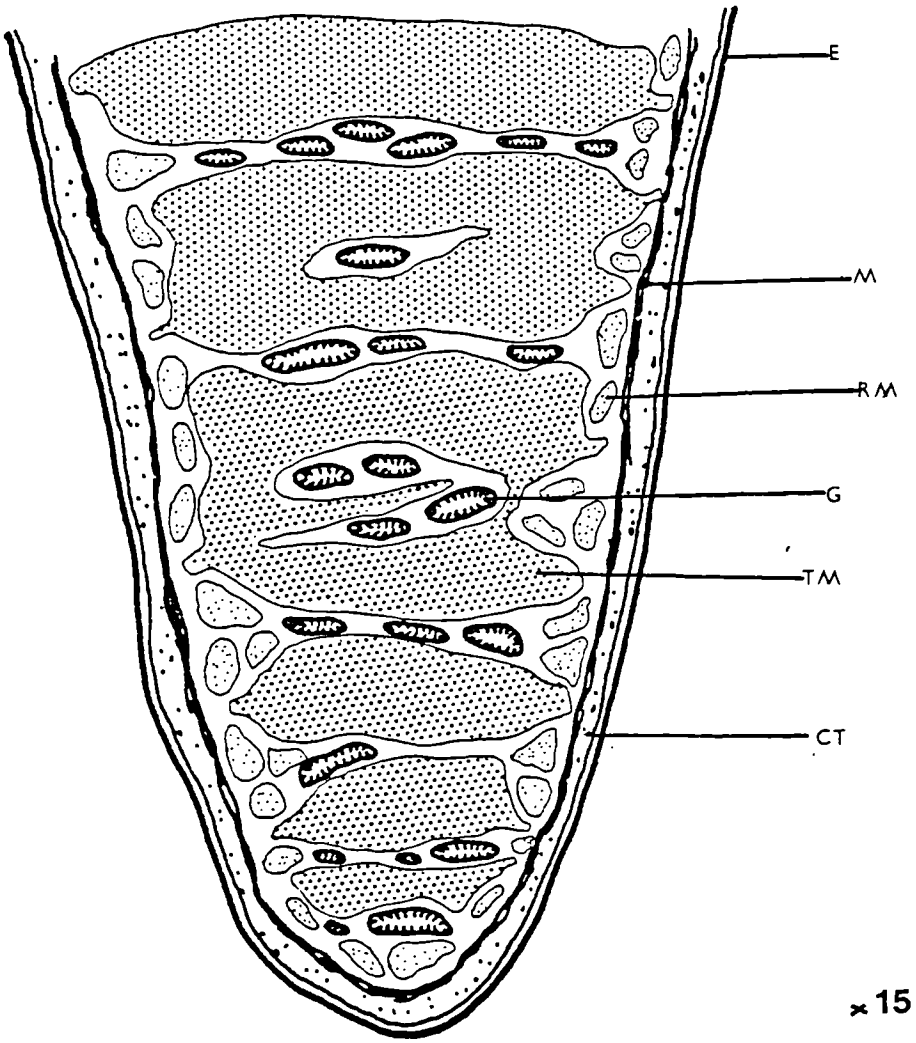


Figure 2.12. Lutraria. Semi-diagrammatic drawing of a transverse section through the heel of the foot showing the extension of the gonadial tissue into the musculature.

Key

E ciliated epithelium of foot

M muscle fibres

RM retractor muscle tissue

TM transverse muscle

CT connective tissue

G gonad

2.5.4. Pericardium

The position of the pericardium and the paired kidneys are shown in figure 2.9. The pericardial cavity lies anterior to the kidneys, and posterior to the visceral mass. The heart consists of a large muscular ventricle with a pair of thin walled auricles entering on either side. The auricles are extensions of the efferent branchial blood vessels. Blood is carried from the ctenidia via the auricles to the ventricle, which on contraction drives blood into the anterior and the posterior aortae. In Lutraria there is a fairly large posterior aortic bulb. The hind gut runs through the ventricle and posterior aortic bulb.

The pericardial glands of the Lamellibranchia have been described by White (1942) and those of Lutraria lutraria briefly discussed by her. They are found in bivalves generally as paired, oval, pale brown patches in the mantle either dorso-lateral or anterior to the heart. Most authors now agree that the pericardial gland is an organ of excretion passing waste into the pericardium which is then removed via the main excretory organs.

A pair of reno-pericardial pores are situated on the antero-ventral wall of the kidneys and open from the posterior ventral part of the pericardium. The kidneys of Lutraria lie directly anterior to the posterior adductor muscle. They are large and dark red in colour. Although highly ramified, histologically they show no difference from other bivalve kidneys (Fig. 2.13.).

Connective tissue surrounding the kidneys contains blood spaces amoebocytes and muscle fibres. The kidneys are lined with columnar cells, often containing an apical vacuole and a number of concretions. It is the latter that colours the kidneys dark brown. The nuclei

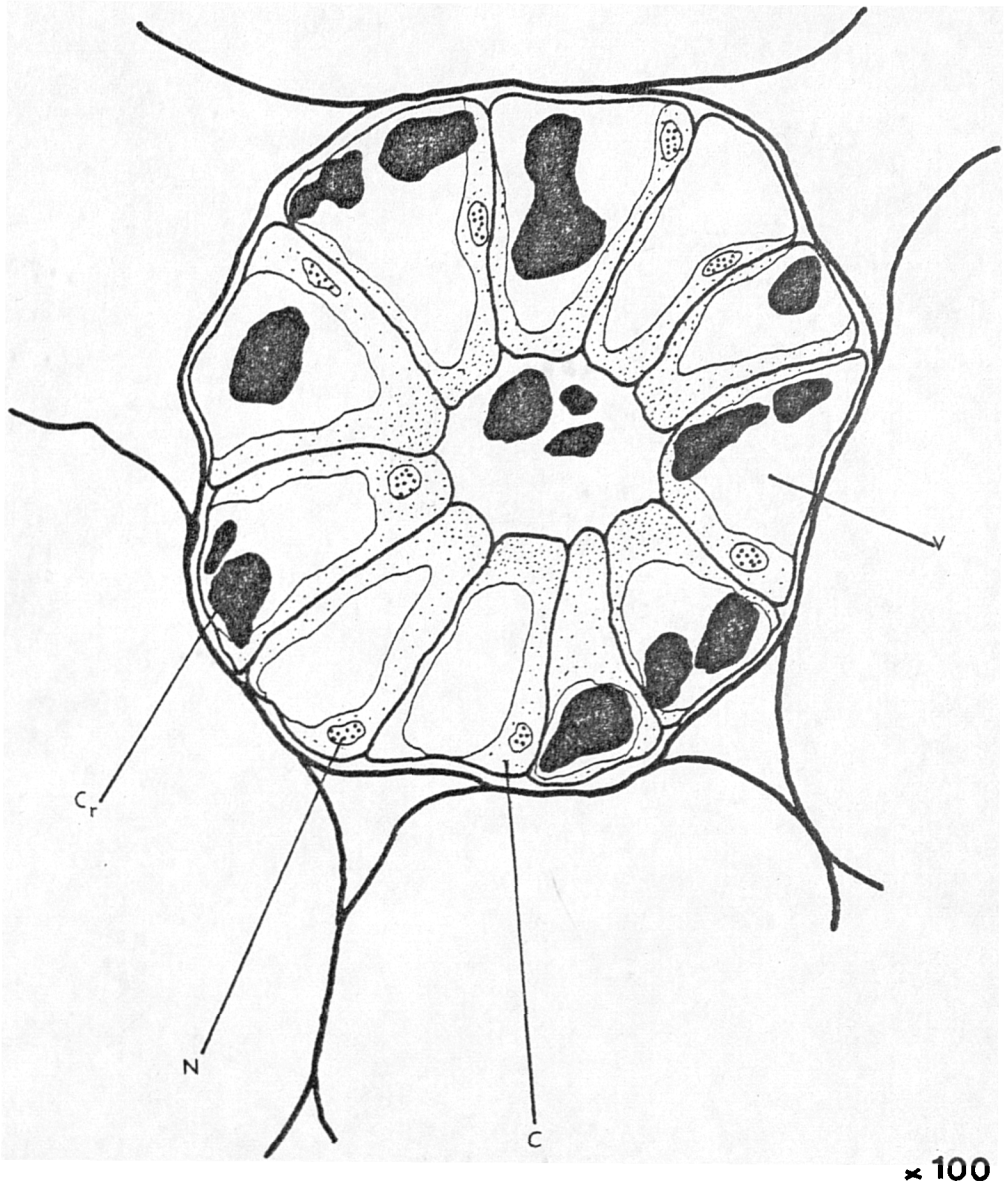


Figure 2.13. Lutraria. Transverse section through a single kidney tubule.

Key

C_r	concretions
N	nucleus of tubule cell
C	columnar cells
V	vacuolated region of cell

and mitochondria usually lie towards the base of the cell, while the surface generally has a brush border. Scattered amongst these columnar cells are a few ciliated cells (Potts, 1967).

The nephridopores open from the posterior walls of the kidneys on either side of the visceral ganglia into the posterior part of the suprabranchial cavity.

2.5.5. Nervous system

The nervous system of Lutraria is that of a typical eulamellibranch. The cerebropleural ganglia lie slightly anterior to, and on either side of, the oesophagus close to the mouth. In Lutraria they are exceedingly small in size and difficult to find in dissection. From the cerebropleural ganglia the cerebrovisceral connectives pass lateral to the anterior pedal retractor muscle, through the viscera to terminate in a pair of visceral ganglia. The cerebropedal connectives pass through the anterior pedal retractor and extend posteriorly and ventrally into the foot to connect with the pedal ganglia. An anterior pallial nerve from the cerebropleural ganglia supplies the anterior regions of the mantle. A separate nerve supplies the anterior adductor muscle. Because the cerebropleural ganglia are responsible for the co-ordination of pedal and valve movements, their small size might indicate that Lutraria is a relatively inactive animal.

The visceral ganglia are situated ventrally on the anterior face of the posterior adductor muscle and are in close contact with the epithelium covering the muscle.

The visceral ganglia also are very small and lie close together. They give rise to a combined pallial and siphonal nerve which branches

posterior to the posterior adductor muscle giving a nerve to the gill axis and a nerve to the posterior adductor muscle. Visceral ganglia control the posterior adductor muscles.

The pedal ganglia are the largest of the three ganglia in Lutraria lutraria and they are found at the junction of foot and body wall musculature, approximately a third in from the anterior wall of the visceral mass. From the ganglia nerves pass to each side of the foot. Foot movement is under the control of the pedal visceral and cerebropleural ganglia.

The margin of the mantle lobe, particularly the middle fold, is the principal location of most mantle sense organs in bivalves. In Lutraria the middle fold is very much reduced and the only pallial tentacles that are present are restricted to the siphonal apertures (Plate 2.2.).

2.5.6. The Alimentary Canal

The oesophagus opens into the anterior wall of the stomach. The mid gut is separate from the style sac and lies anterior to it. From the postero-ventral wall of the stomach the mid gut penetrates the foot ventrally towards the heel, and then curves antero-ventrally continuing as a series of coils of the hind gut within the body before passing through the pericardium and then dorsal to the posterior adductor muscle to the anus. Dorsal to the anus is an anal papilla.

Except for that part of the stomach region secreting the gastric shield a ciliated epithelium lines the lumen of the gut from the mouth to the posterior end of the mid gut. For the most part the hind gut is unciliated, instead the wall of the hind gut and part of the mid gut

has associated muscle fibres. A large typhlosole almost fills the lumen of the mid gut. The mid gut epithelium is densely ciliated with scattered mucous cells present.

Both circular and longitudinal muscles are present in the wall of the hind gut (Fig. 2.14.). The inner epithelium is of columnar cells, variable in height, with very few cilia present interspersed with many mucous cells. This confirms similar observations by Jegla and Greenberg (1968) on species of the closely related family Mactridae. The lumen of the hind gut is small, oval in cross section (0.9 x 0.7mm) with a faecal rod (0.5 x 0.4mm) that does not occupy the full lumen of the gut.

The stomach of Lutraria lutraria lies antero-dorsally in the visceral mass, close to the body wall. Digestive diverticula surround the antero-dorsal part stomach but do not extend posterior to the stomach. Ducts to the digestive diverticula open from the stomach via the left pouch, and the left and right caeca. In addition an independent duct opens directly into the stomach above the right caeca. Figure 2.15. shows a typical digestive duct.

The gastric shield is in the normal position largely to the left side of the stomach. Phlanges of the gastric shield penetrate the left pouch and dorsal hood (Fig. 2.16.). Purchon (1960) describes the gastric shield of the Mactridae as unusual in being extensively emarginated postero-ventrally. This is also true of Lutraria. The crystalline style is large and firm approximately 2mm in diameter and 10mm in length.

Unlike Mactra mera, described by Purchon (1960), Lutraria has an area that lies along the anterior wall of the stomach, possibly homologous to the minor typhlosole (Fig. 2.16.). The major typhlosole flattens out within the stomach and penetrates both right and left caeca. Penetration of both caeca is very deep the perimeter of each

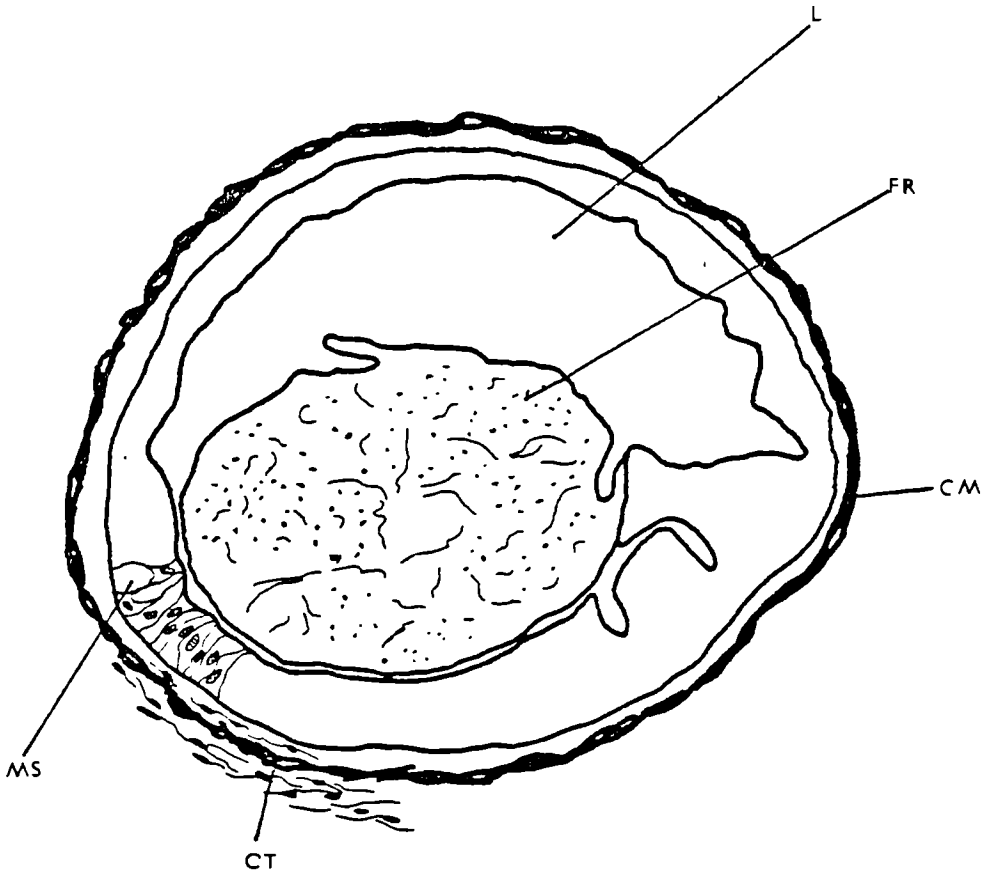


Figure 2.14. Lutraria. Semi-diagrammatic drawing of a section through the hind gut.

Key

CT	connective tissue
FR	faecal rod
L	lumen of hind gut
MS	mucous secreting cell in gut epithelium
CM	circular muscle

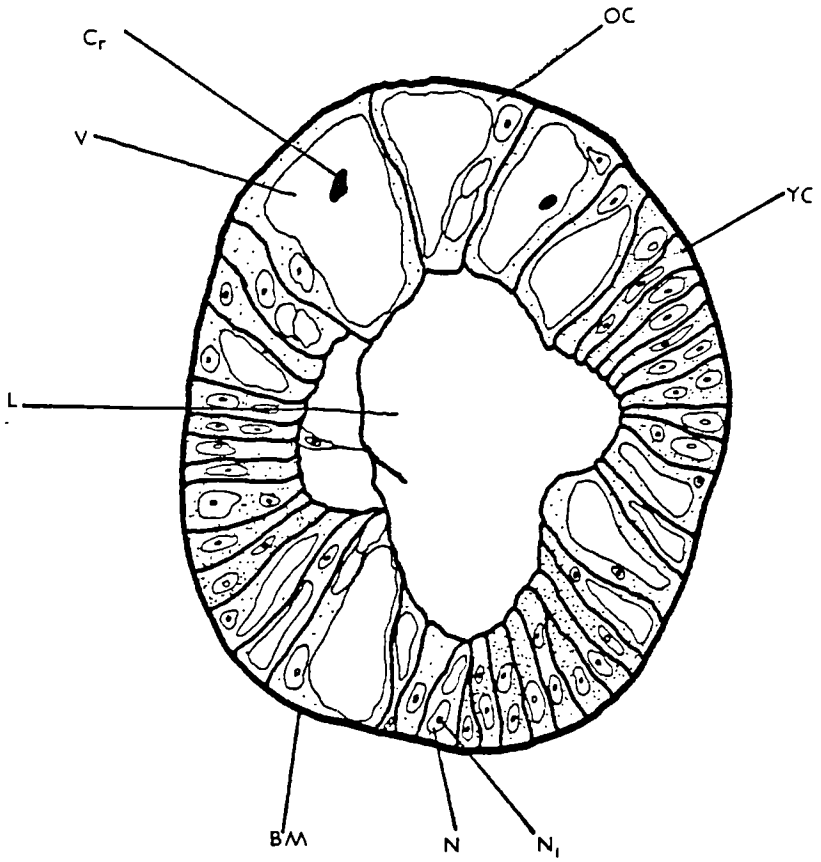


Figure 2.15. Lutraria. Transverse section through a tubule of the digestive gland.

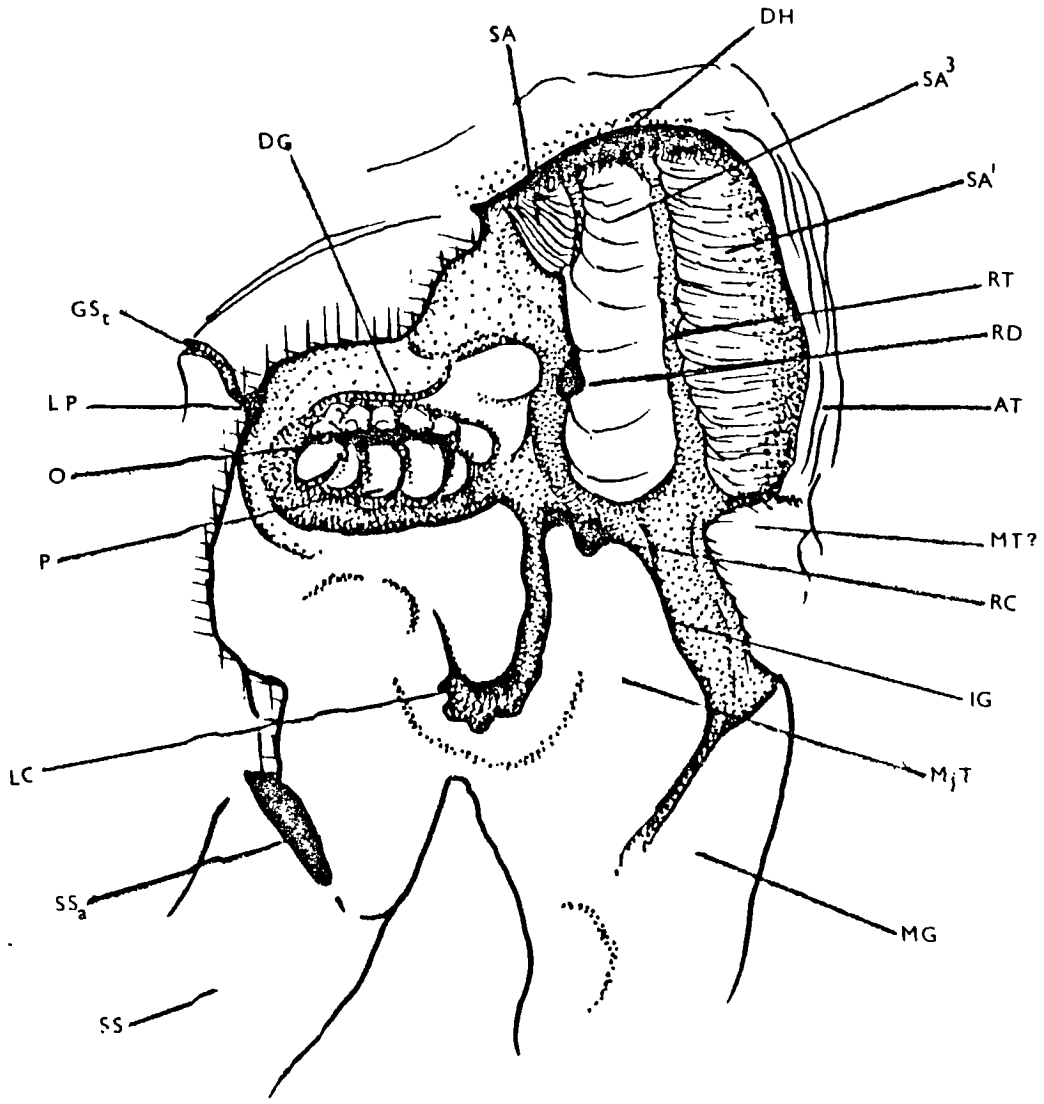
Key

C_r	concretions in vacuole of tubule cell
V	vacuolated region
L	lumen
N	nucleus
N_1	prominent nucleolus
BM	basement membrane
YC	young darkly staining cells
OC	older highly vacuolated cells

Figure 2.16. Lutraria. Lateral view of the stomach opened along the mid posterior wall from the base of the dorsal hood to the mid gut.

Key

DH	dorsal hood
SA^3	third sorting area
SA^1	posterior sorting area
RT	rejection tract
RD	right duct
AT	acceptance tract
MT?	minor typhlosole
RC	right caecum
IG	intestinal groove
M_jT	major typhlosole
MG	mid gut
SS	style sac
SS_a	style sac aperture
LC	left caecum
P	papillae
O	oesophagus
LP	left pouch
GS_t	gastric shield tooth
DG	dorsal groove
SA^2	second sorting area



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being surrounded by a broad semi-circular rim of the typhlosole. The major typhlosole is accompanied by the intestinal groove. The dorsal hood is well developed.

Three sorting areas are present. The principal sorting area of the dorsal hood originates on the anterior wall of the dorsal hood and extends over the right wall of the stomach. It is bordered on its anterior side by a major rejection tract which passes material to the intestinal groove.

There is a small sorting area on the posterior wall of the dorsal hood and this also terminates on the right side of the stomach. A third sorting area is present on the right side of the stomach extending from the oesophageal aperture into the dorsal hood. The oesophageal aperture is surrounded by large papillae, in place of the fold seen in other families.

2.6. DISCUSSION

In life *Lutraria* lies buried in fairly fine, stable, sandy mud substrates from extreme low water of spring tides to shallow water. A deep burrowing bivalve, it leads a safe but fairly stationary existence and at the size attained by the present population is probably not predated upon to any great extent. Special adaptations are required for such a protected life, deep in the sediment.

The shell of *Lutraria* is streamlined, laterally flattened, smooth and slightly elongate, clearly adapted to a burrowing habit. The smooth shell valves offer minimum resistence to movement through the substrate.

Elongation of the shell has produced, by convergence, a number of deep burrowers such as *Mya* (Myacea), *Lutraria* (Mactracea), *Panope*

(Saxicavacea) and Glauconome (Veneracea). In all, there is great elongation of the shell and reduction of the foot. The more flattened shell of Lutraria allows for a much greater degree of burrowing than does the more globular shell of the cockle Cardium edule. The valves of Lutraria are thin and gape widely at the posterior end to accommodate the extremely extensible siphons. The foot is not greatly enlarged and only slightly directed anteriorly and Lutraria does not make frequent digging movements, unlike Ensis.

The shells of Mya arenaria and Lutraria lutraria are very similar in shape, both are equivalve and inequilateral but Mya truncata has a blunt as opposed to rounded posterior margin of the shell and which may be an adaptation to living in a coarser muddy gravel sediment.

The hinge dentition in Lutraria is well developed with cardinal and smaller lateral teeth. This is in contrast to deep burrowing members of the Saxicavacea who have reduced dentition with no more than one tooth in each valve and often being lost in the adult (Yonge, 1971).

Nevertheless, the hinge mechanism of Lutraria is fairly weak though about 1.5 times more powerful than that of Mya arenaria despite their similar form and habit. It is generally thought that deep burrowing forms are derived from less specialised shallow burrowing forms. This would seem to be true in the case of Lutraria, it probably being derived from a mactrid-like form similar to Spisula solidissima with its powerful ligament. The ligament of Spisula solidissima is about 3.5 times more powerful than Mya arenaria, in terms of opening moment (Russell Hunter and Grant, 1962).

In Lutraria, as in Mya, the ligament may not be the most important antagonist to adductor muscle contraction preventing the excessive gape

of the shell valves. Hydrostatic pressure within the mantle cavity in conjunction with extensive ventral mantle fusion probably gives rise to a greater opening moment than that of the ligament. Owen (1953) noted in Glossus humanus the poor elastic qualities of the hinge ligament allowed less thrust into the sediment. In situ the pressure of the sand on either side of Lutraria provides sufficient additional support to the adductors against the hydrostatic pressure to keep valves to the right degree of closure and the ligament intact. On removal to aquaria with no substrate, the adductors tire, the valves gape, the ligament then becomes stretched and eventually torn, and the animal consequently dies. An elastic band placed around the valves prevents this.

In Lutraria the adductor muscles are somewhat distant from the shell margin and in a position in which they are more efficient than they would be nearer the margins of the valves.

It seems probable that bivalves living in the deep mud and muddy sand environments rely, to a great extent, on the support of the substrate to keep the valves from gaping and in consequence the adductor muscles are not adapted to prevent gaping and consequent enfeeblement of the animal.

A major problem to burrowers, particularly those in soft shore and shallow sea sediment, is that with strong water movements, sediment may gain easy access to the mantle cavity, yet circulation of respiratory water is essential for the animal. Characteristic of deep burrowers is the extensive mantle fusion which helps to reduce sediment intake. In Lutraria only four restricted openings remain, the inhalant and exhalant at the lip of large combined siphons, the pedal and the fourth pallial apertures. This extensive fusion not only limits the quantity of sediment entering the mantle via two small apertures but also makes

easier the maintenance of the hydrostatic pressure of the mantle cavity.

Yonge (1971) states that in the case of the deep burrower Panomya (Saxicavacea) its highly successful exploitation of the deep burrowing mode of life is due to the complete covering of shell and exposed tissues by a thick periostracum and to the exceptionally extensive area of extended pallial tissue ventrally and to some extent anteriorly as well as posteriorly.

Lutraria also has a surrounding protective layer of relatively thick periostracum, although it is not so thick as that of Mya and Panomya. In contrast the Solenidae (Yonge, 1952) although they are deep burrowers have a finer periostracum, however their habit of rapid vertical movement and form of the mantle shell differs greatly from these three genera.

The occurrence of mucous glands at the area of the pedal gape possibly help to consolidate waste material rejected from the palps and ctenidia. Extra mantle folds covering the main ciliated rejection tract are present in other eulamellibranch families than the Mactridae. Yonge (1948) states that in the Mactridae the presence of these mantle folds appears to be correlated with the presence of a siphonal membrane initially directing the in current ventrally, clear of the gills. In Lutraria no siphonal membrane is present but here the mantle folds direct waste to a fourth pallial aperture.

In the case of other sand dwelling bivalves, the Tellinacea have mantle folds that are used to prevent excessive quantities of sediment from clogging ctenidia and palps (Yonge, 1949). The mantle folds confine the sediment to the waste channel. Folds are also found in Siliqua patula, an intertidal occupant of high energy sand beaches, but are not present in the more specialised Ensis (Yonge, 1952) in which the pedal gape is greatly reduced.

A fourth pallial aperture is also present in other lamellibranch species. In the Solenidae (Graham, 1934), it would appear that the fourth aperture acts as a safety valve which permits the ventral extrusion of water from the mantle cavity and prevents the rupture of tissues due to the high pressures generally due to the piston-like movement of the foot when these animals burrow rapidly. It is not primarily associated with waste removal as in Lutraria. In Lutraria rapid withdrawal of the siphons might impose high pressure but for the aperture, Bloomer (1903) noted that frequently there was a sudden ejection of water from the fourth pallial aperture in Lutraria and that this was used for ridding any objectionable material from the pedal cavity. Bloomer (1903) further suggested that the fourth aperture originated as a tentacular fringe on a portion of the pedal aperture. This then extended posteriorly, the pallial walls coalesced,and finally the fourth aperture migrated to its present position. Graham (1931) related shell differences with the variation and the extent of the fourth aperture in Ensis.

As illustrated in figure 2.3., in Lutraria the waste canal can be closed by the folds and then hydrostatic pressure used to eject material through the fourth aperture. Transverse muscles in the area of the mantle fold suggest a muscular and a hydrostatic component in the function of the canal. The pallial muscles of the inner mantle fold in the region of the aperture are also greatly enlarged and on contraction these open the aperture.

To enable them to burrow to great depths the bivalves either have an elongate shell, and strong foot (Ensis) or long siphons with a more moderately developed foot and less elongate shell (Lutraria). In Lutraria massive fused siphons are protected by a periostracal layer. The siphons can extend between two and three times the length of the shell (Plate 2.1.). Hunt (1973) has shown that the siphon sheath of

Lutraria lutraria is bilayered, consisting of an inner loose flexible layer of chitin protein complex, and an outer periostracal sheath. The periostracum alone provides resistence to abrasion and the inner layer contains flexion and extension of siphons. The inner layer is most noticeable in preserved specimens.

Differences in the form of the siphons reflect important differences in the habits of different species. Tentacles around the inhalent opening tend to be better developed in those suspension feeding species living under conditions where there is much sediment in the water. The tentacles of Lutraria are sensitive to quantities of large particles entering the mantle and they act to prevent clogging of the ctenidia and mantle cavity. They are very mobile. In contrast, Yonge (1949) found no such tentacles in the deposit feeding Tellinacea.

There is much variation in siphonal musculature and in its complexity within the Lamellibranchia. Work by Duval (1963) has shown that in species in which the siphons are large, joined and relatively thick walled (Veneridae, Petricolidae, Lutraridae, Myidae and Pholadidae) there are four longitudinal haemocoels more or less equally placed around the walls. The use of the haemocoels in Mya arenaria was investigated by Chapman and Newell (1956). They found that siphonal extension was due to water from the mantle cavity being forced into siphonal canals by the action of the adductor muscle. Previously it was thought that influx of blood was responsible for promotion and extension of molluscan siphons. Much greater quantities of water can be used than blood. A similar system is thought to occur in Lutraria.

The longitudinal siphonal muscle blocks are responsible for retraction. In Lutraria lutraria where the siphons are very long the longitudinal muscles are well developed, as are the siphonal retractor muscles. In deep burrowers good control of the extension and retraction

of the siphons is of the greatest importance. Well defined circular muscles control the diameter of the siphonal passage and radial muscles regulate the thickness of the walls of the siphon.

Pohlo (1967) suggests that suspension feeders require straining tentacles, large ctenidia closely joined to body and mantle and small palps. The size of the palps is related to the quantity of suspended material entering the mantle cavity. In Lutraria the palps are moderate in size (approximately $\frac{1}{3}$ to $\frac{1}{2}$ the length of the ctenidia) suggesting the animal takes in a moderate amount of material. In deposit feeders the palps tend to be very large e.g. in Macoma baltica the palps are larger than the ctenidia themselves.

The ctenidia of Lutraria are plicate and homorhabdic. The extent to which variability in plication in bivalves can be related to either food or habitat is uncertain and much variation can be found within a single genus (Atkins, 1937a). No special sorting mechanisms were found in Lutraria lutraria and the bulk of material is transferred from the gills to the palps in the normal way.

In Glossus humanus, Owen (1953) attributed deep plication to the need to deal with large volumes of water containing small quantities of suspended material. Plication in Lutraria is thought to be a means of increasing the pore area rather than the sorting area.

The visceral mass is large, but the foot relatively small. The reduction of the foot is a feature of other families of deep burrowers (Myacea, Saxicavacea) where the adult is permanently embedded in the sediment and has little need to change its position. Mya, Lutraria and Panope are all deep burrowing suspension feeders. The foot in Lutraria is the least reduced of the three being completely atrophied in Panope generosa. Lutraria has retained some use of its foot and can burrow.

There is no need in Lutraria for a large foot to give a great degree of mobility. The size and length of siphons ensures that the adult leads a sedentary life. In association with this the power of the hinge has also decreased, there is little need for valve movement once it has established its life position.

In Lutraria the style sac and mid gut are completely separate, as they are in Mya arenaria (Yonge, 1923). The combined condition occurs in all protobranchs and primitive lamellibranchs suggesting that it is the primitive condition, however Yonge (1939) attaches no functional significance to the separation of the two as both situations can occur within one family.

There is a certain degree of coiling of the mid gut anterior to the Style sac. Longer mid guts appear to be found in species that take large quantities of sand into the mantle cavity e.g. Macoma balthica (Yonge, 1949). The length of the hind gut is correlated in part with the need to consolidate faecal pellets. In Lutraria the hind gut is short. The muscle surrounding the posterior part of the gut would suggest that peristalsis is used to pass material through the hind gut region. The faecal rod is small in relation to the lumen of the hind gut suggesting that Lutraria lutraria has an efficient system for selecting and sorting food. The rest of the alimentary canal is well ciliated.

Mya arenaria has a very thick muscular layer surrounding the hind gut. Jegla and Greenberg (1968) state that the rectum of the Bivalvia is a non adaptive structure which has undergone little change since the divergence of the families, and while subtle species specific differences in rectal physiology and internal ridging are present and while they must be related to functional differences, there are no such relationships at the level of gross histology. The faeces in Lutraria appear to be in

non-compacted threads as opposed to well formed pellets. These are light and possibly easier to transport up the long siphon, as Yonge (1971) found in Panope.

Purchon (1960) classified the stomach of the Mactridae as type V. The diagnostic features of this stomach are 1) the extension of the major typhlosole and the intestinal groove into left and right caeca, 2) the left pouch on the left wall of the stomach invested with a lobe of gastric shield receives ducts from the digestive diverticula, 3) a relatively large dorsal hood, invested by a phlange of the gastric shield, and with a well developed sorting area on its anterior wall.

The basic functions of the stomach are to a large extent invariable. Material from the ctenidia and palps is circulated and sorted by ciliary currents. The sorting areas in Lutraria are not very large suggesting that the bulk of the sorting may be left to the ctenidia and palps. The dorsal hood is not particularly large also indicating a lack of material being brought into the stomach.

Both Purchon (1960) and Dinamani (1967) studying Mactra mera and Standella pellucida respectively observed a row of papillae surrounding the oesophageal orifice. These are also present in Lutraria and clearly show familial relationship. Dinamani (1967) suggests that they too have a sorting function in the anterior region of the stomach but whether this is true for Lutraria lutraria is uncertain.

The reproductive system and excretory system in Lutraria merit little comment here.

The nervous system is that of a typical eulamellibranch, however, the three pairs of ganglia are exceedingly small. Of the three, the pedal ganglia being the largest. Presumably because of its deep burrowing stationary life style, Lutraria does not require a highly developed sensory system. Thus the middle sensory lobe is greatly reduced

to an insignificant ridge lying close to the periostracal groove in the area of the pedal gape.

Pallial tentacles are restricted to the siphonal apertures and do not fringe the pedal aperture. This in contrast to Siliqua patula (Yonge, 1952) living on high energy sandy shores. No additional sense organs are found in Lutraria.

In conclusion it can be said that Lutraria lutraria is very well adapted to a virtually sedentary deep-burrowing life.

CHAPTER 3

REPRODUCTION

CHAPTER 3

REPRODUCTION

3.1. INTRODUCTION

Studies on the reproductive cycle of bivalves include work on the shallow-burrowing mactrids Spisula solidissima (Ropes, 1968), Spisula sachaliensis (Takahashi and Yamamoto, 1970). Other studies pertinent to the present include that on the deep-burrowing species Mya arenaria (Ropes and Stickney, 1965; Pfitzenmeyer, 1965) and that on Venus striatula (Ansell, 1961) from shallow sands of the Clyde Sea Area.

Knowledge of the reproduction of any animal is paramount to the understanding of the biology of that animal. The basis of the reproductive cycle of a population is the combination of the underlying gametogenic cycles of the individuals.

The gametogenic cycle in terms of the gonad development, spawning and the number of cycles annually, are described for Lutraria lutraria over the period March 1979 to March 1981. The extent of the correlation between the spawning cycle and certain environmental variables is briefly discussed.

3.2. REPRODUCTIVE ANATOMY

The reproductive system of Lutraria has been briefly described in Chapter 2. Sexual reproduction is characteristic of bivalves - the majority being dioecious, gonochoric or unisexual. Very few exhibit

hermaphroditism. Lutraria is dioecious. No cases of hermaphroditism were found over the two year study period.

Male and female specimens can only be identified with certainty histologically. There is no variation in the colour of the gametes as in Chlamys operculatis or Mytilus edulis where the ripe female is orange or red and the male is cream or white. In the ripe female Lutraria the gonad appears granular, whereas the ripe male appears creamy, but the body wall is thick and the differences can only be seen on dissection.

Prior to spawning, the gonadial tissue totally overlies and penetrates between the lobes of the digestive gland and occupies much of the visceral mass, extending well into the foot ventrally. Because of the great extension in all directions (except in the region of the gonoducts), the paired gonads become indistinguishable from each other. Gametes are released through the genital pores via the gonoducts into the epibranchial chamber from whence they are carried in the exhalant current, through the exhalant siphon, into the surrounding water. After spawning the visceral mass becomes flaccid and the digestive gland more obvious.

In Lutraria rapid increase in food reserves after spawning may result in the visceral mass looking full. This is the main reason why gonad distension as an index of gonad ripeness is not used here.

3.3. MATERIALS AND METHODS

3.3.1. Reproductive Cycle

Samples of Lutraria lutraria were collected on a monthly basis from March 1979 to March 1981, with the exception of December 1979 when there

was adverse sampling weather. Ten animals were used each month for histological examination of gonad tissue. The small sample size was dictated by availability of the animal.

Immediately on return to the laboratory after collection, the visceral mass of each individual was removed and fixed overnight in seawater Bouin's fluid. This was to prevent loss of eggs and sperm by premature release triggered by physical disturbance. Because of the large size of the viscera, a small portion of gonad tissue postero-dorsal to the heel of the foot, was removed and refixed for at least a further three hours. This was then embedded in paraffin wax, sectioned at 6-8μm and stained using Erlhrich's haematoxylin and eosin.

The state of the gonad was assessed from the sections and classified using the arbitrary scheme adopted by Seed and Brown (1975) shown in Table 3.1. The general reproductive condition of each sample was assessed by a mean index of gonad ripeness. This was calculated from the sum of the number of individuals at each stage times the numerical value of each stage, divided by the total number of individuals in the sample. The index can vary from zero if the entire sample is in the resting/spent condition, to five when fully ripe. An increase in index is generally taken to indicate development, a decrease to indicate spawning.

TABLE 3.1. Arbitrary scheme of classification of gonad

	Brief Description of Gonad	Stages for L. lutraria
(i)	Resting or spent gonad	
	Undifferentiated ; no gametes present	0
(ii)	Developing stages	
	Developing gametes appear; no ripe gametes detectable	1
	Ripe gametes appear but developing	2
	Gonad half full of ripe gametes.	3
	Majority of gametes ripe, a few developing still present	4
(iii)	Ripe gonad	
	Gonad full of ripe gametes	5
(iv)	Spawning stages	
	General reduction in density of gametes occur	4
	Gonad half empty: unlike developing gonad very few early gametes present	3
	Gonad approximately three-quarters spawned	2
	Only residual gametes present; cytolysis in progress	1

3.3.2. Gametogenesis

The processes of spermatogenesis and oogenesis in Lutraria were observed from high power examination of the slides.

3.3.3. Experiments on Spawning

The main experiments on spawning were carried out between May and July 1979 and 1980. The aim was to produce young Lutraria to aid in the identification of larvae in plankton samples and complete the part of the reproductive cycle in terms of development and growth.

3.3.3.1. Natural Spawning

Specimens of Lutraria, maintained in running seawater in aquarium tanks in the laboratory, were closely observed for any occurrence of spawning.

3.3.3.2. Induced Spawning

Individual specimens were placed in aquarium tanks containing filtered seawater (0.3µm). Various techniques for inducing spawning were used.

(i) Animals were kept in temperatures of 7°C for four hours then rapidly transferred to room temperature (between 16-18°C).

Alternatively the temperature was raised rapidly by 5°C from room temperature.

(ii) Pricking of the adductor muscle and, in a few animals, actually cutting the muscle.

(iii) Addition of 5mls sperm or egg suspension from stripped individuals.

(iv) Injection of 5mls 1M KCl into the mantle cavity.

3.3.3.3. Stripping of Ripe Adults

Adult Lutraria were stripped following the method of Loosanoff and Davis (1963).

The gonads were cut with a sterile scalpel and eggs and sperm were siphoned off with a sterile pipette. After separately washing the eggs and sperm to remove excess body fluids and tissues, sperm suspension was added to the eggs in sterile seawater and stirred. 50mg ml^{-1} of streptomycin sulphate was added to control bacteria. The success or failure of artificial fertilisation was determined by microscopic examination of the eggs after one hour.

3.4. RESULTS

3.4.1. Reproductive Cycle

The change in mean index of gonad ripeness over the two year period of study is shown in figure 3.1. Tables 3.2. and 3.3. illustrate the distribution of animals in reproductive stages 0 - 5 from which the index is calculated. Figure 3.2. gives a graphic illustration of the percentage of animals in stages 0 - 1 and 4 - 5.

From figure 3.1. it can be seen that Lutraria shows marked cyclical

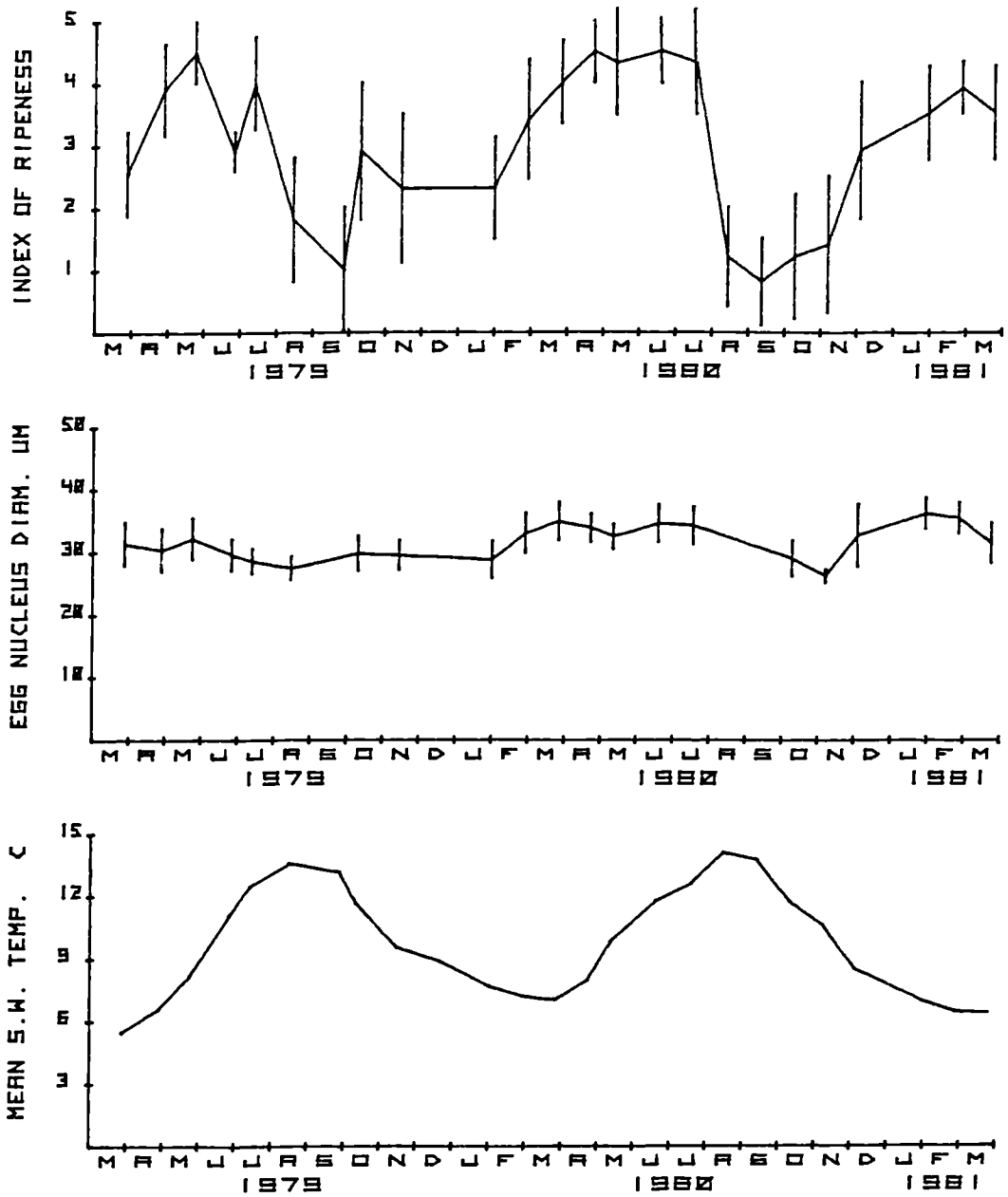


Figure 3.1. Lutraria. Changes in the mean index of ripeness and the mean diameter of the egg nucleus (um) and of the mean seawater temperature at Keppel Pier. (Vertical lines indicate standard deviation).

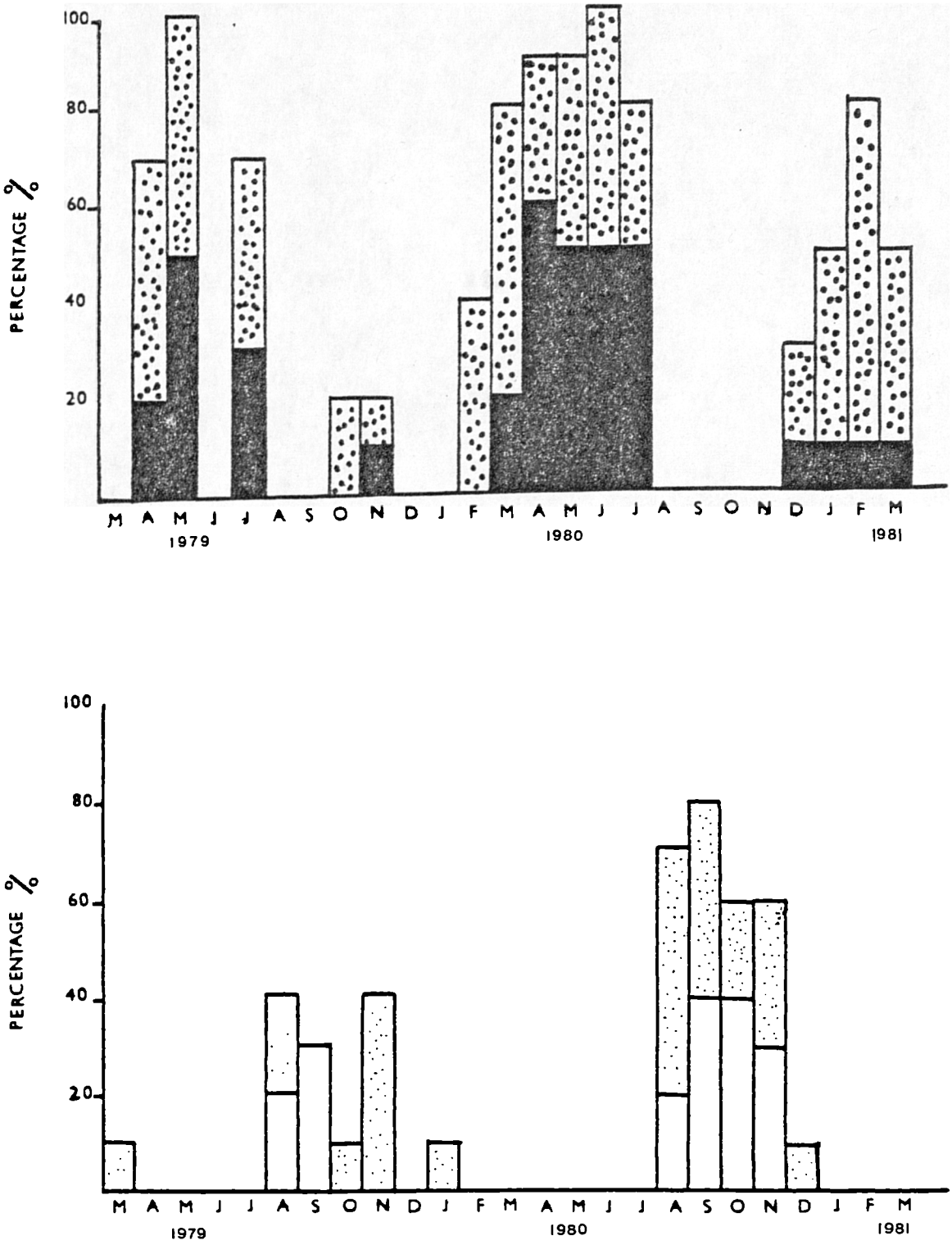


Figure 3.2. Lutraria. Histograms of the percentage distribution of the stages 4 and 5 (▣ and ■) and spent and almost spent (□ and ▣) throughout the sampling period.

late 3.1. *Lutraria*. Photomicrographs of sections through the testis.

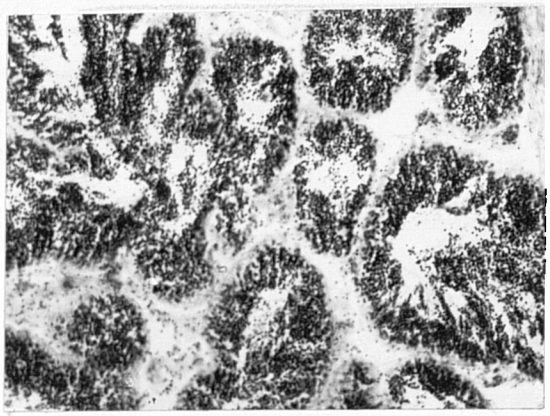
A. early developing phase (stage 2)

B. late developing phase (stage 3)

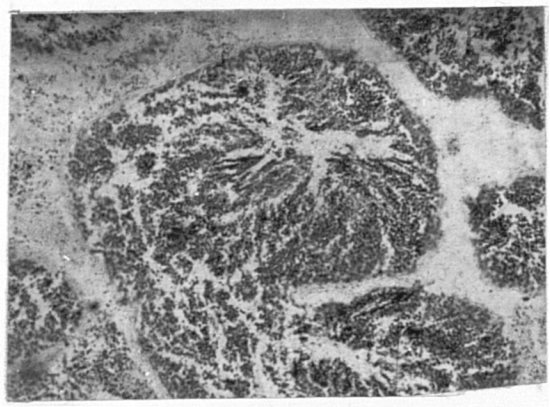
C. ripe phase (stage 5)

D. almost spent phase (stage 1)
(fc - follicle cell)

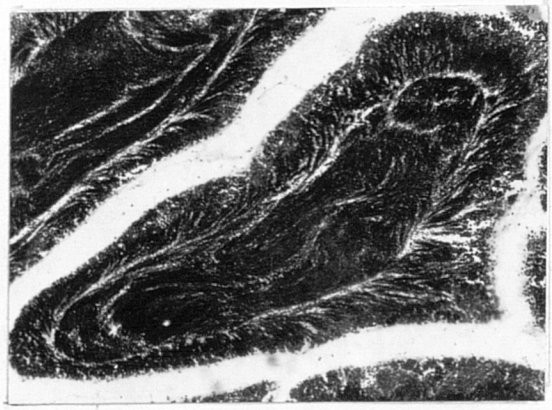
A



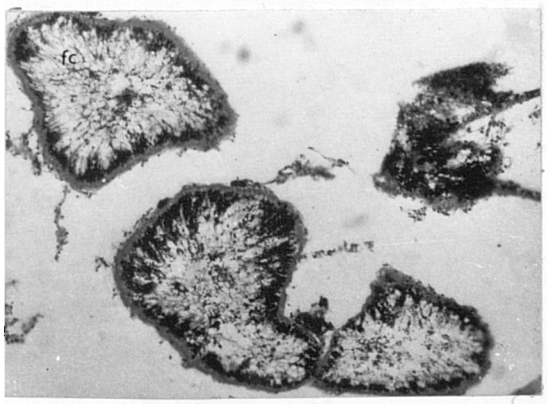
B



C



D



0·1 mm

Plate 3.2. Lutraria. Photomicrographs of sections through the ovary.

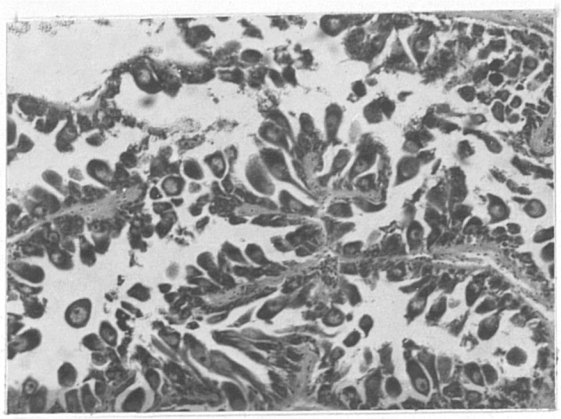
A. early developing phase (stage 2)

B. late developing phase (stage 3)

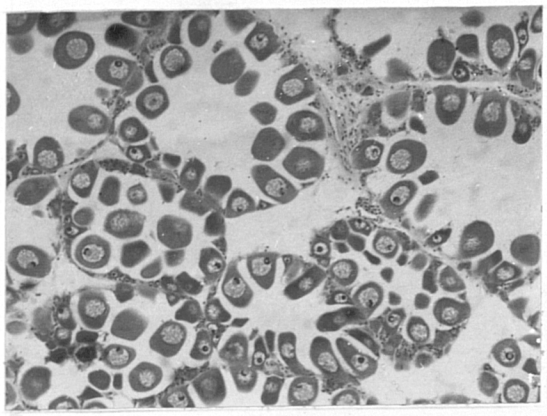
C. ripe phase (stage 5)

D. partially spawned phase (stage 3)

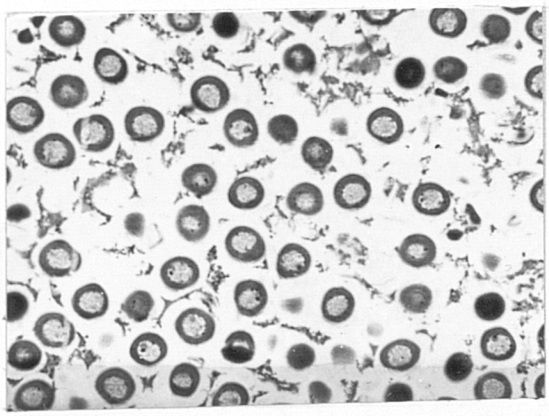
A



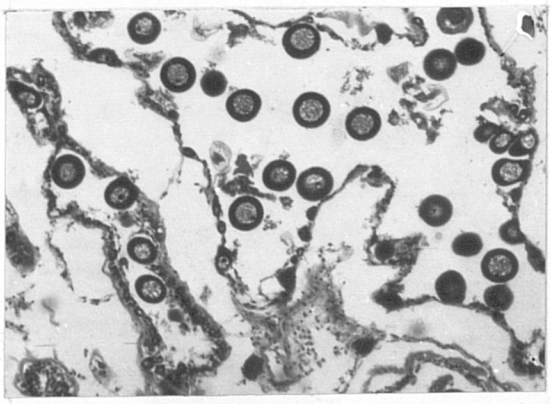
B



C



D



0·1 mm

TABLE 3.2. Lutraria. Distribution of the stages of development and spawning of the ovary.

DATE	DEVELOPING				RIPE	SPAWNING				RESTING
	1	2	3	4	5	4	3	2	1	0
1979										
MAR.	1	1	111							
APR.			111	111						
MAY				111	11111	1				
JUNE							1111111	1		
JULY		1		1		1	1			
AUG.							1	11	1	11
SEPT.										111
OCT.	1			1		11		11		
NOV.					1				111	
DEC.										
1980										
JAN.	1	11	11				1	11		
FEB.		11	111	111						
MAR.			1	1111	11					
APR.			1		111	1				
MAY					11	1				
JUNE					111	11				
JULY					111	11	1			
AUG.								1	111	1
SEPT.									11	11
OCT.								11	1	11
NOV.							1		11	11
DEC.			111	11	1					
1981										
JAN.		1	111	111						
FEB.			11	1111		1				
MAR.			1	11		1		1		

TABLE 3.3. Lutraria. Distribution of the stages of development and spawning of the testis.

DATE	DEVELOPING				RIPE	SPAWNING				RESTING
	1	2	3	4	5	4	3	2	1	0
1979										
MAR.	1	11	111							
APR.				11	11					
MAY				1						
JUNE							11			
JULY				11	111	1				
AUG.							111		1	
SEPT. (only 5)							1	1		
OCT.				1			11	1		
NOV. (only 9)						1	11	1	1	
DEC.								11	1	11
1980										
JAN.		1	1							
FEB.				1	1					
MAR.			1	11						
APR.				11	111					
MAY				1	111	1	11			
JUNE					11	111				
JULY					11	1	1			
AUG.							1	1	11	1
SEPT.								11	11	11
OCT.							11		1	11
NOV.							11	1	1	1
DEC.	1	1	1							
1981										
JAN.			1	1	1					
FEB.				11	1					
MAR.			1		1	1	1	11		

reproductive activity. The index was high in May and July 1979, April - July 1980 and February 1981. Animals appear to ripen earlier in 1981 than in previous years.

In years I and II (March 1979 - February 1980 and March 1980 - March 1981 respectively), the index is at a low level in August and September, and corresponds to the spent stage. However, the two years differ during the late autumn/early winter months. In year I the index increases to a value of over 2.5 in October 1979 and remains at this value until increasing again in January. Unfortunately sampling problems prevented collection from the sublittoral site in December, although specimens were collected from an adjacent beach population.

In year II the index of gonad ripeness remained low until November and only by December had it reached the October 1979 value. Thereafter it steadily increased to a high value in February 1981.

In the summer of 1979 phytoplankton was particularly plentiful. Plankton samples taken from July to September were particularly rich, with Ceratium species as the dominant alga. Plankton samples taken in the summer of 1980 were very poor by comparison. No quantitative data is available for the Clyde Sea Area, though a similar phytoplankton picture was noted in Loch Striven (Tett, 1980).

The main spawning period for Lutraria is during the summer months when the index of gonad ripeness is highest and the diameter of the egg nucleus is also high (Fig. 3.1.). Spent and almost spent animals (0 + 1) are found from August to November in both years. Individual animals in the pre-spawning or ripe condition are found through most of the period of study except in the months of August and September. By February 1980 and 1981 most animals have developed to at least Stage 3. A high index of gonad ripeness is maintained through the summer months.

Initial histological investigations on Lutraria began in January 1979 at a time when I was beginning to develop the histological techniques. Slides from January and February 1979 show very little development and compare with the low index of ripeness recorded in March 1979. The temperature in March 1979 fell below 6°C, a lower figure than that recorded in the spring of the following two years 6.96°C and 6.30°C. Maximum seawater temperatures were recorded in August in both years 13.50°C and 14.05°C and little change was seen in the temperature regime over the two year period (Fig. 3.1.).

It is interesting to note that the index of gonad ripeness falls to its lowest value at the maximum seawater temperature.

3.4.2. Development

Gametogenesis in Lutraria follows the same basic pattern as that of many other bivalves.

In the male, spermatogonia lying embedded in the thickened alveolar wall, give rise to primary and secondary spermatocytes which lie free in the lumen of the follicles. These in turn give rise to spermatids which develop into spermatozoa.

In the ripe male, spermatozoa fill most of the lumen. The sperm may appear either as a 'swirl' in the centre of the alveoli, or have their tails orientated toward the centre or form a homogeneous mass as described for Spisula solidissima (Ropes, 1968).

Ripe males are first seen in some number in April 1979, and slightly earlier in 1980 and 1981. The majority, however, are found during the summer months.

There is no evidence of an atypical spermatogenesis as reported by Loosanoff (1937) for Mercenaria mercenaria where multi-nucleated bodies developed from spermatogonia and eventually become cytolysed.

Spent and late spawning stages are found in August through to December.

In the spent condition, in both males and females, the lumen of the follicles is empty except for a few residual gametes. There are many spaces in the tissue where the alveolar walls have broken down following the release of gametes.

Plate 3.2. (D) of a spent male shows the development of vacuolated follicle cells in the lumen with primary gonial cells at the periphery. Coe (1943) found this condition in Teredo navalis. He suggests that the follicle cells provide the nutrient for the developing gametes and consequently they decrease in number during gametogenesis. The resting gonads of the genera Pecten, Mytilus, Modiolus and Pamphia are composed of gonial cells with only minute follicle cells and probably take up nutrient from the surrounding connective tissue (Sastry, 1979). Very little connective tissue surrounds the follicles in Lutraria.

In Lutraria there is only a very short recuperative phase when sex cells are not present. This was observed in some individuals during August and September of both years. Following this period, spermatogonia and oogonia are seen in the alveolar walls. Very early oocytes can be distinguished by a sharply defined nucleolus in an almost clear nucleoplasm.

As development progresses the oocytes increase in diameter from 7μm to a maximum value of 36μm. They became more obviously attached by a stalk to the basement membrane and the nucleoplasm becomes granular. In the ripe female oocytes lie free in the lumen of the alveoli. The

diameter of the nucleus of the ripe eggs varies from 26.07μm to 36.00μm (Figure 3.1.) and is greatest when the index of gonad ripeness is greatest.

In both males and females, as development continues the alveoli lie closer together and the whole gonad takes on a fuller appearance.

3.4.3. Experiments on Spawning

Natural spawning was only observed on one occasion in the laboratory and this during a 'pumping' experiment in April 1981 (see page 90). The animal was buried in sandy mud and emitted sperm in an almost constant stream through the exhalant siphon.

Injection of KCl proved successful in summer 1979 with the emission of gametes within 30 to 60 minutes of the injection. Methods (i), (ii) and (iii) (page 34) were unsuccessful in inducing spawning.

Artificial fertilization was achieved using gametes from KCl injection and stripping of adults in 1979 but a similar success was not achieved in 1980. Examination of the eggs after one hour showed cleavage and development proceeded to the ciliated late blastula - early gastrula stage, thereafter the cultures died. Straight hinge larvae were never obtained nor were larvae identified in plankton samples.

3.5. DISCUSSION

Spawning in Lutraria takes place from late spring reaching a peak in May with the major spawning effort being completed in August/September.

From September to November various spawning stages are found but by

December the majority are in the spent or almost spent condition.

The index of gonad ripeness shows slight difference in value between the autumn of 1979 and 1980. In 1979 the index shows an increase in October, the level then is maintained until January, after which there is an increase to the high spring level. It is possible that a minor spawning took place at this time (October) in a small proportion of the population. Alternatively, the animals may have developed fairly rapidly - due to high phytoplankton abundancy - and then development slowed down over the winter months.

The mactrid Spisula solidissima (Ropes, 1968) has such a biannual cycle, which is characterised by a major mid-year spawning and a minor late year spawning. Ropes (1968) suggests that the second annual reproductive cycle may be neither typical for surf clams throughout their geographical range nor always an annual event in clams in New Jersey. Pfitzenmeyer (1962) found two separate spawnings in May and September/October for Mya arenaria and suggested that they were the result of two separate maturations and not a cessation in spawning due to the high summer temperatures.

Unfortunately in the present work it was not possible to obtain a December sample from the study site, however, samples of Lutraria from the beach close by at Hunterston had specimens present in a spent or redeveloping state.

Individuals with ripe gonads were found outside the major spawning period throughout most of the two years of study.

From the assessment of monthly samples of Lutraria it is thought that the animal does not completely empty the follicles at one spawning but may continue spawning throughout the summer months. However, because continuous histological studies of one individual are impossible this cannot be confirmed. Haines (1976) and Holland and Chew (1974)

report a similar situation for Macrocallista nimbosa and Venerupis japonica respectively. Loosanoff and Davis (1950) also found that in Venus (Mercenaria) mercenaria all eggs were not discharged at once.

Animals from the same site and collection date exhibit different stages of development and of spawning. This is similar to the results of Loosanoff (1937) for Venus (Mercenaria) mercenaria and which led him to suggest that the whole population of a certain bed does not spawn at exactly the same time and hence the spawning season is extended. Furthermore, within Lutraria, different follicles of an individual may be at a different stage, i.e. some follicles may have discharged their gametes, while in others gametogenesis is still occurring.

Thus difficulties arise in the classification of the gonadial condition and the interpretation of the reproductive cycle. Other methods previously used for assessment of gonad include excision of gametes (Allen, 1951, 1953) and for Placopecten magellanicus change in gonad colour (Merrill and Burch, 1960). The most reliable results are thought to be obtained from microscopic examination of gonadial tissue. An arbitrary scheme of classification was used here. The distinction between stages in what is essentially a continuous process is naturally subjective and intermediate stages are inevitable. Thus, examination of later spawning stages of Lutraria also show signs of early redevelopment and young oocytes. Furthermore, when the gonad appears to be in spawning condition, there is no certainty that active emission is taking place. Haines (1976) found that strip-spawning of the Sunray Venus Clam (Macrocallista nimbosa) was not successful over the entire period that the animal is histologically ripe but is confined to a much narrower period than would be expected.

Direct observations of spawning in the field are critical in determining that part of the annual cycle. Such observations are often very difficult, and for Lutraria were found impossible to obtain. Observations of laboratory spawnings, either natural or induced, are of limited value because numerous environmental variables in nature may act as controls in modifying the cycle. Only if laboratory conditions emulate natural ones, are they meaningful. Factors that induce spawning are possibly not the same as those which induce gametogenesis.

The summer months were chosen for experimental larval work as the probability of the animals being in Stage V of ripeness was high at this time. However, as previously stated histological and physiological ripeness need not be the same and the adults used may not have been in the required condition.

Fertilization was achieved on two occasions but the larvae never developed to the straight hinge stage. The lack of success in rearing larvae of Lutraria is attributed to several factors. There were laboratory problems in maintaining appropriate temperature regimes and the eggs and embryos were unfortunately subjected to temperature fluctuations. Contaminants may have been present in the filtered seawater and rough handling of eggs in washing may have contributed to the death of the cultures. It is thought by some workers that, in general, larvae obtained by stripping do not develop normally.

Larvae of Lutraria lutraria were never identified in the plankton samples. Previous workers have used hinge and pigmentation of the larvae of Lutraria for identification (Rees, 1951), however, the accuracy of this identification is not certain.

The identity of larvae raised in the laboratory from known adults cannot be questioned.

Different species of bivalves have different lengths of periods of sexual development and spawning periods of different duration. In some lamellibranchs gonad development begins at the end of the winter or the beginning of the spring as the water temperature begins to rise e.g. Tivela stultorum (Coe, 1947), Crassostrea virginica (Loosanoff and Davis, 1963). These animals 'hibernate' and spawn late from mid-summer to autumn. In others development starts in summer and autumn and in these winter causes a temporary pause in the cycle e.g. Venus (Mercenaria) mercenaria (Loosanoff, 1937), Mytilus edulis (Chipperfield, 1953) Macoma balthica (Lammens, 1967). These animals tend to spawn from spring until early summer.

Lutraria belongs to the second group although it seems not to have complete cessation of sexual development during the winter. During the autumn and early winter the animals are in the late spawning stages with the residual gametes being cytolysed by December. The main period of gametogenesis appears to be from December to January, though in October 1979 some development was seen. Literature shows that Cyprina (Arctica) islandica (Loosanoff, 1953), Pecten maximus (Mason, 1957), Venus striatula (Ansell, 1961) and Argopecten irradians (Sastry, 1963) also have no complete cessation of development in winter.

Workers on other members of the Mactridae have found similar spawning cycles. Ropes (1968) found the breeding cycle in Spisula solidissima was from July to August and mid-October to early November. In Spisula sachaliensus, Takahashi and Yamamoto (1970) showed that development commenced in December and January and with rapid growth until spawning in early May and summer months. Golikova and Scarlato (1970) also working on Spisula sachaliensis found the breeding season of their population extended from June to October.

Sastry (1966) used mean oocyte size to assess the average stage of gonad development. Similarly, in Lutraria the diameter of the egg

nucleus is greatest when the index of gonad ripeness is greatest.

Many factors are thought to influence reproductive cycles of marine invertebrates. Giese and Pearse (1974) and Wilson and Hodgkin (1967) believe that a complex of physical variables in the environment influence, if not control, the sequence and timing of events in the reproductive cycle, while Sastry (1970) states that the reproductive cycle of a species is a genetically controlled response to the environment.

Environmental factors, including temperature, salinity, light, food, day length and endogenous factors within the animal itself are involved. Only temperature and food will be discussed here.

Temperature has received greatest attention in the field of factors influencing reproductive activity. Giese (1959) considers growth and maturation of gametes are probably influenced more by temperature than by any other factor. Spawning may occur with rising temperatures e.g. Cyprina (Arctica) islandica (Loosanoff, 1953), decreasing temperature e.g. Argopecten irradians (Sastry, 1963) and maximum temperature e.g. Mercenaria mercenaria (Loosanoff and Davis, 1950).

In Lutraria the major spawning period occurs as the water temperature increases. Spawning has largely ceased by August when the seawater temperature has reached its maximum. Gamete development occurs when the water temperatures are still decreasing and when they reach their lowest values. Loosanoff (1937) found a similar pattern in Venus (Mercenaria) mercenaria and commented that it was unusual that the development of gametes occurs during the season when water temperature is rapidly decreasing and the ecological conditions for gonad development appear less favourable than in spring and early summer. Sastry (1966,1968)

suggested that gonad growth and gametogenesis takes place under temperature conditions at which nutrient mobilization at the gonads is permitted after basic needs of the animal have been met.

In animals already undergoing gametogenesis, development may be accelerated by an increase in temperature. Chipperfield (1953) indicated that the rate of gametogenesis in Mytilus edulis was roughly proportional to the rate of temperature increase. Colder temperatures were found to delay gamete development to maturation in Mercenaria mercenaria (Loosanoff and Davis, 1963) and Mytilus edulis (Bayne, 1965).

In the winter of 1979 minimum water temperatures occurred in March (5.40°C). Histological examination of Lutraria lutraria in January and February 1979 showed the animals to be in very early stages of development. This was in contrast with the two following years when the index of gonad ripeness was higher at this time. The unusually cold weather at the beginning of 1979 is thought to have delayed gamete development.

Saleuddin (1964) reported that in Astarte sulcata gametogenesis also began in January when temperatures are at a minimum. Ropes (1968) found that Spisula solidissima spawned when the temperature was approximately 10°C in May and continued to spawn until July, stopping before the temperature rose to a maximum of approximately 18°C in August. Animals then spawned again from October to November when the temperatures decreased from 18°C to 10°C. In the years when the fall in temperature was lower than normal, spawning was delayed and the second cycle did not occur.

The population of Lutraria lutraria studied was from the Clyde Sea Area only. Consequently no comment can be made on possible variation in the gametogenic cycle of geographically separated populations. In

many species southern populations have more than one breeding cycle through the year. Ropes and Stickney (1965) showed for Mya arenaria that gametes developed in the fall and spring in areas south of Cape Cod, while to the north only one period of reproductive activity was seen in the summer.

The temperature regime for the Clyde Sea Area showed little change over the two year period of study apart from low winter temperatures in 1979. This suggests that another factor was involved in the high index of gonad ripeness recorded in the autumn of 1979 which may have resulted in a minor spawning. Large phytoplankton blooms were seen in the Clyde Sea Area in the summer of 1979. Severe fish kills were recorded in Loch Striven (Tett, 1980) in May and June 1979. Plankton samples taken from June to October were very rich, the principal phytoplankton species being Ceratium spp. In the following summer, phytoplankton was noticeably less abundant.

Sastry (1968) suggests that both a minimum temperature requirement for gamete development and the abundance of food in the environment limit the reproductive period of the scallop Aequipecten irradians to the summer. The adequacy of phytoplankton as a food for suspension feeders e.g. Lutraria, is dependent on its concentration, rate of production and its availability to the animal. A rapidly growing and maturing animal needs food for basic metabolism, gonad development and for growth, whereas in a mature but spent animal the needs are metabolic and to build up reserves to spawn again. The deposition of reserves long before the breeding season occurs and complicates the relationship between growth and gamete production and the two may become obscured. Furthermore when food availability is high, reserves may be built up and stored until a later date.(Ansell, 1972; Ansell and Trevallion, 1967).

The relationship between food availability, reproductive cycle and reserves for Lutraria is discussed further in the following chapter, but it is thought that the high phytoplankton levels in the summer 1979 were responsible for the increase in index of gonad ripeness at that time.

Because so few young Lutraria were obtained there is insufficient data to determine the relationship between age, gametogenesis and size at maturity. Some workers have found that the size of an individual appears to relate to gonad development, thus, in Mya arenaria(Brousseau, 1978) observed a positive correlation between female body size and oocyte production. The life history of the sampled population of Lutraria was discussed in Chapter 1.

Such evidence as exists on the effect of light and day length on reproductive cycles was reviewed by Giese (1959) and Giese and Pearse (1974), however, no conclusions were reached. Similarly, there have been few studies on the effects of salinity and tides and nothing in the present study relates to these factors.

In summary the major spawning period of Lutraria was found to be during the summer months as the water temperatures were increasing. Spent and late spawning stages were recorded from August to early winter although early development was also recorded at this time. The main period of development, with a consequent increase in the index of gonad ripeness, was recorded from December/January. A plentiful supply of phytoplankton in the summer of 1979 probably resulted in a higher index of gonad ripeness in the winter of 1979 than in 1980.

A minor spawning may have occurred in the late autumn of 1979, although this cannot be stated conclusively. It is possible that the animals merely remained in greater state of development through the winter.

CHAPTER 4

SEASONAL CHANGES IN WEIGHT AND BIOCHEMICAL COMPOSITION

CHAPTER 4

SEASONAL CHANGES IN WEIGHT AND BIOCHEMICAL COMPOSITION

4.1. INTRODUCTION

Many studies exist on the seasonal cycles in condition and biochemical composition of bivalves including species from the Clyde Sea Area, e.g. Chlamys opercularis (Taylor and Venn, 1979), Chlamys septemradiata (Ansell, 1974b), Pecten maximus (Comely, 1974), Donax vittatus (Ansell, 1972) and Abra alba, Nucula sulcata, Lima hians (Ansell, 1974a,c,d).

Reviews on biochemical changes in bivalves include those by Giese (1969), Gabbot (1975, 1976) and Bayne (1976).

The present work describes the seasonal changes in body weight and biochemical composition of Lutraria lutraria from the Clyde Sea Area.

4.2. MATERIALS AND METHODS

Specimens of Lutraria were collected at monthly intervals using the methods described in Chapter 1.

A sample of twenty animals was used for determination of wet and dry weights and shell lengths. The soft tissues were removed, blotted dry and weighed. They were then divided into five components namely adductor muscles, gonad and visceral mass, siphon, digestive gland and the remaining tissues as 'other'. Each component was then further blotted dry and weighed, then placed in a weighed dish in an oven at 95°C for twenty four hours to obtain the dry weight.

The shell was washed to remove any excess sand or mud, and left to dry overnight at room temperature. The shell weight and length were then found.

Tissues were removed from a further sample of five animals and dissected as above. The individual tissues were rinsed in distilled water, homogenized, then freeze dried for biochemical analysis.

Protein was determined using the method of Lowry et al., (1951) as described by Taylor and Venn (1979). 10mg of freeze dried tissue was homogenized in 10ml 0.1N sodium hydroxide and left overnight. After centrifugation (10 mins 8,000 rev/min.), the pellet was discarded and 1ml of supernatent added to 2ml 10% trichloroacetic acid and left overnight. Further centrifugation resulted in the formation of a pellet which was redissolved in 1ml 0.1N sodium hydroxide. 0.5ml of the redissolved precipitate was placed in a test tube and 5ml Lowry reagent 'C' (Lowry et al., 1951) was added and the mixture incubated at 50°C for 15 mins. 0.5ml reagent 'E' (Folin's Ciocalteau reagent) was added and after thorough mixing the solution was incubated for one hour at 50°C. The optical density was read at 750nm initially using a Cecil CE 273 spectrophotometer; later a Unicam SP. 600 spectrophotometer was used. A calibration curve using casein was constructed.

Determination of carbohydrate (total) was carried out using the anthrone - sulphuric method of Hewitt (1958) as described by Taylor and Venn (1979). 2mg freeze dried tissue was homogenized in 10ml of distilled water. 0.5ml was then removed and placed in a test tube and 5ml anthrone - sulphuric reagent (Hewitt, 1958) was added. The solution was thoroughly mixed and incubated at 100°C for 10 mins.

On rapid cooling the optical density at 620nm was determined. A calibration curve using glucose as a standard was constructed.

Lipid was determined by the sulphosphovanillin method of Barnes and Blackstock (1973) as described by Taylor and Venn (1979). Extraction of lipid was first carried out using the method of Folch, Lees and Sloane Stanley (1957).

50mg freeze dried tissue was homogenized in 25ml chloroform: methanol 2:1 (v/v) and left for an hour in a stoppered bottle. 5ml 0.9% sodium chloride was then added, thoroughly mixed and left overnight at 5-6°C. The two resultant phases were separated using phase separating paper, Whatman 1PS. 0.5ml of the chloroform-methanol mixture was placed in a test tube and reduced to dryness. 0.5ml concentrated sulphuric acid was added and the mixture incubated at 100°C for 10 mins. 0.2ml of this solution was then transferred to a test tube and 5.0mls phosphovanillin reagent (Barnes and Blackstock, 1973) was added. The optical density was read at 520nm.

Cholesterol was used to calculate the calibration curve with a correction for total lipids (Barnes and Blackstock, 1973).

Results from the gravimetric method on tissues of Lutraria were compared to the results obtained from the sulphosphovanillin method at the onset of the period of study. The gravimetric method was found to give more variable results on the quantities of tissues used and the lipids were consequently determined using the colorimetric method.

Comparison of results of biochemical analysis on freeze dried and oven dried tissue showed higher and more variable results from the oven dried samples, particularly the carbohydrate and protein.

Ashing was carried out at 500°C - 600°C. 0.20g or 0.02g of freeze dried tissue was oven dried at 85-95°C, cooled in a dessicator, reweighed and then placed in the muffle furnace for a minimum of five hours.

Regression analysis between shell length and wet and dry weights of the total animal and all the component parts was used to estimate the weights of a standard animal of 11.00cm length.

Covariance analysis was carried out using the methods of Snedecor (1956) (see Appendix I for detailed results). Each group of regressions was compared by covariance analysis and the values calculated from a common slope. Very few significant differences in slope were found, and these occur mainly in June 1980. The reason for this is unclear, however, in June the animals are in spawning condition. Larger animals may be decreased in weight due to release of gametes, whereas small, ripe animals may be heavier. Alternatively the nutritive condition of the animals may be in an unusual but undefined state.

The lack of significant difference in slope is probably because the range of animals used in the experiment is small, too small to show any significant variation in weight and biochemical composition due to size.

The significance of the overall F value (Regression Coefficient) is dependent to some extent on whether or not the June 1980 figure is included. Neglecting the June data the F value is not significant, but if June figures are included, then in a few cases the F value is significant. The overall F value (Adjusted Means) is significant in all cases showing that changes in weight are likely to be seasonal.

Total tissue dry weight was found by summation of dry weights of each component. Total weight of the intact animal was not found for Lutraria owing to the variable quantity of water in the mantle cavity.

Biochemical results have been presented in terms of percentage composition and as composition of the tissue (dry) of a standard animal length 11.00cm. This was calculated by multiplying percentage composition of each tissue by the estimate of dry weight of that tissue in the standard animal.

This has the advantage of preventing biochemical changes in percentage of one biochemical component reflected by a reciprocal change in the others.

Values for both male and female have been combined throughout calculations of weight and biochemical composition.

4.3. RESULTS

4.3.1. Seasonal Changes in Weights and Water Content

4.3.1.1. Gonad

The seasonal changes in tissue weight and percentage water of the gonad are summarised in figure 4.1. The index of gonad condition taken as $\frac{\text{dry wt. gonad (g)}}{\text{total dry wt. (g)}} \times 100$ is also shown.

It can be seen that the results from the two years differ. In 1979 both wet and dry weights remained fairly low during the summer, then increased rapidly from August reaching maximum values of 21.77g wet weight and 6.70g dry weight in October, decreasing through the winter. In 1980 neither wet or dry weights reached the high values of the previous year. Highest values were recorded in June 1980, 16.07g wet weight and 4.33g dry weight decreasing by July and remaining fairly constant between 2.0 - 3.0g dry weight for the remainder of the year.

The water content of the gonadial tissues remains fairly high and constant over the two year period with a mean value 75.85%. The minimum value was recorded in October 1979 corresponding to maximum dry weight values. There appears to be no seasonal trend in water content associated with spawning.

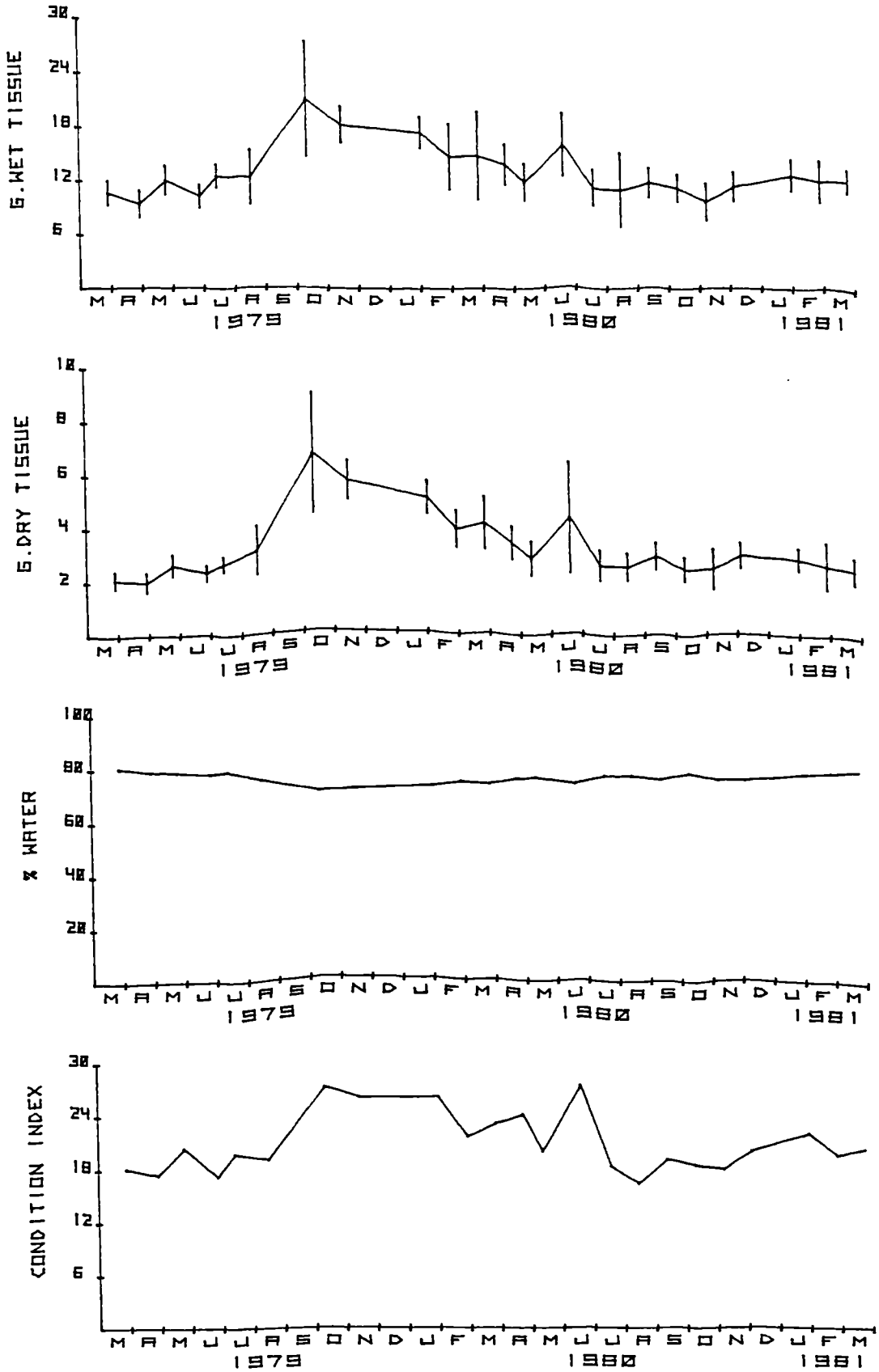


Figure 4.1. Lutraria. Changes in tissue wet weight, dry weight, percentage water and condition index of the gonad of a standard animal. (Vertical lines = confidence limits).

The index of gonad condition increases through the winter of 1979 to a maximum 26.61% in October 1979 and remains high until February when a slight decrease was recorded. During the summer 1980 the index remains fairly high until decreasing from the June 1980 value of 27.06% to a minimum of 16.20% in August 1980.

The total percentage changes in the index of gonad condition cannot be attributed to the events of the spawning cycle in 1979. However in 1980 the events follow more closely the changes in index of gonad ripeness (Chapter 3). The fall in the index of gonad condition from 27.06% in June to 16.20% in August, corresponds to the change from ripe to spent animals. From this it can be seen that the actual gonad is represented by about 44.11% of the 'gonad' index, (i.e. 10% of the body is equivalent to gonad), the remainder to visceral mass and foot. The index of gonad condition increases slowly over the winter 1980 reaching a high value of 21.90% by January 1981.

4.3.1.2. Digestive Gland

The seasonal changes in tissue weight and percentage water of the digestive gland are summarised in figure 4.2. The index of condition of the digestive gland is also shown.

The digestive gland is the smallest of the five components ranging between 1.41% of body weight in January 1980 to 4.80% in June 1979.

Wet and dry weights are highest through the summer and early autumn of 1979, decreasing in October 1979 to remain between 1.50 - 2.21g wet weight and 0.27 - 0.47g dry weight for the remainder of the period of study. The percentage of water was high and fairly constant for 1979 and 1980 between 76.96 - 81.99%.

There is a reciprocal relationship between index of condition of the digestive gland and index of condition of the gonad.

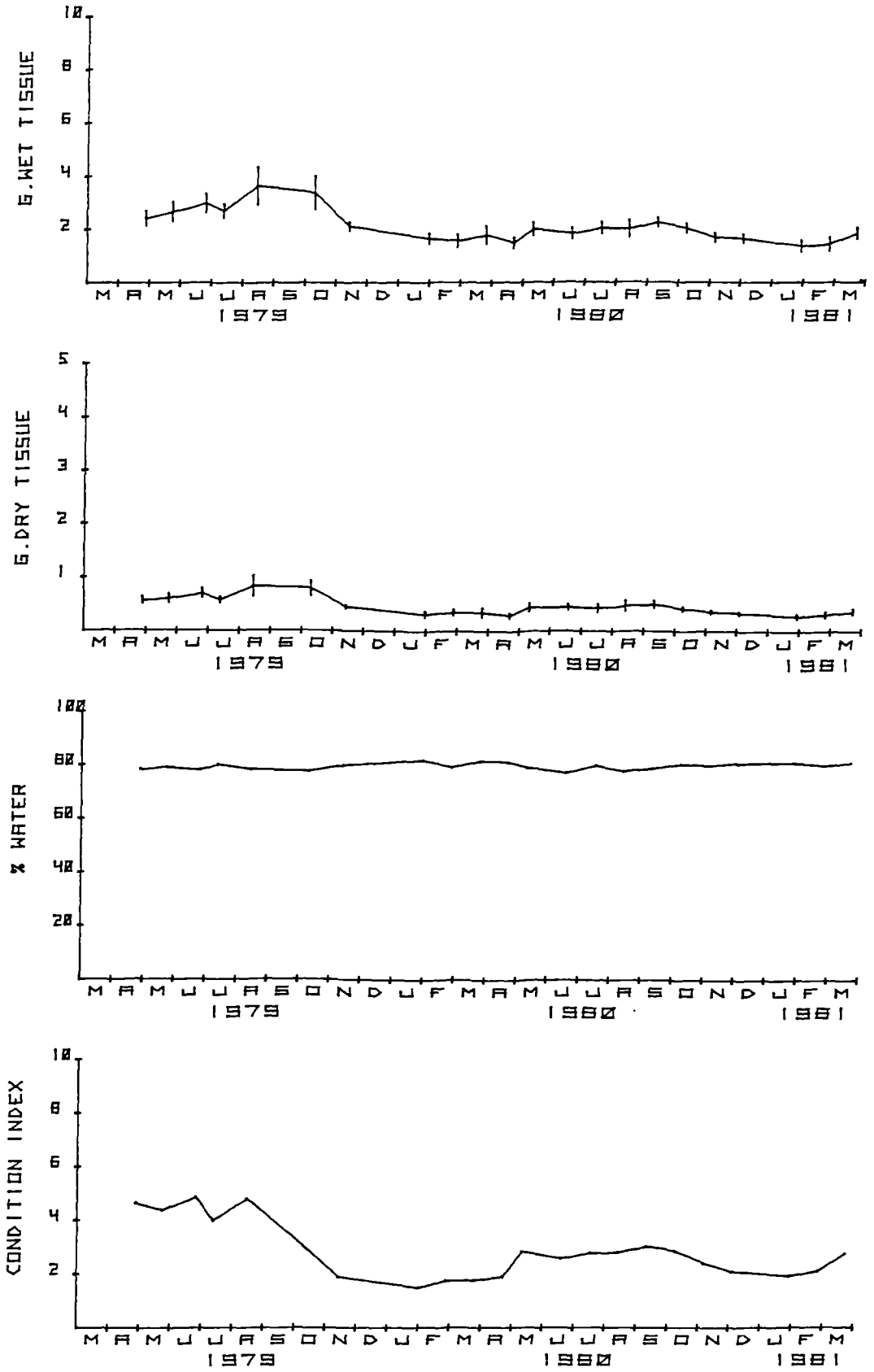


Figure 4.2. Lutraria. Changes in tissue wet weight, dry weight, percentage water and condition index in the digestive gland of a standard animal. (Vertical lines = confidence limits).

4.3.1.3. Adductor Muscle

The adductor muscle comprises a small part only of the total animal. The seasonal changes in tissue weight and percentage water of the adductor muscle are summarised in figure 4.3. The change in adductor muscle index is also shown.

In 1979 muscle tissue weight increased to a maximum 5.75g wet weight and 1.59g dry weight. There is a decrease over the winter months to a minimum value in February 1980. Muscle tissue weight fluctuates slightly through the summer 1980 with no increase in the autumn. A small decrease was recorded during the winter months 1980/1981.

There is no clear seasonal trend in the water content. The minimum value (69.80%) was recorded in April 1980.

The condition index for the adductor muscle increased throughout 1979 and 1980 reaching a maximum value in April 1980 (9.36%). A low value (4.97%) was recorded in March 1979.

4.3.1.4. Siphon

The siphon constitutes the largest body component in Lutraria. The seasonal changes in the weight and the percentage of water of the siphon are summarised in figure 4.4. The change in condition index is also shown.

The change in siphonal weight differs in 1979 as compared to 1980. In 1979, as in the case of gonad and adductor muscles, the wet and dry tissue weight increased from a July value of 34.67g and 7.13g respectively to a maximum value in October of 45.71g wet weight and 11.00g dry weight. In 1980 the weight remained fairly constant though a slight decrease was recorded through the winter months. This decrease occurred in both years with the decrease in weight in 1979 being the greater (Fig. 4.4.).

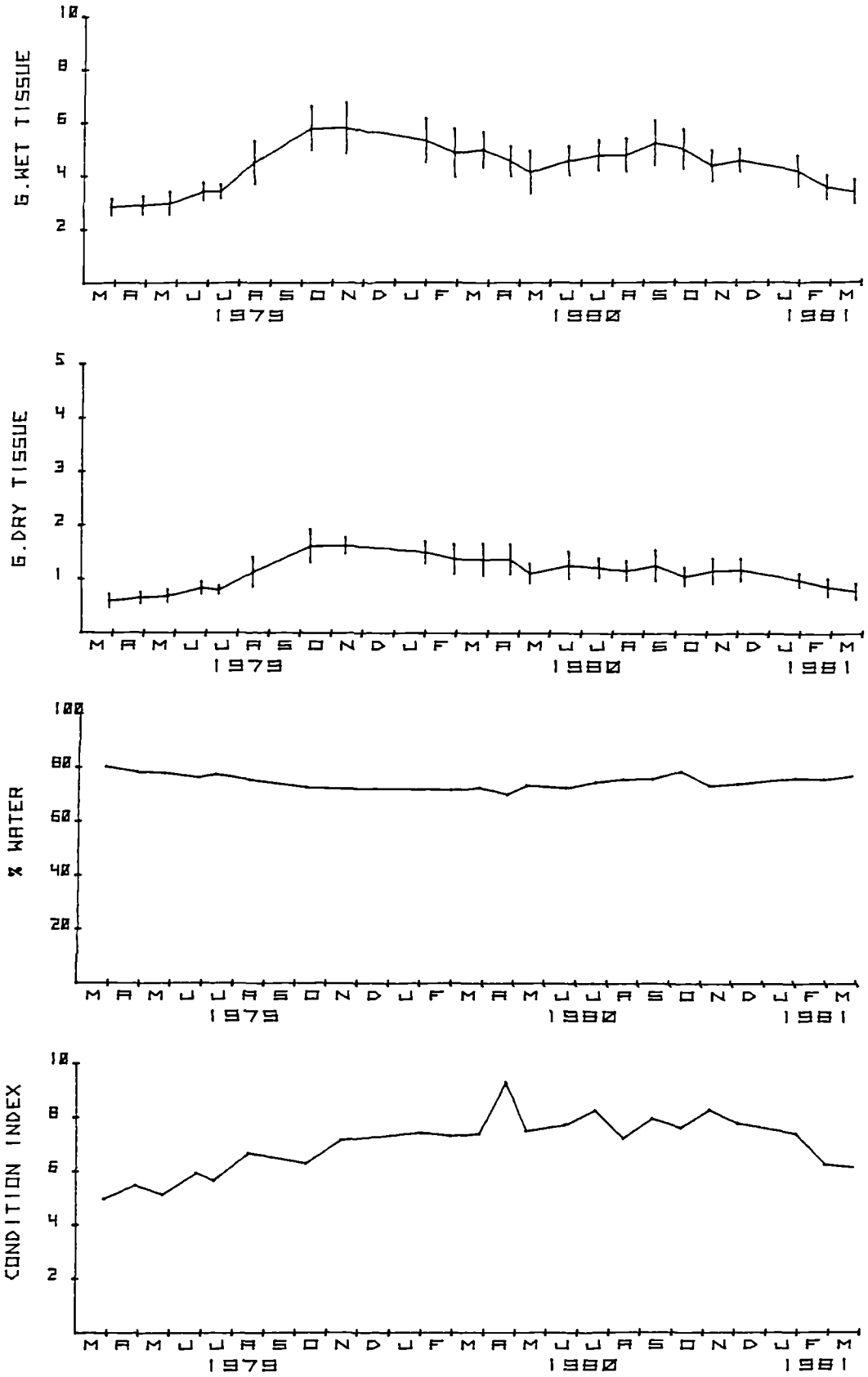


Figure 4.3. Lutraria. Changes in tissue wet weight, dry weight, percentage water and condition index in the adductor muscle of a standard animal. (Vertical lines = confidence limits).

No clear seasonal trend can be seen in the water content of the siphonal tissues. The minimum value (75.94%) was recorded in both October and November 1979, corresponding to the highest dry weight values. For the rest of the period the water content remains at a consistently high value of between 75-80%.

4.3.1.5. 'Other' Tissue

The seasonal changes in weight and the percentage water content in the 'other' tissue are summarised in figure 4.5. The change in condition index is also shown. 'Other' tissue comprises mantle, *ctenidia* and palps and kidney, heart.

The changes in 'other' tissue weight are similar to those of the siphon, adductor muscles and gonad tissue. A maximum weight of 21.38g wet weight and 4.76g dry weight was recorded in October 1979 and decreas - through the winter. In 1980 the weight fluctuates through the summer and shows a slight decrease in November.

The water content remains high and fairly constant throughout the period of study, as does the condition index.

4.3.1.6. Whole Animal

The seasonal changes in total tissue weight, percentage water and shell weight of the whole animal are summarised in figure 4.6.

The graph showing changes in total tissue weight reflects the changes in weight of each of the body components, except that of the digestive gland. The results of the two years differ significantly.

Both wet and dry weight reach a maximum in October 1979, 102.23g wet weight and 25.18g dry weight respectively. Minimum values in 1979 were recorded in March 62.60g wet weight and 11.48g dry weight.

Tissue weight decreases through the winter of 1979 and by March 1980 the dry weight had fallen to 14.42g.

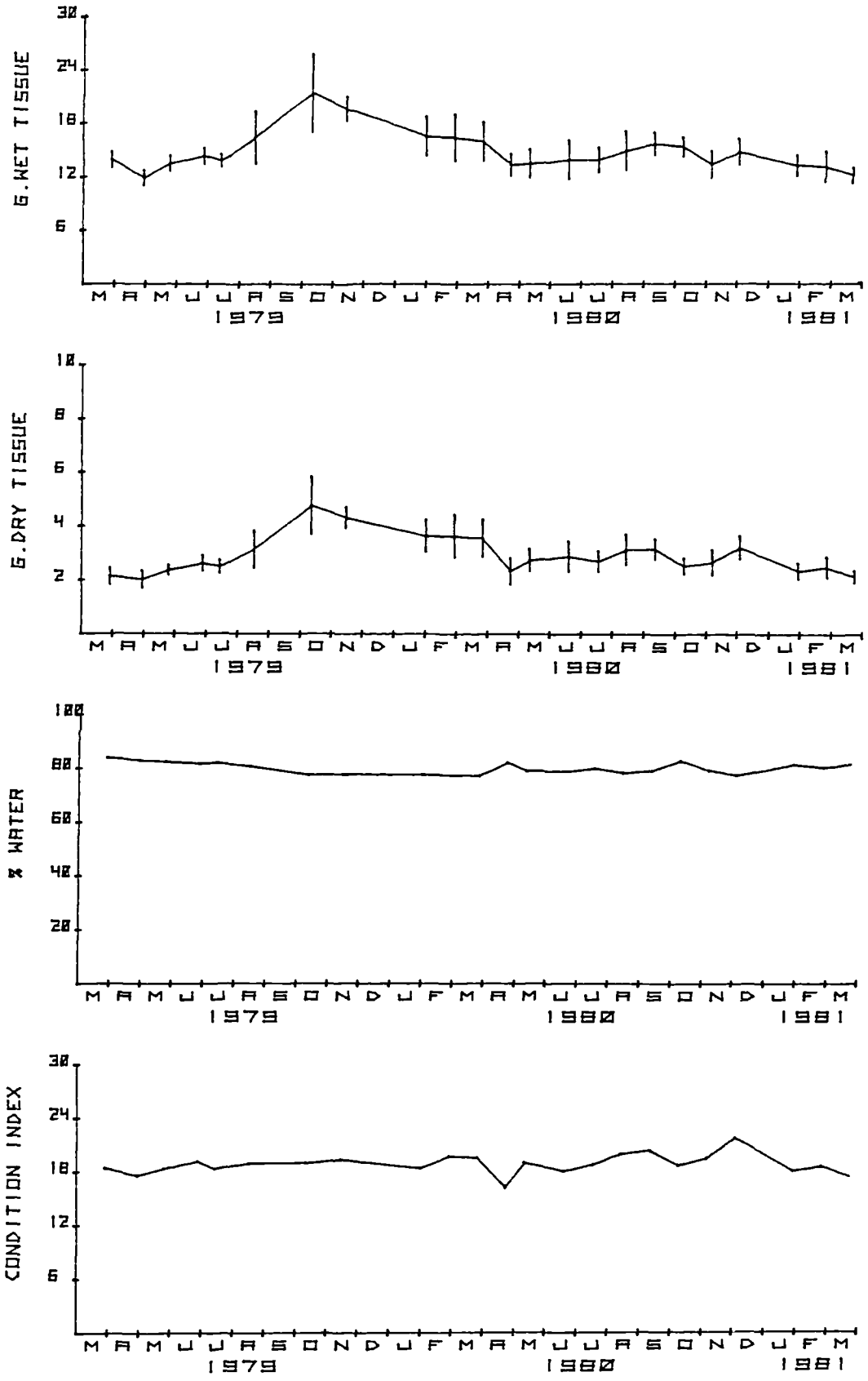


Figure 4.5. Lutraria. Changes in tissue wet weight, dry weight, percentage water and condition index in the 'other' tissue of a standard animal. (Vertical lines = confidence limits).

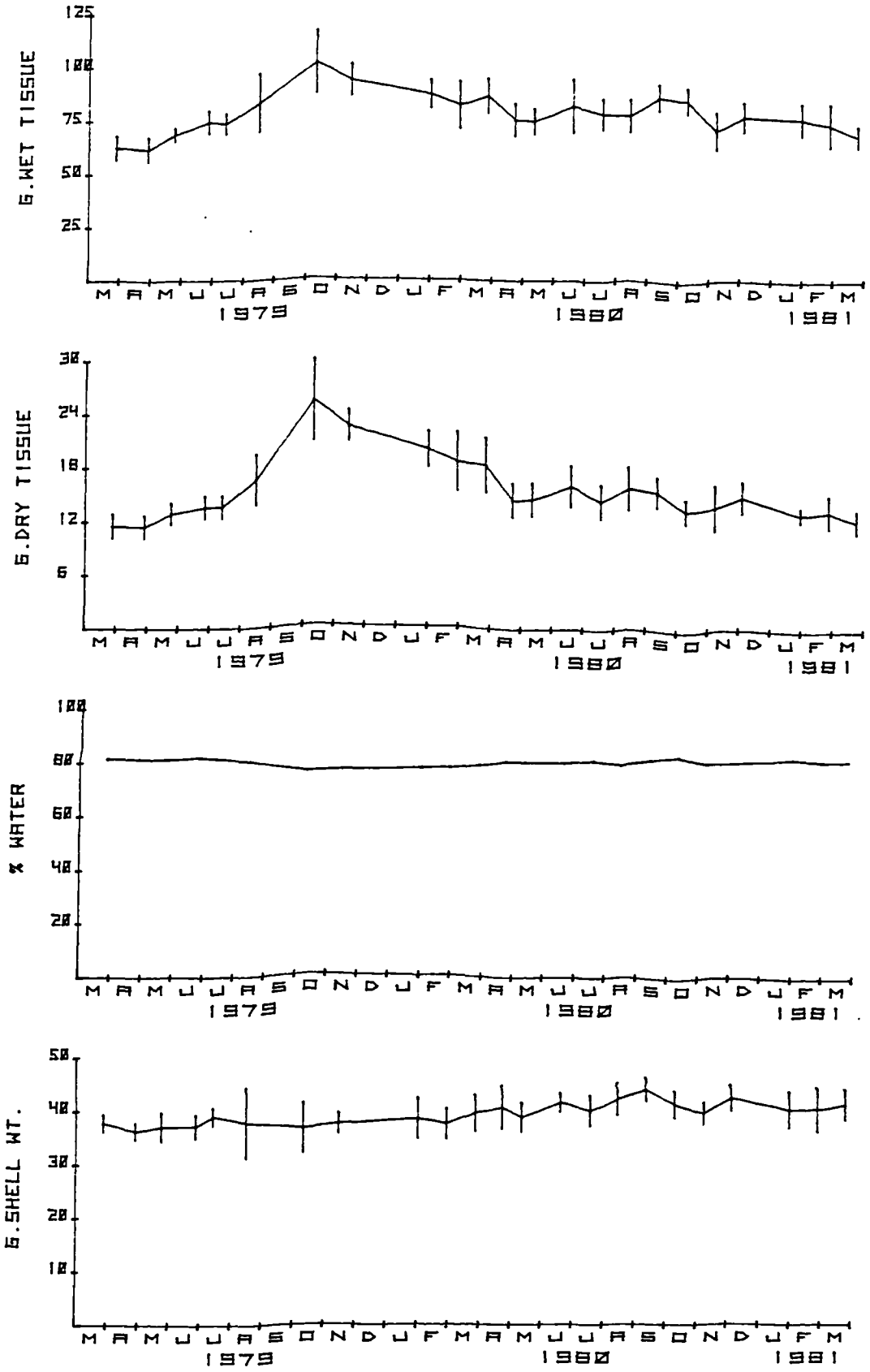


Figure 4.6. Lutraria. Changes in tissue wet weight, dry weight, percentage water and shell weight for a total standard animal. (Vertical lines = confidence limits).

Fluctuations in tissue weight were recorded throughout the summer of 1980 with values never reaching the minimum recorded in 1979. By February 1981 the dry weight had fallen to 13.37g which is comparable to the value of March 1979. No October peak was recorded in 1980.

Shell weight shows no consistent seasonal trend. A maximum value of 44.14g was recorded in September 1980.

4.3.2. Seasonal Changes in Biochemical Composition

4.3.2.1. Gonad

The percentage dry weight of the biochemical components measured and their composition in g dry weight of the gonad are summarised in figures 4.7. and 4.8. respectively.

The two years differ:-

The percentage protein content was high in the summer of 1979 and low in the winter. In 1980 the percentage protein remained fairly high although fluctuating. The lowest value was recorded in October 1980.

The carbohydrate content showed a large increase from 8.91% in July 1979 to a maximum of 41.74% in September 1979, and 53.79% in January 1980. The carbohydrate value remained high throughout the winter, decreasing in February of 1980. A similar decrease in carbohydrate was recorded from November 1980 to January 1981 (Fig. 4.7.).

The percentage content of lipid appears to be highest in both winters though high values were recorded in the early summer of 1979.

Barnes and Blackstock (1973) found the lipid level in gonad and digestive gland of Lutraria to be 3.5% in crude and 3.0% in purified extract. No indication of the time of year was given. This value corresponds to summer 1980 values in Lutraria.

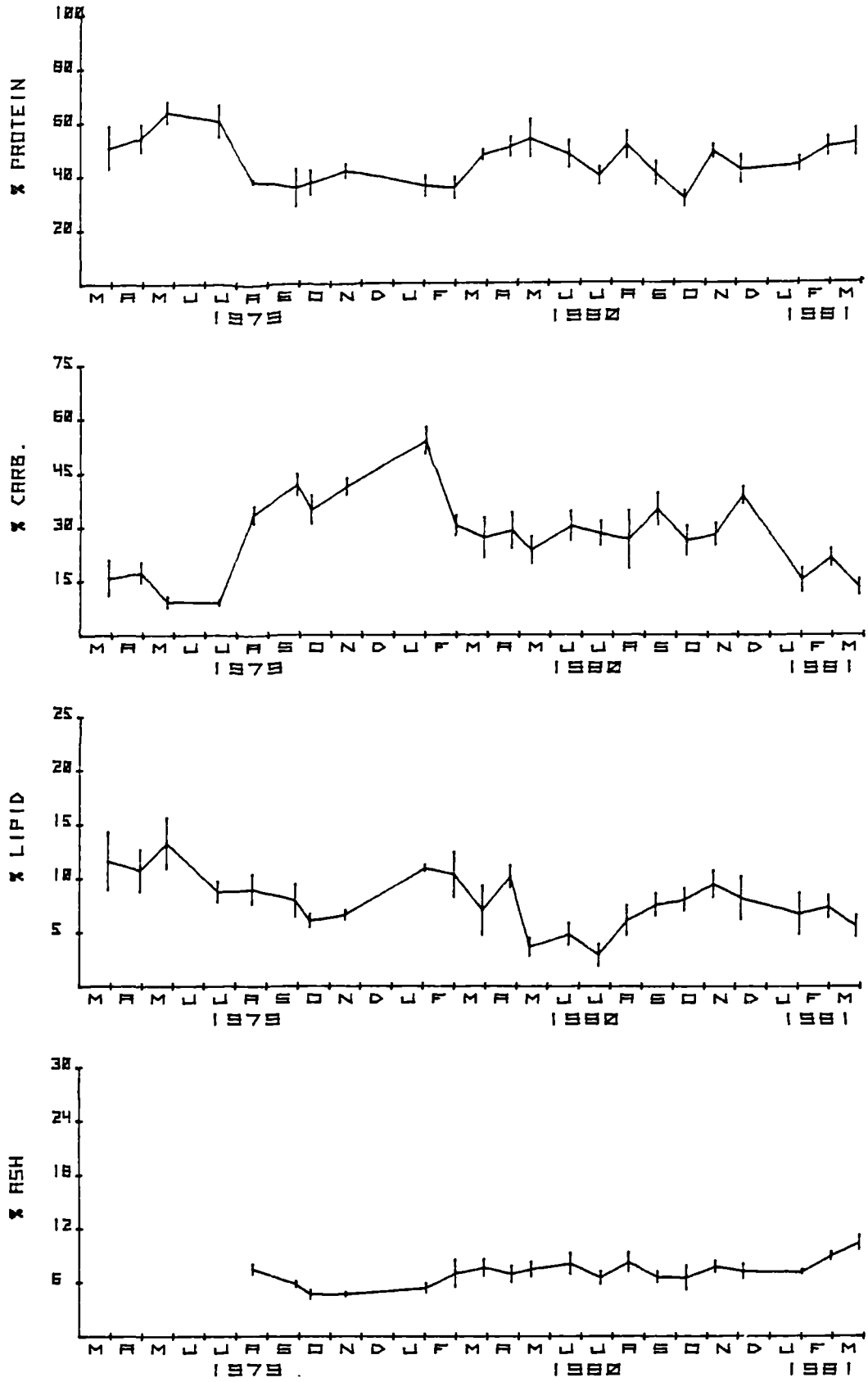


Figure 4.7. Lutraria. Changes in the percentage biochemical composition of the gonad of a standard animal. (Vertical lines = standard deviation).

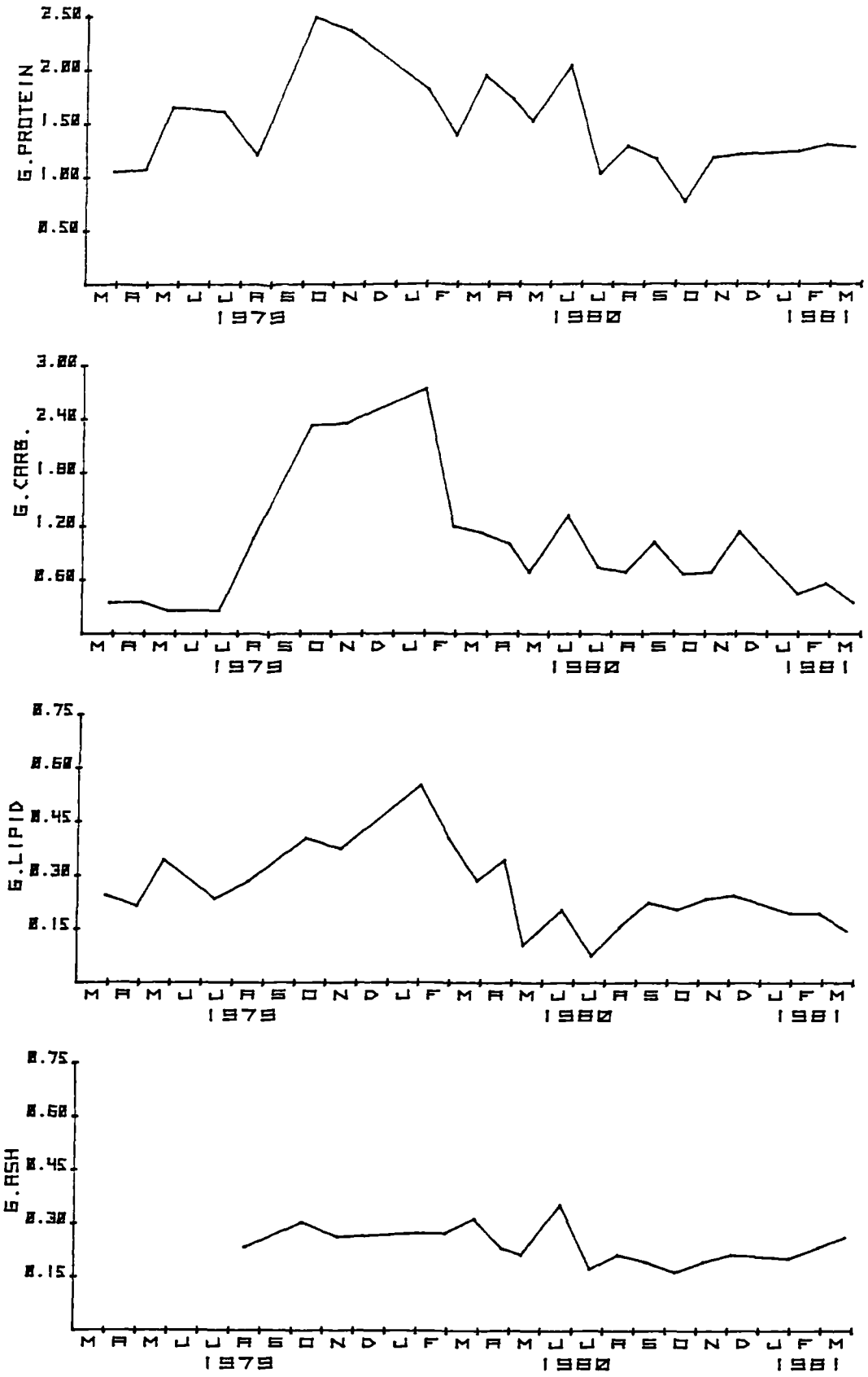


Figure 4.8. Lutraria. Changes in the biochemical composition (grammes dry weight) of the gonad of a standard animal.

The percentage ash remained fairly constant throughout the two year period and showed no clear seasonal trend.

The changes in the dry weight of the biochemical components are comparable to the changes seen in the dry weight of the gonad and total animal. An increase in all biochemical components was recorded throughout the winter of 1979. The carbohydrate content increases rapidly between July and October 1979 and remains high until February. The increase in lipid is more gradual, peaking in January 1980. The protein content is most variable with a peak seen in both summer and winter 1979, the latter being larger.

In 1980 high values of carbohydrate were recorded through the summer with a decrease in winter. The amount of protein is high in the early summer of 1980, decreasing to a minimum in October 1980 and then gradually recovering through the winter, though never reaching the levels of the previous winter.

Ash weight is variable throughout.

4.3.2.2. Digestive Gland

The percentage dry weight of the biochemical components and the biochemical composition in g dry weight of the digestive gland are summarised in figures 4.9. and 4.10. respectively.

There appears to be no clear seasonal trend in any of the components in terms of percentage dry weight. All fluctuate throughout the two year period but with no recognisable pattern.

The percentage lipid level is consistent in that it was always the highest of the five biochemical components analysed.

The changes seen in the dry weight of the biochemical components also show little seasonal trend. The values of all five were highest in

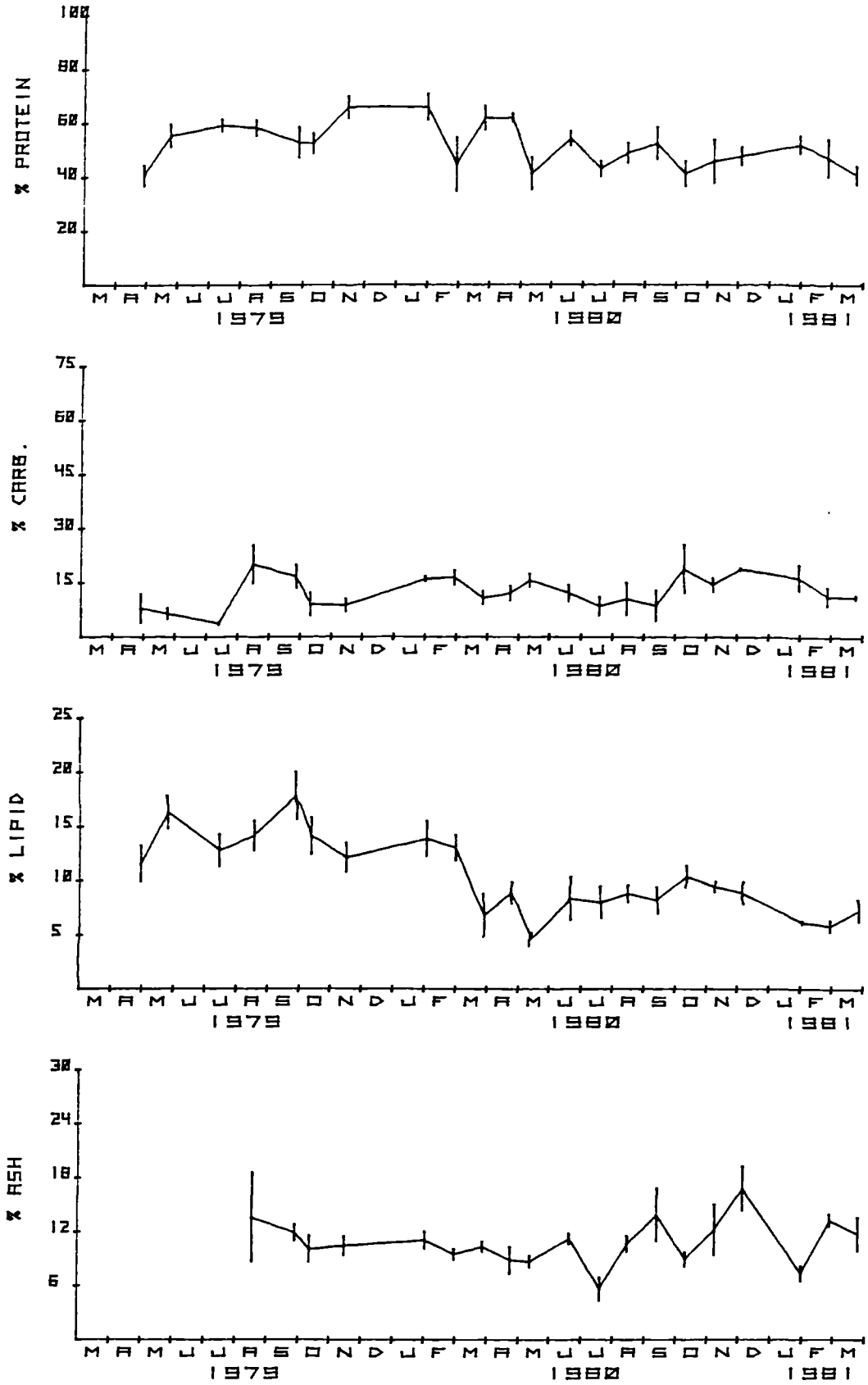


Figure 4.9. Lutraria. Changes in the percentage biochemical composition of the digestive gland of a standard animal. (Vertical lines = standard deviation).

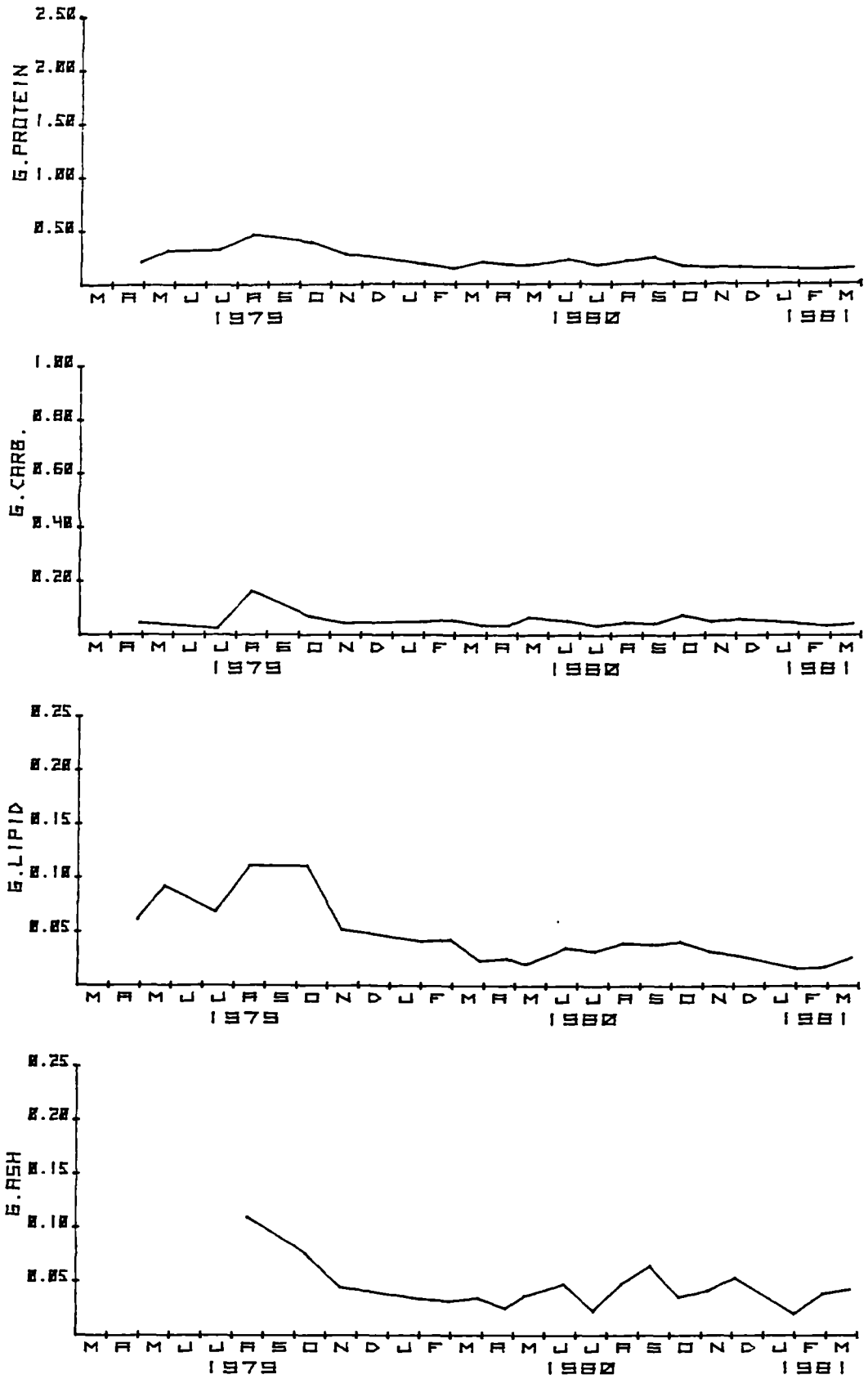


Figure 4.10. Lutraria. Changes in the biochemical composition (grammes dry weight) of the digestive gland of a standard animal.

the late summer of 1979 and then fell to low levels. Ash, which is variable throughout the period, is the exception.

4.3.2.3. Adductor Muscle

The percentage dry weight of the biochemical components and the biochemical composition in g dry weight of the adductor muscles are summarised in figures 4.11. and 4.12. respectively.

The changes in the percentage protein and percentage carbohydrate of adductor muscle tissue are similar to those in gonadial tissue. The percentage carbohydrate content was at a maximum in January 1980 (49.94%), decreasing to a low level in March 1980 (26.37%), fluctuating through the summer of 1980 and decreasing again by March 1981 (20.86%). Values in the summer of 1980 never fell below 24%.

Except in April (1.23%) the percentage lipid content is high throughout 1979. The low value is similar to that of 1.8% found by Barnes and Blackstock (1973) for Lutraria. In 1980 lipid was present in low levels throughout the summer, then increased to a maximum of 8.50% by December 1980.

Again percentage ash content is variable.

The biochemical composition of the adductor muscle in terms of g dry weights shows an increase from July 1979 to November 1979 (except in g ash), reflecting the increase in dry weight at the end of the summer.

An increase in the weight of both lipid and carbohydrate was recorded in the late autumn of 1980 when it decreased to a minimum by March 1981. The protein content is the least variable and remained fairly constant in 1980.

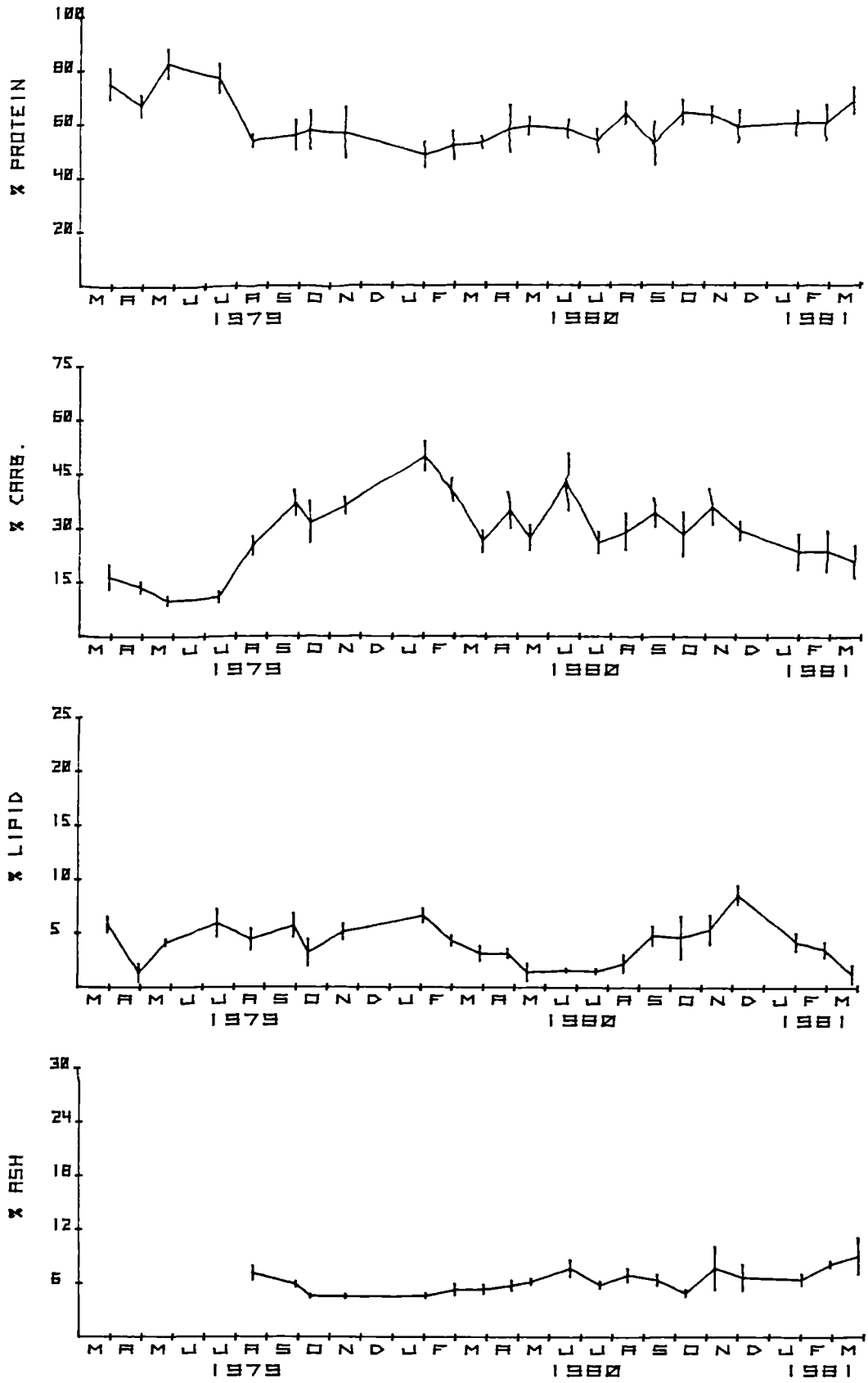


Figure 4.11. Lutraria. Changes in the percentage biochemical composition of the adductor muscle of a standard animal. (Vertical lines = standard deviation).

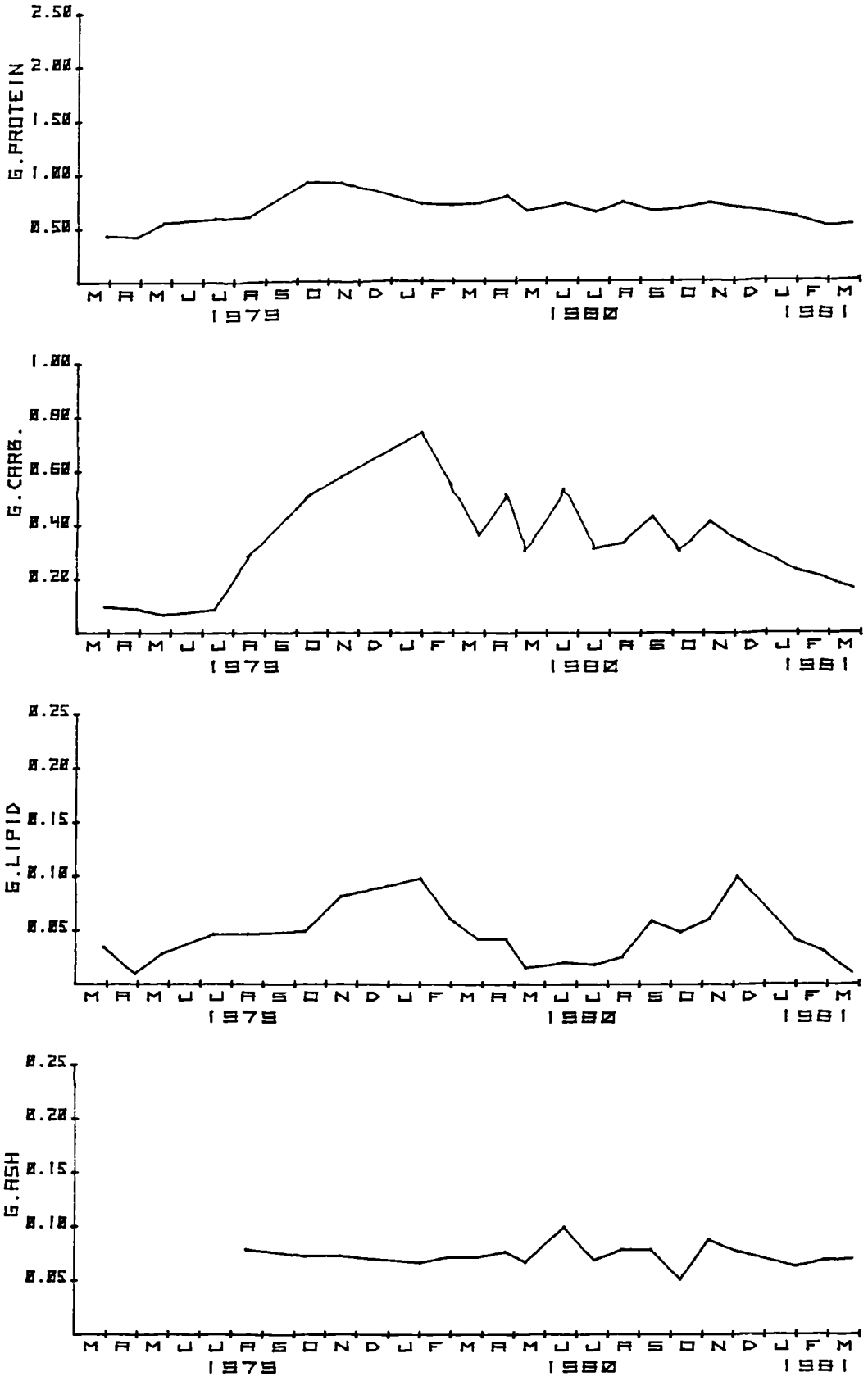


Figure 4.12. Lutraria. Changes in the biochemical composition (grammes dry weight) of the adductor muscle of a standard animal.

4.3.2.4. Siphon

The percentage dry weight of the biochemical components and the biochemical composition in g dry weight of the siphon are summarised in figures 4.13. and 4.14. respectively. The changes in biochemical composition of siphonal tissue, both as percentage and as dry weight, follow a similar pattern to those of gonadial tissue and adductor muscle.

Ash dry weight decreased throughout the two year study period.

As would be expected, siphon and adductor muscle both have a high percentage protein content over most of the two year period.

4.3.2.5. 'Other' Tissue

The percentage weight of the biochemical components and the biochemical composition in g dry weight of the 'other' tissue are summarised in figures 4.15. and 4.16.

No clear seasonal trend is seen in the percentage biochemical components. Values for percentage carbohydrate are at a maximum in January 1980 (45.00%).

The dry weight of all biochemical components reflects the increase in body weight in the late summer of 1979 then decreasing through the winter. The decrease is continuous throughout the winter of 1980 while during the summer of 1980, all components fluctuated widely.

4.3.2.6. Whole Animal

The biochemical composition of the standard animal is shown in figure 4.17.

All the biochemical components reflect the increase in total weight recorded in October 1979. Total protein follow more closely the changes in the dry weight of the animal. Values for the beginning of each year are similar (7.30g March 1979, 8.21g February 1980 and 7.43g March 1981).

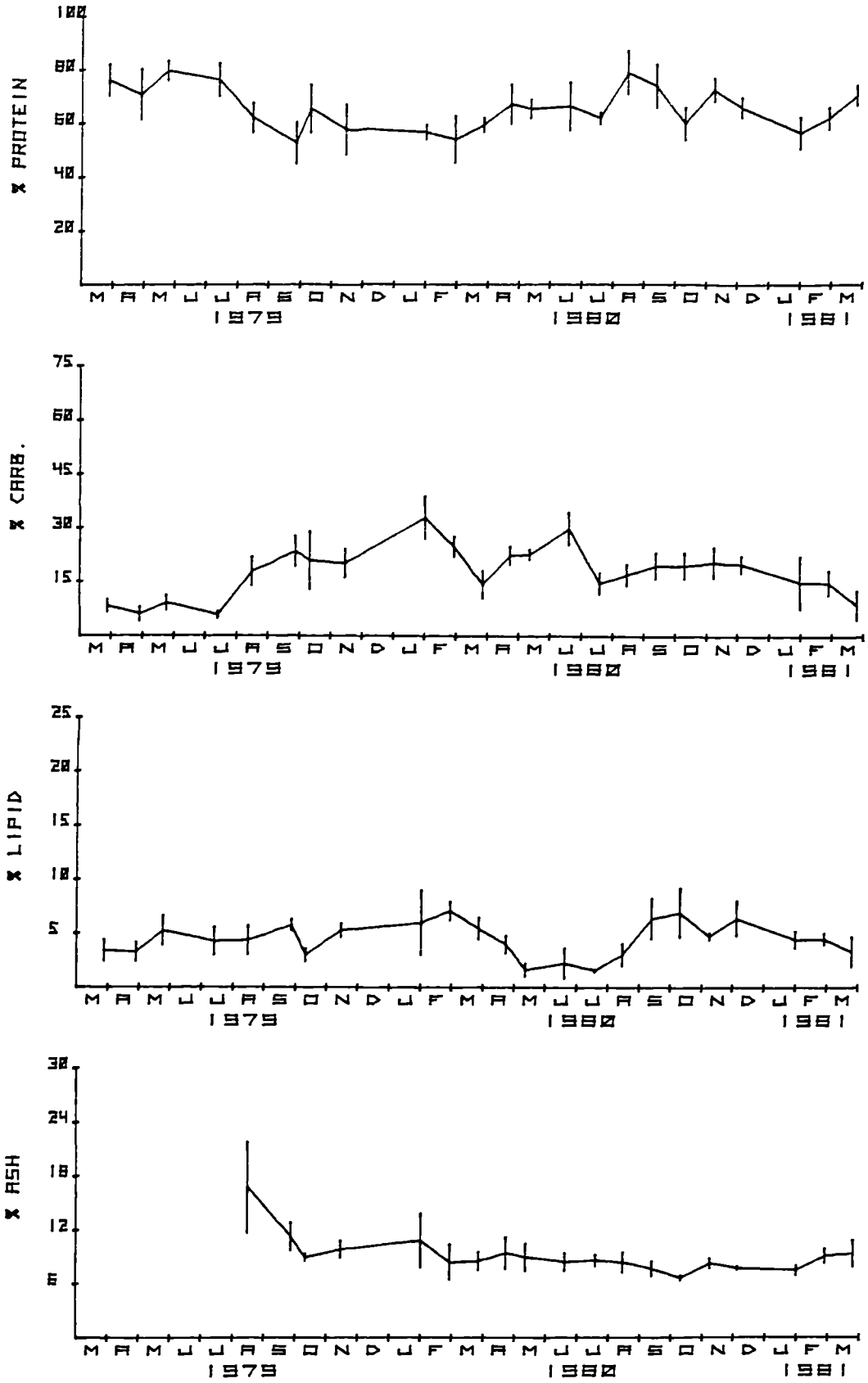


Figure 4.13. Lutraria. Changes in the percentage biochemical composition in the siphon of a standard animal. (Vertical lines = standard deviation).

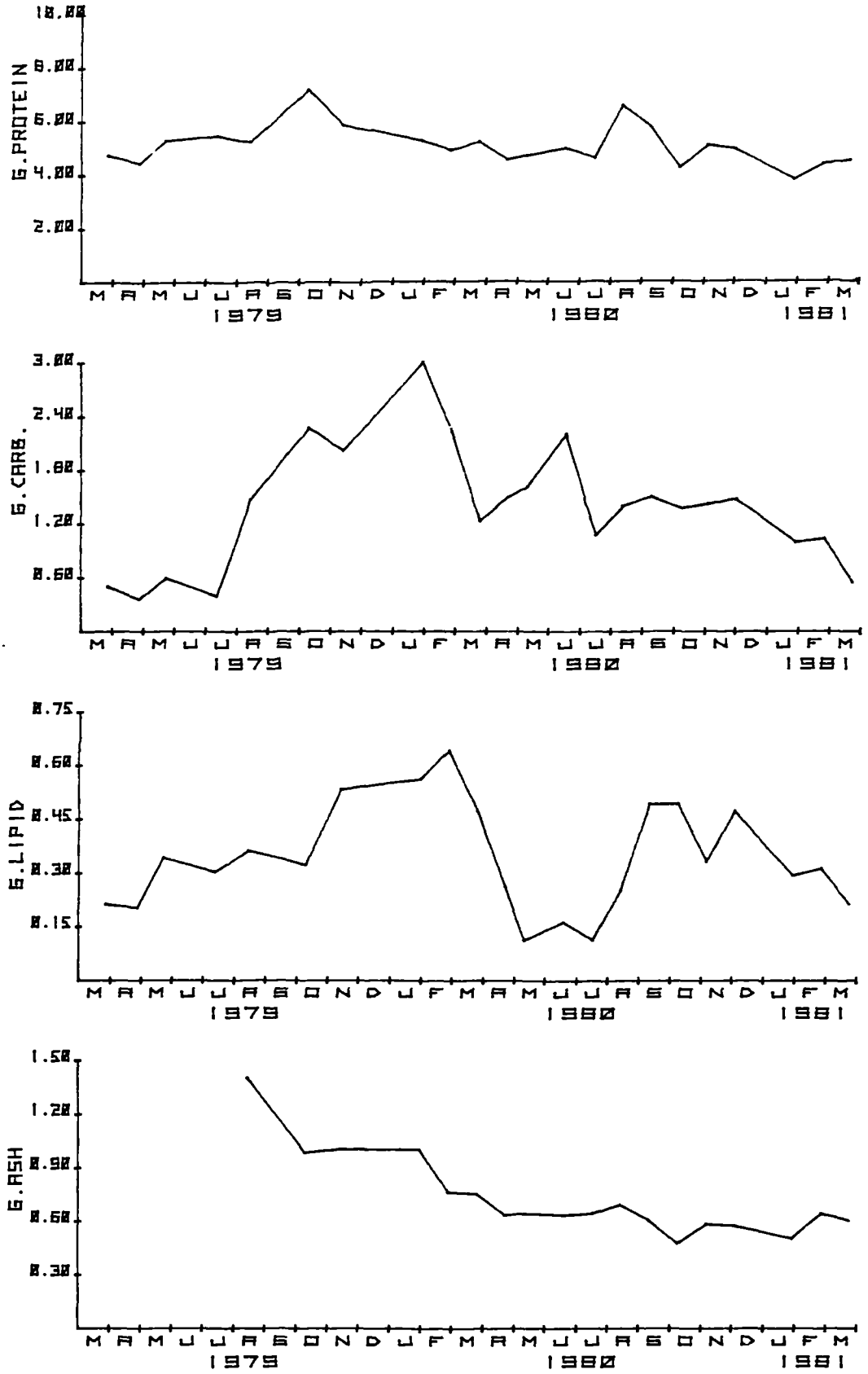


Figure 4.14. Lutraria. Changes in the biochemical composition (grammes dry weight) of the siphon of a standard animal.

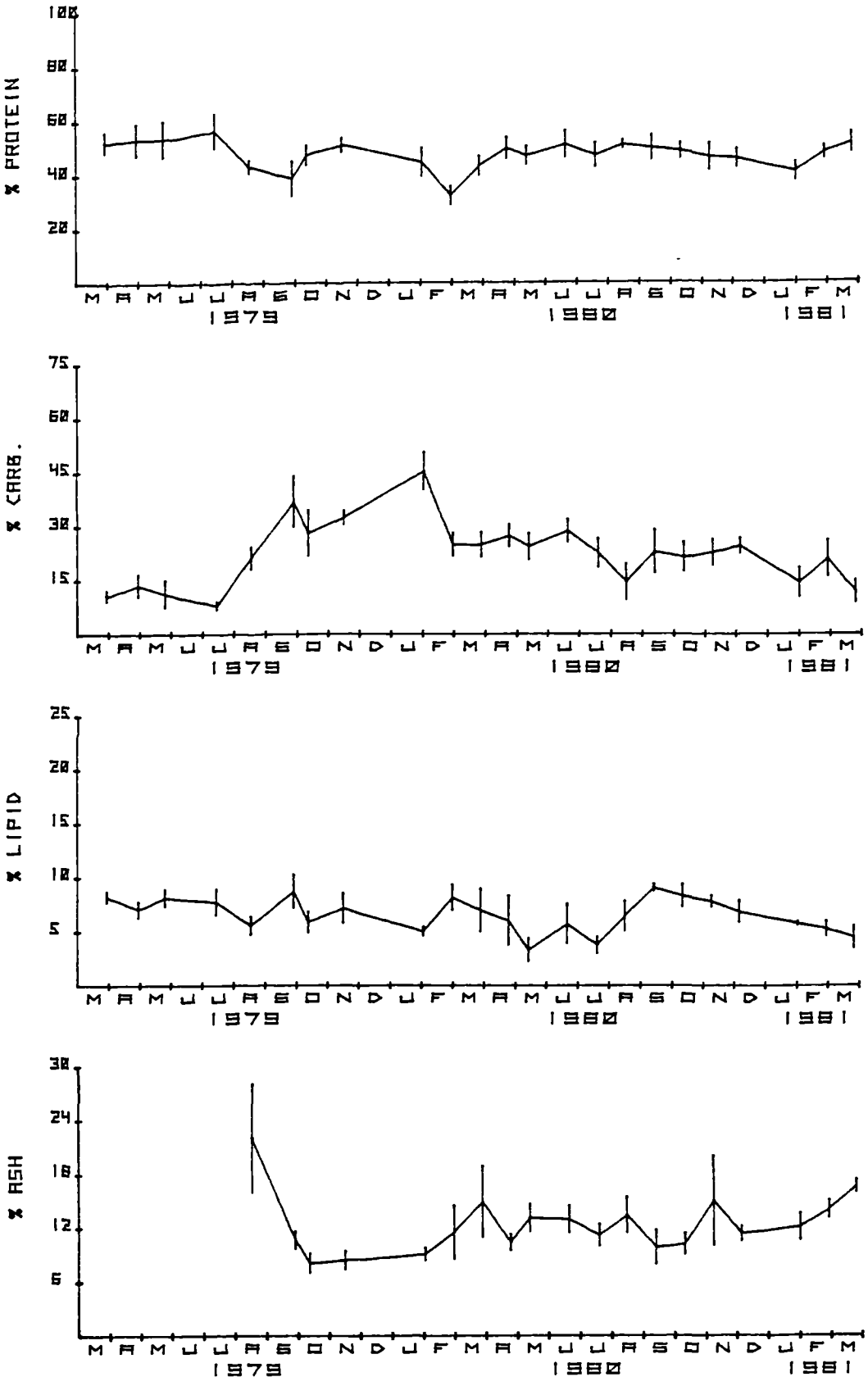


Figure 4.15. Lutraria. Changes in the percentage biochemical composition of 'other' tissue of a standard animal. (Vertical lines = standard deviation).

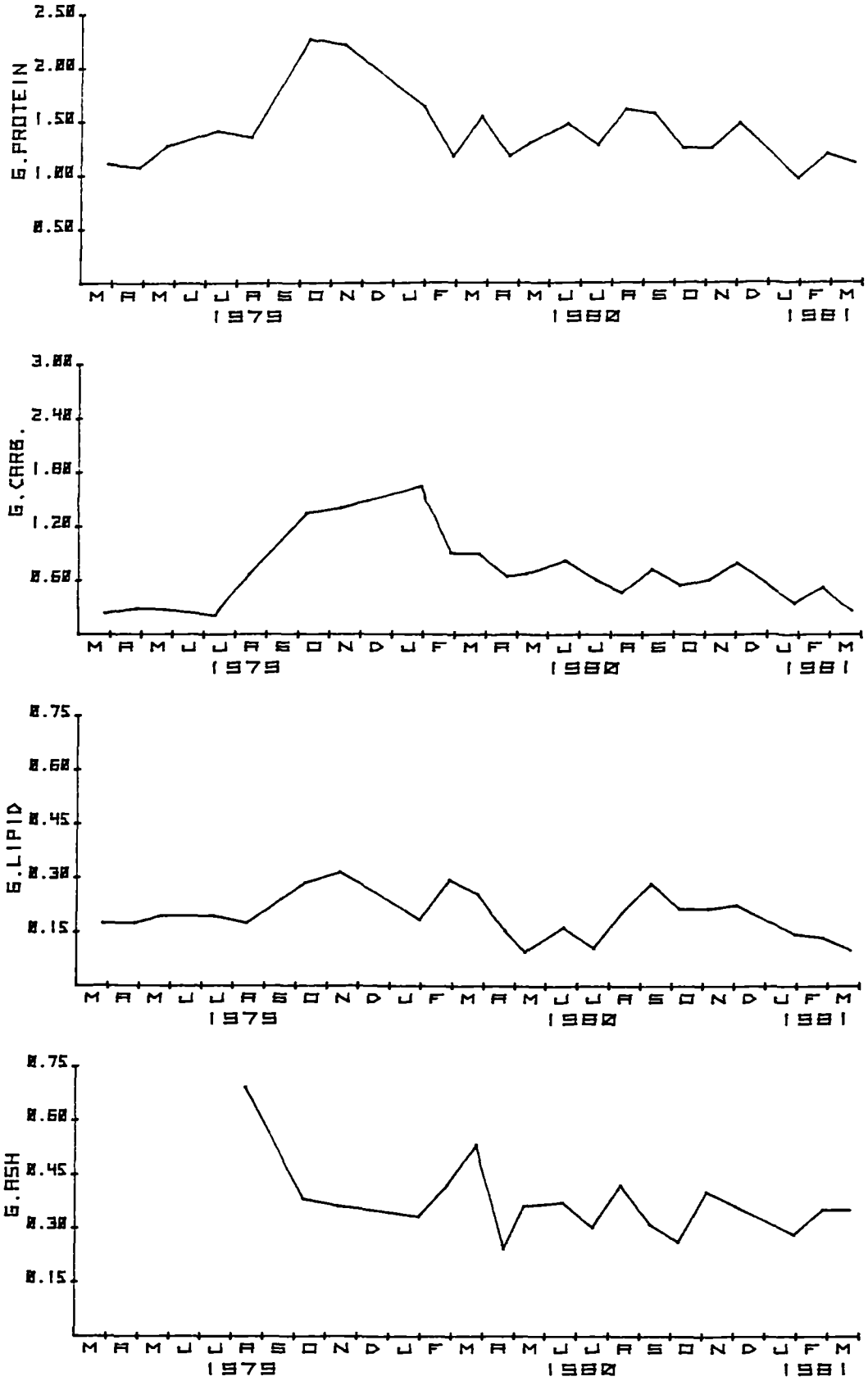


Figure 4.16. Lutraria. Changes in the biochemical composition (grammes dry weight) of 'other' tissue in a standard animal.

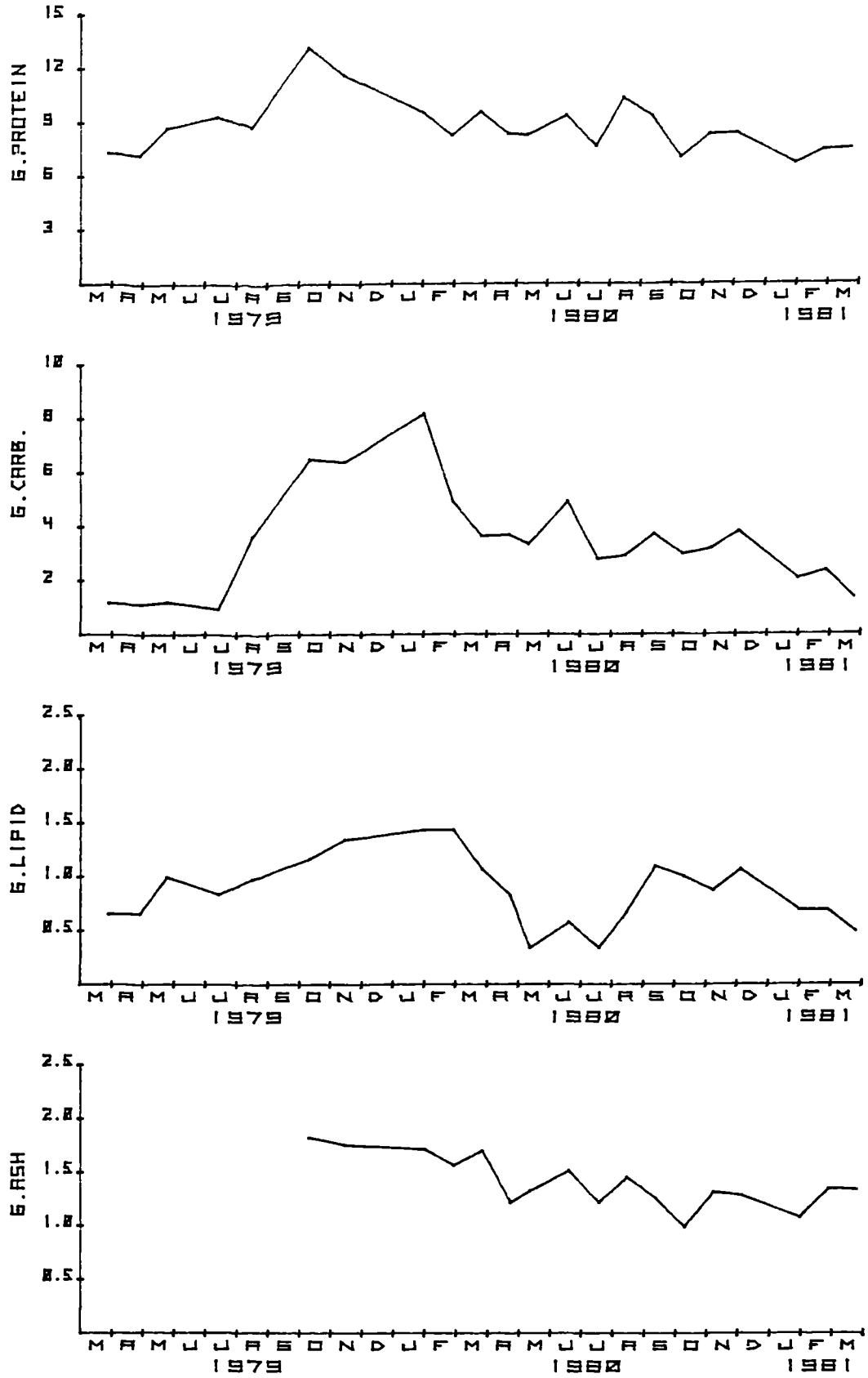


Figure 4.17. Lutraria. Changes in the biochemical composition (grammes dry weight) of the whole standard animal.

The total weight of carbohydrate remained high during the winter 1979 decreasing in January 1980. Minimum values of carbohydrate were recorded in March 1979 (1.14g) and March 1981 (1.31g). Carbohydrate also decreased through November and December of 1980.

Total lipid increased in the late fall in both years and was maintained at high levels throughout the winters. Low levels were recorded in the spring/early summer of each year (0.65g March 1979, 0.33g May 1980 and 0.48g March 1981).

Total ash weight was highest in the late summer of 1979 and then decreased gradually throughout 1980 although with the occasional peak being recorded.

4.4. DISCUSSION

There is a major spawning period during the summer and redevelopment of the gonad occurs during the winter, accelerating in December and January (see Chapter 3). Changes in weight and biochemical composition are discussed here in relation to this reproductive cycle.

Earlier workers studied changes on the biochemical composition of bivalve molluscs in the animal as a whole. In recent years it has been thought to be more informative to study changes within the body components of the animal. The large size of the adult *Lutraria* allows easy separation into five component parts (siphon, adductor muscle, digestive gland, gonad and visceral mass, and 'other'). In the following discussion the term 'gonad' is used in reference to the body component containing the gonad. It must be remembered that this component includes other tissues of the visceral mass and foot from which the gonad is not easily separable. The gonad itself constitutes only a small portion of the total animal (see Section 4.3.1.1.).

The indices of condition for siphon and other tissues show little change over the two years. The adductor muscle tends to increase slightly throughout the period. Indices of gonad and digestive gland show the most variation, with an apparent reciprocal relationship between the two which is more noticeable in Year I.

In year I the index of condition of the gonad reflects an increase in reserves over the winter period. In year II the index reflects the changes in the ripeness of the gonad i.e. the changes within the gonad in terms of development and spawning.

The gonad is thought to represent no more than 10% of the total dry weight of the body (see Section 4.3.1.1.). The small size of the gonad will probably limit the effect of its maturation on the total weight and biochemical changes of the animal, and changes in these totals associated with the reproductive cycle may well be masked. A gravid gonad in Crassostrea virginica by comparison constitutes 31.2 - 40.7% of the wet weight of the animal (Galstoff, 1964) and in Venus (Mercenaria) mercenaria (Ansell, Loosmore and Lander, 1964) may constitute 50% of the total body weight.

Although changes in both wet and dry weight are recorded for Lutraria, changes in condition are discussed in terms of dry weight only. Due to the greater inaccuracies involved in its calculation, wet weight is thought to be an unreliable index.

Changes in total dry weight in Lutraria and changes in weight of the body components are thought to reflect the main changes in the nutritional state of the animal rather than changes due to the proliferation of the gonad and spawning. In the discussion of the results, the two years of study must be dealt with separately.

In year I (March 1979 - March 1980) the total weight of soft tissues remained low until a dramatic increase in October, when the

weight was doubled. This increase was reflected in all the body components, though least in the digestive gland. Weight then decreased through the winter but did not fall to the low spring values of 1979.

In year II (March 1980 - March 1981) weight showed a series of fluctuations up to August after which it remained constant for the remainder of the year. There was no large increase in October 1980.

In year I weight increases at a time when the mean index of gonad ripeness is at its lowest and the majority of the animals are in the later spawning stages. In year II apparently no decrease in weight accompanies spawning and no increase accompanies gonad proliferation in the late winter. This is not unknown in bivalves. Thus, in Tivela stultorum (Giese, 1969) the total mass of the body does not increase with breeding season. In Tivela, however, the gonad does increase in weight and this is accompanied by a decrease in the body fluid index. In Lutraria utilisation of reserves from the visceral mass and foot, inescapably included as 'gonad' component, may mask any increase in gonad itself.

In many other bivalves proliferation of the gonad is accompanied by an increase in tissue weight and spawning results in a rapid decrease. In Tellina tenuis from the Clyde Sea Area (Ansell and Trevallion, 1967) body weight is at its maximum before spawning and water content is at its minimum. After spawning the reverse is true. Water levels remain steady over the winter as body weight recovers i.e. an increase in weight. A similar situation occurs in Venus (Mercenaria) mercenaria (Ansell et al., 1964, Ansell and Lander, 1967) except that water content decreases steadily over the winter i.e. weight is maintained. Except in October 1979 when minimum water levels correspond to maximum levels of dry weight, water content in Lutraria remains fairly steady and consistently high in all components. A similar situation was found in Tivela stultorum

(Giese, Hart, Smith and Chung, 1967), however, in this case indeterminate gonads contained less water (65.6%).

Sastry (1966) has shown in Argopecten irradians that during spawning in August and September the index of condition of the gonad decreases and is accompanied by a decrease in body weight. A decrease in the index of condition of the gonad in Lutraria was recorded after spawning in year II, though an increase was seen in year I. The differences in the change in weight between 1979 and 1980 are attributed to the phytoplankton blooms of the summer of 1979 which resulted in a large increase in weight in October 1979.

All components show a large increase in carbohydrate at this time, suggesting that in an animal of this size all organs that can do so, are used for the primary storage of the metabolised food. A corresponding widespread increase in protein and lipid reserves also occurs.

In the Pectinacea (Comely, 1974; Ansell, 1974b; Taylor and Venn, 1979) storage of nutrients seems to be principally associated with the large adductor muscle, the 'other' tissues showing only slight seasonal variation. Ansell (1974b) suggests that this may, in part, be related to the enlargement of the muscle in the monomyarian condition and a corresponding reduction in the foot and visceral mass. In Lutraria the proportions of the parts are greatly different. The adductor muscle constitutes a mean value of 7.00% of the total body weight, whereas the siphon and the 'other' tissues consitute mean values of 50% and 19% respectively. The carbohydrate level remained high until the beginning of January 1980 and then decreased in all components.. Carbohydrate levels remained low in the digestive gland for the rest of the period, elsewhere fluctuations of carbohydrate were recorded throughout the summer of 1980 though values never returned to the figures recorded in the summer 1979.

It is thought that the animal opportunistically builds up reserves when food is available, but would normally utilise them for gonad development as the summer progresses when planktonic food is usually scarce. A steady decline in carbohydrate content was seen throughout the winter of 1980. Carbohydrate values for March 1979 and March 1981 are comparable.

Changes in protein levels in all components closely follow changes in dry weight and monthly variations bear no relation to the maturation of the gonad in year I. In year II the protein level in the gonad is high when the index of gonad ripeness is high and decreases in September when the index is at its lowest. This suggests that high levels of protein present in the gonad are related to maturity.

Except for the digestive gland, lipid levels are highest during the winter months. In the gonad, high lipid levels may be correlated to the presence of developing and maturing gametes, but immature gonads may contain large stores of reserves, especially lipids. In year I decreasing lipid levels in the digestive gland correspond to increasing lipid levels in the gonad. This was less obvious in year II. The digestive gland has the highest lipid content of all the components and is well known as a site of lipid storage in bivalves (Owen, 1966b). Giese (1969) has shown an inverse relationship between the size of the digestive gland and development of the gonad, suggesting transference of material from the digestive gland to the gonad.

Gametogenesis in Lutraria occurs during the winter with an accompanying increase in the mean index of ripeness. As this occurred in January 1980 and in November/December 1980 when food is least abundant, the animals must therefore be utilising reserves accumulated when food is plentiful. In this respect Lutraria is similar to

Mytilus edulis (Bayne and Thompson, 1970), Pecten maximus (Comely, 1974) and Chlamys opercularis (Taylor and Venn, 1979), but is in contrast to other bivalves, including Chlamys septemradiata (Ansell, 1974b), in which gametogenesis occurs in the spring and coincides with the spring phytoplankton bloom.

Ansell (1961) found that Venus striatula depended more on available food from the environment than on food reserves. Gonad development in this case occurred when the amount of food obtained exceeded that required for other metabolic processes.

Animals such as Lutraria that mature through the winter months are able to take advantage of the increasing seawater temperatures in the spring to spawn early, planktonic larval development coinciding with the phytoplankton increase but occurring before the zooplankton increase.

In conclusion the seasonal changes in tissue weights of Lutraria appear to bear little relation to the reproductive cycle of the animal. This is in part due to the small size of the gonad in comparison to the total animal.

In 1979 massive build up of reserves in all body components during the summer resulted in a large increase in weight. This probably was an opportunistic event and not repeated in 1980.

The decrease in protein, carbohydrate and lipid during the winter months in both 1979 and 1980 is attributed to the requirements of the animal for normal metabolic processes during the period when food is in short supply. The extent to which the reserves are also utilised for gamete development is not clear. Changes recorded within the 'gonad' component itself may be complicated by corresponding changes in the tissues of the visceral mass and foot.

All organs are utilised for the storage of nutrient reserves, however, the digestive gland is mainly concerned with lipid storage.

Carbohydrate and lipid reserves appear to show more correlation to the reproductive cycle than does protein.

Protein reserve decreases from October whereas the main decrease in carbohydrate was from December/January in 1980 and from November/December in 1981 and at a time when the index of gonad ripeness is increasing rapidly.

Because whole animals could not be sexed, separate biochemical analysis was not carried out for males and females. It is unlikely that any significant differences in biochemical composition between the sexes would have been found because of the small proportion that the testis and ovary makes to the total weight and volume of the body.

CHAPTER 5

PHYSIOLOGY

CHAPTER 5

PHYSIOLOGY

5.1. RESPIRATION

5.1.1. INTRODUCTION

Gaseous exchange in bivalves takes place as water moves through the mantle cavity adjacent to the epithelia and across the gills. By virtue of its large surface area, rich blood supply and the passage of water (pumping activity, Section 5.3.) through it, the structure of the lamellibranch gill (Atkins, 1937a,b) is well suited to its respiratory function.

In reviews by Ghiretti (1966) and Vernberg and Vernberg (1972) and Vernberg (1981) internal and external factors that may affect respiration in bivalves are discussed. Internal factors include body size, sex, starvation, diet, locomotor activity, level of cellular metabolic activity, growth and internal physiological chemicals. External factors include temperature, oxygen levels, salinity, photoperiod and chemical composition of the external milieu (Vernberg, 1981).

Respiration rate is studied here in terms of the oxygen consumption of Lutraria (mlsO_2/g. dry wt./hour) and the level of oxygen in the surrounding seawater, i.e. the oxygen tension (mlsO_2/l.).

The effect of stress on the respiration rate of various species has been studied by Mangum and Van Winkle (1973). Other studies include those on Mya arenaria (Van Dam, 1935; Collip, 1921), scallops (Van Dam, 1954), Mytilus edulis (Bayne, 1971a,b; Bayne and Livingstone, 1977) and Arctica islandica (Taylor and Brand, 1975a,b).

Brand and Roberts (1973) discuss three types of imposed respiratory stress on cardiac response of Pecten maximus. These are, (i) gradually induced hypoxia, (ii) rapidly induced hypoxia and (iii) aerial exposure. Investigations into these types of respiratory stress have been carried out on Lutraria and related to respiration and heart rate.

Vernberg (1981) describes two types of respiratory response to reduced oxygen tension: (i) oxyconformation i.e. rate of oxygen uptake decreases in relation to drop in oxygen tension (conformer); (ii) oxyregulation i.e. rate of oxygen uptake is relatively constant over a wide range of ambient oxygen tensions until a critical oxygen level is reached (regulator).

These responses are determined in Lutraria.

The subject of respiratory stress and anaerobiosis in bivalves is well documented and includes reviews by Berkely (1921), Tang (1933), Hochachka, Fields and Mustafa (1973) and Hochachka and Mustafa (1972). The ability of bivalves to respire anaerobically was also reviewed earlier by Von Brand (1946) and more recently, intermediate metabolites and biochemical pathways involved in anaerobiosis have been discussed by De Zwaan and Zandee (1972), De Zwaan and Wijsman (1976).

The effect of temperature on the respiration rate of Lutraria is also investigated.

5.1.2. MATERIALS AND METHODS

5.1.2.1. The Respirometer

Lutraria were collected from the Clyde Sea Area and kept in running seawater in outside tanks until required. Recordings of respiration rate were made as soon as possible after collection, usually within two weeks, and not later than one month.

The apparatus consists of a cylindrical glass respirometer (capacity 2.5 litres) with a specially designed perspex lid, held in place by two strips of copper (Fig. 5.1.). The oxygen electrode (Yellow Springs Instrument) fits into the centre of the lid. On either side, rubber tubing attached to the small pipes through the lid, connects with a small Schuco peristaltic pump to allow water circulation. Two 3-way taps control the flow. During the period of acclimatisation, the water flows from a reservoir into the respirometer, preventing a fall in oxygen tension before the onset of the experiment.

At the beginning of the experiment, the flow from the reservoir is stopped and localised depletion of oxygen around the electrode is prevented by continued pumping round the closed system.

The respirometer and reservoir were placed in a temperature controlled water bath, although for some experiments the apparatus was set up in an air conditioned room at $10^{o}C \pm 2^{o}C$.

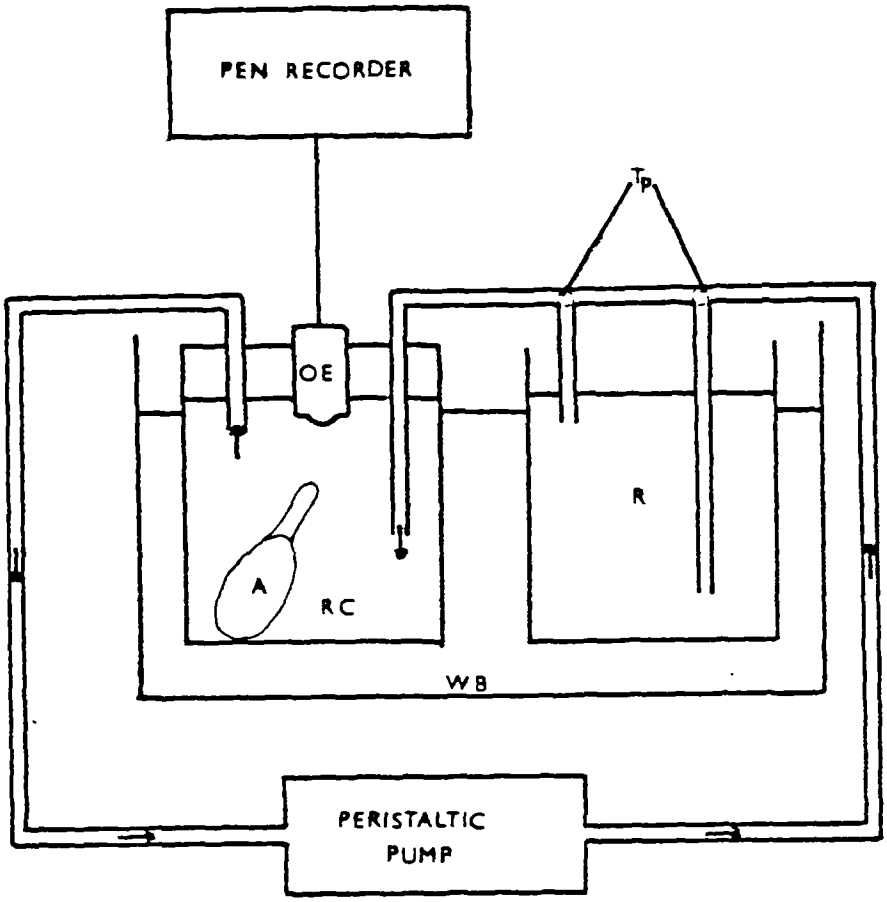
The oxygen electrode was linked to a flat-bed pen recorder (Tekman TE200) and was calibrated daily against solutions of known oxygen concentration as determined by Winkler titration.

In all respiration experiments, membrane filtered seawater was used (0.3µm) and equilibrated to the appropriate temperature over a minimum of twenty-four hours. Before placing in the respirometer animals were cleaned of any mud, sand or epibiota. Oxygen consumption was determined by recording the fall in oxygen concentration over a given time period (usually one hour). The chamber was then flushed with well oxygenated water for 30 mins. and at least one further recording was made. Consecutive experiments on a specimen generally gave close results and the mean value from the recordings was taken. Blank runs, using the respirometer filled with water, showed that the oxygen tension at any level remained fairly constant.

Figure 5.1. Diagrammatic representation of the experimental system used for the determination of respiration and heart rate.

Key

OE	oxygen electrode
A	animal
RC	respiratory chamber
R	reservoir containing aerated seawater (air stone not shown)
WB	water bath
T_p	3-way taps
$\rightarrow$	indicate direction of water flow


PEN RECORDER
T_p
OE
R
A
RC
WB
PERISTALTIC
PUMP

Preliminary experiments showed that the oxygen uptake by Lutraria reached a steady state within two hours of handling (Table 5.1.). At the end of each experiment the soft parts were removed and dried in an oven at 95°C to a constant weight and the length of the shell was noted. Respiration rate was expressed as $ml\,O_2/g$ dry weight/hour. No experiments were performed with natural sediment present.

5.1.2.2. Seasonal respiration

Recordings from ten individuals were taken every two months from January 1980 to January 1981 to determine the seasonal change in oxygen consumption for Lutraria. The experiments were carried out at 10°C using membrane-filtered seawater at a salinity of $32‰ \pm 1‰$.

The respiration rate was found for a standard 20g animal after a double log transformation (regression) had been used for each group of determinations.

5.1.2.3. The effect of temperature on respiration rate

Experiments were carried out at five different temperatures (10°, 15°, 20°, 25° and 30°C) in April and August 1980 and at these temperatures, and additionally at 5-6°C, in October 1980.

Five animals were used individually at each experimental temperature. The animals were transferred from ambient seawater to the experimental temperature with the minimum of handling and without exposure to air during the process, i.e. both the respirometer and the animal were kept submerged in seawater throughout the process. Recordings were taken after a two hour 'settling' period (see above) and three consecutive recordings made.

The oxygen consumption of a standard 20g animal was determined for each of the different temperatures. Q_{10} values were calculated.

TABLE 5.1. Lutraria. Changes in respiration rate of 5 individuals over a period of 3 hours in November 1979.

ANIMAL NO.	RESPIRATION RATE ($mls O_2$/g dry wt/hr)						
	INITIALLY	AFTER ½ HOUR	AFTER 1 HOUR	AFTER 1½ HOURS	AFTER 2 HOURS	AFTER 2½ HOURS	AFTER 3 HOURS
1	0.1058	0.0988	0.0943	0.08531	0.0741	0.0730	0.0735
2	0.1120	0.0880	0.0840	0.0760	0.0660	0.0640	0.0640
3	0.0950	0.0820	0.0800	0.0720	0.0620	0.0600	0.0620
4	0.0953	0.0710	0.0678	0.0662	0.0646	0.0631	0.0650
5	0.1180	0.0950	0.0820	0.0800	0.0840	0.0830	0.0835

5.1.2.4. The effect of hypoxia on respiration rate

5.1.2.4.1. Gradually induced hypoxia

Ten individuals were used in May and in November to determine the effect of gradually declining oxygen tension on Lutraria. Each individual was placed in the respirometer and after two hours the system was closed and the respiration rate recorded over a period of four hours as described by Taylor and Brand (1975b).

The decrease in oxygen content of the circulating water over the period is due to respiratory activity. The changes in respiration rate were determined individually, and then a mean change in rate over four hours for ten animals calculated.

5.1.2.4.2. Rapidly induced hypoxia

Individual animals were placed in the respirometer in seawater of reduced oxygen tension. Prior to the experiment, nitrogen was bubbled through the seawater for two hours until a constant level of oxygen tension was reached.

The effect on respiration rate was determined.

5.1.2.4.3. The effect of anaerobic conditions on the survival of Lutraria

Because information was needed for the conduct of heart rate experiments, preliminary experiments were carried out on the survival of individuals under anaerobic conditions. Five animals were placed individually into respiratory chambers maintained at 10°C and examined daily. From the seasonal respiration results, an average value for oxygen consumption for a standard animal was calculated to be 0.0846 mls O_2/g. dry wt./hr. Thus in a 2.5 litre respirometer at normal oxygen tension at 10°C (6.5 mls O_2/l.), it can be calculated that an individual would use all the available oxygen in approximately ten hours assuming that the oxygen was depleted at a standard rate throughout the period.

5.1.2.5. The effect of long term maintenance in the laboratory on respiration rate

The respiration rate of ten animals from the May sample was determined at 10°C as part of the seasonal respiration study. A further ten animals from this sample were maintained in the laboratory in running seawater in an outside tank for a period of three months. The respiration rate of these animals was then determined at 10°C and compared with the May sample.

Note, because the effect of extended maintenance on the weight of an animal was unknown, it was necessary to sacrifice the original animals immediately after the experiment in order to calculate the seasonal respiration data.

5.1.3. RESULTS

5.1.3.1. Seasonal respiration

Covariance analysis was carried out using the methods of Snedecor (1956) (see Appendix II for detailed results). Because the slopes of the regression lines were not significantly different, a common regression coefficient was calculated. Using the value -1.096, respiration rates at different times during the year were calculated and, in each case, were found to differ significantly. Thus a significant seasonal change in respiration rate is seen in figure 5.2. which shows the recalculated oxygen values over a one year period.

Unfortunately over the limited size range available there is no significant difference in oxygen consumption between different sized individuals (see page 53, for discussion). The animals ranged in length from 9.72 - 12.91cm, and in weight from 8.06 - 40.10g, with an average of 19.40g. The majority of animals varied between 11.00 - 12.00cm and 15 - 25g.

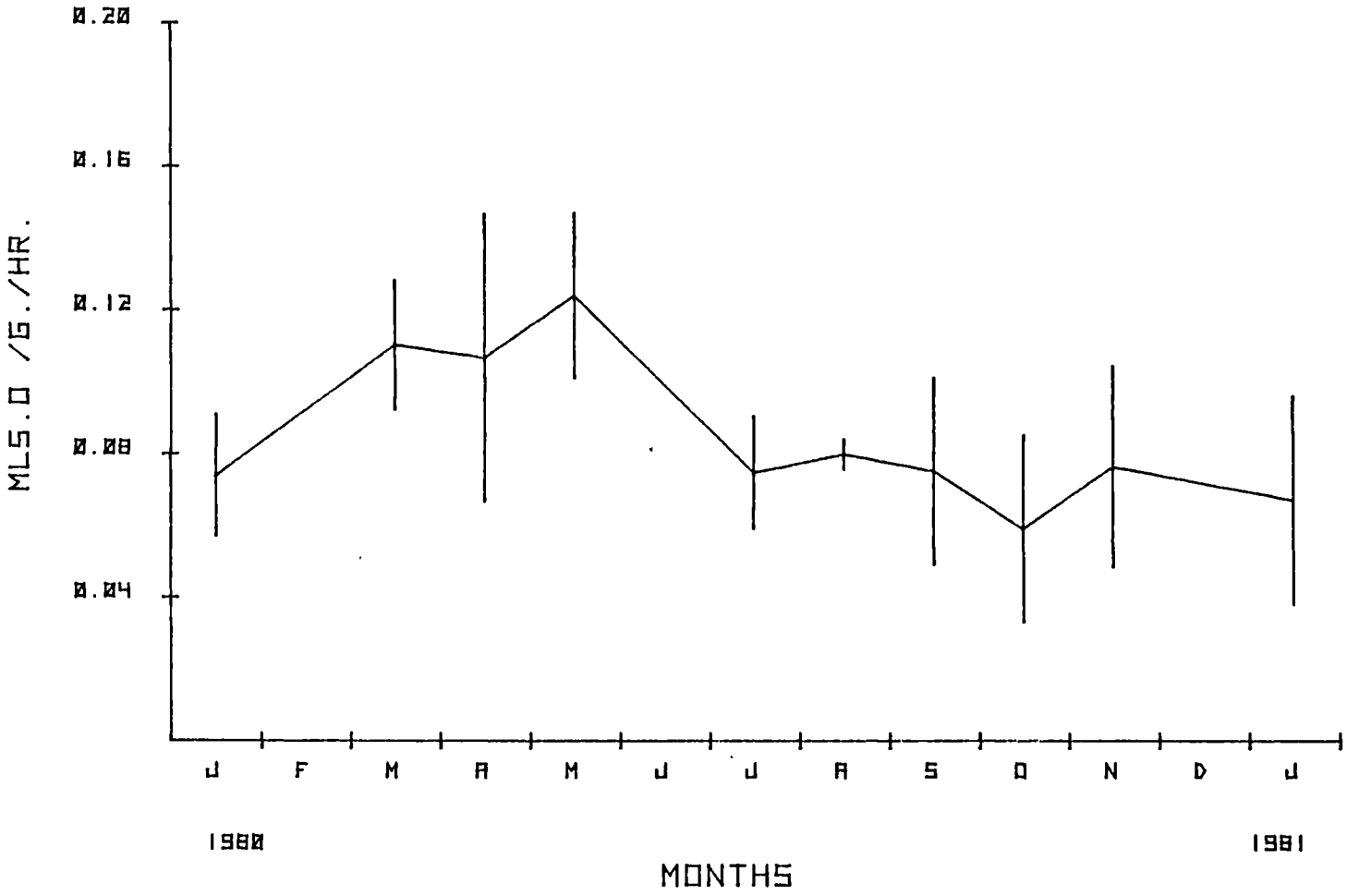


Figure 5.2. Lutraria. Changes in respiration rate (mls O_2/g. dry wt./hr.) of a standard animal (20g) with time.

The respiration rate at 10°C of a standard 20g animal was also calculated from the values obtained for five animals in April, August and October respectively, as part of experiments on respiration rate at different temperatures. The values were then incorporated in the seasonal studies on respiration.

The respiration rate of a standard animal increases through spring to a maximum value in May 1980 of 0.1283mls O_2/g. dry wt./hr. A decrease then occurs to minimum value in October 1980 of 0.059mls O_2/g. dry wt./hr. Although the level increases slightly in November 1980, it remains fairly low throughout the winter. The oxygen consumption in January 1980 is similar to that in January 1981 (0.07389mls O_2/g. dry wt./hr. and 0.067mls O_2/g. dry wt./hr. respectively.

Seawater temperatures in the Clyde Sea Area reach a maximum in August, thus the maximum respiration rate of Lutraria occurs when the temperature of the seawater is still increasing. Comparison of figure 5.2. and figure 3.1. in Chapter 3, suggests that respiration rate may be determined more by the physiological state of the animal and less by the thermal regime of the sea.

The late spring / early summer months appear to be the metabolically expensive time in the life cycle of Lutraria (see Chapter 4.).

5.1.3.2. The effect of temperature on respiration rate

Except on one occasion, covariance analysis showed no significant difference in the slopes of the regression lines (for details of the analysis see Appendix II). A common regression coefficient of -0.952 was used to recalculate the respiration rate at different temperatures at different times of the year. This reveals significant differences.

Figure 5.3. shows the changes in respiration rate with varying temperatures in April, August and October 1980. The mean seawater

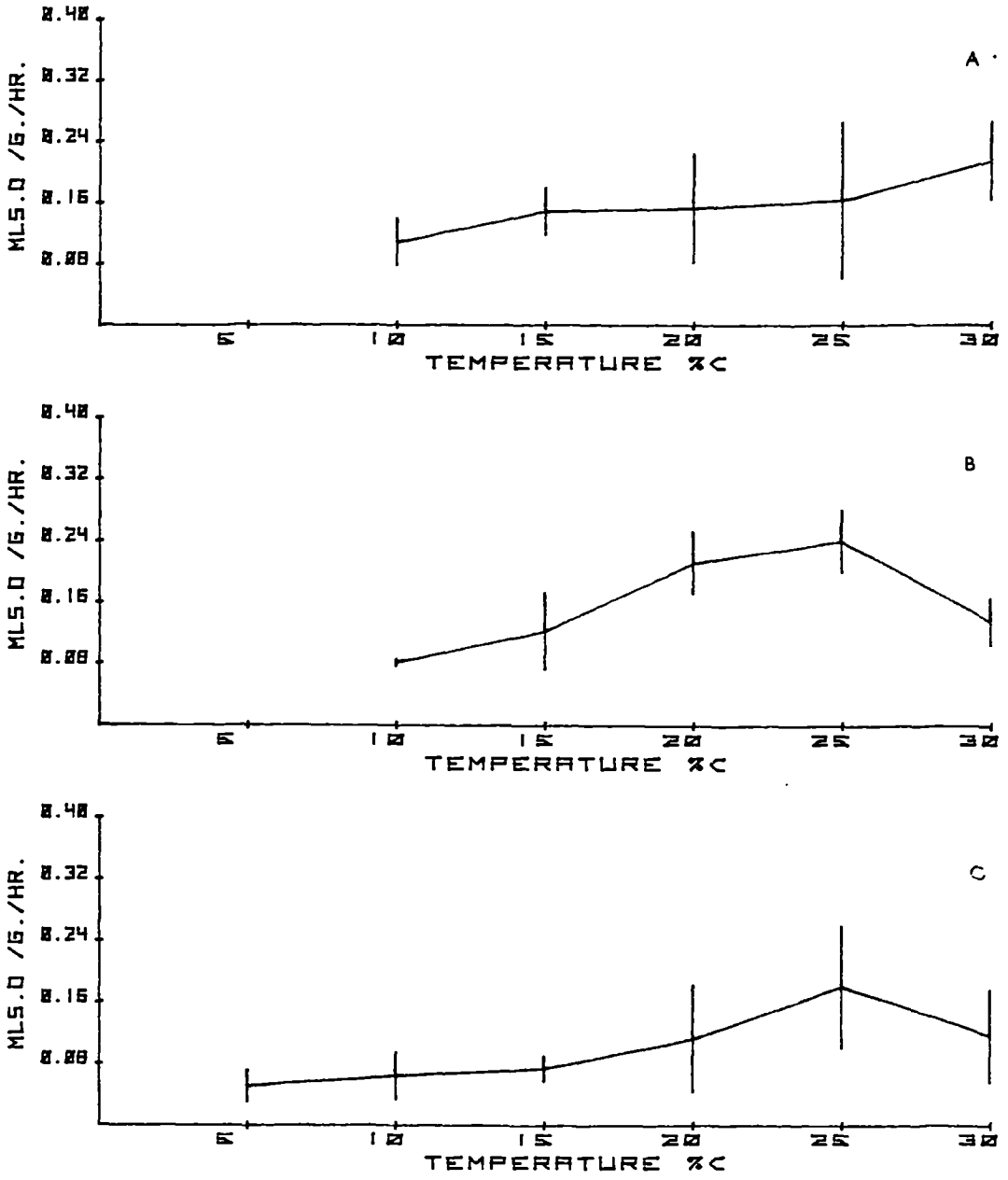


Figure 5.3. Lutraria. Changes in respiration rate (mls O_2/g. dry wt./hr.) of a standard animal (20g) with the different temperatures in April (A), August (B) and October (C).

temperature for these months was 7.91°C, 14.05°C and 11.69°C respectively.

Table 5.2. shows the Q_{10} values for the different months.

Q_{10} values give an indication of the sensitivity of the animal to temperature. Thus, Q_{10} values in April were low (<1.5) indicating relative insensitivity to temperature change. The respiration rate at 30°C was significantly higher than at 10°C, but no other significant differences were found, even though respiration rate appears to increase slightly with increasing temperatures in a linear fashion. In August and October 1980 the respiration rate reached a maximum value at 25°C, and decreased at 30°C. When returned to aerated seawater at 10°C, survival of the animals used in the 30°C experiment was low in both months. Respiration rate at 30°C was comparable to that at 15°C in August and 20°C in October.

Q_{10} values were much higher in August and in October suggesting that as the ambient temperature increases there is greater sensitivity to temperature change.

Covariance analysis of the results obtained at the same temperatures at different times of the year show significant differences.

5.1.3.3. The effects of hypoxia on respiration rate

5.1.3.3.1. Gradually induced hypoxia

Figures 5.4. and 5.5. show the changes in respiration rate in ten individuals under conditions of declining oxygen tension. The change in rate of respiration is given in terms of the percentage change from the initial rate, the initial rate being taken as 100%.

The two graphs show two types of response, namely a gradual decrease in the rate with decreased oxygen tension or a marked decrease.

The range of response to declining oxygen tension is similar in May and November 1980, although the seasonal effect on respiration rate

TABLE 5.2. *Lutraria*. Q_{10} values in April, August and October.

MONTH	5-15°C	10-20°C	15-25°C	20-30°C
April	-	1.34	1.09	1.44
August	-	2.63	1.97	0.64
October	1.46	1.78	2.46	1.09

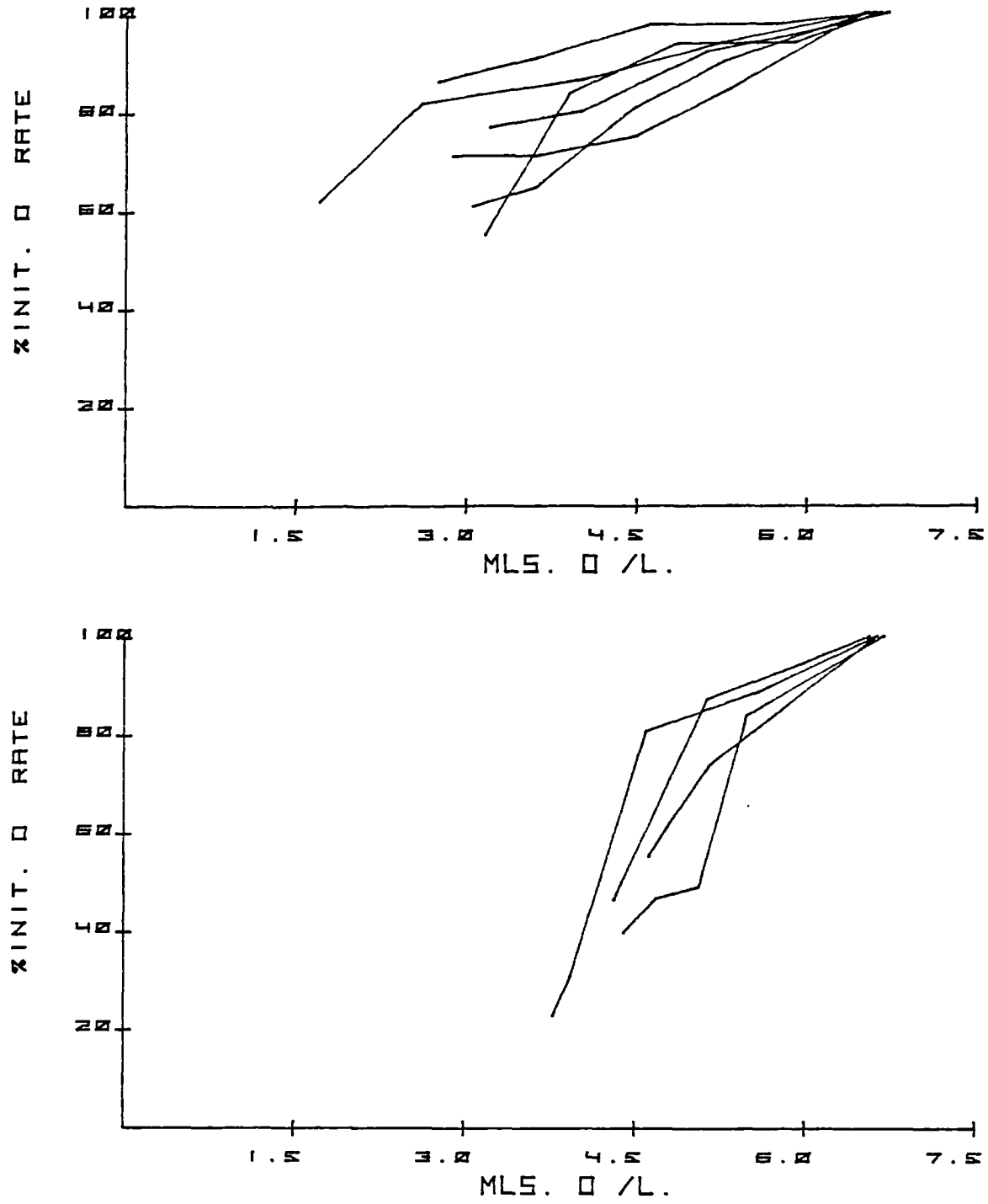


Figure 5.4. Lutraria. Changes from the initial respiration rate in percentage terms of ten individuals under conditions of declining oxygen tension in May 1980.

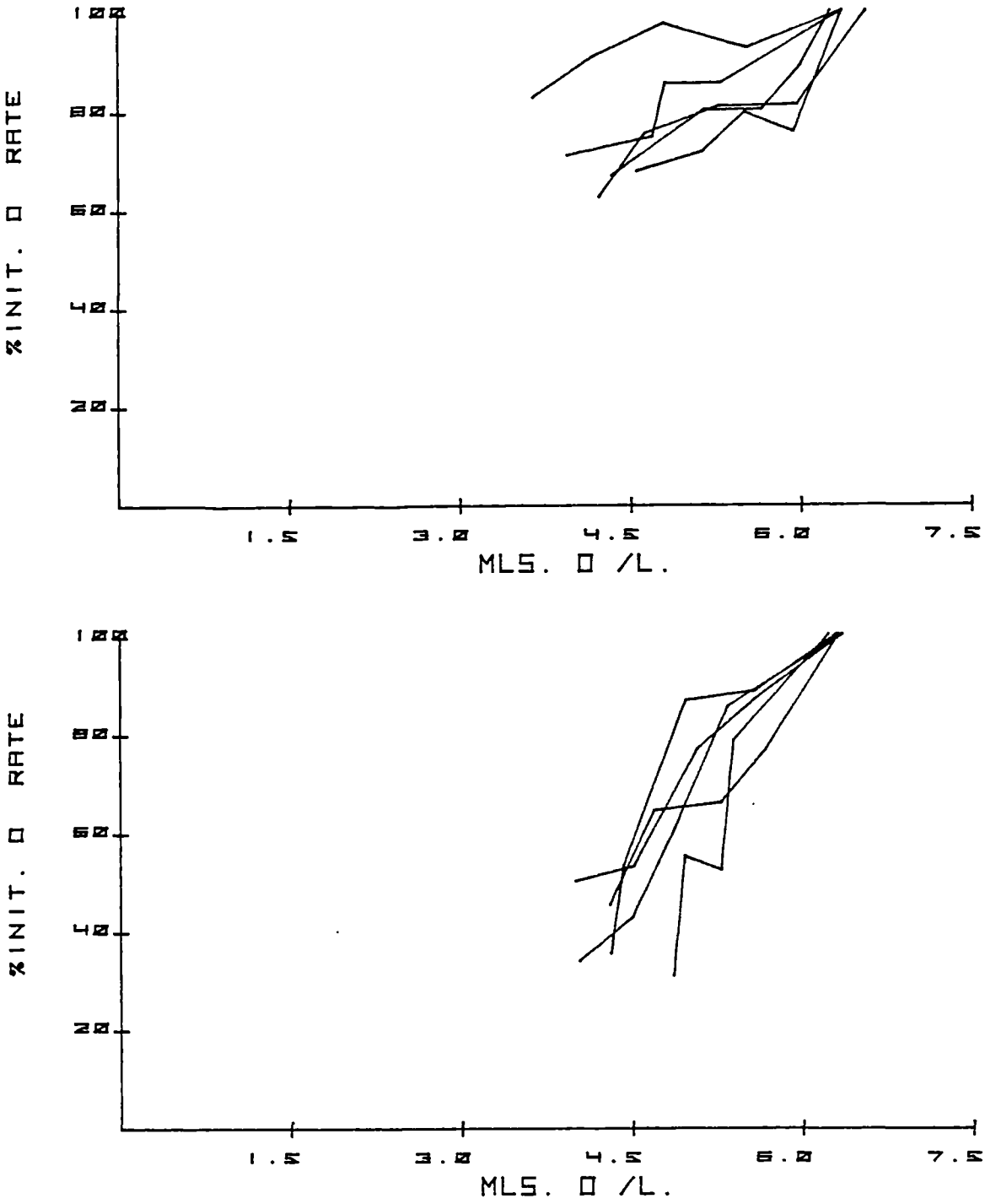


Figure 5.5. Lutraria. Changes from the initial respiration rate in percentage terms of ten individuals under conditions of declining oxygen tension in November 1980.

is again seen, with May values much higher than those in November. The range of lengths and weights of the experimental animals is similar in both months.

Figure 5.6. shows the decrease in the mean respiration rate of the ten animals to declining oxygen tension. The decrease is almost linear at both times of the year, indicating that, in general, Lutraria is a conformer. However, some individuals show a certain ability to regulate (see figures 5.4. and 5.5. and Section 5.1.1.).

5.1.3.3.2. Rapidly induced hypoxia

In these experiments, oxygen tension of the seawater was reduced to an average value of 2.00mls 0_2/l. In experiments involving three individuals in March 1981, the respiration rate was 0.0345, 0.032 and 0.0227mls 0_2/g. dry wt./hr. respectively.

Difficulties were experienced in the earlier experiments and the results given here are for animals used in heart rate experiments.

The normal seasonal respiration value for March 1980 was 0.11005mls 0_2/g. dry wt./hr. at an oxygen tension of 6.5ml 0_2/l. compared with an average respiration rate of 0.0297mls 0_2/g. dry wt./hr. at 0_2 tension 2.00mls 0_2/l. The decrease from the initial rate of respiration is 27% as compared with a decrease in oxygen tension of 30%.

5.1.3.3.3. Survival under anaerobic conditions

Only one animal out of five survived longer than three days in a closed experimental vessel at 10°C. After 48 hours, the animals' siphons were fully extended and flaccid. In some, the pedal aperture was gaping with the foot slightly extended. As a result of these preliminary experiments, later experiments involving effect of anaerobiosis on heart rate did not exceed 48 hours.

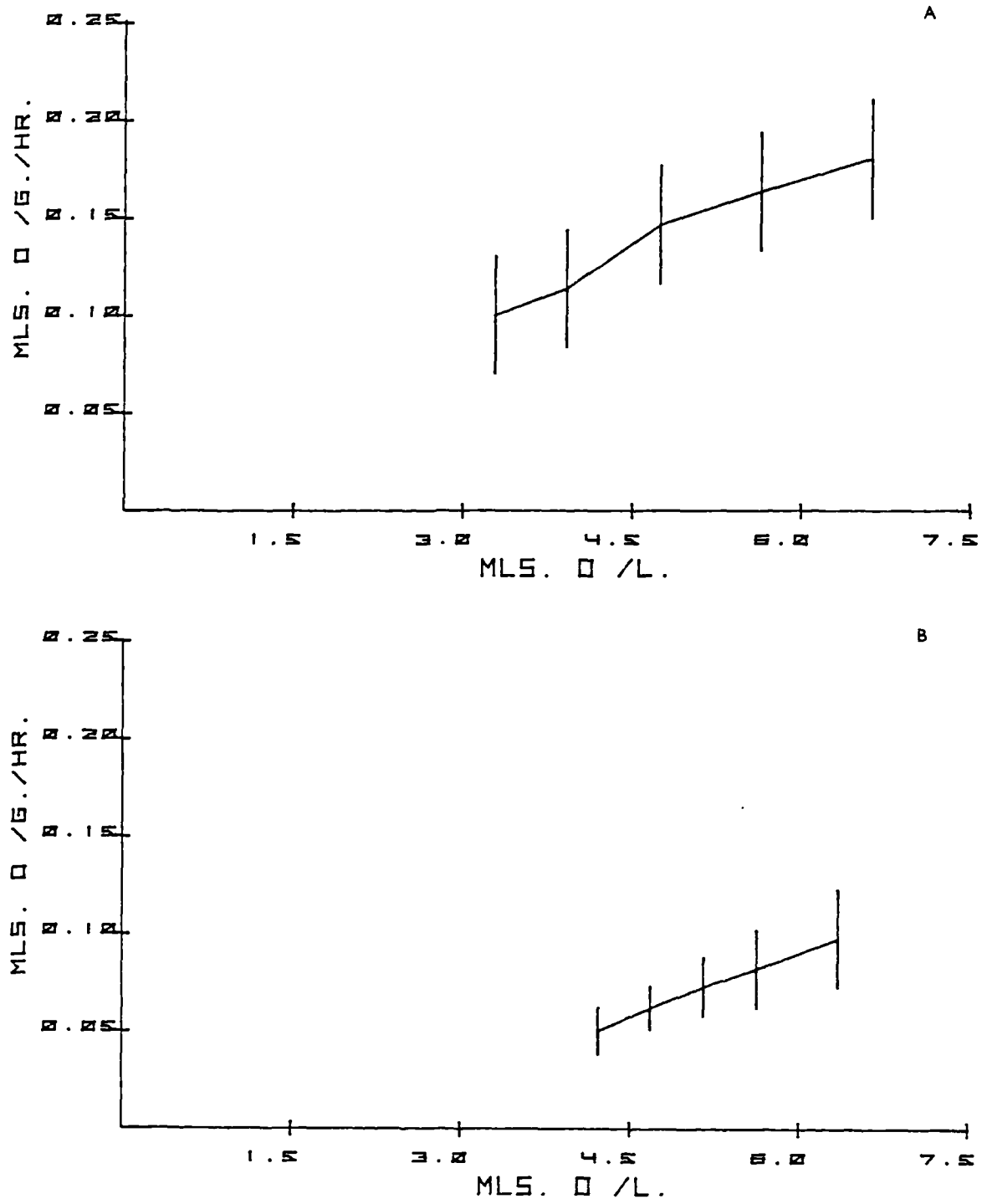


Figure 5.6. Lutraria. Changes in mean respiration rate (mls O_2/g. dry wt./hr.) of ten individuals in May (A) and November (B) under conditions of gradually reduced hypoxia. (Vertical lines = standard deviation).

TABLE 5.3. Lutraria. Change in respiration rate after 3 months in laboratory. (Value of common slope = -0.711).

MONTH	NO. OF ANIMALS	ORIGINAL OXYGEN CONSUMPTION ($mls0_2$/g dry wt/hr)	RECALCULATED OXYGEN CONSUMPTION ($mls0_2$/g dry wt/hr)	NEW INTERCEPT	RANGE OF WEIGHTS (g)
May	10	0.1416	0.1697	0.15479	10.54-20.66
August	10	0.0976	0.0968	-0.0889	6.57-19.74

F (adj. means) = 14.965 (significant at 1%)

F (reg. coeff.) = 0.0009 (not significant)

5.1.3.4. The effect of long term maintenance in the laboratory on respiration rate

Covariance analysis of the results of respiration rate in May and August 1980 showed no significant difference in slope and values were recalculated. This gave a common regression coefficient of -0.711.

The respiration rate in May was 0.1697ml O_2/g. dry wt./hr. for a standard 20g animal while in August the value was significantly lower at 0.0968mls O_2/g. dry wt./hr., i.e. 57.04% of the previous rate (Table 5.3.).

Seasonal experiments gave figures of 0.1238mls O_2/g. dry wt./hr. for May and of 0.0798mls O_2/g. dry wt./hr. for August, i.e. 64.45% of the previous rate. The difference is slightly greater than the seasonal effect and suggests that the reduction is due, in part, to the maintenance of the animals in the laboratory.

5.2. HEART ACTIVITY

5.2.1. INTRODUCTION

The anatomy of the heart of Lutraria is described in Chapter 2. Recent reviews on the physiology of the bivalve heart and its activity have been given by Krijsman and Davis (1955) and Hill and Welsh (1966). Details of heart rate and activity in the natural habitat are given by Coleman (1974).

In the past, two methods have been used for measuring heart rate, the first by direct observation of the heart, 'in situ', through a hole in the shell (Segal, 1956; Pickens, 1965) or second, by the use of impedance pneumographs (Trueman, 1967a; Hoggarth and Trueman, 1967).

Changes in heart activity have been related to environmental change. Various forms of respiratory stress have been listed in Section 5.1.1. and investigations on the cardiac responses of bivalves to respiratory stress include those of Trueman (1967a)on Donax and Cardium, Trueman and Lowe (1971) on Isognomon alatus, Coleman and Trueman (1971) on Mytilus edulis and Modiolus modiolus, Boyden (1972) on Cerastoderma edule and Cerastoderma glaucum, Brand and Roberts (1973) on Pecten maximus, Deaton and Mangum on Noetia ponderosa (1976) and Coleman (1976) on Modiolus modiolus.

In general, species show a reduction in heart rate with hypoxia followed by an increase in heart rate on return to aerated conditions. Bayne (1971b) in the case of M. edulis and Taylor and Brand (1975a) in the case of A. islandica found a slight increase in heart rate as oxygen tension decreased before the gradual decline.

Increase in temperature has been found to cause an increase in heart rate, e.g. Lowe (1974), C. gigas and M. arenaria, Pickens (1965), mussels.

Heart rate and valve activity have been found to be related and this is discussed by Coleman (1974). Generally an increase in heart rate follows adduction with consequent reduction on closure of the shell. Coleman (1974) suggests that in M. arenaria a reduction in heart rate can be related to closure and partial,(sometimes complete), retraction of the siphon. Lutraria is similar to M. arenaria in being unable to completely close the shell.

Heart rate has been used to indicate changes in metabolic activity of bivalves to certain environmental changes. Thompson and Bayne (1972) however, describe changes in metabolic level in relation to feeding in M. edulis which do not affect heart rate. Trueman, et al., (1973) discuss the possibilities of developing continuously recordings of heart rate and activity of molluscs to act as environmental sensors.

The heart activity of Lutraria was monitored by use of impedance pneumographs, and the effects of some environmental factors investigated.

5.2.2. MATERIALS AND METHODS

5.2.2.1. Method for recording heart rate of Lutraria

Animals were kept in running seawater and used within two weeks of collection.

Heart rate was measured by using the technique of Hoggarth and Trueman (1967) and Trueman (1967a). The animals were scrubbed clean and two small holes were drilled in the left valve to enable two fine silver electrodes to be inserted at either side of the heart. Both holes were drilled in one valve in order to prevent interference in the recording due to movement of the valves. The electrodes were held in place using 'Powabo nd' and a small oscillatory current was passed between them. Changes in impedence were recorded by a multichannel pen recorder (Physiograph VI. Narco Biosystems, Inc.). The electrodes were fitted to the animal twenty four hours prior to the experiment and the animal kept overnight in running seawater in a constant temperature room to allow it to recover.

Length and dry weight were measured at the end of each experiment.

5.2.2.2. Cardiac responses to acute temperature changes

Five animals were subjected to each of five temperatures, 10°C, 15°C, 20°C, 25°C and 30°C in August 1980. The initial heart rate was recorded with each animal in running seawater at ambient temperature. Each animal was then placed in the respirometer and the effect of temperature change on the heart rate and respiratory rate monitored simultaneously. There was no evidence of respiratory stress during

the experiments at 10°, 15° and 20°C, however, at higher temperatures (25° and 30°C) the heart rate became erratic and, in some cases, difficult to determine.

5.2.2.3. Cardiac responses to respiratory stress

5.2.2.3.1. Gradually induced hypoxia

The heart rate of five individuals was monitored individually over a period of four hours in the respirometer in June and in January 1981.

5.2.2.3.2. Rapidly induced hypoxia and anaerobic conditions

The heart rate of six individuals was measured in aerated seawater, then in seawater for forty eight hours, with reduced oxygen tension after passing nitrogen through. The animals were then replaced into well aerated seawater and the heart rate measured and then again after a twenty four hour recovery period.

5.2.2.3.3. Cardiac response to aerial exposure

The heart rate of six individuals was monitored in aerated seawater, then during exposure to air over a period of three hours and then following reimmersion in aerated seawater. These experiments were carried out in an air conditioned room at 10°C.

5.2.3. RESULTS

5.2.3.1. Normal heart rate

The range of heart rate in all experiments using aerated water varied from 4-15 beats per minute. Seasonal changes were not regularly determined, however, in January 1981 a heart rate of 4-5 beats/min was recorded although on this occasion difficulty was experienced in placing electrodes.

5.2.3.2. Cardiac responses to acute temperature changes

Although five individuals were used for each experiment, not all the traces recorded were usable, thus the results are based on a minimum of three animals at each temperature. The holding seawater temperature 14°C is used as a base-line for describing mean heart rate at other temperatures (Fig. 5.7.). Figure 5.8. shows extracts of initial heart rate recordings and those at the experimental temperature.

At 10°C the heart rate was lowered in all cases and at 15°C there was little change from that at 14°C. The rate was raised at 20° and 25°C, though at 25°C it became erratic two hours after the beginning of the experiment. At 30°C one individual showed a marked increase in rate while two others showed a decrease. A corresponding decrease in respiration rate was recorded at 30°C.

The mean percentage increase or decrease of heart rate from the initial value of each individual (Fig. 5.9.) shows that the relationship of heart rate with temperature is almost linear between 10°C and 25°C.

5.2.3.3. Cardiac responses to respiratory stress

5.2.3.3.1. Gradually induced hypoxia

The response of five individuals in both June and January 1981 to declining oxygen tension was variable (Fig. 5.10. and Tables 5.4. and 5.5.).

Oxygen tension over a four hour period fell from an average of 6.55mls 0_2/l. to an average of 3.80mls 0_2/l.

In June the animals either maintained a normal heart beat or bradycardia (Fig. 5.11.) occurred; in January 1981, although one animal showed an increase in heart rate, the responses were similar to those recorded in summer.

In June all animals recovered on return to seawater but three

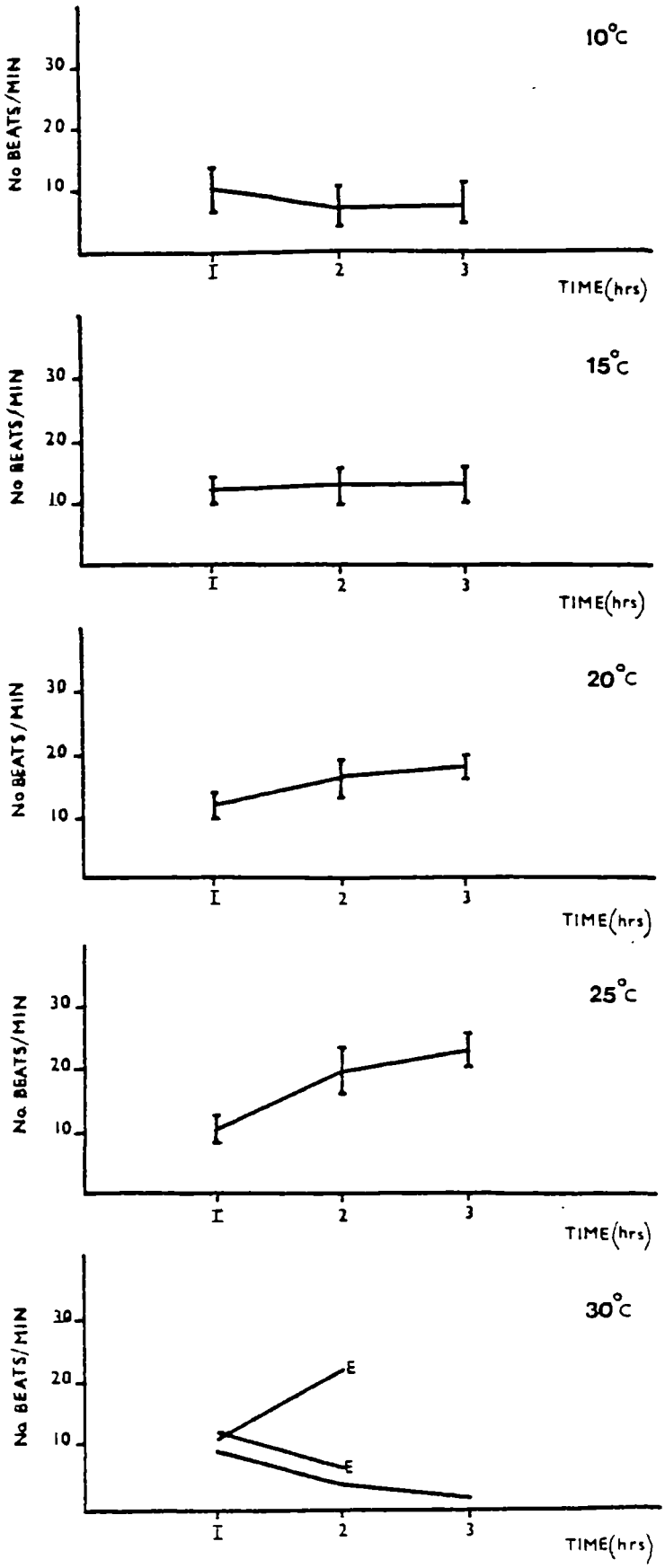
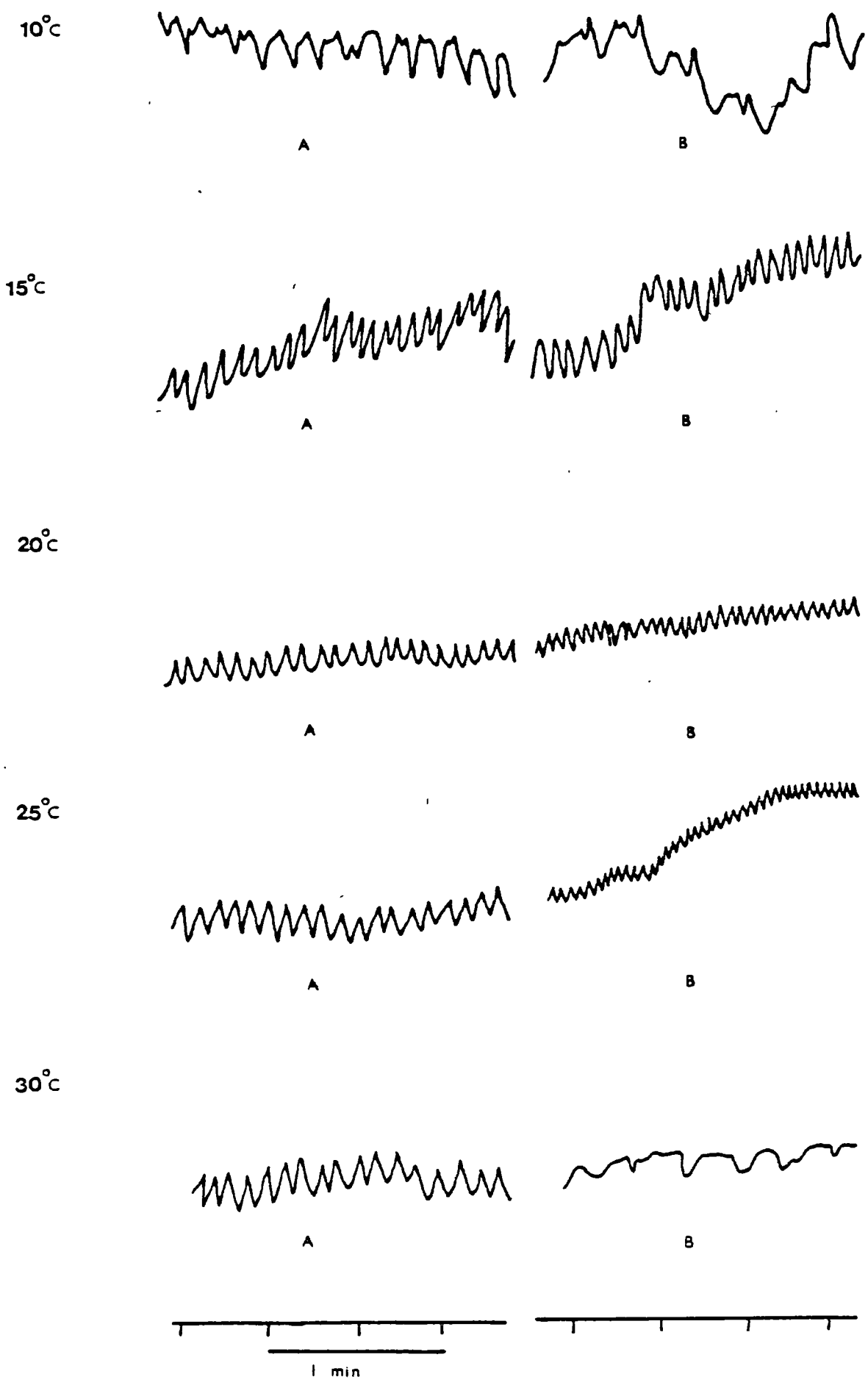


Figure 5.7. Lutraria. Changes in mean heart rate (beats per minute) at different temperatures Initially (I) and after 2 hours and 3 hours. (Vertical lines = standard deviation).

Figure 5.8. Lutraria. Extracts from the traces of heart activity. A - initially at 14°C; B - after 1 hour at the experimental temperature.


10°C
A
B
15°C
A
B
20°C
A
B
25°C
A
B
30°C
A
B
1 min

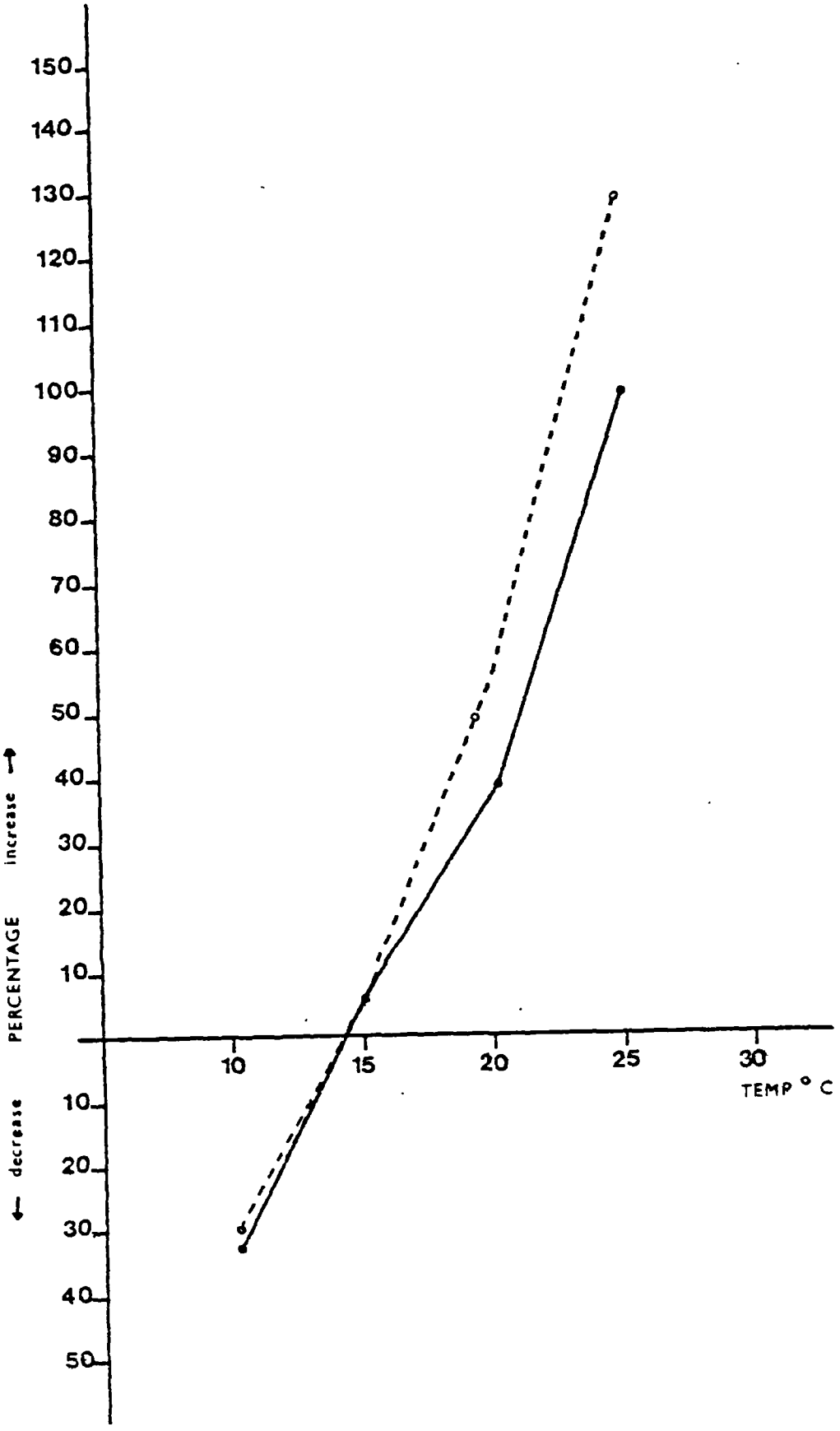


Figure 5.9. Lutraria. The percentage change in the heart rate with increasing temperatures (— after 2 hours, ---after 3 hours).

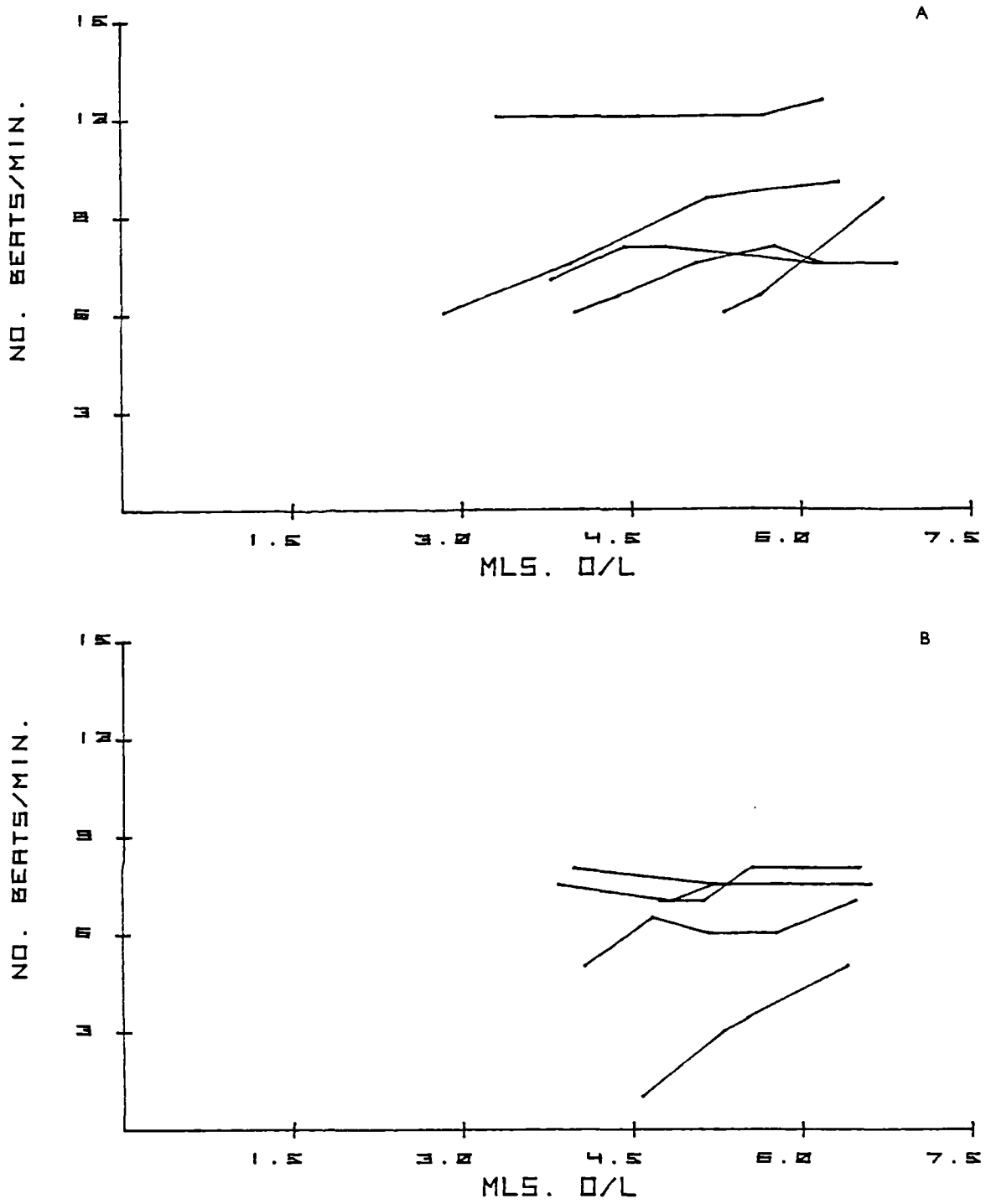


Figure 5.10. Lutraria. Changes in the heart rate (beats per minute) of five individuals in June 1980 (A) and January 1981 (B) under gradual hypoxia.

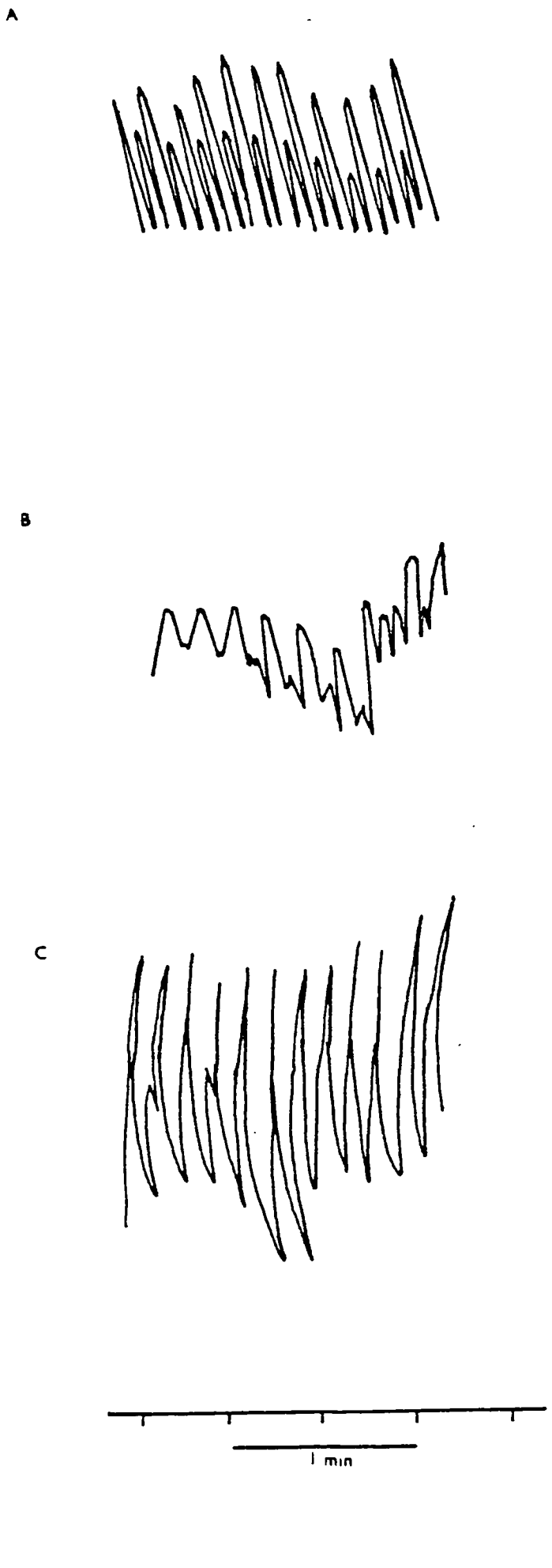
TABLE 5.4. Lutraria. Changes in the heart rate of 5 individuals in June 1980 over a period of 4 hours in a closed respirometer and on recovery.

ANIMAL NO.	LENGTH (cm)	WEIGHT (g)	OXYGEN CONSUMPTION ($mls0_2$/g dry wt/hr)	INITIAL HEART RATE (BEATS/MIN)	HEART RATE AFTER 4 HOURS (BEATS/MIN)	HEART RATE ON RE-AERATION (BEATS/MIN)	HEART RATE AFTER 24 HOURS (BEATS/MIN)
1	11.595	16.22	0.1047	7-8	7	8-9	8
2	11.10	18.37	0.05	9-10	6	6-7	9
3	11.41	6.39	0.2034	7-8	6	7-8	7
4	11.915	16.60	0.1416	10	5-6	10	10
5	10.70	18.63	0.1342	12-13	12	12-14	12

TABLE 5.5. Lutraria. Changes in the heart rate of 5 individuals in January 1981 over a period of 4 hours in a closed respirometer and on recovery.

ANIMAL NO.	LENGTH (cm)	WEIGHT (g)	OXYGEN CONSUMPTION ($mls O_2$/g dry wt/hr)	INITIAL HEART RATE (BEATS/MIN)	HEART RATE AFTER 4 HOURS (BEATS/MIN)	HEART RATE ON RE-AERATION (BEATS/MIN)	HEART RATE AFTER 24 HOURS (BEATS/MIN)
1	11.595	18.16	0.0606	7	5	8	7-8
2	11.95	15.62	0.0832	8	7	8	8
3	11.90	8.60	0.1395	7-8	8	erratic	dead
4	12.02	16.94	0.0885	7-8	7-8	erratic	dead
5	11.60	13.95	0.0980	5	1	erratic	dead

Figure 5.11. Lutraria. Extracts from the traces of heart beat of an individual. A - initially; B - after 4 hours in a closed respirometer; C - on re-immersion.


A
B
C
1 min

animals died in the January experiment. On return to aerated seawater some animals showed a slight increase in rate but in no case was there a significant overshoot of the heart rate and the majority returned to a normal value (Tables 5.4. and 5.5.).

There is no apparent link between the initial respiration rate and a cardiac response, i.e. if respiration rate is high it does not mean that heart rate remains constant.

5.2.3.3.2. Rapidly induced hypoxia and anaerobic conditions

The effect of rapidly induced hypoxia and anaerobic conditions on six individuals is shown in figure 5.12.

Two types of response are recorded for animals placed in seawater with an oxygen tension of 2.00mls. 0_2/l.; either there is an initial increase in rate (tachycardia) followed by a gradual decrease over the experimental period, or there is an initial decrease in rate (brachycardia) followed by a slight increase after three hours and then a decrease. In all cases, after twenty four hours the heart rate was lowered and by forty eight hours it had become very erratic (Fig. 5.13. and Fig. 5.14.).

On return to well aerated seawater recovery to the normal rate was fairly rapid, though an initial overshoot was seen in some cases.

5.2.3.3.3. Aerial exposure

Lutraria, exposed to air, (range of animals 10.90-12.00cm) at first eject water through the siphon. On continued exposure, the siphons become extended and flaccid and the usual response of the heart is a gradual brachycardia (Figs. 5.15. and 5.16.). Mean heart rates decline slowly from 12 beats/min. to 5 beats/min. On reimmersion the rate increases slowly to normal within twenty four hours.

In the case of a few individuals on immediate exposure and/or on reimmersion, the heart rate became very erratic.

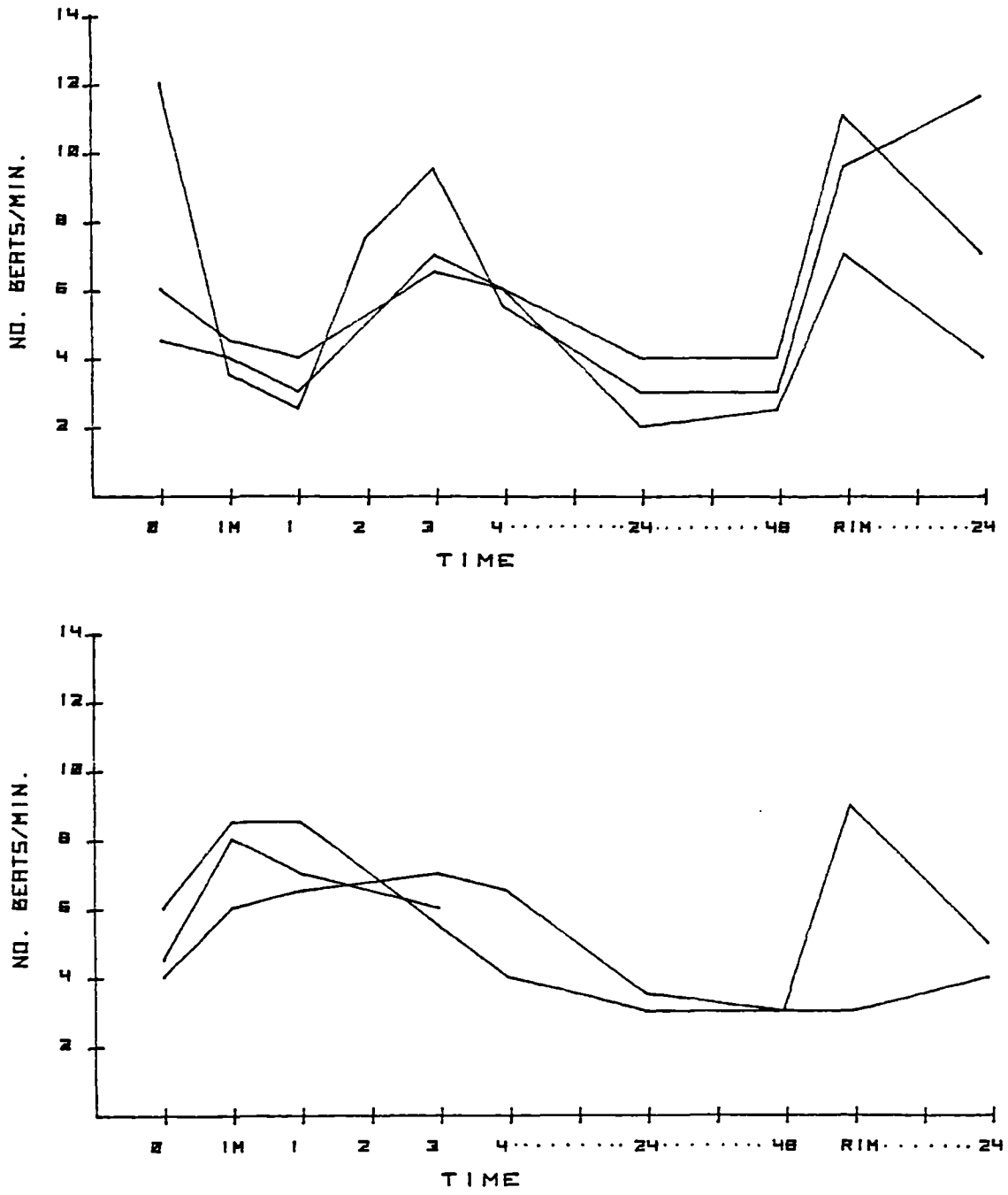


Figure 5.12. Lutraria. Changes in heart rate (beats per minute) of six individuals initially and following immersion in water of reduced oxygen tension (IM) for 48 hours then following re-immersion (RIM) and 24 hours later.

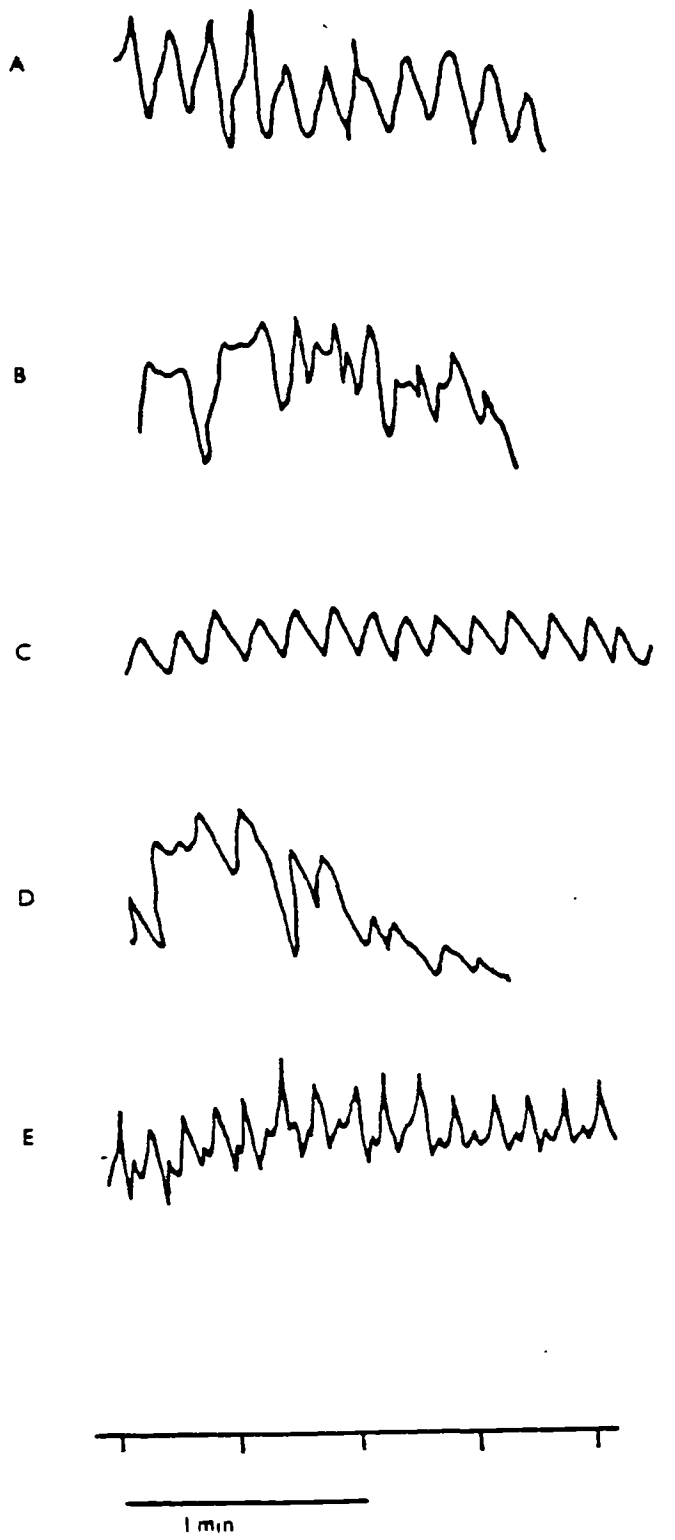


Figure 5.13. Lutraria. Extracts from the traces of heart activity of an individual. A - initially; B - on immersion in water of reduced oxygen tension (decrease); C - after 3 hours (increase); D - after 24 hours; E - on re-immersion in aerated seawater.

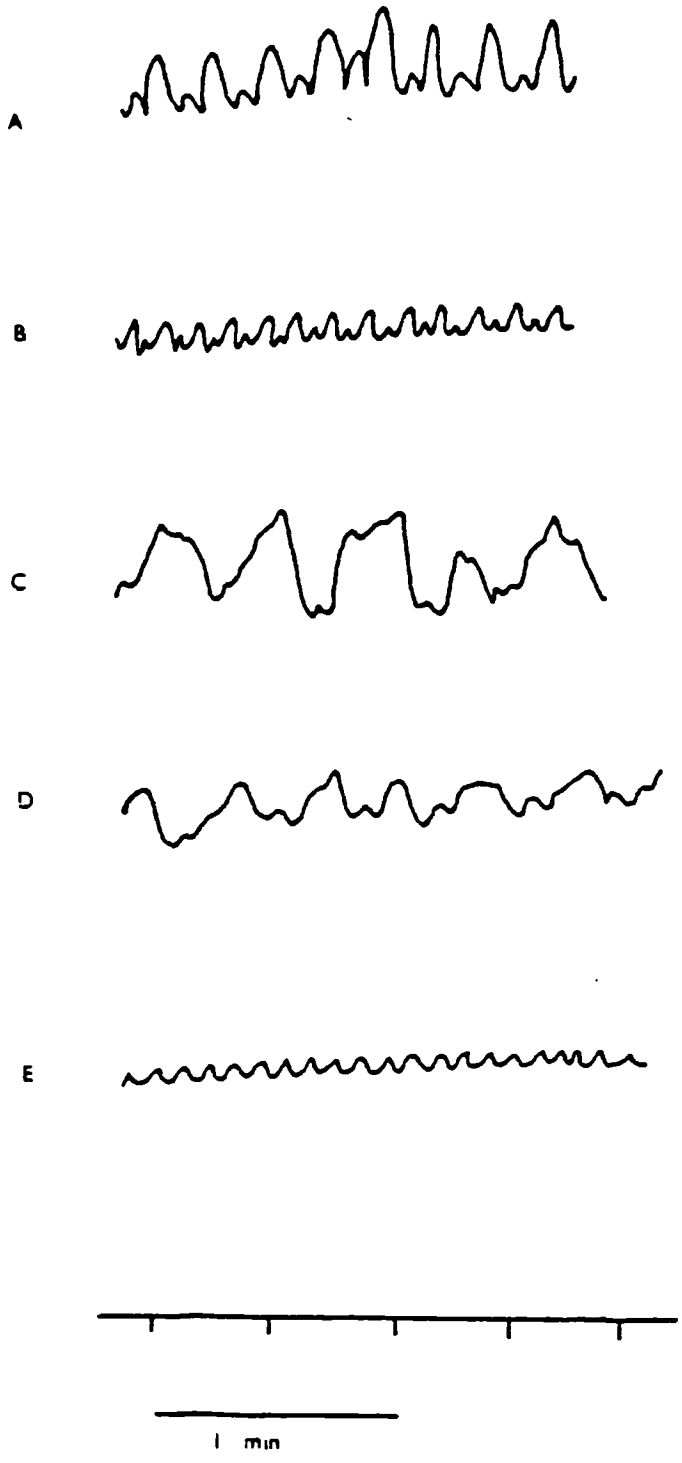


Figure 5.14. Lutraria. Extracts from the traces of heart activity of an individual. A - initially; B - on immersion in water of reduced oxygen tension (increased); C - after 24 hours; D - after 48 hours; E - on re-immersion in aerated seawater.

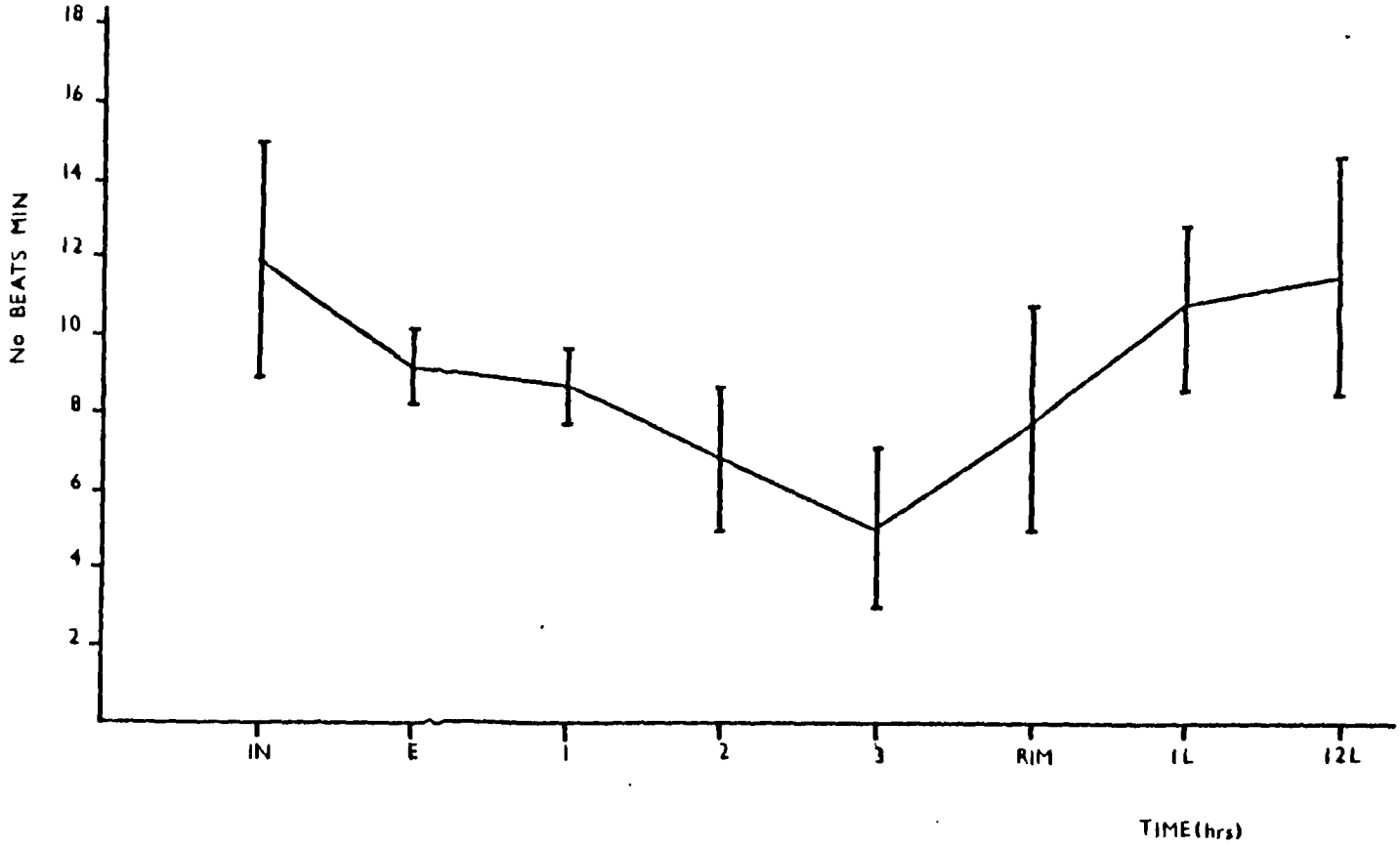


Figure 5.15. Lutraria. Change in mean heart rate of six individuals on exposure to air. Initially (IN); on exposure (E) for 1, 2 and 3 hours; on re-immersion (RIM) and after 1 hour (1L) and 12 hours (12L). (Vertical lines = standard deviation).

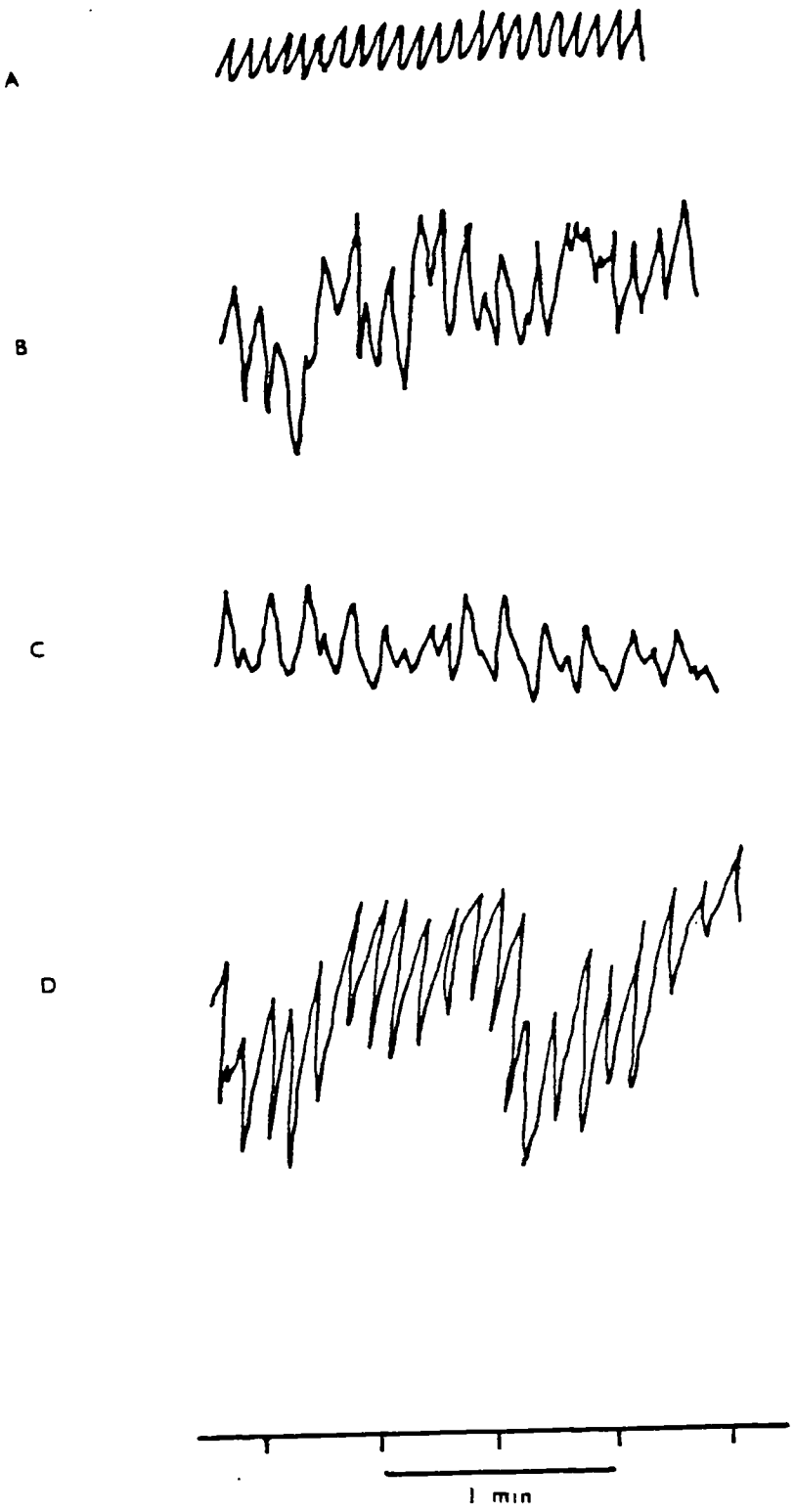


Figure 5.16. Lutraria. Extracts from the heart rate traces of an individual showing effects of exposure to air. A - initial heart rate; B - exposure causing disruption of heart rate; C - after two hours exposure heart rate reduced; D - on re-immersion.

5.3. PUMPING ACTIVITIES OF LUTRARIA LUTRARIA

5.3.1. INTRODUCTION

Recent reviews by Ali (1970) and Winter (1969) discuss the methods used for measurements of filtration rate and/or pumping rate of bivalves. Filtration rate is defined as the volume of water cleared of particles in unit time and its measurement gives an indirect measurement of the pumping rate. Pumping (ventilation) rate is defined as the volume of water flowing through the gills in unit time. If the retention efficiency of the animal is 100% then the filtration rate and pumping rate have the same value. When the retention efficiency is < 100% the pumping rate is higher than the filtration rate, however, the latter is never so inefficient as not to give a good indication of water flow rate.

Indirect measurements of pumping rate (by use of filtration rate) include the work of Willemsen (1952) M. edulis using silt, Loosanoff and Engle (1947) Ostrea virginica, Winter (1969) A. islandica and M. modiolus using natural food, and Allen (1962) M. arenaria, O. edulis, Venus striatula and Cuspidaria cuspidaria using Phaeodactylum labelled with P^{32}.

Direct methods (Drinnan (1964), Davids (1964), Hildreth (1976) and Coughlan and Ansell (1964)), have the obvious advantage of measuring the actual volume passed through the mantle cavity and therefore are not dependant on high concentrations of particles or varying retension efficiencies.

Whichever method is used, the experimental procedure should be so designed as not to affect either the filtration rate or the pumping rate. Thus, Coughlan and Ansell (1964) used a coloured dye for siphonate bivalves, while Loveland and Chu (1969) predicted pumping rates

from measurements of oxygen consumption.

In the present study, direct measurements were made by using thermistors. These have been used by other workers to determine pumping activity, in bivalves (Brand and Taylor, 1974; Foster-Smith, 1976; Earll, 1975 and Lowe and Trueman,1972), in brachiopods (McCammon, 1965, 1971) and in Demospongia (Reiswig, 1971).

Several factors have been reported as affecting pumping rate in bivalves, among these are particle size and particle concentration (Winter, 1969; Vahl, 1972; Davids, 1964), animal size (Thompson and Bayne, 1974) and environmental temperature (Widdows and Bayne, 1971).

The effect of reduced oxygen tension on the pumping activity of Lutraria is examined here.

5.3.2. MATERIALS AND METHODS

5.3.2.1. Pumping activity under simulated normal conditions

Specimens of Lutraria were collected and kept in tanks of running seawater containing natural sediment in which they were allowed to rebury. At the start of each experiment a specimen was partially buried in an aquarium tank half filled with natural sediment. Recordings were made after the animal had completely buried itself and when the tip of the siphon was flush with the surface.

The thermistor flowmeter used was similar in design to that used by Taylor and Brand (1974) and based on a Wheatstone Bridge circuit designed by McCamman (1965) (Fig. 5.17.).

Two bead thermistors (RS bead type GL23 2K) with a resistance of 2KΩwere individually sealed in hollow glass rods. One was used as a flowmeter probe and the other was to compensate temperature changes. A potentiometer completed the other half of the bridge. A heating

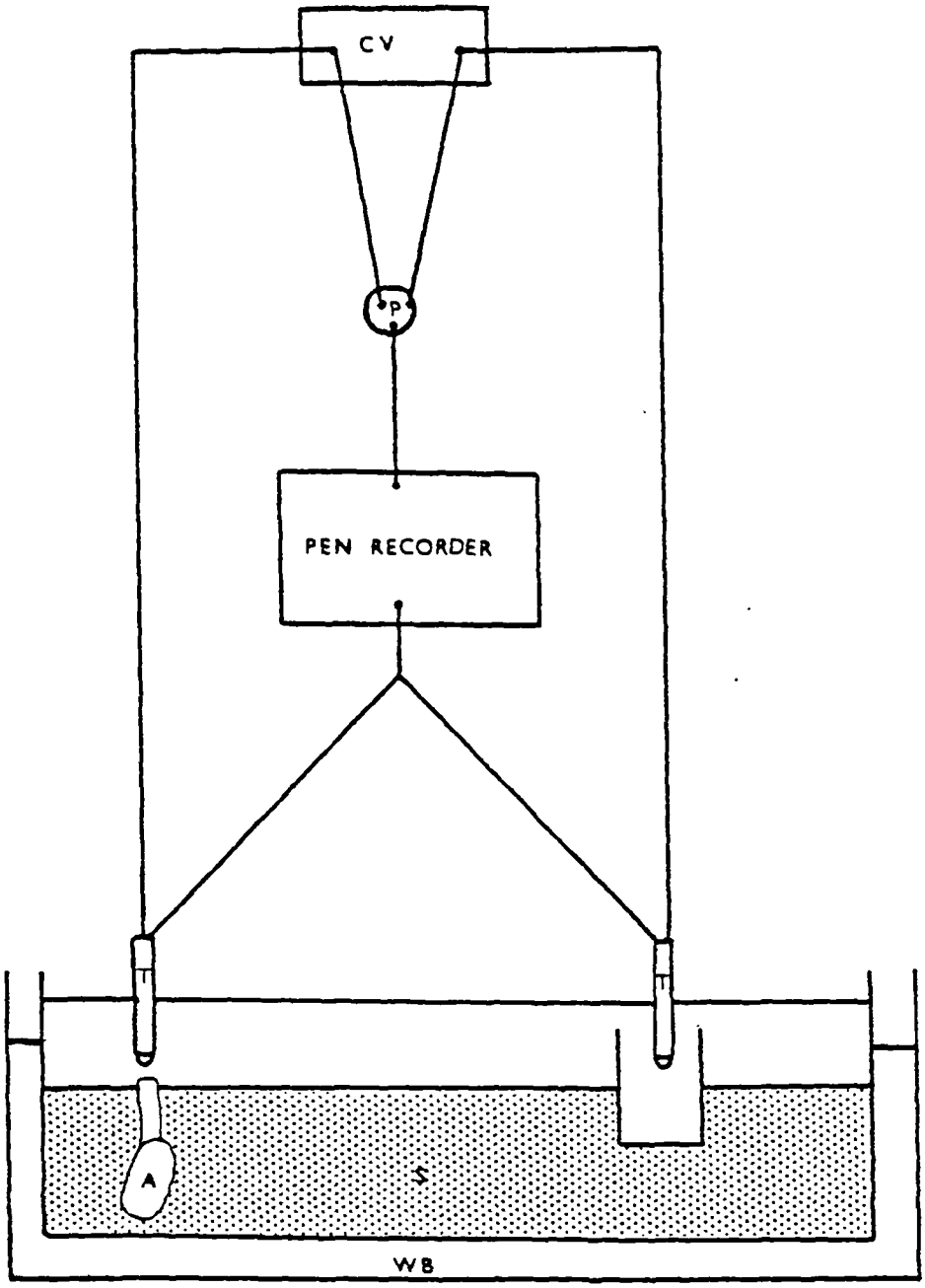


Figure 5.17. Diagram of the experimental system used in pumping experiments.

Key

CV	constant voltage
P	potentiometer
T	thermistor
T_1	temperature compensating thermistor
A	animal
S	sediment
WB	water bath

current of 8mA through the probe (from constant voltage) showed sufficient sensitivity at the range of velocities experienced.

Recordings of changes in velocity were made on a flat-bed pen recorder (Tekman Te200). Experiments were carried out at $10^{o}C \pm 0.5^{o}C$ in an air conditioned room.

At the beginning of each experiment the flowmeter probe was calibrated. Seawater was pumped at known rates through a glass tube of diameter 2.5mm (similar to the average diameter of the exhalant siphon of an undisturbed Lutraria to calibrate the probe.

During the experiment the flowmeter probe was placed at approximately 2mm from the exhalant siphon of the animal and in the direct line of the exhalant stream. The temperature thermistor was placed in the same tank within a beaker to shield it from the effects of currents. Each experiment ran for approximately one hour and no water flowed through the tank during this time. After the experiment the aquarium tank was flushed with seawater for approximately half an hour and another recording was made.

Some preliminary experiments were also carried out to determine the amount of time spent pumping. The pumping rate was determined by calculating the volume of water pumped over a known time.

At the end of each experiment the soft parts of the animal were removed and dried in an oven at $95^{o}C$. Length was also determined.

5.3.2.2. Pumping activity under reduced oxygen conditions

Seven animals were used to determine the effect of reduced oxygen tension on pumping activity and pumping rate.

The oxygen tension of the seawater was measured using an oxygen electrode (see Section 5.1.1.) and was then reduced by passing nitrogen through for 30 minutes. Pumping activity was then recorded. Only

animals with their siphons extended, and seen to be opening and closing, were used in the experiments and great care was taken not to disturb the animals. It is assumed that the pumping activity recorded was close to that in nature.

5.3.3. RESULTS

5.3.3.1. Pumping activity under simulated normal conditions

The animals used varied in length from 9.72-12.25cm with an average weight of 17.5g. Pumping rates varied from 0.382 - 1.023 l./hr. in normal seawater to 0.665 - 1.528 l./hr. under reduced oxygen conditions.

The size range is too small to determine the effect of size on the rate of pumping. The pumping rate obtained, expressed in litres per hour, is fairly constant for each individual (Table 5.6.). A typical recording of pumping activity of Lutraria is shown in figure 5.18.

Lutraria shows a pattern of intermittent pumping that varies between individuals. The amount of time spent pumping expressed as a percentage of the total period of observation for ten animals was found to be 35.58% $\pm$ 5.72%.

5.3.3.2. Pumping activity under reduced oxygen conditions

The changes seen in pumping activity due to decreasing oxygen tension are shown in figure 5.18. The percentage of time spent pumping increased to 65.75% $\pm$ 11.24%. The pumping rate for seven animals at reduced oxygen (between 2.96-3.55mls O_2/l.) increased from an average value of 0.692 l./hr. to 1.0634 l./hr.

TABLE 5.6. Lutraria. Pumping rates of individuals at normal and reduced oxygen tension.

ANIMAL NO.	LENGTH (cm)	WEIGHT (g)	PUMPING RATE (LITRES/HOUR)	TIME SPENT PUMPING (%)	PUMPING RATE AT REDUCED OXYGEN (LITRES/HOUR)	% INCREASE OF TIME SPENT PUMPING (LITRES/HOUR)	OXYGEN TENSION ($mls0_2/l$)
1	12.21	24.51	0.911	37.50%	1.495	64.11%	3.51
2	11.95	21.26	0.873	29.09%	-	-	-
3	11.65	19.40	1.023	31.21%	1.528	55.00%	3.30
4	10.95	11.98	0.480	44.17%	0.950	85.00%	3.32
5	11.89	18.25	0.382	31.25%	0.883	71.67%	3.55
6	12.25	25.00	0.937	41.09%	-	-	-
7	12.15	20.53	0.740	35.27%	-	-	-
8	10.92	10.25	0.582	30.00%	1.112	65.00%	3.47
9	12.15	14.42	0.525	43.75%	0.811	68.75%	3.11
10	9.72	9.81	0.473	32.52%	0.665	50.75%	2.96

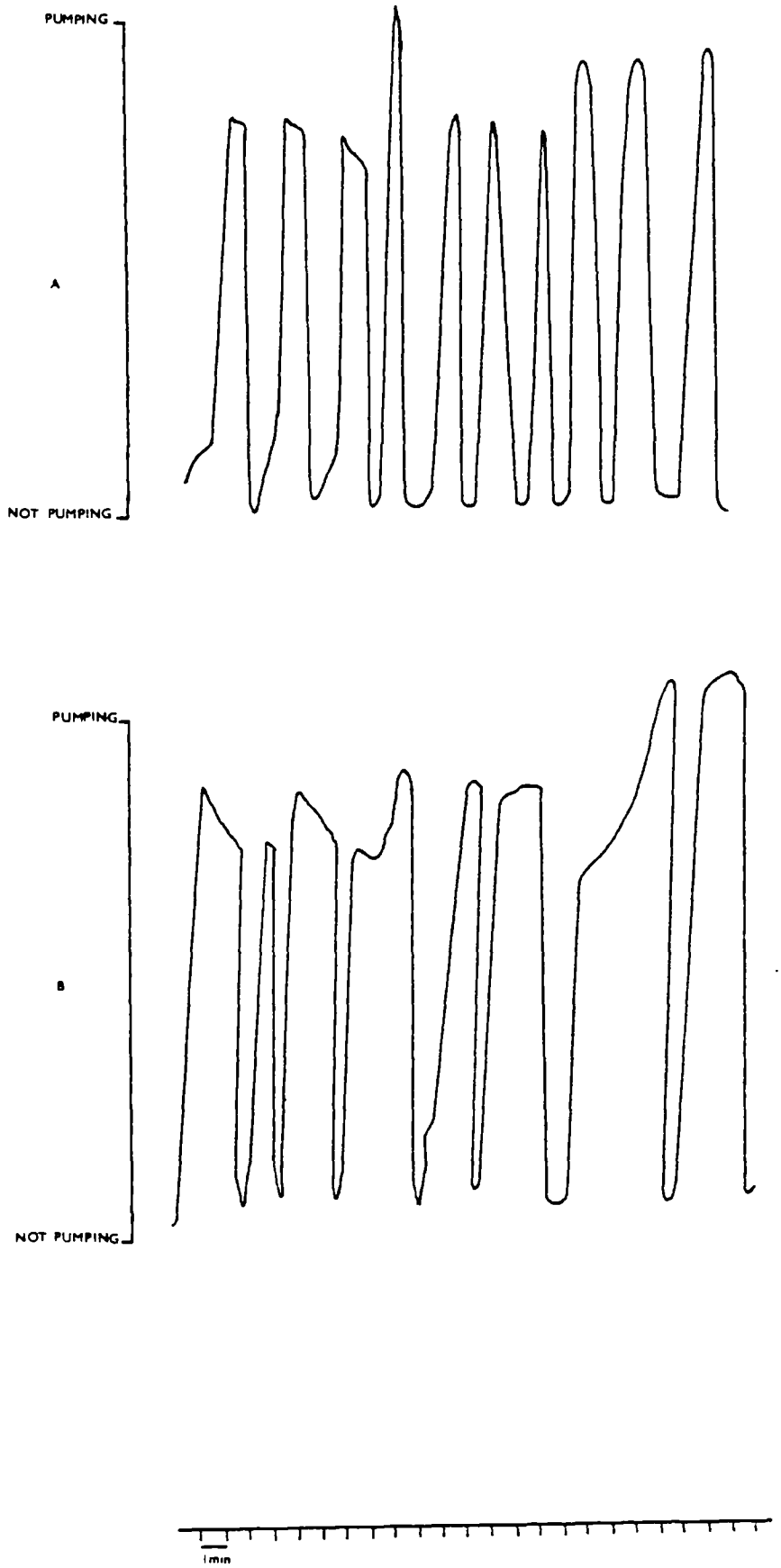


Figure 5.18. Lutraria. Extracts from traces of the pumping activity of an individual. A - under normal oxygen conditions and B - under reduced oxygen conditions.

5.4. DISCUSSION

Physiological rates of various kinds vary widely within the class Bivalvia. The heart rate of *M. edulis* in seawater at 17°C is in the order of 24-26 beats/min. (Helm and Trueman, 1967) and 24-44 beats/min. (Pickens, 1965), whereas that of *Crassostrea gigas* is 5 beats/min. (Feng, 1965). Variation within a species may depend in part on the activity patterns of the individual and in part on the internal conditions of the individual, and the range of normal values for physiological rates can only be determined from extensive experiments on many individuals throughout its geographic range. Thus, in comparing different rates reported by workers, it is essential to know the temperature at which each experiment was conducted, and the normal temperature range of the animal.

Respiration rate (≡oxygen consumption), heart rate and pumping rate are examples of physiological rates that can be used to give an indication of the general well being of the individual (or population) and the effect of certain environmental variables upon this. Coleman (1974) reported that 'the heart rate provides an index of extreme levels of activity and responses to drastic changes in environmental conditions or internal physiological states' but 'it does not provide a comprehensive document of molluscan activity' under normal conditions.

Differences in physiological rates have been recorded in animals of different size and Taylor and Brand (1975b) discuss relationship between oxygen consumption and body weight for *A. islandica*. In the present study the average size range of *Lutraria* was relatively small 9-13cm in length and the majority with body weight in the range 15-25g. Statistical analysis suggests there is no significant differences in

respiration rate over this range and consequently the effect of varying size on respiration cannot be discussed for Lutraria.

Difficulty in 'sexing' Lutraria (discussed in Chapter 3) precludes the determination of any variation in physiological rate between male and female in the present study, and this remains a hidden variable throughout.

Bayne, Thompson and Widdows (1973) define three different levels of oxygen consumption in terms of activity for M. edulis which are applicable to suspension feeding bivalves in general:

1) A standard rate associated with negligible filtration activity, i.e. incurring minimum physiological and mechanical metabolic costs.
2) An active rate associated with maximum filtration, i.e. incurring maximum physiological and mechanical metabolic costs.
3) A routine rate by an animal fully acclimated at a ration which exceeds the maintenance requirement.

The standard rate has been found for Lutraria but no experiments involving feeding were carried out.

The respiration rate of Lutraria was found to vary between 0.059mls O_2/g. dry wt./hr. and 0.1238mls O_2/g. dry wt./hr. for a standard 20g. animal at 10°C over a period of one year. This gives an average value of 0.0846mls O_2/g. dry wt./hr. Lutraria is a bottom dwelling, relatively inactive mollusc, and the respiration rate is relatively low compared with the shallow burrowing, intertidal cockle which has a range of 0.35mls O_2/g. dry wt./hr. - 0.89mls O_2/g. dry wt./hr. (Newell and Bayne, 1980). However, the respiration rate of Lutraria is similar to A. islandica (Taylor and Brand, 1975b) which occupies the same sublittoral sands as Lutraria, but is a more shallow burrower. Chlamys islandica, a fairly mobile species, has a respiration rate comparable to the cockle (Vahl, 1978).

The average heart rate of Lutraria at 10°C is 7-8 beats/min. and is comparable to other sublittoral eulamellibranch bivalves, e.g. Mercenaria mercenaria 10 ± 2 beats/min. (Dykens and Mangum, 1979), M. arenaria 6-10 beats/min. (Smith and Davies, 1965), C. virginca 5 beats/min. (Feng, 1965) but lower than the intertidal filibranch bivalves Mytilus californianus (21 beats/min.) and M. edulis (28 beats/min.) (Pickens, 1965) and the more active eulamellibranch bivalves, e.g. P. maximus (18 beats/min.) (Brand and Roberts, 1973).

Normal pumping rates of Lutraria of 0.382 l/hr. - 1.023 l/hr. compare with those of M. arenaria 0.6-1.3 l/hr. (Allen, 1962), C. virginca 0.763 l/hr. (Loosanoff, 1958), Ostrea edulis 0.13-1.0 l/hr. (Allen, 1962), Venus mercenaria 0.78 l/hr. (Coughlan and Ansell, 1964) and M. mercenaria 0.794 l/hr. (Loveland and Chu, 1969). Winter (1969) showed that both M. edulis and M. modiolus had higher filtration rates than M. arenaria, M. truncata and Venerupis pallustra. These filibranch species inhabit waters with a high seston content and seem adapted to high food concentrations and may not be able to compensate for low concentrations by higher filtration rates.

Approximately 35% of the time is spent pumping by Lutraria. Brand and Taylor (1974) found values of 40%-60% for subtidal species (excluding Chlamys) and > 90% for intertidal species that are submerged, and for Chlamys. The respiration rate, heart rate and pumping rate (under laboratory conditions) of Lutraria are relatively low and indicate a low level of metabolism in this deep burrowing, fairly inactive species. Respiration shows a seasonal pattern, with late spring and early autumn being metabolically more expensive times of year. Seasonal variation in respiration has been recorded in other bivalves including Chlamys islandica (Vahl, 1978), 'mussels' (Brajko and Dereshkeveich, 1978) and M. edulis (Widdows, 1978).

The relationship between gametogenesis, body reserves and oxygen consumption has been discussed for M. edulis by Bayne and Thompson (1970) and for C. edule by Newell and Bayne (1980). M. edulis, in the resting stage during the summer, has large reserves and a large amount of metabolically inert material present in the body. Consequently the respiration rate is low. In Lutraria the low respiration rate in the autumn coincides with the post spawning period and increasing reserves (see Chapter 4). The precise extent to which the reproductive condition affects physiological rates is uncertain. It is widely thought that developing gametes impose a high energy demand on the animal, i.e. a high oxygen uptake which falls after spawning has occurred. Thus, Ansell (1973) found that Donax vittatus in spawning condition has an increased respiration rate. The seasonal respiration rates of Lutraria show a greater correlation with the reproductive condition of the animal than with the thermal regime of the sea, thus maximum values were recorded in May when the sea temperature is still increasing.

Seasonal changes in heart rate have been shown to occur in certain bivalves (Pickens, 1965). In Lutraria changes in heart rate throughout the year were not determined, but difficulty was experienced in recording the heart beat in January 1981 and it is thought that this was possibly due to the physiological condition of the animals in turn related to low ambient temperatures. The internal and external factors affecting physiological rates have been mentioned (see Section 5.1.1.). The effect of changes in temperature and oxygen concentration on the respiration rate and heart rate of Lutraria have been studied. The change in pumping activity at reduced oxygen tensions has also been investigated. Reviews by Newell and Northcroft (1967), Tribe and Bowler (1968) and Newell and Bayne (1973) on the effects of temperature

on the metabolism of marine invertebrates, show that the effect of increasing temperature generally results in an increase in the metabolism in bivalves. The degree of thermal insensitivity usually in terms of Q_{10} values, is variable. Acute temperature effects were investigated for Lutraria but no acclimatisation experiments were performed.

In Lutraria, low Q_{10} values (<2.0) were recorded between 5°C and 30°C except on two occasions yet, the animal lives in a relatively stable environment compared,. say, to M. edulis where Q_{10} values are > 2.00 over its normal range of temperature (Bayne, 1976). Low Q_{10} values would seem to be of more benefit to an animal living in a habitat with widely fluctuating temperatures. As illustrated above, thermal insensitivity is not always the case.

The effect of temperature on the respiration rate of Lutraria varies at different times of the year. This is possibly due to acclimation to different seawater temperatures but may also be due to the varying physiological condition of the animal. In August and October high respiration rates were recorded at 25°C. At higher temperatures (30°C) the respiration rate decreased in these months, although in April, it was significantly increased, perhaps indicating that a critical level had been reached.

Kennedy and Mihursky (1972) found that the respiratory rates of Macoma balthica, Mulinia lateralis and M. arenaria tend to increase with increasing size and, in general, vary directly with temperature. They also found that at high temperatures (30°C) depression of metabolism occurred in cold acclimated Mulinia and Mya. Read (1962) found that M. edulis and Brachiodontes demissus plicatus were capable of compensating for changes in environmental temperature and he suggested that poikilotherms used some kind of homeostatic mechanism to regulate

their temperature.

The differences in respiration rate of Lutraria between April and both August and October may be as much due to the condition of the animal as to the temperature. Lutraria in autumn is in a post spawning period and is likely to be in 'poor condition'. Animals in poor condition are considered to be under stress and hence more susceptible to changes in environmental factors. Bayne (1975) defines stress as 'a measureable alteration of a physiological (or behavioural, biochemical or cytological) steady state which is induced by an environmental change and which renders the individual (population or community) more vulnerable to environmental change'.

That the condition of animals prior to an experiment is not changed from what it was in the natural environment is therefore of utmost importance. To prevent respiratory stress, specimens were maintained in running seawater in an outside tank and used as soon as possible after collection. A significant decrease in respiration rate was recorded in animals kept for three months.

Lowe and Trueman (1972) found that M. arenaria exhibited a marked response in the heart rate to changes in temperature during activity - activity being measured in terms of flow of water through the mantle cavity. Pickens (1965) investigated the heart rate of mussels in relation to latitude, intertidal height and temperature acclimation, and found that the heart rate was lowered by both decreasing temperature and increasing size. Although differences occur the rates are predictable, the effect of temperature alone cannot account for all the variations in rate. The heart rate of Lutraria in August showed an almost linear increase with increasing temperature up to 25°C.

Ventilation response to increased temperature was not studied,

although from the studies of a number of workers it is likely that there would be an increase with increasing temperature. Temperature effects the volume of water pumped rather than the filtering efficiency of the gill (Owen, 1966a). Bayne and Widdows (1971) showed that the filtration rate of M. edulis increases with increase in temperature from 5°C to 20°C. Winter (1969) also found that the filtration rate and food utilization in A. islandica and M. modiolus differed at different temperatures. The optimal food density at 12°C lies between 10 x 10^6 and 20 x 10^6 cells/l., whereas at 20°C the optimal range lies between 20 x 10^6 and 40 x 10^6 cells/l. Galstoff (1928) found in C. virginica no ventilatory current was produced below 5°C and that this was due to the lack of co-ordination of ciliary motion along the surface epithelia.

Changes in external oxygen tension influence metabolism. The respiratory response may vary from complete independance (regulator) to complete dependance (conformer), however, Taylor and Brand (1975b), suggest that the division of species into oxy-regulators and oxy-conformers is not merited because they relate to extremes of what is a variable capacity to maintain respiratory independance during hypoxia. The ability to certain bivalves to regulate oxygen consumption is discussed by Mackay and Shumway (1980) who found that C. delicatula, L. crassum and A. islandica showed least ability to regulate in terms of Baynes' K/K perfusion index, although all were capable of regulating.

The degree of regulation has been shown to vary with size in Mytilus perna (Bayne, 1967) and A. islandica (Taylor and Brand, 1975b). Small M. perna may regulate oxygen consumption down to 70% saturation whereas larger animals regulate down to 50% saturation. Furthermore, Bayne (1971a) found that for M. edulis, starved in the laboratory, oxygen consumption is linearly dependant of oxygen tension, i.e. they lose any capacity to regulate when in poor physiological condition.

Karandeeva (1959) found that M. phaseolia and M. galloprovincalis showed a gradual decline in respiration rate with declining oxygen tension, rather than a sudden drop. Lutraria subjected to gradually induced hypoxia shows a range of responses. In the main, respiration rate showed dependence on oxygen tension, though individual responses did suggest a small capacity to regulate. Ghiretti (1966) suggested that lack of independence may be due to incomplete saturation of the tissues with oxygen or possibly an increase in oxidative processes as a consequence of increased oxygen tension. No critical oxygen tension can be derived for Lutraria.

Bayne (1973) suggests that increasing oxygen dependence related to decreasing likelihood of encountering low oxygen conditions. Many bivalves experience periods of temporary anaerobiosis and the ability to withstand oxygen deficiency is of value to animals living intertidally or deep in sublittoral soft sediments. Thus, Collip (1921) found that M. arenaria could withstand temporary anaerobiosis while more recently Taylor (1976) found that A. islandica could survive anaerobically for periods between 1-7 days. Lutraria can survive temporary periods of anaerobiosis of 2-3 days duration but further experiments involving more individuals are necessary to confirm this.

The general cardiac response of bivalves to declining oxygen tension is a gradual bradycardia (Bayne, 1971b; Lowe and Trueman, 1972; Brand and Roberts, 1973), though some species show slight trachycardia (Booth and Mangum, 1978). In Lutraria, hypoxia results in a variety of responses, but a definite decrease in heart activity was seen after a twenty four hour period in a closed respirometer. After forty eight hours the heart rate becomes erratic. Bayne (1971b) suggested a link between the oxygen tension of the mantle cavity water and the heart rate, acting through changes in the oxygen tension of the blood, as a

possible mechanism for controlling the onset of brachycardia. Aerial exposure of Lutraria results in brachycardia similar to that described by other workers for M. edulis and M. modiolus (Coleman and Trueman, 1971; Helm and Trueman, 1967). Recovery on return to aerated seawater resulted in a small overshoot of heart rate before it returned to normal.

Some bivalves are able to operate an 'air-gaping' system of respiration when exposed, e.g. M. demissus (Coleman and Trueman, 1971), Isognoman alatus (Trueman and Lowe, 1971). This is an intertidal adaptation and is not shown by Lutraria.

There are two ways in which a bivalve may maintain respiratory independence during declining oxygen tension. The ventilation rate may be reduced and the oxygen utilisation increased as in M. edulis (Bayne, 1971b) or the reverse may happen as in A. islandica (Taylor and Brand, 1975a). In both, an adequate supply of oxygen reaches the tissues.

The ability of many bivalves to increase the ventilation rate may be limited by their normal pumping activity. If the animal pumps continually and the ciliary beat is invariable then there is no capacity for increasing the pumping rate, e.g. C. opercularis, M. edulis, M. arenaria (Brand and Taylor, 1974). Nevertheless, M. arenaria is able to increase the oxygen utilization from 3-10% to 25% after periods of anaerobiosis during recovery from an oxygen debt (Van Dam, 1935). In contrast Lutraria has an intermittent pattern of pumping activity and preliminary experiments under reduced oxygen conditions show an increase in pumping activity and pumping rate, thus indicating a regulatory role of the ventilatory current in respiratory control.

Sublittoral species are likely to be less restricted by respiratory and/or feeding demands than are intertidal species. Intermittent pumping should then be adequate to fulfil both these functions. The

degree of individual variation found in the present study precludes discussion of a 'typical' response of Lutraria, especially in terms of heart rate. The species shows only a limited capacity to regulate respiration rate and heart rate under conditions of respiratory and temperature stress.

The rate of metabolism is fairly low and correlates well with the life style of a large, sessile animal.

CHAPTER 6

BURROWING IN *LUTRARIA LUTRARIA*

CHAPTER 6

BURROWING IN LUTRARIA LUTRARIA

6.1. INTRODUCTION

Visual observations of burrowing activity and the use of Kymograph recordings were methods used by early workers to determine the burrowing activity in bivalves (Morton, 1964). These early studies include those of Quayle (1949) and Ansell (1962) on species of the family Veneridae, Allen (1958a) on the Lucinacea and Pohlo (1963) on the Solenacea.

In 1967 Hoggarth and Trueman developed electronic techniques to measure activity that involved the recording of pressure and changes in impedance. These latter were adopted here for Lutraria. Reviews on the mechanism and dynamics of burrowing as determined by the use of these instruments include those by Trueman and Ansell (1969) and Trueman, Brand and Davis (1966a).

The aim of the present work was to determine the burrowing ability of Lutraria and consequently the possible fate of animals disturbed and exposed after the use of the suction bin. Recordings were made of the rate of burrowing, supplemented by visual observations, and the pattern of burrowing activity of the animal as indicated by internal pressure changes and valve movements.

The natural orientation in life and depth to which the animal is buried are also discussed in the light of observations taken during the sampling process.

6.2. MATERIALS AND METHODS

Preliminary observations of the burrowing activity of Lutraria were made immediately after collection in the laboratory. The animals were placed on sediment taken from the sample area in tanks of running seawater in an air conditioned room kept at $10^{o}C \pm 2^{o}C$. A few of the animals were partially buried as an aid to their re-burial. Only animals that successfully buried themselves within 24 hours were used in the experiments that followed.

Burrowing activity was recorded in three ways:-

(i) The downward pull exerted (retraction strength) due to burrowing. Using 'Powabond', a fine thread was attached to the posterior-dorsal region of the shell of each individual. This region of the shell had previously been wiped dry to allow better contact. The thread was then attached to a microdisplacement myograph calibrated to 10 or to 100 grammes.

(ii) Pressure changes in the mantle cavity.

For these studies, a small hole was drilled in the postero-ventral region of the shell and a very fine tube filled with distilled water and linked to a linear core pressure transducer calibrated to 10mmHg was inserted into the mantle cavity and sealed in place using 'Powabond'.

(iii) Movements of the valves.

Two fine silver electrodes were attached by 'Powabond' to the mid-posterior region of the shell and linked to an impedence pneumograph.

The output of the transducers was recorded on a multichannel pen recorder Physiograph Six (Narco Bio Systems Inc.). In addition, the heart beat rate was determined for some individuals using the procedure described in Section 5.2. After the experiments, the length and dry

weight of each animal was determined (see Section 4.2.).

Each individual was gently pulled to the sediment surface and the recording equipment attached with the minimum disturbance. After a few experiments it was thought the results indicated that drilling through the shell to insert the pressure recording capillaries caused gross disturbance to the animal. Thereafter the tube was inserted through the ventral mantle edge being sealed in place by the natural closure of the tissues around it.

6.3. RESULTS

Over a period of ten weeks the burrowing activity of approximately 50 individuals was examined. The animals ranged from 10.50cm to 12.23cm in length and 10.87g to 23.31g dry weight.

About two-thirds of the animals collected proved capable of re-burrowing on their immediate return to the laboratory, and most of these burrowed when placed on their side, i.e. they were not partially buried. Complete burial took place within 48 hours. It was soon apparent that these laboratory kept specimens when pulled up again and linked to the physiograph were not then able to resume burrowing from the horizontal position and so these experiments were started with the individual partially buried.

A complete digging period was not obtained for any individual Lutraria under experimental conditions and in no case did an animal burrow until it was completely covered by the sediment. Although many of the animals attached to the instruments showed little activity, probing cycles and digging cycles were obtained for several. Figures 6.1. - 6.6. illustrate the type of traces recorded during the digging period of different individuals.

Figure 6.1. Lutraria. Recordings of burrowing activity in an individual. A - using an isotonic myograph, upstroke representing movement into the sediment. B - pressure changes in the mantle cavity accompanying probing and digging cycles.

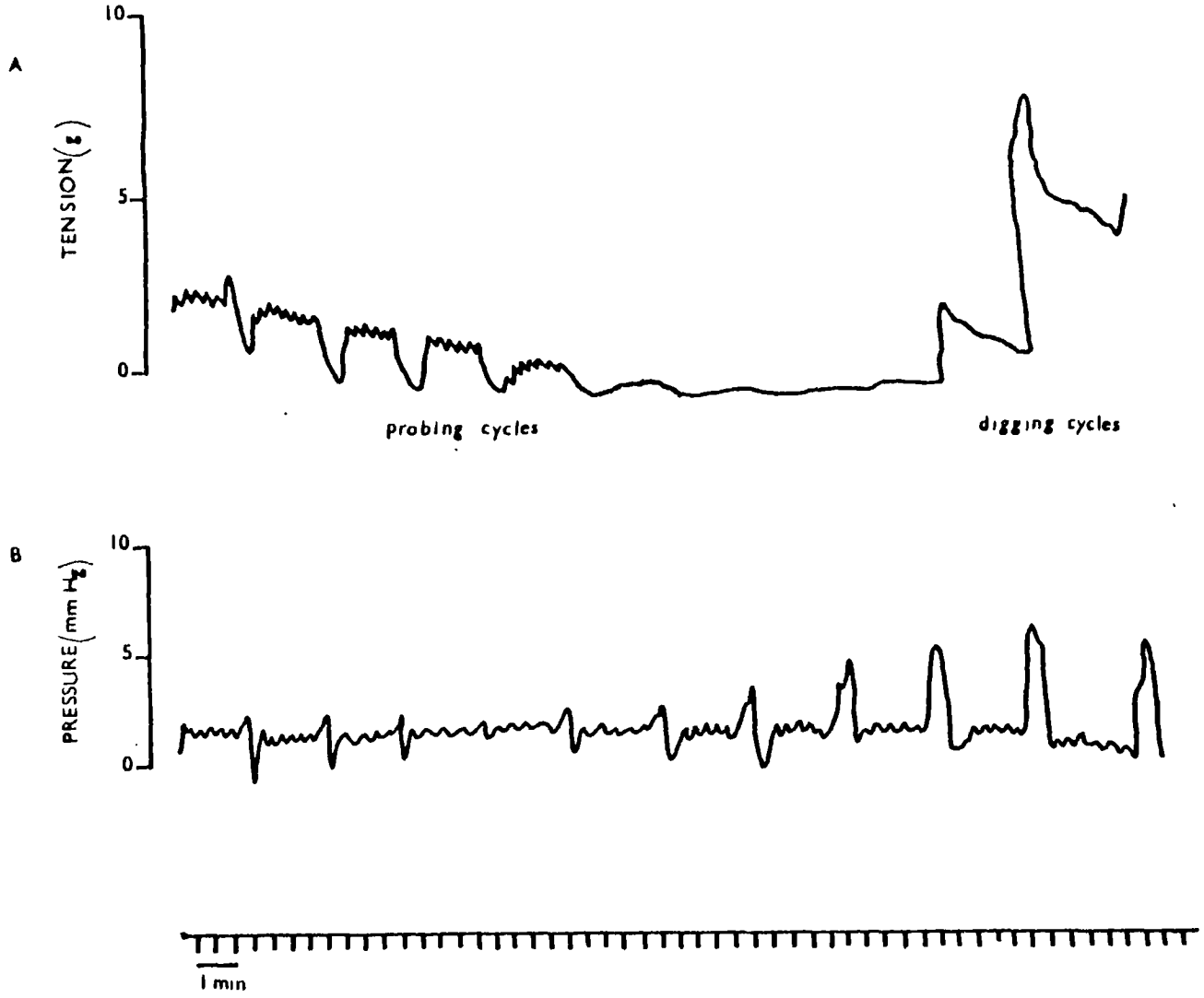
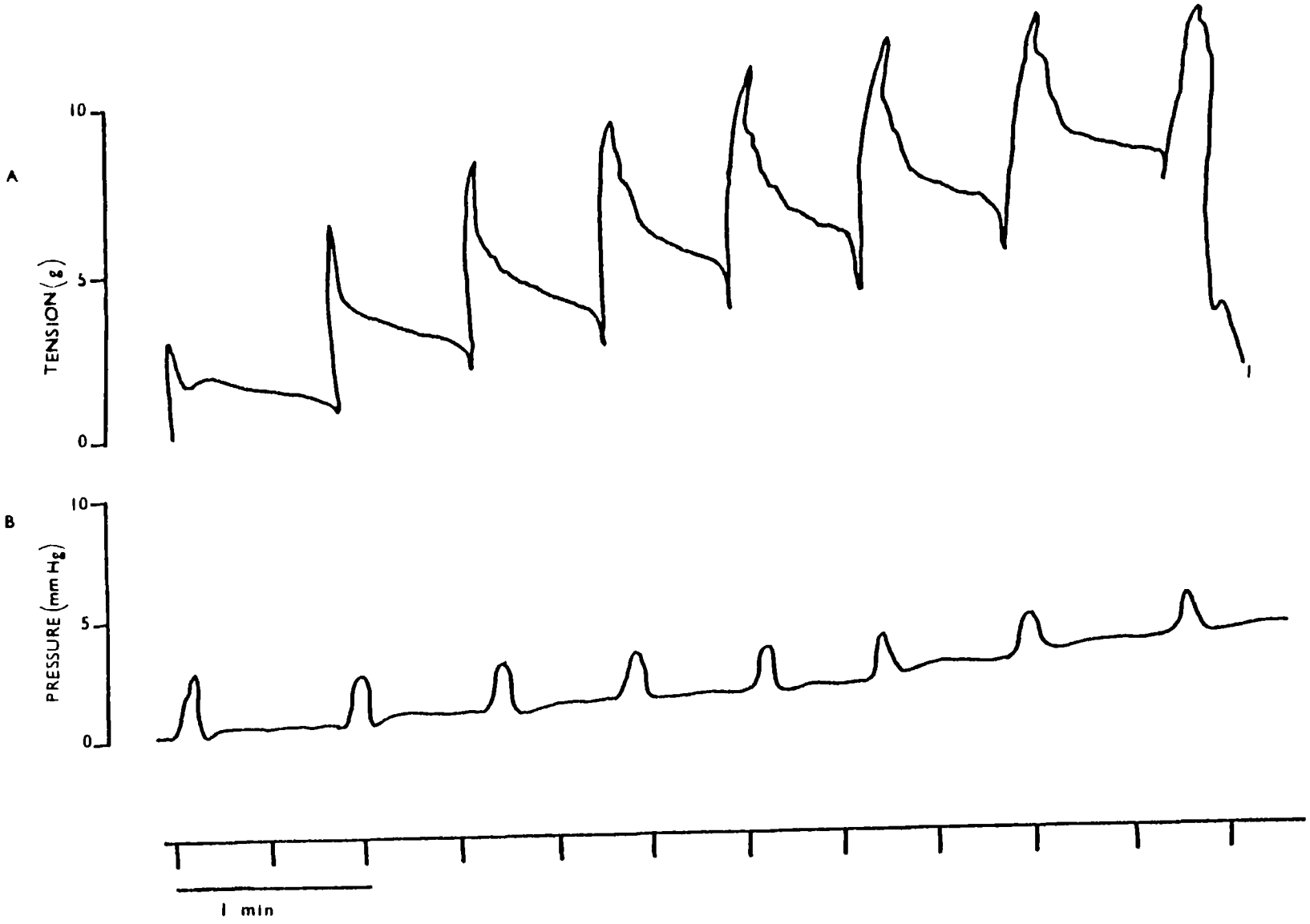

A
10
5
0
TENSION(g)
probing cycles
digging cycles
B
10
5
0
PRESSURE(mm Hg)
1 min

Figure 6.2. Lutraria. Recordings of the burrowing activity in an individual showing digging cycles as step-like movements into the sediment. A - using an isotonic myograph, upstroke representing movement into the sediment. B - pressure changes in the mantle cavity. (l = string loosened).


A
10
5
0
TENSION (g)
B
10
5
0
PRESSURE (mm Hg)
1 min

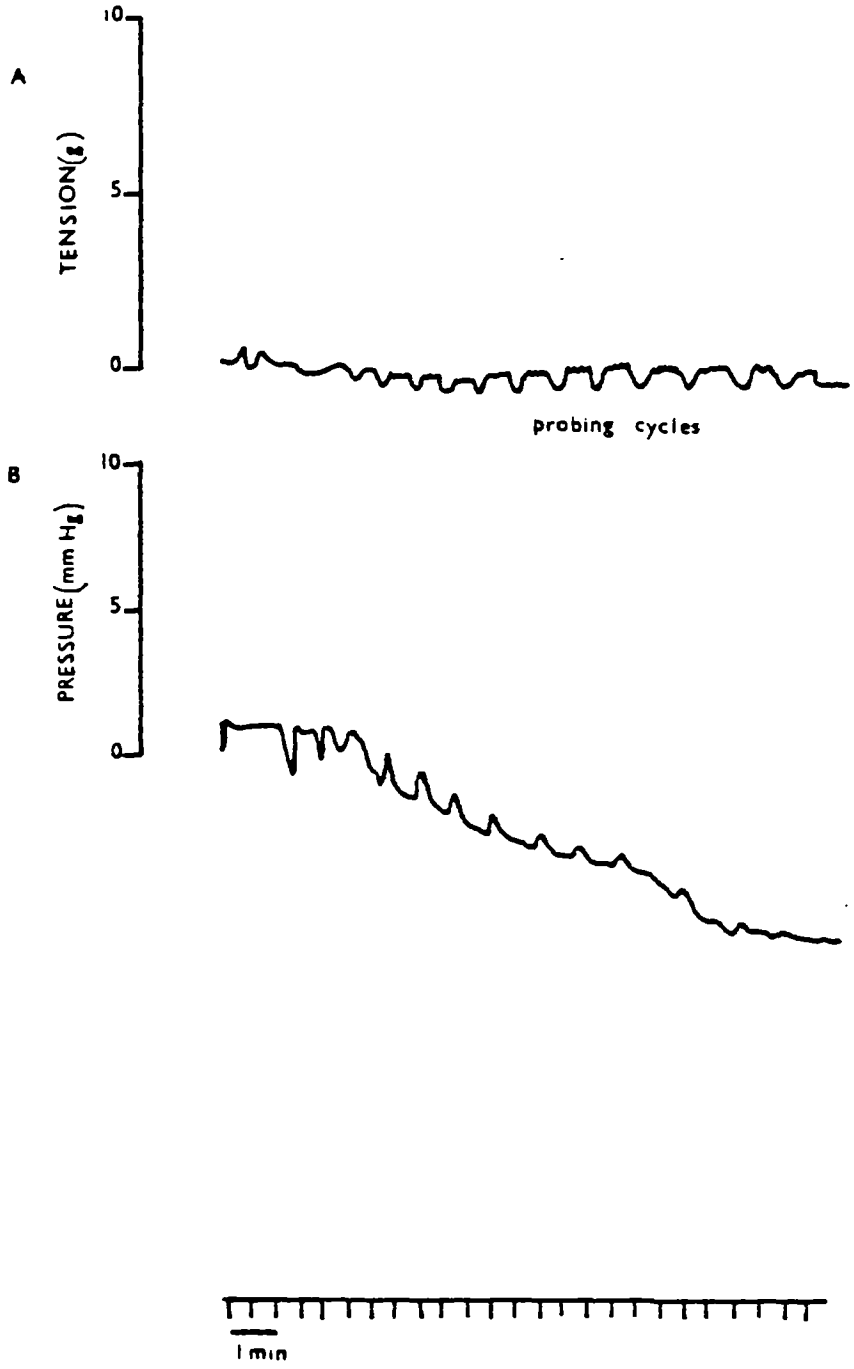


Figure 6.3. Lutraria. Recordings of burrowing activity in an individual showing a large number of probing cycles. A - using an isotonic myograph, upstroke represents movement into the sand. B - pressure changes in mantle cavity.

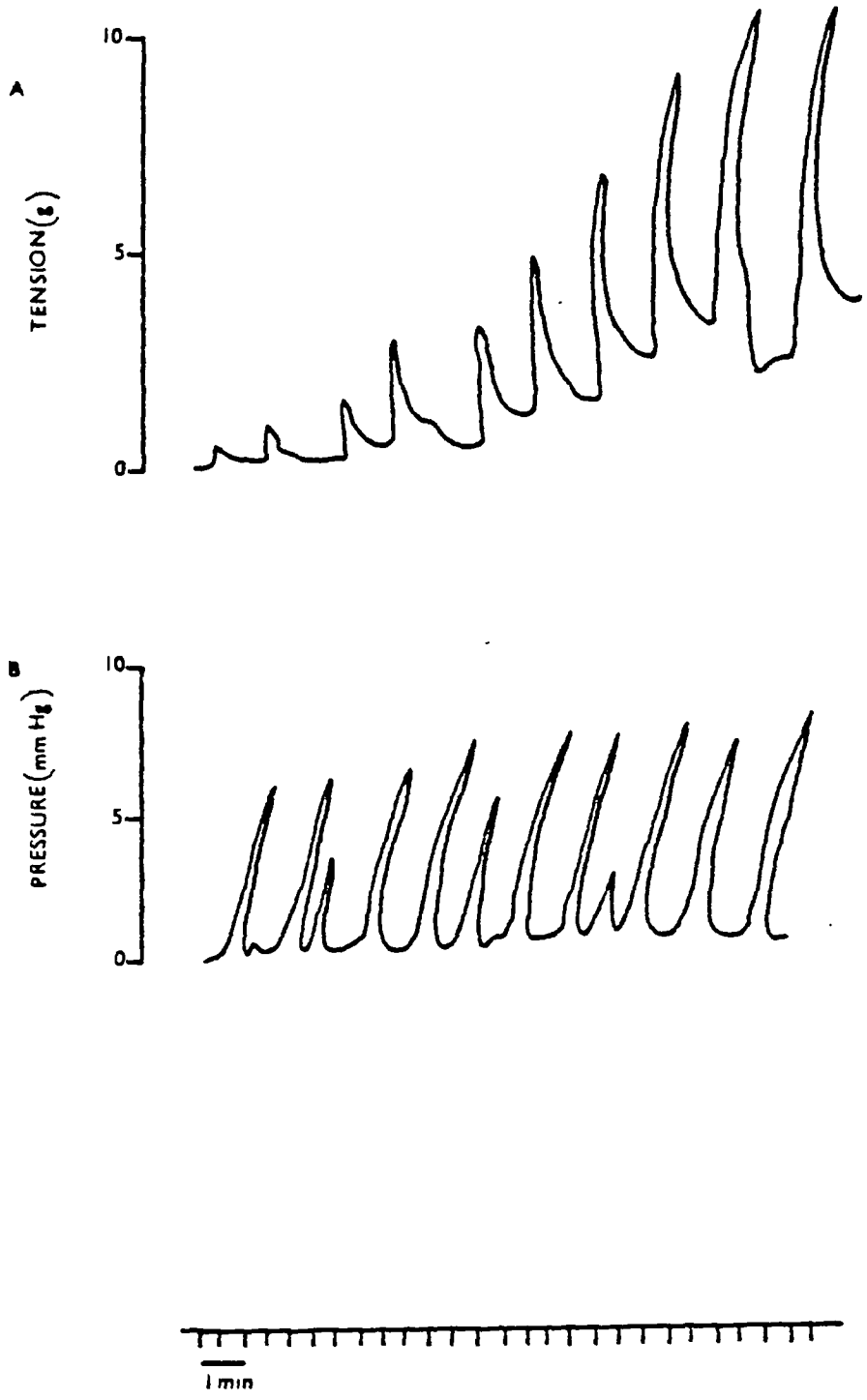
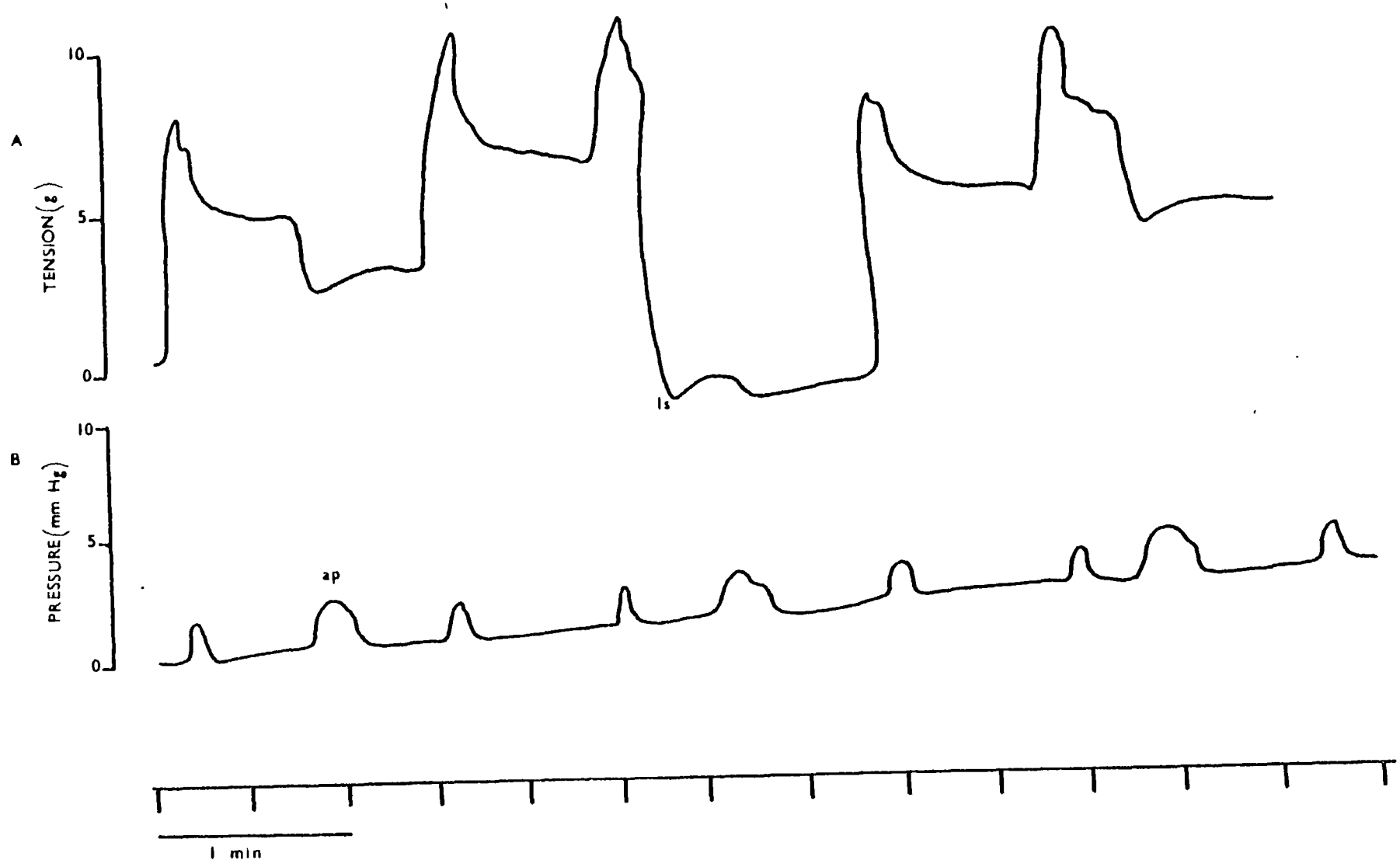


Figure 6.4. Lutraria. Recordings of burrowing activity in an individual approximately one-third buried. A - using an isotonic myograph, upstroke representing movement into the sediment. B - pressure changes in mantle cavity.

Figure 6.5. Lutraria. Recordings of the burrowing activity in an individual approximately half buried and showing two pressure peaks. A - using an isotonic myograph, upstroke representing movement into the sediment. B - pressure changes in the mantle cavity. (ap = additional pressure peak; l = string loosened).


A
10
5
0
TENSION (g)
ls
B
10
5
0
PRESSURE (mm Hg)
ap
1 min

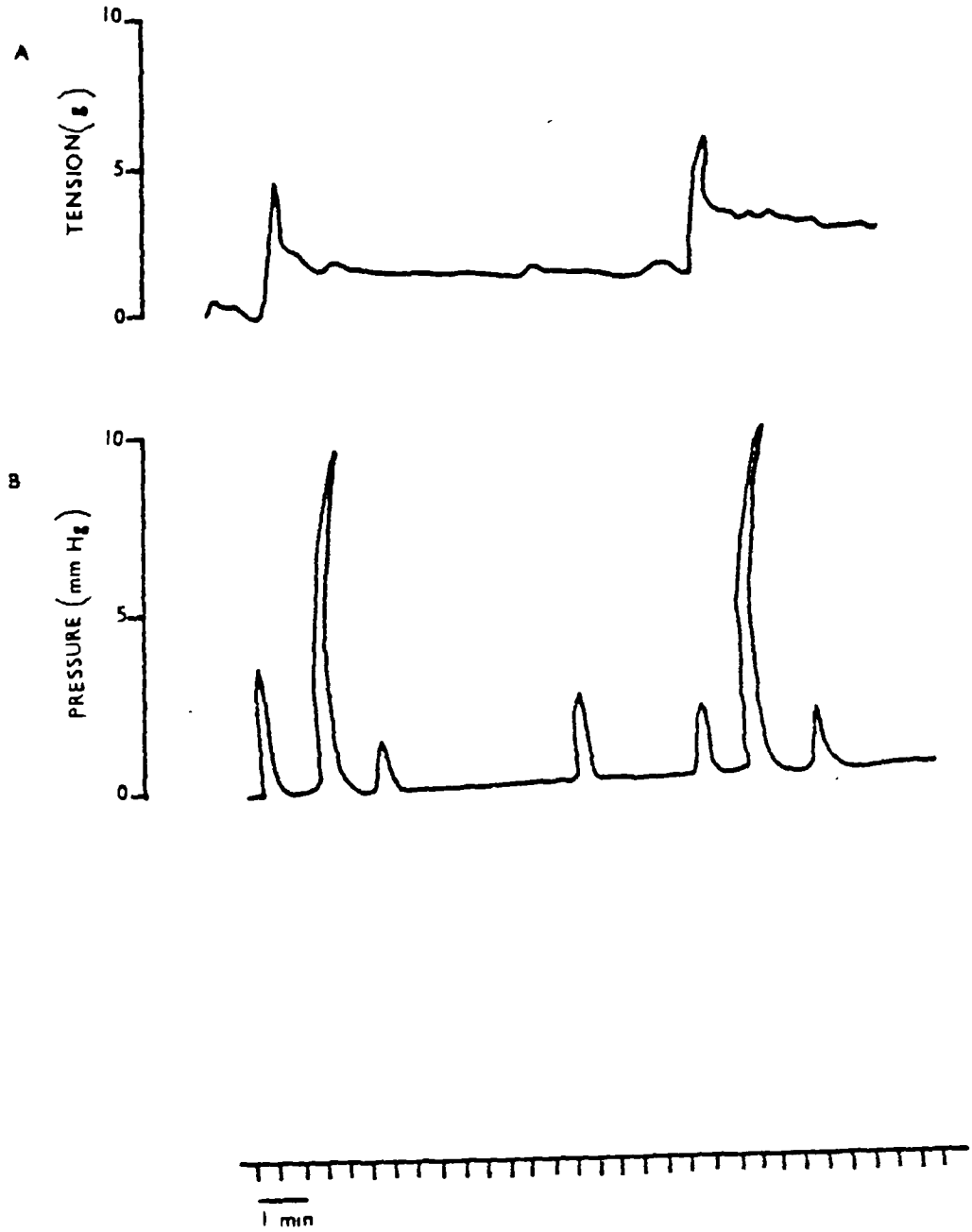


Figure 6.6. Lutraria. Recordings of burrowing activity in a half buried individual. A - using an isotonic myograph, upstroke representing movement into the sediment. B - pressure changes in mantle cavity.

From visual observations of animals 'free' burrowing and those showing some burrowing activity when linked to a physiograph, it is clear that Lutraria burrows in the normal bivalve pattern (Trueman, 1968a).

Six distinct stages were observed.

(i) The foot makes a major downward probe tending to raise the shell if penetration by the foot is not easily achieved.

(ii) The siphon aperture closes preventing the water from being expelled, particularly at adduction (iii). The foot continues to probe reaching its maximum extension. Dilation of the foot may commence.

(iii) Rapid adduction of the valves causes the water to be ejected from the mantle cavity via the pedal and fourth apertures. An increase in blood pressure produces maximum dilation of the foot. This causes a firm anchorage prior to retraction (iv).

(iv) Contraction, first of the anterior, and second of the posterior retractor muscles, results in the shell being pulled into the sand. The siphonal apertures re-open at or just before termination of retraction.

(v) Relaxation of the adductors, the valves open, pedal dilation and anchorage of the foot is maintained.

(vi) A 'static period' during which the shell does not move down through the sediment, but the foot is re-extended with repeated probings.

In the present study no successful recording was made of burrowing activity and combined with heart rate, and combined burrowing activity and valve movements, however, figure 6.1. illustrates probing cycles prior to the onset of digging cycles with the accompanying changes in pressure in the mantle cavity. About four probes per minute were recorded before the start of a digging cycle.

In figures 6.1. to 6.6. the myograph traces are read from left to right and an upstroke indicates movement into the sand. Increases in pressure in the mantle cavity are more marked during the digging cycles than during probing. An increase in pressure corresponding to adduction of the valves (stage (iii)) occurs immediately prior to the downward movement and this is followed by contraction of the retractor muscles (stage (iv)). A strong expulsion of water from the pedal and possibly fourth aperture was also recorded at stage (iii) when the surface of the sediment was obviously disturbed.

There is some degree of individual variation in the time taken for these movements. Thus, in figure 6.1., one digging cycle is 120 secs. in length while in figure 6.2. the length is 30 secs. increasing to 48 secs. High pressure is maintained for approximately 6 secs. in the 30 secs. cycle and approximately 30 secs. in the second cycle. Figure 6.3. illustrates the increase in probing as time increases, although in this particular case the individual moved around the tank rather than burrowing. Figure 6.4. shows other changes in mantle cavity pressure towards the end of the digging cycle in stage (v). These are additional peaks and are related to the opening of the valves. The siphons are closed and retracted, the foot (although not actually seen) also probably retracts at this stage. The resulting increase in pressure assists in the opening of the valves. This additional peak was not observed until the animals were partially buried. In figure 6.4. and 6.5. the individuals are approximately one third buried and in figure 6.6. the individual is approximately half buried and the peak is greater in amplitude. A similar activity was also described by Ansell and Trueman (1967) for Glycymeris glycymeris. In Glycymeris the ligament proved to be ineffective in opening the valves after more than one third of the shell had penetrated the substrate. Similarily

in Lutraria, retraction of siphon and foot assist a weak ligament in the opening of the valves. Stage (iv) in Lutraria results in an obvious rocking movement of the shell, however, secondary contractions of the pedal retractors as described by Trueman (1968b) for Mactra corallina were not recorded.

6.4. DISCUSSION

Lutraria lutraria, a member of the benthic macrofauna, leads a sheltered infaunal existence. After establishing itself in the sediment there appears to be little need for movement other than to accommodate growth and to possibly reorientate itself when disturbed by gales. Pohlo (1964) found in the mactrid Tresus nuttalli that there was a gradual change in mode of life during ontogeny with a progressive loss in burrowing ability in larger specimens. Unfortunately the very narrow size range of the Lutraria population precluded experimentation into possible changes in form and activity in different sized individuals.

Observations on Lutraria in the suction bin core suggest that the animal lies almost vertical in the sediment with siphons extended with the tips flush with the surface. The majority of the bivalves occupy a more-or-less similar vertical position when buried but a few e.g. Cochlodesma (Allen, 1958b) and some tellinid species (Holme, 1961) take up a horizontal position on one side. Holme (1961) found that members of the Tellinidae lie on the left side, 'in situ', and in the burrowing experiments if initially placed on the right side moves so that the right side becomes uppermost.

In the present study the tip of the siphon was not always visible in individuals that had reburied. A similar situation was reported for Mya arenaria (Pfitzenmeyer and Droebeck, 1967).

Glycymeris glycymeris (Ansell and Trueman (1967) burrows until it is a few centimeters below the surface, but when covered by fine sand, digging ceases and the animal raises itself in the sediment. Ansell (1962) suggests that the control of the depth of burial might be due to sensory impulses from proprioreceptors in the siphon wall. Nair and Ansell (1968) suggest also that termination of burrowing may result from increased resistance encountered by the foot when probing as the depth of sand increases. This may be the case in the conditions affecting the Lutraria experiment.

Trueman (1968b) found in species of Mactra that 'once a digging period has commenced, cycles normally continue until burial is complete for there appears to be little alternative to this behavioural pattern apart from cessation of digging'. In the case of many Lutraria attempts to reburrow were made but when the animals were unable to completely rebury themselves, digging ceased. Pohlo (1964) for T. nuttalli and Pfitzenmeyer and Droebeck (1967) for M. arenaria report similar results.

The general principals of burrowing are reviewed by Trueman (1968a) and Trueman and Ansell (1969). They find it is essential for the individual to obtain a firm anchorage in the substratum before movement into it can take place. Thus, the digging period (Ansell, 1962) comprises both a probing and a digging cycle (Trueman, Brand and Davis, 1966a). Both of these are repeated many times during a digging period.

Trueman (1967a) also discusses pedal anchorage and the factors affecting it. Pedal anchorage is achieved in different ways by different bivalves, e.g. dilation of the foot over a broad area as in

Tellina, bulbous swelling as in Ensis, or outward spreading of a cleft foot in Glycymeris. The rate of probing varies:- Ensis arcuatus 90 probes/min., Mercenaria mercenaria 16 probes/min., Mya arenaria 1 probe/min. In Lutraria the rate is 4-6 probes/min. and is in accordance with the form and habit to which these rates apply.

Lutraria, described in Chapter 2, has both anterior and posterior retractor muscles but no protractor muscle. The animal initially extends its laterally flattened foot through the pedal gape and into the sediment in order to erect the shell. The contraction of the transverse pedal muscles together with the relaxing of the retractors, causes extension of the foot. At the same time, contraction of the adductor muscles increases the internal hydrostatic pressure of the foot. Together, these result in the foot penetrating the substrate. Once the animal has established itself in the upright position, penetration becomes dependant also on shell shape and ornamentation. Sculpturing, such as ribs may enhance the ease in which the shell penetrates the substrate (Trueman, Brand and Davis, 1966b; Stanley, 1968).

The shell structure of Lutraria in relation to burrowing ability has been discussed in Chapter 2. The hinge is "fairly weak", although the hinge dentition itself is well developed. Increased water pressure within the mantle cavity, following the contraction of siphon and foot, in addition to the elastic properties of the ligament, ensure that the valves continue to open against the increasing resistance of the substrate as the depth of burial increases. The process is aided by the form of hinge mechanism and the posterior gape of the shell which permits a rocking motion of the valves and also by water forced out of the pedal opening.

Penetration is also aided by the anterio-posterior rocking of the shell, a habit more usually seen in tumid bivalves.

Trueman (1967a) found that in general the haemocoelic pressure of various bivalves was low during the probing activity while higher pressures were associated with adduction. Similar pressure differences are seen in Lutraria.

In Ensis, because of the extensive mantle fusion (Yonge, 1952) the pressure peaks in both pericardial and mantle cavities are of comparable duration and a pressure gradient does not occur between them (Trueman, 1967b). In Margaritifera margaritifera where the ventral margin of the mantle cavity is not fused, the pressure peak in the mantle cavity is less than that in the pericardial cavity (Trueman, 1968c). As Trueman (1966) states, the increase in pressure results in both pedal dilation and ejection of water from the ventral margin. The ejection of water is such that it loosens sand particles in the vicinity of the foot and produces a small cavity into which the animal can move. Stanley (1970) found that the ventral expulsion of water is strongest in species with fused mantle margins and concluded that mantle fusion led to improved burrowing ability and which was a major factor in post Paleozoic adaptive radiation. Earlier, Yonge (1948) had noted the greatly enlarged ventral margins in both Lutraria and Mya and suggested that probably when these were filled with blood they assisted the ligament in pushing the valves against the substrate.

In the present experiments the rate of burrowing was not determined by experimental means, however a few free burrowing individuals were seen to bury themselves within four hours. Pfitzenmeyer and Droebeck (1967) found that in Mya arenaria, which has a smaller foot in an animal of similar size, at fastest, took between four and eight hours to bury itself. Similarly, Pohlo (1964) found Tresus nuttalli, greater than 60mm in length took more than two hours to bury themselves.

Lutraria, unlike some other members of the Mactracea has little need to burrow rapidly. Ansell and Trevallion (1969) found the speed of burrowing movements of three intertidal molluscs on a tropical sandy beach (including Mactra olorina) were unequalled elsewhere. In comparison, M. corallina from Millport (14°C), the digging cycle took five seconds. A complete digging cycle occupied 1.5 seconds. They suggest that high temperatures (30°C) are possibly a prerequisite for the development of the rapid response. Stanley (1970) determined a burrowing rate index (BRI) for bivalves which give S. solidissima another rapid burrower (Ropes and Merrill, 1966) -,a BRI value of 4, Mactra fragilis BRI = 1 and Mya arenaria BRI = 0.2.

$$BRI = \frac{\sqrt[3]{\text{Mass (g)}}}{\text{Burrowing time}} \times 100$$

Although the index was not determined for Lutraria, it is likely, because of its convergent morphological similarities, to have a similar index to Mya arenaria.

Unlike Tellina, disturbance does not stimulate burrowing in Lutraria but merely results in the withdrawal of the siphons. The difference must presumably relate to the relatively calmer conditions in which Lutraria lives and the difference in feeding behaviour of the two animals.

Burrowing is the principal defence of infaunal animals against predators and the limitation of this activity by environmental factors is of interest, but unfortunately due to the partial success of the experiments involving burrowing activity no experiments on environmental effects were carried out.

Work by Savage (1976) and Pfitzenmeyer and Drobeck (1967) on Mercenaria mercenaria, Spisula solidissima and Mya arenaria shows that

thermal optima, upper levels of activity and burrowing rates were species specific, and that, whereas the burrowing of M. mercenaria was not severely impaired by conditions of reduced oxygen tension, that of S. solidissima was. Pfitzenmeyer and Drobeck (1967) also found that water temperature, size and sediment particle size were all important in the reburial activities.

The burrowing ability of Lutraria is adapted to its mode of life. Although actual burrowing rates were not obtained for individuals linked to recording instruments, observations of free burrowing animals suggest that the animal has retained the capability of burrowing, albeit slowly. The specimens used in the present study are from an aging population and older, larger individuals have slower burrowing rates than the younger, smaller ones. The observations suggest that at least some of the Lutraria disturbed after sampling could actively reburrow and divers using the suction bin corroborated this, when they found that Lutraria at the sample site had moved further into the sediment.

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APPENDIX I

APPENDIX I

The tables included in this appendix give the numerical values for the various analyses referred to in Chapter 4.

Tables I.1. - I.7. - Changes in shell weight (g) body (flesh weight) and the weights (g) of the five body components of a standard animal over a two year period (March 1979-March 1981) showing original and recalculated data, and the new intercept.

Tables I.8. - I.10. - Changes in the water content (%) of the body (flesh weight) and the five body components and the changes in condition index of the five body components over a two year period (March 1979-March 1981) showing original and recalculated data.

Tables I.11. - I.15. - Changes in the percentage biochemical composition of the five body components of a standard animal over a two year period (March 1979-March 1981).

Tables I.16. - I.21. - Changes, given as gramme weights, in the biochemical components (original and recalculated) over a two year period (March 1979-March 1981).

Tables I.22. - I.34. - Covariance analysis for flesh weight and the five body components (wet and dry).

TABLE I.1. Changes in dry shell weight (g) of a standard animal over a two year period (March 1979 - March 1981) showing original and recalculated data, and the new intercept. (Value of common slope = 2.29).

	DRY WEIGHT			
MONTHS	ORIG. VAL.	NEW INT.	RECAL. VAL.	CONF. LIMITS
MAR 1979	38.71	-0.808	37.74	1.55
APR	36.12	-0.826	36.21	1.45
MAY	37.55	-0.816	37.05	2.63
JUNE	35.92	-0.815	37.14	2.16
JULY	39.16	-0.794	38.97	1.57
AUG	41.09	-0.808	37.74	6.57
SEPT				
OCT	38.41	-0.825	36.29	4.61
NOV	37.48	-0.814	37.22	1.87
DEC				
JAN 1980	37.80	-0.802	38.26	3.78
FEB	31.17	-0.814	37.22	2.81
MAR	37.97	-0.789	39.43	3.40
APR	40.49	-0.775	40.72	4.05
MAY	38.57	-0.796	38.80	2.70
JUNE	42.00	-0.766	41.57	1.68
JULY	40.71	-0.782	40.07	2.85
AUG	42.30	-0.760	42.15	2.96
SEPT	43.92	-0.740	44.14	2.20
OCT	41.73	-0.766	41.57	2.50
NOV	39.89	-0.787	39.61	2.00
DEC	41.71	-0.757	42.44	2.42
JAN 1981	38.33	-0.777	40.53	3.44
FEB	41.67	-0.777	40.53	4.17
MAR	41.25	-0.767	41.47	2.89

TABLE I.2. Changes in body (flesh) weight (g) of a standard animal (wet and dry) over a two year period (March 1979-March 1981) showing original and recalculated data, and the new intercept. (Value of common slope = 2.551 (wet) and 2.528 (dry)).

	WET WEIGHT				DRY WEIGHT			
MONTHS	ORIG. VAL.	NEW INT.	RECAL. VAL.	CONF. LIMITS	ORIG. VAL.	NEW INT.	RECAL. VAL.	CONF. LIMITS
MAR 1979	62.65	-0.860	62.60	5.64	11.45	-1.573	11.48	1.37
APR	61.96	-0.865	61.89	5.58	11.42	-1.575	11.43	1.26
MAY	69.44	-0.820	68.64	2.78	13.09	-1.524	12.85	1.18
JUNE	75.53	-0.784	74.57	5.29	13.75	-1.500	13.58	1.24
JULY	77.05	-0.790	73.55	4.65	13.65	-1.500	13.58	1.23
AUG	80.65	-0.735	83.48	13.71	15.73	-1.414	16.56	2.83
SEPT								
OCT	106.54	-0.647	102.23	14.92	25.60	-1.232	25.18	4.61
NOV	93.82	-0.683	94.10	7.51	22.27	-1.283	22.39	1.78
DEC								
JAN 1980	82.58	-0.716	87.24	6.61	18.40	-1.335	19.86	2.02
FEB	73.84	-0.742	82.15	11.08	15.79	-1.365	18.53	3.31
MAR	81.90	-0.720	86.40	8.19	17.23	-1.372	18.24	3.10
APR	76.09	-0.780	75.26	7.61	14.59	-1.474	14.42	1.89
MAY	73.88	-0.785	74.40	5.91	14.46	-1.472	14.49	1.88
JUNE	89.35	-0.745	81.58	12.51	17.67	-1.429	16.00	2.30
JULY	79.03	-0.765	77.91	7.11	14.50	-1.475	14.39	1.89
AUG	75.85	-0.771	76.84	7.59	15.99	-1.436	15.74	2.40
SEPT	85.91	-0.724	85.62	6.01	15.38	-1.443	15.50	1.69
OCT	83.26	-0.731	84.25	5.83	13.35	-1.500	13.58	1.34
NOV	72.01	-0.813	69.76	8.64	14.16	-1.497	13.68	2.55
DEC	76.12	-0.774	76.31	6.85	14.61	-1.462	14.82	1.75
JAN 1981	73.34	-0.780	75.26	7.33	12.16	-1.517	13.06	0.73
FEB	70.97	-0.796	72.54	9.93	11.81	-1.507	13.37	1.77
MAR	68.19	-0.830	67.08	4.77	12.49	-1.545	12.25	1.25

TABLE I.3. Changes in gonad weight (g) of a standard animal (wet and dry) over a two year period (March 1979-March 1981) showing original and recalculated data, and the new intercept. (Value of common slope = 2.906 (wet) and 2.973 (dry).

	WET WEIGHT				DRY WEIGHT			
MONTHS	ORIG. VAL.	NEW INT.	RECAL. VAL.	CONF. LIMITS	ORIG. VAL.	NEW INT.	RECAL. VAL.	CONF. LIMITS
MAR 1979	10.17	-1.999	10.64	1.32	2.01	-2.78	2.08	0.31
APR	9.24	-2.055	9.35	1.48	1.96	-2.80	1.98	0.35
MAY	12.36	-1.944	12.08	1.61	2.69	-2.68	2.61	0.40
JUNE	10.70	-2.013	10.30	1.28	2.38	-2.73	2.32	0.28
JULY	12.72	-1.924	12.65	1.27	2.67	-2.67	2.67	0.28
AUG	12.23	-1.930	12.47	3.05	2.86	-2.60	3.13	0.91
SEPT								
OCT	20.86	-1.688	21.77	6.67	6.23	-2.27	6.70	2.30
NOV	19.36	-1.474	19.01	2.13	5.81	-2.34	5.70	0.75
DEC								
JAN 1980	16.23	-1.772	17.95	1.80	4.50	-2.39	5.08	0.63
FEB	13.47	-1.848	15.14	3.78	3.32	-2.50	3.94	0.70
MAR	14.77	-1.846	15.14	5.02	3.99	-2.48	4.13	1.00
APR	14.21	-1.877	14.09	2.27	3.51	-2.56	3.44	0.63
MAY	12.12	-1.945	12.05	2.09	2.90	-2.64	2.86	0.64
JUNE	17.91	-1.820	16.07	3.58	4.35	-2.46	4.33	2.09
JULY	11.29	-1.970	11.38	2.03	2.60	-2.68	2.61	0.57
AUG	9.70	-1.982	11.07	4.17	2.42	-2.69	2.55	0.51
SEPT	11.83	-1.954	11.80	1.66	2.94	-2.63	2.92	0.50
OCT	11.01	-1.969	11.40	1.54	2.38	-2.70	2.49	0.45
NOV	10.23	-2.036	9.77	2.15	2.62	-2.71	2.43	0.76
DEC	11.19	-1.963	11.56	1.68	2.78	-2.63	2.92	0.47
JAN 1981	12.63	-1.917	12.85	1.77	2.99	-2.64	2.86	0.42
FEB	10.23	-1.943	12.10	2.35	2.27	-2.68	2.61	0.88
MAR	12.58	-1.937	12.27	1.29	2.59	-2.70	2.49	0.49

TABLE I.4. Changes in adductor muscle weight (g) of a standard animal (wet and dry) over a two year period (March 1979-March 1981) showing original and recalculated data, and the new intercept. (Value of common slope = 2.400 (wet) and 2.571 (dry)).

	WET WEIGHT				DRY WEIGHT			
MONTHS	ORIG. VAL.	NEW INT.	RECAL. VAL.	CONF. LIMITS	ORIG. VAL.	NEW INT.	RECAL. VAL.	CONF. LIMITS
MAR 1979	2.85	-2.05	2.82	0.30	0.51	-2.93	0.57	0.12
APR	2.89	-2.04	2.88	0.34	0.65	-2.88	0.63	0.10
MAY	2.91	-2.03	2.95	0.43	0.66	-2.86	0.66	0.11
JUNE	3.49	-1.97	3.39	0.32	0.83	-2.77	0.81	0.11
JULY	3.39	-1.97	3.39	0.24	0.76	-2.79	0.77	0.07
AUG	4.04	-1.85	4.47	0.81	0.98	-2.63	1.11	0.28
SEPT								
OCT	5.90	-1.74	5.75	0.83	1.63	-2.48	1.59	0.31
NOV	5.72	-1.74	5.75	0.96	1.61	-2.47	1.61	0.15
DEC								
JAN 1980	5.05	-1.78	5.25	0.83	1.40	-2.51	1.48	0.20
FEB	4.16	-1.82	4.79	0.92	1.18	-2.54	1.36	0.28
MAR	4.58	-1.81	4.90	0.66	1.29	-2.55	1.35	0.30
APR	4.10	-1.84	4.47	0.56	1.34	-2.55	1.35	0.28
MAY	4.02	-1.89	4.07	0.80	1.07	-2.64	1.09	0.18
JUNE	5.00	-1.84	4.47	0.54	1.39	-2.58	1.24	0.25
JULY	4.50	-1.83	4.68	0.57	1.15	-2.60	1.19	0.18
AUG	4.37	-1.83	4.68	0.62	1.14	-2.63	1.14	0.18
SEPT	5.13	-1.79	5.13	0.83	1.29	-2.58	1.24	0.29
OCT	4.91	-1.81	4.90	0.74	1.04	-2.66	1.04	0.17
NOV	4.35	-1.87	4.27	0.58	1.13	-2.63	1.14	0.23
DEC	4.43	-1.85	4.47	0.42	1.17	-2.61	1.16	0.21
JAN 1981	3.82	-1.89	4.07	0.57	0.91	-2.69	0.97	0.12
FEB	3.02	-1.96	3.47	0.43	0.70	-2.75	0.84	0.16
MAR	3.39	-1.98	3.31	0.44	0.77	-2.80	0.76	0.15

TABLE I.5. Changes in siphon muscle weight (g) of a standard animal (wet and dry) over a two year period (March 1979–March 1981) showing original and recalculated data, and the new intercept. (Value of common slope = 2.208 (wet) and 2.290 (dry)).

	WET WEIGHT				DRY WEIGHT			
MONTHS	ORIG. VAL.	NEW INT.	RECAL. VAL.	CONF. LIMITS	ORIG. VAL.	NEW INT.	RECAL. VAL.	CONF. LIMITS
MAR 1979	30.37	-0.823	29.99	3.35	6.26	-1.592	6.22	0.70
APR	30.06	-0.820	30.20	3.01	6.18	-1.589	6.25	0.74
MAY	32.81	-0.787	32.58	1.00	6.73	-1.565	6.61	0.61
JUNE	35.58	-0.745	35.89	2.85	7.25	-1.522	7.30	0.65
JULY	34.51	-0.760	34.67	3.45	7.11	-1.532	7.13	0.85
AUG	40.01	-0.694	40.36	6.00	8.30	-1.461	8.40	1.33
SEPT								
OCT	48.26	-0.640	45.71	7.72	11.84	-1.343	11.00	2.25
NOV	42.64	-0.673	42.35	3.42	10.10	-1.377	10.19	0.91
DEC								
JAN 1980	37.15	-0.716	38.67	3.34	8.86	-1.418	9.28	0.97
FEB	32.34	-0.731	37.01	4.53	7.80	-1.427	9.08	1.25
MAR	34.91	-0.728	37.33	3.84	8.17	-1.440	8.81	1.47
APR	31.62	-0.806	31.16	3.48	6.85	-1.557	6.74	0.89
MAY	33.00	-0.778	33.24	3.96	7.14	-1.528	7.20	0.86
JUNE	36.93	-0.764	34.38	5.17	8.09	-1.511	7.49	1.29
JULY	36.18	-0.745	35.99	3.98	7.50	-1.512	7.46	0.90
AUG	35.21	-0.736	36.73	3.87	8.05	-1.465	8.32	1.53
SEPT	38.96	-0.707	39.14	3.90	7.82	-1.490	7.85	1.47
OCT	39.73	-0.692	40.51	2.78	6.99	-1.533	7.11	0.63
NOV	33.22	-0.786	32.66	4.32	7.21	-1.539	7.02	1.37
DEC	34.98	-0.755	35.05	3.50	7.35	-1.514	7.43	0.96
JAN 1981	30.74	-0.773	33.68	4.30	6.14	-1.560	6.69	0.98
FEB	33.77	-0.779	33.18	6.08	6.43	-1.539	7.02	1.16
MAR	30.11	-0.827	29.76	2.11	6.50	-1.578	6.41	0.58

TABLE I.6. Changes in 'other' tissue weight (g) of a standard animal (wet and dry) over a two year period (March 1979-March 1981) showing original and recalculated data, and the new intercept. (Value of common slope = 2.437 (wet) and 2.712 (dry).

	WET WEIGHT				DRY WEIGHT			
MONTHS	ORIG. VAL.	NEW INT.	RECAL. VAL.	CONF. LIMITS	ORIG. VAL.	NEW INT.	RECAL. VAL.	CONF. LIMITS
MAR 1979	14.81	-1.395	13.90	0.85	2.41	-2.500	2.11	0.30
APR	11.92	-1.464	11.86	0.83	2.01	-2.522	2.00	0.31
MAY	13.69	-1.409	13.46	0.82	2.36	-2.453	2.35	0.17
JUNE	14.20	-1.385	14.23	0.85	2.59	-2.412	2.59	0.28
JULY	13.90	-1.395	13.91	0.69	2.47	-2.430	2.48	0.23
AUG	14.69	-1.324	16.35	2.94	2.79	-2.330	3.12	0.70
SEPT								
OCT	27.18	-1.208	21.38	4.35	4.91	-2.146	4.76	1.08
NOV	19.38	-1.246	19.59	1.36	4.27	-2.189	4.31	0.38
DEC								
JAN 1980	15.54	-1.323	16.39	2.18	3.32	-2.264	3.63	0.60
FEB	14.41	-1.328	16.23	2.59	3.08	-2.264	3.63	0.80
MAR	15.41	-1.338	15.84	2.16	3.48	-2.278	3.55	0.70
APR	13.29	-1.416	13.24	1.20	2.34	-2.458	2.32	0.49
MAY	13.22	-1.413	13.34	1.59	2.71	-2.387	2.74	0.41
JUNE	15.34	-1.399	13.77	2.15	3.28	-2.366	2.87	0.56
JULY	13.84	-1.401	13.71	1.38	2.71	-2.394	2.69	0.38
AUG	14.42	-1.370	14.71	2.16	3.10	-2.328	3.13	0.56
SEPT	15.28	-1.348	15.48	1.22	3.07	-2.326	3.15	0.37
OCT	14.97	-1.358	15.14	1.05	2.50	-2.420	2.53	0.28
NOV	13.36	-1.419	13.15	1.47	2.75	-2.399	2.66	0.47
DEC	14.38	-1.376	14.53	1.44	3.01	-2.317	3.22	0.42
JAN 1981	12.70	-1.423	13.04	1.14	2.24	-2.452	2.35	0.29
FEB	12.17	-1.428	12.87	1.70	2.10	-2.432	2.47	0.38
MAR	12.04	-1.462	11.91	0.84	2.18	-2.500	2.13	0.22

TABLE I.7. Changes in digestive gland weight (g) of a standard animal (wet and dry) over a two year period (March 1979-March 1981) showing original and recalculated data, and the new intercept (Value of common slope = 1.985 (wet) and 2.180(dry)).

	WET WEIGHT				DRY WEIGHT			
MONTHS	ORIG. VAL.	NEW INT.	RECAL. VAL.	CONF. LIMITS	ORIG. VAL.	NEW INT.	RECAL. VAL.	CONF. LIMITS
MAR 1979								
APR	2.38	-1.686	2.40	0.26	0.52	-2.544	0.53	0.06
MAY	2.73	-1.647	2.63	0.35	0.59	-2.522	0.56	0.08
JUNE	2.86	-1.596	2.96	0.34	0.66	-2.450	0.66	0.08
JULY	2.67	-1.640	2.68	0.24	0.53	-2.541	0.54	0.05
AUG	3.44	-1.508	3.62	0.72	0.74	-.2366	0.80	0.19
SEPT								
OCT	3.52	-1.542	3.35	0.63	0.84	-2.392	0.76	0.13
NOV	2.11	-1.748	2.08	0.15	0.42	-2.652	0.42	0.03
DEC								
JAN 1980	1.47	-1.859	1.61	0.18	0.26	-2.810	0.29	0.05
FEB	1.40	-1.880	1.54	0.22	0.30	-2.764	0.32	0.05
MAR	1.68	-1.823	1.75	0.32	0.29	-2.770	0.32	0.08
APR	1.46	-1.902	1.46	0.18	0.27	-2.835	0.27	0.04
MAY	1.92	-1.774	1.96	0.23	0.41	-2.652	0.41	0.07
JUNE	2.06	-1.818	1.78	0.19	0.48	-2.652	0.41	0.05
JULY	1.96	-1.769	1.99	0.20	0.39	-2.665	0.40	0.07
AUG	1.85	-1.773	1.97	0.30	0.42	-2.625	0.44	0.09
SEPT	2.19	-1.723	2.21	0.15	0.46	-2.600	0.47	0.06
OCT	1.99	-1.768	1.99	0.16	0.39	-2.676	0.39	0.04
NOV	1.71	-1.849	1.65	0.15	0.36	-2.753	0.33	0.03
DEC	1.63	-1.860	1.62	0.15	0.31	-2.777	0.31	0.03
JAN 1981	1.31	-1.944	1.33	0.20	0.20	-2.871	0.25	0.04
FEB	1.40	-1.924	1.39	0.24	0.30	-2.821	0.28	0.05
MAR	1.88	-1.811	1.80	0.19	0.35	-2.744	0.34	0.05

TABLE I.8. Changes in the water content (%) of the body (flesh weight), and the water content (%) and condition index of siphon tissue over a two year period (March 1979-March 1981) showing original and recalculated data (see text).

MONTHS	FLESH TISSUE				SIPHON TISSUE			
	% WATER		CON. INDEX		% WATER		CON. INDEX	
	ORIG.	RECAL.	ORIG.	RECAL.	ORIG.	RECAL.	ORIG.	RECAL.
MAR 1979	81.73	81.70			79.39	79.25	54.67	54.18
APR	81.57	81.54			79.54	79.30	54.07	54.68
MAY	81.15	81.28			79.49	79.71	51.41	51.44
JUNE	81.80	82.11			79.63	79.66	52.73	53.76
JULY	82.28	81.54			79.39	79.43	52.09	52.50
AUG	80.50	80.16			79.19	79.19	52.89	50.72
SEP								
OCT	75.96	75.37			73.61	75.94	46.25	43.69
NOV	76.26	76.21			76.32	75.94	45.36	45.51
DEC								
JAN 1980	77.72	77.24			76.11	76.00	48.17	46.73
FEB	78.62	77.44			75.89	75.47	49.39	49.00
MAR	78.96	78.89			76.60	76.40	47.42	48.30
APR	80.82	80.84			78.34	78.37	46.95	46.74
MAY	80.43	80.52			78.37	78.34	49.38	49.69
JUNE	80.22	80.39			78.10	78.24	45.78	46.81
JULY	81.65	81.53			79.28	79.27	51.72	51.84
AUG	78.92	79.52			77.14	77.35	50.34	52.86
SEPT	82.10	81.90			79.93	79.43	50.85	50.65
OCT	83.97	83.88			82.41	82.44	52.36	52.36
NOV	80.34	80.39			78.93	78.51	50.91	51.32
DEC	80.81	80.58			78.99	78.80	50.31	50.13
JAN 1981	83.42	82.65			80.01	80.14	50.49	51.23
FEB	83.36	81.59			80.96	78.84	54.45	52.50
MAR	81.68	81.74			78.42	78.46	52.04	52.33

TABLE I.9. Changes in the water content (%) and condition index of gonad and adductor muscle tissue over a two year period (March 1979-March 1981) showing original and recalculated data (see text).

MONTHS	GONAD TISSUE				ADDUCTOR TISSUE			
	% WATER		CON. INDEX		% WATER		CON. INDEX	
	ORIG.	RECAL.	ORIG.	RECAL.	ORIG.	RECAL.	ORIG.	RECAL.
MAR 1979	80.24	80.45	17.55	18.12	82.11	79.79	4.45	4.97
APR	78.79	78.82	17.16	17.32	77.51	78.13	5.70	5.51
MAY	78.24	78.39	20.56	20.31	77.44	77.63	5.04	5.14
JUNE	77.75	77.48	17.31	17.08	76.22	76.11	6.04	5.96
JULY	79.01	78.90	19.56	19.66	77.52	77.29	5.57	5.67
AUG	76.62	74.90	18.18	18.90	75.85	75.17	6.22	6.70
SEP								
OCT	70.13	69.22	24.34	26.61	72.37	72.34	6.37	6.31
NOV	70.00	70.02	26.08	25.45	71.86	72.00	7.23	7.19
DEC								
JAN 1980	72.22	71.70	24.46	25.57	72.78	71.81	7.61	7.45
FEB	75.35	73.98	21.03	21.26	71.64	71.60	7.47	7.34
MAR	72.99	72.72	23.16	22.64	71.84	72.45	7.49	7.40
APR	75.28	75.59	24.06	23.86	67.32	69.80	9.18	9.36
MAY	76.07	76.27	20.06	19.74	73.39	73.22	7.40	7.52
JUNE	75.72	73.10	24.62	27.06	72.20	72.25	7.87	7.75
JULY	76.97	77.07	17.93	18.14	74.35	74.57	7.93	8.30
AUG	75.06	76.96	15.13	16.20	73.92	75.64	7.13	7.24
SEPT	75.15	75.25	19.12	18.84	74.85	75.83	8.39	8.00
OCT	78.36	78.16	17.83	18.34	78.82	78.76	7.79	7.66
NOV	74.34	75.13	18.50	17.76	74.06	73.30	7.98	8.33
DEC	75.16	74.74	19.03	19.70	73.59	74.05	8.01	7.83
JAN 1981	76.32	77.74	24.59	21.90	76.29	76.18	7.48	7.43
FEB	77.86	78.43	19.22	19.52	76.67	75.79	5.93	6.29
MAR	79.39	79.71	20.74	20.33	77.20	77.04	6.16	6.20

TABLE I.10. Changes in the water content (%) and condition index of 'other' tissue and digestive gland over a two year period (March 1979-March 1981) showing original and recalculated data (see text).

MONTHS	OTHER TISSUE				DIGESTIVE GLAND TISSUE			
	% WATER		CON. INDEX		% WATER		CON. INDEX	
	ORIG.	RECAL.	ORIG.	RECAL.	ORIG.	RECAL.	ORIG.	RECAL.
MAR 1979	83.73	84.82	21.05	18.38				
APR	83.14	83.14	17.60	17.50	78.15	77.92	4.55	4.64
MAY	80.35	82.54	18.03	18.29	78.39	78.71	4.51	4.36
JUNE	81.77	81.80	18.84	19.07	76.92	77.70	4.81	4.86
JULY	82.23	82.17	18.10	18.26	80.15	79.85	3.88	3.98
AUG	81.01	80.92	17.74	18.84	78.50	77.90	4.70	4.80
SEP								
OCT	81.94	77.74	19.17	18.90	76.14	77.31	3.28	3.02
NOV	77.97	78.00	19.17	19.25	80.01	79.80	1.89	1.88
DEC								
JAN 1980	78.64	77.85	18.05	18.28	82.32	81.99	1.41	1.46
FEB	78.63	77.63	19.51	19.59	78.58	79.22	1.90	1.73
MAR	77.42	77.59	20.20	19.46	82.74	81.71	1.68	1.75
APR	82.39	82.48	16.04	16.10	81.51	81.51	1.85	1.87
MAY	79.50	79.46	18.74	18.91	78.65	79.08	2.84	2.83
JUNE	78.62	79.16	18.56	17.94	76.70	76.96	2.72	2.57
JULY	80.42	80.38	18.69	18.69	80.11	79.90	2.71	2.78
AUG	78.50	78.72	19.39	19.89	77.23	77.66	2.63	2.80
SEPT	79.91	79.65	19.96	20.32	79.00	78.73	2.99	3.03
OCT	83.30	83.29	18.73	18.63	80.41	80.40	2.92	2.87
NOV	79.41	79.77	19.42	19.44	79.24	80.00	2.54	2.41
DEC	79.07	77.84	20.60	21.73	80.99	80.86	2.12	2.09
JAN 1981	82.35	81.98	18.42	17.99	81.68	81.20	1.97	1.91
FEB	82.75	80.81	17.78	18.47	78.58	79.86	2.54	2.09
MAR	81.90	82.11	17.45	17.39	81.51	81.11	2.80	2.78

TABLE I.11. Changes in the percentage biochemical compositon of the gonad of a standard animal over a two year period (March 1979-March 1981).

MONTHS	% AND SD BIOCHEMICAL COMPONENTS							
	% PROT.	SD	% CARB.	SD	% LIPID	SD	% ASH	SD
MAR 1979	50.57	8.55	15.75	4.40	11.48	2.70		
APR	54.11	5.19	17.25	2.63	10.59	1.95		
MAY	63.23	3.77	9.15	1.44	13.13	3.27		
JUNE								
JULY	60.29	6.25	8.91	0.65	8.59	0.93		
AUG	38.19	0.51	33.52	2.33	8.85	1.36	7.29	0.49
SEPT	35.33	7.10	41.74	2.92	7.78	1.48	5.67	0.28
OCT	37.15	4.42	34.68	4.94	5.92	0.56	4.54	0.41
NOV	41.62	2.33	41.21	2.19	6.47	0.39	4.54	0.21
DEC								
JAN 1980	35.63	3.69	53.79	3.68	10.82	0.26	5.24	0.47
FEB	34.91	3.85	30.31	2.73	10.21	2.17	6.85	1.96
MAR	46.99	1.65	26.85	5.62	6.87	2.27	7.54	0.87
APR	49.97	3.41	28.88	2.98	10.02	0.98	6.82	0.86
MAY	52.90	7.22	23.34	3.68	3.51	0.87	7.35	0.75
JUNE	46.96	5.69	30.14	4.13	4.70	0.99	7.99	1.15
JULY	38.91	3.06	27.90	3.24	2.77	0.97	6.41	0.66
AUG	50.23	4.89	26.32	8.14	5.96	1.36	8.13	1.05
SEPT	39.84	4.24	34.74	5.50	7.43	1.28	6.49	0.55
OCT	30.39	2.62	26.00	5.42	7.91	1.10	6.41	1.38
NOV	48.00	2.27	27.75	4.01	9.36	1.25	7.63	0.59
DEC	41.12	5.70	38.66	2.27	8.07	2.13	7.13	0.76
JAN 1981	42.99	2.50	15.06	3.27	6.61	1.25	7.01	0.22
FEB	49.44	3.43	21.24	2.25	7.25	1.50	8.83	0.40
MAR	50.85	5.34	13.12	2.10	5.45	0.96	10.33	0.74

TABLE I.12. Changes in the percentage biochemical composition of the adductor muscle tissue of a standard animal over a two year period (March 1979-March 1981).

	% AND SD BIOCHEMICAL COMPONENTS							
MONTHS	% PROT.	SD	% CARB.	SD	% LIPID	SD	% ASH	SD
MAR 1979	75.36	5.87	16.60	3.44	5.72	0.69		
APR	67.20	3.95	13.70	1.53	1.23	0.81		
MAY	82.90	5.47	9.91	1.20	4.02	0.28		
JUNE								
JULY	76.87	5.46	10.87	1.42	5.81	1.30		
AUG	53.76	2.27	25.16	2.56	4.31	0.98	7.06	0.74
SEPT	55.65	5.59	37.00	3.44	5.59	1.09	5.82	0.28
OCT	57.46	7.22	31.63	5.76	3.05	1.22	4.50	0.17
NOV	56.52	9.60	36.26	2.23	4.99	0.71	4.45	0.23
DEC								
JAN 1980	48.01	4.77	49.94	4.16	6.54	0.62	4.50	0.28
FEB	51.47	5.37	40.64	3.15	4.21	0.46	5.20	0.61
MAR	52.58	2.11	26.37	3.02	3.03	0.67	5.24	0.49
APR	57.58	8.78	37.42	5.00	3.03	0.38	5.65	0.53
MAY	58.46	3.22	27.40	3.56	1.31	0.80	6.10	0.31
JUNE	57.34	3.23	42.74	7.97	1.50	0.15	7.59	0.90
JULY	52.92	4.23	25.95	2.95	1.42	0.24	5.75	0.36
AUG	62.94	4.04	29.00	5.18	2.12	0.79	6.84	0.70
SEPT	51.77	10.99	34.32	3.93	4.71	1.84	6.33	0.58
OCT	63.20	4.50	28.41	6.17	4.53	2.70	4.83	0.37
NOV	62.25	2.98	36.02	4.99	5.25	1.36	7.63	1.45
DEC	58.01	8.98	29.53	2.54	8.50	0.86	6.59	1.46
JAN 1981	59.35	4.54	23.69	6.19	4.13	1.04	6.35	0.61
FEB	59.44	6.58	23.84	5.81	3.43	0.67	8.04	0.34
MAR	67.37	4.97	20.86	4.55	1.16	0.83	9.02	2.07

TABLE I.13. Changes in the percentage biochemical composition of the siphon of a standard animal over a two year period (March 1979-March 1981).

MONTHS	% AND SD BIOCHEMICAL COMPONENTS							
	% PROT.	SD	% CARB.	SD	% LIPID	SD	% ASH	SD
MAR 1979	75.92	5.87	7.88	1.65	3.32	0.96		
APR	70.56	9.53	5.63	1.80	3.18	0.88		
MAY	79.53	3.59	8.76	1.94	5.16	1.38		
JUNE								
JULY	76.04	6.22	5.36	0.81	4.19	1.30		
AUG	61.74	5.60	17.37	3.00	4.28	1.34	16.69	5.71
SEPT	52.20	7.72	23.03	3.21	5.69	0.48	11.24	1.52
OCT	64.84	9.06	20.53	6.09	2.92	0.57	8.90	0.38
NOV	57.29	9.34	19.70	4.00	5.22	0.60	9.82	0.92
DEC								
JAN 1980	55.94	2.63	32.53	5.95	5.99	3.00	10.78	2.19
FEB	53.30	8.65	24.50	2.73	7.04	0.82	8.36	2.02
MAR	58.54	2.52	13.86	3.80	5.37	1.00	8.50	0.99
APR	66.28	7.31	21.95	2.10	3.93	0.79	9.39	1.76
MAY	64.44	3.38	22.27	1.30	1.54	0.56	8.91	1.52
JUNE	65.44	9.86	29.21	4.55	2.16	1.40	8.41	0.95
JULY	60.82	1.92	14.26	2.87	1.49	0.09	8.61	0.59
AUG	77.76	8.96	16.61	2.88	2.95	1.01	8.35	1.09
SEPT	72.69	8.20	19.16	3.60	6.32	1.92	7.64	0.81
OCT	58.69	6.20	19.17	3.57	6.87	1.28	6.62	0.24
NOV	71.25	4.15	20.10	4.33	4.67	0.31	8.25	0.51
DEC	64.97	3.62	19.64	2.30	6.35	1.60	7.69	0.18
JAN 1981	55.46	5.84	14.63	7.35	4.37	0.75	7.46	0.50
FEB	60.78	3.96	14.51	3.43	4.43	0.50	9.08	0.75
MAR	69.13	3.64	8.28	4.30	3.22	1.40	9.35	1.56

TABLE I.14. Changes in the percentage biochemical composition of 'other' tissue of a standard animal over a two year period (March 1979-March 1981).

MONTHS	% AND SD BIOCHEMICAL COMPONENTS							
	% PROT.	SD	% CARB.	SD	% LIPID	SD	% ASH	SD
MAR 1979	52.19	3.59	10.50	1.30	8.18	0.43		
APR	53.18	5.95	13.30	5.00	7.02	0.68		
MAY	53.36	6.73	11.05	3.68	8.08	0.72		
JUNE								
JULY	56.41	6.45	7.68	0.94	7.69	1.04		
AUG	43.10	2.13	20.88	2.94	5.53	0.79	21.99	5.20
SEPT	38.54	6.44	36.55	7.05	8.69	1.50	10.56	0.93
OCT	47.19	3.43	27.89	6.28	5.84	0.94	7.98	1.66
NOV	51.06	2.38	32.22	1.72	7.10	1.20	8.32	0.97
DEC								
JAN 1980	44.27	5.15	45.00	4.22	4.98	0.37	8.96	0.63
FEB	31.92	3.17	24.58	3.10	8.10	1.15	11.45	3.10
MAR	42.86	3.29	24.69	3.34	6.93	2.80	14.90	2.41
APR	49.24	3.79	27.03	3.11	5.99	2.20	10.33	0.84
MAY	46.50	3.20	24.12	3.56	3.26	1.00	13.04	1.58
JUNE	50.58	4.81	28.39	3.10	5.67	1.21	12.92	1.49
JULY	46.53	4.30	22.26	3.89	3.71	0.72	11.11	1.19
AUG	50.47	1.29	14.27	5.92	6.39	1.31	13.37	2.04
SEPT	49.19	4.36	22.63	5.21	9.03	0.28	9.78	1.92
OCT	48.06	2.62	21.12	4.00	8.29	0.09	10.14	1.16
NOV	45.75	4.88	22.30	3.50	7.76	0.49	15.03	0.52
DEC	45.09	3.16	24.23	1.92	6.83	0.98	11.33	0.77
JAN 1981	40.13	3.18	14.05	2.40	5.75	0.14	12.10	1.48
FEB	47.22	2.08	20.62	4.10	5.25	0.63	14.03	0.95
MAR	50.63	3.58	11.40	3.00	4.42	1.08	16.61	0.65

TABLE I.15. Changes in the percentage biochemical composition of the digestive gland of a standard animal over a two year period (March 1979-March 1981).

MONTHS	% AND SD BIOCHEMICAL COMPONENTS							
	% PROT.	SD	% CARB.	SD	% LIPID	SD	% ASH	SD
MAR 1979								
APR	40.30	3.83	7.60	4.00	11.53	1.69		
MAY	54.98	4.20	6.12	1.50	16.28	1.54		
JUNE								
JULY	58.85	2.09	3.34	0.27	12.72	1.50		
AUG	58.03	2.80	19.80	5.27	14.12	1.40	13.44	6.20
SEPT	52.30	5.73	16.29	3.19	17.80	2.22	11.77	0.88
OCT	51.89	3.70	8.66	5.31	14.08	1.72	9.92	1.78
NOV	65.62	4.11	8.47	1.64	12.07	1.37	10.29	1.03
DEC								
JAN 1980	62.56	4.84	15.70	0.62	13.84	1.63	10.95	0.92
FEB	44.12	14.28	16.13	1.86	12.98	1.19	9.33	0.57
MAR	61.22	4.35	10.56	1.79	6.77	2.00	10.19	0.55
APR	61.21	1.38	11.88	1.24	8.82	0.98	8.68	1.55
MAY	40.64	5.97	15.36	1.71	4.56	0.64	8.54	0.61
JUNE	53.54	2.53	11.86	2.19	8.32	2.32	11.10	0.56
JULY	42.31	2.65	8.21	2.50	7.95	1.47	5.48	1.31
AUG	48.11	3.67	10.18	4.53	8.77	0.75	10.51	0.84
SEPT	51.61	5.93	8.34	4.25	8.15	1.21	13.79	3.79
OCT	40.52	4.50	18.52	6.67	10.35	0.99	8.77	0.76
NOV	45.00	9.51	14.13	1.81	9.39	0.47	12.09	2.88
DEC	46.83	3.24	18.53	2.27	8.83	1.25	16.70	2.50
JAN 1981	51.04	3.18	16.07	4.90	6.10	0.14	7.19	0.84
FEB	46.33	6.90	10.99	2.57	5.82	0.59	13.19	0.65
MAR	40.07	3.29	10.81	0.44	7.22	1.12	11.61	1.99

TABLE I.16. Changes, given as gramme weights, in the biochemical components (original and recalculated) of gonad tissue over a two year period (March 1979-March 1981).

	g. DRY WT. PROTEIN		g. DRY WT. CARB.		g. DRY WT. LIPID		g. DRY WT. ASH	
MONTHS	ORIG.	RECAL.	ORIG.	RECAL.	ORIG.	RECAL.	ORIG.	RECAL.
MAR 1979	1.02	1.05	0.32	0.33	0.22	0.24		
APR	1.06	1.07	0.34	0.34	0.21	0.21		
MAY	1.71	1.65	0.25	0.24	0.35	0.34		
JUNE								
JULY	1.61	1.61	0.24	0.24	0.23	0.23		
AUG	1.09	1.20	0.96	1.05	0.25	0.28	0.21	0.23
SEPT								
OCT	2.31	2.49	2.16	2.32	0.37	0.40	0.28	0.30
NOV	2.42	2.37	2.39	2.35	0.38	0.37	0.26	0.26
DEC								
JAN 1980	1.60	1.81	2.42	2.73	0.49	0.55	0.24	0.27
FEB	1.16	1.38	1.01	1.19	0.34	0.40	0.23	0.27
MAR	1.87	1.94	1.07	1.11	0.27	0.28	0.30	0.31
APR	1.75	1.72	1.01	0.99	0.35	0.34	0.24	0.23
MAY	1.53	1.51	0.68	0.67	0.10	0.10	0.21	0.21
JUNE	2.04	2.03	1.31	1.31	0.20	0.20	0.35	0.35
JULY	1.04	1.02	0.75	0.73	0.07	0.07	0.17	0.17
AUG	1.22	1.28	0.64	0.67	0.14	0.15	0.20	0.21
SEPT	1.17	1.16	1.02	1.01	0.22	0.22	0.19	0.19
OCT	0.72	0.76	0.53	0.65	0.19	0.20	0.15	0.16
NOV	1.26	1.17	0.73	0.67	0.21	0.23	0.20	0.19
DEC	1.14	1.20	1.07	1.13	0.22	0.24	0.20	0.21
JAN 1981	1.29	1.23	0.45	0.43	0.20	0.19	0.20	0.20
FEB	1.12	1.29	0.48	0.55	0.16	0.19	0.20	0.23
MAR	1.32	1.27	0.34	0.33	0.14	0.14	0.27	0.26

TABLE I.17. Changes, given as gramme weights, in the biochemical components (original and recalculated) of adductor muscle tissue over a two year period (March 1979-March 1981).

	g. DRY WT. PROTEIN		g. DRY WT. CARB.		g. DRY WT. LIPID		g. DRY WT. ASH	
MONTHS	ORIG.	RECAL.	ORIG.	RECAL.	ORIG.	RECAL.	ORIG.	RECAL.
MAR 1979	0.38	0.43	0.085	0.095	0.029	0.033		
APR	0.44	0.42	0.089	0.086	0.008	0.008		
MAY	0.55	0.55	0.065	0.065	0.026	0.027		
JUNE								
JULY	0.58	0.59	0.083	0.084	0.044	0.045		
AUG	0.53	0.60	0.25	0.28	0.042	0.045	0.069	0.078
SEPT								
OCT	0.94	0.91	0.52	0.50	0.05	0.048	0.073	0.072
NOV	0.91	0.91	0.58	0.58	0.08	0.08	0.071	0.072
DEC								
JAN 1980	0.67	0.71	0.70	0.74	0.092	0.097	0.063	0.066
FEB	0.61	0.70	0.48	0.55	0.05	0.06	0.061	0.071
MAR	0.68	0.71	0.34	0.36	0.039	0.041	0.068	0.071
APR	0.77	0.78	0.50	0.51	0.041	0.041	0.076	0.076
MAY	0.63	0.64	0.29	0.30	0.014	0.014	0.065	0.066
JUNE	0.80	0.71	0.59	0.53	0.021	0.019	0.105	0.099
JULY	0.61	0.63	0.30	0.31	0.016	0.017	0.066	0.068
AUG	0.72	0.72	0.33	0.33	0.024	0.024	0.078	0.078
SEPT	0.67	0.64	0.44	0.43	0.061	0.058	0.082	0.078
OCT	0.66	0.66	0.30	0.30	0.047	0.047	0.050	0.050
NOV	0.70	0.71	0.41	0.41	0.059	0.059	0.086	0.087
DEC	0.68	0.67	0.35	0.34	0.099	0.099	0.077	0.076
JAN 1981	0.54	0.58	0.22	0.23	0.038	0.04	0.058	0.062
FEB	0.42	0.50	0.17	0.20	0.024	0.029	0.056	0.068
MAR	0.52	0.51	0.16	0.16	0.009	0.009	0.069	0.069

TABLE I.18. Changes, given as gramme weights, in the biochemical components (original and recalculated) of siphon over a two year period (March 1979-March 1981).

	g. DRY WT. PROTEIN		g. DRY WT. CARB.		g. DRY WT. LIPID		g. DRY WT. ASH	
MONTHS	ORIG.	RECAL.	ORIG.	RECAL.	ORIG.	RECAL.	ORIG.	RECAL.
MAR 1979	4.75	4.72	0.49	0.49	0.21	0.21		
APR	4.40	4.41	0.35	0.35	0.20	0.20		
MAY	5.35	5.26	0.59	0.58	0.35	0.34		
JUNE								
JULY	5.40	5.42	0.38	0.38	0.29	0.30		
AUG	5.14	5.19	1.45	1.46	0.36	0.36	1.39	1.40
SEPT								
OCT	7.68	7.13	2.43	2.26	0.35	0.32	1.05	0.98
NOV	5.79	5.84	1.99	2.01	0.53	0.53	0.99	1.00
DEC								
JAN 1980	4.96	5.19	2.88	3.01	0.53	0.56	0.96	1.00
FEB	4.16	4.84	1.92	2.22	0.55	0.64	0.65	0.76
MAR	4.78	5.16	1.13	1.22	0.44	0.47	0.69	0.75
APR	4.54	4.47	1.50	1.48	0.27	0.26	0.64	0.63
MAY	4.60	4.63	1.59	1.60	0.11	0.11	0.64	0.64
JUNE	5.29	4.90	2.36	2.19	0.17	0.16	0.68	0.63
JULY	4.56	4.53	1.07	1.06	0.11	0.11	0.66	0.64
AUG	6.26	6.47	1.34	1.38	0.24	0.25	0.67	0.69
SEPT	5.68	5.68	1.49	1.49	0.49	0.49	0.60	0.60
OCT	4.10	4.17	1.34	1.36	0.48	0.49	0.46	0.47
NOV	5.13	5.00	1.45	1.41	0.34	0.33	0.59	0.58
DEC	4.78	4.83	1.44	1.46	0.47	0.47	0.57	0.57
JAN 1981	3.41	3.71	0.90	0.98	0.27	0.29	0.46	0.50
FEB	3.91	4.27	0.93	1.02	0.28	0.31	0.48	0.64
MAR	4.49	4.43	0.54	0.53	0.21	0.21	0.61	0.60

TABLE I.19. Changes, given as gramme weights, in the biochemical components (original and recalculated) of 'other' tissue over a two year period (March 1979-March 1981).

	g. DRY WT. PROTEIN		g. DRY WT. CARB.		g. DRY WT. LIPID		g. DRY WT. ASH	
MONTHS	ORIG.	RECAL.	ORIG.	RECAL.	ORIG.	RECAL.	ORIG.	RECAL.
MAR 1979	1.25	1.10	0.25	0.22	0.20	0.17		
APR	1.06	1.06	0.27	0.27	0.17	0.17		
MAY	1.26	1.26	0.26	0.26	0.19	0.19		
JUNE								
JULY	1.40	1.40	0.19	0.19	0.19	0.19		
AUG	1.07	1.34	0.58	0.65	0.15	0.17	0.61	0.69
SEPT								
OCT	2.37	2.25	1.40	1.33	0.29	0.28	0.39	0.38
NOV	2.18	2.20	1.38	1.39	0.30	0.31	0.36	0.36
DEC								
JAN 1980	1.47	1.61	1.49	1.63	0.17	0.18	0.30	0.33
FEB	0.98	1.15	0.76	0.89	0.25	0.29	0.35	0.42
MAR	1.49	1.52	0.85	0.88	0.24	0.25	0.52	0.53
APR	1.15	1.15	0.63	0.63	0.15	0.15	0.24	0.24
MAY	1.26	1.27	0.65	0.66	0.08	0.09	0.35	0.36
JUNE	1.76	1.45	0.93	0.81	0.27	0.16	0.42	0.37
JULY	1.26	1.25	0.60	0.60	0.10	0.10	0.30	0.30
AUG	1.56	1.58	0.44	0.45	0.20	0.20	0.41	0.42
SEPT	1.51	1.54	0.69	0.71	0.28	0.28	0.30	0.31
OCT	1.20	1.22	0.53	0.53	0.21	0.21	0.25	0.26
NOV	1.26	1.22	0.61	0.59	0.25	0.21	0.41	0.40
DEC	1.35	1.45	0.73	0.78	0.21	0.22	0.34	0.36
JAN 1981	0.90	0.94	0.31	0.33	0.13	0.14	0.27	0.28
FEB	0.99	1.17	0.43	0.51	0.11	0.13	0.29	0.35
MAR	1.10	1.08	0.25	0.24	0.096	0.094	0.36	0.35

TABLE I.20. Changes, given as gramme weights, in the biochemical components (original and recalculated) of digestive gland over a two year period (March 1979-March 1981).

	g. DRY WT. PROTEIN		g. DRY WT. CARB.		g. DRY WT. LIPID		g. DRY WT. ASH	
MONTHS	ORIG.	RECAL.	ORIG.	RECAL.	ORIG.	RECAL.	ORIG.	RECAL.
MAR 1979								
APR	0.21	0.21	0.04	0.04	0.06	0.06		
MAY	0.32	0.31	0.036	0.034	0.096	0.091		
JUNE								
JULY	0.32	0.32	0.02	0.02	0.067	0.067		
AUG	0.43	0.46	0.15	0.16	0.10	0.11	0.099	0.108
SEPT								
OCT	0.43	0.39	0.073	0.066	0.12	0.11	0.083	0.075
NOV	0.28	0.28	0.04	0.04	0.051	0.051	0.043	0.043
DEC								
JAN 1980	0.16	0.18	0.041	0.046	0.036	0.040	0.028	0.032
FEB	0.13	0.14	0.048	0.052	0.039	0.042	0.028	0.030
MAR	0.18	0.20	0.03	0.033	0.020	0.022	0.030	0.033
APR	0.17	0.17	0.032	0.032	0.024	0.024	0.023	0.023
MAY	0.17	0.17	0.063	0.063	0.019	0.019	0.035	0.035
JUNE	0.26	0.22	0.057	0.049	0.04	0.034	0.053	0.046
JULY	0.17	0.17	0.032	0.032	0.031	0.031	0.021	0.021
AUG	0.20	0.21	0.043	0.044	0.037	0.039	0.044	0.046
SEPT	0.24	0.24	0.038	0.038	0.037	0.037	0.063	0.063
OCT	0.16	0.16	0.072	0.072	0.04	0.04	0.034	0.034
NOV	0.16	0.15	0.051	0.047	0.034	0.031	0.044	0.040
DEC	0.15	0.15	0.057	0.057	0.027	0.027	0.052	0.052
JAN 1981	0.12	0.13	0.039	0.040	0.015	0.015	0.017	0.018
FEB	0.14	0.13	0.033	0.031	0.017	0.016	0.04	0.037
MAR	0.14	0.14	0.038	0.038	0.025	0.025	0.041	0.041

TABLE I.21. Changes, given as gramme weights, in the biochemical components (original and recalculated) of total animal over a two year period (March 1979-March 1981).

	g. DRY WT. PROTEIN		g. DRY WT. CARB.		g. DRY WT. LIPID		g. DRY WT. ASH	
MONTHS	ORIG.	RECAL.	ORIG.	RECAL.	ORIG.	RECAL.	ORIG.	RECAL.
MAR 1979	7.40	7.30	1.15	1.14	0.66	0.65		
APR	7.17	7.17	1.09	1.08	0.65	0.65		
MAY	9.19	8.72	1.201	1.180	1.01	0.99		
JUNE								
JULY	9.31	9.34	0.91	0.91	0.82	0.83		
AUG	8.26	8.79	3.39	3.60	0.90	0.97	2.38	2.51
SEPT								
OCT	13.73	13.17	6.63	6.48	1.18	1.16	1.88	1.81
NOV	11.58	11.60	6.38	6.37	1.34	1.34	1.72	1.74
DEC								
JAN 1980	8.86	9.50	7.53	8.16	1.32	1.43	1.59	1.70
FEB	7.04	8.21	4.26	4.90	1.24	1.43	1.32	1.55
MAR	9.00	9.53	3.42	3.60	1.02	1.06	1.61	1.69
APR	8.48	8.29	3.72	3.64	0.84	0.82	1.23	1.20
MAY	8.19	8.22	3.27	3.29	0.36	0.33	1.30	1.31
JUNE	10.15	9.31	5.25	4.89	0.70	0.57	1.58	1.50
JULY	7.64	7.60	2.75	2.73	0.33	0.33	1.22	1.20
AUG	9.96	10.26	2.79	2.87	0.65	0.66	1.40	1.44
SEPT	9.27	9.26	3.68	3.68	1.09	1.09	1.24	1.24
OCT	6.84	6.97	2.76	2.91	0.97	0.99	0.94	0.97
NOV	8.51	8.25	3.25	3.13	0.89	0.86	1.33	1.30
DEC	8.10	8.30	3.65	3.77	1.03	1.06	1.24	1.27
JAN 1981	6.26	6.59	1.92	2.01	0.65	0.68	1.01	1.06
FEB	6.58	7.36	2.04	2.31	0.59	0.68	1.07	1.33
MAR	7.57	7.43	1.31	1.30	0.48	0.48	1.35	1.32

TABLE I.22. Covariance analysis for total flesh weight (wet) - S = significant at 5%; * = significant at 1%. (Value F (reg. coeff.) = 2.1813, Value F (adj. means) = 11.0567).

F (reg. coeff.)

F (adj. means)

MONTHS	MAR	APR	MAY	JUNE	JULY	AUG	SEPT	OCT	NOV	DEC	JAN	FEB	MAR	APR	MAY	JUNE	JULY	AUG	SEPT	OCT	NOV	DEC	JAN	FEB	MAR
MAR																									
APR	S																								
MAY	S	S																							
JUNE	*	*	S																						
JULY	*	*																							
AUG	*	*	*	S	S																				
SEPT																									
OCT	*	*	*	*	*	*																			
NOV	*	*	*	*	*	*																			
DEC																									
JAN	*	*	*	*	*			*	S																
FEB	*	*	*	*				*	*							*									
MAR	*	*	*					*	S							*									
APR	*	*		*		S		*	*		*		*												
MAY	*	*						*	*				S			S									
JUNE	*	*	S					*	S		S						S	*	S	*		S	*	S	S
JULY	*	*	*					*	*		*		S												
AUG	*	*	*					*	*				*				S								
SEPT	*	*	*	*	*			*	S					S	*		S								
OCT	*	*	*	*	*			*	S		*				*		S	S							
NOV	S	S				*		*	*		*	S	*				S		*	*					
DEC	*	*	*					*	*		*		*				S		S	S					
JAN	*	*	S			S		*	*		*		*						*	*					
FEB		S				*		*	*		*	*	*						*	*					
MAR	*			*	S	*		*	*		*	*	*	S	S	*	*	*	*	*			*		

TABLE I.23. Results of covariance analysis for total flesh weight (dry) - S = significant at 5%; * = significant at 1%. (Value F (reg. coeff.) = 1.8822, Value F (adj. means) = 17.4244).

F (reg. coeff.)

F (adj. means)

MONTHS	MAR	APR	MAY	JUNE	JULY	AUG	SEPT	OCT	NOV	DEC	JAN	FEB	MAR	APR	MAY	JUNE	JULY	AUG	SEPT	OCT	NOV	DEC	JAN	FEB	MAR
MAR																									
APR																S									
MAY	*															S									
JUNE	*	*																							
JULY	*	S														S									
AUG	*	*	*	*	S											S									
SEPT																									
OCT	*	*	*	*	*	*																			
NOV	*	*	*	*	*	S		S								S									
DEC																									
JAN	*	*			*			*	*																
FEB			*	*	*	S		*	*					S											S
MAR	*	*	*	*				*	*							S									
APR	*	*						*	*			*	*			S									
MAY	S				S			*	*			S	*			S									
JUNE	*	*	S	*				*	*			*	S				S	S	S	S		S	S	S	
JULY	*	*	S	S	S			*	*			S	*												
AUG	*	*	*	S				*	*			S	S												
SEPT	*	*	*	S	S			*	*				S												
OCT		S						*	*			*	*												
NOV	*	S	*			S		*	*			*	*												
DEC	*	*						*	*			S	*												
JAN	S					*		*	*			*	*				S	*	*			*			
FEB						*		*				*	*			S	S	*	*			*			
MAR			S			*		*				*	*	S	S	*	*	*	*			*			

TABLE I.24. Results of covariance analysis for gonad weight (wet) - S = significant at 5%; * = significant at 1%. (Value F (reg. coeff.) = 1.8209, Value F (adj. means) = 12.8487).

F (reg. coeff.)

F (adj. means)

MONTHS	MAR	APR	MAY	JUNE	JULY	AUG	SEPT	OCT	NOV	DEC	JAN	FEB	MAR	APR	MAY	JUNE	JULY	AUG	SEPT	OCT	NOV	DEC	JAN	FEB	MAR
MAR																									
APR	*															S									
MAY	*	*																							
JUNE	S		*																						
JULY	*	*		*																					
AUG	*	*		*																					
SEPT																									
OCT	*	*	*	*	*	*																			
NOV	*	*	*	*	*	*																			
DEC																									
JAN	*	*	*	*	*	*										S									
FEB	*	*	S	*		S		*	*		S					S									
MAR	*	*	*	*		*		*	*		*														
APR	*	*		*	S			*	*		*					S									
MAY	S	S						*	*		*														
JUNE	*	*	*	*	*			*							*					*		S	S	*	*
JULY	*	S			*			*	*		*	S	*	S		*									
AUG								*	*		*	S	*	S		*									
SEPT	S	S						*	*		*	S	*	S		*									
OCT		S						*	*		*		S	S		*									
NOV			S		S	*		*	*		*	*	*	*		*									
DEC	S	S						*	*		*	S	*	S		*									
JAN	S	*		*				*	*		*		*								*				
FEB	*	S		S				*	*		*	*	*												
MAR	S	*		S				*	*		*		*								S				

TABLE I.25. Results of covariance analysis for gonad weight (dry) - S = significant at 5%; * = significant at 1%. (Value F (reg. coeff.) = 1.0512, Value F (adj. means) = 17.6946).

F (reg. coeff.)

F (adj. means)

MONTES	MAR	APR	MAY	JUNE	JULY	AUG	SEPT	OCT	NOV	DEC	JAN	FEB	MAR	APR	MAY	JUNE	JULY	AUG	SEPT	OCT	NOV	DEC	JAN	FEB	MAR
MAR																									
APR	*																								
MAY	*	*																							
JUNE	*		S						S																
JULY	*	*										S								S					
AUG	*	*	S	*	S																				
SEPT																									
OCT	*	*	*	*	*	*																			
NOV	*	*	*	*	*	*																			
DEC																									
JAN	*	*	*	*	*	*		*	S																
FEB	*	*	*	*	*	*		*	*		*														
MAR	*	*	*	*	*	*		*	*		*									S					
APR	*	*	*	*	*			*	*		*														
MAY	*	*		S				*	*		*		*												
JUNE	*	*	*		*			S			*				S										
JULY	*	S						*	*		*	*	*	*		*									
AUG	S					S		*	*		*	*	*	*		S									
SEPT	*	*		*				*	*		*	S	*			S									
OCT	*	S						*	*		*	S	*	*		*									
NOV	S							*	*		*	*	*	*		*									
DEC	S	*		*				*	*		*	*	*			S									
JAN	*	*		*	S			*	*		*	*	*												
FEB	*					S		*	*		*	*	*	S		*									
MAR		S				S		*	*		*	*	*	S											

TABLE I.26. Results of covariance analysis for adductor muscle weight (wet) - S = significant at 5%; * = significant at 1%. (Value F (reg. coeff.) = 1.4371, Value F (adj. means) = 17.0192).

F (reg. coeff.)

F (adj. means)

MONTHS	MAR	APR	MAY	JUNE	JULY	AUG	SEPT	OCT	NOV	DEC	JAN	FEB	MAR	APR	MAY	JUNE	JULY	AUG	SEPT	OCT	NOV	DEC	JAN	FEB	MAR
MAR																*									
APR	S															*									
MAY	*	*	S													*									
JUNE	*	S	S													S									
JULY	*	*	*	*	*																				
AUG																									
SEPT	*	*	*	*	*	*										S									
OCT	*	*	*	*	*	*																			
NOV																									
DEC	*	*	*	*	*	*			*							S									
JAN	*	*	*	S	S			*	*		S					S									
FEB	*	*	*	*	*			*	*				S												
MAR	*	*	*	*	*			*	*																
APR	*	*	*	*	*			*	*		*		S												
MAY	*	*	*	*	*			*	*		S							S	S				*	*	
JUNE	*	*	*	*	*			*	*																
JULY	*	*	*	*	*			*	*		S														
AUG	*	*	*	*	*										*										
SEPT	*	*	*	*	*	S			S						S										
OCT	*	*	*	*	*			*	*		*								S						
NOV	*	*	*	*	S			*	*		*								*	*	*				
DEC	*	*	*	*	S			*	*		*	*	*				*	S	*	S		*			
JAN	S	S	S			*		*	*		*	*	*	*	S		*	*	*	*	S	*	*		
FEB	S	S				*		*	*		*	*	*	*	*	*	*	*	*	*	*	*	*		
MAR																									

TABLE I.27. Results of covariance analysis for adductor muscle weight (dry) - S = significant at 5%; * = significant at 1% (Value F (reg. coeff.) = 1.4048, Value F (adj. means) = 54.7654.)

F (reg. coeff.)

F (adj. means)

MONTHS	MAR	APR	MAY	JUNE	JULY	AUG	SEPT	OCT	NOV	DEC	JAN	FEB	MAR	APR	MAY	JUNE	JULY	AUG	SEPT	OCT	NOV	DEC	JAN	FEB	MAR
MAR																									
APR																									
MAY	*																								
JUNE	*	*	*																						
JULY	*	S														S									
AUG	*	*	*	*	*											S									
SEPT																									
OCT			*	*	*	*																			
NOV	*	*	*	*	*	*										S									
DEC																									
JAN	*	*	*	*	*	*										S									
FEB	*	*	*	*	*	*			*							*									
MAR	*	*	*	*	*	*		S	*							S									
APR	*	*	*	*	*											S									
MAY	*	*	*	*	*			*	*		*		S			S	*								
JUNE	*	*	*	*	*			*	*	S															
JULY	*	*	*	*	*	*		*	*		*	*	*	*	S										
AUG	*	*	*	*	*	*		*	*		*	*	*	*	*	*	*									
SEPT	*	*	*	*	*			*	*		*	S	S	S		S	*	*								
OCT	*	*	*	*	*			*	*		*		S				*	*								
NOV	*	*	*	*	*			*	*		*						*	*								
DEC	*	*	*			S		*	*		*	*	*	*			*	*			S					
JAN	S	S	S			*		*	*		*	*	*	*	S	S	*	*	S	*	*	S				
FEB						*		*	*		*	*	*	*	*	*	*	*	*	*	*	*	*			
MAR		*				*		*	*		*	*	*	*	*	*	S	*	*	S	*	*	*	S		

TABLE I.28. Results of covariance analysis for siphon weight (wet) - S = significant at 5%; * = significant at 1%. (Value F (reg. coeff.) = 1.7316, Value F (adj. means) = 7.7403).

F (reg. coeff.)

F (adj. means)

MONTHS	MAR	APR	MAY	JUNE	JULY	AUG	SEPT	OCT	NOV	DEC	JAN	FEB	MAR	APR	MAY	JUNE	JULY	AUG	SEPT	OCT	NOV	DEC	JAN	FEB	MAR
MAR												S													
APR																									
MAY												S													
JUNE		*	S																						
JULY		S														S									
AUG		*	*	*																					
SEPT																									
OCT		*	*	*	*	*																			
NOV		*	*	*	*			S				S													
DEC																									
JAN		*	*	S				*	S						S										
FEB		S	S					*	*																
MAR		*	*			*		*	S																
APR				S		*		*	*			S								S					
MAY						*		*	*																
JUNE						*		*	*		S							*	S				S		
JULY		*	S			*		*	*					S											
AUG		*	*					*	*					*											
SEPT		*	*		S									*	S	S	S								
OCT		*	*	*	*	S		*				*		*	*			*							S
NOV						*		*	*		*	*	*					*	*	*					
DEC		S				*		*	*		*	*		S				*	S	*					
JAN						*		*	*		*	*	S					*	*	*					
FEB						*		*	*		*	*	S					*	*	*					
MAR			*	*	*	*		*	*		*	*	*		S	S	*	*	*	*		*	S	*	

TABLE I.29. Results of covariance analysis for siphon weight (dry) - S = significant at 5%; * = significant at 1%. (Value F (reg. coeff.) = 1.1496, Value F (adj. means) = 10.5055).

F (reg. coeff.)

F (adj. means)

MONTHS	MAR	APR	MAY	JUNE	JULY	AUG	SEPT	OCT	NOV	DEC	JAN	FEB	MAR	APR	MAY	JUNE	JULY	AUG	SEPT	OCT	NOV	DEC	JAN	FEB	MAR
MAR																S									
APR												S													
MAY												S													
JUNE	S	S																							
JULY	S		S													S									
AUG	*	*		*																					
SEPT																									
OCT	*	*	*	*	*	*						S													
NOV	*	*	*	*	*	*																			
DEC																									
JAN	*	*	*	*	*	S		*	S																
FEB	*	*	*	*	S	*		*	*					S											S
MAR	S	*	*	*	S	S		*	*																
APR	S		*			*		*	*		*	*	*												
MAY	*					S		*	*		*	S	S												
JUNE								*	*		S												*	S	
JULY	*	S	S	S		S		*	*		*	S	S												
AUG	*	*	*					*	*			*		*											
SEPT		*	*					*	*	S				S											
OCT	*	S						*	*		*	S	S												
NOV	*					S		*	*		*	S	*				S	S							
DEC	*	*	*		S	*		*	*		*	*	*	*	*		S	S	S							
JAN	*					*		*	*		*	*	*				S	*	S	S		*			
FEB						*		*	*		*	*	*				*	S	S			*			
MAR				*		*		*	*		*	*	*				*	*	*			*			

TABLE I.30. Results of covariance analysis for 'other' tissue weight (wet) - S = significant at 5%; * = significant at 1%. (Value F (reg. coeff.) = 1.8562, Value F (adj. means) = 17.0887).

F (reg. coeff.)

F (adj. means)

MONTHS	MAR	APR	MAY	JUNE	JULY	AUG	SEPT	OCT	NOV	DEC	JAN	FEB	MAR	APR	MAY	JUNE	JULY	AUG	SEPT	OCT	NOV	DEC	JAN	FEB	MAR
MAR																									
APR	S				S											S									
MAY	S	S														*									
JUNE	*	*																							
JULY	*	*	*	S																					
AUG	*	*	*	S	S																				
SEPT																									
OCT	*	*	*	*	S	*																			
NOV	*	*	*	*	*	*		*																	
DEC																									
JAN	*	*	*	*	*			*	*																
FEB	*	*	*		*			*	*							S									
MAR	S	*	*	S				*	*																
APR	S				*	*		*	**		*	*	*			S									
MAY	*					S		*	*		*		S			S	*		*	*		*	S		
JUNE	S	S			*	*		*	*		S	S	*												
JULY	S	S				S		*	*		*	S	*			S									
AUG	S	*			*			*	*		S					S									
SEPT	*	*	*	S	*			*	*					*	S	S	S								
OCT	*	*	*		*			*	*					S	S		S								
NOV						*		*	*		*	S	*						*						
DEC	*	*			*			*	*		S									*					
JAN	*			S	*	*		*	*		*	*	*					*	*		S	*				
FEB				S		*		*	*		*	*	*					*	*	*		*				
MAR			*	*		*		*	*		*	*	*	S		S	*	*	*	*	S	*	*			

TABLE I.31. Results of covariance analysis for 'other' tissue weight (dry) - S = significant at 5%; * = significant at 1%. (Value F (reg. coeff.) = 1.7053, Value F (adj. means = 15.7570).

F (reg. coeff.)

F (adj. means)

MONTHS	MAR	APR	MAY	JUNE	JULY	AUG	SEPT	OCT	NOV	DEC	JAN	FEB	MAR	APR	MAY	JUNE	JULY	AUG	SEPT	OCT	NOV	DEC	JAN	FEB	MAR
MAR																S									
APR																S									
MAY	S															S									
JUNE	*	S	*													S									
JULY	*	*		*												*									
AUG	S		*	*	S											*									
SEPT																									
OCT		*	*	*	*	*																			
NOV	*		*	*	*	*		*																	
DEC																									
JAN	*		*	*	*	*		*								*									
FEB	*	*	*		*	S		*								*								S	
MAR	S		*		*	S		*	*							*									
APR	*	*				*		*	*		*	*	*												
MAY	*	*						*	*		*	S	*			*	*	*	*			*	*		
JUNE	*	*			S	S		*	*		*	S	*												
JULY	*	*	*	*	*	*		*	S		*	S	*												
AUG	*	*	*		*			*	S		S			S											
SEPT	*	*		*				*	*		*		*	*				S							
OCT	*	*		S				*	*		*	S	*					S							
NOV	*	*	*		S			*	*					*											
DEC	*			*		*		*	*		*	*	*					*			*				
JAN	*			*		*		*	*		*	*	*		*			*			*			S	
FEB			S	*	S	*		*	*		*	*	*		*	*		*	*	*	*		S		
MAR			S	S	*	*		*	*		*	*	*		*	*		*	*	*	*		*	S	

TABLE I.32. Results of covariance analysis for digestive gland weight (wet) - S = significant at 5%; * = significant at 1%. (Value F (reg. coeff.) = 1.7171, Value F (adj. means) = 80.3173).

F (reg. coeff.)

F (adj. means)

MONTHS	MAR	APR	MAY	JUNE	JULY	AUG	SEPT	OCT	NOV	DEC	JAN	FEB	MAR	APR	MAY	JUNE	JULY	AUG	SEPT	OCT	NOV	DEC	JAN	FEB	MAR
MAR																S									
APR																									
MAY	S																								
JUNE	*	*																							
JULY																									
AUG	*	*	*	*	*																				
SEPT																									
OCT	*	*	*		*																				
NOV	*	S	*	*	*	*		*																	
DEC																									
JAN	*	*	*	*	*	*		*	*																
FEB	*	*	*	*	*	*		*	*																
MAR	*	*	*	*	*	*		*	*			S													
APR	*	*	*	*	*	*		*	*		*														
MAY	*	S	*	*	*	*		*				*	*	*											
JUNE	*	*	*	*	*	*		*	*				S	S											
JULY	*	*	*	*	*	*		*			*	*	*	*		S									
AUG	*	*	*	*	*	*		*			*	*	*	*											
SEPT			*	*	*	*		*			*	*	*	*		*	S	S							
OCT	*	*	*	*	*	*		*			*	*	*	*					S						
NOV	*	*	*	*	*	*		*	*			*	*		S		*	S	*	*					
DEC	*	*	*	*	*	*		*	*						*		*	*	*	*					
JAN	*	*	*	*	*	*		*	*		*	S	*		*	*	*	*	*	*	*				
FEB	*	*	*	*	*	*		*	*		*	*	*	*	*	*	*	*	*	*	*	*			
MAR	*	*	*	*	*	*		*	*			*	*	*					*			*	*	*	

TABLE I.33. Results of covariance analysis for digestive gland weight (dry) - S = significant at 5%; * = significant at 1%. (Value F (reg. coeff.) = 1.7210, Value F (adj. means) = 57.89).

F (reg. coeff.)

F (adj. means)

MONTHS	MAR	APR	MAY	JUNE	JULY	AUG	SEPT	OCT	NOV	DEC	JAN	FEB	MAR	APR	MAY	JUNE	JULY	AUG	SEPT	OCT	NOV	DEC	JAN	FEB	MAR
MAR																									
APR	*															*									
MAY	*	*														S									
JUNE	*	*	*													S									
JULY	*	*	*													*									
AUG	*	*	*	S	*											S									
SEPT																									
OCT	*	*	*	*	S	*										S									
NOV	*	*	*	*	*	*		*								S									
DEC																									
JAN	*	*	*	*	*	*		*	*																
FEB	*	*	*	*	*	*		*	*		*					S								S	S
MAR	*	*		*	*	*			*		*	*				S									
APR	*	*	*	*	*	*		*	*		*														
MAY	*	*	*	*	*	*		*			*	*	*	*		*								S	
JUNE	*	*	*	*	*	*		*	*		*	*	*	*	*										
JULY	*	*	*	*	*	*		*			*	*		*		*					S	S		S	
AUG	*	S		*	*			*	*		*	*		*		*									
SEPT	*		S	*	S	*		*	S		*	*		*		*		*							
OCT	*	*	*	*	*	*		*	*		*	*	*	*	*	*		*	*						
NOV	*	*	*	*	*	*		*	*		*			*	*		S	*	*	*					
DEC	*	*	*	*	*	*		*	*				*		*			*	*	S	*				
JAN	*	*	*	*	*	*		*	*		*	*	*	*	*	*	*	*	*	*	*	*			
FEB	*	*	*	*	*	*		*	*		*	*		*	*	S	*	*	*	S	S				
MAR	*	*	*	*	*	*		*	*		*			S	*		S	*	*	*		*			

TABLE I.34. Results of covariance analysis for shell weight - S = significant at 5%; * = significant at 1%. (Value F (reg. coeff.) = 0.9604, Value F (adj. means) = 4.900).

F (reg. coeff.)

F (adj. means)

MONTHS	MAR	APR	MAY	JUNE	JULY	AUG	SEPT	OCT	NOV	DEC	JAN	FEB	MAR	APR	MAY	JUNE	JULY	AUG	SEPT	OCT	NOV	DEC	JAN	FEB	MAR
MAR	\																								
APR		\																							
MAY			\																						
JUNE				\																					
JULY					\																				
AUG						\																			
SEPT							\																		
OCT								\																	
NOV									\																
DEC										\															
JAN											\														
FEB												\													
MAR		S						S					\												
APR		S												\											
MAY															\										
JUNE	*	*	*		*			*	*		*	*				\									
JULY	S	*	S	S				S	S			S					\								
AUG	*	*	*	*	*	*		*	*		*	*	*		*	*		\							
SEPT	*	*	*	*	S	*		*	*		*	*	*		*	*	*		\						
OCT	*	*	*	*				S	*			S				*	*			\					
NOV	*	*		S	*	S		S	S			*									\				
DEC	*	*	*	*		S		*	*		*	*			S							\			
JAN	*	S	S		*			*				S	S				*		S				\		
FEB	S	*	*	S		S		*	*			*					*							\	
MAR	S	*	*	*				*	*			*													\

APPENDIX II

APPENDIX II

The tables included in this appendix give the numerical values for the various analyses referred to in Chapter 5.

Tables II.1. and II.3. - Changes in respiration rate of a standard animal with season and temperature respectively showing original and re-calculated values.

Tables II.2. and II.4. - Covariance analysis for respiration data.

TABLE II.1. Changes in respiration rate ($mls0_2$/g dry wt/hr) of a standard animal over a year period (January 1980-January 1981) showing original and recalculated values. (Value of common slope =-1.096).

MONTHS	NO. OF ANIMALS	ORIGINAL OXYGEN CONSUMPTION ($mls0_2$/g dry wt/hr)	RECALCULATED OXYGEN CONSUMPTION ($mls0_2$/g dry wt/hr)	NEW INTERCEPT	RANGE OF WEIGHTS (g)
January 1980	10	0.0689	0.07389	0.2945	14.52-40.10
March	10	0.0864	0.11005	0.4676	15.23-34.94
April	5	0.1045	0.1065	0.4534	14.70-25.24
May	10	0.1416	0.1238	0.5187	10.54-20.66
July	10	0.0729	0.0747	0.2995	14.18-24.16
August	5	0.0796	0.0798	0.3289	17.59-22.93
September	10	0.0734	0.0751	0.3016	13.70-27.95
October	5	0.0622	0.0590	0.2094	11.05-19.76
November	10	0.0537	0.0763	0.3085	13.84-20.11
January 1981	10	0.0649	0.0670	0.2519	8.06-26.39

TABLE II.2. Covariance analysis for seasonal respiration
S = significant at 5%; * = significant at 1%.
(Value F (reg. coeff.) = 1.3508, Value F (adj. means) = 1.3508).

F (reg. coeff.)

F (Adj. means)

MONTH	Jan. 1980	MAR.	APR.	MAY	JULY	AUG.	SEPT.	OCT.	NOV.	Jan. 1981
JAN. 1980										
MAR.	*									
APR.	S									
MAY	*	S	*							
JULY		*	*	*						
AUG.		*	S	*						
SEPT.	*	*	S	*						
OCT.		*	*	*		*				
NOV.	*	*	*	*	*	*	*	S		
JAN. 1981	*	*	S	*		*	*		*	

TABLE II.3. Changes in the respiration rate of a standard animal with temperature in April, August and October 1980 showing original and recalculated values. (Values of common slope =-0.952).

TEMP. °C	NO. OF ANIMALS	ORIGINAL OXYGEN CONSUMPTION (mlsO_2/g. dry wt/hr)	RECALCULATED OXYGEN CONSUMPTION (mlsO_2/g. dry wt/hr)	NEW INTERCEPT	RANGE OF WEIGHTS (g)
APRIL					
10°C	5	0.1045	0.10717	0.2687	14.70-25.24
15°C	5	0.1384	0.1472	0.4067	15.77-21.86
20°C	5	0.1399	0.1511	0.4179	15.66-22.12
25°C	5	0.1516	0.1608	0.4448	15.48-23.16
30°C	5	0.1598	0.2110	0.5627	12.90-23.25
AUGUST					
10°C	5	0.0796	0.0800	0.1418	17.59-22.93
15°C	5	0.1329	0.1211	0.3215	15.84-21.49
20°C	5	0.2132	0.2105	0.5617	16.10-21.00
25°C	5	0.2521	0.2389	0.6167	14.77-22.78
30°C	5	0.1308	0.1338	0.3648	13.05-23.91
OCTOBER					
5°C	5	0.0508	0.0503	0.0599	12.37-20.68
10°C	5	0.06212	0.0638	0.04365	11.05-19.76
15°C	5	0.0702	0.0736	0.1052	11.08-20.49
20°C	5	0.1102	0.1133	0.2926	10.26-19.71
25°C	5	0.2335	0.1812	0.4967	7.44-24.92
30°C	5	0.1202	0.1166	0.3053	9.20-20.39

TABLE II.4. Covariance analysis for respiration at different temperatures S = significant at 5%;
* = significant at 1%. (Value F (reg. coeff.) = 1.6097, Value F (adj. means) = 20.9784.

F (reg. coeff.)

F (Adj. means)

	$10A_p$	$15A_p$	$20A_p$	$25A_p$	$30A_p$	$10A_g$	$15A_g$	$20A_g$	$25A_g$	$30A_g$	5 O_c	10 O_c	15 O_c	20 O_c	25 O_c	30 O_c
$10A_p$																
$15A_p$									S							
$20A_p$																
$25A_p$																
$30A_p$	*															
$10A_g$	*	*	*	*	*											
$15A_g$		*			*	*										
$20A_g$	*	*				*	*									
$25A_g$	*	*	*			*	*	S								
$30A_g$		*		*	*	*		*	*							
5 O_c	*	*	*	*	*	*	*	*	*	*						
10 O_c	*	*	*	*	*	*	*	*	*	*	*					
15 O_c	*	*	*	*	*		*	*	*	*	*	*				
20 O_c		*		*	*	*		*	*	*	*	*	*			
25 O_c	*	*				*	*		*	*	*	*	*	*		
30 O_c		*			*	S	*	*	*	*	*	*	*		*	