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REPRODUCTIVE ECOLOGY OF *LITTORINA RUDIS* (MATON) IN THE ESTUARINE FIRTH OF FORTH

by

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'Let us consider in what situation the mollusca are placed. They are, as you know, exposed to the dashing of the waves, borne by the violence of storms against rocks; and carried down rapid rivers. You can readily imagine the consequences of their being situated amidst such perils'.

from 'Lessons on shells'
as taught in a Pestalozzian
School at Cheam, Surrey in
1832.

CONTENTS

ABSTRACT

Reproductive ecology of Littorina rudis (Maton) was investigated at three localities in the Firth of Forth from virtually open sea at Aberdour to near the up-estuary limit of the species at Culross some 27 km west. Striking inter-site differences in abundance, population size-composition and minimum size at maturity were observed.

Maximum brood-pouch counts (up to 612 embryos per female) occurred in late spring/early summer and minima(including several empty) occurred in late summer/early autumn. These seasonal changes in embryo numbers were more prounced at the estuarine than the marine sites. Corresponding changes occurred in the condition of ovaries and testes. Seasonal fluctuations in body protein, energy and C : N ratios were also related to reproductive condition. Numbers of embryos contained in brood-pouches on the upper shore at Aberdour were consistently 2 - 3 X those at Torrybay. Values on the lower shore at Aberdour and at Culross fell between these extremes. Embryo weight between sites varied significantly, differences in weight tending to compensate for varying numbers.

Complete development of eggs in vitro at 32 ‰ salinity took 41 - 115 days between 5 - 15°C indicating a Q_{10} of 3 between 5 - 15°C. Embryos failed to develop at 20°C. Successful development was severely restricted at salinities of less than 20 - 24 ‰

at 10°C. Newly released juveniles were less tolerant of reduced salinity than adults on the same shore. L. rudis from the estuarine sites of Torrybay and Culross tolerated low salinities better than those at the marine Aberdour.

Cyclical patterns of juvenile release were observed in a laboratory tide tank with maximum release close to successive new moons. Discrepancies in reproductive production estimates from brood-pouch loads and from juvenile release indicated that not all eggs entering the brood-pouch complete development. A tentative model to predict release from brood-pouch loads is proposed.

Estimated production of juveniles at Torrybay (63.31 kJ m^{-2} y^{-1}) was more than 2 X that on the upper shore at Aberdour (27.08 kJ m^{-2} y^{-1}) and 16 X that on the lower (3.86 kJ m^{-2} y^{-1}). At Torrybay an estimated 29% of the biomass was turned over annually as newborn compared with 14.8% and 10.3% on the upper and lower shore respectively at Aberdour.

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INTRODUCTION

Rough periwinkles of the Littorina saxatilis group are common and widespread on rocky and stony shores of northern Eurasia and America. The great variability within the group has stimulated many attempts to resolve their taxonomy (Fretter and Graham, 1962; James, 1968a; Fischer-Piette and Gaillard, 1971; Heller, 1975a,b,; Smith 1981). After an extensive study, Heller (1975a) concluded that the saxatilis complex comprises the distinct and sympatric species L. patula (Thorpe), L. nigrolineata (Gray), L. neglecta (Bean) and L. rudis (Maton) which is the most abundant and widespread.

The variation within the saxatilis aggregate includes great polymorphism for a number of shell characteristics such as shape, sculpture, thickness, colour and pattern (Pettitt, 1973a, b). Variation is also encountered in the anatomy of tentacles, radula and penis. This polymorphism has clearly contributed to the confusion in the literature concerning classification of this group. In particular, the naming of varieties by such workers as Dautzenberg and Fischer (1912), Gaillard (1972) and James (1968a) based on external features including shell colour and pattern has tended to add to this confusion.

L. rudis is of further special interest as it is one of only four British prosobranch molluscs which are ovoviviparous (Fretter and Graham, 1962). Eggs are retained in the female until they develop into crawling minature adults and are consequently deposited on the

same shore as their parents. This form of reproduction with low dispersal rates and presumed geographic isolation of populations has led several authors to regard L. rudis as a worthy candidate for studies of micro-geographic differentiation and geographic speciation (Fretter and Graham, 1962; James, 1968a; Struhsaker, 1968; Smith, 1981). Snyder and Gooch (1973) consider that there must be some flow of genes between populations of rough periwinkles, otherwise countless different species would be found throughout the wide geographic range of the animal. They suggest that interpopulation communication may be aided by rafting of juveniles or adults. Snails may be swept off-shore by storms and some random dispersal of juveniles may occur by air in severe wind. Either process might account for the population of periwinkles, almost alone among littoral invertebrates, upon Rockall.

The evolution of ovoviviparity in L. rudis can be viewed as one of several tendencies throughout the littorinid family towards a terrestrial mode of life. Such trends are also evident in the occurrence of uricotely and rich vascularisation of the mantle with a concomitant reduction of the gills, the vascularisation increasing proportionately with the dryness of the habitat (Nicol, 1960; Yapp, 1960).

The rough periwinkle has a wide range in Europe and N. America, extending from the Black, Mediterranean and Baltic seas westward to Iceland and Greenland (Bequaert, 1943) and in an arc down the east coast of N. America from Labrador to Virginia. It is the most widely distributed mollusc in Great Britain (James, 1968a) occurring in the littoral zone from the most sheltered to the most exposed rocky shores.

The range of L. rudis in the intertidal zone extends from near mean tide level up to and above extreme high water springs where there is abundant spray or up to between mean high water neaps and mean high water springs on more sheltered shores (Gowanloch and Hayes, 1926; Orton, 1928; Colman, 1933; Lebour, 1937; Spooner and Moore, 1940; Evans, 1947; Newell, 1954; Berry, 1961; Fretter and Graham, 1962; Kensler 1967). The upper limit of the animals range is often more sharply defined than the lower limit (Gowanloch and Hayes, 1926; Colman, 1933; Evans, 1947; Cousin, 1971; Daguzan, 1975) and its general distribution in Britain has been reviewed by Lewis (1964). Typically it lives at levels slightly below L. neritoides (L.) but higher than L. littorea (L.)

Throughout its extensive range the population density of the rough periwinkle varies greatly (Table 1). Emson and Faller-Fritsch (1976) and Raffaelli and Hughes (1978) consider that the density of L. rudis is related to the availability of crevices into which the snails can retire after foraging. These crevices include cracks, holes or depressions in rocks, interstices between boulders, empty barnacle shells and among clumps or mussels. Raffaelli and Hughes (1978) also consider that much of the variation between shores in the population size composition of L. rudis is closely related to the sizes of the available crevices especially on exposed shores. On more sheltered boulder shores or salt marshes, the size-frequency distribution is modified more by independent size-specific mortality factors such as crushing by shifting stones, predation, or differences in growth and recruitment.

TABLE 1. Summary of population densities of *Littorina rudis*

Locality	Numbers of animals m^{-2}	Authority
Exe estuary	26	Holme, 1949
Wood's Hole	32	Allee, 1923
Canada	181	Gowanloch and Hayes, 1926
Landshipping, Pembroke	200	Faller-Fritsch, 1975
Danish Waddens	300	Linke, 1939
Whitstable, Kent	305	Berry, 1961
Tamar estuary	1100	Spooner and Moore, 1940
Murmansk Coast	1160	Matveeva, 1948
Greenhithe, Thames estuary	1400	Faller-Fritsch, 1975
Rum Bay, Plymouth	3000	Moore, 1940
Plymouth breakwater	3000	Southward and Orton, 1954
Semi-exposed shore: Murmansk	3620	Matveeva, 1974
Iceland	3720	Thorson, 1941
Murmansk coast	9200	Kuznetsov and Matveeva, 1948
Denmark	30000	Muus, 1967
Exposed shore: Murmansk	3 to 43218	Matveeva, 1974

The lifespan of L. rudis also appears to vary between populations. Thorson (1944) suggested that the oldest specimens in the populations were at least four years old. Moreteau (1975) suggested that some animals can live up to six years but do not often live longer than four years. On the Murmansk coast, Kuznetsov and Matveeva (1948) found that the oldest snails were usually six or seven years old with occasional specimens of up to 17 years. In contrast, in an East Canadian estuary, Burke (1974) found no animals older than one year.

There is considerable evidence of predation on littorinids by members of a number of taxa, especially seabirds and littoral crustaceans (Pettitt, 1975). Fish, predatory molluscs and mammals probably exert a lesser predation pressure on littorinids. Heller (1975b) showed that the various colour morphs of L. rudis have positive survival values and probably do not arise randomly as genetic accidents as has been suggested in the literature. It is probable that seabirds and littoral crustaceans, which are mainly visual predators, exert most selection pressure on these colour morphs.

L. rudis is largely inactive when submerged (Berry, 1961). Most activity including feeding, movement and copulation seems to take place when the shore is exposed at low tide but still wet (Linke, 1933; Thamdrup, 1935: Berry, 1956, 1961: Faller-Fritsch, 1975). They feed by rasping single-cell or filamentous green algae from the surface of the intertidal stones and occasionally browsing over Pelvetia, Ascophyllum, Ulva and Enteromorpha (Kuznetsov, 1946; Fretter and Graham, 1962; Beskulskaya, 1963; Sokolova, 1963; Wolff, 1973).

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Diatoms are taken but according to Berry (1961) most are not digested. Copulation rarely occurs after snails have been exposed for long periods and has not been observed when they are submerged (Berry, 1961). Linke (1933) and Daguzan (1976) reported that copulation occurs throughout the year but is more usual in the spring. Linke (1933) also noted that copulation even occurs when the brood pouch of the female is already distended with eggs.

The reproductive systems of Littorina spp. while sharing a common plan vary in detail (Linke, 1933, Fretter and Graham, 1962). Differences in the c o mponents of the female glandular duct often relate to the habits of (a) releasing pelagic eggs as in L. littorea and many others (b) attaching egg capsules to the substratum as in L. littoralis (L) and (c) ovoviviparity. Descriptions of reproduction and development of the ovoviviparous L. rudis have been given by Pelseneer (1911), Delsman (1914), Linke (1933, 1934) and Ankel (1936) and have been summarised by Thorson (1946).

The albumen and shell glands are retained but the capsule gland is replaced by a thin-walled brood-pouch (Figs 1 and 2) extending accross the mantle roof to the female aperture at the right side (Fretter and Graham, 1962). Along the ventral wall of the pouch are two longitudinal folds bordering a seminal channel (Fig 2) which leads from the bursa copulatrix back to the receptaculum seminis (Ankel, 1936). From the longitudinal folds arise transverse folds forming connected compartments in which the embryos are grouped. The wall of the pouch is highly vascularised, its epithelium is ciliated and has mucus and protein secreting cells. These glands

FIG. 1. General structure of mature male and female *L. rudis* removed from shell.

ag = albumen gland

bp = brood pouch

dg = digestive gland

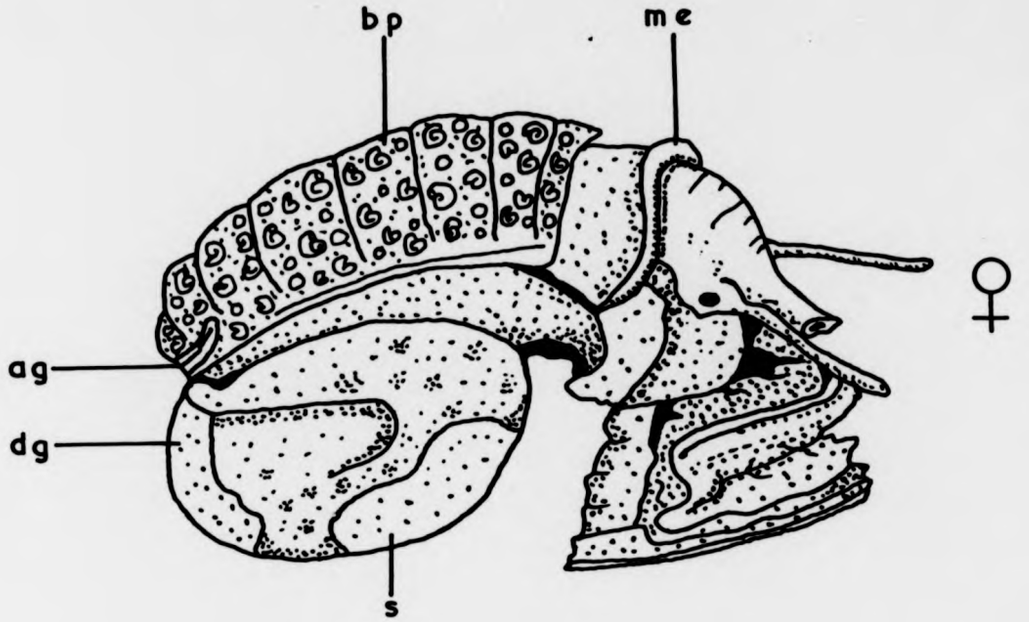
me = mantle edge

o = ovary

s = stomach

sg = seminal groove

t = testis



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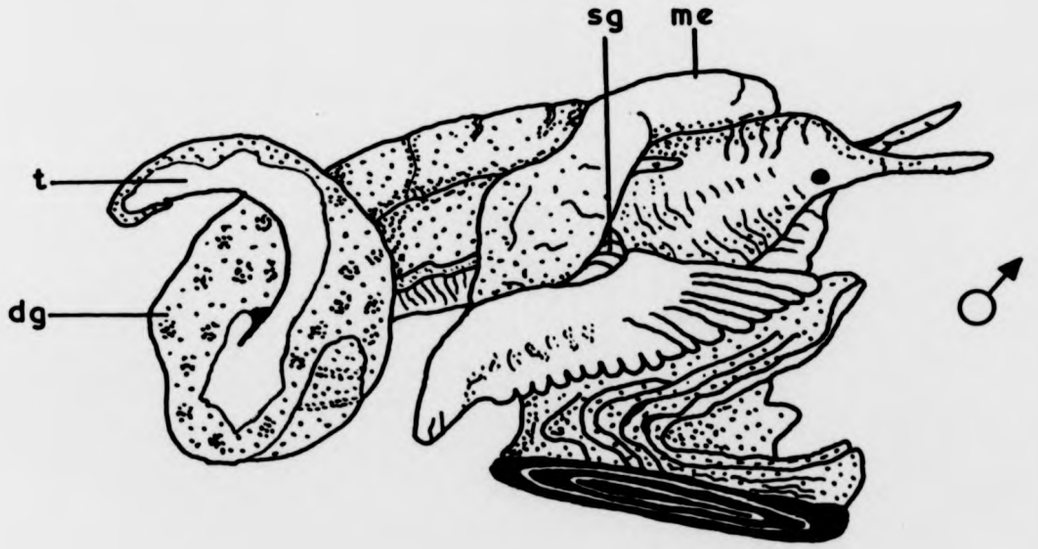


FIG. 2. Semi-diagrammatic representation of the female reproductive system of *L.rudis.* (after Berry,1961).

a = anus

ag = albumen gland

bc = bursa copulatrix

cg = ciliary groove

h = head

k = kidney

m = mantle (cut)

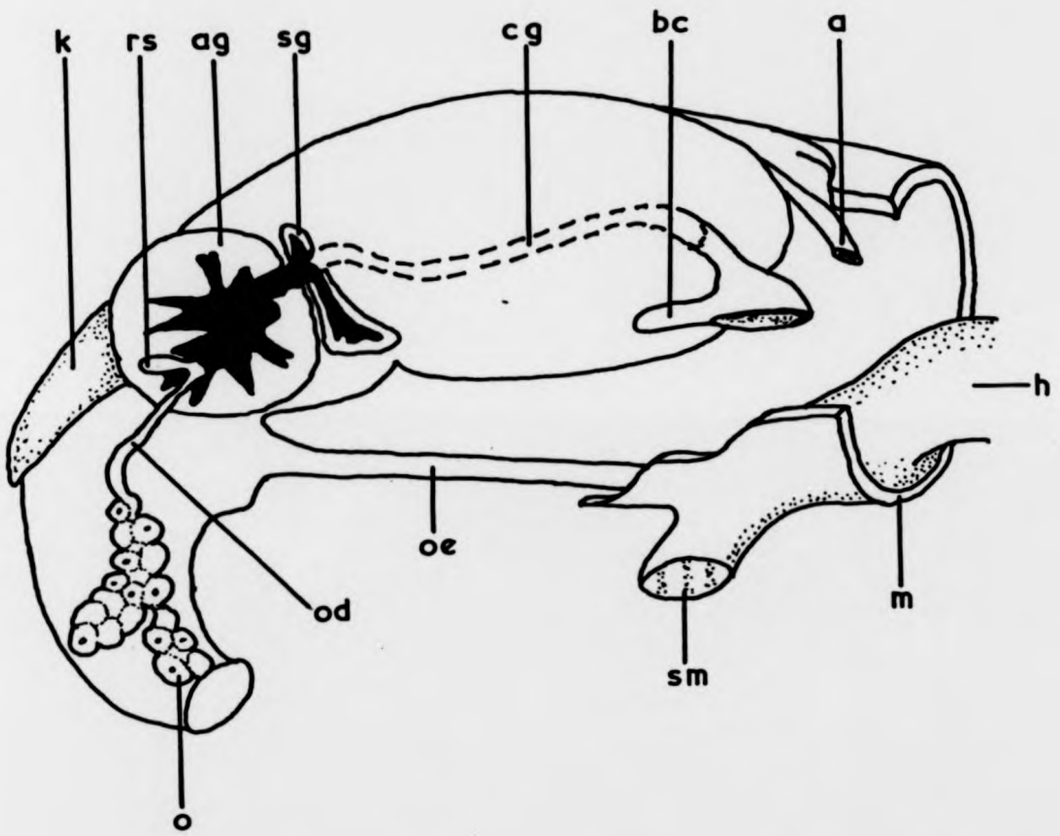
o = ovary

oe = oesophagus

od = oviduct

rs = receptaculum seminis

sm = shell muscle



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y, 1961).

produce a fluid which surrounds the embryos and is kept in circulation by ciliary currents. The pronounced vascularisation of the brood pouch is considered to be concerned with the respiratory requirements of the brood although to date there has been no evidence that the embryos obtain nourishment from the brood-pouch fluid or directly from the maternal tissues themselves.

When egg production is in progress the pink-orange ovary is distended with eggs of greatest diameter 90-300 µm (Berry, 1961). Pelseneer (1935) suggested that the number of eggs produced in one ovulation is 28 to 37. Berry (1961) considers that ovulation is a more continuous process but did confirm the finding of Pelseneer (1934) that pink-orange eggs are transferred to the brood pouch within some 17 hours after fertilisation. Sperm becomes available for the fertilisation of eggs in the receptaculum seminis and albumen gland within five hours of copulation (Berry, 1961).

Prior to entering the brood-pouch each embryo is provided with "albumen" from the albumen gland and a thin membranous egg covering from the shell gland. The "albumen" supplements the yolk provided during development in the ovary and is jelly-like except in the vicinity of the embryo where it is fluid. Eggs develop into veliger-like embryos which rotate in this fluid and later, when all the albumen has been utilised, they creep around the inside of the egg covering before finally rasping a hole through to the exterior using their radulae (Linke, 1933). Freed individuals move amongst the embryos in the lower part of the brood pouch before leaving the female via the genital aperture to live at least initially, on the

same rock surfaces as the adults.

Embryos at all stages of development from eggs to developed juveniles occur together in the brood pouch (Pelseneer, 1911, 1934; Delsman, 1914; Linke, 1933; Ankel, 1936; Thorson, 1946; Berry, 1961; Fretter and Graham, 1962). Thorson (1946) classified the embryos into five arbitrary groupings: (a) eggs and undifferentiated embryos (b) young unshelled veligers (c) veligers with unpigmented shells (d) older veligers with pigmented shells, eyes, statocysts etc. and (e) young hatched from the egg membrane ready to leave the female (Fig 3). Occasionally abnormal embryos are produced, including twinning, possession of an extra eye and sinistral instead of the usual dextral coiling (Pelseneer, 1926). Almost nothing is known of the rate of development in the brood-pouch nor of the rate and pattern of release of juveniles.

The number of young carried by females varies within broad limits and the extent of this variation is apparently related both to locality and season. Thorson (1946) found up to 900 embryos in the brood-pouches of females in Heligoland which was comparable with the findings of Linke (1933). Pelseneer (1911, 1935) reported a maximum of 600 embryos per female and on the Murmansk coast Kuznetsov and Matveeva (1948) found between 103 and 958 embryos per female. At Whitstable, Kent, Berry (1956, 1961) reported a maximum of 300 embryos in large females at the height of the breeding season whereas Roberts and Hughes (1980) found maxima of only 200 in females from three shores in North Wales.

FIG. 3. Examples of different developmental stages of embryos from the brood-pouch of *Littorina rudis*.

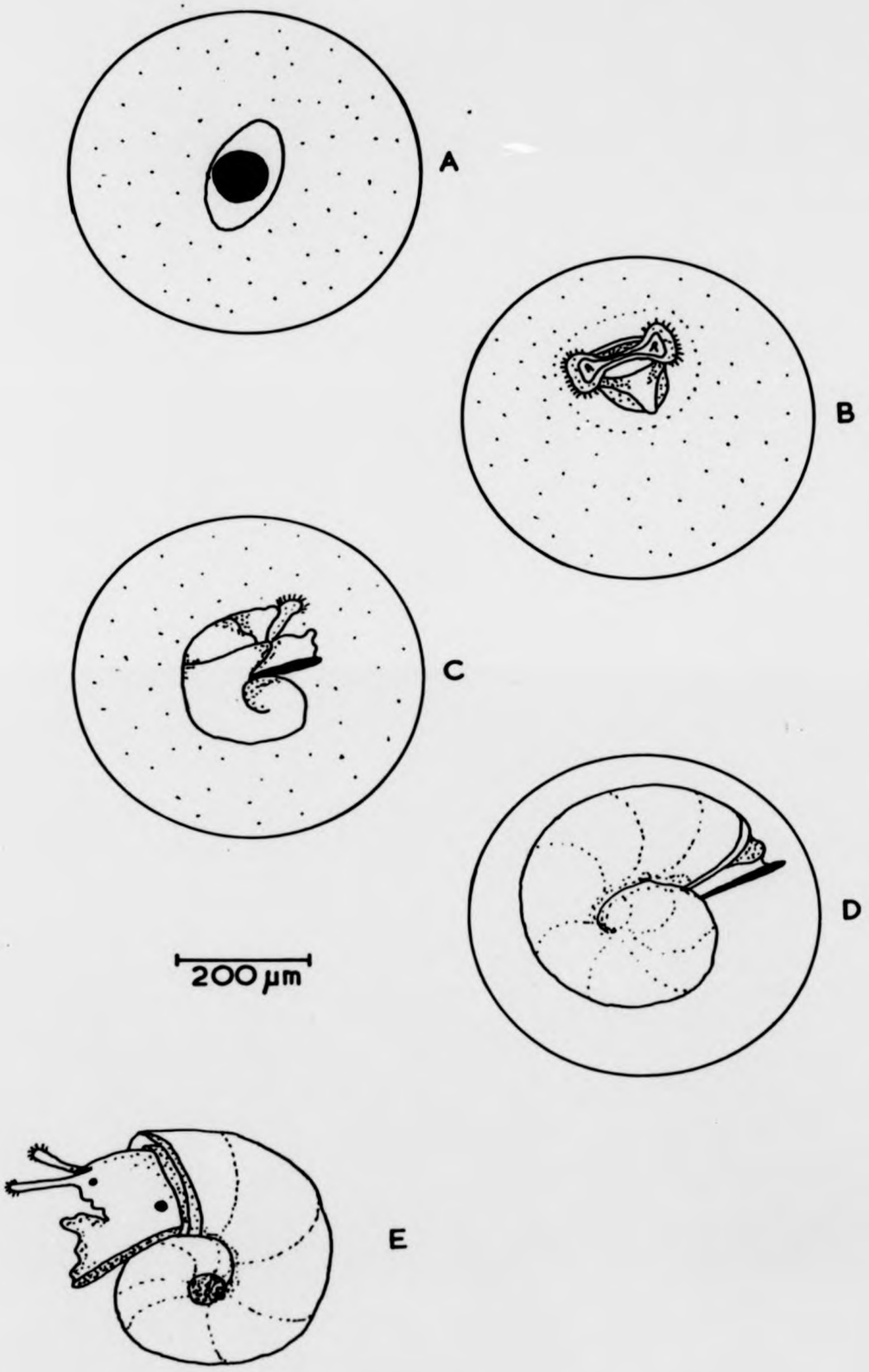
A = Egg stage

B = Early veliger

C = Late veliger

D = Fully formed juvenile prior to leaving capsule

E = Pre-release juvenile


A
B
C
D
200 µm
E

Lebour (1937) revealed that L. rudis breeds throughout the year at Plymouth. Continuous reproductive activity was reported by Beland (1974) in Nova Scotia with peaks in the number of embryos per brood-pouch in both the spring and autumn. At Roscoff, Moreteau (1976) found increased reproduction in the winter and again in early summer. Two peaks in brood-pouch loads were also found by Daguzan (1976), in February and September, at Penvins, France. A single peak in brood-pouch counts was reported in May/June by Berry (1961) at Whitstable and by Faller-Fritsch (1975) at Greenhithe in the Thames estuary and at Landshipping in Pembroke. Emson and Faller-Fritsch (1976) found that the single peak in brood-pouch counts at Newhaven in Sussex was slightly earlier in April/May. Berry(1961) reported a marked decline in brood-pouch loads between June and August. Thus in southerly populations two breeding peaks have been observed but these reduce to a single peak in late spring in some northerly populations. It appears that much of the variability could be attributed to differences in latitude.

In conjunction with the decline in the number of embryos per female from June to August, Berry (1961) found that the condition of other reproductive organs varied. In the female, the ovary was reduced in size while in the male the testes, and in particular the seminal vesicles which are normally conspicuous white tubules full of sperm, decreased in size. At the same time the penis in most males was much reduced in size, with regrowth usually occurring in the autumn. Linke (1934) suggested that material gained from the regression of the genital system at the end of the breeding season is stored in connective tissue.

At Roscoff, Bergerard (1975) found that the annual regression of the genital systems only occurred in some populations. In one population, only old and large animals of both sexes showed this annual reduction. In the winter following regression only a few of the large, old females regrew ovaries and produced embryos, but in most cases those which did so rarely reproduced normally. Essentially then, only the young females in this population were responsible for reproduction. The exclusion of older females from breeding might bear upon the computation of overall reproductive output from populations.

Seasonal cycles of reproduction in a number of marine prosobranch gastropods eg. Patella vulgata (L.) (Blackmore, 1969), Haliotis cracheroidii (L.) (Webber and Giese, 1969; Webber, 1970), Thais lamellosa (Gmelin) (Stickle, 1973; Lambert and Dehnel, 1974) and L. littorea (Williams, 1970; Grahame, 1973; Aliferakis, 1978) are accompanied by changes in the biochemical composition of the animal. Lipid, protein, glycogen, total energy and condition factor have all been shown to be correlated with seasonal phases of growth and reproduction. Although these relationships are likely to be less clear in continuously breeding species they may still be of value in assessing flow of energy into reproduction.

The incidence of parasites in L. rudis has been shown to affect reproduction both directly and indirectly (Pelseneer, 1906; Linke, 1933; Callien and de Larambergue, 1938; James, 1960, 1968a, 1969). Pelseneer (1906) reported that trematode parasites occur in the male reproductive organs and he considered that Cercaria emasculans

(Pelseneer) cuases castration. Permanent reduction in the size of the gonad may be brought about by trematode infection and as the gonad is destroyed the secondary sexual structures are reduced to vestiges. This connection between the state of development of the gonad and the condition of the secondary sexual organs was pointed out by Linke (1933) and Callien and de Larambergue (1938).

Reproductive performance is also likely to be affected indirectly by parasitic infections of non-reproductive tissues which may become heavy enough to diminish the overall condition of the animal. James (1969) described twelve different parasites in L. rudis with up to three species occurring simultaneously in any one individual. During an extensive study at Aberystwyth, he showed that not only the percentage infection but the kind of trematode varies with the size of the snail. Cercaria ubiquita (Lebour) was found only in snails of 6 to 14 mm shell height. C. littorinae-rudis (Lebour) occurred in snails of shell height 4.5 to 10mm while in the 0.6 to 6 mm size class James (1960) reported on unclassified gymnophalline parasite.

Berry (1961) found the incidence of larval trematodes in L. rudis fluctuated in relation to the changing reproductive condition of the snails. In spring, sporocysts were found in small bunches and the digestive gland was rarely severely eroded. In the summer months the gland was often very largely replaced by many invading sporocysts. Although the gonad was never injured by the parasites, heavy infection was accompanied by a reduction of the ovary or testis even while unparasitised snails were still in

reproductive condition. In such cases the males often contained no sperm and the brood-pouches of the females became empty.

A holotrichous ciliate Protophyra ovicola (Kojoid) occurs in the mantle cavity and brood-pouch of L. rudis where it is seen to creep around the surface of the eggs. Cepede (1910) found that they may penetrate the egg covering and enter the embryo and he believed that infection could be brought about in this way. He also reported that heavily infected females produced abnormal offspring. Fenchel (1965) found that P. ovicola is more common in females than males and that the populations in females are greater than in males. It is likely that these aspects of parasitic infection are of significance in the reproductive energetics of L. rudis.

In most studies of reproduction in L. rudis, little attention has been paid to the influence of the estuarine environment even though in many crucial respects estuaries differ from open sea coasts. They exhibit increased gradients and fluctuations of abiotic and biotic factors (Kinne, 1966). Most of the substrate and food matter of estuaries is derived from the land, transported to the estuary by freshwater and there deposited in a region subject to considerable influence from the sea (McLusky, 1971). Ecologically estuaries represent zones of reduced competition in which physical rather than biotic factors determine population dynamics. Most of the animal species in estuaries are of marine origin (Emery and Stevenson, 1957) although the number of species is usually considerably reduced (Kinne, 1966).

Gowanloch and Hayes (1926) reported that the rough periwinkle can live actively and indefinitely at salinities of 15‰ but cannot survive below 13.75‰. Avens and Sleigh (1965) however, considered the lower limit to be 9‰. In the Baltic, Nordensrjold (1900), Jaeckel (1951) and Remane (1958) found rough periwinkles in salinities as low as 6‰. According to Johansen (1918) the typical form only develops where water movements are strong and the salinity is greater than 14‰ and Jaeckel (1951) noted that the maximum size attained decreases with decreasing salinity. Thorson (1946) reported reduced fertility and higher incidences of embryonic abnormalities at low salinities.

It is clear that patterns of reproduction, growth and survival vary in different locations and that several environmental factors might contirbute to this variation. It has not been made clear what part different factors may play in regulating reproduction and it has been very uncertain whether part of the observed variation arises from taxonomic differences between the populations.

While estimates of the fraction of production directed to reproduction have been made in several intertidal and estuarine invertebrates eg. Modiolus demissus (Dillwyn) (Kuenzler, 1961), Scrobicularia plana (da Costa) (Hughes, 1970) and L. littorea (Grahame, 1973) this has not been done for L. rudis. Ovoviviparity might offer particular opportunities for estimating reproductive output by using brood-pouch counts as an index (Kuznetsov and Matveeva, 1948; Berry, 1961) coupled, however, with information on sizes and weights of eggs and embryos, rates of development in the

brood-pouch and of release of young, which have not been presented hitherto. The central aim of this work has been to investigate these features of reproduction in a clearly defined species located in a single estuary in order to assess reproductive output in L. rudis and the effects upon it of the range of different environments encountered in an estuary.

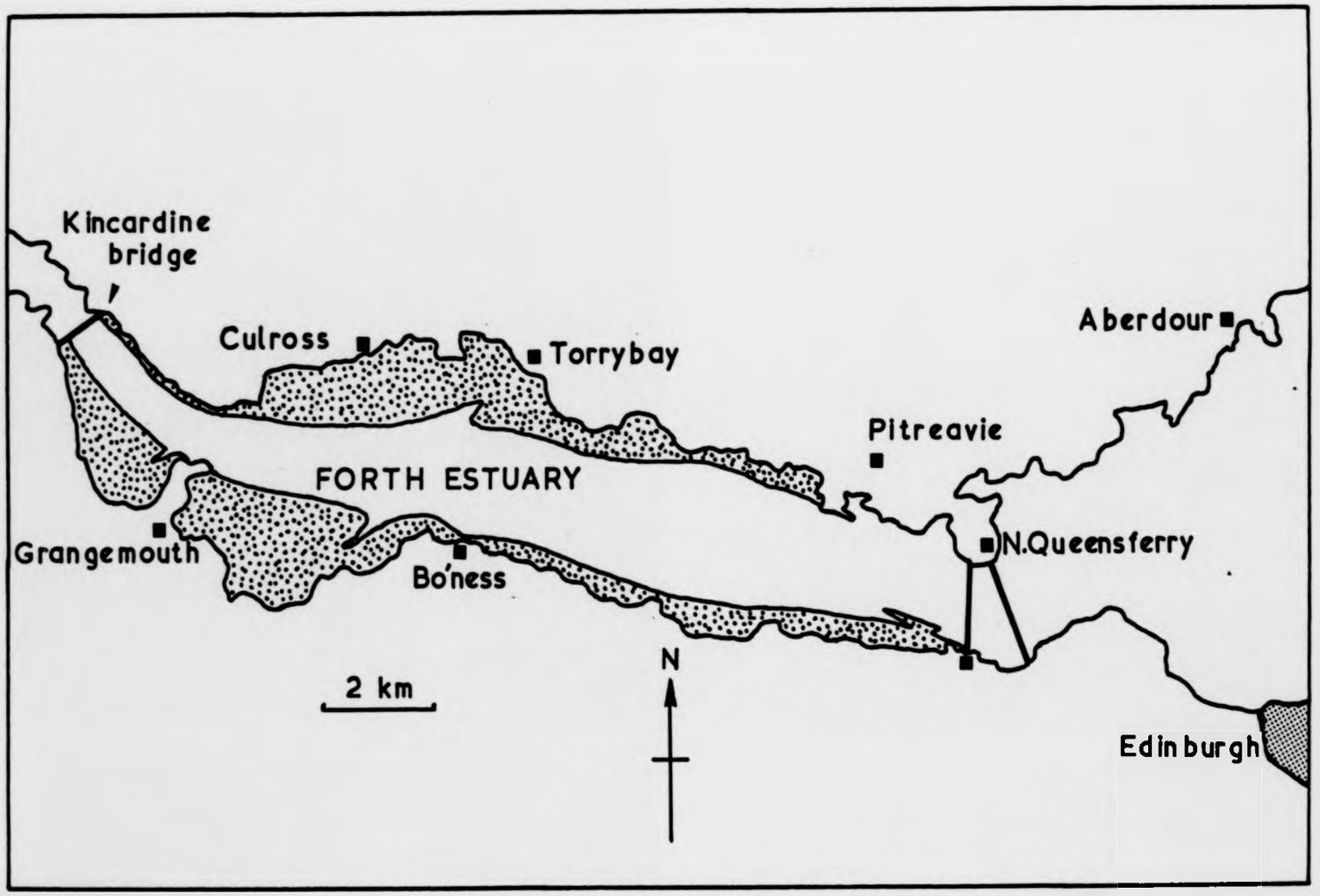
SITES, MATERIALS AND METHODS

1. SITES

The Firth of Forth widens out east of Queensferry to waters that are predominantly marine, whilst above Stirling freshwater enters from the rivers Forth, Teith, and the Allan water. Between these limits the Forth estuary stretches from 48 km subject to regular environmental fluctuations with a gradation of salinity from fresh to salt waters (McLusky, 1978). Below Alloa the Forth gradually widens to 5 km wide at high tide east of Kincardine Bridge with the large mudflats of Skinflats, Kinneil, Torrybay and others revealed at low tide (Fig. 4). The tidal inflow at Queensferry is over 350 x 10^6 m^3 per tide which is more than 130 times the mean volume of land water entering the estuary during an equivalent period (Stout, 1976) hence the dominance of marine conditions in the east.

Following a preliminary inspection of the distribution of L. rudis in the estuarine Forth of Forth, three sampling localities were chosen on the north shore at Aberdour, Culross and Torrybay (Fig. 4). Aberdour (O.S. ref NT 194847) located beyond the estuarine reaches of the Forth, experiences almost totally marine conditions and comprises typically marine rocky and sandy shores. On the rock at this location the population was studied at two levels. The first was near to the upper limit of L. rudis high on the shore and will be referred to as Aberdour 'H'. The second level was near to its down shore limit and will be referred to as Aberdour 'L'.

FIG. 4. The estuarine Firth of Forth, with place-names as indicated in the text. The stippled areas represent mud-flats exposed at low water.


Kincardine
bridge
Culross
Torrybay
Aberdour
Pitreavie
FORTH ESTUARY
Grangemouth
Bo'ness
N.Queensferry
2 km
N
Edinburgh

Shingle and low rock at Culross (O.S. ref NS 985858) supports the last major population upstream except for very few winkles on a 30m stretch of shingle below the northern end of the bridge at Kincardine.

Torrybay (O.S. ref NT 025855) was selected for investigation because it supports an abundant population of L. rudis on shingle and low rock in the middle reaches of the estuary.

The shores were surveyed using an Abney level and the height of sampling sites above chart datum was then determined by reference to Admiralty Tide Tables (1974, 1975, 1976). It was subsequently confirmed that high tides at the stations consistently reached heights very close to the predicted levels within minutes of the predicted times. Thus it was made possible to compare tidal regimes between the sites.

While salinity and temperature were not measured systematically in the course of this work, regular records of salinity and temperature taken twice monthly at the waters edge on spring tides were made available by the Forth River Purification Board (F.R.P.B.) Data from North Queensferry, Bo'ness and Kincardine Bridge provided information for locations close to the sampling sites. Records of mean monthly, mean monthly maximum and mean monthly minimum air temperatures were obtained from the Meteorological Office in Edinburgh, the data having been collected at Pitreavie in Fife, some 7km from Torrybay (Fig 4).

2. Populations

The population structure of L. rudis at the three locations was examined, not with a view to presenting detailed analysis of the populations, but in sufficient detail to provide a background to the studies on reproduction and reproductive ecology. The Aberdour population was the most extensively studied because it provides a fairly typical marine situation against which the more estuarine populations upstream might be compared.

Surveys of the distribution and abundance of L. rudis on the shore at Aberdour were carried out in November 1974 and in January, May and July 1975. The numbers of L. rudis in three 0.25 m^2 quadrats at 2.5, 3.0, 5.0, 10.0, 15.0, 20.0, 25.0 and 30.0m down the shore were counted. These distances were later expressed as vertical heights above chart datum. In addition, twelve monthly samples between November 1974 and October 1975 were collected from the Aberdour 'H' and Aberdour 'L' sites which correspond to the 10 m and 25 m stations cited above. At both of these sites the numbers of L. rudis in three 0.25 m^2 quadrats were noted each month. A vernier caliper was used to measure shell heights (aperture tip to apex) of the snails in each quadrat. Minute examination of crevices, barnacle shells and gravel indicated a tendency to underestimate the numbers of the smallest L. rudis although it is also likely that some of the small snails of other littorinid spp. were included in the counts.

At Torrybay, population density was determined for subsequent reproductive production estimates by counting numbers of L. rudis in five 0.25 m^2 quadrats in November 1974, January, May and September 1975. Since most of the population of L. rudis under study at Culross lived in an old stone jetty it was not feasible to estimate population density at this site as the majority of the snails resided in inaccessible crevices in the wall.

In November 1974 and May and July 1975 additional collections of all L. rudis greater than 2 mm found within an area 1 m^2 were made at each of the four sampling stations. After determining the sizes at the four sites, these animals were examined to find the minimum size of maturity for both females and males. Females were considered to be mature when the ovary was full and eggs were first found in the brood-pouch. Males were examined to determine the size at which they grew a penis and the testes became full.

Single samples of approximately 200 animals were examined from each of the four sites and the shell height-to-mouth diameter ratios were calculated in order to see if different ratios occurred as correllated by Heller (1975a) with degree of exposure.

3. Body composition

One of the aims of this study was to investigate whether seasonal changes in the reproductive performance of L. rudis were accompanied by parallel changes in the general condition of the snails.

Four parameters, total flesh weight, condition factor, protein content and energy content were selected as indices of overall condition.

Changes in flesh weight were derived from the relationships between ash-free dry weight (AFDW) and shell height over the year. Thirty animals were collected from each site in November 1974, January, May and September 1975. Since it was the condition of the breeding population which was under consideration, only mature snails were selected. The minimum size of maturity in each population was 7.5 mm at Aberdour 'H' and Culross, 6.5 mm at Aberdour 'L' and 4.5 mm at Torrybay. On returning to the laboratory the animals were held in aerated sea water at 10^{o}C without food for 48h. During this time the animals voided most of their gut contents prior to dry weight determinations. The flesh and shell were dried separately in pre-weighed aluminium foil dishes at 60^{o}C to constant weight (Lovegrove, 1962). Ash content was then determined by heating the dried samples at 450^{o}C in a muffle furnace for 24 h after which time all of the organic material had been combusted.

The shell height: ash-free dry weight relationship can be expressed as $w = a\ h^{b}$ (Ricker, 1968) where w = ash-free dry weight, a = a constant, h = shell height and b is an exponent with a value nearly always between 2 and 4. If the height of the animals shell grows in proportion to the whole organism, b should be exactly 3 i.e. with isometric growth. Usually however, it is slightly but significantly different from 3 indicating allometric growth (Crisp, 1971). The line of best fit for $\log_{10}$ ash-free dry weight

($\log_{10}W$) on $\log_{10}$ shell height ($\log_{10}h$) was calculated using least-squares regression. The equation is in the form :-

$$\log_{10}W = a + b\log_{10}h$$

The measurements obtained for the determinations of regressions of ash-free dry weight on shell height were also used to calculate the condition factors of the animals. The condition factor, or coefficient of condition, is often used in attempts to investigate seasonal and habitat differences in 'condition', 'fatness' or general 'well being' (Ricker, 1968). The equation for the condition factor (CF) takes the form : -

$$CF = \frac{W}{h^3} \times 100$$

Elemental analysis is being used increasingly as an accurate and convenient method of determining carbon and nitrogen content (Kerambrun, 1975; Champalbert and Kerambrun, 1978) from which energy and protein levels can be estimated (Salonen et al, 1976). The method has the added advantage of requiring only a very small sample of material (between 1 and 3 mg).

A Perkin Elmer Model 240 Elemental Analyser was used to monitor the levels of carbon, nitrogen and hydrogen in the entire flesh of female and male L. rudis in order to investigate seasonal changes in protein and energy and also in C : N and C : H ratios.

The Elemental Analyser accurately determines the carbon, nitrogen and hydrogen content of organic compounds by detecting and measuring their combustion products ie CO_2, N_2 and H_2O. Combustion occurs in pure oxygen and the products are analysed automatically in a self-integrating thermal conductivity analyser. Results were recorded in bar graph form on a 0.1 mV Perkin Elmer Recorder. Use of this machine eliminates the need for tedious classical gravimetric analysis.

Between November 1974 and November 1975 monthly samples of 3 males and 3 females were collected from each site for elemental analysis. Since each animal was analysed at least twice to confirm the results, this represents a total of at least 1532 separate determinations. It was not considered feasible to analyse a larger sample of animals as each determination took 15 minutes.

Shell samples from the monthly collections were also analysed. It was not found necessary to analyse shells from males and females separately as no sexual differences in carbon or nitrogen content were revealed.

All material for analysis was dried at 60°C for 48 h. The dried flesh was then ground with mortar and pestle and stored in labelled tubes in a desiccator in the dark. When required for analysis an aliquot of between 1 and 3 mg of each sample was weighed out accurately on a pre-weighed platinum boat on a Beckmann Model LM - 500 microbalance prior to introduction to the analyser.

4. Reproductive condition and brood-pouch contents

From November 1974 to November 1975 collections of 60 mature L. rudis from each site were made 5 days before each full moon for brood-pouch content analysis. During 1976, samples were taken every 2 months, except during the spring when collections were again taken monthly. Sampling was timed on the lunar as opposed to the calendar month in order to avoid any possible differences attributable to the phase of the lunar cycle.

On returning to the laboratory, snails were stored at - 20°C prior to examination. Each sample of 60 snails was examined until the numbers of eggs and embryos in the brood-pouches of between 15 and 20 females had been counted. Brood-pouch contents of 1260 females in all were thus analysed from a total of 21 collections from each station. (This does not include further counts made of females used in other aspects of this work).

The shell height of each female was noted and the condition of the ovary was recorded upon inspection as either : -

A Reduced : barely visible, thin, pale, usually pink

B Full : a conspicuous pink organ, branched over the digestive gland with some eggs usually visible.

C Very full: swollen, pink, distended with clearly visible eggs.

Any conspicuous parasitism of the visceral coil and gonads was noted. The brood-pouch of each female was then dissected free

and the total number of embryos and numbers of each of the four developmental stages were recorded. Eggs and embryos were classified into four arbitrary developmental stages based on the system of Thorson (1946).

Stage 1 : "Egg stage". This includes cleaving eggs and pre-veliger embryos.

Stage 2 : Young veligers without shells.

Stage 3 : Shelled veligers.

Stage 4 : Fully developed juveniles with shells, eyes, statocysts and with the velum reduced.

Any incidences of abnormal embryonic development including twinning and sinistral as opposed to the usual dextral coiling were noted.

The number of males found while examining each sample of 60 snails was recorded to give a monthly sex ratio. The condition of the testis was inspected visually and recorded as either A : reduced, B : full or C : very full. The length of the penis and any conspicuous parasitism in the visceral coil were also noted.

5. The development of eggs and embryos

Two approaches were taken to estimate the duration of development in the brood-pouch : - (a) Examination of the numbers of each of the four developmental stages in the brood-pouch for peaks in abundance through consecutive collections. (b) The culture of eggs *in vitro*. Females were taken from the field and acclimated for 48 h to 32‰ seawater at 10°C. Then their brood-pouches were removed and the contents dissected out. Samples of 50 representatives of

each of the four developmental stages from each of the four sites (total 800) were placed in four separate petri-dishes containing filtered, UV-treated sea water at 32‰ salinity. The dishes were kept at 10°C and development was observed at regular intervals. The sea water was changed every 2 days. This procedure, using 800 specimens, was carried out on three occasions thus affording observations on a total of 2400 developing embryos. In practise, it was found difficult to culture eggs through to fully developed juveniles. The development of the four different stages could, however, be successfully recorded to give a composite whole.

Since there were no significant differences between sites in the time taken for eggs to develop to juveniles, the effects of temperature and salinity on development were subsequently assessed on embryos from Aberdour 'H' only. The effects on development of temperatures of 5°C, 10°C, 15°C and 20°C on each of the four developmental stages were recorded. Again groups of 50 embryos were held in petri-dishes containing well aerated sea water of salinity 32‰. The influence of salinity on development involved holding embryos in water of salinities 0, 2, 4, 8, 12, 16, 20, 24 and 32‰ at 10°C.

6. Embryo size and growth of newly released juveniles

Determinations of the size, weight and energy content of embryos were made to compare the investment by females into individual embryos from each of the 4 sampling stations. In October 1975 and February 1976 the diameters of at least 500 stage 1 and 500 stage 4

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embryos, taken from between 20 and 30 females from each site, were measured using a micrometer eyepiece in a Vickers Binocular Microscope. This procedure was carried out in sea water to minimise any osmotic swelling or shrinkage.

On both these sampling occasions three batches each of 500 stage 1 embryos and three batches of 500 stage 4 embryos from each of the four sites were dried separately in pre-weighed aluminium foil dishes at 60°C for 48 h to constant dry weight. The samples were then heated at 450°C in a muffle furnace for 24h to determine their ash content and subsequently their ash-free dry weights. All weighings were made on a Beckmann Model LM-500 microbalance. The carbon and hence energy content of dried samples of stage 1 and stage 4 embryos from each of the four sites were determined on each of the two sampling occasions using a Perkin Elemental Analyser, as described in section 3.

The growth ratesof newly released juveniles were determined to give some indication of the age at maturity of L. rudis from each sampling site. It was not feasible to obtain sufficient juveniles by natural release in the laboratory. Instead growth was measured in approximately 500 fully developed juveniles which had been removed from the brood-pouches of females from each of the four sampling stations. The height from aperture tip to apex of each juvenile was measured using a binocular microscope and micrometer eyepiece. From these measurements the mean heights of fully developed juveniles from

each site were determined. Batches of 50 juveniles were taken from each of these samples for dry weight determinations. The remaining juveniles were held in glass tanks of well aerated sea water of salinity 32‰ at 10°C. Food was provided in the form of algal-encrusted native rocks, and a light regime of 12 h light and 12 h darkness was maintained.

At approximately monthly intervals the young snails were measured and samples of 50 animals were taken for dry weight determinations. Unfortunately, after one or two months, in each of three attempts, the young snails from both the Aberdour stations died. It was found that death was a result of heavy nematode infections. The infection was not apparent in the Torrybay and Culross animals which continued to grow.

7. Release of young from the brood-pouch

Release of young from the brood-pouch was investigated in order first to determine the rates of emergence in nature and to compare rates at the marine and estuarine sites. Secondly, using these release rates the intention was to estimate recruitment into whole populations at each site throughout the year. Finally the existence of possible relationships between release rates and brood-pouch contents was investigated. If such relationships exist, it may become possible to predict reproductive output and hence recruitment using brood-pouch contents as an index.

In the laboratory three release experiments each of two months duration were carried out at two monthly intervals in 1976. The first was from January to March, the second from May to July and the third from October to December. In addition, one short field experiment was performed in May. As well as giving data on mean rates of release, the laboratory experiments were designed to yield information on the effects of tidal levels and also to indicate whether any inherent release cycles were present.

(a) Release in the laboratory

The release of young was investigated in an aquarium tide tank modified from the design of de Blok (1964). A simple, constant inflow of sea water was maintained but the outlet from the tank was carried in vertical circular motion on a balanced arm turning one revolution every 12 h 50 min, (Fig 5). Adjustments to flow allowed precise sinusoidal tidal changes in water level. Amplitude could be altered by extending the rotating arm carrying the outlet pipe, (Fig 5).

Snails were held in the tide tank in rectangular perspex containers 302 mm by 210 mm by 35 mm deep. Each container had a removable lid and was divided into twenty four equal compartments. Circular holes approximately 15 mm in diameter were drilled into the base and lid of each compartment and fitted with monel gauze of 400 µ m mesh size to allow free movement of water while retaining the newly released juveniles. The snails were provided with food in the form of native algal-encrusted stones.

FIG. 5. Diagrammatic representation of tide-tank used in this work. (not to scale).

av = air vent

cw = counterweight

ft = flexible drain tube

ec = experimental containers

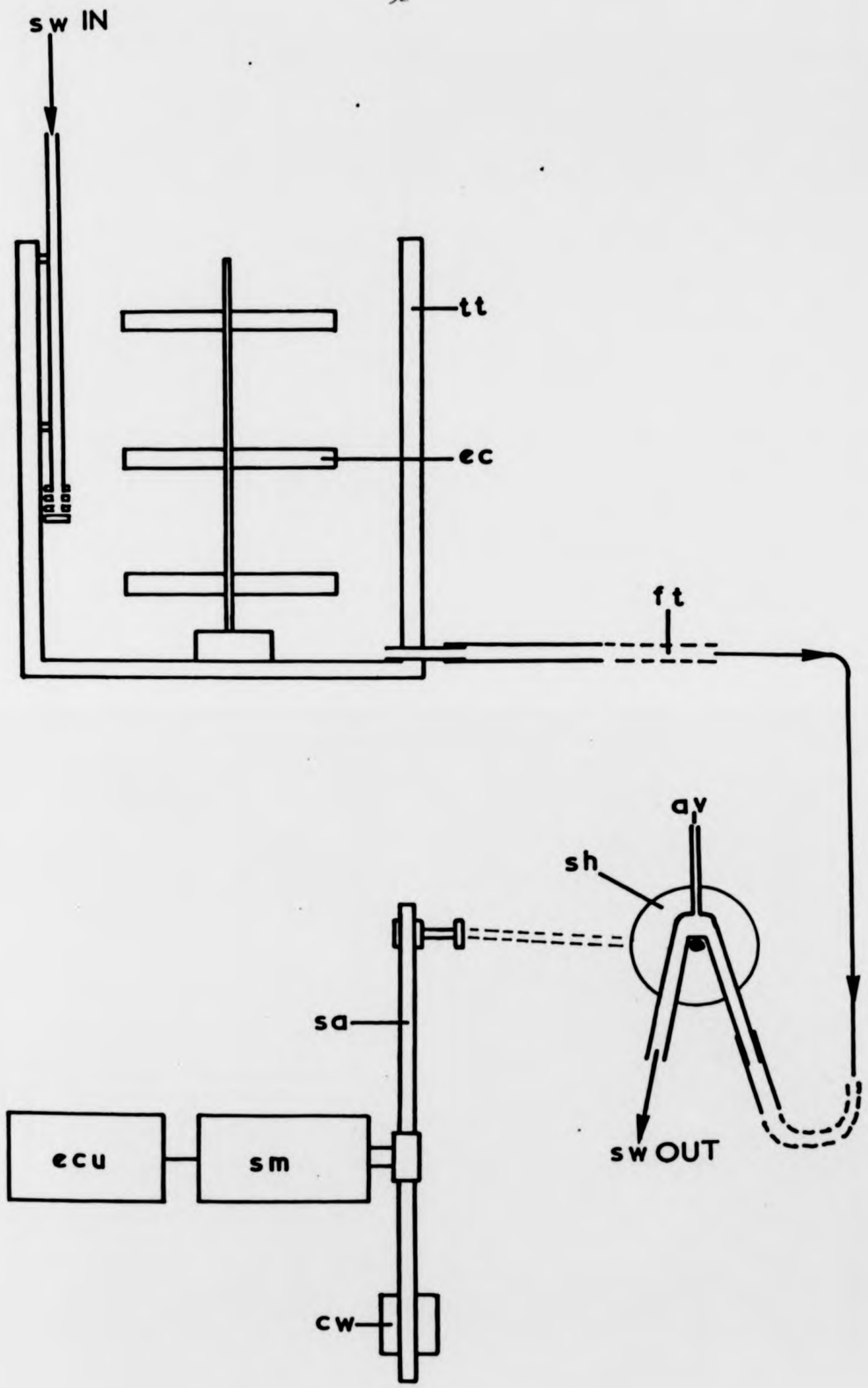
ecu = electronic control unit

sa = swivelling arm

sm = stepping motor

sw IN = sea water inlet

sw OUT = sea water outlet


sw IN
tt
ec
ft
av
sh
sa
ecu
sm
sw OUT
cw

The containers were clamped at levels corresponding, in terms of exposure and immersion times, to high, mid and low tide levels. High tide level (HTL) in the tide tank was equivalent to between MHWN and MHWS, mean tide level (MTL) to MTL in the field and low tide level (LTL) to MLWN. Animals from Aberdour 'H' and Aberdour 'L' were held at all three tidal levels but, due to limited space, snails from Culross and Torrybay were held at mid tide level only.

As it is difficult and time consuming to sex L. rudis, three randomly selected mature snails near to average size for each population, were placed in each compartment. Every three or four days each container was inspected with the aid of a Vickers binocular microscope and the juveniles appearing in each compartment were counted and removed.

At the termination of each experiment the adults were measured and stored in buffered formalin. Post mortems were carried out to determine the sex of each animal and in the case of the females, the brood-pouches were dissected out and the numbers of each of the four developmental stages noted. At the beginning and end of each experiment females were collected from each field site to compare brood-pouch loads with those of the experimental animals.

(b) Release in the field

In order to verify the rates of release obtained in the laboratory, a field investigation of release was conducted at Aberdour and Culross during May/June 1976. Difficulties experienced in securing containers to the more open substrate precluded the possibility of carrying out a similar experiment at Torrybay. Three mature snails, together with algal-encrusted stones were held in 110 mm x 70 mm plastic cylinders whose top and base were constructed of 400 µm monel gauze. Ten containers were secured to the substrate at each site i.e. Aberdour 'H', Aberdour 'L' and Culross. At Aberdour the containers were anchored to the substrate with metal rods and surrounded by rocks while at Culross they were lodged in the jetty wall.

The number of young released was noted every 5 days and the juveniles removed from the containers. At the termination of the experiment after 30 days, post mortems were carried out to sex the adults and to determine the brood-pouch loads of the females. As in the laboratory experiments females were collected from each site to compare their brood-pouch loads with those of the experimental animals at the beginning and end of the experiment.

8. Salinity tolerances of adults, juveniles and embryos

Tolerances of varying salinities by adults, juveniles and embryos were determined in order to decide whether particular phases

of the life cycle of L. rudis are critically susceptible to lowered salinity.

Three replicate sets of 20 adults, 50 juveniles, 50 stage 1 and 50 stage 4 embryos from each of the four sites, were held at 10°C in aerated sea water at each of the salinities 0, 2, 4, 8, 12, 16, 20, 24 and 32‰. In all therefore, 18360 individuals were tested in October, November and December 1976. It was necessary to prevent the snails from having access to air to ensure that they did not simply react to adverse salinity levels by avoidance. Food was provided in the form of native algal-encrusted stones, although Berry (1956, 1961) and Faller-Fritsch (1975) consider that feeding rarely occurs when adult L. rudis is submerged. The experiments were carried out in a light regime of 12 h light and 12 h darkness.

Tolerance was measured in terms of LT 50 ie the number of days taken for 50% of the snails to die. It was sometimes found difficult to be certain whether snails were dead or comatose. This was overcome by placing snails which failed to respond to physical stimuli into full strength sea water to see whether they recovered. Those which were still alive usually showed signs of movement within minutes.

The behaviour of snails was monitored using an activity scale based on the three point system of Arnold (1972).

Animal alive, but operculum closed; score = 1

Foot extended, but not attached; score = 2

Animal moving in container; score = 3

At any salinity the product of the numbers surviving and the total activity score give what will be referred to as the mean integrated response (M.I.R.). This type of index is widely used in other invertebrate studies (Fingerman et al, 1967). The maximum score would be awarded if all of the animals survived and each had been given an activity score of 3. This is equivalent to an M.I.R. of 100%.

RESULTS

1. SITES

The four sampling stations include a wide range of conditions from a rocky open sea coast to almost the up-estuary limits of L. rudis. The different conditions of tidal regime, substrate-type flora and fauna at these sites are summarised in Tables 2 and 3.

At Aberdour, the rocky shore (Plate 1) slopes gradually across a horizontal distance of some 40 m to sand flats at about MLWN (2.1 m above chart datum). The Aberdour 'H' site (4.8 to 5.0 m above chart datum) supported the densest populations of L.rudis and is also near to the upper limit of L. rudis on the shore. Plate 2 shows that the terrain at this site is mainly large boulders and smaller rocks set upon coarse gravel and shingle. There is a paucity of large algae but rather a thin general carpet of microscopic green algae. L. rudis is the predominant littorinid with a few, mostly small, L. littorea but no L. neritoides or L. littoralis.

The Aberdour 'L' site (3.0 m above chart datum) coincides approximately with MTL at Aberdour and is near to the lower limit of L. rudis on the shore. Plate 3 shows that the area consists mainly of small rocks lying on muddy sand with only a few larger boulders. As at Aberdour 'H', the rocks are encrusted with microscopic algae, but there is also a dense covering of macroscopic algae of which Ascophyllum nodosum (L) and Fucus vesiculosus (L) predominate. L. littorea is the predominant littorinid with L. littoralis also commonly found.

TABLE 2. Standard tidal heights (m) above Chart Datum from Admiralty Tide Tables.

Tidal level	Heights above chart datum (m)			
	Aberdour 'H'	Aberdour 'L'	Torrybay	Culross
MHWS	5.6		5.7	5.8
MHWN	4.6		4.5	4.5
MTL	3.3		3.4	3.5
MLWN	2.1		1.9	2.0
MLWS	0.8		0.5	0.6
Collection level	4.8 - 5.0	3.0	4.8	4.5 - 5.0

TABLE 3. Substrate type and relative abundance of major flora and fauna at Aberdour 'H' and 'L', Torrybay and Culross

	Aberdour 'H'	Aberdour 'L'	Torrybay	Culross
	Large rocks and boulders on coarse shingle	Small rocks on muddy sand	Beds of shale and shingle on mudflats	Derilict stone wall on mudflats
Fucus spiralis (L)	+	0	0	0
Fucus vesiculosus (L)	0	++	++	++
Fucus serratus (L)	0	+	+	+
Ascophyllum nodosum (L)	+	+++	++	++
Enteromorpha intestinalis (L)	0	+	++	+
Ulva lactuca (L)	+	++	+	0
Zostera marina (L)	0	0	+++	++
Littorina littorea (L)	+	+++	+++	++
Littorina littoralis (L)	0	++	+	0
Patella sp.	+	+++	+	0
Nucella lapillus (L)	0	++	0	0
Barnacles	++	+++	+	++
Mytilus edulis (L)	0	+	+++	++

0 = Absent
+ = Occasional
++ = Common
+++ = Abundant

PLATE 1. General view of the shore at Aberdour.

PLATE 2. The sampling area at Aberdour H.

PLATE 3. The sampling area at Aberdour L.

The shore at Torrybay is composed of large areas of mudflat below mid tide level with occasional beds of low shale and shingle further upshore (Plate 4). Dense beds of Zostera marina (L) are found on the upper, sandier mudflats and extensive mussel beds are located on the middle and lower shores. Ascophyllum nodosum and Fucus vesiculosus are found on the stone at Torrybay, but only small specimens of the latter occurred within the area sampled. While lacking the marine fauna of Aberdour, Torrybay supports a few barnacles, limpets and flat periwinkles neither of which are present further up the estuary at Culross (Table 3).

At Culross L. rudis was sampled from a derelict stone jetty which was almost the only suitable habitat as the area consists mainly of extensive mudflats with a few rocky outcrops and a narrow band of shingle (Plate 5). The stones making up the jetty are encrusted with microscopic algae but the diversity of macroscopic algae and the variety of animal species are greatly reduced compared with shores further east (Table 3).

The tidal regimes at all three sites are very similar with the sampling stations at Aberdour 'H', Torrybay and Culross being located at approximately corresponding levels between MHWS and MHWN (Table 2). This contrasts with the Aberdour 'L' station where sampling was from a level which coincides approximately with MTL.

The salinity data from the Forth River Purification Board (FRPB) show that at North Queensferry (8 km west of Aberdour) conditions are almost totally marine with very little fluctuation in

PLATE 4. The sampling area at Torrybay.

PLATE 5. The sampling area at Culross; collections were made from the derelict stone jetty.

salinity (Fig. 6). By contrast, at Kincardine Bridge some 6 km above Culross, wide fluctuations in salinity occurred with salinities of below 10‰ having been experienced in the winter of 1974/75 (Fig. 6). Bo'ness, almost opposite Torrybay, falls between these two situations with fluctuations in salinity occurring, but with the amplitude of their fluctuations being less than at Kincardine Bridge (Fig. 6). The profiles of water temperatures, also from FRPB data, are very similar at these 3 stations (Fig. 7). The maximum water temperature recorded was 20°C with a minimum of 4°C.

Meteorological data from the weather centre at Pitreavie, Fife confirms that the range of air temperatures was greater than the range of water temperatures (Fig. 8). It should be noted however, that the extremes of air temperatures are not given as the data is in the form of mean maximum and mean minimum temperatures. Air and water temperatures and salinities at the sites inhabited by L. rudis certainly vary more widely than indicated by Figs. 6, 7 and 8, especially at the up-estuary stations. Indeed, temperatures of up to 38°C were recorded using thermocouples on rocks high on the shore at Culross and salinities as low as 5 to 10‰ in puddles on the shore exposed by the tide at Torrybay after rain.

FIG. 6. Salinities in the Forth estuary.
(data from the Forth River
Purification Board)

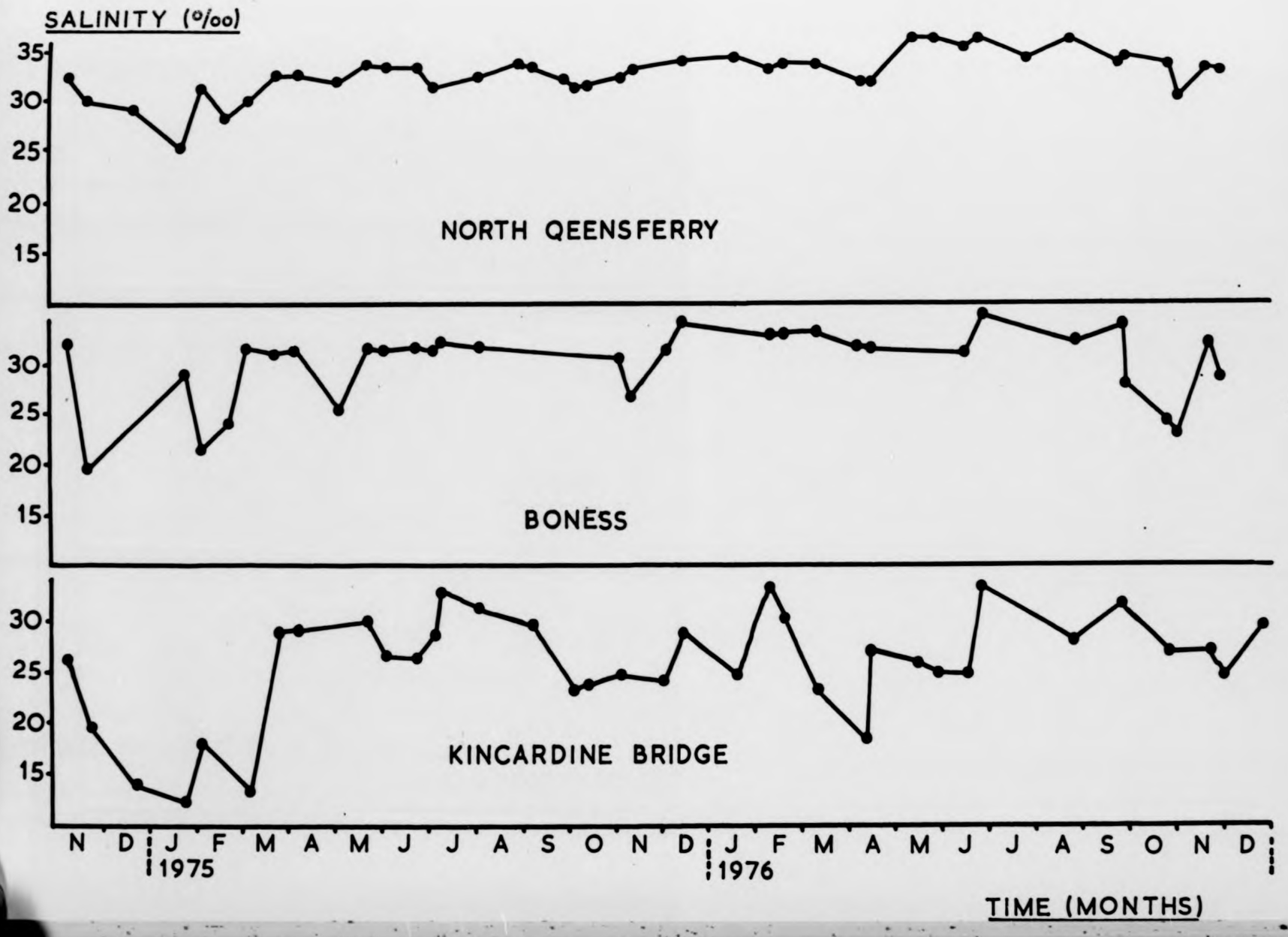

SALINITY (‰)
35
30
25
20
15
NORTH QEENSFERRY
30
25
20
15
BONESS
30
25
20
15
KINCARDINE BRIDGE
N D J F M A M J J A S O N D J F M A M J J A S O N D
1975
1976
TIME (MONTHS)

FIG. 7. Water temperatures in the Forth estuary.

(Data from the Forth River

Purification Board)

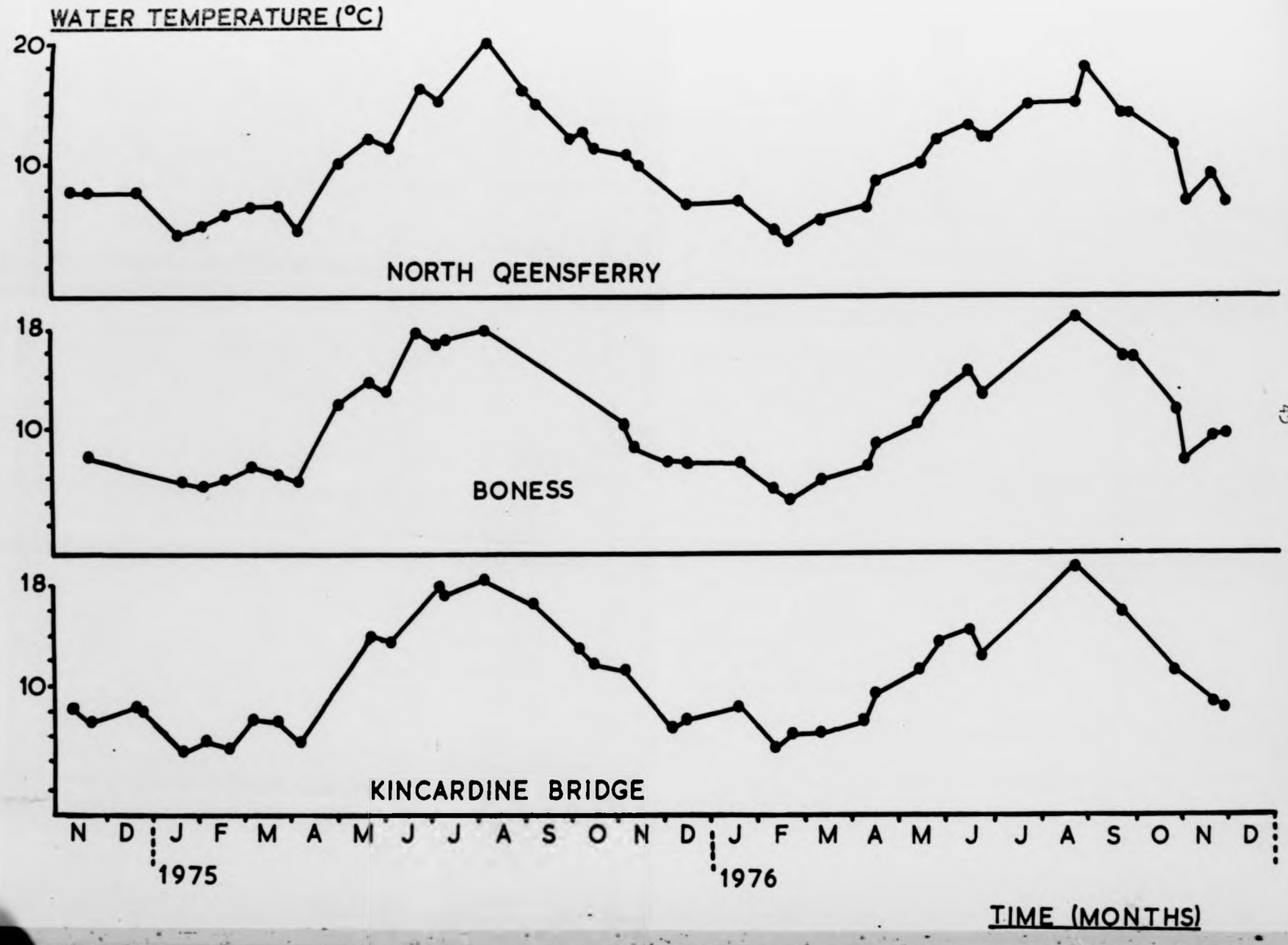
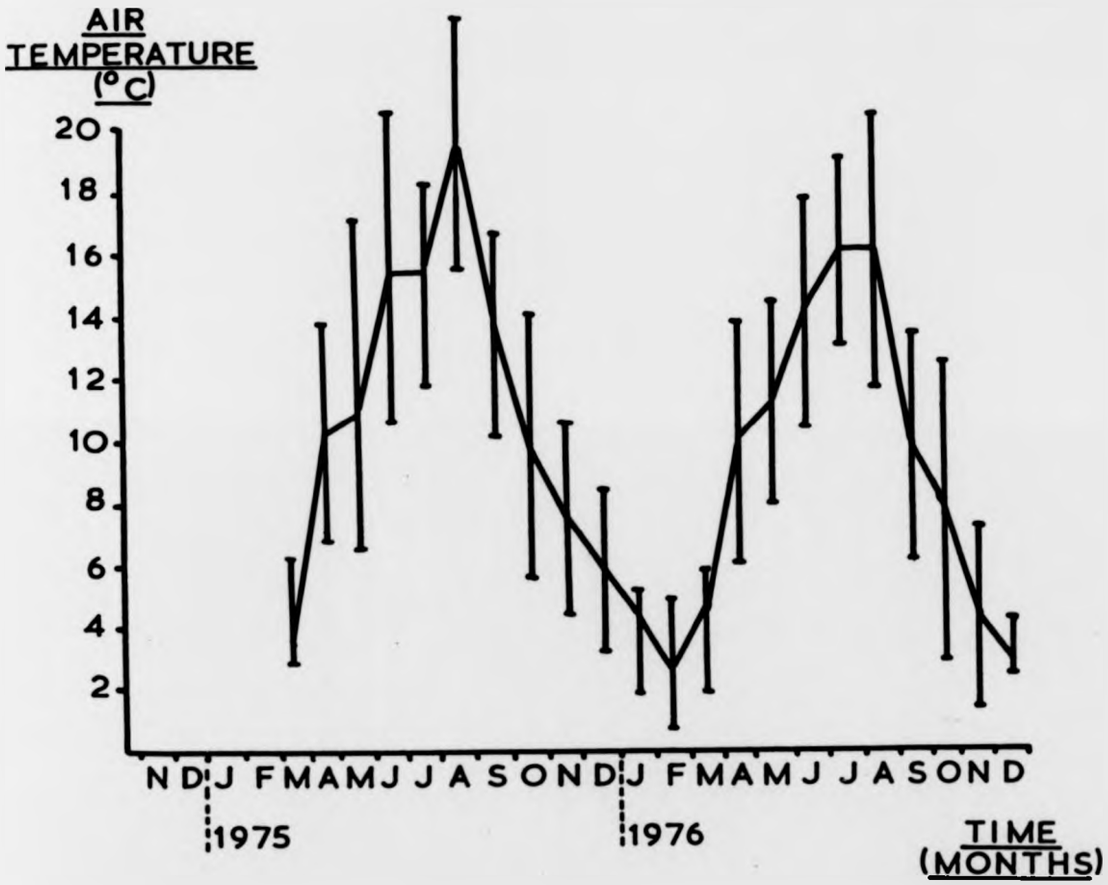

WATER TEMPERATURE (°C)
20
10
NORTH QEENSFERRY
18
10
BONESS
18
10
KINCARDINE BRIDGE
N D J F M A M J J A S O N D J F M A M J J A S O N D
1975
1976
TIME (MONTHS)

FIG. 8. Mean monthly air temperatures at Pitreavie, Fife. The vertical bars extend from the mean monthly minimum to the mean monthly maximum values.


AIR TEMPERATURE (°C)
20
18
16
14
12
10
8
6
4
2
N D J F M A M J J A S O N D J F M A M J J A S O N D
1975
1976
TIME (MONTHS)

2. POPULATIONS

The size range of L. rudis at the four sites differed conspicuously (Table 4). The largest animals occurred at Culross where the maximum shell height was 17 mm and the mean was 11.8 mm. By contrast, the smallest animals were found at Torrybay where the maximum size attained was only 11.5 mm and the mean shell height only 7.3 mm. At Aberdour, the mean shell height at the upper shore site was 11.5 mm while that on the lower shore was only 9.2 mm, both therefore lying between the values at Culross and Torrybay. Although the difference in mean shell height between snails from Aberdour 'H' and Culross was only some 0.3 mm, the maximum shell height at Culross was nearly 2 mm greater than at Aberdour 'H'.

There was considerable variation in the minimum size at which females and males reached maturity at each of the four sites (Table 4). Females from Aberdour 'H' and Culross came to bear eggs and embryos at approximately 7.5 mm whereas females from Aberdour 'L' and Torrybay matured at the significantly smaller sizes of 6.5 mm and 4.5 mm respectively. Males at each site were found to mature (indicated by the growth of a penis and filling of the testes) at about 1 mm smaller than females.

In addition to differences in the size ranges of adults and sizes at maturity, there were also significant differences between the sites in the size of the shell aperture in relation to shell height. The ratio of shell height (SH) to mouth diameter (MD) decreased gradually up the estuary from 1.534 at Aberdour 'H' to

2. POPULATIONS

The size range of L. rudis at the four sites differed conspicuously (Table 4). The largest animals occurred at Culross where the maximum shell height was 17 mm and the mean was 11.8 mm. By contrast, the smallest animals were found at Torrybay where the maximum size attained was only 11.5 mm and the mean shell height only 7.3 mm. At Aberdour, the mean shell height at the upper shore site was 11.5 mm while that on the lower shore was only 9.2 mm, both therefore lying between the values at Culross and Torrybay. Although the difference in mean shell height between snails from Aberdour 'H' and Culross was only some 0.3 mm, the maximum shell height at Culross was nearly 2 mm greater than at Aberdour 'H'.

There was considerable variation in the minimum size at which females and males reached maturity at each of the four sites (Table 4). Females from Aberdour 'H' and Culross came to bear eggs and embryos at approximately 7.5 mm whereas females from Aberdour 'L' and Torrybay matured at the significantly smaller sizes of 6.5 mm and 4.5 mm respectively. Males at each site were found to mature (indicated by the growth of a penis and filling of the testes) at about 1 mm smaller than females.

In addition to differences in the size ranges of adults and sizes at maturity, there were also significant differences between the sites in the size of the shell aperture in relation to shell height. The ratio of shell height (SH) to mouth diameter (MD) decreased gradually up the estuary from 1.534 at Aberdour 'H' to

TABLE 4 Mean and maximum shell heights of L. rudis (≥ 2 mm) and minimum shell height of mature females.

	Mean shell height of L. rudis ≥ 2mm (mm) (± S.D)	Maximum Shell height (mm)	Minimum shell height at maturity of females (mm)
Aberdour 'H'	11.5 (± 2.3)	15.1	7.5
Aberdour 'L'	9.2 (± 1.8)	14.6	6.5
Torrybay	7.3 (± 1.5)	11.5	4.5
Culross	11.8 (± 2.0)	17.0	7.5

1.413 at Culross (Table 5a). The differences between the ratios of shell height to mouth diameter for each population were tested using the special form of the t-test for samples over 30 where

$$^{d}(n_1 + n_2) = \frac{\bar{x}_1 - \bar{x}_2}{\sqrt{\frac{s_1^2}{n_1} + \frac{s_2^2}{n_2}}}$$

n = number in the sample, s = standard deviation of the sample. The confidence interval of the means and values of d show that this ratio is significantly different between all four populations (Table 5b). It is clear that as this ratio decreases, then the area for surface contact through the aperture increases in relation to shell height.

In order to assess in outline the seasonal changes in population density and size composition, a detailed study was carried out at the marine Aberdour site. The highest level occupied by L. rudis on the Aberdour shore was just below MHWS at 5.4 m above chart datum and the lowest level just below MTL at 2.9 m above chart datum (Fig. 9). Although total numbers fluctuated over the year, the distribution across the shore changed little and the greatest numbers always occurred some 10 m down the 40 m length of the rocky shore close to MHWN at 4.8 m above chart datum (Fig. 9).

The annual mean density of snails of shell height $\geq$ 2mm at Aberdour 'H' was 472 m^{-2} (range 360 m^{-2} to 604 m^{-2}) which was about three times the annual mean density of 156 m^{-2} at Aberdour 'L' (range 76 m^{-2} to 232 m^{-2}). Monthly counts at the two stations were generally greater in spring and summer than in winter (Table 6;

TABLE 5a Ratio of shell height (SH) to mouth diameter (MD) for L. rudis at Aberdour 'H' and 'L', Torrybay and Culross.

Site	N	Mean ratio of SH : MD (± SE)	95% Confidence Interval
Aberdour 'H'	201	1.534 (± 0.006)	± 0.012
Aberdour 'L'	210	1.502 (± 0.007)	± 0.015
Torrybay	193	1.459 (± 0.007)	± 0.013
Culross	189	1.413 (± 0.010)	± 0.019

TABLE 5b Calculated values of d for comparison of SH : MD between sites.

	$d_{calc.}$ (df)	Level of significance (P)
Aberdour 'H' vs Aberdour 'L'	3.37(409)	0.001
Aberdour 'H' vs Torrybay	8.19(392)	"
Aberdour 'H' vs Culross	33.31(388)	"
Aberdour 'L' vs Torrybay	56.80(401)	"
Aberdour 'L' vs Culross	9.11(397)	"
Torrybay vs Culross	3.84(380)	"

Tabulated d = 3.291; P = 0.001, d.f. = ∞

FIG. 9. Distribution of **L.rudis** down the shore at **A**berdour.

rdour.

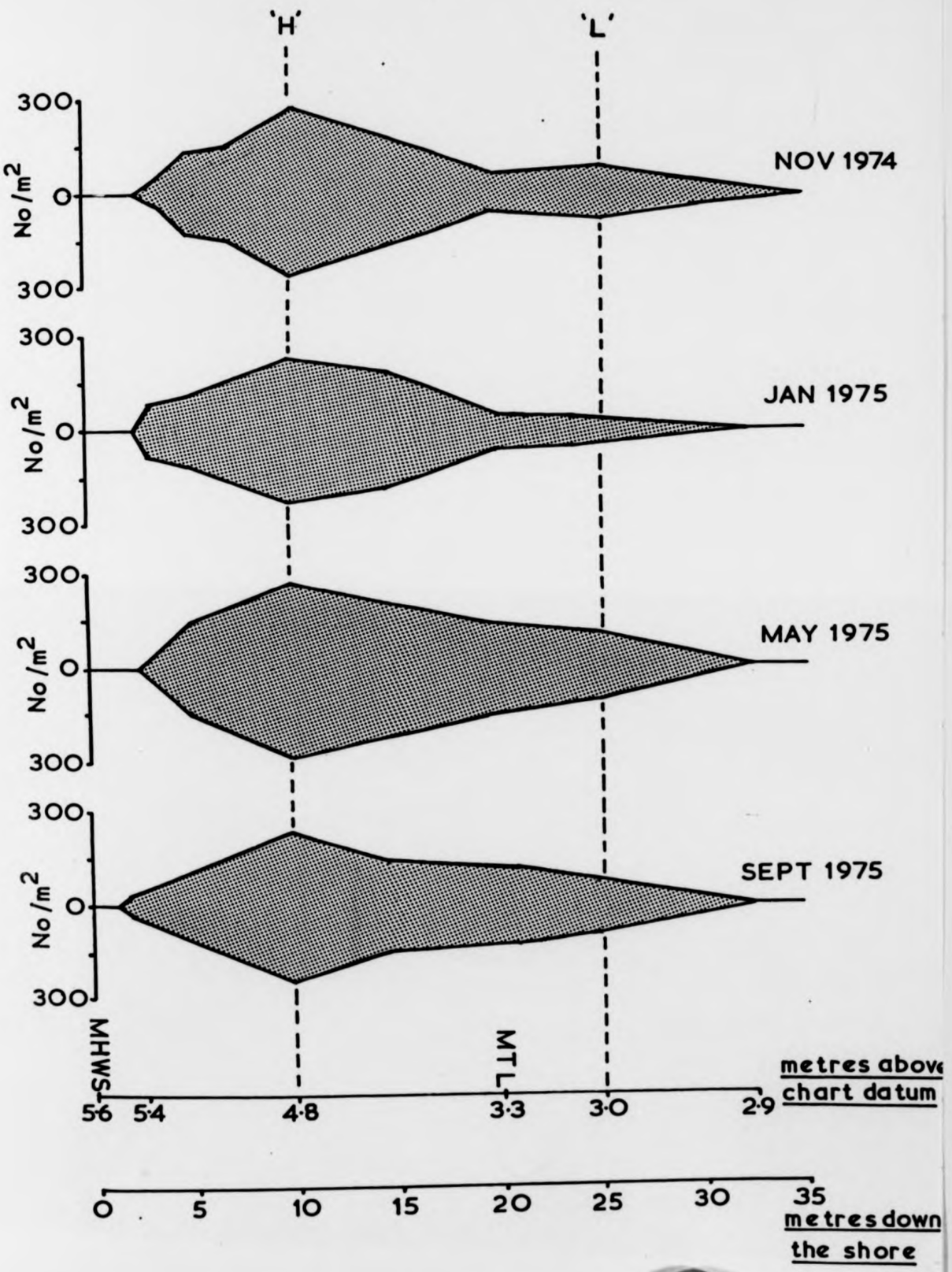

'H'
'L'
300
No/m²
0
300
NOV 1974
JAN 1975
MAY 1975
SEPT 1975
MHWS
MTL
5·6
5·4
4·8
3·3
3·0
2·9
metres above chart datum
0
5
10
15
20
25
30
35
metres down the shore

TABLE 6. Total numbers ($\geq$ 2mm) and numbers of mature and immature L. rudis m^{-2} at Aberdour 'H' and 'L'

Month	Aberdour 'H'				Aberdour 'L'			
	Total numbers m^{-2} ($\geq$ 2mm)	Number mature L. rudis ($\geq$ 7.5mm) m^{-2}	Number immature L. rudis ($\leq$ 7.5mm $\geq$ 2mm) m^{-2}	% Mature L. rudis	Total numbers m^{-2}	Number mature L. rudis ($\geq$ 6.5mm) m^{-2}	Number immature L. rudis ($\leq$ 6.5mm $\geq$ 2mm) m^{-2}	% mature L. rudis
Nov 1974	484	408	76	84	125	97	28	78
Dec	400	356	44	89	76	76	0	100
Jan 1975	472	412	60	87	76	72	4	95
Feb	438	392	46	89	68	56	12	82
Mar	360	292	68	81	193	146	47	76
Apr	370	352	18	95	232	192	40	83
May	560	519	41	93	204	159	45	78
June	604	528	76	87	180	132	48	73
July	561	450	111	80	192	160	32	83
Aug	590	458	132	78	167	136	31	81
Sept	464	306	158	66	144	104	40	72
Oct	360	252	108	70	210	130	80	62
Mean	472	394	78	83	156	122	34	78

Figs. 10, 11). At Aberdour 'H' numbers peaked at 604 m^{-2} in June with lowest counts of 360 m^{-2} in both March and October (Fig. 10). At Aberdour 'L', maximum counts of 232 m^{-2} occurred earlier, in April with low counts of 76 m^{-2} in both December and January (Fig. 11).

Both the upper and lower shore populations were found to be composed predominantly of mature animals (Figs. 12 and 13). It should be noted however, that these distributions do not take into account juveniles of less than 2 mm shell height and in addition it is likely that some animals in the 2 to 4 mm size group were overlooked in counting.

The population on the upper shore was composed of between 66 and 95% mature animals with an annual mean of 83% (Table 6). This calculation was made using the minimum size of mature females (7.5 mm), but as males were found to mature at approximately 1 mm smaller than females, then these figures will be slight underestimates of the true proportion of mature snails in the population.

The Aberdour 'L' population was similarly found to be composed predominantly of mature animals (Table 6). In December 1974 the population consisted entirely of mature animals although this had fallen to 62% by the following October. The annual mean proportion of mature snails in the population was 78% which was slightly lower than the 83% on the upper shore.

Between February and March 1975 there was an almost three-fold increase in the population density at Aberdour 'L' from 68 m^{-2}

FIG.10. Numbers of Littorina rudis per m^2 at Aberdour 'H'.

■ = Total numbers per m^2.

● = Numbers of mature snails per m^2.

o = Numbers of immature snails per m^2.

FIG.11. Numbers of Littorina rudis per m^2 at Aberdour 'L'.

■ = Total numbers per m^2.

● = Numbers of mature snails per m^2.

o = Numbers of immature snails per m^2.

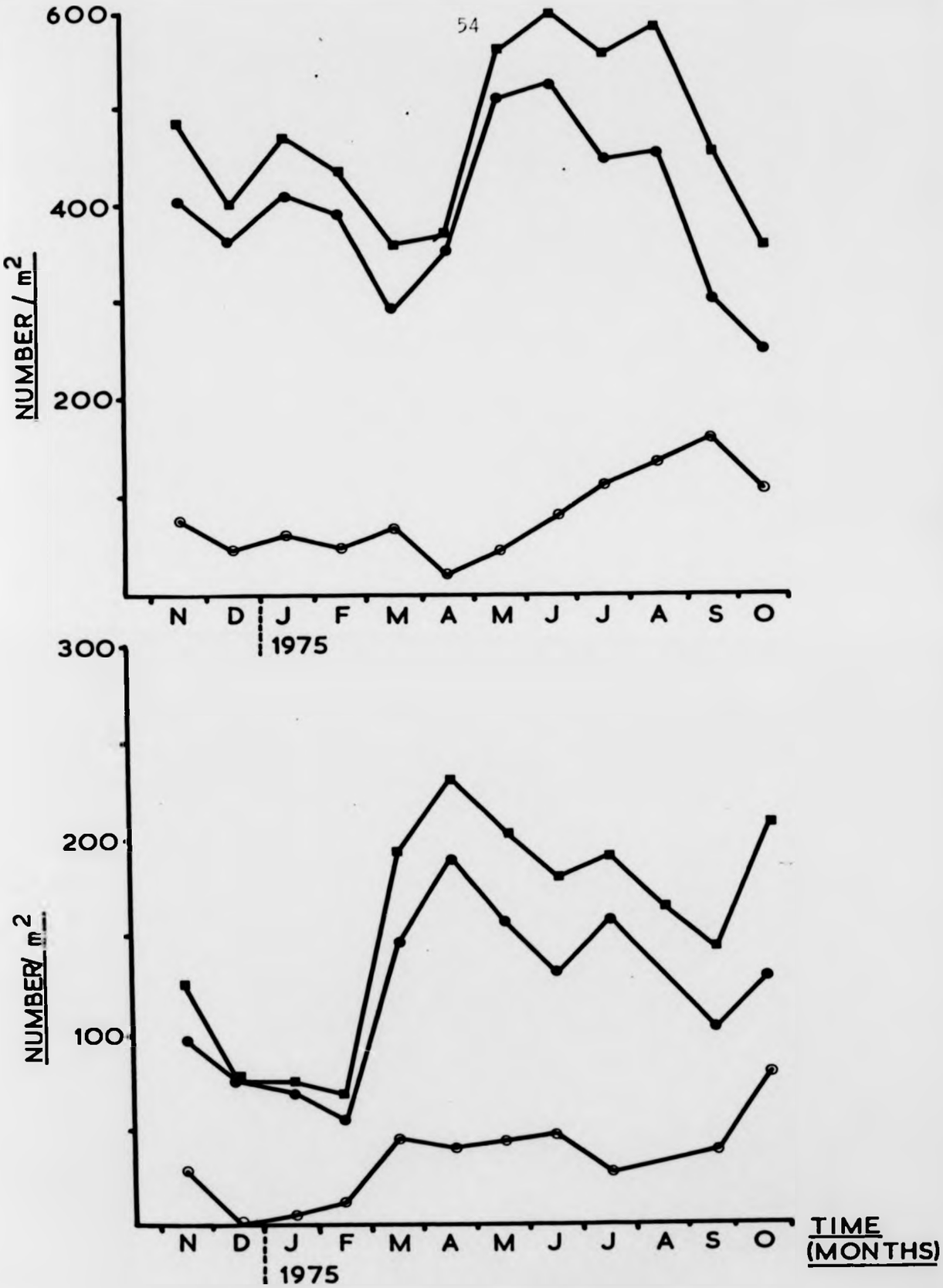

600
400
200
NUMBER / m²
N
D
J
F
M
A
M
J
J
A
S
O
1975
300
200
100
NUMBER / m²
N
D
J
F
M
A
M
J
J
A
S
O
1975
TIME (MONTHS)

FIG.12. Monthly size-frequency histograms for snails greater than 2mm length taken from $1m^2$ quadrats at Aberdour 'H'.

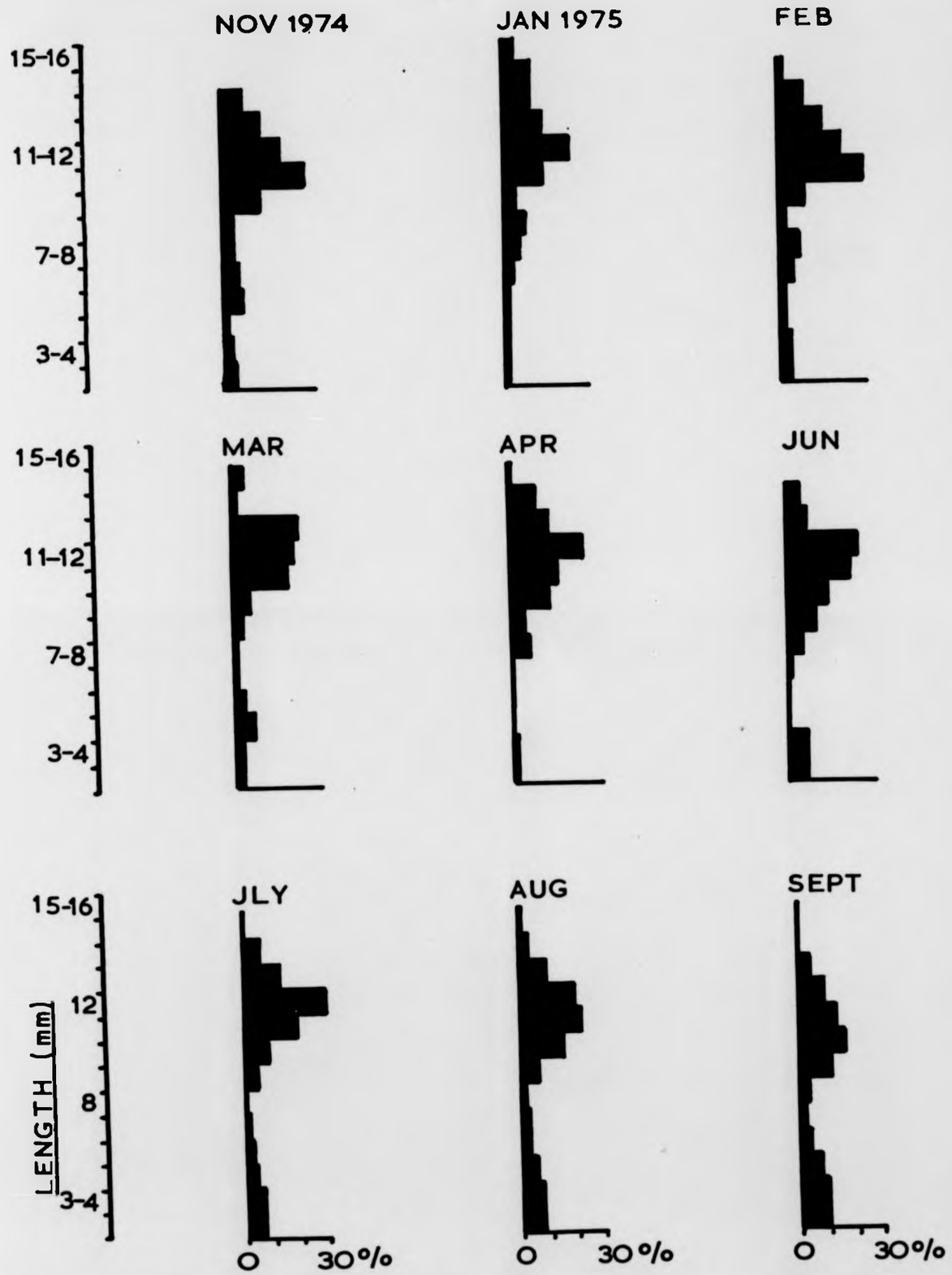
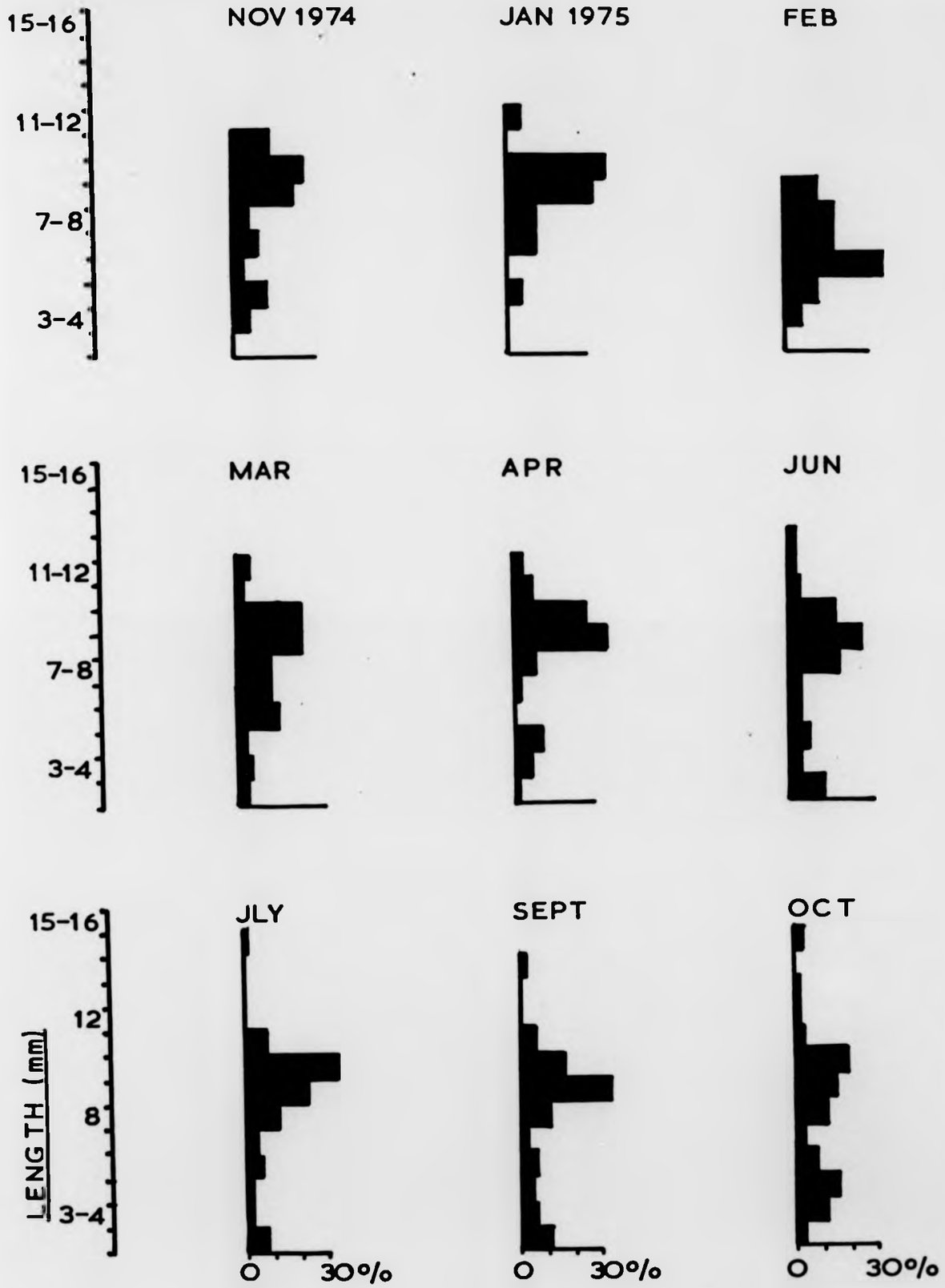

NOV 1974
JAN 1975
FEB
MAR
APR
JUN
JLY
AUG
SEPT
15-16
11-12
7-8
3-4
12
8
LENGTH (mm)
0
30%

FIG. 13. Monthly size-frequency histograms for snails greater than 2mm length taken from $1m^2$ quadrats at Aberdour 'L.'


NOV 1974
JAN 1975
FEB
MAR
APR
JUN
JLY
SEPT
OCT
15-16
11-12
7-8
3-4
12
8
LENGTH (mm)
0
30%

to 193 m^{-2} (Table 6). This increase could only partly be accounted for by recuitment of juveniles into the size classes $\geq$ 2 mm since the number of immature snails rose by only 35 m^{-2} from 12 to 47 m^{-2}. Most of the increase appears to have been the result of recruitment of adults into the population since the number of mature snails rose by 90 m^{-2} from 56 to 146 m^{-2}. At the same time there was a fall in the density of snails on the upper shore from 438 m^{-2} to 360 m^{-2} (Table 6). The number of immature snails rose, however, by 22 m^{-2} from 46 to 68 m^{-2}, therefore the fall in numbers was due either to heavy adult mortality or to adults emigrating. This sudden fall in population density on the upper shore, coupled with a rise on the lower shore suggests possible downshore migrations.

At Aberdour 'H', the density of immature snails ($\geq$ 2 mm $\leq$ 7.5 mm) was relatively constant at between 44 and 76 m^{-2} through the winter from November to March (Fig. 10). Numbers fell between March and April to only 18 m^{-2} before rising gradually through the spring and summer to more than 150 m^{-2} in September, falling again in October. As with the mature snails, immatures at Aberdour 'L' ($\geq$ 2 mm $\leq$ 6.5 mm) changed slightly differently from those at Aberdour 'H' (Fig. 11). Numbers were very low in mid-winter, rose to nearly 50 m^{-2} from March to September, except for a decrease to 32 m^{-2} in July, and reached a maximum of 80 m^{-2} in October. In very broad terms, the changing numbers at the two Aberdour shore levels followed similar trends but with the low shore snails leading the upshore ones by about 3 months (Figs. 10, 11).

The continuous nature of reproduction in L. rudis renders the study of population cohorts extremely difficult. Shifts of relative abundance among the size classes however, provide some slight evidence of growth rate (Figs. 12 and 13). At Aberdour 'H' the total number of mature animals rose from 292 m^{-2} to 352 m^{-2} between March and April 1975, corresponding to an increase of 14% from 81 to 95% of the population. Concomitantly, there was a fall in the proportion of immature snails in the 4 - 6 mm size class, from 11 to 2% of the population, which could not be accounted for by growth into the next size classes (Fig. 12). This "marker-gap" had moved to the 5 - 7 mm size class in June and the 7 - 8 mm group in July. The rate at which the "marker-gap" moved through the size classes of the population suggests that young snails grew at a rate of about 1 mm per month, at least within the 4 - 8 mm size range.

Similar trends were found at the lowshore site (Fig. 13) where the proportion of immature L. rudis in the population fell by 7% from 24 to 17% between March and April 1975 (Table 6). The number of snails in the 5 - 6 mm size group appears to have been the most severely affected since this size class contained 14% of the population in March but none in April (Fig. 13). This fall could not be explained by the growth of snails into the 6 - 8 mm size class since numbers in this size range also fell between March and April. There is some evidence of passage of a cohort of snails of shell height 2 to 3 mm in June/July to the 5 to 6 mm size class in September/October. This again suggests a growth rate of about 1 mm per month between sizes 2 mm to 6 mm.

3. BODY COMPOSITION

When plotted on logarithmic scales the relationships between ash-free dry weight (AFDW) and shell height (SH) at each site were found to be linear (Table 7; Fig 14). Regression equations include values for both males and females since sexual differences were found not to be significant.

Upon considering seasonal weight changes (derived from these equations) in animals of mean size in each of the populations (Table 8) a winter decline in flesh weight was observed at Aberdour 'H' (23.81 mg in November 1974 - 22.31 mg in January 1975 for an 11.5 mm snail), Torrybay (8.94 mg - 8.40 mg for a 7.3 mm snail) and Culross (29.37 mg - 26.82 for an 11.8 mm snail). At Aberdour 'L' however flesh weight of a 9.2 mm snail rose slightly from 13.77 mg in November 1974 to 14.31 mg in January 1975. Between January and May 1975 the weight of an 11.8 mm snail at Culross is indicated as having fallen slightly to 25.33 mg but at Aberdour 'H', Aberdour 'L' and Torrybay flesh weight rose to 24.61 mg, 14.64 mg and 9.07 mg respectively. During the late spring and summer the weights of snails from Aberdour 'H' and 'L' remained relatively constant and were 17.78 mg and 17.22 mg respectively in September. Over this period the weight of a 7.3 mm snail at Torrybay fell to 8.07 mg whereas the weight of an 11.8 mm snail at Culross rose slightly to 26.14 mg (Table 8).

Differences in flesh weight between sites can only be evaluated by comparing the weights of standard-sized animals.

TABLE 7 Linear regression equations correlating $\log_{10}$ ash-free dry weight (w) to $\log_{10}$ shell height (h) for L. rudis from Aberdour 'H' and 'L', Torrybay and Culross in November 1974 and January, May and September 1975

Site	Month	Regression equation	S.E. of b	r	P	n
Aberdour 'H'	Nov 1974	$\log_{10} w = 2.583 \log_{10} h - 1.363$	0.142	0.974	0.001	30
	Jan 1975	$\log_{10} w = 3.057 \log_{10} h - 1.894$	0.192	0.981	"	"
	May 1975	$\log_{10} w = 2.441 \log_{10} h - 1.198$	0.131	0.962	"	"
	Sep 1975	$\log_{10} w = 2.302 \log_{10} h - 1.051$	0.089	0.982	"	"
Aberdour 'L'	Nov 1974	$\log_{10} w = 3.602 \log_{10} h - 2.336$	0.195	0.973	0.001	30
	Jan 1975	$\log_{10} w = 3.269 \log_{10} h - 1.998$	0.221	0.961	"	"
	May 1975	$\log_{10} w = 2.986 \log_{10} h - 1.715$	0.132	0.974	"	"
	Sep 1975	$\log_{10} w = 2.334 \log_{10} h - 1.098$	0.116	0.970	"	"
Torrybay	Nov 1974	$\log_{10} w = 2.661 \log_{10} h - 1.346$	0.201	0.952	0.001	30
	Jan 1975	$\log_{10} w = 1.952 \log_{10} h - 0.761$	0.320	0.821	"	"
	May 1975	$\log_{10} w = 1.750 \log_{10} h - 0.553$	0.090	0.965	"	"
	Sep 1975	$\log_{10} w = 2.746 \log_{10} h - 1.464$	0.238	0.936	"	"
Culross	Nov 1974	$\log_{10} w = 2.821 \log_{10} h - 1.560$	0.174	0.972	0.001	30
	Jan 1975	$\log_{10} w = 2.652 \log_{10} h - 1.418$	0.185	0.957	"	"
	May 1975	$\log_{10} w = 2.857 \log_{10} h - 1.663$	0.162	0.958	"	"
	Sep 1975	$\log_{10} w = 2.703 \log_{10} h - 1.484$	0.183	0.961	"	"

FIG. 14. The relationship between $\log_{10}$ length and $\log_{10}$ ash-free dry weight (A.F.D.W.).

A = November 1974

B = January 1975

C = May 1975

D = September 1975

□ = Aberdour 'H'

■ = Aberdour 'L'

▲ = Torrybay

● = Culross

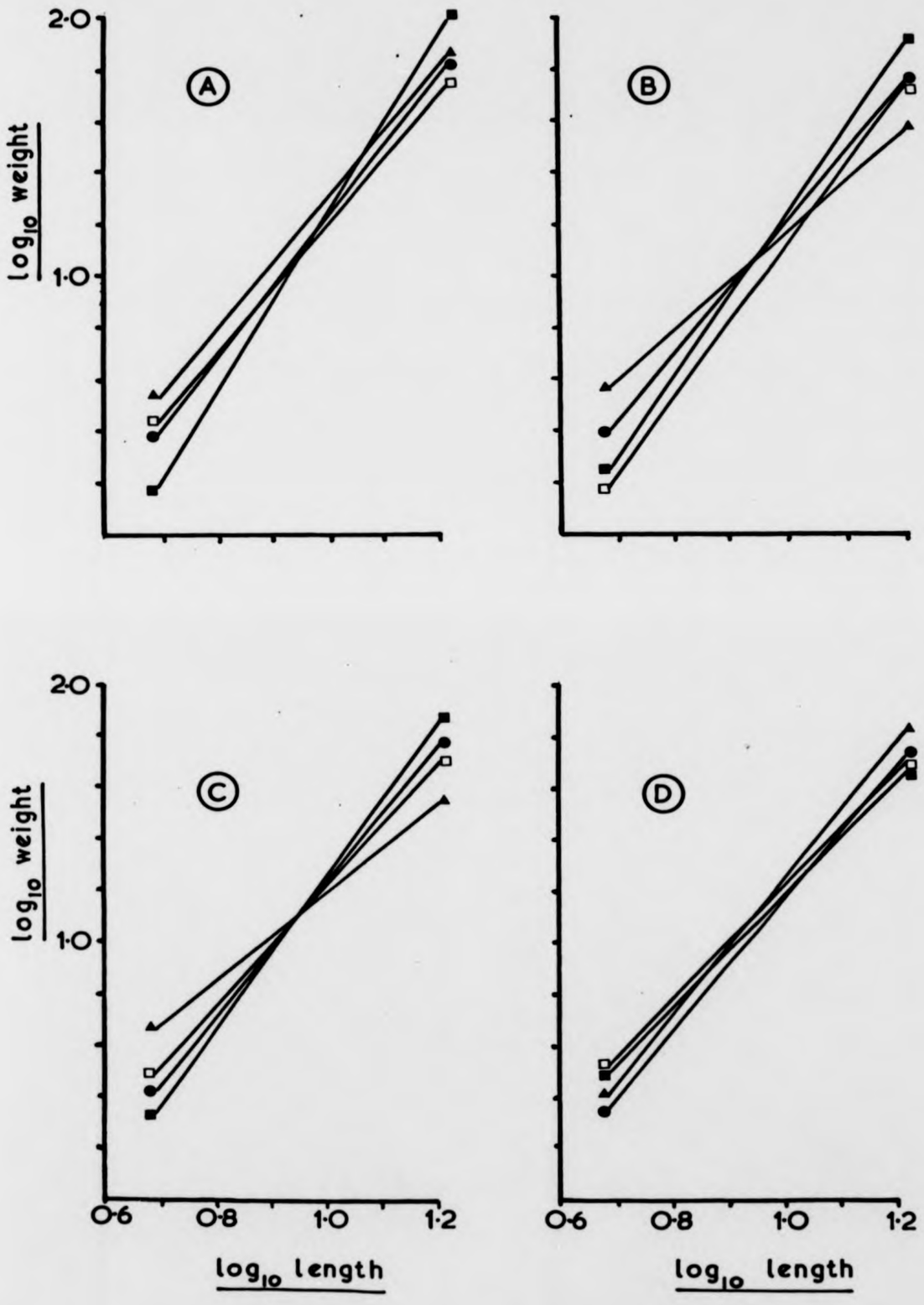

2·0
1·0
log10 weight
A
B
C
D
0·6
0·8
1·0
1·2
log10 length

TABLE 8 Ash-free dry weight of a standard 10 mm *L. rudis* and of an animal representing the mean shell height at Aberdour 'H', Aberdour 'L', Torrybay and Culross

Site	Shell height (mm)	Ash-free dry weight (mg)				
		Nov 1974	Jan 1975	May 1975	Sept 1975	Annual mean
Aberdour 'H'	10.0	16.60	14.55	17.50	17.78	16.61
	11.5	23.81	22.31	24.61	24.59	23.83
Aberdour 'L'	10.0	18.45	18.62	18.66	17.22	18.24
	9.2	13.77	14.31	14.64	14.25	14.25
Torrybay	10.0	20.65	15.52	15.74	19.14	17.76
	7.3	8.94	8.40	9.07	8.07	8.62
Culross	10.0	18.24	17.14	15.63	16.56	16.89
	11.8	29.37	26.82	25.33	26.14	26.92

TABLE 8 Ash-free dry weight of a standard 10 mm L. rudis and of an animal representing the mean shell height at Aberdour 'H', Aberdour 'L', Torrybay and Culross

Site	Shell height (mm)	Ash-free dry weight (mg)				
		Nov 1974	Jan 1975	May 1975	Sept 1975	Annual mean
Aberdour 'H'	10.0	16.60	14.55	17.50	17.78	16.61
	11.5	23.81	22.31	24.61	24.59	23.83
Aberdour 'L'	10.0	18.45	18.62	18.66	17.22	18.24
	9.2	13.77	14.31	14.64	14.25	14.25
Torrybay	10.0	20.65	15.52	15.74	19.14	17.76
	7.3	8.94	8.40	9.07	8.07	8.62
Culross	10.0	18.24	17.14	15.63	16.56	16.89
	11.8	29.37	26.82	25.33	26.14	26.92

10 mm was selected as the most appropriate size for a standard animal at Aberdour 'H', Aberdour 'L' and Culross, although 10 mm lay near to the upper size limit of snails from Torrybay (Table 4).

Seasonal changes in flesh weight were most pronounced at Torrybay where the estimated weight of a standard 10 mm animal fluctuated between 20.65 mg in November 1974 and 15.52 mg in January 1975 (Table 8). Seasonal trends in weight were least discernable in snails from Aberdour 'L' where the weight of a standard 10 mm snail changed by only 1.4 mg from 18.66 mg in May to 17.22 mg in September 1975. The amplitude of weight changes at Aberdour 'H' (14.55 mg in January to 17.78 mg in September) and Culross (15.63 mg in May to 18.24 mg in November) fell between the situations at Torrybay and Aberdour 'L'.

Although scarce at this site, Torrybay supported the heaviest standard 10 mm animals (20.65 mg in November 1974) contrasting with the lightest (14.55 mg in January 1975) at Aberdour 'H', a gross difference of almost 30% when considered in terms of annual mean weights (Table 8), the heaviest 10 mm snail occurred at Aberdour 'L' (18.23 mg) followed by Torrybay (17.76 mg), Culross (16.89 mg) and the lightest at Aberdour 'H' (16.61 mg).

There were no significant seasonal changes in condition factor (Tables 9, 10) at any of the sampling sites. This suggests that the flesh of the snails grew in proportion to the shell throughout the year and that there were no sudden changes in condition associated with overwintering or increased reproductive activity.

TABLE 9 Condition factor of L. rudis on four occasions between November 1974 and September 1975.

Site	Month	Size range (mm)	Condition factor	SE *
Aberdour 'H'	November 1974	7.9-12.6	1.640	0.036
	January 1975	8.0-14.1	1.639	0.080
	May 1975	8.1-13.2	1.672	0.026
	September 1975	7.8-13.8	1.736	0.060
	Annual mean		1.672	
Aberdour 'L'	November 1974	7.6-12.9	1.830	0.059
	January 1975	7.2-10.8	1.817	0.044
	May 1975	8.5-11.6	1.868	0.021
	September 1975	6.8-12.8	1.813	0.067
	Annual mean		1.832	
Torrybay	November 1974	6.1-10.0	2.241	0.055
	January 1975	6.4-9.3	2.168	0.083
	May 1975	6.0-9.5	2.260	0.058
	September 1975	5.9-9.7	2.077	0.101
	Annual mean		2.1865	
Culross	November 1974	8.5-14.3	1.691	0.036
	January 1975	8.8-12.9	1.620	0.043
	May 1975	7.8-13.1	1.570	0.039
	September 1975	8.2-13.7	1.651	0.059
	Annual mean		1.633	

TABLE 10 Significance of differences in condition factor of L. rudis between sites and between months

Source of variation	Level of significance (P)
Within sites between months	Not significant
Between Aberdour 'H' and Aberdour 'L'	0.01
Between Aberdour 'H' and Torrybay	0.001
Between Aberdour 'H' and Culross	Not significant
Between Aberdour 'L' and Torrybay	0.001
Between Aberdour 'L' and Culross	0.01
Between Torrybay and Culross	0.001

* n = 30

Analysis of variance did reveal significant differences in condition factor between sites in all cases except between Aberdour 'H' and Culross (Table 10). L. rudis from Torrybay had the highest annual mean condition factor (2.1865) and those from Aberdour 'H' (1.672) and Culross (1.623) the lowest. The condition factor of Aberdour 'L' snails (1.832) fell between these extremes. Thus these values reflect the relationship established above in AFDW's of standard 10 mm animals.

At each of the 4 sampling sites, levels of carbon, nitrogen and hydrogen in both females and males fluctuated over the period November 1974 to November 1975 (Tables 11, 12, 13, 14). There were no statistically significant differences in the levels of carbon, nitrogen and hydrogen between sites, but within all sites, values between males and females were always found to be significantly different (Table 15). Generally, levels of both carbon and nitrogen in males were higher than in females at all sites (Tables 11 - 14) even though AFDW's were not significantly different.

Levels of carbon in females fluctuated about a mean of 372.2 mg g^{-1} dry flesh weight within the range 340 to 413 mg g^{-1} dry flesh weight (Tables 11 - 14) while in males, the mean carbon level was 393.3 mg g^{-1} dry flesh weight with an annual range of 346 to 433 mg g^{-1} dry flesh weight. The mean level of nitrogen in females was 91.3 mg g^{-1} dry flesh weight (range = 77 to 101 mg g^{-1}). Males had an annual nitrogen content of 100.6 mg g^{-1} (range = 81 to 115 mg g^{-1}).

Although shifts in carbon: nitrogen ratios (C : N) were apparent (Fig 15; Tables 11 - 14), the interpretation of these was

TABLE 11 Mean monthly carbon, nitrogen and hydrogen content of male and female L. rudis from Aberdour 'H'

Month	Carbon (mg g^{-1})			Nitrogen (mg g^{-1})			Hydrogen (mg g^{-1})		C : N		C : H	
	Female	Male	Shell	Female	Male	Shell	Female	Male	Female	Male	Female	Male
Nov 1974	379.3	428.0	129.2	89.6	104.3	negligible	59.2	67.5	4.23	4.10	6.41	6.34
Dec	406.1	425.6	120.7	92.2	102.7	"	63.2	65.8	4.40	4.14	6.43	6.47
Jan 1975	388.7	397.8	116.2	94.5	99.2	"	60.3	63.7	4.11	4.01	6.45	6.24
Feb	374.9	397.2	120.9	84.9	97.6	"	56.1	64.6	4.42	4.07	6.68	6.15
Mar	372.1	410.5	129.4	87.0	105.1	"	55.7	64.0	4.28	3.91	6.68	6.41
Apr	360.2	419.0	122.0	77.5	100.9	"	55.0	65.3	4.65	4.15	6.55	6.42
May	356.2	422.9	123.3	78.1	103.1	"	55.9	68.2	4.56	4.10	6.37	6.20
June	367.3	412.6	122.6	83.6	107.9	"	54.6	67.4	4.39	3.83	6.73	6.12
July	374.0	367.4	117.7	90.9	92.6	"	54.3	54.8	4.11	3.97	6.89	6.70
Aug	376.6	398.9	122.4	93.2	105.9	"	60.1	63.2	4.04	3.77	6.27	6.31
Sept	378.2	402.0	118.8	97.2	100.1	"	58.8	61.0	3.98	4.02	6.59	6.59
Oct	341.6	384.4	128.8	80.7	96.0	"	50.7	56.6	4.23	4.00	6.74	6.79
Nov	358.5	369.5	127.5	83.8	91.6	"	51.8	53.9	4.28	4.03	6.92	6.86
Mean	372.5 (±4.6)	402.8 (±5.5)	123.0 (±1.2)	87.2 (±1.8)	101.3 (±1.4)	"	56.6 (±1.0)	62.8 (±1.1)	4.27	3.98	6.58	6.42

TABLE 12 Mean monthly carbon, nitrogen and hydrogen content of male and female L. rudis from Aberdour 'H'

Month	Carbon (mg g^{-1})			Nitrogen (mg g^{-1})			Hydrogen (mg g^{-1})		C : N		C : H	
	Female	Male	Shell	Female	Male	Shell	Female	Male	Female	Male	Female	Male
Nov 1974	356.1	378.2	118.0	85.2	97.7	negligible	52.6	59.0	4.18	3.87	6.77	6.41
Dec	384.3	427.1	119.6	94.1	114.2	"	54.8	64.6	4.08	3.74	7.01	6.61
Jan 1975	374.3	400.6	112.0	98.6	101.4	"	58.4	61.3	3.80	3.95	6.41	6.54
Feb	396.0	413.5	126.0	99.1	102.5	"	56.1	61.0	4.00	4.03	7.06	6.78
Mar	357.3	382.8	115.9	90.0	97.3	"	52.2	52.7	3.97	3.93	6.84	7.26
Apr	368.6	396.2	117.7	96.7	109.5	"	55.0	65.3	3.81	3.62	6.70	6.07
May	364.8	380.7	119.3	93.9	105.1	"	55.9	63.5	3.89	3.62	6.53	6.00
June	361.7	370.6	117.6	89.3	100.2	"	56.3	62.8	4.05	3.70	6.43	5.90
July	364.4	367.7	116.7	91.7	97.4	"	54.5	59.4	3.97	3.78	6.69	6.19
Aug	387.2	393.3	121.8	97.0	102.6	"	60.6	62.8	3.99	3.83	6.39	6.26
Sept	388.3	393.1	123.6	100.8	102.3	"	60.5	59.6	3.85	3.84	6.42	6.60
Oct	354.1	382.7	123.3	91.5	103.3	"	53.3	62.2	3.87	3.70	6.64	6.15
Nov	365.6	391.7	134.1	92.7	107.6	"	53.6	63.7	3.94	3.64	6.82	6.15
Mean	371.0 (±3.8)	390.6 (±4.6)	120.4 (±1.5)	93.9 (±1.2)	103.2 (±1.4)	"	55.7 (±0.9)	61.4 (±0.9)	3.95	3.79	6.66	6.36

TABLE 13 Mean monthly carbon, nitrogen and hydrogen content of male and female L. rudis from Torrybay

Month	Carbon (mg g^{-1})			Nitrogen (mg g^{-1})			Hydrogen (mg g^{-1})		C : N		C : H	
	Female	Male	Shell	Female	Male	Shell	Female	Male	Female	Male	Female	Male
Nov 1974	387.9	380.1	119.5	93.2	97.9	negligible	60.9	59.1	4.16	3.88	6.37	6.43
Dec	412.3	432.1	121.9	92.1	107.7	"	56.9	64.2	4.48	4.01	7.25	6.73
Jan 1975	353.1	412.6	131.3	87.0	89.3	"	53.9	54.2	4.06	4.62	6.55	6.62
Feb	381.6	405.0	122.5	90.0	85.8	"	55.6	57.7	4.24	4.72	6.86	7.02
Mar	382.0	386.0	114.8	101.0	109.8	"	58.7	59.7	3.78	3.51	6.51	6.47
Apr	377.5	383.9	118.0	97.6	94.9	"	60.5	59.0	3.87	4.05	6.24	6.51
May	371.5	374.1	119.6	93.8	95.4	"	61.2	60.3	3.96	3.92	6.07	6.20
June	365.4	385.6	120.0	92.9	93.0	"	60.0	61.4	3.93	4.15	6.09	6.28
July	352.4	401.9	125.8	86.2	89.9	"	53.3	60.1	40.0	4.47	6.61	6.69
Aug	382.6	381.5	130.6	93.3	97.1	"	61.4	66.4	4.10	3.93	6.23	5.75
Sept	394.6	381.6	127.3	98.6	92.2	"	58.5	57.0	4.00	4.14	6.75	6.69
Oct	357.9	347.4	134.0	86.6	92.7	"	56.8	56.1	4.13	3.75	6.30	6.19
Nov	340.4	346.5	120.0	81.8	81.0	"	49.7	49.1	4.16	4.28	6.85	6.59
Mean	373.8 (±5.5)	386.0 (±5.3)	123.5 (±1.6)	91.9 (±1.5)	94.4 (±1.8)	"	57.5 (±1.0)	58.8 (±1.2)	4.07	4.09	6.50	6.57

TABLE 14 Mean monthly carbon, nitrogen and hydrogen content of male and female L. rudis from Culross

Month	Carbon (mg g^{-1})			Nitrogen (mg g^{-1})			Hydrogen (mg g^{-1})		C : N		C : H	
	Female	Male	Shell	Female	Male	Shell	Female	Male	Female	Male	Female	Male
Nov 1974	381.1	399.5	119.2	92.6	89.8	negligible	58.8	62.4	4.12	4.45	6.48	6.40
Jan 1975	373.9	402.6	126.2	92.2	105.8	"	56.4	61.9	4.06	3.81	6.63	6.50
Feb	390.0	401.4	122.5	91.0	99.4	"	58.8	61.1	4.29	4.04	6.63	6.57
Mar	363.2	408.2	119.3	92.6	112.5	"	58.5	62.3	3.92	3.63	6.21	6.55
Apr	366.8	385.2	126.7	94.1	109.3	"	59.0	65.4	3.90	3.80	6.56	6.35
May	358.9	375.8	122.3	91.8	106.4	"	58.8	64.8	3.91	3.53	6.10	5.80
June	356.7	416.0	118.5	89.9	107.2	"	59.2	65.0	3.97	3.88	6.65	6.40
July	393.5	398.4	122.2	96.6	95.6	"	52.9	59.5	4.07	4.17	6.76	6.70
Aug	373.2	388.5	117.3	92.8	100.8	"	58.2	66.0	4.02	3.85	6.41	5.89
Sept	345.3	383.4	117.6	85.1	100.0	"	52.7	59.1	4.06	3.83	6.55	6.49
Oct	354.6	390.1	117.8	89.2	105.6	"	53.7	59.1	3.98	3.69	6.60	6.60
Nov	398.0	376.2	120.8	99.7	108.3	"	58.2	62.1	3.99	3.47	6.84	6.06
Mean	371.3 (±4.8)	393.8 (±3.6)	120.9 (±0.9)	92.3 (±1.1)	103.4 (±1.7)	"	57.1 (±0.7)	62.4 (±0.7)	4.02	3,81	6.50	6.31

TABLE 15 Significance of differences in carbon, nitrogen and hydrogen content of *L. rudis* between sites and between males and females

Source of variation	Level of significance (P)		
	Carbon	Nitrogen	Hydrogen
Between males and females	0.001	0.025	0.01
Between sites	Not significant	Not significant	Not significant

FIG.15. Seasonal variation in carbon:nitrogen ratio in male and female L.rudis.

A = Aberdour 'H'

B = Aberdour 'L'

C = Torrybay

D = Culross

■ = male

● = female

FIG.15. Seasonal variation in carbon:nitrogen ratio in male and female L.rudis.

A = Aberdour 'H'

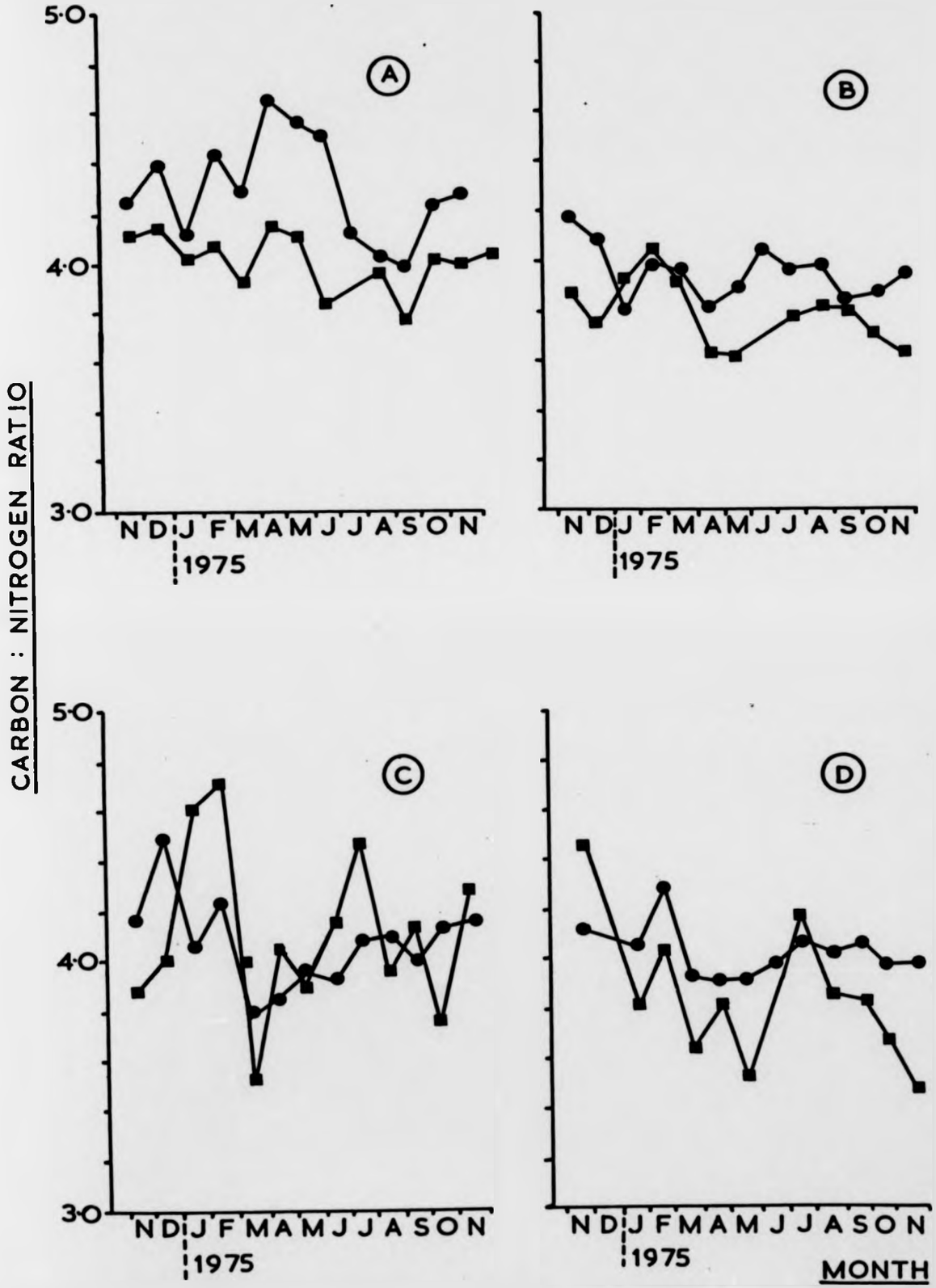
B = Aberdour 'L'

C = Torrybay

D = Culross

■ = male

● = female


5·0
4·0
3·0
A
B
C
D
N D J F M A M J J A S O N
1975
CARBON : NITROGEN RATIO
MONTH

complicated by the absence of a discrete breeding season in L. rudis The C : N ratio of males fluctuated least at the two Aberdour sites (between 3.62 and 4.15) whereas at Torrybay (3.51 - 4.72) and Culross (3.47 - 4.45) males experienced relatively wide fluctuations in C : N ratios (Fig 15). At Culross, C : N ratios of males peaked in both November 1974 (4.45) and July 1975 (4.07) compared with February 1975 (4.72) and July 1975 (4.47) at Torrybay (Fig;15 Tables 11 - 14).

Females at Aberdour 'L'(range =3.8 - 4.18) and Torrybay (range = 3.78 - 4.48) exhibited similar trends in C : N ratios, with peak values in winter followed by minima in the spring, gradually rising again during the summer and autumn (Fig 15; Tables 11 - 14). At Aberdour 'H' however the peak C : N ratio did not occur until April 1975 (4.65) after which there was a gradual decline to the lowest levels in September (3.98). C : N ratios of females at Culross exhibited the least seasonal variation (3.90 - 4.29).

Levels of nitrogen per g flesh dry weight were converted to protein by employing the generally accepted conversion factor of 6.25 (Fig 16; Table 16). Protein content per g flesh dry weight ranged from 714 mg in males from Aberdour 'L' in December 1974 to 484 mg in females from Aberdour 'H' in April 1975 (Fig 16).

In general, protein levels derived from these results fell in the spring and/or the summer suggesting possible utilisation of proteins for reproductive products at this time (Fig 16). It was difficult from these analyses to establish whether the snails stored fats prior to overwintering, but since snails were heaviest between

FIG.16. Seasonal variation in protein levels in male and female L.rudis.

A = Aberdour 'H'

B = Aberdour 'L'

C = Torrybay

D = Culross

■ = male

● = female

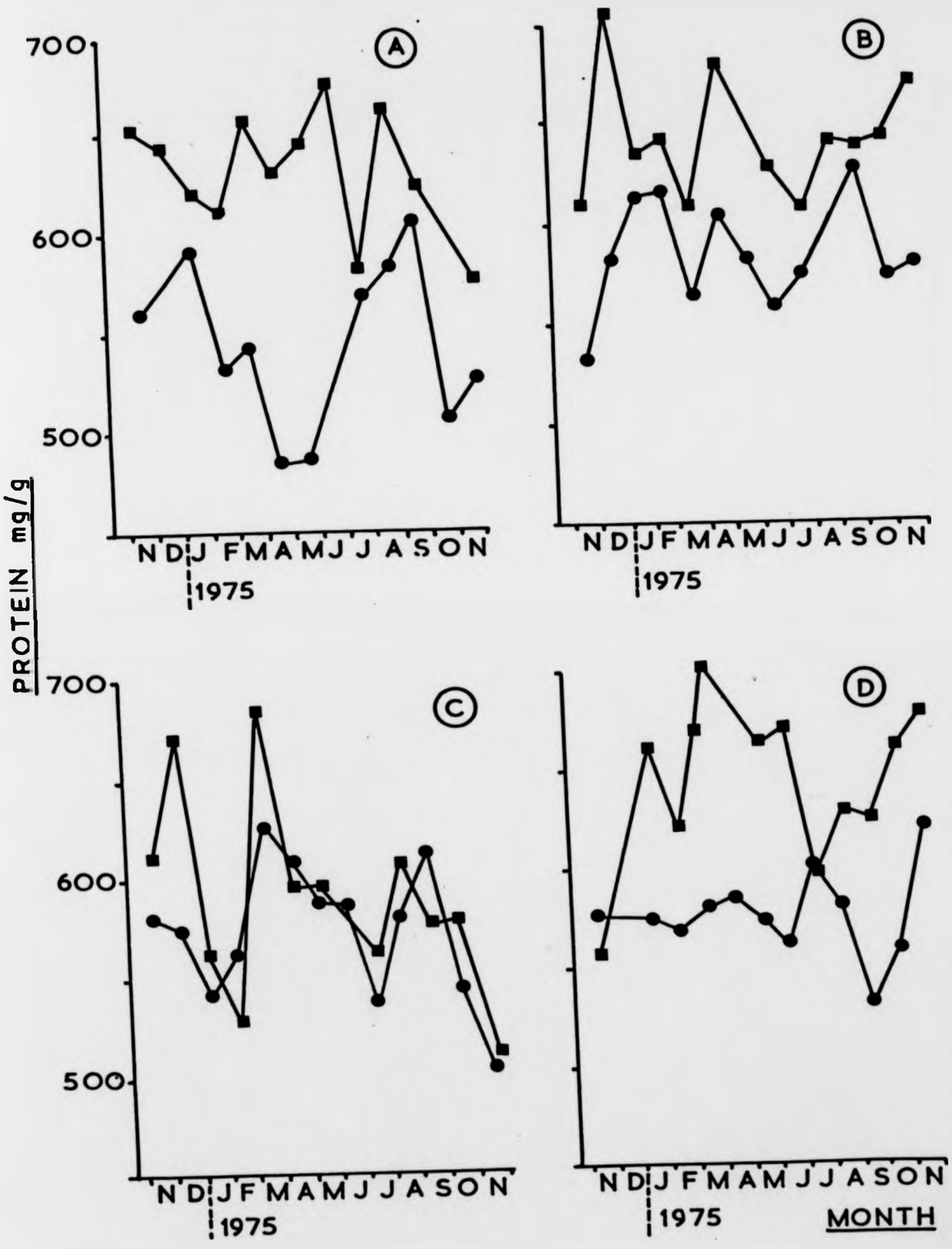

A
B
C
D
700
600
500
PROTEIN mg/g
N D J F M A M J J A S O N
1975
MONTH

TABLE 16 Mean energy and protein content and ratio of carbon to nitrogen of male and female L. rudis from Aberdour 'H', Aberdour 'L', Torrybay and Culross.

Site	Energy						Protein mgg^{-1} DW		C : N	
	Female			Male						
	gCg^{-1} flesh DW	gCg^{-1} AFDW	kJg^{-1} AFDW	gCg^{-1} flesh DW	gCg^{-1} AFDW	kJg^{-1} AFDW	Female	Male	Female	Male
Aberdour 'H'	0.3725	0.4388	19.00	0.4028	0.4744	20.54	545	628	4.27	3.98
Aberdour 'L'	0.3710	0.4370	18.92	0.3906	0.4601	19.92	587	645	3.95	3.79
Torrybay	0.3738	0.4403	19.06	0.3860	0.4547	19.68	574	590	4.07	4.09
Culross	0.3713	0.4373	18.93	0.3938	0.4638	20.08	577	646	4.02	3.81

September and November (Table 8) and since C ; N ratios generally rose at this time (Fig 15), there is some evidence to suggest that this was the case.

Salonen et al (1976) established a direct correlation between carbon levels and energy in a wide range of aquatic invertebrates. Carbon levels in this study were converted to energy values (Fig 17; Table 16) in accordance with their method. A mean conversion factor of 43 kJ $g^{-1}C$ was calculated which compares favourably with the figure of 46 kJ $g^{-1}C$ derived by Salonen et al (1976). Energy content ranged from 21.75 kg g^{-1} AFDW in males from Torrybay in December 1974 to 17.30 kJ g^{-1} AFDW in females from Torrybay in November 1975. In general, energy levels were highest in autumn but fell during the winter and spring to minima in the late spring and early autumn (Fig 17).

FIG.17. Seasonal changes in energy content of male and female L.rudis.

A = Aberdour 'H'

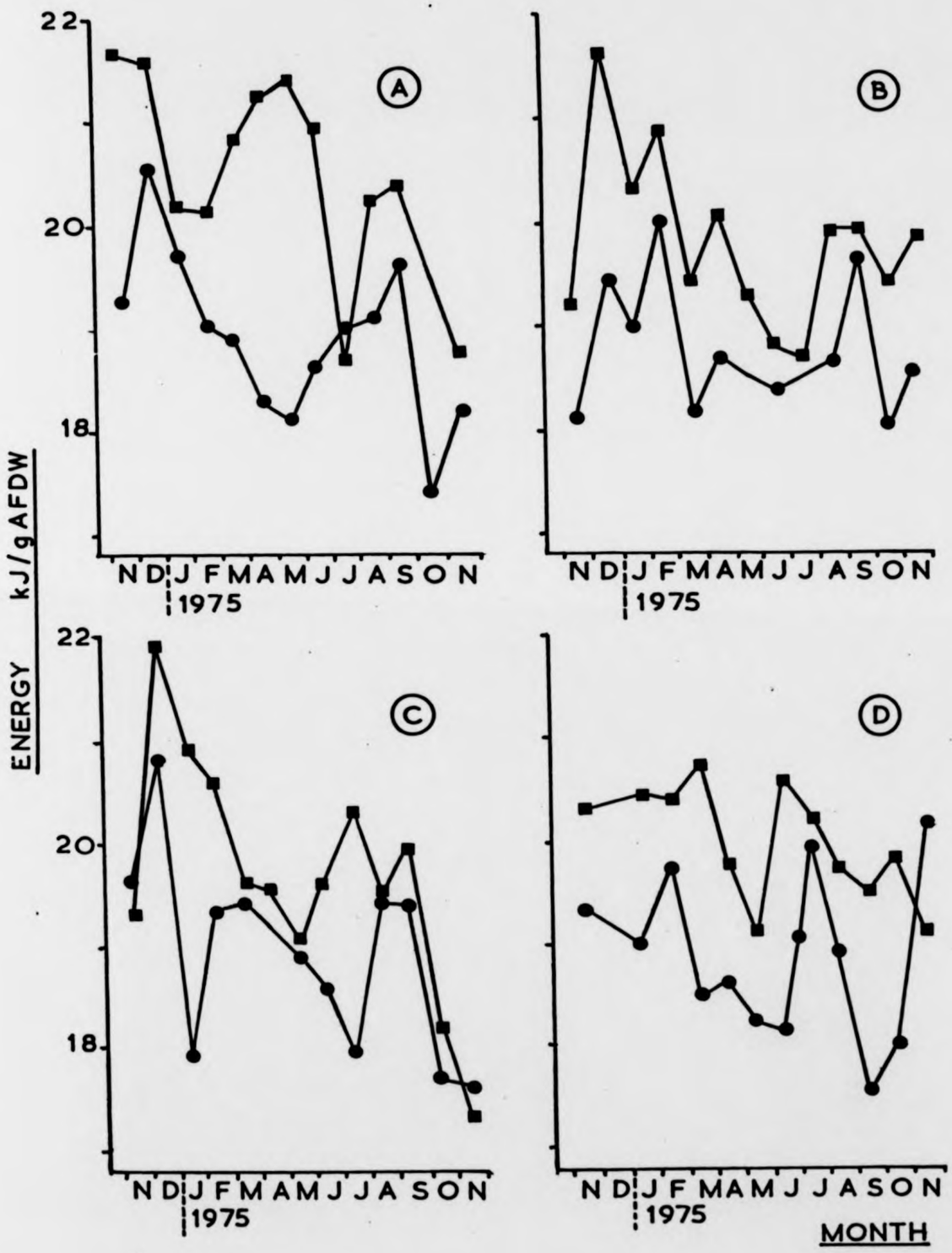
B = Aberdour 'L'

C = Torrybay

D = Culross

■ = male

● = female


22
20
18
A
B
C
D
ENERGY kJ/g AFDW
N D J F M A M J J A S O N
1975
MONTH

4. REPRODUCTIVE CONDITION AND ANALYSIS OF BROOD-POUCH CONTENTS

Two major facts emerge from the brood-pouch counts. Firstly, there were marked seasonal changes in numbers, broadly similar at all stations, with rising numbers in spring and early summer and falling numbers in late summer and autumn (Fig. 18). This fluctuation differed in detail between the 4 stations and between the 2 years (Figs. 19, 20, 21, 22). Secondly, numbers of eggs and embryos differed consistently between the stations with largest numbers at Aberdour 'H' followed by Culross, Aberdour 'L' and with fewest at Torrybay.

In general, maximum brood-pouch counts occurred in late spring and early summer with means exceeding 300 at Aberdour 'H' and Culross. Numbers fell rapidly to mean minima close to 100 in September to December at Aberdour and Culross and as low as 12.4 at Torrybay in September 1975. (Tables 17, 18, 19, 20; Fig. 18). Individual counts ranged much wider with single females carrying up to 612 eggs and embryos, at Culross in June 1976, and many bearing empty brood-pouches especially at Torrybay in August and September 1975. Maximum individual counts at Aberdour 'H', Aberdour 'L' and Torrybay were 535 in May 1975, 400 in May 1976 and 181 in June 1975 respectively.

While seasonal changes over the two years study were broadly similar (Figs. 19, 20, 21, 22) they differed significantly in certain respects. In 1974/75, peak brood-pouch numbers occurred in March at Culross, in May at both Aberdour 'H' and Torrybay and in

FIG. 18. Seasonal variation in the mean monthly brood-pouch contents per female.

A = Aberdour 'H'

B = Aberdour 'L'

C = Torrybay

D = Culross

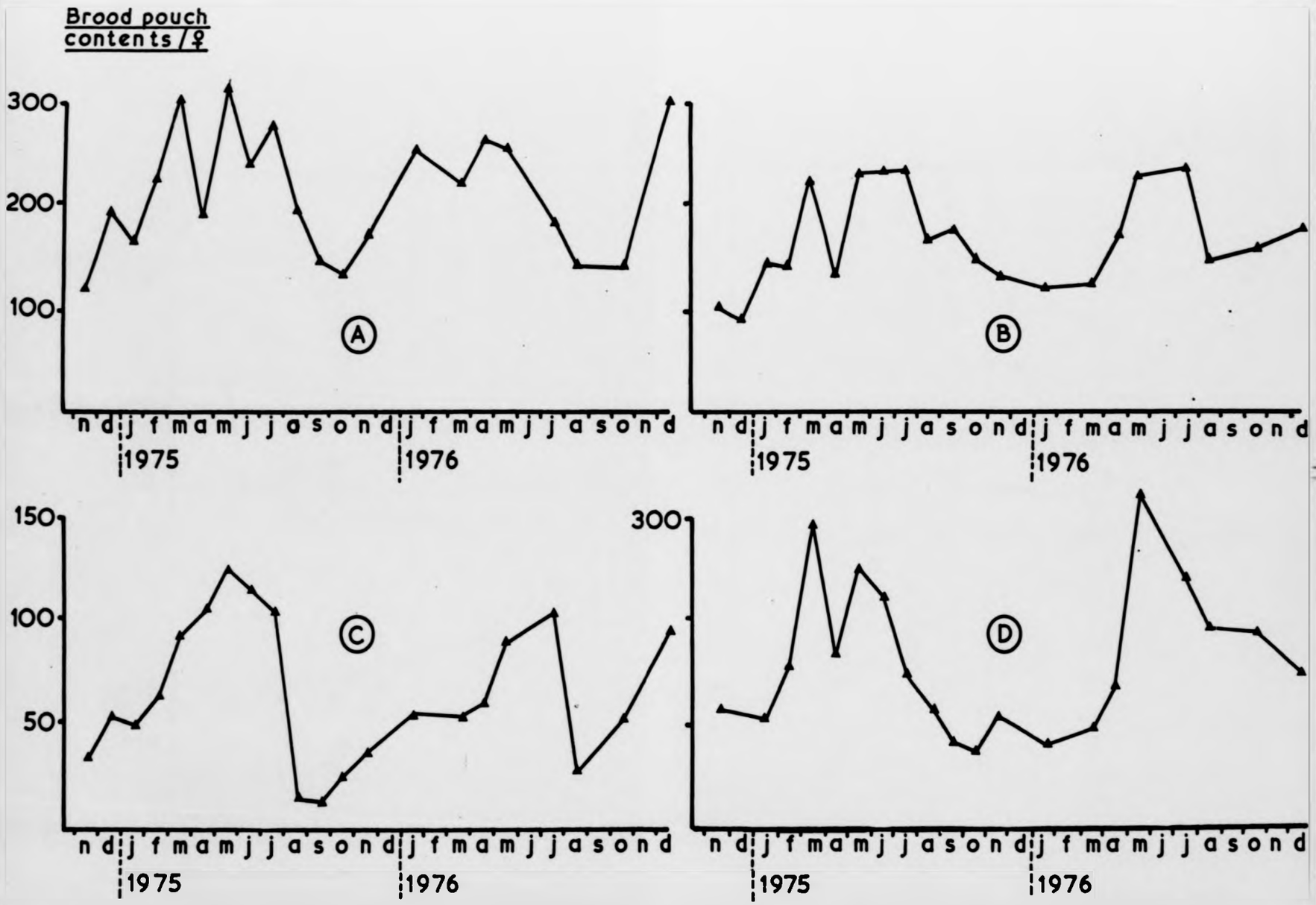

Brood pouch contents / ♀
300
200
100
A
n d j f m a m j j a s o n d j f m a m j j a s o n d
1975
1976
B
n d j f m a m j j a s o n d j f m a m j j a s o n d
1975
1976
150
100
50
C
n d j f m a m j j a s o n d j f m a m j j a s o n d
1975
1976
300
D
n d j f m a m j j a s o n d j f m a m j j a s o n d
1975
1976

FIG.19. Comparison of the mean monthly brood-pouch loads per female for the 1974/1975 and 1975/1976 seasons at Aberdour 'H'.

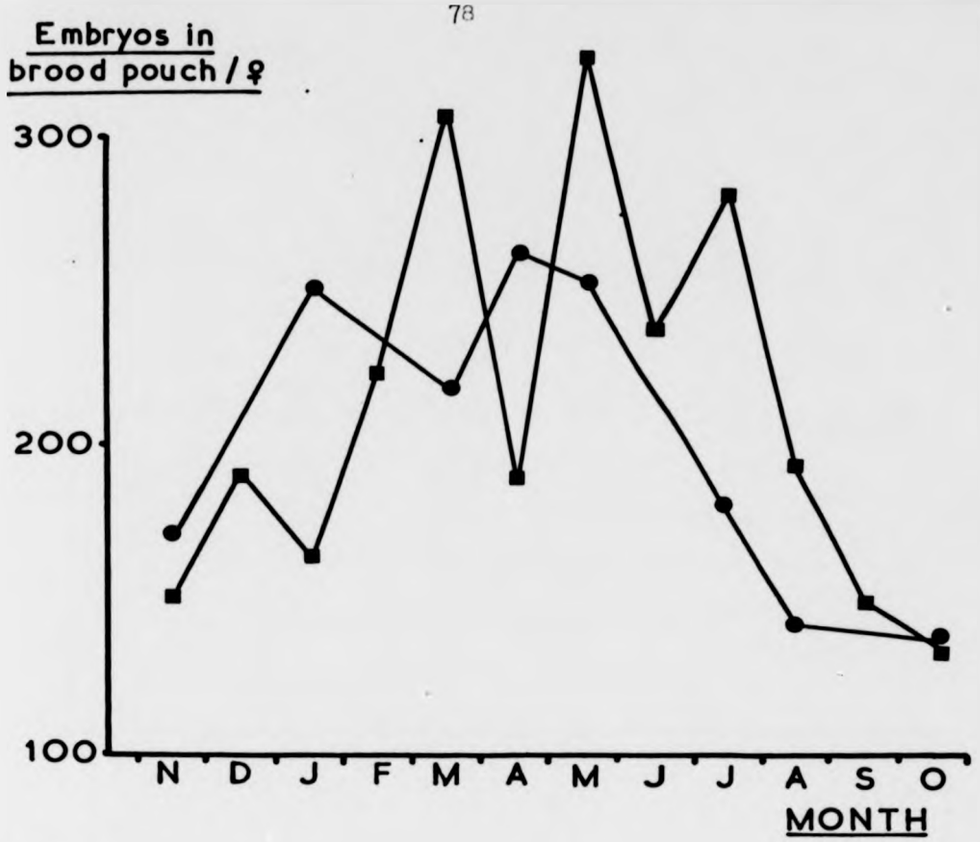
■ = 1974/1975

● = 1975/1976

FIG.20. Comparison of the mean monthly brood-pouch loads per female for the 1974/1975 and 1975/1976 seasons at Aberdour 'L'.

■ = 1974/1975

● = 1975/1976


Embryos in
brood pouch / ♀
300
200
100
N D J F M A M J J A S O
MONTH

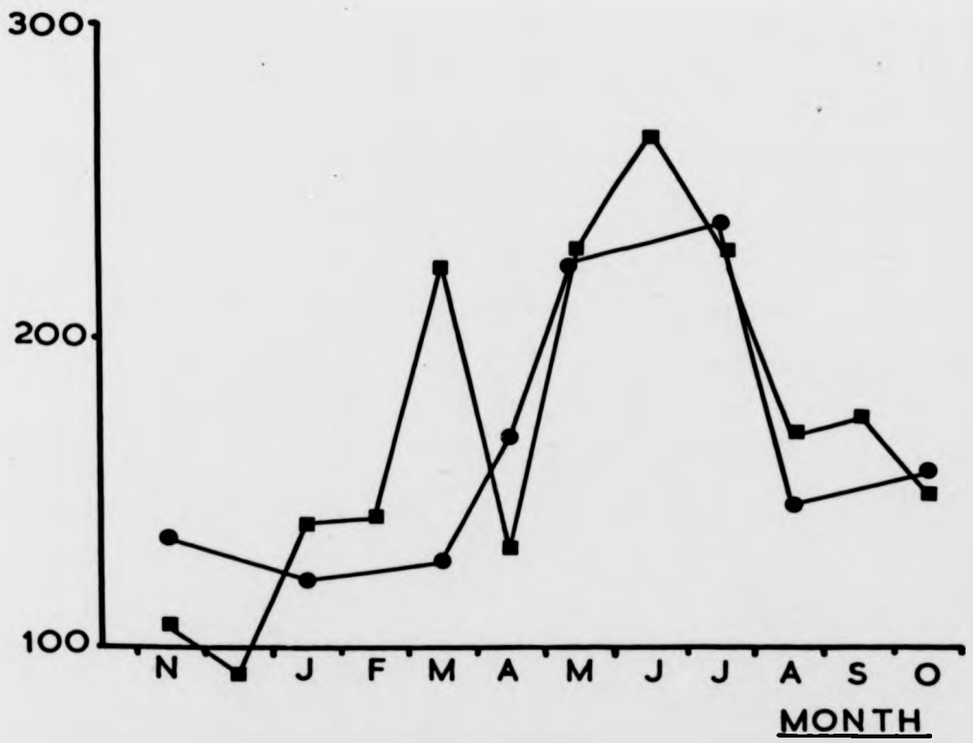

300
200
100
N J F M A M J J A S O
MONTH

FIG.21. Comparison of the mean monthly brood-pouch loads per female for the 1974/1975 and 1975/1976 seasons at Torrybay.

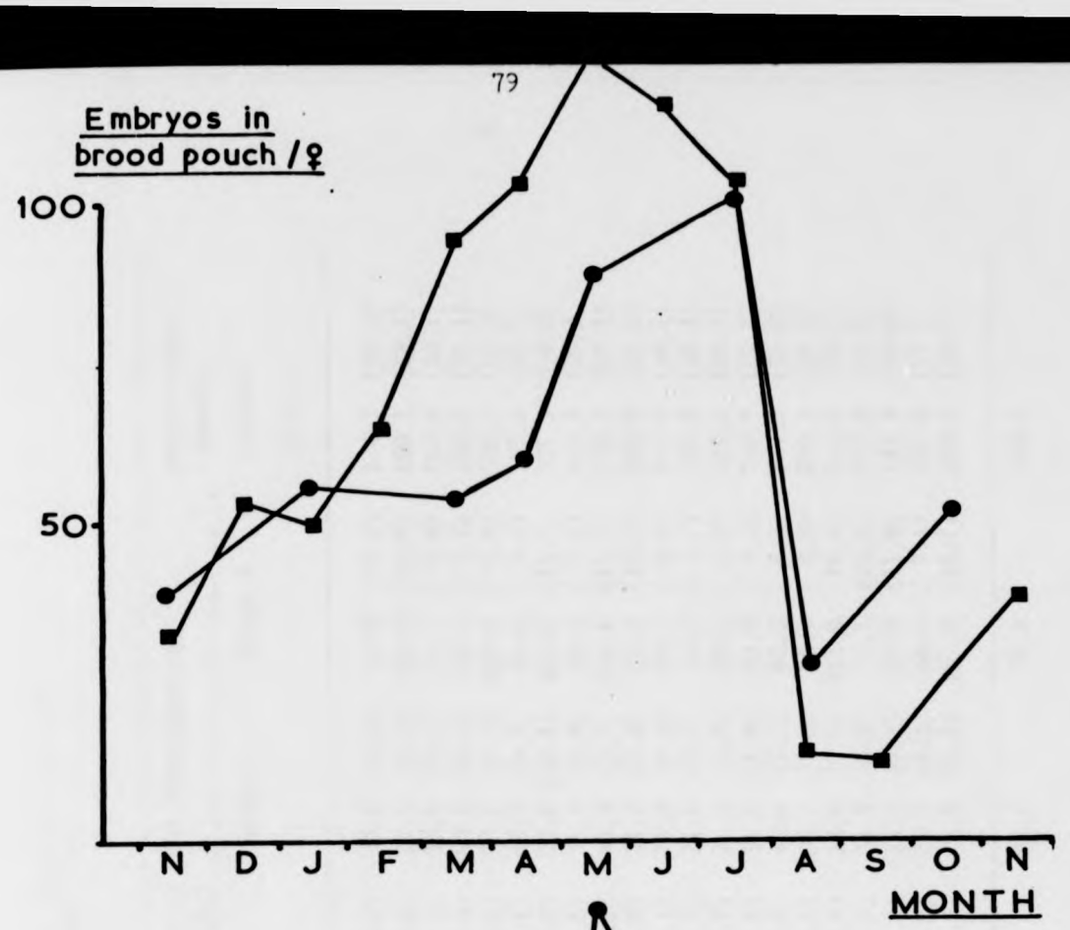
■ = 1974/1975

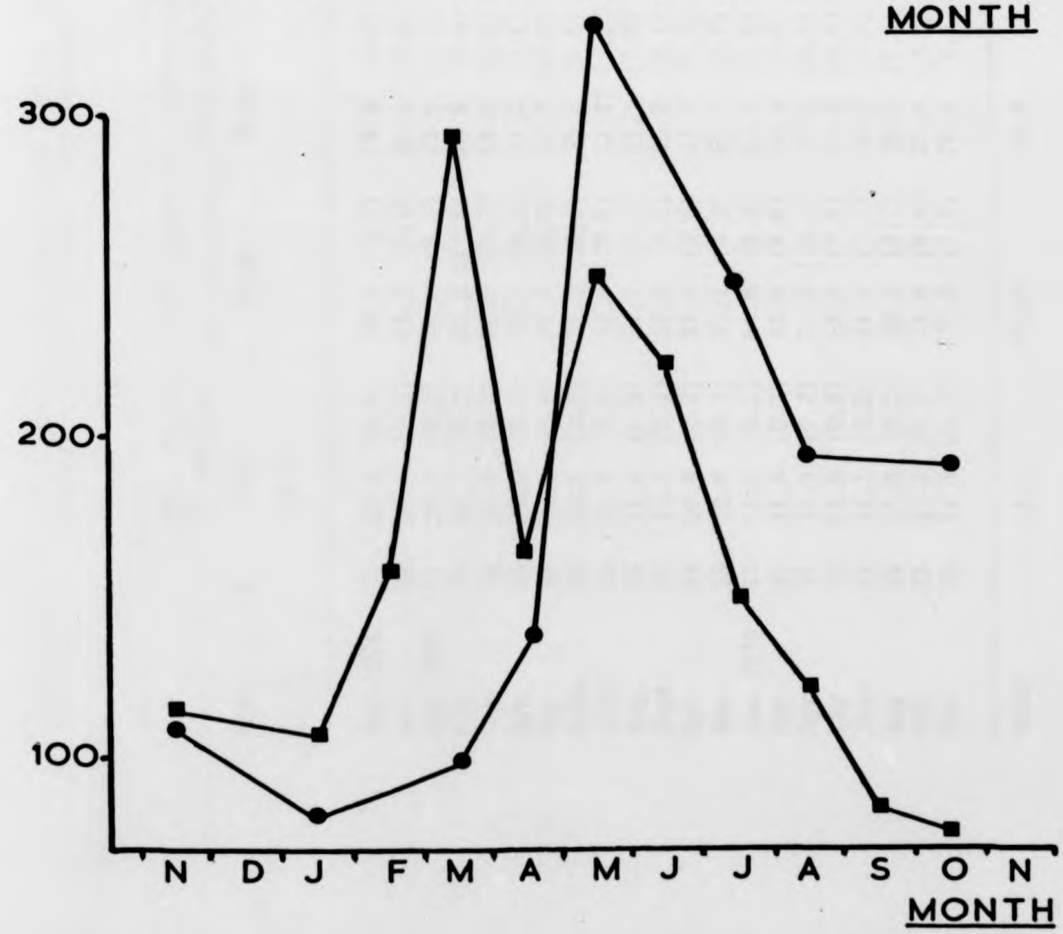
● = 1975/1976

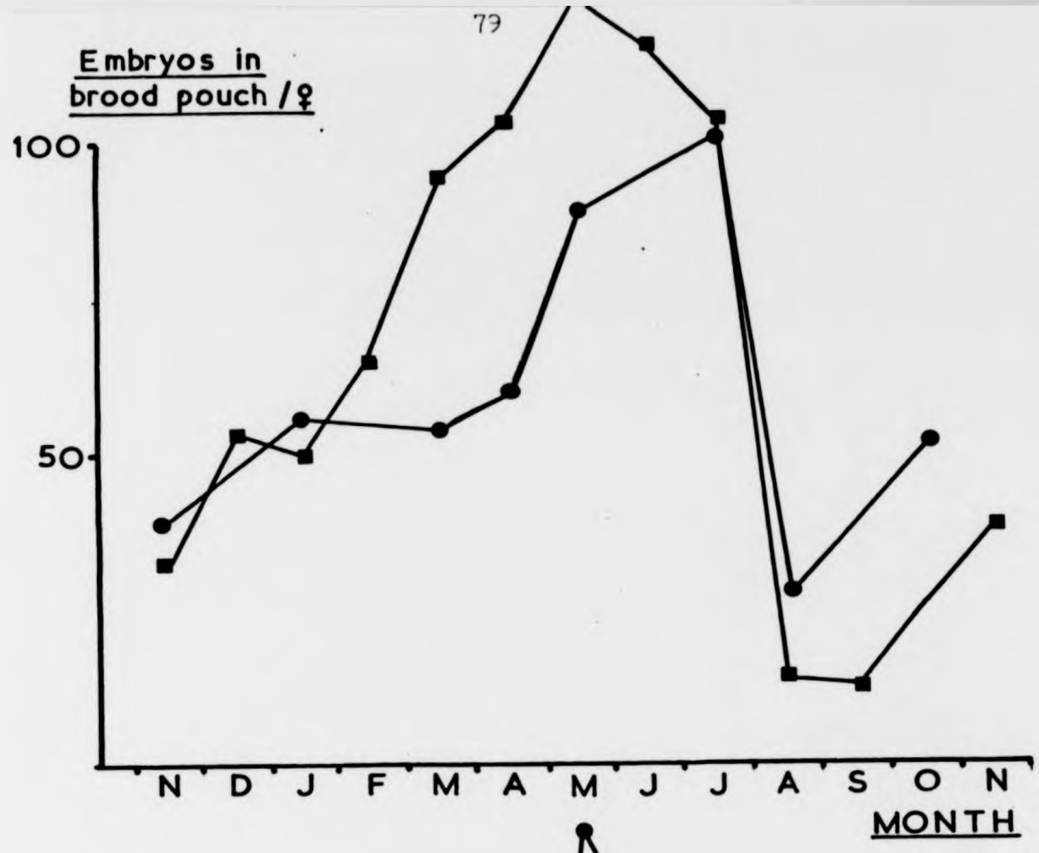
FIG.22. Comparison of the mean monthly brood-pouch loads per female for the 1974/1975 and 1975/1976 seasons at Culross.

■ = 1974/1975

● = 1975/1976


Embryos in
brood pouch / ♀
100
50
N D J F M A M J J A S O N
MONTH


300
200
100
N D J F M A M J J A S O N
MONTH


Embryos in
brood pouch / ♀
100
50
N D J F M A M J J A S O N
MONTH

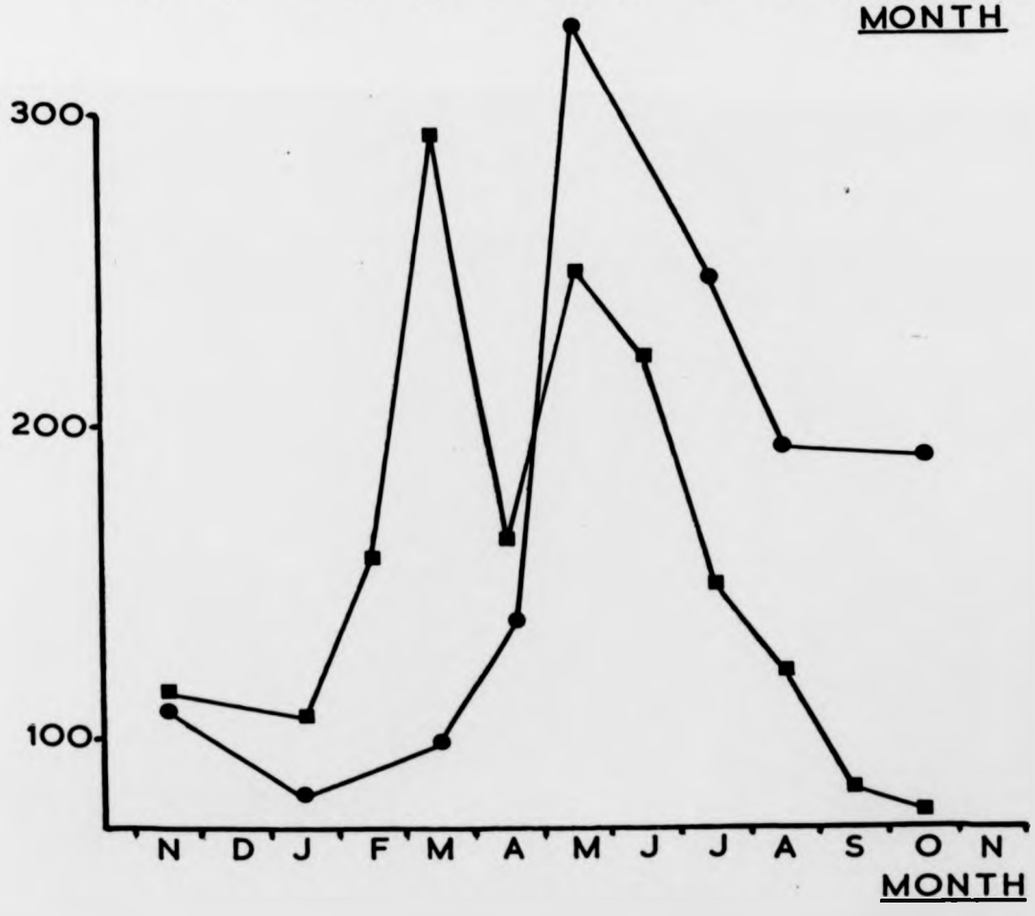

300
200
100
N D J F M A M J J A S O N
MONTH

TABLE 17 Mean monthly brood-pouch loads between November 1974 and December 1976 of L. rudis from Aberdour 'H'

Month	n	Mean height of females mm (S.E.)	Mean number of embryos in each developmental stage (S.E.)				Total brood-pouch content (S.E.)
			Stage 1	Stage 2	Stage 3	Stage 4	
Nov 1974	15	10.4 (0.4)	29.2 (3.2)	19.9 (3.4)	22.8 (3.9)	52.8 (9.5)	124.7 (16.2)
Dec	15	11.8 (0.3)	43.3 (7.1)	31.9 (4.4)	24.5 (4.5)	90.4 (10.7)	190.1 (23.3)
Jan 1975	15	10.9 (0.2)	49.6 (5.2)	23.9 (4.2)	38.5 (7.6)	51.4 (8.0)	163.4 (20.1)
Feb	15	10.7 (0.2)	81.2 (12.8)	43.9 (5.0)	50.6 (8.1)	46.6 (7.7)	222.3 (19.1)
Mar	15	11.9 (0.3)	90.6 (8.2)	58.0 (6.4)	57.1 (4.2)	100.4 (6.6)	306.1 (17.9)
Apr	15	11.0 (0.3)	50.1 (6.5)	31.2 (2.4)	49.3 (5.7)	56.5 (5.6)	187.1 (12.7)
May	15	11.1 (0.2)	75.3 (9.0)	52.7 (10.3)	90.0 (10.4)	107.5 (11.7)	325.5 (4.0)
June	15	11.3 (0.2)	75.1 (9.6)	38.6 (5.5)	36.4 (4.9)	86.4 (7.1)	236.5 (16.2
July	15	11.6 (0.3)	82.1 (7.8)	31.9) (5.3)	43.3 (3.5)	121.4 (11.7)	278.5 (17.2)
Aug.	15	11.4 (0.3)	23.7 (3.7)	51.7 (7.9)	24.2 (3.6)	91.3 (10.3)	190.9 (20.6)
Sept	13	11.1 (0.3)	34.4 (6.5)	25.2 (4.1)	28.0 (4.2)	59.7 (8.5)	147.3 (19.1)
Oct	15	10.8 (0.2)	23.3 (3.4)	32.7 (4.7)	24.6 (3.4)	54.7 (6.2)	135.3 (14.4)
Nov	15	10.8 (0.2)	35.1 (4.0)	27.7 (2.7)	25.9 (3.6)	80.8 (5.9)	169.5 (10.3)
Jan 1976	15	11.6 (0.1)	64.6 (8.9)	62.5 (5.5)	33.6 (4.8)	89.0 (6.2)	249.7 (11.1)
Mar	15	11.3 (0.2)	63.6 (8.6)	33.3 (3.0)	40.6 (5.1)	80.2 (8.4)	217.7 (21.8)
Apr	15	11.3 (0.2)	75.8 (10.7)	47.5 (5.6)	50.7 (7.0)	86.9 (9.9)	260.9 (29.3)
May	15	11.6 (0.3)	63.6 (9.8)	43.9 (4.6)	33.8 (5.5)	111.9 (16.8)	253.2 (28.7)
July	15	11.3 (0.2)	41.5 (7.1)	30.6 (4.5)	34.3 (5.9)	71.1 (10.0)	177.5 (22.6)
Aug	15	11.8 (0.2)	35.8 (4.2)	25.5 (5.2)	23.2 (4.1)	57.8 (11.6)	142.3 (20.6)
Oct	15	11.2 (0.2)	23.9 (5.6)	27.4 (3.2)	29.7 (4.3)	56.5 (7.4)	137.6 (17.1)
Dec	15	11.7 (0.3)	70.5 (7.2)	76.0 (9.5)	48.8 (5.4)	102.9 (15.7)	298.2 (29.4)
Mean		11.3	53.9	38.9	38.6	78.9	210.2

TABLE 18 Mean monthly brood-pouch loads between November 1974 and December 1976 of *L. rudis* from Aberdour 'L'

Month	n	Mean height of females mm (S.E.)	Mean number of embryos in each developmental stage (S.E.)				Total brood-pouch content (S.E.)
			Stage 1	Stage 2	Stage 3	Stage 4	
Nov 1974	17	9.2 (0.2)	18.0 (2.5)	16.0 (2.3)	14.5 (1.6)	52.3 (6.6)	100.8 (11.1)
Dec	18	8.9 (0.2)	18.1 (2.0)	20.0 (2.4)	8.5 (1.5)	46.0 (4.0)	92.6 (7.4)
Jan 1975	15	9.4 (0.2)	33.9 (4.6)	24.9 (3.2)	28.2 (3,4)	54.1 (6.8)	141.1 (13.0)
Feb	15	9.4 (0.3)	38.2 (3.9)	24.5 (2.7)	27.5 (2.1)	51.8 (7.1)	142.0 (12.5)
Mar	15	9.9 (0.1)	72.0 (6.3)	31.3 (4.4)	40.0 (7.3)	81.8 (13.3)	275.1 (26.6)
Apr	15	10.3 (0.2)	35.4 (5.0)	31.3 (4.8)	29.7 (6.3)	36.1 (2.6)	132.5 (15.0)
May	15	10.1 (0.2)	60.4 (4.4)	47.8 (2.9)	56.6 (4.4)	64.8 (4.1)	229.6 (12.0)
June	15	9.8 (0.2)	62.1 (7.4)	53.6 (4.1)	30.5 (3.3)	80.3 (4.1)	226.5 (13.3)
July	15	10.7 (0.2)	56.3 (6.3)	63.6 (2,1)	41.3 (2,4)	68.7 (7.2)	229.9 (10.6)
Aug	15	10.0 (0.2)	30.7 (2.9)	38.5 (3.1)	30.5 (2.5)	67.2 (5.0)	166.9 (9.7)
Sept	15	9.7 (0.2)	38.6 (5,0)	43.5 (6.0)	27.0 (3.2)	64.9 (8.0)	174.0 (18.4)
Oct	15	9.5 (0.1)	32.5 (4.4)	30.7 (2.7)	26.0 (2.3)	61.1 (4.0)	150.3 (16.8)
Nov	15	9.7 (0.2)	34.0 (10.5)	19.3 (3.4)	21.8 (4.0)	60.8 (7.2)	135.9 (18.5)
Jan 1976	15	9.6 (0.1)	25.2 (4.9)	27.7 (3.4)	25.8 (3.2)	43.0 (6.2)	121.7 (16.1)
Mar	15	9.6 (0.1)	43.1 (3.3)	20.2 (1.6)	25.1 (2.5)	38.3 (3.3)	126.7 (8.7)
Apr	15	10.6 (0.1)	46.2 (4.3)	36.0 (4.2)	31.3 (3.2)	52.2 (5.1)	165.7 (9.7)
May	15	10.1 (0.2)	42.4 (7.5)	46.9 (5.3)	54.7 (6.2)	79.8 (6.2)	223.8 (20.2)
July	15	10.1 (0.1)	49.4 (6.3)	51.7 (3.2)	43.1 (5.1)	90.4 (9.6)	234.6 (16.1)
Aug	15	9.7 (0.2)	40.8 (6.7)	38.9 (6.2)	17.1 (2,5)	49.5 (8.2)	146.3 (9.6)
Oct	15	8.9 (0.1)	41.2 (7.3)	29.0 (2.3)	23.5 (1.9)	63.1 (5,6)	156.8 (9.3)
Dec	15	9.9 (0.2)	42.5 (9.5)	36.7 (3.3)	26.4) (2.5)	66.8 (6.4)	172.4 (14.2)
Mean		9.8	41.0	34.9	30.0	60.6	166.4

TABLE 19 Mean monthly brood-pouch loads between November 1974 and December 1976 of L. rudis from Torrybay

Month	n	Mean height of females mm (S.E.)		Mean number of embryos in each developmental stage (S.E.) Stage 1		Stage 2		Stage 3		Stage 4		Total brood-pouch content (S.E.)	
Nov 1974	16	7.4	(0.1)	9.1	(2.1)	6.2	(1.2)	4.7	(1.2)	12.1	(3.0)	32.1	(5.5)
Dec	15	7.9	(0.4)	7.6	(1,5)	12.3	(1.6)	11.8	(1.7)	21.0	(4.6)	52.7	(7.2)
Jan 1975	19	7.2	(0.2)	6,2	(1.4)	10.5	(1.8)	10.1	(1.3)	22.3	(3.0)	49.1	(4.8)
Feb	16	8.2	(0.3)	18.5	(2.6)	7.6	(2,1)	11.3	(1.5)	27.4	(2.4)	64.8	(5.3)
Mar	15	8.5	(0.2)	32.2	(2.0)	18.7	(3.6)	16.3	(3.1)	26.1	(4.2)	93.3	(8.0)
Apr	15	8.4	(0.2)	33.0	(2.0)	18.3	(3.3)	31.4	(1.4)	20.5	(2.5)	103.2	(6,1)
May	15	8.4	(0.2)	24.5	(2.5)	17.7	(1.6)	31.7	(4.8	50.2	(2.8)	124.1	(8.6)
June	14	8.6	(0.2)	33.8	(7.4)	13.9	(2.4)	23.7	(3,1)	44.1	(3,9)	115.0	(8.6)
July	15	9.2	(0.1)	11.8	(2.5)	7.8	(1,5)	17.1	(3.1)	66.4	(6,9)	103.1	(11.6)
Aug	15	8.6	(0.2)	2.6	(1.0)	3,0	(1.3)	0.6	(0.3)	6.9	(2.0)	13.1	(2.7)
Sept	14	8.5	(0.2)	2.2	(0.9)	4.1	(1.0)	2.7	(0.6)	3.4	(0.9)	12.4	(2.3)
Oct	15	7.4	(0.2)	5.3	(1.5)	3.2	(0.9)	3.6	(0.6)	13.1	(1.7)	25.2	(2.7)
Nov	15	7.9	(0.1)	5.1	(0.9)	5.8	(1.5)	6.5	(1.5)	20.9	(4.7)	38.3	(6.5)
Jan 1976	15	8.0	(0.2)	11.9	(1.9)	12.6	(1.9)	10.7	(1.8)	20.6	(3.6)	55,8	(5.5)
Mar	15	7.6	(0.1)	13.5	(1.5)	9.9	(1.5)	11.5	(2.4)	18.9	(2.6)	53.8	(5.9)
Apr	15	7.8	(0.1)	14.9	(2,6)	12.8	(2.5)	10.2	(1,5)	21.1	(3.8)	59.0	(7.7)
May	15	7,8	(0.2)	11.6	(1.6)	21.7	(2,6)	20.0	(1.7)	34.4	(3.3)	87.7	(7.7)
July	15	7.9	(0.2)	7,7	(1,2)	23.7	(3.7)	12.2	(2.3)	58.7	(5.9)	102.3	(10.3)
Aug	15	8,8	(0.1)	3.2	(1.0)	4.4	(1.6)	2.2	(0.6)	17.2	(2.7)	27.1	(4.6)
Oct	15	8.5	(0.1)	7.9	(1.5)	14.2	(1.8)	8,1	(2,0)	21.1	(4.6)	51.3	(5.0)
Dec	15	8.7	(0.1)	17.6	(5.3)	19.9	(1.1)	23.7	(2.7)	36.5	(3.3)	97.7	(8.4)
Mean		8.1		13.3		11.8		12.9		26.8		68.8	

TABLE 20 Mean monthly brood-pouch loads between November 1974 and December 1976 of L. rudis from Culross

Month	n	Mean height of females mm (S.E.)	Mean number of embryos in each developmental stage (S.E.) Stage 1	Stage 2	Stage 3	Stage 4	Total brood-pouch content (S.E.)
Nov 1974	15	12.2 (0.5)	29.6 (5.9	15.2 (3.6)	24.9 (4.0)	46,1 (7.4)	115.8 (17.6)
Jan 1975	15	11.7 (0.3)	26.3 (4.0)	20.7 (4.3)	25.5 (6.2)	34.0 (4.3)	106.5 (15.7)
Feb	15	11.3 (0.3)	42.8 (7.8)	31.8 (2.9)	34.8 (3.0)	45.8 (7.2)	155.2 (12.8)
Mar	14	12.4 (0.2)	100.1 (11.5)	58.2 (7.0)	45.9 (4.2)	89.6 (6.8)	293.8 (24.8)
Apr	16	12.6 (0.2)	37.6 (6.6)	31.6 (4,4)	36.5 (6.3)	54.8 (10.4	160.5 (17.1)
May	15	11.6 (0.3)	46.3 (4.8)	48.9 (3.5)	46.5 (4.2)	109.0 (8.0)	250.7 (17.4)
June	15	11.9 (0.2)	61.2 (3.8)	31.7 (5.9)	34.7 (4,3)	94.1 (7.7)	221.7 (14.0)
July	15	11.5 (0.1)	21.7 (3.5)	24.4 (2.2)	31,0 (5,2)	71.8 (7.0)	148.9 (13.6)
Aug.	15	11.6 (0.3)	13,0 (2.9)	30.8 (5,6)	16.0 (2.6)	58.8 (8.9)	118.6 (17.7)
Sept.	15	12.0 (0.2)	10.5 (2.3)	22.8 (3,9)	19.3 (3.7)	30.7 (5.4)	83.3 (12.5)
Oct	15	11.3 (0.1)	9.6 (1.5)	10.7 (1.5)	12.3 (1.6)	42.5 (4.9	75.1 (7.3)
Nov	14	11.3 (0.2)	23.1 (3.6)	18.8 (2.4)	26.6 (4,0)	39.4 (7.0)	107.9 (15.2)
Jan 1976	15	11.2 (0.3)	25.7 (4.4)	15.8 (3.6)	16.6 (4.0)	22,7 (5.0)	80.8 (13.8)
Mar	15	11.4 (0.3)	27.3 (5,0)	18.8 (4.0)	21.4 (3.6)	29.8 (4.3)	97.3 (13.4)
Apr	15	11.8 (0.3)	42.3 (4.9)	22.7 (1,9)	29.5 (4.8)	41.1 (6.1)	135.6 (12.3)
May	15	12.6 (0.3	60.2 (5.3)	82.1 (9.5)	88,7 (7.7)	98.9 (7.1)	329.9 (17.1)
July	15	12.0 (0.3)	40.0 (7.3)	42.7 (8.3)	39.5 (7.1)	121.7 (11.9)	243.9 (32.7)
Aug	15	12.7 (0.3)	31.9 (5.1)	53.8 (8.0)	20.6 (5.3)	86.5 (12.4)	192.8 (38.3)
Oct	15	12.4 (0.2)	14.2 (2.4)	47.9 (6,7)	32.9 (3.9)	95.6 (17.1)	190.6 (29.1)
Dec	15	12.0 (0.3)	36.1 (4,4)	28.4 (3.5)	28.0 (4.3)	59.8 (9.4)	152.3 (16.0)
Mean		11.9	35.0	32.9	31.6	63.6	163.1

June at Aberdour 'L'. In 1975/76, peak brood-pouch counts at Aberdour 'L' occurred again in June (Fig. 20). At Aberdour 'H' however (Fig. 19), peak numbers occurred one month earlier, in April, while at Culross and Torrybay (Figs 22, 21) they were two months later in May and July respectively. With the exception of Torrybay, brood-pouch counts declined sharply between March and April 1975 but this was not repeated in 1976. Peak brood-pouch counts were generally higher in 1974/75 than in 1975/76 but global analysis of variance showed that there was no significant difference in overall brood-pouch loads between the 2 years.

The seasonal ranges in mean brood-pouch counts at Aberdour represent close to a 2.5-fold increase from 124.7 (November 1974, Aberdour 'H') and 92.6 (December 1974, Aberdour 'L') to 325.5 (May 1975, Aberdour 'H') and 229.9 (July 1975, Aberdour 'L'). At Culross the range of means was greater, spanning a 3.9-fold difference between 75.1 in October 1975 and 293.8 in March 1975. At Torrybay, where numbers were consistently low, means ranged 10-fold between 12.4 in September 1975 to 124.1 in May 1975 (Fig. 18).

Brood-pouch loads were consistently higher at Aberdour and Culross than at Torrybay. Overall, there was a 3-fold difference between the 2-year grand mean brood-pouch count for Aberdour 'H' of 210.2 and that of 68.8 for Torrybay. Corresponding 2-year grand means for Aberdour 'L' (166.4) and for Culross (163.1) fell between these extremes (Tables 17, 18, 19, 20).

These differences in brood-pouch counts were tested for significance using analysis of variance. This showed that the differences between all four sites each month were highly significant ($P = 0.0001$).

In conclusion it becomes clear (a) that there were major annual fluctuations in numbers of eggs and embryos which formed repeated seasonal cycles in the two years of observations, (b) that there were major real differences in brood-pouch loads between the four sites which were not simply related to position in the estuary and (c) that at the station where the comparison can be made, brood-pouch loads were significantly greater upshore than downshore.

When numbers of the four different stages of development in the brood-pouch are considered separately, their relative abundance as a proportion of the total counts varied conspicuously at different times but were, at any one time, broadly similar among the four stations (Figs. 23, 24; Tables 17, 18, 19 20). With almost no exception, stage 4 late juveniles were the most abundant comprising from 20% (Aberdour 'H', February 1974) to 65% (Torrybay, July 1975) of the total (Figs. 25, 26, 27, 28). Peak numbers of stage 4 embryos generally occurred one to two months later than the maximum total brood-pouch counts (Figs. 18, 23, 24).

Stage 1 eggs and early embryos comprised between 7.5% (Torrybay July 1976 and Culross October 1976) and about 30 to 35% of the total brood-pouch counts on several occasions in the spring of 1974 and 1975 (Figs. 25, 26, 27, 28). The seasonal

FIG.23. Mean monthly numbers of each of the four developmental stages in the brood-pouch during the 1974/1975 season.

■ = Numbers of stage 1 embryos.

■ = Numbers of stage 2 embryos.

■ = Numbers of stage 3 embryos.

□ = Numbers of stage 4 embryos.

AH = Aberdour "H"

AL = Aberdour "L"

T = Torrybay

C = Culross

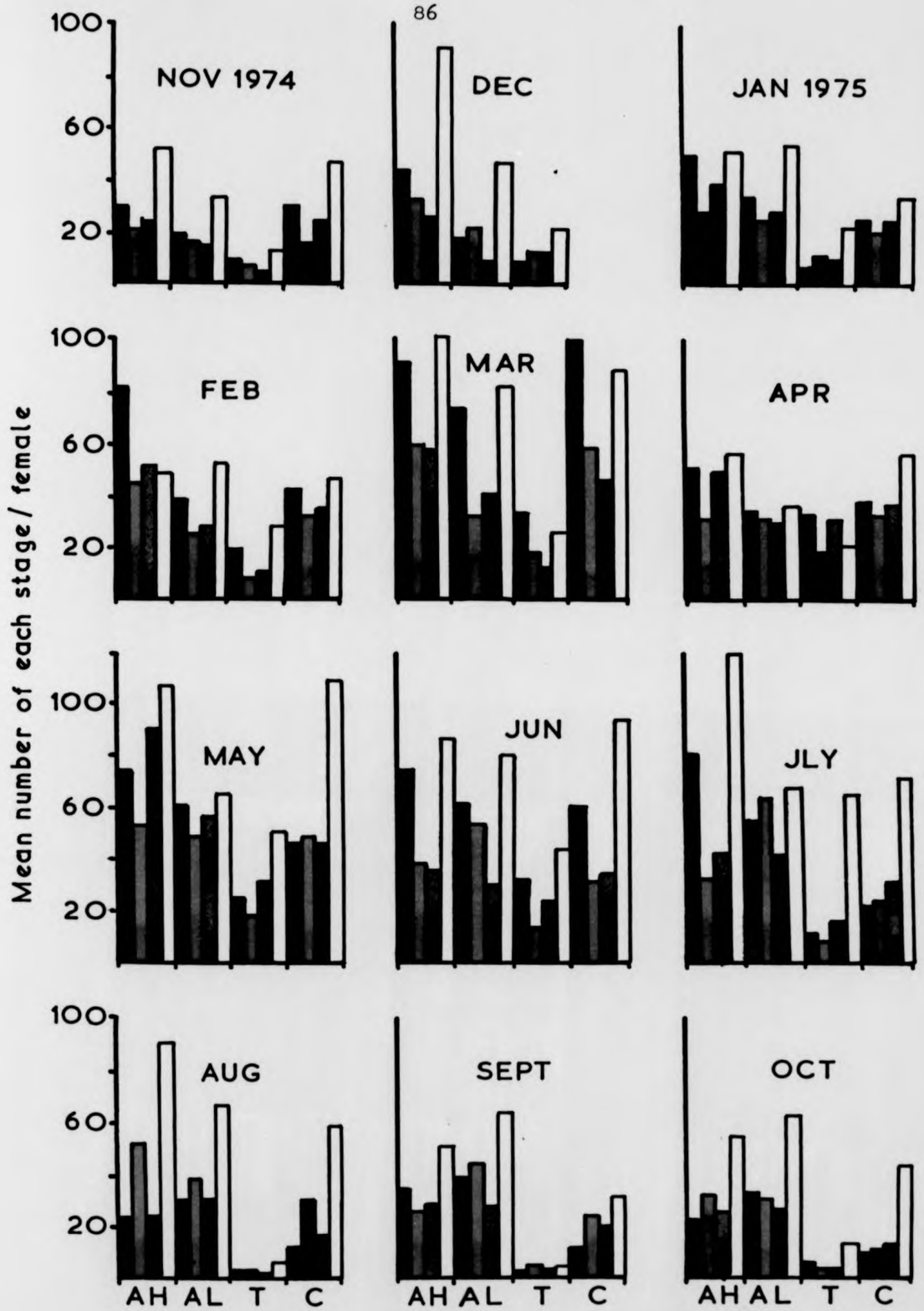

NOV 1974
DEC
JAN 1975
FEB
MAR
APR
MAY
JUN
JLY
AUG
SEPT
OCT
100
60
20
Mean number of each stage / female
AH AL T C

FIG.24. Mean monthly numbers of each of the four developmental stages in the brood-pouch during the 1975/1976 season.

■ = Numbers of stage 1 embryos.

■ = Numbers of stage 2 embryos.

■ = Numbers of stage 3 embryos.

□ = Numbers of stage 4 embryos.

AH = Aberdour "H"

AL = Aberdour "L"

T = Torrybay

C = Culross

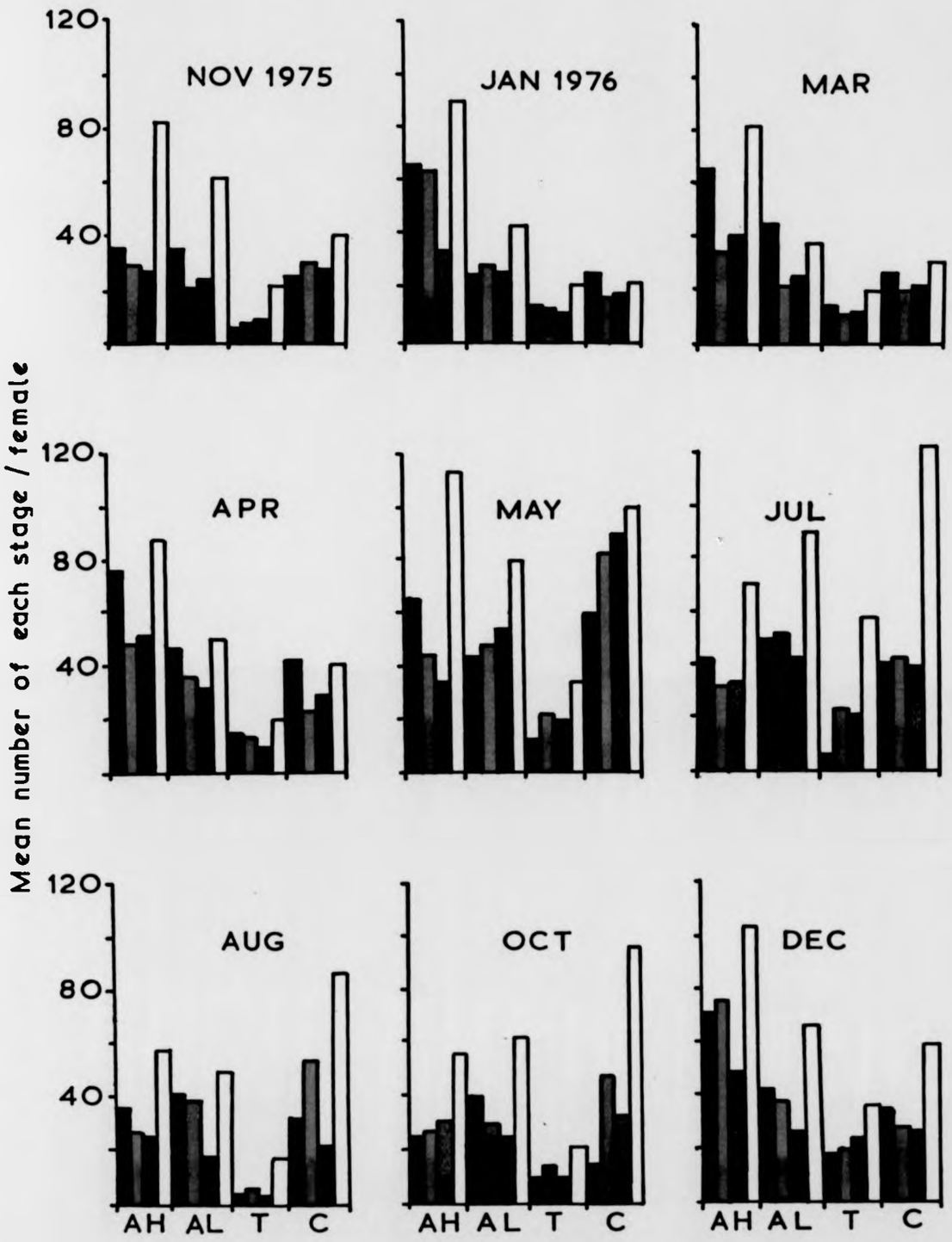

NOV 1975
JAN 1976
MAR
APR
MAY
JUL
AUG
OCT
DEC
120
80
40
AH AL T C
Mean number of each stage / female

FIG.25. Seasonal variation in the percentage of developmental stages in the brood-pouch at Aberdour 'H.'

A = Stage 1 embryos.

B = Stage 2 embryos.

C = Stage 3 embryos.

D = Stage 4 embryos.

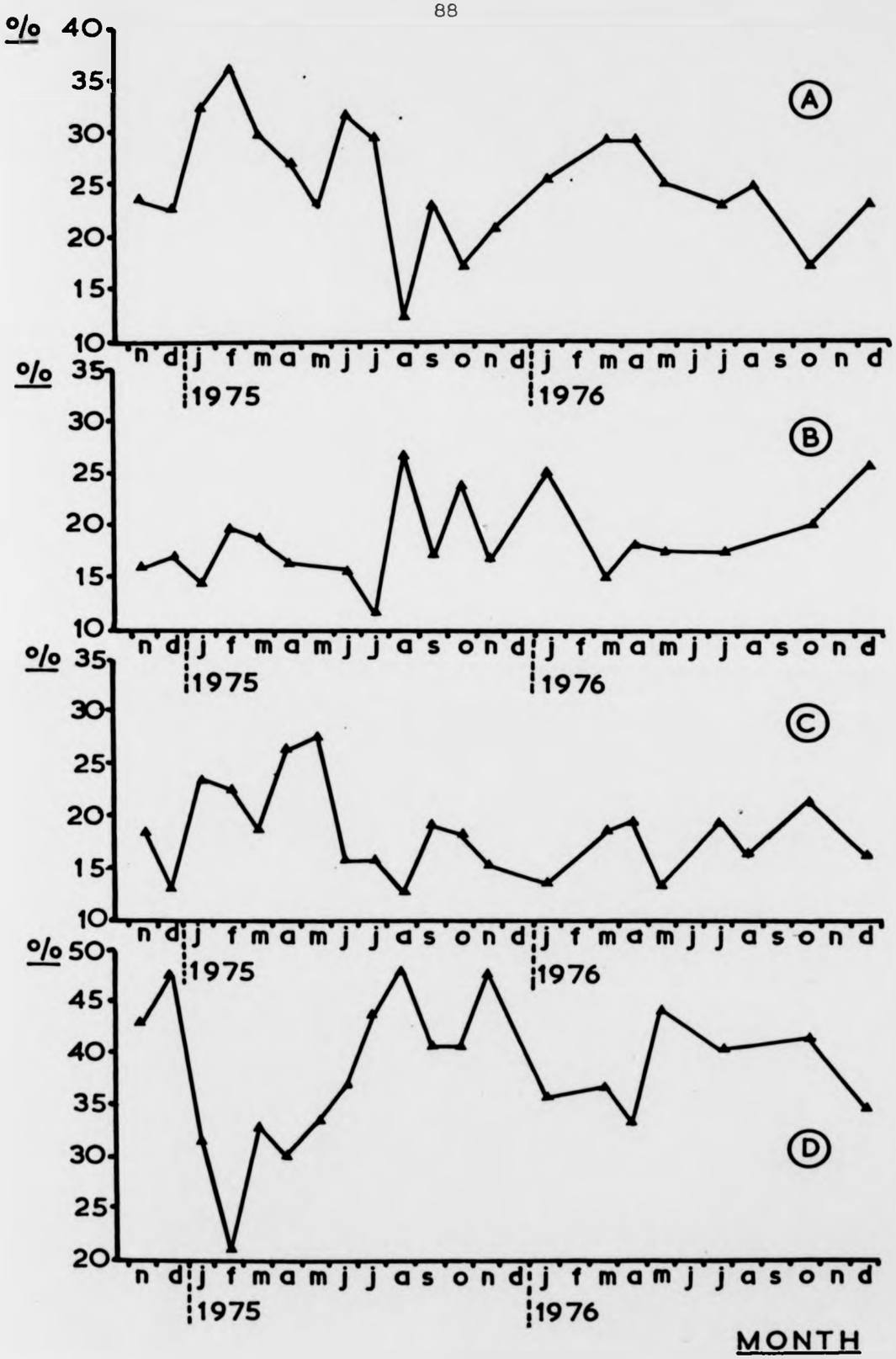

%
40
35
30
25
20
15
10
A
n d j f m a m j j a s o n d j f m a m j j a s o n d
1975
1976
%
35
30
25
20
15
10
B
n d j f m a m j j a s o n d j f m a m j j a s o n d
1975
1976
%
35
30
25
20
15
10
C
n d j f m a m j j a s o n d j f m a m j j a s o n d
1975
1976
%
50
45
40
35
30
25
20
D
n d j f m a m j j a s o n d j f m a m j j a s o n d
1975
1976
MONTH

FIG.26. Seasonal variation in the percentage of developmental stages in the brood-pouch at Aberdour 'L.'

A = Stage 1 embryos.

B = Stage 2 embryos.

C = Stage 3 embryos.

D = Stage 4 embryos.

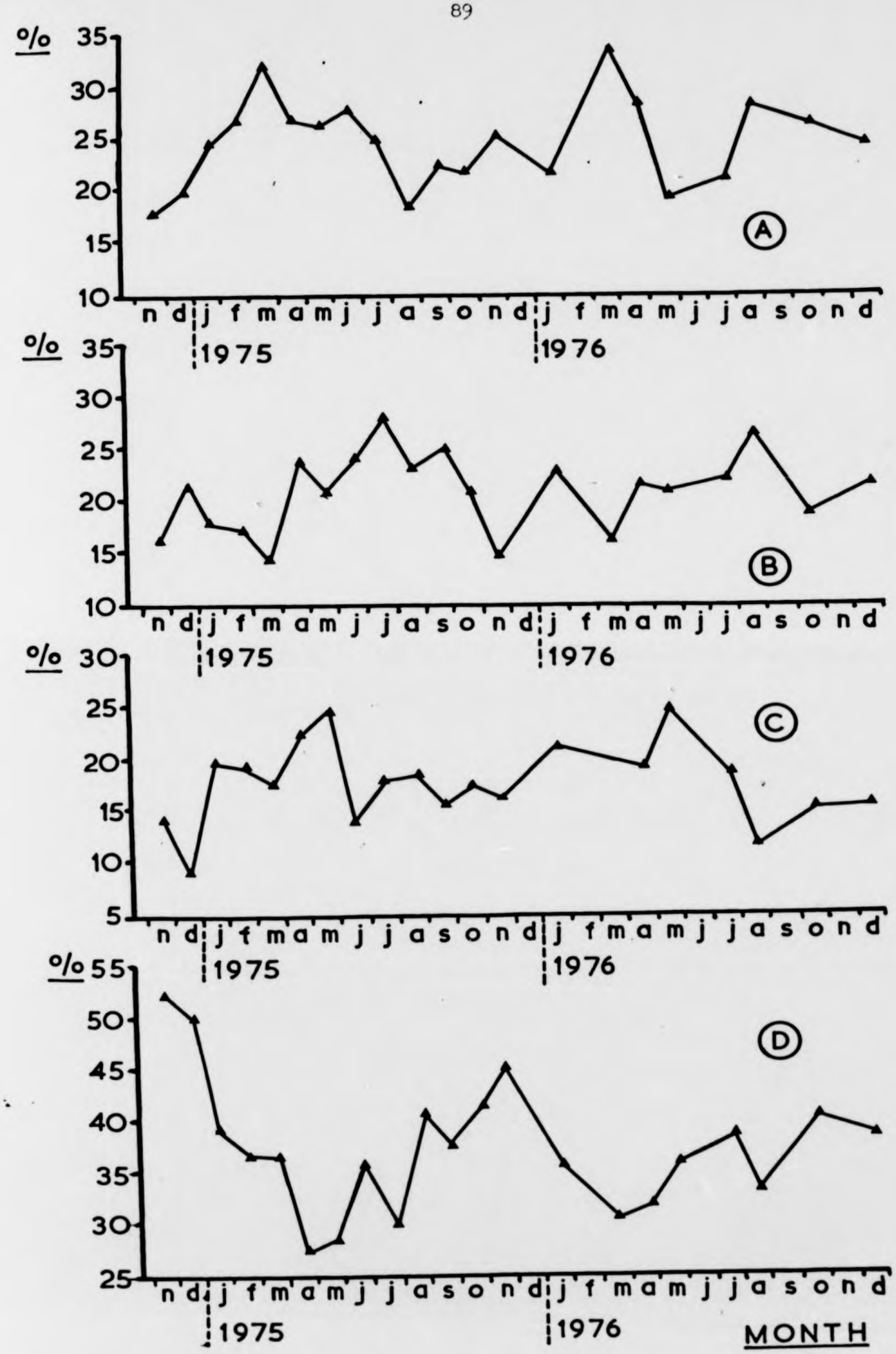

%
35
30
25
20
15
10
A
n d j f m a m j j a s o n d j f m a m j j a s o n d
1975
1976
%
35
30
25
20
15
10
B
n d j f m a m j j a s o n d j f m a m j j a s o n d
1975
1976
%
30
25
20
15
10
5
C
n d j f m a m j j a s o n d j f m a m j j a s o n d
1975
1976
%
55
50
45
40
35
30
25
D
n d j f m a m j j a s o n d j f m a m j j a s o n d
1975
1976
MONTH

FIG.27. Seasonal variation in the percentage of developmental stages in the brood-pouch at Torrybay.

A = Stage 1 embryos.

B = Stage 2 embryos.

C = Stage 3 embryos.

D = Stage 4 embryos.

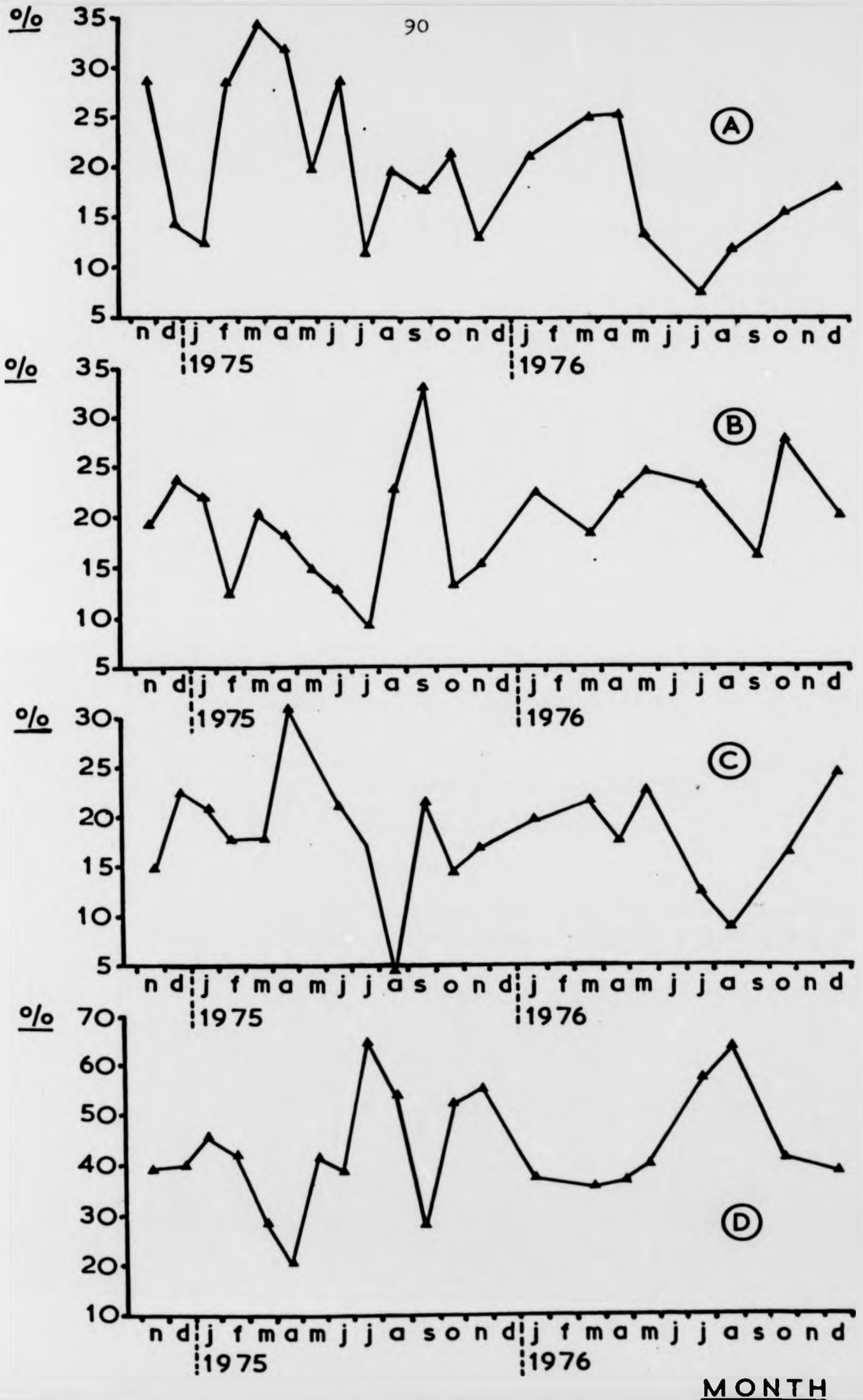

%
35
30
25
20
15
10
5
A
n d j f m a m j j a s o n d j f m a m j j a s o n d
1975
1976
%
35
30
25
20
15
10
5
B
n d j f m a m j j a s o n d j f m a m j j a s o n d
1975
1976
%
30
25
20
15
10
5
C
n d j f m a m j j a s o n d j f m a m j j a s o n d
1975
1976
%
70
60
50
40
30
20
10
D
n d j f m a m j j a s o n d j f m a m j j a s o n d
1975
1976
MONTH

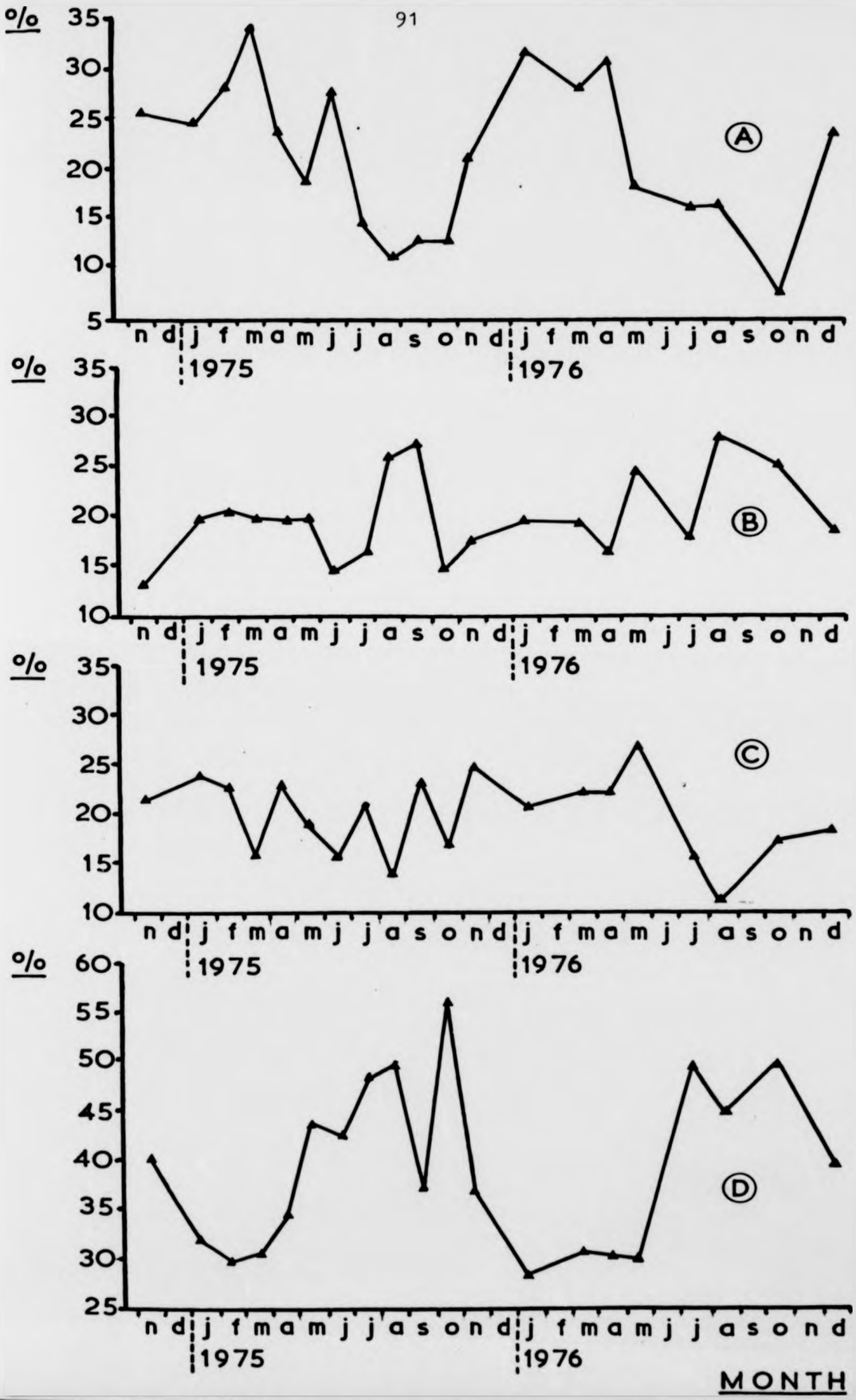
FIG.28. Seasonal variation in the percentage of developmental stages in the brood-pouch at Culross.

A = Stage 1 embryos.

B = Stage 2 embryos.

C = Stage 3 embryos.

D = Stage 4 embryos.


%
35
30
25
20
15
10
5
A
n d j f m a m j j a s o n d j f m a m j j a s o n d
1975
1976
%
35
30
25
20
15
10
B
n d j f m a m j j a s o n d j f m a m j j a s o n d
1975
1976
%
35
30
25
20
15
10
C
n d j f m a m j j a s o n d j f m a m j j a s o n d
1975
1976
%
60
55
50
45
40
35
30
25
D
n d j f m a m j j a s o n d j f m a m j j a s o n d
1975
1976
MONTH

pattern of changing numbers of stage 1 embryos was generally very similar to that for the total brood pouch counts with maximum numbers between March and May (Figs. 23, 24). There was a reciprocal relationship between the proportions of stage 1 and stage 4 embryos (Figs. 25, 26, 27, 28). In general, the highest proportion of stage 1 eggs occurred between January and April which reflects the build-up in reproductive activity at this time. The maximum proportion of stage 4 embryos occurred much later however, between August and November. This coupled with the concomitant low egg and low overall brood-pouch counts, shows that the brood-pouch in autumn was largely occupied by late juveniles which had developed from a high rate of egg production in spring.

The intermediate embryos comprised 7.5% to 33% (stage 2) and 4.5% to 27.5% (stage 3) of the total brood-pouch counts. Throughout the year counts of stages 2 and 3 were broadly similar with maximum numbers occurring in the late spring and early summer (Figs. 23, 24). Increases in the proportion of stage 2 embryos generally followed peaks in abundance of stage 1 embryos by some months when egg production had apparently declined and most eggs had developed to later stages (Figs. 25, 26, 27, 28).

The overall proportional make-up of the brood-pouch loads followed similar patterns in both 1974/75 and 1975/76 and at all sites (Table 21).

At each site a direct linear relationship existed between brood-pouch counts and size over most of the size range of mature

TABLE 21 Proportion of each developmental stage in the brood-pouch of L. rudis between November 1974 and December 1976.

Year	Numbers of each developmental stage expressed as per cent of total brood-pouch counts (± SE)			
	Stage 1	Stage 2	Stage 3	Stage 4
Aberdour 'H'				
Nov. 1974-Oct 1975	25.6(± 1.9)	17.9(± 1.2)	19.3(± 1.4)	37.3(± 2.3)
Nov. 1975-Dec 1976	24.4(± 1.3)	19.2(± 1.2)	17.1(± 1.0)	39.3(± 1.6)
Nov. 1974-Dec 1976	25.1(± 1.2)	18.5(± 0.9)	18.3(± 0.9)	38.2(± 1.5)
Aberdour 'L'				
Nov. 1974-Oct 1975	24.0(± 1.2)	20.9(± 1.2)	17.5(± 1.2)	37.6(± 2.2)
Nov. 1975-Dec 1976	25.2(± 1.5)	20.5(± 1.2)	17.9(± 1.3)	36.5(± 1.5)
Nov. 1974-Dec 1976	24.4(± 0.9)	20.7(± 0.8)	17.7(± 0.9)	37.2(± 1.4)
Torrybay				
Nov. 1974-Oct 1975	22.4(± 1.3)	18.0(± 2.0)	18.9(± 1.9)	40.6(± 3.5)
Nov. 1975-Dec 1976	16.8(± 2.0)	21.1(± 1.4)	17.5(± 2.2)	44.6(± 3.6)
Nov. 1974-Dec 1976	20.0(± 1.6)	19.3(± 1.3)	18.3(± 1.3)	42.3(± 2.5)
Culross				
Nov. 1974-Oct 1975	21.0(± 2.3)	19.1(± 1.3)	19.5(± 1.1)	40.3(± 2.5)
Nov. 1975-Dec 1976	22.0(± 2.2)	20.8(± 1.4)	19.8(± 1.6)	37.8(± 2.9)
Nov. 1974-Dec 1976	21.4(± 1.7)	19.9(± 0.9)	19.6(± 0.9)	39.1(± 1.9)

females. Based on this relationship the brood-pouch loads of standard 10 mm females could be described by

$$BP_{10} = \frac{BPx}{(x - m)} \times (10 - m)$$

Where BPx = brood-pouch load of female of shell height x mm, m = minimum height in mm of maturity. While it is desirable to compare findings in terms of a standard-size female, in the field a 10 mm snail was near the maximum size found at Torrybay while it was more common at the other 3 sites.

This formula accurately describes the relationship between size and brood-pouch loads for females of all sizes except where snails had recently matured and hence only started to produce eggs.

Brood-pouch loads derived for standard 10 mm females from the marine site of Aberdour were clearly greater than those from the up-estuary sites of Torrybay and Culross (Fig. 29). Comparison of brood-pouch loads of standard 10 mm females from Aberdour 'H' and 'L' revealed that the number of embryos carried by a 10 mm female on the low shore was higher than that carried by a 10 mm female on the upper shore (Fig. 29). Mean monthly brood-pouch counts for the whole 2 year sampling period were 178.2 at Aberdour 'L' and 139.4 at Aberdour 'H'.

Standard 10 mm females at Torrybay and Culross carried very similar brood-pouch loads of between 48 and 175 embryos per month

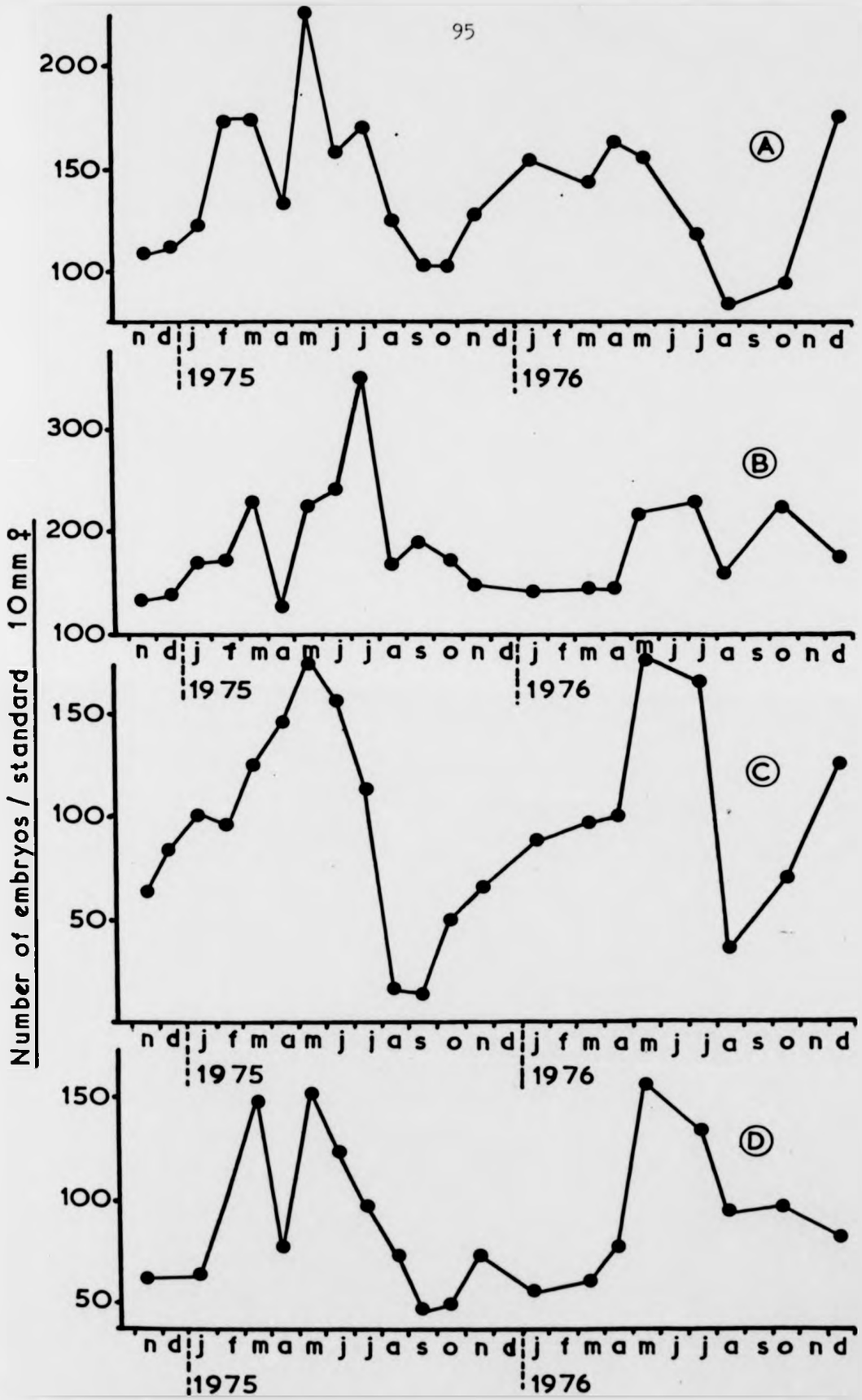
FIG.29. Seasonal variation in the brood-pouch loads of a standard 10mm female.

A = Aberdour 'H.'

B = Aberdour 'L.'

C = Torrybay.

D = Culross.


Number of embryos / standard 10mm ♀
200
150
100
A
n d j f m a m j j a s o n d j f m a m j j a s o n d
1975
1976
300
200
100
B
n d j f m a m j j a s o n d j f m a m j j a s o n d
1975
1976
150
100
50
C
n d j f m a m j j a s o n d j f m a m j j a s o n d
1975
1976
150
100
50
D
n d j f m a m j j a s o n d j f m a m j j a s o n d
1975
1976
MONTH

(Fig. 29) with mean monthly values for the 2 year sampling period of 98.2 at Torrybay and 93.2 at Culross.

Sex ratios and condition of gonads

The sex ratio was close to 1 : 1 at all sites over the 2 year sampling period from November 1974 to December 1975.

Ovaries and testes of L. rudis were full and active in the spring and early summer (Figs 30, 31) when brood-pouch counts were highest (Fig 18) but were reduced in the late summer and autumn when brood-pouch counts and especially egg counts were at a minimum. These results were based on the condition of the ovaries and testes of between 22 and 36 females and 22 and 30 males (Appendices 1 - 8).

Seasonal changes in condition of the ovary were broadly similar between 1974/75 and 1975/76 at all 4 sites (Fig. 30: Appendices 1, 3, 5, 7). The proportion of ovaries in the "very full" condition ranged from 88% at Aberdour 'H' in February 1975 to 0% for several months during the autumn at all sites. With the exception of Aberdour 'H', there were occasions between August and October when all ovaries were in the "reduced state" (Fig. 30). Ovaries of females from Aberdour 'H' were generally active for a greater part of the year than those from the other 3 sites (Fig 30a) This is in contrast to the situation at Torrybay where a phase of almost complete reduction of all ovaries was noted between August and October 1975 (Fig. 30c).

FIG.30. Seasonal variation in the condition of the ovary of *Littorina rudis*.

A = Aberdour 'H'.

B = Aberdour 'L'.

C = Torrybay.

D = Culross.

▒ = % females with reduced ovary.

□ = % females with full ovary.

■ = % females with very full ovary.

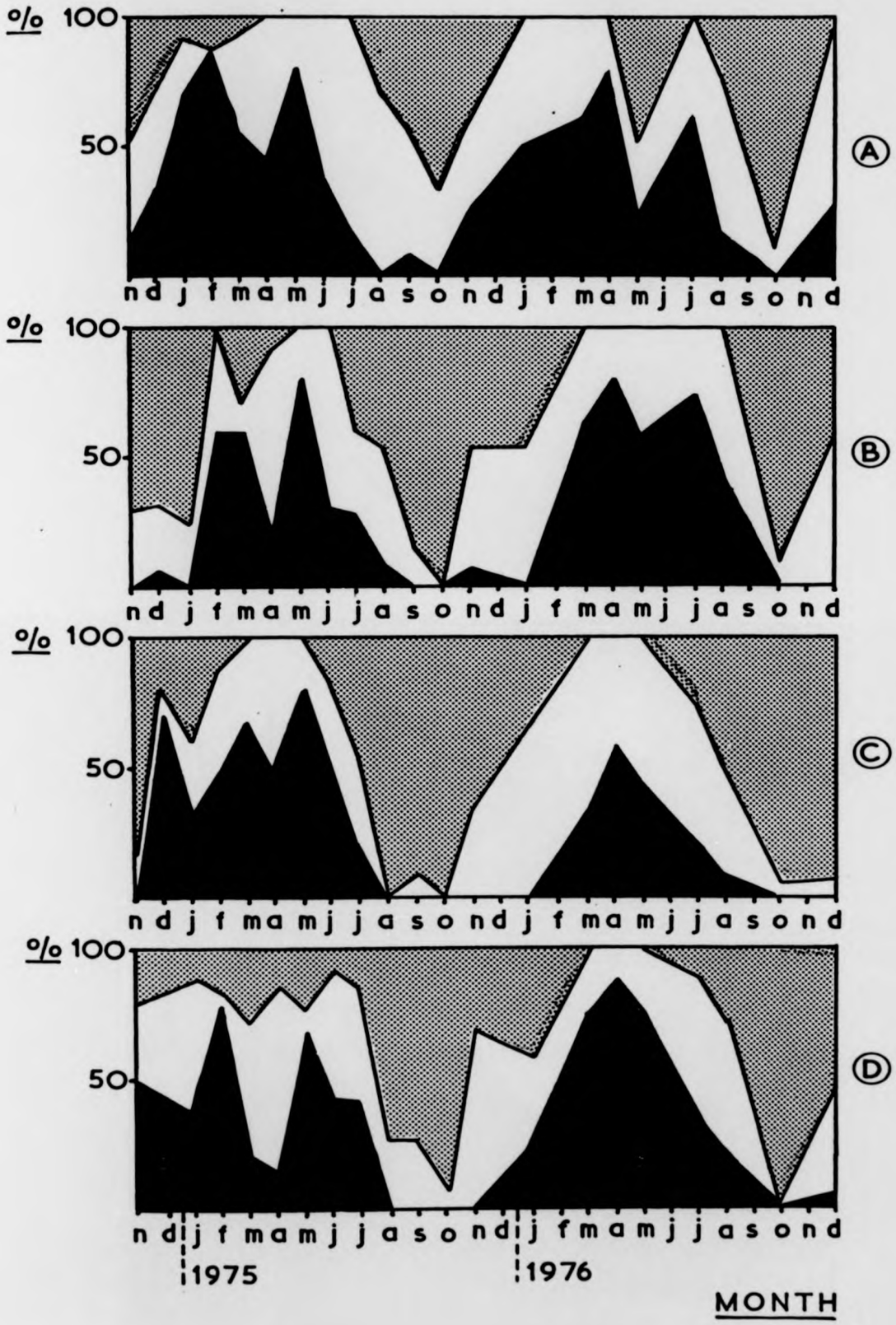

%
100
50
A
n d j f m a m j j a s o n d j f m a m j j a s o n d
%
100
50
B
n d j f m a m j j a s o n d j f m a m j j a s o n d
%
100
50
C
n d j f m a m j j a s o n d j f m a m j j a s o n d
%
100
50
D
n d j f m a m j j a s o n d j f m a m j j a s o n d
1975
1976
MONTH

FIG. 31. Seasonal variation in the condition of the testis in *Littorina rudis*.

A = Aberdour 'H'.

B = Aberdour 'L'.

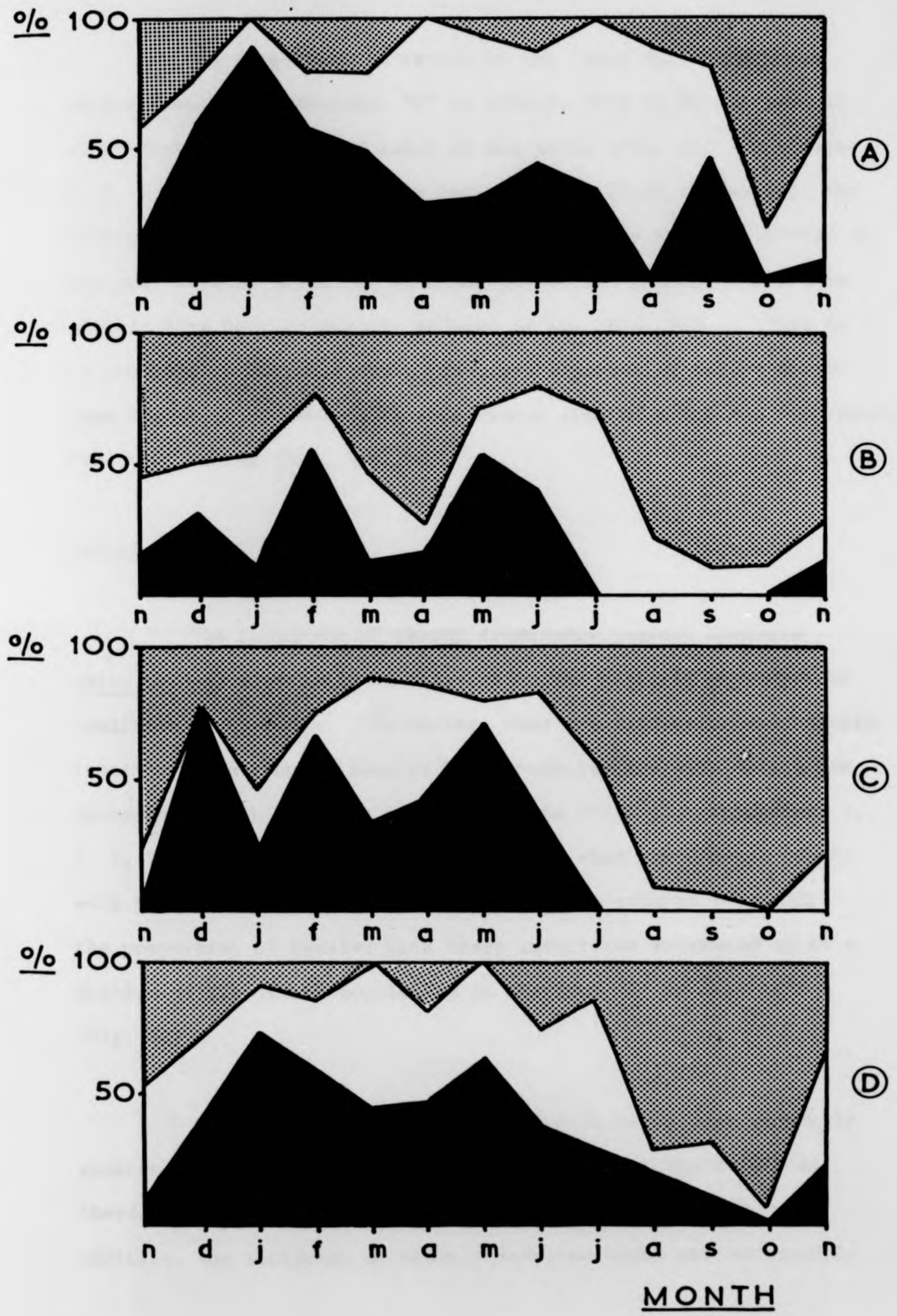
C = Torrybay.

D = Culross.

▒ = % males with reduced testis.

□ = % males with full testis.

■ = % males with very full testis.


%
100
50
n d j f m a m j j a s o n
A
B
C
D
MONTH

The proportion of testes in the "very full" condition ranged from 87% at Aberdour 'H' in January 1975 to 0% for several months between July and October at all sites (Fig. 31; Appendices 2, 4, 6, 8). As had been the case with condition of ovaries, the testes of snails at Aberdour 'H' were active for a longer period of the year than at any other site and at no time did 100% of snails at this site have completely reduced testes (Fig. 31a). This is in contrast to Torrybay where there was a period of some 4 months from August to November 1975 when almost 100% of males had completely "reduced" testes (Fig. 31c).

Parasitism

The incidence of larval trematodes (mainly Cercaria ubiquitoides) fluctuated in relation to the changing reproductive condition of L. rudis. In spring, when egg production was highest, levels of infection in females were generally low with only a few sporocysts visible in the digestive gland (Fig. 32; Appendices 1, 3, 5, 7). In the late summer and autumn when brood-pouch counts were at a minimum (Fig. 18) and ovaries were reduced (Fig. 30) the proportion of females with heavy infections increased up to a maximum of 22% of the population at Aberdour 'L' in July 1975 (Fig. 32).

The frequency and severity of infections were generally greater in males than females with up to 58% (in March 1975 at Aberdour 'L') of males heavily infected in any one month. In addition, the incidence of heavily infected males was not usually

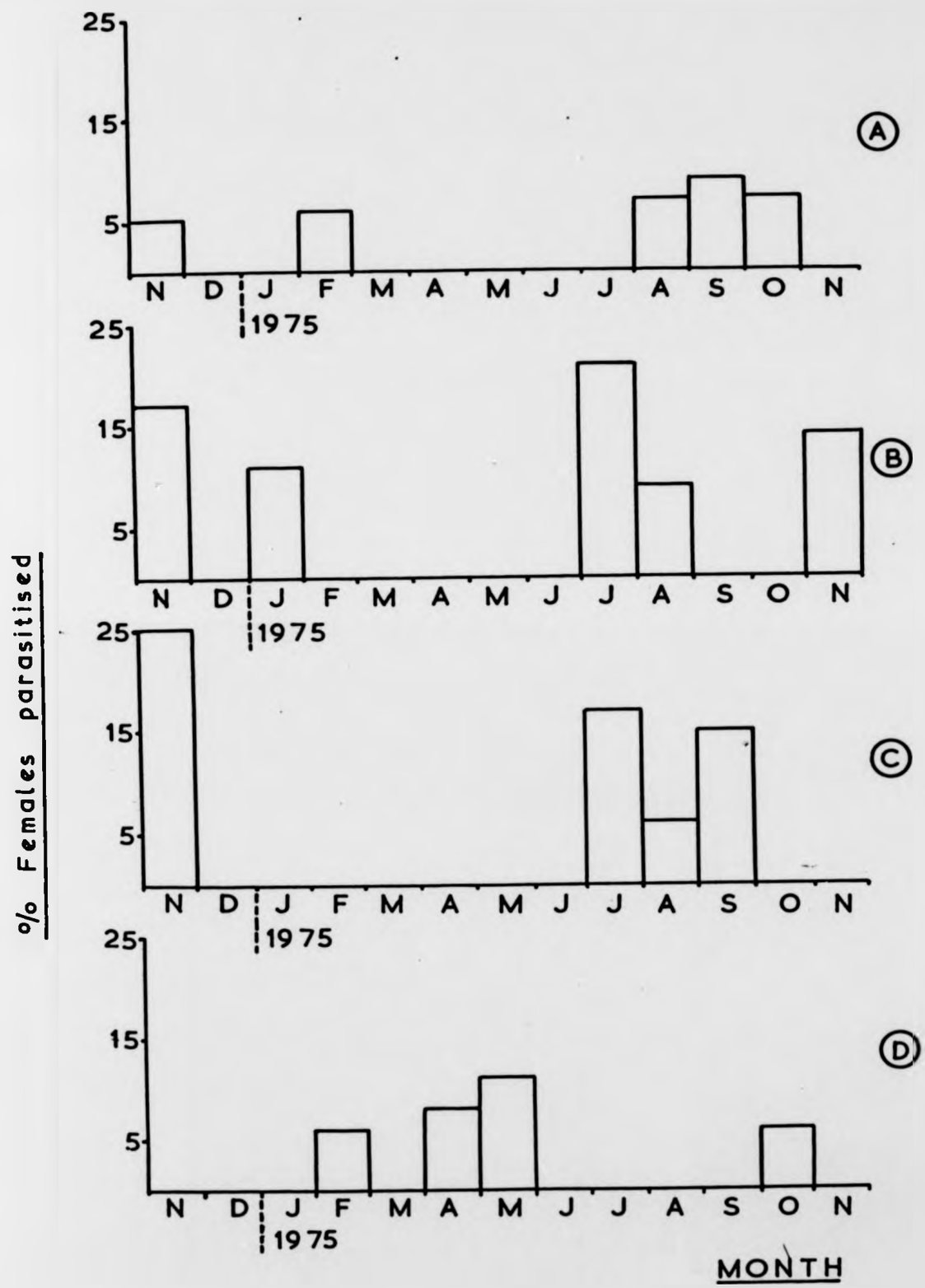
FIG.32. Histograms of the proportion of mature female Littorina rudis with conspicuous parasitism.

A = Aberdour'H!

B = Aberdour'L!

C = Torrybay.

D = Culross.


25
15
5
A
N D J F M A M J J A S O N
1975
B
C
D
% Females parasitised
MONTH

confined to the autumn (Fig. 33; Appendices 2, 4, 6, 8). Males with the digestive gland almost completely replaced by many invading sporocysts were found occasionally, especially at Aberdour 'L', whereas infections of this severity were rarely seen in females.

In both males and females the heaviest levels of infection occurred on the lower shore at Aberdour with a maximum of 58% of the males severely parasitised in March 1975 and 22% of females in July (Figs. 32, 33). The severity and frequency of infection was lowest on the upper shore at Aberdour with a maximum of 22% of the males (February 1975) and 8% of the females (September 1975) carrying heavy parasite loads. Levels of infection at Torrybay and Culross fell between these extremes (Figs. 32, 33). At Torrybay males carried the heaviest infections in August 1975(50%) and females in July (17%) while at Culross infections were heaviest in November 1974 in males (44%) and May in females (12%).

The proportion of males with a reduced penis (less than 3 mm) was not confined to any one period of the year (Fig. 34; Appendices 2, 4, 6, 8) rather there appeared to be a close correlation with the percentage of males heavily infected with parasites (Fig.33)

FIG.33. Histograms of the proportion of mature male Littorina rudis with conspicuous parasitism.

A = Aberdour 'H'

B = Aberdour 'L'

C = Torrybay

D = Culross

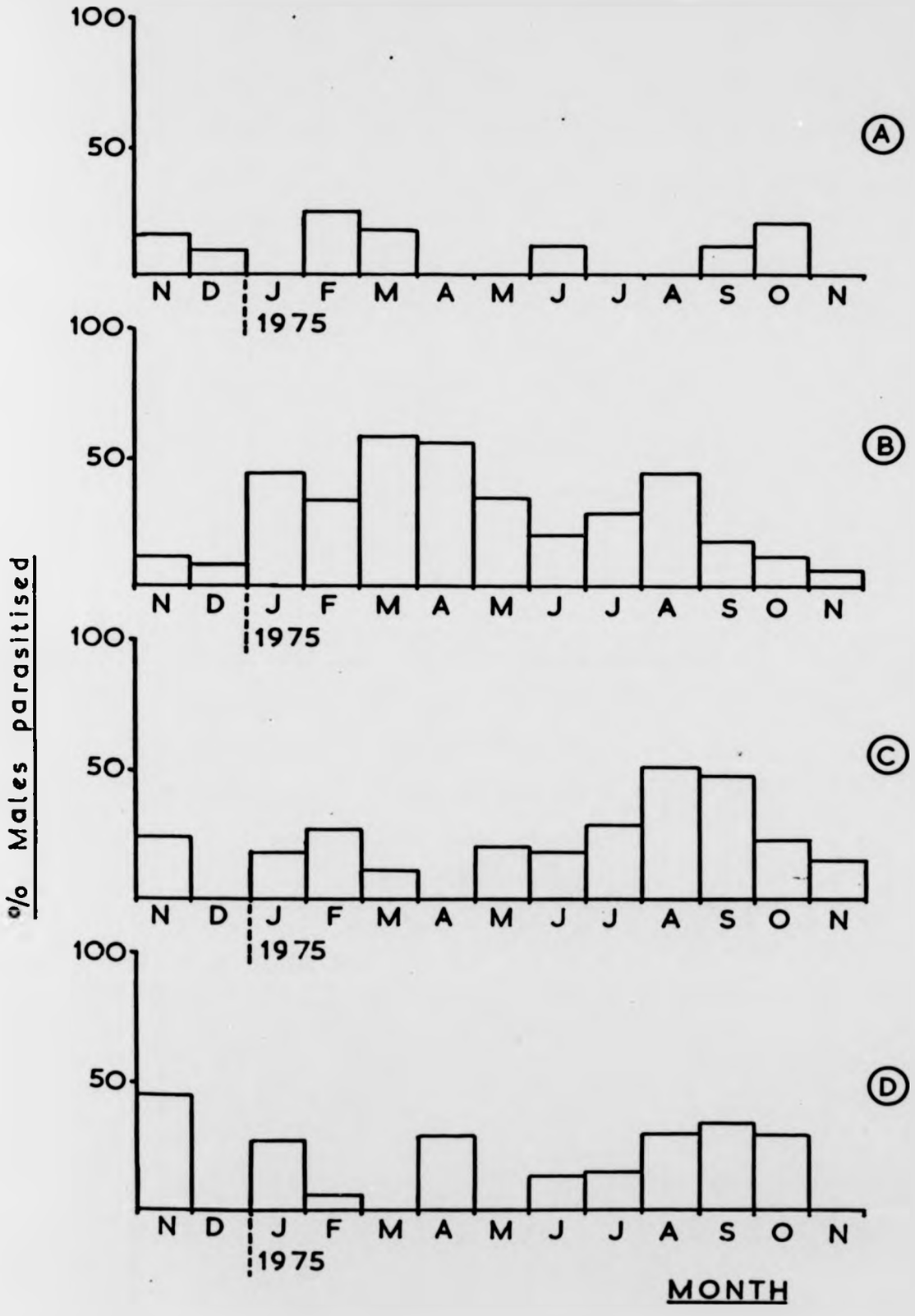

100
50
A
N D J F M A M J J A S O N
1975
100
50
B
N D J F M A M J J A S O N
1975
100
50
C
N D J F M A M J J A S O N
1975
100
50
D
N D J F M A M J J A S O N
1975
% Males parasitised
MONTH

FIG.34. Histograms of the proportion of mature male Littorina rudis with a reduced penis (less than 3mm).

A = Aberdour 'H'.

B = Aberdour 'L'.

C = Torrybay.

D = Culross.

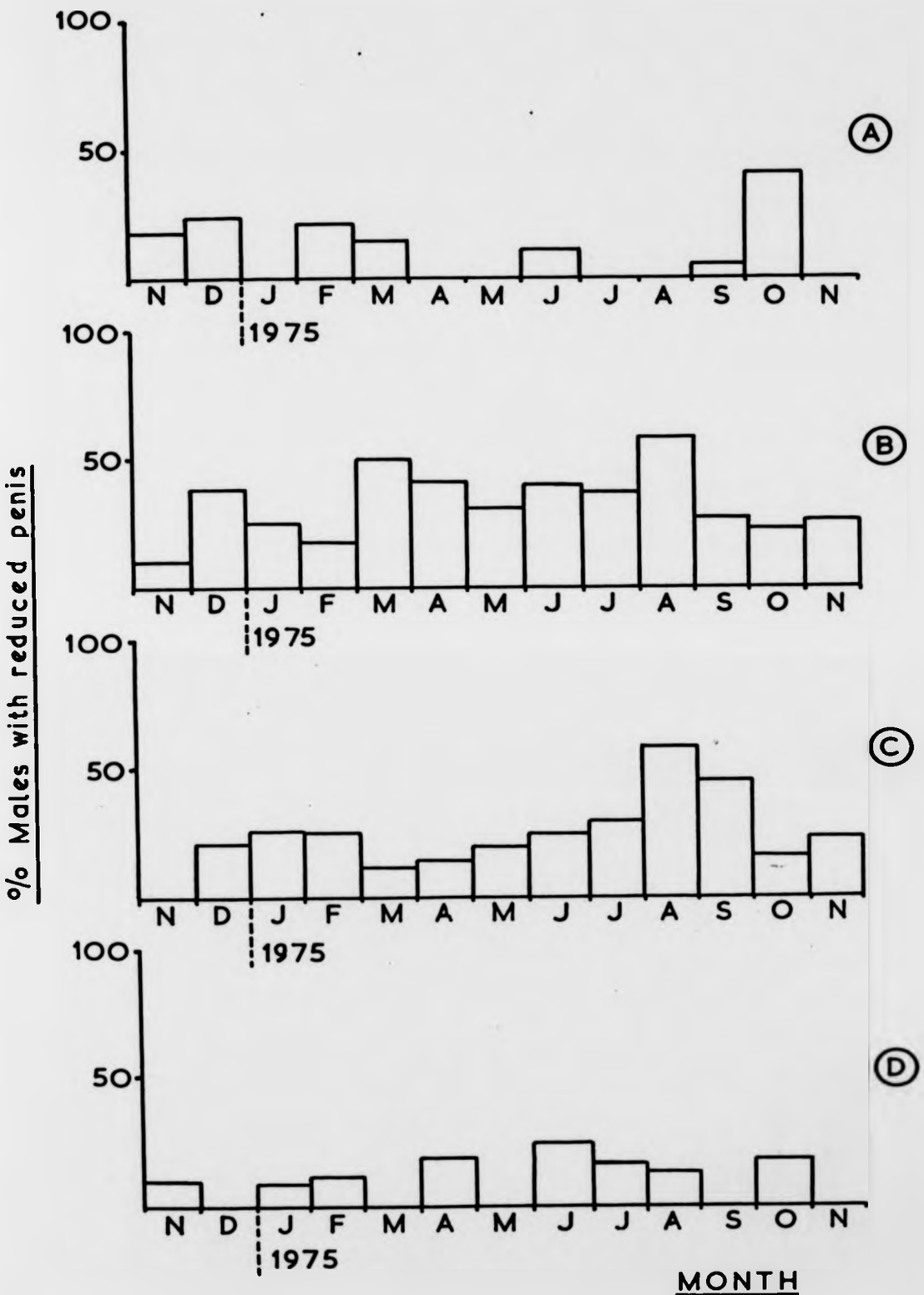
FIG.34. Histograms of the proportion of mature male Littorina rudis with a reduced penis (less than 3mm).

A = Aberdour 'H'.

B = Aberdour 'L'.

C = Torrybay.

D = Culross.


100
50
A
N D J F M A M J J A S O N
1975
100
50
B
N D J F M A M J J A S O N
1975
100
50
C
N D J F M A M J J A S O N
1975
100
50
D
N D J F M A M J J A S O N
1975
% Males with reduced penis
MONTH

5. THE DEVELOPMENT OF EGGS AND EMBRYOS

A preliminary assessment of development out of the brood-pouch of 150 representatives of each of the four embryonic stages from each site (total of 2400 embryos) carried out at 10°C and 32‰ salinity, showed that between sites there were no differences in development rates in the laboratory from egg to pre-release juvenile. 150 Stage 1 embryos (eggs, cleaving and undifferentiated early stages) took an average of 8 days (range = 6 to 9 days) to develop to early veliger embryos (stage 2). The range in parentheses gives the fastest and slowest times of apparently normal development although widely discrepant values of aberrant development were excluded. The development of these embryos beyond stage 2 appeared normal in all respects except that shell production did not proceed beyond the formation of a small disc on the visceral mass. Because of this difficulty it was not possible to follow the complete sequence of normal development starting from the egg stage. To overcome this, development of each of the four embryonic stages was followed separately through to the subsequent stage in order to compile a complete sequence of developmental steps.

Stage 2 embryos took an average of 30 days (range = 27 to 32 days) to reach stage 3, and stage 3 embryos took a further 30 days (28 to 34 days) to develop to pre-emergence stage 4 juveniles. Hence, eggs took a total of 68 days (61 to 74 days) at 10°C and 32‰ salinity to develop to pre-emergence juveniles. Hatching from the egg capsule in these laboratory conditions usually occurred up to 5 days later resulting in a total of 73 days from egg stage to hatched,

free-living juveniles.

Effects of Temperature on development

The effects of temperature on development were assessed on embryos from Aberdour 'H' only. More than 90% of the stage 1 embryos held at 5, 10 and 15°C in water of 32‰ salinity developed to early veligers (stage 2) in 10 (range = 9 to 11 days), 8 (6 to 9 days) and 5 (4 to 6 days) days respectively (Table 22). At 15°C, although some development beyond stage 2 did take place, fungal and bacterial growth on the capsules became very heavy and the embryos had all died by the 12th day. At 20°C only 16 of the 150 eggs reached stage 2 in an average of 4 days (2 to 5 days) but development did not continue beyond this stage and fungal and bacterial growth on the capsules was very heavy.

At 10°C, 96% of the 150 stage 2 embryos developed to stage 3 in an average of 30 days (27 to 32 days) but only 52% succeeded at 5°C taking 40 days (38 to 46 days). Although development at 15°C from stage 2 to stage 3 took an average of only 16 days (15 to 17 days) the mortality rate was almost 70%. In addition, growth of fungi and bacteria on the capsules was heavy and abnormally high numbers of the ciliate Protophyra ovicola were present. Development of stage 2 embryos at 20°C was negligible. Again, fungal and bacterial contamination of the capsules was heavy and eventually all of the embryos died.

TABLE 22 Effects of temperature on *in vitro* development of embryos from Aberdour 'H' *L. rudis* at 32‰ salinity

Temp. (°C)	Mean development times in days of 150 embryos (range) and success rate (%)						
	Stage 1 to Stage 4	Success rate (%)	Stage 2 to Stage 3	Success rate (%)	Stage 3 to Stage 4	Success rate (%)	Total time from Stage 1 to Stage 4
5	10(9-11)	100	40(38-46)	52	65(61-70)	100	115(108-127)
10	8(6- 9)	100	30(27-32)	96	30(28-34)	100	68(61- 74)
15	5(4- 6)	90	16(15-17)	30	20(18-21)	88	41(37- 44)
20	4(2- 5)	10	N/D	0	18(15-23)	9	-

N/D = No Development

TABLE 23 Day - degrees for *in vitro* development of *L. rudis* from Aberdour 'H' at different temperatures at 32‰ salinity

Temp. (°C)	Day degrees for development between Stage 1 and Stage 4			
	Stage 1 to Stage 2	Stage 2 to Stage 3	Stage 3 to Stage 4	Total from Stage 1 to Stage 4
5	50	200	325	575
10	80	300	300	680
15	75	240	300	615
20	80	-	360	-

At 10°C all of the 150 stage 3 embryos developed successfully to stage 4 in an average of 30 days (28 to 34 days) and subsequently emerged from their capsules (Table 22). On leaving the capsule, juveniles were very active, moving to the edge of the petridish and onto the lid. Faecal pellets were observed in the gut within 2 days indicating that feeding began immediately. At 5°C development from stage 3 to 4 was much slower taking an average of 65 days (61 to 70 days) but the juveniles tended to be smaller and less active on leaving the capsules than those at 10°C.

At 15°C, 132 of the 150 stage 3 embryos developed to stage 4, but only 26 of these left their capsules and these died within 2 to 3 days. Fungal and bacterial growth on the capsules of the remaining embryos was extensive and eventually they all died. Large numbers of P. ovicola were present and were observed to consume dead individuals and on a few occasions even attacked embryos which were still alive but in very poor condition.

At 20°C, development to stage 4 occurred in only 13 of the 150 stage 3 embryos, these eventually left their capsules but died almost immediately. In the remaining 137 death was not immediate but the embryos were largely inactive and their capsules were surrounded by large numbers of P. ovicola which eventually consumed them.

While it can be seen that development out of the broodpouch was most rapid at 15°C, taking an average of only 41 days, mortality was high (Table 22). At 10°C embryos survived well but

full development to stages matching those released naturally by females took an average of 73 days. The linear dependence of development on temperature can be demonstrated using the concept of day degrees (Ricker, 1968). Over the range of temperatures studied, full development took between 575 and 680 day degrees with most variation occurring between stages 2 and 3 (Table 23). While these experiments have provided information on development rates, it is still unclear how long fully developed juveniles may remain in the brood-pouch prior to release. Therefore, conditions promoting or preventing release are also likely to be significant to the relationship between brood-pouch loads and rate of production of young.

Effects of Salinity on development

The effects of salinity on development were assessed on embryos from Aberdour 'H' only (Table 24). In salinities of 0 - 8‰ embryos at all stages of development died within 1 - 8 days. Eggs rapidly became granular in appearance with fungal and bacterial growth on the capsules. In freshwater, 10% of the 150 eggs burst within 24 h. Later stage embryos survived for up to 8 days but with no observable development having taken place.

Development out of the brood-pouch was far more successful in salinities between 12 and 32‰. Cleavage began normally in 43 of the 150 stage 1 embryos held at 12‰. A further 14 appeared viable for up to 5 days but the contents of the remaining 93 became granular. By the 8th day all were dead.

TABLE 24 Effects of salinity on *in vitro* development of embryos from Aberdour 'H' *L. rudis* at 10°C

Test Salinity (‰)	Mean development times in days of 150 embryos (range) and success rate (%)						
	Stage 1 to Stage 2	Success rate (%)	Stage 2 to Stage 3	Success rate (%)	Stage 3 to Stage 4	Success rate (%)	Total time from stage 1 to stage 4
0-8	N/D	-	N/D	-	N/D	-	-
12	N/D	-	35(32-39)	90	33(31-40)	38	-
16	13(10-15)	11	35(30-38)	59	33(32-37)	52	81(72-90)
20	14(9-18)	18	34(32-37)	63	32(30-35)	56	80(71-90)
24	13(12-15)	31	33(32-35)	77	30(27-32)	68	76(71-82)
32	7(6- 9)	98	33(31-34)	100	30(28-31)	100	70(65-74)

N/D = No Development

At 24‰ , 47 of the 150 stage 1 embryos reached stage 2 after an average of 13 days (12 to 15 days), the remaining 103 were either dead or in poor condition. Development of the 47 embryos which successfully reached stage 2 continued to stage 3 but shell development was severaly stunted.

Of the 150 stage 2 embryos held at a salinity of 12‰ , 136 died within 8 days. The remaining 14 embryos developed to stage 3 in an average of 35 days (range = 32 to 39 days) but all were very small and in poor condition and none developed further. At 16‰ , 88 of the 150 stage 2 embryos also took an average of 35 days (30 to 38 days) to develop to stage 3 (Table 24), but the remaining 62 died without developing further. The 88 embryos which had developed successfully to stage 3 continued to stage 4 and although shell growth was retarded initially, all eventually formed a complete but thin shell. These embryos were alive and moving in their capsules at the end of the experiment (100 days) despite heavy growth of fungi and bacteria.

At 24‰ salinity, 117 of the 150 stage 2 embryos reached stage 3 after an average of 33 days (range = 32 to 35 days) and about half of these developed to stage 4 although none had left their capsules at the end of the 100 day trial. Stage 2 embryos therefore developed almost as well in 24‰ as in water of 32‰ (Table 24).

At salinities between 12 and 24‰ development rates of stage 3 embryos to stage 4 were very similar taking an average of 33 days (range = 31 to 40 days) at 12‰ , 33 days (32 to 37) at 16‰

and 30 days (27 to 32) at 24‰ . Mortality rates varied however, with only 38% of the 150 embryos surviving at 12‰ , 52% at 16‰ and 68% at 24‰ .

At 12‰ , 24 of the 150 stage 4 pre-emergence embryos had left their capsules after 47 days but only 3 survived until the end of the 100 day trial. The remaining 126 died without leaving their capsules. This is in contrast to the 150 stage 4 embryos at 32‰ which all left their capsules within 5 days. At 16‰ 33% of the 150 stage 4 embryos had left their capsules after 20 days but they were relatively inactive. At 24‰ , all 150 stage 4 embryos had left their capsules within 8 days but only 68% survived (Table 24).

These results have shown that embryonic development is severely restricted at salinities of less than 24‰ . The egg stage was most affected by low salinity and stage 4 pre-emergence embryos most tolerant although there was a tendency for juveniles to remain in their capsules at very low salinities. The results also suggest that lowered salinity leads to retardation of shell development resulting in partially formed or very thin-walled shells. P. ovicola survived in salinities as low as 8‰ .

6. EMBRYO SIZE AND GROWTH OF NEWLY RELEASED JUVENILES

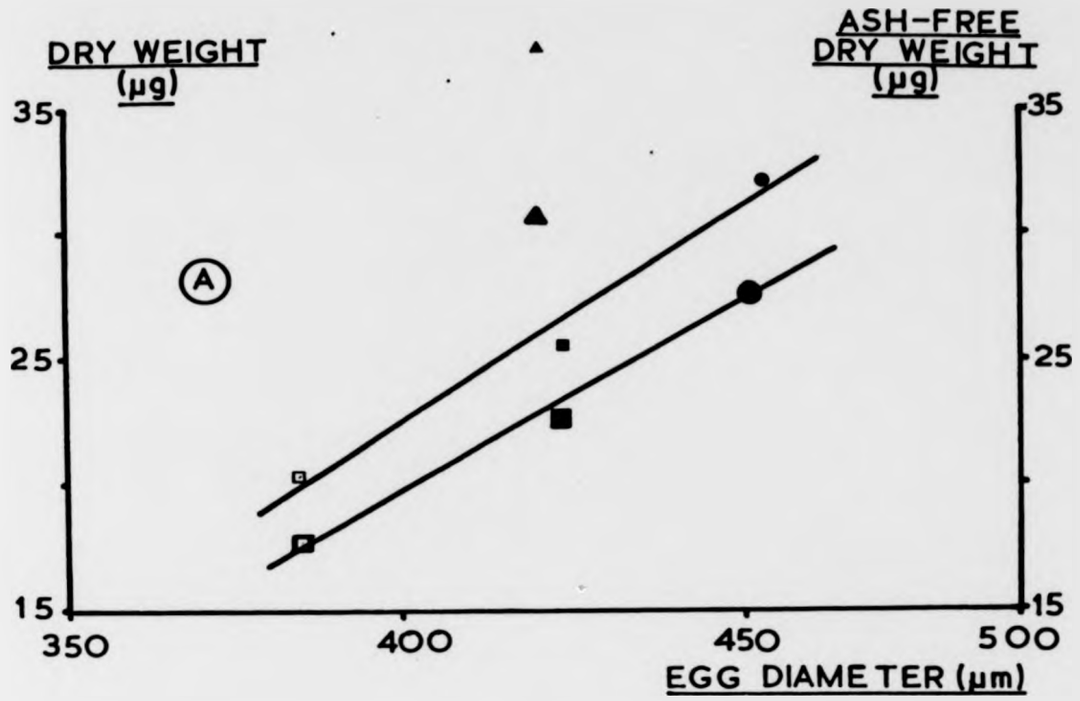
Stage 1 embryos varied in size and weight between the four sites (Table 25) but not with time of year. Of 1000 eggs measured from each site, the largest in terms of diameter were produced at Culross (452 ± 0.92 μm) followed by Aberdour 'H' (424 ± 1.06 μm), Torrybay (420 ± 1.14 μm) and the smallest at Aberdour 'L' (385 ± 0.94 μm). This order did not hold however when weight was considered as Torrybay females produced the heaviest eggs (37.5 ± 0.76 μg dry weight) followed closely by Culross (32.3 ± 0.34 μg dry weight). Eggs of these up-estuary snails were conspicuously heavier than those of Aberdour 'H' (25.7 ± 0.33 μg dry weight) and Aberdour 'L' (20.4 ± 0.45 μg dry weight).

Ash-free dry weights of eggs followed the same order as dry weight with up-estuary values much greater than at Aberdour (Table 25), and this held despite the ash content also being greater at Torrybay (17% of dry weight) and Culross (16%) than at Aberdour 'L' (14%) and Aberdour 'H' (12%). Thus, up-estuary eggs were heavier than those from Aberdour because of both greater organic and inorganic constituents (Table 25).

The relationship between dry weight and diameter and also of ash-free dry weight and diameter was virtually constant among eggs produced at Aberdour 'H', Aberdour 'L' and Culross but differed in Torrybay eggs which were markedly heavier for their size (Fig. 35). When dry weight was plotted against ash-free dry weight however (Fig. 36), the points for all 4 stations, including Torrybay, fell

TABLE 25 The diameter, weight and energy content of stage 1 and stage 4 embryos of L. rudis

Site	Developmental stage	Mean diameter (µm) of 1000 embryos (± SE)	Mean dry weight (µg) of 3000 embryos (± SE)	Increase in dry weight from stage 1 to stage 4 (%)	Ash content (µg)	Ash content as % of dry weight	Increase in ash content from stage 1 to stage 4 (µg)	Ash-free dry weight µg (± SE)	Energy content ($kJx10^{-4}$)
Aberdour 'H'	1	424(±1.06)	25.7(±0.33)	-	3.2	12	-	22.5(±0.30)	4.97
	4	454(±1.41)	38.8(±0.36)	50.9	14.2	36	11.0	24.6(±0.42)	5.24
Aberdour 'L'	1	385(±0.94)	20.4(±0.45)	-	2.8	14	-	17.60(±0.78)	3.89
	4	415(±1.06)	29.3(±0.76)	43.6	12.4	42	9.6	16.94(±0.75)	3.61
Torrybay	1	420(±1.14)	37.5(±0.76)	-	6.5	17	-	31.05(±0.41)	6.86
	4	498(±1.57)	55.5(±0.63)	48.0	24.7	44	18.2	30.83(±1.27)	6.57
Culross	1	452(±0.92)	32.3(±0.34)	-	5.3	16	-	27.0 (±0.96)	5.97
	4	509(±1.54)	48.1(±0.18)	48.9	18.7	39	13.4	29.4 (±0.90)	6.27


DRY WEIGHT (µg)
ASH-FREE DRY WEIGHT (µg)
35
25
15
A
350
400
450
500
EGG DIAMETER (µm)

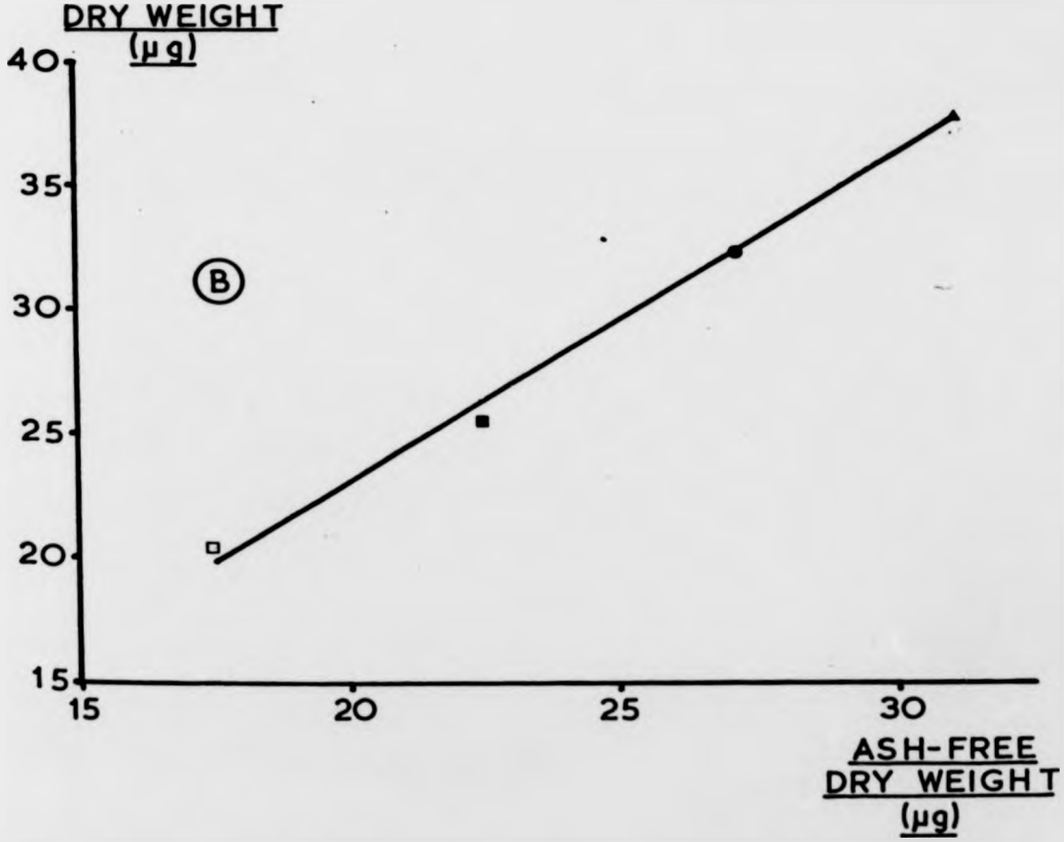

DRY WEIGHT (µg)
40
35
30
25
20
15
B
15
20
25
30
ASH-FREE DRY WEIGHT (µg)

FIG.35. The relationship between egg dry weight, egg ash-free dry weight and egg diameter.

■ = Aberdour 'H' egg dry weight.

□ = Aberdour 'L' " " " .

▲ = Torrybay " " " .

● = Culross " " " .

■ = Aberdour 'H' egg ash-free dry weight.

□ = Aberdour 'L' " " " " " .

▲ = Torrybay " " " " " .

● = Culross " " " " " .

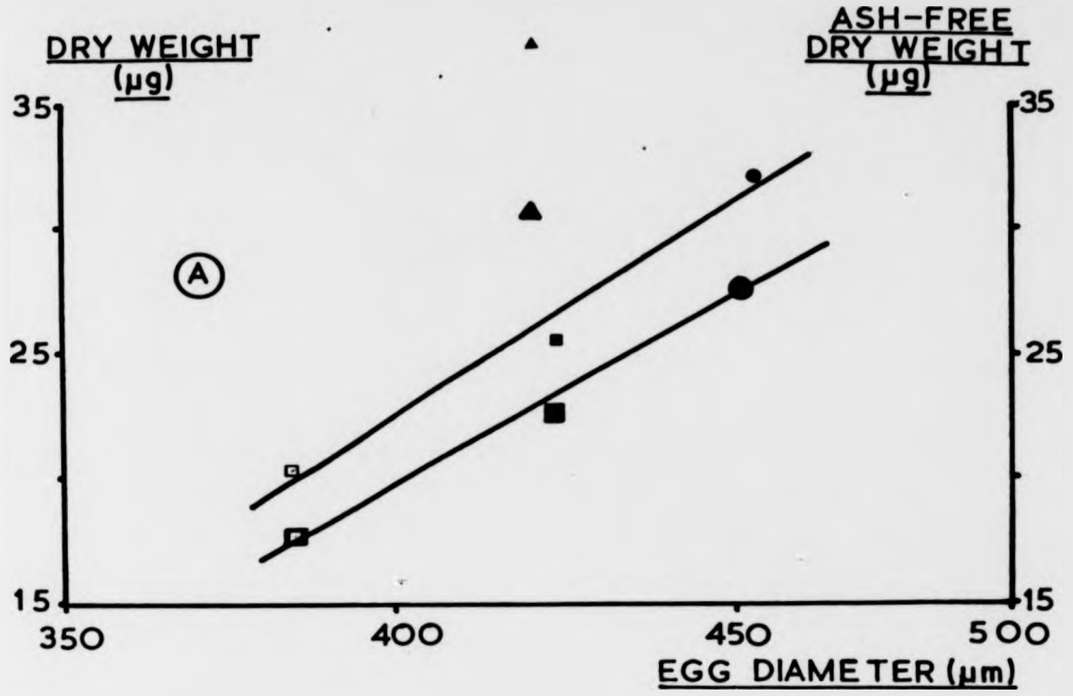
FIG.36. The relationship between egg dry weight and egg ash-free dry weight.

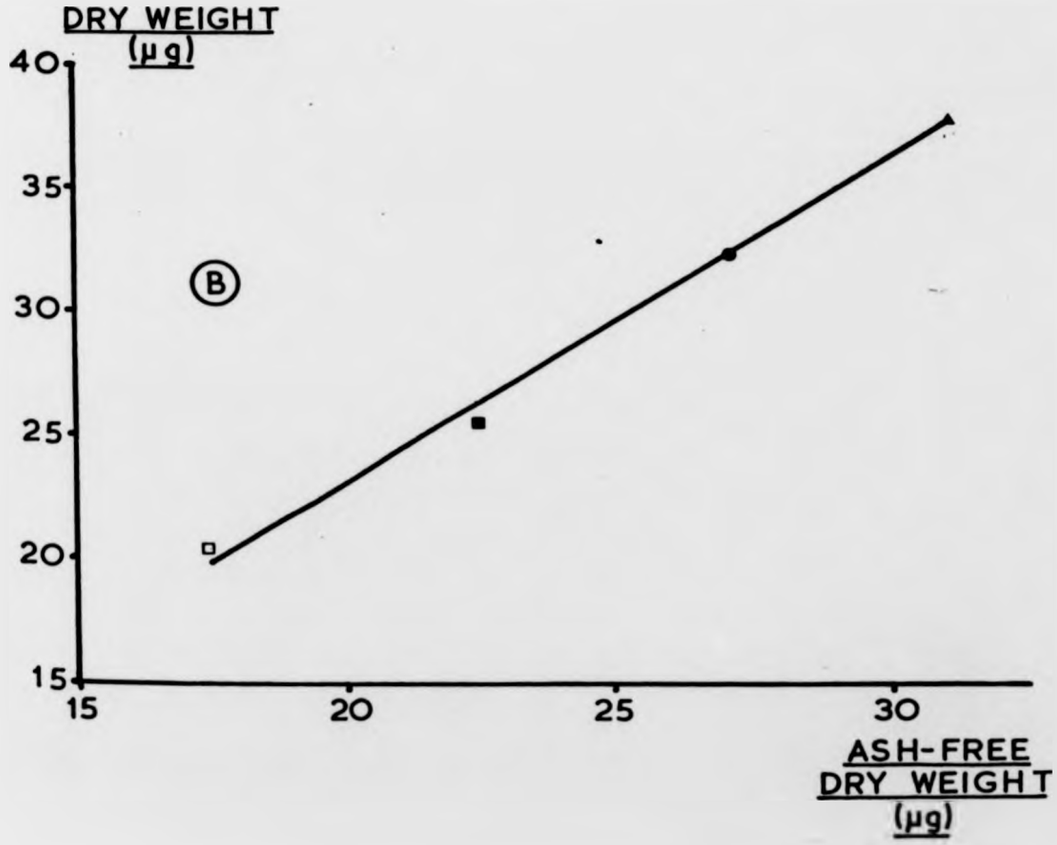
■ = Aberdour 'H'

□ = Aberdour 'L'

▲ = Torrybay

● = Culross


DRY WEIGHT (µg)
ASH-FREE DRY WEIGHT (µg)
35
25
15
A
350
400
450
500
EGG DIAMETER (µm)


DRY WEIGHT (µg)
40
35
30
25
20
15
B
15
20
25
30
ASH-FREE DRY WEIGHT (µg)

onto a straight line described by : -

Egg dry weight = 1.3 egg AFDW - 3 This linear relationship between organic and inorganic contents for eggs from all sites shows that Torrybay eggs must be more dense in order to explain the anomalous relationship between diameter and weight noted in Fig. 35.

The largest stage 4 brood-pouch juveniles were produced at the up-estuary sites of Culross (509 ± 1.5 µm) and Torrybay (498 ± 1.57 µm) followed by Aberdour 'H' (454 ± 1.41 µm) and the smallest at Aberdour 'L' (415 ± 1.06 µm). Again Torrybay juveniles were heaviest with a dry weight of 55.5 ± 0.63 µg and Culross juveniles (48.1 ± 0.18 µg) were heavier than those from both Aberdour 'H' (38.8 ± 0.36 µg) and Aberdour 'L' (29.3 ± 0.76 µg). Ash-free dry weights of stage 4 embryos followed the same order as dry weights with the up-estuary values again much greater than those from Aberdour (Table 25). The relationship between weight and size was more constant for late-brood-pouch juveniles than for the eggs, but again Torrybay juveniles were denser than the slightly bigger Culross juveniles (Fig. 37).

The variation in ash content (36 to 44% of the dry weight) did not account for the weight differences between the marine and estuarine stage 4 embryos (Table 25).

The dry weight of late-brood-pouch juveniles increased exponentially with increasing ash-free dry weight (Fig. 38). As the ash-free dry weight constitutes the organic component and the dry weight includes both the inorganic and organic fractions, then

FIG.37. The relationship between dry weight, ash-free dry weight and diameter of juveniles taken from the brood pouch.

■ = Aberdour 'H' juvenile dry weight.

□ = Aberdour 'L' " " " .

▲ = Torrybay " " " .

● = Culross " " " .

■ = Aberdour 'H' juvenile ash-free dry weight.

□ = Aberdour 'L' " " " " " .

▲ = Torrybay " " " " " .

● = Culross " " " " " .

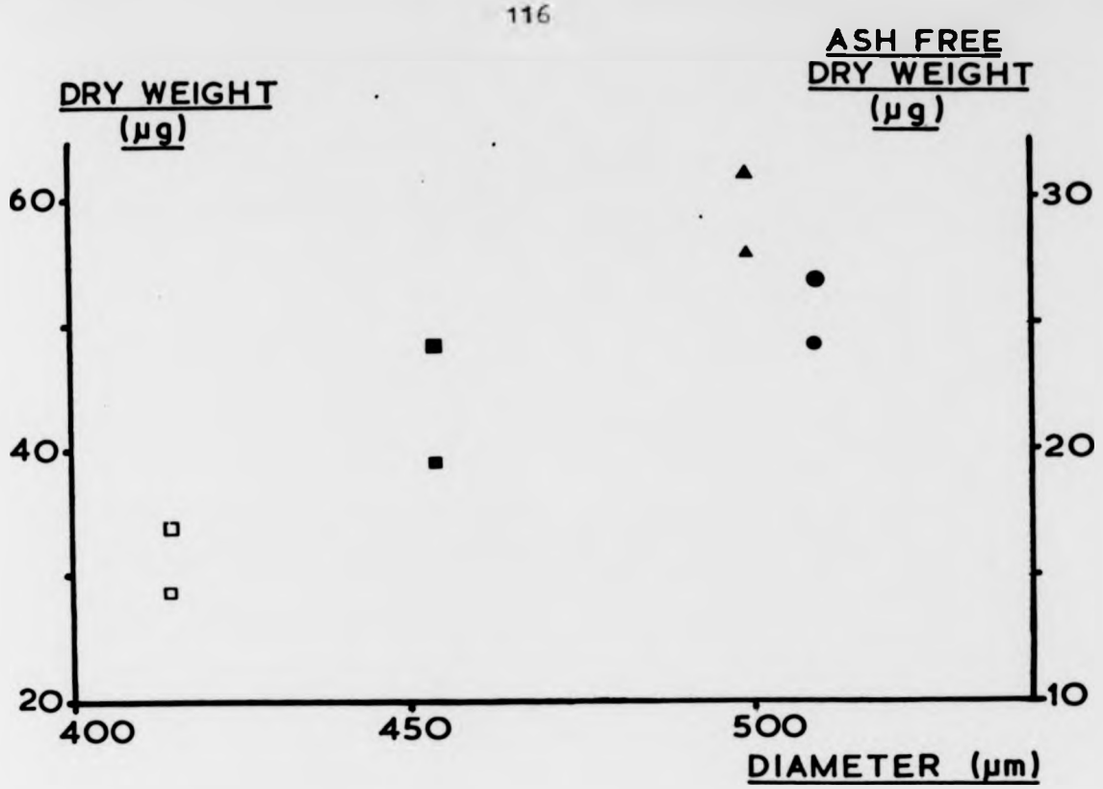
FIG.38. The relationship between juvenile dry weight and juvenile ash-free dry weight.

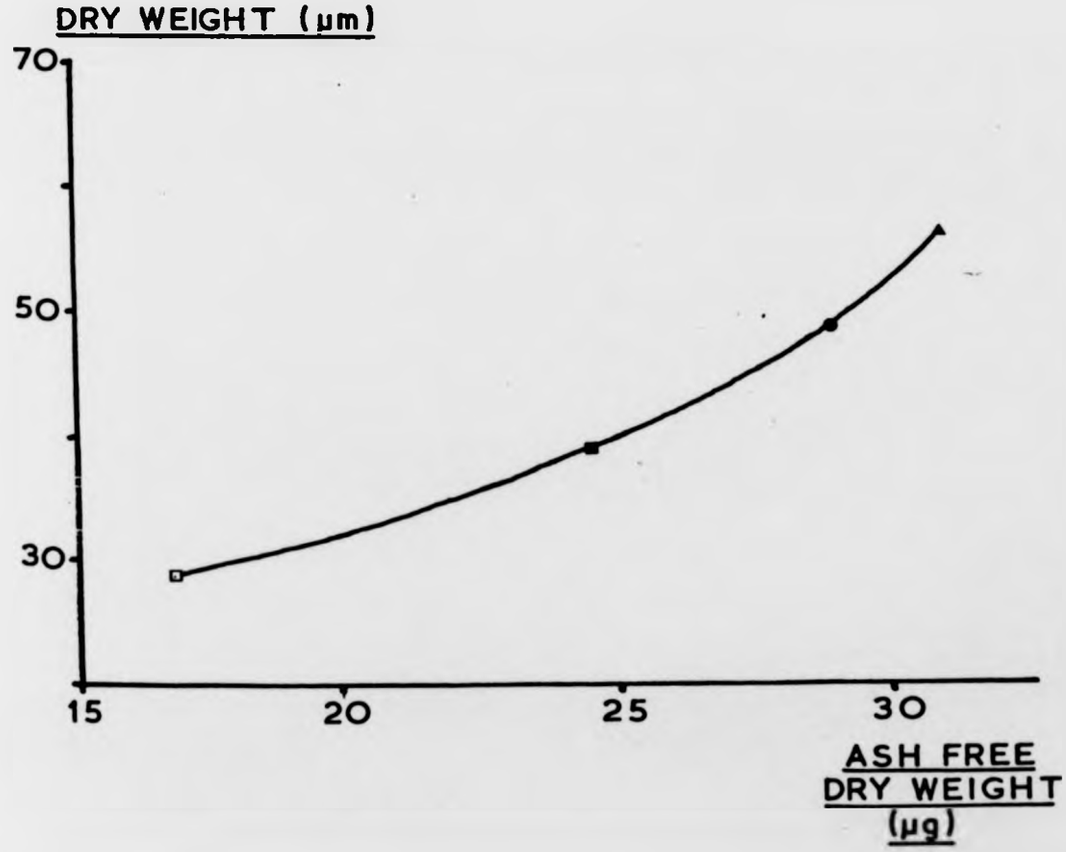
■ = Aberdour 'H'

□ = Aberdour 'L'

▲ = Torrybay

● = Culross


DRY WEIGHT
(µg)
ASH FREE
DRY WEIGHT
(µg)
60
40
20
30
20
10
400
450
500
DIAMETER (µm)


DRY WEIGHT (µm)
70
50
30
15
20
25
30
ASH FREE
DRY WEIGHT
(µg)

the results indicate that the juveniles from Torrybay and Culross had a larger shell weight per unit flesh weight than the smaller juveniles from Aberdour 'H' and 'L'.

At Aberdour 'H', Torrybay and Culross, the increase in dry weight from egg to late juvenile was virtually uniform between 48 and 50%, whereas at Aberdour 'L' the increase was only 43.6% (Table 25). These increases during development consisted predominantly of increases in the ash content while the ash-free dry weights at each site remained virtually constant (Table 25). Thus it appears that the increase in dry weight from egg to juvenile was almost entirely attributable to growth of a shell.

The energy content of stage 1 eggs derived from elemental analysis was 22.10 kJ g^{-1} AFDW while pre-emergence juveniles had an energy value of 21.32 kJ g^{-1} AFDW. Thus the energy expended on each stage 1 embryo by females at Torrybay (6.86×10^{-4} kJ) was almost twice that invested by females at Aberdour 'L' (3.89×10^{-4} kJ) with the values for Culross (5.97×10^{-4} kJ) and Aberdour 'H' (4.99×10^{-4} kJ) falling between these two extremes (Table 25).

Newly emerged young from Torrybay and Culross were cultured successfuly at 10°C and 32‰ salinity in the laboratory for 24 weeks with an estimated overall mortality of 13% and 21% respectively. During the 166 day trial there was an almost 6-fold increase in weight (Tables 26 and 27). Snails from Torrybay grew from 477 to 2618 µ m shell height and 53 to 1495 µ g dry weight, while those from Culross grew from 530 to 3243 µ m (49 to 1750 µg dry weight). This

TABLE 26 Growth of juvenile L. rudis from Torrybay in the laboratory at 10°C and 32‰ salinity.

Age (days)	n	Mean shell height (h) µm	$Log_e h$	Mean weight (w) µg	$Log_e w$	Specific growth rate (SGR)
1	150	477	6.155	53	3.970	-
30	150	653	6.487	123	4.812	2.81
45	150	820	6.709	201	5.303	3.27
62	150	985	6.893	266	5.585	1.67
95	150	1390	7.237	589	6.378	2.40
131	150	2071	7.636	1051	6.958	1.61
166	150	2618	7.870	1495	7.309	1.00

TABLE 27 Growth of juvenile L. rudis from Culross in the laboratory at 10°C and 32‰ salinity

Age (days)	n	Mean shell height (h) µm	$Log_e h$	Mean weight (w) µg	$Log_e w$	Specific growth rate (SGR)
1	150	530	6.273	49	3.892	-
30	150	752	6.623	98	4.585	2.31
45	150	807	6.693	199	5.293	4.72
62	150	1091	6.995	263	5.572	1.64
95	150	1540	7.340	499	6.213	1.94
131	150	2495	7.822	1120	7.021	2.24
166	150	3242	8.084	1750	7.467	1.27

represents, over the entire 166 days, an average increase in dry weight of 8.67 $\mu g\ d^{-1}$ per individual by Torrybay snails and 10.25 $\mu g\ d^{-1}$ by Culross individuals.

Growth was exponential however, with serial doublings of weight after about (a) 20 days (b) 45 days (c) 60 to 80 days and (d) 110 to 120 days (Tables 26, 27; Figs. 39a and 40a), therefore a natural log transformation was carried out on the data (Figs. 39b and 40b) and the following regression equations were derived to relate dry weight to shell height: -

(1) $\log_e w = 1.929 \log_e h - 7.743$ ..... Torrybay

(2) $\log_e w = 1.975 \log_e h - 8.311$ ..... Culross

where w = weight and h = shell height.

The specific growth rate (SGR), which gives the daily gain in weight as a percentage of the body weight, was calculated according to the expression: -

$$SGR = \frac{\ln w_t - \ln w_o}{t_2 - t_1} \times 100\%$$

where $\ln w_t$ = natural log of weight at time t, lnwo = natural log of weight at time zero and $t_2 - t_1$ is the time interval. Maximum SGR's of 3.27% and 4.72% for Torrybay and Culross snails respectively occurred between the 30th and 45th days of the experiment (Tables 26, 27). After the 45th day, the SGR gradually fell to 1.00% for Torrybay snails and 1.27% for Culross snails. The overall SGR's for the 166 days of the experiment were 2.02% and 2.17% for Torrybay

FIG. 39a. Growth in the laboratory at 10 °C of juveniles taken from Torrybay females.

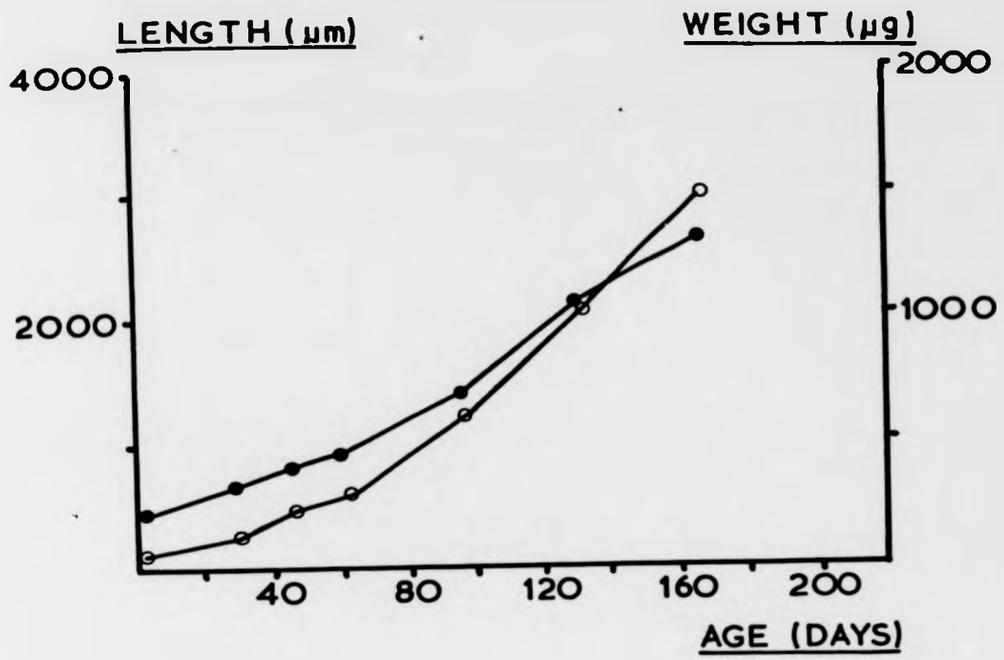
● = length

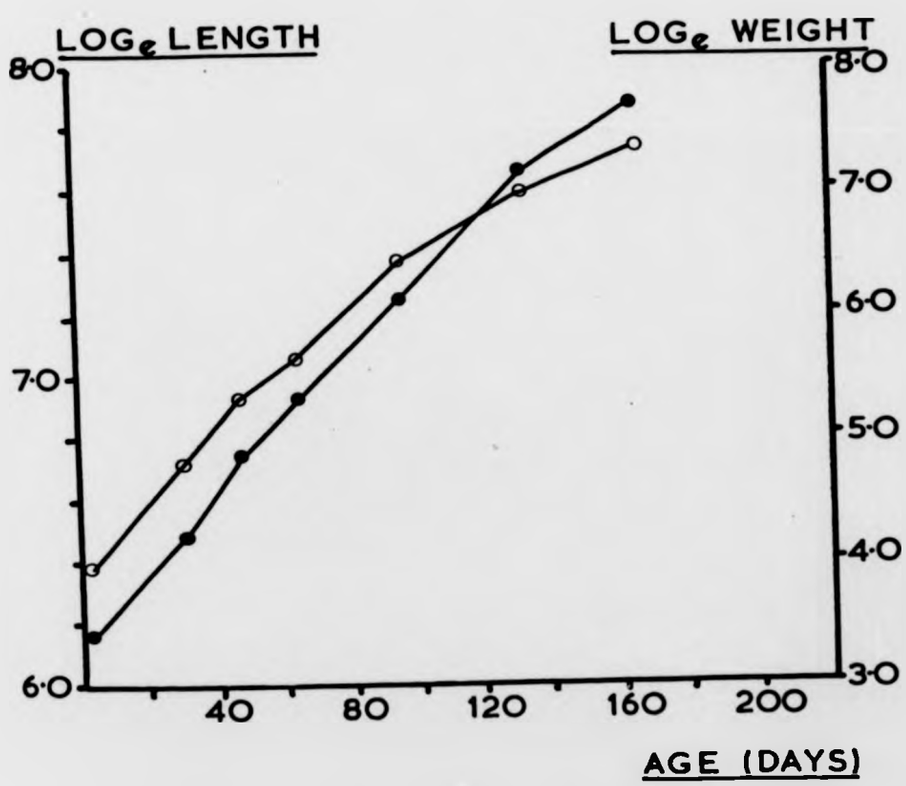
o = weight

FIG. 39b. Log_e transformations of growth data depicted in FIG. 39a.

● = log_e length

o = log_e weight


LENGTH (µm)
WEIGHT (µg)
4000
2000
2000
1000
40
80
120
160
200
AGE (DAYS)


LOGe LENGTH
LOGe WEIGHT
8·0
7·0
6·0
8·0
7·0
6·0
5·0
4·0
3·0
40
80
120
160
200
AGE (DAYS)

. 39a.

FIG.40a. Growth in the laboratory at 10°C of juveniles taken from Culross females.

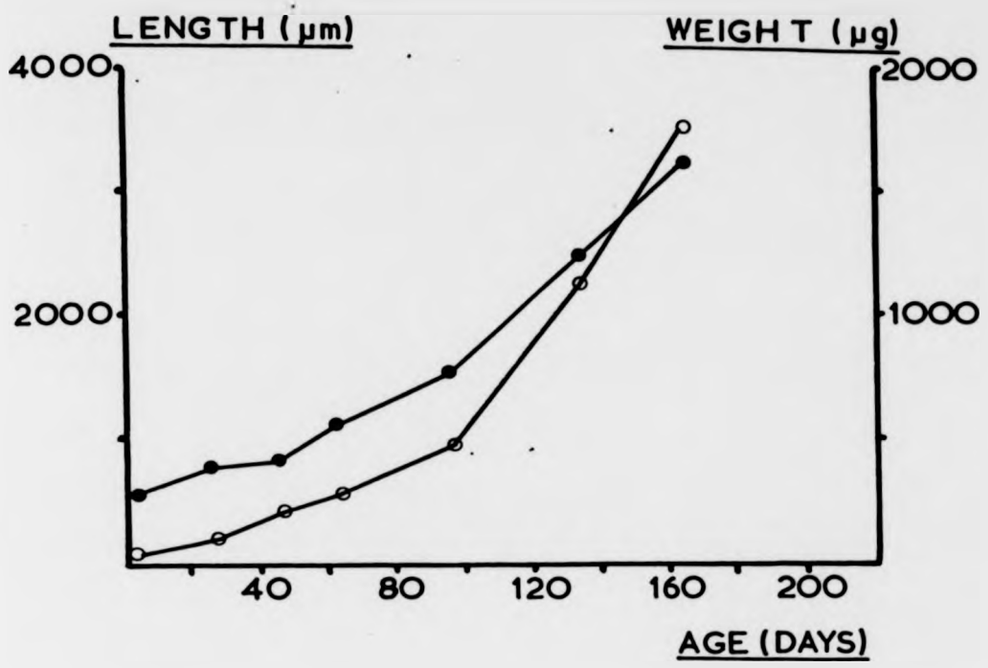
● = length

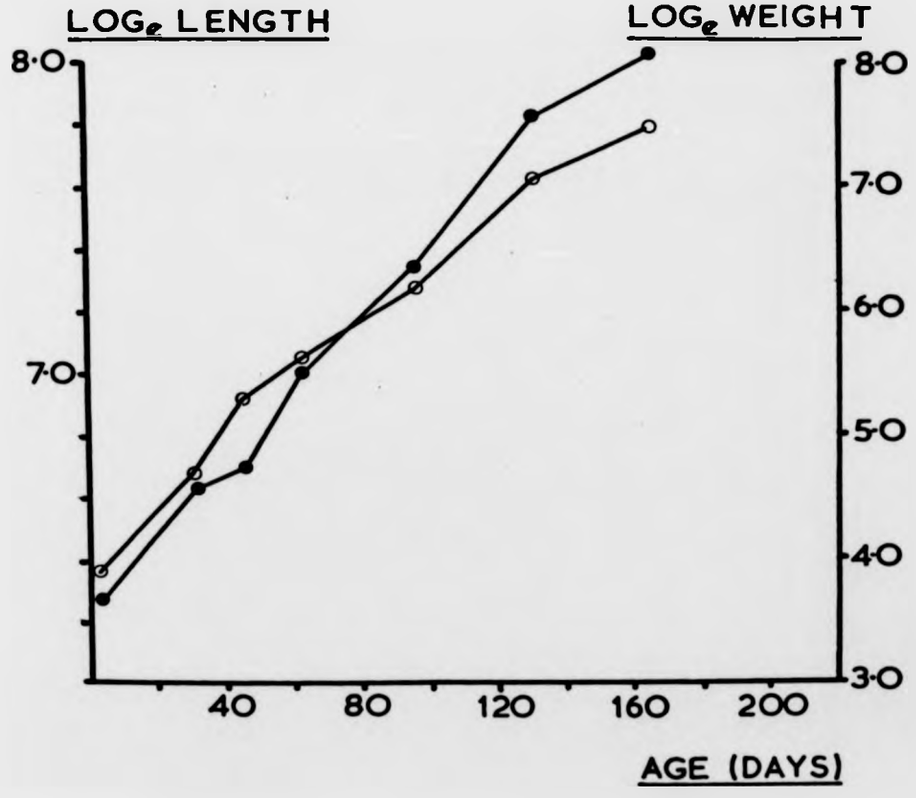
o = weight

FIG.40b. Log_e transformations of growth data depicted in FIG.40a.

● = log_e length

o = log_e weight


LENGTH (µm)
WEIGHT (µg)
4000
2000
2000
1000
40
80
120
160
200
AGE (DAYS)


LOG$_e$ LENGTH
LOG$_e$ WEIGHT
8·0
7·0
8·0
7·0
6·0
5·0
4·0
3·0
40
80
120
160
200
AGE (DAYS)

and Culross snails respectively.

It was not possible to compute growth using the Ford-Walford plot as only the curve where growth rate is declining can be fitted to the Bertalanffy (1934) equation.

No growth data were obtained for juveniles from either of the Aberdour sites as, on each of three occasions that the experiment was attempted, all of the animals died within the first 3 weeks. Death appeared to have been a direct consequence of heavy nematode infections.

7. RELEASE OF YOUNG FROM THE BROOD-POUCH

L. rudis proved to be a good experimental animal, feeding from algal - encrusted stones and producing faeces even after 3 months in the laboratory aquarium. Females released juveniles at fairly steady rates over the 60 days of each trial which allowed investigation of the rates of release from females of different origins and in different tidal regimes corresponding to different tide levels.

(a) Effects of tide tank levels on release

(i) Mid tank level

In terms of times of cover and exposure the tidal regime at this level closely corresponds to the field situation of L. rudis from Aberdour 'L' but corresponds with lower levels than those occupied by snails from Aberdour 'H', Torrybay and Culross.

Significantly fewer juveniles were released per female over the 60 days of the January to March 1976 experiment than in either the May/July 1976 or the October/December 1976 trials (Fig. 41). This difference applied to numbers released by females from each of the 4 sampling sites and was especially marked for females from Torrybay and Culross which exhibited consistently low levels of release in the January/March experiment. In the January/March trial, females from Torrybay and Culross ceased to release juveniles after the 21st day and had only released 4 and 3 young per female respectively during this period. This compares with release of between 30 and 37 juveniles per female in the May/July and October/December trials (Fig. 41). Numbers of juveniles released by

FIG.41. Cumulative numbers of juveniles released per female Littorina rudis held at mid-tide level in the tide tank.

A = January to March 1976

B = May to July 1976

C = October to December 1976

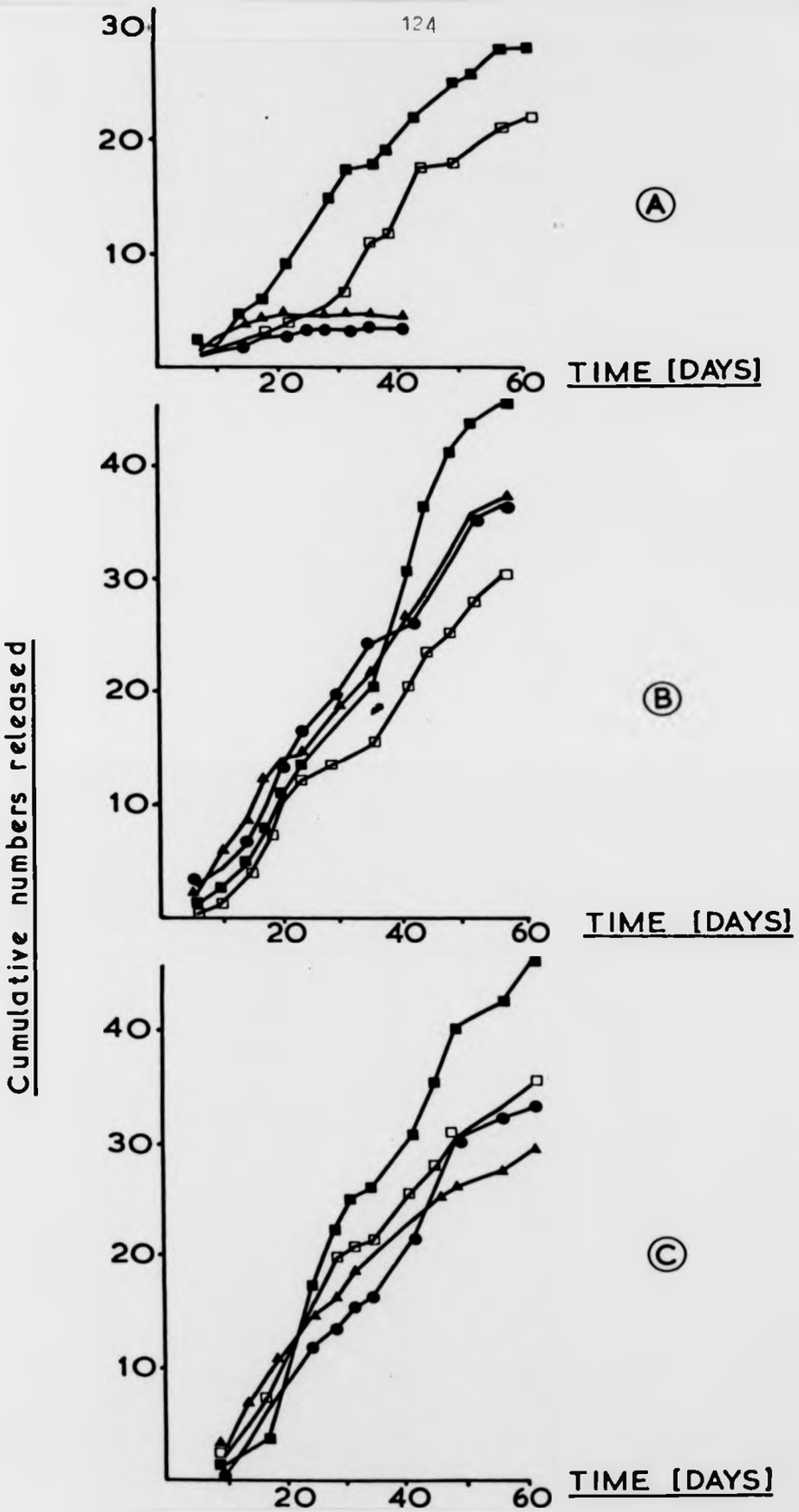
■ = Aberdour 'H'.

□ = Aberdour 'L'.

▲ = Torrybay.

● = Culross.

Littorina


Cumulative numbers released
30
20
10
20
40
60
TIME [DAYS]
A
40
30
20
10
20
40
60
TIME [DAYS]
B
40
30
20
10
20
40
60
TIME [DAYS]
C

Aberdour 'L' females varied less and ranged between 22 per female in the January/March trial and 30 to 35 in the May/July and October/December experiments respectively.

Aberdour 'H' females held at mid-tank level released more juveniles in each of the 3 trials than females from all other stations (Fig. 41; Table 28). Numbers varied in the foregoing fashion between the 3 test times with 28 per female released in the January/March trial and 45 and 46 in the May/July and October/December trials respectively. This lead of Aberdour 'H' over the other stations appeared early in the January/March trial, with Aberdour 'L' females also releasing more juveniles than females from Torrybay and Culross. In the May/July and October/December trials however, females from all 4 stations released comparable numbers of juveniles during the first 25 days or so, with Aberdour 'H' females taking the lead only after 25 days in October/December trial and 40 days in the May/July trial (Fig. 41).

These differences between test-times are in accordance with the seasonal increases of ripe ovaries from January to June (Fig. 30) followed by increasing brood-pouch counts and especially late brood-pouch juveniles from May to July (Tables 17, 18, 19, 20) indicating that these experimental release rates result from seasonal changes in production of eggs and young.

At mid-tank levels, release rates by females from the 4 sites were significantly different at the 0·001% level except between Torrybay and Culross. Release rates between trials were all

TABLE 28 Daily release rates of juveniles by L. rudis from Aberdour 'H' and 'L', Torrybay and Culross at mid-tank level in the laboratory

Time of Experiment	Daily release of juveniles per female Aberdour 'H'			Aberdour 'L'			Torrybay			Culross		
	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min
Jan-Mar 1976	0.48	0.76	0.29	0.38	0.90	0.14	0.18	0.39	0.04	0.13	0.46	0.04
May-July	0.81	1.38	0.45	0.54	0.79	0.27	0.66	0.91	0.37	0.72	1.07	0.43
Oct-Dec	0.76	1.12	0.35	0.53	1.08	0.3o	0.49	0.80	0.18	0.50	1.18	O.o3

TABLE 29 Daily release rates of juveniles by L. rudis from Aberdour 'H' and 'L' at high-tank level in the laboratory

Time of Experiment	Daily release of juveniles per female Aberdour 'H'			Aberdour 'L'		
	Mean	Maximum	Minimum	Mean	Maximum	Minimum
January-March 1976	1.14	2.57	0.22	0.38	0.59	0.07
May - July	1.30	2.30	0.93	0.90	1.50	0.63
October-December	1.32	2.61	1.02	0.86	1.65	0.63

TABLE 30 Daily release rates of juveniles by L. rudis from Aberdour 'H' and 'L' at low-tank level in the laboratory

Time of Experiment	Daily release of juveniles per female Aberdour 'H'			Aberdour 'L'		
	Mean	Maximum	Minimum	Mean	Maximum	Minimum
January-March 1976	0.33	0.46	0.25	0.20	0.41	0.03
May-July	0.73	1.46	0.37	0.48	0.88	0.24
October-December	0.66	0.83	0.57	0.38	0.53	0.23

significantly different at the 0.001% level except between May/July and October/December for females from Aberdour 'H' and 'L'.

Overall annual daily release rates per female at mid-tank level were 0.68, 0.48, 0.44 and 0.45 by females from Aberdour 'H', Aberdour 'L', Torrybay and Culross respectively (Table 31).

(ii) High and Low-tank levels

Snails from Aberdour ('H' and 'L') alone were held at high and low levels in the tide-tank in an attempt to assess any effects upon release rate of regimes of tidal cover and exposure matching high and low shore levels. The high-tank snails were held at a level equivalent to between MHWN and MHWS in the field and the low-tank snails at a level equivalent to MLWN. Thus the high-tank regime matched approximately the tidal conditions at Aberdour 'H' whereas the low-tank regime matched a shore level well below that inhabited by any L. rudis in the field.

In each of the 3 trials and at each tank level females from Aberdour 'H' again released more juveniles than females from Aberdour 'L' (Fig. 42, 43; Table 29, 30). In addition, females of any origin placed at the high-tank level always released more juveniles than females from the same source held at lower levels (Fig. 42, 43; Table 29).

Females at low-tank levels consistently released the least. The range of juveniles released by females from Aberdour 'H' over

TABLE 31 Overall daily release rates of juveniles by female *L. rudis* held in a laboratory tide-tank.

Source of females	Overall daily release of juveniles per female		
	High-tank level	Mid-tank level	Low-tank level
Aberdour 'H'	1.25	0.68	0.57
Aberdour 'L'	0.71	0.48	0.35
Torrybay	-	0.44	-
Culross	-	0.45	-

TABLE 32 Daily release rates by *L. rudis* in the field at Aberdour 'H' and 'L' and Culross

Site	Number of juveniles released per female per day		
	Mean	Maximum	Minimum
Aberdour 'H'	0.74	1.08	0.48
Aberdour 'L'	0.50	0.52	0.44
Culross	0.61	0.94	0.20

FIG.42. Cumulative numbers of juveniles released per female *Littorina rudis* from Aberdour 'H', held in a tidal tank.

A = January to March 1976

B = May to July 1976

C = October to December 1976

● = High tide level in tidal tank.

■ = Mid tide level in tidal tank.

▲ = Low tide level in tidal tank.

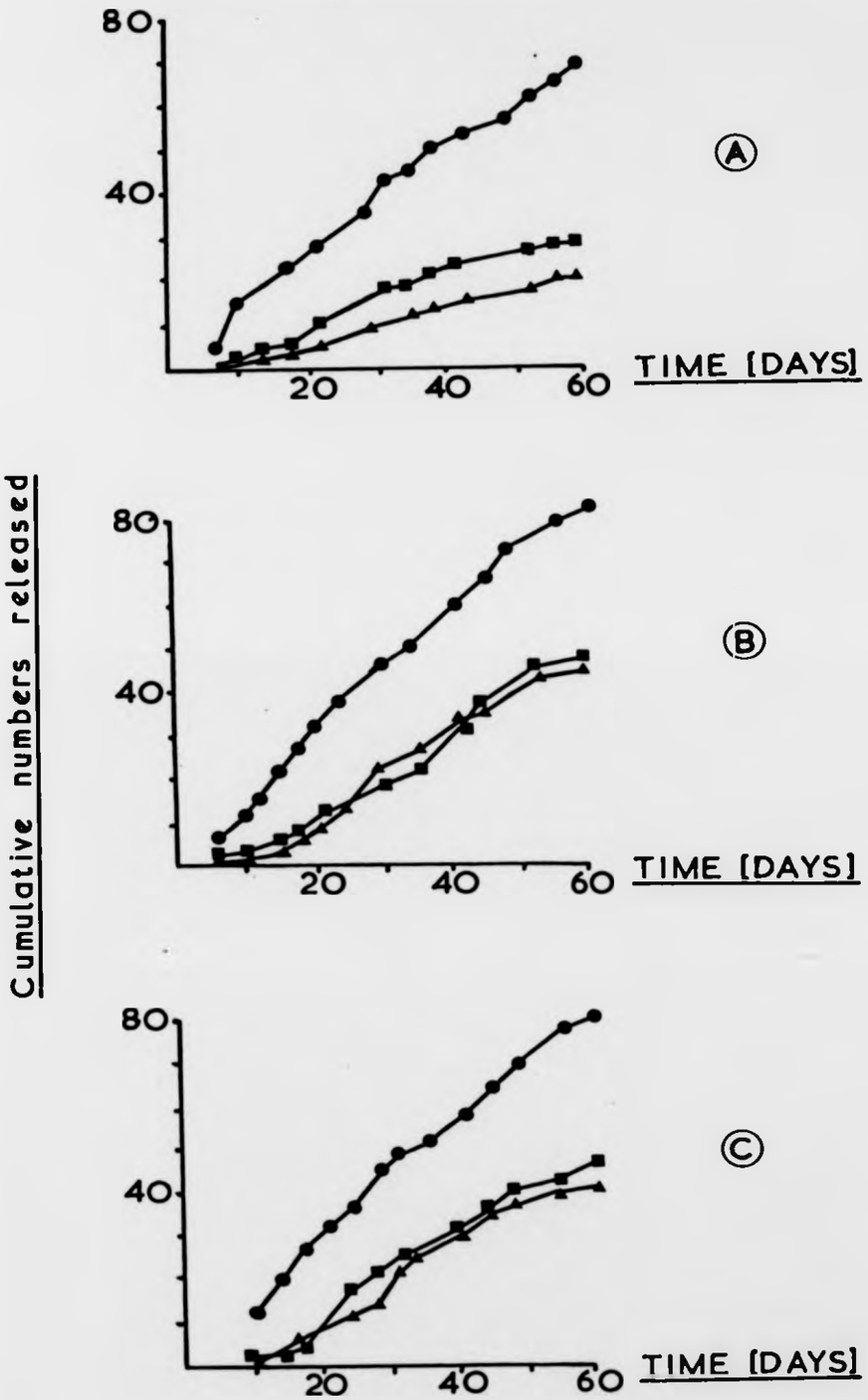

Cumulative numbers released
80
40
20
40
60
TIME (DAYS)
A
B
C

FIG.43. Cumulative numbers of juveniles released per female *Littorina rudis* from Aberdour 'L', held in a tidal tank.

A = January to March 1976

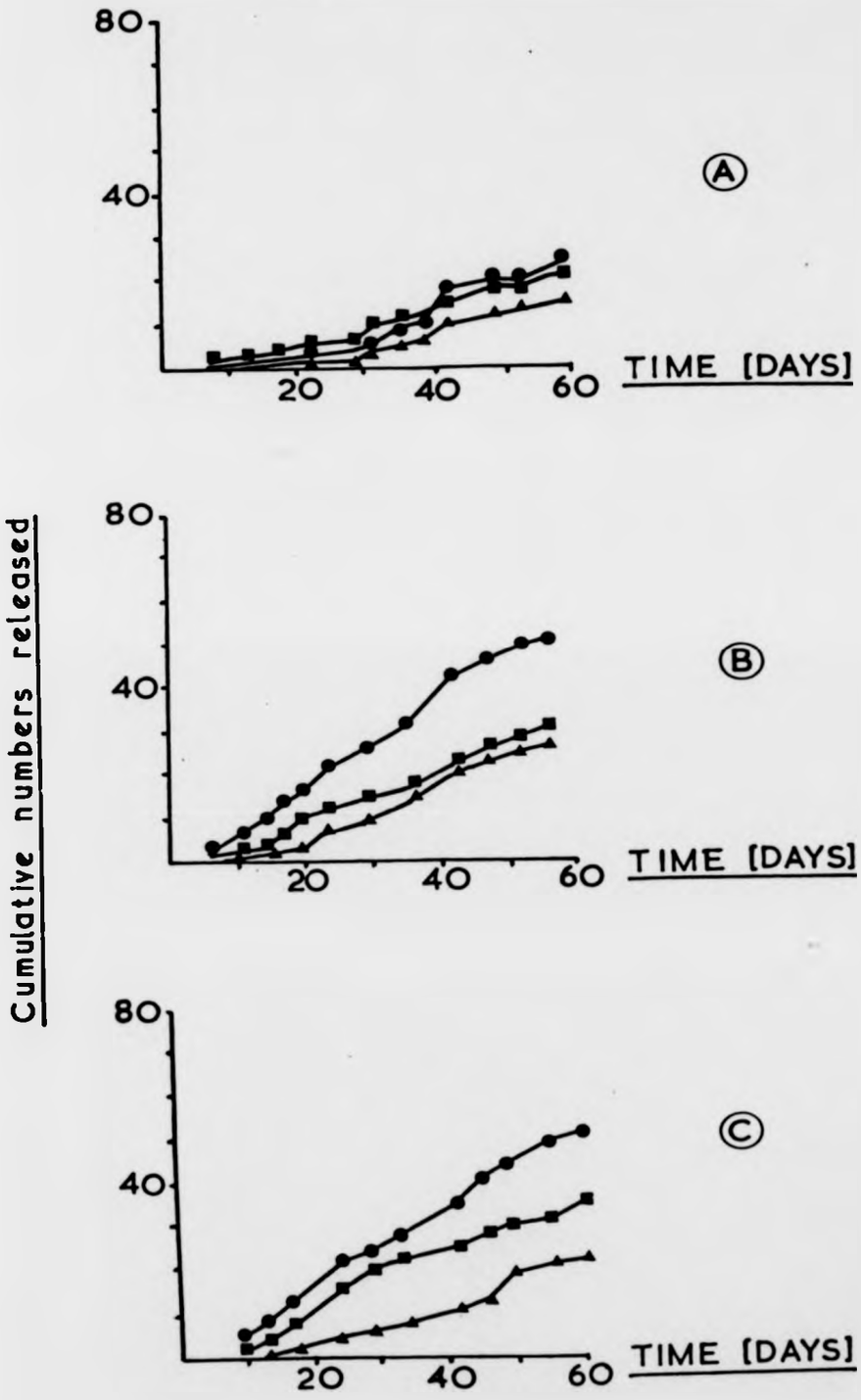
B = May to July 1976

C = October to December 1976

● = High tide level in tidal tank.

■ = Mid tide level in tidal tank.

▲ = Low tide level in tidal tank.


Cumulative numbers released
80
40
20
40
60
TIME [DAYS]
A
B
C

the 3 trials was 68 to 80 per female at high-tank level, 28 to 46 at mid-tank level and 20 to 43 at low tank level. Equivalent ranges for Aberdour 'L' females were 26 to 52 at high-tank level, 22 to 35 at mid-tank level and 15 to 27 at low-tank level. Thus the raised release rate at high-tank level was especially marked in snails from Aberdour 'H' where females placed at this level released close to double the number of juveniles released by similar females at the lower levels.

Earlier results implied that high shore females bear more juveniles than low-shore females (Fig. 18) and these release trials indicate that high shore tidal regimes also increase the release rate of juveniles from all females.

These observations also confirm that females at all tank levels and from all sources released more juveniles in the May/July and October/December trials than in the January to March trial, implying again that the seasonal changes in the ovary condition and brood-pouch contents noted earlier are matched by similar changes in the rates of release (Fig. 42, 43).

Aberdour 'H' females held at high-tank level exhibited the least "seasonal" variation with mean numbers released ranging from 68 juveniles per female in the January/March trial to 82 and 80 in the May/July and October/December experiments respectively (Fig. 42). Seasonal fluctuations in release rates were most apparent in the release patterns of Aberdour 'L' females. In the January/March trial females from all three tank levels released between 15 and 26

juveniles per female whereas in the May/July and October/December trials they released 22 to 51 and 27 to 52 respectively (Fig. 43).

Mean daily release rates per female clearly confirm differences in release resulting from position in the tidal range, shore of origin and season (Tables 28, 29, 30). The highest mean daily release rate per female by snails from Aberdour 'H' was 1.32 (maximum (m_1) = 2.61, minimum (m_o) = 1.02) in the October/December trial at high-tank level and the lowest 0.33 (m_1 = 0.46, m_o = 0.25) in January/March at low-tank level. The highest rate by females from Aberdour 'L' was 0.90 (m_1 = 1.5, m_o 0.63) in May/July at high-tank level and the lowest 0.20 (m_1 = 0.41, m_o = 0.03) in January/March at low-tank level. At mid-tank level the highest values for females from Torrybay and Culross occurred in the May/July trial and were 0.66 (m_1 = 0.91, m_o = 0.37) and 0.72 (m_1 = 1.07, m_o = 0.43) respectively (Table 28).

Analysis of variance showed that release by females from Aberdour 'H' and Aberdour 'L' were significantly different at the 3 tidal levels at the 0.001 and 0.025% levels respectively. There were significant differences in release between the January/March and May/July and January/March and October/December trials by Aberdour 'H' and Aberdour 'L' females at the 0.001 and 0.01% levels respectively but release rates between May/July and October/December were not significantly different.

Taken over the three trials, at high-tank level females from Aberdour 'H' had an overall release rate of 1.25 juveniles per

day and females from Aberdour 'L' 0.71 per day. At low-tank level, overall release rates were 0.57 and 0.35 juveniles per day by females from Aberdour 'H' and 'L' respectively (Table 31).

Release rates by L. rudis in the field during the 30 day experiment during May 1976 were very similar to values obtained at mid-tank level in the laboratory (Table 32). The highest field release rate was 0.74 per female per day by snails at Aberdour 'H'. Females at Aberdour 'L' and Culross released 0.50 and 0.61 juveniles per day respectively.

(b) Patterns of release

Patterns of release at mid-tank level are again considered first (Figs. 44, 45). In the January/March trial (when fewest juveniles were released), release by females from Aberdour 'H' and 'L' appeared erratic (Fig. 44a). Females from Aberdour 'L' released juveniles at a low rate for the first 31 days before producing 2 peaks of 1.10 and 1.50 juveniles per day on the 35th and 42nd days respectively, after which release again fell to a low level.

By contrast, Aberdour 'H' females did not exhibit this initial lag in release, rather a relatively even high rate of release between the 14th and 31st days of between 1.7 and 1.9 juveniles per day followed by a short lull of approximately 10 days before release rates again increased to 1.7 per day (Fig. 44).

During this first January/March experiment, maximum release rates by Torrybay and Culross females at mid-tank level

FIG.44. Daily release rates of juveniles per female from Aberdour 'H' and Aberdour 'L' held at mid tide level in the tide tank.

A = January-March 1976

B = May-July 1976

C = October-December 1976

■ = Aberdour 'H'

● = Aberdour 'L'

○ = Full moon

● = New moon

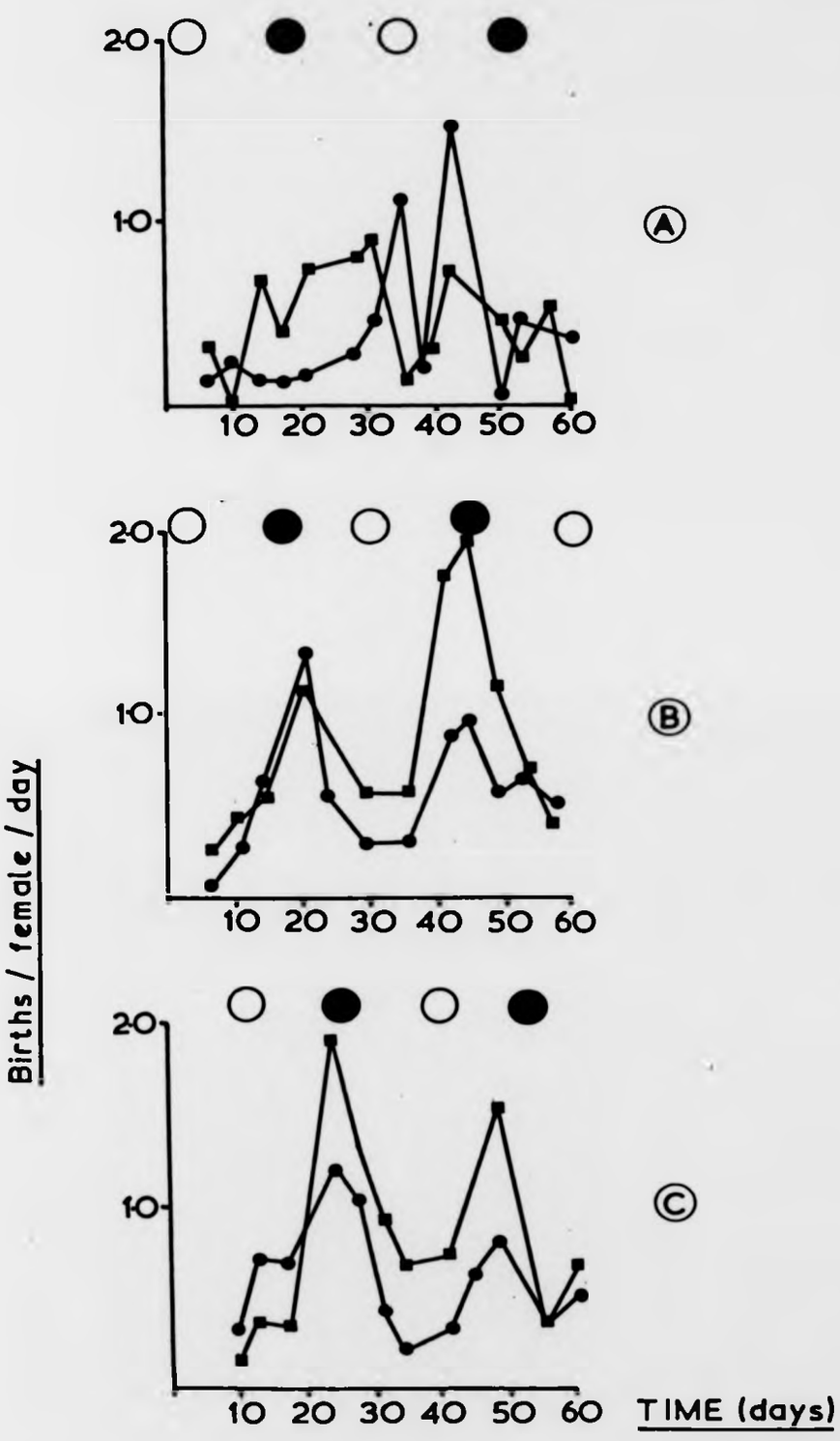

20
10
10 20 30 40 50 60
A
B
C
Births / female / day
TIME (days)

FIG.45. Daily release rates of juveniles per female L.rudis from Torrybay and Culross held at mid tide level in the tide tank.

A = January-March 1976

B = May-July 1976

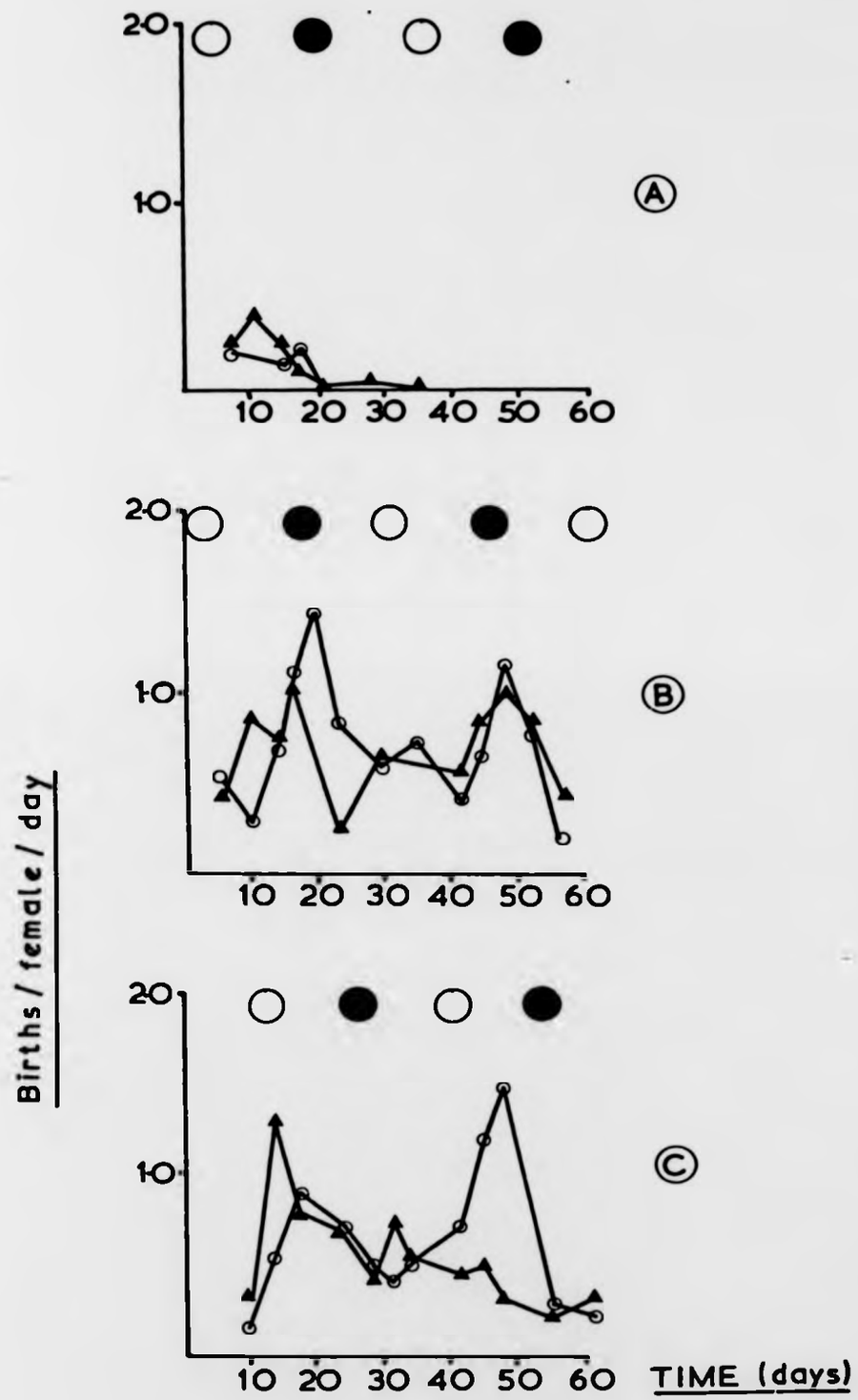
C = October-December 1976

▲ = Torrybay

● = Culross

○ = Full moon

● = New moon


20
10
A
10 20 30 40 50 60
20
10
B
10 20 30 40 50 60
20
10
C
10 20 30 40 50 60
TIME (days)
Births / female / day

were very low being only 0.4 and 0.2 juveniles per day respectively (Fig. 45a). After the 21st day, release by both Torrybay and Culross females ceased.

The relatively low levels of release exhibited by females from all 4 sites at low-tank level do not appear to have proceeded according to any regular, cyclical pattern during this generally unproductive early part of the year.

In the May/July experiment, Aberdour 'H' females produced 2 marked peaks of release 24 days apart on the 20th (1.13 juveniles per day) and 44th (1.9 juveniles per day) days of the trial (Fig. 44b) Both peaks coincided with consecutive new moons with minima at intervening full moons. Maxima of release by Aberdour 'L' females (Fig. 44b) coincided with those of the Aberdour 'H' snails although, in contrast to the Aberdour 'H' females, the first peak (1.36 per day) was greater than the second (0.93 per day). Females from Torrybay and Culross produced 2 peaks of release which approximately coincided with consecutive new moons (Fig. 45b). The peaks produced by the Torrybay females were of equal amplitude (1.0 juveniles per day) and occurred some 31 days apart on the 17th and 48th days of the trial. Maxima of release by Culross females occurred 28 days apart on the 20th and 48th days of the trial and had values of 1.40 and 1.66 juveniles per day respectively (Fig. 45b).

In the October/December trial peaks of release by Aberdour 'H' and 'L' females held at mid-tank level occurred on the 24th and 48th days of the trial, coinciding with consecutive new moons (Fig.44c)

In both cases the first peak was greater than the second being 1.9 and 1.5 juveniles per day for the Aberdour 'H' females and 1.20 and 0.83 for the Aberdour 'L' females. Culross females also produced 2 peaks of release (Fig. 45c) on day 17 (0.92 juveniles per day) and 31 days later on day 48 (1.48 juveniles per day). On this occasion the peaks fell after full and before new moons. Torrybay females produced only one early peak in release which fell on the 14th day (1.33 juveniles per day) after which release rates gradually fell to a very low level (Fig. 45c).

Taken overall, the results indicate that many snails from the 4 sampling sites held at mid-tide level in the tide tank exhibited monthly cyclical patterns of release during the summer and autumn. These cyclical patterns appear to have been based on the lunar month with maximal release close to successive new moons.

Patterns of release by females from Aberdour 'H' and 'L' at high-tank level are considered next. In the January/March trial the Aberdour 'L' females maintained relatively constant slow release rates not exceeding 0.6 juveniles per day (Fig. 46a). Rates of release by Aberdour 'H' females were substantially higher but tended (as at mid-tank level) to be erratic and although 3 release peaks did occur at about 21 to 22 day intervals they did not appear to be related to regular phases of the lunar month (Fig. 46a).

In the May/July trial Aberdour 'H' females again produced peaks of release which coincided with consecutive new moons (Fig. 46b) The first peak of 2.25 juveniles per day fell on the 17th day while

FIG.46. Daily release rates of juveniles per female L.rudis from Aberdour 'H' and Aberdour 'L' held at high tide level in the tide tank.

A = January-March 1976

B = May-July 1976

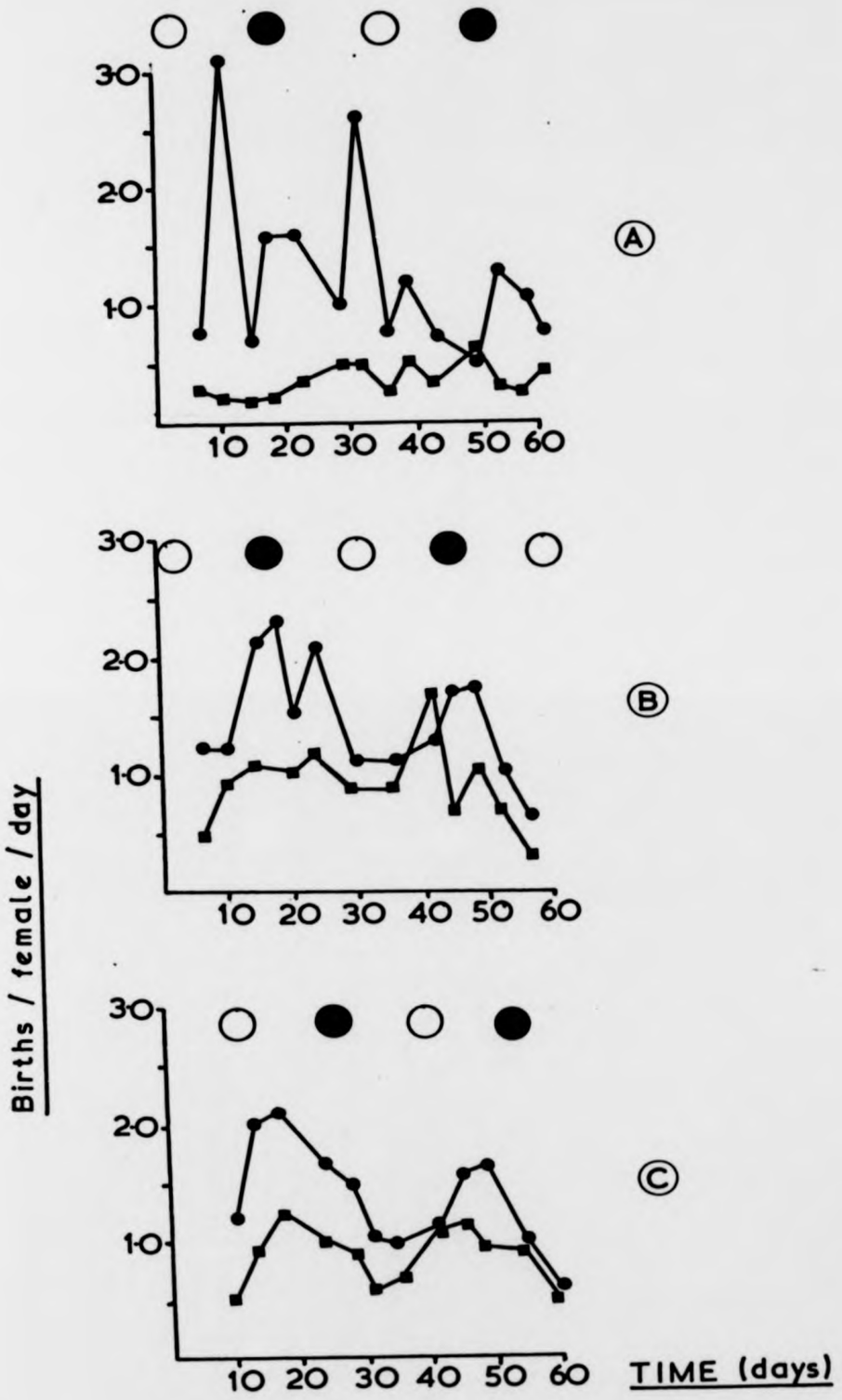
C = October-December 1976

● = Aberdour 'H'

■ = Aberdour 'L'

○ = Full moon

● = New moon


Births / female / day
30
20
10
10 20 30 40 50 60
A
B
C
TIME (days)

the second of 1.75 juveniles per day occurred some 31 days later on the 48th day. Aberdour 'L' females produced only one distinct peak on the 42nd day of the trial with only a hint of faster release from 15th to 25th days (Fig. 46b).

During the October/December trial, females from Aberdour 'H' and 'L' each produced two marked peaks of release some 31 and 28 days apart respectively. (Fig. 46c). These peaks occurred between new and full moons as in the corresponding trials at mid-tank level. The peaks produced by the Aberdour 'L' females were of approximately equal amplitude (1.25 and 1.15 juveniles per day) whereas the first peak produced by the Aberdour 'H' females, 2.10 juveniles per day, was greater than the second, 1.65 juveniles per day (Fig. 46c).

At low-tank level where smaller numbers of juveniles were released, no clearly discernable patterns of release were apparent (Fig. 47). This was especially the case during the January/March trial where rates of release by both Aberdour 'H' and 'L' females were very low and erratic (Fig. 47a). Although rates of release in the May/July and October/December experiments were somewhat higher and some peaks of release appeared (Fig. 47 b, c), no regular patterns of release were in evidence.

The results from animals of all 4 sites held at mid and high tank levels (summarised in Table 33) strongly suggest the existence of cyclical patterns of release based on the lunar month since the time interval between peaks ranged from 24 to 31 days with a mean value of 27.6 ± 1.05 days. In most cases peaks of release were found to coincide with consecutive new moons implying that the

FIG.47. Daily release rates of juveniles per female L.rudis from Aberdour 'H' and Aberdour 'L' held at low tide level in the tide tank.

A = January-March 1976

B = May-July 1976

C = October-December 1976

● = Aberdour 'H'

■ = Aberdour 'L'

○ = Full moon

● = New moon

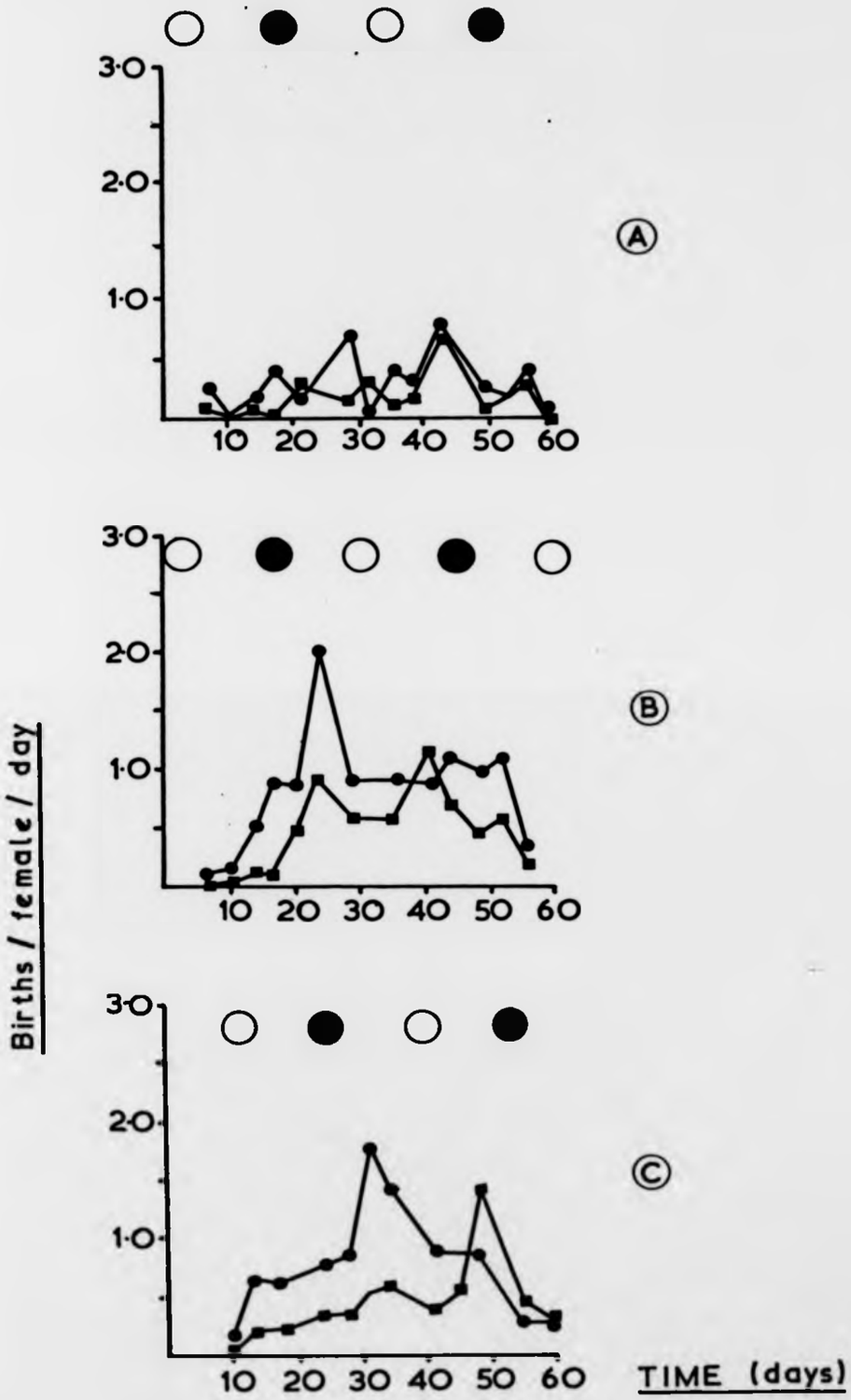

3·0
2·0
1·0
10 20 30 40 50 60
A
B
C
Births / female / day
TIME (days)

TABLE 33 Timing of peaks of release of juveniles from L. rudis held in a laboratory tide-tank

Site	Level in Tide Tank	Experiment	Days of consecutive new moons (in experiment)	Peaks of release				Days between consecutive peaks
				Day of first peak	Release rate	Day of second peak	Release rate	
Aberdour 'H'	High	May/July 1976	16.44	17	2.26	48	1.75	31
Aberdour 'H'	High	Oct/Dec 1976	25.53	17	2.10	48	1.65	31
Aberdour 'H'	Mid	May/July 1976	16.44	20	1.13	44	1.90	24
Aberdour 'H'	Mid	Oct/Dec 1976	25.53	24	1.90	48	1.50	24
Aberdour 'L'	High	Oct/Dec 1976	25.53	17	1.25	45	1.15	28
Aberdour 'L'	Mid	May/July 1976	16.44	20	1.36	44	0.93	24
Aberdour 'L'	Mid	Oct/Dec 1976	25.53	24	1.20	48	0.83	24
Torrybay	Mid	May/July 1976	16.44	17	1.00	48	1.00	31
Culross	Mid	May/July 1976	16.44	20	1.43	48	1.17	28
Culross	Mid	Oct/Dec 1976	25.53	17	0.92	48	1.48	31

spring tides associated with new moons were acting as a "cue" for increased release of juveniles.

(c) Effects of tide tank level on brood-pouch counts

The foregoing different rates of release of juveniles might reflect directly the altered rates of egg production or else speed of development in the different materials and conditions tested. Alternatively, different rates of release might have resulted simply from differential speeds of emptying of brood-pouches without altered egg production or rate of development. Examination of brood-pouch contents of experimental females at the end of release experiments, and comparison of these with brood-pouch loads of females from the field at the start and finish of the experiments, allows these alternatives to be tested.

Trends in brood-pouch loads of control females in the field (Tables 34,35, 36, 37, 38) were dealt with in section 4.

With the exception of one release trial, the total numbers of embryos in females from all four sites held at mid-tank level declined over each of the 3 experimental periods (Fig. 48). The single exception was during the January/March experiment when brood-pouch loads of Culross females rose from an average of 80.8 to 108 per female (Table 37, Fig. 48). In general, trends in brood-pouch contents of snails at mid-tank level were very similar to those in the field with the exceptions of the Aberdour 'H' and Torrybay females in the October/December trial where field brood-pouch contents rose

TABLE 34 Terminal brood-pouch loads of L. rudis from Aberdour'H' held at high, mid and low levels in a laboratory tide-tank for 60 days in January-March, May-July and October-December 1976 Brood-pouch loads of L. rudis in the field at the beginning and end of each trial are also shown.

Experiment	Treatment	n	Mean height (mm)	Number of embryos in each developmental stage (±S.E.)				Total brood-pouch load (± S.E.)
				Stage 1	Stage 2	Stage 3	Stage 4	
Jan/Mar 1976	Field Jan 1976	15	11.6(0.1)	64.4(8.9)	62.5(5.5)	33.6(4.8)	89.0(6.2)	249.7(11.1)
	Field Mar 1976	15	11.3(0.2)	63.6(8.6)	33.3(3.0)	40.6(5.1)	80.2(8.4)	217.7(21.8)
	HTL Mar 1976	11	11.9(6.3)	13.3(4.0)	14.4(4.3)	18.9(4.1)	48.9(6.2)	95.5(16.1)
	MTL Mar 1976	12	11.6(0.2)	16.7(1.4)	13.3(2.1)	30.2(1.5)	109.0(10.7)	170.2(12.0)
	LTL Mar 1976	14	11.8(0.3)	15.5(0.8)	54.1(7.3)	50.7(5.0)	134.5(6.8)	241.8(16.4)
May/July 1976	Field May 1976	15	11.6(0.3)	63.6(9.8)	43.9(4.6)	33.8(5.5)	111.9(16.8)	253.2(28.7)
	Field July 1976	15	11.3(0.2)	41.5(7.1)	30.6(4.5)	34.3(5.9)	71.1(10.0)	177.5(22.6)
	HTL July 1976	14	11.5(0.2)	15.7(3.6)	14.7(4.0)	25.1(7.8)	75.9(17.4)	131.4(28.0)
	MTL July 1976	14	11.2(0.2)	17.4(4.8)	23.4(5.5)	31.3(9.9)	80.5(18.3)	152.6(30.6)
	LTL July 1976	15	11.2(0.3)	50.1(16.1)	30.9(8.2)	31.3(7.6)	86.3(16.5)	198.5(38.5)
Oct/Dec 1976	Field Oct 1976	15	11.2(0.2)	23.9(5.6)	27.4(3.2)	29.7(4.3)	56.6(7.4)	137.6(17.1)
	Field Dec 1976	15	11.7(0.3)	70.5(7.2)	76.0(9.5)	48.8(5.4)	102.9(15.7)	298.2(29.4)
	HTL Dec 1976	16	11.1(0.2)	17.6(3.9)	12.1(4.4)	9.3(2.5)	41.7(8.1)	80.7(15.3)
	MTL Dec 1976	13	10.8(0.3)	20.5(10.1)	14.5(3.6)	10.8(1.7)	48.9(5.3)	94.7(18.7)
	LTL Dec 1976	14	10.7(0.3)	16.3(3.5)	13.8(1.9)	19.4(2.7)	74.8(7.8)	124.5(17.8)

HTL = High tank level in laboratory tide tank
MTL = Mid tank level in laboratory tide tank
LTL = Low tank level in laboratory tide tank

TABLE 35 Terminal brood-pouch loads of L. rudis from Aberdour 'L' held at high, mid and low levels in a laboratory tide tank for 60 days in January - March, May-July and October - December 1976. Brood-pouch loads of L. rudis in the field at the beginning and end of each trial are also shown

Experiment	Treatment	n	Mean height (mm)	Number of embryos in each developmental stage (±S.E.)				Total brood-pouch load (±S.E.)
				Stage 1	Stage 2	Stage 3	Stage 4	
Jan/Mar 1976	Field Jan 1976	15	9.6(0.1)	25.2(4.9)	27.7(3.4)	25.8(3.2)	43.0(6.2)	121.7(16.1)
	Field Mar 1976	15	9.6(0.1)	43.1(3.3)	20.2(11.6)	25.1(2.5)	38.3(3.3)	126.7(8.7)
	HTL Mar 1976	12	9.6(0.3)	1.7(1.0)	3.0(1.8)	16.8(5.3)	36.7(3.8)	58.2(8.9)
	MTL Mar 1976	11	9.7(0.2)	3.2(1.0)	2.3(0.5)	14.8(1.6)	41.5(4.1)	61.8(5.3)
	LTL Mar 1976	12	9.5(0.2)	15.8(3.1)	18.6(2.8)	26.6(3.8)	71.3(13.0)	132.3(20.0)
May/July 1976	Field May 1976	15	10.1(0.2)	42.4(7.5)	46.9(5.3)	54.7(6.2)	79.8(6.2)	223.8(20.2)
	Field July 1976	15	10.1(0.1)	49.4(6.3)	51.7(3.2)	43.1(5.1)	90.4(9.6)	234.6(16.1)
	HTL July 1976	16	10.2(0.3)	21.2(5.2)	12.6(1.9)	22.6(3.8)	52.1(4.6)	108.5(13.4)
	MTL July 1976	16	9.8(0.3)	28.9(6.2)	15.3(3.5)	25.5(4.0)	64.9(8.2)	134.6(12.6)
	LTL July 1976	14	9.7(0.2)	25.8(3.3)	31.9(2.9)	37.1(4.2)	94.2(8.0)	190.0(18.8)
Oct/Dec 1976	Field Oct 1976	15	8.9(0.1)	41.2(7.3)	29.0(2.3)	23.5(1.9)	63.1(5.6)	156.8(9.3)
	Field Dec 1976	15	9.9(0.2)	42.5(9.5)	36.7(3.3)	26.4(2.5)	66.8(6.4)	172.4(14.2)
	HTL Dec 1976	15	9.5(0.2)	9.5(2.3)	7.9(1.7)	11.5(2.1)	43.1(4.8)	72.0(9.5)
	MTL Dec 1976	15	9.9(0.2)	10.6(3.9)	8.0(1.5)	12.4(2.7)	48.2(5.6)	79.2(8.8)
	LTL Dec 1976	17	8.7(0.1)	17.9(4.0)	15.4(2.2)	22.6(3.0)	60.3(3.8)	116.2(9.1)

HTL = High tank level in laboratory tide tank
MTL = Mid tank level in labroatory tide tank
LTL = Low tank level in laboratory tide tank

TABLE 36 Terminal brood-pouch loads of L. rudis from Torrybay held at mid level in a laboratory tide tank for 60 days in January - March, May - July and October - December 1976. Brood-pouch loads of L. rudis in the field at the beginning and end of each trial are also shown.

Experiment	Treatment	n	Mean height (mm)	Number of embryos in each developmental stage (± S.E.) Stage 1	Stage 2	Stage 3	Stage 4	Total brood-pouch load (±S.E.)
Jan/Mar 1976	Field Jan 1976	15	8.0(0.2)	11.9(1.9)	12.6(1.9)	10.7(1.8)	20.6(3.6)	55.8(5.5)
	Field Mar 1976	15	7.6(0.1)	13.5(1.5)	9.9(1.5)	11.5(2.4)	18.9(2.6)	53.8(5.9)
	Tide tank Mar 1976	14	7.7(0.2)	4.1(1.6)	12.9(2.3)	7.5(1.7)	11.9(2.0)	36.4(5.4)
May/July 1976	Field May 1976	15	7.2(0.2)	11.6(1.6)	21.7(2.6)	20.0(1.7)	34.4(3.3)	87.7(7.7)
	Field July 1976	15	7.9(0.2)	7.7(1.2)	23.7(3.7)	12.2(2.3)	58.7(5.9)	102.3(10.3)
	Tide tank July 1976	12	8.0(0.2)	6.4(0.8)	9.0(1.6)	20.5(3.4)	67.7(7.1)	103.6
Oct/Dec 1976	Field Oct 1976	15	8.5(0.1)	7.9(1.5)	14.2(1.8)	8.1(2.0)	21.1(4.6)	51.3(5.0)
	Field Dec 1976	15	8.7(0.1)	17.6(5.3)	19.9(1.1)	23.7(2.7)	36.5(3.3)	97.7(8.4)
	Tide tank Dec 1976	13	9.1(6.3)	4.5(0.9)	7.6(2.9)	9.2(1.9)	24.4(3.1)	45.7(5.5)

TABLE 37 Terminal brood-pouch loads of L. rudis from Culross held at mid level in a laboratory tide tank for 60 days in January - March, May - July and October - December - 1976. Broad-pouch loads of L. rudis in the field at the beginning and end of each trial are also shown.

Experiment	Treatment	n	Mean height (mm)	Number of embryos in each developmental stage (±S.E.)				Total brood-pouch load (±S.E.)
				Stage 1	Stage 2	Stage 3	Stage 4	
Jan/Mar 1976	Field Jan 1976	15	11.2(0.3)	25.7(4.4)	15.8(3,6)	16.6(4.0)	22.7(5.0)	80.8(13.8)
	Field Mar 1976	15	11.4(0.3)	27.3(5.0)	18.8(4.0)	21.4(3.6)	29.8(4.3)	97.3(13.4)
	Tide tank Mar 1976	12	11.5(0.2)	12.4(3.4)	16.9(3.6)	27.3(4.0)	51.4(8.7)	108.0(14.1)
May/July 1976	Field May 1976	15	12.6(0.3)	60.2(5.3)	82.1(9.5)	88.7(7.7)	98.9(7.1)	329.9(17.1)
	Field July 1976	15	12.0(0.3)	40.0(7.3)	42.7(8.3)	39.5(7.1)	121.7(11.9)	243.9(32.7)
	Tide tank July 1976	16	11.8(0.2)	16.9(4.4)	31.7(8.6)	35.1(5.9)	92.7(13.2)	176.4(28.5)
Oct/Dec 1976	Field Oct 1976	15	12.4(0.2)	14.2(2.4)	47.9(6.7)	32.9(3.9)	95.6(17.1)	190.6(29.1)
	Field Dec 1976	15	12.0(0.3)	36.1(4.4)	28.4(3.5)	28.0(4.3)	59.8(9.4)	152.3(16.0)
	Tide tank Dec 1976	15	11.5(0.3)	10.7(2.3)	15.7(4.3)	10.2(1.7)	26.1(5.0)	62.7(9.5)

TABLE 37 Terminal brood-pouch loads of L. rudis from Culross held at mid level in a laboratory tide tank for 60 days in January - March, May - July and October - December - 1976. Broad-pouch loads of L. rudis in the field at the beginning and end of each trial are also shown.

Experiment	Treatment	n	Mean height (mm)	Number of embryos in each developmental stage (±S.E.)				Total brood-pouch load (±S.E.)
				Stage 1	Stage 2	Stage 3	Stage 4	
	Field Jan 1976	15	11.2(0.3)	25.7(4.4)	15.8(3.6)	16.6(4.0)	22.7(5.0)	80.8(13.8)
Jan/Mar 1976	Field Mar 1976	15	11.4(0.3)	27.3(5.0)	18.8(4.0)	21.4(3.6)	29.8(4.3)	97.3(13.4)
	Tide tank Mar 1976	12	11.5(0.2)	12.4(3.4)	16.9(3.6)	27.3(4.0)	51.4(8.7)	108.0(14.1)
	Field May 1976	15	12.6(0.3)	60.2(5.3)	82.1(9.5)	88.7(7.7)	98.9(7.1)	329.9(17.1)
May/July 1976	Field July 1976	15	12.0(0.3)	40.0(7.3)	42.7(8.3)	39.5(7.1)	121.7(11.9)	243.9(32.7)
	Tide tank July 1976	16	11.8(0.2)	16.9(4.4)	31.7(8.6)	35.1(5.9)	92.7(13.2)	176.4(28.5)
	Field Oct 1976	15	12.4(0.2)	14.2(2.4)	47.9(6.7)	32.9(3.9)	95.6(17.1)	190.6(29.1)
Oct/Dec 1976	Field Dec 1976	15	12.0(0.3)	36.1(4.4)	28.4(3.5)	28.0(4.3)	59.8(9.4)	152.3(16.0)
	Tide tank Dec 1976	15	11.5(0.3)	10.7(2.3)	15.7(4.3)	10.2(1.7)	26.1(5.0)	62.7(9.5)

TABLE 38 Terminal brood-pouch loads of L. rudis held in captivity at Aberdour 'H', Aberdour 'L' and Culross for 30 days during May/June 1976 Brood-pouch loads of non-captive females at the Beginning and end of each trial are also shown.

Site	Treatment	n	Mean height (mm)	Number of embryos in each developmental stage (S.E.)				Total brood-pouch load (±S.E.)
				Stage 1	Stage 2	Stage 3	Stage 4	
Aberdour 'H'	Non-captive (S)	15	11.3(0.2)	67.8(9.1)	47.5(10.5)	81.1(10.8)	96.9(11.9)	293.3(17.5)
	Non-captive (T)	15	11.2(0.2)	66.1(8.6)	34.2(4.2)	32.1(7.1)	76.5(7.8)	209.3(19.2)
	Captive (T)	16	10.9(0.1)	61.5(8.3)	34.9(5.0)	36.7(2.9)	68.8(4.1)	201.8(7.7)
Aberdour 'L'	Non-captive (S)	15	9.8(0.1)	59.8(7.2)	47.3(3.5)	56.0(8.9)	64.2(8.7)	227.3(28.7)
	Non-captive (T)	15	9.6(0.2)	63.4(5.0)	54.7(4.4)	31.1(5.4)	81.9(7.0)	231.1(19.6)
	Captive (T)	14	9.5(0.2)	41.5(3.8)	33.3(1.9)	45.8(2.8)	61.7(4.6)	183.0(17.3)
Culross	Non-captive (S)	15	11.9(0.2)	39.8(2.8)	42.2(3.1)	40.1(8.3)	94.0(11.1)	216.1(23.3)
	Non-captive (T)	15	12.2(0.3)	51.4(6.1)	26.6(4.0)	29.2(4.4)	79.1(6.8)	186.3(27.1)
	Captive (T)	12	12.3(0.1)	36.3(8.3)	21.8(2.2)	49.2(7.3)	57.3(8.0)	163.7(13.1)

S = brood-pouch load at the start of each 30 day trial
T = brood-pouch load at the end of each 30 day trial

FIG.48. Trends in brood pouch loads of *Littorina rudis* in field and laboratory release trials.

A = Aberdour 'H'.

B = Aberdour 'L'.

C = Torrybay.

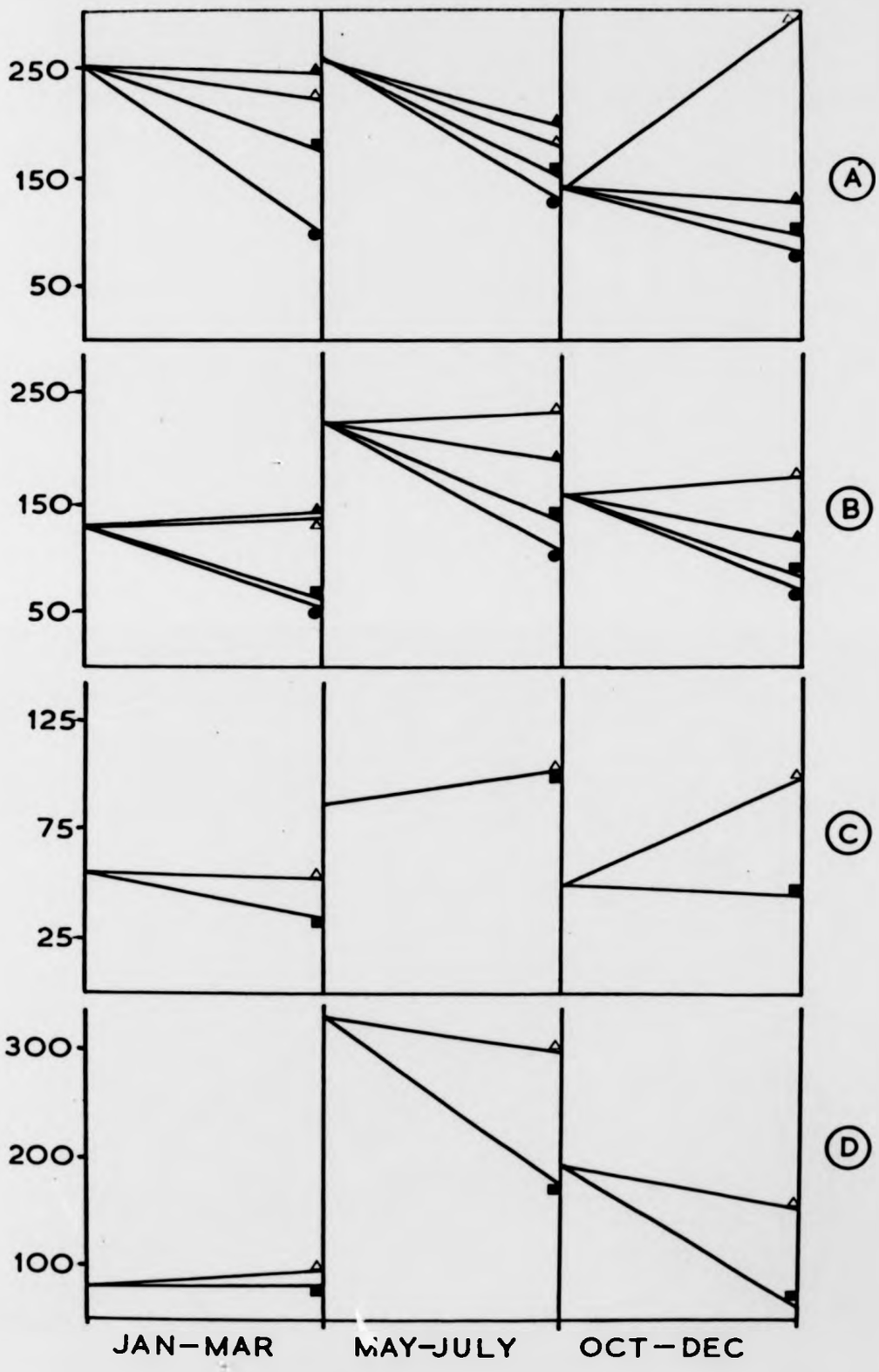
D = Culross.

△ = Brood pouch loads of females in the field.

● = Brood pouch loads of females at high tide level in the tidal tank.

■ = Brood pouch loads of females at mid tide level in the tidal tank.

▲ = Brood pouch loads of females at low tide level in the tidal tank.



ield.

tide

ide

ide

by 117 and 90% respectively but laboratory values fell by 31 and 11% respectively. At the end of the experiments, laboratory females contained on average fewer embryos than those in the field with the exception of the Culross females in the January/March trial which contained marginally more embryos than their field counterparts (Fig. 48).

When different numbers of each of the 4 embryonic stages were examined, it became apparent that the main discrepancies in total brood-pouch counts between field and mid-tank laboratory females were due largely to variation in the numbers of the first two embryonic stages and in particular of stage 1 embryos (Tables 34, 35, 36, 37). Thus, although egg production continued in females from all 4 sites under laboratory conditions, the level of ovulation at mid-tank level was depressed by between 14 and 87% when compared with that in the field.

The highest laboratory release rates occurred when Aberdour 'H' females were held at high tide level in the tide tank (Table 29). It was found upon dissection however, that the terminal brood-pouch counts of these females were only between 31 and 87% of the field counts (Table 34). Again most of the variation was accounted for by the stage 1 and 2 embryos, although the counts of the later embryonic stages were also lower than their field counterparts. It thus appears that in addition to ovulation having been depressed, the snails had released juveniles at a faster rate than embryos were able to develop to compensate for the loss of the late stages. It would appear therefore, that the relatively high levels of release

at high tank level could not have been maintained indefinitely and that release is not merely a consequence of pressure of numbers in the brood-pouch.

At low-tank levels the brood-pouch counts of the Aberdour 'H' females at the end of both the January/March and May/July trials were 12% higher than those in the field (Table 34; Fig. 48). In the October/December experiment however, terminal brood-pouch loads were only about 42% of those in the field although they were 30 to 55% higher than those of females held at both high and mid-tank levels (Table 34; Fig. 48) The wide discrepancy between laboratory and field counts can probably be attributed to a 2-fold increase in brood-pouch loads in the field, from 137.6 to 298.2 per female, which was not achieved in the laboratory. The low release rates of Aberdour 'H' females at low-tank level (Table 30) in conjunction with higher brood-pouch counts (Table 34) indicate that females were with-holding juveniles which suggests that conditions at this level were unsuitable for normal release of juveniles.

Females from Aberdour 'L' were also found to withhold juveniles at low-tank levels while at high-tank levels they released young at rates in excess of that which could be supported by development from earlier embryos (Tables 30, 35). Again, ovulation was depressed by between 37 and 66% at low-tank level in the laboratory although counts of stage 1 and 2 embryos suggest that it was not depressed to the same extent as had been the case at high and mid-tank levels (Table 35).

The average brood-pouch counts of females held in containers in the field at Aberdour 'H', Aberdour 'L' and Culross during May 1976 were very close to those of the non-captive females at the respective sites (Table 38). In addition, there appears to have been very little depression of ovulation in these field captives(up to 30% at Aberdour 'L') but since the experiment was only of some 30 days duration, compared with 60 days in the laboratory, it may have been that this was too short a period to show any effects of captivity on brood-pouch counts.

8. SALINITY TOLERANCES OF ADULTS, JUVENILES AND EMBRYOS

L. rudis from the up-estuary sites of Torrybay and Culross were much more tolerant of lowered salinity at 10°C than snails from the marine site (Table 39; Figs. 49 and 50). In freshwater, 60 adults from Torrybay had an average LT50 (number of days taken for 50% of the snails to die) of 15 days (range = 13 to 17 days) compared with 12.7 (10 to 16), 8.7 (7 to 13) and 6.0 days (3 to 7) for adults from Culross, Aberdour 'L' and Aberdour 'H' respectively (Table 39). (The range in parentheses gives the time taken for the first and last snails to die). Adults from Torrybay survived for the duration of the 35 day trial in salinities down to 12‰ whereas those from Aberdour 'H' did not survive below 20‰ (Fig 49). Adults from Culross and Aberdour 'L' fell between these extremes, surviving down to 16‰ .

Juveniles, which had been removed directly from brood-pouches and consequently had not been in immediate contact with the prevailing salinity regimes at each site, were much less tolerant of lowered salinity than adults from the same shore (Table 39; Fig. 51). Juveniles survived for only 3 to 5 days in freshwater which compares with 6 to 15 days by adults (Table 39). As with adults, juveniles from the up-estuary sites were more tolerant of reduced salinity at 10°C than those from the marine site (Fig. 50). Juveniles taken from the brood-pouches of females from Torrybay and Culross survived down to salinities of 16 and 20‰ respectively for the duration of the 35 day experiment while those from Aberdour 'H' and Aberdour 'L' did not survive below 24‰ (Table 39).

TABLE 39 Salinity tolerances expressed as LTSO's of adult and juvenile L. rudis at 10°C from Aberdour 'H' and 'L', Torrybay and Culross.

Test Salinity (‰)	LTSO's (days) of 60 adults and 150 juveniles Figures in parentheses show days when first and last animals died.							
	Aberdour 'H'		Aberdour 'L'		Torrybay		Culross	
	Adults	Juveniles	Adults	Juveniles	Adults	Juveniles	Adults	Juveniles
0	6.0(3,7)	3.(1,4)	8.7(7,13)	4(1,5)	15.0(13,17)	5(2,6)	12.7(10,16)	5(1,5)
2	7.3(3,8)	3.(1,5)	8.3(4,11)	6(2,7)	13.3(8,17)	10(3,15)	9.3(8,13)	7(2,7)
4	8.0(4,13)	5.(3,8)	9.7(8,15)	7(2,8)	14.0(10,18)	10(5,14)	12.3(8,13)	9(4,11)
8	12.0(6,14)	10.(5,12)	10.3(7,13)	10(4,12)	16.3(10,17)	12(7,19)	13.3(7,15)	11(4,16)
12	12.7(8,15)	10.(7,11)	12.0(7,15)	10(6,17)	>35	15(11,23)	16.3(7,17)	13(8,18)
16	15.0(8,20)	12.(7,15)	>35	15(10,16)	>35	>35	>35	18(8,12)
20	>35	15.(9,18)	>35	19(11,22)	>35	>35	>35	>35
24	>35	>35	>35	>35	>35	>35	>35	>35
32	>35	>35	>35	>35	>35	>35	>35	>35

FIG.49. Salinity tolerances of adult L.rudis.

■ = Aberdour 'H'

□ = Aberdour 'L'

▲ = Torrybay

● = Culross

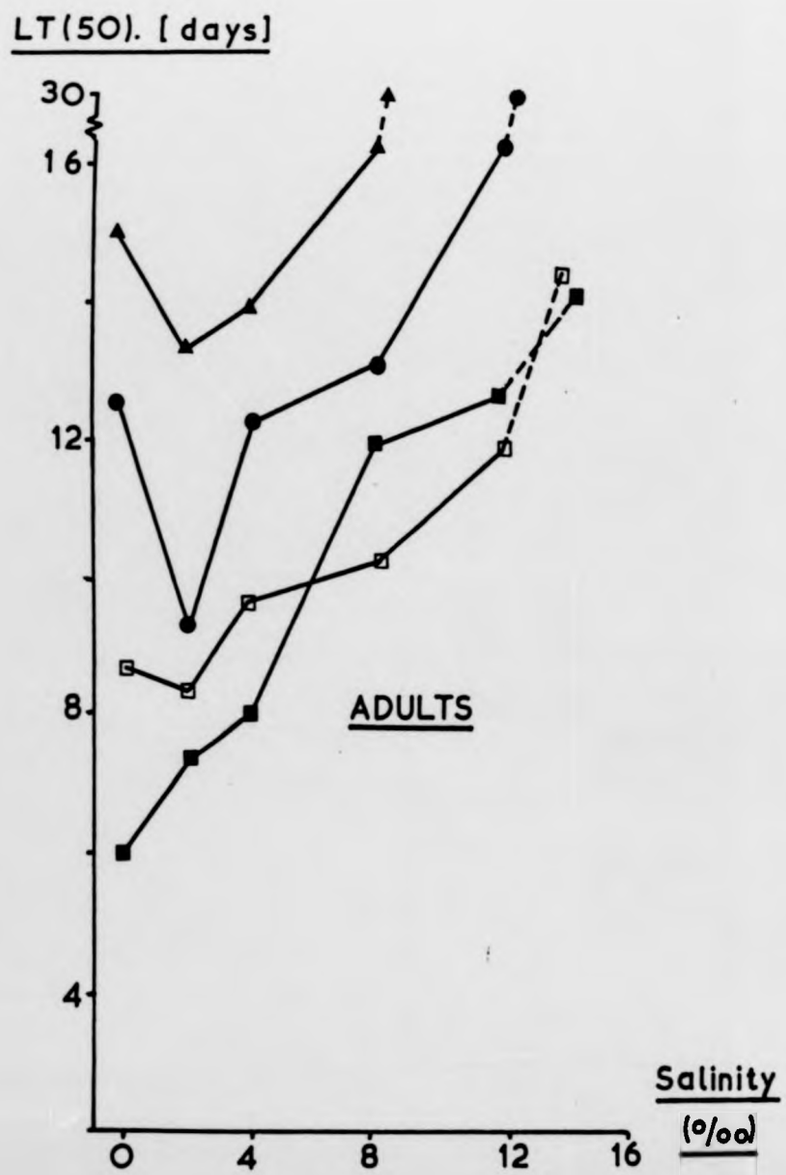
FIG.50. Salinity tolerances of juvenile L.rudis.

■ = Aberdour 'H'

□ = Aberdour 'L'

▲ = Torrybay

● = Culross


LT(50). [days]
30
16
12
8
4
ADULTS
0
4
8
12
16
Salinity
(o/oo)

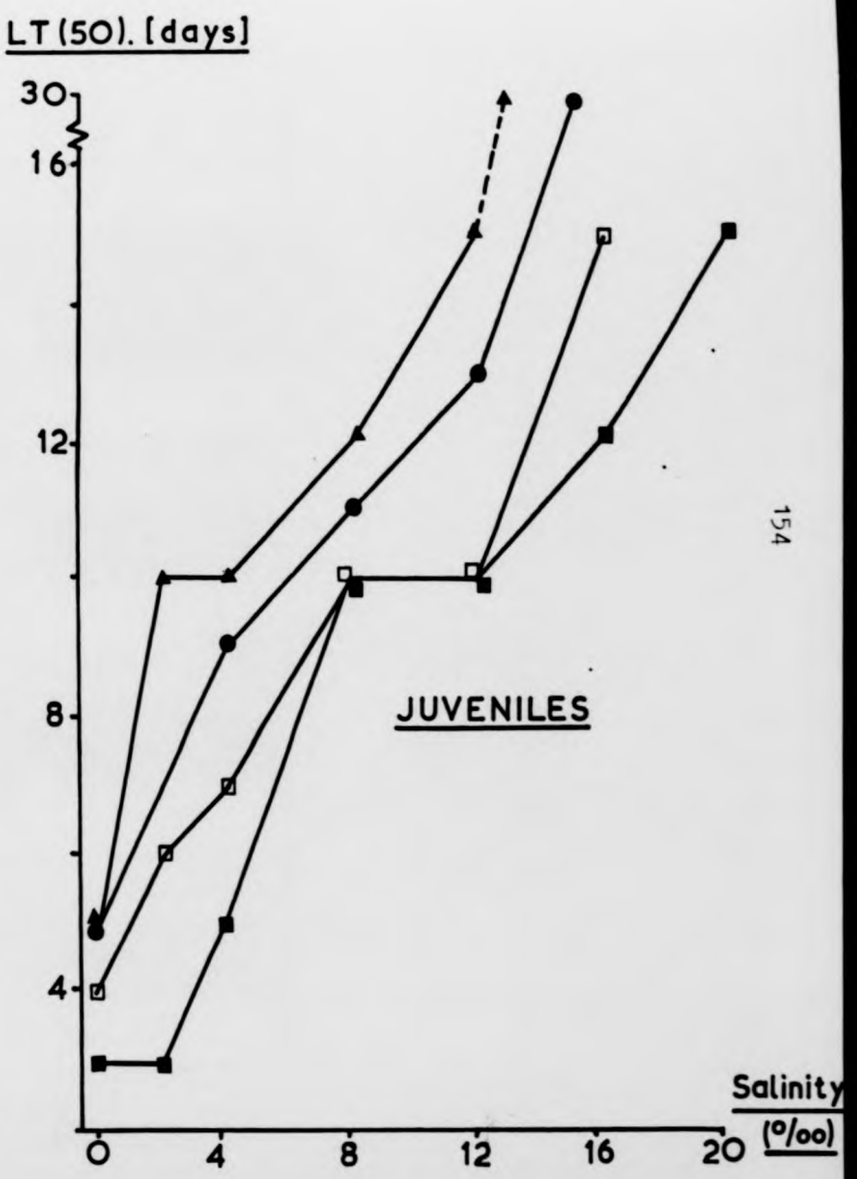
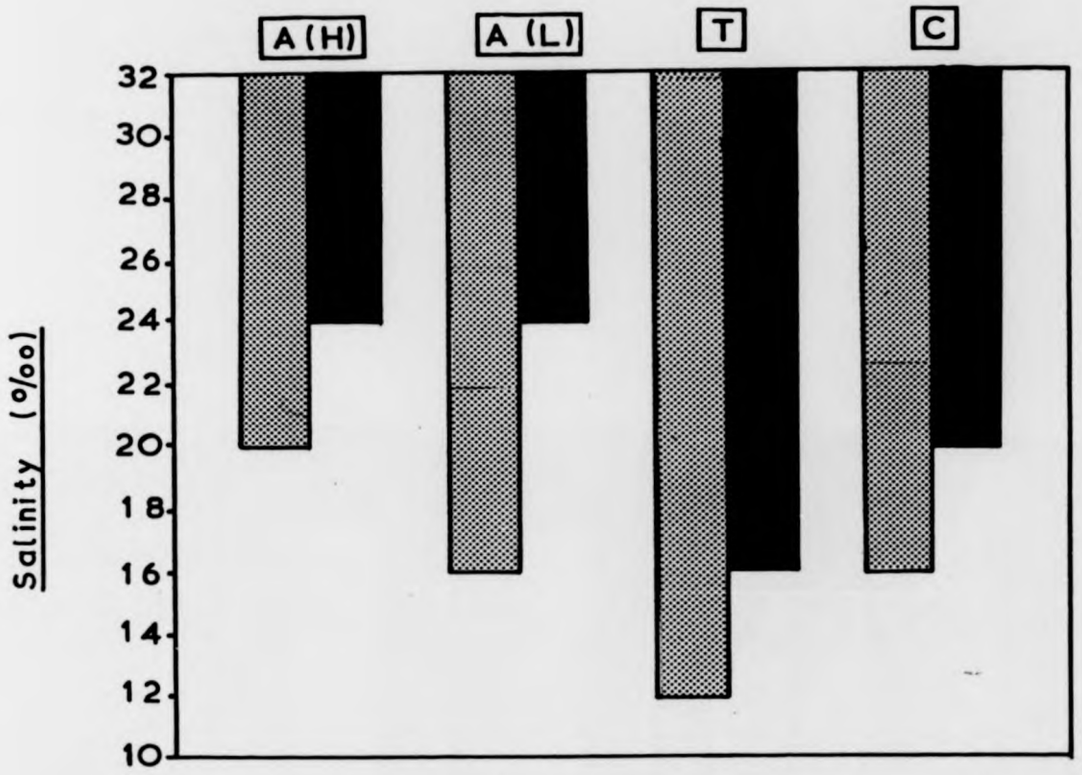

LT(50). [days]
30
16
12
8
4
JUVENILES
0
4
8
12
16
20
Salinity
(o/oo)

FIG.51. Survival of adult and juvenile L.rudis at different salinities. Shaded areas represent 50% or better survival over a 30 day period.

= Adults

= Juveniles


A (H)
A (L)
T
C
Salinity (‰)
32
30
28
26
24
22
20
18
16
14
12
10

Adults from both Aberdour 'H' and Aberdour 'L' approached maximal survival and activity (mean integrated response, MIR) only at salinities of 24‰ and above (Tables 40, 41; Figs 52a, b). In contrast, adults from Torrybay, after an initial period of reduced activity of about 3 days at 16‰ , approached maximum activity at salinities of 16‰ and above (Table 42; Fig. 52c). For the first 3 to 5 days adults from Culross exhibited maximal survival and activity at salinities of 16‰ and above, but the MIR fell gradually over the following 15 days (Table 43; Fig. 52d).

When the overall MIR's for the entire experimental period were calculated it became apparent that for all sites there was a relatively narrow range of critical salinities, between 12‰ and 20‰ below which survival and activity were low and above which the MIR approached a maximum (Fig. 53).

Comparing these survivals of adults and juveniles with effects of salinity on embryonic development (Section 5), it becomes apparent that developing embryos, and in particular eggs, are far less tolerant of lowered salinity than juveniles and adults.

TABLE 40. Time course of Mean Integrated Response (MIR) at different salinities for adult L. rudis from Aberdour 'H'

Salinity (‰)	MIR *							
	Day 1	Day 3	Day 5	Day 8	Day 10	Day 13	Day 15	Day 17
0	33	33	22	8	3	0	0	0
2	33	33	28	14	6	0	0	0
4	33	33	33	17	8	0	0	0
8	33	33	28	22	14	8	3	0
12	33	33	28	22	17	14	6	0
16	39	39	47	44	31	33	22	19
20	39	51	57	58	57	55	54	50
24	56	86	92	83	83	83	78	69
32	100	92	92	89	86	81	75	75

TABLE 41 Time course of Mean Integrated Response (MIR) at different salinities for adult L. rudis from Aberdour 'L'

Salinity (‰)	MIR *							
	Day 1	Day 3	Day 5	Day 8	Day 10	Day 13	Day 15	Day 17
0	33	33	22	17	3	0	0	0
2	33	33	28	14	6	3	0	0
4	33	33	33	19	8	6	0	0
8	33	33	33	22	14	6	0	0
12	33	36	31	25	19	11	3	0
16	44	47	58	50	50	39	39	22
20	47	63	61	58	57	55	54	48
24	78	83	100	86	86	86	92	81
32	89	94	94	89	86	92	89	83

* MIR = $\frac{\text{Number surviving x activity}}{\text{Total number x 3}}$ x 100%; see text

FIG.52. Time course of the Mean Integrated Response (MIR) of adult L.rudis held at different salinities.

A = Aberdour 'H'

B = Aberdour 'L'

C = Torrybay

D = Culross

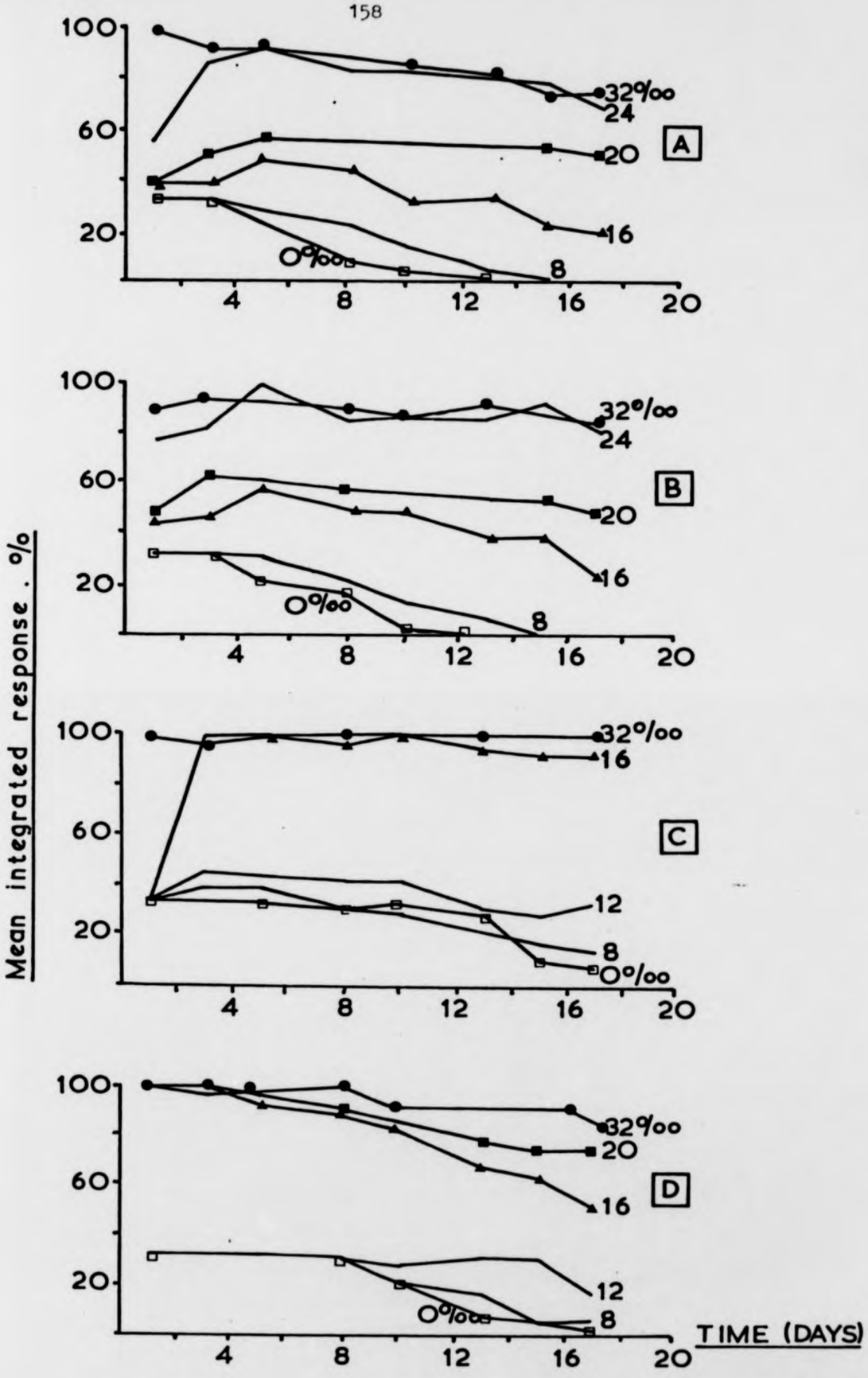

100
60
20
32‰
24
20
16
8
0‰
A
B
C
D
12
4
8
12
16
20
Mean integrated response . %
TIME (DAYS)

TABLE 42 Time course of Mean Integrated Response (MIR) at different salinities for adult L. rudis from Torrybay

Salinity (‰)	MIR *							
	Day 1	Day 3	Day 5	Day 8	Day 10	Day 13	Day 15	Day 17
0	33	33	33	31	33	28	11	8
2	33	33	31	28	28	19	11	3
4	33	33	33	31	31	19	11	6
8	33	39	39	31	28	22	17	14
12	33	44	44	42	42	31	28	33
16	33	100	100	97	100	94	92	92
20	89	100	100	98	97	100	100	100
24	94	100	89	100	100	100	95	100
32	100	97	100	100	100	100	100	100

TABLE 43 Time course of Mean Integrated Response (MIR) at different salinities for adult L. rudis from Culross.

Salinity (‰)	MIR *							
	Day 1	Day 3	Day 5	Day 8	Day 10	Day 13	Day 15	Day 17
0	33	33	33	31	22	8	6	3
2	33	33	31	17	17	6	6	3
4	33	33	33	31	22	14	0	0
8	33	33	33	31	22	17	6	6
12	33	33	33	31	28	33	31	17
16	100	100	94	89	83	69	64	53
20	100	98	97	91	86	79	75	75
24	100	94	100	97	89	92	100	86
32	100	100	94	100	92	92	92	81

* MIR = $\frac{\text{Number surviving x activity}}{\text{Total number x 3}}$ x 100%; see text

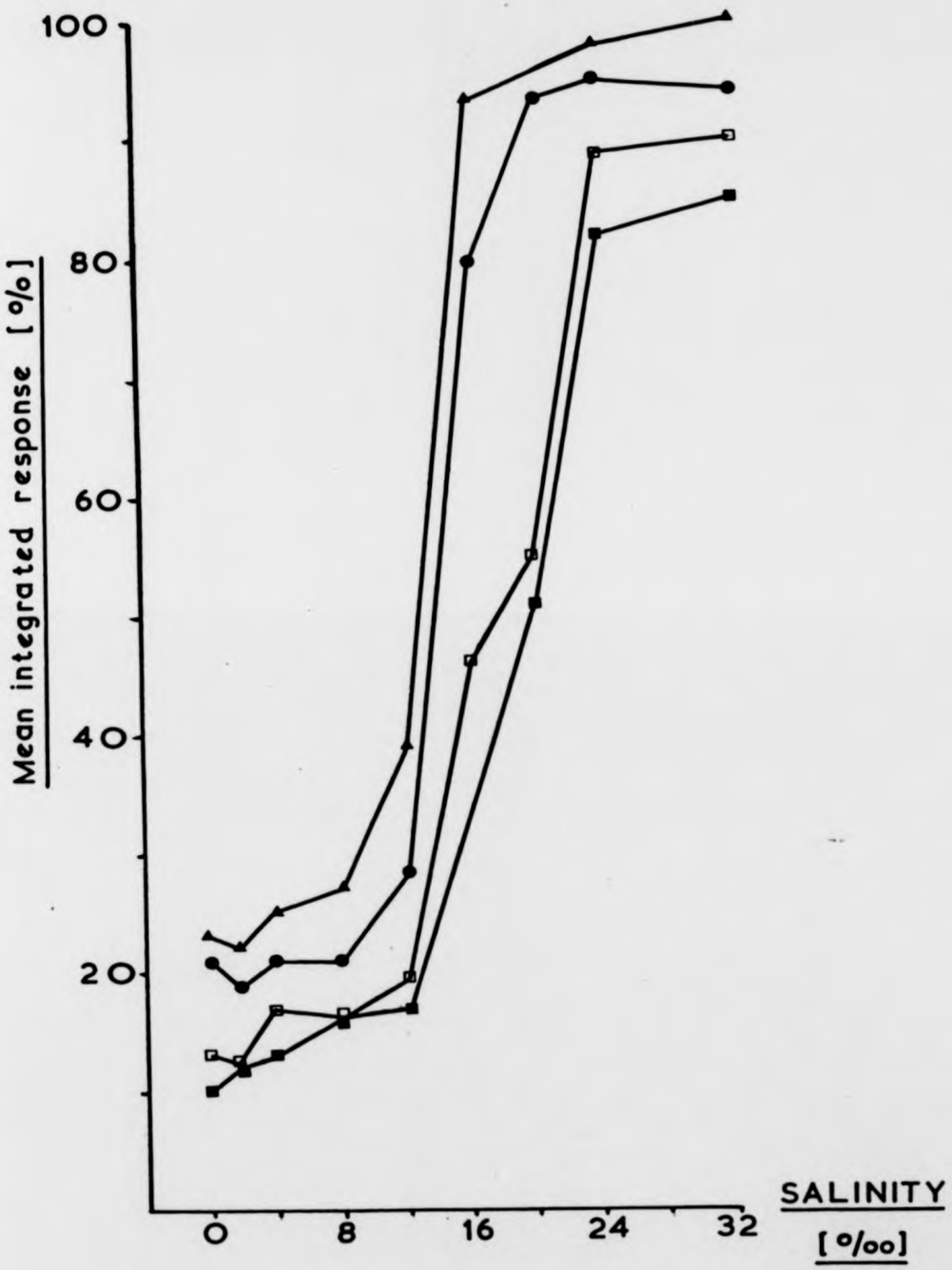
FIG.53. Overall Mean Integrated Response (MIR) to salinity of adult L.rudis.

■ = Aberdour 'H'

□ = Aberdour 'L'

▲ = Torrybay

● = Culross


100
80
60
40
20
Mean integrated response [%]
0
8
16
24
32
SALINITY
[‰]

DISCUSSION

(i) Populations

The two populations studied at Aberdour experienced typically marine conditions but there were striking differences in their composition, presumably related to their position on the shore. The highest densities occurred towards the upper limit of L. rudis on the shore (Fig. 10) confirming at Aberdour, as elsewhere (e.g. Berry, 1961 at Whitstable and Matveeva, 1974 in the White and Barents Sea) that L. rudis is commonly more abundant at the higher than the lower levels within its range.

These Aberdour counts averaging 472 m^{-2} upshore and 156 m^{-2} downshore were far lower than counts on the Murmansk coast or the Danish Waddens (Kuznetsov and Matveeva, 1948; Matveeva, 1974; Muss, 1967) and were more comparable with values at the lower end of the range reported (Table 1). Caution must be exercised in comparisons of this type however, as it is not always clear which member of the 'Saxalitis' aggregate is being considered by other workers.

Both Aberdour populations were composed predominantly of mature snails with few smaller than 7.5 mm and 6.5 mm on the upper and lower shores respectively (Table 6). The monthly mean percentage of these smaller animals was only 18% on the upper shore (7.5 mm) and 25% on the lower shore (6.5 mm). While many of the very smallest were inevitably omitted from these counts, the predominance of large

mature snails emphasises the importance of reproductive output as a proportion of total energy flow in the populations.

In addition to differing densities of L. rudis at the two Aberdour sites, their size composition varied (Figs. 12, 13). The mean and maximum shell heights on the upper shore were 11.5 mm and 15.1 mm respectively compared with a mean of only 9.2 mm and a maximum of 14.6 mm on the lower shore (Table 4).

This pattern of distribution with greater overall densities and more large snails on the upper shore is consistent with the findings of Berry (1961), Underwood (1975), Daguzan (1976), Faller-Fritsch (1977) and is presumably the consequence of a number of interacting factors.

a) The quantity of food available

b) Inter-specific competition for the available food.

These factors are likely to have a greater effect on the lower shore population since L. rudis is the predominant littorinid on the upper shore with only a few L. littorea and no L. littoralis, whereas on the lower shore, L. littorea predominates with L. littoralis commonly found (Table 3).

c) Time available for foraging.

As L. rudis only feeds when uncovered by the tide (Berry, 1961,; Faller-Fritsch, 1975), then more time would be available for

feeding on the upper shore which is exposed by the tide for longer than the lower.

d) The nature of the substratum and availability of crevices.

Since large boulders on the upper shore at Aberdour (Plates 1, 2) are more stable and are buffeted less frequently by the sea than the smaller stones on the lower shore (Plates 1, 3), then the risk of mortalities due to crushing is likely to be greater on the lower shore. Littorinids frequently retire into crevices after foraging (Foster, 1966; Behrens, 1972, 1974; Chow, 1975; Emson and Faller-Fritsch, 1976; Raffaelli and Hughes, 1978) and the availability of suitable crevices has been shown to influence the abundance and size composition of L. rudis (Emson and Faller-Fritsch, 1976; Raffaelli and Hughes, 1978). The relative paucity of crevices at Aberdour may partly explain the low densities at this site compared with other localities (Table 1).

e) Predation pressures

f) Migrations up or down the shore.

There was no evidence of any upshore migration by L. rudis ≥ 2mm at Aberdour although there was a hint of downshore movement by mature L. rudis (≥7.5 mm) between February and March 1975 (Table 6). Berry (1961) reported a slight, passive, upshore drift of small winkles but his observations of long-term movement of L. rudis with those of Daguzan (1976) indicate that the effect on distribution is slight and random.

The estuarine site of Torrybay supported much higher densities of L. rudis than those at Aberdour with an average of 1197 snails m^{-2} on the shale beds. This density is close to the values reported by Spooner and Moore (1940) in the Tamar estuary, Matveeva (1948) on the Murmansk coast and Faller-Fritsch (1975) in the Thames estuary (Table 1). This population at Torrybay was composed however of much smaller snails (mean height 7.3 mm, maximum 11.5mm) than at Aberdour (Table 4). It has been suggested by Jaeckel (1951, 1952) and Remane (1958) that lowered salinity results in the production of smaller shells. This discrepancy in size between the marine Aberdour and the estuarine Torrybay cannot however, be attributed wholly to lowered salinity since L. rudis at the upstream Culross had a mean shell height of 11.8 mm with individuals up to 17 mm. It is possible that the scarcity of suitable, large crevices on the flat beds of shale at Torrybay (Plate 4) rather than lowered salinity was a contributing factor in the paucity of large individuals at this locality.

When the Forth populations are compared with those from other localities, it is found that the size composition of the Torrybay snails was very similar to that of populations on other bedrock shores, whereas the size-structures of the Aberdour and Culross populations were consistent with those of L. rudis on boulder shores (Table 44).

In addition to variation in size composition between the Forth populations, there were also differences in shell morphology (Table 5). The ratios of shell-height (SH) to mouth diameter (MD) between the upper and lower Aberdour populations were found to be significantly different (1.534 on the upper shore and 1.502 on the

on the lower). This indicates that the snails on the lower shore had slightly increased mouth diameter in relation to their shell height which would increase the relative area of foot adherence to the rock. The significantly lower ratio of 1.459 at Torrybay supports the theory that L. rudis at this site was situated in a relatively exposed position on open beds of shale. The SH: MD ratio at Culross (1.413) does not appear to follow the trend of snails possessing a larger foot area in relation to shell height under exposed conditions. Abundance and size of predatory crabs have also been shown to be correlated with mouth diameter, so on sheltered shores narrow-mouthed shells are favoured to discourage crab predation (Heller 1975a). Since L. rudis at Culross was well protected from most predators, the main consideration, even in the relative shelter of the jetty, would have been maintaining position on the wall which would favour wider-mouthed shells.

There was a close correspondence between size at maturation and population size composition (Table 4). Females at Torrybay matured at a significantly smaller size (4.5 mm) than females from the other 3 sites which is consistent with the smaller sizes at this site. Burke and Mann (1974) also found that L. rudis matured at 4.5 mm in an East Canadian estuary, in addition he found that L. rudis at this site did not usually live for longer than a year and that few attained a size greater than 10 mm.

At the Aberdour upper shore site and at Culross, females did not mature until 7.5 mm while at the Aberdour lower shore site maturation occurred at the slightly smaller size of 6.5 mm (Table 4). Again these findings are consistent with those of Emson and Faller-Fritsch

(1976) who found that L. rudis matured at 6 - 8 mm on boulder shores but 2.5 mm on bedrock (Table 44). It should be noted that these reported values refer to the size of maturation of males; in this study males were found to mature at about 1 mm smaller than females. Presumably in those populations where large animals are relatively abundant, it would be advantageous for snails, initially, to devote all of their energy to somatic growth which would result in them quickly attaining a size where they would be less susceptible to predation and crushing by boulders (Heller, 1975a; Faller-Fritsch, 1975; Emson and Faller-Fritsch, 1976). In addition, larger L. rudis have been shown in this study and by Raffaelli (1976) and Roberts and Hughes (1980) to have greater reproductive capacity. These considerations must be balanced with the advantage conferred by maturation at a smaller size of increasing the time period over which reproductive contribution can be made.

Growth of cohorts through the population at Aberdour (Fig. 12, 13) indicated that L. rudis on both the upper and lower shore grew at a rate of about 1 mm per month, at least between 2 and 8 mm. Such a growth rate would result in females maturing at about 7 months on the upper shore and 6 on the lower. Berry (1961) also found that L. rudis matured at slightly different ages on the upper and lower shore at Whitstable; 8 and 9-10 months respectively. Differential growth was responsible for this difference however, since snails matured at about the same size, 7 - 7.2 mm, at both shore levels.

Newly-emerged juveniles from the estuarine sites of Torrybay (mean size 0.477 mm) and Culross (0.530 mm) grew at rates of

TABLE 44 Relationship between population size composition and size at maturity in 11 populations of *L. rudis* from bedrock and boulder substrates.

Site and substrate type	Mean shell height (mm)	Maximum shell height (mm)	Height at maturity (mm)
Bedrock			
* Torrybay	7.3	11.5	4.5 (F)
▲ Newhaven, Sussex	3.7	6.0	3.0-4.0(m)
▲ Watchet, Somerset	3.8	8.0	2.0-3.0(m)
▲ Newhaven	4.9	13.0	4.0-5.0(m)
Boulders			
* Aberdour 'H'	11.5	15.1	7.5 (F)
* Aberdour 'L'	9.2	14.6	6.5 (F)
* Culross	11.8	17.0	7.5 (F)
▲ Newhaven	11.7	17.0	7.0-8.0(m)
▲ Watchet	10.5	17.0	7.0-8.0(m)
▲ Greenhithe, Thames estuary	7.2	13.0	6.0-7.0(m)
▲ Landshipping, Pembroke	5.7	14.0	6.0-7.0(m)

* Data from this study

▲ Data from Emson and Faller-Fritsch (1976)

(F) Females

(M) Males

0.49 and 0.39 mm per month at 10°C in the laboratory over a 6 month period (Tables 26, 27; Figs. 39, 40). Although these growth rates can only be considered as approximations to the field situation since they were carried out at a constant temperature and food was not limiting, they indicate that females at Torrybay matured at about 10 months, 6/7 months at Aberdour and 14 months at Culross. L. rudis at Penvins, France matured at about the same age as snails at Culross (Daguzan, 1976) but they then already had a shell height of 11 mm compared with only 7.5 at Culross

(ii) Fluctuations in reproductive condition and effects of trematode infections

In general, there was a build-up of eggs and developing young in the brood-pouch through the winter and spring to peak numbers in early summer after which numbers declined sharply giving the smallest loads in the late summer and early autumn (Fig. 18; Tables 17 - 20). This seasonal trend, with a single, annual peak in brood-pouch loads is broadly consistent with the findings of Lebour (1937) at Plymouth, Faller-Fritsch (1975) at Greenhithe and Landshipping, Emson and Faller-Fritsch (1976) at Newhaven, Sussex and Roberts and Hughes (1980) at Aber in N. Wales.

Two peaks in brood-pouch loads were reported by Berry (1961) at Whitstable in spring and winter, by Beland (1974) in Nova Scotia in the spring and autumn, by Moreteau (1976) at Roscoff in the winter and early summer and by Daguzan (1976) in February and September at Penvins. Nevertheless a summer decline in reproductive activity was a constant feature in all these populations and probably reflects

changes in temperature optima during the year. Higher mean annual temperatures in more southerly latitudes could easily result in spring and autumn temperature optima alternating with temperatures too high in the summer and too low in the winter.

Seasonal fluctuations in brood-pouch loads in the Forth were much more pronounced at the estuatine than the marine sites (Fig. 18). This was particularly the case at Torrybay where brood-pouch counts fell to almost zero in the late summer before gradually rising again through the winter whereas at the lower shore site at Aberdour, seasonal trends were much less pronounced.

At the 3 sampling localities in the Forth, there was a negative correlation between brood-pouch loads (Fig. 18) and air and water temperatures (Fig. 8, 9) during the summer. Ovaries and testes were generally reduced at this time (Fig. 30, 31) confirming that low brood-pouch counts were a direct result of depressed reproductive activity and did not merely reflect faster turnover rates of embryos in the brood-pouch. These elevated temperatures could have depressed gonad activity directly, alternatively its action may have been indirect by reducing adult foraging ability.

Parallel with these seasonal fluctuations in gonadal condition and brood-pouch loads were distinct changes in body composition (Tables 11 - 16; Figs. 15 - 17). The interpretation of these changes is complicated by the absence of a discrete breeding season in L. rudis unlike studies of L. littorea (Williams, 1970; Grahame, 1973a; Alifierakis, 1978). Patella vulgata (L)

(Blackmore, 1969), Thais lamellosa (Stickle, 1973), Mytilus edulis(L) (Dare and Edwards, 1975) and Venus mercenaria (L) (Ansell et al, 1964) where loss of energy and utilisation of protein and lipids were clearly correlated with loss of gametes during spawning.

Energy content and dry flesh weight of L. rudis in the Forth were generally highest (maximum emergy content = 21.75 kJ g^{-1}; maximum weight of a 10 mm animal = 20.65 mg) in the autumn prior to overwintering (Figs. 17; Table 8). Storage of fats at this time was also indicated by increased C : N ratios (Tables 11 - 14; Fig. 15) Protein levels were highest in the spring (maximum = 714 mg g^{-1}) at the height of the breeding season then fell through late spring and summer indicating utilisation of protein for reproductive products. Overwintering resulted in depletion of energy reserves (Fig. 17) and the continued fall in energy content through spring to minima in the summer also reflects the loss of materials as gametes.

The incidence of larval trematodes (mainly Cercaria ubiquitoides) was also found to fluctuate in relation to the changing reproductive condition of L. rudis (Fig. 32, 33). In general, the level of infection was greatest in the late summer and autumn, although males on the low shore at Aberdour tended to be infected at a relatively high level throughout the year (Fig. 33b). The frequency and severity of infection in the Forth was significantly greater in males (58%) than females (22%). This is consistent with the findings of Pohley (1976) although Berry (1961) found males and females at Whitstable were infected in approximately equal numbers.

Heavy larval trematode infections were usually accompanied by a reduction of the ovary or testis and a fall in brood-pouch loads indicating that these infections directly or indirectly affected gamete production with a consequent decline in numbers of embryos. Parallel effects on fecundity have been demonstrated in a wide range of molluscs (Hurst, 1927; Malek, 1952; Coelho, 1954; Pan, 1965; Etges and Gresso, 1965; Sturrock, 1967).

High levels of infection in male L. rudis in the Forth were also correlated with reduction in the size of the penis and in some cases complete castration (Figs 33, 34). This is consistent with the findings of Pelseneer (1906), Linke (1934) and Berry (1961) and has also been observed in a wide range of prosobranchs including L. littorea (Linke, 1934; Rees, 1936), L. neritoides (Lysaght, 1941), Hydrobia ulvae (Pennant) (Krull, 1935; Rothschild, 1938; Ankel, 1962; Muus, 1967)and Bithynia tentaculata (L) (Neuhaus, 1940). Levels of infection generally declined over the winter (Fig. 33) and, in all but the most severely affected, snails resumed reproductive activity.

Levels of infection in both males and females were higher at the estuarine sites of Torrybay and Culross than the upper shore site at the marine Aberdour (Figs. 32, 33). This is in accordance with the finding of Matveeva (1974) that infection increases in proportion to distance from the open sea. L. rudis on the lower shore at Aberdour, however, carried much heavier infections than at any other site. Thus reduced salinity does not appear to be of paramount importance since the degree of variation imposed by tidal

level was greater than that of salinity. The availability of a secondary host, temperature and tidal regime influence the distribution of larval trematodes (James, 1968b). Differences in parasite loads across the shore at Aberdour (Figs. 32, 33) may also have been related to difference in size composition of L. rudis since it has been shown that their parasites are size-specific (James, 1968b; Pohley, 1976). Conversely, varying levels of parasites down the shore may have influenced the growth and size distributions of L. rudis

Little mention has been made in the literature of the role played by the ciliate Protophyra ovicola. During in vitro studies of development, P. ovicola survived well in water of salinity down to 8‰. P. ovicola crept round the surface of eggs and embryos and was observed to consume dead embryos and occasionally severely stressed embryos were attacked and consumed. No evidence was found to substantiate the theory of Ce pede (1910) and Pelseneer (1920) that young contained in heavily infected brood-pouches were frequently abnormal.

(iii) Development rates of embryos

Development times of invertebrate embryos depend on hatching form, taxonomic affinity, egg size,temperature and native thermal regime (Spight, 1975). Temperate prosobranch species generally produce larvae with a planktonic phase (Thorson, 1946, 1950) and the evolution of ovoviviparity in L. rudis with no planktonic larval stage is exceptional.

Egg size has been shown to affect development time in a wide range of invertebrates. Large eggs develop more slowly than small ones among tunicates (Berril,1935), copepods (McLaren *et al*, 1969), amphipods (Steele and Steele, 1973) decapods (Wear, 1974) and Muricacean gastropods (Spight, 1975).

Although there were significant differences in both the diameters and weight of eggs produced by females from each of the four sampling stations in the Forth (Table 25),under constant environmental conditions no inter-site differences in development times were revealed. This suggests that egg-size differences of this magnitude between members of a given species are not great enough to exert a significant influence.

Little information on development times of *L. rudis* could be gained by following cohorts or peaks in abundance in monthly, brood-pouch data (Tables 17 - 20), since most brood-pouches contained embryos at all stages of development. Development rates of embryos *in vitro* were affected profoundly by ambient temperature (Table 22) in accordance with the observations of Ganaros (1958), Mackenzie, (1961), Phillips,(1969) and Scheltema (1967) that embryos of porikilotherms will hatch sooner at higher temperatures as long as temperatures are compatible with normal development.

Full development of *L. rudis* from egg to pre-emergence juveniles took 41 days at 5^{o}C, 68 days at 10^{o}C and 115 days at 15^{o}C (Table 22) thus the Q_{10} for development between 5 and 15^{o}C is about 3.

A thermal effect of this magnitude will have a major effect on the turnover rate of embryos in brood-pouches since the range of air temperatures in the Forth during the study period was some 23°C from 0.5°C to 23.5°C (Fig. 9).

The optimum temperature for development in terms of maximal survival was 10°C (Table 22). The failure of embryos to develop at 20°C in the laboratory accords with the decline in brood-pouch loads during the summers of 1975 and 1976 (Tables 17 - 20; Fig. 18) when air temperatures exceeded 20°C (Fig. 9), although this effect will have been moderated by sea cover and evaporation providing periodic cooling. The rate of egg production by ovaries is also affected by fluctuations in temperature (Guyomarc'h Cousin, 1973). It has been shown here that the size of ovaries and consequently their capacity for egg production is reduced in the summer (Fig. 32). High temperatures at this time (Fig. 8, 9) may have been a major contributing factor in this reduction in activity. Similar reductions in the size of testes were also recorded during the summer (Fig. 33), which may also have been related to temperature levels unsuitable for sperm production.

The condition of invertebrate gonads is affected by a wide range of other factors however, including food availability and parasitism, therefore it would not be reasonable to postulate that the summer decline in activity is solely a temperature effect. Egg production at these temperatures would in any event be wasteful because further development is shown to be unlikely.

Salinity also had a profound effect on both the ability of embryos to develop and on development rates *in vitro* (Table 24). Successful development at 10°C was severely restricted at salinities of less than 20 - 24‰ . This compares with a minimun of 18‰ salinity required for normal development of embryos taken from *L. rudis* in the White and Barents Seas (Berger, 1971) and salinities of 20‰ and above to allow eggs from *L. littorea* to develop (Hayes, 1926). In this study the egg stage was least tolerant of lowered salinity (Table 24) and although late embryos were affected to a slightly lesser extent, there was a tendency for fully formed juveniles to remain in their capsules at very low salinities. In addition there was no evidence, either in *in vitro* development studies or during regular examinations of brood-pouch loads, to support the suggestion of Thorson (1946) that lowered environmental salinity increases the incidence of abnormal embryonic development such as twinning and sinistral as opposed to normal dextral coiling.

Both in the case of low salinities and temperatures of 15°C and above, fungal and bacterial infections of embryos taken from *L. rudis* tended to be heavy. Since these developmental studies were carried out *in vitro* however, it is probable that within the brood-pouch itself infections of this sort are less common and where they do arise can be combated.

High temperatures and reduced salinity also retarded shell development resulting in partially formed or very thin shells. In addition, it was found that stage 1 embryos cultured *in vitro* rarely developed beyond stage 2, and those which did failed to form a shell

although otherwise they appeared normal. These results suggest that for normal shell development embryos obtain calcium from the external medium. Furthermore, the brood-pouch must contain calcium at concentrations elevated with respect to sea water since embryos were apparently unable to obtain sufficient calcium when cultured in sea water alone. How these factors affect shell development in L. rudis is not fully understood and would warrant further investigation.

The penetration of L. rudis into water of reduced salinity will be governed primarily by the requirements of that stage in the life history which is least tolerant of lowered salinity. L. rudis survived and bred successfully at Torrybay and Culross where salinities fell to 12‰ in the winter (Fig. 6). This is not consistent with the finding in this study that embryonic development and survival is seriously affected at salinities of 20 - 24‰ and below (Table 24). However, Berger (1971) found that at salinities of between 10 and 20‰ the brood-pouch fluid of L. rudis is hypertonic with respect to the external medium but below 10‰ snails are unable to maintain an elevated osmotic pressure. Dutton (1980) reported that L. rudis from the Forth held at a salinity of 12‰ maintained their brood-pouch fluid at about 19‰ . Therefore, although embryos of L. rudis have a relatively high salinity threshold for normal development and survival, the capacity of females to regulate, within limits, the osmotic pressure of the brood-pouch fluid, means that the salinity requirements of embryos should not itself limit the penetration of L. rudis into estuaries at least down to salinities of 10‰.

At each sampling location adults were consistently more

tolerant of reduced salinity than juveniles (Table 39; Fig. 51). Thus the penetration of L. rudis into estuaries will be limited, at least in part, by the tolerances of the very young rather than those of adults. These findings in conjunction with the effects of salinity on development of embryos, indicate that the degree of euryhalinity increases with the ontogenesis of L. rudis. This could be due to shell development rather than osmoregulatory capability.

Differential mortality of adults and juveniles at the estuarine sites of Torrybay and Culross appears likely since salinities fell to 12‰ in winter (Fig. 6) but juveniles at 10°C in the laboratory only survived down to 16‰ (Torrybay) and 20‰ (Culross) whereas adults were better able to withstand these low salinities (Table 39). However, the capacity to withstand lowered salinity has been shown to be modified by temperature (Todd, 1964; Arnold, 1972; Berry and Hunt, 1980). In addition, Stickle and Ahohas (1974) showed that the ability of aquatic invertebrates to withstand reduced salinity increases if the transition is gradual.

L. rudis does not penetrate further up the Forth estuary than Kincardine Bridge 6 km west of Culross (Fig. 4) despite a few physically suitable sites further west (Berry and Hunt, 1980). Above Kincardine Bridge there are extensive periods when salinities fall below 12‰ (FRPB). In such regions juveniles can be expected to die, especially in winter conditions even where adults might survive.

The lower salinity tolerance threshold of L. rudis in the Forth (12‰ by Torrybay adults) is close to the value of 13.75‰ reported by Gowanloch and Hayes (1926) although rough periwinkles have been reported in salinities as low as 6‰ in the Baltic (Nordensrjold, 1900; Jaeckel, 1951; and Remane, 1958).

(iv) Patterns of release

Release of juveniles by L. rudis from the Forth at high and mid tide levels in a laboratory tide tank strongly indicated cyclical patterns of release during spring and autumn (Fig. 44 - 47; Table 33), with maximal release close to successive new moons. This suggests that it is advantageous both for individual offspring and ultimately for populations if release of juveniles is concentrated around new-moon spring tides. Similar monthly peaks of release have been recorded for the mangrove gastropod Littorina melanastoma (Gray) by Berry and Chew (1973) which like L. rudis breeds throughout the year but releases eggs once monthly at full moon, and for the annelid Platynereis dumerillii (Aud. and M. Edw) which releases most of its eggs shortly after full moon (Korringa, 1947).

The significance of cycles of release in L. rudis is less clean than in those high-shore littorinids L. neritoides and Littorina anguilifera (Lam.) which shed their eggs when covered by fortnightly spring tides in order to ensure survival and dispersal (Lysaght, 1941; Lenderking, 1954; Sacchi and Testard, 1971; Hughes and Roberts, 1980). The ovoviviparous L. rudis has to a certain extent overcome some of the problems of laying pelagic egg capsules at high shore levels by

producing shelled-young able to resist dessication. However, it has been shown that prolonged exposure leads to high mortalities of newly released juveniles (Dickson, 1975; Houston, 1976; Berry and Hunt, 1980) but that juveniles are able to overcome this problem to some extent by taking refuge in small crevices (Emson and Faller-Fritsch, 1976). Since juveniles are only active when submerged (Berry and Hunt, 1980) chances of locating a suitable crevice would be improved if release occurred when the shore is covered, as at spring tides.

If juvenile survival is enhanced by release being synchronised with spring tides, then it may be expected that maximum release would coincide with all fortnightly spring tides, this was apparently not the case. Furthermore, maximum release did not coincide with the bigger of the two spring tides each month, which suggests that there are other, less immediately apparent factors, which favour monthly cycles of release coinciding with new moons in particular.

The rate of development of embryos might be expected to influence release patterns, but the considerable influence of temperature on development noted in this work (Q_{10} of 3 between 5 and 15^{o}C); Table 22) will cause development times to vary. Furthermore, L. rudis can withhold juveniles under adverse conditions, as at low tide levels in the tide tank (Figs. 42, 43; Tables 30, 31) or alternatively, release them faster than embryos are able to develop and replenish losses, as at high tide level in the tide tank (Figs. 42, 43; Table 29, 31).

The ability of L. rudis to withhold embryos means that cycles of release are not exclusively endogenous. This is further supported by the findings of Dutton (1980) that speeding up the tidal cycle causes females to speed up their release cycle to some extent and that females held without tidal stimulation do not show any discernable rhythms of release. These observations suggest that L. rudis might use tidal movement as a basic"counting cue" in a similar manner to that reported by Alifierakis and Berry (1980) for L. littorea which exhibits fortnightly peaks of egg release coinciding with spring tides (Grahame, 1975; Fish 1979; Berry and Alifierakis, 1980).

(v) Embryo size

Significant differences were found in the size and weight of eggs and embryos produced by estuarine and marine L. rudis and by high and low shore females (Table 25). Eggs and pre-emergence juveniles from Torrybay (37.5 μg DW and 55.5 μg DW respectively) were almost twice as heavy as those from the low shore Aberdour site (20.4 μg DW and 29.3 μg DW). The greater weight of Torrybay pre-emergence juveniles could only partly be attributed to the production of a bigger shell since their flesh weight also was 25% greater than that of Aberdour low shore juveniles (Table 25).

Variation in embryo size was less marked between the estuarine sites,Torrybay and Culross, than between the estuarine and marine localities (Table 25). Indeed the shell size and flesh weight of Culross pre-emergence juveniles (509 μm and 29.4 μg AFDW)

were very similar to those of the Torrybay juveniles (498 μm and 30.8 μg AFDW), thus the discrepancy in dry weight of juveniles between these sites (48.1 μg DW at Culross and 55.5 μg DW at Torrybay) must have resulted from Torrybay embryos forming thicker shells.

Eggs produced by females on the upper shore at Aberdour (22.5 μg AFDW) were 28% heavier than those produced on the lower shore (17.6 μg AFDW). This difference had increased to 45% in release stage juveniles (24.6 μg AFDW on the upper shore, 16.94 μg AFDW on the lower shore).

There was no variation in the size of eggs produced by females of different sizes at each site. Neither was there a direct correlation between size of female and egg size between sites, indeed the smallest females at Torrybay, produced the biggest juveniles (Tables 4, 25). Thus differences in embryo size must result from habitat differences and are presumably related to maximising survival rates of offspring.

The striking differences in embryo size between the estuarine and marine sites (Table 25) indicates that salinity might have an important effect on hatching size, resulting in bigger juveniles produced under conditions of reduced salinity. This is supported by the finding of Faller-Fritsch (1977) that eggs of L. rudis were much bigger at Greenhithe in the Thames estuary (661 μm) than at Newhaven on the Sussex coast (521 μm). This difference between Greenhithe and Newhaven is unlikely to be an effect of latitude since the size range of L. rudis hatchlings at a number of

sites in France varied between 400 and 500 μm (Cousin, 1971; Daguzan, 1976; Moreteau, 1976) which is very close to the range of 415 - 509 μm in the Forth. The effect of salinity on hatching size is further supported by the observation of Rasmussen (1951) that the size of offspring of the opisthobranch Brachystomia rissoides( ) decreases with increasing salinity.

It has been shown that females transferred from one locale to another continue to produce eggs and embryos of the same size as they had at the original site, but the numbers produced change to match those of the locals (Faller-Fritsch, 1975). This indicates that embryo size is primarily genetically determined whereas the number produced is more easily influenced by environmental conditions such as food availability.

Since embryos vary in weight between sites (Table 25) then numbers of embryos will not alone accurately reflect reproductive effort. Thus in the year 1974/75 the monthly mean number of embryos per brood-pouch of a female of characteristic size at the Aberdour upper-shore site (11.5 mm) was 226.0 (Table 45) compared with only 158.9 (Table 46) for an 11.8 mm female at Culross. However, when dry weight is taken into account (Table 25) the discrepancy in brood-pouch loads becomes much less marked, 7.447 mg DW per female on the upper shore at Aberdour and 6.590 mg DW at Culross.

Females of characteristic size on the lower shore at Aberdour (9.2 mm) had a mean brood-pouch load of 131.6 embryos in 1974/75 (Table 46) which was 2 X that of an average-sized female at Torrybay

TABLE 45 Monthly mean number and weight of each developmental stage in the brood-pouch of a standard 10 mm female and of a female of mean height (11.5 mm) at Aberdour 'H'

Developmental stage	Standard 10 mm female				11.5 mm female			
	1974/75		1975/76		1974/75		1975/76	
	Mean number embryos per female per month	Dry weight per female per month (mg)	Mean number embryos per female per month	Dry weight per female per month (mg)	Mean number per female per month (mg)	Dry weight per female per month (mg)	Mean numbers embryos per female per month	Dry weight per female per month (mg)
1	37.1	0.954	33.8	0.869	59.3	1.524	54.1	1.390
2	24.9	0.804	26.7	0.862	39.8	1.286	42.7	1.379
3	27.6	0.892	22.8	0.736	44.1	1.424	36.5	1.179
4	51.8	2.010	52.5	2.037	82.8	3.213	84.0	3.259
Total	141.4	4.660	135.8	4.504	226.0	7.447	217.3	7.207

TABLE 46 Monthly mean number and weight of each developmental stage in the brood-pouch of a standard 10 mm female and of a female of mean height (9.2 mm) at Aberdour 'L'

Developmental stage	Standard 10 mm female				9.2 mm female			
	1974/75		1975/76		1974/75		1975/76	
	Mean number embryos per female per month	Dry weight per female per month (mg)	Mean number embryos per female per month	Mean weight per female per month (mg)	Mean number per female per month (mg)	Dry weight per female per month (mg)	Mean numbers embryos per female per month	Dry weight per female per month (mg)
1	45.3	0.924	43.0	0.877	35.2	0.718	33.4	0.681
2	38.8	0.966	36.1	0.899	30.2	0.752	28.0	0.697
3	32.8	0.817	31.7	0.789	25.5	0.635	24.7	0.615
4	66.5	1.949	64.1	1.878	51.7	1.515	49.8	1.459
Total	183.4	4.656	174.9	4.443	142.6	3.620	135.9	3.452

TABLE 47 Monthly mean number and weight of each developmental stage in the brood-pouch of a standard 10 mm female and of a female of mean height(7.3 mm) at Torrybay.

Developmental stage	Standard 10 mm female				7.3 mm female			
	1974/75		1975/76		1974/75		1975/76	
	Mean number of embryos per female per month	Dry weight per female per month (mg)	Mean number of embryos per female per month	Dry weight per female per month (mg)	Mean number of embryos per female per month	Dry weight per female per month (mg)	Mean number of embryos per female per month	Dry weight per female per month (mg)
1	23.0	0.863	15.9	0.596	11.7	0.439	8.1	0.304
2	15.3	0.712	21.2	0.986	7.8	0.363	10.8	0.502
3	20.5	0.953	17.9	0.832	10.4	0.484	9.1	0.423
4	38.8	2.153	42.3	2.348	19.8	1.099	21.5	1.193
Total	97.6	4.681	97.3	4.762	49.7	2.385	49.5	2.422

TABLE 48 Monthly mean number and weight of each developmental stage in the brood-pouch of a standard 10 mm female and of a female of mean height (11.8 mm) at Culross.

Developmental stage	Standard 10 mm female				11.8 mm female			
	1974/75		1975/76		1974/75		1975/76	
	Mean number of embryos per female per month	Dry weight per female per month (mg)	Mean number of embryos per female per month	Dry weight per female per month (mg)	Mean number of embryos per female per month	Dry weight per female per month (mg)	Mean number of embryos per female per month	Dry weight per female per month (mg)
1	21.1	0.682	19.0	0.614	36.6	1.182	33.0	1.066
2	17.3	0.696	20.9	0.840	30.0	1.206	36.3	1.459
3	17.3	0.696	19.2	0.772	30.1	1.210	33.3	1.339
4	35.8	1.722	37.6	1.809	62.2	2.992	65.3	3.141
Total	91.5	3.796	96.7	4.035	158.9	6.590	167.9	7.005

(49.7 embryos; Table 47), but the weight of embryos on the lower shore at Aberdour (3.620 mg DW) was only 1.5X that at Torrybay (2.385 mg DW). Similar values were obtained in 1975/76 (Tables 46 - 48) confirming that varying weights tended to compensate for varying numbers.

Size composition at the 4 sites varied conspicuously (Table 4) and so brood-pouch loads were recalculated in terms of a standard 10 mm female (Tables 45 - 48). Brood-pouch loads in 1974/75 of such a standard female on the upper shore at Aberdour (4.660 mg DW), the lower shore at Aberdour (4.656 mg DW), Torrybay (4.681 mg DW) and Culross (3.796 mg DW), were more closely similar than foregoing values for actual females of characteristic sizes thus supporting the possibility that comparable energy available for reproduction at different sites can be partitioned into many small embryos or few large ones as proposed for Muricidae by Spight (1975).

The dry weight of embryos increased by 43 - 50% between egg and pre-emergence juvenile stages (Table 25). This increase was found to be almost entirely due to the production of a shell since the ash-free dry weight of eggs and juveniles remained almost constant (Table 25). Since energy must have been expended in respiration, then the development of embryos could not have depended solely on reserves available within the capsule but more probably embryos obtained additional nourishment from the brood-pouch.

(vi) Reproductive effort

Monthly biomass estimates of mature L. rudis at Aberdour between November 1974 and October 1975 (Tables 49, 50; Fig. 54, 55) were calculated using the size-composition data (Figs. 12, 13), length-weight regressions (Table 7) and population density (Table 6). The calculated biomass values in $gAFDWm^{-2}$ were subsequently converted to kJm^{-2} using energy values derived from carbon content of L. rudis (Table 16).

Biomass varied in close accordance with numbers (Figs. 54, 55) On the upper shore at Aberdour biomass fell in November 1974 from 194.93 kJm^{-2} to 147.48 kJm^{-2} in December 1974 before rising to a peak of 192.16 kJm^{-2} in January 1975(Fig. 54). It then fell to 148.28 kJm^{-2} in March before rising steeply to its maximum level of 240.60 kJm^{-2} in June after which it gradually declined to 139.77 kJm^{-2} in October 1975.

On the lower shore at Aberdour the biomass was conspicuously less than upshore and changed in a slightly different pattern (Table 49; Fig. 55) falling from 28.74 kJm^{-2} in November 1974 to a minimum of 11.46 kJm^{-2} in February 1975 before rising steadily to a peak of 60.98 kJm^{-2} in April 1975. It then fell again between April and June before rising to a maximum of 65.45 kJm^{-2} in July 1975.

Monthly mean biomass on the upper shore (182.87 kJm^{-2}) was almost 5 X greater than that on the lower shore (37.57 kJm^{-2}). Based on 4 counts in 1974/75, the mean monthly biomass at the estuarine

TABLE 49 Density and biomass of mature L. rudis at Aberdour 'H' and 'L' between November 1974 and October 1975

Month	Aberdour 'H'			Aberdour 'L'		
	Numbers of mature (≥7.5mm) L. rudis m^{-2}	Biomass (AFDW) gm^{-2}	kJm^{-2}	Numbers of mature (≥6.5mm) L. rudis m^{-2}	Biomass (AFDW) gm^{-2}	kJm^{-2}
Nov 1974	408	9.86	194.93	97	1.48	28.74
Dec	356	7.46	147.48	76	1.17	22.72
Jan 1975	412	9.72	192.16	72	1.07	20.78
Feb	392	9.31	184.06	56	0.59	11.46
Mar	292	7.50	148.28	146	2.02	39.23
Apr	352	8.60	170.02	192	3.14	60.98
June	528	12.17	240.60	132	2.00	38.84
July	450	11.68	230.91	160	3.37	65.45
Aug	458	10.86	214.70	136	2.71	52.63
Sept	306	7.54	149.07	104	1.56	30.30
Oct	252	7.07	139.17	130	2.18	42.34

TABLE 50 Mean density and biomass of mature L. rudis at Aberdour 'H' Aberdour 'L' and Torrybay

Site	Size at maturity (mm)	Numbers of mature L. rudis m^{-2}	Biomass (AFDW) gm^{-2}	kJm^{-2}
Aberdour 'H'	7.5	382	9.25	182.87
Aberdour 'L'	6.5	118	1.94	37.59
Torrybay	4.5	1197	11.27	218.30

FIG.54. Seasonal change in numbers and biomass / m^2 of L.rudis at Aberdour 'H'.

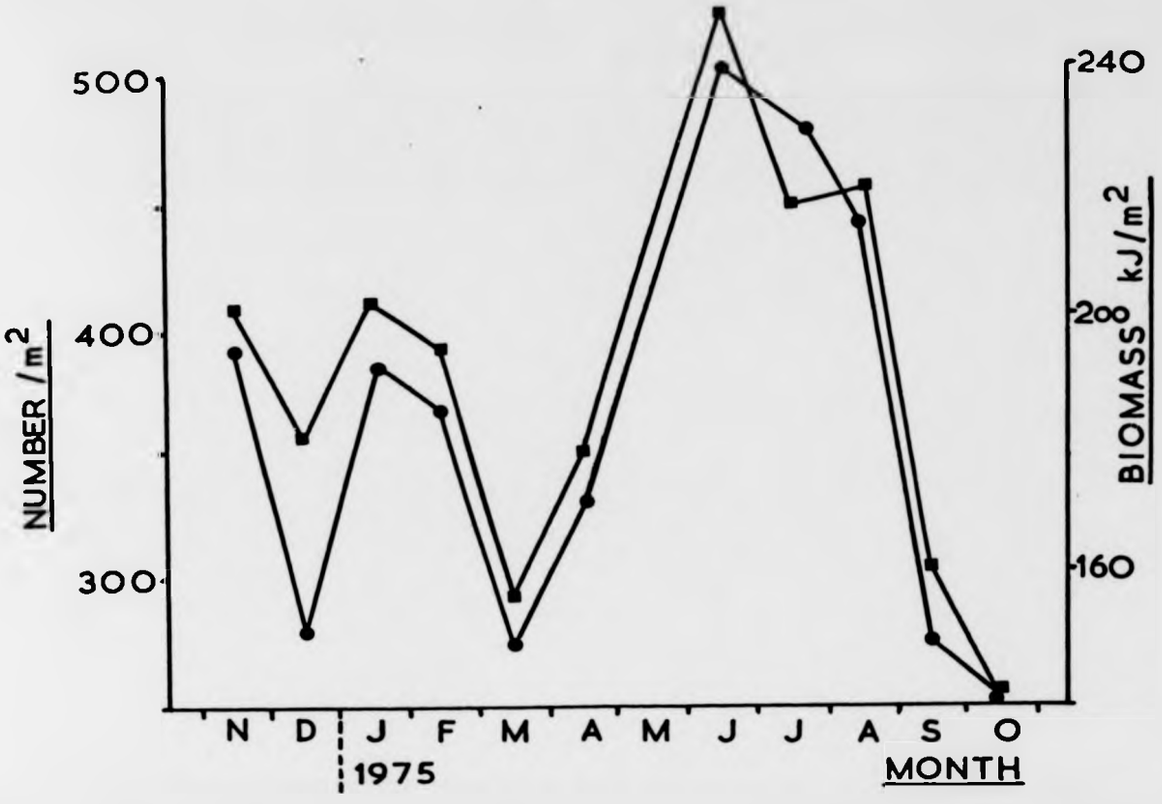
■ = numbers / m^2

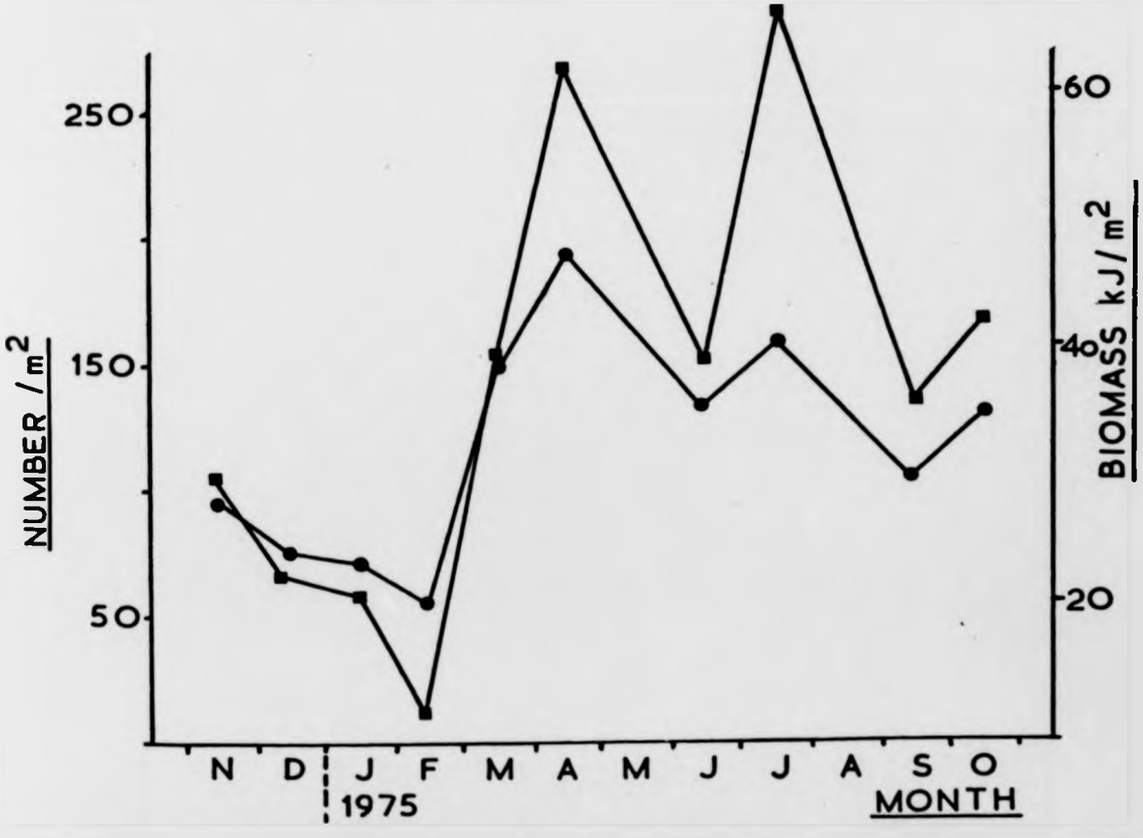
● = biomass / m^2

FIG.55. Seasonal change in numbers and biomass / m^2 of L.rudis at Aberdour 'L'.

■ = numbers / m^2

● = biomass / m^2


500
400
300
NUMBER /m²
240
200
160
BIOMASS kJ/m²
N D J F M A M J J A S O
1975
MONTH


250
150
50
NUMBER /m²
60
40
20
BIOMASS kJ/m²
N D J F M A M J J A S O
1975
MONTH

Torrybay was estimated as 218.30 kJm^{-2} (Table 50). Thus although the Torrybay population was composed of conspicuously smaller individuals than at Aberdour (Table 4), the standing crop was 20% and 580% greater than that on the upper and lower Aberdour shore respectively (Table 50).

Monthly biomasses of embryos carried by females at Aberdour (Tables 51, 52) were calculated on the basis of brood-pouch loads (Tables 17 - 20), weight of embryos (Table 25) and numbers of mature females based on overall sex ratio of 1 : 1 (Table 6).

On the upper shore at Aberdour the estimated biomass of embryos varied from 2.210 g AFDW m^{-2} in May 1975 to 0.491 g AFDW m^{-2} in October 1975 with a yearly mean of 1.082 g AFDW m^{-2} which was equivalent to 10.58% of the total adult biomass (Table 51). On the lower shore, embryo biomass varied between 0.054 g AFDW m^{-2} in January 1975 and 0.240 g AFDW m^{-2} in May 1975 with a yearly mean of 0.145 g AFDW m^{-2} equivalent to only 7.40% of the adult biomass (Table 52). Thus embryo biomass on the upper shore was 7 - 8 X greater than that on the lower shore.

It has been shown that comparisons of brood-pouch counts (Tables 45 - 48) do not accurately reflect reproductive effort at the 4 sampling sites in the Forth since embryo weight varies significantly between sites (Table 25). The mean brood-pouch counts at Culross (163.1 embryos per female; Table 20) and on the lower shore at Aberdour (166.4; Table 18) were very similar but when weight is taken into account (Table 25) embryo biomass per female at Culross amounts to 4.60 mg AFDW compared with only 2.87 mg AFDW on the lower Aberdour

TABLE 51 Monthly biomass of brood-pouch loads in relation to standing crop of adults at Aberdour 'H'

Month	Mean brood pouch load	Mean AFDW in brood-pouch g/female	Number mature females m^{-2}	Biomass of brood-pouch (loads AFDW) gm^{-2} (Bp)	Biomass of adults (AFDW) (≥7.5 mm) (B)	$\frac{Bp}{B} \times 100\%$
Nov 1974	172.0	0.0041	204	0.836	9.86	8.48
Dec	176.8	0.0042	178	0.748	7.46	10.03
Jan 1975	192.2	0.0045	206	0.927	9.72	9.54
Feb	277.9	0.0065	196	1.274	9.31	13.68
Mar	278.3	0.0066	146	0.964	7.50	12.85
April	213.8	0.0050	176	0.880	8.60	10.24
May	361.7	0.0085	260	2.210	-	-
June	248.9	0.0059	264	1.558	12.17	12.80
July	271.7	0.0064	225	1.440	11.68	12.33
Aug	195.8	0.0046	229	1.053	10.86	9.70
Sept.	163.7	0.0039	153	0.597	7.54	7.92
Oct.	164.0	0.0039	126	0.491	7.07	6.95
Mean	226.7	0.0051	191	1.082	9.25	10.58

TABLE 52 Monthly biomass of brood-pouch loads in relation to standing crop of adults at Aberdour 'L'

Month	Mean brood pouch load	Mean AFDW in brood-pouch g/female	Number mature females m^{-2}	Biomass of brood-pouch loads (AFDW) gm^{-2} (Bp)	Biomass of adults (AFDW) (≥6.5mm) gm^{-2} (B)	$\frac{Bp}{B}$ x 100%
Nov 1974	100.8	0.0017	49	0.083	1.48	5.61
Dec	100.4	0.0018	38	0.068	1.17	5.81
Jan 1975	86.2	0.0015	36	0.054	1.07	5.04
Feb	132.2	0.0023	28	0.064	0.59	10.84
Mar	178.8	0.0031	73	0.226	2.02	11.19
April	94.1	0.0016	96	0.154	3.14	4.90
May	172.2	0.0030	80	0.240	-	-
June	185.3	0.0032	66	0.211	2.00	10.55
July	147.8	0.0026	80	0.208	3.37	6.17
Aug	128.8	0.0022	68	0.150	2.71	5.53
Sept	144.8	0.0025	52	0.130	1.56	8.33
Oct.	135.3	0.0023	65	0.150	2.18	6.88
Mean	132.4	0.0023	58	0.145	1.94	7.4

shore. The mean brood-pouch count per female on the upper shore at Aberdour (210.2; Table 17) was 3 X that at Torrybay (68.8; Table 19) but when weight is taken into account (Table 25), there is only a 2-fold difference, 4.95 mg AFDW per female on the upper shore at Aberdour and 2.13 mg AFDW at Torrybay. Thus embryo biomasses per female on the upper shore at Aberdour and at Culross were similar as were those at Torrybay and the lower-shore at Aberdour.

Annual production of embryos per female at each site was estimated using mean brood-pouch biomass and a development rate of 72 days from egg to free-living juvenile based on laboratory trials at 10°C and 32‰ salinity (Table 22). Outputs by females on the upper shore at Aberdour (24.08 mg AFDW y^{-1}) and Culross (23.31 mg AFDW y^{-1}) were close to the value of 23.8 mg AFDW y^{-1} calculated from the data of Faller-Fritsch (1977) at Greenhithe, while the output per female on the lower shore at Aberdour (14.55 mg AFDW y^{-1}) was similar to the 14.0 mg AFDW y^{-1} and 14.4 mg AFDW y^{-1} at Newhaven and Whitstable (calculated from Faller-Fritsch,1977). Output per female at Torrybay was far less at only 10.80 mg AFDW y^{-1}.

The energy expended annually on embryos at Aberdour and Torrybay was calculated using the weight values above, energy content of embryos (Table 25) and numbers of females m^{-2} (Table 6). Thus, L. rudis at Aberdour produced an estimated 103.52 kJ m^{-2} y^{-1} of embryos on the upper shore and only 18.53 kJ m^{-2} y^{-1} on the lower shore. Annual production of embryos at Torrybay was 139.52 kJ m^{-2} y^{-1}.

Using the information on release rates (Tables 31, 32), weight

and energy values of newly released juveniles (Table 25) and numbers of mature females at each site (Table 6), production of newborn was calculated. Daily production due to reproduction (Pr) is the product of numbers released (R) and the weight (w) of newborn, Pr = Rw.

Females on the upper shore at Aberdour released an average of 270.1 juveniles per female, equivalent to a total of 27.08 kJ m^{-2} y^{-1} (Table 53). This field estimate was close to the value of 24.94 kJ m^{-2} y^{-1} calculated from laboratory release rates at mid-tank level in a laboratory tide tank (Tables 31, 53) but was only 60% of the value calculated from release rates at high tank level (45.66 kJ m^{-2} y^{-1}). Since it has been shown that females at high-tank level released juveniles faster than embryonic development could replace the departures (Tables 31, 34) this figure is unlikely to be an accurate reflection of the field situation.

Females at Culross released an estimated 222.7 juveniles per female per year, equivalent to 6.55 mg AFDW y^{-1} which is very close to the field value of 6.65 mg AFDW y^{-1} released by L. rudis on the upper shore at Aberdour (Table 55). Release values at mid-tank level in the tide tank were significantly lower than those in the field (164.3 juveniles per female y^{-1} = 4.83 mg AFDW y^{-1}) but this was probably due to the laboratory tidal level being below that occupied by L. rudis in the field at Culross.

Individual females from Torrybay in the laboratory at mid-tank level released fewer juveniles (160.6 y^{-1}) than females from the other sampling sites held at this tank level (Table 53 - 55). However, when juvenile weight was taken into account, an estimated

TABLE 53 Annual production due to reproduction (Pr) of *L. rudis* from Aberdour 'H'

Source of *L. rudis*	Mean number of juveniles released per female / day	Total numbers released per female y^{-1}	Annual release per female $(DW)_{-1}$ mg y^{-1}	Annual release per female $(AFDW)_{-1}$ mg y^{-1}	Annual release (AFDW) $gm^{-2} y^{-1}$	Annual (Pr) release (AFDW) $kJm^{-2} y^{-1}$
High-tank level	1.25	456.3	17.70	11.23	2.14	45.66
Mid-tank level	0.68	248.2	9.63	6.11	1.17	24.94
Low-tank level	0.57	208.1	8.07	5.12	0.98	20.89
Field	0.74	270.1	10.48	6.65	1.27	27.08

TABLE 54 Annual production due to reproduction (Pr) of L. rudis from Aberdour 'L'

Source of L. rudis	Mean number of juveniles released per female / day	Total numbers released per female y^{-1}	Annual release per female $(DW)_{-1}$ mg y^{-1}	Annual release per female $(AFDW)_{-1}$ mg y^{-1}	Annual release $(AFDW)_{-2}$ gm^{-2} y^{-1}	Annual (Pr) release $(AFDW)_{-2}$ kJm^{-2} y^{-1}
High-tank level	0.71	259.2	7.60	4.39	0.257	5.49
Mid-tank level	0.48	175.2	5.13	2.97	0.174	3.71
Low-tank level	0.35	127.8	3.75	2.17	0.127	2.71
Field	0.50	182.5	5.35	3.09	0.181	3.86

TABLE 55 Annual production due to reproduction (Pr) of *L. rudis* from Torrybay and Culross

Source of *L. rudis*	Mean number of juveniles released per female / day	Total numbers released per female y^{-1}	Annual release per female (DW) $mg\ y^{-1}$	Annual release per female (AFDW) $mg\ y^{-1}$	Annual release (AFDW) $gm^{-2}\ y^{-1}$	Annual (Pr) release (AFDW) $kJm^{-2}\ y^{-1}$
Torrybay Mid-tank level	0.44	160.6	8.91	4.95	2.96	63.31
Culross Mid-tank level	0.45	164.3	7.90	4.83	-	-
Culross field	0.61	222.7	10.71	6.55	-	-

4.95 mg AFDW per female y^{-1} was released which compares with 6.11, 4.83 and 2.97 mg AFDW y^{-1} by females from the upper shore at Aberdour, Culross and the lower Aberdour shore respectively (Tables 53 - 55). Using the laboratory value, as estimated 63.31 kJ m^{-2} y^{-1} was released by L. rudis at Torrybay which is more than 2 X the output on the upper shore at Aberdour and 16 X that on the lower shore (Tables 53 - 55).

On the upper shore at Aberdour an estimated 14.8% of the biomass was turned over annually as newborn (Pr : B = 27.08 kJm^{-2} y^{-1}/ 182.87 kJ m^{-2} = 0.148), whereas on the lower shore annual turnover was only about 10.3% of the biomass (3.86 kJ m^{-2} y^{-1}/ 36.12 kJ m^{-2} = 0.103) (Table 56). At Torrybay estimated reproductive turnover was almost three times greater than on the low-shore at Aberdour (63.3k kJ m^{-2} y^{-1}/ 218.30 = 0.290) and was comparable with values obtained by Grahame (1973a) for L. littorea (33.6%) and Hughes (1970) for low shore S. plana (31.3%). Other examples of the proportion of biomass turned over annually as reproductive production include 4.9% by Modiolus demissus (Dillwyn) (Kuenzler, 1961) and 59% in short-lived orabatid mites (Engelmann, 1961). Variation in the ratio of reproductive production to biomass (Table 56) is an example of the life history effect described by McNeill and Lawton (1970) and indicates that gamete production in relation to biomass generally falls in longer-lived animals.

The ratio of annual production of newborn, Pr to annual assimilation, A, gives the population reproductive efficiency (Table 56). Since assimilation values for L. rudis were not determined in this study, the value of 191.23 g^{-1} dry body weight per day

TABLE 56 Biomass, assimilation and reproductive yield in populations of L. rudis and four other invertebrates

SPECIES		Biomass (B) kJm^{-2}	Assimilation* (A) $kJm^{-2}y^{-1}$	Reproductive yield (Pr) $kJm^{-2}y^{-1}$	Ratio A/B	Ratio Pr/B	Ratio Pr/B	Authority
L. rudis	Aberdour 'H'	182.87	654.54	27.08	3.58	0.148	0.042	Present work
	Aberdour 'L'	37.57	129.81	3.86	3.46	0.103	0.030	
	Torrybay	218.30	786.51	63.31	3.60	0.290	0.081	
Littorina littorea		582.4	1915.8	195.8	3.39	0.336	0.102	Grahame (1973a)
Scrobicularia plana	Upper shore	80.9	302.3	17.6	3.69	0.217	0.058	Hughes (1970)
	Lower shore	856.2	2515.8	268.4	3.94	0.313	0.107	Hughes (1970)
Modiolus demissus		241.1	234.8	11.7	0.975	0.049	0.050	Kuenzler (1961)
Oribatid mites		1.13	8.63	0.67	7.60	0.590	0.078	Engelman (1961)

* Assimilation values were calculated using the data of Grahame (1973 b)

TABLE 56 Biomass, assimilation and reproductive yield in populations of *L. rudis* and four other invertebrates

SPECIES		Biomass (B) kJm^{-2}	Assimilation* (A) $kJm^{-2}y^{-1}$	Reproductive yield (Pr) $kJm^{-2}y^{-1}$	Ratio A/B	Ratio Pr/B	Ratio Pr/B	Authority
L. rudis	Aberdour 'H'	182.87	654.54	27.08	3.58	0.148	0.042	Present work
	Aberdour 'L'	37.57	129.81	3.86	3.46	0.103	0.030	
	Torrybay	218.30	786.51	63.31	3.60	0.290	0.081	
Littorina littorea		582.4	1915.8	195.8	3.39	0.336	0.102	Grahame (1973a)
Scrobicularia plana	Upper shore	80.9	302.3	17.6	3.69	0.217	0.058	Hughes (1970)
	Lower shore	856.2	2515.8	268.4	3.94	0.313	0.107	Hughes (1970)
Modiolus demissus		241.1	234.8	11.7	0.975	0.049	0.050	Kuenzler (1961)
Oribatid mites		1.13	8.63	0.67	7.60	0.590	0.078	Engelman (1961)

* Assimilation values were calculated using the data of Grahame (1973 b)

calculated by Grahame (1973b) for L. littorea was adopted. As L. littorea occupies a similar habitat and has similar feeding habits to those of L. rudis then the use of this figure as a first approximation is not unreasonable.

Annual assimilation in kJ m^{-2} y^{-1} was estimated as biomass gm^{-2} X 191.20 x 365. Assimilation values for the upper and lower shore sites at Aberdour and for Torrybay were estimated as 645.54, 129.81 and 786.5 kJ m^{-2} y^{-1} respectively. Using these values, the population reproductive efficiency at Aberdour becomes 4.2% (27.08 kJ m^{-2} y^{-1}/ 645.54 kJ m^{-2} = 0.042) on the upper shore and 3% (3.86 kJ m^{-2} y^{-1}/ 129.81 kJ m^{-2} = 0.030) on the lower shore. Reproductive efficiency at Torrybay (63.31 kJ m^{-2} y^{-1}/ 786.51 kJ m^{-2} = 0.081) was twice that at Aberdour indicating that the population at Torrybay devoted more energy to reproduction than to maintenance and growth than was the case at Aberdour (Table 56).

Annual reproductive outputs calculated from monthly brood-pouch loads (103.52 kJ m^{-2} y^{-1} at Aberdour 'H', 18.53 kJ m^{-2} y^{-1} at Aberdour 'L' and 139.52 kJ m^{-2} y^{-1} at Torrybay) were 2 - 5 X greater than those calculated from juvenile release (27.08 kJ m^{-2} y^{-1} at Aberdour 'H', 3.86 kJ m^{-2} y^{-1} at Aberdour 'L' and 63.31 kJ m^{-2} y^{-1} at Torrybay). This suggests either (a) release rates determined in this study were underestimates or (b) not all of the eggs entering the brood-pouch completed development to be released as juveniles. The closeness of the field and laboratory release rates (Tables 31, 32) indicates that reproductive outputs calculated from these values were fairly representative of actual output from the brood-pouch.

Counts of eggs in the brood-pouch probably represent less than a third of total monthly production as on average eggs develop to early veligers in approximately 8 days at 10°C and 32‰ salinity in the laboratory. Total monthly egg production will thus be about 3.5 X greater than numbers present at any given time. Observations of brood-pouch loads several times during one month discounted the possibility that sampling at the same time in the lunar month coincided with a single release of a batch of eggs into the brood-pouch. It is clear however, that only about a quarter of the expected number of eggs survive to the next developmental stage (Table 17 - 20). This suggests that either (a) egg mortalities/infertility was high, although little evidence of this was found in the *in vitro* studies of development (Tables 22, 24) or (b) fully developed juveniles awaiting release cannibalised the eggs or (c) some embryos were released at the veliger stage (Hannaford-Ellis (1978) reported the release of a small number of veligers in *L. rudis*)or (d) a high proportion of the eggs broke down and were resorbed or used to nourish the surviving eggs and embryos. Since it appears that developing embryos require supplemental nourishment to complete development, the production of extra eggs which act as "nurse eggs" may possibly provide this additional nourishment. The fate of eggs entering the brood-pouch is central to the full understanding of ovoviviparous development and productivity. In particular the success rate of egg development to pre-release juvenile, and the source and nature of apparent extra-capsular nourishment warrant further investigation.

From evidence presented in this thesis, we may construct a tentative model for prediction of numbers of juvenile *L. rudis*

emerging from the brood-pouch using counts of embryos at any given time. This may be described by the expression

$$BP_n \times \frac{t}{d_{T,S}} \times k$$

where BP_n = total number of embryos in the brood-pouch at any given time, t, t = time interval under consideration, $d_{T,S}$ = development rate at a given temperature (T) and salinity (S) and k is a constant representing the proportion of embryos developing successfully from egg to pre-release juveniles. From this work the value of k is between 0.2 and 0.5.

As embryos have been shown to vary significantly in weight between locations, then production estimates must take this into account. The equation may thus be modified to

$$(BP_n \times w_e) \times \frac{t}{d_{T,S}} \times k$$

where w_e = mean weight of an embryo.

A simple model of this type provides a rapid estimate of reproductive output and thus allows approximate comparisons between different localities. In addition, such a formula may hopefully focus attention on those aspects of reproduction in L. rudis which are not yet fully clear.

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Appendix 1 Condition of ovary and level of parasitism in female *L. rudis* from Aberdour 'H'

Month	n	Condition of ovary			Level of parasitism		
		Very full	Full	Reduced	Heavy	Medium	Negligible
Nov 1974	36	4	14	18	0	2	34
Dec	32	11	12	9	0	0	32
Jan 1975	27	19	6	2	0	0	27
Feb	32	28	0	4	0	2	30
Mar	28	16	10	2	0	0	28
Apr	32	14	18	0	0	0	32
May	31	25	6	0	0	0	31
June	30	11	19	0	0	0	30
July	29	5	24	0	0	0	29
Aug	29	0	21	8	0	2	27
Sept	33	3	16	14	0	3	30
Oct	30	0	10	20	0	2	28
Nov	31	8	10	13	0	0	31
Jan 1976	28	15	13	0	0	0	28
Mar	27	16	11	0	0	0	27
Apr	23	18	5	0	0	0	23
May	27	6	8	13	0	2	25
June	29	17	12	0	0	0	29
Aug	31	5	19	7	0	0	31
Oct	32	0	3	29	0	0	32
Dec	30	8	20	2	0	0	30

n = total number of females examined each month

Appendix 2 Condition of testis, level of parasitism and number of L. rudis from Aberdour 'H' with penis reduced (> 3mm).

Month	n	Reduced penis (3mm)	Condition of testis			level of parasitism		
			Very full	Full	Reduced	Heavy	Medium	Negligible
Nov 1974	26	5	4	12	10	1	3	22
Dec	22	5	13	3	6	2	0	20
Jan 1975	30	0	26	4	0	0	0	30
Feb	27	6	15	6	6	2	4	21
Mar	30	5	15	9	6	0	5	25
Apr	26	0	7	19	0	0	0	26
May	27	0	8	17	2	0	0	27
June	28	3	12	12	4	0	3	25
July	30	0	11	19	0	0	0	30
Aug	27	0	0	24	3	0	0	27
Sept	25	1	12	9	4	0	3	22
Oct	29	12	0	6	23	3	3	23
Nov	28	0	2	15	11	0	0	28

n = total number of males examined each month

Appendix 2 Condition of testis, level of parasitism and number of L. rudis from Aberdour 'H' with penis reduced (> 3mm).

Month	n	Reduced penis (3mm)	Condition of testis			level of parasitism		
			Very full	Full	Reduced	Heavy	Medium	Negligible
Nov 1974	26	5	4	12	10	1	3	22
Dec	22	5	13	3	6	2	0	20
Jan 1975	30	0	26	4	0	0	0	30
Feb	27	6	15	6	6	2	4	21
Mar	30	5	15	9	6	0	5	25
Apr	26	0	7	19	0	0	0	26
May	27	0	8	17	2	0	0	27
June	28	3	12	12	4	0	3	25
July	30	0	11	19	0	0	0	30
Aug	27	0	0	24	3	0	0	27
Sept	25	1	12	9	4	0	3	22
Oct	29	12	0	6	23	3	3	23
Nov	28	0	2	15	11	0	0	28

n = total number of males examined each month

Appendix 3 Condition of ovary and level of parasitism in female *L. rudis* from Aberdour 'L'

		Condition of ovary			Level of parasitism		
Month	n	Very full	Full	Reduced	Heavy	Medium	Negligible
Nov 1974	30	0	9	21	1	4	25
Dec	36	2	9	25	2	0	34
Jan 1975	28	0	7	21	0	3	25
Feb	27	16	11	0	0	0	27
Mar	29	17	4	8	0	0	29
Apr	31	6	23	3	0	0	31
May	29	23	6	0	0	0	29
June	31	9	22	0	0	0	31
July	28	8	9	11	2	4	22
Aug	32	3	15	14	3	0	29
Sept	32	0	5	27	0	0	32
Oct	30	0	0	30	0	0	30
Nov	28	2	10	16	2	2	24
Jan 1976	26	0	14	12	0	0	26
Mar	32	20	12	0	0	2	30
Apr	30	24	6	0	0	0	30
May	27	15	12	0	0	0	27
June	26	19	7	0	0	0	26
Aug	28	12	16	0	0	0	28
Oct	30	0	2	28	0	0	30
Dec	27	0	16	11	0	0	27

n = total number of females examined each month

Appendix 4 Condition of testis, level of parasitism and number of *L. rudis* from Torrybay with penis reduced (>3mm)

Month	n	Reduced penis (>3mm)	Condition of testis			Level of parasitism		
			Very full	Full	Reduced	Heavy	Medium	Negligible
Nov 1974	26	3	5	7	14	2	1	23
Dec	22	9	7	4	11	2	0	20
Jan 1975	27	7	3	12	12	6	6	15
Feb	27	5	15	6	6	6	3	18
Mar	31	16	4	10	17	15	3	13
Apr	25	15	4	3	18	10	4	11
May	27	9	14	6	7	9	0	18
June	25	10	10	10	5	5	0	20
July	27	10	0	19	8	8	0	19
Aug	25	14	0	6	19	5	6	14
Sept	27	7	0	3	24	0	5	22
Oct	26	6	0	3	23	2	1	23
Nov	27	7	4	4	19	2	0	25

n = total number of males examined each month

Appendix 5 Condition of ovary and level of parasitism in female *L. rudis* from Torrybay

		Condition of ovary			Level of parasitism		
Month	n	Very full	Full	Reduced	Heavy	Medium	Negligible
Nov 1974	28	0	1	27	0	7	21
Dec	31	22	3	6	0	0	31
Jan 1975	27	8	8	11	0	0	27
Feb	32	15	13	4	0	0	32
Mar	31	21	10	0	0	0	31
Apr	30	14	16	0	0	0	30
May	28	22	6	0	0	0	28
June	28	14	9	5	0	0	28
July	29	5	11	13	5	0	24
Aug	31	0	0	31	0	2	29
Sept	27	0	2	25	0	4	23
Oct	27	0	0	27	0	0	27
Nov	30	0	10	20	0	2	28
Jan 1976	30	0	19	11	0	0	30
Mar	31	10	21	0	0	0	31
Apr	28	16	12	0	0	0	28
May	27	11	16	0	0	0	27
June	30	6	16	8	0	0	30
Aug	26	2	11	13	0	0	26
Oct	26	0	1	25	0	0	27
Dec	30	0	2	28	0	0	30

n = total number of females examined each month

Appendix 6 Condition of testis, level of parasitism and number of *L. rudis* from Torrybay with penis reduced (>3mm)

Month	n	Reduced penis (3mm)	Condition of testis			Level of parasitism		
			Very full	Full	Reduced	Heavy	Medium	Negligible
Nov 1974	25	0	1	5	19	1	5	19
Dec	27	5	21	0	6	0	0	27
Jan 1975	28	7	7	6	15	3	2	23
Feb	26	7	17	2	7	2	5	19
Mar	28	3	9	16	3	3	0	25
April	28	4	12	12	4	0	0	28
May	25	5	18	4	3	3	2	20
June	22	5	8	10	4	4	0	18
July	29	8	0	17	12	4	4	21
Aug	26	15	0	2	24	0	13	13
Sept	30	13	0	2	28	2	12	16
Oct	26	4	0	0	26	1	5	20
Nov	27	6	0	6	21	0	4	23

n = total number of males examined each month

Appendix 7 Condition of ovary and level of parasitism in female *L. rudis* from Culross

		Condition of ovary			Level of parasitism		
Month	n	Very full	Full	Reduced	Heavy	Medium	Negligible
Nov 1974	28	13	9	6	0	0	28
Jan 1975	30	11	15	4	0	0	30
Feb	31	24	2	5	0	2	29
Mar	27	6	14	7	0	0	27
Apr	26	4	18	4	0	2	24
May	28	19	6	3	3	0	25
June	30	13	15	2	0	0	30
July	30	13	13	4	0	0	30
Aug	30	0	8	22	0	0	30
Sept	28	0	8	22	0	0	30
Oct	31	0	2	29	2	0	29
Nov	25	0	17	8	0	0	25
Jan 1976	29	7	10	12	0	0	29
Mar	30	22	8	0	0	0	30
Apr	28	24	4	0	0	0	28
May	29	25	4	0	0	0	29
June	28	9	16	3	0	0	28
Aug	28	6	14	8	0	0	28
Oct	25	0	0	25	0	0	25
Dec	27	2	11	14	0	0	27

n = total number of *L. rudis* examined each month

Appendix 8 Condition of testis, level of parasitism and number of *L. rudis* from Culross with penis reduced (>3mm).

Month	n	Reduced penis (3 mm)	Condition of testis			Level of parasitism		
			Very full	Full	Reduced	Heavy	Medium	Negligible
Nov 1974	27	3	2	12	13	2	10	15
Jan 1975	23	2	17	4	2	2	4	17
Feb	28	3	17	8	3	2	0	26
Mar	25	0	9	14	0	0	0	25
April	24	5	11	8	5	1	6	17
May	26	0	16	8	0	0	0	26
June	24	6	9	9	6	3	0	21
July	28	5	8	16	4	4	0	24
Aug	28	4	0	8	20	0	8	20
Sept	26	0	3	6	17	0	0	26
Oct	28	5	0	2	26	4	4	28
Nov	27	0	6	12	9	4	5	18

n = total number of males examined each month

II

ABBREVIATIONS AND CHEMICAL FORMULAE

I. Abbreviations

A.	Actinomyces
B.	Bacillus
c.	circa
cv.	cultivar
d	days
diam.	diameter
E	Enzyme
EM	Electron microscope
EPS	Extracellular polysaccharide
f	form
HR	hypersensitive response
lx	lux
min	minutes
NCPPB	National Collection of Plant Pathogenic Bacteria
OD	Optical density
P.	Pseudomonas
SDW	sterile distilled water
SEM	standard error of the mean
spp.	species
TCH	Trihydroxybenzoic
TLC	Thin layer chromatography

5. Chemical formulae

EtOH	Ethanol
H_2O_2	Hydrogen peroxide
$MgSO_4$	Magnesium sulphate
$Na_3(C_6H_5O_7)\cdot 5H_2O$	Sodium citrate
NaCl	Sodium chloride
NaOH	Sodium hydroxide
OsO_4	Osmium tetroxide
$Pb(NO_3)_2$	Lead nitrate