Some aspects of the ecology of the rough periwinkle Littorina rudis Maton (Gastropoda: Prosohranchia) at Marsden Bay,

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Some aspects of the ecology of the rough periwinkle *Littorina rudis* Maton (Gastropoda: Prosobranchia) at Marsden Bay.

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General Introduction

Representatives of the gastropod family Littorinidae, the periwinkles, are amongst the commonest members of the rocky-shore biota in most parts of the world. In Britain, only one genus is represented - Littorina - comprising four species: the edible periwinkle Littorina littorea (L.), the small "grape-pip" periwinkle L. neritoides (L.), the flat periwinkle L. littoralis (L.) and the rough periwinkle L. saxatilis (Olivi). Each of these species tends to occupy a definite position on the shore. The largest periwinkle, L. littorea, is usually found in the region between the Mean Low Water Mark of Spring Tides (MLWS) and the Mean High Water Mark of Neap Tides (MHWN) on shores which are not exposed to too great a degree of wave action. This species has a planktonic larval stage, and thus depends upon prevailing water currents for its distribution around the country. The flat periwinkle, L. littoralis, has no planktonic larval stage and occurs on that part of the shore occupied by the fucoid algae Fucus vesiculosus and Ascophyllum nodosum, whose bladders it closely resembles. This zone is very similar to that occupied by L. littorea ie. MLWS-MHWN on fairly sheltered shores.

The remaining two species are frequently so common among the upper-shore lichens as to form a characteristic "littorina-zone". The small L. neritoides is usually found on the more exposed coasts, and may extend up to sixty feet above the highest water mark (Lewis 1972). This species is dependent upon the sea for reproduction however, as it has a planktonic larval stage. The last species, L. saxatilis, is possibly the most widespread of the four geographically, and is the subject of this study. It is known to occupy almost all the levels on the shore, although it is usually at its most abundant in the upper half of the "barnacle-zone". It occurs on shores with very different patterns of exposure, and has been recorded on the Atlantic coast of North America from Labrador to Virginia, in Europe from the Arctic Circle to the Mediterranean, and on the Pacific coasts of N.America, Asia and Japan(Bequaert 1943).

L. saxatilis has long been the subject of taxonomic controversy. It exhibits many morphological variations in terms of shell shape and thickness (James 1964), and populations tend to show a wide range of colour patterns (Pettitt 1973). Although this species was described by various authors under no less than three generic and nineteen specific names between 1782 and 1893, it was Dautzenberg and Fischer (1912) who decided that only one species was in fact involved. They considered that this species, which they called Littorina saxatilis (Olivi), was "polymorphic" and consisted of six separate forms which did not intergrade, which they termed "subspecies", with several "varieties" in each. These are fully described by James (1968b), who has also based a key (James 1968a) upon the characteristics of the shell ie. the thickness (the density of the shell and contained animal), the shape (the shell length/breadth ratio), the spire height (shell length/aperture length) and the aperture width (aperture length/aperture breadth). The dimensions he uses are shown in figure 3. The overlap between many of these characteristics however, frequently makes an accurate identification to subspecies and variety almost impossible, since several forms often exhibit similar combinations of dimensions. Thus, while such authors as Thorson (1941), Seshappa (1948), and Fischer-Piette et.al. (1960, 1963, 1964, 1971) have contributed many observations on the variety of forms occuring on the British and European coasts, this taxonomic confusion could influence the ecological significance of their data. With a habitat as complex and variable as the seashore, the extrapolation of ecological data must depend all the more upon the accurate identification of the organisms concerned.

L. saxatilis was long thought to be the only viviparous member of the family Littorinidae, until Seshappa (1947) observed one variety laying eggs. Although the accuracy of this observation has been disputed (Mileikovsky 1975), Sacchi (1975) has raised to full species status one form of L. saxatilis (L. saxatilis subsp. rudis var. nigrolineata) as L. nigrolineata Gray, based upon a detailed study of its oviparous reproductive habit.

Another useful contribution to the taxonomic problem was provided by Heller (1975a) in his analysis of the subspecies and varieties of L. saxatilis in Britain. On the basis of conchological proportions, sculpturing, size of shell, range of colour patterns, anatomy of the genitalia and isozyme patterns, Heller determined that four separate species are represented. These are Littorina rudis Maton, L. patula Jeffreys, L. nigrolineata Gray and L. neglecta Bean. Full taxonomic descriptions and synonyms are given in Heller (1975a).

Whilst this controversy may well continue, Heller's concept of the classification into four species is a useful framework, and has been used throughout this study.

Each of the new species in Heller's classification tends, in turn, to occupy a distinct part of the shore. The most common species, L. rudis, usually occurs between the Mean High Water of Neap Tide Level (MHWN) and the Mean High Water of Spring Tide Level (MHWS) amongst the channelled wrack (Pelvetia canaliculata). L. patula, the most similar to L. rudis, tends to occupy a slightly higher level on the shore, amongst the black lichen Verrucaria spp. L.nigrolineata seems to occur in the region between Mid Tide Level (MTL) and the Mean High Water of Neap Tides, while L. neglecta, the smallest of the four, appears mainly to colonise small crevices and the cavities of dead barnacles around the Mid Tide Level. The absence of one or more species and different conditions of exposure may however alter these patterns considerably.

Emson and Faller-fritsch (1976) have observed that, despite its abundance on most shores, L. rudis has been the subject of few ecological investigations. This study has therefore concentrated upon one area of the North East coast of England in order to compare some aspects of the ecology of the populations of L. rudis which occur there with similar aspects reported in the literature for populations elsewhere. L. rudis, as defined by Heller (1975a), comprises many of the subspecies and varieties described by James (1968a) as being amongst the commonest members of L. saxatilis on most shores (especially L. saxatilis rudis). It is thus hoped that studies in the literature which have regarded L. saxatilis as comprising one single polymorphic species can be included in such a comparison, since they are likely to refer to populations comprised, at least in part, of individuals now known as L. rudis.

L. rudis is very abundant at Marsden Bay, and is characterised on this shore by a shell composed of four to six whorls with a generally pronounced sculpturing of narrow, prominent ridges and wide, shallow grooves. Many large individuals may, however, be worn almost smooth, but any repaired shell material resulting from damage is usually of this obviously sculptured pattern. The aperture is oval in shape, tending to be slightly broader towards the lower part. The colour of the organisms at Marsden is a fairly uniform dull grey, without any of the conspicuously coloured forms often recorded for the Welsh shores (Heller 1975b). The most characteristic feature used in the diagnosis of this species is the arrangement of the small glands on the penis. In L. rudis, the tip of the penis is elongated since the proximal gland is situated much more than its own width away from the exit of the sperm groove. The glands are small, and on this shore varied in number between five and fourteen in the specimens examined. The glands occur in a single row in all but one or two of these individuals.

The parameters investigated in this study have followed published data as far as possible in terms of methods and analyses to facilitate comparisons with other areas covered in the literature. These parameters include estimates of the abundance (with an examination of possible factors affecting the abundance), and studies of the sexual maturity, growth rates and longevity of the populations of L. rudis at three selected sites at Marsden Bay. Each of these parameters is dealt with in turn. A description of the study area, both geographical and biological, is included as the first part of this work.

Part One - The Study Area

1. The Location of Marsden Bay

This bay is situated on the North East coast of England, approximately three miles south of Tynemouth and adjacent to South Shields. The northern part of the bay, where the work was carried out, is located in National Grid one kilometre square NZ 3965 of the Ordnance Survey series for Great Britain, and is shown in figure 1.

2. The Nature of the Shore

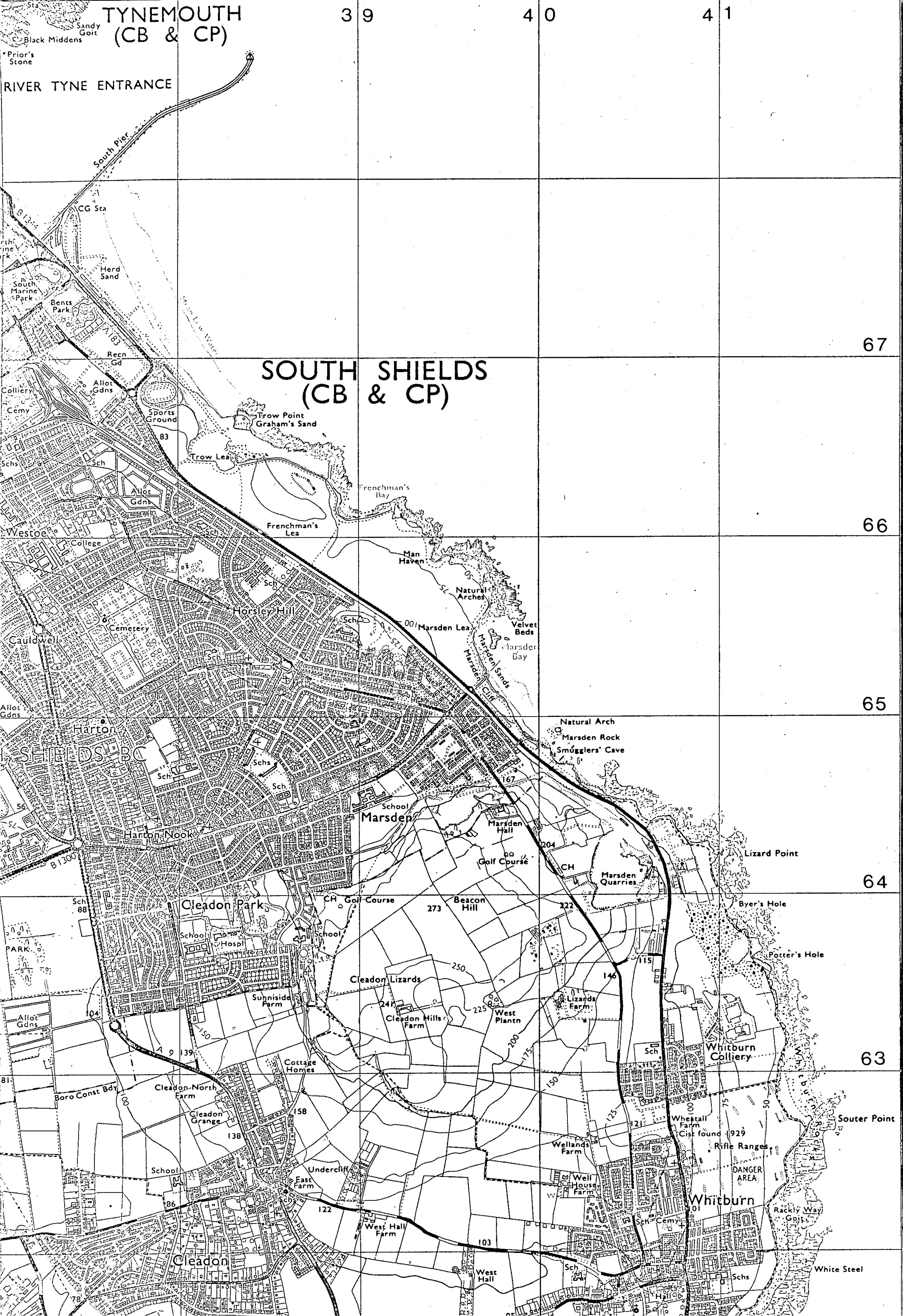
The underlying rock of this area is Magnesian Limestone, which characteristically weathers to form massive arches and caves (as typified by Marsden Rock to the south of the study area) and rough, broken platforms dissected by gullies and crevices.

The aspect of the shore is due East, facing a part of the North Sea that has been described as "chronically polluted" with industrial, colliery and domestic waste (Jones 1973). The effects of such pollution on the shore fauna have not been investigated in this study, but no direct visual evidence of pollution was noted.

The tidal range on this part of the coast is some eighteen feet, with a spring tide range of approximately fourteen feet and a neap tide range of approximately seven feet. The mean ranges are as follows, with heights expressed

Figure 1.

Extract from Ordnance Survey 1:25,000 series for Great Britain. Sheet NZ46 (South Shields).



TYNEMOUTH (CB & CP)
39
40
41
Sandy Goit
Black Middens
Prior's Stone
RIVER TYNE ENTRANCE
South Pier
CG Sta
Herd Sand
South Marine Park
Bents Park
Recn Gd
Allot Gdns
Colliery
Cemy
Sports Ground
67
SOUTH SHIELDS (CB & CP)
Trow Point
Graham's Sand
Trow Lea
Frenchman's Bay
Frenchman's Lea
Westoe
College
66
Man Haven
Natural Arches
Horsley Hill
Cemetery
Cauldwell
Marsden Lea
Velvet Beds
Marsden Bay
Marsden Sands
Marsden Cliff
65
Natural Arch
Marsden Rock
Smugglers' Cave
Harton
SHIELDS BC
Schs
Sch
School
Marsden
Marsden Hall
Harton Nook
Golf Course
CH
Lizard Point
Marsden Quarries
64
Cleadon Park
Golf Course
Beacon Hill
Byer's Hole
PARK
Hospl
Cleadon Lizards
Potter's Hole
Sunniside Farm
Lizards Farm
Allot Gdns
Cleadon Hills Farm
West Plantn
Whitburn Colliery
63
Cottage Homes
Boro Const Bdy
Cleadon North Farm
Cleadon Grange
Wheatall Farm
Cist found 1929
Souter Point
Rifle Ranges
Wellands Farm
DANGER AREA
Undercliff
East Farm
Well House Farm
Whitburn
Rackly Way Goit
West Hall Farm
Cemy
Cleadon
West Hall
White Steel
Hall

in feet above Chart Datum:

Mean High Water Spring Tides (MHWS)	16.4
Mean High Water Neap Tides (MHWN)	12.9
Mean Low Water Neap Tides (MLWN)	6.0
Mean Low Water Spring Tides (MLWS)	2.3

(Data from Admiralty Tide Tables Vol.I 1977)

3. The Algae and Fauna of the shore

A two-foot vertical interval transect was taken up a relatively unbroken part of the shore, from low water mark until no further intertidal life was encountered. The abundance of all macroscopic algae and fauna within a quarter square metre quadrat was estimated at each interval site using a scale modified after Ballantine (1961). For this, Ballantine's five point scale was replaced by a seven point scale (table 1) which gives greater flexibility where fewer organisms are present. The results of this survey are presented as tables 2 and 3, where the figures correspond to the abundance values of each section of table 1. A few isolated starfish were noted during general collections (chiefly Asterias rubens and one or two Henricia oculata), but crabs of all species were conspicuously absent.

Whilst the diagrams given by Ballantine (1961) are slightly inaccurate with regard to the ranges of many of his "indicator" species on the shore, the overall pattern of zonation at Marsden accords quite well with the typical

Table 1. The scale of abundance used to determine the distribution pattern of fauna and algae at Marsden Bay.

Lichens, Encrusting Algae and Sponges.

7 More than 80% cover.
6 50-80% cover.
5 20-50% cover.
4 1-20% cover.
3 Large scattered patches.
2 Widely scattered patches, all small.
1 Only one or two patches.

Seaweeds.

7 More than 90% cover.
6 60-90% cover.
5 30-60% cover.
4 5-30% cover.
3 Less than 5% cover, zone still apparent.
2 Scattered plants, zone indistinct.
1 Only one or two plants.

Littorina neritoides, young L.littorea, L.neglecta and barnacles.

7 More than 5 per sq.cm.
6 3-5 per sq.cm.
5 1-3 per sq.cm.
4 10-100 per sq decimetre
3 1-10 per sq decimetre, never more than 10 cm apart.
2 1-100 per sq metre, few within 10 cm of each other.
1 Less than 1 per sq metre.

Littorina littorea, L.rudis, L.littoralis and Patella spp.

7 More than 200 per sq metre.
6 100-200 per sq metre.
5 50-100 per sq metre.
4 10-50 per sq metre.
3 1-10 per sq metre
2 1-10 per sq decametre
1 Less than 1 per sq DECA metre

Topshells, Whelks, Anemonies and Chitons.

7 More than 100 per sq metre.
6 50-100 per sq metre.
5 10-50 per sq metre.
4 1-10 per sq metre, locally sometimes more.
3 Less than 1 per sq metre, locally sometimes more.
2 Always less than 1 per sq metre.
1 Less than 1 per sq decametre.

Mytilus edulis.

7 More than 80% cover.
6 50-80% cover.
5 20-50% cover.
4 Large patches, but less than 20% cover.
3 Many scattered individuals and small patches.
2 Scattered individuals, but no patches.
1 Less than 1 per sq metre.

Table 2. The pattern of distribution and abundance of marine algae at Marsden Bay (from a vertical interval transect carried out 26 / 4 / 77).

Tidal zones.	MLWS		MLWN			MHWN		MHWS			
Height (ft.) above Chart Datum.	2	4	6	8	10	12	14	16	18	20	22
Station no.	1	2	3	4	5	6	7	8	9	10	11
Ulva lactuca		2	2								
Laminaria digitata	4	3									
L. hyperborea	2										
Fucus serratus		6	4	2							
F. vesiculosus				4							
Ascophyllum nodosum			4								
Corallina officinalis		1									
Gigartina stellata	2	2	1								
Laurencia pinnatifida	2	1									
Lithothamnion sp	4	3	2								
Lomentaria articulata		1									
Ceramium rubrum	2	2	2								
Polyides rotundus	1	1									
Rhodymenia palmata	2	2									
Dilsea carnosa	4	2									
Porphyra umbilicalis			2	2							
Polysiphonia lanosa			2								
Verrucaria maura							3	4			
Lichina pygmaea						2	3				

Table 3. The pattern of distribution and abundance of the intertidal fauna of Marsden Bay (from a vertical interval transect carried out 26 / 4 / 77).

Tidal zones Height (ft.) above Chart Datum	2	4	6	8	10	12	14	16	18	20	22
Station no.	1	2	3	4	5	6	7	8	9	10	11
Actinia equina		4	4	4							
Balanus balanoides	4	4	4	4	4	3	2	1			
Patella sp	4	5	6	7	6	5	3				
Gibbula umbilicalis	4	4									
Littorina neglecta			2	2	2	2					
L. rudis					4	4	5	6	6	7	7
L. littorea		3	3	3	4	4	4	5	5		
L. neritoides				2	2	2	2	2	2		
Nucella lapillus		4	4	4							
Mytilus edulis		3	3	3							
Halichondria panicea	2	2									
Lepidochitona cinereus	4	4	4								

"exposed" shore (ie. grade 3) that he has documented from Wales. He describes this grade of shore as having Laminaria digitata abundant at or below the low water mark of spring tides, Alaria rare (one or two plants are occasionally found washed up at Marsden), Pelvetia rare on the seaward slopes, Fucus serratus occuring occasionally, and the other fucoids being largely absent. Lithothamnia and Corallina are common on such a shore, but barnacles (predominantly Balanus balanoides on this shore) and limpets (Patella spp.) dominate the mid-shore. Top shells are typically represented by Gibbula umbilicalis, Nucella is common on the open rock, and Mytilus is generally confined to cracks. Although not open to the two thousand miles of ocean that Ballantine suggests for the West coast exposed shores, the distribution of the algae and the fauna at Marsden Bay is in reasonable accord with this description.

4. The Study Sites

Much of the published work on the rough periwinkle has stressed the differences that may occur between populations at the top and bottom of the shore (Berry 1961, Bergerard 1971, Daguzan 1976a and 1976b, Moreteau 1976) and between bedrock areas and boulders (Emson and Faller-Fritsch 1976). Accordingly, three sites were chosen at Marsden Bay for the detailed study of L. rudis to represent as far as possible these extremes. These were as follows:-

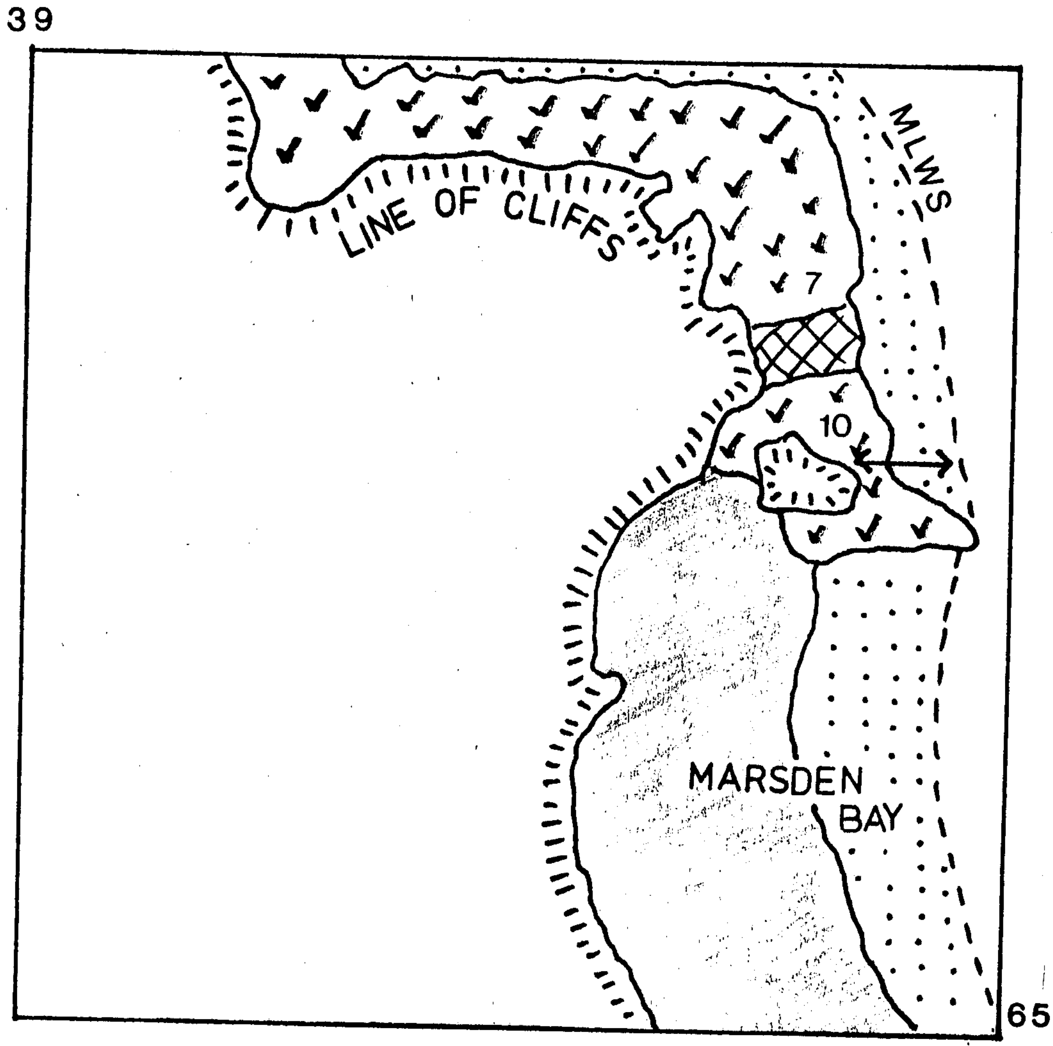
(A) The lowest station of the transect at which L. rudis was recorded in any quantity was used, and is refered to as Station 7. This was at a height of approximately fourteen feet above Chart Datum, just above the Mean High Water of Neap Tide Level.

(B) The highest of the transect stations that could be conveniently sampled was also used, and is referred to as Station 10. This was at a height of approximately twenty feet above Chart Datum, and was above the Mean High Water of Spring Tide Level.

(C) In addition, a group of boulders were selected from the region of broken rock marked on figure 2 (which also shows all of the sample sites and the line of the transect). The boulders were at a height of approximately sixteen feet above Chart Datum, and thus could offer a reasonable comparison with Station 7 on the bedrock.

The site of Station 7 was moved north from the line of the transect simply for convenience, since the rock offered better facilities for collecting. The pattern of zonation here was, however, identical to that of the original transect line.

Figure 2. The Study Area



Beach

100 YARDS.

Cliffs

7 Site of Station 7

10 Site of Station 10

Rock Platform

Area of kelps and broken rock

Boulders

MLWS Mean Low Water Spring Tide Level

⟷ Line of Transect

Part Two - The Abundance and Size Distribution of L. rudis

1. Introduction

Estimates of these two parameters have been shown to vary considerably, both between different shores and between different levels on the same shore. Values for the abundance of the rough periwinkle have varied from five to almost four thousand per square metre from shore to shore ie. Moore (1940) counted up to three thousand animals per square metre in Rum Bay, South Devon, but only four hundred per square metre nearby; Spooner & Moore (1940) counted eleven hundred per square metre in the Tamar estuary and in Iceland Thorson (1941) collected three hundred and seventy animals from an area of one tenth of a square metre; Fischer-Piette, Gaillard & James (1964) estimated values of between five and fourteen hundred on the shores they studied in Brittany and Spain, and Berry (1961) had estimates varying from forty to more than two hundred and sixty per square metre at Whitstable, Kent. In all of these estimates, the values have been shown to increase consistently towards the upper part of the tidal range. Whilst this part of the study deals with the measurement of the abundance of L. rudis at different parts of the shore at Marsden Bay, some possible explanations for these variations are considered in Part Three.

The variation in the mean shell length of the rough periwinkle from shore to shore has also been the subject of several studies. Berry (1961) observed that the average shell length of the animals he studied at Whitstable increased with height upshore. He attributed this to a variety of factors including the longer time available for feeding at these higher levels (he observed that these organisms tend to be fairly inactive when submerged) and more food being present there (based upon his observations that a richer algal growth occurred on his upper shore boulders than on his lower shore boulders). Additionally, many studies on the growth of the rough periwinkle have given the mean shell lengths of sampled populations on various shores, principally in Greenland and France (Thorson 1946, Moreteau 1976, Daguzan 1976b). These have suggested that shell lengths may attain as much as eighteen millimetres when the organism is fully grown, and suggest that sexual maturity is not usually reached until a shell length of ten millimetres. Whilst this subject is considered more fully in part five of this study, it is introduced here to illustrate the size distribution of the populations at Marsden Bay.

2. Methods

The abundance of L. rudis was estimated at each of the two-foot interval sites of the initial transect carried out on 26 / 4 / 77 (described in part one, page 8). All individuals within the quarter square metre quadrat which could be clearly identified as L. rudis were collected and counted. Those gastropods which could not be so clearly identified ie. young L. neglecta and young L. littorea, were ignored in this estimate. Care was taken to examine all the dead and empty barnacle cases and all the crevices within the rocks, and any algae were carefully searched to ensure that even the smallest individuals were recorded.

The length of each individual was then measured along the columellar axis (figure 3) with a pair of vernier callipers accurate to one tenth of a millimetre.

3. Results

The numbers of individuals at each site are recorded in table 4, expressed as numbers per square metre. The mean shell lengths, from all the measurements at each site, are presented in table 5.

4. Discussion

The values for the abundance of L. rudis at Marsden Bay can be seen to increase with height up-shore (table 4), thus following the general trend mentioned in the introduction to this section. Although little work has been documented on comparing the abundance of this organism on shores with different exposures, the overall pattern of distribution accords quite well with personal observations

Figure 3. *Littorina rudis:* Shell Measurements

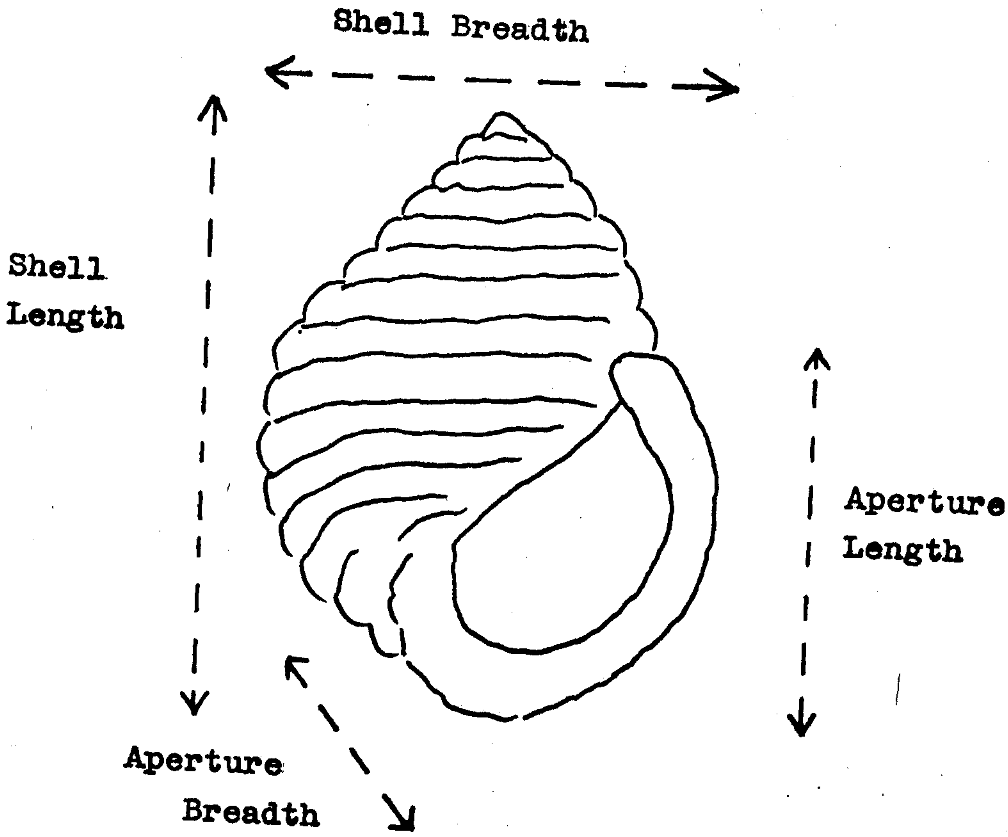


Table 4. The Abundance of L. rudis at Marsden Bay (from a transect carried out 26 / 4 / 77).

Station no.	5	6	7	8	9	10	11
Height above Chart Datum (feet)	10	12	14	16	18	20	22
Nos / m^2	24	60	172	432	648	1044	676

Table 5. The Mean Shell Lengths of L. rudis at Marsden Bay (samples taken 26 / 4 / 77).

Station no.	5	6	7	8	9	10	11
Height above Chart Datum (feet)	10	12	14	16	18	20	22
Mean Length (mms) ± S.D.	4.4 ±1.0	5.6 ±1.7	5.0 ±1.5	5.6 ±1.3	5.9 ±1.3	8.1 ±1.5	6.3 ±1.5
No. Indvls. Measured	6	15	43	108	162	261	169

made in the past on shores of similar exposure elsewhere.

The maximum shell lengths of L. rudis at Marsden are less than those quoted for other shores, ie. Moreteau (1976) gives an "ultimate" shell length of eighteen point five millimetres for the populations he studied in Brittany France, Daguzan (1976b) gives eighteen point six millimetres, and James (1968b) suggests that up to twenty four millimetres may be attained on some sheltered shores in Britain. However, the same general trend of size distribution mentioned by these authors (ie. with the shell length increasing with height up-shore) is noticeable at Marsden (table 5).

The largest individual encountered during this study measured less than twelve millimetres in length, yet as mentioned in parts four and five sexually mature individuals are found on this shore with shell lengths well below this (between three and four millimetres). The relationship between shell length and exposure is poorly known, other than a general observation that the largest shells seem to occur on the most sheltered shores (Ballantine 1961, James 1968b). Heller (1976) has studied the influence of exposure and predation on the shell shape of some British populations of winkles, and has suggested that small shells may in fact be favoured on exposed shores. He considers that they would be better able to make use of the shelter afforded by such habitats as empty barnacle cases and small crevices than would larger shells which would thus suffer more from the effects of wave action and predation. At

Marsden however, the abundance of crevices and cracks of all sizes is such that few individuals could fail to find shelter.

5. Conclusions

(i) At Marsden Bay, the levels on the shore occupied by populations of L. rudis extend between approximately ten and twenty two feet above Chart Datum ie. from approximately Mid Tide Level to high above Mean High Water Spring Tide Level.

(ii) The abundance of L. rudis between April and July 1977 varied between approximately twenty four and one thousand and forty four per square metre over this vertical range, and increased progressively towards the upper part of the shore.

(iii) The mean shell lengths varied between four point four millimetres and eight point one millimetres during this same period, again showing a tendency to increase towards the upper part of the tidal range.

Part Three - Some Factors Affecting the Abundance of L. rudis

1. Introduction

As mentioned in part two of this study, values for the abundance of the rough periwinkle are very variable both from shore to shore and between different levels on the same shore. Various authors have contributed suggestions as to why this should be so.

Ballantine (1961) suggested that on at least one shore which he studied in South Wales, the smoothness of the rock surface - and hence the lack of suitable areas for attachment and protection - may have influenced the abundance and pattern of distribution of the periwinkles.

Emson and Faller-Fritsch (1976) demonstrated the importance of crevices in the rock surface by increasing the number of habitats available on a shore in Sussex, England. By drilling holes into the chalk boulders making up the shore they were able to show that the numbers of periwinkles per unit area could be increased by as much as five hundred and fifty percent. They also noted that the actual sizes of the organisms increased as larger habitats became available. Another important part of their work was to investigate a point made by Berry (1961) that food may prove to be a limiting factor on certain parts of the shore. This, it was assumed, could result in increased growth at the preferred levels leading in turn to an increased breeding potential.

As the estimation of habitat availability, in terms of mumbers of crevices etc., is both difficult and some what subjective, this part of the study has concentrated upon the possibility that on the shore at Marsden, food may be a limiting factor affecting the abundance of L. rudis. A discussion of all of these possible mechanisms is included, together with the roles of migration and predation.

2. Methods

The method used by Emson and Faller-Fritsch (1976) to determine if food availability may prove to be limiting to abundance has been followed here. This method compares the relationship between the shell length and the tissue dry weight of periwinkles at different points on the shore. The underlying principle presumes that for any two such points, the regression value of the tissue dry weight on the shell length of a well fed population will be significantly different from that of a poorly fed population. Although both parameters are known to be highly variable, it is hoped that any general trends would be detected.

Thus, from the collections of organisms used for the estimates of growth and longevity (part five), subsamples of fifty individuals were removed from each sample site (stations 7 and 10, and the boulder area) during each of the months of May, June and July 1977. Each individual was killed by a short immersion in boiling water, and was then measured along the columellar axis (figure 3) using a binocular microscope with a graticule accurate to one tenth of a millimetre. The shell was then broken along this axis and the animal removed, careful inspection with the same microscope ensuring that no tissue remained behind. The organism, minus its shell and operculum, was then dried to constant weight at seventy degrees centigrade. Weighing was carried out on a standard laboratory balance accurate to one tenth of a milligram.

The regression coefficient "b" of the tissue dry weight on the shell length was then determined from the standard formula of $b=c/Sx^2$ (Bailey 1975) where:

$$Sx^2 = \frac{\Sigma(x^2) - (\Sigma x)^2/n}{n-1} \quad \text{and}$$

$$c = \frac{\Sigma(xy) - \frac{(\Sigma x)(\Sigma y)}{n}}{n-1} .$$

The intercept was determined from:

$$q = \bar{y} - b\bar{x}.$$

An arithmetic plot yielded a curvilinear relationship, so the values of shell length (x) and tissue dry weight (y) were transformed to logarithms (base 10).

The regression coefficients calculated for each of the sample sites during each of the months of May, June and July were then compared with the assumption that the difference between any two estimates would be equal tb the sum of their individual variances ie.

$$d = \frac{b_1 - b_2}{\sqrt{\dfrac{S_1^2}{\Sigma x^2 - \frac{1}{n}(\Sigma x)^2} + \dfrac{S_2^2}{\Sigma x^2 - \frac{1}{n}(\Sigma x)^2}}}$$ and where

$$S^2 = \frac{1}{n-2}\left[\Sigma y^2 - \frac{(\Sigma y)^2}{n} - \frac{\left(\Sigma(xy) - \frac{(\Sigma x)(\Sigma y)}{n}\right)^2}{\Sigma x^2 - \frac{1}{n}(\Sigma x)^2}\right].$$

If the numerical value of "d" (ie. irrespective of the sign) was found to be greater than 1.96, it was assumed that a significant difference existed between the two estimates (at the five percent level).

3. Results

The data used for the estimates of the regression coefficients for each sample site in each month of the study are presented in the Appendix as tables I - IX.

The actual regression lines are plotted on figures 4 - 12, to illustrate the spread of the measurements taken.

The values of the regression coefficient "b", and the values of S^2 and of the term $\Sigma x^2 - \frac{1}{n}(\Sigma x)^2$ for each sample site during each month are presented as table 6. For convenience, this expression has been shortened to $\Sigma(x-\bar{x})^2$ in table 6.

The comparisons of the regression coefficients are presented as table 7.

Table 6. Values for the Regression Coefficients of Tissue Dry Weight on Shell Length for Sub Samples of *Littorina rudis* at Marsden Bay.

Station		May 1977	June 1977	July 1977
	Regression Coefficient	3.44	2.16	2.33
7	s^2	0.015	0.042	0.012
	$\Sigma(x-\bar{x})^2$	0.23	0.83	0.68
	Regression Coefficient	2.15	2.17	2.43
10	s^2	0.013	0.024	0.008
	$\Sigma(x-\bar{x})^2$	0.53	1.12	0.33
	Regression Coefficient	2.37	1.96	2.00
Boulder	s^2	0.033	0.031	0.140
	$\Sigma(x-\bar{x})^2$	0.39	1.11	0.50

Table 7. Comparisons of the Regression Coefficients of Tissue Dry Weight on Shell Length for Sub Samples of *Littorina rudis* at Marsden Bay.

Coefficients compared		Value of "d"
Boulder, May	: Boulder, June	1.20
Boulder, June	: Boulder, July	-0.07
Station 10, May	: Station 10, June	-0.09
Station 10, June	: Station 10, July	-1.23
Station 7, May	: Station 7, June *	0.54
Station 7, June	: Station 7, July	-0.65
Station 7, June	: Station 10, June	-0.04
Station 7, June	: Boulder, June	0.71
Station 10, June	: Boulder, June	0.95
Station 7, July	: Station 10, July	-0.50
Station 7, July	: Boulder, July	0.60
Station 10, July	: Boulder, July	-0.78

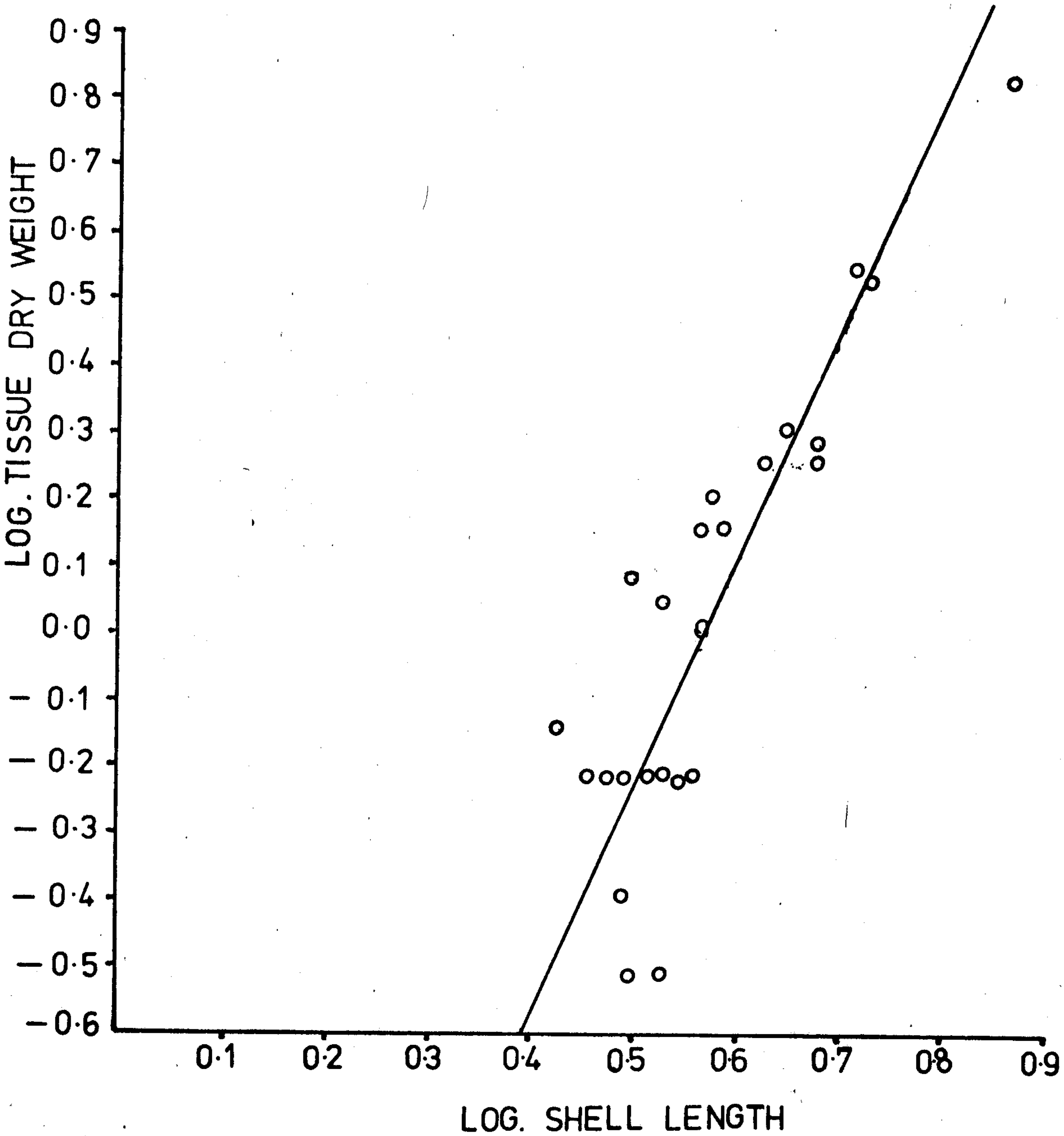
* In this comparison the sample size was below thirty, therefore the following expression was used (Bailey 1975):

$$t = \frac{b_1 - b_2}{S\sqrt{\frac{1}{\Sigma(x-\bar{x})^2} + \frac{1}{\Sigma(x-\bar{x})^2}}} \quad \text{where}$$

$$S^2 = \frac{(n_1 - 2)\, S_1^2 + (n_2 - 2)\, S_2^2}{n_1 + n_2 - 4}$$

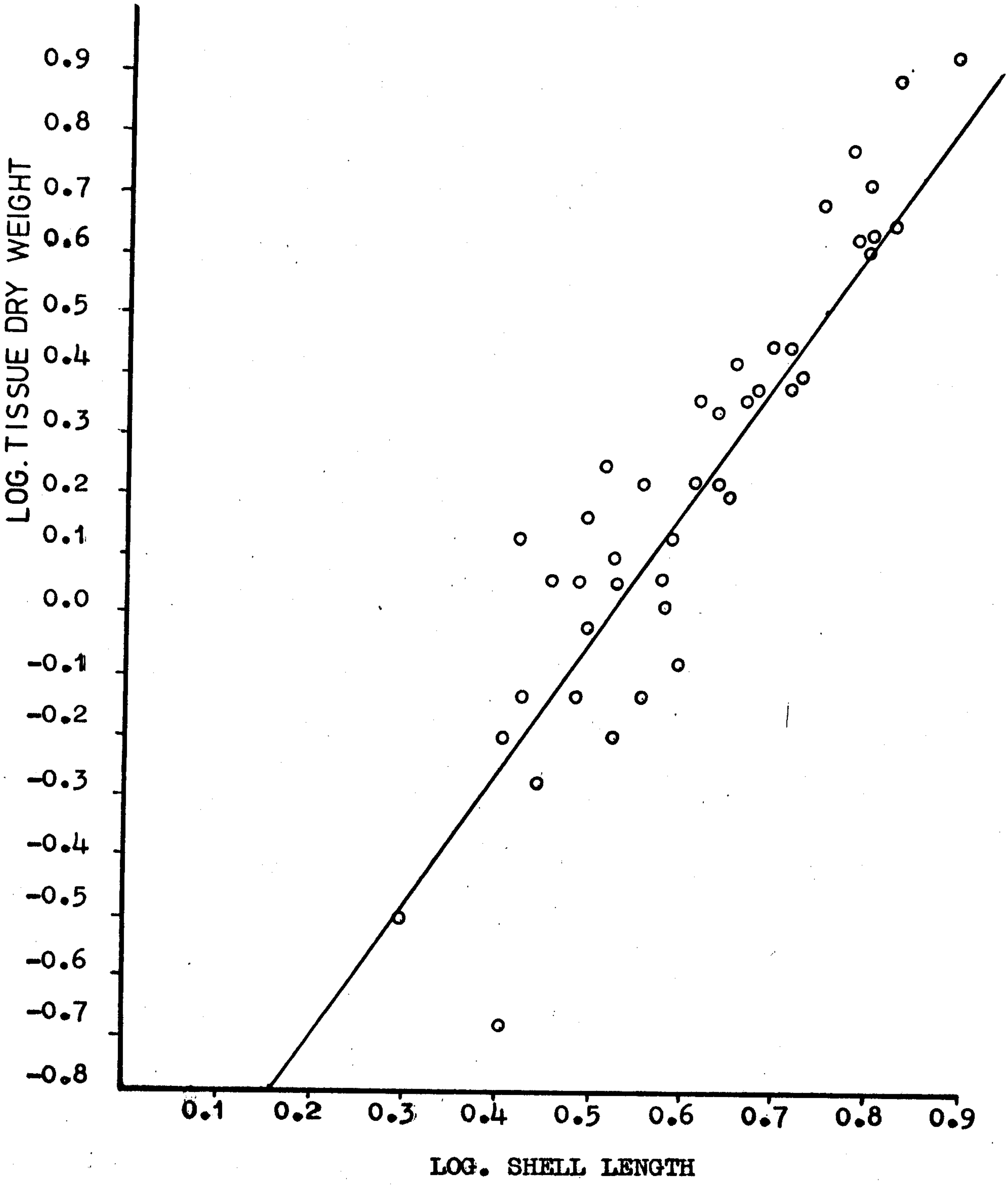
($S = 0.18$).

Figure 4. Plot of Log. Shell Length against Log. Tissue Dry Weight with fitted regression line. Station 7. May 1977.



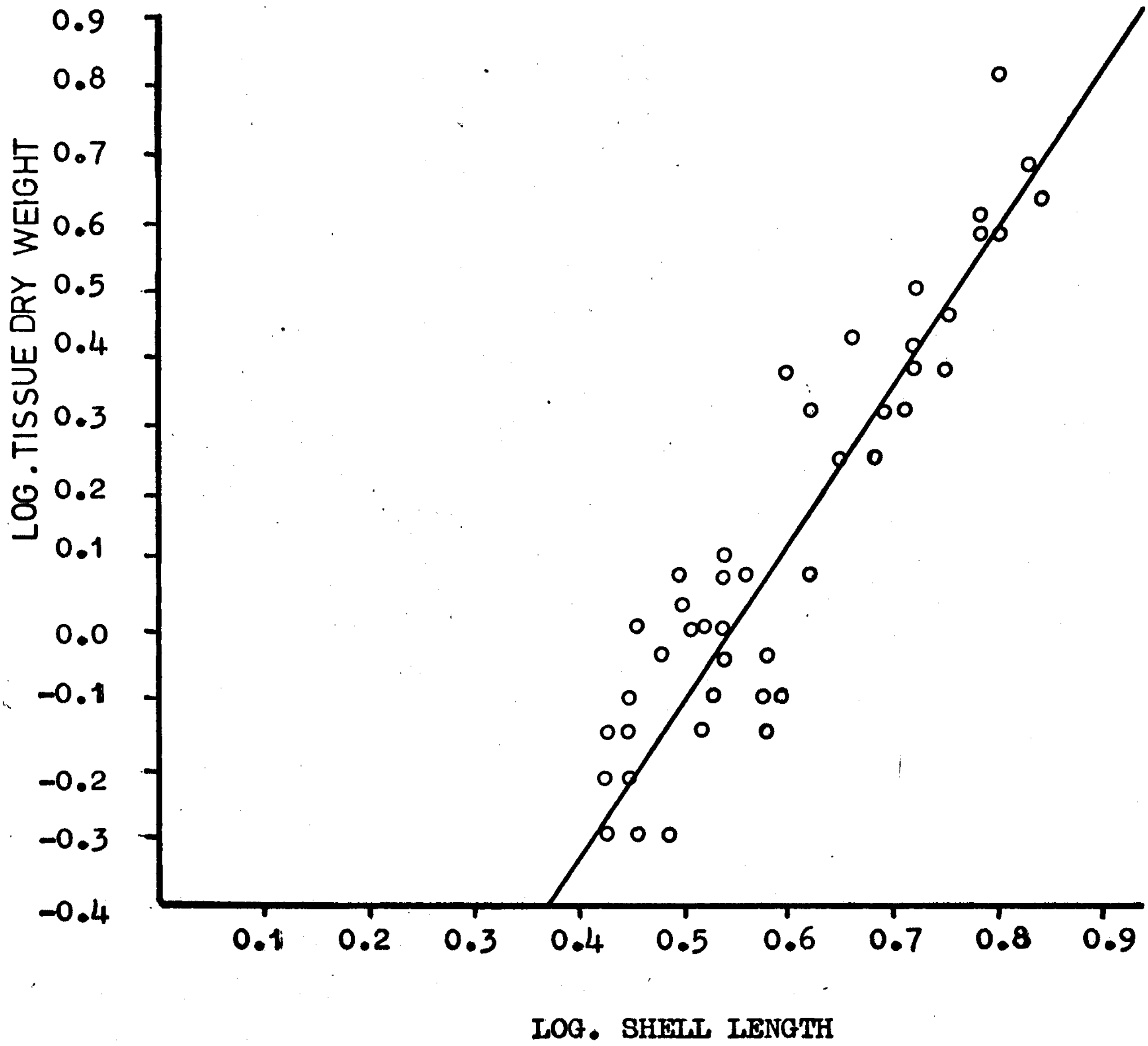
Log.y = 3.44 log.x -1.95

Figure 5. Plot of Log. Shell Length against Log. Tissue Dry Weight with fitted regression line. Station 7. June 1977.



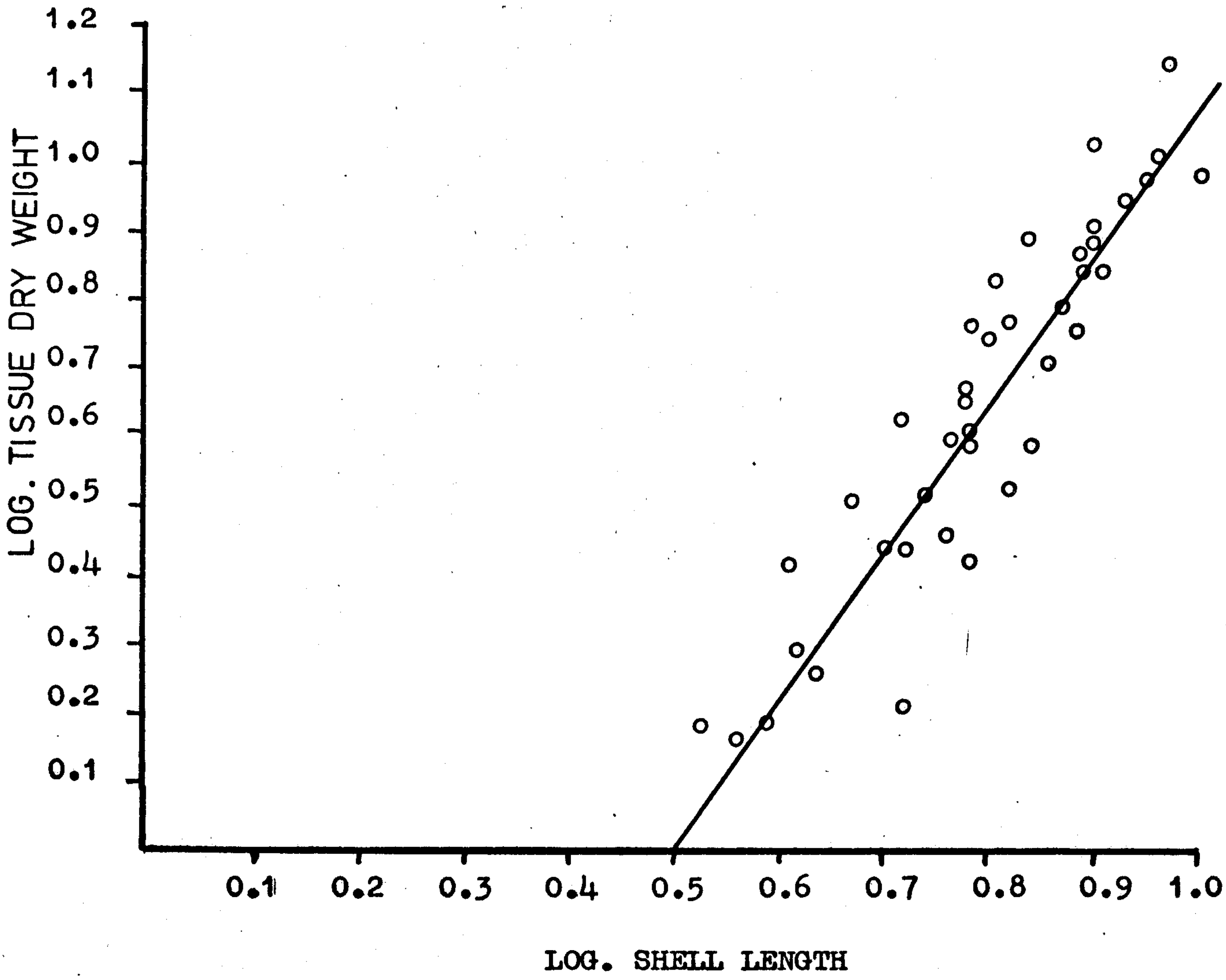
Log. y = 2.16 log. x - 1.13

Figure 6. Plot of Log. Shell Length against Log. Tissue Dry Weight with fitted regression line. Station 7. July 1977.



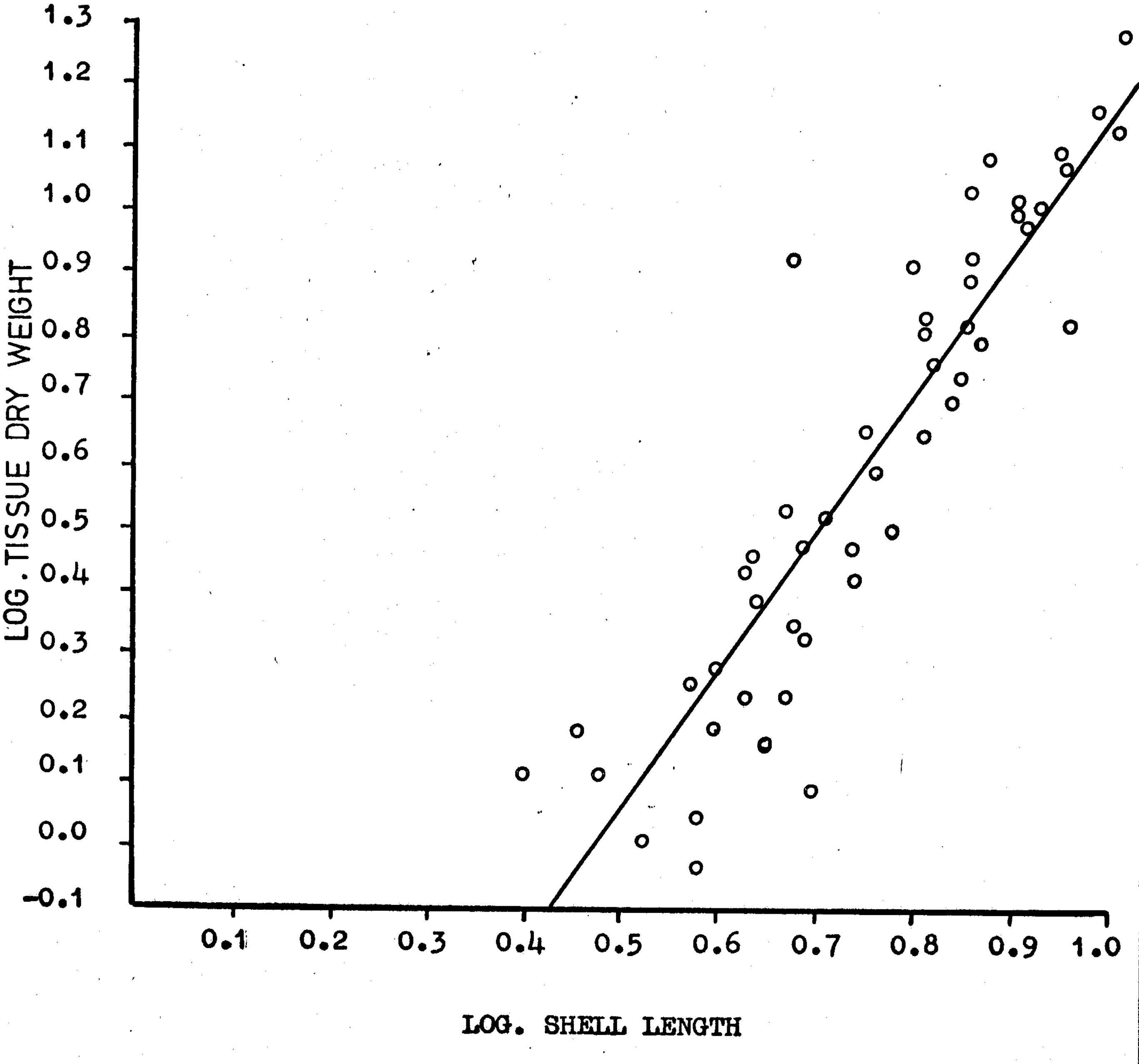
Log. y = 2.33 log. x - 1.26

Figure 7. Plot of Log. Shell Length against Log. Tissue Dry Weight with fitted regression line. Station 10. May 1977.



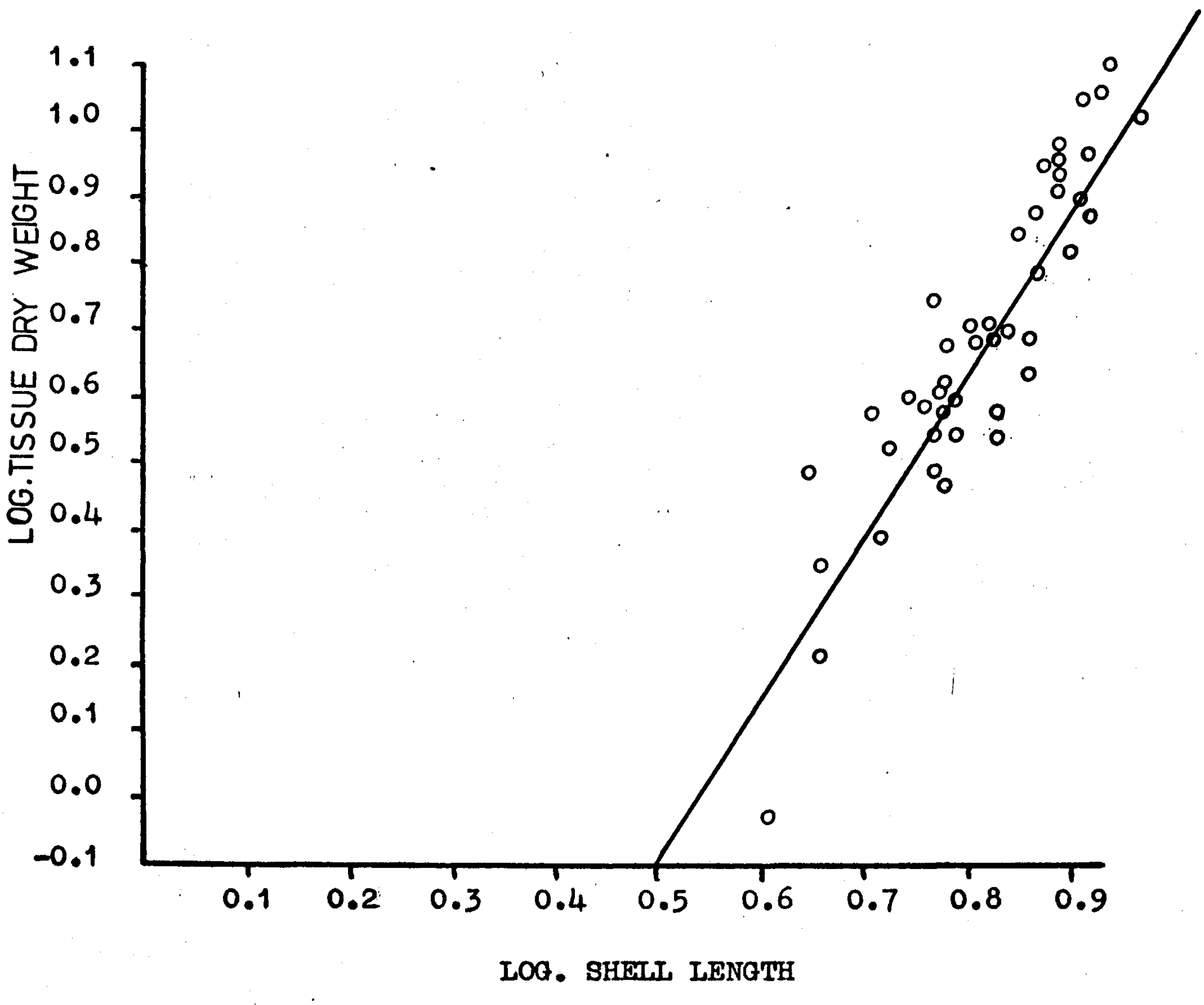
Log. y = 2.15 log. x - 1.07

Figure 8. Plot of Log. Shell Length against Log. Tissue Dry Weight with fitted regression line. Station 10. June 1977.



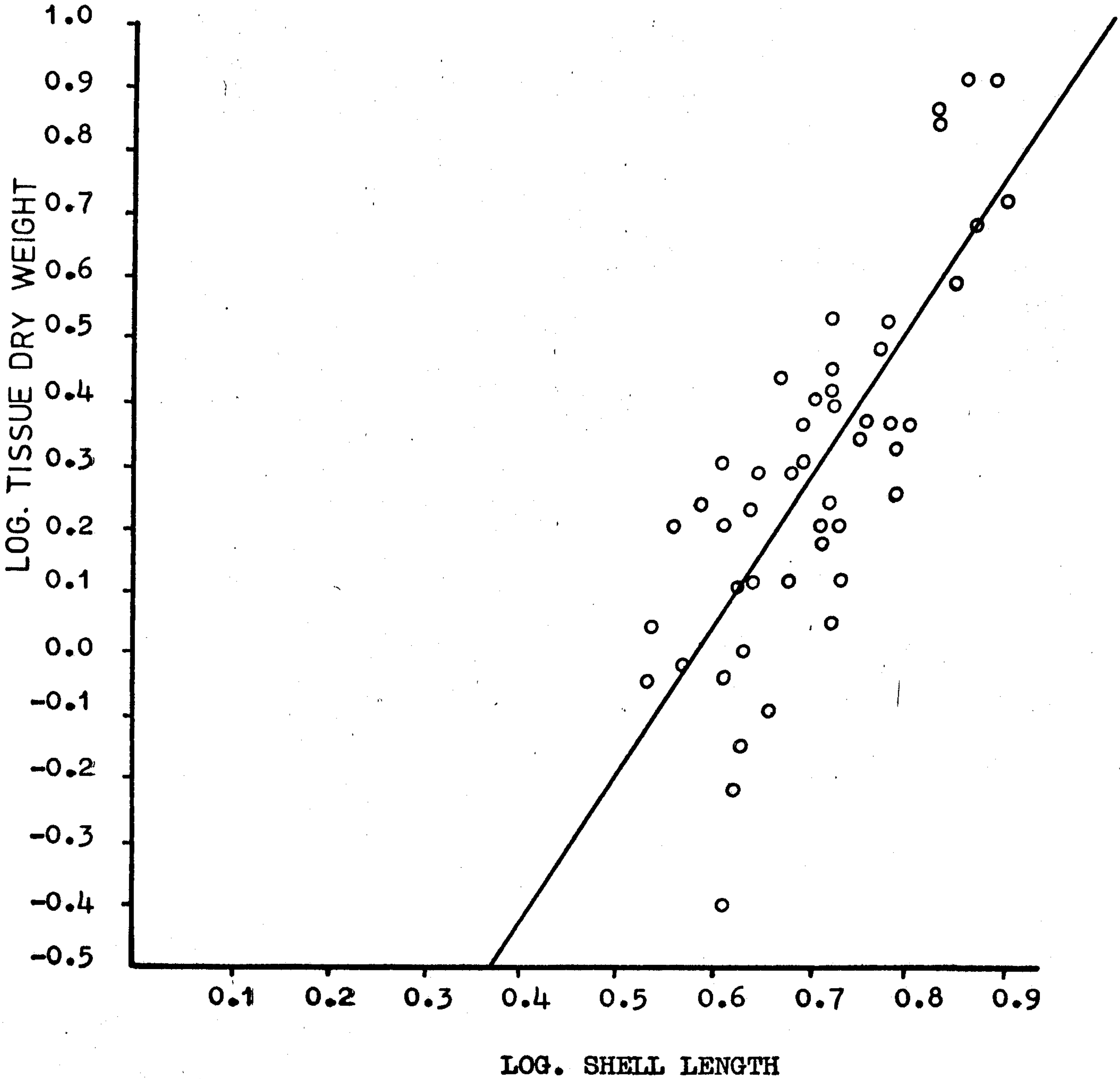
$$\text{Log. } y = 2.17 \text{ log. } x - 1.03$$

Figure 9. Plot of Log. Shell Length against Log. Tissue Dry Weight with fitted regression line. Station 10. July 1977.



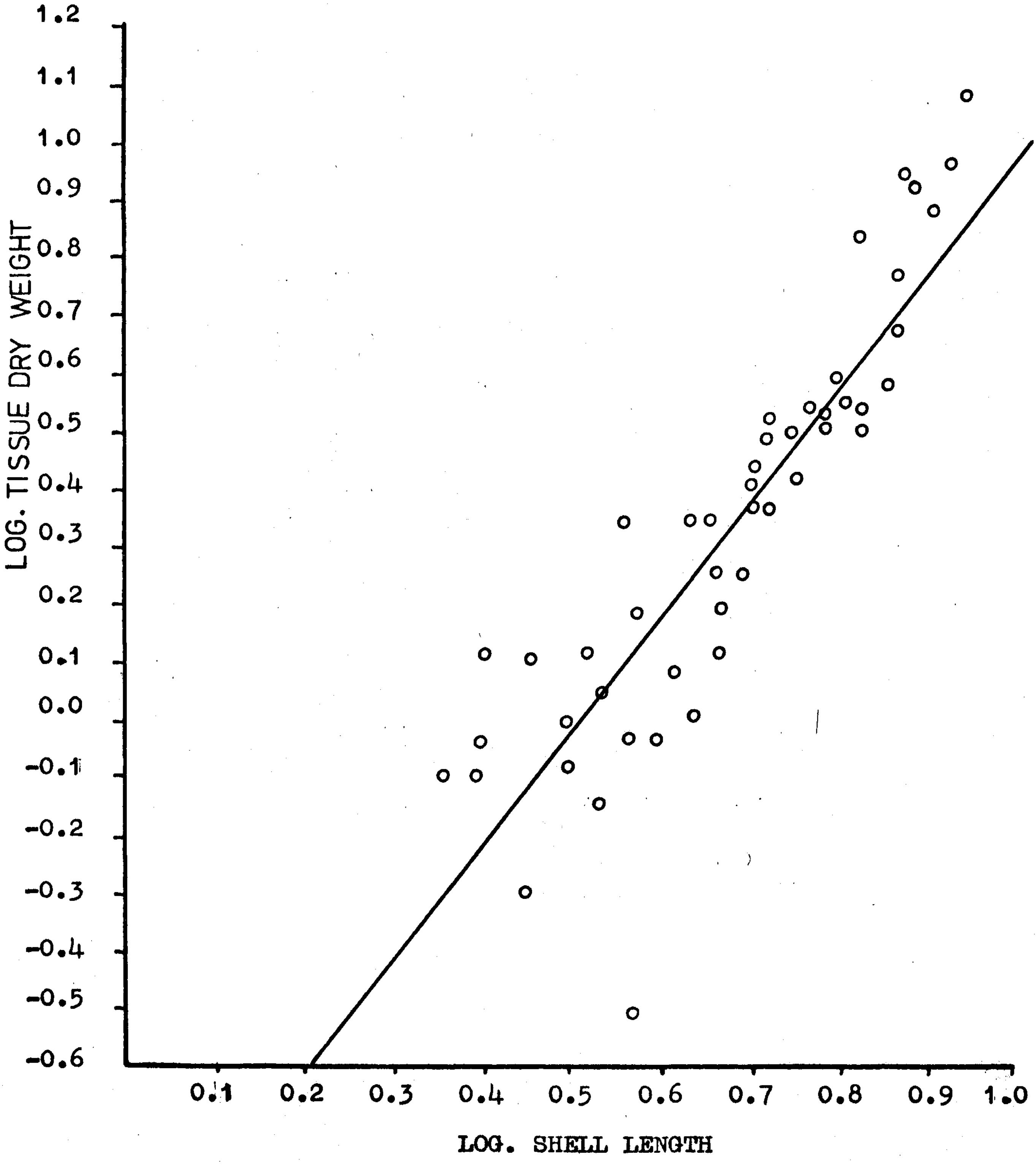
Log. y = 2.43 log. x - 1.30

Figure 10. Plot of Log. Shell Length against Log. Tissue Dry Weight with fitted regression line. Mid shore Boulders. May 1977.



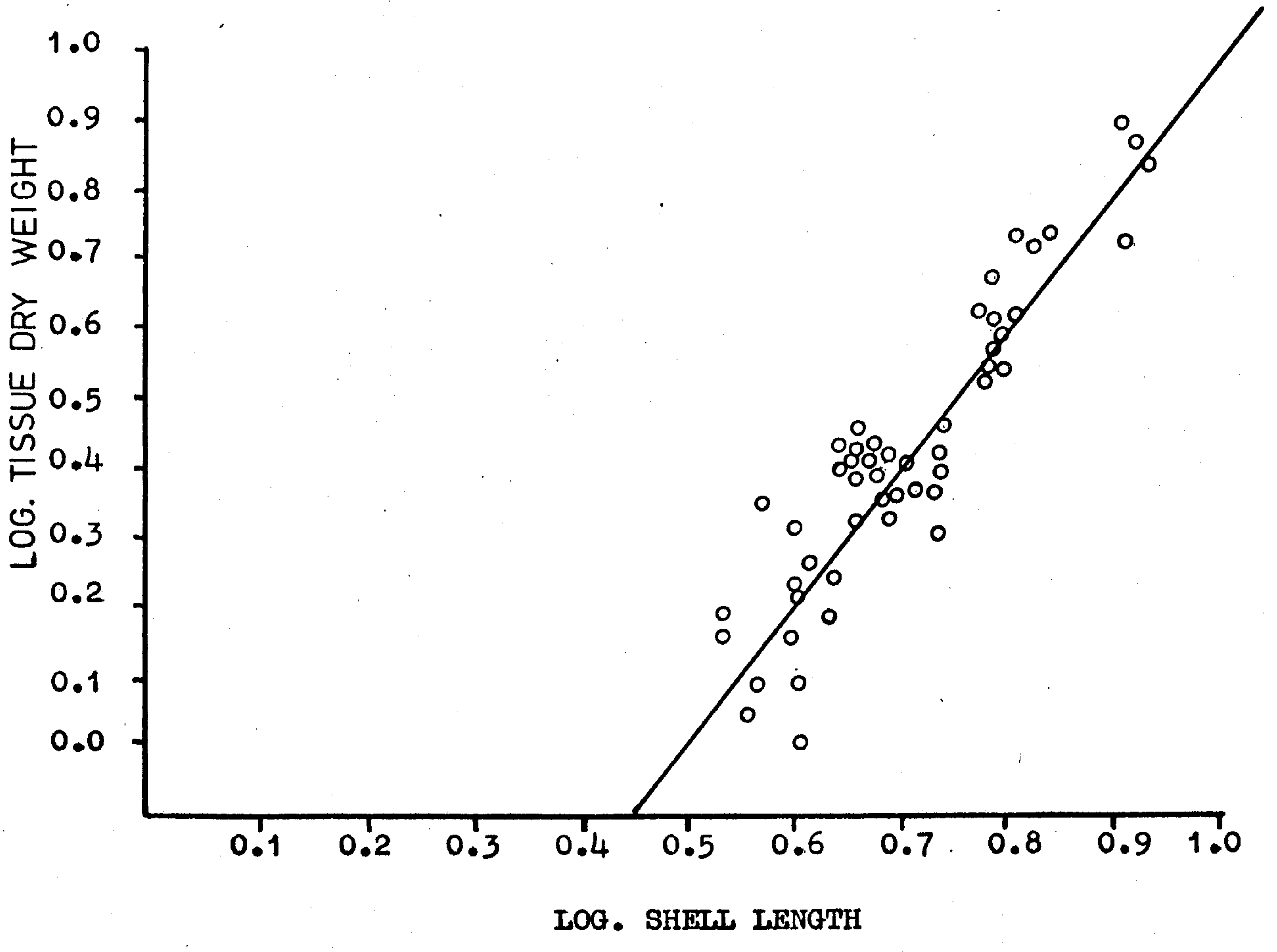
Log. y = 2.37 log. x - 1.37

Figure 11. Plot of Log. Shell Length against Log. Tissue Dry Weight with fitted regression line. Mid shore Boulders. June 1977.



Log. y = 1.96 log. x - 1.00

Figure 12. Plot of Log. Shell Length against Log. Tissue Dry Weight with fitted regression line. Mid shore Boulders. July 1977.



Log. y = 2.00 log. x - 1.00

4. Discussion

James (1968b) has shown that the rough periwinkle normally undertakes only limited migrations, but in his detailed study of the Whitstable shore Berry (1961) considered that a passive upshore migration of periwinkles might take place. He suggested that the young individuals, being small and light, may simply float up with the rising tide to be deposited at a higher level on the shore. Whilst being difficult to prove or disprove on the large scale, observations made on the shore at Marsden with a rising tide on a calm day, did show that small individuals (with a shell length below approximately four millimetres) had a tendancy to float if unprotected by a crevice overhang. Buoyed, usually, by an air bubble in the aperture, many of these individuals were seen to float for some minutes but generally sank again often coming to rest below the level from which they started. Larger individuals were not observed to float so readily. However, on a shore as exposed as Marsden, few individuals would be in a position to take advantage of a gently rising tide since prolonged wave action would seem to encourage most of them to dwell in protected crevices and cracks rather than on the bare rock surface.

Equally at Marsden, estimation of the significance of habitat availability is difficult since the entire rock surface is pitted with cavities and cracks of all sizes. Whilst the numbers of barnacles increase slightly with height up-shore, and hence the number of empty cases left by dead individuals also increases up-shore, the wealth of natural habitats would seem to dwarf their importance. In fact, general observations made whilst collecting would indicate that only about twenty five percent of the available barnacle cases were occupied on this shore - many by the small L. neglecta (especially around the Mid Tide Level). Thus on the shore at Marsden, habitat availability would seem unlikely to be a factor limiting the abundance of L. rudis, although as stated by Emson and Faller-Fritsch (1976) "the probability that an animal will encounter a suitable crevice after a feeding excursion must decrease as winkle density increases and limitations may be imposed on the population at densities much lower than those which might utilise all crevices".

The bulk of this part of the study has been made up of a series of comparisons between the regression coefficients of tissue dry weight on shell length for populations of L. rudis at three different parts of the shore at Marsden Bay over the months of May, June and July 1977. The results indicate that for any given shell length at any two of these sample sites, the dry weights of the animals tissues will not be significantly different. Differences are not detected between the sample sites in any of the months of the study, and no differences are detected for any of the sample sites between the months of the study. In all, therefore, it would appear that food was not a limiting factor affecting the abundance of L. rudis at Marsden Bay during this period. Although this method has only a limited sensitivity, often depending on very small differences between the tissue dry weights of the organisms to yield significant results, it is hoped that any broad trends could be predicted between the sites examined. One principal drawback with this method however, is its inability to estimate the food availability over the shore as a whole unless comparisons are made with many other shores at the same time. Values such as those in table 7 could also be obtained if food was limiting at every station, but in fact, many parts of this shore became well covered by microscopic green algae towards the end of the study period, and imparted, from a distance, a greenish tinge to many areas of rock. Large clumps of Enteromorpha spp. were common, even on the boulders, and gave good visual evidence of potentially abundant food for grazing herbivores.

Although many organisms have been shown to prey upon Littorina species (Pettitt 1975), the role of predation in keeping down population numbers is difficult to assess in this case. As mentioned in part one of this study, crabs are conspicuously absent from the shore at Marsden - at least at low water. However, the type of damage often attributed to crabs (Heller 1976) was noticeable on some five to ten percent of the shells of L. rudis examined. This damage (usually in the form of a chip removed from the central part of the outer lip of the shell) was observed on shells of all lengths at Marsden, often well repaired by the gastropod, but usually of a slightly different colour from the rest of the shell. Predation by birds cannot be ruled out on this shore due to the presence of large numbers of gulls in the region of Marsden Rock approximately half a mile from the study area. Although no such predation was actually observed on the shore, quantities of shells of *L. rudis*, broken across the columellar axis, were frequently found at the higher sample site, especially after periods of calm weather. However, since considerable difficulty was usually experienced in removing periwinkles from their crevices for examination during this work, it is not felt that the gulls would gain sufficient reward for the energy expended by this method of feeding.

Predation by man is also possible, since the shore at Marsden is popular with tourists. Large edible periwinkles (*L. littorea*) are abundant on this shore (sizes in excess of three centimetres are not uncommon) and it is possible that if these are collected in any quantity, then some large specimens of *L.rudis* may be taken as well. It is, however, very difficult to assess the significance of this factor in affecting the overall pattern of distribution and abundance of *L. rudis* in the long term.

Predation by fish - especially by the Blenny (*Blennius pholis*) - may be a little more common at high tide, and periwinkle shell fragments have often been observed in small pools at all levels on the shore where these organisms occur together.

5. Conclusions

(i) Although a passive upshore migration of small individuals is seen to be possible, it is not felt that this will significantly affect the pattern of distribution or abundance of *L. rudis* on this shore.

(ii) The abundance of natural crevices of all sizes on this shore would suggest that habitat availability is unlikely to operate as a factor limiting periwinkle numbers. The role of empty barnacle cases as habitats is not seen to be vital for the populations on this shore.

(iii) As judged by comparisons of the regression coefficients of tissue dry weight on shell length, the abundance of food is not seen to be a limiting factor at any of the sample sites during the period of study.

(iv) The role of predation is difficult to assess, but the effects of crabs, gulls, man and fish cannot be ruled out. These may operate in isolation or in combination at any level on the shore.

Part Four - The Sexual Maturity of L. rudis during the Study Period

1. Introduction

L. rudis is one of three ovoviviparous members of the family Littorinidae occuring in the British Isles, together with L. patula and L. neglecta (Heller 1975a). In his detailed study of the sexual cycles of the rough periwinkle on the French coast, Bergerard (1971) emphasises that the reproductive behaviour of this organism is complex and poorly known. He also considers that this very complexity must play a major part in causing the different patterns of distribution and abundance observed on many shores. Berry (1961) has discussed the reproductive physiology of rough periwinkles on the sheltered shore of Whitstable, Kent, and has determined that as well as numbers and mean shell lengths of the organisms increasing with height up shore, the weights of the female ovaries and the numbers of embryos present in the brood pouches also increase towards the upper part of the tidal range.

Both Berry (1961) and James (1968b) have described the reproductive cycle of the rough periwinkle on British shores as comprising two peaks of activity - January to February and July to August - with a degeneration of the reproductive organs between these times. In his study of the populations of the rough periwinkle at Penvins in France, Daguzan (1976a) has reviewed these points but has stated that his organisms are sexually active throughout the year. This, together with the fact that Heller (1975a) has stated as one of his key features of the taxonomy of L. rudis that it may contain embryos at any time of the year, illustrate the point that many of the variations recorded in the literature may reflect the more complex taxonomic background.

This part of the study has attempted to investigate the state of sexual maturity of the populations of L.rudis at Marsden Bay in the latter part of the spring and early part of the Summer of 1977, ie. in the months of May, June and July.

2. Methods

This work was carried out using the same sub samples that were described in part two of this study ie. the fifty individuals that were taken from each sample site during each of the months of May, June and July. In the initial choice of organisms to compose each subsample, care was taken to select as representative a collection as possible from all of the sizes present. It was while extracting the organism from its shell to measure its tissue dry weight that the opportunity was taken to assess its state of maturity.

Bergerard (1971) distinguishes between three grades of maturity for female periwinkles, and two for males. For females these are :

Grade 1) "Femelles gestantes". These are characterised by having ovaries containing large oocytes, and by having embryos in various stages of development in the brood pouch.

Grade 2) "Femelles mûres, mais non gestantes". These are mature females, but are not gestating ie. they have no embryos in the brood pouches. The associated glands - the albumen glands and the shell glands - are underdeveloped and whitish in colour. The ovary, however, does contain well developed oocytes.

Grade 3) "Femelles immatures". These characteristically show no development of their reproductive structures.

For males, the grades of maturity are:

Grade 1) "Mâles mûrs". These males show a well developed penis with numerous very obvious glands along its length. The prostate is large and rosy red in colour, the vesicula seminalis is white and distended with sperm, and the testes are massive and usually clear in colour.

Grade 2) "Mâles immatures". Here the penis, if present at all, is small with possibly only a stub indicating its position. The prostate is reduced, and the vesicula seminalis is small, brownish in colour and is devoid of sperm.

Bergerard also points out that many individuals may show characteristics between these various grades. In practice, it frequently proved very difficult to reliably distinguish between immature males and females. Therefore only females actually containing embryos, and only males with a well developed penis ie. one which actually showed the growth of penial glands along its length, were recorded as Grade 1. All others were grouped together as "immature".

For the mature females, the state of development of their embryos was assessed by a grouping based on Thorson (1946). This distinguishes between five stages of maturity ie.

Stage E - Eggs from uncleaved ova to trochophore like balls of cells.

Stage V - Young, unshelled, veliger like embryos.

Stage S - Shelled, veliger like embryos having no more than the first shell whorl complete.

Stage C - Shelled, veliger like stages with more than the first shell whorl, and some reduction of the velum.

Stage F - Well formed young free from their egg capsules with a dark, heavy shell of up to two complete whorls and no velum.

This study concentrated upon five aspects of the sexual maturity of L. rudis at Marsden Bay.

The first aspect was an estimation of the percentages of sexually mature individuals (ie. those males and females that accorded with Bergerard's Grade 1 individuals) in each subsample during each month, where the number of Grade 1 individuals was expressed as a percentage of the total number of individuals examined in each subsample. These estimates were further subdevided to record separately the percentages of sexually mature males and females to determine if either sex predominated during the study period.

The second aspect compared the mean shell lengths of the sexually mature males and females, both with each other and with the mean shell length of the whole subsample.

The third aspect compared the percentages of sexually mature individuals at each sample site between the months of the study; the values obtained for each month were compared by the standard test of "d" for the comparison of two percentages based upon two large samples (Bailey 1975).

The fourth aspect was a comparison between the percentages of sexually mature individuals at each of the sample sites during each of the months of the study, using the same statistical treatments as above.

The fifth aspect was an examination of the states of development of the embryos present in the brood pouches of the females (using the groupings of Thorson described on page 28), and of the states of development of the reproductive organs of the males.

3. Results

The percentages of sexually mature (ie. Grade 1) individuals at each sample site during each month of the study period are presented in table 8, which also includes the subdivisions of this total monthly percentage into the separate percentages of sexually mature males and females.

The mean shell lengths of the sexually mature males and females, together with the mean shell lengths of each subsample during each month are presented as table 9.

The comparisons of the percentages of sexually

Table 8. Percentages of sexually mature *L. rudis* at each sample site during the period of study, 1977. Figures in parenthesis indicate relative proportions of sexually mature males : females in each sample.

Station	May	June	July
7	22 (50:50)	29 (45:55)	11 (64:36)
Boulder	20 (60:40)	26 (61:39)	10 (60:40)
10	45 (67:33)	42 (43:57)	40 (45:55)

Table 9. Mean lengths of sexually mature male and female *L. rudis* at each sample site during the period of study. Values expressed as mms ± S.D. Figures in parenthesis indicate numbers of individuals measured.

Station		May	June	July
7	Mean of Whole Sample	3.7±1.2(37)	4.4±1.5(44)	4.2±1.3(46)
	Mean of Mature Males	5.3±1.9(3)	5.2±1.4(6)	6.6±0.4(3)
	Mean Mature Females	4.6±0.7(3)	5.8±1.3(7)	6.1±0.2(2)
B.	Mean of Whole Sample	5.2±1.1(50)	5.1±1.7(50)	5.3±1.3(50)
	Mean of Mature Males	6.4±0.8(6)	6.8±1.3(8)	8.3±0.2(3)
	Mean Mature Females	6.7±1.0(4)	7.3±0.8(5)	7.5±1.0(2)
10	Mean of Whole Sample	6.5±1.7(40)	6.0±2.0(50)	6.7±1.2(50)
	Mean of Mature Males	6.9±1.9(12)	6.5±1.4(9)	7.3±0.7(9)
	Mean Mature Females	7.6±0.9(6)	7.4±1.2(12)	8.1±0.6(11)

Table 10. Comparisons of percentages of sexually mature <u>L. rudis</u> at each sample site between the months of the study. (* indicates values significant at the five percent level).

Sites / Months compared		Value of "d"
Station 7, May	: Station 7, June	0.66
Station 7, June	: Station 7, July	2.14 *
Station 7, May	: Station 7, July	1.22
Station 10, May	: Station 10, June	0.29
Station 10, June	: Station 10, July	0.10
Station 10, May	: Station 10, July	0.48
Boulder, May	: Boulder, June	0.71
Boulder, June	: Boulder, July	2.00 *
Boulder, May	: Boulder, July	1.43

Table 11. Comparisons between the percentages of sexually mature <u>L. rudis</u> at each of the sample sites during each month of the study. (* indicates values significant at the five percent level).

Sites / Months compared		Value of "d"
Station 7, May	: Station 10, May	1.93
Station 10, May	: Boulder, May	2.55 *
Boulder, May	: Station 7, May	0.21
Station 7, June	: Station 10, June	1.35
Station 10, June	: Boulder, June	1.68
Boulder, June	: Station 7, June	0.34
Station 7, July	: Station 10, July	3.31 *
Station 10, July	: Boulder, July	3.45 *
Boulder, July	: Station 7, July	0.15

mature individuals at each of the sample sites between the months of the study are presented as table 10.

The comparisons between the percentages of sexually mature individuals at each of the sample sites during each month of the study are presented as table 11.

The data used to compound all of these results, and the data for the states of embryo development and penis length are presented in the Appendix as tables X to XVIII.

4. Discussion

The examination of subsamples of the populations of L. rudis at Marsden Bay would seem to indicate that less than one quarter of the individuals at the lowest sample sites (Station 7 and the Boulders), and less than half at the highest site, are in obvious breeding condition between the months of May and July (table 8). Whilst prolonged studies over several years, with the examination of many hundreds of individuals, would be needed to determine more accurately the rates of development of sexual maturity of L. rudis on this shore, it does not seem that the obvious pause in the sexual cycle mentioned by James (1968b) and Berry (1961) occurs here. Peaks of activity may well occur on either side of this study period, but enough individuals are breeding at this time to emphasise that interpretation of the data on breeding on other shores may be complicated by taxonomic differences not fully recognised prior to Heller's studies. Daguzan

(1976a) suggests that such differences may be due to combinations of latitude, temperature and the localities of the shores themselves, but admits that on his shore at Penvins, in Brittany, the organisms are breeding at all times of the year. In this same study, Daguzan also points out that although the sex ratio averages out at approximately 1:1, one or other of the sexes tends to be dominant at different times of the year. He observes that, at Penvins, the females seem to dominate between October and February, and the males dominate between March and September. This is the opposite of the pattern of dominance noted by Berry (1961) on the Kent coast of England, who has reported that the males decrease in numbers during the summer months. Although the results of this study show a slight tendency for the males to dominate the females over the period May to July at Marsden Bay, a chi-squared test shows no significant departure at the five percent level from a 1:1 sex ratio at any of the study sites.

The measurements of the shell lengths of the individuals at each of the sample sites over the three months of the study (table 9) show a tendency for the mature individuals to be larger than the immature ones, and a standard "t" test for comparing the means of two large samples (Bailey 1975) indicates that, with a significance at the five percent level, the mature females are larger than the mature males. This accords quite well with observations from elsewhere ie Berry (1961), Bergerard (1971) and Daguzan (1976b). More accurate comparisons of the various values are difficult due to the small numbers of individuals involved in this part of the study, but it would appear that individuals may have attained sexual maturity on this shore with shell lengths of three point two millimetres (males) and three point eight millimetres (females) - much smaller than the ten millimetres suggested by Moreteau (1976) for the shore at Roscoff (Brittany), the six millimetres suggested by Berry (1961) at Whitstable (Kent) or the four millimetres suggested by Daguzan (1976a) at Penvins (Brittany).

The comparisons made of the percentages of sexually mature individuals at each site between the months of the study (table 10) indicate that a significant decrease has occurred in the numbers of mature individuals at both Station 7 and the Boulders between the months of June and July. No such decrease is noted at Station 10 however, which maintains a larger percentage of mature individuals throughout the study period than the two lower sites. The remainder of the values for the other sites are reasonably constant throughout the study period.

Comparisons made between the percentages of sexually mature individuals at each of the sample sites during each month of the study (table 11) emphasise these differences between the highest station and the two other sites. Significant differences occur between the values for station 10 and both of the lower sites in July. Again the other values tend to be fairly constant throughout the study period.

It is not possible to discuss quantitatively how the embryo numbers and ovary weights in the females, as described by Berry (1961), vary between sites on this shore. Total numbers of embryos in the brood pouches were not counted, but no obvious differences could be noticed between samples other than may be expected due to individual size differences between the organisms themselves. The brood pouches of mature females from each of the sites were distended with embryos in all stages of development. It was a general impression that a greater proportion of embryos from Station 10 females seemed to have reached the "F" stage of maturity ie. were well formed, with dark heavy shells. Equally, many of the Station 7 females contained embryos mainly at the "V","S" and "C" stages, but contained sufficient numbers at stage "F" to have the same overall spread of maturity as those from Station 10.

The size and state of development of the male penis is significant not only in assessing the state of maturity of the individual, but also as a taxonomic aid to the species. The appearance of the penis of L. rudis has been discussed in detail in the general introduction to this study (pages 5-6). The function of the penial glands is generally regarded as being one of adhesion ie. to hold the female securely during copulation (Fretter and Graham 1962). James (1968b) observed that organisms which inhabit the more exposed shores tend to have more penial glands than those of sheltered shores.

Berry (1961) has stated that the average length of the penis in a reproducing male rough periwinkle is four point five millimetres or more in length, degenerating to less than three millimetres during the summer and regrowing in the autumn. The mean length of the penis in individuals at Marsden increases with height upshore, and values range between one point two millimetres and five point nine millimetres over the shore as a whole (Appendix tables X to XVIII). However no indication is given by such a short term study as to whether the mean lengths during the remainder of the year are significantly different. Equally, it is difficult to tell from a short term study if the stubs of the penises observed in some of the immature individuals are developing or degenerating. Although Daguzan (1976a) has stated that males in the intermediate stages may be regarded as having penises that are still growing, the numbers of individuals which were recorded as immature - some with shell lengths as great as ten point two millimetres - may give a disproportionate idea of the state of maturity of the population. It has been observed that a male periwinkle is capable of shedding its penis without any ill effect (Pettitt 1973), thus the true state of maturity of organisms of all sizes is often difficult to assess.

The Littorinidae are also prone to infestation by trematode parasites (Rees 1936; James 1965, 1968c, 1968d, 1968e) which infect principally the digestive glands. Berry (1961) states that although the gonads of the periwinkles are never injured by the parasites, heavy infection is accompanied by a reduction of the ovary or testis, and regrowth of the penis in autumn is prevented. Although the presence of trematodes was not investigated in this study, parasitism may provide an additional modifying factor to affect the state of maturity of a periwinkle population.

5. Conclusions

(i) During the months of May and June 1977, the percentages of sexually mature L. rudis at each sample site at Marsden Bay remained approximately constant. In the month of July, the values for the lowest sites fell to approximately half of their June totals. The values for the highest sample site also showed a slight decline at this time.

(ii) The percentages of sexually mature individuals at the highest sample site were approximately double those of the lowest sites throughout the study period. In the month of July, the differences were significant at the five percent level.

(iii) Although males had a slight tendency to dominate over the females in numbers, a chi-squared test detected no significant departure from a 1:1 sex ratio during the study period.

(iv) Mature females at all sample sites were distended with embryos in all stages of development. It appeared that a greater proportion of embryos at Station 10 were more advanced in their maturity than at the lower stations.

(v) Mature females are significantly larger (ie. have greater shell lengths) than mature males on this shore. Sexually mature males were recorded with shell lengths of three point two millimetres, and sexually mature females with shell lengths of three point eight millimetres. These lengths are smaller than those reported from many shores investigated by other workers.

(vi) The lengths of the penises in the males studied on this shore ranged between one point two millimetres (with a shell length of three point six millimetres) and five point nine millimetres (with a shell length of eight point two millimetres), and the mean lengths increased with height upshore. The mean number of penial glands at each sample site was 9, and in every individual but one, the glands were in a single row.

Part Five - The Growth and Longevity of *L. rudis*

1. Introduction

Detailed studies on the growth rates and longevities of the rough periwinkle have only recently appeared in the literature. Although Berry (1961) mentions the growth rates for populations of *L. saxatilis* at Whitstable, Kent, the most detailed mathematical studies of this matter are presented by the French workers Moreteau (1976) and Daguzan (1976b). The latter author briefly traces the history of growth studies on littoral prosobranchs, but emphasises that for much of this work no attempt was made to distinguish between any sub species of *L. saxatilis*.

This part of the study has attempted to estimate the rates of growth and the longevity of the populations of *L. rudis* at Marsden Bay, on the North East coast of England. The study areas are the same as those used earlier in this work ie. Stations 7 and 10, and the mid-shore boulders.

Although the published works mentioned above were carried out over periods of at least two years, the studies from Marsden could only utilise a maximum of four months data. It is hoped however, that even this short time may allow some approximate values to be determined.

X

2. Methods

Various methods have been reviewed by Haskin (1954) for the determination of the ages of molluscs, and have included using the lines of growth on the shell or on the operculum, the use of mark-release-recapture, and the study of the size distribution of organisms in a collection.

This study followed the methods used by Moreteau (1976) and Daguzan (1976b), and compared the size distributions of winkles over several monthly intervals. The collection of the large numbers of individuals necessary for such a study is difficult on a shore as pitted with crevices as Marsden. Thus, the method used by Daguzan (1976b) of collecting everything within a quarter square metre quadrat for detailed examination in the laboratory, was found to be impractical. The "constant effort" method of Moreteau (1976) was therefore used, and each of the sample sites on the shore was searched thoroughly for a unit of time and all individuals of L. rudis that were encountered were collected. The time chosen was one hour at each site, as this seemed to offer the best opportunity to thoroughly search a wide area. Collections were made around the middle of each of the months of May, June, July and August 1977, and the organisms found were returned to the laboratory for accurate measurement with a binocular microscope and graticule.

The first samples collected, in May 1977, were divided into one millimetre size classes for data analysis, but it was found that so few classes were present (ie. the range of values recorded only covered about ten millimetres) that half millimetre size classes were used subsequently. Again, published methods were followed as far as possible, and the linear dimension of Colman (1932) ie. the shell length along the columellar axis, was used for all of the measurements.

Each months data were was plotted in the form of a histogram for each sample site, and the percentages of the total numbers of individuals in each size class indicated that a polymodal size distribution occured in each case. This is typical of the pattern of size distributions described by Berry (1961), Moreteau (1976) and Daguzan (1976a, 1976b).

To analyse the polymodal distributions, ie. to produce a mean value from each mode which could be followed, for each site, throughout the study period, the logarithm transformation method of Bhattacharya (1967) was used. In this method, the number of individuals in each size class is transformed to a logarithm (base 10), and each value so obtained is then subtracted from the preceding class value. This produces a series of values of $\Delta \log . y$ which are plotted on arithmetic graph paper against the mid point values of each size class. The regions where the resulting graph is a straight line with a negative slope correspond to the number of components in the population. The mean values for these components, and their standard deviations, can be calculated from two equations. The mean value of each component is given by the expression:

$$\overline{x} = \lambda + h/2$$

where "λ" is the x-intercept of the line in question, and "h" is equal to the class interval. The standard deviation of each value is given by:

$$\sigma^2 = (dh\ \text{Cot.}\theta\ /\ b) - (h^2/\ 12)$$

where θ is the angle made by the line of the graph with the negative direction of the axis of x, and the x-intercept, and the terms "b" and "d" denote the relative scales of x and Δ log.y respectively.

Although this method is more complex to apply than a probit transformation (Harding 1949, Cassie 1954, Harris 1968), the subjectivity of having to fit the points of inflection by eye is eliminated, and the mathematical results tend to be more accurate.

As will be seen later, between two and three modes could be followed at each sample site during each month, but the calculation of the growth rates dealt only with the largest values obtained to ensure, as far as possible, that the maximum potential growth rate was estimated.

The growth equation of Von Bertalanfy, as described by Lockwood (1974) for following the seasonal growth of fish, was used for the estimation of the growth rates of L. rudis in this study. This equation is given as:

$$l_t = L_\infty \left[1 - \exp.(-k(\ t-t_o\ )) \right]$$

where "l_t" is the shell length at any time "t", and "L_∞" is the theoretical maximum shell length of the population.

This parameter has no biological significance, and represents only a simple estimate of the theoretical maximum length of the shell given by the observed data (Knight 1968). The value of L_{∞} is given, together with the value of the term "k", by the graphical method of Walford (1946). With this method, the shell lengths at times 1,2,3...n are plotted on the x-axis against the lengths at times 2,3,4...n+1 respectively on the y-axis. The slope of the line joining these points gives the value of k from the relationship $b = e^{-k}$ (where "b" is the regression coefficient of the line through the points) and where $k = -\log.b$. The value of L_{∞} is given by the point on the x-axis below the intersection of the line described above with a line drawn at forty five degrees through the zero point. The term "t_o" cannot be given directly since it is almost impossible to place the exact date of birth of a given age class (t=0) on the time axis. However, the methods employed by both Daguzan (1976b) and Moreteau (1976) introduce the term t'_o which corresponds to the time of first capture of individuals of the species. Utilising the accepted size of the young periwinkles at emergence from the brood pouch of approximately nought point four five millimetres (the stage "F" embryos at all sample sites at Marsden were of this length), both of these authors have determined that t_o has the approximate value of point four. The equation used to determine the growth rates of L. rudis on the shore at Marsden was thus

$$l_t = L_\infty \left[1 - e^{-k(t+0.4)} \right].$$

The longevity of each sub sample was estimated from the time, at this calculated rate of growth, that would be needed to reach the theoretical maximum shell length L_∞.

3. Results

The histograms plotted for each sample site to illustrate the polymodal patterns of size distribution over the period of study are presented as figures 13 - 16. The histograms for all three of the sample sites during the month of May are presented separately (figure 13) as the size class interval used in these collections was greater than for the subsequent months (as explained in the methods, page 39).

The graphical plots of the log. transformations from the data at each sample site during each month of the study period are presented as figures 17 - 28.

The mean shell lengths for the components of each of the sub samples followed over the study period are presented as table 12. As explained in the methods (page 40) only the largest size group was followed at each sample site for the estimate of the growth rates, to give the maximum potential growth rate from the data available.

The overall spread of the mean values of each of the two major components at each sample site over the study period are presented as figures 29 - 31. The values used

Table 12. The mean shell lengths of the principal components in the monthly collections of L. rudis from Marsden Bay. Figures in parenthesis indicate the values used to determine the growth rates.

Station	May	June	July	August
	3.31±0.74	2.80±0.72	2.90±1.06	3.15±0.97
7	6.35±1.10	6.63±0.44	7.10±0.27	7.20±0.12
	(5.25)	(6.19)	(6.83)	(7.20)
	3.60±1.35	3.15±0.61	4.27±1.04	4.63±0.88
Boulder	6.95±0.54	7.50±0.09	7.70±0.21	8.22±0.21
	(6.41)	(7.50)	(7.90)	(8.22)
	4.85±0.58	4.07±1.04	4.52±0.88	4.90±1.01
10	6.30±1.40	6.77±0.92	7.25±0.52	7.55±0.68
	(4.90)	(6.77)	(7.77)	(8.23)

Values expressed as mms. ± S.D.

Table 14. The rate of growth and the estimated longevity of <u>L. rudis</u> at Station 10, Marsden Bay.

Where $L_\infty = 8.8$

and $k = -\log_e 0.509 = -0.675$

$$l_t = 8.8 \left[1 - e^{-0.675(t+0.4)} \right].$$

Age	Shell Length (mms.)
6.0 weeks	2.5
12.0 weeks	3.2
6.0 months	4.0
1.0 years	5.4
1.5 years	6.4
2.0 years	7.0
2.5 years	7.6
3.0 years	7.9
3.5 years	8.2
4.0 years	8.4
4.5 years	8.5
5.0 years	8.6
5.5 years	8.6
6.0 years	8.7

Table 15. The rate of growth and the estimated longevity of <u>L. rudis</u> on the mid shore boulders, Marsden Bay.

Where $L_{\infty} = 8.3$

and $k = -\log_e 0.454 = -0.79$

$$l_t = 8.3 \left[1 - e^{-0.79(t+0.4)} \right].$$

Age	Shell Length (mms.)
6.0 weeks	2.8
12.0 weeks	3.4
6.0 months	4.3
1.0 years	5.6
1.5 years	6.5
2.0 years	7.1
2.5 years	7.6
3.0 years	7.8
3.5 years	8.0
4.0 years	8.1
4.5 years	8.2
5.0 years	8.3

Figure 13. Frequency of L. rudis in 1 mm. size classes at each sample site at Marsden Bay. May 1977.

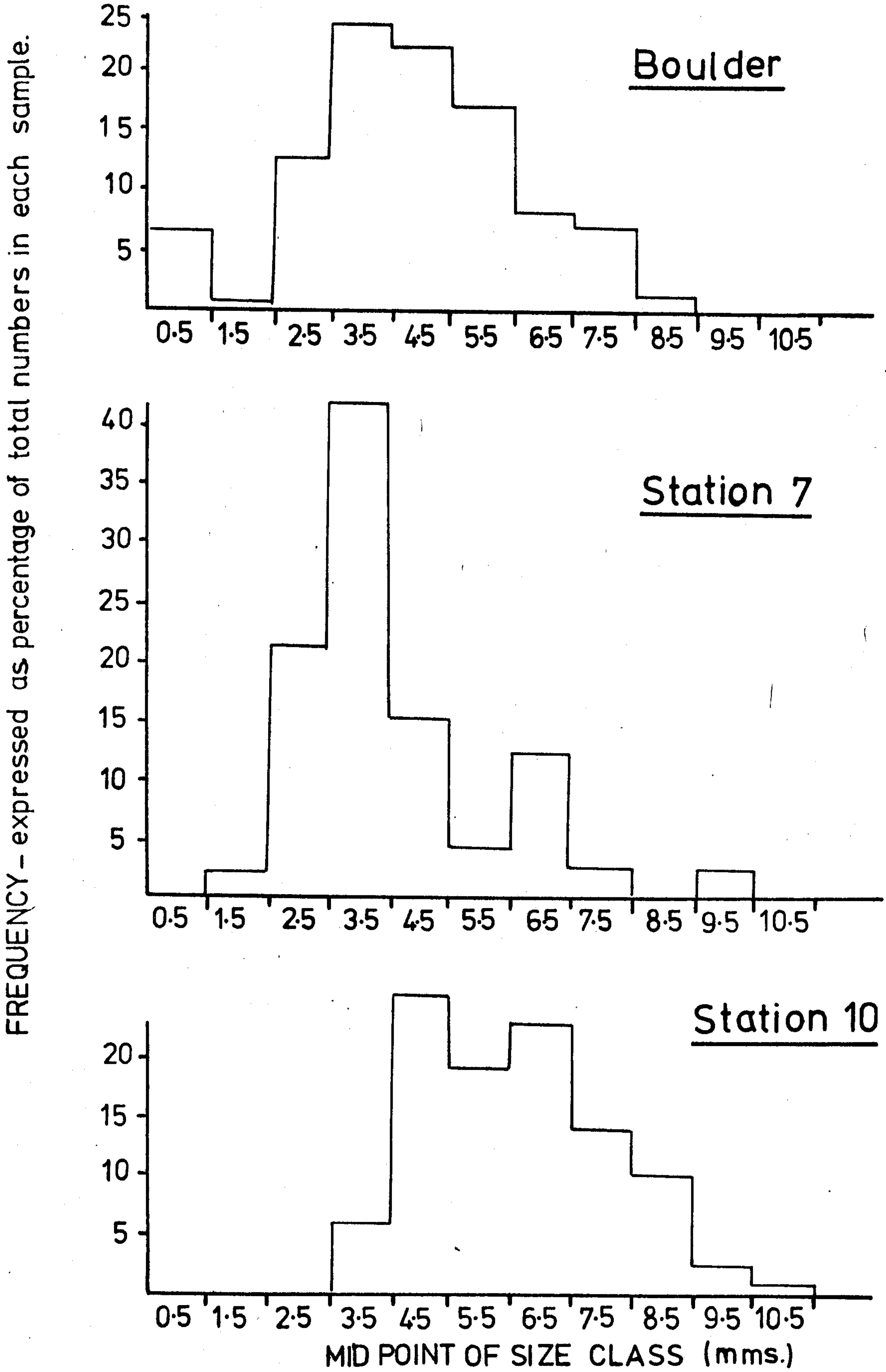


Figure 14. The frequency of L. rudis in 0.5 mm size classes. Station 7, Marsden Bay.

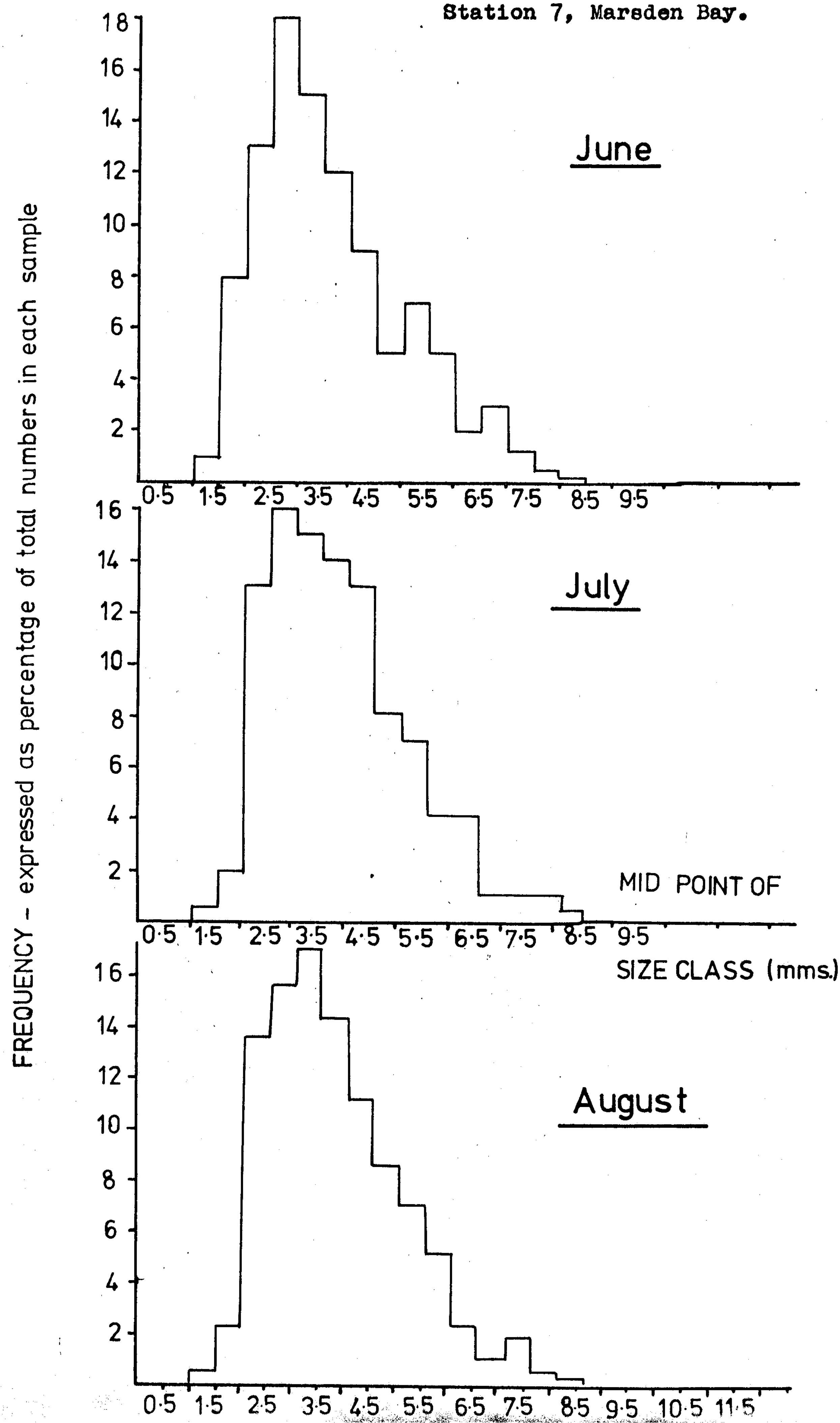


Figure 15. The frequency of <u>L. rudis</u> in 0.5 mm size classes. Station 10, Marsden Bay.

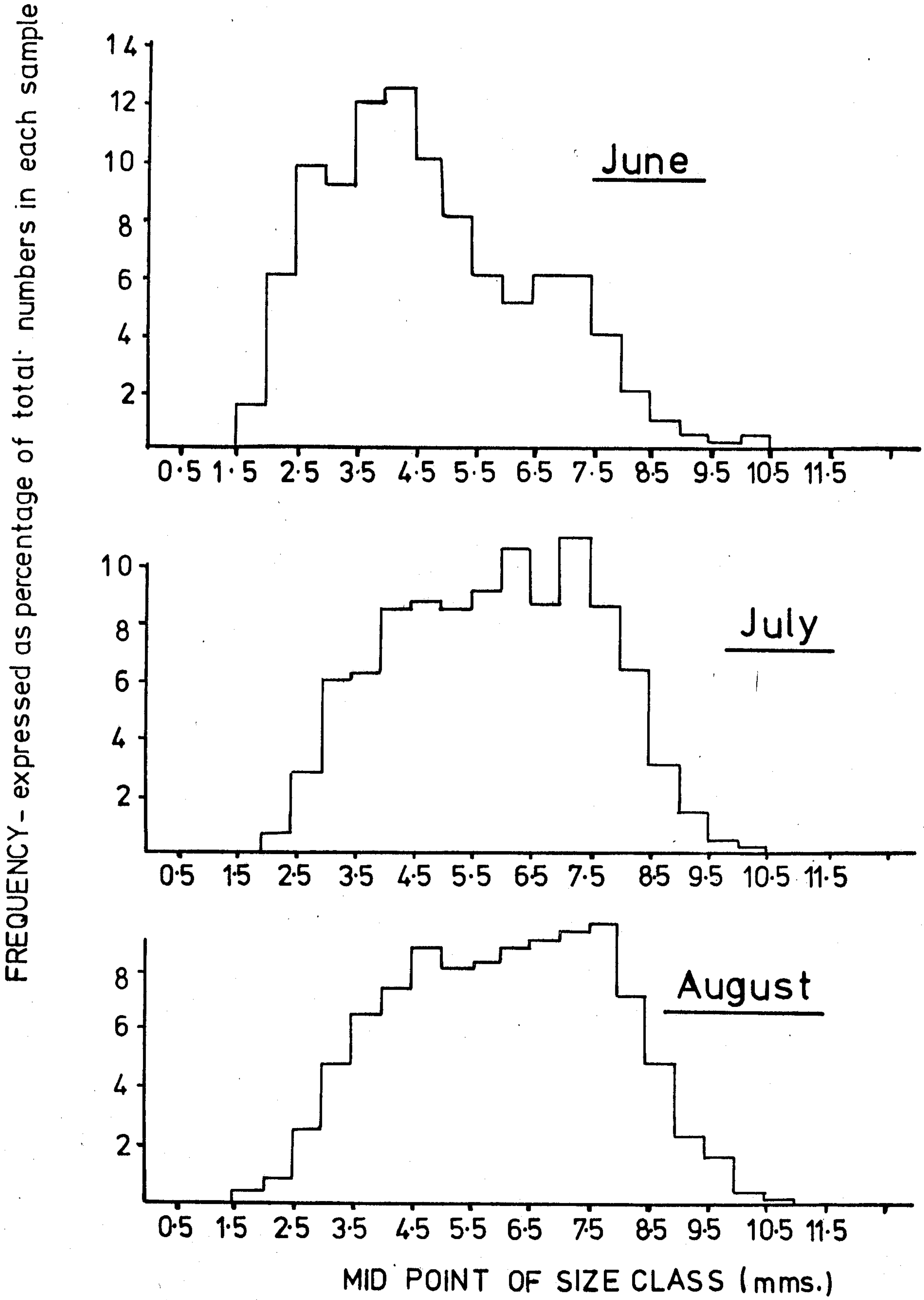


Figure 16. The frequency of L. rudis in 0.5 mm size classes. Mid shore boulders, Marsden Bay.

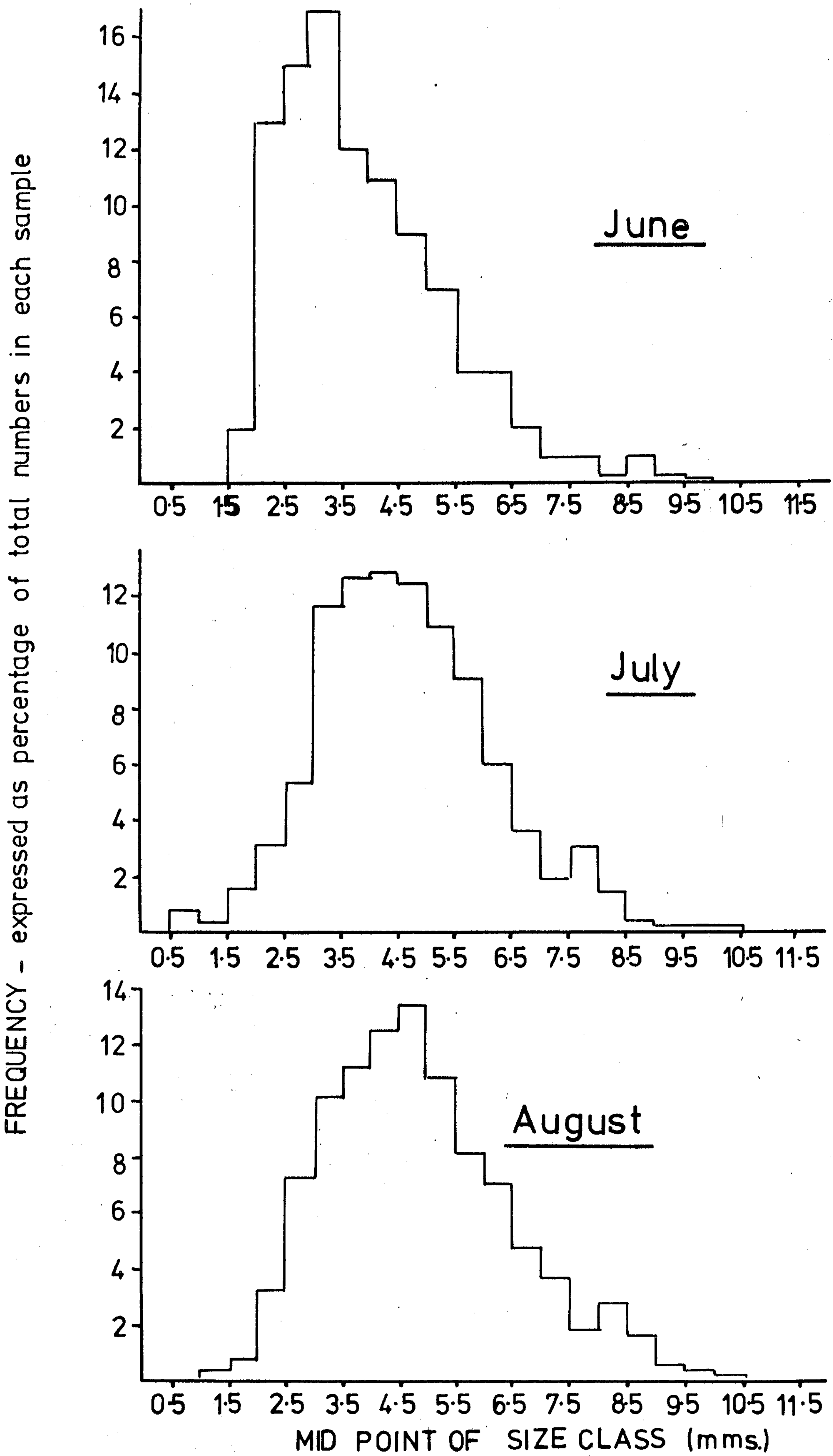
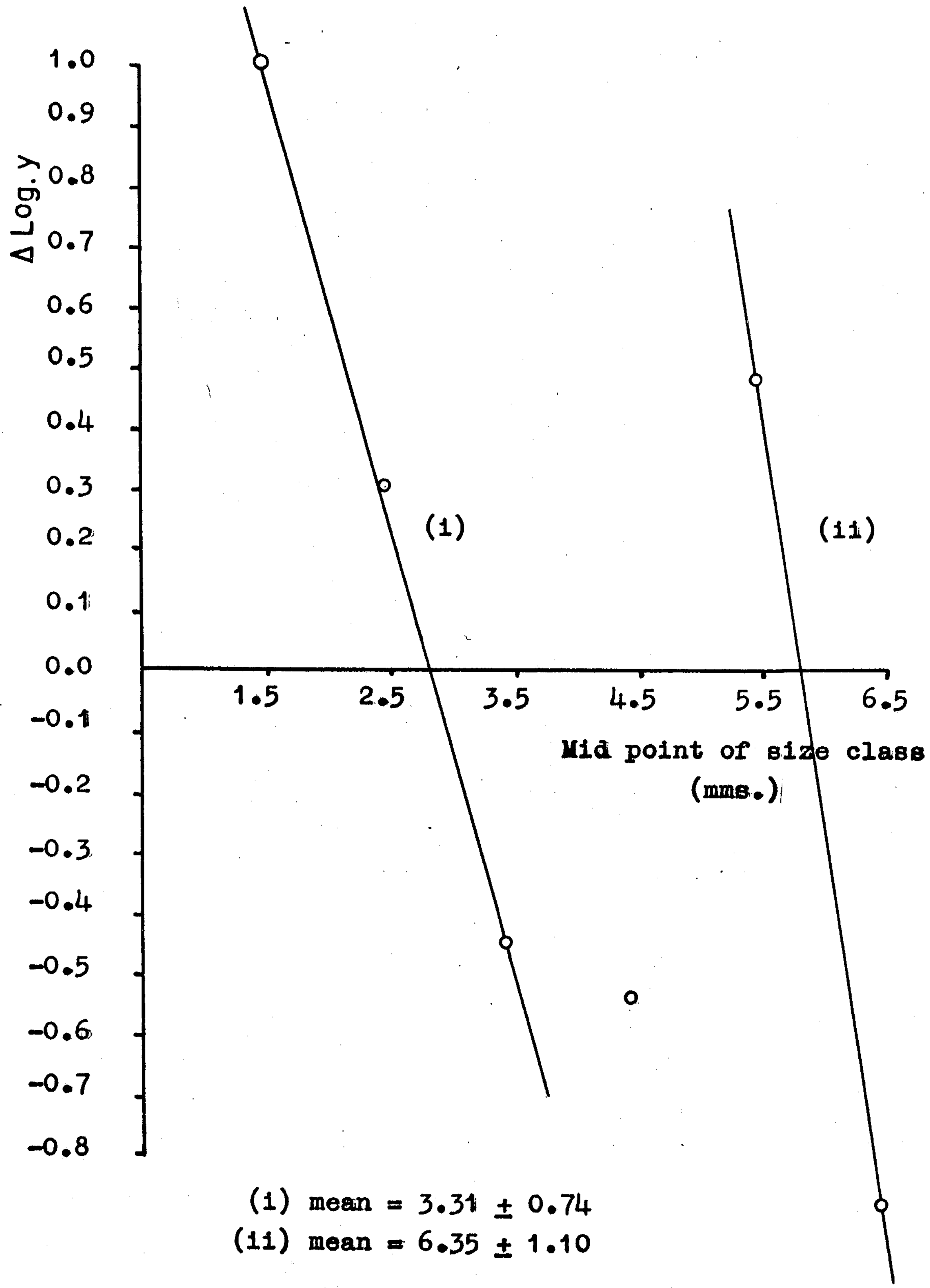


Figure 17. Graph of logarithmic differences of the class frequencies against the mid points of the classes. Station 7. May 1977.



(i) mean = 3.31 ± 0.74
(ii) mean = 6.35 ± 1.10

Figure 18. Graph of logarithmic differences of the class frequencies against the mid points of the classes. Station 10. May 1977.

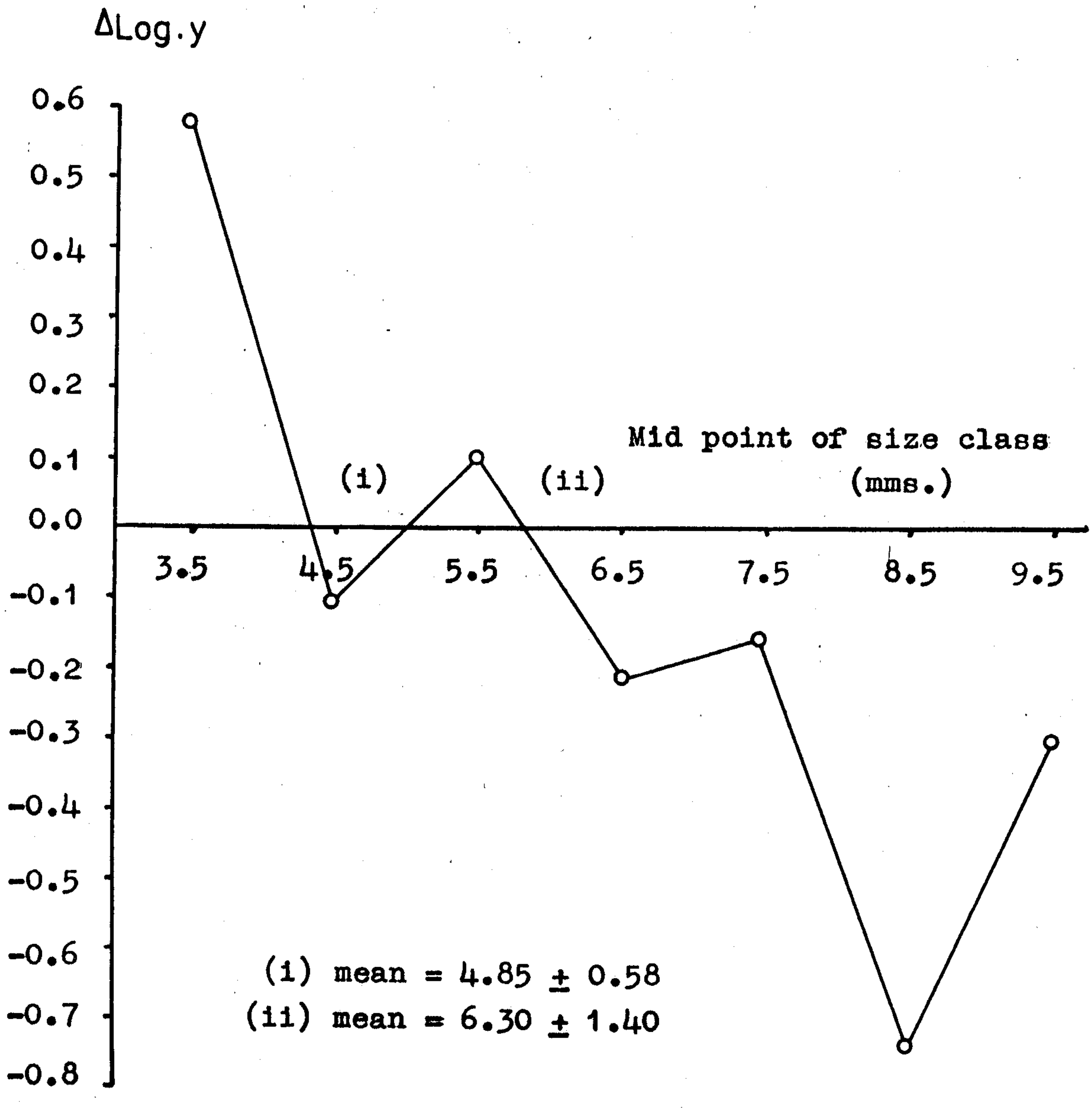


Figure 19. Graph of logarithmic differences of the class frequencies against the mid points of the classes.
Mid shore boulders. May 1977.

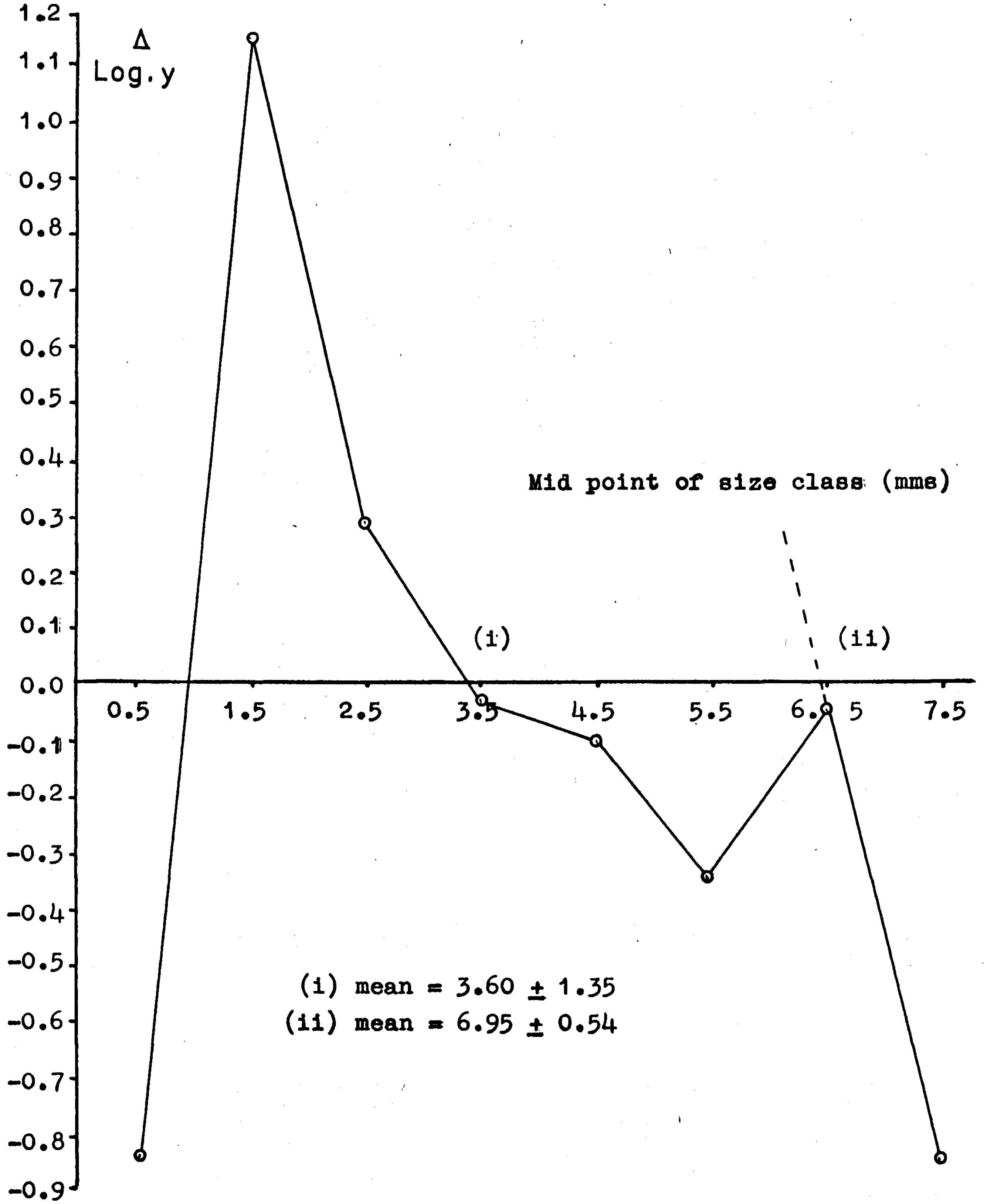


Figure 20. Graph of logarithmic differences of the class frequencies against the mid points of the classes. Station 7. June 1977.

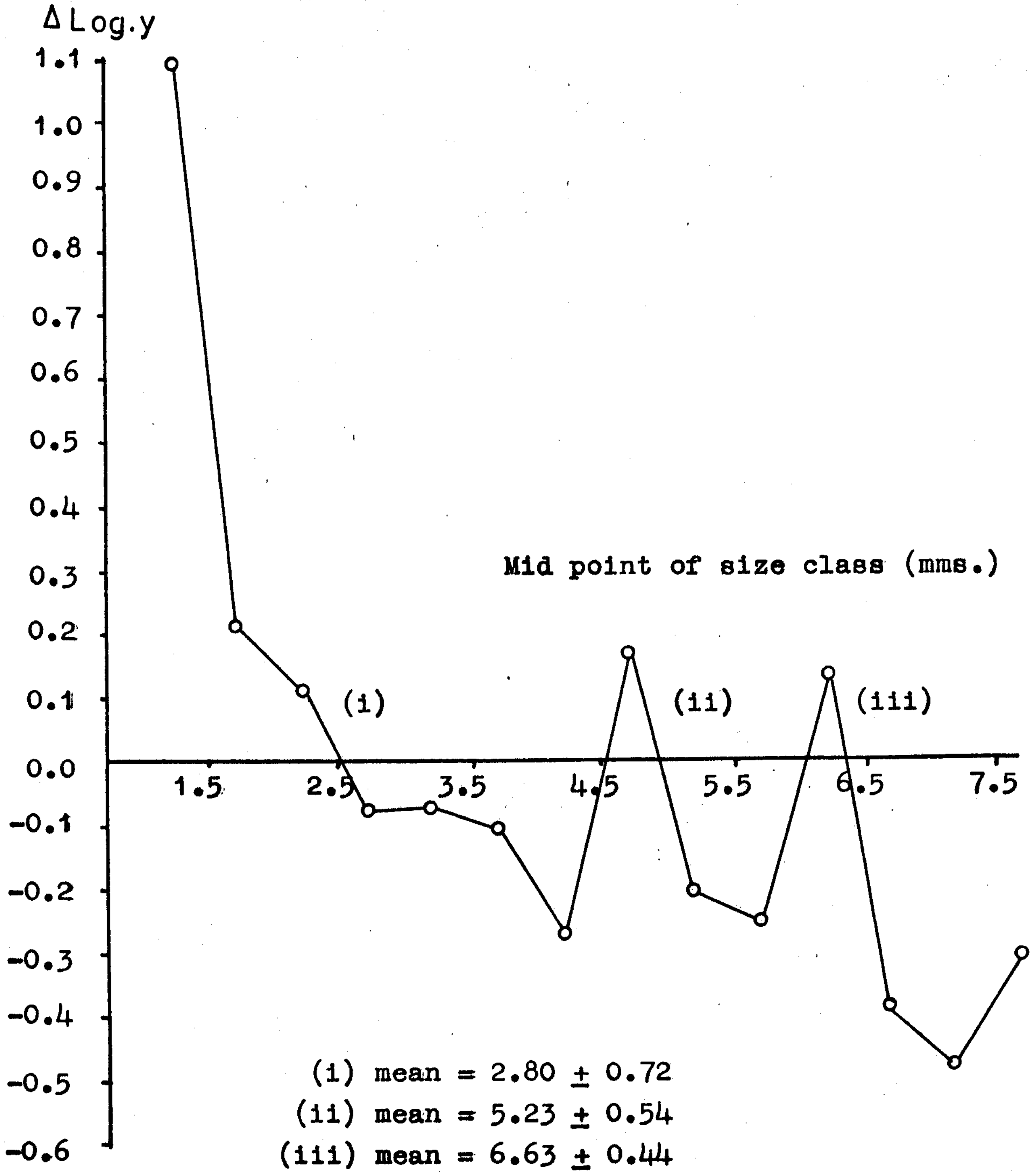


Figure 21. Graph of logarithmic differences of the class frequencies against the mid points of the class. Station 10. June 1977.

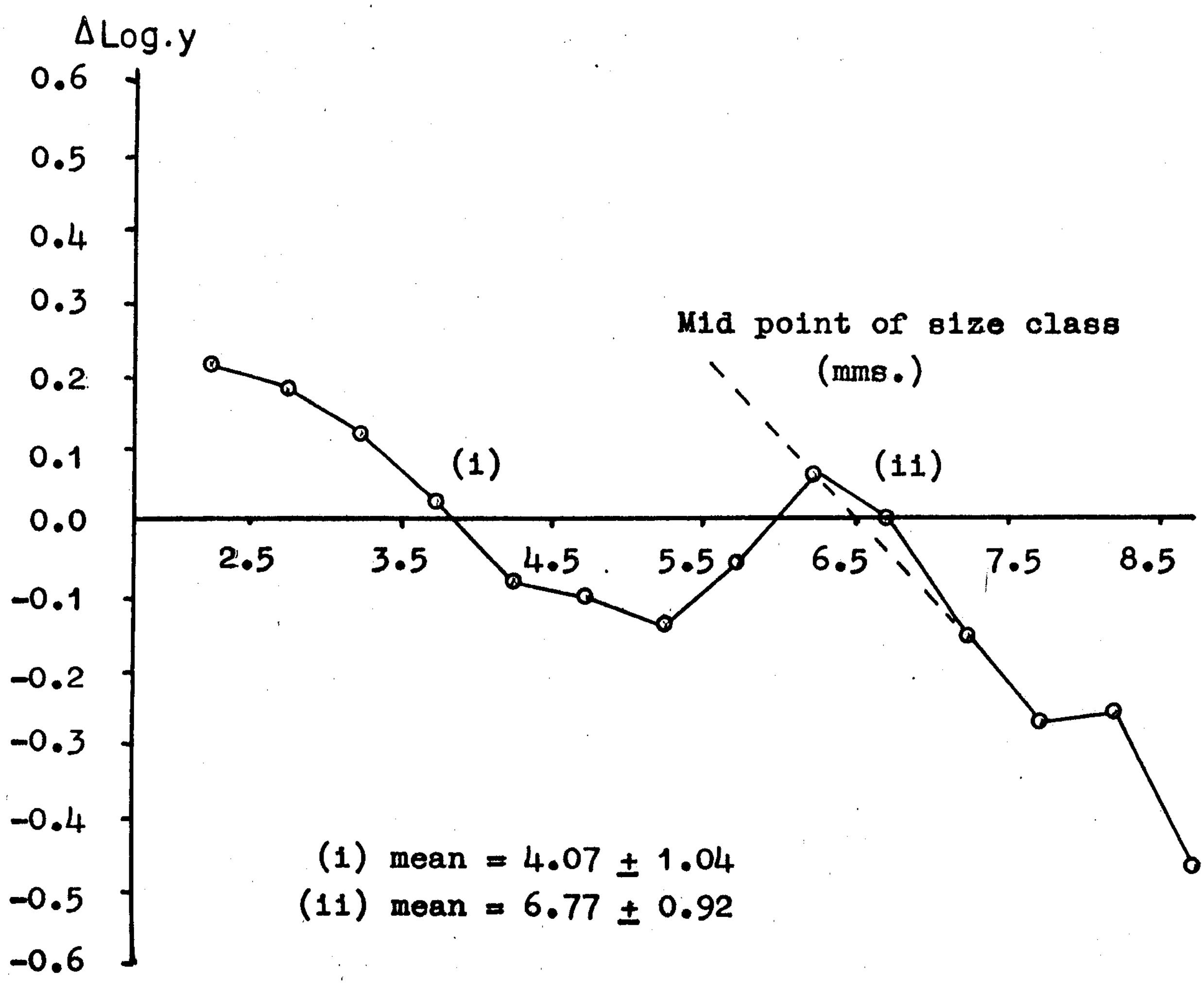


Figure 22. Graph of logarithmic differences of the class frequencies against the mid points of the classes.
Mid shore boulders. June 1977.

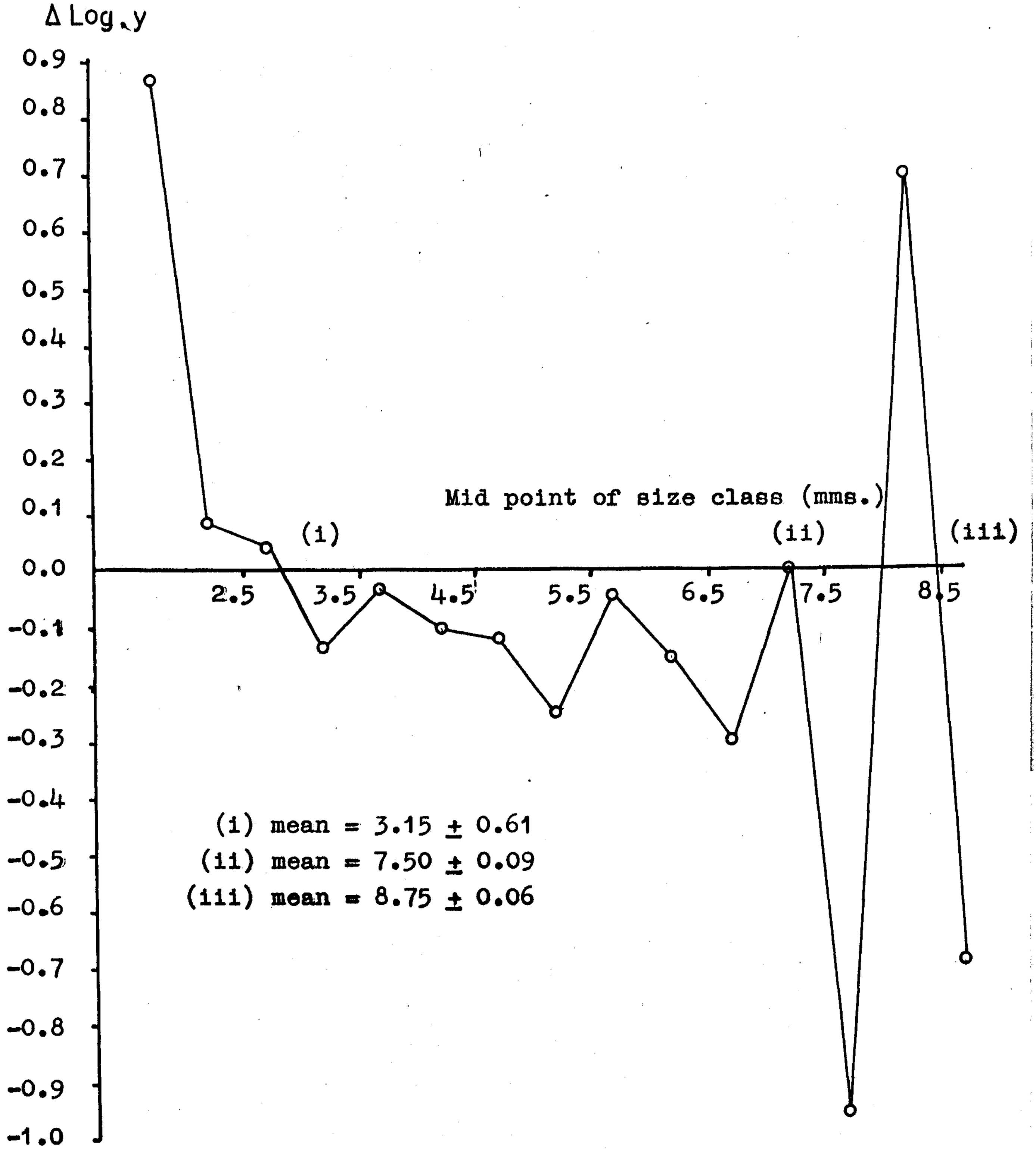


Figure 23. Graph of logarithmic differences of the class frequencies against the mid points of the classes. Station 7. July 1977.

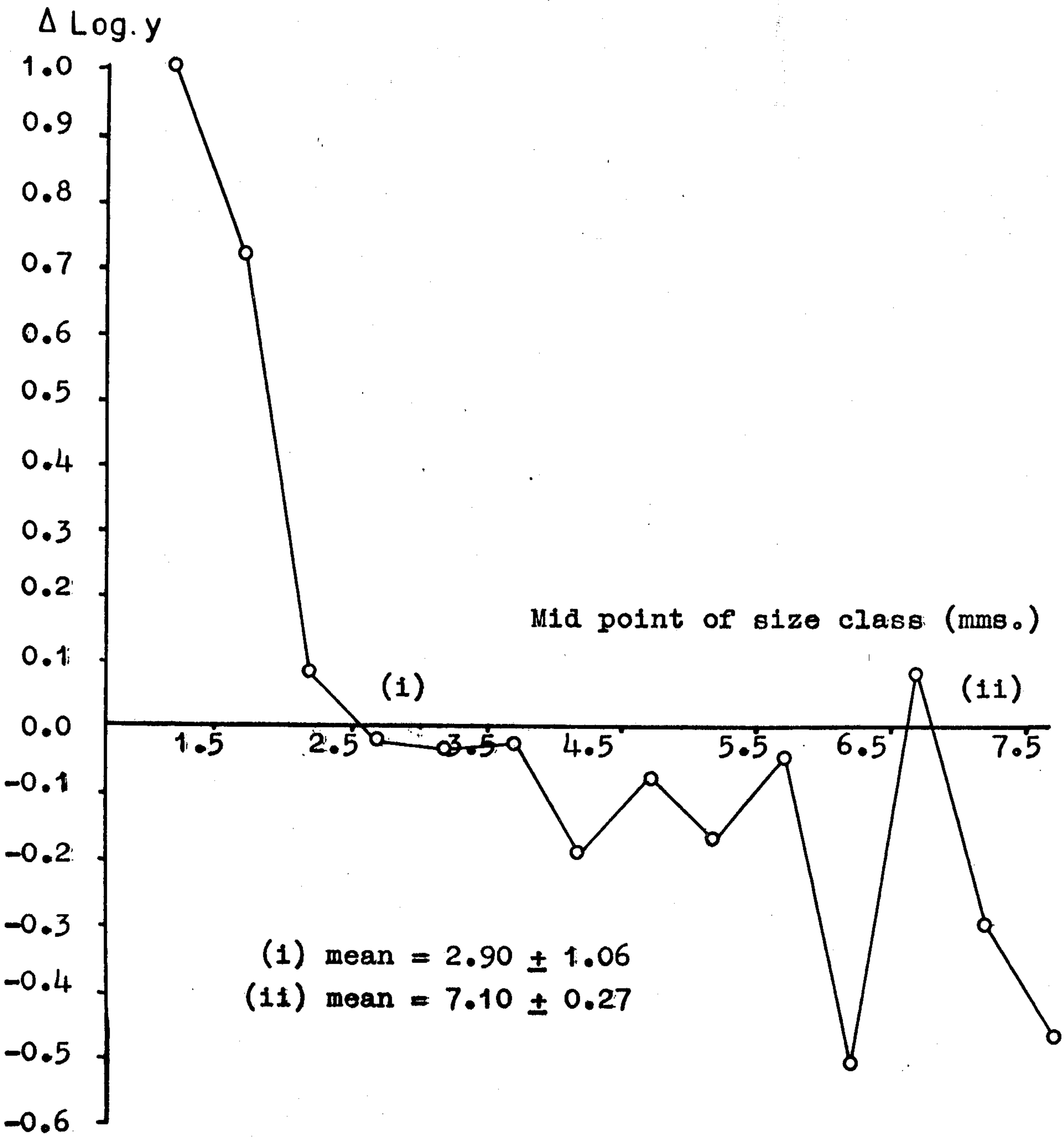


Figure 24. Graph of logarithmic differences of the class frequencies against the mid points of the classes. Station 10. July 1977.

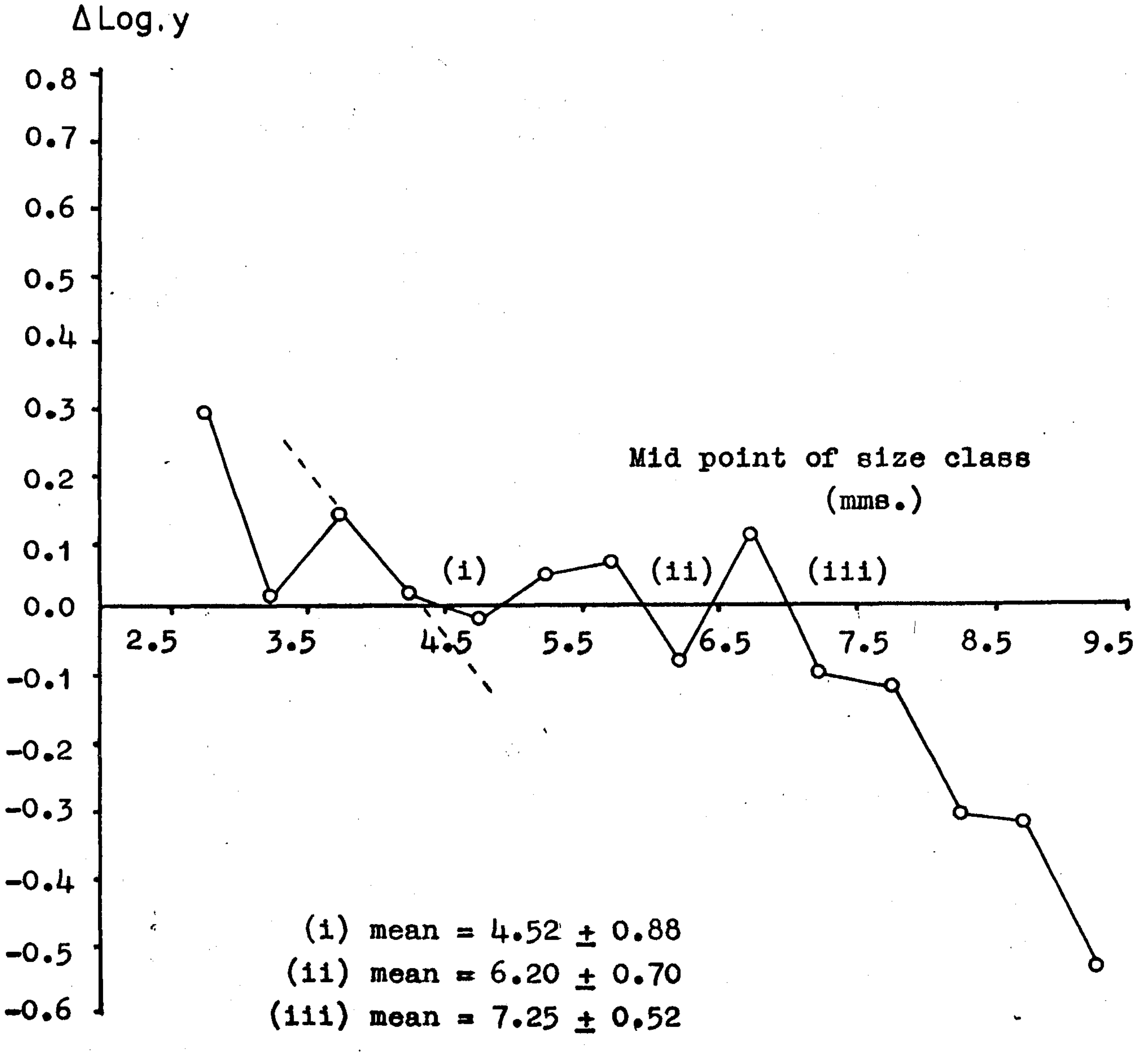


Figure 25. Graph of logarithmic differences of the class frequencies against the mid points of the classes.
Mid shore boulders. July 1977.

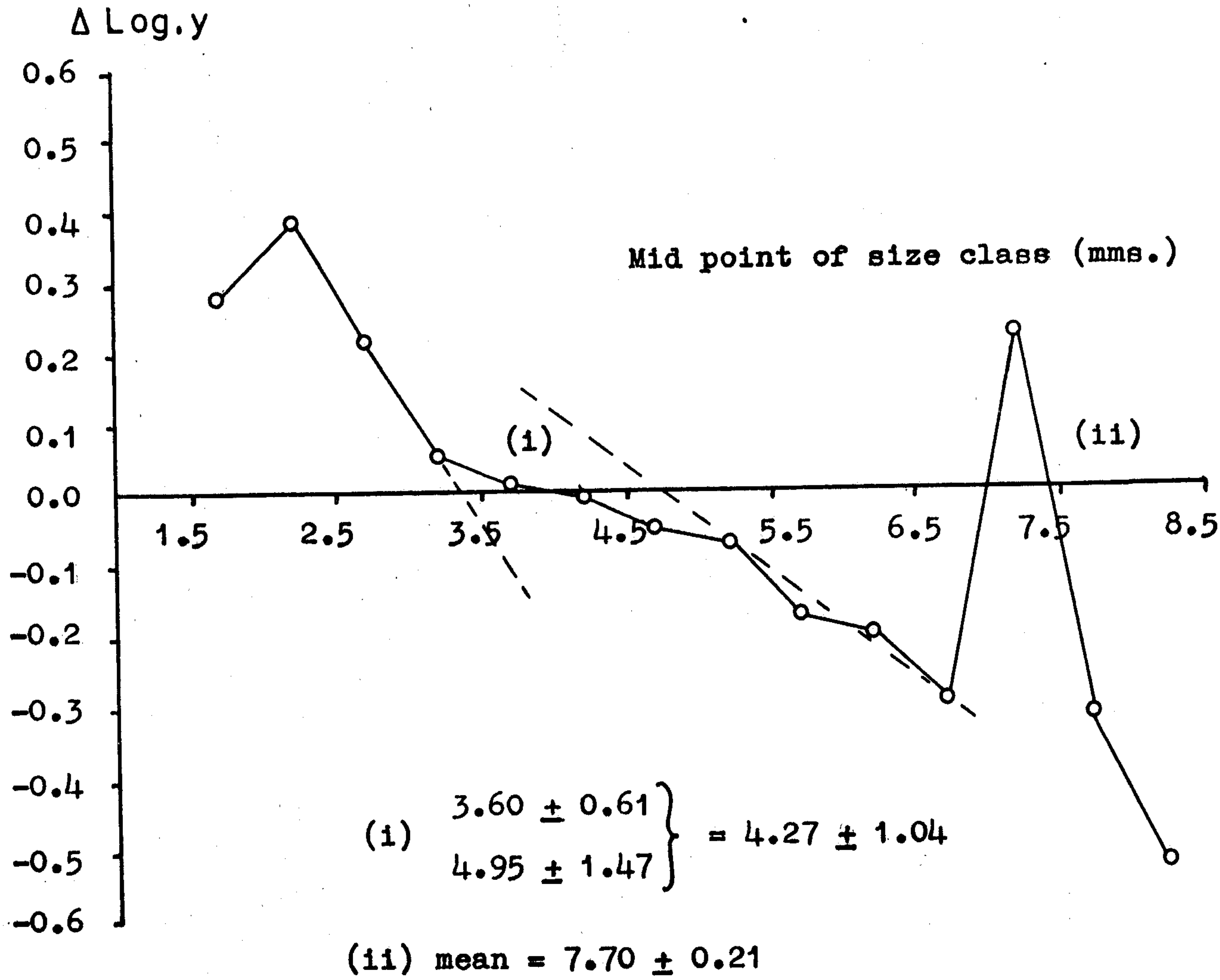


Figure 26. Graph of the logarithmic differences of the class frequencies against the mid points of the classes. Station 7. August 1977.

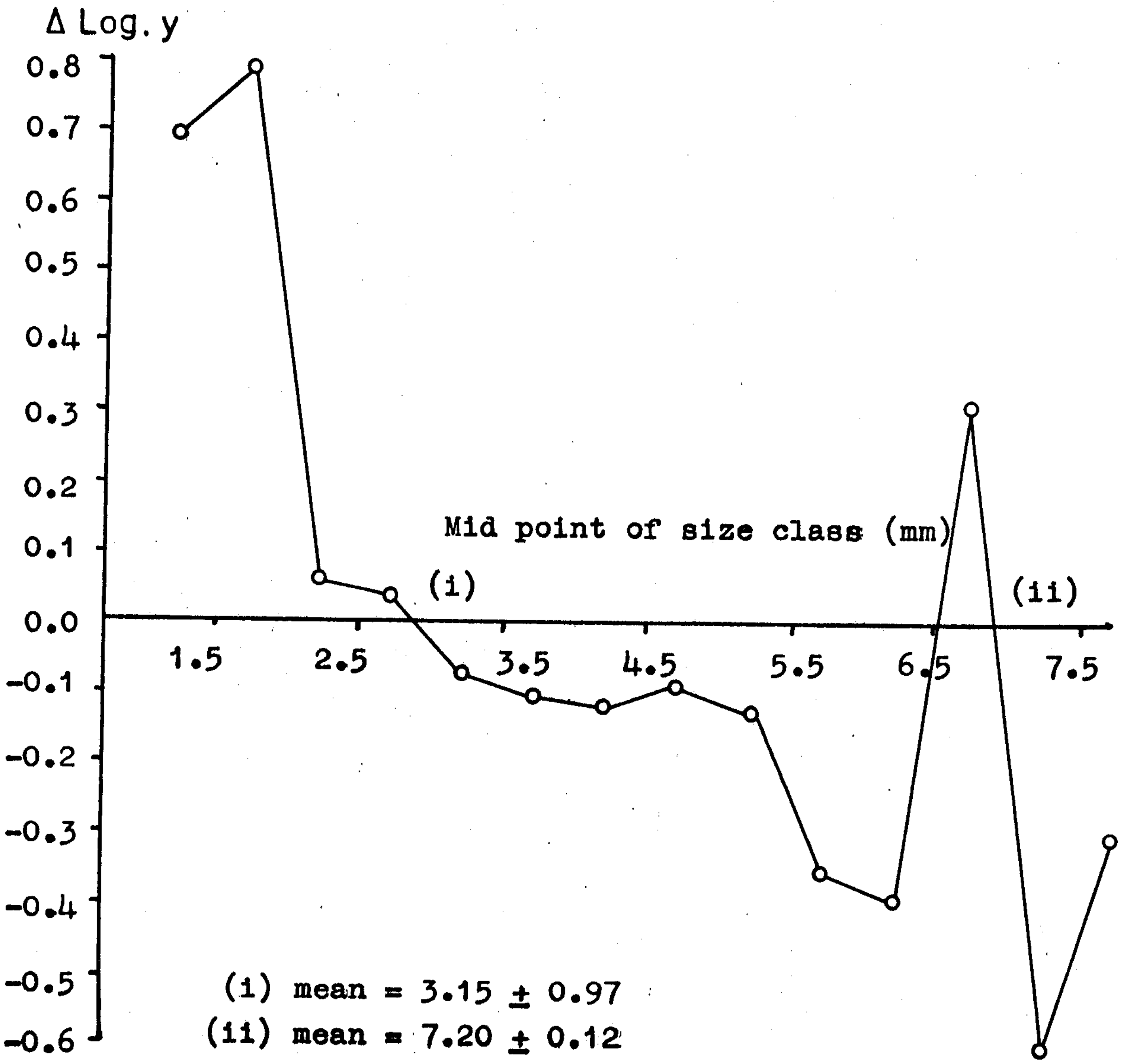


Figure 27. Graph of logarithmic differences of the class frequencies against the mid points of the classes. Station 10. August 1977.

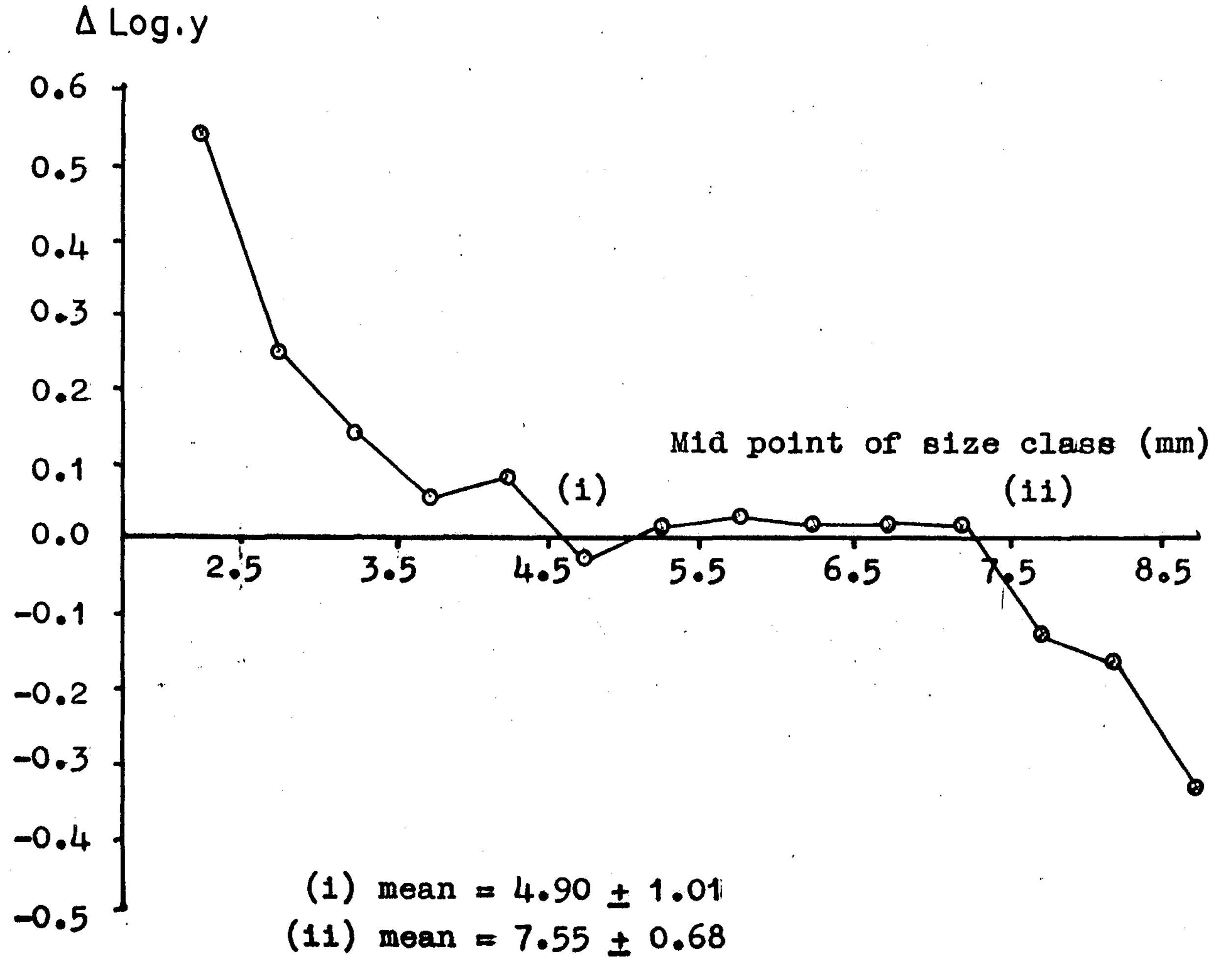


Figure 28. Graph of logarithmic differences of the class frequencies against the mid points of the classes. Mid shore boulders. August 1977.

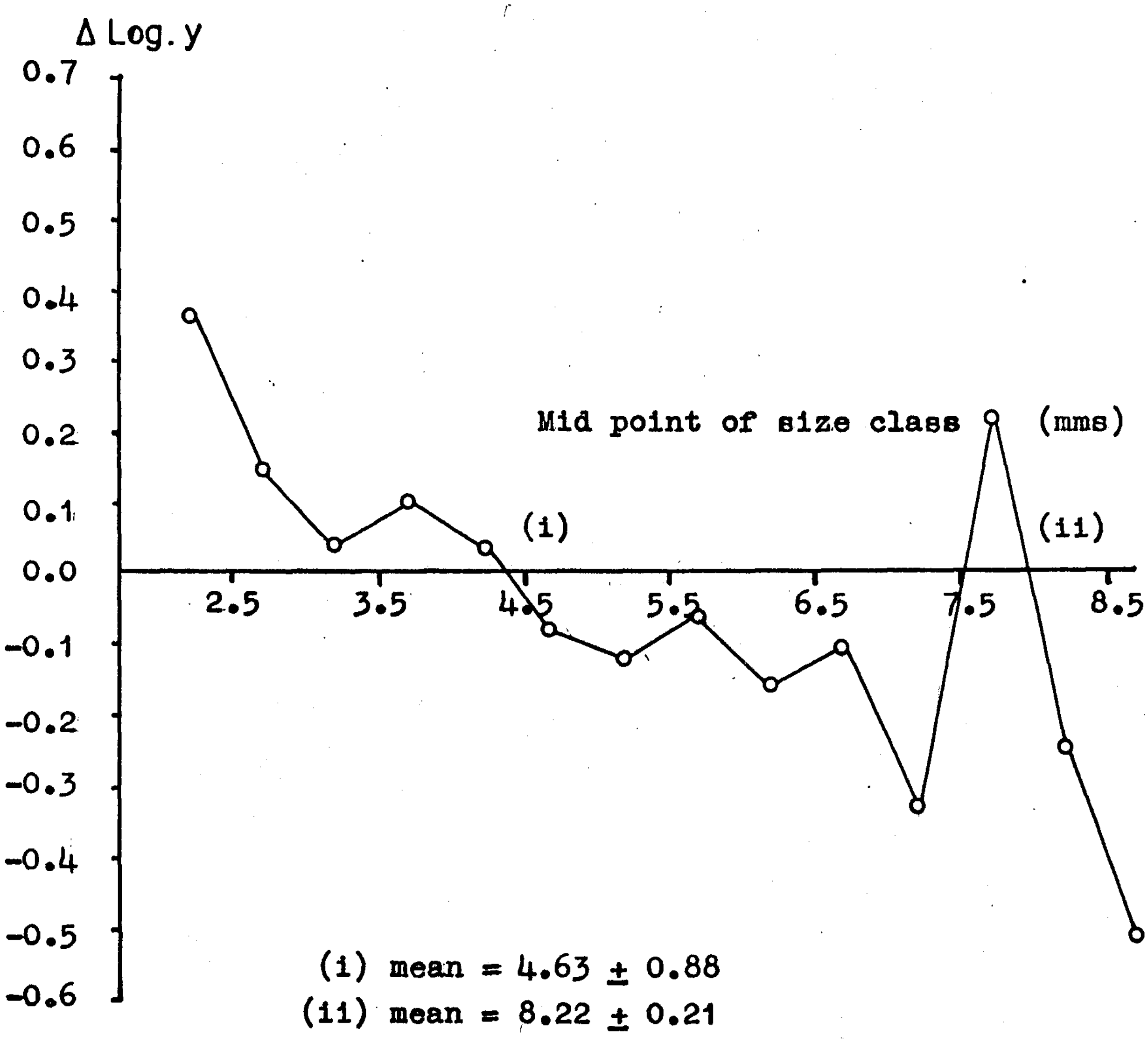
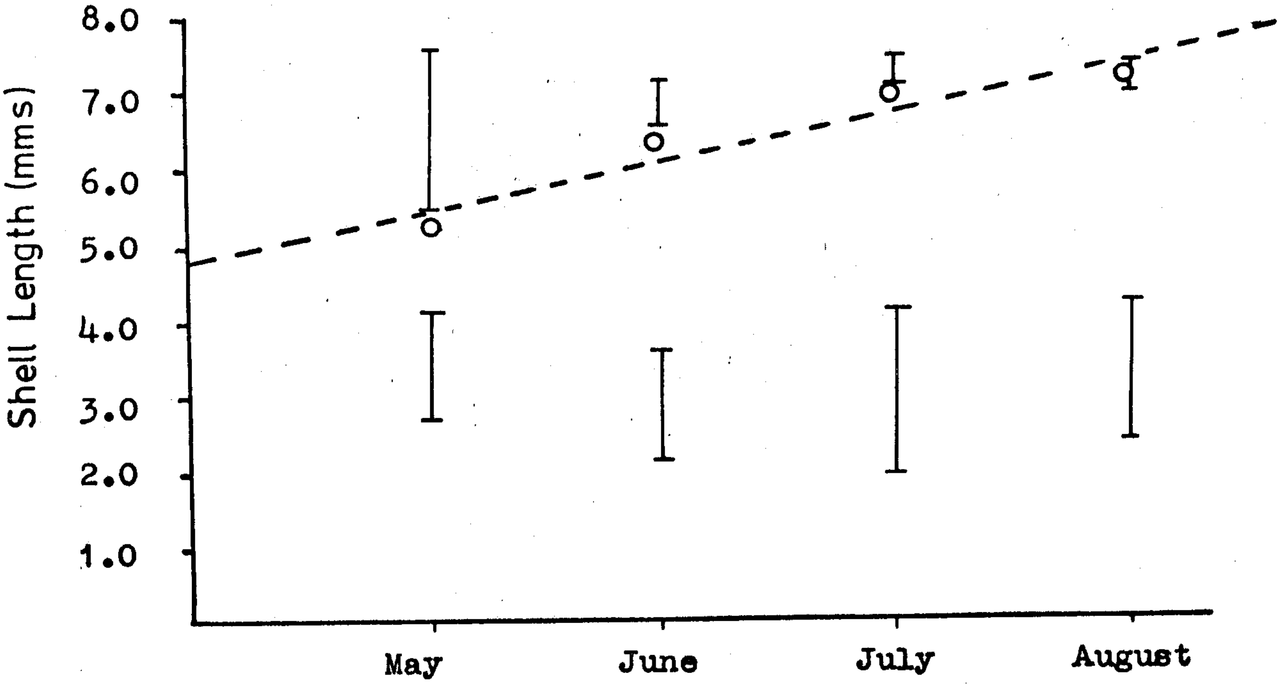


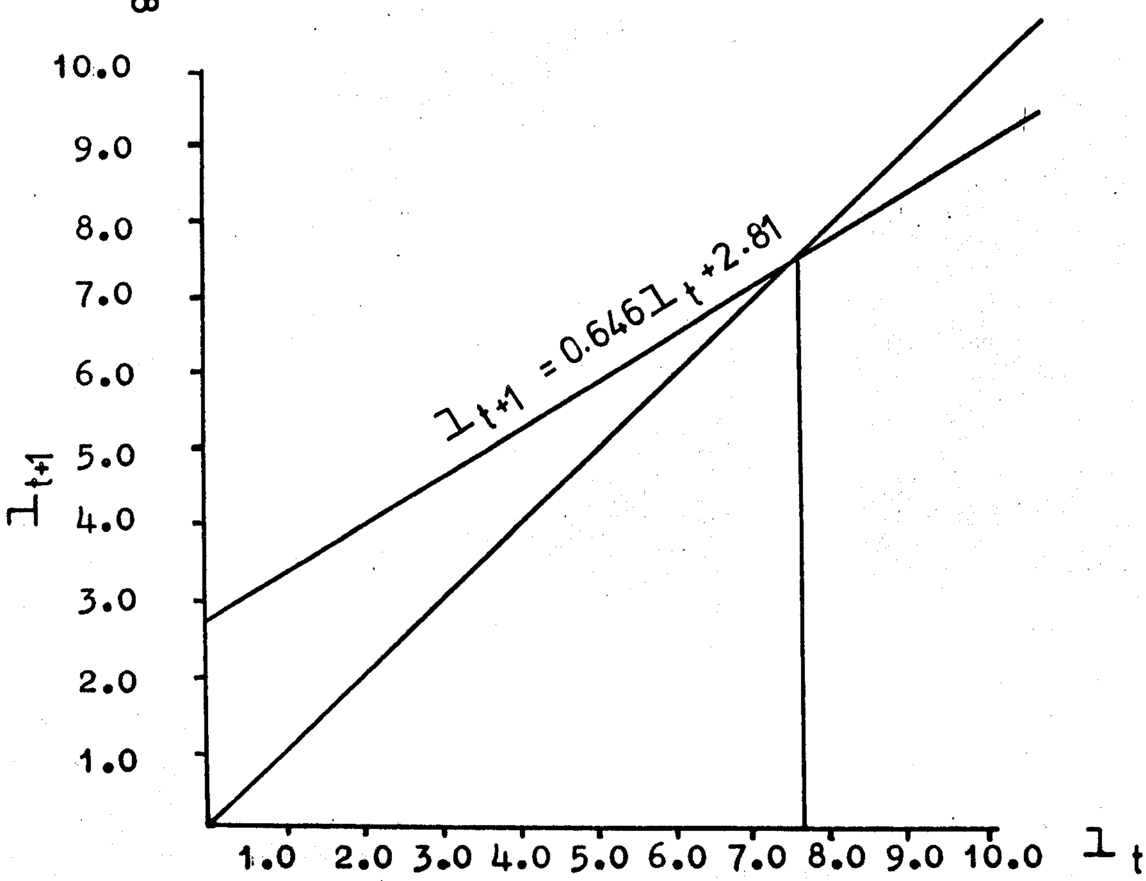
Figure 29. Station 7.

The progression of the modes (values ± S.D.) of the shell length of L. rudis through the study period.

Dotted line indicates trend of growth and circles indicate values used below.



Walford-type plot of l_{t+1} against l_t for the determination of L_∞ - the theoretical maximum shell length.

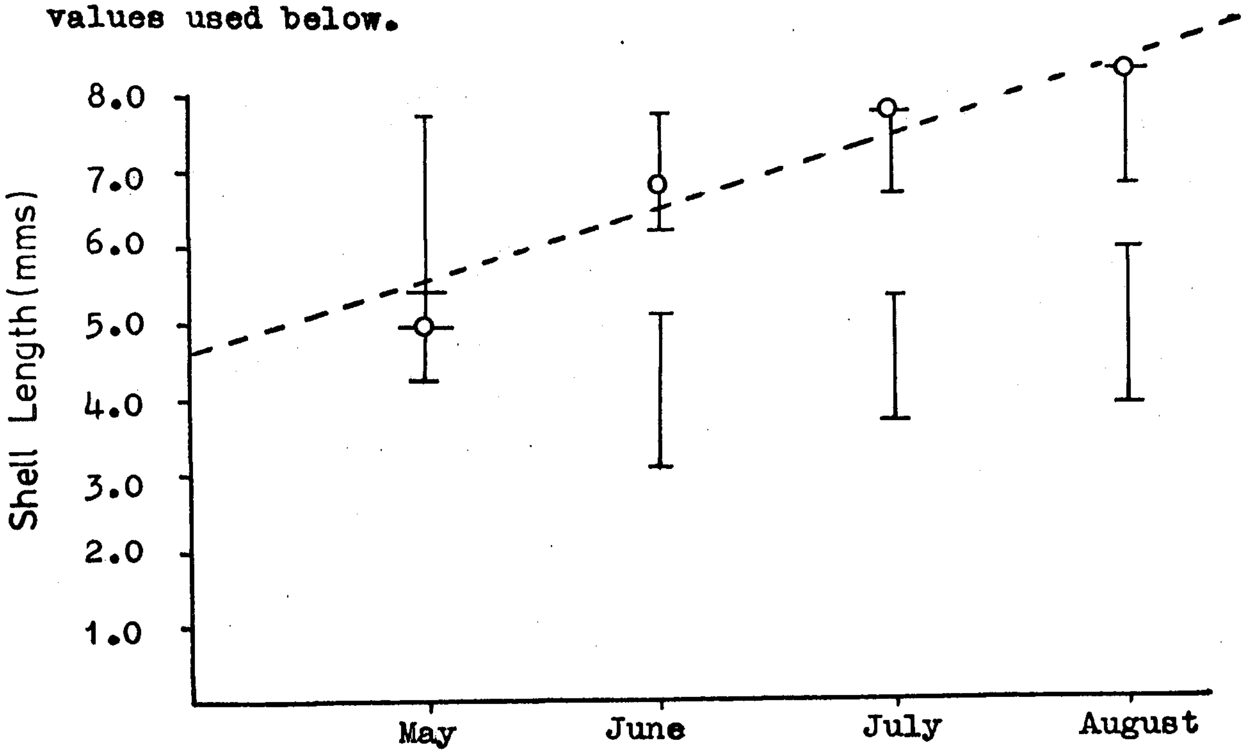


$L_\infty = 7.7$

Figure 30. Station 10.

The progression of the modes (values ± S.D.) of the shell length of L. rudis through the study period.

Dotted line indicates trend of growth and circles indicate values used below.



Walford-type plot of l_{t+1} against l_t for the determination of L_{∞} - the theoretical maximum shell length.

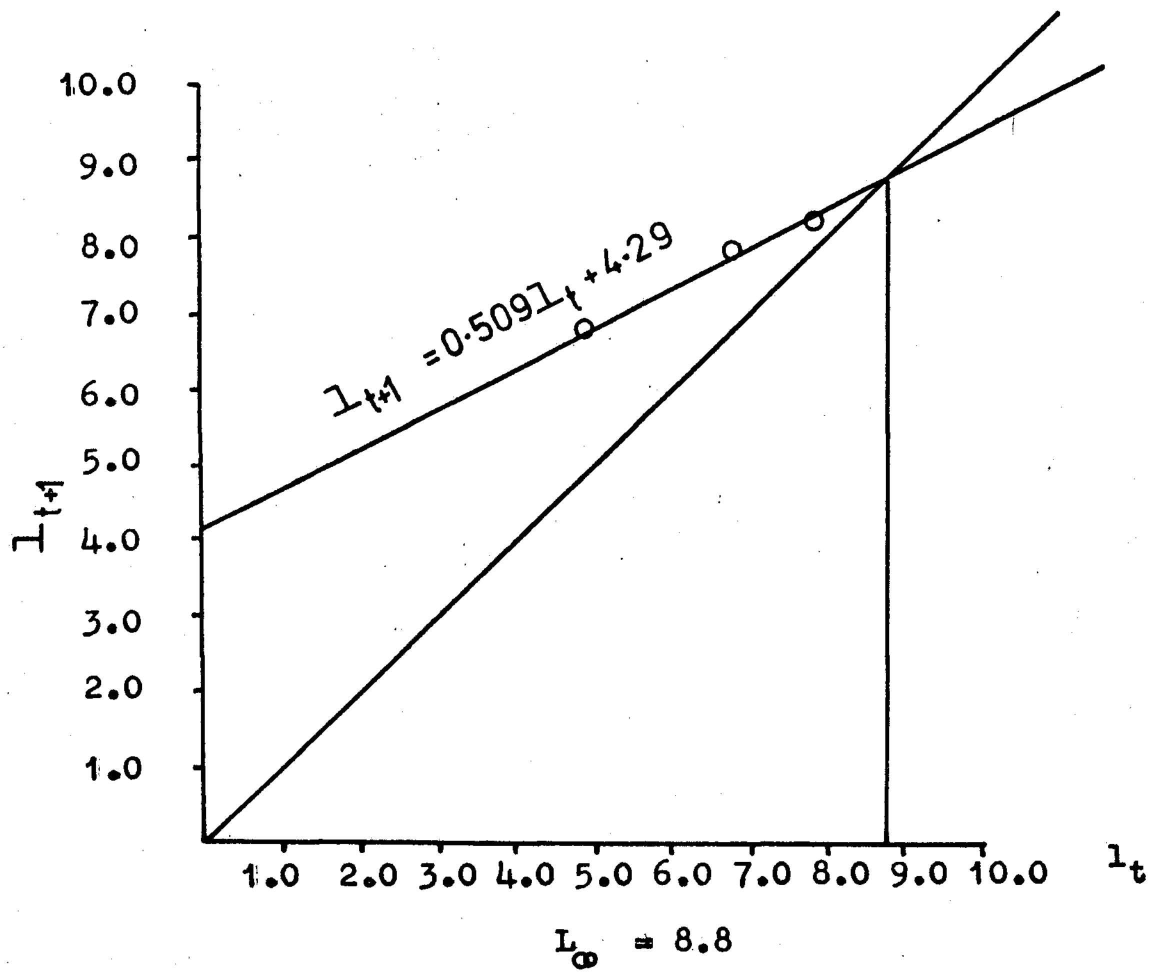
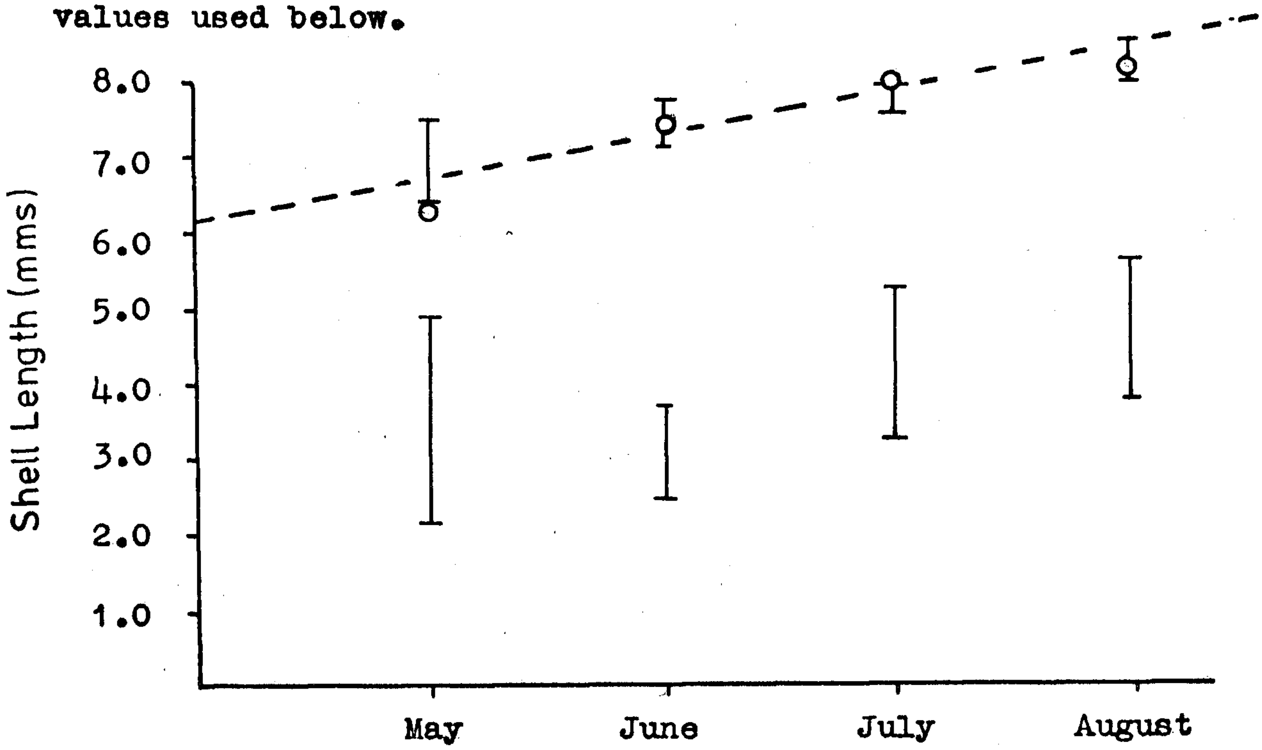


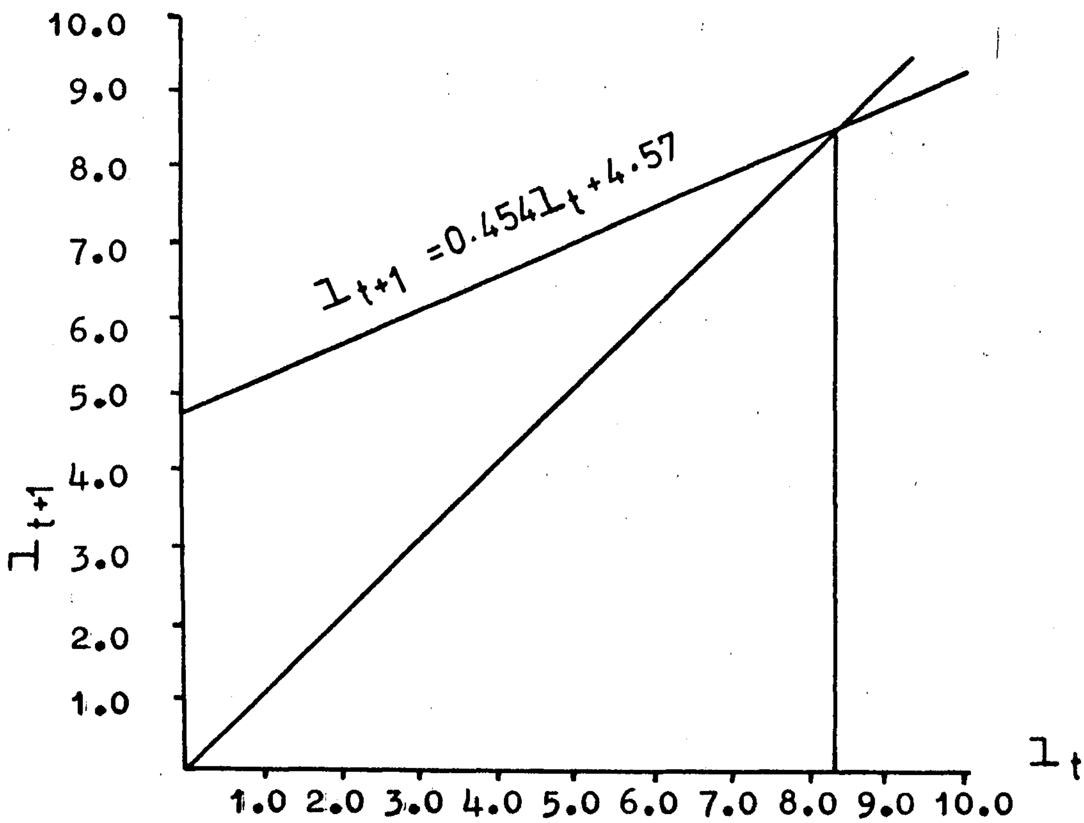
Figure 31. Mid shore Boulders.

The progression of the modes (values ± S.D.) of the shell length of L. rudis through the study period.

Dotted line indicates trend of growth and circles indicate values used below.



Walford-type plot of l_{t+1} against l_t for the determination of L_∞ - the theoretical maximum shell length.



$L_\infty = 8.3$

in the estimates of the growth rates are added in parenthesis to each sample site on table 12, and are indicated on figures 29 - 31 by the lines through the spread of mean values.

The graphical plots to estimate the values of L_{∞} and k for each sample site are also presented on figures 29 - 31.

The final values for the estimated growth rates and longevities at each of the study sites are presented as tables 13 - 15.

The data used to compound all of these results are presented in the appendix as tables XIX to XXX.

4. Discussion

Studies on the growth rates of rough periwinkles by Berry (1961) and Moreteau (1976) have suggested that the shell length at the end of the first year of life is of the order of ten millimetres in the populations with which they have worked. At Marsden, however, few individuals attain this length at all, suggesting that either every rough periwinkle on this shore is less than one year old, or that their growth rates are much slower. Daguzan (1976b) quotes the work of Gaillard (1965) on the influence of latitude on the growth rates of these organisms, and emphasises that southern populations of periwinkles tend to have a greater annual growth rate than those from more northerly latitudes. The effects of exposure may also be significant here however, for the shores used in much of this earlier work have all been more sheltered than Marsden ie. Daguzan (1976b) mentions the abundance of fucoid algae on his shore, Berry (1961) was working in the Thames estuary, and Moreteau (1976) quotes a Ballantine exposure grade of between four and five (ie. semi exposed) for the shore at Roscoff. This may also account for the differences in the maximum shell lengths recorded by these authors from those at Marsden Bay. Thus a slowing of the growth rate of L. rudis at Marsden Bay seems quite possible due perhaps to a combination of the effects of latitude and exposure.

This same study by Gaillard (1965) also compares the growth rates and longevities of populations of periwinkles at different levels on the shore. He has determined that growth rates tend to be faster at higher levels on the shore, but that the longevity tends to be greater for the organisms living at lower levels. The results from Marsden Bay would seem to follow these general trends, as the organisms at Station 10 and on the mid shore boulders grow to a shell length of two point five millimetres after only about six weeks, whilst those at Station 7 require in the order of six months (tables 13 - 15). Equally, the longevity of organisms at Station 7 would seem to be greater than for the other sites, reaching a maximum theoretical longevity of approximately six and one half years (table 13) as against the five years on the mid shore boulders (table 15) and the six years at

Station 10 (table 14). The rates of growth of the youngest individuals estimated for the two higher sample sites also accord quite well with the estimates of Berry (1961), who measured an early growth from approximately nought point seven to three millimetres in about seven weeks for winkles at Whitstable in Kent.

Moreteau (1976) has emphasised that growth is not constant in these organisms however, but is seasonal and may cease during periods of reproductive activity. He considers that many discrepancies between estimates of growth rates may be due to this matter being overlooked.

The values for the longevity of L. rudis at Marsden estimated by this method take no account of the youngest and smallest individuals in the population, but only of the largest size classes that can be recognised in collections and whose progress can be easily followed by repeated samplings. None the less, the values obtained for the longevity of the populations of L. rudis at Marsden would seem to accord quite well with published estimates from elsewhere. Thorson (1946) suggests that the rough periwinkles of the northern North Sea coasts of Denmark may live for about six years, Moreteau (1976) suggests between five and six years at Roscoff (Brittany), Daguzan (1976b) has suggested five years at Penvins (Brittany) and has recorded estimates by Gaillard (1965) of ten years at Dinard, fifteen years at Roscoff and eight years in the estuary of Rance.

The ages at which the males and females attain sexual maturity have also been shown to vary between different levels on the shore. Berry (1961) suggests that females at the higher levels on the shore at Whitstable are mature at an age of approximately eight months, but that lower on the shore the age of maturity is between nine and ten months. Daguzan (1976b) has suggested that on the shore as a whole at Penvins, the young periwinkles become adult at an age of about five and one half months with a shell length of approximately four point three millimetres. At Marsden, sexually mature male L. rudis have been found at the lowest sample site with shell lengths of three point two millimetres (Appendix table XI), and females with shell lengths of three point eight millimetres (Appendix table X). This would put both sexes at around one year old at maturity, with the females being slightly older than the males (table 13). At the highest sample site, the smallest male with a well developed penis had a shell length of three point six millimetres (Appendix table XVI), and the smallest female containing embryos had a shell length of five point eight millimetres (Appendix table XVII). This would seem to put the males at an age of about six months for attaining maturity at this level, and the females at a little over one year (table 14).

Thus little difference is noticeable on this shore between the ages of attaining maturity at different levels, but data collected over a longer period of time may well modify all of these estimates somewhat.

5. Conclusions

(i) Growth rates of the populations of L. rudis at Marsden Bay would appear to be slower than those recorded for other shores. This may be due to the difference in latitude between the North East coast of England and the shores of Brittany in France where much of this earlier work has been done, or to differences in exposure between the shores themselves.

(ii) The growth rates of L. rudis at the lowest sample site at marsden would appear to be slower than those at the highest sites.

(iii) The longevity of individuals at the lowest site appears greater than that for the highest site.

(iv) On this shore, sexual maturity would seem to be attained at ages of between six months and one year in both sexes. Females would appear to reach this state at a later age than males at all three sample sites.

(v) The longevity for L. rudis on this shore would appear to be in the order of five to six years.

SUMMARY

(i) A review of the taxonomic controversy surrounding the rough periwinkle is presented, together with a description of the characteristics of Littorina rudis at Marsden Bay.

(ii) Marsden Bay is described, both geographically and topographically, and an account is given of the distribution and abundance of the typical shore fauna and macrophytic algae. This is a barnacle dominated shore of magnesian limestone, exposed to continuous wave action from the North Sea. Three sites were chosen for the detailed study of L. rudis at Marsden to illustrate any differences that may occur in the population parameters between the upper shore, the mid shore and the lower shore.

(iii) The area on the shore occupied by populations of L. rudis at Marsden Bay is seen to extend from approximately Mid Tide Level to high above the Mean High Water Spring Tide Level, and abundances are recorded of between twenty four and one thousand and forty four individuals per square metre over this range. The abundance is seen to increase with height upshore, together with an increase in the mean shell length of the individuals themselves. The maximum shell length recorded on this shore was eleven point five millimetres.

(iv) The abundance of L. rudis on this shore is not seen to be limited by the availability of food at any of the sample sites investigated. Although the entire shore area is pitted with cracks and crevices of all sizes, a

large proportion of the available habitats are seen to be unoccupied at all levels. It is thus possible that population numbers are maintained at a level below that which both the habitat and the food supply could support by some density dependant process.

(v) The proportion of sexually mature L. rudis at the highest sample site on the shore was consistently greater than at the lower sites throughout the study period. This factor could help to account for the different patterns of abundance noted earlier.

(vi) Growth rates at all levels on the shore at Marsden are shown to be slower than for many other shores recorded in the literature. This may be due to differences in latitude or exposure between the various study areas. The growth rates are faster at the higher levels on the shore, but the longevity is less than is experienced lower down. The longevity would seem to be around five to six years on this shore, with reproductive maturity being attained at ages between six months and one year in both sexes.

ACKNOWLEDGMENTS

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TABLE I contd.

$$c = \frac{0.87 - \frac{14.34 \times 0.23}{25}}{24} = 0.031$$

$$\text{Regression Coefficient} = \frac{0.031}{0.009} = 3.44$$

$$\text{Intercept} = 0.009 - (3.44 \times 0.57) = -1.95$$

$$\text{Log. } y = 3.44 \text{ log. } x - 1.95$$

TABLE II. Legend as for Table I. Station 7. June 1977.

Shell length mms.	Log. shell length = x	x^2	Dry weight mgs.	Log. dry wt. = y	xy.
6.2	0.79	0.62	4.1	0.61	0.48
7.0	0.84	0.70	7.5	0.87	0.73
6.1	0.78	0.61	5.8	0.76	0.59
5.4	0.73	0.53	2.4	0.38	0.28
5.3	0.72	0.52	2.3	0.36	0.26
8.0	0.90	0.81	8.1	0.91	0.82
6.3	0.80	0.64	5.0	0.70	0.56
6.1	0.78	0.61	4.1	0.61	0.47
5.3	0.72	0.52	2.7	0.43	0.31
3.5	0.54	0.29	1.1	0.04	0.02
4.1	0.61	0.37	1.6	0.20	0.12
4.6	0.66	0.43	2.5	0.40	0.26
3.8	0.58	0.34	1.1	0.04	0.02
4.2	0.62	0.38	2.2	0.34	0.21
3.9	0.59	0.35	1.3	0.11	0.06
6.7	0.83	0.69	4.2	0.62	0.51
3.4	0.53	0.28	1.1	0.04	0.02
6.3	0.80	0.64	3.9	0.59	0.47
2.9	0.46	0.21	1.1	0.04	0.02
4.8	0.68	0.46	2.3	0.36	0.24
3.6	0.56	0.31	1.6	0.20	0.11
5.3	0.72	0.52	2.7	0.43	0.31
2.6	0.41	0.17	0.6	-0.22	-0.09
2.0	0.30	0.09	0.3	-0.52	-0.15
3.8	0.58	0.34	1.0	0.00	0.00
6.8	0.83	0.69	4.3	0.63	0.52
4.4	0.64	0.41	2.1	0.32	0.20
3.4	0.53	0.28	0.6	-0.22	-0.12
4.5	0.65	0.42	1.5	0.18	0.12
3.4	0.53	0.28	1.2	0.08	0.04
3.1	0.49	0.24	0.7	-0.15	-0.07
3.6	0.56	0.31	0.7	-0.15	-0.08
4.0	0.60	0.36	0.8	-0.10	-0.06
4.4	0.64	0.41	1.6	0.20	0.13

TABLE II contd:

Shell length mms.	Log.shell length = x	x^2	Dry weight mgs.	Log.dry wt. = y	xy.
3.2	0.50	0.25	0.9	-0.04	-0.02
3.3	0.52	0.27	1.7	0.23	0.12
2.6	0.41	0.17	0.2	-0.70	-0.29
3.1	0.49	0.24	1.1	0.04	0.02
5.7	0.75	0.56	4.7	0.67	0.50
4.7	0.67	0.45	2.2	0.34	0.23
2.7	0.43	0.18	1.3	0.11	0.05
3.2	0.50	0.25	1.4	0.15	0.07
2.7	0.43	0.18	0.7	-0.15	-0.06
2.8	0.45	0.20	0.5	-0.30	-0.13
	27.15	17.58		9.44	7.59

$n = 44$ $(\Sigma x)^2 = 737.12$ $\overline{x} = 0.62$ $\overline{y} = 0.21$ $(\Sigma y)^2 = 89.11$

$\Sigma y^2 = 7.53$

$$\text{Log. } y = 2.16 \text{ log. } x - 1.13$$

TABLE III. Legend as for Table I. Station 7. July 1977.

Shell length mms.	Log. shell length = x	x^2	Dry weight mgs.	Log. dry wt. = y	xy.
6.9	0.84	0.71	4.3	0.63	0.53
5.7	0.75	0.56	2.3	0.36	0.27
6.3	0.80	0.64	6.4	0.81	0.65
6.3	0.80	0.64	3.8	0.58	0.46
6.2	0.79	0.62	3.8	0.58	0.46
5.2	0.72	0.52	3.2	0.50	0.36
5.6	0.75	0.56	2.4	0.38	0.29
4.2	0.62	0.38	1.2	0.08	0.05
3.8	0.58	0.34	0.9	-0.04	-0.02
6.8	0.83	0.69	4.8	0.68	0.56
4.2	0.62	0.38	2.1	0.32	0.20
5.1	0.71	0.50	2.1	0.32	0.23
6.0	0.78	0.61	4.1	0.61	0.48
5.6	0.75	0.56	2.9	0.46	0.35
5.2	0.72	0.52	2.6	0.41	0.30
4.8	0.68	0.46	1.8	0.25	0.17
4.0	0.60	0.36	2.4	0.38	0.23
6.2	0.79	0.62	3.8	0.58	0.46
4.9	0.69	0.48	2.1	0.32	0.22
5.3	0.72	0.52	2.4	0.38	0.27
4.5	0.65	0.42	1.8	0.25	0.16
4.6	0.66	0.44	2.7	0.43	0.28
3.5	0.54	0.29	1.2	0.08	0.04
3.8	0.58	0.34	0.8	-0.10	-0.06
3.5	0.54	0.29	1.0	0.00	0.00
3.8	0.58	0.34	0.7	-0.15	-0.09
3.5	0.54	0.29	0.9	-0.04	-0.02
3.1	0.49	0.24	0.5	-0.30	-0.15
3.3	0.52	0.27	1.0	0.00	0.00
3.8	0.58	0.34	0.8	-0.10	-0.06
3.3	0.52	0.27	1.0	0.00	0.00
3.2	0.50	0.25	1.1	0.04	0.02

TABLE III (contd).

Shell length mms.	Log. shell length = x	x^2	Dry weight mgs.	Log. dry wt. = y	xy.
3.5	0.54	0.29	1.3	0.11	0.06
3.6	0.56	0.31	1.2	0.08	0.04
3.4	0.53	0.28	0.8	-0.10	-0.05
2.8	0.45	0.20	0.7	-0.15	-0.07
2.7	0.43	0.18	0.7	-0.15	-0.06
2.8	0.45	0.20	0.8	-0.10	-0.05
2.9	0.46	0.21	1.0	0.00	0.00
2.9	0.46	0.21	0.5	-0.30	-0.14
3.0	0.48	0.23	0.9	-0.04	-0.02
3.2	0.50	0.25	1.2	0.08	0.04
2.7	0.43	0.18	0.5	-0.30	-0.13
3.3	0.52	0.27	0.7	-0.15	-0.08
2.7	0.43	0.18	0.6	-0.22	-0.09
2.8	0.45	0.20	0.6	-0.22	-0.10
	27.93	17.64		7.24	5.95

$n = 46$ $\quad \overline{x} = 0.61$ $\quad (\Sigma x)^2 = 780.08$ $\quad \overline{y} = 0.16$

$(\Sigma y)^2 = 52.42$ $\quad \Sigma y^2 = 5.25$

$$\text{Log. } y = 2.33 \text{ log. } x - 1.26$$

TABLE IV. Legend as for Table I. Station 10. May 1977.

Shell length mms.	Log. shell length = x	x^2	Dry weight mgs.	Log.dry weight = y	xy.
8.0	0.90	0.81	7.6	0.88	0.79
8.5	0.93	0.86	8.8	0.94	0.87
6.0	0.78	0.61	4.0	0.60	0.47
7.4	0.87	0.76	6.0	0.78	0.68
6.9	0.84	0.70	3.8	0.58	0.49
8.9	0.95	0.90	9.5	0.98	0.93
7.8	0.89	0.79	7.0	0.84	0.75
5.8	0.76	0.58	2.8	0.45	0.34
5.2	0.72	0.52	1.6	0.20	0.14
4.4	0.64	0.41	1.8	0.25	0.16
9.1	0.96	0.92	10.0	1.00	0.96
10.1	1.00	1.00	9.4	0.97	0.97
6.6	0.82	0.67	3.3	0.52	0.43
8.2	0.91	0.83	6.7	0.83	0.75
9.4	0.97	0.94	13.8	1.14	1.10
7.8	0.89	0.79	7.2	0.86	0.76
6.0	0.78	0.61	2.6	0.41	0.32
7.9	0.90	0.81	7.8	0.89	0.80
8.9	0.95	0.90	9.3	0.97	0.92
7.2	0.86	0.74	5.0	0.70	0.60
8.0	0.90	0.81	10.4	1.02	0.92
6.9	0.84	0.70	7.6	0.88	0.74
6.0	0.78	0.61	4.6	0.66	0.51
7.7	0.89	0.79	5.7	0.75	0.67
6.0	0.78	0.61	4.5	0.65	0.51
5.9	0.77	0.59	3.9	0.59	0.45
6.2	0.79	0.62	5.7	0.75	0.59
6.6	0.82	0.67	5.8	0.76	0.62
5.2	0.72	0.52	4.2	0.62	0.45
6.3	0.80	0.64	5.5	0.74	0.59
6.0	0.78	0.61	3.8	0.58	0.45
6.5	0.81	0.66	6.6	0.82	0.66
5.3	0.72	0.52	2.7	0.43	0.31
3.6	0.56	0.31	1.4	0.15	0.08
5.2	0.72	0.52	2.7	0.43	0.31

TABLE IV (contd).

Shell length mms.	Log. shell length = x	x^2	Dry weight mgs.	Log.dry wt. = y	xy.
4.2	0.62	0.38	1.9	0.28	0.17
4.1	0.61	0.37	2.6	0.41	0.25
3.9	0.59	0.35	1.5	0.18	0.11
3.4	0.53	0.28	1.5	0.18	0.09
4.7	0.67	0.45	3.2	0.50	0.33
	32.02	26.16		26.17	22.04

$n = 40$ $\bar{x} = 0.80$ $(\Sigma x)^2 = 1025.3$ $\bar{y} = 0.65$

$(\Sigma y)^2 = 684.87$ $\Sigma y^2 = 19.88$

$$\text{Log. } y = 2.15 \text{ log. } x - 1.07$$

TABLE V. Legend as for Table I. Station 10. June 1977.

Shell length mms.	Log.shell length = x	x^2	Dry weight mgs.	Log.dry wt. = y	xy.
8.2	0.91	0.83	10.2	1.01	0.92
10.2	1.01	1.02	13.1	1.12	1.13
7.6	0.88	0.77	12.0	1.08	0.95
7.1	0.85	0.72	5.4	0.73	0.62
6.6	0.82	0.67	5.6	0.75	0.61
6.3	0.80	0.64	7.9	0.90	0.72
7.3	0.86	0.74	10.6	1.02	0.88
9.2	0.96	0.92	11.4	1.06	1.01
8.9	0.95	0.90	12.1	1.08	1.03
8.5	0.93	0.86	10.0	1.00	0.93
6.5	0.81	0.66	6.4	0.81	0.66
7.2	0.86	0.74	7.7	0.89	0.76
7.3	0.86	0.74	8.3	0.92	0.79
9.1	0.96	0.92	6.5	0.81	0.78
10.5	1.02	1.04	18.6	1.27	1.29
5.5	0.74	0.55	2.6	0.41	0.30
5.7	0.75	0.56	4.5	0.65	0.49
8.3	0.92	0.85	9.4	0.97	0.89
5.8	0.76	0.58	3.8	0.58	0.44
6.5	0.81	0.66	4.4	0.64	0.52
4.8	0.68	0.46	8.3	0.92	0.62
4.7	0.67	0.45	3.3	0.52	0.35
8.2	0.91	0.83	9.8	0.99	0.90
9.7	0.99	0.98	14.2	1.15	1.14
6.9	0.84	0.70	4.9	0.69	0.58
6.5	0.81	0.66	6.6	0.82	0.66
4.9	0.69	0.48	2.9	0.46	0.32
5.1	0.71	0.50	3.2	0.51	0.36
4.4	0.64	0.41	2.8	0.45	0.29
7.4	0.87	0.76	6.0	0.78	0.68
3.8	0.58	0.34	1.1	0.04	0.02
4.5	0.65	0.42	1.4	0.15	0.10
5.5	0.74	0.55	2.9	0.46	0.34
6.1	0.78	0.61	3.1	0.49	0.38

TABLE V (contd).

Shell length mms.	Log. shell length = x	x^2	Dry weight mgs.	Log.dry wt. = y	xy
4.9	0.69	0.48	2.1	0.32	0.22
7.2	0.86	0.74	6.4	0.81	0.70
4.8	0.68	0.46	2.2	0.34	0.23
3.4	0.53	0.28	1.0	0.00	0.00
5.0	0.70	0.49	1.2	0.08	0.06
3.8	0.58	0.34	0.9	-0.04	-0.02
3.0	0.48	0.23	1.3	0.11	0.05
4.3	0.63	0.40	2.7	0.43	0.29
4.4	0.64	0.41	2.4	0.38	0.24
4.0	0.60	0.36	1.5	0.18	0.11
4.3	0.63	0.40	1.7	0.23	0.14
3.7	0.57	0.32	1.8	0.25	0.14
4.7	0.67	0.45	1.7	0.23	0.15
4.0	0.60	0.36	1.9	0.28	0.17
2.9	0.46	0.21	1.2	0.08	0.04
2.5	0.40	0.16	1.3	0.11	0.04
	37.74	29.61		29.92	25.02

$n = 50$ $\overline{x} = 0.75$ $(\Sigma x)^2 = 1424.3$ $\overline{y} = 0.60$

$(\Sigma y)^2 = 895.21$ $\Sigma y^2 = 24.36$

$$\text{Log. } y = 2.17 \text{ log. } x - 1.03$$

TABLE VI. Legend as for Table I. Station 10. July 1977.

Shell length mms	Log.shell length = x	x^2	Dry weight mgs.	Log.dry wt. = y	xy.
8.4	0.92	0.85	7.5	0.87	0.80
7.2	0.86	0.74	4.8	0.68	0.58
7.5	0.87	0.76	7.4	0.87	0.76
8.0	0.90	0.81	6.5	0.81	0.73
7.6	0.88	0.77	8.8	0.94	0.83
5.9	0.77	0.59	3.0	0.48	0.37
6.2	0.79	0.62	3.9	0.59	0.47
7.9	0.90	0.81	7.7	0.89	0.80
6.8	0.83	0.69	4.8	0.68	0.56
8.4	0.92	0.85	9.1	0.96	0.88
6.8	0.83	0.69	3.7	0.57	0.47
9.4	0.97	0.94	10.3	1.01	0.98
5.2	0.72	0.52	2.4	0.38	0.27
6.2	0.79	0.62	3.5	0.54	0.43
4.6	0.66	0.44	2.2	0.34	0.22
6.0	0.78	0.61	4.0	0.60	0.47
6.1	0.78	0.61	4.7	0.67	0.52
6.0	0.78	0.61	3.7	0.57	0.44
6.0	0.78	0.61	4.1	0.61	0.48
6.8	0.83	0.69	3.4	0.53	0.44
8.7	0.94	0.88	12.4	1.09	1.02
8.2	0.91	0.83	10.9	1.04	0.95
6.0	0.78	0.61	4.1	0.61	0.48
5.4	0.73	0.53	3.3	0.52	0.38
5.8	0.76	0.58	3.8	0.58	0.44
8.6	0.93	0.86	11.3	1.05	0.98
4.6	0.66	0.44	1.6	0.20	0.13
7.1	0.85	0.72	7.0	0.84	0.71
6.1	0.78	0.61	2.9	0.46	0.36
6.6	0.82	0.67	4.8	0.68	0.56
6.4	0.81	0.66	5.0	0.70	0.57
4.5	0.65	0.42	3.0	0.48	0.31
6.6	0.82	0.67	5.0	0.70	0.57
7.2	0.86	0.74	4.3	0.63	0.54
6.1	0.78	0.61	4.0	0.60	0.47

TABLE VI (contd).

Shell length mms.	Log. shell length = x	x^2	Dry weight mgs.	Log.dry wt. = y	xy.
7.0	0.84	0.71	4.9	0.69	0.58
6.8	0.83	0.69	5.3	0.72	0.60
9.2	0.96	0.92	10.4	1.02	0.98
7.7	0.89	0.79	9.0	0.95	0.85
6.0	0.78	0.61	4.0	0.60	0.47
5.1	0.71	0.50	3.7	0.57	0.40
5.6	0.75	0.56	3.9	0.59	0.44
7.8	0.89	0.79	9.3	0.97	0.86
8.1	0.91	0.83	7.7	0.89	0.81
5.9	0.77	0.59	3.5	0.54	0.42
4.1	0.61	0.37	0.9	-0.04	-0.02
7.8	0.89	0.79	8.6	0.93	0.83
7.5	0.87	0.76	6.1	0.78	0.68
7.7	0.89	0.79	7.9	0.90	0.80
5.9	0.77	0.59	5.5	0.74	0.57
	41.00	33.95		34.62	29.24

$n = 50$ $\bar{x} = 0.82$ $(\Sigma x)^2 = 1681.00$ $\bar{y} = 0.69$

$(\Sigma y)^2 = 1198.50$ $\Sigma y^2 = 26.52$

$$\text{Log. } y = 2.43 \text{ log. } x - 1.30$$

TABLE VII. Legend as for Table I. Mid shore boulders. May 1977.

Shell length mms.	Log.shell length = x	x^2	Dry weight mgs	Log.dry wt. = y	xy.
7.9	0.90	0.81	5.1	0.71	0.64
4.7	0.67	0.45	1.7	0.23	0.15
7.1	0.85	0.72	3.9	0.59	0.50
6.3	0.80	0.64	2.3	0.36	0.29
6.2	0.79	0.62	2.3	0.36	0.28
4.9	0.69	0.48	2.0	0.30	0.21
6.2	0.79	0.62	1.8	0.25	0.20
5.1	0.71	0.50	1.6	0.20	0.14
5.4	0.73	0.53	1.6	0.20	0.15
5.4	0.73	0.53	1.3	0.11	0.08
4.8	0.68	0.46	1.3	0.11	0.07
4.1	0.61	0.37	0.4	-0.40	-0.24
4.6	0.66	0.43	0.8	-0.10	-0.07
4.3	0.63	0.40	0.7	-0.15	-0.09
5.2	0.72	0.52	1.1	0.04	0.03
4.2	0.62	0.38	0.6	-0.22	-0.14
7.5	0.87	0.76	4.8	0.68	0.59
5.2	0.72	0.52	1.7	0.23	0.16
4.3	0.63	0.40	1.0	0.00	0.00
5.8	0.76	0.58	2.3	0.36	0.27
6.7	0.83	0.69	7.2	0.86	0.71
5.6	0.75	0.56	2.2	0.34	0.25
5.3	0.72	0.52	3.4	0.53	0.38
5.9	0.77	0.59	3.0	0.48	0.37
7.7	0.89	0.79	8.2	0.91	0.81
3.5	0.54	0.29	1.1	0.04	0.02
5.1	0.71	0.50	2.5	0.40	0.28
5.1	0.71	0.50	1.5	0.18	0.13
4.3	0.63	0.40	1.3	0.11	0.07
4.4	0.64	0.41	1.3	0.11	0.07
7.2	0.86	0.74	8.1	0.91	0.78
4.8	0.68	0.46	1.9	0.28	0.19
5.3	0.72	0.52	2.8	0.45	0.32
4.4	0.64	0.41	1.7	0.23	0.15
6.0	0.78	0.61	3.3	0.52	0.40

TABLE VII (contd).

Shell length mms	Log.shell length = x	x^2	Dry weight mgs.	Log.dry wt. = y	xy.
5.2	0.72	0.52	2.5	0.40	0.29
3.9	0.59	0.35	1.7	0.23	0.13
4.7	0.67	0.45	2.7	0.43	0.29
4.9	0.69	0.48	2.3	0.36	0.25
3.9	0.59	0.35	1.7	0.23	0.13
3.6	0.56	0.31	1.6	0.20	0.11
4.1	0.61	0.37	1.6	0.20	0.12
4.1	0.61	0.37	2.0	0.30	0.18
3.5	0.54	0.29	0.9	-0.04	-0.02
3.7	0.57	0.32	0.6	-0.02	-0.01
4.5	0.65	0.42	1.9	0.28	0.18
6.8	0.83	0.69	7.0	0.84	0.70
5.2	0.72	0.52	2.6	0.41	0.29
4.1	0.61	0.37	1.1	0.04	0.02
	35.18	25.14		14.39	11.06

$n = 50$ $\bar{x} = 0.70$ $(\Sigma x)^2 = 1237.60$ $\bar{y} = 0.29$

$(\Sigma y)^2 = 207.07$ $\Sigma y^2 = 7.96$

$$\text{Log. } y = 2.37 \text{ log. } x - 1.37$$

TABLE VIII. Legend as for Table I. Mid shore boulders. June 1977.

Shell length mms.	Log.shell length = x	x^2	Dry weight mgs.	Log.dry wt. = y	xy.
4.7	0.67	0.45	1.3	0.11	0.07
5.1	0.71	0.50	2.3	0.36	0.25
3.7	0.57	0.32	0.3	-0.52	-0.30
5.4	0.73	0.53	3.3	0.52	0.38
4.5	0.65	0.42	1.0	0.00	0.00
4.4	0.64	0.41	1.0	0.00	0.00
5.1	0.71	0.50	2.7	0.43	0.30
5.3	0.72	0.52	3.0	0.48	0.34
3.7	0.57	0.32	0.9	-0.04	-0.02
4.6	0.66	0.43	2.2	0.34	0.22
3.6	0.56	0.31	2.2	0.34	0.19
3.8	0.58	0.34	1.5	0.18	0.10
4.2	0.62	0.38	1.2	0.08	0.05
3.2	0.50	0.25	1.3	0.11	0.05
4.4	0.64	0.41	2.2	0.34	0.22
3.4	0.53	0.28	0.7	-0.15	-0.08
3.5	0.54	0.29	1.1	0.04	0.02
3.3	0.52	0.27	1.3	0.11	0.06
2.6	0.41	0.17	1.3	0.11	0.04
2.5	0.40	0.16	0.9	-0.04	-0.02
2.3	0.36	0.13	0.8	-0.10	-0.04
2.9	0.46	0.21	1.3	0.11	0.05
3.2	0.50	0.25	1.0	0.00	0.00
2.8	0.45	0.20	0.5	-0.30	-0.13
2.5	0.40	0.16	0.8	-0.10	-0.04
7.6	0.88	0.77	8.6	0.93	0.82
6.5	0.81	0.66	3.5	0.54	0.44
6.2	0.79	0.62	3.2	0.50	0.39
8.6	0.93	0.86	9.0	0.95	0.88
9.0	0.95	0.90	11.7	1.07	1.02
7.4	0.87	0.76	4.6	0.66	0.57
6.3	0.80	0.64	3.8	0.58	0.46
7.2	0.86	0.74	3.7	0.57	0.49
5.1	0.71	0.50	2.3	0.36	0.25
6.8	0.83	0.69	3.4	0.53	0.44

TABLE IX. Legend as for Table I. Mid shore boulders. July 1977.

Shell length mms.	Log. shell length = x	x^2	Dry weight mgs.	Log. dry wt. = y	xy.
8.2	0.91	0.83	7.8	0.89	0.81
6.2	0.79	0.62	3.7	0.57	0.45
6.1	0.78	0.61	3.3	0.52	0.41
6.1	0.78	0.61	4.2	0.62	0.48
6.5	0.81	0.66	4.1	0.61	0.49
5.1	0.71	0.50	2.5	0.40	0.28
5.0	0.70	0.49	2.6	0.41	0.29
6.2	0.79	0.62	4.1	0.61	0.48
6.3	0.80	0.64	3.5	0.54	0.43
6.8	0.83	0.69	5.2	0.72	0.60
6.9	0.84	0.71	5.4	0.73	0.61
8.5	0.93	0.86	7.0	0.84	0.78
5.5	0.74	0.55	2.6	0.41	0.30
6.3	0.80	0.64	3.9	0.59	0.47
4.5	0.65	0.42	2.7	0.43	0.28
6.5	0.81	0.66	5.4	0.73	0.59
8.4	0.92	0.85	7.3	0.86	0.79
4.7	0.67	0.45	2.1	0.32	0.21
5.2	0.72	0.52	2.3	0.36	0.26
4.6	0.66	0.44	2.4	0.38	0.25
4.9	0.69	0.48	2.2	0.34	0.23
8.1	0.91	0.83	5.2	0.72	0.66
5.5	0.74	0.55	2.5	0.40	0.30
6.2	0.79	0.62	4.7	0.67	0.53
4.8	0.68	0.46	2.7	0.43	0.29
4.5	0.65	0.42	2.6	0.41	0.27
5.5	0.74	0.55	2.9	0.46	0.34
5.4	0.73	0.53	2.3	0.36	0.26
4.4	0.64	0.41	1.7	0.23	0.15
4.6	0.66	0.44	2.8	0.45	0.30
4.4	0.64	0.41	1.5	0.18	0.12
5.0	0.70	0.49	2.3	0.36	0.25
5.5	0.74	0.55	2.0	0.30	0.22
4.9	0.69	0.48	2.1	0.32	0.22
4.6	0.66	0.44	2.6	0.41	0.27

TABLE IX (contd).

Shell length mms.	Log.shell length = x	x^2	Dry weight mgs.	Log.dry wt. = y	xy.
4.1	0.61	0.37	1.0	0.000	0.00
4.3	0.63	0.40	1.8	0.25	0.16
3.6	0.56	0.31	1.1	0.04	0.02
4.2	0.62	0.38	1.8	0.25	0.16
4.5	0.65	0.42	2.5	0.40	0.26
4.8	0.68	0.46	2.4	0.38	0.26
6.3	0.80	0.64	3.5	0.54	0.43
4.0	0.60	0.36	1.4	0.15	0.09
4.1	0.61	0.37	2.0	0.30	0.18
4.1	0.61	0.37	1.2	0.08	0.05
3.8	0.58	0.34	2.2	0.34	0.20
4.1	0.61	0.37	1.7	0.23	0.14
3.7	0.57	0.32	1.2	0.08	0.05
3.5	0.54	0.29	1.4	0.15	0.08
3.5	0.54	0.29	1.5	0.18	0.10
	35.51	25.72		20.95	15.85

$n = 50$ $\quad \overline{x} = 0.71$ $\quad (\Sigma x)^2 = 1260.96$ $\quad \overline{y} = 0.42$

$(\Sigma y)^2 = 121.66$ $\quad \Sigma y^2 = 11.03$

$$\text{Log. } y = 2.00 \text{ log. } x - 1.00$$

TABLE X. The state of sexual maturity of individual *L. rudis* at Marsden Bay. Station 7. May 1977.

Measurements in millimetres.

Grade 1 males:	Shell Length	Penis Length	No. of Glands
	4.8	2.3	8
	7.4	2.1	8
	3.6	1.2	5

Grade 1 females:	Shell Length	State of Embryos
	4.8	V - S
	5.2	V - F
	3.8	V - F

Immature:	4.5	4.3	3.4	2.9	3.9	3.3	3.1
	5.4	3.5	3.7	3.0	3.7	3.2	3.1
	3.6	3.2	3.0	3.4	2.7	1.3	1.2

Total number examined = 27
Total number mature = 6
Percent mature = 22.2 %

Mean Length of Whole Sample = 3.67 ± 1.22
Mean Length of Mature Males = 5.27 ± 1.94
Mean Length of Mature Females = 4.60 ± 0.72
Mean Length of Penis = 1.87 ± 0.58

TABLE XI. The state of sexual maturity of individual *L. rudis* at Marsden Bay. Station 7. June 1977.

Measurements in millimetres.

Grade 1 males:

Shell Length	Penis Length	No. of Glands
3.8	1.2	9
3.2	1.3	7
5.4	2.2	7
6.3	2.8	11
6.1	2.6	7
6.3	2.6	8

Grade 1 females:

Shell Length	State of Embryos
4.5	V - F
5.7	V - F
4.7	V only
7.0	V - F
6.1	V - F
4.6	V - F
8.0	V - F

Immature:

6.8	4.0	2.6	2.8	3.5	3.9
3.4	4.4	3.1	6.2	4.1	6.7
3.4	3.2	2.7	5.3	3.8	3.4
3.1	3.3	2.7	5.3	4.2	2.9
4.8	3.6	5.3	2.6	2.0	4.4
3.6					

Total number examined = 44
Total number mature = 13
Percent mature = 29.5%

Mean Length of Whole Sample = 4.4 ± 1.5
Mean Length of Mature Males = 5.2 ± 1.4
Mean Length of Mature Females = 5.8 ± 1.3
Mean Length of Penis = 2.28 ± 0.78

TABLE XII. The state of sexual maturity of individual *L. rudis* at Marsden Bay, Station 7. July 1977.

Measurements in millimetres.

Grade 1 males:	Shell Length	Penis Length	No. of Glands
	6.9	1.4	Poorly developed
	6.2	3.1	9
	6.8	1.4	Glands developing

Grade 2 males:

(penis as small stub).	6.3	5.1	6.2	3.6
	5.6	5.6	4.9	

Grade 1 females:	Shell Length	State of Embryos
	6.3	V - F
	6.0	V - F

Immature:	5.7	5.2	4.2	3.8	4.2	5.2
	4.8	4.0	5.3	4.5	4.6	3.5
	3.8	3.5	3.8	3.5	3.1	3.3
	3.8	3.3	3.2	3.5	3.4	2.8
	2.7	2.8	2.9	2.9	3.0	3.2
	2.7	3.3	2.7	2.8		

Total number examined = 46
Total number mature = 5
Percent mature = 10.9%

Mean Length of Whole Sample = 4.2 ± 1.3
Mean Length of Mature Males = 6.6 ± 0.4
Mean Length of Mature Females = 6.1 ± 0.2
Mean Length of Penis = 2.0 ± 1.0

TABLE XIII. The state of sexual maturity of individual <u>L. rudis</u> at Marsden Bay. Boulder. May 1977.

Measurements in millimetres.

Grade 1 males:

Shell Length	Penis Length	No. of Glands
7.1	3.9	8
6.2	2.4	9
7.5	2.0	12
5.9	3.3	10
6.8	2.4	8
5.2	2.6	8

Grade 1 females:

Shell Length	State of Embryos
6.7	V - F
5.3	V - F
7.7	V - F
7.2	V - F

Immature:

7.9	6.2	5.1	4.8	4.3	5.2	5.6
4.7	4.9	5.4	4.1	5.2	4.3	3.5
6.3	6.2	5.4	4.6	4.2	5.8	5.1
5.1	4.3	4.8	5.3	4.4	6.0	5.2
3.9	4.7	4.9	3.9	3.6	4.1	4.1
4.1	3.5	3.7	4.5	4.1		

Total number examined = 50
Total number mature = 10
Percent mature = 20%

Mean Length of Whole Sample = 5.18 $\pm$ 1.13
Mean Length of Mature Males = 6.45 $\pm$ 0.84
Mean Length of Mature Females = 6.72 $\pm$ 1.03
Mean Length of Penis = 2.77 $\pm$ 0.70

TABLE XIV. The state of sexual maturity of individual *L. rudis* at Marsden Bay. Boulder. June 1977.

Grade 1 males:

Shell Length	Penis Length	No. of Glands
6.5	1.2	8
9.0	2.4	12
7.4	2.4	8
6.3	2.3	7
7.2	2.6	8
7.5	3.5	11
6.1	3.1	12
4.7	2.1	8

Grade 1 females:

Shell Length	State of Embryos
7.6	V - F
6.2	V - F
7.8	V - F
6.8	V - C
8.2	V - F

Immature:

8.6	5.8	6.2	5.1	4.7	5.4
5.1	6.8	5.1	4.7	5.1	4.5
6.8	5.6	5.0	4.0	3.7	4.4
5.1	5.3	3.7	4.6	3.6	3.8
4.2	3.2	4.4	3.4	3.5	3.3
2.6	2.5	2.3	2.9	3.2	2.8
2.5					

Total number examined = 50
Total number mature = 13
Percent mature = 26.0%

Mean Length of Whole Sample = 5.10 $\pm$ 1.74
Mean Length of Mature Males = 6.84 $\pm$ 1.26
Mean Length of Mature Females = 7.32 $\pm$ 0.81
Mean Length of Penis = 2.45 $\pm$ 0.68

TABLE XV. The state of sexual maturity of individual *L. rudis* at Marsden Bay. Boulders. July 1977.

Measurements in millimetres.

Grade 1 males:

Shell Length	Penis Length	No. of Glands
8.5	3.3	13
8.4	3.3	10
8.1	3.1	10

Grade 2 males (penis as small stub, but glands often present):

6.2	5.1	6.2	6.3	6.5	5.2
5.4	6.1	5.0	5.5	4.5	4.7
4.9	4.4	5.0	4.1	4.3	3.6

Grade 1 females:

Shell Length	State of Embryos
8.2	V - F
6.8	V - F

Immature:

6.1	6.5	6.3	6.9	4.6	5.5
6.2	4.8	4.5	5.5	4.6	4.4
5.5	4.9	4.6	4.2	4.5	4.8
6.3	4.0	4.1	4.1	3.8	4.1
3.7	3.5	3.5			

Total number examined = 50
Total number mature = 5
Percent mature = 10.0 %

Mean Length of whole sample = 5.3 ± 1.3
Mean Length of mature males = 8.3 ± 0.2
Mean Length of mature females = 7.5 ± 1.0
Mean Length of penis = 3.2 ± 0.1

TABLE XVI. The state of sexual maturity of individual *L. rudis* at Marsden Bay. Station 10. May 1977.

Measurements in millimetres.

Grade 1 males:	Shell Length	Penis Length	No. of Glands
	6.9	2.5	12
	7.7	3.1	9
	5.3	2.7	8
	3.6	1.4	9
	5.2	2.0	5
	4.2	1.6	8
	8.5	3.4	9
	10.1	4.8	9
	8.2	5.9	8
	7.8	3.1	10/11
	7.9	3.2	14 *
	7.2	3.2	6

(* glands present in two rows).

Grade 1 females:	Shell Length	State of Embryos
	8.0	V - F
	6.6	V - F
	6.5	Mainly V
	8.9	V - F
	7.8	V - C
	8.0	V - F

Immature:							
9.1	6.0	7.4	6.9	5.8	5.2	4.4	
6.6	9.4	6.0	8.9	6.0	6.0	5.9	
6.2	5.2	6.3	6.0	4.1	3.9	3.4	4.7

Total number examined = 40
Total number mature = 18
Percent mature = 45.0 %

Mean length of whole sample = 6.54 ± 1.69
Mean length of mature males = 6.88 ± 1.92
Mean length of mature females = 7.63 ± 0.92
Mean length of penis = 3.07 ± 1.27

TABLE XVII. The state of sexual maturity of individual *L. rudis* at Marsden Bay. Station 10. June 1977.

Measurements in millimetres.

Grade 1 males:	Shell Length	Penis Length	No. of Glands
	7.1	2.6	10
	9.2	4.1	13
	6.5	3.4	12
	4.8	1.7	7
	6.9	1.5	9
	6.5	2.8	8
	4.4	2.1	8
	6.1	2.9	8
	7.2	1.5	10

Grade 1 females:	Shell Length	State of Embryos
	8.2	V - F
	7.6	V - F
	7.3	V - F
	8.9	V - F
	8.5	V - F
	7.2	V - F
	7.3	V - F
	10.5	V - F
	8.3	V - F
	5.8	V - C
	8.2	V - F
	9.7	V - F

Immature:	10.2	9.1	6.5	5.1	4.5	4.8	3.8	6.6
	5.5	4.7	7.4	5.5	3.4	3.0	6.3	5.7
	4.9	3.8	4.9	5.0	4.3	4.4	4.0	4.3
	3.7	4.7	4.0	2.9	2.5			

Total number examined = 50
Total number mature = 21
Percent mature = 42.0 %

Mean length of whole sample = 6.0 ± 2.0
Mean length of mature males = 6.5 ± 1.4
Mean length of mature females = 8.1 ± 1.2
Mean length of penis = 2.5 ± 0.9

TABLE XVIII. The state of sexual maturity of individual *L. rudis* at Marsden Bay. Station 10. July 1977. Measurements in millimetres.

Grade 1 males:

Shell Length	Penis Length	No. of Glands
8.4	3.6	8
7.2	3.2	12
7.9	3.5	13
6.8	2.8	9
7.0	2.9	10
7.7	3.2	12
6.0	2.8	12
7.5	3.3	9
7.7	2.4	7

Grade 1 females:

Shell Length	State of Embryos
7.5	Mainly V
8.0	Mainly V
9.4	V - F
8.4	Mainly V
8.7	V - F
8.2	Mainly F
8.6	V - F
7.2	V - F
7.8	V - F
8.1	V - F
7.8	V - F

Immature:

5.9	4.6	6.0	6.6	5.9	6.2	6.0	6.0
9.2	6.4	7.6	6.8	5.2	6.0	5.8	7.1
6.6	6.1	6.2	6.8	6.1	5.4	4.6	6.1
4.5	6.8	5.1	5.6	5.9	4.1		

Total number examined = 50
Total number mature = 20
Percent mature = 40.0 %

Mean length of whole sample = 6.7 ± 1.2
Mean length of mature males = 7.3 ± 0.7
Mean length mature females = 8.1 ± 0.6
Mean length of penis = 3.1 ± 0.4

TABLE XIX. Frequency distribution of L. rudis at Marsden Bay. Station 7. May 1977.

Size Class (mm)	Mid Point (mm)	Nos.	%	Log_{10} y	Δ Log_{10} y
0.0 - o.9					
1.0 - 1.9	1.5	1	2	0.000	1.000
2.0 - 2.9	2.5	10	21	1.000	0.301
3.0 - 3.9	3.5	20	42	1.301	-0.456
4.0 - 4.9	4.5	7	15	0.845	-0.544
5.0 - 5.9	5.5	2	4	0.301	0.477
6.0 - 6.9	6.5	6	12	0.778	-0.778
7.0 - 7.9	7.5	1	2	0.000	
8.0 - 8.9					
9.0 - 9.9	9.5	1	2	0.000	
		48			

TABLE XX. Frequency distribution of L. rudis at Marsden Bay. Station 10. May 1977.

Size Class	Mid Point	Nos.	%	$Log_{10}y$	$\Delta Log_{10} y$
0.0 - 0.9					
1.0 - 1.9					
2.0 - 2.9					
3.0 - 3.9	3.5	7	6	0.845	0.586
4.0 - 4.9	4.5	27	25	1.431	-0.109
5.0 - 5.9	5.5	21	19	1.322	0.093
6.0 - 6.9	6.5	26	23	1.415	-0.211
7.0 - 7.9	7.5	16	14	1.204	-0.163
8.0 - 8.9	8.5	11	10	1.041	-0.740
9.0 - 9.9	9.5	2	2	0.301	-0.301
10.0 - 10.9	10.5	1	1	0.000	
		111			

TABLE XXI. Frequency distribution of L. rudis at Marsden Bay. Boulders. May 1977.

Size Class (mm)	Mid Point (mm)	Nos.	%	Log_{10} y	Δ Log_{10} y
0.0 - 0.9	0.5	7	7	0.845	-0.845
1.0 - 1.9	1.5	1	1	0.000	1.114
2.0 - 2.9	2.5	13	13	1.114	0.284
3.0 - 3.9	3.5	25	24	1.398	-0.036
4.0 - 4.9	4.5	23	22	1.362	-0.107
5.0 - 5.9	5.5	18	17	1.255	-0.352
6.0 - 6.9	6.5	8	8	0.903	-0.058
7.0 - 7.9	7.5	7	7	0.845	-0.845
8.0 - 8.9	8.5	1	1	0.000	
		103			

TABLE XXII. Frequency distribution of L. rudis at Marsden Bay. Station 7. June 1977.

Size Class (mm)	Mid Point (mm)	Nos.	%	Log_{10} y	Δ Log_{10} y
0.0 - 0.5					
0.5 - 1.0					
1.0 - 1.5	1.25	3	1	0.477	1.091
1.5 - 2.0	1.75	37	8	1.568	0.210
2.0 - 2.5	2.25	60	13	1.778	0.108
2.5 - 3.0	2.75	77	18	1.886	-0.080
3.0 - 3.5	3.25	64	15	1.806	-0.074
3.5 - 4.0	3.75	54	12	1.732	-0.109
4.0 - 4.5	4.25	42	9	1.623	-0.281
4.5 - 5.0	4.75	22	5	1.342	0.163
5.0 - 5.5	5.25	32	7	1.505	-0.204
5.5 - 6.0	5.75	20	5	1.301	-0.260
6.0 - 6.5	6.25	11	2	1.041	0.135
6.5 - 7.0	6.75	15	3	1.176	-0.398
7.0 - 7.5	7.25	6	1.25	0.778	-0.477
7.5 - 8.0	7.75	2	0.5	0.301	-0.301
8.0 - 8.5	8.25	1	0.25	0.000	
		446			

TABLE XXIII. Frequency distribution of L. rudis at Marsden Bay. Station 10. June 1977.

Size Class (mm)	Mid Point (mm)	Nos.	%	Log_{10} y	Δ Log_{10} y
0.0 - 0.5					
0.5 - 1.0					
1.0 - 1.5					
1.5 - 2.0	1.75	8	1.5	0.903	0.602
2.0 - 2.5	2.25	32	6.0	1.505	0.211
2.5 - 3.0	2.75	52	9.75	1.716	0.176
3.0 - 3.5	3.25	48	9.0	1.681	0.118
3.5 - 4.0	3.75	63	12.0	1.799	0.027
4.0 - 4.5	4.25	67	12.5	1.826	-0.086
4.5 - 5.0	4.75	55	10.0	1.740	-0.107
5.0 - 5.5	5.25	43	8.0	1.633	-0.142
5.5 - 6.0	5.75	31	6.0	1.491	-0.060
6.0 - 6.5	6.25	27	5.0	1.431	0.060
6.5 - 7.0	6.75	31	6.0	1.491	0.000
7.0 - 7.5	7.25	31	6.0	1.491	-0.169
7.5 - 8.0	7.75	21	4.0	1.322	-0.281
8.0 - 8.5	8.25	11	2.0	1.041	-0.263
8.5-9.0	8.75	6	1.0	0.778	-0.477
9.0 - 9.5	9.25	2	0.5	0.301	-0.301
9.5 - 10.0	9.75	1	0.25	0.000	0.301
10.0 - 10.5	10.25	2	0.5	0.301	
		531			

TABLE XXIV. Frequency distribution of <u>L. rudis</u> at Marsden Bay. Boulders. June 1977.

Size Class (mm)	Mid Point (mm)	Nos.	%	Log_{10} y	Δ Log_{10} y
0.0-0.5					
0.5-1.0					
1.0-1.5					
1.5-2.0	1.75	11	2	1.041	0.867
2.0-2.5	2.25	81	13	1.908	0.088
2.5-3.0	2.75	99	15	1.996	0.041
3.0-3.5	3.25	109	17	2.037	-0.139
3.5-4.0	3.75	79	12	1.898	-0.029
4.0-4.5	4.25	74	11	1.869	-0.106
4.5-5.0	4.75	58	9	1.763	-0.120
5.0-5.5	5.25	44	7	1.643	-0.245
5.5-6.0	5.75	25	4	1.398	-0.036
6.0-6.5	6.25	23	4	1.362	-0.158
6.5-7.0	6.75	16	2	1.204	-0.301
7.0-7.5	7.25	8	1	0.903	0.051
7.5-8.0	7.75	9	1	0.954	-0.954
8.0-8.5	8.25	1	0.3	0.000	0.699
8.5-9.0	8.75	5	1	0.699	-0.699
9.0-9.5	9.25	1	0.3	0.000	
9.5-10.0	9.75	1	0.3	0.000	
		644			

TABLE XXV. Frequency distribution of <u>L. rudis</u> at Marsden Bay. Station 7. July 1977.

Size Class (mm)	Mid Point (mm)	Nos.	%	Log_{10} y	Δ Log_{10} y
0.0-0.5					
0.5-1.0					
1.0-1.5	1.25	1	0.5	0.000	1.000
1.5-2.0	1.75	10	2	1.000	0.724
2.0-2.5	2.25	53	13	1.724	0.082
2.5-3.0	2.75	64	16	1.806	-0.021
3.0-3.5	3.25	61	15	1.785	-0.037
3.5-4.0	3.75	56	14	1.748	-0.032
4.0-4.5	4.25	52	13	1.716	-0.198
4.5-5.0	4.75	33	8	1.518	-0.087
5.0-5.5	5.25	27	7	1.431	-0.176
5.5-6.0	5.75	18	4	1.255	-0.051
6.0-6.5	6.25	16	4	1.204	-0.505
6.5-7.0	6.75	5	1	0.699	0.079
7.0-7.5	7.25	6	1	0.778	-0.301
7.5-8.0	7.75	3	1	0.477	-0.477
8.0-8.5	8.25	1	0.5	0.000	
		406			

TABLE XXVI. Frequency distribution of L. rudis at Marsden Bay. Station 10. July 1977.

Size Class (mm)	Mid Point (mm)	Nos.	%	Log_{10} y	Δ Log_{10} y
0.0-0.5					
0.5-1.0					
1.0-1.5					
1.5-2.0					
2.0-2.5	2.25	6	0.6	0.778	0.713
2.5-3.0	2.75	31	3.1	1.491	0.287
3.0-3.5	3.25	60	6.0	1.778	0.007
3.5-4.0	3.75	61	6.1	1.785	0.134
4.0-4.5	4.25	83	8.4	1.919	0.010
4.5-5.0	4.75	85	8.6	1.929	-0.015
5.0-5.5	5.25	82	8.3	1.914	0.040
5.5-6.0	5.75	90	9.0	1.954	0.063
6.0-6.5	6.25	104	10.5	2.017	-0.088
6.5-7.0	6.75	85	8.5	1.929	0.104
7.0-7.5	7.25	108	10.9	2.033	-0.109
7.5-8.0	7.75	84	8.4	1.924	-0.125
8.0-8.5	8.25	63	6.3	1.799	-0.322
8.5-9.0	8.75	30	3.0	1.477	-0.331
9.0-9.5	9.25	14	1.4	1.146	-0.544
9.5-10.0	9.75	4	0.4	0.602	-0.125
10.0-10.5	10.25	3	0.3	0.477	-0.477
10.5-11.0	10.75	1	0.1	0.000	0.000
11.0-11.5	11.25	1	0.1	0.000	
		995			

TABLE XXVII. Frequency distribution of L. rudis at Marsden Bay. Boulders. July 1977.

Size Class (mm)	Mid Point (mm)	Nos.	%	Log_{10} y	Δ Log_{10} y
0.0-0.5					
0.5-1.0	0.75	4	0.8	0.602	-0.301
1.0-1.5	1.25	2	0.4	0.301	0.602
1.5-2.0	1.75	8	1.6	0.903	0.273
2.0-2.5	2.25	15	3.1	1.176	0.380
2.5-3.0	2.75	36	7.3	1.556	0.207
3.0-3.5	3.25	58	11.7	1.763	0.036
3.5-4.0	3.75	63	12.7	1.799	0.007
4.0-4.5	4.25	64	12.9	1.806	-0.014
4.5-5.0	4.75	62	12.5	1.792	-0.060
5.0-5.5	5.25	54	10.9	1.732	-0.079
5.5-6.0	5.75	45	9.1	1.653	-0.176
6.0-6.5	6.25	30	6.1	1.477	-0.222
6.5-7.0	6.75	18	3.6	1.255	-0.301
7.0-7.5	7.25	9	1.8	0.954	0.222
7.5-8.0	7.75	15	3.1	1.176	-0.331
8.0-8.5	8.25	7	1.4	0.845	-0.544
8.5-9.0	8.75	2	0.4	0.301	-0.301
9.0-9.5	9.25	1	0.2	0.000	0.000
9.5-10.0	9.75	1	0.2	0.000	
10.0-10.5	10.25	1	0.2	0.000	
		495			

TABLE XXVIII. Frequency distribution of L. rudis at Marsden Bay. Station 7. August 1977.

Size Class (mm)	Mid Point (mm)	Nos.	%	Log_{10} y	Δ Log_{10} y
0.0-0.5					
0.5-1.0					
1.0-1.5	1.25	2	0.5	0.301	0.699
1.5-2.0	1.75	10	2.2	1.000	0.785
2.0-2.5	2.25	61	13.5	1.785	0.060
2.5-3.0	2.75	70	15.5	1.845	0.036
3.0-3.5	3.25	76	16.9	1.881	-0.075
3.5-4.0	3.75	64	14.2	1.806	-0.107
4.0-4.5	4.25	50	11.1	1.699	-0.119
4.5-5.0	4.75	38	8.4	1.580	-0.089
5.0-5.5	5.25	31	6.9	1.491	-0.129
5.5-6.0	5.75	23	5.1	1.362	-0.362
6.0-6.5	6.25	10	2.2	1.000	-0.398
6.5-7.0	6.75	4	0.9	0.602	0.301
7.0-7.5	7.25	8	1.8	0.903	-0.602
7.5-8.0	7.75	2	0.5	0.301	-0.301
8.0-8.5	8.25	1	0.3	0.000	
		450			

TABLE XXIX. Frequency distribution of <u>L. rudis</u> at Marsden Bay. Station 10. August 1977.

Size Class (mm)	Mid Point (mm)	Nos.	%	Log_{10} y	Δ Log_{10} y
0.0-0.5					
0.5-1.0					
1.0-1.5					
1.5-2.0	1.75	4	0.4	0.602	0.301
2.0-2.5	2.25	8	0.8	0.903	0.528
2.5-3.0	2.75	27	2.6	1.431	0.250
3.0-3.5	3.25	48	4.7	1.681	0.138
3.5-4.0	3.75	66	6.5	1.819	0.050
4.0-4.5	4.25	74	7.3	1.869	0.080
4.5-5.0	4.75	89	8.7	1.949	-0.030
5.0-5.5	5.25	83	8.1	1.919	0.005
5.5-6.0	5.75	84	8.2	1.924	0.030
6.0-6.5	6.25	90	8.8	1.954	0.010
6.5-7.0	6.75	92	9.0	1.964	0.014
7.0-7.5	7.25	95	9.3	1.978	0.013
7.5-8.0	7.75	98	9.6	1.991	-0.140
8.0-8.5	8.25	71	7.0	1.851	-0.170
8.5-9.0	8.75	48	4.7	1.681	-0.339
9.0-9.5	9.25	22	2.2	1.342	-0.138
9.5-10.0	9.75	16	1.6	1.204	-0.903
10.0-10.5	10.25	2	0.3	0.301	-0.301
10.5-11.0	10.75	1	0.2	0.000	
		1018			

TABLE XXX. Frequency distribution of L. rudis at Marsden Bay. Boulders. August 1977.

Size Class (mm)	Mid Point (mm)	Nos.	%	Log_{10} y	Δ Log_{10} y
0.0-0.5					
0.5-1.0	0.75	1	0.2	0.000	0.301
1.0-1.5	1.25	2	0.4	0.301	0.398
1.5-2.0	1.75	5	0.7	0.699	0.623
2.0-2.5	2.25	21	3.2	1.322	0.359
2.5-3.0	2.75	48	7.2	1.681	0.145
3.0-3.5	3.25	67	10.1	1.826	0.043
3.5-4.0	3.75	74	11.2	1.869	0.093
4.0-4.5	4.25	83	12.5	1.919	0.030
4.5-5.0	4.75	89	13.4	1.949	-0.092
5.0-5.5	5.25	72	10.8	1.857	-0.125
5.5-6.0	5.75	54	8.1	1.732	-0.069
6.0-6.5	6.25	46	6.9	1.663	-0.172
6.5-7.0	6.75	31	4.7	1.491	-0.111
7.0-7.5	7.25	24	3.6	1.380	-0.339
7.5-8.0	7.75	11	1.7	1.041	0.214
8.0-8.5	8.25	18	2.7	1.255	-0.255
8.5-9.0	8.75	10	1.5	1.000	-0.523
9.0-9.5	9.25	3	0.5	0.477	-0.176
9.5-10.0	9.75	2	0.4	0.301	-0.301
10.0-10.5	10.25	1	0.2	0.000	
		662			