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*Some aspects of the biology of Gibbula Cineraria (L.)
with observations on Gibbula Umbilicalis (Da Costa)
and Gibbula Pennanti (PHIL.). (Mollusca :
Prosobranchia)*

D. A. S. Smith

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ABSTRACT

Some aspects of the biology of Gibbula cineraria(L.) with observations on Gibbula umbilicalis(da Costa) and Gibbula pennanti(Phil.). (MOLLUSCA:PROSOBRANCHIA).

by D.A.S.SMITH

The primary aim of this study was to establish the breeding season, growth rate and life history of Gibbula cineraria in north-east England. Sampling was carried out over a period of 13 months on the rocky shore at Whitburn, County Durham. The population was sampled at five different tidal levels and on different substrata.

The principal conclusions were that breeding took place over a long period from September to March. The young animals settled from the plankton mainly below tidal levels and moved up into the tidal zone at about 18 months of age when they became sexually mature for the first time. Rapid growth continued for about three years. There was good evidence that the population at higher shore levels was derived by immigration from lower levels and it was also clear that there was a general movement of animals downshore in the autumn and upshore in the spring. The boulder areas of the beach supported a much higher density of animals than the open rocks and this was probably due to greater protection from predators. Density also declined with increase in level above Chart Datum. The rate of growth was in every case greater where the population density was low which suggested that intra-specific competition for resources was occurring.

G. cineraria populations, together with Gibbula umbilicalis and Gibbula pennanti where they occurred, were examined at many other stations between the Faeroe Islands(^{62°}~~28~~ N.) and the Canary Islands(28° N.). It was concluded that where two or three species of Gibbula were present on the same shore inter-specific competition occurred which was variously manifested by a restricted distribution, slower growth rate or reduced density. Two biogeographical effects were also noted: a gradual size diminution and restricted intertidal range from north to south.

SOME ASPECTS OF THE BIOLOGY OF
GIBBULA CINERARIA (L.) WITH OBSERVATIONS
ON GIBBULA UMBILICALIS (DA COSTA) AND
GIBBULA PENNANTI (PHIL.).
(MOLLUSCA : PROSOBRANCHIA)

By

D. A. S. SMITH, M.A. (Cantab.)

A thesis presented to the University of Durham for the Degree
of Master of Science

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I. INTRODUCTION

Gibbula is a genus of prosobranch gastropod belonging to the family Trochidae. Gaillard (1953, 1954a, and 1954b) lists 18 species for France of which 13 are confined to the Mediterranean whilst the other five occur on the Atlantic seaboard. With the possible exception of some eastern Mediterranean species, Gaillard's check-list for France probably applies to all European waters and certainly to the Atlantic coasts.

Of the five Atlantic species, Gibbula tumida (Montagu) ranges from Iceland to the Mediterranean being found offshore from 7-174 metres (4-95 fathoms). Gibbula magus (L.) occurs fairly commonly between the British Isles and the Mediterranean from the lowest level of equinoctial spring tides down to 73 metres (40 fathoms). The remaining three species of Gibbula which are found intertidally on the Atlantic coasts of Europe, Gibbula cineraria (L.), Gibbula umbilicalis (da Costa) and Gibbula pennanti (Phil.) form the subject of study presented in this thesis.

Previous work.

The literature contains numerous references to these three species in a wide variety of contexts but the only reasonably complete ecological study of any species is that of Williams (1964) on G. umbilicalis. Other major works are Deshpande's (1957) study

of British trochids which is mainly anatomical and Gaillard's (1952-54) publications which are for the most part taxonomic. Observations on reproduction have been made by Robert (1902) for G. magus, Gersch (1936) for G. tumida and G. cineraria, Lebour (1937) for G. cineraria and G. umbilicalis and Gaillard (1952) for G. permanti but none of these authors has given anything like a complete account and the subject remains little known. Compared with Littorina and Patella, Gibbula has received little attention from seashore ecologists.

Aims of the work.

The primary aim of this study was to answer certain questions regarding the ecology of G. cineraria. For this purpose, an area of rocky shore at Whitburn, County Durham, inhabited by a large population of G. cineraria, was chosen as the main study area. Investigations at Whitburn involved the collection of G. cineraria at intervals of approximately three months from areas of standard size in order to provide data for the elucidation of the life history and growth rate. Collections were made simultaneously at several different levels and from distinct substrata on the beach to investigate differences in growth rate, population density and population structure between various habitats. Answers were also sought to the following questions: What is the mean life expectancy? What is the annual mortality rate in each age group? Do animals migrate from one part of the shore to another? What is their spatial distribution and which factors limit density and growth rates?

The secondary aim was to look at G. cineraria and the other two littoral species, G. umbilicalis and G. pennanti in a wider context. Many seashore ecologists e.g. Lewis (1953, 1954, 1957), Lewis and Powell (1960), Evans (1947a, 1947b), Southward (1953), Southward and Crisp (1954), Crisp and Southward (1958), Crisp and Fischer-Piette (1959), Ballantine (1961), and Moyses and Nelson-Smith (1963) recorded observations on the habitat preferences of Gibbula species and it was clear from these accounts and also from my own observations that all three species had similar habitat preferences which can be summarized as follows:-

- (1) All species are most abundant in semi-exposed and sheltered areas.
- (2) G. cineraria and G. umbilicalis extend further into shelter than G. pennanti, though all are rare in extremes of shelter from wave action.
- (3) G. cineraria and G. umbilicalis extend further towards exposure in the north, particularly on flat mussel dominated shores and G. umbilicalis is less common in shelter.
- (4) All species avoid extremes of exposure to wave action.
- (5) All species are intolerant of brackish water, particularly G. pennanti.

- (6) All species, but particularly G. umbilicalis, are reduced in numbers by heavy weed cover.
- (7) All species prefer broken or flat rock surfaces and boulders avoiding verticals and steep faces.
- (8) All species are intolerant of scour by sand or pebbles, and of turbid water and mud, though not to the same extent. G. cineraria is the most tolerant and G. pennanti the least.
- (9) All species avoid surf and strong tidal currents. Here, G. umbilicalis is the most and G. pennanti the least tolerant.
- (10) G. cineraria, G. umbilicalis, and G. pennanti (personal observation) are common in pools, particularly near the upper limit of their vertical range.

Because of the similar habitat preferences interspecific competition seemed theoretically probable where two or more species occurred on the same shore and their vertical ranges overlapped. I have attempted to show that interspecific competition does occur in Gibbula and that it affects such matters as zonation, growth, and density. Observations were also made on the predators of Gibbula and after a review of my own and other author's observations, I advance an hypothesis to explain the importance of Gibbula habitats in relation to protection from predators. Finally, visits to a large number of rocky shores between the Canary Islands (28°N.) and the Faeroes (62°N.) have enabled me to observe all three species

over their entire geographical range. I am therefore able to make some general points with regard to changes in zonation, habitats, growth, competitors, predators and breeding seasons based on a wide range of latitudes and climatic conditions.

Geographical range of the species studied.

G. cineraria is described by Fretter and Graham (1962) as "abundant Iceland to Mediterranean", and Gaillard (1953) gives the distribution on French coasts as "Atlantic and Channel". According to Crisp and Southward (1958) the range is from northern Norway to the Mediterranean. Thorson (1941) gives the northern part of its range in some detail recording its presence on the west coast of Iceland and the Norwegian coast north of the Lofoten Islands, and absence from the north, south, and east coasts of Iceland, from Greenland and north-east America.. Apparently the species is rare and of spasmodic occurrence in Iceland and he suggests that, although it may be transported there from time to time through its pelagic larval phase, it is not a regular member of the fauna. I have found G. cineraria in northern Norway at Tromso (69°40'N.) and the abundant populations in the Faeroe Islands (62°N.) are discussed in section VII (p.85). References to the occurrence of this species in the Mediterranean are probably incorrect since Gaillard (op.cit.) excludes mention of it there. I have searched extensively myself from Spain to the Lebanon and failed to find a single specimen. The species is present on the Atlantic coast of the Iberian Peninsular (personal observation), although rarely in the inter-

tidal zone, and north Africa (Crisp and Fischer-Piette, 1959).

It is possible that it occurs in deeper water in the Mediterranean and perhaps further south in the Atlantic though no record for the latter has been found. It occurs on all coasts round the British Isles.

G. cineraria is therefore a species of Boreal distribution ranging from northern Norway (the exact northern limit is unknown) to Atlantic North Africa. It is probably no more than a casual in Iceland.

The northern limit of G. umbilicalis is known in some detail. Rendell (1956) records it in the Orkney Islands and Lewis (1951) gives full details of its local distribution on the north coast of the Scottish mainland. On the west coast of Scotland the species is more generally distributed and according to Lewis (1957) and Lewis and Powell (1960) it occurs on most suitable beaches southwards to the north shore of the Solway Firth. The distribution around the Irish Sea is intermittent. Crisp and Southward (1958) studied its distribution in the English Channel and found that, along with several other littoral species including Chthamalus stellatus (Poli), Monodonta lineata (da Costa), Balanus perforatus Bruguiere, Patella aspera Lamarck, Patella depressa Pennant and Littorina neritoides (L.), it becomes locally scarce on the Dorset coast and reaches its eastern limit on the west coast of the Isle of Wight. On the French side however it extends as far as Calais. Apart from the areas mentioned G. umbilicalis is abundant on all

suitable shores in Ireland, Wales and south-west England. It is entirely absent from the east coasts of the British Isles between Caithness and the Isle of Wight and it does not occur across the North Sea in the Low Countries, Denmark or Norway. The range outside Britain includes the Channel Islands and French coast from Calais westwards and southwards and the whole Atlantic coast of Spain and Portugal. Nicklés (1947) gives the southern limit as Mauretania (approximately 20°N.). I have found it in Tenerife (Canary Islands) and Madeira but was unable to find it in the Azores. Gaillard (1954b) makes no reference to it in the Mediterranean and my own searches there have failed to reveal it.

G. umbilicalis is therefore, a warm temperate species showing a Lusitanian distribution, Its British range shows that it tolerates northern latitudes only where the influence of the Gulf Stream/Atlantic Drift is strong.

The third species, G. pennanti, was only recognized as being distinct from G. umbilicalis in 1954 (Gaillard 1954a, 1954b). The southern limit of this species is unknown though it certainly extends south to Portugal (personal observation). I was unable to find it in the Canaries, Madeira or the Azores. The northern limit is reached on the French side of the English Channel at Alderney where it is abundant (Crisp and Southward 1958 and personal observation). The eastern limit in the Channel is at Barfleur on the north-east tip of the Cherbourg Peninsula.

The distribution of G. pennanti is therefore similar to that of G. umbilicalis though not extending so far north.

II. A POPULATION OF GIBBULA CINERARIA: GROWTH AND
LIFE HISTORY.

INTRODUCTION

Study area

The area of rocky shore chosen for the study is situated immediately north of Sunderland in County Durham (map ref. NZ 415615). The aspect is E.N.E. and although the shore is open to the North Sea, the prevailing winds blow predominantly offshore and heavy wave battery is unusual. Most of the locality conforms closely to the definition of a semi-exposed shore (Lewis 1964 p.289) though restricted areas might be called sheltered.

The shore offers two rather distinct types of environment to its inhabitants. The greater area to the north consists of boulders and pebbles, more or less unsorted both as regards size and origin. The majority are derived from magnesian limestone which outcrops in the cliffs, but there is also a great quantity of rock of Carboniferous origin and some Cretaceous and Devonian fragments which have been transported considerable distances. Igneous and metamorphic pebbles also occur, probably derived from local boulder clay. The majority of the boulders are small enough to be thrown by a heavy sea and sufficiently soft to be smashed in the process.

Lying to the south of the boulder bank, between it and a sandy beach, is an area of magnesian limestone reefs, much broken and pitted, and of very uneven profile. This area is quite

distinct ecologically from the boulder bank, though boulders have accumulated in depressions in some places.

Both areas are backed by low cliffs, consisting of magnesian limestone overlain by boulder clay. Both deposits, though particularly the latter, are much subject to marine erosion. After equinoctial spring tides, the whole shore may be covered for several weeks by mud derived from the boulder clay and the area is never completely free of it.

The ecological differences between the boulder bank and reef areas may be summarized as follows:-

- (1) The boulder bank is almost devoid of Fucaee excepting a lower fringe of Fucus serratus L. which rarely exceeds 50% cover. On the reefs, F. serratus below and Fucus spiralis L. above, give 100% cover in places. In between, mixed populations of Fucus vesiculosus L. and Ascophyllum nodosum (L.) Le Jol. flourish in the more sheltered areas.
- (2) Balanus balanoides (L.) and Patella vulgata L. dominate the boulder bank. On the reefs they are also present but only dominant on upstanding areas which are too exposed for Fucaee.
- (3) Littorina saxatilis (Olivi) is the most abundant prosobranch over most of the boulder bank, excepting the lower part where G. cineraria replaces it. Littorina littorea (L.) and L. saxatilis (on rocks and in pools) and Littorina littoralis (L.) (on weed) are the dominant species on the reefs. G. cineraria is much scarcer here.

A third distinct type of habitat is offered by the rock pools. A large pool supporting abundant growths of Laminaria digitata (Huds.) Lamour., Laminaria saccharina (L.) Lamour., F. serratus and Halidrys siligiosa (L.) Lyngh. occurs at +0.5 ft. C.D. Many small pools are found at all levels on the reefs, and several extensive pools are present on both reefs and the boulder bank between + 8.6 ft. C.D. and + 9.6 ft. C.D.

The sublittoral fringe is uniformly clothed by L. digitata above and Laminaria hyperborea (Gunn.) Fosl. below, the latter extending well below tidal levels. Most of this area is well carpeted by Rhodophyceae: Gigartina stellata (Stackh.) Batt. and Corallina officinalis L. beneath L. digitata and Rhodymenia palmata (L.) Grev. under and epiphytic upon L. hyperborea. An additional feature of the sublittoral fringe is the presence of Lithothamnion spp. which give almost 100% cover on rocks and boulders. Their most important effect is to cement boulders firmly together making them stable. At this low level, therefore, the contrasting features of the reefs and boulder areas are by no means so apparant.

Methods

To calculate rates of growth and density changes it was clear that fairly regular collections would have to be made from the same area. Monthly collections were clearly desirable but time was not available for this. Accordingly it was decided

to make a collection in each of the seasons winter, spring, summer and autumn with a second winter collection as an overlap. It became clear later that the months March to June were of particular interest and collections were made monthly during this period. All collections for growth studies were made at + 2.3 ft. C.D. \pm 1.3 ft. on the boulder bank (a belt easily recognized by the presence of F. serratus and therefore requiring no special marking). The precise locality sampled was changed on each occasion to avoid error due to collecting from the same area twice.

Collections at four levels on the boulder bank viz - 1.1 ft. C.D., + 0.3 ft. C.D., + 4.8 ft. C.D., and + 8.6 ft. C.D. were made periodically so that a comparison of population structure and growth rates at different levels could be made. Some collections were made from the limestone reefs at + 2.3 ft. C.D. and + 4.8 ft. C.D. to assess the effect of the considerable habitat differences from the boulder bank independently of the changes due to level.

The animals were collected from quadrats of size one square metre. The quadrat frame was placed on the beach and all large weeds removed after inspection for G. cineraria. All boulders and pebbles within the quadrat were then removed and inspected. Due to the very large numbers of pebbles this proved to be a time consuming process, from a half to one hour being

required to complete each square. The aim was to remove every snail from each quadrat and in the case of the adults this was probably largely realized. The younger animals, particularly the youngest which measure no more than 3 mm. in breadth, were almost certainly consistently under-represented in spite of the greatest care exercised in searching them out. The young were entirely confined to the undersides of stones where they often occupied pits and crevices and they were frequently difficult both to spot and remove. Wherever possible at least five quadrats were completed on each occasion. Full details of all the Whitburn samples are given in Appendix I.

The G. cineraria from each quadrat were preserved in 5% formaldehyde in seawater. They were taken to the laboratory where they were measured and the breeding condition investigated. Each quadrat sample was treated separately so that an estimate both of the mean and standard deviation of population density could be calculated.

Two measurements were used to provide an index of growth: the shell breadth from the outer edge of the outer lip to the opposite point on the body whorl and the height of the shell from umbilicus to apex. Measurements were approximated to the nearest millimetre.

Results

Analysis of growth at + 2.3 ft. C.D.

Figures 1 and 2 show the results obtained from the seven sets of samples taken. It is clear that all samples show a

polymodal frequency distribution, though the number of modes apparent from visual inspection is not constant. For instance most of the height kite diagrams (Figure 2) show four modes but that for December shows only three. The majority of the kite diagrams for breadth (Figure 1) show three modes and that for November only two. The differences between the kite diagrams for height and breadth can only be explained if the growth rate in these two dimensions is not identical and indeed this must be the case since the ratio breadth: height is generally about 2:1 in young specimens and approaches 1:1 in adults.

In order to distinguish the size groups with greater precision, each monthly sample was subjected to analysis using arithmetical probability paper by the method described by Harding (1949). By calculating the percentage of each size group and plotting these percentages cumulatively, a curve was obtained from which the various component size classes (=year classes) could be identified. The data for each size class were plotted separately on the assumption that where the frequency distribution for a whole population was polymodal, that for each of its components would conform to a normal distribution. A normal distribution plotted cumulatively on paper of this type would give a straight line and accordingly if straight lines could be obtained for each component size class, the assumption would be justified. Additional advantages of the method were that the mean and standard deviation of each component

Figure 1.

The distribution of size groups (shell breadth in mm.)
at +2.3 ft.C.D., Whitburn 1962-63.

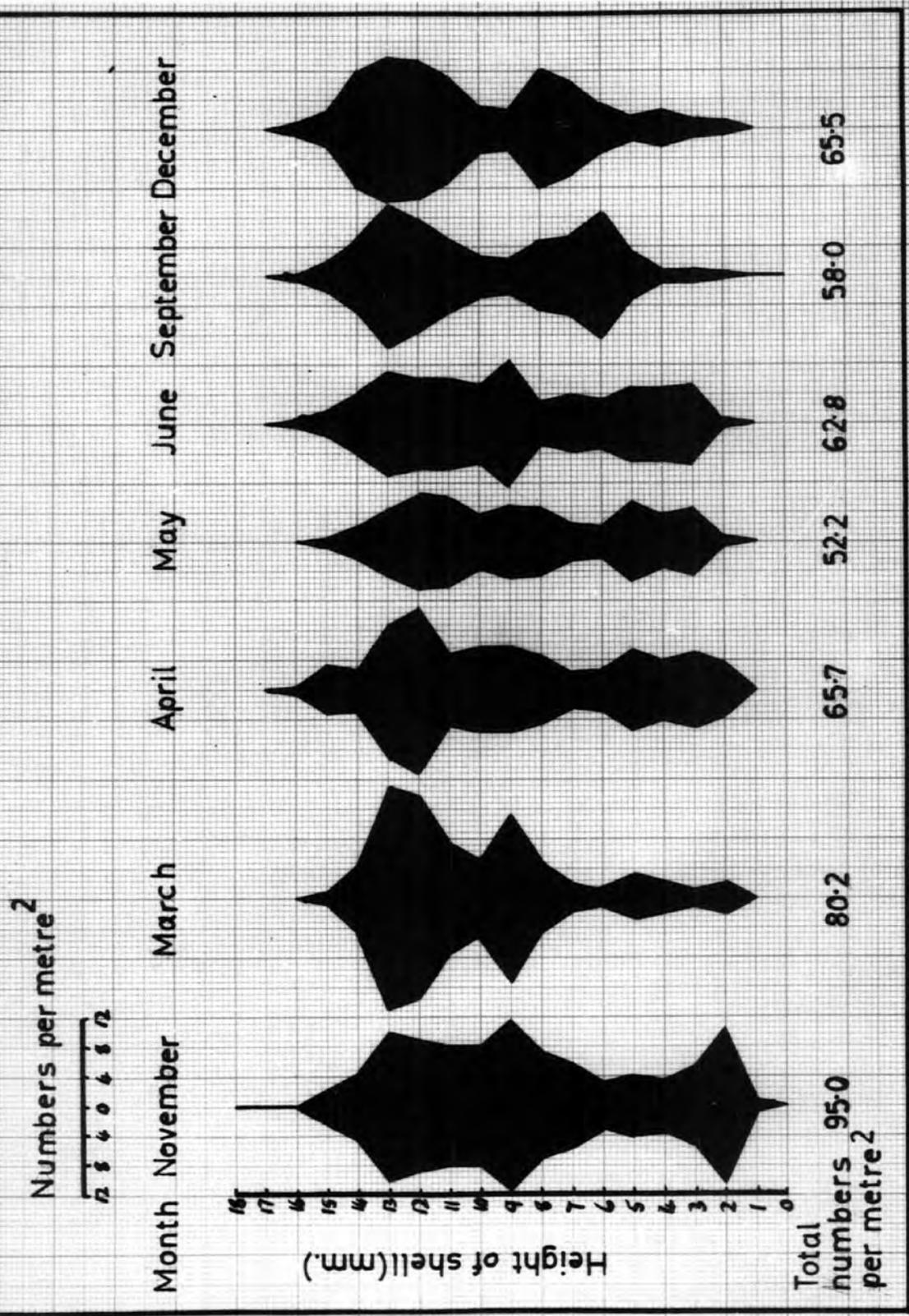


Figure 2.

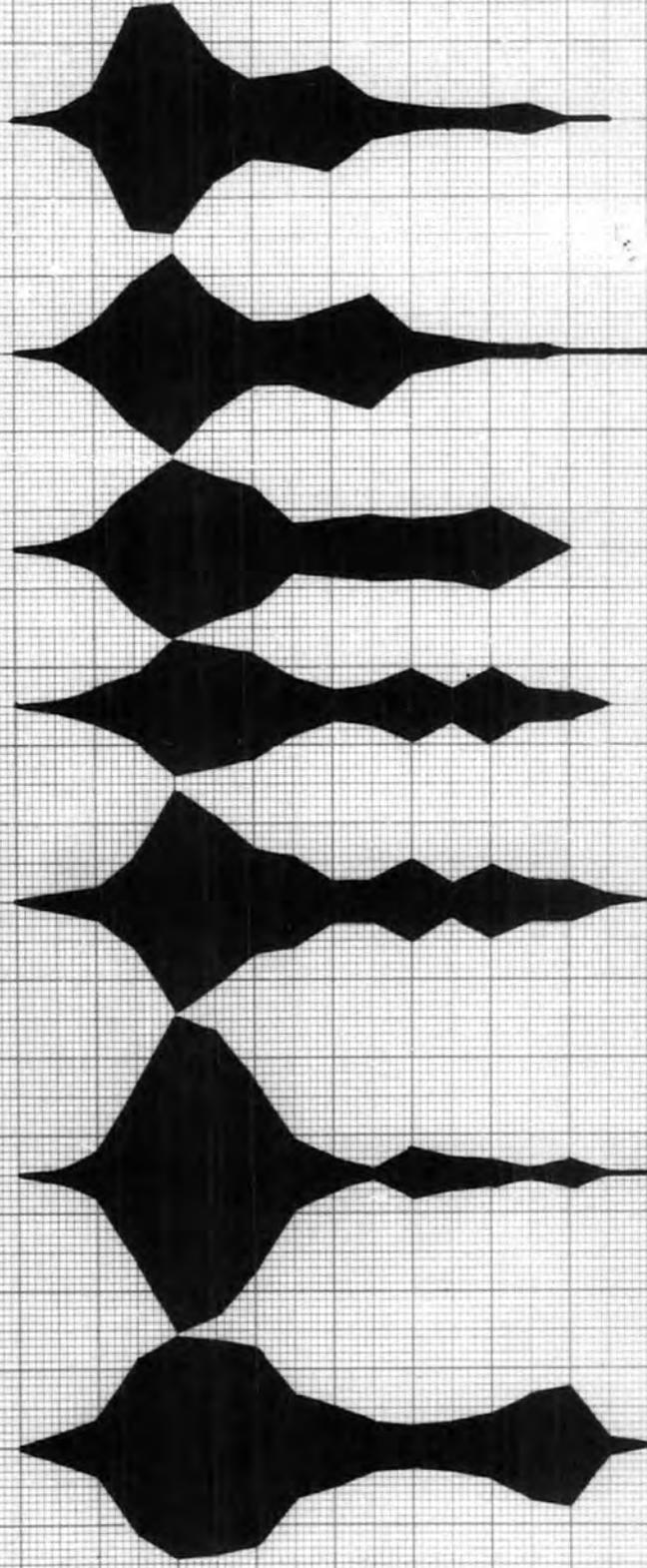
The distribution of size groups (shell height in mm.)
at Whitburn 1962-63 at +2.3 ft.C.D.

Numbers per metre²

15 10 5 0 5 10 15

Month November March April May June September December

Breadth of shell(mm.)
17
16
15
14
13
12
11
10
9
8
7
6
5
4
3
2



Total numbers per metre²
95.0 80.2 65.7 52.2 62.8 58.0 65.5

and the percentage each component constituted of the total, could be read directly from the graph. Two examples of the 40 analyses made during this study are shown in Figures 3 and 4. It was generally not difficult to recognize the straight lines and if after replotting the composite graph, the points were close to the original ones it was clear that a correct solution had been found. If the straight lines were not obtained at the first attempt, trial and error was employed until the best possible fit had been obtained. The histograms in figures 3 and 4 are not part of the method but have been added in order to show its advantages, particularly apparent for the November sample (Figure 3), in demonstrating the presence of four size classes where only two were clearly apparent from the untreated data.

When work was begun in November 1962, four size classes could be distinguished with dimensions for shell breadth at 13.6 ± 1.1 mm., 11.0 ± 1.5 mm., 6.3 ± 1.2 mm. and 3.9 ± 0.6 mm. (Figure 3). These size classes were labelled respectively A, B, C and D. Four size classes could also be recognized after analysis of the shell height data. The height dimensions were respectively 11.7 ± 1.3 mm., 8.2 ± 1.2 mm., 4.5 ± 1.0 mm., and 1.8 ± 0.7 mm. In addition, a fifth size class of height 13.8 ± 0.6 mm. was recognized but it proved impossible to distinguish these from size class A in all other samples (see Appendix III).

Figure 3.

Analysis of the size groups at +2.3 ft.C.D. at
Whitburn in November 1962.

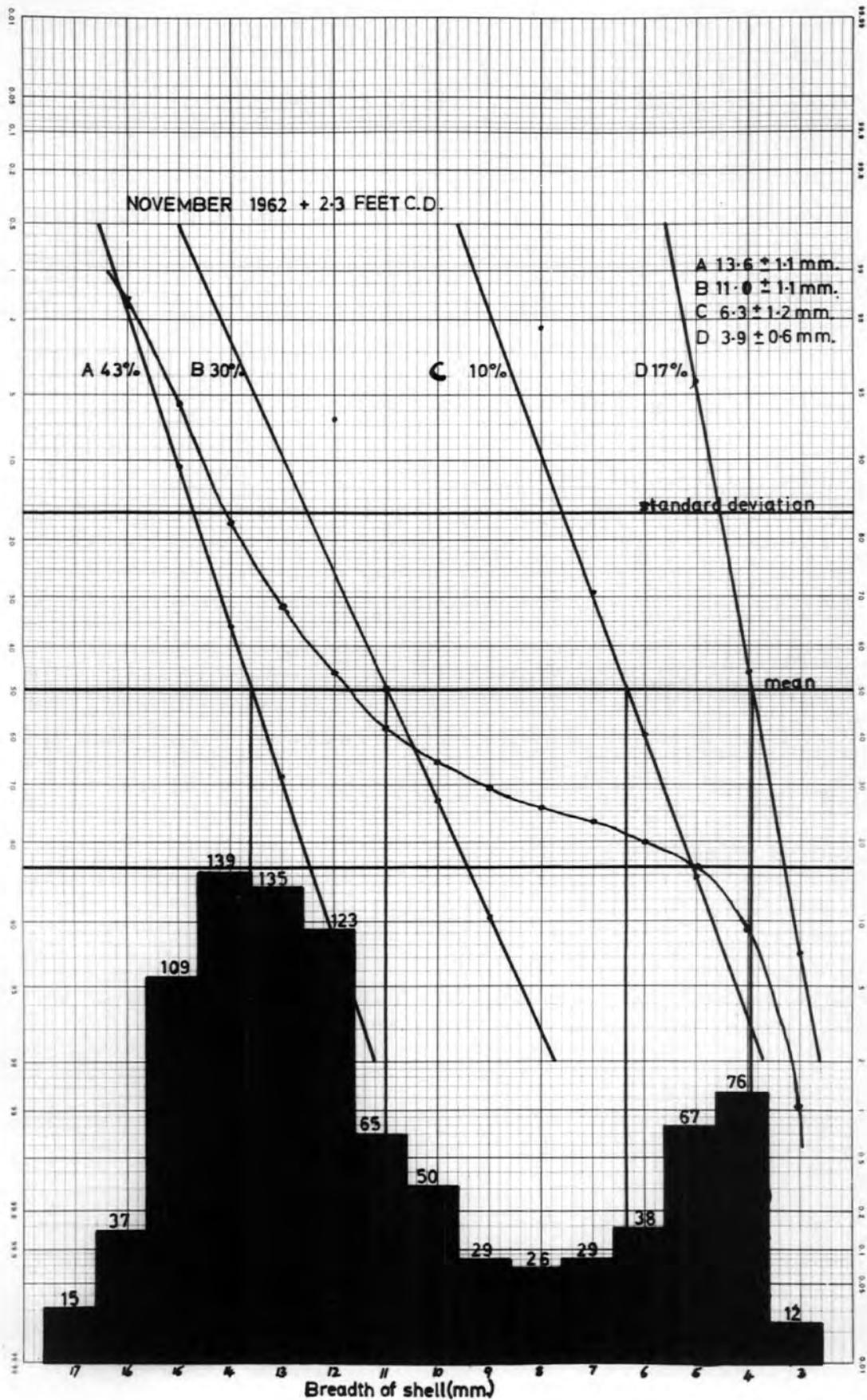
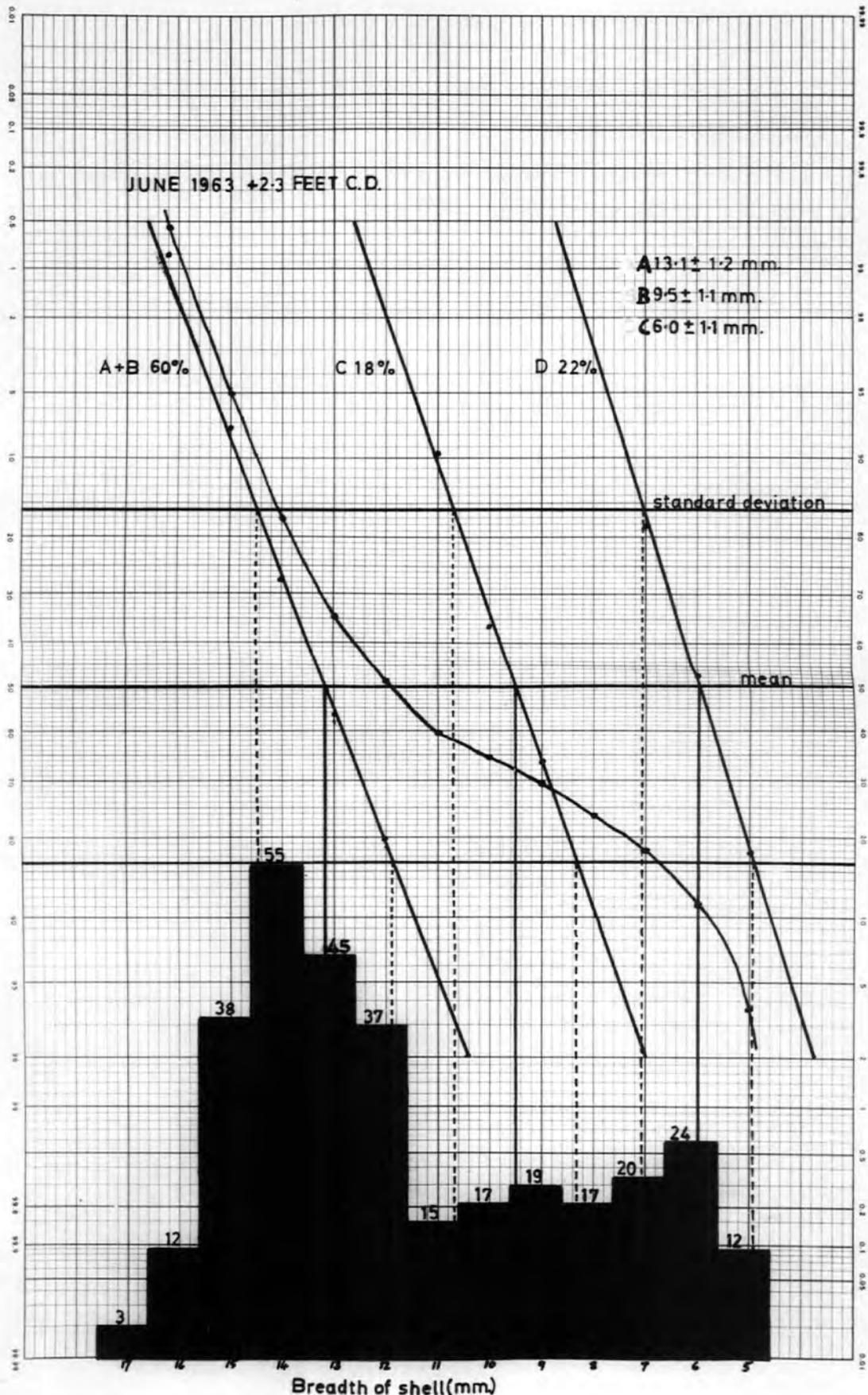


Figure 4.

Analysis of the size groups at +2.3 ft.C.D. at
Whitburn in June 1963.



The percentages indicated by the analysis were as follows (height figures in parentheses): size class A, 43% (38% + 5% for the fifth large size class); B, 30% (29%); C, 10% (12%); and D, 17% (17%). It was clear that the two independent analyses agreed closely. While size class A probably contained elements from two or more year groups, which explained its high proportion of the total, size classes C and D were clearly under-represented. One possible source of error, sampling bias, has already been mentioned, but even taking this into account, it seemed likely that these size classes, particularly D which represented the young brood, were not present within the sampling area in near sufficient numbers to account for the large adult size class. Mortality in the newly settled size class was probably very high (evidence will be produced to this effect) and large numbers would be needed to account for the high density of adults recorded. Therefore, it seemed likely at the outset that size classes C and D were centred elsewhere, possibly below tidal levels.

Owing to the extreme cold of the 1962-63 winter it proved impractical to collect on the shore in January and February since the work had to be done with bare hands. Samples were collected in March, April, May, June, September and December, 1963 and treated in the manner already outlined. The results are given in Table I and Appendices II - IV. It will be seen that size

classes A, B, C and D were recognizable in every sample until June when size classes A and B become so close in size as to be indistinguishable on the breadth data. The height data (Appendix III) show that these two populations had merged by September, but were still distinguishable in June. A fifth size class, labelled E, appeared in small numbers in September and was still present in December. This represented the new year class which was never present in anything like the numbers of size class D in the previous autumn.

TABIE I

The analysis of a population of G. cineraria between + 1.0 ft. and + 3.6 ft. C.D. at Whitburn between November 1962 and December 1963. The figures in the upper line give the mean shell breadth (mm.) with the standard deviation in parentheses. The figures in the lower line refer to the proportion each/year group comprises of the whole population.

Month	Number of samples	Mean nos. 2 per metre	Number examined	Size/year classes (year of origin in parentheses)				
				A (1959)	B (1960)	C (1961)	D (1962)	E (1963)
Nov.	10	95.0 (37.6)	950	13.6 (1.1)	11.0 (1.5)	6.3 (1.2)	3.9 (0.6)	—
				43%	30%	10%	17%	—
Mar.	5	80.0 (50.4)	401	13.3 (0.8)	11.5 (1.4)	7.0 (1.3)	3.9 (0.7)	—
				63%	26%	8%	3%	—
Apr.	3	65.7 (16.7)	197	13.3 (0.8)	11.0 (0.9)	7.6 (0.8)	4.5 (0.7)	—
				45%	25%	15%	15%	—
May	6	52.2 (17.3)	313	13.7 (0.8)	11.5 (0.9)	7.7 (0.8)	5.2 (1.4)	—
				25%	40%	18%	17%	—
June	5	62.8 (16.9)	314	13.1 (1.2)	merged with A	9.5 (1.1)	6.0 (1.1)	—
				60%		18%	22%	—
Sept.	10	58.0 (15.2)	580	13.5 (1.2)	"	9.3 (1.0)	7.3 (1.3)	3.2 (0.5)
				60%		30%	9.5%	0.5%
Dec.	8	67.5 (19.7)	525	13.6 (1.2)	"	9.9 (0.9)	6.8 (1.0)	4.6 (0.4)
				60%		25%	7.5%	2.5%

Although samples were obtained at irregular intervals, it was possible to fit growth lines to the results obtained (Figure 5). Where the results indicate a marked change in rate of growth, separate growth lines have been fitted for each phase. The data proved insufficient to calculate a growth line for size class D between November and March and from September to December. Lines of best fit were calculated by the method of least squares using the formula :

$$y = mx + c$$

where y = size, x = time, m = slope and c = the value of the intercept on the y axis.

Comparison of growth rates at different levels.

During April, 1963, samples were taken from five different levels on the boulder bank between + 8.6 ft. C.D. and - 1.0 ft. C.D. in order to compare the distribution of size groups at the various levels.

Figure 6 illustrates the differences of size distribution between three samples F, G and J separated from each other by height increments above chart datum of approximately 4 ft. It is apparent that the distribution of size groups (shell breadth in mm.) is different in all three cases. Analysis with probability paper showed sample J from + 0.3 ft. C.D. to have four modes at 12.6 ± 1.0 mm., 10.1 ± 0.9 mm., 6.4 ± 0.9 mm. and 0.7 mm. (Table II). Three modes at 14.7 ± 1.0 mm., 11.6

Figure 5.

The growth of Gibbula cineraria at +2.3 ft.C.D. at Whitburn 1962-63. The figures refer to the growth rate in mm. per month.

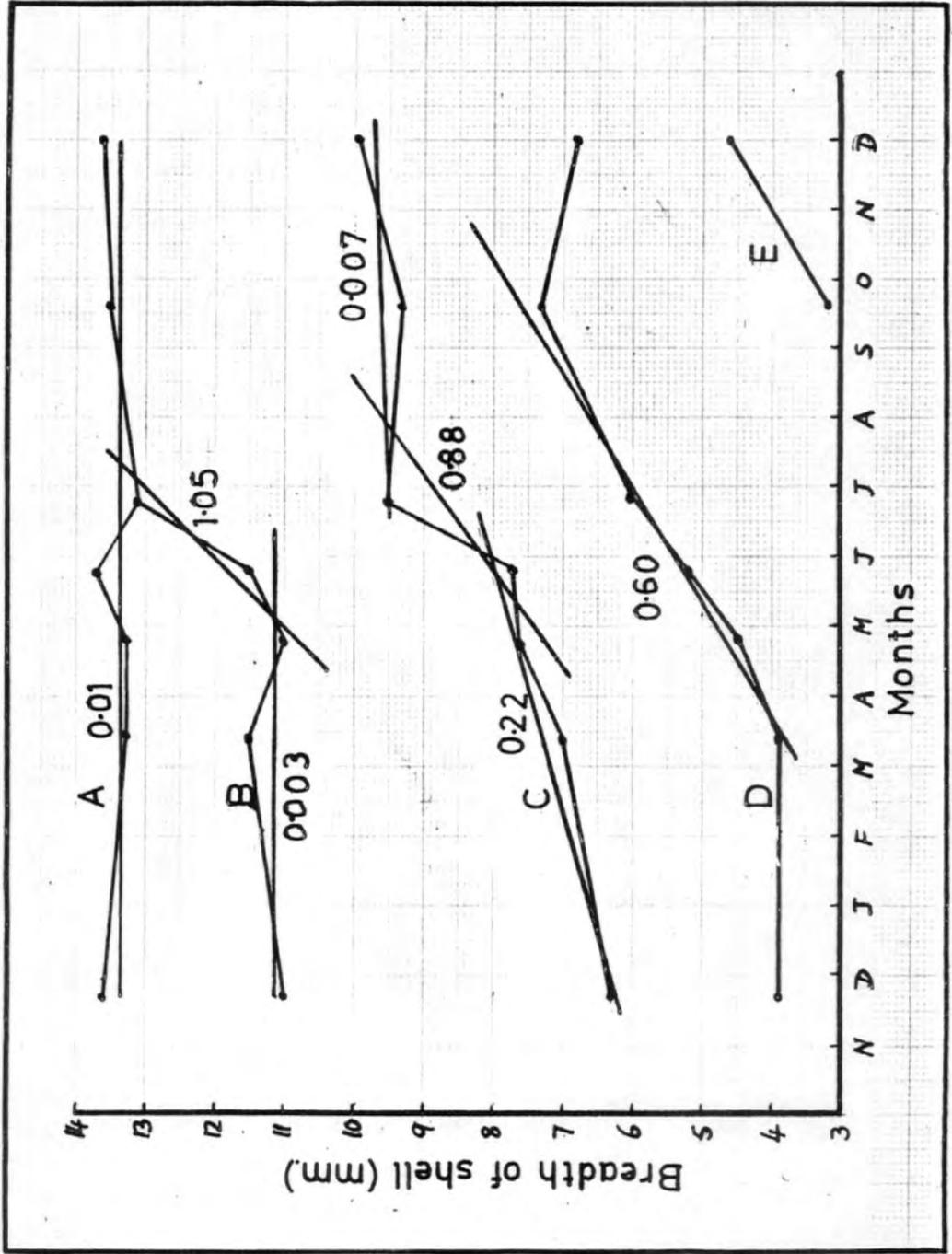
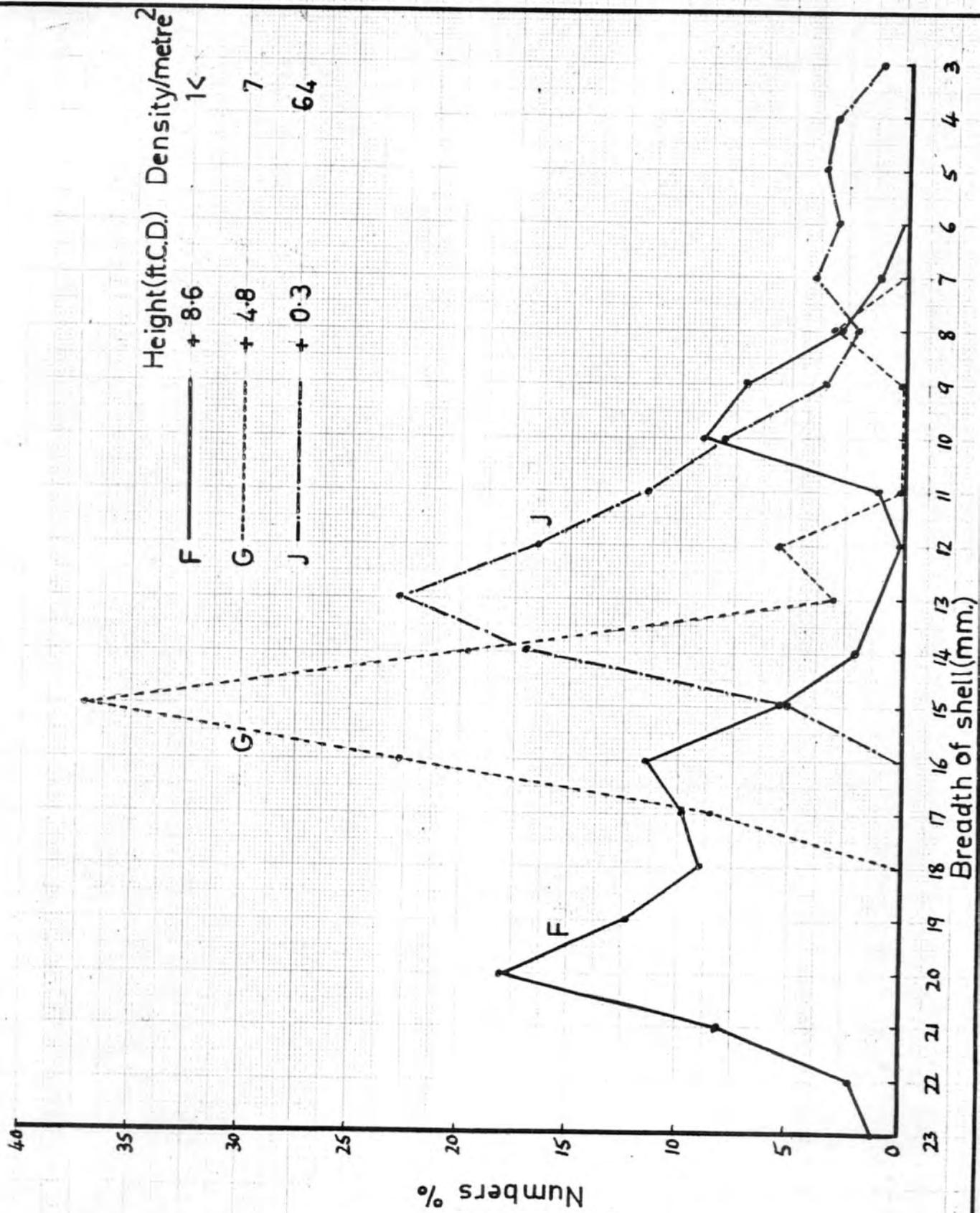


Figure 6.

A comparison of the frequency distribution of size groups at three different levels at Whitburn, April 1963.



± 0.8 mm. and 8.0 ± 0.0 mm. were detected in sample G from + 4.8 ft. C.D. Sample F showed peaks at 19.8 ± 1.1 mm., 16.2 ± 1.2 mm. and 9.3 ± 0.9 mm.

It is not surprising that the youngest element in sample J could not be detected at the two higher levels (samples G and F) where it was scarce at all times of the year. If spat chanced to settle so high up it is probable they did not survive very long. If the other three peaks in the three samples did correspond with respect to years of origin then there were remarkable differences in growth rate between them. The differences in distribution of size groups are statistically highly significant. For samples F and G, $X^2 (2) = 50.86$; $P < 0.001$ and for samples G and J, $X^2 (2) = 107.1$; $P < 0.001$. However, correspondence between the elements of samples G and J is highly likely in that, although the youngest element was missing from G in April, at other times of the year, samples from both levels, (+ 0.3 ft. and + 4.8 ft. C.D.) showed four recognizable modes.

Sample F came from high level pools. The size these animals attained was much greater (maximum breadth = 23 mm.) than any existing record for the species. Whether or not the adults at 19.8 ± 1.1 mm. corresponded to other adult groups in age could be disputed because active growth may have continued for a longer period at this level resulting in a considerable

TABLE II

The analysis of collections from five different levels on the boulder bank at Whitburn in April, 1963. The figures in the upper line give the mean shell breadth (mm.) with the standard deviation in parentheses (where known). The lower line of figures refers to the proportion each year group comprises of the whole population.

Collection	Level (ft. C.D.)	Mean nos. per metre	Number exam- ined	Year groups						
				0-1 yr.	1-2 yr.	2-3 yr.	3-4 yr.	4-5 yr.		
F	+ 8.6	< 1.0	112	—	—	9.3 (0.9)	16.2 (1.2)	19.8 (1.1)	—	—
G	+ 4.8	7.0 (7.2)	35	—	8.0 (?)	11.6 (0.8)	14.7 (1.0)	—	—	—
H	+ 2.3	65.7 (16.7)	197	4.5 (0.7)	7.6 (0.8)	11.0 (0.9)	13.3 (0.8)	—	—	—
J	+ 0.3	63.8 (15.9)	263	3.9 (0.7)	6.4 (0.9)	10.1 (1.0)	12.6 (1.0)	—	—	—
K	- 1.0	59.4 (8.7)	297	3.5 (0.6)	6.5 (1.0)	10.0 (0.9)	12.5 (0.9)	—	—	—

size difference between fourth and fifth year individuals. As four modes excluding first year animals could be discerned at the same level in October (Table III), it is most likely that the 19.8 ± 1.1 mm. animals were in their fifth year. If this is so, then the fourth year group at 16.2 ± 1.2 mm. showed a size superiority over its suggested counterpart in sample G.

Figure 7 shows a comparison of the three low level samples, H, J and K separated by height increments of 2 ft. or less. All were shown to have four modes (details of probability analyses in Table II). Although the three samples had a similar distribution of size groups, it is clear that, mode for mode, growth per unit time was greatest in sample H (+ 2.3 ft. C.D.) and least in sample K (- 1.0 ft. C.D.). Moreover, the size differences between the three samples are statistically significant: $\chi^2 (24) = 49.19; 0.01 > P > 0.001$.

Samples taken from the same five levels in October, 1963, followed a similar pattern. The October samples were labelled F', G', H', J', and K' respectively from the uppermost to the lowest levels, so that for instance, F' (October) corresponds with F (April), K' (October) with K (April) with respect to the shore level from which the samples were taken. The results are shown graphically in Figures 8 and 9 and the probability analyses for the October samples are given in Table III. All the data available on growth rates at different levels are summarized in Figure 12 and Appendix II.

Figure 7.

A comparison of the frequency distribution of size groups at three different levels at Whitburn, April 1963.

Height C.D. Density/metre²

H - - - + 2.3 ft. 66

J - · - · + 0.3 ft. 64

K ——— - 1.0 ft. 59

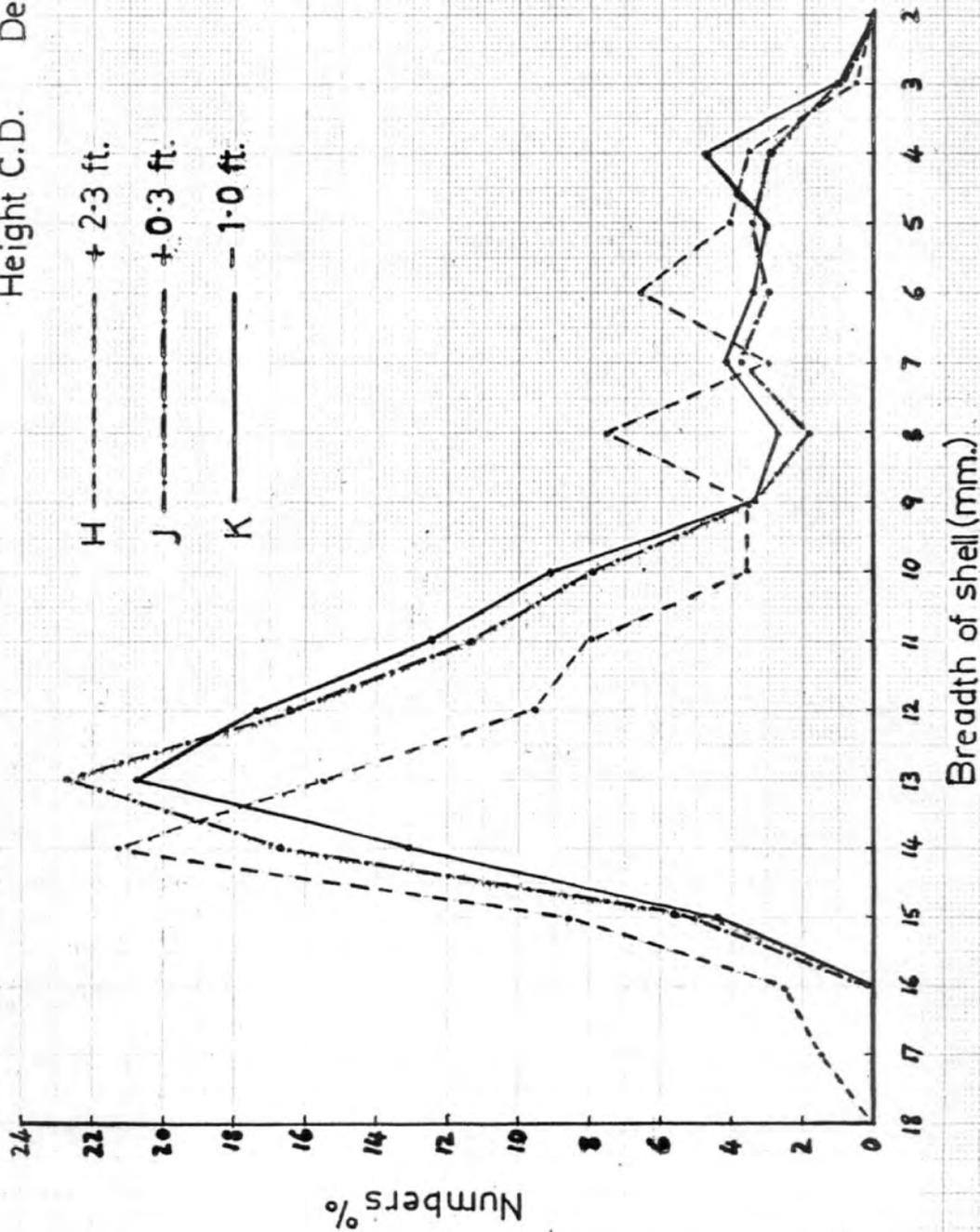


Figure 8.

A comparison of the frequency distribution of size groups at three different levels at Whitburn, October 1963.

Height (ft.C.D.) Density/metre²

——— + 9.1
 - - - + 0.3
 ——— - 1.0

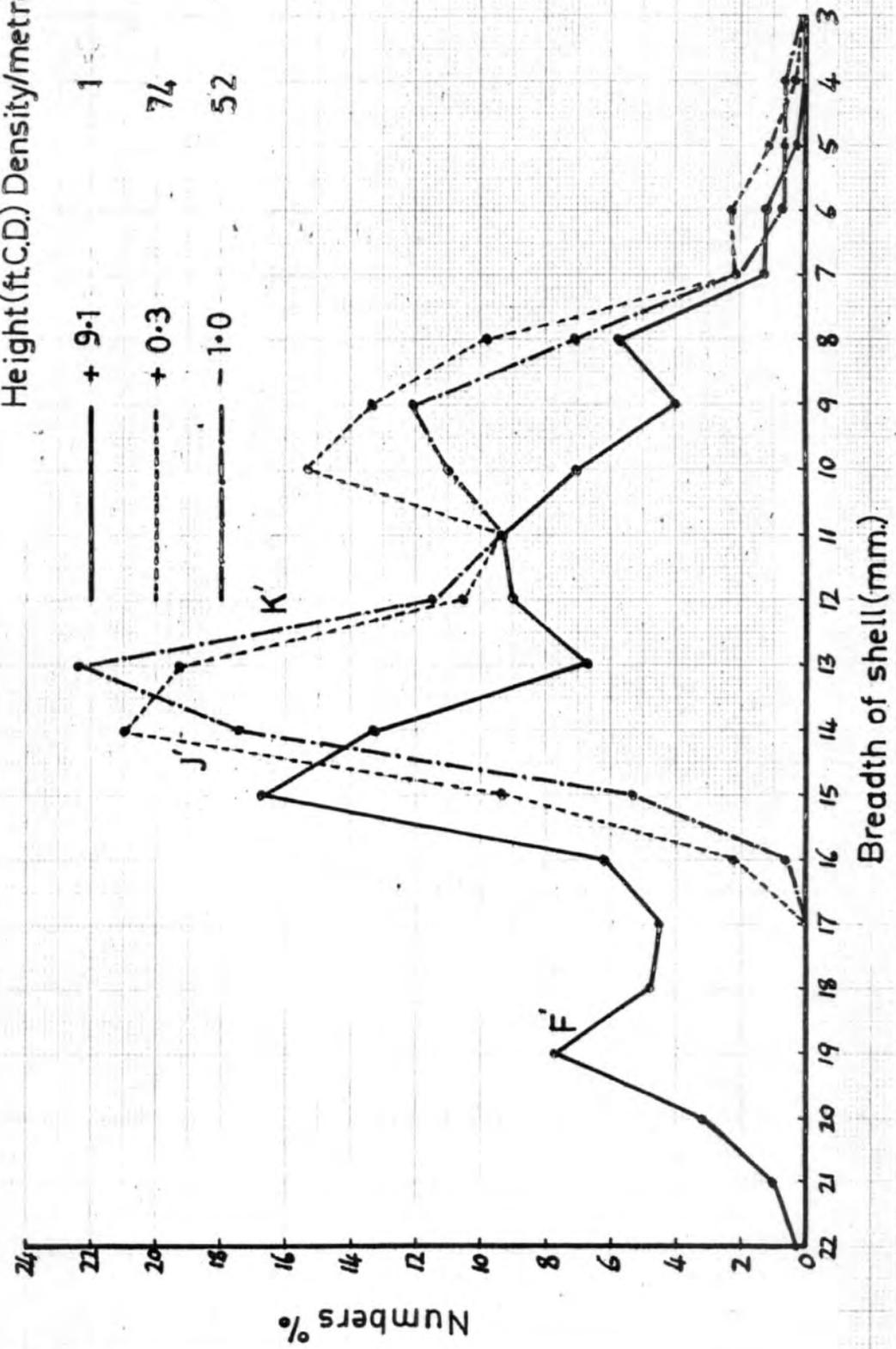


Figure 9.

A comparison of the frequency distribution of size groups at three different levels at Whitburn, October 1963.

F' (Figure 8) showed four modes, the upper three of which can easily be matched with the three found for F in April. The fourth mode at 7.8 ± 0.7 mm. represents two year olds which had arrived in the area during the intervening six months and there were even a few one year olds present. This confirmed the suggestion already made that the mode at 19.1 ± 1.0 mm (19.8 ± 1.1 mm. mm. April) consisted of five year olds. G', H', J', and K' all showed four modes after analysis with probability paper, although the smallest one (size class E of the previous section) was barely detectable. χ^2 tests on the distribution of size groups give the following results : F' and J', $\chi^2 (3) = 166.83$; $P < 0.001$; J' and K', $\chi^2 (4) = 14.17$; $0.01 > P > 0.001$; G' and H' $\chi^2 (4) = 164.93$ $P < 0.001$; H' and K', $\chi^2 (3) = 55.66$; $P < 0.001$. All these results are statistically significant at a high level of probability.

Comparison of growth rates on different substrata.

In order to investigate the effect of differences of substratum on growth rate, the populations on the limestone reefs was sampled at two levels, + 2.3 ft. C.D. and + 4.8 ft. C.D. in October, 1963. These samples were labelled respectively H" and G" and correspond with respect both to level and time of collection with samples H' and G'. The data are given in Figures 10 and 11 and in Table IV.

As has already been indicated (p.10), there were several habitat differences between the reefs and the boulder bank. At the lower level (+ 2.3 ft. C.D.) there was 100% cover from F. serratus on the reefs whereas the average on the boulder bank was about 20% at the same level, At + 4.8 ft. C.D., the reefs were covered 100% with mixed A. nodosum, F. vesiculosus and F. serratus but the boulder bank supported no weed at all being covered mainly by B. balanoides and P. vulgata. At both levels, the major differences can be attributed to the greater availability of sheltered habitats beneath the boulders than in the crevices of the reefs. There are highly significant differences between animals from the two habitats with respect to the distribution of size groups. For samples G' and G'' at + 4.8 ft. C.D., (Figure 11), $\chi^2 (12) = 53.14$, $P < 0.001$; for H' and H'' at + 2.3 ft. C.D. (Figure 10), $\chi^2 (12) = 58.0$, $P < 0.001$. t tests were carried out to discover if the population densities were significantly different in the two habitats; for samples H' and H'', $t (18) = 8.0$, $P < 0.001$; for G' and G'', $t (19) = 1.52$, $0.20 > P > 0.10$. The first result shows a statistically significant difference, but the second is not significant.

It is clear, that, at the lower level, population density on the boulder bank is greater than that on the reef, whereas the reef populations grow significantly faster.

Figure 10.

A comparison of the frequency distribution of size groups from the reefs and the boulder bank at Whitburn, October 1963. The level is +2.3 ft.C.D.

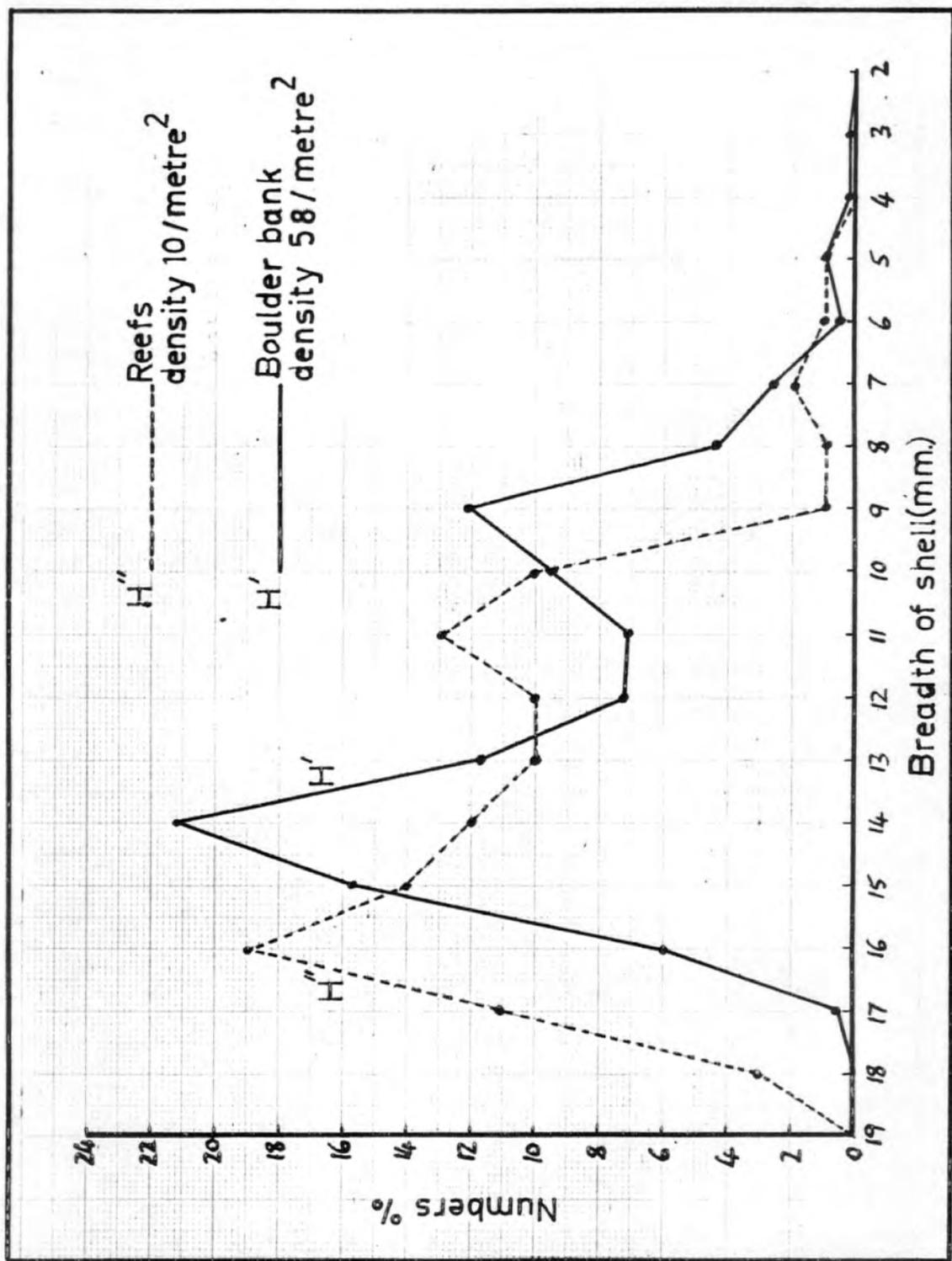


Figure 11.

A comparison fo the frequency distribution of size groups from the reefs and the boulder bank at Whitburn, October 1963. The level is +2.3 ft.C.D.

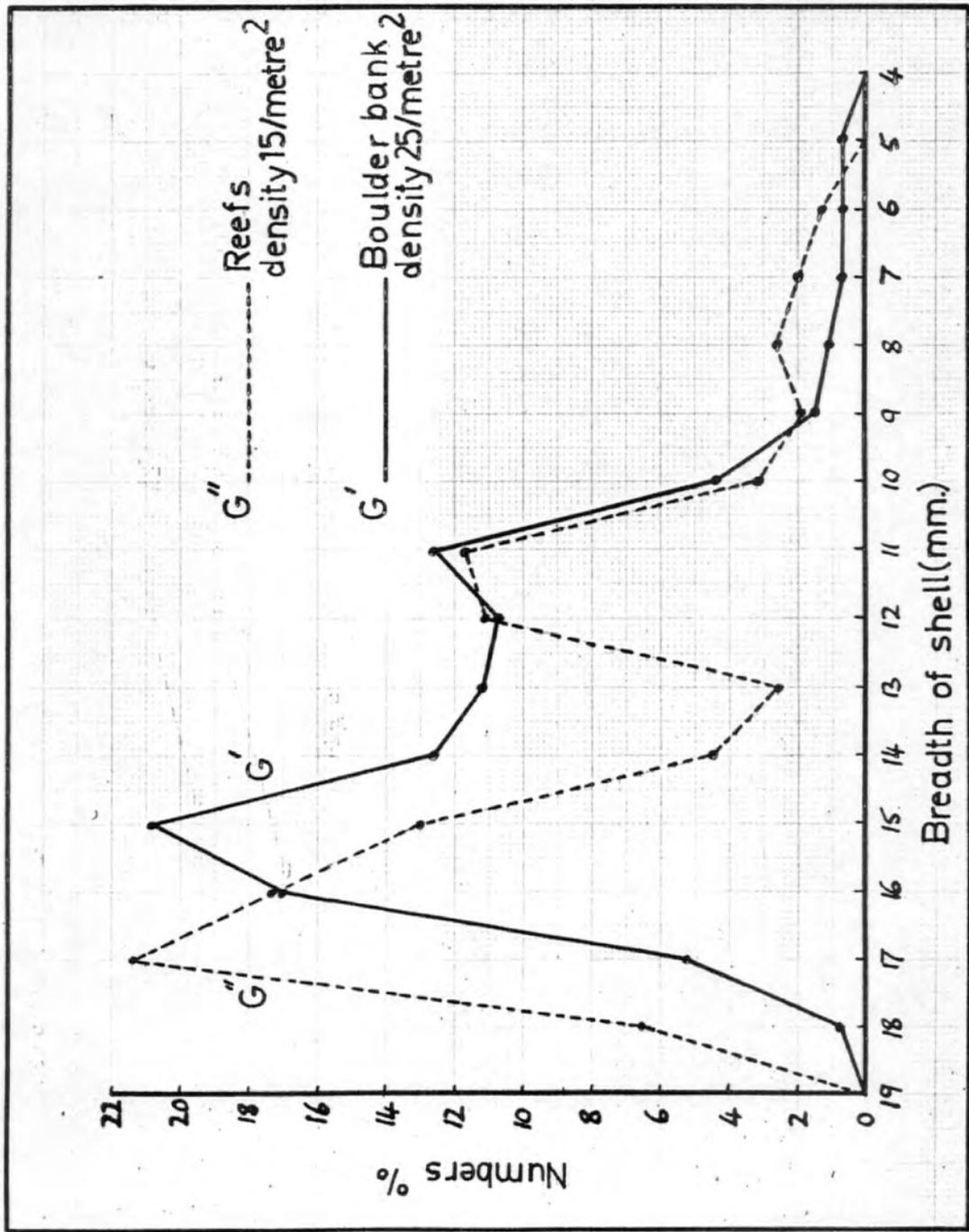


TABLE III

The analysis of collections from five different levels on the boulder bank at Whitburn, in October, 1963. The figures in the upper line give the mean shell breadth (mm) with the standard deviation in parentheses (where known). The lower line of figures refers to the proportion each year group comprises of the whole population.

Collection	Level (ft. C.D.)	Mean nos. ² per metre	Number examined	Year groups					
				0 yrs.	1 yr.	2 yr.	3 yr.	4 yr.	5 yr.
F'	+ 9.1	1.0	312	---	7.8 (0.7) 8%	11.1 (1.1) 30%	14.8 (1.1) 45%	19.1 (1.1) 17%	19.1 (1.0) 17%
G'	+ 4.8	24.5 (16.5)	269	5.1 (0.8) 2%	8.4 (0.9) 3%	11.2 (1.0) 39%	14.8 (0.9) 56%	indistinguishable from 3 yr olds.	
H'	+ 2.3	58.0 (15.2)	580	3.2 (0.9) 0.5%	7.3 (1.3) 9.5%	9.3 (1.0) 30%	13.5 (1.2) 60%		
J'	+ 0.3	74.4 (22.1)	744	3.4 (0.7) 0.5%	5.8 (0.8) 5.5%	9.0 (1.0) 42%	13.0 (0.9) 52%		
K'	- 1.0	52.6 (18.6)	475	4.2 (0.8) 1.4%	6.5 (0.6) 3.6%	9.2 (1.0) 40%	12.7 (0.9) 54%		

TABLE IV

Comparison of samples from the boulder bank and limestone reefs. Whitburn, October, 1963.

<u>Collection</u>	<u>Habitat</u>	<u>Level (C.D. ft.)</u>	<u>Total No.</u>	<u>Nos. per metre²</u>	<u>Shell breadth of age groups in mm.</u>		
					<u>1 year.</u>	<u>2 years.</u>	<u>3 years +</u>
G'	boulders	+ 4.8 ± 1.1	269	24.5 ± 16.5	8	11	15
G''	reefs	+ 4.8 ± 0.5	154	15.4 ± 7.6	8	11	17
H'	boulders	+ 2.3 ± 1.3	580	58.0 ± 15.2	7	9	14
H''	reefs	+ 2.3 ± 1.0	100	10.0 ± 9.1	7	11	16

Discussion

Life history and growth rates.

The 0 year class settled on the shore during the autumn and spring (the greater part of it below tidal levels) at a shell breadth of 3 -4 mm. After one year, it had reached a size of 6 - 7 mm. and after two years, 10 - 11 mm. Between June and September of the third year, adult size was reached at 13.5 mm. and growth thereafter was very slow. As most individuals reached sexual maturity at approximately 8 mm. breadth, the majority of animals was unlikely to breed before the second year on the shore. These results are summarised in Figure 5. It is apparent that little if any growth took place in size class D between November and March. Steady growth at 0.6 mm./month occurred during late spring and summer followed by a decline in the autumn. Size class C grew slowly in winter (0.22 mm./month) and rapidly in spring (0.88 mm./month) but almost ceased growing between June and December. It is possible that the maturation of the gonads in late summer, might have been responsible for the growth pause (see p.106). Size class B also achieved little growth between November and March but the rate increased rapidly to 1.05 mm./month in summer until June. The slow rate after June can probably be attributed either to its having reached more or less adult size or to the onset of gonad maturation or both. Size class A showed little fluctuation through the years. The decreasing trend from November to June should probably be

interpreted as mortality of the older and larger animals following spawning. Size class E was represented by too few animals for the growth rate to be calculated.

The probable years or origin of all the size classes are shown in Appendix VI.

The relation between population density, growth rate and living space.

Three related factors, growth rate, population density and available microhabitats, need to be discussed if the data based on samples from the different levels and substrata, are to be correctly interpreted and understood.

At low shore levels, the population density was fairly uniform up to about + 3.0 ft. C.D. (see Figure 15). Consequently, samples H, J and K (Figure 7) showed similar densities, but small differences in growth rate were apparent. It would appear that the higher level groups, while maintaining slightly higher densities (though not significantly different at the 5% level) also achieved a faster growth rate. The positive influence of increasing level on the growth rate has been demonstrated independently for each age group in the population.

At equivalent levels, it has also been demonstrated that a higher density of animals was supported on the boulder bank than on the limestone reefs. This was almost certainly as a result of the severe shortage of protected microhabitats on the reefs. On the other hand, the individuals comprising the reef populations were

larger in most age groups (Table IV). This fact suggests that the growth rate on the boulder bank where plentiful microhabitats permitted a dense population to develop, was limited by the availability of some resource, possibly food.

There are two other possibilities which need to be considered. Firstly, the largest G. cineraria on the boulder bank may have been selectively eaten by carnivores. The most likely species at Whitburn is Asterias rubens L. which was seen eating G. cineraria on numerous occasions. Connell (1961a) showed that the predation of B. balanoides by Thais lapillus (L.) can follow this pattern, Thais attacking only the largest Balanus and leaving the smaller ones to continue their growth. However, selective predation of all the largest G. cineraria on the boulder bank could not account for size differences between boulder bank and reef animals in the smaller (= younger) size classes which would, according to this explanation, be subject to predation in neither habitat.

Secondly, inter-specific competition with other grazing species is a theoretical possibility. The difficulty here is that G. cineraria is most dense at the lower levels on the boulder bank where obvious possible competitors such as L. saxatilis and L. littorea are either absent or becoming scarce. Since it is here, and not at the higher levels, where these theoretical competitors are abundant and that growth in G. cineraria is slowest, intra-specific competition does seem to be the most likely cause of the differing rates of growth in the various habitats.

The high level animals (+ 8.6 - 9.6 ft. C.D.) were at low density and yet the individuals grew to a great size. It is not simply that they lived longer, though this may have occurred: the evidence (Tables II and III) shows that growth was more rapid in all age groups and there are also good grounds for believing that rapid growth continued into the fifth year by which time the growth rate had declined almost to zero at lower levels. It may be asked why, if resources were available to support such rapid growth, is the population density consistently so small ($<1/\text{metre}$)?

The curious nature of these groups needs to be emphasized. Only one instance has been reported in the literature (Lewis, 1954) of G. cineraria living at such high levels (+ 8.6 to + 9.6 ft. C.D. i.e. just below E.H.W.N.). The Whitburn animals existed only in pools at this level and were separated from the main littoral population by about a 3 ft. height difference. The shore shelves gradually and the distance over the ground separating the two groups on the boulder was everywhere more than 30 yards. Only one specimen was found on the boulder bank separating the main shore population from the pools in spite of repeated searching.

It seems probable that individuals must have reached this habitat via the upper part of the boulder bank only in very small numbers. Spat were occasionally found during the autumn, but they seem to have died quite rapidly (monthly searches confirmed this)

and it is felt that the bulk of the animals must have been recruited by migration from lower levels. One possible route exists via the pools on the reefs which are present at intervals all the way up. Having reached the upper pools, it is possible that the snails spread laterally, so arriving in the pools, at the top of the boulder bank. Chance transport by waves might also have been responsible for recruitment, but the clear age structure of the groups in the pools suggests that most of the animals had grown up there, at least from two years of age. A comparison of the samples F (Figure 6) and F' (Figure 8) shows that there was an influx of animals of around 8 mm., probably two year olds, between April and October, 1963.

The question of low population density in the high level pools may then be answered by the suggestion that this habitat was rather isolated from the main sources of recruitment. Migrants from lower levels arrived only in small numbers and any spat which chanced to settle there failed to survive more than a few weeks. The latter points to the fact that the tolerance of young animals to conditions in midshore was inferior to that of the adults and all other available evidence supports this conclusion (pp.39). They may have been less able to withstand the fluctuations in temperature or salinity or perhaps they were eliminated by a predator from which the older animals were protected. Alternatively, they may have had special food requirements which were lacking. The overall result was a high

level population at low density consisting mainly of three, four and five year olds. Conditions seem to have been ideal for these animals.

Summary

- (1) In November, 1962, G. cineraria showed four modes corresponding to year groups. The largest mode probably embraced two or more year groups. The two youngest year groups were scarce and probably lived mainly offshore. The third year group reached adult size between June and September.
- (2) The new brood was first detected in September. It settled mainly offshore at a size of 3 mm. shell breadth. Animals reached 6-7 mm. after one year, 10-11 mm. after two years and 13.5 mm. after three years. Sexual maturity was reached at about 8 mm. Animals bred for the first time in their second year.
- (3) In all size groups except the largest, growth was rapid in summer and slow in winter. The adults (over three years) showed little growth throughout the year. Sexually mature animals almost stopped growing in late summer and autumn, probably due to breeding activity.
- (4) Above + 2.3 ft. C.D. growth rate increased with level, and below + 2.3 ft. the rate decreased with level. Animals at the highest levels grew rapidly for at least one year longer (i.e. four years) than the others.
- (5) Comparison of reef and boulder bank samples showed an inverse relationship between density and growth rate. The availability

of suitable habitats was thought to be of paramount importance in determining density and growth rate was determined by intra-specific competition for resources.

III A POPULATION OF GIBBULA CINERARIA STRUCTURE AND DYNAMICS

Introduction

The studies on growth rate in G. cineraria at Whitburn indicated a number of apparent anomalies. In some cases, growth was unexpectedly slow e.g. in size class D between November and March and from September to December. In other cases, much growth seemed to have occurred in a short time e.g. in size class C between May and June. It was felt that some of these anomalies might have been due to the movement of animals into or away from the main sampling zone at + 2.3 ft. C.D. \pm 1.3 ft. It has already been demonstrated that growth rate varies with level (Figure 12 and Appendix II) and also between distinct substrata at the same level. Upshore or downshore migration of animals which had grown either faster or more slowly than the majority of animals in the main study area, would substantially influence the results at any particular level, and large scale movements of animals could not be ruled out.

Desai (1959) showed that upshore and downshore migrations occurred in M. lineata populations and similar results were reported by Gowanloch and Hayes (1929) for L. littorea in Nova Scotia. In both cases, downward movement took place in the autumn followed by upshore migration in spring. A west African intertidal

Figure 12.

A comparison of the growth rates of the different size classes at three shore levels, Whitburn 1962-63.

prosobranch, Nerita senegalensis L. moves considerable distances up and downshore with each tide, (personal observation). Although I never observed movements of this kind in G. cineraria, seasonal movements cannot be ruled out. Compared with M. lineata, though not L. littorea, G. cineraria posed a special difficulty in that at all times of the year its range extended well below tidal levels and the sublittoral populations could not be counted during the survey. Even the lowest intertidal levels could be sampled only twice at equinoctial spring tides. However, although necessarily incomplete, the data exhibit certain trends in population levels which indicate some movement of animals within the tidal zone.

Methods

The samples used for growth studies were also used to estimate density. Each quadrat sample was kept separate until all the animals had been counted and measured. Values for the mean density and variance were calculated for each component size class as it seemed possible that all size classes did not behave identically (see Appendix IV). Variance ratios were calculated for each component size class and the total population at each level sampled and for every time interval between sampling dates, in order to establish that the variances did not differ to a significant degree. As no variance ratios exceeded the 5% probability level, they were considered not statistically significant and t tests were performed to test the significance of the differences between

means. Separate t tests were carried out (a) for the total population at all levels combined; (b) for the component size classes at all levels combined; (c) for the total population at each separate level; (d) for the component size classes at each separate level. In all cases, unless it is specifically stated otherwise, the results of t tests mentioned in the text are a comparison of the mean population densities in different months of the samples specified. Bessel's Correction has been applied in every case.

The various levels from which the samples were collected were identified by their floral and faunal characteristics. Although these changed to some extent with season, for instance the large algae were much sparser in winter, it was never difficult to identify the zones concerned. The levels of the lower and upper boundaries of these zones were determined by the method described by Evans (1947a). To apply this method all that is necessary is that the time at which the tide reaches the level concerned be noted. It makes no difference whether the tide is ebbing or flowing. Using the Admiralty Tide Tables (Volume I) for the year in question, the height above chart datum can be calculated for any given time using the tidal curves and data for the locality provided. It is important that the sea should be calm and the wind slight to minimize error. Each level sampled was calculated on at least five different occasions and the mean taken.

The samples from the upper shore pools are excluded from this

analysis since no quadrat frame was used in their collection and therefore the density is not known with any degree of precision.

Results

Seasonal variation in total population density.

With the exception of the animals in the upper shore pools, the distribution of G. cineraria on the boulder bank was continuous from about + 5.9 ft. C.D. down to the sublittoral. There were no apparent obstacles to movement between levels nor were there obvious differences in substratum associated with changes of level. It therefore seems reasonable to compare the mean density of the entire intertidal population in different months. Sufficient data are available for this to be done for the four months indicated in Figure 13. Data for the lowest level at - 1.0 ft. C.D. could only be obtained for April and October but apart from this the samples are comparable.

A slight decline in density occurred between November 1962 and June 1963 from 57/metre² to 46/metre². Although a similar decrease was recorded for all levels independently it cannot be considered significant: $t(33) = 1.63$; $0.20 > P > 0.10$. Neither can the slight increase between June and October 1963, although consistent at all levels, be considered significant from the data: $t(33) = 1.12$; $0.30 > P > 0.20$. It can therefore be tentatively concluded that significant changes in density within the intertidal area did not occur in 1962-63. A greater number of samples would be required for a confident statement to be made.

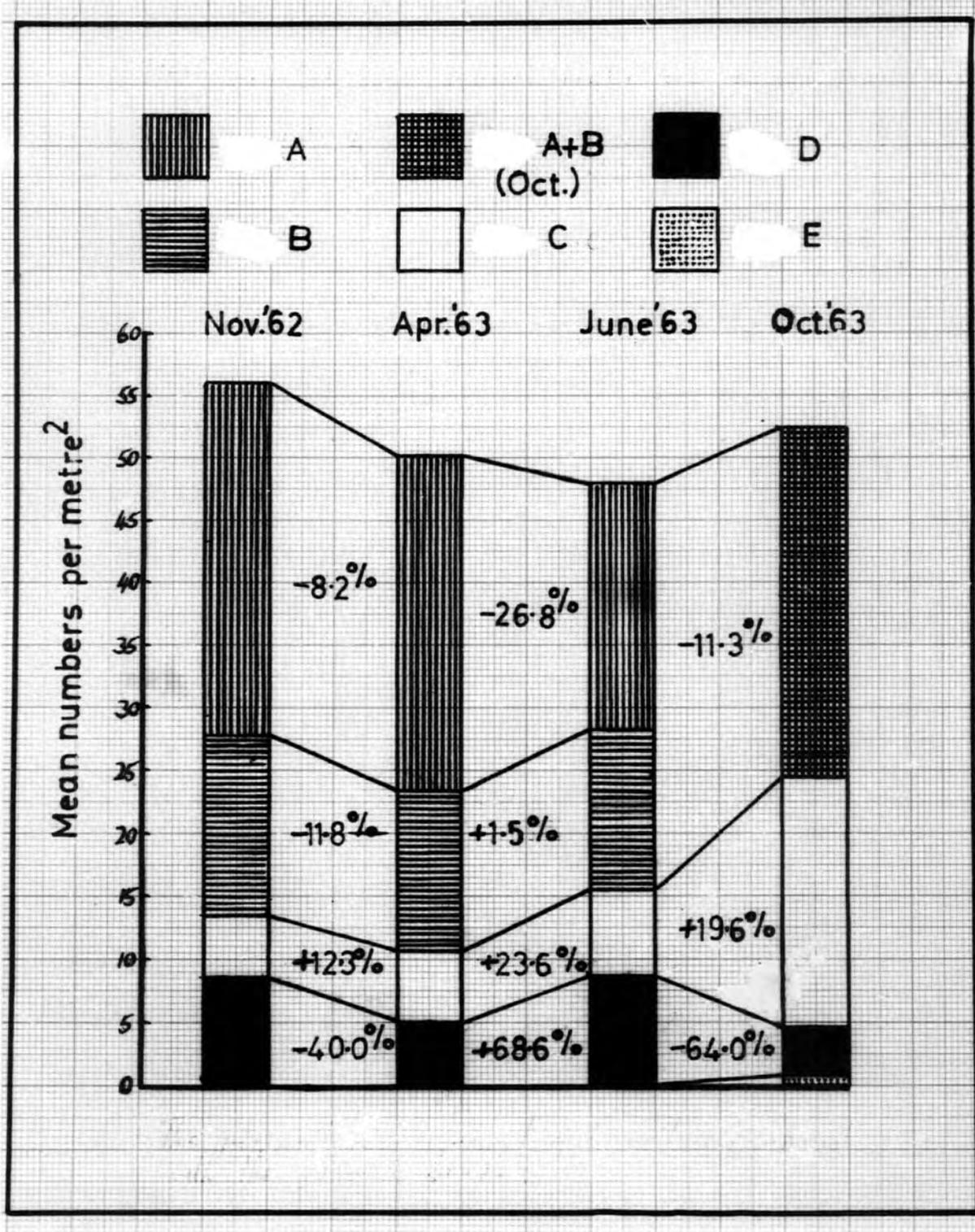
Seasonal variations in density of component size classes at all levels.

Figure 13 shows that although the total population density changed little through the year, there were variations within size classes (= age groups) which could be significant. Between April and June, size class A decreased by 26.8% and this is statistically significant ($t(35) = 3.05; 0.01 > P > 0.001$). After June, size classes A and B could not be separated and the combined decrease of 11.3% from June to October is not significant. The animals lost from size class A were replaced by size class C which began to increase significantly in April. The increases were 23.6% from April to June ($t(35) = 2.26; 0.05 > P > 0.02$) and 19.6% from June to October ($t(53) = 8.4; P < 0.001$). These animals were shown to be two year olds which were preparing to breed for the first time in the autumn (p.27). It appears that many of them moved up into the tidal zone to do so. Incidentally a substantial movement of size class C from lower levels where growth rates were slower (p.46), probably explains why growth appeared to be so slow in this size class at + 2.3 ft. C.D. between June and September (p.27).

Significant changes were also recorded in size Class D. When work began in November 1962, large numbers of newly settled individuals were present. By April 1963, numbers were reduced by 48% ($t(40) = 3.9; P < 0.001$). Between April and June, numbers increased by 68.6% ($t(35) = 1.79; 0.10 > P > 0.05$). The change

Figure 13.

The density of the different size classes on the boulder bank at Whitburn 1962-63. The percentages indicate changes in density between adjacent months.



approaches significance. A further decline of 64% occurred between June and October which is highly significant ($t(53) = 3.24; 0.01 > P > 0.001$). It was clear that many young animals died during the winter, but the continued appearance on the shore of the smallest forms (3 mm. shell breadth) until April together with the absence of growth already noted between November and March, suggested that these animals hardly survived at all in the littoral zone. The animals settled in the autumn had probably perished and been replaced by other animals newly settled in the spring. This would explain why no growth was recorded for this period in size class D. The overall decline in numbers between the end of the 1962-63 breeding season in April and the beginning of the 1963-64 season in October is statistically significant at the 1% level of probability.

Clearly, settlement occurred within the intertidal zone from September 1962 to November 1962 with a maximum in November and also from March 1963 to April in much smaller numbers. It may have taken place throughout the winter but information is lacking for December, January and February (see p.16). The young survived only in small numbers and it must be concluded that their initial development took place largely below tidal levels. There is good evidence that the animals appeared on the shore permanently during their second summer when they had reached a size of 8.5 to 10.5 mm. shell breadth. The upshore movement began in April and reached a

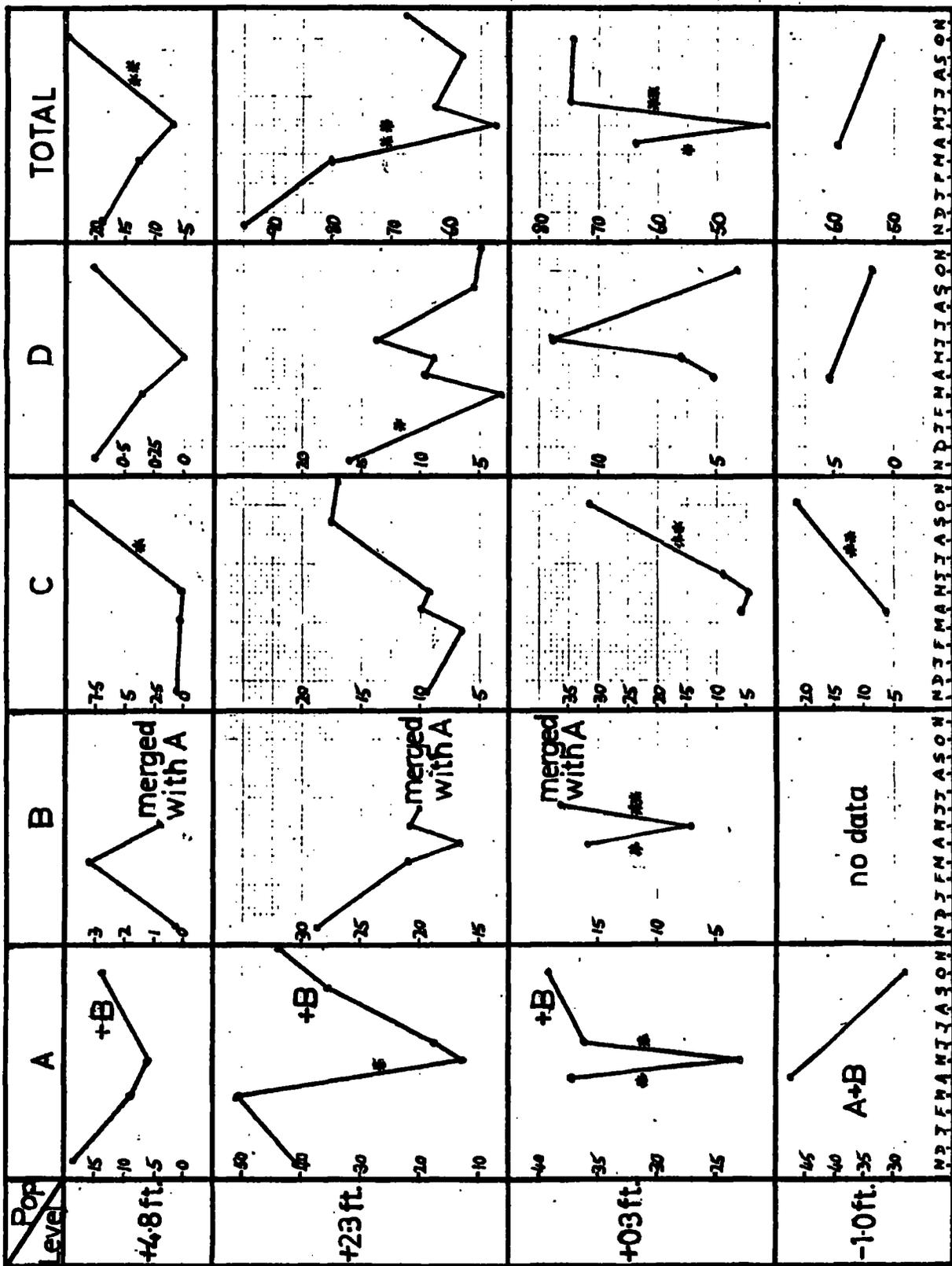
maximum between June and September. From September onwards, they bred for the first time. Fluctuations in size class B were small and in no case did they reach a statistically significant level. Size class A showed a steady drop in numbers from November to April and a further highly significant reduction between April and June. The latter was possibly related to mortality of the older members at the conclusion of the breeding season. Death following the very cold winter cannot be ruled out but if this was responsible, it should not be expected, either that the decline be restricted to adults or that it should occur mainly from April onwards when the cold weather ended in February.

Seasonal variations in density at different levels.

The population density in the Balanus zone at + 4.8 ft. C.D. \pm 1.1 ft. showed considerable fluctuations dropping from 19.6 \pm 14.6/metre² in November 1962 to 7.0 \pm 7.4/metre² in May 1963 (Figure 14). The large standard deviations (see Appendix I) indicate that the animals have a patchy distribution, the actual range per metre² being 3-51 in November and 1-20 in May. A variance ratio test for these months gives the value $F = 4.0$ ($f_1=9$, $f_2=4$): the variances do not show a significant difference at the 5% level. A greater number of samples would be needed to show a statistically significant difference between the sample means by the t test: ($t(13) = 1.68$; $0.20 > P > 0.10$). The May to October increase from 7.0 \pm 7.4/metre² to 24.5 \pm 16.5/metre² gives $t(14) = 2.14$; $P = 0.05$ and is regarded as marginally significant.

Figure 14.

The densities of the component size classes and the total population at four different levels, Whitburn 1962-63.



N P I E N A M I J I A S O N N P I E N A M I J I A S O N N P I E N A M I J I A S O N N P I E N A M I J I A S O N N P I E N A M I J I A S O N

The densities in the F. serratus zone at + 2.3 ft. C.D. \pm 1.3 ft. showed a steady decline from November ($95.0 \pm 37.6/\text{metre}^2$) to May ($52.2 \pm 17.3/\text{metre}^2$). The reduction in density is statistically significant ($t(14) = 2.46; 0.05 > P > 0.02$). The increased density observed between May and December is not significant.

At + 0.3 ft. C.D. \pm 0.7 ft. in the Laminaria zone, the main changes occurred between April and June. Between April and May, a considerable decrease occurred from 63.8 to $41.3/\text{metre}^2$ which approaches significance ($t(19) = 1.9; 0.10 > P > 0.05$). From May to June the density increases most significantly from 41.3 to $74.7/\text{metre}^2$ ($t(10) = 3.46; 0.01 > P > 0.001$).

Seasonal variations in the component size classes at different levels.

Figure 14 summarizes all the data available for the mean densities of the component size classes at each level studied and the variances are given in Appendix IV. Where a t test for the significance of the difference between means gives a positive result, the relevant section of the graph is asterisked. A single asterisk denotes approaching significance at the 10% level, double ones, significance at the 5% level, and treble ones, significance at the 1% level. The vertical scales indicate mean density per metre^2 and it is important to note that they differ in almost every case. The graphs for size class A include size class B from June onwards, since the two components could not be distinguished beyond that month, except for- 1.0 ft. C.D. where only two sets of samples were taken and size classes A and B were

combined throughout. This explains why the graphs for size class B continue only to June in the top three boxes and the absence of data from the bottom box.

Size class A showed a decline in numbers from April to May at + 4.8 ft., + 2.3 ft. and + 0.3 ft. It is hard to resist the conclusion that such a sudden lowering in density at all three levels independently, was due to mortality following spring spawning. The older and larger members of size class A probably constituted the majority of dying animals since at the two upper levels, a drop of 0.5 mm. and 0.3 mm. respectively, in the mean size of the adult population was recorded between March and May. The evidence provided by size classes C and D certainly does not support the view that mortality was general at this time of the year. From May onwards, numbers of size class A rose steadily, though only at + 0.3 ft. did the change approach statistical significance. Unfortunately, because of the state of the tides, it was impossible to collect at - 1.0 ft. in May, but the drop in numbers recorded for size classes A and B combined between April and October is worthy of note. Since this coincided with increases in density for the same size classes at higher levels, upshore movement of adults in the summer can be inferred.

It is impossible to be sure exactly what happened to size class B because it lost its separate identity after June. Numbers at + 4.8 ft. were always low ($5/\text{metre}^2$) and no statistical significance could be attached to the results there. At + 2.3 ft.,

numbers dropped until April and increased thereafter, but the t tests show that these results too, could well be due to chance. Clear statistical significance is shown only by the increase between May and June at + 0.3 ft. which was probably due to the upshore movement of adults already mentioned.

One other feature connected with size class A requires comment. Between November and March its density fell from 18.4 to 8.8/metre² at + 4.8 ft. and rose from 40.8 to 50.5/metre² at + 2.3 ft. A winter downshore movement seems the obvious explanation. However, the variances of both pairs of samples are large in relation to the means and a t test fails to show statistically significant changes in density at either level. At + 2.3 ft., variances were much greater for November and March than at other times (Appendix II). F tests to compare the variances for November and March with those for May and September give the following results: March/May, $F = 8.5$; $0.05 > P > 0.02$; March/ September, $F = 11.0$; $0.01 > P > 0.001$; November/May, $F = 4.7$; not significant: November/September, $F = 6.1$; $0.05 > P > 0.02$. Three of these four results show that the winter variances were significantly greater than the summer ones indicating greater aggregation.

From observation it appeared that there was a greater tendency for the animals to be concentrated in areas where water remained when the tide was out. In the 1962-63 winter, such behaviour might have been important in protecting the animals from the severe cold.

It has been shown by Southward (1958) that G. cineraria can survive no more than 2-3 hours at 5°C. Temperatures well below this were recorded many times at night over a period of two months in January and February 1963: low water at springs occurs in the early evening and early morning at Whitburn, the latter especially being a period when temperatures are likely to be minimal: at + 2.3 ft., the animals are emersed for well over two hours at spring tides. High mortality did not happen at this time and it is concluded that clumping occurred in the wetter areas where the animals could remain under water when the tide was out, and that this was responsible for the avoidance of high mortality. These arguments would be expected to apply with even more force to the animals which wintered at + 4.8 ft. but F test results do not reach the 5% significance level, no doubt due to the small number of samples.

The conclusion that animals concentrated in the wetter areas in winter does not rule out the additional possibility that downshore movement had occurred. The figures point to this, even to the extent that the gain over the November-March period at + 2.3 ft. in size class A was approximately 10/metre² and this was almost exactly balanced by the loss at + 4.8 ft. However, it must be stressed that a larger number of samples would be required to establish the statistical significance of this.

Discussion

Variations in density associated with level.

The total population density varied with level on the boulder bank. In April, the maximum ($66/\text{metre}^2$) was at + 2.3 ft. In October, it was a little lower at + 1.0 ft. (Figures 15). In both months, the variation between approximately + 3.5 ft. and E.L.W.S. was not great, though numbers dropped somewhat below M.L.W.S. There was a tendency for the spring population to be centred slightly lower on the shore than the autumn one, in spite of the fact that the maximum density was a little higher up. For instance; spring numbers were higher than autumn ones at E.L.W.S.; numbers dropped more sharply above + 2.3 ft. and the upper limit was approximately 0.5 ft. lower (excluding the animals in the uppermost pools). Taking the year as a whole, the maximum densities lay between M.L.W.S. and M.L.W. There can therefore be no doubt that, at least in this locality, G. cineraria is a truly intertidal species.

Figure 16 shows the distribution of the component size classes on the boulder bank for three different months. In April, size class A was maximal at + 0.3 ft. and remained so in June and October. Size classes B, C, and D were concentrated higher at + 2.3 ft. in April and June. Size class B could no longer be separately recognized in September, but size class C was centred at + 0.3 ft. and D at + 2.3 ft. In view of what has been said earlier about the poor survival

Figure 15.

Kite diagrams showing the population density of
Gibbula cineraria at Whitburn.

Numbers per metre²



F.I.C.D. F.T.O.D.

April, 1963 October, 1963 (boulders) October, 1963 (reefs)

10
9-2
8-1
7-0
6-1
5-2
4-3
3-4
2-5
1-6
0-7
-1-8
-2-9

- MTL
Ordnance datum
- ELWN
- MLWN
- MILW
- MLWS
- Chart datum
- ELWS

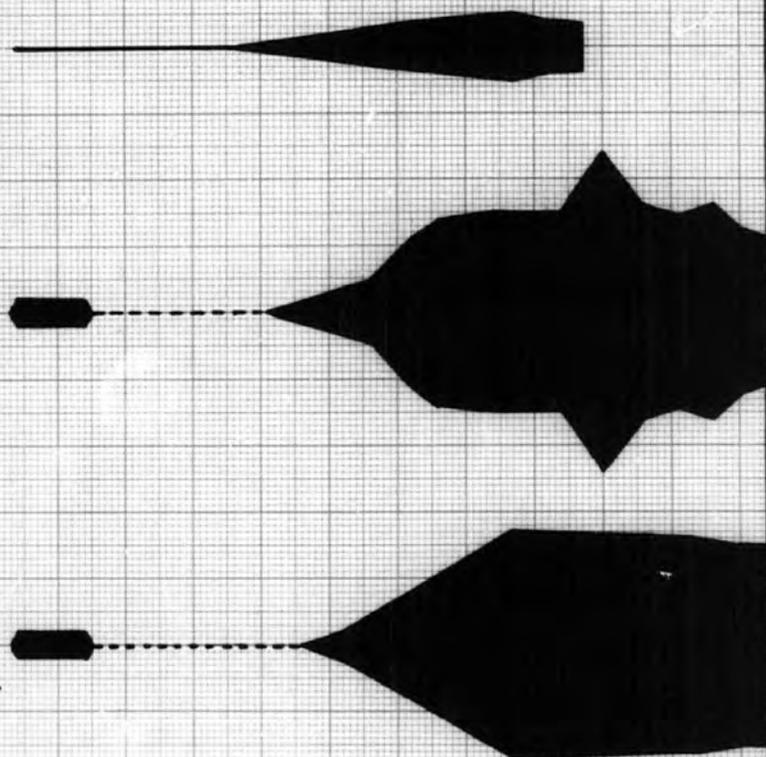


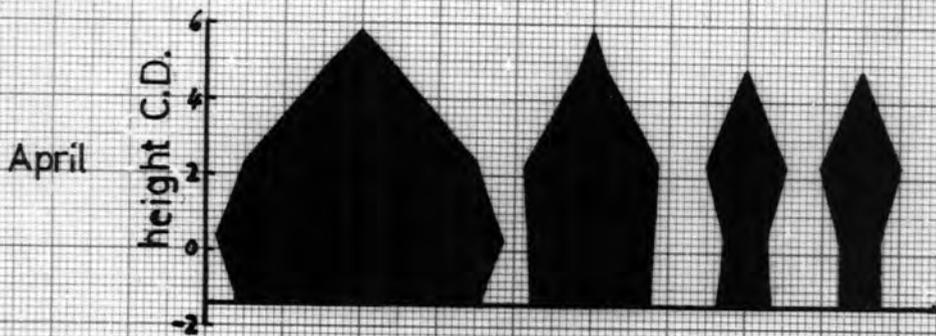
Figure 16.

Kite diagrams showing the densities of the component size classes in three different months at Whitburn.

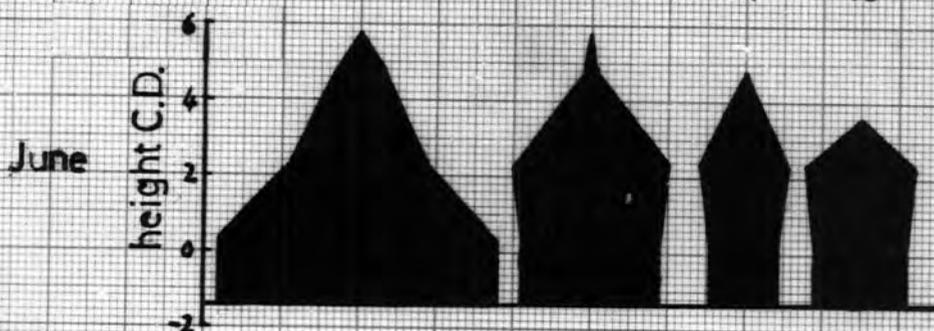
Numbers per metre²

40 20 0 20 40

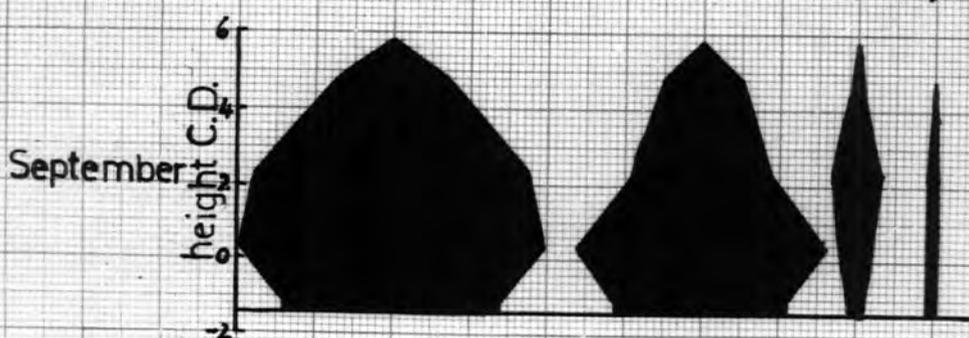
% of total A 57 B 25 C 9 D 9



% of total A 53 B 23 C 11 D 13



% of total A+B 55 C 38 D 6 E 1



of young animals on the shore, it was surprising to find that their maximum density was not at the lowest levels. In the case of size classes C (before the mid-summer of their second year) and D, the animals were below 7.5 to 8.5 mm. in shell breadth (Figure 12). Their precise habitat was quite different from that of the adults. They were rarely found anywhere but underneath stones even in pools. Sometimes they occurred on the topside of stones lying deeply buried beneath other stones but hardly ever on an exposed surface. As already mentioned (p. 11), the stones at the two lower levels were extensively cemented by Lithothamnion spp. which rendered the undersides inaccessible to young G. cineraria. Their numbers throughout the tidal zone were always low, but it is probable that suitable habitats were more abundant at + 2.3 ft. than at lower levels. This fact does not alter the conclusion already reached that the main concentration of young was below tidal levels.

The cases of size classes C and D differ somewhat. Size class C was approaching sexual maturity and it has already been shown (p. 38), and is evident from Figure 16 that its numbers increased from April onwards and particularly after June. The main concentration in September was around + 0.3 ft. as the majority of these animals had only recently arrived on the shore. Around 9 mm. shell breadth, the habits of the animals changed. They began to appear in more exposed places, grazing the algae from the upper surfaces of stones during the day. Their chances of survival without lying

permanently protected under stones may have increased. Since they bred for the first time from the autumn onwards the altered behaviour may have been related to this fact. Adequate dispersal of the planktonic trochophore larvae would almost certainly be hindered if the animals remained confined beneath several layers of stones.

The conclusions are that the main adult part of the population was centred around + 0.3 ft. between April and September. The density remained fairly constant between 36 and 39 per metre² at this level. Members of size class A which died before June seem to have been completely replaced by members of size class B which reached adult size between June and September. Size class C was centred mainly below tidal levels until the onset of sexual maturity when it assumed the habitat of the adults. Size classes C (before sexual maturity), D and E were never well represented on the shore, but they seem to have been concentrated around + 2.3 ft.

Variations in density associated with substratum.

Discussion of the differing habitats of young and adults necessitates some mention of those areas on the limestone reefs which are more or less free from boulders. It is clear that, if what has already been said about the habitats of the young be true, then their chances of survival on the reefs would have been slender. Although only two sets of samples were taken from this habitat in October, 1963, the facts supported this conclusion.

From both levels, size class E was entirely absent and D present only in very small numbers. Size classes A + B and C comprised about 95% of the total. It was also apparent (Figure 15) that the mean density was much lower, particularly at + 2.3 ft. ($10/\text{metre}^2$ as compared with $60/\text{metre}^2$ on the boulder bank). At + 4.8 ft. the difference was less ($15/\text{metre}^2$ as compared with $25/\text{metre}^2$).

It is clear that the reef population must have been derived from the boulder bank by immigration. The smaller number of protected habitats presumably acted as a decisive limiting factor to the numbers of size class C which could survive there. They were mostly confined to crevices and pools. At the higher level, the reef animals seem not to have been at such a comparative disadvantage. It is possible that the weed cover, in assisting the retention of moisture in crevices, to some extent counter-balanced the absence of protective stones. It has already been noted that the boulder bank animals showed a clumped distribution at the higher levels, for which the chief factor responsible was thought to be moisture.

It has been shown (p.24) that the differences in mean density of the reef and boulder bank populations was statistically significant at + 2.3 ft. but not at + 4.8 ft. This supports the argument that at the lower level, habitat differences were of crucial importance while, at the upper level, where both populations were reaching their upper distribution limit, this was not the case.

However, it must additionally be noted that both sets of samples showed highly significant differences in growth rate (p.24). In both cases the animals at lower density on the reefs achieved more rapid growth. It is therefore, unlikely that shortage of food could limit the density of the reef populations. The availability of suitable microhabitats is suggested to be the most important factor limiting density in different areas of the shore. The fact that the growth rate is extremely plastic results in more rapid growth where density is low and intraspecific competition for resources consequently less severe (see p.29).

Mortality and mean life expectancy.

When investigations began in November, 1962, the mean density of size class A over the whole study area was approximately 28/metre² and of size class B, 14/metre² (Figure 13). It was therefore considered probable that A was composed of two or more year groups. While the mean density of B altered comparatively little through the year, its percentage of the sum of size classes A and B increased from 33% in November to 43% in June. Mortality in the two size classes combined was 33% for the whole year. As mortality in B was never heavy where it could be distinguished from A, it is reasonable to suppose that the 33% mortality was mainly accounted for by the older elements of A, i.e. approximately 50% of size class A died during the 12 months November 1962 to October 1963. By October, A + B were at a density of 28/metre², i.e. the two adult classes

combined were in identical numbers to the previous year.

Although numbers of size class A fell steadily until June, over 25% of the annual mortality occurred in April and May. Since the mean shell diameter of size class A fell slightly at this time (Figure 5), it seems likely that more of the older and larger animals had died. Deaths at this time of the year might be attributed to exhaustion following breeding rather than any special climatic or other factors.

Mortality cannot be assessed in size classes C and D because only a fraction of these groups was available for examination. It can be stated with certainty however, that size class C showed constant increase throughout the investigation period, particularly in the summer months. By October 1963 it had reached a mean density of 20/metre², i.e. a level slightly higher than that of size class B, its equivalent in age, a year earlier. Size class D showed high mortality (40%) between November and April and again (64%) from June to September. The continued presence of these animals on the shore was probably due to chance settlement right through the winter period from September 1962 to April 1963 at a tidal level unsuited to their survival. True mortality over this period was probably much higher than 40% (see p.39).

If size class A represented two year groups, as seems most probable, the mean life expectancy of animals which survived the first few months, was approximately five years. In November, 1962,

for instance, size class D consisted of animals newly settled, C of one year olds, B of two year olds and A of three and four year olds. Most of the four year olds would have died during the ensuing year i.e. in their fifth year.

Summary

(1) The overall mean density did not change significantly during the year. Size class A decreased from November to June and particularly after April. Size class B maintained a fairly uniform density through the year. Size class C increased throughout, but particularly after April, due to upward migration from the sublittoral. Size class D fluctuated according to breeding production, but individuals failed to survive long in the tidal zone.

(2) At the higher levels, the total density fell between November and April and rose thereafter. At the lowest level sampled (- 1.0 ft.) total density fell between April and October. Down-shore migration took place in winter followed by an upshore movement after April.

(3) Distribution was less clumped at lower levels at all times of the year. At upper levels, aggregation due to animals congregating in the wetter areas was marked, particularly in winter.

(4) Maximum total densities were found between M.L.W. and M.L.W.S. Young animals living intertidally showed a maximum density at a higher level than old ones. The importance of stones under which to live has been emphasized in the case of the young animals. The

animals' habits altered at about 9 mm. shell breadth: they began grazing in more exposed places. Before sexual maturity at 8-9 mm. shell breadth, most of the individuals were below tidal levels.

(5) The boulder areas supported higher densities than the limestone reef areas. Young animals did not survive at all on the reefs and the population was derived by immigration from the boulder areas.

(6) Size class A represented two year groups and suffered an annual mortality of 50%. Mortality was particularly high following the breeding season. Mortality of first year animals was very high in the intertidal area. Mean life expectancy for animals surviving the first year is about five years.

IV SYMPATRIC POPULATIONS OF *G. CINERARIA*AND *G. UMBILICALIS* : *G. CINERARIA*Introduction

The majority of suitable shores on the west coasts of Britain, support populations of *G. umbilicalis* in addition to *G. cineraria*. One such shore at Seaton, Devon (map reference SY235894), was examined on four occasions, the main object being to establish whether competition between the two species influenced the ecology of *G. cineraria*. The shore chosen for this study could not be visited sufficiently often to establish precise growth rates or breeding seasons, but the population density and size distribution of the two species was measured in August 1962 and in March, July, and December 1963.

Study area.

The shore at Seaton was specially chosen for its similarity to the north-eastern shore at Whitburn, which it closely resembles with respect to geology and exposure. It consists almost entirely of boulders varying greatly in size, which have descended in cliff falls from the Upper Greensand and Arenaceous Chalk cliffs above. The upper shore consists largely of barren shingle but the middle and lower levels are well covered with Fucaceae although these are not too dense to exclude the acorn barnacles, *B. balanoides* and

G. stellatus. The gradient is uniform and slight except for a stretch astride M.L.W.N. which is almost flat and contains many shallow pools. From M.L.W.S. downwards, there is a good deal of sand and the rock does not extend beyond E.L.W.S.

In August, 1962 the shore supported large populations of G. umbilicalis and the high level trochid M. lineata. L. littorea, and L. saxatilis were all abundant and L. neritoides was present in small numbers in the supralittoral fringe. At low levels, Lacuna pallidula (da Costa) occurred on F. serratus and the Laminaria spp. Three species Patella, P. vulgata, P. depressa, and P. aspera were also present. Four species of grazing gastropod viz. M. lineata, G. umbilicalis, P. depressa and P. aspera occurred which were absent at Whitburn, the first two in large numbers. Since both are closely related to G. cineraria it was considered possible that the species might be in competition where their vertical ranges overlapped.

Effects of the 1962-63 winter.

Due to the exceptionally severe winter of 1962-63, the faunal composition of the shore was totally altered when the second visit was made in March 1963. M. lineata had entirely disappeared and G. umbilicalis was so reduced in numbers as to be difficult to find. (It was incorrectly stated by Crisp and Southward in Crisp D.J. ed. (1964) that G. umbilicalis had entirely disappeared from Seaton and several neighbouring beaches). G. cineraria had

survived with much reduced numbers but the littorinids seemed to have survived quite well. The almost complete disappearance of G. umbilicalis upset the original aim of the work at Seaton, but quite fortuitously made possible some interesting observations relating to the nature of competition between intertidal grazing prosobranchs.

Methods

G. cineraria and G. umbilicalis populations were measured using a metre² quadrat in August 1962, March, July and December 1963 and a further visit was made in September 1965. On the first occasion, collections were made at three different levels, + 8.5, + 4.4 and + 1.3 ft. C.D. On the second visit, collections were made at the same three levels and also at - 0.3 and - 1.0 ft. C.D., levels, which were only accessible at equinoctial spring tides. The July and December collections were confined to the + 1.3 and - 0.3 ft. levels since the upper levels were barren and the lowest was not uncovered by the tide (Appendix V). Two transects were made over the collecting area in August 1962 and March 1963 to establish the vertical ranges of both species.

Results

Population density

The first samples in August 1962 showed that G. cineraria at + 1.3 ft. C.D. in the F. serratus zone had a much lower summer density than at Whitburn, the mean being 24/metre². At a comparable

level, the summer density (June) at Whitburn was $62/\text{metre}^2$. However at Seaton, G. cineraria shared this habitat with G. umbilicalis the density of which had a mean value of $65/\text{metre}^2$. The total density of Gibbula spp. ($89/\text{metre}^2$) at this level was therefore considerably higher than at Whitburn at the same time of year. G. cineraria was entirely confined to pools even at this low level and it was also clear that its vertical range on the shore at Seaton was much less. Apart from a single specimen found at M.L.W.N. the species did not extend above M.L.W. The smaller vertical range could have been due either to climatic factors such as inadequate resistance to the higher temperatures experienced during emersion in the south or it might have been caused by competition with G. umbilicalis. Low water during spring tides at Seaton always occur in the middle of the day when temperatures are likely to be at their greatest. On the other hand, G. umbilicalis was clearly a successful species on the Seaton shore and considering its high density, competition between the two species could not be discounted.

In March 1963 when the second visit was made, the density of G. cineraria at + 1.3 ft. C.D. had fallen to $3.6/\text{metre}^2$. The many empty shells found indicated that the severe weather had taken its toll. A downshore migration might have occurred as this had been demonstrated at Whitburn. The low tides made it possible to sample lower levels than on the previous visit. At - 0.3 ft. C.D. the density was $6.7/\text{metre}^2$ and at - 1.0 ft., $8.4/\text{metre}^2$. Therefore,

although the density was greater at lower levels it could not nearly account for the population density recorded in August. An additional important point needs to be made. Below E.L.W.S. the bottom consists entirely of sand and it was no surprise that G. cineraria could not be found there. This also suggested that the species could not retire further than the sublittoral fringe when conditions became adverse. It was concluded that mortality had been considerable. Since the density was not estimated at the lower levels before the severe weather, a downshore movement cannot be proved, but seems probable.

By July, density at + 1.3 ft. C.D. had recovered to 7.1/metre² but had not reached the level of the previous summer. At - 0.3 ft., density had also risen to 15.8/metre² and an upshore summer movement seems the obvious explanation for these increases. A real change in density from the March level at + 1.3 ft. is supported by a t test: $t(34) = 2.45$; $P = 0.02$. At - 0.3 ft., the change is not statistically significant: $t(16) = 1.95$; $0.10 > P > 0.05$ (Bessel's Correction applied in both cases). At + 1.3 ft. the density had fallen again by December to 4.3/metre², but the result is not quite significant: $t(34) = 1.88$; $0.10 > P > 0.05$.

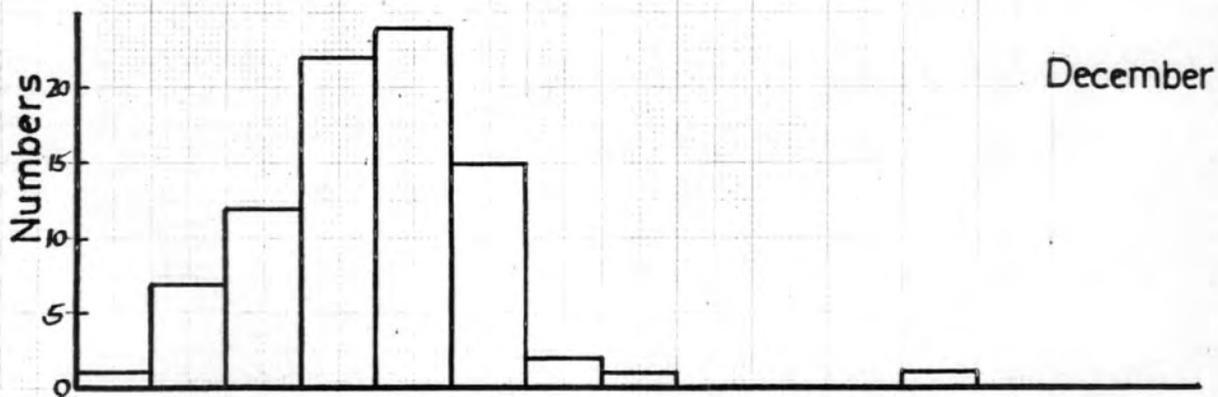
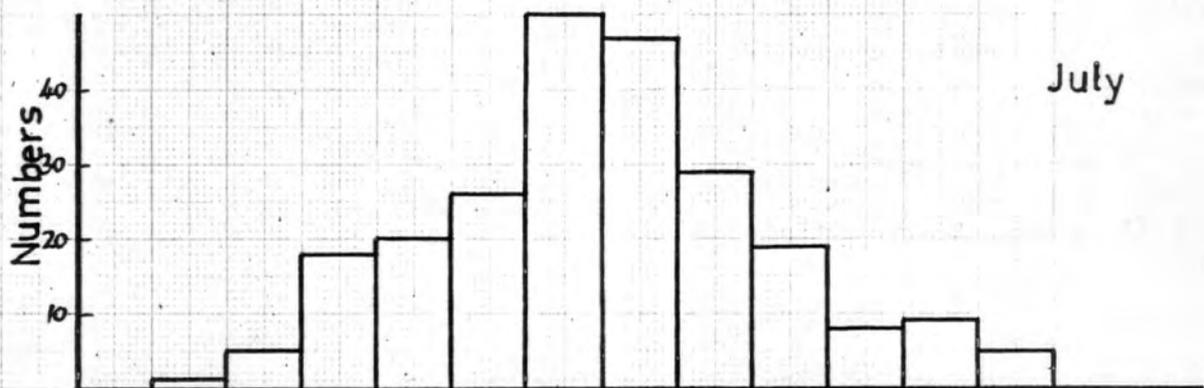
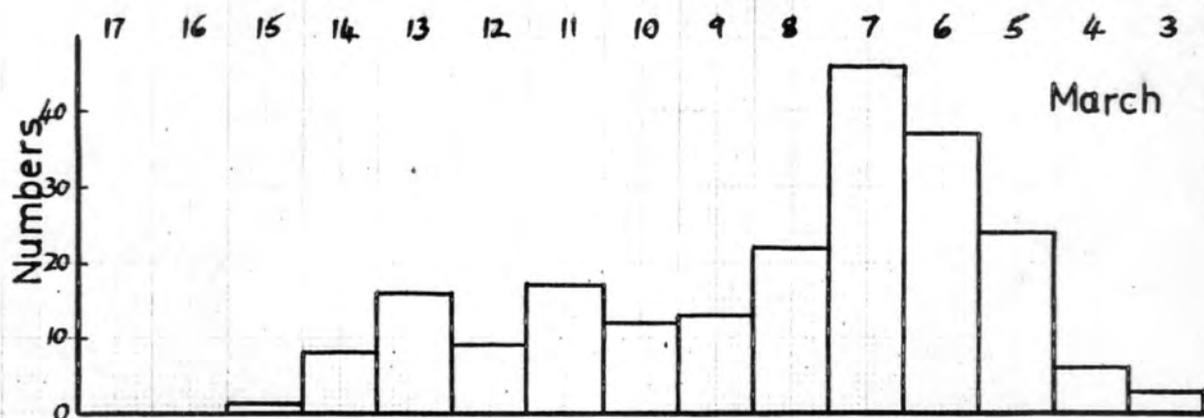
Growth rate.

The distribution of size groups (Figure 17) shows a pattern similar to the Whitburn samples. The figures for March, July and December were analysed using arithmetical probability paper to

Figure 17.

Histograms showing the frequency distribution of size classes at Seaton 1963, in three different months.

Size: shell breadth(mm)



show the true distribution of the population's age components and their percentages of the total. The details are given in Appendix V.

In March 1963, four component size classes, W, X, Y and Z were discerned after analysis with probability paper. The size classes had a mean size (shell breadth in mm.) of 12.7 ± 0.8 , 10.4 ± 0.8 , 5.9 ± 1.2 and 3.4 ± 0.7 respectively. As at Whitburn, size class Z which consisted of newly settled animals constituted a small (5%) proportion of the total. Size classes W and X which were the breeding animals made up 12% and 18% respectively of the total. The great majority of animals (65%) belonged to size class Y which was probably just over one year old. Compared with the situation at Whitburn in March 1963 the age structure of the population was in marked contrast, the only similarity being the small percentage of first year animals. At Whitburn, the two adult size classes, (A and B) constituted 89-95% of the total, depending on level, at this time of year. Corresponding age components (W and X) at Seaton composed only 30% of the total for which the high mortality among adults was probably responsible. The high percentage of second year animals (size class Y) at Seaton might have been due to the fact that they escaped heavy mortality because of their low level habitat during the severe weather. It cannot be stated at what time of year these animals would have been expected to appear in numbers in a normal year., but it is quite possible that the

extensive mortality of adults and the decimation of G. umbilicalis left a vacant niche which they were able to exploit. In any case, it has been shown that second year animals at Whitburn began a massive upshore movement in April. The same probably happened at Seaton.

In July, 1963, only three classes could be distinguished with probability paper. The mean shell breadths were 13.3 ± 1.5 mm., 10.0 ± 1.5 mm. and 5.3 ± 0.7 mm. and the respective proportions 11%, 82% and 7%. The largest animals at 11% were undoubtedly size class W. The 82% group consisted of size classes X and Y which had merged. Size class Z remained distinct at 7%. By December, the population was almost unimodal. Only one animal of 6 mm. was found representing size class Z. The other size classes, (99%) could not be separated using probability paper, though the use of finer measurements, say to the nearest 0.25 mm. might have made this possible. It was concluded that size classes W, X and Y had merged by December 1963.

Discussion

The relation between population density and growth rate.

These results are of interest because they provide a clue to the nature of the relationship between population density and rate of growth. Such was the effect of the reduction of density on the growth rate of the remaining animals that three modes (= year groups) had merged into one in less than 12 months, due to the

greatly accelerated growth rate in size class Y. By analogy with the Whitburn population, it is likely that size classes W and X would have merged in any case during a normal year as a result of the latter attaining adult size. What is exceptional here is that size class Y achieved what would normally be two years' growth in one year. It could be argued that this more rapid growth might be normal on the south or west coasts but this cannot be the valid explanation for two reasons. First, the population was clearly tetramodal in March; secondly, all the other populations of G. cineraria from south or west coasts examined during this survey (p.74^l et seq.) showed a polymodal frequency distribution.

It is impossible to say whether the reduced density of G. cineraria could alone be responsible for the accelerated growth rate of size class Y. It is likely that the sudden exodus of G. umbilicalis had an appreciable effect.

First year animals were always uncommon on the shore, as at Whitburn. Their numbers fell almost to zero through the year. Even when the overall density was low it seemed that they were unable to survive between the tidemarks. Since they were present in March but not by the following December it is concluded that breeding occurred chiefly in spring and not in the autumn as in the north-east. In view of the polymodal structure of the population, which implies a restricted annual breeding period,

and the failure to find the smallest animals except in spring, the Plymouth Marine Fauna (Marine Biological Association, 1957) is almost certainly incorrect in stating that G. cineraria breeds throughout the year.

When the Seaton animals were first measured for size in March, 1963, comparing similar levels between M.L.W.S. and M.L.W., the northern animals had a distinct size advantage in all age groups except the first year (Table V). However, by the end of the year, the Seaton animals were no longer smaller. The size of the largest animals had increased by 3 mm. and the second and third year animals had completely overtaken their Whitburn counterparts. When a further visit was paid to Seaton in September, 1965, animals measuring 17 mm. were abundant. In August 1962, only one animal measuring 14 mm. (the maximum) could be found. The majority of adults was 12 mm. Again we have evidence that reduced density allowed not only accelerated growth but also a greater maximum size to be attained. The results summarized in Table V show that the growth rate was plastic within the Seaton population and that it could be adjusted extremely rapidly to exploit available resources. It had already been concluded from the work at Whitburn that the species had a plastic growth rate.

Inter-specific competition.

In March, 1963, G. cineraria was collected from three different levels, at - 1.0 ft., - 0.3 ft. and + 1.3 ft. C.D.

As at Whitburn, a comparison of the size distribution at the different levels showed that the growth rate was not identical in each case (Figure 18): $\chi^2 (6) = 15.99$; $0.02 > P > 0.01$.

However, whereas, at Whitburn the high level animals at lower density showed the more rapid growth rate, the reverse was the case at Seaton. Although the higher level animals were at lower density here too, their growth rate was also markedly less. This difference between the localities is considered likely to have been caused by the presence of G. umbilicalis at Seaton. Its vertical range extended down to approximately + 0.3 ft. C.D. (M.L.W.S.). Therefore at + 1.3 ft. the two species could have been in competition, whereas at the two lower levels, where G. umbilicalis was absent, the reduced competition resulted in G. cineraria attaining more rapid growth. It might be objected that other potential competitors for G. cineraria existed at + 1.3 ft. and it must be conceded that L. littorea, living in similar situations to Gibbula spp. could have been important in this respect. However, L. littorea was also present at Whitburn whereas G. umbilicalis was not. At Whitburn, L. littorea was abundant but at Seaton, although plentiful, it was much outnumbered by G. umbilicalis before the 1962-63 winter. The vertical range of the two species was almost identical, but at + 1.3 ft., G. umbilicalis had a density of 65/metre² whereas L. littorea was quite scarce. It is therefore concluded that G. umbilicalis was in competition with G. cineraria where their ranges overlapped and that this reduced the growth rate and perhaps also the density of the latter.

Figure 18.

A comparison of the distribution of size groups
at three different levels, Seaton, March 1963.

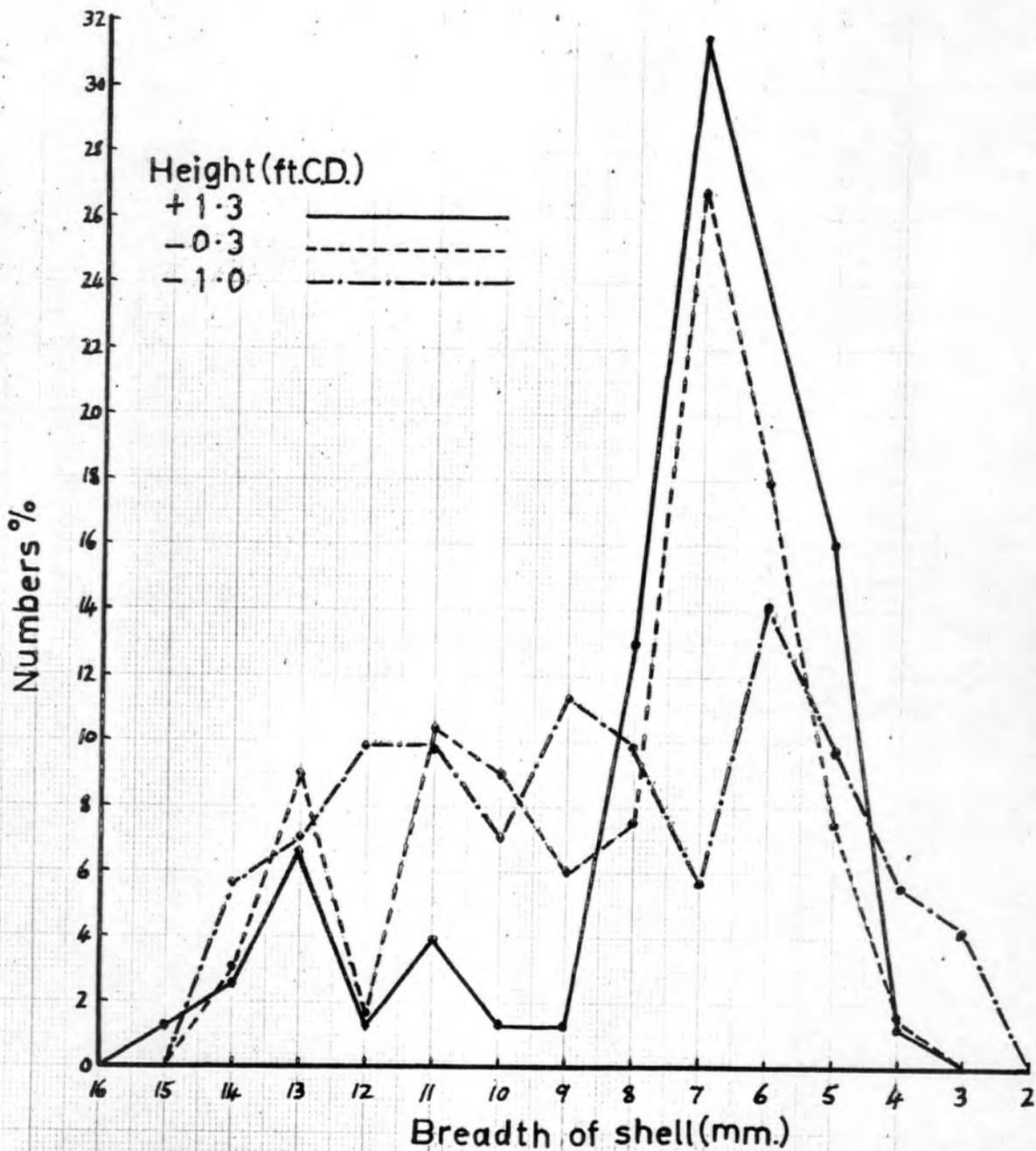


TABLE V

Comparison of the sizes attained by the different year groups at Whitburn and Seaton between M.L.W.S. and M.L.W.

<u>Date</u>	<u>Locality</u>	<u>Mean size (shell breadth in mm)</u>				<u>Maximum</u>
		<u>1st yr.</u>	<u>2nd yr.</u>	<u>3rd yr.</u>	<u>4th yr.</u>	<u>size</u> <u>(mm.)</u>
3/63	Whitburn	3.9	7.0	11.5	13.3	17
3/63	Seaton	3.4	5.9	10.4	12.7	14
6/63	Whitburn	6.0	9.5	13.1	13.1	17
7/63	Seaton	5.3	10.0	10.0	13.3	16
12/63	Whitburn	4.6	6.8	9.9	13.6	17
12/63	Seaton	?	13.2	13.2	13.2	17

04.

Summary.

- (1) The density of G. cineraria was much lower at Seaton than at Whitburn, and in extending only up to M.L.W., the vertical range was less extensive at Seaton.
- (2) Mortality of G. cineraria was severe during the 1962-63 winter.
- (3) Density in March was greater at lower levels, but increased at upper levels in summer. Upshore migration in summer was inferred.
- (4) Four component size classes were found in March. The majority of animals was one year old. Adults and newly settled animals were scarce. By December, the three oldest size classes had merged.
- (5) Rapid growth of the one and two year olds is ascribed to the low density and this to reduced intra-specific competition.
- (6) Breeding took place in Spring. The first year animals were scarce between the tidemarks and failed to survive there.
- (7) G. cineraria grew faster at Whitburn than at Seaton before the 1962-63 winter but after the winter, level for level, the Seaton animals grew faster.
- (8) High level G. cineraria grew more slowly than low level ones at Seaton (c.f. Whitburn), a fact which is ascribed to inter-specific competition between G. cineraria and G. umbilicalis where the vertical ranges overlapped.

V SYMPATRIC POPULATIONS OF *G. CINERARIA*
AND *G. UMBILICALIS* : *G. UMBILICALIS*

Introduction

In August, 1962, *G. umbilicalis* was the most abundant midshore gastropod at Seaton. It had an extensive vertical range from just above M.L.W.S. (at + 0.3 ft. C.D.) up to M.H.W.N. (+ 8.7 ft. C.D.). Like *G. cineraria* it grazed mainly on rock surfaces which were not over-exposed. It was most numerous where there was a plentiful supply of boulders, pits and crevices. Neither loose shingle nor sand was favoured, though the latter was tolerated to a small extent. In the upper part of its range it occurred mainly in pools. Where weed cover approached 100% it was rarely found but neither was it common on rocks covered with acorn barnacles. It seemed to favour the intermediate situations where barnacles, Fucaceae and limpets were competing for living space.

Methods

Samples were taken at three levels in August 1962, viz. + 1.3 ft., + 4.4 ft., and + 8.5 ft. C.D. (see Appendix V). These stations were respectively midway between M.L.W.S. and M.L.W., at M.L.W.N. and midway between E.H.W.N. and M.H.W.N. The lowest level was identical with the highest level from which *G. cineraria* was collected and the dominant alga was *F. serratus*. The middle

level supported a mixed vegetation of F. serratus and F. vesiculosus. Here, apart from one specimen of M. lineata, G. umbilicalis was the only trochid. Weed cover at the upper level was entirely F. vesiculosus and G. umbilicalis shared this habitat with M. lineata. Above M.H.W.N. where F. spiralis became the dominant weed, G. umbilicalis was absent.

The animals were collected from within a 20 cm. square which was cast backwards over the shoulder, 40 times at each level, to achieve randomness. In practice, the method proved difficult to operate due to the frequent tendency of the square not to fall flat because of the uneven terrain. After this occasion, the method was abandoned in favour of the larger metre square.

Results

Population density.

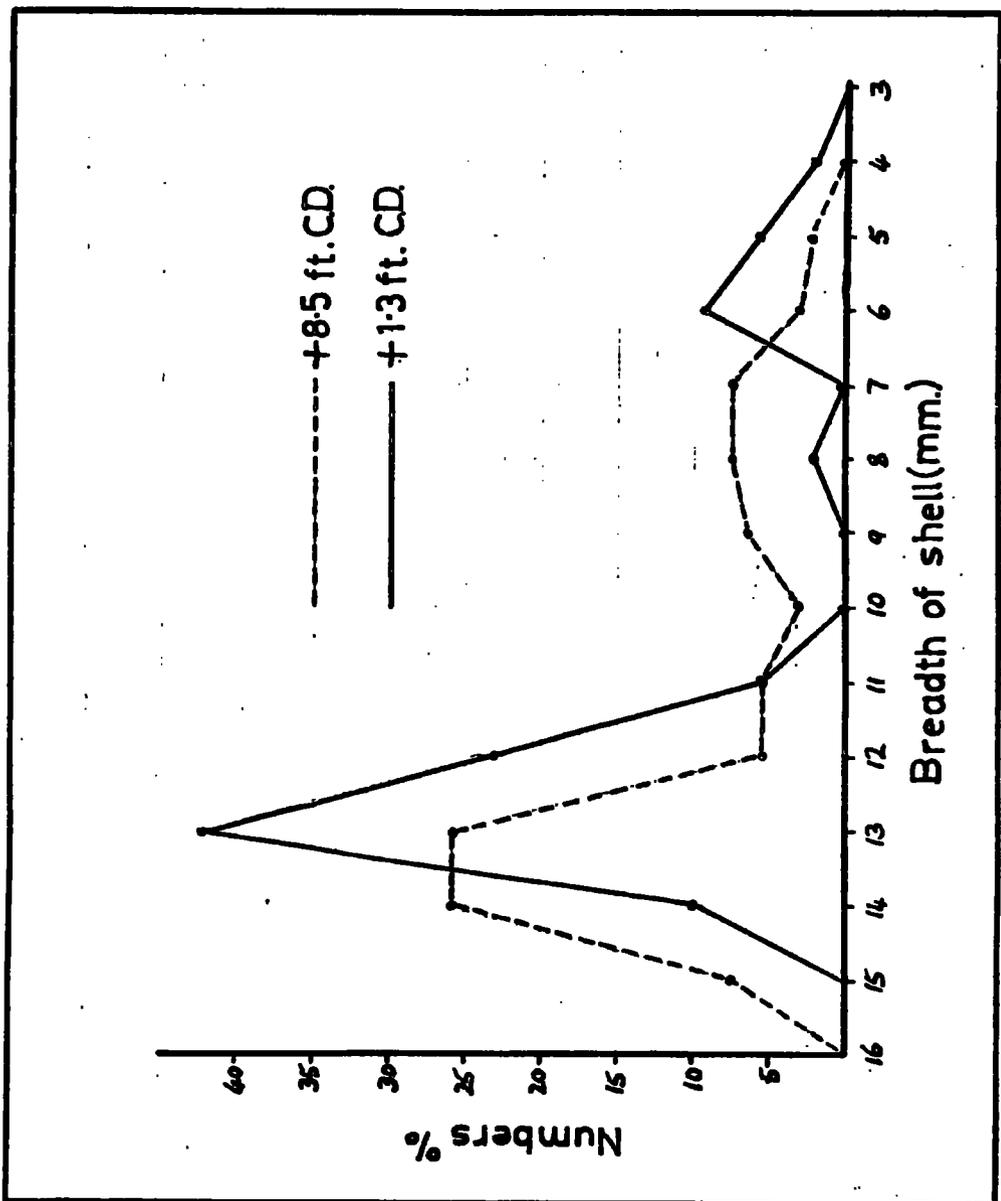
The mean density of G. umbilicalis was 65/metre² at + 1.3 ft., 165/metre² at + 4.4 ft. and 59/metre² at + 8.5 ft.

Growth rate and breeding.

The distribution of size groups at + 1.3 ft. and + 8.5 ft. are compared in Figure 19. It is apparent that the two samples were not identical: $X^2 (3) = 18.24; P < 0.001$. At the upper level, growth was more rapid. The overall distribution pattern supports the conclusion of Williams (1964) that this species reaches adult size in two years i.e. one year less than G. cineraria. Although

Figure 19.

A comparison of the distribution of size groups
at two levels, Seaton, August 1962.



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few young specimens were found, the presence of small animals (< 4 mm. shell breadth) suggests that breeding took place in the immediately preceding months, May, June and July. Summer breeding by G. umbilicalis at this latitude has been recorded by Williams (1964) in Cardigan Bay and Cornet and Marche-Marchad (1951) for Roscoff, Brittany.

At + 8.5 ft., M. lineata was present but seemed to exploit slightly different situations from G. umbilicalis. Of the 39 squares from which specimens were collected, 17 were free from weed, 22 contained some weed and one was barren shingle. The distribution of the two species is shown in Table VI and the results certainly suggest a different pattern in each case. A X^2 test on the data in Table VII based on the same 39 squares gives the result $X^2 (1) = 56.7$; $P < 0.001$ (Yates' Correction applied). The habitat difference between the species was very significant indeed on this particular shore. M. lineata frequented bare rock and G. umbilicalis, rock where at least some weed was present (p. 69). At Seaton it is probable that G. umbilicalis was restricted in its distribution at + 8.5 ft. to the areas where weed was present because M. lineata occupied the bare areas rather than vice-versa. M. lineata in my experience is rarely found in weed covered areas whereas G. umbilicalis is capable of colonizing bare rocks. Where M. lineata is absent e.g. in west Scotland, G. umbilicalis is certainly found on bare rocks.

TABLE VI

The comparative frequency of M. lineata and G. umbilicalis in areas of rock surface with and without seaweed.

<u>Species status</u>	<u>Squares with weed</u> (22)	<u>Squares without weed</u> (17)
<u>M. lineata</u> only	0	6
<u>M. lineata</u> > <u>G. umbilicalis</u>	0	6
<u>G. umbilicalis</u> > <u>M. lineata</u>	6	0
<u>G. umbilicalis</u> only	15	2
Neither species present	1	3

TABLE VII

Numbers of M. lineata and G. umbilicalis found in 39 squares (20 cm.²) according to the presence or absence of weed.

	Weed	No weed	Total
<u>M. lineata</u>	13	46	59
<u>G. umbilicalis</u>	80	15	95
Total	93	61	154

Discussion

Inter-specific competition

The reality of competition with G. cineraria is again supported by the fact that the growth rate of G. umbilicalis at + 1.3 ft. where the species were living together, is slower than at + 8.5 ft. where G. cineraria was absent. The mean densities of G. umbilicalis were similar at the two levels, so intra-specific competition was unlikely to be the cause.

In view of the distinct habitats occupied it is unlikely that competition between G. umbilicalis and M. lineata was severe on this shore.

Effects of the 1962-63 winter.

In March 1963, the density of G. umbilicalis was 0.3/metre² at + 1.3 ft. and 0.2/metre² at + 4.4 ft. All the animals found were adults. At the higher levels not a single specimen was found. The ability of G. umbilicalis to survive at lower levels probably saved it from the extinction suffered by Monodonta. In July and December, the population still survived at the same low density and by December, most of the animals were 16 mm. in breadth which is larger than any individual recorded in 1962.

By September 1965 the species was still scarce but a long search produced 48 animals and it was concluded that the population was recovering slowly. The distribution of the size groups provided yet more evidence of the flexible growth rate in Gibbula.

A comparison of the size distribution in August 1962 (both levels combined) and September 1965 is given in Figure 20. It is noticeable that in 1965, the largest animals were 3 mm. bigger than in 1962. Also, the 1965 population had an additional mode at 16 mm. Active growth probably continued longer when the density was low (cf. G. cineraria p.30), in which case the mode at 16 mm. represents three year olds, at 13 mm. two year olds and at 9 mm., one year olds.

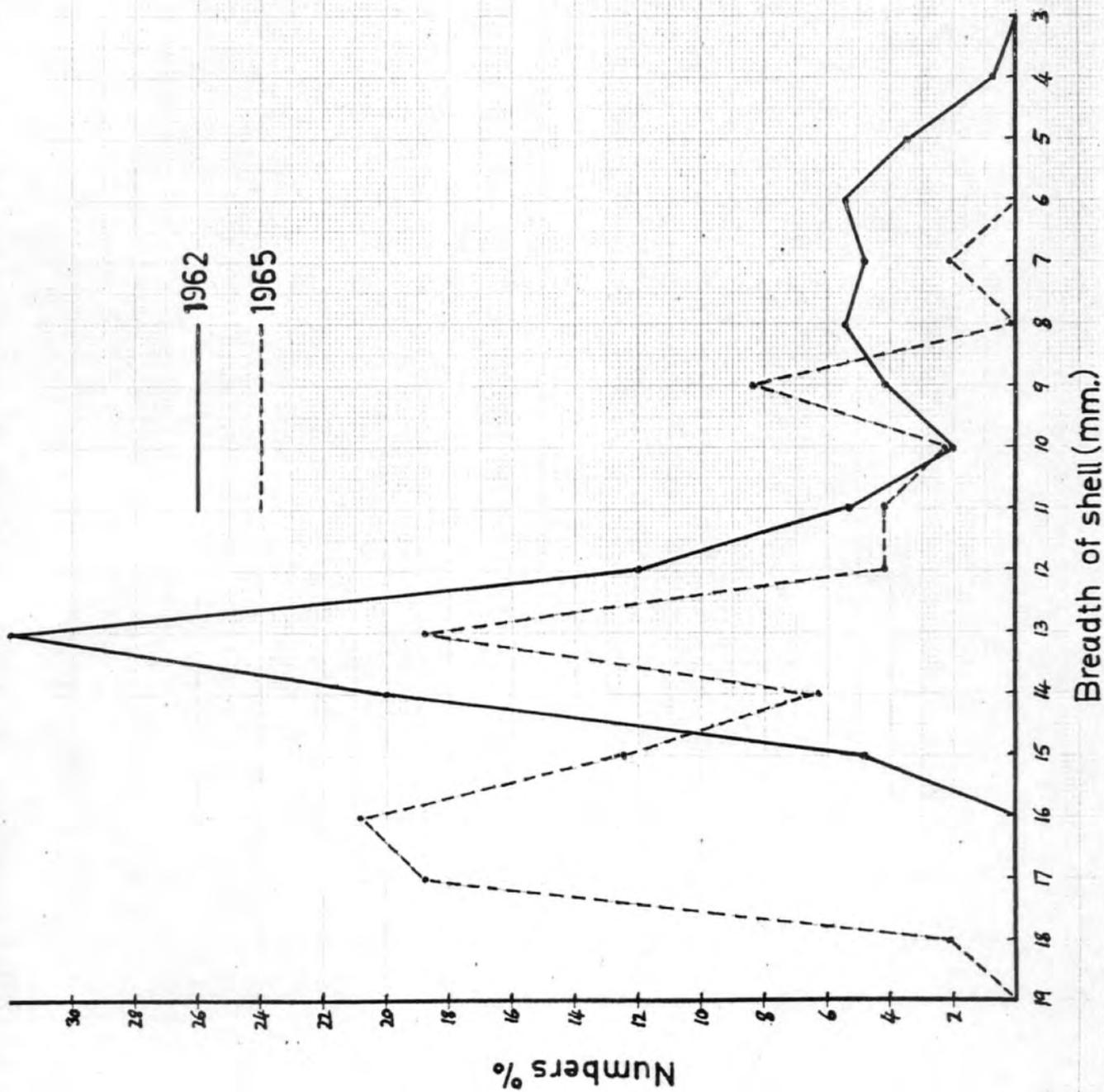
A brief visit to Seaton in September 1968, showed that G. umbilicalis was completely re-established.

The recovery of the population.

Recruitment of larvae may have occurred in 1963 from populations further afield since it must be doubtful if the depleted Seaton stock could have bred successfully that year. The nearest G. umbilicalis population to survive the 1962-63 winter without serious loss was at Teignmouth in Torbay, a distance of about 20 miles from Seaton, with no intervening headlands and a favourable current. The question is whether larvae with a planktonic phase lasting at most seven days and possibly no more than two days (Robert, 1902; Lebour, 1937; Gaillard 1952) could travel so far in the time. The current speed at the relevant time is not known. In September 1965 an estimate was obtained at Seaton by observing the rate of eastward drift of a bright red rubber ball kicked as far as possible offshore. It travelled east at 150 yards per hour, equivalent to 14.3 miles/week. This rate

Figure 20.

A comparison of the distribution of size groups
in Gibbula umbilicalis at Seaton in 1962 and 1965.



would not have been sufficient to transport Gibbula larvae over the required distance in a week. But, naturally, several qualifications need to be made. The current speed may vary a great deal between Teignmouth and Seaton with regard both to the locality and weather conditions. The day in question was calm. A strong south-west wind could make a lot of difference to the surface current speed. Again, current speed measured at the surface or close inshore may not be relevant. The issue as to whether or not the younger animals (13 mm. and below) observed at Seaton in 1965 could have been recruited from further afield must remain in doubt. On balance the evidence suggests that this was not possible.

M. lineata had failed to reappear at Seaton by 1965 or by 1968 and its breeding biology is very similar to that of G. umbilicalis (Williams, 1964; Desai, 1959). Populations of Monodonta survived the 1962-63 winter though much reduced in numbers, west of Teignmouth (Crisp ed. 1964). The alternative explanation is that the few remaining G. umbilicalis produced enough spawn to make possible a small recruitment in the summer of 1963. These animals were 13-14 mm. at that time. In 1965, they were represented by the individuals of 16 mm. or more.

Finally, L. littorea had increased its numbers greatly at Seaton between 1962 and 1965. It seems reasonable to suppose that this could have been due to the removal of M. lineata and the reduction of G. umbilicalis. The habitat of L. littorea

is often similar to that of G. umbilicalis in particular. On many sheltered western shores they are co-habitants of the midlittoral: either may be dominant. L. littorea had probably benefited from the removal of, in this case, a dominant competitor.

Summary

- (1) G. umbilicalis extended from M.L.W.S. to M.H.W.N. in 1962. Densities ranged from 59-165/metre², being greatest at + 4.4 ft. C.D.
- (2) The species bred in early summer at Seaton and reached adult size in two years.
- (3) Growth was more rapid at high than at low levels. Lower densities allowed more rapid growth.
- (4) Where the vertical ranges overlapped, the habitats of G. umbilicalis and M. lineata differed. The former preferred weed covered and the latter, weed free areas. Habitat differences between G. umbilicalis and G. cineraria, except for the levels occupied, were not demonstrated.
- (5) Mortality of G. umbilicalis was almost 100% during the 1962-63 winter. By 1965, it was still scarce but had increased. By 1968, it had re-established itself.
- (6) Whether the initial recovery of G. umbilicalis was due to external recruitment or was internally generated could not be determined.
- (7) G. umbilicalis seemed likely to be competing with L. littorea over much of the middle shore.

VI SYMPATRIC POPULATIONS OF G. CINERARIA

G. UMBILICALIS AND G. PENNANTI

Introduction

Alderney was visited in April 1964. All three intertidal Gibbula species were known to be abundant there and it was felt that the additional presence of G. pennanti, not found anywhere north of the English Channel, might throw some light on the ecology of the other two species. Seven shores were examined and two, which supported the densest Gibbula populations I had ever seen, were the subject of fairly detailed observations.

Study Areas.

Alderney is composed entirely of granite. Its coastline consists of steep cliffs, boulder beaches and sandy shores. The sand when present is a coarse unsorted arkose. The two beaches at which most of the work was done, Fort Raz East and Clonque Bay, are both extensive and exhibit a variety of degrees of exposure. Both have areas of steep granite, low lying reefs, boulders, shingles, arkose sand and plentiful pools. The large tidal range (18 ft. at springs) and the gentle gradient over most of the beaches means that a huge area is available for colonization by intertidal organisms. The algal flora of both beaches is astonishingly rich in species and contains a considerable number of Lusitanian forms which are rare in Britain. The prosobranch fauna, possibly as a result

of the variety of algae is extremely diverse. The following herbivorous prosobranchs were recorded:-

<u>Littorina neritoides</u>	<u>Patella vulgata</u>
<u>L. saxatilis</u>	<u>P. depressa</u>
<u>L. littoralis</u>	<u>P. aspera</u>
<u>Lacuna vincta</u> (Montagu)	<u>Patina pellucida</u> (L)
<u>L. pallidula</u>	<u>Acmaea virginea</u> (Müller)
<u>Tricolia pullus</u> (L.)	<u>Calliostoma zizyphinum</u> (L.)
<u>Rissoa parva</u> (da Costa)	<u>Monodonta lineata</u>
<u>Rissiodae unidentified</u>	<u>Gibbula cineraria</u>
<u>Haliotis tuberculata</u> L.	<u>G. umbilicalis</u>
<u>Bittum reticulatum</u> (da Costa)	<u>G. pennanti</u>

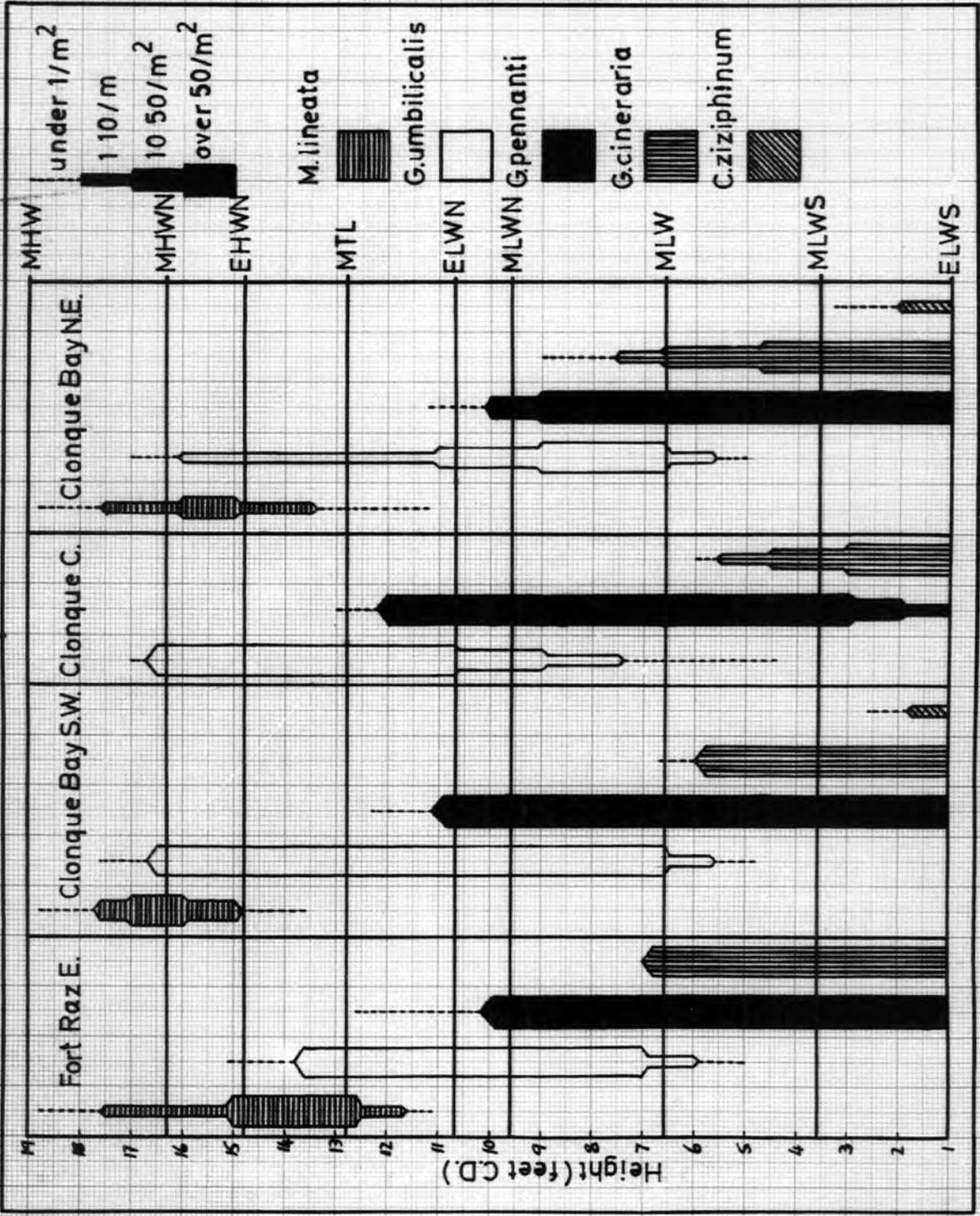
Results.

Zonation

The results of transects carried out at four different points, three in Clonque Bay and one at Fort Raz, show the vertical ranges of the three Gibbula species and the other two trochids, M. lineata and C. zizyphinum (Figure 21). The Evans Method (p. 36) was used. It is clear from all the transects that the range of G. pennanti was intermediate between those of G. cineraria and G. umbilicalis. Since all three species were abundant (exceeding 50/metre²) in the centre of their range, the extent to which their habitats differed where they overlapped, was investigated.

Figure 21.

The vertical ranges of five species of Trochidae
on four rocky shores in Alderney, Channel Islands.



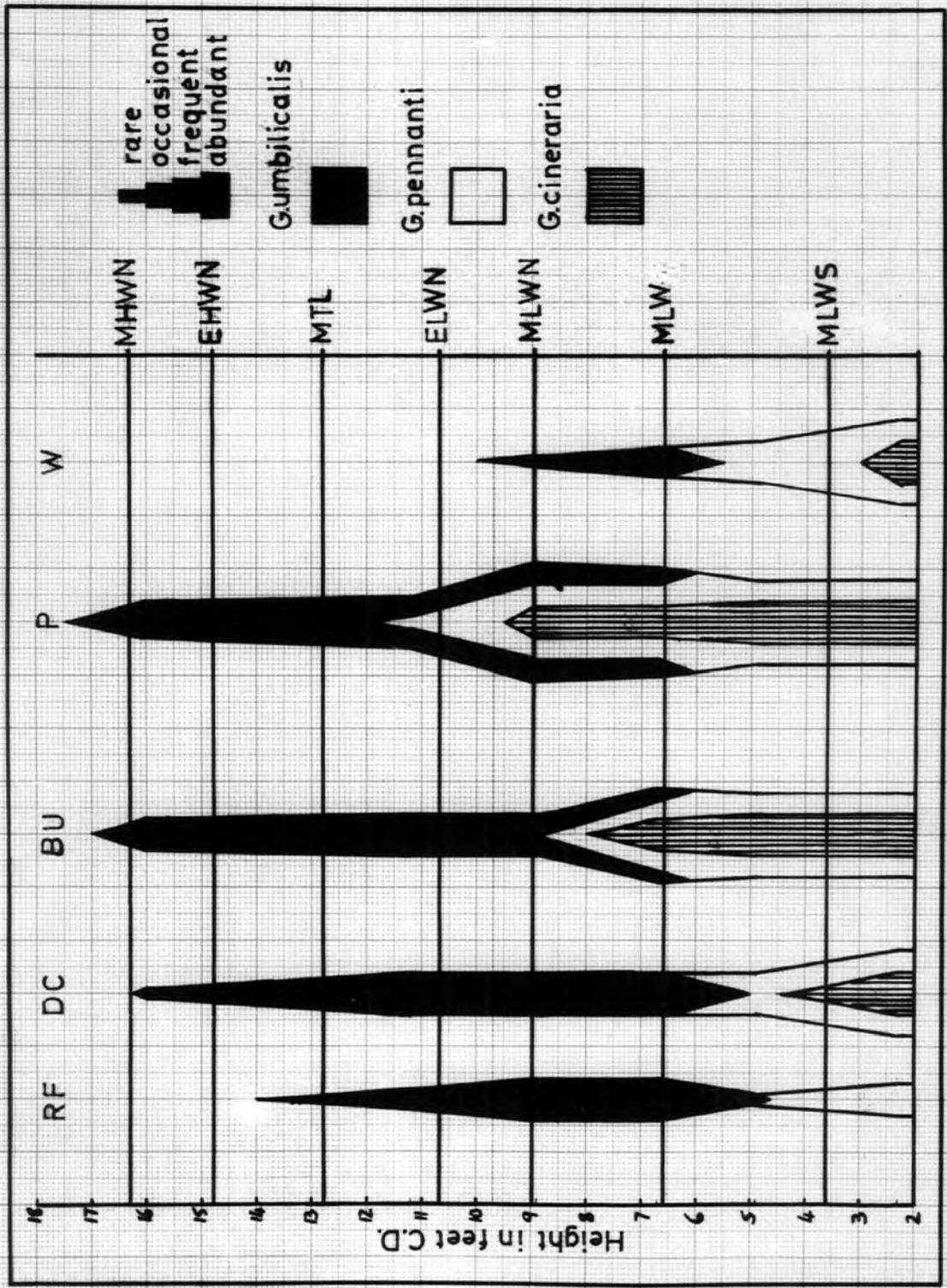
Habitats.

The available habitats were classified as follows: flat rocks without crevices, depressions or weed (R.F.); depressions and crevices (D.C.); undersides of boulders without standing water (B.U.); pools (P.); surfaces of seaweeds (W). Abundance was divided into four categories as follows: some found in over 75% of situations inspected - abundant; some found in 25-75% of situations inspected - frequent; found in less than 25% of situations - occasional; scattered individuals - rare. Four examples of each type of habitat were searched at each of seven levels on the shore between + 2.3ft. C. D. and + 17 ft. The results are shown in Figure 22.

It was clear that the choice of habitats for each species narrowed the further upshore they lived. All extended furthest upshore in pools. The undersides of boulders were also much frequented in the upper range. Open rock was only favoured by G. umbilicalis except at low levels where it was replaced by G. pennanti. Below M.L.W., G. pennanti was the chief browser on weed. Each species seemed to require protection and moisture in its upper range. Below E.L.W.N. G. umbilicalis was progressively replaced by G. pennanti in the more sheltered areas and pools. From M.L.W.N. downwards, G. cineraria joined G. pennanti in the pools and the latter was found more commonly in open situations, at first confined to crevices and then at lower levels, browsing on weeds and

Figure 22.

The habitat preferences of the three species of Gibbula at Clonque Bay, Alderney. (for explanation see text p.76).



open rocks. In some cases between E.L.W.N. and M.L.W.N., G. umbilicalis occurred above the waterline of pools and G. pennanti below, with no more than one inch separating them.

In Clonque Bay, a large sandy pool at + 4.4 ft. C.D. supported a huge population of G. pennanti feeding largely on weeds. No other species of Gibbula occurred there. The dominant weed was the flowering plant, Zostera marina L. but there was an immensely varied algal flora including Codium tomentosum Stackh., Codium fragile (Sur). Hariot and four species of Cystoceira. On reefs at this level, G. pennanti was found feeding in large numbers on the small Rhodophyceae, particularly Furcellaria fastigiata (L.) Lamour, Chondrus crispus Stackh., Gigartina stellata (Stackh) Batt. and Laurencia spp. It was also common among Bifurcaria bifurcata Ross, a southern species of Fucaceae which is abundant on Alderney but rare in Britain. It appeared that G. pennanti was exploiting a niche which G. cineraria and G. umbilicalis rarely fill, though several species of Littorinidae, notably on this shore Lacuna vineta, L. pallidula and Littorina littoralis all feed almost exclusively on the larger algae. However, the Littorinidae feed mainly on the common Fucaceae and Laminariaceae whereas G. pennanti was most abundant on Bifurcaria, Cystoceira (Fucaceae rare in Britain and confined to the south-west), Codium and the Rhodophyceae

(see above). It is possible that the geographical range of G. pennanti is limited by the ranges of its favourite food-plants. It must be stressed, however, that G. pennanti does frequently browse on open rock at low levels and also on algae particularly Rhodophyceae, which are abundant all round the British coast.

Two interesting points in connexion with G. cineraria were noted. Firstly, large numbers of spat were found scattered over a much wider belt of the shore than was inhabited by the adults. The highest spat were found at + 13.2 ft. (M.T.L. + 0.4 ft.). These young animals were omitted from the transect results (Figure 21) because the much smaller range of the adults was taken as an indication that the young do not survive long at this high level and considerable evidence of their inability to survive on the shore had already been given. Connell (1961b) has shown that C. stellatus in Scotland settles over a wide area of shore but the spat are either crushed or overgrown by B. balanoides. It is possible that G. cineraria spat are similarly ousted by more successful species when they settle outside their normal zone. However, the presence of the spat indicated spring breeding.

Secondly, the adults were mostly small (12mm.) and this was probably a result of the extremely high overall densities of Gibbula spp. and perhaps particularly of competition from G. pennanti from which it is free at the lowest levels on

British shores.

Exposure tolerance.

Five more exposed shores were examined briefly to investigate exposure tolerances. Although all three species could be found on shores that would be classified as exposed, all were restricted to sheltered microhabitats. Moving from exposure towards shelter, G. umbilicalis was the first species to appear and G. pennanti the last. On the most sheltered shore where Fucaceae cover was 100% and large quantities of sand and silt were deposited, all three species were scarce. The impression gained was that all three species had similar habitat preferences: where one was abundant, the other two would also be. All preferred semi-exposed and sheltered shores, avoiding extremes of either exposure or shelter. It was felt that the ability of G. umbilicalis to withstand slightly more exposed conditions than the other two species might be aided by its flatter shell which would create less resistance to water movements.

Summary.

- (1) The vertical range of G. pennanti was intermediate between those of G. cineraria and G. umbilicalis. All three species frequented sheltered and damp situations in the upper part of their range.
- (2) Open rock was most favoured by G. umbilicalis. G. pennanti was found more frequently than the other two species browsing

on weed. Silt, sand and heavy weed cover were to some extent avoided by all three species.

(3) G. umbilicalis was the most and G. pennanti the least tolerant of wave action.

(4) The geographical range of G. pennanti might be limited by that of certain algae eg. B. bifurcata and Cystoceira spp.

(5) The small adult size of G. cineraria might be the result of competition with G. pennanti.

(6) G. cineraria spat settle over a much wider area of shore than is colonized by the adults.

(7) G. cineraria was a spring breeder.

VII ZONATION AND HABITATS IN *G. CINERARIA**G. UMBILICALIS* AND *G. PENNANTI*Introduction

Evidence has been presented which shows that competition between *G. cineraria* and *G. umbilicalis* is likely to have an important influence on the ecology of both species where they occur together. In order to seek further evidence of competition between these two species and *G. pennanti*, where it occurs, several other localities both within and outside the British Isles were visited. The questions to which answers were sought mainly involved the effects of inter-specific competition and the influence of latitude (i.e. climate) on the biology of the species. The effect of competition on such factors as vertical range (zonation), growth rate, density and habitat selection was investigated. Additionally, it was sometimes possible to infer a climatic effect where factors like vertical range, growth and adult size, exposure tolerance and breeding seasons were concerned. Since most of the visits were necessarily quite brief, many of the problems regarding growth and breeding seasons are unsolved and attempts to provide answers to others remain at the level of speculation.

Two areas, Port William in south-west Scotland, and Clashnessie in north-west Scotland were examined to see if *G. cineraria* and *G. umbilicalis* interacted in the same way as

in Devon. The populations of G. cineraria in the Faeroe Islands, where it is nearing its northern distribution limit (Thorson, 1941), were investigated. A beach in north Spain where G. cineraria is absent from the littoral zone and the other two species are abundant, was inspected. Finally, several shores in the Canary Islands, Madeira and the Azores were examined briefly.

G. cineraria and G. umbilicalis in Scotland.

Clashnessie, Sutherland (map reference NC 060313)

This shore was examined in March, 1964, it consists of boulders of Lewisian gneiss, some of them extremely large. The substratum had the appearance of being stable except during heavy storms. The degree of exposure is intermediate., the middle shore being largely bare except for B. balanoides and P. vulgata, and weeds are restricted to depressions and pools. There is an upper fringe of Pelvetia canaliculata (L.) and the lower shore is fairly well clothed with F. serratus and Himanthalia elongata (L.). Laurencia spp. and G. stellata form a dense carpet covering the rocks at the lower level. The sublittoral fringe supports a flora of L. digitata, L. hyperborea and Alaria esculenta (L.) Grev. Both the predominance of barnacles in midshore and the presence of H. elongata and A. esculenta lower down, indicated that the shore is fairly exposed and at first glance it would be thought an unlikely habitat for Gibbula. However, the size of the boulders is such

that sheltered habitats are common beneath and between them. Many pools containing small pebbles are formed in depressions between the large boulders and these proved a suitable Gibbula habitat. The degree of protection afforded by the crevices and gullies must be considerable since large plants of F. vesiculosus and A. nodosum were found growing in such places.

Both G. cineraria and G. umbilicalis were abundant in suitably protected places, the former from the sublittoral up to + 8.4 ft. C.D. (just above M.T.L.) and the latter from + 4.5 ft. C.D. (M.L.W.N. - 0.7 ft.) up to + 10.4 ft. C.D. (B.H.W.N.). The upper limit of G. cineraria corresponded exactly with the uppermost pools to which it was confined at this level. It became abundant and generally distributed from M.L.W.N. downwards reaching a maximum density (over 50 per metre²) at + 3.3 ft. C.D. (just above M.L.W.). Below this level, all boulders and stones were cemented together with Lithothamnion which rendered the undersides inaccessible and the density fell, probably due to the scarcity of protective stones under which to crawl. Particularly noticeable was the absence of young animals at the lowest levels though they were common higher up and this observation supports the conclusion reached from the Whitburn data that the survival of the young depends on the presence of loose stones under which to live.

G. umbilicalis is approaching its northern limit at Clashnessie (Rendell, (1956); Lewis, 1957). There was no

indication that it was struggling to survive as its maximum abundance at + 5.6 ft. C.D. (between M.L.W.N. and E.L.W.N.) exceeded 50 per metre². However, the extent of its vertical range (particularly at the lower end,) was certainly less than is usual further south, where it normally reaches M.L.W.S. or thereabout. A lower limit just below M.L.W.N. is also recorded by Lewis (1957) at Scourie, another Sutherland locality. The upper limit at Scourie was just above M.H.W.N. whereas at Clashnessie it extended only to E.H.W.N. This was probably due to the absence of pools to which it is almost completely confined when it occurs above this level.

Port William, Wigtownshire (map reference NX 384413).

This shore was examined in May, 1964. It is a large area of boulder shore with a gentle slope, not so exposed as Clashnessie but by no means covered with weed. This may be attributed as much to the small size and consequent instability of the stones as to exposure. Large populations of both G. cineraria and G. umbilicalis were present.

G. cineraria extended from the sublittoral to E.H.W.N. though above M.L.W.N. it was confined to pools, while G. umbilicalis was present from M.L.W. up to M.H.W.N. Although, G. umbilicalis extended lower than at Clashnessie, its lower range was not so extensive as is usual in Wales or Southern England. G. cineraria did not extend so high as in Sutherland and other parts of Scotland, but its intertidal range was still

in excess of that observed further south.

The distribution of size groups for both species is shown in Figure 23. In the case of G. cineraria, the histogram shows the expected polymodal distribution. It is of interest to note the presence of minute animals (the smallest found on any shore) indicating that breeding was occurring. The largest animals at 18mm. were larger than any found further south on the west side of Britain. The histogram for G. umbilicalis suggests that the breeding performance during 1962 and 1963 was poor, resulting in very low numbers of one and two year olds.

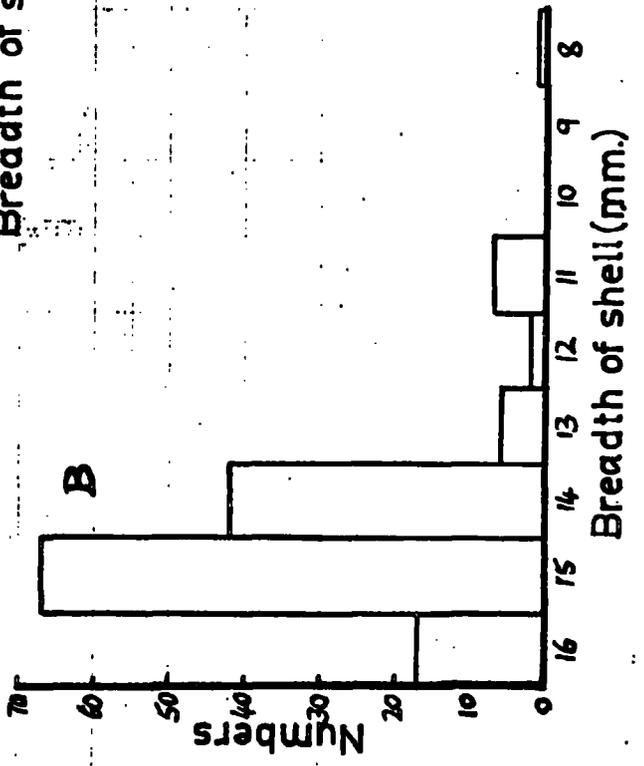
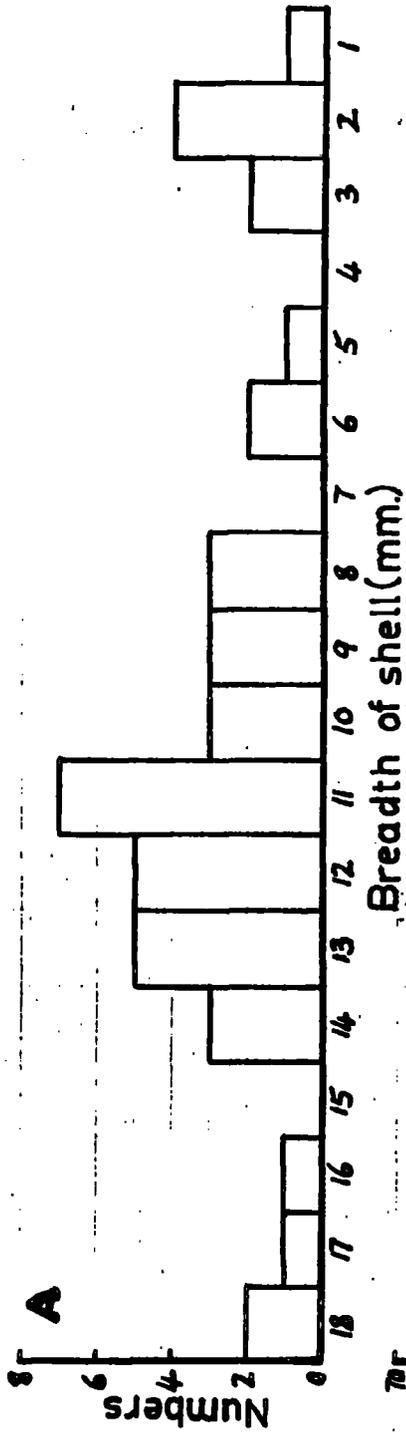
Gibbula cineraria in the Faeroe Islands.

The Faeroe Islands were visited in April 1965. Here, G. cineraria, the only member of the genus present, is approaching the northern limit of its range (Thorson, 1941). Eleven shores varying degrees of exposure were examined on the islands Streymoy and Vagar. The populations of G. cineraria in the Faeroes provided additional evidence in support of some conclusions reached so far.

Of the eleven shores examined, G. cineraria was found on six. It was absent from all very exposed shores excepting one to which further reference will be made. It was also found on only one sheltered shore. Its occurrence was fairly regular on exposed and semi-exposed shores where suitable microhabitats existed. It was abundant on only two shores, both of which had a plentiful supply of boulders and were free from sand.

Figure 23.

Histograms showing the distribution of size groups in G. cineraria (A) and G. umbilicalis (B) at Port William, Wigtownshire.



The single occurrence on a very exposed shore must be the most bizarre habitat ever recorded for G. cineraria. The shore at Hoyvik, Streymoy, which has a tidal range of only one foot at springs, consists of a vertical cliff of basalt from M.L.W.S. up to M.H.W.S. + 4 ft. supporting a fauna of B. balanoides, P. vulgata, and Mytilus edulis L. and a flora composed of A. esculenta, Porphyra umbilicalis (L.) and a turf of small Rhodophyceae. Above M.H.W.S. + 4 ft. lies a series of flat shelves in one of which at M.H.W.S. + 6 ft. there is a large pool. The fauna of the pool was dominated by low level and even sublittoral animals such as Modiolus modiolus, (L.) Tealia felina, (L.) Aeolidia papillosa, (L.) A. virginica, Buccinum undatum L. and M. edulis. G. cineraria and T. lapillus were the most abundant inhabitants.

The dominant climatic features of the Faeroes are the high rainfall, humidity, cloud cover and winds and the low incidence of both sunshine and frost. Sea temperatures (annual range 5.2°C.) and are extremely equable. High rock pools are not exposed to the climatic extremes usual at this level. The high humidity and dense cloud cover reduce evaporation and the incessant swell and spray provide constant renewal of the sea water in the pools. When all these factors are considered, there is no need to suppose that the animals inhabiting this pool were especially tolerant of normal conditions on the upper shore. Conditions in this case were most unusual. Moreover, the steep

sides of the pool provided a comparatively sheltered habitat although the other inhabitants of this shore are all indicators of considerable exposure.

On one exposed shore at Hoyvik, Streymoy, G. cineraria was abundant. As at Clashnessie, the shore was composed of very large boulders, in this case of basalt, and the species was confined to sheltered places mainly beneath the boulders. In the sublittoral, the species was much more numerous. It could be seen in large numbers feeding on the upper sides of boulders even in the heavy swell. A local fisherman volunteered the information that G. cineraria moves upshore in large numbers in the summer and retires again to the sublittoral in the autumn. Such an observation would be much more easily made in the Faeroes than in Britain because (a) the intertidal zone is narrow; (b) this particular shore was free from weed; (c) G. cineraria is the only large intertidal gastropod apart from limpets. If true, this evidence supports conclusions concerning seasonal migration already arrived at from the Whitburn and Seaton populations. Even in April, the vertical range of G. cineraria extended up to M.H.W.S. on this shore, though it was scarce at the upper levels.

A shore of smooth basalt without crevices no more than a few yards from the preceding one produced not a single specimen of G. cineraria. The overall exposure conditions were identical in the two cases and the example indicates the great importance of microhabitats in determining the distribution of the

species. The truth of this statement is reinforced by evidence from the shore at Futaklettur on the island of Vagar. Here the tidal range is 6.6 ft. at springs. The intertidal zone consists of a series of flat wavecut platforms of basalt. Below M.T.L. sheltered habitats were absent, but above this level some crevices and pools supported small numbers of G. cineraria up to M.H.W.N.

Two other shores on Vagar at Sandvag and Midvag, both composed of basal boulders, supported G. cineraria at low density, in the more sheltered areas, from the sublittoral up M.T.L. + 0.5 ft. The individual specimens found were all large adults between 19mm. and 23mm. in shell breadth. These figures are very different from those shown in Figure 22, where most adults measure 14mm. In the latter case, the specimens were collected from a dense population at Hoyvik, Streymoy. Again, we have evidence of the negative relationship between density and adult size referred to in previous chapters.

Two sheltered shores were examined. From the first at Sorvag on Vagar with a tidal range of 6.6 ft., G. cineraria was entirely absent. The intensity of weed cover and the presence of sand under the boulders and pebbles was probably responsible for this. The species is absent from many similar shores in the lochs and sheltered inlets of western Scotland. The other sheltered shore near Thorshaven on Streymoy supported a dense population of G. cineraria, though mostly below tidal levels.

09.

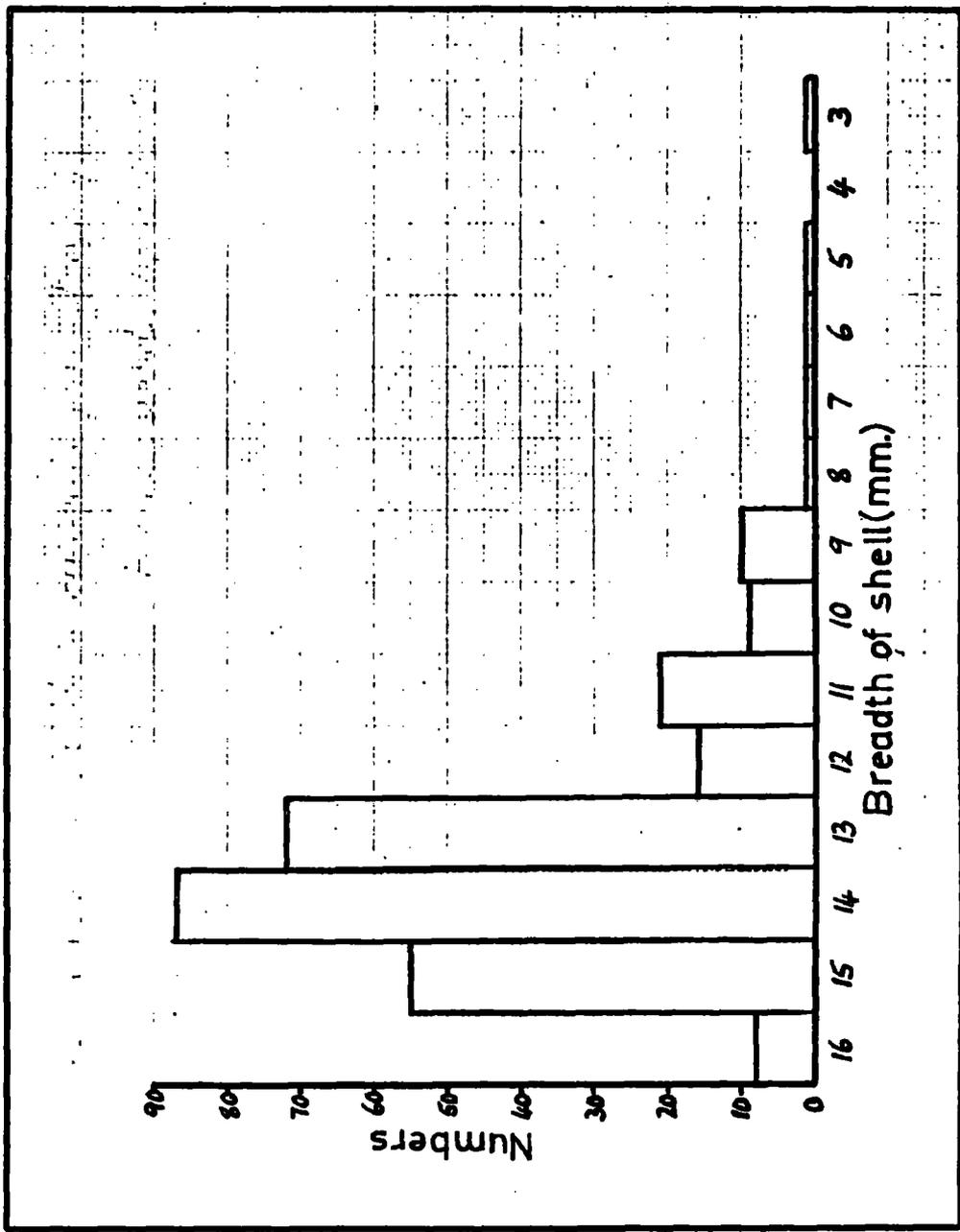
Here although weed cover was almost 100%, there was no sand. The species was feeding extensively on the weeds both in the sublittoral and in several pools. This feature which has also been noticed on sheltered shores in Scotland suggests that G. cineraria is able to feed on weeds only when the water movement is slight (Ebling et. al. 1948; Lewis 1962). Sand and silt are such a frequent feature of shores of this type that the species is often absent from them. Where it is present it faces competition from L. pallidula and L. vineta at low levels and from L. littoralis at higher levels, all of which feed mainly on the larger algae.

Finally, it was noticed that G. cineraria was absent from all Faeroese shores where the basalt was replaced by sand at low levels, even where suitable habitats appeared to exist in midshore. The very small numbers of first and second year animals found (Figure 24) suggests that the species is heavily dependent on the existence of suitable sublittoral habitats for the settlement of larvae. If, in addition, the adults largely retire to the sublittoral in winter, sand at this level would be a limiting factor.

The most interesting point that emerges from the comparative study of Faeroese shores is that G. cineraria can survive here at any level up to M.H.W.S. + 6 ft. where suitable habitats exist. There can be no doubt that increased exposure to wave action allows the species to extend upshore. On sheltered shores

Figure 24.

The distribution of size groups in G. cineraria
from Hoyvik, Streymoy, Faeroe Islands.



the upper limit was at M.L.W.S. + 0.3 ft., on semi-exposed shores at M.T.L. + 0.5 ft. and on exposed shores, above M.H.W.S. The observations of Lewis and Powell (1960) in Argyll are confirmed.

G. cineraria and G. pennanti in Spain.

The shore at Comillas near Santander in the province of Asturias was examined in August, 1964.

It consists of broken limestone rocks, mostly flat, boulders and sand. Where sand was plentiful there were large colonies of Sabellaria alveleolata (L.). Algae were sparse as usual on Iberian shores. An upper fringe of P. canaliculata and F. spiralis and a lower fringe of B. bifurcata and Cystoceira tamariscifolia (Huds) were the only Fucaceae present. Between the algal fringes, C. stellatus, with P. vulgata, P. depressa, P. aspera, and Patella Lusitanica L., was dominant. L. neritoides was abundant over most of the shore. L. saxatilis was rare and no other littorinid was found. The dominant grazing gastropods were the trochids, M. lineata, G. umbilicalis and G. pennanti together with the small turbinid, T. pullus. One specimen of G. cineraria (7.5 mm.) was found at M.L.W.S. At first one gained the impression that Gibbula spp. were more numerous than later transpired: over 50% of the shells seen were occupied by the small hermit crab, Clibanarius misanthropus Risso. The grazing sea urchin, Paracentrotus lividus (Lamarck) was abundant at lower levels and in view of its considerable size, might have

been an important competitor for the trochids.

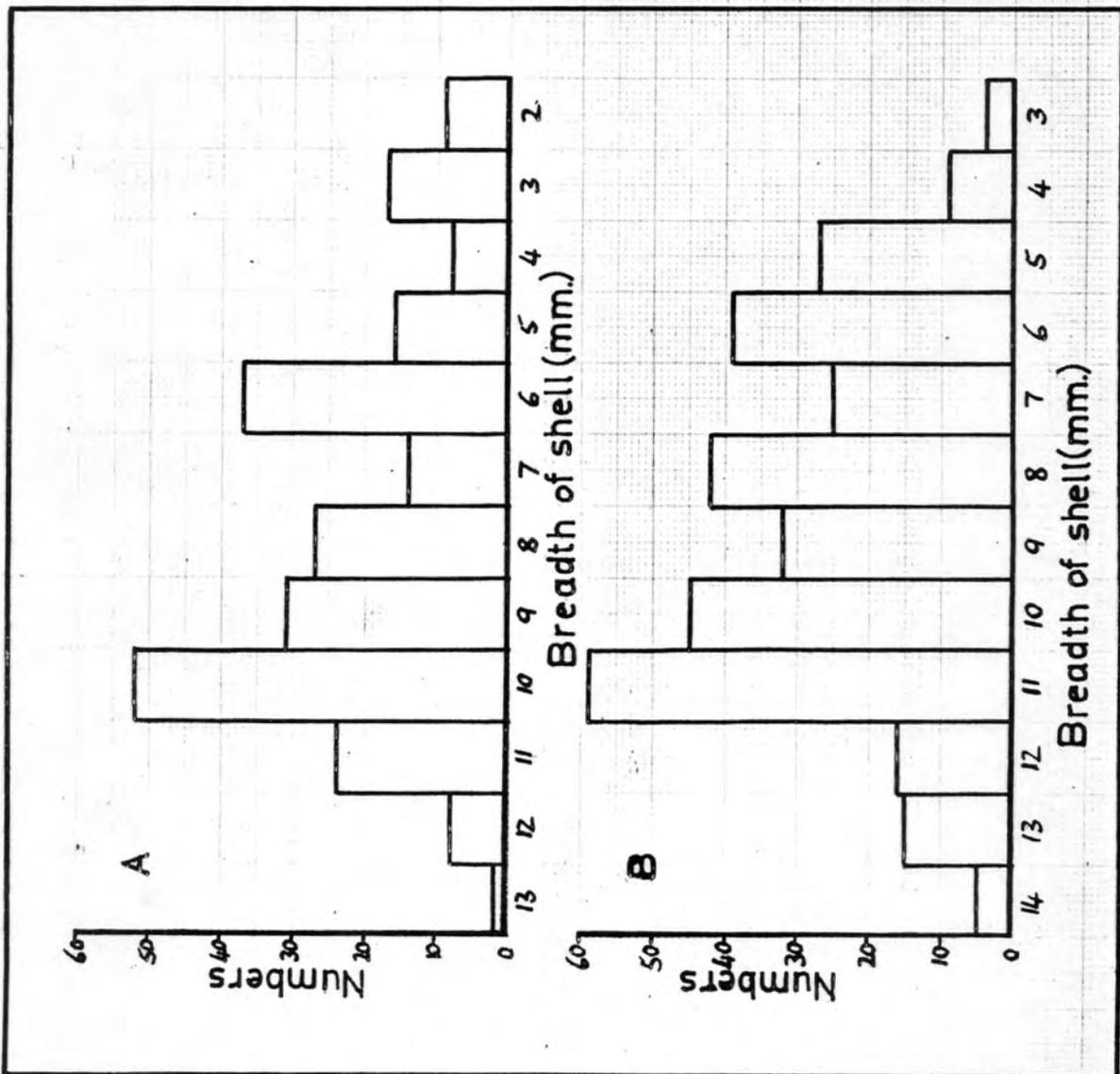
G. pennanti was less abundant than on Alderney. It ranged from M.L.W.S. up to M.T.L. Over the entire range it was much commoner in pools and under stones than anywhere else. Near low water it was seen feeding extensively on Bifurcaria. A large number of young animals of 2-3 mm. shell breadth indicated that breeding was occurring. The frequency distribution judged from the histograms was trimodal (Figure 25 A). The mode at 3mm. could have been no more than a week or two old. The mode at 6mm. probably represents the one year olds and that at 10mm. the two year olds. The adults are much smaller than Alderney specimens, most of which are 14mm. shell breadth.

G. umbilicalis extended from M.L.W.N. to M.H.W.N. Its abundance was about equal to that of G. pennanti. The frequency distribution was trimodal (judged from the histogram, Figure 25 B): the 6mm. animals were probably one year old, the 8mm. ones two years old and those of 11mm., three years old. The small size of most of the adults compared with northern populations was striking. The presence of animals at 3mm. indicated the occurrence of breeding at this time, but the numbers are small. It is possible that breeding had only just begun and would have reached its peak later, say in early autumn.

Crisp and Fischer-Piette (1959) mentioned the fact that G. umbilicalis on the Basque coast rarely exceeded 11-12 mm. After surveying the whole Atlantic coast of France and examining

Figure 25.

The size-frequency distribution of G. pennanti(A)
and G. umbilicalis(B) at Comillas, Asturias, Spain.



museum specimens, they recorded a size diminution from north to south. They did not mention G. pennanti in this regard though it seems justified on present evidence to postulate a similar size diminution in that species. Crisp and Fischer-Piette (op. cit.) also referred to specimens of G. umbilicalis with a closed or almost closed umbilicus in south-west France. At Comillas, 35.9% of the specimens over 10mm. (140 examined) had a closed umbilicus. The smallest specimen with this condition was 8mm. At such a high frequency of closure, this character ceased to be of much value in distinguishing G. umbilicalis from G. pennanti. At Comillas, the different disposition of colour bands on the shell base was regarded as a much more reliable field character.

On this shore a distinct difference between the habitats of young (under 8mm.) and old (over 8mm.) specimens of G. umbilicalis was noticed. The young animals tended to remain in protected places such as crevices, under boulders and in pools, whereas animals over 8mm. seemed largely to have adopted the adult habitat on dry, bare rock surfaces. A change of habitat at approximately the same size and age was demonstrated for G. cineraria at Whitburn (p. 46). It seems likely that G. umbilicalis also adopts the adult habitat on attaining sexual maturity and prior to its first spawning.

Summary.

Scotland.

(1) The upper limit of G. cineraria and the lower limit of G. umbilicalis are both higher than in south England and are higher in north than in south Scotland.

(2) G. cineraria breeds in the spring.

(3) The breeding performance of G. umbilicalis varies from year to year.

Faeroe Islands.

(4) G. cineraria retired to the sublittoral in winter.

(5) G. cineraria was found more frequently on wave beaten shores than in Britain and also had a more extensive vertical range (to M.H.W.S. + 6 ft.). It was scarce in sandy and weed covered areas and absent from exposed flat rocks.

Spain.

(6) G. pennanti and G. umbilicalis both breed in summer.

(7) Both species were smaller than further north.

(8) Many adult G. umbilicalis had a closed umbilicus.

(9) G. umbilicalis changed its habitat at about 8mm. shell breadth, moving from crevices and pools to more open situations. This probably facilitates the dispersal of larvae after breeding.

Canary Islands and Madeira (addendum 1968)

(10) G. umbilicalis was local (see p. 7) but abundant where present at low levels. Neither G. cineraria nor G. pennanti was found.

VIII DISCUSSION

Geographical distribution.

Our knowledge of the geographical distribution of Gibbula and of G. umbilicalis and G. pennanti in particular, has been improved as a result of this work. My own records from the Canary Islands and Madeira (p. 7) go some way towards improving our knowledge of the southern distribution of G. pennanti and G. umbilicalis. The probable absence of both species from the Azores, is interesting reflecting dispersal difficulties in the form of adverse ocean currents. The pelagic trochophore larvae probably have a life of no more than two days (Robert, 1902; Gaillard, 1952; Lebour, 1937) which would be insufficient time for them to complete the long sea passage from Portugal before metamorphosis. L. littorea, another prosobranch with a planktonic larval phase is similarly absent from the Faeroe Islands (Thorson, 1941 and personal observation) though conditions seem most suitable for it there.

Zonation.

(i) G. cineraria.

This species is common in the sublittoral down to 10 fathoms (18.3 metres) (Plymouth Marine Fauna, 1957) or 15 fathoms (27.4 metres) (Isle of Man; Moore 1937). In the south it is probably more numerous below tidal levels (Moore, 1940) and is apparently never confined to the littoral zone. The upper shore limit is frequently around M.L.W.N. (Evans 1947a; Lewis 1957; Moyses and

Nelson-Smith, 1963; Moore, 1940; Southward and Crisp, 1954). However a number of Scottish records show greater upshore penetration to M.T.L. at Scalpay (Moore, 1940) and M.H.W.N. in Caithness (Lewis 1954) while on the south coast the upper limit is frequently around M.L.W. (Colman, 1933). Judging from the results of Crisp and Southward (1958) and Crisp and Fischer-Piette (1959) the species frequently fails to penetrate the littoral zone on shores apparently suitable for other Gibbula species on the French coast, particularly in the south. A tendency for the species to penetrate higher upshore in the north has been apparent from previous work and is confirmed here (section VII).

(ii) G. umbilicalis

This is a midlittoral species though it may occasionally be dredged in shallow water (Plymouth Marine Fauna, 1957) where its lower limit is given as 3 fathoms (5.5 metres). At Wembury, the lower limit is at E.L.W.S. (Colman, 1933). In Cardigan Bay it extends almost to M.H.W.S. in pools (Evans, 1947), though only to E.H.W.N. on bare rock. In Pembroke it can be abundant to M.H.W.N. (Moyses and Nelson-Smith, 1963). In the Menai Straits, it rarely occurs above the barnacle line which is at M.H.W.N. in shelter (Lewis, 1953). Evans (1947b) states that the lower and upper limits are raised by exposure, the ranges being M.H.W.N. - 1 ft. to M.L.W.S. + 1.5 ft. at the most exposed and E.H.W.N. + 0.5 ft. to M.L.W.S. - 1 ft. at the most

sheltered stations near Plymouth. The zone of maximum abundance is variable being M.L.W.S. to M.L.W.N. near Plymouth (Moore, 1940), M.L.W.N. to M.T.L. on shingle in the Menai Straits (Lewis, 1953) and M.T.L. to E.H.W.N. - 1 ft. in Cardigan Bay (Evans, 1947a). It seems that G. umbilicalis can occur from the shallow sublittoral up to M.H.W.S. in pools and can be abundant from M.L.W.S. to M.H.W.N.

(iii) G. pennanti

This work confirms that the vertical range of G. pennanti is intermediate between those of G. cineraria and G. umbilicalis (Gaillard and Fischer-Piette, 1956; Crisp and Fischer - Piette, 1959). Its range at both Alderney and Comillas is from E.L.W.S. to M.T.L.

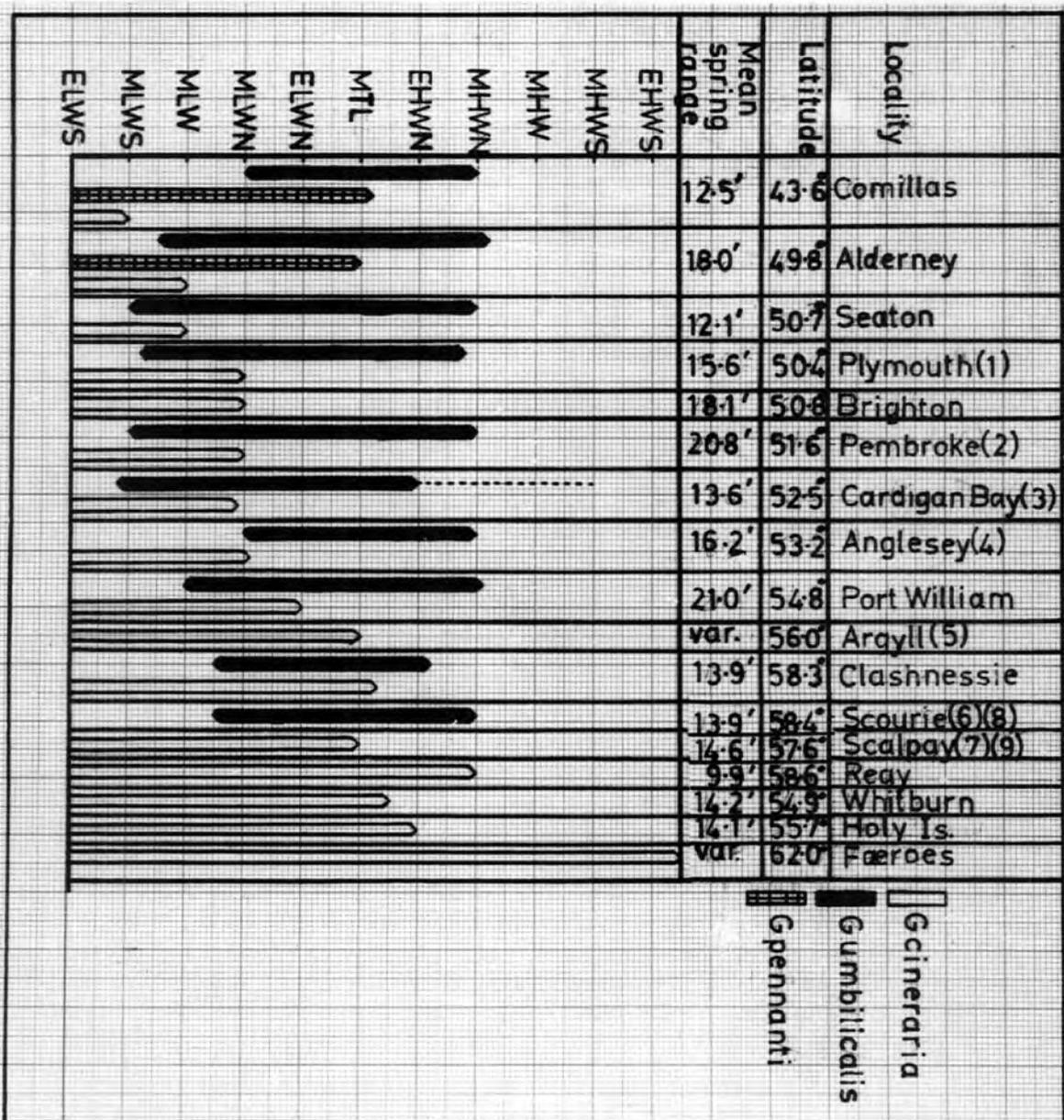
The effects of latitude on zonation.

The vertical ranges of G. cineraria, G. umbilicalis and G. pennanti on shores between Comillas (43° N) and the Faeroes (62° N). are shown in Fig. 26. The data are my own except where indicated otherwise.

(i) G. cineraria. This is a sublittoral species in the south and may extend over the whole shore in the north. The restricted range in the south is probably partly a result of competition from other species but not entirely so. In west Scotland, where G. umbilicalis is also present, it often extends up to E.L.W.N. or M.T.L. It has never been recorded so far up in the south. Where competition from G. umbilicalis is absent as in the Faeroes, Caithness and north-east England, G. cineraria

Figure 26.

The vertical distribution of three Gibbula species on rocky shores between N. Spain and the Faeroe Islands. The data are from:- (1) Evans(1947b); (2) Moyse and Nelson-Smith(1963); (3) Evans(1947a); (4) Lewis(1953); (5) Lewis and Powell(1960); (6) Lewis(1954); (7) Moore(1940); (8) Lewis(1957).



has an even more extensive range. The height to which it extends shows some correlation with latitude. It is concluded that both competition and climate act as factors limiting the vertical range of G. cineraria. G. cineraria also grows to a greater size in the north, where equivalent densities and levels are compared in north and south (e.g. Port William and Alderney). It is difficult to state with certainty whether this effect is caused by changes in competition or some other factor. There is also a trend towards greater exposure tolerance in the north when localities such as Caithness and Alderney are compared.

(ii) G. umbilicalis. An upper shore limit around M.H.W.N. seems to be a remarkably constant feature of this animal's range. Occasionally, it may extend higher in pools (e.g. Cardigan Bay). Where pools are absent from upper levels, it may not extend much beyond E.H.W.N. (e.g. Clashnessie). No geographical trend can be discerned in this case. The lower limit varies considerably, however. In S.W. England and Wales, M.L.W.S. usually marks the lower limit. Both to the north and south of this, the limit is raised to M.L.W. or M.L.W.N. In Scotland, this effect may be the result of the greater abundance and better adaptation to intertidal conditions of G. cineraria. In Alderney and Spain, it seems probable that the additional presence of G. pennanti at lower levels, pushes G. umbilicalis upshore. Like G. cineraria, G. umbilicalis grows much larger in the north.

(iii) G. pennanti. This species was collected only in Alderney and Spain. In both areas, it extended from the sublittoral to M.T.L.

Zonation and physical factors.

(i) Temperature tolerance.

Evans (1948) studied the effect of high temperature on the activity and survival of 11 species of intertidal molluscs (including G. umbilicalis and G. cineraria) immersed in water and Southward (1958) repeated the experiments using Trochidae and barnacles, but in addition investigated the effects of low temperature on the animals in air. The results are given in Tables VIII and IX.

Both authors conclude that the environmental temperatures are not sufficiently extreme to act as factors limiting the animals to the zones in which they occur naturally. However, it is clear that the animals' abilities to withstand both high and low temperatures are related to the levels they occupy on the shore rather than to the geographical range: G. cineraria (a northern species) is much less tolerant of either extremes than M. lineata or G. umbilicalis which are both of southern distribution. The 1962-63 winter has shown that in exceptional circumstances, intertidal species can be severely affected by low temperatures. In this case, M. lineata and G. umbilicalis suffered drastic alterations in their geographical range (Crisp, 1964).

(ii) Resistance to dessication

There are no published results of experiments which investigate resistance to dessication in trochids. As a factor of possible significance in the intertidal zone, I carried out a small series of investigations in November, 1963. The animals were collected in Pembrokeshire. Thirty specimens each of M. lineata, G. umbilicalis and G. cineraria were placed in dessicators with anhydrous calcium chloride, having previously been dried as thoroughly as possible on the outside. Five specimens of each species were removed at 12 hourly intervals, placed in seawater and checked for: (a) ability to move; (b) ability to crawl; (c) response to stimulation (pricking with a pin). If there was no immediate response, the animals were left in seawater for 12 hours, after which, if there was no recovery, they were considered dead. Control groups were kept in aerated seawater to check the animals' abilities to survive under normal conditions. The results are given in Table X. Table XI shows the percentage of time during which G. cineraria and G. umbilicalis are exposed to the air in normal circumstances.

It is clear that the high level M. lineata is able to withstand prolonged periods of continuous emersion. After 36 hours, G. umbilicalis had partly withdrawn into its shell and was unable to maintain its grip on the substratum. It would therefore be exposed to the danger of being moved by the tide

TABLE VIII

The effects of high water temperature on two species of Gibbula and M. Lineata. The data are taken from Evans (1948) and Southward (1958).

<u>Species</u>	<u>Spontaneous</u>	<u>Heat</u>	<u>Lethal</u>	<u>Temperature</u>	
	<u>Movement</u>	<u>Coma</u>		<u>(°C.)</u>	
	<u>Ceases (°C.)</u>	<u>(°C.)</u>	<u>50%</u>	<u>50%</u>	<u>100%</u>
	<u>(Evans)</u>	<u>(Evans)</u>	<u>(Evans)</u>	<u>(South-</u>	<u>ward)</u>
<u>M. lineata</u>	37	38-39	45.8	45.0	45.3
<u>G. umbilicalis</u>	33	33-34	42.1	41.8	42.0
<u>G. cineraria</u>	30-31	34-35	36.2	35.5	36.0

TABLE IX

Time in hours required to produce 50% mortality at various temperatures in two species of Gibbula and M. lineata.

<u>Species</u>	<u>Temperature (°C.)</u>					
	- 10	- 5	0	30	35	40
<u>M. lineata</u>	2-3	6-24	138-179	72-100	-	6-6½
<u>G. umbilicalis</u>	2-3	16	30-79	24-72	10	¾-1
<u>G. cineraria</u>	2-3	2-3	12-30	3¾	1¼-5¼	0

Data from Evans (1948) and Southward (1958).



TABLE X

The effects of continuous exposure to air on two species of Gibbula and M. lineata.

<u>Species</u>	<u>Time in hours required for:</u>			
	<u>Locomotion</u> <u>to cease</u>	<u>Movement</u> <u>to cease</u>	<u>50%</u> <u>mortality</u>	<u>100%</u> <u>mortality</u>
<u>M. lineata</u>	72 +	72+	72 +	72 +
<u>G. umbilicalis</u>	36	48	60	72
<u>G. cineraria</u>	12	24	36	48

TABLE XI

Percentage of time during which two species of Gibbula are exposed to the air at their upper and lower intertidal limits.

Species	<u>% time exposed to air</u>			
	<u>Wembury (Colman, 1933)</u>		<u>Cardigan Bay. (Evans 1947)</u>	
	<u>upper limit</u>	<u>lower limit</u>	<u>upper limit</u>	<u>lower limit</u>
<u>G. cineraria</u>	40	0	21	0
<u>G. umbilicalis</u>	65	5	63	2

and possibly stranded. G. umbilicalis rarely extends higher than M.H.W.N. where the average period of continuous emersion is about two days and the maximum possible period four days. The results suggest that dessication could act as a limiting factor to further upshore extension although wherever this occurs, the species is confined to damp crevices and pools (see p. 65.) G. cineraria needs wetting at every tide to remain healthy, but in nature it always occurs in pools above E.H.W.N. Dessication seems to be more probable than temperature as a limiting factor in both species of Gibbula. In particular, the results of this experiment show how important damp and protected habitats are likely to be near the upper limit of the animals' vertical range.

Habitats.

The numerous observations of previous authors are summarized in the Introduction (p. 3). So far as the habitats of the adult animals are concerned, my own work has added little to this general picture. It has been emphasized, however, that the young animals of all three Gibbula species require particularly well protected and damp habitats. Prior to sexual maturity (about 8mm. shell breadth on most shores), the young cannot be found without searching damp crevices and under stones, In the case of G. cineraria where settlement is mainly below tidal levels, it has been suggested that an unsuitable substratum in the sublittoral, say sand or mud, has an adverse effect on the

density of the intertidal population due to difficulties of recruitment (p.p.57, 89.) It was also felt that the change of habitat recorded for all these species at the onset of sexual maturity might be an adaptation necessary for the successful dispersal of the planktonic trochophore larvae. Similar changes of habitat with age have also been reported in L. littorea (Moore, 1937b) and T. lapillus (Moore, 1938).

Population density and habitat.

Over the whole geographical range of all three species it has been found that boulders and broken, creviced rocks support dense populations. At the same time extreme conditions of shelter where sand and silt often accumulate, are not favoured. The animals probably require the protection from predators afforded by narrow crevices and the undersides of stones and the population density seems to be directly related to the availability of such microhabitats (p.28).

Growth and Life cycles.

Growth varies with age in G. cineraria and G. umbilicalis. It is slow for the first year followed by one year's (G. umbilicalis) or two year's (G. cineraria) rapid growth, at least in the two localities investigated in detail. However the growth rate in both species is sufficiently plastic to make generalization rather risky. I have shown (p.30) that G. cineraria sometimes continues active growth for at least

three years and also (p.60). that it can, in certain circumstances, complete what would normally be two years growth in one year. G. umbilicalis is probably similar in this respect though the evidence for this species is not so complete. After two years (G. umbilicalis) or three years (G. cineraria) growth slows down considerably but may continue for several years longer. Growth in both species is slow in winter, a conclusion supported by Williams (1964a) for G. umbilicalis. Williams (1964b) and Moore (1937b) have both shown that winter growth is slow in L. littorea and also that growth is halted by maturation of the gonads. A similar explanation probably applies to the halt in growth between June and September in adult G. cineraria at Whitburn.

Mortality in newly settled G. cineraria was found to be very great. Moore (1937b) also found this in L. littorea. Mean life expectancy was calculated to be about five years. Sexual maturity was gained after $1\frac{1}{2}$ - 2 years in G. cineraria which compares with 1 - $1\frac{1}{2}$ years in G. umbilicalis (Williams, 1964a) and 2 - 3 years in L. Littorea (Moore, 1937b; Williams 1964b).

Growth and latitude.

Crisp and Fischer-Piette (1959) remarked on the diminution in size from north to south in G. umbilicalis. I have been able to confirm this and also to add that the same effect is apparent in G. pennanti and G. cineraria.

Population density and growth rate.

Stephen (1928, 1929a, and 1929b and 1930) was able to show that the rate of growth in Tellina tenuis da Costa and Cardium edule L. is inversely related to the population density. His findings for T. tenuis in particular have much in common with the situation described in Sections II and III for G. cineraria.

At Whitburn, density and growth rate are inversely related above + 2.3 ft. C.D. and the effect at higher levels is so marked that rapid growth continues for a year longer than lower down. The decreasing suitable habitat space higher up the shore is thought to be responsible for the reduced density. The greater quantity of resources per head of population probably accounts for the faster growth rate and the greater adult size attained at high levels.

The effect of the depletion of the G. cineraria population at Seaton following the 1962 - 63 winter was remarkable. The acceleration of growth rate that followed is regarded as prima facie evidence for the existence of intraspecific competition.

Migration.

Two distinct affects have been noted in G. cineraria. Gowanloch and Hayes (1927) and Hayes (1927, 1929) for L. Littorea, Williams (1964a) for G. umbilicalis, Naylor (1963) for C. maenas and Desai (1959) for M. lineata have noted seasonal changes in the distribution of these species involving downwards

migration in autumn and upwards migration in spring.

G. cineraria has been shown to behave in a similar manner in three separate areas (p.p. 51, 56, 87.)

A second phenomenon is the gradual upshore movement with age of G. cineraria which has been shown to take place at Whitburn (p. 31). The high level groups contain no young animals and the population is recruited entirely by immigration from lower levels. A similar situation has been recorded for L. littorea (Moore, 1937b; Williams, 1964b), T. lapillus (Moore, 1938) and L. neritoides (Lysaght, 1941).

Interspecific competition.

It has already been concluded (p. 96-7) that interspecific competition affects the zonation of all three Gibbula species. The evidence from Seaton (Sections IV and V) also points to the existence of interspecific competition between G. cineraria and G. umbilicalis. The important fact is that the growth rate in both species is lowest where they coexist, in spite of population densities which are lower for each individual species than at other points on the same shore. This evidence must be considered conclusive when the relationship between density and rate of growth in G. cineraria at Whitburn is also taken into account.

Predation.

The recorded predators of Gibbula species are numerous and it is probable that they have many natural enemies.

Ebling et al. (1966) have shown that Marthasterias glacialis (L.) ranging in size from 3 to 20 cm. in radius destroyed 170 out of 216 G. cineraria ranging from 2 to 10 mm. in shell height, in nine days. The animals were placed together in cages which were suspended about one in. below the water surface. These workers also showed conclusively that G. cineraria emerges onto the tops of boulders to feed on the algae exclusively during daylight hours whereas Marthasterias is active mainly at night. They concluded that, although Marthasterias is potentially a dangerous predator of G. cineraria, both populations might be able to survive by virtue of their differing activity rhythms. Asterias rubens L. and Asterina gibbosa (Pennant) are the other asteroid predators present in Lough Ine which might destroy G. cineraria.

My own observations at Whitburn, have shown that Asterias rubens feeds frequently on G. cineraria by day. Asterias is common throughout the year among Laminaria and Fucus serratus and must be regarded as a serious enemy. In the absence of Mytilus edulis at low levels G. cineraria is the chief item in its diet.

Muntz et al. (1965) investigated the predatory activity of several species of large crabs at Lough Ine by field observation, placing predators and potential prey species together in submerged cages and observations in Laboratory tanks. They demonstrated that Carcinus maenas (L), Portunus

puber (L) and Cancer pagurus L. will all destroy and eat G. cineraria. Large and medium sized Garcinus were only able to destroy small G. cineraria (1.5. - 4.0mm in height), but Cancer pagurus could crush large specimens (8 - 9mm height). Portunus puber was the most successful crab with large G. cineraria (8 - 9mm.) one specimen destroying 6 out of 12 snails in one day. Laboratory observations showed that it normally achieved this by chipping the outer lip backwards with the right chela until the body was exposed. Small G. cineraria were often smashed in one attempt by pressure applied either across the base or from base to apex. These authors felt that G. cineraria might be protected from crabs to some extent because the latter feed largely at night when the snails have retired to protected sites in crevices or beneath boulders. The extent to which G. cineraria with chipped outer lips can be found in the field suggests that predation by crabs is quite common.

Nucella lapillus includes both G. cineraria and G. umbilicalis in its diet (Moore, 1938; Largen, 1967; personal observation). It is not possible to assess the importance of this species as a predator of Gibbula on present knowledge but it is certain that young Nucella which are found lower on the shore than the adults, quite frequently attack young G. cineraria. They usually do this by drilling a hole in the shell though on one occasion, I found a specimen drilled through the operculum.

Salomonsen (1934) records G. cineraria in the diet of eider ducks in the Faeroes and the oyster catcher, turnstone, dunlin,

purple sandpiper and curlew as feeders on molluscs in the littoral zone. Gulls also include snails in their diet (Witherby et al. 1938 - 41). Fish such as haddock, plaice, flounder, dab and cod have all been recorded as predators of littoral gastropods (Thorson, 1941). Blennius pholis L. which is known to take molluscs (Gibson, 1967) will probably eat Gibbula on occasion.

It seems probable that crabs and starfish are important predators of G. cineraria in the sublittoral and on the lower shore. Birds, particularly the oyster catcher are probably more important in the midlittoral and G. umbilicalis would be more affected here. The extent of predation by fish and T. lapillus is not known.

While our information on the predators of Gibbula is far from complete the work at Lough Ine is most important in identifying some of the major enemies of G. cineraria. It also indicates that the importance of boulders and crevices as microhabitats for the species is not solely a question of moisture but also of protection from enemies. The most likely explanation for the rarity of G. cineraria (and perhaps the other two species) on open rocks is their vulnerability to attack by crabs and starfishes.

Breeding Seasons.

Evidence from other groups suggests that differences in breeding season between species might be expected to reflect their geographical range. For instance in Britain, P. depressa, a southern species is a summer breeder (Orton and Southward, 1961) and

Dodd 1956). A similar situation is apparent in the acorn barnacles where the southern G. stellatus breeds in summer and the northern B. balanoides in winter (Moore and Kitching, 1939; Moore, 1934).

Williams (1964a) for G. umbilicalis and Gaillard (1952) for G. pennanti have recorded the breeding season for these species as June to September and September respectively. Cornet and Marche-Marched (1957) give April - June as the main breeding season of G. umbilicalis at Roscoff. Both species can be assumed to be summer breeders in the regions of southern Britain and north France.

Records for G. cineraria are less reliable and hard to find. Chumley (1918) mentions spring as the breeding season in the Clyde and this accords with my own observations on the west coasts of Britain. In north-east England, breeding was taking place over a long period between September and March in two successive years 1962-63 and 1963-64. On the whole, the breeding records for topshells do bear some similarity to those for limpets and barnacles. The two Lusitanian species, G. umbilicalis and G. pennanti are summer breeders at the northern end of their geographical range and G. cineraria, a Boreal species spawns over the winter period.

Unfortunately, the trochophore and veliger larvae of the three Gibbula species have not yet been identified and it is therefore not possible to infer the breeding seasons from inshore plankton records. The description of the larval stages of all three species is an important task remaining.

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Appendix I

The collections made at Whitburn, 1962 - 1963.

Date	Habitat	No of samples (each 1 metre ²)	No animals examined	Mean density ² per metre	Standard deviation	Variance
11/62	+ 2.3ft. C.D.	10	950	95.0	37.6	1413.8
3/63	F. serratus	5	401	80.0	50.4	2540.2
4/63	zone	3	197	65.7	16.7	278.9
5/63	"	6	313	52.2	17.3	299.3
6/63	"	5	314	62.8	16.9	285.6
9-10/63	"	10	580	58.0	15.2	231.0
12/63	"	8	525	67.5	19.7	388.1
11/62	+ 4.8ft. C.D.	10	196	19.6	14.6	213.2
3/63	Balanus	10	126	12.6	10.0	100.0
5/63	zone	5	35	7.0	7.3	53.3
9-10/63	"	11	269	24.5	16.5	272.3
4/63	+ 0.3ft. C.D.	4	263	63.8	15.9	252.8
5/63	Laminaria	7	289	41.3	13.9	193.2
6/63	zone	5	373	74.6	15.8	249.6
9-10/63	"	10	744	74.4	22.1	488.4
4/63	- 1.0ft. C.D.	5	297	59.4	8.7	75.7
9-10/63	Lam. zone	9	475	52.6	18.6	346.0
9-10/63	+ 2.3ft. C.D. F. serr. reefs.	10	100	10.0	9.1	82.8
9-10/63	+ 4.8ft. C.D. A. nod. reefs.	10	154	15.4	7.6	57.8
4/63	+ 8.6 - 9.1ft	-	112	1	-	-
9-10/63	upper pools	-	312	1	-	-

Appendix II

The mean shall breadth in mm (\bar{x}) with standard deviation (s) and percentage of total sample of the component size classes at Whitburn, 1962-63.

Date	Habitat	Size/year classes (year of origin in parentheses)					E (1963-64)						
		A (1959-60)		B (1960-61)		C (1961-62)		D (1962-63)					
		\bar{x}	s	%	\bar{x}	s	%	\bar{x}	s	%	\bar{x}	s	%
11/62	+ 2.3-ft C.1)	13.6	1.1	43	11.0	1.5	30	6.3	1.2	10	3.9	0.6	17
3/63	F. serratus	13.3	0.8	63	11.5	1.4	26	7.0	1.3	8	3.9	0.7	3
4/63	zone	13.3	0.8	45	11.0	0.9	25	7.6	0.8	15	4.5	0.7	15
5/63	"	13.7	0.8	25	11.5	0.9	40	7.7	0.8	18	5.2	1.4	17
6/63	"	13.1	1.2	60	merged with A	"	"	9.5	1.1	18	6.0	1.1	22
9-10/63	"	13.5	1.2	60	"	"	"	9.3	1.0	30	7.3	1.3	9.5
12/63	"	13.6	1.2	60	"	"	"	9.9	0.9	25	6.8	1.0	7.5
11/62	+ 4.8ft. C.D.	15.2	1.2	94	10.0	1.2	1	7.5	1.1	1.5	5.0	0.9	4
3/63	Balanus zone	15.0	1.1	70	12.1	1.1	25	7.2	0.9	2	4.9	1.3	3
5/63	"	14.7	1.0	85	11.6	0.8	12	8.0	-	12	---	---	0
9-10/63	"	14.8	0.9	56	merged with A	"	"	11.2	1.0	39	8.4	0.9	3
4/63	+ 0.3ft. C.D.	12.6	1.0	58	10.1	1.0	25	6.4	0.9	8	3.9	0.7	8
5/63	Laminaria zone	12.6	0.9	56	10.1	0.5	17	7.5	0.9	11	4.9	0.8	16
6/63	"	12.8	1.1	48	10.1	0.9	24	7.0	0.9	12	4.9	0.9	16
9-10/63	"	13.0	0.9	52	merged with A	"	"	9.0	1.0	42	5.8	0.8	55
4/63	- 1.0ft C.D.	12.5	0.9	54	10.0	0.9	26	6.5	1.0	11	3.5	0.6	9
9-10/63	Laminaria zone	12.7	0.9	54	merged with A	"	"	9.2	1.3	40	6.5	0.6	36
4/63	+8.6-9.1 ft.	16.2	1.2	34	9.3	0.9	20	---	---	---	---	---	---
9-10/63	upper pools	14.8	1.1	30	11.1	1.1	30	7.8	0.7	8	---	---	---

* A fifth large group A', was present. In 4/63, A' was \bar{x} = 19.8 mm, s = 1.1mm, 46% In 9-10/63 it was \bar{x} = 19.1 mm, s = 1.0 mm, 17%.

Appendix III

The mean shell height in mm. (\bar{x}) with the standard deviation (s) and percentage of total sample of the component size classes at Whitburn, 1962-63. The habitat is + 2.3 ft. C.D. in the *Fucus serratus* zone.

Date	Size/year classes (Year of origin in parentheses).														
	A (1959-60)			B (1960-61)			C (1961-62)			D (1962-63)			E (1963-64)		
	\bar{x}	s	%	\bar{x}	s	%	\bar{x}	s	%	\bar{x}	s	%	\bar{x}	s	%
11/62*	11.7	1.3	38	8.2	1.2	29	4.5	1.0	12	1.8	0.7	17	---	---	---
3/63	11.3	1.3	64	8.4	1.5	25	4.2	0.7	7	1.9	0.6	4	---	---	---
4/63	11.7	0.8	37	8.6	1.3	31	4.3	0.8	18	2.2	0.7	14	---	---	---
5/63	11.1	1.1	40	7.9	0.9	24	4.4	0.8	22	2.2	0.6	14	---	---	---
6/63	12.4		27	9.2		32	7.0		11	3.8		30	---	---	---
9-10/63	12.0	1.3	56	merged with A			7.2	1.0	20	5.4	1.0	22.5	2.4	0.9	2.5
12/63	12.0	1.3	60	"			6.9	1.3	29	4.1	1.2	10	2.0	-	1

* A fifth large group was present, labelled A', for which \bar{x} = 13.8 mm., s = 0.6 mm. It comprised 1% of the total population.

Appendix IV

The mean density per metre² (\bar{x}) with variance (s^2) for each component size class at Whitburn, 1962-63.

Date	Habitat	Size / year classes (year of origin in parentheses)			
		A (1959-60)	B (1960-61)	C (1961-62)	D (1962-63)
		\bar{x} s^2	\bar{x} s^2	\bar{x} s^2	\bar{x} s^2
11/62 3/63	+ 2.3ft. C.D. F. serratus zone	40.8 608 50.5 1600	28.5 424 20.8 660	9.5 14.1 6.4 76.0	16.1 240 2.4 20.3
4/63 5/63 6/63 9-10/63* 12/63*	" " " " "	29.6 125 13.0 74.8 37.7 171 34.8 139 43.8 252	16.4 69.5 20.8 120 merged with A " "	9.9 41.8 9.4 53.8 11.3 51.4 17.4 69.3 16.9 97.0	9.9 41.8 8.9 50.8 13.8 62.8 5.5 22.0 5.1 29.1
11/62 3/63 5/63 9-10/63*	+ 4.8ft. C.D. Balanus zone " "	18.4 200 8.8 70.0 5.8 45.4 13.7 152	0.2 2.1 3.4 25.0 0.8 6.4 merged with A	0.3 3.2 0.3 2.0 0.2 1.6 9.6 106	0.8 8.5 0.4 3.0 ----- 0.8 8.2
4/63 5/63 6/63 9-10/63*	+ 0.3ft. C.D. Laminaria zone " "	37.0 147 23.2 109 35.8 120 38.7 254	15.9 63.2 7.0 33.0 17.9 60.0 merged with A	5.7 22.8 4.5 21.3 9.0 30.0 31.2 205	5.1 20.2 6.6 31.0 11.9 40.0 4.1 26.8
4/63 9-10/63*	- 1.0ft. C.D. Laminaria zone	32.1 40.9 28.4 187	15.4 19.7 merged with A	6.5 8.3 21.1 138	5.3 6.8 1.9 12.5
4/63 9-10/63*	+8.6-9.1ft upper pools	<1.0 -	<1.0 -	<1.0 -	----- -----

* A fifth size/year class E (1963-64) was present in these samples. Details are given in appendix II. The numbers were too small for the calculation of useful means and variances.

Appendix V

The collections of *G. cineraria*, made at Seaton, 1963. The figures in the upper line of the lower table give the mean shell breadth (mm) with the standard deviation in parentheses. The lower line of figures refers to the proportion each year group comprises of the whole population.

<u>Date</u>	<u>No. of samples</u> <u>(each metre²)</u>	<u>No. animals</u> <u>examined</u>	<u>Mean density</u> <u>per metre²</u>	<u>Standard</u> <u>deviation</u>	<u>Variance</u>
3/63	40	214	5.3	3.7	14.21
7/63	24	238	9.9	7.2	51.84
12/63	20	85	4.3	4.1	16.81

Component size classes (year groups in parentheses)

	<u>W (1960)</u>	<u>X (1961)</u>	<u>Y (1962)</u>	<u>Z (1963)</u>
3/63	12.7 (0.8)	10.4 (0.8)	5.9 (1.2)	3.4 (0.7)
	12%	18%	6%	5%
7/63	13.3 (1.5)	10.0 (1.5)	10.0 (1.5)	5.3 (0.7)
	11%	82% (with Y)	82% (with X)	7%
12/63	13.2 (1.4)	13.2 (1.4)	13.4 (1.4)	6.0 (0.0)
	99% with X&Y)	99% with W,Y)	99% (with W,X)	1%

Appendix VI

I. The equivalence of size classes with age and year of origin. G. cineraria, Whitburn. The age is given to the nearest year in December, 1963.

<u>Size class</u>	<u>Age</u>	<u>Year of origin</u>
E	0	1963
D	1	1962
C	2	1961
B	3	1960
A	4	1959
A'	5	1958

II. The equivalence of size classes with age and year of origin. G. cineraria, Seaton. The age is given to the nearest year in December, 1963.

<u>Size class</u>	<u>Age</u>	<u>Year of origin</u>
Z	1	1963
Y	2	1962
X	3	1961
W	4	1960

Appendix VII

Abbreviations

E.H.W.S.	extreme high water at springs.
M.H.W.S.	mean high water at springs.
M.H.W.	mean high water.
M.H.W.N.	mean high water at neaps.
E.H.W.N.	extreme (lowest) high water at neaps.
M.T.L.	mean tide level.
E.L.W.N.	extreme (highest) low water at neaps.
M.L.W.N.	mean low water at neaps.
M.L.W.	mean low water.
M.L.W.S.	mean low water at springs.
E.L.W.S.	extreme low water at springs.
C.D.	chart datum.
O.D.	Ordnance datum.

