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91

A Preliminary Study of Growth-rate in Cockles (Cardium edule L.) in relation to Commercial Exploitation

H. A. Cole, D.Sc.

Introduction

Cockles as marketed in Britain vary greatly in size. Those reaching the London market from Barra, in the Outer Hebrides of Scotland, are uniformly large, often up to, or exceeding, 50 mm. in shell-length, whereas those from the great fishery in the Burry Inlet, South Wales rarely exceed 30 mm. Cockles from Morecambe Bay, Lancashire are intermediate. Such differences may result from basic variations in growth-rate or from varying intensities of exploitation. There is also the effect of minimum size-regulations which differ from one Sea Fishery District to another (in England and Wales) and affect the composition of the stocks remaining on the beds.

In recent years there has been intense exploitation of British cockle fisheries during a period of generally poor bivalve spatfalls. The combined action of these two factors has led to the belief that over-fishing has occurred on some beds. This has led to an investigation of growth and spatfall and a reconsideration of minimum size limits on certain fisheries. The preliminary conclusions from these investigations are presented here; the full data will be given and more fully analysed in a later publication.

The estimation of age and growth

It has long been known that cockles may exhibit on the shell a well-marked series of rings; it was supposed that these represented annual growth checks occurring during the coldest period of the year. Orton (1926), while he confirmed that rings were formed each year, also showed that disturbance rings were easily produced, e.g. by shifting bottoms, by the removal of cockles from their habitat for measurement, even though they were returned within a few hours, or by marking the shell-edge with a file. These disturbance rings were generally much less well-marked than true annual rings but could cause confusion. Stephen (1931, 1932), investigating the growth and spatfall of cockles on the south shore of the Clyde estuary, found well-marked annual growth rings, except in the first year. Kreger (1940) found little difficulty in separating year-classes on Dutch cockle beds, except on high banks where the beds were exposed for a long period. Fraser (1931) found well-marked growth checks in Cardium corbis, but noted that in old cockles the umbonal region might be worn smooth, obliterating the first winter ring.

The conclusions from the present study are that annual growth rings are usually to be clearly discerned but, from grounds on the south coast of Britain, where winter temperatures are relatively high and the cold period of short duration, growth rings may be very faint or absent altogether in young cockles. The first growth ring in particular is liable to be absent. In Poole Harbour, Dorset, a very favourable habitat, the third and subsequent rings are usually clear in practically all cockles but a high proportion show very faint first and second rings or none at all. Sufficient cockles have, however, been found with clear rings on all grounds examined to give an intelligible growth pattern.

In South and North Wales and in Morecambe Bay growth rings are usually very clear, as they are on cockles from Barra, Outer Hebrides. In individuals with many rings erosion of the shell at the umbo may be severe and may obscure the position of the first ring. Such heavily eroded cockles were found commonly in the Salcome estuary, Devon; in many cockles the shell at the umbo was paper-thin and in some had actually broken through.

Under natural conditions disturbance rings are produced most commonly on exposed shifting bottoms where cockles may be buried or uncovered by gale action or strong currents at times of spring tides. It is a commonplace on the Burry Inlet and Morecambe Bay beds for cockles to be washed out of the soil into heaps as streams and drainage channels over the flats change their course; alternatively soil may be deposited over the surface of the beds from which cockles may have difficulty in emerging. Such violent environmental changes inevitably cause checks in growth which may be marked by a slight ring on the shell. Such disturbance rings are less deep and clearly marked than true annual rings and may not encircle the shell, fading away at the margins.

Since annual growth rings may be found in at least a proportion of cockles on all grounds, it is possible in a large sample to separate the year classes and to obtain an estimate of the growth which occurred over the previous three to six years depending upon the age of the cockles examined.

Early post-settlement stages may be widely distributed by tides and currents (Baggerman 1953) and older cockles may be washed out in quantity by gales or disturbed and carried away by streams draining comparatively flat areas. Such movements of older cockles can, however, usually be recognized and by careful selection of grounds reliable information can be obtained regarding growth in relation to tidal level and nature of soil.

In Britain cockles are rarely found below low water mark of spring tides although they may flourish in mud at the bottom of certain enclosed lagoons. The main concentration occurs between mean tide level and low water of average neap tides. The reasons for this zoning are not clear. Verwey (1952) suggests that light is important as influencing the settlement behaviour of the larvae; but gives no evidence in support. Predation by demersal and pelagic forms, e.g. flatfish, will be most severe on the lower levels of the shore, but predation by birds, e.g. oystercatchers (which have recently been shown by R. E. Drinnan, of this laboratory, to take very large numbers) is likely to be most serious on those parts of the beds longest exposed. Whether larval cockles settle gregariously (see Cole & Knight-Jones 1949) is not yet known, such gregarious behaviour tends to result in the major concentration of young settled stages among the parent stock. As Baggerman (1953) has shown, it is difficult to determine the initial settlement pattern since it may quickly be modified by post-larval transport by currents.

<u>Growth-rate in relation to environment</u>

<u>Tidal Level</u>. Although on the major cockle beds the greatest concentration of cockles occurs between mean tide level and low water neaps, this is not the most favourable zone for growth. In a large series collected from widely dispersed stations on the Llanrhidian Sands, Burry Inlet, the most rapidly growing were obtained from the lowest tidal levels. Stephen (1932) reached a similar conclusion. A comparison of growth-rates of 0-group cockles from "high" "medium" and "low" stations is given in Fig. 1. These three stations were spaced over approximately 1,500 metres, with a difference in level of ca. 2 metres (in a tidal range of 8.5 metres at springs) between the high and the low stations.

In Poole Harbour, cockles are found living among the roots of rice-grass (<u>Spartina townsendii</u>), at the level of high water of neap tides (Green 1940). In this situation they can feed for only a limited period around high water and on poor neap tides may be uncovered for several days together. They are protected from dessication by the dense covering of <u>Spartina</u> but it is amazing that in this situation their growth should be only slightly less than that of cockles living at mid-tide level and specimens up to 42 mm. in length have been found. What is even more surprising is that occasional large specimens of <u>Paphia decussata</u> are found in the same situation. Fig. 2 gives a comparison between the size and distribution of cockles (known locally as "floaters") taken from <u>Spartina</u> and those living at a normal tidal level on the flats alongside.

<u>Nature of Soil</u>. Although the occurrence of cockle beds is generally associated with large estuarine flats of firm sand or muddy sand, such as those occurring in the Wash, the Thames estuary, the Burry Inlet, Morecambe Bay or the Waddensee, cockles occur in other localities in a great variety of soils varying from soft mud to hard gravel and stones mixed with sand. In Poole Harbour, Dorset,

there is a great range of soils and cockles are found in all, if they occur at a suitable tidal level. Recent surveys of these beds, which are at present but thinly populated by cockles, allow a preliminary assessment of the effect of soil texture on growth. Water conditions throughout the area examined were very uniform and as the tidal range is very small (about 2m. at springs), and the band of shore occupied by cockles very narrow, the degrees of exposure varied only slightly. The size distributions of a series of samples taken in May, 1955 are plotted in Fig. 3; it shows a considerable degree of uniformity in growth over the range of soils studied and suggests that growth is dependent on temperature and food conditions rather than on the nature of the bottom soil. In Poole Harbour exceptionally rapid growth occurs in all soils from very soft mud, on which a man of average weight in seaboots sinks to his knees or deeper, to hard gravel and stones mixed with sand from which it is impossible to collect cockles except with a strong rake or like instrument.

Conditions in Poole Harbour, however, are somewhat peculiar in that due to the landlocked nature of the inlet and the relatively small tidal range, wave action on the shores is never severe. The coarse soils in the harbour occur in areas of relatively strong currents, the soft soils in areas of weak currents. Kreger (1940), following some analysis of current speeds over certain flats in the Waddensee, concluded that both very weak and very strong currents were unfavourable, the first because of exhaustion of food in the immediate vicinity of cockles lying densely together, the second through bombardment with transported particles leading to closure of siphons and loss of feeding time.

From a comparison of samples from habitats varying in degree of exposure to prevailing winds it seems that in situations exposed commonly to strong wave action growth of cockles is slow and the maximum size small. This is well shown in Table 1 where two samples collected in exposed and sheltered situations in Essex are compared. In each case the soil was shell - gravel and sand with a little mud and the tidal level was the same, viz. low water of neap tides; average salinity was also similar in the two localities.

Table 1

Growth of cockles. Effect of exposure to wave action. The figures in brackets indicate the numbers in each sample.

Locality	Situation	Date	1st ring mm.	2nd ring mm.	3rd ring mm.	4th ring mm.	5th ring mm.
Bradwell, River Blackwater, Essex.	Exposed. W. to N.E.	August 1955	9.3(88)	20.3(74)	26.4(39)	28.8(19)	30.4(11)
Paglesham Pool, River Roach, Essex.	Sheltered.	August 1955	12.3(48)	25.1(40)	31.6(24)	34.8(11)	38.3(3)

Salinity. Cockles extend up-river in British estuaries some distance beyond the limit of toleration of oysters. In the Wareham Channel in Poole Harbour they are found up to Wood Bar Looe (a creek entering the main river estuary) where the daily range of salinity at neap tides in summer is from about 27°/oo to 30°/oo. (Green 1940). In this situation growth is somewhat stunted compared with the main beds in Poole Harbour where the summer salinity ranges from about 32 - 34°/oo (Fig. 4). In such up-river situations cockle beds may be almost totally destroyed in winters which are either exceptionally cold or exceptionally wet. In consequence the maximum size reached is usually rather low. The dwarfing of cockles living in low salinity water has been recorded by Havingan (1922) and others.

Density of Settlement

It is not easy to isolate the effect of density of settlement on growth from the effects of other factors such as tidal level, nature of soil, and exposure. During the course of a fairly comprehensive survey of the Penclawdd, Burry Inlet, cockle beds in April 1953, 21 Stations were worked on the main producing area. The position of the mode of the group of cockles rising two-years old (1+), the group on which the fishery was based at that time, is clearly demarcated in the size distribution curves in 19 of these samples. These stations have been grouped as "dense" (exceeding 1,750 per sq.m.) and "moderately dense" (less than 1,750 per sq.m.). The average density of all stations was 1,614 per sq.m. with a range from 241 to 4,350 per sq.m.

In the seven dense stations the modes lay at 17, 18, 18, 18, 17, 19 and 19 mm; in the 12 moderately dense stations the modes lay at 18, 18, 18, 19, 20, 18, 20, 19.5, 19, 19, 24 and 23 mm. If the stations are grouped in three zones according to their distance from high water mark, the result is as shown in Table 2.

Table 2. Effect of density on growth of cockles

Proximity to high water mark	Moderately dense stations			Dense stations		
	No.	Mean density per sq. metre	Modes mm.	No.	Mean density per sq. metre	Modes mm.
Near	7	1,034	18,18,18, 19,20,18, 19.	3	3,021	17,18,19.
Mid	3	1,339	19.5,19, 19.	3	2,533	18,18,17.
Distant	2	465	24,23	1	1,806	19

There seems to be a slight but definite slowing down of growth at the dense stations in each of three zones. Kreger (1940) records an apparent density effect on the cockle bank known as Staart van Sheringhals in the Waddensee but this effect was not evident on other banks in the same area.

Orton (1934) recorded cockle spat below 5 mm. in length at a density exceeding 100,000 per square metre on the Cark Sands in July 1933. Densities up to 39,000 per square metre have also been described in Germany (Wohlenberg 1937), immediately after settlement, but these were rapidly reduced, so that at two years old only 800 cockles per square metre survived. In the present study the maximum density recorded was 6,142 per square metre on the Llanrhidian Sands, Burry Inlet in December, 1953; these were all 0-group cockles. Older cockles were found in the same area at densities up to approximately 2,300 per square metre, representing a substantially larger volume of flesh, and therefore filtering capacity, per unit area. Wright (1926), when he examined the same grounds in 1923, obtained 5,649 0-group cockles per square metre at one station so that spatfalls at this density must occur fairly frequently. Actual settlement densities must be considerably higher since Wright's estimate was made in April and that from the present study in December. Wohlenberg (1937) showed that losses up to nearly 90% may occur in the first six months after settlement.

Wright recorded no less than 8,000 one year-old cockles per square metre on the Maplin Sands, Thames Estuary, with an average length of 13.9 mm. At such densities there is a solid pavement of cockles with little unoccupied space and it must be concluded that competition for food severely limits growth. Conditions for the spread of epidemic diseases would seem to be very favourable (see Korringa 1955) but only one instance of unexplained mortality in cockles has been recorded (Orton 1934). A similar mortality among Amphidesma Ventrecosum in New Zealand has been recorded by Rapson (1954).

<u>Annual growth increment</u>. Samples of cockles have been examined from Barra, Outer Hebrides; Morecambe Bay; several localities in North Wales; Burry Inlet, South Wales; Milford Haven; Fal estuary, Salcombe and Poole Harbour. Average size at the time of formation of first, second and third growth rings has been determined for each locality; the results are presented in Table 3. Growth is very rapid in the Upper Fal, at Barra, in Poole Harbour and in North Wales, intermediate at Salcombe and in Morecambe Bay and slow at Milford Haven and the Burry Inlet. Comparison of size reached at the first winter ring is not profitable since this may depend to a substantial extent upon time of settlement. The latter may extend from May to early September. It has been observed that late set cockles may be less than 5 mm. at their first winter (see also Stopford 1951) but grow rapidly in favourable areas during their second year.

Table 3. Growth of cockles. Size at the time of the formation of first, second and subsequent winter rings. The figures in brackets are the numbers measured in each sample.

Locality	Date	Mean length - mm.					
		1st ring	2nd ring	3rd ring	4th ring	5th ring	6th ring
Tolverne Reach, River Fal, Cornwall.	July 1953	15.9(94)	28.5(94)	32.7(89)			
Poole Harbour.	July 1954	12.4(101)	25.8(47)	36.1(18)	39.9(15)	41.7(11)	45.0(5)
Barra Outer Hebrides.	Nov. 1953	15.7(69)	25.7(58)	28.5(6)			
Barra Outer Hebrides.	May 1954	15.1(106)	24.5(105)	29.0(81)	31.3(48)	34.1(36)	38.1(12)
Lavan Sands, Menai Straits, North Wales.	March, 1950	10.9(92)	23.4(79)	28.2(54)	31.1(21)	31.60(5)	33.70(3)
Lavan Sands, Menai Straits, North Wales.	Nov. 1953	11.4(10)	25.0(13)				
Cartmel Wharf, Morecambe Bay, Lancashire.	Jan. 1954	8.0(97)	21.0(97)	24.4(97)			
Blanks Mill, Salcombe, Devon.	Apl. 1955	9.5(20)	19.4(38)	24.5(12)			
Llanrhidian Sands, Burry Inlet, South Wales.	Aug. 1949	9.5(106)	17.9(104)	24.3(9)			
Martin Haven, Milford Haven, Pembroke.	May 1955	9.3(80)	17.9(62)	23.1(31)			

The reasons for these variations in growth-rate are not clear in all cases; comparison is made difficult by the great differences in the nature of the habitat. Beds located on firm, gently shelving, sand flats are found in Morecambe Bay, Burry Inlet, Lavan Sands, and Milford Haven. Freshwater influence is much greater in Morecambe Bay and the Burry Inlet than on the North Wales beds or in Milford Haven and this seems to be correlated with reduced growth rate. The beds at Morecambe and in the Burry Inlet are considerably exposed to the prevailing southwest winds and this, it is suggested, adversely affects growth in these two areas. At Barra the beds are sheltered from westerly winds.

Density is highest in the Burry Inlet where the growth-rate is the slowest so far recorded. Milford Haven is, however, little better, yet the bed from which the sample was taken lies on the inner edge of a large area of flats in a situation of practically full salinity where there is a rich and varied fauna. The density of cockles did not exceed 1,000 per square metre and the cause of the poor growth remains obscure.

Although the cockles from the River Fal were the largest at the time of the formation of the second ring, their growth increment in the year after settlement averaged 12.6 mm. compared with 13.4 mm. at Poole. In the next season the Fal cockles increased in length by 4.2 mm. only, whereas those at Poole gained 10.3 mm., and a further 3.8 mm. in the following year. Density may, however, have exerted some effect as the Fal bed was described as "very dense" by the collector, whereas at Poole cockles were sparse. The common feature of the two areas is shelter from severe wave action.

Wave action is heavy at times, particularly during late autumn in both Morecambe Bay and the Burry Inlet and seems to be a factor leading to severe checks in growth and low average annual growth increments. The Salcombe sample, from a sheltered creek, is anomalous in this respect and one can only conclude that some adverse environmental factor, so far unrecognized, was limiting growth. Possibly the occurrence of severe erosion of the shell, noted above, may be the result of acid conditions in the soil which also lead to poor growth.

Sea Temperature

Low winter water temperatures seem to result in a severe check to growth and poor average annual growth increments in comparison with areas where water temperatures are higher and severe cold is unusual. The cockles are larger and grow faster at Barra, in the River Fal and in Poole Harbour, than they do in Morecambe Bay or South Wales. North Wales is intermediate. There seems, therefore, to be a correlation with the duration and intensity of winter cold. Very low winter sea temperatures are not recorded in North Wales or off the outer Hebrides or the south-west coast of Britain. The Milford Haven sample is again anomalous since this is a deep inlet into the relatively mild frost-free peninsula of Pembroke.

Of the beds examined, Poole Harbour probably experiences the highest average summer temperature and it is not surprising to find this reflected in a high growth rate. On the other hand the low summer temperatures off the Island of Barra in the Outer Hebrides do not check growth, as cockles from these beds reach an exceptional size.

Duration of Life and Maximum Size

The largest cockles obtained were from the Island of Barra and from certain West Scottish lochs. A single live individual of shell length 64 mm. was collected from Loch Craignish, Argyll, and several fresh shells of similar size were seen. This giant cockle showed clearly marked rings at 12, 25, 36, 47, 52, 54, 56, 57, 58, 59, 60, 61, 62 and 63 mm. indicating that it had reached an abnormally large size by virtue of both a high growth rate and long life.

A commercial sample from Barra, sent to me by courtesy of Dr. H. J. Thomas, contained cockles up to 51 mm. A cockle of 51 mm. from Barra showed rings at 50, 49, 48, 47, 45, 43, 40, 37, 32, 23 and 12 mm. giving annual growth increments of 11, 9, 5, 3, 3, 2, 1, 1 and 1 mm. respectively after the formation of the first winter ring. Samples from Poole Harbour include individuals up to 54 mm; in that area those below 30 mm. are not usually taken by bona-fide cockle fishermen. Such cockles show from 7-9 rings but growth increments are very small at this age and rings at the edge of the shell are not easily distinguished.

On the Lavan Sands in the Menai Straits, North Wales, the cockle beds are virtually unexploited and the maximum size and age reached is therefore not influenced by commercial gathering. As can be seen from Table 2, there is a marked decline in length increment after the third season. During recent surveys the largest cockles found were 45 mm. in length; competition was not severe since the maximum density recorded did not exceed 100 cockles of all sizes per square metre. On unexploited beds at Bradwell, Essex, in an exposed situation, it was rare to find individuals over 35 mm.; annual growth increments after the third year were very small (Table 1) and after the fifth year generally resulted in an increase in tumidity without a measurable increase in length.

Reference to Table 2 shows that where cockles reach a large size they do so in the main by virtue of continued rapid growth in their third and subsequent seasons. The average growth increments between the second and third rings in Poole Harbour (large) and Morecambe Bay (small) cockles were 10.3 mm. and 3.4 mm. respectively. Continued growth of large cockles is presumably related to the amount of competition for the available food supply, but the possibility of inherent differences in growth pattern should not be overlooked.

On the large commercial fisheries of South Wales and Morecambe Bay cockles showing more than four rings are very scarce and none has been found with more than six rings. Kreger (1940) mentions that he never succeeded in counting more than four winter rings clearly distinguishable in Waddensee cockles. Cardium corbis (Fraser 1931) does not survive beyond seven years in British Columbia.

Growth-rate in relation to commercial exploitation

The accepted method of conserving cockles supplies on beds in England and Wales is to fix a minimum size limit below which cockles may not be removed. Most local Sea Fishery Committees fix such a size limit by bye-law, usually prescribing a gauge with a square aperture through which the cockles taken must not pass. Minimum sizes vary slightly from place to place, the largest being a gauge with a square hole with a side of 1 inch (25.4 mm.) and the smallest one with a side of 11/16 inches (17.5 mm.). The lengths of cockles which pass through these gauges vary somewhat with the tumidity of the shells, young quick-growing cockles being less tumid than older slow-growing cockles of the same shell length. A square gauge of side 17.5 mm. retains most cockles above 21 mm. in length and one with 25.4 mm. side those above 30 mm. Tables 1 and 3 show that cockles 21 mm. in length will have two rings (rising two years old) in South Wales, Morecambe Bay and some parts of Essex, but only one ring in most other localities. Cockles of 30 mm. will be over two years old in all localities and over three years old on many beds.

Conservation aims at retaining on the beds in their second year (the first major breeding period) the bulk of the stock of cockles. With such an accessible animal such a policy appears to be sound having regard to the very limited information regarding replacement rate and natural mortality. The application of this policy can be illustrated by recent changes in the minimum size applicable to the Burry Inlet beds. This fishery showed symptoms of intense exploitation in that large cockles were almost entirely absent and yields fluctuated violently from year to year in consequence of dependence on a single year class (those rising two years old) and irregular spatfalls. Investigation showed that with the minimum size limit then enforced (a gauge with square aperture of side ⅝ inch (16.0 mm.)) it was theoretically possible to remove over three quarters of the breeding stock of 1+ cockles before the peak of the breeding season had been reached. In the absence of any significant number of older cockles this was considered undesirable and the minimum size limit was raised to 11/16 inch (17.5 mm.). The effect of this in conserving the breeding stock is shown diagrammatically in Fig. 5. On this fishery cockles of the group rising two years old average 19 mm. in April when growth recommences after the winter and increase in length on the average by 6 mm. during the following summer and autumn before growth is again checked in October. Thus it is possible assuming a steady growth rate to draw six curves to represent the state of the population of cockles of this year class with modes at intervals of 1 mm. Also shown in Fig. 5 are the breeding season and the old and new size limits. It can be seen that an increase in the minimum size limit of only 1/16 inch (1.5 mm.) has a material effect in conserving breeding stock. Following the change the yield from the fishery has steadied and spatfalls appear to be more uniform. Clearly such changes can only be made on the basis of full knowledge of local growth rates.

Discussion

It has been shown that growth in cockles is influenced by sea temperature, salinity, tidal level, exposure to wave action, food supply, and density and time of settlement. The effect of nature of soil has not been fully investigated but appears to exert less influence than was anticipated from a study of the literature. Cockles are shown to thrive in a great variety of soils and are not restricted as Kreger (1940) reported to clean sand or muddy sand. The "normal" habitat, comprising large estuarine sand flats is shown to be less favourable for growth and survival than sheltered areas with soft soils in creeks and inlets less exposed to wave action or greatly reduced salinity. The level on the beach which carries the densest population is less favourable for growth than lower down on the shore; the reasons for the observed zoning are not clear but are probably the resultant of larvae preferences modified by current transport and predation by flatfish. Since cockles are susceptible to destruction during both exceptionally hot (Orton 1934) and exceptionally cold weather (Smidt 1944) it follows that mass settlement on the middle regions of the shore, as normally observed, leads to increased mortality from these causes when compared with settlement on the lower shore where growth would also be superior. One cannot avoid the conclusion that despite its success as a littoral animal, the cockle is somewhat ill-adapted to its environment in that the behaviour of the larvae at the time of settlement tends to result in vast accumulations of seed cockles in situations which do not lead to rapid growth and a high rate of survival.

The most favourable areas for the settlement of cockle spat in Britain are the large sandy estuaries (Thames, Burry Inlet, Wash and Morecambe Bay), judged by the regularity and extent of their production of market cockles. Information regarding growth rate in the Thames estuary and the Wash is sparse but in Morecambe Bay and the Burry Inlet growth has been shown to be much slower than on the soft soils in southern estuaries and inlets, such as Poole Harbour. There is therefore a possibility of profitable transplantation of seed cockles from the sandy exposed estuaries to these sheltered areas following the system recently developed with great success in Malaya (Soong, personal communication). Initial small-scale transplantations from the Burry Inlet to Poole Harbour have already been made and if successful will be followed by commercial scale operations.

References

Baggerman, B. 1953. Spatfall and transport of Cardium edule L. Arch. Neerl. Zool., 10, 315

Cole, H. A. and Knight-Jones, E. W. 1949. The setting behaviour of larvae of the European flat oyster, Ostrea edulis L., and its influence on methods of cultivation and spat collection. Fish Invest., Ser. 2, 17, No. 3.

Fraser, C. McL. 1931. Notes on the ecology of the cockle, Cardium corbis Martyn. Trans. Roy. Soc. Canada 25, 59.

Green, F. H. W. 1940. Poole Harbour a hydrographic survey 1938-9. London.

Havinga, B. 1922. Mariene mollusken, in Flora en Fauna der Zuiderzee. Den Helder.

Korringa, P. 1955. Oyster culture and production biology. Rapp. et Proc. Verb., 137 (In the press).

Kreger, D. 1940. On the ecology of Cardium edule L. Arch. Neerl. Zool., 4, 157.

Orton, J. H. 1926. On the rate of growth of Cardium edule. Part I. Experimental observations. J. Mar. Biol. Assoc. U.K., 14, 239

Orton, J. H. 1934. Bionomical studies on Cardium edule with special reference to mortality in 1933. James Johnstone Memorial Volume, 97.

Rapson, A. M. 1954. Feeding and control of Toheroa (Ampidesma ventricosum Gray) Eulamellibranchiata) populations in New Zealand. Aust. J. Mar. Freshw. Res. 5, 486

Smidt, E. L. B. 1944. The effects of ice winters on marine littoral faunas. Fol. Geog. Dan. 2, 1.

Stephen, A. C. 1931. Notes on the biology of certain lamellibranchs on the Scottish coast. J. Mar. Biol. Assoc. U.K., 17, 277

Stephen, A. C. 1932. Notes on the biology of some lamellibranchs in the Clyde area. J. Mar. Biol. Assoc. U.K., 18, 51

Stopford, S. C. 1951. An ecological survey of the Cheshire foreshore of the Dee estuary. J. Animal Ecol. 20, 103

Verwey, J. 1952. On the ecology of distribution of cockle and mussel in the Dutch Waddensee, their role in sedimentation and the source of their food supply. (Arch. Neerl. Zool., 10, 171

Wohlenberg, E. 1937. Die Wattenmeer - Lebensgemeinschaften im Königshafen von Sylt. Helgol. Wiss. Meeresunters. 1 (1), 1.

Wright, F. S. 1926. A report on the cockle beds and the cockle industry of England and Wales. Fish. Invest. Ser. 2, 9, No. 5

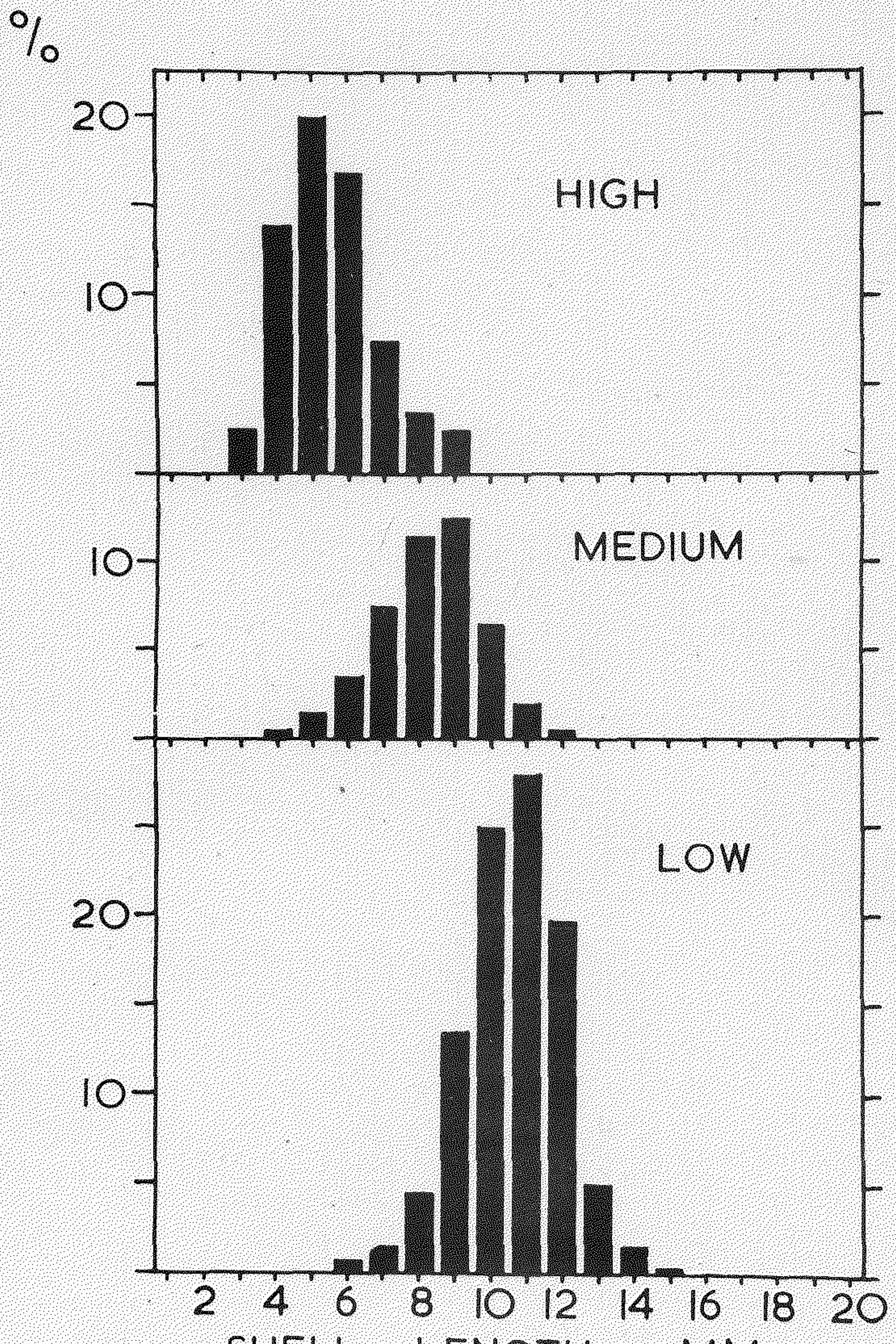

Fig. 1. A comparison of cockle populations (0 group only) from three stations differing in height in relation to low tide level, from Llanrhidian Sands, Burry Inlet, South Wales.

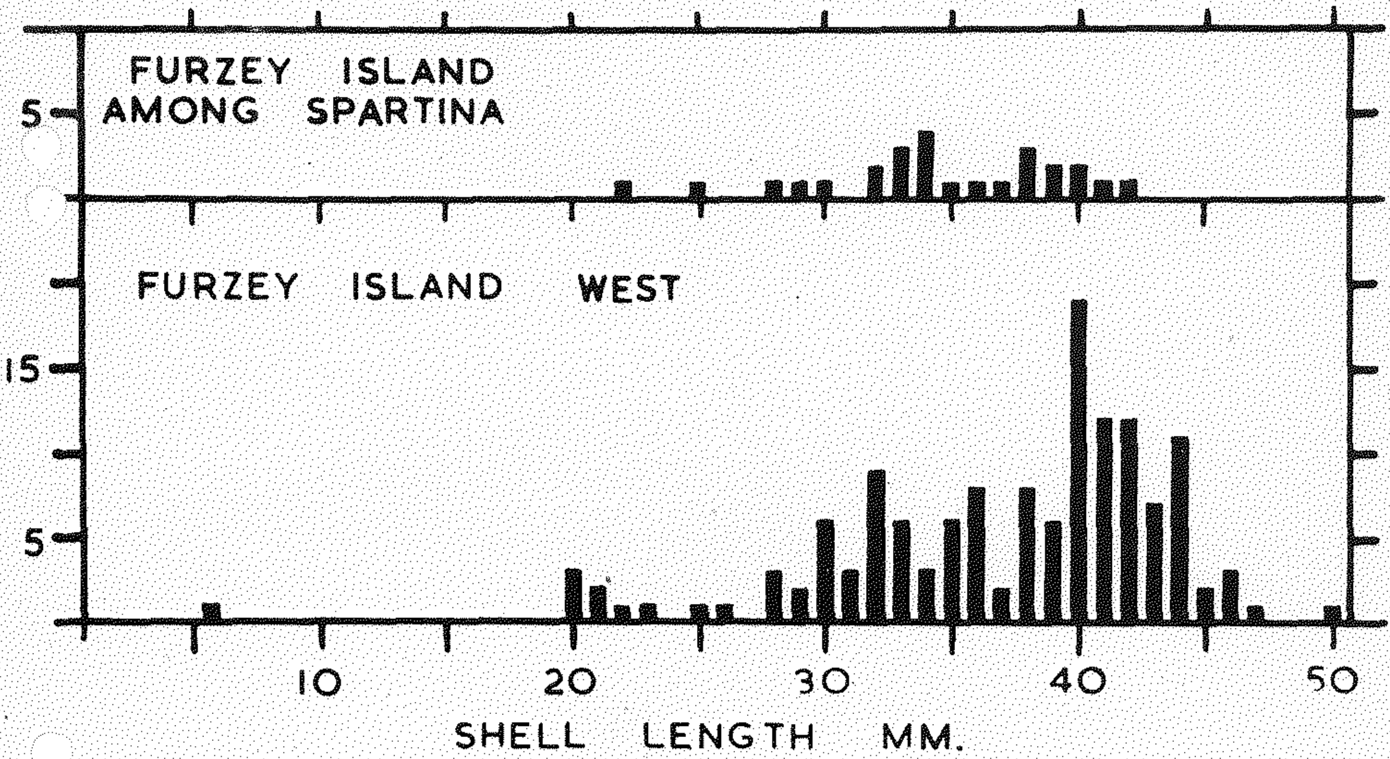

Fig. 2. Cockles living among roots of Spartina townsendii at high water of neap tides, Poole Harbour, Dorset, compared with cockles from the shore nearby.

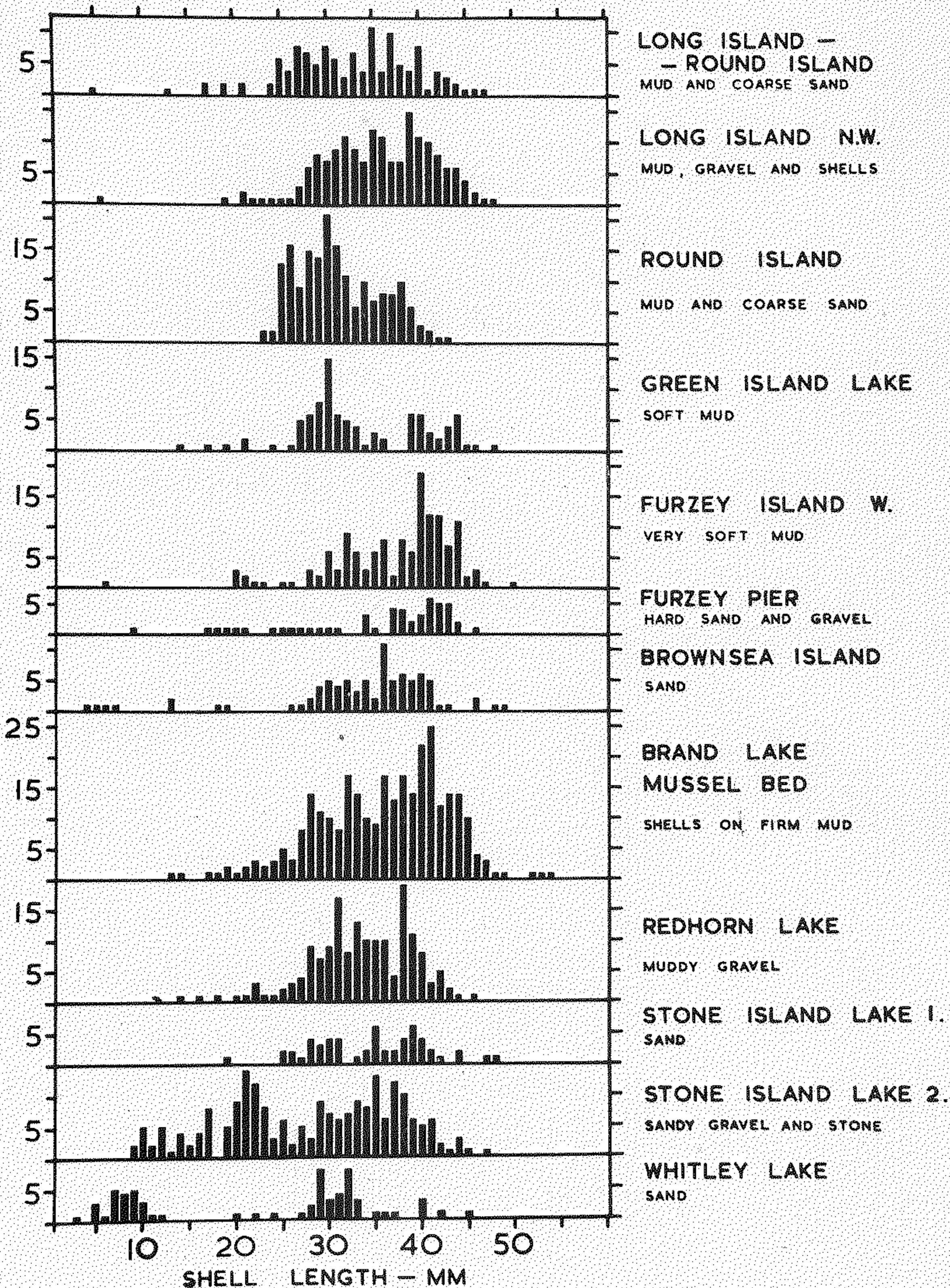

Fig. 3. Size distributions of populations of cockles taken from a variety of soils in Poole Harbour, Dorset.

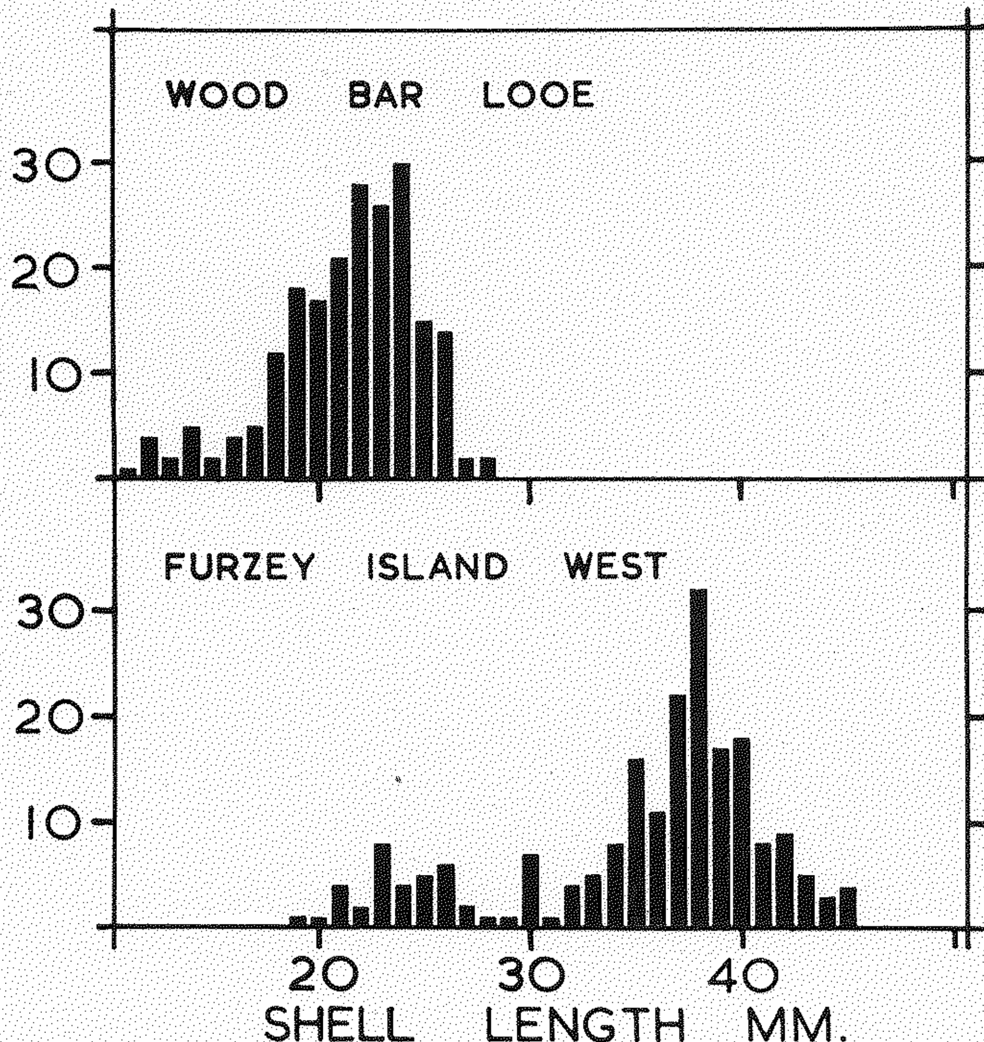

Fig. 4. Effect of reduced salinity on growth of cockles from Wood Bar, Looe, Poole Harbour, subject to strong flow of fresh water, compared with typical station with normal salinity conditions. The bulk of the population at each station comprises 3 and 4 year-old cockles.

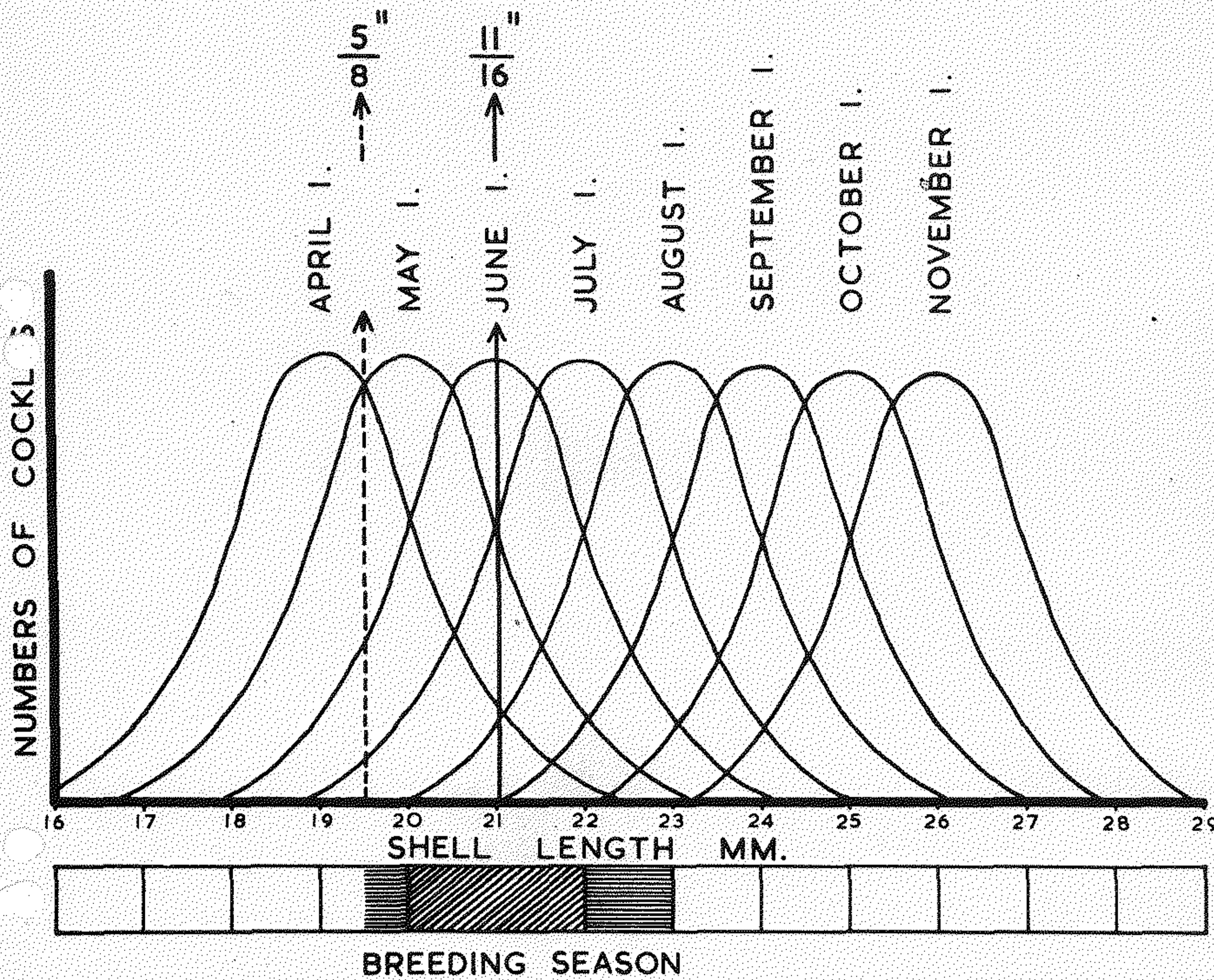

Fig. 5. An analysis of growth and breeding on the Burry Inlet beds in relation to commercial exploitation. The size distribution of the group of cockles rising two years old is shown at the commencement of each month from April to November. The effect of using the present (11/16 inch. square hole) and past ($\frac{5}{8}$ inch. square hole) legal minimum size gauges is shown.