

ON THE RATE OF GROWTH OF *NUCULANA MINUTA* (MÜLLER) (BIVALVIA; NUCULANIDAE)

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INTRODUCTION

The bivalves of the families Nuculidae and Nuculanidae are among the commonest inhabitants of soft substrata in Scottish coastal waters, including the predominantly muddy sediments of the deep waters of the sea lochs which are a feature of the Scottish west coast. The habits, mode of life, and functional morphology of these protobranch bivalves have been well described in such papers as those of Yonge (1939, 1959), and earlier papers by Pelseneer (1891, 1899, 1911) and Heath (1937), while Winckworth (1930, 1931) Moore (1931a,b) and, most recently, Allen (1953, 1954) have made attempts to clarify the nomenclature of the British species, especially of the genus *Nucula*. Edwards (1965) has drawn attention to differences in habits between the species, correlated with differences in the epifaunal organisms attached to their shells.

In contrast to the Nuculidae with five species, all common in inshore waters, only one species of the Nuculanidae occurs commonly in inshore British waters: *Nuculana minuta* (Müller), which Tebble (1966) recorded as living in bottoms of muddy sand and gravel from 5-10 fathoms depth (9.1-18.29 m) particularly off the coasts of Scotland and N.E. England, although it has also been reported off the Isle of Man, Dublin and Sussex and Dorset. For Scottish west coast waters, Chumley (1918) recorded *Nuculana minuta* (as *Leda minuta*) for all areas of the Clyde District (except the Gareloch) in depths of 10-105 fathoms (18.29-192.02m) on muddy and sandy bottoms, but most abundantly in deeper water, and Allen (1962) records the species as common in sandy mud, mud and gravel in depths of 20-210 m in the Clyde Sea Area. Allen (1954) also gives more detailed information on the distribution of this species in the Clyde Sea Area, and is the only author to discuss population structure, rate of growth and length of life.

Recent surveys of the bottom fauna of a number of Scottish sea lochs, including those of the Clyde Sea area, confirm the general conclusions of these earlier authors in respect to the distribution of *Nuculana minuta*. The purpose of this paper is to present the results obtained from these recent surveys, as they concern *Nuculana minuta*, and to present an alternative interpretation of the population structure of *Nuculana* population in the Clyde Sea Area, using new information based mainly on measurements of growth rings on the shells of living animals.

DISTRIBUTION OF *NUCULANA MINUTA* IN SCOTTISH WEST COAST WATERS

The material discussed here was collected during a number of cruises with the M.V. *Calanus* between 1971 and 1975, during which quantitative samples of the benthic macrofauna were

collected using a Van Veen grab, especially on muddy grounds from the sea lochs of the Scottish west coast and from the immediately adjacent waters, in an area roughly bounded by Loch Alsh and Loch Duich, to the north, and the Clyde Sea Area, as defined by Mill (1891), to the south. Within each area, a chain of stations was sampled, roughly following the long axis of each sea loch, and at each station, three Van Veen grab samples were taken, each of 1/10m². In addition, in certain areas, larger non-quantitative samples of the shallow burrowing infauna and epifauna were collected using an Agassiz dredge with a fine-meshed net lining the bag. In the case of *Nuculana*, such samples have produced large numbers of individuals from areas where the species is abundant although, in such samples, the smallest sizes of animals are under-represented or absent, because of losses from the net.

Nuculana minuta was found to be common only in samples collected from certain parts of the Clyde Sea Area. It was not taken from the lochs on the west coast of Argyll. However, the species has been recorded as present in Loch Creran (Gage, 1972a) and Loch Etive (Gage, 1972b; as dead shells only), but it was not taken from Loch Nevis by McIntyre (1961) or from Lochs Eil and Linnhe (Pearson, 1970).

For the Clyde Sea Area, the distribution of samples, and of stations at which *Nuculana minuta* was collected, is summarized in Fig. 1. Six main areas were found where the species could be described as being common or abundant. The six areas are all of deep or moderately deep water; in the upper Loch Fyne Basin; in the Lower Loch Fyne Basin; in Kilbrannan Sound; in the Arran Deep, N.E. of the Island of Arran; in the Cumbrae Deep, between the islands of Great Cumbrae and Bute; and in the Loch Long Basin. The number of stations sampled in each area together with the mean and the maximum densities of *Nuculana minuta* recorded, is given in Table 1. Not all of the areas where *Nuculana* occurs commonly were sampled equally effectively, but the greatest densities were found in Lower Loch Fyne, where there was a mean density of 61 m⁻² and a maximum density of 210 m⁻², in depths of 82-104 m.

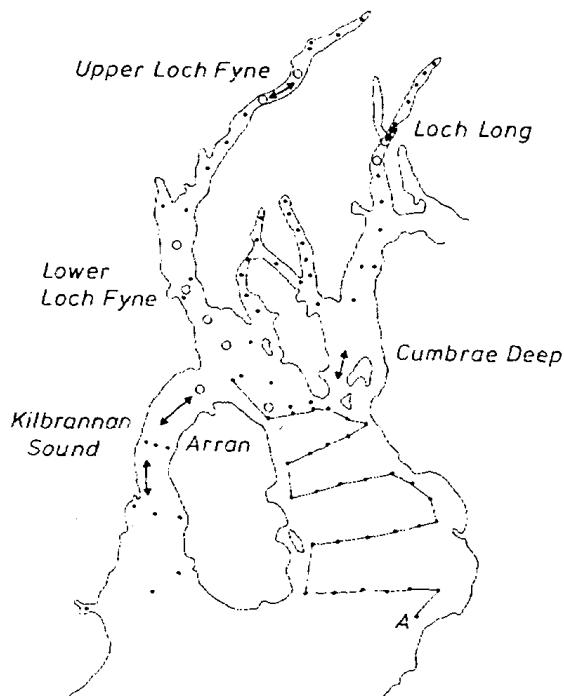


Fig. 1. The distribution of *Nuculana minuta* in the Clyde Sea Area. Dots: Van Veen stations with no *Nuculana*. Circles: Van Veen stations with *Nuculana* present (See Table 2). The chain of samples labelled A were taken by the Marine Laboratory, Aberdeen (See Kennedy, 1975).

Table 1. Summary of population density data for *Nuculana minuta* in the Clyde Sea Area.

Locations	No. of Stations	No. of samples with <i>Nuculana</i>	Mean No. m ⁻²	Maximum No. m ⁻²	Depth (m)
Upper L. Fyne	3	8/9	32	70	137,144,97
Lower L. Fyne	4	11/12	61	210	85,104,82,90
Kilbrannan Snd.			No Van Veen grabs in deep area.		
Cumbræ Deep.			No Van Veen grabs in deep area.		
Loch Long.	2	3/6	13	60	106, 70
Arran Deep..	1	1/3	10	10	73

Table 2. Values of the mean height/length (H/L), width/length (W/L), and width/height (W/H), ratios for shells of *Nuculana minuta* from different locations in the Clyde Sea Area

Location	H/L	W/L	W/H
Upper L. Fyne	0.513	0.286	0.558
Lower L. Fyne	0.531	0.266	0.500
Kilbrannan Snd.	0.530	0.322	0.608
Cumbræ Deep	0.544	0.327	0.601
Loch Long	0.551	0.341	0.619

ASSOCIATED FAUNA

Allen (1954) stated that *Nuculana minuta* in the Clyde Sea Area closely resembles *Nucula sulcata* Bronn in its habitat range, and occurs together with the polychaete *Lipobranchus jeffreysii* (McIntosh), the bivalve *Glossus humanus* (L), and the echinoderms *Amphiura chiajei* Forbes and *Brissopsis lyrifera* (Forbes). In the present survey, *Nucula sulcata* was found to be much more widely and commonly distributed on the lochs on the west coast of Argyll and in the Clyde Sea Area than was *Nuculana minuta*. In the Clyde Sea Area, *Glossus humanus* was not taken, but the other three of the above species were collected both in Van Veen and Agassiz samples from the same areas as *Nuculana minuta*. Various smaller polychaetes, including *Terebellides stroemii* Sars, *Paraonis gracilis* (Tauber) and *Lumbriconereis hibernica* McIntosh occurred at all the stations where *Nuculana minuta* was taken. In addition *Nucula tenuis* (Montagu) and *Thyasira ferruginea* Winckworth were abundant with *Nuculana minuta* in Upper Loch Fyne. *Amphiura filiformis* (Müller) was more abundant than *Amphiura chiajei* at the stations where *Nuculana minuta* occurred in Lower Loch Fyne. The fauna of all the areas sampled will be described in more detail elsewhere.

SIZE STRUCTURE OF THE POPULATION

The size distribution of *Nuculana minuta* in the largest samples collected is shown in Fig. 2. In those samples collected using the Agassiz dredge, the size distribution shown is not representative of the whole population, since the smallest sizes are not all recovered by this method. Measurements of the *Nuculana minuta* taken by the Van Veen grab in the upper and lower Loch Fyne basins show that smaller sizes are, in fact, well represented in the population.

The largest *Nuculana minuta* were found in the Cumbræ deep, while those collected from Loch Fyne were of smaller mean size and had a smaller maximum size than those collected from the Cumbræ Deep, Loch Long and Kilbrannan Sound.

Allen (1954), gave a histogram of the size distribution of *Nuculana minuta* from Kilbrannan Sound, i.e., from the same area as one of the present samples. Allen's histogram shows well-defined size groups which he interpreted as being 'in all probability year groups'. Based on this assumption, he concluded that the maximum age attained by *Nuculana minuta* in this population is 17 years, and that the growth rate 'remains practically constant throughout the life of the species', the yearly shell increment for *Nuculana minuta* having a mean value of 0.98 mm. The animals found in the present survey show no such clear polmodal frequency distributions.

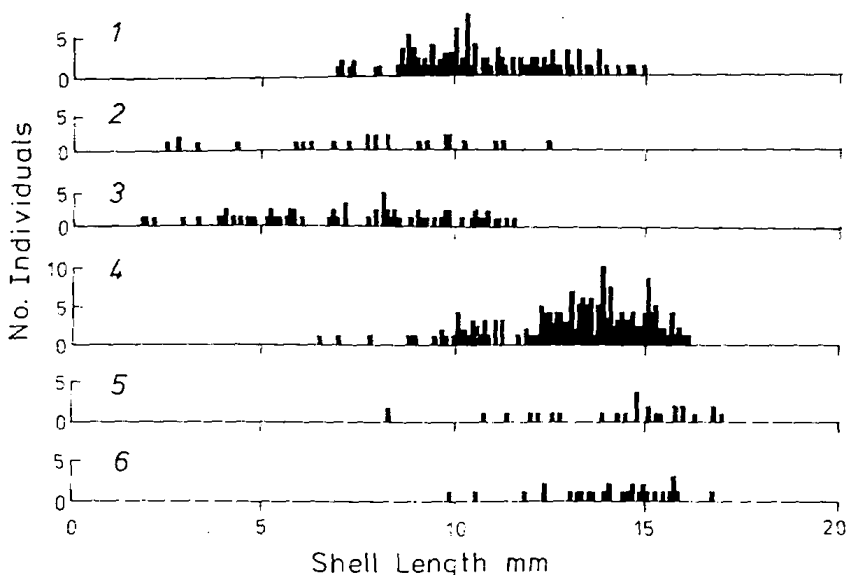


Fig. 2. Size distribution histograms of samples of *Nuculana minuta* from the Clyde Sea Area. 1, Upper Loch Fyne; 2, Upper Loch Fyne; 3, Lower Loch Fyne; 4, Kilbrannan Sound; 5, Cumbrac Deep; 6, Loch Long. 1 and 3 were from Van Veen grab samples; 2, 4 and 5 from Agassiz dredge samples.

Allen's interpretation of the *Nuculana* populations both in terms of age structure, length of life and rate of growth, is based upon the very well-defined size groups present in his data. In our opinion these size groups may have resulted from unconscious bias during the process of measurement rather than being representative of the size distribution of the actual population.

Examination of the frequency histograms in Allen's Text-Fig. 6 shows that there is a mode exactly corresponding with each integer. For example, for *Nucula turgida* (4) there are well-marked modes at the 3, 4, 5, 6, 7, 8, 9, 10 and 11 marks, and for *Nuculana minuta* (11), well-marked modes occur at 7, 8, 9, 10, 11, 12, 13 and 14 mm. The clearest modes in the other size distributions show a corresponding relationship to the integers, with the exception of those for *Nucula nucleus* (8 and 9) which in addition to having modes corresponding with each integer, also have intermediate modes corresponding with the 0.5 mm points. In our opinion, it is unlikely that natural populations would show such a close correspondence either to each other or to the exact whole mm points. To produce such well-defined size groups, maintained throughout the life span of each species, would require the assumption that the settlement seasons were shorter and more well-defined, and the growth of the individual animals much more uniform, than may be reasonably expected from what is known of the biology of protobranchs, or indeed of any bivalve mollusc. Moreover, the growth curve derived from these modes would indicate uniform growth increments maintained throughout the life span of the animal. Such a form of growth has not been found for any other bivalve.

We believe that an alternative, and more likely, interpretation of modes in Allen's data is available, that is, that they arose from unconscious bias introduced by the method of recording measurements made to the nearest 0.1 mm. The tendency for measurements to cluster round particular values where there is doubt as to the final digit in reading a scale has been recognized in the statistical literature (Yule, 1927) but seems rarely to have been quoted. In our experience such bias is common when measurements, for example of bivalve shells, are made using callipers or other means, when the final digit of the measurement is estimated by eye between marks on a scale of, say, 1 mm, or 1 mm and 0.5 mm, intervals. There is an unconscious bias by the observer towards certain final digits, and against others, which, in some cases, may result in the digits nearest to the scale markings being over-represented and those progressively further from a scale-

marking being progressively under-represented. The exact form of the bias may differ with different observers or with the same observer using differently scaled instruments. The presence of such bias in any group of measurements may be checked simply by comparing the actual distribution of the final digits of the recorded measurements, with the equal distribution which would be predicted were no bias present (Fig. 3). Such bias should be avoided by making use of a vernier, but the possibility of such a bias affecting the final digit should always be considered, although the common practice of grouping data for presentation may partially or completely mask its effect, depending on the number of size groups used in grouping.

Allen's data for *Nucula turgida* Leckenby & Marshall (Allen, 1954, Text-Fig. 6, nos. 4, 5, 6) are also discussed in an earlier paper (Allen, 1953) and similar comments apply to the conclusions on age and growth reached in that paper. We hope to discuss the rate of growth, and population structure of species of *Nucula* in Scottish waters in a later paper.

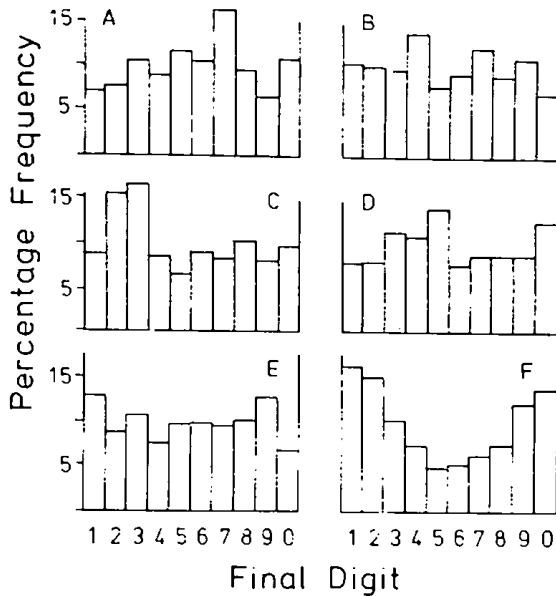


Fig. 3. Histograms of frequency distributions of the final digit in measurements using callipers, when the final digit is estimated. A-E; measurements made by five different observers using callipers scaled in 1 mm units; F; taken from Allen (1954) Text-Fig. 6, No. 11.

AGE STRUCTURE AND RATE OF GROWTH BASED ON SHELL MARKINGS

The shells of most of the individuals of *Nuculana minuta* from all the Clyde stations show more or less well-marked rings (Fig. 4). If it is assumed that one such ring is formed annually, an alternative estimate of the age and growth of *Nuculana minuta* from the Clyde Sea area may be made. Although there is some doubt in individual cases in most shells it is possible both to count the number of rings and measure the length of the shell each represented. As for other bivalves, the greatest errors probably involve (1) the interpretation of rings near the umbone, representing the 1st and possibly the 2nd check to growth and (2) interpretation of the closely-spaced rings near the shell margin in old specimens. The errors involved in estimating the early growth from rings near the umbone are intensified in the case of *Nuculana minuta* by the presence of manganese-rich deposits on the shell, or in some cases by erosion of shell material from near the umbones. Because of these uncertainties, grouping individuals into year classes is also subject to some error.

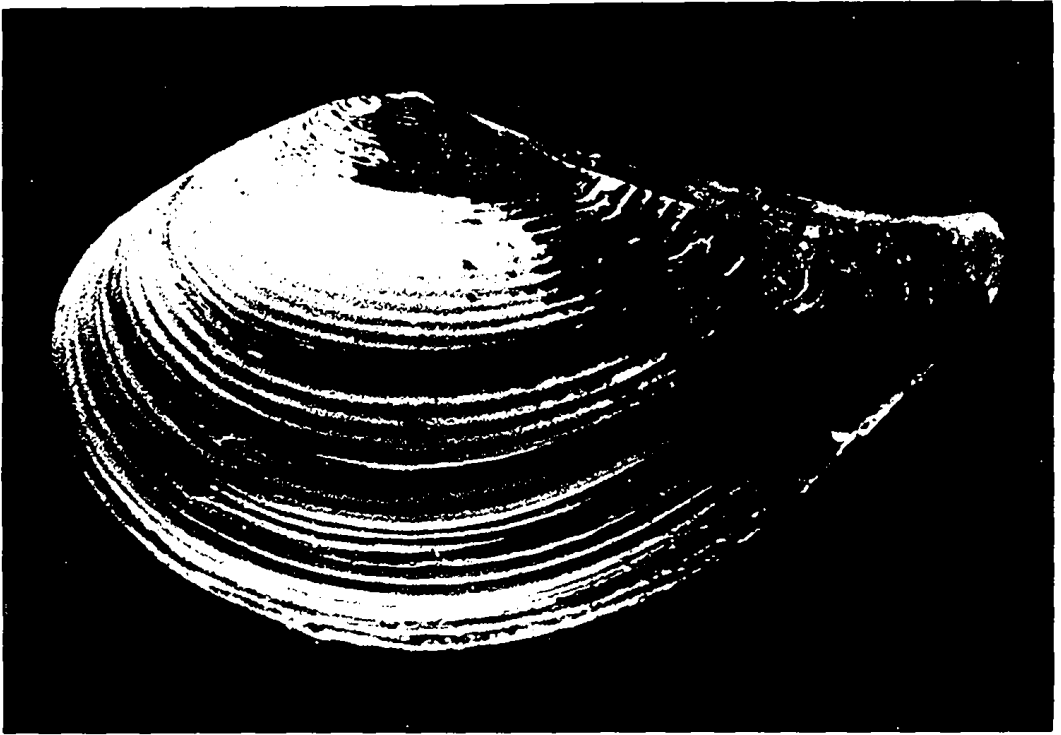


Fig. 4. Photograph of shell of *Nuculana minuta* from the Cumbrae Deep to illustrate the shell rings used to estimated age and growth.

With these limitations in mind the best comparisons between areas may be made by means of Ford-Walford plots (Fig. 5). These indicate that the mean rate of growth of *Nuculana minuta* is greater in the Cumbrae Deep than in Loch Fyne, while the rate for animals from Kilbrannan Sound and Loch Long is intermediate. The data suggest that *Nuculana minuta* may grow to reach the maximum sizes recorded from the Clyde stations in 7-8 years from settlement, rather than the 17 years suggested by Allen (1954). The form of the growth curve derived from ring measurements (Fig. 6) is more typical of that found for other bivalve species, with annual growth increments after the first or second growth checks declining regularly, except where affected by annual fluctuations, presumably reflecting good or bad conditions. There is considerable variation in the rate of growth as indicated by shell marks, both between individuals, and, in the same individual, between years. Such fluctuation is, however, a feature of bivalve growth.

The size-frequency distributions found for the Clyde populations of *Nuculana minuta*, where based on collections made by the Agassiz dredge, indicate a predominance of larger individuals in most of the populations, although there are differences in the estimated age structure: the animals collected in Loch Fyne were predominantly younger than these from Kilbrannan Sound and Loch Long. For Kilbrannan Sound, the size-distribution found in the present survey, made during September 1974, closely resembles that found by Allen (1954) for samples collected in August 1951 (when the peaks in his distribution are smoothed), indicating the probability of long-term stability in the population. The same predominance of large individuals is not confirmed in the samples collected by the Van Veen grab, but the samples available suggest that regular, although variable, annual recruitment takes place to these populations, followed by relatively slow mortality over the life span. The smaller mean and maximum sizes found for the Loch Fyne populations are the result of the slower mean rate of growth, although the variability is great in all cases.

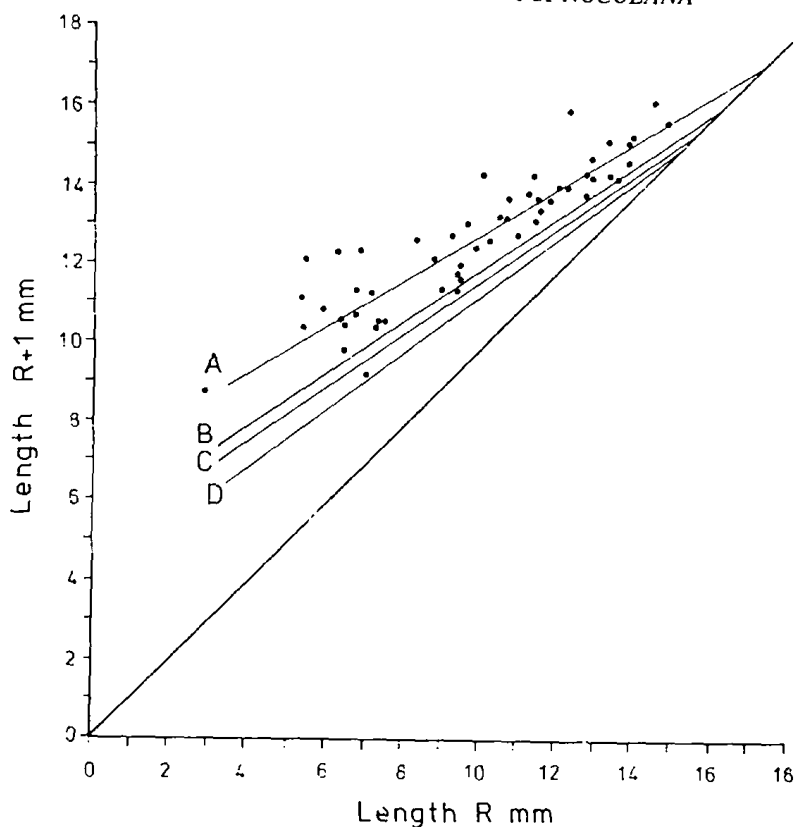


Fig. 5. Regressions fitted to Ford-Walford plots of all ring measurements for *Nuculana minuta* from the Clyde Sea Area. Individual points are shown only for the Cumbræ Deep population. A, Cumbræ Deep; B, Loch Long; C, Kilbrannan Sound; D, Upper and Lower Loch Fyne.

SHELL SHAPE

In addition to length (L) measurements, height (H: umbone to ventral margin) and width (W: at point of greatest obesity) of shells from each locality, were measured. Mean values for the ratios H/L, W/L and W/H were found for animals from the Loch Long Basin, and the lowest values for animals from the Loch Fyne Basins. Values for the Kilbrannan Sound and Cumbræ Deep populations were intermediate.

Relationships between shell length and the total weight of the animal, and between shell length and shell weight were determined only for animals from the Cumbræ Deep. These relationships are adequately fitted by the following equations:

$$\text{total weight (g)} = 0.1025 (\pm 0.0054) \text{ length}^3 \text{ (cm)}$$

$$\text{shell weight (g)} = 0.0570 (\pm 0.0036) \text{ length}^3 \text{ (cm)}$$

Thus the shell accounts for approximately 55% of the total weight of the animal. The mean percentage of wet tissue, following removal from the shell, was 24.6% and for dry tissue, following oven drying at 65-70°C, 4.88% of total body weight, determined for a collection made during March. Experience with other bivalves found in the deep waters of the Clyde Sea Area, including *Nucula sulcata* (Ansell, 1974, a,b,c) suggests that this figure for tissue weight is likely to be near the minimum percentage for the year.

The revised estimates of the life span and rate of growth for *Nuculana minuta* presented here indicate a more rapid turnover in the *Nuculana* populations in the Clyde Sea Area than was previously thought (Allen, 1954). In spite of this, the contribution of *Nuculana minuta* to benthic productivity is low. Assuming a constant rate of mortality, a seven year life span would represent a ratio of production to biomass (P/B ratio) of approximately 1.0.

Skalkin & Tabunkov (1969) and Tabunkov (1974) have studied another nuculanid, *Nucula pernula* (Müller), where it occurs with maximum densities approaching 1800 m⁻² at a depth of 80-85 m on the south-east coast of Sakhalin Island, in the Sea of Okhotsk. The maximum life span of *Nuculana pernula* in this area is five years. The shells show clear growth rings similar to those described here for *Nuculana minuta*. Present evidence, therefore, suggests that the two species show a similar life span although *Nuculana pernula* grows to a larger maximum size than *Nuculana minuta*. Ockelmann (1958) gave the distribution of *Nuculana* (= *Leda*) *minuta* as low-arctic boreal, discontinuously circumpolar; and that of *Nuculana* (= *Leda*) *pernula* as pan-arctic boreal, circumpolar.

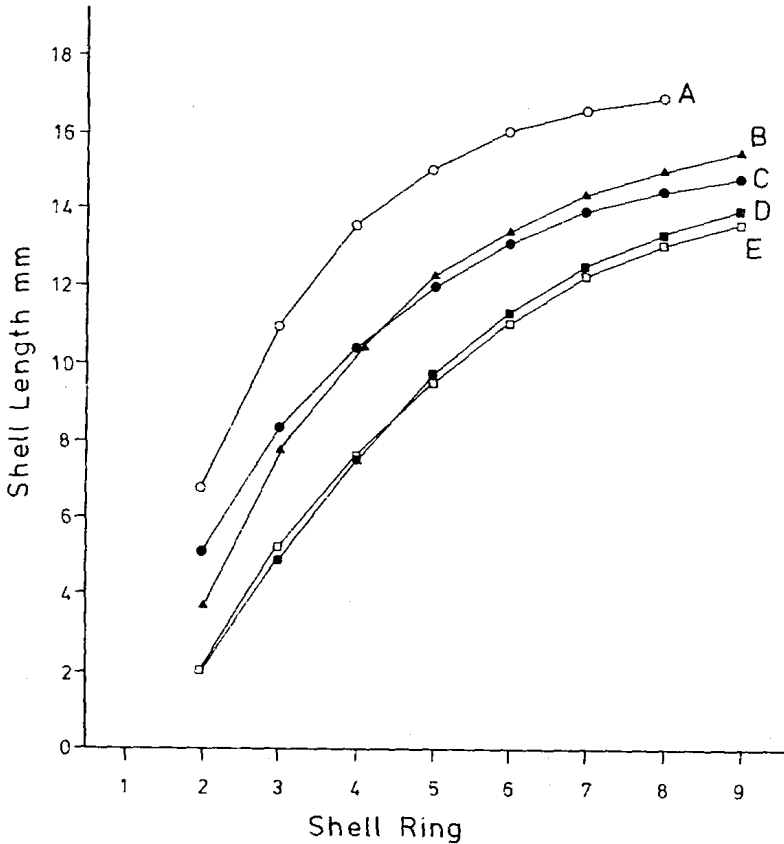


Fig. 6. Mean growth curves for *Nuculana minuta* from the Clyde Sea Area, based on ring measurements. A, Cumbrae Deep; B, Loch Long; C, Kilbrannan Sound; D, Lower Loch Fyne; E, Upper Loch Fyne.

If the clear growth rings on the shell of *Nuculana minuta* are indeed formed annually as suggested here, the interruption of growth which leads to their appearance presumably results from a predictable period when conditions become unsuitable for growth. In those molluscs from shallower British waters which show clear growth rings, the interruption usually results from low temperatures during the winter, accompanied by a low level of suitable phytoplankton food. In the case of *Nuculana*, food supply is unlikely to be a factor: *Nuculana* species burrow shallowly into the sediment, maintaining a water current for respiration, and perhaps partly for feeding, by means of the siphons (Trevallion, 1965; Stasek, 1951, 1955). Food particles are collected from the surface of the sediment by extension of the palp proboscides. In the Clyde Sea Area, at the depth at which *Nuculana minuta* is found in abundance, water temperatures are minimal, between 6° and 7°C during February-March, when the water in the area is practically isothermal. There is a gradual rise of temperature through the summer, and maximal temperatures (10.5 — 12°C) occur in October-November, after the breakdown of the summer thermocline and the mixing of the water column during the autumn. Thereafter temperatures fall steadily. In February-March, the whole water column is saturated with oxygen, but there is a decline in percentage oxygen saturation in the deep layers through the summer to minimal values in September-October. In September-October, therefore, maximum temperatures coincide with minimum oxygen values, although these do not fall below 70% saturation, while oxygen saturation conditions and minimum temperatures occur together in February-March (data from Dr H. Barnes, quoted by Edwards (1965)). The most abrupt change in conditions on the bottom must result from the mixing of the whole water column when the summer thermocline breaks down. In *Nucula sulcata*, which is common in the Clyde Sea Area at similar depths, the tissue weight increases during the period May to late August, following an increase in the content of phaeophytin pigments in the tissues in April and May, which is taken as indication of increased feeding activity (Ansell, 1974). The phaeophytin content of the tissues remains at a high level throughout June and July but falls in August. *Nucula sulcata* spawns in the Clyde in the winter, beginning in October-November, and it is likely that *Nuculana minuta* shows a similar cycle of slow gonadal development through the summer months followed by spawning in the winter at the time of maximal or declining water temperatures. It is possible that cessation of shell growth in *Nuculana* occurs during the winter, and this may coincide with the period of maximum temperature accompanied by a reduction in oxygen saturation, and with the main period of spawning, but this requires confirmation. Such a reversal of the more common situation would be consistent with the arctic-boreal distribution of *Nuculana minuta*.

The egg in *Nuculana minuta* is large, and development is probably entirely lecithotrophic, so that the developing larva is not dependent on planktonic food supplies. As in other protobranchs, spawning success may depend, therefore, on the conditions for feeding encountered by the adult during the period of gonadal development and maturation when the food reserves of the eggs are laid down. The population structure found for *Nuculana minuta* in the Clyde suggests that in most years these conditions are good, leading to successful spawning and recruitment to the populations in all the main areas of its distribution.

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SUMMARY

The protobranch bivalve *Nuculana minuta* (Müller) was found to be present in abundance in six main areas of deep water mud in the Clyde Sea Area, but absent or rare from muddy substrata in sea lochs on the west coast of Argyll, Scotland.

A new interpretation of the age structure of the populations, and of the rate of growth is given, based on the presence of clear shell growth rings. This evidence suggests a life span of about seven years for *Nuculana minuta*, with successful annual recruitment to the population. There are minor differences in shell shape between the populations found in the different major areas of abundance.

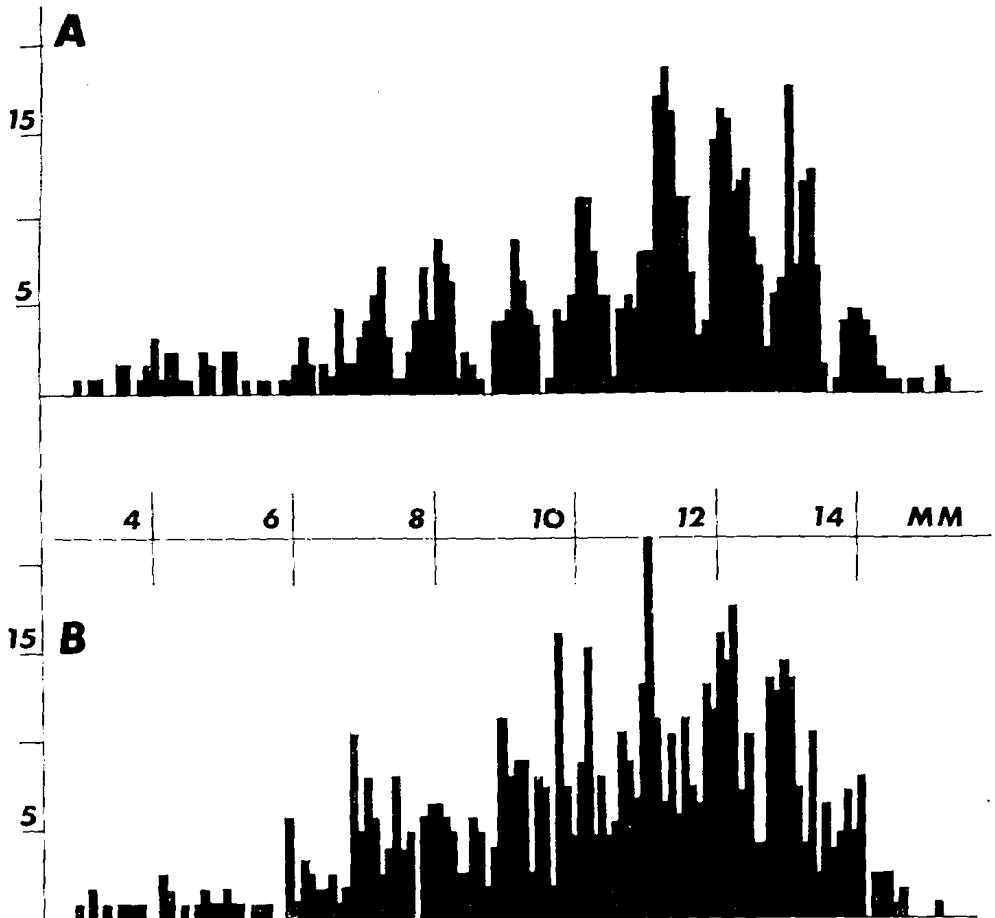


Fig. 7. Size-frequency histogram of a sample of *Nuculana minuta* collected from the Kilbrannan Sound in August 1951, *A* as measured in 1953, *B*, as measured in 1976. Some dissolution of the shell has occurred in the intervening years during which time the specimens have been kept in 70% alcohol.

NOTE ADDED BY J. A. ALLEN

When the results of the 1953 and 1954 investigations on Clyde protobranchs (Allen, 1953, 1954) were reviewed prior to publication the possibility of measurement bias was raised by Mr G. M. Spooner of the Marine Biological Association and repeat measurements were carried out at that time and the previous measurements were confirmed.

By good fortune the sample of *Nuculana minuta* has remained largely intact in the intervening 24 years. Miss Hilary Holliday of the University Marine Biological Station was asked to remeasure the sample, care being taken to ensure that there was no observer bias in the measurements. She was unaware that the sample had been previously measured. Fig. 7 *a* & *b* compare the results of 1953 and 1977. Although some dissolution of the shells has occurred in the intervening years, it can be seen that the coincidence of modes and integers is confirmed. Whether the peaks correspond to year classes is debatable, there are good *a priori* grounds for accepting that the growth curve presented by Dr Ansell and Dr Parulekar is of a type that might be expected and thus, if this is the case, the modes shown in the samples measured by Allen (1953, 1954) are not year classes.

Nevertheless, all the evidence (albeit scanty) (see Mortimer, 1962) is that the protobranch species in the Clyde have well-defined, short breeding seasons. It is also known that growth rate of some protobranches is very slow (Turekian *et al.*, 1975) and that this is true of the post-larvae of species of protobranches in the Clyde (Mortimer, 1962): for example in the case of *Nucula sulcata* in four and one-half months (Feb-June) the post-larvae only increased in size by 7 μ m.

So called 'growth rings' are notoriously difficult to interpret and the disturbance that leads to their formation may or may not be seasonal in occurrence.

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