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Notes on the Ecology of Brachiopods in New Zealand

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Abstract

DESCRIPTIONS are given of occurrences of *Terebratella* (*Waltonia*) *inconspicua* (Sowerby) around low-tide level; of *T. inconspicua, Tegulorhynchia* (*Notosaria*) *nigricans* (Sowerby) and *Pumilus antiquatus* Atkins in an intertidal rock-pool; of *Terebratella* (*Magasella*) *sanguinea* (Leach) and *Neothyris lenticularis* (Deshayes) from a muddy bottom off shore; and of *T. inconspicua* and *T. sanguinea* near the shore of a fiord. All these brachiopods appear to be intolerant of sedimentation and exposure to wave-action, but tolerant of turbidity and temperature fluctuation. *T. inconspicua* is marginally tolerant of emersion above water level. The intertidal species are probably subject to stronger competition for settling space than for food. They show an extremely patchy distribution, which is apparently due to very uneven settling of larvae during successive spatfalls. Living populations of all the species contain a high proportion of large and sexually mature individuals. One population of *T. inconspicua* is analysed in some detail. There is evidence that the rate of growth diminishes progressively in the later stages of the life-history. The life-span of the oldest individuals is probably much greater than the four years suggested by Percival.

INTRODUCTION

DESPITE the great palaeontological importance of the phylum, there are still relatively few published observations on the ecology of living brachiopods (see Hyman 1959, p. 583 ff.). As a result, discussions of the palaeo-ecology of fossil brachiopods are often seriously handicapped.

During a visit to New Zealand in 1959–60 I was able to study five living species. The purpose of this paper is to record some miscellaneous observations on the environment and population structure of these organisms (studies of feeding mechanisms and other aspects of physiology and behaviour will be published elsewhere). A more intensive study, over a longer period than was available to me, would have yielded more conclusive results. But I hope that this will encourage biologists in New Zealand to exploit their geographical advantage by enlarging our knowledge of this once-prolific phylum.

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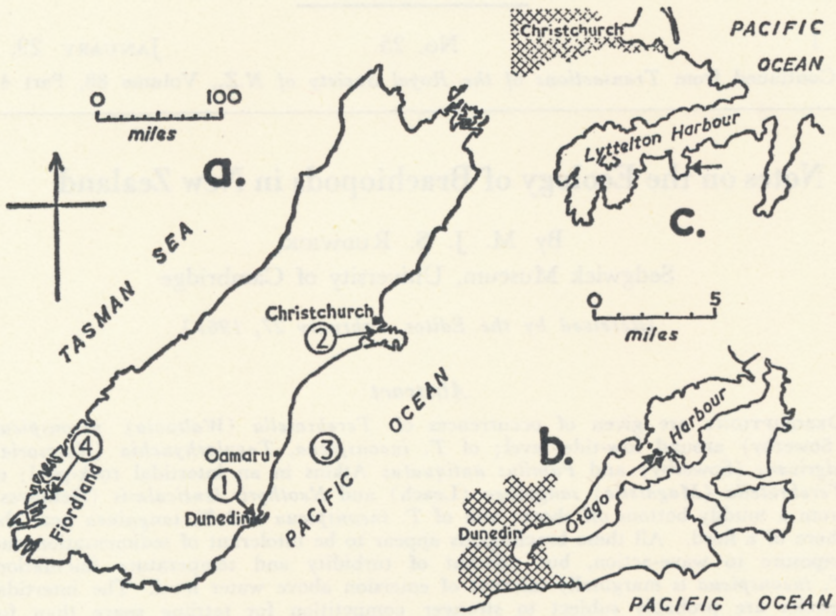
Intertidal Occurrences

(i) *Around low tide level.*

Terebratella (*Waltonia*) *inconspicua* (Sowerby) is locally very abundant around low tide level. I have studied the species in two such localities: (a) on the S.W.-facing shore of Quarantine Island and the nearby Aquarium Point of Portobello Peninsula, in Otago Harbour, near Dunedin; and (b) on the W.-facing shore of Purau Bay in Lyttelton Harbour, near Christchurch (Text-fig. 1).



Text-fig. 1.—Maps to show brachiopod localities mentioned in text. (a) Index map of South Island—(1) Otago Harbour; (2) Lyttelton Harbour; (3) off Oamaru; (4) Doubtful Sound. (b) Localities (arrowed in Otago Harbour. (c) Locality (arrowed) in Purau Bay in Lyttelton Harbour.

Both localities are shores sheltered from the extreme wave action of the open coast (cf. Batham 1958); but during windy weather the wave action is nevertheless considerable. (It is noteworthy that a third and well-known locality—on the shore of Rangitoto Island, near Auckland—is similarly placed.) The shores consist of large boulders of volcanic rock lying in a substratum of sandy or shelly mud. The boulders are probably shifted only by the heaviest storms; but except during periods of unusually calm weather the water is always turbid. Many of the brachiopods are very close to the surface of the substratum, where even the gentlest movement of the water stirs up the mud; yet here, and under similar conditions in the laboratory, they continue to filter-feed normally, and are thus evidently tolerant of turbidity.

The brachiopods are most abundant around the mean level of low spring tides, and they extend only sparsely above and below this level, though Percival (1944, p. 2) recorded that at another locality in Lyttelton Harbour they extend "up to about half tide mark". They occur almost exclusively on the lower surfaces of the boulders, where those surfaces are at least an inch or two clear of the substratum. Since they occur invariably in these protected positions even below the level of extreme low spring tides, their protection must be primarily against excessive wave action rather than against desiccation. But doubtless it is this habitat that enables the species to extend its range upwards on the shore into a zone in which it withstands periodic—though brief—emergence. Its relative rarity immediately below the level of extreme low spring tide is probably governed by the intense competition which seems to characterise this level (Batham, 1956, p. 459); for it is locally abundant at greater depths, extending to 50 fathoms (Allan, 1960, p. 253).

In periods of very calm weather, muddy sediment settles out of the water on to all upward-facing surfaces. Similar sedimentation in the laboratory causes the death of many of the smaller brachiopods: larger individuals stand out further from the surface of sedimentation, and are better able, by more vigorous snapping of the valves, to keep themselves clear of sediment. This probably explains why in the natural habitat the brachiopods are relatively uncommon on upward-facing surfaces, even where such surfaces are sheltered.

At Portobello Marine Biological Station, close to the Otago Harbour localities, the sea temperature fluctuates between mean annual extremes of about 6° and 17° C. Since Otago Harbour is a relatively enclosed body of water (Text-fig. 1*b*), the temperature also fluctuates appreciably from day to day, in accordance with the changing weather. No comparable figures are available for the Lyttelton Harbour locality, but conditions are probably similar. Specimens from both localities were kept under observation in aquaria at Portobello from early February to mid-June, 1960, while the temperature was falling, with much fluctuation, from 16° to 8° C.; but these changes never had any apparent effect on the health or behaviour of the brachiopods. It is possible that, in common with many other marine invertebrates, their breeding activities may demand stricter limits of temperature than their general metabolism; but of this nothing is at present known.

The shells are attached by a short pedicle, usually to the actual surface of the boulder but often to the shell of another brachiopod or of a lamellibranch. A few may be found with the pedicle embedded in the tissues of an ascidian: this habit is known also in *Kraussina rubra* (Gray, 1872). The shells do not appear to have any preferred orientation relative to the horizontal: neither the dorsal (= brachial) nor the ventral (= pedicle) valve can be said to be constantly the "upper" valve in any but a purely morphological sense.

The brachiopods and associated organisms form a dense cover over the sheltered surfaces of the boulders. The assemblage is chiefly remarkable for the large number and variety of filter-feeding organisms. Apart from the brachiopods themselves, these include many ascidians, both simple (*Corella, Pyura*) and compound (*Didemnum*); many sponges (*Aplysilla, Tethya, Leucosolenia*); lamellibranchs (*Ostrea, Modiolaria*); tubeworms (*Galeolaria, Pomatoceros, Spirorbis*); polyzoa (*Escharoides*); and porcellanid crabs (*Petrolisthes*). (Some of the species are named in Batham 1956, but many are still unidentified.) The larger brachiopod shells bear an epifauna which may be so dense that the shell itself is invisible. Sponges, ascidians, polyzoa, tubeworms, hydroids and younger brachiopods are the commonest members of this epifauna. The abundance and density of filter-feeding organisms suggests that competition for settling space is probably a more significant limiting factor to the brachiopods than competition for food.

Starfish, carnivorous gastropods and crabs are all present on the shores, and (by analogy with their predation on lamellibranchs) may be predatory on the brachiopods; but no direct evidence of predation was seen. Possibly the smallest shells, in the earliest period after the larvae have settled, are the chief victims of predation.

In detail, the distribution of the brachiopods is very uneven. One boulder may have a dense cover, with shells packed closely together, whereas on an adjacent boulder, in an apparently similar position, there may be only one or two shells. This gregariousness probably reflects the very short free-swimming larval period (Percival, 1944). Even on a boulder on which the shells are abundant, they tend to occur in small, dense patches a few inches across. Within each patch most of the shells are of roughly uniform size and have probably grown from larvae of the same year-class. This patchy distribution means that a sample of the total population can only be representative if it is taken from a relatively large area of substratum. If many boulders are inspected (thus averaging out the inequalities due to the patchiness), it becomes clear that the population contains a high proportion of large and sexually mature individuals. This is discussed in the final section of this paper.

(ii) *In an intertidal rock-pool.*

On the shore of Lyttelton Harbour there is an intertidal rock-pool which contains three species of brachiopod. *Terebratella inconspicua* is the most abundant; the rhynchonelloid *Tegulorhynchia* (*Notosaria*) *nigricans* (Sowerby), though common sublittorally in up to 30 fathoms elsewhere around New Zealand (Allan, 1960, p. 253), is here at its uppermost known limit; and at present this pool is the only locality from which the small Kraussinid *Pumilus antiquatus* Atkins (1958) is known.

This pool has been described briefly by Percival (1960, pp. 439–440). It is indented in a wave-cut platform of hard volcanic rock. It is shallow, and largely filled with boulders. At low tide the water sinks to about mid-tide level; it is generally somewhat turbid, except at low tide in calm weather. The brachiopods are confined to the lower surfaces and (less commonly) the well-protected upper surfaces of the boulders, and they occur only between the level to which the water sinks at low tide and a level some ten or twelve inches lower. Percival noted that *Tegulorhynchia* is generally abundant in more sheltered positions than *Terebratella.*

It is remarkable that this rich brachiopod fauna should occur in a rock-pool situated relatively high up on the shore, where the water is isolated for about half the tidal cycle; for this must produce very large fluctuations of temperature. No full figures are available; as an example, on one sunny day in January, 1960, the temperature in the pool at low tide (around mid-day) rose to 20.1° C., while on the shore nearby it was only 15.6° C.

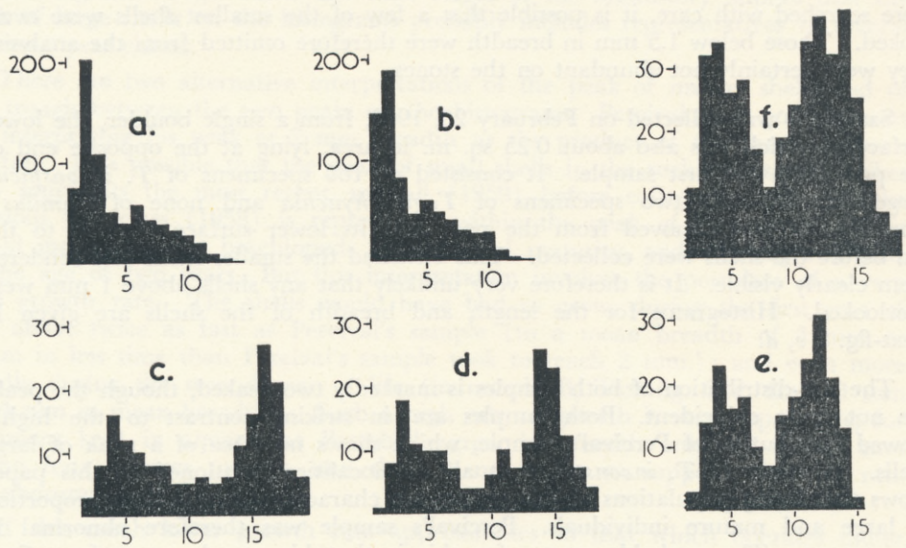
A prolonged search of the adjacent shore at and below low-tide level revealed only a very few specimens of *T. inconspicua*: this is probably due to a degree of exposure greater than in the rock-pool itself. The mode of attachment of the shells, and the general character of the associated fauna, are similar to those at the localities described above. Their distribution is equally patchy. Some boulders bear *T. inconspicua* almost to the exclusion of *N. nigricans;* on others (generally, as Percival noted, the deeper and more sheltered ones) the position is reversed; and on others the two species are intimately mixed. The abundance of *P. antiquatus* is more difficult to estimate; owing to its small size and inconspicuous colouring it is easily overlooked except on a very close inspection. Collections of all three species show a predominance of large and sexually mature individuals.

Subtidal Occurrences

Terebratella (*Magasella*) *sanguinea* (Leach) and *Neothyris lenticularis* (Deshayes) were collected by trawling in 51–54 fathoms (about 100 m), on latitude 45° 0′ off Oamaru (Text-fig. 1*a*, (3)). This assemblage is characteristic of deeper waters in the south of New Zealand (Allan, 1960, p. 253). The substratum was muddy. The temperature was not recorded, but the brachiopods were kept subsequently in aquaria at Portobello for two months in temperatures falling with fluctuations from 12.5° to 8° C., and showed no signs of ill-health during this period. Large and sexually mature specimens are predominant in the collection. The shells were attached to the tangled "horny" tubes of the chaetopterid worm *Phyllochaetopterus socialis* Claparède. Other attached organisms included anemones, ascidians and *Chlamys*. I have commented elsewhere (Rudwick, 1961) on the palaeo-ecological significance of this occurrence.

In the laboratory these brachiopods, like the other species mentioned above, proved to be tolerant of turbidity but not of sedimentation. The muddy substratum suggests that they normally live in turbid water. Their attachment to the worm-tubes probably raises them slightly above the mud, and this may enable them to overcome the hazard of sedimentation.

T. inconspicua and *T. sanguinea* were obtained by skin-diving from a subtidal locality in Fiordland (Text-fig. 1*a* (4)), on the N.E. shore of Doubtful Sound due N. of Ferguson Island. This point is about sixteen miles from the open sea. The brachiopods were attached to boulders at a depth of 12 feet below low tide level. This occurrence is of some interest, for the brachiopods were only about three feet below the level (at low tide) of a pronounced boundary between fully saline water and a surface layer of highly brackish water (cf. Batham 19—). Circumstances precluded a thorough study of the locality; it would be of interest to discover whether the brachiopods range high enough on the shores of the fiord to be subject to intermittent immersion in this brackish layer. At present there is no record of any articulate brachiopod tolerating brackish conditions.



TEXT-FIG. 2.—Histograms to show size-distributions in living populations of *Terebratella inconspicua*. (*a, b.*). Length and breadth of shells in collection of March 30, 1941 from pier at Lyttelton (re-drawn from Percival, 1944, Text-fig. 1). (*c, d.*). Length and breadth of shells in collection of February 28, 1960 (sample B) from rock-pool in Lyttelton Harbour. (*e*) Breadth of shells in collection of December 14, 1959 (sample A) from same rock-pool. (*f*) Summation of breadth-distributions of both samples from rock-pool.

Population Structure

The only published data on the rate of growth and population structure of any living articulate brachiopod are those given by Percival (1944) in the introduction to his work on the embryology of *T. inconspicua.* He collected a sample on March 30, 1941, from a pier at Lyttelton. His frequency graphs are here redrawn as histograms (Text-fig. 2 *a, b*). The sample showed a great preponderance of very small shells. Having collected it shortly before the 1941 breeding season, he interpreted these small shells as members of the 1940 class. He referred to " a second broad crest, less definite than the first ", between 3.5 mm and 7 mm length, interpreting it as the second year class; and he divided the shells of 7 mm upwards into even less clearly defined third and fourth year classes.

This work has been quoted frequently by palaeontologists (e.g., Boucot, 1953; Olson, 1957), and made to bear several far-reaching conclusions—e.g., about mortality rates and the action of natural selection in fossil brachiopods. Therefore the population structure of these living brachiopods urgently needs a thorough long-term study along the lines of Percival's pioneer work. Pending such a study, it seems worthwhile to record an analysis of a population that differs significantly from Percival's, and to discuss the possible meaning of the discrepancy.

Two samples were taken from the population of *T. inconspicua* in the rock-pool in Lyttelton harbour. Sample A was collected on December 14, 1959, from four adjacent large stones, of which the lower surfaces totalled about 0.25 sq. m. in area. This sample consisted of 215 specimens of *T. inconspicua* (together with about 150 specimens of *Tegulorhynchia nigricans* and a few *Pumilus antiquatus*). The shells were measured to the nearest 0.1 mm with vernier or eyepiece micrometer, and the measurements were grouped into 1 mm size classes. A histogram for shell-breadth is shown in Text-fig. 2e. Although the surfaces of the stones were searched with care, it is possible that a few of the smallest shells were overlooked. Those below 1.5 mm in breadth were therefore omitted from the analysis: they were certainly not abundant on the stones.

Sample B was collected on February 28, 1960, from a single boulder, the lower surface of which was also about 0.25 sq. m. in area, lying at the opposite end of the pool from the first sample. It consisted of 180 specimens of *T. inconspicua* (together with only two specimens of *Tegulorhynchia* and none of *Pumilus*). The boulder was removed from the pool and its lower surface exposed to the sun before the shells were collected. This bleached the smaller shells and rendered them clearly visible. It is therefore very unlikely that any shells above 1 mm were overlooked. Histograms for the length and breadth of the shells are given in Text-fig. 2 *c, d*.

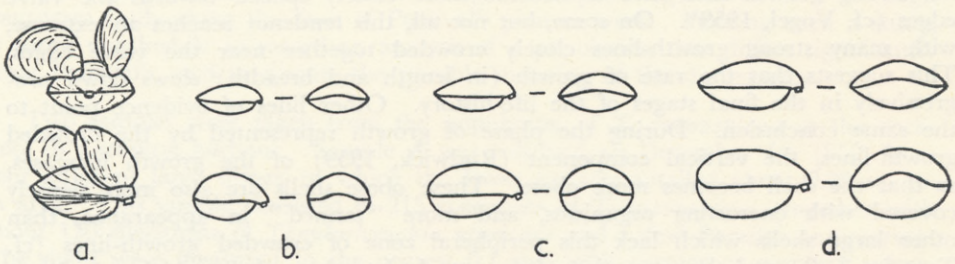
The size-distribution of both samples is markedly two-peaked, though the peaks are not quite coincident. Both samples are in striking contrast to the highly skewed distribution of Percival's sample, which shows no trace of a peak of large shells. A study of *T. inconspicua* at all the localities mentioned in this paper shows that living populations of this species are characterised by a high proportion of large and mature individuals. Percival's sample was therefore abnormal in this respect. The probable reason for this is that his sample came from four stones totalling only 0.023 sq. m. in area. Owing to the very patchy distribution of the shells, this is far too small an area to ensure a representative sample of the population. The stones were apparently occupied by a very dense patch from the most recent spatfall, but evidently did not include any patches of the large and mature specimens that form the bulk of the population. Consequently the larger sizes are seriously under-represented.

Growth-lines on the shells are of some significance in the interpretation of the histograms. Growth-lines are clearly due to temporary cessations of shell-growth (more accurately, of growth in the length and breadth of the shells), affecting both valves simultaneously. Some of them are almost certainly formed at irregular intervals, perhaps during short periods of unfavourable conditions. But on many of the shells the more conspicuous growth-lines are rather regularly spaced on the surfaces of the valves, and often coincide with narrow zones of darker pigmentation. This strongly suggests that shell-growth is halted at regular intervals, possibly seasonally though not necessarily annually. Such regular halts cannot be due to seasonal breeding activities, for the first of these regular growth-lines often occurs near the umbo of each valve and therefore dates from a period when the shell was well below the minimum size for sexual maturity. If the intervals between these growth-lines do in fact represent regular periods of time (the actual duration of the period is irrelevant here), they give some indication of changes in the rate of growth during ontogeny. On most of the larger shells the strong growth-lines tend to become more closely spaced towards the valve edges (cf. Vogel, 1959). On some, but not all, this tendency reaches an extreme, with many strong growth-lines closely crowded together near the valve edges. This suggests that the rate of growth (in length and breadth) slows down progressively in the final stages of the life-history. Other lines of evidence point to the same conclusion. During the phase of growth represented by the crowded growth-lines, the vertical component (Rudwick, 1959) of the growth increases, so that the shell becomes more obese. These obese shells are also more densely covered with encrusting organisms, and more "tanned" in appearance, than other large shells which lack this peripheral zone of crowded growth-lines (cf. Text-fig. 3 *d*); and they sometimes have attached to them shells which are almost equally large but necessarily derived from a later spatfall (Text-fig. 3 *a*). A diminishing rate of growth in the later stages of the life-history implies that the peak of large shells on the histograms probably includes representatives of several different year-classes.

There are two alternative interpretations of the peak of smaller shells and of the trough between the two peaks on the histograms. Percival gave good reasons for interpreting his peak at 2 mm breadth as the product of the previous year's spatfall. It is possible that the peak of small shells in the rock-pool samples likewise represents the most recent spatfall (1959) before collection, and that the previous year-class (1958) is represented within the peak of large shells. This would mean that the brachiopods reach sexual maturity, and virtually full size, at the age of two years. But this interpretation involves the postulate of a very high growth rate. The shells would have had to grow, during the first year of life, about twice as fast as Percival's sample (to a mean breadth of 3 mm or 4 mm in less time than Percival's sample took to reach 2 mm.); and even more rapidly during the second year of life (in sample B, Text-fig. 2 *d*, from 3 mm to 14 mm in mean breadth). Such a high rate of growth is very improbable, for specimens kept in aquaria at Portobello grew in breadth only 0.7 to 1.3 mm during four summer months, and there is no reason to suppose that this rate was abnormally slow.

If this much lower growth rate approximates to that which operates under natural conditions, an alternative interpretation of the histograms is indicated. If certain year-classes are poorly represented in a sample—for whatever reason—the histogram will tend to show troughs at those points. Thus in the samples A and B from the rock-pool the one-year-old shells (which are so abundant in Percival's sample) may be very poorly represented; and the peak at 3 mm or 4 mm breadth may be composed chiefly of two-year-old shells (1958 spatfall), perhaps with the elision of a group of slightly larger shells from the 1957 spatfall (compare especially Text-fig. 2 *a* and *c*). Similarly, the trough between the peaks may be due to under-representation of the classes of still earlier years. Poor representation of certain year-classes might be due to the patchy distribution of the shells: even an area ten times that from which Percival's sample came may still be too small to ensure an accurately representative sample of the population. Alternatively, since the troughs are almost coincident in the two samples (Text-fig. 2 *d, e, f*), there may have been a general failure in spatfall throughout the rock-pool during the years in question (I owe this suggestion to Dr K. A. Joysey).

This interpretation of the histograms implies that the brachiopods grow relatively slowly (the rate indicated would suggest that the regular growth-lines may be formed annually); that they take several years to reach maturity (perhaps 5 to 7 years if the growth-lines are indeed annual); and that some survive thereafter for several years, growing less and less in length and breadth but increasing slowly in height, and gathering an increasingly dense epifauna on the surface of the shell.



Text-fig. 3.—*Terebratella inconspicua*: shells from sample A. (*a*) Posterior and lateral views of large shell with two other shells attached. (*b, c*) Lateral and anterior views of normal immature shells (upper figures) and obese, stunted (?), mature shells of approximately same length and breadth (lower figures). (*d*) Lateral and anterior views of normal mature shell (upper figures) and obese, old-aged (?), mature shell. All figures natural size.

Sample A contains a few shells with all the characters—obesity, crowded peripheral growth-lines, tanned appearance and heavy encrustation—here interpreted as signs of considerable age, yet at an absolute size much below the normal for such shells (Text-fig. 3 *b, c*). This probably indicates phenotypic stunting (cf. Vogel, 1959). In view of the nature of the rock pool, slight differences in position of attachment may cause significant differences in the degree of wave-action, temperature fluctuation, etc., to which individual brachiopods are subjected; and those attached in the less favourable positions may grow more slowly, and reach maturity at a lesser size, than the normal. Indeed, sample A may have come from an *average* position less favourable than sample B, for its peak of large shells is at a slightly lower size (Text-fig. 2 *e, d*).

It seems both premature and hazardous to form any conclusions about the rate of mortality in *T. inconspicua*. Rowell's (1960) size-distribution graph for a collection of the inarticulate brachiopod *Crania anomala* (Müller), like Percival's graph for *T. inconspicua*, shows a high peak of very small shells; and Rowell concludes that there is a high rate of mortality in the early stages. This may be true also of *T. inconspicua*, although the samples analysed here do not give any clear evidence for it.

The lack of direct evidence on the rate of growth and mortality has necessarily limited this discussion to an interpretation which seems to satisfy the available indirect evidence. Although this interpretation must therefore be tentative, its divergence from Percival's should warn palaeontologists to await the results of a more thorough study of the growth of a brachiopod population before attaching too great significance to either.

CONCLUSIONS

These brachiopods appear to be intolerant of sedimentation and exposure to wave-action, but tolerant of turbidity and temperature fluctuation. *Terebratella inconspicua* is marginally tolerant of emersion above water level. The intertidal species are probably subject to stronger competition for settling space than for food. They show a characteristically patchy distribution, due probably to very uneven settling of larvae during successive spatfalls. Living populations contain a high proportion of large and sexually mature individuals. There is evidence that the rate of growth diminishes progressively in the later stages of the life-history. The life-span of the oldest individuals of *T. inconspicua* is probably much greater than the four years suggested by Percival.

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