ECOLOGY AND POPULATION STRUCTURE OF THE RECENT BRACHIOPOD *TEREBRATULINA* FROM SCOTLAND

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ABSTRACT. The ecology and population structure of the Recent articulate brachiopod *Terebratulina retusa* (Linnaeus) are described. The population studied occurs around the margins of a depression of more than 220 m in the Firth of Lorne, Scotland, and is predominantly attached to the horse-mussel *Modiolus modiolus* (Linnaeus). Spawning occurs regularly in late spring and late autumn, and is initiated at temperatures of 10–11 °C. The highly synchronized reproductive cycle, from spawning to spatfall, occurs within 3 weeks in nature. Length-frequency histograms prepared from large representative samples collected at regular intervals during 1977–1979 are unimodal and right-skewed due to the predominance of juveniles. Regularly spaced subsidiary peaks in the histograms correspond to biannual settlement cohorts; in later life successive peaks merge to form a single annual peak. This pattern is identical to that predicted by computer-based simulations. Recently settled specimens grow rapidly to an average length of 2·75 mm within 3 months during both spring and autumn; thereafter the animals grow (initially by 4 mm per year) throughout life, although at a progressively reducing rate from the third year of life onwards. Growth slows or ceases in winter in all but recently settled specimens. The maximum life span is 7 years. The mortality rate remains constant, although the causes of death are not apparent. The growth-lines form biannually, at times of pronounced environmental and physiological disturbance.

I T is not generally realized that the Recent brachiopod fauna of the British Isles (21 species of 17 genera, Brunton and Curry 1979) is significantly more diverse than that of New Zealand (12 species of 9 genera). Considering the relative diversity of the two faunas, it may appear strange that New Zealand has become the classic area for Recent brachiopod research. However, this apparent anomaly is readily explained since the New Zealand species are far more accessible, with 25% of the species abundant intertidally and a further 30% common in nearshore shallow subtidal habitats. By contrast, British brachiopods are very rarely found intertidally and the majority of species have only been collected in small numbers from widely dispersed and often inaccessible localities.

Intermittent research during the last 100 years has demonstrated that several of the British species are locally abundant, especially off the west coast of Scotland and in the Western Approaches (Atkins 1959a, b, 1960a, b, c, 1961; Davidson 1886–1888; Chumley 1918; see summary maps in Brunton and Curry 1979), although dredging is the only practicable method of sampling these predominantly deeper-water populations. The recent upsurge of interest in palaeoecology has emphasized the need for precise data on the life-habits and ecology of Recent representatives of fossil phyla, and more data are needed to augment the patchy and often contradictory information available to the brachiopod palaeoecologist. The present study was initiated in the light of such inadequacies, and when it became clear that the comprehensive dredging facilities available at Dunstaffnage Marine Research Laboratory, nr. Oban, Scotland, could ensure access to the abundant brachiopod populations off the west coast of Scotland.

Although dealing entirely with living animals, this study was conducted from a palaeontological viewpoint. As such, the main interest was the interpretation of features on the shell, in particular the analysis of population structure and dynamics based on size-frequency histograms prepared from large samples of brachiopods collected at regular intervals throughout 1977–1979. The main advantage of working with living, as opposed to fossil, populations is that it is possible to seek

confirmatory evidence for conclusions reached by direct observations on the living population. This paper first describes aspects of the biology and ecology of the animal, and goes on to apply the results to the interpretation of size-frequency histograms.

MATERIAL

The species under investigation was *Terebratulina retusa* (Linnaeus), which is the most abundant of the Recent British brachiopods. Initially the intention was to collect regular bulk samples from the large populations of *T. retusa* which were known to occur in the Sound of Mull (text-fig. 1). However, during an exploratory cruise in March 1977 an extremely abundant population, ideally situated for regular sampling, was discovered near a depression in the nearby Firth of Lorne (text-fig. 1). This depression, which reaches a maximum depth in excess of 220 m, is mid-way between the Island of Kerrera and the south-west coast of the Island of Mull (Grid. ref. NM 745 265; Stn. 1 in text-fig. 1), and is thought to lie along the Firth of Lorne Fault (a subsidiary splay of the Great Glen Fault, Barber *et al.* 1979). At this locality the brachiopods are predominantly attached to the horse-mussel *Modiolus modiolus* (Linnaeus) which occurs in dense beds around the smoothly sloping margins of the depression.

The samples were collected, by the R/V *Calanus* or *Seol Mara*, using a conventional 'clam-dredge' (1·2 m wide × 2 m long), the body of which consists of an outer framework of interlocking iron chain and an inner nylon meshwork with a maximum aperture of 15 mm. This dredge is designed to collect material resting on, or partially buried within, the substrate, and proved to be extremely efficient at sampling the Firth of Lorne mussel beds. For each sample the dredge was trawled slowly along the substrate for approximately 5–10 minutes, in a
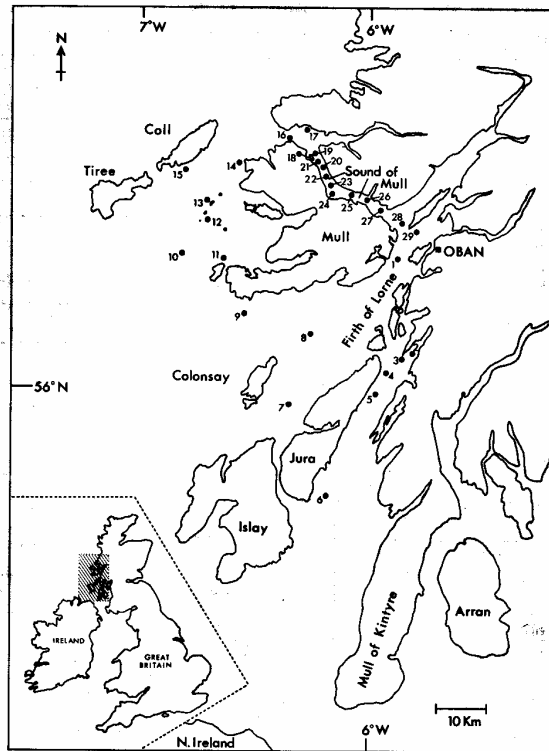
TEXT-FIGURE 1. Map showing locations of R/V *Calanus* sample stations off the west coast of Scotland; station numbers refer to Table 1 (see opposite).

north-easterly or south-westerly direction. Once landed on deck, the sample was washed with sea-water to remove any adherent sediment, and then placed in plastic baths supplied with flowing fresh sea-water.

The disturbance caused by the dredging was minimal, and the majority of the sample had become 'acclimatized' to the plastic baths and commenced feeding within half an hour of arriving on deck. Mechanical damage during dredging was not significant, and only seven specimens out of the 818 brachiopods collected in March 1977 (i.e. 0·85%) proved unmeasurable because of shell damage. Due to the efficiency of the 'clam-dredge', and the density and abundance of both mussels and brachiopods, all attempts to sample the Firth of Lorne populations were successful. In addition, the Firth of Lorne depression is a prominent submarine feature, easily recognizable using the ship's depth-sounding equipment, and it was therefore possible to ensure that all samples were collected from the same population.

TABLE 1. Results of the dredging operations of the R/V *Calanus*, west coast of Scotland, 1977-1979 (a = abundant, c = common, r = rare, x = absent).

STATION No.	LOCATION.	DEPTH.	SEDIMENT.	T. retusa abund.	T. retusa attachment.	C. anomala abund.	C. anomala attachment.	ASSOCIATED FAUNA.
1	Firth of Lorne	146-183m.	fine mud	a	Modiolus	a	Modiolus	see text.
2	Rabbit Island	13m.	--	c	rocks	r	rocks	Pecten
3	Garbh Reisa	20m.	--	X	--	X	--	Pecten
4	Sound of Jura (north-east)	73-128m.	--	X	--	X	--	Modiolus and hydrozoans
5	Sound of Jura	110m.	--	r	vesicular basalt	X	--	large no. of dis-articulated Modiolus
6	Sound of Jura (south)	37m.	--	X	--	X	--	Pecten, Balanus.
7	E. of Colonsay	37m.	sand	X	--	X	--	seaweed, crabs.
8	North-east of Colonsay	55m.	--	c	rocks and clinker	c	rocks and clinker	--
9	Torran Rocks	91-110m.	--	X	--	X	--	--
10	North-west of Iona	73-110m	--	r	rocks	X	--	--
11	North of Iona	73-128m.	sand	X	--	X	--	--
12	Treshnish Is.	29-55m.	--	X	--	X	--	Balanus, serpulids on rocks
13	Lunga	37m.	--	X	--	X	--	Balanus on rocks
14	North-west of Mull	37-46m.	--	X	--	X	--	Pecten, echinoids
15	East of Coll	146-183m.	--	X	--	c	rocks	--
16	Ardmore Point, Mull	73-213m.	mud	X	--	X	--	--
17	Mingary Bay, Ardnamurchan	37m.	mud	X	--	c	rocks	--
18	Tobermory Bay, Mull	73m.	mud	c	clinker	a	clinker and rocks	Modiolus
19	Sound of Mull (north)	110m.	mud	c	rocks	a	rocks	--
20	Sound of Mull (north)	91m.	mud	a	modiolus	c	Modiolus	--
21	Sound of Mull (north)	91m.	mud	X	--	c	rocks	--
22	Sound of Mull (north)	91m.	mud	a	Modiolus	a	Modiolus	--
23	Sound of Mull (north)	91-146m.	mud	r	Modiolus	r	Modiolus	--
24	Sound of Mull (north)	18- 37m.	--	c	shell fragments	X	--	--
25	Sound of Mull (south)	110-128m.	mud	a	Modiolus	a	Modiolus	--
26	Sound of Mull (south)	128-146m.	mud	c	clinker	r	clinker	--
27	Sound of Mull (south)	18-37m.	mud	c	clinker	r	clinker	--
28	Lismore Island	37m.	--	r	vesicular basalt	r	vesicular basalt	--
29	Lismore Island	15-26m.	--	r	rocks	X	--	--

The samples were transported back to the laboratory and placed in an outside aquarium through which fresh sea-water was continually being circulated. Because of the difficulty in seeing very small brachiopods (recently settled post-larvae are less than 0·5 mm in length and their shells are transparent), the surfaces of all mussels and other potential brachiopod substrates were examined using a binocular microscope. Once detected, each brachiopod was removed from its substrate by severing its pedicle with a sharp scalpel, measured to the nearest 0·1 mm using 'MITUTOYO' dial calipers, and then preserved in either 10% formalin or 70% alcohol. The samples have been deposited in the Department of Palaeontology, British Museum (Natural History), London, and the registration numbers quoted in the text (with the prefix ZB) refer to the Recent brachiopod collections in that museum.

ECOLOGY OF *TEREBRATULINA RETUSA*

Distribution. The precise geographic limits of the distribution of *T. retusa* are unknown, as there are two morphologically similar and often confused species of *Terebratulina* in the North Atlantic. Positively identified *T. retusa* have been collected from as far north as Norway (the type area) and as far south as Spain and the Mediterranean. The species would appear to be confined to the north-eastern North Atlantic, although it has been recorded from the east coast of Greenland (Wesenberg-Lund 1940). The possibility that the two named species are members of a *Terebratulina* cline has been considered by several authors (e.g. Wesenberg-Lund 1941), and certainly the presence of individuals with intermediate morphological characteristics in the mid North Atlantic could explain the confusion over the geographic distribution of the two species, which are quite distinct.

T. retusa is relatively common off the west coast of Scotland, and has been recorded from many of the sea-lochs (Davidson 1886–1888; Chumley 1918). On a more local scale the comprehensive dredging equipment available on the R/V *Calanus* provided an opportunity to investigate the pattern of distribution of *T. retusa* around the Islands of Mull and Jura (text-fig. 1). The results of these dredging operations provide strong evidence of an essentially patchy distribution, which is illustrated by the results of a comprehensive sampling programme in the Sound of Mull (Stns. 18–27 in text-fig. 1 and Table 1). In most of these samples the horse-mussel *M. modiolus* formed the bulk of the sample, whilst *T. retusa* varied from being the numerically dominant constituent (e.g. Stn. 22), to being a minor constituent (e.g. Stn. 23), or being totally absent (e.g. Stn. 21). Suitable substrate for brachiopod attachment was present at the latter station, and the fact that the habitat occupied by *T. retusa* is not occupied by other sessile epibenthos suggests that competition for space is not an important factor in these deeper water localities. It is likely, therefore, that the patchy distribution is an inherent feature of the *T. retusa* population, reflecting the short duration, and hence limited dispersal range, of the pelagic larval stage (see below). Many other Recent brachiopod populations appear to be patchily distributed (Rudwick 1970, p. 156).

It is appropriate to sound a cautionary note on the use of benthic dredging to determine the distribution pattern of sessile epibenthos such as *T. retusa*. Benthic dredges will only collect free-lying or loosely attached material which falls within a restricted size range, and it is clear that the substrates used by brachiopods are very variable both in grain-size and in the extent to which they are anchored to the sea bed. Therefore the absence of brachiopods in a particular sample may simply be due to the inability of the dredge to sample substrates such as large boulders or rock-faces. This feature was evident during the present study, as dredged samples from the Sound of Jura yielded no brachiopods (Stn. 4), and yet divers have reported quantities of *T. retusa* attached to large boulders in this region (R. Harvey, pers. comm. 1978). Benthic dredging is only a satisfactory method of sampling populations in which the predominant substrate is of a size and nature that can readily be collected, as is the case with the mussel beds in the Firth of Lorne.

Depth. Within the study area the most abundant populations of *T. retusa* occur at depths of 100–200 m, although a few specimens have been collected from an estimated depth of 3 m in the Sound of Raasay (M. K. Howarth, pers. comm. 1978), and a reasonably abundant population is known to occur at a depth of 13–20 m off the coast of Rabbit Island (Stn. 2 in text-fig. 1 and Table 1). Despite these occurrences, *T. retusa* is not a common constituent of the shallow subtidal ecosystem along the Scottish west coast, and there is no record of any dead shells being washed up on beaches in this

region. The known depth range of *T. retusa* is from 3–1478 m, although it is most commonly found between 100 and 500 m. Environmental conditions vary considerably with depth, and it is the tolerance of an organism to such variations which determines its depth range; depth in itself is not considered to be a controlling factor (Moore 1958). Presumably, therefore, *T. retusa* is prevented from colonizing intertidal or shallow tidal habitats by the combined effects of biological and physio-chemical factors characteristic of such habitats, such as competition with other organisms, rapid daily temperature fluctuations, the possibility of increased predation intensity, periodic desiccation, salinity fluctuations, wave turbulence, and intensity of incident light. Competition for space is certainly an inhibiting factor, as was illustrated during the present study when brachiopods collected from the Sound of Mull were reintroduced into the shallow marine environment of Dunstaffnage Bay in recoverable cages. These brachiopods were killed by a dense settlement of fast-growing barnacles which engulfed and smothered them within 3 months. Prolific swarms of barnacles are common in shallow-water habitats along the Scottish coast, but in the deep-water localities where *T. retusa* is abundant they are rare and solitary (in fact a different species). Clearly the relatively slow-growing *T. retusa* is at a considerable disadvantage in areas where suitable substrates are in short supply.

Temperature. Temperature is one of the most important environmental parameters for cold-blooded marine invertebrates (Moore 1958), limiting their geographic range, and affecting all aspects of life by virtue of its controlling effect on the rates of metabolic processes (i.e. Van't Hoff's Law—see Prosser 1973). The general pattern of temperature fluctuation experienced by *T. retusa* in the Firth of Lorne depression was determined (sea-water samples were collected from the vicinity of the brachiopod population using insulated sampling bottles), and has been compared with surface water temperatures in text-fig. 2. The temperature of bottom waters in the Firth of Lorne range from a February minimum of 6·5 °C to a maximum of 13 °C in August, an annual range of 6·5 °C which is smaller than would be expected at this latitude because of the warming effect of the North Atlantic Drift Current. The over-all pattern and range is similar in surface waters, (minimum in January of 6 °C and a maximum of 14 °C in August—annual range of 8 °C), although it is apparent from text-fig. 2 that the bottom and surface waters are virtually never isothermal and can differ by as much as 2·5 °C. This vertical stratification of the water column, the thermocline, is a common feature of Scottish sea-lochs and, although complex, can be considered as reflecting the greater susceptibility of
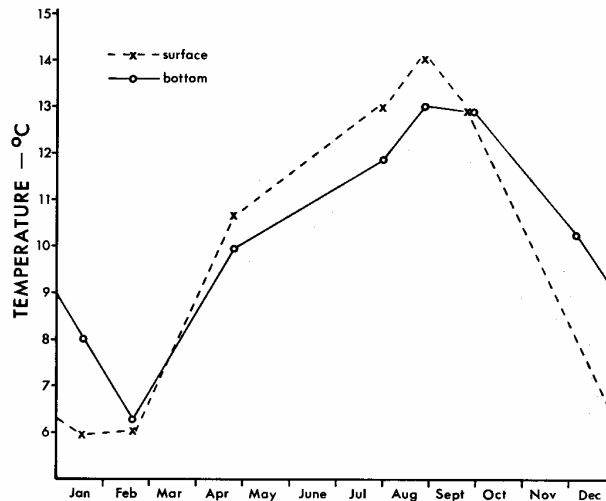
TEXT-FIGURE 2. Annual temperature curves for the surface and bottom (approx. 150 m) waters in the Firth of Lorne, Scotland.

surface waters to prevailing air temperatures (e.g. being warmer in summer and cooler in winter). Other factors which enhance this vertical stratification are density and salinity gradients produced by the high levels of surface run-off of fresh water from the surrounding land. The thermocline breaks down during two short periods in spring and autumn when the water column becomes thoroughly mixed, isothermal, and uniformly saturated with oxygen (i.e. the points at which the curves in text-fig. 2 cross).

Substrate. The predominant utilization of *M. modiolus* as substrate by the brachiopods in the Firth of Lorne depression is well illustrated by the analysis of the substrate of attachment of the 786 specimens of *T. retusa* collected on 5 May 1977 (Table 2). The sample contained 204 living mussels, 166 of which

Substrate	No. of Occurrences	No. of Brachiopods	°/₀ of Total
Living mussel	166	591	75
Dead mussel	27	53	7
Mussel frags.	33	63	9
Hydrozoan	10	13	2
Dead gastropod	5	14	2
Dead brachiopod	4	10	1
Living & dead bivalve	4	8	1
Sponge/ascidian	4	16	2
Unattached	4	8	1
Rock	2	9	1
Tube-worm	1	1	0.1

TABLE 2. Substrate of attachment of the 786 specimens of *T. retusa* collected on 5 May 1977 from the Firth of Lorne.

(i.e. 81%) had been utilized as substrate by *T. retusa*. A total of 707 brachiopods (91% of the sample) were attached to living or dead mussels or to fragments of mussel shell. Mussels are ideal substrate for brachiopods, being sessile and of much longer life span (at least 20 years (Comley 1978) as compared with a maximum of 7 years for *T. retusa*). The relatively large surface area of the mussels is readily bored by the anchoring pedicle rootlets of *T. retusa*, and is free of obstructions which would hinder the rotation of brachiopods around their pedicles, a procedure which enables them to move away from localized disturbances and to take up preferred feeding orientations. In addition, the majority of brachiopods are attached anteriorly, close to the inhalant and exhalant feeding currents of the mussels, and are likely to benefit from the enhanced flow of nutrient-rich sea-water in such regions. The selective sampling bias of the benthic dredge makes it impossible to determine to what extent the data in Table 2 can be considered representative. However, the thin covering of fine-grained glauconitic mud in this area is likely to preclude dense settlements directly on to rock surfaces, because of the high risk of being smothered or choked by suspensions of sediment stirred up by bottom currents. Under such circumstances the elevated position resulting from attachment to mussels would be all the more advantageous for brachiopods, especially as the mussels' ability for limited reorientation will ensure that their anterior region remains above the substrate in the event of sediment accumulations. Nevertheless, direct attachment to substrates such as boulders or rock-faces is to be expected in the Firth of Lorne depression when suitable surfaces are free of sediment due to inclination or current scour.

Current. Little can be said about the currents in the vicinity of the Firth of Lorne population, as direct measurements of velocity was beyond the scope of this study. However, indirect evidence of strong bottom currents comes from the fact that the great majority of dead shells are moved away from the living population and have presumably accumulated in the deepest regions of the depression. This phenomenon is being investigated with the aim of assessing the fossilization potential of the Firth of Lorne brachiopod population. A strong and constantly flowing current is a necessity for sessile benthic invertebrates such as *T. retusa*, which feeds on material carried in suspension in the surrounding sea-water.

Associated fauna. Apart from *T. retusa* the surfaces of the Firth of Lorne mussels are used as substrate by a wide variety of sessile organisms and plants, the most numerous of which being the cemented inarticulate brachiopod *Crania anomala* (Müller), hydroids, sponges, chitons, spirorbid worms, foraminifera, the bivalve *Anomia*, and gastropods (e.g. *Cappula*). The dredged samples also contained abundant ophiuroids (*Ophiothrix* and *Ophiura*), and asteroids (*Crossaster*, *Solaster*, and *Asterias*) are often present but in much smaller numbers. Occasionally echinoids (*Echinus*) and decapods (*Munida* and *Galathea*) have been recovered. As compared with shallow-water localities in the Firth of Lorne, this fauna is impoverished, especially in sessile epibenthic organisms which would be in direct competition with *T. retusa* for space and nutrients. Burrowing animals, such as bivalves and polychaetes, are rare, presumably because of the thin sediment cover. The external shell surfaces of *T. retusa* are themselves used as substrate by a wide variety of animals and plants, in particular sponges, hydroids, bryozoans, and spirorbid worms. Shallow borings, almost entirely confined to the primary shell layer of *T. retusa*, are thought to be the work of phoronids and fungi (B. Akpan, pers. comm. 1980). These borings are not predatory, and none of the major predators in this fauna appears to feed on *T. retusa*, although it is impossible to assess the effect of all potential predators (e.g. fish). Some small worms have been found in the brachial cavity of a few specimens of *T. retusa*, but it is not clear if these are parasitic or have merely been drawn in by the feeding currents.

REPRODUCTION

It was of great importance to accurately determine the timing and frequency of spawning in *T. retusa*, as such information is necessary to establish the population structure and dynamics. In *T. retusa* the sexes are separate and can be distinguished on the basis of colour (males are whitish, whilst the tissues of females are orange-red), and by the examination of the gonads. Males and females are approximately equally represented (342 adult specimens could be sexed in the sample collected on 26 October 1977, 181 of which were male, and 161 female). One pair of gonads is present in each valve, developing within the mantle canals between the inner and outer mantle epithelium and extending posteriorly into the body cavity. Individual gametes develop along narrow interconnecting genital canals, which are anchored to the outer epithelium by linear membranes (Hancock 1859). Columns of tissue, situated in the interstices between the genital canals, prevent the gonads from being damaged or crushed between the two layers of tissue. It seems likely that the gonadal pits which have been recognized on the internal surfaces of some fossil brachiopods represent the points of attachment of the supportive columns rather than, as Rudwick (1970) suggests, the points at which the gonad itself was attached. Rigid calcareous spicules are present in many regions of the body tissues of *T. retusa*, but are particularly densely developed above the gonads thereby providing further protection.

The periodicity of larval recruitment was determined by monitoring the state of development of gonadal tissues throughout the year (by comparing at least twenty adult specimens from each sample), and by microscopically examining the surfaces of all potential brachiopod substrate for recently settled post-larvae. It became clear that the gonads of *T. retusa* pass through two full development cycles per year, culminating in the release of gametes in late spring and late autumn. Recently settled post-larvae have only been observed at these times, and the spawning event must be highly synchronized, of short duration, and affecting the vast majority of sexually mature individuals. For example, the entire reproductive cycle, from spawning through to spatfall, was completed within the 3-week period between samples collected in early and late May 1977. The precise timing of the natural spawning event must be related to temperature, as *T. retusa* spawns at a temperature of 10–11 °C in both autumn and spring. A similar temperature control on the timing of spawning activity has been recognized in both articulate (Rickwood 1968) and inarticulate brachiopods (Paine 1963; Yatsu 1902).

To investigate the spawning behaviour in greater detail, ripe individuals collected immediately prior to one of the autumn spawning periods were induced to spawn in the laboratory by rapid controlled fluctuations of temperature and the addition of mobile mature sperm teased from males.

Temperature variation is a common method of inducing spawning.in marine invertebrates (P. Redfern, pers. comm. 1978) because the resulting stress stimulates the release of gametes. This method had previously been used by the author and Dr. J. Richardson in a successful attempt to induce spawning in the Recent New Zealand brachiopod *Terebratella inconspicua* (Sowerby). It seems that synchronization of spawning in neighbouring specimens depends upon the presence of male sperm, or perhaps hormones secreted along with it, in the surrounding sea-water; it was noticeable, both with *T. inconspicua* and *Terebratulina retusa*, that spawning commenced shortly after suspensions of sperm had been drawn into the brachial cavity by feeding current. Once spawning is initiated the ova and sperm are moved from the gonads to the brachial cavity via the metanephridia, and then extruded from the valves by a series of snapping movements similar to those used during the ejection of faecal or pseudofaecal pellets (Rudwick 1970).

Fertilization occurs both in the brachial cavity of females and on the surrounding substrate, and a high degree of synchronization is obviously vital as the sperm remain in suspension and is rapidly carried away from the breeding population by bottom currents. The ova, by contrast, settle in dense clusters around the margin of the parent. Only a small proportion of ova ejected during the laboratory experiment were fertilized, although in nature the proportion may be greater. Both fertilized and non-fertilized ova appeared to be particularly susceptible to bacteriological attack, although once again this may have been due to atypical laboratory conditions, in particular unavoidable increases in sea-water temperature due to the heat from the microscope lamps. The free-swimming larvae which developed from ova fertilized in the laboratory appeared to be very similar in size, shape, and activity to those of *T. septentrionalis* (Couthony) from the coast of Maine (Morse 1873) although no attempt was made to study them in detail. The laboratory-reared larvae of *T. retusa* had reached an advanced stage of development (with a third peduncular segment indicating settlement was imminent) within 5 days of spawning, which is in keeping with the observed maximum duration of 3 weeks in nature.

During one of the natural spawning periods, attempts were made to collect pelagic larvae from the Firth of Lorne using a plankton net trawled at the surface and at an estimated depth of 100 m. No brachiopod larvae were recovered, indicating perhaps that the larvae remain close to the sea-floor during their pelagic stage. However, the evidence for this is not conclusive, especially as the pelagic stage appears to be of at most a few days' or perhaps hours' (see below) duration, and it was impossible to conduct a comprehensive plankton study for the expected duration of the spawning period. Some pelagic larvae are known to actively swim towards light sources during their early development stages (e.g. Paine 1963), and certainly the larvae of the abyssal inarticulate *Pelagodiscus atlanticus* (King) has been recovered at the surface (Ashworth 1915). An alternative explanation for the lack of brachiopod larvae in the plankton samples is that the larvae are brooded to an advanced stage of development within the brachial cavity of adult females, thereby further curtailing the duration of the free-swimming stage. Such a phenomenon has been observed in *T. septentrionalis* from the Bay of Fundy, Canada (Webb *et al.* 1976), and is of particular significance as no special brood pouches are developed. Instead the brooded larvae are simply held between the filaments of the lophophore and the body wall. In the Firth of Lorne the disturbance caused by the dredging process would almost certainly cause the release of any brooded larvae within *T. retusa* and hence it will be difficult to determine if such a phenomenon is widespread. However, the space available for brooded larvae within the brachial cavity of *T. retusa*, assuming a mechanism similar to that of *T. septentrionalis*, would be insufficient to hold all ova shed by one individual during a spawning period, and therefore a proportion must still be extruded from the brachial cavity.

The density of larval settlement on the Firth of Lorne mussel beds following each spawning event is remarkable. The number and size of brachiopods attached to each mussel collected on 24 May 1977 was recorded, and the percentage of mussels with attached brachiopods from each year-class was plotted (text-fig. 3). Representatives of the '0' year-class (which in this sample had settled within the 3 weeks prior to collection) and the 1st year-class (the two 1976 cohorts) were both present on more than 50% of the mussels in the sample, which represents a considerably greater proportion of the available substrate, as the mussels live in dense clusters with the lowermost specimens being less
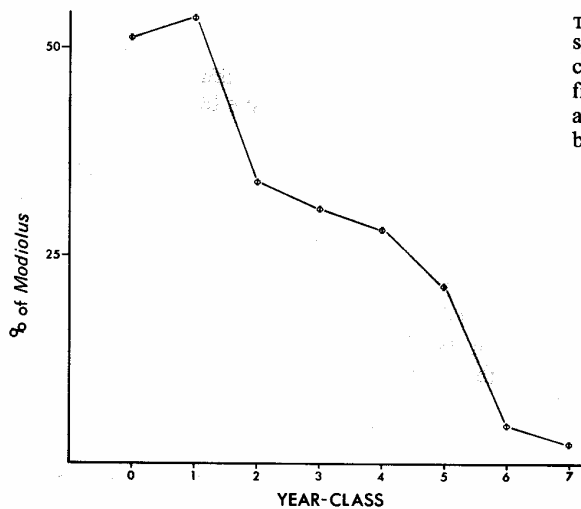
TEXT-FIGURE 3. Percentage of the total number of specimens of *Modiolus modiolus* (Linnaeus) collected on 24 May 1977 which had brachiopods from each of the seven year classes of brachipods attached. The sample yielded 127 mussels and 554 brachiopods; a total of 21 mussels (= 16·5%) had no attached brachiopods.

accessible for brachiopod larvae. The fact that fewer mussels had '0' year-class than 1st year-class brachiopods attached is probably due to the difficulty in picking out the former, and the trend of the graph would suggest that more than 50% of the mussels are covered at a spawning event. As many as thirty brachiopods of different ages have been found on a single mussel, and on average each mussel in a sample has 3–4 brachiopods attached. The density of settlement provides further indirect evidence of a short pelagic larval stage, as the degree of dispersion increases with the length of the free-swimming stage. Both autumn and spring spawnings appeared to be equally successful, although there was no practicable method of comparing the numbers of larvae produced.

POPULATION STRUCTURE AND DYNAMICS

Problems such as biased sampling, selective preservation, and *post-mortem* transportation have bedevilled attempts to interpret fossil population structure and dynamics by means of size-frequency distributions. Size-frequency distribution does, however, have considerable potential as an analytical tool in palaeontology, provided the fundamental problem of obtaining a representative sample can be overcome. The simplest and most effective method of checking for 'representativeness' is to collect a series of large samples from the population in question and to compare the resulting size-frequency distributions. Providing adequate care has been taken to eradicate recurring sampling inadequacies, similar results from a series of samples can be considered as good evidence that such results are an accurate reflection of the situation in the parent population. The ability to rationalize the recurring pattern of size-frequency distribution within the limits of theoretical population biology can be regarded as a further useful check on the validity of such results. In this study both approaches provided strong evidence that the regular samples from the Firth of Lorne population were representative, and certainly the favourable situation of the *T. retusa* population makes sampling bias unlikely, and obviously the distortion resulting from preservational bias is not pertinent to studies of living animals. The number of specimens in a sample is certainly a critical factor, however, and the necessity of having a large sample has been stressed by several authors (see Hallam, in discussion at end of Craig and Oertel 1966). The density and abundance of brachiopods at the Firth of Lorne locality, combined with their favourable situation for sampling, facilitated the collection of acceptably large samples.

Further problems have arisen because of confusion over the descriptive terminology applied to size-frequency diagrams, which warrants mention for the sake of clarity. In conventional statistical

usage the term 'skewed' refers to the gradually sloping 'tail' of an assymetrical distribution (Simpson *et al.* 1960), and therefore a unimodal skewed distribution which slopes away gradually on the right-hand side (e.g. text-figs. 4, 6) would be described as right-skewed, or positively skewed. A left-skewed, or negatively skewed, distribution slopes gradually from the left-hand side to a prominent mode on the right-hand side of the diagram. This convention has been reversed by some authors, who relate 'skewed' to the mode rather than the 'tail' (e.g. Raup and Stanley 1978; Thayer 1978). Throughout this study the more conventional usage has been adopted.

The over-all shape of a size-frequency distribution reflects the relative proportion of animals of different age-groups, and is an important diagnostic feature. All samples analysed during this study yielded a unimodal right-skewed length-frequency histogram (e.g. text-fig. 4) with sexually immature juveniles forming considerably more than 50% of the sample at all seasons. For example, 71% of the 811 specimens collected in March 1977 were less than 9·6 mm in length (i.e. not more than 2 years old—see below). This predominance of juveniles is not unexpected, as the long-term success of any brachiopod population depends upon the regular influx of large numbers of larvae. The population structure of *T. septentrionalis* from the Bay of Fundy, Canada, is also unimodal and right-skewed at all seasons (Noble *et al.* 1976), although, just as in *T. retusa*, the position of the main mode varied slightly depending on the average size of the most recently settled cohort.

Significantly there is no over-all bimodality discernible in any of the length-frequency histograms of *T. retusa*. A bimodal size-frequency distribution is characteristic of some living brachiopod populations (e.g. Rudwick 1962; Doherty 1976, 1979), and it is now generally accepted that the secondary (right-hand) mode forms as a result of the merging of older age-groups because of the gerontic slowing or cessation of growth. Such a growth strategy (known as determinate growth (Doherty 1976) because adults continue to survive without growing after attaining their maximum, or determinate, size) is very different to that of *T. retusa*, which continues to grow throughout life.

When examined in greater detail, it is apparent that the length-frequency histograms of *T. retusa* are characterized by regularly spaced subsidiary peaks (e.g. text-fig. 4). Once the biannual spawning season and its timing had been determined by direct observation, it was then possible to interpret these peaks in terms of settlement cohorts. The underlying principle on which this analysis is based is that each of the peaks represents a cohort of brachiopods which settled on the mussel beds after one
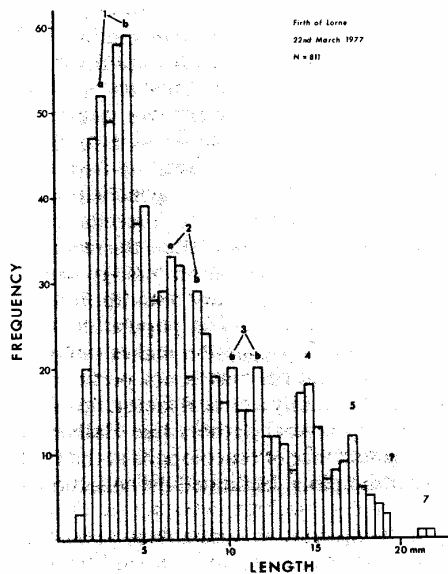

TABLE 3. Analysis of the March 1977 length-frequency histogram (Fig. 4). All measurements are in mm.

| Annual Increment	Peak	Biannual Increment	Date of Settlement	Year-Class
	2.75	1.5	Autumn 1976	1a
4	4.25		Spring 1976	1b
4	6.75	1.5	Autumn 1975	2a
3.5	8.25		Spring 1975	2b
3.5	10.25	1.5	Autumn 1974	3a
	11.75		Spring 1974	3b
3	14.75		1973	4
2.5	17.25		1972	5
2.5	19.75		1971	6
1.75	21.50		1970	7

TEXT-FIGURE 4. Length-frequency histogram of *T. retusa*, March 1977 sample (ZB3727–ZB3736). 1*a*, *b*, etc., refer to settlement cohorts (see text).
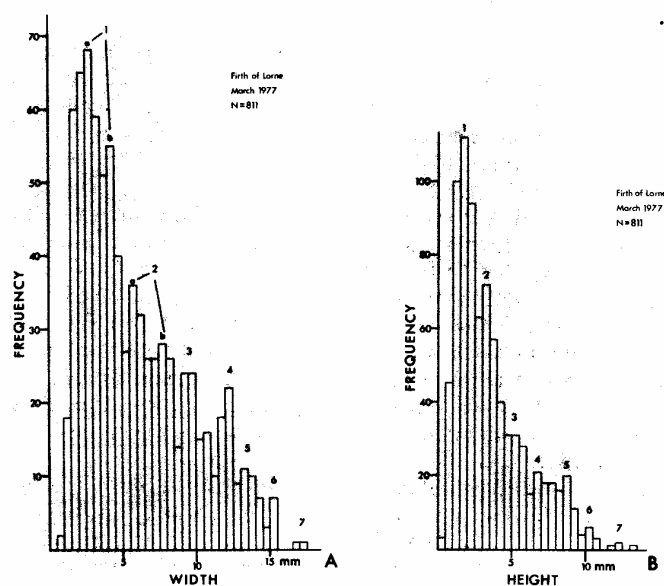
TEXT-FIGURE 5. Width-frequency (A) and height-frequency (B) histogram of *T. retusa*, March 1977 sample (ZB3727–ZB3736). 1*a*, *b*, etc., refer to settlement cohorts (see text).

of the biannual reproductive events. Such a technique has been widely used, and is a logical assumption provided that the animals have a sharply defined breeding season, and that the average growth-rate of individual cohorts is such that successive peaks do not merge (at least in the early stages of life). The majority of these subsidiary peaks can be recognized in all histograms, but the March 1977 length-frequency histogram (text-fig. 4) has been selected as a standard and will be analysed in detail. It can be demonstrated that the width-frequency histogram (text-fig. 5A), and to a lesser extent the height-frequency histogram (text-fig. 5B), yield essentially the same results as the length-frequency histogram, but in *T. retusa* the maximum incremental increase in shell dimensions occurs anteriorly (i.e. in length) throughout ontogeny, and hence the measured shell width and height dimensions are of smaller absolute value with the result that the resolution between peaks in the frequency distribution is reduced. An alternative method of analysing length-frequency data, in which the data is plotted on probability paper, is described in the Appendix.

The March 1977 sample was collected approximately 2 months prior to the spring 1977 spawning period, and therefore the first two peaks on the left-hand side of text-fig. 4 (at 2·75 mm and 4·25 mm) correspond to the autumn and spring cohorts in 1976, and are therefore labelled 1(*a*) and 1(*b*) respectively in text-fig. 4 and Table 3. Similarly the paired peaks at 6·75 mm (2*a*) and 8·25 mm (2*b*) represent the two cohorts which settled in autumn and spring 1975 respectively; the autumn and spring cohorts in 1974 are likewise clearly represented by twin peaks at 10·25 mm (3*a*) and 11·75 mm (3*b*). Each of these pairs of peaks have identical spacing (i.e. 1·5 mm—'Biannual' Increment in Table 3), and the interval between cohorts which settled 1 year apart remains remarkably constant (i.e. approx. 4 mm—Annual Increment in Table 3). Clearly the rate of growth of *T. retusa* remains constant throughout the first 3 years of life, at least within the limits of resolution of this method of mensuration. Another striking feature of this analysis is that each of the biannual spawning periods in the previous 3 years has been highly successful, indicating that this relatively deep-water population is not subject to environmental disturbances known to cause aperiodic disruption to the
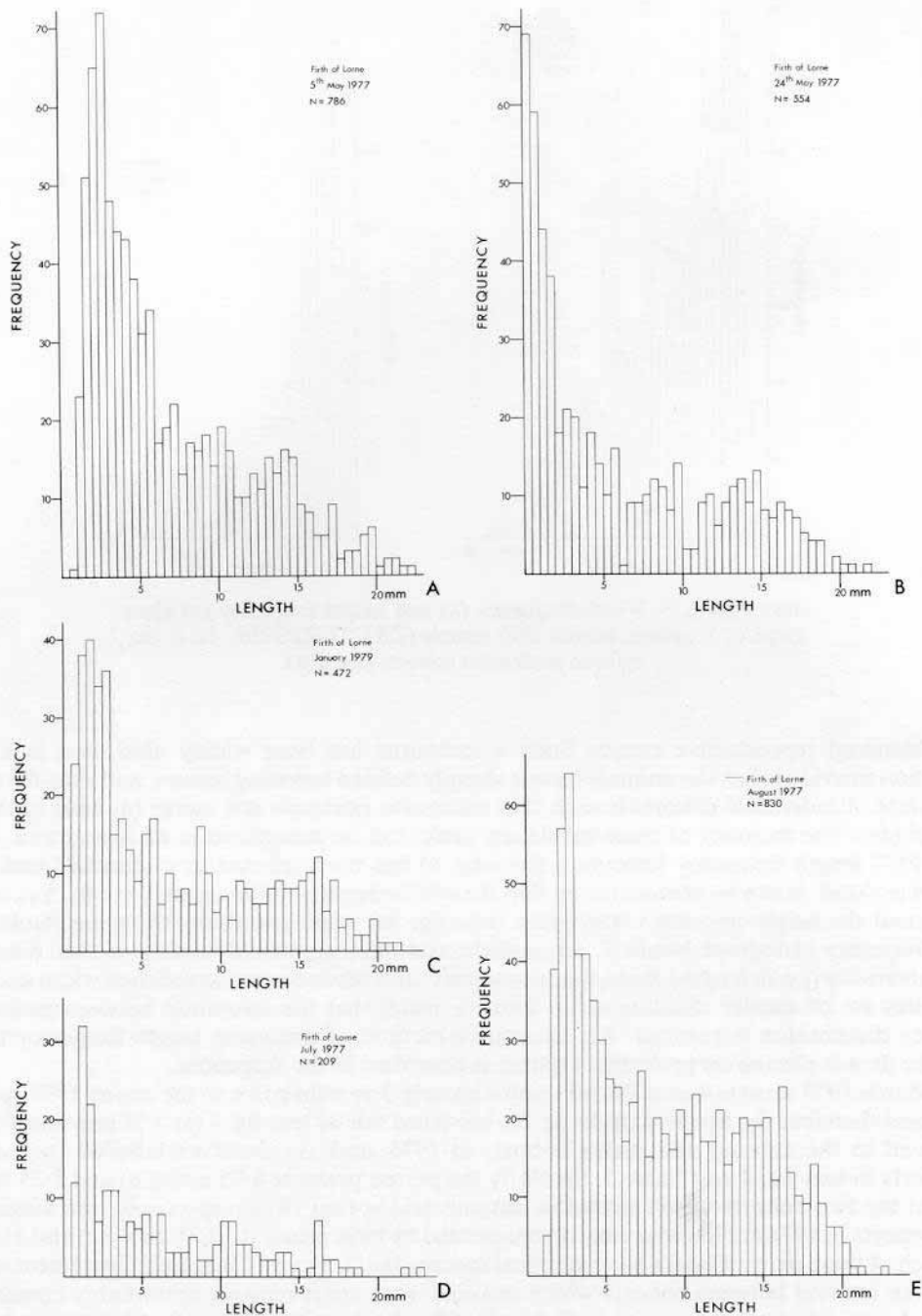
TEXT-FIGURE 6. Length-frequency histograms of *T. retusa* A, 5 May 1977 sample (ZB3737–ZB3746). B, 24 May 1977 sample (ZB3747–ZB3756). C, January 1979 sample (ZB3717–ZB3726). D, July 1977 sample (ZB3757–ZB3766). E, August 1977 sample (ZB3767–ZB3776).

reproductive cycle of shallow-water marine invertebrates. As mentioned above, the spawning events observed subsequently during 1977-1979 appeared to be equally successful.

The position and spacing of the remaining peaks in text-fig. 4, indicates that the growth-rate progressively decreases from the third year of life onwards, resulting in the merging of the paired peaks to form a single broad peak representing the biannual cohorts in 1973 (14·73 mm—labelled 4 in text-fig. 4 and Table 3) and in 1972 (17·25 mm—labelled 5). There is no peak corresponding to the 1971 cohorts in text-fig. 4, but such a peak is present at 19·75 mm in the 5 May 1977 sample (text-fig. 6A) and such a value is included in Table 3 for the sake of completeness (as described below there is very little movement of peaks between March and May). Ambiguity over the position of the peaks corresponding to the older age-groups is not surprising considering the rarity of specimens—the grouping tentatively identified as representing the 1970 cohorts in text-fig. 4 (i.e. 21·75 mm—labelled 7) includes a mere two specimens out of a total sample of 811. However, similar groupings of slightly more specimens do occur in other samples, and its interpretation as a 7th year-class can also be justified on the basis of the spacing between previous peaks in text-fig. 4 (see Table 3).

Age Group	Year of Settlement	Size Range	No. of Specimens	% of Total	% Rate of Mortality
1	1976	up to 5.5	365	45	
2	1975	5.6 - 9.5	213	26	42
3	1974	9.6 - 13.5	121	15	43
4	1973	13.6 - 16.0	63	8	45
5	1972	16.1 - 18.5	40	5	40
6	1971	18.6 - 20.0	7	0.9	83
7	1970	over 20.0	2	0.2	71

TABLE 4. *T. retusa* age-groups in the March 1977 sample; size range refers to maximum shell length measured in mm.

Following on from this analysis it was possible to divide the March 1977 sample into age-groups (= year-classes) on the basis of a range of lengths (Table 4). The boundaries of the age-groups are somewhat arbitrary, and the higher and lower values in each grouping include specimens which rightly belong in the age-groups on either side. Nevertheless, the exercise is useful as it quantifies the relative proportions of age-groups and provides an estimation of mortality-rates.

Comparison with theoretical model. One of the most significant contributions to the study of population structure and dynamics in recent years has been the comprehensive theoretical simulations of Craig and Oertel (1966). Having identified five main factors which influence the over-all shape of a size-frequency distribution, Craig and Oertel programmed a computer to produce an exhaustive series of histograms using various combinations of these five factors. Having established the characteristic population structure of *T. retusa* in nature, it was obviously of interest to identify which of Craig and Oertel's experiments was conducted using a combination of factors similar to those prevailing in the Firth of Lorne population, and to compare the theoretical simulation with the actual population structure.

Craig and Oertel's five factors are (1) recruitment strategy, (2) growth-rate, (3) coefficient of variation of growth-rate, (4) mortality-rate, (5) cessation of growth. *T. retusa* clearly falls within the 'boreal' recruitment strategy of Craig and Oertel, which was defined as two short spawning periods in autumn and spring. The growth-curve of *T. retusa* is intermediatory between the 'linear' and the 'high-to-low' curves used by Craig and Oertel, but is closer to the former than the latter. The third factor, the coefficient of variation of growth-rate, was an attempt to allow for the effects of the varying growth-rates of individuals in a single cohort. There is no indication of the extent of such variability in *T. retusa*, but Craig and Oertel mostly used a coefficient of 2, which they believed to be an acceptable average value. The mortality-rate of *T. retusa* remains constant, at least during the first 5 years of life (see below). The final factor related to the timing and duration of any cessation of growth during the year, and there is good evidence that *T. retusa* falls within Craig and Oertel's category (a), namely a winter stoppage of 3 months' duration (see below).

This permutation of factors was combined in Craig and Oertel's experiment number 34, and the resulting size-frequency histogram (Craig and Oertel, 1966, fig. 17, p. 346) is strikingly similar to the length-frequency histograms of *T. retusa*. The over-all shape of all these distributions is identical,

being unimodal and right-skewed. The computer simulation had evenly spaced peaks corresponding to the biannual cohorts, which merge into a single annual peak in later life, exactly as in the natural population. Craig and Oertel described this experiment as follows:

Boreal recruitment, three winter months cessation of growth with doubling of mortality, coefficient of variation 2 ... growth-rate linear ... mortality constant.

Boreal recruitment consists of two equal waves in late spring and early autumn, separated by a short summer interval and a long winter interval. This forms twin peaks in the living population ... the groups of twin peaks are equidistant, and the twins have identical intervals. This peak spacing is diagnostic for linear growth.

Obviously there are differences in detail between the theoretical and the actual, especially as the critical factors in nature tend to vary slightly with increasing age rather than remain constant. Nevertheless, the results of this comparison are very encouraging, and demonstrate the potential of a combined theoretical and empirical approach to the study of population structure and dynamics.

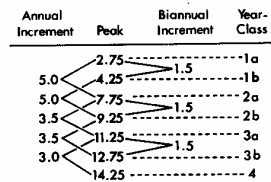| Annual Increment	Peak	Biannual Increment	Year-Class
	2.75		1a
5.0	4.25	1.5	1b
5.0	7.75		2a
3.5	9.25	1.5	2b
3.5	11.25		3a
3.0	12.75	1.5	3b
	14.25		4

TABLE 5. Analysis of the peak spacing in the width-frequency histogram of *Rostricellula rostrata*, Ulrich and Cooper (data, in mm, are from Walker and Parker 1976).

Relevance for fossil populations. The analysis of the population structure and dynamics of fossil brachiopods is best conducted using both size-frequency histograms and growth-line counts, as the inherent deficiences of one method are compensated for by the strengths of the other. However, under ideal conditions of preservation, a frequency histogram prepared from a sample of fossil brachiopods can, on its own, yield precise data on the autecology of that species. In preparing a width-frequency histogram from a sample of the Middle Ordovician species *Rostricellula rostrata*, Ulrich and Cooper from Tennessee, Walker and Parker (1976) used the same grouping adopted for the *T. retusa* histograms (i.e. 0·5 mm), and hence the prominent peaks in the *R. rostrata* histogram can be analysed in the usual tabular form (i.e. Table 5) allowing direct comparison with the living population (i.e. Table 3).

This method of analysis emphasizes the remarkable similarity in the population structure between the living and fossil population, especially in the pattern of peak spacing. Both histograms have prominent regularly spaced twin peaks, with the separation between each peak in a twin (i.e. the 'biannual increment'—see Tables 5 and 3) being identical in both populations (i.e. 1·5 mm). Just as in the *T. retusa* histogram, these twin peaks are not discernible on the right-hand side of the diagram, because the slowing of the growth-rate in older specimens has resulted in the merging of the twins to form a single peak representing the total annual recruitment (e.g. at 14·25 mm in Table 5). There are differences in the absolute values of comparable increments (e.g. annual increments—compare column 1 in Tables 5 and 3) and the fossil species had a shorter life span and a more rapidly decreasing growth-rate, but such differences are of minor significance compared to the similarity in the over-all pattern of peak spacing. Both theoretical and empirical data indicate that this pattern of regularly spaced twin peaks is characteristic of animals inhabiting temperate latitudes, and the fossil population can reasonably be assumed to have experienced broadly similar seasonal cycles of temperature, food supply, etc., to those prevalent today in the Firth of Lorne or other temperate habitats. Apart from comparison with equivalent living populations, the reconstruction of population structure and dynamics in fossil brachiopods would, under ideal circumstances, be based on the analysis of several large samples rather than just one, and would also take into consideration pertinent localized environmental and biological factors; as mentioned above, the interpretation of growth-lines can further refine the resulting data. Nevertheless, the success of this preliminary comparison between the population structure of living and fossil brachiopods augers well for this technique.

Seasonal growth pattern. To obtain a more precise picture of the pattern of seasonal growth in *T. retusa*, the position of peaks corresponding to individual cohorts was recorded in samples collected throughout the year. The results (Table 6) suggest that the growth-rate of adults decreases significantly in winter months, as the peaks appear to remain stationary between January and May.

TABLE 6. Movements of peaks corresponding to the 4th and 5th year-classes of *T. retusa* (measurements, in mm, refer to maximum shell length).

Age Group	Mar	May	Aug	Oct	Jan	Expected in Mar
4	14.75	14.75	16.25	17.25	17.25	17.25
5	17.25	17.25	18.25	18.75	19.75	19.75

The evidence for this is based on the assumption that the mid-point of a particular peak is an acceptable measure of the average length of specimens in a cohort; although the growth-history of individuals within a cohort will vary depending on localized environmental conditions. The slowing of growth in winter is an expected and readily explained phenomenon, bearing in mind the direct relationship between decreasing temperature and a reduction of the rate of metabolic activity in cold-blooded invertebrates. It seems likely that the rate of growth of *T. retusa* slows progressively during the autumn and winter, and reaches a minimum, or perhaps ceases altogether, in mid-winter when temperatures are lowest and food supplies minimal. There is some evidence that sexually-mature females have a slightly slower rate of growth than mature males (text-fig. 7A), perhaps indicating that the production of ova is more demanding in terms of available nutrients. However, the pattern of modes in text-fig. 7A is rather confused and far from unequivocal, and this facet of sexual dimorphism does not appear to be noticeable in the combined length-frequency distributions. The increments involved, like those produced by variable growth-rates in a single cohort, are so small as to be outside the limits of resolution of the length-frequency histogram.

In contrast, the growth of recently settled post-larvae appears to proceed rapidly during the first 3 months of settled life, and to be independent of prevailing environmental conditions. For example, the cohort which settled in late autumn 1976 had attained an average length of 2·75 mm by the following March (i.e. 1(*a*) in text-fig. 4), a rate of growth greater than at any other stage of life. Similarly, the cohort which settled in May 1977 had grown to an average length of 2·75 m by the following August (compare text-figs. 6B, 6E). The growth-history of *T. retusa*, therefore, has three distinct phases: (1) approximately 3 months of rapid growth immediately following settlement in both autumn and spring; (2) the remainder of the first 3 years of life, when the annual growth-rate remains constant, but varies seasonally depending upon ambient sea-water temperatures; (3) the remainder of life, during which annual growth-rates decrease progressively.

The initial period of rapid post-settlement growth is a prudent feature, as the early development of a rigid protective exo-skeleton will reduce mortality rates during this most vulnerable stage of settled life. The ability of the autumn cohorts to grow in winter months indicates perhaps that their modest nutrient requirements are adequately satisfied by even the reduced winter food supplies. It may also be of significance that the volume of the feeding 'chambers' in juveniles is considerably greater than that enclosed by the valves of the shell, as the filaments of the lophophore extend a considerable distance beyond the shell margin when feeding. In adults the filaments are almost entirely contained within the brachial cavity when feeding; in juveniles the increased risk of predation resulting from the exposed filaments and widely gaping shell (as much as 45° as compared to ≈ 15° in adults) may be offset by the advantages gained by the relatively rapid shell growth due to the proportionately high levels of nutrient intake. The reduction in the rate of annual growth-rate at the end of 3 years coincides with the onset of sexual maturity, and probably reflects a fundamental change, with the nutritional requirements of the developing gonads receiving precedence over other metabolic processes.

Growth-line analysis. The analysis of the pattern of growth-line formation in brachiopods is best conducted on a cumulative basis using a large number of individuals from a single population. The main difficulty of attempting a growth-line analysis of an individual is that the pattern is often incomplete, and hence difficult to interpret. Nevertheless, a sample analysis of a single adult specimen
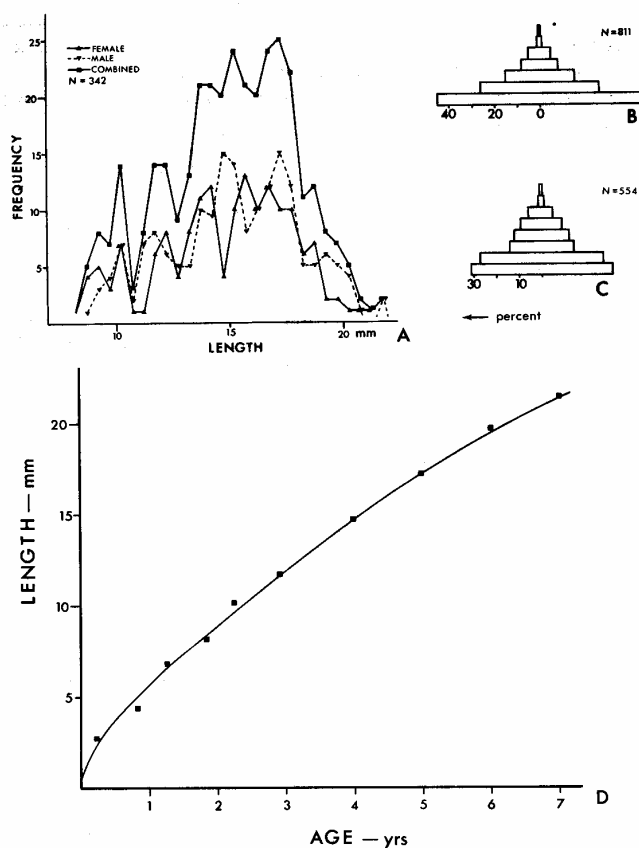
TEXT-FIGURE 7. A, sexual dimorphism in shell growth as determined
from 342 sexually mature specimens of *T. retusa* collected 26 October
1977 from the Firth of Lorne population. B, C, age pyramids for *T.
retusa* population in the Firth of Lorne before (B, from March 1977
sample) and after (C, from 24 May 1977 sample) spatfall. D, Growth
curve for *T. retusa* as determined from the analysis of the March 1977
sample (i.e. Table 3).

of *T. retusa* with a complete record of growth-line formation is included at this stage as it contributes
further to our knowledge of the growth history of the population. The specimen (ZB 3717) was
collected during January 1979 at an approximate depth of 165 m from the Firth of Lorne, and was
15·5 mm in length. Having measured the distance to each growth-line from the posterior margin of
the shell along the medial axis of the pedicle valve (Table 7), and determined the spacing between
individual growth-lines (column 2 in Table 7), it was then apparent that growth-lines form biannually.
The age-group analysis in Table 4 indicates that a specimen of length 15·5 mm should be 4 years old; a
conclusion which is confirmed by growth-line analysis which indicates that the 1st growth-line on this
specimen was formed in autumn 1975 (Table 7) and therefore it must have settled in spring 1975.

The spacing between growth-lines (column 2 in Table 7) on this specimen indicates that
approximately two-thirds of the annual growth occurs during the 'summer' period, whilst the

remaining one-third occurs during 'winter'. The exact timing of growth-line formation has not been determined, but is assumed to occur in autumn and spring, and at times of pronounced environmental and physiological stress. If so, the 'summer' and 'winter' periods would therefore be of approximately 6 months' duration, and would probably be more accurately designated as 'summer/autumn' and 'winter/spring' respectively.

TABLE 7. Analysis of growth lines on single specimen of *T. retusa* (ZB3717) collected from the Firth of Lorne on 21 January 1979 (data in mm).

Increment	Growth-line	Date of Formation
	2.0	Autumn 1975
Winter -----1.4	3.4	Spring 1976
Summer -----2.9	6.3	Autumn 1976
Winter -----1.6	7.9	Spring 1977
Summer -----2.9	10.8	Autumn 1977
Winter -----2.0	12.8	Spring 1978
Summer -----1.4	14.2	Autumn 1978
Winter -----1.3	15.5	Spring 1979

Mortality. The data in Table 4 indicates that roughly 40% of the brachiopods in each age-group die per year. This estimation applies only to specimens more than 1 year old, as there is no viable method of determining the mortality rate during the periods prior to and immediately following settlement. Significantly higher mortality-rates are likely to occur during these early stages of life, as has been determined in other living brachiopod populations (e.g. Doherty 1976, 1979). As the number of specimens in the older age-groups is so small, the significant increase in mortality-rates amongst the 6th and 7th age-group (Table 4) may not necessarily be representative, although older specimens may indeed be more susceptible to disease, stress, etc.

The causes of mortality in the *T. retusa* population are not apparent, although it was not possible to examine large numbers of dead shells for signs of predation. There is, however, very little evidence of repaired shell damage in living specimens, which suggests that the level of predation is low. Probably a large proportion of deaths occur in winter because of the stress caused by less favourable environmental conditions. It may be significant that Craig and Oertel (1966) incorporated a doubling of the mortality rate in winter in the experiment which yielded a size-frequency distribution similar to that of *T. retusa*. The fact that a few adult specimens did not develop gonads during spawning periods may be symptomatic of diseases or infections which may account for a small proportion of the annual mortality. However, as gonad development is discernible during winter months, it would appear that starvation is not a major cause of death.

The small tissue content of brachiopods probably partially explains the apparent lack of predators on *T. retusa*, although predatory gastropod borings have been found in other species (e.g. Logan 1979). Because of their low nutritional value, it may indeed be more reasonable to look for potential predators at the 'micro' rather than the 'macro' level, and certainly carnivorous micro-organisms could readily gain access to the brachial, and perhaps body, cavity via the feeding currents. Some nematoid worms do appear to feed on brachiopod lophophoral filaments (McCammon 1971) although there has been no detailed study of the extent and effect of such predation/parasitism.

CONCLUSIONS

The large population of *T. retusa* in the Firth of Lorne is well established, and the species is relatively abundant in deeper waters off the west coast of Scotland. The main reasons for this success are the recurring efficiency of the reproductive activity and the absence of competing organisms or readily apparent predators. Representatives of the genus *Terebratulina* have a long history, and have been present in the North Atlantic since its inception. It survives as one of the most cosmopolitan and abundant of living brachiopod genera, occurring in all oceans. The longevity and success of this genus are probably due to an adaptability of pedicle morphology which greatly increases its range of substrates, combined with an ability to colonize habitats (such as the Firth of Lorne depression) inimical to other more 'successful' epibenthonic organisms. Critical factors in this latter capability may

be a generally low level of nutrient requirements, and the ability to survive prolonged periods of adverse conditions by a virtual cessation of metabolic processes, as demonstrated by the specimens which survive in the outside aquarium at Dunstaffnage despite being subjected to rapid daily temperature fluctuations. Clearly another important factor in the longevity and success of the genus is its remarkable morphological conservatism, with Cretaceous and Recent species being almost indistinguishable. *T. retusa* is unlikely, however, to reassume the role of its ancestors as a common constituent of shallow marine ecosystems because of its inability to compete for available space in such environments.

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APPENDIX. The use of probability graph paper for the analysis of polymodal length-frequency histograms

By way of an additional check on the interpretation of the population structure of *T. retusa*, the length-frequency data used to construct text-fig. 4 was also plotted on probability graph paper (text-fig. 8). By this means it is
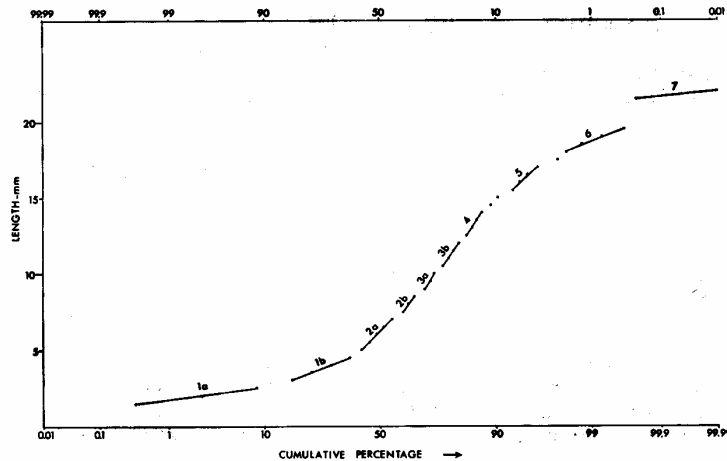
TEXT-FIG. 8. Length-frequency data collected 22 March 1977 ($n = 811$) plotted on probability graph paper.

possible to check that text-fig. 4 is indeed composed of a series of more or less overlapping normal distributions corresponding to individual settlement cohorts. Harding (1949) was the first to realize that the ability of probability paper to pick out individual normal distributions in a polymodal distribution would be of great use to population biologists, but few workers have made use of this method (Cerrato 1980). The methodology of this method of analysis is straightforward. The data is plotted as a cumulative percentage (i.e. % of total sample less than x mm) on a non-linear horizontal scale, which is so arranged that a plot of points corresponding to a normal distribution yields a straight line. As Harding (1949) demonstrated, a polymodal distribution plots out as a series of straight lines corresponding to each of the constituent normal distributions. Although there is no information as to the size distribution of animals in each settlement cohort in the Firth of Lorne, it is a reasonable and widely accepted assumption that each cohort would plot out as an essentially normal distribution. By this method of analysis, therefore, it is possible to check that each peak in text-fig. 4 does represent a settlement cohort (or amalgamation of two cohorts in the adult specimens) as suggested in the main text.

When the March 1977 data is plotted in this manner the results (text-fig. 8) confirm the interpretation of population structure outlined in the text. Short discrete lines are clearly distinguishable amongst juvenile specimens, and correspond to biannual cohorts. The degree of differentiation is less amongst 3- and 4-year-old specimens, which is consistent with growth-rates decreasing following the onset of sexual maturity. The suggestion that biannual cohorts coalesce in later life to form annual peaks is confirmed by text-fig. 8, and the pattern of growth amongst adults is more discernible than in the original length-frequency histogram. For example, a 6th year-class is clearly marked in text-fig. 8, but could only be inferred from text-fig. 4 (i.e. Table 3). However, the clearly differentiated 7th year-class in text-fig. 8 must be considered as artificial, as the gap in the histogram before the last two specimens automatically results in a strong differentiation from the preceding groups of specimens.