

Growth and Size Distribution of the Brachiopod *Terebratalia transversa* Sowerby

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ABSTRACT: Relatively synchronized samplings of man-made structures of known but varying ages have been used to generate a growth curve for *Terebratalia*. Modes indicative of the first four or five year classes were recognized, and seem internally consistent with each other. Older year classes were indistinguishable. In the vicinity of Seattle, Washington, this species probably does not survive more than nine to ten years. Growth lines, though conspicuous shell features, are not related to age.

LENGTH-FREQUENCY DISTRIBUTIONS are given in Figure 1 for two samples from populations of the brachiopod *Discinisca strigata* Broderip. Both samples were collected from the intertidal, one from near Puertocitos, Baja California, Mexico (Paine, 1962), the other from Mata de Limon, on the west coast of Costa Rica. The obvious difference in population structure represents a problem of major importance to both ecologists and paleoecologists, namely, the interpretation of size-frequency graphs. In this instance, the Puertocitos sample could represent the size structure of (1) an annual species some time after settlement, or (2) an isolated patch of individuals containing one or a few year classes of a perennial species which had received no subsequent recruitment; the Mata de Limon sample might represent (1) continuous recruitment, and hence breeding, in an annual, or (2) a long-lived species subject to constant recruitment and mortality. The facts that the former sample was drawn from a cobble patch of about 9000 m² while the latter was taken from a single 0.06 m² rock surface, and that both samples were made by the same individual with similar care but at different times and places, further confound the problem of interpretation. A final resolution of these *Discinisca* size distributions obviously must await data on growth patterns and rates; they have been presented only to typify the problem inherent in the interpretation of size-frequency distributions, well illustrated in the literature on both recent (Rudwick, 1962;

Percival, 1944; Paine, 1962, 1963; Rowell, 1960) and fossil (Hallam, 1962; Fagerstrom, 1964; Ferguson, 1963) brachiopods.

Satisfactory age determinations, fundamental to further elaboration of brachiopod size-frequency data, have been based in general on two procedures: the growth of a cohort has been followed in the laboratory or field (Paine, 1963), and individuals have been marked, released, and recaptured (Chuang, 1961). Both procedures allow the setting up of a growth curve from which age can be inferred, but both are time consuming and laborious. Another method, using growth rings (Vogel, 1959), is less direct and involves assumptions about the rate at which annuli are added to the shell.

There is at least one other approach which seems feasible—the synchronous sampling of comparably placed artificial habitats of known but varying ages. In this way a single set of samples taken from the appropriate structures can indicate growth rates and mortality because the ecologist is gaining, in essence, a historical perspective not otherwise available. The rate of advance in understanding ecological processes is probably directly correlated with the development and acceptance of time- and energy-saving techniques, and with the ability of ecologists to infer dynamics from single samples. Mortality rates (Deevey, 1947), reproductive rates (Edmondson, 1965), and the presumed role of competitive interaction (MacArthur, 1957) are fair examples.

In this paper I will show how a limited number of approximately synchronous samples of brachiopod populations taken from an increas-

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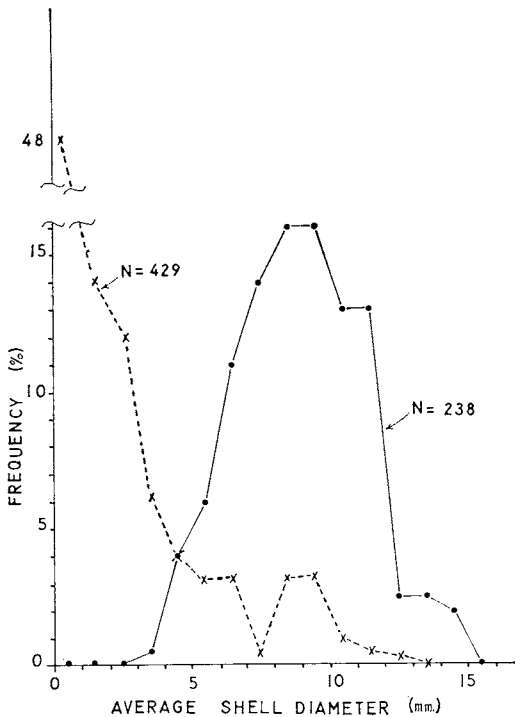


FIG. 1. Size-frequency distributions in *Disciniscia strigata* that are uninterpretable biologically without data on individual age. Samples from Puertocitos, Mexico, are indicated by closed circles (●), and those from Mate de Limon, Costa Rica by (X).

ingly common marine habitat can be used to reveal certain population properties, and in so doing I will add to the sparse ecological literature on brachiopods, a group of considerable paleontological importance.

MATERIALS

The city of Seattle, Washington, is located on Puget Sound, a sheltered, deep, and extensive body of characteristically marine water. Because the area's human population is increasing rapidly, a variety of permanent structures such as marinas, sewage outfalls, bridge abutments, and breakwaters have been completed at known but varying dates. In general, these are placed in shallow water, and, with their associated rock ballast, they provide fresh surfaces for colonization. If it is assumed that the general successional process and availability of colonizers are comparable from year to year and from place to

place, then simultaneous sampling of a few sites should provide a historical perspective on past ecological events.

Three areas adjacent to Seattle, representing structures of four different maximum ages, were sampled by SCUBA in 1967 at depths varying from 0 to 5 meters below MLLW. The data are given in Table 1. U. S. Army Engineer project maps (Anon., 1965) were used as the source for dating the Shilshole and Edmonds structures; the Alki sewer outlet was aged from city of Seattle drawing plans (Anon., 1954). In addition, similar information is given on a more limited sample taken with J. A. Long by wading at an extreme low tide in 1963. For all the samples an effort was made to search a fairly broad, representative area, and to take every brachiopod encountered. All specimens collected belonged to the locally most abundant species *Terebratalia transversa* Sowerby. Shell length and width were measured to the nearest 0.1 mm with vernier calipers.

DATA ANALYSIS

Terebratalia transversa is known to be a morphologically highly variable species with forms ranging from prolate to oblate spheroids, with well defined to poorly defined sulci, with smooth or ribbed shells, and with other variable characters (DuBois, 1916). Because it was not known to what extent shell traits varied between sampling sites, the statistical relationship between width and length was compared between all areas by an analysis of covariance (Snedecor and Cochran, 1967). When all samples were compared, the width-length relationships were not found to be parallel or to share a common regression, with the level of rejection set at the 0.05 level. The covariance analysis supports the reported great variability within this species and suggests that these animals are homogeneous neither in their meristic traits nor, as will be seen, in their more ecological properties.

The regression equations are given in Table 2 for all samples. They indicate that, for instance, at a width of 30 mm a maximum variation in mean length of 3.5 mm might be expected between the most disparate samples. Conversely, at a length of 25 mm the maximum variation in width would be about 4.0 mm.

TABLE 1
COLLECTION DATA FOR *Terebratalia transversa* FROM THE SEATTLE AREA

LOCALITY	DATE CONSTRUCTION COMPLETED	DATE SAMPLED	MAXIMUM POTENTIAL AGE (years)	SAMPLE SIZE
Shilshole Marina, South End	Jan. 1958	6 Aug. 1963	5-6	46
Shilshole Marina, South End	Jan. 1958	25 July 1967	9-10	242
Shilshole Marina, South End	Jan. 1958	7 Dec. 1967	9-10	319
Shilshole Marina, North End	Nov. 1961	25 July 1967	6	63
Edmonds Yacht Basin	Apr. 1962	19 Aug. 1967	5	1
Alki Sewer Outlet	July 1954	8 Oct. 1967	13	121
Alki Sewer Outlet	July 1954	19 Oct. 1967	13	81
Alki Sewer Outlet	July 1954	5 Nov. 1967	13	253

TABLE 2
REGRESSION EQUATIONS OF SHELL WIDTH (X) ON LENGTH (Y)
FOR DIFFERENT SAMPLES OF *Terebratalia transversa*

LOCALITY	DATE COLLECTED	EQUATION	CORRELATION COEFFICIENT	MEAN LENGTH (mm)	MEAN WIDTH (mm)
Shilshole Marina, South End	6 Aug. 1963	$Y = 1.30X + 0.15$	0.98	24.8	33.7
Shilshole Marina, South End	25 July 1967	$Y = 1.22X + 0.10$	0.91	35.6	44.5
Shilshole Marina, South End	7 Dec. 1967	$Y = 1.18X + 0.21$	0.89	35.6	43.9
Shilshole Marina, North End	25 July 1967	$Y = 1.29X + 0.06$	0.92	27.1	35.5
Alki Sewer Outlet	8 Oct. to 5 Nov. 1967	$Y = 1.12X + 0.15$	0.97	29.1	34.2

The majority of individuals collected from all areas bore signs of past or recent attack by some unknown predators, probably crabs. The shell would be chipped away from a localized area of the commissure, leaving a gaping hole in the animal. *Terebratalia* survive such attacks, as is shown by the occurrence of living individuals with damaged margins and many with completely regenerated ones. Since these attacks, if localized, would affect length-width relationships, their position on the animal was determined by dividing the commissure into the five arbitrary areas shown in Figure 2. The epicenter of both past and recent damage was estimated and assigned to a shell region. The distribution of major attacks is not random ($\chi^2 = 30.8$), and, as might be expected, the predator seems to attack the more exposed anterior margins. In this species, however, the sulcus is not greatly indented, and there was no significant difference between the anterior three areas ($\chi^2 = 2.9$).

The incidence and pattern of attack was similar between Alki and Shilshole populations, and

so the variations in length-width relationships probably cannot be attributed to this factor. The single most obvious environmental difference was the tendency for Shilshole animals of all sizes to be heavily encrusted by *Balanus crenatus* Bruguière, and the general absence of an epifauna at Alki. Unfortunately, the degree to which barnacle encrustation alters brachiopod growth patterns is unknown.

Although both length and width measurements were taken from all specimens, neither of these was believed to be sufficient in itself to reflect accurately the animal's size because of the variable position of shell damage, and also, perhaps, because of a high degree of intrinsic shell variation. Therefore, both measurements were averaged to provide an index of body size. Histograms for the pooled Alki samples and each Shilshole sample are given in Figure 3. The interval between successive size groups is 2.0 mm. The regression analysis indicated that the most disparate populations would show a maximum difference of about 4 mm in their respec-

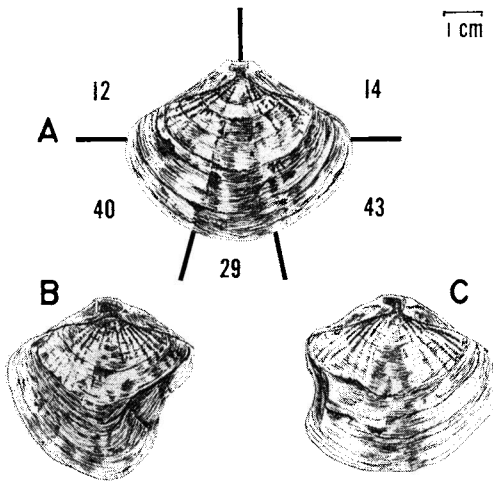


FIG. 2. Line drawings of normal (A) and completely regenerated (B) and (C) individuals of *Terebratalia transversa*. Around the margin of A, counts are given of the instances of major shell damage in the areas indicated. B and C illustrate the difficulty of using width alone as an index of shell size.

tive indices at their mean values. This is equivalent to two index units, suggesting that within these limits some variation in modal position is to be expected in comparisons of the morphologically different populations.

DISCUSSION AND CONCLUSIONS

The size-frequency histograms (Fig. 3) are such as typify many brachiopod populations (Rudwick, 1965); that is, they are polymodal and skewed to the right, the population size structure being dominated by larger and hence presumably older individuals. Further interpretation requires an estimate of age, and the basic design of these samples from populations of known but variable maximum age was intended to reveal the age-length relationship.

Long (1964:28) wrote that the breeding season of *Terebratalia* "... has not been determined with certainty but probably extends from November through February." This conclusion was reached by an examination of the gonads for ripeness, and three observations of natural spawning. On the basis of this work, done in the Seattle area, I have taken February 1 to be an average date of larval settlement for all areas in all years, and have aged the modes in Figure 3 from this date.

The pooled Alki samples show modal peaks at 9, 23, 33, 39, and possibly 43 mm. Assuming that all year classes are represented, these modes correspond to animals 9, 21, 33, 45, and 57 months old. The data from Shilshole South, 1963, and Shilshole North, 1967, have been similarly treated. These individuals could not be more than six years old, and most likely are only five. The current year class is not, or is at best poorly, represented in these samples, presumably due to the difficulty in seeing small individuals against a heterogeneous background. I have assumed them to be present. Modes appear in the 1963 Shilshole sample at 25, 33, and 39 mm, with a suggestion of the current year's recruitment apparent at 9 to 13 mm. There are comparable modes for Shilshole North, 1967, at 26, 33, and 39 mm. Other humps in those data are probably artifacts caused by sampling error and small sample size. The excellent agreement between samples taken four years apart but on approximately the same date in the modal positions suggest that the modes do represent periods of maximum recruitment, and that their displacement can be attributed to growth. These relationships are plotted in Figure 4, which thus represents the growth of a modal individual in its first 57 months.

The data from the south end of Shilshole, 1967, cannot be as clearly interpreted. The first sample (N = 242) taken in late July shows a hint of the current year class at 7 mm, and two distinct modes at 33 and 42 mm. Because this pattern was different from the other samples, a second collection was made from the same general area four months later. The pattern was repeated in this larger sample (N = 319) with clearly distinguished modes solely at 35 and 43 mm. When both samples are considered, and allowance made for some growth, the modes at 33 to 35 mm probably represent the survivors of the 1965 year class. The tendency of both histograms to flatten out near 25 to 28 mm suggests that a few 1966 year-class individuals are present. The relative absence of a 1967 settlement is obvious. The modes at 42 to 43 mm pose the greatest interpretive difficulty, for they can represent either a 1964 class or some earlier group with 1964 missing or underrepresented. A tentative decision was reached by using Figure 4 to estimate the age in months of animals

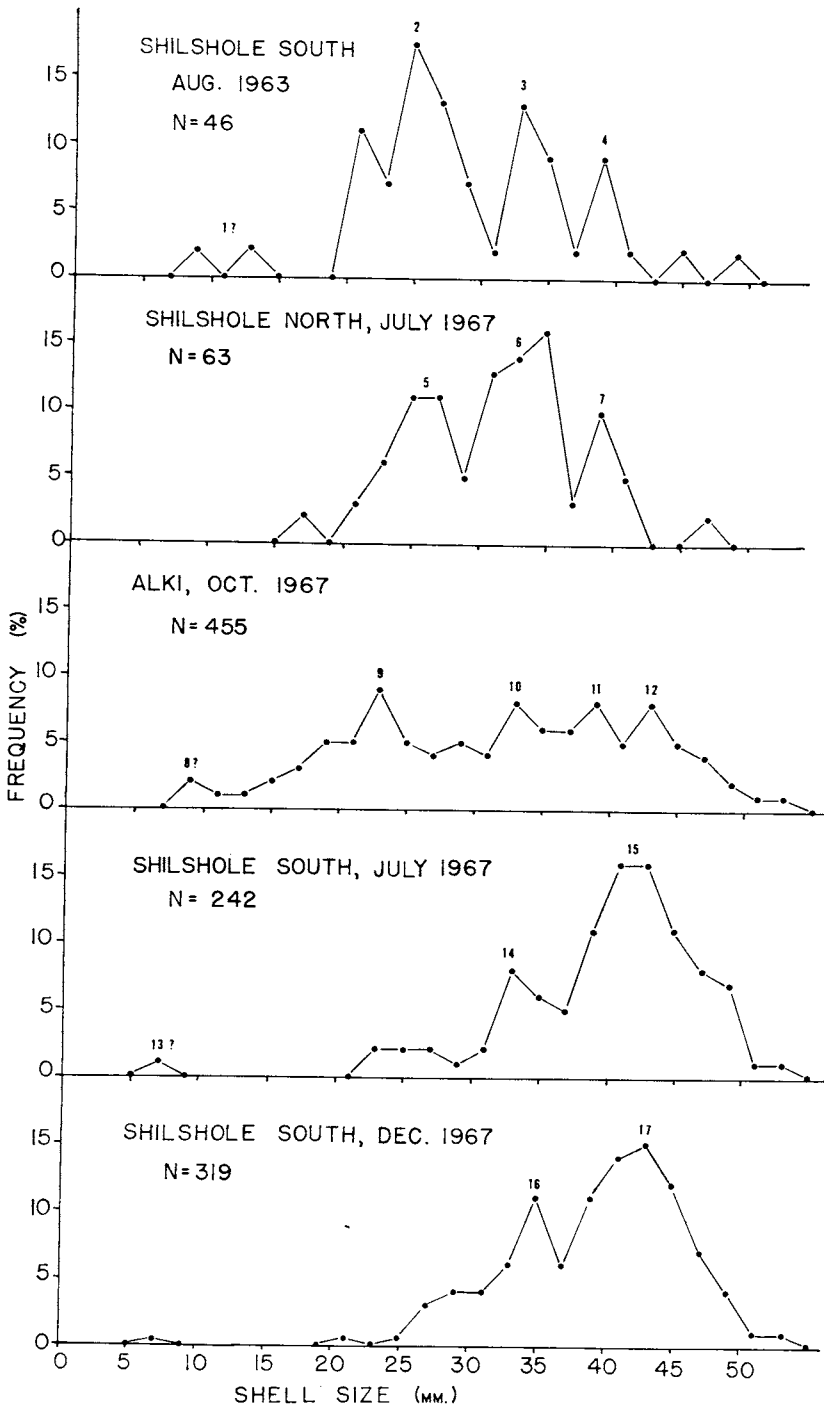


FIG. 3. Size (mean of individual width and length)-frequency data for the five major samples; the numbers indicate the position of modes, or presumed modes, used to construct the growth curve (Fig. 4).

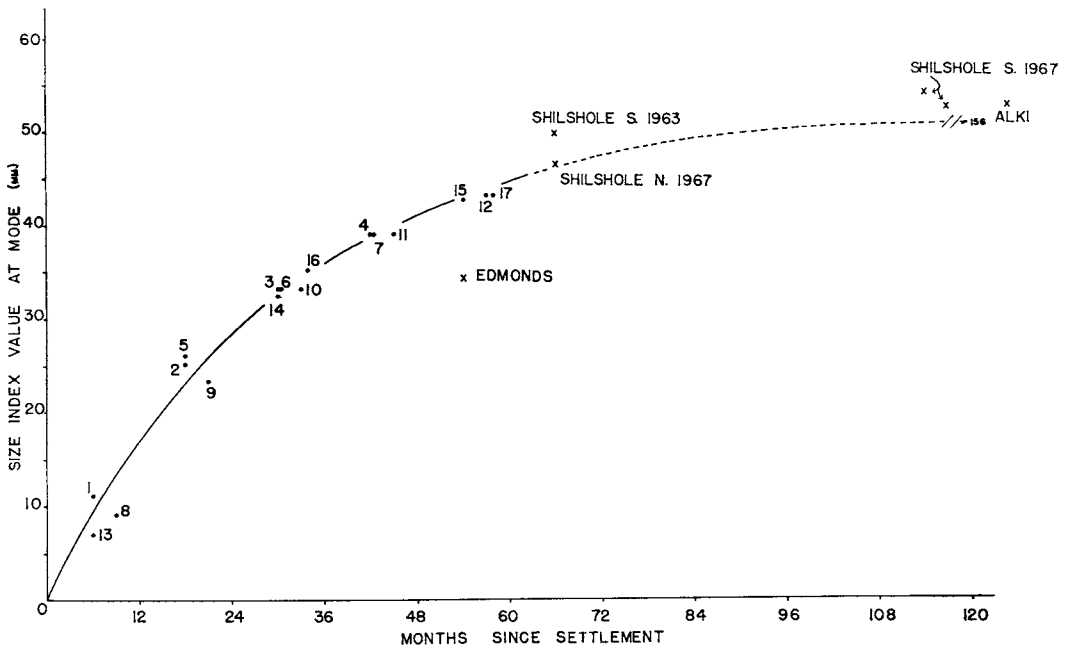


FIG. 4. A growth curve for a modal individual. The numbers identify the modes in Figure 3 while (X) designates the largest specimen found in each area.

this size. Modes 15 and 17 (see Figs. 3 and 4 for explanation), by this criterion, are 54 to 58 months old and apparently belong to the 1963 year class. Although the reasoning becomes entirely circular, I have added these modes to the growth curve to indicate their goodness of fit to the curve, thus strengthening the interpretation of a missing year class.

Another way of expressing growth is to plot on the curve the largest-sized individual found in each collection, assuming maximum possible age. Since we are now evaluating maximum, not modal, growth, it is not surprising that the two largest individuals from the 5½-year maximum age samples fall above the curve. The two 10-year-old maximum age individuals, and the one from Alki representing an "infinitely" old brachiopod (13 years), all fall close to an extrapolation of the curve, at about the same size, indicating either that growth in length and width may cease, or that mortality pressures are so intense that the probability of a *Terebratalia* living more than 10 years is extremely low. The single specimen collected at Edmonds apparently did not settle at the earliest opportunity.

While the data necessary to evaluate *Tere-*

bratalia growth were being compiled, some other aspects of its ecology were noted. This species is common in Puget Sound, but it is far from ubiquitous, and the distributional and age structure irregularities seen in this paper seem characteristic. *Terebratalia* was abundant at Shilshole, yet at Edmonds, on *a priori* grounds a more suitable habitat, only one specimen was found. The missing year classes demonstrated for the population inhabiting the south end of the Shilshole Marina in 1967 have been discussed. Yet both 1967 and 1966 year classes can be found in a small sample ($N = 63$) taken from the same marina's north end. Local heterogeneity of this nature apparently typifies many articulate brachiopod populations (Rudwick, 1965). When small individuals (less than 10 mm shell length) occurred, they tended to be attached to the brachial valve of large individuals, and usually close to the pedicle foramen. However, this sort of conspecific association is rare, and I have never observed the clusters of individuals that may be found in other species. Finally, *Terebratalia transversa* shells exhibit a bewildering array of growth lines. Some shells are almost smooth. Others show the appropriate

number of lines when shell age is judged on the size-age relationship as established in Figure 4, but still more have a number of major growth lines considerably in excess of their maximum potential age. For instance, the single Edmonds specimen, at most five years old, has eight or nine such lines. It seems safest to conclude that lines on the shell of this species, although undoubtedly representing a hiatus in the growth process, do not give an accurate indication of year class.

In summary, sampling artificial structures of known but varying ages seems to provide an effective means of relating size to age in *Terebratalia*. Once this relationship is known, ecologically meaningful differences in age structure may be evaluated, and the size distribution interpretation may be made more accurate. In the absence of this information, few inferences could have been drawn that would have withstood even a minimal level of questioning.

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