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# SOME ECOLOGICAL ASPECTS OF BIVALVE MORTALITY PATTERNS

JEFFREY S. LEVINTON* and RICHARD K. BAMBACH**

ABSTRACT. A logarithmic growth model, D = s ln (T + 1), where D = length, T age, and s is a constant, is proposed as a convention for relating size and relative age in bivalve mollusks. Studies of size-frequency distributions of dead Recent and fossil bivalve mollusks employing this relationship indicate that calculated survivorship curves can be correlated with ecological parameters.

Shallow-water muddy-bottom bivalve associations were studied. Calculated survivorship patterns of *Yoldia limatula* Say (living) and *Arisaigia placida* (Billings) (Siluro-Devonian), both infaunal proboscidial deposit-feeding nuculanids well adapted to life in muds, show a nearly constant probability of mortality through most of the life span. *Yoldia limatula* has a higher juvenile mortality on less stable substrates. *Mulinia lateralis* (Say), a small suspension-feeding mactrid, has very high juvenile mortality in muddy substrates. Clogging of the filtering apparatus (ctenidia), due to high turbidity at the sediment-water interface, is probably the limiting factor in its early life. Because of the large population size of the juveniles and subsequent high mortality, *Mulinia* would appear as a numerically dominant species in a fossil muddy-bottom assemblage, although it is a minor component of the living community at most times.

## INTRODUCTION

Autecological interpretation of size-frequency data has been generally neglected but is a fruitful subject for paleontologic research (see Craig and Hallam, 1963; Kurtén, 1953, 1954, 1958, 1964; and Hallam, 1967, for some discussion). Although the approach of correlating ecology with mortality in natural populations has not been exploited fully (Deevey, 1947), such studies demonstrate that ecological parameters, such as predation and population density, play important roles in the mortality patterns of many species-populations (Hatton, 1938; Murie, 1944). In this paper we examine the survivorship curves of some living and fossil bivalve mollusks and discuss the ecological parameters that might play important roles in shaping these survivorship curves.

The mortality patterns of two distinct adaptive types, deposit-feeding and suspension-feeding bivalves, have been investigated. Both populations were studied live in shallow-water muds (the term mud is used here for fine-grained substrates with a variable silt-clay ratio). Many deposit-feeders are well adapted for living in muds, whereas suspension-feeders seem to do poorly in this biotope (Sanders, 1958; Jörgensen, 1966, p. 106). Comparative study of survivorship between representatives of these trophic types from similar habitats shows differences we believe to be ecologically controlled. The paleontologic utility of survivorship study is

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** Department of Geology, Smith College, Northampton, Massachusetts 01060 illustrated by comparing a Siluro-Devonian deposit-feeder with our living example.

Dead shell size-frequency distributions can be used by both neontologists and paleontologists to infer the survivorship of a given population. Indeed, this is one of the few ways of investigating population dynamics in fossil species.

### A LOGARITHMIC MODEL FOR BIVALVE GROWTH

The ages of death of bivalves may be permanently recorded in the dimensions of the dead shells. In order to know this age one must have a way of linking growth rates and size with age. A common approach is to use bivalve growth rings, which permanently record seasonal events (compare, Orton, 1926). Although the modal analysis of growth rings, as proposed by Craig and Hallam (1963), is an attractive method, it often cannot be employed. In many bivalve species such as *Mytilus edulis* (Craig and Hallam, 1963) annual growth rings are poorly developed and even if well developed may be poorly preserved in fossils. Some bivalves have life spans of only a year or two, giving insufficient ring data for a growth curve. Finally, in some habitats, such as subtidal zones in tropical waters and possibly in deep water below the seasonal thermocline, growth rings on specimens may not reflect seasonal growth, for seasonal changes are slight (Craig, 1967). The ring size-frequency method must therefore be supplemented with a method that can relate age directly to size.

If size were related to age in the form of a linear function one could construct a survivorship curve from a size-frequency diagram by using size classes as age classes. However, the studies of many investigators clearly indicate that growth in bivalve mollusks is not linear but is close to logarithmic (Mason, 1957; Orton, 1926; Weymouth and McMillin, 1930; and others). Hallam's (1967) summary of bivalve growth data shows that, in most cases, the growth rate steadily decreases with age, the rate of decrease varying according to the population studied. In some cases the shape of the curve is sigmoidal (low to high to low growth rate, for example, *Pecten maximus*, Mason, 1957). This results from spawning in the fall, with subsequent initially slow juvenile winter growth (Mason, 1957).

Although there are differences in growth patterns between and within species of bivalve mollusks, all growth curves are decidedly non-linear. Therefore, if one assumes linear growth, this would cause errors in inferences of survivorship from a size-frequency histogram, because lowered rates of growth at older ages (that is, larger sizes) make unit size increments represent a greater length of time than at a younger age (that is, smaller size). More individuals are thus "compressed" into the older age size-classes in a survivorship analysis (Craig and Hallam, 1963). Size-frequency distributions, therefore, must be adjusted systematically in some fashion to correct for nonlinear growth.

As judged from Hallam's (1967) summary of bivalve growth data, a simple logarithmic relationship, such as the following, seems adequately nian deposit-feeder with our liv-

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BIVALVE GROWTH

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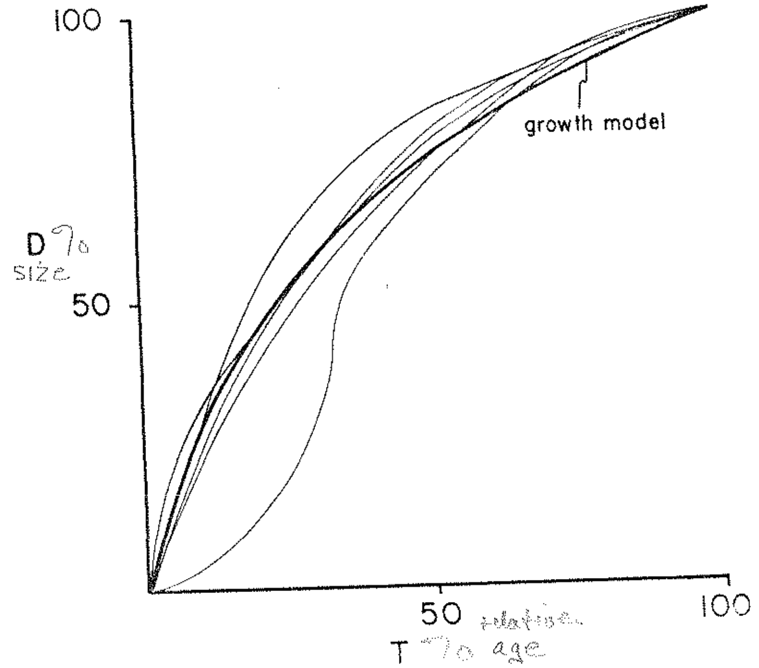

Fig. 1. Fit of five growth curves to the growth model proposed. D and T are both expressed as percentages. Five curves were selected by means of a random number table and were taken from Hallam (1967).

to reproduce bivalve growth patterns:

$$D = s \ln (T + 1),$$

where D is the size, T is the time, and s is a constant.

In practice, since absolute age is not known, we are dealing with relative time and thus can only make generalizations comparing one part of the life cycle with another. If Hallam's (1967) compiled growth curves are normalized to a relativistic scale (fig. 1), most growth patterns lie close to the proposed model growth curve. Although the relationship described is not always precisely correct, it is realistic enough to serve as a growth rate model for most purposes in bivalve survivorship studies.

## MORTALITY PATTERNS OF BIVALVES LIVING IN MUDS

The following cases compare the mortality of a living and a fossil deposit-feeder and a living suspension-feeder from muddy sediments. The cases illustrate the relative adaptiveness of these organisms and the usefulness of survivorship study in determining habitat fitness.

Deposit-feeding bivalves depend for food upon the substrate in which they live, whereas suspension-feeding bivalves obtain food chiefly from water layers near the bottom. Deposit-feeders are abundant in muddy sediments, but suspension-feeders are commonly most diverse and abundant in sandy, well-sorted sediments. Deposit-feeders find optimum condi- *

tions where there is relatively little water movement and low-density organic detritus can accumulate in the sediment. Suspension-feeders depend upon water movement for food transport. Most suspension-feeding bivalves may be poorly adapted for muddy bottoms (Sanders, 1958; Rhoads and Young, 1970).

*Interpretation of survivorship.*—Survivorship curves are constructed in the following manner: The total number of specimens is plotted as the number surviving at the age corresponding to the smallest size individual. The relative age corresponding to each size class limit is calculated, using the logarithmic growth relationship (see above). The number of individuals in a given size class (for example, those between 10 and 12 mm long) can be taken as the number dying for the calculated corresponding age interval. From these data the percentage of the population surviving to each relative age interval can be calculated and a survivorship curve plotted.

In this method bivalve age is assumed to be related to size according to the logarithmic growth model suggested above. None of the cases to be discussed are examples of "instant" mass mortality (for example, due to sudden burial and suffocation by sediment). Such a case would yield a census of the population *alive* at the time of death, and strong yearly variations in reproduction and in population size could give an incorrect picture of the mortality rates for the different life stages (Caughley, 1966; Kurtén, 1964; Slobodkin, 1961, p. 38). If our samples exclude catastrophes that tend to eliminate (census) the whole population, then the dead shell size-frequency distribution can give us the average number dying for any age interval. Finally, it is assumed that the causes of mortality and their relative importance have remained the same over the generations represented by the dead shell assemblage to be analyzed.

*Survivorship of Yoldia limatula (living deposit feeder).*—*Yoldia limatula* is an infaunal deposit-feeding nuculanid, well-adapted for life in muddy substrata (Rhoads, 1963). It is anterior-posteriorly elongate (fig. 2A), smooth-shelled, and lives and feeds in the sediment, communicating to the overlying water by means of siphons (Stanley, 1970). It is an extremely active, rapid-burrowing deposit-feeder, feeding by means of a ciliated palp which conducts particulate matter to the mouth (Drew, 1899).

Two samples of *Yoldia limatula* were taken in Long Island Sound, off West Haven, Connecticut. One was collected at a water depth of about 7 m, where *Yoldia limatula* occurs with (but in greater abundance than) the deposit-feeding nuculid *Nucula proxima*. The other sample was taken in deeper water (20 m) with a more clay-rich, less cohesive mud substratum.

In the shallow-water (fig. 3) *Yoldia limatula* has a *constant* rate of mortality for the growth period of most of the population (fig. 4), the final low mortality stage possibly being an artifact caused by the small number of specimens upon which it is based.

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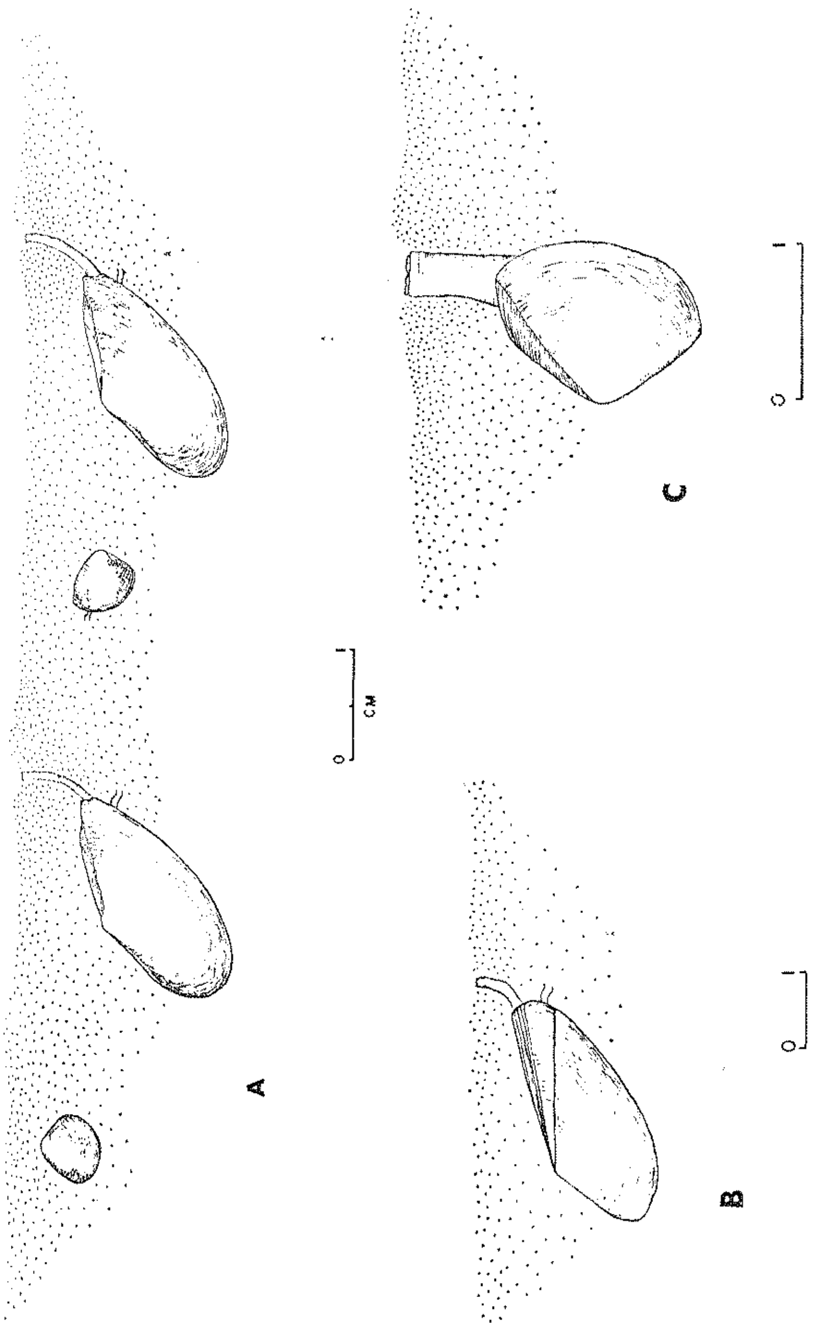

Fig. 2. Form and life-habit of (A) *Yoldia limatula* (smaller species is *Nucula proxima*), (B) *Arisaigia placida* (Siluro-Devonian), and (C) *Mulinia lateralis*.

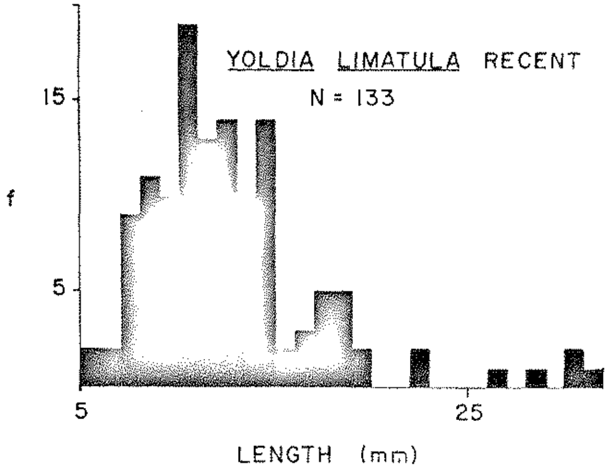

Fig. 3. Size-frequency distribution of dead shells of *Yoldia limatula*. Lower size limit is that of sieve size.

N. smallest size class

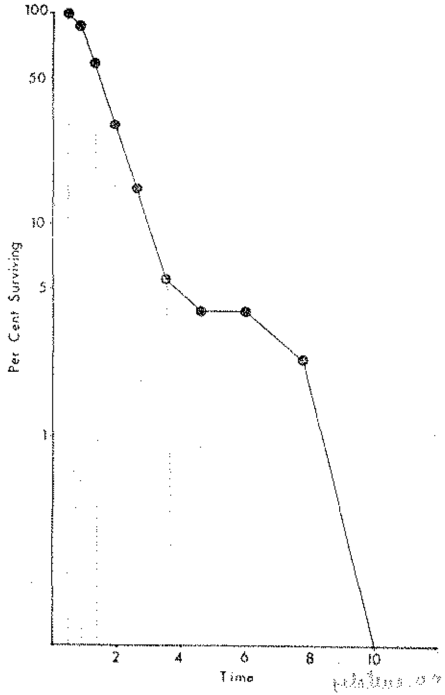

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Fig. 4. Survivorship of *Yoldia limatula* in shallow water mud. Calculated from figure 3.

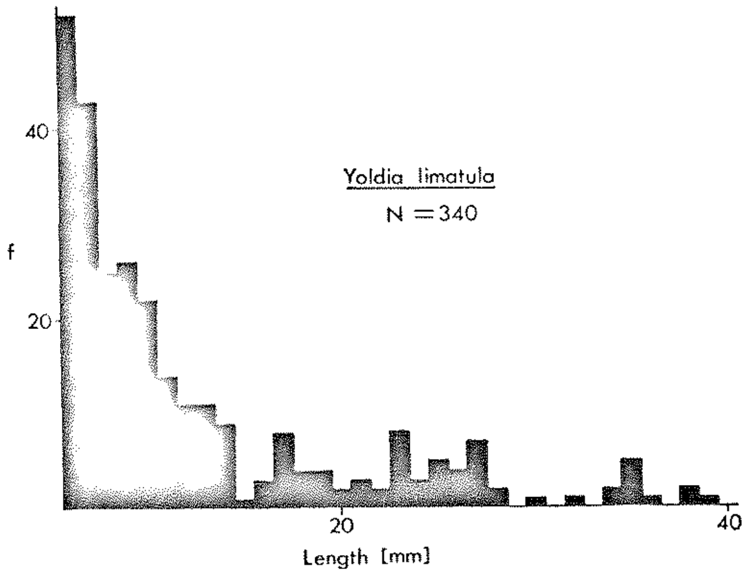

Fig. 5. Size-frequency distribution of *Yoldia limatula*, taken from a habitat different from that of distribution in figure 3. Details in text.

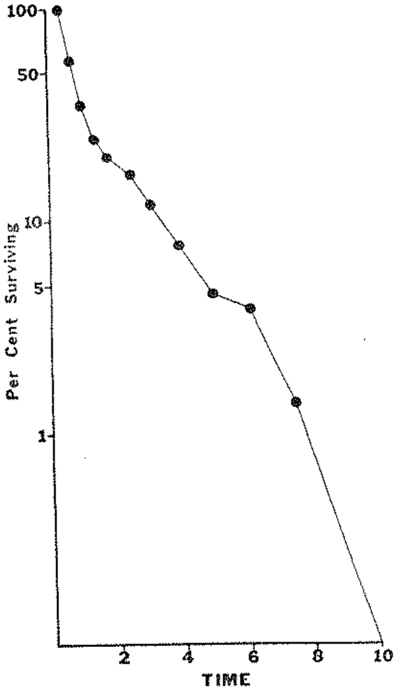

Fig. 6. Survivorship of *Yoldia* calculated from figure 5. Note break in slope at T = 2 (length = 11 mm), from a high to a lower mortality rate.

In the deeper-water sample (fig. 5) mortality of *Yoldia limatula* is not constant, juveniles being more prone to death (fig. 6). This sampling station differs from the other *Yoldia* locality not only in water depth and substratum stability but in faunal makeup as well. Here *Nucula proxima*, which feeds at or near the sediment surface, strongly dominated the fauna. Salinity, temperature, and predation factors are similar or less severe than at the shallow water locality.

*Survivorship of Arisaigia placida (Siluro-Devonian deposit feeder).*—To test the possibility of fossil deposit-feeding species having similar survivorship characteristics, a Siluro-Devonian deposit-feeding bivalve, *Arisaigia placida,* was studied. *Arisaigia placida* is similar in morphology and synecological association to *Yoldia limatula*. It occurs in the Siluro-Devonian Stonehouse formation of Nova Scotia. It is an elongate, moderately inflated nuculanid with two sharp creases, or folds, extending to the posterior margin from the umbo.

*Arisaigia placida* (fig. 2B) probably was a siphonate, laterally mobile, infaunal palp proboscide deposit-feeder. The radial shell folds and radial posterior ridging probably indicate that the animal burrowed into the sediment at an angle (rather than horizontally or vertically). There are no shell gapes, so the shell opened for the extension of the siphon and the proboscides. The folds may indicate some ventral mantle fusion which would have made the animal a more efficient burrower and would have simplified shell sanitation. The palp proboscides were probably extended from the posterior, in association with the siphons, rather than ventrally. Though capable of lateral locomotion *Arisaigia placida* may have been stationary most of the time and moved only to relocate when feeding or when disturbed. The shell was quite thin and fragile, and the animal probably lived and fed completely buried in the sediment.

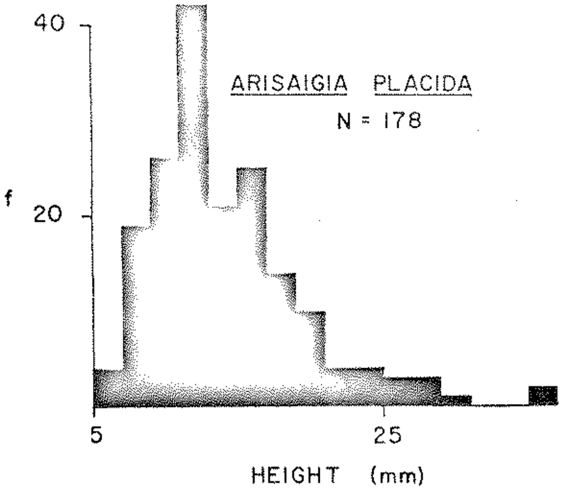

Fig. 7. Size-frequency distribution of *Arisaigia placida*.

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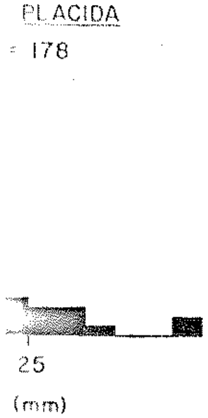


*Arisaigia placida.*

*Arisaigia placida* was a member of a deposit-feeding community dominated by two species of *Nuculites*, which together make up 25 to 40 percent of the shells of the collected Stonehouse fauna. *Arisaigia placida* was a minor though persistent member of the fauna, contributing about 4 percent of the total number of individuals. The Stonehouse sediments represent soft but cohesive muds which were subjected to occasional storm disturbance (Bambach, ms).

The calculated size-frequency distribution (fig. 7) is a composite for collections from 121.92 m of vertical section. Although collecting was not by bulk sampling, a concerted effort was made to collect all bivalve specimens present. It is believed that all sized specimens present were recovered, as evidenced by the many individuals of other species collected which are smaller than the smallest *A. placida* recovered. These collections are believed to represent an unaltered fossil assemblage (see app.).

As shown in figure 8 all stages of a life cycle reconstructed from this collection of *Arisaigia* are about equally prone to death. The size-frequency distribution is also similar to that of the shallow water collection mentioned. This is coincidental, however, since other shallow water collections of *Yoldia limatula* yield somewhat differing size-frequency distributions, although the resultant mortality patterns do not change.

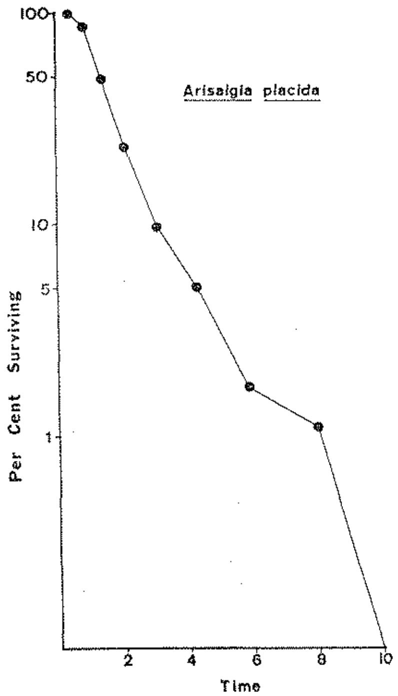


Fig. 8. Survivorship of *Arisaigia placida*. Calculated from figure 7.

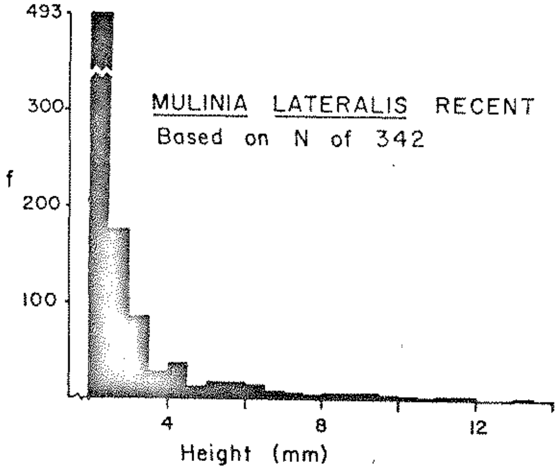


Fig. 9. Dead-shell size frequency distribution of *Mulinia lateralis.* Lowest size limit is that of sieve employed.

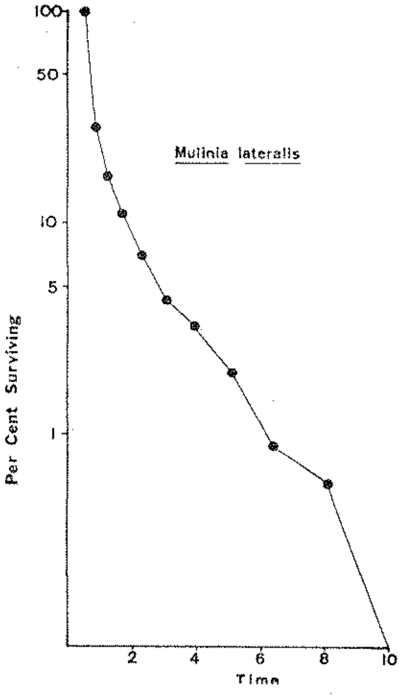
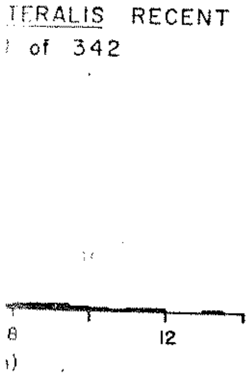


Fig. 10. Survivorship of *Mulinia lateralis.* Calculated from figure 9.



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*Survivorship of Mulinia lateralis (living suspension feeder).*—As suggested above, a suspension-feeder in mud might have a different mortality pattern than a deposit-feeder, since they are generally poorly adapted to very high turbidity at the sediment-water interface. A suspension-feeding bivalve occurring commonly in silty sediments is *Mulinia lateralis* (fig. 2C). This small mactrid lives in a wide variety of muddy bottoms in New England shallow waters (Sanders, 1956, 1960; Stickney and Stringer, 1957; Jackson, 1968). Our collection was taken from shallow water muds (depth about 7 m) in Long Island Sound, off West Haven, Connecticut.

The dead shell size-frequency distribution (fig. 9) is very strongly right-skewed, clearly indicating that the juvenile mortality is much higher than that of the adults (fig. 10). This pattern is distinctly different from that observed for deposit feeders.

## DISCUSSION

The data presented here support the hypothesis that deposit-feeding nuculanid bivalves living in shallow-water cohesive muds have a constant rate of mortality with increasing age. This produces a characteristic size-frequency distribution for accumulated dead shell samples. We have no data on the very youngest (smallest) shelled juveniles or significant numbers of oldest (largest) individuals, so our remarks do not apply to these growth stages.

The conclusion concerning constant mortality is reasonable, since deposit-feeders are active burrowers and are well adapted to this muddy, physically unstable bottom habitat (Savilov, 1957; Rhoads, 1963; Stanley, 1970). Feeding on buried organic detritus allows a deposit-feeding population to be unaffected by short term fluctuations in supply of suspended food. The detritus acts as a "buffer reservoir" of food. Apparently age-specific gastropod predation is not significant, either, in this habitat dominated by deposit feeders. Less than 1 percent of the valves were drilled in either *Yoldia* sample, and none in the *Arisaigia* sample.

In the sample of *Yoldia* taken in deeper water from less cohesive mud, the higher rate of juvenile mortality is probably caused by the soft, floccular nature of the surface of the sediment. This physically unstable sediment-water interface zone is formed by the burrowing and fecal pellet formation activities of *Nucula proxima* and other deposit-feeders (primarily annelids). This provides an unstable and turbid medium offering poor support and fouling juveniles, but not adults (Rhoads and Young, 1970; Sanders, 1960; Moore, 1931). The larger adults are able to stabilize themselves in the more solid substrate below the "soupy" zone. This zone's thickness (1 cm) is approximately equivalent to the maximum depth of burrowing of the smaller individuals having higher mortality. Other possible detrimental effects for a young *Yoldia* in this habitat are spatial interference and competition with the superabundant *Nucula proxima*, as *Yoldia* also feeds near the surface when young, and oxygen deficiency at the sediment-water interface because of the low amount of circulation.

The physical instability and high turbidity of sediments reworked by deposit-feeders is probably a major factor in the high juvenile mortality of the suspension-feeder *Mulinia lateralis*. High turbidity was shown by Loosanoff and Tommers (1948) to inhibit the pumping rate of oysters, and Loosanoff (1962) suggested that suspension-feeding bivalves feed most effectively in relatively clear waters. Glude (1954) has shown that replanted *Mya arenaria* has a higher mortality in silts than in sands. In addition, suspension-feeding bivalve growth is stunted in muds, relative to sands (Pratt, 1953; Pratt and Campbell, 1956; Tenore, Horton, and Duke, 1968; Rhoads and Young, 1970; Kristensen, 1957; Allen, 1954). Allen (1954) found that juveniles of *Mya arenaria* showed poor survival in muddy substrates.

In the presence of weak bottom currents, deposit-feeders reworking the surface sediments make the sediment surface physically unstable (Rhoads and Young, 1970). Sediment resuspension over this bottom type is common, with concomitant clogging of filtering bivalves living at this unstable interface. Juveniles, having smaller siphon diameters and smaller gill surface areas, would be more prone to death. Hence the observed survivorship pattern for *Mulinia*.

Siphonate deposit-feeders, such as *Yoldia limatula*, are probably subject to these same physiological limitations, although not nearly as much as are suspension-feeders.

In years of high reproduction successful larval populations of *Mulinia* attempt to colonize local, hydrographically favorable areas of muddy bottoms. Very high juvenile mortality, however, causes these dense initial populations to die out very quickly and to be very transient. It is curious that *M. lateralis* seems to prefer muddy habitats in New England waters. Perhaps its small size and low bulk density, enabling support in the soft substratum (Savilov, 1957; Hallam, 1965) plus a high reproductive rate, allow it to lead what would otherwise be a tenuous existence. If the shell accumulation from a New England muddy-bottom community were fossilized, *Mulinia lateralis* would appear to be a dominant and permanent member of the fauna. Actually it is a species with very transient and unstable populations (Sanders, 1956). Survivorship study, indicating high juvenile mortality, is helpful in revealing the true nature of the population dynamics. The significance of such transient, opportunistic species in the fossil record will be discussed in another publication.

The data on *Arisaigia placida* indicate that undisturbed shell accumulations can be used for study of population dynamics of species at any point in the geologic column, if appropriate growth models are developed. The logarithmic growth model discussed above seems appropriate for most bivalves.

## ACKNOWLEDGMENTS

This manuscript was examined critically, in various stages of preparation, by G. Y. Craig, Anthony Hallam, R. G. Johnson, D. C. Rhoads,

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Solene Roming Whybrow skillfully prepared figure 2.

## SUMMARY

1. Survivorship data can be inferred from living and fossil bivalve mollusk dead shell size-frequency distributions and can be related to the autecology of the organisms studied.

2. A growth relationship, D = s ln (T + 1) — where D is the size, s a constant, and T the age — is suggested as a correction factor for non-linear growth in bivalve mollusks.

3. *Yoldia limatula,* an infaunal proboscidial deposit-feeding nuculanid, has a constant rate of mortality for most of the life cycle considered, in a habitat where it is a dominant form. It has somewhat higher juvenile mortality in a less favorable (?) habitat.

4. *Arisaigia placida,* a Siluro-Devonian nuculanid, had a constant mortality rate. All evidence points to the fossil assemblage being undisturbed.

5. *Mulinia lateralis,* a small suspension-feeding mactrid living in muds, shows very high juvenile mortality and much lower adult mortality. This is explained by the juveniles' proneness to clogging with silt, relative to the greater hardiness of the adults. High mortality plus sporadic (in time and space) success in colonization make this species locally dominant in the death assemblage, while often being rare or absent as living members of mud bottom communities.

## APPENDIX

All available evidence supports the conclusion that the Stonehouse fauna collected experienced little post-mortem current transport (Bambach, ms). All sediments are highly bioturbated, and associated current structures are lacking in the horizons sampled. Valves of many bivalve species occur in a variety of sizes and are oriented randomly on the bedding surfaces. In many cases bivalves have been found in life position or with the two valves of the organism in close proximity or articulated. The surface detail on the specimens is very well preserved, and valves are almost never found broken. As far as can be judged, all the members of the associated fauna are ecologically compatible and are well adapted to living in muds. This fossil assemblage is believed to be an excellent example of a Johnson (1960) "Type I" *in situ* assemblage.

A composite size-frequency distribution was used in the survivorship analysis. This is because any individual bed yielded too few specimens to give reliable results. However, if one combines the collections of a few localities and compares this with another such combination, one finds very similar size-frequency distributions (fig. 11). This same observation applies to the size frequency distributions of the Upper Cretaceous bivalve, *[illegible]ardia subquadrata,* where year classes may be traced from locality to locality (Speden, ms, and in preparation).

If growth rates and the general ecological setting of a species were similar from place to place, as seems to be the case in the Stonehouse fauna, then one would expect similar mortality patterns and, hence, similar size-frequency distributions in the respective localities. In other words, if size-frequency distributions show similarities from

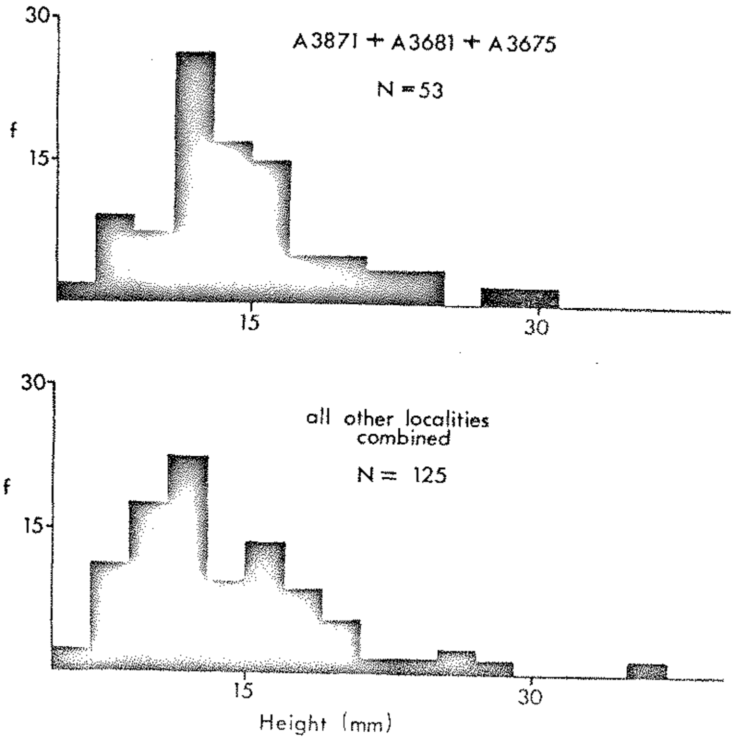


Fig. 11. Similarity of different size-frequency distributions representing different collections, for *Arisaigia placida.* Numbers preceded by "A" are Peabody Museum (Yale University) locality numbers.

locality to locality, then the probability of transport in all localities is minimized. Current sorting, due to a chance distribution of current velocities in widely scattered localities, would produce dissimilar distributions. However, if one finds different size-frequency distributions in different localities, it does not necessarily follow that transport has occurred. It may be that the environmental mosaic varies strongly and thus yields a set of widely differing mortality patterns.

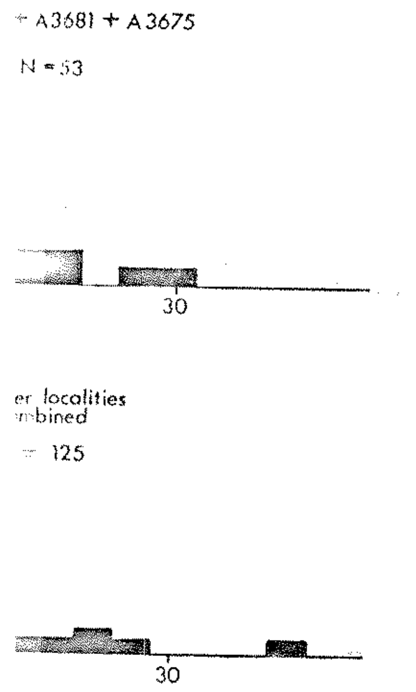
The only effects, other than similar mortality patterns and growth rates, which could yield similar size-frequency distributions, would be diagenetic effects, such as size-preferential solution. But the various bivalve species in the Stonehouse collections have different size-frequency distributions. Since some species collections have high frequency peaks at sizes much smaller than the modal size of the *Arisaigia* distribution presented, significant diagenetic effects are probably precluded. Bivalve shells were certainly dissolved since only composite molds are found. But the fine surface detail on the fossils indicates that the shells were buried and the molds were formed before solution occurred to a significant degree. Still, it is the case that specimens smaller than about 5 mm high were not found. This may be due to low mortality rates, in combination with rapid growth, or poor calcification of small individuals.

## References

Allen, J. F., 1954, The influence of bottom sediments of the distribution of five species of bivalves in the Little Annemessex River, Chesapeake Bay: Nautilus, v. 68, p. 56-65.

Bambach, R. K., ms, 1969, Bivalvia of the Siluro-Devonian Arisaig Group, Nova Scotia: Ph.D. dissert., Yale University.

Caughley, Graeme, 1966, Mortality patterns in mammals: Ecology, v. 47, p. 906-918.



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Devonian Arisaig Group, Nova Scotia:

mammals: Ecology, v. 47, p. 906-918.

g, G. Y., 1967, Size-frequency distributions of living and dead populations of pelecypods from Bimini, Bahamas, B.W.I.: Jour. Geology, v. 75, p. 34-45.

g, G. Y., and Hallam, Anthony, 1963, Size-frequency and growth ring analyses of *Mytilus edulis* and *Cardium edule* and their paleoecological significance: Palaeontology, v. 6, p. 731-750.

ey, E. S., Jr., 1947, Life tables for natural populations of animals: Quart. Rev. Biology, v. 22, p. 283-314.

x, G. A., 1899, *Yoldia limatula*: Johns Hopkins Univ. Biology Lab. Mem. 2, 3 p.

de, J. B., 1954, Survival of soft-shell clams, *Mya arenaria*, buried at various depths: Maine, Dept. Sea and Shore Fish. Research Bull. 22, 26 p.

llam, Anthony, 1965, Environmental causes of stunting in living and fossil marine benthonic invertebrates: Palaeontology, v. 8, p. 132-155.

______ 1967, The interpretation of size-frequency distributions in molluscan death assemblages: Palaeontology, v. 10, p. 25-42.

tton, H., 1938, Essais de bionomie explicative sur quelques espéces intercotidales d'algues et d'animaux: Inst. océanog. Annales, v. 17, p. 241-348.

kson, J. B. C., 1968, Bilvalves: spatial and size-frequency distributions of two intertidal species: Science, v. 161, p. 479-480.

mson, R. G., 1960, Models and methods for the analysis of the mode of formation of fossil assemblages: Geol. Soc. America Bull., v. 71, 1075-1086.

gensen, C. B., 1966, Biology of suspension feeding: Oxford, Pergamon, 357 p.

allec, J. A., and Drury, W. H., 1968, Structure of the New England Herring Gull population: Ecology, v. 49, p. 644-675.

istensen, I., 1957, Differences in density and growth in a cockle population in the Dutch Wadden Sea: Archives néerlandaises Zoologie, v. 12, p. 351-454.

artén, Björn, 1953, On the variation and population dynamics of fossil and Recent mammal populations: Acta Zool. Fennica, v. 76, p. 1-122.

______ 1954, Population dynamics, a new method in paleontology: Jour. Paleontology, v. 28, p. 286-292.

______ 1958, Life and death of the Pleistocene Cave Bear: a study in paleoecology: Acta zool. fennica, v. 95, p. 1-59.

______ 1964, Population structure in paleoecology, *in* Imbrie, John, and Newell, N. D., eds., Approaches to Paleocology: New York, John Wiley, p. 91-106.

oosanoff, V. L., 1962, Effects of turbidity on some larval and adult bivalves: Gulf and Caribbean Fish. Inst., 14th annual session, Proc., p. 80-95.

oosanoff, V. L., and Tommers, F. D., 1948, Effect of suspended silt and other substances on the rate of feeding of oysters: Science, v. 107, p. 68-69.

Mason, James, 1957, The age and growth of the scallop, *Pecten Maximus* (L.), in Manx waters: Marine Biol. Assoc. [U.K.] Jour., v. 36, p. 473-492.

Moore, H. B., 1931, The muds of the Clyde Sea area. III. Chemical and physical conditions, rate of sedimentation and fauna: Marine Biol. Assoc. [U.K.] Jour., v. 17, p. 325-358.

Murie, A., 1944, The wolves of Mount McKinley, *in* Fauna of the National Parks of the U. S.: Washington, D. C., U. S. Dept. Interior, Natl. Parks Service, Fauna Ser. 5, 238 p.

rton, J. H., 1926, On the rate of growth of *Cardium edule*. Part I. Experimental observations: Marine Biol. Assoc. [U.K.] Jour., v. 14, p. 239-279.

Pratt, D. M., 1953, Abundance and growth of *Venus mercenaria* and *Callocardia morrhuana* in relation to the character of the bottom sediments: Jour. Marine Research, v. 12, p. 60-74.

Pratt, D. M., and Campbell, D.A., 1956, Environmental factors affecting growth in *Venus mercenaria*: Limnology and Oceanography, v. 1, p. 2-17.

Rhoads, D. C., 1963, Rates of sediment reworking by *Yoldia limatula* in Buzzards Bay, Massachusetts, and Long Island Sound: Jour. Sed. Petrology, v. 33, p. 723-727.

Rhoads, D. C., and Young, D. K., 1970, The influence of deposit feeding benthos on bottom sediment stability and community trophic structure: Jour. Marine Research, in press.

Sanders, H. L., 1956, Oceanography of Long Island Sound, 1952-1954. X. Biology of marine bottom communities: Bingham Oceanog. Colln. Bull., v. 15, p. 345-414.

______ 1958, Benthic studies in Buzzards Bay. I. Animal-sediment relationships: Limnology and Oceanography, v. 3, p. 245-258.

______ 1960, Benthic studies in Buzzards Bay. III. The structure of the soft-bottom community: Limnology and Oceanography, v. 5, p. 138-153.

Savilov, A. I., 1957, Biological aspect of the bottom fauna groupings of the North Okhotsk Sea: *in* Nikitin, B. N., ed., Marine Biology: Inst. Oceanography Trans., v. 20, p. 67-136.

Slobodkin, L. B., 1961, Growth and regulation of animal populations: New York, Holt, Rinehart and Winston, 184 p.

Speden, I. G., ms, 1965, Paleozoology of Lamellibranchia from the type area of Fox Hills Formation (Upper Cretaceous, Maestrictian), South Dakota: Ph.D. dissert., Yale Univ.

Stickney, A. P., and Stringer, L. D., 1957, A study of the invertebrate bottom fauna of Greenwich Bay, Rhode Island: Ecology, v. 38, p. 111-122.

Stanley, S. M., 1970, Relation of shell form to life habits in the Bivalvia (Mollusca): Geol. Soc. America Mem. 125, in press.

Tenore, K. R., Horton, D. B., and Duke, T. W., 1968, Effects of bottom substrate on the brackish water bivalve *Rangia cuneata*: Chesapeake Science, v. 9, p. 238-248.

Weymouth, F. W., and McMillin, H. C., 1930, The relative growth and mortality of the Pacific razor clam (*Siliqua patula* Dixon) and their bearing on the commercial fishery: Washington, Bur. Fisheries Bull., v. 46, p. 543-567.