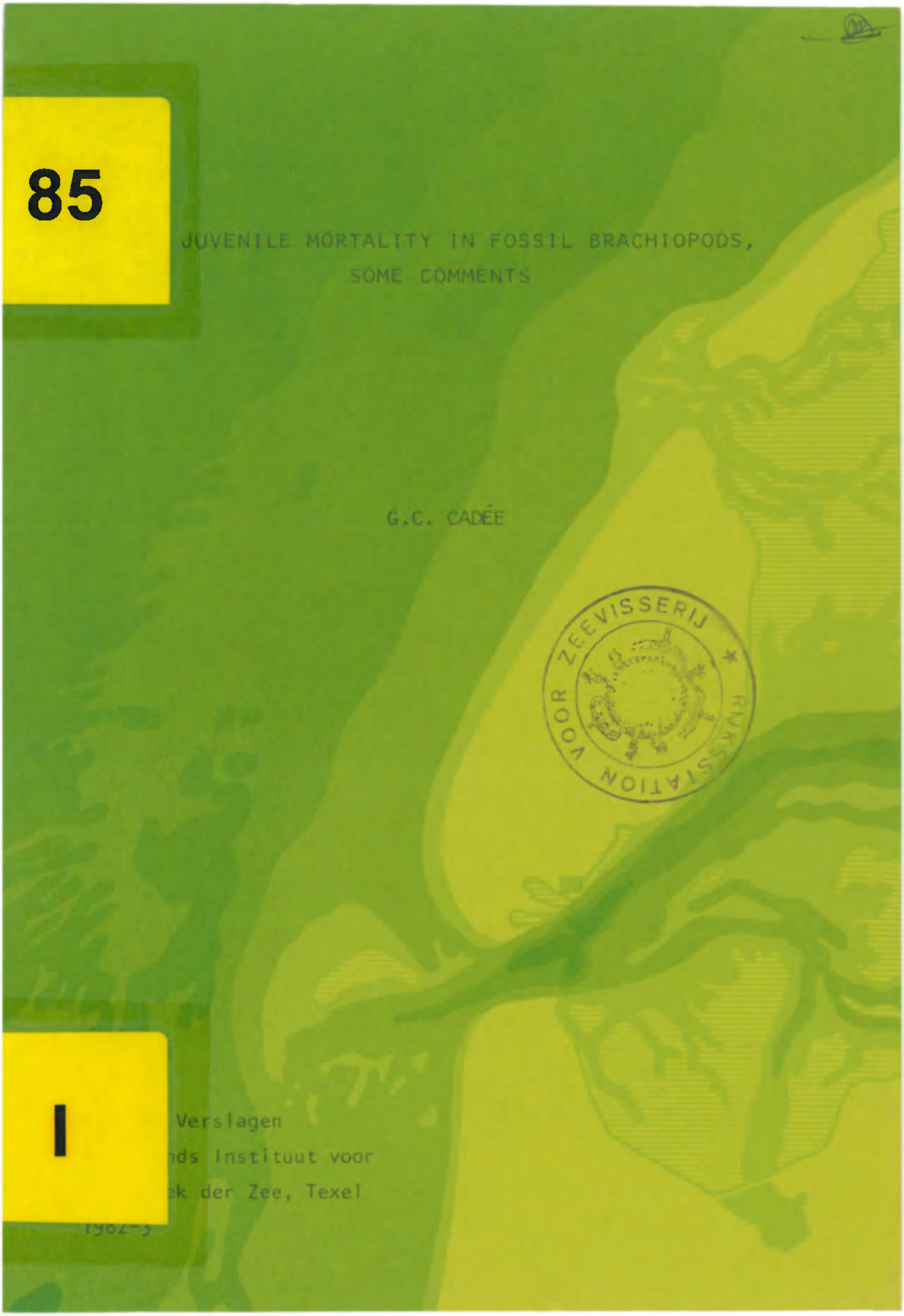

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JUVENILE MORTALITY IN FOSSIL BRACHIOPODS, SOME COMMENTS

G.C. CADÉE

RIJKSSTATION VOOR ZEEVISSERIJ

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Verslagen
nds Instituut voor
ek der Zee, Texel
1982-5

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LOW JUVENILE MORTALITY IN FOSSIL BRACHIOPODS, SOME COMMENTS

by

G.C. CADÉE

CONTENTS

SUMMARY

Assemblages of fossil brachiopods are often characterized by the absence of juvenile specimens. This absence may be due for instance to method of collection, transport by currents, mechanical destruction, diagenetic solution, predation, factors that all may work selectively on small specimens. In some instances, where it was assumed from a taphonomic analysis that these factors could be excluded, low or even absence of juvenile mortality was given as an explanation. These cases are reviewed and alternative explanations are proposed. So, the assemblage could be the result of mass-mortality (census-assemblage) of a population without juveniles due to the fact that this "census" was taken some time after the last successful recruitment. Another explanation is that adults and juveniles live spatially separated, the assemblage of shells accumulating

at localities where the adults live then contains no juvenile specimens. Recent examples of spatial separation of adults and juveniles are given for different groups of marine organisms which shows this phenomenon to be widespread and not only occurring in vagile animals.

As long as other explanations are available, low juvenile mortality should be used with great reservation to explain the absence of juveniles in fossil assemblages, as such mortalities are rarely observed in present-day marine animals.

Although juvenile mortality is usually high in the planctonic larval stage it is by no means restricted to this stage as stated sometimes. Also just settled benthic organisms are highly vulnerable to predation and other causes of mortality.

I. INTRODUCTION

BOUCOT (1953) suggested that a not transported fossil assemblage would contain many juvenile specimens due to high juvenile mortality; transported fossil assemblages would be characterized by bell-shaped size-frequency distributions. BOUCOT's paper has stimulated research in size-frequency both for Recent organisms and for fossils. This resulted in the opinion that size-frequency distributions are not well suited to distinguish transported and not-transported assemblages. Bell-shaped size-frequency distributions were found in assemblages supposedly not transported (HALLAM, 1961; CADÉE, 1968; SURLYK, 1972 a.o.), whereas transported assemblages may contain numerous juvenile specimens (SAMTLEBEN, 1973; TREWIN, 1973; own observations in Wadden Sea).

Another use of size-frequency data seems more promising as these data can give an insight into the population dynamics of fossils. An assemblage of fossil or Recent organic remains represents the preserved deaths of a population. If growth-rate is known, size can be related to age. Growth-rate can be measured if annual growth-rings are present, or by postulating a simple logarithmic relationship: $D = s \ln(T + 1)$, where D is size, T is time and s is a constant (LEVINTON & BAMBACH, 1970). From the size-frequency data survivorship curves can be constructed (KURTÉN, 1953, 1964; CRAIG & HALLAM, 1963; CADÉE, 1968; LEVINTON & BAMBACH, 1970; HALLAM, 1972). To obtain reliable survivorship curves obviously it is of great importance that all deaths be preserved.

Many size-frequency distributions of fossils are bell-shaped (BOUCOT, 1953; OLSON, 1957) leading to convex survivorship curves (survivors plotted on a logarithmic scale) which would indicate a low or even absent juvenile mortality. High juvenile mortality seems to be normal, however, in Recent marine invertebrates (MOORE, 1958, p. 12; THORSON, 1966), although complete data exist for only a few species. HALLAM (1967, p. 33) cites examples from Recent Mollusca. For brachiopods PAINE (1963) also found a high juvenile mortality after settlement in *Glottidia pyramidata*, but NOBLE et al. (1976) report a high mortality over the whole life of *Terebratulina septentrionalis*, and THAYER (1977) found a constant mortality in *Terebratalia transversa* amounting to 32.7% in the first year after settlement. But, as THAYER's mortality data are based on one census annually, juvenile mortality was presumably much higher; the number of spat which settled after one census and died before the next one is unknown (THAYER, 1977, p. 105). DOHERTY (1979) observed a mortality from egg to settlement of

98% and mortality in the first year after settlement was of the same size in a Recent subtidal population of *Terebratella inconspicua* in New Zealand. Some adults survived at least 14 years. CRAIG & OERTEL (1966), varying recruitment, growth-rate and mortality-rate in their computer experiments, always found a great number of small individuals in their simulated dead populations.

Different explanations have been suggested for this discrepancy between Recent and fossil examples. The absence of juveniles in fossil assemblages may be due to collection failure, current transport, mechanical destruction and diagenetic solution, factors that all may work selectively on smaller specimens. Also predation may be size selective (BROADHURST, 1974; SEED, 1975) reducing chances for fossilisation.

Careful bulk-sampling has produced several fossil brachiopod assemblages with many juveniles, indicating that high juvenile mortality may occur (VEEVERS, 1959, sample B; SURLYK, 1972, 1973, 1974; RICHARDS & BAMBACH, 1975; PEDLEY, 1976). However, the same authors found also bell-shaped size-frequency distributions, which were supposed not to be affected by collection failure, transport, mechanical destruction or solution. In these cases low juvenile mortality was given as an explanation for the absence of juveniles.

In this paper, reviewing literature data, suggestions are given for alternative explanations for the absence of juveniles in samples. One of these was already provided by CADÉE (1968): if juveniles and adults live spatially separated, a non transported assemblage of skeletal remains from the site where the adults live will consist of adult specimens only and a "survivorship-curve" based on the size-frequency distribution in this assemblage will erroneously suggest a low juvenile mortality. Spatial separation of juveniles and adults occurs in different groups of marine organisms and is probably widespread not only in vagile animals.

II. EXAMPLES OF SPATIAL SEPARATION OF JUVENILES AND ADULTS IN MARINE ORGANISMS

Migration from a nursery area to the adult habitat occurs frequently among marine organisms. It is best documented for shallow water and intertidal species. Some samples are given in Table I. YONGE (1962) and THORSON (1964) give more examples of juveniles of infaunal bivalves which start their benthic life bysally attached. A mechanism by which young postlarval bivalves migrate is "byssus drifting": by secretion of a primary byssus thread they are easily transported even by small currents (SIGURDSON, et al., 1976). This postlarval migration might be widespread among bivalves; it was found in all the 20 species tested by these authors even in species not possessing a byssus in adult life. YONGE (1962, p. 113) suggests a byssal apparatus to be universally present in bivalve postlarvae.

For those brachiopods which live their whole life attached by a pedicle or cemented to the substrate with a valve or spines, migration will be possible. THAYER (1977) observed this for the pediculate *Terebratalia transversa* which was unable to reattach itself when detached. However, RICHARDSON & WATSON (1975) have demonstrated that a pedicle is not always used for attachment to a solid substratum but may also occur in free-living brachiopods: the Recent *Magadina cumingi* lives in loose sediments and uses its pedicle for elevating

TABLE I

Recent examples of spatial separation of juveniles and adults in respectively fishes, crustaceans, polychaetes, bivalves, gastropods, echinoderms and brachiopods.

Species	Juvenile habitat	Adult habitat	Reference
Anguilla anguilla	Sargasso Sea	European rivers	SCHMIDT, 1922
Pleuronectes platessa	Shallow coastal waters (Wadden Sea)	Deeper water, North Sea, small and large individuals spatially separated	GARSTANG, 1909; ZIJLSTRA, 1972
Solea solea	Shallow coastal waters (Wadden Sea)	Deeper water, North Sea	ZIJLSTRA, 1972
Clupea harengus	Shallow coastal waters (Wadden Sea)	Deeper water, North Sea	ZIJLSTRA, 1972
Clupea sprattus	Shallow coastal waters (Wadden Sea)	Deeper water, North Sea	ZIJLSTRA, 1976
Gadids	Pelagic, North Sea	Near bottom, often small and large individuals spatially separated	MUUS, 1966
Carcinas maenas	Tidal flats, on algae, Wadden Sea	Gullies, Wadden Sea, North Sea	KLEIN BRETELER, 1976
Crangon crangon	Tidal flats, Wadden Sea	Gullies, Wadden Sea, North Sea	BODDEKE, 1975; HAVINGA, 1930
Penaeids	Shallow water	Deeper water	GREEN, 1968
Arenicola marina	High, nearshore tidal flats, Wadden Sea	Also lower flats, whole Wadden Sea	THAMDRUP, 1935 p. 85; SMIDT, 1951, p. 70
Nereis virens	Sublittoral	Littoral	BASS & BRAFIELD, 1972
Amphidesma ventricosum	Subtidal, Australia	Exposed beaches	CASSIE, 1955
Gemma gemma	Main tidal flat, quiet places	More exposed parts of same tidal flat	BRADLEY & COOKE, 1959
Macoma balthica	High, near coastal tidal flats, Wadden Sea	Wadden Sea and adjacent part of North Sea	DE VLAS, 1973; BEUKEMA,
Mytilus edulis	On filamentous substrates	On existing mussel beds	BAYNE, 1964; DE BLOK & GEELEN, 1959

TABLE I (Cont.)

Species	Juvenile habitat	Adult habitat	Reference
Mya arenaria	Bysally attached as epifauna	Infaunal	KELLOGG, 1899; YONGE, 1962
Chlamys islandicus	Bysally attached outside entrance fjords, north Norway	Free-living, inner parts fjords	GRUFFYDD, 1976
Chlamys opercularis	Bysally attached restricted part Ria de Arosa	Free-living widespread Ria de Arosa	CADÉE, 1968
Littorina littorea	Zostora leaves, stones Wadden Sea	Tidal flats	SMIDT, 1951
Nassarius pygmaeus	On Ulva, shallow water Ria de Arosa	On mud, deeper water	CADÉE, 1968
Turritella communis	Shallow water, Millport, Plymouth	Deeper water	FRETTER & GRAHAM, 1962, p. 571
Low intertidal gastropods	High intertidal	Low intertidal	VERMEIJ, 1972
High intertidal gastropods	Low intertidal	High intertidal	
Asterias rubens	On Zostera, algae, Wadden Sea	Deeper water, mussel beds	MORTENSEN, 1927; own observations
Neothyris lenticularis	Attached	Free, rolling over sea bottom	NEALL, 1970
Glottidia pyramidata	On sand	In seagrass meadows	PAINE, 1963

the shell when it becomes burried by sediment. Moreover, RICHARDSON (1981 a, b, c) observed that *Neothyris lenticularis*, *Terebratella sanguinea* & *T. inconspicua* live either attached or free-lying and CURRY (1981) found free-lying and attached living *Terebratulina septentrionalis* in one and the same sample from 241 m depth off Nova Scotia.

A number of brachiopods live attached as juveniles but free as adults. MUIR-WOOD & COOPER (1960) and GRANT (1966) give examples of productoids where juveniles live attached by spines and adults are free living. SURLYK (1973) demonstrated that two inarticulate Cretaceous brachiopods (*Isocrania)* were free living when adult, whereas juveniles lived attached with one valve to small objects. In adult free-living brachiopods with juveniles living attached by a pedicle, the pedicle atrophies later as can be judged for example by the gradual shrinking and final plugging of the foramen or by a progressive incurving of the ventral umbo and final blocking of the foramen (RUDWICK, 1965; 1970). A Recent example is *Neothyris lenticularis* (NEALL, 1970). MANCENIDO & WALLEY (1979) describe ontogenetical alterations of the shell of *Septirhynchia numidiensis*, which changes during life from attached epifaunal to an attached semi-infaunal mode of life. FÜRSICH & HURST (1981) demonstrated that juveniles of the Silurian *Sphaerirhynchia wilsoni* had a functional pedicle but in adults this was atrophied to a non-functional pedicle. The smaller individuals, living attached by means of a pedicle were capable of withstanding agitated environments. The adults lacking a functional pedicle lived in very calm environments where no rapid sedimentation or erosion occurred.

This change from attached to not attached may be accompanied by a change in habitat: *Neothyris lenticularis* adults were found rolling over the sea bottom away from the attached juveniles (NEALL, 1970).

III. TYPES OF FOSSIL ASSEMBLAGES

A fossil assemblage is any group of fossils from a suitably restricted stratigraphic interval and geographic locality (FAGERSTROM, 1964). Following largely the classification of FAGERSTROM (1964) we can distinguish several types of fossil assemblages:

1. a community assemblage (or fossil community) consisting of the gradually accummulated remains of organisms at the place where these organisms once lived and where they died by predominantly natural causes;
2. a census assemblage consisting of the remains of organisms that died by a catastrophic event (mass-mortality);
3. a residual assemblage consisting of only part of the organic remains of the original community whereas the other part, usually the smaller specimens, were transported by currents;
4. a transported assemblage consisting of organic remains which were all transported;
5. a mixed assemblage consisting of a mixture of transported and not transported remains.

BOUCOT's (1953) life assemblage and the fossil community of FAGERSTROM (1964) included both the community assemblage and the census assemblage. A separation between these assemblages is necessary, however, as the size frequency distribution may be quite different. For the construction of survivorship curves a census assemblage can only be used when the recruitment was constant, which seldom occurs. In community assemblages the accumulation of organic remains is due to natural mortality over a longer time that therefore reflects an average mortality rate of many fossil generations that build up the assemblage. The assemblage represents a time-averaged community censu FÜRSICH (1978). Such assemblages are suitable for survivorship studies, but they will provide only meaningful data for the population dynamics of its components if conditions remained relatively stable during their formation.

Size frequency distributions found in census assemblages represent the census of a fossil population at the time of the catastrophe and therefore reflect the casual size frequency distribution of a living population. For Recent brachiopods size frequencies in living populations have been studied now by many authors. THAYER (1975a) gives a review of the types of size frequency distributions found. From his survey it appears that any type may be found: left-skewed, right-skewed, bell-shaped and polymodal. The distributions found will be largely due to the time lapse between the census and the last successful recruitment. If the census is taken shortly after a successful recruitment many juveniles will be present, one or more peaks of older successful years may be found. When the census is taken long after a successful recruitment only large specimens will be found. The success of recruitment may differ from year to year: for the bivalve *Macoma balthica* SEGERSTRÅLE (1960) reports a period of 25 years between two successful spatfalls in a deep water population (35 m deep). In shallower water this period was shorter, which is closer to what is normally found in molluscs.

According to RHOADS (1966), RAUP & STANLEY (1971) and KRANZ

(1974) census assemblages may be more important in the fossil record than formerly recognized. HALLAM (1961, p. 658) supposed the clusters of brachiopods he found in Middle Liassic deposits in England to be the result of mass mortality (census assemblage). Absence of specimens smaller than 3 and 5 mm in these clusters is in my opinion due to the time lapse between recruitment and census, selective predation as suggested by HALLAM seems less likely.

From the study of Recent brachiopods it appears that they can occupy areas with strong currents (McCAMMON & BUCHSBAUM, 1968; NEALL, 1970; THAYER, 1975b), they are certainly not confined to areas with relatively weak currents as supposed by RUDWICK (1965, p. 212 ; 1970, p. 160). Most brachiopods live as epifauna attached to substrates i.e. above the sediment. But RICHARDSON (1981 a, b) points to the great versatility of some Recent species, which have the capacity, as larvae, to utilize virtually any surface - hard substratum or soft bottom - for settlement. In those brachiopods which live attached with a pedicle, the pedicle will decay after death and some transport to a place where the organic remains can be embedded in the sediment and may fossilize will occur. Although such transport may occur over short distance, differences between the living and the dead populations will be the result. Infaunal organisms have a greater chance of being embedded in situ. However, in situ preservation of pediculate brachiopods in life orientation occurs; RICHARDS (1972) gives excellent examples. These in situ preservations can be explained, as HALLAM (1961) did, by mass mortality due to rapid deposition of a layer of sediment.

For a better understanding of size frequency distributions in brachiopods the study of Recent brachiopod populations is helpful. However, not only the size frequency distributions in the living population has to be studied but also that of the accumulated dead remains. As far as the author is aware, the size frequency distributions in both living and dead populations were studied only by STEWART (1981). One of the reasons will be that accumulation in many cases is not at the site where the brachiopods live. CADÉE (1968) for instance found many dead *Crania anomala* specimens in his samples but failed to collect them alive and supposed transport from nearby rocks. NOBLE et al. (1976) must have had the opportunity to study both types of size frequency distributions as they found the accumulation of empty shells of *Terebratula septentrionalis* near the site where the species lived. DOHERTY (1979) extensively studied size frequency distribution of living *Terebratella inconspicua* but mentioned only once that many large intact empty shells were present on the floor of the canyon studied. Moreover, the area was one of occasional, but intense, wave surge so that the sediments will not contain all size classes equally represented (DOHERTY, 1981, in litt.). RICHARDSON (1981 a, b, c) studied both living and dead assemblages, but his data are not yet published in full.

STEWART (1981) provides the first quantitative study of brachiopod populations, both living and dead, from soft substrates. In coastal waters of Stewart Island, New Zealand, death assemblages of *Terebratella inconspicua* were right skewed in shallow subtidal stations, but bell shaped in somewhat deeper stations 15 mm : juvenile shells smaller than 15 m were totally absent, in the same sample also empty shells of *Neothyris lenticularis* smaller than 29 mm were lacking. According to STEWART (1981) the absence of juvenile shells in the death assemblages of Stewart Island may be due to low mortality rates (although in shallower stations high juvenile mortality occurred), to the removal by transport (less likely as the current was not sufficiently strong to remove the silt), or to disintegration of shellsubstance. Decalcification was apparent in large numbers of empty shells. Also the total absence of empty shells smaller than 15 mm strongly favours in my opinion solution: low juvenile mortality would always yield some small shells. Survivorship curves based on death assemblages of the shallow stations of Stewart Island indicating high juvenile mortality are more realistic in my opinion than those based on the deeper water samples, where explanations other than low juvenile mortality are mentioned for the absence of smaller shells.

IV. LOW JUVENILE MORTALITIES FOR BRACHIOPODS AS FOUND IN THE LITERATURE

By careful bulksampling in Danish chalk deposits SURLYK (1972) found assemblages of brachiopods, where transport could not have played a role. Most species were small and apparently had lived attached to small hard substrates mainly delicate bryozoans at the site of burial. For these attached species he found size-frequency distributions with many small specimens, suggesting high juvenile mortality. Their position close to the sediment-water interface was thought to be dangerous, as they could be easily overturned by vagile benthic animals that made them die (in my opinion predation might be more important). Some species *(Magas chitoniformis, Terebratulina gracilis, Trigonosemus pulchellus)* had a different size frequency distribution in some cases almost a bell-shaped one and never an overweight of juvenile individuals. Of these species the adults were free living whereas only the juveniles lived attached. SURLYK gives no illustration of size frequency distribution of these species, in fact the only as adult free living species for which size frequency distributions are given (*Cretirhynchia* sp. and *Carneithyris subcardinalis*, Fig. 16) show many small specimens. As an explanation for the absence of juvenile specimens in these species SURLYK suggests a low mortality rate together with a rapid growth rate for the juveniles. This high growth rate was assumed necessary to pass rapidly through the vulnerable small growth stages. From his growth data (Fig. 22), however, no clear difference in growth rate is apparent in the first 2 years in an adult free living and an adult attached living brachiopod which attained respectively 4 mm and 3.7 mm length after 2 years. It seems therefore that juveniles of both groups of brachiopods were equally vulnerable.

Tentatively one might suggest another explanation for the bell-shaped size frequency distribution in these adult free living species. If the juveniles do not live in the habitat of the adults i.e. when the adults move or are moved away from a nursery area, a bell-shaped size frequency distribution will be found at the place where the adults lived. As long as this possibility is still open, a low juvenile mortality is not proved.

For *Isocrania costata* an Upper Cretaceous brachiopod from northern Europe, also with juveniles living attached and adults free living, SURLYK (1973) reports a size frequency distribution with a juvenile peak and an adult peak. This indicates that also in this as adult free-living species juvenile mortality is high. The adult peak - compared by SURLYK with the adult peak he found in other adult free-living brachiopods - is not very clearly present in his 14 histograms.

These histograms are, however, all based on few specimens (9 to 18 per sample). Although it is not justified to combine all SURLYK's 171 measurements of *Isocrania costata* collected at different localities, it is surprising that this offers a histogram with a neatly right-skewed size frequency distridution (more juveniles than adults)!

BROOKFIELD (1973) explains the absence of juveniles in his sample of *Torquirynchia inconstans* from the Upper Jurassic of southern England by low juvenile mortality. His sample is small (64 specimens used for size frequency distribution) and not collected by bulk sampling. No indication is given whether collection failure might play a role. In adults of 30 to 35 mm length the pedicle lost its function as a supporting structure (BROOKFIELD, 1973, p. 251). The mode of life of these adults is thought to be comparable to that of adult *Neothyris lenthcularis* which are free living on current swept bottoms (NEALL, 1970). BROOKFIELD does not explain the absence of juveniles in his samples as NEALL did for *Neothyris* viz. adults living separated from the juveniles. This explanation finds support in BROOKFIELDS data on distribution of juveniles and adult specimens in the different localities studied: only juveniles are found in location G; juveniles and adults are found in the nearby localities J and I and also in G; in other localities farther away only adults occur (BROOKFIELD, 1973, p. 244).

SHELDON (1974) published 2 roughly bell-shaped size frequency distributions respectively for *Productus hibernicus* and *Rugochonetes* sp. from a Lower Namurian shale (Lancashire, England). Absence of juveniles was explained by low mortality during the first years. Several specimens of both species were collected with complete spines, which indicates that the brachiopods are preserved where they lived. The absence of juveniles can perhaps be explained in a different way. *Productus hibernicus* apparently was free living - the spines are used to stabilize the shell against overturning (RUDWICK, 1970, p. 91). Chonetaceans were also adult free living and could possibly swim (RUDWICK, 1970, pp. 91, 109). In both species juveniles lived presumably attached and possibly not in the same habitat as the adults.

RICHARDS & BAMBACH (1975) studied in situ assemblages of brachiopods from the Upper Ordovician Richmond group (Indiana and Ohio). In 12 populations representing 6 species they found strong right-skewed size frequency distributions indicative of high juvenile mortality. In 4 populations representing 3 species they found left-skewed size frequency distributions suggesting (in their opinion) low juvenile mortality. Their material stems from 9 bulk collections and "life assemblages" (clusters of brachiopods partly preserved in life orientation). These life assemblages are comparable to those of HALLAM (1961). It is remarkable that all the bulk collections provided samples rich in juveniles, whereas 3 of the "life assemblages" yielded samples with many juveniles and from 4 "life assemblages" juveniles were absent. With HALLAM (1961) I am inclined to see these "life assemblages" as the result of mass mortality. The resulting census assemblage may have a right-skewed or a bell-shaped size frequency distribution as explained above. For *Holtedahlina sulcata* a pediculate species (see also RICHARDS, 1972), most of the specimens were found in their life position in a cluster several individuals thick. Some of the brachiopods had their commissure overgrown but were still in life orientation. According to RICHARDS & BAMBACH, this is not in keeping with a mass mortality of the whole cluster. However, this cluster closely resembles a *Mytilus* bank, where the upper ones are alive, living attached to the lower dead specimens, still intact but buried in sediment which accumulated due to the activity of the suspension-feeding *Mytilus*. This leaves open the possibility that a catastrophe killed the upper layer of living *Holtedahlina*.

WALKER & PARKER (1976) studied size frequency distribution and growth of 2 Middle Ordovician brachiopods from Tennessee. In both species juvenile specimens were absent. For *Strophomena basilica* they constructed a survivorship curve with almost absence of mortality over the first 2 years of life. According to the authors the animal probably changes at the age of 2½ year from a pediculate to a free living semi-infaunal life habit. In my opinion this opens the possibility that the attached juveniles and the free living adults did not live at the same locality. Shells accumulating at the place where the adults lived give information only on adult mortality. Moreover RUDWICK (1965, p. 202) suggests that some Strophomenidae were able to swim like free-living pectinids. For *Rostricellula rostrata* WALKER & PARKER (1976) found clusters with all sizes represented, probably due to catastrophic death (op. cit. p. 193). They are comparable to the clusters studied by HALLAM (1961), which were also the result of catastrophic death. They thus represent a census assemblage and hence of doubtful value for the construction of a survivorship curve (see above). The examples given by WALKER & PARKER (1976) are not indicative of low juvenile mortality. Other explanations for the absence of juveniles are possible.

In Miocene deposits on Malta, PEDLEY (1976) found different size frequency distributions for *Terebratula terebratula* in a bioherm margin and the adjacent green sand deposits. Many juveniles were present in the bioherm margin but in the green sand only adults were found. PEDLEY (1976, p. 224) suggests that strong currents or wave action prevented colonization of *Terebratula terebratula* in the greensand area, except during brief periods of ameliorating conditions. Providing that these calmer conditions prevailed for the greater part of the first year of life, then the young terebratulids would become sufficiently large to withstand the rougher conditions which subsequently occurred. Such a long quiet period in an area where strong currents and wave action are reported to prevail seems improbable. The absence of juveniles in the green sand could be due to transportation by these currents. The green sands are found east of the bioherm, PEDLEY (1976, p. 232) gives arguments for a net eastward transport of sea water. Clusters of *Terebratula* in the greensands apparently consisted of specimens which lived attached to each other as shown by borings in the shells due to the pedicle attachment, comparable to those reported by BROMLEY (SURLYK (1973). These clusters might be torn loose from the bioherm and transported to the area, comparable to clusters of mussels bysally attached to each other which may be transported and found on tidal flats away from the mussel banks.

WEST (1977) suggests low juvenile mortality and recruitment failure of successive generations to be responsible for the presence of only few juveniles in a cluster of the strophomenide brachiopod *Meekella striatocostata* in life orientation (Pennsylvanian, Iowa). According to WEST an influx of fine grained sediment overwhelmed the individuals of this cluster. In my opinion therefore this is nice example of a census assemblage and the "census" is taken long after the last successful recruitment. This cluster cannot be used for the construction of a survivorship curve as WEST does, because recruitment was not constant.

HALLAM (1972) and RICHARDS & BAMBACH (1975) cite an *Epithyris oxonica* sample of McKERROW et al. (1969) as an example of low juvenile mortality in brachiopods. However, McKERROW et al. state that their sample comes from an intertidal channel (p. 56) where smaller shells are clearly selectivly transported (p. 71).

According to RICHARDS & BAMBACH (1975), VEEVERS (1959, p. 892) sample C (*Schizophoria apiculata* from the Upper Devonian of W. Australia) could be another case of low juvenile mortality. VEEVERS, however, suggests that sample C is a transported assemblage.

V. LOW JUVENILE MORTALITY IN RECENT MOLLUSCS

Brachiopods are relatively unsignificant in the Recent marine environment, they were far more abundant in earlier periods, especially during the Paleozoic. The Permian extinction affected brachiopods profoundly, but bivalves only little; as a result bivalves occupied much of the ecospace vacated by brachiopods during the Permian crisis (GOULD & GALLOWAY, 1980). Recent molluscs are far better studied than Recent brachiopods and population dynamic studies of many Recent bivalves are published. Therefore various authors have tried to find examples of low juvenile mortality in the literature on Recent bivalves for comparison with supposed low juvenile mortality in fossil brachiopods.

SAVAGE (1956) is often cited as giving an example of low juvenile mortality in *Mytilus edulis* (CRAIG & HALLAM, 1963; McKERROW et al., 1956, p. 72; WORSLEY & BROADHURST, 1975).

SAVAGE describes a very heavy spatfall in spring 1940 in the Conway estuary after the severe winter of 1939/1940. Exact data on the mortality of this spatfall cannot be found in his paper. Juvenile mortality would have been very difficult to measure especially as the young mussels migrated. Those which had settled on the sand were removed in summer by the wind. Some of the juveniles were stranded at high water mark and died. REYNOLDS (1969) studied *Mytilus* beds in the same Conway estuary and reports on the heavy predation especially on the juveniles by *Carcinus maenas* (REYNOLDS, 1969 pp. 10, 13). DARE (1976), working in the nearby Morecambe Bay, observed 96.6-100% mortality in *Mytilus* in the first year after settlement. SEED (1976) reviews data on mortality in *Mytilus edulis* and cites no case of low juvenile mortality. This apparently did not occur in the Conway estuary in 1940, but spatfall had been so enormous that, although juvenile mortality was high, large numbers survived. In tank experiments (SAVAGE, 1956, p. 17) little mortality occurred. This, however, cannot be cited as an example of low natural mortality as CRAIG and HALLAM (1963, p. 774) did. In the tanks mortality was low because predators (*Asterias*, *Carcinus*, *Purpura*, birds) were absent as also was removal by currents.

Low juvenile mortality in *Mytilus edulis* and *Cardium edule* reported by CRAIG & HALLAM (1963) and often cited (*e.g.* DODD & STANTON, 1981, p. 358) as a recent example in molluscs, has already been criticized by CADÉE (1968) and SAMTLEBEN (1973). Absence of juvenile shells in their (storm) beach samples - transported assemblages - can have causes other than juvenile mortality. Under comparable conditions SAMTLEBEN (1973), TREWIN (1973 and CADÉE (unpublished) found samples with many juveniles.

SHELDON (1965) cites *Urosalpinx cinerea* studied by HANCOCK (1959) as an example of low juvenile mortality in a Recent gastropod. From HANCOCK's paper it is evident that the absence of juveniles in his sample of empty gastropod shells may be due to collection failure the mesh size of his dredge being too large to collect juveniles quantitatively.

SHELDON (1974) quotes WEYMOUTH et al. (1931) who described populations of the pacific razor clam *Siliqua patula* where 95% survived to 5 years. However, these authors clearly state that 95% survived after their first winter, mortality in the first year is not included. Moreover, the 95% survival is a maximum. They give a range of 1.7% to 95.8%. Data on mortality in the first year were not given. WEYMOUTH et al. (1925) followed the settlement and survival in 1923 of *Siliqua patula* on Copalis beach, Washington. From 1 August to 4 December they found a growth from 2.5 mm to over 16 mm and a mortality of 66%. A heavy storm shortly after 4 December destroyed almost the whole population and from the 1.2% remaining, nothing remained in the next summer. The example quoted by SHELDON (1974) gives no idea of juvenile mortality. Moreover the method of estimating mortality from the frequency of the year classes in one census of the living population as used by WEYMOUTH et al. (1931) seems questionable when recruitment varies strongly from year to year as in *Siliqua patula*.

It is not always realized (RIGBY, 1958; STUMP, 1976) that survivorship curves normally are given with survivors plotted on a log-scale. RIGBY constructs the size frequency distribution of empty shells of a hypothetical shelled organism, with a growth rate declining with age and a J-shaped survivorship curve following DEEVEY (1947, p. 312) who suggests J-shaped survivorship curves to be characteristic for oysters.

However, DEEVEY used a log-scale, and RIGBY plots this J-shaped curve on a linear scale. Transforming RIGBY's survivorship curves to curves with a log-scale for survivors; we see that RIGBY in fact used a convex survivorship curve for his hypothetical population. The bell-shaped size frequency distribution which results will therefore not surprise us. Recalculating his data we find a mortality of 30% in the first year and about 64% in the second and third year: a relatively low juvenile mortality which is not in accordance with the high juvenile mortality suggested by DEEVEY to be characteristic of oysters.

STUMP (1975) constructed survivorship curves with survivors plotted on probability paper. Without being aware of this difference from the normally used semi-logarithmic paper, he compares his curves with those of others who used a log-scale.

Moreover, some of his survivorship curves (Figs. 9, 14, 15) show the impossibility of an increase in survivors with increasing time.

High juvenile mortality is not confined to planctonic larval stages as stated by CRAIG & HALLAM (1963), RAUP & STANLEY (1971) and DODD & STANTON (1981) *i.a.* In *Mytilus edulis* larval mortality is high (see e.g. BARKER JÖRGENSEN, 1981), but mortality is also high during the first year after settlement (REYNOLDS, 1969; DARE, 1976; SEED, 1976). For *Ostrea edulis* KORRINGA (1941) calculated that out of one million larvae produced only about 250 attach themselves and metamorphose. Of this newly set spat 95% die before the onset of winter! Such high mortalities in planctonic larval and early bottom stages observed in bivalves are in accordance with results obtained by DOHERTY (1979) in studying the Recent brachiopod *Terebratella inconspicua* (see p. 3-4).

VI. SOME OTHER EXPLANATIONS FOUND IN LITERATURE FOR THE ABSENCE OF JUVENILE BRACHIOPODS

BOUCOT (1953) found a bell-shaped size frequency distribution for brachiopods in 5 out of 6 samples from the Lower Devonian of Maine. They are explained as belonging to transported assemblages ("death assemblages"). OLSEN (1957) explains the absence of juveniles in 5 samples of Paleozoic brachiopods by "size selective physical and biological factors".

HALLAM (1961, p. 658) gives mass mortality as an explanation for his bell-shaped size frequency distribution in Middle Lias brachiopod clusters from Leicestershire (census assemblage). NEAL (1970) compares his Pleistocene sample of *Neothyris ovalis* consisting of adults only with the Recent *Neothyris lenticularis* where adults are free living on current-swept bottoms and juveniles live attached at a different site.

Juveniles of *Isocrania egnabergensis* in Upper Cretaceous deposits in Scandinavia were thought to be transported causing a bell-shaped size frequency distribution of the remaining shells (SURLYK, 1973). SURLYK & CHRISTENSEN (1974) explained an assemblage of *Crania stobaei* as a census assemblage to account for the absence of juveniles. WORSLEY & BROADHURST (1975) describe their Atrypid population from the Silurian of southern Norway in which juveniles are missing as a residual assemblage.

This enumeration, which is by no means exhaustive, indicates that in some cases explanations other than low juvenile mortality have been given to account for the absence of juvenile brachiopods in assemblages.

VII. CONCLUSION

Low juvenile mortality in fossil brachiopods was concluded from the absence of juvenile shells in not transported fossil assemblages, where selective transport and/or destruction could not account for this absence. In most cases reviewed however, other explanations could be envisaged for this absence of juvenile shells. Data on low juvenile mortality in Recent molluscs, extracted from the literature for comparison with the supposed low juvenile mortality in fossil brachiopods, appeared to be misquotations. In the light of studies of the Recent marine environment low juvenile mortality seems highly unlikely to occur. On the contrary, high juvenile mortality seems to prevail in Recent macro-benthic organisms. This can best be illustrated with a quotation from THORSON (1966, p. 286) based largely on work published later by MUUS (1973): "Actually, so many different types of true and even potential predators are ready to attack the macrobenthos at all levels of its development and upgrowth, that it may seem surprising that, in spite of all, a number of macrobenthic animals large enough to secure the next generation can survive to full adult size and maturity".

High juvenile mortality is not confined to the planctonic larval stages as stated by some authors. Studies of mortality in Recent brachiopods suggest high juvenile mortality after settlement (PAINE, 1963; NOBLE et al., 1976; THAYER, 1977; DOHERTY, 1979):

The examples of low juvenile mortality in brachiopods from the literature are not conclusive. We have suggested other explanations for the absence of juveniles in the samples. One of these possibilities - adult and juveniles living spatially separated - was given special attention. BROADHURST (1964) a.o. stressed the importance of size selective predation and the possible cooperation of different factors together. As long as other explanations for the absence of juveniles exist, the size-frequency data cannot be used for the construction of meaningful survivorship curves. The many variables operating in the establishment of fossil assemblages make analysis of population dynamics in fossil organisms very difficult if not impossible.

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