SOME ASPECTS OF THE PALAEOECOLOGY OF THE E_1b ZONE OF THE EDALE SHALES (NAMURIAN) IN THE EDALE VALLEY, DERBYSHIRE

by

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Summary

The sediments and faunal composition of the E_1b zone of the Edale Shales at Edale were examined and recorded. The faunal diversity was plotted by means of a rarefaction graph, the value of which in palaeoecological interpretations is questioned. It is concluded that the sediments were deposited in the bathyal marine zone under either aerobic or anaerobic conditions. The posidonoid bivalves are considered to have led an epifaunal benthonic existence as suspension feeders. They are further analysed to determine (1) the opportunistic and specialist species, (2) the natality and mortality structuring of their populations, and (3) the variation of death rates with sexual maturity and age within each population.

Introduction

The Namurian Edale Shales of north Derbyshire form a sequence of dark grey mudstones and limestones, often carbonaceous, containing disseminated pyrite. They vary in thickness from about 200 m in the type area (the Edale valley) to about 400 m in the Alport valley (Hudson and Cotton, 1943, 1945; Stevenson & Gaunt, 1971), and have been interpreted as a sequence of basinal marine shales formed by the deposition of mud from the suspension load in a low energy environment. The marine nature of these sediments is indicated by the presence of goniatites, and the disseminated pyrite suggests stagnant bottom conditions (Walker, 1966; Collinson, 1969; Selley, 1976).

The 7 m of sediment which comprise the *Eumorphoceras pseudobilingue* zone (E_1b) of the Edale Shales (Table 1) in the Edale valley, are exposed in the banks of the River Noe at the core of the Edale anticline. The top of this zone has not been defined by Hudson and Cotton (1945), but it is taken by the authors of this article to be represented by a thin band of extensively burrowed argillaceous limestone exposed in the River Noe, (SK 10858481). The burrows in this band represent a number of organisms which displayed a complex behaviour pattern in their excavating or burrowing activities. The upper 6 m of the sequence consist of flaggy, well bedded carbonaceous, paper shales, while the lower 1 m is a fossiliferous black shale containing some rounded calcareous nodules.

All the lithologies examined were fossiliferous, with the calcareous fossils occuring in small lenses, less than 1 m in diameter, and irregularly distributed. No trace fossils or sedimentary structures, other than parallel laminations, were observed in the entire sequence, and all the macrofossils examined possessed a crushed recrystallised calcareous skeleton.

For the purposes of this study the distribution, composition, and population structure, in terms, for example, of size and numbers of the faunas, were examined both laterally and vertically through the sequence.

Mercian Geol., Vol. 6, No. 3,
1977, pp. 179-196, 6 text-figs.

Table 1 Faunal zones of the Pendleian (E_1), Arnsbergian (E_2), Chokierian (H_1) and Alportian (H_2) stages present in the Edale Shales of North Derbyshire.

Stage	Zone No.	Goniatite index fossil
Alportian	H_2c	*Homoceras magistrorum*
	H_2b	*Homoceras undulatum*
	H_2c	*Hudsonoceras proteus*
Chokierian	H_1b	*Homoceras beyrichiacum*
	H_1a	*Homoceras subglabosum*
Arnsbergian	E_2d	*Nuculoceras nuculum*
	E_2c	*Nuculoceras stellarum*
	$E_2b(2)$	*Cravenoceratoides nititoides*
	$E_2b(1)$	*Cravenoceratoides edalensis*
	$E_2a(2)$	*Eumorphoceras bisulcatam*
	$E_2a(1)$	*Cravenoceras cowlingense*
Pendleian	E_1c	*Cravenoceras malhamense*
	E_1b	*Eumorphoceras pseudobilingue*
	E_1a	*Cravenoceras leion*

Composition of the Fauna

Comprised either goniatites and/or bivalves, between 3% and 5% of the latter occurred as articulated valves, both gaping and closed.

The macrofauna observed is listed as follows, and its distribution through the succession is illustrated in text-fig. 1:

(1) Bivalvia

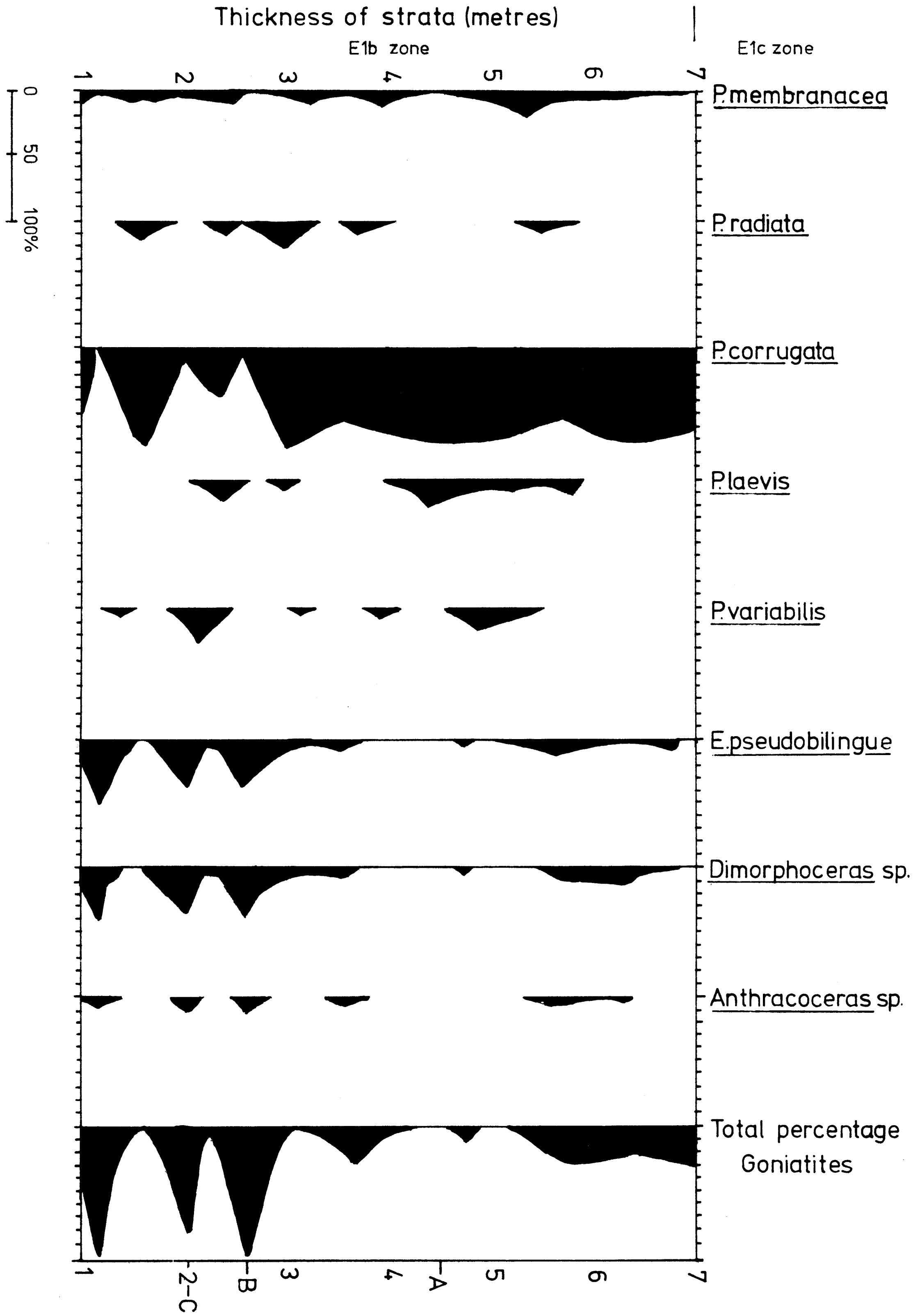
Posidonia corrugata (Etheridge)
Posidonia membranacea (McCoy)
Posidonomya radiata (Hind)
Posidoniella laevis (Brown)
Posidoniella variabilis (Hind)

(2) Ammonoidea (Goniatites)

Anthracoceras sp.
Dimorphoceras sp.
Eumorphoceras pseudobilingue (Bisat)

(3) Others

Fish fragments and plant debris constitutes from 0.1% to 1% of the rock by volume as particles greater than 1 mm.



Text-fig. 1. Distribution of the fauna through the E_1b zone.

A rarefaction graph has been drawn for the fauna as a measure of faunal diversity (text-fig. 2). No broad interpretations in terms of climatic provinces and depth, such as those produced by Duff (1975) and Calef and Hancock (1974), have been made from the graph because we have doubts as to the validity of its usage, for the following reasons:

(1) The current ecological rarefaction curves which are used as a basis for palaeoecological interpretations are drawn using both the soft bodies and the calcareous shelled members of the fauna (Sanders, 1968). Among fossils, examples of soft bodies organisms preservation are a rarity, and even burrows are no real indication of the actual diversity of the soft bodied content of the benthonic substrate (Davis, 1964, 1965, 1967). These factors must be considered when comparing past and living faunas.

(2) Rarefaction curves from modern shell deposits are rarely comparable with those of the fauna from which the deposit was derived (Antia, in press, and text-fig. 2).

(3) Rarefaction curves from adjacent beds deposited under similar conditions may be vastly different, reflecting sedimentological processes rather than biological diversity (text-fig. 2). As Antia (in press) has shown changes in this diversity, in both its gradiational and varietial components, are mirrored in the fossils only when sedimentological transport of the sediment is minimal. Since the species composition of the live and dead faunas at a given locality tend to be dissimilar, (Antia, in press) except where both the fossils occur in life orientation, little reliance can be placed on an ecological interpretation of faunal diversity when the fossils are dispersed.

An examination of relative percentages of Bivalvia left and right valves reveals that although they occur in approximately equal numbers throughout the sequence, occasionally some lenses may be almost completely devoid of left or right valves. Such biased concentrations are rare, and indicate that some differential sedimentological sorting has taken place (Van Straaten, 1952; Craig, 1967). All the single valves were orientated concave down.

Numerical Analysis of the Fauna

1. Size Frequency Distributions

Biogenetic growth rings of the bivalves proved impossible to differentiate, so size has been used as a measure of age (Hallam, 1972). The reliability of external growth ring analysis in palaeoecology, has been questioned by Farrow (1971 a, b; 1972).

As bivalves are often without a calcareous skeleton for part of their first year of life and achieve their highest mortality rates in that year, no truly representative trace of their first year of life can be expected to occur in the fossil record. A representative sample of the population later in life can be expected as fossils, if it is first assumed that little sedimentological sorting of the bivalves has taken place and secondly that all mortalities were preserved. In reality, both assumptions fail.

Explanation of text-fig. 2.

Fig. 2(a)	for selected beds in the E_1b zone (letters correspond with those given in Fig. 1).
Fig. 2(b)	for the molluscan faunas of (1) the littoral mudmound topography of Sales Point, Bradwell, Essex (see Greensmith and Tucker, 1967) (2) for the subtidal benthonic muds seaward of the offshore shell bank at Sales Point. In both instances the prefix "L" by a curve indicates that it represents the actual diversity of the living molluscan community, the prefix "D" indicates the dead molluscan fauna represented on the benthos at the same location at which the community was sampled.
Fig. 2(c)	for the top five beds of the shelly Waltonian Red Crag, at Walton on the Naze, Essex, representing beds 7 - 11 of Kendall (1931). The beds are labelled with Kendall's lettering on the graph, s.d. is the standard deviation from the mean of the collections. A total of 14,000 individual specimens were considered.

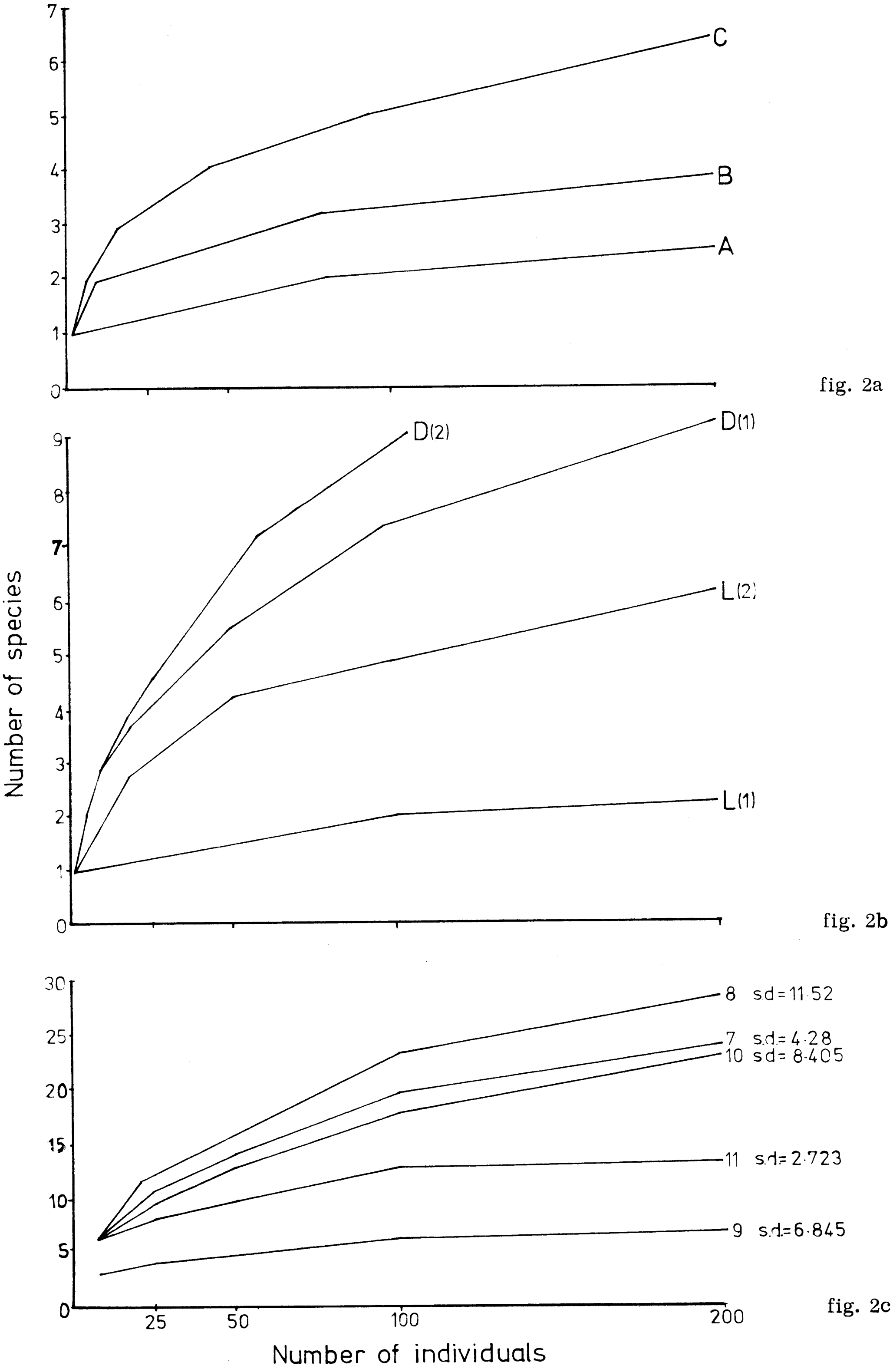


fig. 2a

fig. 2b

fig. 2c

Text-fig.2. Rarefaction curves (Explanation on facing page).

The size frequency distribution of the bivalve faunas of the Edale Shales are shown in text-fig. 3 alongside similar distributions for (1) a sedimentologically unsorted life assemblage of *Anodonta* sp., collected by Miss C.E. Rodgers at Stoney Cove Quarry, Leicestershire (SP. 495952), and (2) a sedimentologically sorted death assemblage of *Glycimeris glycimeris* (Linn) from the Waltonian Red Crag (Pleistocene) at Walton on Naze, Essex, (collected by D.D.J.A.). These graphs suggest that the Edale Shale bivalve fauna has undergone minimal sedimentological sorting and may be regarded as representative of the original life population.

As it is not possible to conduct detailed population growth studies on fossils, their populations will be discussed in terms of a life-table. Detailed explanations of the applicability of such tables to fossils are given by Reyment (1971); the tables form a convenient and informative way of presenting geological data on population deaths and numbers in the fossil record in a manner which allows conclusions on the probabilities of death and survivorship to be made. Life-tables for the fauna under consideration are given in Table 2, while their age pyramids and survivorship curves are given in text-fig. 3 and 4 respectively.

Table 2 Life Tables for the Bivalve fauna of the E_1b zone of the Edale Shales, Edale, Derbyshire. (Continued on the opposite page).

Key to the interpretation of the colums of the tables:

1. Age interval in standard time-spans x to x+1 (where x is given in terms of shell length in mm.)
2. Age interval in standard time units x to x+1 (where x is given as the number of age intervals lived)
3. Proportion dying in interval (x, x+1)
4. Number living at age x (represents number of survivors at each age x)
5. Number dying in interval (x, x+1) expressed as 3 (m) x 4 (m)
6. Number of time-spans lived in interval (x, x+1) expressed as 4 (m) - $\frac{1}{2}$ (5 (m))
7. Total number of time-spans lived beyond age x, expressed as the total sum of the number standard time-spans lived in each age interval beginning with age x
8. Observed expectation of life at age x. This is the average number of time-spans yet to be lived by an individual, now aged x.
9. Proportion of survivors over the age interval (x, x+1)

Life table for *Posidonia corrugata* (Etheridge)

Sample Size	1	2	3	4	5	6	7	8	9
29	2-4	1	0.193334	10000	1933	9034	21203	2.1203	0.81
48	4-6	2	0.396694	8067	3200	6467	12169	1.5085	0.60
43	6-8	3	0.58904	4867	2867	3434	5702	1.17156	0.41
19	8-10	4	0.63333	2000	1267	1367	2268	1.134	0.37
7	10-12	5	0.63636	733	466	500	901	1.229	0.36
1	12-14	6	0.25	267	67	234	398	1.4906	0.75
1	14-16	7	0.33333	200	67	167	167	0.835	0.67
2	16-18	8	1.00000	133	133	-	-	-	-

Life table for *Posidonia membranacea* (McCoy)

Sample Size	1	2	3	4	5	6	7	8	9
9	4 - 5	1	0.2143	10000	2143	8929	16547	1.65	0.7875
18	5 - 6	2	0.5455	7857	4286	5714	7618	0.97	0.4545
14	6 - 7	3	0.9335	3571	3334	1904	1904	0.53	0.0665
1	7 - 8	4	1.0000	238	238	-	-	-	-

Life table for *Posidoniella laevis* (Brown)

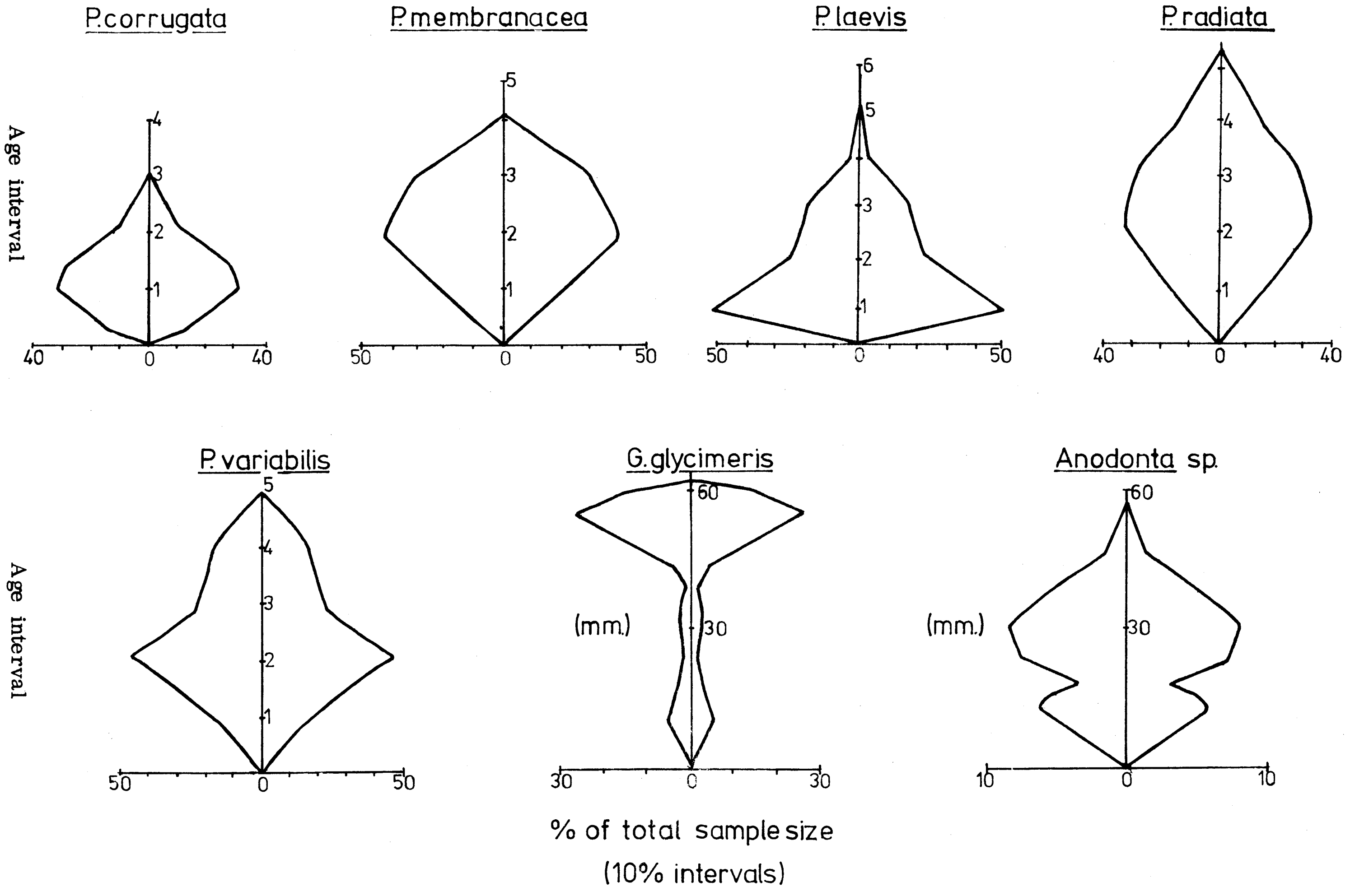
Sample Size	1	2	3	4	5	6	7	8	9
46	2 - 4	1	0.5652	10000	5652	7174	14156	1.42	0.4348
20	4 - 6	2	0.2001	4348	870	3913	6982	1.61	0.7999
16	6 - 8	3	0.7985	3478	2777	2090	3069	0.88	0.2015
4	8 - 10	4	0.5000	870	435	653	979	1.13	0.5000
2	10 - 12	5	0.5011	435	218	326	326	0.75	0.4999
1	12 - 14	6	1.0000	217	217	-	-	-	-

Life table for *Posidoniealla variabilis* (Hind)

Sample Size	1	2	3	4	5	6	7	8	9
9	2 - 4	1	0.128	10000	1280	1360	17360	1.736	0.972
24	4 - 6	2	0.6471	8500	5500	5750	8000	0.9417	0.3329
9	6 - 8	3	0.5000	3000	1500	2250	2250	0.750	0.5000
9	8 - 10	4	1.000	1500	1500	-	-	-	-

Life table for *Posidonomya radiata* (Hind)

Sample Size	1	2	3	4	5	6	7	8	9
13	0 - 2	1	0.1711	10000	1711	9145	20790	2.08	0.8289
25	2 - 4	2	0.39679	8289	3289	6645	11645	1.40	0.6032
22	4 - 6	3	0.579	5000	2895	3553	5000	1.00	0.421
10	6 - 8	4	0.6251782	2105	1316	1447	1447	0.69	0.375
6	8 - 10	5	1.000	789	789	-	-	-	-



Text-fig. 3. Size frequency distribution (age pyramids) of the bivalve faunas referred to in the text compiled from data in Table 2.

By comparing the age pyramids produced from the life-table with those of recent age (Clapham, 1972, p. 94) certain conclusions can be reached about the bivalve fauna, provided it is first assumed that only limited sedimentological size sorting has occurred. These conclusions are summarised in Table 3.

From a comparison of the survivorship curves for the bivalve faunas (text-fig. 4) and the hypothetical patterns for organism survivorship outlined by Deevey (1950) and Valentine (1973), the following conclusions can be drawn about the mortality within the Edale Shale bivalve species:

(1) *Posidonia membranacea* initially has a low mortality rate which then increases rapidly over a narrow time span.

(2) *Posidonia corrugata*, *Posidonomya radiata* and *Posidoniella variabilis* have constantly increasing mortality rates with age.

(3) *Posidoniella laevis* has a constant mortality rate at all ages.

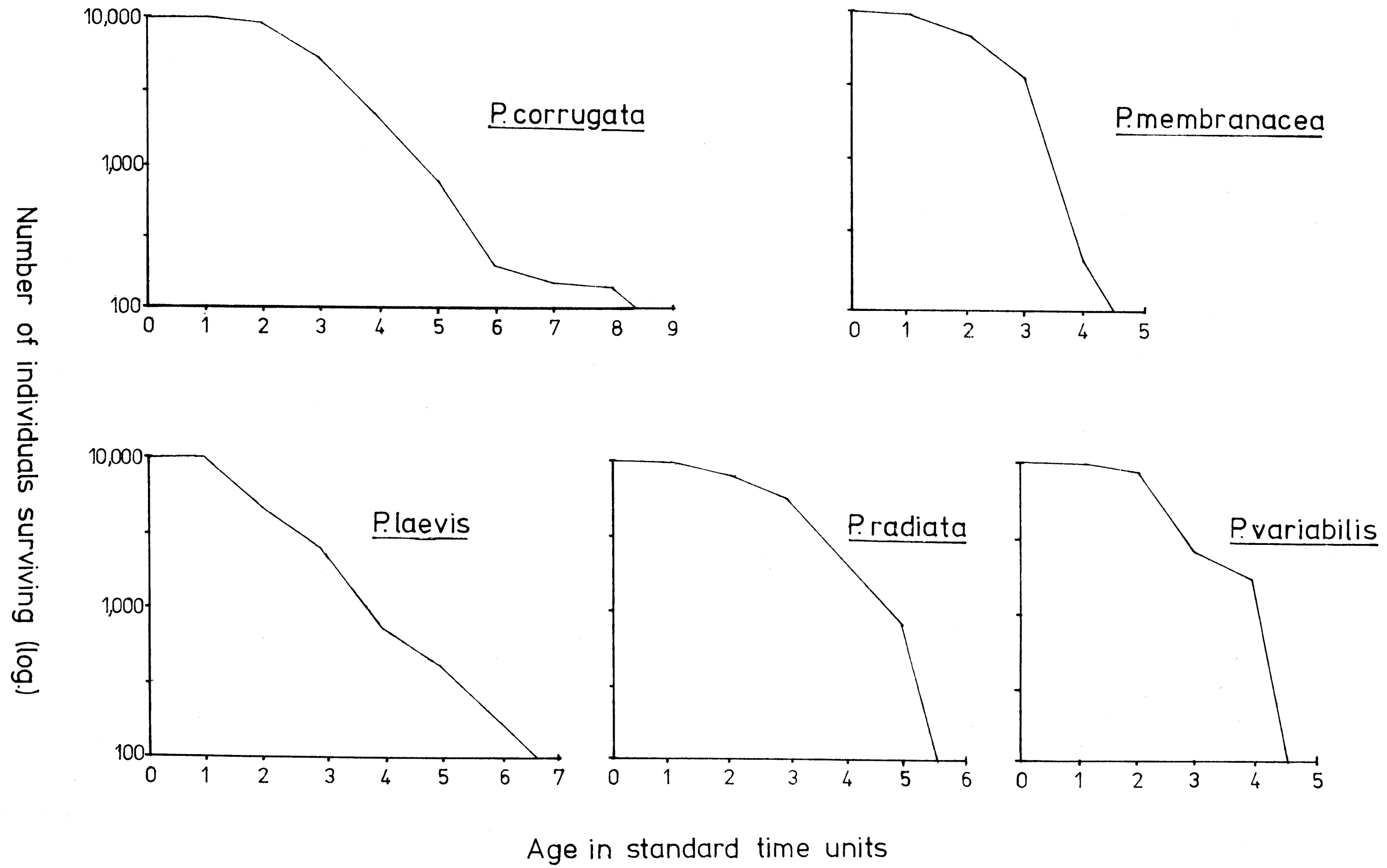
Text-fig. 5 depicts the age mortality distributions of the bivalve faunas. It is assumed that a high juvenile mortality rate exists in these species during the larval planktonic stage. Although some of the graphical irregularities of the various population figures (Table 2) may be due to sample error, they will be treated here as if such error was non-existent, according to the principles outlined by Sellmer (1967). A benthonic mode of life (to be discussed later) is assumed throughout for these bivalves.

Table 3. An age structure table to illustrate relative natality and population structure. (Interpretation based on the graphs in text-fig. 3.

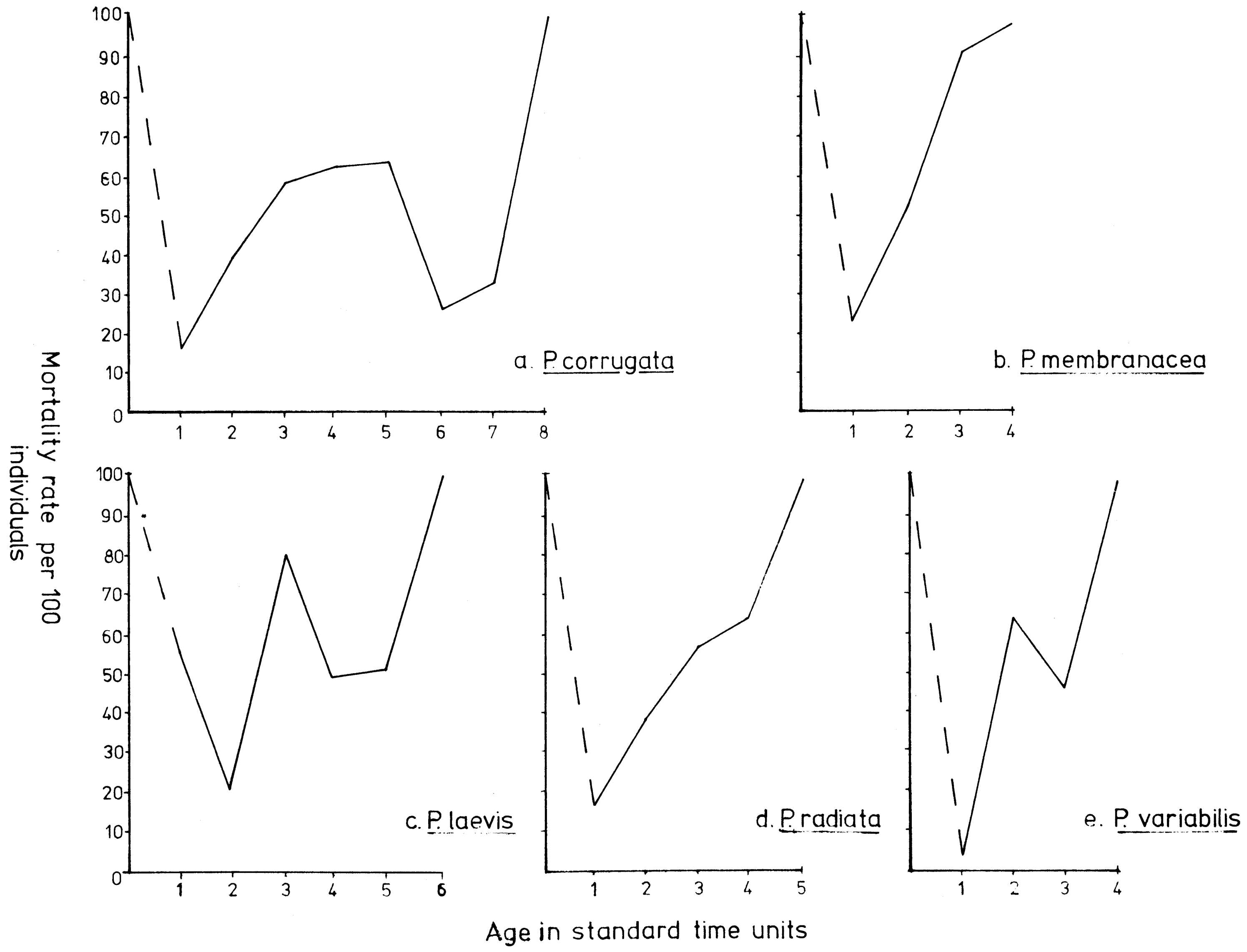
	Age distribution of:	Very few young	Species producing intermediate number of young	Many young
1.	Stable population	-	-	*P. laevis*
2.	Expanding population	-	*P. membranacea*	*Anodonta* sp.
3.	Contracting population	-	-	*P. radiata*
4.	Over exploited population	-	-	*P. corrugata* *P. variabilis*
5.	Sedimentologically sorted population	-	*Glycimeris glycimeris*	

(1) *Posidonia corrugata* (text-fig. 5a) The mortality rate at time unit 1 may represent the normal death rate, due largely to predation on sexually immature animals. The increasing mortality rate between time units 1 and 3 may reflect the sexual maturation of the species, with the increased death rate being a by-product of a drain on the animals physiological resources due to reproduction. The higher constant mortality rates of time units 3, 4, and 5 may result from the combined effects of a population of sexually mature adults and the environment (including predation) acting together possibly in equilibrium on the death rate. The removal of the reproductive survivorship constraint, due to senility, may explain the lower mortality rate in time units 6 and 7. The high mortality rate during time unit 8 presumably represents physiological breakdown due to gerontism.

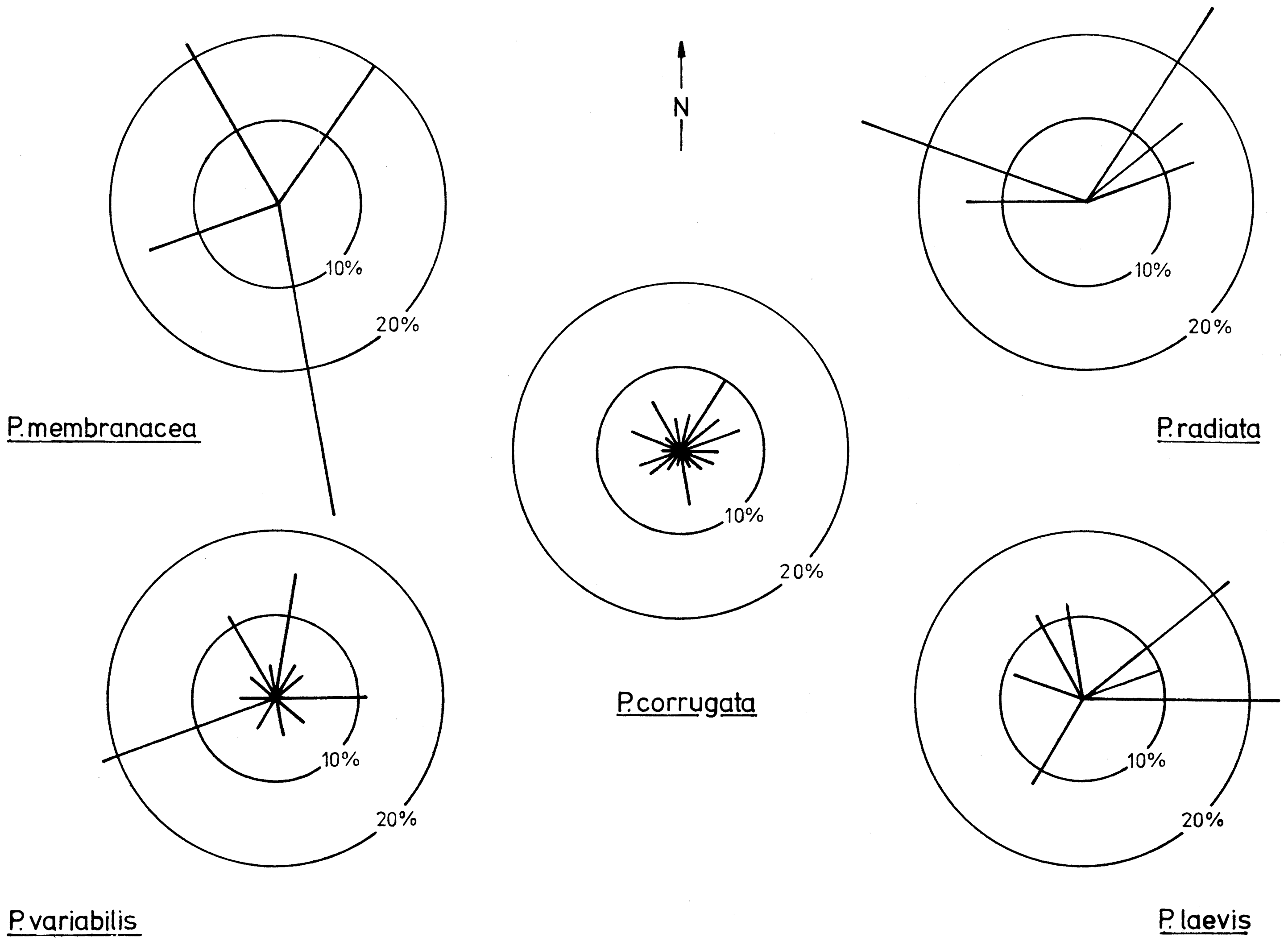
(2) *Posidonia membranacea* (Fig. 5b) Time unit 1 again represents the mortality rate of a sexually immature population. The constraints on survivorship are emphasised by the increased mortality rates in time spans 2 and 3, resulting, presumably from the sexual maturation of the population and associated fatalities, and in time span 3 from the additional burden of deaths due to ageing; the latter being the prime cause of the high mortality rate in time unit 4.



Text-fig. 4. Survivorship curves for the bivalve fauna of the Edale Shales compiled from data in table 2, pp. 184-5).



Text-fig. 5. Age mortality graphs compiled from data in table 2 (p.184-5).



Text-fig. 6. Orientation of the bivalves. Plot represents dorso-ventral axis.

(3) *Posidoniella laevis* (Fig. 5c) The decrease in the mortality rate between the first and second time units may be due partially to the physiological adjustment of the stresses and strains of an independent life on the benthos. The mortality rate at time unit 2 probably represents the natural mortality rate for a population of sexually immature individuals suffering from normal predation and physiological wastage. The increased mortality rate forming a peak in time unit 3 may result from a readjustment of the animals physiology on reaching sexual maturity, and its levelling off to an even rate during time units 4 and 5, may represent the equilibrium mortality rate of a sexually mature population. The increase in mortality depicted in time unit 6 again indicates physiological breakdown of the population due to ageing.

(4) *Posidonomya radiata* (Fig. 5d) A low mortality rate at time unit 1 suggests a population of sexually immature individuals. As the population becomes sexually mature the mortality rate increases (time units 2 and 3) until a steady state equilibrium is reached between mortality due to strains on the physiological resources caused by reproduction, and other normative mortality causes (time units 3 and 4). Due to gerontism, this "equilibrium" is disturbed by the physiological breakdown of the population, causing an increase in the mortality rate (time unit 5).

(5) *Posidoniella variabilis* (Fig. 5e) Following previous examples, time unit 1 probably represents the mortality rate of a sexually immature population, caused primarily by predation. The increase in the mortality rate in time unit 2 reflects an increase in mortality due to primary alterations in physiology, the result of sexual maturation. The subsequent decrease in the mortality rate (time unit 3) suggests either equilibrium readjustment of the population or an increase in senility. Physiological breakdown due to ageing is invoked as the primary cause of the increase in mortality in time unit 4.

2. Numerical Frequency Distributions

(1) *Temporal.* The faunal species population variation with time illustrated in text-fig. 1 (p. 181) shows that when bivalves are present goniatites tend to be rare, and that the bivalve *Posidonia corrugata* tends to represent between 83% and 50% of the fauna and is the most successful specialist in this environment (Valentine, 1973), while the "explosive" increases in abundance of some other species, *Posidoniella variabilis*, *Posidoniella laevis* and *Posidonomya radiata* for example, is the criterion used to indicate that they are opportunistic species. The remaining bivalve species, *Posidonia membranacea*, is regarded as a less successful specialist. All the goniatites are regarded as specialist species. The significance of layers composed entirely of goniatites and the mode of life of the bivalve will be discussed later.

(2) *Spatial.* The fossils are distributed in three modes, the first as scattered, randomly distributed skeletons, most of which are bivalves. The second and most common mode of occurrence is as ovoid lenses distributed randomly over the surface of the bedding planes and the third and rarest mode, is that of thin (4 - 9 cm thick) perched shell gravel banks. Such faunal modes of occurrence are known to the authors in close proximity in the lower Lias of Houghton-on-the-Hill, (Leicestershire) in association with the bivalve *Posidonia* sp., and in the Holocene sediments of the River Blackwater, Essex. Here they form either as a result of current activity, or as *in situ* bivalve reef growths.

Mode of Life of the Fauna

Previously the goniatites are considered to have led a planktonic existence (Selley, 1976), while the posidonoid type bivalves are thought to have led a pseudoplanktonic or even bethonic mode of life. The latter are now discussed.

(1) The bivalves may have been pseudoplanktonic, occurring as organisms which were byssally attached to drift wood or seaweed, as suggested by Hudson and Cotton (1943, pp. 149 - 150). It would be difficult to prove that they had been attached byssally during life, and that the wood had been floating rather than lying on the sea floor (Craig, 1954, p. 119). None of the

bivalves seen in this study occurred in intimate association with driftwood or organic remains.

(2) They may have led a planktonic existence, as suggested by Jefferies and Minton (1965). The evidence for this hypothesis is restricted to the presence of anterior and posterior gapes, thin shells, experimental hydrodynamic evidence, and the wide angle of opening of the valves in life. However, much of the interpretation of the evidence used in this hypothesis is speculative.

The thin shelled nature of the shells may be due to a swimming adaptation similar to that found in Pectinacea (Yonge, 1938, p. 81), indicating an adaptation to a shallow benthonic (less than 450 m) (Craig, 1954), or a nectoplanktonic, (Jefferies and Minton, 1965, p. 164), or it may represent an adaptation to a deep basinal (greater than 2,000 m depth) benthonic mode of life, (Lemche and Wingstrand, 1959, p. 63).

Anterior and posterior gapes in the recent Pectinidae and Limidae serve to release the swimming jets, and as a general rule the larger the gapes the greater the swimming ability of the animal (Jackson, 1890; Verrill, 1897). Jefferies and Minton claim that large posterior gapes occur in posidonoid bivalves, but since it is difficult to establish the existence of a nonplanar commisure, an essential attribute of a swimming bivalve, such claims should be treated with caution, especially after suggestions that the commisure can deform, due to the thin elastic nature of the shell, both before and after death (Jefferies and Minton, 1965).

If these gapes do exist they by no means prove a swimming ability, as similar gapes are also found in the benthonic burrower *Mya* where the foot protrudes through the anterior gape and the siphons through the posterior gape. On taxonomic grounds it is unlikely that the posidonoids were burrowers, but their shape, when analysed by the functional morphological methods outlined by Stanley (1975), suggests that they could have survived successfully as such; indeed the vertical orientations recorded for specimens of *Bositra buchi* Romer (a posidonoid) by Hess (1960, p.377) and Jefferies and Minton (1965, p. 168) could be taken as conclusive evidence for a burrowing habitat in some posidonoids.

Jefferies and Minton (1965, p. 157) regard the nature of the sediments in which these bivalves occur to be indicative of an anaerobic benthos which was unable to maintain a molluscan or annelid fauna. Studies of recent sediments, have shown that both hydrogen sulphide and pyrite may be formed in anaerobic conditions which are confined to the subsurface, for example the estuarine muds of the River Blackwater, Essex, and that their presence does not necessitate a foetid benthonic environment for the Edale Shales (Bruce, 1928; Craig, 1954) The fallacy of this facies argument is highlighted by Davis (1967, p. 7) who has found annelids and bivalves living in a foetid environment. Jefferies and Minton suggest that articulated posidonoid valves are nearly always gaping and orientated on the bedding plane concave up. They also suggest that the valve-open position is indicative of swimming ability, yet other bivalves which commonly occur in a similar position on the benthonic muds and beaches of Essex today, *Cerastoderma edule*, *Barnea* sp., and *Scrobicularia* sp. do not possess this ability.

71 articulated bivalves, 56 of which possessed closed articulated valves, orientated with their commisures aligned roughly parallel to the bedding, were recorded in the E_1b zone. This observation is contrary to the posidonoid orientations recorded by Jefferies and Minton (1965, p. 168). Their specimens were orientated with the commisure perpendicular to the bedding. Such orientations can be used as evidence for a burrowing ability, as suggested earlier, but have been interpreted (Jefferies and Minton, 1965, p. 168) as posidonids that fell into a liquid anaerobic mud, closed up and died. If this idea is correct and posidonoid bivalves were nectoplanktonic, then the vertical orientations must, by analogy with the cephalopods, be indicative of a "shallow" benthos, since Weaver and Chamberlain (1976) suggest that vertically orientated ammonoids will not occur if the benthos was deposited at a depth greater than 10 m.

(3) A third hypothesis suggests that *Posidonia corrugata* led a benthonic existence in near foetid conditions (Craig, 1954) and by analogy this mode of life could be extended to the bivalve fauna of the E_1b zone, as a whole and will be briefly discussed along with the environment of the zone.

The currently accepted hypothesis for the environment and ecology of the fauna of the Edale shales suggests a deep basinal environment with foetid bottom conditions containing a planktonic fauna (Hudson and Cotton, 1943, 1945; Selley, 1976; etc. The Edale shales may not have presented foetid bottom conditions. They were certainly marine, deposited in the bathyal zone, above the carbonate compensation depth, shown by the presence of thin shelled calcareous bivalves and in low latitudes, indicated by the nearby Castleton reef complex; (Stevenson & Gaunt, 1971) and from palaeomagnetic data.

The substratum was swept by currents capable of disarticulating bivalved shells, but the absence of shell fragments, despite the fragility of the shells, suggests that the currents were weak, possibly following a north-east to south-west trend as determined by valve orientations (text-fig. 6). *Posidonia membranacea* was orientated both parallel, to and normal, to the direction of current flow.

The goniatites occur throughout the sequence (tex-fig. 2) and are thought to have led a planktonic existence. The bivalves are absent from certain beds which may be due to changes in the conditions operating on the sea floor from time to time, for example fluctuations in the anaerobic nature of the benthos. The bivalves could well have led a benthonic life.

Craig and Jones (1967) suggest that the predominant benthonic organisms on shallow muddy substrates are infaunal, but we saw no evidence for this except in the basal bed of the *Cravenoceras malhamense* (E_1c) zone. In oceanic basins, bivalves may be distributed patchwise on a dark muddy substrate, where they are epifaunal and possess thin shells (Lemche and Wingstrand, 1959). This is comparable to the distribution and nature of the bivalve fauna of the Edale Shales. We conclude posidonoid bivalves of the E_1b zone were motile benthonic swimmers or nestlers rather than nectoplanktonic swimmers or pseudo planktonic attached forms.

Although *Posidonia corrugata* is a specialist species in this environment, the evidence presented by Craig (1954) suggests that in a shallow subtidal environment it is an opportunistic species inhabiting semi-foetid muds. Thus it can be shown that some posidonoids have a wide tolerance range in benthonic environments. If they are benthonic, then they can be described as eurybathic (pertaining to a wide depth range, *Posidonia corrugata* for example) and stenoecious (pertaining to a narrow habitat range), as most prefer a similar habitat of dark (?) semi-foetid muds.

The bivalve trophic nucleus of the E_1b zone (where the trophic nucleus is defined as those species which numerically comprise 80% of the fauna (Neyman, 1967) contains *Posidonia corrugata* as its prime species, with occasional influxes into the nucleus by the opportunistic species. It is thought likely that all the bivalves examined were epifaunal suspension feeders since there is no evidence of bioturbation within this zone. If this is so then the influxes of opportunistic species could be a response to variations in some aspect of environment, such as nutrient content, temperature, salinity or oxygen.

Conclusion

Throughout this study we have tried to produce a palaeoecological interpretation of the fauna, which, although factual in content, is not sacrosanct. In doing so we have appealed to "Occums razor" (as in the instance dealing with the bivalve mode of life) and used techniques which assume that the observed fauna is truly representative of the original, for instance in natality and mortality interpretations. The latter assumption we admit may be invalid but we feel some interpretation of both natality and mortality rates is required from a palaeoecological study such as this, where the operation of bottom currents and hence sedimentological sorting of shells on the benthos was minimal.

The 7 m of sediment which represent the E_1b zone of the Edale shales at Edale, possess a low diversity fauna of bivalves and goniatites, occurring in thin interbedded carbonaceous shales and limestones. The sediments contained no primary sedimentary structures, other than parallel lamination, and no evidence for bioturbation of the substratum. The distribution of the fauna through the sequence, and along individual bedding planes, along with their morphology, and the nature of the sediments leads us to suggest that the bivalves led an epifaunal benthonic, rather than a pseudoplanktonic or nectoplanktonic, existence, in an ocean basin, situated in the bathyal zone, possessing an aerobic or anaerobic benthos. (Davis (1967) has demonstrated that bivalves do live in both types of benthos.)

The individual bivalve species were considered, to determine whether they were specialist or opportunistic species. A life-table has been used to help determine the natality, mortality and age structuring of the population. Further analysis of the mortality rates has enabled discussion of sexually immature and mature populations, and enabled predictions to be made about the size at which the bivalves become sexually mature.

Although we have not been able to prove that our faunal assemblages are life assemblages, we hope that the methods (natality and mortality rate interpretation) introduced in this study will become more widely used by palaeoecologists in the analysis of faunal assemblages found either as life assemblages or as assemblages suffering from minimal sedimentological sorting, thus enhancing our understanding of the organism and its ecology.

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