

The platycopid signal: a means of detecting kenoxic events using Ostracoda

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ABSTRACT — It has been shown that during Jurassic and Cretaceous kenoxic events, while other groups of benthonic Ostracoda severely decline and eventually disappear, the Platycopina tend to survive. The survival of the platycopids is attributed to their being filter feeders who, in dysaerobic conditions manage to obtain sufficient oxygen by virtue of the greater volume of water which they circulate across their respiratory surface in the course of their normal feeding behaviour. The podocopid ostracods, which are predators, scavengers and deposit feeders, are unable to survive the diminished oxygen concentrations which characterise these events. The platycopid genus *Cytherella* is shown to dominate the oxygen minimum zone in two different parts of the Atlantic at the present day.

INTRODUCTION.

All ostracods require oxygen to respire, although some species seem able to survive in surprisingly low levels of oxygen. Infaunal estuarine taxa such as various species of *Leptocythere* and species living among plant and other detritus, for example *Cyprideis torosa* tolerate very low oxygen levels in such dysaerobic environments. Some non-marine members of the Cypridacea also seem able to survive in surprisingly low levels of oxygen concentration. The great majority of species of all the major groups of Ostracoda and especially those living in marine environments, however, seem quite incapable of tolerating even relatively small reductions in oxygen availability.

APPENDAGE MORPHOLOGY: RESPIRATION AND ALIMENTATION

With the exception of some few members of the largely oceanic Myodocopina which, like *Cylindroleberis* possess gills, ostracods lack specific organs for oxygen interchange and it is thought that respiration takes place through the chitinous-like polysaccharide which forms the ventral surface of the body of the animal. Oxygenated water is circulated continuously across this surface by branchial plates situated on two or more of the normally 7 pairs of appendages.

The following synopsis of those appendages of the major groups of marine benthonic Ostracoda which bear branchial plates is of necessity simplistic and intentionally ignores the complications of sexual dimorphism etc. In the Cythereacea (the most abundant and diverse post-Palaeozoic ostracod group), branchial plates occur only on the 3rd (mandibles) and 4th (maxillae) appendages; the Cypridacea bear an additional such plate on the 5th appendage the (first thoracic appendage) although this appendage is more pediform in marine than in freshwater cyprids. The entirely marine Bairdiacea also possess a large branchial plate on the pediform 1st thoracic leg. In these three groups which are essentially benthonic scavengers, predators and deposit feeders, (although at least some marine cyprids can swim

short distances), the circulation of water within the carapace is entirely associated with respiration.

The essentially marine (some brackish species have been described from West Africa) and benthonic Platycopina, as typified by such early Mesozoic to Recent genera as *Cytherella* and *Cytherelloidea* are filter feeders. This is reflected in their appendage morphology where none of the thoracic legs are pediform, the 3rd is lacking and locomotion is effected by means of greatly expanded posterior furcae. In order to perform the functions of alimentation, a larger number of branchial plates circulate water over the ventral surface and the appendages are provided with numerous tufts of pilate setae which effectively sieve out suspended food particles and transport them to the mouth. The thesis of the present paper is that a secondary advantage of such an enhanced circulation is improved respiratory ability which could allow platycopid ostracods to survive in environments of reduced oxygen (Whatley, 1990). Because they circulate more water across the ventral surface in order to feed, they also provide more oxygen which, during a kenoxic event (Cepek & Kemper, 1981) could allow platycopid ostracods to survive while other, non-filter feeding ostracods perished.

PLATYCOPID REPRODUCTIVE STRATEGY

An additional feature which would militate in favour of platycopid survival in dysaerobic conditions is associated with their reproductive strategy. All platycopids brood their young within the carapace and, therefore, the instars will also enjoy the same survival benefits as the adults during periods of low oxygen concentration. Many other marine benthonic ostracods release their eggs into the environment where, during kenoxia, they will neither develop nor survive. Others among the Cythereacea, such as the Xestoleberidae, for example, which although they brood their young, not being filter feeders would have perished anyway.

A further likely advantage to filter feeders during times of low

oxygen levels would be the greater availability of particulate carbon as a food source. Thus the platycopids would have enjoyed a threefold advantage over the other ostracods in these times of crisis based upon their respiration, reproduction and feeding biology.

PLATYCOPIDS AND KENOXIC EVENTS

Although mostly referred to as “anoxic” events (Schlanger & Jenkyns, 1976) times when oxygen levels fell to the point of total anaerobiosis are very rare and possibly have never happened on an oceanic scale. Kenoxic events, resulting in dysaerobiosis, are probably much more common. The distinctions between these two types of event are discussed elsewhere (Whatley, 1990).

A classic example of a kenoxic event is that which took place in the Upper Cretaceous late Cenomanian, and whose effects persisted into the Turonian and which has been documented with respect to Ostracoda (among other organisms) in southern England by Jarvis *et al.* (1988), and Horne *et al.* (1990). These authors (Jarvis *et al.* 1988, pp. 35-44, figs 13, 14; Horne *et al.*, 1990, pp. 125-129, fig. 31; Babint & Crumiere-Airaud, 1990, p. 34, fig. 6) all demonstrate that with the onset of this Upper Cretaceous kenoxic event various elements of the fauna begin to disappear until virtually only platycopids remain.

This is very striking qualitatively when assessed at the generic and specific levels; it is dramatic when actual numbers or percentages of individuals are calculated. For example, in the Cassis section in Provence in the part of the late Cenomanian *Pentagonum Zone*, Babinot & Crumiere-Airaud (1990) found that “the platycopids dominate with *Cytherella ovata* (Roemer) making up 70-80% of the total fauna”. It is interesting to note that the authors record that the remainder of the fauna is made up by *Bairdia* and “some specimens of *Pontocyprilla*”. It has been noted above that the Bairdiacea possess an additional branchial plate on the 1st thoracic appendage; by increasing the amount of water passed over the ventral surface this may assist their survival in dysaerobic environments.

Babinot & Crumiere-Airaud (1990) go on to show that while *Cytherella* together with *Bairdia* remain dominant for a certain interval of the overlying early Turonian, higher up in the succession they are progressively joined by cytheracean species and other taxa such as a *Polycope* and *Macrocypris*. Similarly, in the Cenomanian-Turonian succession of Dover, Jarvis *et al.* (1988) and Horne *et al.* (1990) demonstrate the successive disappearance of podocopid ostracods through the late Cenomanian and early Turonian so that, for example, the former authors state (p.37) that their Bed 8 at the top of the late Cenomanian *Plenus* Marls “yielded an even lower diversity assemblage consisting almost entirely of platycopids”. The less than 5% of podocopids in the bed belonged to a single cytheracean species, *Imhotepia euglyphea*. The same authors (p.44) note that in the overlying lowest Turonian, the fauna is dominated by 5 platycopid species with *Cytherella ovata* making up over 70% of the total fauna. Both groups of authors show that at Dover, as at Cassis, although the same platycopid taxa persist, they are gradually joined by more and more podocopids through the Turonian. The overall increase in diversity is at the expense of the overwhelming dominance of the platycopids.

These two examples from the same Cenomanian—Turonian kenoxic event provide clear evidence of the greater ability of platycopid ostracods to survive episodes of reduced oxygen concentration in comparison with other podocopids. It should be possible, therefore, within the biostratigraphical range of the Platycopina, to use their dominance as evidence of dysaerobic bottom conditions which are

the hallmarks of kenoxic events. This must be done with some care and with the exercise of our knowledge of the ecology and distribution of living representatives of the Cytherellidae. This family (which is virtually synonymous at the present day with the Platycopina) is widely distributed in modern seas and oceans, occurring from the intertidal zone (in the tropics) down to abyssal depths (Whatley, 1988). The family approaches dominance (in terms of numbers of species rather than numbers of individuals) today only in shallow water tropical environments, but these are not oxygen impoverished. On the contrary, they are oxygen rich and sustain rich and varied invertebrate (including reefs), vertebrate and plant communities.

PLATYCOPIDS AND THE OXYGEN MINIMUM ZONE

If the thesis that the platycopids are best able to survive dysaerobiosis is to be considered in the modern context, then the oxygen minimum zone of the oceans is an area in which they might be expected to thrive. In the Atlantic, the oxygen minimum layer lies anywhere between 200 and 800m and is characterised by oxygen concentrations of less than 4ml/l; these are commonly around 3ml/l for the zone in much of the Atlantic but may be as low as 0.5ml/l in such areas as off southwestern Africa (Bubnov, 1966).

Of the two most common living platycopid genera, *Cytherelloidea* is thermophilic and is not found, even in low latitudes, at anything but shallow depths. *Cytherella* on the other hand has been recorded commonly in bathyal and abyssal environments (Whatley, 1983; Whatley & Coles, 1987) and ranges from those depths through the oxygen minimum zone.

Unfortunately, relatively few studies of the Ostracoda of the outer shelf and upper slope have been conducted in such a way as to provide clear evidence of the relationship of the various taxa at oxygen concentrations. However, two studies of Atlantic ostracods provide some evidence to support the hypothesis. Cronin, (1984) studied a transect across the Florida—Hatteras slope, the Straits of Florida and the Blake Plateau off the southeastern United States. He records three species of *Cytherella* and of these, two are most abundant in the oxygen minimum zone of the upper bathyal (*Cytherella* spp. A & B, Fig. 8) while the other, although its depth range is 462-1070m, is most abundant below the oxygen minimum zone (*Cytherella* sp. B, Fig. 9, which from the illustration is clearly *C. serratula* Brady). This species has been found to much greater depths (Whatley & Coles, 1987) but its presence below the oxygen minimum zone, where it usually occurs in the Atlantic, does not negate the importance of *Cytherella* spp., A and B in that zone. The latter two species in several samples within the zone together account for between 50 and 70% of the total Ostracoda (Cronin, 1984).

Dingle *et al.* (1989) in their study of the Ostracoda and their relationship to water masses off southwestern Africa, show that between 200m and 650m “the ostracod assemblage is numerically dominated by *Krithe* and *Cytherella* spp...”. This depth range embraces the oxygen minimum zone.

In order to check whether or not the overwhelming dominance of platycopids at any level in the stratigraphical column was due to conditions being inimical to podocopids rather than being particularly favourable to the filter feeders, it would be necessary, as with the Cenomanian—Turonian examples cited above, to check whether either prior or subsequent to the time in question, podocopids progressively disappeared and/or reappeared.

KENOXIA AND THE PLATYCOPID SIGNAL

It is probable that there are numerous examples in the Mesozoic—Recent interval where the platycopid signal is indicative of a kenoxic event. One such in the Toarcian of Spain gives a distinct platycopid signal in the *Tenuicostatum* Zone (Whatley & Arias, in press). Also in the Lower Jurassic of the Mochras borehole in North Wales, there is an alternation throughout the mid and late Toarcian of Cardigan Bay of dominance between the Cytheracea and the Cytherellidae (Boomer, 1991). It is suggested that the periods of platycopid dominance may be associated with periods of reduced oxygen levels induced by periodic relatively high sea level stands in this basin. The author is currently investigating other Mesozoic, and two Tertiary examples, where platycopid ostracods dominate which may well also be indicative of the prevalence of dysaerobic conditions.

Metacopid ostracods were almost certainly filter feeders. Their frequent monospecific or near monospecific occurrence in Lower and Middle Liassic sequences worldwide, often associated with extensive pyrite, is also a probable signal of kenoxia.

CONCLUSIONS

Platycopid ostracods, because of their filter feeding habit were, by virtue of the increased amount of water passed over their respiratory surface, able to survive in water of such reduced oxygen concentration as to preclude the survival of other benthonic ostracods.

Known kenoxic events in the Cenomanian/Turonian and Liassic of Europe are shown to be typified by the overwhelming dominance of platycopids, and *Cytherella* also dominates in the oxygen minimum zone of the modern North Atlantic.

The platycopid signal should be used to identify kenoxic events in the Mesozoic—Recent interval and other filter-feeding ostracods could be used to pinpoint similar events in the Palaeozoic.

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