

Faunal responses to temporal disequilibrium in the deep sea

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Abstract: The concept of the constant environment in the deep sea at both spatial and temporal scales has been challenged over the last 20 years. Spatial variation is recognised at a variety of scales from centimeters to kilometers. As temporal sampling programmes have taken the place of snapshot observations, we are now aware that spatial heterogeneity varies with time. The main cause of temporal variation in the deep sea is the input of organic carbon from the surface. Fluxes from the surface include large food falls of both animal and macrophyte origin and the seasonal pulse of small particles from surface primary production. There is an increasing body of evidence that, at all latitudes, these inputs can have a seasonally varying component. The response to this temporal variation can be observed in a number of deep-sea species from both temperate and subtropical latitudes, although the dominant response appears to ameliorate the periodic effects and demonstrate quasi-continuous life history processes. This paper will examine the evidence for a temporarily varying environment in the deep sea and assess how life histories of deep-sea invertebrates have adapted to temporal disequilibrium.

Introduction

Constancy and continuity were believed to be the conditions that prevailed in the deep sea below the permanent thermocline. Thirty years ago, MENZIES (1965), in his review of conditions for the existence of life at the deep-sea floor, could find no evidence of temporal variation on an annual or sub-annual basis. This and many other accounts failed to grasp the significance of a single paragraph in MOSELEY's (1880) letter to "Nature" in which he suggested there may be "a little annual excitement at the deep sea floor" generated by the falling of material from the surface. Subsequent data suggested that any such pulse from the surface would be so slow that any seasonal or periodic signal would be dampened out (MENZEL 1974). Conversely, from the earliest deep-sea sampling, spatial variation had been recognised at a gross scale in that the fauna of soft sediment and rock in the sea were different. With the advent of the spade box corer (HESSLER and JUMARS 1974), variation on a small scale could be analysed and this led to a rapid understanding of the small-scale spatial variation at the deep-sea bed that resulted from small-scale disturbances. This spatial heterogeneity has been invoked as the cause of the high species diversity recognised in the deep sea (see GAGE and TYLER 1991).

The understanding of temporal variation was less rapid as it required time series studies and did not lend itself to the rigorous experimentation that was very tractable in understanding spatial variation. Early evidence for temporal variation came in the form of variation in reproduction or population structure (GEORGE and MENZIES 1967, 1968, SCHOENER 1968, ROKOP 1974), whilst understanding of temporal variation in environmental parameters was not forthcoming for at least another 10 years (DICKSON et al. 1982, BILLETT et al. 1983). In this short review I want to explore physico-chemical temporal disequilibrium in the deep sea and examine how faunal response to this disequilibrium occurs. Temporal disequilibrium does not imply seasonal, i.e., annual variation, but a process that varies through time on a scale of days to 1 year.

Temporal variation in the physico-chemical environment

Temporal variation in the physico-chemical environment in the deep sea may be unpredictable or predictable. Unpredictable temporal variations include turbidity currents, benthic storms, and the arrival of large food falls at the deep-sea bed. The only time the last variation may have a predictable component is when the seabed underlies a whale migration route (see TYLER 1988) or when there are known seasonal spawning migrations with subsequent population mortalities that input food packages to the deep-sea bed as in the case of the blue whiting (*Micromesistius poutassou*) (see BISHOP 1982, GORDON and MAUCLINE 1984). Another unpredictable variation is the casting of moults, particularly by crustaceans, when the carapace forms a substratum for the attachment of another (epizoid) species (see below).

The only predictable feature of the deep sea according to the older literature was its lack of variation with time. The last 15 years have conclusively shown that a number of predictable environmental events occur here. Annual variations are seen in the eddy kinetic energy reaching the deep-sea bed in the NE Atlantic (DICKSON et al. 1982, DICKSON et al. 1986), whilst on a smaller time scale semidiurnal tidal variation has been measured at bathyal and abyssal depths (GOULD and MCKEE 1973, LONSDALE and HOLLISTER 1979, ELLIOT and THORPE 1983, LAMPITT et al. 1983, YOUNG et al. 1993). In the clearest waters of the sea, solar radiation will penetrate as deep as 1000 m; this is known to elicit immediate responses in crustaceans but evidence of annual seasonality or other periodicity is lacking.

More significant in controlling deep-sea biological processes is the input of organic matter. On a global scale the dominant input is in the form of particulate organic matter from surface primary production, which in many

parts of the world's oceans has been shown to have a significant seasonal, i.e., annual, component (BILLETT et al. 1983, DEUSER 1986, TYLER 1988, THIEL et al. 1990, RICE et al. 1994). The sinking rate of this material is $\sim 100 \text{ m d}^{-1}$ and during the late spring and early summer it carpets the deep-sea floor in a layer of green phytodetritus. Macrophyte debris may also contribute on seasonal basis, with seagrasses and macroalgae entering the deep sea as a result of seasonal storms and wood entering from spring thaws bringing trees into the ocean (TURNER 1973, TYLER 1988). Although faunal remains contribute to the downward vertical flux (see WIEBE et al. 1979, SMITH 1985), the periodicity (if present) of their temporal variation remains to be determined.

Faunal responses to temporal disequilibrium

As in case of the environmental variation, faunal responses fall into two classes: unknown periodicity and predictable or known periodicity.

Unknown periodicity

From the data available, faunal responses of unknown periodicity are seen in the contrasting life styles of the stalked barnacle *Poecilasma kaempferi* and the wood-boring bivalve *Xylophaga* n.sp.. *Poecilasma kaempferi* lives epizoically on the carapace and legs of the stone crab *Neolithodes grimaldi* at $\sim 2200 \text{ m}$ depth in the NE Atlantic. The rapid reproductive cycle of this barnacle is suggested as being a response to the moulting periodicity of the crab (GREEN et al. 1994). Adult *N. grimaldi* are believed to moult every two years so that *P. kaempferi* has to complete its life cycle before its substratum is shed and the exoskeleton and barnacle sink into the soft sediment. *P. kaempferi* produces egg lamellae within 170 d of settlement (GREEN et al. 1994) and if this production continues for the period between crab ecdyses, sufficient progeny will be released to ensure successful colonisation of another host.

Xylophaga n. sp. relies on the presence of wood in the sea for settlement, growth, and reproduction. Wood is an ephemeral resource in the deep sea, which together with macrophyte remains is known to be colonised by deep-sea invertebrates (KNUDSEN 1961, WOLFF 1976, 1979). Wood may have a seasonal component (TURNER 1973), as may some macrophyte debris in subtropical regions (YOUNG et al. 1994). Experimental evidence from spruce and oak colonization panels deployed for 3 and 6 month periods at 500m depth in the Bahamas indicate that colonisation occurs year round, although there may be greater settlement in the spring (YOUNG and TYLER pers. observ.).

Xylophaga also grows and reproduces rapidly - a strategy adaptive to a temporally as well as spatially varying substratum and food source. As with *Poecilasma* there is a finite time before the usefulness of the resource is exhausted and this has led to a rapid reproductive cycle.

Known periodicity

Predictable or periodic responses are found in a number of deep-sea invertebrate species. The best examples are those that are behavioural or life history responses.

The clearest behavioural patterns involve responses to tidal currents. LAMPITT et al. (1983) have shown that scavenging amphipods are attracted to bait only during periods of low tidal current velocity. LAMPITT and PATERSON (1988) have demonstrated with deep-sea photography that the orientation of the abyssal anemone *Sicyonis tuberculata* is determined by the prevailing tidal current, which aids feeding. GUENNEGAN and RANNOU (1979) suggested that tidal currents could be used for orientation by mobile animals or may act as signals for synchronous spawning. Caution must be exercised in analysing this type of data, as the response to tidal currents may be passive rather than active, especially in sessile species.

Life history responses are best observed in the few deep-sea invertebrates that appear to breed on an annual basis. It should, however, be emphasized that the dominant reproductive pattern in the deep sea is asynchronous "continuous" reproduction. Deep-sea echinoderms are the best examples of predictable, temporally varying reproductive patterns. In the NE Atlantic, *Ophiura ljungmai*, *Ophiocten gracilis*, *Plutonaster bifrons*, *Dytaster grandis* and *Echinus affinis* have seasonally synchronous reproductive cycles (see TYLER 1988, TYLER et al. 1991). At bathyal depths in the Bahamas, practically all the echinoids examined, with the exception of the echinothurids, show a seasonal pattern of reproduction. *Stylocidaris lineata*, for example, exhibits a seasonal reproductive behaviour of "pairing" superimposed on the seasonal gametogenic pattern (YOUNG et al. 1992). The seasonal reproductive pattern in many of these echinoderms is supported by population studies that indicate seasonal life history processes (SCHOENER 1968, GAGE and TYLER 1981a, b, GAGE 1990). In the deep sea, seasonal reproduction is not confined to the echinoderms. ROKOP (1974) presented some early convincing evidence on the brachiopod *Friellia halli* and the scaphopod *Cadulus californicus* from 1250m depth in the San Diego Trough. An annual reproductive pattern has been proposed for protobranch bivalves from 2900 m in the NE Atlantic (LIGHTFOOT et al. 1979, TYLER et al. 1993) as well as for the anemone *Amphianthus inornata* epizoic on the gorgonian *Acanella arbuscula* at 2200

m (BRONSDON et al. 1994). At least one species of polychaetes from 2000 m in the NW Atlantic reproduces seasonally (BLAKE 1993). HARRISON (1988), on the other hand, found variation in the breeding intensity of deep-water isopods rather than a strong seasonal signal.

The dominant driving force for this periodicity of reproduction is apparently the downward vertical flux from surface production. Compelling evidence, from dietary analysis and time lapse photography, is provided to support this idea in *Echinus affinis* (CAMPOS-CREASEY et al. 1994). TYLER et al. (1993), however, pointed out that, in addition to the role of the vertical flux of POM in the diet of the seastar *Plutonaster bifrons*, food from the seasonal occurrence of dead blue whiting at the deep-sea bed may also be a proximal force. Dietary evidence has been difficult to obtain for the protobranchs and *Amphianthus inornata* in the NE Atlantic, although the evidence of flux and faunal response remain correlative.

Experimental evidence from bathyal depths off the Bahamas has shown that macrophyte debris features strongly in the diet of *Stylocidaris lineata*, with the macroalga *Sargassum* being taken in preference to the seagrass *Thalassia* (YOUNG et al. 1993). Although it has been difficult to determine the seasonality of supply of the macrophytes, time lapse video evidence suggests that the input of macroalgal material coincides with the hurricane season (C.M. YOUNG pers. comm.)

Growth is an additional feature that may show periodic variation in the deep sea. GAGE (1990) presents convincing evidence that the lines observed on the vertebral ossicles of *Ophiura ljungmani* and *Ophiomusium lymani* are annual growth bands. A similar pattern is seen in the test ossicles of *Echinus affinis* (see GAGE and TYLER 1991). Although there has been some discussion as to whether these represent **annual** growth lines, there can be little doubt they represent growth lines of some periodicity. The xenophyophore *Reticulammina labyrinthica* at 4944m on the Madeira Abyssal Plain provides a stunning visual image of periodic growth in the deep sea (GOODAY et al. 1993). Growth in this protozoan occurred in distinct phases lasting 2-3 d with some 60 d of inactivity between growth phases. Whether the control of this growth cycle was environmental or internal could not be determined.

More intriguing still is the possibility of temporal variation in environments where this prediction would be unexpected. In hydrothermal and cold seep environments the ready supply of inorganic energy for chemosynthesis would mitigate any temporally varying patterns. However, along the Mid-Atlantic Ridge the mussel population at a vent at 14°45'N appears to be formed from three cohorts (VAN DOVER 1995). Also, four distinct cohorts in the population

structure of a large sample of *Bathymodiolus* from the Brine Pool on the Louisiana slope suggest periodic recruitment events. In *Rimicaris exoculata* from the TAG hydrothermal vent on MAR, gametogenic development appears to be related to size; this indicates a periodicity in the gametogenic biology, although the low number of individuals carrying eggs mitigates this (WILLIAMS and RONA 1986, P. TYLER pers. observ.).

Conclusions

Of all the aspects of understanding the deep sea, the analysis of temporal variation has proved to be one of the most intractable. The cost of ship time and the analytical effort involved has hampered a concerted effort to establish time series studies in this environment. The data available are from disparate sources and much of the discussion is based on correlative evidence, with only a small amount of experimental testing having been attempted. In exploring the faunal responses to temporal changes in the deep-sea environment, one should not ignore the phylogeny of deep-sea organisms. ECKELBARGER and WATLING (1995), for example, argue that reproductive pattern in deep-sea organisms is driven as much by their phylogeny as by environmental controls. This provocative argument provides deep-sea biologists with an excellent framework to test the effect of phylogeny against local environmental control.

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