



Temporal variability in polychaete assemblages of the abyssal NE Atlantic Ocean

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ABSTRACT

Temporal variability in deep-sea polychaete assemblages was assessed at the Porcupine Abyssal Plain Sustained Observatory, NE Atlantic, over a 9-year period (eight cruises between August 1989 and September 1998). The polychaete communities were characterized by large number of individuals (abundance) and high family richness. The highest abundances occurred in the upper 1 cm sediment layer (53.2% of total abundance). The most abundant families were the Cirratulidae, Spionidae, Opheliidae and Paraonidae. Surface deposit feeders were the dominant trophic group (67.4% of total abundance). Significant temporal variability was evident in polychaete abundance with significant differences in polychaete abundance between sampling periods (cruises; $p < 0.01$). Stepwise increases in abundance in September 1996 and March 1997 coincided with similar increases in abundance in large invertebrates (megafauna) in the same area (known as the 'Amperima Event' after a species of holothurian that increased in abundance by over three orders of magnitude). Similar patterns were observed for abundances across different layers of the sediment, main families and trophic groups showing significant differences between cruises ($p < 0.05$). A comparison of samples taken (1) before the 'Amperima Event' (1989–1994) and (2) during the 'Amperima Event' (1996–1998) showed significant differences in the polychaete abundance in the upper 3 cm of the sediment. There were significant differences in some trophic groups (predators, deposit feeders and burrowers) and the dominant families (Cirratulidae, Spionidae and Opheliidae). Not all elements of the polychaete community showed a response (e.g. the Paraonidae). Changes in surface deposit feeders were particularly evident. The temporal variability is likely to be related to seasonal and interannual variability in organic matter input. Greater food supply in some years may allow the growth and development of deposit-feeding polychaetes.

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1. Introduction

Studies of abyssal assemblages have shown tentative relationships between the flux of organic material to the ocean floor and the abundance and biomass of benthic assemblages in some areas (Sibuet et al., 1993; Glover et al., 2002; Smith et al., 2006; Smith and Rabouille, 2002). However, these studies were unable to reveal how intimately climate and upper ocean events might be linked to benthic processes. Links between climate, surface production and deep-sea processes are becoming clearer as a

result of long time series in the NE Pacific and NE Atlantic Oceans. In the NE Pacific there have been two long time series, one centred on 'Station M' (Smith and Druffel, 1998) and the other at the Hawaiian Ocean Time Series (HOT) station (Smith et al., 2002; Karl and Lucas, 1996). A comprehensive set of benthic samples have been taken at 'Station M'. Changes have been observed in both the abundances of benthic communities (larger macrofauna and megafauna) and community oxygen consumption over a 7-year period. These variations have been tentatively linked to seasonality in food supply (Lauerman et al., 1996; Smith and Druffel, 1998; Smith et al., 2006; Ruhl, 2007).

In the NE Atlantic a similar long-term study of particle flux and benthic communities has been conducted on the Porcupine Abyssal Plain (PAP). This site has been the focus of several European Union-funded projects, including BENGAL (High-resolution temporal and spatial study of the BENThic

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Table 1
Cruise, sampling period, station number and samples number.

| Cruise | Date | Station | Number of box core samples |
|---------------------------------------|-----------------------------|--------------|----------------------------|
| RRS <i>Discovery</i> 185 | 18 August–17 September 1989 | 11908 | 1 |
| RRS <i>Challenger</i> 79 | 12 May–3 June 1991 | 52701 | 6 |
| RRS <i>Challenger</i> 111 | 29 March–25 April 1994 | 53201, 53205 | 4 |
| RRS <i>Discovery</i> 222 ^a | 29 August–24 September 1996 | 12930 | 7 |
| RRS <i>Discovery</i> 226 ^a | 12 March–10 April 1997 | 13077 | 6 |
| RRS <i>Discovery</i> 229 ^a | 2–31 July 1997 | 13200 | 5 |
| RRS <i>Discovery</i> 231 ^a | 1–31 March 1998 | 13368 | 2 |
| RRS <i>Discovery</i> 237 ^a | 25 September–8 October 1998 | 13627 | 3 |

^a Samples taken in the BENGAL project.

biology and Geochemistry of a northeastern Atlantic Locality; Table 1) in the NE Atlantic since 1989 (Billett and Rice, 2001). Significant temporal changes have been observed in protozoan meiofaunal (Gooday et al., 2010), metazoan meiofaunal (Vanreusel et al., 2001; Kalogeropoulou et al., 2010), macrofaunal (Galéron et al., 2001) and megafaunal communities (Bett et al., 2001; Billett et al., 2001). Changes in the vertical distribution of some components of the infaunal sediment community were evident and were thought to be related to the apparent impoverishment of organic matter at the sediment surface and/or the effects of increased disturbance and bioturbation (Vanreusel et al., 2001). Long-term changes were most clearly seen in the abundances of the invertebrate megafauna. Changes occurred in the abundances of actinarians, annelids, ophiuroids, pycnogonids and tunicates and particularly in holothurians (Billett et al., 2001). The sudden increase in abundance of some holothurians in the mid 1990s, such as *Amperima rosea* and *Ellipinion molle*, by three orders of magnitude, had important consequences for organic material cycling at the sediment surface (Bett et al., 2001). This event was known as ‘The *Amperima* Event’ (Billett and Rice, 2001).

Macrofaunal studies at PAP indicated potential long-term changes in this size fraction of the benthic community. An increase in the abundance of opportunistic species was recorded, with various taxa, such as foraminiferans, opheliid polychaetes and other polychaetes responding to the changes on the seabed at different rates (Galéron et al., 2001; Vanreusel et al., 2001). Polychaetes are the dominant component of the deep-sea macrofauna, constituting between 30% and 70% of the macrofaunal abundance (Blake and Grassle, 1994; Gage and Tyler, 1991; Glover et al., 2001; Grassle and Maciolek, 1992; Paterson et al., 1994; Tyler, 2003). Polychaetes generally also dominate the macrofauna in terms of biomass (Brown, 1991). Nevertheless, long-term variability in deep-sea polychaete assemblages is very poorly understood, and to date there have been no studies on this subject. This study addresses the gap in long-term studies of polychaete population succession, recruitment and reproductive patterns.

Other studies have shown links between surface productivity and benthic parameters, at both seasonal and interannual time scales (Billett et al., 1983; Lampitt, 1985; Rice et al., 1994). In the current investigation, long-term variability in deep-sea polychaetes at the PAP time series was studied. In particular we test whether the polychaetes respond to changes in the biogeochemical environment as noted for other elements of the abyssal fauna, and, if so, whether all elements of the assemblage do so equally. We also test whether there are changes in the vertical distribution of polychaetes within the sediment. The large number of megafaunal sediment deposit feeders was thought to affect the quantity and quality of nutrient available in the surface layers. We test whether the abundances of polychaetes, particularly surface deposit feeders, were diminished as a result.

2. Methods

2.1. Study site

All samples were collected from a central locality (48°50'N 16°30'W) on the Porcupine Abyssal Plain Sustained Observatory (PAPSO) NE Atlantic about 270 km southwest of Ireland, and of 4850 m depth (Fig. 1). It was chosen because it is a relatively flat area, remote from both the continental slope to the east and the mid-ocean ridge to the west, and so is unlikely to be influenced strongly by downslope or advective processes (Billett and Rice, 2001). This abyssal region is known to be subject to strong seasonal fluctuations in fluxes of organic matter that reflect the seasonal cycle of primary production in the euphotic layer with pronounced maxima in summer (Rice et al., 1994; Lampitt et al., 2001). The depth of winter mixing of the upper water column is about 500 m (Rice et al., 1994). Table 2 gives a summary of the main geochemical characteristics of the study area.

2.2. Sampling and processing

Polychaete samples were collected using an USNEL spade boxcorer (total surface area 0.25 m²; Hessler and Jumars, 1974). Samples were processed immediately after recovery. The core was subsampled routinely using a subcore with square cross-section (92 × 92 mm²) and another with circular cross-section (55 mm diameter). Large xenophyophores and perforated tubes were removed before the core was subdivided into six horizontal layers (0–1, 1–3, 3–5, 5–10, 10–15, 15–20 cm) manually with a trowel. The 0–1 and 1–3 cm layers were immediately placed into 4% borax-buffered formaldehyde until they were sieved in order to avoid the deterioration of organisms. The deeper layers were placed in cold sea water. Sieving was carried out on a stack of 1000, 500, 300 and 250 μm sieves for the four upper layers, while the two deepest (10–15 and 15–20 cm) layers were washed through two sieves (1 mm and 500 μm). In the laboratory, all preserved samples were sorted into higher taxa (Polychaeta, Peracarida, Mollusca, etc.) and counted to evaluate abundance.

Polychaete family identification was carried out by stereo microscope (Leica, model WILD MZ8) and light microscope (Olympus) with video camera support (Panasonic F10 CCD). Unknown specimens were drawn using a light microscope with camera lucida attached (Olympus). A photographic record was kept of unknown and main species using a digital photograph camera.

All macrobenthic samples and data were taken during eight oceanographic cruises between 1989 and 1998 (Table 1). While further sampling for macrofauna has been undertaken since 1998, it was not possible to include this material in a 3-year Ph.D. study. These later samples will be analysed in a subsequent study.

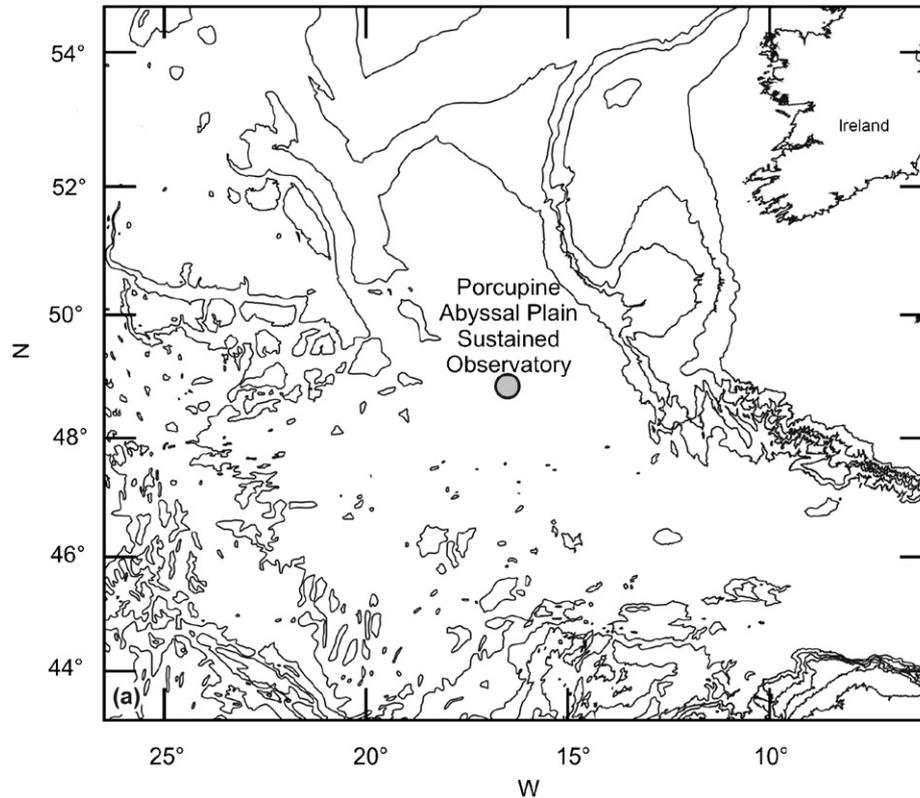


Fig. 1. Study site at Porcupine Abyssal Plain (PAP). NE Atlantic Ocean.

Table 2
Main biogeochemical characteristics measured at PAP.

| Nutrient regime | Seasonal phytoplankton bloom |
|--|---|
| Sedimentation accumulation rate ^a | 3.5 cm kyr ⁻¹ |
| Sediment median grain size ^a | 8–8.6 μm (calcareous ooze) |
| TOC surface sediment ^b | 0.35–0.45% |
| C:N ratio ^c | 4.8–7.8 |
| POC flux ^d | 10.6 mg C m ⁻² d ⁻¹ (average) |

^a Rice et al. (1991).

^b Rabouille et al. (2001).

^c Santos et al. (1994).

^d Lampitt et al. (2010).

2.3. Statistical analyses

The temporal variation in polychaete abundance was analysed. In addition to total abundance, a hierarchical approach was taken to identify whether all elements of the fauna responded in a similar way. So abundances of polychaetes in different sediment horizons, dominant families and finally different trophic groupings were analysed. The trophic group classification applied for each family was simplified from the scheme proposed by Fauchald and Jumars (1979) with individuals being assigned to broad feeding categories—predators (carnivores plus omnivores), surface deposit feeders, burrowing subsurface deposit feeders (hereafter termed burrowers) and filter feeders. Family richness also was calculated. To get a consistent data set the statistical analyses were made only on a specific subset of samples. This was because of (1) the high variability in the number of samples available for each sampling period and (2) the different types of data available for each cruise. Consequently, analyses were carried out only on data from individuals retained in the 300–500 μm

fractions. We are confident that while this will have reduced the overall abundance it did not affect the overall comparison between cruises or pre- and post-‘*Amperima* Event’ analyses significantly. An analysis of samples, where a full set of sieve fractions was retrieved, indicates that the greatest abundance of polychaetes (62.9%) occurred in the 300–500 μm size fraction (Fig. 2).

Analyses of variance (ANOVA) and a non-parametric Kruskal–Wallis test (only cruises with >2 samples) were used to test for significant differences in abundance between sampling periods (cruises), while a *t*-test was used for pre-‘*Amperima*’ versus ‘*Amperima* Event’ periods. Data were log transformed, and ‘STATISTICA’ statistical software was used (www.statsoft.com). For the comparison between pre-‘*Amperima*’ and ‘*Amperima* Event’ periods, samples from August 1989, May 1991 and April 1994 were used as pre-‘*Amperima*’ and from September 1996, March 1997, July 1997, March 1998 and September 1998 for the ‘*Amperima* Event’. No corrections were made for multiple testing when multiple comparisons were made.

3. Results

3.1. Temporal variability in polychaete abundance

A total of 3338 polychaetes were recorded during eight cruises between August 1989 and September 1998. Mean abundance varied with sampling period (cruise). The greatest abundances were recorded in July 1997 (145 ± 31 specimens per 0.25 m², *n* = 5). The lowest mean abundance was recorded in 1989 (45 specimens per 0.25 m², *n* = 1), which may be influenced by a single sample being available for this analysis. A stepwise increase in the abundance of polychaetes occurred between 1994 and 1996, and then again in early 1997. The trend with time after

July 1997 was a small but consistent decrease in mean abundance with time (Fig. 3). ANOVA demonstrated significant differences between sampling periods ($F_{5,25} = 20.3$, $p < 0.05$). A non-parametric Kruskal–Wallis test confirmed that observed differences were highly significant between cruises ($p < 0.001$). A t -test conducted on the same data demonstrated significant changes between pre-‘Amperima’ samples (1989–1994) and ‘Amperima Event’ samples (1996–1998; $p < 0.001$). The mean abundance in pre-‘Amperima’ samples was 54.4 ± 14 ($n = 11$) specimens per 0.25 m^2 , while the mean abundance in the ‘Amperima Event’ was 195.7 ± 37 ($n = 23$) specimens per 0.25 m^2 . The mean abundance

of polychaetes during all periods (1989–1998) was 98.2 ± 44 ($n = 34$) specimens per 0.25 m^2 .

3.2. Temporal change in abundance in relation to depth in sediment

Only results from the 0–1, 1–3 and 3–5 cm sediment layers were analysed because they were the only layers processed using a $300 \mu\text{m}$ sieve. A total 1596 specimens (53.2% of polychaete total numbers) were recorded in the top 1 cm and 958 specimens between 1 and 3 cm (31.9%). Between 3 and 5 cm 446 specimens were recorded. (14.9%). A total of 3000 individuals were recorded in the upper (0–1, 1–3 and 3–5 cm) sediment layers (all sieve sizes). For the 0–1 and 1–3 cm layers, polychaete abundances changed with time (Fig. 4). In contrast, polychaete abundances in the 3–5 cm layer showed no obvious trends (Fig. 4).

Statistical analysis (ANOVA) confirmed significant differences in the two first layers between sampling periods (0–1 cm layer, $F_{4,23} = 4.3$, $p < 0.01$ and 1–3 cm layer, $F_{4,23} = 11.9$, $p < 0.001$). No significant changes were recorded in the 3–5 cm layer between sampling periods ($F_{4,23} = 1.8$, $p > 0.1$). A t -test of pre-‘Amperima’ and ‘Amperima Event’ periods showed significant differences in the two uppermost sediment layers (0–1 cm layer, $p < 0.005$ and 1–3 cm layer, $p < 0.01$), but not in the 3–5 cm sediment layer ($p > 0.05$).

3.3. Temporal change in family richness

A total of 44 polychaete families were recorded from the eight cruises between August 1989 and September 1998. The lowest richness (10 families) was recorded in August 1989, which probably reflects the fact that only one sample was processed. Family richness was the greatest at the time of the ‘Amperima Event’, increasing from 16 families in April 1994 to 36 families in September 1996. Subsequently the number of different families

Abundance distribution by size (sieve hole diameter)
PAP time series 1989–1998.

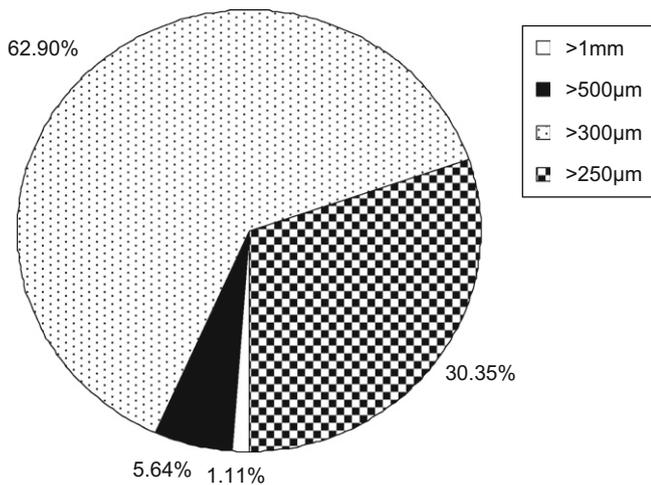


Fig. 2. Total number of individuals by size (mesh diameter). All sieve fractions considered.

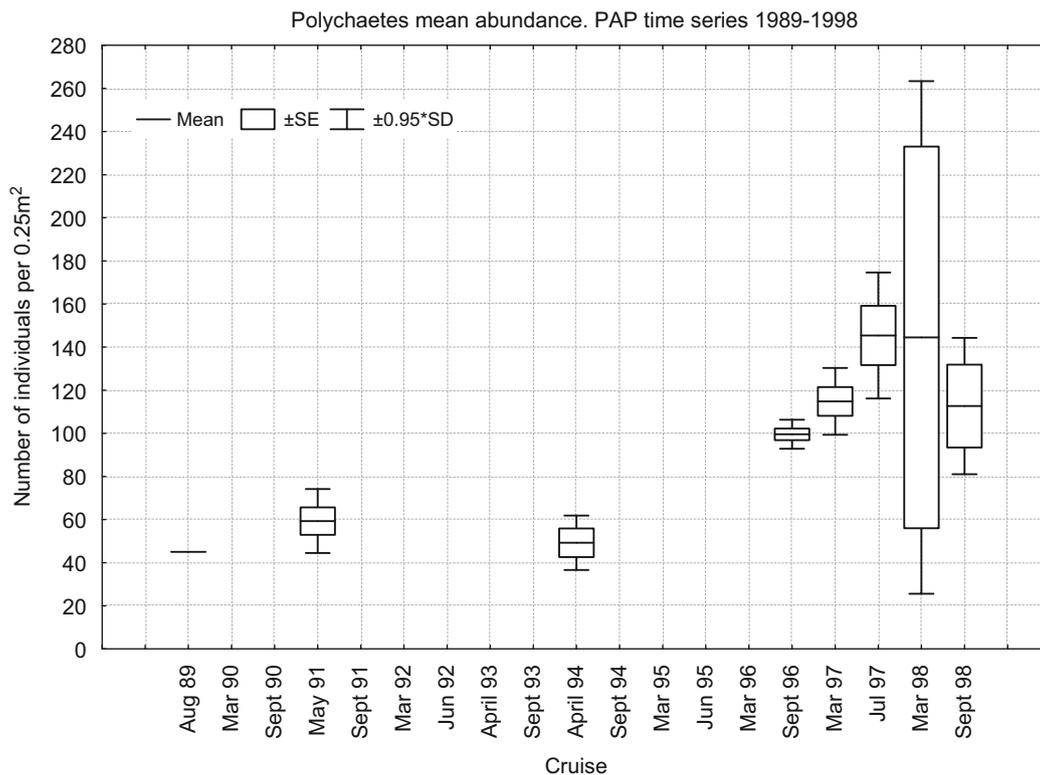


Fig. 3. Temporal variability in mean abundance of polychaetes. PAP 1989–1998. Mean abundance, standard error and standard deviation (95%).

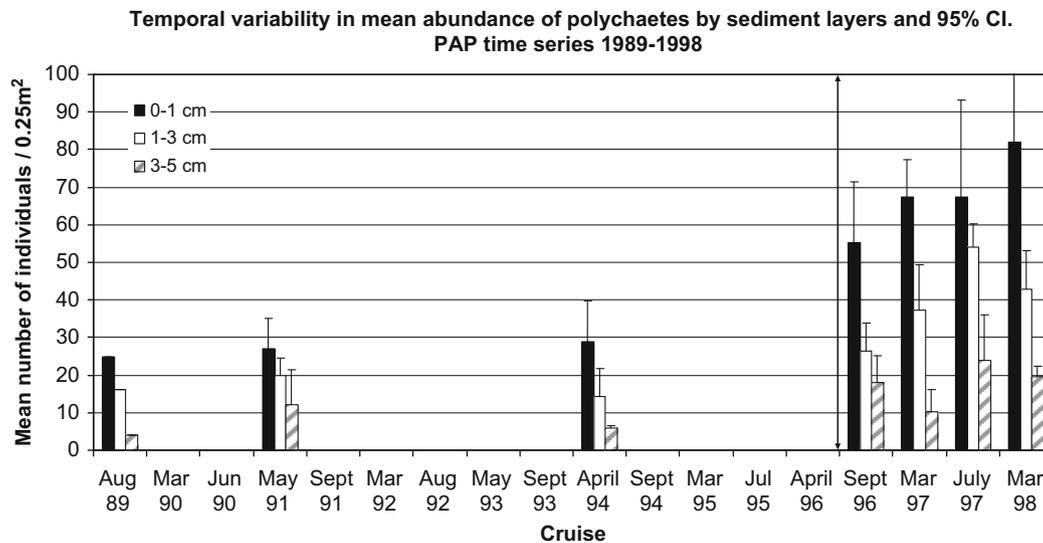


Fig. 4. Temporal variability in mean abundance of polychaetes by sediment layers. The double headed arrow marks the start of the *Amperima* Event. There was no layer information in September 1998.

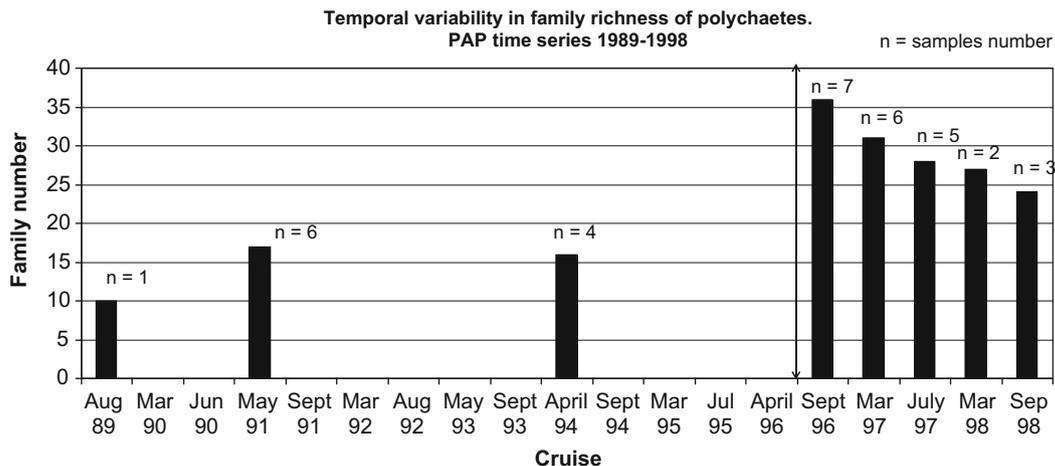


Fig. 5. Temporal variability in family richness of polychaetes. The double headed arrow marks the start of the *Amperima* Event.

declined (Fig. 5). The apparent changes in family richness were not sample-size dependent ($R^2 = -0.1$). Pre-'*Amperima*' and '*Amperima* Event' samples showed highly significant differences in family richness and faunal composition. Some families were present during all sampling periods, such as Ampharetidae, Chrysopetalidae, Cirratulidae, Paraonidae, Pilargidae and Spionidae. Others, such as Nepthyidae, Nereididae, Pisionidae and Trochochaetidae were recorded only once or twice with only one individual. The rarity of some families and constancy of others is typical of deep-sea polychaete communities. Some families such as Acrocirridae, Maldanidae and Oweniidae that were not recorded in 1994 were present in 1996. Some families that occurred only in low abundances in 1994, such as Opheliidae, Fauveliopsidae, Glyceridae and Lumbrineridae, became abundant in September 1996.

3.4. Temporal changes in abundance of the dominant polychaete families

Cirratulidae was the most abundant family sampled at the PAP (29.8%), followed by Spionidae (20.9%). Paraonidae and Opheliidae accounted for 8.1% and 5.4%, respectively. Changes in abundances

of these families over the study period were not uniform. Cirratulidae, Spionidae and Opheliidae increased in abundance, reaching a peak during the '*Amperima* Event', with the greatest abundances during July 1997 (Cirratulidae and Spionidae) and March 1998 (Opheliidae; Fig. 6). In contrast, the abundance of Paraonidae did not vary greatly during the study. ANOVAs showed significant differences between sampling periods for Cirratulidae ($F_{5,25} = 9.16$, $p < 0.001$), Spionidae ($F_{4,23} = 3.75$, $p < 0.05$) and Opheliidae ($F_{5,26} = 15.83$, $p < 0.001$). These differences were not observed for Paraonidae ($F_{5,25} = 1.33$, $p > 0.1$). Differences in the number of individuals of opheliids were evident from September 1996 cruise owing to a recruitment event of small opheliids during that period (Vanreusel et al., 2001). A *t*-test for pre-'*Amperima*' and '*Amperima* Event' periods showed significant differences for Cirratulidae, Spionidae and Opheliidae ($p < 0.05$). No significant changes were observed in Paraonidae between these periods ($p > 0.05$).

3.5. Changes in abundance of trophic groups

Polychaete families present could be assigned to various feeding guilds, including surface deposit feeders, burrowers

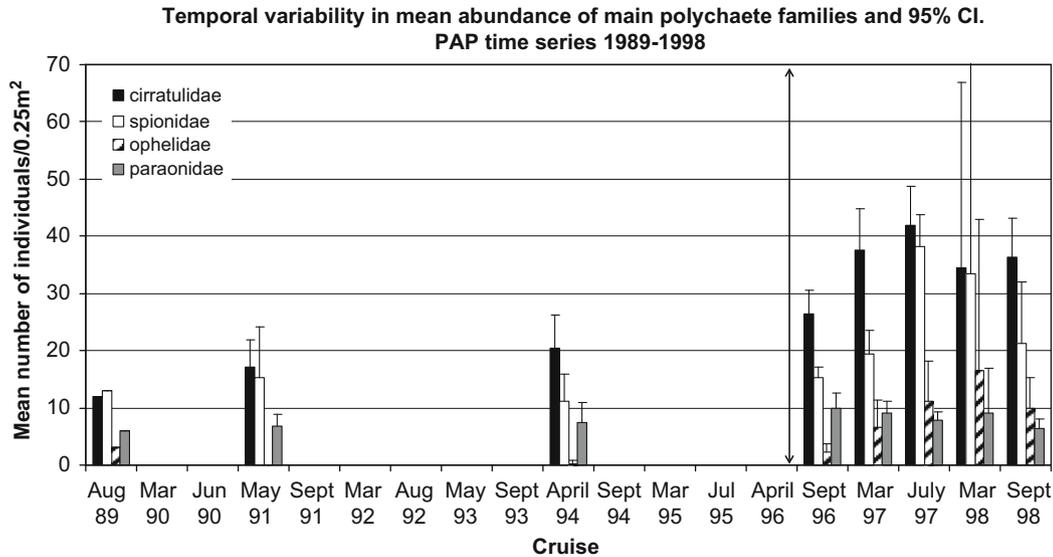


Fig. 6. Temporal variability in mean abundance of main polychaete families. The double headed arrow marks the start of the *Amperima* Event.

(subsurface deposit feeders), filter feeders and predators (carnivores plus omnivores). Surface deposit feeders were the dominant trophic group (67.4%), with Cirratulidae and Spionidae as the main families. Burrowers contributed 16.5% of the individuals, mainly opheliid polychaetes. Predators and filter-feeding polychaetes were represented by 13.7% and 2.4% of total number of individuals, respectively. Despite the clear dominance of surface deposit feeders, large numbers of predators and burrowers were found during several cruises (group richness). In burrowers, highly significant differences were recorded with time ($F_{5,25} = 7.25$, $p < 0.001$). Significant changes between sampling periods were observed also for surface deposit feeders ($F_{5,25} = 9.2$, $p < 0.001$), and predators ($F_{6,26} = 2.8$, $p < 0.05$). There were no significant differences in the abundances of filter feeders between cruises ($F_{5,25} = 0.9$, $p > 0.1$). A *t*-test made on pre-*Amperima* and the *Amperima* Event periods showed significant differences for predators ($p < 0.01$) and highly significant differences in surface deposit feeders and burrowers ($p < 0.005$). In filter feeders the changes observed between periods were not significant ($p > 0.1$).

4. Discussion

4.1. Abundance

Polychaete abundance showed a significant increase during the *Amperima* Event. The size of the increase was, however, smaller than observed for the holothurian megafauna species, being just two to three times the abundance of pre-*Amperima* samples, compared to two orders of magnitude for the megafauna. Polychaete abundances before the *Amperima* Event were comparable to abundances determined for other abyssal localities lying under eutrophic and seasonally productive surface waters. However, polychaete abundances at the PAP during the *Amperima* Event were much greater than any other abyssal region measured previously, highlighting that there has been a response to a changing nutrient regime (Table 3).

Polychaetes were not the only infaunal group to increase during the *Amperima* Event. Galéron et al. (2001) noted that infaunal bivalves showed an increase during this period. Within the meiofauna, Gooday et al. (2010) reported a similar response in

protozoan meiofauna, while Kalogeropoulou et al. (2010) observed increases in abundance with metazoan harpacticoid copepods and nematodes. However these increases in the infaunal elements were again considerably smaller than observed for the megafauna, particularly the holothurians (Billett et al., 2001, 2010; Bett et al., 2001) by two orders of magnitude. These results suggest that whatever the process that resulted in the increase in abundance of the megafauna, it was also affecting the infauna. The reduced magnitude of the response of the infauna in comparison with the surface-dwelling megafauna points to some mediation or amelioration of the effects. In other words while there may have been an increase in nutrient flux to the ocean floor a smaller proportion of it appears to have been available to the infauna.

The *Amperima* Event may be a response to increases in the flux of organic matter to the seabed. Water column fluxes in total organic carbon (TOC) and total nitrogen (Kiriakoulakis et al., 2001), phytopigments (Fabiano et al., 2001) and biogenic silica (Lampitt et al., 2001) were the greatest during the July 1997 and September 1998 periods. In sediments, bacterial carbon production (Eardly et al., 2001), phytopigments (Witbaard et al., 2001), lipid compounds (Galéron et al., 2001) and biogenic silica components (Ragueneau et al., 2001) were the greatest in September 1996. These values coincide with the first increase in abundance in the polychaete assemblages. Unfortunately, there were no sediment trap data available just prior to the *Amperima* Event (Lampitt et al., 2001), but subsequent work has shown that fluxes at this site can change by an order magnitude from year to year (Lampitt et al., 2010). It is possible, therefore, that enhanced organic matter inputs to the deep-sea floor have caused changes in the meiofaunal, macrofaunal and megafaunal size fractions of the benthic community (Billett et al., 2001; Gooday, 2002). However, the relationship between the *Amperima* Event and surface ocean export flux is still tentative (Billett et al., 2010).

In considering the response of polychaete assemblages, two potential factors must be considered. Firstly, there was an increase in the nutrient flux to the abyssal ocean floor and, secondly, the massive increase in surface-feeding megafauna, particularly holothurians, may have acted as competitors for this influx. We do not consider holothurians to be potential consumers of the polychaete infauna as many species appear to be quite restricted in particle size selection (Hudson et al., 2003), although ophiuroids may impact small juveniles and settling larvae. The

Table 3Site, depth, sieve fraction size, number of USNEL spade box core samples, mean number of individuals per 0.25 m², number of species and references.

| Site | Depth (m) | Sieve fraction size | No. of box cores | Abundance per 0.25 m ² (SE) | No of species | Reference |
|---|-----------|---------------------------------|--|--|---------------|---|
| JGOFS Equatorial Pacific Study 0°N | 4300 | 300 μm | 3 | 84 (27.9) | 73 | Glover et al. (2002) |
| JGOFS Equatorial Pacific Study 2°N | 4400 | 300 μm | 4 | 60 (6.4) | 82 | Glover et al. (2002) |
| JGOFS Equatorial Pacific Study 5°N | 4400 | 300 μm | 3 | 80 (19.1) | 76 | Glover et al. (2002) |
| JGOFS Equatorial Pacific Study 9°N | 4900 | 300 μm | 3 | 13 (2.3) | 23 | Glover et al. (2002) |
| Hawaii Ocean Time Series 23°N (HOT) | 4800 | 300 μm | 4 | 9 (1.7) | 14 | Glover et al. (2002) |
| Deep Ocean Mining Environmental Study A | 5100 | 300 μm | 47 | 16 (0.8) | 104 | Glover et al. (2002) and Paterson et al. (1998) |
| Preservation Reserve Area (PRA) | 4800 | 300 μm | 16 | 65 (16.8) | 100 | Glover et al. (2002) |
| ECHO 1 | 4500 | 300 μm | 15 | 42 (5.5) | 113 | Glover et al. (2002) |
| CLIMAX II | 5010 | 300 μm | 10 | 15.6 (1.7) | 46 | Hessler and Jumars (1974) |
| Cape Verde Abyssal Plain (CAP) | 4580–4647 | 250 μm | 5 | 37.8 | 39 | Cosson-Sarradin et al. (1998) |
| Cape Verde Abyssal Plain (CAP) | 4600 | 1 mm, 500 μm and 250 μm | 8 | 35.8 (10) | 75 | Glover et al. (2001) and Sibuet et al. (1993) |
| Tagus Abyssal Plain (TAP) | 5035 | 300 μm | 6 (Vegetatic SBC 0.09 m ²) | 64.5 (25.8) | 57 | Glover et al. (2001) and Gage et al. (1995) |
| Madeira Abyssal Plain (MAP) | 4900 | 1 mm, 500 μm, 300 μm and 250 μm | 5 | 17.5 (7.8) | 29 | Glover et al. (2001) and Paterson et al. (1994) |
| Porcupine Abyssal Plain (PAP) | 4800 | 1 mm, 500 μm, 300 μm and 250 μm | 5 | 81 (20.25) | 101 | Glover et al. (2001) and Paterson et al. (1994) |
| Porcupine Abyssal Plain (PAP) | 4850 | 1 mm, 500 μm, 300 μm and 250 μm | 23 | 252.00 | No data | Galéron et al. (2001) |
| This study (1989–1994) | 4850 | 300 μm | 11 | 54.4 (4.4) | 23 (family) | Soto et al. (this paper) |
| This study (1996–1998) | 4850 | 300 μm | 23 | 195.7 (7.8) | 43 (family) | Soto et al. (this paper) |

megafauna may, however, repackage the available nutrients in the form of excretory products such as faeces and so increase nutrients, albeit of a reduced and potentially different nature, which may then be available for infaunal groups. Holothurian assimilation efficiencies are estimated to be around 30% when phytodetritus is present but drop and become negative when it is absent (Ginger et al., 2001; Sibuet, 1988). Holothurians appear to be selective, able to preferentially feed on newly deposited phytodetritus (Wigham et al., 2003). Therefore, nutrients may be still available to sediment-dwelling infauna given the assimilation efficiencies, but it may be of reduced 'quality' in that key sterols have been removed or reduced. Lipid concentrations such as phytoplankton-derived sterols and other labile lipids were dramatically depleted in the surficial sediments in 1997 (Ginger et al., 2001). The absence of phytodetritus and chlorophyll concentrations (Witbaard et al., 2001) in the surficial sediments was apparent also between 1997 and 1998. As phytosterols are energetically 'expensive' to biosynthesise, Ginger et al. (2001) suggest that their availability may be an important factor controlling the abundance of some deep-sea taxa.

Two further aspects of megafaunal feeding need to be considered. Firstly it is still not clear what the assimilation efficiency of ophiuroids is. They are also surface deposit feeders but they are less likely to be selective and so may be reducing available nutrients. Secondly it is unknown how often the same area of the ocean floor is revisited by mobile deposit-feeding megafauna. So while 30% efficiency would perhaps appear to leave a considerable amount of nutrient available, it may in fact be much less as the sediment may be processed a number of times and the 'quality' of the remaining nutrients much reduced. Separating competition and/or alternative nutrient effects is not possible with the data available, particularly given the lack of sediment trap data. As long as 100% assimilation efficiency of the added nutrient flux by the mobile epifauna was not achieved, increased infaunal abundance would be expected. Repackaging and conversion of chemical form by the mobile epifauna might be expected to favour some infaunal taxa more than others.

4.2. Abundance: vertical distribution (sediment layers)

Polychaetes were the most abundant in the top 1 cm layer of sediment (Fig. 4), confirming the PAP results of Galéron et al. (2001), who used all sieve size fractions in which 62% of the polychaetes occurred in the top 1 cm layer of the sediment. This is similar to results reported from PAP and MAP (Glover et al., 2002). By contrast, results from the oligotrophic EUMELI site on the Cap Verde Abyssal Plain showed that the 0–1 cm layer contained >80% of the fauna and in the mesotrophic ECHO site in the Pacific the top 0–1 cm layer accounted for 75% of the fauna (Paterson et al., 1998) (Table 3).

Temporal changes in abundance were observed in the 0–1 and 1–3 cm sediment layers, but not in deeper layers within the sediment. Downward and upward movements within the sediment were not evident in total abundance following the 'Amperima Event'. Overall proportions of polychaete abundance in the upper layers did not change substantially with time; so there appeared to be a general up-lift in abundance within the 0–3 cm layers. This suggests that whatever process was operating it affected the surface and upper sediment rather than occurring within the sediment column as a whole. The nature of the response of polychaetes supports the observation that they were affected by the same process(es) that drove the 'Amperima Event'.

A similar vertical distribution and dominance was reported for harpacticoid copepods (>63%), bivalves (45–80%), tanaidaceans (~40%) and isopods (>60%) at the PAP (Galéron et al., 2001). The abundances recorded in this study declined significantly with depth in the sediment ($p < 0.005$). This may be related to lipid concentrations (Galéron et al., 2001) and phytopigments (Witbaard et al., 2001) in the surficial sediment. Between September 1996 and July 1997, the total organic carbon content of the sediment declined from 0.37% at the surface to 0.15% at 15-cm depth, except in September 1996, when the surficial TOC content was 0.45% (Rabouille et al., 2001). The TOC profiles in September 1996 suggest that a large phytodetritus deposition event had occurred in the sediment surface. This is consistent with the presence of phytodetritus on core surfaces collected during this month, and concentrations of chlorophyll *a*,

phaeophorbides and hydrolysable proteins, which were higher than during 1997 (Witbaard et al., 2000; Fabiano et al., 2001).

4.3. Faunal composition and family richness

Variabilities in faunal composition, diversity and family richness are evident in benthic communities on a variety of spatial scales relating to depth (Paterson and Lambshead, 1995) and regional biogeography (Rex et al., 1993). Changes in the faunal composition may also be caused by disturbance (Grassle and Morse-Porteous, 1987; Gage, 2003) or physical effects (Grassle and Maciolek, 1992). Seasonal or interannual variability has been recorded for only a few taxa and at a limited number of localities (Billett et al., 2001). In the current study, a stepwise increase in the number of polychaete families was recorded from September 1996 onward, coincident with the 'Amperima Event'. The increase was not directly correlated with sampling effort and so appeared to be the result of a general increase in the overall abundance of polychaetes. At the PAP, 23 families were recorded prior to the 'Amperima Event' and 43 families during the event (Table 3). Dominant families did not change during the study; rather, polychaetes increased in abundance generally and represented a corresponding immigration of individuals from a greater range of families.

The families that showed the greatest response were those that most often dominate deep-sea polychaete infaunal assemblages—Cirratulidae, Paraonidae and Spionidae (Hilbig and Blake, 2006). The former families were described by Smith and Hessler (1987) as opportunists (species that wait for optimal conditions and respond quickly to high levels of organic enrichment to accumulate energy). Nowell et al. (1984) have showed that some Spionids change their feeding type from suspension to deposit feeding in the case of changing food supply. Two of these families (Cirratulidae and Spionidae) showed temporal variation, increasing in abundance at the time of the 'Amperima Event'. Cirratulidae dominated the polychaete families in seven of eight cruises. Spionidae dominated only in July 1989 (Fig. 6). By contrast the Paraonidae did not show any significant changes in abundance.

One other family that increased notably in abundance was the Opheliidae. Opheliids are burrowers and appear to be non-selective subsurface deposit feeders. Studies made by Hermans (1978) in shallow-water opheliids and Renaud et al. (1999) on

opheliids on the shelf off North Carolina also suggest that they are opportunists. Vanreusel et al. (2001) found a large influx of post-larval individuals of an unknown opheliid species at PAP during the 'Amperima Event' and suggested that this influx was an opportunistic response to an increase in nutrient flux. Jumars (1978) similarly observed patches of opheliids of homogeneous length, suggestive of cohorts. These life history traits may explain the temporal variability noted for the PAP opheliid polychaetes.

The rise in overall abundance and the response of opportunistic polychaetes point to a quantitative rather than a qualitative change in nutrient input. In experiments using a variety of different substrates, early colonisers are usually from different families from those observed here. In particular, members of the Dorvilleidae are particularly common (Grassle and Morse-Porteous, 1987; Snelgrove et al., 1994) in sediment rich enough in organic material to approach or reach anoxia. In the PAP samples there was not a major shift in the dominant families, although there was a large increase in the abundance of opheliids; this is thought to be a recruitment event of one species.

4.4. Trophic groups

The nature of the polychaete response in the upper sediment layers suggests that trophic groups that exploit the surface were favoured. At PAP, surface deposit feeder polychaetes were indeed the most important trophic group, representing 67.4% of total abundance. Their temporal variability showed a trend of increasing abundance from September 1996 (Fig. 7) probably owing to surface sediment enrichment by a summer 1996 pulse of organic supply (Lampitt et al., 2001; Witbaard et al., 2000). Burrowing polychaetes represented 16.6% of total abundance. The observed increase in abundance was due partly to a large number of opheliid polychaetes (juveniles) recorded from March 1997. Predators (13.7%) and filter feeders (2.4%) were minor components of the polychaete community. These trophic groups did not show any significant temporal trends despite the density of predators being higher than deposit feeders in several cruises.

Qualitative changes in the organic flux might regulate essential dietary compounds required by benthic populations (Ginger et al., 2001), and changes in the composition of phytodetritus may drive changes in the composition of the benthic communities

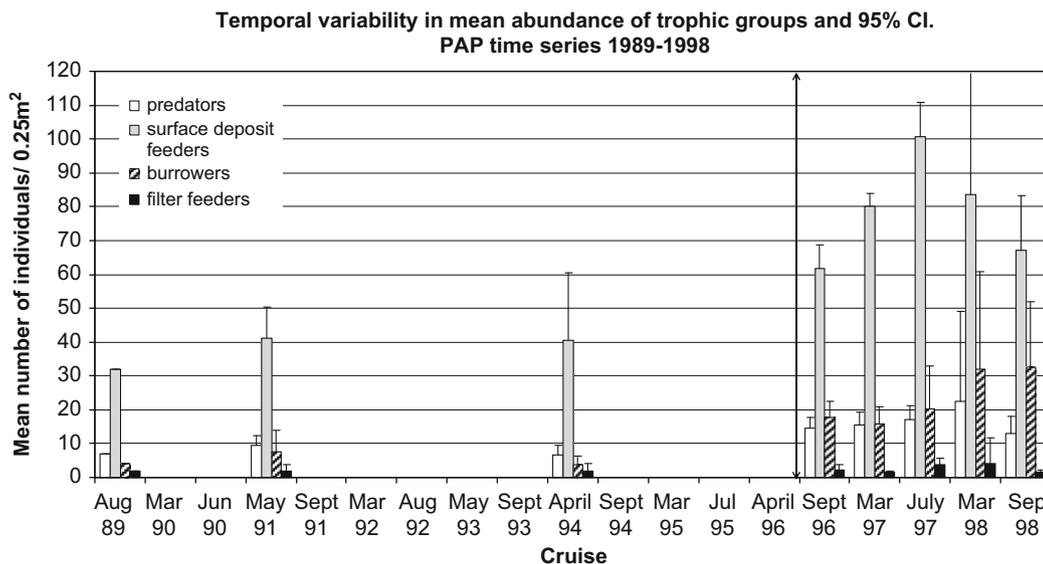


Fig. 7. Temporal variability in mean abundance of polychaete trophic groups. The double headed arrow marks the start of the Amperima Event.

(Wigham et al., 2003). However there were no obvious changes in the trophic composition of the polychaete groups to support this conclusion. Once again it appears there was a general increase in surface deposit and burrowing deposit feeders, with exceptional increase of the opportunistic opheliid deposit feeders.

Deposit feeders are the dominant trophic group in the deep sea (Dauer, 1983; Jumars et al., 1990). Studies made by various authors have recorded similar trophic groups' composition and dominance. Glover et al. (2001) found deposit-feeder dominance in PAP, EOS and MAP sites. Only at TAP did they find that burrowers dominated (opheliid polychaetes). Similar results were found by Aberle and Witte (2003) during May and June 2000 from PAP, Paterson and Lamshead (1995) in the Rockall Trough and at the Climax II, ECHO, PRA and Domes sites in the Pacific Ocean (Hessler and Jumars, 1974; Paterson et al., 1998).

5. Conclusion

Temporal variability in the abundance and family richness of polychaete assemblages was evident on the PAP between August 1989 and September 1998. Significant differences in abundance through time among families, trophic groups and in different layers within sediment were observed. These changes may be the response to changing ecological and oceanographic factors, the main one being an increase in food supply generated by seasonal nutrient inputs and particulate flux to the seabed from the water column through the deposition of phytodetritus. While it is not possible to rule out a response to the sediment alteration and disturbance caused by large numbers of holothurians, this is perhaps less likely as the dominant families and trophic groups did not change. The reduced responses of the polychaetes and other infaunal elements do suggest that the holothurians have been more successful in utilizing the nutrient influx. Further studies of the polychaetes at the species level will enable us to test this idea further.

The response of the infaunal polychaetes within the same time frame as both the megafauna and other infaunal components, such as the meiofauna, points to a widespread phenomenon operating on short ecological time scales. This rapid response indicates that there may be a close linkage between the processes operating in the upper ocean and the abyss. Climatic forcing, which has been implicated in upper water column ecology, may have a much more direct role in abyssal sediment systems than was first thought.

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