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Temporal changes (1989–1999) in deep-sea metazoan meiofaunal assemblages on the Porcupine Abyssal Plain, NE Atlantic

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ABSTRACT

Trends among major metazoan meiofaunal taxa were investigated based on 56 deployments of a multicorer at 10 time points over a period of 11 years (1989–1999) at the Porcupine Abyssal Plain Sustained Observatory site (PAP-SO: 48°50′N 16°30′W, 4850 m depth). This area is characterised by a strong seasonality in the deposition of organic matter to the seafloor and by the massive increase in the density of holothurian species since 1996, the so-called '*Amperima* event'. Total meiofaunal densities ranged from 346 to 1074 ind. $\times$ 10 cm^{-2} and showed a significant increase with time when time was represented by cruises, years and the '*Amperima* period' (1996–1999) vs. the pre-*Amperima* period (1989–1994). This pattern was driven mainly by the nematodes, which were the dominant taxon ($\sim$90% of total abundance). The third most abundant group, the polychaetes, also increased significantly in abundance over the time series, while the ostracods showed a significant decrease. Most other taxa, including the second-ranked group, the copepods (harpacticoids and nauplii), did not exhibit significant temporal changes in abundance. Ordination of taxon composition showed a shift from the pre-*Amperima* to the *Amperima* periods, a trend supported by the significant correlation between the x-ordinate and time. The majority (52–75%) of meiofaunal animals inhabited the top 2 cm of the 5 cm sediment cores analysed. There were significant increases in the proportion of total meiofauna, nematodes and copepods (but not polychaetes) inhabiting the 0–1 cm layer over time (represented by cruises) and between the pre-*Amperima* and *Amperima* periods in the case of copepods and polychaetes. During the intensively sampled period (1996–1997), there were indications of seasonal changes in the vertical distribution patterns of total meiofauna and nematodes within the sediment. We discuss the potential link between temporal variations in organic matter flux to the seafloor and meiofaunal populations, considering both qualitative and quantitative changes in fluxes and how they may be linked to climate variations.

1. Introduction

Quantitative studies of deep-sea meiofaunal ecology have been conducted in all major ocean basins including the Atlantic, Pacific, North Sea, Mediterranean, Red Sea, Gulf of Mexico, and Weddell Sea (e.g. Vincx et al., 1994; Soltwedel, 2000). These deep-sea investigations focused mainly on bathymetric gradients of abundance and relationships between community structure, food availability and other environmental factors. Time-series studies are much less common. Most have been of short duration ($<$5 years) and carried out in bathyal continental margin settings (Guidi-Guilvard, 2002; Gooday, 2002; Hoste et al., 2007), although a few have extended over longer periods (Gooday et al., 2010). In the abyssal, open-ocean, studies of temporal trends in benthic communities over decadal time scales ($>$10 years) have been conducted at only two sites, namely the Porcupine Abyssal Plain (PAP) in the NE Atlantic and Station M in the NE Pacific (34°50′N, 123°00′W). Both these time-series studies were initiated in 1989 and have revealed long-term changes in megafaunal communities, possibly linked to climate fluctuations that influence organic matter supply (Billett et al., 2001; Ruhl and Smith, 2004; Ruhl, 2007).

A series of European Union-funded projects conducted at the PAP site during the late 1980s and 1990s (Rice et al., 1994; Billett and Rice, 2001) reported a strong seasonal deposition of phytodetritus (Bett et al., 2001) and a radical shift in the abundances and

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community structure of the invertebrate megafauna (Billett et al., 2001). This so-called '*Amperima* Event' (Fig. 1) involved significant increases in the abundance of various benthic species, notably the holothurians *Amperima rosea* and *Ellipinion molle* (Bett et al., 2001; Billett et al., 2001). It is considered to be related to changes in the quantity and/or quality of organic matter reaching the seafloor (Wigham et al., 2003). This, in turn, may be influenced by climatic oscillations, although there has been no obvious trend in total organic flux to the seabed (Lampitt et al., 2001; Lampitt et al., 2010). A similar phenomenon was observed during the same period (1989–2005) in the NE Pacific, where intense fluctuations in the populations of certain species, especially holothurians, were potentially linked to climate changes (Ruhl and Smith, 2004; Ruhl, 2007).

Apart from the observed changes in the larger benthic components, evidence is accumulating that the smaller benthic size classes at the PAP site also underwent shifts in abundance during the 1990s. Based on a study of samples from September 1996 to October 1998, Vanreusel et al. (2001) described an opheliid polychaete mass recruitment event that they interpreted as a rapid population response to a flux event. Galéron et al. (2001) demonstrated that both meiofaunal and macrofaunal taxa responded to the food pulse with increased abundance and showed vertical movements within the sediment depending on the burial of labile particulate organic matter (POM). Gooday and Rathburn (1999) present preliminary data on foraminiferal trends over time at the PAP. Other contributions in the present volume report on temporal trends among invertebrate megafauna (Billett et al., 2010), macrofaunal polychaetes (Soto et al., 2010) and foraminifera (Gooday et al., 2010).

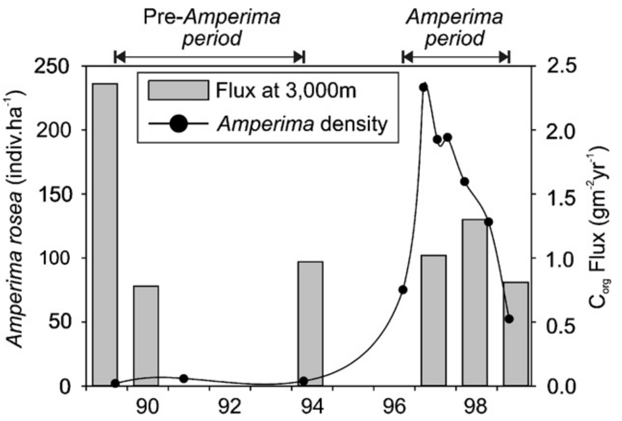

Fig. 1. Temporal variations in *Amperima rosea* (holothurian) density and organic carbon flux at the Porcupine Abyssal Plain Sustained Observatory site. "Pre-*Amperima*" and "*Amperima*" periods are indicated as referred to in the text. (After: Billett et al., 2010; Lampitt et al., 2010).

It is known that the seasonal deposition of phytodetritus to the deep-sea floor increases the density, activity and biomass of small faunal groups in general (Pfannkuche et al., 1999). A rapid respond of the smaller size-fractions of the benthic community, such as meiofauna, therefore might be expected. The spatial distribution of meiofauna (Rice and Lambshead, 1994) seems to be linked to the patchy distribution of phytodetritus on the sea bed and their vertical distribution in the sediments may also be affected by the presence of phytodetritus at the sediment surface (Lambshead et al., 1995). Here we provide the first comprehensive assessment of metazoan meiofauna from the PAP site for the decade 1989–1999. The main objective of this paper is to describe the trends in density and vertical distribution within the sediment of meiofauna over this 10-year period. Two questions are addressed: (1) do meiofaunal communities exhibit significant changes over long time scales, (2) are these changes similar for the different meiofaunal taxa and how do they compare to the changes observed for other faunal groups?

2. Materials and methods

2.1. Study area

The study area is located in the centre of the Porcupine Abyssal Plain (PAP) about 270 km southwest of Ireland (PAP-SO, 48°50′N, 16°30′W) at 4850 m water depth (Fig. 2). It has been sampled frequently for more than 15 years under a series of European Union-funded projects (Billett and Rice, 2001). The PAP site is characterised by an absence of significant topography, making the benthic environment spatially uniform and remote from both the continental slope and the foothills of the mid-ocean ridge. The site is not significantly influenced by benthic storms or by down slope processes. It is characterised, however, by large seasonal variations in the flux of particulate organic matter (POM) derived from surface production (Rice et al., 1994; Lampitt et al., 2001; Lampitt et al., 2010). Fluxes are highest during the summer months, late

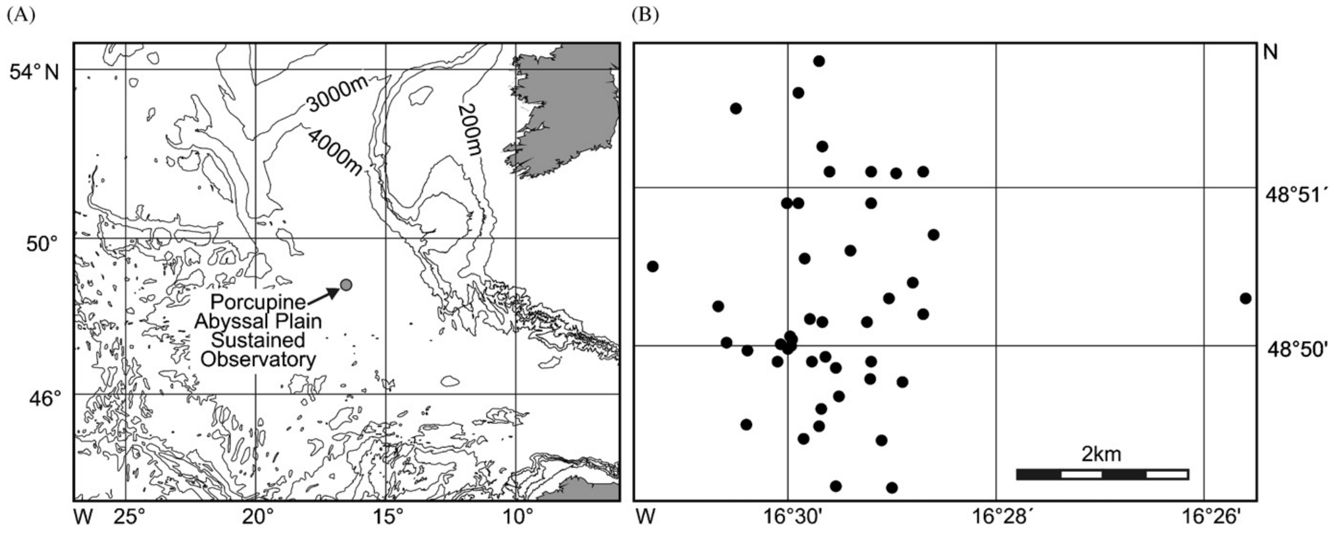

Fig. 2. Charts showing (A) the general location of the Porcupine Abyssal Plain Sustained Observatory site and (B) the disposition of samples assessed in the present study (see also Table 1).

May or early June, although peaks sometimes occur later in the year (Lampitt et al., 2010). As in other parts of the NE Atlantic, the settling material sometimes forms a patchy carpet of phytodetritus on the seabed (Thiel et al., 1989), although this was notably absent during the later years of the time series (Bett et al., 2001). During the most intensively sampled period (1996–1998), seasonal changes were evident in organic compounds such as labile lipids (Kiriakoulakis et al., 2001) and phytopigments (Fabiano et al., 2001; Witbaard et al., 2001). Near-bottom current speeds are low, with a mean speed of 3.5 cm s^{-1} and maximum of 9 cm s^{-1} (Vangriesheim et al., 2001). The sediment consists of biogenic carbonates, characterised as foraminiferal ooze, with a median grain size of 8.3 μm (Varnavas et al., 2001) and a sedimentation rate of 3.5 cm ky^{-1} (Rice et al., 1991). Oxygen concentration profiles show a decrease from 266 μmol l^{-1} at the sediment water interface to 25 μmol l^{-1} at depths ranging from about 6.2 cm in September 1996 to 7.5 cm in July 1997 and about 10 cm in March 1997 (Witbaard et al., 2000). The surficial sediment has a total organic carbon content of about 0.35% decreasing to 0.15% at 18 cm depth (Rabouille et al., 2001); the C:N ratio varies between 4.8 and 7.8 (Santos et al., 1994).

2.2. Shipboard procedures

Samples were collected using a hydraulically-damped, SMBA-type multiple corer (Barnett et al., 1984), equipped with 12 core tubes of 57 mm internal diameter. A total of 56 undisturbed core samples, obtained from 44 separate corer deployments during 10 cruises to the PAP, were analysed for meiofaunal metazoans (Fig. 2, Table 1). Immediately after recovery, the cores were processed as follows in the ships' constant temperature laboratories (5–8 °C). Any phytodetritus present, together with a small volume (1–2 ml) of surface sediment, was removed using a Pasteur pipette and stored separately, together with the lower few centimetres of overlying water. The core was then cut into horizontal slices by extruding it into a ring and slicing the sediment with a metal plate. During earlier cruises (1989–1994, Stations 11908, 52701, 53201), the cores were cut into 1-cm-thick slices to a depth of at least 10 cm. From 1996 onwards, the cores were cut into 0.5-cm slices to a depth of 2 cm and thereafter into 1-cm slices to at least 10 cm depth. All samples were fixed in 4% formalin buffered with sodium borate (borax), made up with filtered (32 μm) seawater.

2.3. Laboratory procedures

The core samples were analysed to a depth of 5 cm. Meiofauna are conventionally defined to include animals that pass through a 1000-μm mesh sieve and are retained on a 63-μm mesh sieve (Giere, 1993). However, because deep-sea organisms are generally smaller than their shallow-water counterparts (Kaariainen and Bett, 2006), a 32-μm mesh sieve was used as the lower limit in this study. Meiofauna were extracted by density gradient centrifugation with Ludox as a flotation medium (de Jonge and Bouwman, 1977). The technique typically extracts 95–99% of organisms over all sediment grain sizes (Burgess, 2001). The treated samples were stained with Rose Bengal (0.5 g l^{-1}) and all metazoan meiofaunal taxa were counted and sorted under a stereoscopic microscope. Although the samples were sorted by different people in two laboratories (DZMB and Universiteit Gent), there were no statistically significant differences between counts of samples from the same cruise (paired *t*-test; $p > 0.05$). Both temporary and permanent meiofaunal taxa were analysed.

2.4. Statistical methods

Univariate statistical procedures were carried out using the Minitab® (v. 15.1.1.0., Minitab Inc.) software package; all methods employed are as described by Zar (1999). Prior to the analyses, data from multiple samples from single deployments (e.g. a–c samples indicated in Table 1) were averaged to a single representative sample, i.e. only true replicates (from independent deployments) were included in the analyses. Variations in meiofaunal density were assessed by analysis of variance (ANOVA), the data having first been subject to a log(x+1) transformation in an attempt to 'improve' normality and homoscedasticty (e.g. Bartlett's test of log-transformed total meiofauna data assessed by year gives a non-significant result, $p > 0.05$). ANOVA was also employed to examine variations in the vertical distribution of meiofaunal taxa using the percentage of specimens recovered in the 0–1 cm layer, relative to the total recovered in the 0–5 cm sample, as an indicator of vertical distribution. These percentage data were subject to an arcsine transformation prior to analyses in an attempt to 'improve' normality. For presentation, both the density and vertical distribution results are shown with 95% confidence intervals based on pooled variances; note that in the case of density, back transformation yields geometric mean (not arithmetic mean) values. Some correlation analyses were also carried out (as described in Section 3); in all cases these were implemented using the Spearman's rank (non-parametric) technique.

Potential variation in meiofaunal taxon composition was assessed by multivariate analyses (cluster analysis and non-metric multi-dimensional scaling ordination) using the PRIMER (v. 5.2.0, PRIMER-E Ltd.) software package. The Bray–Curtis similarity index was employed in all analyses (Clarke and Green, 1988). The significance of taxon composition variation between periods (pre-*Amperima* to *Amperima*) was assessed by analysis of similarities (ANOSIM); a range of data transformations (none, $\sqrt{}$, $\sqrt{}\sqrt{}$ and log[x+1]) was tested.

3. Results

3.1. Meiofaunal assemblage composition

Meiofaunal organisms, belonging to 14 major taxa, were extracted from the core samples collected between 1989 and 1999. Nematodes were clearly the dominant group, representing 68–96% of the assemblage; harpacticoid copepods, including all developmental stages, were the second most abundant taxon, contributing 3–14% to the total; polychaetes were the third most abundant representing 0.2–4.4% of the meiofauna. The latter were dominated (>97%) by larval specimens of an opheliid, as reported by Vanreusel et al. (2001). Other taxa, namely oligochaetes, gastrotrichs, ostracods, tardigrades, loriciferans, kinorhynchs, molluscs, nemertines and tantulocarids, were regularly found but in very low abundances and generally contributed no more than 1% to the assemblage. Rotifers and halacarids were also encountered during sample processing; these are believed to be contaminants either from clothing fibers, or plastic vials, i.e. halacarids, or tap water, i.e. rotifers (Pedro Martinez Arbizu, personal communication) and have been excluded from all results presented here.

3.2. Temporal changes in densities

Mean abundances of metazoan meiofauna and major taxa are summarised in Table 2 and trends in mean densities of selected taxa over time are shown in Fig. 3. Mean densities of total

Table 1
Station data for meiofauna samples obtained from the Porcupine Abyssal Plain Sustained Observatory site 1989–1999.

Date	Cruise	Station number	Position		Depth (m)	Sorting
			N	W		
Aug. 1989	R.R.S. *Discovery* 185	11908#39	48° 49.9′	16° 30.1′	4845	NOC
		11908#70	48° 49.5′	16° 30.4′	4847	NOC
May 1991	R.R.S. *Challenger* 79	52701#10	48° 51.1′	16° 28.7′	4843	DZMB
		52701#24	48° 50.9′	16° 29.2′	4845	DZMB
		52701#27	48° 51.1′	16° 29.2′	4847	DZMB
		52701#51	48° 50.9′	16° 29.9′	4843	DZMB
April 1994	R.R.S. *Challenger* 111	53201#7	48° 51.5′	16° 30.5′	4837	DZMB
		53201#9	48° 51.8′′	16° 29.7′	4845	DZMB
		53201#11	48° 51.6′	16° 29.9′	4847	DZMB
		53201#17	48° 51.1′	16° 29.6′	4846	DZMB
Sep. 1996	R.R.S. *Discovery* 222	12930#10	48° 49.86′	16° 29.54′	4838	DZMB
		12930#15a	48° 50.55′	16° 29.84′	4837	UG
		12930#15b	48° 50.55′	16° 29.84′	4837	DZMB
		12930#18	48° 50.30′	16° 29.03′	4837	UG
		12930#29a	48° 50.15′	16° 29.24′	4839	UG
		12930#29b	48° 50.15′	16° 29.24′	4839	UG
		12930#36a	48° 51.26′	16° 29.67′	4837	UG
		12930#36b	48° 51.26′	16° 29.67′	4837	DZMB
		12930#66	48° 50.25′	16° 30.67′	4840	DZMB
Mar. 1997	R.R.S. *Discovery* 226	13077#6a	48° 50.90′	16° 30.01′	4843	UG
		13077#6b	48° 50.90′	16° 30.01′	4843	UG
		13077#6c	48° 50.90′	16° 30.01′	4843	DZMB
		13077#12	48° 50.17′	16° 29.79′	4846	DZMB
		13077#21	48° 50.02′	16° 30.59′	4845	UG
		13077#24	48° 49.97′	16° 30.39′	4844	DZMB
		13077#58a	48° 50.04′	16° 29.96′	4844	UG
		13077#58b	48° 50.15′	16° 29.67′	4844	DZMB
		13077#60	48° 50.00′	16° 29.97′	4845	UG
		13077#69	48° 50.01′	16° 30.07′	4843	DZMB
Jul. 1997	R.R.S. *Discovery* 229	13200#1a	48° 49.98′	16° 30.00′	4843	UG
		13200#1b	48° 49.98′	16° 30.00′	4843	DZMB
		13200#1c	48° 49.98′	16° 30.00′	4843	UG
		13200#12	48° 49.60′	16° 29.68′	4842	UG
		13200#24	48° 49.79′	16° 29.21′	4844	UG
		13200#32	48° 49.77′	16° 28.90′	4843	DZMB
		13200#46	48° 49.41′	16° 29.85′	4844	DZMB
Oct. 1997	R.R.S. *Challenger* 135	54301#9b	48° 50.50′	16° 31.3′	4843	DZMB
		54301#10a	48° 50.7′	16° 28.6′	4843	UG
		54301#10b	48° 50.7′	16° 28.6′	4843	UG
		54301#14	48° 50.4′	16° 28.8′	4839	UG
		54301#16	48° 50.6′	16° 29.4′	4842	UG
		54301#21	48° 49.1′	16° 29.0′	4840	DZMB
Mar. 1998	R.R.S. *Discovery* 231	13368#3	48° 49.11′	16° 29.54′	4846	UG
		13368#7	48° 49.49′	16° 29.70′	4844	DZMB
		13368#15	48° 49.68′	16° 29.51′	4845	UG
		13368#19a	48° 51.09′	16° 28.96′	4842	UG
		13368#19b	48° 51.09′	16° 28.96′	4842	UG
		13368#19c	48° 51.09′	16° 28.96′	4842	DZMB
		13368#28a	48° 50.06′	16° 29.98′	4841	UG
		13368#28b	48° 50.06′	16° 29.98′	4841	DZMB
Sep. 1998	R.R.S. *Discovery* 237	13627#12	48° 49.90′	16° 29.77′	4836	DZMB
		13627#15	48° 49.93′	16° 29.64′	4837	UG
Apr. 1999	R.R.S. *Challenger* 142	54901#11	48° 50.3′	16° 25.6′	4840	DZMB
		54901#12	48° 50.2′	16° 28.7′	4837	DZMB
		54901#13	48° 49.4′	16° 29.1′	4839	DZMB
		54901#14	48° 49.9′	16° 29.2′	4841	DZMB

Station number (xxxxx#yyz: x, unique coding for cruise and sampling location; y, unique coding for consecutive equipment deployments; z, indicator for multiple samples from single deployment). Sorting, indicates the laboratory where the samples were analysed (DZMB: Deutsches Zentrum für Marine Biodiversitätsforschung; NOCS: National Oceanography Centre, Southampton; UG: Universiteit Gent).

meiofauna ranged from the lowest (346 ind. × 10 cm^{-2}) in April 1994 to the highest (1074 ind. × 10 cm^{-2}) in April 1999 and increased from an overall mean of 475 ind. × 10 cm^{-2} during the 1989–1994 period to 824 ind. × 10 cm^{-2} in the 1996–1999 period. The dominant taxon, the nematodes, also showed a three-fold density range from the lowest (301 ind. × 10 cm^{-2}) in April 1994 to the highest (935 ind. × 10 cm^{-2}) in April 1999. Mean nematode densities increased over the time series from 418 ind. × 10 cm^{-2} (1989–1994) to 740 ind. × 10 cm^{-2} (1996–1999). Polychaete densities were even more variable, ranging from 2 ind. × 10 cm^{-2} (August 1989) to 19 ind. × 10 cm^{-2} (September 1996) with means of 3 ind. × 10 cm^{-2} (1989–1994) and 11 ind. × 10 cm^{-2} (1996–1999) during the earlier and later parts of the time series. Harpacticoid copepods (including their nauplii) fluctuated in abundance with the highest peaks in May 1991 (55 ind. × 10 cm^{-2}) and April 1999 (58 ind. × 10 cm^{-2}). However, mean densities during the 1989–1994 and 1996–1999 periods were similar (42 and 45 ind. × 10 cm^{-2}; Table 2).

Nested ANOVA revealed that the densities of total metazoan meiofauna, as well as those of nematodes and polychaetes, varied significantly ($p < 0.001$) between periods (i.e. 1989–1994 vs. 1996–1999) (Table 2; Fig. 3) and between years within periods ($p < 0.05$). Several other taxa (oligochaetes, gastrotrichs, ostracods, kinorhynchs) showed significant ($p < 0.05$) variations with either period, year or cruise (see Table 2). However, the densities of copepods and some of the less common taxa did not change significantly. When density data were arranged by month, irrespective of year, significant variations ($p < 0.05$) were found only for polychaetes, oligochaetes and ostracods (Table 2).

Hierarchical cluster analysis and multi-dimensional scaling analysis were carried out on meiofaunal taxon composition without performing any data transformation. The two-dimensional plot revealed a fairly good separation, although with some overlap, between samples from the pre-*Amperima* (1989–1994) and *Amperima* (1996–1999) periods (Fig. 4A). There was also a significant correlation (r_s 0.617, $p < 0.001$) between *n*MDS*x*-axis values and time (Fig. 4B), driven mainly by the changes in nematode and polychaete density. (We repeated these analyses using principal components analysis, implemented with PRIMER, and achieved identical results). ANOSIM results strongly support the pre-*Amperima* to *Amperima* period variation (*p* values range from 0.001 to 0.006, depending on transformation), again largely reflecting the increasing abundances of nematodes and polychaetes.

3.3. *Vertical distribution*

Vertical distribution profiles of the major meiofaunal taxa are shown in Fig. 5. Densities decreased with sediment depth with the single exception of nematodes in the August 1989 samples, where similar densities were present in both the 0–1 and 1–2 cm layers. Assessed across all samples, the median proportion of specimens present in the 0–1 cm layer was 44.9% (36.8–51.6% interquartile range) for the total meiofauna, with similar median values for the nematodes (median: 43.0%; 35.0–49.8% interquartile range). Copepods were more superficially distributed (median: 67.9%; 62.0–75.1% interquartile range), with polychaetes largely restricted to the surface layer (median: 81.1%; 73.3–95.1% interquartile range).

Temporal trends in the vertical distribution of meiofaunal taxa, assessed on the basis of the relative abundance of specimens in the 0–1 cm layer, were examined by ANOVA (Fig. 6, Table 3). Significant variations were found between months (irrespective of year) for nematodes ($p < 0.001$), copepods ($p = 0.010$) and total meiofauna ($p < 0.001$). Significant (see Table 3) temporal

Table 2
Temporal variation in the meiobenthos of the Porcupine Abyssal Plain Sustained Observatory site (1989–1999).

Taxon	Cruise mean density (indiv. × 10 cm^{-2})										Nested ANOVA (p)			ANOVA (*p*)	Period mean density (indiv. × 10 cm^{-2})	
	Aug. '89	May '91	Apr. '94	Sep. '96	Mar. '97	Jul. '97	Oct. '97	Mar. '98	Sep. '98	Apr. '99	Period	Year	Cruise	Month	1989–1994	1996–1999
Nematodes	409.2	584.8	301.3	671.4	609.7	842.2	777.9	747.5	756.5	935.5	<0.001	0.011	ns	ns	417.7 (345.2–505.5)	739.7 (666.9–820.1)
Copepods	35.5	54.7	34.4	51.6	40.0	45.3	44.8	40.4	29.2	58.1	ns	ns	ns	ns	41.7	44.5
Polychaetes	1.6	7.6	1.9	18.8	12.3	10.1	10.5	9.2	6.5	8.7	<0.001	<0.001	ns	0.001	3.3 (2.2–5.0)	11.2 (9.1–13.8)
Oligochaetes	0	0	0	0	0.1	0.5	0	0	0	0	ns	ns	0.031	0.010	0	0.1
Gastrotrichs	0	0.9	0	0.9	0.4	0	0.2	0.3	0.5	0.5	ns	0.021	ns	ns	0.2	0.4
Ostracods	4.2	2.4	2.1	0.8	0.5	0.5	0.3	0.4	0.9	3.0	0.019	ns	ns	0.007	2.5 (1.3–4.8)	0.7 (0.4–1.1)
Kinorhynchs	0.3	0.3	0.2	0.2	0.1	0.1	0	0	0	0.9	ns	0.015	ns	ns	0.2	0.1
Molluscs	0.4	0.4	0	0.2	0.1	0	0	0.2	0.2	0.1	ns	ns	ns	ns	0.2	0.1
Loriciferans	0	1.6	0.4	0.8	0.7	0.4	0.2	0.4	0.3	1.8	ns	ns	ns	ns	0.6	0.6
Tantulocarids	0	0.4	0.5	0	0.1	0.2	1.1	0	0	0.4	ns	ns	ns	ns	0.3	0.2
Others	1.2	0.3	1.3	1.1	0.9	2.2	0.1	0.2	0.5	0.5	ns	ns	ns	ns	0.7	0.7
Total	453.6	667.2	346.6	754.6	677.7	920.1	897.8	807.0	799.6	1073.5	<0.001	0.008	ns	ns	475.3 (393.4–574.5)	823.5 (743.3–912.6)

Mean densities of major taxa are given on a by cruise basis (see also Fig. 3), together with nested ANOVA results for between period (1989–1994 vs. 1996–1999), year within period and cruise with year comparisons. ANOVA results are given for month irrespective of year comparisons. Period mean densities are also given with 95% confidence intervals (in parenthesis) for those taxa exhibiting significant between period variations. (ns—not significant).

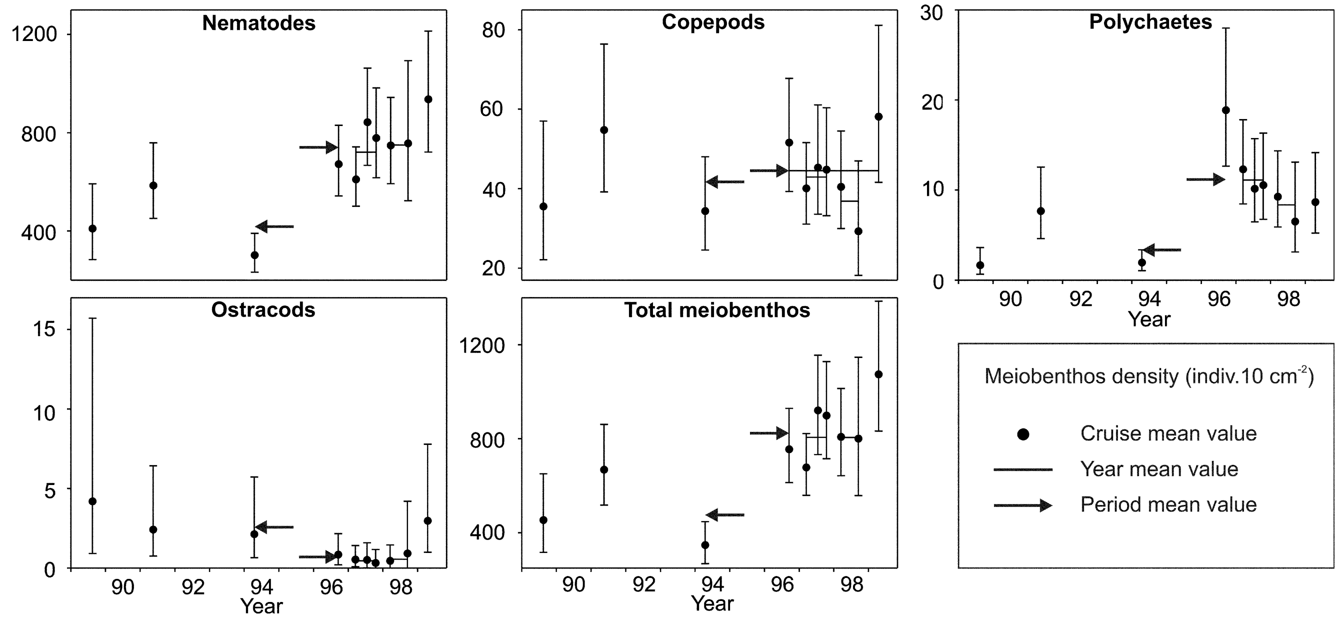

Fig. 3. Plots of temporal variations in the density of selected meiobenthic taxa at the Porcupine Abyssal Plain Sustained Observatory site; cruise means with 95% confidence intervals are shown together with indications of year means (1997 and 1998) and period means (1989–1994 and 1996–1999).

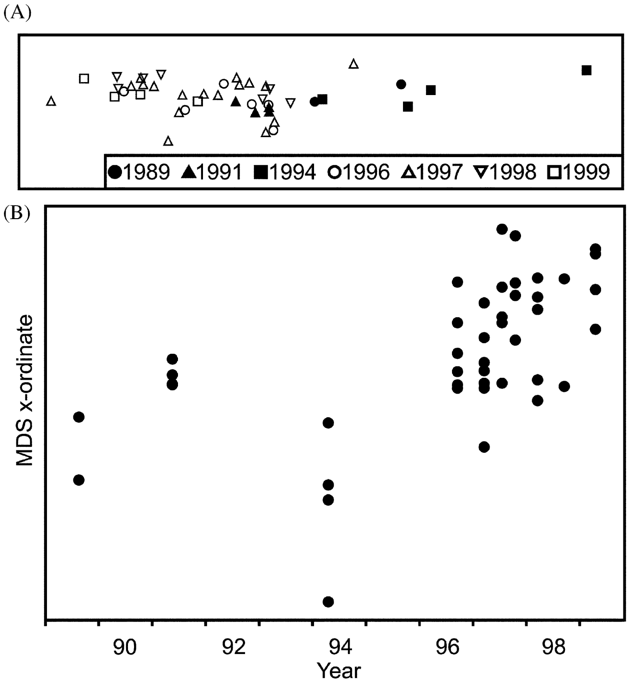

Fig. 4. Temporal variations in the composition of meiobenthic taxa at the Porcupine Abyssal Plain Sustained Observatory; (A) non-metric multi-dimensional scaling (MDS) ordination, note filled symbols represent the "pre-*Amperima* period" (1989–94) and open symbols the "*Amperima* period" (1996–99) (*n*MDS stress, 0.02); (B) plot of temporal variation in the MDS-*x* ordinate.

variations were also detected between cruises (nematodes, copepods and total meiofauna), years (copepods) and periods (copepods and polychaetes) (Table 3). Both copepods and polychaetes were concentrated closer to the surface sediment in the 1996–1999 (*Amperima*) period; the median relative abundance of copepods in the 0–1 cm layer increasing from 55.6% (51.1–63.9% interquartile range) to 69.6% (63.7–78.1% interquartile range) and that of polychaetes increasing from 64.6% (43.8–97.9% interquartile range) to 88.9% (77.4–94.7% interquartile range) between periods, respectively.

4. Discussion

4.1. Comparison of PAP meiofauna standing stocks with other deep-sea areas

The number of higher taxa (14 excluding rotifers and halacarids) in our PAP time-series samples, and the dominance of nematodes (>90% of the total meiofauna) followed by harpacticoid copepods and polychaetes, is consistent with previous studies of deep-sea meiofauna (Thiel, 1983; Shirayama, 1984a; Tietjen et al., 1989; Alongi, 1992; Vincx et al., 1994; Vanhove et al., 1995; Vanreusel et al., 2000). Total meiofaunal abundances at the PAP ranged from 200 to 1417 ind. × 10 cm^{-2}, with mean values per time point ranging from 347 to 1074 ind. × 10 cm^{-2}. Previous studies have reported abundances of the same order of magnitude in deep eastern Atlantic basins (Pfannkuche, 1985; Soltwedel, 1997) and lower values, by up to a factor of two, in western basins (Tietjen et al., 1989; Thistle et al., 1991; Tietjen, 1992; Soltwedel, 2000). According to Soltwedel (2000), meiofaunal abundances in polar regions are approximately twice as high as those in temperate areas such as the PAP. On the other hand, densities in subtropical Atlantic regions, as well as in the Western and Eastern Mediterranean and the northwest Indian Ocean, are 2–3 times lower (Dinet and Vivier, 1977; Tahey et al., 1994; Danovaro and Fabiano, 1995; Tselepides and Lampadariou, 2004) than those at the PAP. In abyssal Pacific basins, meiofaunal densities are similar to those in our samples (Shirayama, 1984a; Alongi, 1992).

These geographical variations in meiofaunal densities at similar abyssal depths can be explained by differences in productivity. The PAP is a relatively eutrophic area with strong seasonal fluxes (Lampitt and Antia, 1997; Lampitt et al., 2001), whereas much lower POM fluxes have been reported at several sites in the western Atlantic (Lampitt and Antia, 1997). The Mediterranean, particularly the Eastern basin, is characterised by very low standing stocks, reflecting the very low primary

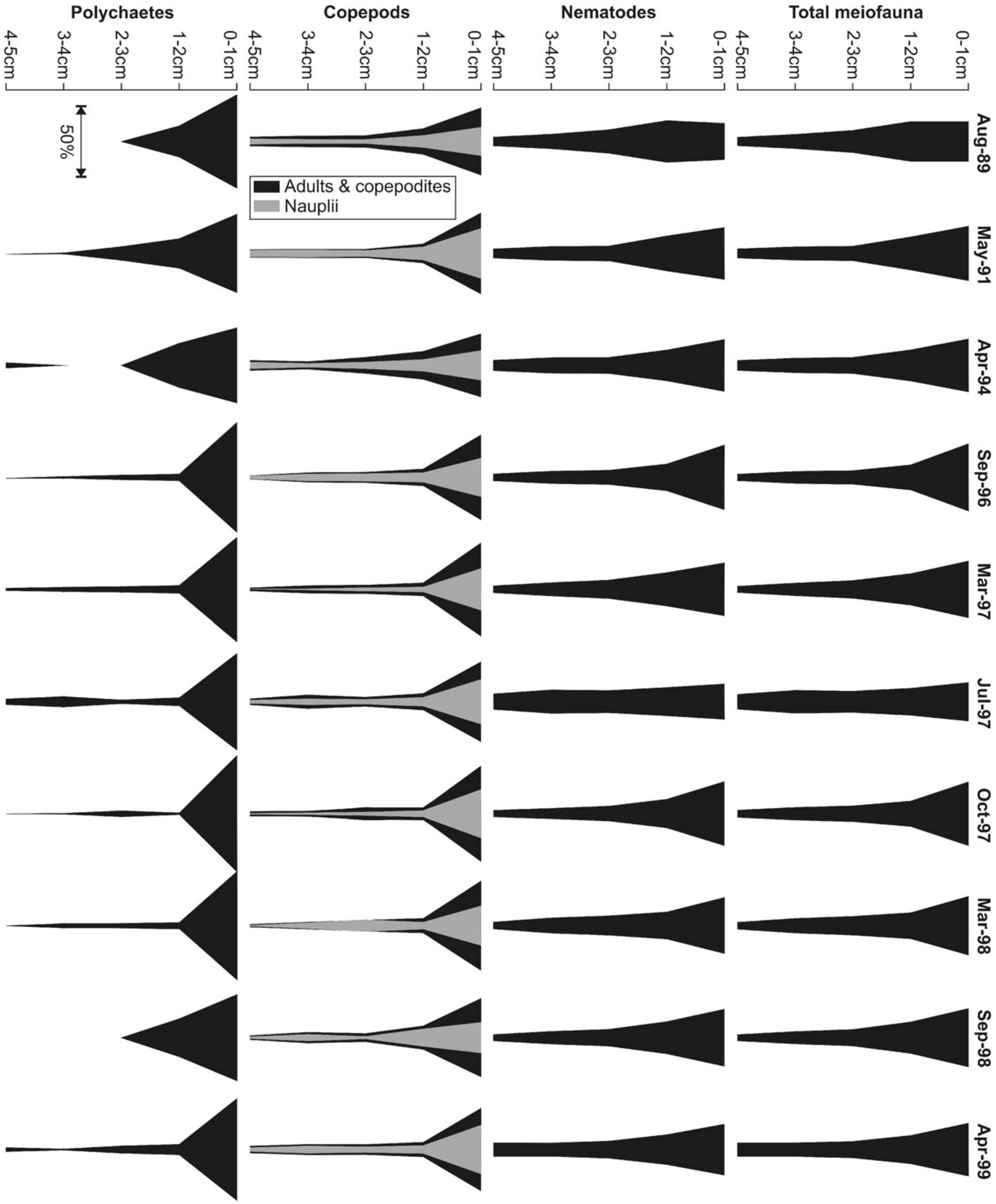

Fig. 5. Temporal variations in the vertical profiles of mean relative abundance in 1 cm horizons (0–5 cm) for the dominant meiofaunal taxa at the Porcupine Abyssal Plain Sustained Observatory site.

productivity of the area (Danovaro et al., 1995a). Rex et al. (2006) compiled a global dataset of meiofaunal abundance, their regression equation predicts an abundance of 206 ind. × 10 cm^{-2} for a water depth of 4850 m. This value is some 2–4 times lower than the period mean values at the PAP (1989–1994, 475 ind. × 10 cm^{-2}; 1996–1999, 824 ind. × 10 cm^{-2}) supporting the relatively eutrophic status of the site. Moreover, Mokievskii et al. (2007) presented a stable correlation between the abundance of meiofauna in the deep sea and the productivity of the surface water. The results of the present study clearly suggest that, as in other oceanic regions, meiofaunal organisms at the PAP are sensitive to food supply and that they show a similar response to carbon limitation in terms of standing stock (Pfannkuche, 1993; Vincx et al., 1994).

4.2. *Meiofaunal response to phytodetritus fluxes*

When densities of the total meiofauna and of individual taxa from this study were arranged by month, irrespective of year, the

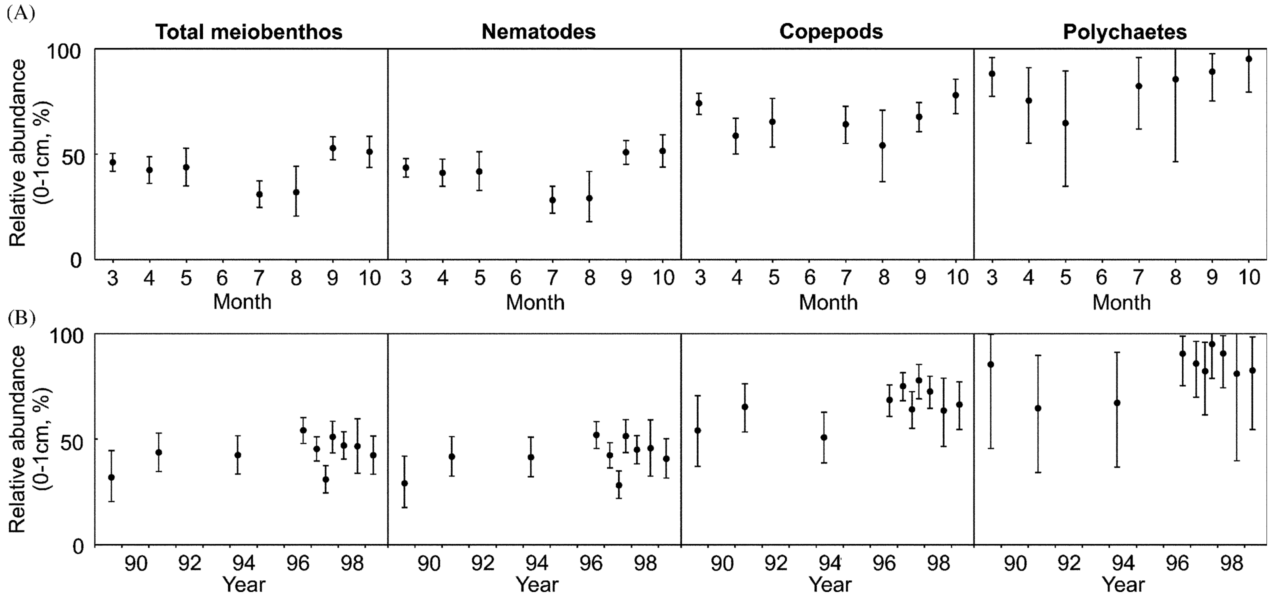

Fig. 6. Temporal variation in the relative abundance (mean and 95% confidence interval) of selected meiofaunal taxa in the 0–1 cm sediment layer at the Porcupine Abyssal Plain Sustained Observatory site; (A) data arranged by month irrespective of year; (B) data arranged by cruise date.

Table 3
Temporal variation in the vertical distribution of selected meiofaunal taxa from the Porcupine Abyssal Plain Sustained Observatory site (1989–1999).

Taxon	ANOVA			
	Month	Cruise	Year	Period
Nematodes	<0.001	0.001	ns	ns
Copepods	0.010	0.016	0.034	0.002
Polychaetes	ns	ns	ns	0.032
Total meiobenthos	<0.001	0.001	ns	ns

ANOVA results for comparisons of relative abundance in the 0–1 cm sediment horizon. Tests are shown for between cruise, year and period (1989–1994 vs. 1996–1999) comparisons. The results of by month (i.e. irrespective of year) comparisons are also given. (ns—not significant).

only numerically important group to exhibit significant variations, were the polychaetes (Table 2). In our samples, this taxon was dominated by juvenile opheliids. Vanreusel et al. (2001) studied the abundance and size spectra of these small worms during the period September 1996–October 1998. They found evidence for a recruitment event in 1996, when populations were dominated by small individuals, followed by growth of the cohort in terms of body size over the next 2 years.

It is difficult to interpret seasonal data compiled from different years. However, the lack of a significant seasonal pattern in other taxa, notably the nematodes and harpacticoids (Table 2), contrasts with the strong seasonal signal in the organic matter flux detected by sediment traps (Lampitt et al., 2001, 2010). Similarly, there were no seasonal changes in meiofaunal densities at a nearby site (BIOTRANS, 47° N, 20°W, 4450 m water depth) in the abyssal NE Atlantic (Pfannkuche, 1992, 1993), nor in the bathyal NE Atlantic (Gooday et al., 1996) and NW Pacific (Shimanaga and Shirayama, 2000). However, at the BIOTRANS site, Soltwedel et al. (1996) observed significant increases in nematode size spectra, indicating intense reproductive activity and therefore seasonal recruitment stimulated by the increased input of organic matter. Moreover, there are indications in our data of a response by some taxa during the intensively sampled period between 1996 and 1997 (Billett and Rice, 2001). As noted by Galéron et al. (2001), total meiofauna, nematodes and harpacticoids decrease in abundance between September 1996 (when phytodetritus was present; Bett et al., 2001) and March 1997. Our new data show that the same groups increased in abundance between March and July 1997, when a ‘faint green veneer’ was observed on the seafloor and chlorophyll-*a* values in surficial sediments were higher compared to March 1997 (Witbaard et al., 2000). More detailed sampling during other years may have revealed similar seasonal variations. It is also possible that the metazoan meiofauna exhibit time-lagged responses to food pulses, similar to those reported in the North Sea (Faubel et al., 1983), Kiel Bight (Graf et al., 1982, 1984) and the deep Eastern Mediterranean (Danovaro et al., 2000).

4.3. *Multi-year trends*

Over the decadal time scale, total meiofaunal abundances increased significantly in 1996 and persisted at a similar or even higher level until 1999, showing a significant correlation with time. The densities of nematodes and polychaetes exhibited a similar trend. These changes paralleled those in other faunal groups. Among the macrobenthos, Galéron et al. (2001) observed an increase in population densities that lagged behind the timing of POM input. Soto et al. (2010) report increases in the abundance of macrofaunal polychaetes, particularly surface deposit-feeding taxa. Gooday et al. (2010) report that the densities of live foraminifera, and particularly trochamminaceans, were significantly higher in 1996–2002 than in 1989–1994. Most remarkably, there was a spectacular rise in the abundance of megafauna, particularly the holothurians *A. rosea* and *E. molle*, over the same time period (Billett et al., 2001). Similar long-term shifts in the abundance of megafaunal animals are documented at Station M in the NE Pacific (Ruhl and Smith, 2004; Ruhl 2007). Short-term temporal changes without any seasonality, recorded for the meiofaunal assemblages in adjacent areas in the NE Atlantic (Pfannkuche, 1993) as well as the NW Pacific (Shimanaga and Shirayama, 2000), are consistent with the results of the current study. Studies with ^{13}C-labelled phytodetritus at PAP have shown that macrobenthic (and presumably megabenthic) organisms can effectively out compete meiobenthos and bacteria in terms of the immediate consumption of newly arrived phytodetritus (Witte et al., 2003).

The rise in meiofaunal densities is coincident with increased activity by megafaunal animals (Bett et al., 2001). Large consumers play an important role in the removal and repackaging of POM (Jumars and Self, 1986; Boudreau, 1994), strongly interacting with the meiofauna, as suggested by the *in situ* experiment conducted by Thistle et al. (2008). Moreover, Gallucci et al. (2008) suggest that larger benthic organisms significantly influence nematode assemblages, although megafauna may not fully account for the high nematode species coexistence in deep-sea sediments. At the PAP, the massive increase in the abundance of megafaunal detritus feeders referred to above meant that fresh POM was consumed rapidly, reworked and repackaged into smaller aggregates, which may then have been available to the infaunal meiobenthos. This repackaging may also have altered bacterial populations, which may be a key resource for the meiobenthos. The increased densities of large animals may also have favoured 'disturbance opportunists', as suggested by Gooday et al. (2010) in the case of foraminifera at the PAP.

We have compiled a summary set of environmental and biological (meio- and mega-benthos) parameters for the PAPSO site and present their intercorrelations in Table 4. -Note that in the case of modeled flux and climatic index data we have also considered one-year time lags in the correlation analyses, as have proved valuable in other deep-sea studies (see e.g. Smith et al., 2006). The quantity of phytodetritus present at time of sampling (phytodetritus index; Bett et al., 2001) exhibited no significant correlations with other environmental or biological parameters. Bett et al. (2001) indicate that phytodetritus accumulation is dependant upon both its supply and the rate of 'removal' by the megabenthos. Consequently, given the extreme variation in megabenthos activity at the PAPSO site (Bett et al., 2001), it is not a good proxy for organic matter supply to the benthos. Direct measurements of particulate organic matter (POM) supply to the seabed are not available for all of our sampling periods (see Lampitt et al., 2010) we have therefore considered modeled POM flux as provided by Lampitt et al. (2001). Modeled flux is significantly ($p<0.05$) correlated with both a climatic index (see below) and all bar one of the biological parameters included in our analysis. The correlations with most quantitative biological parameters (*A. rosea*, nematode, polychaete and total meiobenthos densities) are negative, i.e. high modeled flux is associated with lower benthos densities. Kiriakoulakis et al. (2001) have noted that there are systematic variations in the biochemical composition of POM over the PAPSO site related to high and low flux conditions. Such qualitative variations in POM have been linked with ecosystem change on the PAP (Wigham et al., 2003) where the supply of specific biochemicals may be critical to the reproductive and recruitment success of key species such as *A. rosea* (FitzGeorge-Balfour et al., 2010).

Smith et al. (2006) were able to link climatic indices with the potential supply of POM to the abyssal seafloor in both the NE Pacific and NE Atlantic (PAPSO site), in the latter case linking it with the North Atlantic Oscillation (NAO) index (see e.g. Jones et al., 1997). In our assessment we have considered the NAO Winter index (NAO$_{\mathrm{DJFM}}$), the mean monthly value for the December–March period. NAO$_{\mathrm{DJFM}}$ exhibits a good ($p = 0.005$) positive correlation with modeled POM flux. Positive (high) NAO$_{\mathrm{DJFM}}$ values are associated with stormy conditions and may therefore positively correlate with flux through a link to the depth of winter mixing in the surface ocean (see e.g. Lampitt et al., 2001). Variations in the NAO$_{\mathrm{DJFM}}$ may also influence the composition of surface ocean phytoplankton communities (Irigoien et al., 2000) and hence the biochemical composition of exported POM (Smythe-Wright et al., 2010). It is interesting to

Table 4

Spearman's rank correlations between selected environmental and biological variables for the Porcupine Abyssal Plain Sustained Observatory site, based on cruise mean values for the period 1989–1999 ($n = 10$).

	Phyto[a] score	Model[b] flux	Model[c] flux-1	NAO[d] DJFM	NAO[e] DJFM-1	*A. rosea*[f]	Mega[g] MDS*x*
Model flux	0.184						
Model flux-1	0.593	0.000					
NAO DJFM	−0.079	*0.800* *0.005*	0.000				
NAO DJFM-1	0.217	0.550	0.125	0.125			
A. rosea	−0.428	*−0.874* *0.001*	−0.357	*−0.702* *0.024*	*−0.640* *0.046*		
Mega MDSx	−0.279	*−0.886* *0.001*	−0.246	*−0.689* *0.027*	*−0.689* *0.027*	*0.976* *0.000*	
Nematodes[h]	−0.240	*−0.665* *0.036*	−0.025	−0.320	−0.320	0.527	0.552
Copepods[h]	0.084	−0.351	0.572	−0.388	0.289	0.030	0.055
Polychaetes[h]	−0.156	*−0.862* *0.001*	−0.025	*−0.911* *0.000*	−0.172	*0.758* *0.011*	*0.733* *0.016*
Ostracods[h]	0.389	*0.671* *0.034*	0.535	*0.659* *0.038*	0.474	*−0.855* *0.002*	*−0.794* *0.006*
Total meiob[h]	−0.279	*−0.665* *0.036*	−0.025	−0.320	−0.320	0.539	0.564
Meiob MDS*x*[i]	0.240	*0.665* *0.036*	0.025	0.320	0.320	−0.527	−0.552

Significance levels are given where $p<0.05$ and are highlighted in italics.

[a] Phytodetritus index from Bett et al. (2001).

[b] Modelled organic carbon flux to seafloor from Lampitt et al. (2001).

[c] The same lagged by 1 year.

[d] Winter (December–March) average North Atlantic Oscillation index (Jones et al., 1997).

[e] The same lagged by 1 year.

[f] *Amperima rosea* mean density from Billett et al. (2010).

[g] Megabenthos taxon composition as multi-dimensional scaling *x*-ordinate from Billett et al. (2010).

[h] Meiobenthos taxon mean density from present study.

[i] Meiobenthos taxon composition as multi-dimensional scaling *x*-ordinate from present study.

note that the NAO_{DJFM} for 1996 is the second most extreme negative value recorded since 1828. Consequently 1996, the onset of the '*Amperima* period', may have been a particularly unusual year with respect to both the quantity and quality of organic matter supplied to the seafloor at the PAPSO site.

As noted above the link between the incoming POM flux and meiobenthic communities might be mediated by the megabenthos. There are significant ($p < 0.05$) correlations between both *A. rosea* density and megabenthos composition and meiofaunal polychaete and ostracod densities; though correlations with nematodes, copepods, total meiobenthos and meiobenthos composition are not significant. Overall, modeled POM flux to the seafloor is best correlate with the biological parameters considered here. That the relationship with quantitative biological parameters is negative is perhaps surprising. There is certainly the potential for climatic control of both qualitative and quantitative attributes of export flux; clearly much of the fine detail in bentho-pelagic coupling in the deep sea remains to be elucidated.

4.4. Contrasting responses by metazoan meiofauna and foraminifera

In a general sense, the overall increase in abundance of metazoan meiofauna over time resembles the temporal patterns shown by the foraminifera (Gooday et al., 2010). Nevertheless, meiofaunal animals are often less responsive than foraminifera to episodic pulses of phytodetritus (Pfannkuche, 1993; Gooday et al., 1996; Gooday 2002). For example, in the bathyal Porcupine Seabight, there was no obvious increase in the abundance of metazoan meiofauna following a phytodetrital input, whereas the foraminifera exhibited a clear response. The foraminiferal response is most evident in the case of the small, opportunistic 'phytodetritus species' that undergo short-term fluctuations in population densities related to inputs of phytodetritus (e.g., Gooday, 1988; Gooday et al., 1992; Ohga and Kitazato, 1997; Kurbjeweit et al., 2000; Kitazato et al., 2000; Gooday and Hughes 2002). Over the course of the PAP time series, several groups, particularly the trochamminaceans, showed substantial increases in abundance. The ability of foraminifera to respond in this way seems to reflect their opportunistic life-histories (Gooday, 1993), highly efficient food-gathering mechanisms and an ability to rapidly activate their metabolic processes after periods of dormancy (Linke, 1992; Gooday et al., 1992). As a group, however, the metazoan meiofauna seem to have generally slower turnover rates as well as higher energy requirements for egg production. Moreover, the predominantly bacterial diets of many deep-sea nematodes probably make them less directly dependant on inputs of fresh phytoplankton-derived material than opportunistic, shallow-infaunal foraminifera.

Similar lifestyles and, consequently, responses to varying phytodetrital flux and megafaunal reprocessing may be evident among the polychaetes. The harpacticoids, however, exhibited no significant temporal change in their abundance (neither by month, cruise, and year nor between pre-*Amperima* and *Amperima* periods). These copepods may be predominantly surface feeders, and certainly their shallow-water counterparts can rapidly assimilate sedimented planktonic diatoms (Palmer, 1984; Decho, 1986; Rudnick, 1989) and may be closely associated with phytodetritus (Fleeger and Shirley, 1990). It is conceivable that their lack of abundance response is as a result of intense competition with the markedly enhanced populations of surface deposit-feeding megabenthos (particularly the ophiuroid *Ophiocten hastatum* and the holothurian *A. rosea*; Bett et al. 2001). Although, it is difficult to establish direct competition for food resources between copepods and the megabenthos, stable isotope studies at the PAP-SO (Iken et al., 2001) and at two bathyal sites in Sagami Bay (Nomaki et al., 2008) do suggest that the two groups do not have distinct $\delta^{15}N$ signatures. The phytodetritus associated foraminiferan *Epistominella exigua* was reduced in abundance at the onset of the "*Amperima* Event", again potentially as a result of competition from the megabenthos (Gooday et al., 2010).

4.5. Temporal changes in vertical distribution

Availability of organic matter and oxygen are considered to be the main factors limiting the penetration of meiofauna into the sediment (Thiel, 1983; Shirayama, 1984b; Danovaro et al., 1995b; Vanreusel et al., 1995). According to oxygen profile data (Witbaard et al., 2000), oxygen was never severely depleted in the upper 5 cm of sediment during our time-series study. Therefore, food availability and quality were probably the main factors determining vertical distribution patterns. During most years, the sediment surface was enriched by the supply of organic matter from the water column (Witbaard et al., 2000; Lampitt et al., 2001). Our data show that all meiofaunal taxa were aggregated to a greater or lesser extent in the upper sediment layer (Fig. 5). This was consistent with the higher values of oxygen and respiration profiles found in the reactive top layer (Witbaard et al., 2000).

It is possible, however, that oxygen played some role in the decrease from September 1996 to March and July 1997 in the proportion of total meiofauna inhabiting the upper 1-cm layer (Figs. 5 and 6). During September 1996, the vertical oxygen profile within the sediment was steeper compared to July and March 1997. At the same time, the relatively fresh phytodetritus present on core surfaces during September 1996 had disappeared by March 1997, the surficial layer became impoverished in both labile lipids and phytopigments, and higher quantities of phytopigments were detected in the 1–2 cm layer (Witbaard et al., 2001). Nematodes, in particular, showed a downward movement into the sediment, increasing in abundance in the 1–3 cm layer where they encountered more degraded organic material. In addition to the possible influence of oxygen, they may have been forced to move deeper by the availability of food in the sub-surface layers and to avoid physical disturbances, such as the intense reworking of the sediment, competition or predation pressure from larger organisms, as suggested by Thiel (1983) and Lambshead et al. (1995). It is interesting to note that the foraminiferan species *Quinqueloculina* sp. also migrated deeper into the sediment between September 1996 and July 1997 (Gooday et al., 2010). Our observations over this well-sampled portion of the time-series support the suggestion that small infaunal species can respond on seasonal time scales to the chemical properties of the sediment by changing their vertical distributions (Danovaro et al., 1995b; Lambshead et al., 1995; Soetaert et al., 1997). There were also indications of seasonality when vertical distribution data for nematodes, copepods and total meiofauna were analysed by month, irrespective of year (Fig. 6), although it is difficult to interpret this pattern based on composite data.

Polychaetes did not penetrate deeply into the sediment at any time over the course of the study. Similarly, harpacticoids were predominantly associated with the surface sediment layer; perhaps not surprisingly given their surface feeding behaviour and possible association with phytodetritus (see Section 4.4. above). Compared to adult harpacticoids and copepodites, copepod nauplii were more abundant and inhabited deeper sediment layers during May 1991, April 1994, July 1997 and April 1999, possibly suggesting enhanced reproductive activity. In marked contrast, nematodes were much more extensively distributed through the sediment column, again presumably linked with their bacterial/sub-surface deposit feeding and potentially their greater tolerance of dysoxic conditions (e.g. Heip et al., 1985).

5. Concluding remarks

We analysed temporal patterns among metazoan meiofauna at the higher taxon level. However, species within each taxonomic group are characterized by different biological and physiological characteristics, feeding preferences, life cycles and reproduction rates. They probably react individually to changes in parameters such as the quantity and quality of available food. Therefore, some meiofaunal responses to seasonal or interannual environmental changes may be masked at the level of higher taxa (Gooday et al., 1996). Thiel et al. (1989) noted elevated abundances of nematodes on aggregates of freshly deposited phytodetritus sampled from 4500 m in the NE Atlantic, suggesting that metazoan meiofauna may colonise and utilize freshly sedimented material. There is a clear need for detailed microscopic observations in order to recognize species, at least for the dominant groups, the nematodes and harpacticoid copepods. These should be coupled with morphological studies of mouthparts and other structures from which aspects of their trophic ecology could be inferred. In this way, it may be possible to detect any short-term or long-term changes that have occurred in the structure and composition of meiofaunal assemblages over the PAP time series.

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