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Long-term change in the abyssal NE Atlantic: The 'Amperima Event' revisited

D.S.M. Billett^{1*}, B.J. Bett¹, W.D.K. Reid^{1,3}, B. Boorman¹, I.G. Priede²

¹ National Oceanography Centre, Ocean Biogeochemistry & Ecosystems (DEEPSEAS Group), Southampton SO14 3ZH, UK.

² Oceanlab, University of Aberdeen, Newburgh, Aberdeenshire AB41 6AA, UK.

³ Present address: School of Marine Science and Technology, Newcastle University, Newcastle upon Tyne NE1 7RU, UK.

* Corresponding author

Tel.: +44 (0)23 80596014

Fax: +44 (0)23 80596247

E-mail address: dsmb@noc.soton.ac.uk (D.S.M. Billett)

Abstract

The results from a time series study (1989 to 2005) at a depth of 4850m on the Porcupine Abyssal Plain, NE Atlantic, are presented showing radical changes in the density of large invertebrates (megafauna) over time. Major changes occurred in a number of different taxa between 1996 and 1999 and then again in 2002. One species of holothurian, *Amperima rosea*, was particularly important, increasing in density by over three orders of magnitude. There were no significant changes in total megafaunal biomass during the same period. Peaks in density were correlated to reductions in mean body size indicating that the increases were related to large-scale recruitment events. The changes occurred over a wide area of the Porcupine Abyssal Plain. Comparisons made with changes in the density of protozoan and metazoan meiofauna, and with macrofauna, showed that major changes in community structure occurred in all size fractions of the benthic community at the same time. This suggests that the faunal changes were driven by environmental factors rather than being stochastic population imbalances of one or two species. Large-scale changes in the flux of organic matter to the abyssal seafloor have been noted in the time series, particularly in 2001 and may be related to the sudden mass occurrence of *A. rosea* the following year. Time-varying environmental factors are important in influencing the occurrence of megafauna on the abyssal seafloor.

Keywords: megabenthos; density; biomass; time-series; temporal change; deep sea; Porcupine Abyssal Plain; NE Atlantic

1. Introduction

In recent years large-scale changes have been noted in the density and species dominance of abyssal benthic megafauna in both the NE Atlantic (Billett et al., 2001; Wigham et al., 2003a) and the NE Pacific (Smith and Druffel, 1998; Lauermaun et al., 1996; Bailey et al., 2006; Ruhl, 2007). Some species have changed in density by over 3 orders of magnitude within a two-year period, with significant effects on how organic matter is processed at the seabed (Bett et al., 2001; Ruhl and Smith, 2004). These two study areas have established long-term time series stations from 1989 to the present day measuring changes in both the fauna and the downward flux of organic matter (Smith and Kaufmann, 1999; Lampitt et al., 2001). Recent temporal fluctuations in deep-sea biota have been linked to environmental changes in other areas (Danovaro et al., 2001, 2004) and variations in deep-sea sediment fauna are evident over geological timescales (Stuart et al., 2003; Yasuhara et al., 2008). Knowledge of how species density and dominance change in relation to environmental variables in the present will help in interpreting the geological record and will allow predictions of how deep-sea fauna might alter in relation to climate change.

In the NE Pacific, echinoderms in particular holothurians, dominate the invertebrate megabenthos (Lauermaun et al., 1996). Changes in the density of the megafauna appeared to be related to long-term, climate-driven variations in the flux of Particulate Organic Carbon (POC) and hence to productivity in the overlying surface waters (Ruhl and Smith, 2004). Increases in density were associated with decreases in mean body size, suggesting that recruitment events had occurred (Ruhl, 2007). Sharp declines in density were believed to be related to competitive faunal interactions and survivorship (Ruhl, 2007).

In the NE Atlantic, large-scale changes in the density of megafauna occurred in 1996. Some species that had been a rare component of the fauna for many years became very abundant. One of these, the holothurian *Amperima rosea*, was particularly notable for the change in its density and became the dominant megafaunal species (Billett et al., 2001). Wider spatial sampling (c. 250 km) of the Porcupine Abyssal Plain showed that the faunal changes had occurred over a very large area. This, coupled with the simultaneous increase in density of a number of different taxa, indicated that the change seen on the Porcupine Abyssal Plain was a large-scale temporal phenomenon rather than the result of spatial patchiness and/or random recruitment events of various species (Billett et al., 2001).

While the large-scale change on the NE Atlantic abyssal seafloor was characterised as the 'Amperima Event', several other species also exhibited radical short-term (e.g. <1 year) changes in density, including the holothurian *Ellipinion molle* and the ophiuroid *Ophiocten hastatum*. These species, together with *A. rosea*, led to a reduction in the time necessary for the benthic megafauna to rework the entire sediment surface from a period greater than 2.5 years to one of less than 6 weeks (Bett et al., 2001). The reworking of

the sediment surface was so rapid that phytodetritus arriving in large quantities at the seabed in summer months (as determined from sediment traps, Lampitt et al., 2001) never accumulated as a distinct layer on the sediment, as it had in previous years (Lampitt, 1985). Analysis of the reproductive strategies of *A. rosea* and *O. hastatum* showed that their life history patterns were suited to opportunistic reproductive responses to periodic inputs of organic matter (Wigham et al., 2003b; Gage et al., 2004).

At the time when the 'Amperima Event' occurred, gear failures and problems in cruise planning meant that the sediment trap record was imperfect for the period immediately prior to the 'Event'. It was not possible to relate the changes in fauna with any change in the supply of organic matter. Analysis of satellite imagery coupled with downward particle flux model predictions did not suggest any episodic event in surface waters that might have led to the increases in *Amperima*. Nor was there any evidence of a progressive increase in organic matter supply to the seafloor over a number of years (Lampitt et al., 2001).

A stable isotope analysis of the fauna collected during the 'Amperima Event' indicated that those species that had increased significantly in density had fed on fresh detritus arriving at the seabed (Iken et al., 2001). Analysis of the lipid biochemistry of the fauna also highlighted notable differences between benthic species, leading to the hypothesis that qualitative changes in the supply of organic matter to the seabed with time, selective feeding and competition for resources by the fauna might be responsible for the observed changes in species composition (Ginger et al., 2000, 2001; Billett and Rice, 2001). The pigment biochemistry of phytodetritus, holothurian gut contents, gut wall and ovary appeared to indicate that differences in the biochemical requirements of different species might lead to periodic changes in their dominance, depending on the supply (quantity and composition) of detrital organic matter derived from surface waters (Wigham et al., 2003a). Competition for resources during the 'Amperima Event' had a significant adverse effect on the fecundity of the holothurian *Oneirophanta mutabilis* (Ramirez-Llodra et al., 2005) illustrating one mechanism by which densities of some species could decrease.

In order to examine what environmental factors might influence radical changes seen in faunal communities on the abyssal seafloor this paper extends the time series described by Billett et al. (2001) for the period 1989 to 1998, with further samples taken in the years from 1999 to 2005. It relates the work on megafauna to 1) time series data on other benthic faunal components, notably the protozoan meiofauna (Gooday et al., this volume), metazoan meiofauna (Kalogeropoulou et al., this volume) and macrofauna (Soto et al., this volume), 2) further work on the reproductive chemistry of benthic megafauna (Smith et al., this volume) and 3) and to characteristics of the flux of organic matter to the Porcupine Abyssal Plain (Lampitt et al., this volume; Smythe-Wright et al., this volume).

2. Materials and Methods

2.1 Study Area

The Porcupine Abyssal Plain (PAP) is situated off the southwest coast of Ireland in the Northeast Atlantic. All the samples were collected between 1989 and 2005. Most samples were taken within a 20 nautical mile (37 km) radius of a central position for time series studies (48°50'N and 16°30'W) (Figure 1 and Table 1). This site became known as the 'BENGAL Station' following a major European project on seabed biology and geochemistry that focussed its work there (Billett and Rice, 2001). The site is now known as the Porcupine Abyssal Plain Sustained Observatory (PAP-SO). The site was chosen to be as far as possible from the influence of the continental slope to the east and the foothills of the Mid-Atlantic Ridge to the west. The aim was to reduce perturbations caused by slope-related process on the continental margin and the ocean ridge to a minimum. This allowed processes linking the sea surface to the abyssal seabed through the transfer of organic matter to be studied. The seabed depth at the sampling site ranges between 4800m and 4850m. The site was a level area of seabed with little topographic and environmental heterogeneity. It had a strong seasonal signal in the flux of organic material (phytodetritus) (Billett et al., 1983).

2.2 Sampling

Sampling for megafauna was undertaken using a semi-balloon otter trawl (OTSB14). The wing-end spread was 8.6 m and the net height was approximately 1.5 m from the footrope to the headline. Towing speed was a nominal 0.75 ms⁻¹. The net was constructed of 44 mm stretch mesh in the main part, 37 mm stretch mesh in the central part and a 13 mm stretch mesh liner in the cod-end. Contact of the net with the seafloor, and hence an estimate of the area fished, was assessed by changes in wire tension during trawling operations. The acoustic beacon used with trawls between 1989 and 1999 to monitor performance was unavailable from 2000 onwards. We are nevertheless confident that our estimates of seafloor area fished remain consistent throughout the time series.

On completion of a trawl, samples were sorted into major taxonomic groups on board the ship before being fixed in 5% borax-buffered formaldehyde in seawater. The samples were transferred into 80% methylated spirit once the samples were returned to the laboratory. The samples were then sorted into finer taxonomic groups, and wet weight and length was measured for each individual.

Apart from sampling at the time series station in the middle of the Porcupine Abyssal Plain a number of other stations were sampled over the years to give spatial relevance (c. 40-100 nm from PAP-SO). Specific sampling was undertaken deeper than 4800m to the southeast, east and north of the time series station (Fig 1, Table 1). In addition, advantage was taken of other trawling at abyssal depths closer to the base of the continental slope as part of science programmes conducted by the Oceanlab, University of Aberdeen and the National Oceanography Centre, Southampton. The samples came mainly from close to the mouth of the

Porcupine Seabight (Fig 1). This area had been sampled many times during the IOS Deep-Sea Biology Programme from 1976 to 1989 (Rice et al., 1991).

Some of the larger abundant holothurians collected in the trawls, namely *Psychropotes longicauda*, *Oneirophanta mutabilis*, *Pseudostichopus villosus* and *Paroriza prouhoi*, were enumerated and weighed at sea (fresh wet weight biomass) before the samples were used for other analyses, in the years 1998 and 1999. Where this occurred the fresh wet weights were converted to preserved wet weight by applying a factor of 0.6 to the fresh wet weight in order to allow a comparison of wet weight biomass over the whole time series. Conand (1989) has shown that holothurians lose about 40% of their wet weight on preservation.

2.3 Statistical analyses details

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). Variations in megafaunal density and biomass 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 homoscedasticity (e.g. Bartlett's tests of log-transformed total megabenthos density, holothurian density, *Amperima rosea* and total megabenthos biomass data assessed by cruise gives a non-significant result, p>0.05, in all cases). For presentation, both density and biomass data are given as means with 95% confidence intervals based on pooled variances; note that back transformation (i.e. from logs) yields geometric mean (not arithmetic mean) values. In the assessment of spatial variation in the density of *A. rosea* a multiple comparisons test was also employed (Tukey's test with a 5% family error rate). Some correlation analyses were also carried out (as described in the results section below); in all cases these were implemented using the Spearman's rank (non-parametric) technique.

Variation in megafaunal taxon composition was assessed by multivariate analyses (non-metric multi-dimensional scaling ordination) using the PRIMER (v. 5.2.0, PRIMER-E Ltd) software package. A square-root transformation and the Bray-Curtis similarity index were employed in all analyses (Clarke and Green, 1988). The significance of taxon composition variations was assessed by analysis of similarities (ANOSIM).

3. Results

3.1 Temporal variation in megafaunal invertebrate density, biomass and composition.

Large changes in the density of total benthic invertebrate megafauna on the Porcupine Abyssal Plain were evident between 1989 and 2005 (Fig. 2-A, Table 2). Corresponding changes in wet weight biomass (Fig 2-B, Table 3), however, were not significant. Samples indicate that prior to 1996 the density of benthic megafauna in trawls varied from 63 to 92 individuals per hectare (ind. ha⁻¹). Holothurians accounted for about 60% of the individuals. The holothurian *Amperima rosea* was present only rarely. Prior to 1996 biomass varied between 1637 and 2327 g preserved wet weight per hectare (g wet wt. ha⁻¹). Holothurians accounted for about 90% of the wet weight biomass.

A major change occurred in the megafauna in 1996. Density, as estimated in trawls, increased and peaked at 378 ind. ha⁻¹ in March 1997, before declining back to 112 ind. ha⁻¹ in October 2000. A second peak in megafaunal density of 435 ind. ha⁻¹ was evident in October 2002. Subsequent sampling in 2004 and 2005 indicated that the density of megafauna had declined to 127 ind. ha⁻¹ and 115 ind. ha⁻¹ respectively. There were no significant changes in biomass during the same period.

The increase in megafaunal density between 1996 and 1999 and again in 2002 was driven principally by the holothurians, mainly *Amperima rosea* (Figs 2-A, 3-A, N). Significant increases in density therefore had little effect on the total megafaunal wet weight biomass (Fig. 2-B) as *Amperima* is among the smallest of holothurians. Nevertheless, there was a significant difference in the biomass of *Amperima rosea* over the time series (Table 3, Fig 4-A).

Differences in several key taxa, including a number of holothurian species, occurred over the period of the time series (Table 2, Fig 3). These changes in density were not as great as those seen in *A. rosea*. An Analysis of Variance (ANOVA) over the time series was used to detect significant changes in density between cruises and between sampling years for each taxon. Significant differences were detected for a number of different taxa between cruises and between years (Table 2). The patterns in changes in density with time were not the same for all taxa (Fig 3). Patterns of change in density with time were closely matched by changes in biomass for individual taxa (Table 3; Fig 4).

The elpidiid holothurians *Amperima rosea* and *Ellipinion molle* increased rapidly in density and biomass in 1996 and 1997, but whereas *Ellipinion* decreased almost as quickly as it appeared, *Amperima* densities showed a more gradual decline (Fig 3-A,B; Fig 4-A,B). *Amperima* increased in density again in 2002, but not *Ellipinion*. *Pentagone diaphana*, another elpidiid holothurian, showed great variability in density and biomass and an inverse relationship to *A. rosea* (Fig 3-G; Fig 4-F). It was consistently rare during the 'Amperima Event' period.

Psychropotes longicauda, a psychropotid holothurian (Hansen, 1975), and *Pseudostichopus aemulatus*, a synallactid holothurian (Solis Marin et al., 2004), showed a more gradual and generally consistent

increase in density and biomass through the 'Amperima Event' period (Fig 3-C, E; Fig 4-C, E). Both species decreased significantly in density between April 1999 and October 2000, returning to densities seen between 1989 and 1994. No significant increase was evident at the time of the second peak in *Amperima* density.

Pseudostichopus villosus, another synallactid species, showed little variation in mean density over the time series apart from a peak in density in April 1999 (Fig 3-F). While an ANOVA between years showed a significant difference ($p < 0.05$) this was not apparent between cruises. There were no significant variations in biomass between cruises or years. In all sampling periods there was considerable variation in the number of *P. villosus* collected.

Oneirophanta mutabilis, a deimatid holothurian, did not show a significant change in density between the period before the 'Amperima Event' (1989-1994) and the 'Amperima Event' (1996 to 1999). However, there were significant differences in density over the whole time series, owing to lower densities between 2000 and 2005 (Fig 3-D, Table 2). Using Spearman's rank correlation to detect consistent trends with time, *O. mutabilis* showed a significant decrease in density with time ($p = 0.011$, comparing years). A similar trend is evident in biomass ($p < 0.001$). It was the only species to show a general decrease in density and biomass over the time series. This decrease was associated with a decrease in mean body size (see below).

In contrast, the Actiniaria showed a significant increase in density over the time series (Spearman's rank correlation, $p = 0.007$, comparing years). There was a significant increase in the density of Actiniaria between the 'pre-Amperima Event' (1989-1994) and 'Amperima Event' (1996-1999) periods (Fig. 3-H). The Tunicata showed a similar significant rapid increase in density at the time of the 'Amperima Event' and like the actinarians maintained their higher levels of density after the 'Amperima Event'. There was, however, no significant trend detected with time, possibly owing to low densities recorded in April 1999 (Fig. 3-O). The Annelida show a similar trend, a three-fold increase in mean density at the time of the 'Amperima Event', and a further increase after the 'Amperima Event' (Fig. 3-J) although there was great variability between samples.

The Pycnogonida showed highly significant differences in density (Fig 3-K). While there was no significant trend over the whole time series, there was a highly significant increase in density during the 'Amperima Event' period (Spearman's rank correlation $p = 0.001$, comparing cruises between 1996 and 1998). The Pycnogonida showed a secondary peak in density in June 2004.

The Ophiuroidea showed high variability in density (Fig 3-M). While there were significant variations between cruises, no significant changes were evident between years (Table 2). The reasons for this are not readily apparent. Many of the ophiuroid species at the time series site were small, e.g. *Ophiocten hastatum*, and so many individuals would have passed through the mesh of a bottom trawl. Consequently, trawl-sampled ophiuroids are not good indicators of

change in this time series. Similarly taxa that are not common at abyssal depths, or are poorly represented in the megafauna, such as the Cephalopoda, Gastropoda, Bivalvia and Scaphopoda, are poor indicators. Non-segmented worms, termed "vermes" in this analysis, and including echiurans and sipunculids, showed little variation (Fig 3-I).

Temporal variations in the major taxon composition of the megabenthos at the PAP-SO were assessed by non-metric multi-dimensional scaling ordination (Fig 5-A). The ordination very clearly separates samples collected in the pre-BENGAL and BENGAL project periods (1989-1994, 1996-1999; Billett & Rice, 2001), the BENGAL period corresponding with what we term the 'Amperima Event'. Post- the BENGAL period, samples generally group with those of the pre-BENGAL period with the notable exception of those collected in 2002 which group with those of the 'Amperima Event' period. Fig 5-B re-plots the x-ordinate data as cruise means with 95% confidence intervals. This plot (necessarily) closely matches the plot of temporal variation in *Amperima* density (Fig 3-A), but variations in the density of other taxa also contribute to the distinctiveness of the 2002 samples, for example the low densities of *Peniagone diaphana* (Fig 3-G).

3.2 Spatial variation in megafaunal invertebrate density, biomass and composition.

The time taken to obtain a trawl sample at abyssal depths generally precludes undertaking both temporal and spatial studies in the deep sea. However, it is important to set temporal studies within a spatial context and to determine if the changes seen at one locality are representative of the larger area. Variations in the composition of all recognised taxa in all PAP samples are illustrated in a non-metric multi-dimensional scaling (MDS) ordination plot (Fig 6-A). Samples from 'Amperima Event' periods (1996-1999 and 2002) are clearly distinguished from those from other periods. Among the 'Amperima Event' periods samples there is little indication of any systematic variation between the Sustained Observatory and other PAP sites. When examined on a by cruise by cruise basis, MDS plots show some separation of the time series station samples in both 1998 (Fig 6-B) and 1999 (Fig 6-C) from those taken at other localities on the Porcupine Abyssal Plain. This difference is significant (ANOSIM $p < 0.001$) in the case of 1999 samples (note that there are insufficient replicates to assess the 1998 data by ANOSIM). The most variant sample, Station 54902, collected in 1999, was notable for very high densities of *A. rosea* and markedly lower densities of *Pseudostichopus villosus* than in corresponding time series site samples. Fig 6-D illustrates temporal and spatial variation in *A. rosea* density for the 1998-1999 period; only the difference between Station 54902 and the corresponding time series site samples (Station 54901) is statistically significant (Tukey's test $p < 0.05$). While there was short-term spatial variation among PAP sites (e.g. Fig 6-D) it is clear that 'Amperima Event' conditions are common to all the analysed PAP sites and that they are

very clearly distinguished from non-'Amperima Event' conditions (e.g. Fig 6-A).

3.3 Relationship between density and size distributions

The cumulative body length frequency distributions of three holothurians species are presented in Fig 7. The size of the specimens of *A. rosea* decreased notably during the 'Amperima Event' (Fig 7-A, B) and has generally remained small since then; i.e. small individuals dominate. Prior to the 'Amperima Event' there were greater proportions of large individuals, although in 1991 there is an indication of two 'cohorts' with a substantial number of small individuals in the population. Generally, samples with the lowest densities (i.e. 1989-1994) had the greatest proportion of large individuals, to the extent that there is a significant negative relationship between mean body length and mean density (Spearman's rank correlation $p < 0.05$).

The body size distributions of *P. longicauda* also showed an increase in the proportion of small individuals during the 'Amperima Event' (Fig 7-C, D). In the years 1999-2005 there was a general trend for an increasing proportion of larger individuals. As in the case of *Amperima*, *Psychropotes longicauda* exhibited a significant negative relationship between mean body length and mean density (Spearman's rank correlation $p = 0.003$).

In contrast to the two species detailed above, *Oneirophanta mutabilis* exhibited a general trend for reducing body size throughout the time series (Spearman's rank correlation $p < 0.001$) (Fig 7-E, F). When assessed on a by year basis the density of this species also showed a general trend for decrease throughout the time series (Spearman's rank correlation $p = 0.011$). Consequently, there was no indication of an inverse relationship between mean body length and mean density in this species.

4. Discussion

4.1 Temporal variation in megafaunal invertebrate density and biomass.

Time series studies at the Porcupine Abyssal Plain Sustained Observatory have shown that abyssal ecosystems can change radically over short periods (e.g. <6 months). Large-scale (e.g. order of magnitude change in density) changes have occurred in the invertebrate megafauna (Fig. 2). These changes have been mirrored in protozoan and metazoan meiofauna (Gooday et al., this volume; Kalogeropoulou et al., this volume) and macrofaunal polychaetes (Soto et al., this volume). Similar large-scale changes have been noted in the invertebrate megafauna of the NE Pacific Ocean (Ruhl and Smith, 2004; Ruhl, 2007).

Based on trawl data, the megafauna increased in density by a factor of about three. However, the density of benthic megafauna is underestimated by trawls (Billett, 1991; Bett et al., 2001). The problem is particularly acute for small, fragile and neutrally buoyant species, such as *Amperima rosea*, which may be pushed aside by the bow wave of a trawl, or be damaged by, and pass through, the trawl mesh. While densities of c. 350 ind. ha⁻¹ were recorded for *A. rosea* in trawls (Fig. 2) time-lapse photography (Bett, 2003) showed that the true density of the species was in excess of 6000 ind. ha⁻¹ (Bett et al., 2001). Using these data Bett et al. (2001) demonstrated that the invertebrate megafauna on the Porcupine Abyssal Plain increased in density by a factor of at least ten during the 'Amperima Event'. This compares with an increase in density of a factor of three for the small infaunal components (Gooday et al. this volume; Kalogeropoulou et al. this volume; Soto et al. this volume). The changes in the benthic community density on the Porcupine Abyssal Plain, therefore, while evident in all size fractions, were greatest in the invertebrate megafauna.

This has important implications for how organic matter is reprocessed on the deep-sea floor and how changes in the density of megafaunal species impact the rest of the benthic community. The majority of deep-sea animals feed directly on detritus. Fresh detritus derived from surface water productivity gathers either as a fine layer on the sediment surface or is redistributed by near-bottom currents into pockets around mounds and within hollows (Billett et al., 1983; Lampitt, 1985). Deep-sea megafauna compete directly with the smallest protozoans for this resource. Indeed, megafauna may have a distinct advantage. They are able to forage large surface areas for a thinly spread resource and can seek out pockets of organic matter (Billett, 1991; Roberts et al., 2000; Lauermaun et al., 1996). Megafauna, therefore, are primary consumers of fresh detritus.

Bett et al. (2001) demonstrated that changes in the density of megafauna affected significantly the rate at which phytodetritus is reworked at the sediment surface, reducing the time taken to rework the entire sediment surface from a period of two and a half years to one of less than six weeks between the 'pre-Amperima Event' (1989 to 1994) and 'Amperima Event' (1996 to 1998) periods respectively. While there was considerable influx of organic matter during the

'Amperima Event' there was very little evidence of it on the seafloor owing to the increased activity of the megafauna (Bett et al., 2001). Much of this increased activity related to increases in the densities of the ophiuroid *Ophiocten hastatum* (Bett et al., 2001; Gage et al., 2004) as well as *A. rosea*. As shown experimentally for macrofauna by Witte et al. (2003) the larger sediment fauna preferentially rework fresh detritus ahead of the meiofaunal and microbial size fractions when the detritus first arrives on the seabed.

The assimilation rate of organic matter by the megafauna is about 20% (Khrupounoff and Sibuet, 1980). Significant quantities of organic matter therefore will be available for the rest of the benthic community following reworking by the megafauna. However, the organic matter will be 'stripped' of many of its more labile and biologically important compounds, such as carotenoids and poly-unsaturated fatty acids, and the detritus will be repackaged into a different physical form. These factors are likely to have important effects on other components of the benthic community. The decrease in phytodetritus foraminiferan indicator species (Gooday et al., this volume) and the significant reduction in the fecundity of the holothurian *Oneirophanta mutabilis* (Ramirez-Llodra et al., 2005) during the 'Amperima Event' are examples of possible faunal competitive interactions. The reduction in fecundity of *O. mutabilis* appears to have had a significant effect on its density over a long period (Fig 7-E, F). The large increases in the density of opportunistic species such as *Amperima rosea* and *Ophiocten hastatum* while being comparatively short in duration (a few years) can have longer-lasting effects on benthic ecosystems.

Not all the interactions between the size fractions of the benthic community were negative. A number of taxa, such as the meiofaunal foraminiferan *Trochammina*, nematodes and polychaete worms increased in density. The changes may reflect additional organic inputs to the seabed, but may also be due to the reworking of the detritus and sediment by the megafauna (Thistle et al., 2008; Gooday et al., this volume; Kalogeropoulou et al., this volume; Soto et al., this volume). The increase in Pycnogonida densities evident between 1996 and 1998 (Fig 3-K) may have been related to the greater availability of prey.

4.2 Organic matter deposition and benthic community change on the deep-sea floor.

The effectively contemporary increases in the density of protozoan and metazoan meiofauna, macrofaunal polychaetes and a number of different megafaunal taxa indicate that the 'Amperima Event' was driven by environmental change that affected all of the benthic community rather than being stochastic population imbalances of one or two species. If the changes on the Porcupine Abyssal Plain had been driven by a random increase in *Amperima rosea* followed by a cascade through the ecosystem then a lag would be evident between the various species and size fractions. This was not the case and it is difficult to conceive that such a mechanism could cause statistically significant, three-fold increases in the densities of protozoan and

metazoan meiofauna as well as the polychaete macrofauna.

Sampling at a number of locations on the Porcupine Abyssal Plain between 1998 and 2002 (Fig. 1, Table 1; Billett et al., 2001) showed that the 'Amperima Event' was not confined to the time series site (Fig 6-A). Some of these additional locations were on the abyssal plain close to the mouth of the Porcupine Seabight, an area that was sampled regularly from November 1976 as part of the Institute of Oceanographic Sciences benthic biology programme (Rice et al., 1991). In all these previous samples *Amperima rosea* was a very minor component of the benthic megafaunal community (Billett, 1987). *Amperima rosea* was also a minor element of, or absent from, trawl samples taken by Ifremer (Sibuet and Segonzac, 1985) and the Netherlands Institute for Sea Research (NIOZ) (Rutgers van der Loeff and Lavaleye, 1986) on the Porcupine Abyssal Plain in the 1970s. Only on one other occasion, in 1911, has *A. rosea* been sampled in great density in the region (Hérouard, 1923).

Both *Amperima* density (Fig. 3-A) and megabenthos taxon composition (Fig. 5) appear to show a discrete 'boom-bust' event spanning 1996-1999 and a second equivalent peak in 2002. This suggests there may have been two 'Amperima Events' during the time series to date, having peaks in 1997 and 2002. Accepting the limitations of the historical data, it may be that wide-area 'Amperima Events' are unlikely to have occurred on the Porcupine Abyssal Plain for more than 20 years previously. However, large aggregations of another elpidiid holothurian, *Kolga hyalina*, have occurred on at least two occasions (Billett and Hansen, 1982; Billett, 1991).

While the 'Amperima Event' occurred over a very large part of the Porcupine Abyssal Plain (Fig. 6-A), it is evident that within the area there has been patchy recruitment. Samples taken at locations distant from the time series site but within the same month (Table 1, Fig. 1) have shown that while *A. rosea* was dominant numerically, there were differences in the relative proportions of species and differences in the total density of *A. rosea* (Fig. 6-B-D). There is a mixture of temporal and spatial patchiness set within a larger-scale change. However, the major changes associated with the 'Amperima Event' were typical of the whole area and indicate a major environmental driver. As Hérouard (1923) noted, it is remarkable that a species that can occur so abundantly has been sampled on so few occasions. This indicates that time varying processes are important in influencing the occurrence of *Amperima rosea* and other species on the abyssal seafloor.

For the megafauna, stable isotope analyses showed close linkages to the supply of phytodetritus (Iken et al., 2001). In addition, *A. rosea* had a significantly different requirement for certain lipids than other species (Ginger et al., 2000). When the 'Amperima Event' was first described (Billett et al., 2001) it was not possible to demonstrate a direct correlation to variations in organic matter input owing to gear malfunctions and logistical difficulties in maintaining the time series (Billett and Rice, 2001). An

alternative approach using satellite ocean colour data coupled with modelling did not identify any stepwise changes or longer-term trends in downward particle flux that could account for the 'Amperima Event' (Lampitt et al., 2001).

At the time large-scale changes in the flux of organic matter to abyssal depths of an order large enough to stimulate changes in the density of benthic organisms were unknown. It was thought therefore that the quality rather than the quantity of organic matter flux might influence abyssal benthic communities. The results of the extended time series sediment trap measurements presented by Lampitt et al. (this volume) now show that variations in the supply of organic matter to the Porcupine Abyssal Plain can vary by an order of magnitude between years. Levels of organic input equivalent to those that commonly fuel benthic communities at 500m depth, can on occasion be found at 5000m. Smythe-Wright et al. (this volume) also demonstrate how changes in the nature of the surface ocean phytoplankton community can modify the composition of exported organic matter.

The frequency of the years with large fluxes appears to be low. In the sediment trap time series, only one large deposition of organic carbon is evident in the late summer of 2001 (Lampitt et al., this volume). The following year the density of *Amperima rosea* was at its greatest (Fig. 2-A). While there is no direct evidence that an increase in organic matter input caused the original 'Amperima Event' in 1996, all subsequent observations have supported rather than contradicted this hypothesis.

As in the NE Pacific (Ruhl, 2007) significant increases in the density of benthic megafauna at the PAP-SO were associated with a greater proportion of small individuals (Fig. 7). The main driver for change on the Porcupine Abyssal Plain, therefore, was one that stimulated the greater recruitment of juveniles to the benthic community. For *A. rosea* it is known that the species produces a large number of small eggs of a size (max. egg diameter 180µm) indicative of abbreviated lecithotrophic development (Wigham et al., 2003b). This would allow the rapid colonisation of large areas of the seafloor as part of an opportunistic life history pattern. This life history pattern is likely to apply to other elpidiid holothurians that have occurred periodically in great density in the deep sea, such as *Kolga hyalina* (Billett and Hansen, 1982; Billett, 1991) and *Elpidia glacialis* (Gutt and Piepenburg, 1991).

Small egg size, however, was not a feature of all species that increased in density during the 'Amperima Event'. *Psychropotes longicauda*, one of the largest invertebrates at the PAP-SO site, produces one of the largest eggs known in echinoderms, about 4.5mm in diameter (Hansen, 1975). These eggs lead to direct development in the abyssopelagic domain (Billett et al., 1985). Juveniles settle on the seabed only when they are several centimetres long. In the Porcupine Abyssal Plain time series significant increases in *P. longicauda* density were associated with decreases in body size distributions indicative of a recruitment event (Billett et al., 2001; Fig 7-C, D). While *P. longicauda* appears to produce a slow and steady supply of large eggs, its

recruitment on the seafloor appears to be patchy and to be associated with variations in the availability of organic matter.

Kiriakoulakis et al. (2001) noted that there was intra-annual variability in the composition of the organic matter flux. When downward flux was considered to be high there were more unsaturated fatty acids and low molecular weight alcohols. When downward flux was low other compounds dominated, including sterols and steroidal ketones. Inter-annual differences are also evident in the gross composition of the downward flux (Lampitt et al., 2001) and carotenoids deposited on the seafloor (Smith et al. this volume). Wigham et al. (2003a) proposed that differences in the quality of organic matter flux might be important in driving ecosystem change in the food-limited deep-sea environment. Smith et al. (this volume) demonstrate that different holothurian species have different carotenoid signatures in their body wall and ovaries. In particular, *Amperima rosea* shows high carotenoid concentrations and consistency in its carotenoid composition among individuals. Smith et al. (this volume) indicate that diet and reproduction in deep-sea holothurians are linked intimately and that changes in the supply of critical compounds might influence the reproduction and recruitment of particular species, notably *A. rosea*.

5. Conclusions

Radical changes have occurred in the density and species composition of the invertebrate megafauna on the Porcupine Abyssal Plain, NE Atlantic, 4850m, in recent years. One species of holothurian, *Amperima rosea*, was particularly important, increasing in density by over three orders of magnitude. Peaks in density were correlated to reductions in mean body size indicating that the increases were related to large-scale recruitment events over a wide area of the Porcupine Abyssal Plain. In total the invertebrate megafauna increased by an order of magnitude. This compares with increases in the density of other size fractions of the benthic community (macrofauna, protozoan and metazoan meiofauna) by a factor of two to three (Gooday et al., this volume; Kalogeropoulou et al., this volume; Soto et al., this volume). The greatest changes in density have occurred in the invertebrate megafauna. Major changes occurred in all size fractions of the benthic community at the same time. This suggests that the faunal changes were driven by environmental factors rather than being stochastic population imbalances of one or two species. Large-scale changes in the flux of organic matter to the abyssal seafloor have been noted in the time series (Lampitt et al., this volume). An exceptionally large downward flux of organic material in 2001 may have led to the sudden mass occurrence of *A. rosea* the following year (potentially a second 'Amperima Event'). Large-scale changes occur in abyssal communities. They may be related to inter-annual variability in the supply of organic matter from the sea surface, and hence ultimately to factors influencing global change.

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Table 1

Dates, positions and depths of trawls taken on the Porcupine Abyssal Plain from 1999 to 2005. For 1989 to 1998 sampling data see Billett et al. (2001). Stations from the Porcupine Abyssal Plain Sustained Observatory (PAPSO) site are marked with an asterisk. For other stations their distance from the PAPSO site is indicated (nm, nautical miles).

Station	Date	Position Start		Position End		Depth (m)	Fished area (ha)	Dist. from PAPSO (nm)
		Lat. (N)	Long. (W)	Lat. (N)	Long. (W)			
RRS Challenger Cruise 142								
54901#2*	26-04-99	48°42.2'	16°51.6'	48°48.0'	16°50.4'	4811-4837	10.25	-
54901#5*	28-04-99	48°44.9'	16°40.5'	48°48.2'	16°36.2'	4835-4838	8.21	-
54901#7*	29-04-99	48°47.5'	16°48.9'	48°50.8'	16°46.0'	4836-4838	6.15	-
54901#9*	30-04-99	48°46.9'	16°41.6'	48°50.6'	16°36.4'	4837-4841	8.4	-
54902#1	02-05-99	48°26.4'	15°39.7'	48°24.4'	15°34.9'	4843-4845	6.03	41
54903#1	03-05-99	49°32.1'	15°56.0'	49°28.1'	15°56.5'	4810-4817	6.37	45
54905#1	04-05-99	50°32.7'	16°57.8'	50°28.7'	16°59.4'	4764-4786	6.68	100
54906#1	11-05-99	49°41.3'	14°29.1'	49°37.9'	14°34.2'	4306-4380	-	89
RRS Discovery Cruise 250								
13907#1	20-09-00	49°55.9'	14°30.3'	50°02.6'	14°36.0'	4128-4220	-	100
13925#1*	07-10-00	48°53.5'	16°45.9'	48°56.8'	16°54.7'	4835-4845	14.02	-
RRS Discovery Cruise 255								
14137#1	19-08-01	49°36.9'	14°04.6'	49°37.8'	14°07.8'	4108-4146	-	102
14158#1	28-08-01	49°32.2'	14°23.3'	49°33.0'	14°19.3'	4286-4311	-	91
RRS Discovery Cruise 260								
14317#1	19-03-02	49°39.4'	14°15.5'	49°35.7'	14°20.2'	4190-4263	-	95
RRS Discovery Cruise 266								
15054#6*	03-10-02	48°51.9'	16°40.9'	48°48.7'	16°52.8'	4843-4844	15.44	-
15054#22*	09-10-02	48°53.7'	16°54.1'	48°58.4'	17°02.0'	4842-4845	11.6	-
15054#25*	12-10-02	48°54.2'	16°29.5'	48°55.2'	16°39.3'	4844-4845	10.32	-
15055#2	13-10-02	49°29.3'	16°52.3'	49°29.5'	16°58.7'	4783-4822	7.12	42
RRS Charles Darwin Cruise 158								
56506#1*	20-06-04	48°54.4'	16°38.7'	48°55.8'	16°30.6'	4841-4841	9.37	-
56515#1*	21-06-04	48°53.3'	16°29.4'	48°50.6'	16°37.3'	4831-4841	9.8	-
56523#1*	23-06-04	48°55.6'	16°44.6'	48°56.6'	16°51.7'	4834-4835	7.81	-
RRS Discovery Cruise 296								
15711#1*	16-07-05	48°50.8'	16°38.5'	48°48.5'	16°54.6'	4838-4839	17.47	-
15717#1*	18-07-05	48°53.1'	16°46.0'	48°57.2'	16°56.6'	4837-4841	12.79	-

Table 2

Geometric mean density of dominant megafaunal taxa expressed as numbers of individuals per hectare with 95% confidence limits in parentheses for the years 1999-2005. ANOVA results (p values) comparing different cruises and years for the complete 1989-2005 time series are also shown (ns - not significant).

	Apr-1999	Oct-2000	Oct-2002	Jun-2004	Jul-2005	ANOVA Cruises	ANOVA Years
PORIFERA	0.06 (0.0-0.2)	0.21 (0.0-0.6)	0.16 (0.0-0.4)	0.1 (0.0-0.3)	0.14 (0.0-0.4)	ns	ns
OCTOCORALLIA	0.27 (0.1-0.5)	0.29 (0.0-0.7)	0.14 (0.0-0.3)	0.41 (0.2-0.7)	0.24 (0.0-0.5)	ns	ns
ACTINIARIA	17.53 (13.1-23.4)	10.99 (5.9-19.8)	14.16 (10.0-19.9)	12.7 (9.0-17.8)	14.9 (9.8-22.5)	0.001	0.006
Other HEXACORALLIA	0.91 (0.3-1.9)	0.21 (0.0-1.8)	3.64 (1.9-6.5)	7.32 (4.1-12.5)	5.19 (2.4-10.2)	0.001	0.001
"Vermes"	0.85 (0.2-1.8)	3.21 (0.9-8.4)	5.16 (2.9-8.8)	4.28 (2.3-7.4)	6.05 (3.0-11.5)	0.037	0.007
ANNELIDA	10.02 (6.3-15.6)	23.11 (9.6-53.7)	17.19 (10.3-28.2)	13.12 (7.8-21.7)	10.25 (5.3-19.1)	0.002	0.001
DECAPODA	1.14 (0.6-1.8)	0.29 (0.0-1.3)	0.42 (0.0-1.0)	6.57 (4.5-9.5)	3.56 (2.1-5.8)	0.001	0.001
Other Crustacea	0.15 (0.0-0.5)	0.36 (0.0-1.2)	0.21 (0.0-0.6)	0.56 (0.2-1.1)	0.41 (0.0-1.0)	ns	ns
PYCNOGONIDA	0.03 (0.0-0.1)	0.07 (0.0-0.3)	0.03 (0.0-0.2)	0.47 (0.3-0.6)	0.12 (0.0-0.3)	0.001	0.001
GASTROPODA	0.68 (0.3-1.1)	0.14 (0.0-0.8)	0.48 (0.1-1.0)	0.39 (0.1-0.8)	0.25 (0.0-0.8)	ns	ns
SCAPHOPODA	0.08 (0.0-0.2)	0 (0.0-0.2)	0.14 (0.0-0.3)	0.12 (0.0-0.3)	0.14 (0.0-0.3)	ns	ns
BIVALVIA	0.29 (0.1-0.5)	0.07 (0.0-0.5)	0.18 (0.0-0.4)	0.52 (0.2-0.9)	0.51 (0.2-0.9)	0.025	ns
CEPHALOPODA	0.16 (0.0-0.3)	0 (0.0-0.3)	0.03 (0.0-0.2)	0.58 (0.3-0.9)	0.19 (0.0-0.5)	0.035	0.021
ASTEROIDEA	3.84 (2.1-6.6)	2.43 (0.4-7.4)	6.88 (3.7-12.2)	6.36 (3.4-11.3)	9.12 (4.4-18.0)	ns	ns
OPHIUROIDEA	3.16 (2.0-4.8)	2.92 (1.0-6.7)	2.53 (1.4-4.2)	1.34 (0.6-2.4)	3.02 (1.5-5.5)	0.001	ns
ECHINOIDEA	0 (0.0-0.1)	0 (0.0-0.2)	0 (0.0-0.1)	0.4 (0.3-0.5)	0.08 (0.0-0.2)	0.001	0.001
HOLOTHUROIDEA	144.71 (94.8-220.6)	57.43 (24.3-134.2)	289.07 (177.7-469.8)	64.87 (39.6-105.9)	56.43 (30.7-102.9)	0.001	0.001
CRINOIDEA	0 (0.0-0.3)	0 (0.0-0.6)	0.62 (0.2-1.1)	0.78 (0.3-1.4)	0.08 (0.0-0.5)	ns	0.028
TUNICATA	0.27 (0.0-1.0)	4.34 (1.1-12.6)	5.02 (2.5-9.3)	3.04 (1.4-5.9)	2.51 (0.8-5.8)	0.001	0.001
Total invertebrates	193.76 (133.5-281.1)	112.34 (53.0-236.8)	364.56 (237.3-559.7)	126.62 (82.2-194.7)	113.79 (67.0-192.8)	0.001	0.001

Table 3

Biomass (g wet wt.ha⁻¹) of selected megabenthos groups; geometric mean with 95% confidence limits in parentheses. ANOVA results for between cruise (Cr) and between year (Yr) comparisons are also listed (ns-not significant).

Cruise	Other invertebrates	Other holothurians	<i>Amperima rosea</i>	Total invertebrates
Sep-89	211.1 (130-342)	1453.1 (946-2232)	10.5 (5-21)	1680.7 (1108-2548)
May-91	354.2 (196-639)	2127.3 (1257-3599)	18.4 (8-41)	2507.9 (1506-4175)
Apr-94	181.4 (119-276)	1485.1 (1024-2154)	29.9 (17-52)	1714.6 (1196-2459)
Sep-96	174.7 (120-254)	1629.6 (1169-2273)	264.0 (161-431)	2082.6 (1509-2875)
Apr-97	191.0 (118-310)	2062.4 (1343-3168)	541.5 (288-1019)	2846.1 (1877-4315)
Jul-97	183.4 (121-279)	2227.6 (1536-3231)	395.3 (228-684)	2864.0 (1997-4107)
Oct-97	294.7 (163-532)	1872.7 (1107-3168)	256.2 (118-556)	2426.3 (1457-4039)
Mar-98	114.4 (75-174)	1486.2 (1025-2155)	184.9 (107-320)	1806.1 (1259-2590)
Oct-98	323.6 (179-584)	2088.6 (1234-3533)	162.2 (74-353)	2583.4 (1552-4301)
Apr-99	155.2 (102-236)	2765.7 (1907-4011)	34.8 (20-61)	2968.3 (2070-4256)
Oct-00	105.6 (45-244)	1275.3 (606-2683)	17.3 (5-54)	1398.3 (680-2875)
Oct-02	239.0 (147-387)	1189.5 (774-1827)	328.3 (174-618)	1777.0 (1172-2694)
Jun-04	171.0 (105-277)	1609.3 (1048-2472)	24.1 (12-46)	1811.1 (1194-2746)
Jul-05	212.6 (118-384)	1711.0 (1011-2895)	21.7 (9-48)	1945.6 (1169-3239)
ANOVA-Cr	ns	ns	p<0.001	ns
ANOVA-Yr	ns	ns	p<0.001	ns

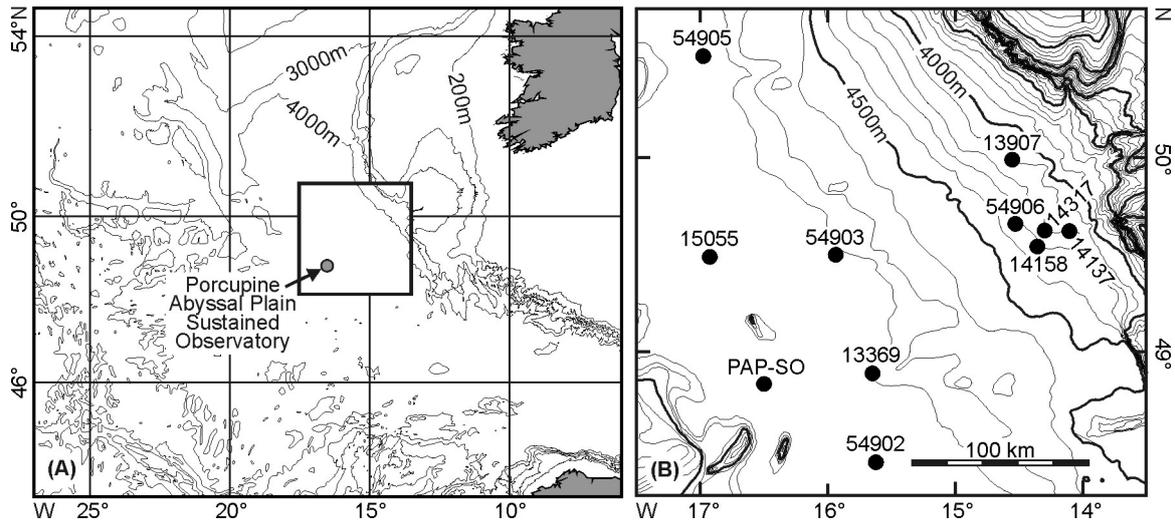


Figure 1. Charts showing (A) the general location of the Porcupine Abyssal Plain Sustained Observatory site (PAP-SO) and (B) the locations of other Porcupine Abyssal Plain sampling sites referred to in the text (identified by their station numbers).

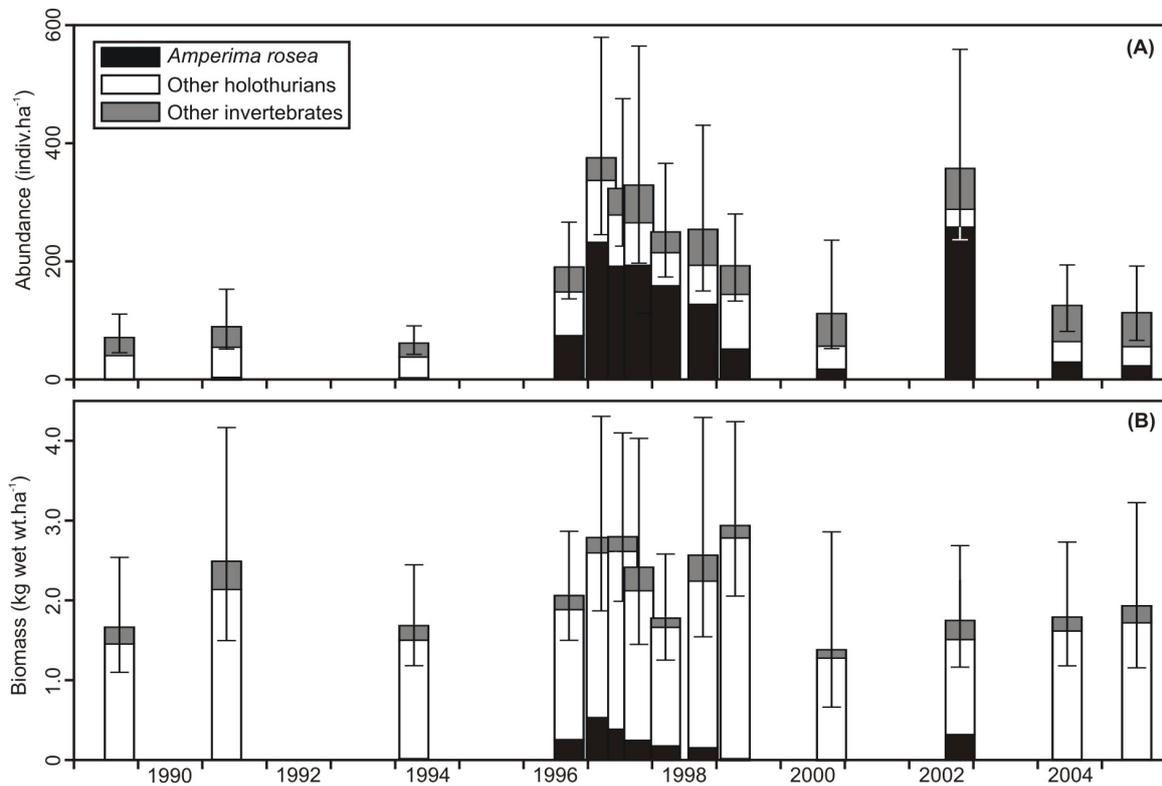


Figure 2. Histograms illustrating temporal variations in the (A) density and (B) biomass of selected megafaunal groups at the Porcupine Abyssal Plain Sustained Observatory site (means and 95% confidence intervals are shown).

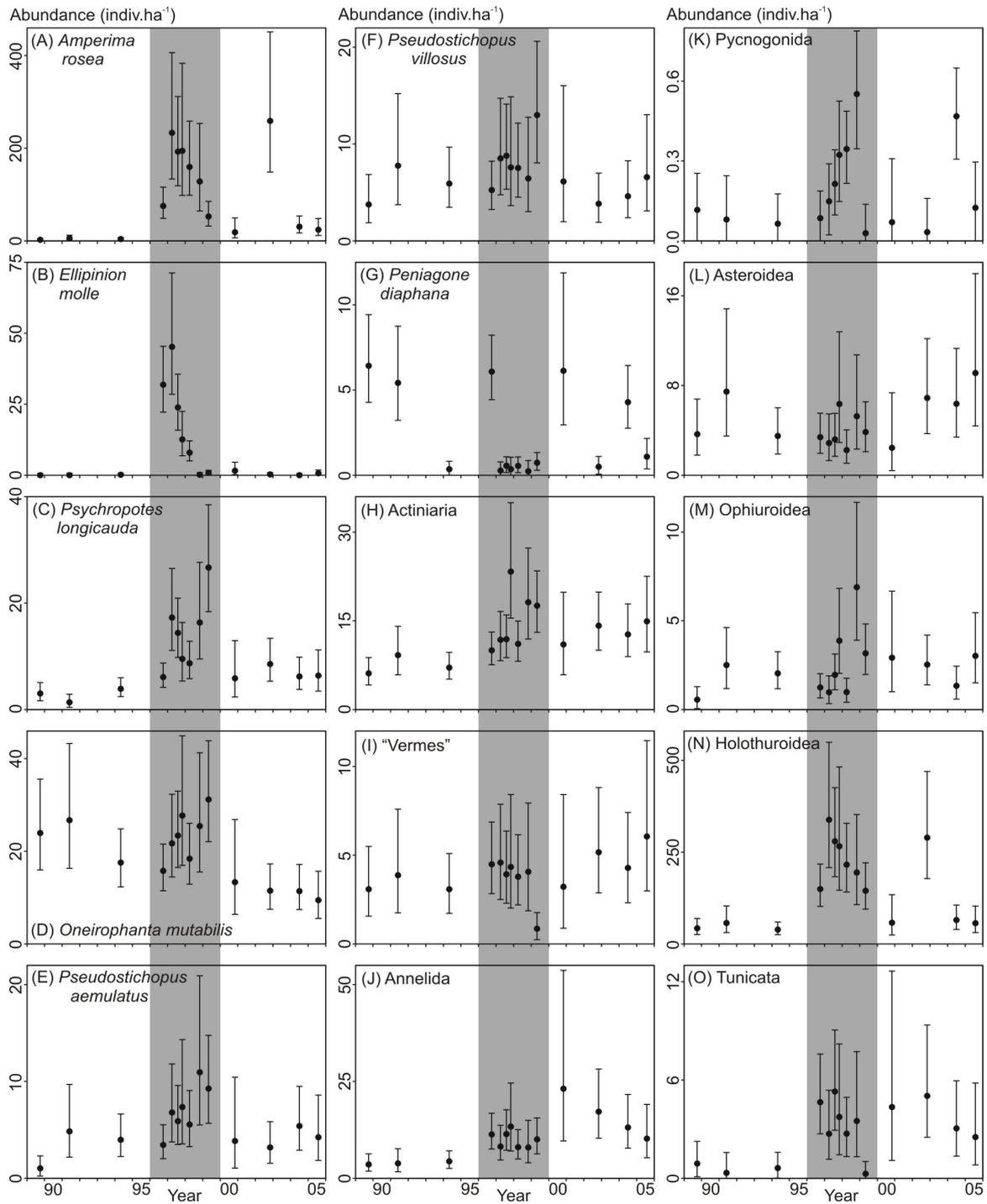


Figure 3. Plots of temporal variations in the density of selected holothurian species and megafaunal groups at the Porcupine Abyssal Plain Sustained Observatory site, the 'Amperima Event' is indicated by the shaded area (means and 95% confidence intervals are shown).

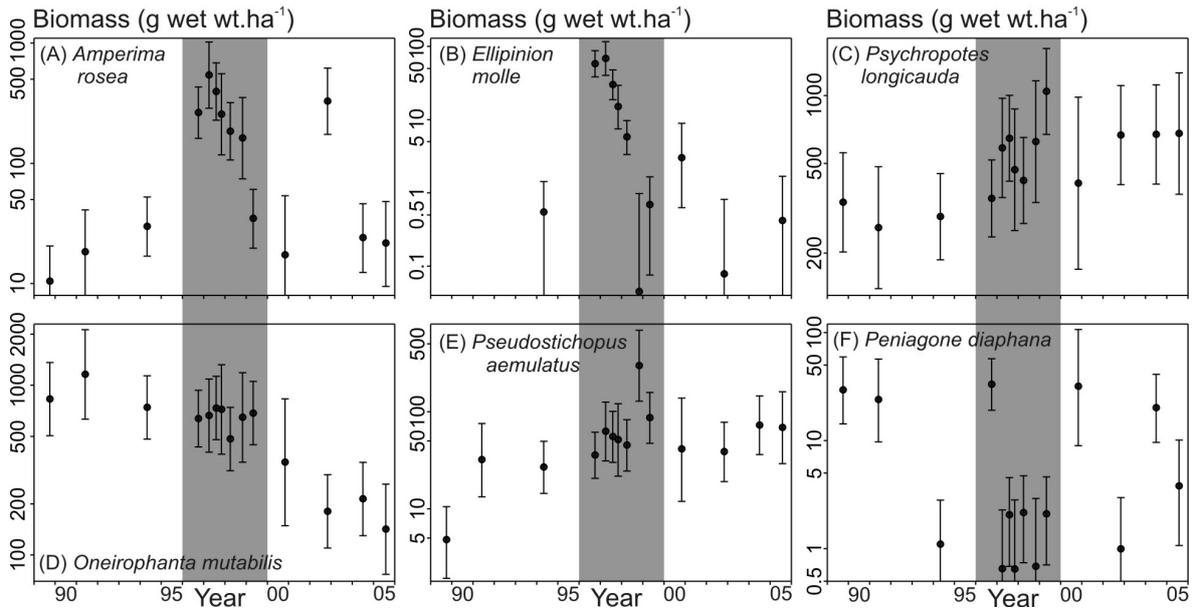


Figure 4. Plots of temporal variations in the biomass of selected holothurian species at the Porcupine Abyssal Plain Sustained Observatory site, the 'Amperima Event' is indicated by the shaded area (means and 95% confidence intervals are shown). All species illustrated exhibit statistically significant ($p < 0.05$) biomass variations between cruises and between years.

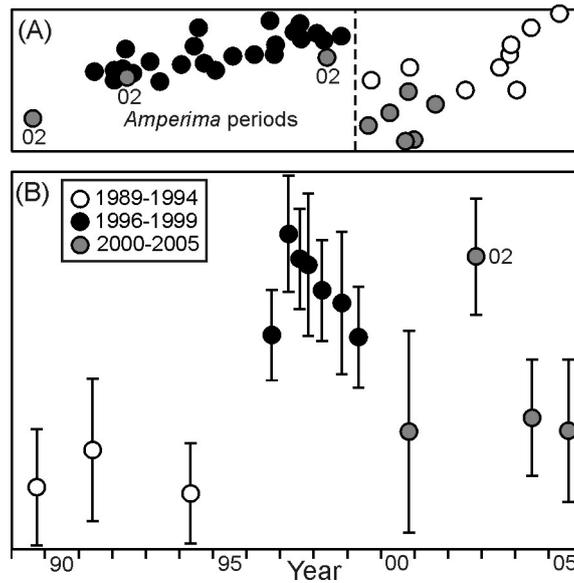


Figure 5. Temporal variation in major taxon composition of Porcupine Abyssal Plain Sustained Observatory site megabenthos: (A) non-metric multi-dimensional scaling (MDS) ordination plot of megabenthos composition; (B) MDS x-ordinate data from (A) plotted as cruise means with 95% confidence intervals. Samples collected in 2002 (02) are highlighted on both plots.

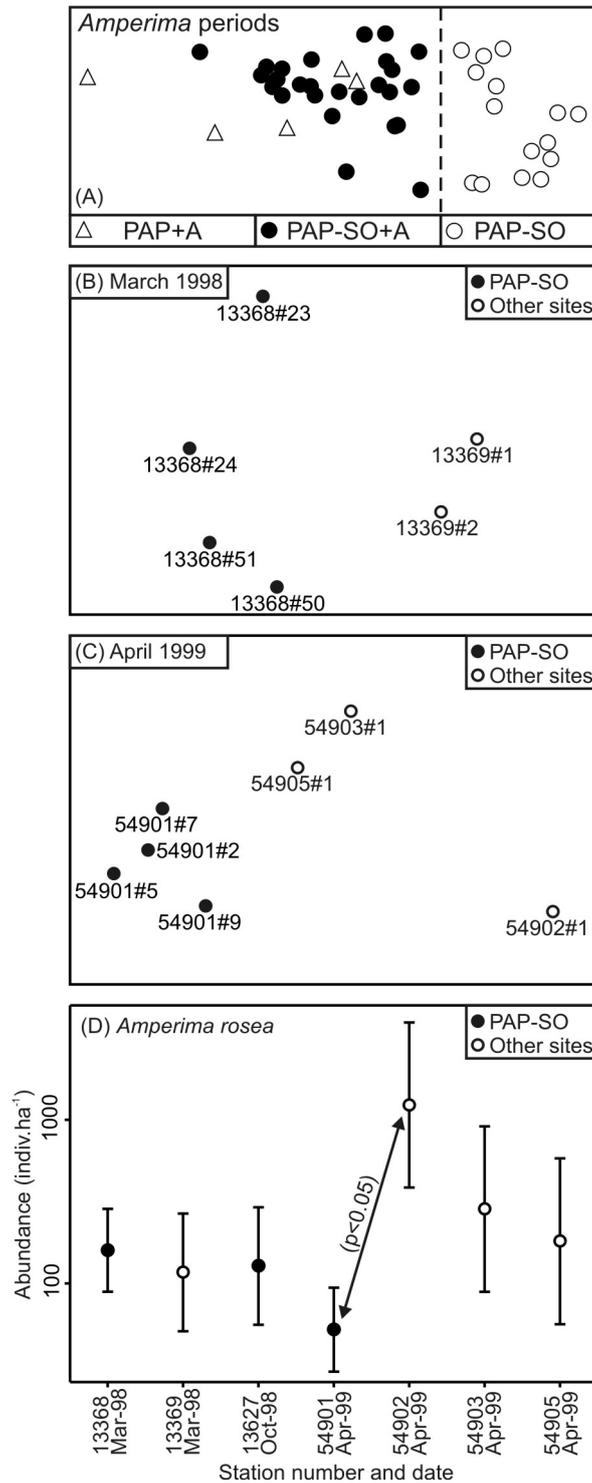


Figure 6. Large-scale spatial variation of Porcupine Abyssal Plain (PAP) megabenthos: (A) non-metric multi-dimensional scaling (MDS) ordination plot of megabenthos composition across all Porcupine Abyssal Plain sites; (B) MDS plot of megabenthos composition for March 1998 samples and (C) in April 1999 samples; (D) temporal and spatial variations in the density of the dominant holothurian, *Amperima rosea*, during 1998-1999. (PAP-SO, sustained observatory site; +A, 'Amperima Event' periods).

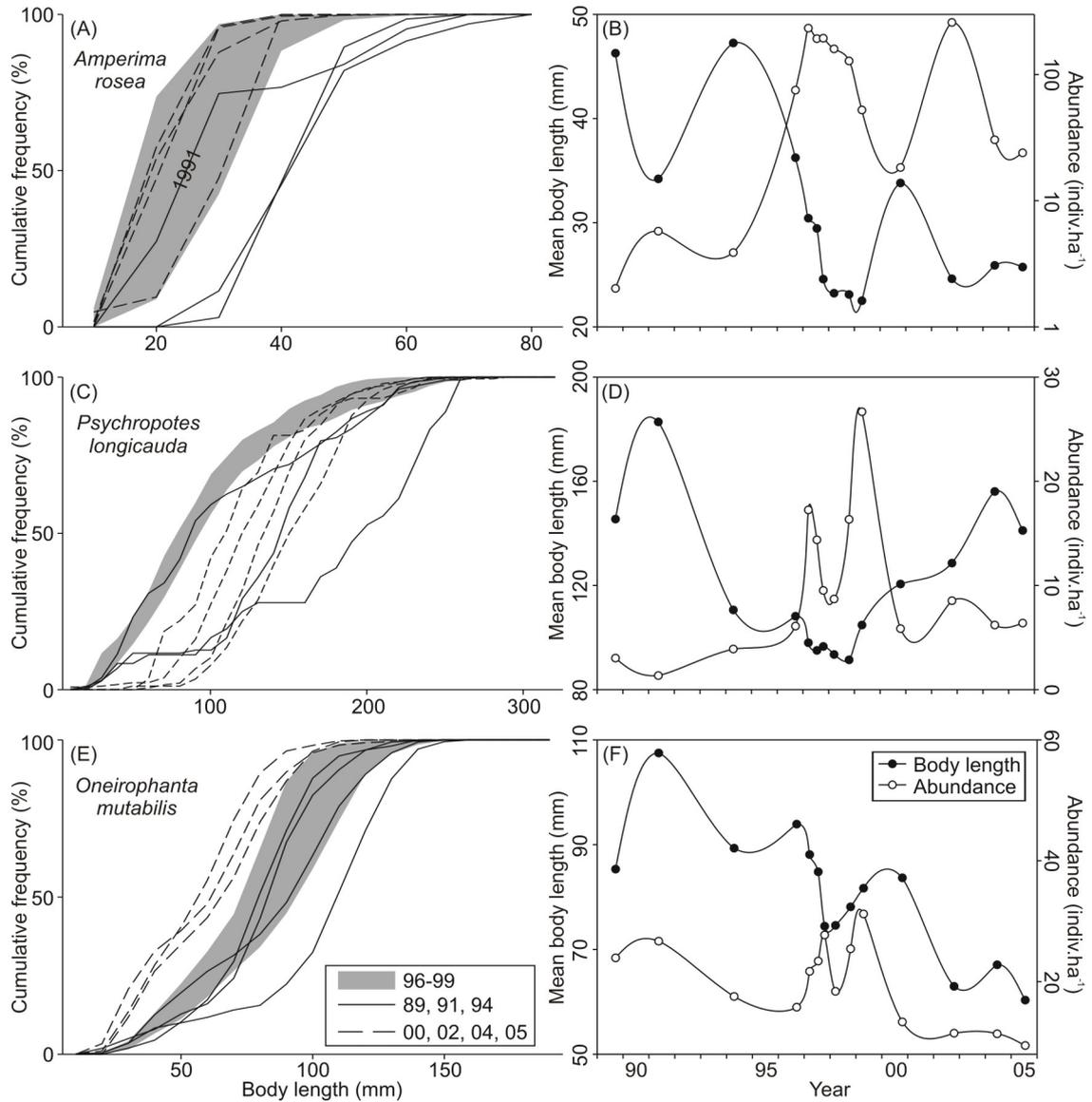


Figure 7. Temporal variations in the body sizes of selected holothurians species from the Porcupine Abyssal Plain Sustained Observatory site: (A, B) *Amperima rosea*, (C, D) *Psychropotes longicauda*, and (E, F) *Oneirophanta mutabilis*. Left-hand plots illustrate cumulative frequency distributions of body length; right-hand plots show variations in mean body length together with corresponding changes in the density of that species.