



Inter-annual dynamics of abyssal polychaete communities in the North East Pacific and North East Atlantic—A family-level study

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ABSTRACT

Characterising how deep-sea communities change on contemporary time-scales and understanding underlying ecosystem processes has become important under changing climate and the rise in the exploitation of deep-sea resources. However, little is known about these dynamics and processes. Long-term observations from which inter-annual variations can be detected are scarce in the deep sea. This study examines inter-annual changes in density, family richness and evenness, family and functional group rank abundance distributions of infaunal polychaetes at two abyssal stations in the North East Pacific (Station M, 1991 to 2005) and in the North East Atlantic (Porcupine Abyssal Plain, 1991 to 1999). The two long-term data sets were used to investigate not only if polychaete community structure and composition varied at inter-annual scales in terms of diversity and rank abundance distributions but also if any changes were related to previous observations in megafauna and environmental factors at each locality. The polychaete community structure at each locality was analysed using univariate statistics as well as multivariate ordination techniques based on Bray-Curtis similarity of the yearly family density. Sub-surface deposit feeders, such as Paraonidae, dominated the North East Pacific, whereas surface deposit feeders, such as Cirratulidae, dominated the North East Atlantic. Both stations showed inter-annual variations in density, family evenness and rank abundance distributions. The greatest changes occurred in 1998 in both time series when polychaete densities peaked, and switches in the rank abundance of the most abundant families and functional groups took place. Inter-annual variations in the polychaete community were correlated with a limited number of holothurian species changes, but no correlation was found with particulate organic matter flux or climate indices. Ecological and environmental factors behind the family-level changes remain elusive. Overall, changes in the dominance of functional groups imply changes in abyssal ecosystem functioning with potential consequences on carbon cycling at the seabed.

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1. Introduction

Understanding temporal variations in deep-sea system is becoming more important because of the increasing exploitation of deep-sea resources such as fisheries, hydrocarbons and minerals (Glover and Smith, 2003; Thiel, 2003). In addition, global warming is likely to impact ocean conditions with consequences on primary and export of that production to the deep ocean (Bopp

et al., 2005; Sarmiento and Gruber, 2006; Richardson, 2008; Steinarcker et al., 2010). Most deep-sea fauna depend on such export production as sinking particulate organic carbon (POC) flux provides food through pelagic–benthic coupling (Smith, 1987). In a food-limited environment, such as the deep sea, the supply of food is important in structuring deep-sea communities (Billett, 1991) and has links to many long-term carbon processes such as bioturbation, remineralisation, and burial (Smith et al., 1997, 2001, 2009; Witte and Pfannkuche, 2000; Bett et al., 2001; Ruhl et al., 2008). Characterising deep-sea system temporal variations is important to assess how ecosystem processes are linked to climatic variations, stochastic events and long-term trends (Smith et al., 2009; Glover et al., 2010). In recent years, significant inter-annual changes have been found in abyssal macro-infaunal

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communities in the North-East Pacific (Ruhl et al., 2008) and North-East Atlantic (Soto et al., 2010), including changes in polychaete densities, the dominant macrofaunal taxon in many areas of the ocean. In order to achieve a mechanistic understanding of processes shaping abyssal communities in time, the inter-annual variations of macrofauna community structure defined as density, family richness, evenness, family and functional group (FG) compositions have been characterised.

To date, only two abyssal (>4000 m) soft-bottom habitats have been studied for a period greater than 20 years: Station M (Sta. M) in the North East Pacific and the Porcupine Abyssal Plain Sustained Observatory (PAP) in the North East Atlantic. Previous research has characterised pelagic–benthic coupling and abyssal fauna ecology, especially in terms of temporal patterns (Smith and Druffel, 1998; Billett and Rice, 2001; Lampitt et al., 2010a). Results from sediment traps have shown that POC flux has intra- and inter-annual variations in quantity and quality at both stations (Baldwin et al., 1998; Smith et al., 2006; Lampitt et al., 2010b). Climate has been proposed as a key factor generating inter-annual variations in POC flux, in particular the variations of the El Niño Southern Oscillation (ENSO) and North Atlantic Oscillation (NAO). Changes in POC flux at Sta. M were significantly and positively correlated with the North Oscillation Index (NOI, an ENSO indicator) where changes in POC flux lagged NOI variations by 6 months. Similar correlations also found that POC flux at PAP lagged variations in the NAO by 5 months (Smith et al., 2006). At Sta. M, POC flux variations appeared to impact megafauna species in different ways: some increased in density during periods of high food supply whereas others decreased. The most striking examples include the holothurians *Elpidia minutissima*, the echinoid *Echinocrepis rostrata* as well as less dominant species like holothurians *Scotoplanes globosa* at Sta. M (Ruhl and Smith, 2004). At PAP, the densities of the holothurians *Amperima rosea*, *Ellipinion molle*, and the ophiuroid *Ophiocten hastatum* varied by several orders of magnitude between 1989 and 2005 (Billett et al., 2010; Bett et al. 2001).

Less is known about sediment macrofauna community temporal variations. From 1989 to 1998, Ruhl et al. (2008) found significant correlations between POC flux, the NOI and some macrofauna phyla densities at monthly and inter-annual scales at Sta. M. At PAP, during the first 'Amperima Event' (1996–1998), macrofauna also displayed taxon-specific temporal variations in density (Galéron et al., 2001). Focusing on infaunal polychaetes, Soto et al. (2010) showed that density and total family number changed between 1989–1994 and 1996–1998, the latter period coinciding with the first 'Amperima Event'. *In situ* enrichment experiments conducted at Sta. M and PAP have shown that macrofauna can ingest carbon quickly and mix it into deeper sediment layers (Aberle and Witte, 2003; Sweetman and Witte, 2008). Therefore, macrofauna temporal variations could provide important insights in assessing deep-sea carbon flow dynamics (Ruhl et al., 2008). However, a better mechanistic understanding of macrofauna inter-annual variations is needed to make such insights.

Examining macrofauna community structure variation at a finer taxonomic resolution than has been done previously will provide greater knowledge of the functional role of macrofauna at Sta. M and PAP. Intra-annual variations in POC flux are related to seasonality with both stations located at temperate latitudes, where seasonality influences food quantity and quality. While there is evidence to suggest that intra-annual changes in polychaete community structure and composition occur (e.g., Drazen et al. 1998), our study focuses on longer term change. In this study, polychaetes were examined at the family-level because: (1) polychaetes dominate a majority of deep-benthic soft-bottom macrofaunal communities in terms of density and species number

(Olsgaard et al., 2003; Paterson et al., 2009); (2) few polychaete families have been reported as being exclusively abyssal and those families have apparently limited adaptations compared to shallow water forms (Glover, 2000; Paterson et al., 2009); (3) polychaetes have varied life-histories and perform important ecological functions such as sediment reworking, bioturbation and carbon recycling (Rouse and Pleijel, 2001; Olsgaard et al., 2003); (4) polychaetes are clearly responsive to changes in organic matter supply (e.g., Ruhl et al., 2008; Soto et al., 2010).

In addition to finer taxonomic level, a better characterisation of Sta. M and PAP macrofauna community inter-annual variations requires the use of various ecological descriptors. Based on niche theories, Rank Abundance Distribution (RAD) provides a useful way to describe resource division among a community (MacArthur, 1957; Hubbell, 1979; Magurran, 2004). In time series research, the investigation of RAD variation can facilitate mechanistic insights into community inter-annual variations. Analysing switches in rank composition over time can investigate the potential role of biological or environmental processes in community temporal variations (Thibault et al., 2004; Magurran, 2007; Ruhl, 2008). When used with more classical indexes such as density, richness and evenness, RADs can provide an informative description of change (Magurran and McGill, 2011). Ruhl (2008) used temporal RAD analyses to show that benthic community-level megafauna changes at Sta. M from 1989 to 2004 were modulated by climate-driven resource variations rather than random ecological drift.

This study examines inter-annual variations in polychaete density, family richness and evenness, family RAD (RAD_F) and functional group RAD (RAD_G) at Sta. M from 1991 to 2005 and PAP from 1991 to 1999. Using the two long time-series polychaete data sets, three main questions were addressed: (1) Did polychaete community structure and composition change at inter-annual scales in terms of diversity both as family richness and as Pielou's Evenness Index? (2) Did polychaete community structure and composition change in terms of RAD_F and RAD_G at inter-annual scales? (3) Did inter-annual changes in polychaete family community composition or structure relate to previous observations in megafauna and environmental factors at each locality?

2. Materials and methods

2.1. Study areas and macrofauna sampling

From 1991 to 2005, 22 of the research cruises to Sta. M (50°00N, 123°00W, in the North East Pacific, 4100 m depth, see details in Smith and Druffel 1998) included macrofauna sampling using a Free-Vehicle Grab Respirometer (FVGR, Smith et al. (2001)). The FVGR is a sampling system comprised of four 413-cm² grabs separated by 25 cm (square design) collecting the top 15 cm of sediment (Table 1). After recovery, material was sieved through a 300 μm mesh and preserved in 10% borate-buffered formalin solution (Drazen et al., 1998). While FVGR samples were collected from 1989 to 1990, these were no longer available for further analysis.

From 1991 to 1999, ten research cruises to PAP, (48°50N, 16°30W, in the North East Atlantic, 4850 m depth, Billett and Rice, 2001) sampled macrofauna using a 0.25 m² USNEL box-corer (Table 1). Overlying water and five top centimetres of sediment were sieved using a 300 μm mesh and retained material was similarly preserved in a 10% formalin solution (Soto et al., 2010).

Before identification, Sta. M samples were sorted to phylum level at the Scripps Institution of Oceanography prior to 2006, and thereafter at the Monterey Bay Aquarium Research Institute.

Table 1

Stations, dates, number of chamber grab and drop (Sta. M) or box-corer (PAP) and locations of macrofauna samplings at Sta. M and PAP.

Station	Year	Month	Chamber grab (drop) or Box-corer	Latitude °N	Longitude °W
Sta. M	1991	February	1 (1)	34.84	122.93
		June	7 (2)	34.90	123.05
		July	2 (2)	34.89	123.07
		October	3 (1)	34.88	123.11
	1992	February	5 (2)	34.88	123.12
		June	5 (2)	34.91	123.11
		July	3 (1)	34.78	122.95
		October	6 (2)	34.85	123.15
	1993	February	3 (1)	34.79	122.92
		July	3 (1)	34.82	123.07
		November	5 (2)	34.80	122.93
	1994	February	2 (2)	34.78	122.92
	1995	February	5 (2)	34.93	123.12
		June	1 (1)	34.95	123.13
	1996	February	4 (2)	34.72	122.98
		June	3 (1)	34.68	122.94
		October	5 (2)	34.69	122.90
	1998	April	2 (1)	34.93	123.03
		August	3 (2)	34.78	123.03
December		2 (1)	34.78	123.00	
2005	February	3 (1)	34.853	123.20	
	June	3 (1)	34.93	123.25	
PAP	1991	May	6	48.85	16.50
	1994	April	4	41.85	16.50
	1996	September	7	48.85	16.48
	1997	March	6	48.83	16.50
		July	5	48.83	16.48
	1998	March	2	48.84	16.49
		September	3	48.83	16.50
	1999	May	3		

Samples for PAP were sorted at the Natural History Museum (NHM) of London. In both cases, samples were stained for 24-h in Rose Bengal, rinsed in distilled water, transferred to a 70% isopropyl alcohol solution and sorted at phylum-level. Sta. M annelids were then sent to NHM for taxonomic identification. PAP polychaetes sampled prior to 1999 were identified to family level by E. Soto.

2.2. Taxonomic identification

Taxonomic identification was undertaken under high power microscopes (Zeiss Discovery v20 Stereo and high power Leica DM 5000 B) by comparing the external morphology of specimens with published identification keys (Fauchald, 1977; Rouse and Pleijel, 2001). Family-level identification was a first step before a more detailed taxonomic analysis. For family identification, only specimens with a head were used leading to a conservative assessment of density and diversity (Paterson et al., 2009). Overall, only 2 and 5% of fauna were unknowns at Sta. M and PAP, respectively.

Each family was assigned to a single functional group among those defined by Fauchald and Jumars (1979) and amended by subsequent authors (e.g., Pagliosa, 2005). The choice of the retained functional group was based on the feeding strategy most likely to be encountered in an abyssal environment, e.g., direct herbivory was not meaningful in abyssal systems. Fauchald and Jumars' classification was mainly derived from shallow water specimen observations; such a classification must therefore be used with caution in an abyssal context. However, as few polychaete families have been reported as being exclusively abyssal (Glover, 2000), analogy with shallower species is not

unreasonable. Polychaete functional group research is still ongoing (e.g., Lindsay and Woodin, 1995; Mistri et al., 2002; Würzberg et al., 2011) with evidence suggesting that many polychaetes may be multimodal and may adapt to utilize what resources are available (Dr. L. Lovell, pers. com.). However, so far, Fauchald and Jumars (1979) FG classification remains the only unified classification, based on polychaete morphological traits and appeared the most relevant for this analysis.

2.3. Statistical analysis of polychaete community diversity at inter-annual scale

After identification, persistence over time defined as percentage of occurrence over the time-series was computed for each family and functional group. Only data from three or more FVGR chamber grabs at Sta. M and box-corerers at PAP for each sampled month (Table 1) were used. Data were averaged by year for further analyses. Because the sampling methods were different at Sta. M and PAP any comparisons between them must be undertaken with caution. First, Sta. M was sampled over a greater range of seasons than PAP (respectively February–December vs. March–October). Sta. M data statistical analyses were therefore computed for both the full range of samples across months February–December and the range which overlaps with samples at PAP, March–October. The results were not dependant on seasonal range, and therefore only results of the full data set are presented here. Second, although using a common analytical treatment is an asset to compare stations, we acknowledge there are important limits to quantitative comparison between Sta. M and PAP because different sampling technologies were employed. For example, the box corer samples a larger continuous area than the FVGR grabs and the two systems have different so-called bow-wave effects (Bett et al., 1994). These bow-wave effects can cause systematic differences in the level of disturbance to the seafloor sample as the coring device operates. The main results rely on examining the variations at each site rather than direct quantitative comparison.

Polychaete mean densities were computed for each sampling year, as well as Pielou's evenness Index (Primer v.6, Clarke and Gorley (2006)). Family numbers were estimated by rarefaction technique to account for uneven sampling effort in each time-series (Coleman technique, EstimateS, Colwell (2009)). Rarefaction curves were computed for each sampling year and tested by Kruskal–Wallis rank test (SigmaPlot v.11). Family richness at each locality was compared by using family accumulation curves (EstimateS) and Mann–Whitney Rank Sum Test (SigmaPlot v.11). Relationships between univariate indexes were investigated with non-parametric Spearman rank correlation (r_s , SigmaPlot v.11).

The polychaete community structure at each locality was analysed using multivariate ordination techniques (Primer v.6). Family composition as Bray–Curtis Similarity of the 4th root-transformed yearly family density data was computed. Prior to further temporal analyses, the effects of spatial heterogeneity were tested. Two similarity matrices were created, one with spatial distances and one with linear temporal distances between each sample. Using the RELATE routine (Mantel test, ρ , Primer v.6) relationships between polychaete community similarity matrix and these two matrices were investigated. A non-parametric Multi-Dimensional Scaling (MDS) method was then applied to polychaete similarity matrices. Inter-annual changes were assessed using multivariate Analysis Of SIMilarity (ANOSIM [R], Primer v.6), which uses randomisation testing of significance with 999 permutations. Also, the MDS x-ordinate was used as a summary univariate parameter to characterise community structure and composition over time.

2.4. Statistical analysis of polychaete community structure as RAD_F and RAD_G at an inter-annual scale

Family and functional rank abundance distributions (RAD_F and RAD_G) were obtained by ranking, respectively, family and functional group densities for each year (rank 1 being the most abundant). In each case, the density values were retained and the distributions were only re-order by ranking these densities without applying any transformation on the data. Ranked composition as Bray–Curtis similarities of the 4th root-transformed yearly ranked data were computed (Primer v.6). A RELATE test was performed with a matrix of linear temporal time between each sample and RAD_F, RAD_G matrices. In other words we examined if the similarity of various RAD distributions was more similar when the samples were taken closer together in time. Similarity data were also used for hierarchical clustering (group average linkage, Primer v.6) and MDS. For FG analysis, the ratio between surface and sub-surface feeder density (SB ratio) was examined. Non-parametric Spearman rank correlations (r_s , SigmaPlot v.11) were computed between families and between FG variables to assess potential compensatory effects as defined by negative co-variation (*sensu* Houlahan et al., 2007).

2.5. Statistical analysis of relationships with megafauna and environmental factors

Spearman-rank correlations were used to investigate potential relationships between polychaete community and megafauna/environmental factors (SigmaPlot v.11). Several polychaete community descriptors were tested: mean density, rarefied family number, MDS x-ordinate of the Bray–Curtis similarity, family, functional group and rank densities. For family, FG and rank densities, only those with a coefficient of variation (CV, standard deviation to mean ratio) less than one were used representing 15 most abundant families and 7 functional groups. Also, for megafauna, only species or indicators representative of marked temporal changes were used. At Sta. M, *Elpidia minutissima*, *Echinocrepis* sp., *Scotoplanes globosa*, total echinoderm biomass and density were examined (Ruhl and Smith, 2004; Ruhl, 2007). At PAP, *Amperima rosea*, *Peniagone diaphana*, *Oneirophanta mutabilis*, total echinoderm biomass and density, total holothurian surface deposit feeder biomass and density, total holothurian sub-surface deposit feeder biomass and density were used (Iken et al., 2001; Billett et al., 2010). A distinction between surface and sub-surface deposit feeding megafauna was applied at PAP only because the Sta. M data did not include sub-surface deposit feeders (*cf.* photography data were used to quantify megafauna at Sta. M while trawl data were obtained at PAP).

In terms of environmental factors, the climate indicators NAO at PAP and NOI at Sta. M were tested, as well as site-specific records of POC flux to the seafloor. At Sta. M, a near-continuous monthly data record of POC flux was made possible by a composite measure of POC flux integrated from sediment trap data at 50 and 600 mab and a model based on satellite data to fill in the gaps in the record (Ruhl et al., 2008). No such gap filling data are available for PAP, where much of the need for gap filling

pre-dates the availability of suitable satellite colour data. Monthly and yearly cross-correlations were used to test relationships over a distribution of monthly and yearly temporal lags between the environmental factors (climate and food supply) and polychaete community features. Because data sets were highly gapped, serial autocorrelation was not tested. Significance was assessed with several criteria regarding correlation sign, p -value and involved time lags. These tests were aimed to understand if climate processes, productivity and POC fluxes had a direct but lagged impact on the abyssal polychaete communities at both stations.

3. Results

3.1. Taxonomy

At Sta. M, a total of 3000 specimens were identified, belonging to 39 families and 10 FG. At PAP, a total of 4984 specimens were identified representing 41 families and 9 FG. Three families were present at all sampled times at Sta. M: Capitellidae, Lumbrineridae, Paraonidae and eight families were present at least 80% of the sampled time: Cirratulidae, Cossuridae, Opheliidae, Orbiniidae, Phyllodocidae, Pilargidae, Spionidae, Syllidae. At PAP, six families were found 100% of the sampled times: Ampharetidae, Cirratulidae, Paraonidae, Pilargidae, Sabellidae, Spionidae and seven families occurred 80% or more of the sampled times: Capitellidae, Chrysopetalidae, Fauveliopsidae, Flabelligeridae, Opheliidae, Phyllodocidae, and Scalibregmatidae. In terms of functional groups, BMx, OMJ, PMJ, PMx, SBMx, SMT and SDT (see Table 2) occurred at least 80% of the sampled times at both Sta. M and PAP. Overall, the two localities shared 34 families, among which seven were present in at least 80% of the samples. One family, the Paraonidae, was present in all samples. At Sta. M, oligochaetes (Phylum Annelida) occurred in substantial and variant numbers, but were notably absent from PAP.

3.2. Polychaete community density and diversity

Polychaete density varied inter-annually at both stations (Fig. 1a and b). The highest densities were found in 1998 at both sites with 1893 ± 393 ind. m⁻² at Sta. M and 839 ± 285 ind. m⁻² at PAP. The lowest densities were approximately four times less and were recorded in 2005 at Sta. M with 490 ± 219 ind. m⁻² and in 1994 at PAP with 203 ± 52 ind. m⁻².

In terms of diversity, rarefied family number changed between years (Fig. 1c and d) but without significant statistical difference at Sta. M ($p > 0.05$). In contrast, significant differences occurred at PAP between the periods 1991–1994 and 1996–1999, the ‘Amperima Event’ ($p = 0.022$) with rarefied family numbers higher during the ‘Amperima Event’. Pielou’s evenness index also varied inter-annually at both stations (Fig. 1e and f) albeit without correlation to density or rarefied family number over the whole time-series (Spearman rank correlation, $p > 0.05$). Greater evenness occurred in 1995 at Sta. M and 1996 at PAP. The highest dominance was found in 1991 at Sta. M and 1994 at PAP.

Overall family composition changed at inter-annual scale ($R = 0.151$, $p = 0.01$ at St M, $R = 0.636$, $p < 0.001$ at PAP with year

Table 2
Three-letter code key of polychaete functional groups as defined by Fauchald and Jumars (1979).

First letter feeding mode	Second letter mobility	Third letter feeding apparatus
B—Subsurface deposit feeder	D—Discretely motile	J—Jaw
F—Filter feeder	M—Motile	T—Tentacle
P—Predator	S—Sessile	x—non-armed structure
S—Surface deposit feeder		

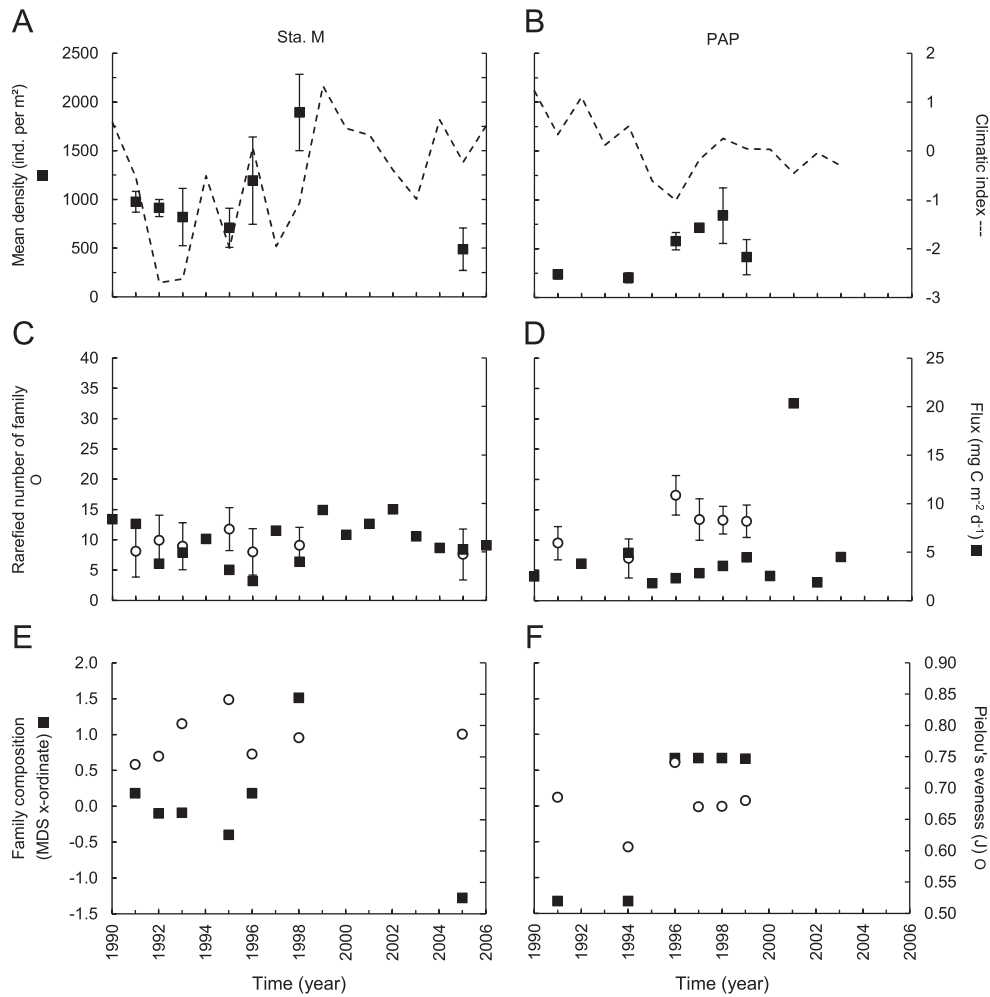


Fig. 1. Polychaete community structure univariate indexes at Sta. M and PAP over 1991–2005 (A) Sta. M mean polychaete density as individuals per m^{-2} (■) with associated standard error and yearly-averaged NOI index (dashed line) (B) PAP mean polychaete density as $ind. m^{-2}$ (■) with associated standard error and yearly-averaged NAO index (dashed line) (C) Sta. M rarefied family number with 18 individuals (○) with associated standard error and mean annual POC flux (') (D) PAP rarefied family number with 50 individuals (○) with associated standard error and mean annual POC flux (') (E) Sta. M MDS x-ordinate (■) and Pielou's evenness Index (○) (F) PAP MDS x-ordinate (■) and Pielou's evenness Index (○).

as a factor). As no relationship was found between the spatial distance between samples and their similarity ($\rho < 0.1, p > 0.1$) at either locality, these changes were not found to be linked to spatial variations among sampling. However, a significant relationship was obtained between the temporal distance between samples and their similarity: samples taken further apart in time were less similar to each other than samples taken near in time ($\rho = 0.303, p < 0.001$ for Sta. M and $\rho = 0.582, p = 0.061$ for PAP). The inter-annual variations in family composition were thus linked to temporal rather than spatial processes. Family composition MDS x-ordinate had an opposite sign in 1991, 1996 and 1998 compared to 1992, 1993, 1995 and 2005 at Sta. M (Fig. 1e, 0.063 stress value) with a marginally significant difference among the two groups of years (ANOSIM, $R = 0.463, p = 0.029$). At PAP, MDS x-ordinate (0.001 stress value) also had different signs between 1991, 1994 compared to the 'Amperima Event' period (Fig. 1f). These two groups of years were significantly different (ANOSIM, $R = 1, p = 0.069$). In other words, family composition was different over periods of time rather than from year to year.

Comparing the two stations, allowing for different sampling methodologies, Sta. M had twice the standardised density of PAP.

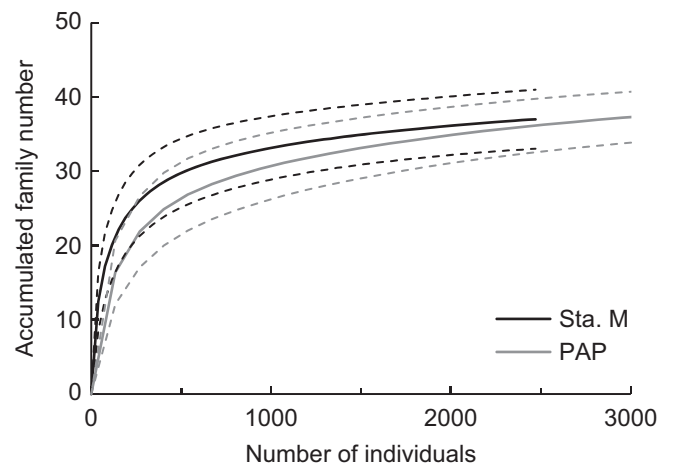


Fig. 2. Family accumulation curves for Sta. M (black line) with 95% confidence interval (black dashed line) and PAP (grey line) with 95% confidence interval (grey dashed line).

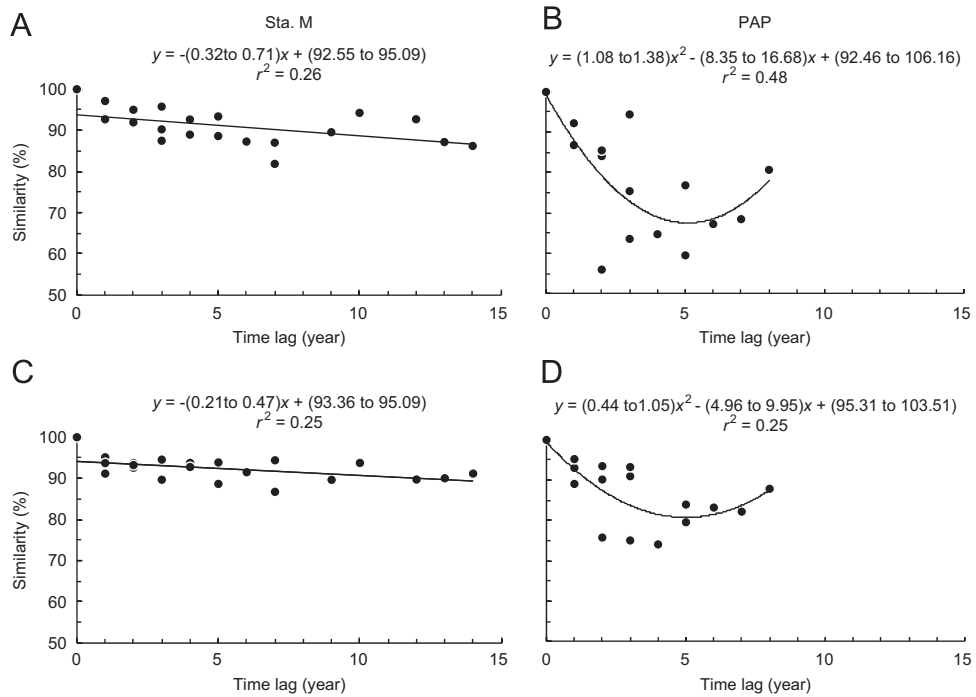


Fig. 3. Scatter-plots of Bray-Curtis Similarity (%) for (A) all possible RAD_F pairs in 1991–2005 at Sta. M and (B) 1991–1999 at PAP and for (C) all possible RAD_C pairs in 1991–2005 at Sta. M and (D) 1991–1999 at PAP. The regression lines are best fit only shown for visual purposes (the statistical results of the Mantel test are given in Sections 3.3 and 3.4).

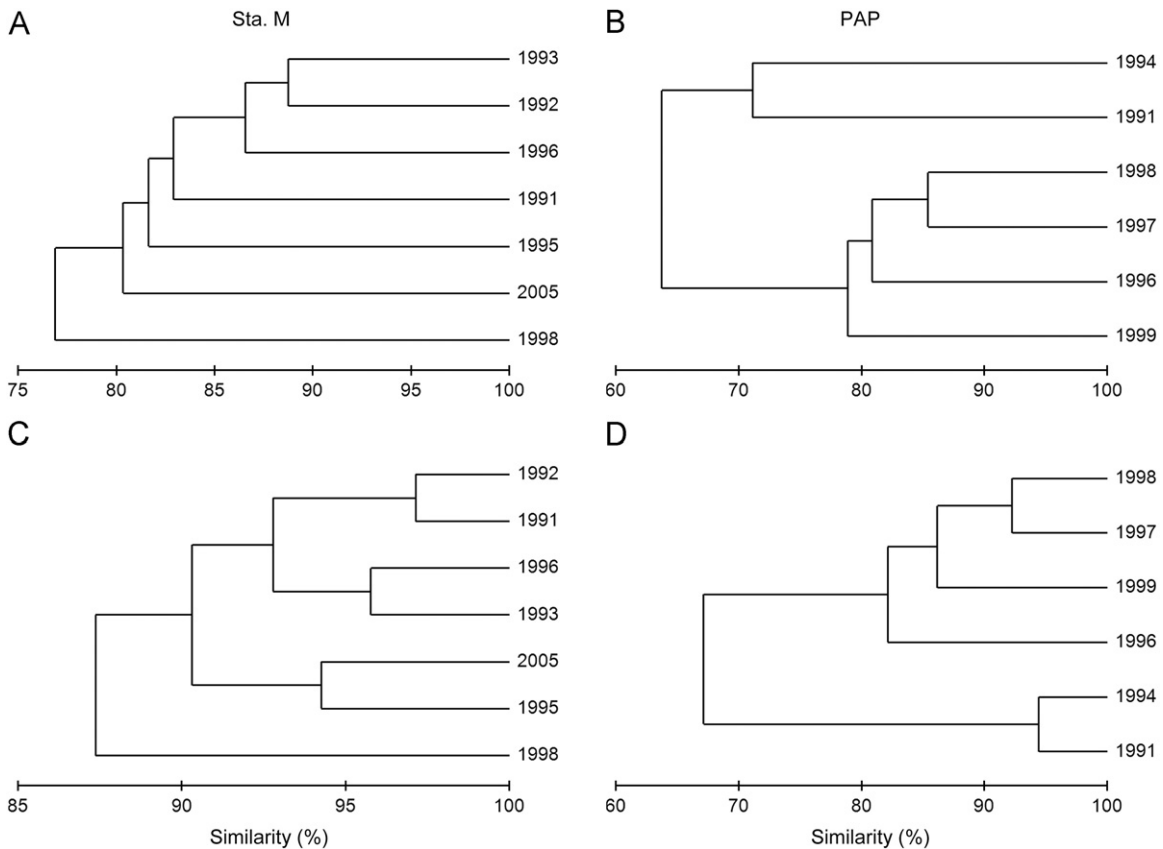


Fig. 4. Bray-Curtis dendrograms of (A) Sta. M yearly family composition, (B) PAP yearly family composition, (C) Sta. M yearly RAD_F and (D) PAP yearly RAD_F.

However, both stations had similar density trends over years: decreasing from 1991 to 1995 and increasing from 1996 to 1998. In terms of family numbers, Sta. M and PAP had similar accumulation rates (Fig. 2, Mann Whitney, $U=21$, $p > 0.05$).

3.3. Polychaete community structure as RAD_F

Directional changes in family rank abundance distribution (RAD_F) occurred at both stations at inter-annual scales (Fig. 3a

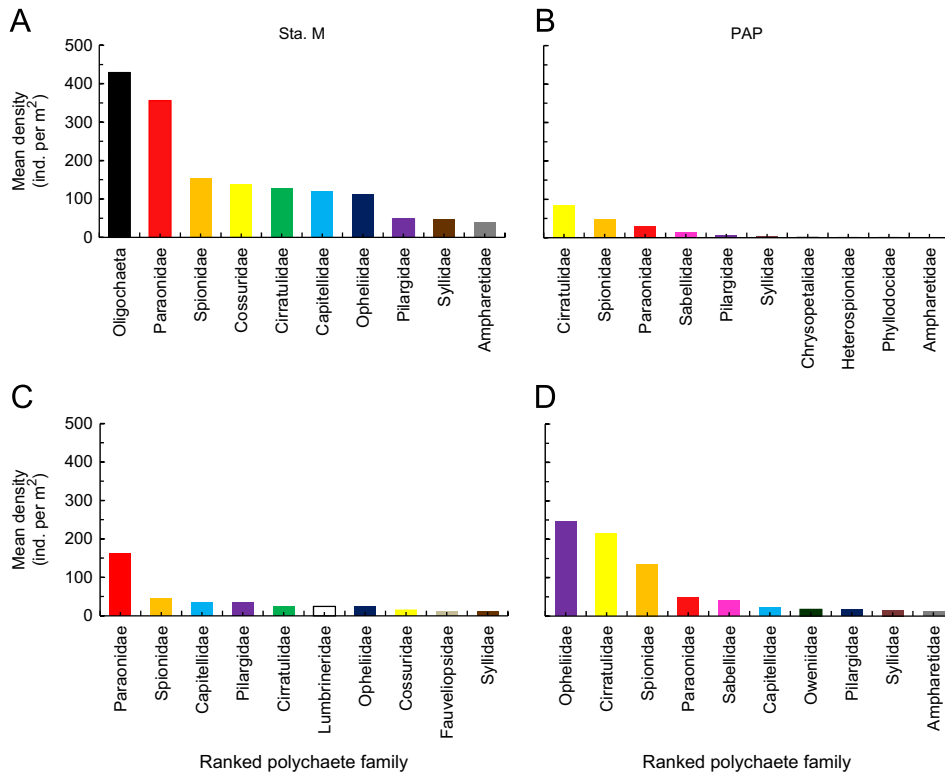


Fig. 5. RAD_F for (A) Sta. M in 1998, year of high polychaete mean density (HD), (B) PAP in 1994, year of low polychaete mean density (LD), (C) Sta. M in 2005, year of low polychaete mean density (LD) and (D) PAP in 1998, year of high polychaete mean density (HD). Rank 1 on the left is the most abundant. Families occupying each rank are given below. Rank densities are given in individuals per m⁻².

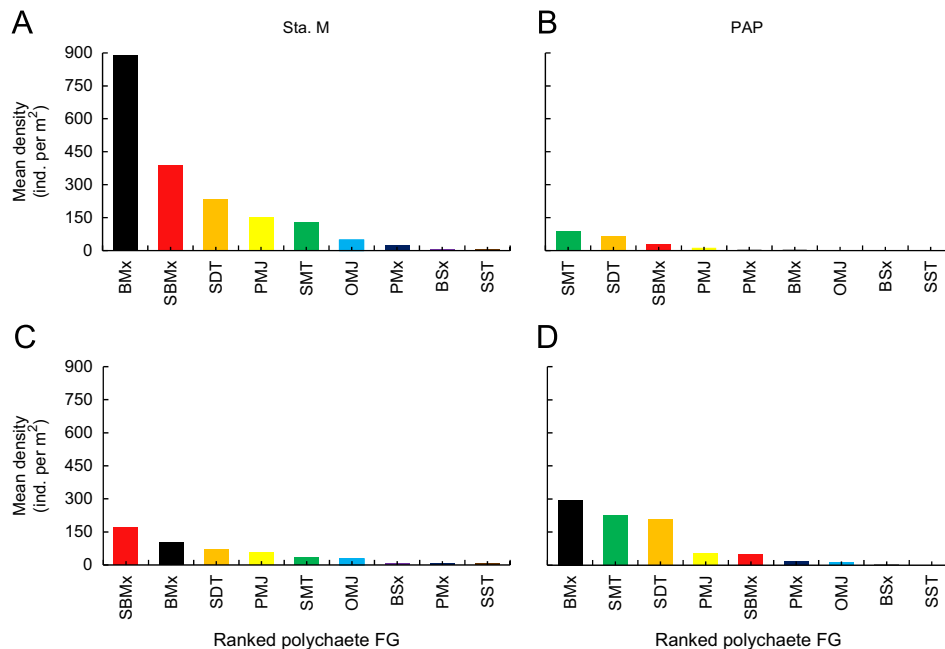


Fig. 6. RAD_C for (A) Sta. M in 1998, year of high polychaete mean density (HD), (B) PAP in 1994, year of low polychaete mean density (LD), (C) Sta. M in 2005, year of low polychaete mean density (LD) and (D) PAP in 1998, year of high polychaete mean density (HD). Rank 1 on the left is the most abundant. Functional groups occupying each rank are given below. Rank densities are given in individuals per m⁻².

and b). Samples taken closer together in time were generally more similar to those taken with longer time intervals between samples: $\rho=0.269$, $p=0.051$ at Sta. M and $\rho=0.780$, $p < 0.001$ at PAP. The RAD_F similarity dendrogram showed three clusters at Sta. M: 1998, 2005 and 1991–1996 (Fig. 4c). At Sta. M, no significant clustering was found with family composition dendrograms (Fig. 4a). At PAP, two clusters were found in both cases: 1991–1994 and 1996 to 1999, the 'Amperima Event' period (Fig. 4b and d). At each locality, year of greatest and least densities belonged to different clusters and their corresponding rank abundance distribution (RAD_F) varied in density level, shape and composition (Fig. 5). Sta. M rank 1 was occupied by Paraonidae, except in 1998 when oligochaetes became dominant, whereas other ranks had four or more switches. From 1991 to 1999, PAP rank 1 to 3 only switched once or twice and lower ranks five or six-times. Cirratulidae, Spionidae and Paraonidae occupied the first three density ranks at PAP, with relative density changes over time, except in 1998 when Opheliidae became the most dominant family.

Non-parametric Spearman rank correlations between family densities ($CV < 1$) at both stations were only positive, if significant.

3.4. Polychaete community structure as RAD_G

Polychaete communities also had directional changes in yearly RAD_G (Fig. 3c and d). Samples closer together in time were generally more similar to those with longer time intervals between them: $\rho=0.353$, $p=0.006$ at Sta. M and $\rho=0.654$, $p=0.031$ at PAP. RAD_G dendrograms of both stations gave similar clusters to RAD_F plots. The FG rank abundance distributions (RAD_G) changed in terms of composition, shape and level at both stations (Fig. 6). At Sta. M, rank 1 and 2 switched four times between 1991 and 2005, Rank 3 switched only once. Surface deposit feeders as BMx occupied rank 1 in 1991, 1992, 1995 and 2005. Sub-surface deposit feeders as BMx dominated in 1993, 1996, 1998. Some predators such as PMJ or tentaculate surface

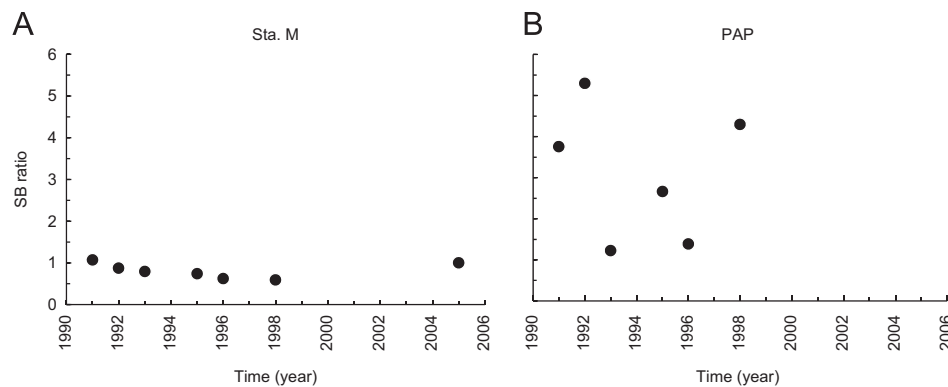


Fig. 7. RAD_G yearly dynamics represented by the ratio of surface to sub-surface deposit feeder densities (SB ratio) over year at (A) Sta. M and (B) PAP.

Table 3

Spearman rank correlation of *Scotoplanes globosa* with Sta. M polychaete community descriptors, $n=6$ and of *Amperima rosea*, *Oneirophanta mutabilis*, Total Echinoderm Density (TED), Total Holothurian Surface deposit feeder Density (THS D), Total Holothurian Sub-surface deposit feeder Biomass (THB B) with PAP polychaete community descriptors, $n=6$. R is the coefficient of correlation with its associate p -value (SigmaPlot v.11). Ord. stands for ordinate. MPD stands for mean polychaete density.

Station	Megafauna descriptor	Polychaete descriptor	R	p	Polychaete descriptor	R	p	
Sta. M	<i>S. globosa</i>	RAD_F MDS x-ord.	1	0.028	Cirratulidae	1	0.028	
		RAD_G MDS x-ord.	0.943	0.017	Spionidae	0.943	0.017	
		Ampharetidae	0.943	0.017	SDT	1	0.028	
		Capitellidae	0.886	0.033	SMT	0.943	0.017	
PAP	<i>A. rosea</i>	MPD	0.943	0.017	Spionidae	0.886	0.033	
		RAD_G MDS x-ord.	0.943	0.017	Syllidae	0.886	0.033	
		MDS x-ord.	0.926	0.017	PMJ	0.810	0.010	
		Ampharetidae	0.943	0.017	SDT	0.943	0.017	
		Cirratulidae	0.886	0.017	SMT	0.943	0.017	
		Sabellidae	0.886	0.033				
	<i>O. mutabilis</i>	SB ratio	0.943	0.017				
	TED	MPD	MPD	0.886	0.033	RAD_G MDS x-ord.	0.886	0.033
			Lumbrineridae	0.899	0.017	SBMx	0.886	0.033
			Sabellidae	0.943	0.017	SDT	0.943	0.017
			Spionidae	0.943	0.017	SMT	0.943	0.017
			SB ratio	0.943	0.017			
THS D	MPD	MPD	0.943	0.017	Spionidae	0.886	0.033	
		MDS x-ord.	0.926	0.017	Syllidae	0.943	0.017	
		RAD_G MDS x-ord.	0.943	0.017	PMJ	0.943	0.017	
		Ampharetidae	0.899	0.017	SMT	0.886	0.033	
		Cirratulidae	0.886	0.033	SDT	0.886	0.033	
		Sabellidae	0.886	0.033				
THB B	Lumbrineridae	Lumbrineridae	0.928	0.017	OMJ	0.943	0.017	
		Sabellidae	0.886	0.033	SDT	0.886	0.033	
		Spionidae	0.886	0.033				

feeders such as SMT and SDT were mainly in ranks 3 to 5 albeit with different positions over time.

At PAP, rank 1 was occupied by surface deposit feeders as SMT in 1991, 1994, 1996, 1997, 2002 and SDT in 1989 and 1999. Only in 1998, sub-surface deposit feeders as BMx became the most dominant FG (due mainly to the influx of one family: the Opheliidae). Between rank 3 and 5, two types of functional group, the deposit feeders (SBMx, BMx) and predators (PMJ) were found most of the time. Both stations were dominated by deposit feeders but the relative proportion of surface and sub-surface deposit feeders was different: surface (S) dominated at PAP and sub-surface (B) deposit feeders at Sta. M. The SB ratios had inter-annual variations also relating to RAD_G changes (Fig. 7). Correlations (Spearman) between FG ($CV < 1$) at both stations were only positive, if significant.

3.5. Polychaete community relationships with megafauna and environmental factors

In terms of statistical relationships between polychaetes and megafauna, several Sta. M polychaete community descriptors were correlated with *S. globosa* but not with any other species or megafauna indicators (Table 3). At PAP, many polychaete community descriptors were correlated with *A. rosea*, total echinoderm density, total holothurian surface deposit feeder density, and total holothurian sub-surface deposit feeder biomass (Table 3). No correlations with compatible statistical and mechanistic rationale were found with POC flux or climate indices at either locality.

4. Discussion

4.1. Inter-annual variations in abyssal polychaete community structure

Sta. M and PAP polychaetes showed significant changes in family composition, family evenness, RAD_F and RAD_G in addition to the density variations reported by Ruhl et al. (2008) and Soto et al. (2010). At both stations, structural changes occurred, the strongest being in 1998 when polychaete densities peaked at both localities, and switches in the densities of most abundant families and functional groups took place. The changes in dominance were initiated in 1996 when switches started to occur in RAD_F and RAD_G composition and evenness. At PAP, changes observed during the 'Amperima Event' lasted through 1999. However, the persistence of these changes could not be assessed at a later date than 1999 owing to low replication and gear change issues from 2002 to 2010. A study to assess gear change impact on macrofauna when sampling abyssal systems is underway as done by Bett et al. (1994) on meiofauna.

The main difference in inter-annual variations of the polychaete communities at Sta. M and PAP was the constancy of Sta. M rarefied family richness over years. Although it may be due to a sampling artefact of the FVGR, consistently missing some polychaete families, it may also be linked to differences in the regional family pool in the vicinity of both stations. Thibault et al. (2004) also observed changes in RAD and not in species richness in a long-term study of a desert rodent community, suggesting that RAD and species richness may not be as closely connected as previously thought (e.g., MacArthur, 1957).

Despite inter-annual variations, the polychaete community compositions at Sta. M and PAP showed some consistent features. These were more evident in community structure than in the specific composition of the families. Both localities shared 34 families. This is not surprising because few polychaete families are endemic to the deep sea and many have broad geographic and bathymetric distributions (Paterson et al., 2009). The Paraonidae was the only family present during each sampling time at both stations. Most species

belonging to this family are thought to be opportunistic and may be more suited to environments with seasonal and limited food supply (Smith and Hessler, 1987; Levin et al., 1999; Hilbig and Blake, 2000). Paraonidae was the dominant family at Sta. M, representing 25 to 30% of the community, except in 1998 when oligochaetes became dominant. The presence of oligochaetes in benthic macro-infaunal communities has been scarcely reported at abyssal depths. Blake (1997) described oligochaetes from Santa Maria basin and Western Santa Barbara Channel seafloor off the California coast. Oligochaetes could be present in the regional species pool associated with Sta. M and not in the one associated with PAP. Although Sta. M and PAP were sampled with different gear, recent sampling at PAP using a megacorer did not sample macrofaunal oligochaetes. Another difference between the stations was that the Paraonidae was never the dominant family at PAP; Cirratulidae was. This difference is unlikely to be an artefact of the different sampling methodologies because Sweetman and Witte (2008) also noticed this difference between Sta. M and PAP during enrichment experiments conducted with the same design of incubation chambers at the two localities. At PAP, Cirratulidae represented 25 to 30% of the polychaete community except in 1998 when Opheliidae became dominant. Differences in regional family and species pools and/or environmental settings may explain Sta. M and PAP dissimilarities in composition.

Ecological and environmental factors could also be forcing variables. Switches in polychaete RAD_F and RAD_G observed in 1998 at both localities may indicate competitive interactions in an environment where resources were variable in supply, and/or niche-based difference environmental tolerances. The main changes in 1998 were not accompanied by negative correlations between polychaete families or functional group suggesting no compensatory effect as defined by Houlahan et al. (2007). However, oligochaetes became more dominant than Paraonidae at Sta. M and Opheliidae were more dominant than Cirratulidae at PAP in 1998. The change in dominance could be due to a greater numbers of individuals collected following a particularly good recruitment due to factors unrelated to competition, although biomass data may be better at unravelling competition processes (Ernest and Brown, 2001). However, in fragile deep-sea samples there are many fragmented polychaete specimens precluding a biomass analysis at the family level. Vanreusel et al. (2001) suggested that a synchronised recruitment event occurred in Opheliidae at PAP in fall 1996 as only small juveniles were present in meiofauna at a single period of time over the time-series. Episodic growth and/or reproduction events could also influence the population structure (Smith, 1994).

The lack of obvious compensatory effects could also be related to some taxon pairs belonging to mis-matched trophic levels (Houlahan et al., 2007). Houlahan et al. (2007) suggest in such cases that, if there were compensatory effects, they may have been weaker than other forcing variables such as megafaunal abundance and sediment reworking rates, food supply or environmental factors. The inter-annual variations in polychaete family community structure and composition were not isolated in time from the other faunal changes noted in both time series, but were part of broad-scale changes observed across all abyssal faunal-size groups (Ruhl et al., 2008; Gooday et al., 2010; Kalogeropoulou et al., 2010). Such comprehensive variations suggest forcing variables rather than ecological drift as drivers of changes (Ruhl, 2008; Smith et al., 2009; Billett et al., 2010).

4.2. Inter-annual variations in polychaete community, megafauna and environmental factors

At both stations, changes in the megafauna and polychaete communities were synchronous even though the polychaete density shifts were not as great in magnitude as for the

megafauna (Ruhl and Smith, 2004; Ruhl et al., 2008; Billet et al., 2010). Several polychaete community features were positively and significantly correlated with *S. globosa* (not a dominant species) at Sta. M and *A. rosea* and other megafauna descriptors at PAP. Positive correlations between megafauna and polychaete community features indicate a lack of substantial compensatory effect. However, it does not preclude ecological interactions because several processes may be interrelated between megafauna and macrofauna over time. Holothurians have been shown to ingest the bulk of phytodetritus pulses, at least at PAP during the 'Amperima Event', and may have more direct access to the more liable food fraction (Bett et al., 2001) changing the amount and/or nature of food available for polychaetes. There is also some evidence that benthic megafauna may facilitate macrofauna density via bioturbation leading to oxygenation of sediments and mixing of organic matter to deeper depths (Thistle et al., 2008). At PAP, the positive correlation in polychaete community variations with total echinoderm density and total surface deposit feeder holothurian density provides limited evidence that facilitation processes could be important for polychaetes, particularly for polychaete surface feeders (Table 3).

In addition to ecological interactions, megafauna and macrofauna may have been influenced by the same environmental forcing variables. At Sta. M, *S. globosa* was positively and significantly correlated with a 14-month lagged NOI and an 8-month lagged POC flux (Ruhl and Smith, 2004). At PAP, POC flux quantity/quality has been proposed as a likely driver of inter-annual variations in *A. rosea* density (Billett et al., 2001, 2010; Iken et al., 2001; FitzGeorge-Balfour et al., 2010). Even if a satisfactory mechanistic understanding of pelagic–benthic coupling has not been reached yet (Lampitt et al., 2010b; Smythe-Wright et al., 2010), climate is likely to influence POC flux. Positive NAO have been associated with increased primary production and POC flux (Ruhl and Smith, 2004; Smith et al., 2009) and therefore will have effects on benthic communities. However, polychaete community descriptors did not show correlations with POC flux or climate indexes at the family level at either Sta. M or PAP.

The lack of correlation between polychaete community descriptors and POC flux, NOI or NAO does not rule out environmental factors as drivers of inter-annual variations. Synchronous variations between megafauna and polychaete density variation give some support to this hypothesis. Several reasons may account for the lack of direct correlation between environmental factors and polychaete community features: (1) small-scale spatial heterogeneity may introduce unexplained variation in time-series. Heterogeneity in space is likely to be as small as centimetre-scale for polychaetes (Jumars, 1975). However, any spatial patterns in the analysed samples were less important than time in explaining variation; (2) some important forcing variables may have not been accounted for; (3) the temporal extent of sampling may be critical to infer mechanisms underlying patterns in time. Chalcraft et al. (2004) highlighted that extending the temporal extent of time series observations increases the likelihood of including extreme and episodic data that often drive ecological patterns. With a larger data set including 1989 and 1990 polychaete density data, Ruhl et al. (2008) found a positive significant correlation between Annelida density, mostly dominated by polychaetes, and 9-month lagged NOI. Herein, in the current study, we did not have family level data for 1989 and 1990, perhaps leading to the 9-month correlation between polychaete density and NOI not being significant; (4) gaps in the time-series may prevent identification of correlations with the present method. While there is tantalising evidence to suggest non-random processes as drivers of inter-annual variations of polychaete communities, the factors behind these processes remain elusive likely because of numerous interactions between all potential forcing variables.

4.3. Inter-annual variations in polychaete community in terms of abyssal system functioning

Although POC flux did not directly correlate with density, evenness, RAD_F , RAD_C at both Sta. M and PAP, several lines of evidence suggest that POC flux played a role in polychaete community temporal variations for the following reasons: (1) higher density and major changes in RAD composition occurred during higher POC flux as seen for megafauna (Ruhl and Smith, 2004; Ruhl et al., 2008; Billett et al., 2010); (2) POC flux seems to influence at least mean polychaete density at each station. Station M had a higher mean annual POC flux and polychaete density compared to PAP: $1.9 \text{ g C m}^{-2} \text{ y}^{-1}$ at Sta. M in 1990–1996 and $1.3 \text{ g C m}^{-2} \text{ y}^{-1}$ at PAP in 1989–1999 (Baldwin et al., 1998; Smith et al., 2001; Lampitt et al., 2001). At an inter-annual scale, POC flux may drive less family structure and composition variations than density variations, because there was no statistical difference in family accumulation rate at the two localities despite the difference in organic matter input. One critical difference that may occur is the connection to and size of regional family and species pools. The mechanisms of family turnover may be different in the two areas and may be linked to factors other than POC flux (Shurin, 2007); (3) while POC flux may be an important factor for abyssal systems, it may not be the best surrogate of polychaete energy supply (Drazen et al., 2008). For example, there may be a threshold in POC flux quality/quantity to impact polychaete community structure that may be different for surface and sub-surface deposit feeders (Iken et al., 2001); (4) little is known about food web flows in deep-sea systems (Witte et al., 2003; Brandt, 2008; Soetaert and Van Oevelen, 2009). Because stable isotope analysis remains difficult to perform on abyssal polychaetes (Witte, pers. comm.), the food compounds polychaetes rely on, in particular for their reproductive biochemistry, are unknown in contrast to megafauna, such as holothurians (e.g., Wigham et al., 2003; FitzGeorge-Balfour et al., 2010). Stable isotopes and fatty acid studies conducted in deep-sea systems have confirmed that polychaetes responded to a fresh input of food (Levin et al., 1999; Witte et al., 2003; Sweetman and Witte, 2008). However, these experiments often exclude a portion of the food web such as megafauna (Witte et al., 2003) or give ambiguous results with stable isotope signatures suggesting that deposit feeders may switch mode in completely unexpected or unseen/unobserved way (e.g., Opheliidae, Sweetman and Witte, 2008). Overall, the lack of knowledge in abyssal infaunal polychaete natural history, particularly regarding reproduction, dispersal and recruitment restricts our understanding of the mechanisms that shape polychaete communities in time.

Whatever processes underpin polychaete community inter-annual variations, changes in density and functional group dominance has consequences on abyssal system functioning. Infaunal polychaetes influence not only sediment biogeochemistry (Cosson et al., 1997; Olsgaard et al., 2003), but also interact with infaunal meiofauna, protists and bacteria via competition, predation and facilitation mechanisms (Smith, 1994; Levin and Edesa, 1997; Witte et al., 2003; Van Nugteren et al., 2009). In this context, a shift from surface deposit feeder to sub-surface deposit feeder dominance or vice-versa, as seen at both localities between 1991 and 1999, may have important consequences, in particular for carbon processes. For example, Sweetman and Witte (2008) have suggested that the dominance of Cirratulidae at PAP and Paraonidae at Sta. M could explain the difference in carbon processing rates measured at the stations. Surface deposit feeders such as Cirratulidae may have access to fresher food increasing carbon degradation rates. In fact, this study suggests that not only Cirratulidae, but also surface deposit feeders in general were relatively more abundant at PAP than Sta. M. This observation points to faster bioturbation rates at Sta. M than PAP,

taking nutrients away from the surface down to the subsurface more quickly. Sta. M may be more suitable for sub-surface rather than surface deposit feeder polychaetes. Overall a clearer characterisation of the relationship between POC flux, megafauna, macrofauna and carbon process rates would help understanding of carbon cycle processes, particularly over longer time scales (Ruhl, 2007).

5. Conclusion

Abyssal infaunal polychaetes showed inter-annual variation in density, family number, family composition, and functional group rank abundance distributions at Sta. M and PAP and in family richness at PAP. In particular, in 1998, both stations had increases in polychaete density with a shift in the dominance of the most abundant family and functional group ranks. Changes occurred in synchronicity with other taxa, in particular to some holothurian species during periods of greater POC flux. These results suggest a common driver for change. There is, at present, no reason to believe that observed intra- and inter-annual changes in polychaetes would not extend to longer period changes that are expected with climate change related to global warming. However, factors behind these processes remain elusive likely due to numerous biological and environmental interactions. Future work to better constrain factors driving changes and carbon processing by polychaetes at abyssal seafloor will include: (1) the addition of new time points at each station; (2) analysis of small-spatial scale heterogeneity at each station; (3) analyses of body size distribution of the same samples over time to investigate possible reproduction and/or recruitment events and biomass variation; (4) species-level analysis of the same samples as family level results are the combination of numerous species responses, which can obscure patterns, and (5) the development of experimental approaches *in situ* on the seafloor.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.dsr.2012.12.007>.

References

- Aberle, N., Witte, U., 2003. Deep-sea macrofauna exposed to a simulated sedimentation event in the abyssal NE Atlantic: *In situ* pulse-chase experiments using ¹³C-labelled phytodetritus. *Mar. Ecol. Prog. Ser.* 251, 37–47.
- Baldwin, R.J., Glatts, R.C., Smith Jr., K.L., 1998. Particulate matter fluxes into the benthic boundary layer at a long time-series station in the abyssal NE Pacific: composition and fluxes. *Deep Sea Res. Part II* 45, 643–665.
- Bett, B.J., Malzone, M.G., Narayanaswamy, B.E., Wigham, B.D., 2001. Temporal variability in phytodetritus and megabenthic activity at the seabed in the deep Northeast Atlantic. *Prog. Oceanogr.* 50, 349–368.
- Bett, B.J., Vanreusel, A., Vincx, M., Soltwedel, T., Pfannkuche, O., Lamshead, P.J.D., Gooday, A.J., Ferrero, T., Dinert, A., 1994. Sampler bias in the quantitative study of deep-sea meiobenthos. *Mar. Ecol. Prog. Ser.* 104, 197–203.
- Billett, D.S.M., 1991. Deep-sea holothurians. *Oceanogr. Mar. Biol.: Annu. Rev.* 29, 259–317.
- Billett, D.S.M., Bett, B.J., Reid, W.D.K., Boorman, B., Priede, I.G., 2010. Long-term change in the abyssal NE Atlantic: the “*Amperima* Event” revisited. *Deep Sea Res. Part II* 57, 1406–1417.
- Billett, D.S.M., Bett, B.J., Rice, A.L., Thurston, M.H., Galéron, J., Sibuet, M., Wolff, G.A., 2001. Long-term change in the megabenthos of the Porcupine Abyssal Plain (NE Atlantic). *Prog. Oceanogr.* 50, 325–348.
- Billett, D.S.M., Rice, A.L., 2001. The BENGAL programme: introduction and overview. *Prog. Oceanogr.* 50, 13–25.
- Blake, J.A., 1997. Taxonomic Atlas of the Benthic Fauna of the Santa Maria Basin and Western Santa Barbara Channel. vol. 4. The Annelida Part I—Oligochaeta and Polychaeta: Phyllococida (Phyllococidae to Paralacydoniidae). Santa Barbara Museum of Natural History, CA.
- Bopp, L., Aumont, O., Cadule, P., Alvain, S., Gehlen, M., 2005. Response of diatoms distribution to global warming and potential implications: a global model study. *Geophys. Res. Lett.* 32, L1 9606.
- Brandt, A., 2008. Deep-sea ecology: infectious impact on ecosystem function. *Curr. Biol.* 18, R1104–R1106.
- Chalcraft, D.R., Williams, J.W., Smith, M.D., Willig, M.R., 2004. Scale dependence in the species-richness–productivity relationship: the role of species turnover. *Ecology* 85 (10), 2101–2708.
- Clarke, K.R., Gorley, R.M., 2006. Primer v6: user manual/tutorial. Primer-E, Plymouth.
- Colwell, R.K., 2009. EstimateS: statistical estimation of species richness and shared species from samples. Version 8.2. User guide and application, <<http://purl.oclc.org/estimates>>.
- Cosson, N., Sibuet, M., Galéron, J., 1997. Community structure and spatial heterogeneity of the deep-sea macrofauna at three contrasting stations in the tropical northeast Atlantic. *Deep Sea Res. Part I* 44, 247–269.
- Drazen, J.C., Baldwin, R.J., Smith Jr, K.L., 1998. Sediment community response to a temporally varying food supply at an abyssal station in the NE Pacific. *Deep Sea Res. Part II* 45, 893–913.
- Drazen, J.C., Phleger, C.F., Guest, M.A., Nichols, P.D., 2008. Lipid, sterols and fatty acids of abyssal polychaetes, crustaceans, and a cnidarian from the northeast Pacific Ocean: food web implications. *Mar. Ecol. Prog. Ser.* 372, 157–167.
- Ernest, S.K.M., Brown, J.H., 2001. Homeostasis and compensation: the role of species and resources in ecosystem stability. *Ecology* 82, 2118–2132.
- Fauchald, K., 1977. The polychaete worms: definitions and keys to orders, families and genera. *Nat. Hist. Mus. Los Angeles County Sci. Ser.* 28, 1–188.
- Fauchald, K., Jumars, J.A., 1979. The diet of worms: a study of polychaete feeding guilds. *Oceanogr. Mar. Biol.: Annu. Rev.* 17, 193–284.
- FitzGeorge-Balfour, T., Billett, D.S.M., Wolff, G.A., Thompson, A., Tyler, P.A., 2010. Phytopigments as biomarkers of selectivity in abyssal holothurians; interspecific differences in response to a changing food supply. *Deep Sea Res. Part II* 57, 1418–1428.
- Galéron, J., Sibuet, M., Vanreusel, A., Mackenzie, K., Gooday, A.J., Dinert, A., Wolff, G.A., 2001. Temporal patterns among meiofauna and macrofauna taxa related to changes in sediment geochemistry at an abyssal NE Atlantic site. *Prog. Oceanogr.* 50, 303–324.
- Glover, A., 2000. Abyssal Polychaete Assemblages along Latitudinal Gradients of Productivity in the Equatorial Pacific and North Atlantic Oceans. Thesis. University of Southampton, School of Ocean and Earth Science.
- Glover, A.G., Gooday, A.J., Bailey, D.M., Billett, D.S.M., Chevaldonné, P., Colaço, A., Copley, J., Cuvelier, D., Desbruyères, D., Kalogeropoulou, V., Klages, M., Lampadariou, N., Lejeune, C., Mestre, N.C., Paterson, G.L.J., Perez, T., Ruhl, H., Sarrazin, J., Soltwedel, T., Soto, E.H., Thatje, S., Tselepidis, A., Van Gaever, S., Vanreusel, A., 2010. Temporal change in deep-sea benthic ecosystems: a review of the evidence from recent time-series studies. *Adv. Mar. Biol.* 58, 1–95.
- Glover, A.G., Smith, C.R., 2003. The deep-sea floor ecosystem: current status and prospects of anthropogenic change by the year 2025. *Environ. Conserv.* 30, 219–241.
- Gooday, A.J., Malzone, M.G., Bett, B.J., Lamont, P.A., 2010. Decadal-scale changes in shallow-infaunal foraminiferal assemblages at the Porcupine Abyssal Plain, NE Atlantic. *Deep Sea Res. Part II* 57, 1362–1382.
- Hilbig, B., Blake, A.J., 2000. Long-term analysis of polychaete-dominated benthic infaunal communities in Massachusetts Bay, USA. *Bull. Mar. Sci.* 67 (1), 147–164.
- Houlahan, J.E., Currie, D.J., Cottenie, K., Cumming, G.S., Ernest, S.K.M., Findlay, C.S., Fuhlendorf, S.D., Gaedke, U., Legendre, P., Magnuson, J.J., McArdle, B.H., Muldavin, E.H., Noble, D., Russell, R., Stevens, R.D., Willis, T.J., Woivod, I.P., Wondzell, S.M., 2007. Compensatory dynamics are rare in natural ecological communities. *Proc. Nat. Acad. Sci.* 104 (9), 3273–3277.
- Hubbell, S.P., 1979. Tree dispersion, abundance, and diversity in a tropical dry forest. *Science* 203, 1299–1309.
- Iken, K., Brey, T., Wand, U., Voigt, J., Junghans, P., 2001. Food web structure of the benthic community at the Porcupine Abyssal Plain (NE Atlantic): a stable isotope analysis. *Prog. Oceanogr.* 50, 383–405.

- Jumars, P.A., 1975. Environmental grain and polychaetes species' diversity in a bathyal benthic community. *Mar. Biol.* 30, 253–266.
- Kalogeropoulou, V., Bett, B.J., Gooday, A.J., Lampadariou, N., Martinez Arbizu, P., Vanreusel, A., 2010. Temporal changes (1989–1999) in deep-sea metazoan meiofaunal assemblages on the Porcupine Abyssal Plain, NE Atlantic. *Deep Sea Res. Part II* 57, 1383–1395.
- Lampitt, R.S., Bett, B.J., Kiriakoulakis, K., Popova, E.E., Ragueneau, O., Vangriesheim, A., Wolff, G.A., 2001. Material supply to the abyssal seafloor in the Northeast Atlantic. *Prog. Oceanogr.* 50, 27–63.
- Lampitt, R.S., Billett, D.S.M., Martin, A.P., 2010a. The sustained observatory over the Porcupine Abyssal Plain (PAP): insights from time series observations and process studies. *Deep Sea Res. Part II* 57, 1267–1271.
- Lampitt, R.S., Salter, I., de Cuevas, B.A., Hartman, S., Larkin, K.E., Pebody, C.A., 2010b. Long-term variability of downward particle flux in the deep Northeast Atlantic: causes and trends. *Deep Sea Res. Part II* 57, 1346–1361.
- Levin, L.A., Edesa, S., 1997. The ecology of cirratulid mudballs on the Oman margin, northwest Arabian Sea. *Mar. Biol.* 128, 671–678.
- Levin, L.A., Blair, N.E., Martin, C.M., Demaster, D.J., Plaia, G., Thomas, C.J., 1999. Macrofaunal processing of phytodetritus at two sites on the Carolina margin: *In situ* experiments using ¹³C-labeled diatoms. *Mar. Ecol. Prog. Ser.* 182, 37–54.
- Lindsay, S.M., Woodin, S.A., 1995. Tissue loss induces switching of feeding mode in spionid polychaetes. *Mar. Ecol. Prog. Ser.* 125, 159–169.
- MacArthur, R.H., 1957. On the relative abundance of bird species. *Proc. Nat. Acad. Sci. U.S.A.* 45, 293–295.
- Magurran, A.E., 2004. *Measuring Biological Diversity*. Oxford Univ. Press, Oxford.
- Magurran, A.E., 2007. Species abundance distributions over time. *Ecol. Lett.* 10, 347–354.
- Magurran, A.E., McGill, B.J., 2011. *Biological Diversity-Frontiers in Measurements and Assessment*. Oxford Univ. Press, Oxford.
- Mistri, M., Fano, E.A., Ghion, F., Rossi, R., 2002. Disturbance and community pattern of polychaetes inhabiting Valle Magnavacca (Valli di Comacchio Northern Adriatic Sea, Italy). *Mar. Ecol.* 23, 31–49.
- Olsgaard, F., Brattegard, T., Holthe, T., 2003. Polychaetes as surrogates for marine biodiversity: lower taxonomic resolution and indicator groups. *Biodivers. Conserv.* 12, 1033–1049.
- Pagliosa, P.R., 2005. Another diet of worms: the applicability of polychaete feeding guilds as a useful conceptual framework and biological variable. *Mar. Ecol.* 26, 246–254.
- Paterson, G.L.J., Glover, A.G., Barrio Frojan, C.R.S., Whitaker, A., Budaeva, N., Chimonides, J., Doner, S., 2009. A census of abyssal polychaetes. *Deep Sea Res. Part II* 56, 1739–1746.
- Richardson, A.J., 2008. In hot water: zooplankton and climate change. *ICES J. Mar. Sci.* 65 (3), 279–295.
- Rouse, G., Pleijel, F., 2001. *Polychaetes*. Oxford Univ. Press, Oxford.
- Ruhl, H.A., 2007. Abundance and size distribution dynamics of abyssal epibenthic megafauna in the northeast Pacific. *Ecology* 88, 1250–1262.
- Ruhl, H.A., 2008. Community change in the variable resource habitat of the abyssal NE Pacific. *Ecology* 89, 991–1000.
- Ruhl, H.A., Ellena, J.A., Smith Jr., K.L., 2008. Connections between climate, food limitation, and carbon cycling in abyssal sediment communities. *Proc. Nat. Acad. Sci.* 105, 17006–17011.
- Ruhl, H.A., Smith Jr., K.L., 2004. Shifts in deep-sea community structure linked to climate and food supply. *Science* 305, 513–515.
- Sarmiento, J.L., Gruber, N., 2006. *Ocean Biogeochemical Dynamics*. Princeton Univ. Press, Princeton, New Jersey.
- Shurin, J.B., 2007. How is diversity related to species turnover through time? *Oikos* 116, 957–965.
- Smith, C.R., 1994. Tempo and mode in deep-sea benthic ecology: punctuated equilibrium revisited. *Palaios* 9, 3–13.
- Smith, C.R., Berelson, W., Demaster, F.D.J., Dobbs, F.C., Hammond, D., Hoover, D.J., Pope, R.H., Stephens, M., 1997. Latitudinal variations in benthic processes in the abyssal equatorial Pacific: control by biogenic particle flux. *Deep Sea Res. Part II* 44, 2291–2317.
- Smith, C.R., Hessler, R.R., 1987. Colonisation and succession in deep-sea ecosystems. *Trends Ecol. Evol.* 2, 359–363.
- Smith Jr., K.L., 1987. Food energy supply and demand: a discrepancy between particulate organic carbon flux and sediment oxygen community consumption in the deep ocean. *Limnol. Oceanogr.* 32, 201–220.
- Smith Jr., K.L., Baldwin, R.J., Ruhl, H.A., Kahru, M., Mitchell, B.G., Kaufmann, R.S., 2006. Climate effect on food supply to depths greater than 4000 m in the northeast Pacific. *Limnol. Oceanogr.* 51, 166–167.
- Smith Jr., K.L., Druffel, E.R.M., 1998. Long time-series studies of the benthic boundary layer at an abyssal station in the NE Pacific. *Deep Sea Res. Part II* 45, 573–586.
- Smith Jr., K.L., Kaufmann, R.S., Baldwin, R.J., Carlucci, A.F., 2001. Pelagic-benthic coupling in the abyssal eastern North Pacific: an 8-year time-series study of food supply and demand. *Limnol. Oceanogr.* 46, 543–556.
- Smith Jr., K.L., Ruhl, H.A., Bett, B.J., Billett, D.S.M., Lampitt, R.S., Kaufmann, R.S., 2009. Climate, carbon cycling, and deep-ocean ecosystems. *Proc. Nat. Acad. Sci.* 106, 19211–19218.
- Smythe-Wright, D., Boswell, S., Kim, Y.-N., Kemp, A., 2010. Spatio-temporal changes in the distribution of phytopigments and phytoplanktonic groups at the Porcupine Abyssal Plain (PAP) site. *Deep Sea Res. Part II* 57, 1324–1335.
- Soetaert, K., Van Oevelen, D., 2009. Modeling food web interactions in benthic deep-sea ecosystems—a practical guide. *Oceanography* 22, 128–143.
- Soto, E.H., Paterson, G.L.J., Billett, D.S.M., Hawkins, L.E., Galéron, J., Sibuet, M., 2010. Temporal variability in polychaete assemblages of the abyssal NE Atlantic Ocean. *Deep Sea Res. Part II* 57, 1396–1405.
- Steinacher, M.J.F., Frolicher, T.L., Bopp, L., Cadule, P., Cocco, V., Doney, S.C., Gehlen, M., Lindsay, K., Moore, J.K., Schneider, B., Segsneider, J., 2010. Projected 21st century decrease in marine productivity: a multi-model analysis. *Biogeosciences* 7, 979–1005.
- Sweetman, A.K., Witte, U., 2008. Response of an abyssal macrofaunal community to a phytodetrital pulse. *Mar. Ecol. Prog. Ser.* 355, 73–84.
- Thibault, K.M., White, E.P., Ernest, K.M., 2004. Temporal dynamics in the structure and composition of a desert rodent community. *Ecology* 85, 2649–2655.
- Thiel, H., 2003. Anthropogenic impacts on the deep sea. In: Tyler (Ed.), *Ecosystems of the World 28: Ecosystems of the Deep Oceans*. Elsevier, Amsterdam, pp. 427–471.
- Thistle, D., Eckman, J.E., Paterson, G.L.J., 2008. Large, motile epifauna interact strongly with harpacticoid copepods and polychaetes at a bathyal site. *Deep Sea Res. Part I* 55, 324–331.
- Van Nugteren, P., Herman, P.M.J., Moodley, L., Middelburg, J.J., Vos, M., Heip, C.H.R., 2009. Spatial distribution of detrital resources determines the outcome of competition between bacteria and a facultative detritivorous worm. *Limnol. Oceanogr.* 54, 1413–1419.
- Vanreusel, A., Cosson-Sarradin, N., Gooday, A.J., Paterson, G.L.J., Galéron, J., Sibuet, M., Vincx, M., 2001. Evidence for episodic recruitment in a small opheliid polychaete species from the abyssal NE Atlantic. *Prog. Oceanogr.* 50, 285–301.
- Wigham, B.D., Hudson, I.R., Billett, D.S.M., Wolff, G.A., 2003. Is long-term change in the abyssal Northeast Atlantic driven by qualitative changes in export flux? Evidence from selective feeding in deep-sea holothurians. *Prog. Oceanogr.* 59, 409–441.
- Witte, U., Pfannkuche, O., 2000. High rates of benthic carbon remineralisation in the abyssal Arabian Sea. *Deep Sea Res. Part II* 47, 2785–2804.
- Witte, U., Wenzhofer, F., Sommer, S., Boetius, A., Heinz, P., Aberle, N., Sand, M., Cremer, A., Abraham, W.-R., Jorgensen, B.B., Pfannkuche, O., 2003. *In situ* experimental evidence of the fate of a phytodetritus pulse at the abyssal sea floor. *Nature* 424, 763–766.
- Würzberg, L., Peters, J., Schüller, M., Brandt, A., 2011. Diet insights of deep-sea polychaetes derived from fatty acid analyses. *Deep Sea Res. Part II* 58, 153–162.