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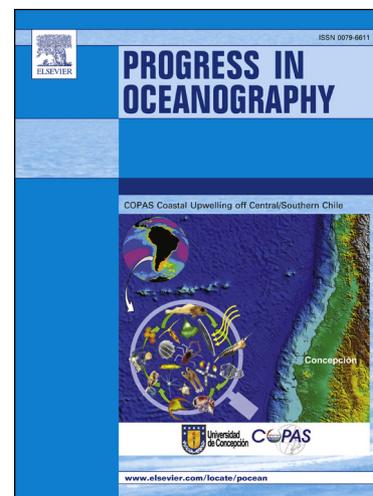
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Title

Inter-annual species-level variations in an abyssal polychaete assemblage (Sta. M, NE Pacific, 4000 m)

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Abstract

Understanding the dynamics of abyssal community structure and function has become increasingly important as deep-sea resource exploitation and climate change pressures are expected to ramp up. This time-series study investigates macrofaunal polychaete dynamics at a station in the North East Pacific (Sta. M; 35° N 123° W, 4000 m, 1991-2011). Infaunal polychaete species were identified and their proxy biomass and proxy energy use rate estimated. The assemblage comprised 167 species, having a composition consistent with other abyssal areas globally. Significant changes in univariate and multivariate parameters (rank abundance distribution, Simpson's diversity index, and species and functional group composition) were detected across 1991-2011. However, no change in biomass or energy use rate was apparent through the time-series. The largest changes in the polychaete assemblage coincided with both an increase in sinking particulate organic carbon flux to the seafloor in 2007, and a 40 km relocation of the sampling location to a site 100 m shallower, preventing a conclusive assessment of which might drive the observed variation. Analyses prior to the change of sampling location showed that the polychaete assemblage composition dynamics were primary driven by food supply variation. Changes in several species were also lagged to changes in POC flux by 4 to 10 months. The polychaete fauna exhibited a significant positive relationship between total density and total energy use rate, suggesting population-level tracking of a common resource (e.g. POC flux food supply). Neither compensatory nor energetic zero-sum dynamics were detected among the polychaete assemblage, but the results suggest that the latter occur in the macrofaunal community as a whole. The results do indicate (a) potential control of species composition, and the density of individual key species, by food supply, when the time-series prior to the sampling location was analysed separately, and (b) generally sensitive detection of environmental change by species-level analysis of the abyssal polychaete assemblage.

Key word

Deep sea; Polychaeta; Time-series; Ecology; Abyssal; Compensatory dynamics; Zero-sum dynamics

1 Introduction

Temporal changes in food supply, quantified as particulate organic carbon (POC) flux, have been shown to influence abyssal benthic communities (e.g. Billett et al., 2010; Ruhl and Smith, 2004; Smith et al., 2009). However, the mechanisms by which environmentally-driven resource variations impact the structure and function of abyssal faunas are challenging to disentangle. A better understanding of the ecological and biogeochemical processes behind these dynamics is necessary to assess: (a) how deep-sea systems will respond to climate change (Jones et al., 2014; Mora et al., 2013), (b) increasing seabed resource exploitation (Ramirez-Llodra et al., 2011), and (c) how long-term carbon cycles such as remineralisation, bioturbation, and burial (Smith et al., 2009), are influenced by benthic community dynamics. Significant inter-annual changes have been observed in abyssal macrofaunal communities (North East Pacific, Ruhl et al., 2008; North East Atlantic, Laguionie-Marchais et al., 2013; Soto et al., 2010) as exemplified by polychaetes, typically the dominant macrofaunal taxon (Paterson et al., 2009).

One of the longest time-series studies of abyssal system dynamics has been conducted at Station M (Sta. M) in the North-East Pacific. Over 25 years of study, the POC flux reaching the benthos underwent significant variations both in quantity and quality (Smith et al., 2006; Smith et al., 2013). In turn, POC flux variations have driven changes in the structure and function of the benthic community, in particular the mobile epibenthic megafauna (Kuhnz et al., 2014; Ruhl and Smith, 2004; Ruhl et al., 2014).

The extent to which mechanisms of megafaunal change can be generalised to other abyssal faunal groups is not known. At the Porcupine Abyssal Plain in the North East Atlantic, changes in megafaunal composition and density were also observed at macro- and meio-faunal levels (Billett et al., 2010). At Sta. M, the macrofauna is dominated by polychaetes that varied between 1991-2005 in terms of total density, family and functional group compositions, and in family rank abundance distributions (RADs; Laguionie-

Marchais et al., 2013). The latter authors showed that potential relationships between POC flux and polychaete assemblage attributes were complex. Polychaete and megafauna density changes occurred in apparent positive correlation suggesting that common external factors may be driving dynamics across the different faunal groups. Sta. M polychaetes have been shown to respond within days to the input of fresh phytodetritus during feeding experiments (Jeffreys et al., 2013; Sweetman and Witte, 2008; Witte et al., 2003). Variations in the Sta. M polychaete fauna might then be expected to depend directly on food supply, with the deep sea generally regarded as a food limited environment (Rex and Etter, 2010).

Resource limitation is a central concept in many ecological theories, whether niche-based or neutral (Hubbell, 2001; Tilman, 1982). It gives an ultimate limit to total community-level carrying capacity (e.g. Ernest and Brown, 2001). Under compensatory dynamics, density compensation should occur where any increase in the density of one species is compensated by a decrease in others, **Hypothesis A:** species covariance will be significantly negative (see 2.4 below). Note that species level compensatory dynamics may occur with or without community level compensation (Gonzalez and Loreau, 2009). Ernest et al. (2008) suggested that energetic demand may be a more suitable currency than density to address the occurrence of compensatory dynamics. Further they suggest that under a metabolism-based zero-sum framework there could be a direct trade-off between population density and mean individual energy use rate (see also Ernest et al., 2009), **Hypothesis B:** under zero-sum dynamics, there will be a significant negative relationship between density and mean individual energy use.

In this study we examine a range of polychaete assemblage descriptors (density, biomass, rate of energy use, diversity, species composition, functional group composition, and rank abundance distributions) to test: (a) if inter-annual variations in assemblage structure and dynamics are detectable; (b) if assemblage variation is linked to food supply; and (c) if there is evidence for compensatory dynamics (**Hypothesis A**) and/or zero-sum dynamics (**Hypothesis B**).

2 Methods

2.1 Study area, macrofauna sampling and species identification

We used data from twenty-two research cruises (Table 1) from 1991 to 2011, conducted at Sta. M in the North East Pacific (Smith and Druffel, 1998). To accommodate the water depth limitations of the remotely operated vehicles *Tiburón* and *Doc Ricketts* used during later collections, the sampling area was relocated some 40 km between the 1991-2005 period (34° 50' N, 123°00' W, c. 4100 m water depth) and the present (35° 10' N, 122° 59' W, c. 4000 m water depth; Fig. 1). Macrofauna were sampled with a free-vehicle grab respirometer (FVGR; Smith et al., 2001), a system comprised of four 413-cm² grabs that collected the top 15 cm of the sediment column (Table 1). After recovery, sediment from each grab was sieved through a 300 µm mesh and preserved in 10% borax-buffered formalin solution.

Table 1

Station M macrofauna samples assessed, date and location (Lat. for latitude and Long. for longitude), number of grabs (and deployments) available per month.

Year	Month	Grab (deployments)	Lat. °N	Long. °W
1991	Jun	7 (2)	34.90	123.05
	Oct	3 (1)	34.88	123.11
1992	Feb	5 (2)	34.88	123.12
	Jun	5 (2)	34.91	123.11
	Jul	3 (1)	34.78	122.95

1993	Oct	6 (2)	34.85	123.15
	Feb	3 (1)	34.79	122.92
	Jul	3 (1)	34.82	123.07
	Nov	5 (2)	34.80	122.93
1995	Feb	5 (2)	34.93	123.12
1996	Feb	4 (2)	34.72	122.98
	Jun	3 (1)	34.68	122.94
	Oct	5 (2)	34.69	122.90
1998	Aug	3 (2)	34.78	123.03
2005	Feb	3 (1)	34.85	123.20
	Jun	3 (1)	34.93	123.25
2009	Feb	4 (1)	35.12	122.92
	Nov	4 (1)	35.14	122.92
2010	May	4 (1)	35.15	122.90
	Nov	4 (1)	35.16	122.92
2011	May	4 (1)	35.15	122.93
	Nov	4 (1)	35.14	122.93

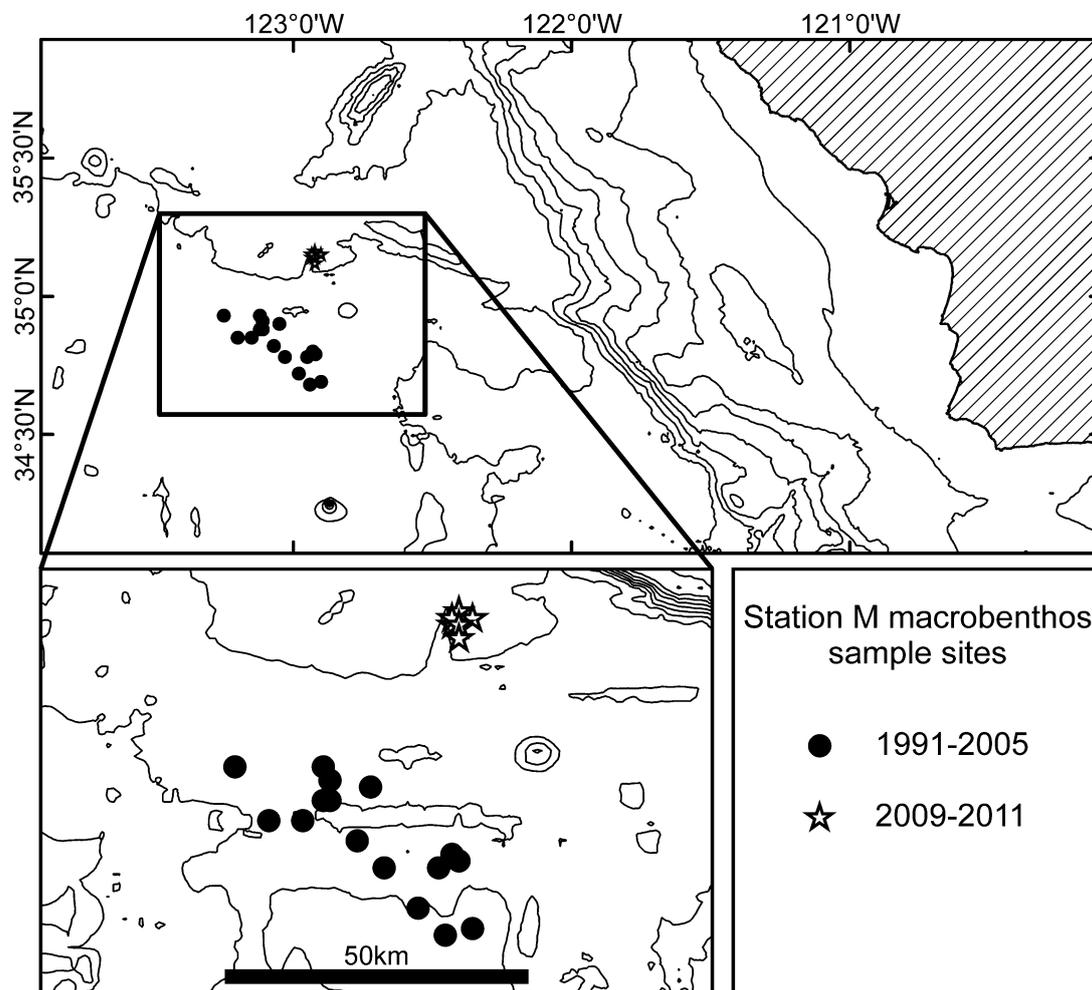


Fig. 1. Chart showing location of Station M area, North East Pacific, 220 km off the California coast.

Inset: sampling sites occupied during the two periods of study, 1991-2005 (solid symbols), 2009-2012 (open symbols).

All polychaete specimens recovered from the grab samples were identified to species level using high-power microscopes (Zeiss Discovery v20 Stereo and high power Leica DM 5000 B), published identification keys, and original taxonomic descriptions (e.g. Fauchald, 1972, 1977, 1981). Only individuals with a head were considered in the subsequent analyses, to give an objective assessment of density and diversity with respect to individual counts (Paterson et al., 2009). Of the 3800 headed-individuals, 3646 could be classified to family level and 3077 to species level. Many species appeared to be undescribed, and were designated as sp. A, sp. B, and so forth. Each family was assigned to a single functional group among those defined by Fauchald and Jumars (1979), as detailed in Laguionie-Marchais et al. (2013) and in Table 2.

Table 2

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

1. Feeding Mode	2. Mobility	3. 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		

2.2 Proxies of polychaete biomass and energy use rate

Of the 3077 identified specimens, only 100 were complete individuals, consequently a proxy of polychaete body volume was employed. The width of the first chaetiger (W_1) was measured for all specimens (see Paterson et al., 2006) and cubed as a proxy for individual body mass ($=W_1^3$). Proxy rates of energy use (respiration, R) were then estimated for each specimen using standard mass scaling (e.g. $\text{mass}^{3/4}$, Brown et al., 2004), such that proxy energy use rate $R = (W_1^3)^{3/4} = W_1^{2.25}$. Neither a proportionality coefficient, nor a temperature coefficient was applied as *in situ* temperature was near-constant at Sta. M (Ruhl et al., 2014). Hereafter, the terms proxy biomass and proxy energy use rate are simply referred to as biomass and energy use rate.

2.3 Analyses of polychaete assemblage temporal variations

For the statistical analyses, the primary sampling unit was FVGR deployment. Data from individual grabs were pooled within deployment to yield deployment-level data (i.e. grabs regarded as subsamples, not independent replicates). The deployment-level data were then averaged within cruise to provide 'month-level' data ($n = 22$), and the month-level data were then averaged within year to yield give 'year-level' data ($n = 10$) (i.e. sampled months are given equal weight within year). It should be noted that time of sampling was not fixed within year. A change of primary sampling area occurred during the time-series. In terms of POC flux, the expected difference between the two sampled depths (4000 and 4100m) would be of order 2% (Martin et al., 1987), a quantity greatly out-scaled by recorded temporal variability in POC flux at Sta. M (Smith et al., 2013, Fig. 2). Nevertheless, to acknowledge the potential significance of the shift in sampling area during the time-series, where possible, we conducted separate tests of the 1991-2011 and 1991-2005 data (i.e. with and without the influence of the change in location).

Analysis of Variance (ANOVA, Minitab v17.1; see e.g. Sokal and Rohlf, 2012) of $\log(x+1)$ transformed month data was used to test temporal and sampling location differences for total density (D_{tot}), total biomass (B_{tot}), and total rate of energy use (R_{tot}). Diversity was assessed with estimated species richness (S_{est}), an asymptotic richness estimator (Chao1), the Shannon index, and Simpson's index (Magurran, 2004). In each case, diversity was estimated for (a) an individual-based rarefied sample of 91 individuals, and (b) a sample-based rarefaction to the two grab level, encompassing a range of 90-113 individuals (EstimateS, v.9.1.0; Colwell et al., 2012). Comparisons of diversity were made by visual inspection of the confidence intervals produced by the EstimateS package (see e.g. Chao et al., 2014; Colwell, 2013).

Multivariate analyses of the polychaete assemblage were conducted at both species- and functional group-levels. Similarity in composition was calculated as the Bray-Curtis index, based on $\log(x+1)$ transformations of density, biomass and energy use rate at monthly and yearly scales. 2d non-metric

multi-dimensional scaling ordinations (MDS; Kruskal and Wish, 1978; Primer v.6; Clarke and Gorley, 2006) were then applied to examine the resultant similarity matrices (S_D , species density composition; S_B , species biomass composition; S_R , species energy use rate composition; S_{FD} , for functional group [FG] density composition; S_{FB} , for FG biomass composition; S_{FR} , for FG energy use rate composition). Where possible, inter-annual and sampling site changes were assessed using analysis of similarities (ANOSIM; Primer v.6; Clarke, 1993; 999 permutations employed). A nested ANOSIM, with years nested in site, was also run to investigate temporal variation without the influence of site.

MDS x- and y-ordinates were used as summary variables of species composition (MDS- x_D , species density; $-x_B$, species biomass; $-x_R$, species energy use rate; $-x_{FD}$, functional group [FG] density; $-x_{FB}$, FG biomass; $-x_{FR}$, FG energy use rate). These parameters were tested for potential correlations with spatial variables (latitude, longitude, water depth), and temporal variables (date, measures of food supply), using the Spearman's rank method (r_s , Minitab v17.1; see e.g. Sokal and Rohlf, 2012). For these assessments of potential temporal and spatial variations, several transformations (no transformation, square-root, fourth-root, $\log[x+1]$, presence-absence) were applied to the data in order to assess both (a) the robustness of the results, and (b) the relative importance of abundance- and identity-related changes. The measures of potential food supply tested were: (a) total POC flux in the 6-month preceding period, (b) in the 12-month preceding period, and (c) total polychaete density, as a proxy of food consumption. The POC flux data (Fig. 2) represented a near-continuous monthly dataset obtained as a composite measure from sediment trap data at 50 and 600 mab, as provided by Smith et al. (2013).

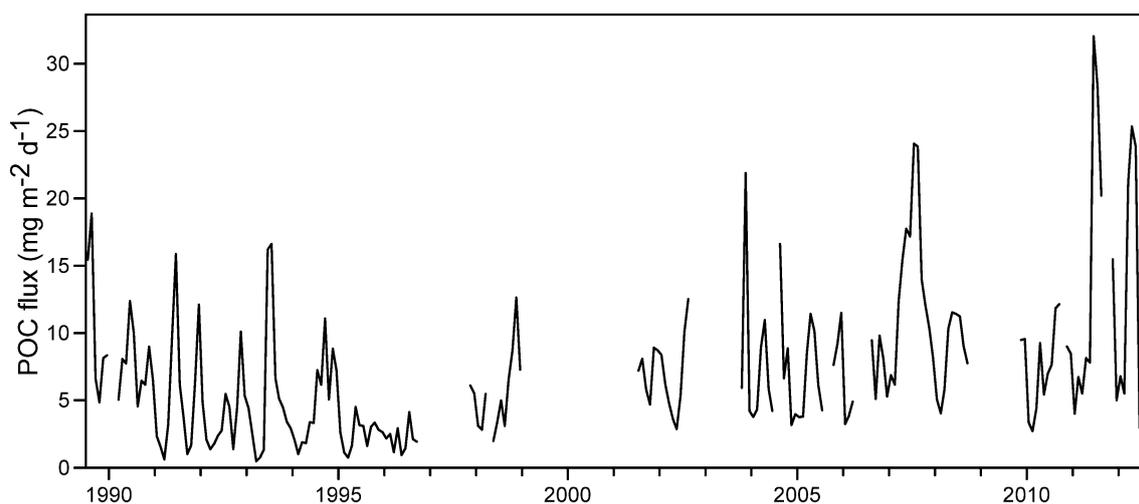


Fig. 2. Temporal variation in particulate organic carbon (POC) flux to the seabed at Station M (data from Smith et al., 2013).

Variations in polychaete assemblage composition (density, biomass, energy use rate) were also assessed by examining rank abundance distributions. Changes in species rank switching were visualised using a method based on top-down correlation (see e.g. Zar, 1999). For each parameter separately, only the top 50 species, determined across all deployments, were included in these analyses. These top 50 species were then ranked within deployment and the rank values (1 high; 50 low) converted to Savage scores (Savage, 1956; i.e. in the 50 species case, rank 1 becomes 4.50, and rank 50 becomes 0.02), giving greater weight to higher ranks. The resultant species by deployment matrices of Savage scores were then plotted using principal component analysis (using a correlation approach; Primer v.6).

2.4 Analyses of potential mechanisms of change

To further assess the potential importance of food supply, we examined the correlations of polychaete assemblage parameters with 1-11 month lags in particulate organic carbon flux (for 1991-2011 and 1991-2005 periods separately). To reduce the multiplicity of correlations, we limited species-level testing to density and biomass parameters only, and included only the most abundant species. In an attempt to

reduce the reporting of ‘false positive’ results, we followed the method of Benjamini and Hochberg (1995) in controlling the false discovery rate.

Compensatory dynamics as defined by Houlahan et al. (2007), (**hypothesis A**) were tested using the variance ratio (VR) method (Ernest and Brown, 2001; Hallett et al., 2014; Klug et al., 2000; Schluter, 1984). Both species and functional group density, biomass and energy use rate were assessed in this manner (Eq. 1), with $\text{var}(X)$ the variance across sampling units of a given parameter at the assemblage level, and $\text{var}(Y_i)$ the variance of the same parameter at species level, for species $i = 1$ to n

$$VR = \frac{\text{var}(X)}{\sum_{i=1}^n \text{var}(Y_i)} \quad \text{Eq. 1}$$

VR was then tested for difference from unity with a χ^2 -test ($VR \cdot n$ distributed as χ^2 ; Schluter, 1984). VR values significantly less than unity suggest negative covariance among species, potentially indicative of compensatory dynamics. These tests were conducted at year, month and deployment level to assess potential compensatory dynamics at different levels of data organisation.

The energetic zero-sum dynamics hypothesis, (Ernest et al., 2008, 2009), was tested by correlation (Spearman’s rank method, r_s) of geometric mean individual polychaete energy use rate with polychaete total density, D_{tot} (**hypothesis B**). Similarly, the correlation between the total energy use rate and total density was also computed.

3 Results

3.1 Taxonomic results

A total of 3077 specimens were identified belonging to 167 species. Only 14 species were recorded every year: two Cirratulidae, *Aphelochaeta* sp. A and *Chaetozone* sp. A, one Cossuridae, *Cossura* cf. *rostrata*, one Fauveliopsidae, *Laubieriopsis* cf. *brevis*, one Lumbrineridae, *Abyssoninoe* sp. B, one Nephtyidae, *Aglaophamus* sp. A, one Opheliidae, *Ophelina* cf. *farallonensis*, five Paraonidae species, *Aricidea* *abbranchiata*, *Aricidea* sp. A, B, and D, *Levinsenia* sp. A, one Pilargidae, *Ancistrostylis* sp. A, one Syllidae, *Sphaerosyllis* sp. A. Overall, 33 species were recorded through at least 80 % of the time-series, 65 species in at least 50 % of the time-series and 50 species were recorded only in a single year. Across all samples, five species represented 30% of the total density: *Cossura* cf. *rostrata*, *Sphaerosyllis* sp. A, *Paradoneis* sp. A, *Levinsenia* sp. A and *Aphelochaeta* sp. A. One species represented 30% of the total biomass (*Notomastus* cf. *latericeus*) with four species comprising 50% of the total biomass: *N.* cf. *latericeus*, *N.* sp. A, *N.* sp. B and *Paradoneis* sp. A.

3.2 Polychaete density, biomass, energy use rate and diversity

Polychaete assemblage total density, D_{tot} , varied between years, Fig. 3a. The highest D_{tot} was recorded in 1998 (1232 ± 134 SE ind m^{-2}) and the lowest in 2005 (377 ± 170 SE ind m^{-2}) c. 3.5 fold range over the study period. Total biomass (Fig. 3c), B_{tot} , ranged 4.4 fold and total energy use rate (Fig. 3e), R_{tot} , 3.4 fold over 1991-2011. ANOVA indicated significant differences between years only in the case of D_{tot} in 1991-2011 and 1991-2005 (Table 3). No significant variation in D_{tot} , B_{tot} , or R_{tot} was detected between sampling locations. There was no evidence of significant variation in species diversity (Fig. 3b,d).

Table 3

ANOVA results (F statistic with degrees of freedom, dof) for variation in polychaete total density (D_{tot}), total biomass (B_{tot}), and total energy use rate (R_{tot}) by year and location. Significant ($p < 0.05$) results highlighted in bold.

Period	Polychaete	Factor	F (dof)	p-value
1991-2011	D_{tot}	Year	5.04 (9, 21)	0.001
		Location	0.33 (1, 29)	0.568
	B_{tot}	Year	1.52 (9, 21)	0.205
		Location	0.75 (1, 29)	0.394
	R_{tot}	Year	1.92 (9, 21)	0.105
		Location	0.57 (1, 29)	0.457
1991-2005	D_{tot}	Year	5.36 (6, 18)	0.002
	B_{tot}	Year	1.28 (6, 18)	0.315
	R_{tot}	Year	1.93 (6, 18)	0.131

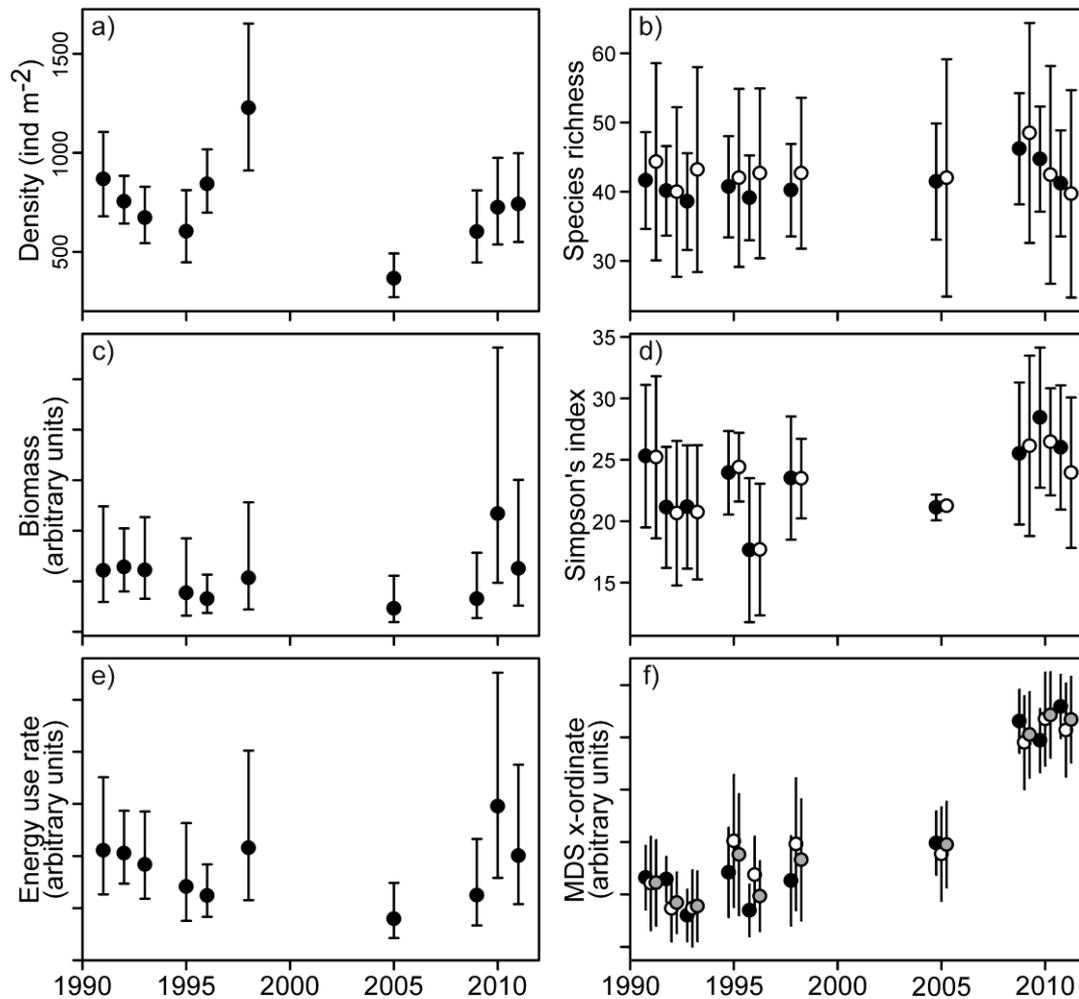


Fig. 3. Temporal variation in annual mean polychaete assemblage parameters, shown with estimated 95% confidence intervals: a) total density, D_{tot} ; b) rarefied species richness (solid symbol, 91 individuals; open symbol, two grabs); c) total biomass, B_{tot} ; d) rarefied Simpson's index (inverse form; solid symbol, 91 individuals; open symbol, two grabs); e) energy use rate, R_{tot} ; f) species composition represented by yearly x-ordinate of 2d non-metric multi-dimensional scaling ordination (solid symbol, density, $MDS-x_D$; open symbol, biomass, $MDS-x_B$; shaded symbol, energy use rate, $MDS-x_R$).

3.3 Species and functional group composition

Species and functional group composition varied significantly by density, biomass, and energy use rate across years and between 1991-2005 and 2009-2011 (Fig. 3f, Fig. 4 and Table 4). Assessed over 1991-2005 only, species composition by density, and functional group composition by density also exhibited significant differences between years ($p < 0.05$, Table 4). When assessed via two-way nested ANOSIM, S_D , S_B , and S_R showed highly significant ($p = 0.008$) differences between periods (locations), but no significant ($p > 0.05$) differences between years.

Table 4

ANOSIM results of one- and two-way nested comparisons of year and/or location for polychaete species composition (by density, S_D ; biomass, S_B ; energy use rate, S_R) and functional group composition (by density, S_{FD} ; biomass, S_{FB} ; energy use rate, S_{FR}). Significant ($p < 0.05$) results highlighted in bold.

Period	ANOSIM	Variable	Factor	R	p-value		
1991-2011	1-Way	S_D	Year	0.409	0.001		
			Location	0.768	0.001		
		S_B	Year	0.299	0.007		
			Location	0.696	0.001		
		S_R	Year	0.300	0.005		
			Location	0.700	0.001		
		S_{FD}	Year	0.303	0.005		
			Location	0.215	0.068		
		S_{FB}	Year	0.100	0.152		
			Location	0.169	0.083		
		S_{FR}	Year	0.099	0.164		
			Location	0.107	0.082		
			2-Way nested	S_D	Year	0.171	0.051
					Location	0.859	0.008
				S_B	Year	0.050	0.317
					Location	0.897	0.008
S_R	Year			0.050	0.306		
	Location			0.897	0.008		
S_{FD}	Year			0.236	0.012		
	Location			0.183	0.192		
S_{FB}	Year			0.030	0.366		
	Location			0.250	0.108		
S_{FR}	Year			0.027	0.354		
	Location			0.272	0.100		
1991-2005	1-Way			S_D	Year	0.185	0.047
				S_B	Year	0.066	0.271
				S_R	Year	0.066	0.269

S_{FD}	Year	0.232	0.015
S_{FB}	Year	0.026	0.386
S_{FR}	Year	0.026	0.382

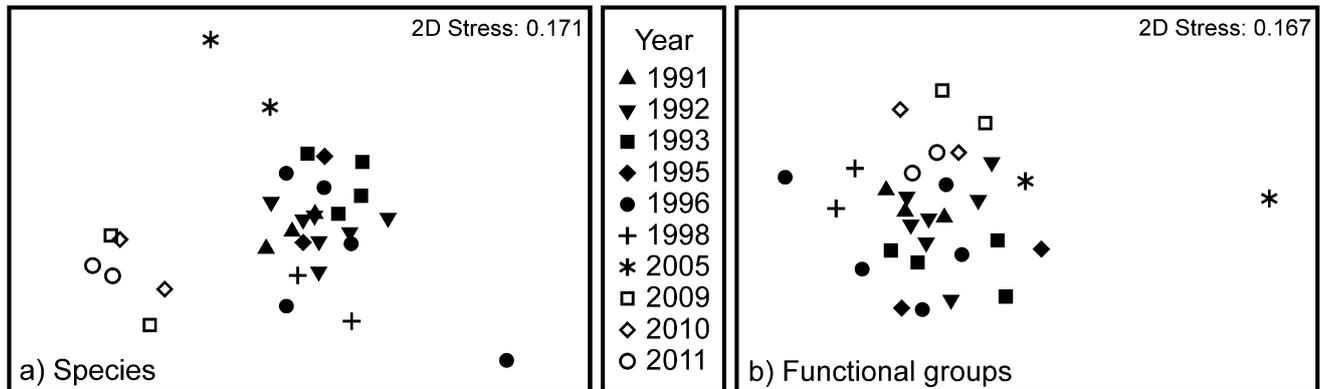


Fig. 4. 2d non-metric multi -dimensional scaling ordination, (a) polychaete species density composition, S_D , and (b) polychaete functional group density composition, S_{FD} .

Correlations with selected spatial and temporal variables showed that regardless of data transformation, the strongest correlations with primary faunal variation (MDS-x) during 1991-2011 were with latitude and depth (Table 5). Secondary variation (MDS-y) appeared to be linked with potential resource supply (POC, density). When assessed over 1991-2005 alone (i.e. the influence of location removed), the primary variation appeared to be linked with potential food supply.

Table 5

Spearman's rank correlations of selected environmental variables with descriptors of polychaete species composition by density (2d MDS ordinates), for the full dataset (period 1991-2011) and the period 1991-2005 alone. Note that the absolute value of the correlation is shown. For each polychaete descriptor, the two strongest, significant ($p < 0.05$), correlations are highlighted. (Long., longitude; Lat., latitude; POC6M, particulate organic carbon flux in preceding 6-months; 12M, preceding 12-months; Den., total polychaete density; ord., ordinate; Transformations: None, no transformation; Sqrt, square-root; Fort, forth-root; Log, $\log(x+1)$; P/A, presence-absence).

	Period 1991-2011							Period 1991-2005							
	Long.	Lat.	Depth	Date	POC6M	POC12M	Den.	Long.	Lat.	Depth	Date	POC6M	POC12M	Den.	
Lat.	0.144							0.792							
Depth	0.087	0.802						0.377	0.624						
Date	0.444	0.264	0.404					0.132	0.398	0.125					
POC6M	0.167	0.628	0.550	0.251				0.474	0.519	0.404	0.090				
POC12M	0.138	0.746	0.600	0.281	0.875			0.580	0.589	0.343	0.236	0.839			
Den.	0.164	0.328	0.271	0.250	0.404	0.308		0.304	0.334	0.232	0.194	0.415	0.301		
MDS x-ord.	None	0.165	0.668	0.545	0.508	0.235	0.483	0.190	0.272	0.214	0.166	0.096	0.537	0.417	0.676
	Sqrt	0.094	0.748	0.615	0.455	0.293	0.516	0.150	0.288	0.244	0.148	0.143	0.593	0.398	0.667
	Fort	0.090	0.782	0.674	0.463	0.414	0.584	0.225	0.158	0.078	0.220	0.014	0.470	0.477	0.068
	Log	0.216	0.632	0.516	0.493	0.201	0.465	0.125	0.323	0.317	0.279	0.033	0.563	0.491	0.471
	P/A	0.148	0.658	0.597	0.552	0.473	0.576	0.157	0.175	0.037	0.321	0.198	0.229	0.220	0.148
MDS y-ord.	None	0.174	0.373	0.292	0.210	0.606	0.444	0.732	0.355	0.526	0.254	0.030	0.147	0.150	0.629
	Sqrt	0.217	0.263	0.160	0.165	0.515	0.297	0.643	0.104	0.214	0.017	0.137	0.243	0.258	0.286
	Fort	0.280	0.205	0.285	0.061	0.521	0.404	0.154	0.182	0.146	0.351	0.390	0.058	0.130	0.099
	Log	0.193	0.266	0.155	0.149	0.519	0.318	0.645	0.316	0.397	0.083	0.151	0.099	0.010	0.641
	P/A	0.032	0.100	0.096	0.291	0.168	0.274	0.208	0.153	0.078	0.171	0.448	0.213	0.307	0.003

As visualised by the principal component analysis of the Savage scores, species rank distributions by density (RAD_D), and energy use rate (RAD_R) varied substantially between periods (1991-2005 and 2009-2011, i.e. locations), with only modest, if any, variation between years within locations (Fig. 5a,d). The underlying drivers of this distinction between locations were examined by reference to rank switching among selected key species, e.g. note opposing patterns in the Savage scores of: (a) *Paradoneis* sp. A

(Fig. 5b) and *Chaetozone* sp. A (Fig. 5c) density, and (b) *Notomastus* cf. *latericeus* (Fig. 5e) and *Notomastus* sp. C (Fig. 5f) energy use rate.

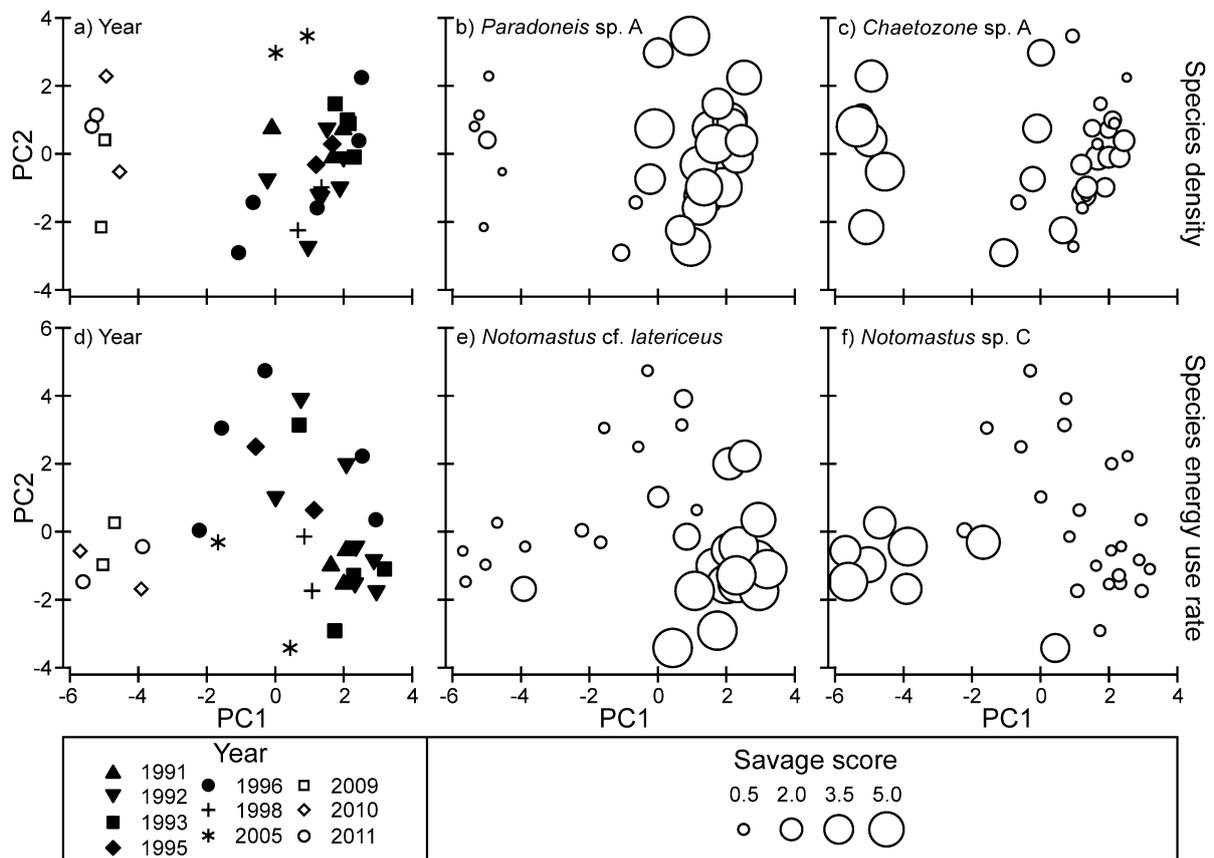


Fig. 5. Principal component ordinations analysis of species rank Savage scores by density (a-c) and energy use rate (d-e), with year coding (a,d), and bubble plots of selected species' Savage scores.

3.4 Analyses of potential mechanisms of change

No significant cross-correlation was detected between POC flux and D_{tot} , B_{tot} or R_{tot} at the month scale, over 1991-2011, or 1991-2005. There was, however, significant correlation of POC flux with species composition (MDS-x) by density, biomass, and energy use rate (Table 6) over 1991-2011. Significant correlations were also detected between POC flux and some species and functional groups (Table 6). In

particular, *Cossura cf. rostrata*, *Aricidea* sp. B and BMx exhibited significant correlations with similar lags during both 1991-2011 and 1991-2005 (i.e. with and without the location change).

Table 6

Spearman's rank correlations of biological variables with 1-11 month lags of particulate organic carbon flux, for the full dataset (period 1991-2011) and the period 1991-2005 alone. Correlations are highlighted by significance level (for period 1991-2011 $p \leq 0.019$, FDR=0.02, $p \leq 0.011$, FDR=0.01; for period 1991-2005 $p \leq 0.021$, FDR=0.02, $p \leq 0.011$, FDR=0.01; FDR, false discovery rate). (Variables: B, biomass; D, density; E, energy use rate. Parameters: MDS-x, x-ordinate of 2d non-metric multidimensional scaling ordination; BMx and PMJ, feeding groups as detailed in Table 2).

	Biological parameter	Variable	Particulate organic carbon flux, months of lag										
			2	3	4	5	6	7	8	9	10	11	
Period 1991-2011	<i>Abyssoninoe</i> sp. B	B	0.167	0.180	0.395	0.629	0.314	0.329	0.141	0.217	0.226	0.414	
	<i>Aricidea</i> sp. A	D	0.007	0.052	0.319	0.206	-0.061	-0.117	-0.068	-0.081	0.010	0.592	
	<i>Aricidea</i> sp. B	D	0.205	-0.139	-0.167	-0.276	0.204	0.108	0.546	0.578	0.163	0.046	
	<i>Chaetozone</i> sp. A	B	0.332	0.165	0.188	0.220	0.350	0.299	0.288	0.525	0.326	0.386	
	<i>Cossura cf. rostrata</i>	D	-0.536	-0.524	-0.651	-0.565	-0.519	-0.347	-0.155	-0.391	-0.619	-0.577	
	<i>Cossura cf. rostrata</i>	B	-0.402	-0.489	-0.591	-0.529	-0.388	-0.115	0.096	-0.168	-0.544	-0.358	
	<i>Notomastus</i> sp. B	D	-0.013	-0.199	-0.280	-0.473	-0.539	-0.356	-0.282	-0.203	-0.202	-0.425	
	<i>Notomastus</i> sp. B	B	-0.054	-0.241	-0.350	-0.532	-0.528	-0.164	-0.166	-0.182	-0.321	-0.512	
	<i>Orbiniidae</i> sp. A	B	-0.466	-0.590	-0.313	-0.135	-0.164	-0.018	-0.303	-0.409	-0.339	-0.187	
	<i>Paradoneis</i> sp. A	D	-0.250	-0.341	-0.247	-0.405	-0.310	-0.150	-0.340	-0.518	-0.241	-0.166	
	<i>Paradoneis abbranchiata</i>	D	-0.214	-0.272	-0.177	-0.469	-0.560	-0.667	-0.279	-0.243	-0.243	-0.351	
	<i>Paradoneis abbranchiata</i>	B	-0.149	-0.230	-0.248	-0.393	-0.546	-0.369	-0.279	-0.232	-0.341	-0.431	
	<i>Sphaerosyllis</i> sp. A	D	-0.142	-0.243	-0.220	-0.402	-0.641	-0.461	-0.263	-0.219	-0.473	-0.405	
	<i>Sphaerosyllis</i> sp. A	B	-0.093	-0.244	-0.182	-0.323	-0.555	-0.276	-0.185	-0.105	-0.421	-0.333	
	BMx	D	-0.211	-0.282	-0.453	-0.545	-0.487	-0.243	-0.121	-0.211	-0.439	-0.518	
	PMJ	D	-0.052	-0.244	-0.102	-0.277	-0.537	-0.370	-0.284	-0.195	-0.406	-0.263	
	MDS-x	D	-0.496	-0.382	-0.365	-0.482	-0.662	-0.501	-0.329	-0.552	-0.684	-0.643	
MDS-x	B	0.518	0.465	0.458	0.606	0.636	0.461	0.277	0.481	0.649	0.562		
MDS-x	E	-0.532	-0.477	-0.484	-0.626	-0.620	-0.421	-0.265	-0.494	-0.672	-0.581		
Period 1991-2005	<i>Ancistrosyllis</i> sp. A	B	0.141	0.029	0.179	0.218	0.656	0.550	0.121	-0.003	0.146	0.244	
	<i>Aricidea</i> sp. B	D	0.138	-0.212	-0.158	-0.364	0.095	0.090	0.531	0.637	0.068	-0.133	
	<i>Cossura cf. rostrata</i>	D	-0.416	-0.393	-0.642	-0.440	-0.283	-0.025	0.128	-0.228	-0.611	-0.367	
	<i>Cossura cf. rostrata</i>	B	-0.279	-0.462	-0.636	-0.474	-0.144	0.182	0.335	-0.050	-0.571	-0.165	
	BMx	D	-0.049	-0.137	-0.388	-0.570	-0.336	0.029	0.046	-0.063	-0.404	-0.433	

The variance ratios of species and functional group density, biomass, and energy use rate were either not significantly different from unity ($p > 0.05$), or were significantly greater than unity ($p < 0.05$) over 1991-

2011, 1991-2005 and 2009-2011 (Table 7). Consequently, we detected no evidence of compensatory dynamics (**hypotheses A**).

Table 7

Variance ratio of species (S) and functional group (FG) density (D), biomass (B), and energy use (R) over 1991-2011, 1991-2005 and 2009-2011 at deployment-, month-, and year-level with associated number of data points (n). Values significantly different ($p < 0.05$) from unity are highlighted in bold. .

Period/Location	Level	n	S-D	S-B	S-R	FG-D	FG-B	FG-R
1991-2011	Deployment	31	3.043	1.375	1.650	1.824	1.085	1.193
	Month	22	3.566	1.302	1.676	2.069	0.966	1.125
	Year	10	5.157	1.493	1.672	2.277	1.155	1.556
1991-2005	Deployment	25	3.737	1.465	1.882	2.119	1.285	1.513
	Month	16	5.248	1.404	2.157	2.678	1.242	1.688
	Year	7	8.460	1.238	1.200	2.960	1.199	1.595
2009-2011	Deployment	6	1.016	1.580	1.824	0.905	0.915	0.972
	Month	6	1.016	1.580	1.824	0.905	0.915	0.972
	Year	3	2.116	2.424	2.729	1.850	1.484	1.539

No significant relationship was detected between yearly total density and (geometric) mean individual energy use rate over 1991-2011 ($r_s = -0.285$, $p = 0.425$, $n = 10$) or 1991-2005 ($r_s = -0.424$, $p = 0.294$, $n = 7$). Consequently, we detected no direct evidence of “zero-sum dynamics” (**hypothesis B**). In contrast, total density and total energy use rate were significantly correlated over 1991-2011 ($r_s = -0.782$, $p = 0.008$, $n = 10$) and 1991-2005 ($r_s = 0.821$, $p = 0.023$, $n = 7$).

4 Discussion

4.1 Sta. M polychaete assemblage

The Sta. M polychaete assemblage was composed of families and genera often reported in abyssal sediments (Paterson et al., 2009). Cossuridae, Paraonidae, Syllidae, Cirratulidae, Lumbrineridae and

Capitellidae dominated polychaete density and biomass over 1991-2011. The main difference in polychaete composition between Sta. M and other well studied abyssal areas (NE North Atlantic: Porcupine, Madeira, Tagus, and Cape Verde Abyssal Plains; Equatorial Pacific: DOMES, ECHO1, and PRA sites) was the low relative abundance of Spionidae (Glover, 2000; Glover et al., 2001, 2002). When comparing Sta. M and the Porcupine Abyssal Plain (NE Atlantic), Laguionie-Marchais et al. (2013) suggested that the difference in Spionidae relative abundance might be at least partly explained by differences in surface productivity and consequently POC flux to the seafloor. Members of the family Spionidae have previously been noted for their occurrence in organically enriched sediments (Grassle and Morse-Porteous, 1987). They are considered to be potential opportunists (Grassle and Grassle, 1974; Smith and Hessler, 1987), capable of rapid population growth and switching from suspension to deposit feeding when food is in abundance (Blake, 1996). Detailed comparison of abyssal sites is hampered by the difficulty in assigning specimens to formally (or informally) described species, a continuing problem in deep-sea polychaete taxonomy and ecology (Paterson et al., 2009).

4.2 Inter-annual variation in the polychaete assemblage and its energetics

Our examination of polychaete species-level variation provides the most detailed view of temporal changes in the Sta. M macrofaunal assemblage undertaken to date. Significant, and substantive, change was observed in a number of descriptors, including total density and multivariate measures (rank distributions, species and functional group composition), between the periods 1991-2005 and 2009-2011. Thus, it was not possible to conclusively isolate sampling location or temporal change per se. In contrast, no significant change was detected in yearly measures of biomass, energy use rate, or species richness (though note that some variation in species dominance between locations was suggested, Fig. 3d). Across the time-series (1991-2011), polychaete energy use rate (respiration) ranged by a factor of 3 among annual means. These variations were of similar magnitude to that recorded for the Sta. M megafauna (factor of 4, Ruhl et al., 2014). In addition to respiration, polychaetes perform other important carbon

cycle functions such as bioturbation and sediment reworking (Olsgaard et al., 2003; Rouse and Pleijel, 2001), that may all vary with a similar magnitude.

4.3 Assemblage variation links to environmental variables

In a number of attributes, the polychaete assemblage appeared to vary with food supply, as indicated by several significant correlations with POC flux. Interpretation is, however, complicated by the coincidence of the change in sampling location with an apparent increase in organic matter supply to the seabed in the latter years of the time-series. For the macrofauna sampling years between 1991 and 2005, mean annual POC flux was estimated as $1.7 \text{ gCm}^{-2}\text{yr}^{-1}$, for the period 2009-2011 the corresponding value was $3.7 \text{ gCm}^{-2}\text{yr}^{-1}$ (data from Smith et al., 2013). No simultaneous sampling of the polychaete fauna at both locations was undertaken, such that we were not able to directly assess that change. Consequently, we consider two non-mutually exclusive options in assessing the nature of the changes detected in the polychaete assemblage: (a) that it may be consistent with continuous change in species composition over a 100 m bathymetric interval (i.e. between locations), likely driven by a suite of co-varying environmental factors, and/or (b) that it may have been driven by a change in POC flux to the seabed.

Evidence of the former option (a) seems to be suggested by the substantive change in faunal composition (Fig. 3f, 4a, 5), despite no corresponding change in faunal abundance or diversity (Fig. 3a-e). There has been change in community structure, but no change in headline community function (e.g. resource use). Such change is potentially consistent with change in the background environment (location), not change in food supply (POC flux). Nonetheless, evidence of the latter option (b) also seems to be apparent in our analyses. Secondary variation in polychaete assemblage composition (MDS-y) appeared to be correlated with food supply over 1991-2011, a potential relationship that was maintained as primary variation (MDS-x) when analysed over 1991-2005 alone (Table 5). Similarly, two important species, *Cossura* cf. *rostrata* (rank 1 across the time-series) and *Aricidea* sp. B (rank 8) exhibited significant lagged-

correlations with POC flux at consistent lags in analyses of both periods (1991-2011, and 1991-2005; Table 6). Some species were consistently positively correlated with potential food supply (e.g. *Aricidea* sp. B), while others were consistently negatively correlated (e.g. *C. cf. rostrata*), suggesting differential responses to food supply, as previously noted among holothurians at Sta. M (Ruhl, 2007).

Significant changes have occurred more generally among Sta. M megafauna during both periods, (i.e. at both locations, 1991-2005 [1989-2004; Ruhl et al., 2014] and 2009-2011 [2006-2012; Kuhnz et al., 2014]). It is conceivable that small active surface deposit feeding megafauna may have intercepted much of the incoming organic matter flux, reducing the magnitude of temporal variation experienced by the infaunal benthos (Bett et al., 2001). We should also note that the FVGR sampler may also suffer from a bow-wave effect that impacts the quantitative recovery of smaller polychaetes (e.g. Bett, 1994). The latter may be the most reactive to organic enrichment as noted in the case of an opheliid in the Porcupine Abyssal Plain time-series. Vanreusel et al. (2001) reported that 95% of the opheliids were restricted to the unconsolidated superficial sediment layer, i.e. the most subject to sampler bow-wave effect. The only sampling of polychaetes conducted in 2007 at Sta. M was done during a feeding experiment (Jeffreys et al., 2013). The latter authors reported that Spionidae was one of the three most dominant families at that time. As Jeffreys et al. (2013) used a different sampler, it is not possible to ascribe the presence of Spionidae to either a reduced bow-wave effect or an increase of opportunistic surface deposit feeders under enrichment conditions as observed in other deep-sea systems (Levin et al., 1999; Smith and Hessler, 1987). On abyssal plains, greater numbers of surface deposit feeders have previously been linked to higher POC flux (Laguionie-Marchais et al., 2013).

Resolving the influence of above average POC flux deposition events on abyssal benthic polychaetes may become important under various climate change scenarios. Smith et al. (2013) noted that the frequency and magnitude of such events had increased at Sta. M since 2007, with a particularly marked salp deposition event in 2012. Continued time-series research will be needed to evaluate if and how the

polychaete assemblage responds to such large POC flux events and which aspects of these events (quality, quantity) might trigger assemblage change. It is conceivable, for example, that salp-derived POC flux may have sufficiently different characteristics to drive assemblage responses despite minimal change in total organic carbon supply.

4.4 Mechanisms of polychaete assemblage structure dynamics

Compensatory dynamics *sensu* Houlihan et al. (2007) were not detected in Sta. M polychaete assemblage density, biomass, or energy use rate (**Hypothesis A**, not supported). Overall, a similar lack of compensatory dynamics was also reported for Sta. M megafauna by Ruhl et al. (2014), as has been noted in other ecosystems (Houlihan et al., 2007). Hubbell (2001) suggested that compensatory mechanisms could be hidden when studying species that are not at the same trophic level. Although the Sta. M polychaete fauna belong to several different feeding groups that are all ultimately dependant on POC flux (Jeffreys et al., 2013), little is known about their species-specific feeding characteristics. Recent experiments conducted at Sta. M have shown that the polychaetes have a $\delta^{15}\text{N}$ value indicating omnivory (Jeffreys et al., 2013). Given their relatively low densities and small body sizes, performing gut content analyses remains a challenge, and the life-histories of deep-sea polychaetes remain speculative (Jumars et al., 2015). Finally, compensatory dynamics may be most detectable in assemblages with limited species richness; the Sta. M polychaete fauna is rich, with 167 species recorded to date, many as singletons.

Energetic zero-sum dynamics were not observed among the Sta. M polychaete assemblage (**Hypothesis B**, not supported). Total polychaete density, although not correlated with mean individual energy use, was significantly and positively correlated with total energy use rate. This may indicate synchronous change, as might be expected if density was tracking a common resource. Energetic zero-sum dynamics may, nevertheless, operate among the wider Sta. M macrofaunal assemblage. Using total measured density and biomass to estimate mean individual mass (data from Drazen et al., 1998) over the period 1991-2005,

macrofaunal density was negatively correlated with mean individual mass ($r_s = -0.564$, $p = 0.006$, $n = 7$). Although calculating mean individual mass by this method is not ideal, the significant relationship might suggest that energetic zero-sum dynamics operate among the macrofauna in total, if not among the polychaetes alone.

It is worth considering a number of other issues in connection with the detection of zero-sum dynamics among the Sta. M polychaete assemblage: (a) In common with the concept of ‘constant final yield’ (Weiner and Freckleton, 2010), the detection of zero-sum dynamics may be limited to particular circumstances; both most readily detected where the resource in question is constant and limiting. At Sta. M there is substantial intra- and inter-annual variation in organic matter supply to the seafloor (Smith et al., 2013). (b) Continuing change in assemblage body size distribution once resource limitation/carrying capacity has been reached (e.g. successional change introducing biomass dominants, Warwick, 1986) also improves the likelihood of detecting zero-sum dynamics. Indeed, the absence of zero-sum dynamics in the polychaete assemblage may suggest temporal stability in the body size structure. (c) Using a body mass proxy rather than direct measurements may have impacted our detection of zero-sum dynamics. However, as less than 3% of the specimens were complete, the use of a proxy was inevitable in this case. Nevertheless, the proxies were based on direct body size measurements of each specimen, and consequently the best possible predictors of population biomass and respiration. We suspect that a direct assessment of variations in the body size distributions of density, biomass, and energy use would help resolve a number of these issues.

5 Conclusions

The polychaete assemblage at Sta. M appeared to exhibit temporal stability in some attributes (biomass, energy use rate, diversity) while displaying significant changes in density, composition and rank abundance distribution between 1991-2005 and 2009-2011. Across the same time period there has been

substantial intra- and inter-annual variation in the supply of organic matter to the seabed. The changes in species and functional group composition that we have detected appear to be associated with both (a) change in food supply, and (b) change in the location of the Sta. M study area. Although we cannot definitively weight the relative influence of these factors, it seems likely that both were responsible for substantive change. Analyses prior to the change of sampling location showed that the polychaete assemblage composition dynamics were primarily driven by food supply variation. Changes in several species were also lagged to changes in POC flux by 4 to 10 months. We did not detect compensatory, or zero-sum dynamics, in the Sta. M polychaete assemblage; however, zero-sum dynamics operated at the macrofaunal community level. Overall the synchronous change in polychaete density and energy use rate suggested the tracking of a common resource, presumed to be particulate organic carbon flux. Our results do suggest the sensitive detection of environmental change (food supply and/or bathymetry) through the species-level study of deep-sea polychaete assemblages.

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Contributors

Dr. Laguionie-Marchais conducted the laboratory work, identified all polychaetes, analysed the data, wrote and edited the manuscript.

Dr. Paterson conceived and designed the project. He helped identified polychaetes, analysed the data and participated in the critical revision of the manuscript and gave final approval of the article.

Dr. Bett analysed the data, participated in the critical revision of the manuscript and figures and gave final approval of the article.

Dr. Smith collected the data and participated in the critical revision of the manuscript and gave final approval of the article.

Dr. Ruhl conceived and designed the project. He helped collected the data, analysed the data and participated in the critical revision of the manuscript and gave final approval of the article.

Highlights

- the polychaete assemblage comprised 167 species over the time-series;
- species structure and composition changes between 1991-2005/2009-2011;
- species composition dynamics were linked to POC flux variation;
- dynamics suggest possible tracking of POC flux rather than zero-sum dynamics.

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