

# Spatial and temporal patterns of benthic polychaete communities on the northern Gulf of Mexico continental slope

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**Abstract** Community structure and abundance of benthic polychaetes along a transect on the central northern Gulf of Mexico continental slope were examined. Spatial, seasonal, short- (~1 year), and long-term (~16–17 years) temporal comparisons of assemblages were conducted with samples collected in 1983–1984 and 2000–2001. Polychaete abundance did not consistently decrease between 325 and 1500 m, but sharply decreased between 1500 and 2100 m. On the upper slope (325–1500 m) polychaete abundance approximately doubled between fall 1983 and spring 1984, but had returned to initial levels by fall 1984. On the lower slope (2500 m) seasonal variations in abundance were less pronounced. The taxonomic composition of the polychaete assemblages changed continuously along a depth gradient; however, temporal variations of the assemblages at all water depths were generally minor. This study provides a baseline for naturally occurring spatial

and temporal dynamics of benthic polychaete communities on the northern Gulf of Mexico continental slope.

**Keywords** Temporal dynamics · Distribution patterns · Deep sea · Abundance · Diversity

## Introduction

The premise that benthic communities in the deep sea are stable over time has been challenged by a number of contrasting findings (e.g., Billett et al., 2001; Galéron et al., 2009; Laguionie-Marchais et al., 2013). Seasonal events such as algae blooms, long-term cycles such as the El Niño Southern Oscillation (ENSO), and stochastic events affect benthic communities not only in shallow water but also in bathyal and abyssal depths (Aller, 1997; Drazen et al., 1998; Levin et al., 2002).

Yet, little is known about temporal dynamics of deep-sea habitats because only few deep-sea locations have been resampled over time scales of years or decades (for a list see Glover et al., 2010). This is because deep-sea sampling is technically demanding and expensive and available resources are usually allocated to unexplored parts of the world's oceans. However, in order to understand temporal patterns of the deep-sea benthos, it is crucial to resample the same locations.

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We studied the benthic polychaete fauna along a bathymetric gradient on the central northern continental slope of the Gulf of Mexico. Numerous sampling stations on the transect were sampled multiple times during different seasons and years (Table 1), allowing for analyses of seasonal, short-, (~1–2 years) and long-term (~16–17 years) dynamics of the polychaete communities. The two surveys from which we obtained data were the “Northern Gulf of Mexico Continental Slope Study” (NGoMCS) in the years 1983–1985 (Gallaway, 1988) and the “Deep Gulf of Mexico Benthos Study” (DGoMB) in the years 2000–2002 (Rowe & Kennicutt, 2009). Both were initiated by the Minerals Management Service (now Bureau of Ocean Energy Management, Research and Enforcement) to create baseline data of benthic assemblages and to study potential impacts of oil and gas exploration and exploitation at the northern Gulf of Mexico continental margin (Pequegnat, 1983).

Polychaetes are among the most prominent benthic macrofauna organisms in any marine benthic sample. On the northern Gulf of Mexico continental slope, polychaetes accounted for 37.5% of macrofaunal specimens (Rowe & Kennicutt, 2009). Haedrich et al. (2008) found that meiofauna biomass was the best predictor for polychaete species richness on the northern Gulf of Mexico continental slope. The different polychaete families have a wide variety of morphology, mobility, and diets (Fauchald & Jumars, 1979; Reuscher & Shirley, 2014; Jumars et al., 2015). These diverse adaptations make them an interesting indicator group because environmental variables affect different taxa and different functional groups in different ways. Furthermore, polychaetes may be a viable surrogate for benthic macrofauna diversity measurements (Olsgard et al., 2003).

In our study we addressed the questions: (1) Did polychaete abundance or community structure change along the depth gradient of the transect? (2) Did polychaete abundance or community structure change between different seasons or years? We tested the hypotheses that polychaete abundance and composition change considerably along the depth gradient. We also tested the hypothesis that abundance and composition are stable over time. Understanding the natural dynamics in polychaete assemblages of the northern Gulf of Mexico continental slope as a baseline will be vital for benthic impact studies of the 2010 Deepwater

Horizon oil spill (Montagna et al., 2013) and possible future disturbances.

## Materials and methods

### Study sites

Samples were collected during three cruises of the NGoMCS in fall 1983 and spring and fall of 1984 (Gallaway, 1988) and two cruises of the Deep Gulf of Mexico Benthos Study (DGoMB) in spring 2000 and summer 2001 (Rowe & Kennicutt, 2009) (Table 1). Sampling stations were arranged along a transect, with a depth range of approximately 325–3000 m (Fig. 1). Station names consist of “C” (for central transect) and numbers. The original transect consisted of five stations, with C1 being the shallowest and C5 being the deepest. During the third NGoMCS cruise six additional stations, increasing in depth from C6 to C12 (C10 was not sampled for macrofauna) were sampled (Fig. 1). During the first DGoMB cruise C1, C4, C7, and C12 were resampled, and a new station C14 was added. During the second DGoMB cruise only C7 was revisited (Table 1). The maps of the sampling sites were generated with ArcMap.

Additional transects sampled during the NGoMCS and DGoMB surveys were not included in this study because they were not sampled multiple times.

### Sampling methods and replication

All samples were collected with box corers. A TAMU (Texas A&M University) modified version of the Gray-O’Hara modified J&O box corer was used during the NGoMCS cruises and a GOMEX box corer was used for the DGoMB surveys. Six replicate cores were analyzed for NGoMCS stations with core sizes of 0.0569 m<sup>2</sup> during the first cruise and 0.0475 m<sup>2</sup> during the remaining cruises. Three replicate cores with a size of 0.1725 m<sup>2</sup> were analyzed for DGoMB. In both surveys 300 µm sieves were used to retain macrofaunal organisms.

### Taxonomy

Polychaete species lists of NGoMCS were obtained from Gallaway et al. (1988). Polychaete species lists of DGoMB were retrieved from unpublished material

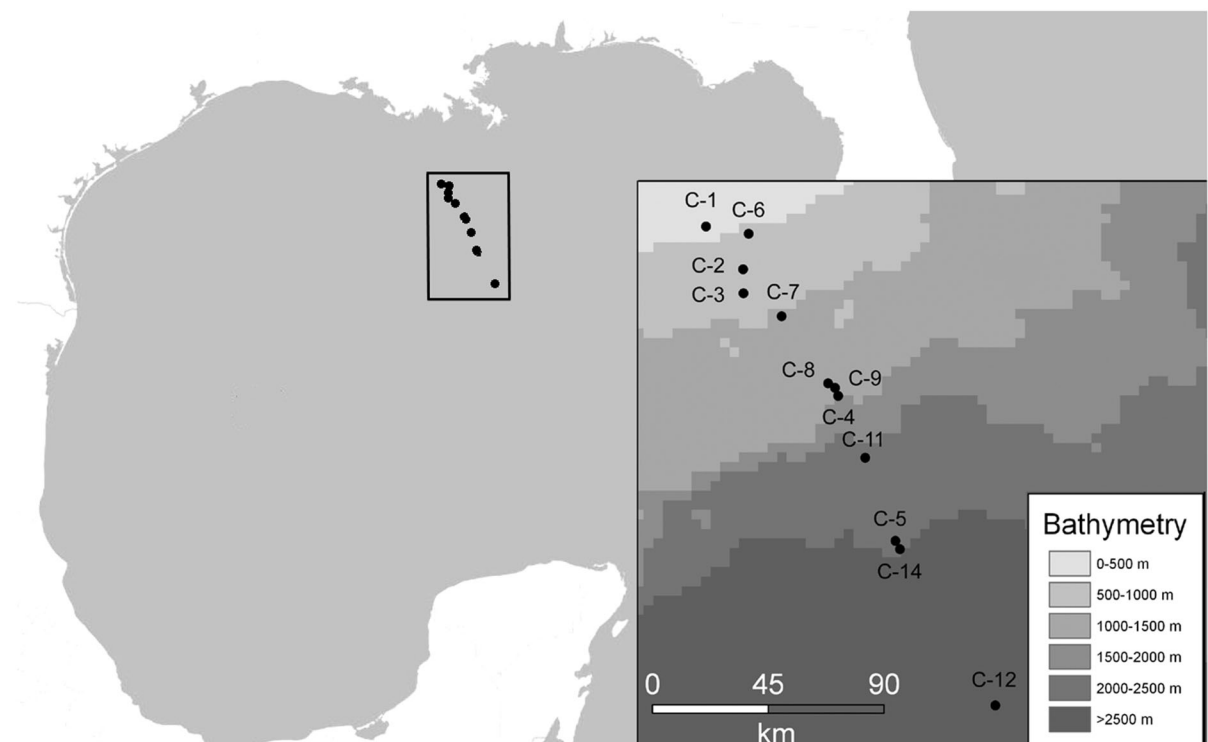
**Table 1** List of sampling stations

Study	Sampling date	Station	Latitude	Longitude	Depth (m)	Replicates	Core size (m <sup>2</sup> )	Sampled area (m <sup>2</sup> )	Abundance (n/m <sup>2</sup> )	No. of families
NGoMCS	Nov 1983	C-1	28.053 N	90.235 W	320	6	0.0569	0.341	1,224	30
			28.062 N	90.255 W	356					
NGoMCS	Nov 1983	C-2	27.905 N	90.098 W	603	6	0.0569	0.341	1,503	31
			27.907 N	90.102 W	632					
NGoMCS	Nov 1983	C-3	27.752 N	90.113 W	845	6	0.0569	0.341	1,095	28
			27.827 N	90.142 W	853					
NGoMCS	Nov 1983	C-4	27.472 N	89.760 W	1325	6	0.0569	0.341	1,069	30
			27.492 N	89.785 W	1440					
NGoMCS	Nov 1983	C-5	26.963 N	89.517 W	2467	6	0.0569	0.341	627	20
			26.990 N	89.543 W	2490					
NGoMCS	Apr 1984	C-1	28.055 N	90.253 W	348	6	0.0475	0.285	2,018	28
				90.260 W	358					
NGoMCS	Apr 1984	C-2	27.905 N	90.098 W	595	6	0.0475	0.285	2,849	33
			27.908 N	90.103 W	605					
NGoMCS	Apr 1984	C-3	27.752 N	90.113 W	845	5	0.0475	0.238	2,269	33
			27.827 N	90.142 W	853					
NGoMCS	Apr 1984	C-4	27.472 N	89.780 W	1320	6	0.0475	0.285	2,137	33
			27.473 N	89.783 W	1355					
NGoMCS	Apr 1984	C-5	26.948 N	89.570 W	2377	6	0.0475	0.285	832	27
			26.965 N	89.621 W	2400					
NGoMCS	Nov 1984	C-1	28.068 N	90.256 W	353	5	0.0475	0.238	1,187	27
			28.069 N	90.265 W	361					
NGoMCS	Nov 1984	C-2	27.912 N	90.073 W	625	6	0.0475	0.285	877	27
			27.914 N	90.109 W	639					
NGoMCS	Nov 1984	C-3	27.826 N	90.117 W	870	6	0.0475	0.285	965	29
			27.827 N	90.121 W	892					
NGoMCS	Nov 1984	C-4	27.461 N	89.785 W	1433	6	0.0475	0.285	1,544	23
			27.469 N	89.789 W	1506					
NGoMCS	Nov 1984	C-5	26.953 N	89.565 W	2482	6	0.0475	0.285	375	20
			26.958 N	89.570 W	2540					
NGoMCS	Nov 1984	C-6	28.029 N	90.098 W	482	6	0.0475	0.285	1,628	26
			28.030 N	90.100 W	505					
NGoMCS	Nov 1984	C-7	27.736 N	89.983 W	1007	6	0.0475	0.285	2,639	36
			27.744 N	90.987 W	1032					
NGoMCS	Nov 1984	C-8	27.507 N	89.817 W	1147	6	0.0475	0.285	1,512	30
			27.510 N	89.823 W	1232					
NGoMCS	Nov 1984	C-9	27.486 N	89.790 W	1389	6	0.0475	0.285	1,898	26
			27.496 N	89.798 W	1507					
NGoMCS	Nov 1984	C-11	27.245 N	89.690 W	2075	6	0.0475	0.285	291	20
			28.250 N	89.693 W	2124					
NGoMCS	Nov 1984	C-12	26.380 N	89.232 W	2915	6	0.0475	0.285	256	17
			26.387 N	89.243 W	2959					
DGoMB	May 2000	C-1	28.059 N	90.249 W	334	3	0.1725	0.5175	1,397	33
			28.060 N		336					

**Table 1** continued

Study	Sampling date	Station	Latitude	Longitude	Depth (m)	Replicates	Core size (m <sup>2</sup> )	Sampled area (m <sup>2</sup> )	Abundance (n/m <sup>2</sup> )	No. of families
DGoMB	May 2000	C-4	27.452 N 27.459 N	89.763 W 89.786 W	1452 1476	3	0.1725	0.5175	970	33
DGoMB	May 2000	C-7	27.728 N 27.733 N	89.977 W 89.984 W	1066 1080	3	0.1725	0.5175	1,407	38
DGoMB	May 2000	C-12	26.379 N 26.383 N	89.241 W	2920 2922	2	0.1725	0.3450	380	18
DGoMB	May 2000	C-14	26.930 N	89.564 W 89.571 W	2487 2495	3	0.1725	0.5175	539	23
DGoMB	June 2001	C-7	27.730 N 27.735 N	89.981 W 89.985 W	1045 1072	3	0.1725	0.5175	1,115	36

Station data of replicates are lumped and indicated as ranges



**Fig. 1** Map of the Gulf of Mexico showing the location of the transect. The *inset* is a detailed map showing the station locations of the transect and bathymetry

of Wang (2004). Additional unsorted replicates of DGoMB were identified by the first author of this study.

We used the taxonomic sufficiency approach (Ellis, 1985) and converted the species lists into lists of polychaete families. One reason for this decision was that specimens were identified by three different

individuals [G.F. Hubbard (NGoMCS and DGoMB), Y. Wang (DGoMB), and M.G. Reuscher (DGoMB)]. Inconsistencies in species identifications between the different taxonomists would impair the analysis. In contrast, family-level identifications of polychaetes are straightforward and far less prone to misidentifications.

Most importantly, we chose to use taxonomic surrogates because a large portion of the collected polychaete specimens could not be identified to species level. The main reasons were: (1) Specimens were in overall poor condition; (2) Fragmented specimens lacked crucial morphological characters; (3) Poorly resolved taxonomy of some taxa; (4) The difficulty in drawing the line between intraspecific variation and interspecific distinguishing characters in some of the taxa. Of the polychaetes sampled during the three NGoMCS cruises, approximately 18, 46, and 26%, respectively, could not be identified to species level. Excluding these considerable portions of polychaetes from the analyses would have caused an extensive loss of information. Furthermore, the unidentifiable specimens were not a uniform or random subset of the species list. Instead, the portion of unidentified species was consistently higher for some families than for others. For example, polychaetes of the prominent families Terebellidae and Acrociiridae were almost entirely identified to only genus or family level. Ampharetidae, Hesionidae, and Phyllodocidae had consistently low rates of species identification. Other families had a large variance in the success rate of species identifications between different cruises. For example, only about 9% of the family Maldanidae could be identified to species in the samples of the second NGoMCS cruise. In contrast, 95% of the specimens of the third NGoMCS cruise were identified to species. Therefore, the exclusion of the unidentified polychaetes would have introduced taxonomic artifacts, skewing the results of our multivariate community analysis.

We considered family-level identification as a taxonomic surrogate to be a more solid and less skewed approach for the polychaete community analysis. The use of taxonomic surrogates of the family level is an efficient and robust alternative for benthic community analyses (Dethier & Schoch, 2006; Terlizzi et al., 2009). Polychaetes, in particular, have been successfully used in taxonomic sufficiency studies (Olsgard & Somerfield, 2000; Muniz & Pires-Vanin, 2005; Soares-Gomes et al., 2012).

#### Analysis of polychaete abundance

Only complete specimens or anterior fragments were counted to avoid multiple counts of fragmented specimens. We converted the counts to number of

individuals per square meter ( $n/m^2$ ) to account for unequal sample sizes. Average abundances and standard errors were computed in Microsoft Excel. Bar graphs were generated in Microsoft Excel. A 2-way analyses of variance (ANOVA) was performed in R to test for significant differences in polychaete abundances between different sampling periods and sampling stations, described by the model  $Y_{ijk} = \mu + \alpha_j + \beta_k + \alpha\beta_{jk} + e_{(i)jk}$ , where  $Y_{ijk}$  is the dependent response variable (abundance),  $\mu$  is the overall sample mean,  $\alpha_j$  is the main effect of sampling periods  $j = 1-5$ ,  $\beta_k$  is the main effect of sampling stations  $k = 1-12$ ,  $\alpha\beta_{jk}$  is the interaction term between sampling period and sampling station, and  $e_{(i)jk}$  is the random error for replicates  $i = 1-6$ . One-way ANOVAS were performed in R to test for significant differences between sampling periods at individual sampling stations and between sampling stations during individual sampling periods.

#### Multivariate analyses of polychaete communities

For measuring the spatial turnover and temporal dynamics of the continental slope polychaete fauna, replicates of each station were pooled. Stations with less than 100 polychaete specimens were excluded because the statistical error is too large for such a small sample size (Wolda, 1981). Abundances were square-root transformed to decrease the relative weight of abundant taxa over rare ones in the analysis. The Morisita–Horn index (Horn, 1966) was used to measure similarity between assemblages of different stations or sampling periods ( $\beta$ -diversity). The Morisita–Horn index was calculated with the equation

$$C_\lambda = \frac{2 \sum n_{1i} \times n_{2i}}{(\sum n_{1i}^2 / N_1 + \sum n_{2i}^2 / N_2) \times N_1 \times N_2}$$
, where  $n_{1i}$  and  $n_{2i}$  are the counts of species  $i$  in the first and second sample, respectively, and  $N_1$  and  $N_2$  are the numbers of individuals in the first and second sample, respectively. This index outperforms other indices when samples of unequal sizes are compared (Wolda, 1981). Calculations of  $\beta$ -biodiversity values were performed in Microsoft Excel. Ordination of the similarity matrix by means of non-metric multidimensional scaling (MDS) was performed with Primer 6 (Clarke & Gorley, 2006). The same program was used to perform “analyses of similarity” (ANOSIM) to test for significant differences among different sampling periods. “Similarity percentage” (SIMPER) was performed to

measure the contributions of different polychaete families to the dissimilarity among samples of different sampling periods. For the ANOSIM procedure, we used the Bray–Curtis similarity index when the sample size compared was equal and the Morisita–Horn index when sample size was unequal. For the SIMPER procedure we converted the abundance of each family of the compared samples to  $n/m^2$  to account for unequal sample sizes.

## Results

### Abundance

Polychaete abundance was significantly different between sampling stations ( $F = 11.52$ ,  $df = 11$ ,  $P < 10^{-13}$ ) and sampling periods ( $F = 13.66$ ,  $df = 4$ ,  $P < 10^{-8}$ ). The interaction between sampling station and period was also significant ( $F = 2.39$ ,  $df = 11$ ,  $P = 0.01$ ), indicating that temporal variability was not equal among different stations.

In neither one of the NGoMCS samples did we observe a consistent, or even an exponential, decrease with depth in polychaete abundance between 325 and 1500 m. Density at these upper slope stations, including C1–C4, C6, C8, and C9, was approximately 1000–2000  $n/m^2$  during fall and approximately 2000–3000  $n/m^2$  during spring (Table 1, Fig. 2). Station C7 was exceptional for its unusually high polychaete abundance in November 1984 ( $2639 \pm 594$   $n/m^2$ ). During all three sampling events there was a sharp decline of abundance in the lower slope stations, including C-11 (2100 m), C-5 (2400–2500 m), and C-12 (about 2900 m). These stations had average densities of 265–627  $n/m^2$ .

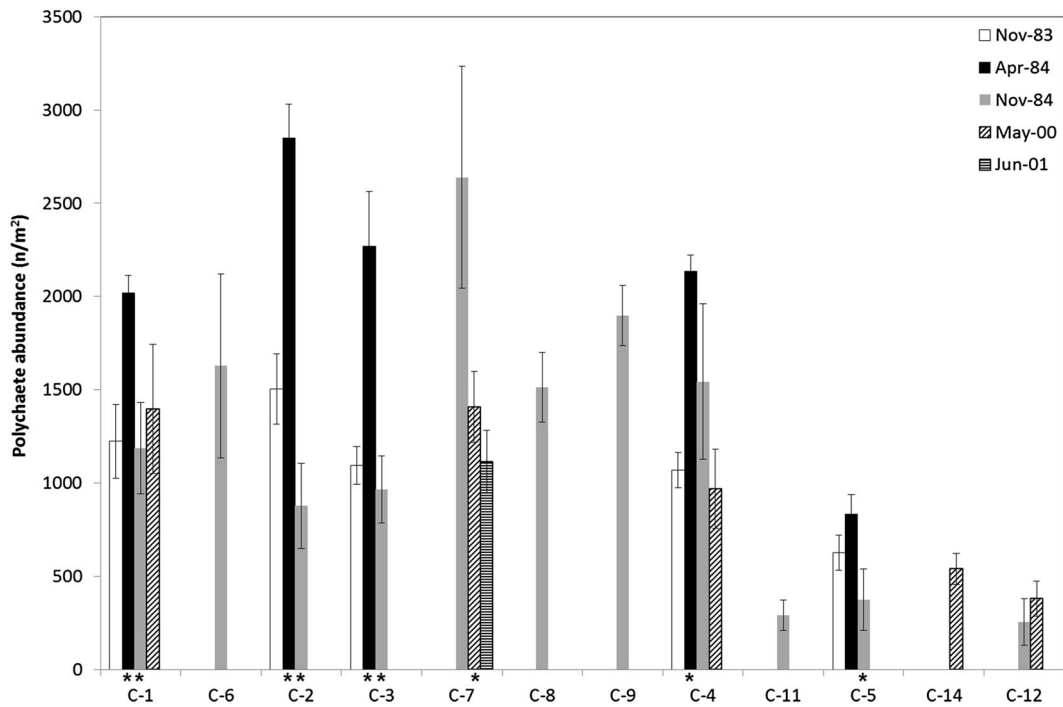
The most abundant family overall was Spionidae, which attained densities of up to 821  $n/m^2$  at the shallow stations C1 and C6 during spring 1984 and decreased continuously with depth. Other prominent families peaked at station C2, including Syllidae, Opheliidae, and Pilargidae, or at C3, including Trichobranchidae and Flabelligeridae. Polychaetes of the family Maldanidae had a very distinct peak at station C4 in approximately 1400 m, with up to 901  $n/m^2$  in the spring samples of 1984.

In November 1983 there was no significant difference in polychaete abundance between any of the upper slope stations C1–C4. However, each of the four

stations had significantly higher abundances than the lower slope station C5 ( $P < 0.01$ ). In April 1984, C2 had the highest polychaete abundance of any station included in the study. Abundance at C2 was significantly higher than at C1 and C4. No other significant differences between upper slope stations were found during April 1984. However, C5 had significantly lower polychaete abundance than each of the upper slope stations ( $P < 0.001$ ). During November 1984 polychaete abundance at C2 and C3, the stations with the highest densities during April 1984, had dropped conspicuously, making them the upper slope stations with the lowest polychaete abundances. C2 and C3 had significantly lower abundances than C7 and C9. Abundances at the lower slope stations C5, C11, and C12 were all significantly lower than at the upper slope stations ( $P < 0.05$ ), with the exception of the non-significant difference between C2 and C5 ( $P = 0.10$ ). In May 2000, only abundances between the upper slope station C7 and the lower slope station C12 were significantly different ( $P < 0.05$ ).

In April 1984, polychaete numbers at the upper slope stations were at about twice the level of the fall samples. The increase between November 1983 and April 1984 was highly significant at the upper slope stations C1–C4 ( $P < 0.005$ ) (Table 2). The decrease in the abundance between the April and November 1984 was also highly significant at the upper slope stations ( $P < 0.01$ ), except for station C4 (Table 2). Polychaete abundance at station C5 had moderately, but not significantly, increased between November 1983 and April 1984, but it did significantly decrease ( $P < 0.05$ ) between April 1984 and November 1984 (Table 2). Polychaete abundances of fall samples of 1983 and 1984 were not significantly different at any of the stations compared.

A closer look at abundances of the individual polychaete families during the different sampling periods revealed that the spring peak in abundance was especially pronounced with deposit feeders. The most dominant family that peaked in spring was Spionidae, mostly composed of surface deposit-feeding species, some of which are also able to utilize their palps for suspension feeding (Fauchald & Jumars, 1979; Reuscher & Shirley, 2014; Jumars et al., 2015), with average abundances over the five stations C1–C5 of 219  $n/m^2$  in November 1983, 502  $n/m^2$  in April 1984, and 200  $n/m^2$  in November 1984. Other prominent families, which contain mostly or exclusively deposit-



**Fig. 2** Polychaete abundance of different stations and sampling periods. Error bars indicate standard errors. Stations are arranged according to increasing depth from left to right.

Asterisks indicate significant differences in polychaete abundances from previous sampling periods

**Table 2** P values of ANOVA tests for significant differences in the polychaete abundances during different sampling periods

Samples compared	C1	C2	C3	C7	C4	C5	C12
N1 vs. N2	<b><math>P &lt; 0.005</math></b>	<b><math>P &lt; 5 \times 10^{-4}</math></b>	<b><math>P &lt; 0.005</math></b>	n.d.	<b><math>P &lt; 1 \times 10^{-5}</math></b>	$P = 0.179$	n.d.
N1 vs. N3	$P = 0.907$	$P = 0.061$	$P = 0.540$	n.d.	$P = 0.294$	$P = 0.212$	n.d.
N2 vs. N3	<b><math>P &lt; 0.01</math></b>	<b><math>P &lt; 1 \times 10^{-4}</math></b>	<b><math>P &lt; 0.005</math></b>	n.d.	$P = 0.195$	<b><math>P &lt; 0.05</math></b>	n.d.
N1 vs. D1	$P = 0.652$	n.d.	n.d.	n.d.	$P = 0.632$	n.d.	n.d.
N2 vs. D1	$P = 0.052$	n.d.	n.d.	n.d.	<b><math>P &lt; 5 \times 10^{-4}</math></b>	n.d.	n.d.
N3 vs. D1	$P = 0.628$	n.d.	n.d.	$P = 0.199$	$P = 0.391$	n.d.	$P = 0.615$
N3 vs. D2	n.d.	n.d.	n.d.	$P = 0.121$	n.d.	n.d.	n.d.
N3 vs. D pooled	n.d.	n.d.	n.d.	<b><math>P &lt; 0.05</math></b>	n.d.	n.d.	n.d.
D1 vs. D2	n.d.	n.d.	n.d.	$P = 0.313$	n.d.	n.d.	n.d.

N1, N2, and N3 indicate first, second, and third NGoMCS cruise, respectively; D1 and D2 indicate the first and second DGoMB cruise, respectively; n.d. indicates no data, as the station was not sampled during at least one of the compared sampling periods. Bold indicate significant differences

feeding species, with markedly elevated abundances in the spring samples included Maldanidae, Capitellidae, Paraonidae, Ampharetidae, Cirratulidae, Opheliidae, Trichobranchidae, and Flabelligeridae. Some of the more abundant families with other feeding strategies that peaked in the spring samples included the mostly carnivorous and omnivorous Hesionidae,

Lumbrineridae, Glyceridae, Onuphidae, and Paracynodiidae. Another abundant family with an abundance peak in spring was Syllidae, which contains a wide variety of species with feeding strategies ranging from carnivory to deposit feeding. Overall, 32 out of the 44 families who were recorded during the NGoMCS surveys peaked in spring.



Polychaete abundances in the DGoMB samples of late May 2000 and June 2001 were generally similar to the fall samples of NGoMCS. Station C7 did not have conspicuously high abundance as it did in November 1984, but instead was similar to the other sampled upper slope stations C1 and C4. Abundances at C1, C4, and C12 were not significantly different between the DGoMB samples and the November samples of NGoMCS (Table 2). Compared to the spring samples of NGoMCS, abundance at C4 was significantly lower ( $P < 0.001$ ), while at C1 the difference was not significant. At station C7 no significant differences were found between the samples of 1984, 2000, and 2001. However, because of the low number of DGoMB replicates analyzed, we pooled the samples of 2000 and 2001. The pooled DGoMB samples of station C7 had a significantly lower abundance ( $P < 0.05$ ) than those of NGoMCS (Table 2).

#### Community composition analysis

The polychaete communities of the different stations at transect C clustered into four groups at a similarity level of 85% (Fig. 3). One group consisted of the shallow upper slope assemblages of stations C1, including all four different sampling periods, and C6. The depth range of the samples of this cluster was approximately 325–500 m. The second cluster included the intermediate upper slope stations C2 and C3 of all three sampling periods, respectively, located in depths of approximately 600–900 m and station C7 sampled twice during DGoMB at approximately 1070 m. The next cluster contained the deeper upper slope stations C4, including all four sampling periods, C8, and C9, in depths between 1150 and 1500 m. The polychaete community of station C7, sampled in approximately 1020 m during NGoMCS, also clustered with these deeper stations. Among all stations sampled repeatedly, polychaete assemblages had shifted most at C7. In 1984 station C7 was most similar to the deeper stations C4, C8, and C9, in 2000 and 2001 the station was most similar to the next shallower stations C2 and C3. The fourth cluster included the lower slope stations C5, C12, and C14, in depths between approximately 2400 and 3000 m. NGoMCS samples of the stations C11 and C12 were excluded because they contained fewer than 100 specimens.

A consistent noteworthy trajectory occurred in the polychaete communities of stations C1, C2, and C3 sampled during three consecutive NGoMCS cruises:

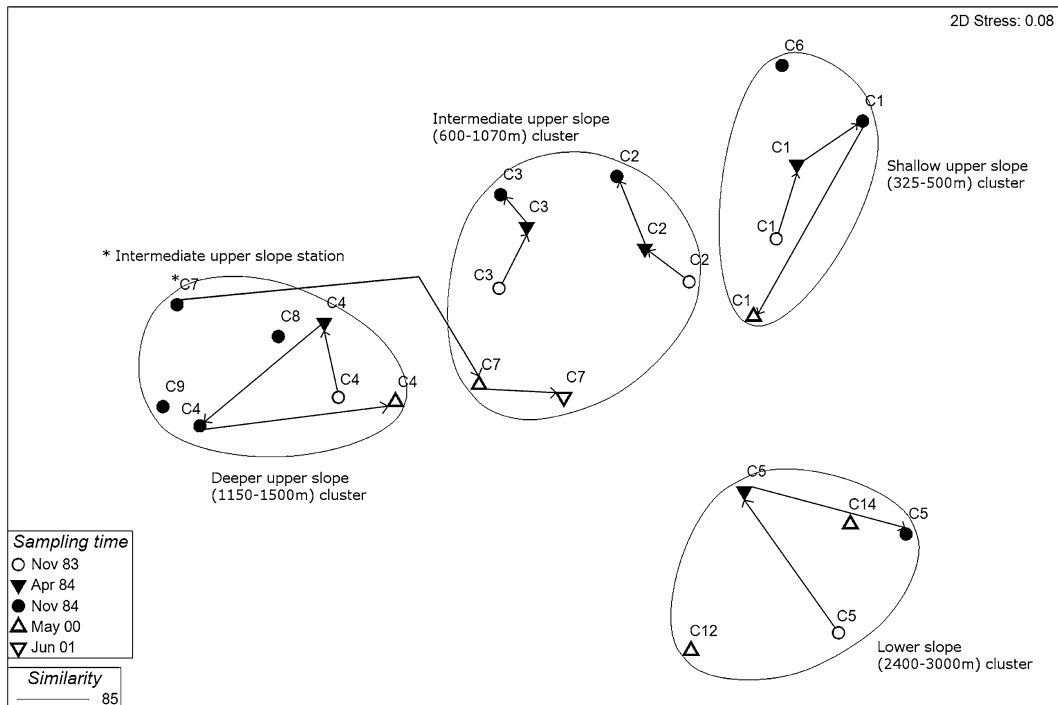
stations had an approximately parallel trend in the ordination plot with the samples of November 1983 on bottom, samples of April 1984 in the middle, and samples of November 1984 on top (Fig. 3). During the approximately 16 years between the third NGoMCS cruise and the first DGoMB cruise, the dynamics in the polychaete community at station C1 reversed and the assemblage returned beyond the position of the first NGoMCS cruise (Fig. 3). Similarly, in the transition of station C4 the polychaete community of the first DGoMB cruise approximately returned to the position of the first NGoMCS cruise after a non-linear trajectory between the three NGoMCS samples (Fig. 3).

Polychaete communities at C1 were significantly different between each sampling period, except between November 1983 and late May 2000 (Table 3). At each sampling event the assemblages were mainly characterized by Spionidae, Paraonidae, Nephtyidae, and Capitellidae. Two different patterns of change occurred between the three NGoMCS sampling periods. First, the numerically dominant Spionidae, Capitellidae, Syllidae, and Lumbrineridae were more abundant in April 1984 and therefore contributed more to the dissimilarity between spring and fall samples. Second, families that either continuously increased (e.g., Ampharetidae and Nephtyidae) or decreased (e.g., Amphinomidae, Maldanidae, and Opheliidae) contributed most to the dissimilarity between the samples of November 1983 and November 1984. In 2000 Ampharetidae, Nephtyidae, Maldanidae, and Opheliidae had approximately returned to their initial levels of 1983. Syllidae were more abundant than in any of the NGoMCS samples.

At station C2, the polychaete community had not changed significantly between November 1983 and April 1984, but had significantly changed in November 1984 (Table 3). Temporal differences in the abundance of Spionidae, Opheliidae, and Paraonidae contributed most to the dissimilarity between different sampling periods at station C2.

Polychaete assemblages at C7 were significantly different between NGoMCS and DGoMB (D1 and D2 pooled). Most importantly, the high numbers of Maldanidae had decreased by about 80% between November 1984 and late May 2000. This decline is reflected in the results of the SIMPER analysis, in which the maldanid polychaetes contributed by far the most to the dissimilarity between NGoMCS and DGoMB samples.





**Fig. 3** MDS ordination plot based on similarity of the polychaete fauna of the different stations and sampling periods. *Arrows* indicate the trajectories of the different stations over time

Polychaete assemblages at C3, C4, and C5 were not significantly different between different sampling periods. SIMPER analyses were not performed at stations without significant differences among sampling periods.

## Discussion

### Abundance

The finding that polychaete density did not consistently decrease with depth among the stations between 325 and 1500 m differs from observations by Carvalho et al. (2013), who found a steady exponential decline of polychaete abundance and biomass with depth at the northern Gulf of Mexico continental slope. Pérez-Mendoza et al. (2003) reported an unusual inverse parabolic distribution in the western Gulf of Mexico, with decreasing densities along the continental slope and abundance peaks on the Sigsbee abyssal plain. Despite the relatively uniform abundances between 325 and 1500 m, polychaete biomass likely decreased with depth as a consequence of the

decrease of the average polychaete body size with depth (Carvalho et al., 2013).

The unusually high polychaete abundance at station C7 in November 1984 was mainly caused by bamboo worms of the family Maldanidae. However, their distribution was quite patchy, which is reflected in the large standard error of the average abundance (Fig. 2). Gallaway (1988) found evidence of hydrocarbon seeps in the vicinity of the station. He observed high concentrations of hydrocarbons typically found near seeps and bivalves common in chemosynthetic environments. Five specimens of an unidentified species of “Pogonophora” were also found in the replicate sample with the highest polychaete density (5368  $n/m^2$ ). The pogonophorans, now considered polychaetes of the family Siboglinidae, lack a digestive tract and rely exclusively on endosymbiotic, chemoautotrophic bacteria for their nutrition. Therefore, they are obligate dwellers of hydrocarbon seeps and hydrothermal vents in other oceans. The same replicate had conspicuously high numbers of Maldanidae and elevated levels of Glyceridae and Terebellidae. None of these families are restricted to chemosynthetic environments, but each has species known to

**Table 3** *P* values of ANOSIM tests for significant differences between polychaete assemblages of different sampling periods

Samples compared	C1	C2	C3	C7	C4	C5
N1 vs. N2	<b><i>P</i> &lt; 0.005</b> (2/462)	<i>P</i> = 0.0974 (45/462)	<i>P</i> = 0.115 (53/462)	n.d.	<i>P</i> = 0.288 (133/462)	<i>P</i> = 0.286 (132/462)
N1 vs. N3	<b><i>P</i> &lt; 0.05</b> (10/462)	<b><i>P</i> &lt; 0.01</b> (4/462)	<i>P</i> = 0.190 (88/462)	n.d.	<i>P</i> = 0.0844 (39/462)	<i>P</i> = 0.193 (89/462)
N2 vs. N3	<b><i>P</i> &lt; 0.01</b> (3/462)	<b><i>P</i> &lt; 0.005</b> (1/462)	<i>P</i> = 0.519 (240/462)	n.d.	<i>P</i> = 0.132 (61/462)	<i>P</i> = 0.773 (357/462)
N1 vs. D1	<i>P</i> = 0.131 (11/84)	n.d.	n.d.	n.d.	<i>P</i> = 0.357 (30/84)	n.d.
N2 vs. D1	<i>P</i> < 0.05 (1/84)	n.d.	n.d.	n.d.	<i>P</i> = 0.179 (15/84)	n.d.
N3 vs. D1	<i>P</i> < 0.05 (2/56)	n.d.	n.d.	<i>P</i> = 0.452 (38/84)	<i>P</i> = 0.238 (20/84)	n.d.
N3 vs. D2	n.d.	n.d.	n.d.	<i>P</i> = 0.250 (21/84)	n.d.	n.d.
N3 vs. D pooled	n.d.	n.d.	n.d.	<b><i>P</i> &lt; 0.005</b> (1/462)	n.d.	n.d.
D1 vs. D2	n.d.	n.d.	n.d.	<i>P</i> = 0.200 (2/10)	n.d.	n.d.

*N1*, *N2*, and *N3* indicate first, second, and third NGoMCS cruise, respectively; *D1* and *D2* indicate the first and second DGoMB cruise, respectively; brackets indicate numbers of permutations with *R* equal or bigger than the real dataset over all possible permutations. *n.d.* indicates no data, as the station was not sampled during at least one of the compared sampling periods. Bold indicate significant differences

occur in the vicinity of cold seeps (Miura & Hashimoto, 1991; Levin et al., 2000; Reuscher et al., 2012). Hydrocarbon seeps are common in the Gulf of Mexico and abundance and biomass in their vicinity are much higher than in the surrounding deep sea (MacDonald et al., 1989). Thus, the considerable difference in polychaete abundance at station C7 is likely attributed to the coincidental sampling at or near a hydrocarbon seep during the third NGoMCS cruise.

Reasons and mechanisms for the approximately 2-fold increase in polychaete abundance in April 1984, compared to November 1983 and November 1984 at the upper slope stations are unknown. Comparable increases in deep-sea polychaete abundances in the abyssal Northeast Atlantic were caused by a pulse of POC flux (Vanreusel et al., 2001; Soto et al., 2010). Similarly, Wang (2004) found that polychaete abundance in the northern Gulf of Mexico is directly correlated to POC flux from the surface. Vanreusel et al. (2001) found direct evidence for an episodic recruitment event of an opportunistic deposit-feeding

opheliid polychaete species in the deep Northeast Atlantic, following the deposition of phytodetritus. Blake (1993) found that the deposit-feeding species *Cossura longocirrata* showed distinct spring recruitment patterns on the continental slope off North Carolina, which he hypothesized to be a response to phytoplankton sedimentation during spring. Similar mechanisms may be at work in the Gulf of Mexico, where the import of nutrients through the Mississippi–Atchafalaya river system peaks during spring (Turner et al., 1998; Aulenbach et al., 2007), causing phytoplankton spring blooms.

DGoMB samples were collected at a different time of the year (May, June) than the NGoMCS samples. Therefore, it is impossible to unravel the relative importance of seasonal and annual variations. The annual nutrient input from the Mississippi–Atchafalaya river system in 2000 and 2001 was much lower than in 1983 and 1984.

The only non-significant difference in polychaete abundance on the upper continental slope between

spring and fall samples was between April and November 1984 at station C4. Five of the six replicates of the fall samples had lower densities (484–1537  $\text{n/m}^2$ ) than the six replicates of the spring samples (1835–2505  $\text{n/m}^2$ ). However, one replicate of the fall sample had an unusually high number of 3453  $\text{n/m}^2$ , mainly attributed to the high density of the polychaete family Maldanidae (1934  $\text{n/m}^2$ ). This replicate inflated the standard error of the average abundance at N3–C4 substantially (Fig. 2) and caused the  $P$  value to increase over the significance threshold (Table 2).

### Polychaete community

Our findings that the polychaete fauna changed gradually down the continental slope corroborate the observations by Pequegnat et al. (1990) and Wei et al. (2010) on the macrofauna of the same area. Hydrostatic pressure, temperature, oxygen levels, contaminants, and, most importantly, nutrient availability, are compounding factors that affect the assemblages (Carney, 2005). Furthermore, changes in the community composition were independent from abundance. Stations shallower than 1500 m had significant seasonal changes in abundance that were not mirrored in the multivariate analysis of the polychaete communities.

The composition of the polychaete assemblages at C1 and C4 changed little over 16–17 years. Even more intriguing is that the DGoMB samples are most similar to the samples of the first NGoMCS cruise, suggesting that the short-term trajectory of the polychaete communities observed between N1 and N3 had reversed. This trend is mirrored by the continuous decrease of Amphinomidae and Opheliidae and the increase of Ampharetidae and Nephtyidae between November 1983 and November 1984. In May of 2000 the numbers of all four families had approximately returned to the levels of 1983. Reasons for the trends of the polychaete community in general and the four families mentioned remain speculative.

A possible explanation could be that stable conditions, favoring  $k$ -selected species, and episodic disturbances, such as gravity-driven turbidity currents (Niedoroda et al., 2003) and mass wasting events (Santschi & Rowe, 2008), oil contamination from natural seeps (Kennicutt et al., 1989) or spills (Montagna et al., 2013), and trawling (Watling & Norse, 1998), which would favor  $r$ -selected species, lead to communities in different succession stages (Smith,

1994). Species level data are needed to test this hypothesis effectively because polychaete families may contain both opportunistic and sensitive species. Additionally, it should be kept in mind that each sampling event represented only a snapshot of the polychaete communities and any possible disturbance(s) in between the sampling events remain elusive.

It is also possible that imperfect sampling of replicate cores during the NGoMCS, particularly during the first cruise in November 1983, introduced a bias. Replicate cores of the first NGoMCS cruise at stations C1 and C4 were as far apart as 2.3 and 3.7 km, respectively. The depth ranges of the 1983 cruise replicates at C1 and C4 were 320–355 and 1325–1440 m, respectively. When all three NGoMCS cruises and the DGoMB cruise are taken into account, samples at C1 and C4 came from locations as far apart as 2.9 and 5.3 km, respectively. Depth ranges at C1 and C4 across all cruises and replicates were 320–361 and 1325–1506, respectively. Therefore, some of the community variability that seems to occur across sampling periods might actually be explained by the slightly different sampling locations and depths during the different research cruises.

The almost parallel trajectories of the upper slope stations over time could also be an artifact of different sampling procedures during the various cruises. Overall, three different box cores with different sizes were employed. Additionally, procedures for washing the box core samples and specimen extraction techniques may have varied between cruises.

### Conclusions

- (1) Polychaete abundance at the central Gulf of Mexico continental slope undergoes significant temporal changes.
- (2) Polychaete abundance did not consistently decline with increasing depth between 325 and 1500 m, but sharply declined below 1500 m.
- (3) Changes in the composition of polychaete communities were independent from changes in abundance. Doubling in abundance during spring 1984 did not affect  $\beta$ -diversity measurements. Also, communities changed consistently with depth, while abundances did not.

- (4) Depth (and its correlated variables) is an important factor for polychaete community structure.

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