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ORIGINAL RESEARCH ARTICLE

Natural and anthropogenic factors influencing abundance of the benthic macrofauna along the shelf and slope of the Gulf of Guinea, a large marine ecosystem off West Africa

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Summary The West African continental margin belongs to the least known areas in terms of the ecology of benthic ecosystems. At the same time, this region is influenced by various threats associated with human activities, including industrialisation and oil excavation. Here, we analyse the abundance and distribution patterns of macrozoobenthic communities along the coast of Ghana. The material was collected in 2012 on nine transects at depths ranging from 25 to 1000 m. Over 200 quantitative samples were collected using a 0.1-m^2 van Veen grab. Generally, the mean density of macrozoobenthos decreased gradually from the shallow zone (25 m: 231.4 $\pm$ 262.2 ind./0.1 m^2) down to bathyal depths (1000 m: 55.4 $\pm$ 51.4 ind./0.1 m^2), but we observed intermediate scale variability in distribution patterns among the transects along the Ghanaian coast. Analysis of environmental factors showed no evidence of substantial pollution, although levels of hydrocarbons, barium and some other toxic metals show some local increases at particular stations, especially on the continental slope. Cluster analysis based on Bray—Curtis similarity and abundance of higher taxonomic groups of macrofauna yielded five groups of stations, while SIMPER analysis demonstrated that polychaetes and amphipods contributed most

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significantly to within-group similarity. Canonical Correspondence Analysis demonstrated that PAH, THC and toxic metal levels (Ba, Cd, Pb), as well as oxygen concentration, were the most important factors structuring benthic communities.

1. Introduction

Understanding the continental margin benthic community structure is crucial in marine studies. Continental margins are major marine oil repositories and host important fishery resources. Thus, studies describing ecological gradients may lead not only to a comprehensive description of ecological processes, but also guarantee the appropriate development of future management plans (Levin and Sibuet, 2012). The distribution of benthos along an oceanic depth gradient is influenced by a number of factors including dissolved oxygen concentration, sediment structure, the total organic carbon level in the sediment as well as various disturbance processes and pollution events (e.g. Bakus, 2007; Edros et al., 2011; Ellis et al., 2012 and references therein; Solan et al., 2012; Włodarska-Kowalczuk et al., 2004). Rex et al. (2006), in their global-scale analysis of the meio-, macro- and megafauna, have demonstrated that the abundance of benthic communities decreases with depth, although there are still numerous discrepancies between the global scale models (e.g. Rex and Etter, 2010; Rex et al., 2006) and specific studies conducted on the regional or local scale (e.g. Aller et al., 2002; Coleman et al., 1997; McCallum et al., 2015). Moreover, studies describing the changes in benthic fauna from the shallow shelf areas down to bathyal or abyssal depths are still scarce, and many regions have almost completely been neglected in earlier research programmes (Rex and Etter, 2010).

The benthic marine fauna of the West African continental margin is largely unknown. The majority of ecological studies have focused on the shallow coastal areas, often with a low sampling effort. For example, some studies have investigated coastal brackish lagoons and river estuaries on the Nigerian coast (Akanabi Bamikole et al., 2009; Brown and Ajao, 2004; Edokpayi et al., 2010; Ewa-Oboho et al., 2008), and on the Ivory Coast (Kouadio et al., 2008), while some focused on tidal flats on the Mauritanian coast (Duineveld et al., 1993; Wijnsma et al., 1999). Longhurst (1959) analysed the shelf macrobenthic communities of the coast of Sierra Leone, while Le Loeuff and Intés (1999) focused their attention on the spatio-temporal dynamics of the benthic fauna of the Ivory Coast shelf. The macroepifauna associated with oil platforms in Gabon was also a subject of a recent study (Friedlander et al., 2014). On the other hand, the area of the Angola-Congo margin (south-eastern part of the Gulf of Guinea) was subject of comprehensive hydrological, hydrographical and ecological studies in the framework of the programme BIOZAIRE (Sibuet and Vangriesheim, 2009). However, this initiative concentrated on the deep-sea benthic communities associated with highly restricted areas influenced by high levels of organic matter inflow from the Congo River (e.g. Brind'Amour et al., 2009; Gaever et al., 2009; Galeron et al., 2009; Menot et al., 2009) and on a giant pockmark area (Menot et al., 2009).

The northern part of the Gulf of Guinea, including the Ghanaian coast, is almost completely unsurveyed, including the shallow areas. The only studies of the marine benthic fauna of the coast of Ghana were performed in the 1950s and 1960s and concentrated on distribution patterns of the macrobenthic fauna of the shallow areas, down to a depth of 80 m (Bassindale, 1961; Buchanan, 1957; Longhurst, 1958).

Marine ecosystems of the tropical and subtropical part of the West African coast are shaped by a highly dynamic and diversified set of factors, including natural hypoxia (oxygen minimum zones) (Levin et al., 2009) and high dynamics of water masses (Djagoua et al., 2011), making it a separate marine ecoregion (Spalding et al., 2007). In this sense, there is an urgent need for studies describing the influences of those complex processes and numerous factors on marine fauna.

The Gulf of Guinea is also an area of high economic interest. It constitutes the Large Marine Ecosystem (LME) characterised by significant fishery resources and oil reserves (Ukwe et al., 2003). Human pressure on this ecosystem has constantly been increasing since the last 30 years due to high population growth, the development of various industrial activities and the excavation of oil deposits (Ayamdoo, 2016; Scheren et al., 2002). Therefore, studies analysing the influences of those processes are needed to find benchmarks against which we can assess the level of future changes and create baselines for further monitoring and environmental protection in this region. Such studies are especially important for scarcely studied regions and countries, such as the West African coast, which is highly influenced by the uncertain economic situation and have poorly developed environmental protection systems.

In this context, the aim of this study was to analyse distribution patterns and factors shaping benthic macrofauna communities along a 25—1000 m depth gradient off the Ghanaian coast of the Gulf of Guinea, including areas affected by oil excavation activities. The material was collected in the framework of the Oil for Development (OfD) program, supported by the Food and Agriculture Organization of the United Nations (FAO). This initiative offers assistance to developing countries in their efforts to manage petroleum resources in a sustainable manner and to develop environmental protection systems based on ecological studies.

2. Material and methods

2.1. Study area

The Gulf of Guinea is a large open bay on the Atlantic coast of West Africa between latitudes 5°N and 5°S and longitudes 8°W to 12°E (Ukwe et al., 2003), with a coastline of about 3000 km (Chukwuone et al., 2009). It is influenced by the Guinea Current, by the Benguela Current and by the South Equatorial Counter Current (Schneider, 1990; Ukwe et al., 2006). The area is characterised by the occurrence of oxygen minimum zones (Levin, 2003; Levin et al., 2009) as well as by dynamic sedimentation phenomena associated with coastal erosion (Ukwe et al., 2003). The coastal areas of Ghana are located in the atypical tropical climate region (Le Loeuff and Cosel, 1998) and characterised by high dynamics of water masses and upwellings (Djagoua et al., 2011). This part of the coastline contains no large river systems, except for the Volta River estuary, which is located in the eastern part of the coast. The Ghanaian coast stretches along a distance of 565 km.

2.2. Sampling

Material was collected in October and November of 2012 on nine transects distributed along the entire coast of Ghana, starting from New Town and ending near the Togo (Fig. 1). Samples were collected using a 0.1-m^2 van Veen grab supported with the VAMS (Video Assisted Monitoring System) allowing for appropriate sediment penetration. Each transect consisted of six stations: 25, 50, 100, 250, 500 and 1000 m. Five samples were collected at each station. The material was sieved through a 0.3-mm sieve and preserved in 4% formaldehyde solution. The methodology was consistent with the recommendations of the *Oil Spill Prevention, Administration and Response Fund* (OSPAR) guidelines (OSPAR, 2011).

2.3. Environmental data

Physical and chemical properties, including sediment structure, total organic matter (TOM) content in the sediments, level of hydrocarbons and various toxic metals, were analysed at each station. We also determined temperature, conductivity and oxygen level (Seabird 911 CTD Plus and SBE 21 Seacat thermosalinographs were used). Sediment grain size was determined by mixing the sediment with water and sieving it through a 0.063-mm sieve. Larger particles were then sieved through Endecott sieves; for calculation, the equations of Buchanan (1984) and Folk and Ward (1957) were used. Total organic matter was determined as the weight loss in a 2—3-g dried sample (dried at 105°C for 20 h) after 2 h of combustion at 480°C. Petroleum hydrocarbon content was determined using a gas chromatograph with a flame ionisation detector (GC/FID), as outlined in the Intergovernmental Oceanographic Commission, Manuals and Guides No. 11, UNESCO (1982). Metals (Ba, Cd, Cr, Cu, Pb, Zn, Hg) were analysed via Inductively Coupled Plasma-Atomic Emission Spectrometry (ICP-AES), except for mercury, which was determined via Cold Vapour Atomic Emission Spectrometry (CVAAS) after drying, sieving and digestion (Elezz et al., 2018; Jarvis and Jarvis, 1992).

2.4. Statistical analysis

To analyse trends in abundance along a depth gradient of the Ghanaian shelf, slope mean values of abundance with standard deviations (SD) were calculated for each station (25, 50, 100, 250, 500 and 1000 m) for the entire macrozoobenthos and for the most abundant taxonomic groups. Mean values were calculated separately for each transect and for the entire material. To determine statistically significant differences in macrozoobenthic abundance among depths, Kruskal—Wallis test was used. Post hoc testing was performed with the use of Dunn's test in the software package Statistica 6.

Multivariate analysis was performed in the Primer 7 package. Hierarchical agglomerative clustering analysis, based on the Bray—Curtis formula, was used to check faunistic

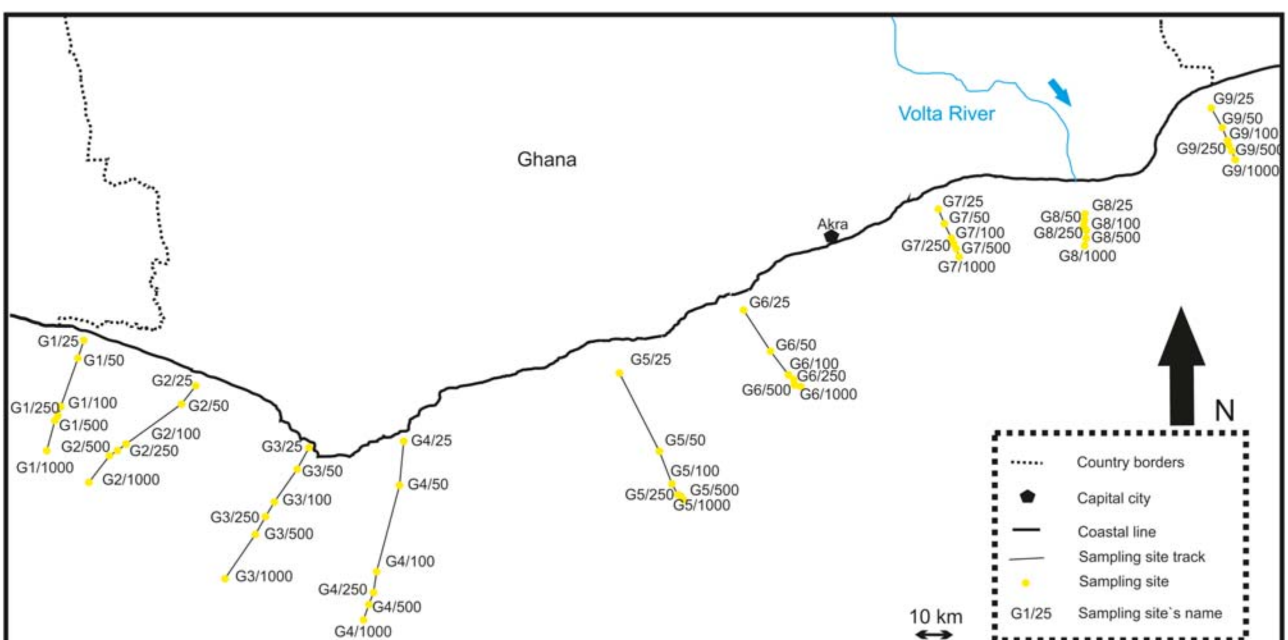

Figure 1 Distribution of sampling stations along the Ghanaian coast.

similarity among the samples. For the purpose of the cluster analysis, we used mean values of abundance calculated for each station; the analysis was based on higher taxa level. Data were square root-transformed, and the group average method was used. A SIMPROF test with 1% significance level was performed to check the multivariate structure within groups (Clarke and Gorley, 2015). Mean values of macrozoobenthos abundance and mean values of environmental variables with standard deviations were calculated for each group of stations (clusters). Frequency of occurrence (*F*, percentage of samples where a taxonomic group was found in the total number of samples) was calculated for each taxon in each cluster. We performed SIMPER analysis to determine the dissimilarity among groups separated by cluster analysis, using the R Studio environment (Clarke, 1993; Warton et al., 2012).

Canonical Correspondence Analysis (CCA) was performed in the R Studio (Legendre and Legendre, 2012; R Core Team, 2013) with the vegan package (Oksanen et al., 2019). For this, we used the Variance Inflation Factor (VIF) to determine which factors are significant in shaping biodiversity on each station (Fox, 2016; Fox and Monette, 1992). Subsequently, we removed factors with the highest VIF value and repeated the VIF analysis. Finally, nine factors remained in the analysis. Permutational Multivariate Analysis of Variance Using Distance Matrices (PERMANOVA) was performed for these nine factors to determine which were significant in the CCA. In addition, we calculated the Adjusted *R* Square (Zapala and Schork, 2006).

3. Results

Altogether, we found 28,754 individuals in the studied material; the fauna was dominated by polychaetes, bivalves and amphipods (Fig. 2).

The mean abundance of macrozoobenthos gradually decreased from shallow shelf areas (25 m: 231.4 $\pm$ 262.2 ind./0.1 m^2) down to bathyal depths (1000 m: 55.4 $\pm$ 51.4 ind./0.1 m^2) (Fig. 3). Statistically significant results were found between the shallowest (25—50 m) and the deepest stations (500—1000 m) (Kruskal—Wallis test, Dunn's test $p < 0.05$). On the other hand, general trends in abundance differed among the investigated transects (Fig. 4). On most of the transects, highest mean abundance was recorded on 25 m (five transects, including G3, G6—G9) or on 50 m (three transects G1, G2 and G5), while the lowest mean values were found on 1000 m (five transects: G4, G5, G 7—G9) or on 500 m (two transects, G2 and G6). Nevertheless, on transect G4, highest mean densities were observed on 500 m (125.6 $\pm$ 95.8 ind./0.1 m^2), while on transect G3, the lowest values were found on the lower shelf (250 m: 58.6 $\pm$ 23.3 ind./0.1 m^2). The highest mean values of macrozoobenthos abundance were recorded on transect G7 at the depth of 25 m (786.4 $\pm$ 466.0 ind./0.1 m^2). There were no statistically significant differences among the stations at five transects (G1—G4 and G8). Statistically significant results were found between the shallowest and the deepest stations on transects G5, G6, G7 and G9 (Kruskal—Wallis test, Dunn's test, $p < 0.05$).

General trends in abundance differed strongly among the various taxonomic groups. For example, polychaetes followed the general pattern observed for the entire macrofauna, with the highest abundance observed in the shallowest areas and a gradual decrease along the depth gradient. Amphipods were most abundant at 25 m (34.6 $\pm$ 43.7 ind./0.1 m^2) and 50 m, but their density sharply decreased at 100 m (Table 1). Nevertheless, the values of the abundance of particular taxonomic groups differed among the transects. The abundance of bivalves, polychaetes and amphipods varied among the transects, with highest densities observed on various depths, depending on the transect. The highest abundance of fauna, including exceptionally high polychaete densities (292.2 $\pm$ 279.4 ind./0.1 m^2 at station 25 m), was found on transect G7, while the lowest abundance values were found on transect G9, especially on the deepest stations (Table 2). Total organic matter content increased with depth on most of the transects. Oxygen depletion was recorded at 250-m stations. On most of the transects, the concentrations of barium and hydrocarbons were highest at 500 and 1000 m (Fig. 5). We also

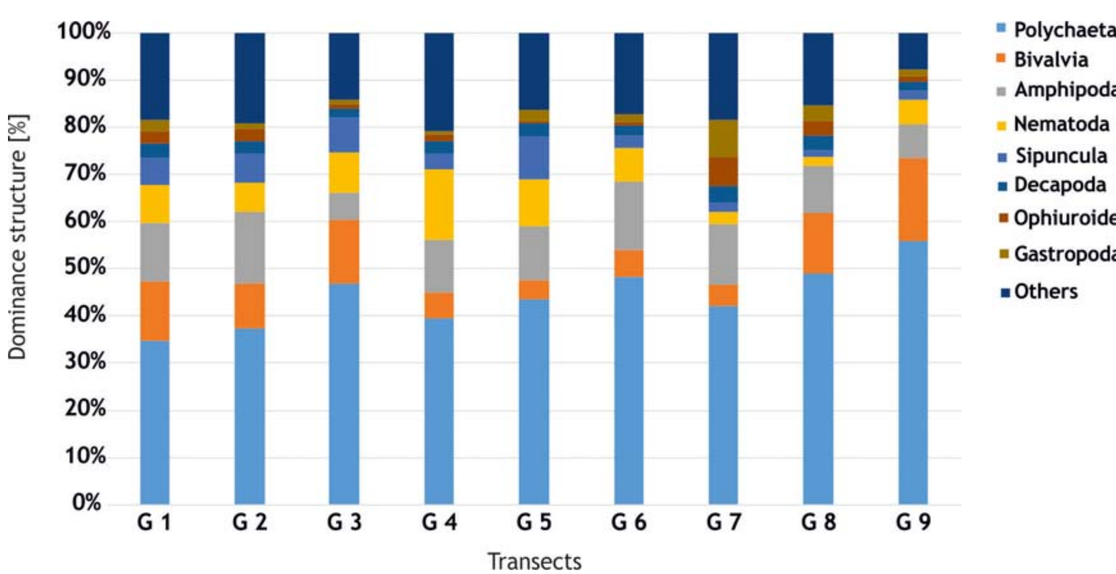

Figure 2 Dominance structure of macrozoobenthos at each of the depths.

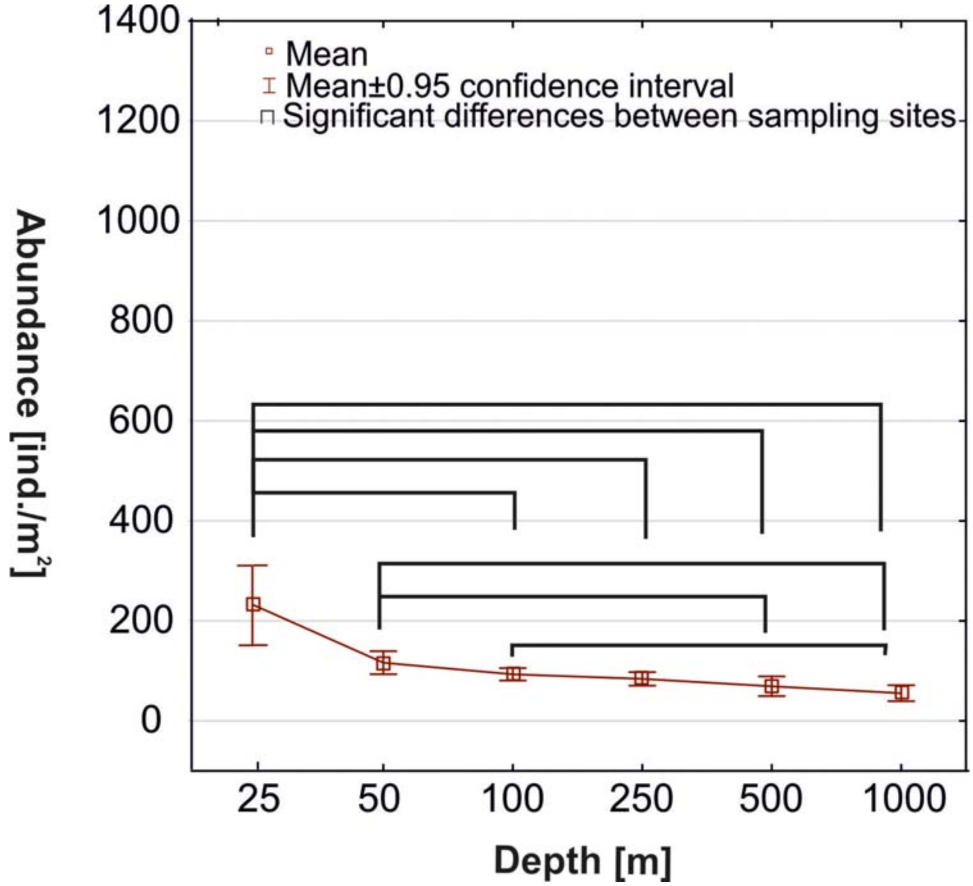

Figure 3 Mean densities at each of the studied depths (data from all transects analysed together).

noticed sediment changes with depth. Shallower shelf stations were characterised by sandy sediments, while on the slope, silt and clay fractions dominated (Table 3).

Five groups of stations were distinguished in the cluster analysis (Fig. 6). All groups were created at high levels of similarity (more than 50%) and significantly differentiated in SIMPROF analysis. The first two clusters grouped the stations characterised by higher levels of disturbance (e.g. higher contents of barium and THC), while clusters 3—5 grouped less disturbed or undisturbed stations. **Cluster 1** consisted of six samples representing various depths (from 50 to 1000 m). This group was characterised by generally low densities of macrozoobenthos (28.2 $\pm$ 12.5 ind./0.1 m^2). Stations were dominated only by polychaetes (15.6 $\pm$ 6.6 ind./0.1 m^2) and bivalves (3.8 $\pm$ 4.0 ind./0.1 m^2) (Table 4). Only 22 taxonomic groups were found in the samples from this group, and all stations from this cluster were characterised by high levels of barium, chromium, copper and THC as well as high levels of organic matter (Table 5). **Cluster 2** grouped the stations from a depth of 100 to 500 m. The macrofauna was dominated by polychaetes (25.4 $\pm$ 2.2 ind./0.1 m^2), with a high frequency of occurrence of some other taxonomic groups including nematodes, isopods, bivalves and amphipods (Table 4). Only 26 taxonomic groups were found in samples from this group. Generally, it was characterised by a low total macrozoobenthos abundance (65.9 $\pm$ 12.8 ind./0.1 m^2) and by high levels of barium, copper and nickel, as well as by silt and clay bottom deposits. **Cluster 3** grouped five shallow-water stations (25—50 m depth range) dominated by polychaetes (28.3 $\pm$ 7.9 ind./0.1 m^2) and amphipods (29.1 $\pm$ 17.1 ind./0.1 m^2), with 28 taxonomic groups across recorded. The total macrozoobenthos densities were considerably higher than in the previous two clusters (105.12 $\pm$ 32.8 ind./0.1 m^2). This area was characterised by lower contents of toxic metals and THC (Table 5). **Cluster 4** grouped 26 samples representing various depths from 50 to 1000 m, dominated by polychaetes (42.6 $\pm$ 12.7 ind./0.1 m^2) followed by bivalves, nematodes and amphipods (Table 4); in total, 40 taxonomic groups were found in samples from this group. Mean densities of macrozoobenthos equalled 92.7 $\pm$ 26.0 ind./0.1 m^2, and the stations were characterised by low levels of toxic metals and THC as well as by fine sand bottom deposits. **Cluster 5** grouped mostly shallow-water samples collected at 25 and 50 m (one sample from 250 m). It showed the highest mean densities of macrozoobenthos (185.1 $\pm$ 71.5 ind./0.1 m^2). The bottom fauna was dominated by polychaetes and characterised by a high diversity of taxa, with 42 taxonomic groups. Stations from this cluster were characterised by the lowest levels of barium, chromium, nickel and THC (Table 5).

Based on the results of the SIMPER analysis, polychaetes and amphipods contributed most significantly to within-group similarity (Table 6).

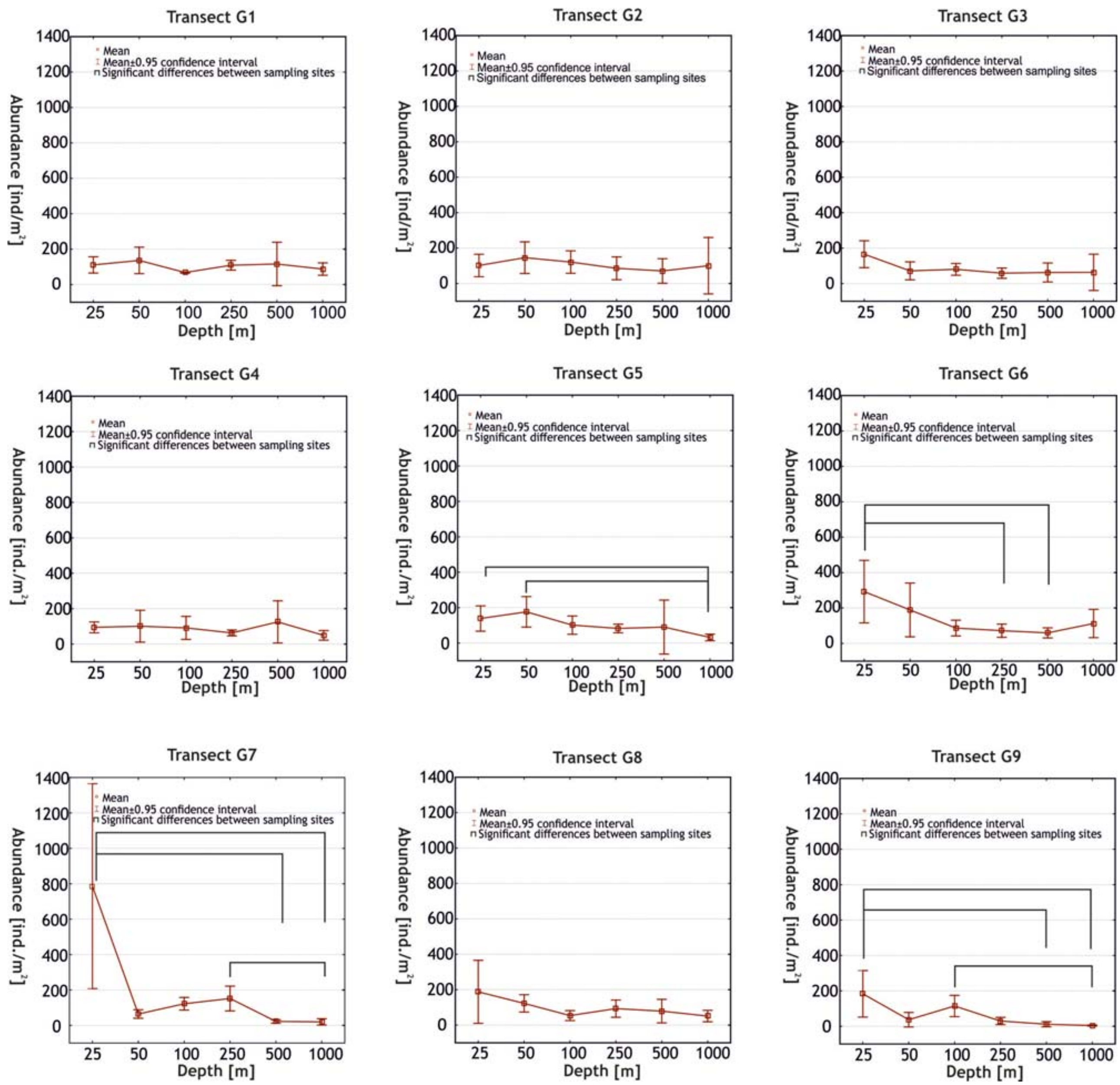

Figure 4 Mean densities at each of the studied depths on each of the transects.

The CCA demonstrated that PAH, THC, metal levels (Ba, Cd, Pb) and oxygen concentration plays a significant role in shaping biodiversity on the Ghanaian coast (Fig. 7). All these factors were statistically significant, and the VIF values were <10.0 (Table 7). The CCA represented 58% of all data from our analysis (Adj. $R^2 = 0.4114759$). The coefficient of determination of the CCA for this dataset is 0.5835628.

4. Discussion

The depth-related decrease in macrozoobenthos abundance was consistent with the general pattern observed for the deep-sea (Rex et al., 2006) and can be explained by the substantial decrease in nutrient supply in bathyal and abyssal depths as well as the distance from productive coastal waters (Carney, 2005; Nephin et al., 2014; Rex et al., 2006). At the same time, on the coast of Ghana, the highest TOM values were recorded for the deepest areas, and on most of the transects, the level of TOM increased along the depth gradient. In his study of the meiofauna of the West African coast, Soltwedel (1997) found areas characterised by high organic matter contents and low fauna densities, suggesting that the lighter fraction of organic matter, transported over longer distances with subsurface currents, probably does not have the same energy content. Discussions about the quality of detritus along a depth gradient pose the question about a meaningful assessment of poor- and high-quality detritus (Carney, 2005), although there are studies showing different levels of organic matter bioavailability in the deep-sea

Table 1 Mean and maximum density values [ind./0.1 m^2] with standard deviation (SD) on each of the depths (only most abundant taxa, data from all transects analysed together). The highest values are marked in bold.

Taxonomic group	25 m		50 m		100 m		250 m		500 m		1000 m	
	Mean ± SD	Max	Mean ± SD	Max	Mean ± SD	Max	Mean ± SD	Max	Mean ± SD	Max	Mean ± SD	Max
Polychaeta	**94.9 ± 131**	674	**41.6 ± 41.8**	161	**49.1 ± 21.2**	99	**46.6 ± 32.3**	123	**28.6 ± 24.9**	97	**24.7 ± 25.3**	115
Amphipoda	**34.6 ± 43.7**	189	**25.2 ± 23.3.**	91	7.1 ± 6.2	25	4.3 ± 4.4	81	2.2 ± 2.8	10	3.0 ± 3.5	15
Bivalvia	**22.7 ± 27.5**	154	**10.3 ± 19.2**	113	8.6 ± 13.7	53	7.4 ± 14	81	6.8 ± 11.5	51	2.0 ± 3.1	13
Nematoda	9.0 ± 11.4	41	5.9 ± 8.6	35	7.4 ± 10.2	45	4.6 ± 9.1	48	**10.3 ± 20.0**	91	6.5 ± 8.8	38
Sipuncula	5.4 ± 6.9	33	2.2 ± 2.5	9	4.2 ± 3.7	14	9.1 ± 11.1	46	6.1 ± 9.9	58	0.9 ± 1.8	9
Gastropoda	**13.5 ± 50.9**	329	2.5 ± 2.7	12	0.8 ± 1.9	9	1.2 ± 4.5	29	0.6 ± 1.1	4	0.3 ± 0.6	2
Tanaidacea	5.9 ± 18.7	90	4.5 ± 6.7	22	0.8 ± 1.6	7	0.6 ± 1.5	9	2.7 ± 4.9	29	4.0 ± 6.4	30
Decapoda	7.4 ± 9.8	40	5.1 ± 4.8	19	3.3 ± 3.4	13	1.5 ± 1.3	8	0.8 ± 1.3	6	0.1 ± 0.4	2
Ophiuroidea	8.5 ± 20.3	92	4.6 ± 4.2	22	0.9 ± 1.2	5	1.2 ± 1.7	8	0.3 ± 1.0	6	0.1 ± 0.4	2
Isopoda	5.0 ± 10	48	1.8 ± 2.2	9	1.0 ± 1.4	6	0.2 ± 0.7	18	1.8 ± 2.3	8	4.4 ± 5.2	18
Cumacea	2.3 ± 4	19	2.6 ± 3.2	12	1.5 ± 2.2	10	2.2 ± 2.8	12	1.2 ± 2.0	11	1.0 ± 1.4	6
Nemertea	2.7 ± 2.7	10	1.9 ± 1.7	6	1.2 ± 1.5	6	0.7 ± 1.1	4	0.4 ± 0.9	4	0.9 ± 1.3	6

Table 2 Mean and maximum density values [ind./0.1 m^2] with standard deviation (SD) on each of the transects (only most abundant taxa). The highest values are marked in bold.

	25 m		50 m		100 m		250 m		500 m		1000 m	
	Mean ± SD	Max	Mean ± SD	Max	Mean ± SD	Max	Mean ± SD	Max	Mean ± SD	Max	Mean ± SD	Max
G1												
Polychaeta	**34.6 ± 15.5**	59	**49.2 ± 28.3**	79	**32.2 ± 8.3**	41	**36.8 ± 21.7**	68	**54.8 ± 34.2**	97	**25.6 ± 16.2**	41
Amphipoda	**18.2 ± 6.8**	25	**42.2 ± 15.6**	66	5.4 ± 4.0	12	5.2 ± 3.3	11	6.3 ± 3.5	10	**7.6 ± 4.6**	15
Bivalvia	**27.8 ± 21.0**	60	3.2 ± 2.4	6	2.8 ± 4.1	9	**30.6 ± 32.3**	81	**9.5 ± 6.0**	18	5.2 ± 4.8	13
Nematoda	**7.2 ± 5.4**	14	6 ± 6.7	17	**8.6 ± 6.1**	17	3.4 ± 4.8	10	**19.0 ± 21.7**	42	**12.6 ± 4.8**	20
Sipuncula	5.8 ± 4.4	12	5.4 ± 2.4	8	5.2 ± 2.6	8	**13.8 ± 13.4**	31	**7.0 ± 5.4**	15	0.8 ± 0.8	2
Gastropoda	4.4 ± 4.8	12	3.0 ± 2.1	5	0.2 ± 0.4	1	**7.4 ± 12.6**	29	1.0 ± 0.8	2	0.4 ± 0.5	1
Tanaidacea	0.6 ± 0.9	2	4.6 ± 2.6	8	1.0 ± 2.2	5	—	—	1.3 ± 2.5	5	3.2 ± 4.1	9
Decapoda	3.6 ± 4.5	11	**10.8 ± 4.5**	18	4.0 ± 1.9	6	2.2 ± 1.9	5	0.5 ± 1.0	2	—	—
Ophiuroidea	1.4 ± 1.5	3	**11.4 ± 8.6**	21	1.2 ± 1.3	3	1.4 ± 1.5	3	—	—	—	—
Isopoda	0.8 ± 0.8	2	0.8 ± 0.8	2	0.4 ± 0.9	2	0.2 ± 0.4	1	1.3 ± 1.9	4	**13.8 ± 3.3**	18
Cumacea	3.4 ± 3.8	8	3.0 ± 2.7	7	1.6 ± 2.6	6	2.4 ± 2.2	6	2.3 ± 2.1	4	2.4 ± 1.5	4
Nemertea	5.2 ± 3.3	10	1.4 ± 1.1	3	0.6 ± 0.9	2	—	—	1.3 ± 1.0	2	1.0 ± 1.0	2
G2												
Polychaeta	**42.4 ± 14.9**	61	**28.6 ± 25.1**	56	**45.8 ± 8.3**	84	**43.8 ± 44.2**	112	**23.6 ± 14.3**	42	**56.8 ± 54.5**	115
Amphipoda	**16.8 ± 11.8**	37	**56.0 ± 33.7**	91	**11.2 ± 4.0**	25	5.8 ± 7.0	17	3.2 ± 4.1	10	2.0 ± 2.4	5

Table 2 (*Continued*)

	25 m		50 m		100 m		250 m		500 m		1000 m	
	Mean ± SD	Max	Mean ± SD	Max	Mean ± SD	Max	Mean ± SD	Max	Mean ± SD	Max	Mean ± SD	Max
Bivalvia	**22.4 ± 40.1**	94	4.2 ± 2.7	8	**10.8 ± 4.1**	27	**8.8 ± 11.6**	29	**7.6 ± 8.4**	22	4.8 ± 5.9	12
Nematoda	0.8 ± 1.8	4	5.2 ± 6.3	16	**17.4 ± 6.1**	45	4.8 ± 5.0	12	4.8 ± 6.0	15	3.5 ± 3.0	6
Sipuncula	2.8 ± 2.8	7	3.2 ± 2.8	6	**9.0 ± 2.6**	12	**11.6 ± 13.0**	32	**10.4 ± 4.8**	16	2.5 ± 4.4	9
Gastropoda	0.4 ± 0.5	1	1.2 ± 1.6	4	4.4 ± 0.4	9	0.2 ± 0.4	1	0.8 ± 1.8	4	0.3 ± 0.5	1
Tanaidacea	0.6 ± 1.3	3	5.4 ± 4.5	12	3.2 ± 2.2	7	2.0 ± 3.9	9	**7.0 ± 12.4**	29	0.5 ± 0.6	1
Decapoda	3.8 ± 3.1	7	6.8 ± 5.4	15	4.2 ± 1.9	13	1.4 ± 1.1	3	0.2 ± 0.4	1	—	—
Ophiuroidea	2.0 ± 2.1	5	**12.8 ± 7.1**	22	0.6 ± 1.3	2	1.0 ± 0.7	2	—	—	0.5 ± 0.6	1
Isopoda	0.2 ± 0.4	1	2.2 ± 1.8	5	1.0 ± 0.9	2	0.2 ± 0.4	1	2.8 ± 3.0	8	1.8 ± 2.2	5
Cumacea	0.4 ± 0.9	2	3.8 ± 4.0	9	1.2 ± 2.6	4	1.8 ± 1.1	3	0.6 ± 0.9	2	0.5 ± 1.0	2
Nemertea	1.2 ± 1.6	4	1.6 ± 1.1	3	2.0 ± 0.9	5	0.2 ± 0.4	1	—	—	2.3 ± 2.6	6
G3												
Polychaeta	**57.6 ± 51.4**	126	**39.8 ± 35.4**	94	**47.2 ± 9.2**	59	**41.4 ± 17.8**	64	**25.6 ± 13.1**	42	**21.5 ± 26.0**	59
Amphipoda	4.6 ± 4.8	12	7.2 ± 6.9	19	**7.6 ± 4.3**	13	4.6 ± 5.4	13	1.6 ± 1.5	3	4.0 ± 3.7	8
Bivalvia	**56.0 ± 58.9**	154	6.0 ± 3.3	9	1.2 ± 0.8	2	1.2 ± 1.3	3	1.4 ± 2.2	5	1.3 ± 1.5	3
Nematoda	8.8 ± 8.3	18	4.2 ± 5.6	14	2.4 ± 5.4	12	2.8 ± 5.2	12	**15.6 ± 20.2**	41	**10.5 ± 10.8**	24
Sipuncula	**16.0 ± 11.7**	33	2.0 ± 2.0	5	2.8 ± 1.5	5	2.8 ± 1.3	4	**11.2 ± 6.2**	19	2.8 ± 2.8	6
Gastropoda	1.4 ± 1.1	3	2.8 ± 1.6	5	0.6 ± 0.5	1	0.2 ± 0.4	1	0.4 ± 0.5	1	—	—
Tanaidacea	—	—	1.6 ± 3.0	7	1.6 ± 1.1	3	0.4 ± 0.5	1	1.4 ± 1.5	3	4.0 ± 4.3	10
Decapoda	3.2 ± 2.3	7	1.0 ± 1.2	3	3.4 ± 5.3	12	1.0 ± 1.4	3	1.0 ± 1.2	3	0.3 ± 0.5	1
Ophiuroidea	1.8 ± 1.6	3	1.2 ± 1.6	4	1.0 ± 1.0	2	0.2 ± 0.4	1	—	—	0.5 ± 1.0	2
Isopoda	1.2 ± 0.8	2	0.2 ± 0.4	1	2.0 ± 2.3	5	0.4 ± 0.5	1	1.6 ± 3.6	8	**6.8 ± 6.7**	16
Cumacea	0.8 ± 1.1	2	1.2 ± 1.3	3	1.8 ± 2.5	6	1.4 ± 2.2	5	0.6 ± 1.3	3	1.0 ± 1.4	3
Nemertea	4.6 ± 2.6	7	0.8 ± 1.3	3	2.0 ± 1.9	5	0.6 ± 1.3	3	—	—	1.3 ± 1.5	3
G4												
Polychaeta	**22.4 ± 20.6**	45	**34.8 ± 27.1**	74	**46.8 ± 19.3**	77	**29.6 ± 12.5**	42	**57.6 ± 24.8**	79	**13.6 ± 5.7**	22
Amphipoda	**17.6 ± 24.3**	61	**21.2 ± 16.6**	40	**8.8 ± 9.0**	22	5.6 ± 4.2	12	0.6 ± 0.5	1	3.4 ± 2.2	7
Bivalvia	**13.0 ± 5.7**	22	4.6 ± 5.4	13	3.6 ± 3.8	9	4.4 ± 3.0	7	2.0 ± 1.6	4	1.2 ± 1.3	3
Nematoda	**9.0 ± 9.2**	24	5.0 ± 4.7	10	**16.6 ± 12.9**	30	3.6 ± 3.2	8	**38.8 ± 41.5**	91	4.8 ± 5.8	12
Sipuncula	4.8 ± 3.7	9	3.2 ± 3.5	9	4.6 ± 5.5	14	3.8 ± 3.2	8	—	—	0.8 ± 0.8	2
Gastropoda	0.6 ± 0.9	2	2.0 ± 2.1	5	—	—	0.4 ± 0.5	1	—	—	0.4 ± 0.9	2
Tanaidacea	1.2 ± 1.6	4	**9.0 ± 8.2**	18	0.2 ± 0.4	1	1.2 ± 0.4	2	1.8 ± 1.3	4	**13.2 ± 9.9**	30
Decapoda	3.6 ± 3.6	8	3.6 ± 2.4	7	2.2 ± 2.9	7	1.6 ± 0.9	3	2.4 ± 2.5	6	—	—
Ophiuroidea	3.8 ± 2.6	7	1.4 ± 1.1	3	0.2 ± 0.4	1	2.6 ± 3.1	8	—	—	—	—
Isopoda	1.6 ± 2.1	5	2.2 ± 2.2	5	—	—	—	—	0.4 ± 0.5	1	3.8 ± 2.3	7
Cumacea	1.0 ± 1.7	4	4.4 ± 4.3	9	1.2 ± 1.3	3	5.2 ± 3.1	8	0.4 ± 0.9	2	1.0 ± 1.0	2
Nemertea	—	—	1.0 ± 1.2	3	0.2 ± 0.4	1	0.2 ± 0.4	1	0.4 ± 0.9	2	0.8 ± 1.3	3
G5												
Polychaeta	**47.2 ± 41.5**	112	**71.0 ± 65.0**	138	**58.2 ± 27.8**	90	**37.4 ± 18.7**	51	**37.5 ± 34.0**	85	**19.0 ± 6.6**	25
Amphipoda	**16.6 ± 5.0**	22	**40.2 ± 11.8**	59	**8.0 ± 4.6**	13	3.2 ± 2.9	8	1.5 ± 2.4	5	3.2 ± 4.0	10

Table 2 (*Continued*)

	25 m		50 m		100 m		250 m		500 m		1000 m	
	Mean ± SD	Max	Mean ± SD	Max	Mean ± SD	Max	Mean ± SD	Max	Mean ± SD	Max	Mean ± SD	Max
Bivalvia	**13.0 ± 4.9**	20	6.0 ± 3.7	10	2.4 ± 1.9	5	0.6 ± 0.9	2	1.5 ± 1.0	2	1.0 ± 0.7	2
Nematoda	**22.6 ± 16.8**	38	**13.8 ± 11.7**	33	**10.8 ± 11.3**	23	1.8 ± 2.0	5	5.8 ± 9.5	20	1.6 ± 1.7	4
Sipuncula	1.6 ± 3.0	7	2.2 ± 1.3	4	4.4 ± 3.5	9	**30.2 ± 9.6**	46	**22.0 ± 24.4**	58	–	–
Gastropoda	**10.4 ± 22.7**	51	3.0 ± 2.5	7	0.2 ± 0.4	1	–	–	1.5 ± 1.7	4	0.4 ± 0.5	1
Tanaidacea	0.4 ± 0.5	1	**10.8 ± 9.4**	22	1.0 ± 1.0	2	0.2 ± 0.4	1	2.5 ± 4.4	9	2.0 ± 2.8	6
Decapoda	4.2 ± 1.6	6	6.6 ± 8	19	4.2 ± 3.2	9	1.2 ± 1.3	3	1.0 ± 2.0	4	–	–
Ophiuroidea	0.8 ± 0.8	2	1.8 ± 3.5	8	1.2 ± 2.2	5	–	–	0.3 ± 0.5	1	–	–
Isopoda	2.0 ± 0.7	3	2.4 ± 2.7	7	1.0 ± 1.2	3	–	–	2.3 ± 3.3	7	2.6 ± 1.8	5
Cumacea	1.8 ± 1.5	4	2.4 ± 2.9	6	1.0 ± 1.7	4	4.2 ± 1.3	6	1.3 ± 1.0	2	0.4 ± 0.9	2
Nemertea	2.2 ± 1.5	4	2.0 ± 2.0	5	0.8 ± 0.4	1	0.6 ± 1.3	3	1.0 ± 1.4	3	0.2 ± 0.4	1
G6												
Polychaeta	**139.2 ± 133.1**	286	**77.6 ± 78.8**	161	**59.0 ± 26.9**	99	**38.6 ± 19.0**	66	**22.2 ± 16.5**	48	**54.8 ± 20.7**	77
Amphipoda	**60.2 ± 14.1**	71	**35.4 ± 18.6**	58	5.0 ± 3.4	9	**8.4 ± 5.8**	18	1.2 ± 0.4	2	6.0 ± 2.6	9
Bivalvia	**22.6 ± 18.0**	46	**12.0 ± 12.6**	32	1.8 ± 1.9	5	4.2 ± 2.3	8	3.2 ± 2.6	7	3.3 ± 3.4	8
Nematoda	6.6 ± 4.4	12	**16.2 ± 14.5**	35	4.8 ± 8.2	19	1.2 ± 1.3	3	**9.0 ± 6.9**	18	**23.8 ± 11.4**	38
Sipuncula	2.0 ± 2.1	5	1.6 ± 2.5	6	3.4 ± 4.1	10	6.6 ± 3.9	13	5.8 ± 5.8	12	0.3 ± 0.5	1
Gastropoda	8.2 ± 17.2	39	3.2 ± 5.0	12	0.2 ± 0.4	1	1.2 ± 1.1	2	0.4 ± 0.9	2	0.5 ± 1.0	2
Tanaidacea	1.0 ± 1.0	2	7.2 ± 9.1	19	0.4 ± 0.9	2	–	–	3.6 ± 3.5	8	2.8 ± 4.9	10
Decapoda	9.0 ± 5.8	18	3.2 ± 2.9	7	1.6 ± 1.5	4	1.4 ± 1.1	3	1.4 ± 0.9	2	0.8 ± 1.0	2
Ophiuroidea	1.6 ± 1.5	3	2.6 ± 2.7	7	0.8 ± 1.1	2	0.4 ± 0.9	2	–	–	–	–
Isopoda	7.2 ± 3.8	12	4.6 ± 3.4	9	0.8 ± 0.8	2	0.8 ± 1.8	4	4.0 ± 2.3	7	**7.8 ± 6.8**	17
Cumacea	9.2 ± 7.2	19	6.4 ± 4.6	12	1.0 ± 2.2	5	3.0 ± 5.1	12	1.0 ± 1.0	2	1.8 ± 1.0	3
Nemertea	3.0 ± 4.1	8	3.0 ± 2.1	6	0.6 ± 1.3	3	1.0 ± 1.2	3	1.2 ± 1.6	4	2.0 ± 1.8	4
G7												
Polychaeta	**292.2 ± 279.4**	674	**18.6 ± 16.6**	36	**63.0 ± 23.2**	91	**95.4 ± 26.2**	123	**12.0 ± 2.0**	14	**12.0 ± 5.9**	20
Amphipoda	**126.8 ± 64.0**	189	**14.8 ± 13.6**	37	6.4 ± 4.4	13	2.0 ± 1.4	4	0.4 ± 0.9	2	0.6 ± 0.5	1
Bivalvia	**17.0 ± 13.9**	31	6.4 ± 4.1	10	**22.8 ± 16.3**	49	4.0 ± 5.8	14	3.0 ± 2.2	7	0.6 ± 0.5	1
Nematoda	4.6 ± 4.5	9	0.2 ± 0.4	1	1.4 ± 2.2	5	**23.0 ± 17.2**	48	0.2 ± 0.4	1	0.2 ± 0.4	1
Sipuncula	6.4 ± 5.0	15	0.2 ± 0.4	1	4.8 ± 2.4	8	**8.6 ± 5.9**	16	1.4 ± 1.9	4	0.2 ± 0.4	1
Gastropoda	**90.8 ± 135.9**	329	1.8 ± 1.1	3	0.2 ± 0.4	1	0.6 ± 0.9	2	0.2 ± 0.4	1	–	–
Tanaidacea	**48.0 ± 35.2**	90	0.6 ± 0.9	2	–	–	1.6 ± 1.1	3	1.4 ± 1.1	3	2.4 ± 3.8	9
Decapoda	**30.8 ± 11.3**	40	4.6 ± 3.8	9	6.2 ± 3.5	8	2.6 ± 1.3	4	0.2 ± 0.4	1	–	–
Ophiuroidea	**59.6 ± 26.8**	92	6.0 ± 5.3	15	1.4 ± 1.1	3	2.4 ± 2.2	6	0.6 ± 0.9	2	–	–
Isopoda	**28.2 ± 15.8**	48	1.6 ± 1.8	4	0.8 ± 1.3	3	0.2 ± 0.4	1	1.6 ± 1.8	4	1.4 ± 1.1	3
Cumacea	0.8 ± 1.8	4	1.0 ± 1.0	2	4.0 ± 3.8	10	1.4 ± 2.2	5	0.8 ± 0.8	2	1.2 ± 2.7	6
Nemertea	2.0 ± 1.6	4	1.2 ± 1.6	4	0.8 ± 0.8	2	1.2 ± 1.3	3	–	–	0.6 ± 0.5	1
G8												
Polychaeta	**107.0 ± 83.8**	200	**39.0 ± 22.4**	61	**37.4 ± 16.7**	56	**75.4 ± 34.3**	116	**23.4 ± 25**	67	**28.2 ± 12.9**	45
Amphipoda	**36.5 ± 31.1**	79	7.2 ± 6.1	17	0.8 ± 1.3	3	2.4 ± 1.7	5	5.2 ± 2.9	9	0.8 ± 0.8	2

Table 2 (*Continued*)

	25 m		50 m		100 m		250 m		500 m		1000 m	
	Mean ± SD	Max	Mean ± SD	Max	Mean ± SD	Max	Mean ± SD	Max	Mean ± SD	Max	Mean ± SD	Max
Bivalvia	**11.0 ± 8.3**	20	**40.2 ± 46.3**	113	0.4 ± 0.5	1	4.4 ± 4.2	10	**31.6 ± 18.1**	51	1.2 ± 1.3	3
Nematoda	2.8 ± 3.0	7	2.6 ± 2.6	6	1.8 ± 0.8	3	0.2 ± 0.4	1	0.2 ± 0.4	1	5.2 ± 5.4	14
Sipuncula	7.5 ± 10.5	23	1.6 ± 1.5	4	–	–	0.2 ± 0.4	1	0.4 ± 0.5	1	1.0 ± 1.7	4
Gastropoda	0.8 ± 0.5	1	3.8 ± 3.3	9	0.4 ± 0.5	1	0.4 ± 0.5	1	1.0 ± 1.7	4	0.6 ± 0.5	1
Tanaidacea	0.3 ± 0.5	1	0.6 ± 0.9	2	–	–	0.2 ± 0.4	1	4.6 ± 4.4	11	6.8 ± 9.6	23
Decapoda	4.8 ± 2.5	8	7.4 ± 4.3	11	2.2 ± 2.0	4	1.8 ± 0.4	2	0.2 ± 0.4	1	–	–
Ophiuroidea	3.3 ± 2.5	6	4.6 ± 5.7	13	0.8 ± 0.4	1	0.4 ± 0.9	2	1.4 ± 2.6	6	–	–
Isopoda	1.8 ± 3.5	7	1.4 ± 1.5	3	0.2 ± 0.4	1	–	–	1.8 ± 1.6	4	2.6 ± 1.8	5
Cumacea	2.3 ± 4.5	9	0.4 ± 0.5	1	–	–	–	–	3.8 ± 4.5	11	0.2 ± 0.4	1
Nemertea	3.0 ± 0.0	3	4.2 ± 1.1	5	2.6 ± 2.2	6	2.0 ± 1.4	4	0.4 ± 0.9	2	0.6 ± 0.9	2
G9												
Polychaeta	**113.8 ± 86.3**	247	**16.0 ± 8.4**	27	**52.0 ± 21.8**	76	14.5 ± 3.9	18	**8.0 ± 8.1**	21	3.0 ± 1.6	5
Amphipoda	14.2 ± 9.5	24	2.4 ± 3.4	8	**10.4 ± 7.8**	20	0.5 ± 0.6	1	0.6 ± 0.9	2	–	–
Bivalvia	**19.0 ± 12.3**	35	**9.8 ± 17.5**	41	**31.2 ± 19.4**	53	**8.5 ± 7.4**	18	0.6 ± 0.5	1	0.2 ± 0.4	1
Nematoda	**17.0 ± 20.2**	41	–	–	3.0 ± 4.5	11	–	–	–	–	–	–
Sipuncula	1.8 ± 1.5	4	–	–	3.4 ± 3.1	8	2.8 ± 2.5	6	–	–	–	–
Gastropoda	2.0 ± 2.9	7	1.6 ± 3.6	8	1.2 ± 1.6	4	0.5 ± 1	2	0.4 ± 0.5	1	–	–
Tanaidacea	–	–	0.6 ± 0.9	2	0.2 ± 0.4	1	–	–	–	–	0.2 ± 0.4	1
Decapoda	3.2 ± 3.1	7	2.0 ± 1.6	4	1.8 ± 1.5	4	–	–	–	–	0.2 ± 0.4	1
Ophiuroidea	1.0 ± 1.7	4	–	–	1.0 ± 1.7	4	2.5 ± 1.3	4	0.6 ± 0.9	2	0.2 ± 0.4	1
Isopoda	1.0 ± 0.9	2	0.4 ± 0.5	1	2.4 ± 2.3	6	0.25 ± 0.5	1	0.4 ± 0.5	1	–	–
Cumacea	1.4 ± 2.2	5	0.6 ± 0.9	2	1.8 ± 1.3	3	–	–	0.2 ± 0.4	1	0.4 ± 0.9	2
Nemertea	3.4 ± 3.0	8	2.0 ± 1.6	4	1.2 ± 1.6	3	–	–	–	–	–	–

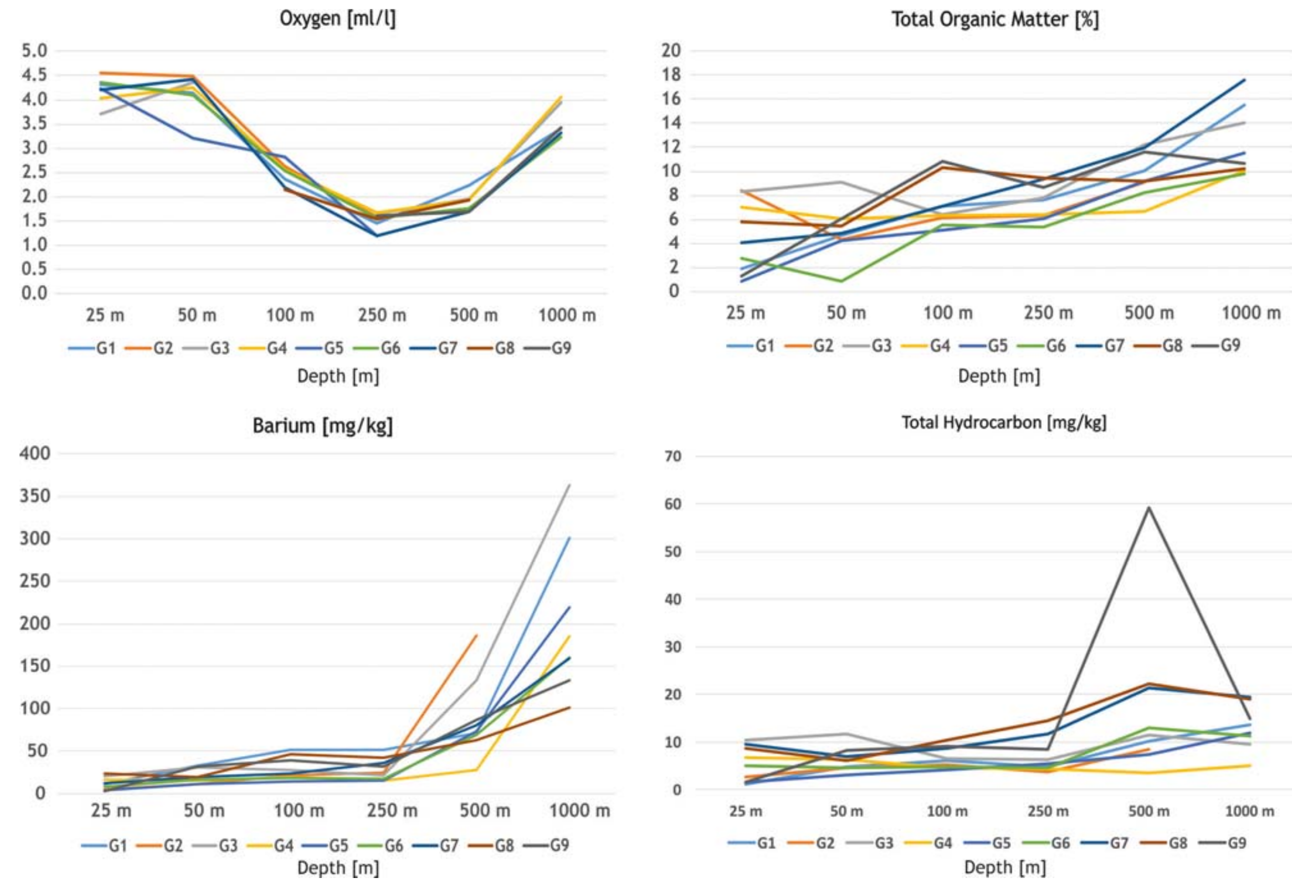

Figure 5 Concentrations of total organic matter, oxygen, barium and hydrocarbons on each of the studied transects.

Table 3 Characteristics of bottom deposits along a depth gradient on each of the transects.

	25 m	50 m	100 m	250 m	500 m	1000 m
G1	Fine sand	Very Fine sand	Very Fine sand	Fine sand	Silt clay	Silt clay
G2	Silt clay	Very Fine sand	Very Fine sand	Medium sand	Silt clay	—
G3	Silt clay	Silt clay	Very fine sand	Very fine sand	Silt clay	Silt clay
G4	Silt clay	Silt clay	Very fine sand	Very fine sand	Very fine sand	Silt clay
G5	Coarse sand	Fine sand	Very fine sand	Very fine sand	Silt clay	Silt clay
G6	Silt clay	Very fine sand	Fine sand	Fine sand	Silt clay	Silt clay
G7	Coarse sand	Very fine sand	Silt clay	Silt clay	Silt clay	Silt clay
G8	Medium sand	Silt clay	Silt clay	Silt clay	Silt clay	Silt clay
G9	Coarse sand	Fine sand	Silt clay	Silt clay	Silt clay	Silt clay

sediments (Dell'Anno et al., 2013). Moreover, deposit feeders associated with different depth zones might exploit different components of detritus (Carney, 2005). However, such functional analysis of the macrofauna is impossible on a higher taxa level. On the other hand, the highest values of polychaete and amphipod densities, observed at the 25-m station on transect G7, corresponded with the highest values of TOM observed for this depth at any of the transects, confirming the importance of TOM for macrofauna in the shallow shelf sites. The relationships between organic matter and the abundance of benthic communities might also be altered by the presence of oxygen minimum zones occurring in this region (Levin et al., 2009), although the lowest oxygen levels in our study were found between 250 and 500 m. Nevertheless, the highest values were recorded in the 25—50-m stations, which strongly corresponded with the areas of highest macrozoobenthos densities. Moreover, values below 0.5 ml/l (true oxygen minimum zone) (Levin, 2003) never occurred in our study. Nevertheless, it is also worth mentioning that the abundance of macrozoobenthos in the oxygen minimum zones might be relatively high. For example, in a study from northern Namibia, macrozoobenthos densities varied between 300 and 3350 ind./m^2 (Zettler et al., 2009) and were comparable to the highest values recorded on Ghana's coast, although the Namibian coast is characterised by a high productivity (Sakko, 1998).

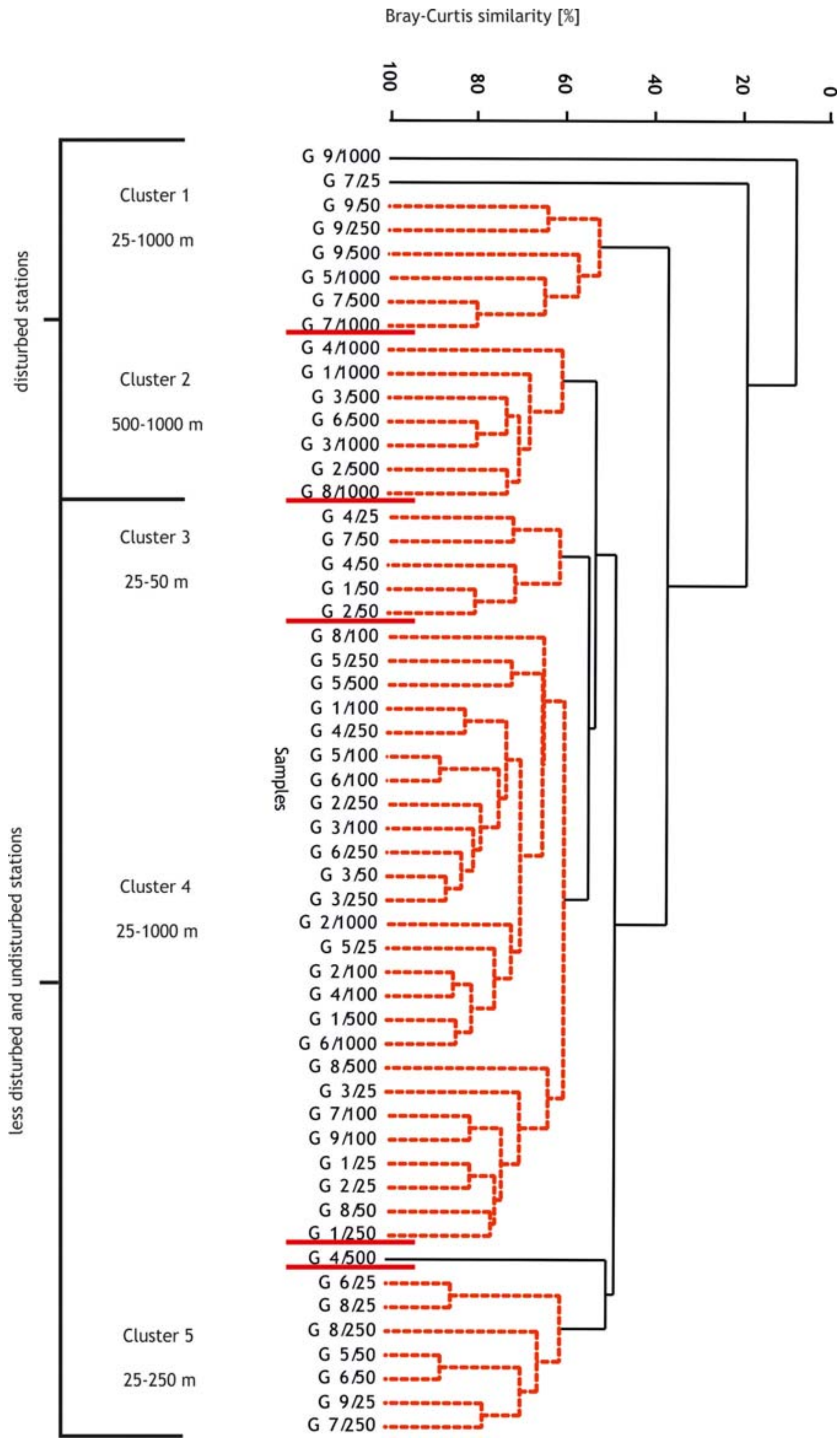

Figure 6 Dendrogram of stations for the Bray—Curtis similarity square root-transformed data and group average grouping method. (Spotted lines indicate the stations that cannot be significantly differentiated by SIMPROF.)

In the analysis of particular transects, the differences between the shallowest and the deepest stations were not statistically significant, while on one transect, the highest abundance was recorded for a depth of 500 m. These findings stress the importance of local conditions at the intermediate spatial scale along the coast of Ghana. Generally, such differences in abundance or diversity of benthic fauna across a scale of tens or hundreds of kilometres might be related to differences in sedimentary processes or productivity (Brind'Amour et al., 2009) and might be observed in vast

Table 4 Mean and maximum density values [ind./0.1 m^2] with standard deviation (SD) and frequency of occurrence *F* [%] in each of the groups of samples according to Bray—Curtis similarity analysis (only most abundant taxa). The highest values are marked in bold.

	Cluster 1			Cluster 2			Cluster 3			Cluster 4			Cluster 5		
	Mean ± SD	Max	*F* [%]	Mean ± SD	Max	*F* [%]	Mean ± SD	Max	*F* [%]	Mean ± SD	Max	*F* [%]	Mean ± SD	Max	*F* [%]
Polychaeta	**15.6 ± 6.6**	26.7	100.00%	**25.4 ± 2.2**	28.2	100.00%	**28.3 ± 7.9**	37.2	100.00%	**42.6 ± 12.7**	63.0	100.00%	**102.4 ± 30.6**	144.4	100.00%
Amphipoda	1.3 ± 1.2	3.2	100.00%	3.0 ± 2.5	7.6	100.00%	**29.1 ± 17.1**	56.0	100.00%	**7.5 ± 4.3**	18.2	100.00%	**17.0 ± 20.3**	54.6	100.00%
Bivalvia	**3.8 ± 4.0**	9.8	100.00%	3.4 ± 2.5	7.6	100.00%	6.2 ± 4.1	13.0	100.00%	11.6 ± 14.0	56.0	100.00%	**11.5 ± 7.3**	22.6	100.00%
Nematoda	0.4 ± 0.6	1.6	66.67%	**9.4 ± 4.2**	15.6	100.00%	4.4 ± 3.3	9.0	100.00%	**6.9 ± 6.6**	22.6	100.00%	8.7 ± 7.3	22.6	100.00%
Sipuncula	0.6 ± 1.0	2.2	50.00%	3.8 ± 4.1	11.2	100.00%	3.1 ± 1.7	4.8	100.00%	5.0 ± 4.1	16.0	100.00%	3.4 ± 3.2	8.6	100.00%
Gastropoda	0.5 ± 0.6	1.6	83.33%	0.5 ± 0.2	0.8	100.00%	1.5 ± 0.6	2.0	100.00%	1.4 ± 1.9	7.4	95.65%	5.2 ± 6.5	18.8	100.00%
Tanaidacea	1.1 ± 1.0	2.4	83.33%	4.2 ± 2.2	7.0	100.00%	3.9 ± 3.4	9.0	100.00%	1.1 ± 1.2	4.6	82.61%	3.1 ± 3.8	9.8	85.71%
Decapoda	0.4 ± 0.8	2.0	50.00%	0.5 ± 0.6	1.4	66.67%	5.5 ± 2.3	9.0	100.00%	2.6 ± 1.9	7.4	95.65%	5.2 ± 3.3	10.0	100.00%
Ophiuroidea	0.7 ± 1.1	2.8	50.00%	0.1 ± 0.2	0.5	16.67%	7.1 ± 4.9	12.8	100.00%	1.2 ± 1.0	4.6	95.65%	3.5 ± 4.9	14.5	100.00%
Isopoda	1.1 ± 0.9	2.6	100.00%	**5.2 ± 4.5**	13.8	100.00%	1.6 ± 0.7	2.2	100.00%	1.3 ± 1.5	6.7	91.30%	3.2 ± 3.2	7.4	85.71%
Cumacea	0.5 ± 0.4	1.2	83.33%	1.0 ± 0.8	2.4	100.00%	2.5 ± 1.6	4.4	100.00%	1.9 ± 1.2	5.2	100.00%	3.3 ± 3.3	9.2	85.71%
Nemertea	0.5 ± 0.8	2.0	66.67%	0.7 ± 0.6	1.4	66.67%	0.9 ± 0.6	1.6	80.00%	1.5 ± 1.4	5.2	95.65%	2.5 ± 0.8	3.4	100.00%
Total macrozoobenthos abundance	28.2 ± 12.5	45.9	—	65.95 ± 12.8	87.6	—	105.12 ± 32.8	145.8	—	92.7 ± 26.0	165.6	—	185.1 ± 71.5	308.76	—
No. of higher taxa per sample	13.2 ± 2.9	18	—	17.3 ± 3.6	23.0	—	22.0 ± 1.6	24	—	19.9 ± 2.6	24	—	24.1 ± 5.8	35	—

basins that can be considered Large Marine Ecosystem (Piacenza et al., 2015). Our results show also strong local discrepancies (even on neighbouring transects) and demonstrate that depth-related patterns of distribution (Table 3) might differ from the global scale patterns observed by Rex et al. (2006). As already shown, such differences can be seen in patterns of standing stock and diversity, depending on local oceanographic processes (Aller et al., 2002; Coleman et al., 1997; McCallum et al., 2015). For example, mean values of polychaete densities at the same depths varied from tens to hundreds of individuals, depending on the transect. At the same time, patterns observed for different taxonomic groups such as amphipods, polychaetes or bivalves differed strongly, even on the same transect. Similar discrepancies might be associated with differences in species composition and functional diversity of benthic communities at particular zone depths (Carney, 2005; Levin and Sibuet, 2012).

Disturbance processes associated with human activities also influenced faunal densities at some of the investigated stations. This was clearly visible in the results of the CCA analysis and the cluster analysis, where various shelf and slope stations were grouped together if the levels of barium and other toxic metals or hydrocarbons were elevated. Barium compounds are used during oil extraction and are poorly soluble in water, enabling them to survive for a long time in bottom sediments (Olsgard and Gray, 1995) and to move with the bottom currents (Guiavarch et al., 2008). Metals such as barium or cadmium may affect the development of benthic invertebrates and reduce their abundance (Lira et al., 2011); however, in case of some tolerant species, their densities in polluted areas might be elevated (Ellis et al., 2012). On the Ghanaian coast, the highest concentrations of metals and hydrocarbons were recorded in the deepest stations in the silt and clay sediments, and those factors might additionally affect the abundance of benthic communities. Only the arsenic values were elevated mostly in the shallowest sites, but there was no clear influence of this metal visible in our study. Since there are no obvious anthropogenic sources of this metal in the shallow areas (25—50 m), we suppose that it originated from a type of geological formation in the study region. Generally, the environmental status of the investigated sites was good, and the levels of barium and other toxic metals were similar to the background levels according to the OSPAR and KLIF (Norwegian Pollution Authority) guidelines (Iversen et al., 2011), although some local disturbance was visible even in the analysis of the higher taxa, stressing the need for repeated monitoring in this region. In the case of the Ghanaian coast, even low pollution in the deepest areas might be reflected in the lower abundance of benthic communities as a result of joint effect of various natural and anthropogenic causes. It is also worth mentioning that even relatively small levels of pollution might result in responses of the benthic community, depending on the studied region and on other factors specific for a given area (Olsgard and Gray, 1995). For example, hydrocarbons might affect deep-sea benthic oxygen uptake (Main et al., 2015).

The need for the further monitoring of Ghanaian waters is obvious, since data about the influences of oil platforms and other human activities on the benthic fauna of this region is extremely limited (Ayamdoo, 2016; Scheren et al., 2002). Our

Table 5 Mean and maximum values of environmental variables (means with standard deviation) for each of the clusters according to Bray—Curtis similarity analysis.

	Cluster 1			Cluster 2			Cluster 3			Cluster 4			Cluster 5		
	Mean ± SD	Max	Min	Mean ± SD	Max	Min	Mean ± SD	Max	Min	Mean ± SD	Max	Min	Mean ± SD	Max	Min
As	10.9 ± 6.4	23.4	5.9	9.7 ± 5.9	21.6	5.8	32.5 ± 41.6	106.8	12.4	27.6 ± 41.0	185.8	4.6	25.1 ± 37.5	109.5	4.7
Ba	101.5 ± 74.4	219.6	31.6	192.3 ± 116.8	363.3	69.5	19.2 ± 8.0	32.6	11.5	33.2 ± 33.4	160.5	3.5	20.1 ± 14.6	42.6	3.3
Cd	0.3 ± 0.1	0.4	0.2	0.2 ± 0.03	0.3	0.2	0.1 ± 0.02	0.1	0.0	0.1 ± 0.06	0.31	0.02	0.1 ± 0.1	0.2	0.0
Cr	63.3 ± 9.9	78.1	48.6	60.9 ± 8.4	71.8	46.4	58.3 ± 19.8	90.9	42.4	48.9 ± 16.9	89.2	15.1	37.0 ± 15.4	56.3	15.0
Cu	16.5 ± 5.0	22.1	9.7	15.7 ± 5.4	22.6	8.3	4.0 ± 0.9	5.4	3.1	6.3 ± 3.8	15.2	0.5	6.7 ± 5.7	14.6	1.4
Ni	32.8 ± 6.9	39.1	22.4	31.9 ± 7.4	43.2	22.4	15.6 ± 4.3	23.0	12.3	17.1 ± 7.3	29.5	2.4	14.5 ± 10.4	26.7	3.0
Pb	6.2 ± 1.5	7.6	4.4	4.7 ± 2.5	9.2	2.4	8.78 ± 8.5	24.0	4.8	5.4 ± 4.2	19.8	1.4	5.4 ± 3.8	12.7	1.4
Zn	64.2 ± 9.6	74.5	47.5	62.3 ± 11.3	76.7	47.9	51.4 ± 18.5	84.2	39.6	52.6 ± 23.7	102.0	8.1	36.4 ± 22.9	71.4	6.2
Hg	0.02 ± 0.01	0.02	0.01	0.02 ± 0.01	0.04	0.01	0.01 ± 0.004	0.01	0.01	0.01 ± 0.01	0.03	0.01	0.01 ± 0.01	0.04	0.01
THC	21.4 ± 19.3	59.2	8.3	12.5 ± 3.7	18.9	8.4	5.9 ± 1.1	6.9	4.6	6.8 ± 4.6	22.2	1.1	7.0 ± 4.8	14.5	1.6
PAH	241.5 ± 429.8	1117.1	36.0	44.4 ± 21.9	86.7	27.2	25.0 ± 23.9	67.0	8.5	22.5 ± 20.6	91.6	4.6	51.9 ± 70.9	204.0	6.7
NPD	88.4 ± 72.6	229.6	34.3	41.2 ± 14.2	67.1	27.5	24.6 ± 6.7	35.1	18.0	26.5 ± 19.6	87.1	4.1	32.4 ± 25.9	69.6	9.3
TOM [%]	11.2 ± 3.9	17.6	6.1	11.5 ± 2.8	15.5	8.3	5.34 ± 1.1	7.0	4.3	6.9 ± 2.4	10.8	0.9	4.8 ± 3.6	9.5	0.9
Grain size distribution %															
<	79.5 ± 24.6	99.5	41.5	90.3 ± 9.7	99.5	77.4	44.3 ± 10.1	56.9	34.5	48.8 ± 26.7	98.9	3.7	50.6 ± 38.2	97.9	1.1
Sand	19.9 ± 23.6	55.3	0.5	9.6 ± 9.5	22.1	0.5	52.8 ± 8.4	65.1	43.1	49.8 ± 26.0	94.0	1.1	39.2 ± 28.9	72.5	2.1
Gravel	0.6 ± 1.3	3.1	0.0	0.1 ± 0.2	0.5	0.0	3.0 ± 5.4	12.6	0.0	1.4 ± 1.4	5.2	0.0	10.2 ± 13.4	30.2	0.0
Pressure	636.6 ± 323.2	975.0	246.0	735.8 ± 334.3	1187.0	492.0	41.2 ± 10.4	48.0	23.0	209.3 ± 243.8	1010.0	23.0	107.2 ± 114.6	267.0	18.0
Temperature	23.4 ± 10.7	28.2	4.2	10.0 ± 10.2	28.1	4.2	27.3 ± 1.9	28.9	24.8	23.4 ± 7.1	28.9	6.2	28.3 ± 0.3	28.9	28.1
Salinity	34.9 ± 0.3	35.5	34.6	34.7 ± 0.1	34.8	34.7	35.4 ± 0.1	35.5	35.3	35.3 ± 0.5	35.9	34.1	35.3 ± 0.2	35.5	35.1
Oxygen	2.4 ± 0.9	3.5	1.6	2.7 ± 1.0	3.9	1.8	4.3 ± 0.2	4.5	4.0	2.7 ± 1.1	4.6	1.5	3.1 ± 1.4	4.4	1.2

Table 6 SIMPER analysis for groups from dendrogram cluster.

Group 1_2	Average	Group 1_3	Average	Group 1_4	Average	Group 1_5	Average
Polychaeta	15.83%	Amphipoda	18.85%	Polychaeta	25.87%	Polychaeta	37.60%
Nematoda	8.44%	Polychaeta	14.01%	Bivalvia	7.86%	Amphipoda	10.85%
Tanaidacea	5.68%	Ophiuroidea	4.85%	Amphipoda	5.98%	Nematoda	4.82%
Sipuncula	4.42%	Decapoda	4.02%	Nematoda	4.77%	Bivalvia	3.49%
Isopoda	4.37%	Bivalvia	3.66%	Sipuncula	4.36%	Gastropoda	2.61%
		Group 2_3	Average	Group 2_4	Average	Group 2_5	Average
		Amphipoda	14.12%	Polychaeta	12.31%	Polychaeta	29.11%
		Polychaeta	4.66%	Bivalvia	6.43%	Amphipoda	8.99%
		Ophiuroidea	3.85%	Nematoda	3.84%	Nematoda	3.26%
		Decapoda	3.13%	Sipuncula	3.49%	Bivalvia	3.13%
		Nematoda	3.09%	Tanaidacea	2.96%	Tanaidacea	1.98%
				Group 3_4	Average	Group 3_5	Average
				Amphipoda	10.17%	Polychaeta	23.60%
				Polychaeta	8.20%	Amphipoda	7.51%
				Bivalvia	5.08%	Nematoda	3.19%
				Ophiuroidea	2.86%	Bivalvia	2.17%
				Nematoda	2.68%	Ophiuroidea	1.96%
						Group 4_5	Average
						Polychaeta	18.87%
						Amphipoda	7.73%
						Bivalvia	4.08%
						Nematoda	3.26%
						Sipuncula	1.87%

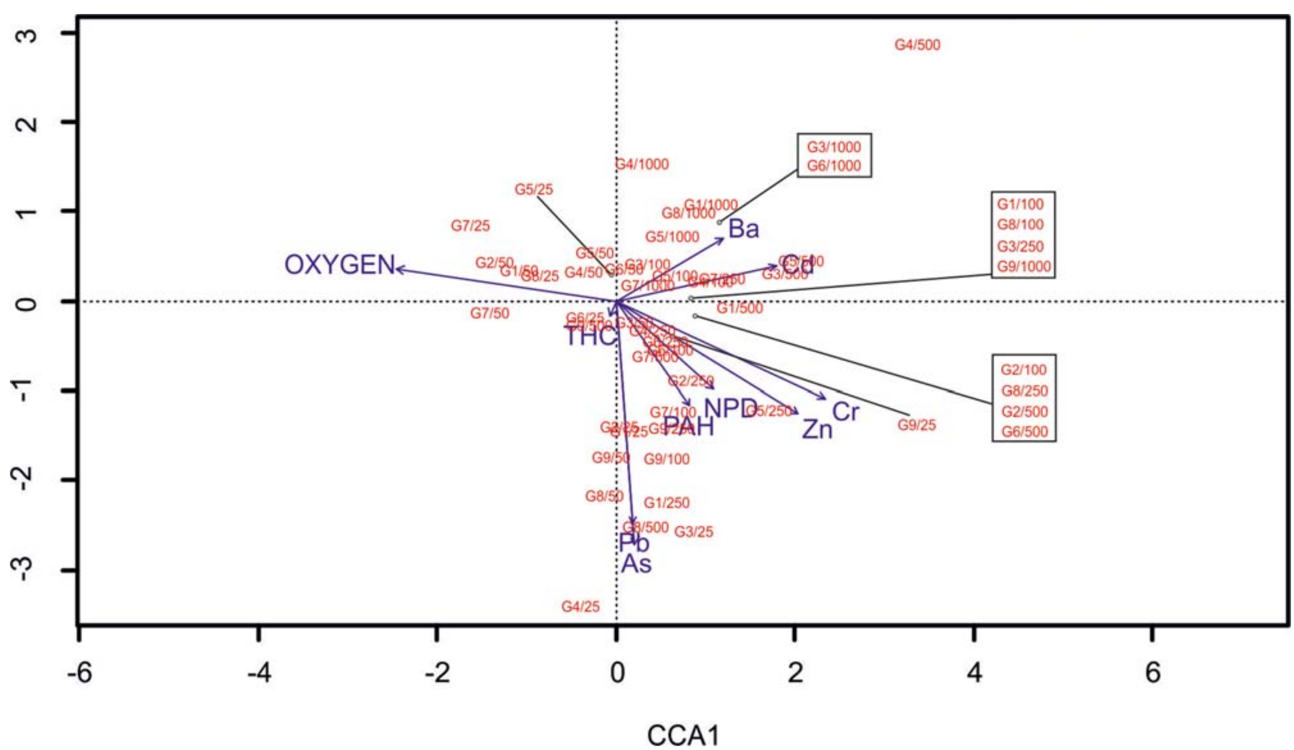

Figure 7 Distribution of stations according to environmental factors (Canonical Correspondence Analysis).

results might therefore be important for the development of sustainable management strategies under the concept of the "Large Marine Ecosystem" (Ukwe et al., 2003). The influence of low pollution levels, visible even in the analysis of higher taxa, might suggest vulnerability of those communities to such disturbance events. Włodarska-Kowalczuk and Kędra

Table 7 VIF and statistical significance of factors used in CCA.

	VIF	Significance
As	7.923847e+00	0.001
Ba	4.448803e+00	0.001
Cd	4.037395e+00	0.001
Cr	9.461655e+00	0.001
Pb	1.112333e+01	0.020
Zn	1.687098e+01	0.013
THC	4.069166e+00	0.012
PAH	1.462323e+01	0.001
NPD	1.419567e+01	0.017
Oxygen	4.417467e+00	0.002

(2007) have demonstrated that even data on generic level might be used as surrogate in the analysis of disturbance processes in benthic marine ecosystems. Nevertheless, further studies should include the analysis of species richness and diversity, especially in the case of the most important indicatory taxa such as amphipods and polychaetes (Olsgard et al., 2003; Ossa-Carratero et al., 2012). The spatial variation of abundance along the coast of Ghana also suggests the need for a closer investigation of the functional analysis of benthic communities based, for example, on the classification into various trophic guilds.

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