

Diversity, distribution patterns and indicatory potential of echinoderm communities of the tropical East Atlantic (Gulf of Guinea): Influence of multiple natural and anthropogenic factors along a 25–1000 m depth gradient

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ABSTRACT

All earlier studies of the West African echinoderm fauna have focused on taxonomy, and general knowledge about benthic community responses to various human related threats are poorly diagnosed and not monitored along the whole African coast. Our analysis of diversity and distribution patterns of Ghanaian echinoderms yielded 36 species. Material was collected at nine transects distributed along the coast of Ghana (25–1000 m depth range, total of over 270 samples). Gradual decreases in species richness, diversity, evenness and abundance were observed along the depth gradient, with the most diverse fauna being recorded on the shelf (25–50 m). The most abundant species were *Ophiactis luetkeni* and *Ophiothrix congensis*, although both had very patchy distributions. Cluster analysis separated shelf communities (25–100 m) from slope communities (500–1000 m), although on a low level of similarity. Our analysis allowed to select most vulnerable benthic habitats that should be amongst priorities of the future monitoring. Local influence of arsenic was observed at some shelf sites, while slope fauna was affected by elevated levels of hydrocarbons and barium. Changes in salinity and fluorescence also influenced echinoderm assemblages. The most general trend showed patchily distributed, diverse shallow water fauna being influenced by increased microhabitat diversity and food availability, while depauperate slope fauna was affected by local disturbances associated with oil extraction. Tropical echinoderm communities have a great potential as indicators of even minor and local pollution, although high patchiness and low abundance creates difficulties in the multivariate analysis. High sampling effort and high number of replicates allowed to minimise those problems and demonstrated small scale microhabitat diversity.

1. Introduction

Echinoderms are recorded from shallow shelf sites, down to abyssal depths (Mah and Blake, 2012; Stohr et al., 2012), but can also be found inhabiting the hadal zone (Zhang et al., 2021). They are the fourth most speciose marine taxon after crustaceans, molluscs and annelids. Moreover, according to some estimates, the true number of species might be as much as double the currently known number (Appeltans et al., 2012). This underestimation is especially obvious in tropical regions and deep-sea habitats that are poorly sampled and characterised by a very low rate of new species descriptions (Alvarado et al., 2012, 2022; Gondim et al., 2014; Mah and Blake, 2012; Rodrigues et al., 2011; Stohr et al., 2012).

Echinoderms can occur at high abundance and biomass in some ecosystems and habitats (Uthicke et al., 2009; Bergmann et al., 2010; Tilot et al., 2018; Rosellon-Druker and Stokesbury, 2019), and are key components of benthic biomass in particular (Pabis et al., 2011; Piepenburg and Juterzenka, 1994). This makes them an important element of energy transfer from pelagic to benthic zones (Ambrose et al., 2001; Lebrato et al., 2010). Echinoderms display a variety of feeding strategies representing a high functional diversity ranging from bioturbators (Belaústegui et al., 2017), to deposit feeders, omnivores, scavengers and predators, with the potential of ontogenetic changes in their role (Stohr et al., 2012). However, details of ecology and feeding habits for many echinoderm species are unknown (Dearborn et al., 1996; Fernandez and

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Boudouresque, 2000).

Despite the important roles of echinoderms in marine benthic ecosystems, the majority of community ecology studies have been conducted at shallow shelf sites (e.g. Rowe and Richmond, 2004; Jones et al., 2006; Iken et al., 2010; Alvarado et al., 2012; Rosellon-Druker and Stokesbury, 2019), and knowledge about deep-sea communities is incomplete or lacking (e.g. Fujita and Ohta, 1990; Hughes et al., 2011; Ruhl et al., 2014; Christodoulou et al., 2020). There is limited research into depth-related trends (Gage and Tyler, 1982; Howell et al., 2002; Nephin et al., 2014), and studies describing the influence of anthropogenic factors on deep-sea communities (Jones et al., 2007; Ross et al., 2016; De Smet et al., 2021). At the same time echinoderms are susceptible to ocean acidification (Dupont et al., 2010) and to other global changes, including warming (Gooding et al., 2009; Morley et al., 2014) and oxygen deficiency (Parameswaran et al., 2018). They might be an important indicators of pollution, physical disturbance associated with oil drilling and other types of anthropogenic changes (Joly-Turquin et al., 2009; Jones et al., 2006; Li et al., 2021; Lukyanova et al., 2017; Portocali et al., 1997; Skold and Gunnarsson, 1996; Temara et al., 1998). Heavy metals and/or hydrocarbons might accumulate in their digestive system (Besten et al., 2001; Gounin et al., 1995) and gonads, influencing reproduction, development and growth (Lukyanova et al., 2017; Schroder et al., 2005), or affect fitness by altering some important adaptations, like bioluminescence (Deheyn et al., 2000). Particular toxic agents might cause sex-specific reactions (Wang et al., 2021b). Moreover, echinoderm larvae are characterized by rapid response to wide range of stressors (Morrone et al., 2023). Recent studies suggested also that similarity of echinoderm genome to vertebrate genomes and their complex immune systems results in high adaptive potential (Pinsino and Matranga, 2014). Therefore, studies of the echinoderm responses might have implications not only for monitoring and assessment of invertebrate communities but also as proxy for describing potential responses of vertebrate fauna. Pollution may result in decline of abundance, even at early stage of disturbance, morphological malformations or avoidance of contaminated sites (Chiarelli et al., 2019; Lenihan et al., 2003; Ryder et al., 2004), on the other hand more mobile forms might indicate recovery of the habitat after disturbance (Fernandez-Torquemada et al., 2013), while some taxa display rapid decontamination abilities and are resistant to particular pollution agents (Joly-Turquin et al., 2009).

Nevertheless, earlier studies are focused on ecotoxicological responses of single model species that are easy to breed in laboratory conditions, like *Paracentrotus lividus* (Warnau et al., 1998; Chiarelli et al., 2016, 2019) or recently also *Holothuria polii* (Rakaj et al., 2019; Morrone et al., 2020). Those species mostly represent North Atlantic of Mediterranean shallow water fauna (Newton and McKenzie, 1995; Sarly et al., 2023; Schroder et al., 2005). Narrow geographic and taxonomic range of available data contrasts with very high diversity of echinoderms and their wide distribution in different habitats, depth zones and regions (Mah and Blake, 2012; Stohr et al., 2012). There are more detailed studies of species representing less than one permille of the known echinoderm diversity and we lack information from the tropics. We especially lack studies of community level responses, where numerous species interact with each other and are affected by various natural and anthropogenic factors. Multiple stressors may differently affect particular species, making some changes visible only at community level (Kroeker et al., 2011; O'Brien and Keough, 2013). Moreover, other factors might potentially enhance or diminish the influence of pollution. Some echinoderm studies demonstrated combined effects of temperature and pollution (Hutchins et al., 1996; Li et al., 2021) or hypoxia and organic enrichment (Nilsson, 1999). Large organisms like echinoderms may have importance in mutual interaction occurring at small and intermediate scale in natural systems. For example it was suggested that presence of echinoderms may induce modifications in biodisponibility of heavy metals for other deposit feeders (Gounin et al., 1995). Bio-turbation by echinoderms may also increase abundance of other invertebrates in the contaminated sediments or cause shifts in species

composition (Lenihan et al., 2018). In the areas like Gulf of Guinea, region prone to climate changes, characterized by presence of oxygen minimum zones and influenced by different pollution agents (Ukwe et al., 2003; Pabis et al., 2020), such complicated interactions might be an important element of ecosystem responses. Nevertheless, such multifactor studies cannot be done in the experimental conditions.

Published analyses of the long term echinoderm responses to changes are very scarce (Gates and Jones, 2012; Ross et al., 2016) and in the tropical regions, including the East Atlantic, there is a lack of even basic knowledge about echinoderm distribution patterns and diversity. Overall our knowledge about tropical benthic community responses to disturbance or assessments of ecosystem health is extremely scarce (Soares et al., 2022). Such data could constitute a benchmark for future monitoring, and improve understanding of ecological processes and their potential responses to global changes or local pollution events. Moreover, such baseline knowledge could facilitate an understanding of ecosystem recovery processes, help in the development of management plans and allow the identification of regional indicator species.

Basins like the Gulf of Guinea, which is a Large Marine Ecosystem (LME) and a separate ecoregion (Spalding et al., 2007) are considered of key importance for our understanding of global patterns in benthic ecology and diversity. At the same time, they suffer from enormous lack of sampling, which prevents meaningful analyses of zoogeographic trends and benthic community composition, and limits reliable diversity estimates (Menegotto and Rangel, 2018). The bias in basic knowledge about the diversity of the Ghanaian upwelling ecoregion was recently demonstrated for cumaceans (Stepien et al., 2021), tanaidaceans (Jozwiak et al., 2022) and polychaetes (Sobczyk et al., 2023), with large numbers of species new to science being recorded in each of these taxonomic groups.

As far as the echinoderms of this region are concerned, there is not a single quantitative study dedicated to the community ecology of this group along a 10 000 km stretch of the West African coast. However, some earlier studies based on analysis of bottom images and ROV movies analysed megaepibenthic communities in Ivory Coast (Lebrato and Jones, 2009), Mauretania (Jones and Brewer 2012), Nigeria (Jones et al., 2013) and Angola (Biede et al., 2022). The majority of studies, mostly published in the first half of the 20th century, has been focused on echinoderm taxonomy (e.g. Koehler, 1914; Clark 1955; 1974, Madsen, 1950; Bohn, 2006; Gluck et al., 2012). Moreover, the Gulf of Guinea has generally been neglected in studies of benthic ecology and diversity. There are only a few shallow water analyses from Ghana (Bassindale, 1961; Buchanan, 1957; Longhurst, 1958), and a few more recent research studies from deeper areas (Jozwiak et al., 2020; Pabis et al., 2020; Sobczyk et al., 2021, 2023; Stepien et al., 2021). The benthic macrofaunal communities of the Angola-Congo margin have also been studied, but material was mostly identified only to higher taxonomic units (Brind'Amour et al., 2009; Gaever et al., 2009; Galeron et al., 2009; Menot et al., 2009), making the analyses of benthic biodiversity uncertain.

General knowledge about diversity, distribution patterns and functioning of species in the Gulf of Guinea benthic ecosystem is poor. Currently we know nothing about about the benthic community responses in the tropical part of the Atlantic. This basin is exposed to enormous anthropogenic pressures that are constantly increasing. They are mostly associated with warming, pollution, industrialisation and other human activities (Ukwe et al., 2003; Scheren et al., 2002; Ayam-doo, 2016) and their influence on marine fauna is entirely unmonitored. The benthic ecosystem here is also influenced by various natural factors, including upwelling and the presence of oxygen minimum zones (Levin et al., 2009; Djagoua et al., 2011), which make it an area characterised by a very complicated set of ecological and functional interactions (Sobczyk et al., 2021). The Gulf of Guinea might be considered a natural laboratory for studies of tropical benthic ecology in times of global change and a regional model of benthic ecosystem health assessment in the tropics. It is an important region for meaningful analysis of

zoogeography and bioregionalism of the Atlantic, as well as an area of growing economic interest. The aim of this study, therefore, was to analyse the diversity and distribution patterns of echinoderm communities in the coastal waters of Ghana, against a background of natural factors (e.g. sediment structure, organic matter content, salinity) and human-related disturbance associated with oil extraction (e.g. heavy metal concentrations, hydrocarbon content), along a 25–1000 m depth gradient. We also aimed to identify the priority monitoring sites and potentially vulnerable habitats or depth zones.

2. Material and methods

2.1. Study area

The Gulf of Guinea is a large, open gulf in the tropical East Atlantic. It is treated as a separate zoogeographic province (Spalding et al., 2007) and includes fragments of two abyssal provinces (Watling et al., 2013). The Gulf is influenced by the Guinea, South Equatorial, and Benguela Currents (Le Loeuff and Cosel, 1998), making it interesting from a zoogeographic point of view (Fig. 1). This area suffers from processes associated with coastal erosion, oxygen minimum zones, and seasonal upwelling (Levin, 2003; Ukwe et al., 2003; Hahn et al., 2014; Nieto and Mèlin, 2017; Pabis et al., 2020). The coastal areas of Ghana, in particular, fall within an atypical climatic region (Loeuff and Cosel, 1998) and form a separate marine ecoregion (Spalding et al., 2007). The 565 km-long coast of Ghana is affected by various human activities that might result in local pollution and disturbance. The most important anthropogenic factors shaping the Ghanaian coast are related to oil and gas extraction, the dyeing industry and the removal of sand (Acquah, 1995; Addo, 2010; Jonah et al., 2017; Hanson and Kwarteng, 2019). The sampling stations were uniformly distributed along the coast of Ghana, also in vicinity of areas potentially affected by oil extraction like Sekondi-Takoradi. Fig. 1 identifies some of the more important points of pollution sources. However, particular pollution agents cannot be

associated with an individual point of origin, because oil blocks are distributed along the whole coast of Ghana (Fiave, 2018).

2.2. Sampling

Material was collected using a 0.1 m² van Veen grab, supported with a VAMS (Video Assisted Monitoring System), which enabled monitoring of the sampling process and appropriate sediment penetration for each sample. Sampling stations were distributed along almost the whole length of the Ghanaian coast. Altogether, nine transects were designated, with six sampling stations along each transect (25, 50, 100, 250, 500 and 1000 m depth; Fig. 1). Five samples were collected at each station. The material was sieved through a 0.3 mm mesh sieve and preserved in a 4 % formaldehyde solution. Material was collected under the Oil for Development (OfD) framework and with support from the Food and Agriculture Organisation of the United Nations (FAO).

2.3. Environmental data

Sea-Bird 911 CTD Plus and SBE 21 SeaCat thermo-salinograph instruments were used to measure temperature (°C), fluorescence (µg/l) for Chl-a, and dissolved oxygen concentrations (ml/l) at each sampling station at seafloor depth. Sediment structure and total hydrocarbon concentration (THC, mg/kg), arsenic (As, mg/kg), barium (Ba, mg/kg), cadmium (Cd, mg/kg), chromium (Cr, mg/kg), copper (Cu, mg/kg), nickel (Ni, mg/kg), lead (Pb, mg/kg), zinc (Zn, mg/kg), and total organic matter (TOM, %) were also analysed. Sediment grain size (gravel: 16–2 mm; sand: 2–0.063; silt < 0.0063) was determined by mixing the sediment with water and sieving it through a 0.063 mm sieve and Endecott sieves. Particle diameter was calculated following Buchanan (1984) and Folk and Ward (1957). THC was analysed using a gas chromatograph with a flame ionisation detector (GC/FID), as outlined in the Intergovernmental Oceanographic Commission Manuals and Guides No. 11 (UNESCO Intergovernmental Oceanographic Commission, 1982). Toxic

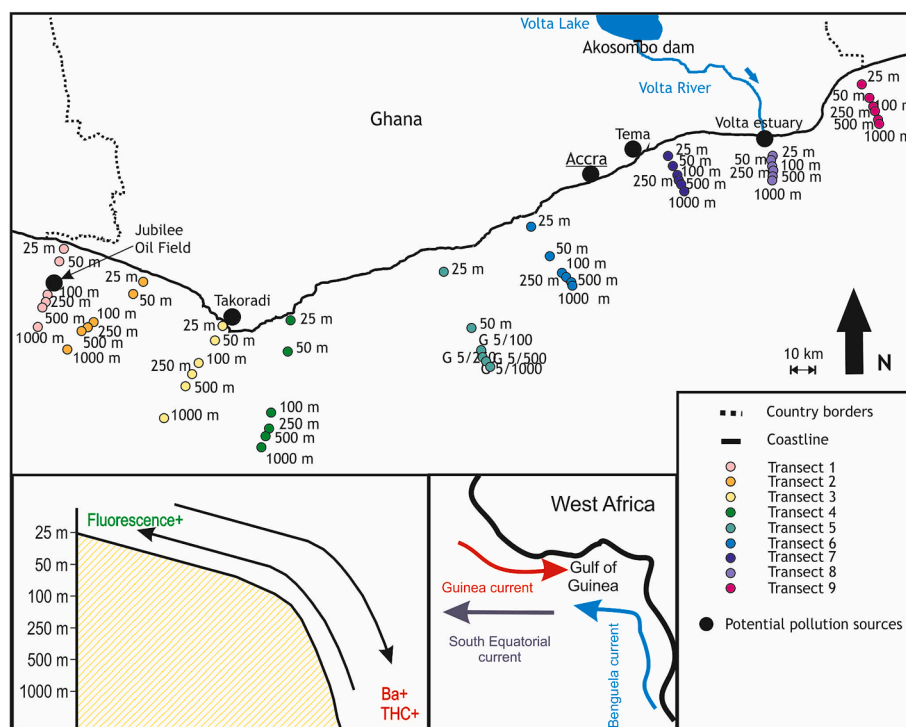


Fig. 1. Map of the study area located off the coast of Ghana. Potential pollution sources were marked as black dots. In addition, depth-dependent relationship of some variables was showed at the left bottom corner of the figure. Note that fluorescence reached the highest values at continental shelf and decreased along a depth gradient, while barium and total hydrocarbons concentration in sediments were the highest at deepest stations. Currents influencing the Gulf of Guinea were also indicated.

metal contents were analysed via Inductively Coupled Plasma-Atomic Emission Spectrometry (ICP-AES) (Elez et al., 2018; Jarvis and Jarvis, 1992). Total organic matter was measured as the weight loss of a 2–3 g dried sample (105 °C for 20 h) after 2 h of combustion at 480 °C.

2.4. Data analysis

The majority of echinoderms were identified to the species level, although part of the holothuroids and echinoids were identified to the family level only due to the poor condition of the material. The number of rare species represented by one (singletons), two (doubletons) or three (tripletons) individuals only, as well as the number of species recorded in only one (uniques), two (duplicates) or three (triplicates) samples was calculated.

Mean and maximum abundance with standard deviation (ind./0.1 m²) and frequency of occurrence (F - percentage of samples where a species was found in total number of samples or total number of samples from particular depth and particular station) in samples were calculated for all taxa. Selected indices, including species richness (S = number of species per sample), Shannon Index, Pielou's evenness, as well as abundance, were calculated for each depth zone. For these calculations, samples from all stations from a given depth (25, 50, 100, 250, 500, 1000 m) were averaged (N = 45 for each depth, 0.1 m²). Species richness and Shannon Index were calculated using functions (*decostand* for species richness, and *diversity* for Shannon) from the vegan community ecology package in R software (Oksanen et al., 2020). Statistica 13 software was used to conduct the Levene test for checking the homogenisation of variance. Next, the non-parametric Kruskal-Wallis test and the post-hoc Dunn's test were used to check differences between each depth zone.

Cluster analysis was done using PRIMER 7 software to check the faunistic similarity between the stations (for each station mean abundance from all replicates was used). Hierarchical agglomerative clustering, based on the Bray-Curtis formula (non-transformed data, group average method), was used. SIMPROF test with a 5 % significance level was performed to inspect the heterogeneity of the structure within the groups (Clarke and Gorley, 2015). Cluster analysis was based on mean values calculated for samples from each station (N = 5). Mean values, standard deviations and maximum values of echinoderm abundance and environmental variables were calculated for each cluster.

All other analyses were performed using R software (R Core Team, 2017). To evaluate species richness from the results of sampling, rarefaction curves were performed using the *specaccum* function from the vegan package (Jackknife1, Jackknife2, Chao1 and Chao2 were used for bias correction) (Oksanen et al., 2020). All samples were included into analysis without averaging.

Pearson's correlation coefficients between all predictors were used (*corrplot* function from *corrplot* package; Wei and Simko, 2017) to check for correlations with each environmental variable. The most correlated variables ($r > 0.60$) were removed, and six of them were included in further analysis (Fig. S1).

Principal Component Analysis (PCA) was performed to investigate community structure at each sampling site (averaged samples from each station; N = 5), along with the passive projection of selected environmental variables within the salinity gradient. To achieve this, Yeo-Johnson power transformations (using the *preProcess* and *predict* functions from the *caret* package (Kuhn, 2020) were performed to reduce biases between analysed variables (*rda* function was used). Next, selected environmental variables were fitted into the ordination by using the *envfit* function from the *vegan* package (Oksanen et al., 2020). Additionally, the same function was used to check the statistical significance of the variables. The salinity gradient was added to the plot by using the *ordisurf* function from the *vegan* package (Oksanen et al., 2020).

PCA axis and species richness of ophiuroids (dominant taxon) were used to fit linear models for PCA axes 1 and 2 and generalised linear

models with Poisson distribution for species richness of ophiuroids with seven environmental variables (As, Ba, Cr, THC, Fluorescence, gravel and salinity) as fixed effects, using *lm* and *glm* functions, respectively (R Core Team, 2020). Corrected Akaike Information Criterion (AICc) was used to choose the best fitting models (*dredge* function from the MuMIn package; Bartoń, 2018). Model averaging was performed by using the *model.avg*, *confset95p* and *avgmod.95p* functions from the MuMIn package (Bartoń, 2018) to calculate estimates of function slopes for the subset of models with $\Delta AICc > 2$ produced by the MuMIn *dredge* function.

To check the percentage value of the independent effect of each analysed variable, and its joint contribution to all other predictors for ophiuroids richness and PCA axes 1 and 2, hierarchical partitioning was done (*hier.part* function from the *hier.part* package; Walsh and Mac Nally, 2013). Gaussian (for PCA axes 1 and 2) or Poisson distribution (species richness) were used to compute goodness-of-fit measures for all model combinations with all predictors. The *Rand.hp* function from the *hier.part* package (Walsh and Mac Nally, 2013) was used to check statistical significance by computed randomisation tests with implementing P-values and z-scores (confidence limit < 0.05). Lastly, the *labdsv/indval* function (Roberts, 2019) was used to check the number of significant indicator species for the content of selected heavy metals Indicator Value Analysis (IndVal) allows to select indicator species by combining their relative abundance with its relative frequency of occurrence in the various groups of sites (Dufrene and Legendre, 1997). It provides information on species fidelity and specificity and it is widely used in various terrestrial and aquatic studies (Vilches et al., 2013; Al et al., 2022).

3. Results

A total of 36 echinoderm species (743 individuals) were found in the study material. Five taxa were identified to the family level. The abundance of the majority of species was very low, with 32 % of taxa being classified as rare. From this group, seven taxa were represented in the material by only one individual (singletons), while there were five doubletons and one tripleton. Additionally, 34 samples contained only one specimen (uniques), 21 contained two specimens (duplicates) and 17 samples contained three specimens (triplicates).

Most taxa were recorded only in the 25–50 m depth range. Twenty-four species were found at 25 m, 21 species at 50 m, 14 at 100 m, 9 at 250 m, 5 at 500 m and only 4 at 1000 m depth. Only two species of ophiuroids, *Ophiactis luetkeni* (4.20 ± 12.60 ind./0.1 m²) and *Ophiothrix congensis* (1.60 ± 4.80 ind./0.1 m²), had mean abundances of more than 1 individual/0.1 m². (Table 1). We observed a gradual decrease in species richness, diversity, evenness and abundance along a depth gradient (Table 1). We recorded statistically significant differences between the shallowest (25–50 m) and deepest stations (500–1000 m) (Fig. 2). Moreover, echinoderms were rarely found in all samples collected at the same station (Appendix 1), while many species were recorded only in one or two out of 5 samples collected at each station (Appendix 2).

The species accumulation curves did not reach their asymptotes (Fig. 3), indicating that inadequate sampling had taken place and that more effort was required.

Four clusters were distinguished in the cluster analysis, all of them at very low levels of similarity (below 20 %) (Fig. 4). At this level of similarity, cluster 3 is sub-dividing into 3a and 3b, however the sub-groups are not significantly different based on SIMPROF at 5 %. First cluster grouped two stations from the 1000 m. The group was characterized by elevated concentration of heavy metals (e.g. barium and chromium), contribution of mud and percentage of total organic matter in bottom sediments. Presence of *Amphiura segenalensis* was detected. Overall, only two taxa were found in samples from this group. The second cluster grouped three stations from the shallowest stations. This group was characterised by overall low species richness as well as presence of

Table 1
Mean \pm standard deviation of abundance, maximum and frequency of occurrence for echinoderms taxa (per 0.1 m²) with total number of specimens from each taxa at specific depth and total number of individuals in the whole material.

	25 m Mean \pm SD	Max	Freq	Σ	50 m Mean \pm SD	Max	Freq	Σ	100 m Mean \pm SD	Max	Freq	Σ	250 m Mean \pm SD	Max	Freq	Σ	500 m Mean \pm SD	Max	Freq	Σ	1000 m Mean \pm SD	Max	Freq	Σ	Total
Cidaridae	0.15 \pm 0.53	3	11 %	8	–	–	–	0	–	–	–	0	–	–	–	0	–	–	–	0	–	–	–	0	8
Echinometridae	0.16 \pm 0.47	3	11 %	7	–	–	–	0	–	–	–	0	–	–	–	0	–	–	–	0	–	–	–	0	7
Fibulariidae gen sp.	0.02 \pm 0.07	1	11 %	1	–	–	–	0	–	–	–	0	–	–	–	0	–	–	–	0	–	–	–	0	1
Parechinidae	–	–	–	0	0.33 \pm 0.49	4	56 %	16	–	–	–	0	–	–	–	0	–	–	–	0	–	–	–	0	16
Schizasteridae gen sp.	–	–	–	0	–	–	–	0	–	–	–	0	–	–	–	0	–	–	–	0	0.04 \pm 0.09	1	22 %	2	2
Spatangidae gen sp.	–	–	–	0	0.02 \pm 0.07	1	11 %	1	–	–	–	0	–	–	–	0	–	–	–	0	–	–	–	0	1
Cucumariidae gen sp.	–	–	–	0	–	–	–	0	0.04 \pm 0.13	2	11 %	2	–	–	–	0	–	–	–	0	–	–	–	0	2
Sclerodactylidae	0.04 \pm 0.09	1	11 %	2	0.15 \pm 0.21	2	44 %	7	0.07 \pm 0.14	1	22 %	3	–	–	–	0	–	–	–	0	–	–	–	0	12
Synaptidae	–	–	–	0	0.17 \pm 0.40	5	22 %	8	0.20 \pm 0.40	4	22 %	9	0.02 \pm 0.07	1	11 %	1	0.02 \pm 0.07	1	11 %	1	–	–	–	0	19
<i>Amphilepis ingolfiana</i>	–	–	–	0	–	–	–	0	–	–	–	0	0.05 \pm 0.10	1	22 %	2	–	–	–	0	–	–	–	0	2
<i>Amphilepis olivacea</i>	–	–	–	0	0.11 \pm 0.28	2	22 %	6	–	–	–	0	–	–	–	0	–	–	–	0	–	–	–	0	6
<i>Amphioptus aciculatus</i>	0.13 \pm 0.17	1	44 %	6	0.29 \pm 0.45	2	33 %	14	–	–	–	0	–	–	–	0	–	–	–	0	–	–	–	0	20
<i>Amphioptus archeri</i>	0.02 \pm 0.07	1	11 %	1	–	–	–	0	–	–	–	0	–	–	–	0	–	–	–	0	–	–	–	0	1
<i>Amphioptus aurensis</i>	0.02 \pm 0.07	1	11 %	1	0.87 \pm 1.53	12	67 %	44	–	–	–	0	–	–	–	0	–	–	–	0	–	–	–	0	45
<i>Amphioptus congensis</i>	0.61 \pm 0.93	6	33 %	25	0.51 \pm 0.92	8	44 %	24	–	–	–	0	–	–	–	0	–	–	–	0	–	–	–	0	49
<i>Amphioptus</i> sp.	–	–	–	0	0.34 \pm 0.73	5	33 %	16	0.02 \pm 0.07	1	11 %	1	–	–	–	0	–	–	–	0	–	–	–	0	17
<i>Amphipholis bananensis</i>	–	–	–	0	0.02 \pm 0.06	1	11 %	1	–	–	–	0	–	–	–	0	–	–	–	0	–	–	–	0	1
<i>Amphipholis nudipora</i>	0.34 \pm 0.59	3	44 %	15	0.93 \pm 0.84	6	89 %	44	0.20 \pm 0.22	2	56 %	9	–	–	–	0	–	–	–	0	–	–	–	0	68
<i>Amphipholis squamata</i>	0.20 \pm 0.60	4	11 %	9	0.02 \pm 0.07	1	11 %	1	–	–	–	0	–	–	–	0	–	–	–	0	–	–	–	0	10
<i>Amphiura atlantica</i>	0.04 \pm 0.13	2	11 %	2	0.02 \pm 0.07	1	11 %	1	0.13 \pm 0.20	3	44 %	6	0.29 \pm 0.47	3	44 %	13	–	–	–	0	–	–	–	0	22
<i>Amphiura atlantidea</i>	–	–	–	0	–	–	–	0	0.07 \pm 0.10	1	33 %	3	0.16 \pm 0.33	3	33 %	7	0.13 \pm 0.40	5	11 %	6	–	–	–	0	16
<i>Amphiura chiajei</i>	–	–	–	0	–	–	–	0	–	–	–	0	–	–	–	0	0.09 \pm 0.18	2	22 %	4	–	–	–	0	4
<i>Amphiura filiformis</i>	–	–	–	0	–	–	–	0	0.02 \pm 0.07	1	11 %	1	0.02 \pm 0.07	1	11 %	1	–	–	–	0	–	–	–	0	2
<i>Amphiura incana</i>	0.07 \pm 0.14	1	22 %	3	0.02 \pm 0.06	1	11 %	1	0.02 \pm 0.07	1	11 %	1	–	–	–	0	–	–	–	0	–	–	–	0	5
<i>Amphiura senegalensis</i>	–	–	–	0	–	–	–	0	–	–	–	0	–	–	–	0	–	–	–	0	0.02 \pm 0.07	1	11 %	1	1

(continued on next page)

Table 1 (continued)

	25 m Mean ± SD	Max	Freq	Σ	50 m Mean ± SD	Max	Freq	Σ	100 m Mean ± SD	Max	Freq	Σ	250 m Mean ± SD	Max	Freq	Σ	500 m Mean ± SD	Max	Freq	Σ	1000 m Mean ± SD	Max	Freq	Σ	Total
<i>Amphiura unguolata</i>	0.16 ± 0.28	2	33	7	–	–	–	0	–	–	–	0	–	–	–	0	–	–	–	0	–	–	–	0	7
<i>Ophionephtys lowelli</i>	0.09 ± 0.20	1	22	7	0.11 ± 0.28	2	22	6	–	–	–	0	–	–	–	0	–	–	–	0	–	–	–	0	13
<i>Ophiophragmus acutispina</i>	0.16 ± 0.20	2	56	9	0.38 ± 0.67	5	44	18	0.13 ± 0.22	1	33	6	0.34 ± 0.63	3	33	14	–	–	–	0	–	–	–	0	47
<i>Ophiostigma abnorme</i>	0.20 ± 0.60	3	11	9	–	–	–	0	0.02 ± 0.07	1	11	1	–	–	–	0	–	–	–	0	–	–	–	0	10
<i>Ophiactis lymani</i>	–	–	–	0	0.16 ± 0.28	3	33	8	–	–	–	0	–	–	–	0	–	–	–	0	–	–	–	0	8
<i>Ophiactis luetkeni</i>	4.20 ± 12.60	62	11	189	–	–	–	0	0.02 ± 0.07	1	11	1	–	–	–	0	–	–	–	0	–	–	–	0	190
<i>Ophiactis savignyi</i>	0.09 ± 0.27	3	11	4	–	–	–	0	–	–	–	0	–	–	–	0	–	–	–	0	–	–	–	0	4
<i>Ophiocomella pumila</i>	–	–	–	0	–	–	–	0	–	–	–	0	0.02 ± 0.07	1	11	1	0.02 ± 0.07	1	11	1	–	–	–	0	2
<i>Ophiopsila guineensis</i>	0.02 ± 0.07	1	11	1	0.10 ± 0.10	1	56	5	–	–	–	0	–	–	–	0	–	–	–	0	–	–	–	0	6
<i>Ophioderma longicaudum</i>	0.02 ± 0.07	1	11	1	–	–	–	0	–	–	–	0	–	–	–	0	–	–	–	0	–	–	–	0	1
<i>Ophiolepis paucispina</i>	0.13 ± 0.40	5	11	6	–	–	–	0	–	–	–	0	–	–	–	0	–	–	–	0	–	–	–	0	6
<i>Ophiopteron atlanticum</i>	0.07 ± 0.20	2	11	3	–	–	–	0	–	–	–	0	–	–	–	0	–	–	–	0	–	–	–	0	3
<i>Ophiothrix congensis</i>	1.60 ± 4.80	31	11	72	–	–	–	0	–	–	–	0	0.02 ± 0.07	1	11	1	–	–	–	0	–	–	–	0	73
<i>Ophiothrix nociva</i>	–	–	–	0	0.02 ± 0.07	1	11	1	–	–	–	0	–	–	–	0	–	–	–	0	–	–	–	0	1
<i>Ophiura carnea skoogi</i>	–	–	–	0	0.02 ± 0.07	1	11	1	0.04 ± 0.13	1	11	2	–	–	–	0	–	–	–	0	0.06 ± 0.17	1	11	2	5
<i>Ophiura grubei</i>	–	–	–	0	0.57 ± 0.72	6	67	28	–	–	–	0	0.04 ± 0.13	2	11	2	–	–	–	0	–	–	–	0	30

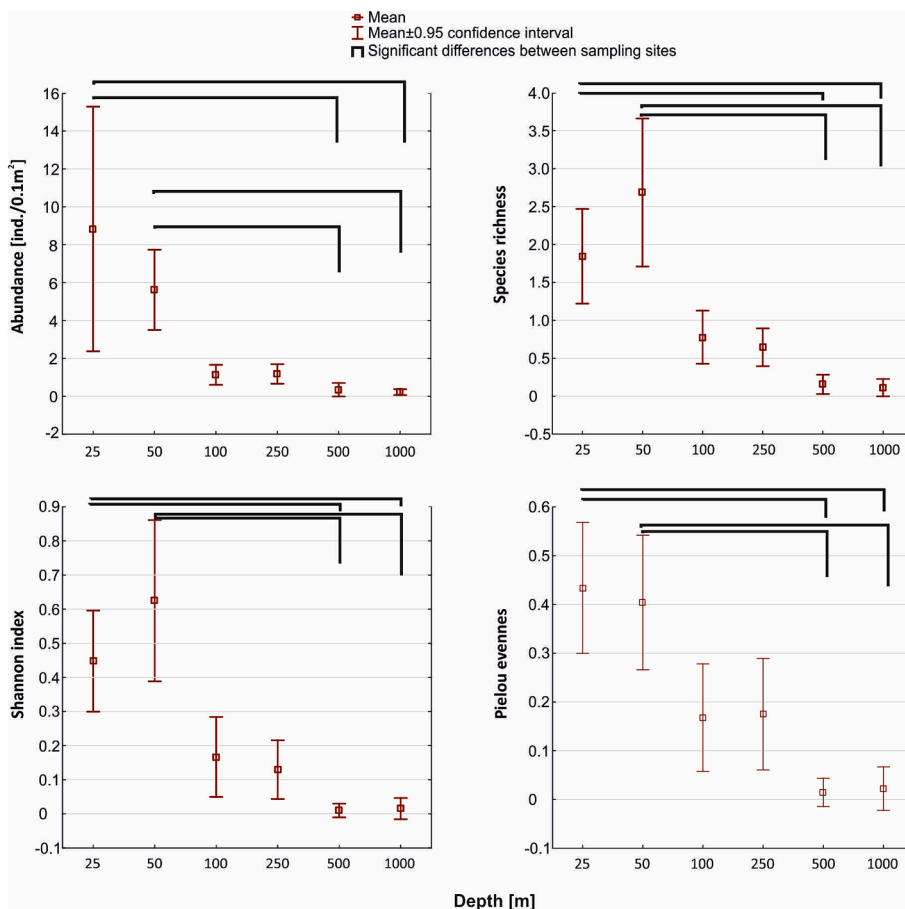


Fig. 2. Mean and 95% confidence intervals for abundance, species richness, Shannon index and Pielou evenness. Note that statistical significant differences (Kruskal-Wallis, Dunn's post-hoc test) between the specific depth were marked by black line.

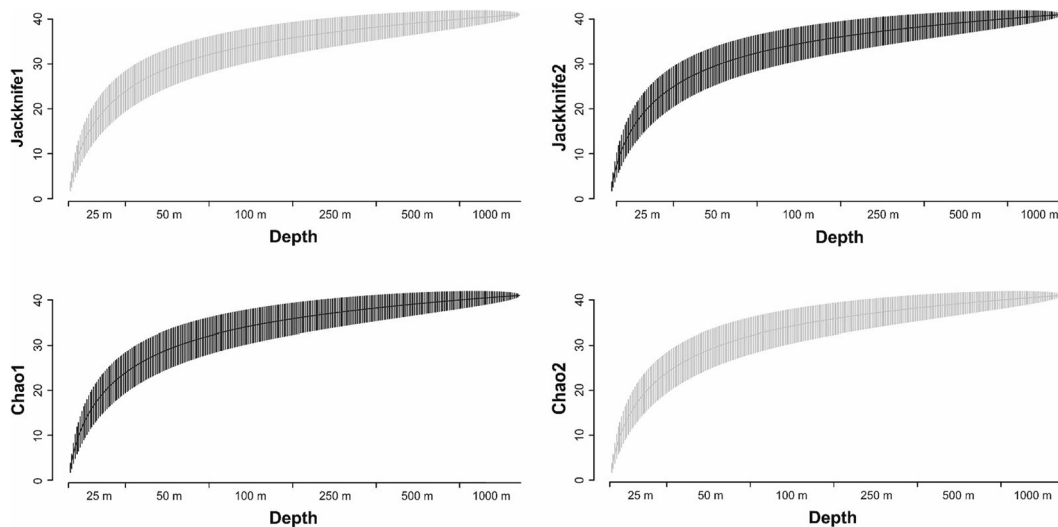


Fig. 3. Accumulation curves for each depth with (Jackknife1, Jackknife2, Chao1 and Chao2).

Amphioplus archeri and *Amphiura unguata* but only the latter species was found at all stations. Stations in this cluster were characterised by lower concentrations of heavy metals and total hydrocarbons, as well as higher sediment heterogeneity compared to other clusters. Organic matter content was also low. The third group was divided into two subgroups (shallows vs deeper shelf and upper slope). Cluster 3a grouped 15 stations (Fig. 3) that were characterised by the highest species richness.

Some of these stations also showed elevated levels of arsenic and lead. Twelve deeper stations were grouped in cluster 3b (Fig. 3). The presence of *Amphiura atlantidea* characterised the group 3b. These stations showed the lowest oxygen concentrations along with elevated levels of chromium and zinc. Finally, cluster four grouped four stations from the bathyal zone (Fig. 3). *Amphiura chiajei* and *Ophiocoma pumila* were present only in this group. Low concentration of arsenic as well as

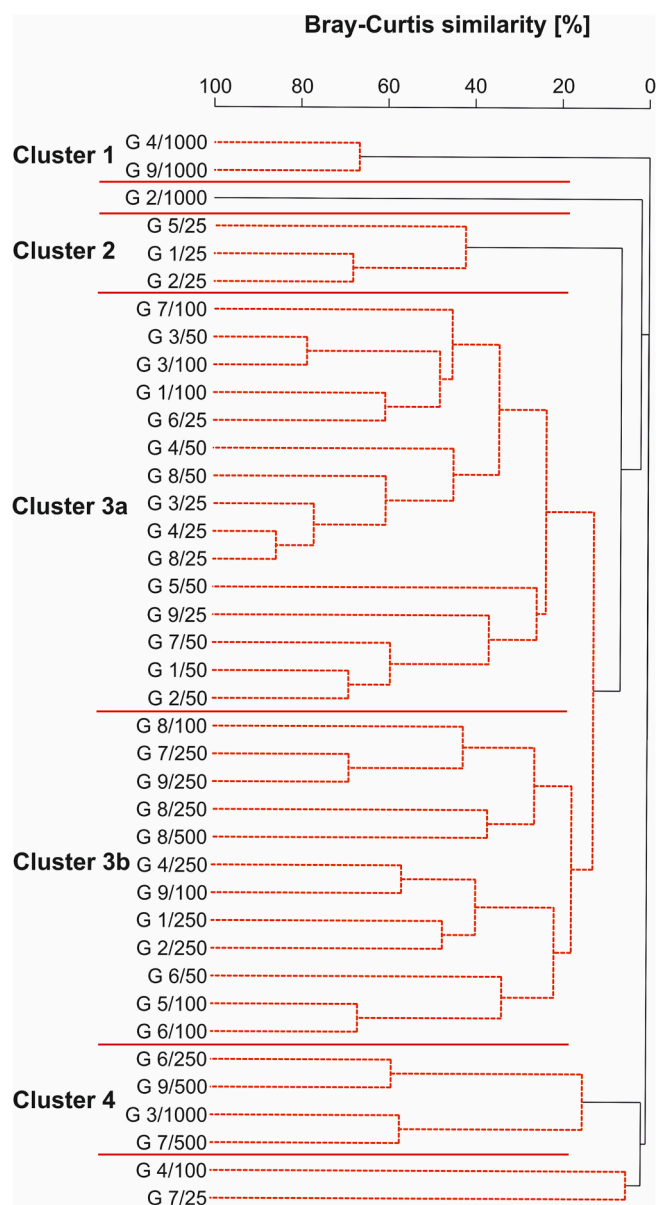


Fig. 4. Similarity of samples (Bray-Curtis similarity, square-root transformed data with 1 000 iterations). SIMPROF [5%] analysis showed which samples cannot be significantly differentiated.

elevated concentration of barium and total hydrocarbons were specific to the cluster.

Principal Component Analysis (PCA) explained 33.1 % of the variance (Fig. 5). Stations were distributed by specific pollutants rather than depth or transect. Axis 1 explained 18.2 % of the variance and divided stations into two groups. The right side of axis 1 contained stations from the continental shelf that were characterised by elevated concentrations of arsenic and higher fluorescence values. The left side of axis 1 contained stations with higher barium and total hydrocarbon concentrations. Axis 2 grouped stations affected by high barium and total hydrocarbons concentration (lower part of the axis) and those with elevated level of chromium (upper part of the axis).

From the four linear models best describing the species composition along axis 1 (containing Ba, fluorescence, gravel, salinity, and THC), only barium, salinity, and fluorescence were statistically significant. Higher salinity content (estimated slope: 0.13, $p = 0.01$) and fluorescence (estimated slope: 0.28, $p < 0.001$) had a positive impact, while Ba (estimated slope: -0.19 , $p = 0.02$) had a negative influence on

echinoderm species richness along axis 1 (Fig. 6, Table 2, Table 3). Hierarchical partitioning revealed that only fluorescence (62 % of relative contribution) and salinity (relative contribution: 12 %) had significant influence for PCA axis 1 (Fig. 7).

From the four most parsimonious ($\Delta\text{AICc} < 2$) linear models for PCA axis 2, only salinity (out of As, gravel, salinity and fluorescence) had a significant positive influence (estimated slope: 0.26, $p < 0.001$) on species composition (Fig. 6, Table 2, Table 3). The relative contribution of salinity to explaining variation was 67 %, while the variable fluorescence contributed 11 % (Fig. 7).

The five most parsimonious generalised linear models describing the species richness of ophiuroids showed the significantly negative impact of barium concentration (estimated slope: -0.75 , $p < 0.01$) and positive influence of arsenic levels (estimate slope: 0.29, $p = 0.02$) and salinity (estimated slope: 0.39, $p < 0.01$; Fig. 8, Table 2, Table 3). Based on the results of hierarchical partitioning, barium had the greatest relative contribution (34 %), while three other variables (viz. salinity, arsenic and fluorescence) had relative contributions of 17 %, 12 % and 12 %, respectively, and all had significantly positive impacts on ophiuroid species richness (Fig. 7).

Four species, namely *Amphioplus aciculatus* (indicator value: 0.44, $p = 0.001$), *Amphiura unguolata* (indicator value: 0.77, $p = 0.011$), *Ophiactis lymani* (indicator value: 0.68, $p = 0.015$) and *Ophionephthys lowelli* (indicator value: 0.59, $p = 0.027$) may be considered as vulnerable to barium pollution. Only *Ophiopsila guineensis* (indicator value: 0.28, $p = 0.033$) was identified as possibly vulnerable to pollution by hydrocarbons.

4. Discussion

4.1. Overall distribution and diversity along a depth gradient

The general impoverishment of benthic communities in the bathyal zone and gradual decrease in abundance and diversity along a depth gradient is an interesting feature of the Ghanaian coast (Pabis et al., 2020; Sobczyk et al., 2021, 2023; Stepien et al., 2021), except of tanaidacean fauna (Jozwiak et al., 2022), but this peracarids are often diverse on the slope (Pabis et al., 2015a,b; Stepien et al., 2019). Earlier studies from the North East Atlantic reported high diversities of benthic echinoderm communities in this zone (e.g. Howell et al., 2002; Hughes et al., 2011), and continental slopes are often described as biodiversity hot spots for benthic fauna in general (Danovaro et al., 2009; Rex and Etter, 2010), although with some exceptions (Coleman et al., 1997; McCallum et al., 2015). On the other hand, some studies, like one from Icelandic waters, have demonstrated low diversity and low abundance of echinoderms in the 800–1100 m depth range, coupled with high patchiness, and occasional large aggregations of individuals representing single species (Piepenburg and Juterzenka, 1994). On the Beaufort Sea slope, diversity was relatively low, and communities were highly dominated by only one species. Moreover, many taxa had low frequencies of occurrence and highly patchy distributions (Nephtin et al., 2014), demonstrating some similarities with our results. The character of slope communities might reflect the steep topography present in the 250–1000 depth range off Ghana (Sobczyk et al., 2022), a generally typical feature of the slope in this region.

The benthic communities off Ghana may also reflect the influence of sediment slides (Jacobi, 1976), quality of organic matter (Soltwedel, 1997), and/or local disturbance associated with oil industry activities, and their influence on the postlarval development of echinoderms, a key moment in the life history which influences the distribution of adult forms (Sumida et al., 1998). Although, direct comparisons between regions characterised by different hydrological regimes and geological characteristics are difficult, or even impossible. Good reference data about tropical deep-sea echinoderm communities is lacking, especially in the East Atlantic. Generally, the pattern observed in waters off Ghana seems to be associated with the influence of multiple factors, including

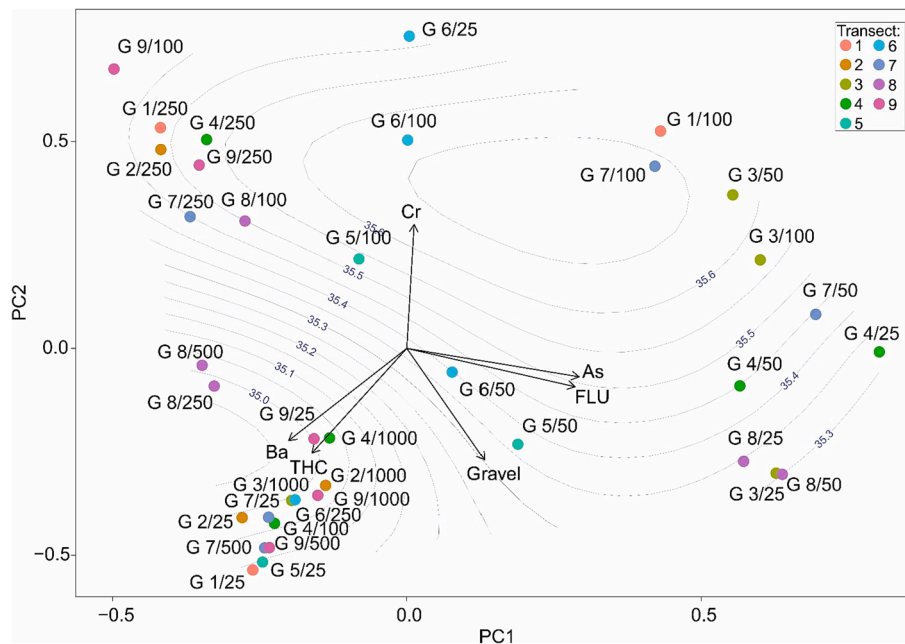


Fig. 5. Results of PCA ordination showing differences in species composition of ophiuroids at the plot level with passive projection of environmental variables fitted to the ordination results and presented by arrows. Points represent stations. Blue isolines are ranges of salinity. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

high habitat heterogeneity and coarser sediment fractions in the shallows (high diversity area), or the presence of oxygen minimum zones and higher concentrations of barium and hydrocarbons in the slope sediments (species poor areas) (Pabis et al., 2020; Sobczyk et al., 2021, 2023), where fauna did not form stable assemblages and only single, randomly distributed individuals were recorded.

We recorded over 30 species in the 25–50 m depth range, which is similar to the number of species (36 taxa) recorded in the earlier study of Ghanaian echinoderms that was focused on the taxonomy of shallow shelf fauna in the vicinity of Accra (Clark, 1955). The sea star *Astropecten michaelsoni* was abundant in the 7–50 m depth range in this survey (Clark, 1955; Bassindale, 1961), but was absent from our material. Buchanan (1959) mentioned three other shallow water species that were also absent from our samples, namely *Schizaster edwardsi*, *Centrostephanus longispinus* and *Ophiotrix nociva*. Those results demonstrate that shallow shelf communities are likely even more diverse than recorded in our study, while the absence of the above-mentioned species in our collection might be a result of a highly patchy distribution and low abundance in this area.

The current findings are confirmed by the results of the ROV recordings that were performed off the coast of Ghana (Jóźwiak and Pabis unpublished results). The videos revealed a lack of crinoids and very patchy and rare occurrences of large sea stars, holothurians and sea urchins. There were no large echinoderms at the majority of stations, and samples collected using point scale van Veen grabs effectively reflected the distribution of fauna in the studied area. At the same time, this quantitative approach allowed the description of small-scale distribution patterns that may reflect microhabitat characteristics, including levels of patchiness, as we already know that the microhabitat diversity is high along the coast of Ghana (Sobczyk et al. 2021; 2023). Trawling devices that are often used in the study of echinoderms tend to mix all the animals collected over a large distance, and from various microhabitats, resulting in the underestimation of smaller-sized animals and the inability to link distribution patterns with data about environmental properties (Jozwiak et al., 2020). West African studies conducted mostly in batyal and based on bottom images and movies demonstrated relatively low number of species and low abundances (Lebrato and Jones, 2009; Jones and Brewer, 2012; Jones et al., 2013; Biede et al.,

2022). At the same time, our results suggests important disproportions between data from van Veen grabs and movies, especially in species richness and species composition and bottom imaging techniques are certainly omitting the small species buried in the sediments.

4.2. Influence of natural and anthropogenic factors

Our analysis showed great complexity of interactions and factors influencing bottom communities along the continental margin off Ghana, including character of bottom deposits, food availability or human related disturbance. Echinoderms are not independent of sediment structure and often show preferences for a given type of bottom deposits (Boos et al., 2010). However, being much bigger and more sclerotised, their relationships with soft bottom habitats are different from those of polychaetes, nematodes and small crustaceans, that are only a few millimetres long (Blazewicz-Paszkowycz et al., 2012; Jumars et al., 2015; Snelgrove, 1999), and often build protective tubes from sediment grains (Blazewicz-Paszkowycz et al., 2012; Pabis and Sobczyk, 2017). It was, nevertheless, somewhat surprising to find, in the current study, that the sediment structure did not significantly influence the distribution of echinoderm communities in Ghana which were, according to our analysis, mostly driven by food availability (described by fluorescence) and salinity, or by some local minor disturbances associated with elevated levels of barium and arsenic. Echinoderms certainly may react to pollution, as was demonstrated for Ghanaian taxa like *A. filiformis* and *A. chiajei* (Newton and McKenzie, 1995; Temara et al., 1998), while barium compounds used during oil extraction are generally toxic to benthic invertebrates (Lira et al., 2011). Echinoderm aggregations are also often related to high organic matter availability (Calero et al., 2018), while salinity may influence their development and growth (Allen et al., 2017; Santos et al., 2022). However, earlier studies demonstrated that some sea stars could detect and avoid crude-oil contaminated sediments (Ryder et al., 2004), and pollution could at least partially result in extremally low abundance in the deep-sea samples.

On the other hand, it is noteworthy that multivariate analysis of speciose but patchily distributed marine taxa, characterised by very low abundance, might be difficult to interpret, and observed patterns are

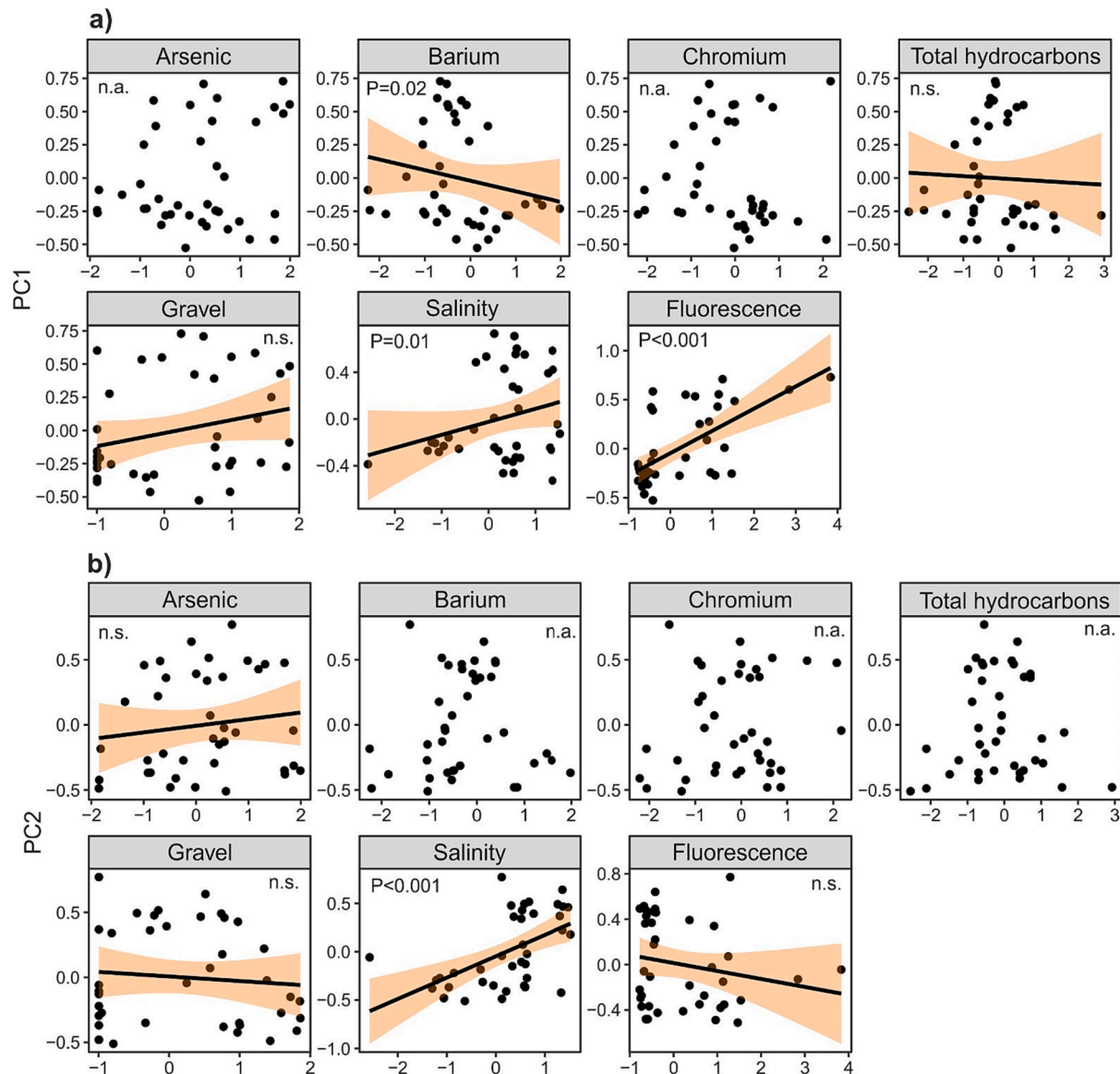


Fig. 6. Visualization of linear models testing for effects of environmental factors on species composition of ophiuroids, expressed as site scores along PCA ordination axis 1 (a) and axis 2 (b). Code “n.a.” indicates that predictor was not included in a set of the most parsimonious models. Code “n.s.” indicates that predictor was included in a set of the most parsimonious models, but its explanatory power was not significant.

rarely clear and meaningful (Reiss et al. 2015), although low abundances are often recorded in the deep-sea samples and they still allow for use of various ordination methods or clustering techniques (e.g. Kaiser et al., 2007; Pabis et al., 2015b; Zemko et al., 2017; Rybakova et al., 2019). Nevertheless, the results often reflect only co-occurrence of species and are similar to the presence/absence data. It is visible in the results of our cluster analysis which allowed to discriminate only more general trends (shelf vs slope) at low or very low similarity. Small clusters mixing samples from shelf and slope at very low similarity level (like cluster 4) are rather an artefact than a true pattern. For this reason, we also cannot exclude the role of sediments in shaping echinoderm assemblages along the coast of Ghana. Gravel was included in the analysis due to its low correlation with any other predictors (the highest being its correlation with mud $r = -0.52$, $p < 0.001$), although the results were not significant. Nevertheless, sediments and food availability shape faunal communities, especially on the shelf, and it was evident that the highest sediment heterogeneity and highest organic matter content were recorded in the 25–50 m depth range (Pabis et al. 2020; Sobczyk et al., 2021, 2023). Heterogeneous sediment structure might

increase habitat complexity for small invertebrates (Leduc et al., 2012), and the activity of larger, burrowing taxa might also create more heterogeneous habitats for other invertebrates, thereby facilitating numerous mutual interactions (Thistle et al., 1993). One larger organism could also potentially have much greater (or completely different) effects on sediments, than high numbers of smaller animals (De Smith et al., 2021), which may also have implication for whole community reaction to pollution (Gounin et al., 1995; Lenihan et al., 2018). Therefore, it would be interesting to investigate potential role of echinoderms in mitigation of the pollution effects on other organisms, especially in the shallow shelf sites of the Ghanaian waters, where all other benthic invertebrates including polychaetes and peracarid crustaceans had very small size (Jozwiak et al., 2020; Pabis et al., 2020; Sobczyk et al., 2021; Stepień et al., 2021). Therefore, even small echinoderms were the largest members of the communities, increasing their role in the ecosystem despite low abundance. More detailed studies of those problems are important for analysis of recovery processes or community resilience to pollution (Sobczyk et al., 2021; Wang et al., 2021a), while small size of the benthic invertebrates might also suggest

Table 2

Most supported ($\Delta AIC < 2$) models testing for impacts of environmental factors on species composition (site scores along PCA ordination axis 1 and 2) and richness of ophiuroids. Note that for testing impacts of environmental factors on ophiuroids composition the linear regression was performed, while regarding species richness the generalized linear model with Poisson distribution was employed.

Response variable	Model	df	logLik	AICc	$\Delta AICc$	weight
Site scores along PCA ordination axis 1	Ba + FLU + Gravel + Salinity	6	-1.23	17.30	0.00	0.15
	Ba + FLU + Gravel + Salinity + THC	7	0.14	17.60	0.31	0.13
	Ba + FLU + Salinity	5	-3.41	18.60	1.50	0.07
	FLU + Salinity + THC	5	-3.53	19.00	1.73	0.06
Site scores along PCA ordination axis 2	As + FLU + Salinity	5	-5.74	23.40	0.00	0.12
	As + FLU + Gravel + Salinity	6	-4.41	23.60	0.20	0.11
	As + Gravel + Salinity	5	-6.54	25.00	1.60	0.05
	Gravel + Salinity	4	-8.03	25.30	1.90	0.04
Richness of ophiuroids	As + Ba + Salinity	4	-69.66	148.20	0.00	0.16
	As + Ba + Cr + Salinity	5	-68.68	148.70	0.50	0.12
	As + Ba + Salinity + THC	5	-68.82	148.90	0.77	0.10
	As + Ba + Cr + Salinity + THC	6	-68.09	150.10	1.88	0.06
	As + Ba + Salinity	5	-69.39	150.10	1.91	0.06

Table 3

Estimates of function slopes of variables present in set of most parsimonious models testing for impacts of environmental factors on species composition (site scores along PCA ordination axis 1 and 2) and richness of ophiuroids. Note that for testing impacts of environmental factors on ophiuroids composition the linear regression was performed, while regarding species richness the generalized linear model with Poisson distribution was employed.

Response variable	Predictor	Estimate	Adjusted SE	Z	P
Site scores along PCA ordination axis 1:	Intercept	-0.04	0.05	0.83	0.40
	Ba	-0.19	0.08	2.17	0.02
	FLU	0.28	0.05	5.06	<0.001
	Salinity	0.13	0.05	2.33	0.01
	THC	0.10	0.06	1.60	0.10
Site scores along PCA ordination axis 2:	Intercept	-0.04	0.05	0.74	0.45
	As	0.11	0.05	1.95	0.05
	FLU	-0.10	0.05	1.77	0.07
	Gravel	-0.10	0.06	1.59	0.11
	Salinity	0.26	0.06	4.30	<0.001
Richness of ophiuroids:	Intercept	0.12	0.17	0.73	0.46
	As	0.29	0.12	2.29	0.02
	Ba	-0.75	0.24	3.07	<0.01
	Cr	-0.18	0.16	1.13	0.25
	Salinity	0.39	0.15	2.57	<0.01
	THC	0.25	0.20	1.24	0.21

exclusion of larger individuals (Tung et al., 2023).

In the current study, we found only one location with abundant aggregations of echinoderms. The ophiuroids *O. luetkeni* and *O. congensis* had high abundances at 25 m, in the G7 transect, with up to 62 individuals of one species in a single sample, and we might speculate based on earlier studies of genus *Ophiothrix* that such aggregations might have importance in the transfer of heavy metals within a thin layer between water and bottom sediments (Gounin et al., 1995). Nevertheless, apart from this single, small sampling point, the abundances of species most often varied between 1 and 3 individuals per sample, and the frequency of occurrence was low. Therefore, high patchiness resulted in low similarity values in all clusters.

Gulf of Guinea certainly is prone to potential risk of increasing pollution, especially taking into account new investments in the oil industry that occurred during last 10 years and the fact that Ghana became one of fastest-growing hydrocarbon markets (Kimiagari et al., 2023). Our studies of polychaete fauna suggested that barium may accumulate deeper in the sediments (Sobczyk et al., 2021) and have more pronounced influence on burrowing fauna resulting in lack of sediment-dwelling echinoderms on the slope, probably as a result of environmental filtering (Kraft et al., 2015), although this interpretation should be treated cautiously. Taking into account potential long term influence of even small amounts of barium compounds and other heavy metals that originate from oil excavation and dying industry (Ukwe et al., 2003; Scheren et al., 2002; Ayamdo, 2016; Fiave, 2018; Pabis et al., 2020; Sobczyk et al., 2021) we might expect further changes in the community structure, potentially also on the shelf.

4.3. Eco-functional characteristics of the communities

The functional diversity of echinoderms is generally high (Stohr et al., 2012), and the increased species richness on the shallow shelf (25–50 m) might be associated not only with organic matter content but also with higher availability of food for predatory or necrophagic taxa. Unfortunately, we do not know the biology and/or feeding strategies of the majority of African echinoderms, although our knowledge is more comprehensive than in the case of African polychaetes or peracarids, of which we know almost nothing. Moreover, large numbers of species collected during recent research in Ghana are new to science (Sobczyk et al., 2023; Jozwiak et al., 2022; Stepien et al., 2021). Despite these limitations in knowledge, we have tried to describe the known eco-functional characteristics of the echinoderm species representing shallow shelf communities in Ghana.

There were no clear dominant species recorded amongst the echinoderms of the shallow shelf communities, although *O. luetkeni* and *O. congensis* were slightly more abundant at the shallowest stations. Both species have been recorded previously on a soft bottom along the shelf of Angola (Lange, 2013). *O. luetkeni* is a shelf-related species associated with the presence of gravel (Micael et al., 2012), a sediment fraction that played a very important role in shaping polychaete and cumacean communities at Ghanaian shallow shelf sites (Sobczyk et al., 2021, 2023; Stepien et al., 2021). *O. congensis* and *O. longicauda* were the most common ophiuroids in the stony bottom shallow water communities in Ghana (Gauld and Buchanan, 1959), and the second of those species was also recorded from shallow rocky shores (Micael et al., 2012). In Sierra Leone, *O. congensis* was an element of the shelf communities distributed above the thermocline on muddy sediments, or on sandy mud with shells (Heymans and Vakily 2004). *O. longicauda* is a very common and widely distributed Atlanto-Mediterranean species that forms a cryptic species complex driven by factors that influence development, especially trophic of the habitat and temperature (Boissin et al., 2011; Anh-Thu Weber et al., 2013). The ecological requirements of the particular genetic lineages may therefore differ. *O. savigny* is a cosmopolitan species with a planktonic larval stage and the ability to disperse as drifting juveniles. It was most probably transported to the Atlantic by humans and is also a cryptic species complex (Roy and Spooner, 2002). It is associated with

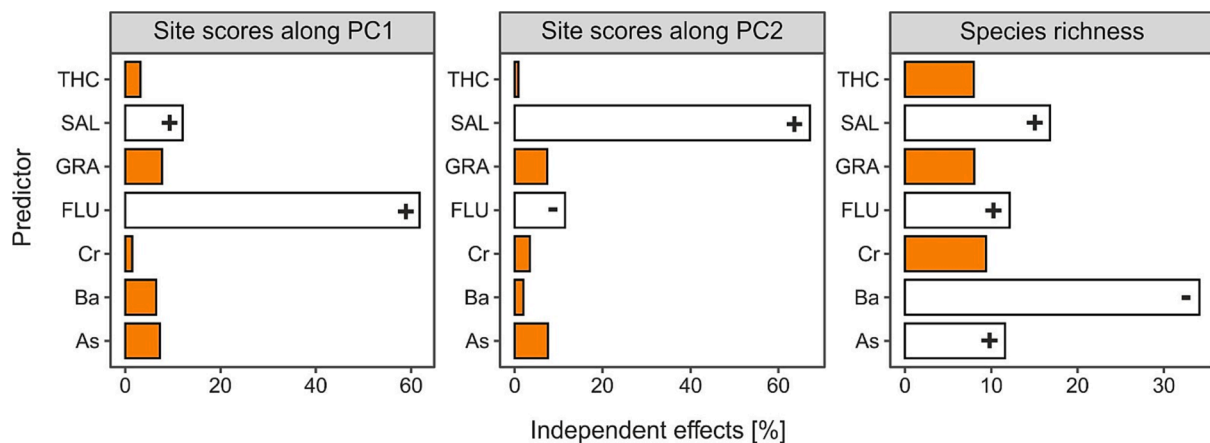


Fig. 7. Relative contribution of each predictor to shared variability of full models testing for effects of environmental factors on species composition (expressed as site scores along PCA ordination axis 1 and 2) and richness of ophiuroids. Predictors that had significant effect on response variables are given in white. Plus (+) signs express positive impact of predictors on response variables and minus (-) signs express negative influences.

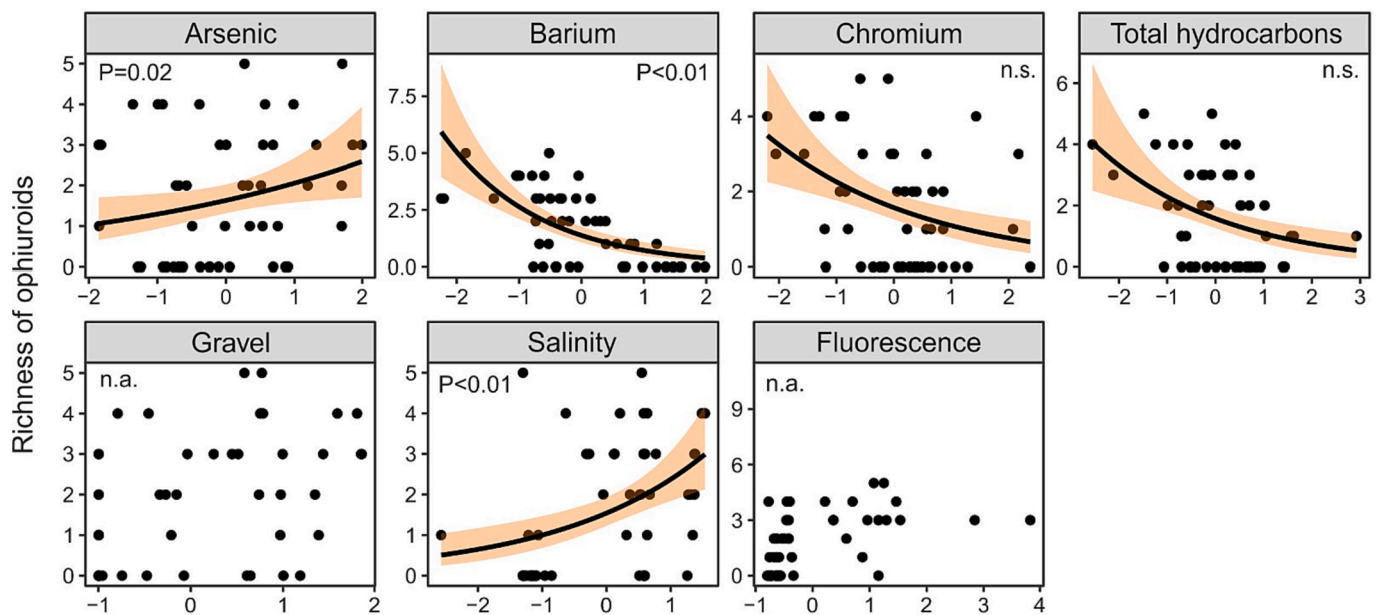


Fig. 8. Visualization of generalized linear model testing for effects of environmental factors on species richness of ophiuroids. Code “n.a.” indicates that predictor was not included in a set of the most parsimonious models. Code “n.s.” indicates that predictor was included in a set of the most parsimonious models, but its explanatory power was not significant.

epifaunal suspension-feeding communities, mainly sponges (Chao and Tsai, 1995), which were poorly represented in the shallows of Ghana (Pabis et al., 2020). *A. unguata* is most probably a burrowing species (Woodley et al., 1975), while *O. nociva* is probably a suspension feeder.

Another species representing the genus *Ophiothrix* is known from large aggregations at continental slope sites off Northwest Africa, in areas characterised by high primary production outside the oxygen minimum zones (Calero et al., 2018). *A. squamata* is a hermaphroditic species which disperses by rafting on macroalgae (Roy and Spooner, 2002), and is probably an omnivore (Jones and Smaldon, 1989), although it also shows cryptic diversity (Roy and Spooner, 2002; Boissin et al., 2010). Representatives of the genus *Ophiura* might be carnivores or carrion feeders (Stohr et al., 2012). Species like *O. carnea* often co-occur with *A. chiajei* and *A. filiformis* (Rodriguez et al., 2011), as was also reported in our study at 100 m depth. *A. chiajei* is an infaunal ophiuroid that is strongly associated with muddy and sandy sediments. It mostly occurs in low abundances, although it can be found in high densities at sites with elevated levels of organic matter (Munday and

Keegan, 1992). *A. filiformis* has a similar ecology (Skold and Gunnarsson, 1996), and both species were recorded on the lower shelf and upper slope regions in the muddy bottom off the coast of Ghana. The important feature of the Ghanaian shelf communities is also dominance of ophiuroids, complete lack of asteroids and crinoids and very small abundance of sea cucumbers and sea urchins, that constitute only a very small fraction of the material. This pattern cannot be explained by disproportions in the total number of species in particular echinoderm classes (Mah and Blake, 2012; Stohr et al., 2012; Uthicke et al., 2009), but earlier studies of echinoderm communities already showed that ophiuroids strongly dominate the soft bottom communities and often form aggregations (Bergmann et al., 2010; Tilot et al., 2018; Rosellon-Druker and Stokesbury, 2019). Those results may partially reflect differences in distribution patterns of particular taxa (especially crinoids) in relation to small scale sampling using van Veen grab (Summers and Nybakken, 2000), although this explanation is doubtful taking into account very high sampling effort. The result may be associated with fact that ophiuroids use complex arm musculoskeletal physiology for rapid

locomotion, while other echinoderms are typically slow moving (Clark 2019), which makes them also potentially more sensitive to disturbance, but this explanation concerns only disturbed areas of the seafloor. Moreover, some ophiuroids like *A. chiajei* and *A. filiformis* may even increase their abundance in disturbed areas as a result of high organic enrichment or simply in areas with higher organic matter content (Uthicke et al., 2009). Nevertheless, this aspect requires further, more detailed studies.

This very incomplete overview of the biology of species recorded in Ghanaian waters suggests that shallow water echinoderm fauna forms functionally and ecologically diverse communities that are characterised by highly patchy distribution and low abundance. High functional and taxonomic diversity of echinoderm fauna point at potentially high resilience of the shelf communities e.g. in case of increasing pollution (Carturan et al., 2022; Nasi et al., 2023). Our results suggest high level of niche partitioning which may result in higher functional redundancy (Biggs et al., 2020), one of the important elements of ecosystem responses to pollution in various terrestrial and aquatic ecosystems, especially in the longer time scale (Bruno et al., 2016; Salminen et al., 2001). High functional and taxonomic diversity was also demonstrated for polychaetes in the 25–50 m depth range. Those marine annelids were represented by predators, omnivores, filter feeders, burrowers and deposit feeders, as well as by different mobility types and taxa representing various dispersal abilities (Sobczyk et al., 2021). Similar observations were also found for decapod communities in the same region (Podwysocki et al. unpublished results). The 25–50 m zone is likely to be characterised by high microhabitat diversity resulting in highly patchy distribution, high species richness and complex functional interactions (Pabis et al., 2020; Sobczyk et al., 2021).

4.4. Baseline for further studies and priority monitoring sites

Our results constitute a baseline dataset for future ecological studies of the tropical echinoderm communities of the East Atlantic. Large Marine Ecosystems, like the Gulf of Guinea, might be a reference point for temporal studies associated with the impacts of human-induced disturbance or climate warming. Currently, it is the only fragment of the tropical East Atlantic with more comprehensive ecological and taxonomic knowledge about benthic fauna (e.g. Bassindale, 1961; Brind'Amour et al., 2009; Buchanan, 1957; Gaever et al., 2009; Galeron et al., 2009; Menot et al., 2009; Pabis et al., 2020; Sobczyk et al., 2021, 2023; Jozwiak et al., 2022; Stepień et al., 2021), although there are still substantial gaps in our understanding of processes occurring along the seabed of the African continental margin in this region. Some earlier studies have already demonstrated that echinoderms recorded in our study, like *O. longicauda*, might be influenced by changes related to global warming in the near future (Anh-Thu Weber et al., 2013). Our study demonstrated that elevated levels of barium and some other toxic metals already influenced echinoderm communities, but we know nothing about changes that have occurred in the last 10 years since our material was collected. Low abundance and high number of rare species in highly diverse shallow shelf communities makes them potentially prone to modifications of the ecosystem functioning and local species extinctions. Less abundant but larger organisms like echinoderms may play important role in stability and resilience of such ecosystem (Dee et al., 2019). Shallow shelf sites are the most diverse and constitute potential species repository (in case of many eurybathic species also for slope communities) and should be urgently included in conservation actions, also taking into account the importance of benthic communities in a wide range of ecosystems services. They also host a large number of unique species, 16 echinoderms were found only in this zone. Therefore, the Ghanaian shallows requires special protection, especially taking into account some local arsenic pollution and increasing level of anthropogenic disturbances, mostly in the vicinity of large cities like Accra and in Ghanaian centres of dying industry, which is a source of barium pollution. At the same times bathyal communities require repeated sampling

and studies of temporal changes that might be caused by disturbance associated with oil excavation. It is also worth mentioning that 2 out of 3 species recorded at 1000 m were found exclusively in this zone. We urgently need to describe the scale of potential threats and locate potentially small areas with elevated concentrations of pollutants, that might be easily unnoticed in standard monitoring actions.

For these reasons, a monitoring program is urgently needed in this area, as well as studies of the ecology and pollution resistance of particular species. Relatively large, shallow-water echinoderms are good model organisms for such studies (Warnau et al., 1998; Chiarelli et al., 2016, 2019; Morroni et al., 2020). For example, the taxa selected as indicator species in our analysis might be suitable for more comprehensive laboratory observations in future, although due to their very low abundances, their roles as potential indicators should be treated cautiously and should be verified in more detailed eco-toxicological studies. Additionally, our taxonomic analysis revealed taxa that have very poorly known distributions or are known species complexes. The Gulf of Guinea is influenced by different currents (Guinea, South Equatorial, and Benguela Current), making it a very interesting area for zoogeographic studies; the important role of circulation in the Atlantic for the distribution and dispersal of ophiuroids has already been demonstrated (Gluck et al., 2012). In addition, an earlier study of polychaete fauna from the same area has shown that bioregionalism of this poorly recognised but very important part of the Atlantic (Spalding et al., 2007) might be strongly biased due to substantial undersampling (Sobczyk et al., 2023). All above-mentioned questions remain open and can be answered only through repeated sampling in various areas of the Gulf of Guinea and the southern part of the tropical West African coastline.

5. Conclusions

Our results showed that the large sampling effort combined with high number of replicates allows to minimise some of the data analysis problems associated with high patchiness and rarity typical for marine benthic communities, especially in the deep-sea (e.g. Kaiser et al., 2007; Pabis et al., 2015a; McClain, 2021). At the same time the use of the point scale sampler like van Veen grab allowed to detect changes in the microhabitat diversity occurring at the scale of metres. Such high resolution on a small scale seems to be crucial for further monitoring of the tropical marine waters of the West Africa. Our study even suggest that number of replicates at particular station should be higher, since species accumulation curves were steep and each collected sample added important data about species richness and distribution (Appendix 2) suggesting high microhabitat diversity. This concerns also the number of samples collected for analysis of chemical and physical factors, which should also be higher than in standard procedures, when only one sediment sample is collected at each station (e.g. Mavric et al., 2013; Jozwiak et al., 2020). The use of trawling devices, dredges or bottom photographs and movies that are frequently used for echinoderm sampling (e.g. Bergmann et al., 2010; Jones et al., 2007, 2012; Nephin et al., 2014), or lowering of the number of replicates results in sampling bias in the description of the small scale distribution patterns and factors responsible for those patterns. Therefore, we miss the scale of the variability, and therefore the complexity of potential responses and/or future recovery processes. Such approach could also affect future studies, including comparisons of existing reference data with datasets based on molecular techniques like e-DNA (Hestetun et al., 2021). Those problems result mostly from high logistic costs of the deep-sea sampling, especially in the tropical regions, but also in earlier assumptions that standard benthic sampling protocols with 2 or 3 replicated samples at one station will allow reasonable description of community responses (Blazewicz et al., 2019; Jozwiak et al., 2020; Mavric et al., 2013). Nevertheless, if we want to enhance our understanding of processes occurring on deep-sea seafloor, we need to modify the procedures used in monitoring programs and ecological studies.

CRediT authorship contribution statement

Robert Sobczyk: Conceptualization, Data curation, Formal analysis, Writing – original draft, Writing – review & editing. **Piotr Presler:** Investigation. **Patryk Czortek:** Formal analysis. **Bjorn Serigstad:** Project administration, Funding acquisition, Methodology. **Krzysztof Pabis:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Supervision, Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2023.111108>.

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