LIMNOLOGY
and
OCEANOGRAPHY

ASLO

Limnol. Oceanogr. 9999, 2024, 1–13

doi: 10.1002/lno.12632

Seafloor bioturbation intensity on the deep sea: More complex than organic matter

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Abstract

Deep-sea benthic communities are strongly controlled by the quantity and quality of organic matter sinking from the ocean surface. The interaction between benthic fauna and seafloor sediments mainly occurs through bioturbation that modifies substrate properties (e.g., geochemical profiles). The intensity of the bioturbation has long been linked with organic matter and measured as a diffusive process by considering the vertical particle reworking (endobenthic bioturbation), disregarding the seafloor horizontal mixing (epibenthic bioturbation). Here, a novel approach to quantify horizontal mixing is presented: Seafloor Bioturbation Intensity (SBI). SBI calculations were based on seafloor image datasets from eight stations that reflected different environmental conditions in the north-western Pacific (e.g., chlorophyll *a*, silicate). To calculate SBI, we characterized the area occupied by all different types of traces (i.e., lebensspuren) related to epibenthic bioturbation, trace makers, and their ingested sediment thickness. Our results showed a weak negative correlation between organic matter and SBI. This relationship contrast with the traditionally held view on vertical bioturbation intensity, where a dominant positive correlation is expected. It is demonstrated that lebensspuren morphotypes contributed differently to SBI. Not all morphotypes—and, by extension, their corresponding trace makers—are equally controlled by the same environmental factors. This investigation does not dismiss the importance of organic matter content, but emphasizes the importance of other environmental variables that need to be considered when determining the long-term relation between epibenthic fauna and bioturbation intensity. Finally, we emphasize the importance of characterizing horizontal bioturbation for approaching global biogeochemical cycles and conservational strategies.

The deep ocean is the largest environment on Earth. It has been scarcely explored so far and only a tiny fraction has ever been studied through direct observation, mainly due to the technical limitations and costs that deep marine research entails (Gage and Tyler 1991; Brandt et al. 2016). The deep-sea environments (e.g., abyssal hills, plains, trenches) are almost entirely covered by soft sediments, which may well form the dominant landscape on Earth (Ramirez-Llodra et al. 2010; Riehl et al. 2020). In these habitats, the interaction between animals and sediment occurs mainly through bioturbational process (Gage and Tyler 1991). Bioturbation refers to the reworking of sediments as a result of the activity of organisms (Meysman et al. 2006). This interaction is complex as it depends on multiple variables and with tremendous environmental impact. On the one hand, the fauna responsible for bioturbation is constrained by limiting factors, such as temperature, salinity, oxygen concentration, substrate consistency, current energy, and organic matter availability (Buatois and Gabriela Mángano 2011). Bioturbation, on the other hand, is an important mechanism by which physicochemical and ecological features of sediments are modified, creating significant seafloor heterogeneity affecting living communities and global biogeochemical cycles (Aller 1994; Beam et al. 2022).

Based on the impact of benthic fauna on the sedimentary transport of particles and pore water, bioturbation can be divided into two main categories: (1) "particle reworking" (bio-mixing) and (2) "burrow ventilation" (bio-irrigation) (Kristensen et al. 2012; Hülse et al. 2022). Particle reworking

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Additional Supporting Information may be found in the online version of this article.

Author Contribution Statement: OMS and TR led project design. OMS and HS performed the data acquisition and treatment. OMS, TR, HS, and AB wrote the main manuscript text. OMS and HS. prepared all figures, tables, and supplementary material. All authors reviewed and edited the manuscript at multiple stages and approved it for submission.

can occur within the sediment producing both vertical and horizontal particle movement (endobenthic bioturbation), or on the sediment–water interface with a dominant horizontal particle displacement (epibenthic bioturbation). This reworking can get preserved through different types of biogenic structures (lebensspuren) such as burrows, trails, mounds, and fecal casts (ingestion and defecation) among others (Miguez-Salas et al. 2024*a*). The consequences of bioturbation are usually more prominent vertically because most sediment characteristics show strong vertical gradients (Middelburg 2019; Solan et al. 2019). Thus, bioturbation is usually represented as a one-dimensional diffusive process in continuum models where a bioturbation coefficient (D_B; $cm^2\,year^{-1}$) is calculated to numerically describe the intensity of bioturbation within sediments (i.e., endobenthic bioturbation) (Teal et al. 2008; Solan et al. 2019; Zhang et al. 2024). However, the number of studies dealing with the intensity of seafloor (horizontal) bioturbation is much scarcer than studies addressing vertical aspects of bioturbation (e.g., Maire et al. 2008; Robert and Juniper 2012; Miguez-Salas et al. 2020). Consequently, the importance of horizontal particle reworking has been largely overlooked in attempts of modeling the percentage of organic carbon deposited on the seafloor that becomes buried in both modern and geological records (Middelburg 2019).

The deep sea is a food-limited environment where benthic communities are ultimately fueled by organic matter produced through photosynthesis in surface waters (Smith et al. 2009). Thus, these communities are sensitive to variation in food supply, and faunal abundance is positively related to primary production in the overlying water (Smith et al. 2008). Also, it has been shown that organic carbon utilization by these communities is positively linked to the amount of particulate organic matter reaching abyssal depths (Pfannkuche 1993). With regard to bioturbation analysis conducted within the sediments (i.e., endobenthic bioturbation), previous studies have observed a positive relationship between the D_B value and organic-carbon deposition on a global scale (Smith and Rabouille 2002). This positive relationship has been also established for specific lebensspuren types such as echinoid trails where periodic variations in bioturbation were significantly correlated with particulate organic carbon (POC) flux (Vardaro et al. 2009). Nevertheless, the connection between general seafloor bioturbation intensity (i.e., the full lebensspuren assemblage) and environmental factors (e.g., depth, grain size, organic carbon content) has so far not been addressed in detail (Durden et al. 2020).

This research addresses Seafloor Bioturbation Intensity (SBI) in deep-sea stations at the Northwest Pacific Abyssal Plain in the direct vicinity of the Kuril-Kamchatka Trench. The area was selected because the Kuril-Kamchatka Trench and the adjacent abyssal plain are of special scientific interest due to their complex hydrography combined with a high surface productivity which affect the benthic habitat (*see* Sattarova and Artemova 2015). To analyze changes in SBI, we selected eight deep-sea stations based on differences in depth, grain size, organic carbon content in the sediment, and chlorophyll *a* (Chl *a*) concentration. The objectives of this research were: (1) to test if SBI is controlled by some of these environmental variables, with special emphasis on organic carbon content variations; (2) to study if all the lebensspuren morphotypes are equally controlled by the same environmental variables; and (3) to test if the SBI can help to quantify deep-sea animal–sediment interactions (i.e., particle mixing and redistribution). Finally, as a major unknown component of deep-sea bioturbation is the horizontal reworking of particles, this study aims to discuss the implications of the obtained results on global biogeochemical cycles and future deep-sea ecological challenges.

Materials and methods

Sample collection

A total of eight deep-sea stations were studied using still images from Ocean Floor Observation System (OFOS) deployments at the Northwest Pacific Abyssal Plain in the direct vicinity of the Kuril-Kamchatka Trench during SO223 cruise, July 21, 2012 to September 7, 2012 (for OFOS deployment details, *see* Brandt and Malyutina 2015) (Table 1). Two stations were in the upper part of the Kuril-Kamchatka Trench slope, and the other six stations were located at the adjacent abyssal plains (Table 1). The depth of the stations ranged from 4868 to 5768 m. In total, 50 random frames per station were studied, covering a seafloor area of 878 m^2. All still images extracted from the OFOS videos at a frequency of one frame per 5 s are stored in Zenodo (Miguez Salas and Riehl 2023*a*,*b*). These still images were uploaded to the BIIGLE 2.0 software for annotation and area measurements (Langenkämper et al. 2017). The area of 5692 lebensspuren was annotated (Miguez Salas and Riehl 2023*c*). Only lebensspuren with low degradation and clearly distinguishable trace shape have been considered for this study. Lebensspuren classification and trace maker taxonomy are based on the previous research conducted by Miguez-Salas et al. (2024*b*). In addition, megabenthic fauna was quantified manually using BIIGLE 2.0 software and classified as "faunal coverage" at each station, which was the area covered by all individual megabenthic organisms. This "faunal coverage" area is based on the measurements of 4009 individual animals. Lebensspuren and megabenthic fauna raw dataset reports at each station are stored in Zenodo (*see* Miguez Salas and Riehl 2023*b*,*c*).

Seafloor bioturbation quantification

Prior research has approached bioturbation intensity by calculating a bioturbation coefficient with radioisotopes (e.g., ^{14}C, ^{210}Pb, ^{234}Th) to characterize the mixing intensity and the depth over which diffusive mixing occurs (Guinasso and Schink 1975; Solan et al. 2004). Thus, this calculation offers a value mainly for endobenthic bioturbation intensity. Since our study focused on seafloor bioturbation associated to benthic surface deposit feeders as a proxy for sediment disturbance in a deep-sea environment, we developed a new approach based on two indices:

Table 1. The eight deep-sea stations studied in which Ocean Floor Observation System (OFOS) and Multiple Corer (MUC) were deployed at the Northwest Pacific Abyssal Plain in the direct vicinity of the Kuril-Kamchatka Trench (KKT). Overall obtained values of SBA, SBI, and faunal coverage for each station. Chl *a* (μg g^{-1}), Corg (%), Sand (%), and Silty/Clay (%) data retrieved from Sattarova and Artemova (2015) and Schmidt et al. (2019).

Station	Date OFOS (*MUC*)	Start OFOS	End OFOS	Depth (m)	SBA (m^2)	SBI (dm^3)	Faunal coverage (m^2)	Chl *a* (μg g^{-1})	C$_{org}$ (%)	Sand (%)	Silty/ Clay (%)
3	Aug 6, 2012 (*Aug 4, 2012*)	47°14.31′N 154°42.35′E	47°13.80′N 154°43.16′E	4974	3.13	0.456	0.51	19.45	1.55	15.47	84.53
4	Aug 8, 2012 (*Aug 5, 2012*)	46°58.00′N 154°32.48′E	46°58.48′N 154°31.44′E	5679	1.77	0.8503	1.39	6.54	0.98	22.08	77.74
5	Aug 9, 2012 (*Aug 10, 2012*)	43°35.03′N 153°57.95′E	43°34.64′N 153°58.60′E	5378	2.93	8.919	0.45	3.36	0.78	6.58	93.42
6	Aug 13, 2012 (*Aug 13, 2012*)	42°28.97′N 153°59.91′E	42°28.18′N 153°59.90′E	5298	4.11	9.159	1.25	1.24	0.69	8.56	90.94
8	Aug 19, 2012 (*Aug 20, 2012*)	42°14.61′N 151°43.50′E	42°14.42′N 151°42.91′E	5128	2.75	12.543	0.55	1.16	0.58	10.9	89.1
9	Aug 22, 2012 (*Aug 23, 2012*)	40°34.99′N 151°0.03′E	40°34.47′N 151°0.38′E	5406	1.93	1.322	0.6	2.71	1.36	1.76	98.24
10	Aug 25, 2012 (*Aug 26, 2012*)	41°12.01′N 150°5.70′E	41°12.19′N 150°6.40′E	5250	4.76	2.505	0.29	7.23	1.05	3.58	96.42
11	Aug 28, 2012 (*Aug 29, 2012*)	40°12.93′N 148°6.04′E	40°12.92′N 148°5.41′E	5349	2.67	3.083	0.93	11.91	1.45	1.71	98.23

(1) Seafloor Bioturbation Area (SBA) which is the total area occupied by the lebensspuren assemblage and (2) Seafloor Bioturbation Intensity (SBI) where we multiplied the area occupied by each lebensspuren type (A_l) with the hypothesized sediment thickness ingested by the specific trace maker associated to each lebensspuren type (Table 2). For SBA and SBI calculations, we did not consider most of the dwelling lebensspuren (e.g., burrows, mounds, craters) as it is not possible to estimate how much volume of sediment is being disrupted by the trace maker. Sediment thickness was based on field observations (i.e., still images and videos) and literature data (e.g., Billett 1991; Roberts et al. 2000; Vardaro et al. 2009; Durden et al. 2019, 2020). For lebensspuren that have multiple trace makers (Miguez-Salas et al. 2024*b*) with different sediment thickness values (e.g., smooth fecal cast associated with *Psychropotes* sp. and *Benthodytes* sp.; M-ridged trail produced by echinoids and asteroids), an specific value has been selected based on the most abundant trace maker.

Environmental variables

Content of grain fractions (%Sand, %Silt/Clay), organic carbon in the sediment (total weight [wt%] of the sediment), and Chl *a* concentrations (μg g^{-1}) were obtained from previously published data on the studied stations (Sattarova and Artemova 2015; Schmidt et al. 2019). Sampling of environmental variables took place during the same cruise (i.e., SO223), using three multiple corer hauls per station. The time lag between OFOS and multiple corer deployment was always less than 3 d at each station (Table 1).

Additionally, we included seafloor environmental factors (benthic layers for each station) which have been reported as important driving factors of deep-sea species richness in other studies (Gooday et al. 2010; Saeedi et al. 2019, 2022). Benthic environmental layers were extracted from Bio-ORACLE (bio-oracle.org) (Tyberghein et al. 2012; Assis et al. 2018). These included average temperature (°C), salinity (Practical Salinity Scale), dissolved oxygen (mol m^{-3}), current velocity (m s^{-1}), nitrate (mol m^{-3}), phosphate (mol m^{-3}), and silicate (mol m^{-3}) concentrations.

Correlation matrix and PCA analyses

Data analyses and plotting of the results were performed in R 4.2.2 according to the approach of Saeedi et al. (2019). The R packages "tidyverse" and "openxlsx" (Schauberger and Walker 2020) were used for data importing and formatting. The correlation analyses between the number of lebensspuren

Table 2. Lebensspuren and associated trace makers identified in the present study with the hypothesize sediment thickness ingested by taxon (St) (Billett 1991; Roberts et al. 2000; Vardaro et al. 2009; Durden et al. 2019, 2020).

Group	Taxa (for more details, *see* Miguez-Salas et al. 2024*a*,*b*)	S_t (cm) (Billett 1991, Roberts et al. 2000, Vardaro et al. 2009, Durden et al. 2019, 2020)	Lebensspuren morphotypes (Miguez-Salas et al. 2024*a*,*b*)	Notes
Holothuroidea	*Peniagone* sp.	0.1	Knotted FC, wavy FC	
	Scotoplanes sp. *Elpidia*. Sp. 1	0.1	Rounded FC	
	Psychropotes sp. *Benthodytes* sp. cf. *Pseudostichopus* sp. *Synallactidae* morphospecies 1	0.5	Smooth FC	$S_t = 0.5$ was selected because *Psychropotes* morphospecies are the most abundant trace makers of smooth FC
	Psychropotes sp. *Benthodytes* sp.	0.5	Coiled-curly FC	
	Psychropotes sp. *Benthodytes* sp.	0.01	Flat trail	
Echiura		0.1	Rosette	Based on the assumption that this lebensspuren is created by echiuran worms (Miguez-Salas et al. 2023).
Ophiuroidea	Ophiuroidea. Fam. Gen. Sp. 1 to Ophiuroidea. Fam. Gen. Sp. 3	1	Ophiuroid impression	
Asteroidea	Asteroidea. Fam. Gen. Sp. 3, 4, 7, 8, 9	1	Asteroid impression	
	Asteroidea. Fam. Gen. Sp. 1, Asteroidea. Fam. Gen. Sp. 4	0.01	M-ridged trail	$S_t = 0.01$ was selected because there is not precise literature about asteroid morphospecies St while Vardaro et al. (2009) reported a $S_t = 0.01$ for *Echinocrepis*.
	Asteroidea. Fam. Gen. Sp. 3	0.01	Flat trail	
Echinoidea	*Echinocrepis*. Sp. 1; Echinoidea. Fam. Gen. Sp. 5.	0.01	M-ridged trail	
	Echinoidea. Fam. Gen. Sp. 2; Echinoidea. Fam. Gen. Sp. 7	0.01	Flat trail	
	Echinoidea. Fam. Gen. Sp. 6	0.01	Variable thin trail	
Enteropneusta	Enteropneusta gen. Sp. 1 Enteropneusta gen. Sp. 2	0.1	Spiral FC	
	*Torquaratoridae*_gen_sp_1	0.1	Switchback FC	
Gastropoda	Gastropoda. Fam. Gen. Sp. 1 to Gastropoda. Fam. Gen. Sp. 6	0.01	Flat trail	
Unknown	Unknown	1	Mounded fecal cast	Approximate value based on the elevation of the fecal cast mounds.
Unknown	Unknown	1	Mounded trail	Approximate value based on the elevation of the trails. Calculated in function of the size of the shadow in comparison with the shadow of crinoids and sponges which we know their real size.

and number of distribution records with abiotic factors including SBI, SBA, faunal coverage, depth, content of grain fractions (%Sand, %Silt/Clay), organic carbon in the sediment, Chl *a* concentration, temperature, salinity, dissolved oxygen, current velocity, nitrate, phosphate, and silicate were done using "ggcorplot" (Kassambara 2019). We have used the same set of variables to run the principal component analysis (PCA) using "ggbiplot" (Vu, 2016). We used PCA to reduce the dimensionality of all variables to describe the correlation of those variables with fewer dimensions. We have calculated PCA1 and PCA2. Finally, package "vegan" (Oksanen et al. 2022) was also used for calculating and plotting the rarefaction ES50 (expected number of species) against latitudinal bands.

GAM and GLM analyses

We used generalized additive models (GAMs) to examine the impact of environmental predictors as well as SBA, SBI, and faunal cover on the number of lebensspuren per station. The coordinates of each station were collated with the spatial resolution of the environmental variables. All the models were fitted by restricted maximum likelihood, using the automatic predictor selection implemented in the mgcv package (Wood 2012) to control the complexity of smooth terms. For each analysis, an intercept-only model was fitted, with the null hypothesis that response variables were not explained by environment, spatial sampling bias, or spatial autocorrelation. For models built using number of lebensspuren as the response variable, a total number of records per trace was used for each station as an estimate of sampling effort. To model the effects of spatial autocorrelation on predictor and response variables, we used a two-dimensional spherical spline on latitude and longitude of sampling sites (Wood 2012).

For models using number of lebensspuren as a response variable, only one model was fitted using spatial sampling bias, one using only spatial autocorrelation, and one using both sampling bias and spatial autocorrelation. We also fitted a model for each environmental predictor separately, and one that represented the combined impacts of all environmental predictors. Models built using environmental predictors also included sampling effort and the effects of spatial autocorrelation (*see* Saeedi et al. 2019).

We also fitted generalized linear models (GLMs) using a Poisson error distribution, and used number of records per latitudinal bands to control for differences in sampling effort. Latitudinal models were evaluated using the small sample size-corrected Akaike Information Criterion (AIC48), and we selected a statistical method to choose models with optimal fit to the data while controlling for overparameterization (Akaike 1971; Burnham and Anderson 2002). The models with lower AIC scores are those that presented a better compromise between model fit and model complexity. A difference in AIC value (deltaAIC) of less than two was considered to be inconclusive when comparing all models. GLMs relating trait richness to environmental predictors are given in Supporting Information Tables S2 and S3.

Results

The final lebensspuren dataset comprised 5692 records and 15 lebensspuren morphotypes (Fig. 1) (for the raw lebensspuren area dataset, *see* Miguez Salas and Riehl 2023c). Around 93% of these records were assigned to wasting lebensspuren (i.e., fecal casts), where rounded fecal cast was the dominant lebensspuren morphotype (3896 records; Fig. 1). This morphotype was mainly found at Stas. 9 and 11 (i.e., lower latitudes) with a water depth range from 5349 to 5406 m (Fig. 1d–f). The remaining dataset comprised 7% of locomotion-feeding lebensspuren where M-ridged trails (i.e., echinoid and asteroid trails) were the most common lebensspuren morphotype (Fig. 1d–f). The total SBA per station revealed that Stas. 6 and 10 had the highest values even though the number of lebensspuren records was considerably lower than at Stas. 9 and 11 (Fig. 1b). This was related to the occurrence of rosette lebensspuren at Stas. 6 and 10 which cover a much larger area than the rounded fecal casts that dominate Stas. 9 and 11. The total SBI revealed that Stas. 5, 6, and 8 have higher values due to the appearance of smooth and coiled-curly fecal casts which are produced by trace makers with higher levels of ingested sediment (Fig. 1c; Table 2).

The correlation analysis revealed multiple significantly environmental variables affecting faunal coverage, SBA, and SBI. SBA and SBI were overall negatively correlated with depth, silty/clay sediments, and organic carbon; while a positive correlation was observed with sand concentration (Fig. 2; Supporting Information Table S1). The Chl *a* had no significant correlation with SBA and SBI (Fig. 2). Also, faunal coverage showed a non-existent correlation with SBI and SBA with negative correlation with sand sediments (Fig. 2). Faunal coverage is positively correlated with Chl *a* concentration, and organic carbon content (Fig. 2).

The PCA revealed that dissolved oxygen, current, C_{org}, and silt/clay had large positive loadings on component 1. Silicate, nitrate, and phosphate had large negative loadings on component 2 and were negatively correlated. The length of SBA and SBI arrows indicated that they are not strongly correlated to anything. However, the overall variability in SBA and SBI seemed to have a weak negative correlation with organic carbon content, Chl *a* concentration, and silty/clay content (Fig. 3). Their variability appeared to be more related with sand concentration, depth changes, longitude, and latitude. The benthic layers extracted from Bio-ORACLE revealed that SBA and SBI variability seems to match with temperature and silicate while dissolved oxygen and bottom current velocity seems to indicate the opposite. This is consistent with results exposed in Fig. 2. Among the lebensspuren assemblage significant variations could be observed depending on the different lebensspuren morphotypes (Fig. 3). Rounded fecal casts (i.e., the most abundant

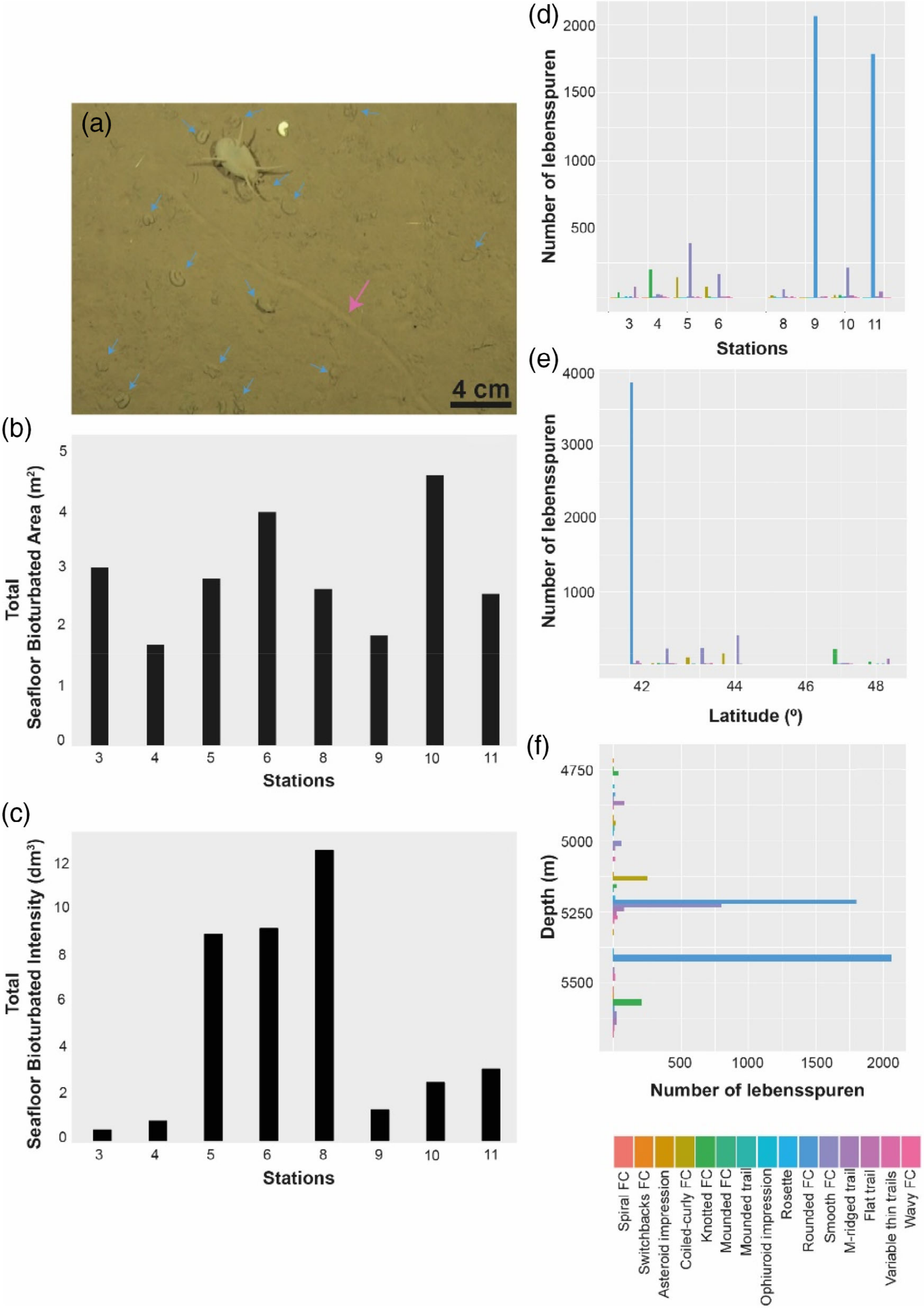
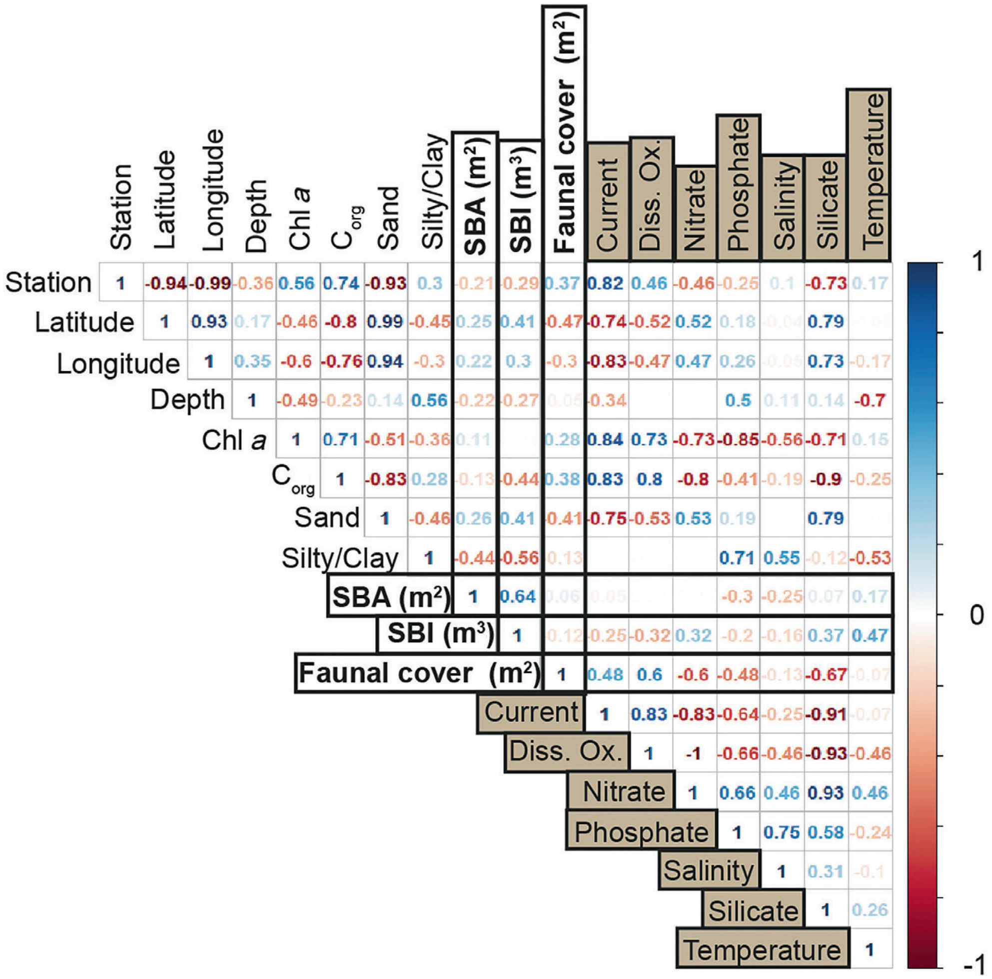


Fig. 1. Still image example from Sta. 9 with one *Scotoplanes* sp., multiple rounded fecal casts (small blue arrows), and a thin flat trail (big pink arrow) (**a**). Total seafloor bioturbated area (**b**) and seafloor bioturbation intensity (**c**) at each station. Distribution of lebensspuren records in function of Station (**d**), latitude (**e**), and depth (**f**).



	Station	Latitude	Longitude	Depth	Chl *a*	C_{org}	Sand	Silty/Clay	SBA (m^2)	SBI (m^3)	Faunal cover (m^2)	Current	Diss. Ox.	Nitrate	Phosphate	Salinity	Silicate	Temperature
Station	1	-0.94	-0.99	-0.36	0.56	0.74	-0.93	0.3	-0.21	-0.29	0.37	0.82	0.46	-0.46	-0.25	0.1	-0.73	0.17
Latitude		1	0.93	0.17	-0.46	-0.8	0.99	-0.45	0.25	0.41	-0.47	-0.74	-0.52	0.52	0.18	-0.04	0.79	[illegible]
Longitude			1	0.35	-0.6	-0.76	0.94	-0.3	0.22	0.3	-0.3	-0.83	-0.47	0.47	0.26	-0.05	0.73	-0.17
Depth				1	-0.49	-0.23	0.14	0.56	-0.22	-0.27	0.05	-0.34			0.5	0.11	0.14	-0.7
Chl *a*					1	0.71	-0.51	-0.36	0.11	[illegible]	0.28	0.84	0.73	-0.73	-0.85	-0.56	-0.71	0.15
C_{org}						1	-0.83	0.28	-0.13	-0.44	0.38	0.83	0.8	-0.8	-0.41	-0.19	-0.9	-0.25
Sand							1	-0.46	0.26	0.41	-0.41	-0.75	-0.53	0.53	0.19		0.79	[illegible]
Silty/Clay								1	-0.44	-0.56	0.13		[illegible]	[illegible]	0.71	0.55	-0.12	-0.53
SBA (m^2)									1	0.64	0.06	0.05	[illegible]	[illegible]	-0.3	-0.25	0.07	0.17
SBI (m^3)										1	0.12	-0.25	-0.32	0.32	-0.2	-0.16	0.37	0.47
Faunal cover (m^2)											1	0.48	0.6	-0.6	-0.48	-0.13	-0.67	-0.07
Current												1	0.83	-0.83	-0.64	-0.25	-0.91	-0.07
Diss. Ox.													1	-1	-0.66	-0.46	-0.93	-0.46
Nitrate														1	0.66	0.46	0.93	0.46
Phosphate															1	0.75	0.58	-0.24
Salinity																1	0.31	-0.1
Silicate																	1	0.26
Temperature																		1

Fig. 2. Correlation matrix of environmental data obtained in the expedition KuramBio (2012), lebensspuren measurements (SBI and SBA) and faunal coverage calculations. The black rectangles indicate the variables calculated through lebensspuren and benthic fauna annotations. Brown boxes indicate environmental variables obtained from Bio-ORACLE data.

morphotype) variability seems to be controlled by C_{org}, current, salinity, and phosphate. The variables faunal coverage and SBI are not likely correlated. Faunal coverage seems to be correlated with dissolved oxygen and Chl *a* concentration.

GAM output models showed that models including depth ($\Delta AIC = 0.000159$) followed by faunal coverage ($\Delta AIC = 0.000319$) compared to other environmental predictors, indicating that much of the predictive power of the environment for determining number of lebensspuren is likely derived by depth and faunal coverage (Supporting Information Table S2). The GLM models revealed that latitude, longitude, bottom current, temperature, dissolved oxygen, and nitrate are the best predictors for the number of lebensspuren ($\Delta AIC > 8.26$) (Fig. 4; Supporting Information Table S3). SBA and SBI were found to be good predictors as well for lebensspuren richness ($\Delta AIC = 8.18–8.22$). We also recovered the model "numrec" ($\Delta AIC = 2.66$), which contains only effects of sampling, with higher ΔAIC than the best models, but lower than other environmental predictors (e.g., sand, depth). This result indicates that a model that contains only total distribution records is for all practical purposes as good as any model that contains an environmental predictor. As such, we cannot say with confidence that any environmental predictor is useful in explaining the number of lebensspuren.

Discussion

Several environmental factors have been proposed to regulate the general bioturbation intensity, including water depth (Middelburg et al. 1997), bottom water oxygen availability (Savrda and Bottjer 1991), sedimentation rate (Boudreau 1994), and sedimentary organic content (Yang and Zhou 2004) among others. The flux of particulate organic carbon may be one of the most important factors because it regulates the food supply for benthic organisms (Smith et al. 2008). In the literature, several studies have observed a positive relationship between bioturbation intensity (D_B value) and organic matter deposition on a global scale (e.g., Boudreau 1998; Smith and Rabouille 2002;

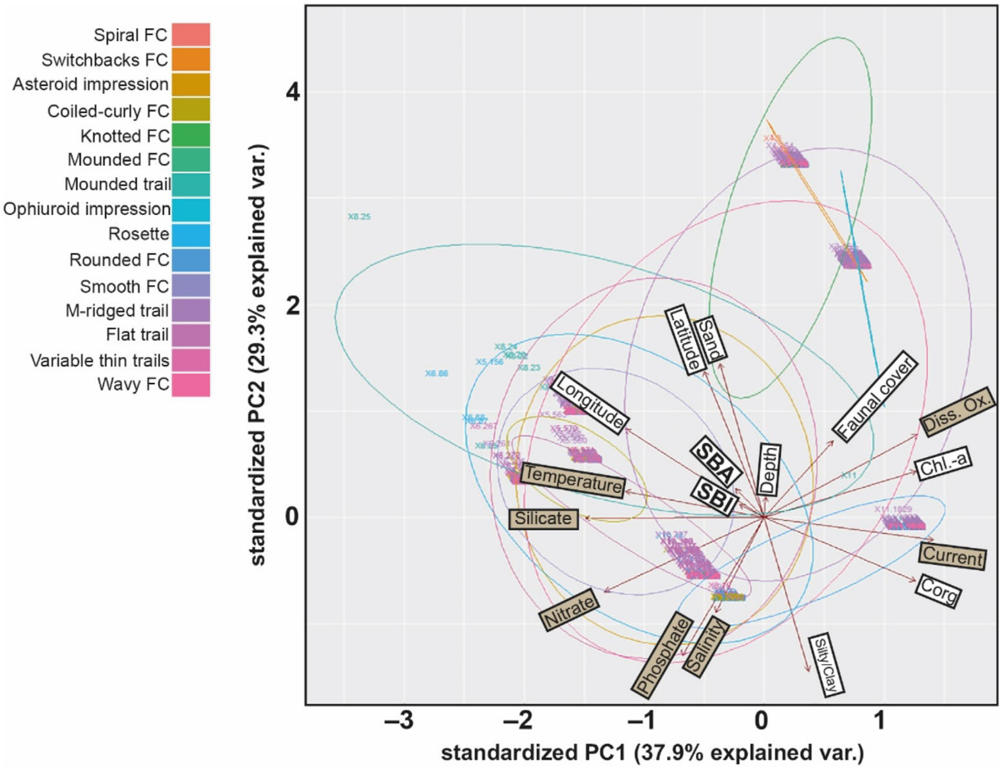


Fig. 3. PCA of environmental variables on diversity and abundance of lebensspuren morphotypes. Brown boxes indicate environmental variables obtained from Bio-ORACLE data.

Yang et al. 2020). Also, this positive relationship has been observed between vertical mixing intensity and animal abundance in the northeast tropical Atlantic (Legeleux et al. 1994). However, even though most studies show this positive relationship, an increase in organic matter is not essential to have high bioturbation intensity. Turnewitsch et al. (2000) found in the Arabian Sea that high food availability can cause deposit feeders to reduce sediment processing rates, decreasing bioturbation mixing intensity. These authors could not find a single functional relation between food supply and sediment mixing in deep-sea environments. Even the environmental drivers are sustainable different, in shallow marine settings in the Baltic Sea, a negative correlation was also found between bioturbation intensities and surface chlorophyll concentrations, indicating that organismal activity is low when food supply is high and fresh (Morys et al. 2016). In summary, even though these studies considered only vertical particle mixing, a global positive correlation between bioturbation intensity and organic matter cannot be generally assumed. Our results exemplify that horizontal mixing may not necessarily be driven by organic matter content either.

In the literature, deep-sea bioturbation intensity has been approached by considering the full endobenthic lebensspuren assemblage to obtain an overall D_B value. One of the main knowledge gaps of studying vertical bioturbation intensity is assigning the contribution of each lebensspuren morphotype (i.e., the contribution of each trace maker) to that global D_B value (Wheatcroft 1992). When approaching seafloor bioturbation (i.e., horizontal reworking of particles), this gap can be partially closed. In the present study, it could be shown that lebensspuren morphotypes contribute differentially to the overall SBI value and how specific environmental factors control the associated trace maker behavior. The obtained results reveal a high degree of variability. The studied fecal cast morphotypes are related with holothurian ingestion and defecation activities. The type of sediments ingested by holothurians varies considerably among the deep-sea taxa (Pierrat et al. 2022). Organic matter, grain size or detrital matter content are important factors for the organisms when choosing the most appropriate food resource (Pierrat et al. 2022). *Scotoplanes* spp., producing rounded fecal casts, show a selective behavior in favor of sediments rich in organic matter (Miller et al. 2000) while some spices of *Peniagone* that produce knotted fecal casts do not have this selectivity (Wigham et al. 2008). This is clearly observed in Fig. 3 where the rounded fecal cast variability is influenced by C_{org} while the knotted fecal casts are not. Also, grain size is important for some deep-sea *Psychropotes* species as well as their predilection for diatomaceous ooze (Khripounoff and Sibuet 1980). Here, the variability of smooth and coiled-curly fecal casts related with this trace maker is substantial but grain size and silicate seem to have a certain degree of control (Fig. 3). Rosette lebensspuren are attributed to echiuran feeding activities while extending their proboscis to collect detritus

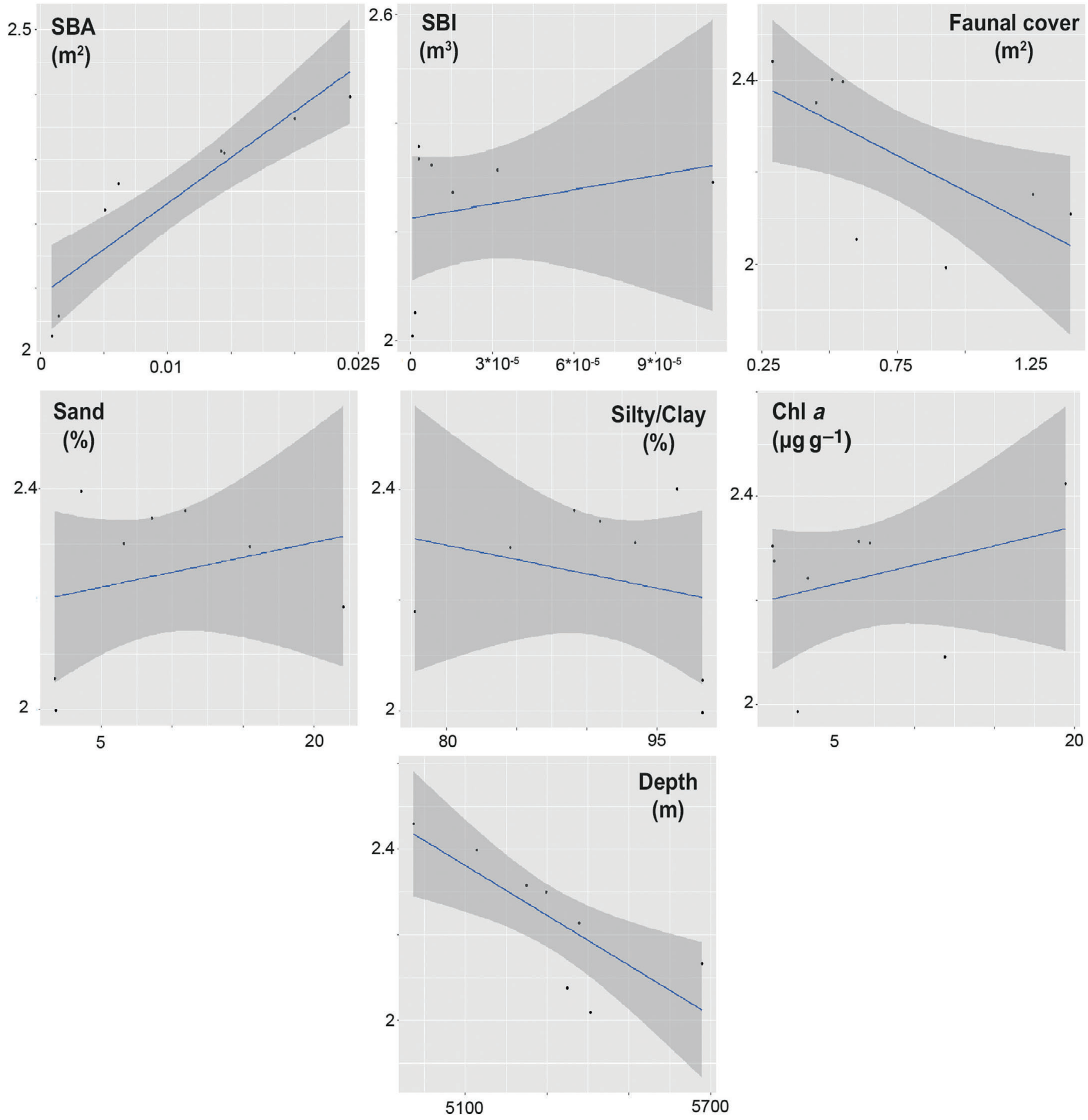


Fig. 4. Effects of each environmental predictor from its respective single-variable model showing the correlation matrix between number of lebensspuren and environmental factors (including SBI and SBA) used in GLMs per latitudinal bands.

(Miguez-Salas et al. 2023). Diatoms have been proposed as the most important food source for some rosette trace makers (Izumi and Yoshizawa 2016). Also, longer digestion times of some echiurans may be favored under reduced POC conditions (Jumars et al. 2015) and relatively larger area coverage by the rosette morphotype has been related with reduced organic availability due to faunal competition (Miguez-Salas et al. 2023). This is clearly observed in Fig. 3 where the rosette morphotype variability is related with silicate concentration while an opposite trend is observed with C_{org} and faunal cover. The question is whether a general negative correlation between SBI and organic matter can be assumed beyond all these specific examples.

When Turnewitsch et al. (2000) found the ambiguity between food supply and bioturbation mixing intensity at the Arabian Sea, they stated that "Bioturbation intensity should be controlled primarily by the composition of the benthic fauna, its specific adaptation to the environmental setting, and the abundance of each species of the benthic community. Food supply can have only an indirect influence on bioturbation intensity." It is well known that in the abyss food supply and faunal abundance are positively related to primary production in the overlying water (Smith et al. 2008). Here, we also found that faunal coverage is positively correlated with C_{org} and Chl *a*. However, the role of organic matter in controlling the activities of deep-sea deposit feeders has been under discussion due to recent progress in understanding their foraging behaviors and dietary preferences. Lately, it has been demonstrated that gut contents of deposit feeders constitute hotspots of organic matter on the abyssal plain that occupy one trophic level above detritus (Amaro et al. 2015; Romero-Romero et al., 2021). Also, it is common that repeated selective enrichment processes of sediment microbiota occur in sea cucumber guts (Pierrat et al. 2022). Moreover, the heterogeneous distribution of nutrients (i.e., organic matter patches; *see* Míguez Salas et al. 2022) together with changing food quality and quantity (e.g., seasonal inputs; Jumars and Wheatcroft 1989; Bett et al. 2001), controls the foraging behavior of some deposit feeders and, by extension, the bioturbation intensity. The implications of gut microbiota, seasonality, and food heterogeneity at each station are hard to evaluate here and are beyond the scope of this manuscript. However, deep-sea deposit feeders seem to have evolved means to cope with variable availability of organic matter.

Our results show a weak negative correlation between food quality/quantity and SBI (Fig. 2), suggesting that the trace maker community needs to look around more to find enough food. But, this type of correlation may not be true for all deep-sea settings. For example, if Stas. 9 and 11 data are isolated, a positive correlation appears between C_{org} and SBI as the assemblage is dominated by rounded fecal casts from *Scotoplanes*, a group with selective feeding behavior for sediments rich in organic matter. Lebensspuren morphotypes contribute differentially to the overall SBI and not all their trace makers are equally controlled by the same environmental factors (Fig. 3). In other words, the correlation between environmental factors and SBI varies because these factors will exert differential pressures on the trace makers and their life style while SBI may depend on the dominant lebensspuren morphotypes of the assemblage. The obtained results provide a more complex picture than expected and we cannot say with confidence that any environmental predictor alone is sufficient to explain the number of lebensspuren morphotypes (Fig. 4). This finding is consistent with recent tree-based machine learning results on how endobenthic bioturbation correlates with environmental and ecological parameters (Zhang et al. 2024).

Building on this, our results show the importance of interactions between epibenthic fauna and deep-sea sediments for global biogeochemical cycles and the challenges for future deep-sea conservation. Organic matter is usually consumed by benthic organisms on the seafloor and in the uppermost layers of the sediment; very little is permanently buried in sediments and varies from less than 1% to a few tens of percent, being positively related with total sedimentation rate (Sarmiento and Gruber 2006; Middelburg 2019). Holothurian fecal casts are usually organically enriched (e.g., C- and N-enriched feces) compared to the surrounding sediment (Amon and Herndl 1991; Ennas et al. 2023). Here, we observed a positive correlation between C_{org} and rounded fecal casts (i.e., *Scotoplanes* trace maker), whereas a negative correlation is observed between smooth, curly-coiled fecal casts (i.e., Psychropotidae trace makers) and C_{org} (Fig. 3). However, rounded fecal casts produce lower SBI while smooth and curly-coiled fecal casts produce higher SBI. Thus, for example, seafloor settings with low C_{org} that are characterized by high SBI values with similar fecal casts may increase the availability of organic carbon at the sediment–water interface that could be consumed again (e.g., by the benthic community, microbiota) or be available for further degradation and burial. In short, to understand how SBI may affect carbon processing at the seafloor, we need to know how much each lebensspuren morphotype contributed to SBI as well as the amount of sediment ingested by each trace makers. We would like to remark that there is a lot of room for improvement in terms of having an accurate value for the sediment ingested by each trace makers. This needs to be the next step for better SBI assessments.

The resettling of surface/subsurface sediments, which occurs in areas with high SBA associated with locomotion-feeding lebensspuren (e.g., M-ridged trails, flat trails), will increase exposure time of previously buried organic matter to different redox conditions at the sediment–water interface and lead to sediment porosity modifications. This will lead to consumption and redistribution of organic particles while this new exposure will allow further degradation and affect the amount that is ultimately buried. Enhanced diffusive transport of dissolved pore water components such as manganese may be affected as well. The implications of this redistribution and increased exposure of the sediments are outside the scope of this research but may be more important than previously anticipated.

It is well known that one of the future marine ecological challenges will be deep-sea mining. Despite the fact that the start of abyssal ferromanganese-nodule mining seems imminent, the potential environmental impact of future deep-sea mining on trace makers is far from being known. The density evolution of some lebensspuren morphotypes has been tested in deep-sea mining scenarios (Vornsand et al. 2024). The results showed that even though the lebensspuren can appear in a disturbed habitat within a few weeks after disturbance (e.g., *Paleodictyon*; Boehringer et al. 2021), epi- and endobenthic lebensspuren were at least 50% less abundant than observed on undisturbed seafloor (Vornsand et al. 2024). It is premature to conclude if other trace makers would continue performing their bioturbational activities with the same effectiveness in a disturbed habitat. However, it is known that both vertical and horizontal bioturbation are necessary for stable biogeochemical cycles. The disappearance of the trace makers by mining activities may cause damage beyond the erased biosphere and disrupt the lithosphere (i.e., global biogeochemical cycles).

In conclusion, our study documents that the characterization of animal–sediment interactions by studying their final products (i.e., lebensspuren) in the abyss emerges as a key tool to understand processes affecting this complex environment and associated ecological changes. Our results showed a weak negative correlation between organic matter content and SBI where lebensspuren morphotypes contributed differently to horizontal bioturbation. However, we cannot say with confidence that any environmental predictor alone (e.g., organic matter content) is sufficient to explain the number of lebensspuren morphotypes and SBI. Also, SBI seems to be a promising method for quantifying horizontal bioturbation intensity and may shed some light on how bioturbation processes are connected with environmental factors in deep sedimentary seafloor habitats worldwide. Further research should address the implications of SBI on global geochemical cycles (e.g., sulfur, nitrogen, phosphate), and how anthropogenic disturbing activities (e.g., deep-sea mining) may inhibit horizontal bioturbation processes in the long term.

Data availability statement

Lebensspuren area data are stored for peer review in the Zenodo GitHub (public repository; doi: 10.5281/zenodo.7848792).

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Acknowledgments

The research of OMS was funded by a Humboldt Postdoctoral Fellowship from the Alexander von Humboldt-Stiftung. The project was undertaken with financial support of the PTJ (German Ministry for Science and Education), grant 03G0223A to A.B., and by the Russian Foundation of Basis Research (project 13-04-02144), the Council of the President of the Russian Federation (project МК-2599.2013.4), Russian Federation Government grant No 11.G34.31.0010, grant of Presidium of the Far East Branch of RAS (12-I-P30-07). The master and crew of R/V Sonne are gratefully acknowledged for their support during OFOS deployments. During the expedition, T.R. was funded by a PhD fellowship from the German National Academic Foundation (Studienstiftung des deutschen Volkes). This is contribution #32 of the Senckenberg Ocean Species Alliance (SOSA) and we extend our profound gratitude for the philanthropic contribution that has empowered SOSA. We are most grateful for the constructive comments of two anonymous referees who helped us to improve the clarity of the manuscript. Open Access funding enabled and organized by Projekt DEAL.

Conflict of Interest

None declared.

Submitted 13 July 2023
Revised 25 March 2024
Accepted 29 June 2024

Associate editor: Florence Schubotz