



# Biodiversity and distribution patterns of deep-sea fauna along the temperate NW Pacific

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## ABSTRACT

The deep NW Pacific has been intensively analyzed in the last decade, during an international collaboration between German and Russian scientists, which has resulted in a vast, unique collection of material from previously unexplored areas. Until now, the environmental forces that could be driving species richness patterns in the deep NW Pacific have not been explored widely. Therefore, in this paper, we utilize new species distribution data from four deep-sea expeditions to the NW Pacific (2010–2016), which include the Sea of Japan, Sea of Okhotsk, the abyssal plain adjacent to the Kuril-Kamchatka Trench (KKT) and the KKT, to better understand species connectivity, biodiversity patterns, and distribution ranges in deep-sea benthos in this region. To determine the best environmental predictors driving these deep-sea species richness patterns, we applied generalized additive (GAMs) and linear models (GLMs). We calculated the total number of geographic distribution records, alpha (total number of species per 10,000 km<sup>2</sup> hexagonal cells) and gamma species richness (total number of species per 1° latitudinal bands), and expected number of species (rarefaction ES15). Our highest number of distribution records and gamma species richness during the last decade peaked at intermediate latitudes (42°–44°N) along the mesopelagic zone (500–1000 m) of the Sea of Japan and abyssopelagic zone (4000–6000 m) of the NW Pacific and KKT. When sampling bias was accounted for, the alpha species richness in bathypelagic zone (1000–4000 m) of Sea of Okhotsk and abyssopelagic zone (4000–6000 m) of the NW Pacific and KKT were as high as mesopelagic zone of the Sea of Japan. The similarity cluster analysis of species presence/absence in lower bathyal/hadal (3000–8500 m) revealed three distinct geographic regions including Sea of Japan, Sea of Okhotsk, and KKT in the NW Pacific. The eastern sector of the Sea of Okhotsk and western KKT had c. 50% of species in common. Several species of deep-sea Bivalves, such as *Dacrydium rostriferum* and *Vesicomya pacifica*, had the greatest latitudinal distribution ranges among all species. Echinoderm *Ophiura leptocenia*, had instead, the broadest bathymetric distribution ranges compared to all other collected species. GAM models indicated that dissolved oxygen was the best explanatory variable for predicting numbers of species, closely followed by the model including all environmental variables plus topography. However, the GLM models of species richness, with latitudinal intervals of 1° and 5°, found that the topography and temperature were the best predictors of number of species. GLM model outputs indicated that a model that contains only the number of distribution records is, for all practical purposes, as good as any model that contains an environmental predictor. This study provides new insights on the NW Pacific deep-sea species richness patterns, where dissolved oxygen might play an important role, especially when considering the Oxygen Minimum Zones (OMZs) in the deep NW Pacific.

## 1. Introduction

The deep ocean makes up 90% of the world's ocean, shaping the largest biome on Earth, while encompassing a wide range of habitats and environmental conditions (Brandt & Malyutina 2015; Danovaro

et al., 2017; Ramirez-Llodra et al., 2010; Raupach et al., 2008). However, less than 0.0001% of the deep sea (deeper than 200 m) has been explored so far, making it the least explored environment on Earth (Brandt & Malyutina 2015; Danovaro et al., 2017). Consequently, deep-sea species richness gradients and their driving factors, remain poorly

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known.

In general, gradients of marine species richness show a declining trend from low to high latitudes (Chaudhary et al., 2017; Hillebrand 2004; Jablonski et al., 2006; Saeedi & Costello 2012; Saeedi & Costello 2019a; Saeedi & Costello 2019b; Saeedi et al., 2019b; Saeedi et al., 2017b; Tittensor et al., 2010), and from shallow water to deep sea (Costello & Chaudhary 2017; Saeedi et al., 2019b), with species richness peaking near the bathyal zone for different taxa, for instance in gastropods and nematodes (Danovaro et al., 2010; Rex 1973; Rex & Etter 2010; Saeedi et al., 2019b). This bathyal species richness peak might be due to evolutionary historical and ecological processes such as speciation and high differentiation rate (Danovaro et al., 2010; Rex 1973; Rex & Etter 2010; Rex et al., 2005b) as well as decreased chemical energy and carbon-flux (McClain et al., 2012; Woolley et al., 2016).

Some chemosynthetic deep-sea habitats, such as cold methane seeps, seamounts, and organic food falls, share many common taxa with broad geographical distribution ranges, likely due to horizontal gene flow (Danovaro et al., 2017; Pawlowski et al., 2007; Samadi et al., 2006). For instance, the wood-boring bivalve, genus *Xylophaga* W. Turton, 1822, was broadly distributed along chemosynthetic deep-sea large organic wood falls (Danovaro et al., 2017; Saeedi et al., 2019a; Voight 2008).

In contrast to broad distribution range and the extensive horizontal gene flow theory, multiple soft-bottom taxa show significant genetic differentiation along bathymetric gradients of only a few kilometres (Carney 2005; Danovaro et al., 2017; Zardus et al., 2006). However, some studies have shown that the narrow distribution ranges of species, for example in seamounts, might be an artefact of sampling bias (Clark et al., 2010; McClain 2007; O'Hara 2007; Samadi et al., 2007). It is therefore unclear whether this is true local endemism (narrow distribution range) or a result of sampling bias (Clark et al., 2010; Hall-Spencer et al., 2007; McClain 2007; O'Hara 2007).

Despite the vast area of the deep sea, its heterogeneous habitats and potential high species richness, distribution and biodiversity patterns and their driving factors (e.g., environmental factors and sampling bias) have not been widely studied along the NW Pacific. The NW Pacific is an important ecosystem to study deep-sea biodiversity patterns, as it includes several deep-sea basins differing in depths, hydrology, and isolation (Grebmeier et al., 2006; Leprieur et al., 2016; Renema et al., 2008). Thus far, as a result of four deep-sea expeditions (SoJaBio, So-khoBio, and KuramBio I and II; 2010–2016), three of the main NW Pacific areas, have been extensively sampled - Sea of Japan, Sea of Okhotsk, and Kuril-Kamchatka Trench (KKT) - providing a *proxy* for the diversity encountered in the deep sea area of these regions. The Sea of Japan, the warm temperate zone of the NW Pacific, and the KKT receive two major currents: warm Tsushima and cold Oyashio Currents (Fujikura et al., 2010; Su et al., 1990). The Tsushima Current splits from the Kuroshio Current and flows from off Kyushu into the Sea of Japan. The Oyashio Current flows southward through Japanese waters from off Hokkaido along the Pacific coast (Fujikura et al., 2010; Su et al., 1990).

In the past few decades, much research effort has been placed on determining the importance of environmental variables, such as temperature, Particulate Organic Carbon (POC) flux, oxygen, current, and nutrients on shaping the deep-sea biodiversity and influencing species richness (Cook et al., 2000; Gooday et al., 2010; Grassle 1991; Levin & Gage 1998; Rogers 2000; Rogers 2015; Sibuet & Vangriesheim 2009; Thurber et al., 2014; Yasuhara & Danovaro 2016). Some studies argued that chemical energy and carbon flux are more likely to control species diversity in the deep sea, not the temperature (e.g., bivalves and gastropods) (McClain et al., 2012; Woolley et al., 2016). Ocean turbidity currents and sediment overflow can transport large amounts of sediment as deep as 4,800 m depth at the Congo channel in Africa, which could also affect the diversity and community structure of deep-sea benthic fauna in this area (Sibuet & Vangriesheim 2009). This deep-water layer in Congo channel is characterized by anomalies in oxygen

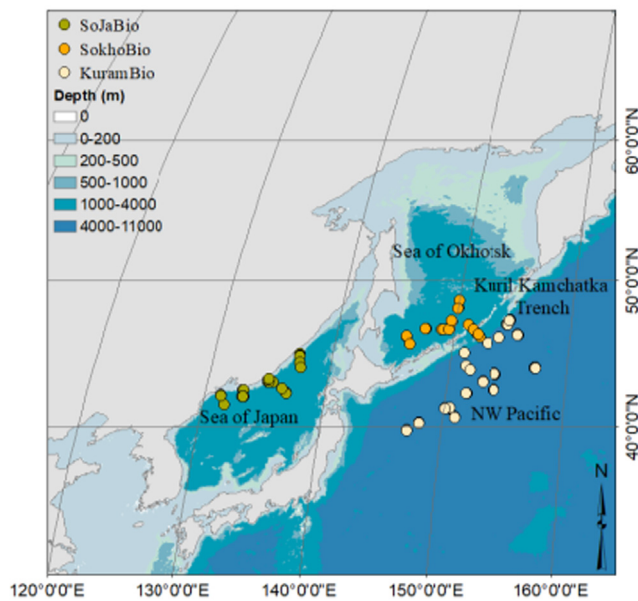
(decreased), silicates and nutrients (increased), which were due to the re-mineralization of particulate organic matter and upward diffusion of silicate from the sediment (Sibuet & Vangriesheim 2009). These current systems thus affect the organic matter content and dissolved oxygen in the deep ocean. (Cook et al., 2000; Gooday et al., 2010; Grassle 1991; Levin & Gage 1998; Rogers 2000; Sibuet & Vangriesheim 2009; Thurber et al., 2014; Yasuhara & Danovaro 2016). Results from both present and past deep-sea assemblages indicate that when a broad range of deep-sea bottom-water temperatures are considered, an unimodal relationship exists between temperature and deep-sea diversity (Yasuhara & Danovaro 2016). Oxygen minimum zones (OMZs), defined as layers of the water column where dissolved oxygen concentrations fall below  $0.5 \text{ ml l}^{-1}$ , have also been found to be an important factor affecting deep-sea faunal biodiversity and abundance in the eastern Pacific Ocean, Indian Ocean, the Arabian Sea, and the Sea of Japan (Cook et al., 2000; Gooday et al., 2010; Huang et al., 2019; Huang et al., 2018; Levin & Gage 1998; Rogers 2000; Tada 2015).

In this study, we aim to determine the: (i) latitudinal and bathymetric deep-sea benthic species richness patterns and distribution ranges; (ii) if number of distribution records, alpha species richness (number of species), expected species richness accounted for sampling bias (ES15), and endemism rate vary based on  $10,000 \text{ km}^2$  hexagons; and (iii) what are the potential explanatory factors driving these species richness patterns, which includes available bottom environmental variables such as temperature, dissolved oxygen, current velocity, salinity, nitrate, topography, and total number of distribution records. We hypothesized that ES15 is the best estimation of species richness compared to the total number of distribution records and alpha species richness. We also hypothesized that dissolved oxygen is the best predictor of deep-sea benthic fauna species richness as found in other similar studies (Huang et al., 2019; Huang et al., 2018; Levin & Gage 1998). This study intends to provide insights on the NW Pacific deep-sea species richness patterns and its potential environmental predictors that might have helped shape the present and future species distribution and richness patterns.

## 2. Methods

### 2.1. Study area and dataset preparation

Our study area includes much of the temperate NW Pacific (c.  $32^\circ$  to  $60^\circ$  in latitude and c.  $130^\circ$  to  $160^\circ$  in longitude). We used two datasets (I and II), depending on our aim and the applied statistical analysis. Dataset I (Beneficial dataset), was prepared from our four benthic deep-sea expeditions to the NW Pacific including the Sea of Japan Biodiversity Study (SoJaBio, 2010) (Malyutina & Brandt 2013), Kuril-Kamchatka Biodiversity Study (KuramBio I and II, 2012–2016) (Brandt & Malyutina 2015), and the Sea of Okhotsk Biodiversity Study (So-khoBio, 2015) (Malyutina et al., 2018). All specimens were collected using our standard gear (CTD, MUC (multicorer); GKG (giant box corer); EBS (epibenthic sled); AGT (Agassiz Trawl), WT (bottom trawl) (Brandt & Malyutina 2014), BC (box corer) (Brandt et al., 2010), and PN (plankton net) (Chernyshev & Polyakova, 2018) being deployed following a standardized method (Brandt & Malyutina, 2014). Dataset I (c.  $40^\circ$  to  $50^\circ$  in latitude and c.  $130^\circ$  to  $160^\circ$  in longitude; and depth from 455 to 8136 m) (Fig. 1), is already published on the Ocean Biogeographic Information System (OBIS) ([www.iobis.org](http://www.iobis.org)) and is publicly available (Saeedi et al., 2019d). During the dataset preparation for OBIS, species names were matched against the World Register of Marine Species (WoRMS) and synonyms reconciled ([www.marinespecies.org](http://www.marinespecies.org)). Distribution records were checked for reliability using quality control tools such as the R package 'robis' (Provoost P, 2018), and uncertain records were corrected (e.g., reversing latitude and longitude fields, duplicate records). Dataset I included 7023 occurrence records with 872 deep-sea taxa, from which 1701 records (c. 24%) were at the species level represented by 366 species. Malacostraca (c. 42% of



**Fig. 1.** Study area and sampling locations in three areas from four expeditions. Colored circles show 303 sampling effort coordinate points (per sampling gear per station per cruise) during four deep-sea cruises including Sea of Japan Biodiversity Study (SoJaBio, 2010), Kuril-Kamchatka Biodiversity Study (KuramBio I and II, 2012–2016), and Sea of Okhotsk Biodiversity Study (SokhoBio, 2015). The area KuramBio is represented by the two expeditions KuramBio I in 2012 (open abyssal of NW Pacific) and KuramBio II in 2016 (Kuril Kamchatka Trench).

data composition) and Bivalvia (c. 10% of data composition) were the most abundant taxa in composition of the dataset I, respectively (Figure S1). Finally, we used dataset I to create latitudinal and bathymetrical biodiversity and distribution range analysis (Figs. 2, 3, and S1).

Dataset II is composed of dataset I, and additional geographic distributional records extracted from OBIS and Global Biodiversity Information Facility (GBIF) ([www.gbif.org](http://www.gbif.org)) collected also by a variety of sampling gear. We searched for any extensive available distribution records of the 366 species in OBIS and GBIF, which were distributed in the NW Pacific and adjacent Arctic Ocean (c. 0° to 90° in latitude and c. 100° to 180° in longitude; and depths from c. 450 to 11,000 m) but absent in our dataset I, resulting in 1888 additional occurrence records (Figure S2 and Table S1). The extracted data was then merged with the dataset I, and duplicates were excluded. In total, dataset II included 3589 occurrence records (1701 + 1888 records) of 366 species. We then used the dataset II in per-hexagon basis analysis (Fig. 3), generalized additive models (GAMs) and generalized linear models (GLMs) (Fig. 6 and supplementary files 1, 2, 3). Hexagon and environmental model analyses require greater numbers of samples and a greater range of geographical distributions to produce outcomes that are more accurate. Finally, latitudinal distribution density-range of deep-sea species at the class level was plotted using dataset II, to discover which species in dataset I are also distributed in higher latitudes of Arctic (Figure S3).

## 2.2. Measurements of biodiversity

The statistical software R 3.4.3 (Team 2017) and ArcMap 10.5.1 were used to analyze the data and plot the graphs. Total number of distribution records and total number of species per 1° latitudinal bands as well as 100 m depth intervals were plotted (gamma species richness). The aggregation of samples into latitudinal bands and depth intervals was made to smooth out the effects of uneven sampling effort. The latitudinal and bathymetric distribution ranges of the most common species were also plotted. This captures the heterogeneity in the

underlying data best, but contains data collected by a variety of methods and sample sizes which are not necessarily comparable (e.g., plankton, whales, turtles, sharks, tracked animals, sediment cores, trawls, Table S1). This introduces considerable variability and bias between latitude bands and depth intervals.

To characterize the latitudinal community composition and density of deep-sea species distribution-range in dataset II, we excluded duplicate latitudinal records for species within a respective class, and created the violin plot built with the R package ‘ggplot2’ (Wickham 2016), to represent the density of data estimated by the kernel method.

Biological samples were collected using unequal sample sizes and a variety of methods (e.g., Camera Epibenthic Sledge (C - EBS), Box Corer (GKG), Multicore (MUC), sediment cores, and trawls) during the four expeditions, which were not necessarily comparable. To normalize the sampling size, we also created c. 10,000 km<sup>2</sup> hexagons to uniformly split the study area. For that, a polygon was created to set limits to the studied area, and converted into regular hexagonal grids of 1° resolution (c. 10,000 km<sup>2</sup>) with R packages, which included ‘geogrid’ (Bailey J, 2018), ‘rgeos’ (Bivand et al., 2018), and ‘sp’ (Pebesma & Bivand, 2005), by assigning the content of the existing polygons to the new grid using the Hungarian algorithm (Kuhn, 2005).

We used four measures of species richness for each hexagonal cell including: (1) the total number of records per hexagon; (2) the total number of species per hexagon (alpha diversity); (3) the total number of unique species per hexagon (endemicity); and (4) the estimated species richness per sampled hexagon using rarefaction (ES15).

The rarefaction method was used to reduce the effect of sampling size on benthic species richness patterns by counting the number of species in a constant number of random samples. We considered each sample as a unique combination of date and location where one or more species were recorded. ES15 does not remove the sampling bias completely, but it reduces the effect of un-even sampling at a certain level. Due to low sampling effort of the deep-sea fauna, we used ES15 to estimate the species richness in 15 samples per hexagon, using the R package ‘vegan’ (Oksanen et al., 2017).

We applied hierarchical cluster analysis separately for bathyal (450–3000 m) and lower bathyal/hadal (3000–8500 m) fauna, using the *vegan* package in R (Oksanen et al., 2015; Oksanen et al., 2010), which uses Euclidean distance, and group-average linkage, which are recommended for analysis of species presence/absence. Bootstrap support was obtained via ordinary bootstrap resampling and multiscale bootstrap resampling (AU) (Shimodaira, 2004) using the R package *Pvclust* (Suzuki et al., 2015).

## 2.3. Environmental models

We extracted five bottom environmental factors (benthic layers) which were reported as important driving factors of the deep-sea species richness by other studies (Cook et al., 2000; Gooday et al., 2010; Grassle, 1991; Levin & Gage, 1998; Rogers, 2000; Sibuet & Vangriesheim, 2009; Thurber et al., 2014; Yasuhara & Danovaro, 2016). Benthic layers were at 5 arcmin (~10 km) spatial resolution corresponding to the maximum depth including average temperature (°C), dissolved oxygen (mol m<sup>-3</sup>), current velocity (m<sup>-1</sup>), salinity (PSS), and nitrate (mol m<sup>-3</sup>) from Bio-ORACLE (<http://www.bio-oracle.org/>) for deep-sea records (> 500 m) (Assis et al., 2018; Tyberghein et al., 2012), and topography (m) from the General Bathymetric Chart of the Oceans (<https://www.gebco.net/>).

We then used generalized additive models and generalized linear models (GLMs) to examine the impact of environmental predictors on the number of species and expected number of species (ES15) on a per-hexagon basis. As predictors, we used the topography layer and five environmental factors.

The GAMs were built using negative binomial error distribution and models fitted via restricted maximum likelihood. Automatic predictor selection was implemented in the R package ‘mgcv’ (Wood, 2013) to



control the complexity of smooth terms. For each analysis we fitted an intercept-only model, which represented the explanatory power of a model that assumes no relationship between response variables and the environment. We also fitted a model for each environmental predictor separately; one that represented the combined impacts of all environmental predictors ('env'), and one that represented the combined impacts of all environmental predictors and topography ('env.topo'). Additionally, we fitted a model that included only a two-dimensional spline and intercept, to examine support for the hypothesis that all signal in the data stemmed from spatial autocorrelation. Due to high correlation of latitude to temperature (Saeedi et al., 2017b), we excluded the model using latitude and longitude as predictors.

All models with the number of species as the response variable included the number of records from each site in order to control for sampling size, with the exception of the intercept only model. Models using ES15 as a response variable excluded this term, as ES15 calculations are themselves intended to control for sampling bias. The GLMs were performed on two latitudinal intervals (1° and 5°), which limited our ability to fit complex functional responses due to the reduced sample size. Hence, we fitted a Poisson error distribution, and used the number of records per band to control for differences in sampling size.

To compare the models for goodness of fit, while penalizing for over-parameterization, we used the small sample size corrected Akaike Information Criterion (AIC; (Akaike, 1973; Guisan et al., 2002; Sakamoto et al., 1986). Variable selection is essentially the same for all regression models, although evaluation criteria like the AIC can be used with GLMs and GAMs (Guisan et al., 2002). In our study, we opted for the AIC method as it chooses the models with optimal fit to the data, while controlling for over parameterization, and avoids the high variance operations, as small perturbations of the response data can sometimes lead to vastly different subsets of the variables (e.g., stepwise regression or shrinkage rules; (Guisan et al., 2002). Thus, lowest AIC score represented the best compromise between model fit and complexity and allows the estimation of the relative support for each model. Here, we used the compression between  $\Delta AIC < 2$  of the top model (lowest AIC score), and the remaining models.

### 3. Results

#### 3.1. Species richness and distribution

##### 3.1.1. Latitude and depth

The greatest number of distribution records (c. 500 records) and total number of species per 1° latitudinal bands or gamma species richness (c. 200 spp.) in our dataset reached its peak at intermediate latitudes (43–44°N) (Fig. 2). The latitudinal gradient of total number of records and gamma species richness were highly correlated. More than half of the 366 species (c. 200 spp.) were collected only at latitudes 42–44°N, and less than 100 species in most of the remaining 1°

latitudinal bands.

The highest number of records (175–225 records) and number of species (c. 100–125 spp.) in our dataset peaked around depth 500 and 5000 m (Fig. 2). Of the total 366 species, c. 120 species (c. 33%) were distributed in depth around 500 m, and c. 100 species (c. 25%) in depth of about 5500 m. The bathymetric gradient of total number of records and gamma species richness were also highly correlated.

Most of the species had broad latitudinal (horizontal) distribution ranges from about 40° to 47°N (Fig. 3). Of 40 species which had more than 10 occurrence records, 22 species (55%) had latitudinal distribution ranges broader than 5° (> ~500 km). The broadest latitudinal distribution ranges were observed in three species of Bivalvia, *Dacrydium rostriferum* F. R. Bernard, 1978, *Vesicomya pacifica* (E. A. Smith, 1885), and *Katadesmia vincula* (Dall, 1908), ranging from latitude c. 40° to 48°N. Porifera *Caulophacus* (*Caulophacus*) *schulzei* Wilson, 1904 and Nemertea *Sonnenemertes cantelli* Chernyshev, Abukawa & Kajihara, 2015 had the narrowest distribution ranges (around 47°N) compared to other species in our study.

Of 40 species, more than half (21 spp.) had their average bathymetric distribution ranges around 4000–6000 m depth (abyssopelagic depth) (Fig. 3). Twelve species (30%) did not reach deeper than 4000 m depth. The bivalve *Rhinoclama filatovae* (Bernard, 1979) had its greatest distribution ranges in the hadal depths (6000–8000 m). More than 50% of the species (22 spp.) had narrow bathymetric (vertical) distribution ranges of less than 1000 m depth. The brittle-star *Ophiura leptoctenia* H.L. Clark, 1911 had the broadest vertical distribution range and was collected from mesopelagic to abyssopelagic depths (500 m to 5000 m).

When additional occurrence records of the NW Pacific and its adjacent Arctic Ocean were added to species listed in dataset I, Bivalvia had the broadest latitudinal distributions ranging from the tropical NW Pacific to the Arctic Ocean (Figure S3). In general, Bivalvia, Polychaeta, Asteroidea, Malacostraca, and Gastropoda had the broadest horizontal distribution ranges among all other classes inhabiting the tropical NW Pacific to the Arctic Ocean. However, more than 50% of the species (10 spp.) were only reported from latitude c. 40–50° N and were absent from the other areas.

##### 3.1.2. Hexagons

The mesopelagic zone of the continental shelf around the Sea of Japan (500–1000 m) had the highest number of records (239 records), number of species or alpha species richness (121 spp.), expected number of species (ES15) (12 – 14 species), and endemism rate (> 60%) per hexagonal cell (Fig. 4). However, the expected species richness in the bathypelagic zone (1000–4000 m) of Sea of Okhotsk and abyssopelagic zone (4000–6000 m) of the NW Pacific and KKT were as high as mesopelagic zone of the Sea of Japan.

##### 3.1.3. Similarity analysis

Bathyal (450–3000 m) cluster analysis clearly showed two distinct

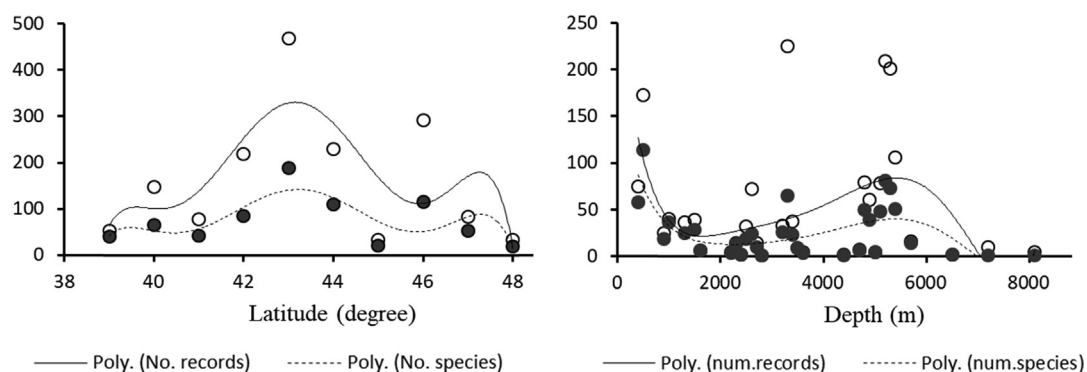
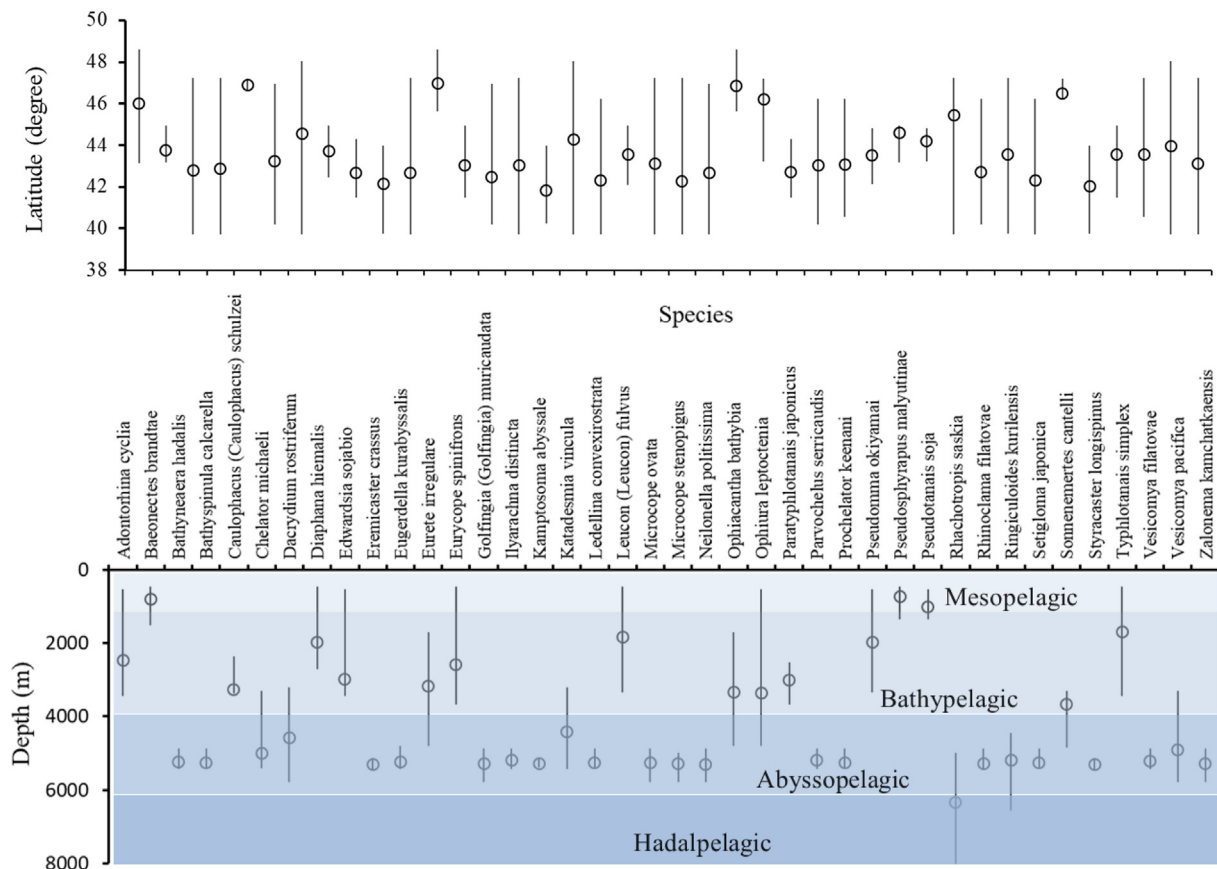


Fig. 2. Total number of records (hollow circles) and gamma species richness (total number of species, black circles) of deep-sea fauna collected from four cruises in three areas against 1° latitudinal bands and 100 m depth intervals using dataset I. The solid and dashed lines show a level-six polynomial trend.



**Fig. 3.** Latitudinal and bathymetric distribution ranges of 40 deep-sea species which had more than 10 distribution records in dataset I. The hollow circles show the average (average latitude and depth calculated by summing up all the values divided to the total number of distribution records reported for that species). The highlighted blue gradients show four ocean depth classifications. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

clusters representing the species composition in the Sea of Japan and Sea of Okhotsk and the area overlapped on the KKT (Fig. 5). For lower bathyal/hadal (3000–8500 m) fauna, the cluster is more informative as there is more number of distribution records in those depths (Fig. 5). The lower bathyal/hadal dendrogram grouped species based on their presence/absence into three distinct geographic regions, which included the Sea of Japan, Sea of Okhotsk, and KKT. However, one hexagonal cell (ID = 4262) from the KKT was grouped with the Sea of Okhotsk and shared c. 50% of species (including Echinodermata, Nemertea, Bryozoa, Arthropoda, Mollusca, and Porifera) together (Table S2).

### 3.1.4. Environmental models

As a result of the GAM analysis, we recovered parallel results for models predicting number of species and ES15 (supplementary material S1, GAM-Supplementary S1). On models predicting number of species, dissolved oxygen was recovered as the best explanatory variable followed by the model ‘env.topo’ ( $\Delta AIC = 0.17$ ), the model ‘env’ ( $\Delta AIC = 0.17$ ), and the predictor nitrate ( $\Delta AIC = 0.17$ ), all with marginally comparable  $\Delta AIC$  values ( $\Delta AIC < 2$ ) (Fig. 6). Similarly, the same models were recovered as best fit, except nitrate, which presented a non-marginal difference of AIC value ( $\Delta AIC = 5.33$ ). For ES15, dissolved oxygen featured as the best predictor in the top model, followed by the model ‘env.topo’ ( $\Delta AIC = 0.00$ ) and the model ‘env’ ( $\Delta AIC = 0.00$ ).

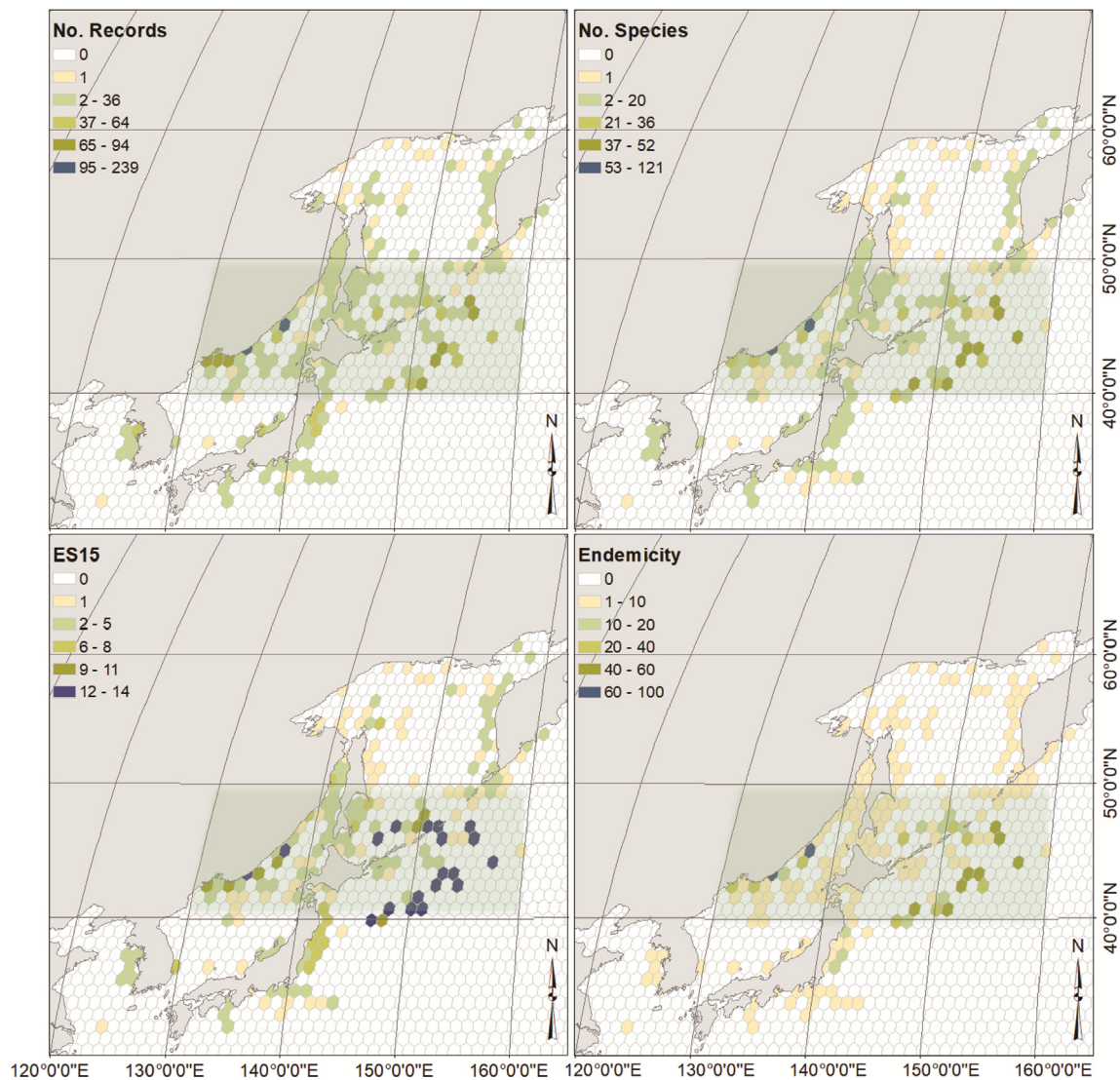
GLMs relating species richness and ES15 values to environmental predictors are given in Fig. 6 and supplementary materials S2 and S3 (GLM-Supplementary S2\_1 deg and GLM-Supplementary S3\_5 deg). In the dataset with latitudinal intervals of  $1^\circ$ , the models for number of

species and ES15 were similar. For the models explaining the number of species, we recovered topography as the best predictor, followed by temperature ( $\Delta AIC > 34.46$ ). We also recovered the model ‘numrec’ ( $\Delta AIC = 82.22$ ), which contains only effects of sampling, with higher  $\Delta AIC$  than the best models, but lower than other environmental predictors (e.g., nitrate, salinity). 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 species. Whereas in models predicting ES15, temperature was found to be the best predictor, along with dissolved oxygen ( $\Delta AIC = 1.63$ ). In the dataset with latitudinal intervals of  $5^\circ$ , we found similar results of explanatory variables for number of species and ES15. For number of species, we solely recovered topography as the best predictor, followed by the model ‘numrec’ ( $\Delta AIC = 6.56$ ), indicating that rarefaction ES15 reduction can influence the response predictors in the model. For ES15, topography was the best predictor, followed by temperature ( $\Delta AIC = 1.13$ ) and dissolved oxygen ( $\Delta AIC = 1.78$ ). Nitrate was marginally recovered as a good predictor, with not a particular strong  $\Delta AIC$  of only 2.41.

## 4. Discussion

### 4.1. Species richness and distribution

The highest latitudinal gamma species richness in this study was observed along the intermediate latitudes ( $42^\circ$ – $44^\circ$ N) in correlation with the greatest number of records in the mesopelagic depths of Sea of Japan (500–1000 m) and abyssopelagic depths of the NW Pacific and



**Fig. 4.** Total number of records, species richness (number of species), expected number of species (ES15), and endemism rate (%) per c. 10,000 km<sup>2</sup> hexagonal cells calculated using dataset II (Fig. S2). The three sampling areas of the four cruises (SoJaBio, KuramBio I and II, and SokhoBio; 2010–2016) is highlighted in light green. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

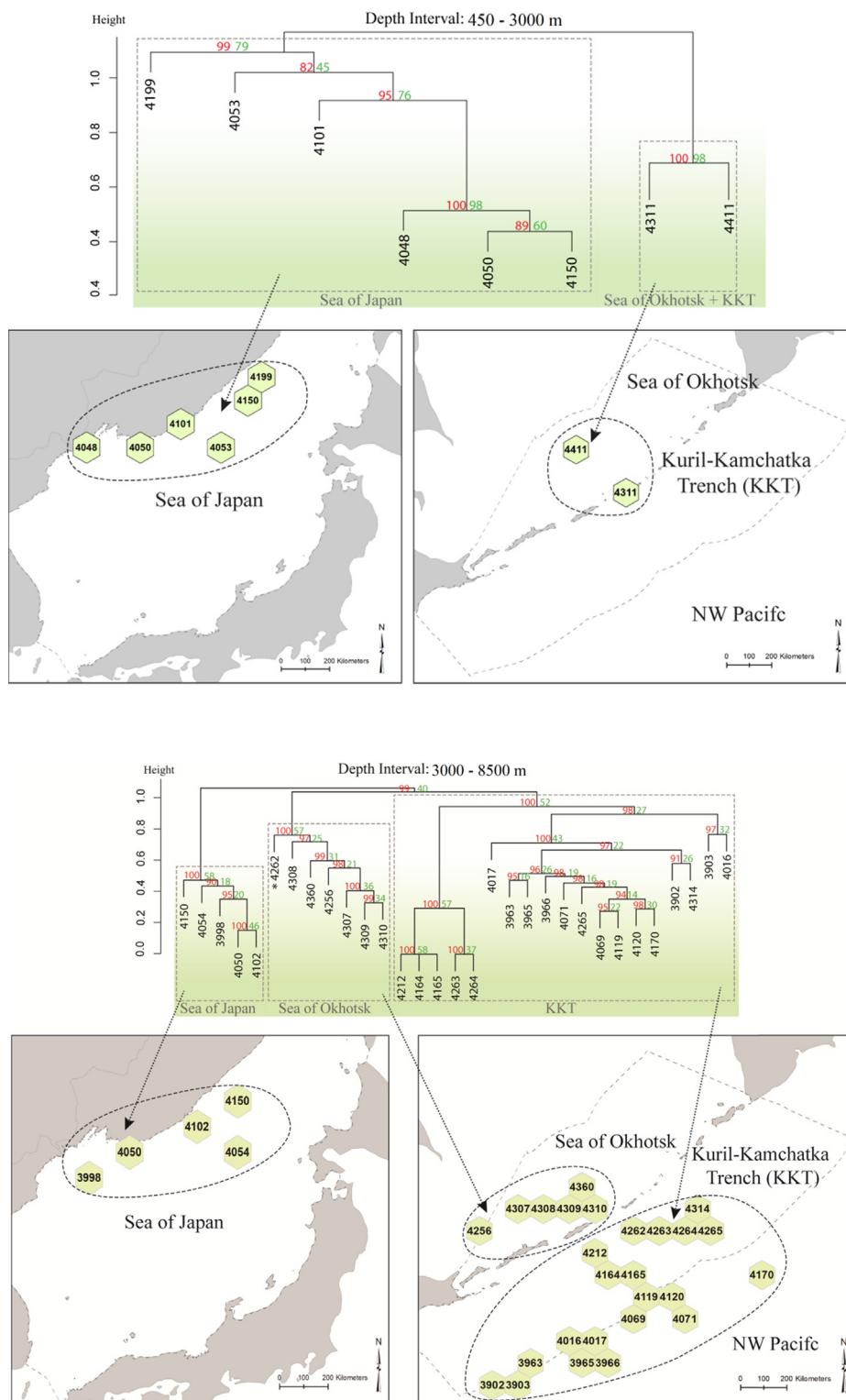
KKT (4000–6000 m). This latitudinal species richness peak around 40° to 45°N is also well documented for other deep-sea fauna such as bivalves, gastropods, and isopods (Rex et al., 2000). Moreover, the high levels of deep-sea species richness along the Sea of Japan and KKT, despite their small area, has been reported by other scientists (Brandt et al., 2015; Frutos et al., 2017; Fujikura et al., 2010). This could be due to heterogeneous environments of the Japanese waters including various topographical, geological, physical and chemical characteristics as well as the high number of distribution records (Brandt & Malyutina, 2015; Fujikura et al., 2010; Malyutina & Brandt, 2013). Sea of Japan also is geographically isolated and has an abnormally high level of dissolved oxygen in its deeper parts; however, its bottom-water oxygen level has declined up to 8–10% in the recent three decades (Elsner et al., 2013; Huang et al., 2019; Huang et al., 2018). When rarefaction ES15 was calculated in our study, the species richness in KKT, southern parts of Sea of Okhotsk, and warm temperate NW Pacific showed high levels of species richness comparable to Japan. This can suggest that there might be still many undiscovered species in areas under/less-sampled along the deep NW Pacific which taking them into account can change the presented biodiversity patterns here. This result could also support the idea that the deep non-isolated Kuril-Kamchatka Trench area might have higher abundance and species richness than the young

geographically isolated deep-sea basin of the Sea of Japan (Brandt et al., 2015; Frutos et al., 2017).

In our study, the bathymetric gamma species richness gradient reached its highest peak at the lower mesopelagic depth (c. 500 m), then decreased by depth and increased again towards the bathypelagic depths (c. 2000–3000 m), and reached its second peak near the abyssopelagic depth (4000–6000 m). This pattern of decreasing bathymetric species richness with lower-slope peaks has been well documented by other studies (Jöst et al., 2019; Rex et al., 2005a; Rex & Etter, 2010; Yasuhara et al., 2012). For instance, diversity in some deep-sea taxa such as gastropods and nematodes increases from the continental shelf to the bathyal and abyssal zones due to increased environmental stability (Danovaro et al., 2010; Rex, 1973; Rex & Etter, 2010). However, the high species richness of some well-studied taxa in some regions might be an artefact of a sampling bias where there are more taxonomic studies and researches in those regions compared to the other less-studied taxa in those areas (Reimer et al., 2019).

We examined latitudinal and bathymetric distribution ranges of some deep-sea fauna and concluded that most of the species had broad horizontal distribution ranges, but rather narrow vertical distribution ranges. Bivalve species, such as *Dacrydium rostriferum* and *Vesicomya pacifica*, had the greatest latitudinal distribution ranges among these

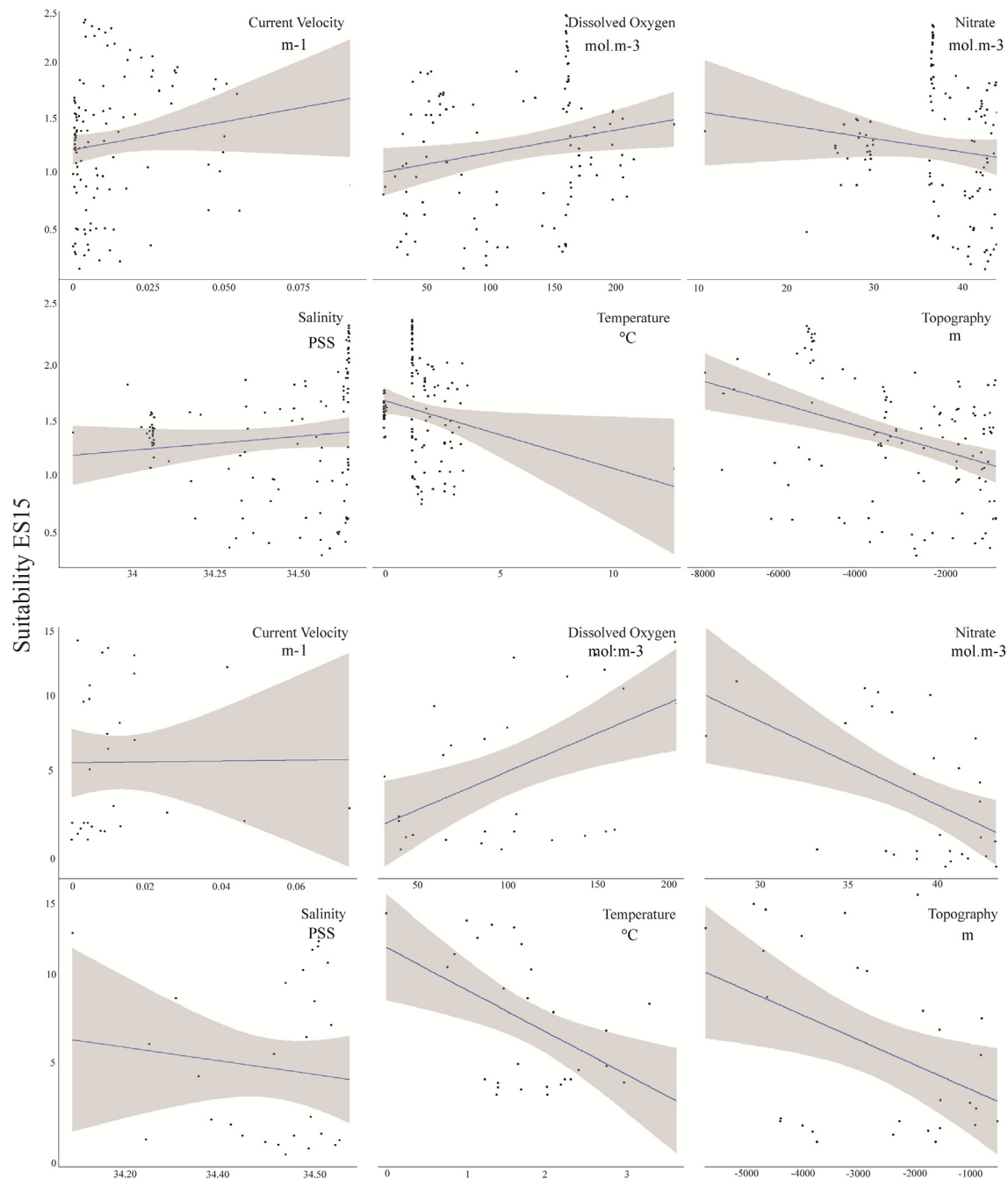




**Fig. 5.** Cluster dendrogram of bathyal (450–3000 m) and lower bathyal/hadal (3000–8500 m), fauna of our sampling collection (dataset I) in c. 10,000 km<sup>2</sup> hexagonal cells in the Sea of Japan, Kuril-Kamchatka Trench, and Sea of Okhotsk. In the clusters, the numbers above each edge show the probability of nodes below that edge occurring as a cluster in resampled trees, via ordinary bootstrap resampling (BP, green) or multi-scale bootstrap resampling (AU, red). The black numerals represent the hexagonal cell ID numbers and the dashed lines correlate to the clusters which were grouped together. \*The only hexagonal cell from KKT which was grouped with Sea of Okhotsk clade not the KKT itself. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

species. This finding supports the hypothesis that many deep-sea species are broadly horizontally distributed, but not vertically, regardless of their habitat type (Danovaro et al., 2017; Jing et al., 2018; Samadi et al., 2006). Even patchy habitats such as seamounts and vents do not appear to differ from the surrounding abyssal plains in this respect (Danovaro et al., 2017). For example, about 80% of the species on a well-studied California seamount possess ranges greater than 1000 km (Danovaro et al., 2017; McClain et al., 2009). Moreover, about half of the deep-sea bivalves and gastropods in the North Atlantic Ocean have

wide distribution ranges along the entire basin (Allen & Sanders, 1996; Rex et al., 2005b). Dover et al. (2002) also found that species of mussels and clams near the vent habitats exhibit no evidence for isolation by distance across thousands of kilometers. He suggested that their larvae, from distant source populations, likely mix in the water column before they settle at hydrothermal sites, which allows for broader distribution ranges (Van Dover et al., 2002). However, other studies suggested that bathymetric gradients might pose significant constraints on species ranges relative to horizontal distances, which could be explained by the



**Fig. 6.** Correlation matrix between expected number of species (ES15) and environmental factors used in GAMs per 10,000 km<sup>2</sup> hexagons (top) and GLMs per 1° latitudinal bands (bottom) using dataset II.

sharp physicochemical gradients along the water depths (Danovaro et al., 2017; Jing et al., 2018). Thus, biodiversity and geographic distribution patterns are likely to vary considerably between the abyssal seafloor and the continental slopes due to heterogeneity in OMZs, carbon flux, topography, sediment type, and current regime (Danovaro et al., 2017; Lamshead et al., 2002; McClain et al., 2009; Van Dover et al., 2002). For example, some studies found that the presence of an OMZs in the Arabian Sea creates a strong vertical gradient in physical and biological parameters which could affect the species richness (Cook et al., 2000; Rogers, 2000). The reduced downward flux of organic material in the OMZs provides more food for organisms immediately below OMZs leading to strong vertical gradients in selective pressures for optimal rates of growth, reproduction, development, and habitat

specialization resulting in higher speciation rates (Rogers, 2000). Carney (2005) also suggested that because abiotic and biotic factors vary greatly with depth, many species often possess restricted vertical ranges despite the potential for broad horizontal distribution ranges.

Our cluster analysis using species presence/absence revealed that species collected in the Sea of Japan were slightly different from the Sea of Okhotsk and KKT for both bathyal and lower bathyal/hadal species, which has been reported in other studies of the author in the study area (Brandt et al., 2019; Brandt et al., 2013). This might be due the fact that most species in the Sea of Japan were sampled at shallower depths (upper bathyal, around 500 m) and were different compared to the deeper dwelling species collected from the Sea of Okhotsk and KKT (Brandt et al., 2019). Moreover, the Sea of Japan is isolated by



shallower straits compared to the Sea of Okhotsk and this isolation could affect the species community composition, endemism, and biodiversity in this area (Brandt et al., 2019; Brandt et al., 2013; Golovan et al., 2013; Kamenev, 2013; Malyutina & Brandt, 2013). The species composition was different between the Sea of Okhotsk and KKT; although, some species were shared at the edge of the eastern Sea of Okhotsk and western KKT. This was also found in another paper by the authors studying the same area, which suggested distinct fauna of the KKT compared to the Sea of Okhotsk despite the bathyal Bussol and Kruzenstern straits (Brandt et al., 2019; Brandt et al., 2013). However, as in one of the hexagons, about 50% of the species were shared between the Sea of Okhotsk and KKT, one can argue that the bathyal Kuril straits might enhance faunal exchange of the open NW Pacific and the Sea of Okhotsk, despite the KKT (Brandt et al., 2019; Kamenev, 2018; Malyutina & Brandt, 2018).

#### 4.2. Environmental drivers

Both GAM and GLM models recovered the dissolved oxygen (GAM), topography and bottom temperature (GLM) as the best explanatory variables in driving species richness, followed closely by the model including all environmental variables. Model outputs indicated that a model that contains only total number of distribution records is, for all practical purposes, as good as any model that contains an environmental predictor. We suggest that using gamma species richness (total number of species per 1° and/or 5° latitudinal bands) in GLM modeling reduced the contribution of dissolved oxygen as a response variable to the species richness because in these models, the geographic points near the OMZs were merged with the geographic points where the oxygen concentrations were higher. That might be the reason that in the GLM models; topography and bottom temperature took over the oxygen as the best predictor of species richness. In general, depth, temperature, and dissolved oxygen have been reported as the most important factors in driving the latitudinal gradients of species richness in both shallow-water (Chaudhary et al., 2016; Saeedi et al., 2017a; Saeedi et al., 2017b) and deep-sea fauna (e.g., ostracods, polychaetes, and ciliates) (Huang et al., 2019; Huang et al., 2018; Levin & Gage 1998; Yasuhara & Danovaro 2016; Zhao et al., 2017). Other studies argue that in the deep sea, chemical energy and carbon flux are more likely to control species diversity, and temperature does not predict variation in rarified diversity of bivalve and gastropod species (McClain et al., 2012; Woolley et al., 2016). In the Sea of Japan, multiple-regression analysis indicated that oxygen content was one of the most significant controlling factors of ostracod dominance and diversity (Huang et al., 2019; Huang et al., 2018).

The correlation between expected species richness (ES15) and dissolved oxygen in GAM output models (Fig. 6) revealed that areas near the OMZs (dissolved oxygen concentrations below 0.5 ml l<sup>-1</sup>) had the lowest suitability for species richness compared to the areas with higher oxygen concentration. GAM modeling also verified that dissolved oxygen is the best predictor of species richness compared to other environmental factors in our study. The impact of OMZs on deep-sea species richness in the Indo-Pacific, East Pacific, the Arabian Sea, and Sea of Japan have been tested and discussed in the last two decades (Breitburg et al., 2018; Cook et al., 2000; Gooday et al., 2010; Karstensen et al., 2008; Levin & Gage 1998; Pierce et al., 2012; Rogers 2000; Van Geen et al., 2006). Gooday et al. (2010) suggested that in the Pacific and Arabian Sea where OMZs were examined, oxygen appears to be the most important driver of alpha and beta diversity in all benthic faunal groups, as well as macrofaunal composition. They later concluded that OMZs probably enhance regional diversity (gamma species richness), particularly in taxa such as Foraminifera, which are more tolerant to hypoxia compared to the other taxa (Gooday et al., 2010). Levin & Gage (1998) hypothesized that for bathyal faunas, oxygen at low concentrations has more influence on species richness, while organic carbon regulates the distribution of individuals among species

(community evenness). They showed that species richness in polychaetes, crustaceans, molluscs, and ostracods reduced within oxygen minimum zones (OMZs) in the Indo-Pacific, which would eventually reduce the macrobenthic diversity in that area (Levin & Gage 1998). Gooday et al. (2010) also suggested that in examined Pacific and Arabian Sea OMZs, oxygen appears to be the primary driver of alpha and beta diversity in all benthic faunal groups for which data exist, as well as macrofaunal assemblage composition regional diversity (gamma species richness) of shallow-water and bathyal foraminifera, which was enhanced by the OMZs in the areas of eastern Pacific, the Arabian Sea, and the Bay of Bengal. In the Sea of Japan, the long-term oxygen variability reported as a major control of deep marginal sea biota (Huang et al., 2018). Huang et al. (2018) discovered five major ostracods' extirpation events which were caused by deoxygenation events during glacial sea level lowstands deeper than 90 m in the Sea of Japan.

GAM and GLM model outputs also supported the relevance of including all environmental factors as explanatory variables as the best predictor of deep-sea species richness, where rarefaction ES15 was used. However, secondly and only with marginally different  $\Delta AIC$  values, models including all environmental variables and models including all environmental variables and topography, rather than single variables, showed high explanatory power for the number of species and ES15. These results are expected, while taking into consideration the ecological theory (Hutchinson, 1957), which recognizes niche as an  $n$ -dimensional hyper-volume, with its  $n$  dimensions characterized by the diverse environmental conditions and resources that define the multidimensional space of conditions allowing a species and populations to survive and reproduce. Thus, despite the complexity of the best models, due to their rich composition of environmental variables, the ability to represent the studied area's environmental space holistically, provides a better view of the environmental factors playing a key role in maintaining the region's diversity.

Well-mapped abiotic data are commonly used, together with data from ecological communities, to model or predict species diversity and distributions (Lawler et al., 2015), and the relationship between environmental heterogeneity and species richness has been established across multiple taxa and spatial scales (Chaudhary et al., 2016; Chaudhary et al., 2017; Saeedi et al., 2017a; Saeedi et al., 2017b; Stein et al., 2014). Here, besides environmental variables, we also tested the inclusion of topography as an explanatory variable, which provided information regarding the depth of the studied area. In our results, topography featured among the most relevant predictor of species richness in GLM and GAM model outputs. The summary of these layer values provides insight into the great topography of the area (min: 517.6; max: 7964.2; med: 2557.8 m), which could be responsible for the explanatory power of this variable in our models. Thus, our results show the relevance of including depth in GAM and GLM modeling processes as this simple measure of topography can improve the biodiversity-environment modeling.

#### 5. Conclusion

The GAM model outputs showed that dissolved oxygen is the best environmental predictor for alpha species richness (total number of species per c. 10,000 km<sup>2</sup> hexagonal cells) in the deep NW Pacific; however, gamma species richness (total number of species per 1° latitudinal bands) was mostly derived by depth and bottom temperature. Climate change has been and is predicted to impact deep-sea species richness through increased temperature, ocean acidification, declining oxygen and productivity (Sweetman et al., 2017; Thomas & Gooday 1996; Yasuhara et al., 2008; Yasuhara et al., 2009; Yasuhara et al., 2014). Estimating the scale and magnitude of these impacts are difficult to predict as the vast majority of the deep-sea environment is still unexplored and remains to be discovered (Saeedi et al., 2019c). Furthermore, the reduced rate of global ocean circulation and human impacts such as deep-sea mining will affect not only the deep-sea habitat, but

also the services (e.g., fisheries, cultural, water circulation and CO<sub>2</sub> exchange, nutrient cycling) that are gained from those habitats. We thus believe that having informative biodiversity baseline studies and exploring potential driving factors, even using our limited dataset coming from these recent expeditions, is necessary to accurately assess concealed deep-sea areas to establish biodiversity conservation and Marine Protected Areas (MPA). Our results provide not only insights in the NW Pacific deep-sea ecosystem biodiversity patterns (vertical and horizontal species distribution ranges), and environmental variables contributing to promote and maintain its diversity (e.g., dissolved oxygen and temperature); but also provide decision makers and stakeholders with a fundamental regional study of the NW Pacific to prioritize conservation criteria across multiple biodiversity conservation initiatives such as Deep Ocean Stewardship Initiative (DOSI) and International Seabed Authority (ISA).

### 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.

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### Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.pocan.2020.102296>.

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