



# Crustaceans of the Northwest Pacific Ocean: Species richness and distribution patterns

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## ABSTRACT

Biodiversity patterns of marine crustaceans are still unknown in many locations or might have been overlooked due to our knowledge gaps, despite increasing sampling and data sharing efforts during the last decades. By analysing big data extracted from open portals such as Ocean Biodiversity Information System (OBIS) and Global Biodiversity Information System (GBIF), we aim to revisit the distribution and biodiversity patterns of the highly speciose and abundant Crustacea in the Northwest Pacific (NWP) from shallowest depths to the deep sea. This study focussed on selected benthic and pelagic crustacean (sub) classes and their species richness, sampling effort, and expected species richness (ES50) using equal/sized hexagonal cells, 5° latitudinal bands, 500 m depth intervals were analyzed. Crustacean species richness was highest in the tropical Philippines as well as around the Japanese islands. Pelagic crustacean species richness peaked at 30° latitude and declined beyond that. Benthic taxa; however, depicted high levels of species richness across most of the latitudinal gradient, reaching its highest point at 45° latitude. Due to the prevalence of certain crustacean orders in the deep sea, benthic species richness showed a distribution pattern with two distinct peaks across bathymetric gradients; with highest species richness recorded at shallow-water depths and also at abyssal depths. The most important environmental drivers of benthic and pelagic crustacean species richness were primary productivity (positive correlation) and salinity (negative correlation). Our study provides first insights into biodiversity patterns of the highly diverse Crustacea in the NWP and highlights strong differences between benthic and pelagic taxa. The results presented here could help us to better understand whether benthic or pelagic taxa might respond differently to climate changes in the NWP based on their distinct physiological and biological characteristics. This information is crucial in establishing species management strategies and ecosystem restorations in both shallow water and deep-sea environments.

## 1. Introduction

Patterns of marine species biodiversity and their distribution at global and regional scales have been the focus of scientific research for the last few decades (e.g., Costello and Chaudhary, 2017; Grassle, 1991; Gray, 1997; Renema et al., 2008). Some studies assumed a unimodal decline of marine species richness against latitudinal gradients following Rapoport's rule and the Mid-Domain Effect (Brown, 2013; Colwell et al., 2004; Rex et al., 2000; Stevens, 1989). More recent studies; however, found a bimodal species richness pattern on a global scale (Chaudhary et al., 2016; Powell et al., 2012; Saeedi et al., 2017, 2019a). Generally,

species richness is assumed to decline from shallow water depths to the deep sea in many taxa – even when accounting for sampling bias (Costello and Chaudhary, 2017). While the deep sea (> 500 m depth, Thistle, 2003) comprises the largest biome on earth, accounting for over 63% of the planet's surface, it remains one of the least explored realms of our planet (Mora et al., 2011; Ramirez-Llodra et al., 2010). Yet, even with our current state of knowledge, several marine taxa – such as gastropods, nematodes or isopods – contradict the trend of decreasing species richness with depth by thriving in bathyal and abyssal depths (Danovaro et al., 2010; Rex, 1973; Saeedi et al., 2022a). In addition, reports of deep-sea species richness reaching similar or greater levels at

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higher latitudes of 30° to 50° than in the tropics have been made for Chordata, Mollusca, Polychaeta and Ophiuroidea (Saeedi et al., 2019a; Saeedi et al., 2019b; Woolley et al., 2016). These apparent differences between shallow-water and deep-sea biodiversity patterns highlight that we are only starting to understand these patterns.

Understanding the potential causes for observed marine biodiversity patterns requires understanding the complex system that might shape species richness and distribution patterns in present days (e.g., Brown, 2013). This is especially important as anthropogenic climate change could dramatically change these patterns; for example, through range shifts of marine taxa to either greater depths or poleward (Abram et al., 2019; Simões et al., 2021). As pointed out by the IPCC, marine biota also face climate-change related challenges as for example decreased oxygen solubility or increased stratification, that severely alter their living conditions (Abram et al., 2019; Hoegh-Guldberg et al., 2014). Evaluations on the influence of environmental conditions on marine biodiversity delivered valuable insights in correlations between biodiversity patterns and abiotic factors: while global shallow-water species richness highly correlates with temperature (Saeedi et al., 2017; Tittensor et al., 2010), the species richness of the temperature-wise relatively constant deep sea (the sole exception being upper bathyal depths that exhibit larger changes in temperature) is influenced by other abiotic factors such as food availability or dissolved oxygen (Golovan et al., 2019; Woolley et al., 2016). As pointed out by Saeedi et al. (2022a), considering the biology (reproduction and larval development) and morphology (locomotive capabilities) of the investigated taxa is also crucial for explaining current distribution patterns. Biodiversity patterns are also interrelated with the topographic complexity and heterogeneity of their marine environment (e.g., Myers, 1997; Stein et al., 2014) and prone to changes due to climate-related alterations of current regimes and associated environmental factors (Bellwood et al., 2005; Renema et al., 2008). On a temporal scale, major historic events such as glaciations, plate tectonics and oxygen minimum zones (OMZ) also proved to alter marine biodiversity patterns, population ranges and their connectivity (Erwin, 2009; Riehl et al., 2020a; Yasuhara et al., 2009). One should also consider that biodiversity patterns and their potential drivers might not only differ among marine taxa, but can also vary at regional or even local scales (Levin et al., 2001; Ramirez-Llodra et al., 2010; Snelgrove and Smith, 2002). Studying these potential drivers of biodiversity patterns thus requires a solid foundation of knowledge on the region to be examined.

The Northwest Pacific (NWP) ranks among the better understood ocean regions on our planet and even its deep sea has been sampled and studied in the past tremendously, increasing our knowledge of that area (Brandt, 2016; Brandt et al., 2010; Brandt and Malyutina, 2015; Malyutina et al., 2018; Werner et al., 2016). In addition, a large fraction of our current knowledge about the NWP fauna is based on the deep-sea expeditions with RV *Vityaz* from the 1950s to 1970s, initiated by Lev Zenkevich (Belyaev, 1989, 1983; Birstein, 1971, 1970, 1963; Kussakin, 1988, 1982, 1979, 1971; Kussakin and Vasina, 1990; Shirshov, 1983; Zenkevich, 1963). The entirety of currently available sampling data on the marine fauna of the NWP revealed high levels of biodiversity across many marine taxa, especially crustaceans.

The high levels of species richness in this region are promoted by the heterogeneity of the NWP that comprises various hadal trenches, vast abyssal plains and several deep-sea basins, all differing in their bathymetry, hydrology and other environmental factors (Saeedi et al., 2020; Saeedi and Brandt, 2020). Previous studies by Renema et al. (2008) and Saeedi et al., 2019a identified the tropical and subtropical areas of the NWP, comprising the Indo–Australian Archipelago, as hosts the highest number of marine species in the World Ocean. The diversity in species richness and geomorphology thus turn the NWP into an ideal area to study more regional effects of biodiversity patterns.

Previous studies focussed mostly on overall species richness or rather specialized (crustacean) taxa (e.g., Saeedi et al., 2022a,a), yet did not cover the highly speciose and abundant group of marine crustaceans as a

whole. Currently, over 66,000 recent species of crustaceans are recognized globally (Zhang, 2011). Marine crustaceans comprise the largest chunk of animal biomass on earth (Bar-On et al., 2018) and are also commonly reported from biological samplings during multiple deep-sea expeditions in the NWP, such as the KuramBio, SokhoBio, SoJaBio, or KuramBio II campaigns (Brandt, 2016; Brandt et al., 2010; Brandt and Malyutina, 2015; Malyutina et al., 2018). These findings are not surprising, given the fact that crustaceans are the dominant taxa throughout the marine water column, extending from intertidal waters down to the Challenger Deep in the Mariana Trench (e.g., Itani, 2004; Lan et al., 2016). While many crustacean species primarily inhabit the shallow coastal waters of the World Ocean (e.g., Decapoda, Stomatopoda), there are several crustacean groups that are particularly known for inhabiting the deep sea, such as several peracarid, ostracod and copepod (sub-)orders, for example, Podocopida, Myodocopida, Ergasilida, and Siphonostomatoida (Hessler and Sanders, 1967; Humes, 1987; Yasuhara et al., 2014). Their omnipresence in our oceans is achieved by a wide spectrum of lifestyle adaptations and changes throughout their ontogenetic development that enable utilization of many unique ecological niches (Thiel and Wellborn, 2018). In addition, many crustacean taxa display complex trophic roles in marine communities (see Thresher and Kuris, 2004; Würzberg et al., 2011). Understanding their biogeographic distribution and species richness patterns during times of rapid anthropogenic climate change is thus crucial in preparing management measures to aid conserve the marine biodiversity far beyond the crustacean realm.

The main objectives of this study were to (i) investigate and compare the biodiversity patterns of benthic and pelagic crustacean taxa in the NWP against latitudinal and bathymetric gradients; (ii) identify hotspots of crustacean species richness in the NWP; and (iii) determine which environmental parameters drive the observed biodiversity patterns and species richness hotspots. Based on comparable big-data studies for other marine taxa we expect an overall decline in crustacean species richness with increasing latitude and depth, yet mainly for shallow-water biodiversity, while deep-sea biodiversity should remain higher even at temperate latitudes (Costello and Chaudhary, 2017; Saeedi et al., 2022a,b). In this regard it is important to test whether the Philippines host the highest number of crustacean species, as they are not only located in lower, tropical latitudes, but also within the particularly species rich Coral Triangle which is regarded as a marine biodiversity hotspot (Renema et al., 2008; Saeedi et al., 2019a). Previous studies on the environmental drivers for marine biodiversity in the NWP identified depth, temperature, and dissolved oxygen as key factors (Saeedi et al., 2020; Saeedi et al., 2022b). We therefore expect similar patterns for crustacean biodiversity in the NWP. If this holds true, the impacts of the anthropogenic climate change on the marine realm would result in major consequences for crustacean distribution and diversity in the NWP.

## 2. Material and methods

### 2.1. Data extraction and cleaning

The considered study area for this research included all of the NWP between latitudes of 0 to 65° N and longitudes between 100 and 180° E. This includes the extensive high sea areas in the southeast of the NWP (< 30° latitude, > 130° longitude) and several marginal seas such as the Sea of Okhotsk, Sea of Japan, East China Sea, South China Sea and Philippine Sea. The vast majority of occurrence records used for this study were extracted from OBIS ([portal.obis.org](http://portal.obis.org); Grassle, 2000) and GBIF ([GBIF.org](http://GBIF.org), 2021), and comprised data of selected crustacean taxa (Thecostraca, Ostracoda, Copepoda, Malacostraca excl. Syncarida). Additional occurrence records of crustacean taxa from the recent deep-sea expedition SO-249 in the Bering Sea (available upon request; Werner et al., 2016) were added to the dataset as well.

The resulting dataset was quality controlled and invalid data were

removed or cleaned in R 4.1.1 (R Core Team, 2021) using the packages “tidyverse” (Wickham et al., 2019), “scrubr” (Chamberlain, 2021) and “obistools” (Provoost and Bosch, 2021). The cleaning process followed Saeedi et al. (2020) by removing records that (i) lacked occurrence geographic coordinates, (ii) were duplicated, (iii) were fossil records, (iv) had coordinate uncertainties exceeding 100 km, and (v) were located on land. All taxa names within the datasets were matched against the World Register of Marine Species (WoRMS; WoRMS Editorial Board, 2021) and excluded if they were not accepted or unified in the case of synonymous names.

In addition, each taxon was assigned to either benthic (i.e., bottom dwelling or demersal/bottom-associated) or pelagic, as inferred from their WoRMS and Encyclopaedia of Life (EoL; Wilson, 2003) database entries. Dubious records (e.g., family level known only) were excluded from analyses involving benthic and pelagic taxa if a distinct lifestyle could not be determined. Our dataset also featured multiple parasitic crustacean taxa. Whether these belong to the benthic or the pelagic lifestyle group was decided based on their specific host taxa, following WoRMS. Crustaceans are also known to change their lifestyle throughout their development (e.g., pelagic larvae and benthic adults). Most crustacean records in our dataset lacked information on whether the record represents a larva or an adult. We therefore considered the lifestyle of specimens with unclear development stage, based on their adult lifeform. This way they did not get excluded from our analyses. Most occurrence records also lacked depth information, and the depth information for benthic taxa were therefore extracted from the maximum water depth of the depth layer of the General Bathymetric Chart of the Oceans (GEBCO Compilation Group, 2021). Because accurate depth information could not be retrieved for pelagic taxa, any depth-related analysis for these taxa was impossible. For the remaining taxa, we chose a depth threshold of 500 m following the World Register of Deep-Sea Species (WoRDSS, Glover et al., 2022; Thistle, 2003) to distinguish between shallow-water and deep-sea taxa.

In the final dataset, all occurrence records were analyzed to measure the sampling effort and abundance, but for species richness analyses, analyses were done at species-level only.

To evaluate the influence of environmental variables on crustacean biodiversity patterns nine environmental factors (both for benthic and pelagic crustaceans) were extracted from Bio-ORACLE (bio-oracle.org) from the surface (i.e., pelagic) and benthic layers (Assis et al., 2018; Tyberghein et al., 2012). These layers comprised average temperature ( $^{\circ}\text{C}$ ), salinity (PSS), dissolved oxygen ( $\text{mol m}^{-3}$ ), current velocity ( $\text{m}^{-1}$ ), primary productivity ( $\text{g m}^{-3} \text{day}^{-1}$ ), nitrate ( $\text{mol m}^{-3}$ ), phosphate ( $\text{mol m}^{-3}$ ), silicate ( $\text{mol m}^{-3}$ ), pH (surface only) and light at bottom (benthic only).

## 2.2. Data analysis

Subsequent analyses of the cleaned dataset and its subsets were performed in R 4.1.1 according to the approach of Saeedi et al. (2019a). The R packages “tidyverse”, “openxlsx” (Schauberger and Walker, 2021), “MASS” (Venables and Ripley, 2002) and “sf” (Pebesma, 2018) provided tools for importing, cleaning, manipulating and plotting the data. The study area was divided into equal-sized hexagons (Fig. 1; approximately  $700,000 \text{ km}^2$  per hexagon cell). We further ran the biodiversity analyses against  $5^{\circ}$  latitudinal bands and 500 m depth intervals to study distribution patterns across latitudinal and bathymetric gradients. For each hexagon cell,  $5^{\circ}$  latitudinal band and 500 m depth interval three different measurements of biodiversity estimation were calculated including: (i) sampling effort (number of distribution records), (ii) species richness (total number of species), and (iii) expected rarefied species richness (ES50), which calculates species richness under consideration of sampling effort. Rarefaction ES50 is done by randomly selecting 50 samples from the available datasets (here: per hexagon, latitudinal band, depth interval) multiple times and subsequently calculating the mean number of species per 50 occurrence records.

Because multiple hexagons comprised solely single-digit records, we tested multiple ES thresholds, yet ultimately decided to use ES50 as the minimum of each samples were just  $>50$  samples. Therefore, low ES50 values remain an artifact of low record numbers rather than actual low biodiversity. Nonetheless, ES50 proved helpful in negating the effects of heavily sampled hexagons to provide a more comparable measure of marine crustacean biodiversity. To calculate ES50 and rarefaction curves the R package “vegan” (Oksanen et al., 2020) was used. These calculations also included records from higher taxonomic ranks other than species level, as based on the records alone we are unable to confirm or deny that these records represent duplicates of potential species records that belong to the same higher taxonomic rank.

To identify potential correlations between environmental variables and crustacean biodiversity measurements in the NWP the R package “corrplot” (Wei and Simko, 2021) was used. This required extracting environmental data from the multiple Bio-ORACLE layers per each occurrence record and calculating the average of each environmental variable per hexagon, which was done in QGIS 3.16 (QGIS.org, 2020). Afterwards, these environmental values were interrelated with each hexagon’s calculated biodiversity measurements using Spearman correlation matrices. We considered the alpha species richness as species richness per hexagon cell, and gamma species richness as species richness per  $5^{\circ}$  latitudinal band following Saeedi et al. (2019a).

## 3. Results

### 3.1. Dataset composition

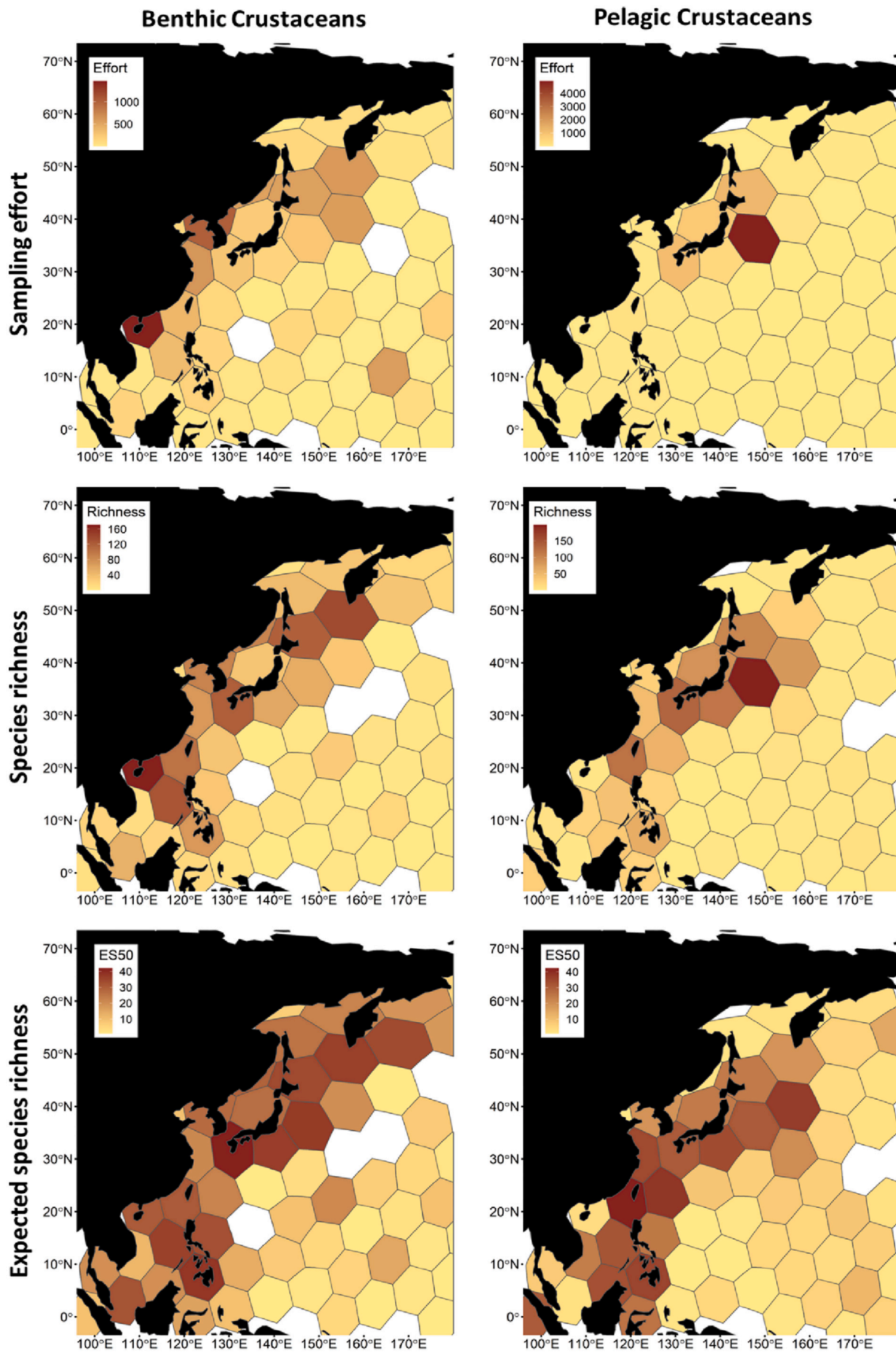
The final dataset comprised 21,694 occurrence records of 2015 deep-sea crustacean taxa. Around 72% of these records were at species level and represented 1613 species in total. The remaining dataset comprised 18% of genus level records, 3% of family level records, 5% of order level records and 2% of class level records. Within the dataset, the most records belonged to Malacostraca (42.8%), followed by Copepoda (41.6%), Ostracoda (15.4%), and Thecostraca (0.2%) (Table 1).

### 3.2. Distribution and diversity

The NWP high seas was characterized by low to non-existing levels of sampling effort (Fig. 1; Fig. A1–A3). Higher levels of sampling effort for benthic crustaceans of 976 and 1412 records respectively were found in the hexagons around the Korean peninsula and the South China Sea, which were mainly related to shallow-water taxa (see Fig. A2). As for pelagic crustaceans, 47% of all the pelagic crustacean records stem from a single hexagon located off the eastern coast of Honshu, Japan, while being low ( $< 1148$  records) in all other hexagons in the NWP.

Species richness was generally higher in coastal areas and marginal seas rather than in the high seas of the NWP (Fig. 1). For benthic crustaceans, the species richness hotspots were located in the South and East China Sea, the Yellow Sea, around the Philippines and Japan as well as Kurile Islands. The hotspot around the Kurile Islands primarily comprises deep-sea benthic taxa, as visible in Fig. A3. On the contrary, pelagic species richness reached a maximum of 199 species in the open NWP off the Japanese islands but was generally elevated around Japan (91–135 species).

ES50 for benthic crustaceans was particularly high in coastal areas and marginal seas around the Philippines, Japan and the Kuril Islands. While shallow-water benthic taxa peaked at all these hotspots (see Fig. A2), the expected species richness of deep-sea benthic taxa was especially increased around the Kurile Islands and Japan between  $30^{\circ}$  and  $60^{\circ}$  latitude (Fig. A3). As for pelagic crustaceans, ES50 was especially high around Japan, the Philippines, and adjacent marginal seas such as the East and South China Sea or the Sea of Japan. It is noteworthy, that ES50-values in pelagic crustacean remained low – in comparison with benthic crustaceans – in the northernmost parts of the NWP and the Sea of Okhotsk beyond  $45^{\circ}$  latitude (Fig. 1).



(caption on next page)

**Fig. 1. Biodiversity patterns of benthic and pelagic crustaceans in the NWP.** Sampling effort (number of distribution records), alpha species richness (number of species per hexagon) and ES50 (expected number of species) of benthic ( $n = 6939$ ) and pelagic crustaceans ( $n = 8612$ ) in the NWP is visualized per hexagonal cells ( $700,000 \text{ km}^2$  per cell). Areas without colouring had zero values. Lower counts of coloured grid cells in species richness and expected species richness than in sampling effort are caused by distribution records that lack taxonomic identification to species level.

**Table 1**

**Taxonomic composition of the NWP crustacean dataset.** Composition and percental share of crustacean (sub)classes and orders within the crustacean dataset of the NWP. The dataset comprises 21,694 occurrence records of 2015 taxa from the crustacean Thecostraca, Ostracoda, Copepoda and Malacostraca excl. Syncarida as extracted from OBIS and GBIF. Additional records stem from a crustacean dataset from the Bering Sea (Knauber et al., in preparation). NA denotes cases in which an order was not given for the respective records.

(Sub-)Class	Order	Number of records	% of dataset	% of (sub-) class
<b>Copepoda</b>		<b>9024</b>	<b>41.6%</b>	
	Calanoida	6937		76.9%
	Cyclopoida	1916		21.2%
	Harpacticoida	168		1.9%
	Monstrilloida	1		0.0%
	Siphonostomatoida	2		0.0%
<b>Malacostraca</b>		<b>9286</b>	<b>42.8%</b>	
	Amphipoda	2576		27.7%
	Cumacea	642		6.9%
	Decapoda	1250		13.5%
	Isopoda	2331		25.1%
	Leptostraca	39		0.4%
	Lophogastrida	66		0.7%
	Mysida	403		4.3%
	Stomatopoda	1876		20.2%
	Tanaidacea	103		1.1%
<b>Ostracoda</b>		<b>3339</b>	<b>15.4%</b>	
	Halocyprida	1328		39.8%
	Myodocopida	308		9.2%
	Platycopina	34		1.0%
	Podocopida	1194		35.8%
	NA	475		14.2%
<b>Thecostraca</b>		<b>45</b>	<b>0.2%</b>	
	Balanomorpha	29		64.4%
	Scalpellomorpha	14		31.1%
	<i>Incertae sedis</i>	2		4.4%

### 3.3. Bathymetric and latitudinal gradients

Sampling effort and gamma species richness were higher in benthic crustaceans than in pelagic crustaceans across most of the NWPs latitudinal gradient (Fig. 2A and B). Pelagic sampling effort and gamma species richness was highest around latitudes  $30\text{--}45^\circ$  (5253 records between latitudes  $35\text{--}40^\circ$ ), where it also exceeded benthic biodiversity measurement levels. The rarefaction curves highlighted, that pelagic species richness around these latitudes is almost fully inventoried, while benthic species richness was recorded constantly across the latitudinal gradient (Fig. A4).

Towards higher latitudes both sampling effort and gamma species richness of benthic and pelagic crustacean taxa declined (Fig. 2A and B). Despite lower sampling effort of pelagic taxa at lower latitudes ( $5^\circ\text{--}25^\circ$ ), ES50 stayed constant between 30 and 42. Benthic sampling effort and gamma species richness declined at latitude  $30^\circ$  and  $< 10^\circ$ . A decline of ES50 at higher latitudes was observable for crustaceans in general (Fig. A5), yet especially pronounced in pelagic crustaceans declining beyond  $30^\circ$  latitude already (Fig. 2D). On the contrary, benthic ES50 reached high levels of ES50 ( $> 30$ ) across most latitudes and solely declined at latitudes  $60^\circ$  and beyond (Fig. 2C), which is especially caused by the deep-sea fraction of benthic taxa ( $< 11$ , see Fig. A6).

Most benthic distribution records belonged to shallow waters above 500 m depth (63.4%, Fig. 3A). The remaining 36.6% of benthic deep-sea records exhibited an overall decline with increasing depth with a sudden increase at the NWP maximum depths around 10,500–11,000 m.

Another peak in number of records ( $n = 1047$ ) became apparent around 5000–5500 m.

In accordance with high benthic sampling effort at shallow depths, species richness also peaked at shallow-water depths of 0–500 m with over 800 recorded species (Fig. 3B), exceeding rarefaction species richness at other deep-sea depth intervals by a large margin (Fig. A7). Species richness of benthic fauna declined significantly with depth and remained low down to 5000–5500 m, where elevated species number were registered. From there on species richness rapidly declines again with increasing depth. The same patterns arise for ES50 with two peaks at shallow-water depths and around 4500–6000 m followed by a rapid decline in ES50 at hadal depths below 6000 m (Fig. 3C).

### 3.4. Community composition

In the final dataset, 45.8% of the distribution records represented benthic records, 48.6% were classified as pelagic, and 5.6% could not be assigned to any lifestyle due to low taxonomic accuracy (Fig. 4). The largest number of pelagic records belonged to Copepoda (85.6%), followed by Ostracoda (12.1%), and Malacostraca (1.9%). However, Malacostraca were the most dominant benthic taxa (83.5%) among all other benthic fauna, followed by Ostracoda (15.9%). Thecostraca and Copepoda had the minimum contribution to the benthic fauna (both  $< 1\%$ ).

Malacostraca and Ostracoda exhibited a latitudinal distribution pattern with two peaks at  $20^\circ$  and  $40^\circ$  as well as around  $10^\circ$  and  $40^\circ$  latitude, respectively (Fig. 5). While Hexanauplia were found at all latitudes of the NWP, they were especially abundant around  $40^\circ$  latitude. Malacostraca, Ostracoda and Hexanauplia exhibited a distinct dip around  $25\text{--}30^\circ$ . However, thecostracan crustaceans peaked in their abundance around these latitudes yet declined below and above these middle latitudes. An overview about the latitudinal abundance patterns of all analyzed crustacean orders is provided in Figs. A8 and A9.

Based on benthic crustacean taxa, abundance distributions across a bathymetric gradient showed that Malacostraca, Ostracoda, and Thecostraca reached highest densities at shallow-water depths above 500 m (Fig. 6). Only Malacostraca and Ostracoda exhibited a depth distribution that reaches down to hadal depths of up to 11,000 m and further featured another abundance increase around 5000 m depth. Thecostraca, in turn, were almost absent from abyssal depths already. The malacostracan and ostracodan orders responsible for this increase at abyssal depths are Isopoda, Tanaidacea as well as Halocyprida (see Figs. A10 and A11).

### 3.5. Environmental correlation

Sampling effort, species richness, and ES50 of NWP crustaceans were overall significantly positively correlated with one another in both the benthic and pelagic dataset on a 5% confidence level respectively (Fig. 7). In addition, the correlation analysis revealed multiple significantly co-varying environmental variables, e.g., light, depth, salinity and productivity in the benthic dataset (Fig. 7A) or dissolved oxygen and temperature in the pelagic dataset (Fig. 7B). Overall, correlations between biodiversity measurements and environmental factors were stronger for benthic than pelagic taxa. Within the pelagic crustacean dataset significant correlations between biodiversity measurements and environmental variables were restricted to a weak to intermediate positive correlation (0.23–0.49) with productivity and a weak to non-existent correlation with current velocity ( $-0.1\text{--}0.13$ , Fig. 7B). Most correlations between pelagic biodiversity measurements and environmental variables not only proved weak to non-existent but were also not

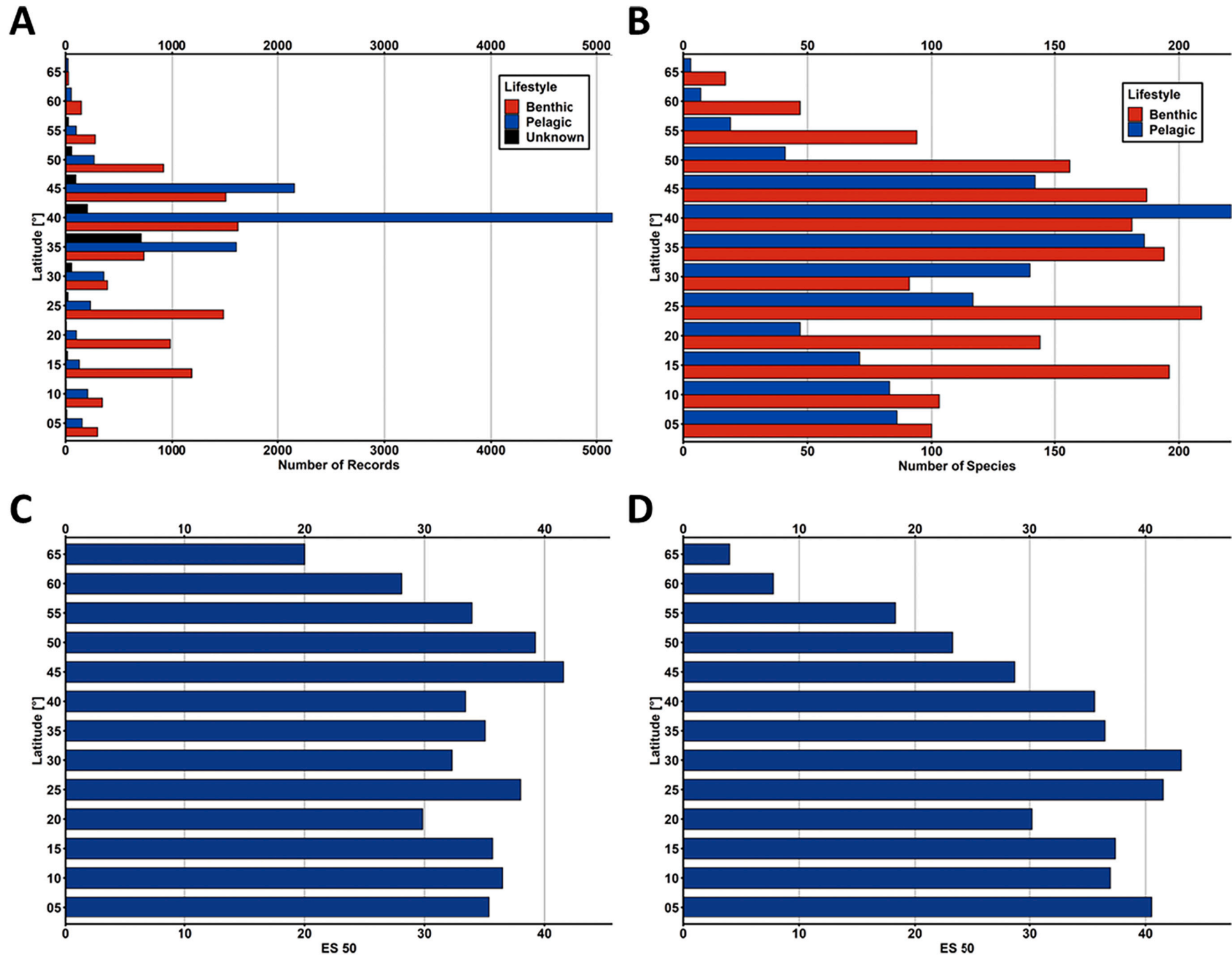
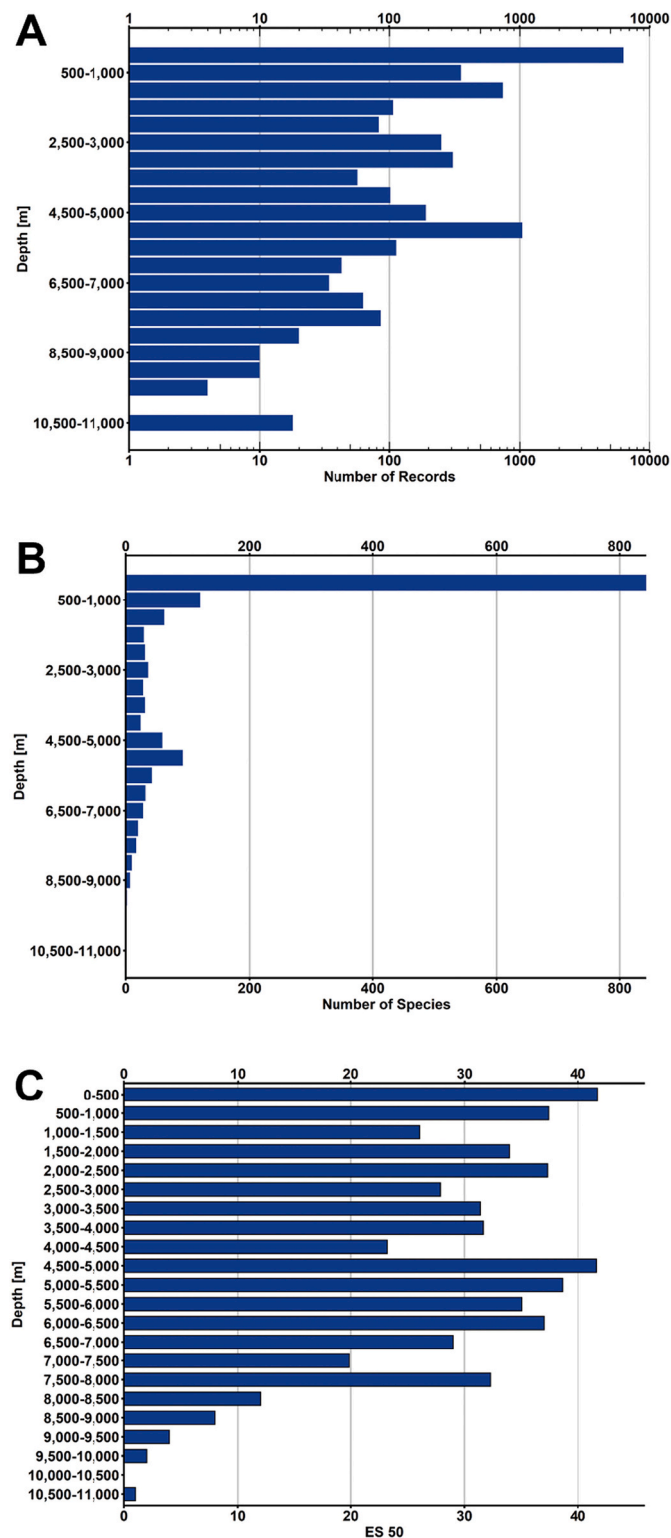


Fig. 2. Distribution of crustacean sampling effort (number of distribution records, A), gamma species richness (number of species per 5° latitudinal band, B) and ES50 (expected species richness) for benthic (C) and pelagic (D) crustaceans across a latitudinal gradient (5° latitudinal bands). Histograms displaying the gradual decline of crustacean biodiversity parameters in the NWP at high latitudes across a latitudinal gradient. Records that could not be identified as either benthic or pelagic with certainty are listed under unknown.



**Fig. 3.** Distribution of benthic crustacean sampling effort (number of distribution records, A), species richness (number of species per 500 m depth interval, B) and ES50 (expected species richness ES50, C) against maximum water depth (GEBCO). Histograms displaying the gradual decline of benthic crustacean taxa biodiversity measures from the NWP against depth (500 m depth intervals) based on the maximum water depth as inferred from the GEBCO layer.

significant on a 5% significance level.

For benthic taxa, temperature, primary productivity, and light at bottom revealed intermediate positive correlation levels with the three biodiversity measurements, ranging between 0.46 and 0.64 (Fig. 7A) on a 5% significance level. On the contrary, nitrate, phosphate and silicate exhibited weak negative correlations with benthic biodiversity measurements. Salinity and depth were the environmental variables with the strongest negative correlations with biodiversity measurements, ranging between  $-0.45$  and  $-0.54$  for depth and  $-0.54$  and  $-0.66$  for salinity, but for the latter only the correlation to species richness was significant. The correlation matrices of shallow-water and deep-sea benthic diversity patterns against the same environmental variables resulted in much milder and less significant correlations for deep-sea than for shallow-water biodiversity (Fig. A12). Splitting benthic biodiversity into shallow-water and deep-sea biodiversity for the correlation analyses highlights, that all significant correlations from the benthic dataset and overall correlation trends are caused by shallow-water rather than deep-sea crustacean records. Within the deep-sea benthic crustacean dataset, the same correlation trends exist – except for nitrate, phosphate and silicate – but on a much weaker and non-significant level.

#### 4. Discussion

This study provides a first overview on the previously unknown, yet surprisingly complex biodiversity patterns of crustaceans in the NWP across latitude and depth. While we could not analyse pelagic biodiversity patterns across a bathymetric gradient due to insufficient data coverage and depth information, benthic species richness was characterized by two distinct peaks in their bathymetric distribution at shallow-water depths and greater abyssal depths (Fig. 3). This finding contradicts other studies that found an overall decline in species richness with increasing depth (Costello and Chaudhary, 2017). Our findings revealed differences in the biodiversity and distribution patterns of benthic and pelagic crustaceans in the NWP: while expected pelagic species richness overall declined across the latitudinal gradient, after a peak around  $30^\circ$  latitude, expected benthic species richness remained at high levels across most of the latitudinal gradients and peaked at higher latitudes of  $45\text{--}50^\circ$  compared to the pelagic taxa (Fig. 2). These differences coincided with the respective hotspots of expected crustacean species richness found here, that – contrary to our initial hypothesis – extended beyond the tropics.

##### 4.1. Biodiversity patterns

As hypothesized, we were able to identify hotspots of crustacean species richness for benthic and pelagic crustaceans around the Philippines (Fig. 1), thus confirming previously detected patterns of high marine species richness at tropical latitudes (e.g., Saedi et al., 2019a; Saedi et al., 2022a). The Philippine Sea is located within the Coral triangle which in turn represents the most species rich area in the world ocean (Renema et al., 2008) for many marine taxa (e.g., Asaad et al., 2017; Carpenter and Springer, 2005; Fautin et al., 2013; Kerswell, 2006; Saedi et al., 2017).

Surprisingly, crustacean species richness also peaked at higher latitudes in the NWP – namely around the Japanese islands (benthic and pelagic) as well as the Kurile islands and the Kamchatka peninsula (primarily benthic). A comparable study identified the Japanese islands as hotspot for algal genera diversity too (Kerswell, 2006), which could hint at a more favourable food availability.

Overall, crustacean species richness hotspots were mainly located in minor coastal regions rather than the vast offshore NWP. An explanation for these patterns might be found in the degree of scientific exploration these particular coastal regions have been exposed to in the last decades (Brandt, 2016; Brandt et al., 2010; Brandt and Malyutina, 2015; Malyutina et al., 2018; Shirshov, 1983; Tadokoro, 2021), as opposed to large fractions of the vast NWP's high seas remaining poorly sampled

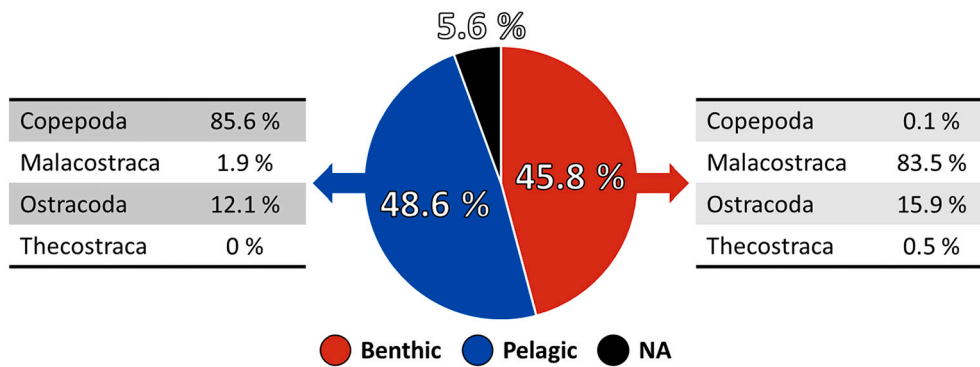


Fig. 4. Taxon and lifestyle composition of crustacean taxa in the NWP. Pie chart displaying the composition of benthic ( $n = 9949$ ) and pelagic NWP crustaceans ( $n = 10,535$ ) in the analyzed dataset by percentage (middle) and the taxonomic (sub-)class composition of each of the two lifestyles by percentage respectively in tables. Records that could not be identified as either benthic or pelagic with certainty are listed under NA ( $n = 1210$ ).

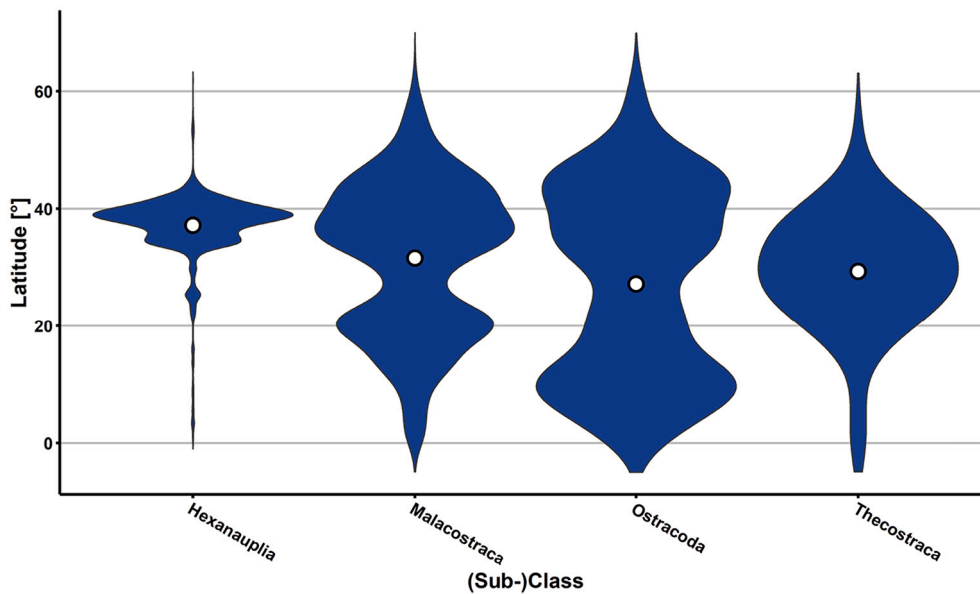


Fig. 5. Abundance of crustacean (sub-)classes in the NWP across a latitudinal gradient. For readability each of these violin plots possesses the same maximum width, which in turn means no informative conclusions regarding comparisons of abundance across (sub-)classes is possible. The median of each plot is highlighted by a white dot.

and consequently crustacean species composition being poorly understood and known (Fig. 1). In addition, large areas of continental shelf (coastal zones) in the NWP might provide the necessary habitat and productivity for crustacean taxa, complementing the findings of Saeedi et al. (2017). However, further research is required to identify why this proxy of available habitat influences species richness.

Outliers in sampling effort were located in two hexagons within the NWP and can be ascribed to single datasets: (i) the National Comprehensive Oceanographic Survey (available online: <http://ipt.iobis.org/seaobis/>) crustacean dataset which surveyed benthic crustaceans in the waters around the Hainan Island province in southern China and (ii) research cruises of the Japan Fisheries and Education Agency (FRA) off the east coast of Japan (Kuroshio-Oyashio transition zone) that investigated zooplankton over multiple decades (Tadokoro, 2021). Despite accounting for sampling bias by utilization of ES50, the FRA-dataset records heavily influenced abundance and composition calculations in later analyses (Figs. 2A and 5, Figs. A4B and A9). Another potential bias in the data used as framework for this study represents the different gears and their respective biases with which crustaceans were sampled in the NWP. The meta-data of crustacean records were very limited in this regard and therefore neglected for this study, yet should be kept in mind

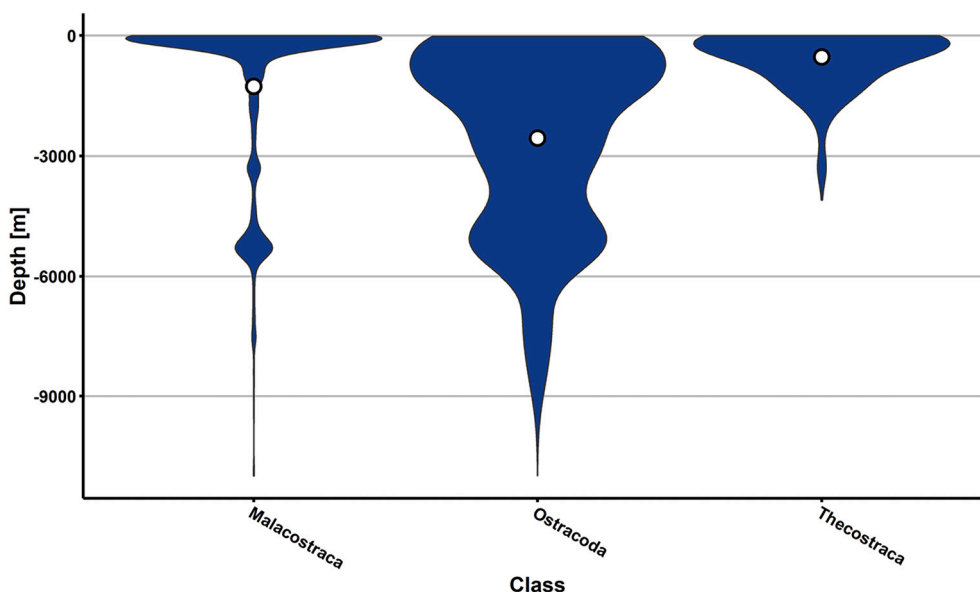
when looking at peaks or troughs in biodiversity data. This underlines again that sampling bias and effort must be considered when investigating large-scale marine biodiversity patterns.

#### 4.2. Bathymetric and latitudinal gradients

Given the poor quantity and quality of depth records for crustacean records, pelagic crustaceans could not be analyzed with our approach and their bathymetric distribution patterns thus remain unknown. We can only hypothesize, that most of the pelagic crustacean taxa analyzed in this study might be bound to shallow water and upper bathyal depths as previous studies on copepods, who make up the majority of the pelagic crustaceans, have shown (Bode et al., 2018; de Dias et al., 2018).

Regardless, we observed a pattern with two separate peaks in benthic crustacean species richness with depth (Fig. 3), contrasting the unimodal decline in species richness with depths as found in other studies (Costello and Chaudhary, 2017; Danovaro et al., 2010; Rosa et al., 2012; Saeedi et al., 2019a). Most crustacean orders were especially abundant and speciose in shallow waters yet declined with increasing depth (Figs. A10 and A11). However, some taxa were present throughout bathyal and abyssal depths, ultimately causing another peak in benthic





**Fig. 6.** Abundance of benthic crustacean classes in the NWP across a bathymetric gradient. For readability each of these violin plots possesses the same maximum width, which in turn means no informative conclusions regarding comparisons of abundance across (sub-)classes is possible. The median of each plot is highlighted by a white dot.

species richness at greater abyssal depths. These taxa comprise various crustacean orders of the Malacostraca and Ostracoda such as Cumacea, Halocyprida, Leptostraca and Podocopida. Other crustacean orders like Isopoda and Tanaidacea comprise taxa that represent typical and speciose deep-sea inhabitants (Blazewicz-Paszkiwicz et al., 2012; Raupach et al., 2004) and thus remain at least as speciose in deep-sea waters as they are in shallow waters. The visible decline in species richness for crustaceans at hadal depths (Fig. 3) is most likely caused by a combination of sampling bias as well as the scarce food availability that occurs in the hadal, resulting in low species numbers of specialized taxa in these depths.

Rex et al. (2006) found varying patterns of standing stock decrease in different deep-sea biota size classes with depths, which adds an aspect we did not consider in our approach: differences in body size across crustacean taxa could result in different responses to abiotic factors such as depth, food availability and productivity and thus aid in understanding crustacean biodiversity patterns even better.

The overall species richness pattern of pelagic crustaceans across the latitudinal gradient of the NWP (Figs. 2B and D) aligns with findings of previous studies on copepods, gastropods and sponges (Chaudhary et al., 2016; Rombouts et al., 2009). Possible explanations for a decline in species richness at higher latitudes may at least be partly caused by the reduced amount of ocean surface within our study area in comparison to its lower latitudes (compare Fig. 1). While this ultimately results in a lower amount of occurrence records, northernmost regions such as the Bering Sea are poorly sampled in general (< 500 records in our dataset). Another potential factor are downward shifts in water temperature and salinity with increasing latitude, which exhibited a negative correlation for pelagic crustacean species richness to a weak degree (Fig. 7B), contrasting the positive correlation between temperature and copepod diversity Rombouts et al. (2009) reported.

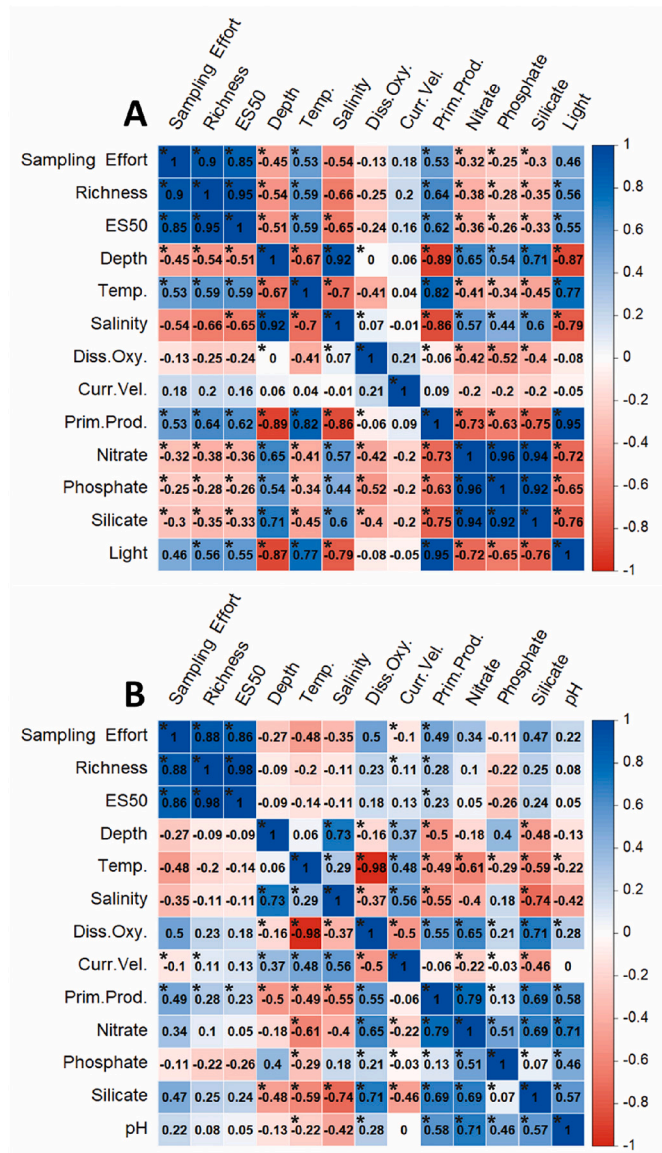
Interestingly, this latitudinal pattern did not apply to benthic crustaceans, whose biodiversity patterns were more evenly distributed across the latitudinal gradient and peaked around 45° latitude (Figs. 2B and C). Hillebrand (2004) found a similar imbalance pattern between benthic and pelagic latitudinal gradients, with the latter being stronger. Elevated levels of biodiversity at higher latitudes were previously estimated for marine taxa in general as well as reported in sea anemones, red algae and the also herein analyzed amphipods (Chaudhary et al., 2016; Fautin et al., 2013). Thus, the apparent differences between

benthic and pelagic biodiversity patterns became particularly noticeable at higher latitudes: even in the Sea of Okhotsk and alongside the Kurile Kamchatka Trench ES50 reached high values for benthic crustaceans yet declined for pelagic taxa. These differences might be caused by high levels of benthic species richness in the deep sea, as the latitudinal gradient for deep-sea benthos was less steep than for shallow-water benthos (Fig. A6), which coincides with the findings of Hillebrand (2004). Within a temperature-wise relatively stable deep sea, benthic crustacean fauna inhabiting the heterogeneous ocean floor of the NWP underlies other environmental drivers as the – hypothesized – shallow water pelagic crustaceans. Such factors range from sedimentation rates, current regimes and consequently habitat heterogeneity (Bellwood et al., 2005; Renema et al., 2008; Riehl et al., 2020b) to limiting factors such as food availability, especially in the deep sea (Golovan et al., 2019; Woolley et al., 2016). Strong bathymetrical gradients formed by hadal trenches and island ridges across a comparably small area might provide the ecological foundation for a speciose benthic crustacean community despite an otherwise environmentally stable deep sea (Ramirez-Llodra et al., 2010).

The absence of several crustacean taxa beyond latitudes of 40° such as the malacostracan Stomatopoda, the copepod order Siphonostomatoida, and the ostracod order Platycopina contrasts the distribution of most crustacean taxa across the whole latitudinal gradient of the NWP (Fig. 5, Figs. A8 and A9). While we cannot rule out that these findings are ultimately caused by sampling bias further investigations on these taxa might provide further context on their distribution patterns. Nevertheless, as these taxa represent a diverse taxa, we do not expect that their distribution patterns can be ascribed to their lifestyle and morphology alone.

#### 4.3. Environmental correlation

Following the trend of strong differences in biodiversity patterns of benthic and pelagic crustaceans, we also found little consensus in the correlation of environmental variables with these patterns across both lifestyles (Fig. 7). While multiple environmental variables showed significant correlation patterns with benthic crustacean abundance and species richness, there was almost no significant environmental variable that could explain the observed pelagic crustacean biodiversity patterns. Based on our findings, one could assume that low nutrient levels



**Fig. 7. Correlation matrices of environmental factors in the NWP and biodiversity measurements of benthic (A) and pelagic (B) crustaceans.** Benthic and pelagic crustaceans were tested against different sets of environmental variables from Bio-ORACLE (bottom and surface) using Spearman correlation to accommodate for their different lifestyles. Correlation scores marked with an asterisk were significant on a 5% confidence level. Significant positive correlations for benthic crustacean biodiversity measurements were found for light, productivity, and temperature whilst depth, nitrate, phosphate, salinity, and silicate were negatively correlated. For pelagic biodiversity measurements significant correlations were restricted to productivity (weak positive) and current velocity (low positive and negative).

(nitrate, phosphate, silicate) and salinity as well as higher levels of temperature, productivity, and light and low levels of seem to drive benthic crustacean biodiversity – especially at shallow-water depths. High levels of crustacean diversity and their apparently strong correlation to primary productivity underline how marine biodiversity benefits from nutrient-rich regions of the World Ocean such as the NWP. Especially within the deep-sea realm, previous studies identified food availability as one of the key restricting factors, as the deep sea lacks sources of primary production (Golovan et al., 2019; Woolley et al., 2016). However, our environmental correlation analysis showed no significant correlation with productivity with deep-sea benthic crustacean species richness.

Identifying the environmental causes for observable marine biodiversity patterns often results in temperature being one of the key environmental drivers (Costello and Chaudhary, 2017; Rombouts et al., 2009; Saeedi et al., 2019a). The positive correlation between temperature and benthic crustacean biodiversity we recorded, especially at shallow water depths, thus coincides with the findings of previous studies (Saeedi et al., 2017; Tittensor et al., 2010). However, this did not apply to pelagic crustacean biodiversity patterns, as we could not retrieve any significant correlations between temperature and biodiversity. Other studies reported positive relationships between temperature and shallow water biodiversity in general and pelagic copepod crustaceans more specifically (Rombouts et al., 2009; Saeedi et al., 2017).

Overall, the weaker environmental correlations for pelagic and deep-sea benthic crustaceans might hint at flaws in our methodological approach yet could also be caused by missing other abiotic factors with higher relevance in our study design. Saeedi et al. (2019a) pointed out, that high spatial heterogeneity within each hexagon (e.g., depth) may also cause poor correlations between species richness and environmental conditions. Many of the considered environmental variables exhibited significant correlations with one another, hinting at covariation. Therefore it seems more plausible to consider multiple, if not all, of the environmental variables together, rather than individually, to increase the certainty in potential findings on the relationship between abiotic factors and marine biodiversity patterns, especially at regional and local geographical scales. Nonetheless, we believe that the stronger, significant correlations we did find with our approach such as primary productivity, salinity and temperature do offer a valuable primary insight into the environmental drivers for crustacean biodiversity in the NWP, despite being complete.

**4.4. Conclusion**

Although it's far from being fully inventoried or understood, the crustacean diversity and distribution in the NWP is summarized for the first time in this study and offers a foundation for future endeavours in uncovering the biodiversity patterns of marine crustaceans, and how they might respond to future climate changes by potential distribution range shifts. This is crucial for evaluating and designing conservation strategies such as the establishment of marine protected areas – especially in times of anthropogenic climate change, where shifts in biodiversity patterns are likely.

Our study highlights the complexity of crustacean biodiversity patterns in the NWP formed along bathymetric and latitudinal gradients and the environmental factors that shape these patterns. However, these patterns are also heavily influenced by the lifestyle of these crustaceans (compare Saeedi et al., 2022a), which became apparent by strong differences between benthic and pelagic biodiversity patterns in our study. It is therefore necessary to incorporate the crustacean biology, comprising factors such as given lifestyle adaptations (pelagic, epibenthic, infaunal), larval development (sessile brooders, pelagic dispersers), body size, physiology, and motility (swimming, walking, digging) characteristic when analysing such a diverse faunal group. Consequently, many crustacean taxa possess distinct distribution patterns, highlighting that biodiversity patterns not only differ between global, regional and local scales but also at taxon level. Therefore, additional research on specific crustacean taxa under consideration of their characteristics (e.g., Rombouts et al., 2009; Saeedi et al., 2022a) is necessary to complement the bigger picture outlined by our approach.

Given the detected differences between shallow-water and deep-sea benthic diversity patterns as well as their environmental causes, we need to rethink where high levels of biodiversity could occur in the 3D marine realm. This requires considering latitude and depth together in a joint approach rather than independently to properly detect potential differences between shallow-water and deep-sea biodiversity.

## 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

The dataset of additional occurrence records from the SO-249 expedition in the Bering Sea is planned to be shared via OBIS and GBIF soon. Meanwhile all the R codes and dataset is available upon 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.seares.2022.102332>.

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