



# Biogeography of polychaete worms (Annelida) of the world

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**ABSTRACT:** The global biogeography of polychaete worms has never been assessed previously. In the present study, we studied the world distribution patterns of polychaetes based on datasets obtained from the Global Biodiversity Information Facility, the Ocean Biogeographic Information System and our recently published checklist of Indonesian polychaete species. Polychaete biogeographic regions were visualized using 'Infomap Bioregions', and the latitudinal species richness gradient of the animals was examined using 3 metrics, i.e. alpha, gamma and estimated species richness (the last metric was adjusted for sampling bias). We identified 11 major polychaete biogeographic regions. The North Atlantic, Australia and Indonesia were the top 3 species-rich biogeographic regions in the world. The total number of polychaete species was higher in the southern hemisphere (~2100 species, 67 families) than in the northern hemisphere (~1800 species, 75 families) despite significantly more data in the latter (>500 000 records compared to >26 000 records). Contrary to the classical idea of a unimodal distribution pattern, the latitudinal gradient of polychaetes was generally bimodal with a pronounced dip north of the Equator (15°N). We suggest that the slightly higher peak of species richness in the southern (30°S) than in the northern (60°N) hemisphere reflects higher southern endemities. These patterns are unlikely to be due to sampling bias but rather represent a natural phenomenon, and we found them most significantly correlated with sea temperature.

**KEY WORDS:** Global distribution · Latitudinal diversity gradient · Endemicity · Biodiversity · Polychaeta

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## 1. INTRODUCTION

Understanding of the world's biodiversity requires biogeographic knowledge, i.e. why species occur where they do. Identifying biogeographic regions, i.e. areas of endemism, is thus the first step in protecting areas with high biodiversity and endemism.

Historically, the first biogeographic schema focused on terrestrial fauna (mainly vertebrate species) such as those of Sclater (1858) and Wallace (1876). Wallace's Line is one of the oldest boundaries in biogeography and divides the Asian from the Australian fauna (Wallace 1860). In the marine realm, the evi-

dence for biogeographic boundaries was first considered unclear (e.g. Ekman 1953, Briggs 1974). However, Spalding et al. (2007) proposed 12 coastal realms based on expert opinion, and more recently, Costello et al. (2017) published a map of 18 and 12 coastal and offshore realms of the world based on species distribution data analysis.

The latitudinal distribution of the world's species was generally believed to show a unimodal pattern, whereby species richness increases from polar to tropical regions with a peak around the Equator (e.g. Kaufman 1995, Gaston 2000). As latitude is strongly correlated with temperature, temperature-

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driven hypotheses have been proposed to explain the underlying mechanisms behind these patterns, including the species–energy hypothesis, which asserts that faster metabolic and speciation rates in warmer temperatures have contributed to higher species numbers in the tropics (e.g. Kaspari et al. 2004), and the species–productivity hypothesis, which states that greater primary productivity has supported more individuals in the tropics (e.g. Rosenzweig 1995, Chase & Leibold 2002).

Contrary to the classical unimodal paradigm, Chaudhary et al. (2016) found the latitudinal gradient of marine species richness to be bimodal with a dip around the Equator. Fernandez & Marques (2017) and Menegotto & Rangel (2018) considered that this pattern was due to sampling bias. However, Chaudhary et al. (2017) used a rarefied species richness estimator to show that the pattern was unlikely to have been caused by sampling bias. In fact, the latitudinal diversity gradient pattern can vary between taxa. Razor clams (Mollusca), for example, show a strong bimodal pattern (Saeedi et al. 2017), whereas the pattern for planktonic radiolarians appears to be unimodal (Boltovskoy & Correa 2016, 2017).

Polychaete worms (phylum Annelida, class Polychaeta) are ubiquitous in virtually all marine and estuarine habitats, at all latitudes, and from the supralittoral to abyssal waters. They typically dominate macrofaunal assemblages in sedimentary environments, representing 25–63% of all species and 39–73% of all individuals (Hutchings 1998). The group also has a high tolerance towards extremes of temperature, salinity and oxygen availability. Some species occur near hydrothermal vents with extremely high temperatures and low available oxygen (McHugh & Tunnicliffe 1994), and others occur in fresh or near-fresh waters (Glasby & Timm 2008).

Since the middle of the 18<sup>th</sup> century, about 11 500 polychaete species (about 1400 genera, 85 families) have been described and accepted (Pamungkas et al. 2019). Over this period, numerous marine expeditions and investigations have been carried out at regional scales. Many polychaete datasets generated from these studies have been archived in the Global Biodiversity Information Facility (GBIF, [www.gbif.org](http://www.gbif.org)) and Ocean Biogeographic Information System (OBIS, [www.obis.org/](http://www.obis.org/)). Despite the availability of these datasets, the global biogeography of polychaetes has never been assessed. In this study, we investigated the geographic world distribution of the animals (including regions of endemism and latitudinal diversity gradient patterns), identified gaps in

the distributional data and compared our findings with those of other marine groups. We thus tested whether the geographic world distribution of the taxon is similar to that of all marine taxa together as studied by Costello et al. (2017). Also, we asked whether polychaetes, like many other marine organisms, show the classical unimodal diversity gradient pattern with peak species richness at the Equator, as suggested by the taxon-limited polychaete study of Giangrande & Licciano (2004). Additionally, we determined the primary environmental variables responsible for shaping polychaete distributional patterns and species richness.

## 2. MATERIALS AND METHODS

### 2.1. Dataset collection and quality control

The datasets used in the present study were primarily obtained from GBIF and OBIS (downloaded on 10 June 2018) (see 'References S1' in the Supplement at [www.int-res.com/articles/suppl/m657p147\\_supp.pdf](http://www.int-res.com/articles/suppl/m657p147_supp.pdf)). We also added Indonesian polychaete records published by Pamungkas & Glasby (2019), as most records in that geographic region were not in GBIF and OBIS (records uploaded to OBIS Indonesia at [http://obis.lipi.go.id:8080/ipt/resource?r=polychaeta\\_pamungkas\\_2019](http://obis.lipi.go.id:8080/ipt/resource?r=polychaeta_pamungkas_2019)). Each dataset from GBIF and OBIS was first prepared by removing records without a species name or geocoordinates. To ensure the use of data with high coordinate accuracy, we omitted records without coordinate uncertainty or with coordinate uncertainty of more than 10 km. This 10 km figure is a compromise between retaining existing record accuracy (most records have less than 1 km of coordinate uncertainty), recognizing small islands, and keeping each record within 1° of latitude (about 111 km). Duplicated records with the same species name, latitude and longitude, depth and collection date, were also removed (see Tables S1 & S2 in the Supplement). Both datasets were then merged, and duplicates between the 2 datasets were removed (Table S3). The World Register of Marine Species (<http://www.marinespecies.org/>) was used as a basis for the higher classification; to reconcile synonyms and misspellings, the nomenclature of polychaete species names was verified using 'Taxon match' (datasets with invalid species names were only used after the names were corrected). The final dataset used for analyses in this study is available at [https://auckland.figshare.com/articles/dataset/Global\\_polychaete\\_data\\_csv/12401993](https://auckland.figshare.com/articles/dataset/Global_polychaete_data_csv/12401993).

## 2.2. Polychaete biogeographic regions and indicator species

All polychaete occurrence records were mapped using ArcGIS version 10.4.1. Records that were mapped inland were either corrected (based on the locality information given in the dataset) or removed (if no locality information was given). The interactive web application 'Infomap Bioregions' (<http://bioregions.mapequation.org>) was then used to identify polychaete biogeographic regions objectively based on latitude–longitude coordinates for all species records (Edler et al. 2017). The analysis was run with the following settings: for the spatial resolution, we used grid cells of 4° to reflect spatial differences in data density (the maximum and the minimum cell capacities were set to 100 and 50 occurrence records, respectively), and for the clustering algorithm, we set the numbers of trials and cluster cost to 1 and 1.5, respectively, to identify major polychaete biogeographic regions. Infomap Bioregions uses neural network theory to map the similarity of cells based on their species composition. In doing so, it identified the most common and indicative polychaete species in each biogeographic region. Because we focussed on major biogeographic regions only, we made no attempt to recognize any hierarchy among the regions (e.g. realms, provinces etc.) and removed isolated cells. In addition, we calculated the percentage of endemic polychaete species in each region.

## 2.3. Analyses

Following the methods of Chaudhary et al. (2017), the latitudinal gradient was examined using 3 metrics, i.e. alpha, gamma and estimated species richness. As alpha and gamma species richness were biased by uneven numbers of records between latitudinal bands (Fig. S1), we performed the rarefaction method of Hurlbert (1971) in R version 3.5.3 (R Core Team 2013) using the 'vegan' package (Table S4). The analysis calculated the expected number of species in each 5° latitudinal band per repeatedly sampled 50 occurrence records, i.e. the so-called E(S50). The equation used was:

$$E(S_n) = \sum_i [1 - (N - N_{in}) / (N_n)] \quad (1)$$

where  $E(S_n)$  is defined as the expected number of species in a sample of ( $n$ ) records, selected randomly from a sample containing ( $N$ ) records, ( $S$ ) species and  $N_i$  records in the  $i$ th species. E(S50) was much less

biased by sampling effort (Fig. S1). We then ran a generalized additive model (GAM) using R (Table S5) to define the best non-linear model fitting the latitudinal gradients in species richness (Hastie & Tibshirani 1990), i.e. whether it shows a uni-, bi- or multimodal pattern.

We investigated a range of environmental variables shown by previous studies (C. R. Smith et al. unpubl. data [www.soest.hawaii.edu/oceanography/mincks/publications/Smith\\_etal\\_Abyssal\\_biogeography\\_synthesis.pdf](http://www.soest.hawaii.edu/oceanography/mincks/publications/Smith_etal_Abyssal_biogeography_synthesis.pdf)) to be correlated with taxon occurrences, i.e. sea surface and bottom temperatures, salinity, primary productivity, particulate organic carbon, depth, slope, distance from land and sea-to-land ratio. Environmental datasets were downloaded on 6 November 2019 from the Global Marine Environment Datasets (GMED) (Basher et al. 2018) and were analyzed using MATLAB R2018. Using the non-parametric Spearman rank correlation analysis, we correlated E(S50) and E(S30) values with various environmental variables for each 5° latitudinal band and 5° cell, respectively.

## 3. RESULTS

### 3.1. Geographical distribution

Most polychaete species records, i.e. over 75%, were coastal (Fig. 1) and within 2.5 km of land (Fig. 2); this, in part, is likely related to greater accessibility of coastal areas for sampling. Consequently, fewer species were found in latitudinal bands with a higher sea-to-land ratio, reflecting the lesser coastal area (Fig. S2). The number of species tended to decline with depth (Fig. 2). The coasts of some temperate and subtropical regions, i.e. Europe, Australia and New Zealand, had the most species records. In the tropics, most species records were centred in Indonesia, whereas in polar waters more occurred in the Antarctic than Arctic (Fig. 1). Of all polychaete families, spionids had the most records (>62 000 records), followed by serpulids and terebelids with >28 000 records each (Table S6).

We identified 11 major polychaete biogeographic regions (Fig. 1). Regions with the most polychaete species records were, in order, the North Atlantic (including eastern and western parts of Mediterranean Sea), Australia and Indonesia, whereas regions with the fewest species records were the eastern Pacific Ocean, Caribbean Sea and Atlantic Ocean (Table 1). Despite being the region with the most polychaete species, the North Atlantic had the

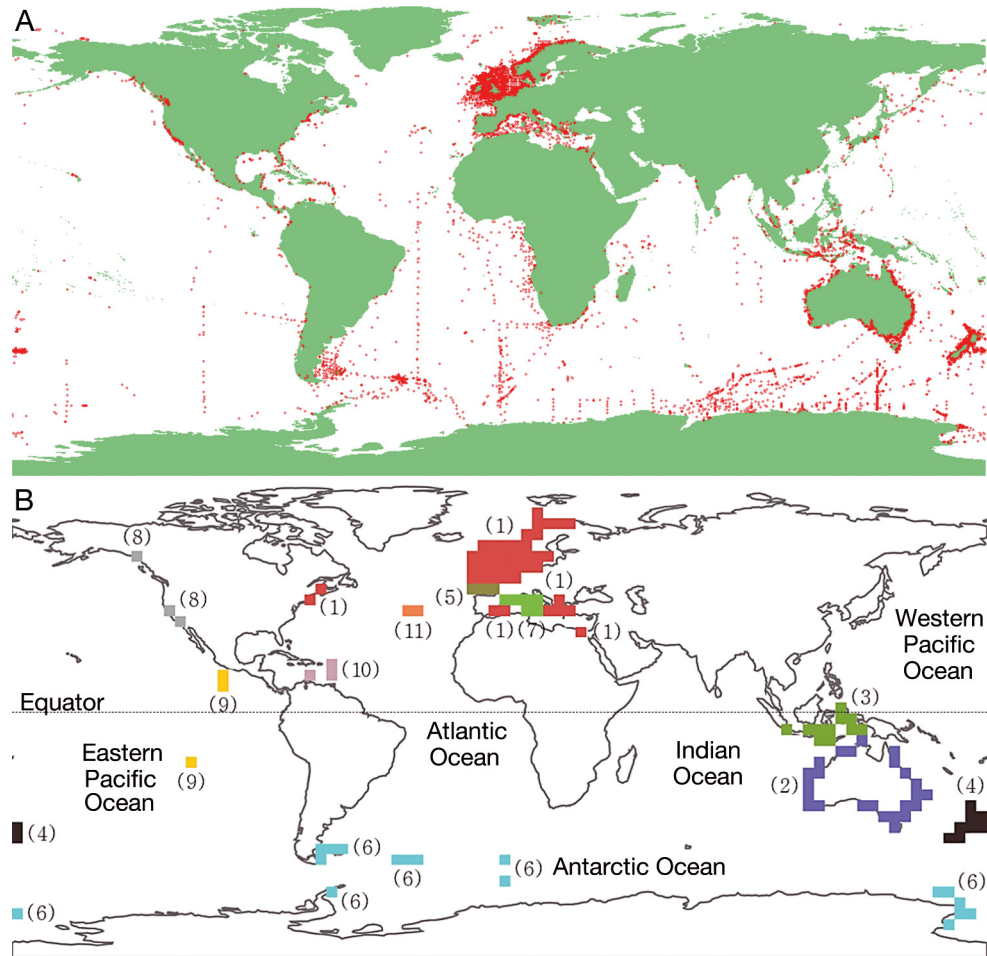


Fig. 1. (A) Polychaete occurrence records and (B) biogeographic regions. Species records were based on Global Biodiversity Information Facility (GBIF) and Ocean Biogeographic Information System (OBIS) datasets, plus our recently published checklist of Indonesian polychaete species (Pamungkas & Glasby 2019). Biogeographic regions were generated by uploading the records to the interactive web application 'Infomap Bioregions' (<http://bioregions.mapequation.org>) (see Table 1 for additional details)

lowest indicative species score (1), whereas Indonesia had the highest indicative species score (291) (Table 1). These scores mean that the indicative species of the North Atlantic have the same frequency of occurrence there as in other regions, whereas those of Indonesia are 291 times more frequent in this biogeographic region than in other regions (the species of Indonesia are, as a whole, far more distinctive than those of the North Atlantic). Of the 11 biogeographic regions, 7 regions had more than 50% endemism of polychaete species (Table 1). The eastern part of the Pacific Ocean and the Central Mediterranean Sea had the highest (100%) and the lowest (5%) percentage of endemic polychaete species, respectively (Table 1) (here, we define 'endemic species' as species unique to a biogeographic region as defined in this study).

### 3.2. Latitudinal distribution

The analysis of >550 000 cleaned polychaete occurrence records (3415 species, 77 families) (Tables S3 & S6) showed significantly more records in the northern (>500 000 records) than the southern hemisphere (>26 000 records) (Fig. 3A). Similarly, the average number of polychaete species, including the data variance, was generally higher in the northern than the southern hemisphere (Fig. 3A). However, the total number of species was higher in the southern (~2100 species, 67 families) than the northern (~1800 species, 75 families) hemisphere (Fig. 3B). A similar pattern of slightly higher species numbers in the southern hemisphere was also observed for each of the 2 subclasses (i.e. Errantia and Sedentaria), although Sedentaria appeared to be relatively less speciose than Errantia between 5° N and 10° S (Fig. 3C).

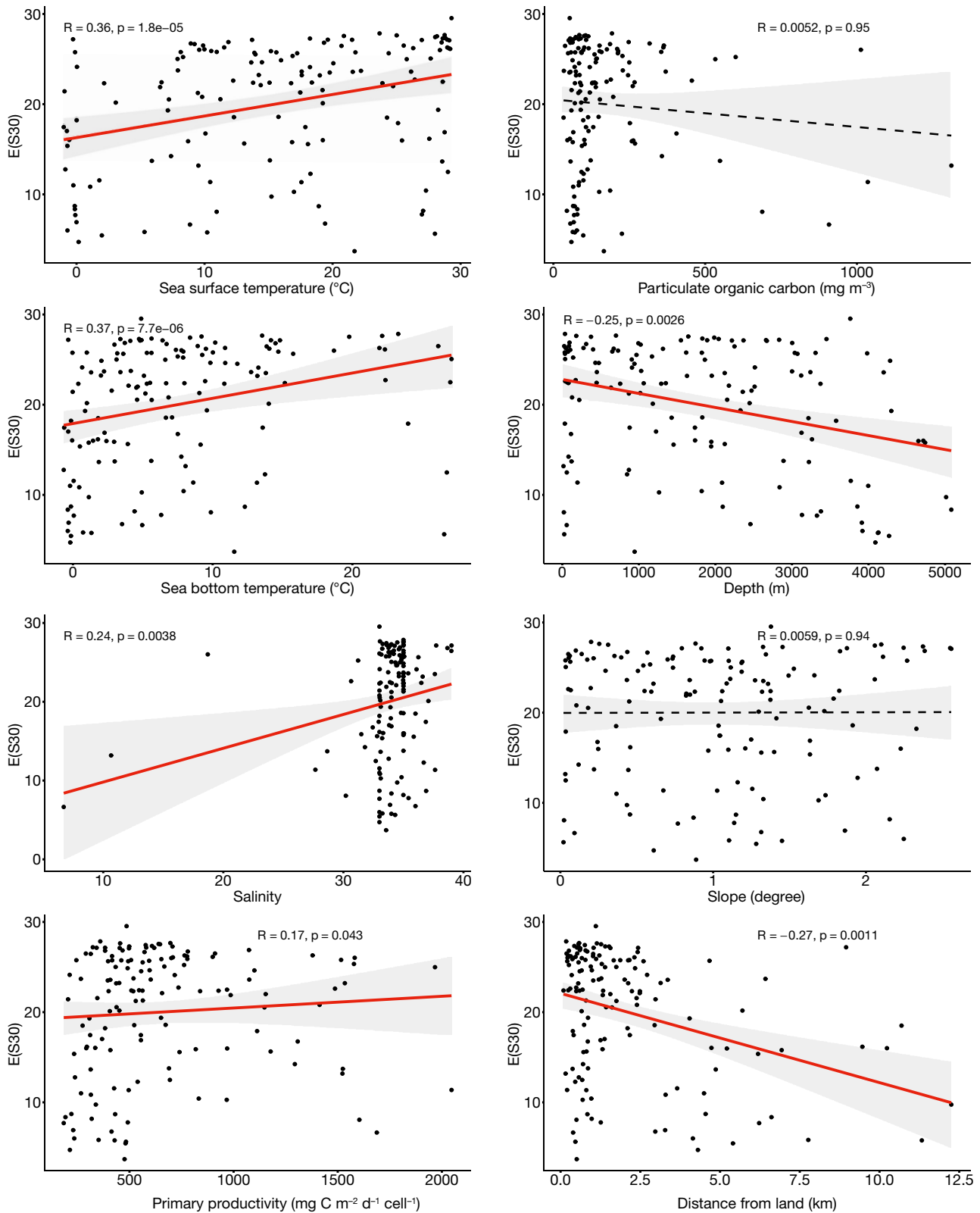


Fig. 2. Spearman correlation analyses between the expected number of species in a sample of 30 records (i.e. the E[S30] value) and various environmental variables in each 5° grid-cell resolution. R is the Spearman's correlation coefficient. Results were considered significant at  $p < 0.05$ . Visually, solid red and dashed black linear regression lines also indicate significant and non-significant analysis results, respectively. Grey shading represents standard error



Table 1. Major polychaete biogeographic regions mapped (sorted by species richness) in comparison with marine regions outlined by Spalding et al. (2007) and Costello et al. (2017). A cell represents an area with 4° grid-cell resolution. Biogeographic regions for which our study lacked data are: Arctic, Western Indo-Pacific and Temperate Southern Africa (in Spalding et al. 2007), as well as Arctic Seas, Gulf of Aqaba, Aden, Suez & Red Sea, South Africa, Black Sea, Chile, Inner Baltic Sea, North American Boreal, Northwest Pacific, Offshore Indian Ocean, Offshore Middle-East Pacific, Offshore South Atlantic, Offshore West Pacific, Tasman Sea and Tropical East Atlantic (in Costello et al. 2017). 'Score' indicates the ratio between the frequency of the species in the region and that in all regions

Region	Location(s)	Records	Species	Cells	Most common species (record)	Most indicative species (score)	% endemic species	Spalding et al. (2007)	Costello et al. (2017)
1	North Atlantic & eastern and western parts of Mediterranean	494766	1144	41	<i>Lanice conchilega</i> (11004)	<i>Pygospio elegans</i> , <i>Nephtys cirrosa</i> , <i>Pholoe baltica</i> , <i>Pseudopolydora pulchra</i> , <i>Scalibregma celticum</i> , <i>Ophelia borealis</i> , <i>Polycirrus norvegicus</i> , <i>Dipolydora caulleryi</i> , <i>Ampharete falcata</i> , <i>Paranaitis kostersi</i> (1) <i>Longicarpus modestus</i> , <i>Pista australis</i> , <i>Spio blakei</i> , <i>Armandia intermedia</i> , <i>Nephtys inornata</i> , <i>Micronephtys oculifera</i> , <i>Galeolaria gemineoa</i> , <i>Prionospio tridentata</i> , <i>Mediomastus australiensis</i> (37)	62.4	Temperate Northern Atlantic	North-east Atlantic, Norwegian Sea & Mediterranean
2	Australia	13292	1111	24	<i>Aglaophamus australiensis</i> (295)	<i>Ceratonereis tenia culata</i> , <i>Tomopteris nationalis</i> , <i>Leanira coeca</i> , <i>Glycera longipinnis</i> , <i>Opisthoyllis australis</i> , <i>Phyllochaetopterus clapariedii</i> , <i>Polydora atrorugosus</i> , <i>Lumbrineris laterelli</i> , <i>Loimia nigrifilis</i> , <i>Lysidice oele</i> (291)	65.9	Central Indo-Pacific & Temperate Australasia	Coral Sea & South Australia
3	Indonesia	1571	513	11	<i>Leodice antennata</i> (38)	<i>Armandia maculata</i> , <i>Ayschis trifloesus</i> , <i>Scolecoplexides benhami</i> , <i>Boccardia syrtis</i> , <i>Sthenelais chathamensis</i> , <i>Lepidonotus polychromus</i> , <i>Pomatoceros caeruleus</i> , <i>Phylo novaezealandiae</i> , <i>Neosabellaria kaiparaensis</i> , <i>Paradiopatra minuta</i> (57)	62.3	Central Indo-Pacific	Indo-Pacific Seas & Indian Ocean
4	New Zealand	5659	381	10	<i>Hyalinoecia tubicola</i> (193)	<i>Armandia maculata</i> , <i>Ayschis trifloesus</i> , <i>Scolecoplexides benhami</i> , <i>Boccardia syrtis</i> , <i>Sthenelais chathamensis</i> , <i>Lepidonotus polychromus</i> , <i>Pomatoceros caeruleus</i> , <i>Phylo novaezealandiae</i> , <i>Neosabellaria kaiparaensis</i> , <i>Paradiopatra minuta</i> (57)	35.5	Temperate Australasia	New Zealand
5	Atlantic coasts of Spain & France	928	216	3	<i>Glycera papillosa</i> (46)	<i>Lumbrineris laubieri</i> , <i>Poecilochaetus fulgoris</i> , <i>Paradoneis abranchiata</i> , <i>Exogone furcigera</i> , <i>Sclerobregma brachiata</i> , <i>Microrbinia linea</i> , <i>Paraonides rubriceps</i> , <i>Lumbrineriopsis gasconensis</i> , <i>Diplobrachia capillaris</i> , <i>Bonellia plumosa</i> (240)	20.7	Temperate Northern Atlantic	Northwest North Atlantic
6	Antarctica & the southern coast of Argentina	1983	207	17	<i>Pelagobia longicirrata</i> (103)	<i>Siophanes tcherniai</i> , <i>Amythas membranifera</i> , <i>Polycirrus kerguelensis</i> , <i>Lanicides vayssierei</i> , <i>Genetyllis polyphylla</i> , <i>Epigamia charcoti</i> , <i>Ophrotrocha notialis</i> , <i>Capitella perarmata</i> , <i>Thelepidetes koehleri</i> , <i>Terebellides</i> spp. (107)	50.8	Southern Ocean & Temperate South America	Southern Ocean & Argentina
7	Central Mediterranean Sea	5066	197	6	<i>Sabella spallanzanii</i> (631)	<i>Perineris macropus</i> , <i>Protobonellia brevirhynchus</i> , <i>Spirobranchus lima</i> , <i>Adercodon plejeji</i> (18)	5.1	Temperate Northern Atlantic	Mediterranean
8	US west coast	419	87	3	<i>Phragmatopoma californica</i> (156)	<i>Phyllocoe medipapillata</i> , <i>Dorvillea moniloceras</i> , <i>Pareurythoe californica</i> , <i>Pista pacifica</i> , <i>Spirobranchus spinosus</i> , <i>Megasyllis nipponica</i> , <i>Glycera robusta</i> , <i>Odontosyllis phosphonea</i> , <i>Lepidonotus spiculus</i> , <i>Herrnadiella truncata</i> (71)	77.4	Temperate Northern Pacific	North Pacific
9	Eastern Pacific Ocean	574	31	3	<i>Paralvinella grasslei</i> (52)	<i>Branchinotoglypta sandersi</i> , <i>Branchiplicatus cupreus</i> , <i>Branchipolynoe symmytilida</i> , <i>Paralvinella pandorae</i> , <i>Thermiphione risensis</i> , <i>Protis hydrothermica</i> , <i>Lepidonotopodium riftense</i> , <i>Nicomache arwidssoni</i> , <i>Sirsoe hessleri</i> , <i>Malacoceros samurai</i> (213)	100	Tropical Eastern Pacific & Eastern Indo-Pacific	Southeast Pacific & Gulf of California
10	Caribbean Sea	243	16	3	<i>Spirobranchus giganteus</i> (67)	<i>Notaulax nudicollis</i> , <i>Eupolyornia crassicornis</i> , <i>Notopygos caribea</i> , <i>Hydroides mongeslopezi</i> (165)	44.4	Tropical Atlantic	Caribbean & Gulf of Mexico
11	Atlantic Ocean	254	15	2	<i>Branchipolynoe seepensis</i> (80)	<i>Lepidonotopodium jouinae</i> , <i>Prionospio unilamellata</i> , <i>Laonice asaccata</i> , <i>Ophrotrocha fabrae</i> , <i>Neomicrobrachis azoricus</i> (138)	62.5	Temperate Northern Atlantic	Northwest North Atlantic

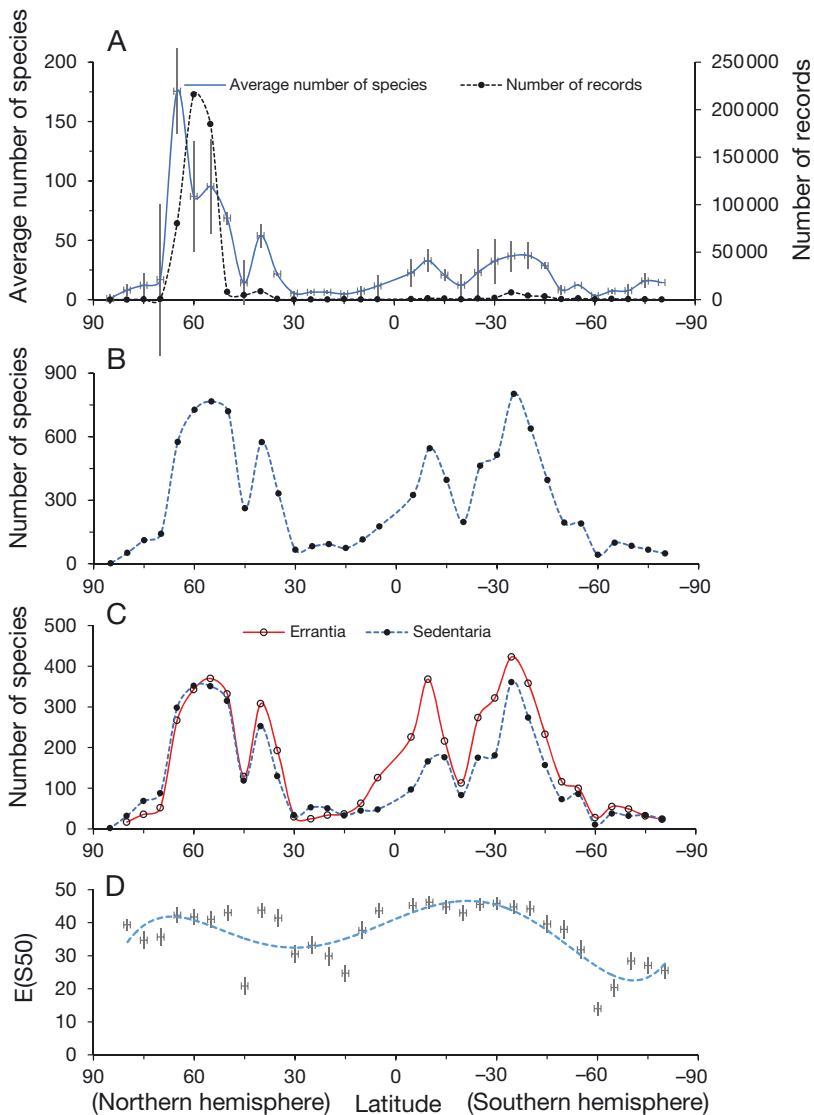


Fig. 3. (A) Alpha species richness (calculated as mean  $\pm$  SE number of species, with a 2-point moving average trend line) and record numbers. (B) Gamma species richness (all species). (C) Gamma species richness (errant and sedentary species). (D) Expected number of species in a sample of 50 records, E(S50)

The latitudinal gradient of alpha species richness (average per latitudinal band) was bimodal and much higher in the northern than southern hemisphere (Figs. 3A & 4A). Gamma (total) species richness for all errant and sedentary species was more symmetrically bimodal, with a peak at around 55°N and slightly higher one at 35°S, and a dip north of the Equator between 15 and 30°N (Figs. 3B,C & 4B). We found that both alpha and gamma species richness were highly correlated ( $p < 0.0001$ ) with the number of occurrence records (Fig. S1), suggesting that the pattern was driven by uneven sampling effort. Although E(S50) was also correlated with the

number of records (Fig. S1), it was far less so ( $p \leq 0.01$ ). Nevertheless, our rarefaction analysis, which adjusted for the uneven sampling effort across latitudinal bands, found that the latitudinal species richness gradient of polychaetes, i.e. the E(S50), remained bimodal with the peaks at around 60°N and 30°S, and a dip at around 15°N (Fig. 3D). Supporting this, our GAM also showed the pattern to be bimodal (Fig. 4C). This further indicates that the bimodality is unlikely to be due to sampling bias, and that the southern hemisphere has higher species richness than the northern hemisphere.

There were significant correlations between the E(S30) and all environmental variables in each 5° cell, except particulate organic carbon and slope (Fig. 2). All correlation coefficients were positive and weak, except the coefficients for depth and distance from land (Fig. 2). For latitudinal bands, there was a moderate positive correlation between the E(S50) and the sea surface temperature and salinity, and a negative correlation with the sea-to-land ratio (Fig. S2).

## 4. DISCUSSION

### 4.1. Geographical distribution

We found that Europe and its surroundings had the most records, and therefore have published (in a broad sense) the most polychaete data, fol-

lowed by Australia and New Zealand. More records were also found in Antarctic than Arctic waters, and in the tropics, Indonesia had more records than other equatorial regions (Fig. 1). That most polychaete records were coastal is in line with the general pattern for marine species found in comparable online-data-based biogeographic studies (Costello et al. 2017, Costello & Chaudhary 2017).

The 11 polychaete biogeographic regions identified in this study largely coincide with the marine biogeographic regions proposed by Spalding et al. (2007) and determined from data analysis by Costello et al. (2017). They also closely coincide with the 24

biogeographic regions outlined by Glasby (2005), which were based on sponge and polychaete distributions, although some adjacent regions of Glasby

(2005) were combined in the present study (e.g. temperate and tropical Australia). However, due to insufficient data, particularly for Africa, South America

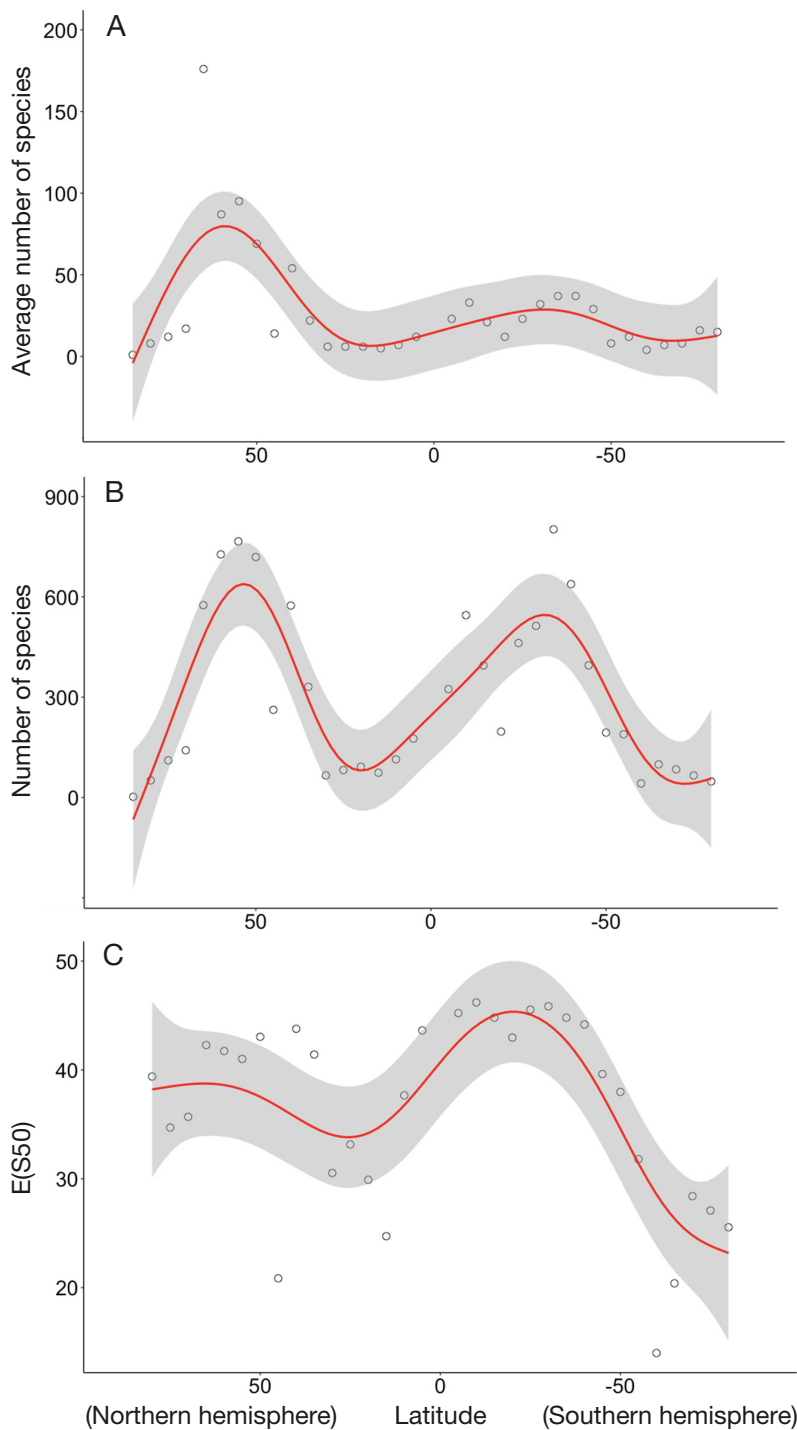


Fig. 4. Generalised additive models of (A) alpha species richness, (B) gamma species richness and (C) expected number of species in a sample of 50 records,  $E(S_{50})$ . The solid red lines are the best non-linear models, smoothed using the restricted maximum likelihood (REML) method (see Table S4). Grey shading represents standard error; circles are the data points

and the deep sea in general, the present study did not recover previously defined biogeographic regions such as the Arctic Seas, Black Sea (studies by Arvanitidis et al. 2002, 2009; Surugiu et al. 2010; and Costello et al. 2017 found the Black Sea to be distinct from the Mediterranean Sea), Chile, Inner Baltic Sea, North American Boreal, Northwest Pacific, offshore Indian Ocean, middle east Pacific, South Atlantic and West Pacific Oceans, South Africa, Tasman Sea, Tropical East Atlantic as well as the Western Indo-Pacific (Table 1). Further, some biogeographic regions recognized in this study were subdivided into smaller units in other studies. For example, Biogeographic Region 6, i.e. Antarctica and the southern coast of Argentina (which here includes the entire Southern Ocean), comprised several distinct regions including the East Antarctic, West Antarctic–South Georgia and Magellan, in the polychaete biogeography study of Glasby & Alvarez (1999) and Glasby (2005). Nevertheless, our recognition of Region 6 agrees with several all-taxa studies considering the Antarctic and Southern Ocean to be one biogeographic region (e.g. Ekman 1953, Spalding et al. 2007, Costello et al. 2017). Reasons for the recognition of a combined Antarctic plus Southern Ocean area seem to reflect the larger amount of data available (Glasby & Alvarez 1999 and Glasby 2005 only analyzed 6 families and 10 clades of polychaetes, respectively); it may also reflect spatial biases where particular geographic areas may have been sampled differently (e.g. sediments or epifauna). Obtaining polychaete data from poorly-known areas and incorporating all available data using a standard biogeographic methodology are thus a priority for further research.

Biogeographic Region 1, i.e. the North Atlantic excluding the coast of Spain



and France facing Biscay Bay, was found to be the region with the most polychaete species reflecting its large area and survey effort. Yet, the score of the indicative species of this region was the lowest among all biogeographic regions (Table 1), as polychaete species from the North Atlantic also occurred in many other geographic regions. By contrast, Indonesia (Region 3) had the highest score and was the third most species-rich biogeographic region in the world despite a relatively low number of records (Table 1). The high polychaete species richness and endemism in this area is not surprising as the region is part of the 'Coral Triangle', so named because it is a globally rich region for corals (Veron et al. 2009), fish and other taxa (e.g. Asaad et al. 2018).

Despite being located near Region 1, the Bay of Biscay coast of Spain and France (Region 5) and the central part of the Mediterranean Sea (Region 7) were identified as distinct biogeographic regions (Fig. 1). However, we caution recognition of the indicative species of these regions as endemic because the data were taken from only 42 locations. To our knowledge, almost all of the indicative species of both regions have not been reported elsewhere since their first descriptions. Moreover, occasionally species in both regions have been reported a considerable distance away—for example, one of the indicative species of Region 5, i.e. *Microrbinia lineata*, was also reported in the China Sea (Liu 2008). This outlier, and others, may represent misidentifications; taxonomic revisions are the basis to improving the accuracy of species names in global datasets. Thus, Regions 5 and 7 may be part of Region 1, following the warm-temperate Lusitania Region proposed by Briggs & Bowen (2012), which includes largely coastal areas of southern Britain and Ireland, extending south to southern Morocco, and eastwards through the Mediterranean Sea. Similarly, Spalding et al. (2007) considered coastal Europe (including the Bay of Biscay) and the Mediterranean Sea as one marine biogeographic region (i.e. Temperate Northern Atlantic) comprising 6 smaller regions. Also, the species distribution data analyses by Costello et al. (2017) defined the North East Atlantic and Mediterranean as one biogeographic region.

Furthermore, we found that most of the polychaete biogeographic regions were coastal, but some were offshore, such as those situated in the offshore northern Atlantic, Antarctic and eastern Pacific Oceans (Regions 11, 6 and 9, respectively) (Fig. 1). These biogeographic regions were dominated by deep-sea polychaete species associated with hydrothermal vent habitat. In fact, all indicative species of Region 11

were described from the deep-sea environment of the area, and 4 of the 5 species were obtained from hydrothermal vents (Zibrowius 1972, Desbruyères & Hourdez 2000, Sigvaldadóttir & Desbruyères 2003, Paxton & Morineaux 2009). Similarly, all indicative species of Region 9 were originally described from a similar hydrothermal vent habitat (Pettibone 1984a,b, 1985a,b, 1986, Blake 1985, 1991, Desbruyères & Laubier 1986, ten Hove & Zibrowius 1986, Hourdez et al. 2006), and were not recorded elsewhere. Whether these regions are really biogeographic regions or reflect sampling of unique deep-sea habitats merits further research comparing data from vents and non-vent habitats in these biogeographic regions.

#### 4.2. Latitudinal distribution

The total number of polychaete species was slightly higher in the southern hemisphere despite the availability of about 20 times more samples in the northern than southern hemispheres (Fig. 3A–C). This finding contradicts the pattern of most marine taxa, where species richness generally peaks in the northern hemisphere (Chaudhary et al. 2016, 2017, Chaudhary 2019), but is similar to the pattern of a few taxa such as fish, sharks and rays, stony corals (Chaudhary 2019) and amphipods (Arfianti & Costello 2020) when sampling bias is accounted for (Table S7). In our case, we suspected that elevated polychaete species richness in the southern hemisphere may be driven by high endemism, as species richness and endemism have been found to be positively correlated (e.g. Costello et al. 2017). Moreover, when the brackish Black and Baltic Seas are excluded, an all-taxon study that mapped global biogeographic 'Realms' equivalent to polychaete biogeographic regions in our study suggested that endemism may be higher in the southern than northern hemisphere (47 vs. 40%) (Costello et al. 2017). Indeed, comparison of the number of endemic species (per biogeographic region) in the present study shows that ca. 1300 endemic species occur in the southern hemisphere compared to ca. 870 endemics in the northern hemisphere (62 vs. 48%).

A less likely explanation for the greater number of polychaete species in the southern than northern hemisphere is the adoption of northern hemisphere species names by polychaete workers of the southern hemisphere (see a review by Hutchings & Kupriyanova 2018). This may have, in small part, artificially inflated the number of species in the southern hemi-

sphere, and at the same time hidden the distinctive, largely endemic fauna in the southern hemisphere, which was first revealed in revisionary morphological taxonomic studies (Hutchings & Glasby 1991), and more recently by molecular studies. Also, our analysis of species occurring in both hemispheres indicated that less than 1% (5 of about 500) of species occurring in both hemispheres are the result of suspected misidentification (Table S8), so taxonomic bias would appear to have little influence on the patterns observed in this study. However, the number of polychaete species documented in the present study (i.e. about 3400) is much smaller than the total named species (i.e. nearly 11 500). Therefore, the use of a larger sample of polychaete species, underpinned by improved taxonomy, will undoubtedly provide additional insights into the large-scale biogeography of polychaetes.

The bimodal latitudinal gradient in alpha, gamma and E(S50) species richness for polychaetes (Figs. 3 & 4) supports the findings of Chaudhary et al. (2016, 2017) of bimodality of overall marine species. Our results are thus in line with the latitudinal species richness gradient of various marine groups such as amphipods (Arfianti & Costello 2020), bivalves (Crame 2000, 2001, 2002), brachiopods (Shen & Shi 2004), planktonic organisms (Brayard et al. 2005), razor clams (Saeedi et al. 2017), sea anemones (Fautin et al. 2013), seaweeds (Bolton 1994, Kerswell 2006) and zooplankton (Rutherford et al. 1999), as well as with the latitudinal species richness gradient of some terrestrial groups like amphibians, reptiles, birds and mammals (McCoy & Connor 1980, Currie 1991, Sax 2001). However, most of the authors of these studies did not explicitly state the pattern to be bimodal, either because the pattern was not noticed, or the drop in species richness near the Equator was considered to be due to a lack of data. The pattern was first noticed and reinterpreted to be bimodal by Chaudhary et al. (2016).

The results of the present study thus strongly contradict the findings of other studies focussed on polychaetes suggesting that the latitudinal gradient species richness either does not exist (Gobin & Warwick 2006) or is unimodal (Giangrande & Licciano 2004). The former study had only 14–77 polychaete species from 15 sampling sites at 4 geographic locations (so the different pattern found in that study may simply reflect a lack of sufficient data), and the latter study was limited to 428 species of the Sedentaria family Sabellidae (so the differences with the bimodal pattern finding in our study are more surprising given that we found the Sedentaria to be relatively less

speciose than Errantia in the vicinity of the tropics, specifically between 5° N and 10° S). The greater taxon sampling in our study, i.e. about 3400 species in 85 families sampled across 10 000 sampling sites around the globe, resulted in a bimodal pattern in polychaete species richness. We show that alpha and gamma species richness-based latitudinal gradients are biased by uneven sampling effort across the globe (Fig. S1). However, our rarefaction index E(S50) and GAM, which corrected for sampling effort, demonstrated that the pattern remains bimodal (Fig. 4C). This indicates that the bimodal pattern in polychaete species richness is not an artefact, but rather a natural phenomenon.

Chaudhary et al. (2016) proposed that sea surface temperature was the primary factor causing the dip in marine species richness in the tropics. That is, the equatorial region may already be too hot from climate warming; some marine species may have been lost and/or moved to higher latitudes as has been observed for marine fish (e.g. Perry et al. 2005, Nye et al. 2009, Last et al. 2011), echinoderms and decapods (O'Hara & Poore 2000) as well as some algae (Phillips 2001). At local scales, polychaete species composition is influenced by a range of abiotic factors such as food availability (e.g. Snelgrove & Butman 1995, Haedrich et al. 2008), sediment type (Etter & Grassle 1992), habitat complexity (Serrano & Preciado 2007), salinity (Stephenson et al. 1979) and environmental disturbances (Gray 1997). However, these factors influence distributions of marine species at local habitat scales rather than biogeographic scales. Sea temperature, by contrast, influences both local and global distributions of marine species due to its pervading effects on individual growth, reproduction and physiology, as well as the limits of species geographic distributions. Of all the potential environmental variables that may affect the latitudinal distribution of the animals (Fig. 2), sea surface temperature is the only one that is relatively symmetrical with latitude, and is possibly the primary factor shaping the bimodal pattern in polychaete species richness, whether due to ecological, environmental and/or evolutionary factors.

Further, polychaete species number tends to decrease with depth (Fig. 2), supporting the findings of Carvalho et al. (2013) and Gunton et al. (2015) for polychaetes, and of Costello & Chaudhary (2017) for marine species in general. Poor food supply in the deep-sea environment (we define 'deep-sea environment' as the pelagic and benthic zones below 200 m), which results in low environmental disturbance, growth and competitive displacement rates, may be

an explanation (Cosson-Sarradin et al. 1998). Habitat homogeneity and lower temperatures have also been linked to lower species richness in the deep sea compared to continental shelves (Costello & Chaudhary 2017). We also note that deep-sea species are in general poorly documented (C. R. Smith et al. unpubl. data [www.soest.hawaii.edu/oceanography/mincks/publications/Smith\\_et\\_al\\_Abyssal\\_biogeography\\_synthesis.pdf](http://www.soest.hawaii.edu/oceanography/mincks/publications/Smith_et_al_Abyssal_biogeography_synthesis.pdf)). In many parts of the world's oceans, as our data indicated, no deep-sea species have even been reported. Information gaps in global polychaete diversity can therefore be filled by further targeting collections in this data-poor habitat, as well as other habitats with high marine species richness such as coral reef ecosystems. More researchers and research institutions also need to make their datasets publicly available, ideally including data of published literature, so that other scientists can make use of them to better study the distribution of marine species (e.g. Costello 2009, Costello et al. 2013). More detailed morphological and molecular studies are also likely to reveal a large increase in polychaete diversity not only in poorly-studied areas, but also in well-studied areas. For example, Lavesque et al. (2017) identified a large intertidal polychaete as a new *Marphysa* species from the *M. sanguinea* complex collected from a well-studied area, i.e. Bay of Biscay, Northeast Atlantic. Indeed, when the data gaps from poorly-sampled geographic areas are filled, and datasets are made fully available as we found by compiling data for Indonesia, and more detailed taxonomic studies are conducted, it may provide new insights into the latitudinal gradients and biogeographic regions recognized here.

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