

# Global biogeography of marine amphipod crustaceans: latitude, regionalization, and beta diversity

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**ABSTRACT:** Studying the biogeography of amphipod crustaceans is of interest because they play an important role at lower trophic levels in ecosystems. Because they lack a planktonic larval stage, it has been hypothesized that marine benthic amphipod crustaceans may have short dispersal distances, high endemism, and spatial turnover in species composition, and consequently high global species richness. In this study, we examined over 400 000 distribution records of 4876 amphipod species, and identified 12 regions of endemism. The number and percent of endemic species peaked at 30°–35° S and coincided with 3 of these regions of high endemism: Australia, New Zealand, and southern Africa. Pelagic species of marine amphipod crustaceans were more cosmopolitan than benthic species. The latitudinal patterns of richness (alpha, gamma, and ES50) and species turnover were at least bimodal. Most occurrence records and greater alpha and gamma richness were in mid-latitudes, reflecting sampling bias. Both ES50 and beta diversity had similar richness in the tropics, mid-latitudes, and on the Antarctic shelf around 70° S. These 2 indices exhibited a sharp dip in the deep Southern Ocean at 55° S. ES50 peaked at 30°–35° S and a small dip was apparent near the equator at 5°–10° N. Beta diversity was driven mostly by turnover rather than nestedness. These findings support the need for conservation in each realm of species endemism—and for amphipods, particularly in Antarctica and the coastal mid-latitudes (30°–35° S) of the Southern Hemisphere.

**KEY WORDS:** Endemism · Latitudinal gradients · Conservation · Species richness · Species turnover

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## 1. INTRODUCTION

Biogeographic information can inform how to prioritize conservation and detect environmental change (Spellerberg & Sawyer 1999, Heads 2015, Lomolino et al. 2017). The biogeography of amphipod crustaceans is of interest because these organisms play a crucial role in ecosystems as a link between lower and higher trophic levels, and between benthic and pelagic communities (Michel et al. 2016, Griffiths et al. 2017). It has been generally believed that species diversity decreases with (higher) latitude and that

equatorial regions have the most species (Hillebrand 2004). However, recent literature reviews and data analysis of 65 000 marine species (Chaudhary et al. 2017), razor clams (Saedi et al. 2017), planktonic foraminifera (Brayard et al. 2005), and amphipod crustaceans (Chaudhary et al. 2016) found a bimodal latitudinal gradient with reduced species richness around the equator. While Menegotto & Rangel (2018) argued that this pattern was due to insufficient sampling near the equator, Chaudhary et al. (2017) used rarefaction indices of diversity to adjust for sampling effort, and still found the pattern.

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The geographic patterns of species endemism indicate how evolutionary history has led to the present patterns of species richness. At a global scale, 30 marine biogeographic realms have been mapped based on the distribution of 65 000 species (Costello et al. 2017). However, each taxon can have distinct patterns of distribution, diversity, and evolutionary history (Briggs & Bowen 2012, Watling et al. 2013). Most amphipod crustaceans are benthic (97% of 9980 valid species) and all lack planktonic larvae (Barnard & Karaman 1991, Arfianti et al. 2018). It has been suggested that these species may have small distribution ranges, high endemism, and show a robust biogeographic pattern (Myers & Lowry 2009). Their patterns of endemism may thus support, modify, and/or subdivide biogeography based on other taxa. If benthic amphipods have greater endemism than other taxa, then their regions of endemism may nest within those of other taxa, such as in the realms proposed by Costello et al. (2017). Myers & Lowry (2009) hypothesized that due to the Gondwanaland fragmentation 150 million years ago (Ma), amphipods will have distinct regions of endemism in Madagascar, India, Australia, New Caledonia, and New Zealand. However, there have been no global-scale analyses of marine amphipod biogeography to place this in context.

There are 3 main indices of species richness used in biogeography; alpha, gamma, and beta diversity. Alpha diversity is the number of species at a local scale, and it is strongly affected by sampling effort. Gamma, the regional scale diversity index, is less sensitive to sampling bias because it accounts for overlap in species composition between adjacent cells (Chaudhary et al. 2017). The amount of turnover in species composition between samples (beta diversity) helps explain the mechanisms that maintain these 2 indices (Kraft et al. 2011, McClain et al. 2012). Thus, biogeographic analyses should report all 3 diversity measures and consider sampling effort. In this paper, we studied marine amphipod biogeography by analyzing regions of endemism and latitudinal gradients for these 3 measures of diversity.

## 2. MATERIALS AND METHODS

### 2.1. Data source and cleaning process

Data on the geographic distribution of amphipods were obtained from the Ocean Biogeographic Information System (OBIS 2019) and the Global Biodiversity Information Facility (GBIF 2019). We checked the

suitability of the data using the ‘SpeciesGeoCoder’ package (Töpel et al. 2017) in R v.3.4.4 (R Core Team 2016), removing data with missing values and non-numeric values in the coordinates. Although Indonesia is at the centre of the world’s most biologically diverse marine region, i.e. the Coral Triangle (Allen 2008, Asaad et al. 2018), only a few occurrence data of amphipods from Indonesian waters were available in OBIS and GBIF. Thus, we added additional data of amphipod occurrences in Indonesian waters from published literature, namely Pirlot (1933, 1934, 1936, 1938), Laubitz (1991), Ortiz & Lalana (1997, 1999), and Arfianti & Wongkamhaeng (2017). Where publications lacked geographic coordinates (i.e. longitude and latitude), we placed the occurrences in the centre of the indicated sea, bay, or strait that had been sampled. All records then were combined into a single data set. We excluded any duplicated records and fossil data. We verified taxonomic names against the World Register of Marine Species (WoRMS) (Horton et al. 2019). All occurrence records at the subspecies level, synonyms, and misspellings were corrected to the valid species name and included. We removed data that were mapped to land using the clip feature in ArcGIS v.10.3 (ESRI). After this process, we had a data set consisting of 428 053 occurrences for 4876 species (Table S1 in the Supplement at [www.int-res.com/articles/suppl/m638p083\\_supp.pdf](http://www.int-res.com/articles/suppl/m638p083_supp.pdf)).

### 2.2. Species richness

Alpha species richness was calculated as the mean and 1 SE of species occurrences in each 5° latitude–longitude cell for each 5° latitudinal band. Gamma species richness was the total number of species in each 5° latitudinal band. Both alpha and gamma (to a lesser extent) richness are biased by sampling effort. Thus, we calculated the expected number of species (ES) among 50 random, repeatedly sampled samples (ES50) to standardize the data and account for sampling effort (Gotelli & Colwell 2011), using the ‘vegan’ package (Oksanen et al. 2013) based on Hurlbert’s (1971) formulation, and the standard errors based on Heck et al. (1975).

### 2.3. Endemism analysis

Pelagic amphipods were excluded (Table S2) from the biogeographic analysis because initial analysis showed they were relatively cosmopolitan and sometimes abundant. Thus, they could bias biogeographic

analysis into grouping often distant cells into the same group. After we removed pelagic species, we had 400 608 occurrences of benthic species. Introduced species of amphipods were removed from the data set based on Ahyong et al. (2019), because initial analyses found they significantly confused biogeographic analyses.

We uploaded the data set to Infomap Bioregions (Edler et al. 2017) and used a minimum latitude–longitude cell size of 4° to get a reasonable balance between sample coverage and spatial resolution. Following initial analyses, we set 100 records for the minimum cell capacity to avoid distortions in the analyses due to small sample sizes. The analysis first mapped geographic areas according to the similarity of their species composition. It also identified which species were common and characteristic of each group of geographic cells (Edler et al. 2017), which we termed biogeographic regions. We termed species with more than one occurrence record but present sequentially in less than five 5° longitude–latitude cells and less than five 5° latitudinal bands as endemic; this classified 1920 species as endemic (Table S3). The proportion of endemism was the proportion of total species listed in Table S3 of gamma richness in each 5° latitudinal band.

#### 2.4. Beta diversity

Beta diversity was studied using 3 components: Sorensen (the overall beta diversity), Simpson (species turnover independent of species richness), and nestedness (Baselga et al. 2007, 2012). Each was calculated in 100 random samples of eleven 5 × 5° cells within 5° latitudinal bands consecutive across longitude to determine a value for each band. Eleven was the minimum number of 5 × 5° cells with occurrence data. Any 5° latitudinal bands with less than 50 species were excluded from the analysis. The turnover and nestedness components were separated to reveal the contribution of each component to overall beta diversity (Baselga et al. 2007, Castro-Insua et al. 2016). All calculations were performed using the 'betapart' package in R (Baselga et al. 2018).

We used the 'strucchange' package in R to compute the number and position of breaks for the optimal partition of latitudinal gradients (Zeileis et al. 2015). The breakpoints of ES50, Sorensen dissimilarity, Simpson dissimilarity, and nestedness were modeled by performing piecewise regressions using the 'segmented' package in R (Muggeo 2008).

### 3. RESULTS

The global map of 4876 marine amphipod species shows that these organisms are distributed worldwide in coastal areas (Fig. 1). The 5 species with most occurrence records were *Monoporeia affinis*, *Corophium volutator*, *Ampelisca brevicornis*, *Bathyporeia elegans*, and *A. tenuicornis*, with 18 217–7400 occurrences, respectively (Table 1). The most widespread species globally were *Themisto gaudichaudii*, *Phronima sedentaria*, *Primno macropa*, *T. abyssorum*, and *T. libellula* from the suborder Hyperiidea, all of which are pelagic species (Table S2). They were found in at least 10 of the 5° latitudinal bands and more than 50 of the 5° cells (Table S2). Many species were rare, with 41 % of benthic and 20 % of pelagic species occurring in only one 5° cell (Fig. 2).

#### 3.1. Species richness patterns with latitude

The number of sample records peaked at 50° N, with 139 812 occurrence records (Fig. 3a). Alpha and gamma richness were at least bimodal, with a dip around the equator. Peaks for alpha richness were found at 70° N and 30° S, with 37 and 34 species, respectively. For gamma richness, peaks were evident at 45° N and 30° S, with 671 and 859 species, respectively (Fig. 3b,c). The observed alpha richness and the number of sample records per 5 × 5° longitude–latitude cell were highly correlated (Spearman rho = 0.89, p < 0.05; Fig. S1). A high correlation was also found between gamma richness and the number of sample records per 5° latitudinal band (Spearman rho = 0.85, p < 0.05; Fig. S1). These correlations indicated that alpha and gamma richness were significantly influenced by sampling effort. In contrast, ES50 and the number of sample records were not correlated (Spearman rho = -0.03, p > 0.05; Fig. S1). Piecewise regressions of ES50 showed 3 latitudinal breakpoints: a sharp dip at 55° S, and peaks at 35° S and 70° N. This increased model fit (r<sup>2</sup> = 0.49) compared to a linear regression (r<sup>2</sup> = 0.003) (Fig. S2). A high value of ES50 was still found around 30° S, as with alpha and gamma richness. A distinct dip was apparent at 55° S, and a small dip near the equator at 5°–10° N (Fig. 3d).

#### 3.2. Beta diversity

The low latitudes around the equator had higher beta diversity, with a peak at 10° N (Fig. 4). Latitudes around Antarctica, 70°–75° S, also showed high beta

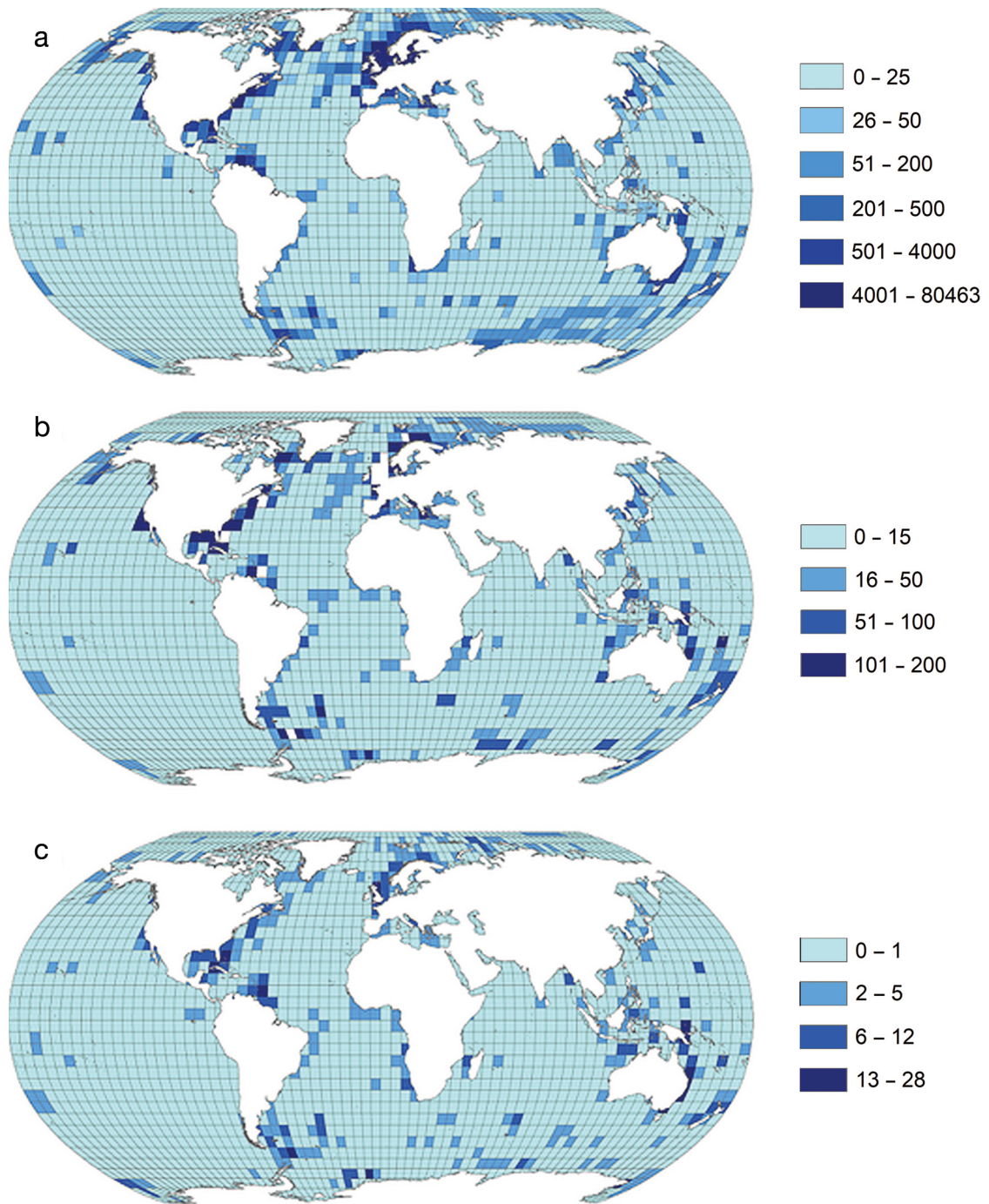


Fig. 1. Global map of marine amphipod crustacean (a) occurrences, (b) species richness ( $\gamma$ ), and (c) expected number of species among 50 random samples (ES50) in 5° cells. White areas: land

diversity. The lowest beta diversity was found at 55°S and 75°N. The partition of this total beta diversity into turnover and nestedness components showed that spatial turnover (Simpson index) contributed most to beta diversity (Simpson = 0.84, nestedness component = 0.13). Thus, the beta diversity

pattern was mostly driven by species replacement rather than nestedness (Fig. 4).

Piecewise regressions of the Sorensen index revealed 3 latitudinal breakpoints: a dip at 55°S, and peaks at 35°S and 35°N (Figs. 4 & S3). This piecewise regression ( $r^2 = 0.87$ ) increased model fit com-

Table 1. The top 20 marine amphipod species with the most occurrence records

Species	No. of records
<i>Monoporeia affinis</i>	18217
<i>Corophium volutator</i>	14817
<i>Ampelisca brevicornis</i>	10440
<i>Bathyporeia elegans</i>	9789
<i>Ampelisca tenuicornis</i>	7400
<i>Ampelisca spinipes</i>	6776
<i>Perioculodes longimanus</i>	6353
<i>Harpinia antennaria</i>	6344
<i>Bathyporeia guilliamsoniana</i>	6272
<i>Urothoe elegans</i>	6140
<i>Urothoe poseidonis</i>	6019
<i>Themisto gaudichaudii</i>	5673
<i>Microdeutopus gryllotalpa</i>	5338
<i>Pontoporeia femorata</i>	4906
<i>Pariambus typicus</i>	4716
<i>Phtisica marina</i>	4210
<i>Themisto abyssorum</i>	4140
<i>Nototropis vedlomensis</i>	3919
<i>Unciola irrorata</i>	3787
<i>Othomaera othonis</i>	3777

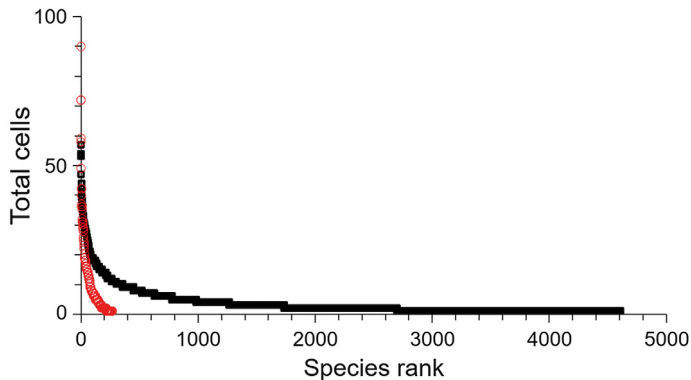


Fig. 2. Occurrence of pelagic (red circles) and benthic (black squares) species in 5° cells. Species are ranked from most to least number of cells present, indicating the far greater number of benthic than pelagic species, and that pelagic species generally occur in more cells

pared to the linear regression ( $r^2 = 0.06$ ). One breakpoint in the Simpson index was found at 10° S, which increased the model fit from  $r^2 = 0.001$  to  $r^2 = 0.83$ . Piecewise regressions of the nestedness component ( $r^2 = 0.71$ ) increased model fit compared to the linear regression ( $r^2 = 0.06$ ), with 2 latitudinal breakpoints at 2° S and 20° N (Fig. S3). Thus, species turnover was highest in the tropics from 35° S to 35° N, and on the Antarctic continental shelf around 70–75° S.

### 3.3. Regions of endemism

We found 12 biogeographic regions for marine benthic amphipod crustaceans (Figs. 5 & S4). All

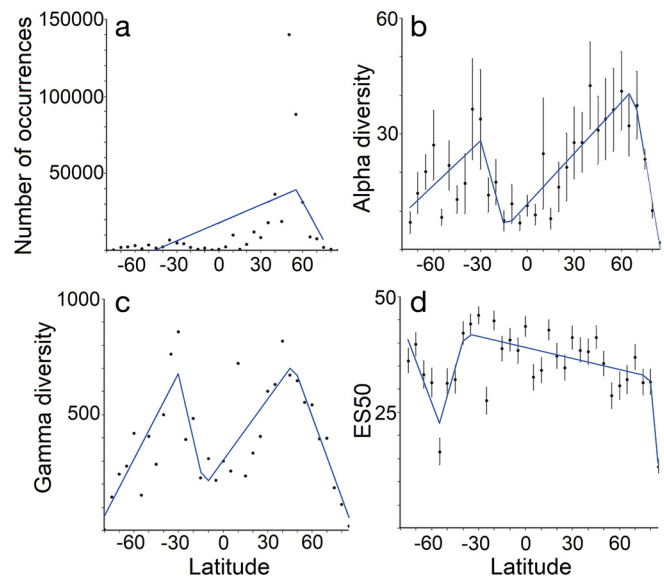


Fig. 3. Latitudinal species richness of marine amphipod crustaceans for (a) total number of records in 5° latitudinal bands, (b) alpha richness  $\pm$  SE, (c) gamma richness, and (d) the expected number of species among 50 individuals (ES50  $\pm$  SE). Lines: piecewise regressions

regions aligned with realms defined in Costello et al. (2017), although there was insufficient data of amphipod occurrences, and thus 9 realms (South-east Pacific; Gulf of California; Gulfs of Aqaba, Aden, Suez, Red Sea; Mid-South Tropical Pacific; Offshore Indian Ocean; Offshore West Pacific; Offshore mid-East Pacific; Gulf of Guinea; and Chile) were not detected in the present study. The highest number of records was in Europe while the 'Laccadive Sea and Bay of Bengal' had the fewest records at 255 (Table 2). The highest number of species was in Australia (region 4) with 1016 species, and the lowest number was in the 'South and East China Sea' with 71 species. The common, characterizing, and endemic species for each region are listed in Tables 2 & S4.

Almost half of the amphipod species were endemic (Table S3). The latitudinal pattern for the number of endemic species and the proportion of all species that were endemic in 5° latitudinal bands showed that latitudes between 30° and 40° S had a high number and proportion of endemic species. Both patterns had a concordant peak at 35° S. In the Northern Hemisphere, latitudes 30°–40° N showed a high proportion and number of endemic species (Fig. 6). The number of endemic species, and the proportion of species that were endemic, were highly correlated (Spearman rho = 0.87,  $p < 0.05$ ; Fig. S6).

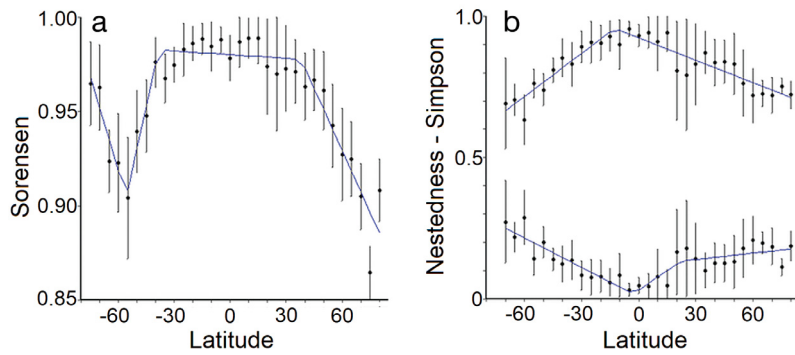


Fig. 4. Latitudinal patterns of beta diversity ( $\pm$ SE) for (a) Sorensen total dissimilarity, (b) Simpson dissimilarity (above) and nestedness component (below) in  $5^\circ$  latitudinal bands. Lines: piecewise regressions

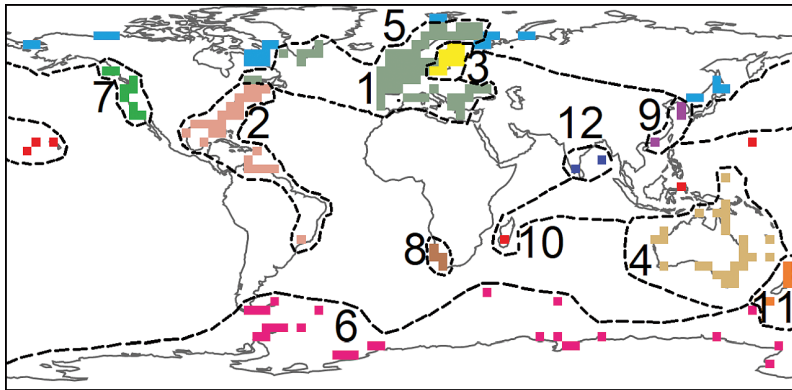


Fig. 5. Biogeographic regions based on benthic marine amphipod crustaceans, showing regions overlaid on the original map (see Fig. S4). For details of characterizing and common species of each region, see Tables 2 & S4

#### 4. DISCUSSION

The 5 species of marine amphipods that we found with the most occurrence records are typically common and abundant in seabed sediments (e.g. Meadows & Reid 1966, Bonsdorff 1992, d'Udekem d'Acoz 2004, Sundelin et al. 2008). Most samples of amphipods were from the continental shelves (Fig. 1a), reflecting the ease of sampling shallow depths near the coast. To account for sampling bias, we calculated ES50 and found that richness was still highest in the shallow waters near the continents (Fig. 1c).

##### 4.1. Benthic and pelagic amphipod richness

It has been proposed that pelagic species, both microscopic plankton and larger nekton, are more widespread than benthic species because of the mobility and relative homogeneity of their habitat

(Costello et al. 2017). In contrast to these groups, macrobenthos is far richer in species, reflecting the heterogeneity of seabed habitats and risk of predation when dispersing. However, pelagic amphipods are of similar size to their benthic relatives. They may avoid predation in the open pelagic waters by being relatively transparent, living within gelatinous zooplankton, having good eyesight, and being agile swimmers. Only 3% of amphipod species are pelagic (Arfianti et al. 2018). As predicted, we found that benthic species were less widespread than pelagic species (Fig. 2). While 20% of pelagic species only occurred in one  $5^\circ$  cell, 41% of benthic species did. The top 5 most widespread species are all pelagic (Table S2) and are sampled regularly in net-based oceanographic sampling programs (e.g. Vinogradov et al. 1996, Zeidler & De Broyer 2009). That there are far fewer pelagic than benthic amphipod species thus supports the hypothesis that higher gene flow in more widespread pelagic species limits speciation (Costello & Chaudhary 2017).

##### 4.2. Biogeographic regions and endemism

A total of 12 biogeographic regions were found for marine benthic amphipod crustaceans, and they matched realms defined by Costello et al. (2017). The fact that this study only employed benthic amphipod crustaceans but revealed the same realms as in Costello et al. (2017) indicates that benthic amphipods are representative species to map marine biogeography based on endemism (i.e. realms). However, 9 other realms were not observed due to gaps in amphipod distribution records. More data may reveal additional biogeographic regions in South America, central East Pacific, Africa, the Red Sea, and the Mediterranean.

The latitudes between  $30^\circ$ S and  $40^\circ$ S had the highest number and proportion of endemic species, peaking at  $30^\circ$ S (Fig. 6). These latitudes are concordant with 3 biogeographic regions, i.e. southern Africa, Australia, and New Zealand. In total, 80%

Table 2. Comparison of the 12 biogeographic regions of benthic marine amphipod crustaceans identified in this study with the realms based on all marine taxa (Costello et al. 2017). Numbers in parentheses correspond to the realms defined in Costello et al. (2017). N: north; NW: north-west; NE: north-east; S: south. Dominant species: those with the highest records; characterizing species: most indicative for each region as identified by Infomap Bioregions software (see Table S4)

Regions for Amphipoda	Realms	Records	Species	Cells	Dominant species	Characterizing species
1	Black Sea, NE Atlantic, Mediterranean Sea, Offshore and NW North Atlantic (in part)	221870	770	61	<i>Ampelisca brevicornis</i>	<i>Apherusa clevei</i> , <i>Bathyporeia tenuipes</i> , <i>Corophium arenarium</i> , <i>Maerella tenuimana</i> , <i>Guernea (Guernea) coalita</i> , <i>Gammarus crinicornis</i> , <i>Lepidopereum longicornis</i> , <i>Apherusa ovalipes</i> , <i>Bathyporeia nana</i> , <i>Iphimedia nexa</i>
2	Caribbean, Gulf of Mexico and Offshore S Atlantic Ocean (in part)	65849	917	26	<i>Unciola irrorata</i>	<i>Eudevenopus honduramus</i> , <i>Acanthohauistorius millsii</i> , <i>Leptocheirus plumulosus</i> , <i>Casco bigelowi</i> , <i>Idunella carinata</i> , <i>Metopella angusta</i> , <i>Chevalia carpenteri</i> , <i>Meximaera diffidentia</i> , <i>Netamelita brocha</i> , <i>Ampelisca parapacifica</i>
3	Inner Baltic Sea	31042	77	10	<i>Monoporeia affinis</i>	<i>Pallaseopsis quadrispinosa</i>
4	Tasman Sea, Coral Sea, S Australia and Indo-Pacific seas and Indian Ocean (in part)	13686	1016	26	<i>Ampelisca euroa</i>	<i>Byblis mildura</i> , <i>Cephalophoxoides kukathus</i> , <i>Podocerus dentatus</i> , <i>Birubius maldus</i> , <i>Hippomedon rodenicki</i> , <i>Birubius maamus</i> , <i>Nagada uwedoae</i> , <i>Birubius jirrandus</i> , <i>Limnoporeia ungamale</i> , <i>Charcotia dempseyae</i>
5	Norwegian Sea, Arctic seas, N Pacific (in part), N American boreal	8653	338	26	<i>Rhachotropis aculeata</i>	<i>Byblis brevirama</i> , <i>Metopa longirama</i> , <i>Orchomene minor</i> , <i>Byblis frigidus</i> , <i>Byblis robustus</i> , <i>Ampithoe tarasovi</i> , <i>Arrhinopsis longicornis</i> , <i>Lepidopereum eoum</i> , <i>Harpinia bidentata</i> , <i>Ischyrocerus nanooides</i>
6	Southern Ocean	6693	653	27	<i>Eusirus perdentatus</i>	<i>Amphilochella simplicarpa</i> , <i>Podocerus danae</i> , <i>Kerguelenia antithorealis</i> , <i>Eusiroides aberrantis</i> , <i>Gondogeneia macrodon</i> , <i>Tonocote introflexidus</i> , <i>Anonychocheirus richardsoni</i> , <i>Stomacantion pepinii</i> , <i>Liljeborgia pseudomacronyx</i> , <i>Lepidopereum infissum</i>
7	N Pacific (in part)	7177	413	9	<i>Ampelisca abdita</i>	<i>Americorophium salmonis</i> , <i>Rhepoxynius daboius</i> , <i>Caprella californica</i> , <i>Foxiphallus obtusidens</i> , <i>Mayerella banksia</i> , <i>Pleusymates subglaber</i> , <i>Cheirimedeia zotea</i> , <i>Foxiphallus similis</i> , <i>Amphideutopus oculatus</i> , <i>Metopa cistella</i>
8	Southern Africa	3134	207	4	<i>Ampelisca anomala</i>	<i>Idunella lindae</i> , <i>Periculodes pallidus</i> , <i>Indischnopus capensis</i> , <i>Hippomedon normalis</i> , <i>Leucothoe euryonyx</i> , <i>Ischyrocerus carinatus</i> , <i>Indischnopus herdmani</i> , <i>Zygomaera emarginata</i> , <i>Urothoe pinnata</i> , <i>Unciolella foveolata</i>
9	South and East China Sea	1128	71	3	<i>Ampelisca brevicornis</i>	<i>Urothoe convexa</i> , <i>Melita longidactyla</i> , <i>Mandibulophoxus hongae</i> , <i>Podocerus hoonsooi</i> , <i>Pholis japonica</i> , <i>Gammaropsis japonica</i> , <i>Eoahustorius spinigerus</i> , <i>Guernea (Prinassus) terelamina</i> , <i>Sunamphitoe chujaensis</i> , <i>Protohyale (Boreohyale) magnaocularis</i>
10	Hawaii, Indo-Pacific seas and Indian Ocean	1025	202	6	<i>Leucothoe hyhelia</i> , <i>Erichthonius brasiliensis</i>	<i>Globosolenbos leापakahi</i> , <i>Wandelia orghidani</i> , <i>Ventojassa ventosa</i> , <i>Leucothoe lihue</i> , <i>Kanaloa manoa</i> , <i>Paranamixis ledoyeri</i> , <i>Azotostoma bunakenensis</i> , <i>Ampithoe alluaudi</i> , <i>Tepidopleustes honomu</i> , <i>Ischyrocerus kapu</i>
11	New Zealand	890	190	5	<i>Ampelisca chiltoni</i>	<i>Otagia neozelanicum</i> , <i>Amphorites hurleyi</i> , <i>Tagua aporema</i> , <i>Melita awa</i> , <i>Paradexamine houtete</i> , <i>Stenothoe moe</i> , <i>Talhape karori</i> , <i>Podocerus karu</i> , <i>Oedicerina loerzae</i> , <i>Pseudopleonexes evensis</i>
12	Laccadive Sea and Bay of Bengal	255	108	2	<i>Ampelisca scabripes</i>	<i>Ampelisca scabripes</i> , <i>Socarnella bonnierii</i> , <i>Mallacoota sokotrae</i> , <i>Amphilochus schubarti</i> , <i>Abdia latipalpus</i> , <i>Anonyx indicus</i> , <i>Grandierella macronyx</i> , <i>Talorchestia gracilis</i> , <i>Periculodes megapleon</i> , <i>Parandantexis spinescens</i>

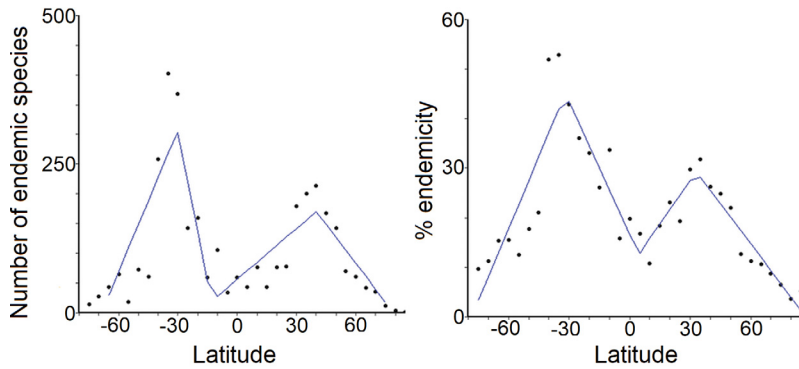


Fig. 6. Latitudinal patterns of (a) number of endemic species and (b) proportion of species (gamma richness) that were endemic, in 5° latitudinal bands. Lines: piecewise regressions

of the southern temperate region species in Australia are believed to be endemic (Condie & Harris 2006). The processes which have generated the high numbers of endemic species in Australia, including 7 endemic genera of amphipods (Myers & Lowry 2009), can be attributed to the continent's long isolation, i.e. its separation from Gondwanaland at least 150 Ma and then from Antarctica about 53 Ma (Veevers & McElhinny 1976, Poore 2001).

New Zealand is a highly isolated continental landmass in the south-western Pacific Ocean. It was part of Gondwana (Cowie & Holland 2006) but separated about 80 Ma and reached its present distance from Australia around 50–60 Ma (Cooper & Millener 1993, McLoughlin 2001). Thus, only a few species can have arrived in New Zealand in recent times, apart from human introductions. Amongst its amphipod fauna, New Zealand's isolation is reflected in the endemic genera *Neocyproidea* and *Paraleptamphopus* and endemic family Rakiroidae. In addition, 15 of 17 species of Phoxocephalidae described from New Zealand are endemic (Myers & Lowry 2009, Webber et al. 2010). Of the 365 New Zealand marine and estuarine amphipods, 55% (194 species and 35 genera) are endemic (Webber et al. 2010). Similarly, 51% of marine species are endemic to New Zealand, which is the highest percent marine endemism of any country (Costello et al. 2010). South Africa also has a high number of endemic marine species: 28–30% of all 12 000 marine species, including 33% of 454 amphipod species (Costello et al. 2010, Griffiths et al. 2010).

The smaller peak of endemism evident at 40°N overlapped with the Mediterranean Sea, an area known to have high amphipod diversity (e.g. Ruffo

1998, 2010, Dauvin et al. 2013). Over one-quarter of the Mediterranean marine biota are endemic (Fredj et al. 1992, Coll et al. 2010) and 46% of Mediterranean amphipod species are considered endemic (Bellan-Santini 1990). This high endemism may be due to the Messinian Crisis, a geological event during which the sea largely, but not entirely, dried out following the closure of the Strait of Gibraltar. Thus, a relict but isolated Tethyan amphipod fauna survived (Bellan-Santini 1990).

#### 4.3. Latitudinal patterns of species richness and beta diversity

The latitudinal pattern of beta diversity (Sorensen index) was like that of ES50 and was mostly driven by turnover in species composition (Simpson dissimilarity index) (Figs. 3d & 4b). High turnover in the equatorial regions could be explained by the high variability of habitats there, such as coral reef and seagrass ecosystems and a range of other habitats (Shurin 2007, Costello et al. 2017, Asaad et al. 2018, Chaudhary 2019). In addition, land masses in this region are a barrier for marine species' dispersal (Chaudhary 2019). In contrast, the smaller area and lack of such barriers in the Arctic and Southern oceans result in higher connectivity and less endemism within their latitudes. Hence, there was only one biogeographic region in each of the Arctic-Boreal and Southern Ocean (Fig. 5), but 10 regions in the tropics to temperate latitudes.

That the peak of species richness, as alpha and gamma diversity, number and percent of endemic species, and ES50, in the southern hemisphere was around 30°–35°S (Fig. 3) contrasts with findings for razor clams (Saeedi et al. 2017) and fossil and marine species (Chaudhary et al. 2016, 2017). These studies found the peak in diversity was in the Northern Hemisphere with respect to gamma diversity for razor clams, and alpha diversity for fossil and marine species. However, Chaudhary et al. (2017) found gamma diversity and ES50 to have equal peaks in the Northern and Southern Hemispheres. That the number of sample records in the Southern Hemisphere was only one-tenth of the number in the Northern Hemisphere confirms that the peak in richness around 30°–35°S was not due to high sampling effort, but



rather due to the patterns of endemism discussed previously.

The dip near the equator at 5°–10° N was observed in alpha, gamma, and ES50, as found in the recent syntheses of 65 000 species and 50 000 fossil marine species by Chaudhary et al. (2016, 2017), although our dip is much smaller and not as obvious. This finding supports the non-unimodality hypothesis in the richness patterns of marine species (Chaudhary et al. 2016, 2017), which is highly correlated with sea surface temperature (Chaudhary 2019). This dip at the equator appears to be due to high temperatures because it has become more prominent in recent decades (Chaudhary 2019), as predicted by climate warming models (Poloczanska et al. 2013).

A sharp dip of species richness in ES50 was apparent at 55° S in the Southern Ocean. Antarctica is surrounded by 4000–6000 m depths, and the depth of the break between the shelf and the slope in the Southern Ocean is at least double the depth of the shelf break on other continents (Knox 2006, Harris et al. 2014). This may form a biogeographic barrier for benthic species. There were sample records for benthic and pelagic amphipod species from 45°–75° S (Fig. S5), and ES50 was low from 45°–70° S, with lowest species richness at 55° S. Another study on the Southern Ocean deep-sea biodiversity reported similar findings; i.e. the Southern Polar Front around 52° S had a low diversity and abundance of many macrofauna taxa including Amphipoda (Brandt & Ebbe 2009). Although an expedition at 748–6348 m depth in the Weddell Sea (70° S) and adjacent areas did not report any amphipod species despite the discovery of 674 isopod species (of which 585 were new to science; Brandt et al. 2007a), this was because the amphipod samples (except for the scavengers caught by baited traps) had not been identified (A. Brandt pers. comm). Thus, whether the number of amphipod species at 55° S is as exceptionally low as our results suggest merits confirmation. Nevertheless, the deep-sea amphipod assemblage at 55° S is distinct from that on the Antarctic shelf as shown by the indices of species turnover (beta diversity) (Fig. 5).

Species richness on the Antarctic continental shelf between 70 and 80° S was similar to latitudes north of 45° S. Clarke (2008) also found that the Antarctic shelf has comparable benthic (including Amphipoda) diversity to some tropical and temperate shelves. This similar richness contrasts with the hypothesis that polar regions have low diversity due to the harshness of the environment (Willig et al. 2003, Payer et al. 2013). That the Arctic is species-poor compared to Antarctica seems to be due to the long

isolation and high endemism of Antarctica since the breakup of Gondwana (Brandt et al. 2007b, Saucède et al. 2014).

Other studies on amphipods in the Southern Ocean have reported the same pattern as we found, i.e. that the shelf area between 0–1000 m had more species than the area deeper than 1000 m (De Broyer et al. 2007, De Broyer & Jażdżewska 2014). These findings contradict the hypothesis that the deep sea has a high richness (Grassle 1989, Snelgrove 1999, Rex & Etter 2010). Even though the deep sea comprises more area, it is cold (<4°C) with low productivity, and contains a more limited number of habitats compared to shallow waters with high primary productivity and complex biogenic habitats like coral reefs, kelp forests, seagrass meadows, shell beds, and other epifaunal assemblages that provide 3-dimensional habitat for many species (Costello & Breyer 2017, Costello & Chaudhary 2017, Havermans & Smetacek 2018). The relative homogeneity of deep-sea environments, varying little in temperate, salinity, and habitat, means that the same deep-sea species may inhabit large geographic areas and depth ranges (Costello et al. 2018).

## 5. CONCLUSIONS

We found that pelagic amphipod species were more widespread and far less species-rich than benthic species. This reflects the greater homogeneity of pelagic than benthic habitats, and thus likely higher gene flow. Similarly, greater homogeneity in deep-sea than shelf depth zones may partly explain the greater number of species on the Antarctic continental shelf compared to the deep-sea Southern Ocean, in addition to the high Antarctic endemism.

Although there were 10 times more sample records from the Northern Hemisphere, species richness peaked in the Southern Hemisphere and thus was not due to sampling effort. These peaks were concordant with the high number and proportion of endemic species, and aligned with 3 regions of high endemism: Australia, southern Africa, and New Zealand. Beta diversity was lower in higher latitudes, probably due to greater connectivity and gene flow of species across a smaller total area of longitudes than in the low latitudes, and fewer land barriers. The 12 regions of endemism found for amphipods matched well with previously proposed marine biogeographic realms. Thus, amphipods do not appear to have a more complex global biogeography than other marine taxa due to their lack of planktonic life

stage. Their latitudinal gradients are broadly similar to other marine taxa but have higher richness in temperature Southern Hemisphere latitudes and Antarctica, reflecting regional endemisms. Conservation planning should note the importance of these regions (realms) of endemism when designing global networks of marine reserves.

Data accessibility. Data underlying this article can be accessed on Figshare (doi:10.17608/k6.auckland.8227784) and used under the Creative Commons Attribution licence (CC BY 1.0).

**Acknowledgements.** Special gratitude goes out to all members of the Oceans of Biodiversity research group (<https://www.oceansofbiodiversity.auckland.ac.nz/>) for stimulating suggestions and encouragement. We thank Dr. Rakhshan Roohi and M. Hafidzt and S. Si (LIPI-Indonesia) for their help in using Geographical Information Systems, Dr. Adrian Castro-Insua and Dr. Chhaya Chaudhary for help with beta diversity, and Sapii S. Kom for assistance with breakpoint analysis. T.A. thanks the New Zealand Ministry of Foreign Affairs and Trade for providing a PhD scholarship through the ASEAN scholarship scheme (NZAS).

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Editorial responsibility: Lisandro Benedetti-Cecchi,  
Pisa, Italy

Submitted: October 7, 2019; Accepted: February 21, 2020  
Proofs received from author(s): March 14, 2020