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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. Due to lacking a planktonic larval stage, it has been hypothesized that marine benthic amphipod crustaceans may have short dispersal distances, high endemicity and spatial turnover in species composition, and consequently high global species richness. Over than 400000 distribution records of 4876 amphipod species were used. Twelve regions of endemicity were identified. The number and percent of species that were endemic peaked at 30° to 35° S and coincided with three of these regions of high endemicity; 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, with a dip at the equator as found for other marine taxa. Most occurrence records and greater alpha and gamma richness were in mid-latitudes reflecting sampling bias. Both ES50 and beta diversity had a similar richness in the tropics, mid-latitudes, and on the Antarctic shelf around 70° S. These two indices had a sharp dip in the deep Southern Ocean at 55° S. The ES50 peaked at 30° to 35° S and a small dip was apparent near the equator at 5° to 10° N. Beta diversity was mostly driven by turnover rather than nestedness. The findings support the need for conservation in each Realm of species endemicity, and for amphipods, particularly in Antarctica and the coastal mid-latitudes (30° to 35° S) of the southern hemisphere.

Keywords: endemicity, latitudinal gradients, conservation, species richness, species turnover.

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 they play a crucial role in ecosystems as a link between lower and higher trophic levels, and benthic-pelagic communities (Michel et al. 2016, Griffiths et al. 2017). It has been generally believed that species diversity decreases with (higher) latitude and that the equator has most species (Hillebrand 2004). However, recent reviews of literature and analysis of data on 65000 marine species (Chaudhary et al. 2017), razor clams (Saeedi 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 the 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.

The geographic patterns of species endemicity 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 65000 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 they may have small distribution ranges, high endemicity, 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 endemicity than other taxa, then their regions of endemicity 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 Ma, amphipods will have

1 distinct regions of endemicity in Madagascar, India, Australia, New Caledonia, and in New

2 Zealand. However, there have been no global scale analyses of marine amphipod biogeography

3 to place this in context.

4   There are three main indices of species richness used in biogeography; alpha, gamma,

5 and beta diversity. Alpha diversity is the number of species at a local scale that is strongly

6 affected by sampling effort. Gamma, the regional scale diversity index is less sensitive to

7 sampling bias because it accounts for overlap in species composition between adjacent cells

8 (Chaudhary et al. 2017). The amount of turnover in species composition between samples (beta

9 diversity) helps explain the mechanisms that maintain these two indices (Kraft et al. 2011,

10 McClain et al. 2012). Thus, biogeographic analyses should report all three diversity measures

11 and consider sampling effort. In this paper, we studied marine amphipod biogeography by

12 analyzing regions of endemicity and latitudinal gradients for these three measures of diversity.

13

14 **2. METHODS**

15 **2.1. Data source and cleaning process**

16 Data on the geographic distribution of amphipods were obtained from the Ocean

17 Biogeographic Information System (OBIS, 2019) and the Global Biodiversity Information

18 Facility (GBIF, 2019). We checked the suitability of the data using the 'speciesgeocodeR'

19 package (Töpel et al. 2017) in R version 3.4.4 (RStudio Team, 2016). This removed data

20 with missing values and non-numeric values in the coordinates. Although Indonesia is at the

21 centre of the world's most biologically diverse marine region, i.e., the Coral Triangle (Allen

22 2008, Asaad et al. 2018), only a few occurrence data of amphipods from Indonesian waters

23 were available in OBIS and GBIF. Thus, we added additional data of amphipod occurrences

24 in Indonesian waters from published literature, namely Pirlot (1933, 1934, 1936, 1938),

25 Laubitz (1991), Arfianti & Wongkamhaeng (2017), and Ortiz & Lalana (1997, 1999). Where

1   publications lacked geographic coordinates (i.e., longitude and latitude), we placed the

2   occurrences in the centre of the indicated sea, bay, or strait that had been sampled. All

3   records then were combined into a single dataset. We excluded any duplicated records and

4   fossil data. We verified taxonomic names against the World Register of Marine Species

5   (WoRMS) (Horton et al. 2019). All occurrence records at the subspecies level, synonyms,

6   and misspellings were corrected to the valid species name and included. We removed data

7   that were mapped to land using the clip feature in 'arcgis 10.3'. After this process, we had

8   428053 occurrences for 4876 species (Table S1).

9

10   **2.2. Species richness**

11   Alpha species richness was calculated as the mean and one standard error (SE) of species

12   occurrences in each 5° latitude-longitude cell for each 5° latitudinal band. Gamma species

13   richness was the total number of species in each 5° latitudinal band. Both alpha and gamma (to

14   a lesser extent) richness are biased by sampling effort. Thus, we calculated the expected

15   number of species (ES) among 50 random, repeatedly sampled, samples (ES50) to standardize

16   the data and account for sampling effort (Gotelli & Colwell 2011) using the 'vegan' package

17   (Oksanen et al. 2013) based on Hurlbert's (1971) formulation, and the standard errors on Heck

18   et al. (1975).

19

20   **2.3. Endemicity analysis**

21   Pelagic amphipods were excluded (Table S2) from the biogeographic analysis because initial

22   analysis showed they were relatively cosmopolitan and sometimes abundant. Thus, they could

23   bias biogeographic analysis into grouping often distant cells into the same group. After we

24   removed pelagic species, we had 400608 occurrences of benthic species. Introduced species of

1 amphipods were removed from the dataset based on Ahyong et al. (2019) because initial

2 analyses found they significantly confused biogeographic analyses.

3   We uploaded the dataset to 'infomap bioregions' (Edler et al. 2017) and used a minimum

4 latitude-longitude cell size of 4° to get a reasonable balance between sample coverage and

5 spatial resolution. Following initial analyses, we set 100 records for the minimum cell capacity

6 to avoid distortions in the analyses due to small sample sizes. The analysis first mapped

7 geographic areas according to the similarity of their species composition. It also identified

8 which species were common and characteristic of each group of geographic cells (Edler et al.

9 2017), which we termed biogeographic regions. We termed species with more than one

10 occurrence record but present sequentially in less than five 5° longitude-latitude cells, and less

11 than five 5° latitudinal bands, as endemic. This classified 1920 species as endemic (Table S3).

12 The proportion of endemicity was the proportion of total species listed in Table S3 of gamma

13 richness in each 5° latitudinal band.

14

15 **2.4. Beta diversity**

16 Beta diversity was studied using three components: Sorensen (the overall beta diversity),

17 Simpson (species turnover independent of species richness), and nestedness (Baselga et al.

18 2007, Baselga et al. 2012). Each was calculated in 100 random samples of eleven 5° x 5° cells

19 within 5° latitudinal bands consecutive across longitude to get a value for each band. Eleven

20 was the minimum number of 5° x 5° cells with occurrence data. Five–degree latitudinal bands

21 with less than 50 species were excluded from the analysis. The turnover and nestedness

22 components were separated to reveal the contribution of each component to the overall beta

23 diversity (Baselga et al. 2007, Castro-Insua et al. 2016). All calculations were performed using

24 the 'betapart' package in R (Baselga et al. 2018).

1   We used the 'strucchange' package in R to compute the number and position of breaks

2   for the optimal partition of latitudinal gradients (Zeileis et al. 2015). The breakpoints of ES50,

3   Sorensen dissimilarity, Simpson dissimilarity, and nestedness were modeled by performing

4   piecewise regressions using 'segmented' package in R (Muggeo, 2008).

5

6   **3. RESULTS**

7   The global map of 4876 marine amphipod species shows that they are distributed worldwide

8   in coastal areas (Fig. 1). The five species with most occurrence records were *Monoporeia*

9   *affinis, Corophium volutator, Ampelisca brevicornis, Bathyporeia elegans,* and *A. tenuicornis*

10   with 18217 to 7400 occurrences, respectively (Table 1). The most widespread species globally

11   were *Themisto gaudichaudii*, *Phronima sedentaria*, *Primno macropa*, *T. abyssorum*, and *T.*

12   *libellula* from the suborder Hyperiidea, and all are pelagic species (Table S2). They were

13   found in at least ten of the 5° latitudinal bands and more than 50 of the 5° cells (Table S2).

14   Many species were rare, with 41 % of benthic and 20 % of pelagic species occurring in only

15   one 5°cell (Fig. 2).

16

17   **3.1. Species richness patterns with latitude**

18   The number of sample records peaked at 50° N with 139812 occurrence records (Fig. 3a).

19   Alpha and gamma richness were at least bimodal with a dip around the equator. The peaks for

20   alpha richness were found at 70° N and 30° S with 37 and 34 species, respectively. For gamma

21   richness, the peaks were evident at 45° N and 30° S with 671 and 859 species, respectively

22   (Fig. 3b & c). The observed alpha richness and the number of sample records per 5° x 5°

23   longitude latitude cells were highly correlated (Spearman rho = 0.89, $p < 0.05$, Fig. S1). A high

24   correlation was also found between gamma richness and the number of sample records per 5°

25   latitudinal band (Spearman rho = 0.85, $p < 0.05$, Fig. S1). These correlations indicated that

1 alpha and gamma richness were significantly influenced by sampling effort. In contrast, ES50

2 and the number of sample records were not correlated (Spearman rho = -0.03, p > 0.05, Fig.

3 S1). Piecewise regressions of ES50 showed three latitudinal breakpoints: a sharp dip at 55° S;

4 and peaks at 35° S and 70° N. This increased model fit (r^2 = 0.49) compared to a linear

5 regression (r^2 = 0.003) (Fig. S2). A high value of ES50 was still found around 30° S, as with

6 alpha and gamma richness. A distinct dip was apparent at 55° S, and a small dip near the equator

7 at 5° N to 10° N (Fig. 3d).

8

9 **3.2. Beta diversity**

10 The low latitudes around the equator had a higher beta diversity with a peak at 10° N (Fig. 4).

11 Latitudes around Antarctica, 70° to 75° S, also showed high beta diversity. The lowest beta

12 diversity was found at 55° S and 75° N. The partition of this total beta diversity into turnover

13 and nestedness components showed that spatial turnover (Simpson index) contributed most to

14 beta diversity (Simpson = 0.84, nestedness component = 0.13). Thus, the beta diversity pattern

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

16   Piecewise regressions of the Sorensen index revealed three latitudinal breakpoints: a dip

17 at 55° S; and peaks at 35° S and 35° N (Fig. 4, S3). This piecewise regression (r^2 = 0.87)

18 increased model fit compared to the linear regression (r^2 = 0.06). One breakpoint in the

19 Simpson index was found at 10° S, which increased the model fit from r^2 = 0.001 to r^2 = 0.83.

20 Piecewise regressions of the nestedness component (r^2 = 0.71) increased model fit compared to

21 the linear regression (r^2 = 0.06) with two latitudinal breakpoints at 2° S and 20° N (Fig. S3).

22 Thus, species turnover was highest in the tropics from 35º S to 35º N, and on the Antarctic

23 continental shelf around 70° to 75° S.

24

25 **3.3. Regions of endemicity**

1   We found twelve biogeographic regions for marine benthic amphipod crustaceans (Fig. 5 &

2   Fig. S4). All regions aligned with the Realms in Costello et al., (2017) although there was

3   insufficient data for nine Realms, i.e., South-east Pacific, Gulf of California, Gulfs of Aqaba,

4   Aden, Suez, Red Sea, Mid-South Tropical Pacific, Offshore Indian Ocean, Offshore West

5   Pacific, Offshore mid-East Pacific, Gulf of Guinea, and Chile. The highest number of records

6   was in Europe while the 'Laccadive Sea & Bay of Bengal' had the fewest records with 255

7   (Table 2). The highest number of species was in Australia with 1016 species, and the lowest

8   number of species was in the 'South & East China Sea' with 71 species. The common,

9   characterizing and endemic species for each region are listed in Tables 2 and S4.

10   Almost half of the amphipod species were endemic (Table S3). The latitudinal pattern

11   for the number of endemic species, and the proportion of all species that were endemic in 5°

12   latitudinal bands showed that latitudes between 30° and 40° S had a high number of endemic

13   species and a high proportion of endemic of all species. Both patterns had a concordant peak

14   at 35° S. In the northern hemisphere, latitudes 30° to 40° N showed a high proportion and

15   number of endemic species (Fig. 6). The number of endemic species, and the proportion of

16   species that were endemic, were highly correlated (Spearman rho = 0.87, $p < 0.05$, Fig. S6).

17

18   **4. DISCUSSION**

19   The five species with most occurrence records are typically common and abundant in seabed

20   sediments (e.g. Bonsdorff 1992, Meadows & Reid 1966, d'Udekem d'Acoz 2004, Sundelin et

21   al. 2008). Most samples of amphipods were from the continental shelves (Fig. 1a) reflecting

22   the ease of sampling shallow depths near the coast. To account for sampling bias, we calculated

23   ES50 and found that richness was still highest in the shallow waters near the continents (Fig.

24   1c).

25

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 the 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° cell, 41 % of benthic species did. The top five 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 endemicity

Twelve biogeographic regions were found for marine benthic amphipod crustaceans, and they matched the Realms of 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) indicated that benthic amphipods are representative species to map marine biogeography based on endemicity (Realms). However, nine other Realms were not observed due to gaps in amphipod distribution records. More data may find additional biogeographic regions in South America, central East Pacific, Africa, Red Sea, and the Mediterranean.

1   The latitudes between 30° S and 40° S had the highest number and proportion of endemic

2   species, peaking at 30° S (Fig. 6). These latitudes are concordant with three biogeographic

3   regions, i.e., southern Africa, Australia, and New Zealand. Eighty percent of the southern

4   temperate region species in Australia are believed to be endemic (Condie & Harris 2006). The

5   processes which have generated the high numbers of endemic species in Australia, including

6   seven endemic genera of amphipods (Myers & Lowry 2009), can be attributed to its long

7   isolation, i.e., the separation of this continent from Gondwanaland at least about 150 Ma and

8   then from Antarctica at about 53 Ma (Veevers & McElhinny 1976, Poore 2001).

9   New Zealand is a highly isolated continental landmass in the south-western Pacific

10   Ocean. It was part of Gondwana (Cowie & Holland 2006) but then separated at 80 Ma and

11   reached its present distance from Australia around 50-60 Ma (Cooper & Millener 1993,

12   McLoughlin 2001). Thus, only a few species can have arrived in New Zealand in recent times,

13   apart from human introductions. Amongst its amphipod fauna, New Zealand's isolation is

14   reflected in the endemic genera *Neocyproidea* and *Paraleptamphopus*, and endemic family

15   Rakiroidae. In addition, 15 of 17 species of Phoxocephalidae described from New Zealand are

16   endemic (Myers & Lowry 2009, Webber et al. 2010). Of the 365 New Zealand marine and

17   estuarine amphipods, 55% (194 species and 35 genera) are endemic (Webber et al. 2010).

18   Similarly, 51% of marine species are endemic to New Zealand, the highest percent marine

19   endemicity of any country (Costello et al. 2010). South Africa also has a high number of

20   endemic marine species, that is, 28-30% of all 12,000 marine species, including 33% of 454

21   amphipod species (Costello et al. 2010, Griffiths et al. 2010).

22   The smaller peak of endemicity evident at 40° N overlapped with the Mediterranean Sea.

23   The Mediterranean Sea is known to have high amphipod diversity (e.g., Ruffo 1998, Ruffo

24   2010, Dauvin et al. 2013). Over one-quarter of the Mediterranean marine biota are endemic

25   (Fredj et al. 1992, Coll et al. 2010) and 46% of Mediterranean amphipod species are considered

1   endemic (Bellan-Santini 1990). The high endemicity may be due to the Messinian Crisis, a

2   geological event during which the sea largely, but not entirely, dried out following the closure

3   of the Strait of Gibraltar. Thus, a relict but isolated Tethyan amphipod fauna survived (Bellan-

4   Santini 1990).

5

6   **4.3. Latitudinal patterns of species richness and beta diversity**

7   The latitudinal pattern of beta diversity (Sorensen index) was like that of ES50 and was mostly

8   driven by turnover in species composition (Simpson dissimilarity index) (Fig. 3d & 4b). High

9   turnover in the equatorial regions could be explained by the high variability of habitats there

10   such as coral reef and seagrass ecosystems as well as the range of other habitats (Shurin 2007,

11   Costello et al. 2017, Asaad et al. 2018, Chaudhary 2019). In addition, land masses in this region

12   are a barrier for marine species dispersal (Chaudhary 2019). In contrast, the smaller area, and

13   lack of such barriers in the Arctic and Southern Oceans, result in higher connectivity and less

14   endemicity within their latitudes. Hence, there was only one biogeographic region in both the

15   Arctic-Boreal and Southern Ocean (Fig. 5), but ten regions in the tropics to temperate latitudes.

16   That the peak of species richness, as alpha and gamma diversity, number and percent of

17   endemic species, and ES50 in the southern hemisphere was around 30° to 35° S (Fig. 3),

18   contrasts with findings for razor clams (Saeedi et al. 2017), and fossil and marine species

19   (Chaudhary et al. 2016, 2017). These studies found the peak in diversity was in the northern

20   hemisphere with respect to gamma diversity for razor clams, and alpha diversity for fossil and

21   marine species. However, Chaudhary et al. (2017) found gamma diversity and ES50 to have

22   equal peaks in the northern and southern hemispheres. That the number of sample records in

23   the southern hemisphere was only a tenth of the number in the northern hemisphere, confirms

24   that the peak in richness around 30° to 35° S was not due to high sampling effort. Rather it is

25   due to the patterns of endemicity as discussed previously.

1   The dip near the equator at 5° to 10° N was observed in alpha, gamma, and ES50 as found

2   in the recent syntheses of 65000 species and 50000 fossil marine species (Chaudhary et al.

3   2016, 2017), although our dip is much smaller and not so obvious. This finding supports the

4   non-unimodality hypothesis in the richness patterns of marine species (Chaudhary et al. 2016,

5   2017), which is highly correlated with sea surface temperature (Chaudhary 2019). This dip at

6   the equator appears due to high temperatures because it is becoming more prominent in recent

7   decades (Chaudhary 2019), as predicted by climate warming models (Poloczanska et al. 2013).

8   A sharp dip of species richness in ES50 was apparent at 55° S in the Southern Ocean.

9   Antarctica is surrounded by 4000 to 6000 m depths, and the depth of the break between the

10   shelf and the slope in the Southern Ocean is at least double the depth of the shelf break on other

11   continents (Knox 2006, Harris et al. 2014). This may form a biogeographic barrier for benthic

12   species. There were sample records for benthic and pelagic amphipod species from 45º S to 75º

13   S (Fig. S5), and ES50 was low from 45º S to 70º S, with lowest species richness at 55º S.

14   Another study on the Southern Ocean deep-sea biodiversity reported similar findings, i.e., the

15   Southern Polar Front around 52° S had a low diversity and abundance in many macrofauna

16   taxa including Amphipoda (Brandt & Ebbe 2009). Although an expedition at 748 to 6348 m

17   depth in the Weddell Sea (70° S) and adjacent areas did not report any amphipod species,

18   despite the discovery of 674 isopod species of which 585 were new to science (Brandt et al.

19   2007a), this was because the amphipod samples (except for the scavengers caught by baited

20   traps) had not been identified (Brandt, pers. comm. 10th July 2019). Thus, whether the number

21   of amphipod species at 55° S is as exceptionally low as our results suggest merits confirmation.

22   Nevertheless, the deep-sea amphipod assemblage at 55° S is distinct from that on the Antarctic

23   shelf as shown by the indices of species turnover (beta diversity) (Figure 5).

24   Species richness on the Antarctic continental shelf between 70° S and 80° S was similar

25   to latitudes north of 45° S. Clarke (2008) also found that the Antarctic shelf has a comparable

1 benthic (including Amphipoda) diversity with some tropical and temperate shelves. This

2 similar richness contrasts with the hypothesis that polar regions have low diversity due to the

3 harshness of the environment (Willig et al. 2003, Payer et al. 2013). That the Arctic is species

4 poor by comparison with Antarctica seems due to the long isolation and high endemicity of

5 Antartica since the breakup of Gondwana (Brandt et al. 2007b, Saucède et al. 2014).

6   Other studies on amphipods in the Southern Ocean reported the same pattern as we found,

7 i.e., the shelf area between 0-1000 m had more species than the area deeper than 1000 m (De

8 Broyer et al. 2007, De Broyer & Jażdżewska 2014). These findings contradict the hypothesis

9 that the deep sea has a high richness (Grassle 1989, Snelgrove 1999, Rex & Etter 2010). Even

10 though the deep sea has more area, it is cold ($< 4\ ^{\circ}C$) with low productivity, and a more limited

11 number of habitats compared to shallow-waters with high primary productivity and complex

12 biogenic habitats like coral reefs, kelp forests, seagrass meadows, shell beds, and other

13 epifaunal assemblages provide three-dimensional habitat for many species (Costello & Breyer

14 2017, Costello & Chaudhary 2017, Havermans & Smetacek 2018). The relative homogeneity

15 of deep-sea environments, varying little in temperate, salinity and habitat, mean that the same

16 deep-sea species may inhabit large geographic areas and depth ranges (Costello et al. 2018).

17

18 **5. CONCLUSION**

19 We found that pelagic species of amphipod were more widespread and far less species-rich,

20 than benthic species. This reflects the greater homogeneity of pelagic than benthic habitats, and

21 thus likely higher gene flow. Similarly, greater homogeneity in deep sea than shelf depth zones

22 may partly explain the greater number of species on the Antarctic continental shelf compared

23 to the deep-sea Southern Ocean, in addition to the high Antarctic endemicity.

24   Although there were ten times more sample records in the northern hemisphere, species

25 richness peaked in the southern hemisphere and thus was not due to sampling effort. These

1   peaks were concordant with the high number and proportion of endemic species, and aligned

2   with three regions of high endemicity, i.e., Australia, southern Africa, and New Zealand. Beta

3   diversity was lower in higher latitudes, probably due to greater connectivity and gene flow of

4   species across a smaller total area of longitudes than in the low latitudes, and fewer land

5   barriers. The 12 regions of endemicity found for amphipods matched well with previously

6   proposed marine biogeographic realms. Thus, amphipods do not appear to have a more

7   complex global biogeography than other marine taxa due to their lack of planktonic life stage.

8   Their latitudinal gradients are broadly similar to other marine taxa but had higher richness in

9   temperature southern hemisphere latitudes and Antarctica reflecting regional endemicities.

10 Conservation planning should note the importance of these regions (Realms) of endemicity in

11 designing global networks of marine reserves.

12

13

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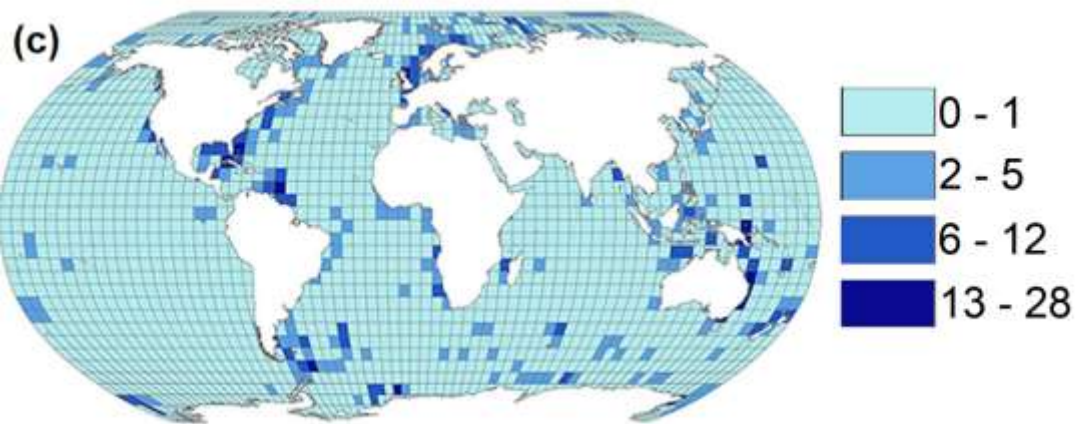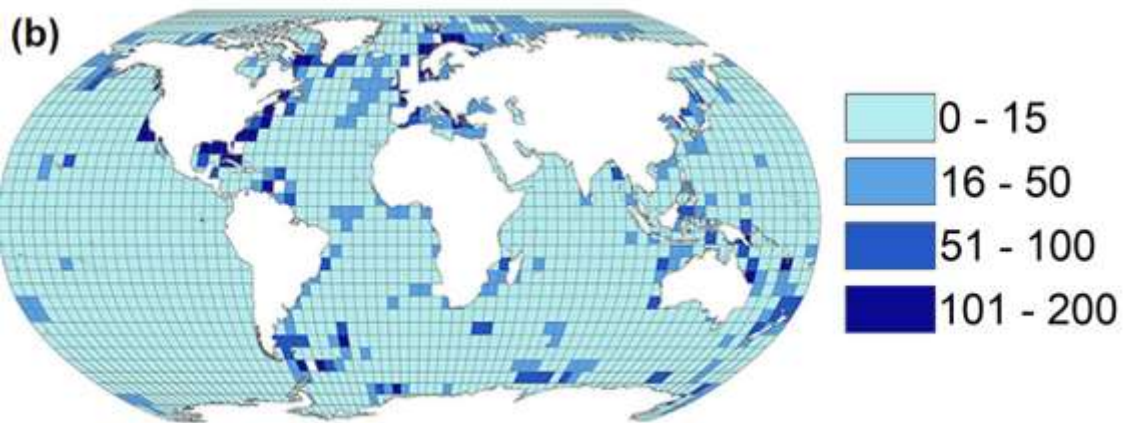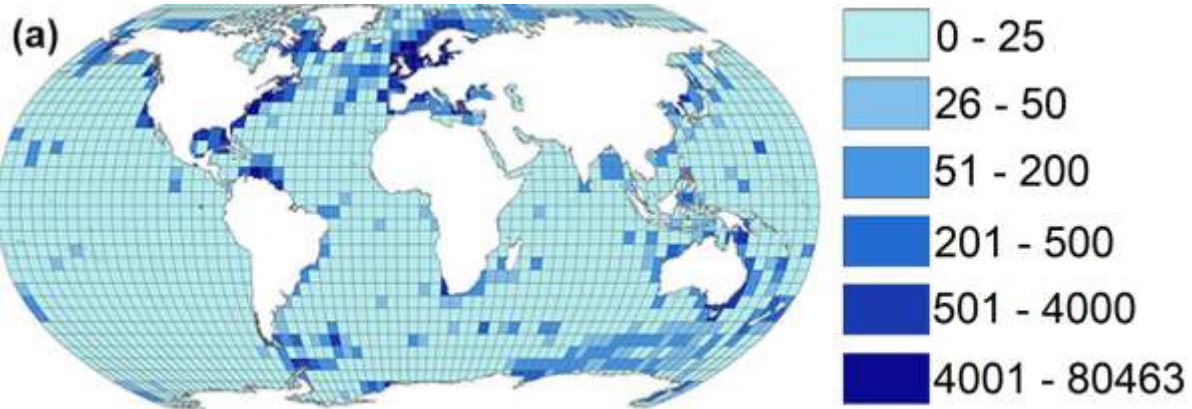
Data Acessibility Statement

Data underlying this article can be accessed on Figshare (DOI 10.17608/k6.auckland.8227784) and used under the Creative Commons Attribution licence.

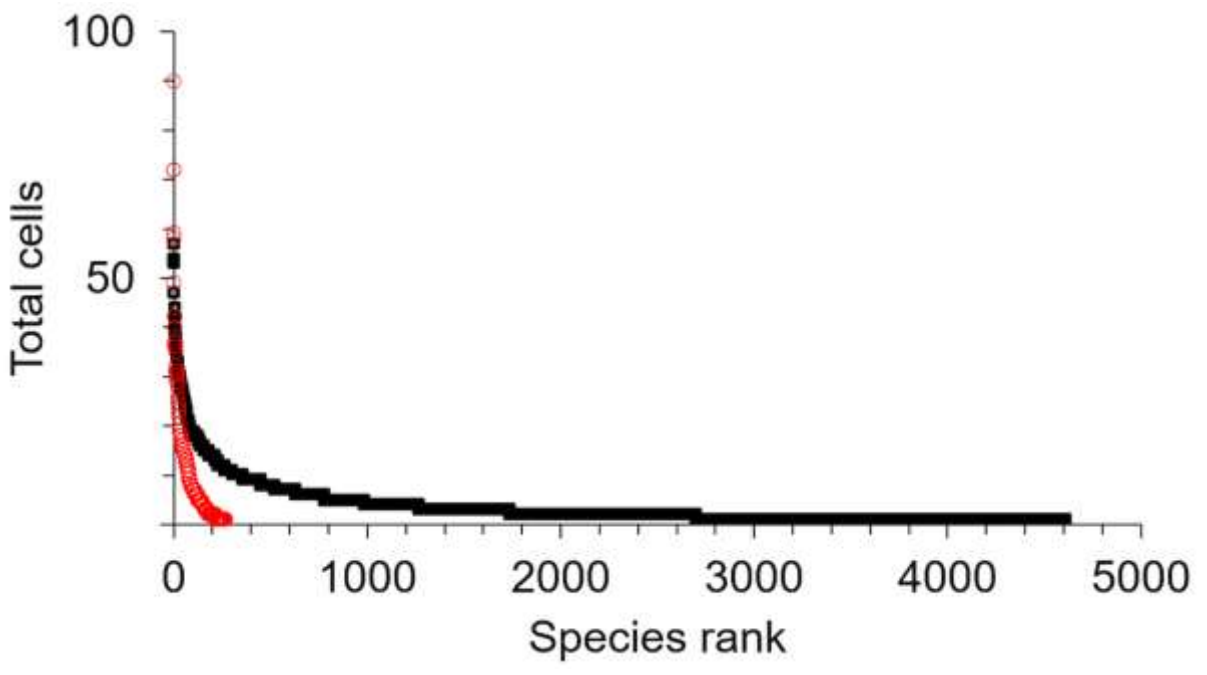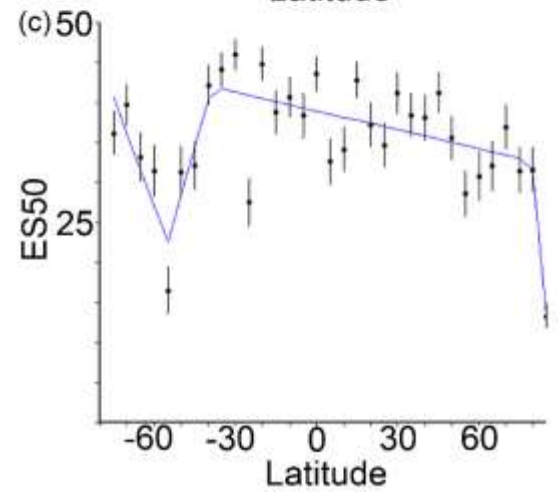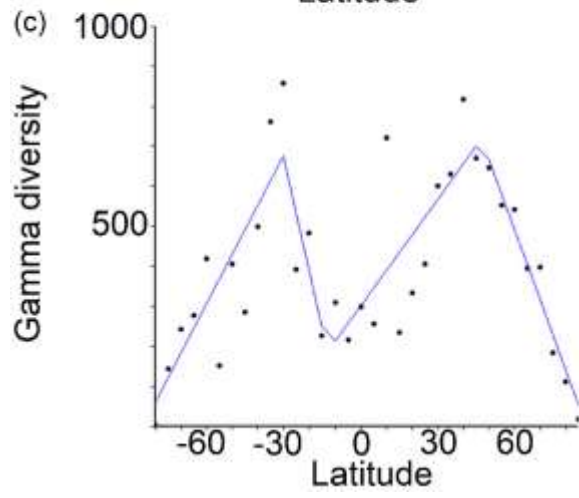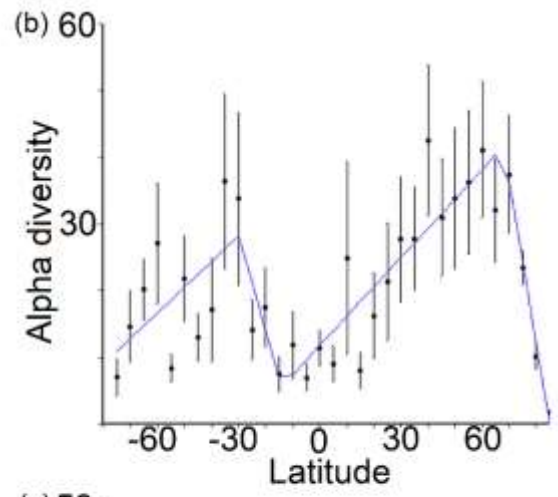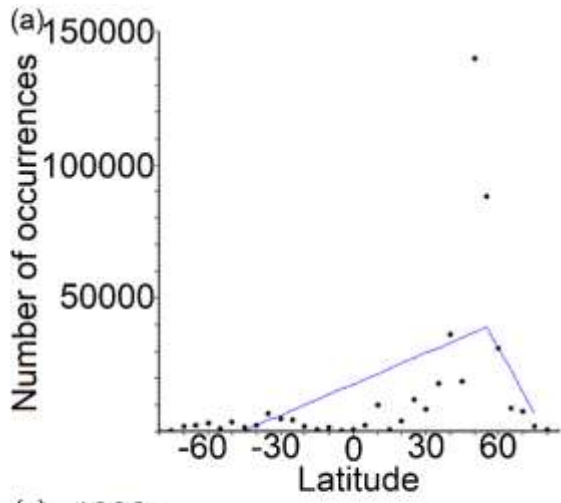**Figure Legend**

Figure 1. Global map of marine amphipod crustaceans for (a) occurrences, (b) species richness (gamma), and (c) the expected number of species among 50 random samples (ES50) in 5° cells. Land is white.
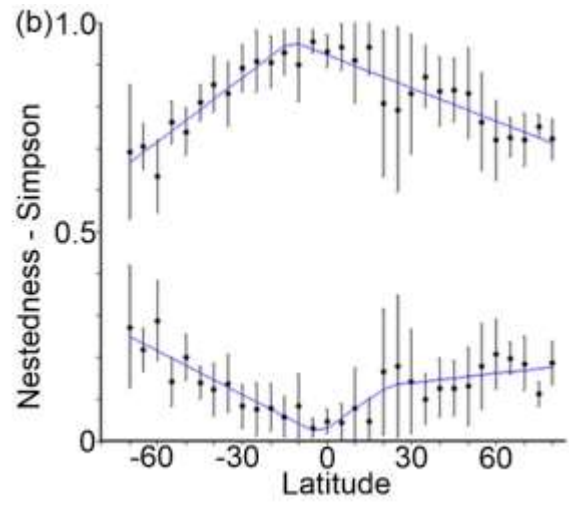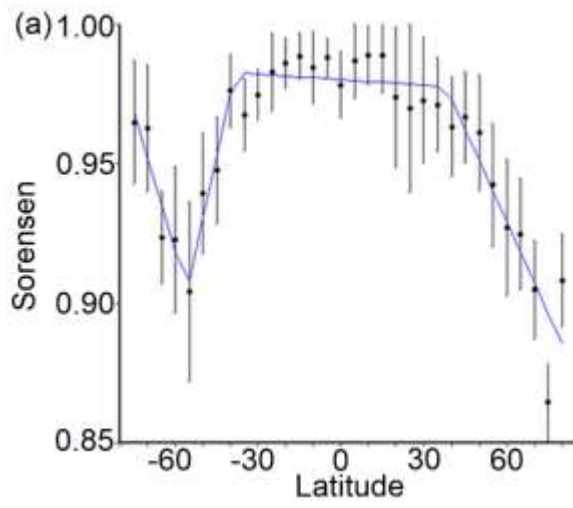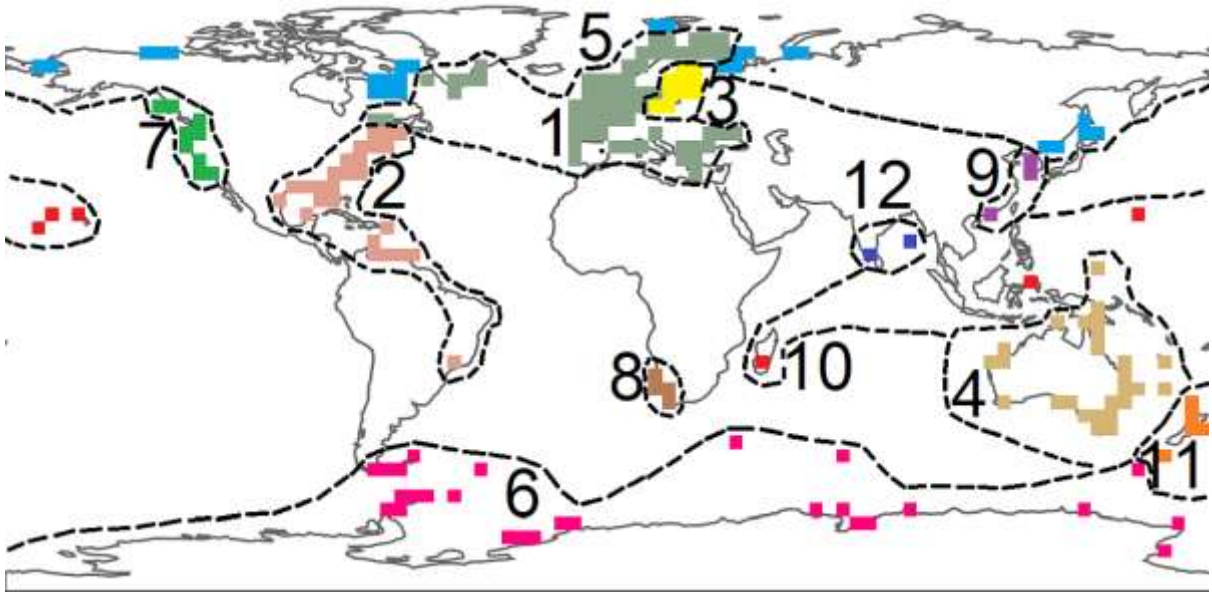
1   Figure 2. The occurrence of pelagic (red circles) and benthic (black squares) species in 5° cells.
2   Species are ranked from most to least number of cells present, indicating the far greater number
3   of benthic than pelagic species, and that pelagic species generally occur in more cells.

4   Figure 3. Latitudinal species richness of marine amphipod crustaceans for (a) total number of
5   records in 5° latitudinal bands, (b) alpha richness ± standard error, (c) gamma richness, and (d)
6   the expected number of species among 50 individuals (ES50 ± standard error). Lines are
7   piecewise regressions.

8   Figure 4. Latitudinal patterns of beta diversity and its standard error for (a) Sorensen total
9   dissimilarity, (b) Simpson dissimilarity (above) and nestedness component (below) in 5°
10   latitudinal bands. Piecewise regressions are shown as lines.

11   Figure 5. Map of biogeographic regions based on benthic marine amphipod crustaceans. It
12   shows regions overlaid on the original map (Figure S4). For details of characterizing and
13   common species of each region see Tables 2 and S4.
14
15   Figure 6. Latitudinal patterns of (a) number of endemic species, and (b) proportion of species
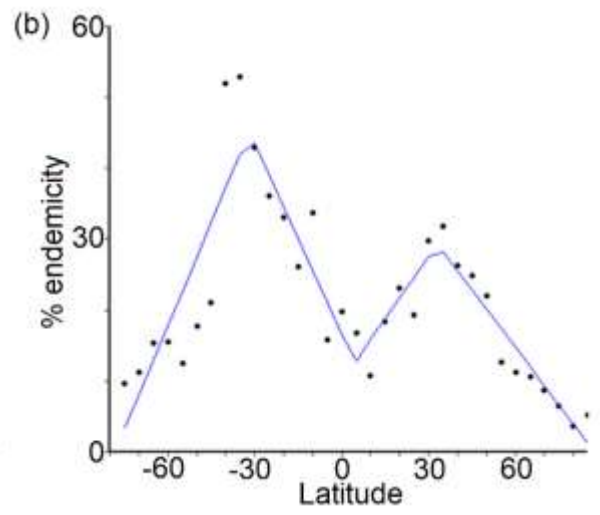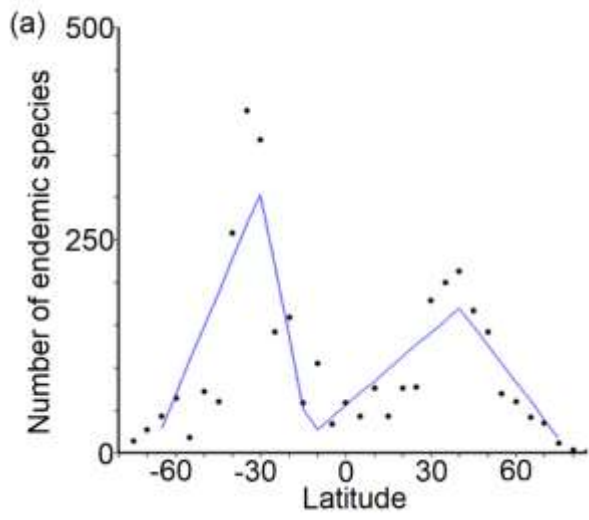16   (gamma richness) that were endemic, in 5° latitudinal bands. Lines are piecewise regressions.

17

18

(a)

	0 - 25
	26 - 50
	51 - 200
	201 - 500
	501 - 4000
	4001 - 80463

(b)

	0 - 15
	16 - 50
	51 - 100
	101 - 200

(c)

	0 - 1
	2 - 5
	6 - 12
	13 - 28

1

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

2

3

Species	Number of records
Monoporeia affinis	18217
Corophium volutator	14817
Ampelisca brevicornis	10440
Bathyporeia elegans	9789
Ampelisca tenuicornis	7400
Ampelisca spinipes	6776
Perioculodes longimanus	6353
Harpinia antennaria	6344
Bathyporeia guilliamsoniana	6272
Urothoe elegans	6140
Urothoe poseidonis	6019
Themisto gaudichaudii	5673
Microdeutopus gryllotalpa	5338
Pontoporeia femorata	4906
Pariambus typicus	4716
Phtisica marina	4210
Themisto abyssorum	4140
Nototropis vedlomensis	3919
Unciola irrorata	3787
Othomaera othonis	3777

4

Global biogeography of marine amphipod crustaceans

Table 2. Comparison of the twelve biogeographic regions of benthic marine amphipod crustaceans identified in this study with the Realms based on all marine taxa (Costello et al., 2017). The number in parentheses matches that applied to the Realms in Costello et al. (2017). N = north, NW = north-west, NE = north-east, S = south. Dominant species had the highest records, and characterizing species were the most indicative for each Region identified by Infomap Bioregions software (Table S4).

	Regions for Amphipoda	Realms	Records	Species	Cells	Dominant species	Characterizing species
1	Black Sea, NE Atlantic, Mediterranean Sea, Offshore & NW North Atlantic (in part)	Black Sea (1) NE Atlantic (2) Mediterranean (3) Offshore & NW North Atlantic (4)	221870	770	61	*Ampelisca brevicornis*	*Apherusa clevei, Bathyporeia tenuipes, Corophium arenarium, Maerella tenuimana, Guernea (Guernea) coalita, Gammarus crinicornis, Lepidepecreum longicornis, Apherusa ovalipes, Bathyporeia nana, Iphimedia nexa*
2	Caribbean, Gulf of Mexico & Offshore S Atlantic Ocean (in part)	Caribbean & Gulf of Mexico (5), Offshore S Atlantic (6)	65849	917	26	*Unciola irrorata*	*Eudevenopus honduranus, Acanthohaustorius millsi, Leptocheirus plumulosus, Casco bigelowi, Idunella carinata, Metopella angusta, Chevalia carpenteri, Meximaera diffidentia, Netamelita brocha, Ampelisca parapacifica*
3	Inner Baltic Sea	Inner Baltic Sea (7)	31042	77	10	*Monoporeia affinis*	*Pallaseopsis quadrispinosa*
4	Tasman Sea, Coral Sea, S Australia & Indo-Pacific seas & Indian Ocean (In part)	Tasman Sea (8) Coral Sea (9) South Australia (10)	13686	1016	26	*Ampelisca euroa*	*Byblis mildura, Cephalophoxoides kukathus, Podocerus dentatus, Birubius maldus, Hippomedon rodericki, Birubius maamus, Nagada uwedoae, Birubius jirrandus, Limnoporeia ungamale, Charcotia dempseyae*
5	Norwegian Sea, Arctic seas, N Pacific (in part), N American Boreal	Norwegian Sea (in part) (11), Arctic seas (12), N Pacific (in part) (13), N American Boreal (14)	8653	338	26	*Rhachotropis aculeata*	*Byblis brevirama, Metopa longirama, Orchomene minor, Byblis frigidus, Byblis robustus, Ampithoe tarasovi, Arrhinopsis longicornis, Lepidepecreum eoum, Harpinia bidentata, Ischyrocerus nanoides*
6	Southern Ocean	Southern Ocean (15) Rio de La Plata (16)	6693	653	27	*Eusirus perdentatus*	*Amphilochella simplicarpa, Podocerus danae, Kerguelenia antiborealis, Eusiroides aberrantis, Gondogeneia macrodon, Tonocote introflexidus, Anonychocheirus richardsoni, Stomacontion pepinii, Liljeborgia pseudomacronyx, Lepidepecreum infissum*

Global biogeography of marine amphipod crustaceans

7	N Pacific (in part)	N Pacific (in part) (17)	7177	413	9	*Ampelisca abdita*	*Americorophium salmonis, Rhepoxynius daboius, Caprella californica, Foxiphalus obtusidens, Mayerella banksia, Pleusymtes subglaber, Cheirimedeia zotea, Foxiphalus similis, Amphideutopus oculatus, Metopa cistella*
8	South Africa	South Africa (18)	3134	207	4	*Ampelisca anomala*	*Idunella lindae, Perioculodes pallidus, Indischnopus capensis, Hippomedon normalis, Leucothoe euryonyx, Ischyrocerus carinatus, Indischnopus herdmani, Zygomaera emarginata, Urothoe pinnata, Unciolella foveolata*
9	South & East China Sea	N W Pacific (19)	1128	71	3	*Ampelisca brevicornis*	*Urothoe convexa, Melita longidactyla, Mandibulophoxus hongae, Podocerus hoonsooi, Photis japonica, Gammaropsis japonica, Eohaustorius spinigerus, Guernea (Prinassus) terelamina, Sunamphitoe chujaensis, Protohyale (Boreohyale) magnaocularis*
10	Hawaii, Indo-Pacific seas & Indian Ocean	Indo-Pacific seas & Indian Ocean (20) Mid-tropical North Pacific Ocean (21)	1025	202	6	*Leucothoe hyhelia, Ericthonius brasiliensis*	*Globosolembos leapakahi, Wandelia orghidani, Ventojassa ventosa, Leucothoe lihue, Kanaloa manoa, Paranamixis ledoyeri, Azotostoma bunakenensis, Ampithoe alluaudi, Tepidopleustes honomu, Ischyrocerus kapu*
11	New Zealand	New Zealand (22)	890	190	5	*Ampelisca chiltoni*	*Otagia neozelanica, Amphorites hurleyi, Tagua aporema, Melita awa, Paradexamine houtete, Stenothoe moe, Taihape karori, Podocerus karu, Oedicerina loerzae, Pseudopleonexes evensis*
12	Laccadive Sea & Bay of Bengal	Indo-Pacific seas & Indian Ocean (20)	255	108	2	*Ampelisca scabripes*	*Ampelisca scabripes, Socarnella bonnieri, Mallacoota sokotrae, Amphilochus schubarti, Abdia latipalpus, Anonyx indicus, Grandidierella macronyx, Talorchestia gracilis, Perioculodes megapleon, Parandaniexis spinescens*