ORIGINAL RESEARCH

Antarctica is less isolated with increasing depth - evidence from pycnogonids

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Abstract

No other group of animals typifies the uniqueness of Antarctic life more than Pycnogonida (sea spiders), with 20% of all known species found in the Southern Ocean, and 64% of these endemic to the Antarctic. Despite nearly 200 years of research into pycnogonids and other benthic phyla in Antarctica, the parameters which drive the distribution and diversity of benthic fauna are still poorly understood. This study aimed to investigate the diversity and connectivity of pycnogonid communities on either side of the Antarctic Polar Front, with an emphasis on the role of water depth, using an occurrence dataset containing 254 pycnogonid species from 2187 sampling locations. At depths shallower than 1000 m, communities to the north and south of the Antarctic Polar Front were distinct, while below this depth this geographic structure disintegrated. The Polar Front, or the expanse of deep ocean it bisects, seemingly acts as a semipermeable barrier to species exchange between well-sampled shallow communities. The less sampled and less understood deep sea appears to be better connected, with high levels of shared species following the northward flow of Antarctic Bottom Water. The exceptionally high diversity and endemism of Antarctic pycnogonids may reflect an apparent competitive advantage in cold waters which leaves them vulnerable to ongoing ocean warming, with increased competition and predation pressures.

Keywords Pycnogonida · Biogeography · Antarctic polar front · Species richness · Connectivity

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Introduction

The ocean surrounding Antarctica is a cold but relatively stable deep-sea environment allowing the evolution of a unique and diverse set of cold-adapted benthic taxa, with limited prevalence of otherwise globally diverse and abundant taxa such as shelled gastropods, bivalves, teleost fish and decapod crustaceans (Clarke and Crame 2010). Several taxa have a disproportionately large number of their global species here e.g., polychaetes (12%), bryozoans (10%), holothurians (9%) and isopods (9%), considering the Southern Ocean has only 8% of the Earth's continental shelf (Barnes and Peck 2008). However, no group exemplifies the diversity and uniqueness of the Antarctic benthos more than Pycnogonida (sea spiders). 20% of all known pycnogonid species are found in the Southern Ocean and, of these, ~ 270 species (64%) are endemic to the region (Munilla and Soler Membrives 2009). It is the only place on Earth where all families of pycnogonids are represented, leading to the hypothesis that the Southern Ocean is the evolutionary centre of origin of extant pycnogonids (Griffiths 2010).

The Antarctic benthic environment, i.e., the area of seafloor south of the Antarctic Polar Front (PF), is the coldest marine habitat on Earth, with temperatures ranging from −2 to 2 °C (Clarke et al. 2009). The PF marks a point of species turnover in several groups, whereby there is a change in the species present, with an accompanying increase in species richness across the front moving north to south. Gastropod richness is constant down to 40°S, and increases to a peak of over 600 species south of 60°S (Griffiths et al. 2009; Valdovinos et al. 2003). In demosponges (Porifera: Demospongiae) 30% more species are found south of the PF (McClintock et al. 2005). Similarly, nearly 30% more Asteroidea species are recorded around the Antarctic Peninsula compared to South America (Moreau et al. 2021). For echinoids, richness decreases between 35°S and 55°S before increasing at the polar frontal zone and then reducing again at higher latitudes (Saucède et al. 2014).

At the surface, the PF is defined by a steep temperature gradient and rapid velocities of up to ~100 cm/s (Moore et al. 1999). Despite being recognised as a full water column feature, the temperature gradient decreases with depth (Clarke et al. 2009; Orsi et al. 1995) and is crossed by slower (~5–10 cm/s) northwards flowing Antarctic Bottom Water close to the sea floor, meaning conditions are more homogenous than in the waters above. Antarctic Bottom Water, cold deep water formed around the Antarctic continent, is a major driving force of the thermohaline circulation of the global ocean as it sinks and flows northward. Since their establishment during the early Miocene (Huang et al. 2017), northward flowing Antarctic Bottom Water has provided a pathway by which taxa of Antarctic origin have dispersed across the PF, and subsequently undergone radiations. Molecular studies have shown this to be true in a variety of taxa, octopuses (Strugnell et al. 2008), pleurobranch gastropods (Göbbeler and Klussmann-Kolb 2010), notothenioid fishes (Dornburg et al. 2017), primnoid corals (Taylor and Rogers 2015), headshield sea slugs (Moles et al. 2021), and limpets (González-Wevar et al. 2016) with the common feature being they are mostly benthic taxa. It has also been shown for the pycnogonid genus *Colossendeis* (Dömel et al. 2019). Additionally, there is evidence of the PF moving further north at various times (Kemp et al. 2010) allowing colonisation of the South American continental shelf.

Pycnogonids are an ideal taxon to investigate the biogeographic structure of Antarctic and Sub-Antarctic benthos. They are slow moving benthic animals but, with no known pelagic larval stage, they are assumed to have limited dispersal capabilities (Crooker 2008),

and have a disproportionately high number of species in the region (Munilla and Soler-Membrives 2009). They are the focus of a large presence-only dataset in online portals such as the Ocean Biodiversity Information System (OBIS 2023) and the Global Biodiversity Information Facility (GBIF 2023). For pycnogonids, as is the case with the majority of Antarctic taxa, there is a bias in terms of sampling locations, with most records coming from regions of the continental shelf that are either close to established research bases or are easily accessible e.g., Western Antarctic Peninsula, Eastern Weddell Sea and South Georgia (Griffiths et al. 2011b). Having a biased dataset, with local foci, influences analyses which use grid squares or large defined regions.

Most biogeographic pycnogonid studies have concentrated on circumpolar or predefined regional comparisons. The circumpolar studies tend to support the original findings of (Hedgpeth 1969) of a single circumpolar biogeographic province, distinct from neighbouring regions, where "*circumpolar species are the largest component of any Antarctic shelf region*" with "*little indication of separate regions of development within the waters of the shelf region*", and that "*a very large percentage of some genera are endemic to the regions south of the Antarctic Convergence*". The most recent attempts to analyse the overall distribution patterns add that the most diverse region is the Scotia Arc and northern Antarctic Peninsula, with a high number of endemic species and a potential centre of radiation (Griffiths et al. 2011a; Munilla and Soler-Membrives 2009). Griffiths et al. (2011a) also noted that the shelf fauna differed from that of the deep sea, although eurybathy was prevalent. Finer-scale patterns in pycnogonid species richness, distribution, and community structure have been identified in local or regional investigations (Munilla and Soler-Membrives 2007, 2015; San Vicente et al. 1997; Soler-Membrives et al. 2009)]. These studies found a decrease in richness with depth and distinct communities on the shelf compared to the slope.

The study presented here combines historical presence records for Southern Ocean pycnogonids with a new dataset generated by Maxwell et al. (2022) which contains 5070 individuals (97 species) across 1300 occurrence records and 197 sampling stations within the Southern Ocean. These new data increase the number of sampling points where pycnogonids have been recorded by 11% for the Southern Ocean, and by almost 20% for the study area used here (110°W −5°E, and 40°S- 80°S). The aims of the study were to (a) quantify the observed species richness and sampling effort within the study area; (b) identify diversity hotspots both in terms of locations and depth ranges; and (c) compare diversity and connectivity patterns for the study area and at a range of depth horizons.

Methods

Data compilation

Occurrence data for pycnogonids, within the boundaries of 110°W −5°E, and 40°S −80°S, were extracted from OBIS (OBIS 2020) and GBIF (GBIF 2020) (data accessed on 30/10/2020) and combined with data from (Maxwell et al. 2022). Any duplicates were identified and removed, producing a dataset containing 254 pycnogonid species from 2187 sampling locations. The species list was checked for synonyms using the World Register of Marine Species (WoRMS) Taxon Match tool. All species occurrences were grouped by

sampling event (a unique combination of latitude, longitude, and depth), and each sampling event (Fig. 1) was given its own unique number.

Species richness and sampling effort

The occurrence data were imported into ArcGIS Pro (Esri Inc., 2020) using a South pole Lambert Azimuthal equal area coordinate system, and a tessellated grid composed of 40,000 km^2 hexagons was created to cover the area $110°W - 5°E$, and $40°S - 80°S$. As the subsequent analyses were area based and the data used were spread over 40 degrees of latitude, the equal area coordinate system combined with the equal area tessellated grid were used, rather than the more commonly used latitudinal and longitudinal grid system, to ensure that all hexagons were comparable in area. Using the spatial join tool in ArcGIS, species present, sampling event number and depth data of each station were joined to the corresponding hexagon, resulting in 157 hexagons containing records (Fig. 2). The hexagon layer attribute table was exported to Excel, and a pivot table used to create a matrix of species presence (and therefore assumed absence where there was no record) for each hexagon and similarly by position north and south of the PF and for the depth bins. These pivot tables were used to generate lists and counts of distinct species and sampling locations for each geographic unit (hexagons or north/south of the PF) and depth bin for further analyses.

To account for the influence of sampling intensity, the residuals of a model 1 least-squares regression of the number of species and sampling events per hexagon were calculated (Clarke et al. 2007). Residual value of zero means the observed value is equal to the expected value, negative values infer the observed value is below the expected, with positive values inferring observed values are greater than the expected. All values were natural log transformed. Another method used to account for impact sampling intensity on species richness, less dependent upon the total number of samples taken, was species accumulation curves. The most species rich hexagons for each well sampled geographic area were selected, and smoothed species accumulation curves for the observed number of species were generated in PRIMER 6 (Clarke and Warwick 2001) by averaging 999 curves that drew samples in random order.

The methods above were used to identify pycnogonid diversity hotspots within the study area. These hotspots had the greatest species richness, and the highest diversity according to the species accumulation curves.

Fig. 1 The locations of all the initial sampling stations in the Southern Ocean and from waters surrounding South America. Purple=Maxwell et al. (2022), Green=OBIS and GBIF. Blue line is the mean position of the Antarctic Polar Front (Sokolov and Rintoul 2009)
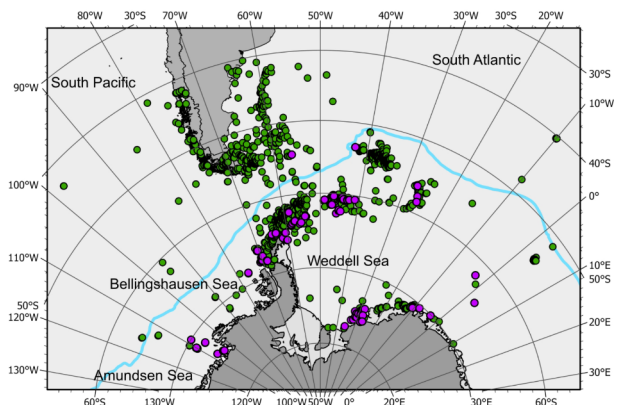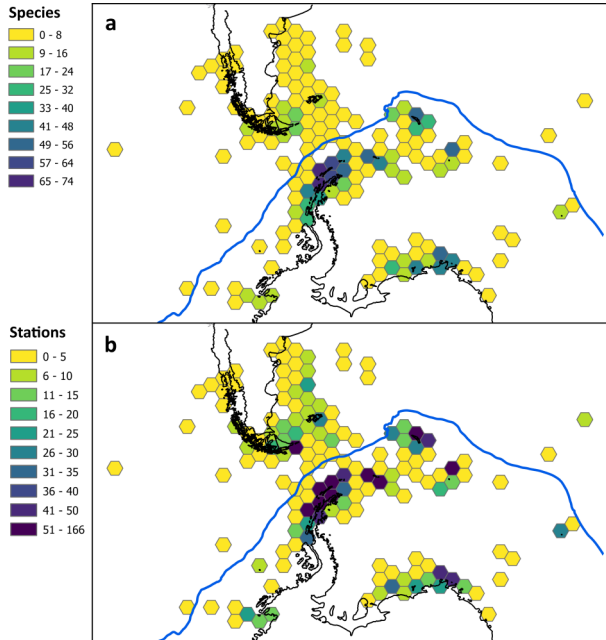
Fig. 2 The species richness and sampling effort for the study area as identified using 40, 000 km² hexagons. (**a**) Number of species stations within each hexagon. (**b**) Number of stations within each hexagon. Station and species data were taken from OBIS and GBIF. Blue line is the mean position of the Antarctic Polar Front (Sokolov and Rintoul 2009)

Faunal similarity

Shared species similarity analyses that combined all depths used the same tessellated grid, but any hexagon that had three or fewer species in it was removed to exclude under-sampled hexagons. The abundance data for each depth bin were transformed into presence/absence data using the overall transform pre-treatment operation in Primer 6 (Clarke and Warwick 2001), and a Bray-Curtis similarity matrix was constructed. Hierarchical clustering analysis used the group average linkage option in Primer 6 with clusters defined via SIMPROF (Similarity Profile Analysis – (Clarke et al. 2008). This analysis was then repeated for separate depth bins (0–200 m, 200–500 m, 500–1000 m and > 1000 m) but included all hexagons (i.e., also those with three or fewer species) to ensure enough samples per depth bin for comparison.

Species accumulation curves

To compare species richness between depths, species accumulation curves were generated in PRIMER 6 (Clarke and Warwick 2001), using the same method as described in Sect. 2.2, for all records grouped by depth bin (0–200 m, 200–500 m, 500–1000 m and > 1000 m) and whether they were north or south of the PF. If a hexagon was bisected by the PF, it was assigned either north or south based on majority coverage.

Drivers of similarity: ANOSIM & SIMPER

In order to investigate the relationship between different depths and the connectivity between regions across the PF, individual hexagons were labelled with their locality (north

or south of the PF) and Primer 6 was used to undertake a SIMPER (Similarity Percentage) analysis and ANOSIM (ANalysis Of Similarities) analysis on a Bray-Curtis similarity matrix (Clarke 1993).

Percentage similarity

A matrix was created showing the number of shared species between each of the depth bins north and south of the PF. This was used to produce a further matrix, giving the percentage of the total species from each bin shared with each of the other bins. The resulting percentage matrix shows the relationship between the bins and the weighting of that relationship, indicating whether the mutually shared species between two bins make up a significant proportion of each bin e.g., does one of the bins contain a community that is a subset of a larger, more diverse community elsewhere.
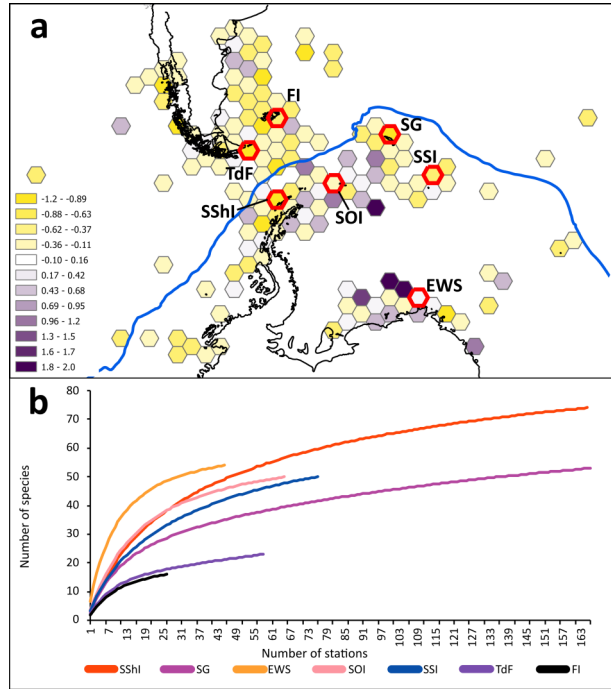
Results

Species richness and sampling effort

The Antarctic Peninsula, South Shetland Islands, Eastern Weddell Sea and South Orkney Islands were identified as regions with high species richness (Fig. 2a). Species richness is higher south of the PF than north of it. Hexagons contained between one and 74 species (Fig. 2a), with 70% having eight or fewer. The highest number of species was recorded around the Bransfield Strait and South Shetland Islands. Other areas with high recorded species numbers are the South Orkneys, Eastern Weddell Sea, South Georgia, and the South Sandwich Islands. The number of stations in an individual hexagon ranged from one to 166 (Fig. 2b) with 60% of hexagons containing five or fewer stations. There were five areas with a high sampling intensity (>50 stations): West Antarctic Peninsula/Bransfield Strait, South Orkney Islands, South Georgia, the South Sandwich Islands and Cape Horn.

Due to the patchy and uneven nature of Southern Ocean benthic sampling, pycnogonid species richness within a hexagon generally reflects the number of samples taken. The model 1 least-squares regression residual values represent a first-order estimate of species richness corrected for sampling intensity (Clarke et al. 2007). Poorly sampled deep-sea hexagons, south of the PF, had the highest residual values, particularly in the eastern Weddell Sea (Fig. 3a). Most hexagons had values close to zero, however, particularly well sampled hexagons (Fig. 3a) had lower than expected residual values. Species richness does not have a linear relationship with sampling intensity, with new species numbers plateauing with increased repeated sampling. For hexagons with greater sampling intensity (>~30 stations) the residual values do not accurately reflect the true diversity of the polygon when compared with less well sampled hexagons which are not approaching the horizontal asymptote.

The species accumulation curves for the richest polygons from each geographic area (Fig. 3b) indicate that the South Shetland Islands (74 species in total from 165 stations, residual value = -0.783577) is the area of highest species richness within the dataset. The Weddell Sea (54 species in total from 45 stations, residual value=0.175518) had the steepest curve but this started levelling off more rapidly than curves for other regions. The two regions north of the PF, the Falkland Islands (16 species in total from 26 stations) and

Fig. 3 Species richness residual values and species accumulation curves to evaluate the interaction between sampling effort and species richness. (**a**) The model 1 least-squares regression residual values for all depths within each hexagon. The hexagons highlighted in red represent the hexagons with the greatest sampling effort around the Falkland Islands (FI), Tierra del Fuego (TdF), South Georgia (SG), South Sandwich Islands (SSI), South Orkney Islands (SOI), South Shetland Islands (SShI), and East Weddell Sea (EWS). Blue line represents the mean position of the Antarctic Polar Front (Sokolov and Rintoul 2009). (**b**) Species accumulation curves for each of the seven hexagons highlighted in Fig. 3a

Tierra Del Fuego (23 species in total from 58 stations) had the shallowest curves and lowest diversity.

Faunal similarity

The all depths combined faunal similarity analysis resulted in 102 hexagons grouped into twenty clusters using SIMPROF (Fig. 4). Three of the clusters were found exclusively north of the PF, with one hexagon in the eastern Weddell Sea forming part of the fourth South American cluster. There are 13 clusters found exclusively south of the PF. The clusters corresponding to the Antarctic Peninsula, South Orkney and South Sandwich Islands, East Weddell Sea, and South Georgia are most similar to each other (approx. 40%). The Southern Ocean Deep cluster has a single hexagon north of the PF, with the remaining hexagons spread across the Weddell Sea, the Scotia Arc, Drake Passage, and the Western Antarctic Peninsula. The Amundsen Sea and the Weddell Sea Deep clusters are sister and have only 22% similarity to the rest of the Southern Ocean clusters. Two clusters (black and white horizontal and diagonal stripes respectively in Fig. 4) did not correspond to any single location or depth.

When divided up by depth bins and whether north or south of the PF, the number of recorded species and sampling stations were skewed towards shallower depths and locations south of the polar front (Table 1). The 500–1000 m depth bin was the least sampled bin north of the polar front, and the >1000 m bin was the South's least sampled, with both bins also being the depths with the least species (Table 1). The shallower depth bins (0-200 and 200–500 m) showed the strongest geographic signal when using SIMPROF (similarity
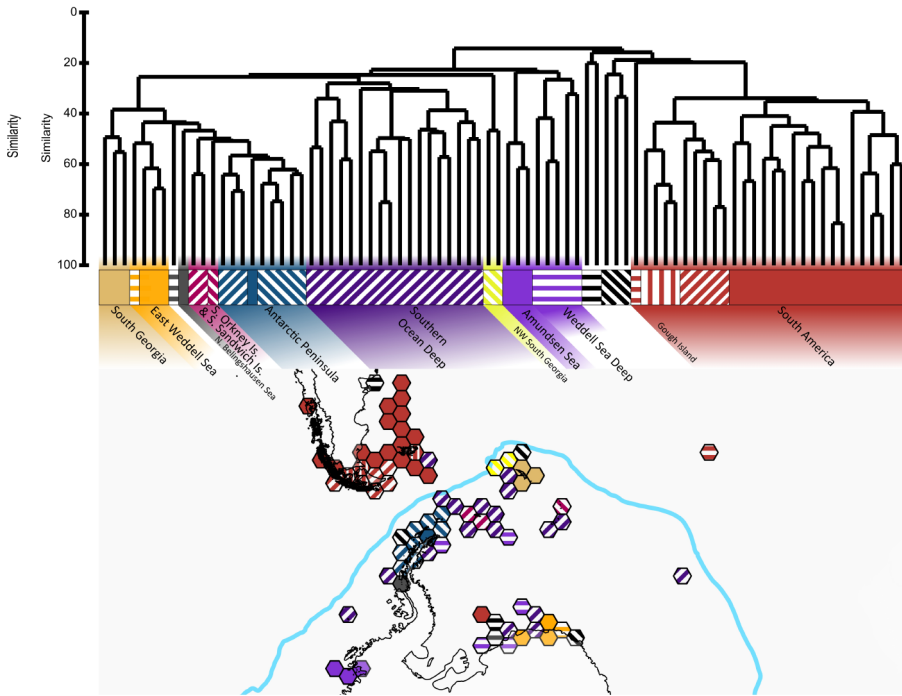
Fig. 4 All depths combined hierarchical cluster analysis of species in 40 000 km^2 hexagons. The dendrogram shows faunal similarity between hexagons, each bar below the dendrogram represents a significant grouping as determined by SIMPROF. The map below is the geographic representation of clusters determined by SIMPROF. The blue line represents the mean position of the Antarctic Polar Front (Sokolov and Rintoul 2009)

Table 1 Summary of data for different depth bins, including total number of species and stations in each depth bin, the number of species and stations for each bin North and South of the Antarctic Polar Front

Depth bin	Total no. species	No. species North	No. species South	Total no. stations	No. stations North	No. stations South
0–200 m	140	51	113	926	251	675
200–500 m	159	36	149	700	81	619
500–1000 m	125	22	112	297	23	274
>1000 m	104	30	92	250	34	216
Totals	254	82	213	2173	389	1784

profile) to determine the structure, with clear splits between hexagons from south of the PF and those in the north, while deeper bins showed less differentiation (Fig. 5).

The 0–200 m depth bin cluster and SIMPROF analysis revealed 25 distinct faunal groups made up of 15 multi-hexagon groups (groups of two or more hexagons with SIMPROF-determined significantly similar assemblages) and a further 10 hexagons that are either singletons (individual polygons with faunal lists that do not significantly group with any other hexagon in the SIMPROF analysis) or very low similarity SIMPROF groupings (with similarity levels of close to 0%) (Fig. 5a). There are four distinct South American multi-hexagon

groups clustering with ∼14% similarity. Nine multi-hexagon groups and four singletons clustering with ∼8% similarity are found only in Antarctica. Three groups had hexagons on both sides of the PF and were either poorly sampled or only contained records for widespread Southern Hemisphere species.

The 200–500 m depth bin formed 27 clusters comprising 15 multi-hexagon groups and 12 singletons (5b). Three multi-hexagon groups clustering with ∼10% similarity were confined to South America waters. Seven multi-hexagon groups and two single hexagons clustering with ∼18% similarity were found only in Antarctica. One group, found mostly in South America, had hexagons on both sides of the PF; this group was influenced by the presence of *Austropallene cornigera*, a common circum-Antarctic and sub-Antarctic species.

Fig. 5 Groups resulting from hierarchical cluster analysis of regions across the Antarctic Polar Front from four different depth bins (**a**) 0–200 m, (**b**) 200–500 m, (**c**) 500–1000 m, and (**d**) >1000 m. Blue line represents the mean position of the Antarctic Polar Front (Sokolov and Rintoul 2009). Bars to the left of the dendrogram represent whether a branch is positioned north (white bar) or south (black bar) of the Antarctic Polar Front
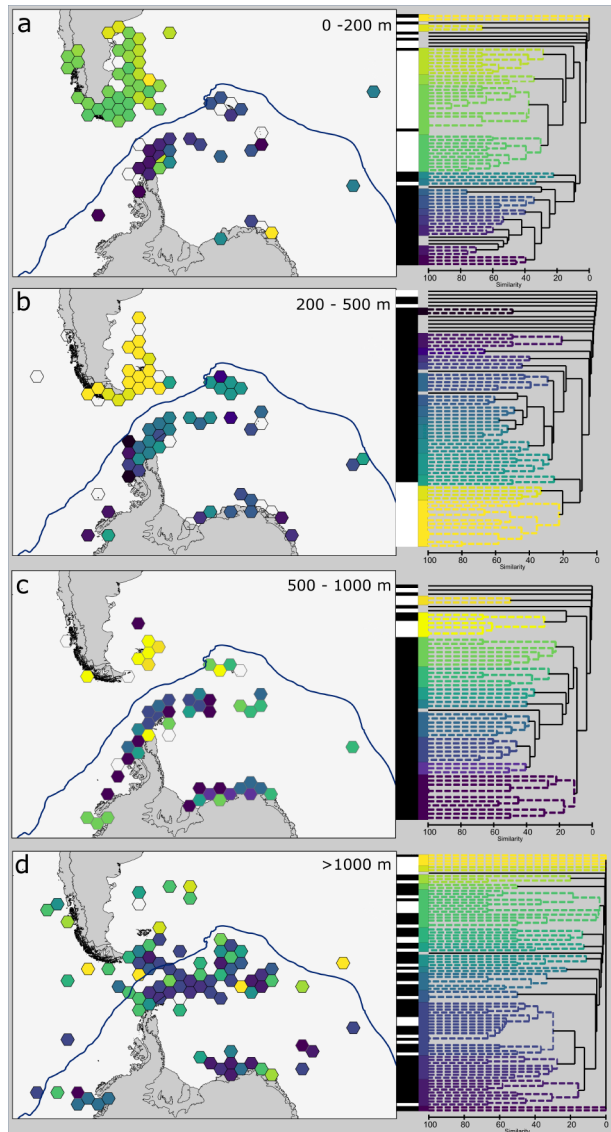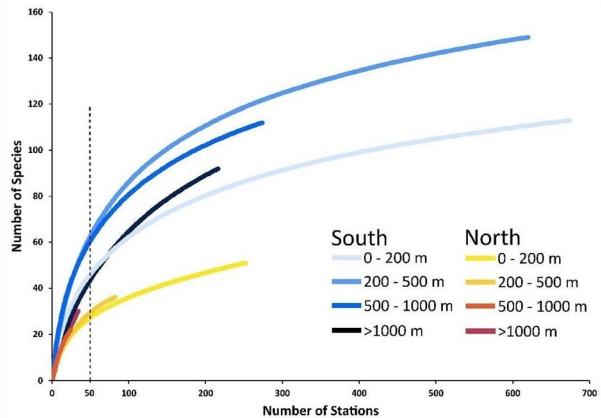
Fig. 6 (**a**) Species accumulation curves for the different depth bins (0–200 m, 200–500 m, 500–1000 m, and > 1000 m) for the regions north and south of the PF

The 500–1000 m depth bin analysis resulted in 16 groups, 10 multi-hexagon groups and six single hexagons (5c). One multi-hexagon group and a single hexagon clustering with ~20% similarity were South American only. A set of eight multi-hexagon groups and one single hexagon sharing~9% similarity were found in Antarctica. Two of the groups, one mainly South American and the other mainly Antarctic, had records on both sides of the PF and consist of a range of general Southern Hemisphere species.

There was no geographic structure in the > 1000 m depth bin in relation to the PF and most groups had a wide geographic distribution (5d). Of the 17 groups (12 of which were multi-hexagon groups and five of which comprised singletons or hexagons with very low similarity to others). There were only two multi-hexagon groups exclusively south of the PF and these were well separated on the dendrogram. Ten groups had records on both sides of the PF and were dominated by eurybathic or deep-sea species such as *Colossendeis megalonyx* (92% SIMPER contribution to one group) and *Colossendeis media*, *Pantopipetta longituberculata*, and *Nymphon hadale*.

Species accumulation curves

Species accumulation curves for the different depth bins for the regions north and south of the PF show that all depths in the south are significantly richer in biodiversity than those in the north. Within the southern groups the richest depth bin was 200–500 m and the least diverse was the 0–200 m (6). North of the PF the most sampled depth bin, 0–200 m, had the highest number of species but the 500–1000 m and > 1000 m bins, despite being the least sampled, had steeper curves meaning they are potentially richer than their better sampled shallower counterparts.

Drivers of similarity: ANOSIM & SIMPER

The results of the ANOSIM analysis of the depth bins across the PF indicated significant faunal composition differences between north and south of the PF between 0 m and 1000 m ($R^2 = 0.361–0.526$ and P values of < 0.01) (Table 2). Areas deeper than 1000 m south of the PF showed a high degree of similarity with all northern depth bins but had least similarity with the 0-200 northern depth bin ($R^2 = 0.327$ and P value of < 0.01). Very little evidence of

Table 2 Results of the ANOSIM analysis of the depth bins (0–200 m, 200–500 m, 500–1000 m, and > 1000 m) across the Polar Front. Numbers give the R^2 values for the pairwise comparisons between bins. Statistically significant results in bold (P value < 0.05). Global Test: Sample statistic (R): 0.222. P value: 0.01. Number of permutations: 999. Number of permuted statistics greater than or equal to R: 0

	North 0 200 m	North 200– 500 m	North 500– 1000 m	North > 1000 m	South 0 200 m	South 200– 500 m	South 500– 1000 m	South > 1000 m
North 0–200 m								
North 200–500 m	0.02							
North 500–1000 m	0.021	-0.081						
North > 1000 m	**0.436**	**0.25**	-0.02					
South 0–200 m	**0.512**	**0.45**	**0.526**	**0.439**				
South 200–500 m	**0.454**	**0.377**	**0.407**	**0.393**	0.03			
South 500–1000 m	**0.488**	**0.403**	**0.421**	**0.361**	**0.084**	0.012		
South > 1000 m	**0.327**	**0.224**	0.2	**0.156**	0.074	**0.078**	**0.069**	

Table 3 SIMPER within group similarity for the depth bins north and south of the Antarctic Polar Front

	0–200 m	200–500 m	500–1000 m	> 1000 m
North	19.86	18.51	18.87	1.62
South	19.13	15.34	13.44	8.03

faunal difference was found between any of the depth bins south of the PF, with very low R^2 values (< 0.09). While the shallower depth bins (0–1000 m) north of the PF were not demonstrated to be different from each other (R^2 values of < 0.03 and P values of > 0.05), the 0–200 m and 200–500 m bins were significantly different to the > 1000 m northern fauna (R^2 = 0.436 and 0.25 respectively and P values of 0.01).

The SIMPER results echoed the ANOSIM, showing highest dissimilarity between the northern and southern bins (> 90%) and lowest dissimilarity among the shallower depth bins in the north and among the shallowest in the south (< 90%) (Table 3 and Supplementary information S1). The northern > 1000 m bin showed a high dissimilarity (> 96%) with all other bins. The within-group similarity for the north showed a dramatic drop off for stations > 1000 m and in the south showed a trend of decreasing similarity with increasing depth (Table 3). For the shallower stations (0–1000 m) the north had higher within-group similarities than their southern counterparts, however for > 1000 m the north had the lowest similarity. The main species contributing to the within-group similarity in the shallow northern bins (0–1000 m) was *Pallenopsis patagonica*, accounting for between 53.5 and 84.8% of the overall similarity. For the deepest northern bin, > 1000 m, *Colossendeis megalonyx* (45%) was the main contributing species, with *C. angusta*, *C. media* and *Nymphon hadale* all accounting for ~14% each. In the south, the greatest contributing species across all depths included *C. megalonyx* (7–43%) and *N. australe* (8–24%). The less speciose northern bins only required between one (500–1000 m) and four (> 1000 m) species to account for 75% of the within group similarity with an average contribution of 32%, whereas the more diverse southern bins required between four (> 1000 m) and 15 (200–500 m) species with an average contribution of 7%.

Percentage similarity

The proportion of shared pycnogonid species either side of the PF is asymmetric. All depth bins north of the PF share over 47% of their species with at least one southern depth bin (Table 4). Conversely the southern stations only share significant percentages with each other and share less than 22% of their species with the less speciose northern bins. The deep (>1000 m) northern bin had a greater affinity with the southern bins (40–63%) than it did with the shallower northern bins (30–40%). The shallowest northern bin (0–200 m) has its highest percentage of shared species with the shallow (0–200 m) southern bin (47%) and has a low percentage of shared with other northern groups (18–41%) but species from this bin account for significant proportions of the 200–500 m (58%) and 500–1000 m (73%) northern bins (Table 4).

Discussion

Pycnogonid richness in the study area was higher south of the Polar Front than north of it (Figs. 2a and 6). The addition of the new data from Maxwell et al. (2022) added a considerable number of records (circa an extra 20% south of PF) to the area and reinforced the findings of previous work (Griffiths et al. 2011a). Other taxa within the same geographic range show similar distinctions in species richness and faunal patterns north and south of the PF, with the PF marking a point of species turnover, south of which species richness increases, e.g., Gastropods (Griffiths et al. 2009; Valdovinos et al. 2003), demosponges, (McClintock et al. 2005). seastars (Moreau et al. 2021), and echinoids (Saucède et al. 2014).

The Antarctic Peninsula, South Shetland Islands, Eastern Weddell Sea and South Orkney Islands were identified as areas of high seaspider richness in the Southern Ocean in the current analysis (Fig. 3), reinforcing previous findings that these areas are biodiversity hotspots for pycnogonids (Griffiths et al. 2011a; Munilla and Soler Membrives 2009; Soler-Membrives et al. 2014) along with Asteroidea (Danis et al. 2014), Bivalvia (Griffiths et al. 2009), Porifera (Downey et al. 2012), benthic Amphipoda (De Broyer and Jazdzewska 2014) and

Table 4 The directional percentage of shared pycnogonid species either side of the PF for different depth bins. Numbers represent the percentage of species from the categories in the vertical labels that are shared with the horizontal categories. Grey shading indicates a sharing ≥ 50%

	North 0–200 m	North 200–500 m	North 500–1000 m	North >1000 m	South 0–200 m	South 200–500 m	South 500–1000 m	South >1000 m
North 0–200 m		58	73	30	21	14	11	12
North 200–500 m	41		82	40	21	18	14	15
North 500–1000 m	31	50		33	11	10	7	9
North >1000 m	18	33	45		14	12	11	21
South 0–200 m	47	67	55	53		64	61	47
South 200–500 m	39	72	64	60	83		81	58
South 500–1000 m	24	42	36	40	60	61		54
South >1000 m	22	39	36	63	38	36	45	

Echinoidea (Saucède et al. 2014). These regions have also been shown to have the greatest species richness in terms of total number of species across all taxa (Griffiths 2010). They are also areas of high richness in terms of different macrobenthic community types, as defined by (Gutt et al. 2013). While this consistent pattern of hotspots could simply reflect greater sampling effort in these areas, the dynamic and heterogenous environments in these regions (e.g., as seen in the Bransfield Strait and surrounding areas) are plausible drivers of the increased biodiversity (Gutt et al. 2019). Species diversification may also have been driven by these dynamic and heterogeneous habitats, or by the isolation of lineages in shelf refugia during glacial cycles, as evidenced by numerous molecular studies revealing the presence of cryptic species (Allcock and Strugnell 2012).

Given the nature of the data used, presence only records from GBIF and OBIS, it is not possible to know whether differences in the numbers of species and sampling locations reflect fewer records due to less effort or lower prevalence of pycnogonids within the northern fauna and samples. Diversity hotspots are also likely to be influenced by the thoroughness of taxonomic work undertaken regionally (Clarke et al. 2007). Fortunately, for the SO pycnogonids the vast majority (>92%) of all pycnogonid records come from identifications made by a small pool of expert taxonomists working from the original specimens, reducing the risk of taxonomic bias (Griffiths et al. 2003; Munilla and Soler Membrives 2009).

Only the shallowest (0–200 m) northern depth bin has been sampled to a level comparable to that recorded in the south (Fig. 6), although absence records are not available for either region, making a true measure of effort impossible. The shallowest sites (0–200 m) had the lowest recorded diversity on the species accumulation curves on both sides of the PF, implying that pycnogonids might prefer deeper water. South of the front, past glaciations and the ice-impacted conditions of present day Antarctica might have adversely impacted the shallow water communities (Smale et al. 2007). If disturbance by ice was the cause of the lower shallow diversity, then the opposite would be expected for the northern shallows where disturbance is minimal. North of the PF benthic shelf waters are warmer than the south, and have wider seasonal temperature ranges, e.g., on the Argentinian shelf there is approximately 10 °C difference between winter and summer (Bastida et al. 1992). If pycnogonids are better adapted to colder waters as the richness of Antarctic species might suggest, than seasonally fluctuating warmer waters would be a physiological barrier to overcome. The higher diversity in the cooler deep northern waters, as inferred by shortest and steepest accumulation curve and low within-group similarity, suggests that this could be the case. In shallower waters north of the PF, the presence of potential competitors and predators also explain the lower species richness in the region. South of the PF, potential competitors e.g., brachyuran and anomuran crabs (Griffiths et al. 2013), and predators, e.g. many types of bony and cartilaginous fish (Aronson et al. 2009) of pycnogonids are either absent or underrepresented compared to the rest of the world. These competitors and predators are believed to excluded by the cold conditions (Clarke and Crame 2010) and their presence in warmer waters north of the PF could be another factor in the lower pycnogonid diversity compared to the South.

The faunal divide between South American and the Antarctic reflects previous findings for the pycnogonids (Griffiths et al. 2011a; Soler-Membrives et al. 2014), while the divisions within Antarctic waters show a split between shallow coastal waters and the deep sea. Only the Southern Ocean deep water cluster crossed the PF. Distinct biogeographic groups forming either side of the front are evident in other taxa such as bryozoans and bivalves

(Griffiths et al. 2009), hydroids (Miranda et al. 2021), polychaetes (Montiel et al. 2005) and demosponges (Downey et al. 2012). Unlike pycnogonids, these faunal groups are sessile and have a pelagic larval stage, allowing the circulation of the Antarctic Circumpolar Current, the associated gyres and the Antarctic Coastal Current (ACC) to directly affect their distribution. The ACC, or the vast expanse of deep water it represents, is believed to be an important barrier to species transfer in and out of Antarctica, with recent studies showing that planktonic or rafting organisms, would face a two-year, circumpolar journey on the ACC to reach Antarctica from South America and that the opposite journey in the surface waters would be near impossible (Fraser et al. 2022).

Our results show there is less distinction between northern and southern deep-water communities (Fig. 5d; Table 2) which could be explained by the weakening of the impact of the PF with depth (Clarke et al. 2009; Orsi et al. 1995) and northward flow of cold Antarctic Bottom Water. Species that live shallower than 1000 m face the double hurdle of the temperature gradient and the vast expanse of the deep Scotia Sea to reach the shelf on the other side of the PF. The difference between pycnogonid species assemblages either side of the PF is not absolute, even at shallow depths, with 22% of all species in our study being recorded on both sides. Molecular evidence suggests that some Antarctic taxa, on multiple occasions, have colonised the South American shelf (Havermans et al. 2011; Sands et al. 2015). These shelf-dwelling species could have moved northwards through the deep sea if they were highly eurybathic or in a stepping-stone manner along the islands of the Scotia Arc (Clarke and Crame 1989)aided by interannual shifts in the position of the PF induced by temperature fluctuations, freshwater input, or windforcing (Giglio and Johnson 2016), or the exchange may have happened during a time when the PF was in a different position due to climate shifts (Kemp et al. 2010).

The commonly found and widely distributed taxa, such as *Pallenopsis patagonica*, *Nymphon australe* and *Colossendeis megalonyx*, were largely responsible for the faunal similarity patterns observed (Supplementary Table S2). The presence or absence of these common species are major contributors to within-group similarity and dissimilarity (Table 3 and Supplementary Table S2). *Pallenopsis patagonica* and *C. megalonyx* are cosmopolitan and eurybathic species found throughout the Southern Ocean and southern South America and are the most extensively studied pycnogonids in the world. Phylogenetic studies have revealed that these species have complex and structured distribution patterns. Molecular evidence revealed that *P. patagonica* and *C. megalonyx* are both species complexes that can be assigned to geographically distinct clades, with South America specimens in different clades to those south of the PF, and with multiple clades within Antarctic waters (Dietz et al. 2015; Dömel et al. 2019, 2020; Weis et al. 2014). The well-distributed Southern Ocean species *N. australe* was thought to represent a single circum-Antarctic species with limited contemporary gene flow (Arango et al. 2011) but more recent evidence suggest that there are two genetically distinct species in West Antarctica (Collins et al. 2018). Although there are regional differences and differentiation across the PF in these pycnogonid species complexes, we still lack molecular evidence of depth differentiation within these complexes. This is probably due to the paucity of deep-sea sampling, with our dataset showing that >74% of all pycnogonid sampling occurred shallower than 500 m, despite ~77% of species having recorded samples that go deeper (Griffiths et al. 2011a). This lack of representative sampling in the deep sea on both sides of the PF restricts our ability to understand connectivity in this vast habitat (Brandt et al. 2007).

The depth bins north of the PF are heavily influenced by taxa also found in the south, with at least 50% of the pycnogonid biodiversity of most northern bins being made up of species shared with the south (Table 4). This suggests greater, but more directional, connectivity across the PF than was revealed by the other analyses. Pycnogonids in the Southern Ocean are highly eurybathic with nearly 40% of species having a depth range greater than 1000 m (Griffiths et al. 2011a). Northward export of the benthic Antarctic water masses in the deep sea (Naveira Garabato et al. 2002) might aid the dispersal of eurybathic and deep water pycnogonids out of the Antarctic, while potentially impeding northern species trying to move south. Weddell and Prydz Bay sourced bottom waters are the main sources of bottom water flowing northwards. They cross the PF into the deep Scotia Sea and are driven north-eastwards by the Antarctic Circumpolar Current into the Atlantic (Solodoch et al. 2022). This Antarctic-sourced seafloor water flows around the Falkland Plateau and into the Argentine Basin of the southwest Atlantic (and to a lesser extent the east side of the Mid-Atlantic Ridge), carrying with it nutrients, oxygen and life (Strugnell et al. 2008).

The high species richness of the Southern Ocean in some taxa, and ability to disperse northwards through the deep sea, supports the suggestion of the Southern Ocean as a cradle of origin or centre of radiation for some groups. Such Antarctic radiations were proposed initially based on morphological features of isopods, with some groups showing polar emergence and others polar submergence (Bober et al. 2018; El-Sayed 1973). Molecular evidence in support of the hypothesis was first provided in octopuses (Strugnell et al. 2008) and subsequently for a diversity of taxa (see Introduction). In pycnogonids, a radiation of the family Colossendeidae began in the Southern Ocean in the Early to Mid-Miocene with species crossing the PF to South America, the Kerguelen Plateau, and northwards through the deep sea, with one species even reaching the Arctic (Dömel et al. 2019) providing strong evidence that our higher Southern Ocean richness is indicative of evolutionary processes in this region.

Conclusions

We found that, in addition to supporting previously recorded differences in pycnogonid richness and species composition between north and south of the PF, this differentiation, like the PF itself, weakens with depth. South of the PF species richness is greatest 200–1000 m, while north of the front richness is highest at depths below 1000 m. This suggests that, as a group, pycnogonids are better adapted to colder, deeper waters. The region deeper than 1000 m shows high and underexplored diversity with connections that resemble the flow of Antarctic Bottom Water northwards into the global ocean. Given that the deep sea comprises ∼ 80% of the Southern Ocean, with direct connections to every other ocean basin except the Arctic, understanding the role of the Southern Ocean in global deep-sea connectivity and speciation are key questions in marine biogeography. With only ∼ 11% of our sampling stations in this study coming from > 1000 m depth, to understand the true nature of these deep connections will require further sampling of the deep sea on both sides of the PF and the use of molecular/genomic analyses to determine the connectivity between these seemingly poorly dispersing organisms. The exceptionally high diversity of Antarctic pycnogonids and an apparent competitive advantage in cold waters leaves them vulnerable to ongoing climate change and ocean warming.

Data availability All data used in this study was sourced from Ocean Biodiversity Information System (https://obis.org/) and the Global Biodiversity Information Facility (https://www.gbif.org/) and is publicly available.

Declarations

Ethical approval Not applicable.

Competing interests The authors declare no competing interests.

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