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Well-connected worms: genetic connectivity of annelids (Melinnidae and Ampharetidae) across a biogeographical break in Australia's eastern abyss

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Abstract. Marked species composition changes are observed between shallow-water (0–200 m) temperate and tropical fauna, however, this transition is not well documented in deep-water fauna (> 200 m). Along the east coast of Australia there is an apparent biogeographic tropical to temperate transition between 30–40°S for bathyal and abyssal fauna. This has been recorded for brittle stars (Echinodermata: Ophiuroidea) and certain benthic megafauna taxa combined but not tested for other taxa individually or tested with genetic data. During the 2017 RV *Investigator* expedition, a series of beam trawl and epibenthic sledge samples were taken from 13 sites along a south to north latitudinal transect along the east coast of Australia, from Freycinet Marine Park, 42°S, to Coral Sea Marine Park, 24°S, from 1,000 to 4,800 m depth. Three of the most abundant segmented worms (Annelida: Polychaeta) species, *Melinnopsis gardelli*, *Melinnopsis chadwicki* (Melinnidae) and *Jugamphicteis galatheae* (Ampharetidae) were morphologically identified, and the COI genetic marker was sequenced for 88 specimens. *Melinnopsis gardelli* was recorded across the biogeographical break from 42°S to 24°S. An AMOVA for the north and south populations revealed significant evidence of populations structuring of this species. The other two species, *M. chadwicki* and *J. galatheae,* were recovered from north and south respectively of the biogeographic break. One haplotype of *M. gardelli* was shared between two sampling locations south of the break, Jervis Marine Park and Freycinet Marine Park (distance 735 km), similarly, haplotypes were shared for *M. chadwicki* between locations 726 km apart and *J. galatheae* 950 km apart. We found genetic evidence of a break occurring at 28–35°S dividing *M. gardelli* populations in the north and south, additionally our data appeared to show a third central population for *M. gardelli*. However, the break was not strongly defined as *M. gardelli* was found to bridge across the transition. Our results indicated deep-sea annelid populations are well connected along sections of the eastern Australian margin, suggesting the designated deep-water Marine Parks function as an important network for these organisms.

Keywords: biogeography; deep sea; Annelida; phylogeography; macrobenthos
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Introduction

Biogeographical provinces are geographic regions that contain groups of plants and animals, and physical features that are distinct or unique from their surroundings at a particular scale (UNEP, 2007). Accurately assigning biogeographic provinces and the transition zones between provinces provides a critical base map to focus the study, conservation and management of biodiversity. Global biogeographical provinces are well delineated for terrestrial (Olson *et al.*, 2001), freshwater (Abell *et al.*, 2008; Collen *et al.*, 2014), and shallow-water marine (coastal and shelf) habitats (Spalding *et al.*, 2007), yet provinces for deeper oceanic habitats such as continental slopes and abyssal plains are less well-defined, particularly at smaller spatial scales (UNESCO, 2009; Watling *et al.*, 2013; Costello *et al.*, 2017). This creates challenges for designing effective deep-sea marine protected areas which prioritize areas of high species distinctiveness.

Biogeographic ranges of species in the deep sea (> 200 m) are thought to be large in comparison with those of shallow-water species (coastal waters < 200 m) owing to the perceived lack of barriers to dispersal and homogeneity of the environment in much of the deep sea (McClain & Hardy, 2010). Traditionally observations of deep-sea species based on morphological data resulted in the theory of wide dispersal and cosmopolitan species (Ekman, 1953), where 'cosmopolitan' distributions are defined as distributions occurring in two or more ocean basins (Hutchings & Kupriyanova, 2018). For example, studies on protobranch bivalves across the deep-sea floor (260 m to 5,800 m) of the Atlantic demonstrated that the average number of cosmopolitan species was higher at greater depths (70% total number of species at 4,500 m) than shallower depths (around 15% at 1,000 m) (Allen & Sanders, 1996). Implementation of genetic techniques over the past decade revealed pan-oceanic and even bipolar distributions for some deep-sea annelids (Georgieva *et al.*, 2015; Eilertsen *et al.*, 2018; Guggolz *et al.*, 2020; Meißner *et al.*, 2023; Budaeva *et al.*, 2024). Yet other findings indicate that deep-sea species described as 'cosmopolitan' using morphological methods may consist of multiple cryptic species when examined using molecular methods (Havermans *et al.*, 2013; Brasier *et al.*, 2016; Nygren *et al.*, 2018).

Species ranges are directly influenced by genetic connectivity between populations, the exchange of genes between populations, which affects the evolutionary processes within populations (Lowe & Allendorf, 2010). Notably, much of the research on genetic connectivity in deep-sea invertebrates has focused on individual species of economic interest (Drengstig *et al.*, 2000; Jorde *et al.*, 2015), species from specialised habitats (reviewed in Taylor & Roterman, 2017), for example, chemosynthetic environments such as hydrothermal vents and cold seeps (Vrijenhoek, 2010; Xiao *et al.*, 2020; DeLeo *et al.*, 2022), seamounts (Miller *et al.*, 2010; Miller & Gunasekera, 2017), or areas of economic interest such as potential deep-sea mining sites with high densities of manganese nodules (Taboado *et al.*, 2018; Janssen *et al.*, 2019; Stewart *et al.*, 2023). Such specialised habitats may not accurately represent the rest of the deep-sea environment, particularly the extensive soft-sediment habitats at bathyal and abyssal depths. Consequently, there is a gap in our understanding of genetic connectivity in the wider deep ocean. Exacerbating this deficit is the sparseness of data from the Southern Hemisphere which make global scale analyses challenging.

Australia has the third largest marine territory in the world, with 48 % of it being deeper than the 3,000 m abyssal boundary (Bond & Jamieson, 2022). This substantial area encompasses multiple biogeographical provinces and transition zones (UNESCO, 2009; Watling *et al.*, 2013). The precise locations of the faunal borders around Australia have been debated (UNESCO, 2009; Watling *et al.*, 2013; Costello *et al.*, 2017), particularly off the eastern coast where geomorphic features and limited biological data were used to produce biogeographic provinces (Harris *et al.*, 2008) from which a network of marine protected areas (Marine Parks) was established. Along the eastern coast demersal fish (> 40 m depth) species occurrence data suggested two biogeographical provinces, Central Eastern Province (CEP) from Southport (Queensland) 27º51'S to Ulladulla (NSW) 35º20'S, and Tasmanian Province (TasP) from Lakes Entrance (Victoria) 148º31'E to Woolnorth Point (Tasmania) 143º50'E. These two provinces had 'biotones' or transitional areas designated as Central Eastern Transition and Southeastern Transition zones where species from adjacent biomes overlap (Last *et al.*, 2011). Modelling of environmental data in the Global Open Ocean and Deep Sea (GOODS) classification indicated that at lower bathyal depths (800–3,000 m), the transition between the West Pacific and New Zealand-Kermadec provinces occurs at around 23°S along the eastern Australian coast. This transition was the same at abyssal depths (3,500–6,500 m). Furthermore the Tasman abyssal plain in southeast Australia was listed as part of the Indian province which stretched from east Africa through to New Zealand, although the authors acknowledged the region was not well studied and may contain species following Antarctic bottom water northward (UNESCO, 2009). Agreeing with the GOODS classification, Watling *et al.* (2013) also proposed two lower bathyal provinces along eastern Australia (BY6 New Zealand-Kermadec and BY12 West Pacific) with the break between them at 23°S. At abyssal depths the province 'AB8' also ended at the same location, at the Tasman abyssal plain, and did not extend northward along the Australian east coast (Watling *et al.*, 2013).

Studies using benthic faunal data (as opposed to demersal fish data and environmental data above) revealed slightly different patterns. For example, Vinogradova (1958) designated abyssal (3,000–4,500 m) West-Pacific and Indian provinces which converged along the east coast of Australia at 40°S. Costello *et al.* (2017) assigned two realms 'Tropical Australia and Coral Sea' and 'South Australia' along eastern Australia with the division between them around 35°S. O'Hara *et al.* (2011) reported a tropical to temperate transition at 30°–40°S along the east coast using benthic ophiuroid data. From shallow water to bathyal depths (0–2,000 m), ophiuroids are distributed in three broad latitudinal bands from the equator to the South Pole, with a tropical-temperate transition at 30°–40°S (O'Hara *et al.*, 2011). This distinction was also seen in mitochondrial (COI) data from ophiuroids collected at bathyal depths (200–3,500 m) (O'Hara *et al.*, 2014). At both lower bathyal (~2,500 m) and abyssal (~4,000 m) depths the transition has been reported at 33°–30°S for megafauna including sponges, anemones, octocorals, barnacles, decapods, pycnogonids,

annelids, echinoderms, gastropods, bivalves, cephalopods and fish (O'Hara *et al.*, 2020a). Interestingly, the transition occurred across almost uniform temperature, salinity and dissolved oxygen and appeared to be linked to the flux of organic matter to the sea floor (O'Hara *et al.*, 2020a). Such a transition has not been tested with individual taxa in the lower bathyal and abyssal zone, indeed, studies using combined taxa may generate patterns driven by one or several individual groups.

Annelids are a dominant macrofauna (>300 µm) taxon in terms of abundance and species diversity in deep-sea soft sediments (Glover *et al.*, 2002; Rex & Etter, 2010; MacIntosh *et al.*, 2018; O'Hara *et al.*, 2020b). They display a fascinatingly diverse range of life history and reproductive strategies, from internal fertilization of brooders which produce a few large, yolky eggs that directly develop into juveniles, to species that spawn many small eggs which are fertilized in the water column where they may stay as planktotrophic larvae for weeks before settling and metamorphosing into juveniles (Rouse *et al.*, 2022). These contrasting modes of reproduction and dispersal likely affect the population connectivity of deep-sea invertebrate species (Baco *et al.*, 2016), making annelids interesting model organisms for phylogeographic and genetic connectivity studies.

In this study we assessed genetic connectivity in three species of annelids from lower bathyal and abyssal along the eastern margin of Australia using mitochondrial DNA data. We tested the hypotheses that: 1) species distribution and genetic patterns of these annelids will coincide with the known biogeographical tropical to temperate transition between 30–40°S along the eastern Australia margin, and 2) populations either north or south of the divide will be well-connected.

Materials and methods

Study area

The eastern Australian landmass is bordered by the Coral Sea in the north, and the Tasman Sea in the south. The eastern continental shelf is narrow compared with that of the rest of the continent, so the abyssal plain can be as close as 60 km to the east coast (Heap & Harris, 2008). Heap and Harris (2008) identified three regions based on the distribution of geomorphic features: Region 1 (northeast) contained plateau, coral reef and trough features, Region 2 (east) narrow shelf, canyon, abyssal plain and seamount features, and Region 3 (southeast) plateau, basin, seamount and canyon features. Marine carbonates dominate the regional sedimentology, with a tropical carbonate margin in the north leading to a mixed-terrigenous-carbonate margin in the south. Sediment shows zoning with depth, terrigenous quartzose sediments on the inner shelf, carbonate dominated sediments on the outer shelf, and calcareous silts and clays occurring at abyssal depths (Keene *et al.*, 2008).

The shallow-water (typically 200 m depth) East Australian Current (EAC) flows from north to south along the east coast (Ridgway & Dunn, 2003), it heads eastward around 32-35°S, and part is deflected offshore around 30°S along the Tasman Front (Rintoul *et al*., 2017). The remainder, the EAC extension, continues poleward. At depths around 1,000 m Antarctic Intermediate Water (AAIW) also flows from north to south along the east coast (Chiswell *et al*., 2015). The AAIW found in the Coral and Tasman Seas has a temperature range 4–8°C and salinity 34.45–35.6 ‰ (Bostock *et al*., 2013). At around 3,000 m depth the Lower Circumpolar Deep Water (LCDW) flows in the opposite direction (south to north) along the continental margin (Chiswell *et al*., 2015). Antarctic Bottom Water (AABW) enters the western Tasman Sea and circulates cyclonically around 4,000 m (Chiswell *et al*., 2015). The mean water mass temperature and salinity for the wider region (80°–160°E) of AABW is −0.17°C and 34.68‰, respectively (Orsi *et al*., 1999). Seafloor sediments are well oxygenated at all water depths, the oxygen minimum zone found at 1,000–2,000 m is weak and does not affect seafloor fauna (Keene *et al*., 2008).

Specimen collection

All samples were collected during research vessel (RV) *Investigato*r voyage 'Sampling the Abyss' (IN2017_V03), the first dedicated expedition to sample the fauna from the Australian eastern lower bathyal and abyssal environments. From 15 May to 16 June 2017 samples were taken along a south to north latitudinal transect of 18 degrees along the east coast of Australia, from 42°S to 24°S (Fig. 1; Suppl. Table 1, Gunton *et al.*, 2025a). Sampling encompassed 13 localities including seven Marine Parks (Freycinet MP, Flinders MP, East Gippsland MP, Jervis MP, Hunter MP, Central Eastern MP and Coral Sea MP). Samples were collected from 2,500 m and 4,800 m depths, with several shallower samples taken around 1,000 m using the CSIRO 4 m wide x 0.5 m high beam trawl (Lewis, 2010) and Brenke epibenthic sledge (Brenke, 2005). Onboard, collected annelids were sorted into families on ice in chilled (5°C) seawater, then fixed in either 95% ethanol or in 10% buffered formalin. A detailed account of onboard processing methods is provided in Gunton *et al.* (2021). Only specimens fixed in ethanol were used for this study.

Annelid identification

Annelid specimens were shipped to and deposited at the Australian Museum Marine Invertebrate Collections. Specimens were examined in 95% ethanol using a dissecting (OLYMPUS SZX7) and compound (OLYMPUS BX53) microscopes. Individuals of *Melinnopsis gardelli* Gunton, Kupriyanova & Alvestad, 2020; *Melinnopsis chadwicki* Gunton, Kupriyanova & Alvestad, 2020 (family Melinnidae); and *Jugamphicteis galatheae* Holthe, 2000 (family Ampharetidae) were used in the present study. These named species were among the most abundant annelid taxa collected during the expedition (Gunton *et al.*, 2021) and had recent or detailed morphological descriptions available. All specimens were registered with the prefix "AM W." and lodged at the Australian Museum, whereas DNA extractions were integrated into the frozen tissue collection of the Australian Centre for Wildlife Genomics, Australian Museum.

Molecular methods

Tissue samples were obtained from 27 *M. gardelli*, 43 *M. chadwicki* and 18 *J. galatheae* specimens. Total genomic DNA was extracted using a Bioline Isolate II genomic DNA

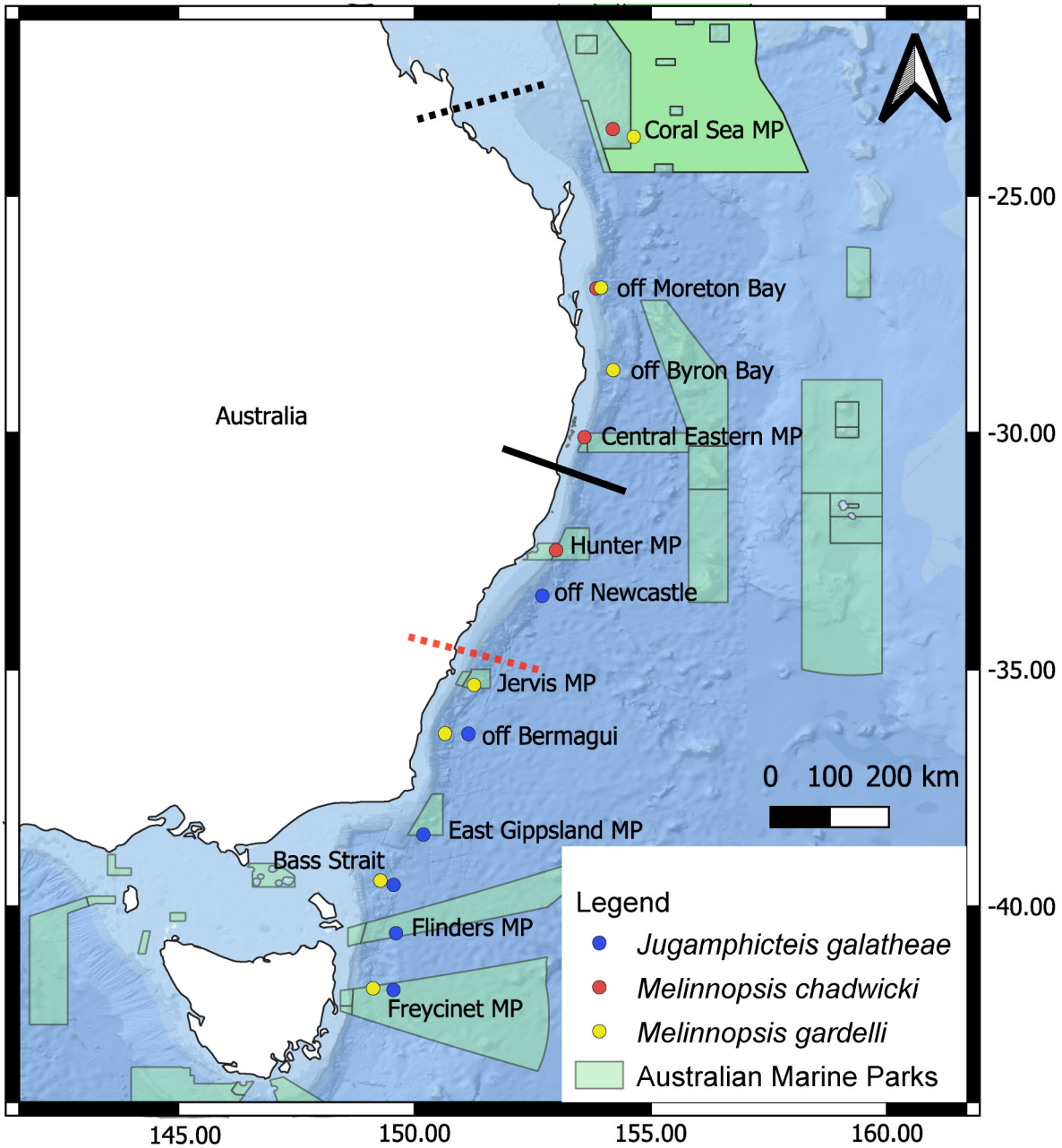

Figure 1. Map of sample sites along the east coast of Australia. Black bar marks faunal boundary recorded in O'Hara *et al.* (2020a). Black dashed line marks faunal boundary from Global Open Ocean and Deep Sea (GOODS) classification (UNESCO, 2009). Red dashed line marks faunal boundary from Costello *et al.* (2017).

kit following the manufacture's protocols. Polymerase chain reaction (PCR) amplification of part of the cytochrome c oxidase subunit I (COI) gene was conducted using two sets of primers (Table 1). PCR mixtures consisted of 0.4 µl of each primer (forward and reverse), 1 µl of template DNA, 2 µl of Coral Load Qiagen PCR buffer, 1.5 µl of $MgCl_2$, 1.5 µl of dNTPs, 0.1 µl of MyTaq DNA Polymerase Bioline and 13.1 µl of water, making a total mixture of 20 µl. PCRs were conducted in a Thermal Cycler with the following conditions: primers polyLCO/ polyHCO and polyLCO/ polyshortHCO - 94°C/1 min, 5 cycles 94°/40 s, 45°/40 s, 72°/60 s, followed by 35 cycles 94°/40 s, 51°/40 s, 72°/60 s, and finally 72°/5 minutes; primers HCO/LCO - 94°C/ 2 min, 35 cycles 94°C/30 s, 50°C /45 s, 72°C/60 s, finally 72°C/3 min. The quantity of PCR products was detected using gel electrophoresis and visualized using a Bio-Rad XR+ Gel Documentation System. Successful PCR products were sent to Macrogen South Korea where they were purified, and standard Sanger sequencing was performed.

Sequence editing and processing

Sequences were manually edited in Geneious Prime 2019.0.4 (https://www.geneious.com). A BLAST analysis (Altschul *et al.*, 1990) was performed to confirm the correct region had been amplified, to compare with other sequences on GenBank, and to check for contamination. Nucleotide sequences were translated into amino acid sequences to confirm stop codons were absent and thus checking for

Table 1. COI primers used for PCR and sequencing

Primer	Sequence 5'-3'	Direction	Reference
LCO	GGTCAACAAATCATAAAGATATTGG	Forward	Folmer *et al*., 1994
HCO	TAAACTTCAGGGTGACCAAAAAATCA	Reverse	Folmer *et al.*, 1994
polyLCO	GAYTATWTTCAACAAATCATAAAGATATTGG	Forward	Carr *et al.*, 2011
polyHCO	TAMACTTCWGGGTGACCAAARAATCA	Reverse	Carr *et al.*, 2011
PolyshortCOIR	CCNCCTCCNGCWGGRTCRAARAA	Reverse	Carr *et al.*, 2011

pseudogene amplification. New sequences were submitted to GenBank (Suppl. Table 2, Gunton *et al*., 2025a).

Phylogenetic analysis

Two separate datasets were compiled because analysed species belonged to families Ampharetidae and Melinnidae. Additional sequences of 13 Melinnidae, 41 Ampharetidae, two Terebellidae and one Alvinellidae were downloaded from GenBank (Suppl. Table 2, Gunton *et al*., 2025a). Sister taxa were used as outgroups following Stiller *et al.* (2020): Alvinellidae for Ampharetidae and Terebellidae for Melinnidae. Sequences were aligned using the Geneious plugin MUSCLE (Edgar, 2004) with the default settings. The optimal evolutionary model for each alignment was identified by jModelTest 2.1.10 (Darriba *et al.*, 2012) using both the Akaike Information Criterion and the Bayesian Information Criterion. The best fit model of nucleotide substitution was GTR+G for the Ampharetidae dataset, and GTR+I+G for the Melinnidae dataset. Bayesian phylogenetic trees were constructed in MrBayes v3.2.6 (Ronquist *et al.*, 2012). The analysis was run for 10,000,000 generations, until the standard deviation of split frequencies was below 0.01 and potential scale reduction factor (PSRF) was 1.0 for all parameters, with the first 25% discarded as burn-in. Results were visualised using the Tracer v1.7 (Rambaut *et al.*, 2018) to ensure convergence and effective sampling size of each parameter was > 200. Trees were visualised in FigTree v1.4.4 (Rambaut, 2018) and edited in Adobe Illustrator.

Population genetics analysis

All sequences of individual species were trimmed to the same length to exclude missing data, and if sequences were too short (> 10% missing, i.e., *M. gardelli* < 549 bp, *M. chadwicki* < 519 bp, *J. galatheae* < 575 bp), they were removed from the alignment. Uncorrected pairwise p-distance matrixes for each species were calculated in MEGA X (Kumar *et al.*, 2018). Haplotype networks were constructed using the Median Joining method in PopART v 1.7 (Leigh & Bryant, 2015) and edited in Adobe Illustrator. For each species, haplotype diversity (*h*), nucleotide diversity (π), number of polymorphic sites (*Np*), and the neutrality test Fu's *Fs* (Fu, 1996) were calculated in DnaSP v6 (Rozas *et al.*, 2017).

Only *M. gardelli* was found at sites spanning the suggested biogeographic break (30–40°S) (Fig. 1). Owing to most sites yielding very low numbers of individuals, sequences from seven sites were *a priori* divided into North (sites: Coral Sea MP, off Moreton Bay and off Byron Bay) and South (sites: Jervis MP, off Bermagui, Bass Strait and Freycinet MP) groups given results from Watling *et al.* (2013) and O'Hara *et al.* (2020a, 2020c). To assess population genetic structure within and between these north and south groups a standard Analysis of MOlecular VAriance (AMOVA) was performed, and the fixation index (F_{ST}) values calculated to test for population genetic divergences in Arelquin v3.5 (Excoffier & Lischer, 2010). The AMOVA was performed using pairwise differences and 1,000 permutations. F_{ST} is a measure of genetic difference between populations where values range from zero to one. A value of zero indicates complete sharing of genetic material between populations and the populations interbreed freely, with no differentiation between populations. A value of one indicates all variation exists within the separate populations, with no sharing of genetic material between populations.

Results

A total of 88 COI partial sequences were obtained, including 27 sequences of *M. gardelli*, 43 of *M. chadwicki* and 18 of *J. galatheae* (Table 2). COI intraspecific genetic distances (pairwise p-distance) within *M. chadwicki* ranged 0–1.61%, *J. galatheae* 0–1.07%, *M. gardelli* 0– 4.39%. The highest intraspecific genetic distance between individuals of *M. gardelli* specimens was 4.39% for two specimens collected at Jervis MP (AM W.53128 and AM W.52988). Within Melinnidae interspecific genetic distance ranged 5.8–33.6% (*Melinna heterodonta* and *M. cristata*; *M. gardelli* AM W.53128 and *Isolda bipinnata* MT166993, respectively). Within *Amphicteis* interspecific genetic distance ranged from 17.05% (between *Amphicteis gunneri* and *A. ninonae)* to 23.74% (between *Amphicteis obscurer* and *A.* sp.).

Phylogeography

Jugamphicteis galatheae was recovered as a well-supported monophyletic clade (posterior probability (pp 1)) (Suppl. Fig. 1, Gunton *et al.*, 2025b). Specimens within the shallow monophyletic clade of *J. galatheae* showed no geographical structuring and were recovered from off Newcastle, off Bermagui, East Gippsland MP, Bass Strait, Flinders MP and Freycinet MP. All specimens were from abyssal depths, 3,800–4,800 m.

Melinnopsis chadwicki and *M. gardelli* were recovered as sister taxa with strong support (pp 1). These taxa fell within the larger polytomy of Melinnidae grouping (*Isolda*, *Melinna*, *Melinnopsis*). *Melinnopsis chadwicki* was recovered as a shallow, well-supported monophyletic clade (pp 1) (Suppl. Fig. 2, Gunton *et al.*, 2025b). Specimens within the *M. chadwicki* clade showed no geographical structuring and were collected from Coral Sea MP, off Moreton Bay, Central Eastern MP, Hunter MP. All specimens were from bathyal depths 1,000–1,190 m.

Table 2. Number of COI sequences/ individuals per location

Location	*J. galatheae*	*M. chadwicki*	*M. gardelli*
Coral Sea MP	—	7	3
Off Fraser Island	—	—	—
Off Moreton Bay	—	32	1
Off Byron Bay	—	—	1
Central Eastern MP	—	3	—
Hunter MP	—	1	—
Off Newcastle	5	—	—
Jervis MP	—	—	18
Off Bermagui	1	—	1
East Gippsland MP	1	—	—
Bass Strait	6	—	1
Flinders MP	2	—	—
Freycinet MP	3	—	2
Total	18	43	27

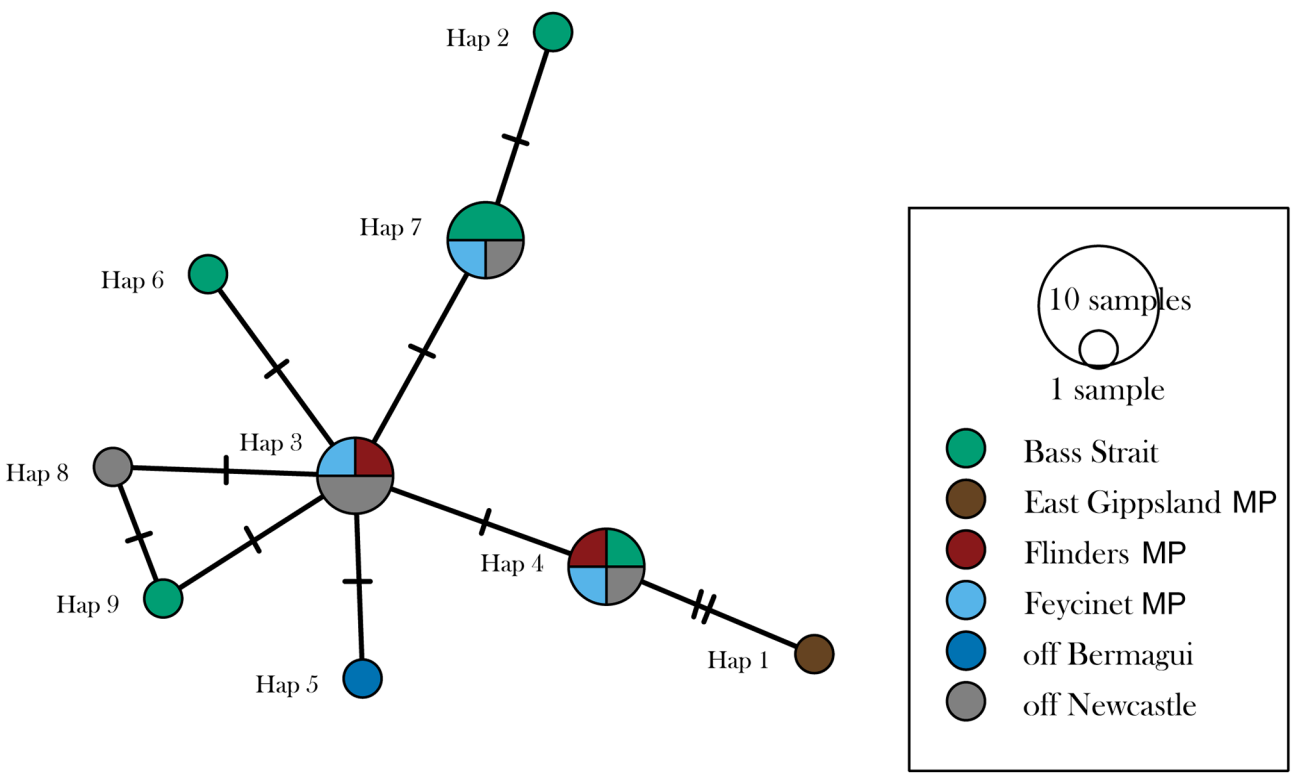

Figure 2. Median-joining COI haplotype network for *Jugamphicteis galatheae.* The size of the circle is proportional to the number of sampled individuals belonging to that haplotype. The colour represents the locality. Lines connect each haplotype to its most similar relative. Bars represent mutational steps between haplotypes.

Melinnopsis gardelli displayed higher genetic variability compared with that of *M. chadwicki* as seen by the more complex branching topology. Within the larger *M. gardelli* well-supported clade (pp 1) three shallow clades corresponding to geographic and bathymetric structuring were nested. Clade A included one specimen (AM W.53128) from Jervis MP (2,650–2,636 m), clade B included 16 specimens from Jervis, Bass Strait and Freycinet MPs (2,650–2,820 m), clade C included five specimens from Coral Sea MP, off Moreton Bay, and off Byron Bay (1,761–2,587 m) and sister to clades A-C, six specimens from Jervis MP and off Bermagui (2,650–2,821 m) (Suppl. Fig. 2, Gunton *et al.*, 2025b).

Geographic distribution of haplotypes

Two main patterns emerged: in *J. galatheae* and *M. chadwicki*, many haplotypes were separated by one or a few nucleotide changes and few haplotypes were widespread (across two or more sites) (Figs 2–3; Haplotype Numbers Supp. Table 2), whereas for *M. gardelli*, the haplotype network could be divided into three main clusters corresponding with the phylogenetic clades, each divided by 14 nucleotide changes, with one outlier (AM W.53128) separated by 19 nucleotide changes (haplogroup A in Fig. 4, clade A in Suppl. Fig. 2). As seen in the phylogenetic tree, these clusters displayed some geographical and bathymetric

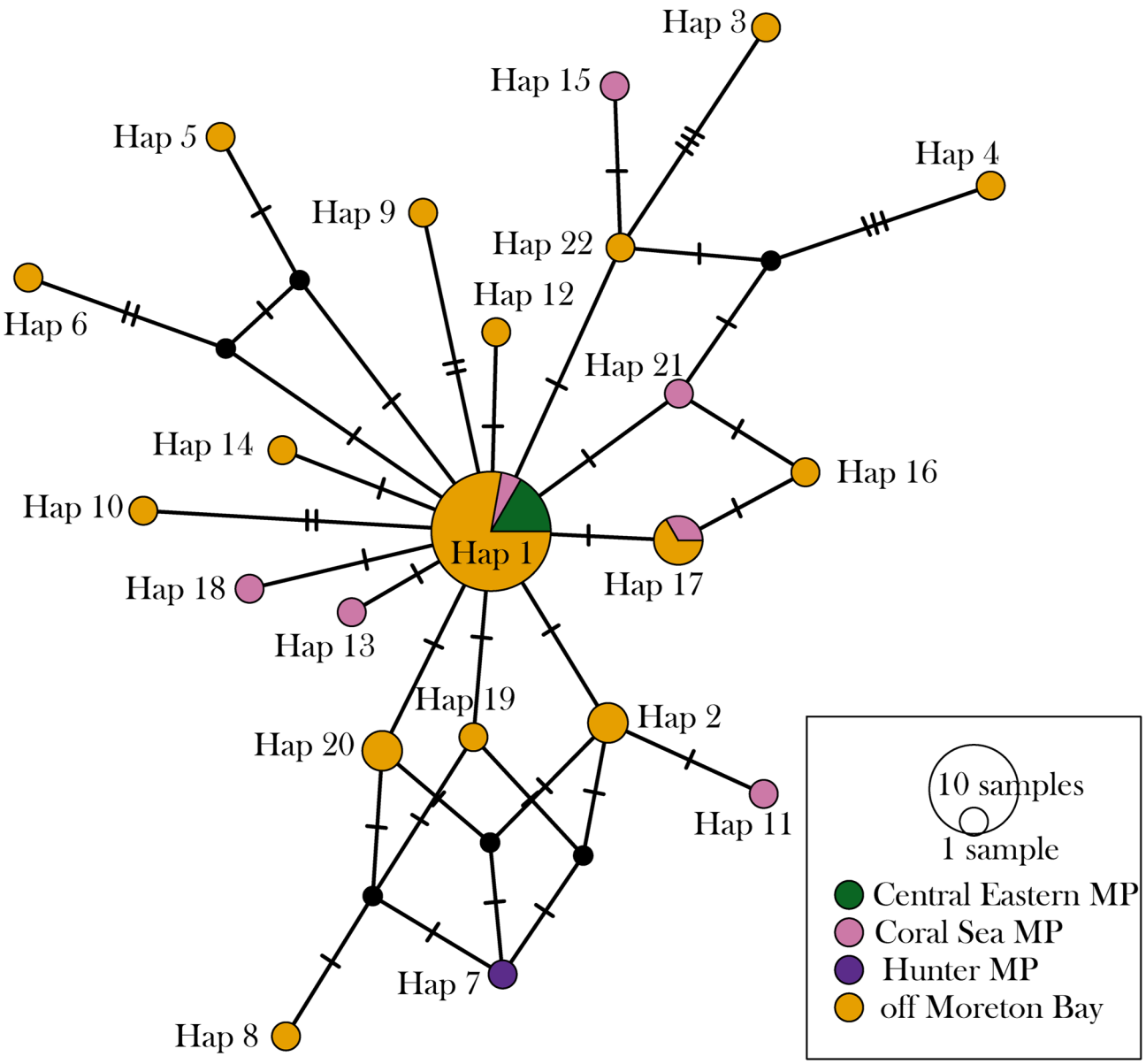

Figure 3. Median-joining COI haplotype network for *Melinnopsis chadwicki*. The size of the circle is proportional to the number of sampled individuals belonging to that haplotype. The colour represents the locality. Lines connect each haplotype to its most similar relative. Bars represent mutational steps between haplotypes.

patterns: group B (clade B in the phylogenetic tree) with specimens from Bass Strait, Jervis and Freycinet MPs collected from 2,650–2,820 m, group C (clade C) with specimens collected from off Moreton Bay, Coral Sea MP and off Byron Bay from 1,761–2,587 m, and group D (six sister terminal nodes) from Jervis MP and off Bermagui 2,650–2,821 m (Fig. 4).

In *J. galatheae,* of nine haplotypes, five were recorded from one site (Bass Strait). Of the three haplotypes that were shared between sites, Hap 4 was shared between four sites: off Newcastle, Freycinet MP, Bass Strait and Flinders MP with a distance of around 950 km from Freycinet MP (operation number (op.) 006) to off Newcastle (op. 065) (Fig. 2). In *M. chadwicki*, of 22 haplotypes, only two were shared between sites, with the most common haplotype (Hap 1) accounting for 42% of individuals at Central Eastern MP, Coral Sea MP and off Moreton Bay, and the second most common haplotype (Hap 17) accounting for 7% of individuals and occurring at Coral Sea MP and off Moreton Bay. The shared haplotypes from Central Eastern MP (op. 080) to Coral Sea MP (op. 121) spanned 726 km. *Melinnopsis gardelli* had 24 haplotypes. One haplotype was shared between sites (Jervis MP op. 056 and Freycinet MP op. 004, distance 735 km). Haplotype and nucleotide diversity was higher for *M. gardelli* (h = 0.989, π = 0.02137) than for *J. galatheae* (h = 0.882, π = 0.00282) and *M. chadwick*i (h = 0.825, π = 0.00392). Within *M. gardelli*, haplotype diversity was higher for the north population, whereas nucleotide diversity was higher in the south (Table 3).

Neutrality

Fu's *Fs*, which detects departures from the neutral model of evolution, produced values which were significantly ($P < 0.05$) negative for all three species, except for the north population of *M. gardelli* (Table 3). Significantly negative

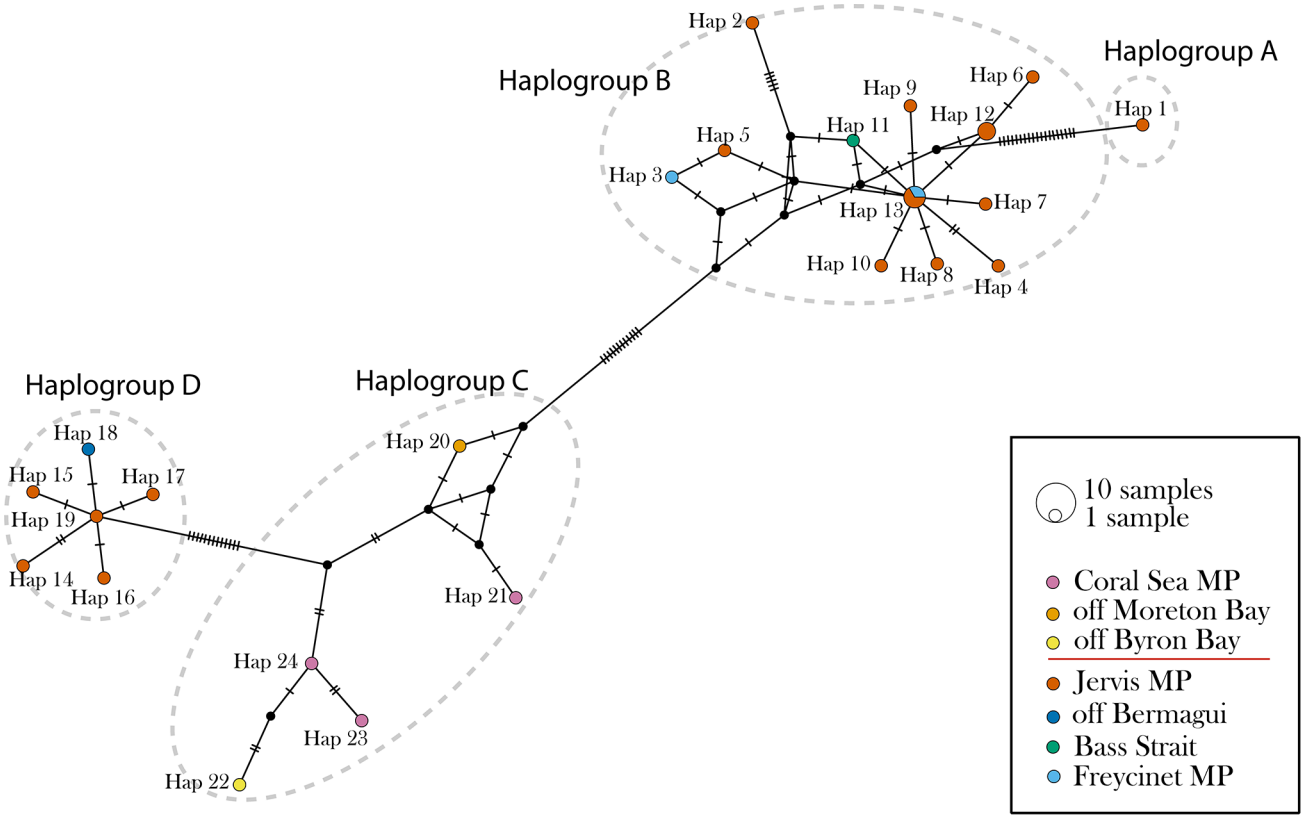

Figure 4. Median-joining COI haplotype network for *Melinnopsis gardelli*. The size of the circle is proportional to the number of sampled individuals belonging to that haplotype. The colour represents the locality. Lines connect each haplotype to its most similar relative. Bars represent mutational steps between haplotypes. Red line in legend indicates biogeographic break between sites. Dashed ovals represent haplogroups.

Table 3. Genetic diversity of COI within *J. galatheae*, *M. gardelli* and *M. chadwicki* populations. Sample size (*n*), sequence length (base pairs), number of haplotypes (*N*h), haplotype diversity (*h*), nucleotide diversity (π), number of polymorphic sites (*Np*) Fu's *Fs* are reported (P < 0.05, in bold)

Species	n	Size (bp)	Nh	h	π	Np	Fs
J. galatheae	18	575	9	0.882±0.047	0.00282±0.00045	8	**-4.65**
M. chadwicki	43	519	22	0.825±0.059	0.00392±0.00065	25	**-20.65**
M. gardelli	27	614	24	0.989±0.015	0.02137±0.00218	56	**-9.26**
M. gardelli north population	5	614	5	1.000±0.126	0.00881±0.00171	11	-1.22
M. gardelli south population	22	614	19	0.983±0.00287	0.01816±0.00287	48	**-6.30**

Fu's *Fs* indicate an excess of rare haplotypes in a population relative to expectations of neutrality and is consistent with either recent demographic expansions following genetic bottlenecks, or selective sweeps/genetic hitchhiking. This excess of rare haplotypes can also be seen in the star-like haplotype networks for the three species (Figs 2–4).

Genetic differentiation between north and south populations

AMOVA calculations were restricted to *M. gardelli* as the only species recovered from both sides of the proposed biogeographical break. The AMOVA for the north and south populations revealed that around half of the genetic variation was between north and south populations, and half was within individual populations (Table 4). The northern and southern populations were genetically distinct with a F_{ST} of 0.47 (P < 0.001).

Discussion

Genetic evidence for tropic to temperate faunal transition

Australia has an exceptionally diverse marine fauna ranging from the warm tropical seas in the north to the cool temperate waters in the south (Butler *et al.*, 2010). The present study found genetic evidence in three annelid species for a faunal transition (around 28–35°S) from tropical to temperate biogeographical province in deep waters (2,500–4,800 m) off eastern Australia as suggested by data of Hara *et al.* (2020c). Our results showed that individual examined species displayed distinct distribution patters. *Jugamphicteis galatheae* and *M. chadwicki* were found south and north of the transition respectively, the faunal shift for these species appeared between Hunter MP and off Newcastle sampling

Table 4. COI standard AMOVA results for *Melinnopsis gardelli*

	Source of variation	d. f.	Sum of squares	Variance components	Percentage of variance	p-value
COI	Among populations	1	42.577	4.59380 Va	47.17	0.00000± 0.00000
	Between populations	25	128.645	5.14582 Vb	52.83	
	Total	26	171.222	9.73962		
Fixation index (F_{ST})	0.47166					
Pairwise F_{ST} values	North population					
South population	0.47166					

The F_{ST} P value=0.00000+-0.0000.

sites (32.5–32.9°S), whereas *M. gardelli* was found to bridge across the transition. This third species displayed genetic structuring patterns in line with the transition. Three main haplogroups were recovered: one to the north of the hypothesised biogeographical break (north of off Byron Bay station 28°S), and two to the south (south of Jervis MP station 35°S). The break between the northern group and the two southern groups coincided with the known biogeographical tropical to temperate transition between 30–33°S in the deep sea (O'Hara *et al.*, 2020c). This agrees with previous work in Australia based on morphological identification of specimens, which divided deep-water fauna (>200 m) along the east coast into two distinct biomes in ophiuroids (O'Hara *et al.*, 2011), squat lobsters (Schnabel *et al.*, 2011) and most recently, two studies on megafauna collected from beam trawl samples, with the first study including annelid, anthozoan, asteroid, barnacle, bivalve, cephalopod, decapod, echinoid, gastropod, holothuroid, ophiuroid, pycnogonid, sponge and tunicate data (O'Hara *et al.*, 2020a), and the second study comprising the aforementioned taxa that included fish data, but omitted tunicate data (O'Hara *et al.*, 2020c).

The genetic structuring of *M. gardelli* across the biogeographical break revealed restricted gene flow. This is likely a consequence of limited dispersal and/or latitudinal environmental gradients and could be consistent with incipient speciation (early and incomplete divergence of one lineage into two), as evidenced by the northern population not sharing any haplotypes with the southern. Individual marine species ranges may bridge across multiple biogeographical regions, which is reflected in their genetic structure, as recorded in a meta-analysis on global benthic fish (Riginos *et al.*, 2011) and on mudprawns from estuarine environments (Teske *et al.*, 2008). In estuarine areas, genetic studies have reported that temperature-mediated selection represents an early stage of marine ecological speciation (Teske *et al.*, 2019). However, along the proposed biogeographical break at both lower bathyal (~2,500 m) and abyssal (~4,000 m) depths in eastern Australia there is no difference in temperature, salinity or dissolved oxygen. Instead the break appears to be linked to the flux of organic matter to the sea floor (O'Hara *et al.*, 2020c). Here, food availability, which is tightly linked with surface waters and depth, may be driving speciation, accounting for the differentiation between the northern and southern populations of *M. gardelli*.

Despite the strong genetic structuring in *M. gardelli,* morphologically all specimens appeared to belong to the same species. In *M. gardelli* intraspecific COI pairwise distances ranged 0–4.39%. These results were high compared with some studies (e.g., COI K2P distances < 1% in Brasier *et al.*, 2016), but comparable with other work on annelids (uncorrected p distances 0–37%, average 4.89% in Kvist (2016)), suggesting that our genetic distances are low enough to support the presence of a single species. One specimen (AM W.53128: Clade A Suppl. Fig. 2 and Hap 1 Fig. 4) collected from Jervis MP 2,650–2,636 m did appear to be genetically distinct from other specimens, thus, further analysis using electron microscopy and additional genetic markers is needed to determine whether this specimen is morphologically different or belongs to a cryptic species. Unfortunately, this is beyond the scope of the present study.

High genetic diversity at bathyal and abyssal depths

Annelid populations north and south of the transition zone were not genetically homogeneous and showed high genetic diversity. Haplotype diversity values for the COI gene in *J. galatheae* were h = 0.882 and in *M. chadwicki* h = 0.825. These values are in the upper range of COI haplotype diversity values for annelids recorded at abyssal sites of the Clarion Clipperton Zone (CCZ) in the Pacific, where values ranged from h = 0.4 to 1.0 (Janssen *et al.*, 2019) and h = 0.1 to 0.9 (Stewart *et al.*, 2023). Similarly high diversity, h = 0.92801, was recorded for the quillworm *Hyalinoecia longibranchiata* at upper bathyal depths (<2,000 m) off New Zealand (Bors *et al.*, 2012). These findings suggest that annelids at bathyal to abyssal depths on the Australian eastern margin exhibit high levels of genetic diversity, similar to those in other bathyal (Etter *et al.*, 2005; Knox *et al.*, 2020) and abyssal regions (Stewart *et al.*, 2023). Our results and those of other genetic studies from abyssal environments

(Stewart *et al.*, 2023) do not support the theory of declining genetic diversity from the bathyal to the abyssal zone (Etter *et al.*, 2005).

Nucleotide diversity values in the present study were low and represented small differences between haplotypes. Levels of nucleotide diversity in our study were similar to those found at the CCZ π = 0.0016–0.0016 (Janssen *et al.* 2019) and π =0.000–0.014 (Stewart *et al.*, 2023), but lower than results based on 16S from annelids from the tropical North Atlantic, Puerto Rico Trench and central Pacific π = 0.0015–0.0101 (Guggolz *et al.*, 2020). Such low levels of nucleotide diversity, combined with significantly negative Fu's *Fs* values, would be consistent with past demographic/range expansions and/or selective sweeps. Additionally, the presence of three distinct haplogroups in *M. gardelli* (and another divergent haplotype) could be consistent with large population fluctuations in the past and/or past geographical isolation with subsequent admixture, which is further supported by individuals collected at Jervis MP belonging to divergent haplogroups B and D (assuming they are not reproductively isolated cryptic species). Given that the southern haplogroups B and D are each more closely related to the northern haplogroup C than to each other, it could be indicative of two separate southward range expansions from a northern refugium (perhaps during glacial episodes) with subsequent admixture in the southern region. However, inferences regarding cryptic speciation, past isolation and admixture, or past demographic expansion are constrained by the single locus mitochondrial dataset used in this study. Future complimentary multilocus datasets incorporating nuclear markers could better address these uncertainties.

Connectivity along the eastern Australian margin

All three annelid species in this study displayed connectivity along portions of the eastern coast of Australia as all species exhibited shared haplotypes between multiple sites. Unfortunately, the degree and extent of connectivity along the eastern margin for all three species cannot be fully tested as very few or no individuals were collected at some sampling sites. For *M. gardelli*, most individuals and haplotypes were collected from Jervis MP, with only five individuals and haplotypes collected across three northern sites. This uneven sample of specimens (a common feature of deep-sea sampling) precluded the use of pairwise F_{ST} to determine the nature and location of the hypothesised biogeographic break. Despite the gaps in sampling, the sharing of haplotypes between sites is consistent with medium-to-long-range dispersal in all three species. Indeed for *J. galatheae* one haplotype was shared between sites off Newcastle, Freycinet, Bass Strait and Flinders MPs, a distance of around 950 km from Freycinet MP (off Tasmania) to off Newcastle. Interestingly, Flaxman and Kupriyanova (2024) reported a new species of Aphroditidae, *Laetmonice hutchingsae,* with specimens recovered along eastern Australia (1,151–2,760 m) from off Tasmania (41° S) up to Fraser Island (25° S), which was confirmed using the 16S and COI gene fragments, although no haplotype networks were constructed to further understand connectivity. Guggolz *et al.* (2020) reported a pan-ocean distribution of several spionid species where identical haplotypes of 16S rRNA were shared between the Atlantic (tropical North Atlantic 5,000–6,000 m depth, and the Puerto Rico Trench around 8,000 m depth) and Pacific Oceans (CCZ 4,000–5,000 m depth). Even within oceans four species occurred in the tropical Atlantic across distances >4,000 km. In Rouse and Kupriyanova (2021) the serpulid *Laminatubus alvini* displayed very little genetic structure, showing only two haplotypes, despite samples being collected around 7,000 km apart from vent communities in Alarcon Rise, Mexico to vents on the East Pacific Rise from depths of 2,200–2,600 m. Shared haplotypes over vast geographical areas have been reported between polychaetes in the abyssal Pacific and Atlantic Oceans, where one haplotype in the goniadid *Bathyglycinde profunda* was shared between the two oceans (Meißner *et al.*, 2023).

In the present study, the shared haplotypes suggest continual dispersal and ongoing gene flow between sites along the eastern Australian coast. Long-distance genetic connectivity in annelids is generally thought to be maintained by larval dispersal (Brasier *et al.*, 2017; Guggolz *et al.*, 2020). The majority of deep-sea invertebrates have lecithotrophic larvae that have been shown to survive long periods in culture (e.g., over one year before settling in Birkeland *et al.* (1971)). Low metabolic rates of these larvae in cold water apparently enable their long-term survival and thus broad dispersal potential (Young *et al.*, 1997), as the lecithotrophic larvae are carried on deep-water currents thus expanding their range beyond the local scale. This mode of dispersal is likely true for the taxa investigated in the present study. Although there is very little information on the life history of these species, only non-feeding larva have been reported in Ampharetidae and Melinnidae (Marshall *et al.,* 2012). Whilst there is no information on the genus *Melinnopsis*, Hutchings (1973a, 1973b) investigated a shallow-water population of another melinnid (*Melinna cristata,* now recognised as *Melinna elisabethae*) in the North Sea. This species has a restricted spawning season of around two weeks once per year. After external fertilization, larvae (non-feeding, Hutchings pers. comm.) settle on the seafloor and within two to three weeks metamorphosize into juveniles (Hutchings, 1973a). Hutchings (1973b) reported fully developed oocytes with a diameter of 240 to 400 µm in the body of *M. elisabethae* specimens*,* while two individuals of *M. gardelli* (AM W.51476, AM W.51480) were observed with eggs (~500 µm diameter) inside the body (Gunton unpubl.), large egg size is generally linked to non-feeding larvae (reviewed in Giangrande *et al.*, 1994). Comparable egg sizes in these closely related species (*M. elisabethae*) suggest similar methods of reproduction in the *Melinnopsis* species investigated here. Another closely related species, the shallow-water *Melinna palmata,* has a lecithotrophic planktonic larval stage that lasts for around seven days (Grehan *et al.*, 1991). Considering that brooders tend to be smaller sized representatives of a group than broadcasters (Strathmann & Strathmann, 1982), we assume the three species in this study are broadcasters with non-feeding planktonic larvae. Recently *Hyalinoecia robusta,* a brooding deep-sea onuphid with no free-swimming larval stage, was found to occur from the western Atlantic to the Indian Ocean (Budaeva *et al.*, 2024). These results confirmed with molecular data suggest that reproductive strategy may not be a good predictor of dispersal ability in the deep sea. Instead, historical events, behavioural traits and abiotic factors should also be considered in species dispersal potential (Budaeva

et al., 2024).

Deep-water currents run along the east coast of Australia and likely facilitate annelid species dispersal. Using Argo float and hydrographic data to model ocean currents Chiswell *et al.* (2015) reported that at around 1,000 m depth Antarctic Intermediate Water flows from north to south along the east coast of Australia, and at around 3,000 m the Lower Circumpolar Deep Water (LCDW) flows in the opposite direction along the margin. These deep-water currents may have the potential to transport *M. gardelli* larvae/juveniles enabling some limited and episodic connectivity across the biogeographic break.

Sediment transport along the Australian continental margin may be a mechanism for dispersal and enhanced genetic connectivity. Meißner *et al.* (2023) suggested that abyssal benthic invertebrate populations may undergo dislodgement through abyssal storms and then be transported *via* bottom currents, thus increasing the distribution and connectivity of species. In Australia 10% of continental shelf is influenced by storms and currents (Harris *et al.*, 2014), which are likely to extend out onto the abyssal plains. The annelids in this study are tubicolous and would therefore require a large storm to dislodge them from the sediment, however, the smaller juveniles are more likely to be dislodged, and sediment transport may be a means of dispersal.

Understanding species ranges and genetic connectivity is essential for constructing accurate biogeographical boundaries in the deep sea, which provide a map to study, conserve and manage biodiversity, and thus design effective Marine Protected Areas. Many of the specimens from this study were recovered from Marine Parks. O'Hara *et al.* (2020c) raised concerns that Australia's Marine Park (MP) network along the east coast, which is grouped into three networks (South-east, Temperate East and the Coral Sea) do not adequately cover the distribution of the deep-water fauna. Our study indicated that at least for the annelids included in this study the current MPs do cover much of the known species' ranges. Future studies using more powerful next generation sequencing techniques such as restriction-site-associated DNA sequencing (RAD-seq) may resolve population-level distinctions between and within individual MP sites providing a clearer picture of the level of protection for deep-sea fauna around Australia.

Conclusions

The present study found genetic evidence for a faunal transition (around 28–35°S) from tropic to temperate biogeographical province in deep waters (1,000 m to 4,800 m depths) off eastern Australia. Two examined species, *J. galatheae* and *M. chadwicki,* were found south and north of the transition respectively. However, the break was not strongly defined as *M. gardelli* was found to bridge across the transition. This third species displayed genetic structuring patterns in line with the transition. Different patterns between individual species ranges suggest that broad generalised patterns of the tropical to temperate transition do not hold true for all annelid taxa.

All three annelid species in this study displayed connectivity along portions of the eastern coast of Australia as all species exhibited shared haplotypes between multiple sites. This pattern is consistent with ongoing gene flow along large portions, but not the entirety of the Eastern Australian coast.

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References

Abell, R., M. L. Thieme, C. Revenga, M. Bryer, M. Kottelat, N. Bogutskaya, B. Coad, N. Mandrak, S. C. Balderas, W. Bussing, M. L. J. Stiassny, P. Skelton, G. R. Allen, P. Unmack, A. Naseka, R. Ng, N. Sindorf, J. Robertson, E. Armijo, J. V. Higgins, T. J. Heibel, E. Wikramanayake, D. Olson, H. L. López, R. E. Reis, J. G. Lundberg, M. H. Sabaj Pérez, and P. Petry. 2008. Freshwater ecoregions of the world: a new map of biogeographic units for freshwater biodiversity conservation. *BioScience* 58(5): 403–414.
https://doi.org/10.1641/b580507

Allen, J. A. and H. L. Sanders. 1996. The zoogeography, diversity, and origin of the deep-sea protobranch bivalves of the Atlantic: The epilogue. *Progress in Oceanography* 38(2): 95–153.
https://doi.org/10.1016/S0079-6611(96)00011-0

Altschul, S. F., W. Gish, W. Miller, E. W. Myers, and D. J. Lipman. 1990. Basic local alignment search tool. *Journal of Molecular Biology* 215(3): 403–410.
https://doi.org/10.1016/S0022-2836(05)80360-2

Baco, A. R., R. J. Etter, P. A. Ribeiro, S. der Heyden, P. Beerli, and B. P. Kinlan. 2016. A synthesis of genetic connectivity in deep-sea fauna and implications for marine reserve design. *Molecular Ecology* 25(14): 3276–3298.
https://doi.org/10.1111/mec.13689

Birkeland, C., F.-S. Chia, and R.R. Strathmann. 1971. Development, substratum selection, delay of metamorphosis and growth in the seastar *Mediaster aequalis* Stimpson. *Biological Bulletin* 141: 99–108.

Bond, T. and A. Jamieson. 2022. The extent and protection of Australia's deep sea. *Marine and Freshwater Research* 73(12): 1520–1526.
https://doi.org/10.1071/MF22156

Bors, E. K., A. A. Rowden, E. W. Maas, M. R. Clarke, and T. M. Shank. 2012. Patterns of deep-sea genetic connectivity in the New Zealand region: Implications for management of benthic ecosystems. *PLoS ONE* 7(11): e49474.
https://doi.org/10.1371/journal.pone.0049474

Bostock, H. C., P. J. Sutton, M. J. M. Williams, and B. N. Opdyke. 2013. Reviewing the circulation and mixing of Antarctic Intermediate Water in the South Pacific using evidence from geochemical tracers and Argo float trajectories. *Deep Sea Research Part I: Oceanographic Research Papers* 73: 84–98. https://doi.org/10.1016/j.dsr.2012.11.007

Brasier, M. J., H. Wiklund, L. Neal, R. Jeffreys, K. Linse, H. Ruhl, and A. G. Glover. 2016. DNA barcoding uncovers cryptic diversity in 50% of deep-sea Antarctic polychaetes. *Royal Society Open Science* 3(11): 160432. https://doi.org/10.1098/rsos.160432

Brasier, M. J., J. Harle, H. Wiklund, R. M. Jeffreys, K. Linse, H. A. Ruhl, and A. G. Glover. 2017. Distributional patterns of polychaetes across the west Antarctic based on DNA barcoding and particle tracking analyses. *Frontiers in Marine Science* 4(356): 1–20. https://doi.org/10.3389/fmars.2017.00356

Brenke, N. 2005. An epibenthic sledge for operations on marine soft bottom and bedrock. *Marine Technology Society Journal* 39(2): 10–21. https://doi.org/10.4031/002533205787444015

Budaeva, N., S. Agne, P. A. Ribeiro, N. Straube, M. Preick, and M. Hofreiter. 2024. Wide-spread dispersal in a deep-sea brooding polychaete: The role of natural history collections in assessing the distribution in quill worms (Onuphidae, Annelida). *Frontiers in Zoology* 21(1): 1. https://doi.org/10.1186/s12983-023-00520-0

Butler, A. J., T. Rees, P. Beesley, and N. J. Bax. 2010. Marine biodiversity in the Australian region. *PLOS ONE* 5(8): e11831. https://doi.org/10.1371/journal.pone.0011831

Carr, C. M., S. M. Hardy, T. M. Brown, T. A. Macdonald, and P. D. N. Hebert. 2011. A tri-oceanic perspective: DNA barcoding reveals geographic structure and cryptic diversity in Canadian polychaetes. *PLOS ONE* 6(7): e22232. https://doi.org/10.1371/journal.pone.0022232

Chiswell, S. M., H. C. Bostock, P. J. H. Sutton, and M. J. M. Williams. 2015. Physical oceanography of the deep seas around New Zealand: a review. *New Zealand Journal of Marine and Freshwater Research* 49(2): 286–317. https://doi.org/10.1080/00288330.2014.992918

Collen, B., F. Whitton, E. E. Dyer, J. E. M. Baillie, N. Cumberlidge, W. R. T. Darwall, C. Pollock, N. I. Richman, A.-M. Soulsby, and M. Böhm. 2014. Global patterns of freshwater species diversity, threat and endemism. *Global Ecology and Biogeography* 23(1): 40–51. https://doi.org/10.1111/geb.12096

Costello, M. J., P. Tsai, P. S. Wong, A. K. L. Cheung, Z. Basher, and C. Chaudhary. 2017. Marine biogeographic realms and species endemicity. *Nature Communications* 8(1): 1057. https://doi.org/10.1038/s41467-017-01121-2

Darriba, D., G. L. Taboada, R. Doallo, and D. Posada. 2012. jModelTest 2: More models, new heuristics and parallel computing. *Nature Methods* 9(8): 772. https://doi.org/10.1038/nmeth.2109

DeLeo, D. M., C. L. Morrison, M. Sei, V. Salamone, A. W. J. Demopoulos, and A. M. Quattrini. 2022. Genetic diversity and connectivity of chemosynthetic cold seep mussels from the U.S. Atlantic margin. *BMC Ecology and Evolution* 22(1): 76. https://doi.org/10.1186/s12862-022-02027-4

Drengstig, A., S.-E. Fevolden, P. E. Galand, and M. M. Aschan. 2000. Population structure of the deep-sea shrimp (*Pandalus borealis*) in the north-east Atlantic based on allozyme variation. *Aquatic Living Resources* 13: 121–128. https://doi.org/10.1016/S0990-7440(00)00142-X

Edgar, R. 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* 32(5): 1792–1797. https://doi.org/10.1093/nar/gkh340.

Eilertsen, M. H., M. N. Georgieva, J. A. Kongsrud, K. Linse, H. Wiklund, A. G. Glover, and H. T. Rapp. 2018. Genetic connectivity from the Arctic to the Antarctic: *Sclerolinum contortum* and *Nicomache lokii* (Annelida) are both widespread in reducing environments. *Scientific Reports* 8(1): 4810. https://doi.org/10.1038/s41598-018-23076-0

Ekman, S. 1953. *Zoogeography of the Sea*. London: Sidgwick & Jackson, 417 pp. https://doi.org/10.2307/1439946

Etter, R. J., M. A. Rex, M. R. Chase, and J. M. Quattro. 2005. Population differentiation decreases with depth in deep-sea bivalves. *Evolution* 59(7): 1479–1491. https://doi.org/10.1111/j.0014-3820.2005.tb01797.x

Excoffier, L. and H. E. L. Lischer. 2010. Arlequin suite ver 3.5: A new series of programs to perform population genetics analyses under Linux and Windows. *Molecular Ecology Resources* 10(3): 564–567. https://doi.org/10.1111/j.1755-0998.2010.02847.x

Flaxman, B. and E. K. Kupriyanova. 2024. New species of *Laetmonice* (Aphroditidae, Annelida) from bathyal and abyssal depths around Australia. *Records of the Australian Museum* 76(4): 195–210. https://doi.org/10.3853/j.2201-4349.76.2024.1900

Folmer, O., M. Black, W. Hoeh, R. Lutz, and R. C. Vrijenhoek. 1994. DNA primers for amplification of mitochondrial cytochrome oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* 3: 294–299.

Fu, Y. X. 1996. New statistical tests of neutrality for DNA samples from a population. *Genetics* 143: 557. https://doi.org/10.1093/genetics/143.1.557

Georgieva, M. N., H. Wiklund, J. B. Bell, M. H. Eilertsen, R. A. Mills, C. T. S. Little, and A. G. Glover. 2015. A chemosynthetic weed: The tubeworm *Sclerolinum contortum* is a bipolar, cosmopolitan species. *BMC Evolutionary Biology* 15(1): 280. https://doi.org/10.1186/s12862-015-0559-y

Giangrande, A., S. Geraci, and G. Belmonte. 1994. Life-cycle and life-history diversity in marine invertebrates and the implications in community dynamics. *Oceanography and Marine Biology: An Annual Review* 32: 305–333.

Glover, A. G., C. R. Smith, G. L. J. Paterson, G. D. F. Wilson, L. Hawkins, and M. Sheader 2002. Polychaete species diversity in the central Pacific abyss: Local and regional patterns, and relationships with productivity. *Marine Ecology Progress Series* 240: 157–170. https://doi.org/10.3354/meps240157

Grehan, A., C. Retière, and B. Keegan. 1991. Larval development in the ampharetid *Melinna palmata* Grube (Polychaeta). *Ophelia Supplement* 5: 321–332. https://doi.org/10.1163/9789004629745_032

Guggolz, T., K. Meißner, M. Schwentner, T. G. Dahlgren, H. Wiklund, P. Bonifácio, and A. Brandt. 2020. High diversity and pan-oceanic distribution of deep-sea polychaetes: *Prionospio* and *Aurospio* (Annelida: Spionidae) in the Atlantic and Pacific Ocean. *Organisms Diversity and Evolution* 20(2): 171–187. https://doi.org/10.1007/s13127-020-00430-7

Gunton, L. M., E. K. Kupriyanova, and T. Alvestad. 2020. Two new deep-water species of Ampharetidae (Annelida: Polychaeta) from the eastern Australian continental margin. *Records of the Australian Museum* 72(4): 101–121. https://doi.org/10.3853/j.2201-4349.72.2020.1763

Gunton, L. M., E. K. Kupriyanova, T. Alvestad, L. Avery, J. A. Blake, O. Biriukova, M. Böggemann, P. Borisova, N. Budaeva, I. Burghardt, M. Capa, M. N. Georgieva, C. J. Glasby, P.-W. Hsueh, P. Hutchings, N. Jimi, J. A. Kongsrud, J. Langeneck, K. Meißner, A. Murray, M. Nikolic, H. Paxton, D. Ramos, A. Schulze, R. Sobczyk, C. Watson, H. Wiklund, R. S. Wilson, A. Zhadan, and J. Zhang. 2021. Annelids of the eastern Australian abyss collected by the 2017 RV 'Investigator' voyage. *Zookeys* 160: 1–198. https://doi.org/10.3897/zookeys.1020.57921

Gunton, L. M., E. K. Kupriyanova, and C. N. Roterman. 2025a. Supplementary Tables. Well-connected worms: genetic connectivity of annelids (Melinnidae and Ampharetidae) across a biogeographical break in Australia's eastern abyss. figshare. Dataset.
https://doi.org/10.6084/m9.figshare.28472045.

Gunton, L. M., E. K. Kupriyanova, and C. N. Roterman. 2025b. Supplementary Figures. Well-connected worms: genetic connectivity of annelids (Melinnidae and Ampharetidae) across a biogeographical break in Australia's eastern abyss. figshare. Dataset.
https://doi.org/10.6084/m9.figshare.28470908.

Harris, P. T., A. D. Heap, T. Whiteway, and A. Post. 2008. Application of biophysical information to support Australia's representative marine protected area program. *Ocean and Coastal Management* 51: 701–711.
https://doi.org/10.1016/j.ocecoaman.2008.07.007

Harris, P. T., M. Macmillan-Lawler, J. Rupp, and E. K. Baker. 2014. Geomorphology of the oceans. *Marine Geology* 352: 4–24.
https://doi.org/10.1016/j.margeo.2014.01.011

Havermans, C., G. Sonet, C. d'Udekem d'Acoz, Z. T. Nagy, P. Martin, S. Brix, T. Riehl, S. Agrawal, and C. Held. 2013. Genetic and morphological divergences in the cosmopolitan deep-sea amphipod *Eurythenes gryllus* reveal a diverse abyss and a bipolar species. *PLOS ONE* 8(9): e74218.
https://doi.org/10.1371/journal.pone.0074218

Heap, A. D. and P. T. Harris. 2008. Geomorphology of the Australian margin and adjacent seafloor. *Australian Journal of Earth Sciences* 55(4): 555–585.
https://doi.org/10.1080/08120090801888669

Holthe, T. 2000. Bathyal and abyssal Ampharetidae (Annelida: Polychaeta) (sedentary species II). *Galathea Report* 18: 57–68.

Hutchings, P. A. 1973a. Gametogenesis in a Northumberland population of the polychaete *Melinna cristata*. *Marine Biology* 18(3): 199–211.
https://doi.org/10.1007/BF00367986

Hutchings, P. H. 1973b. Age structure and spawning of a Northumberland population of *Melinna cristata* (Polychaeta: Ampharetidae). *Marine Biology* 18(3): 218–227.
https://doi.org/10.1007/BF00367988

Hutchings, P. and E. Kupriyanova. 2018. Cosmopolitan polychaetes – fact or fiction? Personal and historical perspectives. *Invertebrate Systematics* 32(1): 1–9.
https://doi.org/10.1071/IS17035

Janssen, A., H. Stuckas, A. Vink, and P. M. Arbizu. 2019. Biogeography and population structure of predominant macrofaunal taxa (Annelida and Isopoda) in abyssal polymetallic nodule fields: Implications for conservation and management. *Marine Biodiversity* 49(6): 2641–2658.
https://doi.org/10.1007/s12526-019-00997-1

Jorde, P. E., G. Sovik, J.-I. Westgaard, J. Albretsen, C. Andre, C. Hvingel, T. Johansen, A. D. Sandvik, M. Kingsley, and K. E. Jorstad. 2015. Genetic distinct populations of northern shrimp, *Pandalus borealis*, in the Northern Atlantic: adaptation to different temperatures as an isolation factor. *Molecular Ecology* 24: 1742–1757.
https://doi.org/10.1111/mec.13158

Keene, J., C. Baker, M. Tran and Potter, A. 2008. *Sedimentology and Geomorphology of the East Marine region of Australia*. Geoscience Australia, Record 2008/10. Canberra: Geoscience Australia, 262pp.

Knox, M., I. D. Hogg, C. A. Pilditch, J. C. Garcia-R, P. D. Herbert, and D. Steinke. 2020. Contrasting patterns of genetic differentiation for deep-sea amphipod taxa along New Zealand's continental margins. *Deep Sea Research Part I: Oceanographic Research Papers* 162: 103323.
https://doi.org/10.1016/j.dsr.2020.103323

Kumar, S., G. Stecher, M. Li, C. Knyaz, and K. Tamura. 2018. MEGA X: Molecular Evolutionary Genetics Analysis across computing platforms. *Molecular Biology and Evolution* 35(6): 1547–1549.
https://doi.org/10.1093/molbev/msy096

Kvist, S. 2016. Does a global DNA barcoding gap exist in Annelida? *Mitochondrial DNA Part A* 27(3): 2241–2252.
https://doi.org/10.3109/19401736.2014.984166

Last, P. R., W. T. White, D. C. Gledhill, J. J. Pogonoski, V. Lyne, and N. J. Bax. 2011. Biogeographical structure and affinities of the marine demersal ichthyofauna of Australia. *Journal of Biogeography* 38(8): 1484–1496.
https://doi.org/10.1111/j.1365-2699.2011.02484.x

Leigh, J. and D. Bryant. 2015. PopART: Full-feature software for haplotype network construction. *Methods in Ecology and Evolution* 6(9): 1110–1116.
https://doi.org/10.1111/2041-210X.12410

Lewis, M. 2010. The CSIRO 4m beam trawl. *CSIRO Marine and Atmospheric Research* Paper 033. Hobart, Tasmania: CSIRO.

Lowe, W. H., and F. W. Allendorf. 2010. What can genetics tell us about population connectivity? *Molecular Ecology* 19: 3038–3051.
https://doi.org/10.1111/j.1365-294X.2010.04688.x

MacIntosh, H., F. Althaus, A. Williams, J. E. Tanner, P. Alderslade, S. T. Ahyong, N. Bax, F. Criscione, A. L. Crowther, C. A. Farrelly, J. K. Finn, L. Goudie, K. Gowlett-Holmes, A. M. Hosie, E. Kupriyanova, C. Mah, A. W. McCallum, K. L. Merrin, A. Miskelly, M. L. Mitchell, T. Molodtsova, A. Murray, T. D. O'Hara, P. M. O'Loughlin, H. Paxton, A. L. Reid, S. J. Sorokin, D. Staples, G. Walker-Smith, E. Whitfield and R. S. Wilson. 2018. Invertebrate diversity in the deep Great Australian Bight (200–5000 m). *Marine Biodiversity Records* 11: 23.
https://doi.org/10.1186/s41200-018-0158-x

Marshall, D. M., P. J. Krug, E. K. Kupriyanova, M. Byrne, and R. B. Emlet. 2012. The biogeography of marine invertebrate life histories. *Annual Review of Ecology, Evolution, and Systematics* 43: 97–114.
https://doi.org/10.1146/annurev-ecolsys-102710-145004

McClain, C. R. and S. M. Hardy. 2010. The dynamics of biogeographic ranges in the deep sea. *Proceedings of the Royal Society B-Biological Sciences* 277(1700): 3533–3546.
https://doi.org/10.1098/rspb.2010.1057

Meißner, K., M. Schwentner, M. Götting, T. Knebelsberger, and D. Fiege. 2023. Polychaetes distributed across oceans—Examples of widely recorded species from abyssal depths of the Atlantic and Pacific Oceans. *Zoological Journal of the Linnean Society* 199: 906–944.
https://doi.org/10.1093/zoolinnean/zlad069

Miller, K. and R. Gunasekera. 2017. A comparison of genetic connectivity in two deep sea corals to examine whether seamounts are isolated islands or stepping stones for dispersal. *Science Reports* 7: 46103.
https://doi.org/10.1038/srep46103

Miller, K., A. Williams, A. A. Rowden, C. Knowles, and G. Dunshea. 2010. Conflicting estimates of connectivity among deep-sea coral populations. *Marine Ecology* 31: 144–157.
https://doi.org/10.1111/j.1439-0485.2010.00380.x

Nygren, A., J. Parapar, J. Pons, K. Meißner, T. Bakken, J. A. Kongsrud, E. Oug, D. Gaeva, A. Sikorski, R. A. Johansen, P. A. Hutchings, N. Lavesque, and M. Capa. 2018. A mega-cryptic species complex hidden among one of the most common annelids in the North East Atlantic. *PLOS ONE* 13(6): e0198356.
https://doi.org/10.1371/journal.pone.0198356

O'Hara, T. D., A. A. Rowden, and N. J. Bax. 2011. A southern hemisphere bathyal fauna is distributed in latitudinal bands. *Current Biology* 21(3): 226–230.
https://doi.org/10.1016/j.cub.2011.01.002

O'Hara, T. D., P. R. England, R. M. Gunasekera, and K. M. Naughton. 2014. Limited phylogeographic structure for five bathyal ophiuroids at continental scales. *Deep Sea Research Part I: Oceanographic Research Papers* 84: 18–28.
https://doi.org/10.1016/j.dsr.2013.09.009

O'Hara, T. D., A. Williams, F. Althaus, A. S. Ross, and N. J. Bax. 2020a. Regional-scale patterns of deep seafloor biodiversity for conservation assessment. *Diversity and Distributions* 26(4): 479–494.
https://doi.org/10.1111/ddi.13034

O'Hara, T. D., A. Williams, S. T. Ahyong, P. Alderslade, T. Alvestad, D. Bray, I. Burghardt, N. Budaeva, F. Criscione, A. L. Crowther, M. Ekins, M. Eléaume, C. A. Farrelly, J. K. Finn, M. N. Georgieva, A. Graham, M. Gomon, K. Gowlett-Holmes, L. M. Gunton, A. Hallan, A. M. Hosie, P. A. Hutchings, H. Kise, F. Köhler, J. A. Konsgrud, E. Kupriyanova, C. C. Lu, M. Mackenzie, C. Mah, H. MacIntosh, K. L. Merrin, A. Miskelly, M. L. Mitchell, K. Moore, A. Murray, P. M. O'Loughlin, H. Paxton, J. J. Pogonoski, D. Staples, J. E. Watson, R. S. Wilson, J. Zhang, and N. J. Bax. 2020b. The lower bathyal and abyssal seafloor fauna of eastern Australia. *Marine Biodiversity Records* 13: 11.
https://doi.org/10.1186/s41200-020-00194-1

O'Hara, T. D., A. Williams, S. N. C. Woolley, A. W. Nau, and N. J. Bax. 2020c. Deep-sea temperate-tropical faunal transition across uniform environmental gradients. *Deep Sea Research Part I: Oceanographic Research Papers* 161: 103283.
https://doi.org/10.1016/j.dsr.2020.103283

Olson, D. M., E. Dinerstein, E. D. Wikramanayake, N. D. Burgess, G. V. N. Powell, E. C. Underwood, J. A. D'amico, I. Itoua, H. E. Strand, J. C. Morrison, C. J. Loucks, T. F. Allnutt, T. H. Ricketts, Y. Kura, J. F. Lamoreux, W. W. Wettengel, P. Hedao, and K. R. Kassem. 2001. Terrestrial ecoregions of the world: a new map of life on earth. *BioScience* 51(11): 933–938.
https://doi.org/10.1641/0006-3568(2001)051[0933:teotwa]2.0.co;2

Orsi, A. H., G. C. Johnson, and J. L. Bullister. 1999. Circulation, mixing and production of Antarctic bottom water. *Progress in Oceanography* 43: 55–109.
https://doi.org/10.1016/S0079-6611(99)00004-X

Rambaut, A. 2018. FigTree v1.4.4. Edinburgh, Scotland: Program distributed by the author (University of Edinburgh).
http://tree.bio.ed.ac.uk/software/figtree/

Rambaut, A., A. J. Drummond, D. Xie, G. Baele, and M. A. Suchard. 2018. Posterior summarization in Bayesian phylogenetics using Tracer 1.7. *Systematic Biology* 67(5): 901–904.
https://doi.org/10.1093/sysbio/syy032

Rex, M. A. and R. J. Etter. 2010. *Deep-Sea Biodiversity: Pattern and Scale*. Cambridge, Massachusetts: Harvard University Press.

Ridgway, K. R. and J. R. Dunn. 2003. Mesoscale structure of the mean east Australian current system and its relationship with topography. *Progress in Oceanography* 56(2): 189–222.
https://doi.org/10.1016/S0079-6611(03)00004-1

Riginos, C., K. E. Douglas, Y. Jin, D. F. Shanahan, and E. A. Treml. 2011. Effects of geography and life history traits on genetic differentiation in benthic marine fishes. *Ecography* 34(4): 566–575.
https://doi.org/10.1111/j.1600-0587.2010.06511.x

Rintoul, S., M. Feng, N. Hardman-Mountford, E. Raes. 2017. Australia's ocean currents. In *Oceans: Science and Solutions for Australia*, ed. B. D. Mapston, 13–24. Melbourne: CSIRO Publishing.

Ronquist, F., M. Teslenko, P. van der Mark, D. L. Ayres, A. Darling, S. Höhna, B. Larget, L. Liu, M. A. Suchard, and J. P. Huelsenbeck. 2012. MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61(3): 539–542.
https://doi.org/10.1093/sysbio/sys029

Rouse, G. W. and E. K. Kupriyanova. 2021. *Laminatubus* (Serpulidae, Annelida) from eastern Pacific hydrothermal vents and methane seeps, with description of two new species. *Zootaxa* 4915(1): 1–27.
https://doi.org/10.11646/zootaxa.4915.1.1

Rouse, G., F. Pleijel, and E. Tilic. 2022. *Annelida*. Oxford: Oxford University Press, 432 pp.
https://doi.org/10.1093/oso/9780199692309.001.0001

Rozas, J., A. Ferrer-Mata, J. C. Sánchez-DelBarrio, S. Guirao-Rico, P. Librado, S. E. Ramos-Onsins, and A. Sánchez-Gracia. 2017. DnaSP 6: DNA sequence polymorphism analysis of large data sets. *Molecular Biology and Evolution* 34(12): 3299–3302.
https://doi.org/10.1093/molbev/msx248

Schnabel, K. E., P. Cabezas, A. McCallum, E. Macpherson, S. T. Ahyong, K. Baba, and G. Poore. 2011. World-wide distribution patterns of squat lobsters. In *The Biology of Squat Lobsters*, eds. G. C. B. Poore, S. T. Ahyong, and J. Taylor, pp. 149–182. Melbourne: CSIRO Publishing.

Spalding, M. D., H. E. Fox, G. R. Allen, N. Davidson, Z. A. Ferdaña, M. Finlayson, B. S. Halpern, M. A. Jorge, A. Lombana, S. A. Lourie, K. D. Martin, E. McManus, J. Molnar, C. A. Recchia, and J. Robertson. 2007. Marine ecoregions of the world: A bioregionalization of coastal and shelf areas. *BioScience* 57(7): 573–583.
https://doi.org/10.1641/b570707

Stewart, E. C. D., G. Bribiesca-Contreras, S. Taboada, H. Wiklund, A. Ravara, E. Pape, B. De Smet, L. Neal, M. R. Cunha, D. O. B. Jones, C. R. Smith, A. G. Glover, and T. G. Dahlgren. 2023. Biodiversity, biogeography, and connectivity of polychaetes in the world's largest marine minerals exploration frontier. *Diversity and Distributions* 29(6): 727–747.
https://doi.org/10.1111/ddi.13690

Stiller, J., E. Tilic, V. Rousset, F. Pleijel, and G. W. Rouse. 2020. Spaghetti to a tree: A robust phylogeny for Terebelliformia (Annelida) based on transcriptomes, molecular, and morphological data. *Biology* 9(4): 73.
https://doi.org/10.3390/biology9040073

Strathmann, R. R. and M. F. Strathmann. 1982. The relationship between adult size and brooding in marine invertebrates. *The American Naturalist* 119(1): 91–101.
https://doi.org/10.1086/283892

Taboada, S., A. Riesgo, H. Wiklund, G. L. J. Paterson, V. Koutsouveli, N. Santodomingo, A. C. Dale, C. R. Smith, D. O. B. Jones, T. G. Dahlgren, and A. G. Glover. 2018. Implications of population connectivity studies for the design of marine protected areas: An example of a demosponge from the Clarion-Clipperton Zone. *Molecular Ecology* 27: 4657–4679.
https://doi.org/10.1111/mec.14888

Taylor, M. L. and C. N. Roterman. 2017. Invertebrate population genetics across Earth's largest habitat: The deep-sea floor. *Molecular Ecology* 26(19): 4872–4896.
https://doi.org/10.1111/mec.14237

Teske, P. R., I. Papadopoulos, B. K. Newman, P. C. Dworschak, C. D. McQuaid, and N. P. Barker. 2008. Oceanic dispersal barriers, adaptation and larval retention: An interdisciplinary assessment of potential factors maintaining a phylogeographic break between sister lineages of an African prawn. *BMC Evolutionary Biology* 8(1): 341.
https://doi.org/10.1186/1471-2148-8-341

Teske, P. R., J. Sandoval-Castillo, T. R. Golla, A. Emami-Khoyi, M. Tine, S. von der Heyden, and L. B. Beheregaray. 2019. Thermal selection as a driver of marine ecological speciation. *Proceedings of the Royal Society B: Biological Sciences* 286(1896): 20182023.
https://doi.org/10.1098/rspb.2018.2023

UNEP. 2007. *Deep-Sea Biodiversity and Ecosystems: A Scoping Report on Their Socio-Economy, Management and Governance*. Cambridge, United Kingdom: UNEP.

UNESCO. 2009. *Global Open Oceans and Deep Seabed (GOODS)-Biogeographic Classification* (IOCTechnical Series, 84). UNESCO-IOC.

Vinogradova, N. G. 1958. The zoogeographical distribution of the deep-water bottom fauna in the abyssal zone of the ocean. *Deep Sea Research* (1953) 5(2): 205–208.
https://doi.org/10.1016/0146-6313(58)90012-1

Vrijenhoek, R. C. 2010. Genetic diversity and connectivity of deep-sea hydrothermal vent metapopulations. *Molecular Ecology* 19(20): 4391–4411.
https://doi.org/10.1111/j.1365-294X.2010.04789.x

Watling, L., J. Guinotte, M. R. Clark, and C. R. Smith. 2013. A proposed biogeography of the deep ocean floor. *Progress in Oceanography* 111: 91–112.
https://doi.org/10.1016/j.pocean.2012.11.003

Xiao, Y., T. Xu, J. Sun, Y. Wang, W. C. Wong, Y. H. Kwan, C. Chen, J.-W. Qiu, and P.-Y. Qian. 2020. Population genetic structure and gene expression plasticity of the deep-sea vent and seep squat lobster *Shinkaia crosnieri*. *Frontiers in Marine Science* 7: 587686.
https://doi.org/10.3389/fmars.2020.587686

Young, C.M., M.A. Sewell, P.A. Tyler, and A. Metaxas. 1997. Biogeographic and bathymetric ranges of Atlantic deep-sea echinoderms and ascidians: the role of larval dispersal. *Biodiversity and Conservation* 6: 1507–1522.
https://doi.org/10.1023/A:1018314403123

Supplementary Information

Supplementary Table 1. Specimens, voucher numbers, latitude and longitude, and sampling gear for specimens used in the analyses.
https://doi.org/10.6084/m9.figshare.28472045

Supplementary Table 2. Specimens, voucher numbers, GenBank numbers and collection localities of specimens used in the analyses.
https://doi.org/10.6084/m9.figshare.28472045

Supplementary Figure 1. Ampharetidae Bayesian inference tree run for 10,000,000 generations using COI gene fragment.
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Supplementary Figure 2. Melinnidae Bayesian inference tree run for 10,000,000 generation using COI gene fragment.
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