Marine Biodiversity Hub

National Environmental Science Programme

The Eastern Australian Marine Parks: Biodiversity, assemblage structure, diversity and origin

Report to Parks Australia

Tim O’Hara, Museums Victoria

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Milestone 5 – Research Plan v3 (2017)

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Important Disclaimer

Contents

Summary

The IN2017_V03 expedition of Australia's premier research vessel 'Investigator' was the first to systematically sample lower bathyal to abyssal habitats (2000-5000 m) in Australia's Exclusive Economic Zone [1]. It traversed seven newly declared marine parks in Commonwealth waters off the eastern margin of Australia from 15th May to 16th June 2017, including Freycinet, Flinders, East Gippsland, Jervis, Hunter, Central Eastern and Coral Sea Marine Parks. The voyage mapped much of the deeper water habitats of these parks using high resolution multi-beam data and systematically sampled the habitats, principally using video transects, small beam trawls and epibenthic sleds.

The scientific objectives of the voyage included:

1. Describe latitudinal and bathymetric patterns of biodiversity of Australia's eastern bathyal (1000-2500 m) and abyssal (4000 m) fauna from 42 to 24°S. Test whether patterns of latitudinal turnover described for the shelf and upper bathyal are replicated at deeper depths.
2. Survey and photograph the lower-bathyal and abyssal ecosystem of Commonwealth marine parks for the first time.
3. Describe the faunal communities and correlate biodiversity patterns against measured and modelled oceanographic and geological environmental factors.
4. Sequence DNA of selected species to examine the evolutionary history of the fauna.
5. Convey the excitement of deep-sea marine science and the conservation importance of Australian Marine Parks to the general public by having specialised science communicators on the voyage.
6. A further objective of the NESP Marine Biodiversity hub was to compare the community composition and richness of beam trawl samples between the IN2017_V03 survey and the various surveys (IN2015_C01, IN2015_C02, IN2017_C01) recently conducted in the Great Australian Bight.

We report here on a diverse set of products and outcomes ranging from real-time information products, delivered through daily blogs and YouTube videos, to a new fundamental understanding of the origins of deep sea biodiversity over the last 100 million years based on new and existing data. This diversity of products was only possible because of the resources and effort given to collaborations, both with communication experts and management agencies (especially Parks Australia) for the extensive communication products, and ecologists and taxonomists over many years for the biogeographic products. Consistent approaches, best practice and verified taxonomies are just some of the tools needed to support these long-term collaborations that enable the results from this "voyage to the abyss" to have a far greater and more enduring impact than might be expected from a single marine survey.

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[1] Voyage report available at http://mnf.csiro.au/~/media/Files/Voyage-plans-and-summaries/Investigator/Voyage%20Plans%20summaries/2017/IN2017_V03%20Voyage%20Summary.ashx

This report contains the analyses and results from these objectives and is structured as follows.

Chapter 1: contains descriptions, maps, seafloor imagery and representative animals that were found to occur in the seven Marine Parks surveyed. These samples provide a baseline for understanding how AMPs are distributed with regard to deep sea biogeography.

Chapter 2: describes the novel biodiversity highlights of the voyage across the dominant faunal groups from sponges to fish. Taxonomic investigations are ongoing, but to date the total number of taxa identified is 1061 from 25,661 specimens, predominantly from the 35 beam trawl samples but also including some taxonomic groups from the 28 Brenke sled samples. Of these taxa, only 405 could be assigned scientific names, indicating that up to 60% of the fauna is new to science. This chapter has been submitted for publication in the scientific journal "Marine Biodiversity Records".

Chapter 3: uses model-based statistics to explore patterns of latitudinal diversity along the east continental margin of Australia at bathyal and abyssal depths. The results indicate that separate faunas occur at each bathymetric layer analysed (~1000, 2500 and 4000 m) and that each of these bathymetric assemblages is separated into a temperate and tropical subgroups. The results are of international significance as this is the first time a temperate-tropical transition has been reported from the deep-sea. This transition occurs despite almost uniform temperature, salinity and dissolved oxygen concentrations occurring across latitudes at these depths. Conversely, the flux of organic matter to the seafloor does vary with latitude, from being relative high in the productive temperate off Tasmania and Bass Strait to low in more-oligotrophic tropical waters, and may drive large scale faunal distribution patterns. This chapter has been submitted for publication in the scientific journal "Deep Sea Research I".

Chapter 4: uses model-based statistics to analyse the difference in abundance, richness and evenness for lower bathyal and abyssal beam trawl samples from the Great Australian Bight and from off the east Australian margin. The results indicate that samples from off SE Australia have the highest abundance and species richness. These indices are correlated with levels of particulate organic carbon flux to the seafloor, which is higher under the seasonal plankton bloom around Tasmania and Bass Strait. The greater abundance leads to increased species richness. Evenness was most closely associated with the seasonality of net primary production. The samples from the Great Australian Bight were collected north of the enhanced temperate plankton belt and thus do not show elevated abundance or richness. However, they are compositionally distinct from samples from the east coast. Some taxonomic groups, such as sponges, are represented by an almost totally distinct set of species. The lower bathyal and abyssal fauna of the Great Australian Bight is thus compositionally different from other sampled regions. Additional sampling, particularly from off the south-western Australian coast and western Bass Strait, is required to determine the spatial extent of this fauna. This chapter has been submitted for publication in the scientific journal "Diversity and Distributions".

Appendix A: is a pre-print of a paper published in the scientific journal Nature in January 2019 [1]. This paper combined DNA sequences from animals collected on the IN2017_V03 voyage with a large dataset accumulated for a previous Marine Biodiversity Hub project (on marine phylogenetic endemism) to examine the origin and regional evolutionary trajectory of the marine fauna from Australia to Antarctica. This project focused on brittle stars, a group of echinoderms that are abundant across the seafloors and make an ideal group to research large scale patterns of marine biodiversity. The results show that patterns of diversity in the deep sea (seafloors deeper than 200 m) were profoundly different from those in shallow water. Although the number of species and genetic diversity were much higher in the tropics at all depths, evolution appears to have proceeded differently in shallow and deep seas. Shallow water patterns were like those that occur on land, tropical regions were generating more species than colder areas. This conforms to the well-known theory that higher temperatures increases evolutionary processes. However, the reverse was true for the deep sea. Speciation rates were highest in the coldest region (Antarctica) and lowest in the tropical deep sea.

The explanation for these patterns lies in the age of these different ecosystems. The rich diversity of the tropical deep sea appears to have been accumulated over a hundred million years. It is not an environment that is rapidly producing new species. Instead it is a refuge for an ancient fauna. This is where the “living fossils” occur, those species that look like relicts from the dinosaur era. Like the Coelacanths, fish that also live in this habitat, they are often the last of their kind. The mild environmental conditions of these waters have been stable over time, unlike shallow water disturbed by sea level changes and extreme weather events, polar regions that suffer from period glaciations, and the very deep abyssal sea that occasionally becomes oxygen depleted. This ancient fauna is like the ‘rainforest of the sea’ and the distinct genetic composition of this diverse ancient fauna adds high conservation value to management actions that seek to preserve its biodiversity. Antarctica on the other hand appears to be still recovering from extinction events, tens of millions of years ago, when ice sheets started to dominate the continent and the temperature of surrounding waters plummeted. A new specialist Antarctic fauna evolved, closely related to the deep sea fauna, which is still in the process of rapidly diversifying.

Biologists have previously explained global terrestrial and shallow water biodiversity patterns in terms of an ‘out of the tropics’ process, where new types of organisms evolve in the tropics that eventually spread out into cooler regions. The new research, backed up by fossil data, suggests that it is better to view the history of the oceans as a ‘contraction of the tropics’. In the dinosaur era, the whole planet was tropical. Over the past 50 million years the earth has progressively cooled due to a rearrangement of tectonic plates. This process created new cold water environments around Antarctica and also at temperate latitudes, which occur half way between the pole and the equator. In temperate shallow waters, a few tropical species managed to adapt to the new conditions and evolved into the endemic fauna we see across southern Australia and New Zealand today. Around Antarctica, the old tropical animals disappeared completely and deep water species evolved to form a new fauna. Thus, the fauna of each region has evolved according to its own geological, climatic and biological history.

Management Implications

From a management perspective, the data indicate that the south-east and eastern networks of Australian Marine Parks (MPs) contain examples of all the deep-sea assemblages identified (SE abyssal, NE abyssal, SE lower bathyal, NE lower bathyal, SE upper bathyal and NE upper bathyal). The identified temperate-tropical transition does not correspond with the administrative division between the south-east, temperate eastern and Coral Sea MP networks along Australia's eastern continental margin. Jervis Bay MP has a fauna that is more similar to the south-eastern than the other eastern MP network, and the fauna of the southern Coral Sea MP is similar to the temperate east MP network. However, the deep-sea temperate-tropical transition is not a sharp biogeographical break, but a gradual change in composition, particularly along the New South Wales coastline. Consequently, regardless of how they are defined, the park networks will never contain homogeneous faunas.

We did not find quantitative evidence that the Key Ecological Feature 'Benthic invertebrate communities of the eastern Great Australian Bight', defined on elevated biodiversity metrics, extends to lower-bathyal or abyssal depths (i.e. > 2000 m). More quantitative research is required to determine whether such a feature exists in shallow water. However, we did find evidence that the deep-water communities of the Great Australian Bight contain a different fauna to that occurring at similar depths off the Australian east coast. A sampling gap (between SE South Australia and western Tasmania) prevented us identifying the transition zone between these two regional faunas.

Tropical upper bathyal (200-1000 m) benthic habitats contain an ancient and diverse fauna, including many evolutionarily distinct lineages. We hypothesise that this fauna has survived through the stability of these habitat over the previous 100 my. The fauna contains remnants of Mesozoic lineages that are now rare in other habitats. This feature deserves more recognition in conservation assessments.

Further Research

Australia's lower bathyal and abyssal (2000-5000 m) fauna is now known from the Great Australian Bight and from off Australia's eastern coast. But many gaps remain. In particular, we have little to no information about the deep sea fauna of the west coast, from off SW WA to the Timor Trench. Other gaps include off Western Bass Strait, southern Tasmania, the Coral Sea Basin, and around all of Australia's offshore islands. This prevents a quantitative bioregionalisation of the fauna at these depths.

However, the sampling regime to cover these gaps need not be dense. Many species have widespread distributions. The sampling design of the "Voyage to the Abyss", taking samples every 1.5° of latitude, was sufficient to characterise the major faunal communities at the target depth along the eastern coast. Moreover, such voyages significantly add to the mapped area of Australia's marine domain; most notably mapping the continental margin of many Australian marine parks.

The specimens collected represent an invaluable addition to Australia's natural history collections - a significant depository of morphological and molecular data from an environment that is expensive to survey. Ongoing research includes connectivity studies (gene flow between deep-sea populations) and numerous descriptions of new species and genera.

The analyses in this report are restricted to the megafauna (organisms over 1 cm) as we did not obtain sufficient funds to identify all the small animals (particularly crustaceans and worms) that were collected by the epibenthic sled. Identifying these animals is an ongoing process with some funding obtained from ABRS (Australian Biological Resources Study, Polychaeta). However, at the time of this report (late 2019) it is not possible to conduct quantitative analyses on these samples.

Chapter 1: Eastern Australian Marine Parks: bathyal to abyssal habitats

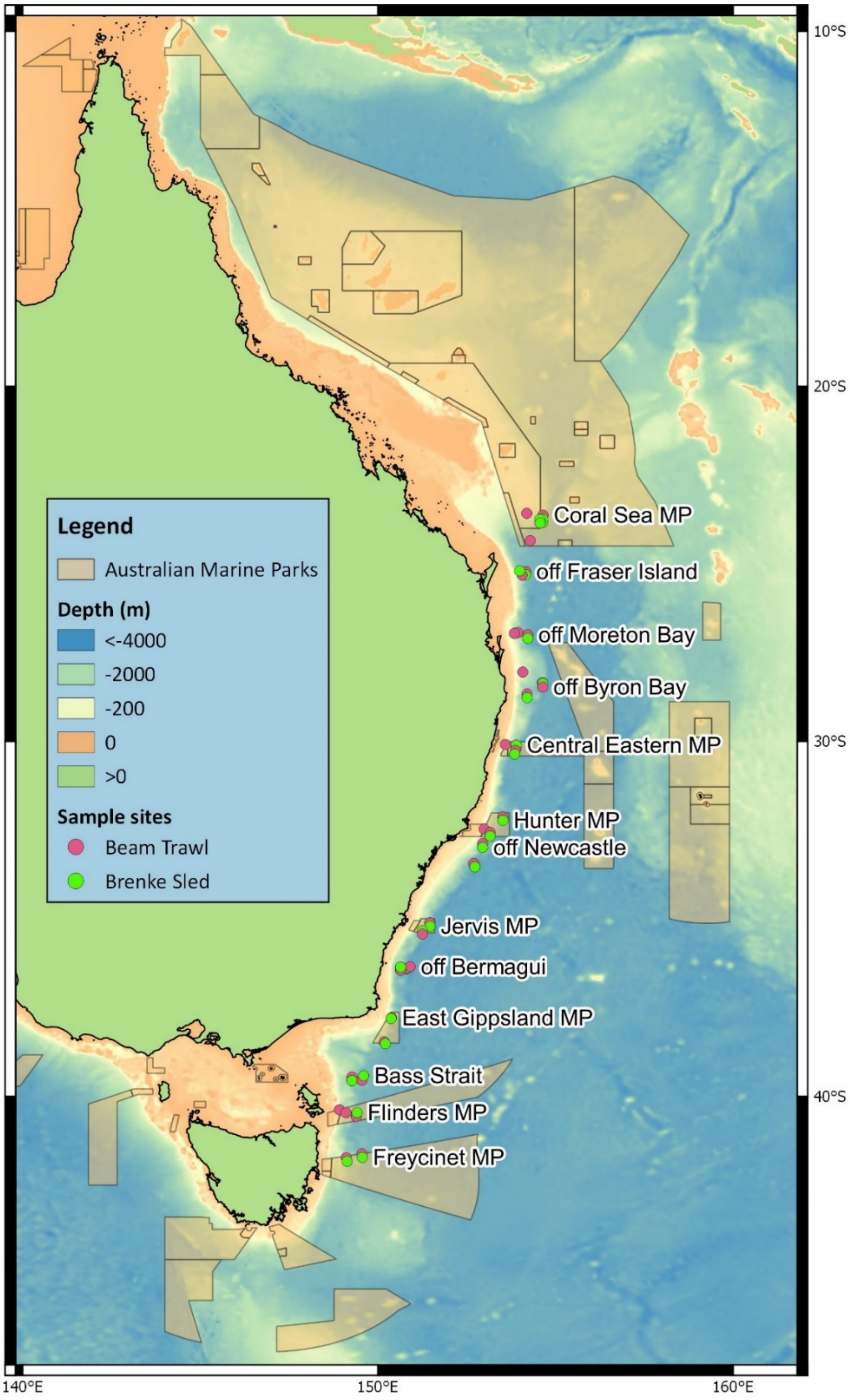

Fig. 1. Map of the eastern Australian continental margin showing the voyage sample sites and Australian Marine Parks.

Freycinet Marine Park

Freycinet Marine Park is a large reserve that extends in a wedge-shape from the continental shelf off the Freycinet Peninsula to the edge of Australia's Exclusive Economic Zone. It is managed as three zones, two occur on the outer continental shelf and upper continental slope (to 1000-1500 m) and include a multiple use zone to the north and a recreation zone to the south, the third, a marine national park zone, extends across the lower continental margin and abyssal plain. The IN2017_V03 voyage only traversed a small area to the north and so much of the park is unmapped and unexplored. Reef areas on the continental shelf have been mapped as a separate Marine Biodiversity Hub project (see https://www.nespmarine.edu.au/project/project-2-analysis-approaches-monitoring-biodiversity-commonwealth-waters).

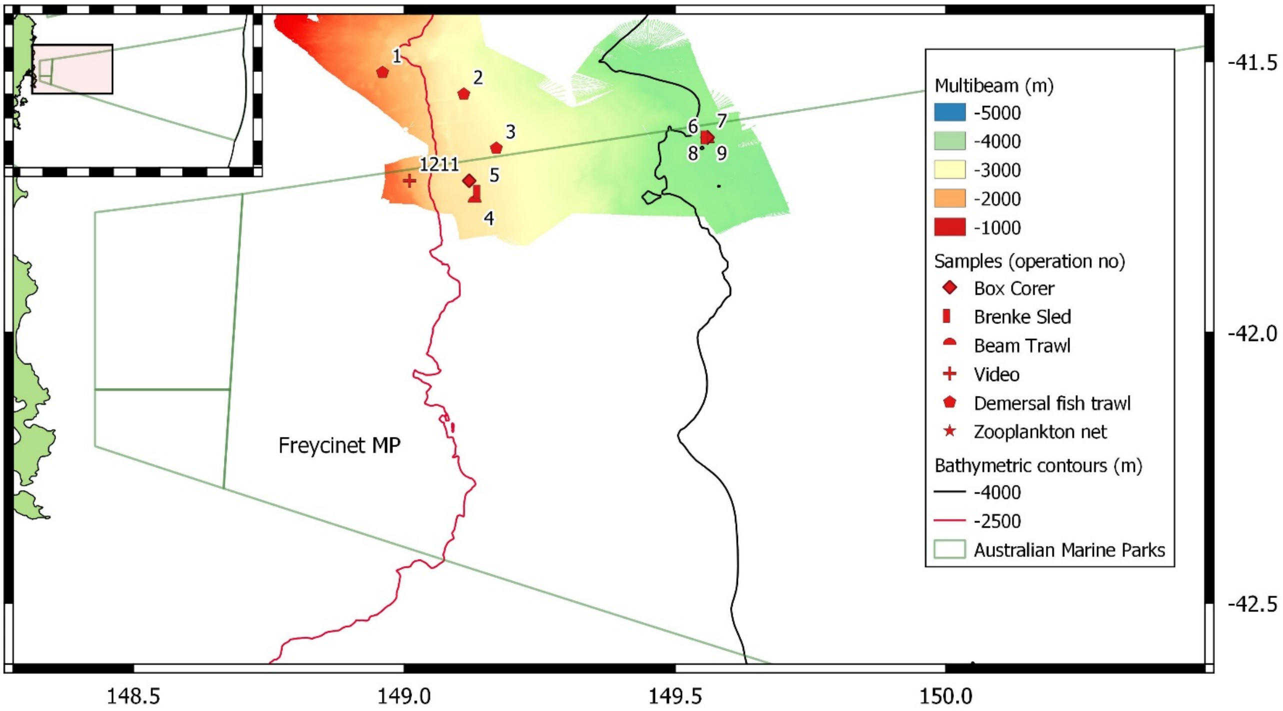

Fig. 2. Freycinet Marine Park, IN2017_V03 sample locations and multibeam coverage.

The areas that have been mapped with modern multibeam technology (Fig. 3) show some linear canyons on the upper slope and at least one box canyon that cuts through the lower bathyal terrace in the centre of the park. The continental slope is gentle and convex. There is evidence of a mid-slope escarpment at ~2500 m. The lower slope terraces are very wide and show some slip scars as they gradually descend to the abyssal plain. There is a notable flat plateau or detached continental block on the continental edge at around 41.9°S.

A video transect near the northern edge of the park at 1600 to 1858 m showed a rocky environment with boulders, gravel patches and expanses of soft sediment (Fig. 4). There were numerous herds of the sea cucumber *Peniagone* that would periodically settle on the mud to feed amongst the seapens. The rocks and boulders supported numerous filter feeders including green crinoids (*Thalassometra*), brittle stars, brisingid seastars, sea urchins (*Histocidaris*) and glass sponges. Halosaurs and basketwork eels were common. A box core at 2793 m brought up an intact section of seafloor that was dominated by sponge colonies that in turn sheltered various brittlestars (*Ophiactis amator*), pericarids and worms (Fig. 5). The beam trawl at 2751-2820 m resulted in the greatest biomass of any operation (>24 kg, see chapter 3), composed particularly of numerous sea cucumbers, seapens and molluscs and worms, a reflection of the organic-rich environment.

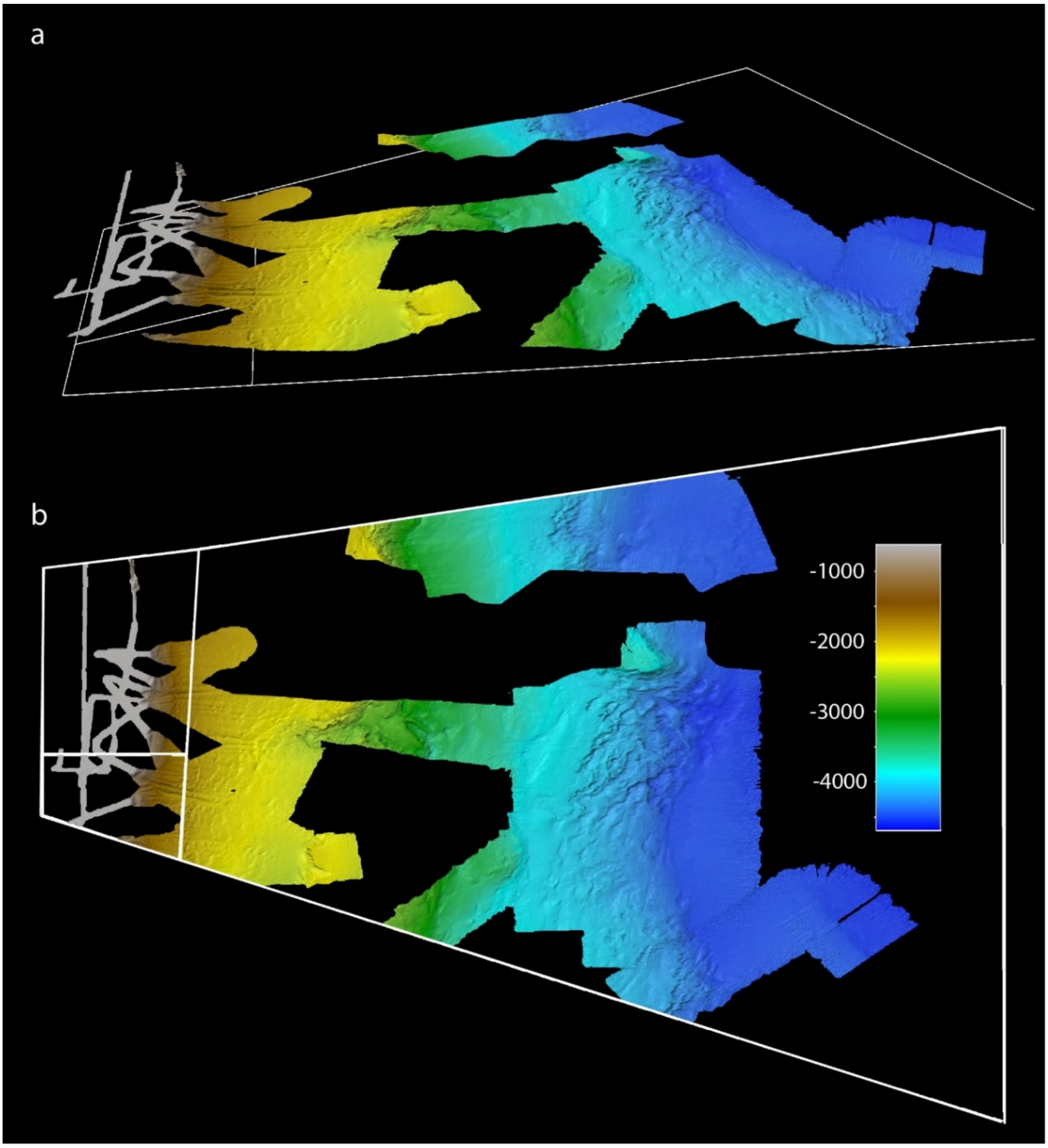

Fig. 3. Freycinet Marine Park, consolidated multibeam coverage (historical + IN2017_V03) with black polygons representing un-swathed areas. (a) Oblique view, (b) vertical view. Images: Amy Nau/CSIRO.

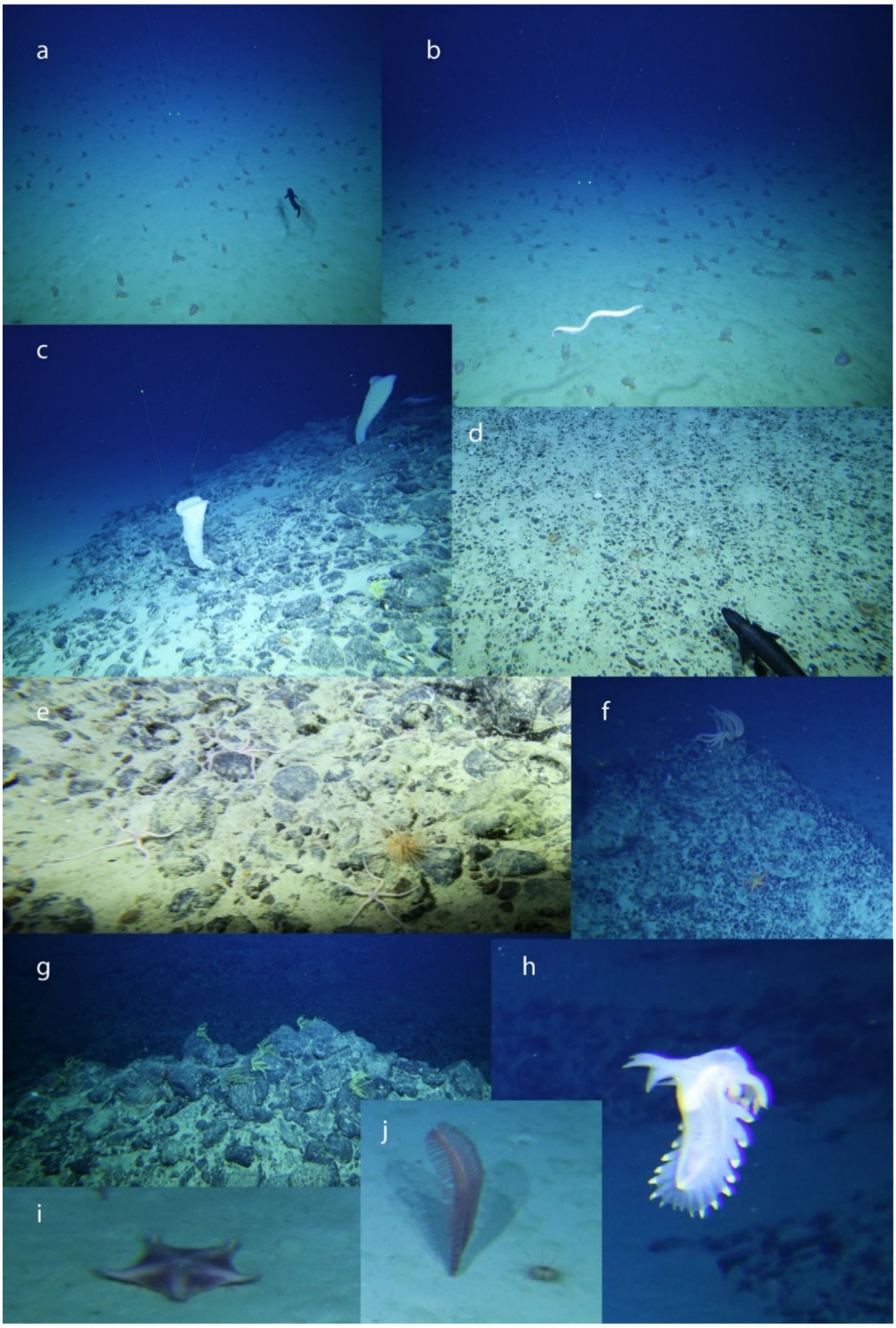

Fig. 4. Freycinet Marine Park, still photos from video transect (op 12, 1671-2516 m). (a-b) Shark and spiny eel swimming through herds of feeding holothurians (*Peniagone* spp); (c) glass sponges on a boulder field; (d) basketwork eel; (e) ophiuroids and sea-urchins (*Histocidaris*) amongst the stones, (f) seastars on a large boulder, including a predatory orange species (*Hyphalaster*) and a suspension feeding brisingid on top of the rock; (g) yellow thalassometrid crinoids; (h) swimming *Peniagone* holothurian; (i) *Hymenaster* seastar; (j) Seapen and urchin on the mud.

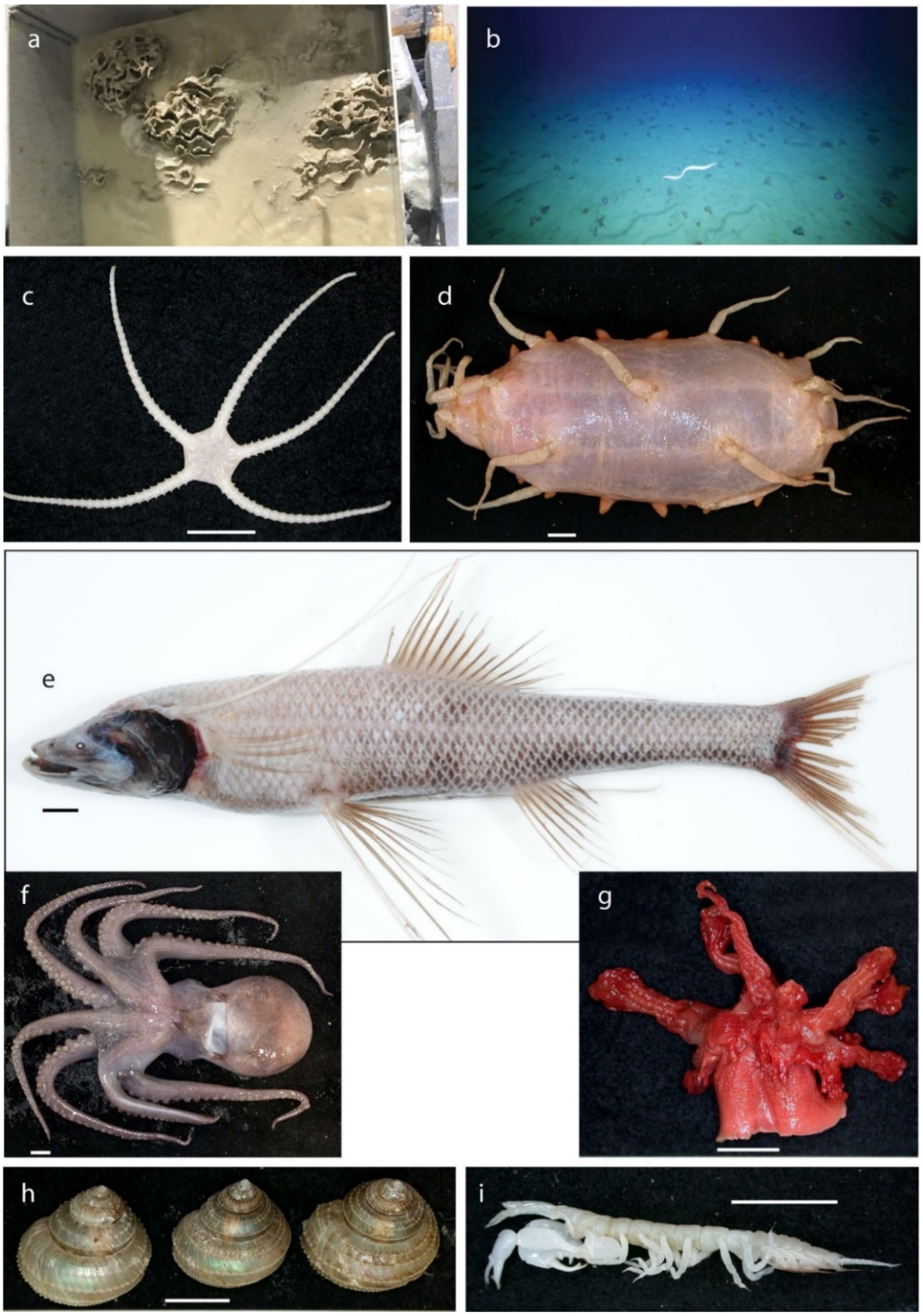

Fig. 5. Animals of the Freycinet Marine Park. (a) sponge *Ijimadictyum* sp QM 4980 collected in a box core (op 011, 2393 m, JM); (b) spiny Eel swimming over a herd of feeding holothurians (op 012, 1671-2516 m, deep-towed video); (c) ophiuroid *Ophiosphalma armigerum* is found from the North Atlantic to the Tasman Sea (op 011, 2393 m, KGH); (d) holothurian *Oneirophanta mutabilis* (op 004, 2820-2751 m, KGH); (e) tripod fish *Bathypterois filiferus* (op 004, 2820-2751 m, JP/AG); (f) undescribed species of Muusoctopus (sp. 1) (op 004, 2820-2751 m, KGH); (g) soft coral *Anthomastus* (op 003, 2948-2787 m, KGH); (h) undescribed species of gastropod, *Calliotropis* (sp. 2) (op 004, 2820-2751 m, KGH); (i) abyssal tanaid (op 006, 4022-4052 m, KGH). Scale bar = 1 cm.

Flinders Marine Park

Flinders Marine Park extends from the outer shelf off Banks Strait to the edge of Australia's Exclusive Economic Zone on the abyssal Tasman Plain. It is managed as two zones, a multiple use zone covering the shelf and upper slope and a Marine National Park Zone covering the lower continental margin and abyssal plain. This description only covers the margin from 1000-4000 m (Fig. 6), the area traversed by the IN2017_V03 expedition. Habitats on the outer shelf have been mapped and characterised by a separate Marine Biodiversity Hub project [2]. The offshore abyssal plain, with deep seamounts, is mostly unexplored.

The upper slope is characterised by numerous small linear canyons that extend from the shelf edge, through the sediments of the convex upper margin until reaching a series of wide lower bathyal terraces at ~2500 m. Several of these linear canyons coalesce into larger box canyons that cut deeply into the terrace, the most southerly of which is named Banks Strait Canyon. Two small cone-shaped features, possibly of volcanic origin, rise 500 m off the terrace in the centre of the park. The lowest terrace is uneven and includes several elevated blocks, possibly resulting from processes associated with the original rifting of Australia from New Zealand, or from slumping off the mid slope. Several of these blocks terminate in a steep scarp facing the abyssal plain. To the north of the park, a winding moat occurs on the abyssal plain, evidence of the strong bottom currents. It is likely that manganese nodules or a manganese pavement would occur further out on the abyssal plain of the Flinders and Freycinet Marine Parks as they are known to occur below 4,300 m from off Sydney to the South Tasman Rise [3]. The formation of nodules is possible as sedimentation rates are low below the lysocline [4].

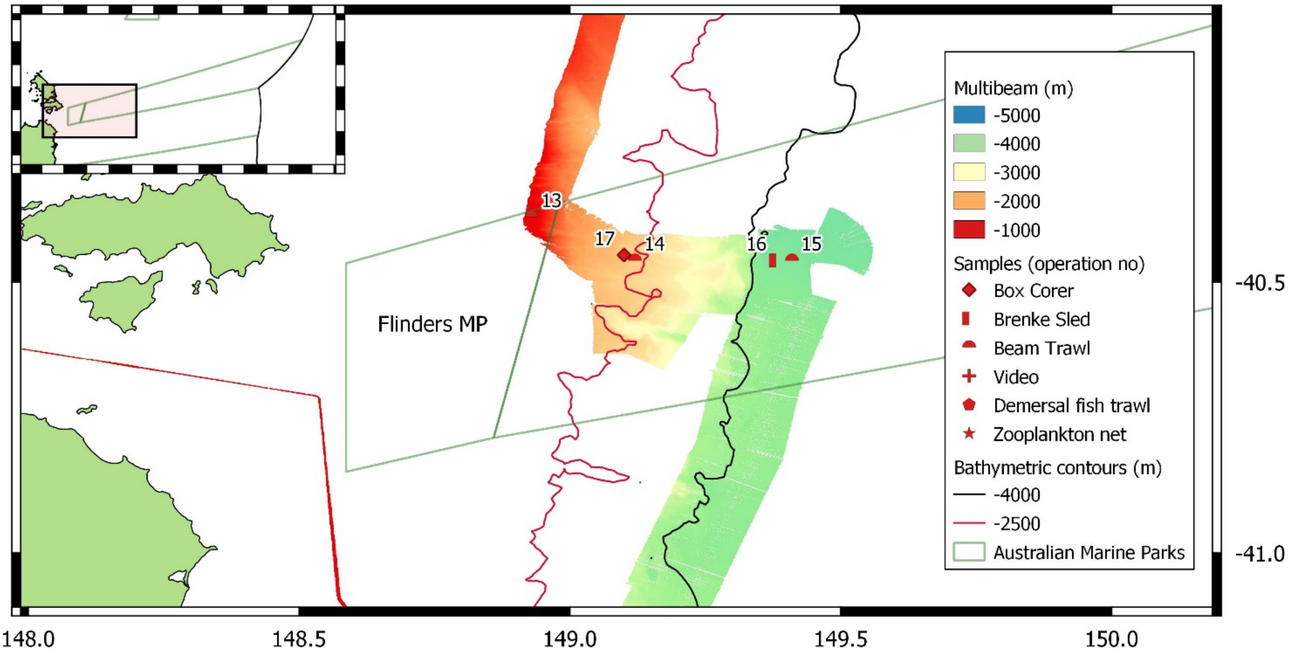

Fig. 6. Flinders Marine Park, IN2017_V03 sample locations and multibeam coverage.

The park experiences elevated phytoplankton production in spring and autumn, which lead to seasonal pulses of organic matter reaching the seafloor. The upper depths of the park experiences southward moving eddies from the Eastern Australian Current. Below this several water masses move up from the south, including Antarctic Intermediate water (temperature of 5.0°C) at around 1000 m, North Atlantic Deep Water (1.9°C) at ~2500 m and Antarctic Bottom Water (1.1°C) on the abyssal plain at ~4500 m. Although these water masses play a role in facilitating horizontal dispersal of larvae, it is unclear whether their differing salinity or dissolved oxygen concentrations are biologically limiting. The differing temperatures, pressure and organic matter availability are more likely to determine faunal niches.

The fauna at 2298-2486 m (op 014) was diverse but not as abundant as the Freycinet sample, without the sea cucumber herds. The fauna was dominated by the brittle star *Ophiocten australis*, the holothurian *Mesothuria cathedralis*, the seastar *Plutonaster complexus* and the pycnogonid *Colossendeis tasmanica*. The beam trawl at 932-1151 m (op 013) was terminated early and did not produce a representative sample. Conversely the trawled sample at 4114-4139 m (op 015) was rich and diverse. The ophiuroids were numerous and included a typical abyssal fauna (*Ophiosphalma armigerum*, *Amphiophiura bullata*, *Ophiacantha cosmica*, *Amphioplus verrilli*, *Astrodia tenuispina*). There were also numerous seapens (*Porupinella* and *Umbellula*), stalked ascidians (*Culeolus anonymus*), seamouse polychaetes (*Laetmonice yarramba*), and a piece of wood with numerous burrowing bivalves (*Xylophaga*). Equipment problems on the voyage prevented the successful deployment of the towed video in this park.

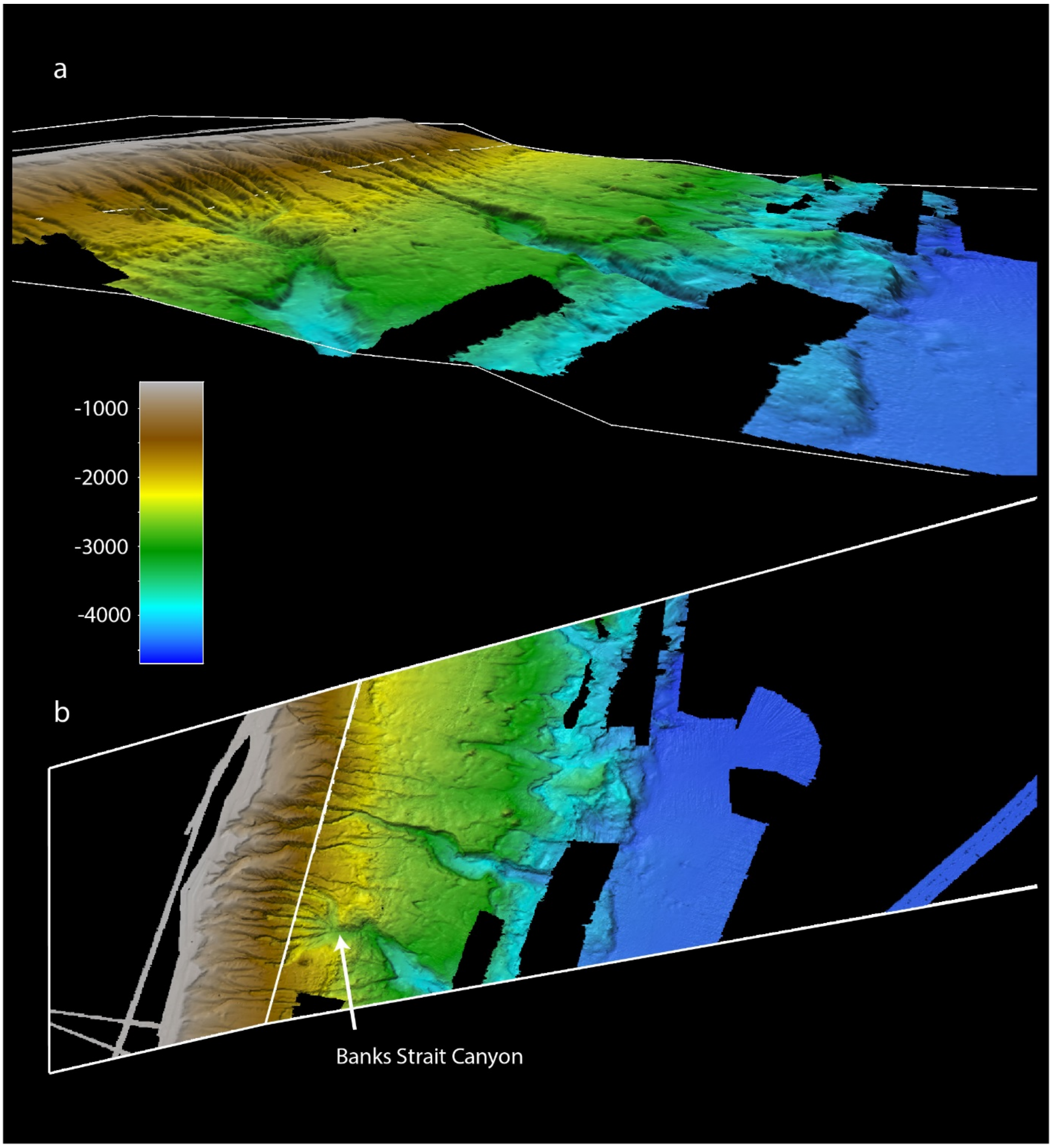

Fig. 7. Flinders Marine Park, consolidated multibeam coverage (historical + IN2017_V03) with black polygons representing un-swathed areas. (a) Oblique view, (b) vertical view. Images: Amy Nau/CSIRO.

Fig. 8. Some seafloor animals of the Flinders Marine Park. (a) undescribed buccinid snail *Neptunea* (sp; 1) (op 015, 4114-4139 m, KGH); (b) Undescribed *Fusinus* (sp; 1) (op 013, 932-1151 m, KGH); (c) ophiuroid *Astrodia* cf *tenuispina* on a soft coral (op 015, 4114-4139 m, KGH); (d) widespread abyssal brittlestar *Amphiophiura bullata* (op 015, 4114-4139 m, KGH); (e) upper bathyal indo-Pacific *Ophiura clemens* (op 013, 932-1151 m, KGH); (f) giant pycnogonid *Colossendeis tasmanica* (op 015, 4114-4139 m, KGH); (g) sponge eating asteroid *Hoplaster kupe* (op 014, 2298-2486 m, KGH); (h) asteropectinid sea star *Proserpinaster neozelanicus* (op 014, 2298-2486 m, KGH); (i) large deep-sea slime-star *Hymenaster carnosus* (op 014, 2298-2486 m, KGH); (j-k) sea toad, *Chaunax* sp (op 013, 932-1151 m, JP/AG). Scale bar = 1 cm.

East Gippsland Marine Park

The East Gippsland Marine Park contains deep-water habitats from the upper continental slope to abyssal plain. The northern end of the park is marked by a plateau at lower bathyal depths (~3000 m) and a large tilted continental block that has become detached from the margin. Around 37.8°S there is large box canyon with a long discontinuous ridge extending through its centre to the abyssal plain. The shape of the ridge suggests that it is the remains of a large slide of sediment and basement rock from the continental margin. Such slumps are thought to be caused by earthquakes or current erosion at the foot of the slope which destabilises sediment further up the slope. Further south (38.2°S), there is a dome-shaped plateau on the upper slope (700-1800 m) which is bordered by relatively steep dissected slopes (1800-3800 m). Evidence of a shallow moat at the start of the abyssal plain suggests that the bottom current flows strongly to the north along this section of the continental margin. After a small canyon, there is a notable quadrangular platform (1600-2400 m) with a steep escarpment along most of the seaward edge and again signs of a margin slump off the northern corner. The southern edge of the plateau is bordered by a large box canyon. The canyon, which is steep at the head with apparent slide scars, incises the lower slope and across the rise before reaching the abyssal plain. The southernmost section of the park is characterised by a relatively gentle slope from 1600 m to the base of the margin.

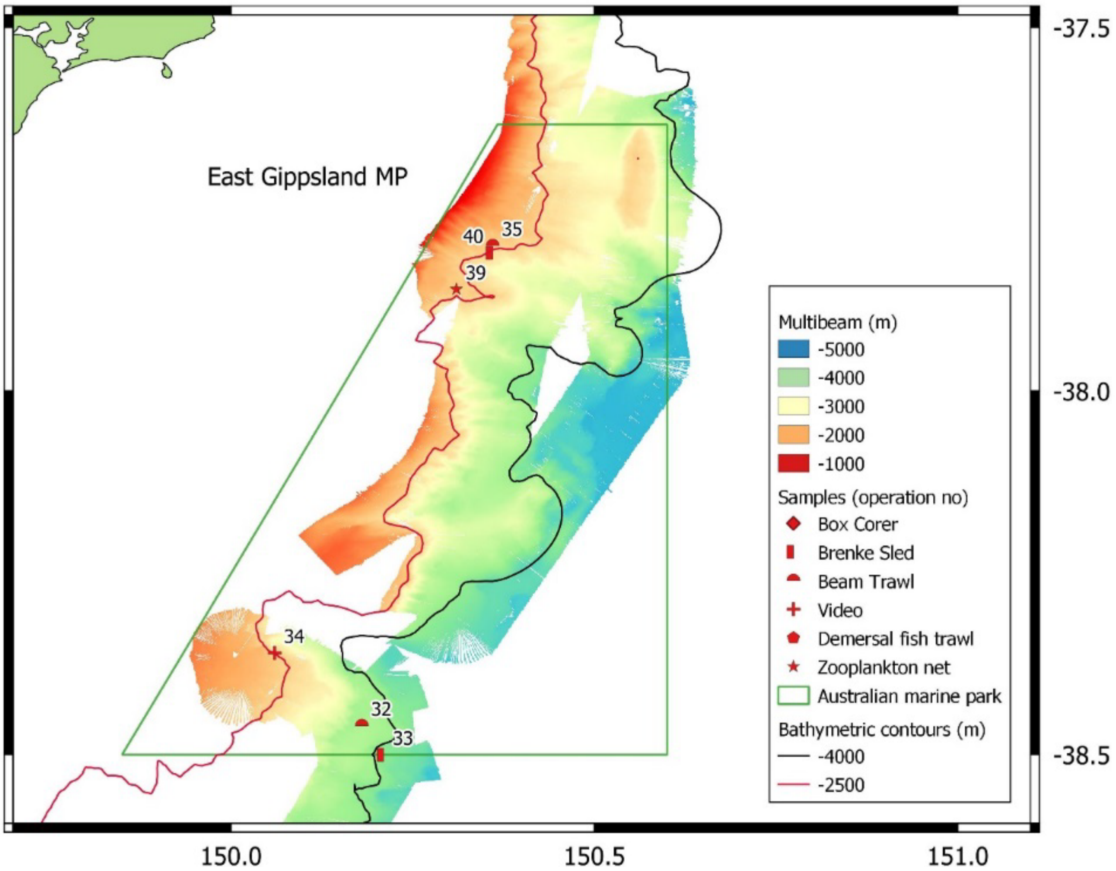

Fig. 9. East Gippsland Marine Park, IN2017_V03 sample locations and multibeam coverage.

During winter and spring, a seasonal current called the Bass Strait cascade would flow through the park. This flow results from the formation of high salinity water in Bass Strait which downwells over the upper continental slope in the Bass Strait Canyon to approximately 300-400 m depth before turning east and north [5]. The signature of this flow has been detected as far north as the Coral Sea [6].

A major input of food for the seafloor is from swarms of oceanic salps that can occur in the upper 200 m of the Tasman Sea [7]. The carcasses and faecal pellets of large salps such as *Thetys vagina* play a significant role in carbon transport to the seafloor due to their fast sinking rates [8]. In nearby Bass Canyon, mean densities of 219 carcasses per 1000 m^2 have been recorded on the seafloor; densities of oceanic salps and pyrosomes are greatest between December and June [7].

The video transect (Fig. 11) across the rectangular plateau showed a muddy plain with a few fish, cnidarians, and lots of plankton in the water. The mid-bathyal beam trawl (op 035) sampled a diverse fauna (Fig. 12). The highlights were a large red spiny king crab (*Neolithodes bronwynae*), many pycnogonids, sea-stars (e.g. *Porcellanaster* and *Zoroaster*), and a finned-octopus. Oher animals included numerous polychaetes (e.g. ampharetids, aphroditids, serpulids), bivalves, ophiuroids and ship-worms. The diverse sea cucumber fauna was in this case dominated by *Amperima furcata.* The deep beam trawl (Op 032) at 3850-3853m included numerous seamice (*Laetmonice yarramba*), the benthic tunicate *Asajirus indicus* (which eats crustaceans and is not a filter feeder), seapens (*Scleroptilum*, *Kophobelemnon*), the small clam *Abra profundorum*, similar ophiuroids to Flinders MP and numerous raphitomid gastropods (*Bathybela*).

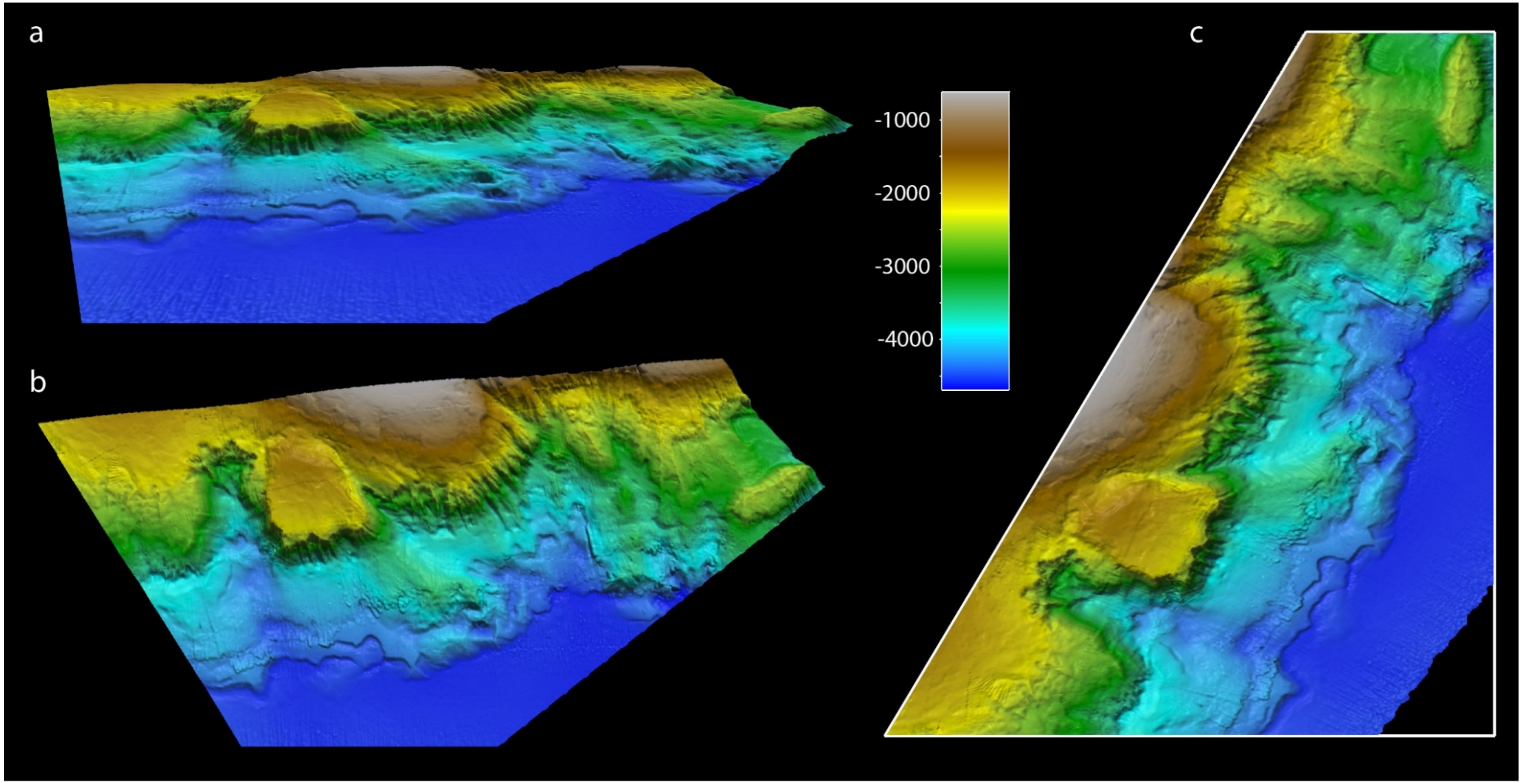

Fig. 10. East Gippsland Marine Park, consolidated multibeam coverage (historical + IN2017_V03) with black polygons representing un-swathed areas. (a-b) oblique views, (b) vertical view. Images: Amy Nau/CSIRO.

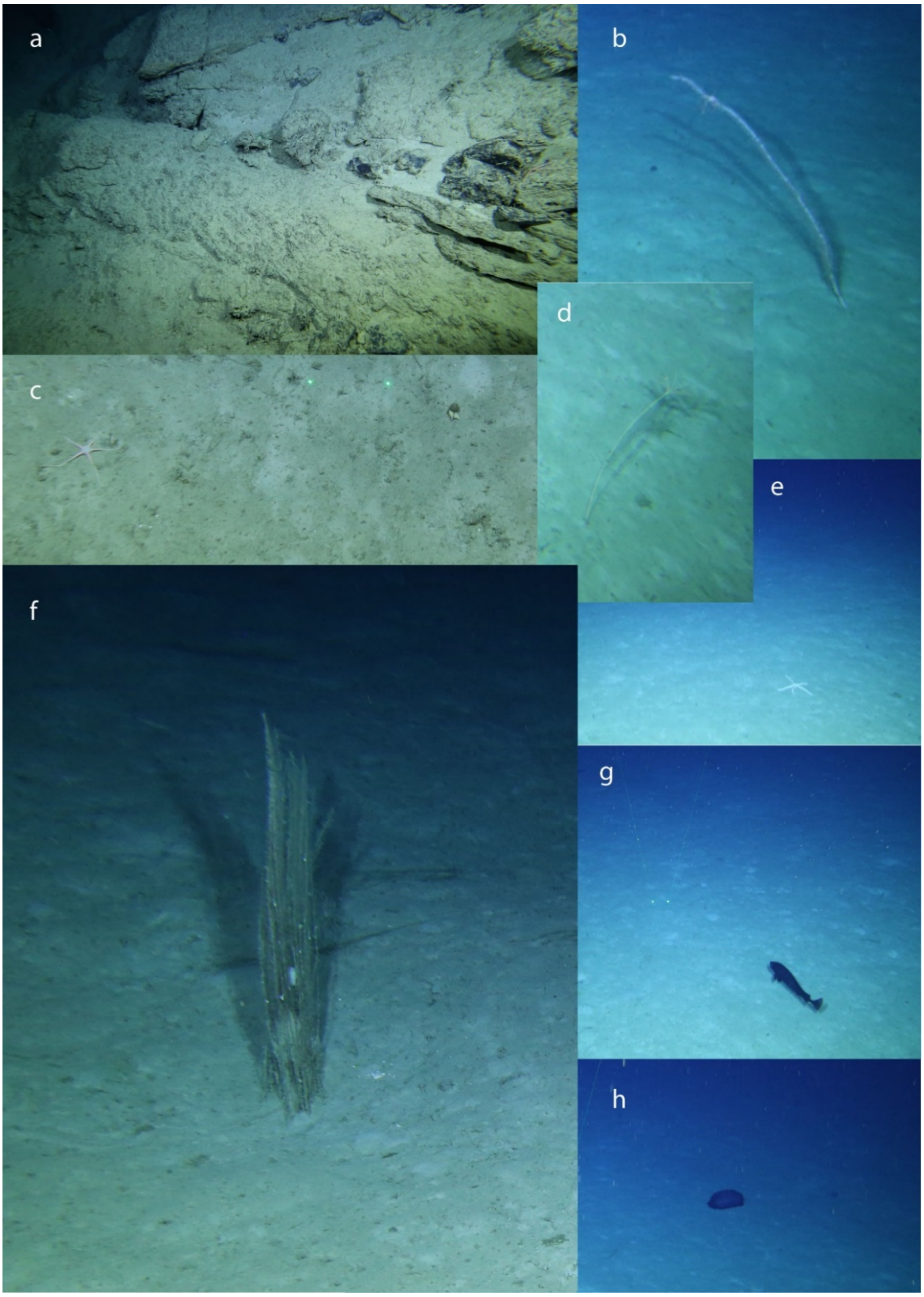

Fig. 11. East Gippsland Marine Park, still photos from video transect (op 34, 2357-2544 m). (a) rocky escarpment; (b) sea=whip (?Primnoidae) supporting the clinging ophiuroid *Asteronyx loveni*; (c) ophiuroid *Ophiocten australis*; (d) bathycrinid crinoid has a fixed stalk; (e) unknown predatory sea-star; (f) sponge or soft coral; (g) a violet cod (*Antimora rostrata*); (h) undescribed *Benthodytes* holothurian.

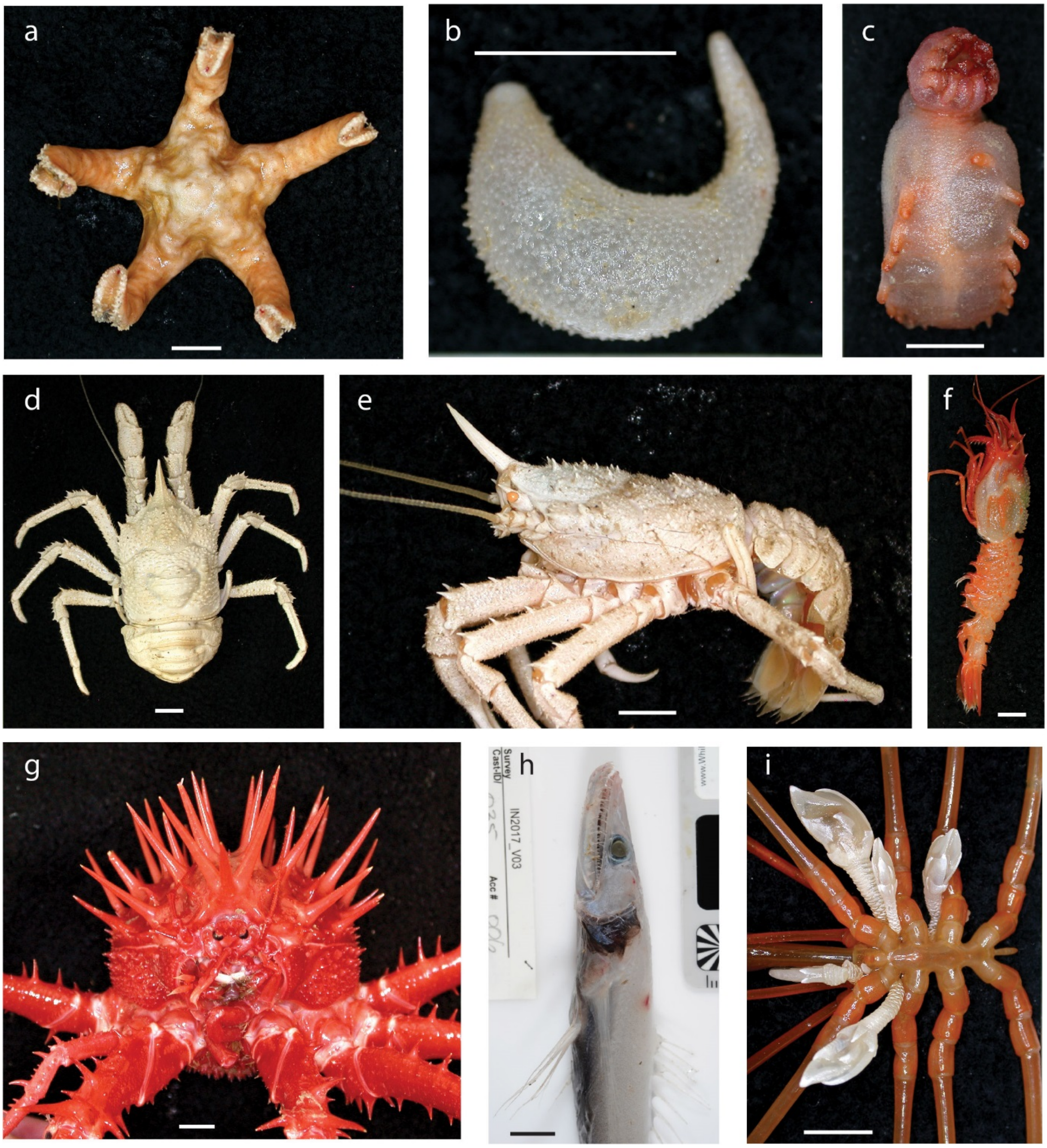

Fig. 12. Some seafloor animals of the East Gippsland Marine Park. (a) unknown poranid seastar (op 032, 3850-3853 m, KGH); (b) U-shaped holothurian *Echinocucumis ampla* has the mouth and anus protruding from the mud (op 035, 2338-2581 m, KGH); (c) deposit feeding elasipod holothurian *Amperima furcata* (op 035, 2338-2581 m, KGH); (d) squat lobster *Munidopsis crassa* (op 032, 3850-3853 m, KGH); (e) female squat lobster *Munidopsis arietina* (op 032, 3850-3853 m, KGH); (f) deep sea armoured shrimp *Glyphocrangon dimorpha* (op 035, 2338-2581 m, KGH); (g) spiny king crab *Neolithodes bronwynae* (op 035, 2338-2581 m, KGH); (h) deep sea lizardfish *Bathysaurus ferox* is widespread in tropical and subtropical seas (op 035, 2338-2581 m, JP/AG); (i) undescribed species of the barnacle genus *Litoscalpellum*, epibiont on the pycnogonid *Colossendeis tasmanica* (op 035, 2338-2581 m, KGH). Scale bar = 1 cm.

Jervis Marine Park

The Jervis Marine Park has five notable linear canyons that incise the sediments of the upper slope, with at least one continuing from the continental shelf [4]. At their upper reaches they are V-shaped and up to 200 m deep, but become wider (400 m) and shallower (100 m) as they proceed down the slope. They are known collectively as the Shoalhaven canyons and the three largest are named Perpendicular, Beecroft and St George. However, there has been some confusion about these canyon's locations. The original paper sites them at 35° 07', 35° 12' and 35° 17'S respectively [9, fig. 1]. A later paper by the same author showed the positions of Beecroft and Perpendicular reversed [10, fig. 23], whereas Harris, et al. [11, fig. 3.24] placed all three canyons north of 35°S. Here, the original positions are preferred and are marked on the map appropriately.

The canyons widen and coalesce into box canyons as they cut through the mid-slope escarpment (2000-3500 m). This escarpment shows evidence of slide scars and gullies along much of its southern length. Both the Perpendicular and Beecroft canyons strongly incise the 15 km wide terrace of the lower slope possibly from turbidity currents flowing down the canyons [4]. The terrace on the northern side of Perpendicular Canyon is marked by a linear trail of slump blocks. Between these two incisions, there is a tall steep (average gradient 25°) scarp along the edge of the abyssal plain, possibly the result of a strike-fault forming before or during the rifting that created the Tasman Sea [4].

Although the canyons have the appearance of river valleys, they are actually caused by the slow de-watering and compaction of sediments over geological time frames. The erosion proceeds head-ward from lower depths up onto the shelf and likely proceeds in stages through sudden collapse of sediments and associated turbidity currents.

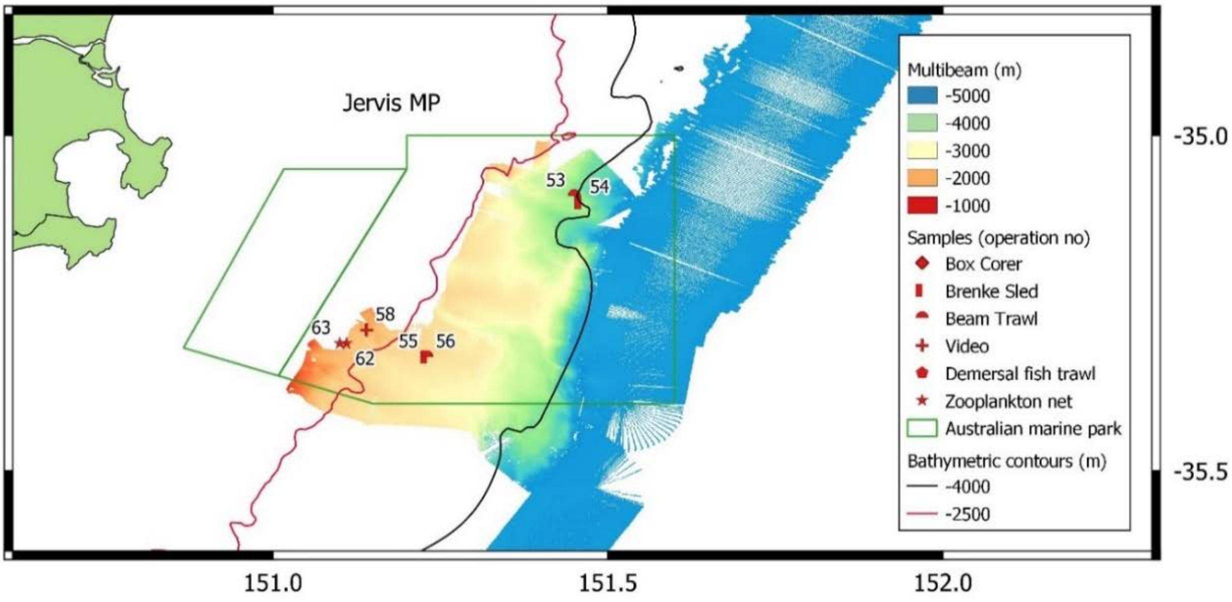

Fig. 13. Jervis Marine Park, IN2017_V03 sample locations and multibeam coverage.

A camera tow (op 058) near the St George Canyon, revealed mostly muddy ground, with some boulders near the end. Visible animals included sea pens, brittle-stars, sea-stars, and sea spiders. The faceless fish which featured prominently in the media reports from the expedition was found on the lower slope terrace (op 53), just to the north of the Beecroft Canyon. The Jervis Marine Park marks the southern limit of many northern species.

The mid bathyal beam trawl (Op 056) at 2650-2636 m included numerous polychaetes (particularly ampharetids, aphroditids and maldanids), *Parapagurus* hermit crabs, a new species of crangonid prawn, barnacles *Gibbosaverruca navicular*, pycnodonid *Ascorhynchus cooki*, the large predatory seastar *Zoroaster barathri*, the infaunal seastars (*Bathybiaster loripes* and *Dytaster exilis*), stalked bathycinid feather stars (*Monachocrinus*), large numbers of ophiuroids (*Ophiocten*, *Ophiura*, *Ophiosphalma*) glass scallops (*Propeamussium*), turritellid and mangeliid gastropods, and the sponge *Chondrocladia clavata.* The deeper trawl (Op 053) at 3952-4011 m resulted in chaetopterid and onuphid polychaetes, *Ophiosphalma armigerum*, *Abra profundorum*, and two species of the holothurian *Molpadia*, amongst many others.

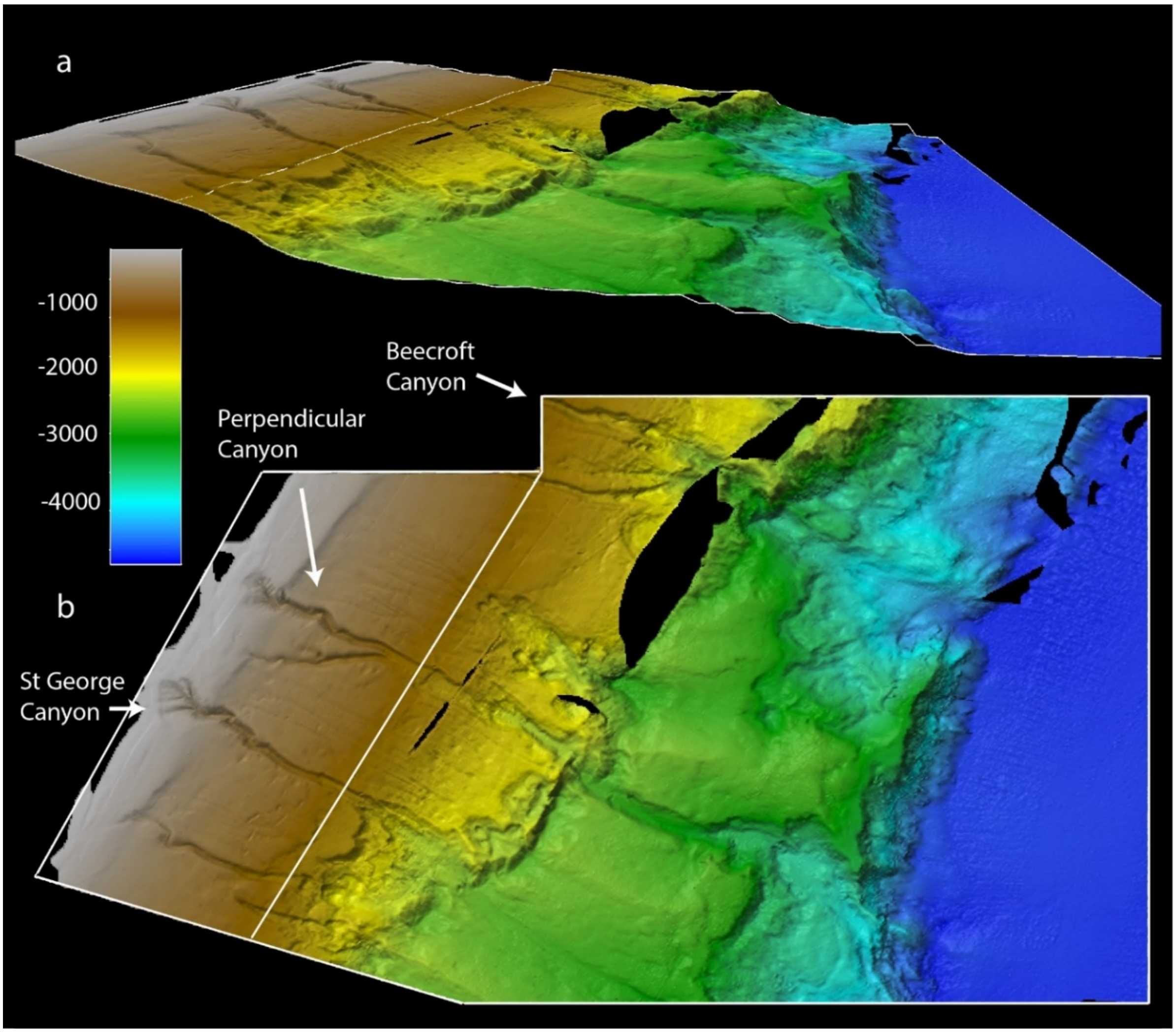

Fig. 14. Jervis Marine Park, consolidated multibeam coverage (historical + IN2017_V03) with black polygons representing un-swathed areas. (a) Oblique views, (b) vertical view. Images: Amy Nau/CSIRO.

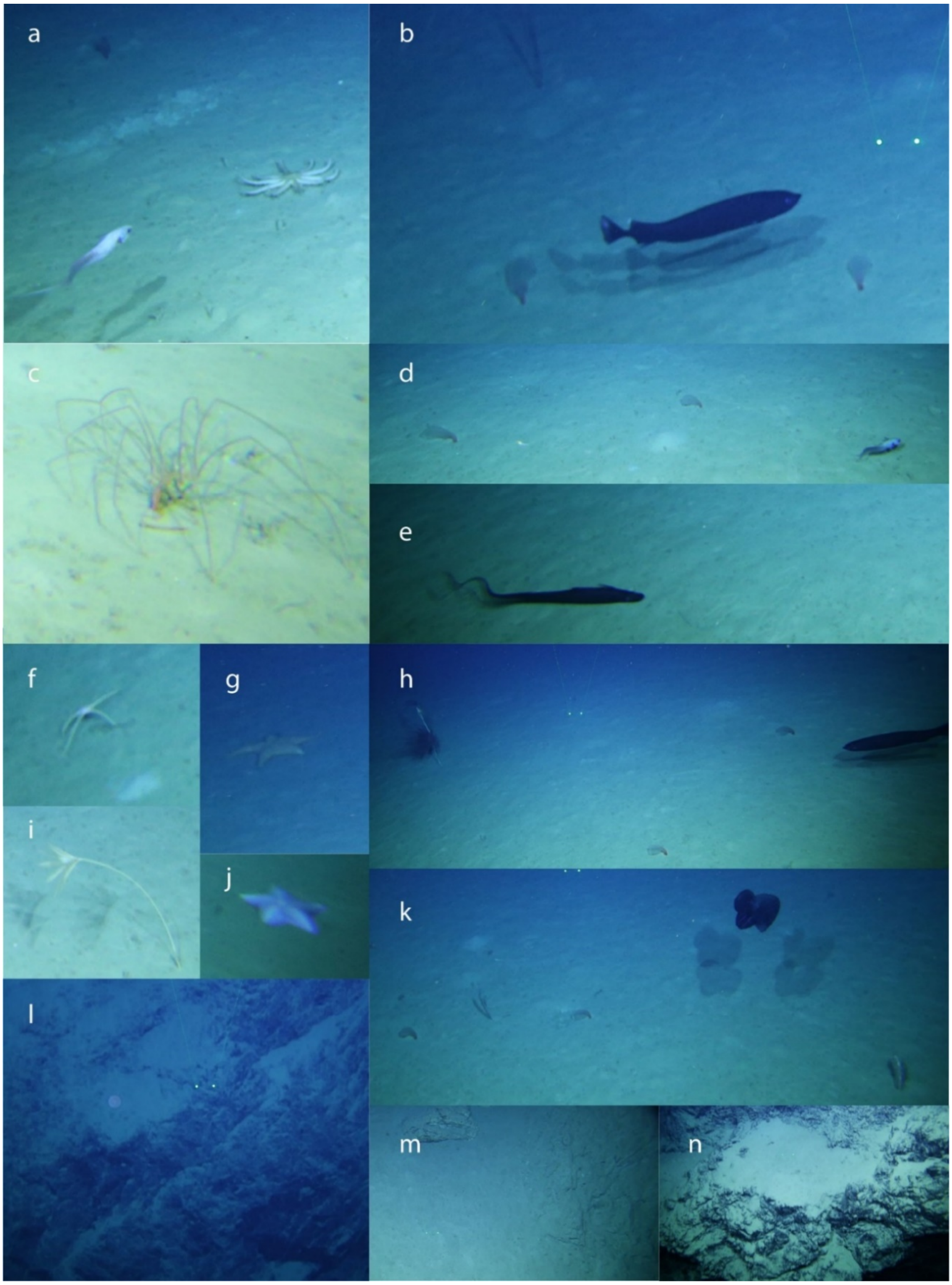

Fig. 15. Jervis Marine Park, still photos from video transect (op 58, 2126-2355 m). (a) a whiptail, perhaps *Coelorinchus*, approaching the seastar *Crossaster multispinus*; (b) violet cod swimming past seapens; (c) the giant sea-spider *Colossendeis*; (d) another whiptail; (e) the black halosaur *Halosauropsis macrochir*; (f) the brittle-star *Ophiomusa lymani* lifts its body free from the mud; (g) unknown seastar; (h) a slickhead, perhaps *Alepocephalus*, approaching an epibiotic anemone to the left; (i) bathycrinidae sea-lily; (j) *Hymenaster* seastar; (k) The holothurian *Benthodytes* swimming above the mud; (l) bare rock; (m) consolidated mud; (n) boulder.

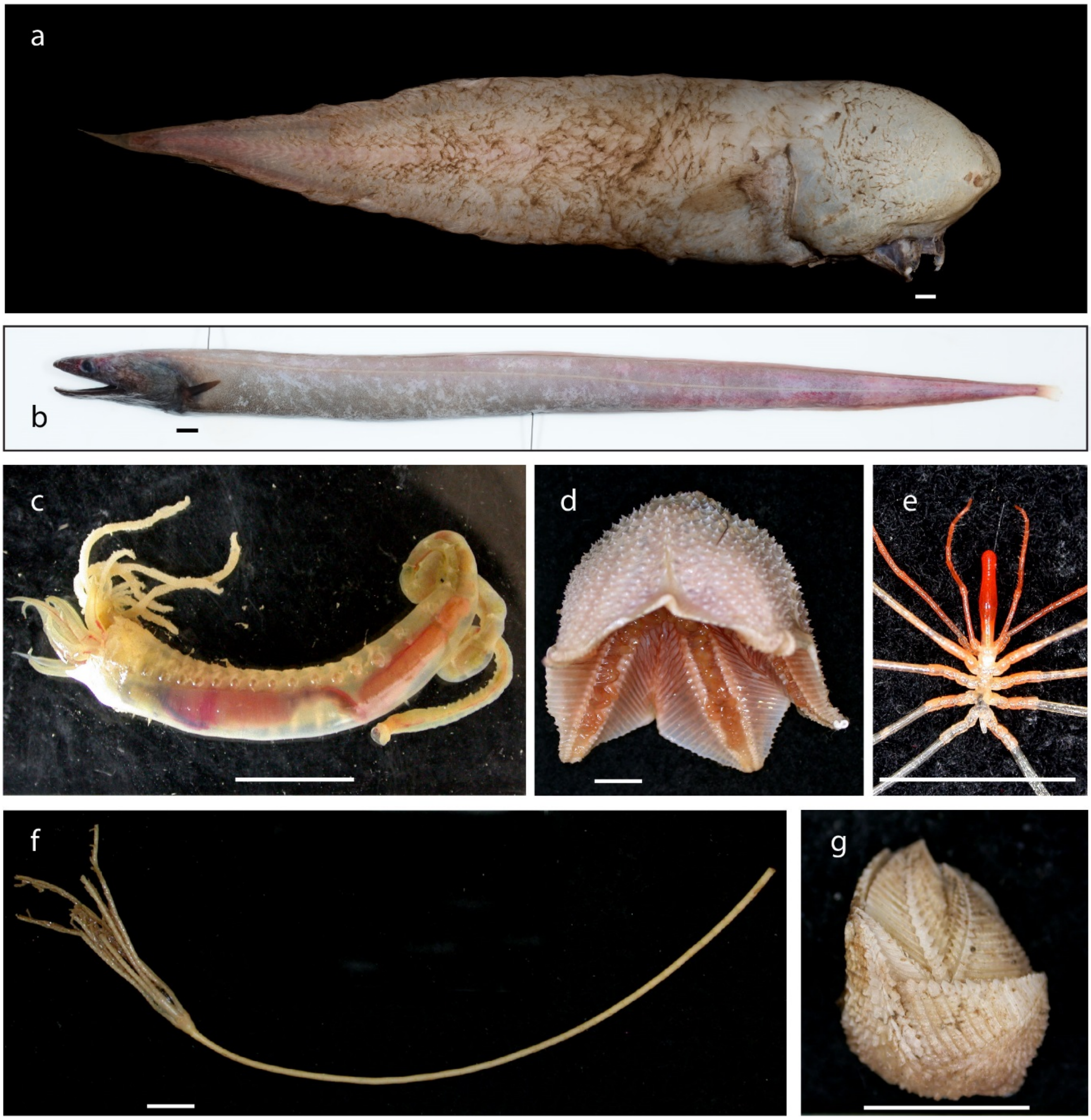

Fig. 16. Some seafloor animals of the Jervis Marine Park. (a) media-famous faceless cusk fish *Typhlonus nasus* (op 053, 3952-4011 m, RZ); (b) southern cut-throat eel *Histiobranchus australis* is widespread in southern oceans (op 056, 2650-2636 m, JP/AG); (c) undescribed ampharetid polychaete (sp; C) (op 056, 2650-2636 m, KGH); (d) pterasterid seastar *Calyptraster gracilis*, originally described from off the Reunion Islands (op 056, 2650-2636 m, KGH); (e) undescribed *Colossendeis* pycnogonid (sp; 3) (op 056, 2650-2636 m, KGH); (f) the stalked crinoid *Monachocrinus* cf *aotearoa* (op 056, 2650-2636 m, KGH); (g) barnacle *Gibbosaverruca navicula* has been found regularly around Australia at mid-bathyal depths (op 056, 2650-2636 m, KGH). Scale bar = 1 cm.

Hunter Marine Park

The Hunter includes a Special Purpose Zone (SPZ) protecting shelf and upper slope (<1000 m) habitats and a deeper Habitat Protection Zone (HPZ) that continues to the abyssal plain. The Hunter SPZ has been the focus of a separate shallow water mapping and habitat classification exercise by the Marine Biodiversity Hub [12]. Consequently, this description of the park is restricted to the deeper habitat protection zone.

Across the Hunter HPZ, the continental margin is marked by a mid-slope escarpment incised by numerous slide scars, gullies and small box canyons with blocks of displaced sediment below. Along the base of the escarpment are a series of wide terraces that step down to the abyssal plain. A series of “pock marks” occur on the lowest terrace near the southern of the park. A narrow moat occurs in the sediments of the abyssal plain along the edge of the lowest terrace. The large box canyon at the southern end of the park is northern section of the Hunter Canyon complex. The head of the section of the canyon is defined by a steep scarp at ~1000 m. The canyon then turns to the south-east before cutting through the lower slope terraces in a series of scoured depressions as water and sediment flows over ridges of resistant bedrock. South of the park tributary linear canyons extend up to the outer shelf. The Manning Canyon lies just to the north of the park.

The rocks of the Hunter Marine Park are of both sedimentary and igneous origin. They outcrop on the escarpments, canyon walls, and as boulders or scree material at their base. These rocks are often coated with Fe-Mn crusts [4]. There is no continental rise formed from terrestrial sediments. Sedimentation is relatively low and results from pelagic biota at lower bathyal and abyssal depths. The strong Eastern Australian current flows offshore, breaking up into eddies across the park. These eddies can disturb seafloor sediments from the outer shelf down to 2000 m [4].

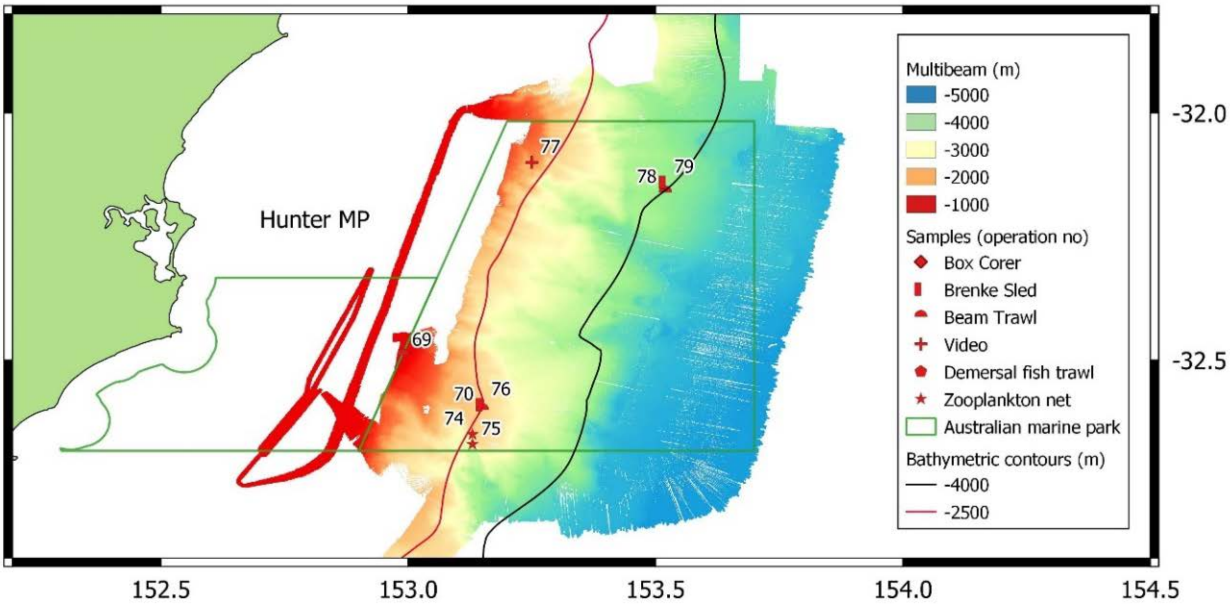

Fig. 17. Jervis Marine Park, IN2017_V03 sample locations and multibeam coverage.

A towed camera was deployed (stn 077) from 1741 to 2115 m seafloor depth near the north-western corner of the Habitat Protection Zone. This revealed a muddy plain with a few boulders. A beam trawl at 1006-1036 m (stn 069) collected a diverse and rich fauna including small bamboo corals, sponge rods, lots of crinoids (*Democrinus* cf *japonicus* and *Thalassometra* cf *gracilis*), climbing (*Ophioplinthaca rudis*) and epibenthic (*Ophiura irrorata*) brittle stars, sea-stars (*Cheiraster* and *Zoroaster*), the holothurian *Amperima furcata*, turrid (*Ptychosyrinx*) and nassariid (*Tritia*) gastropods and a juice bottle. The 2500 m beam trawl in (stn 070) revealed glass sponges, a new species of brittle star (*Amphiophiura* sp nov), saleniid sea urchins (Salenocidaris), squat lobsters, hermit crabs, barnacles (*Gibbosaverruca*), large pieces of pumice, and a can of (empty) fosters beer. This park represents a temperate-tropical transition at this depth, with more animals having tropical affinities (see Chapter 3), for example the southern brittle star *Ophiosphalma armigerum* is replaced by the tropical *O. fimbriatum* at this site. The abyssal beam trawl (op 078) at 3980-4029 m collected a small but diverse range of animals. At this depth, the park also marked a transition but shared more species with the south-east.

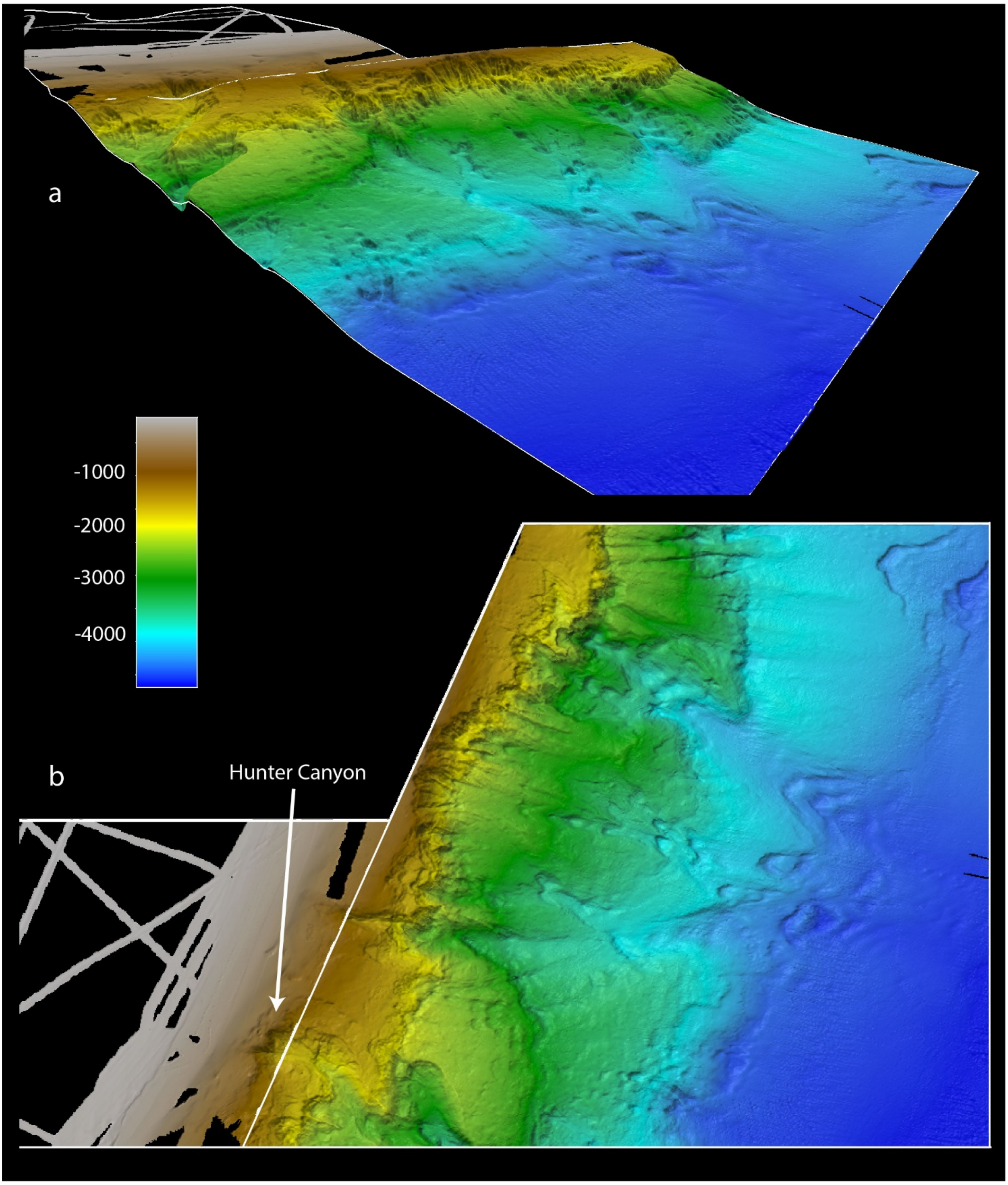

Fig. 18. Hunter Marine Park, consolidated multibeam coverage (historical + IN2017_V03) with black polygons representing un-swathed areas. (a-b) oblique views, (b) vertical view. Images: Amy Nau/CSIRO.

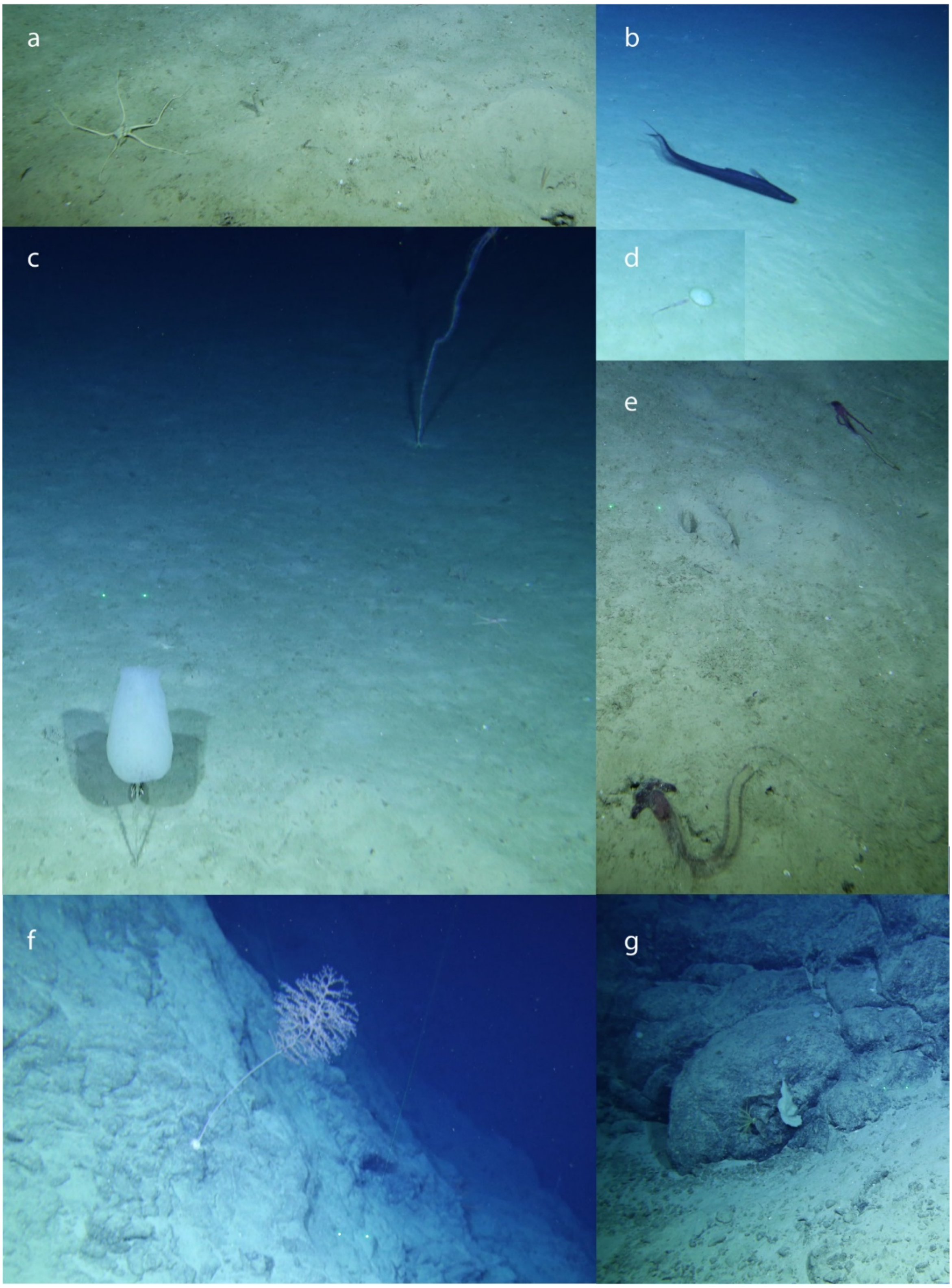

Fig. 19. Hunter Marine Park, still photos from video transect (op 77, 1741-2115 m). (a) Brittle-star *Ophiomusa lymani* on the mud; (b) the black halosaur *Halosauropsis macrochir*; (c) goblet sponge *Haplonema*; (d) pancake urchin of the family Echnothuriidae; (e) acorn worm (Torquaratoridae) winding its way across the mud; (f) gold coral (?*Chrystogorgia*) on a rocky slope; (g) sponge and green crinoid on a boulder.

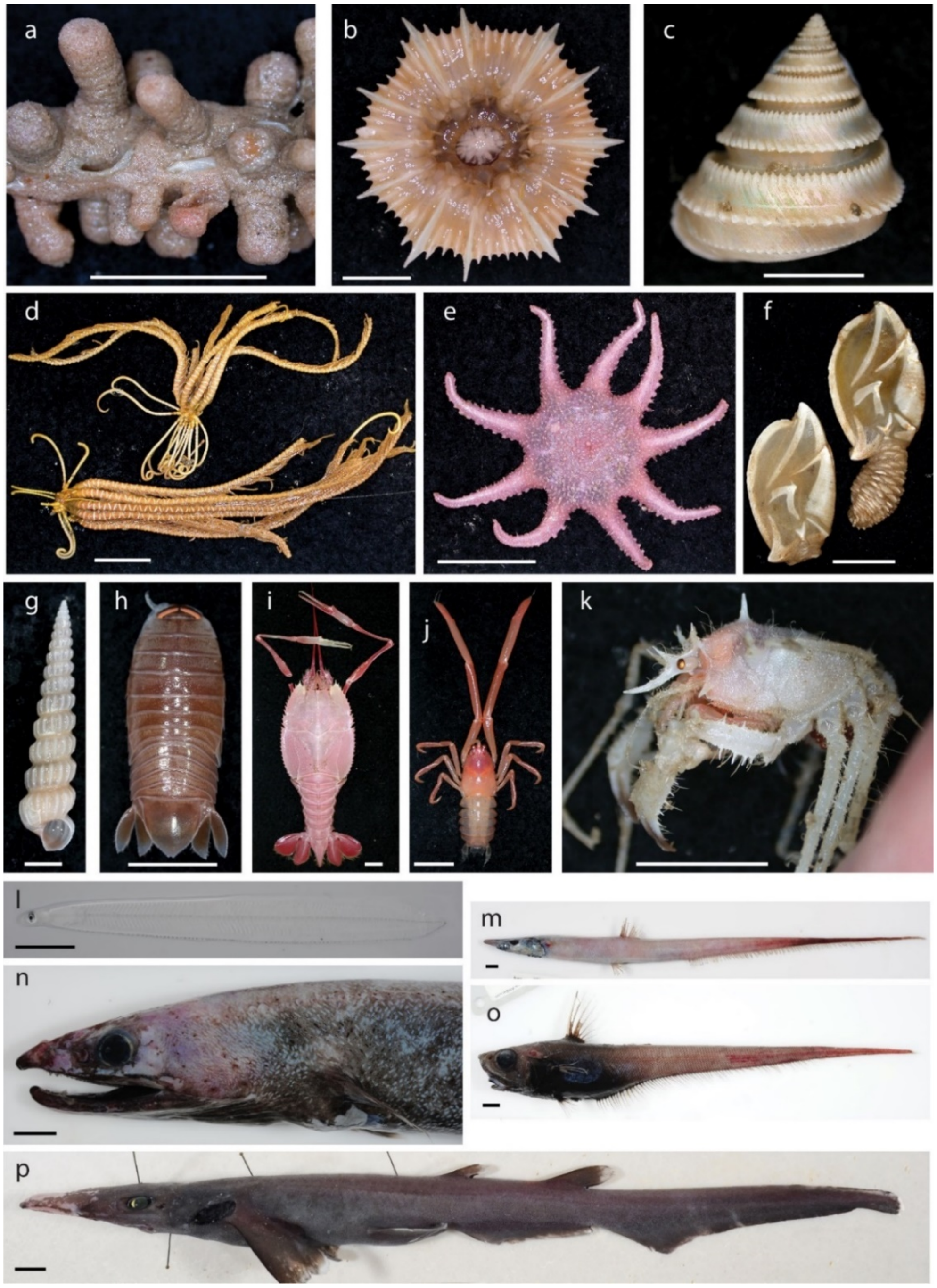

Fig. 20. Some seafloor animals of the Hunter Marine Park. (a) undescribed zoanthid in the family Parazoanthidae (sp; 1) (op 069, 1006-1036 m, KGH); (b) solitary scleractinian cup coral *Stephanocyathus platypus* (op 069, 1006-1036 m, KGH); (c) undescribed gastropod in the genus *Calliotropis* (sp; 3) (op 069, 1006-1036 m, KGH); (d) the crinoid *Thalassometra* cf *gracilis* (op 069, 1006-1036 m, KGH); (e) multi-armed seastar *Crossaster multispinus* (op 069, 1006-1036 m, KGH); (f) stalked barnacle *Neoscalpellum* cf *crosnieri* (op 070, 2595-2474 m, KGH); (g) small predatory wentle-trap sea snail *Epitonium* (sp; 1) (op 069, 1006-1036 m, KGH); (h) isopod *Aega* is parasitic on fish (op 069, 1006-1036 m, KGH); (i) widespread blind lobster *Pentacheles laevis* (op 069, 1006-1036 m, KGH); (j) squat lobster *Uroptychus nigricapillis* (op 069, 1006-1036 m, KGH); (k) deep-sea porter crab *Homologenus levii* (op 069, 1006-1036 m, KGH); (l) transparent *Leptocephalus* larvae of a marine eel in surface waters (op 075, 0-1 m, JP/AG); (m) allied halosaur, *Aldrovandia affinis* (op 069, 1006-1036 m, JP/AG); (n) grey cut-throat eel, *Synaphobranchus affinis* (op 069, 1006-1036 m, JP/AG); (o) kapala whiptail, *Nezumia kapala* (op 069, 1006-1036 m, JP/AG); (p) pinocchio catshark, *Apristurus australis* (op 069, 1006-1036 m, JP/AG). Scale bar = 1 cm.

Central Eastern Marine Park

The Central Eastern Marine Park extends from the Australian upper continental slope at 30.0 to 30.4°S to across the abyssal plain of the Tasman Sea before widening into a T-shape that extends from the Queensland seamount in the north to the Taupo Seamount in the south. The IN2017_V03 voyage traversed the most easterly section of the park which contains the Australian continental margin and the following description will be limited to this area.

A small section of outer shelf and upper slope occurs at the north-western tip of the park, however, the seaward edge of the park is generally below 1200 m. A feature of the upper slope of this region is the presence of hardgrounds, iron rich nodules and phosphate nodules which appear to the result of sediment being removed by strong currents. The most prominent feature is a massive complex box canyon in the northern half of the park. This canyon is fed by several rugose linear canyons, two of which start on the outer shelf within the park. These narrow canyons widen into gullies at ~1800 m before coalescing into the box canyon complex at 3500 m. A smaller canyon complex, known as the Coffs Canyon occurs at the southern end of the park's Multiple Use Zone. Between the two canyons, the western margin of the park runs across a convex sediment-draped upper slope. Several narrow ridges run parallel west to east across this sediment dome possibly indicating volcanic dykes, or faulting or folding of the underlying rock. The lower slope terrace is narrow throughout the park and forms a convex scape adjacent to the abyssal plain. An erosional moat occurs at the base of the scarp in the soft calcareous sediments of the abyss. Several sediment lobes occur on the abyssal plain. Significant areas of manganese nodules and depositional drift deposits possibly occur further out on the abyssal plain within the park [4].

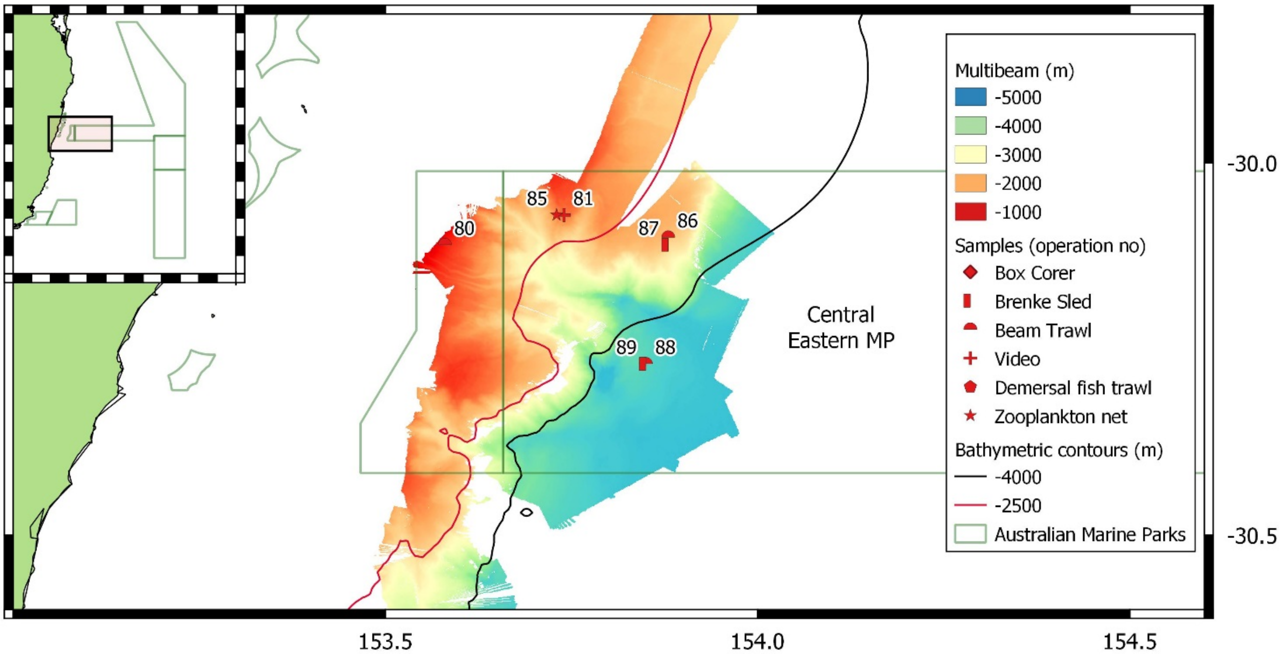

Fig. 21. Central Eastern Marine Park, IN2017_V03 sample locations and multibeam coverage.

The main Eastern Australian current flows mainly to the west of the park, but part of the current is deflected south 30°S along the Tasman Front, which forms the boundary at the water surface between the warm waters of the Coral Sea and the cooler waters of the Tasman Sea. This front is not static but moves further to the south (34°S) during summer. Currents also probably flow up or down the canyons and winnow the sediment on the seabed [4].

The IN2017_V03 camera tow (stn 081) followed a transect down a southwards facing ridge at the northern edge of the large canyon from 1600 to 2100 m. This imagery revealed a muddy plain with rat-tails, eels, glass sponges, and sea-whips. A beam trawl at 1000 m (stn 080) surprisingly netted a 4m wide manta ray carcass, with lots of scavenging amphipods and brittle-stars (*Ophiura flagellata*). There were also lots of associated fish, although these were not scavengers. The collection of a mid-bathyal beam trawl sample was challenging as there was little horizontal seafloor. A site (op 086) across a hill in the north of the park resulted in a catch dominated by stones and rocks. The fauna was distinctly northern. The abyssal beam trawl (op 088) at 4401-4481 m included a cookie-cutter shark, large prawns, and many brittle-stars of six species. There were some whale bones, which were not infested with *Osedax* worms (although a trawl at the nearby Byron Bay site to the north in 1000 m included a whale skull and vertebrae with *Osedax* necrophagous polychaetes and bivalves).

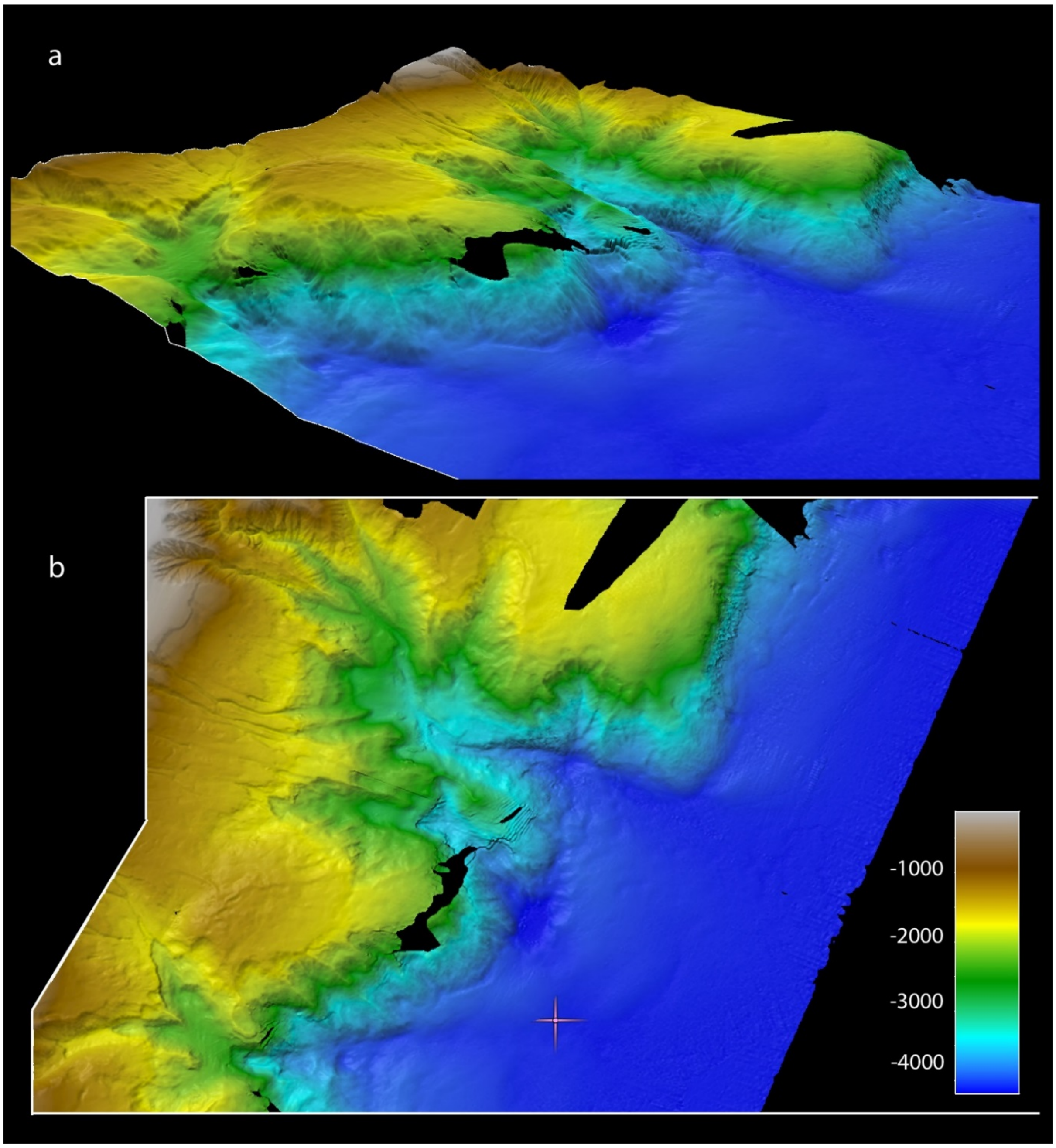

Fig. 22. Central Eastern Marine Park, consolidated multibeam coverage (historical + IN2017_V03) with black polygons representing un-swathed areas. (a-b) oblique views, (b) vertical view. Images: Amy Nau/CSIRO.

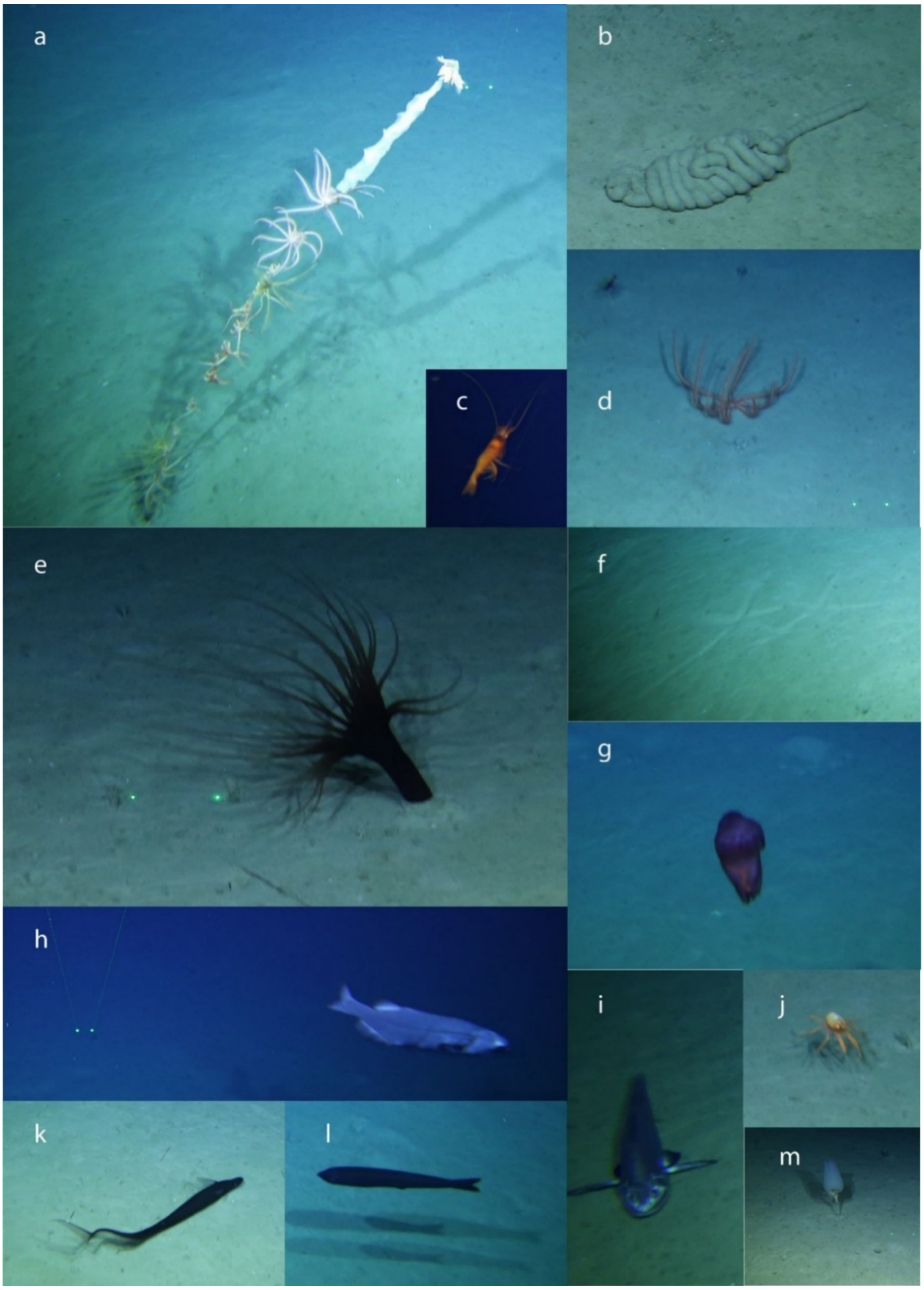

Fig. 23. Central Eastern Marine Park, still photos from video transect (op 81, 1511-2246 m). (a) a roll call of echinoderms along an old whip coral, including 8-armed white brisingid seastars, green crinoids, and red/white serpent stars; (b) faecal cast; (c) shrimp; (d) brisingid seastar; (e) ceriantid anemone; (f) impressions of Zoroaster seastars lurking under the mud; (g) swimming *Benthodytes* sea cucumbers; (h) slickhead, probably *Alepocephalus*; (i) deepsea lizardfish *Bathysaurus ferox;* (j) Munida squat lobster; (k) halosaurs can discard their tails to avoid predators; (l) slickhead, perhaps *Alepocephalus*; (m) *Halponema* sponge.

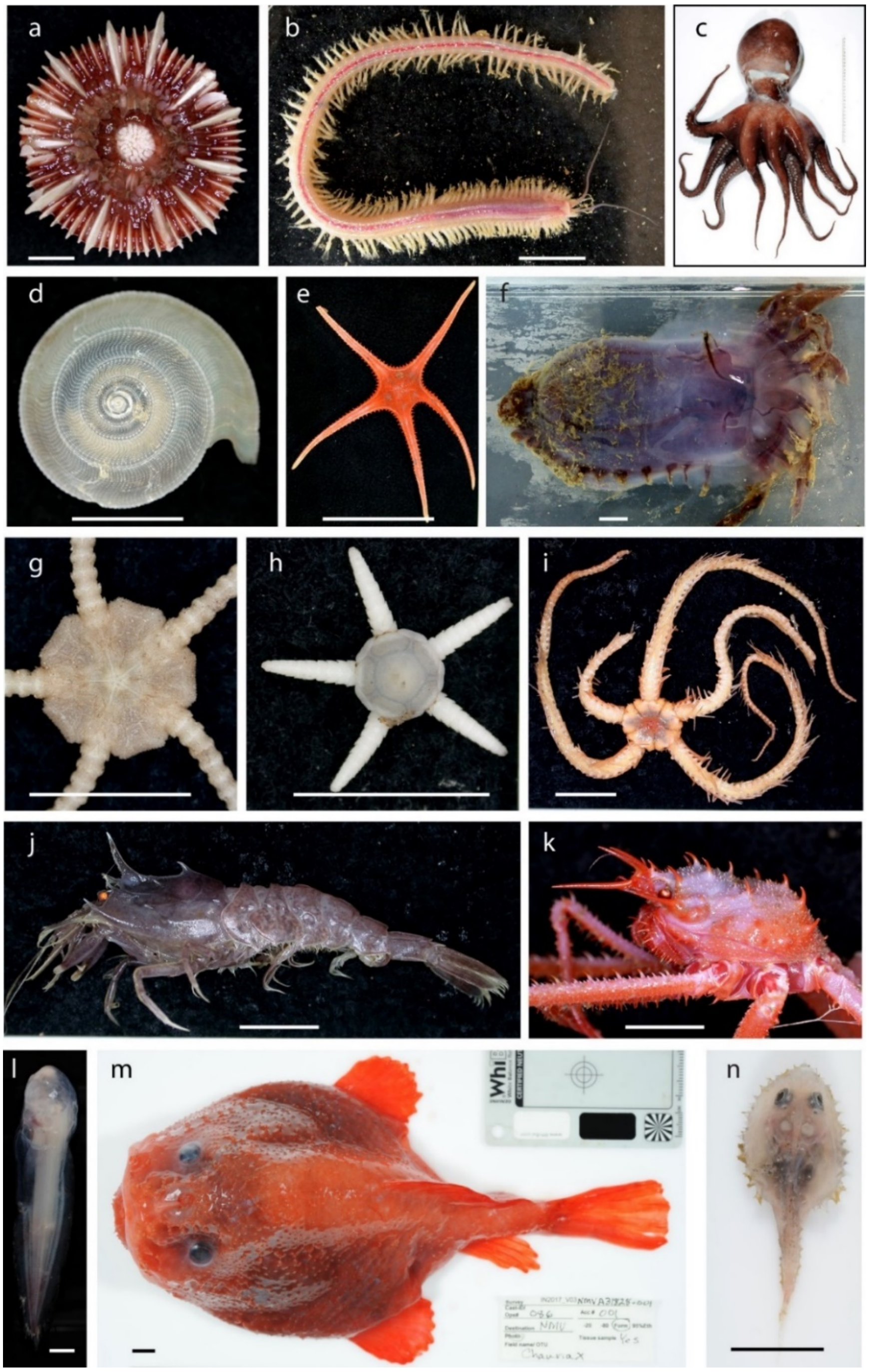

Fig. 24. Some seafloor animals of the Central Eastern Marine Park. (a) cup coral *Stephanocyathus coronatus* (op 080, 1194-1257 m, KGH); (b) sigalionid polychaete worm in the genus *Neoleanira* (op 080, 1194-1257 m, KGH); (c) undescribed *Muusoctopus* species (sp; 1) (op 080, 1194-1257 m, KGH); (d) small deep-water snail in the genus *Ancistrobasis* (sp; 1) (op 086, 2429-2518 m, KGH); (e) abyssal seastar *Plutonaster knoxi* (op 088, 4481-4401 m, KGH); (f) pelagic holothurian *Enypniastes eximia*, photographed in a shipboard aquaria (op 080, 1194-1257 m, KGH); (g) epifaunal *Ophiomusa facundum* (op 086, 2429-2518 m, KGH); (h) paedomorphic widespread brittlestar *Ophiotypa simplex* (op 088, 4481-4401 m, KGH); (i) epizoic ophiuroid, *Ophioplinthaca rudis* (op 080, 1194-1257 m, KGH); (j) deep-sea armoured shrimp *Metacrangon* (sp; 1) (op 080, 1194-1257 m, KGH); (k) deep sea spider crab *Vitjazmaia latidactyla* (op 080, 1194-1257 m, KGH); (l) gelatinous blind cusk eel *Aphyonus gelatinosus* (op 086, 2429-2518 m, JP/AG); (m) red coffin fish *Chaunacops coloratus* (op 086, 2429-2518 m, JP/AG); (n) small juvenile batfish *Halieutopsis* (op 080, 1194-1257 m, JP/AG). Scale bar = 1 cm.

Coral Sea Marine Park

The Coral Sea Marine Park is the largest in Australia, stretching from the northern Coral Sea to the northern Tasman Basin, offshore of the Great Barrier Reef Marine Park. The IN2017_V03 expedition only surveyed the south-eastern corner of the park and so the following description is based only upon that section.

The SE section of the Coral Sea Marine Park encompasses the southern end of the Marion Plateau, the northern margin of the Tasman Basin and the Cato Trough. The eastern section of the plateau forms the Capricorn Basin which is slightly shallower than the Swain Reefs high which runs along the Cato Trough. The Capricorn Basin runs to the SE becoming the Capricorn Sea Valley which persists as a visible feature down the continental slope and onto the abyssal plain. The Marion Plateau is covered with carbonate sediments that are gradually transported down the slope onto the abyssal plain, which is shallower (3500-3700 m) and less distinct than along more southerly Australian coasts [4]. However, sections of the lower slope are exposed bedrock due to erosional currents [4]. The Cato Trough connects the Coral Sea and the Tasman Sea at continental slope depths (1000-3500 m) and was formed late in the tectonic separation of Australia and New Zealand. The trough is only 10 km wide near its southern entrance. The sides are steep due to exposed Palaeozoic basement ridges, although there is some sediment slumps at the base and the flat floor is covered with sediment from pelagic sources and turbidity currents [13].

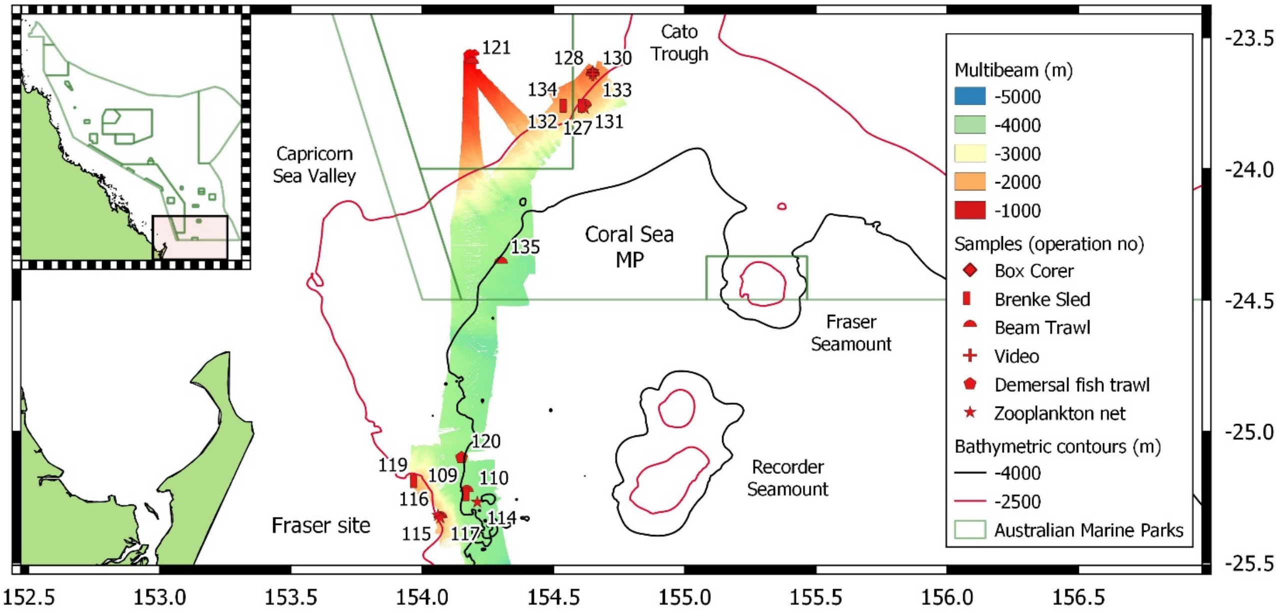

Fig. 25. Coral Sea Marine Park, southern section, IN2017_V03 sample locations and multibeam coverage.

The IN2017_V03 expedition sampled four beam trawls (ops 121: 1019-1093 m, 122: 2329-2369 m, 128: 1700-1761 m, 135: 3968-4034 m), three successful Brenke sleds , three Mantra nets (for microplastics), two zooplankton nets, and one video transect (op 133: 1753-2246 m) along the southern margin of the Marion Plateau within the Coral Sea Marine Park. The video transect (Fig. 26) showed a muddy seafloor with low density of large epifauna and demersal fish, and rare low relief provided by disturbance events or consolidated mud. The beam trawls and Brenke sleds however, resulted in a diverse catch of smaller animals and fish from the thick mud (Fig. 27). There were ~100 species at each of the bathyal stations, mostly sponges, soft-corals and seapens, a range of crabs, worms, seastars, and brittle-stars. The brittle-star *Amphiophiura paraconcava* was very abundant at 1700 m. Diversity fell dramatically with depth from 114 species at ~1000 m, 93 at 1700 m, and 41 at ~2400 m. At ~4000 m, there was only 10 species present in the beam trawl, including hard corals, worms, ophiuroids, a brisingid seastar, two crinoids and some bivalves.

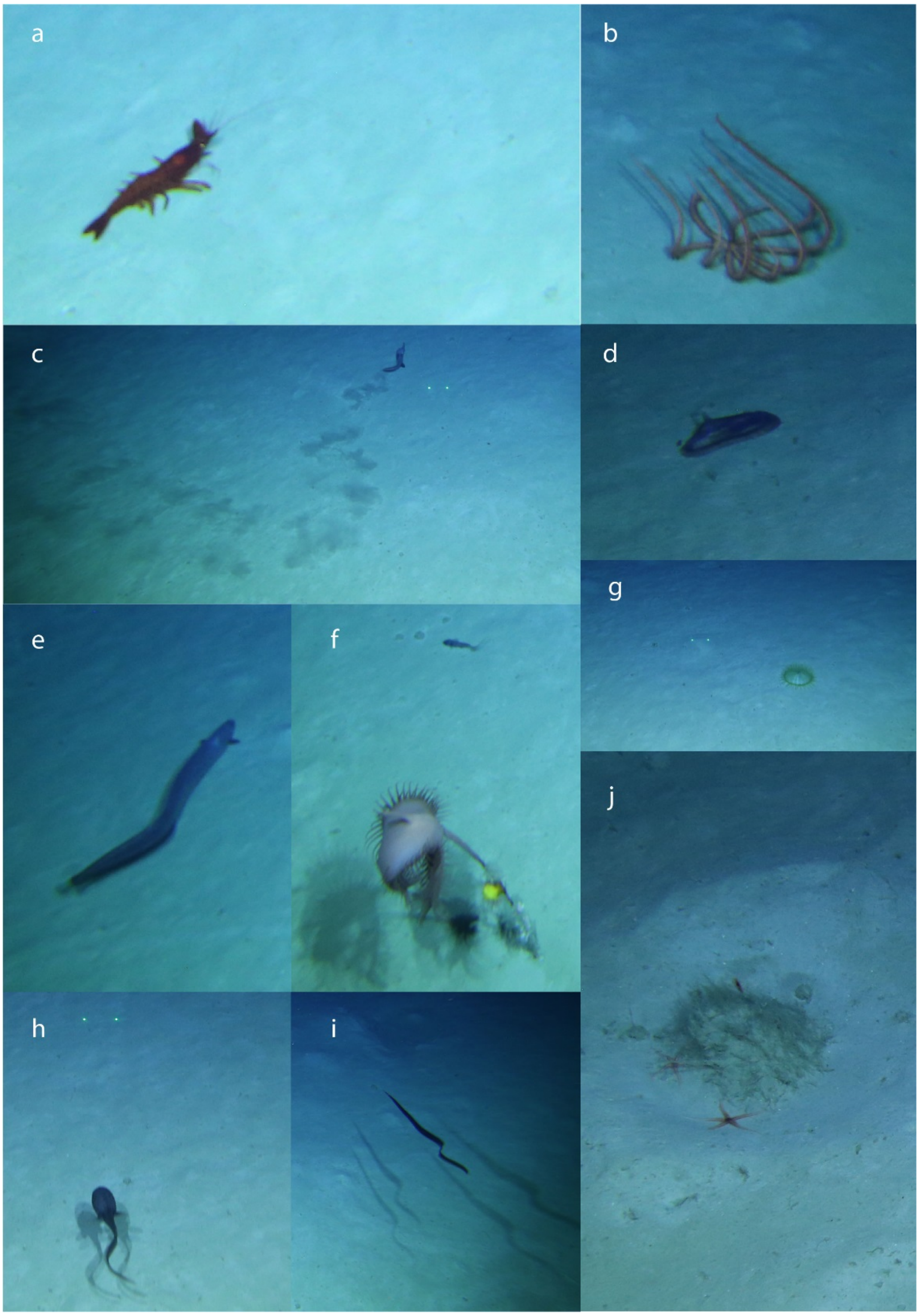

Fig. 26. Coral Sea Marine Park, still photos from video transect (op 133, 1753 m). (a) shrimp; (b) brisingid seastar raises its arms above the seafloor to feed on floating organic matter; (d) the function of the dorsal fin on *Psychropotes* holothurians is not known; (e) basketwork eel, family Synaphobranchidae; (f) venus-flytrap anemone (probably of the family Hormathiidae); (g) echinothuriid sea urchin; (h) whiptail, perhaps *Cetonurus*; (i) duckbill eel (*Venefica*); (j) large brittle-stars (?*Bathypectinura*) feasting on a mound of organic debris.

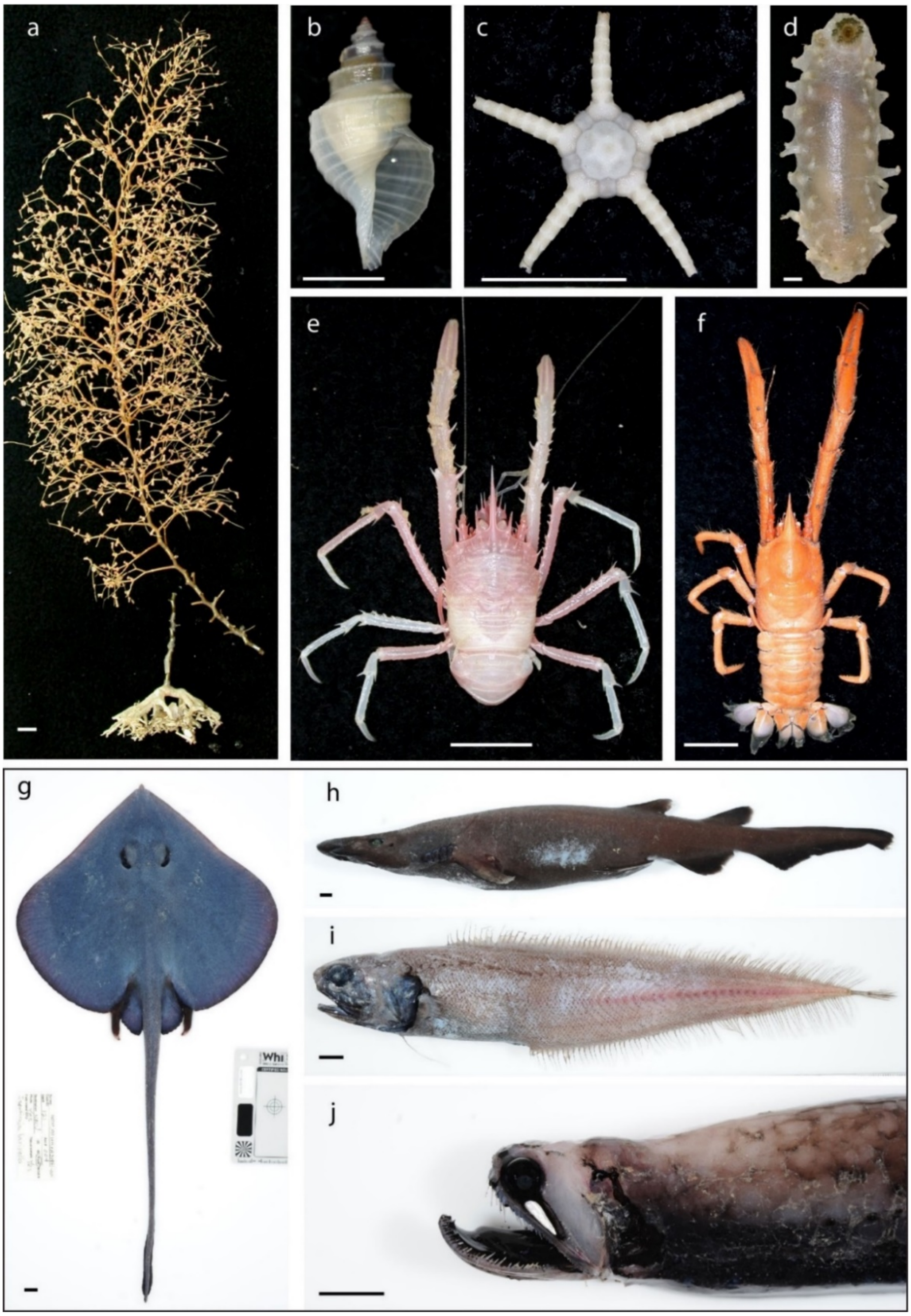

Fig. 27. Some seafloor animals of the southern Coral Sea Marine Park. (a) *Chrystogorgia* soft coral (op 121, 1013-1093 m, KGH); (b) raphitomid gastropod (op 121, 1013-1093 m, KGH); (c) *Ophiopyrgus saccharatus* (op 128, 1770-1761 m, KGH); (d) holothurian *Oneirophanta mutabilis* (op 128, 1770-1761 m, KGH); (e) undescribed *Munida* squat lobster (op 128, 1770-1761 m, KGH); (f) squat lobster *Munidopsis kensleyi* (op 121, 1013-1093 m, KGH); (g) eastern Looseskin Skate *Insentiraja laxipella* (op 121, 1013-1093 m, JP/AG); (h) ghost shark *Apristurus* (op 121, 1013-1093 m, JP/AG); (i) Cusk eel *Monomitopus* (op 121, 1013-1093 m, JP/AG); (j) dragonfish *Photonectes* (op 121, 1013-1093 m, JP/AG). Scale bar = 1 cm.

Box 1: Rubbish

We collected waste, plastics or rubbish from every trawl sample on the IN2017_V03 expedition including from all seven Australian Marine Parks occurring along the east coast. These samples were collected 45-175 km offshore, from seabeds 1000-4800 m deep. Some of the rubbish is old; off New South Wales, there is a lot of coal and clinker (fused impurities from boilers) on the seafloor, discarded from old steam ships. But we also trawled up more modern debris from shipping, including paint cans (still with liquid paint), fishing gear (nets), tar and scrap metal.

We also used a Mantra net to collect microplastics from surface waters. This frequently included tooth brush bristles, netting fragments and other small plastic pieces. Waste constitutes an ongoing impact on the natural values of Australia's deep-sea marine parks.

Acknowledgements

Specimen photographs were on-board by Karen Gowlett-Holmes (KGH, CSIRO) for invertebrates, and John Pogonoski (JP, CSIRO) and Alistair Graham (AG, CSIRO) for fish. Other photographers included Jerome Mallefet (JM, University of Louvain), Robert Zugaro (RZ, Museums Victoria) and Asher Flatt (AF, NESP Marine Biodiversity Hub). In-situ still photos were taken on video transects on the RV Investigator. Amy Nau (CSIRO) composed the 3D seascape images of each park from collected and historical multi-beam data. The numerous taxonomists who identified the animals are outlined in chapter 2. We wish to thank the CSIRO Marine National Facility (MNF) for its support in the form of sea time on RV Investigator, support personnel, scientific equipment and data management. All data and samples acquired on the voyage are made publicly available in accordance with MNF Policy. We also thank all the scientific staff and crew who participated in voyage IN2017_V03. Project funding was provided by the Marine Biodiversity Hub, supported through the Australian Government's National Environmental Science Program (NESP).

Chapter 2: The lower bathyal and abyssal seafloor fauna of eastern Australia

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Background

Deep-sea ecosystems are one of the world's major ecological research frontiers, giving us new perspectives on macro-ecological questions [14]. The deep sea is characterised by very cold water, extreme pressure, little to no light and limited food, with organic matter residues sinking from surface waters or transported down continental margins [15].

Our knowledge of the benthic fauna at lower bathyal to abyssal (LBA; > 2000 m) depths off Eastern Australia is very limited, despite the presence of a large abyssal basin in the Tasman Sea. The H.M.S *Challenger* (U.K.) took a single biological dredge sample (station 165, almost empty) in 1874 in 4754 m [16]. The Galathea expedition (Denmark) collected from 8 abyssal stations across the Tasman Sea in 1951-2 [17]. Cruise 16 of the RV Dmitry Mendeleev (U.S.S.R.) trawled two abyssal samples from the Tasman Sea on its way across Southern Australia and up past Norfolk Island in 1975-1976. Finally, the RV Tangaroa (New Zealand) collected biological material at abyssal depths when searching for manganese nodules in 1982 on a transect between New Zealand and Sydney [3]. However, only three of these samples occurred within the Australian Exclusive Economic Zone (EEZ) and none from the newly created eastern network of Australian Marine Parks. Consequently, the composition of the LBA fauna of the western Tasman Sea is largely unknown.

The Tasman Basin formed 90-52 mya through the tectonic rifting of Australian and New Zealand continental masses [18]. It now extends from the Marion and Chesterfield plateaus off Queensland in the north (24°S) to south of Tasmania (48°S) before opening up into the Southern Ocean. A south-north spreading ridge formerly existed in the centre of the basin [18]. Subsequently, the north-south chain of Tasmantid seamounts were created along the Lord Howe Rise by the Australian plate moving over a crustal hotspot from 33.5-6.4 mya [4].

The upper continental slope along eastern Australia is broadly convex from the shelf break down to 1500 m [4]. At mid slope depths (until 3000 m) it is more concave, with the upper section sometimes forming an escarpment. On the lower slope there can be a series of steplike rocky ledges down to the abyssal plain at 4500-5000 m. The margin is frequently dissected by canyons, some of which start at shelf depths [19], and slumps due to slope failure [20]. Sediment accumulates on the upper slope and sometimes on flatter surfaces at mid and lower slope depths where bottom currents are not too strong [4]. The composition of the sediments is depth-dependent. Terrestrial siliceous and biogenic carbonate sediments occurring on the shelf and upper slope, and finer pelagic-derived sediments (mainly coccolith and foraminifera remains) on the lower slope and abyssal plain [4]. Below the lysocline at 3,600 m, carbonate particles dissolve and sediments form a fine ooze [21].

There are two main current trajectories through the Tasman Sea according to depth [22]. The counter-clockwise southern Pacific gyre circulates shallow water from the Coral Sea, south along the Australian continental margin (East Australian Current) until about 32-35°S before heading eastward to northern New Zealand, although eddies move south as far as Tasmania [23]. Antarctic Intermediate Water (AAIW) is present at ~1000 m, entering the Tasman Sea from two directions, one flowing from the south-west and the other from the north and east, the latter having become entrained by the surface gyre in the southern Pacific east of New Zealand. Both North Atlantic Deep Water (NADW) (at ~2500 m) and Antarctic Bottom Water (ABW) (~4-5,000 m) flow in from the south-west along the Australian margin, forming clockwise eddies at the northern end of the basin, with a net southern flow back down the Lord Howe Rise [24,25]. The northward flow of these deep currents is strong enough to remove sediment from the Australian lower continental slope leaving a rocky surface [4].

Oceanographic factors such as temperature, salinity and oxygen are relatively invariant within each water mass [26]. ABW at 4000 m is relatively cold (1.1°C), salty (34.72‰) and oxygenated (4.49 ml/l). NADW at 2500 m is slightly warmer (1.9°C), the same salinity and slightly less oxygen (4.13 ml/l). AAIW at 1000 m is warmer again (5.0°C), slightly less salty (34.47) and less oxygenated (4.06). There are no hypoxic (O2 <1.7 ml/l) or anoxic (<0.02) oxygen minimum zones in the Tasman Sea [27]. The flux of particulate organic carbon (POC) to the seafloor varies with net primary production (NPP) in surface waters, seasonal variation in NPP (POC is increased if NPP is seasonal), and the depth of the seafloor (more POC gets consumed in the water column) [28]. Both NPP and seasonality of NPP is higher at southern latitudes in the Tasman Sea. Away from the coast, the waters of the northern Tasman Sea are oligotropic. While the sediments of the continental slope are well oxygenated and bioturbation is abundant, the carbon content of the sediments is less than 1% [4], which is poor by global standards [29].

In May-June 2017, the IN2017_V03 expedition of the RV 'Investigator' sampled LBA benthic communities along the lower slope and abyss of Australia's eastern margin from off mid-Tasmania (42°S) to the Coral Sea (23°S), with particular emphasis on describing and analysing patterns of biodiversity that occur within a newly declared network of offshore marine parks. This paper summarises the fauna collected by the expedition. This was the first dedicated biological expedition to sample the abyssal fauna anywhere across Australia’s Exclusive Economic Zone, the third largest of any nation.

Methods

Biological Sampling

The study design was to deploy a 4m (metal) beam trawl (12 mm mesh at mouth, 10 mm mesh at cod end) [30] and Brenke sled (0.5 mm mesh) [31] to collect samples on soft sediment substrata at the target seafloor depths of 2500 and 4000 m at every 1.5 degrees of latitude along the western boundary of the Tasman Sea from 42° to 23°S, traversing seven Australian Marine Parks (AMPs) (Fig. 2). In addition, a few beam trawl samples were collected at 1000 m and a few box-corer samples at southern sites (until technical difficulties precluded its further use). A single deep-towed video transect (1500-2500 m) was completed within each Marine Park. Each site was mapped (bathymetry and backscatter) prior to deployment using a Kongsberg EM 122 multibeam sonar. Environmental data (temperature, salinity, pressure) were collected by a Sea-Bird SBE37SM sensor mounted on the Brenke Sled.

Samples were sorted, weighed and preserved (generally in 95% ethanol, the rest in formalin) on-board into broad taxonomic groups, and sent to taxonomic experts. The following groups of megafauna were subsequently identified to operational taxonomic units (mostly to species, some to genus or family) and counted: sponges, sea anemones, octocorals, barnacles, decapods, pycnogonids, annelids, echinoderms, molluscs and fish. Freshly collected material was photographed on-board the ship, predominantly by Karen Gowlett-Holmes (KGH, invertebrates), John Pogonoski (JP, fish), Alastair Graham (AG, fish), Jerome Mallefet (JM, general) and Robert Zugaro (RZ, general).

Results

The expedition biological sampling included 35 beam trawls, 28 Brenke sleds, 8 box cores, 20 surface meso-zooplankton tows, and 7 Deep Towed Camera transects. Here we present biodiversity highlights from the beam trawls and Brenke sleds (Fig. 1). The multibeam sonar revealed a continental slope topography that was much more complex and rugged than expected, with the margin incised by numerous canyons, sediment slumps, cliffs and other areas of exposed rock (Fig. 2). This complicated the placement and duration of sampling. The depth of the samples differed from the target as follows: 4000 m (3754-4800 m), 2500 m (1761-2963 m), and 1000 m (932-1257 m) (Table 1 & 2). Sample 080 from 1225 m included a decaying manta ray with associated scavengers and predators. Sample 100 included a dead pilot whale skull and vertebrae which hosted *Idas* bivalves and *Osedax* worms (not previously reported from Australia).

In total to date, 25710 specimens have been identified to 1067 taxonomic entities, including 828 species-level, 146 genus-level and 69 family-level and 24 higher-level taxa. Of the species-level taxa, only 417 have been assigned species-level taxonomic names, which implies that up to 50% of the collected fauna is undescribed.

Porifera

M. Ekins

Over one hundred and twenty Porifera specimens were collected during the expedition, of which half were Demospongiae and half were Hexactinellida (the glass sponges). Of the Demospongiae, there were only four orders representing the four families of Ancorinidae, Polymastiidae, Niphatidae and Cladorhizidae. The Cladorhizidae (carnivorous sponges) were by far the most commonly collected family with 40 specimens, which is surprising considering that many of these species are only several millimetres in length.

Most notable from this expedition was the finding of 17 new species of carnivorous sponges, belonging to seven of the nine known genera of Cladorhizidae: *Abyssocladia*, *Asbestopluma*, *Chondrocladia*, *Cladorhiza*, *Lycopodina* and *Euchelipluma*. Also remarkable is that only two previously well-known carnivorous species were collected i.e. *Chondrocladia clavata* and *Lycopodina calyx*. Another commonly collected sponge was *Radiella irregularis* and two potential new species of Radiella. There was only one other Demospongiae sponge that could be identified to a described species *Echinostylinos reticulatus*, the remaining 22 morpho-species of Demospongiae will be new to science.

The class Hexactinellida was represented by four orders, containing eight families in order of number of specimens found: Hyalonematidae, Pheronematidae, Rossellidae, Farreidae, Aulocalycidae, Euplectellidae and the solitary Euretidae with the solitary species *Pleurochorium cornutum*. The most common glass sponges were the large *Pheronema pilosum*, *Semperella schulzei*, and the stunning *Monorhaphis chuni*, with its metre long glass spicules. Amongst the glass sponges there were another seven described species and sixteen new species. Unfortunately all eleven specimens of the Farreidae are a Farreidae/Euretidae *incertae sedis*, which has been repeatedly recovered from Australian and New Zealand seamounts as long dead fragments which cannot yet be assigned to a living species [32].

Overall this assemblage of sponges is to be expected from the Abyssal depths. It consists of glass sponges that have adapted to the 150 fold increase in silicon in the water and use it to create large glass structures, or those that have adapted to carnivory in an attempt to secure more reliable food resources. Many of the sponges collected on this expedition have been described from previous expeditions to the Pacific at Abyssal depths [33-37]. Interestingly there were no sponges collected on this expedition that matched to those previously collected from the Great Australian Bight [38-40]. Whilst more than half of the sponge specimens collected on this voyage are unknown, almost three quarters of the species are new. This indicates the high diversity of sponges on the abyssal plains and continental slopes that are still to be fully described.

Hydrozoa

J.E Watson & T. D. O’Hara

Eight species of thecate hydroids (Leptothecata) were collected from depths of 1151–4173 m, including three previously known species (*Acryptolaria angulata*, *Cryptolarella abyssicola*, *Zygophylax* *concinna*), three newly described species (*Hebella* sp nov, *Amphisbetia* sp nov, *Lytocarpia* sp nov) and two species (*Hebella* sp., *Halecium* sp.) which were too inadequate or in too poor a condition for identification.

Abyssal hydroids recorded from Challenger Station 160 from a depth of 4755 m were previously the only published reports of the abyssal hydroid fauna from Australia. They recorded two species, *Cryptolarella abyssicola* and *Halisiphponia megalotheca* [41]. Hydroids from the continental shelf have been reported from the Great Australian Bight [42-45] and off New South Wales [46]. None of these studies included material deeper than 100 m.

Cryptolarella abyssicola was by far the most abundant species with 12 records. The species is a wide-ranging abyssal hydroid that has previously been recorded under various names from the Southern, Eastern Pacific and Atlantic Oceans in 2470-6328 m [47,48]. The Australian range of *C. abyssicola* is now extended along the south-eastern Australian coast from cool temperate Tasmania in the south to the subtropical Coral Sea. *Acryptolaria angulata* has been found from deep water in the Indian Ocean, Indo-west Pacific, New Caledonia and New Zealand [49]. The two new records of *Zygophylax concinna* extends its range from the only known record found off Sydney [46] and to the depth range of 100 m to 3754 m.

Three new species occur in the collection from the genera *Hebella*, *Amphisbetia* and *Lytocarpia*. The first two were recovered from depths of 4133 m and 4131 m respectively from eastern Bass Strait, Victoria. *Amphisbetia* is a moderately common hydroid genus from shallow coastal environments of southern Australia [50], so the record from 4131 m possibly indicates that it is a floating fragment from a shallow water colony entrained in the trawl net. With more material, the new species of *Lytocarpia* from the Coral Sea, may prove to be a diminutive subspecies of *L. spiralis*, a common deep water species from around New Zealand [49].

There were surprisingly few species and few locality records in the collection considering the extensive latitudinal range of the survey. This may be an artefact of decrease in hydroid diversity with depth, the sampling gear used, or sampling of predominantly sedimentary substrates.

Several siphonophores we also collected, including the characteristic mushroom-shaped bracts of the benthic rhodaliid species *Dendrogramma enigmatica* from off Bermagui (op 044) and in Jervis Marine Park (op 056) in 2650-2821 m. small denuded rhodaliid pneumatophores were also found at station 056 and off Byron Bay (ops 090 and 100) which may or may not be *Dendrogramma*. The pelagic bluebottle *Physalia utriculus* was caught, probably from the sea surface, in an abyssal beam trawl sample (op 030) off eastern Bass Strait.

Actiniaria

M.L. Mitchell & A.L. Crowther

The IN2017_V03 expedition represents the first time we can compare the actiniarian faunal composition by depth and latitude along the Eastern Australian coast. The bathyal and abyssal Actiniaria fauna collected off the Eastern coast of Australia totalled 111 lots (325 specimens) from 29 stations across all latitude and depths. The mid-lower bathyal depths (1500-3500 m) contained the most lots (57 with 126 specimens). However, the highest number of specimens were collected from abyssal depths (< 3500 m), with 34 lots (136 specimens). The remainder (20 lots, 63 specimens) were collected from the upper bathyal depths (> 1500 m). Eleven lots of Corallimorpharia were also collected from mid-lower bathyal and abyssal depths, but not from upper bathyal depths. Corallimorpharians have not been identified lower than order.

Representatives of two families dominated all latitudes of the survey: Hormathiidae and Amphianthidae. These were also the only two families that were collected from the deepest (4800 m) to the shallowest station (1006 m).

Not surprisingly, representatives of Hormathiidae were sampled from all depths, and across the range of latitudes, with 49 lots (149 specimens) collected. Hormathiids are known to consistently dominate the actiniarian fauna catch of deep sea surveys [38,51], as shown here, with hormathiids not only being most sampled (149 specimens), but also the greatest diversity (12 OTUs), compared to other families. The Hormathiid *Paracalliactis rosea* was the most prevalent OTU (21 lots, 60 specimens), found in a wide range of latitudes. This species was not sampled from abyssal depths; however, the deepest collection from this survey (>3000 m) is similar to the depth this species was collected from in the Great Australian Bight [38]. *Actinauge* species were only represented in the lower latitudes of Bass Strait and Freycinet. The few specimens of Hormathiidae collected from abyssal depths were unable to be identified to genus at present.

Representatives of Amphianthidae (24 lots, 121 specimens) were collected from a wide range of depths (1000-4000 m), and throughout the extent of the latitudinal range sampled (Coral Sea MP to Freycinet MP). Specimens were identified to genera, representing eight OTUs; a similar diversity to that found in the Great Australian Bight. More work is needed to determine species identities and distribution. Unlike hormathiids, the Amphianthidae were found mostly at lower depths (> 2500 m), and in greater numbers in the southern latitudes.

The Actinostolidae, another common faunal component of the deep sea, were found in far fewer numbers at shallower depths < 2500 m. Actinostolids were lacking in many sites, although *Sicyonis* species were found in their greatest number near Freycinet. The remaining families; Actiniidae, Actinoscyphiidae, Liponematidae and Sargartiidae were uncommon, and were represented by a single specimen in some instances. The actiniid *Stylobates birtlesi* was collected from one station, at 1000 m, and this fits with the recorded depth range of the specimens but extends the distribution [52]. Previously, this was known only to occur off southern Queensland, and now from off Byron Bay in New South Wales. From the limited representation of four families we are unable to make any inferences regarding faunal contribution via depth or latitude.

Of the specimens we were able to identify to species (*Stylobates birtlesi*, *Paracalliactis rosea*, and *Monactis vestita*), these new records provide a distribution expansion as indicated by the World Register of Marine species (WoRMS, see http://www.marinespecies.org/) and the Great Australian Bight sampling program [38]). Not unlike other deep-sea surveys a proportion of samples (74 %) were taxonomically unresolved to species, genus or family, and eight OTU's could only be resolved to order level. These unresolved identifications may represent new species and distributions; this survey highlights the diversity of the abyssal actiniarian fauna present around Australia and our paucity of knowledge regarding their distribution by not only latitude, but depth as well.

Zoantharia

H. Kise

Species of order Zoantharia are generally known as colonial sea anemones and are characterized by having two rows of tentacles and a unique bilateral arrangement of the mesenteries. Zoantharians can be found in a wide variety of marine environments [53]. Zoantharian taxonomy has been considered chaotic due to few diagnostic morphological characteristics and the presence of large amounts of intraspecific variation [54,55]. However, molecular phylogenetic techniques have improved the taxonomy and systematics of zoantharians. As a result of previous studies using molecular phylogenetic techniques combined with morphological and ecological data, three families and 12 genera have been described since 2007 e.g. [53,56-61].

In Australia, zoantharian diversity and taxonomy in shallow waters have been relatively well documented see [55,62,63,64]. However, little or no information is focused on zoantharians in Australian deep-seas due to difficulty of collection. During RV investigator expedition in 2017, 31 specimens were collected from the deep-seas of Australia. Molecular phylogenetic analyses combined with morphological observations showed that specimens collected from the Australian deep-sea contain 10 different morphological species. At least three species are almost certainly undescribed species; hermit crab-associated species *Epizoanthus* sp. 1 and *Epizoanthus* sp. 2, and echinoderm-associated species *Epizoanthus* sp. 3. Although several hermit crab-associated species and one echinoderm-associated species have been described, specimens collected in this study are morphologically and phylogenetically different from already described species.

Deep-sea zoantharians have recently attracted attention as there is apparently much undiscovered diversity [58,60,65,66]. In fact, several undescribed *Epizoanthus* species were found in this current study. Thus, investigation of deep-sea zoantharian diversity can contribute to a better understanding of the systematics and evolutionary history of zoantharians.

Octocorallia

P. Alderslade & K. Moore

The collection yielded 540 octocoral specimens comprising 15 families across 2 orders (Alcyonacea & Pennatulacea), and included 5 new genera and 15 new species. Because sampling was mostly on soft bottom habitat, pennatulids (sea pens) dominated, accounting for 396 specimens. With a cosmopolitan distribution, the most common abyssal sea pen is Umbellula and it was therefore not surprising that species of this genus represented about a third of the collection.

Of the 95 specimens of the sea pen *Porcupinella*, 63 were identified as the North Atlantic species *P. profunda* described by López-González and Williams [67] from the Porcupine Abyssal Plain. In an earlier paper [68], similar specimens were described under the name *Umbellula carpenteri*, but two different colony forms were illustrated: one lot looking like *P. profunda* from the same original location, and one *Umbellula*-like lot from the South Indian Ocean showing a markedly curved rachis. López-González & Williams synonymised the author's Porcupine Abyssal Plain samples with *P. profunda* but assigned her curved samples, whose main taxonomic feature was not well illustrated, to an unnamed species of the genus *Umbellula*. However, both colony forms are present in the material from our collection, and notably they were collected together from the same stations and with intermediate colony forms present, suggesting that they be treated as the same species (Fig. 1A,B).

Specimens of another species of sea pen, morphologically assignable to *Umbellula*, show traits that suggest it requires a new genus and a putative new family, which could probably accommodate other nominal species of *Umbellula* as well. A new species of *Porcupinella* is also present. There are 26 previous Australian records (GBIF) of the sea pen genus *Kophobelemnon* and of these only 6 have been identified to a species – *K. macrospinosum*. Of the 67 *Kophobelemon* specimens in our collection, nearly one third can be assigned to this species. The remainder represent one known and four new species.

A new species of the rare, small, encrusting soft coral *Scyphopodium* provides a new record for Australia and also a considerable range extension for the genus, only having been previously reported from Iceland and southern Africa. The uncommon genus *Telestula* is represented by 13 nominal species, but the literature is very inadequate and probably fewer than half of these species are valid. Our material contains 9 specimens comprising 3 unidentifiable species and a specimen of *Telestula spicuola robusta* previously only recorded from Hawaii. The collection of the gorgonian *Acanella rigida* is possibly only the 3rd valid report of this species since it was first described from the Challenger expedition, and the first time recorded outside of Indonesia and the Philippines (Fig. 1C). A new genus of gorgonian from the Family Isididae, Subfamily Mopseinae, is also noteworthy for the attractive appearance of the polyp sclerites (Fig. 1D).

Annelida

L. M. Gunton, M. N. Georgieva, E. Kupriyanova, R.S. Wilson, H. Paxton, P. Hutchings, A. Murray, I. Burghardt, J. Konsgrud, T. Alvestad, J. Zhang & N. Budaeva

Over 3100 annelid specimens were recorded from combined bathyal and abyssal beam trawl samples. Samples included representatives of Polychaeta, Sipuncula and Echiura. The polychaetes, the most abundant group (2800 individuals), were composed of 39 families and 116 species/OTUs. Serpulidae (792 individuals), Aphroditidae (377), Ampharetidae (288) and Phyllodocidae (186) were the most abundant polychaete families. These results are similar to those of the global abyssal polychaete fauna, where ampharetids made up 10% of the total number of polychaete species recorded below 2000 m depth and serpulids were also abundant (3% total number of deep-sea species recorded) [69]. The families Ampharetidae and Serpulidae were also dominant in a large scale study of the deep Great Australian Bight (GAB) at 192–5032 m depth [38]. The high total abundance of serpulids in the beam trawl samples is mostly a result of operations 097 and 099 (around 3780 m) where the trawls retrieved numerous pebbles with calcareous tubes of serpulids attached (mainly *Bathvermilia* n. sp.).

The most species-rich families were Serpulidae (17 species), Ampharetidae (14 species), Onuphidae (10 species) and Polynoidae (8 species). Serpulidae, Onuphidae and Polynoidae also had a high species richness in the deep GAB along with the Spionidae, Cirratulidae, Syllidae and Paraonidae [38]. The most abundant species in this study were *Bathvermilia* n. sp. (Serpulidae), and *Laetmonice* cf. *yarramba* (Aphroditidae).

This study yielded around 81 species (70 %) that could not be designated a Latin binomial name and may be new to science. To date, species currently being described include five onuphid species (Genus: *Nothria*), four ampharetid species (*Melinnopsis*, *Amage*, *Anobothrus*), four serpulid species (*Bathyditrupa*, *Bathvermilia*, *Hyglopomatus*), and two sabellariid species (*Gesaia*, *Phalacrostemma*). Descriptions of two new species of the pectinariid genus *Petta, P. investigatoris* n. sp. and *P. janewilliamsoni* n. sp., have been published [70].

As this is the first dedicated study of Australian eastern abyssal fauna, a number of species have been reported for the first time in Australian waters and have geographic range extensions. A new species in the genus *Myriowenia* (Oweniidae) is reported from deep Australian waters (P. Hutchings pers. comm.), the genus having only been reported in Australia once before from 60 m off the coast of New South Wales [71]. *Gesaia* sp. (Sabellariidae) was observed in the present study after being recorded for the first time in deep waters from the GAB [38]. The genus *Boguella* (Maldanidae) is also reported for the first time in Australian waters. The abundant aphroditid scaleworm, *Laetmonice yarramba*, previously recorded from around Australia in 60-523 m depth [72], has been recorded now from the deep GAB (189–3884 m) and from the present study in the lower bathyal and abyssal environments ranging from southern Queensland to Tasmania (932-4800). The wide geographic and bathymetric distribution, as well as its morphological variability, strongly suggest it is a species complex. *Laetmonice yarramba* is likely carnivorous, preying on both mobile macrobenthos, sessile foraminifera and carrion [73], its large (4-8 cm) and robust body may increase the likelihood of its collection during beam trawl sampling methods.

During the beam trawl sampling operation 100 (depth 999–1013 m) the skull and vertebrae of a pilot whale (possibly *Globicephala macrorhynchus*) were collected, the first natural whale fall reported from Australian waters. A high abundance and diversity of annelids was associated with the whale bones. Annelids found on the bones included representatives of the typical ‘bone-eating’ Siboglinidae (*Osedax* n. spp.), numerous specimens of the dorvilleid *Ophryotrocha,* a genus that is often abundant and diverse at whale falls and other organically enriched habitats, as well as Orbiniidae, Phylodocidae (*Eumida* sp.) and Protodrilidae. A detailed study and description of the whale bone associated fauna is ongoing.

Preliminary investigations into the epibenthic and infaunal material collected using a Brenke sled and Box Corer (around 2700 annelids) revealed a polychaete fauna (most abundant families Scalibregmatidae, Sigalionidae, and Flabelligeridae) different at the family level from that collected by beam trawl. Smaller sized fauna which would have slipped through the larger beam trawl mesh (12-10 mm) are retained on the Brenke sled mesh (0.5 mm). Smaller-sized annelids from the Brenke sled and box core sampling may be different adult species, as well as newly settled and juvenile individuals of species already retained in the coarser mesh of the beam trawl. The importance of smaller size classes of organisms increases with depth, at abyssal depths small organisms (meiofauna) have the highest metazoan abundance and biomass values [74]. Further identification of material from Brenke sled sampling will vastly increase the knowledge of the smaller annelid fauna from the Australian eastern abyss.

Cirripeda

A.M. Hosie

A total of 400 cirripede specimens were collected during the survey, comprising 5 families, 18 genera and 34 species/OTUs. The Scalpellidae was the most diverse family, represented by 24 species (143 specimens), however the Verruccidae was the most abundant family with 220 specimens collected (5 species). *Gibbosaverruca navicula* and *Cristallinaverruca* sp.1 were the most abundant species with 106 and 72 specimens collected, followed by *Metaverruca recta* with 28. More than half of the specimens of these species were collected in a single collecting event each, indicative of a patchy distribution within the survey area. Diversity was highest in depths less than 3000 m with 19 species exclusively collected in depths less than 3000 m, compared with 7 found only at depths greater than 3000 m.

The diversity and composition of taxa above species level are consistent with what is known of bathyal and abyssal barnacle fauna in Australia [38,75]. The species identified are largely wide-ranging in tropical and warm-temperate latitudes with only *Arcoscalpellum* cf *gryllum* being a potential Australian endemic and two species, *Teloscalpellum* cf *gracile* and *Trianguloscalpellum hamulus*, which are restricted to the Indo-Australian area. Significantly, only 13 (38%) species are shared with from the eastern part of the Great Australian Bight collected during the only comparable survey of Australian deep sea barnacles [38]. These shared species demonstrate a connection between northern and southern areas of the Australian bathyal and abyssal zone.

Only one species, *Litoscalpellum* sp. nov., is considered to be new to science with any certainty, while the remaining OTUs will require further study of similar species. The newly recorded species for Australia, *Arcoscalpellum* cf *sculptum* and *Litoscalpellum crinitum*, are range extensions south from tropical waters [76], while *Neoscalpellum* cf *crosnieri* was previously known only from the western Indian Ocean [77].

The present collection contains many taxonomically valuable specimens, including good ontogenetic series for *Amigdoscalpellum vitreum* and *Litoscalpellum* sp. nov. This is of particular importance for genera such as *Annandaleum*, *Litoscalpellum*, *Neoscalpellum* that are characterised by significant ontogenetic shifts in the calcification of the capitular plates, making the identification of small numbers of specimens difficult, especially juveniles as these often are indistinguishable from other genera [78]. The specimens will also be of value for phylogeographic studies as these specimens provide a wide geographic and latitudinal coverage that links the specimens collected from the Great Australian Bight to the deep seas of the tropical Indo-West Pacific.

Isopoda

K. L. Merrin

The isopod collection consists of 4229 specimens from both beam trawl and Brenke sleds, all of which have been identified to family level (Table 3), with 94% from the suborder Asellota. This high proportion of asellotes is expected at these depths (beyond 1000 metres) as this suborder is the dominant isopod group in these habitats.

In total, 27 families were identified. The Munnopsidae was the most commonly collected family, making up 39.8% of the total isopod numbers. The next most common family was the Ischnomesidae (14.6%), followed by Desmosomatidae (13.2%) and the Haploniscidae (11.4%). The high prevalence of the Munnopsidae in these samples was not surprising as studies have found that this family is the most common family in the deep sea. In the north Pacific abyssal regions around the Kuril-Kamchatka Trench, Munnopsidae have made up around half of all isopod specimens collected, 53.9% in Golovan, et al. [79] and 47.4% in Elsner, et al. [80], while in the Southern Ocean (Atlantic sector) Munnopsidae have made up 50% of all isopod specimens [81]. In this study, the Ischnomesidae were the second highest in total isopod numbers, in contrast to other studies where the Desmosomatidae were the second most collected [79-81]. The most commonly collected non-asellote isopod was from the family Serolidae. There were twelve families who were represented by ten or less specimens.

In general, the Brenke sled samples collected from 4000 metres showed more isopod diversity (in terms of families) than those from 2500 metres. There were only two non-asellote families, the Gnathiidae and Arcturidae that were collected from 4000 metres, all the other non-asellotes were restricted to depths of 2500 metres and above.

All collected isopod families except one have been previously recorded from Australian waters [38; pers obs], however several have not had any species formally described from them. The family Urstylidae, which until now, has only been recorded from the Argentine Basin and the Clarion-Clipperton Fracture Zone [82] was collected from off Bermagui at 4730 metres (station 042). No Serolidae were collected north of the Hunter region (station 070).

Decapoda

C. A. Farrelly & S. T. Ahyong

The IN2017_V03 survey of 1261 decapods comprised 31 families, 61 genera and 108 species, all from typical deep-water groups. Of these, 17 are new to science, 30 represent new records for the east coast of Australia and 15 for Australia as a whole. Significant extensions in depth ranges were also found for seven species (five dendrobranchiates, one caridean and one munidopsid).

Most new species from the voyage were from the Caridea (8%) and Anomura (5.5%). The highest number of new Australian records was in the Anomura and the highest number of new east coast records was in the Caridea (10%). Six species from the ECA survey are endemic to Australia and five of these (4.6%) are endemic to the east coast. The majority of species from the survey are widespread: 75% (81 species) have wider Indo-West Pacific ranges; 10% (11 species) have broader

Southern Ocean or sub-Antarctic ranges and 28% (30 species) are circumglobal, occurring in both the Atlantic and Indo-Pacific. Three species of hermit crab (Paguridae) represent new generic records for Australia: *Catapaguroides microps*, *Chanopagurus atopos*, and *Icelopagurus crosnieri* and three species of the brachyuran crab *Ethusina* (Ethusidae) are the first identified species of this family and genus recorded in Australia [83].

The 15 new Australian records represent significant range extensions with most of the nearest previous records of these species from neighbouring Indo-West Pacific localities, including New Caledonia, Vanuatu, Wallis and Futuna Islands, and Indonesia, although several species were otherwise only found more distantly, including Taiwan (*Chanopagurus atopos*), the Philippines and the Bay of Bengal (*Munidopsis arietina*) [84]. Other range extensions with more proximate previous records include *Gordonella kensleyi*, *Glyphocrangon tasmanica*, *Neolithodes bronwynae* and *Munidopsis crassa*, all previously known from the northeastern Tasman Sea; and *Ethusina castro* and *E. rowdeni* previously known from only a single specimen each from northeastern New Zealand [83,85]. In addition, the survey extended the range of 30 species from adjacent regions to the north or south, or west from the Lord Howe Rise and Norfolk Ridge. Five species, previously known only from Western Australia were also recorded.

All of the undescribed species belong to genera already recorded from Australian waters, although their nearest congeners may not be Australian. For example, the nearest relatives of two new species of squat lobsters, *Munida* sp and *Munidopsis* sp, occur farther afield in the Indo-West Pacific [84]. *Glyphocrangon* cf *ferox*, has its closest relative in Madagascar [86] and *Lebbeus* sp most closely resembles species from New Zealand and Hawaii [87,88].

Ninety-nine species (92%) were found in the bathyal zone (1000 – 3500 m) with almost two thirds (64) of these recorded between 1000 and 1500 m. Twenty-three species (21%) were collected from the abyss (3500 + m). This represents a decrease in diversity of 77% from bathyal to abyssal depths as 76 species fall out below 3500 m. Fifteen species (65% of abyssal species) were recorded from both bathyal and abyssal depths. Thirty-three species from the voyage were also recorded from the Great Australian Bight surveys [38] with seven of these from abyssal depths. This degree of species overlap probably reflects the geographic proximity of the survey areas (i.e., eastern Australia and southern Australia, respectively) in combination with the southern flowing East Australian Current

The Decapoda of the bathyal sea floor along the eastern coast was dominated numerically by deep-water hermit crabs (Parapaguridae; 37%), followed by the deep-sea lobsters (Polychelidae) (10%), squat lobsters (Munididae, Munidopsidae, Chirostylidae; 5%) and a number of shrimp families (Mematocarcinidae, 8%; Sergestidae, 6%; Crangonidae, 5%; Benthesicymidae, 5%). Several families of brachyuran crabs were also recorded from bathyal depths (Cyclodorippidae, Cymonomidae, Homolidae, Ethusidae, Goneplacidae, Inachidae and Geryonidae), though most of these were from the 1000 m trawls. The abyssal fauna was dominated by the Nematocarcinidae (25%), Crangonidae (20%), Benthesicymidae (17%), Munidopsidae (squat lobsters) (16%), Acanthephyridae (10%) and Aristeidae (4%). Significantly fewer parapagurids, polychelids and sergestids were recorded at abyssal depths (all dominant at bathyal depths) and some groups such as the brachyurans, glyphocrangonids, chirostylids and pagurids were not recorded in any abyssal samples.

A marked increase in species diversity with decreasing latitudes was observed for sample sites close to 1000 m (18 species from the Hunter stations compared to 33 species from the Coral Sea). Many species were recorded from southern to northern stations but the largest number of brachyuran, anomuran and polychelid species was recorded from the northern stations from off Byron Bay and the Coral Sea. In contrast, the survey data of the lower bathyal waters (1500-3500 m) showed no pattern of increasing diversity with decreasing latitude (11 species from Freycinet, Tasmania, and 13 from the Coral Sea with various peaks of higher diversity in between). A latitudinal comparison of abyssal plain Decapoda also showed no increase in diversity from south to north, with four species recorded from Freycinet and three from the Coral Sea.

Pycnogonida

D. Staples

The IN2017_V03 collection is represented by 111 specimens assigned to 6 described species and 16 potentially new species. Seven species were collected using the Brenke Sled and 15 using the beam trawl. Only three species were recorded using both methods. Because the Brenke Sled has not been used elsewhere in Australian deep sea surveys comparison between regions can only be effectively based on the trawled material. It is apparent that had the Brenke Sled been used the number of Great Australian Bight (GAB) species could have been increased significantly. Without exception all Brenke Sled material consists of small, fine specimens that would easily go undetected amongst bulk collections associated with trawls and dredges. In this regard the Brenke Sled is a most effective collection method.

The most abundant and diverse genus represented in this collection is *Colossendeis* with 58 specimens belonging to 8 species. *Colossendeis* is a deep-sea genus that includes the largest pycnogonids, often with far-ranging distributions. Because of their size, with leg spans commonly ranging from 30-50 cm in Australian waters, *Colossendeis* is the most conspicuous genus represented in deep-sea trawls. Observations using ROV cameras of large specimens treading water or ‘swimming’ support the probability that distribution is assisted by slow-moving deep-sea currents whilst suspended in the water column. The most abundant species in this collection with 29 specimens is *Colossendeis tasmanica* recorded from 999-2939 m depth. This species is readily confused with *C. colossea* but differences are well supported morphologically and by (unpublished) molecular data. *Colossendeis tasmanica* is well represented in the GAB and probably in the NORFANZ collections as *C. colossea*. *Colossendeis colossea* is a pan-oceanic species recorded at depths of 420–5200 m worldwide and because of their similarities it is most likely that geographic and bathymetric records of the two species are confused.

A notable record in this collection is that of *Ascorhynchus cooki*. This species is one of seven rarely recorded ‘giant’ species in the genus. Nine specimens were collected from seven sites at depths 2336–2821 m. This species has been collected previously from sites SW of Macquarie I., N of Chatham Rise and SE of Cook Strait at depths of 1463–2992 m. It was also collected on the RV Investigator trial voyage south of Tasmania at 2750 m depth. It is likely that these specimens will enable the synonymy of this species with another, predominantly North Atlantic Ocean species, and if this is correct it will broaden the distribution considerably from the US east coast and the west coast of Africa. Shallow-water specimens of *Ascorhynchus* have been observed burrowing into the sand and it is suspected that grain size plays a part in their distribution. Based on morphological characteristics it can be assumed that a similar partial interstitial existence is shared by deep-water forms such as *A. cooki*. This species is also represented in GAB collections. Nine post-larval specimens found attached to feeding tentacles of the bentho-pelagic holothuroid *Psychropotes* are suspected to be this species. These specimens represent more than one stage of development but the most mature forms are beginning to develop characteristics of *A. cooki* and are suspected to be this species. Hitching a ride on a bentho-pelagic holothuroid not only broadens the spread of the species gene pool but assists settlement on fine sediments which accommodate both the feeding of the holothuroid and the burrowing of the pycnogonid. Presumably the fine sediments also support the food source of the adult pycnogonid. The holothuroid was collected by beam trawl at Jervis MP at 2636 m depth.

The record of *Nymphon trituberculatum* is only the second for this species and the first female specimen. The type locality for this species is recorded as the 'Great Australian Bight' but the coordinates given for this station (Eltanin station 20-134, 59° 48´ S, 144° 45´ E, 3200-3259 m) are on the Southeast Indian Ridge. The finding of this species along Australian eastern coast raises the possibility that the incorrect Eltanin station data has been assigned to the type locality.

Bivalvia

H. MacIntosh

The bivalve fauna consisted of 218 lots with a total of 1563 specimens, comprising 21 families, 33 genera and 59 species. All families and genera of bivalves collected were known from bathyal to abyssal environments, and overall patterns of abundance and diversity match reported trends from other deep sea regions [89-91]. While there are few deep water collections from eastern Australian to make reference to, affinities could be seen with the deep-sea bivalve fauna of neighbouring regions. The southern stations (South of Newcastle) showed considerable overlap with bivalves from the deep Great Australian Bight [38]. North of Newcastle and into the Coral Sea, the fauna resembled that collected in the waters around New Caledonia [92,93].

Almost half of the specimens recovered (n=718, 46%) were from three common, near-cosmopolitan deep-sea species: *Bentharca asperula* (Arcidae, n=147), *Propeamussium meridonale* (Propeamussiidae, n=226) and *Abra profundorum* (Semelidae, n=345). These three species were found in small numbers across multiple sites, but occasionally occurred in high abundances: *B. asperula* n=103 in trawl 102, *P. meridonale* n=153 in trawl 053 and *A. profundorum* n=136 in trawl 065. Most other species were rare or sparsely distributed, with over a quarter of species (n=16, 27%) known only from single specimens; almost half (n=25, 42%) were found only at single sites.

It is interesting to note these three species all exemplify adaptations of suspension-feeding bivalves to deep-sea conditions, where plankton is scarce. *Abra profundorum* is primarily a deposit feeder and employs its ctenidia for particle sorting [94]. *Propeamussium meridonale* retains filamentous gills but has secondarily evolved carnivorous feeding, closing its valves on small prey items [95]. *Bentharca* *asperula* remains a suspension feeder and instead shows adaptations to cope with the paucity of food, including enlarging the ctenidia and lowering metabolic rates [96].

The Protobranchia are primitive bivalves characterised by simple ctenidia and the presence of palps for deposit-feeding. This mode of feeding is well suited to deep-sea soft sediments and protobranchs are often the dominant bivalve fauna in abyssal environments [97]. Here 16 species of protobranchs were recorded, including representatives of the Sareptidae, Siliculidae and Yoldiidae, poorly known in Australian waters. Significantly more protobranch species were recovered in this survey compared to surveys in southern Australia [38], likely due to the use of use of Brenke sleds here, which captured more small infauna than beam trawls.

Carnivory is also common in deep-sea bivalves. In ‘septibranch’ bivalves, the gill filaments are fused into a single muscular septum. This diaphragm-like structure, coupled with a large, sensitive inhalant siphon allows septibranchs to rapidly inhale prey like small crustaceans and larvae [98,99]. Notable septibranchs recovered include the spectacularly sculptured *Spinosipella costeminens* (Verticordiidae) an unknown species of *Halonympha* (Halonymphidae), and two species of *Cetoconcha* (Cetoconchidae). These latter two genera have been previously split from larger families (Cuspidariidae and Poromyidae respectively) on the basis of small morphological characters, and fresh genetic material collected here may allow testing the monophyly of these groupings.

The beam trawls and brenke sleds targeted soft sediment substrates, but in several operations wood and whale bone were serendipitously recovered. These organic falls serve as islands amongst the ooze and host their own unique deep-sea fauna [100]. Associated with whale and fish bones, two species of bathymodioline mussels in the genus *Idas* could be separated on the basis of shell morphology and internal musculature. Identifications of these are tentative, however, as the taxonomy of the Bathymodiolinae is in a state of flux, with genetic studies revealing many cryptic species [101,102].

Woody debris was recovered at several sites, hosting three species of Xylophagaidae. These bivalves are obligate wood-borers, the deep sea counterpart of the shallow-water Teredinidae, or “shipworms”. Both burrow into wood with specially-modified shell valves and derive nutrition from with the aid of symbiotic, cellulose-digesting bacteria [103,104]. Like many deep-water taxa, the diversity of Xylophagaidae in Australian waters remains largely unknown.

Gastropoda

F. Köhler, F. Criscione & A. Hallan

In all, 291 lots of Gastropoda were retrieved from the sampled bathyal to abyssal environments along the eastern Australian coast, containing 963 individuals. Altogether, these lots represented 136 species or morphologically distinguishable Operational Taxonomic Units (OTUs) from at least 88 genera and 45 families. Only fifteen species have so far been assigned an available taxonomic name, while many OTUs have remained tentatively identified to genus- or species level. There is no doubt that several of these yet unidentified OTUs will eventually be assigned with an available species name pending further consultation with experts for various gastropod groups. Nonetheless, a significant proportion of the sampled gastropod fauna is considered to be new to science. For example, we consider the vast majority of the 44 OTUs in the family Raphitomidae (Neogastropoda: Conoidea) as undescribed. With regards to the numbers of collected individuals, the most abundant species were representatives of the families Abyssochrysidae, Eucychlidae, Mangeliidae, Philinidae and Turritellidae. The systematically most diverse family is the Raphitomidae (Conoidea), accounting for nearly one third of all gastropod species.

Our identifications have revealed high rates of bathymetric turnover with little overlap between species present at different depths. We have distinguished 27 species/OTUs among samples collected at about 1,000 m, 79 at about 2,500 m, and 40 at about 4,000-4,800 m depth. Among these, fewer than 20 species have been collected in more than one depth layer. The highest species diversity was generally recorded at mid- to lower bathyal depths of around 2,500 m. Here, we also observed a noticeable decrease in the sampled species diversity along a south-to-north gradient.

The bathyal and abyssal gastropod fauna of Australia has remained poorly documented and few deep water collections are available for a faunal comparison. We recorded some overlap with the fauna of the Great Australian Bight as reported by MacIntosh, et al. [38] particularly at the southernmost sampling sites. Several species have been recorded from both areas, the eastern Australian Abyss and the Great Australian Bight, such as *Bathytoma agnata* (Borsoniidae), *Oocorys sulcata* (Cassidae), *Calliotropis carinata* and *C. canaliculata* (Eucyclidae), *Enixotrophon carduelis* (Muricidae), *Tritia ephamilla* (Nassariidae), and *Globiscala* cf. *boaespei* (Epitoniidae). In addition, nine putatively undescribed species retrieved from the eastern Australian abyss were also reported from the Great Australian Bight. Of these, four belong to the Conoidea, the by far most diverse gastropod superfamily. However, for the majority of species/OTUs, no overlap has been recorded between the eastern Australian abyss and the Great Australian Bight. This observation may be indicative of considerable regional endemism in the gastropod fauna of the Australian deep sea.

The gastropods sampled during the eastern Australian voyage of the Investigator represent altogether six ecological feeding guilds, with predators comprising the vast majority of species, largely belonging to the order Neogastropoda. In addition, deposit-feeders, grazers and parasites were each about equally represented in terms of species numbers, while suspension feeders (Calliostomatidae and Turritellidae) and scavengers (Nassariidae) were the least diverse guilds (four species overall).

The majority of samples and species were collected by beam trawls while the Brenke sledge sampled comparatively few gastropods of small size, which would otherwise slip through the mesh of the beam trawl. Because of the overall low numbers of smaller gastropods in the size range of under 10 mm, we consider the smaller-sized gastropod fauna as under-sampled owing to the specific limitations of the deployed collecting gear.

General patterns of diversity as here described for the gastropods of the eastern Australian abyss are consistent with faunal patterns described for other regions of the world. A high proportion of undescribed species-level diversity has also been recorded in deep-sea surveys in New Caledonia [105].

Similarly, conoideans are frequently found to dominate marine gastropod faunas from the intertidal to abyssal depths, including the deep-sea in New Caledonia [105].

The observed turnover in species composition across depth layers has also been observed for other gastropod faunas. For the northern Atlantic, a three-layered faunal composition has traditionally been described consisting of a shelf fauna (to about 300 m depth), a slope to bathyal fauna (to about 2,500 m depth), and an abyssal fauna (extending to about 6,000 m depth). However, in tropical waters a more frequent turnover between faunal assemblages at additional depth layers between about 200 and 1,500 m depth has been reported [105].

Some notable differences have been observed in comparison with the gastropod fauna of the Southern Ocean where a steep decrease in species diversity has been reported with increasing depth [106]. Brandt, et al. [106] reported that species numbers dropped to around 20 species at depths below 1,200 m, whereas we recorded significantly higher cumulative species numbers at depths of 2,500 m and even 4000m across the eastern Australian continental margin.

Cephalopoda

J. Finn & C.C. Lu

A total of 15 cephalopod specimens were collected in beam trawls over the course of this survey. These specimens represent 4 families and at least 6 species. While the total number of cephalopods collected is quite low, this survey increased the known distribution of multiple species and included at least one new record for Australia.

The majority of specimens collected during this survey were deep-water cirrate octopods, family Opisthoteuthidae. Six specimens of *Opistoteuthis pluto*, were collected at stations 22 (2760-2692 m), 80 (1257-1194 m), 100 (999-1013 m) and 121 (1013-1093 m). While previously reported to occupy a distribution including the continental slope waters from the Great Barrier Reef to Tasmania [107], this survey increased the known maximum depth for this primarily benthic species from 1254 m [107] to at least 2692 m.

Among the cirrate octopods, the most well-known are the Dumbo Octopuses (genus *Grimpoteuthis*), nicknamed on account of their large fins, and deemed by some to resemble the ears of Disney's Dumbo the Flying Elephant. This survey provided the first record of *Grimpoteuthis* from Australian waters. Two specimens of *Grimpoteuthis* were collected at stations 35 (2338-2581 m) and 44 (2821-2687 m). Both specimens were found to be consistent with *Grimpoteuthis abyssicola*, described from a single specimen collected at 3180-3154 m on the adjacent slope (35°35.1'S 160°57.1'E) [108].

The next most numerous taxa collected during this survey were the deep-water incirrate octopuses, *Muusoctopus* spp. (family Enteroctopodidae). Four specimens of *Muusoctopus* spp. were collected at stations 04 (2820-2751 m), 80 (1257-1194 m) and 100 (999-1013 m), including a large specimen with a mantle length of approximately 180 mm. Historically these octopuses have been treated under the invalid name *Benthoctopus* (e.g. [109]). Gleadall, et al. [110] proposed *Muusoctopus* as a replacement name. The specimens collected during this survey will be invaluable to a much-needed review of the deep-water octopods of Australian waters.

Single representatives of two oegopsid squid species (family Mastigoteuthidae) were collected in beam trawls during this survey.

Mastigoteuthis psychrophila is a deep-water meso-bathypelagic squid distributed circumpolarly throughout the Antarctic [111]. A single specimen of *Mastigoteuthis psychrophila* was collected in a beam trawl in the Freycinet CMR off eastern Tasmania (station 04; 41°43.83´S, 149°7.182´E; 2820-2751 m). This specimen represents the most northerly confirmed record of this species, and potentially the deepest. On reporting the catches of the *Dmitry Mendeleyev* in subantarctic and Antarctic waters, Nesis [111] noted that, while the depth of *M. psychrophila* varied with latitude, the species occupied water with consistent hydrological conditions. While in the south specimens were collected at 500m, and in the north at 1500 m, all specimens were encountered in water with a temperature approximately 2.1°C, salinity approximately 34.7 ppt and an oxygen content of about 5 ml/l. The beam trawl specimen collected during this survey appears to be consistent with this latitude/depth trend, being encountered both further north and deeper than the material reported by Nesis [111]. While some doubt exists as to the actual collection depth of this specimen (as it was collected in an open beam trawl and hence may have been caught while the gear was descending or ascending), interestingly the hydrological conditions of the station closely match those reported by Nesis [111] as suitable for this species: temperature 1.8°C, salinity 34.7 ppt, oxygen 4.3 ml/l. While not officially detailed in this report, an additional specimen of *M. psychrophila* was collected in a demersal fish trawl in the early stages of this survey (41°37.608´S, 149°8.958´E; NMV F245709). The northerly locations of these records are consistent with catches at similar latitudes in New Zealand [112] and the suspicion that *M. psychrophila* may exist to approximately 40°S in the Atlantic [113].

The second mastigoteuthid squid collected during this survey was an *Idioteuthis cordiformis*. While previously reported from the survey region [109] and sampled depth [114], the most notable aspect of this specimen (in relation to the survey) is its size. With a mantle length of 270 mm, this specimen is the largest squid collected during this survey. *Idioteuthis cordiformis* is however reported to be the largest of all mastigoteuthid squids, attaining mantle lengths to 1000 mm [113].

During this survey a single sepiolid of the genus *Heteroteuthis* was collected. While eastern Australian records have historically been referred to as *Heteroteuthis serventyi* (e.g. [109]), and more recently *H. dagamensis* (see [115]), a recent report of *H. hawaiiensis* from southern Australia [38] highlights the need for a thorough review of this genus from Australian water. It is anticipated that the collected specimen will aid this review.

Crinoidea

M. Eléaume

In total 498 specimens of crinoid were collected during the 2017 expedition. One deployment only accounted for 402 specimens. Other deployments yielded from 1 to 20 specimens. These specimens represented at least 7 different species for which only tentative identifications are given:

Adelatelecrinus cf. *vallatus*, *Bathycrinus* cf. *australocrucis*, *Democrinus* cf. *japonicus*, *Monachocrinus* cf. *aotearoa*, *Pentametrocrinus* cf. *semperi, Thalassometra* cf. *gracilis* and an unidentified representative of the feather star family Antedonidae.

Most of these species were collected in small numbers except *Thalassometra* and *Democrinus*. Both were collected in large numbers during operation 69, and this station may represent the optimal habitat for these two species. *Adelatelecrinus*, *Pentametrocrinus* and *Democrinus* are all restricted to depths from 1000 to 2000. *Thalassometra* was collected mainly from depths around 1000 with some occurrences to 2500 m (Operation 86). *Monachocrinus* was collected at depths exceeding 2500 m and also at depths around 4000 m. Some Bourgueticrinina occurrences, collected at intermediate depths once attributed to a species may help bridge this gap. *Adelatelecrinus*, *Pentametrocrinus, Democrinus, Thalassometra* and unidentified *Antedonidae*, were collected from the two northernmost explored ecoregions Manning-Hawkesbury and Tweed-Moreton. *Pentametrocrinus* and *Bathycrinus* are restricted to Tweed-Moreton and *Monachocrinus* occurred from Bassian to Manning-Hawkesbury.

The crinoids from the eastern coast of Australia display bathymetric and geographic contrasted distributions. More detailed taxonomic resolution is needed to help understand the biogeographic implication of these preliminary results.

Asteroidea

C. Mah

Surveys of Bathyal and Abyssal regions in Eastern Australia yielded a total of over 52 species of sea stars (Asteroidea) including at least six undescribed species. Nearly all of the identified species were new occurrences for the Australian region.

At least one specimen of an undescribed species of *Evoplosoma* was collected. Based on in situ observations by Mah [116,]Mah [117] *Evoplosoma* has been regularly observed feeding on deep-sea octocorals, particularly those which form large deep-sea “forests” such as the “bamboo” corals (family Isididae), suggesting that these coral habitats occur off the Australian coast.

Among the rarest of the sea stars collected were new occurrences of the velatidans *Pythonaster* and two individuals of *Myxaster*, both in the family Myxasteridae. Both of these genera occur at great depth (>2000m and >1000m respectively) and are among the most seldom encountered of deep-sea asteroids [118]. Fewer than 2 dozen specimens of either genus are known from museum collections. These are the first occurrence records of these mysterious animals from Australian waters.

Multiple occurrences of different “slime stars” in the genus *Hymenaster* and the related genus *Calyptraster* were collected. New discoveries showing gut contents of these taxa from the Great Australian Bight suggest deposit feeding or predation on molluscs present in both genera. *Hymenaster* contains numerous species, some of which occur widely throughout the world but it is likely that several new species occur in Australian waters but taxonomic difficulties must be addressed before this work can progress.

At least three deep-water freyellid sea stars were collected, including *Astrocles*, *Freyella* and *Freyastera*. Freyellids are members of the Brisingida, unusual asteroids which extend their multiple, elongate arms into the water column and capture food as it is caught by pedicellariae present on needle-like arm spines. Of the three genera collected, *Astrocles* represents a likely new species, and the first occurrence of this genus from the Southern Hemisphere.

Of the total number of species recorded, several of them are members of families which occur or have been observed on soft sediment, including the Astropectinidae, the Porcellanasteridae, and to a lesser extent the Zoroasteridae and the Benthopectinidae. These groups are widely different from one another, but have adaptations which permit them to exploit soft-bottom settings in different ways. Porcellanasterids for example, occur on abyssal plains and exploit finer mud than astropectinids which occupy a broad range of habitats and different sedimentary settings.

Ophiuroidea

T.D. O’Hara

The ophiuroid fauna consisted of 78 species, 296 species-sample lots, and 9192 specimens. The abyssal fauna (>3500 m) is very similar to that described for the North Atlantic Ocean [119] including the species: *Ophiosphalma armigerum*, *Perlophiura profundissima*, *Amphiophiura bullata*, *Ophiura irrorata*, *Ophiacantha cosmica*, *Ophiotypa simplex* and *Amphiura daleus/verrilli*. Most of these species have been recorded across the Atlantic, Pacific and Indian oceans, although this needs to be confirmed by genetic data. One exception is *Ophiosphalma armigerum* which is occurs throughout the Atlantic and across the Indian Ocean to southern Australia (as far as Hunter MP), but is replaced in the tropical west Pacific by *O. fimbriatum* and *O. glabrum*.

There was a clear temperate-tropical transition at mid bathyal depths. Temperate species included *Astrodia tenuispina*, *Ophiura spinicantha*, *Ophiocten australis*, *Ophiuroglypha verrucosa*, *Ophioplinthus accommodata*, *Ophiocamax applicatus*, *Ophiacantha sollicita*, *Ophiernus vallincola*, *Amphilepis neozelandica*, and *Ophaictis amator*. Many of these animals have been found previously in the Great Australian Bight and off New Zealand. *Ophiocten australis* occurred in huge numbers at some stations (e.g. n=1685 in beam trawl 022 and n=519 in sample 056). The northern group included *Amphiophiura sculptilis*, *A. ornata*, *A. paraconcava*, *Ophiomusium granosum*, *Ophiosphalma fimbriatum* and *O. coricosum*. These are all typical animals found by French surveys around New Caledonia. *Amphiophiura paraconcava* was often abundant (n=396 from sample 115 and n=1308 from 128).

The widespread carnivore *Ophiura flagellata* was numerous (n=49) in the sample (080) with rotting mantra shark, but also in sample 104 (n=62) which did not contain an obvious carcass. A few specimens represented interesting extensions of geographic range. *Amphiophiura inops* (sample 070) is otherwise known only from the Antarctic. *Ophiotoma paucispina* was previous known only from a few specimens collected by the Albatross in the tropical eastern Pacific (1891-1904). One specimen collected from the abyss off Newcastle (sample 067) has been confirmed by multi-locus DNA data to be a new genus within the Ophiotomidae.

Holothuroidea

P.M. O'Loughlin, M. Mackenzie & T.D. O'Hara

The bathyal and abyssal fauna found off eastern Australia was similar at the genus-level to that found in many similar habitats elsewhere in the Pacific and Atlantic Oceans [120]. In this study, the peak of diversity was at mid to lower bathyal depths (1500-3000 m) again similar to that found elsewhere [120]. More than 41 taxa were identified to species-level, including more than 12 potentially new species in the genera *Psolus*, *Peniagone*, *Ellipinion*, *Molpadiodemas* (numerous), *Benthodytes* (x2), *Paroriza*, *Gephyrothuria*, *Molpadia* (x4), *Protankyra*, *Prototrochus* and *Myriotrochus*. However, several other identifications were tentative. Cryptic species-complexes with wide distributions are known to be common amongst echinoderms and future revisions based both on molecular and morphological data may well distinguish Australian species from those living in other oceans. Conversely, deep-sea holothurian phylogeographies published to date have found complexes of species with overlapping geographic and bathymetric distributions [121,122].

The mid to lower bathyal fauna includes taxa from all seven recognised holothuroid orders [123], although in terms of abundance, the orders the Elasipoda (particularly *Amperima furcata* and *Benthodytes* sp nov 1) and Persiculida (*Pseudostichopus peripatus* and *Molpadiodemas* spp) dominated. The abyssal fauna (>3500 m) was generally a subset of the lower bathyal fauna, with the addition of the unusual U-shaped infaunal species *Ypsilothuria bitentaculata*. The upper bathyal (<1500 m) fauna was also a subset of the lower bathyal fauna with the addition of *Orphnurgus insignis* and an undetermined *Benthodytes*.

Several species found in the survey are widespread and their biology has been studied in more detail elsewhere. *Enypniastes eximia* (sometimes known irreverently as the 'headless chicken'), a pelagic elasipod that only descends to the seabed to feed [124], was opportunistically collected in beam trawl 080 at 1225 m in the Central Eastern MP. Some of the holothurians in the family Elpidiidae are also likely to be able to swim, at least for short periods [125]. *Scotoplanes globosa* (the sea pig), collected at 2785 m in the Freycinet MP, forms vast herds on oceanic abyssal plains and has been called the most common mega-faunal animal on the planet [126]. *Psychropotes longicauda*, a large purple species with a prominent sail-like dorsal appendage of unknown function, is known to be a cryptic species complex [121]. It has one of the largest eggs of any echinoderm (up to 4.4 mm in diameter) and appears as if it can metamorphose directly into juveniles in the plankton, having been found thousands of meters above the seafloor [127]. The majority of the epifaunal and bathypelagic species are likely to be deposit feeders. *Oneirophanta mutabilis* another species complex, [122] has been reported to continuously feed and excrete like a "conveyor belt" [128]. It has been estimated to bioturbate up to one third of the seafloor where it is common [129]. In many locations only females have been found, suggesting it is parthenogenetic or that males become fertile only under certain conditions [130]. Numerous animals that live buried in the sediment (infauna) were also collected, from the tiny *Protankyra* and *Echinocucumis* to the large *Molpadia*. The 'skin-digging' tanaid *Exspina typica* was found in the coelomic cavity of two *Pseudostichpus peripatus* specimens collected from Freycinet CMR at 2820 to 2751m. This is the first record of *E. typica* parasitising this particular species of holothuroid, however it has previously been observed in the intestine and body cavity of other holothuroid hosts, and an association between this parasitism and deep-water environments was confirmed by Alvaro, et al. [131].

Tunicata

M. Ekins

From the one hundred tunicates collected during the IN2017_V03 expedition, there were only six different species from four different families and five genera. All species collected from this voyage have previously been collected in abyssal trawls from Antarctica, Australia, the Indian and Pacific Oceans. There is only one potential new species from this expedition, *Protocholozoa* cf *anthos* but, unfortunately it was damaged during collection and the description of a new species will have to wait until another specimen is recovered. *Asjirus indicus* was the most commonly collected ascidian, collected from Victoria up to the Coral Sea, from 1000 to 4000 m in depth. This is a species with a worldwide deep water distribution. *Culeolus anonymus* was the second most commonly collected ascidian, also collected from Victoria to off Fraser Island, Queensland. This species has been recorded from subantarctic to Antarctic waters in the Pacific and Atlantic Oceans previously. The other species recorded on this voyage include *Culeolus recumbens*, *Pharyngodictyon mirable* and *Dicarpa lata*. There were also recorded on this voyage salps *Metcalfina hexagona* and *Thetys vagina* as well as the ubiquitous *Pyrosoma atlanticum*.

Monniot and Monniot [132] have previously conducted extensive abyssal tunicate work in the Pacific concentrating mainly around New Caledonia and Kott [133,]Kott [134] has studied the deep water Antarctica ascidians. The abyssal fauna collected on this expedition is very similar to abyssal fauna from the Antarctic and deep tropical waters, showing an obvious connection via the deep cold waters. The Tasman Sea and Australia, including the Coral Sea and Great Australian Bight, were surveyed by RV Dmitry Mendeleev during 1975-1976. The ascidians collected during that expedition were described in Sanamyan and Sanamyan [135].

Pisces

M. F. Gomon, J. J. Pogonoski, D. J. Bray, A. Graham

The RV Investigator IN2017_V03 Abyssal Survey was Australia’s first attempt to systematically sample the abyssal benthic communities of a segment of the eastern Australian coastline bordering the continent. Although occasional collections had been previously made at similar depths in Australian waters, those efforts were for the most part one-off serendipitous shots at random localities undertaken during projects with quite different goals [136,137]. Some in fact were part of worldwide sampling efforts, like collections of the Challenger expedition undertaken in the mid-1800s, which meant vast distances between trawls to cover such a wide geographic area [138].

Consequently, little is known about the diversity and distribution of abyssal species in Australian waters and how it compares with this interconnected environment around the world. The initial perception of fish species taken in the recent dedicated survey supported the wide held view that abyssal diversity is low and those present are widely distributed in the world oceans. Although a majority of the species encountered during this abyssal project had been previously collected, a significant number represent new records for Australia's Exclusive Economic Zone.

Although the survey targeted depths of 2500 and 4000 m, the nature of the bottom topography encountered necessitated sampling shallower or deeper on some transects, which meant the overall catch composition included deep slope as well as abyssal and pelagic species, the latter taken in the course of shooting and retrieving non-opening and closing sampling gear. Of the more than 100 fish species collected, a little over two-thirds were bottom associated demersal species, with the remaining third pelagic forms, represented by both adults and/or early life stages, the latter in some cases of inshore species. About half of the bottom living species taken were abyssal with the other half confined to the lower parts of the continental slope. The catch included one carcass, the remains of a greatly deteriorated manta ray *Mobula birostris* with a pelvis almost a metre across.

At least seven of the 33 or more abyssal species (21 %) collected are confirmed first records for Australia's EEZ with a similar number still awaiting definitive identifications. Virtually all of these species have extensive geographical distributions, and despite their obvious limited mobility, some, like the colourless, live-bearing, virtually, if not completely blind gelatinous cusk-eels, likely remain close to “home” their entire lives. An ophidiiform group comprising the live-bearing family Bythitidae and the egg laying Ophidiidae, is one of two dominant evolutionary lines in the deepest parts of our oceans worldwide. The latter includes *Typhlonus nasus*, dubbed the “Faceless Fish” by a member of the fish team for its lack of discernible eyes, eye-like nostrils and underslung mouth, which initially masked its family relationships. In the end, it and the four other examples collected were found to be a species that was originally described from the Coral Sea just outside Australia's EEZ 140 years ago, but is only now verified as occurring in Australian waters. Examples of this ophidiiform group also included the massive *Spectrunculus grandis*, initially described from Japanese waters a year before the previous species, and reaching well over a metre in length. Both are widely distributed in Indian and Pacific oceans. Although the two examples reach quite a large size, many species occurring at these depths tend to be rather small, rarely exceeding 10-20 cm in length. The aphyonid-clade of cusk eels collected by the expedition was reviewed by Nielsen, et al. [139] who recognised five distinct species around Australia.

Another particularly diverse group at abyssal depths is the order Aulopiformes, ranging from the ferocious looking deepsea lizardfishes *Bathysaurus ferox* (family Bathysauridae), their extensive gape so full of needle-like teeth that they spill out onto the sides of the jaws, to the stilt-perched tripodfishes (family Ipnopidae) that await patiently on their prolonged fin rays for meals to come to them. The latter family was represented in the survey by eight long-finned species and two bottom huggers, including the odd looking Spiderfish of the genus Ipnops with large yellowish luminous oval plates where eyes should be and a second Australian specimen of the Shortarse Feelerfish *Bathymicrops brevianalis*. The species identity of the *Ipnops* remains in question as the DNA of the only specimen analysed (Coral Sea) differs from that of specimens collected in the Great Australian Bight. The tripodfishes represented comprised a significant proportion of the total number of species known to occur in the Indian and Pacific Oceans [140].

From a biomass perspective, members of the Basketwork Eel family Synaphobranchidae were important with seven species taken during the survey and the Southern Cut-throat Eel, *Histiobranchus australis*, which attains a length of about 70 cm, present at almost all of the 2500 m collection sites from Tasmania to the Coral Sea, demonstrating its dominance in this environment. Prior to recent deep-water sampling made possible by the Investigators' increased capability, this species was known in Australia from one or two specimens collected during international exploration. So, an apparently rare species is now seemingly common with over 30 specimens known from Australia. Basketwork eels are among the most numerous and often collected of the deep benthic fishes worldwide where they feed indiscriminately on available prey.

The brilliant red-orange Red Coffinfish *Chaunacops coloratus*, previously known only from the northern Pacific and eastern Indian Oceans, is one of the deepest dwelling members of a particularly deep, bottom living family of anglerfishes. Underwater videos taken in the Pacific show this species to puff up by inhaling water in an attempt to intimidate predators before "beating feet" when the ploy doesn't work. Other members of this family are generally confined to the continental slopes of the world.

Some shallow dwelling families of the temperate Northern Pacific, like the scorpionfish relatives the Snailfishes (family Liparidae) and the Eelpouts (family Zoarcidae) are absent in the shallows of the Southern Hemisphere, but do have examples in the southern deep-sea. For the most part these species dwell on the slopes of seamounts above the abyssal plain, but a specimen of the eelpout genus *Lycenchelys antarctica* was represented by a single specimen that is the first record for continental Australia. This is, as the name implies, an Antarctic species, which may have been a vagrant carried northwards by north flowing Antarctic Bottom Water that supplies abyssal waters of the world.

The expedition provided a significant glimpse of Australian ichthyo-diversity at these depths. The results show a similarity with that of other parts of the lower bathyal and abyss in world oceans.

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Stn	Location	Latitude	Longitude	Mid depth (m)	Date (d/m/y)	Area sampled (m^2)
004	Freycinet MP	-41.731	149.120	2785	18/5/17	29584
006	Freycinet MP	-41.626	149.552	4037	18/5/17	30344
013	Flinders MP	-40.386	148.928	1041	20/5/17	7908
014	Flinders MP	-40.464	149.102	2392	20/5/17	15348
015	Flinders MP	-40.473	149.397	4126	20/5/17	10572
022	Bass Strait	-39.462	149.276	2726	22/5/17	11756
030	Bass Strait	-39.552	149.553	4165	23/5/17	29312
032	East Gippsland MP	-38.479	150.184	3851	24/5/17	11580
035	East Gippsland MP	-37.792	150.382	2459	25/5/17	15352
043	Bermagui	-36.351	150.914	4800	27/5/17	14824
044	Bermagui	-36.355	150.644	2754	27/5/17	17972
053	Jervis MP	-35.114	151.469	3981	28/5/17	16792
056	Jervis MP	-35.333	151.258	2643	29/5/17	15976
065	Newcastle	-33.441	152.702	4226	30/5/17	13992
067	Newcastle	-32.985	152.952	2803	31/5/17	19748
069	Hunter MP	-32.479	152.994	1021	3/6/17	12508
070	Hunter MP	-32.575	153.162	2534	3/6/17	26260
078	Hunter MP	-32.138	153.527	4004	4/6/17	19608
080	Central Eastern MP	-30.099	153.596	1225	5/6/17	16096
086	Central Eastern MP	-30.098	153.899	2473	5/6/17	13384
088	Central Eastern MP	-30.264	153.870	4441	6/6/17	18328
090	Byron Bay	-28.677	154.203	2574	7/6/17	15400
097	Byron Bay	-28.355	154.636	3782	8/6/17	27508
099	Byron Bay	-28.371	154.649	3789	9/6/17	14416
100	Byron Bay	-28.054	154.083	1006	9/6/17	18968
101	Moreton Bay	-26.946	153.945	2548	9/6/17	11564
102	Moreton Bay	-27.008	154.223	4269	10/6/17	18332
104	Moreton Bay	-26.961	153.848	1104	10/6/17	13352
109	Fraser Island	-25.221	154.164	4005	11/6/17	18156
115	Fraser Island	-25.325	154.068	2346	11/6/17	11976
121	Coral Sea MP	-23.587	154.194	1053	13/6/17	13352
122	Coral Sea MP	-23.751	154.639	2349	13/6/17	13548
128	Coral Sea MP	-23.631	154.660	1765	13/6/17	13964
135	Coral Sea MP	-24.352	154.291	4001	15/6/17	19812

Table 1. Beam trawl sample location, depth, date.

Stn	Location	Lati-tude	Longi-tude	Mid depth (m)	Date (d/m/y)	Area sampled (m^2)
005	Freycinet MP	-41.730	149.135	2784	18/05/17	2985
009	Freycinet MP	-41.626	149.560	4028	19/05/17	4587
016	Flinders MP	-40.463	149.415	4130	21/05/17	4753
023	Bass Strait	-39.462	149.277	2734	22/05/17	2951
031	Bass Strait	-39.422	149.604	4160	23/05/17	3850
033	East Gippsland MP	-38.521	150.213	4085	24/05/17	2872
040	East Gippsland MP	-37.815	150.373	2673	25/05/17	1724
042	off Bermagui	-36.385	150.863	4730	26/05/17	5897
045	off Bermagui	-36.360	150.644	2787	27/05/17	4587
054	Jervis MP	-35.117	151.473	3953	28/05/17	2827
055	Jervis MP	-35.335	151.259	2666	28/05/17	4074
066	off Newcastle	-33.448	152.733	4286	30/05/17	6193
068	off Newcastle	-32.993	152.957	2854	31/05/17	3941
076	Hunter MP	-32.577	153.161	2507	3/06/17	4548
079	Hunter MP	-32.131	153.527	4031	4/06/17	3909
087	Central Eastern MP	-30.113	153.898	2479	6/06/17	3301
089	Central Eastern MP	-30.263	153.859	4425	6/06/17	3550
096	off Byron Bay	-28.678	154.204	2578	7/06/17	4909
098	off Byron Bay	-28.371	154.647	3782	8/06/17	4324
103	off Moreton Bay	-27.000	154.223	4270	10/06/17	7426
110	off Fraser Island	-25.220	154.160	4007	11/06/17	6648
119	off Fraser Island	-25.206	153.991	2308	12/06/17	3674
123	Coral Sea MP	-23.749	154.641	2305	13/06/17	4125
131	Coral Sea MP	-23.748	154.643	2327	14/06/17	4975
132	Coral Sea MP	-23.756	154.568	2156	14/06/17	4296
134	Coral Sea MP	-23.750	154.572	2124	14/06/17	4054

Table 2. Brenke Sled sample location, depth, date.

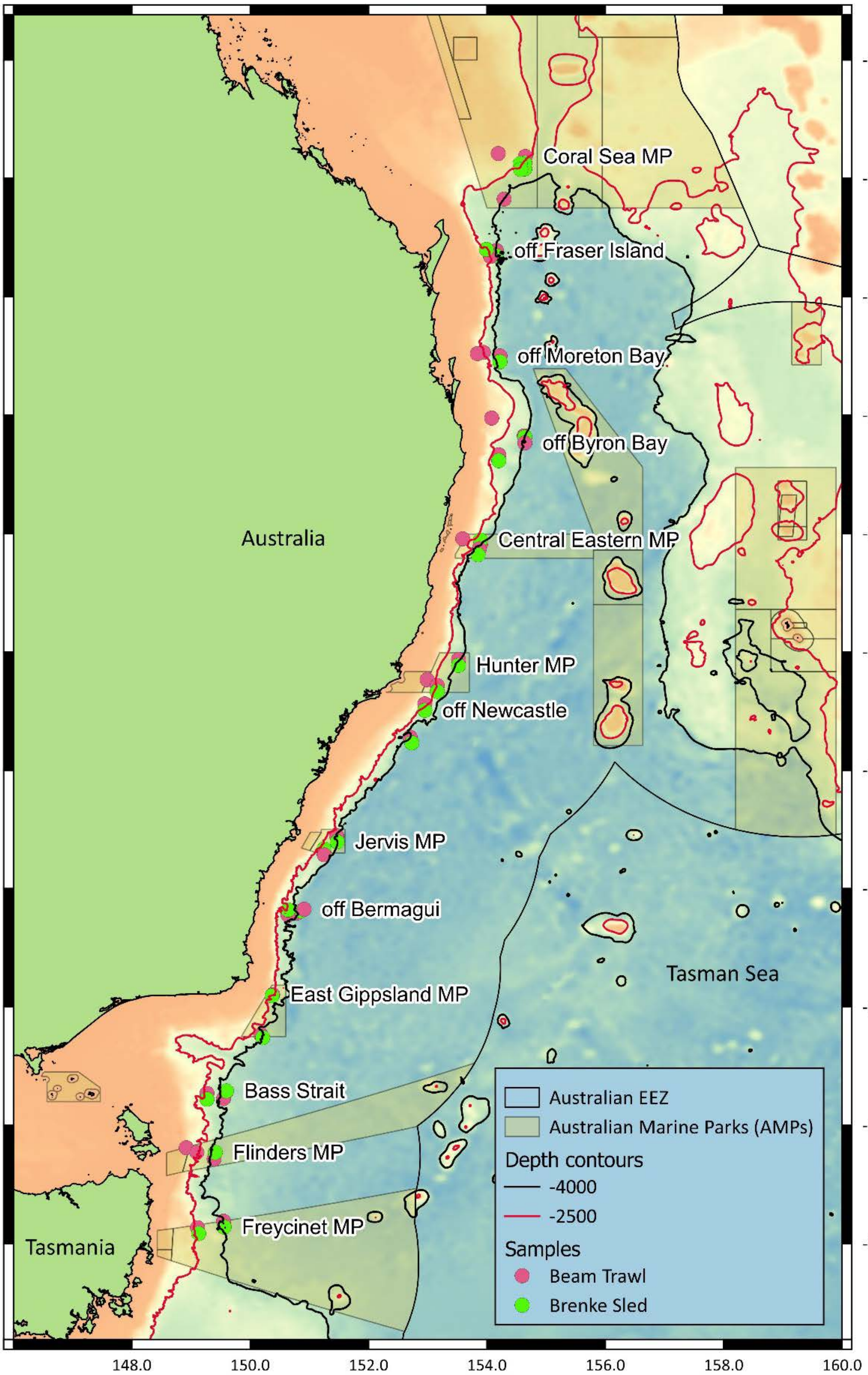

Fig. 1. Map of the eastern Australian continental margin showing the sample sites.

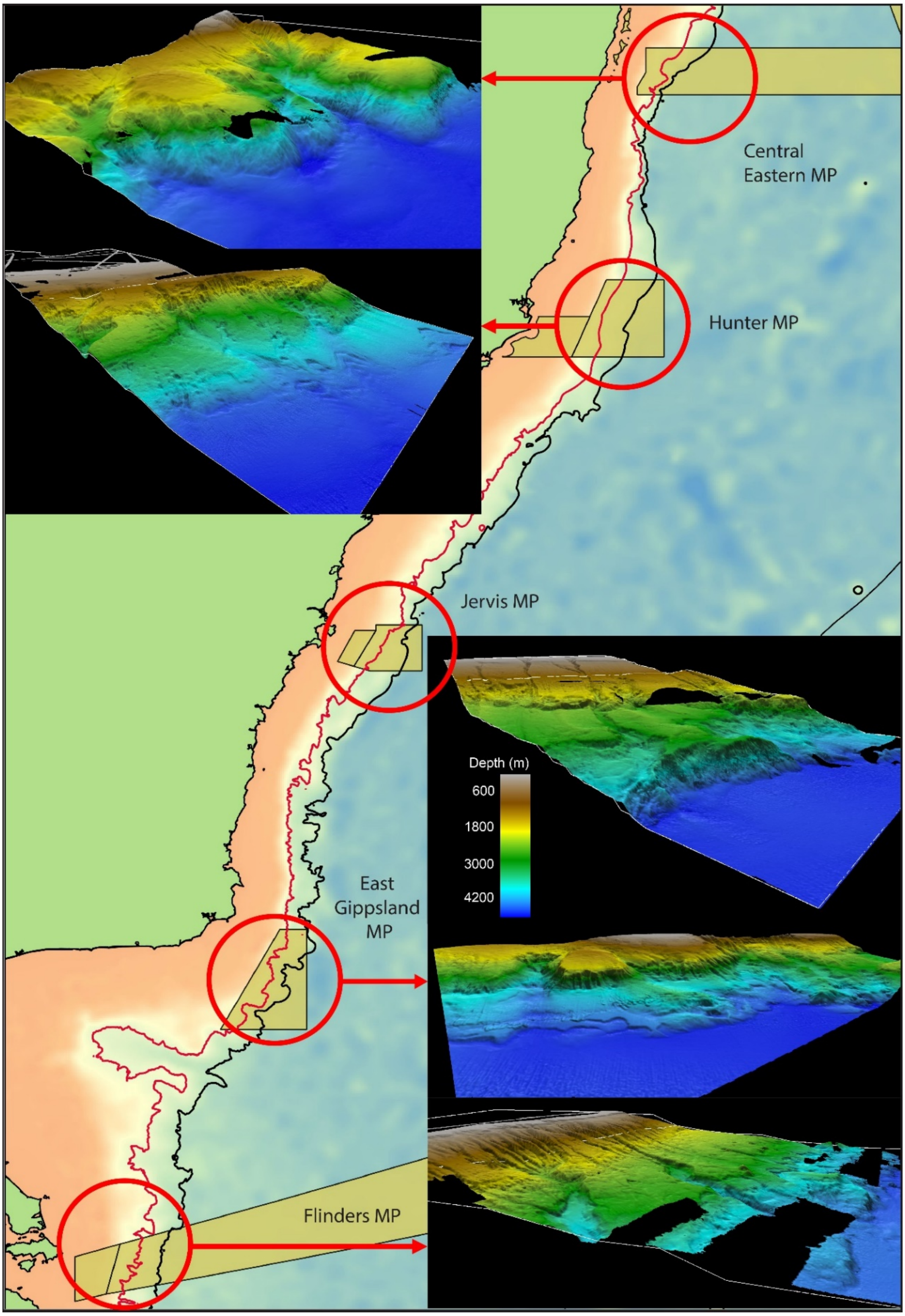

Fig. 2. Multibeam topology of five Marine Parks on the eastern Australian continental margin (map elements as Fig. 1).

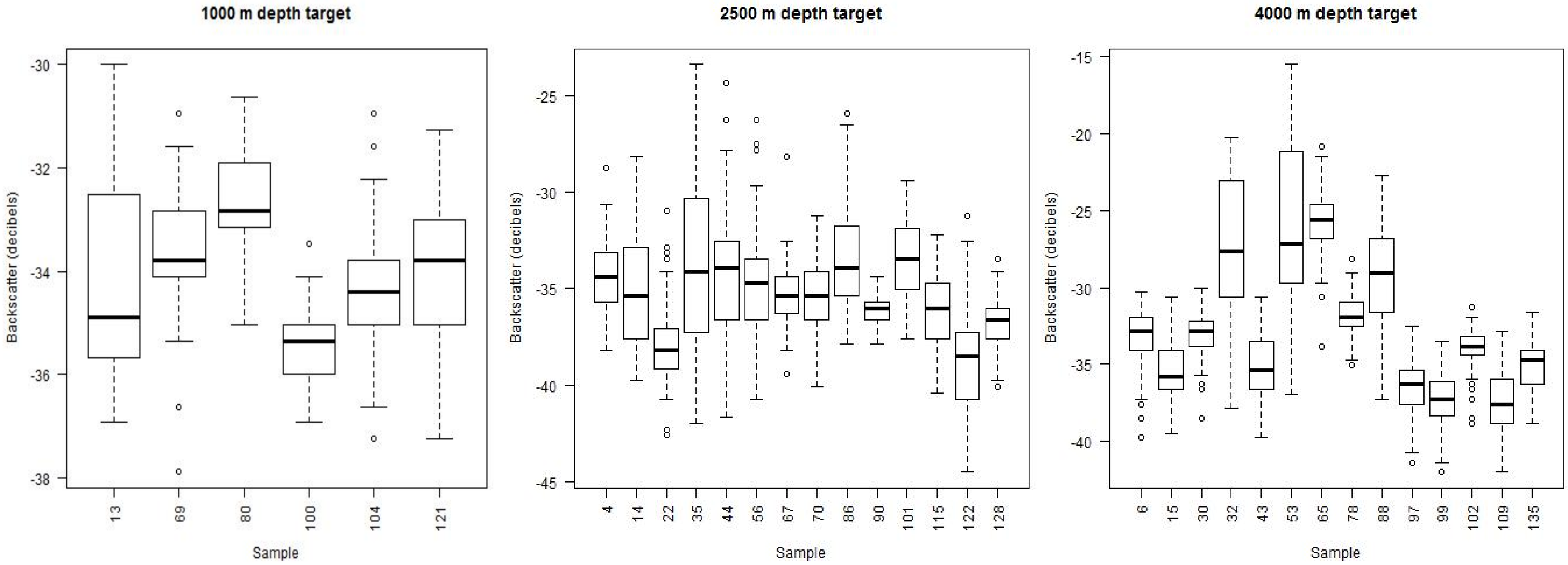

Fig. 3. Backscatter strength (median, quartile and maximum values) along beam trawl samples from the three target depth strata.

Chapter 3. Deep-sea temperate-tropical faunal transition across uniform environmental gradients

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Introduction

Deep-sea ecosystems are one of the world's major ecological research frontiers, giving us new perspectives on macro-ecological questions [14]. The deep sea (below 200 m) is the third biological realm after terrestrial and shallow marine systems, and is characterised by very cold water, extreme pressure, little to no light and limited food, with organic matter residues sinking from surface waters or transported down continental margins. However, our knowledge of large-scale spatial patterns at lower bathyal and abyssal depths (2000-6500 m) is limited, because of the logistical difficulty in sampling the vast extent of this biome (the largest on the planet).

Patterns of faunal distributions are well known for shallow water (0-200 m) marine environments. Here studies have shown marked compositional changes between tropical, temperate and polar assemblages [141]. These patterns were recognised as early as the 1850s, when Edward Forbes composed a global map showing marine life (fish, molluscs, echinoderms and cnidarians) distributed in latitudinal bands or "homoiozoic belts" [142]. These assemblages have formed in the context of a cooling of the earth since the mid Eocene (56 my) which steepened the temperate gradient from equator to pole, creating new niches at temperate and polar latitudes, and the evolution of distinct faunal assemblages e.g. [1,143,144]. The boundaries between these bands are not sharp however, in the southern hemisphere, the temperate-tropical transition gradually occurs between 30-40°S and the temperate polar transition between 50-60°S [145].

Regional evidence suggests that upper to mid bathyal faunas (200-2000 m) are also structured into broad polar, temperate and tropical bands [145]. This may reflect latitudinal variation in temperature (particularly at upper bathyal depths) or other oceanographic variables such as carbon flux [146,147]. However, at mid bathyal depths (~2000 m) the connection between faunal composition and oceanographic gradients is less obvious, although broad polar, temperate and tropical faunal bands persist. O'Hara et al. [145] found that only 6% of ophiuroid species were shared between tropical New Caledonia and temperate southern New Zealand at 1200-2000 m, despite there being only minor differences in environmental variables. The palaeontological record for bathyal faunas are generally too fragmentary to be biogeographically informative [1].

Global abyssal biogeography began with the zoological summary of the HMS Challenger expedition (1872-6). Murray [16] documented the widespread distributions of the abyssal fauna but found few animals were truly cosmopolitan, i.e. there was some biogeographic structure to abyssal faunas. Vinogradova [148] and Menzies et al. [149] produced the first global biogeographic maps of the abyssal fauna based around oceanic basins separated by the newly discovered mid-ocean ridges. However, the biological data were still fragmentary and there were concerns that apparent basin-scale endemism was an artefact of inadequate sampling [150]. However, the emerging consensus was that the abyssal faunas of the Southern, Atlantic, West Pacific and East Pacific Oceans could be distinguished, although with less differentiation than more shallow water faunas. The distinctiveness and relationships of the western Indian Ocean and Arctic faunas were disputed [149,150]. The GOODS classification [151] and a recent update [146] further divided these oceanic faunas based on south-north gradients of the environmental surrogates: temperature, oxygen and phytoplankton production.

The northern boundary of the abyssal Southern Ocean fauna (the polar to temperate/tropical transition) has varied between these analyses. Vinogradova [148] placed it around ~40°S, Menzies et al. [149] at ~10°N, the GOODS classification at the oceanographic Antarctic Convergence (~55°S) and Watling et al. [146] followed the southern Indian and Pacific tectonic ridges, which meander between 30-65°S.

A separate tropical to temperate abyssal transition has been less emphasised, particularly in the southern hemisphere, where the abyssal fauna at temperate latitudes has generally been considered to be continuous with either the Southern Ocean fauna [149] or central Indian/Pacific/Atlantic faunas [146,148,151]. The GOODS classification did distinguish a Central Pacific province (10S to 10°N) based on productivity data, however, this was reduced to a funnel-shaped province in the eastern Pacific by Watling et al. [146] to more accurately reflect areas of enhanced sea surface productivity from equatorial upwelling.

A 2017 voyage of the RV 'Investigator', to survey the deep-sea benthic fauna in newly created marine parks off Australia's eastern continental margin (42-23°S), provided the opportunity to test for the existence of a tropical-temperate faunal transition at lower bathyal (~2500 m) and abyssal (~4000 m) depths. Specifically we investigated whether these lower bathyal or abyssal faunas exhibited latitudinal turnover similar to that found at shallow to mid slope depths (0-2000 m) [145] or whether the faunas are more or less uniformly distributed throughout this study region along the lines predicted by modern maps of abyssal biogeography [146,151]. The question can be reformulated as: how deep does the temperate-tropical faunal transition extend?

Methods

Study area geology and oceanography

The Tasman Sea was formed through the tectonic rifting of Australian and New Zealand continental masses [18]. A rift valley along the eastern Australian margin formed approximately 90 Ma. Separation started south of Tasmania 84 Ma and gradually proceeded northward until spreading stopped approximately 52 Ma. The result was the abyssal triangle-shaped Tasman Basin, flanked on the west by the Australian margin, on the east by the Lord Howe Rise (made up of several conjoined continental fragments) and open to the Southern Ocean in the south [18]. The northern basin apex occurs at 24°S, with the Cato Trough forming a relatively shallow (3400-3500 m) narrow (~10 km wide) channel to the north between the Marion and Chesterfield plateaux [4]. The abyssal Tasman seafloor was generated along a now extinct spreading ridge running south to north [18]. However, the main volcanic feature of the basin is now the offshore Tasmantid chain of seamounts, created by the Australian plate moving over a crustal hotspot from the Oligocene (Kenn, 21°S) to Late Miocene (Taupo, 33°S).

The continental slope along eastern Australia is broadly convex from the shelf break down to 1500 m, then concave until 3000 m, before forming a steep rocky scarp down to the abyssal plain at 4500-5000 m [4]. There is little continental rise present and siltation fans from rivers are small [4]. However, sediment from terrestrial and pelagic sources does accumulate on the upper margin, and can be transported downslope along the numerous submarine canyons [152], via slumping due to slope failure [20] or from particularly productive continental shelves at the northern end of the Tasman Sea [4]. Bottom currents can create large elongate drift mounds on the abyssal plain [4].

Water currents are modified by the topography of the Tasman Basin. Antarctic Bottom Water (ABW) arrives at abyssal depths from the south-west. The enclosed northern end of the Tasman Basin below 3300 m forces the current into clockwise eddies [24] with a net flow south along the Lord Howe Rise [25]. These abyssal eddies cause upwelling near Fraser Island [4], and can modify the course of the eastern Australian current at the surface [24]. The strong northward flow along the Australian margin removes sediment from the lower continental slope leaving a rocky surface, forming shallow (20-50 m deep) moats in the abyssal plain at the base of the margin, and possibly undermining sediment layers further up the slope, causing slumping [4,20]. Moving up the water column, North Atlantic Deep Water (NADW) is present at 2500 m, originating in the North Atlantic Ocean, upwelling into the southern Atlantic, moving east across the Indian Ocean with circumpolar currents, before also entering the Tasman Sea from the south-west [22]. Antarctic Intermediate Water (AAIW) is present around 1000 m which is formed at subantarctic latitudes in the Southern Ocean. However, it enters the Tasman Sea from two directions, one flowing from the south-west and the other from the north and east, the latter having become entrained by the counter-clockwise equatorial gyre in the southern Pacific [22]. Surface currents arrive from north in the form of the East Australian Current (EAC). Most of the surface current turns east from the Australian margin at 32-35°S, although deeper flows and eddies move south as far as Tasmania [23].

The temperature, salinity and oxygen properties of the deeper water masses differ little over the latitudinal range of the study. The CARS2009 dataset [26] indicates that water temperatures rise slowly from 4000 m (1.1°C), through 2500 m (1.9°C) to 1000 m (5.0°C), salinity is very similar at both 4000 and 2500 m (34.72‰), and slightly less at 1000 m (34.47), oxygen levels are slightly higher at 4000 m (4.49 ml/l) compared to 2500 m (4.13) and 1000 m (4.06). There are no hypoxic (O2 <1.7 ml/l) or anoxic (<0.02) oxygen minimum zones within the study region [27].

Net primary production (NPP) is greatest (>700 g C_{org} m^{-2} d^{-1}) at temperate latitudes (48-38°S) across southern Australia Fig. 2; [153]. Offshore from coastal waters, NPP steadily declines with lower latitudes, becoming relatively oligotrophic (300 mg C m^{-2} d^{-1}) north of the Tasman Front (31°S). The

Seasonal Variation Index (SVI), the standard deviation over the mean of NPP, is also elevated at temperate latitudes, particularly south of Tasmania [28]. Phytoplankton communities over the continental margin vary from small to large diatoms typical of the temperate neritic regions to tropical oceanic dinoflagellates off the Queensland coast [154]. Much marine productivity is recycled (consumed) at shallow water depths, and carbon that arrives on the abyssal seafloor is 2-3 orders of magnitude less than is present in surface waters [155]. The slope seafloor is well oxygenated and bioturbation is abundant, although the carbon content of the sediments is less than 1% [4], which is poor by global standards [29]. The composition of the sediments is depth-dependent, with mixed terrestrial siliceous and biogenic carbonate sediments dominating the shelf and upper slope, gradually changing to finer pelagic-derived sediments (mainly coccolith and foraminifera remains) with depth [4]. In the Tasman Sea, the lysocline occurs at ~3,600 m [21], below which carbonate skeletons start to dissolve and the sediments become very fine ooze.

Samples

The study design was to deploy a beam trawl (4 m metal beam) to collect samples on soft sediment substrata at the target seafloor depths of 1000, 2500 and 4000 m at every 1.5 degrees of latitude along the western boundary of the Tasman Sea from 42° to 23°S, traversing seven Australian Marine Parks (AMPs) (Fig. 2). Each site was mapped (bathymetry and backscatter) prior to deployment using a Kongsberg EM 122 12kHz multibeam sonar. Environmental data (temperature, salinity, pressure) were collected by a Sea-Bird SBE37SM sensor. Backscatter data were processed for geometric and radiometric corrections using QPS FMGT software with Angle Varying Gain correction, using a window size of 300 pings, and removal of 25% around the nadir (when possible) to improve the central swath regions. The resulting mosaic values (in decibels re 1.0 µPa) provide a relative measure of the intensity of sound returning from the seafloor which can be used to infer characteristics of the substratum. Values are generally are less negative with increasing substratum hardness. The mosaic values along the trawl transect at 50m resolution were extracted using the ‘Profiles from Lines’ procedure in QGIS software [156].

Beam trawl samples were sorted, weighed and preserved (95% ethanol) on-board into broad taxonomic groups, and sent to taxonomic experts for identification. The following groups of megafauna were subsequently identified to operational taxonomic units (mostly to species, some to genus or family), counted and used as the basis of subsequent statistical analyses: sponges, anemones, octocorals, barnacles, decapods, pycnogonids, annelids, echinoderms, cephalopods, gastropods, bivalves, and fish (see acknowledgements).

Statistical analyses

Exploratory analyses of the data were performed using non-metric multivariate statistics [157]. Species were restricted to those that occurred in at least 2 samples. The species-site abundance data was log(x+1) transformed to down-weight the influence of abundant taxa. A triangular dissimilarity matrix was created using the Bary-Curtis coefficient with the function vegdist(method="bray") function in the ‘vegan’ v2.4.5 package [158]. Hierarchical clustering of sites was performed using hclust() in the stats package ‘cluster’ v2.0.6 [159] and non-metric multidimensional scaling (nMDS) ordination by metaMDS() also in the ‘vegan’ package. The SIMPER method of identifying species that discriminate between groups (available in 'vegan') was not used, as this method does not discriminate species well if there is high variance in within-group abundances [160].

We used a model-based approach for the analysis of community data as this allowed for the direct specification of a statistical model, which correctly describes mean-variance relationships and allows for an estimate of uncertainty in the resulting predictions [161]. We used Species Archetype models (SAMs, SpeciesMix R package v0.3.4) [162,163] to determine whether distinct species-groups existed at tropical and temperate latitudes across the study depth range. This method groups species into 'archetypes' based on the species' shared responses to environmental or geographic (covariates in the model) data. For our study, we fitted a series of negative binomial models which contained an independent intercept for each species [163]. This enables us to correctly model the error distribution of count data derived from the beam trawl catches while also maintaining the species specific density of across all sites. This reduced artefacts in the grouping of 'rare' and/or 'common' species into archetypes based on their prevalence, rather than their response to the model covariates. Crucially for our study, the optimal number of distinct archetypes can be determined based on the model likelihood using the Bayesian Information Criterion (BIC). The fitted Generalised Linear Model (GLM) associated with each archetype can then be used to predict its prevalence and abundance across a landscape. A hard classification of archetypes can be generated by assigning the archetype with the highest predictive value to each pixel.

For the SAMs analysis, we restricted species to those that occurred in 4 or more samples, and explored the potential utility of a range of environmental variables: temperature, salinity, depth and latitude (derived from sample means), annual mean oxygen (ml l^{-1}, from CARS2009), and mean annual net primary productivity (NPP, g C m−2 year−1), seasonal variation of net primary productivity (SVI, g C m−2 year−1; SVI) and carbon flux to the seafloor (POC flux, g C m−2 year−1). NPP and SVI were generated from a vertically generalized production model (VGPM) [164] from satellite-derived chlorophyll (SeaWiFS) data from the years 2003 to 2010 (see http://www.science.oregonstate.edu/ocean.productivity/). POC flux was estimated using NPP and SVI data and a productivity export model [28]. Longitude was considered unimportant in the context of our study region. Many of these variables were highly correlated in our data and the combination of latitude and depth resulted in the lowest BIC for a fixed number of archetypes. We used 2nd degree orthogonal polynomials of the explanatory variables and the interactions between these variables. The area sampled (log transformed) was included as an offset. This had two benefits, accounting for unequal sampling at each site and preserving the data as counts. We used six random initialisations of an Expectation-Maximisation (EM) algorithm (encoded in the SpeciesMix package) to find good starting values for each SAM. Once the best starting values are estimated these values are maximised using Newton-Raphson optimisation of the model log-likelihood [163]. We used model likelihood to describe BIC, which determined the optimum number of archetype groupings (ranging from 2 to 10). Explanatory variables for predictions were transformed via a linear fit to the orthogonal polynomials from the selected SAMs model and the mean of sample-area was used as the offset. Archetype responses to environmental variables were generated by setting non-focal variables to their mean values before transformation [163]. The probability of species belonging to a given archetype was determined from posterior archetype membership (tau) enabling us to understand which species are predicted to belong to each group once they have been estimated [162]. The mixed effects anova.lme()

function from the R library 'nlme' [165] was used to test the relationship between the corrected backscatter results and the mostly likely archetype present at the sample location, with archetype as a fixed factor and sample as a random factor.

Results

The multibeam sonar revealed a continental slope topography that was much more complex and rugged than expected, with the margin incised by numerous canyons, sediment slumps, cliffs and other areas of exposed rock (Fig. 3). Consequently, the location, depth and swept area of each sample varied considerably from the original target due to the need to find relatively flat areas of mostly soft sediment (Table 1). In addition, a number of 1000 m beam trawls at the southern end of the transect were abandoned due to operational difficulties, however we retained the remaining southern 1000 m site (013) as it was informative, particularly in the multivariate analysis (in the model based analysis it appears to be species poor due to the restriction of species to those that occurred in 4 or more samples). Our sampled environmental data was highly correlated (Pearson R=0.993, p<0.001) with modelled oceanographic data of the global CARS2009 dataset. Median backscatter data did not correlate (Pearson, p>0.05) with latitude at any of our target depths, however, several samples (032, 053, 065, 088) from mid-latitudes at ~4000 m did have notably harder substrata and raised relief along the trawl transect.

After adjustment for trawled area, total specimen weight and density varied substantially between samples (Table 1). The highest biomass occurred at 2785 m in the Freycinet AMP (sample 004), which was dominated by a large number of holothurians (*Benthodytes* sp, *Molpadiodemas* sp and *Pseudostichopus peripatus*). Sample 022, from a similar depth but softer substrata, was also characterised by high biomass (of holothurians) and also high density (ophiuroids). Sample 080 from 1225 m included a decaying manta ray with associated scavengers and predators. Sample 100 included a dead pilot whale skull and vertebrae which hosted *Idas* bivalves and *Osedax* worms (not previously reported from Australia). These specialist animals occurred at only one site and thus were not in included in our analyses. All samples from around 4000 m were characterised by relatively low biomass and abundance.

The number of identified taxa was 881, with 432 occurring in 2 or more samples, and 184 in 4 or more samples. The most widespread species, from 19 samples, was an undescribed ampharetid polychaete (sp. C). The MDS ordination was geographically interpretable when overlayed by 6 groups defined from the hierarchical cluster analysis (Fig. 4), which essentially divided the samples into temperate (southern) and tropical (northern) groups across each of the targeted depth strata (groups herein designated as S1000, N1000, S2500, N2500, S4000 and N4000). Within group patterns did not necessarily reflect latitude, although neighbouring samples frequently clustered together. Our failure to obtain all of our targeted southern samples at 1000 m precluded establishing the temperate-tropical transition at this depth for this data, although the sample from Hunter AMP (069, 32.5°S) was closely associated with the N1000 group. At ~2500 m, two samples, off Newcastle (067, 33°S) and Hunter AMP (070) were intermediate between S2500 and N2500 clusters on the MDS plot, although they were included in the temperate group on the cluster dendrogram. At 4000 m, the Hunter sample clustered with the S4000 group, which was distinctly separated from N4000 samples.

Thus the data is consistent with a temperate-tropical transition between 33 and 30°S down to abyssal depths (>3500 m).

In the Species Archetype Model analysis, the model fitted to quadratic transformations of latitude and depth with interactions resulted in the lowest BIC for any combination of environmental parameters (Table S9). When we fixed these environmental covariates as the 'best' model, we identified the optimal number of groups as five (Fig. 5a). If we selected more than five archetype groups, at least one of these extra groups had relatively few species or the predicted density was very low, which suggested an overfitting of the data. The predicted distribution of the five archetypes were again interpretable in terms of latitude and depth (Fig. 5b-e). A single archetype was predicted to occur at relatively high densities at 1000 m across the entire study area (Fig. 5d), although the highest values occurred at northern latitudes (N1000, Fig. 5e). The failure to predict an S1000 group is not surprising given there was only one sample and the analysis was restricted to species that occurred in 4 or more samples. Separate temperate and tropical archetypes were predicted to occur at both 2500 and 4000 m with the transition occurring between 35 and 34°S at 2500 m and slightly to the north (34-33°S) at 4000 m, although the predictions for each archetype (Fig. 5e) indicate that compositional turnover is likely to be gradual between 35 and 30°S. Standard errors (Fig. S10) were greatest for each archetype around the areas with highest predicted densities, indicating high variation in species abundances between samples. The null hypotheses that backscatter results did not differ between archetypes at target depths of 2500 and 4000 m could not be rejected ($p>0.05$) using a mixed effects (nested) ANOVA.

Of the 184 taxa in the SAMs analysis were assigned to the five archetypes as follows: N1000 (15%), S2500 (30%), N2500 (19%), S4000 (28%), and N4000 (9%), i.e. at 2500 m, three times the number of taxa were assigned to the southern than northern groups, and at 4000 m, 1.5 times as many. However, these southern/northern archetypes were compositionally distinct and did not merely reflect differences in species richness. Only 25% of species were predicted to occur in more than one archetype with tau values of > 0.05, including only 2 out of the 16 species (12%) in the N4000 archetype. Nor was this an artefact of the limited sampling. Examination of the known distribution of the N4000 species indicated that half these species were generally longitudinally widespread but restricted to tropical latitudes (< 35°). For example, the Faceless Cusk Fish (*Typhlonus nasus*, Fig. 3d) occurs at abyssal depths throughout the tropical Pacific and Indian Oceans.

Discussion

We found clear evidence for a temperate-tropical turnover of benthic species along the Australian continental margin at lower bathyal to abyssal (LBA) depths (>2000 m). The groups of temperate and tropical species were drawn from across the faunal taxonomic spectrum from fish to sponges. The transition was roughly congruent between our targeted depth layers despite the large turnover of species that also occurs with depth. Although, we did not have enough data to conclusively distinguish a temperate and tropical fauna at 1000 m, earlier spatial analyses of upper (200-2000 m) continental slope data from this region have found distinct faunas in these biomes for ophiuroids [145], squat lobsters [166] and demersal fish [167].

LBA regional species richness is known to be elevated at temperate latitudes in at least one dominant group: ophiuroids [147]. However, the groups identified here were not an artefact of differing species richness, one species group being a subset of the other. Our transitions represented assemblage compositional changes across latitude and depth.

Cluster and model-based analyses placed the latitudinal transition at slightly different latitudes, 33-30°S and 35-33°S respectively. The fine-resolution (0.04 degree) analysis of O'Hara et al. [145] put the boundary of the 200-2000 m ophiuroid fauna just north of 30°S. However, this apparent sharp boundary was an artefact of the clustering algorithm and O'Hara et al. [145] found that mapping species range limits showed a more gradual turnover in the upper bathyal fauna between 40 and 30°S. The individual archetype predictions in Fig. 5e showed a similar pattern for these data; there was considerable overlap around the transition boundary, particularly at 2500 m. Nevertheless, patterns of beta-diversity (or distance-decay relationship) were not uniform along latitudinal gradients, with alternating latitudinal bands and transition zones [145].

Our temperate-tropical transition was broadly congruent with that found by Vinogradova [148], who separated Indo-Pacific and Southern Ocean abyssal faunas at around 40°S. However, pre-1960 sampling around this latitude was sparse and thus her placement of the boundary was approximate. Conversely, our data does not support the abyssal biogeographic schemes of Menzies et al. [149] and Watling et al. [146], who both recognised a very broad 'Austro-Indian Antarctic' area based on temperature and topology, which extended from the Antarctic ridge (~60°S) to the northern apex of the Tasman Sea (23°S). Thus our results were more consistent with previous biogeographies produced from quantitative analyses of biological samples (Vinogradova) rather than environmental factors (Menzies, Watling). These different biogeographies arise because there is a horizontal temperate-tropical transition at 2500-4000 m depths that is not associated with a corresponding change in water temperature, salinity or oxygen (Table 1, SI). The major role of temperature in defining marine species range limits hypothesised to occur in shallow water [168] does not appear to hold for the tropical-temperate benthic LBA fauna.

The transition does not seem to be related to geology either. Maps of geomorphic units (e.g. knoll, terrace, slope, rise, plateau) do show considerable diversity along the Australian eastern margin [152], however, it is unclear whether these units have any direct influence on seafloor faunal composition, apart from altering bottom water flows and the relative abundance of exposed rock and soft sediment habitats [169]. A regional change in substratum composition can generate biogeographic discontinuities e.g. [170]. However, both rocky and soft sediment substrata occurred throughout our study region and do not account for the temperate-tropical LBA transition. Local topography and seafloor characteristics show greater importance at finer scales, while oceanographic properties have greater explanatory power for larger-scale patterns, at least on the continental shelf and slope [171], consistent with the proposed hierarchical structuring of Australian biogeography more generally [167].

One oceanographic variable that does form a latitudinal gradient at the seafloor is particulate organic carbon flux (Table 1), which is dependent on net primary production in surface waters and depth (Fig. 2) [28]. Primary production is both greater and more seasonal near Tasmania and Bass Strait, driven by upwelling of nutrients in spring and to a lesser extent autumn. Seasonal pulses of production increase carbon flux to the seafloor [28] with nutritious sinking aggregates ('marine snow') often visible on the seafloor [172]. Larger zooplankton such as salps can swarm in productive conditions, further enhancing carbon flux to the seafloor through the sinking of faeces and carcasses [8]. Offshore waters north of 30°S are more oligotrophic and less seasonal, in line with much of the tropical ocean away from the continental shelves. Moreover, increased water temperatures are known also to reduce mixing of surface and deeper waters further decreasing export to the seafloor [173]. It is not just the quantity of organic matter that differs. The species of mega-fauna (e.g. whales and sharks/rays) that fall as carcases to the seafloor, important to deep-sea trophic systems [172], will also differ between tropical and temperate latitudes[2]. There are different plankton communities in temperate (large diatoms) and tropical (dinoflagellates) regions [154] that may require specialised physiologies or bacterial intermediates (e.g. symbionts) to exploit. There has been a shift to diatom-based food webs around Antarctica over the last 15 my in response to cooling events [143]. There is evidence that variation in carbon flux to the seafloor can drive differences in both species richness and composition at local scales [174,175] and species richness at regional scales [147]. Various authors have speculated about the biogeographic implications of carbon flux variability on abyssal faunal composition [146] but we are unaware of any studies that have quantified this relationship at large spatial scales.

Extant Biogeographical patterns are also influenced by the history of the biota. The composition and diversity of regional faunas are determined by speciation, extinction and migration over evolutionary timescales [176]. However, the biogeographic boundaries seen today need to be maintained by ecological or neutral processes that prevent homogenisation of regional faunas. These processes can include environmental thresholds, biotic interactions or dispersal limitations [177]. The interaction of water currents and topology can create biogeographic boundaries by creating long-term barriers to dispersal, i.e. species are prevented from dispersing from their ancestral range to all their potential habitat. In the Tasman Basin, water circulates in two patterns. From the surface down to 1000 m (East Australian Current and Antarctic Intermediate Water), currents flow from north to south as part of the Southern Pacific gyre. In deeper waters, however, water inflow is from the south-east, pushed along by circumpolar currents in the Southern Ocean. At 4000 m, the Tasman Basin is enclosed at the northern end (Fig. 2). Consequently, bottom water forms a cyclonic system that flows north along the Australian margin, before forming eddies and turning south along the Lord Howe Rise [24]. A considerable amount of the flow does not penetrate the northern constricted part of the basin thus potentially limiting the northern extension of the temperate bottom fauna. However, this does not explain the presence of tropical abyssal species in the northern section of the basin. Most of these species are eurybathyal to some extent, thus it is not improbable that propagules (or adults for pelagic species) can disperse through the northern Cato Trough (min depth ~3100 m), or even across deeper sections of the northern Lord Howe Rise, forming a continuous fauna with abyssal basins to the north and east (Fig. 6).

However, this discussion is predicated on the assumption that propagules disperse more or less horizontally. However, there are examples of larvae of some benthic invertebrates ascending to water depths that could be affected by a latitudinal gradient in temperature. Planktotrophic larvae of

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[2] www.aquamaps.org, last accessed 31/12/2018.

deep-sea species have been recorded from surface waters [172], where they presumably feed on available phytoplankton. Lecithotrophy is a more common life developmental strategy for LBA animals and some positively-buoyant yolky propagules have been found to migrate vertically [172]. Metamorphosed juveniles of several elasipod holothurians in the NE Atlantic Ocean have been found kilometres off the seafloor [172].

Unravelling the underlying causes of the LBA temperate-tropical transition will require additional descriptive and experimental studies. It would seem profitable to focus on the processes that link LBA communities to the strong latitudinal environmental gradients that occur in shallower waters. The heterotrophic LBA deep sea is heavily dependent on quantity and quality of organic inputs from the surface waters including carcass falls. The upper water column is the medium through which, at least some, species disperse and recruit. Finally, biotic interactions with regionally specific pelagic faunas (e.g. via predation from tropical species) could also influence community composition.

The implication for management is that biodiversity at lower bathyal and abyssal depths is not uniform. Marine parks designs need to incorporate major biogeographic transitions such as the one shown in this study. Fortunately, Australia's newly declared marine park system (see https://parksaustralia.gov.au/marine/) includes seven reserves spaced along the eastern continental margin, although they are grouped into three networks (SE Australia, Temperate Eastern Australia and the Coral Sea) that do not reflect the distribution of the deep-sea fauna faunas identified here.

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Stn	location	Lati-tude	Longitude	Mid depth (m)	Date (d/m/y)	Biomass (g)	Abundance	Area sampled (m^2)	Adj. biomass (g)	Adj. abund.	Temp. (°C)	Salinity (‰)	POC (g $m^{-2}y^{-1}$)	Site cluster	Archetype
004	Freycinet MP	-41.731	149.120	2785	18/5/17	72138	2027	29584	2438	69	1.7537	34.7291	1.998	S2500	S2500
006	Freycinet MP	-41.626	149.552	4037	18/5/17	538	238	30344	18	8	1.0775	34.7074	1.260	S4000	S4000
013	Flinders MP	-40.386	148.928	1041	20/5/17	403	84	7908	51	11	4.4411	34.4686	6.166	S1000	1000
014	Flinders MP	-40.464	149.102	2392	20/5/17	8115	189	15348	529	12	1.9578	34.7166	2.352	S2500	S2500
015	Flinders MP	-40.473	149.397	4126	20/5/17	1306	593	10572	124	56	1.1405	34.7036	1.198	S4000	S4000
022	Bass Strait	-39.462	149.276	2726	22/5/17	15958	2478	11756	1357	211	1.7794	34.7213	2.049	S2500	S2500
030	Bass Strait	-39.552	149.553	4165	23/5/17	896	402	29312	31	14	1.0396	34.6974	1.181	S4000	S4000
032	East Gippsland MP	-38.479	150.184	3851	24/5/17	2235	468	11580	193	40	1.1299	34.7040	1.290	S4000	S4000
035	East Gippsland MP	-37.792	150.382	2459	25/5/17	7503	698	15352	489	45	1.8944	34.7072	2.264	S2500	S2500
043	Bermagui	-36.351	150.914	4800	27/5/17	608	328	14824	41	22	1.1793	34.7013	0.959	S4000	S4000
044	Bermagui	-36.355	150.644	2754	27/5/17	7486	1190	17972	417	66	1.7226	34.6805	1.726	S2500	S2500
053	Jervis MP	-35.114	151.469	3981	28/5/17	1650	140	16792	98	8	1.2244	34.7038	1.045	S4000	S4000
056	Jervis MP	-35.333	151.258	2643	29/5/17	9466	3523	15976	593	221	1.7508	34.7118	1.657	S2500	S2500
065	Newcastle	-33.441	152.702	4226	30/5/17	817	461	13992	58	33	1.1952	34.7011	0.847	S4000	S4000
067	Newcastle	-32.985	152.952	2803	31/5/17	6486	290	19748	328	15	1.8818	34.7039	1.274	S2500	N2500
069	Hunter MP	-32.479	152.994	1021	3/6/17	6478	1900	12508	518	152	5.4223	34.4436	5.352	N1000	1000
070	Hunter MP	-32.575	153.162	2534	3/6/17	8433	715	26260	321	27	1.9117	34.7039	1.405	S2500	N2500
078	Hunter MP	-32.138	153.527	4004	4/6/17	438	79	19608	22	4	1.1873	34.6993	0.793	S4000	N4000
080	Central Eastern MP	-30.099	153.596	1225	5/6/17	16053	1236	16096	997	77	4.2400	34.4640	3.471	N1000	1000
086	Central Eastern MP	-30.098	153.899	2473	5/6/17	2379	373	13384	178	28	2.0119	34.6929	1.193	N2500	N2500
088	Central Eastern MP	-30.264	153.870	4441	6/6/17	1055	377	18328	58	21	1.1856	34.6954	0.687	N4000	N4000
090	Byron Bay	-28.677	154.203	2574	7/6/17	4024	412	15400	261	27	1.8375	34.6998	0.981	N2500	N2500
097	Byron Bay	-28.355	154.636	3782	8/6/17	1635	279	27508	59	10	1.1552	34.6980	0.646	N4000	N4000
099	Byron Bay	-28.371	154.649	3789	9/6/17	1448	646	14416	100	45	1.1550	34.6979	0.646	N4000	N4000
100	Byron Bay	-28.054	154.083	1006	9/6/17	27174	1497	18968	1433	79	5.0321	34.4412	2.369	N1000	1000
101	Moreton Bay	-26.946	153.945	2548	9/6/17	262	216	11564	23	19	1.9569	34.6972	1.017	N2500	N2500
102	Moreton Bay	-27.008	154.223	4269	10/6/17	1049	220	18332	57	12	1.1909	34.6976	0.575	N4000	N4000
104	Moreton Bay	-26.961	153.848	1104	10/6/17	3438	603	13352	257	45	4.4712	34.4483	2.411	N1000	1000
109	Fraser Island	-25.221	154.164	4005	11/6/17	1744	104	18156	96	6	1.1585	34.6972	0.542	N4000	N4000
115	Fraser Island	-25.325	154.068	2346	11/6/17	2213	1274	11976	185	106	2.1208	34.6780	0.905	N2500	N2500
121	Coral Sea MP	-23.587	154.194	1053	13/6/17	5809	763	13352	435	57	4.5996	34.4645	1.674	N1000	1000
122	Coral Sea MP	-23.751	154.639	2349	13/6/17	794	289	13548	59	21	2.0107	34.6884	0.816	N2500	N2500
128	Coral Sea MP	-23.631	154.660	1765	13/6/17	4740	1911	13964	339	137	2.5708	34.6170	1.086	N2500	N2500
135	Coral Sea MP	-24.352	154.291	4001	15/6/17	51	28	19812	3	1	1.1436	34.6996	0.517	N4000	N4000

Table 1. Sample location and environmental data, predicted clusters and archetypes.

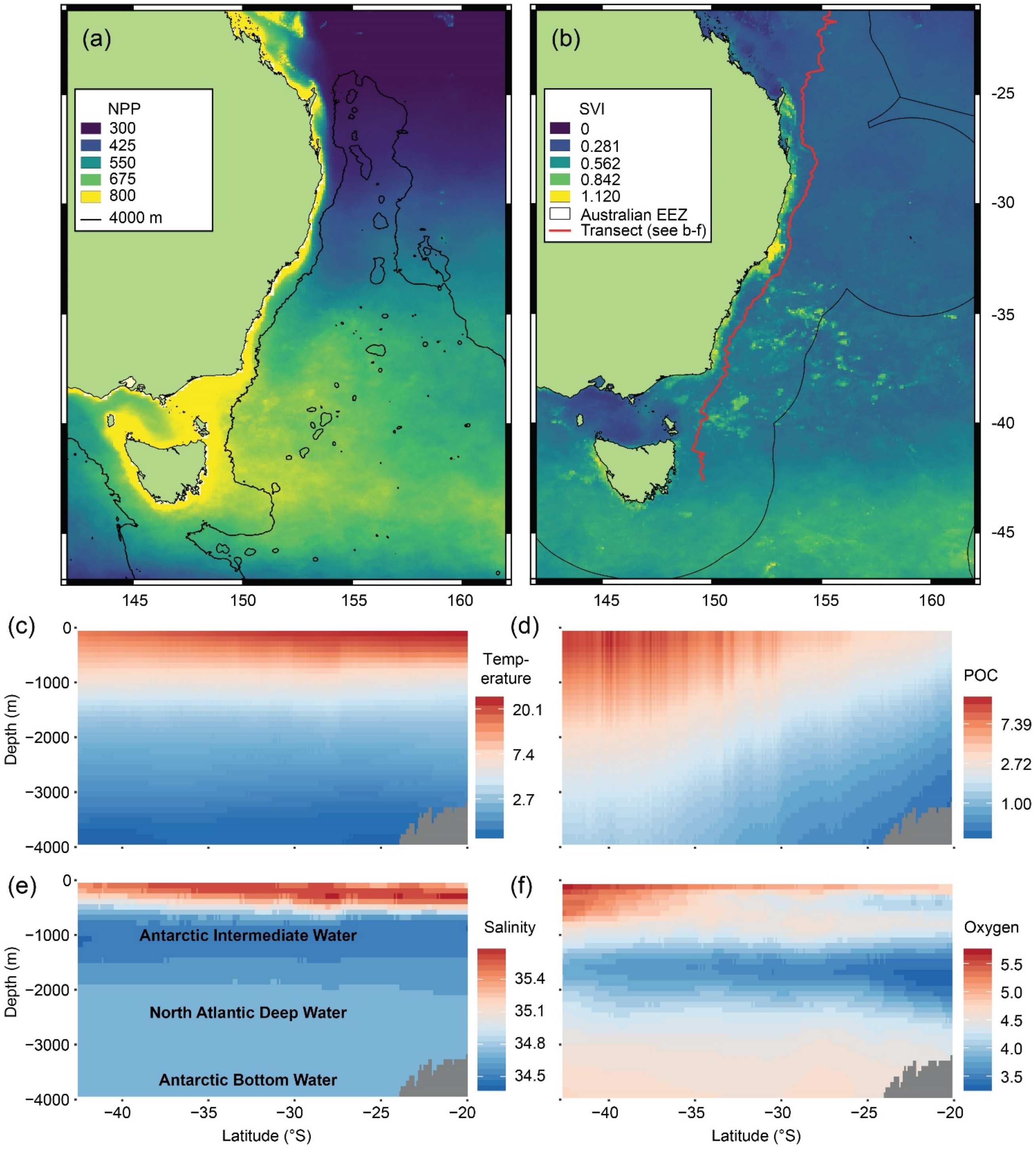

Fig. 1. (a) Net Primary Production (NPP; g C_{org} m^{-2} yr^{-1}) derived from a vertically generalized production model (VGPM) from satellite-derived chlorophyll (see methods). (b) Seasonal Variation Index of NPP (SVI). (c) Sea temperature (°C) interpolated from the CARS2009 dataset. (d) Particulate organic matter flux to depth (POC; g C_{org} m^{-2} yr^{-1}) calculated using the regression equation of Lutz et al. [28]. (e) Salinity (‰) and (f) Oxygen concentration (ml/l) interpolated from the CARS2009 dataset. The transect used to generate the depth-latitude plots (c-f), indicated in red on (b), follows the 4000 m contour north until ~24S after which it enters the Cato Trough (indicated in grey on the lower right corner of c-f). The colour schemes in (c-d) are set to a log scale to emphasise latitudinal variation.

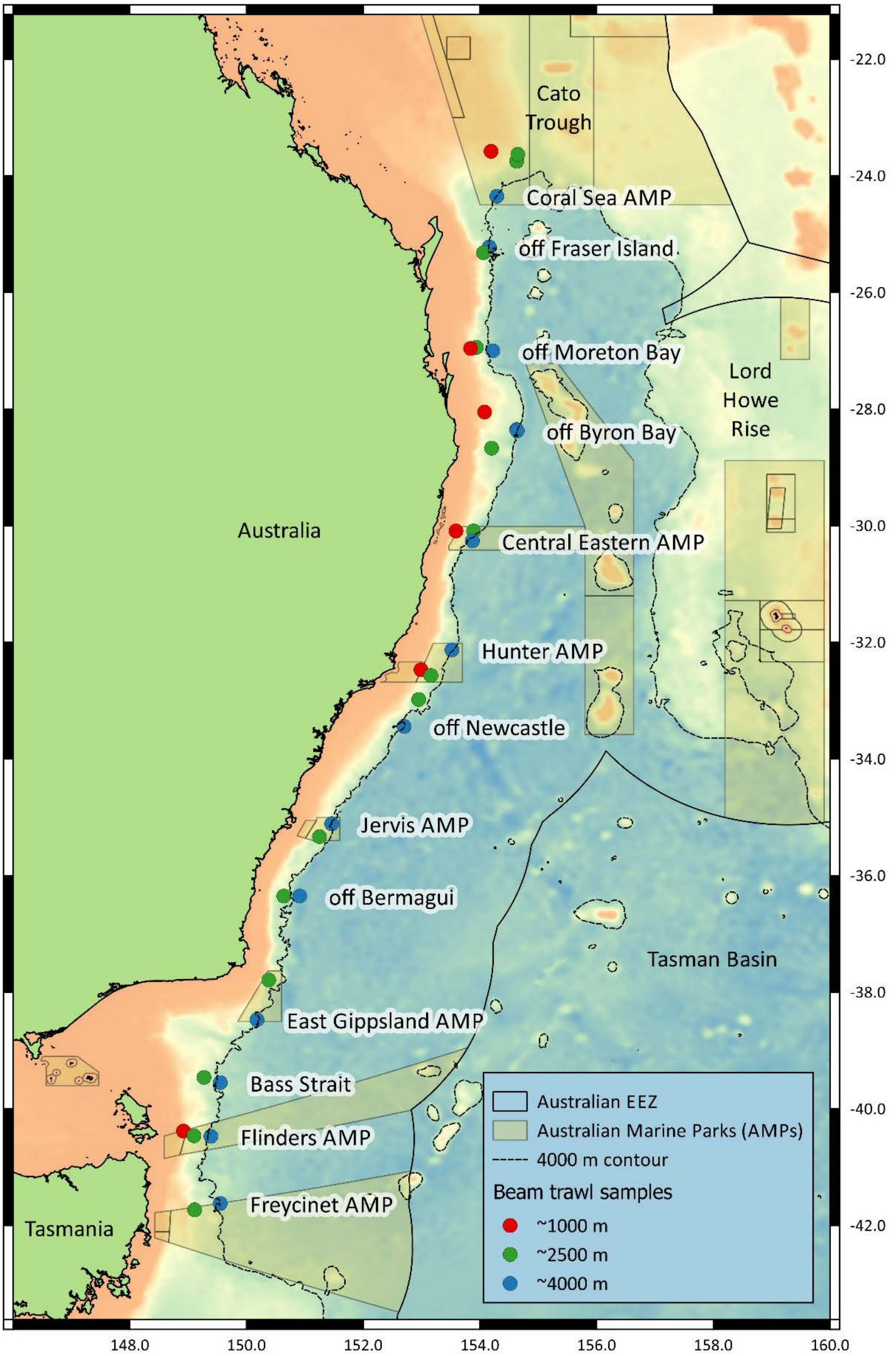

Fig. 2. Map of the eastern Australian continental margin showing sample sites. Note the lateral constriction of the Tasman Basin, at 4000 m water depth, north of Newcastle.

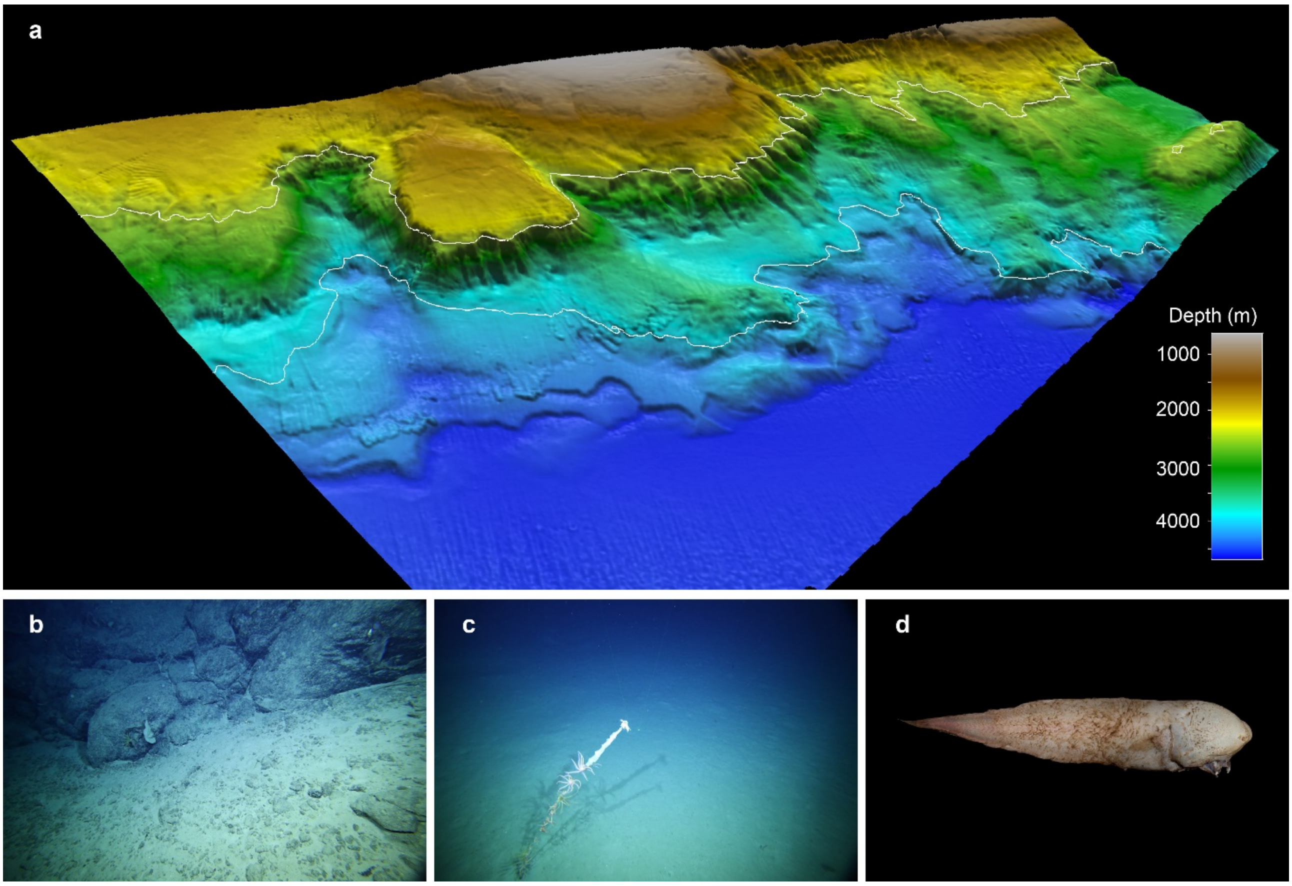

Fig. 3. (a) 3D bathymetric image of East Gippsland AMP (see Fig. 2), showing the difficulty of finding suitable sampling sites along the rugged 2500 and 4000 m depth contours (white lines). The IN2017_V03 voyage mapped this park at high resolution for the first time. (b) Image of a rocky outcrop at ~1800 m from the Hunter AMP. (c) Sea-whip covered in crinoids at ~1900 m on a sediment plain in the Central Eastern AMP. (d) The Faceless Cusk Fish (*Typhlonus nasus*) from beam trawl 053 off Jervis Bay (photo: Rob Zugaro, MV).

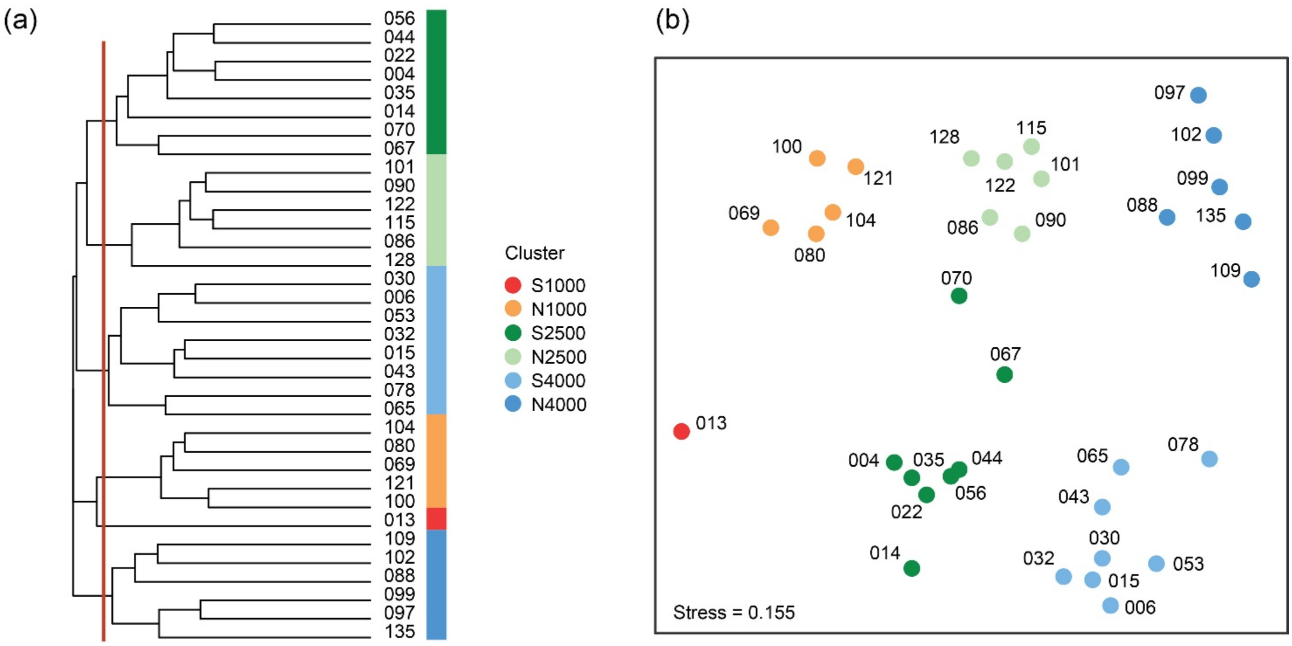

Fig. 4. Non-metric hierarchical clustering and ordination (nMDS) of sample data showing the samples clustered into 6 groups, based on southern temperate (S) and northern tropical (N) locations and target sample depths (1000, 2500 and 4000 m).

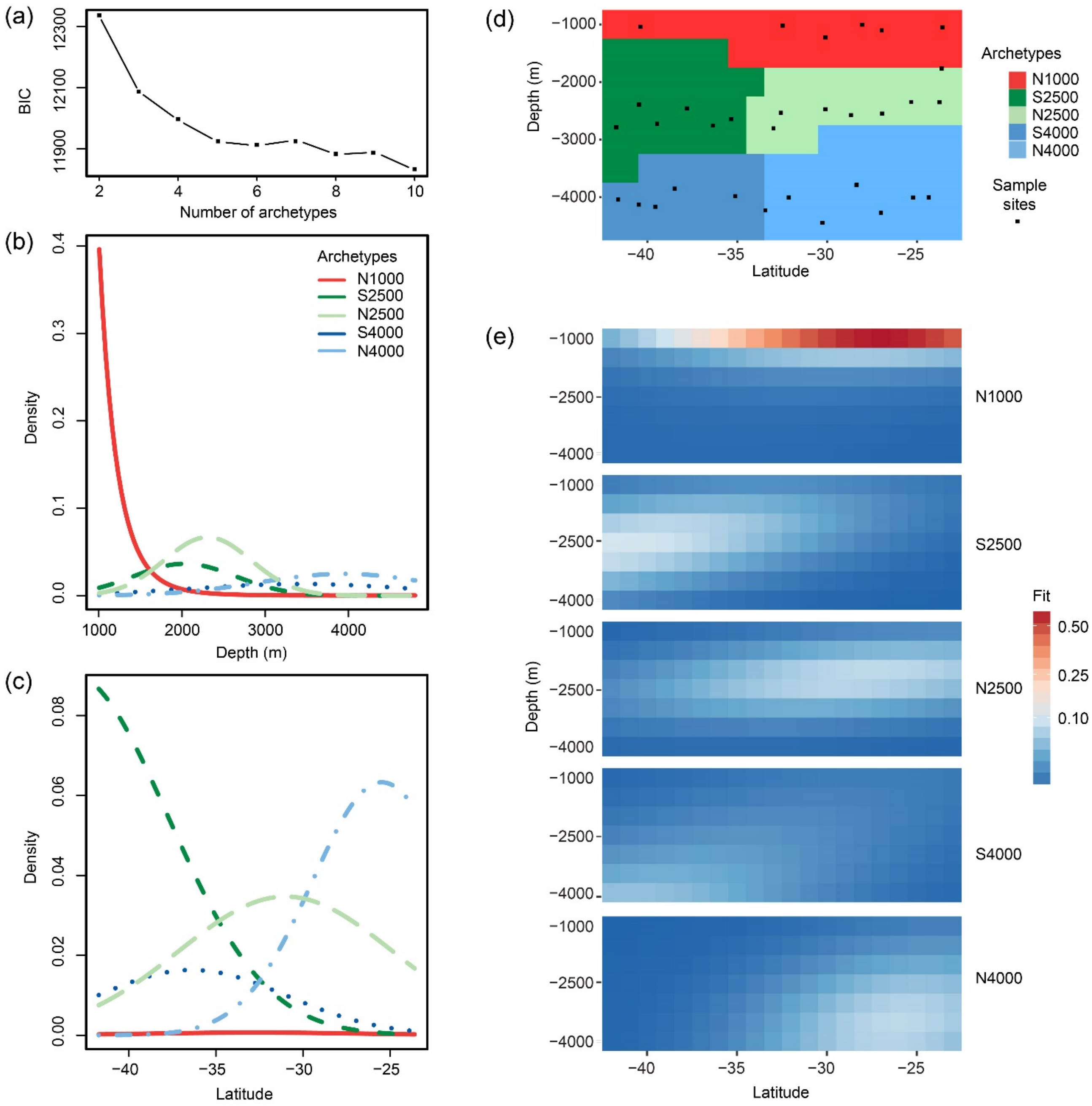

Fig. 5. SpeciesMix model-based analysis to delimit species archetypes. (a) BIC results level off after five clusters which correspond to the N1000, S2500, N2500, S4000 and N4000 groups identified in Fig. 3. (b-c) Responses of the environmental factors, sample depth and latitude, to each archetype. (d) Archetypes with the greatest predicted density (tau) mapped across depth and latitude (500 m x 1° cells). (e) Archetype specific predictions showing the overlap between southern (S) and northern (N) groups at each depth range.

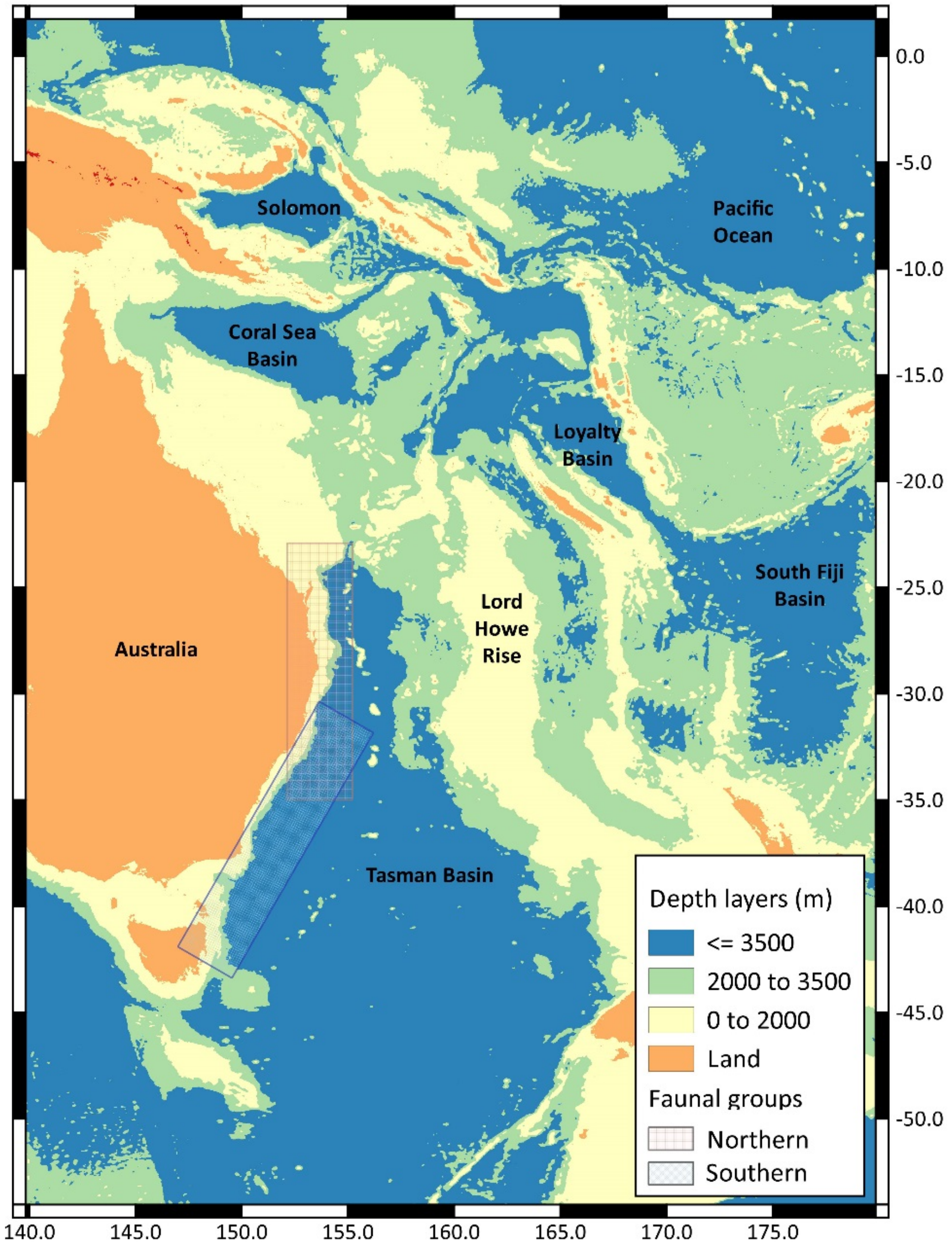

Fig. 6. Map of abyssal basins in the south-west Pacific Ocean, showing the location of northern and southern faunal groups observed in this study.

Chapter 4: Patterns of austral deep-sea benthic assemblages driven by surface productivity

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Introduction

Although deep seafloors cover over half the planet (Ramirez-Llodra *et al.*, 2010), few studies have examined patterns of biodiversity for the deep sea over large spatial scales. This is an important knowledge gap as anthropogenic activities are increasingly targeting deep-sea habitats (Glover & Smith, 2003; Ramirez-Llodra *et al.*, 2011), where inadequate data limit effective Environmental Impact Assessment (Clark *et al.*, 2019). There are plans to mine the deep sea for polymetallic nodules on oceanic abyssal plains, cobalt-rich ferromanganese crusts on seamounts and polymetallic sulphide deposits on volcanically active continental margins and mid-ocean ridges (Miller *et al.*, 2018). Deep-sea sedimentary basins on continental margins are also of interest to the oil and gas industry (Zou *et al.*, 2015), while renewable energy and aquaculture increasingly look to offshore areas to dilute environmental and social concern.

Extractive lease or license areas can be continuous over large areas as they cluster around known resources. For example, exploration areas for polymetallic nodules in the abyssal plains of the Clarion-Clipperton Zone in the NE Pacific cover millions of square kilometres and petroleum protraction areas cover the entire Exclusive Economic Zone of the USA in the Gulf of Mexico. Yet, adequate environmental baselines have been lacking for many of these areas, particularly in deeper water (Cordes *et al.*, 2016; Kaiser *et al.*, 2017). We frequently lack an understanding of how biodiversity is structured at regional scales, such as how much biodiversity could be lost due to catastrophic or accumulated impacts. Our understanding of deep sea biogeography has been 'characterised more by inference than data' with the deep sea fauna having been characterised as both relatively uniform over oceanic scales and characterised by high species turnover at smaller scales (McClain & Hardy, 2010). The paucity in biological data has often led to the use of untested physical surrogates for biogeographical mapping (UNESCO, 2009; Williams *et al.*, 2009; Wedding *et al.*, 2013).

The Great Australian Bight (GAB) has been recognised as one of the world's most prospective, under-explored oil and gas provinces (Begg, 2018). Lying in the centre of the long southern Australian continental margin, this sedimentary basin was predominantly formed by two progradational river deltas in the Late Cretaceous after Australia rifted away from Antarctica (Krassay & Totterdell, 2003).

Oil and gas lease blocks now cover large parts of the basin along the continental slope (Williams *et al.*, 2018).

The GAB has recognised conservation values including a newly proclaimed Australian marine park (Williams *et al.*, 2018). The 'Benthic invertebrate communities of the eastern Great Australian Bight' also have been designated a Key Ecological Feature (KEF). Although KEFs are not listed as matters of national environmental significance under the Australia's Environmental Protection and Biodiversity Conservation Act 1999, they are listed as conservation values in Australia's Marine Bioregional Plans (https://www.environment.gov.au/marine/marine-bioregional-plans), and so are considered as important components of the marine environment, and are frequently referred to in Environment Assessments and Strategic Assessments. The GAB Invertebrate Communities KEF designation was based primarily on a study by Ward *et al.* (2006), who reported relatively high species richness of epibenthic megafauna on the continental shelf of the GAB (0-200 m) which they attributed to the unusual carbonate sediments and overlapping SW and SE Australian faunas. Currie and Sorokin (2014) also suggested that samples of megabenthos from two slope canyons (100-2000 m) may have elevated richness. Uncertainty about the biodiversity of the bathyal (off-shelf) benthic communities resulted in the spatial and bathymetric boundaries of this KEF being left undefined, yet left the impression that developments in the GAB would need to account for threats to a highly endemic fauna.

Few studies have examined patterns of benthic faunal composition in the GAB from seafloors deeper than the continental shelf or upper slope. The exception is Williams *et al.* (2018) who analysed diversity and abundance in epibenthic megafaunal samples from five transects (200-3000 m) across the GAB. However, this study lacked comparable samples from outside the area and could not draw conclusions about comparative richness or abundance. Tanner *et al.* (2018) confirmed that taxa found along these transects were typical of museum collections of epibenthic megafauna from the same region and that their affinities were with other regions along the southern coast compared to those off the eastern coast at similar depths, although the museum samples were largely derived from upper bathyal habitats (200-1000 m).

Over a three year period (2015-2017), a number of voyages of the RV 'Investigator' collected comparative beam trawl samples from lower bathyal (1900-3500 m) and abyssal (3500-5000 m) depths from both the GAB (IN2015_C01, IN2015_C02, IN2017_C01) and off eastern Australia (IN2017_V03) (Fig. 1). This provided the opportunity to assess whether 1) the deep sea benthic diversity of the GAB differed from that of comparable habitats off the east coast, and/or 2) whether the assemblages differed in composition at these spatial scales. In particular, we assessed comparative abundance, richness and evenness using a recently developed community modelling method that models and predicts Rank Abundance Distributions (RADs) from environmental covariates (Foster & Dunstan, 2010; Dunstan & Foster, 2011; Dunstan *et al.*, 2012a; Dunstan *et al.*, 2012b). These covariates included oceanographic variables such as seafloor water temperature, salinity and dissolved oxygen, carbon flux to the seafloor, mean annual and seasonal variation of Net Primary Productivity at the sea surface, as well as geographic variables latitude, longitude and depth.

Methods

Samples

All samples were collected using an identical 4 m wide beam trawl with a 25 mm mesh net on soft sediment substrata in several expeditions to the Great Australian Bight (GAB) and the eastern continental margin of Australia on the RV Investigator (Table 1, Fig. 1). The GAB expeditions included two that formed part of the Great Australian Bight Deepwater Marine Program (IN2015_C01 and IN2017_C01), a partnership of CSIRO and Chevron Australia, and a third that was part of the Great Australian Bight (GAB) Research Program, a collaboration of CSIRO, BP Australia, the South Australian Research and Development Institute, University of Adelaide and Flinders University. The eastern Australian samples were collected as part of the “Sampling the Abyss” voyage (IN2017_V03) that collected samples every 1.5 degrees of latitude from 42° to 23°S. On all voyages, sites were mapped (bathymetry and backscatter) prior to deployment using a Kongsberg EM 122 multibeam sonar. Samples were sorted, weighed and preserved (95% ethanol and/or formalin) on-board into broad taxonomic groups, but subsequently sent to taxonomic experts for post-voyage identification.

For this study we have restricted samples to those that were collected at seafloor depths between 1900 and 5000 m to ensure inter-regional comparability. The depth of 1900 m was chosen as the lower limit so as to include two samples from the GAB, whose mean depth along the tow was slightly shallower than the target depth of 2000 m. We restricted the taxonomic scope to the following megafauna groups that were identified by the same experts (see acknowledgements) across voyages: hexactinellid and demospongid sponges, anthozoans, barnacles, decapods, pycnogonids, polychaetes, asteroids, ophiuroids, echinoids, holothuroids, gastropods, bivalves, cephalopods and tunicates. Important omissions include foraminiferans, hydrozoans, scyphozoans, bryozoans, pericarid crustaceans, ostracods, brachiopods, nemerteans, polyplacophorans, scaphalopods, crinoids and fish. The specimens were identified to operational taxonomic units (mostly to species, some to genus or family), counted and used as the basis of subsequent statistical analyses.

Environmental variables were interpolated from global datasets to produce datasets for model training and prediction (see below). The environmental data was interpolated to mid sample locations (latitude, longitude and depth) for the model training dataset, and at a spatial resolution of 0.1° between 129 and 159°E, 42 and 23°S, and water depths between 2000 and 5000 m, for a prediction dataset. Prediction depths were derived from the ETOPO1 dataset (Amante & Eakins, 2009). Annual mean and standard deviation of seafloor water temperature (°C), salinity (psu), and dissolved oxygen (ml l^{-1}) were interpolated from the CARS2009 dataset (Ridgway *et al.*, 2002). Mean annual net primary productivity (NPP, g C m^{-2} $year^{-1}$) and the seasonal variation of net primary productivity (SVI, g C m^{-2} $year^{-1}$) were generated from a vertically generalized production model (VGPM) (Behrenfeld & Falkowski, 1997) using satellite-derived chlorophyll (SeaWiFS) data from the years 2003 to 2010 (see http://www.science.oregonstate.edu/ocean.productivity/). Carbon flux to the seafloor (C flux, g C m^{-2} $year^{-1}$) was estimated using NPP and SVI data and a productivity export model (Lutz *et al.*, 2007).

Statistical analyses

Most statistical analyses were performed using the R statistical environment v 3.4.3 and maps were produced by QGIS V 3.4.3-MADEIRA. Exploratory analyses of the data were performed using non-metric multivariate statistics. The species-site abundance data was converted into density (m-^{2}) measurements by dividing abundance by the sample area and then log transformed to down-weight the influence of abundant taxa. A triangular dissimilarity matrix was created using the Bray-Curtis coefficient with the vegdist(method="bray") function, clustered using hclust(method="ward.D2"), and ordinated using the non-metric multidimensional scaling (nMDS) function metaMDS() in the R package 'vegan' v2.4.5 (Oksanen *et al.*, 2016). The resulting clusters (biomes) were then used as categorical variables in subsequent analyses. Differences in sample composition according to the fixed factor biome were examined using PERMutational ANalysis Of VAriance (PERMANOVA) (Anderson 2001; Anderson et al. 2008) as implemented in Primer-E software, using the Bray-Curtis coefficient, the conservative Type III SS, and 999 random permutations of sample data amongst the factor groups.

We compared regional diversity patterns using Ranked Abundance Distributions using the R Package 'RAD' v0.3 (Foster & Dunstan, 2010; Dunstan & Foster, 2011). This package models three components of sample biodiversity (N=total abundance of individuals, S=species richness and η=evenness) as functions of environmental covariates, in a sequence that reflects their known conditionality. A forward stepwise selection procedure based on Akaike information criterion (AIC) was used on both linear and orthogonal polynomial predictors (degree=2). Interaction terms were individually assessed to determine if they further lowered AIC of best models. The models were formulated along the recommendations of Foster & Dunstan (2010). The N model included log(sample area) as an offset and negatively binomial error distributions. The S model included the log(sample area) offset, an estimate of N linearly scaled by area, and errors following a negative binomial distribution truncated at the total number of individuals. The η model used a multinomial distribution and is conditional on both N and S scaled by area.

Standard errors (SE) were calculated by sampling from the distribution of each model. Specifically, the SEs were calculated from 10,000 calls to the RAD predict() functions for the selected N, S and η model, using mean values calculated across from randomised subsets (80%) of observed data as the environmental covariates. Response curves for selected covariates were predicted by allowing the focal variable to vary along a selected range while keeping the other terms at their sampled means. Predictive maps for N, S and η were generated sequentially for a band of grid cells (resolution 0.1x0.1 degree) around southern and eastern Australia, restricted to lie between the geographical boundaries of 129 to 156.5°E and 42 to 23°S, and the depth contours of 2000 to 5000 m.

Species richness of each sample was also calculated for a set number of individuals (the smallest number of individuals in any sample = 38) using the rarefaction function rarefy() also in the R package 'vegan', which uses the algorithm of Hurlbert (1971) and the standard error procedure of Heck *et al.* (1975). These results were stratified into bathomes (lower bathyal vs abyssal) and analysed using one-way ANOVA with region (SE, NE and GAB) as the categorical factor (Gotelli & Colwell, 2011) using the EXCEL (v2013) function "ANOVA: Single factor" in the Analysis ToolPak Addin.

The number of species that were collected in one, two or more regions was tabulated by phylum and depth strata (lower bathyal and abyssal, excluding the unmatched shallow – 1900 to 2300 m - samples from the GAB). As species richness varies with collection effort, the number of species was adjusted to the mean number of species per sample multiplied by a standard number of samples (median = 6) per region/depth layer.

Results

The final data matrix was 666 OTUs (Operational Taxonomic Units) across the 49 samples. Speciose taxonomic groups included anthozoans (species=133), gastropods (109), asteroids (72), decapods (70), holothurians (60), ophiuroids (49), bivalves (42), hexactinellid sponges (33), barnacles (31), demosponges (19), pycnogonids (18), echinoids (13), tunicates (11) and cephalopods (7). Eighty-five percent of the OTUs were identified to species-level (including subspecies), 10 % to genus-level, and 5% to higher taxa. Only 251 of the OTUs were assigned species-level taxonomic names and potentially 60 % of the fauna is undescribed. A hierarchical cluster analysis primarily divided samples into lower bathyal and abyssal groups (Fig. 2a). Within each of these groups, regional (GAB, SE Australia, NE Australia) sub-clusters were evident. The exception was for the GAB bathyal samples which were divided into 1) mid (1900-2300 m) and 2) lower bathyal (2300-3200 m) clusters. The NE and SE bathyal samples were limited to > 2300 m (Table 1) and so did not separate in a similar manner. The two-dimensional MDS ordination showed these 7 clusters as discrete groups of points, except for the transitional sample IN2017_V03 067 which grouped with the SE group on the MDS and the NE group on the dendrogram. The analyses were repeated without the Porifera (a taxonomic group for which there were no species in common between the GAB and east coast samples) but showed little difference in pattern (not shown). The 7 clusters outlined above (Fig. 2) were treated as a categorical variable ‘biome’ in subsequent analyses.

Generally, within biome mean Bray-Curtis similarity was high, ranging from 19 % (NE Abyssal) to 32 % (GAB Bathyal 1). Between biome mean similarity was less than 12 %, except between GAB Bathyal 1 and 2 (15 %), GAB Bathyal 2 and SE Bathyal (13 %) (Table 2). An analysis of community composition (PERMANOVA) using biome as a grouping variable resulted in significant p-values for the main effect and all pairwise comparisons (Table 2).

A forward selection process in the RAD modelling procedure identified second order polynomials of Carbon flux (C flux) and seafloor salinity linked to abundance (N); Carbon flux and Latitude (°S) with an interaction term linked to richness (S); and second order polynomials of seafloor salinity, Seasonal Variation Index (SVI) of NPP, and longitude linked to evenness (eta) (Table 3, Fig. 3). The model residuals are given in Fig. 4. Predictive maps (Fig. 5) resulted in elevated abundance and richness at the shallower end of the study bathymetric range (2000-2500 m depth), particularly around SE Australia which is characterised by elevated NPP (Fig. 1). Evenness also was consistently higher around SE Australia (Fig. 5).

Rarefied richness (mean estimated richness per 38 individuals) was not significantly different between biomes when analysed as a single-factor ANOVA (p=0.48), suggesting that abundance drives regional richness patterns. The number of species that were collected from only one region varied according to phylum and depth strata (Fig. 6), ranging from no sponge species being shared between the GAB and eastern Australia to over half the arthropod species being shared.

Discussion

Patterns of regional-scale diversity

Samples with the highest standardised abundance and richness for benthic megafauna within our study area were found at depths of 2500-3000 m off SE Australia (SE). In general, abundance varied inversely with latitude (lowest in the North) across both the lower bathyal (2300-3200 m) and abyssal (>3200 m) depth strata, although abyssal richness was higher for sponges (Fig. 6). Richness at abyssal depths showed a similar regional pattern, but richness at bathyal depths were generally higher off NE Australia (NE) than for the Great Australian Bight (GAB). These patterns do not conform to the typical Latitudinal Diversity Gradient (LDG) reported from shallow waters (Tittensor *et al.*, 2010) and terrestrial environments (Hillebrand, 2004), where richness decreases away from tropical areas. Instead the patterns conform to that reported by Woolley *et al.* (2016b) for ophiuroids (brittle-stars), who found the peak of regional richness for the lower bathyal and abyssal (>2000 m) fauna occurred at mid latitudes in both hemispheres. This can be understood in terms of an energy framework. Whereas richness in the upper oceans (0-2000 m) is correlated with direct kinetic energy inputs (light and heat) that are highest in the tropics, lower bathyal and abyssal (LBA, >2000 m) environments receive the bulk of their energy chemically in the form of organic matter which are highest at temperate latitudes (Woolley *et al.*, 2016b).

Carbon flux has been repeatedly recognised as the key driver of spatial patterns of LBA richness, from local to global scales (Rex & Etter, 2010; Woolley *et al.*, 2016b). Carbon flux to the seafloor was the most important environmental variable driving our RAD models for both abundance and richness (Table 3, Fig. 3). A band of elevated phytoplankton density occurs at austral temperate latitudes (~40°S) across the Atlantic, SE Indian and SE Pacific Oceans, including off southern Australia and the Tasman Sea (Lutz *et al.*, 2007). Many of our samples off SE Australia were collected from directly under this phytoplankton bloom (Fig. 1). Conversely, the GAB samples were located to the north of this band and our samples from the NE were from relatively oligotrophic subtropical waters. It must be emphasised that our carbon flux data is modelled from surface chlorophyll data and depth and doesn’t represent in-situ measurements. Small scale (10-100 m) heterogeneity of particulate organic matter on the seafloor (e.g. Morris *et al.*, 2016) may explain more of the unaccounted for variability in our sampled diversity.

Previous studies have shown that the Bathymetric Diversity Gradient (BDG) for seafloor fauna is generally unimodal, with a diversity peak in the mid bathyal (~2000 m) in the North Atlantic Ocean (Rex & Etter, 2010) and in the upper bathyal (200-1000 m) in the Indo-Pacific Ocean (O'Hara *et al.*, 2019). Biodiversity declines consistently from the mid bathyal to abyss across oceans (Vinogradova, 1962). Our data are consistent with this pattern within each region (GAB, SE, NE). The key variable in our abundance and richness models, Carbon Flux, exponentially declines with depth, and is again a plausible partial explanation for these patterns. The source-sink hypothesis of Rex *et al.* (2005) relates low faunal density to low food supply at abyssal depths. The low density causes species extinction through Allee effects which is only partially balanced by dispersal from bathyal sources on continental margins (Rex *et al.*, 2005) or more productive abyssal areas (Hardy *et al.*, 2015). Under this scenario, SE Australia could be the source of much of the diversity in more oligotrophic regions, although we did find that the GAB and NE regions contained many species not present in the SE (Fig. 6). The decline in abundance and richness at high values of carbon flux may be an artefact of the lack of 1900-2300 m sites of SE and NE Australia and needs to be verified by further sampling.

There are also numerous other environmental variables that vary with depth and it is complex to partition out their effect on diversity. While pressure doubles between 2000 and 4000 m within our study area, water temperature only declines by an average of 1.1°C, salinity by 0.05 psu, and oxygen by 0.7 ml/l, and it is unclear to what extent these differences drive biological patterns. Much of the environmental variation is related to presence of distinct water masses at different depths. At 1000 m, low salinity Antarctic Intermediate Water (AAIW) flows westwards across the GAB in an offshore flow known as the Flinders current (Davis, 2005; Oke *et al.*, 2018). In the Tasman Sea, the same water mass enters via two routes, from the SE as eddies and as a current from the north, where AAIW in the SW Pacific has become entrained by the East Australian Current (Davis, 2005; Ollitrault & de Verdiére, 2013). Although meso-scale direction and velocity of currents at lower bathyal and abyssal depths are less well known, they form part of the thermohaline Global Meridional Overturning Circulation. Cold (~1°C) and oxygen rich Antarctic Bottom Water flows northwards across southern seafloors where it eventually diffuses into shallower waters to form deoxygenated but more saline Indian and Pacific Deep Waters which return southwards (~2000 m at 40°S) to upwell in the Southern Ocean (Talley, 2013; Lee *et al.*, 2019). Water masses in the North Atlantic have been shown to be spatially dynamic at decadal (Yasuhara *et al.*, 2019) to millennial temporal scales (Yasuhara *et al.*, 2009). These flows are consistent with a potential source-sink relationship between the diversity-rich SE and the NE and GAB regions.

Richness is known to be driven by macro-evolutionary processes as well as ecology. The peak at upper to mid bathyal (200-2000 m) depths is, at least partly, due to the age of these environments. The tropical upper to mid bathyal has relatively high diversity but a low lineage diversification rate and thus appears to have been a long-term refuge for deep-sea animals (O'Hara *et al.*, 2019). Conversely, the abyss is characterised by low richness for many groups (Rex & Etter, 2010). From an evolutionary perspective, abyssal taxa can amount to a small disparate subset of the bathyal lineages (e.g. Christodoulou *et al.*, 2019; O'Hara *et al.*, 2019), suggesting multiple infrequent range expansions from bathyal to the abyss over time and little subsequent diversification. The isopod family Munnopsidae is often cited as an exception to this trend, having radiated extensively in the deep sea (Lins *et al.*, 2012). Deep-sea faunal turnover of benthic foraminifera has occurred throughout the Cenozoic Era, possibly due to climate-driven modifications to the thermohaline circulation (Thomas, 2007).

Seasonal variation in seafloor water temperature and salinity did not explain patterns of abundance or richness in our data. However, seasonality in net primary production (SVI, as defined by Lutz *et al.*, 2007) was an informative variable for our model of evenness, along with salinity and longitude. Seasonality in NPP is considered important as organic matter forms aggregates (marine ‘snow’) with increased density, leading to enhanced flux to the seafloor during blooms (Bax *et al.*, 2001; Rex & Etter, 2010). Carcasses and faecal pellets from seasonal salp blooms can provide two thirds of carbon input to the seafloor in the Tasman Sea (Henschke *et al.*, 2013). In our data, evenness increased with increased seasonality, suggesting that numerous benthic species benefit from the plankton blooms. This is unlike the foraminiferan assemblage North Atlantic, where marine snow is exploited by a few dominant species (Corliss *et al.*, 2009). Also, we cannot rule out some inter-annual variation in our data, as our samples were collected in both 2015 and 2017 in the GAB, but in a single 2017 expedition for the SE and NE regions.

The Great Australian Bight

GAB soft sediment assemblages at LBA depths do not have elevated abundance or richness compared to equivalent habitats off Australia's eastern coast. We did not find quantitative evidence for a 'Key Ecological Feature' based on elevated biodiversity metrics that extends to LBA depths.

The evidence for the presence of elevated species richness in the GAB region is largely derived from the studies of Ward *et al.* (2006) and Currie and Sorokin (2014). Both these studies however, only compared total richness of their survey samples (gamma diversity) with a few ad-hoc surveys in other parts of the world. Such comparisons are known to be confounded by differences in habitat heterogeneity, gear type, scale and number of samples, inter-annual variation, and number of individuals (Gray, 2002). For example, claims of elevated richness for deep over shallow seas (Grassle & Maciolek, 1992) have been shown to be incorrect once the number of individuals and sample area were factored out (Gray *et al.*, 1997). None of the regions that Ward *et al.* (2006) (North Sea, Gulf of Carpentaria, Antarctica) or Currie and Sorokin (2014) (North Sea, NE Atlantic, Southern Ocean) compared to the GAB are known to support a particularly elevated regional species pool (e.g. Woolley *et al.*, 2016a). So it is hard to assess why the GAB soft sediment fauna would be considered species rich on a global scale.

However, identifying priority areas for conservation on the basis of species richness alone does not necessarily lead to adequate coverage of biodiversity (Veach *et al.*, 2017). Non species rich areas can have highly endemic biota. Consequently, for conservation purposes it is important to note that LBA samples in the GAB are compositionally distinct from those in the two other Australian regions (SE and NE) that have been surveyed at similar depths to date. Taking a precautionary approach, the GAB must be regarded as potentially having a unique faunal assemblage at these depths, at least until neighbouring regions off SW Australia and off western Bass Strait have been surveyed. The analysis of museum collection data from southern Australia by Tanner *et al.* (2018) indicated that the upper bathyal GAB fauna was generally most similar to that off western Bass Strait to SW Tasmania, and somewhat less similar to that found off SW Australia.

We found that the degree of similarity of the GAB samples to these off SE Australia varies considerably between taxonomic groups (Fig. 6). Most notably, none of the 68 recorded sponge species were collected from both GAB and eastern Australian surveys [although two of the eastern hexactinellid sponge species were found in the GAB using RoV collection devices, *Hyalonema* sp QM4976 and *Lophophysema inflatum*, the latter also known from elsewhere around the Indian Ocean (Tabachnick & Levi, 1999)]. At the other extreme, over half of the arthropod species from the LBA of the GAB were recorded from off the east coast (Fig. 6). At least some of the apparent regional endemism may be due to under-sampling (Coddington *et al.*, 2009) of these inaccessible habitats.

Conclusion

The lower bathyal and abyssal fauna around southern and eastern Australia shows regional diversity and compositional differentiation at the scale of 1-2,000 km along both latitudinal and longitudinal gradients. This has management implications as mineral and petroleum exploration/extraction activities can occur over similar spatial scales, potentially spanning the entire range of some species. Some groups (such as sponges) show higher turnover than others (e.g. arthropods) and appear to be better indicators of regional endemicity at these depths. Additional surveys outside areas of prospective resource development are required to better understand regional scale patterns of biodiversity. This would support more informed evidence-based management of local developments. We were fortunate in this example covering 5000 km of shoreline to have consistent access to expert biologists and taxonomists. In many instances, data for this kind of analysis will need to come from a multitude of academic and commercial surveys. Well-documented best practice survey methods, appropriate metadata and open data will be required to characterise regional biogeography in these instances, or to add to even larger scale analyses in the future.

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Survey	Stn	Region	Location	Latitude	Long-itude	Mid depth (m)	Date (d/m/y)	Area (m^2)	Temp. (°C)	Salinity (‰)	Oxygen (ml/l)	C Flux (g $m^{-2}y^{-1}$)
IN2015_C01	016	GAB	OR02, Area25	-36.069	132.637	4607	31/10/15	5666	0.953	34.710	4.708	0.735
IN2015_C01	026	GAB	OR07, Area19	-35.794	131.711	4517	2/11/15	10927	0.971	34.712	4.709	0.718
IN2015_C01	036	GAB	SZ02, Area20	-35.555	132.283	2242	5/11/15	17687	2.112	34.725	4.014	1.266
IN2015_C01	064	GAB	OR13, Area05	-34.074	129.182	2726	13/11/15	15221	1.787	34.733	4.245	0.974
IN2015_C01	079	GAB	SZ08, Area08	-34.341	129.942	2079	16/11/15	7129	2.245	34.708	3.988	1.192
IN2015_C01	080	GAB	SZ08, Area08	-34.408	130.024	2114	17/11/15	7916	2.214	34.712	4.002	1.197
IN2015_C02	137	GAB	Transect 5	-35.550	134.082	1961	5/12/15	11564	2.286	34.707	3.893	1.433
IN2015_C02	141	GAB	Transect 5	-35.818	134.109	2826	5/12/15	12341	1.761	34.732	4.214	1.067
IN2015_C02	151	GAB	Transect 4	-35.798	132.693	2725	6/12/15	12867	1.766	34.734	4.201	1.054
IN2015_C02	207	GAB	Transect 3	-35.352	131.077	2014	9/12/15	14282	2.288	34.709	3.943	1.282
IN2015_C02	216	GAB	Transect 3	-35.262	131.042	3021	10/12/15	12056	1.723	34.734	4.234	0.950
IN2015_C02	227	GAB	Transect 1	-35.009	130.317	2839	11/12/15	9508	1.726	34.734	4.238	0.938
IN2015_C02	274	GAB	Transect 2	-35.165	130.665	3002	12/12/15	11273	1.647	34.734	4.279	0.910
IN2015_C02	276	GAB	Transect 2	-34.853	130.687	2004	12/12/15	10440	2.299	34.705	3.949	1.279
IN2015_C02	449	GAB	Transect 1	-34.625	130.280	2037	18/12/15	14233	2.305	34.703	3.954	1.251
IN2017_C01	175	GAB	OR21	-35.815	132.021	4090	15/04/17	22871	1.156	34.721	4.570	0.763
IN2017_C01	178	GAB	OR21	-35.716	131.656	3883	16/04/17	21483	1.242	34.724	4.531	0.777
IN2017_C01	179	GAB	OR21	-35.814	131.703	4684	17/04/17	29787	0.925	34.709	4.715	0.706
IN2017_C01	182	GAB	OR26	-35.487	130.378	4961	17/04/17	18706	0.852	34.704	4.814	0.664
IN2017_C01	192	GAB	OR11, Area07	-34.550	129.403	3793	20/04/17	18320	1.258	34.725	4.508	0.745
IN2017_C01	197	GAB	OR11, Area07	-34.447	129.532	3292	21/04/17	14740	1.481	34.732	4.383	0.827
IN2017_C01	198	GAB	OR11, Area07	-34.549	129.602	3464	21/04/17	15875	1.392	34.730	4.455	0.796
IN2017_V03	004	SE	Freycinet MP	-41.731	149.120	2785	18/05/17	29584	1.746	34.735	4.277	1.998
IN2017_V03	006	SE	Freycinet MP	-41.626	149.552	4037	18/05/17	30344	1.041	34.715	4.571	1.260
IN2017_V03	014	SE	Flinders MP	-40.464	149.102	2392	20/05/17	15348	1.988	34.721	4.051	2.352
IN2017_V03	015	SE	Flinders MP	-40.473	149.397	4126	20/05/17	10572	1.045	34.714	4.587	1.198
IN2017_V03	022	SE	Bass Strait	-39.462	149.276	2726	22/05/17	11756	1.788	34.731	4.204	2.049
IN2017_V03	030	SE	Bass Strait	-39.552	149.553	4165	23/05/17	29312	1.077	34.714	4.563	1.181
IN2017_V03	032	SE	East Gippsland MP	-38.479	150.184	3851	24/05/17	11580	1.132	34.718	4.501	1.290
IN2017_V03	035	SE	East Gippsland MP	-37.792	150.382	2459	25/05/17	15352	1.985	34.720	4.108	2.264
IN2017_V03	043	SE	Off Bermagui	-36.351	150.914	4800	27/05/17	14824	1.123	34.713	4.575	0.959
IN2017_V03	044	SE	Off Bermagui	-36.355	150.644	2754	27/05/17	17972	1.785	34.729	4.253	1.726
IN2017_V03	053	SE	Jervis MP	-35.114	151.469	3981	28/05/17	16792	1.170	34.719	4.479	1.045
IN2017_V03	056	SE	Jervis MP	-35.333	151.258	2643	29/05/17	15976	1.855	34.724	4.224	1.657
IN2017_V03	065	SE	Off Newcastle	-33.441	152.702	4226	30/05/17	13992	1.162	34.718	4.475	0.847
IN2017_V03	067	SE	Off Newcastle	-32.985	152.952	2803	31/05/17	19748	1.689	34.728	4.254	1.274
IN2017_V03	070	SE	Hunter MP	-32.575	153.162	2534	3/06/17	26260	1.881	34.724	4.153	1.405
IN2017_V03	078	SE	Hunter MP	-32.138	153.527	4004	4/06/17	19608	1.159	34.718	4.449	0.793
IN2017_V03	080	NE	Central Eastern MP	-30.099	153.596	1225	5/06/17	16096	1.909	34.716	4.104	1.193
IN2017_V03	088	NE	Central Eastern MP	-30.264	153.870	4441	6/06/17	18328	1.168	34.715	4.462	0.687
IN2017_V03	090	NE	Off Byron Bay	-28.677	154.203	2574	7/06/17	15400	1.819	34.723	4.202	0.981
IN2017_V03	097	NE	Off Byron Bay	-28.355	154.636	3782	8/06/17	27508	1.164	34.717	4.473	0.646
IN2017_V03	099	NE	Off Byron Bay	-28.371	154.649	3789	9/06/17	14416	1.164	34.717	4.473	0.646
IN2017_V03	101	NE	Off Moreton Bay	-26.946	153.945	2548	9/06/17	11564	1.811	34.722	4.213	1.017
IN2017_V03	102	NE	Off Moreton Bay	-27.008	154.223	4269	10/06/17	18332	1.161	34.715	4.449	0.575
IN2017_V03	109	NE	Off Fraser Island	-25.221	154.164	4005	11/06/17	18156	1.139	34.715	4.430	0.542
IN2017_V03	115	NE	Off Fraser Island	-25.325	154.068	2346	11/06/17	11976	1.994	34.709	4.029	0.905
IN2017_V03	122	NE	Coral Sea MP	-23.751	154.639	2349	13/06/17	13548	2.030	34.703	3.959	0.816
IN2017_V03	135	NE	Coral Sea MP	-24.352	154.291	4001	15/06/17	19812	1.136	34.715	4.403	0.517

Table 1. Beam trawl sample location and modelled environmental data. C flux= Mean annual carbon flux to the seafloor.

PERMANOVA table of results

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms	P(MC)
Biome	6	82602	13767	5.0266	0.001	997	0.001
Res	42	1.15E+05	2738.9				
Total	48	1.98E+05					

Average Bray-Curtis Similarity between/within groups

	GAB Abyss	GAB Bathyal 1	GAB Bathyal 2	SE Bathyal	SE Abyssal	NE Bathyal	NE Abyssal
GAB Abyss (GA)	23.621						
GAB Bathyal 1 (GB1)	4.7554	32.109					
GAB Bathyal 2 (GB2)	9.9799	14.654	28.213				
SE Bathyal (SB)	5.5416	10.77	12.844	29.951			
SE Abyssal (SA)	10.423	2.0202	5.6307	8.9267	23.434		
NE Bathyal (NB)	5.7388	5.657	11.476	11.484	5.761	29.756	
NE Abyssal (NA)	6.6586	0.88285	1.6827	1.7612	6.368	7.119	19.001

Groups	t	P (permulation)	Permutations	P (Monte Carlo)	Denominator.df
GA, GB1	2.6082	0.001	982	0.001	15
GA, GB2	2.0489	0.001	914	0.001	13
GA, SB	2.3322	0.001	905	0.001	13
GA, SA	2.0007	0.001	969	0.002	15
GA, NB	2.4122	0.001	957	0.001	14
GA, NA	1.896	0.002	789	0.003	12
GB1, GB2	2.056	0.001	851	0.002	12
GB1, SB	2.3208	0.001	859	0.002	12
GB1, SA	2.7157	0.001	923	0.001	14
GB1, NB	2.6734	0.001	930	0.001	13
GB1, NA	2.3986	0.002	684	0.001	11
GB2, SB	1.9891	0.002	410	0.001	10
GB2, SA	2.2464	0.001	854	0.002	12
GB2, NB	2.1135	0.003	761	0.003	11
GB2, NA	2.1249	0.002	422	0.002	9
SB, SA	2.1288	0.001	848	0.002	12
SB, NB	2.175	0.003	762	0.001	11
SB, NA	2.173	0.003	413	0.002	9
SA, NB	2.3805	0.001	919	0.002	13
SA, NA	1.8841	0.001	707	0.003	11
NB, NA	1.9948	0.001	573	0.001	10

Table 2. PERMANOVA results comparing Bray-Curtis similarity of sample composition (log(X+1) transformed) between biomes using Primer-E software, with sums of squares type = Type III (partial), fixed effects sum to zero for mixed terms, unrestricted permutation of raw data, and 7 states of the fixed factor ‘Biome’ (see Fig. 2).

Covariate	Estimate[1]	Standard Error[2]	AIC[2]
Summary of model for total abundance (N_i)			
θ_N	1.72862		
Mean	-3.80259	4.57637	692.91
+ C Flux	3.64231	3.80589	678.40
+ C Flux ^{2}	-1.64429	4.71191	676.85
+ Salinity	0.21956	4.63219	678.53
+ Salinity ^{2}	2.46932	2.87960	672.87
Summary of model for species richness ($S_i \| N_i$)			
θ_S	9.80659		
Mean	-5.97604	0.25500	432.30
+ Scaled abundance	0.23770	0.25649	432.30
+ C Flux	2.09600	0.18554	411.70
+ Latitude	-0.36584	0.17638	411.73
+ C Flux*Latitude	2.14338	0.28738	403.26
Summary of model for evenness ($n_i \| S_i, N_i$)			
θ_n	4.78748		
V	3.58394		
Mean	1.30420	0.00016	6456.39
+ Scaled abundance	0.00469	0.00016	6426.63
+ Scaled richness	-0.04584	0.00018	6414.45
+ Salinity	-0.48157	0.00019	6405.83
+ Salinity ^{2}	0.52365	0.00027	6392.48
+ SVI	1.34297	0.00030	6393.51
+ SVI ^{2}	-1.07033	0.00032	6385.46
+ Longitude	-1.57210	0.00042	6386.06
+ Longitude ^{2}	0.52965	0.00065	6384.54

[1] Final model. [2] From models with terms higher in the table.

Table 3. Summary of final RAD models for Ni, Si|Ni and $n_i|N_i, S_i$. Summary of final RAD (Rank Abundance Distribution) models for total abundance, species richness and evenness of samples. C Flux=Mean annual carbon flux to the seafloor (g C m^{-2} $year^{-1}$), Temp=Seafloor water temperature (°C), NPP=Net primary Productivity (g C m^{-2} $year^{-1}$), SVI= Seasonal variation of net primary productivity (g C m^{-2} $year^{-1}$), AIC= Akaike information criterion.

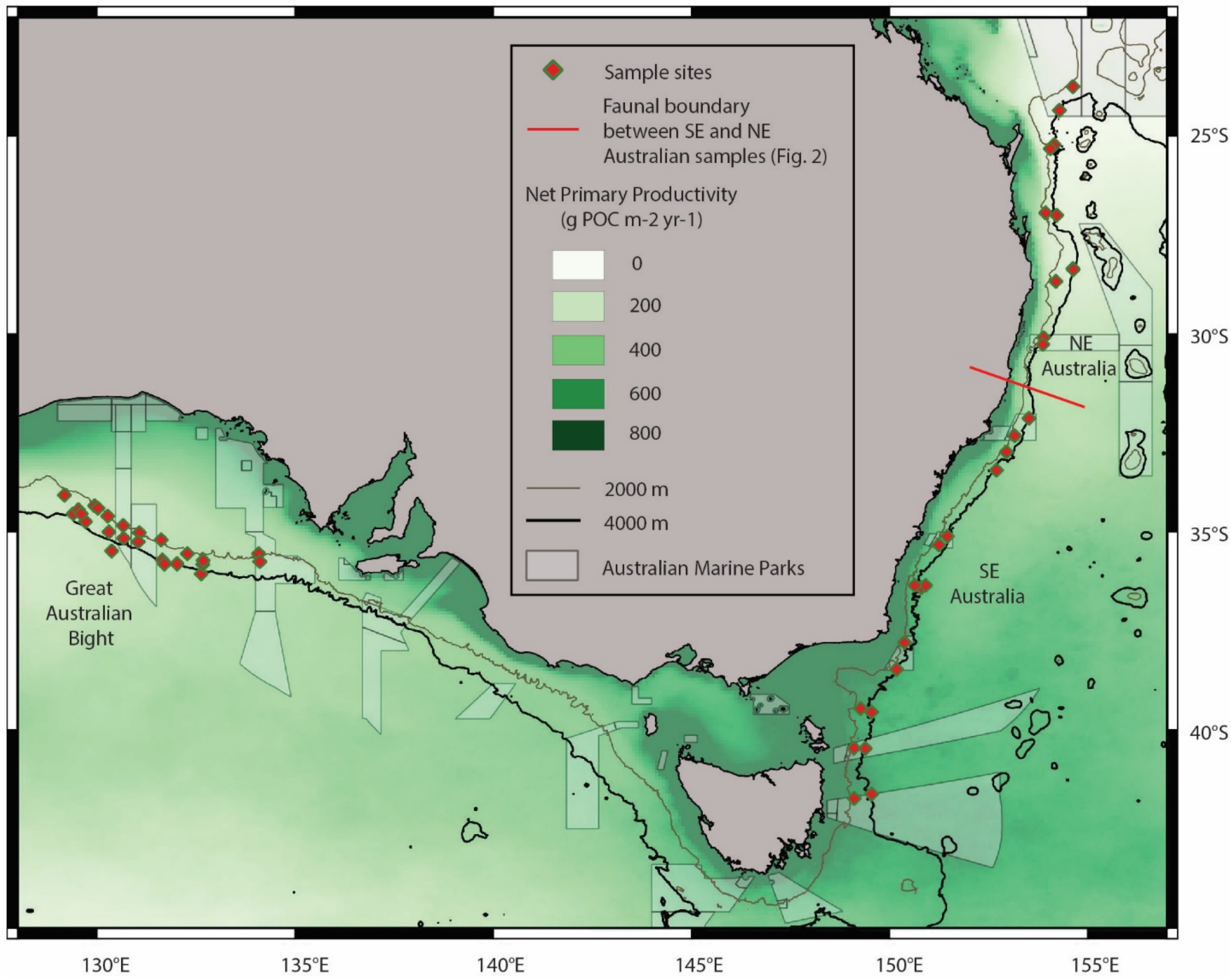


Fig. 1. Map of sample sites (red) and Net Primary Production (NPP) around Southern and Eastern Australia.

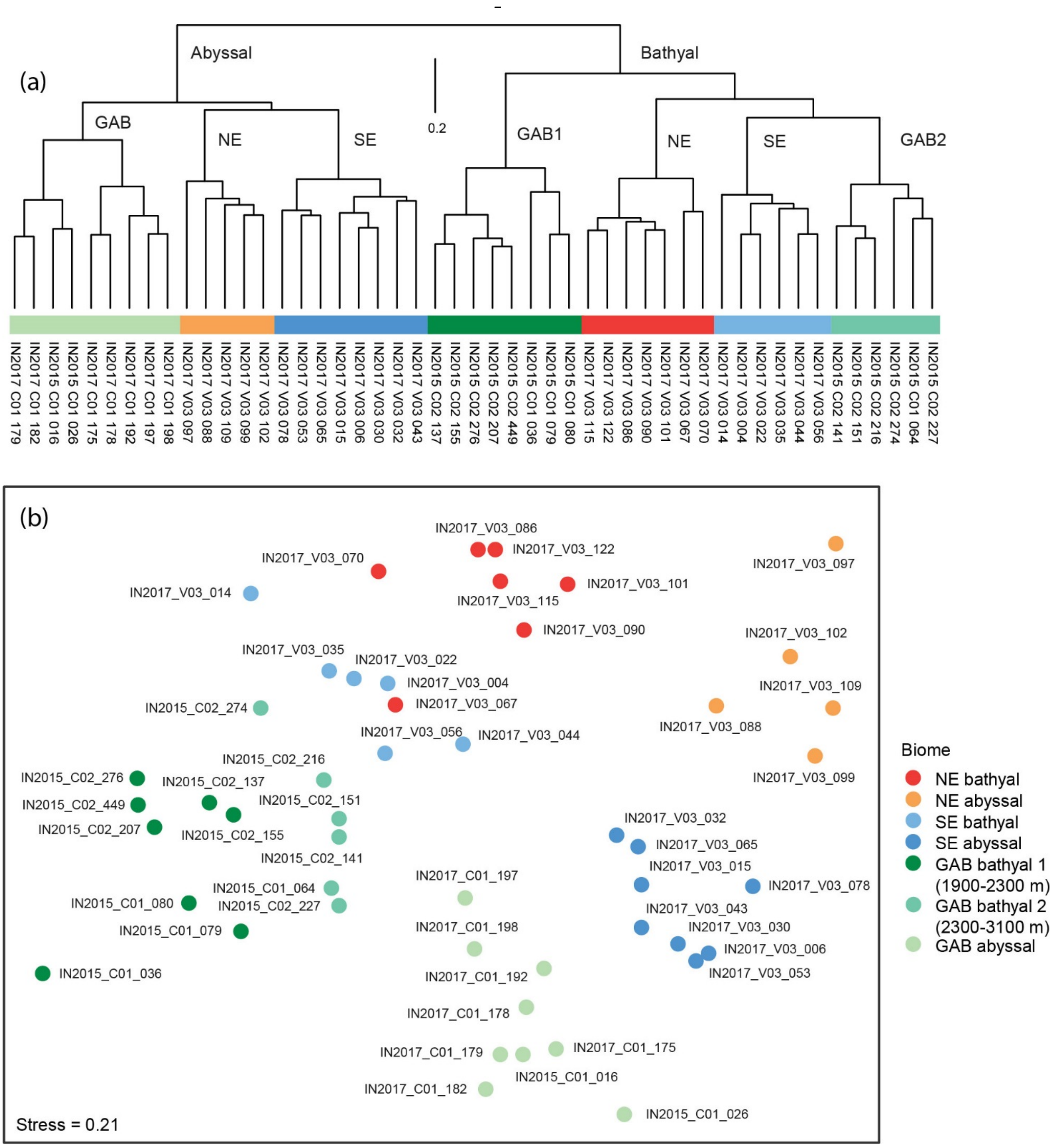


Fig. 2. Multivariate of lower bathyal and abyssal beam trawl samples (2000-5000 m) from the Great Australian Bight (GAB) and off the SE and NE coasts of Australia. (a) Dendrogram showing 7 clusters, and (b) Multidimensional scaling ordination, with points superimposed by biome cluster. Sample details are given in Table 1.

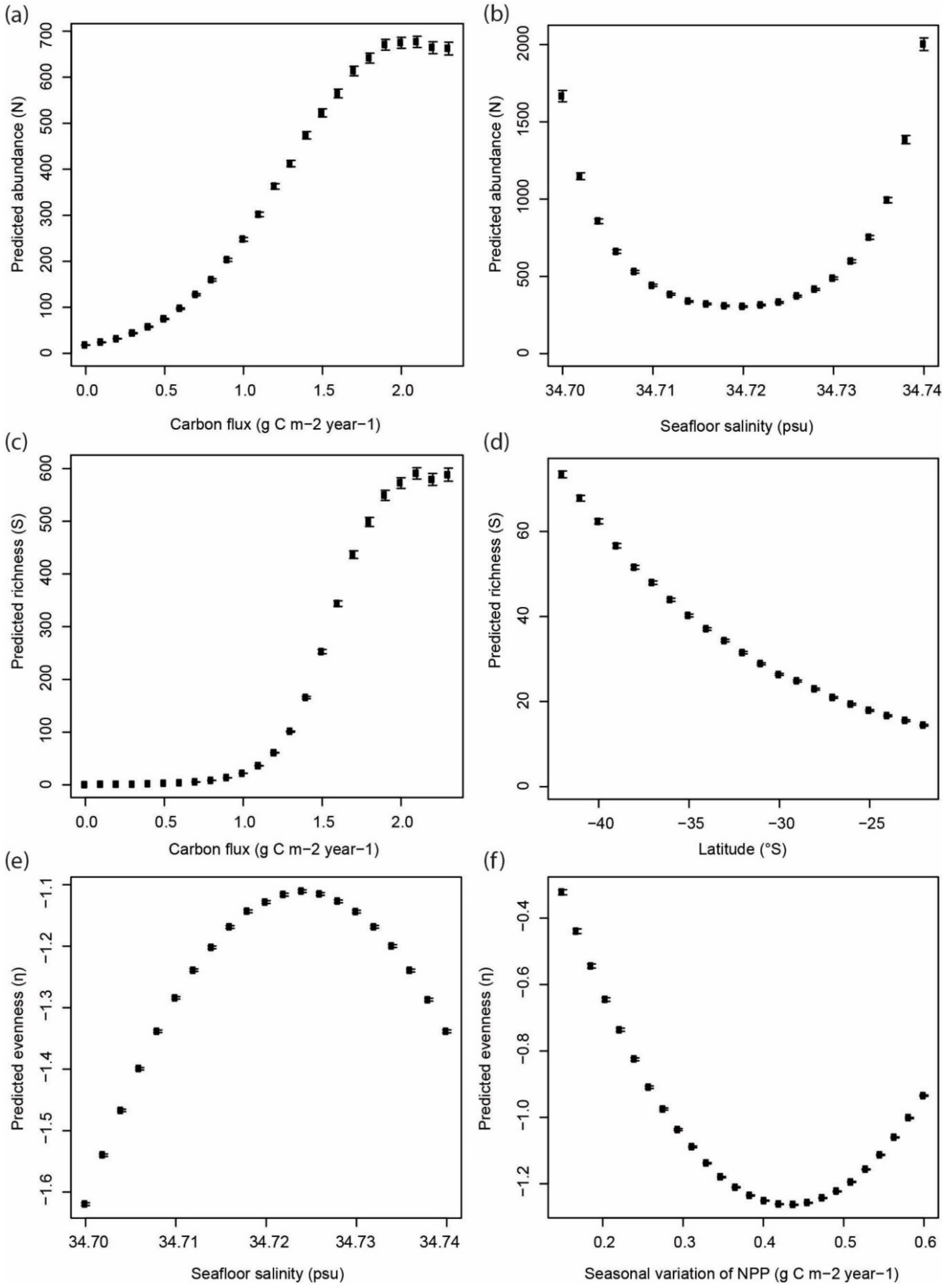
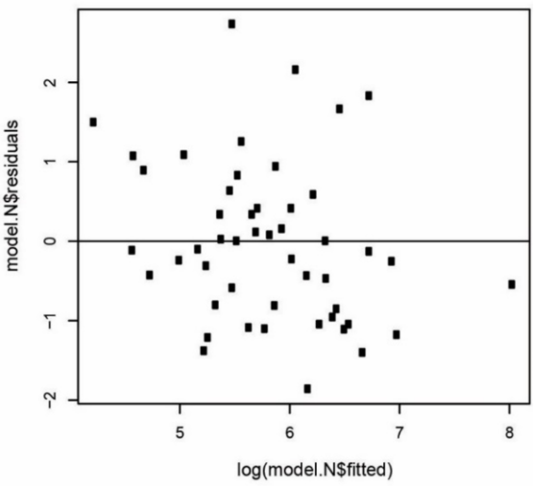
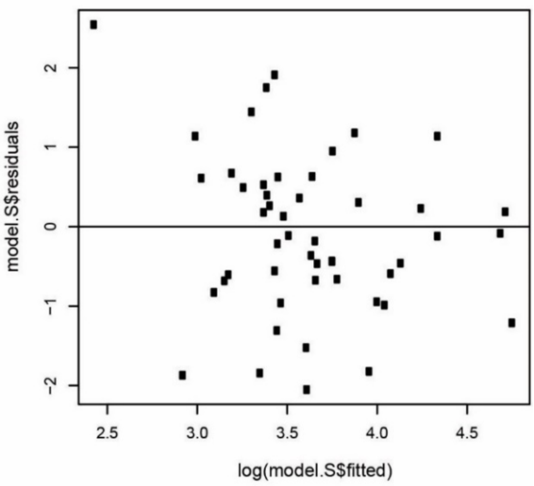


Fig. 3. Key variable responses using final RAD models (Table 2) for (a-b) Abundance, (c-d) Species Richness and (e-f) Richness. The range of the focal variable is set from the sample operations and other environmental variables are held constant to their mean sample values. Mean and confidence intervals (2 x Standard Error) are based on 10,000 bootstrap predictions. Richness is conditional on abundance, and evenness conditional on both richness and abundance of each bootstrap.

(a) RAD abundance (N) model residuals



(b) RAD richness (S) model residuals



(c) RAD Evenness (eta or nij) model residuals

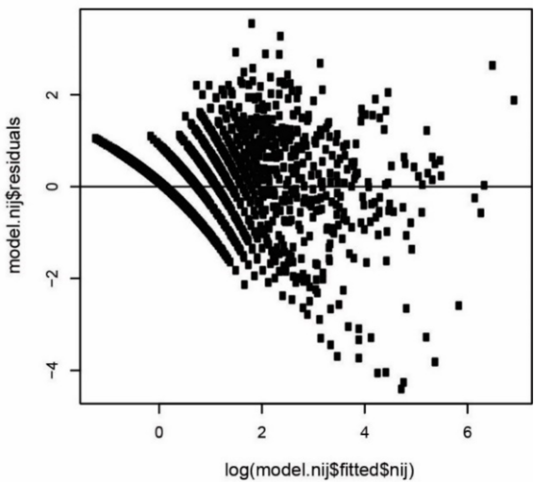


Fig. 4. Residual plots for the selected N, S and η (eta) RAD models (see Table 3).

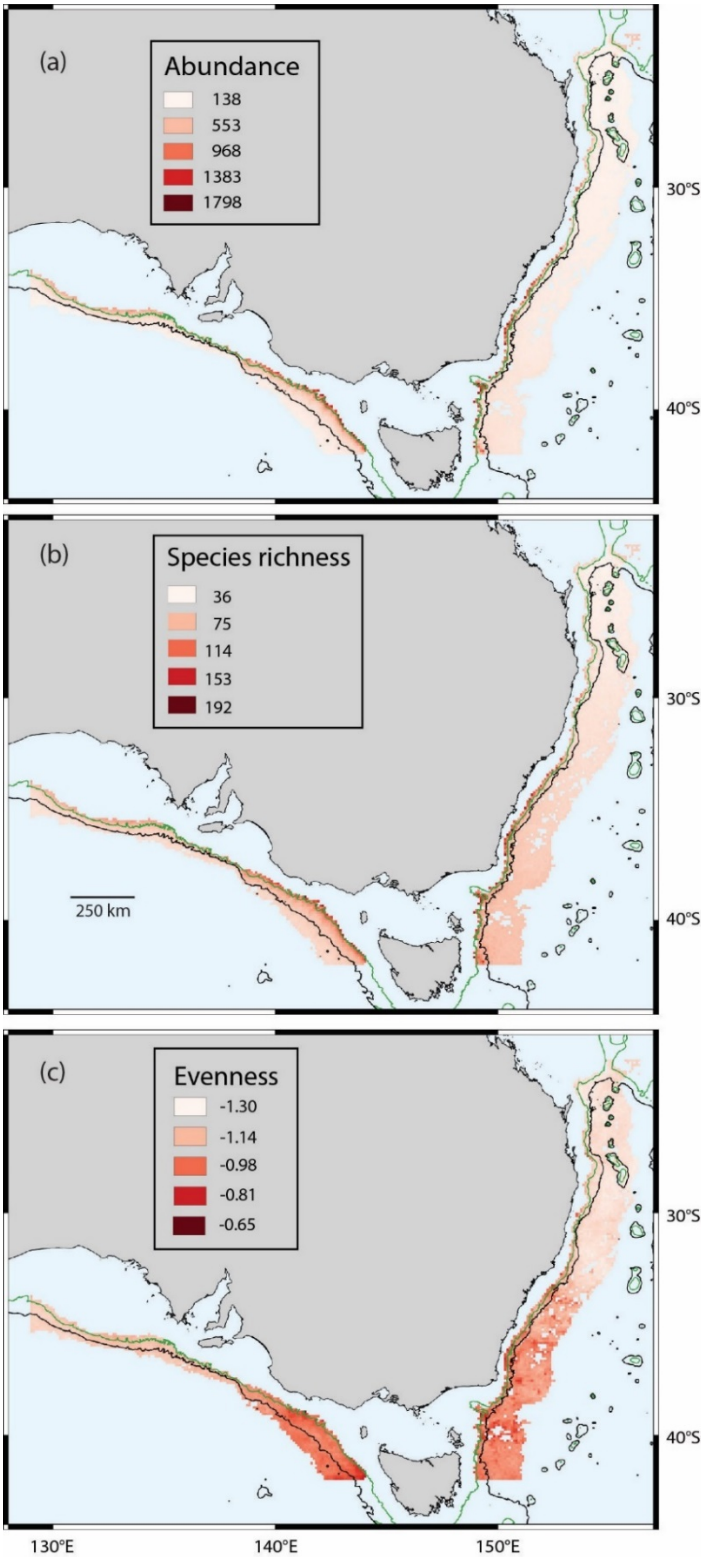


Fig. 5. Predicted (a) Abundance, (c) Species Richness and (e) Evenness on a grid of 0.1° around southern and eastern Australia (2000-5000 m) using final RAD models outlined in Table 2. Bathymetric contours are 2000 m (green) and 4000 m (black).

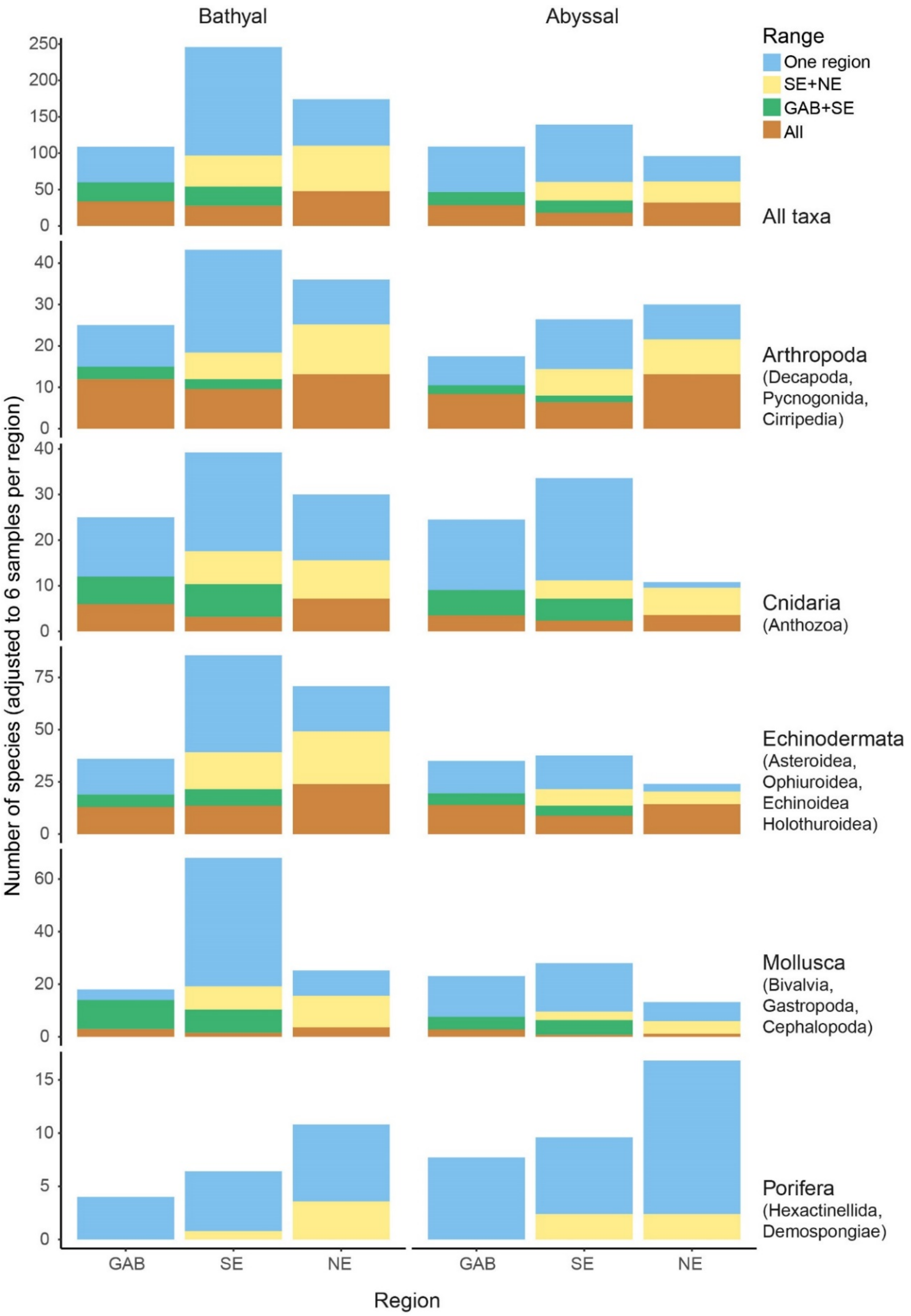


Fig. 6. Number of species collected in one or more regions for a standardised collection effort (6 beam trawl samples per region and depth category). GAB=Great Australian Bight, SE=South-east Australia, NE=North east Australia (See Fig. 1).

Appendix A: Contrasting processes drive gradients in phylodiversity across shallow and deep seafloors.

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Our knowledge of the distribution and evolution of deep-sea life is limited, impeding our ability to identify priority areas for conservation. Here we analyse, for the first time, large integrated phylogenomic and distributional datasets of seafloor fauna from the equator to pole for an entire class of invertebrates. We find that ubiquitous latitudinal diversity gradients are assembled through contrasting evolutionary processes for shallow and deep seas. In the shallow-water tropical-temperate realm, speciation, extinction and migration rates are broadly consistent with an "out of the tropics" process [215]. Speciation rates are reversed for the realm containing the deep sea and Antarctica, being highest at polar and lowest at tropical latitudes, and net migration is from high to low latitudes. The tropical upper bathyal (200-700 m deep), with its rich ancient phylodiversity, is characterised by relatively low background extinction rates. Conversely, the specialised Antarctic fauna is rebounding from episodic extinction events associated with the rapid cooling of polar waters over the mid-Cenozoic.

The decline of species richness with latitude is so prevalent across taxonomic groups and biomes that it has been called the first-order pattern of biodiversity across the planet [216]. However, elucidating the mechanisms that create such patterns remains a major challenge [217]. Different combinations of speciation, extinction and range expansion rates can result in high and low diversity regions. The high diversity tropics are characterised as being a 'cradle' (resulting from high speciation rates) or 'museum' (an accumulation zone with low extinction rates) [218]. Based on marine bivalve fossil data, Jablonski et al. [215] hypothesised an 'out of the tropics' process with lineages originating in the tropics then expanding their range to include both tropical and higher latitudes, the tropics thus being both a cradle and a museum. However, this mechanism has been since investigated only in shallow marine and terrestrial ecosystems. The deep sea (below 200 m) is an important third ecosystem that differs from other environments in that the distribution of life is not primarily driven directly by thermal energy [15,147]. Moreover, it continuously covers a broad range of latitudes. Testing evolutionary and ecological hypotheses in unique environments like the deep sea offers the potential to disentangle some of the numerous interacting variables that potentially affect the distribution of biodiversity [217]. However, until now we have lacked the comprehensive phylogenetic data to investigate these patterns.

Here we combine substantial distributional (160k records) and DNA sequence data (596 species, 267kb) across an entire taxonomic class of invertebrates (Ophiuroidea) to test the 'out of the tropics' hypothesis from shallow to deep-sea environments, from the equator to Antarctica across the Indo-Pacific southern hemisphere (Extended Data Fig. 1). Ophiuroids, or brittle-stars, have become a useful model for examining large-scale patterns of marine biogeography as they occur abundantly on the seafloor of most oceans [145,147,219]. Specifically we test the 'out of the tropics' prediction [217] that speciation rates are higher and extinction rates lower in tropical compared to temperate and polar regions, for both shallow water (0-200 m) and deep-sea systems (> 200 m).

We find a marine latitudinal diversity gradient of varying profile at all depths and at various levels of evolutionary differentiation (Fig. 1 and Extended Data Fig. 2). High species richness occurs at sublittoral (0-200 m) and upper bathyal (200-700 m) depths at tropical latitudes (0-35°S) with moderate richness in temperate (34-46°S) and mid-bathyal (700-2000 m) zones, and a steep decline to Antarctica and the abyss. At the shallowest level (0-100 m) there is a pronounced latitudinal peak south of the equator (13-23°S) while with increasing depths it is more broadly tropical. A non-equatorial peak of richness for shallow marine fauna has been observed for many marine datasets [220]. Across all latitudes the bathymetric peak is in the upper to mid bathyal, shifting southwards with depth. Bathymetric peaks of species richness in the Indo-Pacific at tropical upper bathyal depths have been recorded for other eurybathyal invertebrate groups, such as azooxanthellate scleractinian corals, turrid molluscs, and galatheid crustaceans [221-223]. The deeper temperate latitudinal peak (~1000 m) is compatible with the reported mid-bathyal peak in richness from the northern Atlantic Ocean [15]. With increasing depth, and phylogenetic scale, the gradients become more step-like and pushed further south. Horizontal gradients in the lower bathyal and abyss (>2000 m) differ in being relatively consistent over tropical and temperate latitudes, then gradually declining across the Southern Ocean. Family-level taxa (~110 my) are widespread [224], declining most rapidly at high latitudes and lower bathyal depths (Extended Data Fig. 3a).

Patterns of phylogenetic diversity (PD) are broadly similar, but with the peak restricted to the upper bathyal. Other phylogenetic diversity indices including relative PD (RPD), evolutionary distinctness (ED) and mean lineage diversification rate, highlight the differences between the species diversity and underlying phylogenetic structure. Species with the highest ED, a measure of how isolated they are on the phylogenetic tree, are also concentrated in the tropical upper bathyal. Relative Phylogenetic Diversity (RPD, Fig. 1c), the ratio of observed PD to PD expected from species richness, is significantly low ($p < 0.01$, Extended Data Fig. 3d) in Antarctic waters and the tropical shallows, indicative of phylogenetic clustering or discrete origins and extensive recent speciation (Fig. 2). Conversely, the tropical deep sea, as species rich as the shallows, has a relatively high RPD ($p > 0.95$) reflecting numerous diverse lineages spread across the phylogeny (Fig. 2). Mean lineage diversification rates (Fig. 1d) distinguish the relatively recent phylogenetic radiations evident in Antarctic and older radiations in tropical sublittoral regions.

Simpson's phylo beta diversity ($p\beta_{Sim}$ [225,226]) measures the turnover in phylogenetic composition across the study region. Peak $p\beta_{Sim}$ occurs across a depth gradient between 100 and 300 m at tropical and temperate latitudes (Fig. 1f and Extended Data Fig. 3f). This bathymetric turnover is so pronounced that the seafloor fauna should be considered to form two biological realms, (1) tropical-temperate shallow water (0 to 200-300 m) and (2) the deep sea plus Antarctica. Notable latitudinal compositional changes also occur around 54°S, 45°S and 34°S, allowing five distinct biomes to be defined from multivariate analyses of $p\beta_{Sim}$ across our study region: tropical shallow, temperate shallow, tropical deep sea, temperate deep sea and Antarctica (Fig. 1g). The five bioregions have divergent signatures of speciation, extinction and migration (Fig. 3) that are robust to randomised trials and incomplete sampling (Extended Data Table 4, Extended Data Fig. 5).

The tropical shallows are more a ‘cradle’ than a ‘museum’, with moderate rates of speciation but low rates of extinction, generating high endemic species richness clustered into large discrete radiations (Fig. 2, 3). The temperate shallows are less phylogenetically clustered, have lower speciation rates and higher extinction rates, resulting in reduced species richness despite ongoing exchange between the tropical and temperate shallows (Fig. 3d and Extended Data Table 6). Transition rates between these shallow biomes and Antarctica approximate zero. The temperate shallow water biome currently ends at the southern end of Australia and New Zealand, although it may have continued to 61°S prior to the development of Oligocene polar ice-caps [227]. In summary, faunal distribution across the temperate-tropical shallow water realm is not inconsistent with the ‘out of the tropics’ scenario reported for marine bivalves [215] and various terrestrial clades [228,229]. However, the shallow Antarctic ophiuroid fauna is not part of this process, being phylogenetically related to deep-sea lineages.

The deep-sea and Antarctic realm has an entirely different pattern. The tropical deep sea, with high species diversity but low speciation rate, is a ‘museum’ or accumulation biome, rather than a ‘cradle’. It is phylogenetically dispersed, containing a diverse assemblage of ancient lineages, where both speciation and extinction rates are relatively low but the net diversification rate is still positive, and with low to intermediate rates of immigration respectively from the tropical shallow and temperate deep-sea biomes (Extended Data Table 4). The temperate deep sea is a ‘flux’ biome, containing a transitional fauna, with low net diversification (moderate speciation and high extinction rates) and intermediate to high rates of migration across neighbouring deep-sea latitudes. Net migration is from south to north, both in terms of rate and number of transitions (Extended Data Table 6). Explaining the tropical-temperate transition in the deep sea is one of the unresolved problems of marine biogeography [145], as isotherms occur more or less horizontally from the equator, across both tropical and temperate latitudes, before shoaling in subantarctic waters (Extended Data Fig. 7). Contrary to the hypothesis that thermal energy promotes diversification [230], the Antarctic has the highest rate of speciation of all our biomes, four times the rate of the tropical deep sea. Thus the ‘cradle’ and ‘museum’ are reversed for the deep sea, and regional rates of speciation, extinction and migration do not conform to the predicted ‘out of the tropics’ mechanism. The latitudinal biodiversity gradient in the deep sea has been created or is being maintained by other processes.

Antarctica has a short-branched phylogenetically-clustered ophiuroid fauna indicative of a recent (post mid-Cenozoic) radiation. Numerous ophiuroid families are absent (Extended Data Fig 2, 3) but background extinction rate estimates are only a fifth of the speciation rate (Fig. 3), suggesting other process may account for the current diversity. Fossil evidence indicates that there were elevated rates of extinction in several marine faunal groups coincident with rapidly cooling polar seas, in particular during the development of polar ice-caps at the Eocene-Oligocene (41-34 my) transition, and with a pronounced strengthening of the Antarctic Circumpolar Current during the Middle

Miocene climatic transition (14-12 my) [231]. Remaining fauna had to evolve tolerance to cold water, the presence of ice, and marked seasonal primary productivity. Eurybathy is now a feature of the Antarctic fauna [232] and some deep-sea clades appear to have expanded their range into shallow water. Radiation of surviving lineages would have been facilitated by a combination of vacant niches, removal of predation pressure, and creation of intermittent ice-sheet dispersal barriers [231,233]. Thus the pattern of high speciation rate but modest species diversity for ophiuroids is consistent with a rebound response to episodic extinction events. The Antarctic biome may not be at evolutionary equilibrium.

The low speciation rate for the tropical deep-sea biome is unexpected. Our data is not consistent with hypotheses that the richness is derived from increased speciation rates, generated either from elevated habitat heterogeneity or along the extreme pressure and thermal gradients that characterise the upper oceans [234]. Instead, we argue that low extinction rates and relatively high accumulation rates maintain the high phylodiversity. We hypothesise that the upper-mid bathyal (200-2000 m) has been a stable complex environment and long term refuge for deep-sea animals. Indeed, microfossil ophiuroid assemblages from the late Cretaceous Blake Nose deposits (114 my, palaeo-depth of 800-1500 m), contain the same families as habitats at similar depths in the modern Atlantic Ocean [235]. Upper bathyal waters are the tropical rain forests of the sea, preserving a rich ancient fauna, and a reservoir of phylogenetic diversity. This fauna has not been emphasized in conservation assessments to date.

Conversely, the abyss (> 3500 m) is characterised by low richness for ophiuroids (Fig. 1) and many other faunal groups [236]. This decline has been related to long term environmental drivers (e.g. reduced carbon flux, temperature and increased pressure [147]) or from oceanographic events such as the intermittent development of widespread anoxic conditions in the deep oceans [206]. Unlike for Antarctica, we find that abyssal taxa amount to a small diverse subset of the bathyal lineages, with little evidence for endemic speciation except in polar areas (Fig. 1c-d, 2), suggesting multiple infrequent migrations from bathyal to the abyss. Similar patterns have been found in other animal groups [234,237].

Contrasting patterns and processes in the shallow and deep marine environments suggest reconsideration of conservation priorities. The United Nation's Sustainable Development target 5 goal 14 and Aichi biodiversity target 11 specify that only 10 percent of the coastal and marine areas should be conserved, without consideration of the strong bathymetric and latitudinal turnover in phylodiversity. It may not be appropriate to use extensive deep-sea marine protected areas as a biodiversity offset against lack of shallow water protection. The blue planet requires a global approach to long term marine conservation that addresses the dynamics of oceanic biodiversity.

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Author Contributions T.O'H & A.F.H. designed the research, T.O'H, A.F.H. assembled the data, T.O'H, A.F.H., S.N.C.W. & G.B.-C. performed the analyses, and all authors contributed to writing the paper.

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Methods

Datasets. This study analysed distributional (occurrence) and phylogenetic data of ophiuroids (brittle stars). The global distributional dataset contains over 160,000 collection records, derived and validated from museum databases, the global OBIS database, and literature sources [145,147,219]. After discarding outliers, three-dimensional species ranges were created by interpolating between minimum/maximum latitudinal, longitudinal and bathymetric distributional extents. The deep sea is vast and incompletely sampled (Extended Data Fig. 1) so interpolation was required. We finally used species ranges rather than more complex species distributional (SDM) models as many phylogenetically important species did not have sufficient distribution records to train complex models.

In order to maximise the overlap between biogeographic and phylogenetic datasets while retaining a broad scope, the study area was constrained to marine environments from 70°S to 0°N and 0 to 4,000 m depth. Longitudinal limits were increased with every degree of latitude to ensure a linear latitudinal scale and equal cell areas symmetrical around 150°S, e.g. extending from 109-191°E at 0°S, 100-200°E at 35°S, and 34-267°E at 70°S (Extended Data Fig. 1a). A species or family was recorded as present in a cell if any location in a cell was within its known latitudinal, longitudinal and bathymetric range. This region includes 828 named species, of which 596 (72 %) were represented in the phylodiversity analyses. The number of species sequenced that occurred in each grid cell ranged from 41-94% (Extended Data Fig. 1c).

The phylogeny used here is an extension of the tree used by Bribiesca-Contreras et al. [238] and built using the same methodology [224,239]. Briefly, a RAxML (v8.1.20) [240] bootstrap consensus tree was inferred from a phylogenomic data matrix of 265kb of exon data and the mitochondrial COI gene for 781 taxa, 708 of which have both exon and COI and 73 with only COI data. This tree was then converted into an ultrametric chronogram using Penalized Likelihood Rate Smoothing (PLRS; r8s v7.3) [241] using 12 fossil based calibration points [224]. This methodology has been found to produce robust trees, broadly congruent with Bayesian (BEAST [242]) analyses of the same data, but with fewer computational constraints [224,239,243]. A subtree of 596 taxa from our study region (Fig. 2) was then pruned from this larger reference tree. A single tree was used because uncertainty in absolute age was not important to the analyses herein. We used a new phylogenetically-based taxonomic classification of the Ophiuroidea [224] to map major lineage (~110 mya) distribution patterns. These families form three approximately equal-sized clades (A, B and C) [224,243] each contributing to the overall pattern in varying ways (Fig. 2 and Extended Data Fig. 8).

Environmental plots (seafloor bathymetry, temperature (°C), salinity (‰), oxygen (ml/l), organic carbon flux (g/m^{2}year)) were derived following Woolley et al. [147]. Names of water masses are derived from Tomczak & Godfrey [22].

Phylodiversity analyses. Phylogenetic diversity (PD) calculations summed tree branch lengths for all taxa present in a grid cell [244]. Relative PD [245,246] was calculated by dividing observed PD by the mean from a null model, generated by randomising species present in each cell while retaining cell species richness (1,000 replicates). This index produces similar results to mean phylogenetic pairwise distance between species (MPD or Δ^{+} [247,248] normalised by the mean distance among all species, Extended Data Fig. 3c). Evolutionary distinctness (ED) scales PD by the number of terminal lineages subtending the branch, thus measuring a species' contribution to the total evolutionary history of its clade [249,250]. However, this index is therefore sensitive to the presence of unknown cryptic species, which appear to be prevalent in the oceans [251]. Therefore, each lineage less than 10 my (4% of tree height) was counted as only one terminal for the purposes of calculating ED. We mapped the top 10% of species with the highest levels of ED [252]. The mean lineage diversification rate (Fig. 1d) [253] is the inverse of mean ED [250,252].

We calculated beta diversity (based on morpho species) and phylogenetic beta-diversity (based on phylogenetic branch lengths) [225] following Baselga [254] and Leprieur et al. [226]. For each pair of grid cells we calculated 1) β_{Sor} (Sorensen's dissimilarity index) and β_{Sim} (Simpson's dissimilarity index), and 2) their phylogenetic equivalents ($p\beta_{Sor}$, $p\beta_{Sim}$) for species on our tree. We analysed the resulting dissimilarity matrices in two ways, using 1) ordination and classification to identify spatial clusters of ophiuroid phylodiversity (Extended Data Fig. 9), and 2) a neighbourhood approach (comparing focal cells with their immediate latitudinal and bathymetric neighbours) to investigate fine scale turnover of beta diversity (Fig. 1f, Extended Data Fig. 3e-f). Non-parametric Multidimensional Scaling Ordination was performed using the R function metaMDS() in the 'vegan' v2.4-5 package [158]. Various agglomerative hierarchical and non-hierarchical clustering algorithms were trialled [255] as implemented in the R-package 'cluster' v2.0.1 [256], using mean silhouette scores to discriminate supported clusters.

For further phylogenetic diversification analyses, we defined phylo-regions (or biomes) based on a UPGMA (unweighted Pair-Group Method using arithmetic Averages) cluster analysis of the $p\beta_{Sim}$ dissimilarities, on the basis that it emphasised compositional change rather than species-richness gradients, produced well-supported geographically-cohesive groups, and reasonably reflected the neighbourhood turnover plot. We selected the five cluster solution (Fig. 1g) as a balance between the complexity of the study region and the requirements of multi-state phylogenetic models (see below), including the need to limit the number of parameters being estimated and reduce the unevenness in the numbers of species per state [257]. In particular, abyssal clusters were characterised by very low species richness and we used combined bathyal-abyssal biomes for subsequent analyses. Simpson's beta phylo diversity between biome faunas confirms the distinction between the tropical-temperate shallow water realm and the deep sea+Antarctic realm (Extended Data Fig. 10).

Multiple State Speciation and Extinction (MuSSE) models [258] were fitted across our phylogenetic tree to estimate speciation, extinction and transition rates associated with the five biomes. We used the R package ‘diversitree’ v0.9-10 [258] to report both Maximum Likelihood and Bayesian results (exponential prior, ML solution start, 10,000 MCMC sampled steps, 100 step burnin for chain tuning).

We corrected for incomplete sampling [259,260] by specifying the ratio of species in our tree to all known species for each phylo-region (Antarctica = 85%, temperate shallow = 80%, temperate deep= 80%, tropical shallow = 75%, and tropical deep= 70%). We assigned a single state to each species in the MuSSE analysis by selecting the biome with the maximum number of collection events for that species. We did not cater for multiple states per species, despite some of our species occurring in two (n=123) or three biome (n=2), because 1) current shared-state models (e.g. GeoSSE [261]) can only model two regions, and 2) the addition of multi-regional states to the MuSSE analysis would greatly increase the number of parameters being estimated. Instead, in order to test the robustness of our single biome state assignment, we compared the result against 100 trials of re-sampling species states according to their frequencies of occurrence in each region. These re-sampling rates essentially matched our single state assignment results, indicating its adequacy. As a final check we conducted 100 trials randomising the tree tip states. The lack of any correlation of these random to our observed results (mean Pearson correlation=0.05) further indicated the results were not merely a product of relative biome richness [259]. Results of these re-sampling and randomization analyses are summarized in Extended Data Table 4 and Extended Data Fig. 5.

Biome transition rates were further corroborated [257-260] through the use of ancestral state reconstructions generated from All Rates Determined (ARD) and Equal Rates (EQ) Maximum Likelihood models using the ace(type=”discrete”) function in the R package ‘ape’ v5 [262]. The number of cladogenetic biome transitions were calculated from 1,000 stochastic maps sampled from the ARD marginal state probabilities using the R function make.simmap(Q="empirical") in the package phytools v0.6-44 [263]. For phylogenetic visualisations (Fig. 2), nodes were determined to be decisive if the ER state probability was >= 95%.

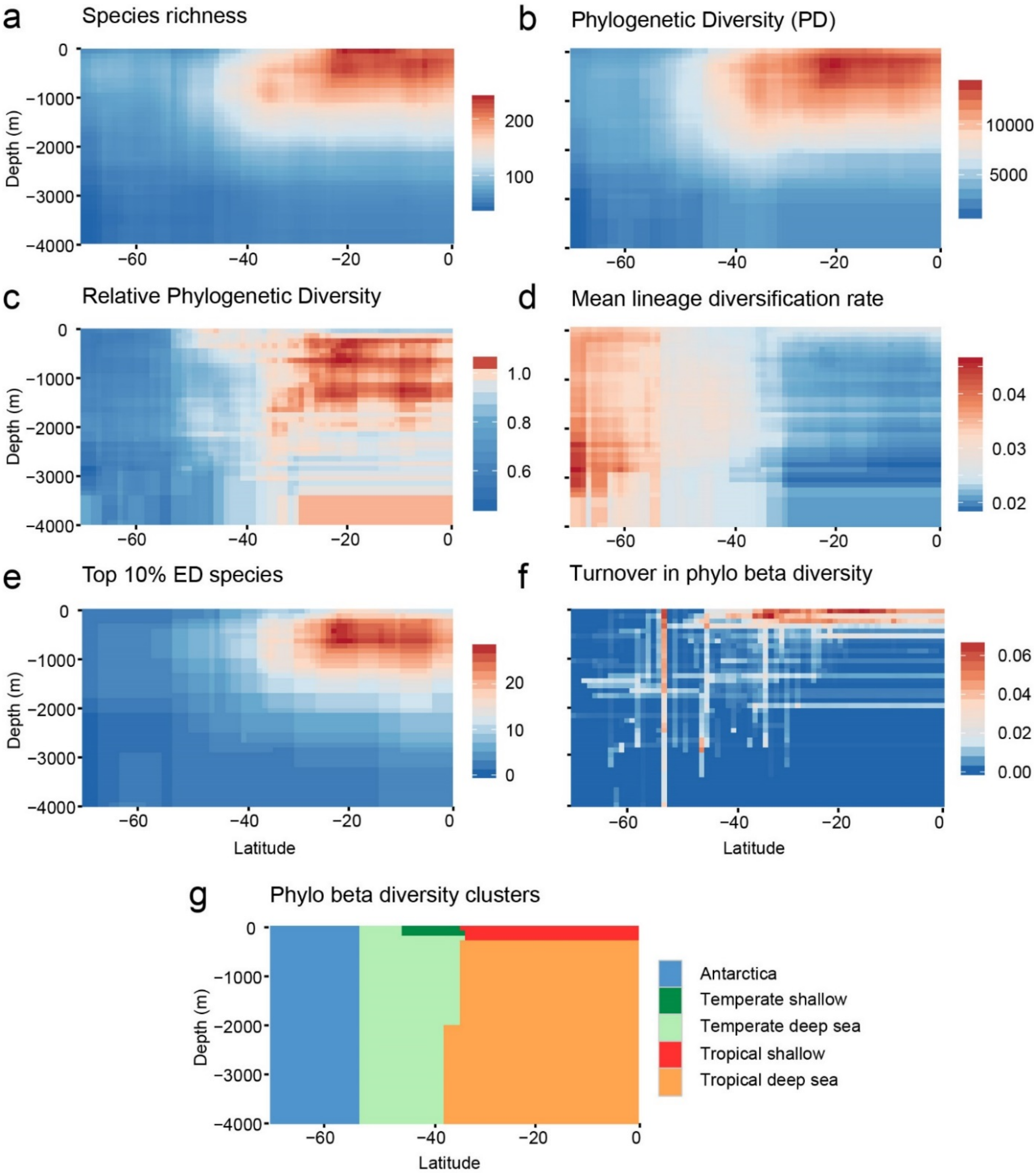


Figure 1 | **The shape of phylodiversity across the seafloor**. (a) Species richness is concentrated in tropical shallow water regions with a steep decline to Antarctica and the abyss. Phylogenetic metrics are all high at tropical latitudes, although they emphasise different aspects of evolutionary assembly with depth. (b) Total Phylogenetic Diversity (PD) peaks at upper bathyal depths. (c) Relative PD given species richness is high at mid bathyal depths and low in Antarctica and tropical shallows. (d) Mean lineage diversification rates are highest in Antarctica and the tropical shallows. (e) Numbers of species with the highest ED peaks in the tropical upper bathyal. (f) Turnover in Simpson's phylogenetic beta diversity (pB_{Sim}) between neighbouring cells is highest across depth in tropical shallow water and across latitudes between temperate and Antarctic latitudes. (g) Latitudinal/bathymetric representations of five clusters derived from pB_{Sim} dissimilarity coefficients.

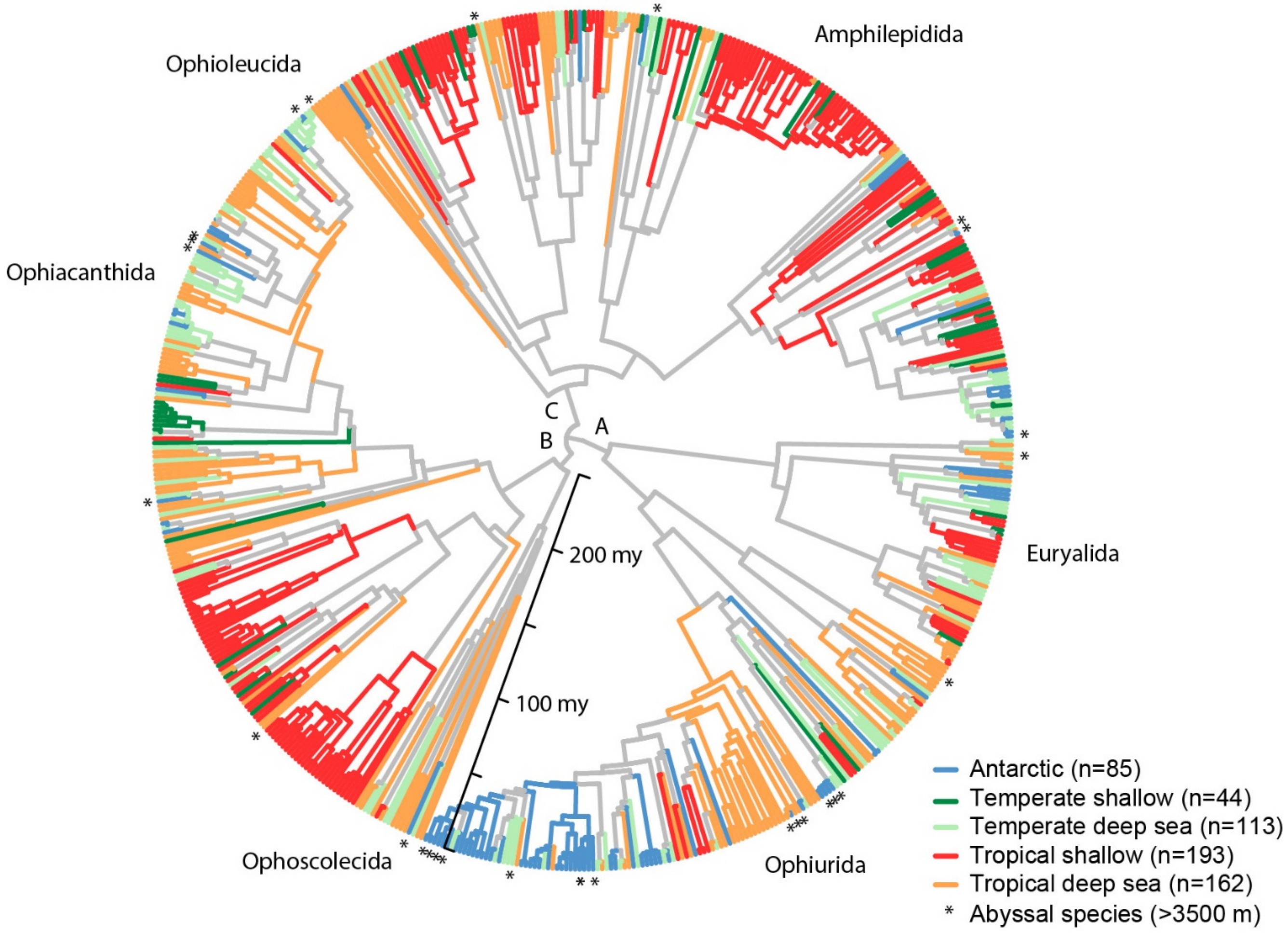


Figure 2 | **Biomes possess divergent phylogenetic signatures.** Maximum Likelihood ancestral state reconstruction shows lineages (n=596) from tropical shallow and Antarctic biomes are phylogenetically clustered compared to those in other biomes. Branch colours on the phylogenomic chronogram follow Fig. 1g, grey indicates indecisive nodes (<95% probability). The three primary clades (A-C) and six orders are indicated, and abyssal taxa marked by asterisk.

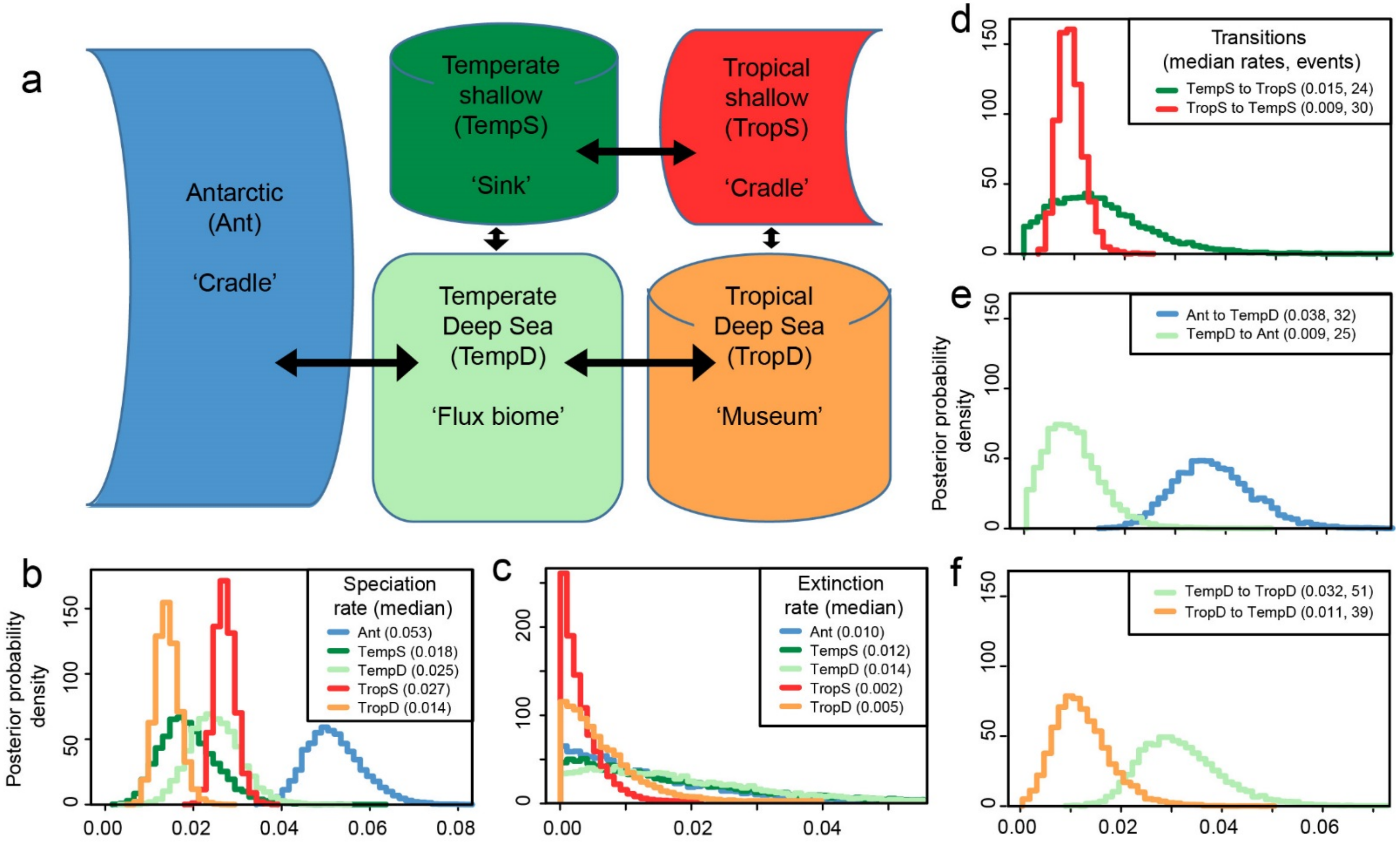
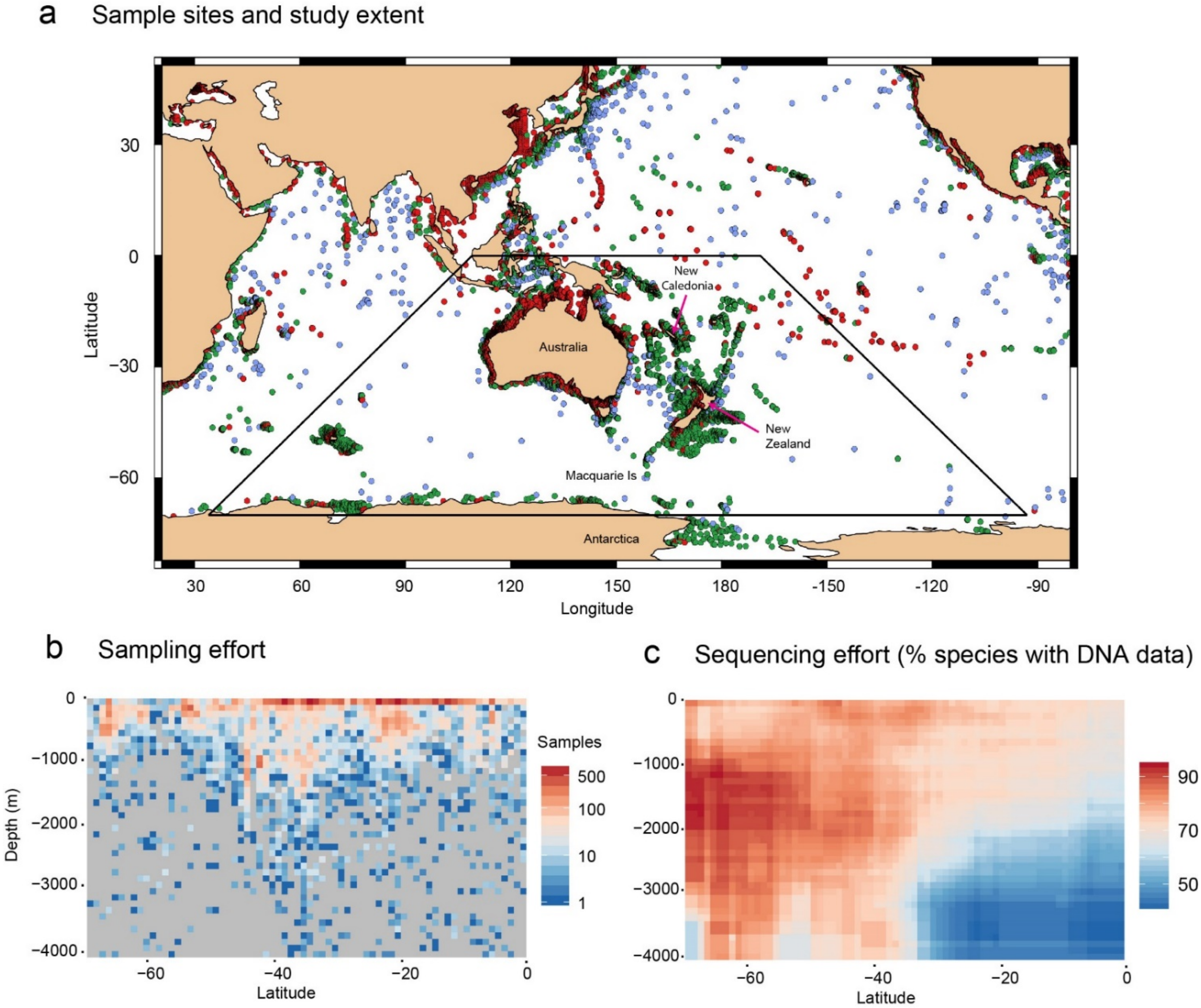
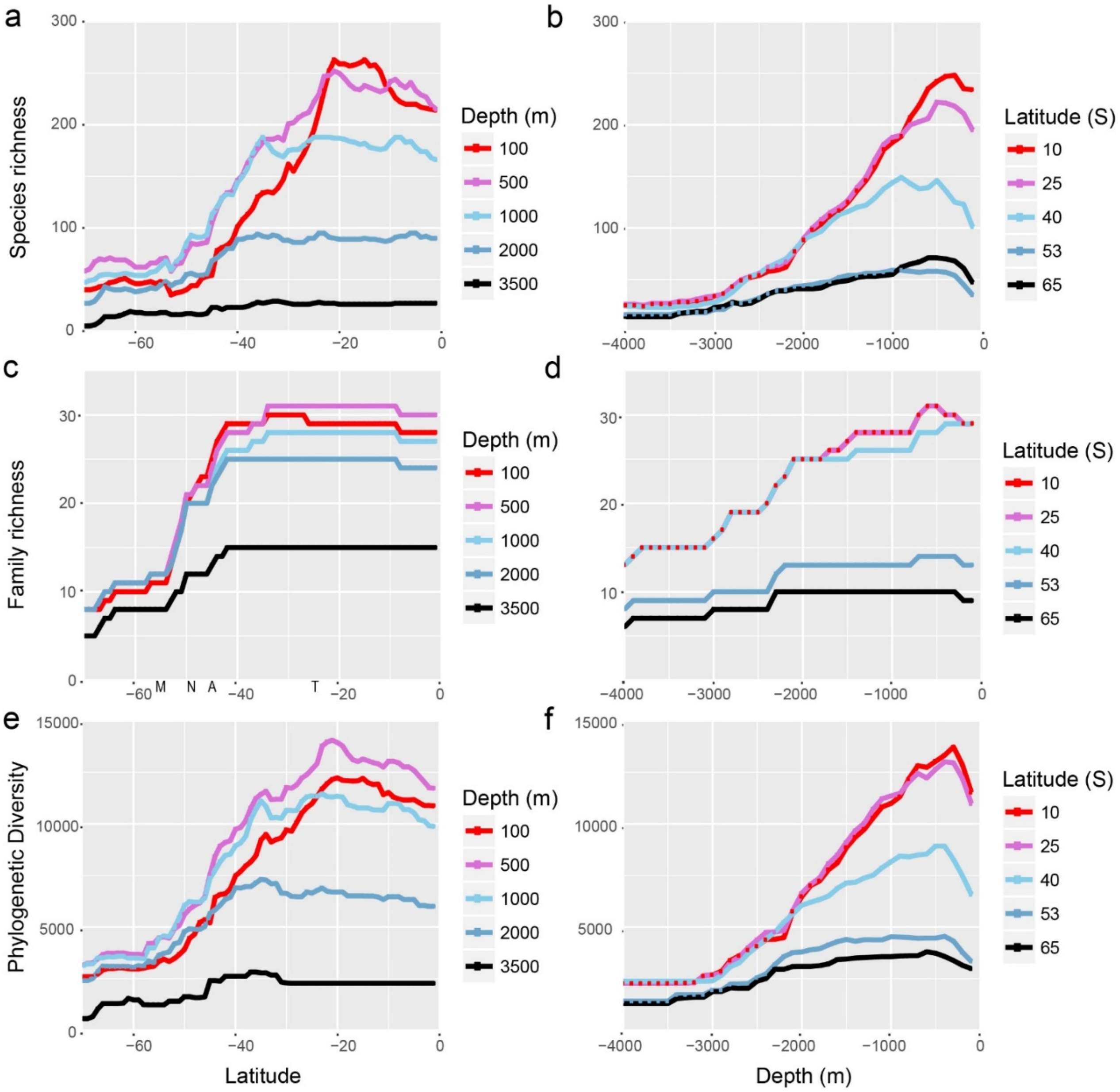


Figure 3 | **Distinct pathways of diversification and migration occur in shallow and deep seas** (a) Schematic of biome interactions from the MuSSE/ARD stochastic mapping analyses, showing the predominately latitudinal pattern of interchange (arrows scaled to the median number of stochastic map events), with Antarctica coupled to deep sea rather than shallow biomes. (b) Speciation rates are highest for the Antarctic biome and lowest for the tropical deep sea. (c) Extinction rates are elevated for temperate and Antarctic biomes and low for tropical ones, with negligible net diversification in temperate biomes. Net migration between neighbouring biomes is similar at shallow depths (d) but towards the tropics in the deep sea (e-f). See Extended Data Tables 4, 6 for full details.

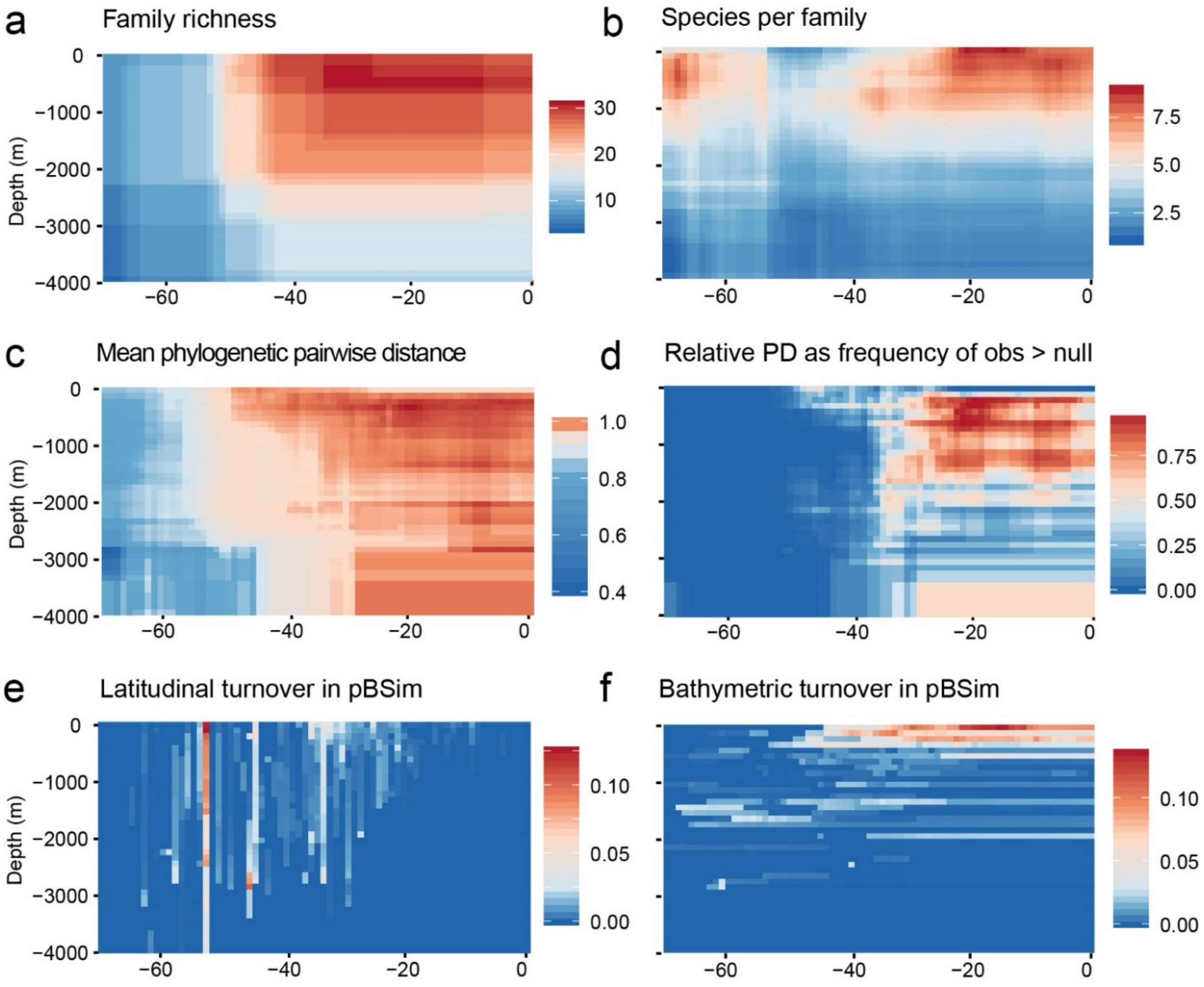
Extended Data



Extended Data Figure 1 | Maps and plots of collection and sequencing effort. (a) Map of sample sites across the study area. The study area, a trapezoid shape on this geographical projection, contains equal area polygons per latitude spaced either side of 150°S. Red dots indicate shallow sites (0-200 m), green are from the upper to mid bathyal (200-2000 m) and blue from the lower bathyal and abyss (>2000 m); many sites overlap. Sampling over our study area has been concentrated around continental margins with few expeditions to the abyssal plain or mid-ocean ridges. Collection effort (e.g. numbers of trawls, dredges, RoV collections) over our study area (b) was, as expected, highest in shallow water (0-100 m) followed by cells at upper to mid bathyal depths. Variation in collection effort does not explain the latitudinal gradient of species richness for this data[211]. Although, collection effort was much lower at lower bathyal and abyssal depths (2000-4000 m), this was offset by a general increase in size of observed species ranges with depth. Many abyssal ophiuroids were widespread across temperate and tropical latitudes. Percentage of species with DNA data (c) was high (>70 %) over the entire study area, except below 2000 m across tropical latitudes (mean 52 %, min 41 %). However, these depths are relatively species poor and sequencing effort across the entire tropical deep sea biome (as defined in Fig. 1g) exceeded 70 %.



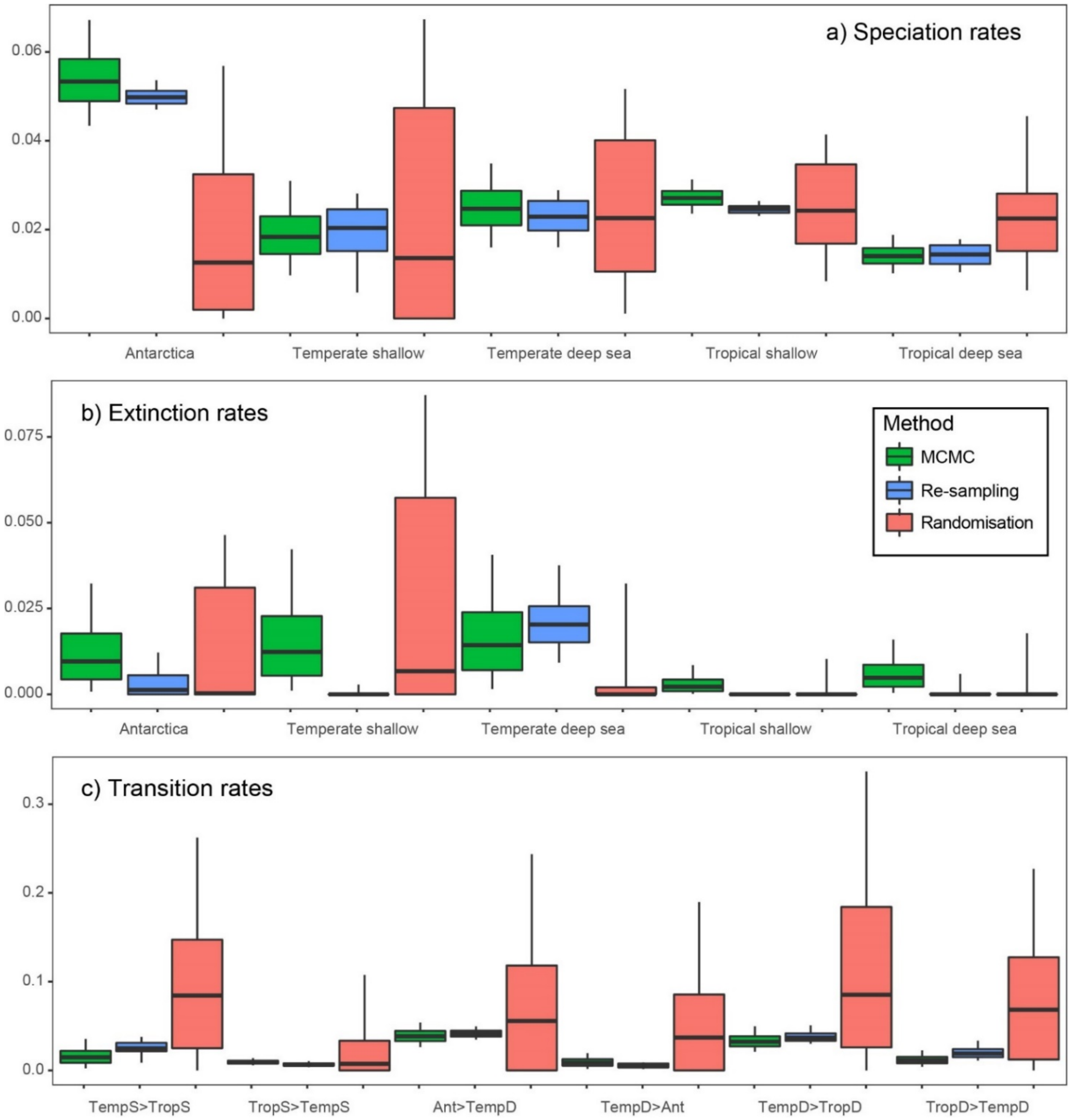
Extended Data Figure 2 | Latitudinal and Bathymetric gradients. Diversity peaks between 13 and 23°S and between 200 and 600 m depth, declining into polar regions and the abyss. Reports (e.g. [15]) that the global ocean fauna exhibit a mid-bathyal species richness (2000 m) are based on a misreading of Vinogradova [236], who included only species occurring below 2000 m in her analysis of the abyssal decline in richness, thus generating an artificial peak of richness at 2000 m. T-Tropical-Temperate transition, A-end of Australian continental shelf, B-end of New Zealand continental shelf, M-Macquarie Island.



Extended Data Figure 3 | **Additional latitudinal/bathymetric plots of diversity indices.** (a) High levels of family-level richness extend into temperate regions and mid bathyal depths. Phylogenetic radiations (b) are concentrated in tropical shallow habitats and Antarctica. (c) Patterns of normalised mean phylogenetic pairwise distance between cells is similar to relative PD (Fig. 1c). (d) The frequency that observed PD exceeded null models that randomised species present in each cell while retaining cell species richness. Simpson's beta phylodiversity turnover (Fig. 1f) factored into latitudinal (e) and bathymetric (f) components.

		MuSSE rates				Stochastic map events from ARD ML ancestral state model (n=1000)	
Rate	Biome(s)	ML	MCMC median	Tip state re-sampling (n=100)	Tip randomisation (n=100)	Mean	SD
Speciation	Antarctica (Ant)	0.050693	0.053309	0.049784	0.013245		
	Temperate shallow (TempS)	0.016091	0.018360	0.020361	0.013721		
	Temperate deep sea (TempD)	0.027735	0.024691	0.022906	0.022841		
	Tropical shallow (TropS)	0.025076	0.027110	0.024599	0.024398		
	Tropical deep sea (TropD)	0.012104	0.014036	0.014409	0.022491		
Extinction	Antarctica (Ant)	0.008355	0.009586	0.001280	0.000363		
	Temperate shallow (TempS)	0.000006	0.012346	0.000000	0.005197		
	Temperate deep sea (TempD)	0.016715	0.014348	0.020324	0.000000		
	Tropical shallow (TropS)	0.000000	0.002225	0.000000	0.000000		
	Tropical deep sea (TropD)	0.000924	0.004813	0.000001	0.000000		
Biome transition	Ant>TempS	0.000002	0.000923	0.000997	0.000000	0.7	0.8
	Ant>TempD	0.039868	0.038453	0.041098	0.052866	32.6	5.9
	Ant>TropS	0.000000	0.000942	0.000000	0.080543	0.4	0.7
	Ant>TropD	0.000003	0.002259	0.000000	0.091123	11.4	4.0
	TempS>Ant	0.000098	0.002101	0.001007	0.022291	2.2	1.2
	TempS>TempD	0.017291	0.012074	0.008190	0.038603	9.3	3.0
	TempS>TropS	0.017048	0.014675	0.024850	0.084110	24.3	6.1
	TempS>TropD	0.004020	0.006957	0.000001	0.074225	7.6	3.2
	TempD>Ant	0.008814	0.008677	0.005229	0.033824	24.1	4.1
	TempD>TempS	0.001091	0.001240	0.000406	0.002308	3.4	1.6
	TempD>TropS	0.002933	0.001606	0.000000	0.109594	4.1	2.0
	TempD>TropD	0.029547	0.032253	0.036919	0.084304	51.9	8.1
	TropS>Ant	0.000000	0.000299	0.000000	0.024469	1.3	1.0
	TropS>TempS	0.008712	0.009134	0.006551	0.008052	29.9	3.8
	TropS>TempD	0.000002	0.000725	0.000001	0.052294	7.4	2.6
	TropS>TropD	0.001751	0.001617	0.004036	0.173270	16.5	3.9
	TropD>Ant	0.002534	0.002803	0.002961	0.038863	9.2	2.7
	TropD>TempS	0.000592	0.001009	0.000001	0.004054	5.3	2.0
	TropD>TempD	0.010703	0.011255	0.019104	0.066857	39.2	6.0
	TropD>TropS	0.000851	0.001137	0.002733	0.195992	14.5	3.6
Log Likelihood (LnL)		-3473.45	-3399.53	-3484.50	-3755.13		

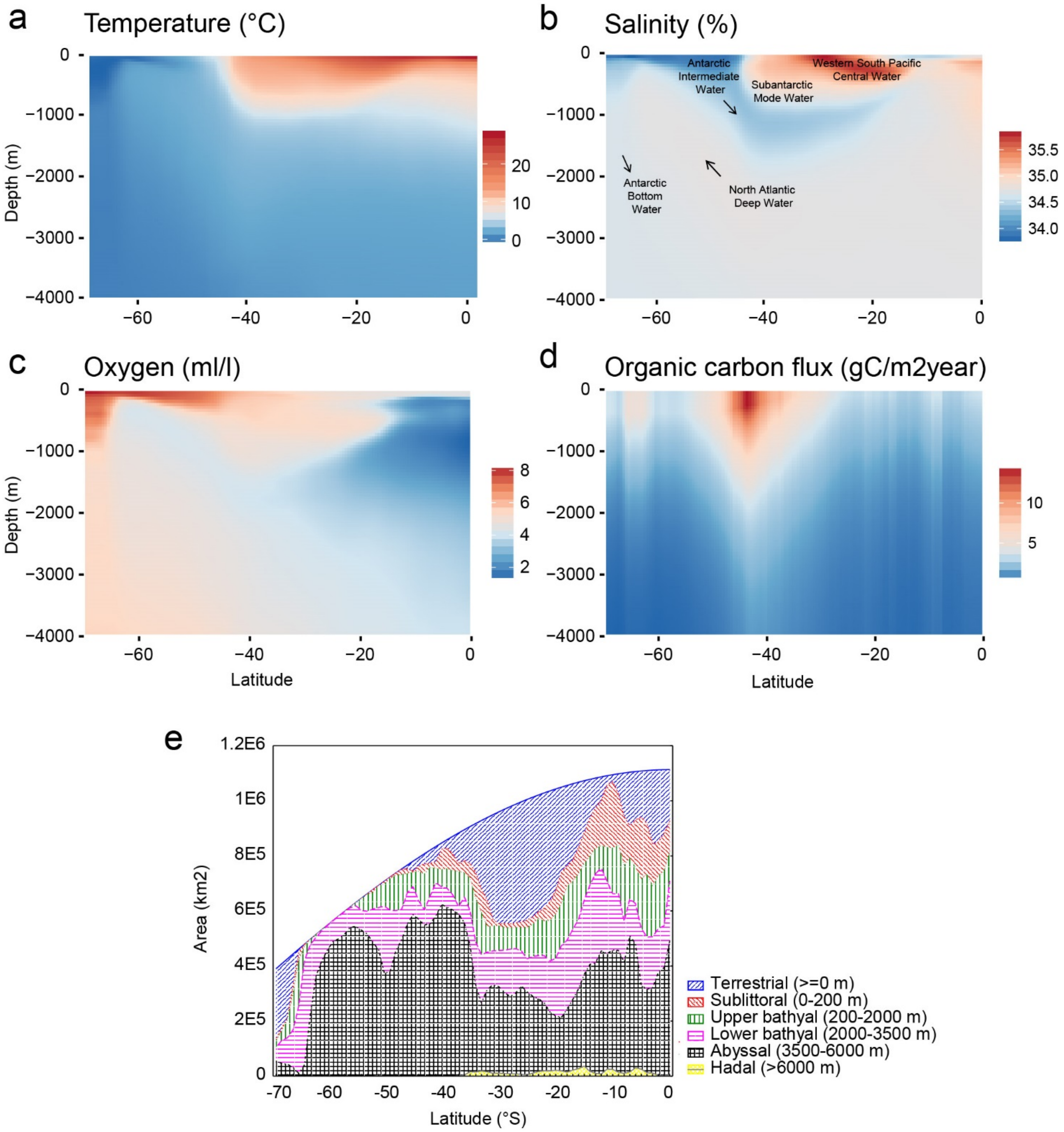
Extended Data Table 4 | MuSSE and stochastic map parameter estimates. MuSSE speciation, extinction and biome transition rates calculated from Maximum Likelihood (ML) and Bayesian (MCMC) methodologies for the entire dataset, and state resampling trials (ML median values), followed by mean and standard deviation of the number of cladogenetic transition events calculated from stochastic maps of marginal All Rates Determined (ARD) ML ancestral state reconstructions. Cells are ranked by colour (Red>White>Blue) independently for each column and rate type. Distributions of MuSSE rates are shown in Extended Data Fig. 5. The rank order of speciation, extinction and transition rates were broadly similar for both Maximum Likelihood (ML) and Bayesian MuSSE methodologies. However, ML extinction rates were considerably lower than the MCMC equivalents, probably due to their wide confidence intervals.



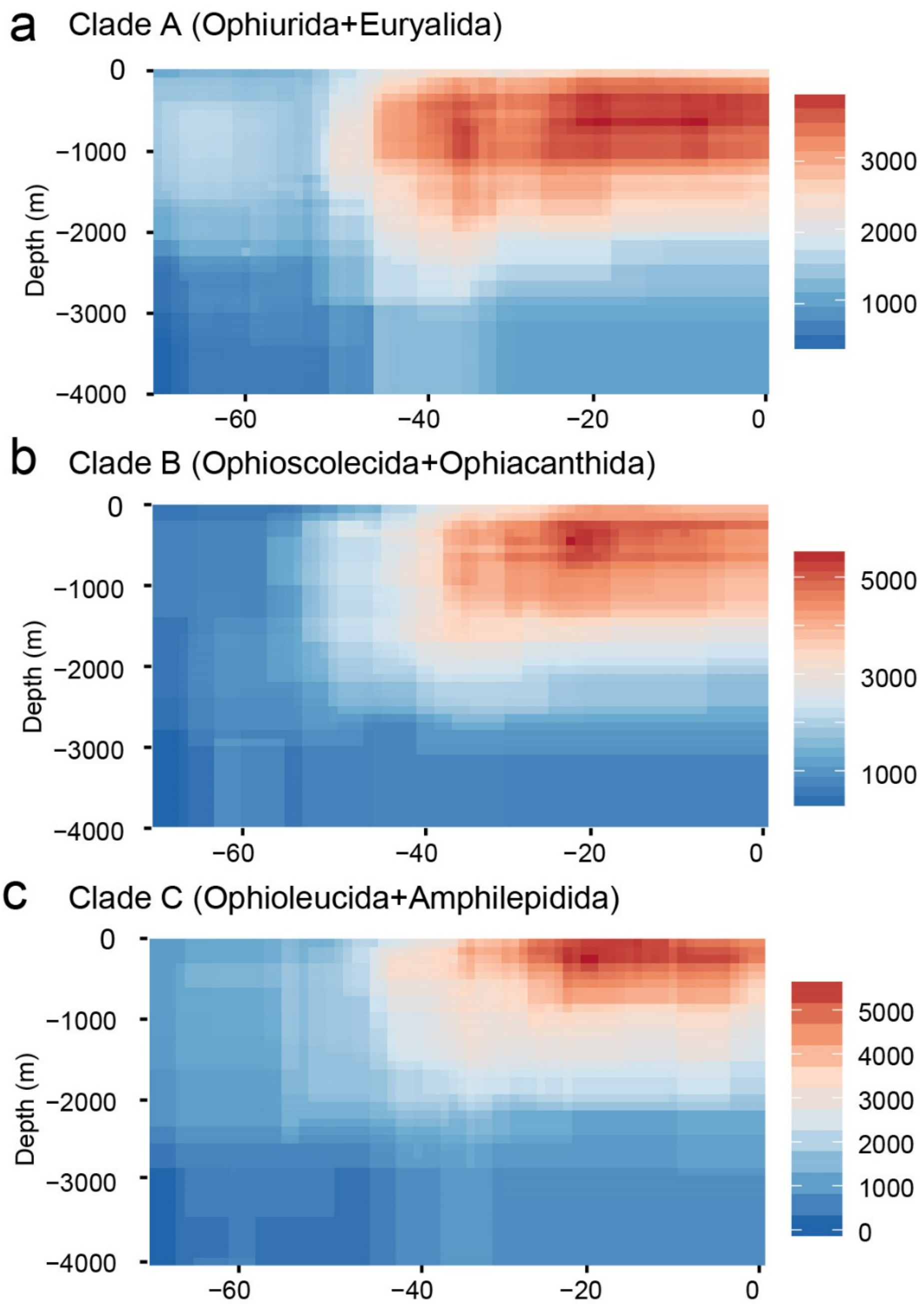
Extended Data Figure 5 | MuSSE randomisation trials. Comparison of (a) speciation, (b) extinction and (c) transition rates generated from our MuSSE Bayesian MCMC analysis compared to ML analyses that i) resampled states (biomes) within species with multi-biome distributions, and ii) randomised tip states while retaining biome richness. The re-sampling results are broadly similar to the original MCMC run, indicating biome misclassification did not significantly affect the results. One exception is the Temperate shallow (TempS) to tropical shallow (TropS) transition rates, which were significantly different for re-sampling due the occurrence of subtropical species across the transition zone. Tip state randomisation produced wide confidence limits as expected, indicating that the results were not merely a product of relative biome richness or chance association.

Parameter significance tests	MuSSE MCMC rate	ARD stochastic mapping events
Antarctic with highest speciation rate	0.9978	-
Ant>TempB greater than TempB>Ant	1.0000	0.860
TempD>TropD greater than TropD>TempD	0.9980	0.879
TropS>TempS greater than TempS>TropS	0.2683	0.771

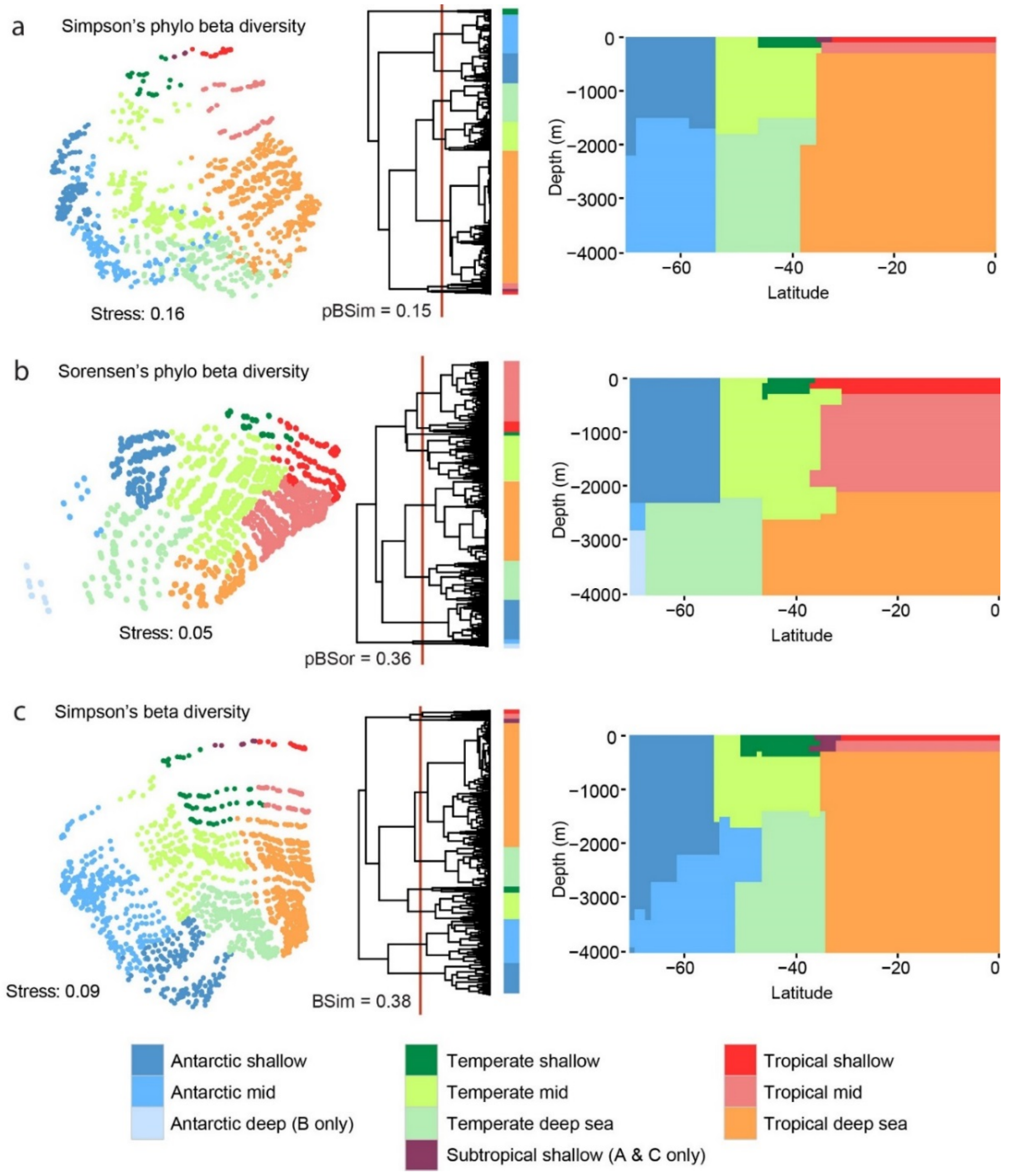
Extended Data Table 6 | Comparison of selected parameters from both the set of 10,000 MuSSE MCMC steps and number of events from 1,000 All Rates Determined stochastic maps. The Antarctic biome had significantly higher speciation rate than the other four biomes. In the deep sea, the net transition across the three biomes (Antarctica to temperate deep sea to tropical deep sea) was from south to north. In shallow water, although the number of north to south events were generally higher, the rates were lower reflecting inequality in species richness; the direction of transition was not significant at $\alpha=0.05$.



Extended Data Figure 7 | Environmental patterns. Mean annual environmental data (a-d) for each latitudinal (1.0°) and bathymetric (100 m) cell across our study area for comparison with phylodiversity analyses. A lens of relatively hot (a) salty (b) water occurs at shallow depths across tropical and temperate latitudes (0-40°S). Antarctic Intermediate Water sinks at subantarctic latitudes and flows north to subtropical latitudes (20°S) at mid-bathyal depths (~1000 m). Deoxygenated (c) 'deep' water flows southwards from the northern hemisphere at lower bathyal depths, shoaling off the Antarctic continent. Cold dense oxygen-rich 'bottom' water sinks near Antarctica, flowing northwards at abyssal depths. Yearly net primary production (d) peaks at temperate latitudes over the study area, driving elevated carbon flux to the seafloor; Antarctic production is highly seasonal. Area of depth strata per degree of latitude across the study region (e), calculated by counting the number of cells of each category for each degree of latitude in the ETOPO1 raster GIS layer (0.01º resolution) and adjusting for the reducing circumference of the Earth with increased latitude. There is limited terrestrial, sublittoral and upper bathyal habitat in the Southern Ocean between the Australian/New Zealand continental masses and Antarctica.



Extended Data Figure 8 | Phylodiversity plots of ophiuroid subclades. The three major clades of extant Ophiuroidea (following O'Hara et al. [224,243]) contribute differently to overall patterns of phylogenetic diversity (PD) across our five biomes (Fig. 2). (a) Clade A is rich in deep-sea and Antarctic species, although individual families had divergent distributions. The Antarctic is dominated by the Ophiopyrgidae while the Ophiomusaidae, Ophiosphalmidae, Astrophytidae and Euryalidae are largely absent from there. Clade A has low species richness in the two shallow water biomes. (b) Clade B is rich in the tropical shallow, tropical deep sea and temperate deep sea biomes. It consists of one suborder (Ophiodermatina) that is heavily represented in tropical shallow water biome and another (Ophiacanthina) that is largely present in deep sea habitats, particularly on hard substrata such as seamounts. (c) Clade C on the other hand is rich in tropical and temperate shallow water biomes, including the families Ophiolepididae, Ophionereididae, Amphiuridae and Ophiotrichidae, and has relatively few lineages in the deep sea or Antarctica.

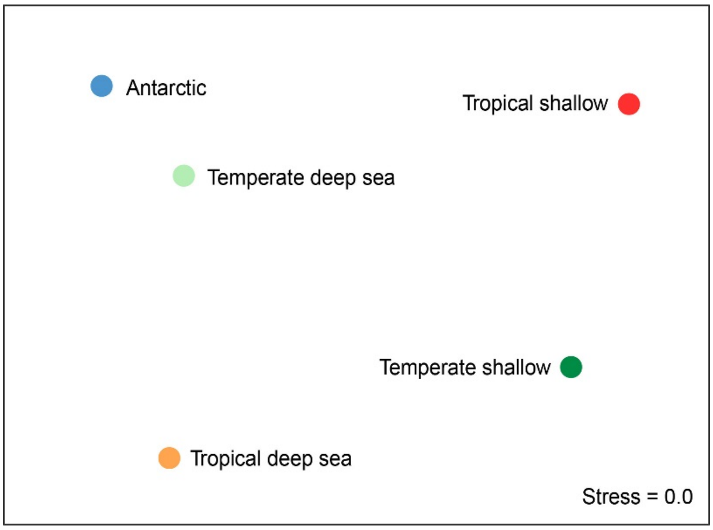


Extended Data Figure 9 | Beta diversity and phylo beta diversity. Ordinations (nMDS), cluster dendrograms (UPGMA) and Latitudinal/bathymetric representations of (phylo) beta diversity clusters for each 1.0° latitude x 100 m depth cell across our study region. (a) Simpson's phylo beta diversity (pB_{Sim}), (b) Sorensen's phylo beta diversity (pB_{Sor}), and (c) Simpson's beta-diversity of presence-absence of species (B_{Sim}). Nine clusters (vertical red lines) are coloured to highlight coherent patterns across latitude and depth. The three methods showed broad similarities in grouping the fauna into tropical, temperate and polar regions and sublittoral, upper bathyal, and lower bathyal/abyssal depth strata, although the cluster hierarchy can differ. The pB_{Sim} and B_{Sim} plots emphasised the strong compositional turnover between 100-300 m at tropical and temperate latitudes (Fig. 1f, ED Fig. 2e). pB_{Sor}, which emphasises species richness gradients in addition to compositional turnover, clustered upper bathyal cells (200-2000 m) separately from those in the lower bathyal/abyss (>~2000 m), reflecting a zone of higher species richness and relative PD (Fig. 1). The pB_{Sim} and B_{Sim} analyses also identified a small shallow water subtropical cluster reflecting the heightened latitudinal turnover between 30-40°S[145]. The pB_{Sor} analysis separated two species poor Antarctic deep-sea regions. The extent of the temperate sublittoral zone varied among analyses, possibly due to it being a small zone of admixture and turnover. The number of clusters was reduced to five (Fig. 1g) for the MuSSE analyses (see methods for rationale).

a

	Antarctica	Temperate shallow	Temperate deep sea	Tropical shallow
Temperate shallow	0.746			
Temperate deep sea	0.392	0.595		
Tropical shallow	0.709	0.394	0.668	
Tropical deep sea	0.491	0.541	0.475	0.770

b



Extended Data Figure 10 | Simpson's phylo beta diversity (pB_{Sim}) between biome faunas. (a) pB_{Sim} results, and (b) a resulting non-parametric MDS. Both the tropical/temperate shallow water biomes and the Antarctic/tropical deep sea/temperate deep sea biomes are compositionally similar (i.e. with low values of pB_{Sim}), consistent with the MuSSE and ARD stochastic map biome transition results (Fig. 3 and Extended Data Table 4).

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