

Regional-scale patterns of deep seafloor biodiversity for conservation assessment

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Abstract

Aim: Mining and petroleum industries are exploring for resources in deep seafloor environments. Lease areas are often spatially aggregated and continuous over hundreds to thousands of kilometres. Sustainable development of these resources requires an understanding of the patterns of biodiversity at similar scales, yet these data are rarely available for the deep sea. Here, we compare biodiversity metrics and assemblage composition of epibenthic megafaunal samples from deep-sea benthic habitats from the Great Australian Bight (GAB), a petroleum exploration zone off southern Australia, to similar environments off eastern Australia.

Location: The Great Australian Bight (34–36°S, 129–134°E) and south-eastern (SE) and north-eastern (NE) Australian continental margins (23–42°S, 149–155°E) in depths of 1,900–5,000 m.

Methods: A species–sample matrix was constructed from invertebrate and fish megafauna collected from beam trawl samples across regions at lower bathyal (1,900–3,200 m) and abyssal (>3,200 m) depths, and analysed using multivariate, rarefaction and model-based statistics. We modelled rank abundance distributions (RAD) against environmental factors to identify drivers of abundance, richness and evenness.

Results: Multivariate analyses showed regional and bathymetric assemblage structure across the region. There was an almost complete turnover of sponge fauna between the GAB and SE. SE samples had the highest total faunal abundance and species richness. RAD models linked total abundance and species richness to levels of carbon flux. Evenness was associated with seasonality of net primary production.

Conclusions: Significant assemblage structure at regional scales is reported for the first time at lower bathyal and abyssal depths in the southern Indo-Pacific region along latitudinal and longitudinal gradients. The GAB fauna was distinct from other studied areas. Relatively high species richness, previously reported from the GAB continental shelf, did not occur at lower bathyal or abyssal depths. Instead, the abundance, richness and evenness of the benthic fauna are linked to surface primary production, which is elevated off SE Australia.

KEY WORDS

benthos, conservation assessment, deep sea, key ecological features, rank abundance distribution

1 | 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, Durden, & Christiansen, 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, Thompson, Johnston, & Santillo, 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 licence 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 United States 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, Smith, & Arbizu, 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 characterized as both relatively uniform over oceanic scales and characterized 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; Wedding et al., 2013; Williams et al., 2009).

The Great Australian Bight (GAB) has been recognized 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 recognized 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, Sorokin, Currie, Rogers, and McLeay (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 (100–2,000 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 (200–3,000 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, Althaus, Sorokin, and Williams (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 (200–1,000 m).

Over a 3-year period (2015–2017), a number of voyages of the RV "Investigator" collected comparative beam trawl samples from lower bathyal (1,900–3,500 m) and abyssal (3,500–5,000 m) depths from both the GAB (IN2015_C01, IN2015_C02, IN2017_C01) and off eastern Australia (IN2017_V03) (Figure 1). This provided the opportunity to assess whether (a) the deep-sea benthic diversity of the GAB differed from that of comparable habitats off the east coast, and/or (b) 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 (Dunstan, Althaus, Williams, & Bax, 2012; Dunstan, Bax, Foster, Williams, & Althaus, 2012; Dunstan & Foster, 2011; Foster

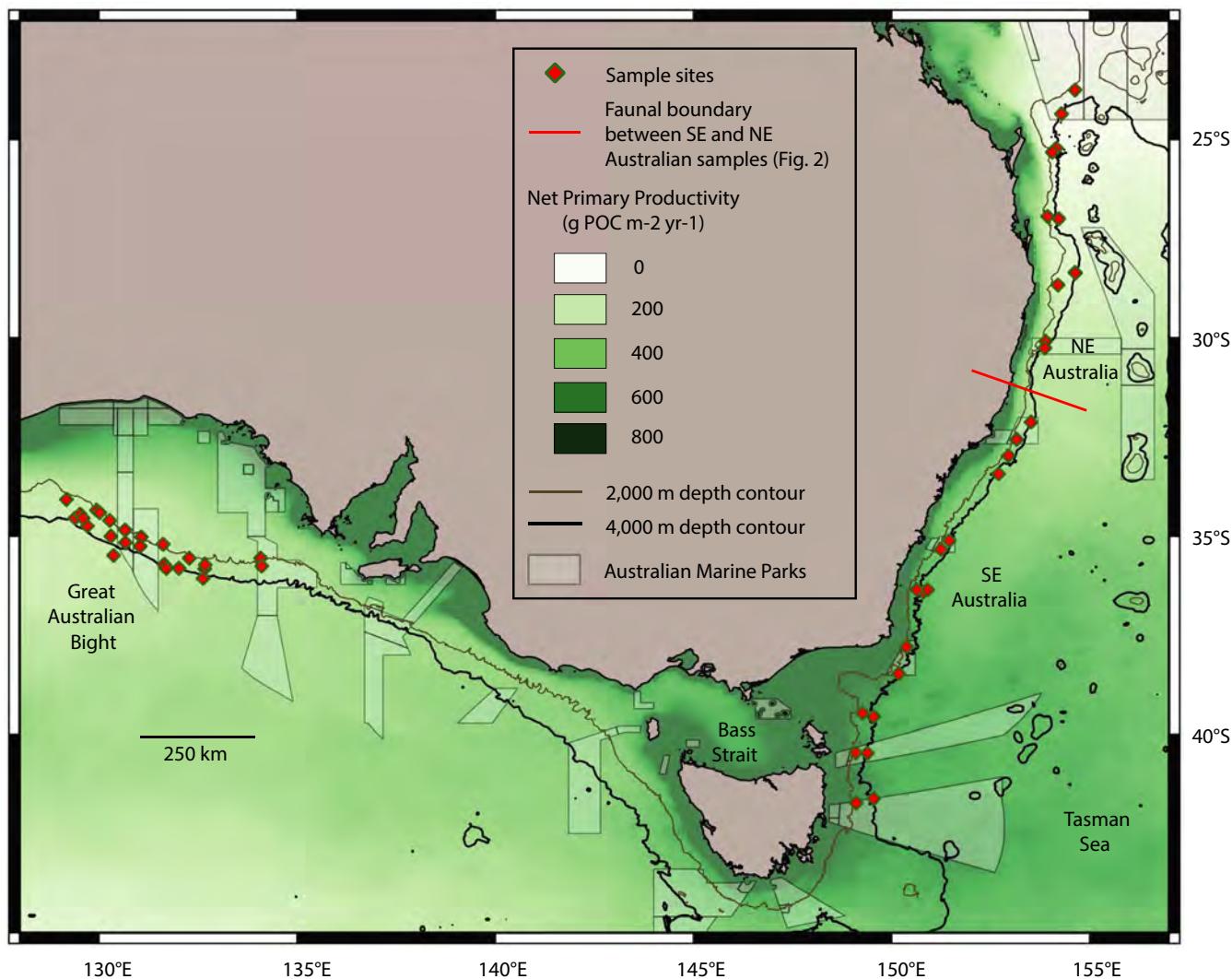


FIGURE 1 Map of sample sites (red) and net primary production (NPP) around southern and eastern Australia

& Dunstan, 2010). 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 geographical variables latitude, longitude and depth.

2 | METHODS

2.1 | 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 and the eastern continental margin of Australia on the RV Investigator (Table 1, Figure 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° 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 1,900 and 5,000 m to ensure inter-regional comparability. The depth of 1,900 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 2,000 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,

TABLE 1 Beam trawl sample location and modelled environmental data

Survey	Stn	Region	Location	Latitude	Longitude	Mid depth (m)	Date (day/month/year)	Area (m ²)	Temp. (°C)	Salinity (‰)	Oxygen (ml/L)	C flux (g m ⁻² year ⁻¹)
IN2015_C01	016	GAB	OR02, Area25	-36.069	132.637	4,607	31/10/15	5,666	0.953	34.710	4.708	0.735
IN2015_C01	026	GAB	OR07, Area19	-35.794	131.711	4,517	2/11/15	10,927	0.971	34.712	4.709	0.718
IN2015_C01	036	GAB	SZ02, Area20	-35.555	132.283	2,242	5/11/15	17,687	2.112	34.725	4.014	1.266
IN2015_C01	064	GAB	OR13, Area05	-34.074	129.182	2,726	13/11/15	15,221	1.787	34.733	4.245	0.974
IN2015_C01	079	GAB	SZ08, Area08	-34.341	129.942	2,079	16/11/15	7,129	2.245	34.708	3.988	1.192
IN2015_C01	080	GAB	SZ08, Area08	-34.408	130.024	2,114	17/11/15	7,916	2.214	34.712	4.002	1.197
IN2015_C02	137	GAB	Transect 5	-35.550	134.082	1,961	5/12/15	11,564	2.286	34.707	3.893	1.433
IN2015_C02	141	GAB	Transect 5	-35.818	134.109	2,826	5/12/15	12,341	1.761	34.732	4.214	1.067
IN2015_C02	151	GAB	Transect 4	-35.798	132.693	2,725	6/12/15	12,867	1.766	34.734	4.201	1.054
IN2015_C02	155	GAB	Transect 4	-35.722	132.681	1,933	7/12/15	10,814	2.286	34.714	3.907	1.423
IN2015_C02	207	GAB	Transect 3	-35.352	131.077	2,014	9/12/15	14,282	2.288	34.709	3.943	1.282
IN2015_C02	216	GAB	Transect 3	-35.262	131.042	3,021	10/12/15	12,056	1.723	34.734	4.234	0.950
IN2015_C02	227	GAB	Transect 1	-35.009	130.317	2,839	11/12/15	9,508	1.726	34.734	4.238	0.938
IN2015_C02	274	GAB	Transect 2	-35.165	130.665	3,002	12/12/15	11,273	1.647	34.734	4.279	0.910
IN2015_C02	276	GAB	Transect 2	-34.853	130.687	2,004	12/12/15	10,440	2.299	34.705	3.949	1.279
IN2015_C02	449	GAB	Transect 1	-34.625	130.280	2,037	18/12/15	14,233	2.305	34.703	3.954	1.251
IN2017_C01	175	GAB	OR21	-35.815	132.021	4,090	15/04/17	22,871	1.156	34.721	4.570	0.763
IN2017_C01	178	GAB	OR21	-35.716	131.656	3,883	16/04/17	21,483	1.242	34.724	4.531	0.777
IN2017_C01	179	GAB	OR21	-35.814	131.703	4,684	17/04/17	29,787	0.925	34.709	4.715	0.706
IN2017_C01	182	GAB	OR26	-35.487	130.378	4,961	17/04/17	18,706	0.852	34.704	4.814	0.664
IN2017_C01	192	GAB	OR11, Area07	-34.550	129.403	3,793	20/04/17	18,320	1.258	34.725	4.508	0.745
IN2017_C01	197	GAB	OR11, Area07	-34.447	129.532	3,292	21/04/17	14,740	1.481	34.732	4.383	0.827
IN2017_C01	198	GAB	OR11, Area07	-34.549	129.602	3,464	21/04/17	15,875	1.392	34.730	4.455	0.796
IN2017_V03	004	SE	Freyenet MP	-41.731	149.120	2,785	18/05/17	29,584	1.746	34.735	4.277	1.998
IN2017_V03	006	SE	Freyenet MP	-41.626	149.552	4,037	18/05/17	30,344	1.041	34.715	4.571	1.260
IN2017_V03	014	SE	Flinders MP	-40.464	149.102	2,392	20/05/17	15,348	1.988	34.721	4.051	2.352
IN2017_V03	015	SE	Flinders MP	-40.473	149.397	4,126	20/05/17	10,572	1.045	34.714	4.587	1.198
IN2017_V03	022	SE	Bass Strait	-39.462	149.276	2,726	22/05/17	11,756	1.788	34.731	4.204	2.049
IN2017_V03	030	SE	Bass Strait	-39.552	149.553	4,165	23/05/17	29,312	1.077	34.714	4.563	1.181
IN2017_V03	032	SE	East Gippsland MP	-38.479	150.184	3,851	24/05/17	11,580	1.132	34.718	4.501	1.290
IN2017_V03	035	SE	East Gippsland MP	-37.792	150.382	2,459	25/05/17	15,352	1.985	34.720	4.108	2.264

(Continues)

TABLE 1 (Continued)

Survey	Stn	Region	Location	Latitude	Longitude	Mid depth (m)	Date (day/month/year)	Area (m ²)	Temp. (°C)	Salinity (‰)	Oxygen (ml/L)	C flux (g m ⁻² year ⁻¹)
IN2017_V03	043	SE	Off Bermagui	-36.351	150.914	4,800	27/05/17	14,824	1.123	34.713	4.575	0.959
IN2017_V03	044	SE	Off Bermagui	-36.355	150.644	2,754	27/05/17	17,972	1.785	34.729	4.253	1.726
IN2017_V03	053	SE	Jervis MP	-35.114	151.469	3,981	28/05/17	16,792	1.170	34.719	4.479	1.045
IN2017_V03	056	SE	Jervis MP	-35.333	151.258	2,643	29/05/17	15,976	1.855	34.724	4.224	1.657
IN2017_V03	065	SE	Off Newcastle	-33.441	152.702	4,226	30/05/17	13,992	1.162	34.718	4.475	0.847
IN2017_V03	067	SE	Off Newcastle	-32.985	152.952	2,803	31/05/17	19,748	1.689	34.728	4.254	1.274
IN2017_V03	070	SE	Hunter MP	-32.575	153.162	2,534	3/06/17	26,260	1.881	34.724	4.153	1.405
IN2017_V03	078	SE	Hunter MP	-32.138	153.527	4,004	4/06/17	19,608	1.159	34.718	4.449	0.793
IN2017_V03	080	NE	Central Eastern MP	-30.099	153.596	1,225	5/06/17	16,096	1.909	34.716	4.104	1.193
IN2017_V03	088	NE	Central Eastern MP	-30.264	153.870	4,441	6/06/17	18,328	1.168	34.715	4.462	0.687
IN2017_V03	090	NE	Off Byron Bay	-28.677	154.203	2,574	7/06/17	15,400	1.819	34.723	4.202	0.981
IN2017_V03	097	NE	Off Byron Bay	-28.355	154.636	3,782	8/06/17	27,508	1.164	34.717	4.473	0.646
IN2017_V03	099	NE	Off Byron Bay	-28.371	154.649	3,789	9/06/17	14,416	1.164	34.717	4.473	0.646
IN2017_V03	101	NE	Off Moreton Bay	-26.946	153.945	2,548	9/06/17	11,564	1.811	34.722	4.213	1.017
IN2017_V03	102	NE	Off Moreton Bay	-27.008	154.223	4,269	10/06/17	18,332	1.161	34.715	4.449	0.575
IN2017_V03	109	NE	Off Fraser Island	-25.221	154.164	4,005	11/06/17	18,156	1.139	34.715	4.430	0.542
IN2017_V03	115	NE	Off Fraser Island	-25.325	154.068	2,346	11/06/17	11,976	1.994	34.709	4.029	0.905
IN2017_V03	122	NE	Coral Sea MP	-23.751	154.639	2,349	13/06/17	13,548	2,030	34.703	3.959	0.816
IN2017_V03	135	NE	Coral Sea MP	-24.352	154.291	4,001	15/06/17	19,812	1.136	34.715	4.403	0.517

Note: C flux, Mean annual carbon flux to the seafloor.

polychaetes, asteroids, ophiuroids, echinoids, holothuroids, gastropods, bivalves, cephalopods and tunicates. Important omissions include foraminiferans, hydrozoans, scyphozoans, bryozoans, pe-racarid 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 were 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 $2,000$ and $5,000$ 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 ($^\circ\text{C}$), salinity (psu) and dissolved oxygen (ml/L) were interpolated from the CARS2009 dataset (Ridgway, Dunn, & Wilkin, 2002). Mean annual net primary productivity (NPP, $\text{g C m}^{-2} \text{ year}^{-1}$) and the seasonal variation of net primary productivity (SVI, $\text{g C m}^{-2} \text{ year}^{-1}$) 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, $\text{g C m}^{-2} \text{ year}^{-1}$) was estimated using NPP and SVI data and a productivity export model (Lutz, Caldeira, Dunbar, & Behrenfeld, 2007).

2.2 | Statistical analyses

Most statistical analyses were performed using the R statistical environment v 3.4.3 (see Data S1 in Appendix S1), 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 (see Table S1 in Appendix S1) were 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, Gorley & Clarke, 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 rank abundance distributions using the R Package "RAD" v0.3 (Dunstan & Foster,

2011; Foster & Dunstan, 2010). 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's information criterion (AIC) was used on both linear and orthogonal polynomial predictors (degree = 2). Interaction terms were individually assessed to determine whether they further lowered AIC of best models. The models were formulated along the recommendations of Foster and Dunstan (2010). The N model included $\log(\text{sample area})$ as an offset and negatively binomial error distributions. The S model included the $\log(\text{sample area})$ 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. The input files for the RAD analyses are contained in Tables S2 and S3 in Appendix S1.

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 models, using mean values calculated across from randomized 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 $0.1 \times 0.1^\circ$) around southern and eastern Australia, restricted to lie between the geographical boundaries of 129 – 156.5°E and 42 – 23°S , and the depth contours of $2,000$ – $5,000$ 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, Belle, and Simberloff (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 add-in.

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– $1,900$ to $2,300$ 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.

3 | RESULTS

The final data matrix was 666 operational taxonomic units (OTUs) across the 49 samples (see Table S1 in Appendix S1). Species-rich 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 per cent 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 (Figure 2a). Within each of these groups, regional (GAB, SE Australia, NE Australia) subclusters were evident. The exception was for the bathyal GAB samples which were divided into (a) mid-bathyal (1,900–2,300 m) and (b)

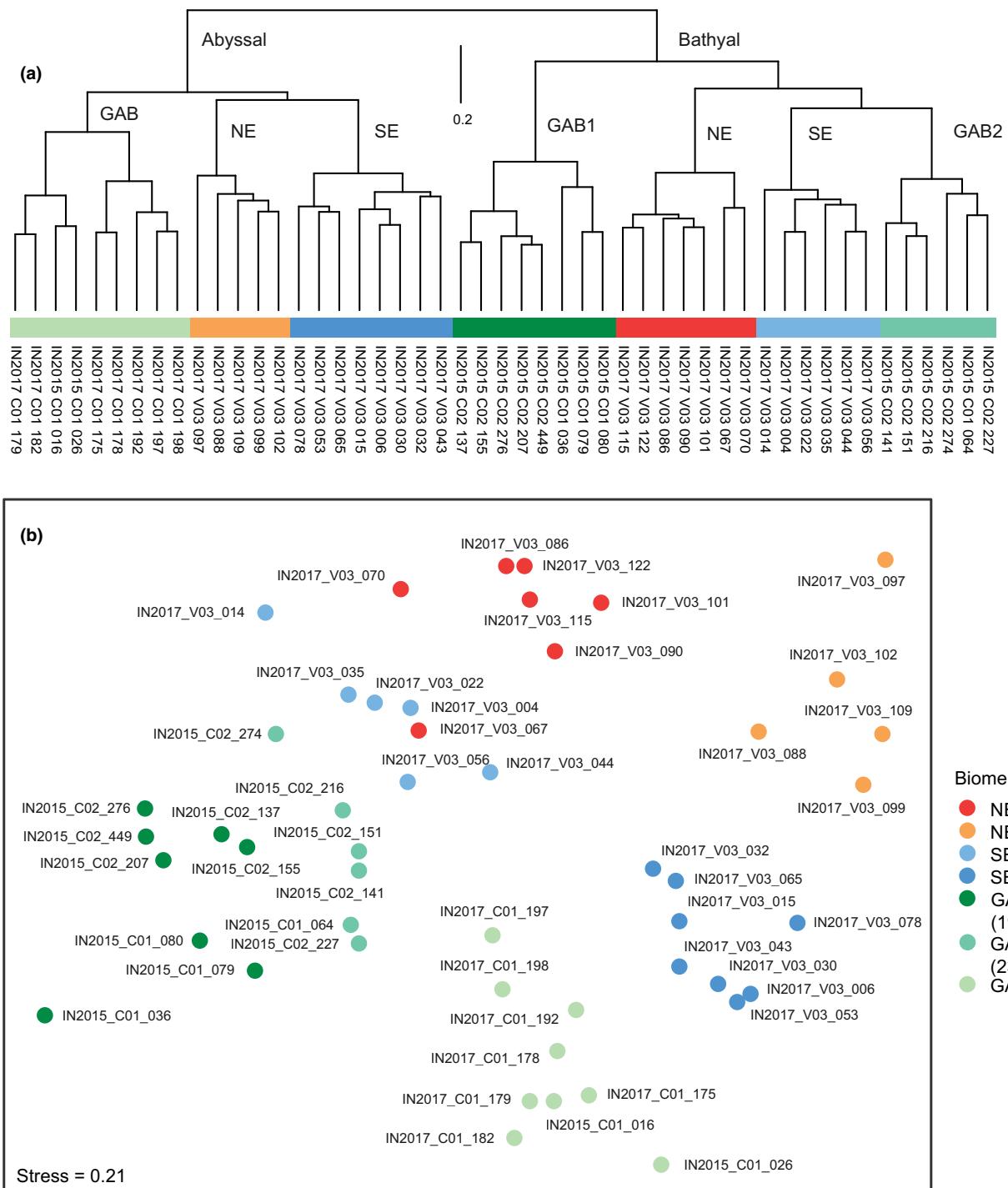


FIGURE 2 Multivariate analyses of lower bathyal and abyssal beam trawl samples (1,900–5,000 m) from the Great Australian Bight (GAB) and off the SE and NE coasts of Australia. (a) Dendrogram showing seven clusters, and (b) multidimensional scaling ordination, with points superimposed by biome cluster. Sample details are given in Table 1

lower bathyal (2,300–3,200 m) clusters. The NE and SE bathyal samples were limited to >2,300 m (Table 1, Table S3 in Appendix S1) and so did not separate in a similar manner. The two-dimensional MDS ordination showed these seven 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 seven clusters outlined above (Figure 2) were treated as a categorical variable “biome” in subsequent analyses.

Generally, within-biome mean Bray–Curtis similarity was high (Table S4 in Appendix S1), ranging from 19% (Abyssal NE) to 32% (Bathyal GAB 1). Between-biome mean similarity was <12%, except between Bathyal GAB 1 and 2 (15%), Bathyal GAB 2 and Bathyal SE (13%). 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 S4 in Appendix S1).

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 ($^{\circ}$ 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 (η) (Table 2, Figure 3). The model residuals are given in Figure S1 in Appendix S1. Predictive maps (Figure 4, Table S5 in Appendix S1) resulted in elevated abundance and richness at the shallower end of the study bathymetric range (2,000–2,500 m depth), particularly around SE Australia which is characterized by elevated NPP (Figure 1). Evenness also was consistently higher around SE Australia (Figure 4).

Rarefied richness (mean estimated richness per 38 individuals) was not significantly different between biomes when analysed as a single-factor ANOVA (Table S6 in Appendix S1), 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 (Figure 5, Table S7 in Appendix S1), ranging from no sponge species being shared between the GAB and eastern Australia to over half the arthropod species being shared.

4 | DISCUSSION

4.1 | Patterns of regional-scale diversity

Samples with the highest standardized abundance and richness for benthic megafauna within our study area (see Table S1 in Appendix

TABLE 2 Summary of final rank abundance distribution (RAD) models for total abundance, species richness and evenness of samples

Covariate	Estimate ^a	SE ^b	AIC ^b
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 ($\eta_i S_i, N_i$)			
θ_η	4.78748		
V	3.58394		
Mean	1.30420	0.00016	6,456.39
+ Scaled abundance	0.00469	0.00016	6,426.63
+ Scaled richness	-0.04584	0.00018	6,414.45
+ Salinity	-0.48157	0.00019	6,405.83
+ Salinity ²	0.52365	0.00027	6,392.48
+ SVI	1.34297	0.00030	6,393.51
+ SVI ²	-1.07033	0.00032	6,385.46
+ Longitude	-1.57210	0.00042	6,386.06
+ Longitude ²	0.52965	0.00065	6,384.54

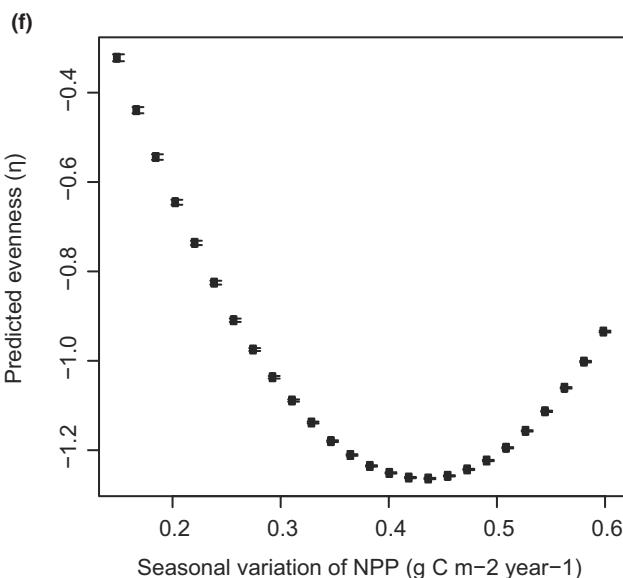
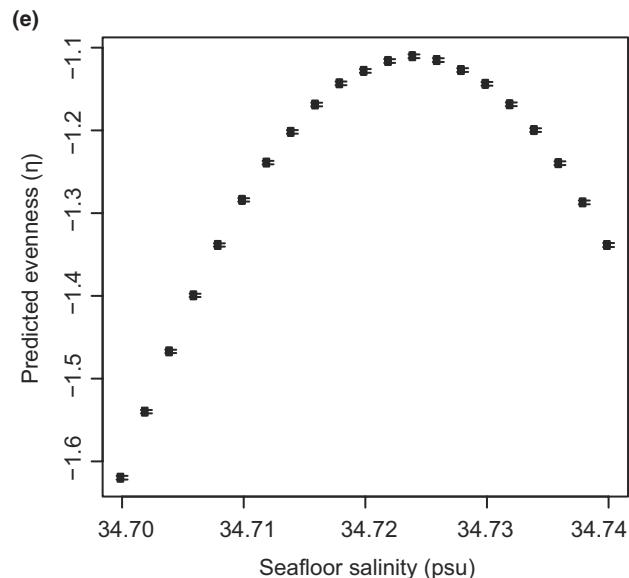
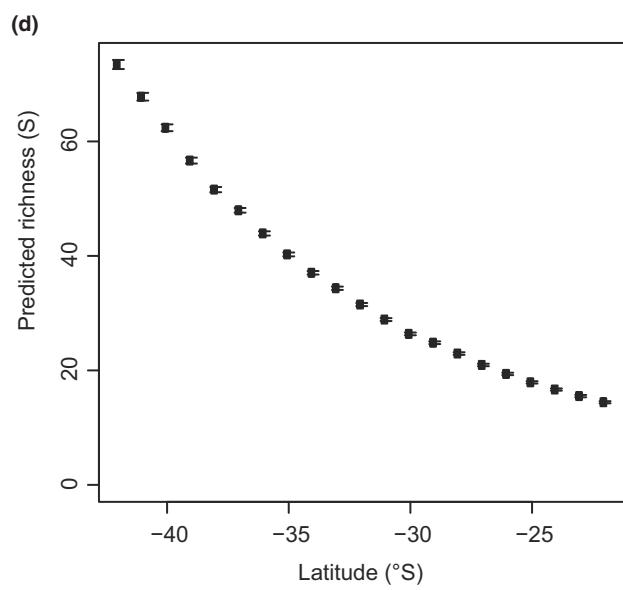
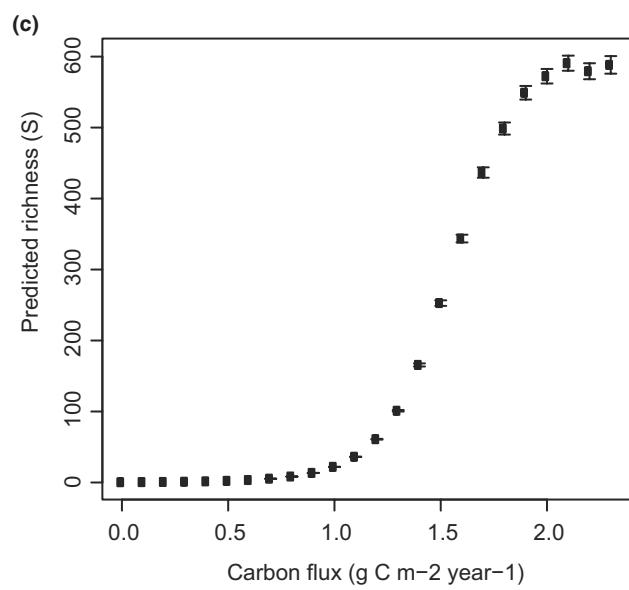
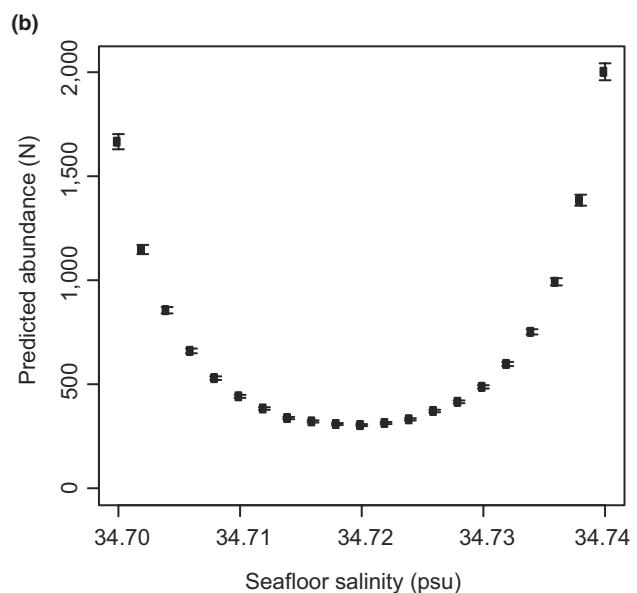
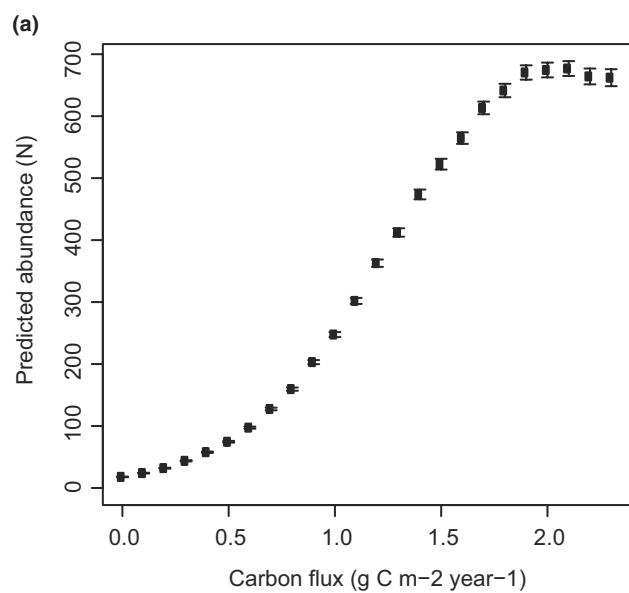
Note: AIC, Akaike's information criterion; C Flux, mean annual carbon flux to the seafloor ($\text{g C m}^{-2} \text{ year}^{-1}$); NPP, net primary productivity ($\text{g C m}^{-2} \text{ year}^{-1}$); SVI, seasonal variation of net primary productivity ($\text{g C m}^{-2} \text{ year}^{-1}$); Temp, seafloor water temperature ($^{\circ}$ C).

^aFinal model.

^bFrom models with terms higher in the table.

S1) were found at depths of 2,500–3,000 m off SE Australia (SE). In general, abundance varied inversely with latitude (lowest in the north) across both the lower bathyal (2,300–3,200 m) and abyssal (>3,200 m) depth strata, although abyssal richness was higher for sponges (Figure 5). Richness at abyssal depths showed a similar regional pattern, but richness at bathyal depths was generally higher off NE Australia (NE) than for the Great Australian Bight (GAB).

FIGURE 3 Key variable responses using final RAD models (Table 2) for (a, b) abundance, (c, d) species richness and (e, f) evenness. 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 ($2 \times \text{SE}$) are based on 10,000 bootstrap predictions. Richness is conditional on abundance, and evenness is conditional on both richness and abundance of each bootstrap



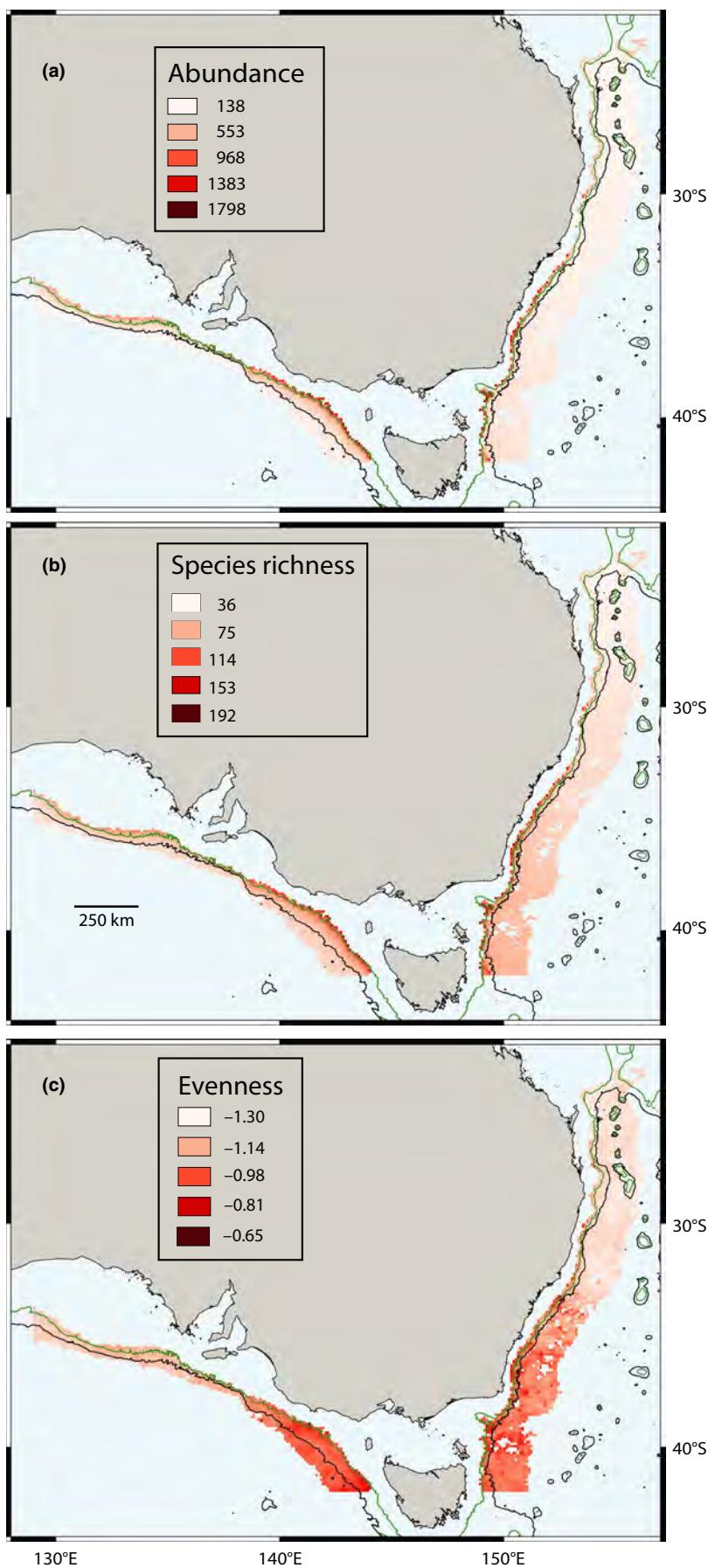
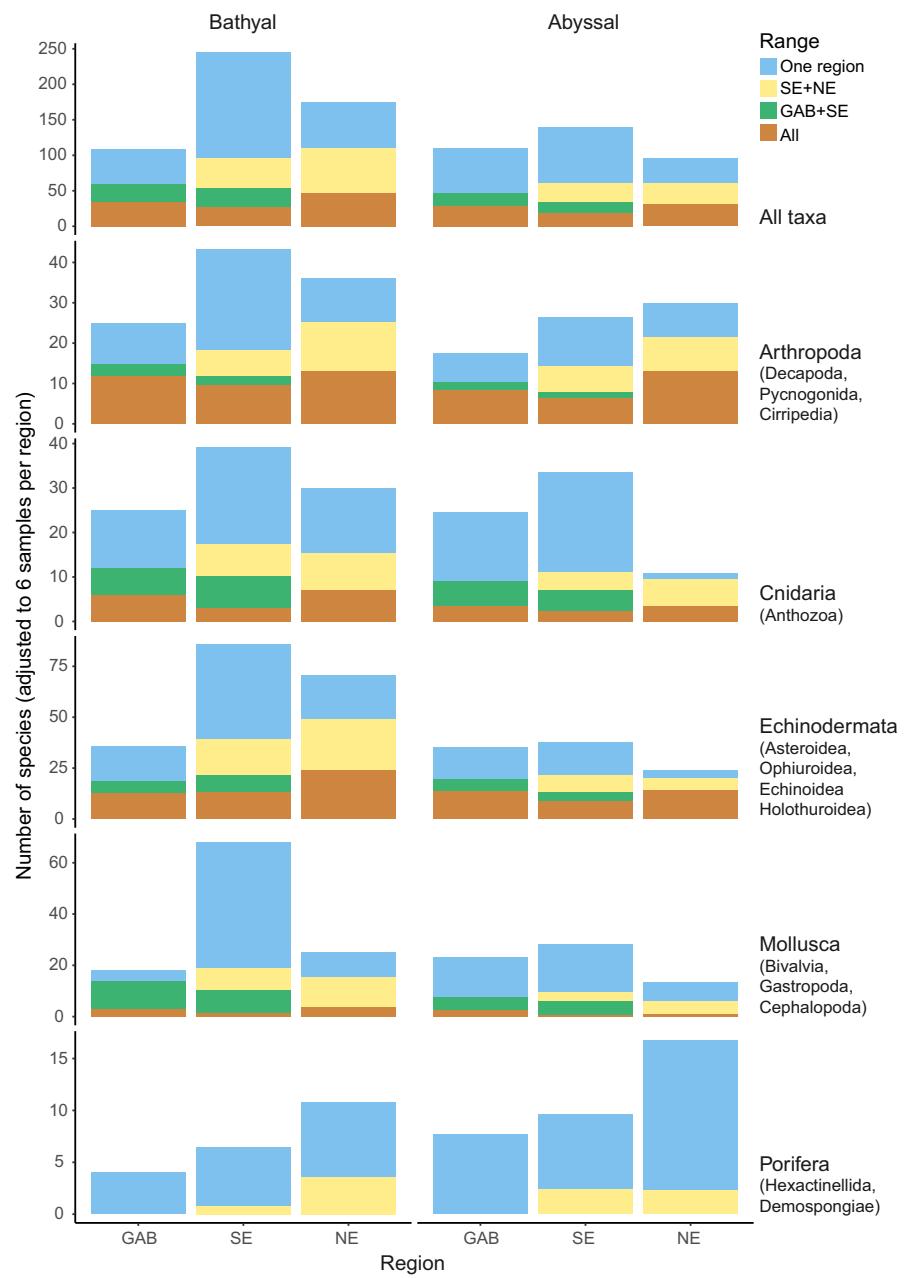


FIGURE 4 Predicted (a) abundance of individuals, (b) species richness and (c) the evenness index, on a grid of 0.1° around southern and eastern Australia (2,000–5,000 m) using final RAD models outlined in Table 2. Bathymetric contours are 2,000 m (green) and 4,000 m (black)

FIGURE 5 Number of species collected in one or more regions for a standardized collection effort (six beam trawl samples per region and depth category). GAB, Great Australian Bight; NE, north-east Australia; SE, south-east Australia (See Figure 1)



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, Tittensor, et al. (2016) for ophiuroids (brittle stars), who found the peak of regional richness for the lower bathyal and abyssal (>2,000 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 (0–2,000 m) is correlated with direct kinetic energy inputs (light and heat) that are highest in the tropics, lower bathyal and abyssal (LBA, >2,000 m) environments receive the bulk of their energy chemically in the form of organic matter which is higher at temperate latitudes (Woolley, Tittensor, et al., 2016).

Carbon flux has been repeatedly recognized as the key driver of spatial patterns of LBA richness, from local to global scales (Rex & Etter, 2010; Woolley, Tittensor, et al., 2016). Carbon flux to the seafloor was the most important environmental variable driving our RAD models for both abundance and richness (Table 2, Figure 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 (Figure 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 (Radke et al., 2017). It must be emphasized that our carbon flux data are modelled from surface chlorophyll data and depth

and do not represent in situ measurements. Small-scale (10–100 m) heterogeneity of particulate organic matter on the seafloor (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 (~2,000 m) in the North Atlantic Ocean (Rex & Etter, 2010) and in the upper bathyal (200–1,000 m) in the Indo-Pacific Ocean (O'Hara, Hugall, Woolley, Bribiesca-Contreras, & Bax, 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, Smith, & Thurnherr, 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 (Figure 5). The decline in abundance and richness at high values of carbon flux (Figure 3a,c) may be a spatial artefact of the lack of 1,900–2,300 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 2,000 and 4,000 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 the presence of distinct water masses at different depths. At 1,000 m, low-salinity Antarctic Intermediate Water (AAIW) flows westwards across the GAB in an offshore flow known as the Flinders Current (Davis, 2005; Oke, Griffin, Rykova, & Bastos de Oliveira, 2018). In the Tasman Sea, the same water mass enters via two routes, from the SE as eddies and from the north as a current, where AAIW in the SW Pacific has become entrained by the East Australian Current (Davis, 2005; Ollitrault & de Verdier, 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 (~2,000 m at 40°S) to upwell in the Southern Ocean (Lee et al., 2019; Talley, 2013). Water masses in the North Atlantic have been shown to be spatially dynamic at decadal (Yasuhara et al., 2019) to millennial temporal scales (Yasuhara, Hunt, Cronin, & Okahashi, 2009). These flows

are consistent with a potential source–sink relationship between the diversity-rich SE and the NE and GAB regions, although this requires further assessment of species range limits.

Richness is known to be driven by macro-evolutionary processes as well as ecology. The peak at upper to mid-bathyal (200–2,000 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 characterized 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 (Christodoulou, O'Hara, Hugall, & Arbizu, 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, Ho, Wilson, & Lo, 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, Burford, Clementson, & Davenport, 2001; Rex & Etter, 2010). Carcasses and faecal pellets from seasonal sulp blooms can provide two thirds of carbon input to the seafloor in the Tasman Sea (Henschke et al., 2013). In our data, evenness peaked at intermediate to high seasonality (Figure 3f, 4c). This is unlike the foraminiferan assemblage North Atlantic, where marine snow is exploited by a few dominant species (Corliss, Brown, Sun, & Showers, 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.

4.2 | The Great Australian Bight

Great Australian Bight 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 extend 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 (Woolley, Foster, O'Hara, Wintle, & Dunstan, 2016). 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, Minin, Pouzols, & Moilanen, 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. Williams et al. (2018) also reported more of their GAB species had been recorded from SE than SW Australia; however, they acknowledge the lack of sampling at lower depths in the west may bias these results. Across the GAB, Williams et al. (2018) found that there was no longitudinal change in species composition, biomass or density at similar depths and considered it a single biogeographical province.

We found that the degree of similarity of the GAB samples to those off SE Australia varies considerably between taxonomic groups (Figure 5). 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 (Figure 5). At least some of the apparent regional endemism may be due to under-sampling (Coddington, Aagnarsson, Miller, Kuntner, & Hormiga, 2009) of these inaccessible habitats.

5 | 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 endemism 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 5,000 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 characterize regional biogeography in these instances or to add to even larger scale analyses in the future.

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Museums Victoria Animal Ethics Committee Approval, MV AEC 17001; and (f) Department of Primary Industries Parks, Water and Environment Animal Ethics Committee Approval, AEC Project 19/2014-15, 2017-02.

DATA AVAILABILITY STATEMENT

All data and R scripts for the analyses used in this study are available in the Appendix S1.

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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