Report

A Southern Hemisphere Bathyal Fauna Is Distributed in Latitudinal Bands

Timothy D. O'Hara,[1,*] Ashley A. Rowden,[2]
and Nicholas J. Bax[3]
[1]Sciences Department, Museum Victoria,
Melbourne 3001, Australia
[2]Marine Ecology Program, National Institute of Water
and Atmospheric Research, Wellington 6021, New Zealand
[3]Wealth from Oceans Flagship, Commonwealth Scientific
and Industrial Research Organisation, Hobart 7001, Australia

Summary

The large-scale spatial distribution of seafloor fauna is still poorly understood. In particular, the bathyal zone has been identified as the key depth stratum requiring further macroecological research [1], particularly in the Southern Hemisphere [2]. Here we analyze a large biological data set derived from 295 research expeditions, across an equator-to-pole sector of the Indian, Pacific, and Southern oceans, to show that the bathyal ophiuroid fauna is distributed in three broad latitudinal bands and not primarily differentiated by oceanic basins as previously assumed. Adjacent faunas form transitional ecoclines rather than biogeographical breaks. This pattern is similar to that in shallow water despite the order-of-magnitude reduction in the variability of environmental parameters at bathyal depths. A reliable biogeography is fundamental to establishing a representative network of marine reserves across the world's oceans [1, 3].

Results and Discussion

Species habitat models were developed and validated for 267 species of ophiuroids (brittle stars) known from more than 20 samples across the predicted region (0°S–70°S, 100°E–170°W, one-eighth of the globe) and depth range (0–2000 m). We used ophiuroids as model organisms because they are an abundant component of the benthic fauna on both hard and soft sediment habitats, from the shore to the deepest trenches, from the equator to the poles, and have a diverse set of trophic (suspension and deposit feeding, carnivory, necrophagy) and life history strategies (planktotrophy, lecithotrophy, viviparity, asexual fissiparous reproduction) [4–8]. Focusing on a single faunal group allowed us to achieve a high level of taxonomic consistency.

Area-based cluster analyses of the species habitat models grouped the component pixels (0.04° resolution) at the highest level into shallow-water (tropical to temperate, 0 to ~250 m, predominantly continental shelf but also some volcanic seamounts and uplifted oceanic crust; hereafter termed the "shelf"), bathyal (tropical to temperate, 250 to ~2000 m), and polar areas (Figure 1). Subsequent divisions successively split the shelf into temperate and tropical regions, the polar into "shelf" (0 to ~1100 m) and "bathyal" regions, and the bathyal into temperate and tropical regions. The temperate shelf group was further split into southern Australia and New Zealand regions.

The shelf and bathyal regions are fundamentally different biomes. There are many more species in common between tropical and temperate shelf regions than between the shelf and bathyal regions within the tropical or temperate areas. This pattern has been apparent (at least qualitatively) since the earliest deep-sea expeditions, although the reported transition depth can vary with region [9]. In our study, the shallower-water Antarctic fauna differs in being more eurybathic [10]; species extend to between 640 and 4350 m and are shared with the temperate regions at bathyal rather than shelf depths.

The boundaries between our tropical, temperate, and polar regions at shelf depths were congruent with those designated previously by qualitative biogeographers [3, 11–13], a confirmation of the overall method used here. The only exception is that we did not recover a separate region at shelf depths around the sub-Antarctic islands, the relevant ophiuroid fauna being relatively species-poor across our study region [14]. In contrast, our bathyal patterns differed from the current internationally accepted bioregionalization [1]. We recognized distinct tropical and temperate/sub-Antarctic bathyal areas stretching across the East Indo-West Pacific region rather than categories based on oceanic basins. The southern Australian bathyal fauna was much more similar to that of the corresponding region around New Zealand and the Macquarie Ridge than that of the tropical Indian Ocean. The overall bathyal pattern was more similar to that of the shelf than that postulated for the abyssal plains [1].

A cluster analysis of species resulted in faunal groups that were broadly congruent with the area-based clusters, with the exception that no bathyal polar fauna was identified. However, the geographical boundaries between these faunal groups were rarely distinct (Figure 2) as a result of overlapping species' range limits (Figure 3). For example, the tropical and temperate bathyal faunas intergraded along the southwestern and eastern coasts of Australia and on the bathyal ridges between New Caledonia and New Zealand, forming broad ecoclines. The widespread distribution and gradual latitudinal turnover of species have confounded previous attempts to bioregionalize the tropical-temperate bathyal fauna [15].

It is not clear what environmental or historical factors may be driving distinct bathyal latitudinal faunas. Latitudinal faunal regions in shelf depths have been related to distinct sea-surface temperature and primary production regimes, which are in turn driven by spatial and temporal variation in solar irradiance [11, 16]. The shelf boundaries at ~30°S and ~45°S are also close to the Tasman Front and the Subtropical Convergence, respectively, suggesting that the oceanographic properties or decreased connectivity across frontal structures could also lead to latitudinal differentiation of the faunas. However, there was an order-of-magnitude reduction in environmental variation at bathyal compared to shelf depths. For example, although only 6% of species in our data set were shared between temperate New Zealand (40°S–42°S, 166°E–168°E) and tropical New Caledonia (22°S–24°S, 166°E–168°E) at 1200–2000 m, environmental conditions

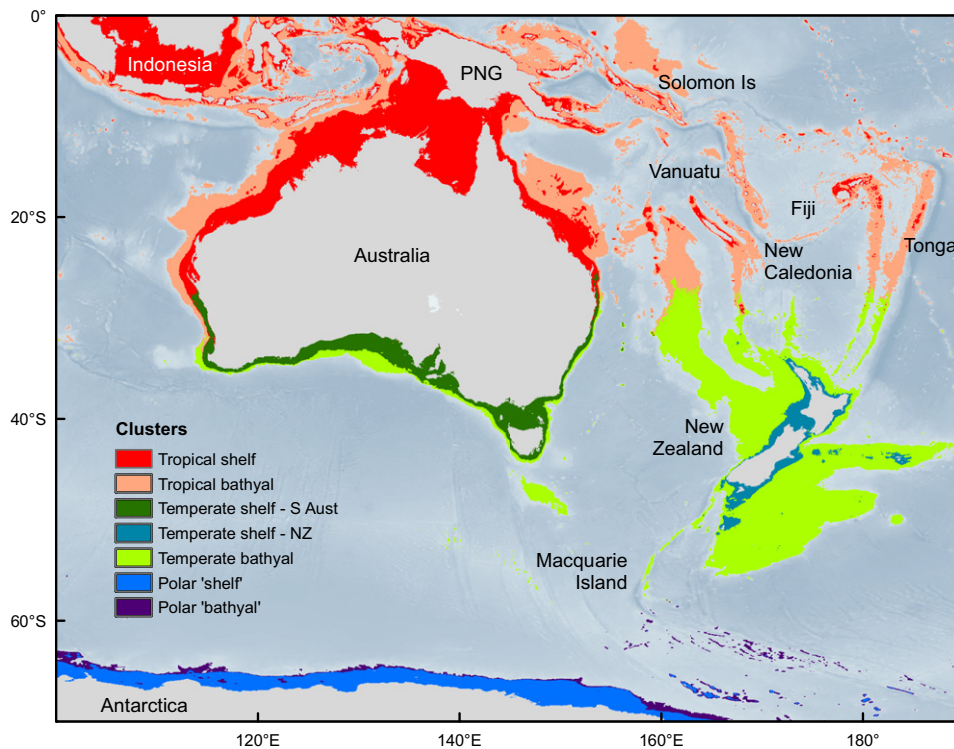*Correspondence: tohara@museum.vic.gov.au

Figure 1. Mapped Seven-Cluster Classification of Seafloor Assemblages
Map generated from multivariate analysis of logistic output predictions from maximum entropy (MaxEnt) modeling of 267 ophiuroid species.

differed only slightly (e.g., at 1500 m, temperature by +0.02°C, oxygen by +0.15 ml/l, salinity by −0.015 parts per thousand, and particulate carbon by +1.5 $\mu g/m^3$), modeled seasonal variation was minimal, and there was no obvious morphological barrier to dispersal, these two regions being connected at this depth via the Norfolk Ridge.

Geospatial variables (latitude, longitude, and depth) contributed substantially to bathyal species habitat models, more so than for the shelf (Figure 4). There were several possible explanations for this situation, the simplest being that the current set of environmental predictors was inadequate, e.g., data sets modeled at coarse resolution may not reflect local sample conditions. Alternatively, there could be demographic or evolutionary processes operating on dispersal and gene flow that prevent species from occupying their potential latitudinal range [17, 18].

Conversely, bathyal species can have widespread longitudinal ranges within their latitudinal bands. For example, in this study we found many of the same species known from southwestern Australia, Tasmania, and the Chatham Rise (Southwest Pacific) [7] at similar depths around the Amsterdam and St. Paul islands, located at temperate latitudes in the middle of the Indian Ocean. Bathyal tropical species can be distributed from Eastern Africa to Hawaii [19]. We found little evidence for separate Indian Ocean and Pacific Ocean bathyal assemblages [1]. Long-term survival of lecithotrophic larvae in the cold temperatures [20] of deep-sea currents, such as the recently discovered "supergyre" spanning the southern Indian and Pacific oceans [21], is one potential explanation for longitudinal dispersal at bathyal depths.

The only faunal groups defined by longitude arising from our analyses were the temperate shelf regions of southern Australia and New Zealand. These regions share only 9% of their ophiuroid fauna. Presumably this faunal distinction has arisen from dispersal limitations, because the two regions experience broadly similar environmental conditions and have been separated by approximately 80 million years. Shelf species can require relatively long larval durations in productive waters to breach an oceanic barrier across the Tasman Sea [22]. The number of species with relatively restricted ranges in our study was otherwise low, although this may reflect the inclusion of only the more frequently found species (>20 sites). Narrow-range marine species can occur in relatively low abundance [23].

It is unclear to what extent species within the broad faunal groups defined in this study share a common biogeographic history. We currently lack a comprehensive phylogeny for the Ophiuroidea, and Tertiary fossils are uncommon. Speciation processes remain obscure, particularly for radiations of sympatric bathyal species [24]. We require further phylogenetic, phylogeographical, paleontological, and population genetic studies to help build a new historical biogeographical paradigm for the bathyal deep sea [18].

Increasing impacts of fishing on the high seas and the increased likelihood of deep-sea mining and oil and gas exploration have stimulated the call for spatial management of deep-sea biodiversity [25]. It is important that any high-seas spatial planning be based on sound biogeographic principles [26]. Recently, the international Convention on Biological Diversity set a target of achieving a network of marine protected areas, including for the high seas by 2012 [27]; recognized the importance of first identifying ecologically and biological significant areas [28]; and agreed on seven criteria to define these areas [29] and a further four criteria to
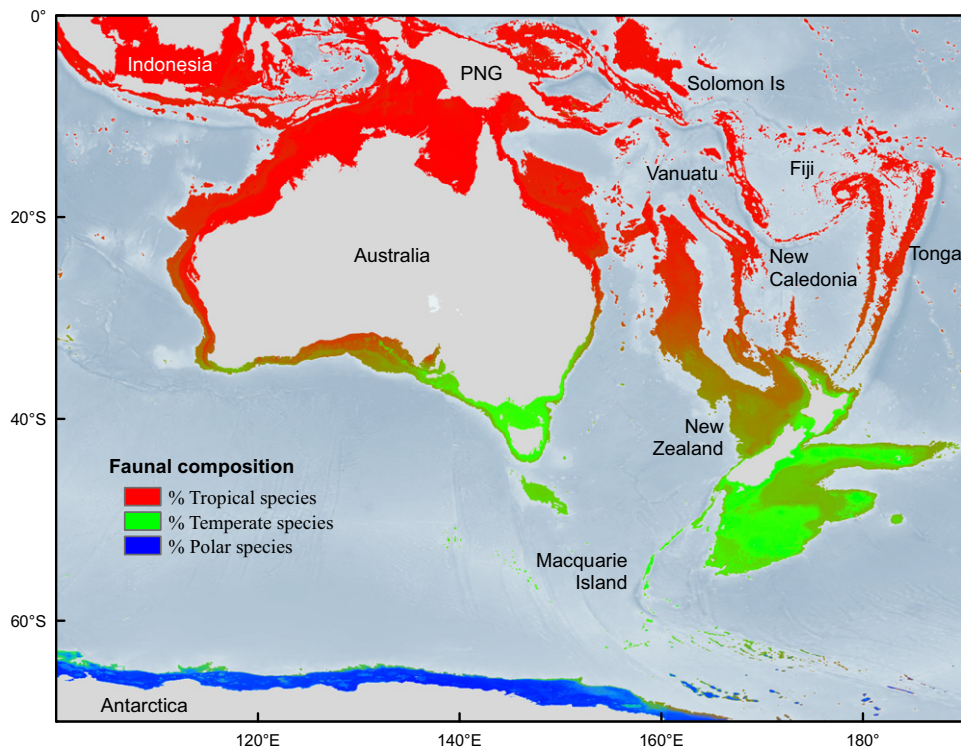
Figure 2. Distribution of Tropical, Temperate, and Polar Species

A visualization of spatial patterns of predicted species distribution, formed by assigning the proportion of tropical, temperate, and polar species from Max-Ent modeling to the red, green, and blue bands of an RGB color image.

define a network. One of the network criteria is "representativity," which is achieved when a network consists of areas representing different biogeographical subdivisions.

It has not been easy to develop informative deep-sea biogeographies based on species' distributions. Analyses have defaulted to untested physical variables [1] or have been restricted to particular geomorphic features supporting restricted communities, such as hydrothermal vents [30]. In this paper, we have provided one of the first regional biogeographies at shelf and bathyal depths for one-eighth of the globe using quality-assured data from 24 museums. It remains to be seen whether the ophiuroids that we modeled are good biological surrogates at this scale for other taxa, or even rare unmodeled ophiuroids, but some initial comparisons are encouraging [31]. A reliable biogeography is fundamental to establishing a representative network of marine reserves across the world's oceans.

Experimental Procedures

Biological Data

Ophiuroid identifications were made or verified by the first author or other expert ophiuroid taxonomists and included records from throughout the Indian, Pacific, and Southern oceans assembled from museum and historical records [6–8, 19]. From the greater study area (26°N–70°S, 60°E–170°W) and depth range (0–2000 m), 27,753 records of 923 species-level taxa from 6,950 samples were available across all extant families of ophiuroids (see Figure S1 available online). There were insufficient samples at depths > 2000 m for detailed analysis. The samples were collected with a variety of gear (mostly trawls, dredges, grabs, and hand collection), and absence of a species from available samples was not considered to be an indicator of absence from a location. Consequently, the data were considered to be presence-only in species habitat modeling.

Environmental Predictors

Environmental predictor variables used included annual mean seafloor temperature, salinity, oxygen, and particulate organic carbon (POC); standard deviation (as a proxy for seasonal variation) of temperature and POC; and depth, latitude, and longitude. Temperature, oxygen, and POC (as a proxy for available food) are well-known drivers of benthic animal biodiversity [32, 33]. Temperature and salinity are characteristic of individual water masses [34]. Seasonal variations in temperature and POC can be regionally important [32]. Depth was chosen as a proxy for pressure [34]. Latitude and longitude were included as proxies for correlated but unmeasured variables such as barriers to dispersal [35].

Bathymetry (m) was derived from the global ETOPO1 ice-surface GIS bathymetric data set [36]. Seafloor temperature (°C), salinity (parts per thousand), and oxygen (ml/l) were derived from the CARS2006 data set, created by averaging and/or interpolating available oceanographic cast data (largely from 1950–2005) across the Southern Hemisphere and equatorial
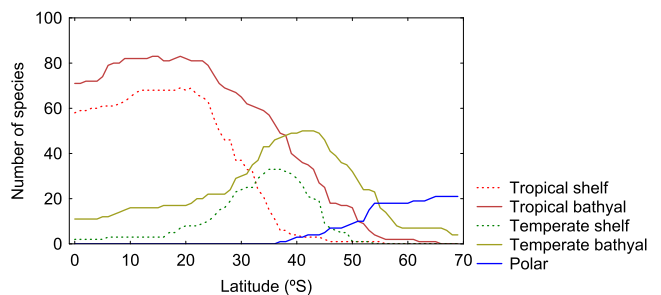

Figure 3. Number of Species in the Major Species Groups for Each Degree of Latitude

For clarity, several groups have been merged. The graph shows that tropical, temperate, and polar groups overlap latitudinally at both shelf and bathyal depths.
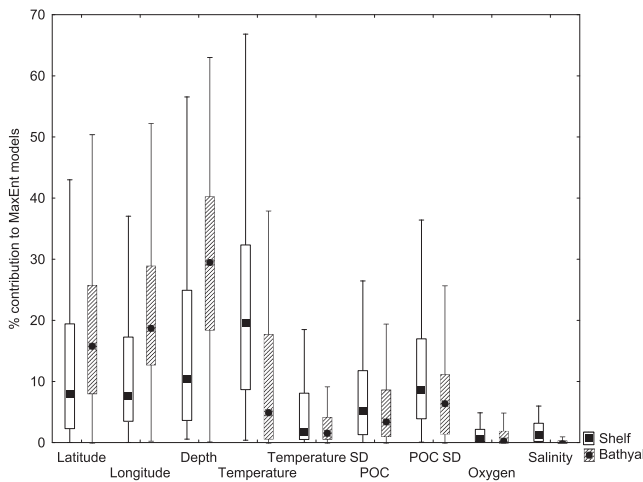
Figure 4. Contribution of Predictors to Species Habitat Models

Comparison of the percentage contribution of geospatial (latitude, longitude, and depth) and environmental (temperature, particulate organic carbon [POC], oxygen, and salinity) predictors to MaxEnt species habitat models for shelf and bathyal species. The filled black symbols represent the median value, the hatched boxes 50% of the included species, and the whiskers the outlier range. The geospatial factors contribute more to bathyal than shelf models.

regions for 79 depth layers at a resolution of 0.5° latitude/longitude [37] (http://www.marine.csiro.au/~dunn/cars2006/). Annual POC was derived from a global NPZD (nutrient-phytoplankton-zooplankton-detritus) model (R. Matear, personal communication), averaged for the years 1980–2010, of resolution 1.875° longitude, 0.9375° latitude, and 31 depth layers by converting the detritus data (mmol N/m^3) to carbon (μg C/m^3) using the 106:16 N:C ratio of seawater multiplied by the molar weight of carbon (12.01 g/mol). The standard deviation of POC was calculated from monthly POC. Depth layers for all oceanographic variables were horizontally interpolated (and extrapolated across coastlines) to 0.02° using the inverse distance-weighted algorithm (ArcMap v9.0 [38]). Environmental values for the seafloor were trilinearly interpolated between these fine-resolution depth layers.

The 0.04° resolution of the environmental layers provided a balance between size (computation time) and precision. However, rapidly changing topography (e.g., around seamounts and coasts) caused a mismatch between recorded sample depth and the corresponding GIS bathymetry layer depth. Training environmental data were therefore interpolated at the actual depth/latitude/longitude of the samples.

Species Habitat Modeling
The "predict then classify" approach to modeling species assemblages was adopted [35, 39] to maximize the use of available "presence-only" museum collection records and to allow each species to respond independently to the environmental predictors. Species habitats were modeled using maximum entropy modeling (MaxEnt v3.2.1), a machine-learning technique that performs particularly well compared to other techniques in predicting species distribution from incomplete information [40, 41].

Only species with more than 20 presence records within the region were modeled, to ensure sufficient coverage across the large study area and reduce the influence of outliers. A stratified random approach was used to select 10,000 background points, reflecting the overall depth and latitudinal profile of the collected samples [42]. The same background points were used to model each species. MaxEnt was set to automatically select feature types, and the regularization multiplier was left at the default level of 1. Models were validated using the area under the receiver operating characteristic curve (AUC) and binomial tests [42–44]. The records were split 75%/25% into training and test data sets. Species with a test AUC of <0.75 were excluded from further analysis [45]. However, AUC may be misleading if a species distribution is small relative to the study area [46]. Consequently, binomial tests were carried out at 11 different thresholds reported by MaxEnt, and the species models were retained if the p values for the tests were

significant at 0.05 for a majority of the thresholds [44]. Two hundred and sixty-seven species habitat models were available for analysis.

The predicted area was defined as 0°S–70°S, 100°E–170°W (Figure S1) to focus on an equator-to-pole latitudinal transect and reduce observed errors in prediction close to the boundaries of the study region. The logistic output was used directly in multivariate analyses because it gave better estimates of probability of presence [47]. However, for comparison, this output was transformed into binary data using several of the thresholds computed by MaxEnt. Multivariate patterns generated using these thresholds were generally highly rank correlated with the logistic scores (see Supplemental Experimental Procedures).

Area-Based Multivariate Analyses
Two-stage clustering was used to handle the large habitat modeling data sets (687,576 pixels for each of the 267 species) [35]. Nonhierarchical (k means) clustering (PATN v3.1 [48]) produced 100 first-stage groups, which were then classified hierarchically using group average clustering (PRIMER v6.1 [49]). The Bray-Curtis similarity measure was used in each case to limit the influence of joint absences on the similarity values [49]. The seven-cluster solution (30% similarity) was chosen to minimize clusters with only one or two first-stage groups (Figure S2A). Clusters were superimposed on two- and three-dimensional multidimensional scaling (MDS) ordinations [49] to explore relationships (Figure S2B) and then mapped (Figure 1). Latitudinal and bathymetric boundaries between area clusters were identified using box plots of the map pixels (Figure S2C).

Species-Based Multivariate Analyses
Species-based rather than area-based groups were generated to display the large-scale latitudinal and bathymetric turnover of species composition. Species groups were defined using group average cluster analysis and MDS ordinations on a random subset of 10,000 pixels, because this was sufficient to determine similarity of ranges between the 267 species. A nine species-group solution was selected (at 33% similarity) with six major and three minor (with 1–3 species) groups (Figure S3).

These nine groups were summed into three broad latitudinal (tropical, temperate, and polar) and two bathymetric (shelf and bathyal) groups for ease of visual interpretation (Figure 3). All of the polar species were considered "shelf," because no polar "bathyal" species group was obtained. The spatial distribution of these groups was shown by summing the outputs from the habitat suitability modeling for each group at each pixel and dividing by the pixel total. For the three latitudinal bands, the relative composition of the shelf and bathyal groups was summed, multiplied by 255, and then assigned to the red, green, and blue bands of a multiband RGB raster data set using the ArcGIS function "composite bands" [38] (Figure 2).

Supplemental Information

Supplemental Information includes three figures, Supplemental Experimental Procedures, and one table and can be found with this article online at doi:10.1016/j.cub.2011.01.002.

References

1. UNESCO. (2009). Global Open Oceans and Deep Seabed (GOODS)—Biogeographic Classification, IOC Technical Series 84 (Paris: UNESCO-IOC).

2. Rex, M.A., and Etter, R.J. (2010). Deep-Sea Biodiversity: Pattern and Scale (Cambridge, MA: Harvard University Press).

3. Spalding, M.D., Fox, H.E., Allen, G.R., Davidson, N., Ferdaña, Z.A., Finlayson, M., Halpern, B.S., Jorge, M.A., Lombana, A., Lourie, S.A., et al. (2007). Marine ecoregions of the world: A bioregionalization of coastal and shelf areas. Bioscience 57, 573–583.

4. Byrne, M. (2001). Echinodermata. In Invertebrate Zoology, D.T. Anderson, ed. (Sydney, Australia: Oxford University Press), pp. 366–395.

5. Byrne, M., and Selvakumaraswamy, P. (2002). Phylum Echinodermata: Ophiuroidea. In Atlas of Marine Invertebrate Larvae, C.M. Young and M.E. Sewell, eds. (London: Academic Press), pp. 483–498.

6. O'Hara, T.D. (2007). Seamounts: Centres of endemism or species-richness for ophiuroids? Glob. Ecol. Biogeogr. 16, 720–732.

7. O'Hara, T.D., Rowden, A.A., and Williams, A. (2008). Cold-water coral habitats on seamounts: Do they have a specialist fauna? Divers. Distrib. 14, 925–934.

8. O'Hara, T.D., and Tittensor, D.P. (2010). Environmental drivers of ophiuroid species richness on seamounts. Mar. Ecol. 31 (Suppl. S1), 26–38.

9. Carney, R.S. (2005). Zonation of deep biota on continental margins. Oceanogr. Mar. Biol. Annu. Rev. 43, 211–278.

10. Brey, T., Dahm, C., Gorny, M., Klages, M., Stiller, M., and Arntz, W.E. (1996). Do Antarctic benthic invertebrates show an extended level of eurybathy? Antarct. Sci. 8, 3–6.

11. Briggs, J.C. (1995). Global Biogeography (Amsterdam: Elsevier).

12. Ekman, S. (1953). Zoogeography of the Sea (London: Sidgwick and Jackson).

13. Wilson, B.R., and Allen, G.R. (1987). Major components and distribution of marine fauna. In Fauna of Australia, General Articles, Volume 1A, G.R. Dyne and D.W. Walton, eds. (Canberra, Australia: Australian Government Publishing Service), pp. 43–68.

14. O'Hara, T.D. (1998). Origin of Macquarie Island echinoderms. Polar Biol. 20, 143–151.

15. Zezina, O.N. (1997). Biogeography of the bathyal zone. Adv. Mar. Biol. 32, 389–426.

16. Longhurst, A.R. (1998). Ecological Biogeography of the Sea (San Diego, CA: Academic Press).

17. Lenormand, T. (2002). Gene flow and the limits to natural selection. Trends Ecol. Evol. 17, 183–189.

18. McClain, C.R., and Hardy, S.M. (2010). The dynamics of biogeographic ranges in the deep sea. Proc. Biol. Sci. 277, 3533–3546.

19. O'Hara, T.D., and Stöhr, S. (2006). Deep water Ophiuroidea (Echinodermata) of New Caledonia: Ophiacanthidae and Hemieuryalidae. In Tropical Deep-Sea Benthos, B. Richer de Forge and J.-L. Justine, eds. (Paris: Muséum national d'Histoire naturelle), pp. 33–141.

20. Young, C.M., Sewell, M.A., Tyler, P.A., and Metaxas, A. (1997). Biogeographic and bathymetric ranges of Atlantic deep-sea echinoderms and ascidians: The role of larval dispersal. Biodivers. Conserv. 6, 1507–1522.

21. Ridgway, K.R., and Dunn, J.R. (2007). Observational evidence for a Southern Hemisphere oceanic supergyre. Geophys. Res. Lett. 34, L13612.

22. Chiswell, S.M., Wilkin, J., Booth, J.D., and Stanton, B. (2003). Trans-Tasman Sea larval transport: Is Australia a source for New Zealand rock lobsters? Mar. Ecol. Prog. Ser. 247, 173–182.

23. O'Hara, T.D. (2002). Endemism, rarity and vulnerability of marine species along a temperate coastline. Invertebr. Syst. 16, 671–684.

24. Machordom, A., and Macpherson, E. (2004). Rapid radiation and cryptic speciation in squat lobsters of the genus Munida (Crustacea, Decapoda) and related genera in the South West Pacific: Molecular and morphological evidence. Mol. Phylogenet. Evol. 33, 259–279.

25. Mills, C.E., and Carlton, J.T. (1998). Rationale for a system of international reserves for the open ocean. Conserv. Biol. 12, 244–247.

26. Hyrenbach, K.D., Forney, K.A., and Dayton, P.K. (2000). Marine protected areas and ocean basin management. Aquat. Conserv. Mar. Freshw. Ecosyst. 10, 437–458.

27. Convention on Biological Diversity. (2004). Report of the Seventh Meeting of the Conference of the Parties to the Convention on Biological Diversity (UNEP/CBD/COP/7/21, April 13, 2004) (Montreal: United Nations Environment Programme).

28. Convention on Biological Diversity. (2008). Report of the Conference of the Parties to the Convention on Biological Diversity on the Work of Its Ninth Meeting (UNEP/CBD/COP/9/29, October 9, 2008) (Montreal: United Nations Environment Programme).

29. Convention on Biological Diversity. (2009). Report of the Expert Workshop on Ecological Criteria and Biogeographic Classification Systems for Marine Areas in Need of Protection (UNEP/CBD/EW-BCS&IMA/1/2, December 22, 2009) (Montreal: United Nations Environment Programme).

30. Bachraty, C., Legendre, P., and Desbruyères, D. (2009). Biogeographic relationships among deep-sea hydrothermal vent faunas at global scale. Deep Sea Res. I 56, 1371–1378.

31. Williams, A., Althaus, F., Dunstan, P.K., Poore, G.C.B., Bax, N.J., Kloser, R.J., and McEnnulty, F.R. (2010). Scales of habitat heterogeneity and megabenthos biodiversity on an extensive Australian continental margin (100-1100 m depths). Mar. Ecol. 31, 222–236.

32. Levin, L.A., Etter, R.J., Rex, M.A., Gooday, A.J., Smith, C.R., Pineda, J., Stuart, C.T., Hessler, R.R., and Pawson, D. (2001). Environmental influences on regional deep-sea species diversity. Annu. Rev. Ecol. Syst. 32, 51–93.

33. Tyler, P.A. (1995). Conditions for the existence of life at the deep-sea floor: An update. Oceanogr. Mar. Biol. Annu. Rev. 33, 221–244.

34. Tomczak, M., and Godfrey, J.S. (2003). Regional Oceanography: An Introduction, Second Edition (Delhi, India: Daya Publishing House).

35. Ferrier, S., Drielsma, M., Manion, G., and Watson, G. (2002). Extended statistical approaches to modelling spatial pattern in biodiversity in northeast New South Wales. II. Community-level modelling. Biodivers. Conserv. 11, 2309–2338.

36. Amante, C., and Eakins, B.W. (2008). ETOPO1 1 Arc-Minute Global Relief Model: Procedures, Data Sources and Analysis (NOAA Technical Memorandum) (Boulder, CO: National Geophysical Data Center).

37. Ridgway, K.R., Dunn, J.R., and Wilkin, J.L. (2002). Ocean interpolation by four-dimensional least squares—Application to the waters around Australia. J. Atmos. Ocean. Technol. 19, 1357–1375.

38. ESRI. (2009). ArcGIS 9.3.1 (computer program) (Redlands, CA: ESRI Software).

39. Ferrier, S., and Guisan, A. (2006). Spatial modelling of biodiversity at the community level. J. Appl. Ecol. 43, 393–404.

40. Phillips, S.J., Anderson, R.P., and Schapire, R.E. (2006). Maximum entropy modelling of species geographical distributions. Ecol. Modell. 190, 231–259.

41. Elith, J., Graham, C.H., Anderson, R.P., Dudík, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehmann, A., et al. (2006). Novel methods improve prediction of species' distributions from occurrence data. Ecography 29, 129–151.

42. Phillips, S.J., Dudík, M., Elith, J., Graham, C.H., Lehmann, A., Leathwick, J.R., and Ferrier, S. (2009). Sample selection bias and presence-only distribution models: Implications for background and pseudo-absence data. Ecol. Appl. 19, 181–197.

43. Fielding, A.H., and Bell, J.F. (1997). A review of methods for the assessment of prediction errors in conservation presence/absence models. Environ. Conserv. 24, 38–49.

44. Fuller, T., Morton, D.P., and Sarkar, S. (2008). Incorporating uncertainty about species potential distributions under climate change into the selection of conservation areas with a case study from the Arctic Coastal Plain of Alaska. Biol. Conserv. 141, 1547–1559.

45. Pearce, J., and Ferrier, S. (2000). An evaluation of alternative algorithms for fitting species distribution models using logistic regression. Ecol. Modell. 128, 127–147.

46. Lobo, J.M., Jiménez-Valverde, A., and Real, R. (2008). AUC: A misleading measure of the performance of predictive distribution models. Glob. Ecol. Biogeogr. 17, 145–151.

47. Phillips, S.J., and Dudík, M. (2008). Modeling of species distributions with MaxEnt: New extensions and a comprehensive evaluation. Ecography 31, 161–175.

48. Belbin, L. (2004). PATN v3.1 (http://www.patn.com.au).

49. Clarke, K.R., and Warwick, R.M. (2001). Change in Marine Communities: An Approach to Statistical Analysis and Interpretation, Second Edition (Plymouth, UK: Natural Environment Research Council and Plymouth Marine Laboratory).