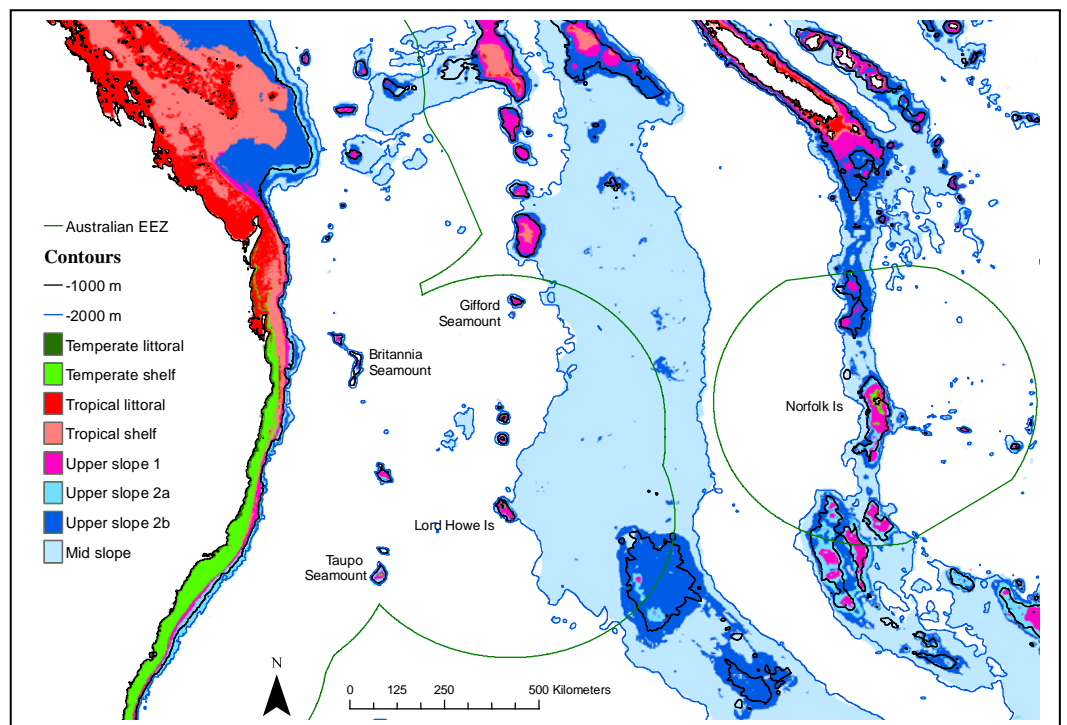


# Bioregionalisation of the waters around Lord Howe and Norfolk Islands using brittle stars (Echinodermata: Ophiuroidea).

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**Australian Government**  
**Department of the Environment,  
Water, Heritage and the Arts**

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## Summary

Ophiuroid assemblages were successfully predicted from current museum sample data using presence-only modeling techniques and a multivariate classification on the resulting species occurrence probabilities across the Coral and Tasman Seas (20-37°S, 148-172°E). The classification involves two-stages. The first uses a non-hierarchical clustering technique to reduce the number of data points (map-pixels) to a manageable number that can be analysed in a second stage with a hierarchical classification method. For both steps, the Bray-Curtis similarity statistic is used.

The benefits of this model-then-classify approach were:

1. It did not rely on consistent sampling techniques. Sample data contributed information to the species distribution patterns regardless of how or when it was collected.
2. It did not depend on accurate absence data. Rarely can we have confidence that a species is truly absent from a given area. This is especially true for large-scale studies, where the pixel resolution is on a scale of square kilometers.
3. Direct multivariate analysis of species occurrence probabilities was threshold independent (ie an arbitrary threshold did not have to be set to distinguish a 'presence' from an 'absence').
4. A two step classification preserved the benefit of a hierarchical classification (ie an explicit hierarchical breakdown of classes) while analysing very large datasets.
5. The Bray-Curtis similarity index is commonly used in ecological studies to reduce the emphasis on joint absences (eg it was not significant if a deep-sea species was absent from both tropical and temperate littoral areas).

The environmental predictors that contributed most to the species models were depth and seafloor temperature, and to a lesser extent nitrate, oxygen and sea-surface temperature. Productivity and surface current velocity were not emphasized.

The resulting maps of ophiuroid assemblages across the study area primarily reflect different depth strata, forming distinct classes at littoral, shelf, upper slope and mid-slope depths and only differentiating into distinct temperate and tropical clusters in shallow water (littoral and shelf depths) along the Australian coastal margin. The temperate New Zealand fauna only partially extends into the SE corner of the study area.

Lord Howe and Norfolk Islands support distinct complexes of tropical, temperate and endemic species, in part reflecting the influence of the East Australia Current. There are a few endemic echinoderms known from both islands, although these are relatively uncommon and may eventually be found elsewhere. The bases of these islands support similar species to habitats with similar depth and environmental profiles elsewhere, including other seamounts in the region and rocky habitats along the continental margins.

Both the Lord Howe Rise and Norfolk Ridges exhibit a north-south transition of species, however, this is less dramatic than for the Australian continental margin. This is in part due to the lack of shallow water habitat along these ridges. Latitudinal gradients are more prominent in shallow water within the study area.

Seamounts within the study areas rarely did not appear to contain more endemic ophiuroid species than similar areas along the continental margins. Instead the majority of species on seamounts appear similar to those occurring elsewhere at similar depths and seafloor temperatures. This suggests that species disperse to these seamounts from surrounding habitat regularly enough to prevent allopatric speciation. These conclusions need to be confirmed by genetic data as cryptic speciation is common in echinoderms. However, it is likely that seamounts have accumulated distinct assemblages of species over time depending on their location, form, depth and age. Seamounts do not show the consistency and specialisation of seafloor assemblages to be considered a single unit for management purposes such as marine-park planning. Until we understand more about the ecological and historical factors that structure seafloor assemblages, 'seamounts' should be evaluated independently to ascertain their conservation status.

This study emphasizes the tropical affinities of many ophiuroid species that live across the Tasman and Coral Seas. This differs from a preliminary pattern for fish described from the NORFANZ expedition in 2003 which emphasized 1) the southern affinities of many fish species, and 2) possible areas of endemism on the Middlesex Bank, Lord Howe Island, Norfolk Island, Norfolk Ridge, Wanganella Bank and Reinga Ridge. However, both ophiuroids and fish were primarily structured by depth.

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## **1. Introduction**

### **1.1 Objective**

The objective of this study was to produce a bioregional analysis of Australian Commonwealth waters surrounding Lord Howe and Norfolk Islands using a numerically dominant invertebrate group (Ophiuroidea or brittlestars). The focus was to produce data and maps that were directly relevant to regional marine planning.

In particular, four tasks were addressed:

1. Were there North-South patterns in brittlestar distributions along the ridges of the Tasman Sea? Were they similar on different ridge systems? How did the results differ from the fish analysis?
2. What were the patterns of brittlestar distribution with depth within this region? Were they similar/different to the strong depth structuring in fish assemblages?
3. Was the brittlestar fauna around Lord Howe and Norfolk Is different from the fauna found on the continental slope of Australia?
4. Was there evidence that supported/refuted the idea that seamounts are centres of endemism within this region?

### **1.2 Geographic Scope**

The geographic scope of the project was the Coral and Tasman Seas bounded by the latitudes 20-37°S and longitudes 148-172°E. This included Australia's Exclusive Economic Zone around Lord Howe and Norfolk Islands, adjoining areas of Australia, New Zealand and New Caledonia, and interspersed international waters. The inclusion of areas outside Australia's EEZ was to place assemblages in their wider geographic context and reduce the analytic artefacts that can occur around study boundaries.

### **1.3 Model taxa**

The taxonomic scope of the project was marine benthic fauna belonging to the class Ophiuroidea. This taxonomic group is useful for benthic biogeographic analyses as they inhabit a wide range of habitats from the coastline to the deepest trench, including rocky, biogenic, sandy, and muddy substrata. They also exhibit a range of life histories from direct development (eg brooding), pelagic larvae (planktotrophic and lecithotrophic) and asexual reproduction (fissiparity). There were 282 ophiuroid species recorded from the study area.

In the long term, investigating biogeographic patterns using a range of taxonomic groups is desirable. However, the practical difficulties in accumulating consistent large-scale datasets across groups are great and for the time being are better analysed independently.

## 1.4 Overall methodology

Analysing large-scale biogeographic data derived from numerous separate surveys was problematic. Many benthic samples could not be directly compared as they had been taken with a variety of gear, under different conditions, and frequently sub-sampled. Stratifying the datasets to factor out collection artefacts reduced the number of samples available for analysis and consequently the scope of the questions that could be answered. Collecting new comprehensive data was prohibitively expensive and not an option.

One alternative was to interpolate or model species distribution data so that an even spread of points (pseudo-samples) were available across the seascape of interest. Species habitat or niche models were the best practical solution, as relevant oceanographic and geomorphological GIS datasets existed the region and the analyses could predict across species distributions across complex three dimensional surfaces. Data did not exist for physiological or other more complex models. Although species habitat models give potential not actual distributions, this can be overcome if necessary by the inclusion of spatial data (eg latitude, longitude) in the habitat models (Ferrier *et al.* 2002). This methodology was adopted to answer tasks 1-3 outlined above, which were really different aspects of the same problem: how species assemblages were spatially distributed across the seafloor in the Tasman and Coral Seas.

A second alternative was to compare observed patterns against null models, derived from random collections of samples drawn from consistently defined areas. This style of analysis was suitable for answering general ecological questions that were not primarily concerned with explicit spatial patterns, and was adopted to answer task 4 of this project.

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## 2. Methods

### 2.1 Data acquisition

#### *Biological data*

The ophiuroid sample data was obtained from two sources: museum collections and taxonomic publications. Collections that were examined include those of major museums in Australia, New Zealand, Europe, United States and Asia. The specimens were collected mainly by scientific expeditions, with some material from fishing vessels and other incidental collections. Sample data includes latitude and longitude (typically of an accuracy of at least 1.0 minute), minimum and maximum depth, collection date and time, vessel, collectors, collection gear, and occasionally substratum or habitat information. The most numerous collections around Australia have been collected by CSIRO voyages (RVs Soela, Franklin and Southern Surveyor), various State based fisheries research vessels (eg FRV Kapala), and naval vessels (HMAS Diamantina, Kimbla). The Tasman and Coral Seas also have been investigated by French, Russian and New Zealand scientific expeditions. A map of the sample locations within the study area is given in Fig. 1. The material was largely the same as that used in O'Hara (2007a, 2007b, 2008) with the addition of material from seamounts across northern New Zealand. Only species with well-known taxonomy were retained for analysis. This included records for undescribed species which were consistently identified by the author.

The samples were collected using a variety of collection gear including trawls, dredges/epibenthic sleds, grabs, cores, and by hand in shallow water. The depth range of samples was restricted to 0-3000 m for the species habitat models (tasks 1-3) and 100-1500 m for the seamount species richness/endemism analysis (task 4). There were very few samples available from the abyssal plain (> 3000 m) in Australian waters and sampled seamounts were restricted to depths less than 1500 m. A possible source of modelling error was the lack of samples from some areas across the study region (Fig. 1). Sparsely sampled areas include 1) the outer Queensland shelf and slope (including areas around Coral Sea atolls such as Wreck and Kenn Reefs), 2) deeper sections of the Lord Howe Rise and Norfolk Ridge, 3) the littoral areas around New Caledonia, 4) the base and mid-slope around many seamounts where only summit samples have been taken (eg Taupo, Gasgoyne).

The sample abundance data was transformed to presence/absence data, as required for both species habitat modelling and the species richness/endemism analysis.

#### *Environmental data*

Nine environmental factors were considered to have some potential to influence ophiuroid species distribution. This included seafloor temperature, salinity, nitrate and oxygen; sea-surface temperature, productivity and current velocity; bathymetry and slope. Temperature and salinity directly affect the physiology of marine organisms. Together, temperature and salinity define oceanographic water masses, such as the East Australian Current (Ridgway & Dunn 2003) that have a three-dimensional distribution throughout the water column. Nitrate and oxygen reflect resources

available to benthic invertebrates. Sea-surface factors were included to reflect the dependence of deep-sea animals on productivity generated at the sea-surface and their potential influence on larval transport. Unfortunately seafloor current velocity was unavailable. Bathymetry is an indirect environmental factor reflecting pressure. Substratum information (eg mean grain size or hardness) was also not available for the entire region. Consequently, slope was included as a crude surrogate, with less sediment expected in areas of steep slope (Bryant & Metaxas 2007).

Other possibly important environmental datasets were also unavailable, including seafloor productivity and a water mass atlas. Water masses (eg Antarctic Intermediate Water) could be potentially very important, combining temperature, salinity and current direction in an ecologically relevant way.

Bathymetry (m) was derived from a Geoscience Australia GIS grid layer of high-quality 0.01 degree data of those parts of the Australian water column jurisdiction lying between 92E & 172E and 8S & 60S. Sea-surface data (temperature, productivity and current velocity) were derived from the National Marine Bioregionalisation raster datasets (Commonwealth of Australia 2005) with a resolution of 0.02, 0.043 and 0.023 degrees respectively. January data was used for temperature and current; annual mean values were used for productivity. Data for both the sample and prediction datasets were generated using the ESRI Spatial Analyst function “extract to point” from the raster datasets. For the sample data, binary interpolation was used to calculate the value at the recorded latitude/longitude of each sample. For the prediction dataset, a regularly-spaced point file was generated for the EEZ at intervals of 0.02 degree of latitude/longitude. Binary interpolation was then used to calculate the value at each prediction point. The resolution of the background and prediction datasets was set at 0.02 degrees latitude/longitude and restricted to a 0-3000 m depth range for practical reasons; finer resolutions produced datasets that were too large to be analysed with chosen statistical tools. Seafloor data (temperature, salinity, nitrate and oxygen) were derived directly from the CARS2000 dataset (Ridgway *et al.* 2002) using latitude, longitude (0.5 degree resolution) and depth categories. Slope (inclination angle) was calculated using the ESRI Spatial Analyst function of the same name which identifies the maximum rate of change in bathymetry around each grid cell.

### **3.1 Biodiversity modelling (tasks 1-3)**

The first three project tasks were addressed by producing a bioregional map of ophiuroid assemblages across the study region and interpreting the results for latitudinal and bathymetric gradients, and island biogeographic affinities. The bioregional map was produced by a) modelling the probability of occurrence of 102 ophiuroid species at each 0.02 degree pixel across the study region, b) using multivariate cluster analyses to group pixels into assemblage categories, and c) mapping the resulting categories.

This methodology follows the ‘modelling-then-classification’ approach of Ferrier *et al.* (2002) and Overton *et al.* (2000). The alternative approaches: ‘classification then modelling’ and ‘classification/modelling together’ (Ferrier & Guisan 2006) were unsuitable for the following reasons. The classification-then-modelling approach is similar to standard multivariate analysis of samples. This approach works best when samples have been consistently collected. The data available for this project consisted



of museum records collected from numerous different surveys over time using a variety of collection gear. Unfortunately ‘Classification/modelling together’ approaches have only been developed for abundance or presence/absence data. The data available for this project is best treated as ‘presence-only’ data. The samples were rarely quantitatively collected (for example using a box-core that captures a set volume of sediment) and large catches are frequently sub-sampled on deck. It is also questionable whether a species can be considered absent from a site just because it was not obtained from a single or even a few samples, particularly at the resolution used in this project (0.02 degrees latitude/longitude, or approximately 4-4.5 km<sup>2</sup> at mid-latitudes). Reliable absence data can be prohibitively-expensive to collect (Ward *et al.* in press). Moreover, preliminary modelling using one presence/absence technique (Multivariate Adaptive Splines, MARS) failed to sensibly model species distributions (O’Hara 2006). Other advantages of a ‘modelling-then-classification’ approach include the ability to 1) model species separately, accounting for their individual response to environmental predictors, and 2) use all available species occurrence data, even that collected by gear that did not sample all species consistently (Ferrier & Guisan 2006).

The modelling technique used in this study was ‘MaxEnt’ (Maximum Entropy modelling), a machine-learning technique that can make species distribution predictions from incomplete information (Phillips *et al.* 2006). Entropy in Information Theory refers to the available information in the system (Legendre & Legendre 1998). MaxEnt performed particularly well in comparative tests against other techniques (Elith *et al.* 2006; Hijmans & Graham 2006; Hernandez *et al.* 2006). As a comparison, an entirely different modeling technique (ENFA) was also performed on 60 species (see Appendix).

MaxEnt allowed for separate modelling and prediction datasets (ie species can be modelled over a different region than predicted). Consequently to improve the quality of the model, samples were included from around the Australian continent and throughout the Tasman and Coral Seas (8-50°S, 102-172°E). Only samples from depths 3000 m or less, and only species sampled 25 or more times, were included. Excluding some inshore samples for which there were no environmental data, 4273 samples containing 102 species were available for analysis.

MaxEnt requires a collection of random points across the region to model species distributions. Several randomization strategies were attempted. Firstly the region was stratified into 2500 latitude/longitude/depth categories from which up to 5 random points were selected (to a total of 10,000). However, in general this strategy performed less successfully (lower average AUC – see below, fig. 2a) than points allocated randomly across the entire region. Experimenting with a range of datasets, 20000 randomly allocated points appeared to offer the best trade-off between model performance and computational time.

The prediction dataset was limited to an area of the Coral and Tasman Seas less than or equal to 3000 m depth from 20-37°S and 148-172°E at a resolution of 0.02 degrees, resulting in 534,552 prediction points.

For validation purposes 75% of the data was included in a training dataset and 25 % in a test dataset. MaxEnt was allowed to automatically select feature types (see

Phillips *et al.* 2006 for details) and the regularization multiplier was left at the default level of one. The models were validated using the Area Under the Curve (AUC) on Receiver Operating Characteristic (ROC) plots. This is a standard modelling validation technique that compares the number of true-positives with false-positives across a range of decision thresholds (Felding & Bell 1997). Values range from 0.5 (random) to close to 1.0 (perfect discrimination). Values better than 0.75 are considered adequate (Pearce & Ferrier 2000, Graham & Hijmans 2006). For MaxEnt modelling, the random background pixels are used instead of absences (Phillips *et al.* 2006).

Several MaxEnt models were run. The first used the nine environmental factors listed above. The second included latitude and longitude in addition to these factors, to see if this improved model predictions across an area that included disjunct north-south continental slopes/ridges and isolated seamounts that may drive patterns of local endemism. The third model included only latitude/longitude and depth to see if sample distribution or spatial factors alone were driving the results.

### *Multivariate analyses*

The result of the species habitat modelling were grids of raw species distribution probabilities (MaxEnt) for a series of ophiuroids across the Tasman Sea region at a resolution of 0.02 degrees. This created very large datasets (eg 102 species across 534,552 pixels) that limited the multivariate statistical techniques that could be applied. Even when the dataset was reduced to pixels with a bathymetry less than or equal to 2000 m (including the vast majority of samples), this resulted in a total of 321,457 points. Ordinations and hierarchical dendrograms are only interpretable up to a few hundred samples (Belbin 2004). The ArcInfo 9.0 multivariate IsoCluster/Maximum Likelihood Classification tools only allowed up to 30 species layers (ESRI 2004).

Consequently, a two step clustering approach was adopted (Overton *et al.* 2000, Snelder *et al.* 2005). Firstly, a non-hierarchical clustering method ALOC was used to reduce the number of data elements from 321,457 to 300 clusters using the software PATN v3.1 (Belbin 2004). The Bray-Curtis similarity measure was chosen as it limited the influence of joint-absences on the similarity values (Clarke & Warwick 2001). The species data were standardised first ( $(x-x_{\min})/x_{\text{range}}$ ) to ensure equal contributions from all species.

The second stage involved a hierarchical classification using Bray-Curtis similarities and a sequential agglomerative clustering technique in PATN v3.1. The mean species probabilities or habitat suitability indices for each species across the 300 first stage clusters were used as the input data. The classification hierarchy was mapped at the levels of 2, 4 and 8 groups (Fig. 8).

### *Tasks 1 and 2. Latitudinal and bathymetric patterns along the Lord Howe Rise and Norfolk Ridge*

The classification hierarchy and the bioregional assemblage maps were analysed for both latitudinal and bathymetric patterns. The hierarchy reflects the most important environmental predictors, which, for example, could reflect latitude for the first classification node (2 groups) and then bathymetry groupings (eg into 4 and 8

groups). The advantage of this technique is that interactions between environmental predictors are reflected in the analysis (eg bathymetric groups can occur in shallower water at higher latitudes).

The MaxEnt modelling software also outputs the relative importance of each environmental predictor in each species model, both in terms of 'gain' (entropy modelling performance) and AUC (modelling validation algorithm). The mean and variance for each predictor can be graphed to reflect their relative importance across all species.

The output probabilities from the MaxEnt models were also used to map the varying composition of tropical and temperate/endemic species over the study area. This analysis built spatial patterns derived from latitudinal gradients or long term evolutionary events. Tropical species were defined as those that are known to occur between and including 20°N and 20°S, across all depth ranges. The proportion of tropical species were calculated for each pixel by summing the standardised MaxEnt scores for all tropical species and dividing by the total for all species and multiplying by a hundred. The resulting ratio of tropical/all species for each pixel was then mapped.

### *Tasks 3. Comparison of the fauna surrounding Lord Howe and Norfolk Islands with the Australian continental margin*

The bioregional assemblage map was used to reflect the faunal relationships of assemblages around Lord Howe (including Elizabeth and Middleton Reefs) and Norfolk Islands with neighbouring regions. The relative contributions of tropical, temperate and endemic species to the fauna of each island were computed for all echinoderms (not just ophiuroids) based on the studies by Hoggett and Rowe (1988), Rowe (1989), Rowe & Filmer-Sankey (1992), Rowe & Gates (1995) and supplemented by new records in Museum Victoria and the New Zealand National Institute of Water & Atmospheric Research (NIWA).

### **3.3 Comparison of narrow-range endemism and species richness of seamounts versus slope samples using null models (task 4)**

The species-richness and narrow-range endemism of seamounts and equivalent areas of non-seamount habitat were compared using the methodology in O'Hara (2007b). Samples were available from 49 seamounts and 3 oceanic islands within the study region (Table 3, Fig. 1) from 100-1500 m. Comparative non-seamount habitat within the target area and depth range included the continental slopes and outer shelves off eastern Australia, New Caledonia and north-western New Zealand, and the fragments of continental crust that form the base of the Lord Howe Rise and the Norfolk Ridge.

Few seamounts were isolated features; many were connected via ridges or clustered together on the same block of elevated crust. Consequently, rather than focus on endemism of single seamounts, this study examined narrow-range endemics, defined as being limited to one degree latitude and longitude, and asked the question are there more narrow-range endemics on seamounts than expected from their distribution across all habitats, including both seamount and non-seamount habitats. This was done by comparing observed levels of narrow-range species found only on seamounts against a null model that assumed that the distribution of narrow-range species is

random with respect to the location and depth of samples. The null model was constructed from 10,000 species lists derived from randomly selecting without replacement between 1 and 50 samples from seamount and non-seamounts throughout the study area and depth range (100-1500 m). A line of best fit was determined by linear regression of the number of narrow-range species versus the number of samples for each species list and 95% prediction interval calculated from the formula  $\mu_y \pm t_{n-2} \sqrt{S\mu^2 + s^2}$  where  $\mu_y$  is the mean of the estimate,  $t$  is the t-value at 95%,  $s$  is the standard error of the estimate and  $S\mu$  the standard error of the predicted value, using the software Statistica v7.1 (StatSoft, 2005).

Null models were also developed to compare the species richness found on seamounts with comparable areas on the continental slope. For these null models, the selection of random samples was constrained to a 50 km radius and  $\pm 250$  m bathymetric range around an initial randomly selected sample (50 km being the mean radius and 500 m the mean depth range of samples from seamounts). A line of best fit was determined by linear regression as above.

The different area sizes between the narrow-range endemic and species-richness analyses were chosen for practical purposes, the 50 km kernel more accurately reflects the size of a seamount; however, this generated too few narrow-range species for a meaningful comparison to be made against a null model.

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## 4. Results

### 4.1 Biodiversity modelling

#### *Species model performance*

MaxEnt was successfully run on 102 species. Model validation was good to excellent for all species, ranging from 0.993 to 0.999 for the training AUC and 0.889 to 0.999 for the test AUC (Table 1, fig. 2b). Models based on non-spatial environmental factors (ie temperature, salinity, nitrate, oxygen, currents, slope, and productivity) performed marginally better than spatial factors (eg latitude, longitude, depth) at predicting ophiuroid distributions across all species (Fig. 2b). The best results occurred if all (environment and spatial) factors were used, suggesting that species were not present in all habitat patches predicted by the environmental factors alone.

The influence of each environmental variable was tested by running each MaxEnt model with one factor alone or by using all factors except one (this indicates which variable has the most information not included in the other variables, ie the least correlated) (Fig. 3). The most important variables were depth and temperature, followed by nitrate and oxygen, and then SST. Slope and longitude had the most information not contained in other variables. Productivity and surface current velocity were not emphasised in any analysis.

An example of a predicted species distribution map is given in Fig. 4. The prediction makes biogeographic sense, in that this tropical upper slope species was predicted to occur at these depths in the north and central sections the study area, ending at approximately Jervis Bay.

Relatively few species endemic to the study area were available in sufficient numbers of specimens to be successfully modelled using MaxEnt. Exceptions include several species along the coast of New South Wales and Southern Queensland, such as *Ophiocoma endeani*, which also occurs at Lord Howe Island. One endemic species was confined to the Lord Howe Ridge and the Taupo and Gasgoyne seamounts (*Dictenophiura platyacantha*), and one to the Lord Howe and Norfolk Ridges (*Amphiophiura bakeri*). Other endemics were relatively rare (see O'Hara 2007b).

#### *Bioregional model*

The community patterns generated, using the two-stage classification on 102 stacked species probability maps resulting from MaxEnt modelling on all environmental variables, reflected both bathymetric and latitudinal gradients (Fig. 3). The primary division (two-class solution) was based on depth, with littoral and shelf seabeds differing from those on the slope (Fig. 5 & 8). The four-class solution was more complicated, the shallow areas dividing latitudinally into a 'tropical' and 'temperate' class, and the slope group bathymetrically into upper and mid-slope classes. The eight class solution again reflects depth, with a) littoral and shelf samples dividing in both temperate and tropical regions, b) the upper slope class separating into three subclasses, and c) the mid-slope group remaining the same. Up to six clusters were represented at different depths along the continental margins (littoral, shelf, upper slope (x3) and mid slope).

Maps were created with 12 and 20 clusters to see if more east-west variation in assemblages became apparent with a finer scale (maps not shown). However, the trend was for clusters to break down into smaller bathymetric units rather than show inter-ridge variability. In particular, the Queensland shelf (including the Great Barrier Reef) and slope showed considerable complexity.

The overall pattern was tested for robustness by using different modelling (ENFA) techniques. The multivariate patterns are broadly similar for the eight-class solution (see appendix).

The MaxEnt model using all environmental variables was also compared to a MaxEnt 'spatial model' that used only latitude/longitude/bathymetry to see if spatial patterns alone drove the patterns. The AUC for species modelled with environmental variables was higher than for those using spatial/bathymetric variables alone (Fig. 2b). The spatial model emphasised an Australian temperate fauna restricted to the temperate Australian coast and offshore seamounts, southern Lord Howe Rise and Norfolk Ridge (Fig. 9). It divided slope categories in slightly different ways (Fig. 9).

#### *Description of classification*

The eight classes from the hierarchical classification of MaxEnt scores based on all factors (environmental and spatial) are described below.

#### **Temperate littoral**

Largely restricted to southern Australia as far north as Fraser Island, Queensland. Also occurred around Lord Howe, Elizabeth, Middleton and Norfolk Islands, and a few anomalous pixels along the northern coast of New Caledonia. Depth range was 0-75 m (mean 16 m).

#### **Temperate shelf**

Largely restricted to southern Australia as far north as Fraser Island, Queensland. Also occurred around Lord Howe, Elizabeth, Middleton and Norfolk Islands, the summits of some shallow seamounts, including Taupo & Gasgoyne and the Wanganella Bank. Depth range was 18-223 m (mean 96 m).

#### **Tropical littoral**

Largely restricted to Queensland, including shallow habitats along the Great Barrier Reef, New Caledonia, tropical atolls including Wreck, Bellona, Chesterfield, Lansdowne Reefs, and around the Loyalty Islands. Also included some non-coral habitat along the Queensland and Northern New South Wales coast to 28°S, with a few pixels south of this latitude, along mid New South Wales and around Lord Howe and Norfolk Islands. Depth range was 0-147 m (mean 28 m).

#### **Tropical shelf**

This class occurred extensively across the Great Barrier Reef region and south along the New South Wales coast to approximately 35°S. Also extensive on the Chesterfield/Bellona banks, Lansdowne banks, around New Caledonia and the

Loyalty Islands, and on the summit of the Capel Guyot. A few pixels occurred near Norfolk Island. Depth range was 0-425 m (mean 131 m).

### **Upper slope 1**

This class occurred at upper slope localities across the region with the exception of the slope offshore of the Great Barrier Reef, where it was replaced with the class Upper Slope 2b. Depth range was 89-1161 m (mean 479 m).

### **Upper slope 2a & 2b**

These classes occur at lower upper slope localities across the region (depth range: 200-2000 m, mean 1024 m). They were considered together here because class 'Upper slope 2b' was best viewed as a composite of two classes (with mean depths of 660 and 1172 m respectively) that sat either side of class 'Upper slope 2a' (mean depth 1020 m). This was seen clearly in the region off Queensland, where a band of "2a" sat between two patches of "2b" around the 1000m contour. In other words, "Upper slope 2" was best considered as 1 or 3 groups (see Fig. 5); the separation of "2a" from "2b" was an artefact of the classification procedure.

### **Mid slope**

This class occurred throughout the study area at the deepest depths considered. The depth range of the pixels was 891-2000 m (mean 1565 m). The apparent absence of this class from the SE Australian coast was an artefact of the steep continental slope in the region, the pixel size (0.01 degrees) too wide to separately record this depth stratum.

## **4.2 Bathymetric gradients (Task 1)**

Bathymetry was the most prominent environmental predictor influencing both the individual species habitat models (fig. 3) and the overall bioregional classification (Figs 5 & 6). The classes resulting from bioregional eight-class solution were categorised by depth (Fig. 7c), with areas broadly based on the littoral, continental shelf, upper and mid-slope. Only in the upper bathymetric zones (littoral & shelf) were these depth classes subdivided into latitudinal categories (temperate & tropical). However, the depth ranges defined by each class were not mutually exclusive, overlapping somewhat, reflecting the local influence of other environmental factors.

## **4.3 Latitudinal gradients (Task 2)**

The eight-class hierarchy shown on the bioregional map (Fig. 6) reflects a latitudinal gradient only in the shallow areas along the Australian coastline, with temperate and tropical classes overlapping in southern Queensland and northern New South Wales.

A finer resolution map of this gradient was obtained by dividing the sum of MaxEnt output probabilities for tropical species (those known to occur north of 20°S) by the total MaxEnt probabilities for each pixel (Fig. 10). This shows the distinctiveness of the shallow water temperate Australian fauna, which occurs along the SE coast to Fraser Island, Queensland. The small area with low numbers of tropical species off the southern Great Barrier Reef is an artefact of lack of sampling; few species were

predicted to occur in this environmentally distinct area. The southern Lord Howe and Norfolk Ridges lack such a distinct temperate fauna, despite the proximity of New Zealand. The lowest proportion of tropical species in this region is 58% adjacent to NW New Zealand. The relatively low proportion of temperate species reflects the bathymetric profiles of these ridges. Temperate faunas are at their most distinct in shallow water (littoral and continental shelf); habitats largely absent from the SE corner of this study area.

#### **4.4 Comparison of the fauna surrounding Lord Howe and Norfolk Islands with the Australian continental margin (Task 3)**

Oceanic islands in the centre of the study area are complex with a mixture of tropical and temperate clusters. Both Lord Howe and Norfolk Islands are surrounded by all eight cluster types.

#### **4.5 Seamount species richness and endemism (Task 4)**

Species richness for individual seamounts ranged from 1 to 37 species from 1 to 43 samples (Table 3). The most species rich samples from seamounts were collected from Blackbourne (25 species, S Norfolk) and Mont K (20, N Norfolk). However, some samples from the continental slope were also rich, particularly some south of New Caledonia (24, 23, 20 & 20) and along the Loyalty Ridge (21 & 18). All seamounts fell within the 95% prediction limits for simulated populations based on areas of 50 km radius and 500 m depth range on the continental slope (Fig. 11).

Forty-seven of the 282 species present in the study area were endemic (ie were not recorded outside the area). Of these 20 (43%) were found only in seamount samples (seamount specialists) and 27 only in non-seamount samples or in both seamount and non-seamount samples (generalists). The majority of seamount specialists (n=17 or 85%) were limited to a single degree of latitude (defined here as 'narrow-range') compared with n=9 (33%) for generalists (Fig. 12). Thirteen species were apparently endemic to a single seamount (Table 3). There were no narrow-range seamount species from the eastern Australian (Tasmantid) seamounts (eg Gasgoyne, Taupo), although they were among the most geographically isolated.

When the number of narrow-range seamount specialists was compared to a null model that assumed the distribution of narrow-range species was random with respect to geographic position, two seamounts fell outside the 95% prediction intervals of the model (Fig. 13). The exceptions were N7 and N9 seamounts on the Norfolk Ridge which had more (n=2) narrow range species than predicted for the sampling intensity (7-8 samples).

All nine generalist species (Fig. 12) that were restricted to one degree latitude/longitude (defined as narrow-range species above) occurred only in non-seamount samples (ie collected from the continental margins or ridges).



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## 5. Discussion

The combination of MaxEnt modelling and a two-stage classification analysis resulted in a large-scale pattern that was biogeographically and ecologically realistic. The MaxEnt species models resulted in high to very AUC (validation) values indicating that they performed significantly better than random.

### 5.1 Bathymetric patterns (Task 1)

Depth was strongly emphasised in all analyses and maps. Depth was the variable contributing the most to MaxEnt models (and ENFA – see appendix). The second most important variable was seafloor temperature which is also influenced by depth. The primary division in the hierarchical classification was between shelf and slope areas across the entire study area. Working down the hierarchy, depth continued to structure the slope (into upper and mid-slope) and shelf classes (into littoral and shelf) across the study area.

Along continental margins, five or six depth clusters were present, typically based on littoral (coastal) areas, the continental shelf, several classes on the upper slope, and the mid-slope. The situation for offshore islands was even more complex (see below).

This division into littoral, shelf and slope classes conforms to the classic bathymetric patterns found in deep-sea systems elsewhere, for example, the coastal, continental shelf, archibenthal zone of transition (upper to mid slope) and abyssal zones (lower slope and abyssal plains) of Menzies *et al.* (1973).

### 5.3 North-south patterns (Task 2)

North-south patterns were also strongly emphasised in most models, particularly for littoral (coastal) areas and the continental shelf. Latitude by itself exerts no influence of the fauna but was a correlate for several environmental gradients including water temperate and primary production. The models consistently recognised distinct temperate and tropical assemblages. This was particularly evident along the Australian continental margin, the lack of temperate shallow water habitat precluding the same pattern in the south-east section of the study area. The situation around Lord Howe and Norfolk Islands is complex, with a mixture of temperate and tropical elements (see below). The northernmost limit of the temperate littoral cluster at Fraser Island, and the southern limit of the tropical littoral cluster in southern New South Wales, was in accordance with traditional qualitative marine zoogeography (Wilson & Allen 1987). The area in between represented a transition zone. The southern extent of the tropical shelf cluster closely matched the position of the East Australian Current (EAC), which separated from the New South Wales coastline around 32°S.

The lack of a strong latitudinal gradient along the Lord Howe Rise and Norfolk Ridge may also be a function of the study area boundaries. Taxonomic studies indicate that there is a considerable difference (90%) between the slope fauna of New Caledonia and southern Tasmania (O'Hara & Stöhr 2006). At slope depths, the zone of transition between tropical and Southern Ocean assemblages may lie further south than the boundary of this study (37°S).

## 5.4 East-west patterns

East-west patterns were not emphasised in the biodiversity maps, in contrast to a previous study that have found strong inter-ridge differences in seamount benthic species, including many ridge endemics (Richer de Forges *et al.* 2000). These earlier studies may have been confounded by artefacts of sampling species-rich communities (Samadi *et al.* 2006, O'Hara 2007b).

Excluding spot endemics (arising from possible sampling artefacts), there were few species that are restricted only to the Lord Howe Rise or the Norfolk Ridge on the continental slope or shelf. In contrast, temperate Australian and New Zealand margins supported many endemics. There were a few endemics restricted to littoral waters around Lord Howe and Norfolk Islands (see below). There were too few data from shallow water (<100 m) around New Caledonia to make an assessment of endemism.

These patterns were possibly driven by the uneven distribution of depth strata throughout the region. Littoral and shelf habitat is limited on the Lord Howe Rise and Norfolk Ridge. The emergent islands were relatively young (older seamounts having subsided) (O'Hara 2007b). Evolutionary processes were likely to be different along large continuous continental shelves than offshore islands and seamounts. In contrast, seafloor at mid-shelf depths (1000-2000 m) is more extensive along the Lord Howe Rise and Norfolk Ridge than the Australian margin. At this depth, however, many species have widespread distributions (Menzies *et al.* 1973).

## 5.5 Lord Howe Island (Task 3)

The modelling of ophiuroid distributions predicted a complex pattern around Lord Howe Island, Balls Pyramid, Elizabeth and Middleton Reefs with a mixture of temperate and tropical elements at littoral, shelf and slope depths. Around Lord Howe Island, temperate species were predicted to dominate at littoral, shelf and mid-slope depths, and tropical species on the upper slope. However, actual surveys around these islands (Hoggett & Rowe 1988, Rowe & Filmer-Sankey 1992) have found that approximately 70% of echinoderms were tropical/subtropical, 5-6% Australian temperate, and the rest had unusual distributions or were endemic to the Tasman Sea. Some of this discrepancy was possibly an artefact of the way subtropical (ie New South Wales-Southern Queensland) species were classified, with Hoggett & Rowe (1988) assigning them to a tropical group and the current analysis clustering them with temperate species. Nevertheless, the presence of a typical (although depauperate) tropical fauna was reflected in the presence of the world's most southerly coral reefs around Lord Howe Island (Hoggett & Rowe 1988). Many of the tropical echinoderm species were uncommon (ie they were not abundant) and are of small size, suggesting that they were representatives of non-reproductive populations living at the limits of their physiological tolerance that arrive occasionally as propagules via the East Australian Current (Hoggett & Rowe 1988).

The NORFANZ expedition collected several samples from shelf and upper slope depths around the islands. Collected species were also largely tropical with a few temperate and trans-Tasman species (O'Hara, O'Loughlin & Mah, unpublished data).

Nine echinoderm species have been recorded as endemic to Lord Howe Island (Hoggett & Rowe 1988) and three (undescribed crinoids) potentially to Elizabeth/Middleton Reefs (Rowe & Filmer-Sankey 1992). But all these species were found rarely (ie were uncommon) and some may be eventually found elsewhere (Hoggett & Rowe 1988).

In conclusion, the fauna of Lord Howe Island was largely shared with the Australian margin with relatively few endemics. In particular, the fauna was similar to that of southern Queensland with its mixture of tropical and warm temperate species.

## 5.6 Norfolk Island

The modelling of ophiuroid distributions around Norfolk Island suggested another complex mixture of tropical and temperate species, although in this case, tropical species were predicted to dominate littoral waters. A biogeographic analysis of the Norfolk Island fauna has not been conducted, however, examination of the species listed by Rowe (1989), and supplemented by new records in Museum Victoria and NIWA, suggested that approximately 63% (38 from 60) of littoral species (0-50 m) were of tropical origin, 33% (20) were shared with temperate Australia and/or New Zealand, 2% (n=1) were endemic to the Tasman Sea (Norfolk, Lord Howe, Elizabeth & Middleton) and 2% (n=1) endemic to Norfolk Island. The single putative endemic to Norfolk Island, the crinoid, *Antedon detonna*, has not been reported since the type description (Rowe & Gates 1995).

The fauna of Norfolk Island was similar to that of Lord Howe Island, except that some warm temperate species were shared with New Zealand (eg *Ophiothrix oliveri*) rather than Australia.

## 5.7 Comparison with fish patterns

The only other taxonomic dataset to have been analysed over the study area was fish collected from the joint Australian/New Zealand NORFANZ expedition in 2003 (Williams *et al.* 2006). The NORFANZ fish samples were analysed using multivariate analysis. The results showed a clear separation of samples by depth. The biogeographic affinities of the fish were preliminary analysed by Roberts & Clark (2006). They divided the fish into four groups, a) widespread, b) southern, c) Norfolk Ridge and d) endemic. They suggested that assemblages a) on the southern Norfolk Ridge (including Wanganella Bank, Reinga Ridge and West Norfolk Ridge) and Lord Howe Rise were similar to those off North-east New Zealand, b) on the northern Norfolk Ridge were similar to New Caledonia, c) around Lord Howe Island with the Australian shelf and d) seamounts on the north Lord Howe Rise with Queensland seamounts. They emphasized the southern affinities of many species and identified possible areas of endemism on the Middlesex Bank, Lord Howe Island, Norfolk Island, Norfolk Ridge, Wanganella Bank and Reinga Ridge.

These patterns showed many similarities to the ophiuroid data analysed here. The presence of temperate species on the southern Lord Howe and Norfolk Ridges (Fig. 10), although at a lower level than the Australian margin: the dominance of tropical (ie New Caledonian) species on the northern sections of the ridges; and the relationship of the fauna around Lord Howe Island to eastern Australia.

Overall, however, the ophiuroid dataset emphasized the tropical affinities of the regions ophiuroids rather than their temperate affinities. This was possibly an artefact of the study area, which did not include the New Zealand continental margin.

There was insufficient data to identify areas of endemism for ophiuroids. Only four species endemic to the study region had been collected frequently enough to warrant inclusion in the species modelling analysis performed here (which was limited to species known from more than 25 samples). The vast majority of the other endemics have been collected one or two times and few biogeographic inferences could be drawn from their distribution at the current time. These species would be best investigated in a phylogenetic context to understand their relationship to more widespread species.

## **5.8 Seamounts as centres of species-richness and endemism**

Seamount species-richness for ophiuroids tended to be consistent with prediction for equivalent areas on the continental slope (Fig. 11), a finding similar to that reported by O'Hara (2007b) for a larger geographic region. These findings were inconsistent with previous reports that have emphasized the relative species-richness of seamounts (Samedi *et al.* 2006).

These findings do not downgrade the potential ecological and biogeographic importance of seamounts. They indicate that some other deep-sea habitats can be equally species rich. The majority of non-seamount samples for this study came from the continental slope around south-eastern Australia and New Caledonia. High continental slope species-richness has been noted previously for both regions (Richer de Forges, 1990; Poore *et al.*, 1994).

This study found that 13 of the 282 species were apparently endemic to a single seamount. Three seamounts contained two endemics. A further four seamount specialists were narrow-range species, restricted to several seamounts within one degree of latitude. Many of these species were rare (i.e. not abundant), collected in 1-2 samples. This level of endemism was within, or slightly higher than, that expected by for random collections of samples found in equivalent sized areas on the continental slope (Fig. 13). Adequate sampling is required before it can be ascertained with certainty whether these species are narrow-range endemics or just rarely found. Expeditions to unexplored regions or habitats will almost always discover new species.

Previous studies into seamount endemism within the study region have reported varying results. Samadi *et al.* (2006) found that all 62 galatheid shrimps reported from the northern Norfolk seamounts had previously been found elsewhere. In contrast, Richer de Forges *et al.* (2000) reported high rates of local endemism (29-34%) for seamounts throughout the south-west Pacific Ocean. The discrepancy may lie in the differing taxonomic composition of these studies or simply from inadequate taxonomy and sampling artefacts. The Richer de Forges *et al.* (2000) study included a large range of macro-invertebrates (but not ophiuroids), some of which may have poor dispersal abilities compared with ophiuroids and galatheids.

However, there was little evidence that geographic isolation influenced community composition within the study depth range (100-1500 m). No narrow-range species were found on the most isolated seamounts such as Gascoyne or Taupo. Instead these species were scattered on a variety of seamounts throughout the Coral and northern Tasman Seas. This was in contrast to shallow water (0-20 m) around oceanic islands within the study area, such as Lord Howe and Norfolk, which were known to support some locally-endemic echinoderm species (see above).

The level of endemism may be understated for ophiuroids. Some shallow-water forms have proven to be suites of similar cryptic species that are genetically divergent but morphologically conserved (e.g. O'Hara *et al.* 2004). Morphological stasis is a feature of ophiuroids, with some extant species being identified from the Miocene (e.g. Ishida 2003) and some genera from the Mesozoic (e.g. Jagt 2000). There is a need for additional molecular studies on deep-sea species. Nevertheless, the limited genetic data from other phyla within the study area have been equivocal for the 'centres of endemism' paradigm. There was little genetic structure between populations of corals, galatheid crustaceans and planktotrophic molluscs, some hundreds of kilometers apart (Smith *et al.* 2004a; Samadi *et al.* 2006). This mirrors the situation for many animals found around hydrothermal vents which have been reported to be able to disperse over long distances (Won *et al.* 2003, Hurtado *et al.* 2004; Miyazaki *et al.* 2004). Other molluscs showed more population structure attributed to poor dispersal capabilities of the species concerned or unusual oceanography of the seamounts (Smith *et al.* 2004b; Samadi *et al.* 2006).

The evidence to date suggested that seamounts in the south-west Pacific support a similar suite of species to that found on neighbouring seamounts or continental crust within the same depth strata (O'Hara 2007b). The isolation of seamount summits suggested that seamount summit faunas have been assembled through dispersal (O'Hara 2007b). Many marine species are capable of long distance dispersal and there are many shallow-water examples of species that are genetically similar across the Tasman Sea from Australia to New Zealand (Poore & O'Hara 2007). The dispersal capability of most deep-sea ophiuroids is unknown, although judging from the size of their eggs many are likely to have lecithotrophic (non-feeding) larvae. Although, long term isolation of populations can lead to allopatric speciation in other environments (Barton 1998), there was little evidence for this in the ophiuroid data (at least leading to species defined by clear morphological differences). This is similar to the situation in other fragmented seafloor habitats such as hot vents, hydrocarbon seeps or whale carcasses (Van Dover 2002; Rouse *et al.* 2004; Stöhr & Segonzac 2005). Species living in these specialized ephemeral habitats can apparently disperse long distances. However, unlike these habitats, in general seamounts did not appear to support a highly specialized fauna (O'Hara 2007b).

The other consequence of the assembly-by-dispersal paradigm is that seamounts are likely to accumulate different sets of species depending on their location, form and longevity. Seamounts within the study area had great diversity of form, size, depth and position, altering local environmental conditions and consequently faunal composition (Rowden *et al.* 2005). The flat-topped structures on the northern Lord Howe Rise had considerable areas of soft-sediments, while volcanic cones were more likely to provide hard substrata, benefiting species that are epizoic on corals (Stocks 2004). Summit assemblages can differ from those along their sides and at the base,

because of different ecological and hydrological conditions. Koslow *et al.* (2001) found that the greatest cover of the habitat-forming coral *Solenosmilia variabilis* on the Tasmanian seamounts was at mid-height, with mud covering much of the summits and bases. In summary, seamounts are not a uniform habitat and do not support uniform assemblages.

The continental slope also contains a variety of habitats, ranging from gentle slopes covered in thick mud to canyons and fracture zones with steep rock-covered sides. Much of the southern Norfolk Ridge is covered by hard basalt without sediment, supporting little visible animal life (Williams *et al.* 2006). The rim of the Horseshoe canyon off eastern Bass Strait has extensive filter feeding communities while the canyon floor is covered in mud (A. Williams *pers. comm.*).

The conclusion to be drawn from this is that ‘seamounts’ appear to be at the wrong scale to be considered a useful seafloor habitat. They have been a convenient mappable geopolitical entity, and may have some usefulness when considered from a fisheries management perspective, but do not show the consistency and specialisation of seafloor assemblages to be considered a single unit for other management purposes such as marine park planning. Until we understand more about the ecological and historical factors that structure seafloor assemblages, ‘seamounts’ should be evaluated independently to ascertain their conservation status.

Seamounts have other important evolutionary and ecological roles besides facilitating speciation, including providing abundant source populations for surrounding regions, refuge habitat during adverse climatic conditions, and acting as ‘stepping stones’ facilitating long distance dispersal of species across oceans (Wilson & Kaufmann 1987; Richer de Forges *et al.* 2000).

## **5.9 Conclusions**

Ophiuroid assemblages were successfully predicted from current sample data using presence-only modeling techniques and a two-stage classification on the resulting species occurrence probabilities across the seascape of interest. The resulting patterns were most clearly structured by depth and latitude, separating into depth clusters within major temperate shelf, tropical shelf, and slope categories. This pattern was best reflected in the environmental predictor ‘seafloor temperature’ which varied with both depth and latitude.

Across this region, there was some east-west variation in littoral habitats, but relatively minor variation at shelf or slope depths. Most of this variation arises from endemics along the Australian continental margin rather than from Tasman Sea endemics.

## **5.10 Future work**

The modelling of species distributions across the study region would be improved by a more consistent spatial availability of samples. In particular, model performance would be improved by the collection of more samples from a) the outer shelf/slope regions off southern Queensland, including offshore seamounts/islands (Cato, Kenn, Wreck, Frederick, Recorder), b) the continental seafloor of the Lord Howe and

Norfolk Rise (most samples to date have come from seamounts), and c) deeper areas (<2000 m) throughout the region.

The models would also be improved with the addition of several environmental datasets including substratum (hardness or sediment composition), bottom currents, and a water mass atlas.

Future studies should increase the study area to include New Zealand and Tasmania. Few species are shared between New Caledonia and Tasmania or southern New Zealand (O'Hara 2007b), and expanding the study area will probably show the separation of slope assemblages into distinct temperate and tropical groups at latitudes south of 37°S.

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Species name	Number of training samples	Regularized training gain	Training AUC	Number of test samples	Test gain	Test AUC
<i>Astrobrachion adhaerens</i>	17	2.3287	0.9593	5	2.0512	0.963
<i>Astrosierra amblyconus</i>	28	4.5822	0.9991	9	5.5844	0.9988
<i>Asteroporpa australiensis</i>	16	3.7918	0.9929	5	3.7786	0.9948
<i>Amphiophiura bakeri</i>	21	3.4694	0.9948	7	3.6556	0.9928
<i>Amphiophiura confecta</i>	46	4.9521	0.9992	15	5.6185	0.9987
<i>Amphiura constricta</i>	107	4.2481	0.9974	35	5.3862	0.9972
<i>Amphioplus depressa</i>	21	2.7643	0.9885	6	2.5315	0.9798
<i>Amphiura elandiformis</i>	111	5.0368	0.9999	37	7.6926	0.9999
<i>Asteronyx loveni</i>	55	2.8808	0.9514	18	3.3398	0.9309
<i>Amphistigma minuta</i>	29	4.7104	0.9979	9	5.0354	0.9961
<i>Amphiophiura paupera</i>	19	3.8229	0.9909	6	4.4546	0.9936
<i>Amphiophiura pertusa</i>	37	3.3867	0.9824	12	4.3305	0.9935
<i>Amphiura poecila</i>	28	5.6279	0.9998	9	6.2978	0.9992
<i>Amphipholis squamata</i>	222	3.0797	0.9907	74	3.8288	0.9861
<i>Amphiophiura urbana</i>	39	3.1074	0.9888	13	3.8148	0.9916
<i>Astrothorax waitei</i>	62	3.6328	0.9927	20	3.9657	0.9842
<i>Bathypectinura heros</i>	36	2.3652	0.9627	12	3.7567	0.9858
<i>Conocladus australis</i>	68	2.9539	0.9859	22	3.6229	0.9923
<i>Clarkcoma bollonsi B</i>	33	4.2706	0.9977	10	4.6826	0.9958
<i>Clarkcoma canaliculata</i>	42	4.9525	0.9995	13	6.287	0.9996
<i>Clarkcoma pulchra</i>	36	5.2809	0.9997	11	4.9113	0.9899
<i>Dictenophiura ctenophora</i>	21	3.9095	0.9971	6	5.3711	0.9986
<i>Dictenophiura platyacantha</i>	33	5.5755	0.9999	10	6.5831	0.9996
<i>Euryale asperum</i>	42	2.3282	0.974	13	2.0153	0.9308
<i>Macrophiothrix longipeda</i>	21	3.5053	0.9954	7	3.167	0.968
<i>Macrophiothrix megapoma</i>	32	3.1755	0.981	10	3.6867	0.9782
<i>Ophiactis abyssicola</i>	60	3.2902	0.9878	19	1.9556	0.8946
<i>Ophiacantha alternata</i>	89	3.6649	0.9953	29	4.3014	0.9916
<i>Ophiiothrix aristulata</i>	92	3.7264	0.9966	30	3.9305	0.9861
<i>Ophiopsammus assimilis</i>	18	3.0259	0.9912	5	3.4249	0.9905
<i>Ophiomyxa australis</i>	165	2.6345	0.9833	54	2.905	0.9787
<i>Ophiacantha brachygnatha</i>	30	4.2316	0.9986	10	5.2539	0.998
<i>Ophiomyxa brevirima</i>	30	3.4993	0.9923	9	3.5454	0.9906
<i>Ophiomaza cacaotica</i>	33	2.5787	0.9714	11	2.3186	0.9598
<i>Ophiiothrix caespitosa</i>	220	3.2054	0.9934	73	3.7169	0.9894
<i>Ophiiothrix ciliaris</i>	102	3.3987	0.9929	33	3.6814	0.9792
<i>Ophiurothamnus clausa</i>	37	2.1472	0.9699	12	2.5245	0.9669
<i>Ophiomitrella conferta</i>	21	3.8329	0.9866	7	2.0814	0.9434
<i>Ophiopeza cylindrica</i>	56	3.0199	0.9881	18	3.4696	0.9888
<i>Ophiothela danae</i>	33	2.7286	0.9841	11	3.6643	0.9897
<i>Ophiactis definita</i>	31	3.4391	0.9885	10	3.4553	0.9812
<i>Ophiomyces delata</i>	26	2.4128	0.9783	8	1.2544	0.9072
<i>Ophiocoma dentata</i>	48	5.0036	0.9991	15	6.4937	0.9988
<i>Ophiarthrum elegans</i>	22	5.0964	0.9992	7	2.2097	0.9641
<i>Ophiocoma endeani</i>	15	5.877	1	5	7.4449	0.9999
<i>Ophiocoma erinaceus</i>	28	4.9889	0.9987	9	5.8011	0.9986
<i>Ophiiothrix exigua</i>	18	2.7877	0.9874	5	3.2752	0.987
<i>Ophiomusium facundum</i>	27	2.4688	0.983	9	2.8123	0.9736
<i>Ophiacantha fidelis</i>	20	4.5651	0.9989	6	4.4283	0.9925
<i>Ophiura flagellata</i>	26	4.5916	0.9984	8	5.2078	0.9753
<i>Ophiarachnella gorgonia</i>	24	3.8304	0.995	8	4.7492	0.9955
<i>Ophiacantha heterotyta</i>	18	3.2041	0.9947	5	3.8351	0.9914

<i>Ophiactis hirta</i>	24	3.0656	0.9916	7	3.6617	0.9837
<i>Ophioplocus imbricata</i>	30	4.3131	0.9989	9	4.1919	0.9934
<i>Ophiomusium incertum</i>	23	4.9756	0.9994	7	4.6381	0.9967
<i>Ophiarachnella infernalis</i>	24	2.6046	0.9811	7	2.5539	0.9595
<i>Ophiura irrorata</i>	32	2.9209	0.9651	10	3.5395	0.9789
<i>Ophiura jejuna</i>	24	4.4932	0.9983	8	5.7638	0.9994
<i>Ophiura kinbergi</i>	113	3.1783	0.9905	37	3.3872	0.983
<i>Ophioplax lamellosa</i>	24	3.7148	0.9977	8	3.4282	0.9881
<i>Ophiothrix lineocaerulea</i>	12	2.0998	0.9626	4	2.9662	0.9886
<i>Ophiomusium luetkeni</i>	56	4.7781	0.9987	18	6.0726	0.9996
<i>Ophiomusium lymani</i>	62	1.8859	0.9562	20	2.1154	0.9521
<i>Ophiactis macrolepidota</i>	22	2.4406	0.9782	7	2.2115	0.9464
<i>Ophiothrix martensi</i>	33	3.3625	0.9881	10	3.652	0.9771
<i>Ophiotreta matura</i>	20	2.0713	0.9745	6	2.0333	0.931
<i>Ophiura micracantha</i>	39	3.8412	0.9963	13	4.1397	0.9804
<i>Ophiocrossota multispina</i>	19	3.5881	0.996	6	2.972	0.9796
<i>Ophiothrix nereidina</i>	28	4.3989	0.9966	9	5.2405	0.9966
<i>Ophiomoeris obstricta</i>	39	3.5786	0.9904	12	4.7794	0.998
<i>Ophiocreas oedipus</i>	17	2.9212	0.9772	5	1.7431	0.9255
<i>Ophiura ooplax</i>	36	3.1835	0.9821	11	3.3631	0.9318
<i>Ophiura palliata</i>	32	4.5651	0.9985	10	5.5708	0.999
<i>Ophiopallas paradoxa</i>	43	4.7068	0.998	14	5.3603	0.9975
<i>Ophiacantha pentagona</i>	32	2.8604	0.9898	10	2.0758	0.918
<i>Ophiocentrus pilosa</i>	95	3.8117	0.996	31	4.555	0.9945
<i>Ophioplinthaca plicata</i>	28	3.7184	0.9896	9	3.0028	0.9471
<i>Ophionereis porrecta</i>	24	4.5072	0.9962	8	5.3471	0.998
<i>Ophiactis profundi</i>	46	2.8313	0.9887	15	3.3957	0.9866
<i>Ophiothrix purpurea</i>	20	3.5249	0.9929	6	4.6479	0.9945
<i>Ophiocoma pusilla</i>	27	5.1515	0.9995	8	5.9544	0.9986
<i>Ophiarachnella ramsayi</i>	30	4.8206	0.9991	9	5.3945	0.9956
<i>Ophiophthalmus relictus</i>	63	2.2437	0.9582	21	3.5206	0.9841
<i>Ophiactis resiliens</i>	162	3.5127	0.9943	54	4.1275	0.9888
<i>Ophiacantha rosea</i>	38	3.8244	0.9934	12	4.8391	0.9979
<i>Ophiactis savignyi</i>	69	3.6798	0.9944	22	3.7428	0.9768
<i>Ophiomusium scalare</i>	30	3.0026	0.9697	10	3.4232	0.889
<i>Ophionereis schayeri</i>	109	3.8968	0.9969	36	4.6354	0.9925
<i>Ophioleuce seminudum</i>	49	3.8492	0.9807	16	3.2051	0.9667
<i>Ophiocreas sibogae</i>	24	2.717	0.9906	7	2.5997	0.9587
<i>Ophiomusium simplex</i>	49	4.0841	0.9967	16	5.321	0.9981
<i>Ophiolimna cf bairdi</i>	21	4.8466	0.9992	7	3.6931	0.9872
<i>Ophiothrix spongicola</i>	91	4.0997	0.9979	30	5.0285	0.9932
<i>Ophiotreta stimulea</i>	39	2.3539	0.9702	13	2.9853	0.9517
<i>Ophiolepis superba</i>	11	4.0022	0.9954	3	3.5534	0.9872
<i>Ophionereis terba</i>	34	4.3348	0.9976	11	4.4777	0.9957
<i>Ophiothrix trilineata</i>	22	5.1866	0.9995	7	6.3161	0.9993
<i>Ophiernus vallincola</i>	32	2.8809	0.9656	10	2.2781	0.9336
<i>Ophiocamax vitrea</i>	82	3.2162	0.9935	27	4.0526	0.9932
<i>Ophiacantha yaldwyni</i>	23	4.1248	0.9969	7	4.6883	0.9947
<i>Ophiopsammus yoldii</i>	28	3.1247	0.9847	9	3.4545	0.9665
<i>Ophioplinthaca rudis</i>	54	2.5375	0.9741	18	3.2938	0.9717

Table 1. List of species used in the MaxEnt modelling. 25% of the species occurrences were retained for model validation (Test dataset). AUC is the ‘Area Under the Curve’ a standard model validation technique, that varies from 0.5 (random) to almost 1.0 (perfect model).

Seamount	Region	Mean latitude (°S)	Mean longitude (°E)	Area sampled (km <sup>2</sup> )	Min depth (m)	Max depth (m)	Mean depth (m)	No samples	No species	No endemics
Lansdowne	N Lord Howe	-20.90	160.86	81.36	500	825	684	3	5	0
Fairway	N Lord Howe	-21.23	162.27	0.00	120	150	135	1	1	0
Nova	N Lord Howe	-22.38	159.34	3428.70	277	1560	479	21	25	2
Argo	N Lord Howe	-23.18	159.52	82.38	279	300	287	4	3	0
Kelso	N Lord Howe	-24.08	159.54	771.45	150	793	292	11	10	1
Joker	N Lord Howe	-24.35	161.71	0.00	816	817	816	1	1	0
Capel	N Lord Howe	-25.16	159.75	5425.40	150	1330	347	18	18	0
Gifford	N Lord Howe	-26.80	159.44	121.50	295	360	323	4	4	0
Gemini	N Norfolk	-20.99	170.12	39.12	190	710	448	6	12	0
Alis	N Norfolk	-22.33	168.70	36.56	255	550	346	10	15	1
Munida	N Norfolk	-23.00	168.31	4.57	200	300	248	3	6	0
Antigonia	N Norfolk	-23.33	168.05	40.06	230	900	350	17	25	0
Cryptothelia	N Norfolk	-23.33	168.27	0.00	340	619	480	1	3	0
Brachiopode	N Norfolk	-23.46	167.84	0.00	276	350	313	1	4	0
Mont D	N Norfolk	-23.56	169.60	0.63	657	845	712	3	12	0
Stylaster	N Norfolk	-23.64	167.72	12.90	418	970	528	8	8	0
Jumeau W	N Norfolk	-23.69	168.01	0.74	229	428	288	8	10	0
Jumeau E	N Norfolk	-23.74	168.28	8.88	379	530	417	7	8	0
Mont J	N Norfolk	-23.88	169.80	26.04	614	715	671	6	25	0
Scarabée	N Norfolk	-24.01	168.64	0.00	1003	1060	1032	1	1	0
Floride	N Norfolk	-24.02	168.01	0.00	1074	1500	1287	1	1	0

Seamount	Region	Mean latitude (°S)	Mean longitude (°E)	Area sampled (km <sup>2</sup> )	Min depth (m)	Max depth (m)	Mean depth (m)	No samples	No species	No endemics
Introuvable	N Norfolk	-24.66	168.65	4.80	562	806	635	4	8	1
Mont K	N Norfolk	-24.74	170.12	6.12	750	855	802	3	26	0
Kaimon Maru	N Norfolk	-24.76	168.14	46.25	235	510	309	15	17	0
Chagrin	N Norfolk	-24.87	168.72	0.00	1133	1280	1206	1	6	0
Eponge	N Norfolk	-24.91	168.36	11.55	500	680	557	4	5	1
Falaise	N Norfolk	-25.05	168.76	0.00	1098	1480	1289	1	1	0
Sud	N Norfolk	-25.28	170.42	268.72	900	1011	938	3	3	0
Athos	N Norfolk	-25.28	168.94	0.00	618	880	749	1	1	0
Zorro	N Norfolk	-25.38	168.33	0.00	625	1250	938	1	2	0
Aramis	N Norfolk	-25.38	168.94	0.00	643	1233	938	1	1	0
N6	N Norfolk	-26.41	167.16	43.77	710	1035	808	4	14	0
Britannia	E Australia	-28.21	155.61	551.77	415	1400	581	5	10	0
Derwent Hunter	E Australia	-30.80	156.22	0.00	288	288	288	1	3	0
Barcoo	E Australia	-32.57	156.29	0.00	285	285	285	1	1	0
Taupo	E Australia	-33.19	156.16	8.96	131	164	142	5	5	0
Gascoyne	E Australia	-36.71	156.18	12.22	143	145	144	2	5	0
N7	S Lord Howe	-29.22	159.01	17.35	292	1395	671	8	21	2
Elizabeth*	S Lord Howe	-29.91	159.13	2.81	420	650	535	2	7	0
Lord Howe Island*	S Lord Howe	-31.60	159.19	1251.63	183	960	473	2	9	0
N9	S Lord Howe	-34.16	162.64	228.80	430	818	695	7	18	2
N4	S Norfolk	-28.88	167.70	13.30	111	812	432	2	13	1
Norfolk Island*	S Norfolk	-29.36	168.04	3643.07	77	732	391	10	17	1
Blackbourne	S Norfolk	-29.78	168.98	0.00	500	500	500	1	14	0



Seamount	Region	Mean latitude (°S)	Mean longitude (°E)	Area sampled (km <sup>2</sup> )	Min depth (m)	Max depth (m)	Mean depth (m)	No samples	No species	No endemics
N3	S Norfolk	-30.04	167.62	255.92	130	1131	641	4	3	0
N21	S Norfolk	-31.99	168.06	1611.87	319	954	590	3	5	0
Wanganella	S Norfolk	-32.57	167.54	1559.66	121	1052	372	20	26	1
N2	S Norfolk	-33.36	170.13	375.75	465	1260	640	8	16	0
N11	S Norfolk	-33.75	167.33	105.20	248	1478	561	4	14	1
N12	S Norfolk	-34.32	168.40	132.10	373	1268	747	7	19	0
N13	S Norfolk	-34.60	168.95	31.37	508	1150	761	4	22	1
N14	S Norfolk	-35.15	169.48	5.33	865	872	868	3	4	0

Table 2. List of sampled seamounts from the study area. Location, depth and area variables refer to samples not actual topography. Seamounts marked by an asterisk emerge to form islands.

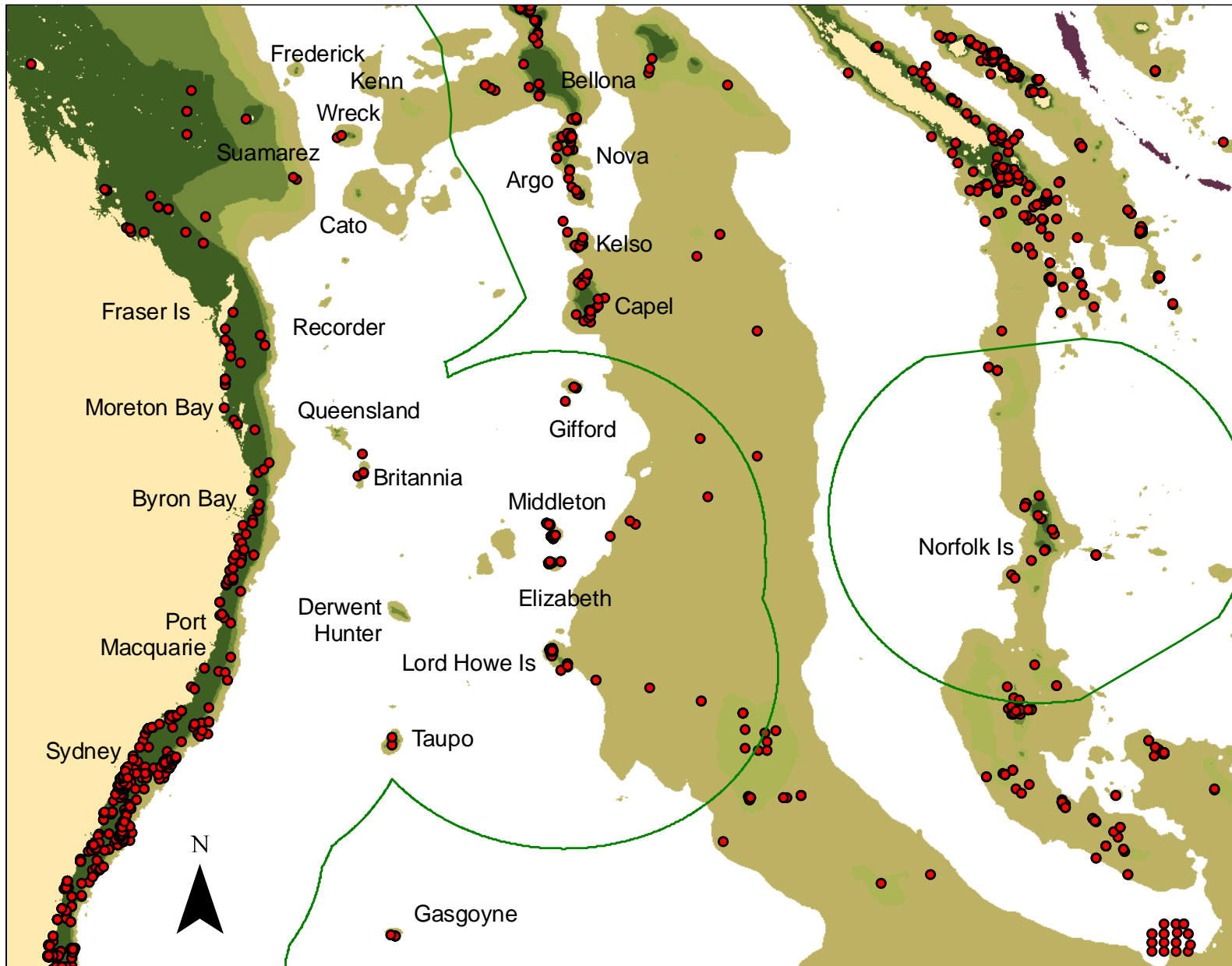


Fig. 1. Map sample sites from the Lord Howe/Norfolk study region (0-3000 m).

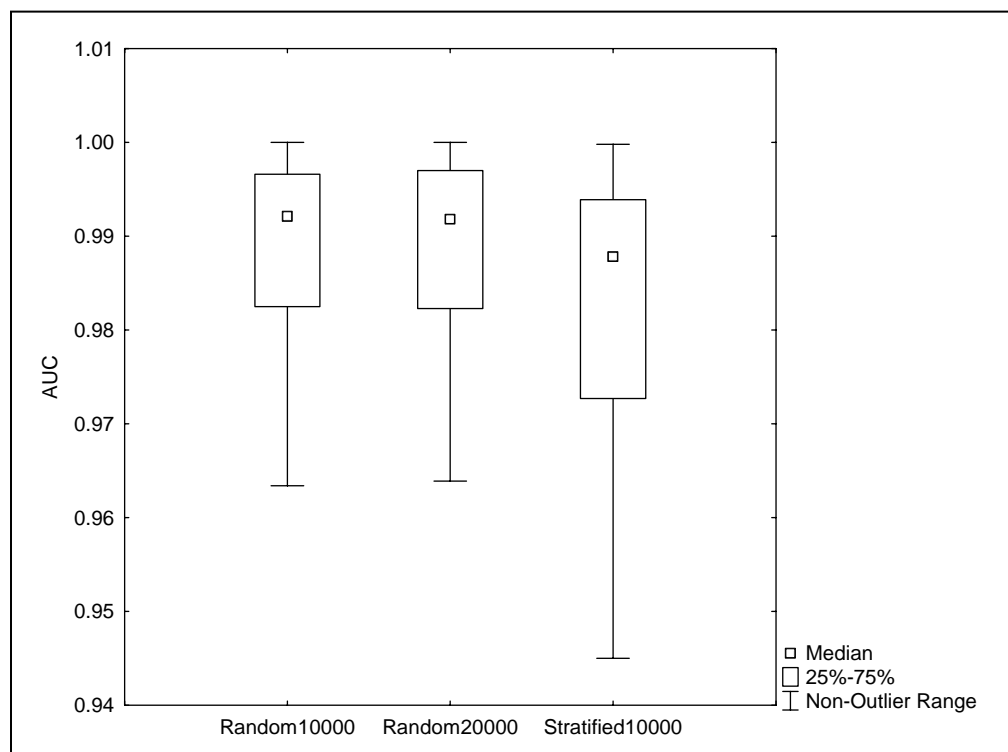


Fig. 2a. Box plots of Training AUC for all 102 ophiuroids derived from analysed with Maximum Entropy modelling using different methods of creating the background random environmental data: using 10000 random points, 20000 random points, and 10000 points using a stratified-random approach (see text for details).

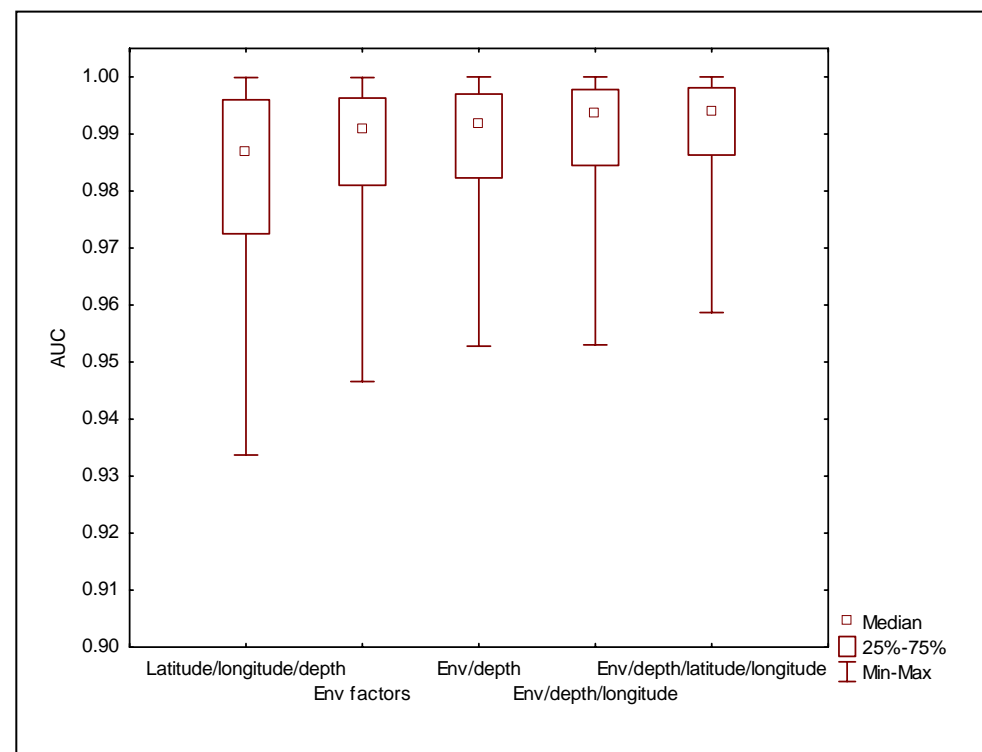


Fig. 2b. Box plots of Training AUC for 102 ophiuroid species analysed with Maximum Entropy modelling comparing various environmental and spatial factors. 'Env' factors include seafloor temperature, salinity, oxygen, nitrate, and slope, and sea-surface temperature, current velocity, and productivity.

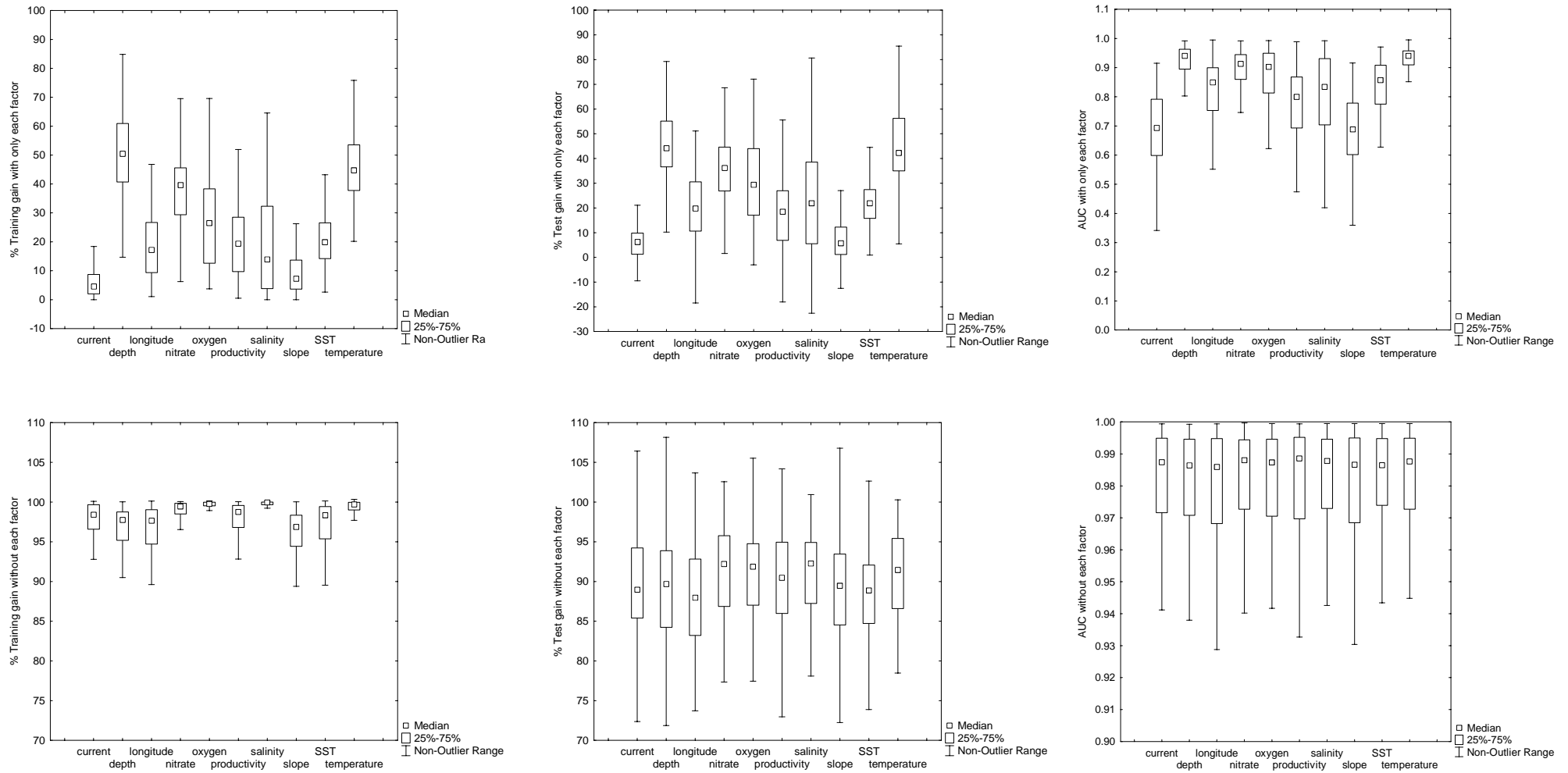


Fig. 3. Graphs showing the importance of each environmental factor in terms of the training dataset gain, test dataset gain and test AUC for 102 ophiuroid species analysed with Maximum Entropy modelling. The upper graphs show the contribution of each factor when used in isolation. The lower graphs show the contribution each factor makes by excluding it from the list. Gain is expressed as a percentage of the gain when all factors are used.

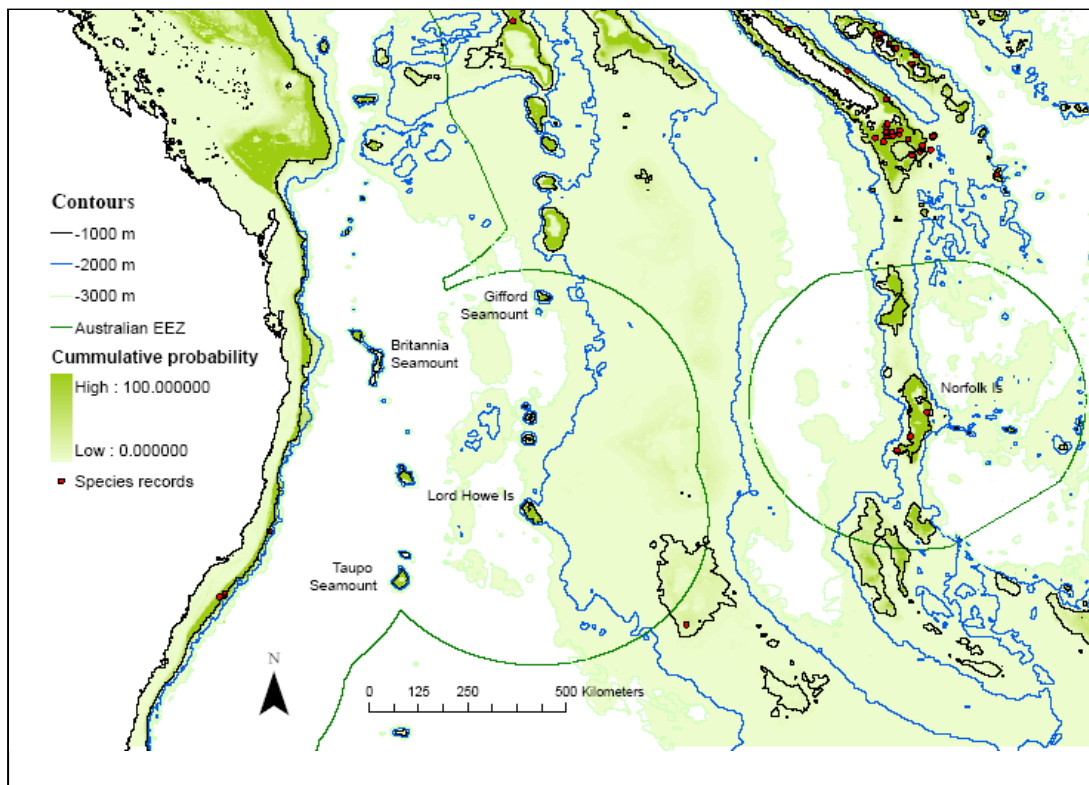


Fig. 4. Map of predicted species distributions for the species *Ophiocamax vitrea* resulting from MaxEnt modelling using all environmental parameters.

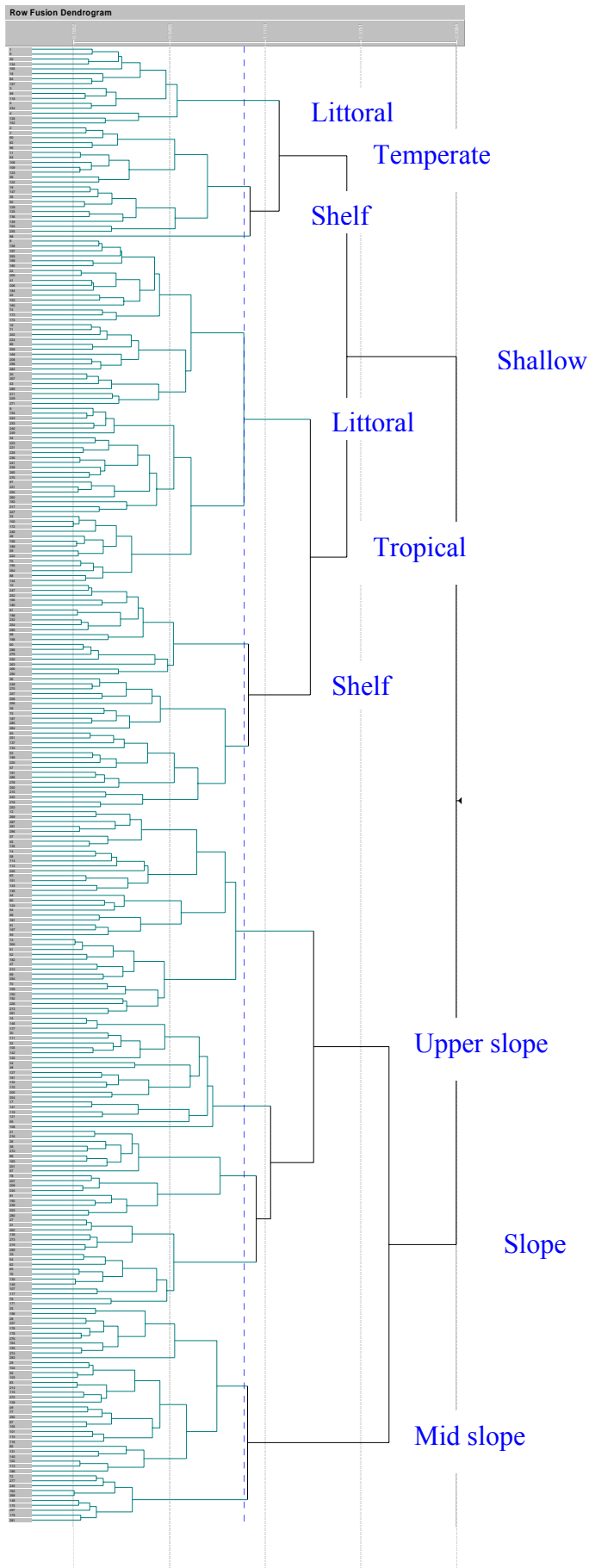


Fig. 5. Dendrogram of the Tasman/Coral Seas MaxEnt classification showing how the classes are progressively amalgamated into 2-300 classes. The blue dashed line shows 12 classes.

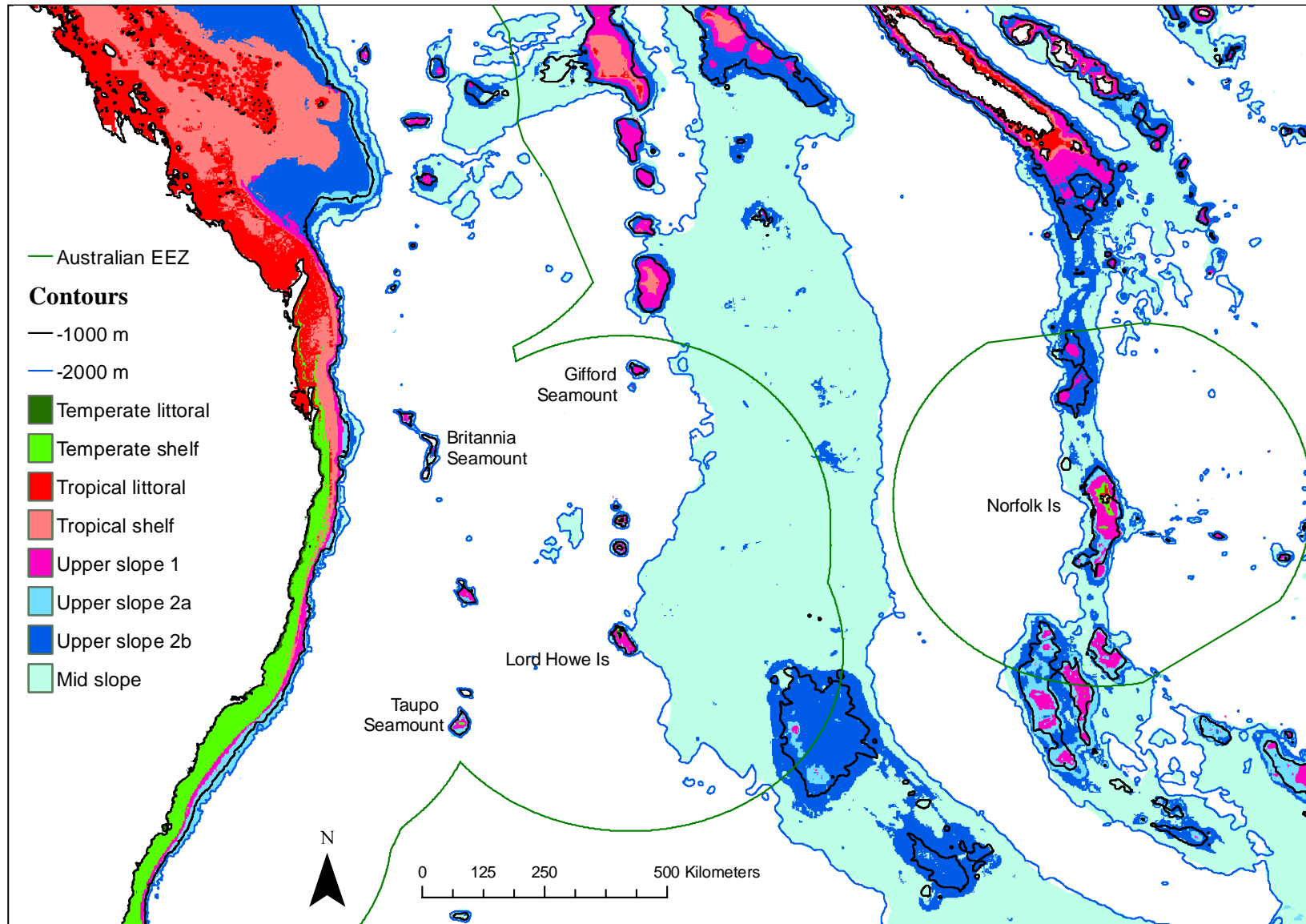


Fig. 6. Eight-class classification of seafloor assemblages generated from cluster analysis of stacked probability predictions from Maximum Entropy modelling of 102 ophiuroid species.

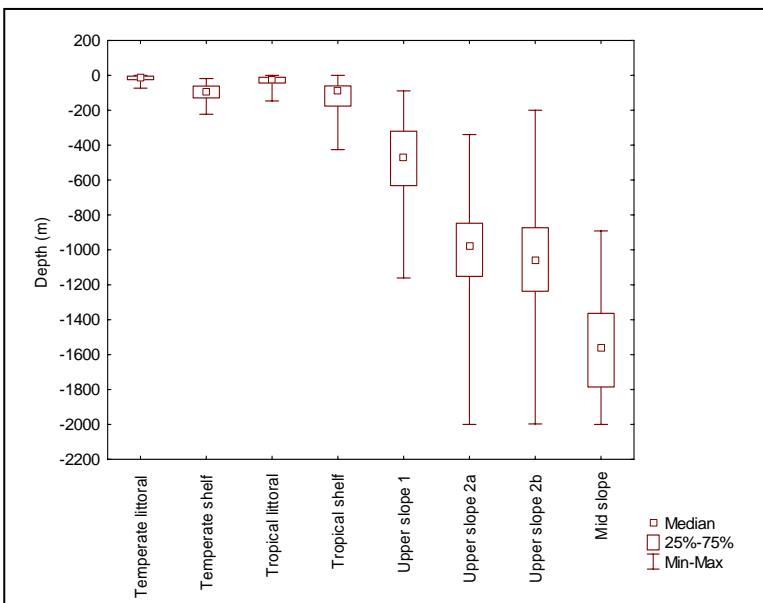
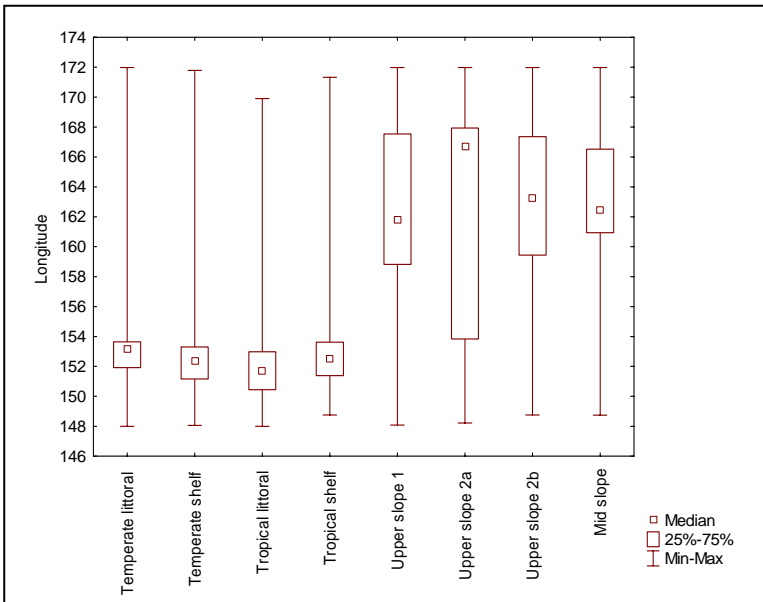
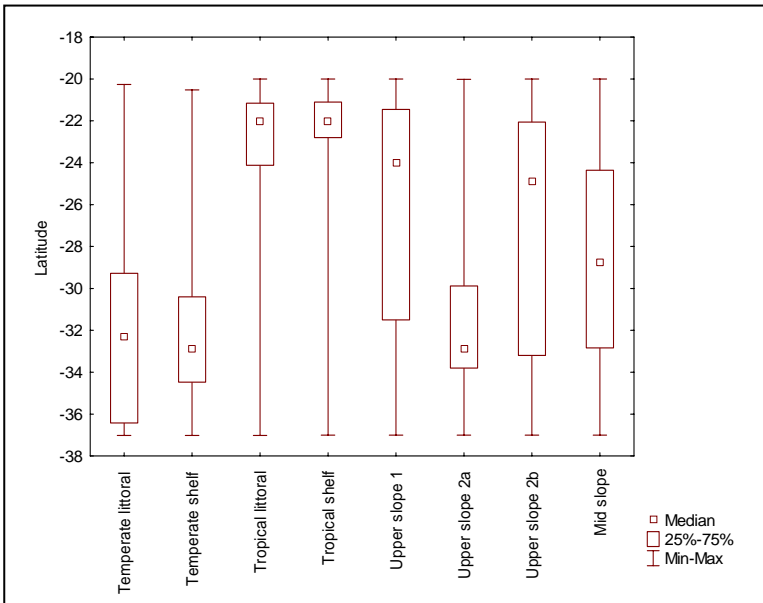


Fig. 7. Box-plots showing the distribution of pixels (see Fig. 5) by latitude, longitude and depth for the MaxEnt eight class solution.

For example, the 50% of the pixels classified as ‘Temperate littoral’ lie approximately between 29-36°S, 152-154°E and 0-20 m depth.



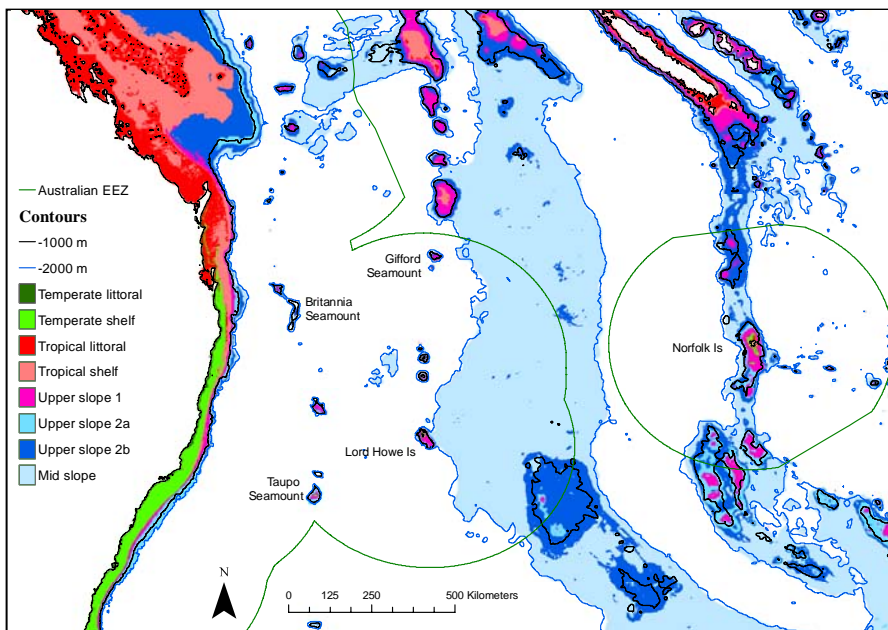
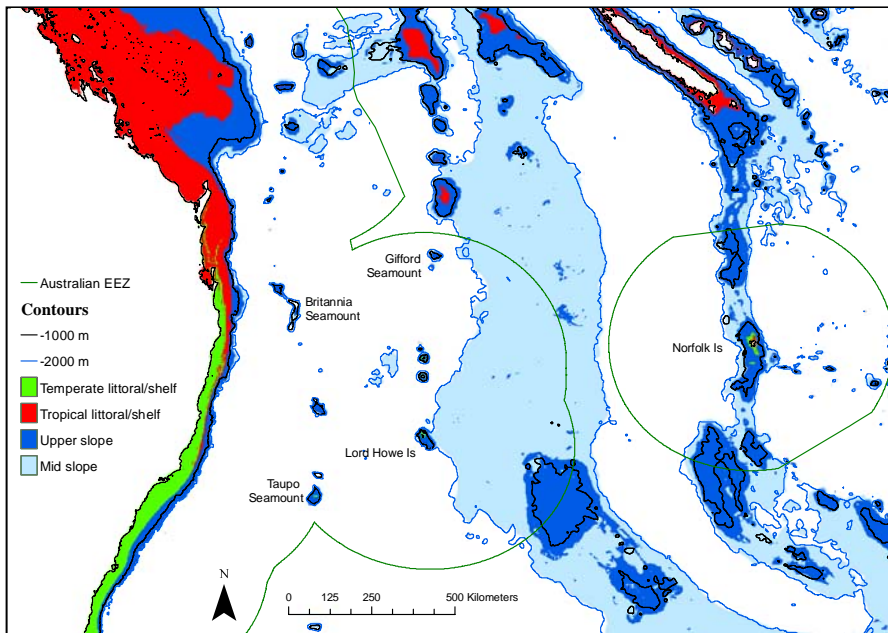
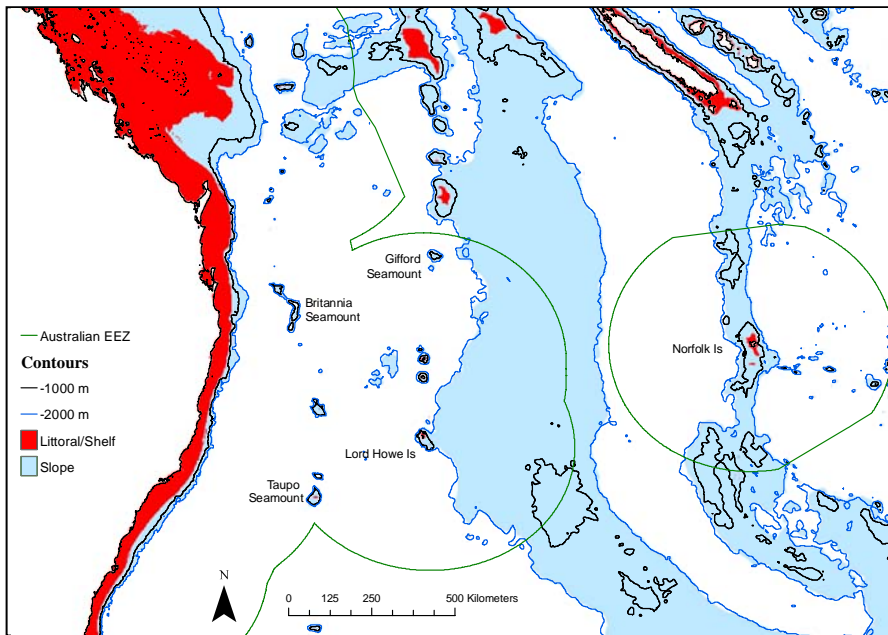


Fig. 8. Hierarchical classification of seafloor assemblages generated from cluster analysis of stacked probability predictions from Maximum Entropy modelling of 102 ophiuroid species. A) Two class solution, B) Four class solution, and C) Eight class solution.

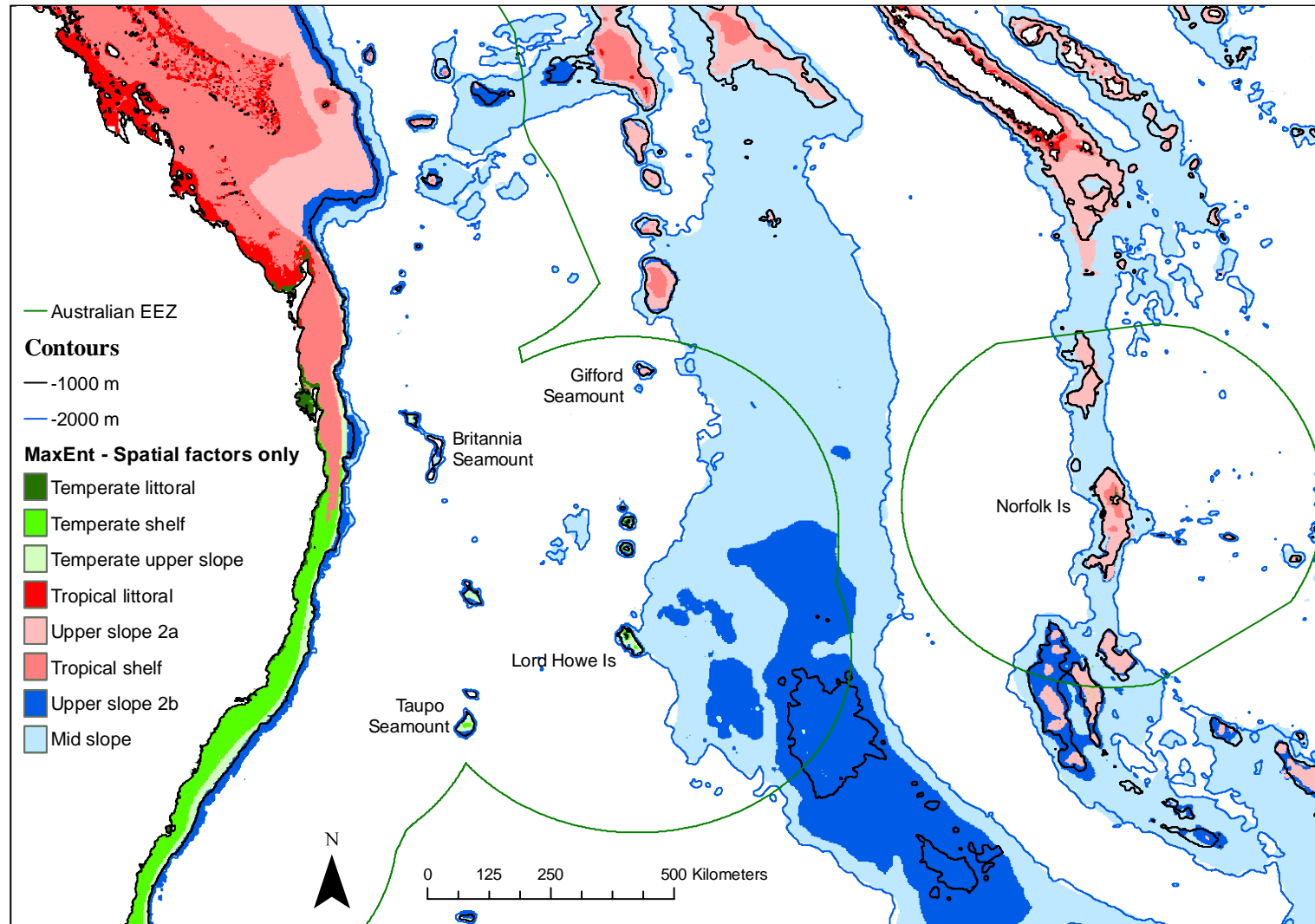


Fig. 9. Eight-class classification of seafloor assemblages generated from a two-stage cluster analysis of stacked probability predictions from Maximum Entropy modelling of 102 ophiuroid species using only spatial and bathymetric environmental factors (latitude, longitude, depth).

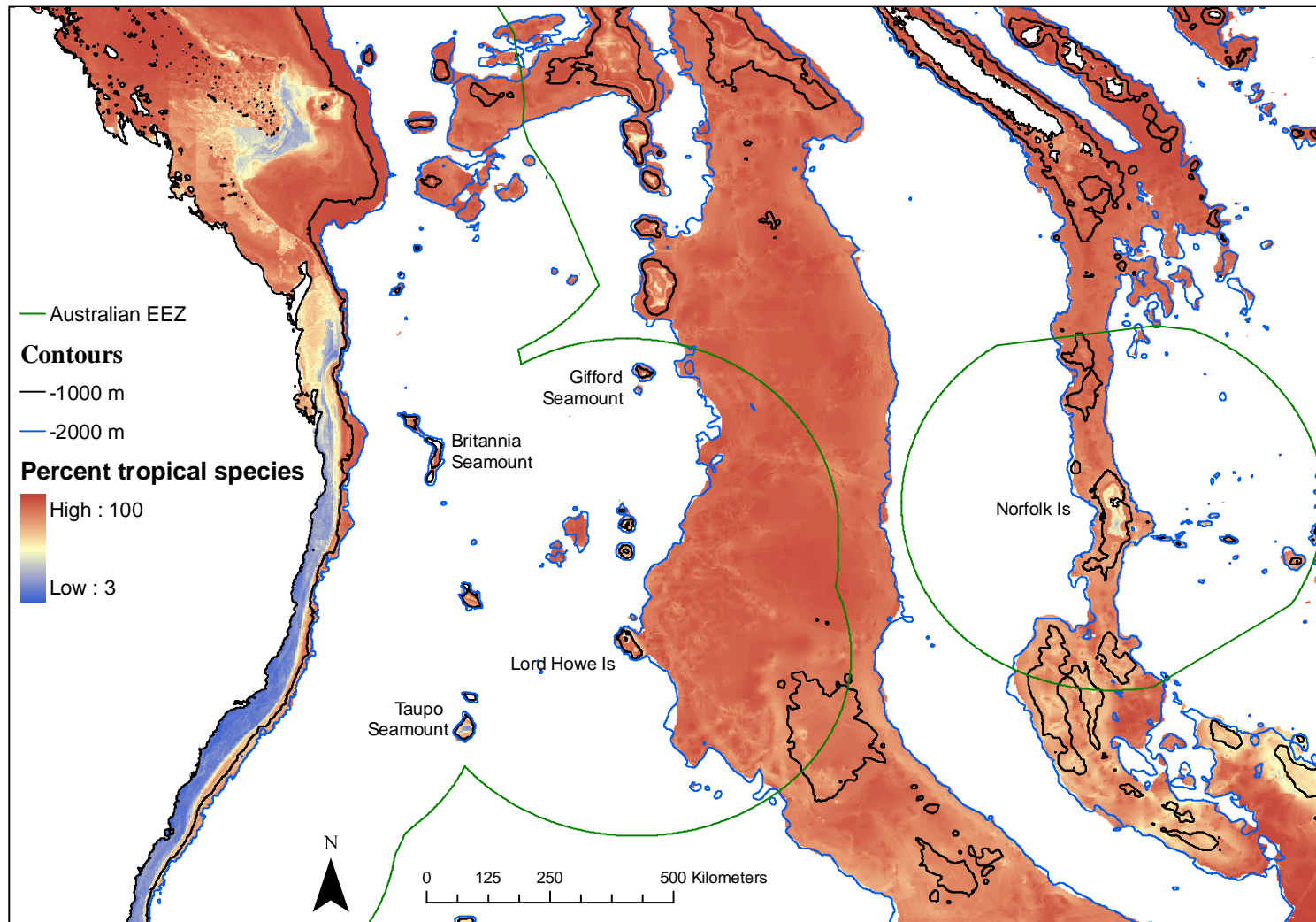


Fig. 10. Map showing the proportion of tropical species across the study area. The proportions are calculated by dividing the sum of MaxEnt output probabilities for tropical species (those occurring north of 20°S) by the total MaxEnt probabilities for each pixel.

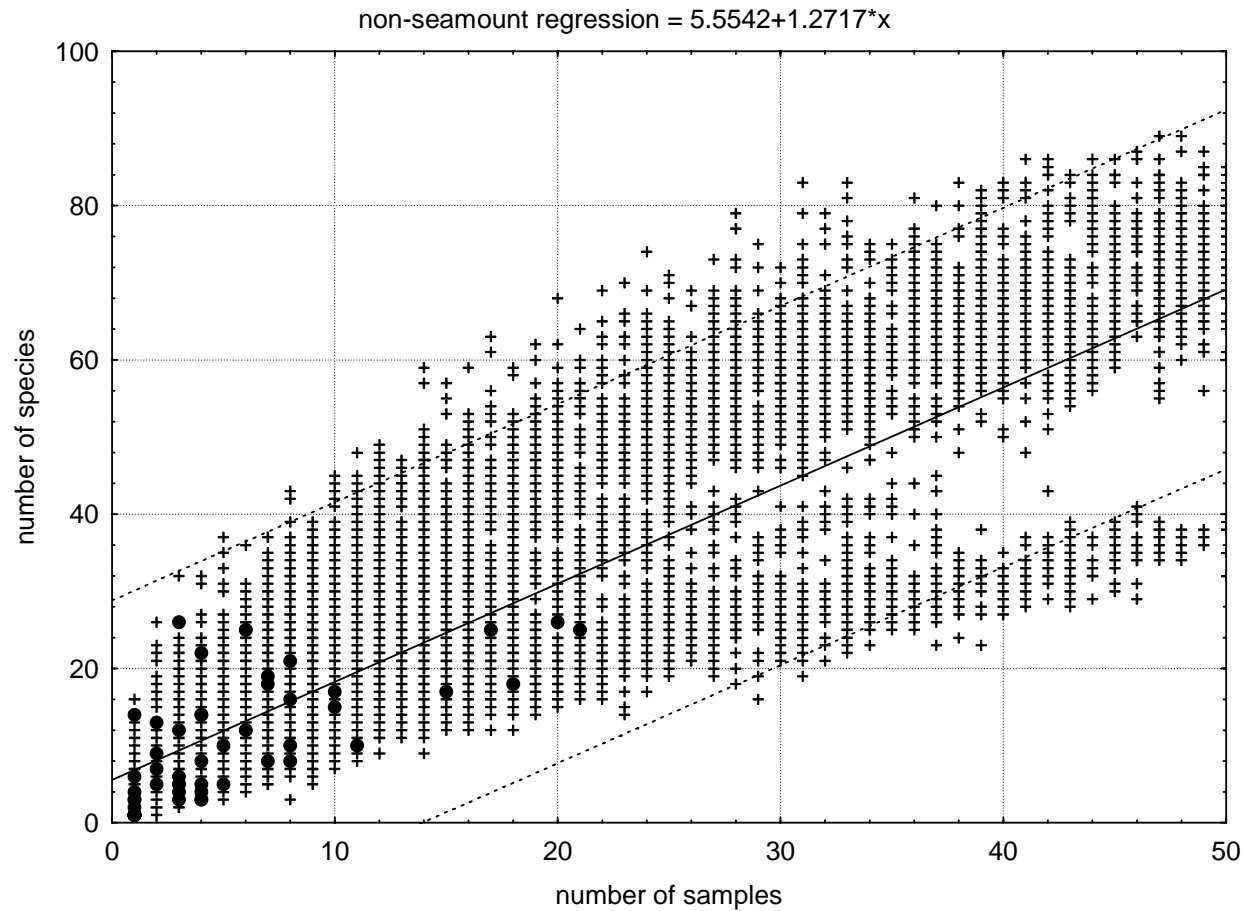


Fig. 11. The relationship between the number of species and number of samples for seamounts and non-seamount areas across the study region. Dots represent each of the 52 seamounts (many overlap). Crosses represent 10,000 randomly-selected populations of between 1 and 50 samples from areas of the continental slope of 50 km radius and 500 m depth range, and the solid and dotted lines show the linear regression and 95 % prediction limits. No seamounts have more the predicted number of species.

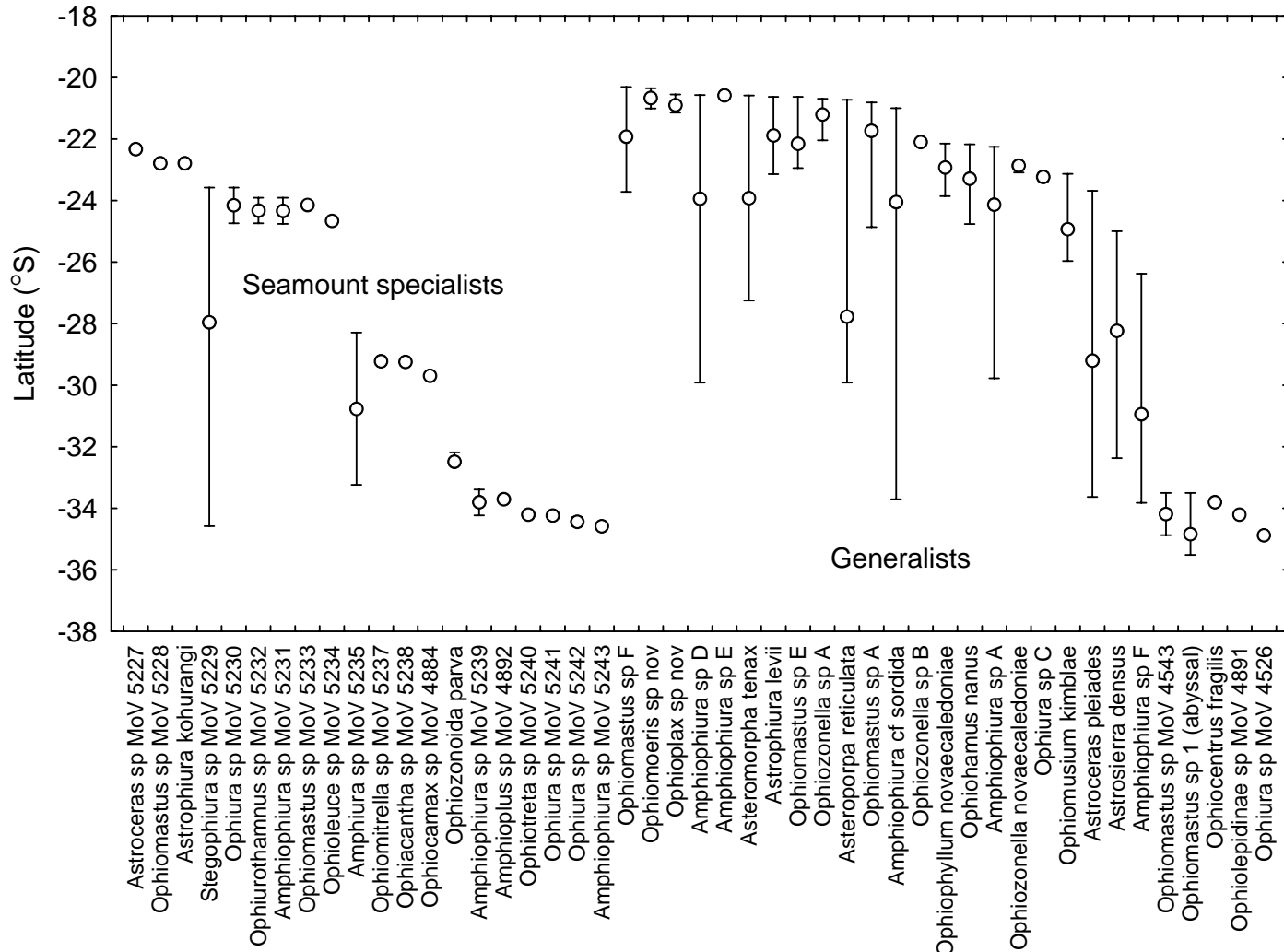


Fig. 12. Latitudinal range of the 47 species endemic to the study area. The left 20 species were only found on seamounts, the remaining ‘generalist’ species were from both seamounts and non-seamounts or non-seamount samples only. Highlighted point of each range indicates the mean collection latitude.

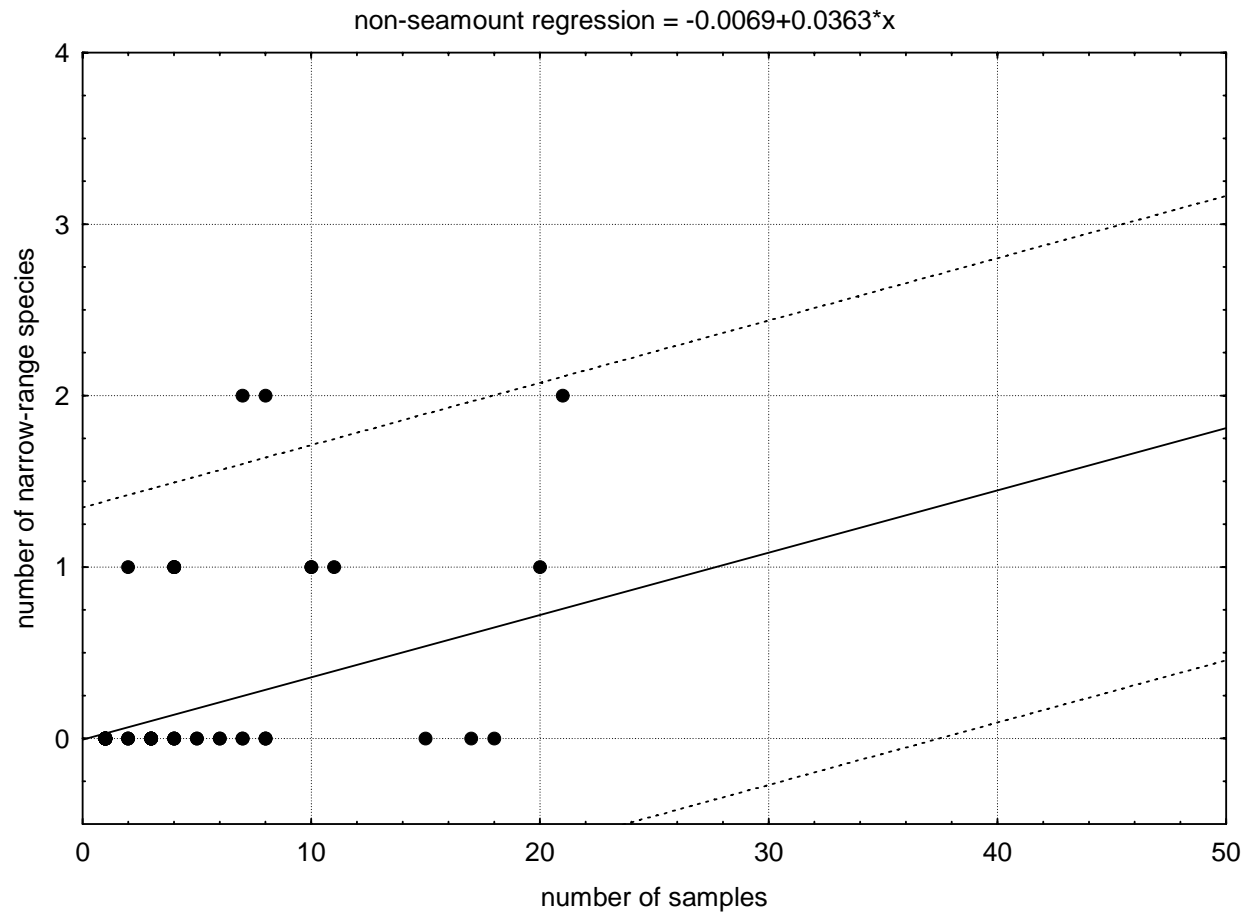


Fig. 13. The relationship between the number of narrow-range species ( $\leq 1$  degree of latitude/longitude) and number of samples within the study area. Dots represent each of the 52 seamounts (many overlap). The solid and dotted lines show the linear regression and 95 % prediction limits for the number of narrow-range species found in 10000 random selections of between 1 to 50 samples from non-seamount samples throughout the study area and depth range (data points are omitted for clarity). Two seamounts on the Norfolk Ridge (N7 and N9) have more than the predicted number of narrow-range species.

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## Appendix S1. ENFA Analysis

A second technique Environmental Niche Factor Analysis (ENFA) (Hirzel *et al.* 2002) was also used as a comparison to the MaxEnt modeling provided above. This technique has been used in the deep-sea environment to model coral distributions over large scales (Clark *et al.* 2006, Bryan & Metaxas 2007). It is similar to principal component analysis in that environmental variables are linearly combined into a series of factors representing the ‘marginality’ and ‘specialisation’ of a species environmental niche. Environmental suitability of a site is then calculated as a distance in the multidimensional niche space.

### *ENFA models*

ENFA modelling as implemented in the Biomapper software, requires that the environmental data and species-distribution data cover the same area, consequently habitat suitability was predicted over the entire Australian EEZ (8-50°S and 102-172°E). However, only a subset of the prediction data covering the same area as predicted by the MaxEnt modelling (20-37°S and 148-172°E) was analysed here.

At least 20-30 species presence records are required for ENFA modelling (Hirzel 2005). However, because ENFA requires the species-distribution data to be input in a binary raster format, sites in close-proximity that fall within a single raster pixel are considered one site. Only 60 ophiuroid species were represented by 20 or more presence records once the data was aggregated into the 0.02 degree raster resolution used in this analysis.

Prior to the ENFA analysis, the environmental data was normalized using the Box-Cox transformation. Habitat suitability maps for each species were prepared using the ‘medians’ method (Hirzel *et al.* 2002) and rescaled to between 0 and 100 using the isopleth method. The number of factors (marginalization plus one or more specialization factors) used was determined by using the broken-stick method. The resulting predictions were cross-validated by allocating the data to four bins and then using a k-fold technique with 10 partitions and Boyce’s continuous index (Hirzel *et al.* 2006).

At the data level there were some mismatches between the depth recorded as part of the biological sample and the mean depth for that 0.02 degree pixel recorded on the bathymetry GIS dataset. This was particularly notable for 1) seamounts, where samples can be several hundred metres higher than the pixel average due to the rugosity of the seafloor and the tendency for biological sampling programs to target seamount summits, and 2) coastal sites, where the recorded depth was often lower than average, collected in very shallow water (eg intertidal or sub-tidally by SCUBA). This was a serious problem for ENFA modelling, where species occurrences and environmental data have to be input in aligned GIS layers. In this case, the pixel depth was altered to the average sample depth, and the seafloor temperature, salinity, oxygen and nitrate re-extracted from the CARS2000 datasets to match the altered depths.

### *Results*

The mean species values (ENFA marginality) differed from the background for all factors except for surface current velocity (Table S1, Fig. S1). This is not surprising as few species would occupy a niche that sits at the mean of environmental factors

across the entire background area from 8-50°S, 102-172°E and 0-3000 m. The main factors driving the difference between species and background variance (ENFA specialisation) were depth, seafloor temperature, and, to a far lesser extent, nitrate, salinity and sea-surface temperature.

The ENFA modelling tended to overfit species distributions, predicting more suitable habitat than the MaxEnt models. For example, *Ophiocamax vitrea* is predicted to occur across a wide section of the continental shelf off Queensland (Fig. S2) although there are no records from such shallow water. On the whole the model validation for the 60 species was poor for the ENFA models (Table S1). This is due partly to the choice of validation methods implemented in the ENFA software package Biomapper which rely on correlation in habitat suitability maps produced by a k-fold partition technique. With relatively few species-presences, the data subsets contained in the partitions span different ecological ranges, resulting in different habitat suitability maps which do not correlate. These techniques work best with more than 50 presence records (Hirzel *et al.* 2006).

However, given the overfitting and validation issues, the ENFA analysis produced a broadly similar eight-class bioregional model to MaxEnt (Fig. S3) when analyses using the two-step classification procedure (see section 2). Important differences include the presence of only one class covering both temperate and tropical regions, a class representing shelf and littoral zones in temperate regions, the extension of the tropical shelf class to southern New South Wales, the division of upper slope pixels into tropical and temperate regions, and the reduction in size of the mid-slope class.



Species	No of presences	Marginality	Specialisation	Explained specialisation - Marginality %	Explained specialisation – Factor 1 %	Explained specialisation – Factor 2 %	No of factors used in HS maps	Mean Boyce's index (4 bins)	Stdev Boyce's index (4 bins)	Mean continuous Boyce's index	Stdev continuous Boyce's index
<i>Amphiophiura insolita</i>	21	1.04	8.542	25	66	4	2	0.00	0.00	0.00	0.00
<i>Amphiophiura urbana</i>	52	1.205	5.374	58	30	5	3	0.44	0.45	0.00	0.05
<i>Amphipholis squamata</i>	260	1.618	4.619	74	18	2	3	0.61	0.38	-0.01	0.08
<i>Asteronyx loveni</i>	71	0.953	4.976	62	21	7	4	0.57	0.39	0.01	0.09
<i>Astrothorax waitei</i>	78	0.846	6.217	64	25	5	2	0.51	0.33	0.01	0.12
<i>Bathypectinura heros</i>	47	0.689	3.982	46	27	17	3	0.40	0.81	0.03	0.17
<i>Clarkcoma bollonsi</i> B	34	1.754	9.693	72	20	4	3	0.25	0.50	0.04	0.11
<i>Conocladus australis</i>	86	1.882	12.663	78	15	5	3	0.51	0.48	-0.01	0.13
<i>Dictenophiura ctenophora</i>	28	1.571	15.077	82	11	4	3	-0.01	0.63	-0.06	0.62
<i>Ophiacantha alternata</i>	117	2.05	22.631	68	27	2	3	0.37	0.23	0.02	0.08
<i>Ophiacantha brachygnatha</i>	41	1.205	9.451	50	39	6	3	0.42	0.50	0.03	0.13
<i>Ophiacantha clavigera</i>	32	2.013	44.761	88	11	1	3	0.40	0.63	0.05	0.14
<i>Ophiacantha fidelis</i>	24	1.419	22.545	71	18	7	3	0.19	0.69	0.05	0.13
<i>Ophiacantha pentagona</i>	41	0.848	3.985	31	46	12	3	0.02	0.77	-0.03	0.14
<i>Ophiacantha rosea</i>	45	1.205	4.773	30	26	25	4	0.46	0.41	0.00	0.10
<i>Ophiacantha yaldwyni</i>	27	1.181	9.136	15	41	34	3	0.51	0.42	0.05	0.08
<i>Ophiactis abyssicola</i>	73	1.085	4.03	49	20	13	5	0.58	0.45	0.01	0.07
<i>Ophiactis definita</i>	40	0.8	7.752	61	19	13	3	0.28	0.63	0.00	0.12
<i>Ophiactis hirta</i>	31	1.149	9.742	75	17	5	3	0.20	0.64	-0.01	0.11
<i>Ophiactis macrolepidota</i>	29	1.399	10.903	85	7	5	4	0.11	0.56	-0.01	0.12
<i>Ophiactis profundi</i>	59	0.97	5.712	78	13	5	3	0.33	0.69	-0.02	0.14
<i>Ophiactis resiliens</i>	176	1.77	8.523	77	14	5	3	0.64	0.28	-0.02	0.09
<i>Ophiernus vallincola</i>	42	0.713	5.35	29	34	23	4	0.11	0.74	-0.03	0.13
<i>Ophiocamax vitrea</i>	99	0.912	9.179	76	18	4	2	0.28	0.19	0.00	0.07
<i>Ophiocentrus pilosa</i>	106	1.95	13.647	61	30	6	3	0.60	0.36	0.02	0.13
<i>Ophioceres bispinosa</i>	21	0.91	10.273	67	22	5	3	0.09	0.79	0.00	0.16
<i>Ophiocreas sibogae</i>	29	0.79	5.361	29	49	9	2	0.10	0.54	0.02	0.12

Species	No of presences	Marginality	Specialisation	Explained specialisation - Marginality %	Explained specialisation – Factor 1 %	Explained specialisation – Factor 2 %	No of factors used in HS maps	Mean Boyce's index (4 bins)	Stdev Boyce's index (4 bins)	Mean continuous Boyce's index	Stdev continuous Boyce's index
Ophiogymna pellicula	22	1.097	30.232	89	8	2	3	0.30	0.58	0.04	0.13
Ophioleuce seminudum	59	1.294	5.653	70	16	8	3	0.78	0.36	0.02	0.07
Ophiolimna cf bairdi	26	1.248	22.652	58	36	5	2	0.28	0.49	0.05	0.10
Ophiomitrella conferta	26	1.083	7.495	42	33	15	3	0.38	0.37	0.02	0.09
Ophiomusium facundum	36	0.744	8.732	53	38	5	2	0.05	0.59	-0.01	0.13
Ophiomusium incertum	30	1.449	15.613	46	38	12	3	0.61	0.30	0.07	0.07
Ophiomusium lymani	78	0.787	8.833	86	9	2	4	0.16	0.68	-0.01	0.14
Ophiomusium simplex	60	1.581	17.25	93	5	1	2	0.64	0.54	0.00	0.10
Ophiomyces delata	34	0.602	3.973	72	16	5	3	0.17	0.55	0.00	0.13
Ophiomyxa australis	210	1.563	4.677	54	31	8	3	0.66	0.41	-0.01	0.13
Ophionereis schayeri	118	2.044	21.668	86	11	2	2	0.33	0.26	0.03	0.09
Ophionereis terba	43	1.835	31.938	74	19	6	2	0.50	0.24	0.07	0.10
Ophiopallas valens	23	1.614	28.383	86	10	3	3	0.15	0.72	0.03	0.13
Ophiopeza cylindrica	80	1.903	26.872	88	10	1	2	0.07	0.40	0.00	0.10
Ophiophthalmus relictus	84	0.924	3.348	30	34	19	4	0.40	0.56	-0.03	0.12
Ophioplax lamellosa	30	0.932	7.531	65	22	7	3	0.35	0.50	0.04	0.13
Ophioplinthaca plicata	36	0.966	5.284	17	40	27	4	0.41	0.62	-0.01	0.12
Ophioplinthaca rudis	72	0.913	7.043	23	63	10	3	0.48	0.58	0.02	0.12
Ophiothrix aristulata	119	1.287	9.934	78	18	2	3	0.94	0.10	0.74	0.07
Ophiothrix caespitosa	273	1.969	15.932	88	9	1	3	0.45	0.36	-0.05	0.10
Ophiothrix ciliaris	103	1.516	19.705	97	2	1	3	0.68	0.38	0.02	0.07
Ophiotreta larissae	21	1.206	21.489	49	43	5	2	0.04	0.63	0.02	0.12
Ophiotreta matura	26	0.795	10.134	10	73	14	3	0.22	0.66	0.03	0.13
Ophiotreta stimulea	51	0.629	4.13	48	29	12	3	0.32	0.61	-0.03	0.11
Ophiura flagellata	32	1.209	11.857	45	34	13	4	0.11	0.64	0.00	0.12
Ophiura irrorata	45	1.153	3.834	22	42	19	3	0.52	0.43	0.03	0.11

Species	No of presences	Marginality	Specialisation	Explained specialisation - Marginality %	Explained specialisation – Factor 1 %	Explained specialisation – Factor 2 %	No of factors used in HS maps	Mean Boyce's index (4 bins)	Stdev Boyce's index (4 bins)	Mean continuous Boyce's index	Stdev continuous Boyce's index
Ophiura jejuna	31	1.05	9.753	13	68	11	2	0.24	0.62	0.03	0.13
Ophiura kinbergi	129	1.93	12.195	77	21	1	2	0.62	0.51	0.01	0.13
Ophiura micracantha	47	1.337	9.176	73	15	8	3	0.58	0.46	0.02	0.08
Ophiura ooplax	49	1.166	4.106	77	9	5	4	0.39	0.61	0.00	0.12
Ophiura palliata	41	1.176	8.454	46	32	15	3	0.45	0.46	0.05	0.11
Ophiura sp MoV 2734	21	1.18	13.541	18	53	13	3	0.43	0.49	0.05	0.12
Ophiurothamnus clausa	48	0.647	4.816	28	46	13	3	0.35	0.54	0.02	0.10

Table S1. List of species used in the ENFA modelling. The number of presences are the number of pixels that the species has been recorded from. Marginality refers how species mean distributions differ from the background. Specialisation refers to how the variance differs from the background. Boyce's index is a k-fold validation statistic which can be calculated by aggregating results into bins or using a 'continuous window'. The mean and standard deviation results represent aggregate values from 10 runs, each retaining a different 10% of the data as the test dataset.

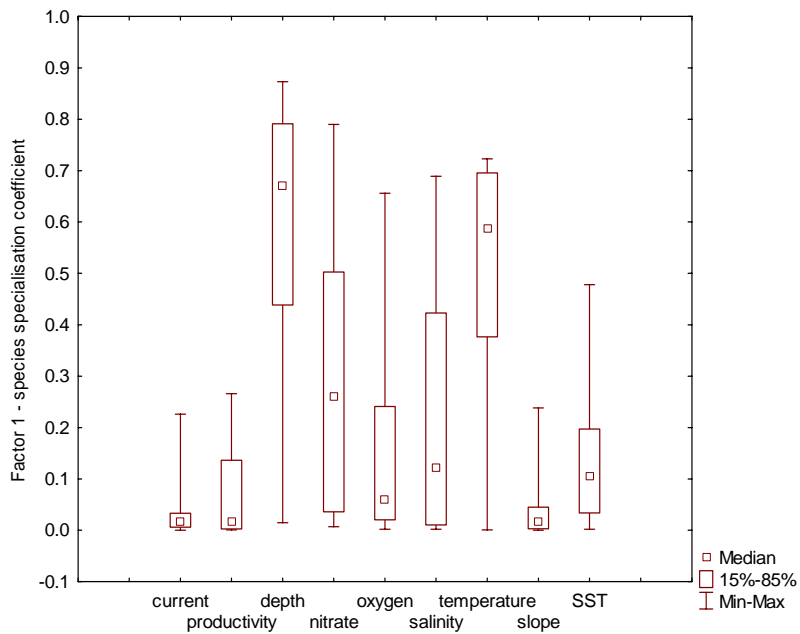
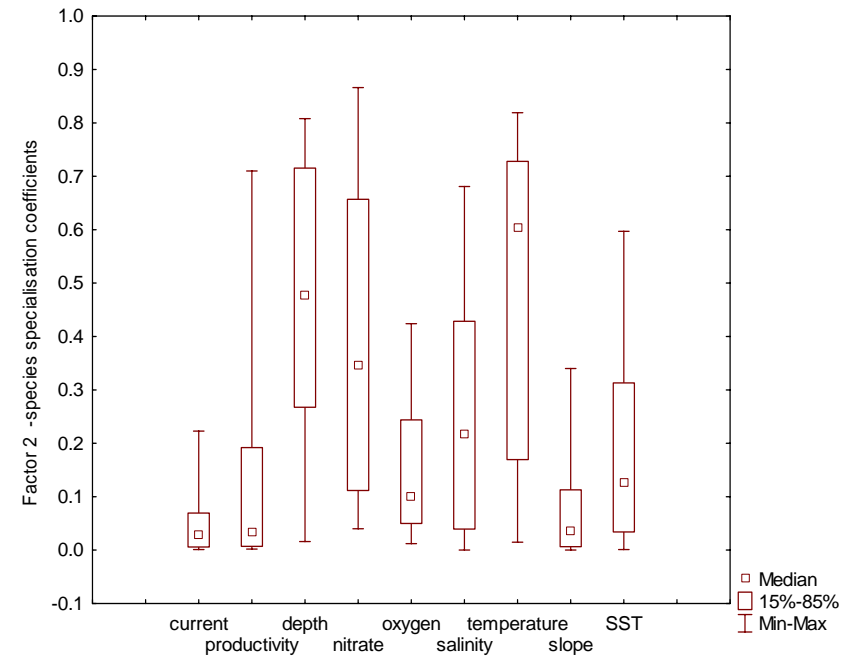
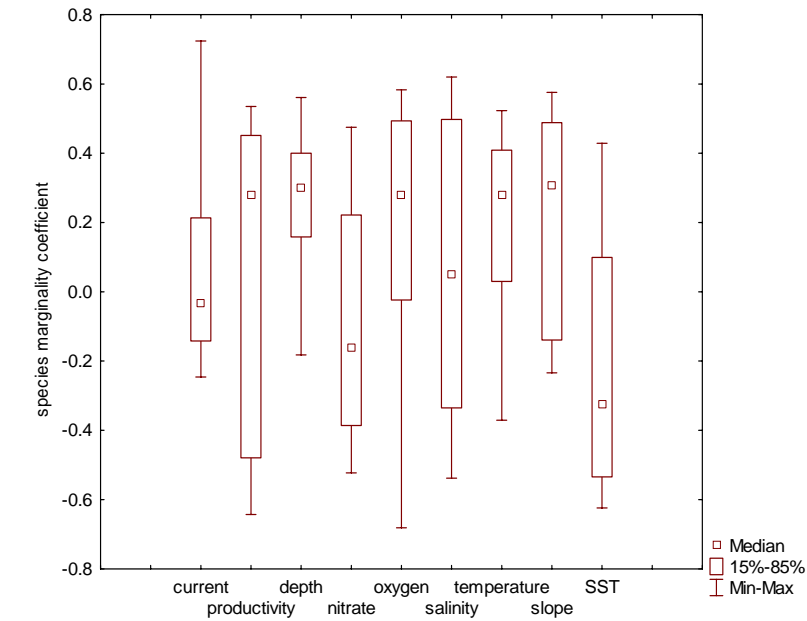


Fig. S1. Box-plots showing the distribution of ENFA marginality and factor 1 & 2 specialisation coefficients across 60 ophiuroid species. The marginality and specialisation indicate how the mean/variance for each species differs from random for each environmental variable. Values furthest from zero indicate a stronger relationship. Marginality can be positive or negative (ie species values are lower than background). Most of the specialisation (variance) is expressed in Factor 1.

These results show that for most species marginality differs from background for most factors except current. Specialisation differs mainly for depth, seafloor temperature and, to a lesser extent, nitrate, salinity and sea-surface temperature (SST).

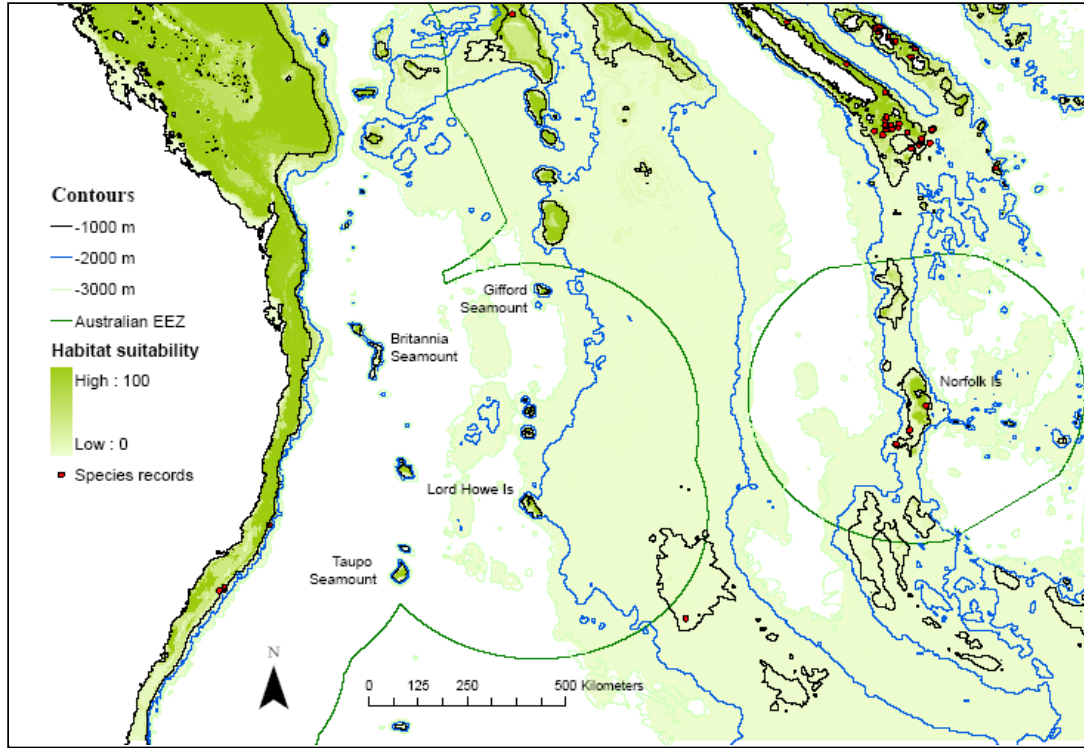


Fig. S2. Map of predicted species distributions for the species *Ophiocamax vitrea* resulting from ENFA modelling using all environmental parameters. The ENFA model tended to overfit the data in shallow water tropical areas.

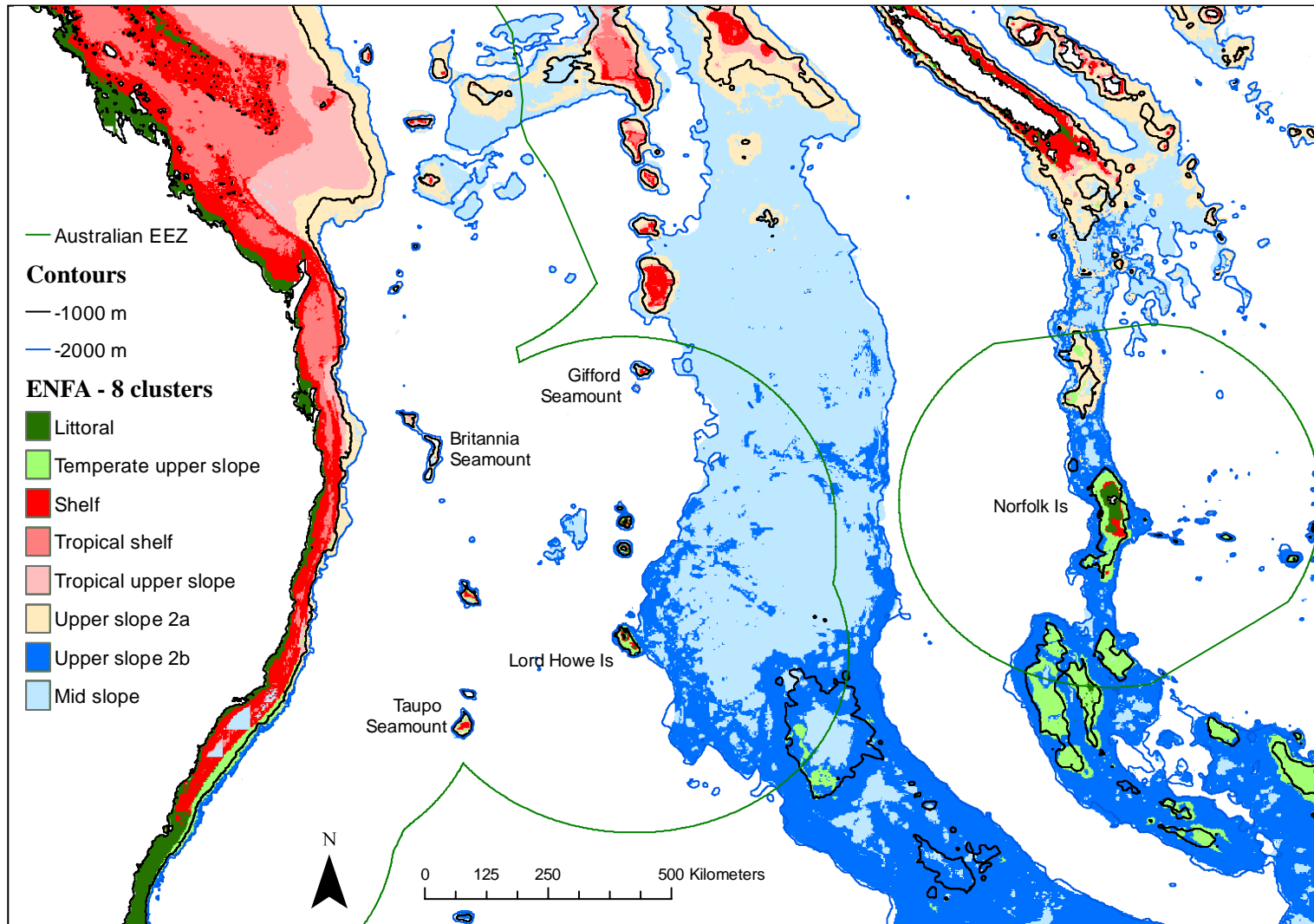


Fig. S3. Map of seafloor assemblages generated from eight-class cluster analysis of the habitat suitability predictions from ENFA modelling of 60 ophiuroid species.

