Bioregionalisation of Australian waters using brittle stars (Echinodermata: Ophiuroidea), a major group of marine benthic invertebrates.

Tim O'Hara

MUSEUMVICTORIA

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

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By O'Hara, Timothy D.

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1. Summary

To date, large-scale marine bioregional analyses in Australia have been largely based on fish data. However, fish are highly mobile and may not act as a surrogate for seafloor communities. Consequently, to inform future regional marine plans in Australia, a bioregionalisation was undertaken for ophiuroids, a group of benthic marine invertebrates. Ophiuroids are dominant members of the benthic community, occurring in all marine habitats and exhibiting a range of reproductive strategies. Ophiuroid distributional data was accumulated from the collections of all museums in Australia; other museums in New Zealand, Europe, Asia and the United States; and from published historical information.

Ophiuroid distributions were modelled in three depth layers (outer shelf 50-300 m, upper slope 300-750 m and mid slope 750-1500 m) for the seafloor of the Exclusive Economic Zone around the Australian continent. This study used the 'modelling-then-classification' (or interpolate then analyse) approach to mapping multivariate data. Three modelling techniques were attempted: 1) a 'String' analysis, similar to that performed for the Fish Bioregionalisation of Last *et al.* (2005); 2) Oceanographic envelopes, analogous to terrestrial climatic modelling (eg BIOCLIM), which predicts presence and absence of species according to their known environmental ranges; and 3) Multivariate Adaptive Regression Splines (MARS) that model complex non-linear relationships between environmental variables and presence distribution data.

The six environmental variables that were used for the Oceanographic Envelope and MARS models included: depth, seabed temperature, seabed salinity, sea surface temperature, sea surface productivity, and sea surface current velocity. To eliminate the remaining correlation between depth, seafloor temperature and salinity, the latter two variables were transformed into the residuals from Generalized Linear Models (GLMs) prior to analysis, using depth as a predictor for temperature, and depth and temperature as predictors for salinity. All variables were interpolated to a cell size of 0.02 degrees. The MARS models failed to accurately predict known distributions and were not analysed further. The resulting predictions from the two remaining models were summarized into cells of 1 degree latitude/longitude for multivariate analysis, including cluster analysis, ordinations and plots of Jaccard dissimilarity between neighbouring cells.

The overall pattern is one of continual species turnover around the Australian continent with few definitive biogeographic breaks, just regions of greater or lesser turnover. Two important biogeographic findings are evident from this study. The first is that the overall patterns do not change substantially with depth, within the range analysed (50-1500 m). The same magnitude of faunal transition occurs at the 750-1500 m layer as the 50-300 m layer. There is an almost complete turnover of ophiuroid species on the upper slope between tropical areas and southern Tasmania. The second is that areas of similar biologically-important habitat exist in separate areas off the east and west of the Australian continent. This implies that many species may have discontinuous distributions, which would invalidate the assumptions made under a 'String'-style analysis. This needs testing with further surveys.

A meta-analysis of the six datasets from the Oceanographic Envelope and ‘String’ analyses resulted in the identification of twelve bioregions around Australia (Figure 4.10). The exact boundaries between these regions differed slightly (1-3 degrees) depending on the technique and depth layer. Nevertheless, there was a remarkable congruity between the various analyses and depth strata within this study, and between this study and the ‘String’ bioregionalisation based on fish distributions.

2. Introduction

Large-scale marine deep-water bioregional analyses in Australia have been largely based on fish data (Butler *et al.* 2005, Last *et al.* 2005). However, fish may not act as a surrogate for benthic communities because they are highly mobile and can migrate as adults, including between areas that form a barrier to animals relying on larval dispersal only. Consequently, to inform future regional marine plans in Australia, it is important to test the fish data against a second national biological dataset based on a benthic invertebrate group.

Results of recent workshops (eg Williams *et al* 2005) have indicated that the most comprehensive dataset we have for any marine invertebrate group across the entire Australian EEZ is the Ophiuroidea (brittle stars, an echinoderm group related to starfish). In addition

- Ophiuroids are one of the most abundant marine invertebrate groups with representatives in all benthic marine habitats. They dominate areas of the deep sea and are collected by most sampling techniques. This is important as large-scale spatial analyses require vast amounts of data.
- Ophiuroids as a group are diverse/abundant enough to be informative and small enough for the taxonomy to be tractable.
- A large amount of material already has been identified and databased from many areas around Australia. This includes collections in major European and New Zealand institutions.
- The majority of identifications have been consistently made or verified by a single taxonomic expert (T. O'Hara) improving the quality of the overall dataset.
- There are known to be large scale changes in ophiuroid community composition between geographic regions in the deep-sea. For example, less than 15% of the species in two families of ophiuroids were found on the continental slopes of both New Caledonia and Tasmania (O'Hara & Stöhr 2006).

Spatial coverage
This study covered the seabed around the Australian continent (50-1500 m). It does not include continental fragments in the Tasman and Coral Seas (including the Lord Howe and Norfolk ridges) or waters around offshore islands such as Cocos, Christmas, Macquarie or Heard Islands because of the lack of complete environmental data from these regions and to be consistent with the fish bioregionalisation previously prepared for the Department of the Environment and Heritage (Last *et al*. 2005). Nor does it include eastern Antarctica because it is a completely different fauna. It does not include seafloor below 1500 m because these waters are also inadequately sampled. Samples from less than 50 m depth are not covered within this project as they were predominantly State waters and the number of unregistered (not databased) specimens was too large to be completed within the available timeframe.

Data was analysed separately for the depth strata: 50-300 m, 300-750 m and 750-1500 m because of the uneven spatial distribution of each depth stratum and to ensure that

depth does not confound spatial patterns in the analysis. The depth strata were based approximately on the habitat concepts of “outer shelf”, “upper slope” and “mid-slope” habitats. The actual depth ranges are not based on any a priori biological information but represent depth bands around the available environmental data from the “2005 National Marine Bioregionalisation of Australia” (Commonwealth of Australia 2005): ie 150, 500 and 1000 m.

3. Methods

The overall methodology for this project consisted of:

1) constructing an integrated dataset for deep-sea ophiuroids of Australia and surrounding waters, including environmental data for each sample location,

2) interpolating or modelling species distributions for areas that have been inadequately sampled, summarising the results into cells of one-degree latitude/longitude, and

3) analysing the results for bioregional patterns using various multivariate statistical approaches.

Biological data at large spatial scales are rarely in a form that can be analysed or mapped directly as they are not spatially dense enough, nor are all areas consistently sampled. For this study, large areas of Australia's Exclusive Economic Zone were known to be inadequately sampled (Last *et al.* 2005). Consequently, the data needed to be interpolated or modelled into a form that can be analysed and mapped. This study used the 'modelling-then-classification' (or interpolate then analyse) approach to mapping multivariate data (Ferrier *et al.* 2002) because the sample database consists of records collected from numerous different surveys over time using a variety of collection gear. The alternative 'classification-then-modelling' (or analyse then interpolate) approach requires a regular sampling protocol.

3.1 Data acquisition

Biological data

The ophiuroid sample data were 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 (Table 3.1). It included all registered specimens from MV, AM, WAM, NTM, QM, and NIWA (see Table 3.1 for acronyms).

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 Sate 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 is given in figure 3.1.

The majority of specimens were identified or verified by Tim O'Hara. The remainder consisted of identifications by established taxonomists (particularly Frank Rowe, Sue

Kingston, Anne Hoggett, and Lyle Vail of the Australian Museum; Loisette Marsh of the Western Australian Museum; Alan Baker of the National Museum of New Zealand; Don McKnight of NIWA). Included published records consisted of type specimens and other voucher material, particularly from the historically important voyages of discovery, including the circumglobal HMS Challenger expedition (Lyman 1878, 1879, 1882), the Siboga expeditions to Indonesia (Koehler 1904, 1905) and Mortensen's Pacific Expeditions to the Indo-Malay region and SE Australia (Koehler 1930, O'Hara 1998). All data were stored on a purpose built taxonomic, distributional and modelling database (Fleet v1.0) developed using Microsoft Access.

Only species with well-known taxonomy were retained for analysis. This included records for undescribed species which were consistently identified by the principal taxonomist for this project (T. O'Hara).

Environmental data

Environmental data were obtained from the "2005 National Marine Bioregionalisation of Australia" (Commonwealth of Australia 2005). See under habitat modeling below for more details.

3.2 Interpolation

The modelling or interpolation was completed for each species in two ways. Both approaches resulted in a grid of species-location cells of one degree of latitude/longitude for three bathymetric layers, 50-300 m, 300-750 m, and 750-1500 m.

The biogeographic approach

The biogeographic approach interpolated species records between known species distribution limits. This approach was similar to that adopted for the 'string-analysis' of Last *et al.* (2005).

First, one-dimensional arrays or 'strings' of cells of one degree latitude and longitude were created along three depth contours around the Australian continental land mass. Where the area of continental shelf or slope was wider than one degree, data from neighbouring cells were merged, at the same latitude along the eastern, western coasts and the Gulf of Carpentaria, and at the same longitude for the southern and northern coasts. The cells along the array were numbered sequentially from 1 to 115, starting from the eastern tip of Torres Strait, around southern Australia and Tasmania, and terminating at the western tip of Torres Strait. There is no deep-water (>100 m) habitat in the Gulf of Carpentaria. Consequently the 'strings' for the two deeper layers (300-750 m, 750-1500 m) were terminated at cell 102. Three special 'extra-limital' cell were added to represent distributional records from north and south of Australia. These were placed in the Arafura Sea (-8°S, 132°E), south of New Guinea (-8°S, 145°E), and south of Tasmania (-45°S, 146°E). This enabled the correct interpolation of distributional ranges for species that occurred outside Australia.

Secondly, the known presence of species with more than five distributional records was then recorded for each cell at the three depth layers. Finally, these actual data were supplemented by interpolated data, generated by recording a species as present

for cells that are between known occurrences, ie species were presumed to occur throughout their known geographic and bathymetric range. The interpolation occurred clockwise around Australia following the numbered cells. The distributions of tropical species were interpolated to the north. For species found to the north and south of Australia, interpolation proceeded to/from the special extra-limital cells. Interpolation was limited to 20 cells, ie large distribution gaps, including gaps to outliers, were not interpolated. This prevented a tropical species being interpolated across Southern Australia or a temperate species across Northern Australia. Known gap in species distributions were removed from the modelled range. Finally all remaining cells without an actual or modelled record were marked as absent for each species. Each species range was reviewed on a map. Outlying records whose identification was not confirmed directly by the author or where there could have been a mistake in location were excluded from the analysis.

Habitat modelling

The habitat approach models species records against environmental data to determine suitable habitat for a given species. This information can then be used to predict species occurrences across a landscape. Consequently, two datasets are required. The first is the sample dataset, consisting of a species/sample matrix with associated environmental data for each of the sample points. The second is the prediction dataset, consisting of environmental data in regular point or raster format across the landscape to be modelled.

Two approaches have been tested in this study. The first was to generate a simple oceanographic envelope for each species, analogous to the climatic envelopes developed for terrestrial applications. The second approach was a relatively novel technique called Multivariate Adaptive Regression Splines (MARS) which is intermediate between machine-learning and regression approaches. The advantage of this technique is that it is computationally inexpensive and can model many species in one analysis (Elith & Leathwick in press).

For these models, only ophiuroid species with more than 10 records in Australia's EEZ in the target depth zone were used. This resulted in a matrix of presence/absence records from 93 species across 2441 sites. To ensure the maximum amount of data was collected for each species, the spatial extent of the sites ranged from 5-50°S and 112-180°E, including areas outside Australia's EEZ but within the extent of available environmental datasets. However, predictions were only made for areas within Australia's EEZ, ranging from 5-47°S and 108-155°E, the scope for this bioregionalisation.

The environmental parameters and predictors were derived from a) datasets in the "2005 National Marine Bioregionalisation of Australia" (Commonwealth of Australia 2005), b) from the CSIRO Atlas of Regional Seas (CARS2000) datasets (Ridgway *et al.* 2002), or c) directly from survey site data.

Twenty-five environmental parameters were available for use in the models, including a digital elevation model (DEM) of seafloor bathymetry; seawater parameters at the surface and seafloor such as temperature, salinity, phosphate, nitrate, oxygen and silicate; and sea surface parameters such current velocity, productivity and chlorophyll. Sea surface temperature, productivity and currents were available

seasonally (January, April, July and September). Unfortunately this list does not include substratum characteristics (e.g. sediment size, composition, geology) as these datasets were not consistently available for the entire EEZ. Among the twenty-five parameters, several were highly correlated which can affect the outcome of many analysis such as MARS (Elith & Burgman 2004). Moreover, a modeling rule of thumb is to limit the number of environmental variables to one for every five species records (Elith pers. comm.). The median number of records across the 93 ophiuroid species was 28. Consequently, the number of environmental variables was reduced to three seafloor and three sea surface variables that were likely to be relevant for the distribution of the target organisms. For the seafloor, depth (m), temperature (°C) and salinity (psu) are known to be critical for limiting the distribution of benthic marine life. 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. On the sea-surface, January temperature (°C) and annual mean productivity were included as surrogates for overall ecosystem productivity. The final variable was January current velocity (m/s).

Environmental data for both the sample and prediction datasets were generated mostly using the ArcInfo Spatial Analyst function “Extract values to point” from various raster datasets. The exception was for depth, where the mean depth recorded from the actual collection event was used for the sample dataset. 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 with the upper left corner at 5°S and 108°E. Binary interpolation was then used to calculate the value at each prediction point if the resolution was coarser than 0.02 degrees. For resolutions less than or equal to 0.02 degrees, the values of the raster cells corresponding to the 0.02 degree points were used. The initial resolution of the environmental raster datasets were 0.01 degree (depth), 0.02 (sea surface temperature), 0.023 (current velocity), 0.043 degree (productivity), and 0.1 degree (seafloor temperature and salinity).

Oceanographic envelopes

Oceanographic envelopes are the marine equivalent of climatic envelopes such as BIOCLIM and BIOMAP that are used extensively to model species distributions in terrestrial systems (Elith & Burgman 2004). Several environmental parameters, including a digital elevation model, are combined to form a multivariate space or ‘envelope’ that characterises the known habitat for a species (Elith & Burgman 2004). This profile can then be used to predict species habitat distribution across a landscape.

For this analysis, an environmental range model was adopted. The envelope was defined by the minimum and maximum values for each environmental parameter. Binary predictions (True, False) were made by assessing whether each point of the prediction dataset fell within or outside this envelope.

This approach was simpler than for terrestrial models such as BIOCLIM, which classify predictions into four categories of habitat suitability. However, the sparsity of available marine data and the lack of available software/datasets for modelling marine environments precluded a more sophisticated analysis within the project timeframes.

Multivariate Adaptive Regression Splines (MARS)

Multivariate Adaptive Regression Splines (MARS) model complex non-linear relationships between a response variable (ie a species) and environmental predictors (Friedman 1991). These relationships can then be used to predict the distribution of species across an area of interest, including locations where there has been no attempt to collect the species but where there is environmental information. The MARS procedure is to break up non-linear response curves into series of connected linear segments called 'basis' functions. The procedure begins by initially creating many segments and then progressively removing segments (and predictors) that don't contribute substantially to the model through a generalised cross-validation technique (Elith & Leathwick, in press). MARS models have preformed well across numerous habitats and taxonomic groups (Elith & Leathwick in press).

The version of MARS implemented in the R statistical environment (Hastie & Tibshirani 1996) has the advantage over other modelling techniques such as Generalised Linear Models (GLMs) or Generalised Additive Models (GAMs) in that it can model many species at once using the "multi-response" option (Elith & Leathwick, in press). This is not only computationally faster than the other techniques but it also improves the prediction of less abundant species by using information included in the distribution of more-abundant species (Leathwick *et al.* in press, Elith & Leathwick, in press). The disadvantage of this implementation is that the fitting assumes normally distributed errors, suitable for abundance and not presence/absence data. This can be overcome by using a Generalised Linear Model (GLM) to constrain prediction values to 0-1 (for details, see Leathwick *et al.* in press).

The multi-response binomial MARS model also assumes that species not collected at a site are actually absent, i.e. it assumes that the data are presence-absence data, rather than presence-only data. This is a reasonable assumption for this study, as, unlike for models based on ad-hoc museum collections, the data have been collected from scientific dredges or trawls where most of the material has been sorted and identified. Moreover, assigning 'pseudo-absences' in this way has been shown to produce superior models to assigning pseudo-absences randomly (Elith & Leathwick in press). However, the uneven bathymetric distribution of the sites produced some modelling artefacts. Initial MARS analyses for example predicted the occurrence of some shallow-water species across the abyssal plain. Consequently, 391 randomly-positioned 'pseudo-absence' sites were added from deeper sections of Australia's EEZ to attempt to make predictions from depth data more realistic.

To eliminate the remaining correlation between depth, seafloor temperature and salinity, the latter two variables were transformed into the residuals from a Generalized Linear Models (GLMs) prior to the MARS analysis, using depth as a predictor for temperature, and depth and temperature as predictors for salinity (Leathwick *et al.* 2006).

Simplifying the model data for multivariate analysis

For the Oceanographic Envelope models, predictions of species distributions were made at a resolution of 0.02 degree. However, this generated far too many points (> 1 million) to be analysed by conventional multivariate statistics. Moreover, the dataset needed to emphasise biogeographical relationships around Australia rather than across the EEZ to be consistent with the fish bioregionalisation. Consequently, the data was simplified in two steps. Firstly, the 0.02 resolution modeled species data were

aggregated into cells of 1.0 degrees (i.e., species were counted as present if they occurred at any 0.02 point within a cell). Secondly, in areas of the EEZ that were greater than 1 degree wide, the 1.0 degree cells were projected onto continuous 'strings' of cells around the Australian continent at the three target depth levels (150-300 m – 115 cells, 300-750 m – 102 cells, and 750-1500 m – 102 cells). The longer string for the shallower depth range reflects the inclusion of the Gulf of Carpentaria. The result was three species/cell matrices that could be analysed for biogeographical turnover.

3.3 Multivariate analyses

The linear 'strings' resulting from both 'String' (biogeographic) and Oceanographic Envelope (habitat) interpolations at the three target depth ranges were analysed using ordination and cluster analyses. The binary form of the Bray-Curtis similarity coefficient (Sorensen coefficient) was used to create the similarity matrices (cell x cell) for each string. Ordinations were prepared using non-metric Multi-dimensional scaling (MDS) and cluster analyses using group-averaging and the hierarchical agglomerative technique. All these analyses were performed using the Primer v5.2 software.

Similarities in faunal composition between adjacent cells were also computed using the Jaccard dissimilarity measure. This dissimilarity measure was used to retain comparability with the Fish Bioregionalisation (Last *et al.* 2005). These values were then graphed sequentially on the x-axis in order from north-east Queensland, across southern and western Australia to the Gulf of Carpentaria (eg Figure 4.7c).

Some sections of Australia's EEZ only contain shallow waters, including parts of Bass Strait (cells 43-44) and northern Australia (cells 104-115). These areas were only analysed for the shallowest depth layer (50-300 m).

The cells along each string were classified into bioregions by identifying clusters that formed at the 80% similarity levels on the cluster diagrams. In some cases, these clusters were further divided if they contained two or more geographically distinct areas. These groupings were then compared with the MDS plots and the Jaccard graphs to further interpret the data. All three analyses were based on the same dataset and thus are expected to be congruent, however, each type of analysis emphasises different aspects of the data. For example, the ordinations were used to explore the structure of clusters that combined two geographically-separate regions. Jaccard analyses emphasise species turnover rather than community composition.

Finally, a meta-analysis of the three depth layers from each of the String and Oceanographic Envelope models was undertaken. Cells from these six datasets were aligned and one bioregionalisation generated from the most commonly occurring regions, with most weighting given to the Oceanographic Envelope 300-750 m layer.

4. Results

4.1. Species/sample data

Samples were available from 2050 sites within the study region. One hundred and fifty one species had more than five distribution records and 93 with more than ten distribution records (Appendix 1). The size of ranges for these species is illustrated in Appendix 2.

4.2. Species predictions

Three modelling techniques were attempted, 1) 'Strings', 2) Oceanographic Envelopes, and 3) Multivariate Adaptive Regression Splines (MARS).

Maps for four species have been figured to illustrate each technique (Figures 4.1-4.3). The 'String' analysis extrapolated between known species distribution limits (except for very large gaps), assuming that species were present continuously throughout their range. It cannot predict species occurrences beyond their known range.

The Oceanographic Envelope analysis only extrapolated to areas with similar environmental conditions to known records. This resulted in gaps in distributions and extrapolations to areas beyond known species limits. For example, *Ophiura flagellata* is predicted to occur off the western Australian coast even though it has not been collected there as yet (Figure 4.2a). *Ophiomusium anisacanthum* is predicted to occur in two populations across Australia's southern coast, separated by a gap from Albany to Esperance (Figure 4.2d). This model correctly predicted almost all known occurrences – the few exceptions occurred at some isolated seamounts (eg Moreton seamount off Queensland) where the resolution of the bathymetry raster dataset used for prediction (0.02 degree) was not sufficient to accurately record the summit depth.

The MARS analysis also predicted species occurrences based on environmental parameters but allowed for non-linear relationships between the environmental and species distribution data. The MARS models failed to successfully predict occurrences at many known collection sites using both single-species and multi-species approaches. For example, *Ophiura flagellata* was only predicted to occur at several tiny areas off the eastern Australian coast (Figure 4.3a), even though it is known from many records from the south-east (Figure 4.1a). *Ophionereis schayeri* was spuriously predicted to occur across large areas of the abyssal plain off southern Australia (Figure 4.3b), even after hundreds of additional pseudo-absences from this region were added to the model. There were no positive predictions for *Ophiopeza cylindrica* (Figure 4.3c) and many other species. The predicted distribution of *Ophiomusium anisacanthum* (Figure 4.3d) omitted the eastern portion of its known range. The likely cause of these modelling failures is the sparsity of records for many species. In general there were not enough records to accurately define a complex non-linear relationship between species occurrences and environmental parameters. Consequently, the results of the MARS models were not included in bioregional analysis.

4.3. Model results

Multivariate analyses were run for six datasets, from the two modeling techniques (String and Oceanographic Envelope) and the three depth layers (50-300, 300-750, 750-1500 m).

The cluster analyses identified 8-13 distinct bioregions with >80% similarity from the six datasets (eg Figure 4.7a). In general, these clusters were also recognisable as separate groups on the MDS plots (eg Figure 4.7b) and the boundaries between these regions as major peaks on plots of Jaccard dissimilarity between adjacent cells (eg Figure 4.7c). These results have been summarized in Table 4.1. Stress values for all MDS plots were very low (0.04-0.07) reflecting the good to excellent fit between the 2-dimensional ordinations and the underlying similarity matrices (Clarke & Warwick 2001).

Overall, the impression from all the analyses is one of continuous change around the Australian coast. Rarely are a group of adjacent cells identical in species composition. However, the rate of change differs for different regions and different datasets, which explains the difference in the number of regions identified. For example, southern Queensland (S Qld) and northern New South Wales (N NSW) are sometimes identified as distinct regions and sometimes as part of larger regions. On the other hand, the region SE South Australia (SE SA) was only identified in one analysis (Figure 4.4a), although lesser east/west substructure was evident in the Southern Australian (S Aust) region from many other analyses.

For the 'String' (biogeographic) analyses, the 50-300 m depth layer separated the EEZ into northern and southern clusters, identifying 12 regions, with each of the north, south, east and west coasts having three regions each. The cells from the Gulf of Carpentaria were very similar reflecting the lack of collecting in that region. Other homogeneous regions included the southern coast (S Aust), northern Queensland (N Qld) and the NW coast (NW WA). Again, this homogeneity maybe in part due to the lack of available collections from the Great Australian Bight, parts of the north Queensland coast and from off Derby to the Cobourg Peninsula (Figure 3.1). The deeper layers (300-750 and 750-1500 m) had fewer regions on the north-eastern and southern coasts, but more around Tasmania and SW Western Australia, the latter due to the presence of specialist seamount faunas. These regions could be biased by uneven collection effort, as many seamounts off southern Australia remain un-sampled.

The 'Oceanographic Envelope' analyses differed in identifying cells from eastern and western Australia with similar environmental characteristics. Cells from northern Queensland (N Qld) consistently clustered with cells from NW Western Australia (NW WA and WA 2), those from southern New South Wales (S NSW) with WA 1, and those from eastern Tasmania (E Tas) with SW Western Australia (SW WA). This implies that many species on the outer shelf and upper slope have discontinuous distributions, separated into eastern and western populations. In contrast to the String analysis, the deeper layers contained more regions from the east and west coasts than for the 50-300 m layer.

When all depth layers were considered together (50-1500m), the results tended to reflect the depth layer with the most species (not shown). For the 'String' analysis this was the 50-300 m layer (with 90 of the 151 species). The all-depth analysis differed only in recognizing a 'S Tas' cluster which included the 'W Tas' cells, placing the 'Peanut' seamount cell with the 'SW WA' region, and 'WA2'/'NW WA' boundary was shifted one cell to the north. The all-depth Oceanographic Envelope analysis was most similar to the 300-750 m layer (with 54 of the 93 species). It differed only is assigning cells 35 and 39 to the 'Tas' region and the addition of the 'N Aust' region (which is only relevant to the 50-300 m layer).

When the regions from the six analyses were aligned (Table 4.2), important similarities became evident. Twelve regions were consistently identified, although their boundaries differed by 1-3 degrees of latitude or longitude depending on the analysis. There was a north Queensland region extending from Cape York to Fraser Island. The east coast was one of continual change, with regions in southern Queensland, northern New South Wales and southern New South Wales. The regionalization around Tasmania differed between the various analyses, but in general the southern tip (S Tas) was distinguished in shallow water by the lack of warm water species and in deeper water by the presence of seamount coral communities. The eastern Tasmanian region (E Tas) was generally distinguished from the rest of the southern coast. The southern coast was recognised as a single region (S Aust) from Western Bass Strait to off Albany, Western Australia, although differences between east and west were sometimes emphasized at the sub-regional level. The western coast was also one of change. Three regions were generally distinguished: the south-west coast (SW WA), a region from Cape Naturaliste to off Coral Bay (WA 1), and another that terminated off Dampier. The northern coast was divided into a long NW region (NW WA) and (for shallow waters only) a northern region (N Aust) off Arnhem Land and the Gulf of Carpentaria. Relying primarily on the boundaries established by the Oceanographic Envelope 300-750 m analysis, the resulting bioregionalisation is mapped in Figure 4.10.

5. Discussion

5.1. Model selection

Off the three modelling techniques attempted for this study, the 'String' analysis (sensu Last *et al.* 2005) is the simplest, assuming that each species will be present throughout their range for a given depth strata. By definition, it will include all known records within the modelled range. It does however, suffer from collection bias. More rare species will be recorded from heavily sampled areas, resulting in more species distribution limits being located in these areas and potentially spurious biogeographic boundaries being identified. The advantage of this technique is that it produces geographically sequential cluster diagrams and ordination plots that can be easily interpreted.

Other modelling techniques partially avoid this collection bias by focusing on the environmental parameters that define a species known habitat. Species can be predicted to occur beyond their known range, in discrete areas of similar habitat. Consequently biogeographic boundaries will be aligned more with important ecological boundaries rather than heavily sampled areas. This study attempted to model ophiuroid distributions using Multivariate Adaptive Regression Splines (MARS) using both the single and multi-response options. This technique combines features of non-linear regression and machine-based learning in a computationally inexpensive way (Elith & Burgman 2004). The multi-response option models all the species together, making the most of sparse sample data (Elith & Leathwick in press). Unfortunately, however, the MARS models failed to sensibly predict the occurrence of many species in this study. Seven different models were attempted with varying numbers of environmental parameters, parameter transformations, and numbers of faunal samples.

The available data was perhaps insufficient to model the complex relationship between species occurrences and the environmental data. Another potential problem is the backward pruning of response curve segments associated with this technique, which may over-simplify the relationship between species and strong environmental gradients such as depth.

Consequently, an Oceanographic Envelope model was developed, analogous to the climate models developed for terrestrial ecosystems, such as BIOCLIM (Busby 1991). It is acknowledged however, that this is a very simple modelling technique that lacks the ability to model complex non-linear relationships between the environmental variables and species data, or allow for interactions between variables. Interactions may be important for marine benthic animals, for example species may tolerate a different range of temperatures depending on depth. Nevertheless, these models have been successfully used for many terrestrial studies and the mapped predictions from this model for this study were generally consistent with what is known about the distribution of ophiuroids around Australia (Figure 4.8).

Future work at Museum Victoria will attempt to model the distribution of common ophiuroid species using 1) a different regression technique, General Additive Models

(GAMs), and 2) a multivariate association method such as Ecological Niche Factor Analysis (ENFA) (Hirzel *et al.* 2002), which has been successfully used at oceanic scales to model deep-sea coral distributions (Clark *et al.* 2006).

5.2. Environmental variables

The environmental variables used in this analysis included depth, various oceanographic data (ie temperature, salinity, oxygen) at the seafloor and surface derived from the CARS2000 datasets, secondary variables derived from the CARS2000 data (surface currents) and surface primary productivity derived from NOAA satellite imagery. These are the variables typically used in modelling benthic species (eg Leathwick *et al*. 2006, Clark *et al.* 2006) because they are readily available as comprehensive GIS datasets and appear to have some ecological relevance to benthic organisms. For example, Leathwick *et al*. (2006) found that depth, chlorophyll, temperature and sea-surface temperature contributed the most to their Boosted Regression Tree analysis. Clark *et al.* (2006) found that productivity and temperature contributed most to the ENFA marginality of their coral analysis, and oxygen and dissolved aragonite (an important component of coral skeletons) to the ENFA specialisation.

The obvious gap in these analyses is substratum, as relevant data only exists for parts of Australia's EEZ (Commonwealth of Australia 2005). Benthic invertebrates are very sensitive to the nature of the seafloor, particularly the division between hard and soft substrates, and, within soft sediments, between coarse (sandy) and fine (muddy) sediments (Hammond & Synnot 1994). However, substratum can vary at quite small scales (eg rocks can be intermingled with sand), and more research is required to determine whether substratum information averaged into cells (eg 0.02 degree) would provide an adequate surrogate for species distribution. The issue here is the variability of environmental variables within each cell. If the variability is too high, it is likely that a variable will be a poor predictor of species distribution at this scale. For example, if animals are collected from an isolated rock within a sea of mud, the average grain size of the area is unlikely to adequately represent species requirements. In recent Australian published work, Passlow *et al*. (2006) found little correlation between benthic community composition and sediments for grab samples in Bass Strait, whereas Post *et al.* (2006) found percent gravel, depth, sediment mobility and to a lesser extent percent mud, explained some of the variation in sled samples from the Gulf of Carpentaria.

Another useful environmental dataset would be a 3-dimensional atlas of water masses. Water masses have defined temperature and salinity signatures but also embody current flow, facilitating dispersal of propagules. Future work needs to examine the usefulness of the newly developed isopycnal maps of temperature and salinity in CARS2006 datasets.

5.3. Bioregionalisation

A meta-analysis of the six datasets from the Oceanographic Envelope and 'String' analyses resulted in the identification of twelve bioregions around Australia (Figure 4.10). The exact boundaries between these regions can differ slightly (1-3 degrees) depending on the technique and depth layer. This emphasises that the turnover of

ophiuroid species on the upper slope around Australia tends to be continuous and there are few definitive biogeographic breaks, just regions of more or less change.

Nevertheless, there is remarkable congruity between the various analyses and depth strata within this study (Table 4.2), and between this study and the 'String' bioregionalisation based on fish distributions produced for the National Oceans Office (see below).

Two important biogeographic findings are evident from this study. The first is that the overall patterns do not change substantially with depth, within the range analysed (50-1500 m). The same magnitude of faunal transition occurs at the 750-1500 m layer as the 50-300 m layer. There is an almost complete turnover of ophiuroid species on the upper slope between tropical areas and southern Tasmania (O'Hara in press).

The second is that areas of similar biologically-important habitat exist in separate areas off the east and west of the Australian continent. This implies that many species may have discontinuous distributions, which would invalidate the assumptions made under a 'String'-style analysis. Such patterns have been described for shallow water species. For example, the warm temperate ophiuroid *Clarkcoma pulchra* occurs in two populations, one along the New South Wales coast, and one along the coasts of south-western and South Australia (O'Hara & Poore 2000). However, not all species will occur in all suitable habitat. The distance between habitat patches may be too distant to facilitate dispersal. Whether slope ophiuroids are continuously distributed needs to be tested with further surveys, particularly in the area of the Great Australian Bight and off NW Australia which are relatively un-sampled.

5.4. Comparisons with the Fish bioregionalisation

The differences between this study and the fish 'string' bioregionalisation (Last *el al.* 2005) are as follows.

This study identified a single region for NE Australia, whereas the fish bioregionalisation identified three, a Cape Province (CP), North Eastern Transition (NET) and North Eastern Province (NEP). The ophiuroid 'NE Aust' region terminates at Fraser Island, whereas the NEP terminates several degrees to the north.

Both bioregionalisations have three regions along the east coast. The main difference is that the fish Central Eastern Province (CEP) is slightly larger than the ophiuroid 'N NSW' region.

Along the southern coast, the fish bioregionalisation identifies three regions, the Tasmanian Province (TasP), the Western Tasmanian Transition (WTasT) and the long Southern Province (SP). The ophiuroid bioregionalisation differs in differentiating a southern Tasmanian region (S Tas), recognising the subantarctic fauna present on the seamounts south of Tasmania (Koslow *et al.* 2001) and the latitudinal decrease in diversity (O'Hara & Poore 2000). The ophiuroid analysis also treats the WTasT and SP units as a single region, although there is some within-region differentiation of eastern and western sections for some ophiuroid datasets. The ophiuroid 'S Aust'

region also terminates near Albany, whereas the fish South Western Transition (SWT) begins at Cape Leeuwin.

Further along the western coast, the fish bioregionalisation recognises the Central Western Province (CWP), the Central Western Transition (CWT) and the North Western Province (NWP). The CWP and CWT correspond with the ophiuroid 'WA 1' region, and the NWP with the ophiuroid 'WA 2' region. The southern and northern sections of the 'WA 1' region are differentiated in some of the ophiuroid analyses but in general not enough to delineate separate regions as for fish.

Finally, the fish North Western Transition (NWT) and Timor Province (TP) correspond almost exactly with the ophiuroid 'NW Aust' region, and the fish Timor Transition (TT) region with the beginning of the ophiuroid 'N Aust' region. The fish bioregionalisation did not consider the Gulf of Carpentaria.

The fish bioregionalisation differentiates between alternating regions of relatively low species turnover (Provinces) and regions of faunal change (Transitions). The ophiuroid regions are not as clear cut. Regions of relatively low species turnover include 'NE Qld', 'S Aust', 'WA 1', and possibly 'S NSW'. Regions off the eastern, Tasmanian and north-western coasts all have large species turnover, and cannot be easily divided into Provinces and Transitions.

The fish bioregionalisation (Last *el al.* 2005) included a second analytic technique besides the Jaccard analysis. This was termed the 'bowler hat' analysis and consisted of analysing the species richness along the 0.5 degree 'string' around Australia. Rather than use raw species-richness values, species presences in each cell were weighted according whether a given cell was near the edge or centre of a species range, assuming a normal distribution. Graphs with all species showed that species richness is generally higher in temperate regions. Using a reduced dataset, with only deeper (>200m) narrow-range species (<25 cells in range), more bioregional structure was evident. This provided some support for the provinces delineated from the Jaccard analyses, with major peaks of narrow-range species richness centred in the NEP, CEP, CWP and NWP provinces on the east and west coast, and a smaller peak in the TasP province.

This style of analysis was not pursued in this study because of the uncertainties regrading the true range of rare ophiuroid species (most narrow-range species also have low abundances, see O'Hara 2001).

5.5. Comparisons with the sponge bioregionalisation

The numerical analysis of shallow water (<70 m) sponge distributions across northern Australia used a slightly different methodology. Only actual sponge records were used (ie there was no interpolation) and small (5 minute) cells were combined into 37 larger but unequal-sized units on the basis of a cluster analysis. A further cluster analysis of these units defined three major and 15 smaller regions. The major biogeographic breaks are at Tweed Heads, Torres Strait and Exmouth, and minor breaks at Fraser Island, Mackay, Lizard Is, Wessel Islands, west of Darwin, and the Abrolhos Islands. Offshore reefs in the Coral Sea and Indian Ocean were also distinct.

A direct comparison between the sponge and ophiuroid bioregionalisations is problematic due to the differences in depths (shallow vs deep) and cell size. However, the ophiuroid study did identify similar regional boundaries to major sponge breaks at Tweed River, Torres Strait and Exmouth, and to the minor break off Fraser Island. However, there was little congruency across Northern Australia. The differences are possibly habitat related, with sponges being sampled from near shore coral reefs and ophiuroids for this study dredged offshore. Reefs are very patchily distributed across northern Australia. Hooper et al. (2005) did note that the Gulf of Carpentaria differed ecologically rather than biogeographically from surrounding regions and that lack of collecting hampered the identification of boundaries across north-western Australia.

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Museum or Institute	Acronym	No lots
Australia		
Museum Victoria	MV	6925
Australian Museum, Sydney	AM	5943
Western Australian Museum	WAM	1332
Northern Territory Museum	NTM	1113
Queensland Museum, Brisbane	QM	428
South Australian Museum, Adelaide	SAM	113
Museum of Tropical Queensland, Townsville	MTQ	102
Tasmanian Museum and Art Gallery, Hobart	TMAG	81
New Zealand		
National Institute of Water and Atmospheric Research	NIWA	3573
National Museum of New Zealand, Wellington	NMNZ	125
Other		
Muséum National D'Histoire Naturelle, Paris	MNHN	2117
Natural History Museum, London	BMNH	378
Museum of Comparative Zoology, Harvard	MCZ	344
Zoological Museum, University of Copenhagen	ZMUC	183
Zoologisch Museum, Universiteit van Amsterdam	ZMA	327
Zoological Survey of India, Kolkata	ZSI	101
United States National Museum, Washington	USNM	7948
Naturhistoriska Riksmuseet, Stockholm	SMNH	5
Published information		579
Total		31717

Table 3.1. Number of ophiuroid lots (species/sample) from each institution available for this study.

Region	Cells	Position	Cluster analysis	Ordination	Jaccard analysis	Comments
N Qld	1-15	9 to 23°S	Cells 1-8 identical, 9 separated slightly	Points linear, closely grouped	Minor peaks at cells 2, 8 and 10 (<0.1). Medium turnover peak at 15 (0.17).	Relatively homogenous tropical region.
S Qld	16-19	24 to 27°S	2 internal clusters: 16-17, 18-19	Two discrete pairs of ordination points	Major peaks at cells 17 (0.14) and 19 (0.24)	Transition zone.
N NSW	20-24	28 to 32°S	Minor substructure	Points closely grouped	Peak at 24 (0.13)	Small homogenous region.
S NSW	25-29	33 to 37°S	Minor substructure	Points spread out	Peak at 29 (0.12)	Transition zone.
Tas	30-46	38°S 149°E around Tasmania to 38°S 141°E	2 clusters: 30-36, 38-46	Points spread out, no major gaps	Peaks at 31 (0.1), 37 (0.1), 40 (0.06) and 46 (0.16)	Relatively homogenous, some differentiation between east and west coasts.
SE Aust	47-50	142 to 137°E	Minor substructure	Points closely grouped	Peak at 50 (0.18)	Small homogenous region, intermediate between Tasmania and Great Australian Bight.
S Aust	51-69	138 to 118°S	3 sub-clusters: 51, 52-62, 63-69	Points closely grouped	Several minor peaks (<0.1) and more pronounced one at 69 (0.11)	Relatively homogenous, in part due to sparse collection effort. Western limit may be an artefact of collection, being the eastern point of the intensive CSIRO SS10/2005 cruise.
SW WA	70-75	35°S 119°E to 31°S 115°E	2 clusters: 70-73, 74-75	Gap between points 73 and 74	Higher values at 73 (0.1), 74 (0.09) and 75 (0.15)	Continuous change between cells, particularly over the northern half of this region.
WA 1	76-81	32 to 25°S	2 clusters 76-78, 79-81, relatively deep	Points spread out	Higher values in most cells (0.9-0.18), highest value at 81	Continuous change, transition zone.
WA 2	82-85	24 to 21°S	2 clusters: 82-84, 85	Points spread	Major peak at 85 (0.18)	Continuous change, transition zone.
NW WA	86-102	20°S 115°E to 10°S 134°E	Shallow terminal clusters	Points grouped closely	Peaks minor except near ends of the region, at 102 (0.13)	Relatively homogeneous region. Coral reef records end at the eastern limit of region. Southern limit possibly influenced by intensive sampling around Dampier.
N Aust	103-115	135 to 141 °E	No sub-clusters	Points overlapping	No peaks	Homogenous area, most cells with similar faunal composition, many records from shallow soft sediment habitats.

Table 4.1a. Regions identified by the ‘String’ analysis for the 50-300 m dataset.

Region	Cells	Position	Cluster analysis	Ordination	Jaccard analysis	Comments
N Qld	1-10	9 to 18°S	4 internal clusters from north to south of 2-5 cells each	Points closely grouped	Peak at cells 10 (0.18).	Relatively homogenous region. Minor turnover near southern limit. Relatively un-sampled region.
S Qld/N NSW	11-24	19 to 32°S	4 internal clusters: 11-14, 15-19, 20-23, 24	Ordination points spread out	Minor peaks at cells 14 (0.10), 16-17 (0.05), and 19 (0.05). High peak at 24 (0.27)	Transition zone.
Tas	25-40	33°S 152°E to 41°S 143°E	3 internal clusters: 25-29, 30-36, 38-40	Points spread out	Peaks at 25 (0.15), 29 (0.18), 37 (0.13) and 40 (0.19)	Northern limit at Sydney. Sub-regional changes at Gabo Is (29) and S Tasmania (37).
W Tas	41-46	40°S 143°E to 38°S 141°E	Minor substructure	Points spread out	Peaks at 41 (0.14), 45 (0.15) and 46 (0.21)	Several species have an easterly range limit to Western Bass Strait.
S Aust	47-68	142 to 119°E	2 clusters: 30-36, 38-46	Points spread out, no major gaps	Peaks at 48 (0.13), 50 (0.15), 60 (0.10) and 68 (0.44)	Relatively homogenous region, major change at western limit. Seamounts in this region unsampled.
Peanut	69	120°E	Only one cell	Grouped with cells from W Tas	Peak at 69 (0.32)	Contains seamounts with similar fauna to Tasmania.
SW WA	70-74	35°S 121°E to 32°S 114°E	2 clusters: 70-72, 73-74	Points spread out	Higher values at 72 (0.14) and 74 (0.33)	Transition zone.
WA 1	75-81	31 to 25°S	3 clusters 75, 76-78, 79-81, relatively deep	Points spread out, 75 distant to the other two groups	Minor peaks at 77 and 79 (<0.1). Major peaks at 75 (0.28) and 81 (0.23)	Transition zone.
WA 2	82-87	24 to 19°S	2 clusters: 82-84, 85-87	Points in two groups reflecting clusters	Highest peaks at 84 (0.2) and 87 (0.25)	Transition zone.
NW WA	88-102	18°S 117°E to 9°S 131°E	Shallow terminal clusters	Points 88 and 89 slightly separate from other points	Peaks minor (< 0.1)	Relatively homogeneous region. Tropical deep sea fauna

Table 4.1b. Regions identified by the ‘String’ analysis for the 300-750 m dataset.

Region	Cells	Position	Cluster analysis	Ordination	Jaccard analysis	Comments
QldNSW	1-24	9 to 33°S	3 internal clusters: 1-10, 11-23, 24	Point 24 distinct, others in 2 neighbouring groups (1-10, 11-23).	Major peak at cells 23-25 (0.18-0.25) and 10 (0.19).	North subregion (1-10) differentiated from southern (11-23). Far southern cell (24) is part of a transition zone. Little data from cells 11-23.
S NSW	25-29	34 to 37°S	2 clusters: 25, 26-29	Point 25 separate, others closely grouped	Peaks at cells 25 (0.18) and 29 (0.2). Constant change between 26-28 (0.3-0.5)	Transition zone.
Tas	30-36	38°S to 44°S	3 internal clusters: 25-29, 30-36, 38-40	Points spread out	Peaks at 35 to 36 (0.15-0.32), constant change from 30-34 (0.02-0.09).	Tasmanian seamounts distinct (36).
S Tas	38-40	43°S 146°E to 41°S 143°E	Minor substructure	Points close together	Peaks at 40 (0.2)	No records from 37 (south of Tasmanian seamounts)
W Tas	41-46	40°S 143°E to 38°S 141°E	2 clusters: 41, 42-46	Point 41 separate	Peak at 46 (0.25)	Western zone homogenous, some transition at the western end (Portland).
S Aust	47-68	142 to 119°E	2 clusters: 30-36, 38-46	Points spread out	Peaks at 48 (0.11), 52-53 (0.11), 59-60 (0.11) and 68 (0.58)	Relatively homogenous region, major change at western limit. Little data from < 500 m.
Peanut	69	120°E	Only one cell	Grouped with cells from W Tas	Major peak at 69 (0.4)	Contains seamounts with similar fauna to W Tas and SE SA.
SW WA	70-74	35°S 121°E to 32°S 114°E	2 clusters: 70-72, 73-74	Points spread out	Major peaks at 70 (0.15), 72 (0.17) and 74 (0.33)	Transition zone. No samples from 74.
WA 1	75-77	31 to 29°S	2 clusters 75, 76-77	Points in two groups, 75 and 76-77	Continuous change 75-77 (0.27, 0.08, 0.33)	Transition zone. No samples from 76.
WA 2	78-87	28 to 19°S	2 clusters: 78-83, 84-87	Points spread out, no notable gaps	Continuous change from 81-84 (0.10-0.11). Major peak at 87 (0.17).	Transition zone.
NW WA	88-102	18°S 117°E to 9°S 131°E	3 clusters: 88-89, 90-94 and 95-101	Points in two groups, 88-94 and 95-101	Major peak at 94 (0.2)	Relatively homogeneous region. Tropical deep sea fauna. Subregions based on sampling artefacts, based on different surveys (S02/82/S01/84 and Siboga) collecting at different depths.

Table 4.1c. Regions identified by the ‘String’ analysis for the 750-1500 m dataset.

Region	Cells	Position	Cluster analysis	Ordination	Jaccard analysis	Comments
N Qld	1-16	9 to 24°S	2 internal clusters: 1-10 and 11-16, NW WA sites 85-87 mixed in.	Points closely grouped, overlap some NW WA points.	Minor peaks (<0.1)	Relatively homogenous tropical region. Clusters with some cells from NW WA with similar habitat.
S Qld-N NSW	17-23	25 to 31°S	2 internal clusters: 17-19, 20-23	Two discrete groups of ordination points, spread out	Major peak at 17 (0.4) and lesser one at 20 (0.3).	Transition zone.
S NSW	24-29	33 to 37°S	Minor substructure	Points in two groups: 24-26, 27-28.	Peak at 24.	Transition zone.
S Aust	30-71	38°S 149°E to 34°S 114°E	2 clusters: 30-45, 46-71. Some SW (66-69) mixed with SE cells. Cells 43-44 (N Bass Strait), 65 (Esperance) form outliers.	Points form a tight ball, except cells 43, 44 and 65.	Large changes between 36-39 and 43-35 (>0.3), reflecting differenced off S Tasmania	Relatively homogenous, some differentiation between SE (to E Bass Strait) and S coasts.
S Tas	36-38	43-44°S, 145-147°E	Long branched cluster	Three spread points	See above	Southern tip of Tasmania, differentiated by oceanographic conditions and lack of some stenothermal species.
WA	73-84	33°S 114°E to 22°S 113°E	2 sub-clusters: 73-81, 82-84, form a larger cluster with NSW.	Form a coherent but spread series of points adjacent to NSW cells.	Minor peaks only (<0.2)	Zone of gradual change.
NW WA	85-94	21°S 113°E to 13°S 126°E	Cells 88-94 form a tight cluster but cells 85-87 are mixed within the N Qld cluster	Cells 88-94 distinct, 85-87 overlap N Qld points	Minor peaks only (<0.2)	Relatively homogeneous region between 88-94 including the shelf around offshore islands. Southernmost cells (85-87) cluster with N Qld
N Aust	95-115	127 to 141 °E	Several chaining clusters, in general not forming geographic subunits. Most of the , Gulf of Carpentaria is identical except cell 110 in the SW corner	Points spread but form a distinct group.	Major region of change, peak at 95 (>0.8) indicating an almost complete change in fauna. Other major peaks at 101, 104 and 111.	Gulf of Carpentaria homogeneous but variable elsewhere. Distinction from NW WA may be because of restriction in habitat availability: much of the region is < 100 m deep. Only western cells (95-102) with areas >100 m.

Table 4.1d. Regions identified by the Oceanographic Envelope analysis for the 50-300 m dataset.

Region	Cells	Position	Cluster analysis	Ordination	Jaccard analysis	Comments
N Qld	1-16	9 to 24°S	Several internal clusters, intermingles with cells from WA 2	Most points group closely, with cells 1 and 16 a little distinct, overlaps WA 2	Region of minor change (<0.2).	Relatively homogeneous tropical region, some substructure. Some ecological similarity with region WA 2, little with S Qld.
S Qld	17-19	25 to 27°S	Some internal structure	Little dispersion	Major change at 17 (0.7)	Transition zone along with N NSW and S NSW.
N NSW	20-23	28 to 31°S	Some internal long branches	Points spread out and linear	Major change at 20 (0.55)	
S NSW	24-26	32 to 34°S	Little internal structure, clusters with WA 1 cells	Points intermediate between N NSW and Tas	Major change at 23 (0.5)	Some ecological similarity with WA 1, but not overlapping.
Tas	27-34	35 to 42°S	Forms two clusters either side cells from SW WA.	Linear spread of points overlapping S Aust points.	Several major peaks between cells 36 and 43 (>0.3) including the S Tas region	The regions S NSW, Tas, S Tas, S Aust and SW WA form a distinct cluster, but internally there is some intermingling, with cells from the eastern and western extremities showing some similarities. Cells from Tas are similar to cells from SW WA.
S Tas	36-38, 42	147 to 145°E	Some long internal branches, clusters apart from Tas cells	Outliers to S Aust and Tas points	See above	S Tas distinct, partially due to the southern seamounts.
S Aust	35, 39-68	144 to 114°E	Three internal clusters, one including cells from the east and west extremities.	Little dispersion except for cells 69-72.	Major peak at 69 (<0.3), rest minor	Relatively homogenous region, except at its eastern and western extremities.
SW WA	69-72	115 to 118°E	Forms a small cluster within two clusters from Tas	Slightly overlaps points from Tas.		Distinct from S Aust, with some similarities to Tas.
WA 1	73-83	33 to 23°S	Two internal clusters, cell 74 clusters with the northern cells	Little dispersion	Minor change (<0.2)	Relatively homogenous region
WA 2	84-87	22 to 19°S	Do not form a coherent cluster, intermingled with cells from N Qld	Overlapping cells from N Qld	Highest peaks at 84 (0.2)	Environmental similarities with cells from N Qld.
NW WA	88-102	18°S 117°E to 9°S 131°E	Two internal clusters, not geographically coherent	Linear grouping	Major peaks at 97-98, 101 (>0.4).	Region of change.

Table 4.1e. Regions identified by the Oceanographic Envelope analysis for the 300-750 m dataset.

Region	Cells	Position	Cluster analysis	Ordination	Jaccard analysis	Comments
N Qld	1-16	9 to 24°S	Two internal clades (1-10,16 and 11-15), WA 2 cells mixed in with first.	Tight group, partially overlapping two of the WA 2 points	Higher peaks in southern section of region, at cell 11, 13 and 16 (<0.3)	Tropical region, relatively homogeneous in the north, more turnover in the south
S Qld	17-19	25 to 27°S	Very long internal branches	Point recognisable as a group but dispersed, distant from N Qld	High peak at 17 (0.7)	Region of transition, more similar to NSW than N Qld
N NSW	20-23	28 to 31°S	Long internal branches	Point recognisable as a group but dispersed, intermediate between S Qld and S NSW	High peak at 20 (0.7)	Region of transition
S NSW	24-26	32 to 34°S	Minor substructure, sister clade to WA 1	Points linear, overlap WA 1 points	High peak at 24	Small region distinct from E Tas, with some similarities to WA 1 region in west
Tas	27-39	35°S 150°E to 42°S 144°E	Two internal clades separating north from south, SW WA cells completely mixed in. Cell 37 distinct.	Point closely grouped with SW WA	Minor peaks at 27 and 30 (~0.1), higher peak at 37 (S Tas)	Relatively homogeneous, some distinction between north and south. Furthest south cell (37) distinct (seamounts)
S Aust	40-68	143°E to 119°E	Continuous substructure. Cell 42 an outlier	Most points tightly grouped, except cells 42 and 45 (W Bass Strait)	Major peak at 42 (0.6), other peaks minor (<0.2)	Homogeneous region, with the exception of two cells from W Bass Strait.
SW WA	69-72	118 to 115°E	Intermingled with cells from Tas	Overlapping points from Tas	Major peak at 69 (0.4)	Small transition region, many similarities to Tas
WA 1	73-83	33 to 23°S	Two internal clades representing north and south sections	Tight linear group, overlapping S NSW	Minor peaks (~0.1)	Homogeneous region, minor differences between north and south
WA 2	84-87	22 to 19°S	Long branches, partially intermingled with N Qld	Little dispersion, partially overlapping with N Qld points	Peak at 84 (0.3)	Small region of change, similar to N Qld
NW WA	88-102	18°S 117°E to 9°S 131°E	Some substructure, not obviously geographic in nature	Points dispersed but identifiable as a group	Peaks at 88 (0.4), 95 (0.4), 96 (0.5), 97 (0.5)	Region of change, particularly eastern section

Table 4.1f. Regions identified by the Oceanographic Envelope analysis for the 750-1500 m dataset.

Cell no	Latitude	Longitude	Oceanographic envelope 50-300 m	300-750 m	750-1500 m	String 50-300 m	300-750 m	750-1500 m
1	-9.5	143.5	N Qld	N Qld	N Qld	N Qld	N Qld	Qld/NSW
2	-10.5	143.5	N Qld	N Qld	N Qld	N Qld	N Qld	Qld/NSW
3	-11.5	143.5	N Qld	N Qld	N Qld	N Qld	N Qld	Qld/NSW
4	-12.5	144.5	N Qld	N Qld	N Qld	N Qld	N Qld	Qld/NSW
5	-13.5	144.5	N Qld	N Qld	N Qld	N Qld	N Qld	Qld/NSW
6	-14.5	145.5	N Qld	N Qld	N Qld	N Qld	N Qld	Qld/NSW
7	-15.5	145.5	N Qld	N Qld	N Qld	N Qld	N Qld	Qld/NSW
8	-16.5	146.5	N Qld	N Qld	N Qld	N Qld	N Qld	Qld/NSW
9	-17.5	146.5	N Qld	N Qld	N Qld	N Qld	N Qld	Qld/NSW
10	-18.5	147.5	N Qld	N Qld	N Qld	N Qld	N Qld	Qld/NSW
11	-19.5	148.5	N Qld	N Qld	N Qld	N Qld	S Qld/NSW	Qld/NSW
12	-20.5	149.5	N Qld	N Qld	N Qld	N Qld	S Qld/NSW	Qld/NSW
13	-21.5	150.5	N Qld	N Qld	N Qld	N Qld	S Qld/NSW	Qld/NSW
14	-22.5	151.5	N Qld	N Qld	N Qld	N Qld	S Qld/NSW	Qld/NSW
15	-23.5	152.5	N Qld	N Qld	N Qld	N Qld	S Qld/NSW	Qld/NSW
16	-24.5	153.5	N Qld	N Qld	N Qld	S Qld	S Qld/NSW	Qld/NSW
17	-25.5	153.5	S Qld/N NSW	S Qld	S Qld	S Qld	S Qld/NSW	Qld/NSW
18	-26.5	153.5	S Qld/N NSW	S Qld	S Qld	S Qld	S Qld/NSW	Qld/NSW
19	-27.5	153.5	S Qld/N NSW	S Qld	S Qld	S Qld	S Qld/NSW	Qld/NSW
20	-28.5	153.5	S Qld/N NSW	N NSW	N NSW	N NSW	S Qld/NSW	Qld/NSW
21	-29.5	153.5	S Qld/N NSW	N NSW	N NSW	N NSW	S Qld/NSW	Qld/NSW
22	-30.5	153.5	S Qld/N NSW	N NSW	N NSW	N NSW	S Qld/NSW	Qld/NSW
23	-31.5	153.5	S Qld/N NSW	N NSW	N NSW	N NSW	S Qld/NSW	Qld/NSW
24	-32.5	152.5	S NSW	S NSW	S NSW	N NSW	S Qld/NSW	Qld/NSW
25	-33.5	152.5	S NSW	S NSW	S NSW	S NSW	Tas	S NSW
26	-34.5	151.5	S NSW	S NSW	S NSW	S NSW	Tas	S NSW
27	-35.5	150.5	S NSW	Tas	Tas	S NSW	Tas	S NSW
28	-36.5	150.5	S NSW	Tas	Tas	S NSW	Tas	S NSW
29	-37.5	150.5	S NSW	Tas	Tas	S NSW	Tas	S NSW
30	-38.5	148.5	S Aust	Tas	Tas	Tas	Tas	Tas
31	-39.5	148.5	S Aust	Tas	Tas	Tas	Tas	Tas
32	-40.5	148.5	S Aust	Tas	Tas	Tas	Tas	Tas
33	-41.5	148.5	S Aust	Tas	Tas	Tas	Tas	Tas
34	-42.5	148.5	S Aust	Tas	Tas	Tas	Tas	Tas
35	-43.5	147.5	S Aust	S Aust	Tas	Tas	Tas	Tas
36	-44.5	146.5	S Tas	S Tas	Tas	Tas	Tas	Tas
38	-43.5	145.5	S Tas	S Tas	Tas	Tas	Tas	S Tas
39	-42.5	144.5	S Aust	S Aust	Tas	Tas	Tas	S Tas
40	-41.5	143.5	S Aust	S Aust	S Aust	Tas	Tas	S Tas
41	-40.5	143.5	S Aust	S Aust	S Aust	Tas	W Tas	W Tas
42	-39.5	144.5	S Aust	S Tas	S Aust	Tas	W Tas	W Tas
43	-38.5	144.5	S Aust			Tas		
44	-38.5	143.5	S Aust			Tas		
45	-39.5	142.5	S Aust	S Aust	S Aust	Tas	W Tas	W Tas
46	-38.5	141.5	S Aust	S Aust	S Aust	Tas	W Tas	W Tas
47	-38.5	140.5	S Aust	S Aust	S Aust	SE SA	S Aust	S Aust
48	-37.5	139.5	S Aust	S Aust	S Aust	SE SA	S Aust	S Aust
49	-36.5	138.5	S Aust	S Aust	S Aust	SE SA	S Aust	S Aust
50	-36.5	137.5	S Aust	S Aust	S Aust	SE SA	S Aust	S Aust
51	-36.5	136.5	S Aust	S Aust	S Aust	S Aust	S Aust	S Aust
52	-35.5	135.5	S Aust	S Aust	S Aust	S Aust	S Aust	S Aust
53	-34.5	134.5	S Aust	S Aust	S Aust	S Aust	S Aust	S Aust
54	-33.5	133.5	S Aust	S Aust	S Aust	S Aust	S Aust	S Aust
55	-32.5	132.5	S Aust	S Aust	S Aust	S Aust	S Aust	S Aust
56	-32.5	131.5	S Aust	S Aust	S Aust	S Aust	S Aust	S Aust
57	-32.5	130.5	S Aust	S Aust	S Aust	S Aust	S Aust	S Aust
58	-32.5	129.5	S Aust	S Aust	S Aust	S Aust	S Aust	S Aust

Table 4.2. Cells (1 degree lat/long) from the String and Oceanographic Envelope analyses at three depth layers with regions identified from the cluster dendrograms.

			Oceanographic envelope			String		
Cell no	Latitude	Longitude	150m	500m	1000m	150m	500m	1000m
59	-32.5	128.5	S Aust	S Aust	S Aust	S Aust	S Aust	S Aust
60	-32.5	127.5	S Aust	S Aust	S Aust	S Aust	S Aust	S Aust
61	-32.5	126.5	S Aust	S Aust	S Aust	S Aust	S Aust	S Aust
62	-33.5	125.5	S Aust	S Aust	S Aust	S Aust	S Aust	S Aust
63	-33.5	124.5	S Aust	S Aust	S Aust	S Aust	S Aust	S Aust
64	-34.5	123.5	S Aust	S Aust	S Aust	S Aust	S Aust	S Aust
65	-34.5	122.5	S Aust	S Aust	S Aust	S Aust	S Aust	S Aust
66	-34.5	121.5	S Aust	S Aust	S Aust	S Aust	S Aust	S Aust
67	-34.5	120.5	S Aust	S Aust	S Aust	S Aust	S Aust	S Aust
68	-34.5	119.5	S Aust	S Aust	S Aust	S Aust	S Aust	S Aust
69	-35.5	118.5	S Aust	SW WA	SW WA	S Aust	Peanut	Peanut
70	-35.5	117.5	S Aust	SW WA	SW WA	SW WA	SW WA	SW WA
71	-35.5	116.5	S Aust	SW WA	SW WA	SW WA	SW WA	SW WA
72	-34.5	114.5	S Aust	SW WA	SW WA	SW WA	SW WA	SW WA
73	-33.5	114.5	WA	WA 1	WA 1	SW WA	SW WA	SW WA
74	-32.5	114.5	WA	WA 1	WA 1	SW WA	SW WA	SW WA
75	-31.5	114.5	WA	WA 1	WA 1	SW WA	WA 1	WA 1
76	-30.5	114.5	WA	WA 1	WA 1	WA 1	WA 1	WA 1
77	-29.5	113.5	WA	WA 1	WA 1	WA 1	WA 1	WA 1
78	-28.5	113.5	WA	WA 1	WA 1	WA 1	WA 1	WA 2
79	-27.5	112.5	WA	WA 1	WA 1	WA 1	WA 1	WA 2
80	-26.5	112.5	WA	WA 1	WA 1	WA 1	WA 1	WA 2
81	-25.5	112.5	WA	WA 1	WA 1	WA 1	WA 1	WA 2
82	-24.5	112.5	WA	WA 1	WA 1	WA 2	WA 2	WA 2
83	-23.5	112.5	WA	WA 1	WA 1	WA 2	WA 2	WA 2
84	-22.5	113.5	WA	WA 2	WA 2	WA 2	WA 2	WA 2
85	-21.5	113.5	NW WA	WA 2	WA 2	WA 2	WA 2	WA 2
86	-20.5	114.5	NW WA	WA 2	WA 2	NW WA	WA 2	WA 2
87	-19.5	116.5	NW WA	WA 2	WA 2	NW WA	WA 2	WA 2
88	-18.5	119.5	NW WA	NW WA	NW WA	NW WA	NW WA	NW WA
89	-17.5	120.5	NW WA	NW WA	NW WA	NW WA	NW WA	NW WA
90	-16.5	121.5	NW WA	NW WA	NW WA	NW WA	NW WA	NW WA
91	-15.5	122.5	NW WA	NW WA	NW WA	NW WA	NW WA	NW WA
92	-14.5	123.5	NW WA	NW WA	NW WA	NW WA	NW WA	NW WA
93	-13.5	125.5	NW WA	NW WA	NW WA	NW WA	NW WA	NW WA
94	-13.5	126.5	NW WA	NW WA	NW WA	NW WA	NW WA	NW WA
95	-13.5	128.5	N Aust	NW WA	NW WA	NW WA	NW WA	NW WA
96	-13.5	127.5	N Aust	NW WA	NW WA	NW WA	NW WA	NW WA
97	-12.5	129.5	N Aust	NW WA	NW WA	NW WA	NW WA	NW WA
98	-10.5	130.5	N Aust	NW WA	NW WA	NW WA	NW WA	NW WA
99	-10.5	131.5	N Aust	NW WA	NW WA	NW WA	NW WA	NW WA
100	-10.5	132.5	N Aust	NW WA	NW WA	NW WA	NW WA	NW WA
101	-10.5	133.5	N Aust	NW WA	NW WA	NW WA	NW WA	NW WA
102	-10.5	134.5	N Aust	NW WA	NW WA	NW WA	NW WA	NW WA
104	-10.5	135.5	N Aust			N Aust		
105	-10.5	136.5	N Aust			N Aust		
106	-12.5	137.5	N Aust			N Aust		
107	-13.5	137.5	N Aust			N Aust		
108	-14.5	137.5	N Aust			N Aust		
109	-15.5	138.5	N Aust			N Aust		
110	-15.5	139.5	N Aust			N Aust		
111	-14.5	140.5	N Aust			N Aust		
112	-13.5	140.5	N Aust			N Aust		
113	-12.5	140.5	N Aust			N Aust		
114	-11.5	141.5	N Aust			N Aust		
115	-10.5	141.5	N Aust			N Aust		

Table 4.2 (cont)

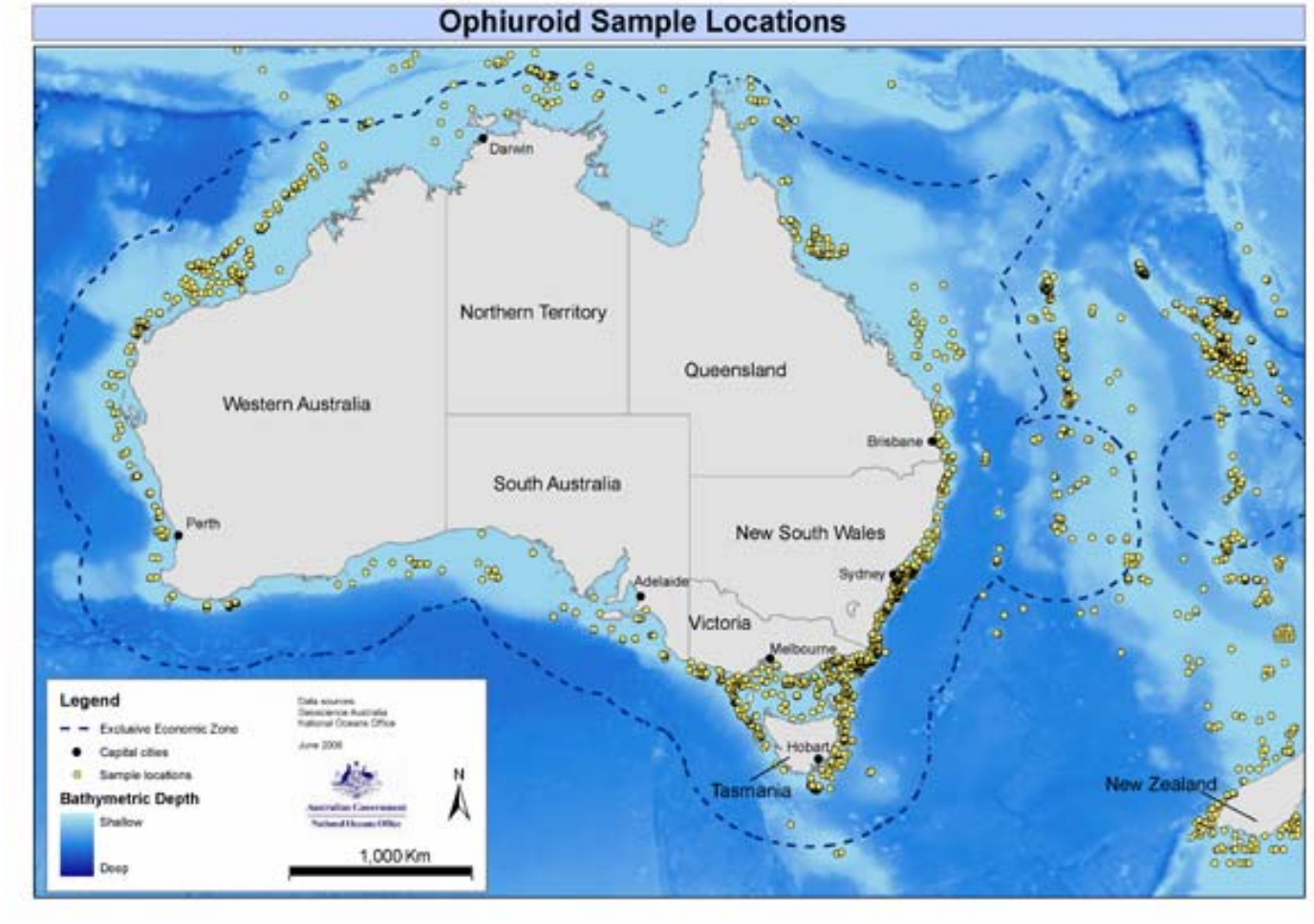
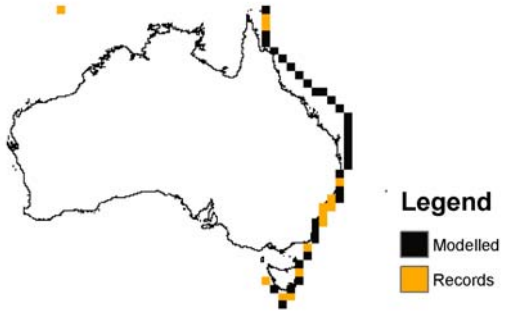
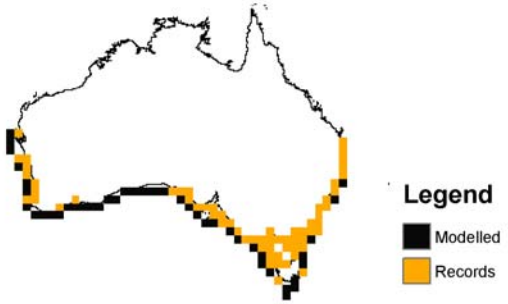


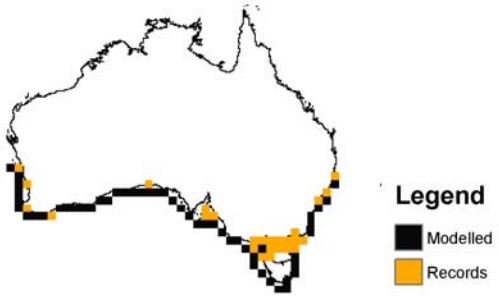
Figure 3.1. Map of the ophiuroid samples available for the study.



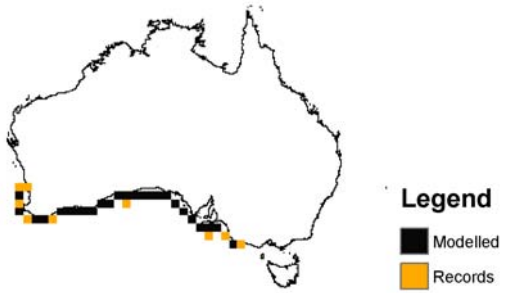
Ophiura flagellata (750-1500 m)



Ophionereis schayeri (50-300 m)

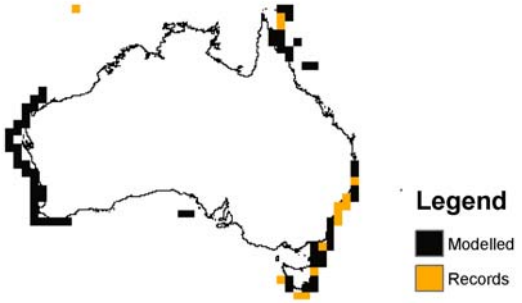


Ophiopeza cylindrica (50-300 m)

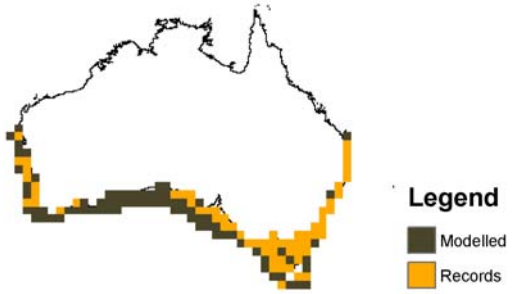


Ophiomusium anisacanthum (50-300 m)

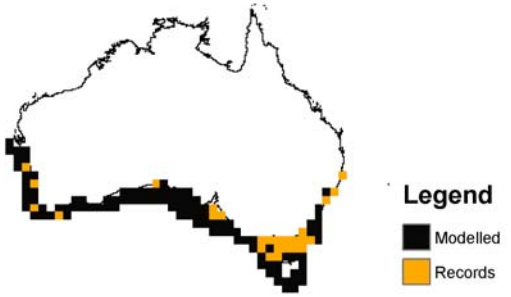
Figure 4.1. Maps of actual records and modelled distributions from the 'String' analysis for four species, summarised into cells of one degree latitude/longitude.



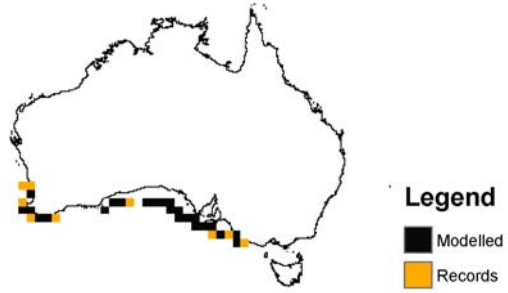
Ophiura flagellata (750-1500 m)



Ophionereis schayeri (50-300 m)

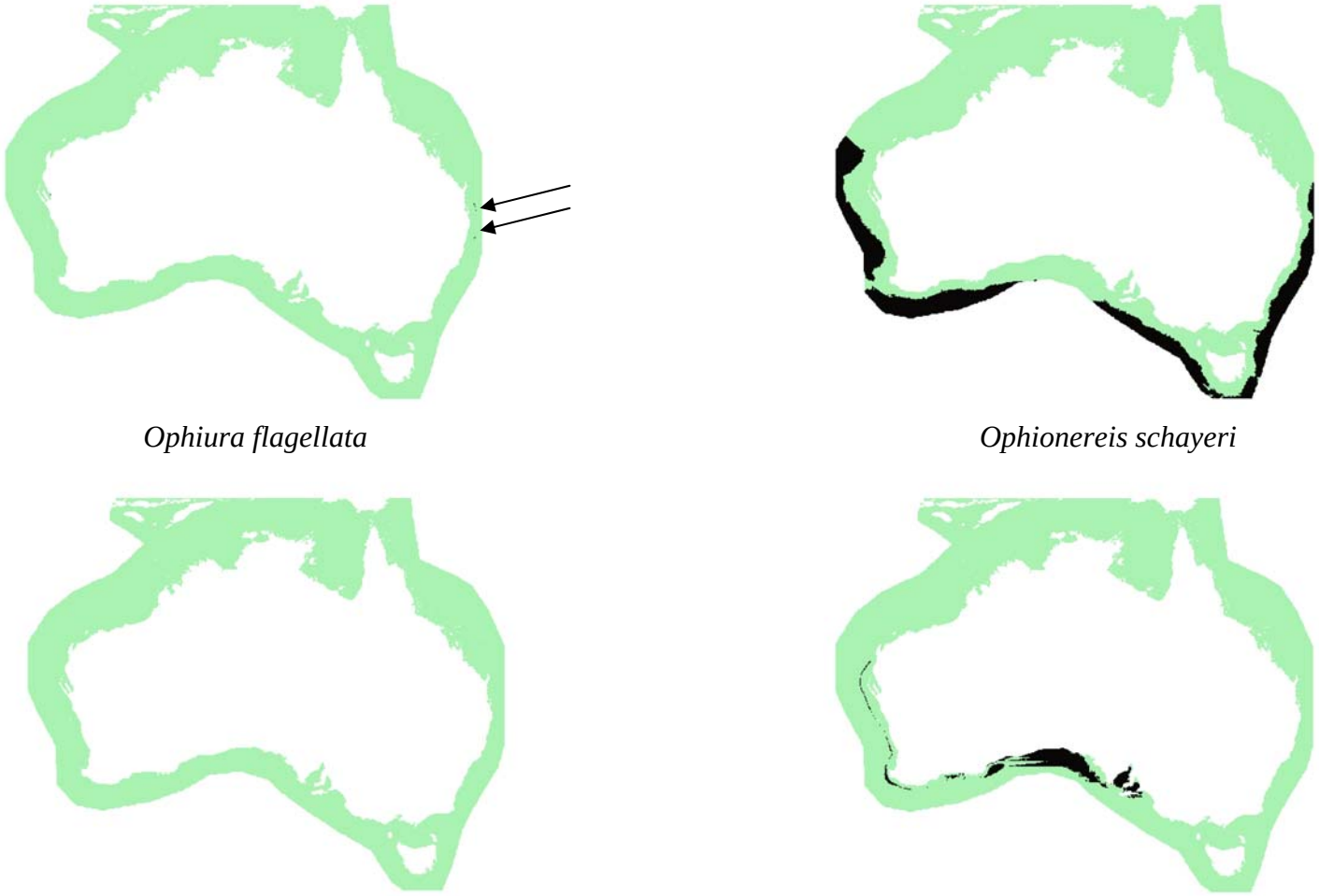


Ophiopeza cylindrica (50-300 m)



Ophiomusium anisacanthum (50-300 m)

Figure 4.2. Maps of actual records and modelled distributions from the Oceanographic Envelop analysis for four species, summarised into cells of one degree latitude/longitude.



Ophiura flagellata

Ophionereis schayeri

Ophiopeza cylindrica

Ophiomusium anisacanthum

Figure 4.3. Maps of modelled distributions from the MARS analysis for four species at a resolution of 0.02 degrees latitude/longitude. The small areas predicted for *O. flagellata* are highlighted by arrows.

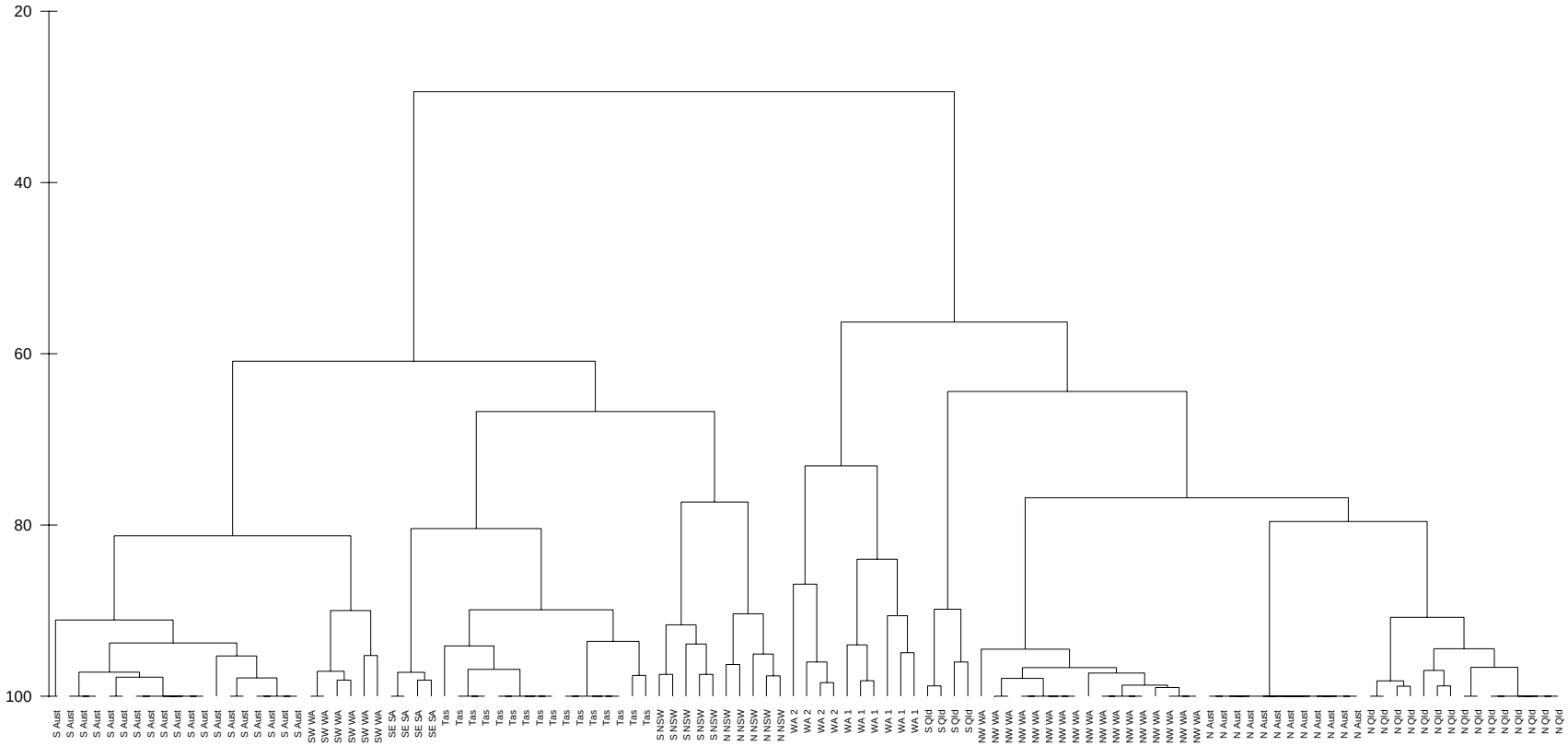


Figure 4.4a. Cluster diagram of cells from the ‘String’ 50-300 m depth layer using presence/absence species occurrence data, the Bray Curtis similarity coefficient and Group Averaging. Branches at 80% similarity have been labeled according to their geographic region.

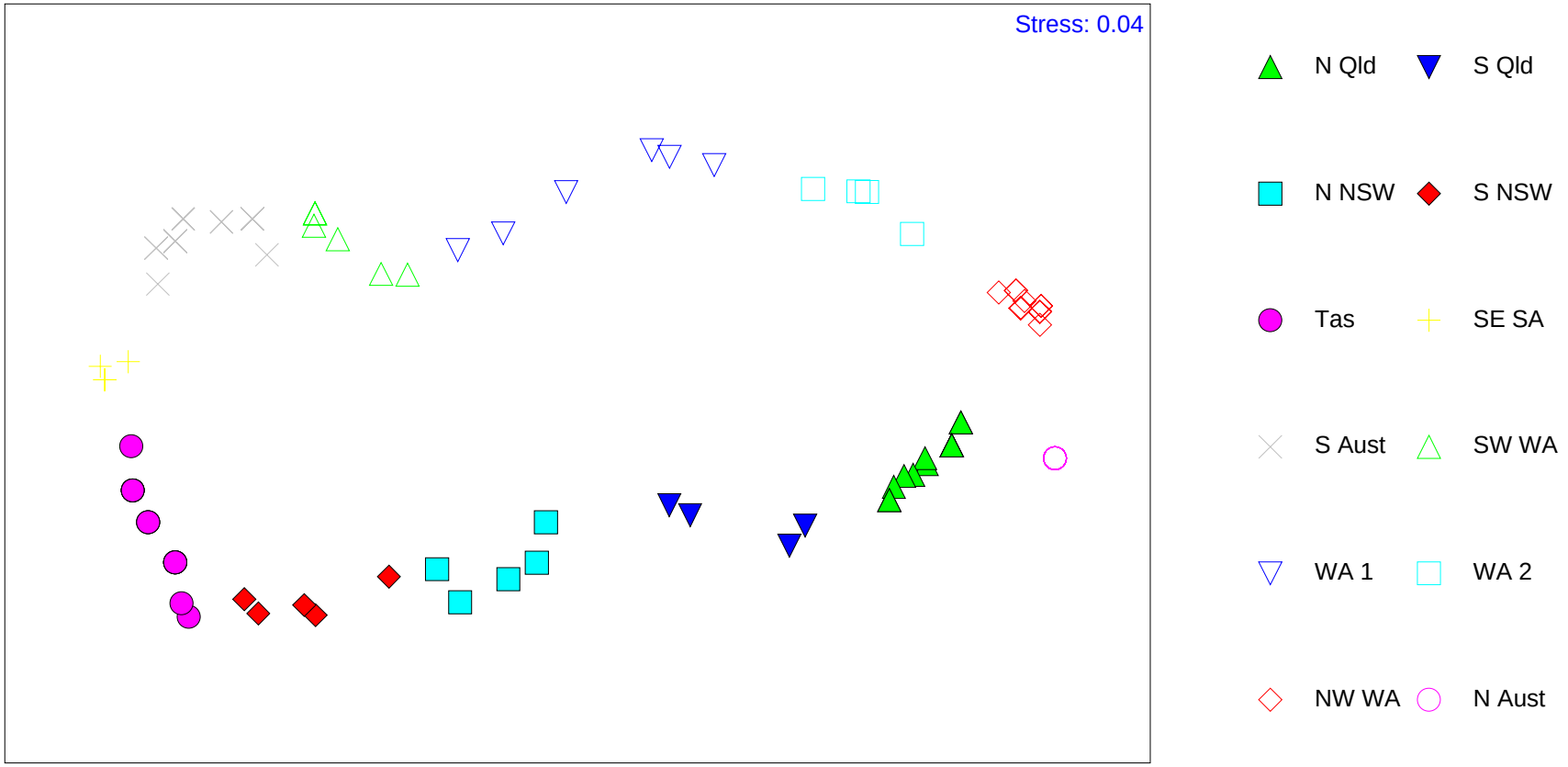


Figure 4.4b. MDS ordination of cells from the 'String' 50-300 m depth layer, labeled by regional clusters.

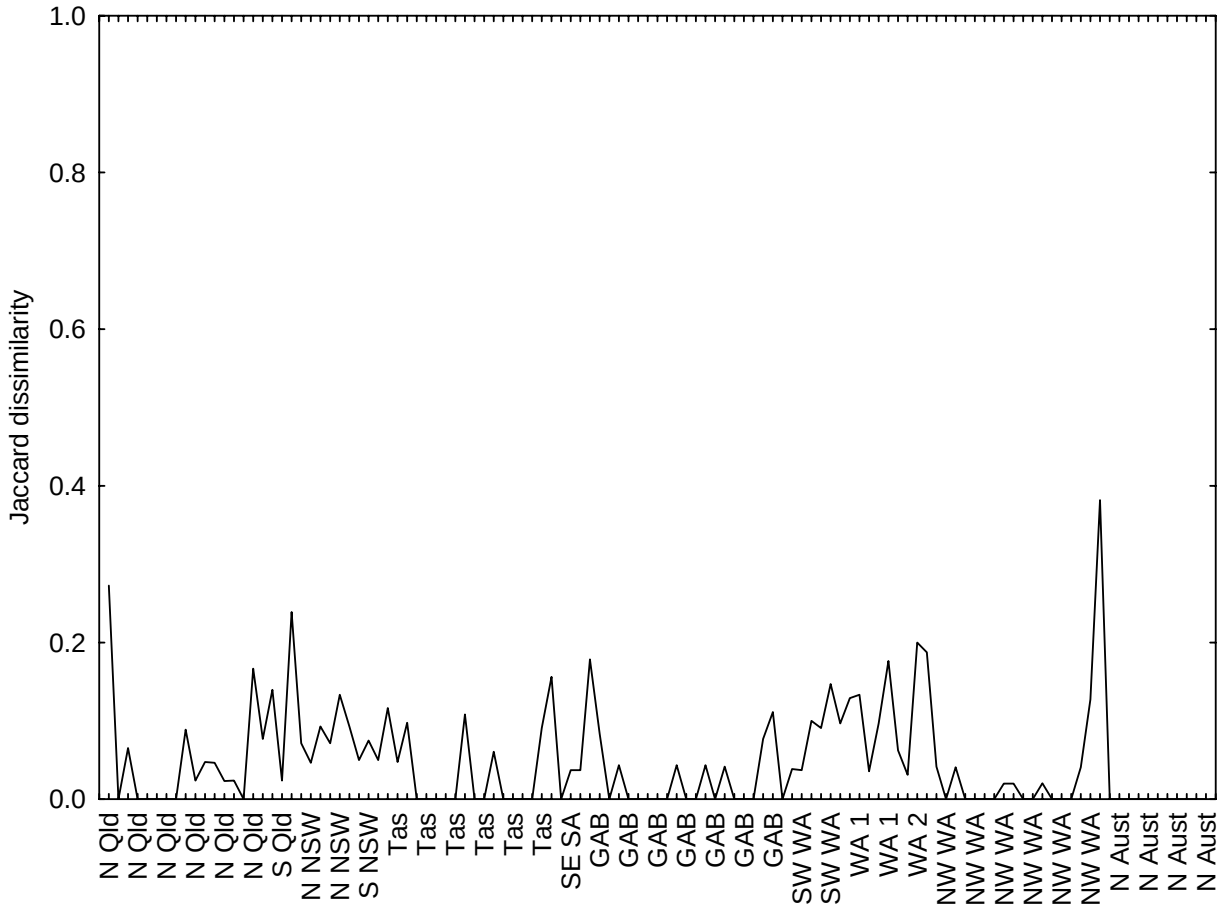


Figure 4.4c. Jaccard dissimilarity measurements between adjacent cells from the ‘String’ 50-300 m depth layer.

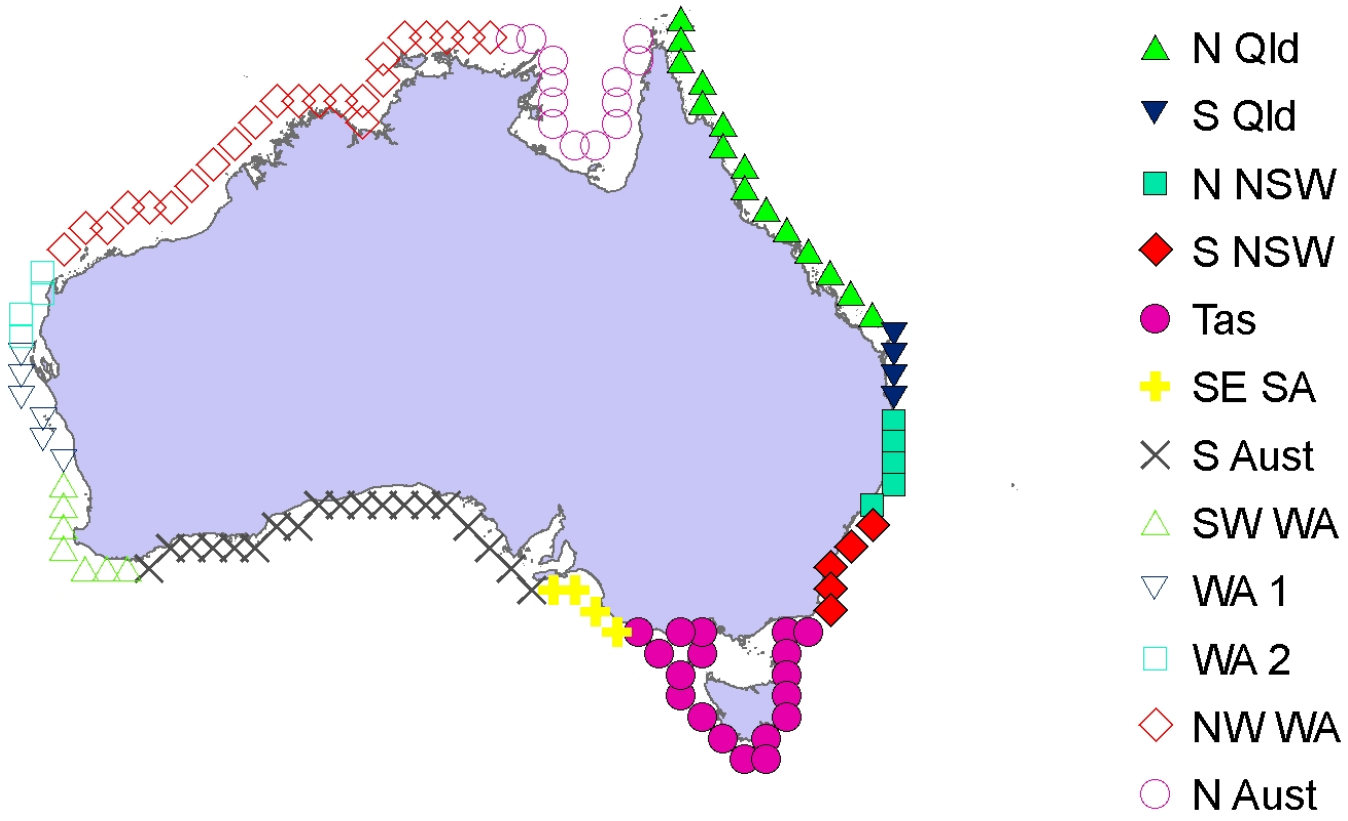


Figure 4.4d. Map of regions from the ‘String’ 50-300 m layer.

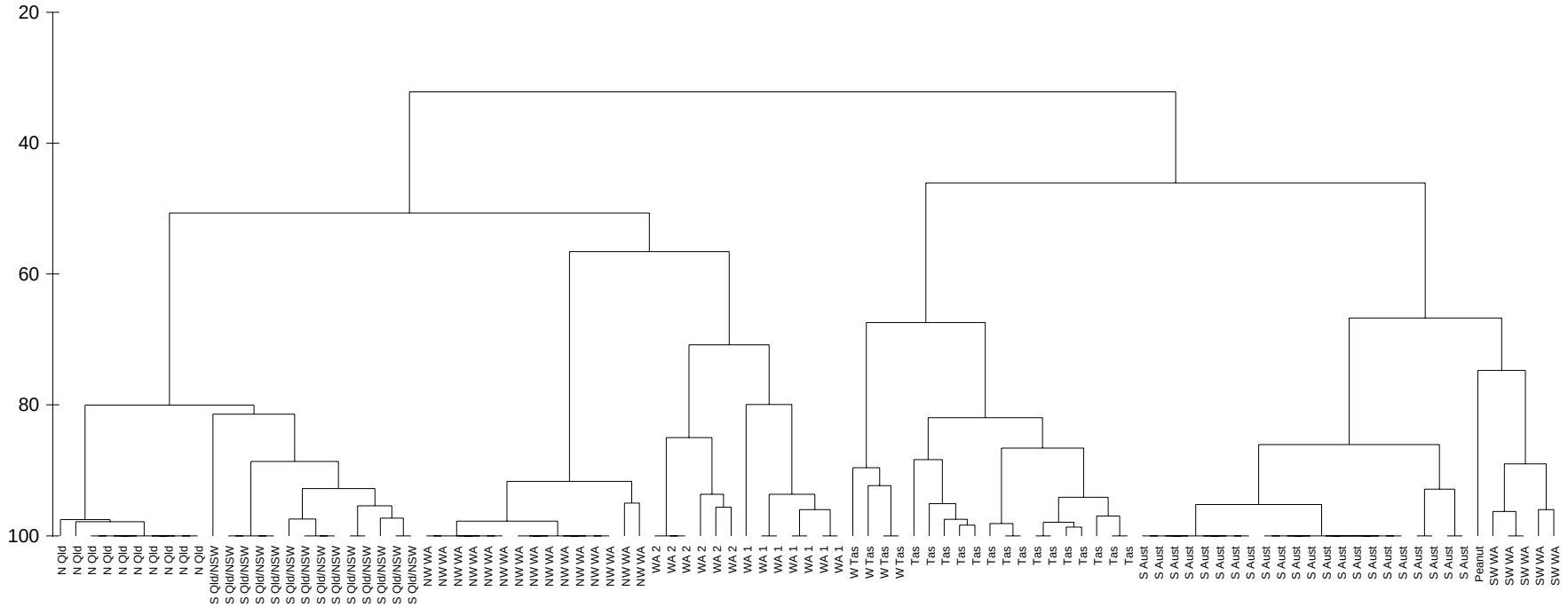


Figure 4.5a. Cluster diagram of cells from the ‘String’ 300-750 m depth layer, labeled by region.

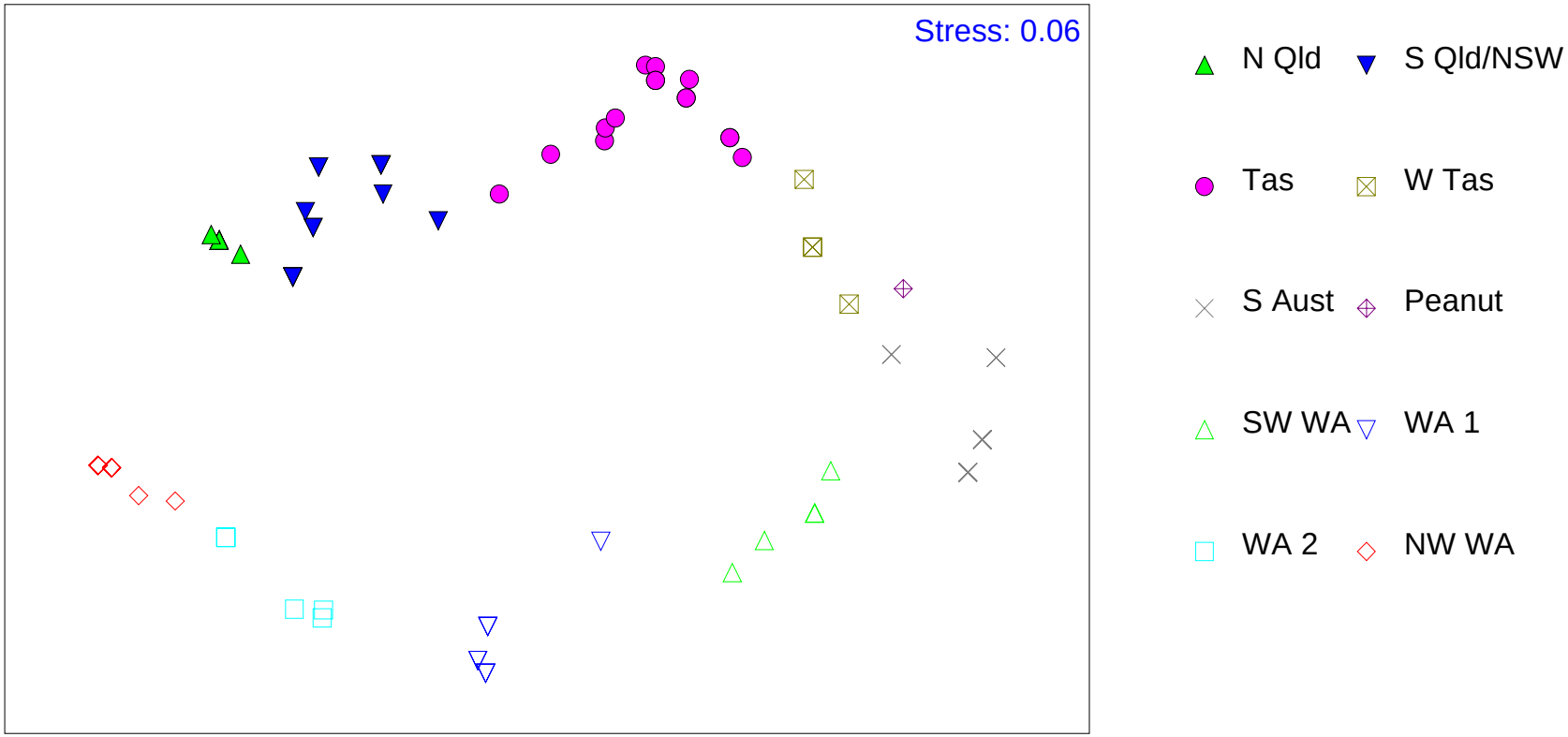


Figure 4.5b. MDS ordination of cells from the ‘String’ 300-750 m depth layer, labeled by regional clusters.

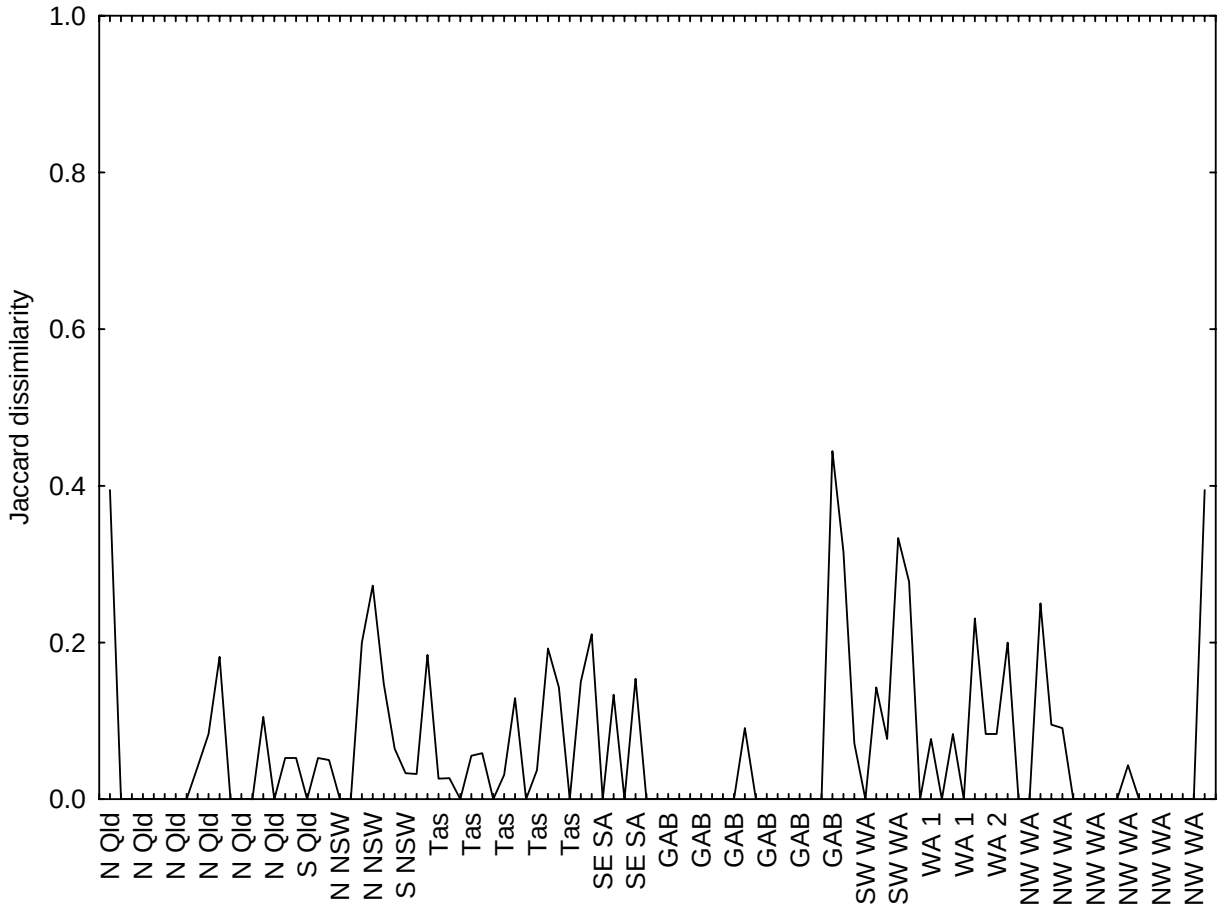


Figure 4.5c. Jaccard dissimilarity measurements between adjacent cells from the ‘String’ 300-750 m depth layer.

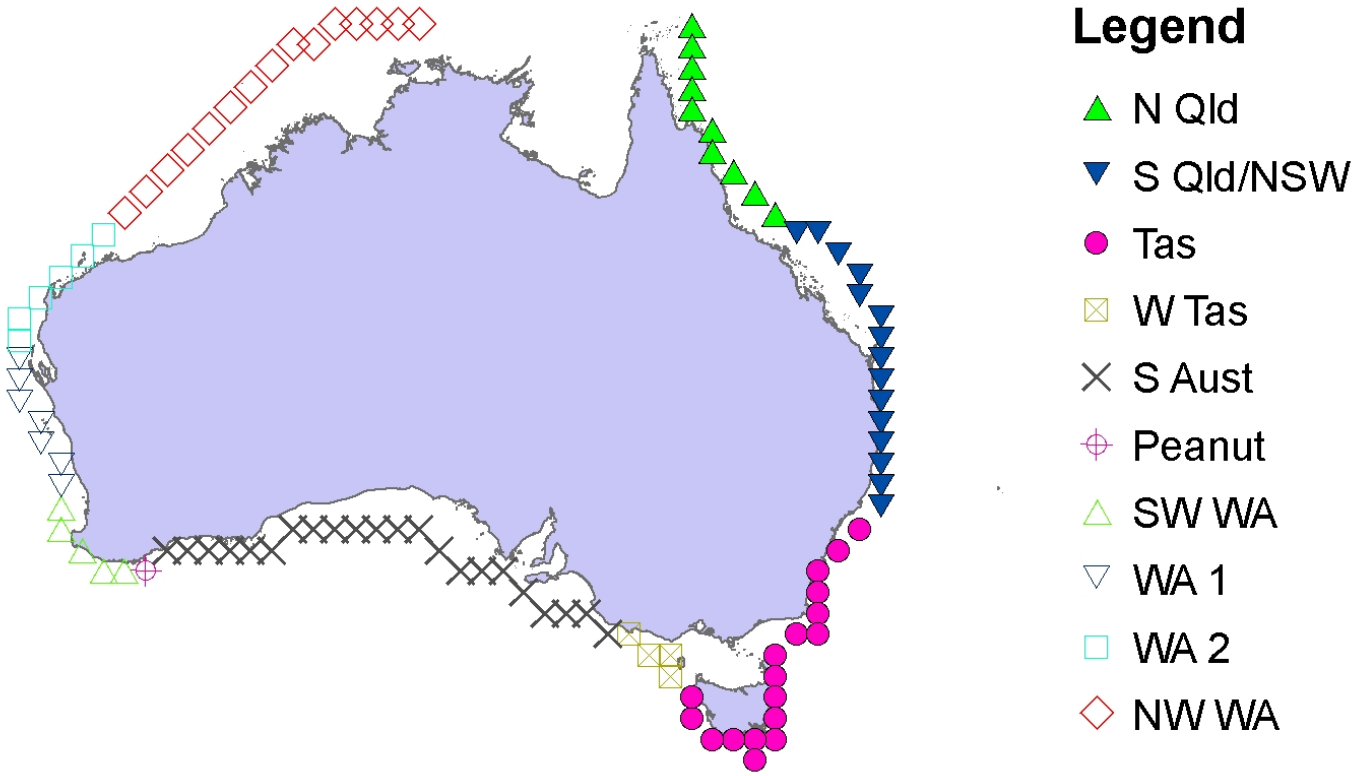


Figure 4.5d. Map of regions from the ‘String’ 300-750 m layer.

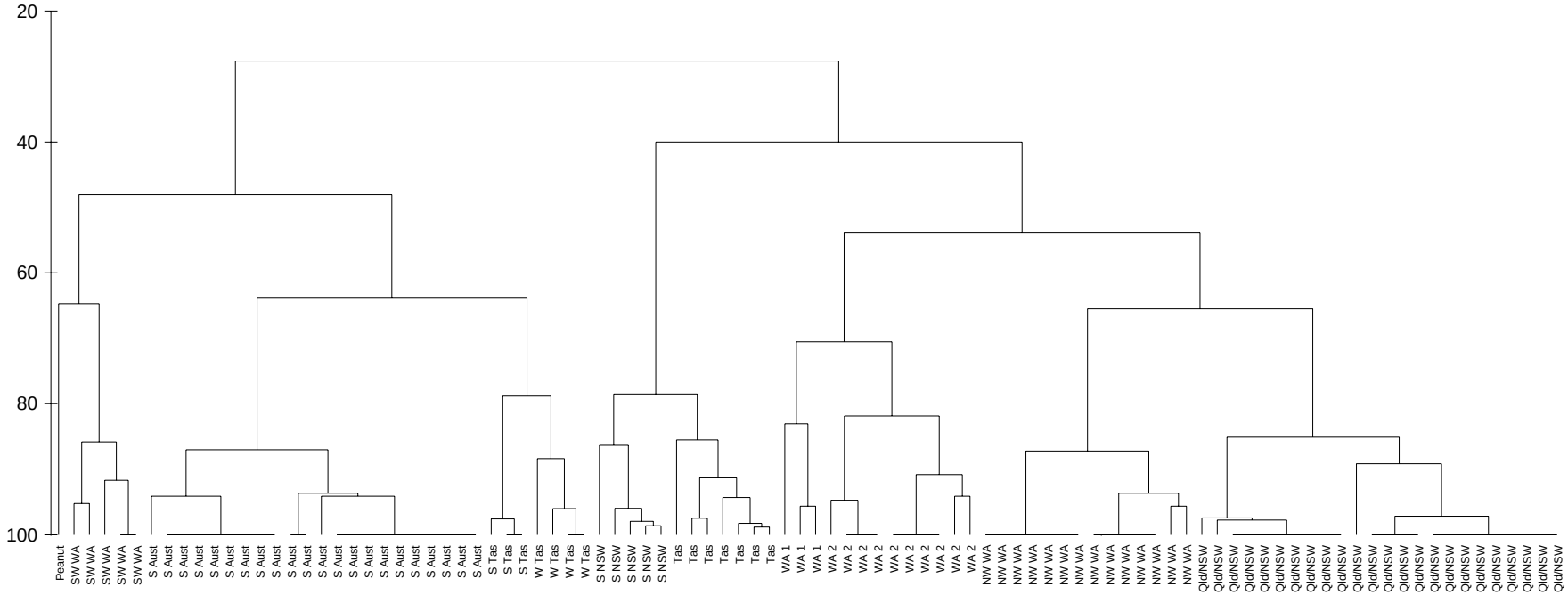


Figure 4.6a. Cluster diagram of cells from the ‘String’ 750-1500 m depth layer, labeled by region.

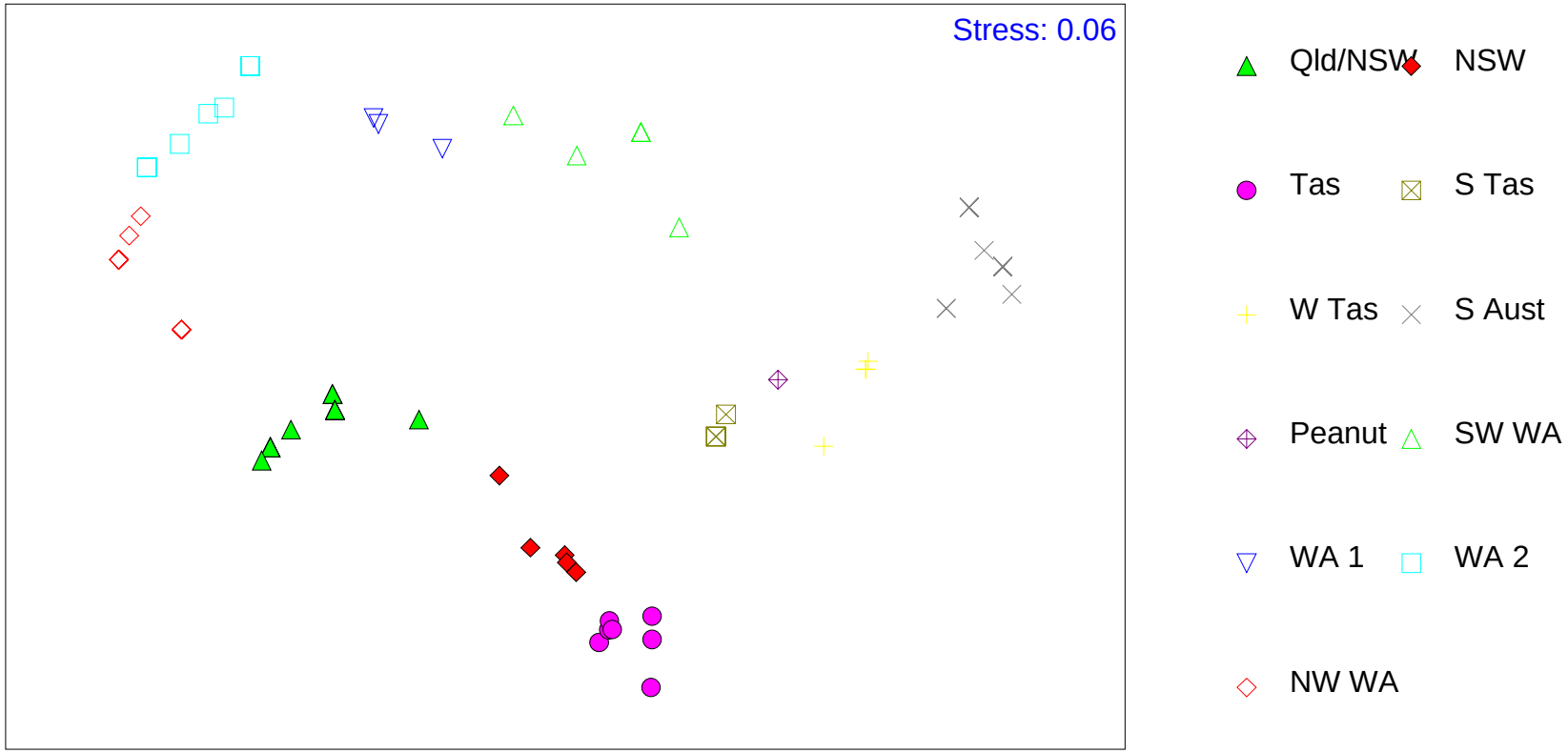


Figure 4.6b. MDS ordination of cells from the 'String' 750-1500 m depth layer, labeled by regional clusters.

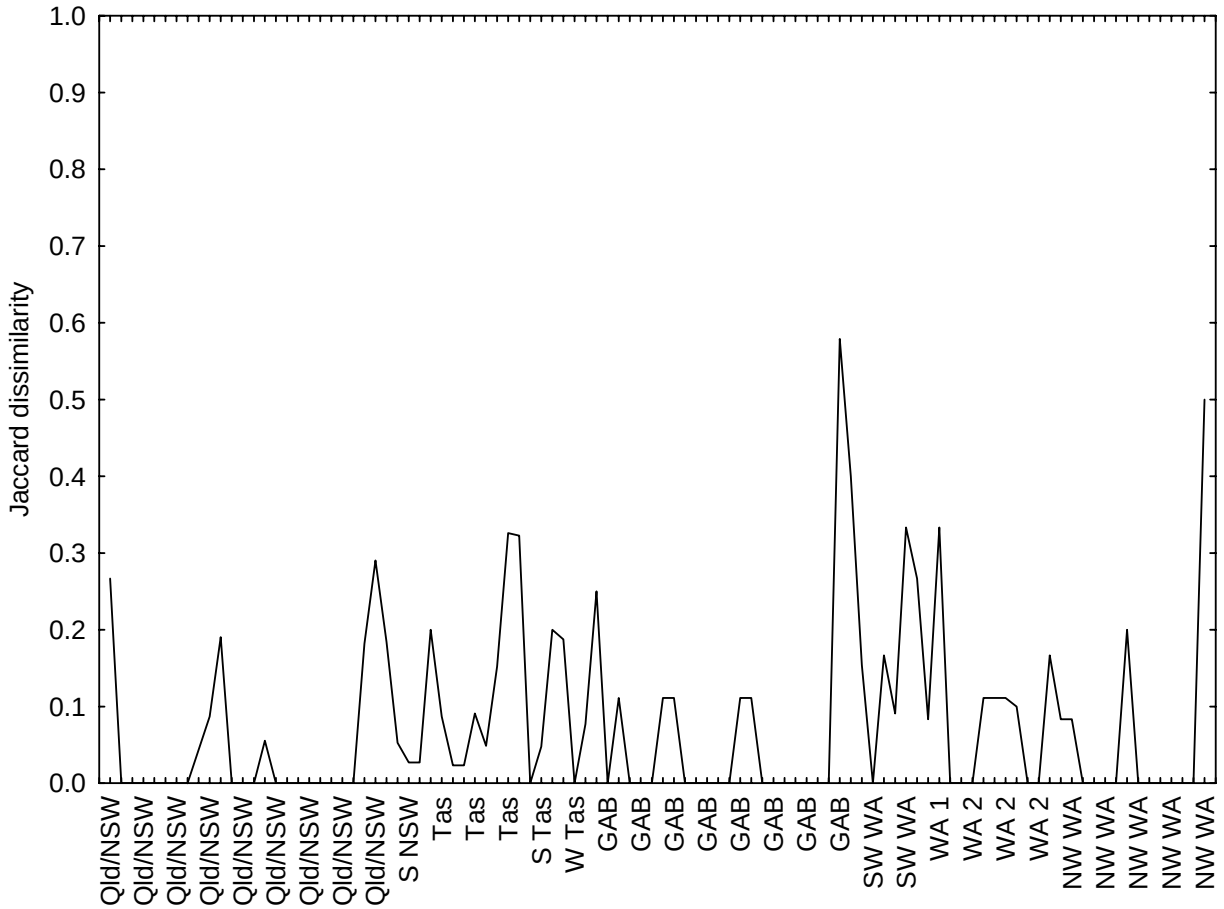


Figure 4.6c. Jaccard dissimilarity measurements between adjacent cells from the ‘String’ 750-1500 m depth layer.

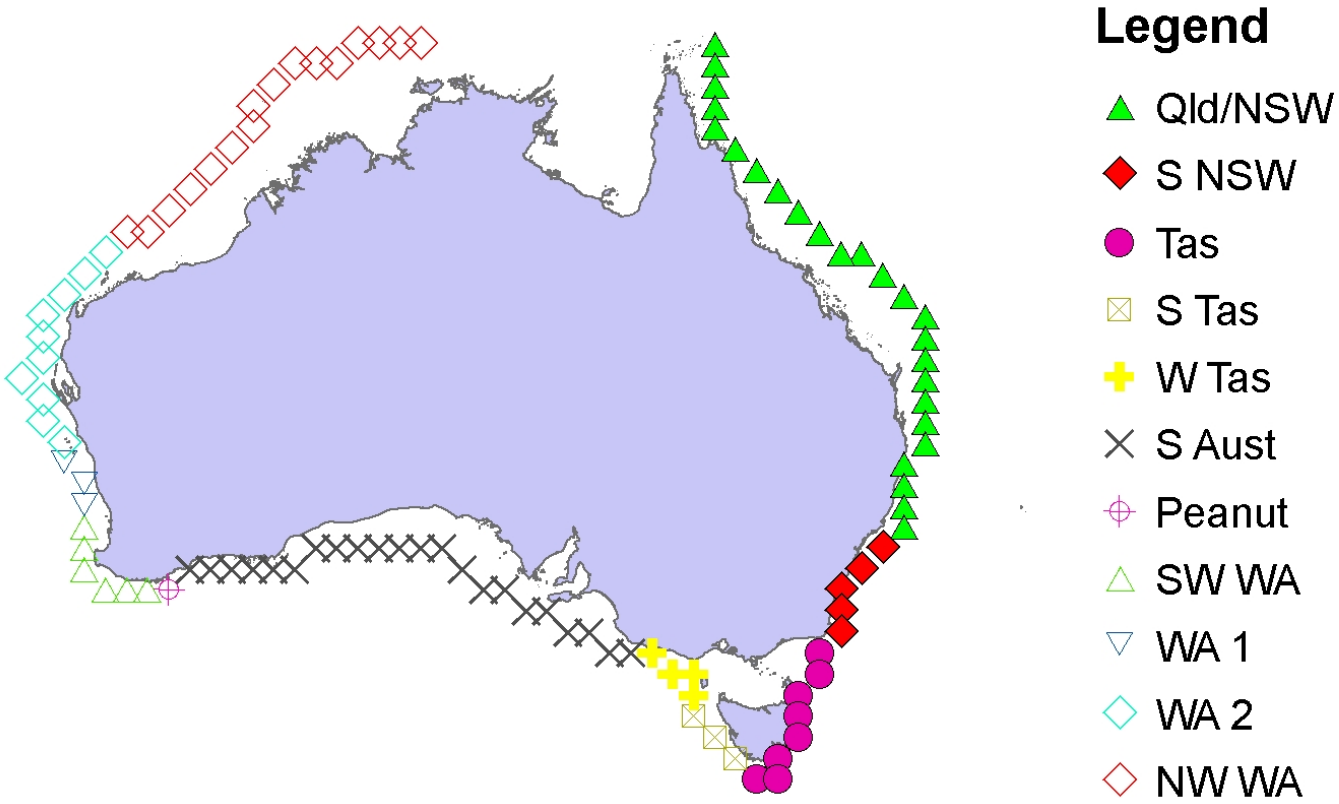


Figure 4.6d. Map of regions from the 'String' 750-1500 m layer.

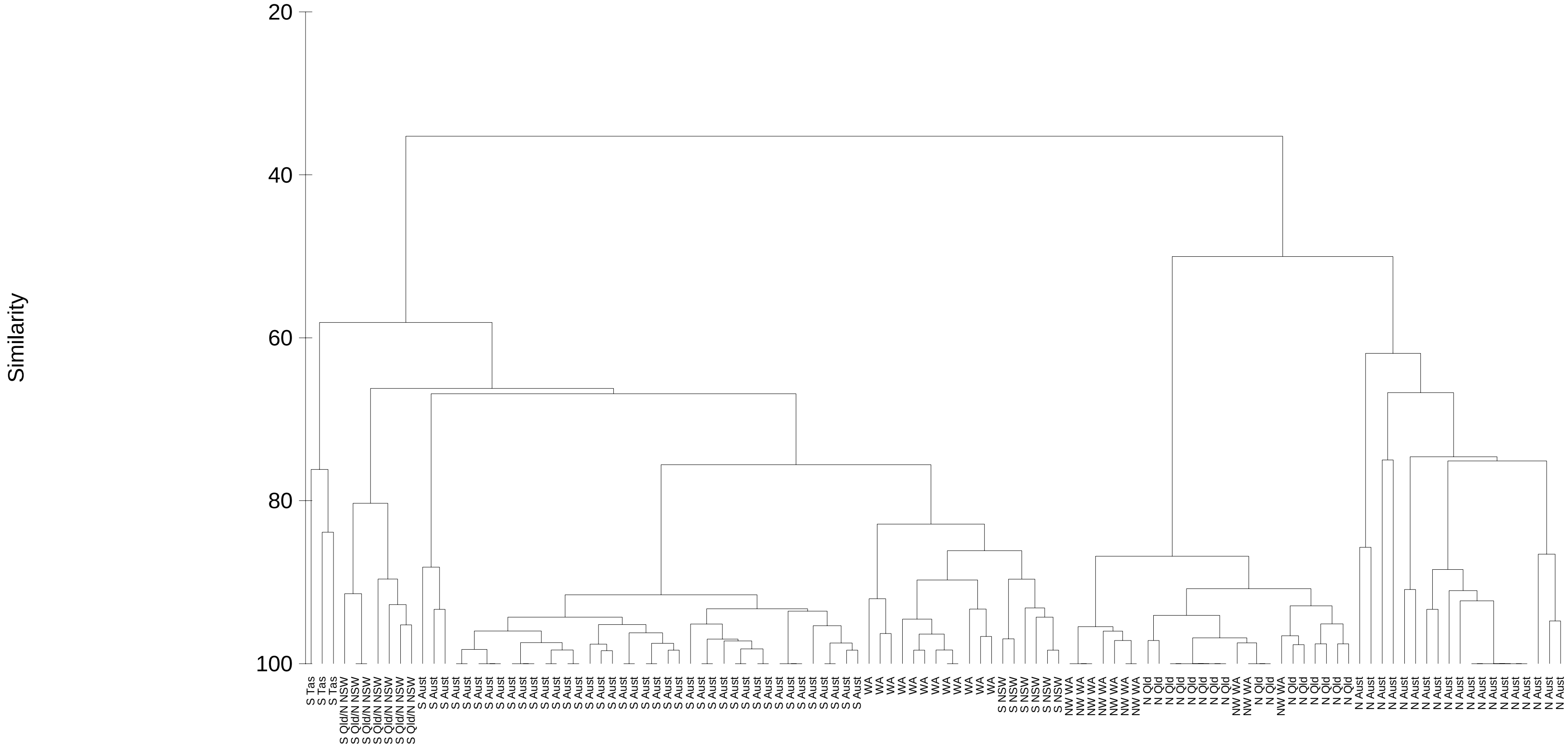


Figure 4.7a. Cluster diagram of cells from the Oceanographic Envelope analysis 50-300 m depth layer using presence/absence species occurrence data, the Bray Curtis similarity coefficient and Group Averaging. Branches at 80% similarity have been labeled according to their geographic region.

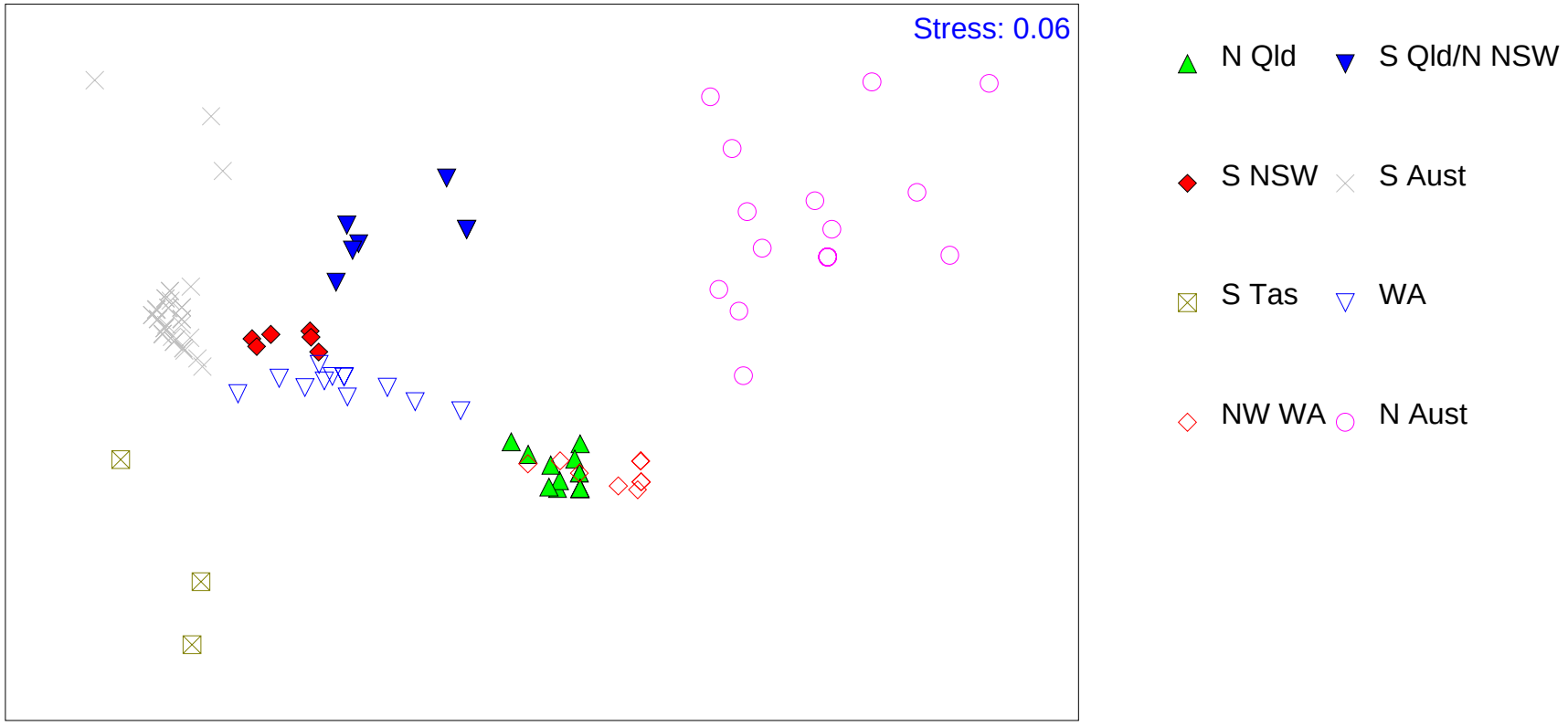


Figure 4.7b. MDS ordination of cells from the Oceanographic Envelope analysis 50-300 m depth layer, labeled by regional clusters.

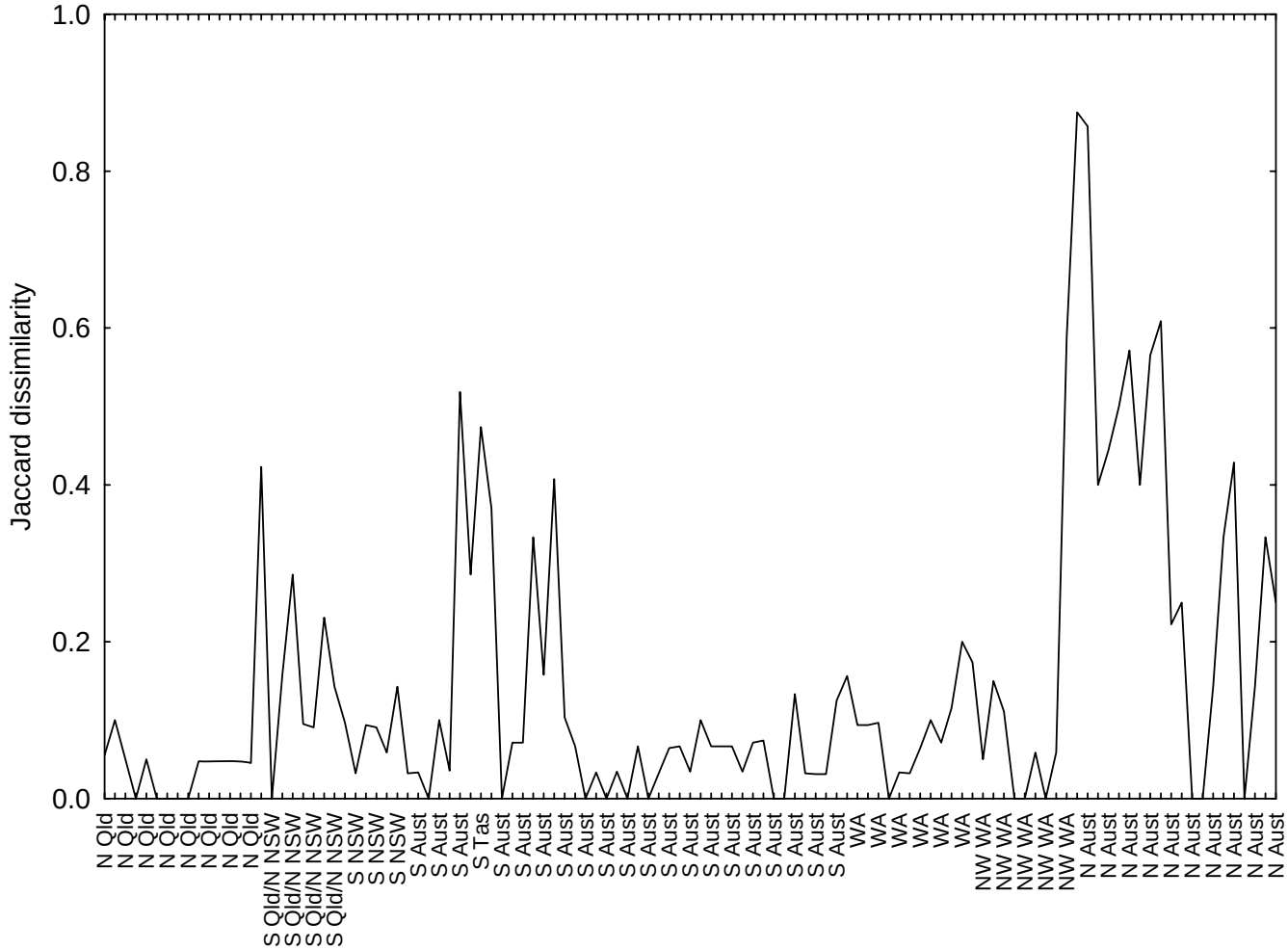


Figure 4.7c. Jaccard dissimilarity measurements between adjacent cells from the Oceanographic Envelope analysis 50-300 m depth layer.

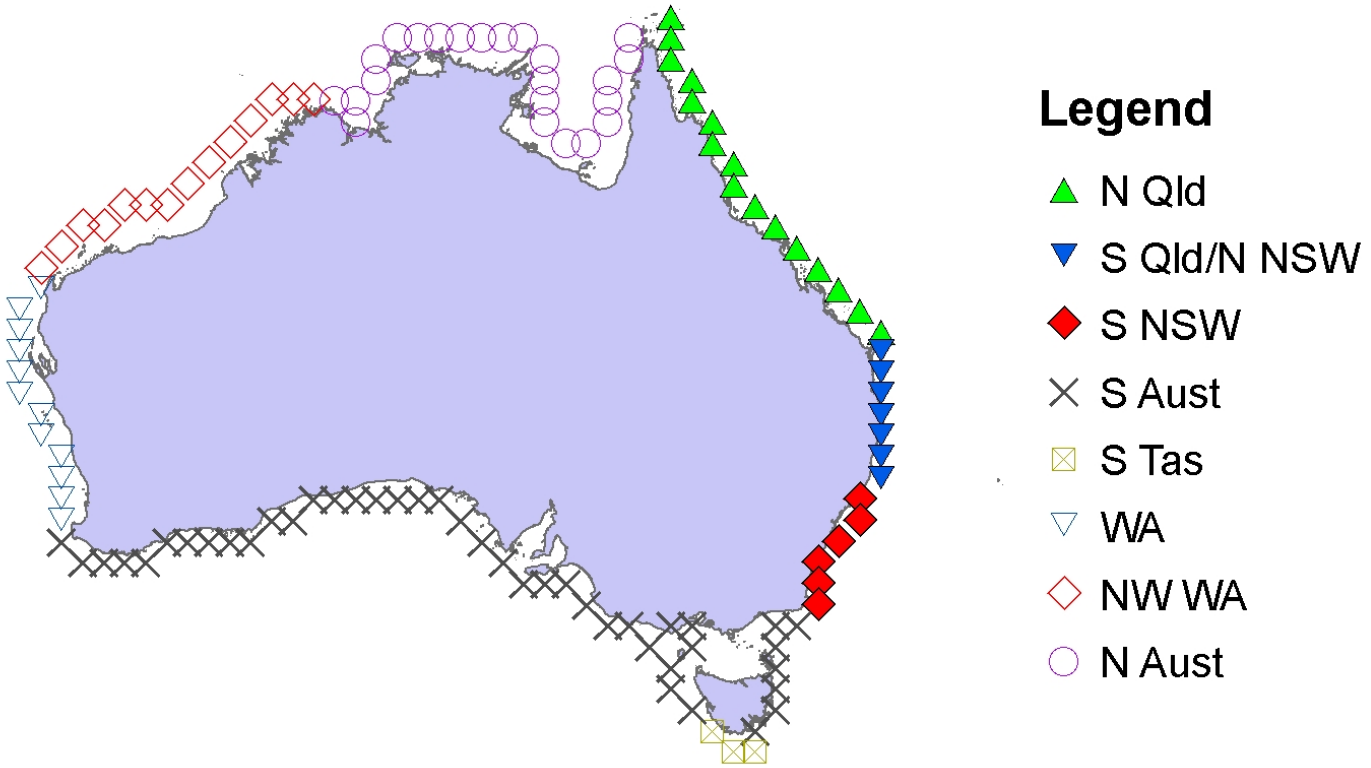


Figure 4.7d. Map of regions from the Oceanographic Envelope 50-300 m layer.

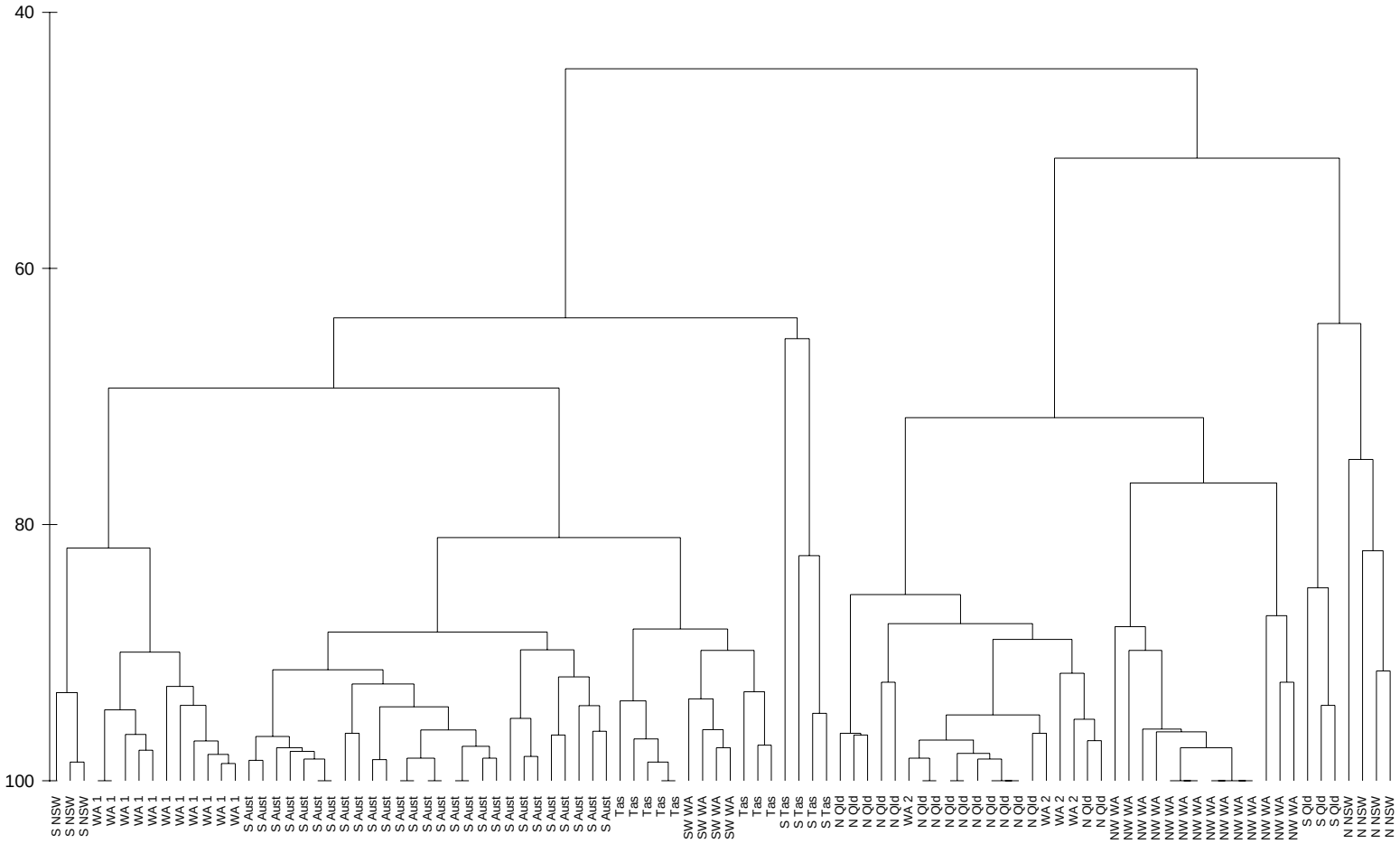


Figure 4.8a. Cluster diagram of cells from the Oceanographic Envelope analysis 300-750 m depth layer, labeled by region.

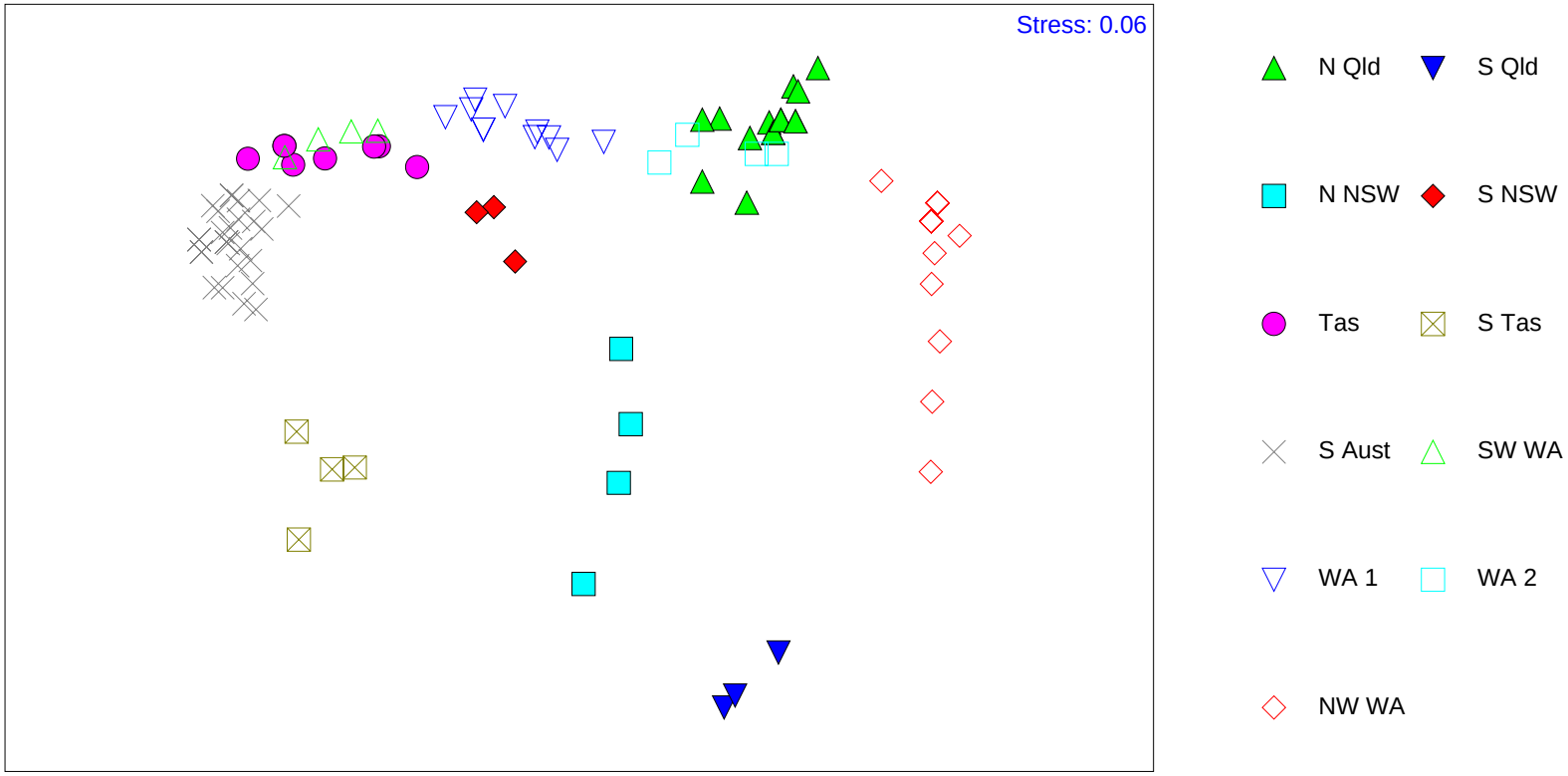


Figure 4.8b. MDS ordination of cells from the Oceanographic Envelope analysis 300-750 m depth layer, labeled by regional clusters.

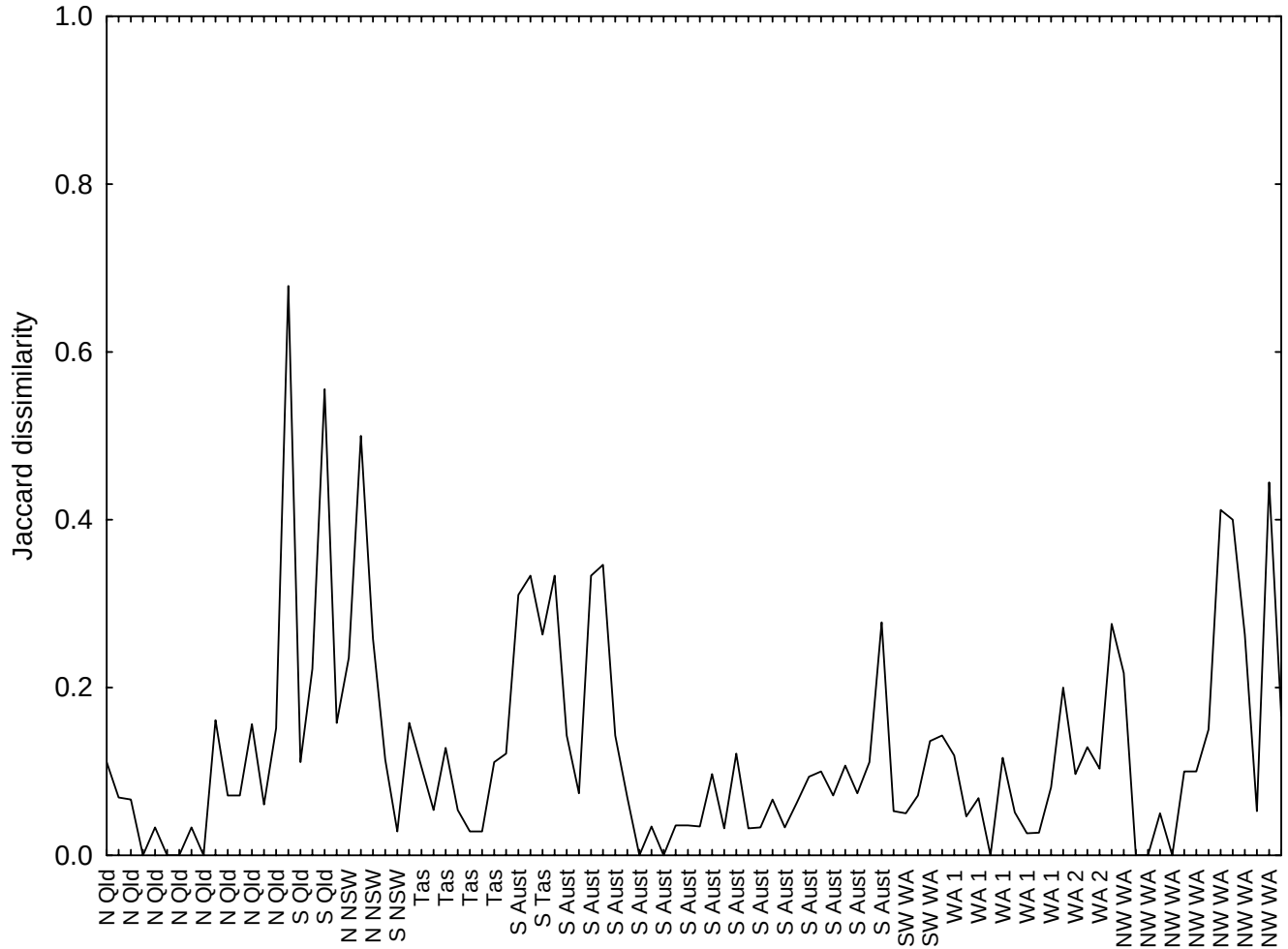


Figure 4.8c. Jaccard dissimilarity measurements between adjacent cells from the Oceanographic Envelope analysis 300-750 m depth layer.

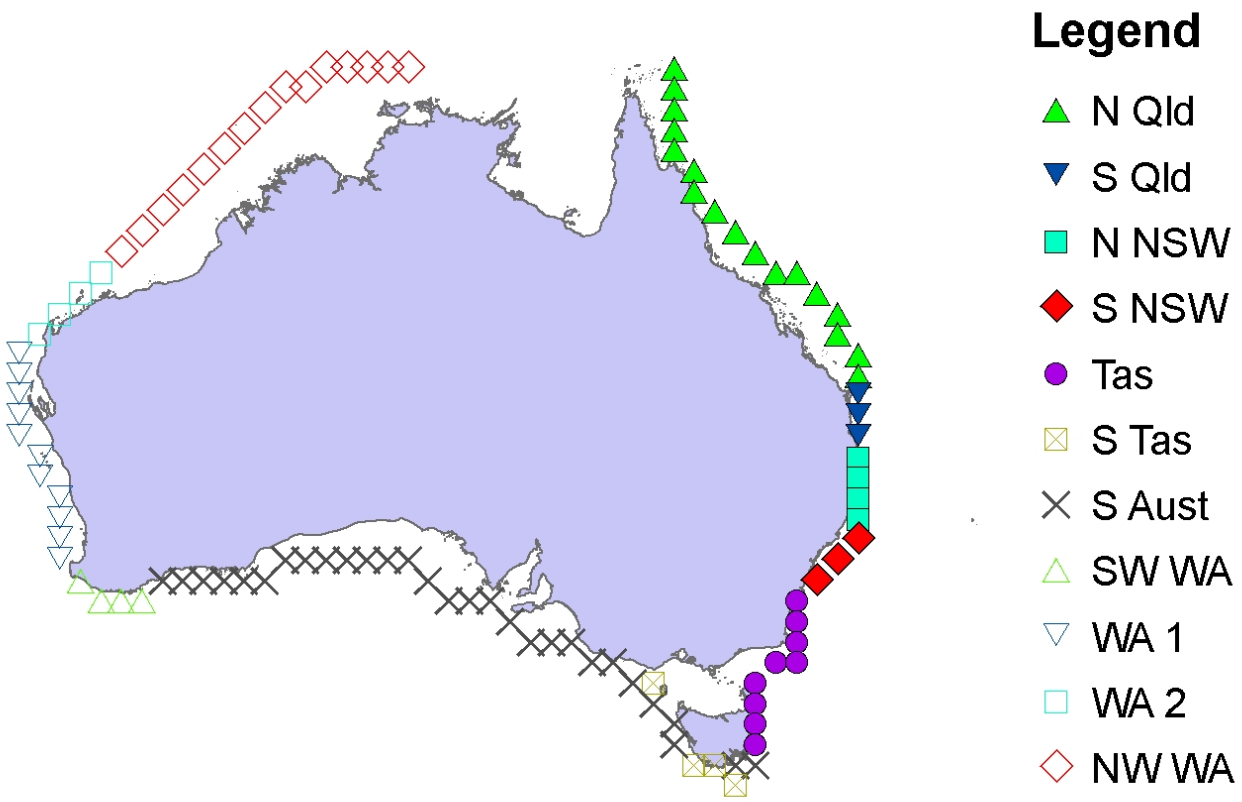


Figure 4.8d. Map of regions from the Oceanographic Envelope 300-750 m layer.

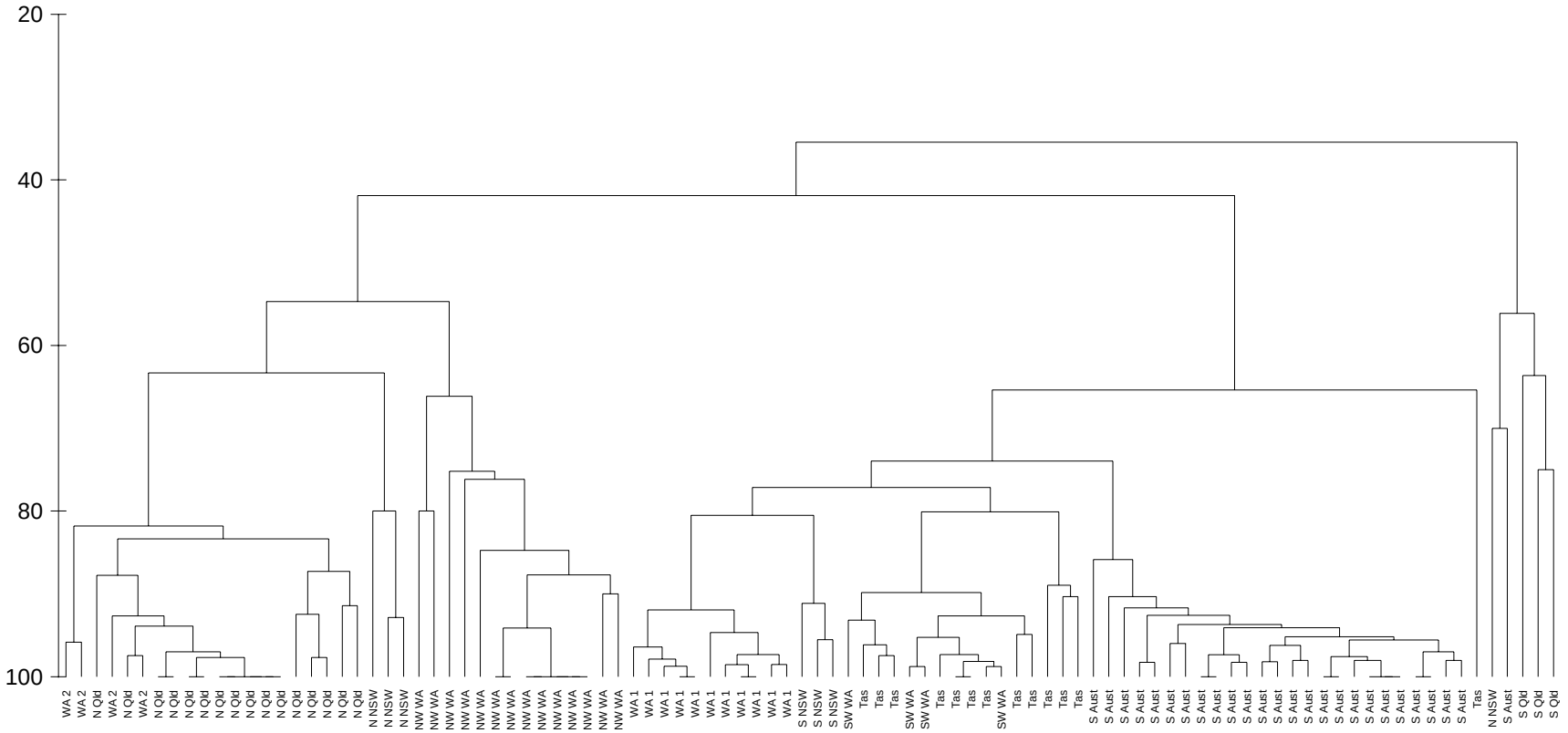


Figure 4.9a. Cluster diagram of cells from the Oceanographic Envelope analysis 750-1500 m depth layer, labeled by region.

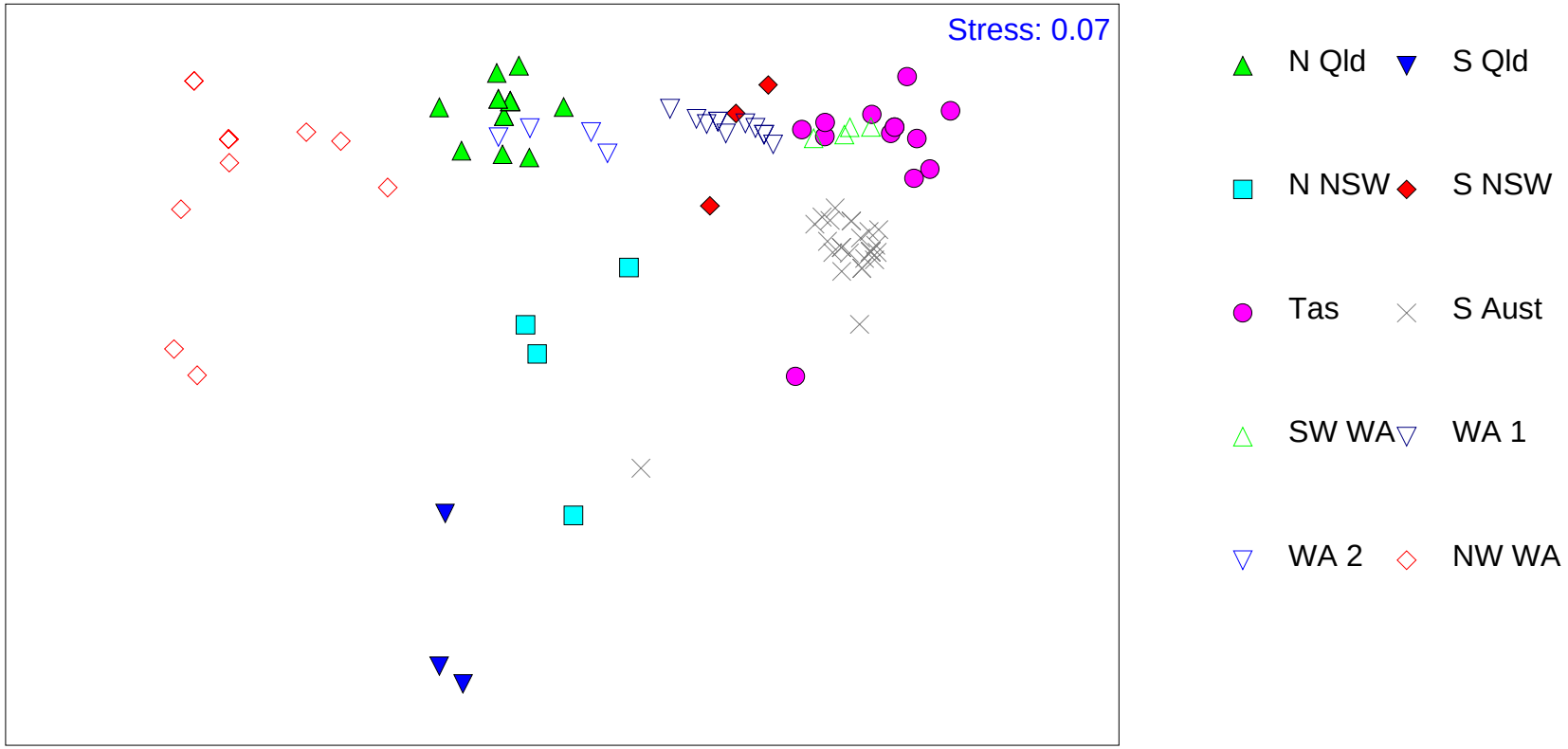


Figure 4.9b. MDS ordination of cells from the Oceanographic Envelope analysis 750-1500 m depth layer, labeled by regional clusters.

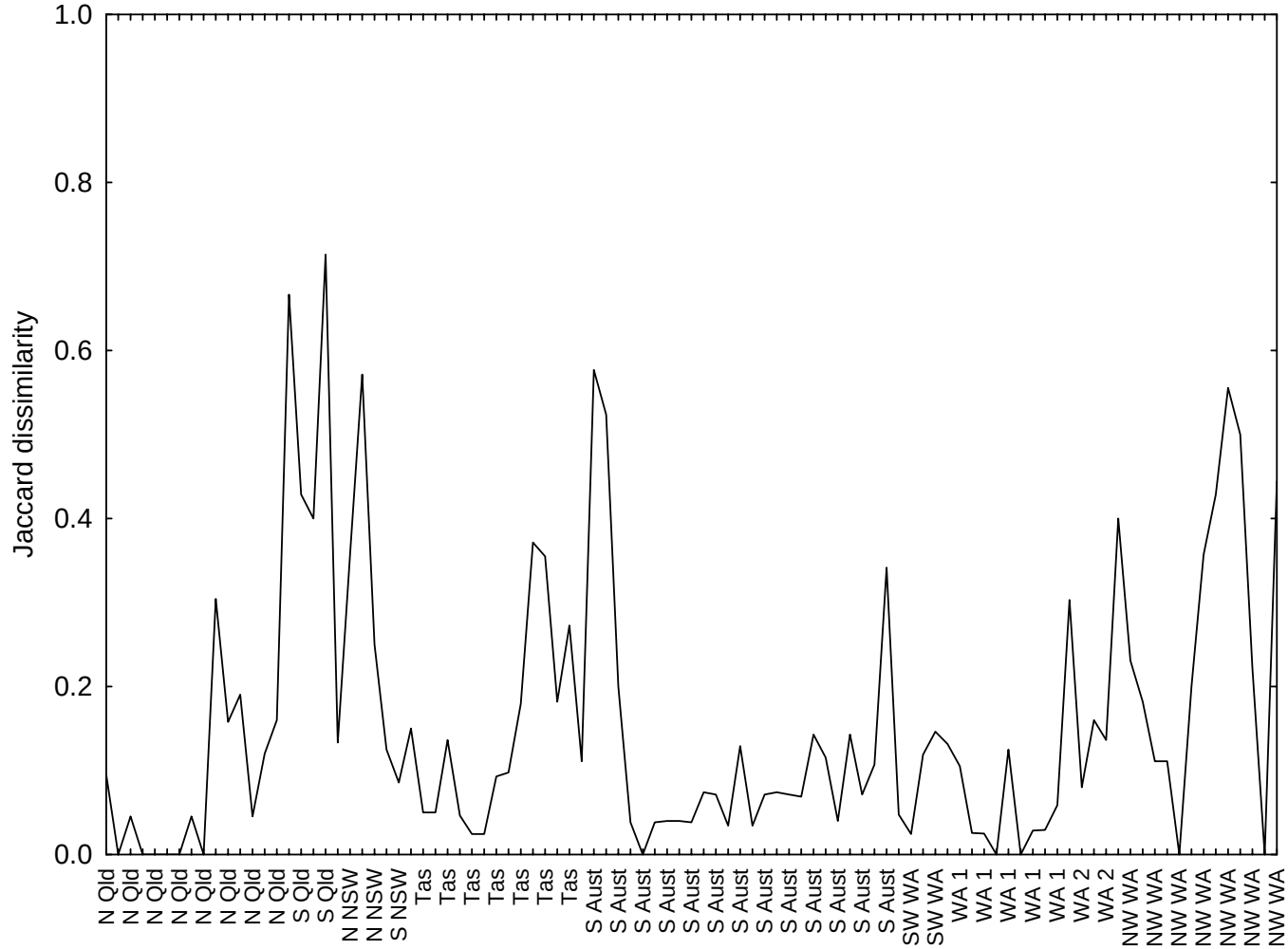


Figure 4.9c. Jaccard dissimilarity measurements between adjacent cells from the Oceanographic Envelope analysis 750-1500 m depth layer.

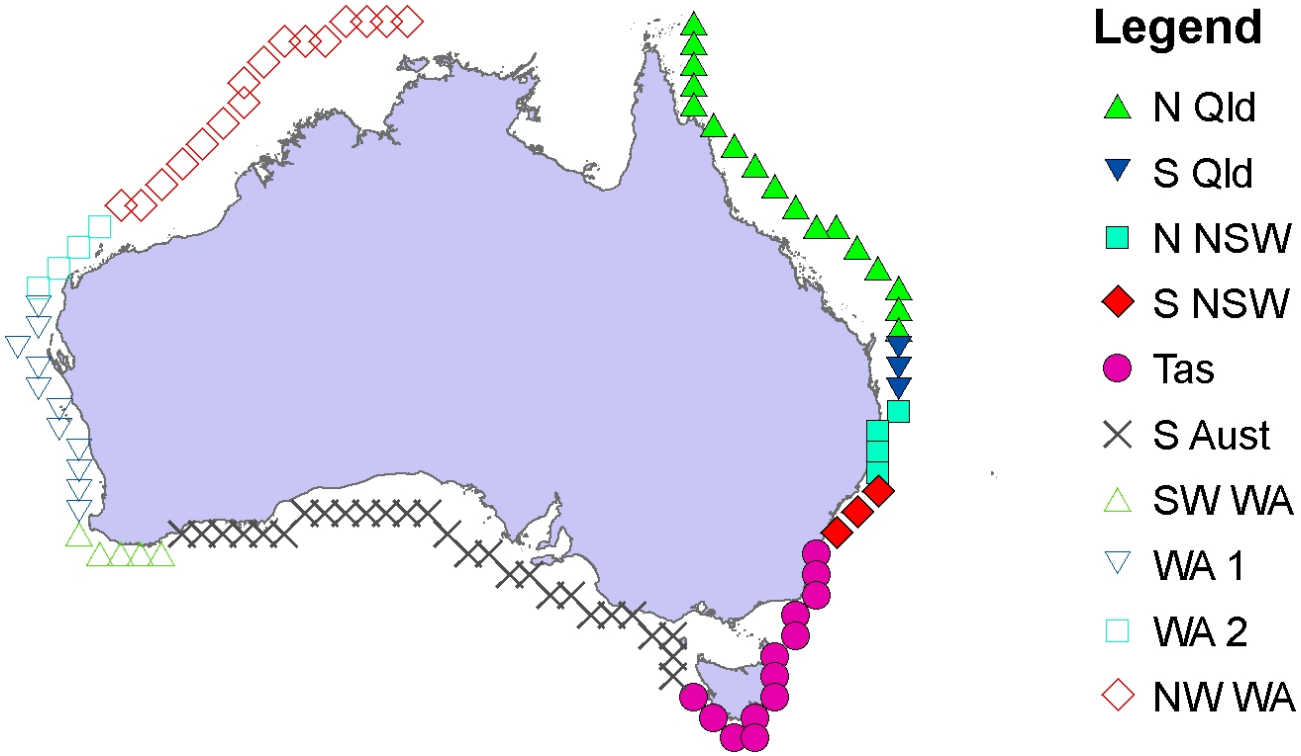


Figure 4.9d. Map of regions from the Oceanographic Envelope 750-1500 m layer.

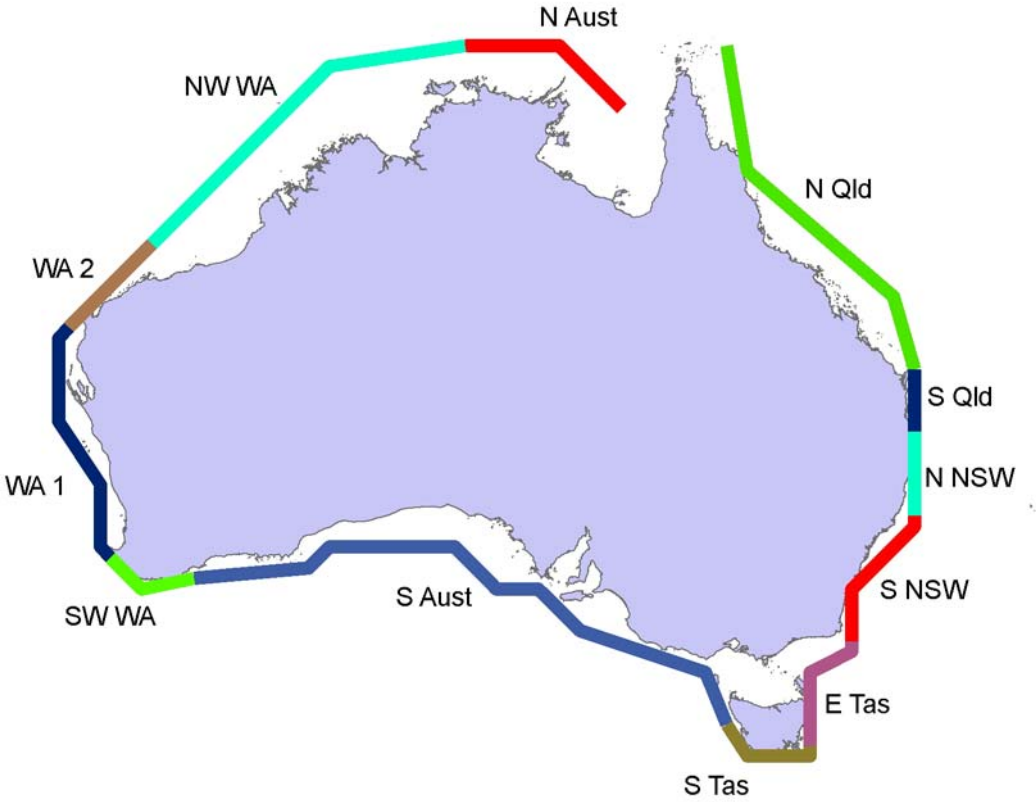


Figure 4.10. Australian marine bioregionalisation (50-1500 m) derived from modelled distribution of ophiuroids. The province 'N Aust' is restricted to outer shelf habitats only.

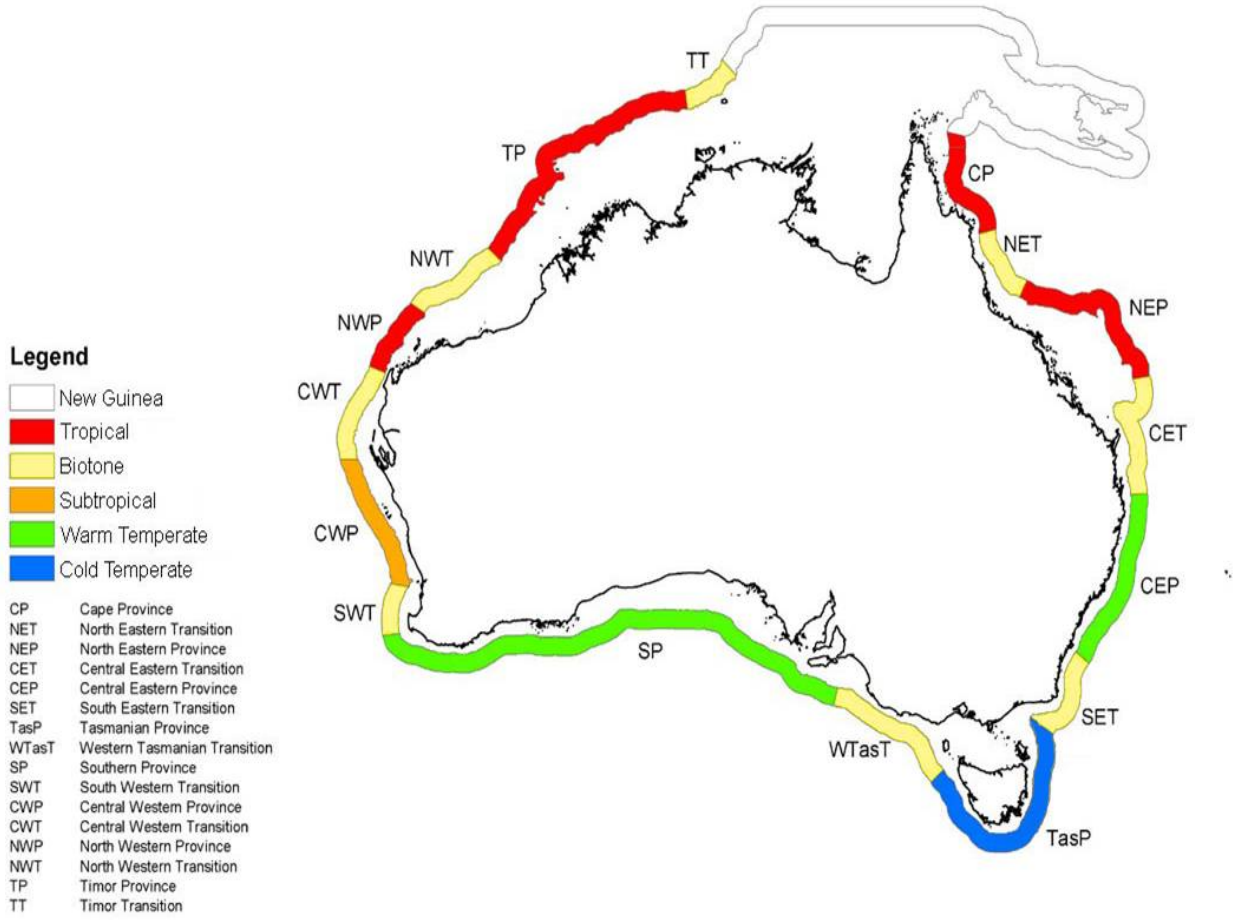


Figure 4.11. Australian marine fish bioregionalisation, reprinted from Last *el al.* (2005).

8. Appendices

Appendix 1. Number of cells with records of ophiuroids for each analysis

Genus	Species	Oceanographic envelope				String			
		50-300 m	300-750 m	750-1500 m	Modelled Range	50-300 m	300-750 m	750-1500 m	Modelled Range
Amphiophiura	*insolita*		5		36		5		35
Amphiophiura	*turgida*	5	6		42	5	6		15
Amphiophiura	*urbana*	23	23		76	23	23		86
Amphioplus	*depressa*	14			48	14			60
Amphioplus	*jarum*		9	10	19		9	10	9
Amphioplus	*ochroleuca*					12			67
Amphioplus	sp MoV 2722							1	1
Amphipholis	*squamata*	79	46		111	79	46		113
Amphiura	*dolia*					8			12
Amphiura	*duncani*					6			44
Amphiura	*elandiformis*					11			24
Amphiura	*magellanica*		8	7	51		8	7	21
Amphiura	sp MoV 3579		8	9	44		8	9	19
Amphiura	sp MoV 4531		5	5	6		5	5	5
Asteronyx	*loveni*	23	20	22	84	23	20	22	75
Asteroporpa	*australiensis*	10			12	10			36
Astroboa	*nigrofurcata*					4			18
Astroboa	*nuda*					8			32
Astrobrachion	*adhaerens*					18			55
Astrobrachion	*constrictum*					7			16

Astrochalcis	*tuberculosus*					11			31
Astrocladus	*exiguus*					6			25
Astrodia	*tenuispina*							3	7
Astroglymna	*sculptum*					6			18
Astrosierra	*amblyconus*					13			11
Astrosierra	*densus*					5	6		8
Astrothorax	*waitei*	11	11	11	98	11	11	11	36
Astrothrombus	*rugosus*					8	8	8	22
Bathypectinura	*heros*		18	18	87		18	18	60
Clarkcoma	*bollonsi B*	23			65	23			36
Conocladus	*australis*	43			65	43			57
Dictenophiura	*ctenophora*	9			29	9			10
Dictenophiura	*stellata*					11			44
Euryale	*asperum*					45			85
Gorgonocephalus	*dolichodactylus*	8	8	8	59	8	8	8	39
Haplophiura	*gymnopora*					4			7
Macrophiothrix	*megapoma*					23			65
Ophiacantha	*alternata*	43			58	42			57
Ophiacantha	*brachygnatha*		16	16	48		16	16	44
Ophiacantha	*clavigera*	18			49	18			29
Ophiacantha	*dallasi*					7			44
Ophiacantha	*densispina*			2	1	2		2	1
Ophiacantha	*fidelis*	10	9		40	9	8		21
Ophiacantha	*heterotyla*	15			41	15			20
Ophiacantha	*indica*					10			52
Ophiacantha	*pentagona*		9	7	59		9	7	15
Ophiacantha	*rosea*		7	7	55		7	7	12
Ophiacantha	sp MoV 2731							1	1
Ophiacantha	sp MoV 2780			2	14			2	11
Ophiacantha	sp MoV 4532							1	1
Ophiacantha	sp MoV 4533							6	9

Ophiacantha	sp MoV 4537							3	7
Ophiacantha	*spectabilis*			3	10			3	5
Ophiacantha	*vepratica*			1	28			1	1
Ophiacantha	*vivipara*			1	11			1	1
Ophiacantha	*yaldwyni*		10	10	32		10	10	15
Ophiactis	*abyssicola*		13	15	76		13	15	29
Ophiactis	*definita*		4	4	18		4	4	10
Ophiactis	*hirta*	13	13	14	56	13	13	14	44
Ophiactis	*macrolepidota*	20			54	20			67
Ophiactis	*profundi*	21	21	20	70	21	21	20	79
Ophiactis	*resiliens*	48			70	47			67
Ophiactis	*savignyi*					49			79
Ophiactis	*tricolor*					20			49
Ophiarachna	*megacantha*					5			11
Ophiarachnella	*infernalis*	20			36	20			44
Ophiernus	*adspersus*						4	4	29
Ophiernus	*vallincola*			10	81			10	35
Ophiobyrsa	*rudis*	11			39	12			35
Ophiocamax	*applicatus*			3	12			3	7
Ophiocamax	sp MoV 4540							2	1
Ophiocamax	*vitrea*	18	19		49	18	19		55
Ophiocentrus	*pilosa*	31			66	31			47
Ophiochasma	*stellata*					35			52
Ophiochiton	*lentus*	4	4	4	56	4	4	4	4
Ophiocnemis	*marmorata*					8			42
Ophiocreas	*oedipus*			10	31			10	33
Ophiocreas	*sibogae*			15	79			15	74
Ophiocrossota	*multispina*					22			54
Ophiocten	*hastatum*			7	27			7	11
Ophiodaphne	*formatus*					4			31
Ophiogymna	*elegans*					8			45

Ophiogymna	*pellicula*	10	8		30	10	8		16
Ophiogymna	*pulchella*					8			19
Ophioleuce	*seminudum*	8	8		57	8	8		45
Ophiolimna	*perfida*		1	2	29		1	2	9
Ophiolimna	*bairdi*			8	17			8	12
Ophiomastus	*tegulitius*		11	11	45		11	11	46
Ophiomaza	*cacaotica*					38			64
Ophiomisidium	*flabellum*					8	7		19
Ophiomisidium	*irene*			3	11			3	7
Ophiomitrella	*conferta*			7	45			7	9
Ophiomitrella	sp MoV 2732			2	5			2	3
Ophiomusium	*anisacanthum*	9	9		24	9	9		30
Ophiomusium	*australe*	10	10		27	10	10		36
Ophiomusium	*facundum*		15	14	32		15	14	28
Ophiomusium	*incertum*	10	10		35	10	10		22
Ophiomusium	*lymani*			19	82			19	74
Ophiomusium	*simplex*	7			42	7			47
Ophiomyces	*delata*	7	8	5	73	7	8	5	66
Ophiomyxa	*australis*	72	48		111	72	48		113
Ophiomyxa	sp. nov.		8		18		8		11
Ophionereis	*schayeri*	59			64	58			63
Ophionereis	*semoni*					15			87
Ophionereis	*terba*	16			50	16			21
Ophiopallas	*valens*	1	1		15	1	1		9
Ophiopeza	*cylindrica*	25			57	25			55
Ophiopeza	*spinosa*					17			54
Ophiophthalmus	*relictus*		15	17	80		15	17	71
Ophioplax	*lamellosa*		6	6	55		6	6	17
Ophioplinthaca	*plicata*		8	8	37		8	8	13
Ophioplinthaca	*pulchra*		8		62		7		14
Ophioplinthaca	*rudis*		23	24	63		23	24	61

Ophiopsammus	*angusta*	12	12		21	12	12		16
Ophiopsammus	*assimilis*	23	17		60	23	17		55
Ophiopsammus	*yoldii*					16			48
Ophiopteron	*elegans*					13			50
Ophiosphalma	*elegans*						7		15
Ophiothamnus	*biocal*		6	6	27		6	6	11
Ophiothela	*danae*					25			70
Ophiothrix	*aristulata*	32	30		94	32	30		52
Ophiothrix	*caespitosa*	65			66	65			66
Ophiothrix	*ciliaris*	51			70	51			70
Ophiothrix	*exigua*					15			53
Ophiothrix	*lineocaerulea*					12			29
Ophiothrix	*martensi*					25			49
Ophiothrix	*melanosticta*					6			37
Ophiothrix	*proteus*					5			45
Ophiothrix	*purpurea*					16			53
Ophiothrix	*smaragdina*					11			31
Ophiothrix	*spongicola*					35			60
Ophiothrix	*striolata*					10			32
Ophiothrix	*vigelandi*					5			35
Ophiotreta	*larissae*		8		23		8		15
Ophiotreta	*matura*		13	12	37		13	12	39
Ophiotreta	*stimulea*		12	10	54		12	10	47
Ophiozonella	*bispinosa*		8	8	55		8	8	28
Ophiozonella	*media*		4	5	30		4	5	17
Ophiura	*flagellata*		13	13	50		13	13	38
Ophiura	*irrorata*			13	58			13	47
Ophiura	*jejuna*			15	51			15	31
Ophiura	*kinbergi*	44			109	44			113
Ophiura	*micracantha*		7		51		6		43
Ophiura	*ooplax*	28	26	26	102	28	26	26	101

Ophiura	*palliata*		16	16	48		16	16	21
Ophiura	sp MoV 2728			1	1			1	1
Ophiura	*trefoli* sp nov.		10	10	44		10	10	20
Ophiurid	sp MoV 2733							3	6
Ophiurolepis	*accomodata*							7	12
Ophiurothamnus	*clausa*			10	72			10	69
Trichaster	*flagellifer*					6			17
Total number of species used for each analysis		53	43	54	90	64	90	59	151

Appendix 2. Histogram of the number of species in distributional range classes, where range is calculated as the number of cells along a ‘string’ around the Australian continent (see Figure 4.10) that each species is predicted to occupy. Note that included species were restricted to those with more than five distributional records for the ‘String’ model and ten for the Oceanographic envelope model, thus removing many short range species from the analysis.