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Extended abstract

Comparison of independently derived benthic invertebrate and demersal fish ecoregionalisations for the Kerguelen Plateau

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Ecoregionalisation is a process that aims to identify areas with distinct biological content and associated environmental conditions. It improves on many traditional approaches to regionalisation by explicitly incorporating biological data into classifications. Ecoregionalisations are useful for improving our ecological understanding of marine ecosystems and for informing spatial management. This includes providing information to aid in defining and prioritising areas for conservation, evaluating current spatial management arrangements, targeting monitoring efforts and managing human activities (e.g. Grant et al., 2006; Douglass et al., 2014). The Kerguelen Plateau is a highly productive region of the southern Indian Ocean that supports lucrative demersal fisheries (Duhamel and Welsford, 2011). It is subject to spatial management in the form of marine protected areas (MPAs) with varying levels of protection (Commonwealth of Australia, 2014; Koubbi et al., 2016). Recently two ecoregionalisations have been independently generated for the northern Kerguelen Plateau; one for benthic invertebrates (Martin et al., 2018) and another for demersal fish (Hill et al., 2017). Here we conduct a preliminary analysis examining the congruence between these ecoregionalisations that represent different components of the demersal ecosystem.

The study region is the French exclusive economic zone (EEZ) on the Northern Kerguelen Plateau ranging from 100 to 1 000 m depth (Figure 1). The two ecoregionalisations examined here use different methodologies that are described in detail in Martin et al. (2018) for benthic invertebrates and in Hill et al. (2017) for demersal fish.

Briefly, presence–absence data for benthic invertebrates was collated from 209 demersal trawls conducted as part of the second Poissons Kerguelen (POKER 2) survey in 2010 (Eléaume et al., 2011). Climatologies (2005–2012) of 15 sea-surface and seafloor conditions likely to affect the distribution of benthic invertebrates, as well as seafloor depth and associated derivatives, were collated at a 0.1-degree resolution from references described in Martin et al. (2018). Six variables that were not highly inter-correlated (spearman's correlation <0.66) were considered in analyses. Invertebrate ecoregions were discriminated using generalised dissimilarity modelling (GDM) (Ferrier et al., 2007) followed by cluster analysis. GDM models the ecological dissimilarity between pairs of sites as a function of the environmental difference between them using a generalised linear model (GLM). This can be conceptualised as modelling the turnover in species' composition in environmental space which can then be predicted into geographical space. The pairwise dissimilarities across the northern plateau predicted by GDM were then clustered using partitioning around medioids (PAM) (Kaufman and Rousseeuw, 1987) and the optimal number of groups, representing ecoregions, determined using the maximum silhouette width (Rousseeuw, 1987). The biological characteristics of each ecoregion was described using indicators (IndVal) (Dufrêne and Legendre, 1997). Here we consider two of the ecoregionalisations presented in Martin et al. (2018) these are: (i) all 111 invertebrate taxa recorded in demersal trawls (all invertebrates) and (ii) the 23 vulnerable marine ecosystem taxa (VME invertebrates) (CCAMLR, 2008). These ecoregionalisations were chosen because (i) is most equivalent to the demersal

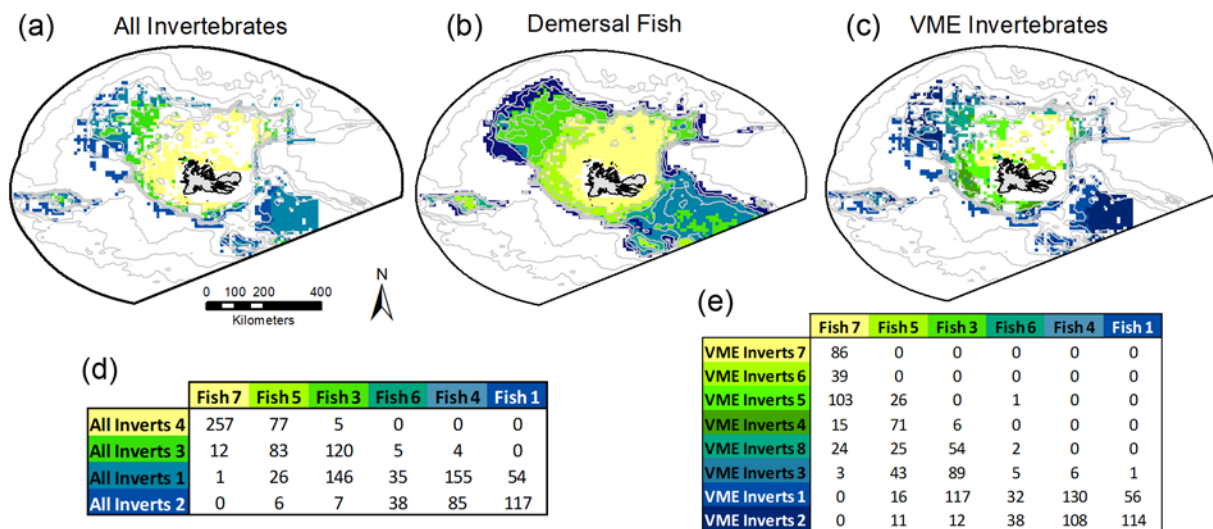


Figure 1: Maps showing the predicted spatial distribution of ecoregions for: (a) all invertebrate taxa, (b) demersal fish, and (c) vulnerable marine ecosystem invertebrates. The black outline indicates the extent of the French EEZ, the grey land mass is the Kerguelen Islands and the grey lines are contour intervals. Contour intervals are 200 m within the depth range of the ecoregionalisations (100–1 000 m) and 1 000 m deeper than 1 000 m. Different colours represent different ecoregions and have been colour-coded within an ecoregionalisation to broadly correspond with depth ranging from shallow (yellow) to deep (dark blue). Contingency tables show the correspondence between (d) the ecoregions of the invertebrate classification that used all taxa and demersal fish ecoregions and (e) the invertebrate ecoregionalisation that used only VME invertebrates and demersal fish. Colours correspond to maps (a) to (c).

fish ecoregionalisation, which includes all fish taxa, and (ii) VME invertebrates are of particular conservation significance. The overall importance of environmental predictors to each regionalisation was inferred from the modelled GDM spline functions (not shown here), where the maximum height of the function for each variable is indicative of their relative importance.

The demersal fish ecoregionalisation presented here is the French EEZ component of an ecoregionalisation for the entire northern plateau (French and Australian EEZs). The ecoregions are shared between the French and Australian EEZs. Details of the data and methodology used are in Hill et al. (2017). Briefly, trawl data on 21 taxa from the 2006, 2010 and 2013 POKER surveys conducted in the French EEZ (Duhamel and Hauteceur, 2009) were combined with random stratified trawl Surveys (RSTS) that were conducted in the same years in the Australian EEZ. This resulted in a total of 1 197 trawl samples from between 200 and 1 200 m depth, with 592 from the French EEZ. Climatologies of 15 environmental variables representing sea-surface and seafloor conditions likely to affect demersal fish communities were obtained from various sources (described in Table 1 in Hill et al. 2017) and the nine variables that were not highly inter-correlated (Pearson's $R < |0.7|$) were considered in analyses.

The demersal fish ecoregionalisation was generated using an analytical method called regions of common profile (RCP) (Foster et al., 2013). RCP is a statistical method based on a multivariate GLMs that

simultaneously groups sites with a similar composition of species and describes patterns of variation in these assemblages using environmental data (Foster et al., 2017). It is a one-step ecoregionalisation method that allows direct interpretation of the environmental characteristics of, and species contained within, ecoregions via model coefficients. It also allows the direct prediction of RCPs into new areas where only environmental predictors exist with appropriate estimates of uncertainty. The occurrences and absences of demersal fish were modelled using RCP models with a Bernoulli sampling distribution and logit link function. The combination of year, season and gear type of each survey was used as the factor within the model that can account for differential catchability of species due to sampling artefacts (see Hill et al. (2017) for more details of the modelling process). The Bayesian information criteria (BIC) was used to choose both the optimal number of ecoregions and select environmental predictors in a forward, step-wise procedure. The 'best' model determined from the forward selection process was used to predict the probability (and associated uncertainty) of each ecoregion occurring across the plateau based on the selected environmental predictors. For the purpose of this paper, probabilistic predictions were converted to hard classes by assigning the most likely ecoregion for each pixel. The importance of environmental predictors was assessed using the change in BIC when included in models (Hill et al., 2017).

The two invertebrate ecoregionalisations were compared with the demersal fish ecoregionalisation by:

(i) mapping and visually inspecting predictions from each ecoregionalisation; and (ii) generating a contingency table that cross-tabulates the number of prediction cells classified as each class for each ecoregionalisation. This tabulation only includes cells that were classified for both of the ecoregionalisations being compared. Larger values indicate a congruence between two classes of the compared ecoregionalisations.

Four ecoregions were identified using all invertebrate taxa, eight ecoregions using VME invertebrates and seven ecoregions using demersal fish (Figure 1). However, the demersal fish ecoregion 2 was sparsely represented in the French EEZ and there was no overlap with cells classified in the invertebrate ecoregionalisation and so it is not considered further. Differences in the spatial coverage of the invertebrate and fish ecoregionalisations can be attributed to the use of environmental datasets with different underlying coverage.

Some congruencies were observed in the spatial patterns of the invertebrate and demersal fish ecoregionalisations that were conducted using different methodologies and environmental data (Figure 1). All ecoregionalisations showed a general depth structuring, which resulted in reasonable congruency between the all invertebrate taxa ecoregionalisation and demersal fish ecoregionalisation (Figures 1a, 1b, 1d). Invertebrate ecoregion 4 corresponded with the two shallowest fish ecoregions. Invertebrate ecoregion 2 mostly corresponded with the deepest fish ecoregion, while cells classified as invertebrate ecoregions 1 and 3 were spread amongst the intermediate depth fish ecoregions. Whilst depth structuring was evident in the VME invertebrate ecoregionalisation, there were less congruencies with the demersal fish ecoregionalisation (Figures 1b, 1c, 1e). The VME invertebrates ecoregionalisation discriminated more ecoregions in shallow areas (ecoregions 4, 5, 6, 7) than the fish ecoregionalisation (ecoregions 5, 7). Conversely, the fish ecoregionalisation discriminated more ecoregions in intermediate to deep waters than the VME ecoregionalisation (Figure 1e).

Depth ranked as the most influential variable in all ecoregionalisations (Table 1). For both invertebrate regionalisations, there appears to be a threshold around 250 m depth separating shallow from deep assemblages (Martin et al., 2018). Furthermore, while it appears to have no strong influence within the shallower assemblages, depth remains a structuring factor deeper than 250 m with a continuous effect on the biological dissimilarity. For demersal fish, the depth structuring appears more continuous across the entire region with two shallow ecoregions identified (<300 m), three intermediate depth ecoregions (300–600 m) and one deep-water ecoregion (>600 m depth) (Hill et al., 2017).

Chlorophyll-*a* was also identified as an important environmental predictor for the VME invertebrate ecoregionalisation and fish ecoregionalisation. It was particularly important for distinguishing the shallow VME invertebrate with ecoregions 6 and 7 in areas of high Chl-*a* compared to ecoregions 4, 5 and 8. For demersal fish, Chl-*a* was influential for intermediate and shallow ecoregions. These patterns reflect the general west to east pattern in satellite-observed Chl-*a* concentrations as eastward-flowing waters become enriched with iron after contact with the plateau and stimulate primary production in Spring (Mongin et al., 2008). Increased surface production in combination with currents are instrumental in determining the export of organic carbon and therefore availability of food to benthic invertebrates (Jansen et al., 2017), and in particular sessile filter feeders such as most VME invertebrates. This may in turn may affect demersal fish directly through food availability or indirectly through habitat availability. Chl-*a* was also identified as relatively important for determining the community composition of all invertebrates. However, the greatest effect occurred between sites where there was virtually no Chl-*a* and those where there was a small amount of Chl-*a* with little effect at greater values of Chl-*a* and so it did not appear to have a large impact on distinguishing the ecoregions.

From 0 to 250 m depth, both the all invertebrate and VME taxa ecoregions are characterised by a relatively high diversity of sessile organisms and high number of indicator species (Martin et al., 2018). This may indicate a stronger structuring of assemblages and greater differentiation of the benthic habitats located in the shallower ecoregions. Within this bathome, the benthic assemblages are dominated by various taxa of sponges (Porifera), sea anemones (Actiniaria) and ascidians (Ascidacea). Furthermore, in the VME ecoregionalisation greater diversity exists in the eastern shallow ecoregions, corresponding with higher Chl-*a* concentrations and a high productivity zone.

For both invertebrate ecoregionalisations, patterns in indicator species at depths greater than 250 m were not as clear. For the VME ecoregionalisation, no distinguishing taxa were identified, while for the all invertebrate ecoregionalisation, only few indicator taxa were identified, mostly various echinoderm taxa (Martin et al., 2018). The number of indicators decreased as the depth of the ecoregion increased and may indicate that the deeper ecoregions are mainly dominated by ubiquitous species with no strong dissimilarity between the benthic habitats

For the demersal fish, some species were prevalent across the entire depth range (e.g. toothfish) while others were restricted to deeper (e.g. grenadiers) or shallower ecoregions (e.g. icefish) and some showed varying preferences across the ecoregions (Hill et al., 2017). In

Table 1: Relative importance of environmental predictors across the entire region for the three ecoregionalisations. Note that the sources of the environmental data are different for the invertebrate and fish ecoregionalisations and have different underlying spatial and temporal resolutions as well as spatial coverage. See Martin et al. (2018) and Hill et al. (2017) for full details of the environmental datasets used. NC – not considered in analyses, NS – not selected in analyses. *Mean Chlorophyll-*a* was calculated of the summer period for the invertebrate ecoregionalisations and over the entire year for the demersal fish ecoregionalisation.

Variable	All invertebrates	VME invertebrates	Demersal fish
Depth	1	1	1
Mean sea surface temperature	4	6	2
Mean Chl- <i>a</i> *	3	3	3
Sea surface salinity variation	1	2	NC
Sediments	5	4	NC
Slope	6	5	NS
Mean seafloor temperature	NC	NC	NS
Mean seafloor current	NC	NC	NS
Mean seafloor NO ₃	NC	NC	NS
Sea surface height variation	NC	NC	NS

general, however, many of the species in the shallow–intermediate ecoregions were endemic to the plateau (e.g. triangular and toad notothen), while many of the deeper species were cosmopolitan (e.g. grenadiers). It is important to note that while all invertebrate and fish taxa were identified to the lowest possible taxonomic resolution, the ecoregionalisations generated for invertebrates use data ranging from species for some well-studied groups (e.g. echinoderms) to broader categories for less studied or less easily identifiable groups (such as sponges) whereas the fish are identified to species or genus. This may have some impact on the patterns observed and modelled between the different ecoregionalisations.

In summary, our preliminary investigations found some congruencies in ecoregionalisation patterns of benthic invertebrates and demersal fish on the northern Kerguelen Plateau. Congruencies were stronger between the all invertebrates and demersal fish ecoregionalisations than for the demersal fish and VME invertebrates, which are a subset of primarily sessile, filter-feeding invertebrates. Both modelling approaches, based on different methods and different taxa, identified depth and the Chl-*a* as important environmental factors affecting the structure of species assemblages. For both fishes and benthic invertebrates, cosmopolitan species are mainly observed in the deeper ecoregions while taxa with a limited distribution are mainly observed in the shallower ecoregions, with a strong influence of Chl-*a* on the VME invertebrate distribution. Future work will focus on refining the ecoregionalisation comparison by using

the same environmental variables and methodology on three datasets: benthic invertebrates, demersal fish and combined benthic invertebrate and demersal data. It will also delve more deeply into the biological patterns and potential ecological connection between benthic invertebrates and demersal fish and explore the management implications of any similarities and differences between the three proposed ecoregionalisations.

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