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Ecoregionalisation and conservation of benthic communities in the French exclusive economic zone of Kerguelen

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Abstract

The deep-sea benthic ecosystems of the French Kerguelen exclusive economic zone remain poorly understood. To address benthic conservation issues, the authors recently contributed expert knowledge to guide the recent extension of the Marine Reserve of the 'Terres australes françaises'. In this new study, we propose a benthic ecoregionalisation of the northern Kerguelen Plateau based on a measurable and repeatable methodology that relies on the generalised dissimilarity modelling technique. Data of macro-epibenthic invertebrate species from the POKER 2 (2010) fish stock assessment survey have been used to compute the models. Our results allow us (i) to characterise and map benthic landscape units based on assemblages of marine invertebrates pooled by taxa and life-history traits, (ii) to highlight the environmental drivers of the spatial distribution of benthic assemblages, (iii) to assess the relevance of the CCAMLR's vulnerable marine ecosystems bioindicator taxa, and (iv) to assess the effectiveness of 'strictly protected areas' of the new Marine Reserve for the conservation of deep-sea benthic ecosystems.

Éco-régionalisation et conservation des communautés benthiques de la zone économique exclusive française des îles Kerguelen

Résumé

Les écosystèmes benthiques des eaux profondes de la zone économique exclusive française de Kerguelen demeurent mal connus. Pour la prise en compte des enjeux de conservation associés, la récente extension de la Réserve naturelle nationale des Terres australes françaises a majoritairement reposé sur une étude à dire d'expert à laquelle ont contribué les auteurs de cet article. Dans cette nouvelle étude, nous proposons une écorégionalisation benthique fondée sur une méthodologie rigoureuse et reproductible, utilisant une technique de modélisation (*generalised dissimilarity modelling*) appliquée aux données de macro-épibenthos issues de la campagne halieutique POKER 2 (2010). Nos résultats permettent notamment i) de caractériser des unités écopaysagères benthiques fondées sur des assemblages d'invertébrés marins rassemblés par taxons et par regroupements fonctionnels, ii) de mettre en évidence les facteurs environnementaux de la structuration spatiale de ces assemblages benthiques, iii) de confirmer la pertinence du choix des taxons retenus par la CCAMLR comme bio-indicateurs des écosystèmes marins vulnérables, iv) de fournir une évaluation de la pertinence des « Zones de Protection Renforcée » de la nouvelle réserve marine au regard de la conservation des écosystèmes benthiques profonds.

Introduction

The Kerguelen Plateau is divided into a northern part situated within a French exclusive economic zone (EEZ) and a southern part situated within an Australian EEZ. Benthic habitats are spatially structured, among other factors, by the proximity of the Polar Front (Améziane et al., 2011; Park and Vivier, 2011). Coastal ecosystems of the Kerguelen archipelago are relatively well-known, and a multi-year monitoring program allows permanent data acquisition (Féral and Poulin, 2011; Féral et al., 2016). In contrast, because of access limitation, benthic ecosystems deeper than 100 m remain under-studied and poorly sampled (Améziane et al., 2011; Hureau, 2011). The MD04 scientific expedition (1975, research vessel *Marion Dufresne*) (Arnaud, 1974) and the POissons de KERguelen (POKER) 2 fish stock assessment survey (2010, fishing vessel *Austral*) (Duhamel, 2011) contributed to provide comprehensive marine invertebrate datasets of these benthic ecosystems (Eléaume et al., 2011b). Studies using these datasets have mostly focused on systematics (e.g. Boury-Esnault and van Beveren, 1982; David and Mooi, 2000; Eléaume et al., 2011b; Monniot and Monniot, 1983). More recently, POKER 2 data has been used to better understand the spatial distribution of deep-sea benthic habitats using a generalist approach that combines biological and environmental data (Eléaume et al., 2011a). Understanding deep-sea ecosystem structure represents a major scientific issue for conservation and sustainable exploitation of commercial species in the French EEZ. In addition to global change (Smith et al., 2006), benthic ecosystems in the French EEZ of Kerguelen are impacted by an industrial deep-sea longline fishing activity, focusing today on Patagonian toothfish (*Dissostichus eleginoides*) (Duhamel et al., 2011).

To prevent potential impacts of longline fishing and following the evolution of international regulation, the 'Terres Australes et Antarctiques Françaises' (TAAF) administration transposed in 2014 CCAMLR Conservation Measures 22-06 and 22-07 about vulnerable marine ecosystems (VMEs) conservation in the French EEZ of Kerguelen (TAAF, 2014). Furthermore, the Muséum national d'Histoire naturelle (MNHN) started to develop in 2015 a permanent VME monitoring program to assess the real impact of the fishery on deep-sea benthic habitats (Martin et al., 2017).

Moreover, the Marine Reserve of Kerguelen, managed by the TAAF administration and originally limited to some coastal areas, has been recently extended to a large portion of deep-sea environments in the French EEZ in 2016 and 2017 (TAAF, 2017). Simple protected areas, and 'strictly protected areas' where fishing is prohibited, have been defined with quantitative objectives regarding the surface to be protected. 'Best available science' and 'expert knowledge' for various environmental components (e.g. marine mammals and birds, fish distribution patterns, benthic units, pelagic physical sub-regions) have been used to design protected areas. A five-days scientific workshop, based on discussions only, with experts from various institutions allowed the production of a report including all scientific elements used to define the protected areas (Koubbi et al., 2016). Conservation issues for deep-sea benthic ecosystems, were addressed using presence data of benthic marine invertebrates available for the area (Eléaume et al., 2011b), outputs of species distribution models initially produced for a former Marine Protected Area project in 2011 (Martin et al., 2017) and expert knowledge have been provided during the workshop by MNHN scientists (Koubbi et al., 2016).

Here we (i) identify sub-regions characterised by homogeneous benthic assemblages using a measurable and repeatable methodology, and (ii) compare these sub-regions to designated protected areas in the French EEZ Marine Reserve to evaluate the relevance of the protection zones for deep-sea benthic habitat conservation.

Materials and methods

Approach and choice of the method

We used an ecoregionalisation method as a 'process method and output of identifying and mapping broad spatial patterns based on physical and biological attributes through classification methods used for planning and management purposes' (Reygondeau et al., 2014). The choice of this approach aims to meet the first main objective of this study, to characterise ecological sub-regions based on homogeneous benthic assemblages and to contribute to our understanding of deep-sea benthic ecology of the study area. Various ecoregionalisation methods have been developed and are commonly used in ecosystem-based spatial management studies (e.g. Berline et al., 2014; Blasi et al., 2011;

Duranton et al., 2006; Hill et al., 2017; Hornsmann et al., 2008; Hunter et al., 2018; O'Hara, 2008). Given its relevance to our objectives, the generalised dissimilarity modelling (GDM) technique has been selected for analysis (Ferrier et al., 2007). GDM is a 'statistical technique for modelling spatial variation in biodiversity between pairs of geographical locations. It allows to make predictions and map biological patterns' (Ferrier et al., 2007). The method relates dissimilarity in community composition to environmental predictors. To perform the GDM and produce interpretable results in terms of benthic assemblages, a complete analysis pipeline developed using the R software (R Development Core Team, 2015) includes different steps, from dataset assembly to statistical analyses. This robust and broadly applied modelling technique (e.g. Ives and Helmus, 2011; Koubbi et al., 2010; Leathwick et al., 2011; Leitao et al., 2015; Rose et al., 2016), including the development of an analysis pipeline, provides a repeatable methodology allowing comparison between models.

Biological data

POKER is a program led by the MNHN, Paris, France, and has been designed to monitor commercial and by-catch fish species within the French EEZ of Kerguelen (Duhamel et al., 2011). This monitoring program is based on systematic random stratified trawl surveys over the northern part of the plateau, from 85 to 1 000 m depth. The POKER 2 cruise (October 2010) included a marine invertebrate by-catch sampling program (Duhamel et al., 2011). The 40 mm mesh bottom trawl used during POKER was designed for catching demersal fish, and benthic invertebrates collected as by-catch were limited to macro-epibenthic invertebrate. All organisms collected have been sorted, weighted, identified and photographed (Eléaume et al., 2011b). Furthermore, representative sub-samples of specimens have been collected and fixed in 96% ethanol to be later identified using molecular and anatomical approaches (Eléaume et al., 2011a). A set of presence/absence data for 111 taxa and morphotypes identified at various taxonomic levels has been produced for the 209 stations of the survey (Figure 1). The dataset is composed of 43% of species or morphotypes, 27% of genus, 2% of families, 9% of orders, 12% of classes and 7% of phyla.

Four types of grouping have been used to pool observations and produce ecoregionalisation

models: life-history traits (trophic mode and motility), protection status and taxonomic identification. Scientific literature (Gutt, 2007; Shojaei, 2016) and taxa listed by CCAMLR as VME bio-indicators (mostly engineer taxa and/or sessile and/or suspension feeders) (SC-CAMLR, 2009) have been used to define relevant groups and classify all the observations in specific tables.

Environmental data

Fifteen environmental variables representing sea floor and sea-surface conditions have been extracted or derived (Guillaumot et al., 2016) from available international databases (Boyer et al., 2013; Douglass et al., 2014; McCoy, 1991; Smith and Sandwell, 1997), and processed to fit the postulated life span and observed bathymetric distribution of species and the POKER 2 spatial coverage (Duhamel et al., 2011) (Table 1). Environmental statistics were averaged over the 2005–2012 period and encompass depths ranging from 85 to 1 000 m with spatial extension from 46° to 52°S and 63° to 73°E. Spatial resolution was set to a common 0.1°. POKER 2 transect mid-points were used to assign environmental statistics to biological occurrences.

Prior to modelling, environmental factors have been compared using the Spearman correlation test. When two factors were highly correlated, the one with the highest spatial resolution or the best ecological explanatory power was selected for modelling. The other factor was removed from the analysis. A threshold of $rs \leq 0.66$ has been defined to consider the factors to be not correlated (Mukaka, 2012).

Statistical analyses

GDM technique is based on analysis of biological dissimilarity between sampling stations according to the variation of related environmental factors (Ferrier et al., 2007).

GDM technique takes into account biological and environmental datasets and produces a dissimilarity matrix that best reflects biological/environment interactions. The process includes various steps. First, a dissimilarity matrix is computed from each of the presence/absence biological tables to obtain the biological distance between pairs of stations. The Jaccard Index is used (Goslee and Urban, 2007). Then, each dissimilarity matrix

Table 1:   Environmental factors used for the ecoregionalisation modelling with references.

| Environmental predictors	Unit	Original spatial resolution	Time period	References
Depth	meter	30 seconds of arc		Guillaumot et al. (2016), derived from Smith and Sandwell (1997)
Average of surface temperature	°C	0.1°	2005–2012	World Ocean Database (2013)
Variance of surface temperature	variance	0.1°	2005–2012	World Ocean Database (2013)
Average of temperature near sea floor	°C	0.1°	2005–2012	Guillaumot et al. (2016), derived from World Ocean Circulation Experiment (2013) sea-surface temperature layers
Variance of temperature near sea floor	variance	0.1°	2005–2012	Guillaumot et al. (2016), derived from World Ocean Circulation Experiment (2013) sea-surface temperature layers
Average of surface salinity	practical salinity scale	0.1°	2005–2012	World Ocean Database (2013)
Variance of surface salinity	variance	0.1°	2005–2012	World Ocean Database (2013)
Average of salinity near sea floor	practical salinity scale	0.1°	2005–2012	Guillaumot et al. (2016), derived from World Ocean Circulation Experiment (2013) sea-surface salinity layers
Variance of salinity near sea floor	variance	0.1°	2005–2012	Guillaumot et al. (2016), derived from World Ocean Circulation Experiment (2013) sea-surface salinity layers
Average of chlorophyll concentration in summer	mg/m^3	0.1°	2002–2009	NASA Goddard Space Flight Center, Ocean Biology Processing Group (2014)
Geomorphology	categorial	1°		ATLAS ETOPO2 2014 (Douglass et al., 2014)
Sediments	categorial	1°		McCoy (1991), updated by Griffiths 2014 (unpublished)
Sea floor slope	index	30 seconds of arc		Smith and Sandwell (1997)
Average of oxygen concentration near sea floor	mL/L	0.1°	2005–2012	Guillaumot et al. (2016), derived from World Ocean Database (2013) sea-surface oxygen concentration layers
Ruggedness	index	30 seconds of arc		Derived from bathymetric layer
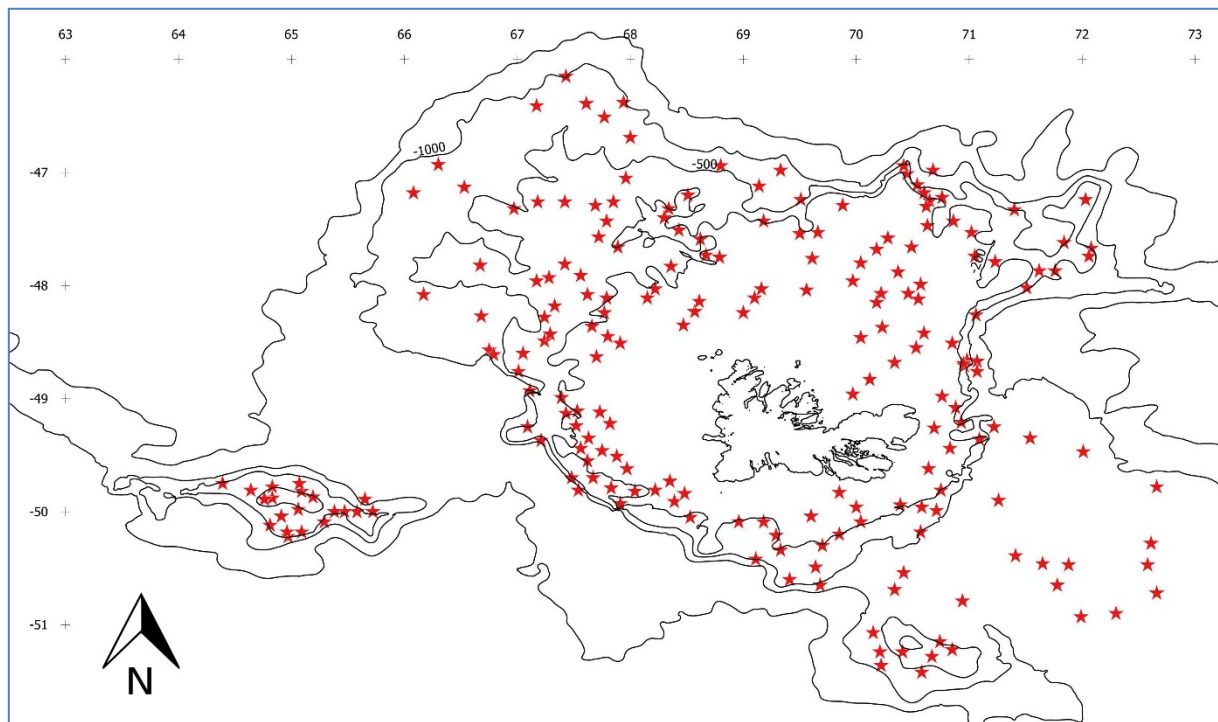
Figure 1:   Geographical distribution of POKER 2 cruise sampling stations over the French exclusive economic zone of Kerguelen.

is crossed to the environmental layers to obtain a new series of tables including for all possible pairs of sampling stations both their biological distance and the environmental statistics of each station. For each table, a generalised linear model (GLM) (McCullagh and Nelder, 1989) is fitted, with the biological dissimilarity as the explained value and the environmental statistics as the explanatory factors. An iterative modelling process is run to select the best GLM and the best set of environmental factors, using the deviance explained as testing criteria (McCullagh and Nelder, 1989).

Models are used to predict biological dissimilarity over the whole study area using all environmental predictors as available across the study domain. Each ecoregionalisation model results therefore in a new distance matrix where the biological distance index between all pairs of pixels is calculated from the GLM. Predictions are limited to the regions that present environmental conditions similar to those observed at the sampling stations. In addition, data gaps are not compensated by interpolation techniques to allow a critical evaluation of the quality of the modelling outputs.

Modelled predictions are then clustered using partitioning around medoids (PAM), an algorithm

that accommodates very large matrices (Kaufman and Rousseeuw, 1987). Each clustering is iterated ten times, starting with three a priori clusters, and finishing the process at twelve clusters. The number of clusters that maximises the 'Sih' silouhette index (Rousseeuw, 1987) is selected.

For each ecoregionalisation model, ecological sub-regions or ecotypes are characterised. Ecotypes are here defined as spatially delimited areas with shared similar environmental factors and benthic assemblages. For this study, the spatially delimited areas are the areas obtained from the clustering of model predictions. To compare the spatial structuring of the models, a principal component analysis (PCA) is applied to the clustering of the predictions. The pixels are set as the individuals of the analysis. The cluster values, associated to each pixel according to the ecoregionalisation models, are set as the variables. Environmental envelope of each ecotype is summarised using environmental statistics of pixels attributed to each cluster, and represented in a series of boxplots.

Benthic assemblages of ecotypes are the taxa detected in sampling stations located within the spatially delimited areas. To characterise species assemblages in a given spatial area, many

techniques are commonly used (e.g. Johnson et al., 1993; Kremen, 1992; Pardo and Armitage, 1997; Ward et al. 1999; Wright and Reeves, 1992). For this study, two methods were applied. First, the ecotypes are compared using a PCA applied to the presence/absence data of the taxa detected within the clusters. The clusters are set as the individuals of the analysis while the taxa are set as the variables. Furthermore, the *IndVal* index is used (Dufrêne and Legendre, 1997). *Indval* attributes a value to each taxon or group of taxa in a given area. This value is the product of a specificity component defined as '*the probability that the surveyed site belongs to the target site group given the fact that the species has been found*', and a sensitivity component defined as '*the probability of finding the species in sites belonging to the site group*' (italics are quoted from Dufrêne and Legendre, 1997). The higher the value of the *IndVal* index attributed to a taxon or a combination of taxa, the higher its value as a bioindicator. *IndVal* statistical significance is also tested and a *p* value is provided (Dufrêne and Legendre, 1997). For this study, we performed an *IndVal* analysis by testing bioindicator values for all taxa that were detected in the various ecotypes of each ecoregionalisation model. We also performed the analysis by testing bioindicator values for all combinations of two and three of those taxa. We assume that testing bioindicator values of larger combinations of taxa (i) would be contradictory with the concept of bioindicators, and (ii) may produce results difficult to interpret. Furthermore, we selected the most robust bioindicators according to a first threshold of *p* value ≤0.05 and a second threshold of *IndVal* ≤ 0.5 (Dufrêne and Legendre, 1997).

The models are compared by considering as a set of complementary quality indices (i) the number of ecotypes obtained, (ii) the number of taxa used to compute each model, (iii) the clusterisation *Sih* index, (iv) the number of computed *IndVal* bioindicators and (v) the number of clusters including bioindicators. According to the parsimony concept, we assume that an informative model must maximise the level of ecological information in the output while using the most limited biological information in the input. For this study, we assume that the best informative model must be based on a lower number of taxa but include a higher number of ecotypes.

Ecotypes are projected onto a map using QGIS (QGIS Development Team, 2017) and surface overlap with marine reserve strictly protected areas (MRSPAs) is computed. Percentage of each ecotype located within MRSPAs is here interpreted as a measurement of the protection level of each ecotype. This level of protection is contextualised according to the degree of rarity of each ecotype calculated as the percentage of each ecotype in the whole study area. These results are used in a preliminary evaluation of the relevance of the protection zones for the conservation of deep-sea benthic assemblages.

Results

Six out of 15 uncorrelated environmental factors are retained for modelling: depth, surface temperature mean, sea-surface salinity amplitude, chlorophyll-*a* summer mean, slope and sediments.

Twenty-one distinct benthic ecoregionalisation models are produced and projected onto a map also showing MRSPA locations. Pixel size indicates the geographical scale of predictions and blank areas indicate missing uninterpolated data.

Thirteen models have been computed using taxa at various identification levels: Actiniaria (Figure 2a), Annelida (Figure 2b), Arthropoda (Figure 2c), Ascidiacea (Figure 2d), Asteroidea (Figure 2e), Cnidaria (Figure 2f), Corals (Figure 2g), Echinodermata (Figure 2h), Echinoidea (Figure 3a), Holothuroidea (Figure 3b), Mollusca (Figure 3c), Ophiuroidea (Figure 3d) and Porifera (Figure 3e). A complete benthic ecoregionalisation model has also been computed by pooling all 111 taxa occurrence data (Figure 3f). Six models have been computed using life-history traits: motility includes sessile (Figure 3g) and vagile (Figure 3h); organisms feeding mode includes detritivore (Figure4a), necrophagous (Figure4b), predator (Figure4c) and suspension feeders (Figure4d). A single model was obtained using CCAMLR VME taxa (Figure 4e).

Although number of ecotypes can differ between models, distribution patterns display similar spatial structures. In models with a lower number of ecotypes, distribution patterns of benthic assemblages are mainly structured according to depth. For example, the suspension feeder model (Figure 4d) includes only three ecotypes, with ecotype 2 associated with habitats shallower than 250 m depth and
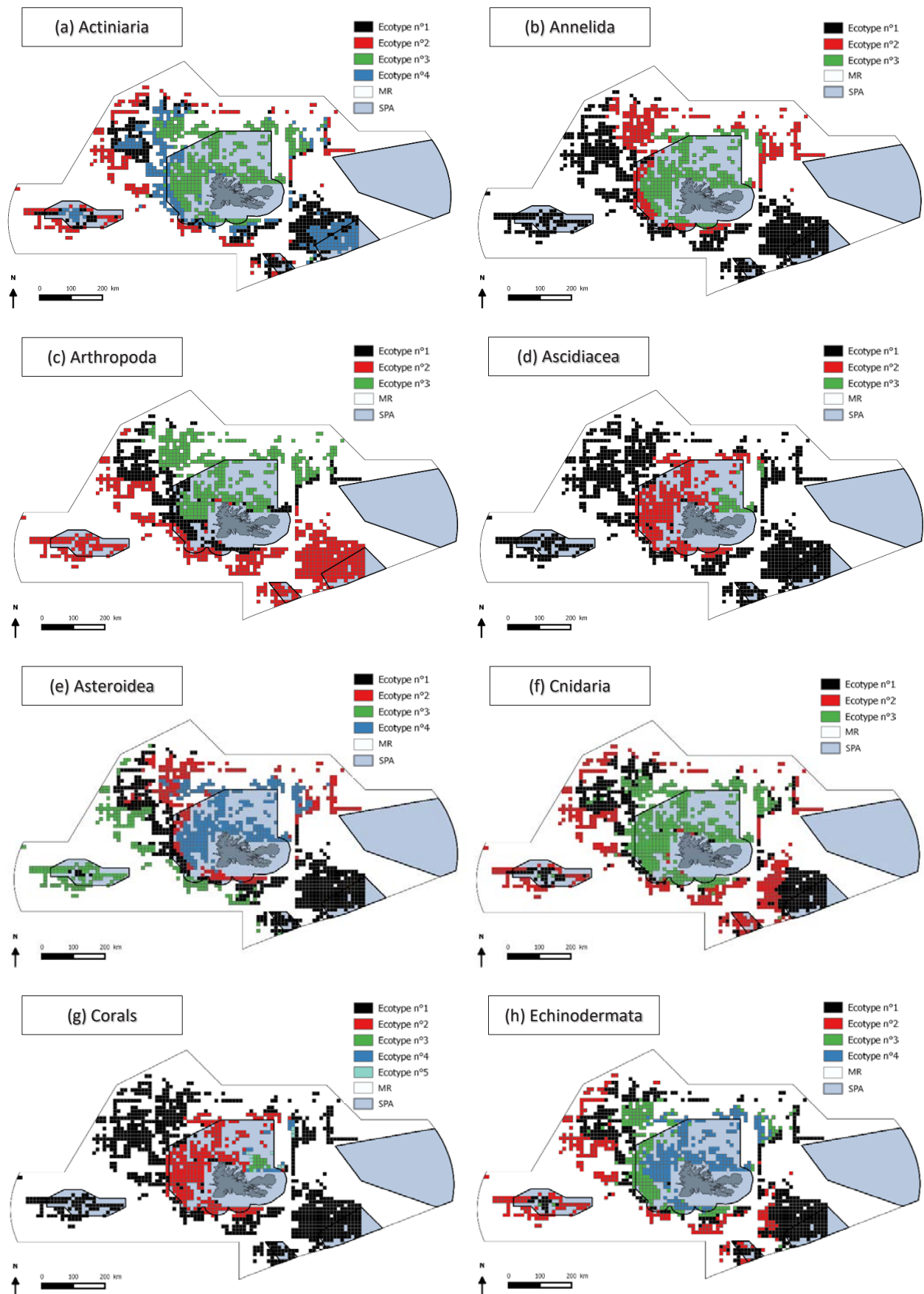
Figure 2: Benthic ecoregionalisation projected into maps showing ecotypes geographical distribution for (a) Actiniaria, (b) Annelida, (c) Arthropoda, (d) Ascidiacea, (e) Asteroidea, (f) Cnidaria, (g) Corals and (h) Echinodermata, Marine Reserve (MR) and strictly protected areas (SPAs).
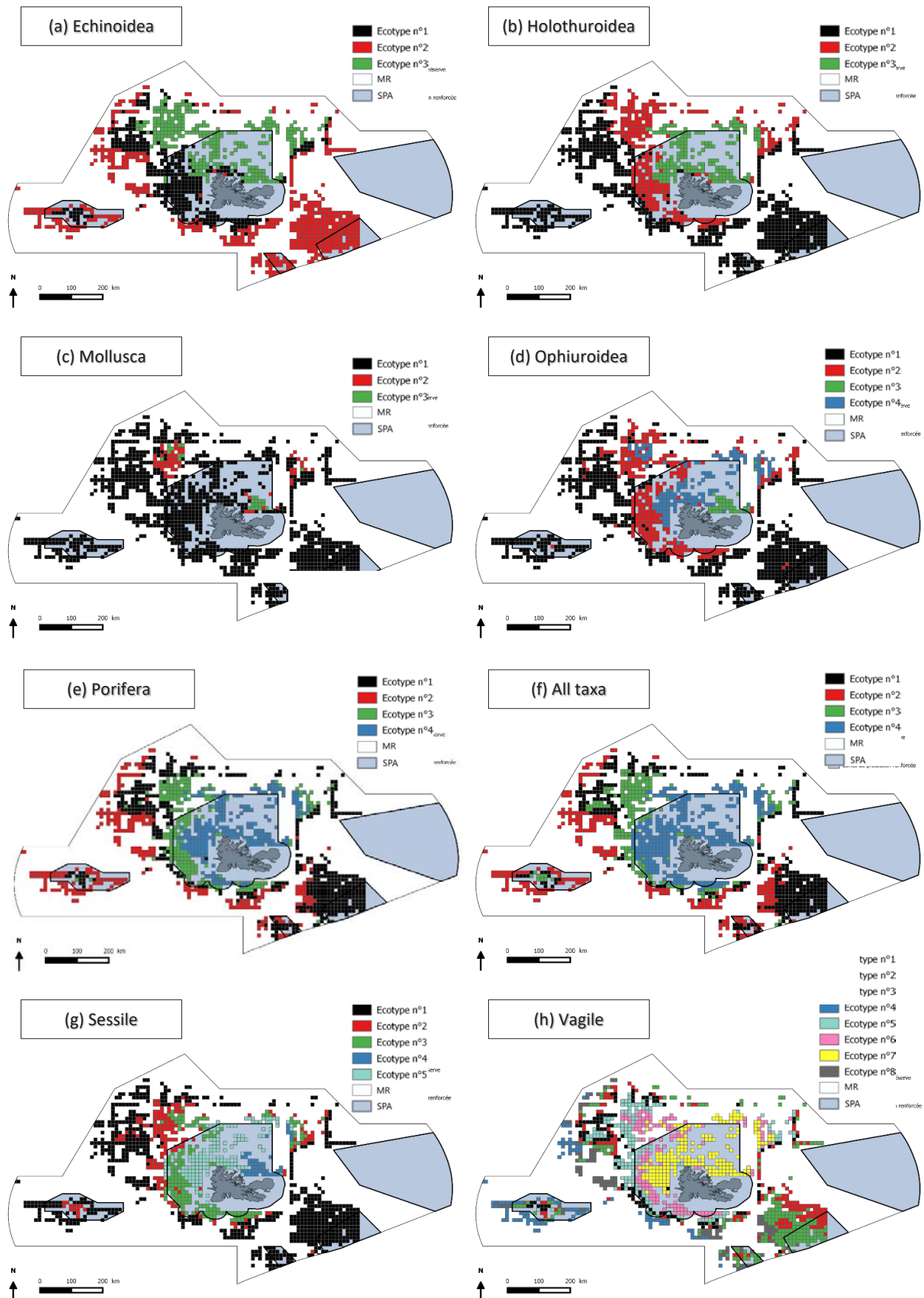
Figure 3:   Benthic ecoregionalisation projected into maps showing ecotypes geographical distribution for (a) Echinoidea, (b) Holothuroidea, (c) Mollusca, (d) Ophiuroidea, (e) Porifera, (f) all taxa, (g) vagile organisms, and (h) sessile organisms, Marine Reserve (MR) and strictly protected areas (SPAs).
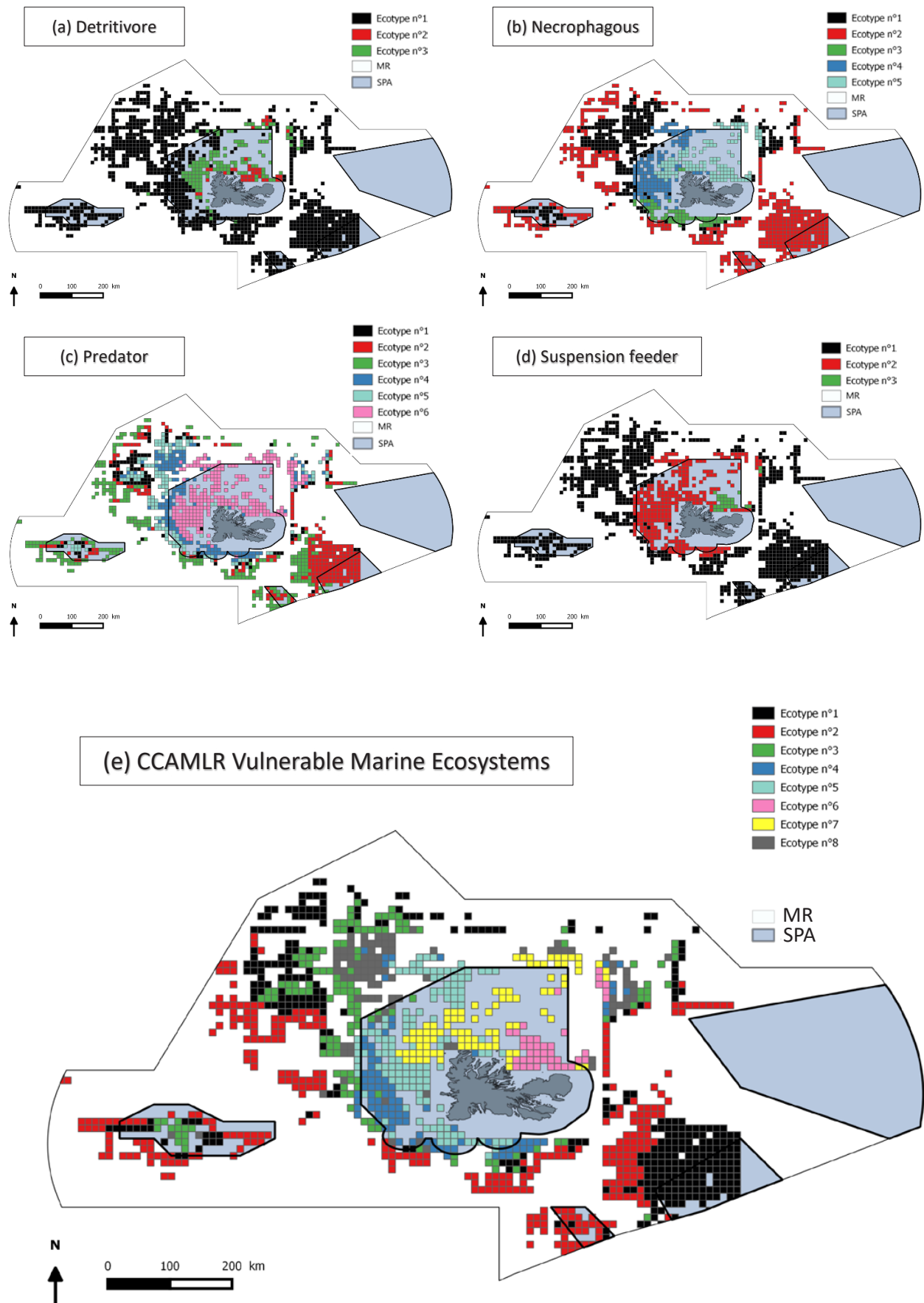
Figure 4:   Benthic ecoregionalisation projected into maps showing ecotypes geographical distribution for (a) detritivore organisms, (b) necrophagous organisms, (c) predator organisms, (d) suspension feeders, and (e) CCAMLR vulnerable marine ecosystems indicators, Marine Reserve (MR) and strictly protected areas (SPAs).

restricted to the immediate vicinity of the Kerguelen archipelago, ecotype 1 associated with habitats deeper than 250 m and largely distributed over the Kerguelen Plateau, and ecotype 3 which appears to be strictly associated with habitats located in a limited shallower area northeast of the archipelago, which has been shown to be a primary productivity peak zone with a high level of chlorophyll-*a* concentration (NASA Goddard Space Flight Center, Ocean Biology Processing Group (2014). Ecoregionalisation models with a higher number of ecotypes tend to show more detailed rather than strongly contrasting distribution pattern structures. For example, the predator model (Figure 4c) results in six ecotypes that depict with more details both deeper and shallower areas, but shows the same threshold in biological dissimilarity around 250 m depth.

The same holds true for ecoregionalisation models using life-history traits and taxa. Furthermore, except the two poorly detailed maps based on Mollusca (Figure 3c) and Detritivore (Figure 4a) ecoregionalisations, all maps show the same threshold of biological dissimilarity around 250 m depth.

The similarity between the distribution pattern structures of the various ecoregionalisation models is confirmed by the PCA. The PCA results in the first two axes representing 58.79% and 9.40% of the variance respectively (Figure 5). While not included in the analysis, clusters of pixels identified using the CCAMLR VME dataset are consistent with the distribution of the PCA individuals obtained with the other ecoregionalisation models (Figure 5). Furthermore, (i) all the ecoregionalisation models appear to be significantly correlated to the first axis of the PCA with *p* values close to zero, and (ii) most of the ecoregionalisation models appear to be strongly correlated, 13 out of 19 models exceeding a correlation value of 0.75 (Table 2). The highest correlation value is 0.93, the lowest correlation value is 0.28, the median value is 0.83 and the mean is 0.74 (Table 2).

Linkage and nesting effects in ecotype distribution patterns across life-history trait and taxa-based ecoregionalisation models are probably also due to the fact that the biological data used is not independent between groups. Life history trait groupings are derived from taxonomic groupings and may correlate in some cases. Asteroidea, for

example, are all vagile organisms and most are predators. One can therefore expect some degree of nestedness between results derived from modelling Asteroidea, vagile or predator groups. However, this may explain only a part of linkage and nesting relations. Indeed, similar observations can be done by comparing ecoregionalisations computed with independent biological datasets. Comparing Actinaria (Figure 2a) versus Echinodermata (Figure 2h) ecoregionalisation, and sessile (Figure 3g) versus vagile (Figure 3h) ecoregionalisation are relevant examples.

Across all ecoregionalisation models, the number of ecotypes varies from 3 to 8 with a mode at 4 and a mean at 4.1 (Table 3). For the taxa-based ecoregionalisation models, the number of ecotypes varies from 3 to 5, with a mode at 3 and a mean of 3.53. For the life-history-traits-based models, the number of ecotypes varies from 3 to 8, with a mode at 3 and a mean of 4.6. The maximum number of ecotypes is found when models are run using vagile or CCAMLR VME groups.

The number of ecotypes across models is not related to the number of taxa used to fit the models. For example, CCAMLR VME ecoregionalisation results in eight ecotypes and is supported by 23 taxa (Table 3). In contrast, Asteroidea ecoregionalisation results in four ecotypes, supported by 30 taxa, and the complete ecoregionalisation, supported by 111 taxa, results in four ecotypes.

The number of taxa used in models varies from 2 for Annelida to 111 for Complete (Table 3). Taxa-based models include from 2 (Annelida) to 52 (Echinodermata) taxa, and life-history-traits-based models include 10 (necrophagous) to 52 (vagile) taxa. Across all models, the mean is 21.6 taxa, the mode is 10 and the median is 10.

The *Sih* index associated to each clustering varies from 0.67 (necrophagous) to 0.93 (Ascidiacea and suspension feeders), with a mean at 0.77 across all groupings (Table 3).

For taxa-based models, the number of *IndVal* bioindicators varies from 0 to 8 combinations of taxa (Table 3). The highest value is obtained for Echinodermata model. For life-history-traits-based models, the number of *IndVal* bioindicators varies from three combinations of taxa for the necrophagous ecoregionalisation to 29 for predator. The

Table 2:   PCA applied to the clusterisation of the model predictions; table of correlated variables according to the Dimension 1 of the PCA; VME ecoregionalisation clusters = supplementary variable.

| Ecoregionalisation model	Correlation	p value	Ecoregionalisation model	Correlation	p value
Sessile	0.9322399	~0	Corals	0.8186677	~0
Porifera	0.9165757	~0	CCAMLR VME	0.7765180	~0
Echinodermata	0.9165757	~0	Cnidaria	0.7663308	~0
Annelida	0.9085115	~0	Asteroidea	0.7648303	~0
Holothuroidea	0.9051280	~0	Detritivore	0.7295518	~0
Ascidiacea	0.8853334	~0	Vagile	0.6576453	~0
Suspension feeder	0.8768481	~0	Arthropoda	0.4634152	~0
Ophiuroidea	0.8491374	~0	Actiniaria	0.3456607	~0
Predator	0.8357889	~0	Echinoidea	0.3039301	~0
Necrophagous	0.8314260	~0	Mollusca	0.2803254	~0
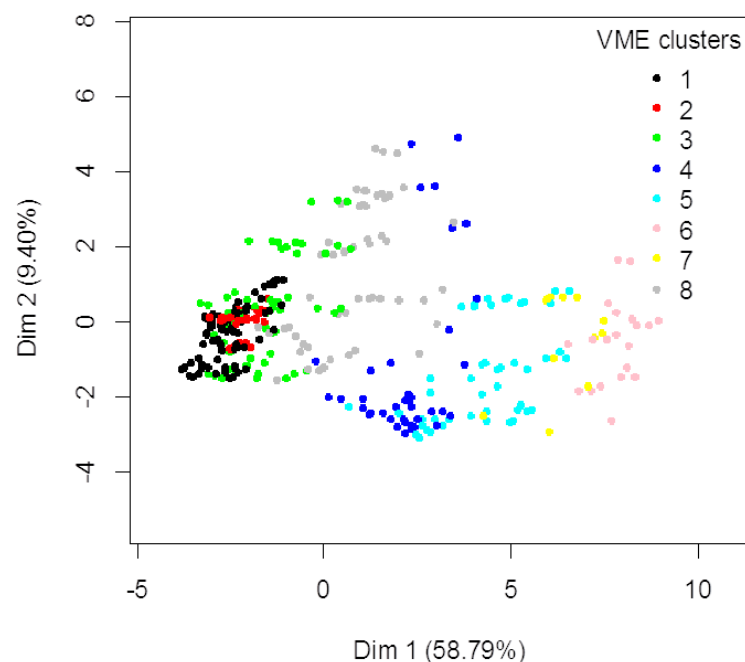
Figure 5: PCA applied to the clusterisation of the models predictions, graph of individuals; individuals = pixels, variables = ecotypes from feeding mode, motility and taxa ecoregionalisations, supplementary variable = VME ecoregionalisation clusters

Table 3:   Quality indices for each ecoregionalisation model: number of ecotypes, number of taxa supporting
the modelling process, *Sih* index of the clustering, number of *IndVal* bioindicators and number of
ecotypes including *IndVal* bioindicators for each output.

Group	Ecoregionalisation model	Number of ecotypes	Number of taxa	*Sih* index	Number of *IndVal* bioindicators	Number of clusters including bioindicators
Taxa	Actiniaria	4	7	0.7	0	0
	Annelida	3	2	0.84	1	1
	Arthropoda	3	10	0.73	0	0
	Ascidiacea	3	3	0.93	1	1
	Asteroidea	4	30	0.75	3	2
	Cnidaria	3	12	0.73	1	1
	Corals	5	5	0.87	0	0
	Echinodermata	4	52	0.69	8	3
	Echinoidea	3	4	0.69	0	0
	Holothuroidea	3	10	0.78	0	0
	Mollusca	3	10	0.88	0	0
	Ophiuroidea	4	8	0.68	0	0
	Porifera	4	3	0.87	0	0
Feeding mode	Detritivore	3	18	0.85	18	1
	Necrophagous	5	10	0.67	3	1
	Predator	6	37	0.73	29	2
	Suspension feeder	3	21	0.93	4	1
Motility	Sessile	5	26	0.7	16	3
	Vagile	8	52	0.7	39	2
Prot. status	CCAMLR VME	8	23	0.77	12	3
Complete	All Taxa	4	111	0.69	16	3

model derived from complete dataset includes 16 combinations of taxa as *IndVal* bioindicators. CCAMLR VME ecoregionalisation includes 12 combinations of taxa as *IndVal* bioindicators for three clusters. Across all models, the mean of *IndVal* bioindicators is 7.19, the minimum is 0, the maximum is 39, the mode is 0 and the median is 1.

The number of clusters including *IndVal* bioindicators within each ecoregionalisation model varies from 0 to 3 (Table 3). No ecoregionalisation model includes *IndVal* bioindicators for all of its ecotypes.

The number of *IndVal* bioindicators for each model and the number of ecotypes including *IndVal* bioindicators are not related to (i) number of taxa supporting the modelling process or (ii) number of resulting ecotypes. For example, only four *IndVal* bioindicators could be computed in a unique ecotype for the suspension feeder ecoregionalisation, with 21 taxa used for the GDM and three ecotypes which could be characterised (Table 3). This can be compared to the detritivore ecoregionalisation, built

with only 18 taxa and resulting in three ecotypes, but including 18 combinations of taxa as *IndVal* bioindicators for one ecotype of the model.

According to the comparison of the quality indices, we consider that the most parsimonious and informative benthic ecoregionalisation model is obtained using CCAMLR VME grouping. While using only 23 taxa, which is close to the mean value of 21.6 and considerably lower than the maximum value of 111 taxa, the CCAMLR VME model displays a maximum value of 8 ecotypes, which is much higher than the mean value of 4.1. Furthermore, the clusterisation appears to be sufficiently robust with a strong *Sih* index of 0.77 equivalent to the mean obtained for the whole set of outputs (Table 3). Moreover, the CCAMLR VME ecoregionalisation includes 12 *IndVal* bioindicators, higher than the mean of 7.19 and considerably higher than the mode of 1. Finally, this model is retained for further analyses of the effect of environmental factors on biological dissimilarity, and to evaluate the relevance of the protection zones of the new Marine Reserve.

Projection onto a map of VME ecoregionalisations (Figure 4e) shows a homogeneous geographical distribution for each of the eight benthic assemblages: no strong fragmentation can be observed, most of the pixels appearing to be located in continuous areas of pixels with same computed ecotype. This strong spatial structuring can be observed both on the plateau and the southwestern Skiff Bank seamount.

Ecotypes 4, 5, 6 and 7 are almost entirely located within the largest MRSPA, close to the Kerguelen archipelago (Figure 4e). Their geographical distribution is structured along a west–east axis around the islands. In deeper areas, the ecotypes 1, 2 and 3 are located all over the plateau and the Skiff Bank, while ecotype 8 remains mainly present in a limited area in the north (Figure 4e). Furthermore, ecotypes 1, 2 and 3 are partly covered by three distinct MRSPAs but ecotype 8 appears to be located mostly outside all MRSPAs.

The effect of environmental factors on biological dissimilarity shows contrasted results (Figure 6). For the CCAMLR VME ecoregionalisation model, depth has a strong continuous effect from 1 000 to 200 m depth approximately (Figure 6a). A strong positive linear correlation between chlorophyll-*a* concentration and biological dissimilarity can also be noted (Figure 6b). Other environmental factors, slope (Figure 6c), salinity (Figure 6d), surface temperature mean (Figure 6e) and sediments (Figure 6f) show more limited effects, with various thresholds.

Environmental envelopes as summarised in Figure 7 show that depth appears to be a main discriminating factor, with a threshold value around 250 m (Figure 7a). A first group includes ecotypes 4, 5, 6 and 7 at depths shallower than 250 m. All display a reduced dispersion of depth value around the median. Ecotype 8 shows a median depth ~250 m and displays a larger dispersion of depth value, from ~85 to ~420 m. A third deeper group with medians depth ~490, 550 and 360 m is composed of ecotypes 1, 2 and 3. All display a comparatively large dispersion of depth value.

Slope is also a good discriminating factor with ecotypes 4, 5, 6, 7 and 8 characterised by small median values and reduced dispersion, and ecotypes 1, 2 and 3 characterised by higher median values and comparatively large dispersion (Figure 7b).

Chlorophyll-*a* concentration also proved to be a relevant explanatory factor (Figure 7c). Ecotypes 6 and 7 are characterised by comparatively higher values of chlorophyll-*a* concentration, all other ecotypes (1, 2, 3, 4, 5 and 8) being characterised by comparatively lower values. In contrast with other factors, chlorophyll-*a* concentration distribution seem homogeneous across ecotypes in terms of dispersion around the median.

Other environmental factors, salinity (Figure 7d), surface temperature mean (Figure 7e) and sediments (Figure 7f), do not appear to be relevant discriminating factors.

PCA results show a strong structuring in the composition of the benthic assemblages of the VME ecoregionalisation ecotypes. The two first axes of the analysis represent 43.84% and 32.64% respectively of the total variance (Figures 8 and 9). The first axis allows to distinguish the ecotype 6, located in a high productivity area, and characterised by (i) the presence of *Molgula pedunculata* Herdman, 1881 (*Ascidiacea* Blainville, 1824), and (ii) a higher probability to observe *Ptilocrinus amezianeae* Eléaume, Hemery, Bowden and Roux, 2011 (*Crinoidea* Miller JS, 1821) and *Scleractinia* Bourne, 1900 organisms (e.g. *Flabellum* Lesson, 1831) (Figures 8 and 9). Furthermore, various associations of *Molgula pedunculata* and specific sets of *Actiniaria* and *Porifera* Grant, 1836 organisms are identified as relevant bioindicators of ecotype 6 according to the *IndVal* analysis (Table 4).

The second axis of the analysis allows to distinguish deep and shallower ecotypes (Figure 8). Shallower ecotypes 4, 5 and 7 are characterised by a higher observed biodiversity with the presence of *Cidaridae* Gray, 1825, *Glyphoperidium bursa* Roule, 1909 (*Actiniaria*), *Gorgonocephalus* Leach, 1815 (*Euryalida* Lamarck, 1816), *Umbellula* Gray, 1870 (*Pennatulacea* Verrill, 1865), *Alcyonacea* Lamouroux, 1812 (*Cnidaria* Verrill, 1865) and various sets of *Actiniaria* and *Porifera* organisms (Figure 9). Biondincators could be obtained only for ecotype 7. Deep ecotypes 1, 2, 3 and 8 are characterised by the presence of two *Euryalida* species, *Asteronyx loveni* Müller & Troschel, 1842 and *Astrotoma agassizii* Lyman, 1875, and by the presence of *Funiculinidae* Gray, 1870 (*Pennatulacea*) (Figure 9). *Asteronyx loveni* is identified as a relevant bioindicator of ecotype 8 according to the *IndVal* analysis (Table 4).
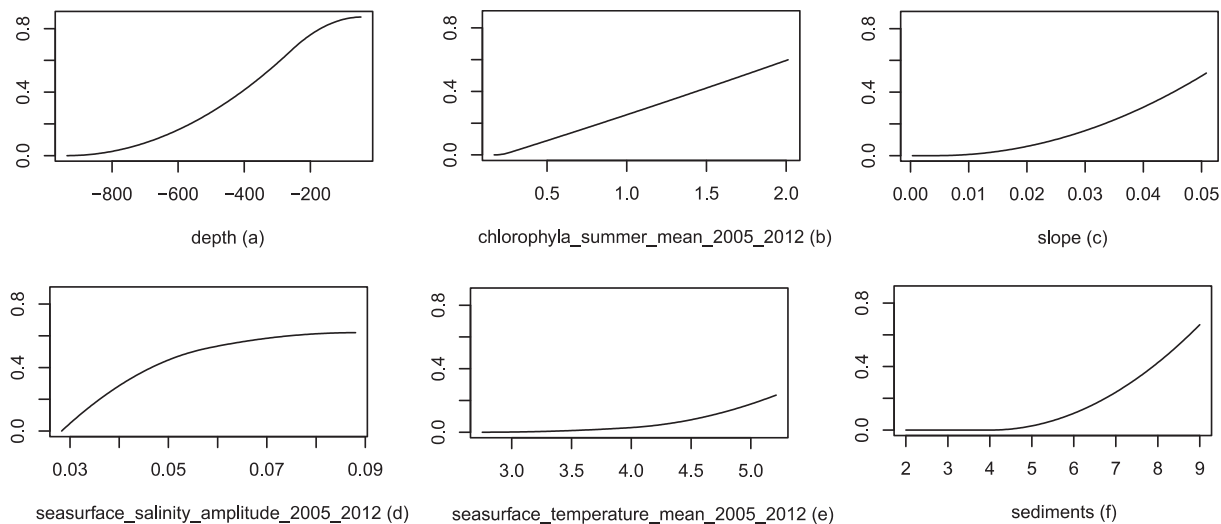
Figure 6:   GLM curves of effects of environmental factors on biological dissimilarity from the CCAMLR VME ecoregionalisation model.
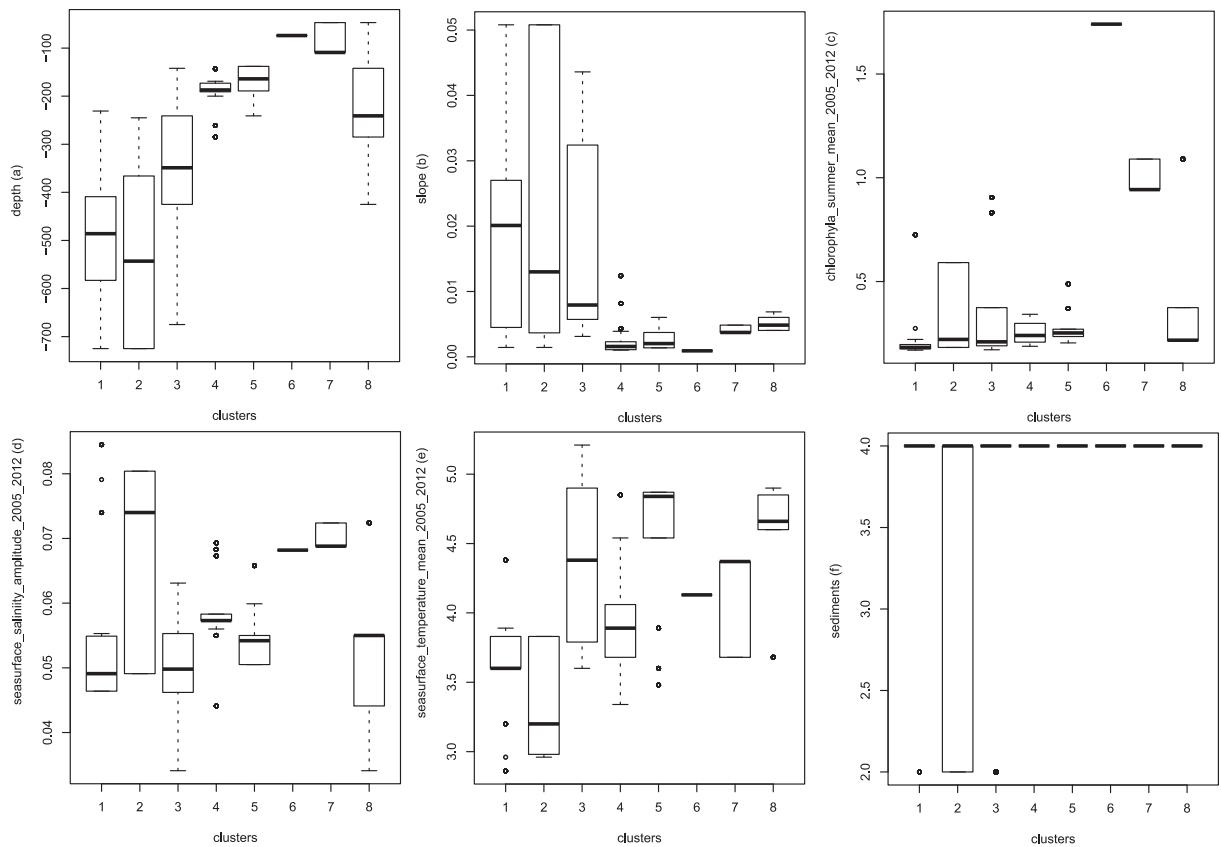

Figure 7:   Boxplots of environmental statistics for ecotypes derived from the CCAMLR VME ecoregionalisation model.
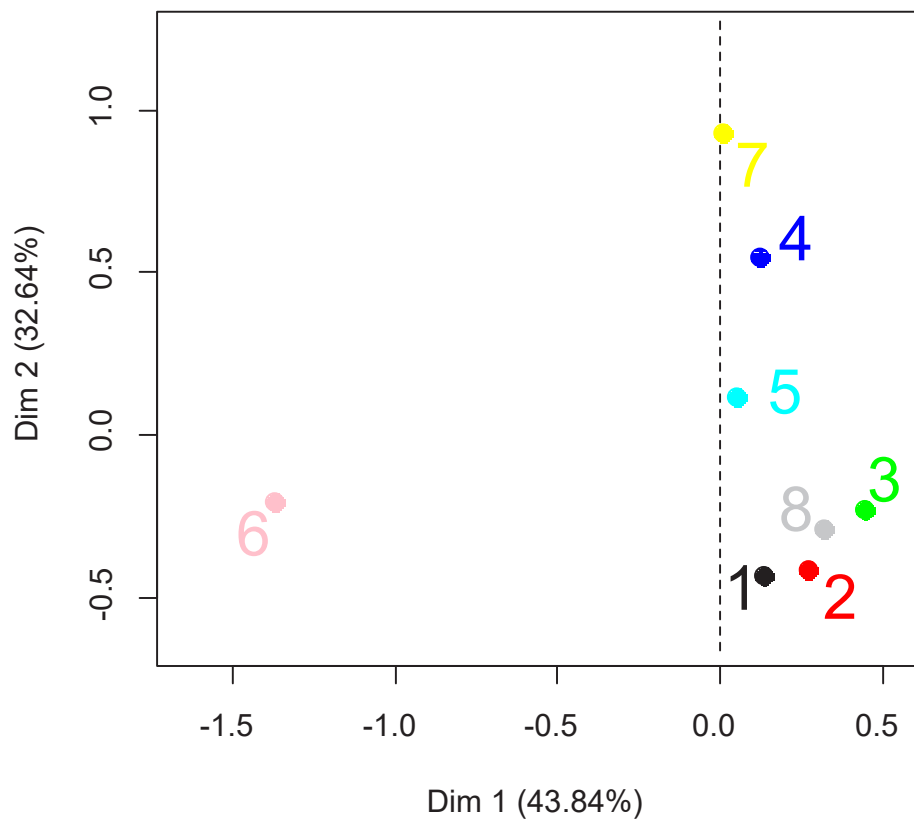
Figure 8:   PCA applied to the biological composition of the VME ecoregionalisation ecotypes, graph of individuals; individuals = VME ecotypes, variables = taxa presence data.
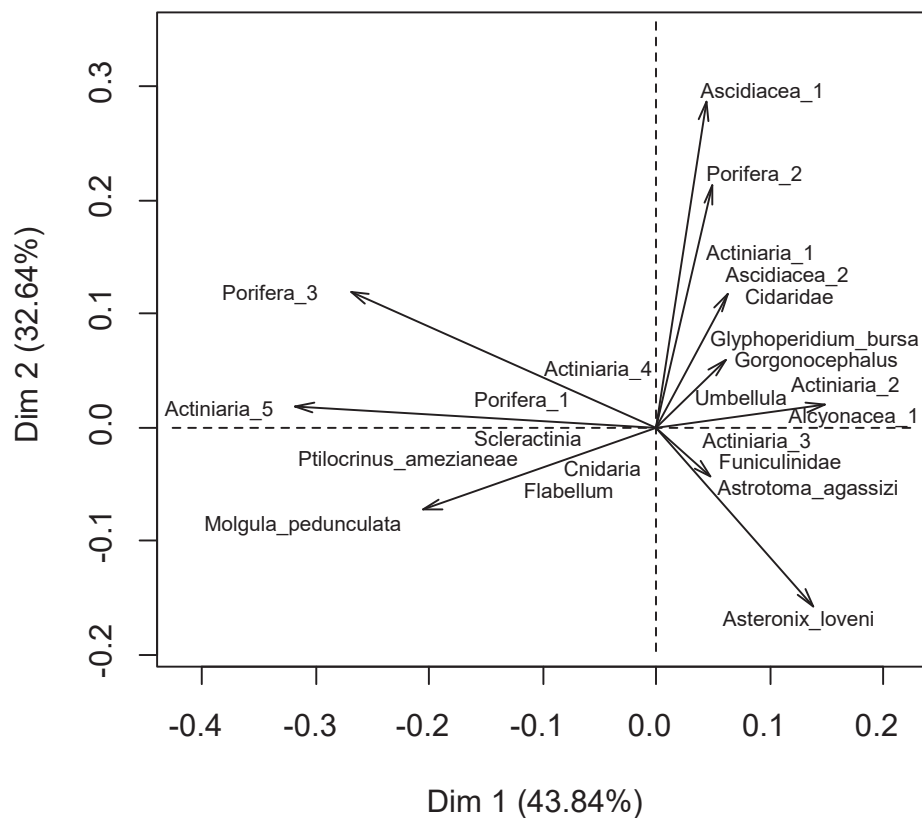

Figure 9:   PCA applied to the biological composition of the VME ecoregionalisation ecotypes, graph of variables (summarised); individuals = VME ecotypes, variables = taxa presence data.

Table 4:   *IndVal* bioindicator taxa (summarised) of the VME ecoregionalisation ecotypes.

Taxa	Stat.	*p* value	Ecotype
Molgula_pedunculata+Actiniaria_5	1.000	0.001	6
Molgula_pedunculata+Actiniaria_5+Porifera_3	1.000	0.001	6
Actiniaria_5+Porifera_3	0.920	0.001	6
Actiniaria_5	0.874	0.001	6
Molgula_pedunculata+Porifera_3	0.798	0.001	6
Porifera_3	0.590	0.032	6
Molgula_pedunculata	0.529	0.018	6
Ascidiacea_2	0.618	0.002	7
Ascidiacea_1+Ascidiacea_2	0.603	0.048	7
Actiniaria_1+Ascidiacea_2	0.522	0.039	7
Ascidiacea_1+Porifera_2	0.516	0.038	7
Asteronix_loveni	0.595	0.045	8

Proportion of VME ecotypes located within a MRSPA varies from 11.66% (ecotype 2) to 80.6% (ecotype 5) with a mean of 45.11% across all ecotypes (Figure 10). Each VME ecotype represent from 3.13% (ecotype 6) to 27.31% (ecotype 1) of the total study area (Figure 11).

Discussion

Quality of the models

Assessing the minimum number of biological records required to compute ecological models constitutes a major methodological issue, especially for data-poor areas such as freshwater and marine habitats (e.g. Bevilacqua et al., 2009; Fraschetti et al., 2011; Guillaumot et al. 2018; Ramos-Merchante and Prenda, 2017; van Proosdij et al., 2016). Our study constitutes a contribution to solve this issue using an ecoregionalisation approach.

The quality indices for each ecoregionalisation model show that (i) number of ecotypes is independent from the number of taxa included in a given model, and (ii) number of *IndVal* bioindicators and number of ecotypes including *IndVal* bioindicators are independent from both the number of sampled taxa and the number of ecotypes resulting from the modeling process.

In the light of this analysis, the biological indicator value of the benthic assemblages appears to be more efficient for ecoregionalisation and ecotypes characterisation than the number and the diversity of sampled taxa. Indeed, increasing the quantity of biological observations by pooling specialist and ubiquitous species, can result in a decrease of model statistical power. This is exemplified here by the highly informative VME model.

Distribution patterns

Due to the field constraints and availability of both biological and environmental data, most of the modelling studies of the deep-sea invertebrates in the Southern Ocean are species-centred and based on species distribution modelling (SDM) techniques (e.g. Guillaumot et al., 2018; Hibbert, 2016; Marshall et al., 2014). In our study, we attempt to go further by modeling benthic assemblages. Our results represent a significant improvement and the first benthic ecoregionalisation models available for the French EEZ of Kerguelen.

One main difficulty in analysing these results lies in the interpretation of ecotypes in terms of ecological relationships between species. In coastal areas, fine-scale in situ observations allow assessing benthic assemblage composition and interactions. Main factors accounting for spatial distribution patterns of macro-zoobenthic communities on the Antarctic shelf are listed in Gutt (2006): competition relations (e.g. Dauby et al., 2001; Gutt, 1991; Gutt and Starmans, 1998), food availability (e.g. Hibbert, 2016; Gutt and Schikan, 1998; Gutt and Starmans, 1998), space availability (e.g. Barnes et al., 2006; Cattaneo-Vietti et al., 2000; Gutt and Starmans, 1998), seasonal changes affecting populations (e.g. Jazdzewski et al., 2001), predation relations (e.g. Dayton, 1972; Dayton et al., 1974; McClintock et al., 2005) and disturbance effects (Dayton and Hessler, 1972; Gutt, 2006). Such a level of analysis still remains inaccessible

Percentage of each cluster located within a Strictly Protected Area
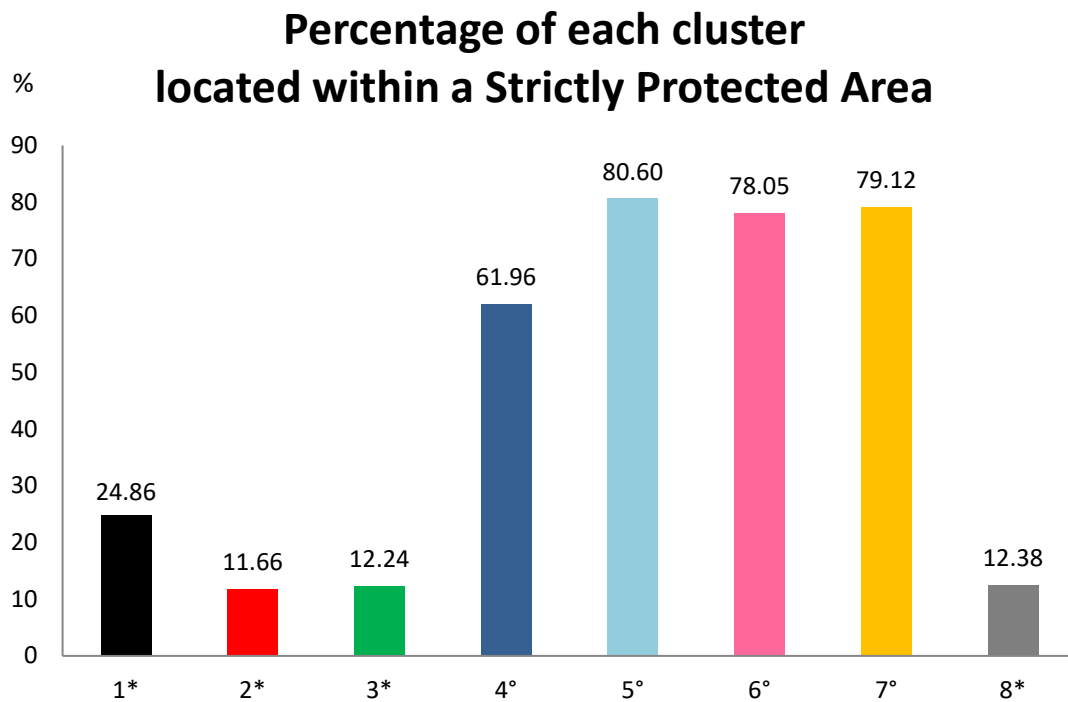

Figure 10: Proportion of each ecotype derived from VME ecoregionalisation modelling located within a strictly protected area; * = ecotypes deeper than 250 m, ° = ecotypes shallower than 250 m.
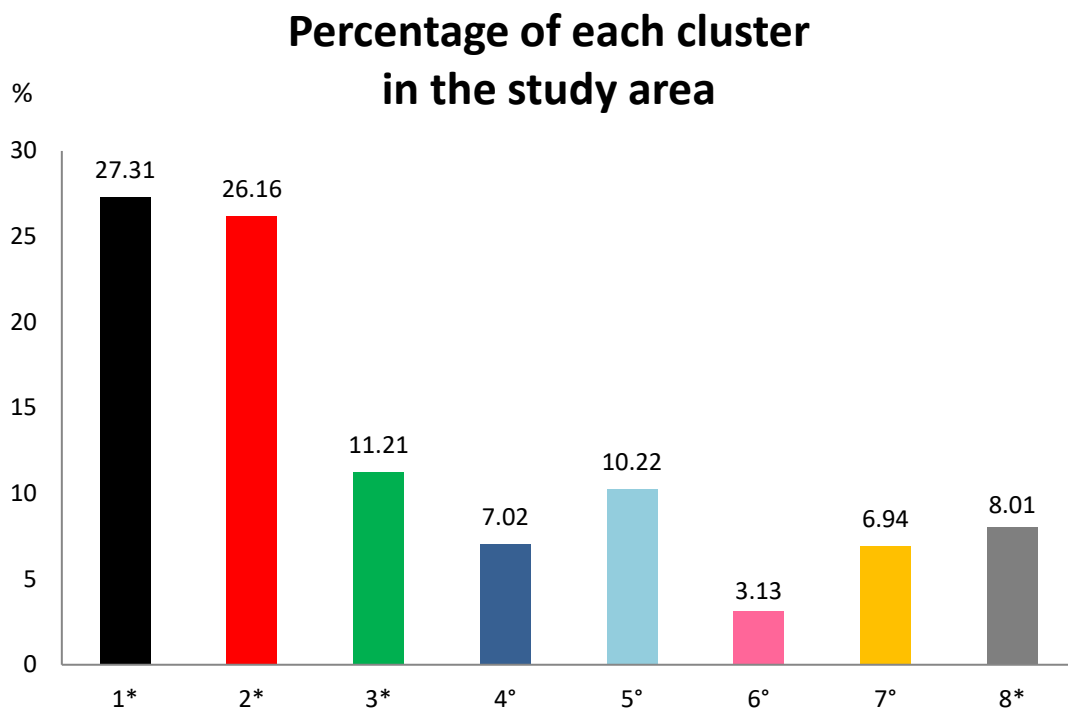
Percentage of each cluster in the study area

Figure 11: Proportion of each ecotype derived from VME ecoregionalisation modelling in the study area; * = ecotypes deeper than 250 m, ° = ecotypes shallower than 250 m.

for deeper areas of the Kerguelen EEZ. However, persistence of linkage and nesting effects over all models may be interpreted as a strong indication that ecotypes and associated benthic assemblages may be understood as benthic landscape units. These benthic landscape units may constitute a relevant spatial framework for the northern Kerguelen Plateau to stratify (i) upcoming deep-sea benthic samplings, and (ii) further studies on deep-sea benthic communities and ecosystems.

Effect of environmental factors

When considering a large geographical scale and a large range of bathomes, depth appears to be a key criterium to describe the spatial distribution of the deep-sea benthic invertebrates of the Southern Ocean (Brandt et al., 2007a, Brandt et al., 2007b), which includes mostly eurybatic species (Arnaud and Hain, 1992; Arntz et al., 1994; Zimmermann and Brandt, 1992). It is widely recognised that depth is a proxy of a series of drivers of Southern Ocean deep-sea benthic ecology, such as food availability (Hibbert, 2016; Gutt and Starmans, 1998; Gutt., 2006; Hibbert, 2016; Piepenburg et al., 2002) or physical factors, which are known in coastal habitats to affect the biology of organisms (Ahn, 1994; Chiantore et al., 2001; Dayton, 1972; Picken, 1980; Thrush et al., 2006). In this study we identify environmental variables other than depth as driving factors for benthic assemblage structuring in the northern Kerguelen Plateau.

Cross examination of GLM effect curves of the VME ecoregionalisation model, and analysis of environmental statistics (Figure 7) help understand the relative effects of each environmental factor on benthic assemblage composition and in particular help better understand the 250 m depth threshold.

In the southern Kerguelen Plateau Heard Island and McDonald Islands (HIMI, Australian EEZ), depth, distance to canyon and concentration of particulate organic carbon (POC, used as a proxy of food availability) appear to be the main factors allowing for prediction of VME taxa biomasses using SDM techniques (Hibbert, 2016).

In the shallower areas of the northern Kerguelen Plateau, at depths ranging between 100 and 250 m, chlorophyll-*a* concentration appears to be the main factor driving the distribution of benthic assemblages. Chlorophyll-*a* is a proxy for a combination

of several factors, including productivity and spatial distribution of surface currents (Park et al., 2011; Park and Vivier, 2011) and may account for the west–east gradient of benthic assemblage variability (Figure 4e). Chlorophyll-*a* concentration is the only environmental factor that shows a significant eastward increase, which is strongly correlated to the pattern of the spatial distribution of ecotypes. This effect is also observed on the faunal composition of the benthic assemblages. The shallower habitats include a higher observed biodiversity in comparison to the deeper habitats. Furthermore, the shallower habitats can also be distinguished from each other according to the relation between the chlorophyll-*a* concentration and their faunal composition. This is in line with previous results obtained for the southern Kerguelen Plateau, where a strong effect of POC concentration on the VME taxa biomass has been described (Hibbert, 2016).

In areas deeper than 250 m on the plateau and southwestern Skiff Bank seamount, depth remains the main environmental factor accounting for spatial distribution of benthic assemblages (Figure 4e). Slope appears as a secondary important factor and contributes to the definition of ecotype 8. This ecotype, including the only bioindicator in the deeper habitats, is located within a deep area, but presenting an original physical structure with a flat surface and a relatively low slope (Figure 4e). Other environmental factors are comparatively weakly significant.

Evaluation of the Marine Reserve

Using different modelling techniques, previous studies have been realised to assess the vulnerability of the southern Kerguelen Plateau benthic ecosystems and guide the creation of the HIMI marine protected area (MPA) within the Australian EEZ (Welsford et al. 2013; Hibbert, 2016). A recent assessment has also been produced for demersal fish (Hill et al., 2017). For the French EEZ, a preliminary evaluation of the Marine Reserve falls into the scope of this study. Needless to say, it is much too soon to evaluate its efficiency in terms of stock or effective ecosystem protection. But it is possible to assess the actual comprehensiveness, adequacy and representativeness of the Marine Reserve albeit if only roughly. Comprehensiveness, adequacy and representativeness are three main concepts that have been retained as key concepts by CCAMLR in designating MPAs (Welsford et

al., 2011). Comprehensiveness ensures that MPAs will include the full range of ecosystems recognised in an area; adequacy ensures that MPAs will have the required level of protection for diversity of life; representativeness ensures that areas protected reflect biotic diversity from a given region. In the case of the TAAF National Marine Reserve, our results are restricted to the northern Kerguelen Plateau. We certainly appreciate the fact that the whole Kerguelen Plateau should be taken into account when assessing protected areas efficiency. To do this will require integration of southern and northern Kerguelen Plateau benthic occurrences, which is well beyond the scope of this study. Adequacy and representativeness are difficult to assess separately from our results. Here we combine these two concepts in one, 'representativity', that may be defined as a level of protection as a function of relative spatial coverage and is calculated as the proportion of each ecotype included in the MRSPA.

As shown in Figure 5, all of the recognised ecotypes have been included in the MRSPA therefore complying with comprehensiveness as understood here.

The calculation of the percentage of each VME ecotype located within an MRSPA shows contrasting results. Shallower ecotypes (4, 5, 6 and 7) ranging from 100 to 250 m depth benefit from higher rates of protection, i.e. 61.96% of protection for ecotype 4, up to 80.60% for ecotype 5 (Figure 10). Ecotypes deeper than 250 m appear to benefit from lower levels of protection, i.e. 11.66% for ecotype 2 up to 24.86% for ecotype 1 (Figure 10).

Comparison with the degree of rarity of each VME ecotype allows a better interpretation. Deeper ecotypes 1 and 2 are protected at a lower level but remain the most common and represented VME benthic assemblages of the French EEZ, representing 27.31% and 26.16% of the whole area (Figure 11). The shallower ecotypes (4, 5, 6 and 7) are well protected by the Marine Reserve and remain the least represented assemblages, from 3.13% for ecotype 6 to 10.22% for ecotype 5 (Figure 11). Both deeper ecotypes 4 and 8 are relatively poorly represented in the French EEZ (11.21% and 8.01%) and also poorly protected by the Marine Reserve (12.24% and 12.38%) (Figure 11). Representativity appears to be unbalanced and some ecotypes could benefit from receiving a better level of protection.

Conclusion

Our results show that increasing the number of taxa in models may have adverse consequences and may decrease the quality of analyses. Analysing datasets restricted to relevant groupings results in more informative ecoregionalisation models. Here we show that VME-based ecoregionalisation unexpectedly appears more informative than the model based on the complete dataset. This finding is of particular interest because VME organisms are regularly collected by longliners and can constitute a source of relevant data for modelling benthic ecosystems at a larger scale, including CCAMLR areas.

In this study we show that three major environmental factors shape deep-sea benthic assemblages in the northern Kerguelen Plateau. At depths shallower than 250 m, chlorophyll-*a* concentration appears to be the main environmental driver. In deeper areas, depth and slope remain the main driving factors. However, other factors that are essential to larval and food transport, larval recruitment and organism existence like current velocity and direction, substratum type, resuspended sediment containing organic matter as potential food source are not sufficiently detailed here. These factors are partly captured in other factors used here and need to be further developed and tested.

Our approach uses a repeatable method and may help evaluate Marine Reserve protection levels of benthic ecosystems. Our preliminary assessment, based on VME-based ecoregionalisation, shows that poorly represented shallower ecotypes (4, 5, 6 and 7) and deeper common ecotypes (1, 2) are given a high level of protection. Two relatively deep and poorly represented ecotypes (3, 8) receive comparatively lower level of protection. Our results partly support MRSPAs as established by expert knowledge (Koubbi et al., 2016). However, more ecotypes than expected have been identified suggesting that expert knowledge should be supplemented with more standardised, quantified approaches when possible. Additional ecoregionalisation results could be used as information layers for an integrative assessment of other conservation issues such as connectivity between ecotypes. Bioindicator organisms could be used as proxies for the design and management of protected areas.

In the near future, existing datasets will be completed by additional biological data collected during

longline fishing activities (Martin et al., 2017) as well as POKER cruises (Martin et al., 2018). Resulting ecoregionalisation models are expected to depict in more detail and help better assess the spatial distribution of benthic ecosystems over the northern Kerguelen Plateau (French EEZ), along the slope where natural resources are currently exploited, and over the southern Kerguelen Plateau (HIMI, Australian EEZ). Environmental data need to be improved in terms of coverage for existing layers. Some important variables such as substrate composition, resuspended organic matter, or current velocity and direction are missing and need to be assessed. To complement this study, which constitutes a first step towards understanding the deep-sea benthic ecology of the Kerguelen EEZ, the future work based on the new datasets may include (i) improved analysis of the faunal composition of the benthic assemblages, (ii) improved comparisons between ecoregionalisation models to allow a (iii) better interpretation about the effects of environmental factors on the benthic assemblage distribution and composition.

Acknowledgments

References

Ahn, I.-Y. Ecology of the Antarctic bivalve *Laternula elliptica* (King and Broderip) in Collins Harbor, King George Island: benthic environment and an adaptive strategy. *Mem. Natl. Inst. Polar Res.*, 50: 1–10.

Améziane, N., M. Eléaume, L. Hemery, F. Monniot, A. Hemery, M. Hautecoeur and A. Dettaï. 2011. Biodiversity of the benthos off Kerguelen Islands: overview and perspectives. In: Duhamel, G. and D. Welsford (Eds). *The Kerguelen Plateau: marine ecosystem and fisheries*. Société Française d'Ichtyologie, Paris: 157–167.

Arnaud, P.M. 1974. Contribution à la bionomie marine benthique des régions antarctiques et subantarctiques. Station marine d'Endoume. *Téthys*, 6: 465–656.

Arnaud, P.M. and S. Hain. 1992. Quantitative distribution of the shelf and slope molluscan fauna (Gastropoda, Bivalvia) of the eastern Weddell Sea (Antarctica). *Polar Biol.*, 12 (1): 103–109.

Arntz, W., T. Brey and V. Gallardo. 1994. Antarctic zoobenthos. Oceanogr. *Mar. Biol. Ann. Rev.*, 32: 241–304.

Barnes, D.K.A., K. Linse, C. Waller, S. Morely, P. Enderlein, K.P.P. Fraser and M. Brown. 2006. Shallow benthic fauna communities of South Georgia Island. *Polar Biol.*, 29 (3): 223–228, doi: https://doi.org/10.1007/s00300-005-0042-0.

Berline, L., A.-M. Rammou, A. Doglioli, A. Molcard and A. Petrenko. 2014. A connectivity-based eco-regionalization method of the Mediterranean Sea. *PLoS ONE*, 9: e111978. https://doi.org/10.1371/journal.pone.0111978.

Bevilacqua, S., S. Fraschetti, A. Terlizzi and F. Boero. 2009. The use of taxonomic distinctness indices in assessing patterns of biodiversity in modular organisms. *Mar. Ecol.*, 30: 151–163.

Blasi, C., G. Capotorti, R. Frondoni, D. Guida, B. Mollo, D. Smiraglia and L. Zavattero. 2011. Vegetation science and the ecoregional approach: a proposal for the ecological land classification of Italy. *Fitosociologia*, 48 (2): 75–82.

Boury-Esnault, N. and M. van Beveren. 1982. Les démosponges du plateau continental de Kerguelen-Heard. *Comité national français pour les recherches antarctiques*, 52: 175 pp.

Boyer, T.P., J.I. Antonov, O.K. Baranova, C. Coleman, H.E. Garcia, A. Grodsky, D.R. Johnson, R.A. Locarnini, A.V. Mishonov, T.D. O'Brien, C.R. Paver, J.R. Reagan, D. Seidov, I.V. Smolyar and M.M. Zweng. 2013. World Ocean Database 2013. In: Levitus, S. and A. Mishonov (Eds). *NOAA Atlas NESDIS 72*. Silver Spring, MD: p. 209, doi: 10.7289/V5NZ85MT.

Brandt, A., C. De Broyer, I. De Mesel, K. Ellingsen, A. Gooday, B. Hilbig, K. Linse, M. Thomson and P. Tyler. 2007a. The biodiversity of the deep Southern Ocean benthos. *Phil. Trans. R. Soc. Lond. B*, 362: 39–66.

Brandt, A., A.J. Gooday, S.N. Brandão, S. Brix, W. Brökeland, T. Cedhagen, M. Choudhury, N. Cornelius, B. Danis, I. De Mesel, R.J. Diaz, D.C. Gillan, B. Ebbe, J.A. Howe, D. Janussen, S. Kaiser, K. Linse, M. Malyutina, J. Pawlowski, M. Raupach and A. Vanreusel. 2007b. First insights into the biodiversity and biogeography of the Southern Ocean deep sea. *Nature*, 447: 307–311.

Cattaneo-Vietti, R., M. Chiantore, M. Gambi, G. Albertelli, M. Cormaci and I. Di Geronimo. 2000. Spatial and vertical distribution of benthic littoral communities in Terra Nova Bay. *Ross Sea Ecology*, Springer: 503–514.

SC-CCAMLR. 2009. Report of the Workshop on Vulnerable Marine Ecosystems. In: *Report of the Twenty-eighth Meeting of the Scientific Committee (SC-CAMLR-XXVIII)*, Annex 10. CCAMLR, Hobart, Australia: 537–571.

Chiantore, M., R. Cattaneo-Vietti, P.A. Berkman, M. Nigro, M. Vacchi, S. Schiaparelli and G. Albertelli. 2001. Antarctic scallop (*Adamussium colbecki*) spatial population variability along the Victoria Land Coast, Antarctica. *Polar Biol.*, 24 (2): 139–143.

Dauby, P., Y. Scailteur, G. Chapelle and C. De Broyer. 2001. Potential impact of the main benthic amphipods on the eastern Weddell Sea shelf ecosystem (Antarctica). *Polar Biol.*, 24 (9): 657–662.

David, B. and R. Mooi. 2000. A new species of subantarctic *Plexechinus* and its phylogenetic position within the Holasteroida (Echinodermata: Echinoidea). *Polar Biol.*, 23 (3): 166–172.

Dayton, P.K. 1972. Toward an understanding of community resilience and the potential effects of enrichments to the benthos at McMurdo Sound, Antarctica. In: Parker, B.C. (Ed.). *Proceedings of the Colloquium on Conservation Problems in Antarctica*. Allen Press, Lawrence, KS: 81–96.

Dayton, P. and R. Hessler. 1972. Role of biological disturbance in maintaining diversity in the deep sea. *Deep-Sea Res.*, 19: 199–208.

Dayton, P.K., G.A. Robilliard, R.T. Paine and L.B. Dayton. 1974. Biological accommodation in the benthic community at McMurdo Sound, Antarctica. *Ecol. Monogr.*, 44: 105–128.

Douglass, L.L., J. Turner, H.S. Grantham, S. Kaiser, A. Constable, R. Nicoll, B. Raymond, A. Post, A. Brandt and D. Beaver. 2014. A Hierarchical classification of benthic biodiversity and assessment of protected areas in the Southern Ocean. *PLoS ONE*, 9: e100551. https://doi.org/10.1371/journal.pone.0100551.

Dufrêne, M. and P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecol. Monogr.*, 67 (3): 345–366.

Duhamel, G. (Ed.). 2011. *Poker 2, 2ème campagne d'évaluation de la biomasse de poissons à Kerguelen*. Muséum national d'Histoire naturelle, Paris: 279 pp.

Duhamel, G., P. Pruvost, M. Bertignac, N. Gasco and M. Hautecoeur. 2011. Major fishery events in Kerguelen Islands: *Notothenia rossi*, *Champsocephalus gunnari*, *Dissostichus eleginoides*. Current distribution and status of stocks. In: Duhamel, G. and D. Welsford (Eds). *The Kerguelen Plateau: marine ecosystem and fisheries*. Société Française d'Ichtyologie, Paris: 275–286.

Duranton, J.-F., A. Monard and R.S. Morales 2006. Contribution à l'étude de la bio-écologie de deux locustes péruviens, *Schistocerca* cf. *interrita* Scudder 1899 et *Schistocerca piceifrons peruviana* Lynch Arribalzaga 1903 (Orthoptera, Cyrtacanthacridinae). *J. Orthoptera Res.*, 15: 157–169.

Eléaume, M., L.G. Hemery, D.A. Bowden and M. Roux. 2011a. A large new species of the genus *Ptilocrinus* (Echinodermata, Crinoidea, Hyocrinidae) from Antarctic seamounts. *Polar Biol.*, 34 (9): 1385–1397.

Eléaume, M., C. Moreau, P. Laffargue, L. Hemery, M. Hautecoeur, N. Gasco, A. Martin, N. Chai, C. Mah and N. Améziane. 2011b. Caractérisation et distribution des assemblages benthiques du Plateau de Kerguelen. In: Duhamel, G. (Ed.). 2011. *Poker 2, 2ème campagne d'évaluation de la biomasse de poissons à Kerguelen*. Muséum national d'Histoire naturelle, Paris: 279 pp.

Féral, J. and E. Poulin. 2011. Kerguelen Islands: a living laboratory to understand the benthic biodiversity of the Antarctic. In: Duhamel, G. and D. Welsford (Eds). *The Kerguelen Plateau: marine ecosystem and fisheries*. Société Française d'Ichtyologie, Paris: 151–156.

Féral, J-P., T. Saucède, E. Poulin., C. Marschal, G. Marty, J.-C. Roca, S. Montreuil and J.-P. Beurier. 2016. PROTEKER: implementation of a submarine observatory at the Kerguelen Islands (Southern Ocean). *Underwater Technol.*, 34 (1): 3–10.

Ferrier, S., G. Manion, J. Elith and K. Richardson. 2007. Using generalized dissimilarity modelling to analyse and predict patterns of beta diversity in regional biodiversity assessment. *Divers. Distrib*, 13 (3): 252–264.

Fraschetti, S., G. Guarnieri, S. Bevilacqua, A. Terlizzi, J. Claudet, G.F. Russo and F. Boero. 2011. Conservation of Mediterranean habitats and biodiversity countdowns: what information do we really need? *Aquat. Conserv.*, 21 (3): 299–306.

Goslee, S.C. and D.L. Urban. 2007. The ecodist package for dissimilarity-based analysis of ecological data. *J. Stat. Softw.*, 22: 1–19.

Guillaumot, C., A. Martin, S. Fabri-Ruiz, M. Eléaume and T. Saucède. 2016. Echinoids of the Kerguelen Plateau – occurrence data and environmental setting for past, present, and future species distribution modelling. *ZooKeys*, 630: 1–17, doi: https://doi.org/10.3897/zookeys.630.9856.

Guillaumot, C., A. Martin, M. Eléaume and T. Saucède. 2018. Methods for improving species distribution models in data-poor areas: example of sub-Antarctic benthic species on the Kerguelen Plateau. *Mar. Ecol. Prog. Ser.*, 594: 149–164.

Gutt, J. 1991. On the distribution and ecology of holothurians in the Weddell Sea (Antarctica). *Polar Biol.*, 11 (3): 145–155.

Gutt, J. 2006. Coexistence of macro-zoobenthic species on the Antarctic shelf: An attempt to link ecological theory and results. *Deep-Sea Res. II*, 53 (8–10): 1009–1028, doi: https://doi.org/10.1016/j.dsr2.2006.02.012.

Gutt, J. 2007. Antarctic macro-zoobenthic communities: a review and an ecological classification. *Ant. Sci.*, 19: 165, doi: https://doi.org/10.1017/S0954102007000247.

Gutt, J. and T. Schickan. 1998. Epibiotic relationships in the Antarctic benthos. *Ant. Sci.*, 10: 398–405.

Gutt, J. and A. Starmans. 1998. Structure and biodiversity of megabenthos in the Weddell and Lazarev Seas (Antarctica): ecological role of physical parameters and biological interactions. *Polar Biol.*, 20: 229–247.

Hibberd, T. 2016. Describing and predicting the spatial distribution of benthic biodiversity in the sub-Antarctic and Antarctic (PhD Thesis). University of Tasmania: 153 pp.

Hill, N.A., S.D. Foster, G. Duhamel, D. Welsford, P. Koubbi and C.R. Johnson. 2017. Model-based mapping of assemblages for ecology and conservation management: A case study of demersal fish on the Kerguelen Plateau. *Divers. Distrib.*, 23: 1216–1230, doi: https://doi.org/10.1111/ddi.12613.

Hornsmann, I., R. Pesch, G. Schmidt and W. Schröder. 2008. Calculation of an Ecological Land Classification of Europe (ELCE) and its application for optimising environmental monitoring networks. In: *Geospatial Crossroads@ GI_Forum'08: Proceedings of the Geoinformatics Forum Salzburg*. Wichmann, Heidelberg: 140–151.

Hunter, J.T. and A.M. Lechner. 2018. A multiscale, hierarchical, ecoregional and floristic classification of arid and semi-arid ephemeral wetlands in New South Wales, Australia. *Mar. Freshw. Res.*, 69 (3): 418–431, doi: https://doi.org/10.1071/MF17006.

Hureau, J. 2011. Marine Research on the Kerguelen Plateau: from early scientific expeditions to current surveys under the CCAMLR objectives. In: Duhamel, G. and D. Welsford (Eds). *The Kerguelen Plateau: marine ecosystem and fisheries*. Société Française d'Ichtyologie, Paris: 5–13.

Ives, A.R. and M.R. Helmus. 2011. Generalized linear mixed models for phylogenetic analyses of community structure. *Ecol. Monogr.*, 81: 511–525.

Jazdzewski, K., C. Broyer, M. Pudlarz and D. Zielinski. 2001. Seasonal fluctuations of vagile benthos in the uppermost sublittoral of a maritime Antarctic fjord. *Polar Biol.*, 24: 910–917.

Johnson, R.K., T. Wiederholm and D.M. Rosenberg. 1993. Freshwater biomonitoring using individual organisms, populations, and species assemblages of benthic macroinvertebrates. In: Rosenberg, D.M. and V.H. Resh (Eds). *Freshwater biomonitoring and benthic macroinvertebrates*. Chapman and Hall: 40–158.

Kaufman, L. and P. Rousseeuw. 1987. Clustering by means of medoids. Data Analysis based on the L1-Norm and Related Methods: 405–416.

Koubbi, P., C. Ozouf-Costaz, A. Goarant, M. Moteki, P.-A. Hulley, R. Causse, A. Dettai, G. Duhamel, P. Pruvost, E. Tavernier, A.L. Post, R.J. Beaman, S.R. Rintoul, T. Hirawake, D. Hirano, T. Ishimaru, M. Riddle and G. Hosie. 2010. Estimating the biodiversity of the East Antarctic shelf and oceanic zone for ecoregionalisation: Example of the ichthyofauna of the CEAMARC (Collaborative East Antarctic Marine Census) CAML surveys. *Polar Sci.*, 4: 115–133, doi: https://doi.org/10.1016/j.polar.2010.04.012.

Koubbi, P., C. Guinet, N. Alloncle, N. Ameziane, C.S. Azam, A. Baudena, C.A. Bost, R. Causse, C. Chazeau, G. Coste, C. Cotté, F. D'Ovidio, K. Delord, G. Duhamel, A. Forget, N. Gasco, M. Hautecœur, P. Lehodey, C. Lo Monaco, C. Marteau, A. Martin, C. Mignard, P. Pruvost, T. Saucède, R. Sinegre, T. Thellier, A.G. Verdier and H. Weimerskirch 2016. Ecoregionalisation of the Kerguelen and Crozet islands oceanic zone. Part I: Introduction and Kerguelen oceanic zone. Document *WG-EMM-16/43*. CCAMLR, Hobart, Australia.

Kremen, C. 1992. Assessing the indicator properties of species assemblages for natural areas monitoring. *Ecol. Appl.*, 2: 203–217.

Leathwick, J.R., T. Snelder, W.L. Chadderton, J. Elith, K. Julian and S. Ferrier. 2011. Use of generalied dissimilarity modelling to improve the biological discrimination of river and stream classifications: River classification for conservation management. *Freshw. Biol.*, 56: 21–38, doi: https://doi.org/10.1111/j.1365-2427.2010.02414.x.

Leitao, P.J., M. Schwieder, S. Suess, I. Catry, E.J. Milton, F. Moreira, P.E. Osborne, M.J. Pinto, S. Linden and P. Hostert. 2015. Mapping beta diversity from space: Sparse Generalised Dissimilarity Modelling (SGDM) for analysing high-dimensional data. *Methods Ecol. Evol.*, 6: 764–771.

McClintock, J.B., C.D. Amsler, B.J. Baker and R.W. Van Soest. 2005. Ecology of Antarctic marine sponges: an overview. *Integr. Comp. Biol.*, 45: 359–368.

McCoy, F.W. 1991. Southern Ocean Sediments: Circum-Antarctic to 30°S. In: Hayes, D.E. (Ed.). *Marine Geological and Geophysical Atlas of the Circum-Antarctic to 30°S*, 54: 37–46.

McCullagh, P. and J. Nelder. 1989. Binary data. In: *Generalized Linear Models*. Springer: 98–148.

Marshall, C.E., G.A. Glegg and K.L. Howell. 2014. Species distribution modelling to support marine conservation planning: The next steps. *Marine Policy*, 45: 330–332, doi: https://doi.org/10.1016/j.marpol.2013.09.003.

Martin, A., M. Eléaume, N. Améziane, P. Pruvost and G. Duhamel. 2017. New data acquisition protocol for benthos by-catch in the French fisheries of the Southern Ocean, presentation of

the protocol and first preliminary results. Document *WG-EMM-17/09*. CCAMLR, Hobart, Australia.

Martin, A., J. Blettery, N. Améziane and M. Eléaume. 2018. Benthos bycatch study and benthic cameras deployment during the Poker 4 fish biomass survey for habitat characterization in the Kerguelen Plateau. In: *Poker 4, 4ème campagne d'évaluation de la biomasse de poissons à Kerguelen*. Muséum national d'Histoire naturelle, Paris, France: 241–254.

Monniot, C. and F. Monniot. 1983. Ascidies antarctiques et subantarctiques: morphologie et biogéographie. *Mémoires du Muséum National d'Histoire Naturelle, Paris*, (A), 125: 168 pp.

Mukaka M. M. 2012. Statistics corner: A guide to appropriate use of correlation coefficient in medical research. *Malawi Med. J.*, 24 (3): 69–71.

NASA Goddard Space Flight Center, Ocean Biology Processing Group 2014. MODIS Ocean Color Data, NASA OB.DAAC, Greenbelt, MD, USA. https://oceandata.sci.gsfc.nasa.gov/MODIS-Aqua/Mapped/Daily/4km/chlor_a/. Maintained by NASA Ocean Biology Distributed Active Archive Center (OB.DAAC), Goddard Space Flight Center, Greenbelt MD.

O'Hara, T. 2008. Bioregionalisation of Australian waters using brittle stars Echinodermata: Ophiuroidea, a major group of marine benthic invertebrates. Department of the Environment, Water, Heritage and Arts, Australia: 69 pp.

Pardo, I., and P.D. Armitage. 1997. Species assemblages as descriptors of mesohabitats. *Hydrobiologia*, 344: 111–128.

Park, Y. and F. Vivier. 2011. Circulation and hydrography over the Kerguelen Plateau. In: Duhamel, G. and D. Welsford (Eds) *The Kerguelen Plateau: marine ecosystem and fisheries*. Société Française d'Ichtyologie, Paris: 43–55.

Picken, G. 1980. Reproductive adaptations of Antarctic benthic invertebrates. *Biol. J. Linn. Soc.*, 14: 67–75.

Piepenburg, D., M.K. Schmid and D. Gerdes. 2002. The benthos off King George Island (South Shetland Islands, Antarctica): further evidence for a lack of a latitudinal biomass cline in the Southern Ocean. *Polar Biol.*, 25: 146–158.

QGIS Development Team, 2017. QGIS Geographic Information System. Open Source Geospatial Foundation Project. http://qgis.osgeo.org.

R Development Core Team. 2015. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

Ramos-Merchante, A. and J. Prenda. 2017. Macroinvertebrate taxa richness uncertainty and kick sampling in the establishment of Mediterranean rivers ecological status. *Ecol. Indic.*, 72: 1–12, doi: https://doi.org/10.1016/j.ecolind.2016.07.047.

Reygondeau, G., S.D. Ayata, C. Gasparini, C. Guieu, J.-O. Irisson and P. Koubbi. 2014. Definition of the Mediterranean eco-regions and maps of potential pressures in these eco-regions. In: *Policy oriented marine Environmental Research in the Southern European Seas (PERSEUS), Deliverable No. 1.6*: 45 pp.

Rose, P.M., M.J. Kennard, F. Sheldon, D.B. Moffatt and G.L. Butler. 2016. A data-driven method for selecting candidate reference sites for stream bioassessment programs using generalised dissimilarity models. *Mar. Freshw. Res.*, 67: 440, doi: https://doi.org/10.1071/MF14254.

Rousseeuw, P.J. 1987. Silhouettes: a graphical aid to the interpretation and validation of cluster analysis. *J. Comput. Appl. Math.*, 20: 53–65.

Shojaei, M. 2016. Developments in German Bight benthic ecology driven by climate change and anthropogenic utilisation (PhD Thesis). University Bremen, Germany: 163 pp.

Smith, C.R., S. Mincks and D.J. DeMaster. 2006. A synthesis of bentho-pelagic coupling on the Antarctic shelf: Food banks, ecosystem inertia and global climate change. *Deep-Sea Res. II*, 53: 875–894, doi: https://doi.org/10.1016/j.dsr2.2006.02.001.

Smith, W.H. and D.T. Sandwell. 1997. Global sea floor topography from satellite altimetry and ship depth soundings. *Science*, 277: 1956–1962.

TAAF. 2017. Arrêté n°2017-28 du 31 mars 2017 instituant un périmètre de protection autour de la réserve naturelle nationale des Terres australes françaises.

TAAF. 2014. Journal Officiel des Terres Australes et Antarctiques Françaises n°63, 3 ème trimestre 2014.

Thrush, S.F., J.E. Hewitt, M. Gibbs, C. Lundquist and A. Norkko. 2006. Functional role of large organisms in intertidal communities: community effects and ecosystem function. *Ecosystems*, 9: 1029–1040.

van Proosdij, A.S.J., M.S.M. Sosef, J.J. Wieringa and N. Raes. 2016. Minimum required number of specimen records to develop accurate species distribution models. *Ecography*, 39 (6): 542–552, doi: https://doi.org/10.1111/ecog.01509.

Ward, T., M. Vanderklift, A. Nicholls and R. Kenchington. 1999. Selecting marine reserves using habitats and species assemblages as surrogates for biological diversity. *Ecol. Appl.*, 9: 691–698.

Welsford, D., A. Constable and G. Nowara. 2011. The Heard Island and McDonald Islands marine reserve and conservation zone: a model for Southern Ocean marine reserves. In: Duhamel, G. and D. Welsford (Eds). *The Kerguelen Plateau: marine ecosystem and fisheries*. Société Française d'Ichtyologie, Paris: 297–304.

Welsford, D.C., G.P. Ewing, A.J. Constable, T. Hibberd and R. Kilpatrick. 2013. Demersal fishing interactions with marine benthos in the Australian EEZ of the Southern Ocean: an assessment of the vulnerability of benthic habitats to impact by demersal gears. The Department of the Environment, Australian Antarctic Division and the Fisheries Research and Development Corporation: 266 pp.

Wright, D.H. and J.H. Reeves. 1992. On the meaning and measurement of nestedness of species assemblages. *Oecologia*, 92: 416–428.

Zimmermann, A. and A. Brandt. 1992. New results of the '"EPOS" leg 3 cruise to Antarctica: Horizontal and vertical distribution of isopods (Crustacea) in the eastern Weddell Sea. In: Hempel, G. (Ed.). *Weddell Sea Ecology*. Springer: 121–128.