

Vulnerable, but still poorly known, marine ecosystems:  
how to make distribution models more relevant and  
impactful for conservation and management of VMEs?

## Authors

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# Abstract

Context: Human activity puts our oceans under multiple stresses, whose impacts are already significantly affecting biodiversity and physicochemical properties. Consequently, there is an increased international focus on the conservation and sustainable use of oceans, including the protection of fragile benthic biodiversity hotspots in the deep sea, identified as vulnerable marine ecosystems (VMEs). International VME risk assessment and conservation efforts are hampered because we largely do not know where VMEs are located. VME distribution modelling has increasingly been recommended to extend our knowledge beyond sparse observations. Nevertheless, the adoption of VME distribution models in spatial management planning and conservation remains limited.

Methods: This work critically reviews VME distribution modelling studies, and recommends promising avenues to make VME models more relevant and impactful for policy and management decision making.

Results: First, there is an important interplay between the type of VME data used to build models and how the generated maps can be used in making management decisions, which is often ignored by model-builders. We encourage scientists towards founding their models on: (i) specific and quantitative definitions of what constitute a VME, (ii) site conservation value assessment in relation to VME multi-taxon spatial predictions, and (iii) explicitly mapping vulnerability.

Policy implications: Along with the recent increase in both deep-sea biological and environmental data quality and quantity, these modelling recommendations can lead towards more cohesive summaries of VME's spatial distributions and their relative vulnerability, which should facilitate a more effective protection of these ecosystems, as has been mandated by numerous international agreements.

## Key-words

Biogeography, Environmental impact assessment, Habitat suitability model, Marine conservation, Marine management, Species distribution model, Vulnerable marine ecosystems.

# 1. Introduction

Deep sea biodiversity is highly diverse, poorly understood (Ramirez-Llodra et al., 2010; Thurber et al., 2014) but threatened by a combination of multiple stresses as a result of human activity (M. R. Clark, Althaus, et al., 2016; Danovaro et al., 2017). Since 2006, the UN General Assembly (UNGA) adopted a series of resolutions dedicated to the protection of fragile benthic biodiversity hotspots in the deep sea, collectively called vulnerable marine ecosystems (VMEs). Resolution 61/105 (UNGA, 2006, p. 105) calls upon States and Regional Fisheries Management Organisations / Arrangements (RFMO/As) to identify areas beyond national jurisdiction where VMEs occur, or are likely to occur, in order to prevent significant adverse impacts from damaging fishing practices. In 2009, the Food and Agriculture Organization (FAO) established five criteria (FAO, 2009) that define VMEs: (i) uniqueness or rareness, (ii) functional significance of the habitat, (iii) fragility, (iv) life-history of species that makes recovery difficult, (v) structural complexity. Overall, the vulnerability refers to the likelihood that an ecosystem will be irreversibly altered by a short-term or chronic disturbance.

Periodic reviews of the implementation of the 61/105 UNGA resolution have noted systematic failures to properly map VMEs, and judged their protection as

insufficient (Bell et al., 2019; Gianni et al., 2016; Rogers & Gianni, 2010; Thompson et al., 2016). VMEs protection is directly hampered by the fact that the vast majority of the deep-sea has not been sampled (M. R. Clark, Consalvey, et al., 2016), hence its benthic composition remains mostly unknown (Weaver et al., 2011). Increasing our knowledge about VMEs, including their spatial distribution, composition, vulnerability and environmental requirements, is crucial in order to provide a more holistic protection (Chimienti et al., 2018). Although many studies urged for the application of the highly precautionary management of deep-sea benthic ecosystems (M. R. Clark, Althaus, et al., 2016; Watling & Auster, 2017), its implementation in the deep sea remains, to date, highly limited (Bell et al., 2019; Norse et al., 2012; Thompson et al., 2016). Therefore, frameworks that can make the best of the data we have (e.g., highlighting where the key uncertainties lie, improve our VMEs knowledge into poorly sampled areas) are valuable.

What we do know about the location of VMEs typically derive from when VME indicator taxa are caught as a bycatch in fisheries gear (Ardrón et al., 2014; Blicher & Arboe, 2021; Carbonara et al., 2020) or, to a lesser extent are captured by scientific surveys (Baco et al., 2020; Dautova et al., 2019; Du Preez et al., 2020; Long et al., 2020; Salinas-de-León et al., 2020). Because the former is destructive and has a limited sampling ability (Watling & Auster, 2017) and the latter is very expensive, these techniques are not suitable to be used at large spatial scales. To extend our knowledge beyond these sparse observations, VME distribution modelling has been increasingly used (Ardrón et al., 2014; Thompson et al., 2016; Vierod et al., 2014). Essentially, VME distribution modelling aims at predicting the suitability of a location for a VME, based

on their observed relationship with environmental conditions. By collating all available information, distribution modelling provides a coherent analysis framework to highlight unsampled, and often remote, areas that may harbour VME. Apart from very recent works in the North Atlantic and South Pacific RFMOs (e.g., (ICES, 2019; A. Rowden & Anderson, 2019)), VME distribution models have yet to realise any substantial impact on conservation and management measures, and translating modelling insights to policy-decisions remains relatively limited (Ardron et al., 2014; Bell et al., 2019; Gianni et al., 2016; A. A. Rowden et al., 2020; Thompson et al., 2016; Vierod et al., 2014). The main reasons for this are: (i) the overall disagreement about what constitutes a VME, (ii) the inherent uncertainty of model predictions, especially since most are fitted on highly imperfect observations from fishery bycatch data, and (iii) model outputs are not always easily understandable or relevant for environmental managers and conservationists.

In this study, we provide a comprehensive and critical review of VME distribution modelling and some perspectives to guide future modelling efforts towards a better integration into policy and management. In particular, we highlight modelling challenges related to the type of data used to build VME models, which model-builders need to be aware of in order to appropriately inform user groups (section 2). Besides, we underline how the lack of quantitative standards of what constitutes a VME limits the models' applicability (section 3), and recommend a multi-criteria and -taxa modelling approach to map the vulnerability of marine ecosystems, to produce VME mappings that are more cohesive and relevant for environmental managers and conservationists (section 4).

## 2. Connections between the type of VME data and model use

The interpretability of VME model predictions directly depends on the underlying data used for model building, meaning the data's characteristics need to match their application (Guillera-Arroita et al., 2015). VME observations mainly come from two sampling methods: (i) by physical sampling, e.g. bycatch of fishing gear and scientific benthic survey, or (ii) using underwater imagery, e.g. towed cameras, Remotely Operated Vehicle or Autonomous Underwater Vehicle. Different gear will have different selectivity. In this section, we discuss the consequences of using a certain type of data on the VME modelling and on its interpretability in regard to the FAO guidelines.

The probability of detecting a VME,  $P$ , at a given location can be expressed by:

$$P(0) = (1 - P_p) + P_p(1 - P_s)$$

$$P(> 0) = P_s P_p$$

where  $P(>0)$  is the probability of detecting a VME when present,  $P_p$  is probability of VME occurrence (which may be expressed as a Poisson distribution), and  $P_s$  is the probability of detecting that a VME is present (which may be a function of a number of variables). VME data may be a function of the full joint Poisson distribution (i.e., abundance data), truncated as a joint Bernoulli distribution (i.e., presence / absence data,  $P(1)$  and  $P(0)$ ), or truncated so that only presence is recorded (i.e., presence-only data as there is no information on  $P(0)$ ). As more information is lost (i.e., going from abundance

to presence-only), model estimation becomes more difficult and the internal variability of both response and covariate data may be such that robust estimation is no longer possible.

(Guillera-Arroita et al., 2015) provide a clear overview of how data characteristics determine how the predictions from species distribution models should be (but often are not) interpreted. Building on (Guillera-Arroita et al., 2015), Fig. 1 illustrates how model interpretation varies depending on the type of estimates yielded by the model, i.e. rank suitability, relative likelihood, true probability of occurrence, or density, which is in turn influenced by the data type. In simple terms, when  $P_s$  decreases, our confidence in being able to have reliable Presence-Absence data decreases. Rank suitability estimation provides a ranked order of suitable sites for harbouring a VME, which is not proportional to the actual probability of occurrence, i.e. does not indicate how suitable a site is for harbouring a VME, with  $P_s$  unreliable. In contrast to rank suitability, the relative likelihood is *proportional* to the probability of occurrence  $P_p$ . Both rank suitability and relative likelihood can be used to discriminate sites, i.e. distinguish between occupied and unoccupied sites better than random. However, to estimate the relative likelihood is not sufficient for comparing across multiple modelled taxa or habitats and / or regions. In order to estimate the true probability of occurrence for a VME, models need to be fitted on presence-absence data with reliable detectability of taxa  $P_s$  (Guillera-Arroita et al., 2015). Further, when abundance data are available, the model can estimate density or percentage cover of indicator taxa.



Biological data	Predictions	Interpretation	Ability									
<p>① Presence-only <math>P_S &lt; 1</math></p>	<p><i>Ranked suitab. of occ.</i></p> <table border="1"> <tr><td>0.4</td><td>0.4</td><td>0.1</td></tr> <tr><td>0.1</td><td>0.1</td><td>0</td></tr> <tr><td>0</td><td>0</td><td>0.1</td></tr> </table>	0.4	0.4	0.1	0.1	0.1	0	0	0	0.1	<p>"VME taxon is <b>more likely</b> to occur <b>here</b> than <b>here</b>."</p>	<p>✓ Discrimination</p>
	0.4	0.4	0.1									
	0.1	0.1	0									
	0	0	0.1									
<p>② Presence-absence <math>P_S &lt; 1</math> but constant</p>	<p><i>Rel. likelihood of occ.</i></p> <table border="1"> <tr><td>0.8</td><td>0.8</td><td>0.4</td></tr> <tr><td>0.4</td><td>0.4</td><td>0</td></tr> <tr><td>0</td><td>0</td><td>0.4</td></tr> </table>	0.8	0.8	0.4	0.4	0.4	0	0	0	0.4	<p>"VME taxon is <b>twice as likely</b> to occur <b>here</b> than <b>here</b>."</p>	<p>✓ Discrimination</p>
	0.8	0.8	0.4									
	0.4	0.4	0									
	0	0	0.4									
<p>③ Presence-absence <math>P_S = 1</math></p>	<p><i>Prob. of occ.</i></p> <table border="1"> <tr><td>1</td><td>1</td><td>0.5</td></tr> <tr><td>0.5</td><td>0.5</td><td>0</td></tr> <tr><td>0</td><td>0</td><td>0.5</td></tr> </table>	1	1	0.5	0.5	0.5	0	0	0	0.5	<p>"VME taxon has <b>50% probability</b> of occurrence <b>here</b>."</p>	<p>✓ Discrimination ✓ Calibration ✓ Comparison across VME taxa</p>
	1	1	0.5									
	0.5	0.5	0									
	0	0	0.5									
<p>④ Abundance <math>P_S = 1</math></p>	<p><i>Density</i></p> <table border="1"> <tr><td>79</td><td>54</td><td>11</td></tr> <tr><td>15</td><td>13</td><td>0</td></tr> <tr><td>0</td><td>0</td><td>9</td></tr> </table>	79	54	11	15	13	0	0	0	9	<p>"VME taxon has a predicted density of <b>15 ind. / m<sup>2</sup></b> <b>here</b>."</p>	<p>✓ Discrimination ✓ Calibration ✓ Comparison across VME taxa ✓ Community composition</p>
	79	54	11									
	15	13	0									
	0	0	9									

**Figure 1. Influence of the VME data characteristics on the interpretability of the model's predictions.** The probability of detectability  $P_S$  directly impacts the characteristics of the model predictions, and therefore their interpretability. Abbreviations: ind.: individuals ; occ.: occurrence ; Prob.: probability ; Rel.: Relative ; suitab.: suitability ; VME: Vulnerable Marine Ecosystem.

Fishing gears have generally a low catchability for benthic organisms, especially for small, fragile and brittle VME taxa (Auster et al., 2011; Watling & Auster, 2017). Fishing gears are typically designed to catch or attract motile species, as opposed to providing representative samples of VME indicator taxa:  $P_S$  is small and unreliable. Moreover, there is a lack of consistency across fisheries management regarding data

collection of VME indicator taxa (Thompson et al., 2016). As a result, taxa may be present (and impacted) by fishing gears, but not all are necessarily caught, brought to the surface and / or reported (Du Preez et al., 2020; Knudby et al., 2013; Watling & Auster, 2017). Therefore, VME data acquired with fishing gear is widely considered as “Presence-only” data (i.e., no “true absence” data,  $P(0)$ , available) with highly imperfect detection (i.e.,  $P_s \ll 1$ ). With poor confidence in estimating  $P_s$ , we are marginalising over  $P_s$  to give a relative measure (see Fig. 1). Besides fisheries bycatch data, some scientific physical sampling gear have been specifically designed for benthic ecosystems, such as benthic sleds, yielding “Presence-absence” or “Abundance” data with reliable benthic species detectability  $P_s$  (Williams et al., 2015). However, physical sampling gear only allows indicator taxa collection, since the identification of habitats generally requires direct observation, e.g. via imagery. Although VME data to date have been largely collected with physical sampling gear, these aforementioned restrictions, both on model predictions and the modelled biotic entity, impact the interpretation against the FAO criteria. Further, because physical sampling methods can permanently impact individuals and assemblages, these methods should be avoided for sampling vulnerable ecosystems (Williams et al., 2015).

Underwater imagery allows sampling the seafloor with a reliable detectability of most taxa  $P_s$  (Long et al., 2020; Williams et al., 2015). It is generally considered that “Presence-absence” data can be derived from these images since most VME taxa are sessile or with a limited mobility. This kind of data can be used to create models that are: (i) discriminative (i.e., occupied vs. unoccupied sites), (ii) well-calibrated (i.e., exact

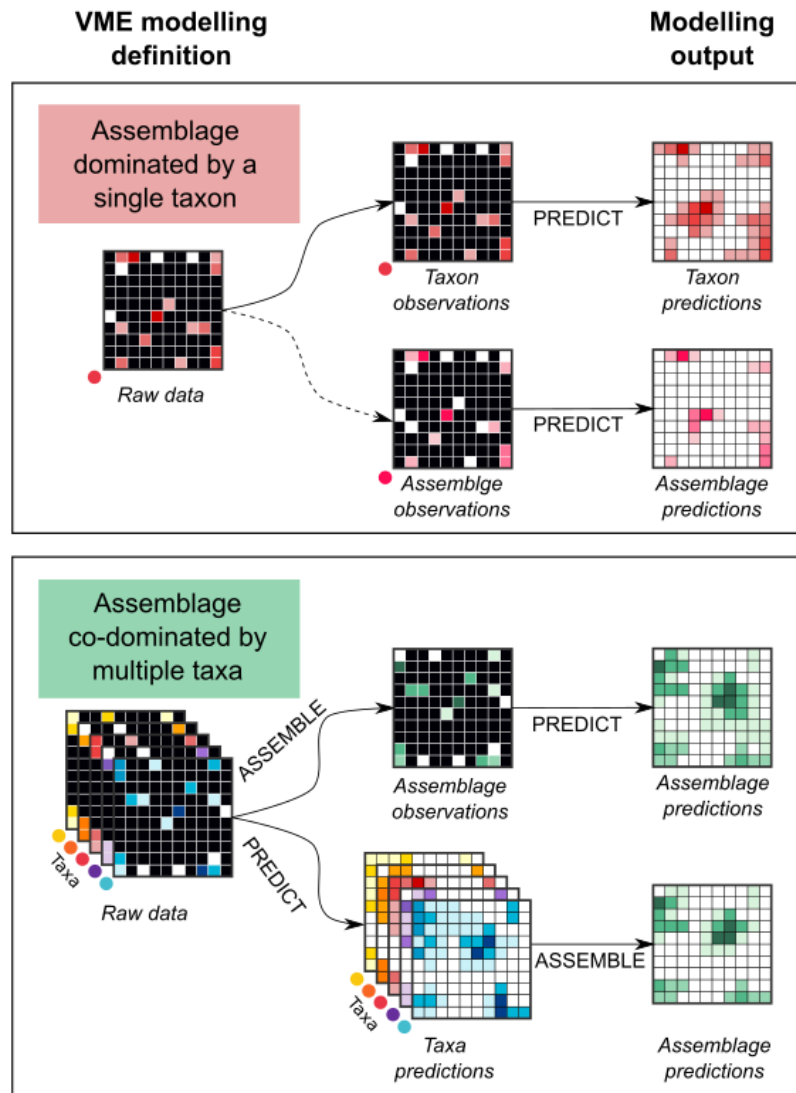
probability, not relative), and (iii) comparable among VME entities and / or regions (see Fig. 1). Importantly, habitat identification and / or accurate VME taxa abundance can be extracted from images (Williams et al., 2015), which is important for addressing the FAO criteria. Underwater imagery allows finer model resolution, e.g. 25 m<sup>2</sup> in (A. A. Rowden et al., 2017). Nevertheless, imagery scientific surveys in the deep sea are rare which restricts the scale of those datasets compared to the ones derived from fishing vessels.

### 3. Limited translation of the FAO criteria into modelling

The FAO guidelines are (intentionally) generic and non quantitative, which makes their interpretation prone to expert-subjectivity (Howell et al., 2011; Watling & Auster, 2017). The UNGA explicitly left to the RFMO/As the responsibility to refine the VME definition relatively to their jurisdiction, which has led to differing interpretations by model-builders and experts in separate RFMO/As (Bell et al., 2019; Long et al., 2020; Thompson et al., 2016). While the original rationale for the UNGA resolutions was to halt the impact to structurally complex, habitat forming, slow growing and brittle assemblages of deep sea benthos, the lack of agreement as to what “vulnerability” means and what a VME is, has been a huge and unproductive time sink.

#### 3.1. Lack of consensus about how to model a VME

In distribution modelling studies, VMEs have most often been considered as either assemblages dominated by a single indicator taxon or co-dominated by multiple indicator taxa. Within these two categories, different modelling approaches have been proposed, each with different implications for identifying VMEs using the FAO criteria. Fig. 2 illustrates the different approaches based on how VMEs have been defined by model-builders.



**Figure 2. VME definition used in distribution modelling.** VMEs can be modelled either considering them as an assemblage either dominated by a single taxon (top), or co-dominated by multiple taxa (bottom). In the first case, the modelling uses the indicator taxon distribution (e.g., cold-water coral *Lophelia pertusa*), or the assemblage dominated by this taxon (e.g., coral reef). When using the multiple taxa approach, the assemblage is modelled with either the “Assemble then Predict” or the “Predict then Assemble” approach.

When VMEs are defined as an assemblage dominated by a single indicator taxon, two approaches are usually employed: either by modelling the distribution of the indicator taxon, as a proxy for the associated assemblage, or by modelling the distribution of the assemblage itself (see Fig. 2, top panel). Most studies model the distribution of the VME indicator taxon instead of the associated assemblage. However, the occurrence of a VME indicator taxon alone is not sufficient to properly identify a VME (FAO, 2009; Howell et al., 2011; Watling & Auster, 2017), as it does not provide evidence of a habitat with important functional significance, see FAO “functionality” criterion. The distribution of a VME assemblage often represents only a small subset of the distribution of its associated dominating indicator taxon, especially when the assemblage requires environmental factors that are more restrictive than for the occurrence of the taxon. For instance, (Howell et al., 2011) model and compare the distribution of a cold-water coral (*Lophelia pertusa*, VME indicator taxon) vs. the reef it forms (assemblage forming a VME habitat), and show that the predicted area of high suitability for the taxon is much broader than for the assemblage (7.17% vs. 0.56% of the studied area). To model VMEs using assemblage data is however limited by the scarce availability of this data type, since it generally requires underwater imagery sampling (see section 2), and by the lack of consensus around the quantitative definition of VME assemblages, e.g. composition or density of taxa (A. A. Rowden et al., 2020).

When VMEs are defined as an assemblage of multiple indicator taxa, there are two components to the modelling approach: defining the assemblage (“Assemble”) and making predictions (“Predict”). These generally occur separately and can be in either

order, i.e. “Assemble first then Predict” or “Predict first then Assemble”, as defined in (Ferrier & Guisan, 2006), see Fig. 2 bottom panel. The “Assemble first then Predict” aims at predicting the occurrence of predefined benthic assemblages, e.g. circalittoral vertical rocky walls with *Caryophyllia cyathus* and *Corallium rubrum* in (Torriente et al., 2019). These assemblages can be defined by: (i) prior knowledge, e.g. biotopes known to occur in the area of interest (Bo et al., 2021), (ii) expert judgement using phylogenetic and functional diversity metrics, or (iii) cluster and ordination analysis (Barrio Froján et al., 2016; Torriente et al., 2019). Importantly, this approach cannot provide insights on environmental requirements of each taxon and can lead to an artificially wide niche description (Brewin et al., 2020; Yesson et al., 2012). The “Predict first then Assemble” approach models and predicts the spatial distribution of each VME taxon before assembling model outputs. It allows assemblage characterisation, e.g. species composition and their environmental requirements (Hill et al., 2020). For instance, (J. W. Chu et al., 2020) combined predictions from individual models developed for each cold-water corals and sponges group to identify areas as suitable assemblage for multiple biogenic habitat-forming species. In VME studies, the individual taxon predictions have mostly been assembled based on *a priori* beliefs about how assemblages are structured (e.g. grouping by higher taxonomic level (Yesson et al., 2012) or functionality (Davies & Guinotte, 2011)), which may not reflect real distribution patterns or confer a limited ecological interpretability (Jansen et al., 2018).

### 3.2. Lack of quantitative standards of what constitutes a VME

To identify a VME in accordance with the FAO guidelines, the five criteria need to be encoded into the modelling approach. However, most VME distribution modelling studies focused on predicting suitable locations for VME indicator taxa, which provides an incomplete assessment according to the multi-criteria guidelines. Nevertheless, the translation of the FAO criteria into modelling terms remains unclear, especially for the “functionality” and “structural complexity” criteria. The “functionality” of an ecosystem cannot be easily modelled given the current FAO VME definition and the available knowledge of these remote ecosystems. The “structural complexity” of a habitat can potentially be assessed if abundance data with excellent detectability is available, e.g. by characterising the density and / or the morphologies of the biotic and abiotic features.

The FAO guidelines do not specify what constitutes a “significant concentration” (Auster et al., 2011; A. A. Rowden et al., 2020; Vierod et al., 2014). A quantitative criteria is needed to distinguish dense aggregations of VME taxa that form a “structurally complex habitat” from low frequency occurrences of VME indicator taxa. Most RFMO/As have established operational definitions based on thresholds of VME indicator taxa caught as fisheries bycatch (Bell et al., 2019), which then triggers precautionary management actions, e.g. CCAMLR conservation measure CM 22-07 (CCAMLR, 2013). However, the relevance of these operational encounter thresholds has been questioned (Ardron et al., 2014; Auster et al., 2011; Geange et al., 2020; Watling & Auster, 2017) because they (i) have undergone limited scientific validation and, (ii) are



not taxon specific, and therefore do not take into account the differential catchability of taxa and their differential vulnerability, distribution or life history characteristics. In addition, VME extent is operationally defined in many RFMO/As by an arbitrary distance around the location where a certain amount of VME indicator taxa has been encountered, e.g. CCAMLR conservation measure CM 22-07 (CCAMLR, 2013), often without further scientific investigation. Further work is then needed to establish quantitative references, scientifically validated, of what constitutes a VME, both in terms of taxon abundance and VME extent.

## 4. Making VME distribution models more relevant for conservation and management decisions

VME distribution models have had limited impact on conservation and management measures to date, partly because their outputs cannot be directly assessed against the FAO criteria and because quantitative standards of what constitutes a VME are lacking. To tackle these issues, our recommendations for the future generation VME models are three fold: VME identification from models should (i) be ruled by a specific and quantitative definition of what constitutes a VME, (ii) assess the entire ecosystem conservation value instead of focusing on a single indicator taxon distribution, and (iii) model the vulnerability of an area instead of its suitability to harbour a vulnerable species.

### 4.1. Establish a quantitative and more specific definition of VMEs

The FAO VME identification guidelines are policy-oriented and their translation into modelling is not straightforward, see section 3.2. There is a need for VME identification criteria which are both model-oriented and user-specific. Therefore, we recommend early and iterative communication between model-users and -builders to converge on quantitative VME identification criteria that are suitable to the user's need.

To find a multi-country and multi-stakeholder consensus is often challenging. Therefore, the involvement of as many parties as possible during the different steps of the modelling process increases the likelihood of models' acceptance and of a successful spatial management planning outcome (Ardron et al., 2014; A. A. Rowden et al., 2019).

Unlike the occurrence or abundance of a species which are absolute measures, vulnerability is relative and qualitative, i.e. it is a spectrum, from hardy and resilient to fragile and vulnerable, and dependent on a specific threat, specific region, etc. To ensure an adequate and precise interpretation of the model's outputs, VME distribution models should be based on criteria that are specific and *a priori* clearly communicated to model-users. In particular, vulnerability criteria should be defined relative to specific threat (e.g., fishing vs. deep sea mining) and to the characteristics of the VME data available for modelling (e.g., model cut-off values should take into account the detectability of the sampling method used to collect the training data). For regional models, the VME policy-oriented criteria defined by some RFMO/As for their area of jurisdiction constitute a relevant starting point. For instance, CCAMLR considers the motility and the larval dispersal as additional VME criteria, as relevant aspects for the Southern Ocean context and the longline fishery (CCAMLR, 2009). To date, VMEs have been mainly modelled in regard to the fishing threat. For applications not only focusing on fisheries management, the seven criteria developed by the Convention on Biological Diversity to identify Ecologically or Biologically Significant Areas (EBSA) should be taken into consideration (Dunn et al., 2014). As shown by (Ardron et al., 2014), the EBSA identification criteria complement the FAO VME criteria with the assessment of

the area naturalness (or ecosystem intactness, i.e., lack of or low level of human induced disturbance or degradation), the biological productivity and diversity (see (Gonzalez-Mirelis et al., 2021)).

Establishing quantitative-based criteria of what constitutes a VME is needed to impede subjectivity in VME identification. To reach a consensual definition of an ecosystem vulnerability, the establishment of cut-off values, data driven and scientifically validated, is needed (Geange et al., 2020; Kenchington et al., 2014; A. A. Rowden et al., 2020). To this end, (A. A. Rowden et al., 2020) model the relationships between the density of a habitat-forming taxon and the number of other epifauna taxa, i.e. correlation between the amount of structurally complex habitat and the associated species richness. This analysis facilitates the translation of the subjective “Structural complexity” FAO criterion into a quantitative model-oriented criterion by determining percentage cover thresholds that are representative of structurally complex habitats. Such methodology has the potential to operationalise FAO’s criteria while providing distribution models with a data-driven and scientifically-validated reference to identify VMEs.

#### 4.2. Assess site conservation value in relation to VME multi-taxa spatial predictions

While most VME modelling studies focus on the distribution of a single indicator taxon, epibenthic community composition analyses would provide a more relevant assessment of both the ecological functionality and structural complexity of an

ecosystem, as per key FAO VME criteria. Therefore, we recommend to model the full list of VME taxa instead of focusing on a single taxon or habitat, and to assess the conservation value of the predicted hotspots by characterising the whole epibenthic community in relation to the predicted VME taxa distributions.

To model the distribution of multiple species, approaches with joint responses among the species, such as Hierarchical Modelling of Species Communities (Tikhonov et al., 2020), Species Archetype Model (Dunstan et al., 2011; Hui et al., 2013) or Regions of Common Profiles model (Foster et al., 2013), should be investigated as they can directly reveal VME' community structure (J. W. F. Chu et al., 2019). Besides the assemblage approaches commonly used in the VME literature (see bottom panel of Fig. 2), future studies could consider the “Analyse simultaneously” approach which simultaneously correlates biological with environmental data to generate regions containing relative homogenous and distinct assemblages within a single model (Hill et al., 2020).

Once hotspots of VME taxa are identified, the ecological value of a site can be evaluated in respect to the biodiversity and productivity of the entire epibenthic community, e.g. by computing the total epibenthic megafauna richness and abundance (Dunstan et al., 2012; Gonzalez-Mirelis et al., 2021). The total epibenthic megafauna richness and abundance can arguably be used as relevant quantitative indicators to assess the “structural complexity” and “functionality” FAO criteria (Gonzalez-Mirelis et al., 2021). Further, since biodiversity and productivity are part of the EBSA identification process, their quantification in VME distribution studies supports a better incorporation

of VME protection within management tools across sectoral authorities and international agreements.

The use of abundance data extracted from underwater imagery is preferable for conducting the community-oriented modelling described above. Imagery-based abundance data provides a significantly more reliable, comprehensive and non-destructive characterisation of benthic communities than other sampling methods (see section 2). Besides, the visual assessment allowed by images is more compelling for non-specialists such as policy-makers. Rapid advances in imaging technologies have recently reduced costs and thus increased underwater imagery coverage (Morato et al., 2018). Further, there has been a substantial global effort to make these images publicly available, e.g. MAREANO video database (Buhl-Mortensen et al., 2015). To increase the spatial and environmental coverage of the training dataset, we encourage model-builders to collate all available data that have been already acquired across the studied region, even when not annotated yet (Etnoyer et al., 2018). Noteworthy recent efforts have been made to standardise protocols for VME identification (Baco-Taylor et al., 2020) and marine reference catalogues (Horton et al., 2021; Howell et al., 2019), both from underwater imagery. While indicator taxa are often defined with a low taxonomic resolution by RFMO/As, the use of images opens the door to higher resolution identifications, which can provide a finer characterisation of ecosystems. In addition, taxonomic groups can be split based on morphological characteristics, e.g. using morpho-taxonomic labels (Gonzalez-Mirelis et al., 2021), or functional traits in order to further appraise the ecosystem vulnerability, e.g. “Fragility” FAO criterion. All in all, the

increase of both quantity and quality of abundance data is likely to underpin the next generation VME distribution models.

### 4.3. Model the vulnerability of marine ecosystems

Most published VME distribution models have focused on mapping the *occurrence* of indicator taxa, which only provides a partial assessment of the entire ecosystem vulnerability. VMEs should instead be identified on the basis of the full suite of vulnerability criteria outlined in the FAO Guidelines (Gianni et al., 2016). Therefore, we recommend future studies to model the vulnerability of an area, rather than its suitability to harbour an indicator taxon. To map the vulnerability of an area, (Morato et al., 2018) propose weighting the VME taxa abundance data by taxa-specific scores for each of the five FAO criteria. This multi-criteria assessment method results in the mapping of a single composite metric, the “VME index”, which represents where a particular location lies on the vulnerability spectrum. Some drawbacks are however inherent to such composite score calculation (Ardron et al., 2014), such as sometimes leading to prioritizing sites harbouring a large number of taxa with low vulnerability, over a habitat dominated by a highly vulnerable taxon. Nevertheless, this methodology has been adopted by the International Council for the Exploration of the Sea (ICES) in the North-East Atlantic (ICES, 2019), and has been recently used to generate the “North Atlantic Ocean basin-scale VME index dataset” (Morato et al., 2020). Building on (Morato et al., 2018) method, (Burgos et al., 2020) map the “VME index” beyond observed sites using the predictions of VME taxa distribution models. Avenues of

improvement include: (i) to use joint-distribution modelling approaches, as detailed in section 4.2, and (ii) to derive vulnerability scores for each taxa from imagery-based analyses that are less prone to expert subjectivity because data-driven and scientifically-validated, see section 4.1.



## 5. Conclusion

Distribution modelling will have an increasingly important role to play in underpinning the next generation of targeted VME management and conservation measures. VME distribution modelling will benefit from the recent increase in both VME data quality and quantity, but several challenges will need to be addressed to make modelling efforts relevant and impactful. First, it is crucial that model-builders understand the connection between the type of data used to build models and what such models are able to estimate to ensure they are appropriate for the intended application. Second, a limitation in the general applicability of VME models occurs because quantitative standards of what constitutes a VME are lacking. We strongly recommend that scientists and RFMO/As work towards generating quantitative definitions and modelling approaches that i) consider the whole ecosystem instead of focusing on a single indicator taxon, and ii) model the vulnerability of an area instead of just its suitability to harbour a vulnerable species. To this end, the combination of models that simultaneously quantify the distribution of a suite of VME taxa with a tailored VME index that considers multiple aspects of the FAO criteria appears a promising way forward. The present work comes at a critical time where there is increased international focus on the sustainable use of oceans, particularly in Areas Beyond National Jurisdiction. International negotiations in Convention on Biological Diversity and Biodiversity Beyond National Jurisdiction are reaching a stage of maturity where having

a science- and data-based framework is important, wherein VME distribution modelling has a key role to play.

## Authors' contributions

CG: Conceptualization, Investigation, Writing – original draft preparation ; JJ: Writing – review and editing, Supervision ; PDK: Writing – review and editing ; DCW: Writing – review and editing ; NAH: Conceptualization, Writing – review and editing, Supervision

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## Conflict of Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## References

- Ardron, J. A., Clark, M. R., Penney, A. J., Hourigan, T. F., Rowden, A. A., Dunstan, P. K., Watling, L., Shank, T. M., Tracey, D. M., Dunn, M. R., & Parker, S. J. (2014). A systematic approach towards the identification and protection of vulnerable marine ecosystems. *Marine Policy*, *49*, 146–154.  
<https://doi.org/10.1016/j.marpol.2013.11.017>
- Auster, P. J., Gjerde, K., Heupel, E., Watling, L., Grehan, A., & Rogers, A. D. (2011). Definition and detection of vulnerable marine ecosystems on the high seas: Problems with the “move-on” rule. *ICES Journal of Marine Science*, *68*(2), 254–264.  
<https://doi.org/10.1093/icesjms/fsq074>
- Baco, A. R., Morgan, N. B., & Roark, E. B. (2020). Observations of vulnerable marine ecosystems and significant adverse impacts on high seas seamounts of the northwestern Hawaiian Ridge and Emperor Seamount Chain. *Marine Policy*, *115*, 103834. <https://doi.org/10.1016/j.marpol.2020.103834>
- Baco-Taylor, A., Ross, R., Althaus, F., Bridges, A., Brix, S., Colaço, A., Clark, M. R., Du Preez, C., Franken, M.-L., & Gonzalez-Mirelis, G. (2020). A Community Consensus on Designating Vulnerable Marine Ecosystems from Imagery. *Ocean Sciences Meeting 2020*.
- Barrio Froján, C., Downie, A.-L., Sacau Cuadrado, M., Kenchington, E., & Kenny, A. (2016). Evaluation of benthic assemblage structure in the NAFO regulatory area

- with regard to the protection of VME. *ICES Journal of Marine Science*, 73(2), 405–419. <https://doi.org/10.1093/icesjms/fsv186>
- Bell, J., Guijarro-García, E., & Kenny, A. (2019). *Scientific approaches for the assessment and management of deep-sea fisheries and ecosystems in RFMOs and RFBs: Final report*. [Website]. Publications Office of the European Union. <http://op.europa.eu/en/publication-detail/-/publication/0f2b559b-4610-11e9-a8ed-01aa75ed71a1>
- Blicher, M. E., & Arboe, N. H. (2021). *Atlas of Vulnerable Marine Ecosystem (VME) indicators observed on Bottom Trawl Surveys in Greenland waters during 2015-2019*. <https://doi.org/10.13140/RG.2.2.35637.81120>
- Bo, M., Coppari, M., Betti, F., Enrichetti, F., Bertolino, M., Massa, F., Bava, S., Gay, G., Cattaneo-Vietti, R., & Bavestrello, G. (2021). The high biodiversity and vulnerability of two Mediterranean bathyal seamounts support the need for creating offshore protected areas. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 31(3), 543–566. <https://doi.org/10.1002/aqc.3456>
- Brewin, P. E., Farrugia, T. J., Jenkins, C., & Brickle, P. (2020). Straddling the line: High potential impact on vulnerable marine ecosystems by bottom-set longline fishing in unregulated areas beyond national jurisdiction. *ICES Journal of Marine Science*. <https://doi.org/10.1093/icesjms/fxaa106>
- Buhl-Mortensen, L., Buhl-Mortensen, P., Dolan, M. F. J., & Holte, B. (2015). The MAREANO programme – A full coverage mapping of the Norwegian off-shore benthic environment and fauna. *Marine Biology Research*, 11(1), 4–17.

<https://doi.org/10.1080/17451000.2014.952312>

Carbonara, P., Zupa, W., Follesa, M. C., Cau, A., Capezzuto, F., Chimienti, G., D'Onghia, G., Lembo, G., Pesci, P., Porcu, C., Bitetto, I., Spedicato, M. T., & Maiorano, P. (2020). Exploring a deep-sea vulnerable marine ecosystem: *Isidella elongata* (Esper, 1788) species assemblages in the Western and Central Mediterranean. *Deep Sea Research Part I: Oceanographic Research Papers*, 166, 103406. <https://doi.org/10.1016/j.dsr.2020.103406>

CCAMLR. (2009). *Report of the Workshop on Vulnerable Marine Ecosystems* (SC-CAMLR-XXVIII/10). CCAMLR.

CCAMLR. (2013). *Conservation Measure 22-07* (No. 22-07). CCAMLR. <https://www.ccamlr.org/en/measure-22-07-2013>

Chimienti, G., Bo, M., & Mastrototaro, F. (2018). Know the distribution to assess the changes: Mediterranean cold-water coral bioconstructions. *Rendiconti Lincei. Scienze Fisiche e Naturali*, 29(3), 583–588. <https://doi.org/10.1007/s12210-018-0718-3>

Chu, J. W. F., Nephin, J., Georgian, S., Knudby, A., Rooper, C., & Gale, K. S. P. (2019). Modelling the environmental niche space and distributions of cold-water corals and sponges in the Canadian northeast Pacific Ocean. *Deep Sea Research Part I: Oceanographic Research Papers*, 151, 103063. <https://doi.org/10.1016/j.dsr.2019.06.009>

Chu, J. W., Nephin, J., Georgian, S., Knudby, A., Rooper, C., Gale, K. S., & Curtis, J. (2020). 1. MaxEnt modelling of biogenic habitat-forming cold-water corals and

- sponges in the Northeast Pacific region of Canada. *PICES Scientific Report*, 57, 1–20.
- Clark, M. (2001). Are deepwater fisheries sustainable? — The example of orange roughy (*Hoplostethus atlanticus*) in New Zealand. *Fisheries Research*, 51(2), 123–135.  
[https://doi.org/10.1016/S0165-7836\(01\)00240-5](https://doi.org/10.1016/S0165-7836(01)00240-5)
- Clark, M. R., Althaus, F., Schlacher, T. A., Williams, A., Bowden, D. A., & Rowden, A. A. (2016). The impacts of deep-sea fisheries on benthic communities: A review. *ICES Journal of Marine Science*, 73(suppl\_1), i51–i69.  
<https://doi.org/10.1093/icesjms/fsv123>
- Clark, M. R., Consalvey, M., & Rowden, A. A. (2016). *Biological Sampling in the Deep Sea*. John Wiley & Sons.
- Danovaro, R., Corinaldesi, C., Dell'Anno, A., & Snelgrove, P. V. R. (2017). The deep-sea under global change. *Current Biology*, 27(11), R461–R465.  
<https://doi.org/10.1016/j.cub.2017.02.046>
- Dautova, T. N., Galkin, S. V., Tabachnik, K. R., Minin, K. V., Kireev, P. A., Moskovtseva, A. V., & Adrianov, A. V. (2019). The First Data on the Structure of Vulnerable Marine Ecosystems of the Emperor Chain Seamounts: Indicator Taxa, Landscapes, and Biogeography. *Russian Journal of Marine Biology*, 45(6), 408–417.  
<https://doi.org/10.1134/S1063074019060026>
- Du Preez, C., Swan, K. D., & Curtis, J. M. R. (2020). Cold-Water Corals and Other Vulnerable Biological Structures on a North Pacific Seamount After Half a Century of Fishing. *Frontiers in Marine Science*, 7.

<https://doi.org/10.3389/fmars.2020.00017>

Dunn, D. C., Ardron, J., Bax, N., Bernal, P., Cleary, J., Cresswell, I., Donnelly, B., Dunstan, P., Gjerde, K., Johnson, D., Kaschner, K., Lascelles, B., Rice, J., von Nordheim, H., Wood, L., & Halpin, P. N. (2014). The Convention on Biological Diversity's Ecologically or Biologically Significant Areas: Origins, development, and current status. *Marine Policy*, *49*, 137–145.

<https://doi.org/10.1016/j.marpol.2013.12.002>

Dunstan, P. K., Bax, N. J., Foster, S. D., Williams, A., & Althaus, F. (2012). Identifying hotspots for biodiversity management using rank abundance distributions. *Diversity and Distributions*, *18*(1), 22–32.

<https://doi.org/10.1111/j.1472-4642.2011.00838.x>

Dunstan, P. K., Foster, S. D., & Darnell, R. (2011). Model based grouping of species across environmental gradients. *Ecological Modelling*, *222*(4), 955–963.

<https://doi.org/10.1016/j.ecolmodel.2010.11.030>

Etnoyer, P. J., Wagner, D., Fowle, H. A., Poti, M., Kinlan, B., Georgian, S. E., & Cordes, E. E. (2018). Models of habitat suitability, size, and age-class structure for the deep-sea black coral *Leiopathes glaberrima* in the Gulf of Mexico. *Deep Sea Research Part II: Topical Studies in Oceanography*, *150*, 218–228.

<https://doi.org/10.1016/j.dsr2.2017.10.008>

FAO. (2009). *International guidelines for the management of deep-sea fisheries in the high seas*. Food and Agriculture Organization of the United Nations.

Ferrier, S., & Guisan, A. (2006). Spatial modelling of biodiversity at the community level.



*Journal of Applied Ecology*, 43(3), 393–404.

Foster, S. D., Givens, G. H., Dornan, G. J., Dunstan, P. K., & Darnell, R. (2013).

Modelling biological regions from multi-species and environmental data.

*Environmetrics*, 24(7), 489–499. <https://doi.org/10.1002/env.2245>

Geange, S. W., Rowden, A. A., Nicol, S., Bock, T., & Cryer, M. (2020). A Data-Informed

Approach for Identifying Move-on Encounter Thresholds for Vulnerable Marine

Ecosystem Indicator Taxa. *Frontiers in Marine Science*, 7.

<https://doi.org/10.3389/fmars.2020.00155>

Gianni, M., Fuller, S. D., Currie, D. E. J., Schleit, K., Goldsworthy, L., Pike, B., Weeber,

B., Owen, S., & Friedman, A. (2016). How much longer will it take. *A Ten-Year*

*Review of the Implementation of United Nations General Assembly Resolutions*, 61(105),

64.

Gonzalez-Mirelis, G., Ross, R. E., Albretsen, J., & Buhl-Mortensen, P. (2021). Modeling

the Distribution of Habitat-Forming, Deep-Sea Sponges in the Barents Sea: The

Value of Data. *Frontiers in Marine Science*.

<http://dx.doi.org/10.3389/fmars.2020.496688>

Guillera-Arroita, G., Lahoz-Monfort, J. J., Elith, J., Gordon, A., Kujala, H., Lentini, P. E.,

McCarthy, M. A., Tingley, R., & Wintle, B. A. (2015). Is my species distribution

model fit for purpose? Matching data and models to applications. *Global Ecology*

*and Biogeography*, 24(3), 276–292. <https://doi.org/10.1111/geb.12268>

Hill, N., Woolley, S. N. C., Foster, S., Dunstan, P. K., McKinlay, J., Ovaskainen, O., &

Johnson, C. (2020). Determining marine bioregions: A comparison of

quantitative approaches. *Methods in Ecology and Evolution*, 11(10), 1258–1272.

<https://doi.org/10.1111/2041-210X.13447>

Horton, T., Marsh, L., Bett, B. J., Gates, A. R., Jones, D. O. B., Benoist, N. M. A., Pfeifer, S., Simon-Lledó, E., Durden, J. M., Vandepitte, L., & Appeltans, W. (2021).

Recommendations for the Standardisation of Open Taxonomic Nomenclature for Image-Based Identifications. *Frontiers in Marine Science*, 8.

<https://doi.org/10.3389/fmars.2021.620702>

Howell, K. L., Davies, J. S., Allcock, A. L., Braga-Henriques, A., Buhl-Mortensen, P.,

Carreiro-Silva, M., Dominguez-Carrió, C., Durden, J. M., Foster, N. L., Game, C.

A., Hitchin, B., Horton, T., Hosking, B., Jones, D. O. B., Mah, C., Marchais, C. L.,

Menot, L., Morato, T., Pearman, T. R. R., ... Wagner, D. (2019). A framework

for the development of a global standardised marine taxon reference image

database (SMarTaR-ID) to support image-based analyses. *PLOS ONE*, 14(12),

e0218904. <https://doi.org/10.1371/journal.pone.0218904>

Howell, K. L., Holt, R., Endrino, I. P., & Stewart, H. (2011). When the species is also a

habitat: Comparing the predictively modelled distributions of *Lophelia pertusa*

and the reef habitat it forms. *Biological Conservation*, 144(11), 2656–2665.

<https://doi.org/10.1016/j.biocon.2011.07.025>

Hui, F. K. C., Warton, D. I., Foster, S. D., & Dunstan, P. K. (2013). To mix or not to mix:

Comparing the predictive performance of mixture models vs. separate species

distribution models. *Ecology*, 94(9), 1913–1919.

<https://doi.org/10.1890/12-1322.1>

ICES. (2019). *Working Group on Marine Habitat Mapping (WGMHM)*.

<https://doi.org/10.17895/ICES.PUB.5578>

Jansen, J., Hill, N. A., Dunstan, P. K., Eléaume, M. P., & Johnson, C. R. (2018).

Taxonomic Resolution, Functional Traits, and the Influence of Species Groupings on Mapping Antarctic Seafloor Biodiversity. *Frontiers in Ecology and Evolution*, 6.

<https://doi.org/10.3389/fevo.2018.00081>

Kenchington, E., Murillo, F. J., Lirette, C., Sacau, M., Koen-Alonso, M., Kenny, A.,

Ollerhead, N., Wareham, V., & Beazley, L. (2014). Kernel Density Surface

Modelling as a Means to Identify Significant Concentrations of Vulnerable

Marine Ecosystem Indicators. *PLOS ONE*, 9(10), e109365.

<https://doi.org/10.1371/journal.pone.0109365>

Knudby, A., Kenchington, E., & Murillo, F. J. (2013). Modeling the Distribution of

Geodia Sponges and Sponge Grounds in the Northwest Atlantic. *PLOS ONE*,

8(12), e82306. <https://doi.org/10.1371/journal.pone.0082306>

Long, S., Sparrow-Scinocca, B., Blicher, M. E., Hammeken Arboe, N., Fuhrmann, M.,

Kemp, K. M., Nygaard, R., Zinglensen, K., & Yesson, C. (2020). Identification of a

Soft Coral Garden Candidate Vulnerable Marine Ecosystem (VME) Using Video

Imagery, Davis Strait, West Greenland. *Frontiers in Marine Science*, 7.

<https://doi.org/10.3389/fmars.2020.00460>

Morato, T., González-Irusta, J.-M., Dominguez-Carrió, C., Wei, C.-L., Davies, A.,

Sweetman, A. K., Taranto, G. H., Beazley, L., García-Alegre, A., Grehan, A.,

Laffargue, P., Murillo, F. J., Sacau, M., Vaz, S., Kenchington, E., Arnaud-Haond,

- S., Callery, O., Chimienti, G., Cordes, E., ... Carreiro-Silva, M. (2020). Climate-induced changes in the suitable habitat of cold-water corals and commercially important deep-sea fishes in the North Atlantic. *Global Change Biology*, 26(4), 2181–2202. <https://doi.org/10.1111/gcb.14996>
- Morato, T., Pham, C. K., Pinto, C., Golding, N., Ardrón, J. A., Durán Muñoz, P., & Neat, F. (2018). A Multi Criteria Assessment Method for Identifying Vulnerable Marine Ecosystems in the North-East Atlantic. *Frontiers in Marine Science*, 5. <https://doi.org/10.3389/fmars.2018.00460>
- Norse, E. A., Brooke, S., Cheung, W. W. L., Clark, M. R., Ekeland, I., Froese, R., Gjerde, K. M., Haedrich, R. L., Heppell, S. S., Morato, T., Morgan, L. E., Pauly, D., Sumaila, R., & Watson, R. (2012). Sustainability of deep-sea fisheries. *Marine Policy*, 36(2), 307–320. <https://doi.org/10.1016/j.marpol.2011.06.008>
- Ramirez-Llodra, E., Brandt, A., Danovaro, R., De Mol, B., Escobar, E., German, C. R., Levin, L. A., Martinez Arbizu, P., Menot, L., Buhl-Mortensen, P., Narayanaswamy, B. E., Smith, C. R., Tittensor, D. P., Tyler, P. A., Vanreusel, A., & Vecchione, M. (2010). Deep, diverse and definitely different: Unique attributes of the world's largest ecosystem. *Biogeosciences*, 7(9), 2851–2899. <https://doi.org/10.5194/bg-7-2851-2010>
- Rogers, A. D., & Gianni, M. (2010). *The Implementation of UNGA Resolutions 61/105 and 64/72 in the Management of Deep-Sea Fisheries on the High Seas* (p. 50). Food and Agriculture Organization of the United Nations.
- Rowden, A. A., Anderson, O. F., Georgian, S. E., Bowden, D. A., Clark, M. R., Pallentin,

- A., & Miller, A. (2017). High-Resolution Habitat Suitability Models for the Conservation and Management of Vulnerable Marine Ecosystems on the Louisville Seamount Chain, South Pacific Ocean. *Frontiers in Marine Science*, 4. <https://doi.org/10.3389/fmars.2017.00335>
- Rowden, A. A., Pearman, T. R. R., Bowden, D. A., Anderson, O. F., & Clark, M. R. (2020). Determining Coral Density Thresholds for Identifying Structurally Complex Vulnerable Marine Ecosystems in the Deep Sea. *Frontiers in Marine Science*, 7. <https://doi.org/10.3389/fmars.2020.00095>
- Rowden, A. A., Stephenson, F., Clark, M. R., Anderson, O. F., Guinotte, J. M., Baird, S. J., Roux, M.-J., Wadhwa, S., Cryer, M., & Lundquist, C. J. (2019). Examining the utility of a decision-support tool to develop spatial management options for the protection of vulnerable marine ecosystems on the high seas around New Zealand. *Ocean & Coastal Management*, 170, 1–16. <https://doi.org/10.1016/j.ocecoaman.2018.12.033>
- Rowden, A., & Anderson, O. (2019). *New data compilation for VME indicator taxa and implications for the review of VME habitat suitability models in the SPRFMO area* (No. SC7-DW12; p. 20). SPRFMO.
- Salinas-de-León, P., Martí-Puig, P., Buglass, S., Arnés-Urgellés, C., Rastoin-Laplane, E., Creemers, M., Cairns, S., Fisher, C., O'Hara, T., Ott, B., Raineault, N. A., Reiswig, H., Rouse, G., Rowley, S., Shank, T. M., Suarez, J., Watling, L., Wicksten, M. K., & Marsh, L. (2020). Characterization of deep-sea benthic invertebrate megafauna of the Galapagos Islands. *Scientific Reports*, 10(1), 13894.

<https://doi.org/10.1038/s41598-020-70744-1>

Thompson, A., Sanders, J., Tandstad, M., Carocci, F., & Fuller, J. (2016). *Vulnerable marine ecosystems—Processes and practices in the high seas* (p. 200). Food and Agriculture Organization of the United Nations.

Thurber, A. R., Sweetman, A. K., Narayanaswamy, B. E., Jones, D. O., Ingels, J., & Hansman, R. L. (2014). Ecosystem function and services provided by the deep sea. *Biogeosciences*, *11*(14), 3941–3963.

Tikhonov, G., Opedal, Ø. H., Abrego, N., Lehikoinen, A., Jonge, M. M. J. de, Oksanen, J., & Ovaskainen, O. (2020). Joint species distribution modelling with the r-package Hmsc. *Methods in Ecology and Evolution*, *11*(3), 442–447.

<https://doi.org/10.1111/2041-210X.13345>

Torriente, A. de la, González-Irusta, J. M., Aguilar, R., Fernández-Salas, L. M., Punzón, A., & Serrano, A. (2019). Benthic habitat modelling and mapping as a conservation tool for marine protected areas: A seamount in the western Mediterranean. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *29*(5), 732–750. <https://doi.org/10.1002/aqc.3075>

UNGA. (2006). *61/105. Sustainable fisheries, including through the 1995 Agreement for the Implementation of the Provisions of the United Nations Convention on the Law of the Sea of 10 December 1982 relating to the Conservation and Management of Straddling Fish Stocks and Highly Migratory Fish Stocks, and related instruments*. UNGA.

Vierod, A. D. T., Guinotte, J. M., & Davies, A. J. (2014). Predicting the distribution of vulnerable marine ecosystems in the deep sea using presence-background models.

*Deep Sea Research Part II: Topical Studies in Oceanography*, 99, 6–18.

<https://doi.org/10.1016/j.dsr2.2013.06.010>

Watling, L., & Auster, P. J. (2017). Seamounts on the High Seas Should Be Managed as Vulnerable Marine Ecosystems. *Frontiers in Marine Science*, 4.

<https://doi.org/10.3389/fmars.2017.00014>

Weaver, P. P. E., Benn, A., Arana, P. M., Ardron, J. A., Bailey, D. M., Baker, K., Billett, D. S. M., Clark, M. R., Davies, A. J., & Durán Muñoz, P. (2011). *The impact of deep-sea fisheries and implementation of the UNGA Resolutions 61/105 and 64/72. Report of an international scientific workshop, National Oceanography Centre, Southampton, 45 p.* Southampton.

Williams, A., Althaus, F., & Schlacher, T. A. (2015). Towed camera imagery and benthic sled catches provide different views of seamount benthic diversity. *Limnology and Oceanography: Methods*, 13(2), e10007. <https://doi.org/10.1002/lom3.10007>

Yesson, C., Taylor, M. L., Tittensor, D. P., Davies, A. J., Guinotte, J., Baco, A., Black, J., Hall-Spencer, J. M., & Rogers, A. D. (2012). Global habitat suitability of cold-water octocorals. *Journal of Biogeography*, 39(7), 1278–1292.

<https://doi.org/10.1111/j.1365-2699.2011.02681.x>