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Three-dimensional conservation planning of fish biodiversity metrics to achieve the deep-sea 30×30 conservation target

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Abstract

Accelerating rate of human impact and environmental change severely affects marine biodiversity and increases the urgency to implement the Convention on Biological Diversity (CBD) 30×30 plan for conserving 30% of sea areas by 2030. However, area-based conservation targets are complex to identify in a 3-dimensional (3D) ocean where deep-sea features such as seamounts have been seldom studied mostly due to challenging methodologies to implement at great depths. Yet, the use of emerging technologies, such as environmental DNA combined with modern modeling frameworks, could help address the problem. We collected environmental DNA, echosounder acoustic, and video data at 15 seamounts and deep island slopes across the Coral Sea. We modeled 7 fish community metrics and the abundances of 45 individual species and molecular operational taxonomic units (MOTUs) in benthic and pelagic waters (down to 600-m deep) with boosted regression trees and generalized joint attribute models to describe biodiversity on seamounts and deep slopes and identify 3D protection solutions for achieving the CBD area target in New Caledonia (1.4 million km^2). We prioritized the identified conservation units in a 3D space, based on various biodiversity targets, to meet the goal of protecting at least 30% of the spatial domain, with a focus on areas with high biodiversity. The relationship between biodiversity protection targets and the spatial area protected by the solution was linear. The scenario protecting 30% of each biodiversity metric preserved almost 30% of the considered spatial domain and accounted for the 3D distribution of biodiversity. Our study paves the way for the use of combined data collection methodologies to improve biodiversity estimates in 3D structured marine environments for the selection of conservation areas and for the use of biodiversity targets to achieve area-based international targets.

KEYWORDS
3D conservation planning, acoustic, biodiversity modeling, BRUVS, deep sea, eDNA, seamounts

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INTRODUCTION

Human disturbances and climate change strongly affect biodiversity worldwide (Andrello et al., 2022) and have severe impacts on the well-being, food security, and socioeconomic situation of billions of people (Eddy et al., 2021). This biodiversity crisis is particularly acute in the oceans (Pacoureau et al., 2021), including on seamounts and other deep-sea environments where overfishing, mining, pollution, and changes in physical and chemical water properties increasingly threaten species and associated ecosystem services (Rogers, 2018). To safeguard ecosystems, a key response of governments, through the Convention on Biological Diversity (CBD), is to set area-based conservation targets, for example, the call to protect 30% of sea areas by 2030 (30×30, target 3) (CBD, 2021). Besides the area goal, the CBD also advocates that protected areas are of particular importance for biodiversity if they are effectively and equitably managed, ecologically representative, and well connected. The 3-dimensional (3D) distribution of biodiversity in the ocean introduces challenges for achieving area-based conservation objectives (Magris et al., 2018; Rogers, 2018).

Marine life occupies a vast vertical expanse, stretching from the ocean's surface to its deepest seafloor. Although species richness decreases with depth, community compositions are distinct in deep continental slopes and mesophotic reefs and are as threatened as shallower ecosystems (Cruz-Acevedo et al., 2018; Rocha et al., 2018; Vieira et al., 2018). These deep ecosystems serve as essential spawning and feeding areas for valuable fish stocks, offer potential refuge for shallow-water species in changing climate, and are essential to the ocean's carbon cycle (Pinheiro et al., 2021; Rutterford et al., 2015). Seamounts are ubiquitous features of the deep sea, spanning a territory as vast as Europe (Kvile et al., 2014), and are among the least studied areas in the ocean, with only 0.002% of world's seamounts sampled for scientific purposes (Rogers, 2018). Very little is known about fish biodiversity on seamounts, and no studies have yet compared seamounts to other deep-sea areas, such as continental or island slopes (Watling & Auster, 2021).

Although they are hotspots and refuges for many different taxa (Letessier et al., 2019), seamounts are presently underrepresented in no-take marine protected areas (MPAs); only 2% of the world's seamounts are in the global MPA network (Letessier et al., 2019; Yesson et al., 2011). Large no-take MPAs are the most efficient tools for protecting many aspects of biodiversity (McClanahan, 2021), but most MPAs have been designated in national coastal waters, without explicit consideration of the different depth domains, and in areas of least necessity and lowest fishing pressure (Devillers et al., 2015; Jacquemont et al., 2024; Levin et al., 2018). Fisheries affect marine ecosystems at all depths and target deep-sea features, such as seamounts (Kerry et al., 2022). Benthic fishing extends to the lower bathyal zones, and mesopelagic fishing is most intense in regions above abyssal depths. This widespread fishing activity disrupts ecosystems, affecting biodiversity and the intricate balance of marine life across these various oceanic layers (Jacquemont et al., 2024). Therefore, 2-dimensional (2D) spatial prioritization schemes may fail to achieve ecological representation and to protect species habitats and refugia from climate change (Brito-Morales et al., 2022; Doxa et al., 2022; Maxwell et al., 2020). Designing MPAs in areas that include seamounts is challenging because the depth gradient between the base and the top of the seamounts leads to highly structured biodiversity across depths. Three-dimensional frameworks for conservation planning are crucial for designing effective protected area systems around seamounts.

Frameworks for planning the use and conservation of the oceans have recently started to include depth so as to consider oceans as a volume and not just a surface and to include climatic data to provide resilient and realistic plans for the future (Brito-Morales et al., 2022; Doxa et al., 2022; Venegas-Li et al., 2018). However, the main obstacle to 3D conservation planning has been the lack of comparable biological data along the depth gradient from the surface to the abyss, a problem that can be overcome thanks to recent technological advances. Environmental DNA (eDNA) metabarcoding, video, and echosounder surveys allow quantitative data to be collected in a standardized way at any depth. The metabarcoding of eDNA, based on the retrieval and analysis of genetic material naturally released by organisms in their environments, was recently shown to outperform dive and video surveys for estimating marine biodiversity (Mathon et al., 2022) and to be efficient in the study of fish assemblages on seamounts (Baletaud et al., 2023; Muff et al., 2022). Yet, the drawback of eDNA metabarcoding is the lack of knowledge about organism size, abundance, and biomass and the relatively small extent of the sampled surface; only a few liters of water are filtered from the vast ocean. Stereo baited remote underwater video stations (BRUVS) can efficiently estimate species abundance and biomass in any marine habitat (Langlois et al., 2020), and acoustic echosounders can provide continuously a proxy of fish biomass across vast oceanic areas (Proud et al., 2018). Thus, these 3 methods seem complementary for surveying marine biodiversity and prioritizing its conservation in 3 dimensions.

We aimed to describe and model biodiversity on seamounts and deep island slopes and to identify 3D protection solutions for achieving the CBD area target in the vast archipelago of New Caledonia (1.4 million km^2). This South Pacific biodiversity hotspot has been a UNESCO World Heritage Site since 2008 and home to the world's second-largest marine park (1.3 million km^2) since 2014. To achieve our objective, we first collected eDNA, BRUVS, and acoustic echosounder data on the benthic and pelagic areas of 15 seamounts and island slopes down to 600-m depth across the archipelago. Using this unique data set, we used modeling to predict fish richness, abundance, and biomass and individual species abundances in 3 dimensions on island slopes, seamounts, and pelagic surroundings. We also identified areas of conservation priority, across 3 depth layers, at the scale of the archipelago to achieve protection of 30% of the spatial domain in high-biodiversity areas. Ours is the first 3D spatial conservation planning exercise for this global biodiversity hotspot.

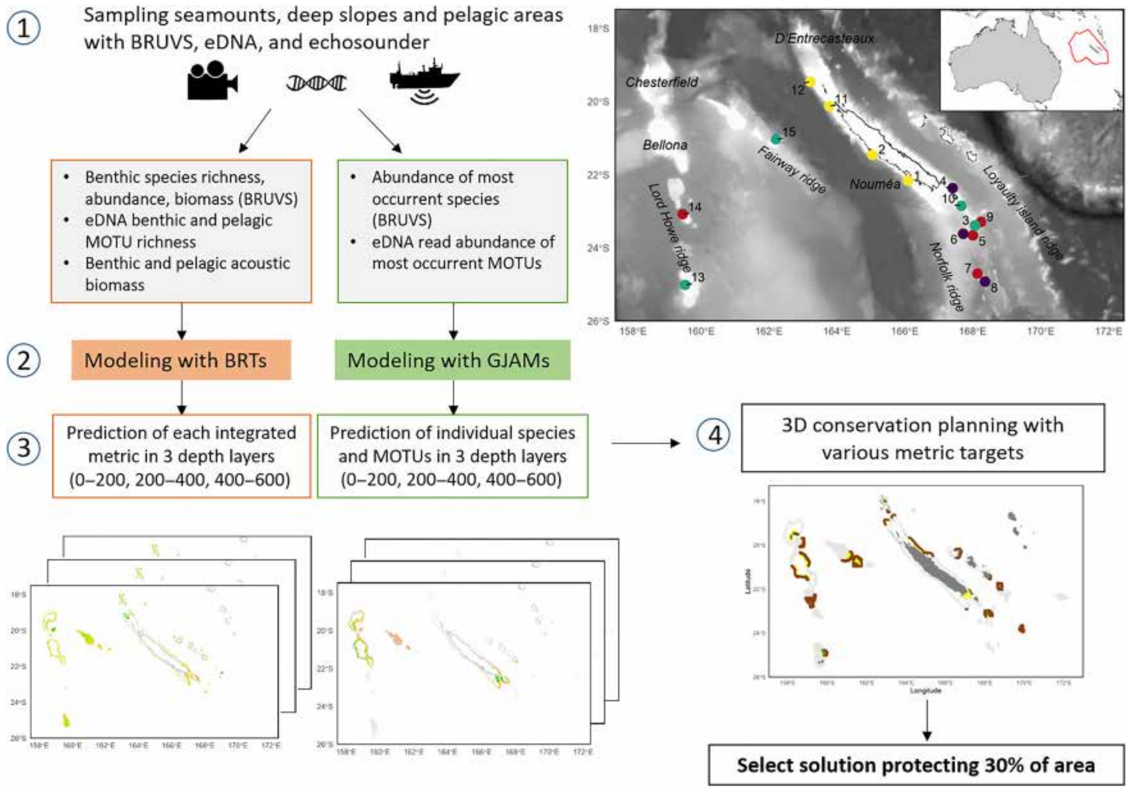

FIGURE 1 Framework of 3-dimensional (3D) conservation planning: (1) sampling at 4 study sites on deep island slopes ~150 m (yellow), 4 sites on seamounts with summit ~50 m (green), 4 sites on seamounts with summit ~250 m (red), and 3 sites on seamounts with summit ~500 m (purple); (2) modeling of diversity metrics with boosted regression trees (BRTs) and generalized joint attribute models (GJAMs); (3) predictions of each diversity metric; and (4) 3D conservation planning (BRUVS, baited remote underwater video stations; eDNA, environmental DNA; MOTU, molecular taxonomic unit).

METHODS

Data collection and processing

Data were collected from April 2019 to September 2020 at 15 sites in New Caledonia, including 11 seamounts and 4 deep island slopes (Figure 1). Sampling sites were spread throughout the archipelago in order to obtain a wide range of human and environmental conditions. Deep slopes were sampled from 100- to 220-m deep. Seamounts were chosen so as to have different summit depths. Four summits were <200-m deep in the euphotic zone, 4 summits were 200- to 320-m deep in the intermediate zone, and 3 summits were 320- to 500-m deep in the aphotic zone.

At each site, we deployed 5–10 stereo BRUVS (total of 120) and collected 10 benthic (total of 150) and 6 pelagic eDNA samples (total of 90). The BRUVS were deployed for 2 h with 1 kg of bait. The eDNA was collected by pumping 32 L of seawater through 0.2-μm filters. Pelagic eDNA was sampled at 6 depths: 20, 80, 150, 250, 500, and 1000 m. Benthic BRUVS and eDNA samples were collected at 45–570 m. Acoustic data were recorded continuously at 38 kHz from depths of 10 to 800 m with an EK60 echosounder (see Appendices S1–S18 for details on data collection).

Fish eDNA metabarcode sequences were amplified with the teleost-specific 12S mitochondrial rRNA gene primer pair teleo (Valentini et al., 2016). There were 12 PCR replicates per sample, conducted by the SPYGEN company. Sequencing was done with Illumina MiSeq or NextSeq sequencers at Fasteris. Reads were clustered with Swarm (Mahé et al., 2015) to estimate the number of species with molecular operational taxonomic units (MOTUs) (Marques et al., 2020). Postclustering cleaning removed errors. Taxonomic assignment of MOTUs was carried out with the lower common ancestor algorithm ecotag implemented in the Obitools toolkit (Boyer et al., 2016). We used the European Nucleotide Archive (ENA; Leinonen et al., 2011) as a reference database (release 143, March 2020). Videos were processed with CAL and EventMeasure software (http://www.seagis.com.au). We used MaxN to estimate abundance (corresponding to the maximum number of individuals of a particular species seen in any one video frame across the video) (Langlois et al., 2020) and the length–weight relationship to derive biomass for each fish species recorded on video. Raw acoustic data were processed with the Matecho software (Perrot et al., 2018) and integrated in 500-m distance by 10-m depth bins, which provided the nautical area scattering coefficient (NASC) (s_A.nmi^{-2}), a proxy for marine organism biomass (Dornan et al., 2019), in 5064 vertical profiles down to 800-m depth. Acoustic data were divided into benthic (mean s_A in the 20 m above the seafloor) and pelagic (vertical profiles of s_A from 10 m to the start of the benthic layer) compartments. Details on eDNA and data processing are in Appendices S1–S18.

Modeling and predicting abundance, richness, and biomass

For each station, we calculated 7 fish community metrics, including benthic species richness, abundance, and biomass (BRUVS); benthic and pelagic MOTU richness (eDNA); and benthic and pelagic acoustic biomass (echosounder). We also extracted individual species abundance and individual MOTU read numbers for species and MOTUs present in at least 30% of stations per habitat (deep slope, shallow, intermediate, deep seamounts).

Seventeen variables were collected as potential explanatory variables for fish biodiversity patterns. At each station, we recorded the sampling depth, the bottom depth, the site type (seamount or deep island slope), and the depth of the summit. We calculated the summit area (km^2) and the summit rugosity. For deep slope stations, the summit depth was set at 0, and the summit area was calculated as the area of cells with a depth <60 m. For each station, we extracted maximum and mean sea surface temperature (SST), mean surface salinity, eastward and northward current velocity, surface suspended particulate matter, seafloor potential temperature, and chlorophyll a over the last 10 years. We calculated the travel time from Nouméa (Januchowski-hartley et al., 2020) and the minimum distances from our sampling sites to reefs and land. Although travel time represents accessibility of the locations to fishers (among other industries) (Maire et al., 2016), the distance to land also reflects the distance to land-based sources of stressors (pollution, sediment run-off) and enrichment from terrigenous inputs, and the distance to reefs is a proxy for the influence of reef productivity and complexity of fish assemblages.

Boosted regression trees (BRTs) (Elith et al., 2008) were used to model total species richness and biomass, benthic and pelagic MOTU richness per sample, and benthic and pelagic acoustic biomass. The BRUVS biomass and abundance, acoustic biomass, and MOTU richness were log transformed. To find the combination of parameters producing the best fit, we used the function gbm.step, which assesses the optimal number of boosting trees using *k*-fold cross validation, from the dismo R package (Hijmans et al., 2017).

Parameters were tree complexity (from 1 to 5), learning rate (0.01, 0.005, or 0.001), and the bag fraction (0.5 or 0.75). All possible combinations of tree complexity, learning rate, and bag fraction were run (number of folds set to 10, initial number of trees set to 700, step size 25). The combination with the lowest deviance and standard error was then selected to identify best parameters. Models were computed with the function gbm.fixed, which uses the best parameters and a fixed number of trees identified previously. The predictors contributing the most to the models were selected, and the final models were computed with gbm.step.

The species abundance data obtained from BRUVS and the numbers of benthic and pelagic eDNA reads were used in generalized joint attribute models (GJAMs) that were run in the gjam function in the gjam R package (Clark et al., 2017). The explanatory variables included in each model were selected with a stepwise procedure. To avoid multicollinearity among variables in our models, only variables with a variance inflation factor (VIF) <10 were kept in the final model. Pearson's correlation coefficient *r* was computed between observed and predicted values to estimate the model's goodness of fit.

Using the best models, we predicted values for the 7 biodiversity metrics and the abundances of individual species and MOTUs at the scale of the New Caledonian EEZ on an equal-size grid with a 1 × 1-km resolution. Predictions from the 7 BRTs were calculated with the function predict from the R package dismo, and predictions from the 3 GJAMs were made with the function gjamPredict from the R package gjam (Appendix S1). The choice of 1 × 1-km grid size corresponded to the resolution of our explanatory variables and was considered appropriate in the context of conservation planning because the smallest MPA in New Caledonia had an area of 1.5 km^2 (Juhel et al., 2019). Using a finer grid scale would unnecessarily slow the computations with regard to the size of the maritime space considered.

All analyses were computed in R 4.2.2 (R Core Team, 2022) (model details in Appendix S1).

Spatial conservation planning in 3 dimensions

The benthic prediction rasters were divided in 3 depth layers (seafloor at 0–200, 200–400, and 400–600 m, approximately corresponding to euphotic, intermediate, and aphotic zones, respectively), and the pelagic predictions were aggregated within these 3 depth layers (sum of S_A and mean of MOTU richness). We used the spatial prioritization prioritizr R package (Hanson et al., 2022) with the Gurobi optimizer (version 10; Gurobi Optimization, LLC, 2023) to identify conservation priority areas across the 3 depth layers.

To perform the 3D spatial prioritization, we modified the input data required for the 2D prioritization to include each 1 × 1 km (horizontal resolution) × 200 m (vertical resolution) cubic unit as a volume. Each planning unit was identified by a unique identifier, a 2D identifier, and a depth identifier. The total number of planning units was 212,684 (85,247 in first depth layer, 69,688 in second depth layer, and 57,749 in third depth layer). Then, we computed the boundary area between each pair of planning units so that each planning unit shared surface boundaries with its 2D neighbors and with units in the upper and lower depth layers.

The prioritization was computed with the minimum set objective function to minimize the cost of the solution while ensuring that all targets were met (Rodrigues et al., 2000) and with an optimality gap of 10%. Instead of an area-based target, we set relative targets to ensure adequate representation for each of the 7 biodiversity metrics and 45 important species distributions (details in "RESULTS"). Specifically, we generated multiple prioritizations under a range of different relative targets for each of the biodiversity metrics (i.e., 10%, 20%, 30%, 40%, and 50%) to examine trade-offs between biodiversity conservation and the total volume of sea protected. We then computed the surface protected by each solution as the 2D spatial coverage to find a solution that would allow protecting 30% of the spatial domain while protecting high-biodiversity areas. We computed a theoretical marine spatial planning (MSP) based solely on biodiversity (not influenced by already protected areas or fisheries impact) because it is usually done for realistic and applicable MSPs. We thus set an equal cost of 1 to all the planning units. We also compared areas prioritized by our theoretical MSP with areas already included in existing MPAs in New Caledonia, including the newly created (2023) MPAs in the archipelago of New Caledonia Sea (Decree n°2023-2955/GNC from 18 October 2023).

The formulation of the problem with prioritizr includes a factor referred to as boundary length modifier (BLM), which controls the compactness of selected units. Lower BLM values provide more spatially fragmented solutions, whereas higher BLM values emphasize compact solutions. Spatially and vertically compact protected areas may more efficiently protect a wide range of species and be easier to manage (cover large spatial and depth ranges, limit the fishing pressure on the edges, and protect the entire water column). For the solution allowing protection of 30% of the spatial domain, we computed 8 iterations of our prioritization problem with BLM values from 0 to 100 (0, 10^{-4}, 10^{-3}, 10^{-2}, 10^{-1}, 1, 10, 100) with the function add_boundary_penalties, which adds penalties to favor solutions that spatially clump planning units based on the overall boundary area, and assessed the efficiency of each solution. For each solution, we computed the total cost and the total boundary area (a proxy of fragmentation). We used the technique for order of preference by similarity to ideal solution (TOPSIS) to rank the solutions and find the best trade-off between total cost and total boundary area (Greene et al., 2011; Hwang & Yoon, 1981) (details in Appendix S1).

The data used for this article are archived in a public repository Zenodo: https://doi.org/10.5281/zenodo.11480777. The codes used for the analyses are available at https://github.com/lmathon/Seamounts_3Dmodeling.

RESULTS

Abundance, richness, and biomass

We identified 190 species from 53 families with the BRUVS and 596 MOTUs from 93 families with eDNA. The species and families had different distributions among site types. Twenty-three species, 12 benthic MOTUs, and 10 pelagic MOTUs were retained for the GJAM analyses (Appendices S19–S24).

The modeling of the 7 fish community metrics with BRTs all reached moderate to high cross-validation accuracy (mean $R = 0.7$) (Figure 2a). The relative contribution of each explanatory variable varied largely among models, but depth (seafloor depth and summit depth), remoteness (travel time to Nouméa, distance to reef and land), and temperature (SST and seafloor temperature) appeared to be the most important factors. Among all models, seafloor depth ranked first (mean [SD] contribution of 20.7% [25]) and was most important in explaining BRUVS fish abundance and biomass, whereas sampling depth most influenced pelagic acoustic biomass. Travel time had a mean contribution of 13.8% (11) and was a major factor explaining eDNA benthic MOTU richness, acoustic biomass, and BRUVS species richness. All the fish community metrics showed varying relationships with the explanatory factors (model results in Appendices S25–S32).

The modeling of 45 individual species abundances and MOTU read numbers with GJAMs provided moderate to high goodness of fit ($R = 0.62$–0.68). The GJAM on BRUVS species abundance revealed 3 clusters, mostly explained by salinity, habitat, and distance to land (Figure 2b). The first cluster included species associated with great depth, either on seamount or deep slopes. The second group was species associated with seamounts and shallow depth, and the third group was species associated with deep slopes and low salinity.

The GJAM on benthic MOTU reads revealed 3 clusters mostly influenced by SST, suspended particulate matter, and distance to reef. The GJAM on pelagic MOTU reads highlighted 2 clusters influenced by salinity, SST, and site type (model results in Appendices S33–S38).

Archipelago-wide predictions

Predictions of the 7 community metrics, the 23 selected species abundances, and the 22 selected MOTU read numbers at the scale of the New Caledonian archipelago reflected well the influence of each explanatory variable and showed spatial heterogeneity horizontally and vertically (prediction results in Appendices S39–S44). For example, fish species richness predicted from the BRUVS data set was higher on shallow seamounts and remote island slopes (e.g., on reefs in the northern and southern lagoons and Fairway) in the first depth layer (0- to 200-m deep) and on deep seamounts (e.g., south of Bellona and Grande Terre) in the third depth layer (400- to 600-m deep) (Figure 3a,b). Likewise, strong spatial differences existed in the 3D distribution of modeled species and MOTUs. For example, the commercially important deep-water snapper (*Pristipomoides filamentosus*) was more abundant on relatively shallow island slopes, whereas the dogfish shark (*Squalus megalops*) was more abundant on deepest slopes and seamounts (Figure 3c,d). To account for such a horizontally and vertically heterogeneous seascape, benthic and pelagic predictions were included in 3 depth layers in the 3D prioritization computation.

Spatial conservation planning in 3 dimensions

The different targets of biodiversity protection yielded solutions with different spatial coverages. There was a strong linear relationship between protection targets of biodiversity metrics and area of the spatial domain protected ($R^2 = 1$, slope = 1.07 [SE 0.001], intercept = 2.84 [0.06]). Protecting 30% of each biodiversity metric led to protecting 34.9% of the spatial domain considered (29,788 km^2 out of 85,247 km^2). Lower biodiversity targets led to solutions protecting <30% of the domain (13.5% and 24.3% for biodiversity targets of 10% and 20%, respectively). Higher biodiversity targets protected larger surfaces

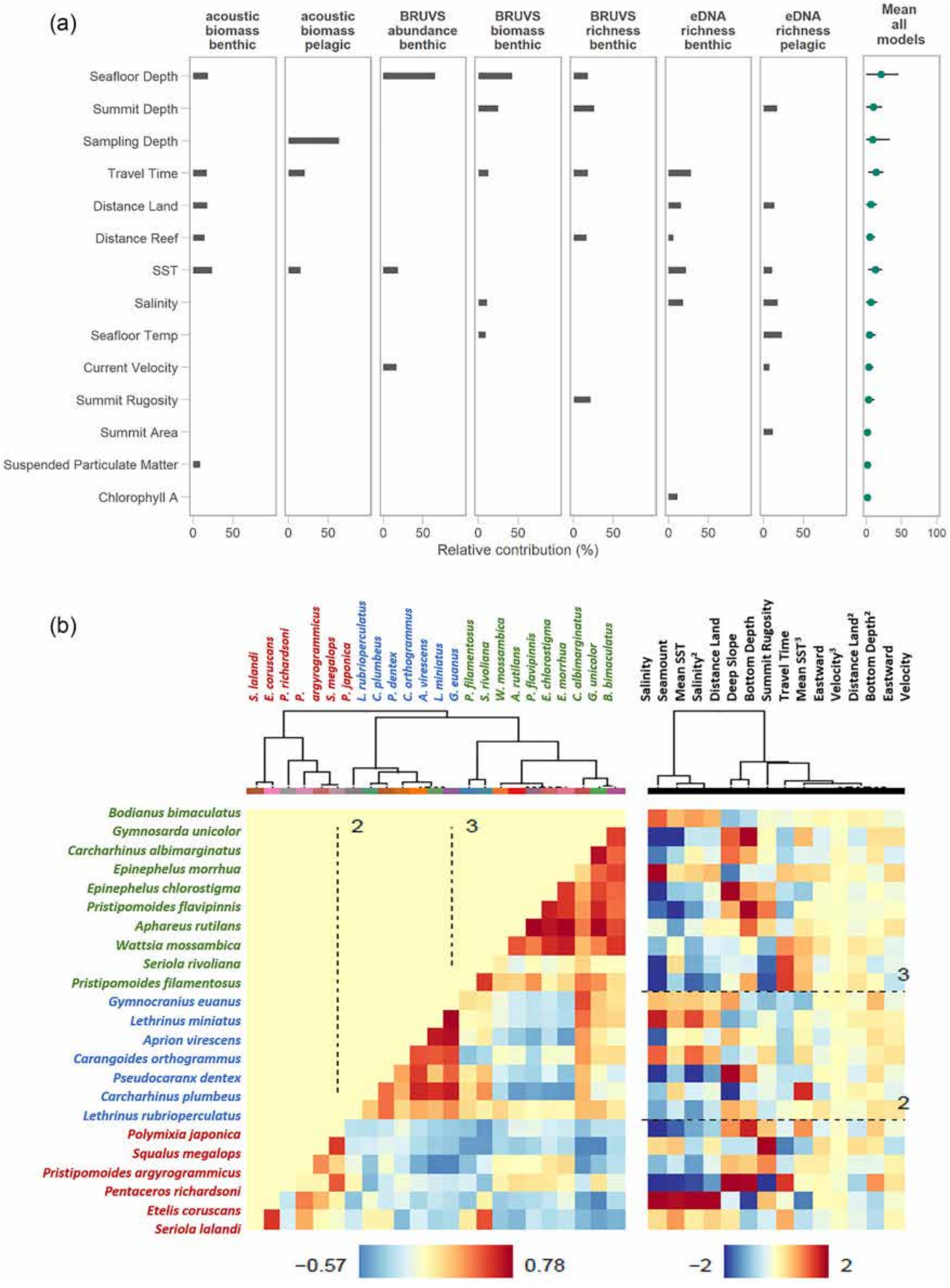

FIGURE 2 (a) Relative contribution of each variable in each boosted regression tree model (0%, variable not included in the model; blue points, mean contribution of each variable among models; error bars, standard deviation among models; BRUVS, baited remote underwater video stations; eDNA, environmental DNA) and (b) strength of correlation between fitted species abundances from BRUVS and predictors of species in the generalized joint attribute model (left panel, correlation among species in terms of their responses to predictors with associated correlation scale; right panel, correlation of each species with predictors with associated correlation scale; dotted lines, 3 species clusters).

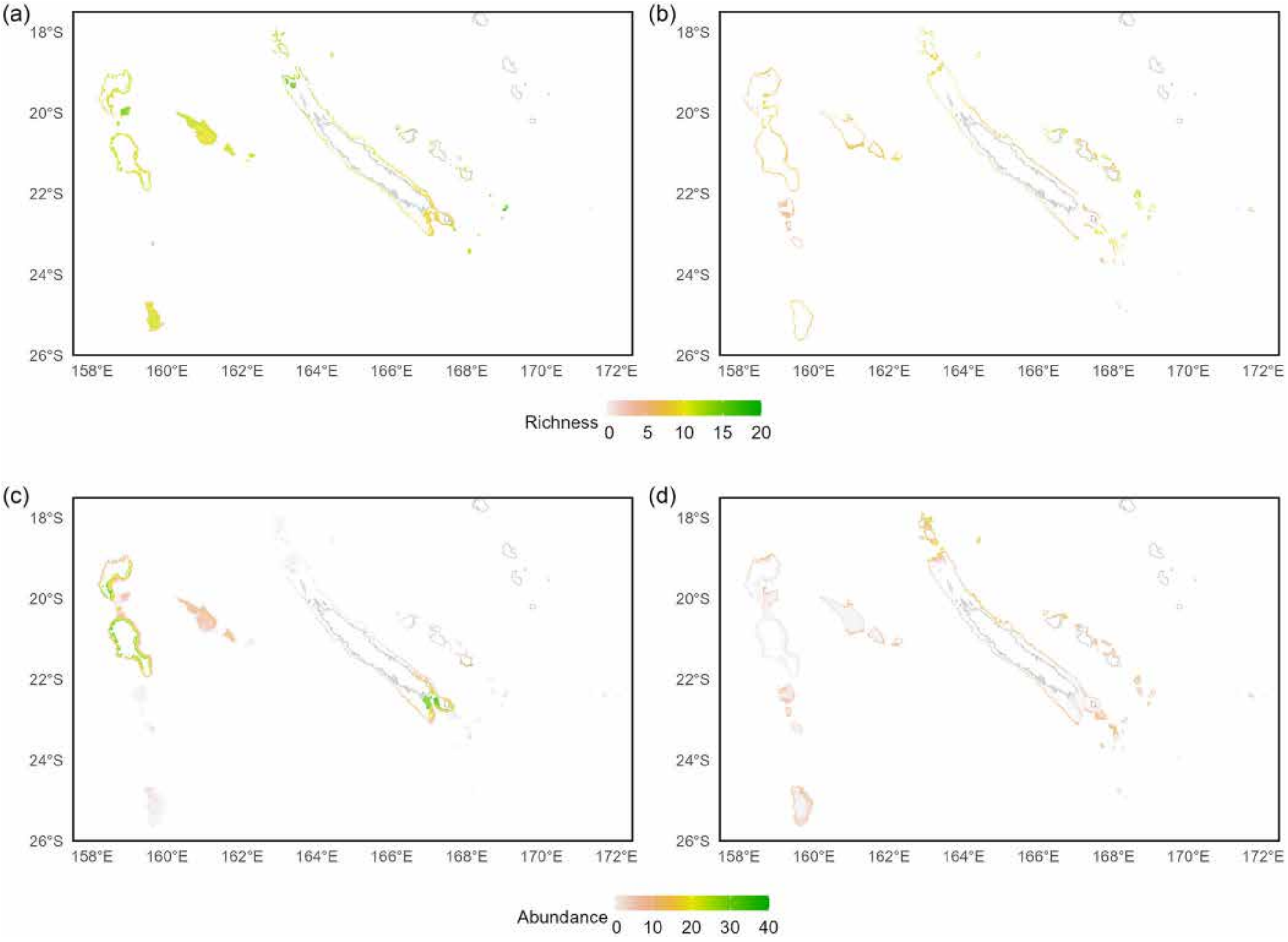

FIGURE 3 Predicted fish (a, b) species richness and (c, d) individual species abundance, as measured from baited remote underwater video stations, from the fitted values of the boosted regression trees and generalized joint attribute models in all seamounts and deep slopes of the New Caledonian economic exclusive zone down to 600-m deep for (a) cells <200-m deep, (b) cells with seafloor 400- to 600-m deep, (c) *Pristipomoides filamentosus* down to 600-m deep, and (d) *Squalus megalops* down to 600-m deep.

(45.7% and 56.3% for biodiversity targets of 40% and 50%, respectively). Details of prioritization results are in Appendix S45.

The solution obtained with biodiversity targets of 30% and no penalty on fragmentation (BLM = 0) was highly fragmented and prioritized 60,241 planning units (Figure 4a). With this solution, 44% of planning units were prioritized across all depth layers, mostly located on remote deep slopes and on several seamounts. Twenty-four percent of planning units were prioritized only in the first depth layer (0–200 m), mostly on the shallow slope around Chesterfield and on shallow seamounts, whereas 8% of planning units were prioritized only in the intermediate depth layer (200–400 m) and 10% only in the deepest depth layer (400–600 m).

The ranking of the different prioritization solutions obtained with the target of 30% and various BLM values with the TOPSIS method identified the best solution with a BLM value of 10 (Appendices S46–S47). This solution had 63,112 planning units, total boundary area of 30,557 km^2 (vs. 51,583 km^2 for BLM0), and total surface of 23,913 km^2, including 13,213 km^2 on slopes and 10,700 km^2 on seamounts (Figure 4b). This corresponded to 28% of the total spatial domain (total area of 85,247 km^2), 30.5% of the slopes, and 25.4% of the seamounts considered in the study down to 600-m depth. More than 70% of planning units prioritized by this solution were across all depth layers. Protection targets were met for all metrics included in the prioritizing algorithm, with low disparity in effective protection (mean = 32.7%, maximum = 47%) (Appendix S48). This conservation solution comprised 17 main areas: 6 areas on slopes and seamounts of the Chesterfield–Bellona alignment (Lord Howe ridge), one area on the Fairway ridge, 2 areas on the slopes of Entrecasteaux and the Great Northern Lagoon, one area on the northeast of Grande Terre, 3 areas on the slopes and seamounts of the Loyalty islands ridge, and 4 areas on slopes in the south of Grande Terre and on southern seamounts (Norfolk ridge). Existing MPAs in the archipelago of New Caledonia cover shallow areas in Grande Terre, the Chesterfield, Bellona, Entrecasteaux, Petri, and Astrolabe remote reefs, and deeper

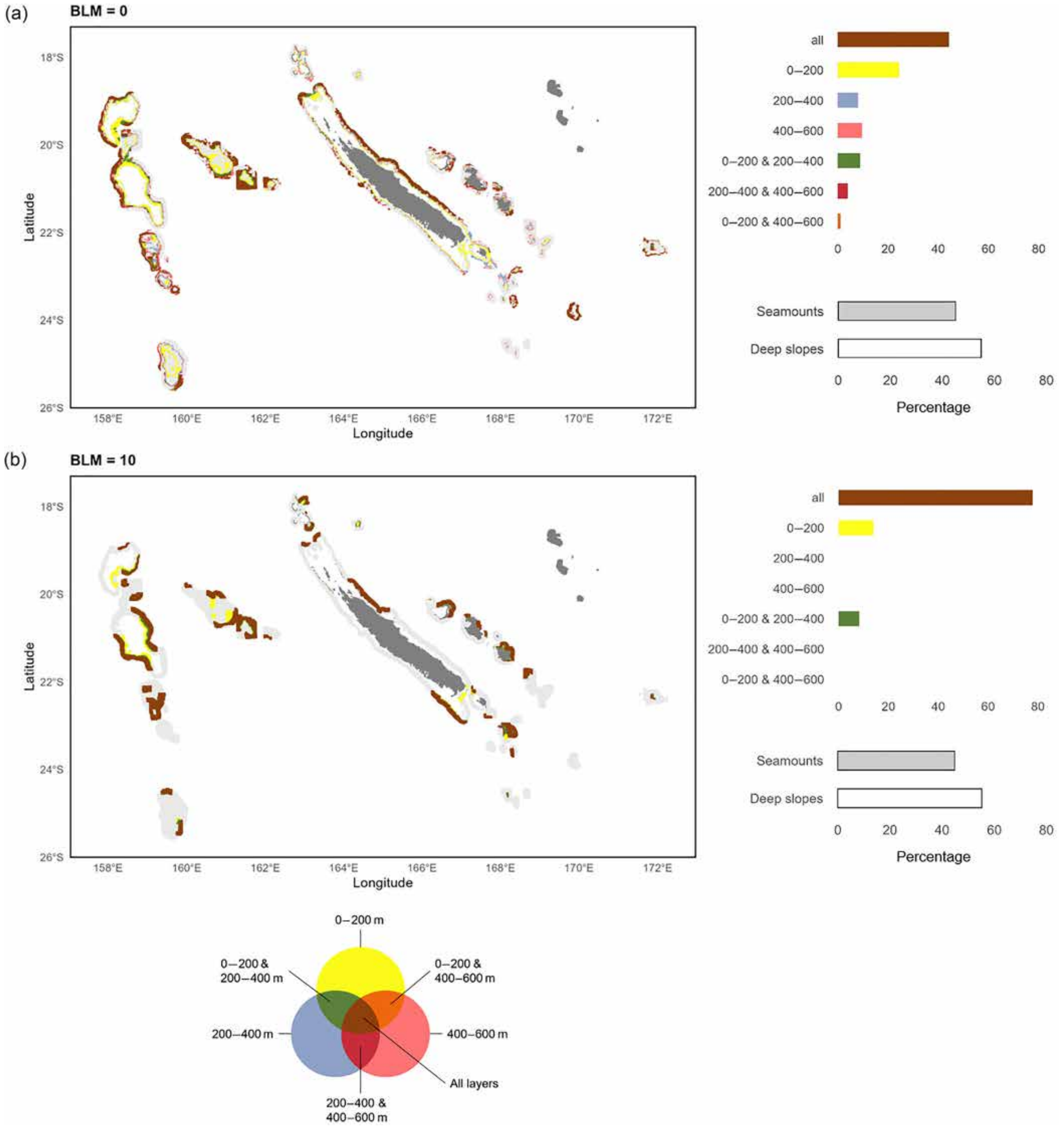

FIGURE 4 Priority conservation areas across space and depth and along a compactness gradient: (a) solution with boundary length modifier (BLM) of 0 (i.e., fragmented solution) and (b) solution with BLM = 10 (best solution identified by technique for order of preference by similarity to ideal solution score) (colors, depth in meters at which each planning unit is prioritized, as shown by the Venn diagram; dark gray, land; light gray, planning units not prioritized by the solution; histograms, percentage of planning units across depth layers and habitats).

areas on the ridges of Fairway and Norfolk. Overall, 36.5% of the areas covered by our solution are already in MPAs, mostly shallow areas on remote reefs and ridges. The remaining unprotected 63.5% covered coastal deep slopes off Grande Terre and Loyalty Islands; deep areas around Chesterfield, Bellona, Capel, and Entrecasteaux; seamounts on the Lord Howe ridge; and the whole area on the Fairway Bank (prioritization results in Appendix S49).

Thus, this solution preserved 30% of the fish biodiversity in ∼30% of the considered spatial domain while accounting for the 3D distribution of biodiversity and offering relative compactness to implement management plans.

DISCUSSION

We collected and modeled a set of biodiversity metrics on 15 seamounts and deep slopes of the New Caledonian archipelago and conducted spatial conservation planning in 3D with different conservation targets for each of our 52 modeled metrics. The conservation solution allowing protection of ~30% (28%) of the area covered by the studied spatial domain, consistent with the 30×30 CBD target, protected at least 30% of each diversity metric (32.7% average) and focused on areas of high importance for biodiversity. This solution was sufficiently compact to provide a reasonable first draft of an area-based management plan while accounting for the 3D distribution of species and biodiversity down to 600-m depth. Furthermore, there was a remarkable linear relationship between biodiversity conservation target and the area of the prioritized solution. Therefore, our biodiversity-based approach seems promising to implement area-based strategic plans in poorly known 3D structured deep-sea environments and other environments where habitats and assemblages cannot be precisely defined.

The strong linear relationship between biodiversity conservation target and the area prioritized ($R^2 = 1$, slope = 1.070, intercept = 2.84) may have resulted from targeting the protection of a wide variety of species with different ecological niches and habitats preferences, which may have led to the protection of a large proportional area comprising all the corresponding habitats. Kujala et al. (2018) found that intermediately rare species occupying mostly species-poor habitats have the greatest influence on the spatial extent of the prioritization, whereas very rare and common species tend to have a small influence. This relationship may not be linear when considering fewer species or a 2D space with little variety. However, further studies are needed in other ecosystems and in other geographic areas to test the generality of this relationship.

The solution of 3D conservation planning with no penalty for compactness was highly fragmented both horizontally and vertically; many planning units were selected in only one or 2 depth layers. Adding a penalty for fragmentation, with a higher value of BLM, led to a more horizontally and vertically compact solution, which may be more efficient in protecting diversity, especially for species with large ranges and species that are more easily managed and surveilled (Edgar et al., 2014). The solution with a BLM of 10 was almost a 2D solution that protected the 3D distribution of biodiversity by favoring the protection of a few large contiguous areas, including all feature types (seamounts and slopes) across the whole water column. The archipelago of New Caledonia hosts one third of global wilderness coral reefs, mostly on Chesterfield, Bellona, and D'Entrecasteaux reefs (Januchowski-hartley et al., 2020), which are currently included in highly protected areas (Claudet et al., 2021). Among the areas prioritized by our best planning solution, derived from the 3D distribution of 52 modeled biodiversity metrics, 36.5% are already included in current MPAs, mostly in shallow waters around Chesterfield, Bellona, and Entrecasteaux reefs and on the Southern Ridges (Norfolk and Fairway). However, our solution also prioritized deeper areas on seamounts and atolls in the Coral Sea Marine Park, where protection may be easy to achieve due to low human pressure and deep slopes along the Grande Terre and the Loyalty Islands.

Our study is one of the few comparing biodiversity from seamounts and deep slopes and combining several novel sampling technologies (Mazzei et al., 2021; Salvetat et al., 2022). Most studies on deep water diversity focus only on one habitat and use no more than one or 2 sampling methods (Cherel et al., 2020; Mejía-Mercado et al., 2019). Our modeling framework revealed that each metric was explained by a different combination of environmental variables and hence had a rather unique distribution. The 3D optimization was therefore essential to selecting the planning units that could protect all metrics in such a heterogeneous seascape. Despite the heterogeneity, depth, remoteness (travel time, distance to land and reefs), and temperature were the strongest predictors of our biodiversity metrics. Most metrics decreased with increasing summit depth or seafloor depth, which is consistent with previous studies of fish diversity along depth gradients (Quattrini et al., 2017). Pelagic acoustic biomass showed a second peak around 500-m deep, which corresponds to the region of micronektonic concentration in the daytime (Ariza et al., 2016). Areas close to land and reefs with a low human impact showed higher diversity levels because they benefit from higher habitat diversity, terrigenous influence (Carassou et al., 2010), and reef areas supporting large populations and individuals (Gove et al., 2016). Most biodiversity metrics increased with moderate travel time, which is concordant with a similar relationship shown for reef biodiversity, where biomass, but also functional and phylogenetic diversity, increased with travel time (Maire et al., 2016).

Our biodiversity predictions were mostly higher on deep slopes around the Grande-Terre and remote atolls (Chesterfield, Entrecasteaux) and on shallow seamounts (Capel, Fairway). Deeper seamounts hosted high abundances of species associated with great depth but had lower biodiversity in general. These results are consistent with recent studies on seamounts showing that deep-sea fish assemblages are strongly correlated with depth, salinity, rugosity, and chlorophyll a (Muff et al., 2022) and that shallow seamounts are refuges for marine predators, such as sharks, jacks, tunas, and billfish (Letessier et al., 2019).

We provide a complete framework for 3D conservation planning, including steps for collecting field data, preparing data for analyses, and subsequently generating spatial prioritizations in 3 dimensions. This framework aligns with the goals and targets of the CBD for 2030 to ensure the sustainable management of wild species and implementation of biodiversity-inclusive spatial planning (targets 1 and 9). Target 3 calls for the protection of 30% of land and sea areas, focusing on well-connected areas of particular importance for biodiversity. By including several biodiversity metrics and targets (richness, biomass, abundance, important species) and the penalty on fragmentation, our framework ensures that the areas selected are diverse, functional, and well connected. The linear relationship between biodiversity and area target suggests that using species-based targets may lead to solutions covering an equivalent area, which can be useful when habitats are not well known, and protecting the water column. The collection of a comprehensive data set, with various methods and metrics, is challenging and costly, but necessary to include the most accurate data in the prioritization process. Video analyses from BRUVS could be more efficient with deep learning algorithms to identify and measure the species automatically (Villon et al., 2021), and the costs of eDNA analyses are decreasing as the method becomes more widely used.

Despite our massive sampling effort, we could not sample temporal replicates; thus, the conservation planning resulting from this sampling reflects a snapshot of the diversity. We could not sample seamounts deeper than 600 m or deep-sea environments, such as abyssal valleys between seamounts. Although sampling on the valleys would be technically challenging, it may bring some evidence for seamounts as hotspots of fish diversity in the open ocean (Campanella et al., 2021). We sampled deep slopes down to 220-m deep and extrapolated the predictions to 600 m so as to have similar depth range as seamounts data. Although other studies confirm that deep island slopes harbor diverse fish and coral assemblages (Cruz-Acevedo et al., 2018), it would be necessary to add samples from deep slopes at 600 m to increase confidence in our interpretation. We sampled modeled and predicted fish biodiversity only. Although our prioritization solution reflects the most important areas for the conservation of fish biodiversity, some other areas may be important for other taxa. Seamounts have been identified as oases of epibenthic megafauna (Rowden et al., 2010) and important feeding areas for cetaceans (Romagosa et al., 2020).

Each of the sampling methods we used had its own limitations. The accuracy of diversity estimates with BRUVS can be limited by the visibility at the station (Langlois et al., 2020). The acoustic estimates obtained with the 38-kHz echosounder corresponded to micronekton and so included mostly fish but also crustaceans and cephalopods. Fish estimates could be incomplete because a large biomass of mesopelagic fish without gas-filled swim bladders may be present but hidden to the acoustic signal by stronger scatterers (Davison et al., 2015). One way to improve our acoustic estimates could be to use multifrequency or wideband acoustic vertical profilers. For the analyses of eDNA metabarcoding data, we used MOTUs curated by a conservative pipeline to decrease the number of MOTUs representing the same taxa and thus better reflect the true level of fish diversity (Brandt et al., 2021; Marques et al., 2020). This methodology may, however, underestimate fish diversity of rare fish species that are more poorly represented in public databases. Moreover, the high number of PCR cycles may influence the detection of species by introducing bias due to PCR errors and reducing the detection of rare species, depending on the primer specificity (Kelly et al., 2019). Our models may also fail to isolate the effect of each variable because our sampling stations were close to each other at each site, and the variables may be locally correlated.

Our 3D conservation planning solution remains theoretical. To obtain a more realistic scenario, we would also have had to include a broader range of taxa in our process, not just fishes, and to have given more weight to rare or endangered species or to areas of special interest (e.g., existing protected areas) and less weight to areas of special use (e.g., fishing areas). This process would require a dialogue with stakeholders, managers, and decision makers to define their interests, needs, opinions, and constraints and guarantee their support in the creation of the conservation plan (André et al., 2021; Frazão Santos et al., 2021; Markantonatou et al., 2021), but this is outside the scope of our work. Integrating predictions of future climate change in the conservation planning and identifying climate change hotspots and refuges would allow placing MPAs in climate-resilient areas and limit the impacts of climate change on ocean ecosystems (Brito-Morales et al., 2022; Queirós et al., 2021). Connectivity may also be an important parameter to include in the conservation planning, through the analysis of species dynamics and dispersal. A well-connected network of MPA may enhance the persistence of both large-range and small-range species, especially at a larger spatial scale (i.e., the Coral Sea) (Magris et al., 2018). To choose the best solution, we used BLM calibration and the TOPSIS method, but finding the best trade-off can be challenging because it depends on a range of factors, and other methods can be used (Arafeh-Dalmau et al., 2021; Brito-Morales et al., 2022; Venegas-Li et al., 2018).

From extensive deep-sea sampling down to 600 m on 15 seamounts and deep slopes across the New Caledonian Archipelago and by combining high-tech methods, we provide a framework for modeling, predicting, and prioritizing biodiversity across space and depth. Our results suggest that fish biodiversity is strongly structured across depth, although each metric had its own spatial distribution in a highly heterogeneous seascape. Three-dimensional conservation planning allowed the definition of a solution that included a few areas of high biodiversity importance across all depths, covering 30% of the spatial domain studied. The selected areas, of different sizes, were scattered throughout the Coral Sea Marine Park at different latitudes and depths, which is an advantage for the conservation of a majority of species and habitats against human pressures and climate change. Our study paves the way for a new methodological framework for the selection of conservation areas in 3D structured environments, taking into account the depth and its biodiversity. This methodology could help provide solutions compatible with the area-based targets agreed by the international community.

AUTHOR CONTRIBUTIONS

Laetitia Mathon and Laurent Vigliola conceived the study. Laurent Vigliola designed the sampling. Florian Baletaud, Laurent Vigliola, Mahé Dumas, Laetitia Mathon, Christophe Menkes, Céline Bachelier, Claire Bonneville, Christine Sidobre, Jacques Grelet, and David Varillon collected the data. Tony Dejean supervised the eDNA laboratory analyses. Laetitia Mathon and Gaël Lecellier performed eDNA bioinformatic analyses, and Florian Baletaud and Mahé Dumas analyzed the BRUVS data. Anne Lebourges-Dhaussy, Jérémie Habasque, Maëlis Peran, and Laurent Vigliola analyzed the acoustic data. Laetitia Mathon performed the modeling and statistical analyses and interpreted outputs. Laetitia Mathon wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

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REFERENCES

André, L. V., van Wynsberge, S., Chinain, M., & Andréfouët, S. (2021). An appraisal of systematic conservation planning for Pacific Ocean Tropical Islands coastal environments. *Marine Pollution Bulletin*, *165*, Article 112131.

Andrello, M., Darling, E. S., Wenger, A., Suárez-Castro, A. F., Gelfand, S., & Ahmadia, G. N. (2022). A global map of human pressures on tropical coral reefs. *Conservation Letters*, *15*(1), Article e12858.

Arafeh-Dalmau, N., Brito-Morales, I., Schoeman, D. S., Possingham, H. P., Klein, C. J., & Richardson, A. J. (2021). Incorporating climate velocity into the design of climate-smart networks of marine protected areas. *Methods in Ecology and Evolution*, *12*(10), 1969–1983.

Ariza, A., Landeira, J. M., Escánez, A., Wienerroither, R., Aguilar de Soto, N., Røstad, A., Kaartvedt, S., & Hernández-León, S. (2016). Vertical distribution, composition and migratory patterns of acoustic scattering layers in the Canary Islands. *Journal of Marine Systems*, *157*, 82–91.

Baletaud, F., Lecellier, G., Gilbert, A., Mathon, L., Côme, J.-M., Dejean, T., Dumas, M., Fiat, S., & Vigliola, L. (2023). Comparing seamounts and coral reefs with eDNA and BRUVS reveals oases and refuges on shallow seamounts. *Biology*, *12*(11), Article 1446.

Boyer, F., Mercier, C., Bonin, A., Le Bras, Y., Taberlet, P., & Coissac, E. (2016). obitools: A unix-inspired software package for DNA metabarcoding. *Molecular Ecology Resources*, *16*(1), 176–182.

Brandt, M. I., Trouche, B., Quintric, L., Günther, B., Wincker, P., Poulain, J., & Arnaud-Haond, S. (2021). Bioinformatic pipelines combining denoising and clustering tools allow for more comprehensive prokaryotic and eukaryotic metabarcoding. *Molecular Ecology Resources*, *21*(6), 1904–1921.

Brito-Morales, I., Schoeman, D. S., Everett, J. D., Klein, C. J., Dunn, D. C., García Molinos, J., Burrows, M. T., Buenafe, K. C. V., Dominguez, R. M., Possingham, H. P., & Richardson, A. J. (2022). Towards climate-smart, three-dimensional protected areas for biodiversity conservation in the high seas. *Nature Climate Change*, *12*(4), 402–407.

Campanella, F., Collins, M. A., Young, E. F., Laptikhovsky, V., Whomersley, P., & van der Kooij, J. (2021). First insight of meso- and bentho-pelagic fish dynamics around remote seamounts in the South Atlantic Ocean. *Frontiers in Marine Science*, *8*, Article 663278. https://doi.org/10.3389/fmars.2021.663278

Carassou, L., Le Borgne, R., Rolland, E., & Ponton, D. (2010). Spatial and temporal distribution of zooplankton related to the environmental conditions in the coral reef lagoon of New Caledonia, Southwest Pacific. *Marine Pollution Bulletin*, *61*(7–12), 367–374.

Convention on Biological Diversity (CBD). (2021). *First draft of the post-2020 Global Biodiversity Framework* (CBD/WG2020/3/3). Secretariat of the United Nations Convention on Biological Diversity.

Cherel, Y., Romanov, E. V, Annasawmy, P., Thibault, D., & Ménard, F. (2020). Micronektonic fish species over three seamounts in the southwestern Indian Ocean. *Deep Sea Research Part II: Topical Studies in Oceanography*, *176*, Article 104777. https://doi.org/10.1016/j.dsr2.2020.104777

Clark, J. S., Nemergut, D., Seyednasrollah, B., Turner, P. J., & Zhang, S. (2017). Generalized joint attribute modeling for biodiversity analysis: Median-zero, multivariate, multifarious data. *Ecological Monographs*, *87*(1), 34–56.

Claudet, J., Loiseau, C., & Pebayle, A. (2021). Critical gaps in the protection of the second largest exclusive economic zone in the world. *Marine Policy*, *124*, Article 104379. https://doi.org/10.1016/j.marpol.2020.104379

Cruz-Acevedo, E., Tolimieri, N., & Aguirre-Villaseñor, H. (2018). Deep-sea fish assemblages (300-2100 m) in the eastern Pacific off northern Mexico. *Marine Ecology Progress Series*, *592*, 225–242.

Davison, P., Koslow, J. A., & Kloser, R. (2015). Acoustic biomass estimation of mesopelagic fish: Backscattering from individuals, populations and communities. *ICES Journal of Marine Science*, *75*(5), 1413–1424.

Devillers, R., Pressey, R. L., Grech, A., Kittinger, J. N., Edgar, G. J., Ward, T. J., & Watson, R. (2015). Reinventing residual reserves in the sea: Are we favouring ease of establishment over need for protection? *Aquatic Conservation: Marine and Freshwater Ecosystems*, *25*, 480–504.

Dornan, T., Fielding, S., Saunders, R. A., & Genne, M. J. (2019). Swimbladder morphology masks Southern Ocean mesopelagic fish biomass. *Proceedings of the Royal Society B: Biological Sciences*, *286*, Article 20190353.

Doxa, A., Almpanidou, V., Katsanevakis, S., Queirós, A. M., Kaschner, K., Garilao, C., Kesner-Reyes, K., & Mazaris, A. D. (2022). 4D marine conservation networks: Combining 3D prioritization of present and future biodiversity with climatic refugia. *Global Change Biology*, *28*(15), 4577–4588.

Eddy, T. D., Lam, V. W. Y., Reygondeau, G., Cisneros-Montemayor, A. M., Greer, K., Palomares, M.-L. D., Bruno, J. F., Ota, Y., & Cheung, W. W. L. (2021). Global decline in capacity of coral reefs to provides ecosystem services. *One Earth*, *4*, 1278–1285.

Edgar, G. J., Stuart-Smith, R. D., Willis, T. J., Kininmonth, S., Baker, S. C., Banks, S., Barrett, N. S., Becerro, M. A., Bernard, A. T. F., Berkhout, J., Buxton, C. D., Campbell, S. J., Cooper, A. T., Davey, M., Edgar, S. C., Försterra, G., Galván, D. E., Irigoyen, A. J., Kushner, D. J., … Thomson, R. J. (2014). Global conservation outcomes depend on marine protected areas with five key features. *Nature*, *506*(7487), 216–220.

Elith, J., Leathwick, J. R., & Hastie, T. (2008). A working guide to boosted regression trees. *Journal of Animal Ecology*, *77*(4), 802–813.

Frazão Santos, C., Agardy, T., Andrade, F., Crowder, L. B., Ehler, C. N., & Orbach, M. K. (2021). Major challenges in developing marine spatial planning. *Marine Policy*, *132*, Article 103248.

Gove, J. M., McManus, M. A., Neuheimer, A. B., Polovina, J. J., Drazen, J. C., Smith, C. R., Merrifield, M. A., Friedlander, A. M., Ehses, J. S., Young, C. W., Dillon, A. K., & Williams, G. J. (2016). Near-island biological hotspots in barren ocean basins. *Nature Communications*, *7*, Article 10581.

Greene, R., Devillers, R., Luther, J. E., & Eddy, B. G. (2011). GIS-based multiple-criteria decision analysis. *Geography Compass*, *5*, 412–432.

Gurobi Optimization, LLC. (2023). *Gurobi optimizer reference manual*. https://www.gurobi.com

Hanson, J., Schuster, R., Morrell, N., Strimas-Mackey, M., Edwards, B., Watts, M., Arcese, P., Bennett, J., & Possingham, H. (2022). *prioritizr: Systematic conservation prioritization in R*. https://prioritizr.net, https://github.com/prioritizr/prioritizr

Hijmans, R. J., Phillips, S., Leathwick, J., Elith, J., & Hijmans, M. R. J. (2017). Package 'dismo'. *Circles*, *9*(1), 1–68.

Hwang, C.-L., & Yoon, K. (1981). Methods for information on attribute given. In C.-L. Hwang & K. Yoon (Eds.), *Lecture notes in economics and mathematical systems* (pp. 58–191). Springer.

Jacquemont, J., Loiseau, C., Tornabene, L., & Claudet, J. (2024). 3D ocean assessments reveal that fisheries reach deep but marine protection remains shallow. *Nature Communications*, *15*(1), Article 4027.

Januchowski-Hartley, F. A., Vigliola, L., Maire, E., Kulbicki, M., & Mouillot, D. (2020). Low fuel cost and rising fish price threaten coral reef wilderness. *Conservation Letters*, *13*(3), Article e12706.

Juhel, J. B., Vigliola, L., Wantiez, L., Letessier, T. B., Meeuwig, J. J., & Mouillot, D. (2019). Isolation and no-entry marine reserves mitigate anthropogenic impacts on grey reef shark behavior. *Scientific Reports*, *9*, Article 2897.

Kelly, R. P., Shelton, A. O., & Gallego, R. (2019). Understanding PCR processes to draw meaningful conclusions from environmental DNA studies. *Scientific Reports*, *9*, Article 12133.

Kerry, C. R., Exeter, O. M., & Witt, M. J. (2022). Monitoring global fishing activity in proximity to seamounts using automatic identification systems. *Fish and Fisheries*, *23*(3), 733–749.

Kujala, H., Moilanen, A., & Gordon, A. (2018). Spatial characteristics of species distributions as drivers in conservation prioritization. *Methods in Ecology and Evolution*, *9*(4), 1121–1132.

Kvile, K. O., Taranto, G. H., Pitcher, T. J., & Morato, T. (2014). A global assessment of seamount ecosystems knowledge using an ecosystem evaluation framework. *Biological Conservation*, *173*, 108–120.

Langlois, T. J., Goetze, J., Bond, T., Monk, J., Abesamis, R. A., Asher, J., Barrett, N., Bernard, A. T. F., Bouchet, P. J., Birt, M. J., Cappo, M., Currey-Randall, L. M., Driessen, D., Fairclough, D. V., Fullwood, L. A. F., Gibbons, B., Harasti, D., Heupel, M. R., Hicks, J., … Harvey, E. S. (2020). A field and video annotation guide for baited remote underwater stereo-video surveys of demersal fish assemblages. *Methods in Ecology and Evolution*, *11*, 1401–1409.

Leinonen, R., Akhtar, R., Birney, E., Bower, L., Cerdeno-Tárraga, A., Cheng, Y., Cleland, I., Faruque, N., Goodgame, N., Gibson, R., Hoad, G., Jang, M., Pakseresht, N., Plaister, S., Radhakrishnan, R., Reddy, K., Sobhany, S., Ten Hoopen, P., Vaughan, R., … Cochrane, G. (2011). The European nucleotide archive. *Nucleic Acids Research*, *39*(Suppl. 1), 44–47.

Letessier, T. B., Mouillot, D., Bouchet, P. J., Vigliola, L., Fernandes, M. C., Thompson, C., Boussarie, G., Turner, J., Juhel, J.-B., Maire, E., Caley, M. J., Koldewey, H. J., Friedlander, A., Sala, E., & Meeuwig, J. J. (2019). Remote reefs and seamounts are the last refuges for marine predators across the Indo-Pacific. *PLoS Biology*, *17*(8), Article e3000366.

Levin, N., Kark, S., & Danovaro, R. (2018). Adding the third dimension to marine conservation. *Conservation Letters*, *11*(3), Article e12408.

Magris, R. A., Andrello, M., Pressey, R. L., Mouillot, D., Dalongeville, A., Jacobi, M. N., & Manel, S. (2018). Biologically representative and well-connected marine reserves enhance biodiversity persistence in conservation planning. *Conservation Letters*, *11*(4), Article e12439.

Mahé, F., Rognes, T., Quince, C., de Vargas, C., & Dunthorn, M. (2015). Swarm v2: Highly-scalable and high-resolution amplicon clustering. *PeerJ*, *3*, Article e1420.

Maire, E., Cinner, J., Velez, L., Huchery, C., Mora, C., Dagata, S., Vigliola, L., Wantiez, L., Kulbicki, M., & Mouillot, D. (2016). How accessible are coral reefs to people? A global assessment based on travel time. *Ecology Letters*, *19*(4), 351–360.

Markantonatou, V., Giakoumi, S., Koukourouvli, N., Maina, I., Gonzalez-Mirelis, G., Sini, M., Maistrelis, K., Stithou, M., Gadolou, E., Petza, D., Kavadas, S., Vassilopoulou, V., Buhl-Mortensen, L., & Katsanevakis, S. (2021). Marine spatial plans focusing on biodiversity conservation: The case of the Aegean Sea. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *31*(8), 2278–2292.

Marques, V., Guérin, P. É., Rocle, M., Valentini, A., Manel, S., Mouillot, D., & Dejean, T. (2020). Blind assessment of vertebrate taxonomic diversity across spatial scales by clustering environmental DNA metabarcoding sequences. *Ecography*, *43*, 1779–1790.

Mathon, L., Marques, V., Mouillot, D., Albouy, C., Andrello, M., Baletaud, F., Borrero-Pérez, G. H., Dejean, T., Edgar, G. J., Grondin, J., Guerin, P.-E., Hocdé, R., Juhel, J.-B., Kadarusman, Maire, E., Mariani, G., McLean, M., Polanco, F. A., Pouyaud, L., … Manel, S. (2022). Cross-ocean patterns and processes in fish biodiversity on coral reefs through the lens of eDNA metabarcoding. *Proceedings of the Royal Society B: Biological Sciences*, *289*, Article 20220162.

Maxwell, S. L., Cazalis, V., Dudley, N., Hoffmann, M., Rodrigues, A. S. L., Stolton, S., Visconti, P., Woodley, S., Kingston, N., Lewis, E., Maron, M., Strassburg, B. B. N., Wenger, A., Jonas, H. D., Venter, O., & Watson, J. E. M. (2020). Area-based conservation in the twenty-first century. *Nature*, *586*(7828), 217–227.

Mazzei, E. F., Pinheiro, H. T., Simon, T., Moura, R. L., Macieira, R. M., Pimentel, C. R., Teixeira, J. B., Floeter, S. R., Ferreira, C. E. L., Ghisolfi, R. D., Francini-Filho, R. B., Quimbayo, J. P., Rocha, L. A., Gasparini, J. L., & Joyeux, J.-C. (2021). Mechanisms of dispersal and establishment drive a stepping stone community assembly on seamounts and oceanic islands. *Marine Biology*, *168*, Article 109. https://doi.org/10.1007/s00227-021-03919-7

McClanahan, T. R. (2021). Marine reserve more sustainable than gear restriction in maintaining long-term coral reef fisheries yields. *Marine Policy*, *128*, Article 104478.

Mejía-Mercado, B. E., Mundy, B., & Baco, A. R. (2019). Variation in the structure of the deep-sea fish assemblages on Necker Island, Northwestern Hawaiian Islands. *Deep Sea Research Part I: Oceanographic Research Papers*, *152*, Article 103086.

Muff, M., Jaquier, M., Marques, V., Ballesta, L., Deter, J., Bockel, T., Hocdé, R., Juhel, B., Boulanger, E., Guellati, N., Polanco, A., Alice, F., Dejean, T., Manel, S., Albouy, C., Durville, P., Mouillot, D., Holon, F., & Pellissier, L. (2022). Environmental DNA highlights fish biodiversity in mesophotic ecosystems. *Environmental DNA*, *5*, 56–72.

Pacoureau, N., Rigby, C. L., Kyne, P. M., Sherley, R. B., Winker, H., Carlson, J. K., Fordham, S. V., Barreto, R., Fernando, D., Francis, M. P., Jabado, R. W., Herman, K. B., Liu, K. M., Marshall, A. D., Pollom, R. A., Romanov, E. V., Simpfendorfer, C. A., Yin, J. S., Kindsvater, H. K., & Dulvy, N. K. (2021). Half a century of global decline in oceanic sharks and rays. *Nature*, *589*(7843), 567–571.

Perrot, Y., Brehmer, P., Habasque, J., Roudaut, G., Behagle, N., Sarré, A., & Lebourges-Dhaussy, A. (2018). Matecho: An open-source tool for processing fisheries acoustics data. *Acoustics Australia*, *46*(2), 241–248.

Pinheiro, H. T., Shepherd, B., Teixeira, J. B., Pimentel, C. R., Pereira, P. H. C., Stein, C. E., Reis-Filho, J. A., Garla, R. C., Macieira, R. M., Delfino, S. D. T., Giarrizzo, T., Joyeux, J. C., Gasparini, J. L., & Rocha, L. A. (2021). Fish aggregations and reproductive behaviour on mesophotic coral ecosystems of a southwestern Atlantic Oceanic archipelago. *Journal of Natural History*, *55*(31–32), 2017–2025.

Proud, R., Cox, M. J., Le Guen, C., & Brierley, A. S. (2018). Fine-scale depth structure of pelagic communities throughout the global ocean based on acoustic sound scattering layers. *Marine Ecology Progress Series*, *598*, 35–48.

Quattrini, A. M., Demopoulos, A. W. J., Singer, R., Roa-Varon, A., & Chaytor, J. D. (2017). Demersal fish assemblages on seamounts and other rugged features in the northeastern Caribbean. *Deep Sea Research Part I: Oceanographic Research Papers*, *123*, 90–104.

Queirós, A. M., Talbot, E., Beaumont, N. J., Somerfield, P. J., Kay, S., Pascoe, C., Dedman, S., Fernandes, J. A., Jueterbock, A., Miller, P. I., Sailley, S. F., Sará, G., Carr, L. M., Austen, M. C., Widdicombe, S., Rilov, G., Levin, L. A., Hull, S. C., Walmsley, S. F., & Nic Aonghusa, C. (2021). Bright spots as climate-smart marine spatial planning tools for conservation and blue growth. *Global Change Biology*, *27*(21), 5514–5531.

R Core Team. (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.r-project.org/

Rocha, L. A., Pinheiro, H. T., Shepherd, B., Papastamatiou, Y. P., Luiz, O. J., Pyle, R. L., & Bongaerts, P. (2018). Mesophotic coral ecosystems are threatened and ecologically distinct from shallow water reefs. *Science*, *361*(6399), 281–284.

Rodrigues, A. S., Cerdeira, J. O., & Gaston, K. J. (2000). Flexibility, efficiency, and accountability: Adapting reserve selection algorithms to more complex conservation problems. *Ecography*, *23*(5), 565–574.

Rogers, A. D. (2018). The biology of seamounts: 25 years on. *Advances in Marine Biology*, *79*, 137–224.

Romagosa, M., Lucas, C., Pérez-Jorge, S., Tobeña, M., Lehodey, P., Reis, J., Cascão, I., Lammers, M. O., Caldeira, R. M. A., & Silva, M. A. (2020). Differences in regional oceanography and prey biomass influence the presence of foraging odontocetes at two Atlantic seamounts. *Marine Mammal Science*, *36*(1), 158–179.

Rowden, A. A., Schlacher, T. A., Williams, A., Clark, M. R., Stewart, R., Althaus, F., Bowden, D. A., Consalvey, M., Robinson, W., & Dowdney, J. (2010). A test of the seamount oasis hypothesis: Seamounts support higher epibenthic megafaunal biomass than adjacent slopes. *Marine Ecology*, *31*(Suppl. 1), 95–106.

Rutterford, L. A., Simpson, S. D., Jennings, S., Johnson, M. P., Blanchard, J. L., Schön, P. J., Sims, D. W., Tinker, J., & Genner, M. J. (2015). Future fish distributions constrained by depth in warming seas. *Nature Climate Change*, *5*(6), 569–573.

Salvetat, J., Bez, N., Habasque, J., Lebourges-Dhaussy, A., Lopes, C., Roudaut, G., Simier, M., Travassos, P., Vargas, G., & Bertrand, A. (2022). Comprehensive spatial distribution of tropical fish assemblages from multifrequency acoustics and video fulfils the island mass effect framework. *Scientific Reports*, *12*, Article 8787.

Valentini, A., Taberlet, P., Miaud, C., Civade, R., Herder, J., Thomsen, P. F., Bellemain, E., Besnard, A., Coissac, E., Boyer, F., Gaboriaud, C., Jean, P., Poulet, N., Roset, N., Copp, G. H., Geniez, P., Pont, D., Argillier, C., Baudoin, J. M., … Dejean, T. (2016). Next-generation monitoring of aquatic biodiversity using environmental DNA metabarcoding. *Molecular Ecology*, *25*(4), 929–942.

Venegas-Li, R., Levin, N., Possingham, H., & Kark, S. (2018). 3D spatial conservation prioritisation: Accounting for depth in marine environments. *Methods in Ecology and Evolution*, *9*(3), 773–784.

Vieira, R. P., Coelho, R., Denda, A., Martin, B., Gonçalves, J. M. S., & Christiansen, B. (2018). Deep-sea fishes from Senghor Seamount and the adjacent abyssal plain (Eastern Central Atlantic). *Marine Biodiversity*, *48*(2), 963–975.

Villon, S., Iovan, C., Mangeas, M., Claverie, T., Mouillot, D., Villéger, S., & Vigliola, L. (2021). Automatic underwater fish species classification with limited data using few-shot learning. *Ecological Informatics*, *63*, Article 101320. https://doi.org/10.1016/j.ecoinf.2021.101320

Watling, L., & Auster, P. J. (2021). Vulnerable marine ecosystems, communities, and indicator species: Confusing concepts for conservation of seamounts. *Frontiers in Marine Science*, *8*, Article 622586.

Yesson, C., Clark, M. R., Taylor, M. L., & Rogers, A. D. (2011). The global distribution of seamounts based on 30 arc seconds bathymetry data. *Deep Sea Research Part I: Oceanographic Research Papers*, *58*(4), 442–453.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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