Received: 17 March 2017 | Accepted: 6 September 2017

DOI: 10.1111/2041-210X.12896

RESEARCH ARTICLE

Methods in Ecology and Evolution BRITISH ECOLOGICAL SOCIETY

3D spatial conservation prioritisation: Accounting for depth in marine environments

Rubén Venegas-Li[1,2] | **Noam Levin**[2,3,4] | **Hugh Possingham**[2,5] | **Salit Kark**[1,2]

[1]The Biodiversity Research Group, School of Biological Sciences, Centre for Biodiversity and Conservation Science, The University of Queensland, St Lucia, Qld, Australia

[2]ARC Centre of Excellence for Environmental Decisions (CEED), The University of Queensland, St Lucia, Qld, Australia

[3]Department of Geography, The Hebrew University of Jerusalem, Jerusalem, Israel

[4]School of Earth and Environmental Sciences, The University of Queensland, St Lucia, Qld, Australia

[5]Conservation Science, The Nature Conservancy, South Brisbane, Qld, Australia

Correspondence
Rubén Venegas-Li
Email: r.venegas@uq.edu.au

Funding information
ARC Centre of Excellence for Environmental Decisions; Australia Research Council (ARC) Centre of Excellence for Environmental Decisions (CEED)

Handling Editor: Barbara Anderson

Abstract

1. While marine environments are three-dimensional (3D) in nature, current approaches and tools for planning and prioritising actions in the ocean are predominantly two dimensional. Here, we develop a novel 3D marine spatial conservation prioritisation approach, which explicitly accounts for the inherent vertical heterogeneity of the ocean. This enables both vertical and horizontal spatial prioritisation to be performed simultaneously. To our knowledge, this is the first endeavour to develop prioritisation of conservation actions in 3D.
2. We applied the 3D spatial conservation prioritisation approach to the Mediterranean Sea as a case study. We first subdivided the Mediterranean Sea into 3D planning units by assigning them a *z* coordinate (representing depth). We further partitioned these 3D planning units vertically into three depth layers; this allowed us to quantify biodiversity (1,011 species and 19 geomorphic features) and the cost of conservation actions at different depths. We adapted the prioritisation software Marxan to identify 3D networks of sites where biodiversity conservation targets are achieved for the minimum cost.
3. Using the 3D approach presented here, we identified networks of sites where conservation targets for all biodiversity features were achieved. Importantly, these networks included areas of the ocean where only particular depth layers along the water column were identified as priorities for conservation. The 3D approach also proved to be more cost-efficient than the traditional 2D approach. Spatial priorities within the networks of sites selected were considerably different when comparing the 2D and 3D approaches.
4. Prioritising in 3D allows conservation and marine spatial planners to target specific threats to specific conservation features, at specific depths in the ocean. This provides a platform to further integrate systematic conservation planning into the wider ongoing and future marine spatial planning and ocean zoning processes.

KEYWORDS
3D planning, biodiversity, marine conservation, Marxan, systematic conservation planning, vertical, zoning

1 | INTRODUCTION

Spatial conservation prioritisation is an established method in conservation biology, used to identify areas where biodiversity conservation targets can be achieved efficiently, usually applied as a step of systematic conservation planning processes (Moilanen, Wilson, & Possingham, 2009). This method uses quantitative techniques to prioritise conservation actions in a repeatable and transparent manner, and can take into account ecological, social and economic factors (Margules & Pressey, 2000; Sarkar & Illoldi-Range, 2010). Prioritising can yield greater benefits from limited resources, while minimising potential conflicts between biodiversity conservation and other uses, possibly increasing the acceptance of conservation actions by a wide range of stakeholders (Pressey, Cabeza, Watts, Cowling, & Wilson, 2007).

Spatial prioritisation is based on the premise that biodiversity and the elements affecting its conservation are not distributed evenly in space. Traditionally, spatial conservation prioritisation has accounted for this heterogeneity by subdividing the study area into two-dimensional (2D) units (referred to as planning units). However, biodiversity features and the factors that influence their conservation vary not only horizontally but also vertically, in a three-dimensional (3D) space. A conspicuous example is the World's oceans, a realm with an average depth of ~3,700 m (Charette & Smith, 2000), in which biodiversity, environmental conditions and human activities can vary substantially with depth. This 3D heterogeneity can give rise to circumstances in which for a given area, biodiversity conservation at a certain depth could be compatible with different uses of the ocean at other depths. In such circumstances, prioritising conservation in 3D (i.e. prioritising actions not only in the horizontal but also in the vertical plane) could deliver better outcomes in comparison with a 2D approach. For example, Grober-Dunsmore et al. (2008) presented a conceptual framework to identify conditions in which recreational pelagic fishing could occur above an area where benthic communities are protected, thus enabling vertical zoning of management actions.

A 3D spatial conservation prioritisation can help guide decisions about which activities should be permitted at different depths, following the core principles of systematic conservation planning (e.g. comprehensiveness, efficiency, representativeness and complementarity). While not yet commonplace, vertical zoning of activities in the ocean is already in place in several locations, especially for protecting benthic ecosystems (Fitzsimons & Wescott, 2008; Helson, Leslie, Clement, Wells, & Wood, 2010). Yet in most of the cases, the planning has not been carried out using quantitative systematic conservation prioritisation techniques, reducing their efficiency in relation to cost and biodiversity protection (Leathwick et al., 2008; Rieser, Watling, & Guinotte, 2013).

In this study, we develop and present a novel 3D spatial conservation prioritisation methodology for the marine realm, where depth is spatially and explicitly accounted for. This approach enables accounting for depth-related variability in biodiversity, human activities, threats to biodiversity, environmental conditions and costs of actions in the oceans, and to determine priorities both horizontally and vertically. We propose adding a third dimension to the planning units, and further subdividing them according to depth. We then illustrate the approach with a case study in the Mediterranean Sea using Marxan, to: (1) evaluate the feasibility of achieving conservation targets by prioritising certain depths of the water column for conservation, (2) assess trade-offs between the cost of priority conservation areas and their spatial arrangement and (3) compare the results of the 3D approach with a standard 2D approach. Finally, we discuss technical and management challenges and opportunities of prioritising conservation in 3D.

2 | MATERIALS AND METHODS

2.1 | Study region

We used the Mediterranean Sea as a case study to test the new 3D spatial conservation prioritisation methodology developed here. The Mediterranean, with its broad bathymetry range (maximum depth 5,276 m), accommodates considerable variety of biodiversity and human activities, and is thus ideal for testing our approach. The Mediterranean Sea diversity of habitats sustain at least 17,000 marine species (Coll et al., 2010). It is bordered by 23 countries and territories that exploit the sea in a variety of ways (Micheli et al., 2013).

2.2 | Developing the 3D prioritisation approach

In the traditional 2D spatial prioritisation, a study region is subdivided into discrete 2D planning units arranged horizontally, occupying a given area in space (Figure 1a). We propose a key modification to this approach in order to carry out a 3D spatial conservation prioritisation: create volumetric planning units by assigning a *z* coordinate to each of them. The *z* coordinates correspond to a given depth below the sea surface. Having 3D planning units enables to further subdivide them vertically (Figure 1b). This subdivision allows considering vertical differences in biodiversity patterns and processes, threats, human activities and conservation costs at different depth layers.

For our case study, we initially created planning units in the horizontal plane by generating a grid of 10 × 10 km using an Albers equal area projection (following Mazor, Giakoumi, Kark, & Possingham, 2014). This grid was clipped using the Mediterranean coastline, rendering some planning units smaller than 100 km^2. These planning units were used to carry out a spatial conservation prioritisation in the traditional 2D approach, to compare the results with those from the new 3D approach.

Subsequently, we transformed the 2D planning units into 3D by assigning a *z* coordinate given by the depth at their centroid. We used the GEBCO bathymetry grid v.20150318 (GEBCO, 2014), with a spatial resolution of 30 arc-seconds (~1 km), as depth reference. We subdivided the 3D planning units vertically into three depth classes (see Figure S1), following ocean zones defined by light penetration characteristics (Nybakken & Bertness, 2005): (1) 0–200 m deep, (2) 200–1,000 m deep and (3) >1,000 m deep. Any given square from the initial grid was composed of one, two or three volumetric planning

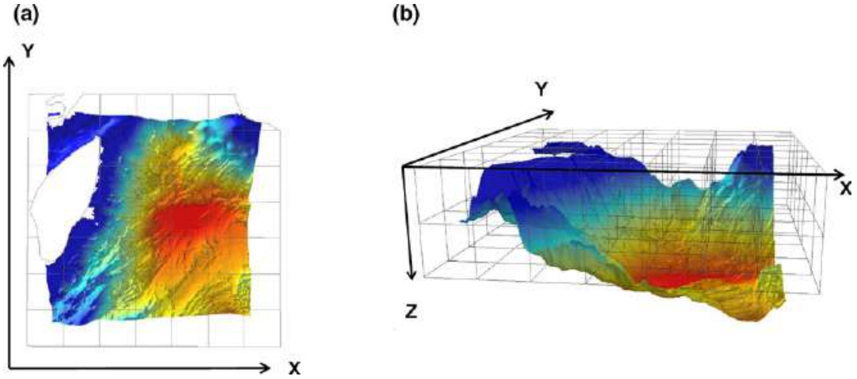


FIGURE 1 The concept of spatial conservation prioritisation in 2D and 3D in marine ecosystems. (a) The traditional approach to marine spatial prioritisation, in which the planning region is subdivided into 2D planning units (*x*, *y* coordinates). (b) The new 3D approach to marine spatial prioritisation, where planning units are defined as a three-dimensional space (*x*, *y*, *z*, coordinates), and subdivided vertically

units arranged vertically, based on the depth at its centroid. For example, a site with a depth of 1,000 m had one planning unit between 0 and 200 m and another between 200 and 1,000 m deep. If the same site was deeper than 1,000 m, a third planning unit was included from 1,000 m and the maximum depth. Overall, we had 61,459 planning units (26,690, 20,049 and 14,720 in the 0–200, 200–1,000 and >1,000 m depth ranges respectively).

2.3 | Biodiversity data

We used spatial distribution data available for 1,011 marine species and 19 geomorphic features occurring at different depths, enabling us to test the methodology of prioritising biodiversity conservation actions in 3D. Marine species range maps, obtained from AquaMaps (Kaschner et al., 2013), included vertebrates (e.g. fish, birds and mammals), invertebrates (e.g. molluscs, bivalves and corals), and green, red and brown algae. These distributions were modelled using species-specific environmental tolerances coupled to local environmental conditions, to produce maps of relative occurrence probability for each species (Kaschner, Watson, Trites, & Pauly, 2006). We used suitability probabilities greater than zero and each species' depth range, to quantify species distribution in each planning unit. Geomorphic features data such as seamounts and trenches were used as a surrogate for benthic habitat and obtained from a global digital seafloor map (Harris, Macmillan-Lawler, Rupp, & Baker, 2014). A full list of biodiversity features is provided in Table S3.

2.4 | Quantifying conservation cost in the Mediterranean Sea

We used a threat index as a surrogate for conservation cost, assuming that it is a proxy of human use of an area. Conservation actions are more easily accepted in areas where their conflicts with other uses are minimised (Ban & Klein, 2009; Joppa & Pfaff, 2009). We created the threat index maps following the cumulative impact mapping methodology of Halpern et al. (2008, 2015), which uses datasets representing threats to biodiversity. Data included different types of fishing and pollution, invasive species and sea surface temperature anomalies. We created a threat map for each depth layer, thus we assumed that certain threats act only at specific depths and not along the entire water column. For the 2D prioritisation approach, we summed the threats of all the vertical planning units in a given location, and assigned it to the planar unit from the original 100-km^2 grid. Detailed information on the methods and datasets used to develop these threat maps is provided in Methods S1.

2.5 | Defining biodiversity conservation targets

We set a target to protect 20% of the total distribution of each biodiversity feature (quantified using volume for species, and area for geomorphic features). This target was set following recommendations by Levin, Mazor, Brokovich, Jablon, and Kark (2015) to achieve solutions that are neither too flexible (resulting in poorly defined conservation networks) or too rigid (where many planning units are considered irreplaceable). We further subdivided the biodiversity features by depth zones, to ensure their representation across zones (Klein, Steinback, Watts, Scholz, & Possingham, 2010) and to ensure that species' conservation targets will not be met within a single depth zone for species distributed across multiple depth zones.

2.6 | Selecting priority conservation areas

2.6.1 | Spatial prioritisation software

We used the spatial prioritisation software Marxan to identify conservation priority areas both through the 2D and the new 3D prioritisation approaches. Marxan uses a simulated annealing algorithm (Possingham, Ball, & Andelman, 2000) to identify a number of near optimal configurations of sites in a study region where defined quantitative conservation targets can be achieved, while minimising cost (Ball, Possingham, & Watts, 2009). Marxan finds alternatives to minimising the total score of an objective function, given by the sum of the total cost of the sites selected for conservation, and a penalty assigned for any unmet targets. It can also incorporate a cost related to the spatial configuration of the selected sites, often measured as the length of the boundaries between selected and non-selected sites. The relative importance in the solution of this "spatial cost" is weighted by a factor referred to as boundary length modifier (BLM), which controls the compactness of selected sites. Lower BLM values minimise the total cost of the solutions, albeit more spatially fragmented; higher BLM values emphasise compact solutions, but the total cost would probably be greater.

In order to perform the 3D spatial conservation prioritisation, we carried out essential modifications to prepare the input data required for the analysis in Marxan. First, as planning units occupy a volumetric space, we quantified the distribution of biotic conservation features within them in volumetric units (km^3) instead of in area units. Second, as we also subdivided the planning region vertically, planning units shared boundaries with planning units that are not only to their sides but also above and below them. Thus, we measured the size of shared boundaries in area units, and not in length units as in the traditional 2D conservation prioritisation. We integrated the third dimension into the objective function that Marxan minimises by creating planning units both horizontally and vertically, assigning boundaries between the different planning units, and quantifying the volume each conservation feature occupies.

We ran Marxan for each the 3D and 2D spatial prioritisation approaches, using arbitrary BLM values between 0 and 1—see Ardron, Possingham, and Klein (2010) for more details on setting BLM values in Marxan. Using scenarios with different BLM values allowed us to examine the effect of compactness on the spatial arrangement of selected sites and on the efficiency of the solutions. All scenarios were run 100 times, resulting in 100 different solutions (configuration of selected sites) for each scenario. Marxan creates a selection frequency output, which is the number of times that an individual planning unit is chosen as part of the solution from all runs in a scenario. Selection frequency provides information about the importance and irreplaceability of each planning unit to achieve efficient solutions (Ball et al., 2009).

2.7 | Examining the efficiency of 3D spatial conservation prioritisation

We evaluated whether conservation targets were met through the 3D spatial conservation prioritisation. We then assessed trade-offs in efficiency (we considered solutions with lower total cost and space required for achieving targets as more efficient) obtained through the various scenarios using different compactness requirements (BLM values). We assessed trade-offs by plotting the mean boundary area between selected and non-selected planning units against the mean cost and volume of the 10 solutions with the lowest objective function score. Trade-off assessment is a standard practice in systematic conservation planning, as it is desirable to balance the increases in cost and total volume of the selected sites incurred by compact solutions (Adams, Pressey, & Naidoo, 2010; Stewart & Possingham, 2005).

We examined whether the total boundary of solutions was minimised in the horizontal or vertical planes as we increased BLM values, for which we summed the total boundary area in both directions separately. We were also interested in understanding how the compactness between planning units in the vertical plane affected the efficiency of the solutions. Thus, we plotted the percentage of areas (areas defined as the horizontal 2D footprint of the planning units as created in the original 100-km^2 grid) in which all the vertically available planning units were selected as part of the best solution against the total cost and total boundary area.

2.8 | Distribution of conservation priorities using the 3D approach

We adopted the Stewart and Possingham (2005) interpretation of selection frequency to classify planning units as conservation priorities. This approach considers as priorities those planning units with a selection frequency higher than would be expected by random. We were especially interested in determining whether the 3D prioritisation approach was successful in identifying priorities in areas of the ocean in which not all the vertically available planning units were included as priorities. We were also interested in understanding whether the requirements for spatial compactness forced Marxan to choose the entire water column in a certain place as a priority or not. Thus, for those areas (again, areas defined here by the horizontal 2D footprint of the planning units as created in the original 100-km^2 grid) where priorities were identified, we calculated the percentage of these in which all the vertically available planning units were classified as priorities. This would mean that protecting the entire space between the surface and the seabed is important to achieve conservation targets, and that vertical zoning of the water column is not ideal. For simplicity, we include the seabed from this point onward when we talk about protecting the entire water column.

2.9 | Comparing efficiency and spatial priorities of the 2D vs. 3D spatial prioritisation

We examined how the 3D spatial conservation prioritisation approach performed in comparison to the traditional 2D approach. To do this, we first compared changes in the average total cost and volume with different requirements for spatial compactness (i.e. BLM values) of the 10 best solutions obtained through the two approaches, as well as the spatial distribution of priority sites. We focused our comparison between those prioritisations in which the BLM was set to zero (which usually produces the lowest cost solution) and "optimal" BLM values. We used the approach of Stewart and Possingham (2005) to calibrate the BLM values to its "optimal," where compactness is minimised without a large increase in cost. This inflection point represents the maximum spatial clustering of priority sites that can be achieved without increasing the cost significantly. It is important to stress that for comparing the results from the 3D and 2D prioritisation approaches, the conservation targets set for the latter were also in units of volume (using the entire volume of the water column under each planning unit, based on its maximum depth) rather than the commonly used area units.

3 | RESULTS

3.1 | Quantification of biodiversity and threats per depth

Subdividing the planning region into 3D planning units and their stratification by depth enabled us to quantify biodiversity (Figure 2) and threats (Figure 3) for different vertical sections of the water column. This stratification, in turn, allowed prioritising conservation actions in 3D, as presented below.

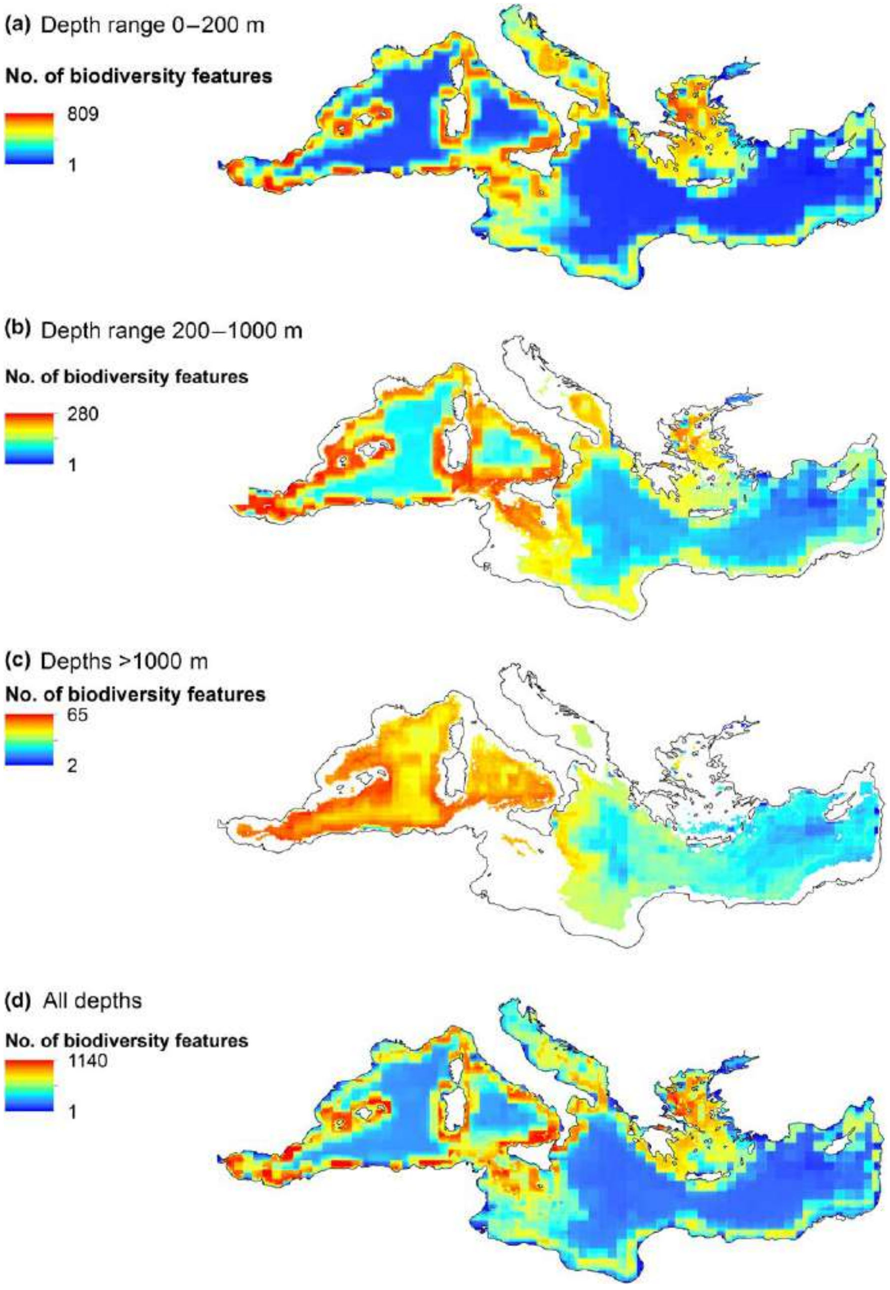


FIGURE 2 The number of biodiversity features subdivided per depth class (a–c), and total number across all depth layers for each grid square (d). The first three layers (a–c) were used as input in the 3D analysis while the summed (d) layer was used in the 2D analysis. White colour within the Mediterranean Sea corresponds to areas that are outside the specific depth layer presented

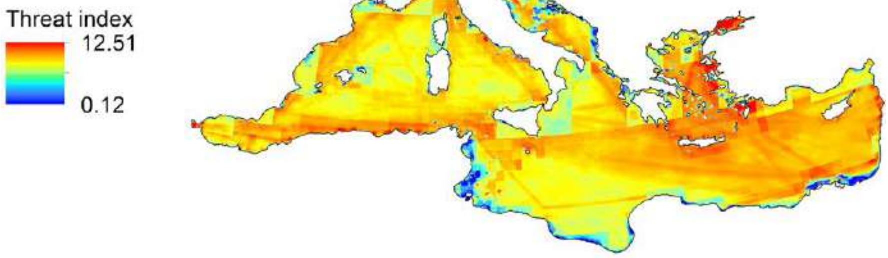
3.2 | Trade-offs in the 3D spatial conservation prioritisation approach

Using the 3D spatial conservation prioritisation method developed here, we were able to meet conservation targets for all biodiversity features. As expected, we found that the total cost, volume, boundary and spatial arrangement of the sites selected to achieve these conservation targets changed with different BLM values (Figure 4), as did the trade-offs between these parameters. For example, as shown in Figure 4a, as we increased BLM values from 0 to 0.09, the boundary area decreased rapidly with only small increases in total cost and volume. The largest decrease in boundary area was observed between planning units that were adjacent vertically, rather than horizontally (Figure 4b), i.e. compactness was favoured in the vertical plane, probably due to the smaller interface area in the vertical direction compared with the horizontal direction. These results show that the efficiency of the solutions (lower cost and volume) was fairly constant even with large changes in the percentage of sites in which the entire water column was considered as a priority for conservation (Figure 4c). This flexibility could provide interesting management options (e.g. vertical zoning), as addressed in the next section.

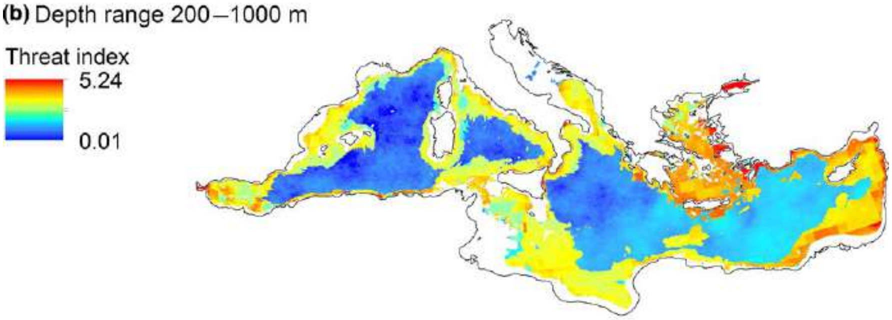
3.3 | Distribution of spatial priorities obtained through the 3D approach

Within the 3D spatial conservation prioritisation scenarios, in areas deeper than 200 m (i.e. where more than two planning units were available vertically), selected planning units often belonged to

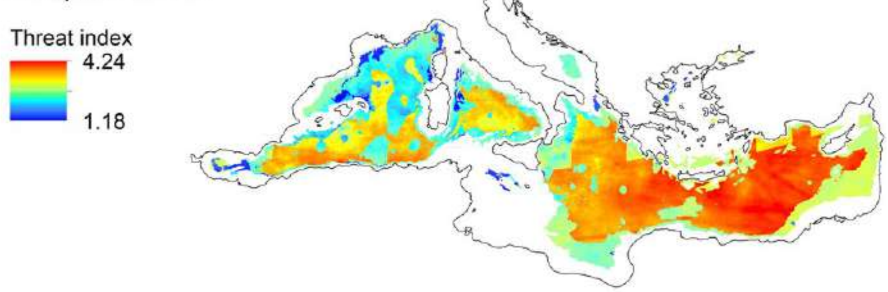
(a) Depth range 0–200 m



(b) Depth range 200–1000 m



(c) Depths >1000 m



(d) All depths

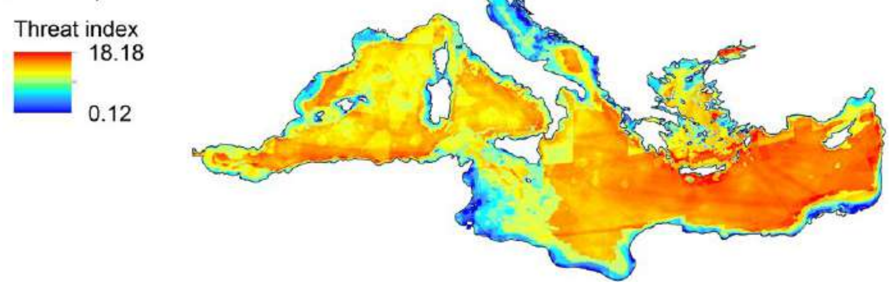


FIGURE 3 Cumulative threat maps per depth class (a–c), and for all depths combined per grid square (d). The first three layers (a–c) were used as input in the 3D analysis. The summed layer presented in d was used in the 2D analysis. White colour within the Mediterranean Sea corresponds to areas that are not within a given depth layer

different depth layers. This means that in a given place, not all the space from the surface to the bottom of the ocean was necessarily selected as a conservation priority, but instead only a section of it. For example, in the scenario where spatial cohesiveness was not required (BLM = 0), in only 10% of the areas the entire water column was identified as a conservation priority. When greater emphasis was given to obtain compact configurations of conservation areas (by increasing the BLM), the percentage of places in which all the vertically available planning units were selected as priorities increased (Figure 5b,c). The resulting planning unit selection frequencies obtained through the 3D spatial conservation prioritisation method are presented in Figures S2–S4.

3.4 | Comparing efficiency and spatial priorities of the 2D vs. 3D spatial prioritisation

We discovered that the 3D prioritisation was more efficient than the traditional 2D approach in terms of minimising total cost of the resulting networks of selected sites for low BLM values between 0 and the "optimal" value (0.05 and 0.007 for the 3D and 2D approaches respectively). The total cost of the 3D planning results was ~13% and 11% less than that from the 2D planning when "optimal" and 0 BLM values were used respectively (Figure 6a). In fact, the total cost in the 3D scenarios only reached a similar total cost to the 2D scenario using a BLM value of 0.5, which produced solutions in which most planning units

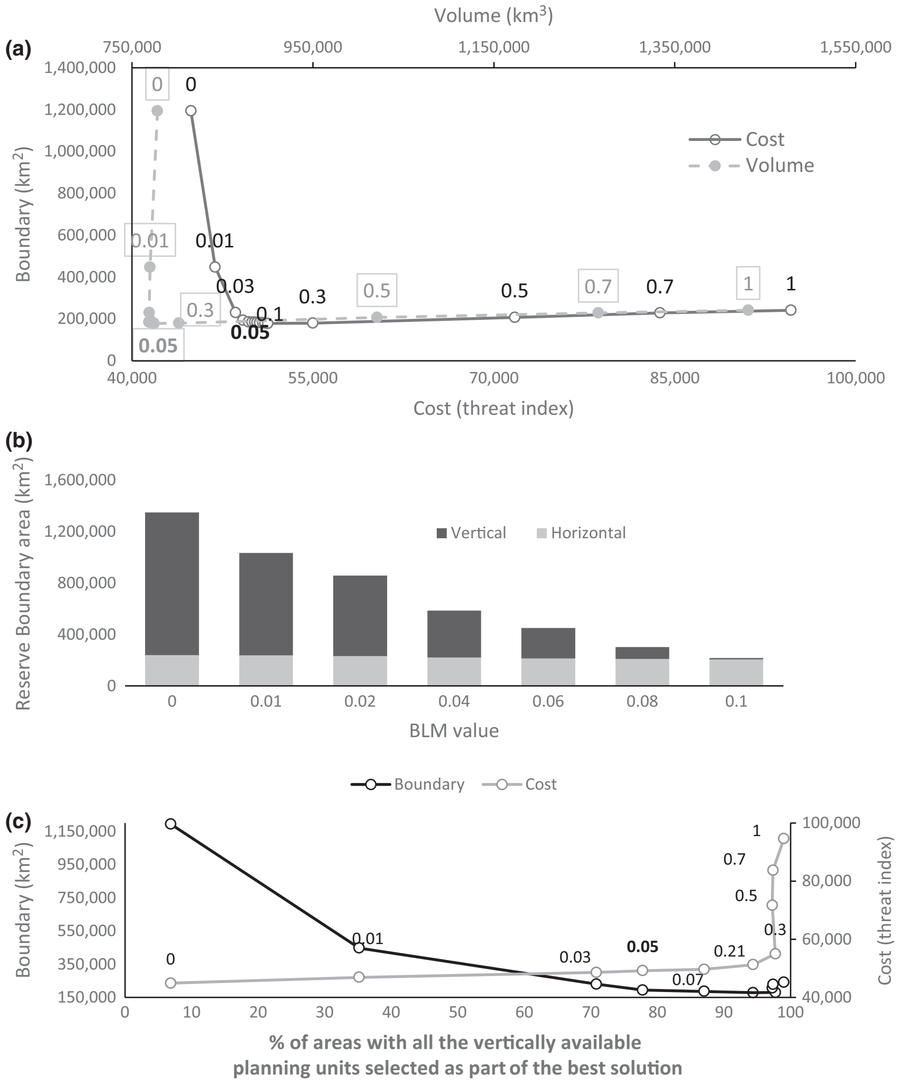


FIGURE 4 Changes in cost, volume, boundary and spatial arrangement of selected sites with different boundary length modifier (BLM) values (requirement for solution compactness). (a) Trade-off between cost and volume of the reserve system with total boundary area; BLM values are shown next to the points (inside a square marker for the volume vs. boundary line). (b) Changes in total horizontal and vertical boundary area. (c) Change of total reserve boundary and cost as a function of the percentage of locations in the resulting solution in which all of the available planning units in the vertical plane were chosen as part of the best solution

were clumped vertically (Figure 4b,c), being far from optimal. Volume, on the other hand, showed only a difference of less than 2% between the optimal scenarios of the 3D and the 2D analysis (Figure 6b). However, the spatial priorities differed between these same two “optimal” scenarios of the 2D and 3D approaches (Figure 7). Only 25% of the priority sites identified with the 3D approach were also identified with the 2D spatial conservation prioritisation. Moreover, most of the matching priorities occurred within planning units in the 0–200 m depth layer, but most of those sites identified as priorities in the 3D approach were not captured in the 2D approach.

4 | DISCUSSION

4.1 | Efficiency of 3D spatial conservation prioritisation

Here, we developed and presented a new spatial conservation prioritisation method for the marine realm that allows accommodating and planning for different uses along different depths in the same region. In the case study presented here, creating 3D planning units and stratifying them by depth enabled us to quantify biodiversity and threats (used as cost surrogate) for different vertical sections of the water column (Figures 2 and 3). In doing so, we successfully identified networks of sites in which conservation targets for over 1,200 biodiversity features were achieved, while minimising conservation cost. These networks included areas of the ocean where only particular depth layers along the water column were identified as priorities for conservation (Figures 4 and 5).

Prioritising in 3D opens the possibility of targeting specific threats to specific features of conservation interest at specific depths, while following core principles of systematic conservation planning such as complementarity, representativeness and efficiency. For example, it could help support systematic conservation planning for benthic habitats, by spatially prioritising areas where conservation could be compatible with other uses (such as recreational fishing) which may not pose a direct threat to other conservation features (Grober-Dunsmore et al., 2008). Thus, it provides an alternative or complementary tool for zoning of management actions, which has been proven to minimise negative socioeconomic impacts from conservation on stakeholders (Grantham et al., 2013; Klein et al., 2010; Mangubhai, Wilson,

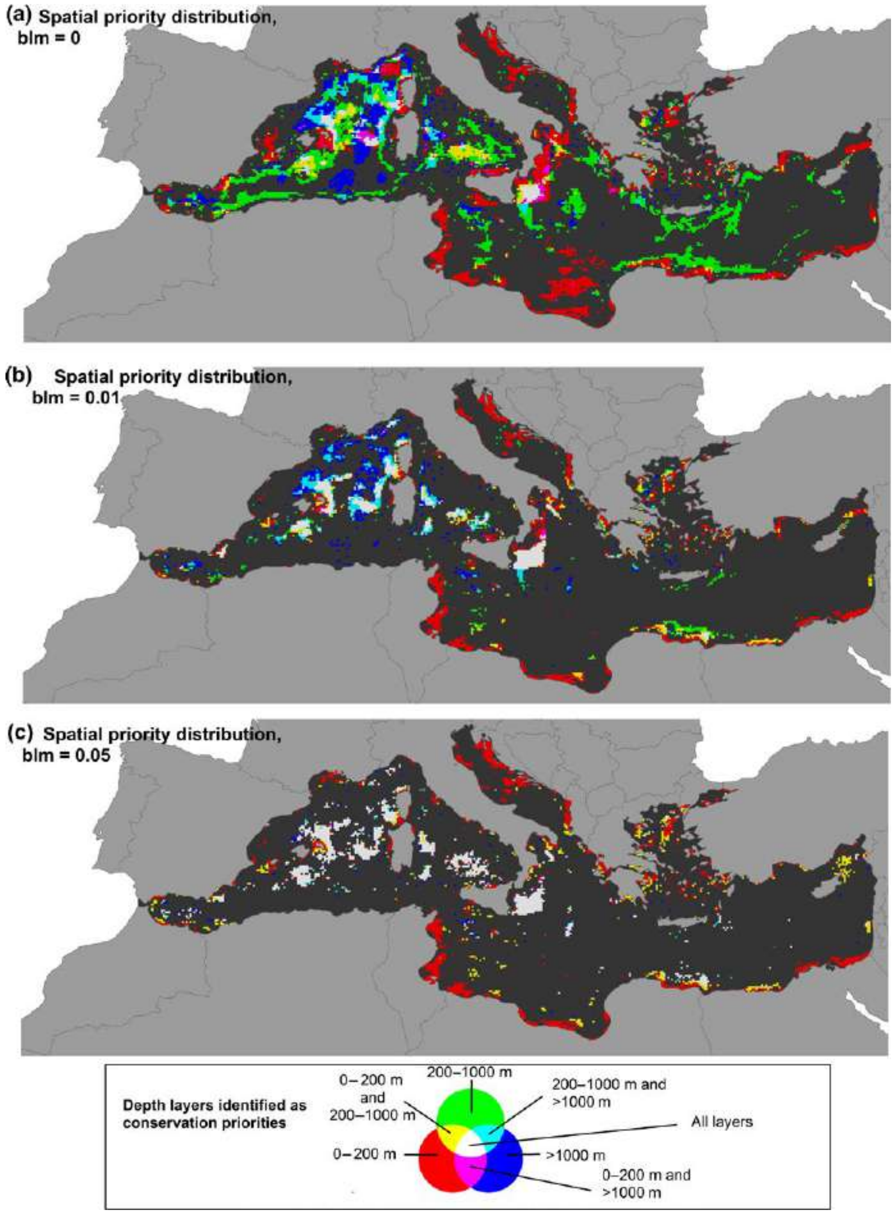


FIGURE 5 Distribution of planning units identified as priorities in a 3D spatial conservation prioritisation approach. Priority planning units are those with a selection frequency higher than would be expected by random. (a–c) Scenarios with different boundary length modifier (BLM) values; with a BLM value of 0, the total cost of the reserve is minimised, without a requirement of spatial compactness. A BLM value of 0.05 represents the optimal solution, in which greater reductions in boundary area are obtained without substantial increases in total cost

Rumetna, & Maturbongs, 2015). For an inherently 3D environment such as the ocean, prioritising actions along both the vertical and horizontal dimensions could allow more efficient use of limited conservation resources, as has been demonstrated for fisheries modelling (Fulton, Smith, & Punt, 2005). Furthermore, given that human activities in the ocean are expanding (Halpern et al., 2015), a more efficient prioritisation approach such as the one presented here is needed to reduce conflicts between stakeholders (Grober-Dunsmore et al., 2008).

The results of the case study examined here indicate that the 3D spatial prioritisation provides flexibility for meeting conservation objectives. This is suggested by two observations: (1) the efficiency of the solutions (lower cost and volume) was fairly constant even with large changes in the percentage of sites in which all the water column was considered as a priority for conservation (Figure 4a,c); and (2) in general, for the different scenarios, fewer than 10% of the planning units in the Mediterranean Sea were identified as priorities. Spatial flexibility is perceived as positive for the planning process, as it provides a broader range of alternative plans for stakeholder consideration, so that the trade-offs between their socioeconomic goals and biodiversity conservation can be optimised (Grantham et al., 2011; Kukkala & Moilanen, 2013; Levin et al., 2015). Regarding the spatial arrangement of the resulting configuration of selected sites, increased BLM values forced solutions to be more compact by minimising boundaries between vertically adjacent planning units (Figure 4b). Vertical clumping occurred as in our study the boundaries between vertically adjacent planning units were much larger than those between horizontally adjacent ones, and thus the algorithm of Marxan reduces these larger values to minimise the score of the objective function. By rescaling the values of the horizontal and vertical boundaries to be in the same order of magnitude (rather than using the exact boundary area values between adjacent planning units), it is possible to achieve more horizontal compactness.

A comparison between the 3D approach and a 2D approach showed that the former was more efficient in terms of cost than the latter for low BLM values (between 0 and the optimal BLM value; Figure 6), which suggests that 3D spatial prioritisation merits use in the planning process. The 3D approach is more efficient as it enables identifying priority areas for certain depth layers, while allowing the rest of the water column to be allocated for other uses in those areas that do not deliver conservation outcomes efficiently. On the contrary, in a 2D analysis, an area with a very important feature in a given depth layer might drive the selection of the rest of the water column for protection, incurring an extra cost and space. This spatially finer resolution used to quantify biodiversity and cost may explain the difference between spatial priorities obtained through the two approaches (Figure 7). The comparison presented here, however, is somewhat constrained by the fact that we based it on the results obtained through the optimal BLM value; in a 3D analysis, large reductions of boundary area are not necessarily as important in comparison to a 2D analysis, given that boundary area will unavoidably remain high if we choose only certain depths for protection along the water column.

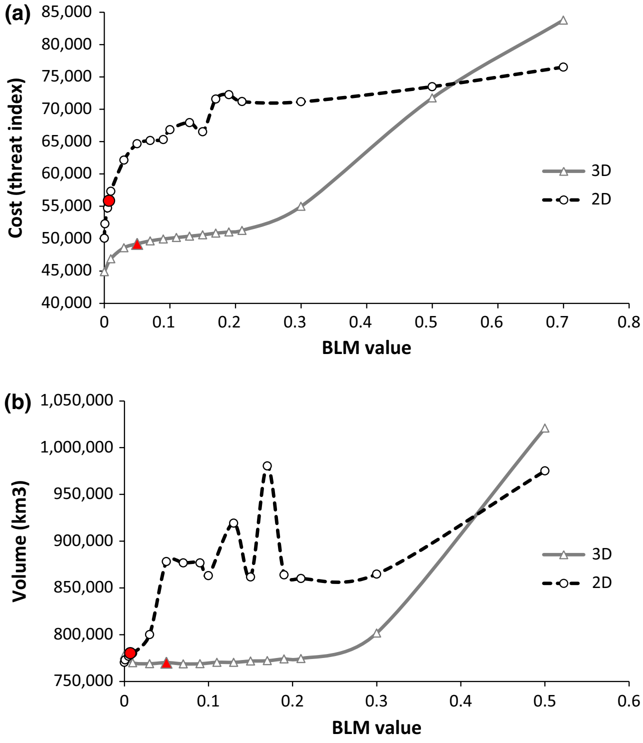


FIGURE 6 Example of total cost (a) and volume (b) of the resulting conservation area configuration for a 3D and a 2D spatial conservation prioritisation approach, at different spatial compactness levels. "Optimal" boundary length modifier (BLM) values for the 3D and 2D approach were 0.05 and 0.007 respectively, shown as full red markers

4.2 | Opportunities and challenges for prioritising in 3D

The 3D conservation prioritisation approach presented here can be modified to address different planning needs. For instance, planning can be restricted to specific areas of the ocean such as near-shore habitats or the high seas. Planning unit size and shape are known to affect the efficiency and spatial pattern of the solutions (Cheok et al., 2016; Nhancale & Smith, 2011), so alternative stratifications could be tested depending on the planning objectives; e.g. using regular divisions from the surface to the bottom, or separating benthic and pelagic habitats. In addition, vertical connectivity between depth layers could be better incorporated by applying methods that have already been developed for spatial conservation prioritisation (Beger et al., 2010). An approach to account for depth as we propose in this study could also be integrated into dynamic ocean management, which takes into account temporal patterns of biodiversity and oceanographic features (Grantham et al., 2011; Hobday, Hartog, Timmiss, & Fielding, 2010; Lewison et al., 2015; Maxwell et al., 2015). These dynamic processes in the ocean occur not only in 2D but also in 3D, so accounting for depth can lead to a more integrated marine spatial planning, in 4D. Moreover, prioritising conservation actions in 3D could contribute to the protection of marine ecosystems currently underrepresented in the global marine protected area system such as pelagic (Game et al., 2009) and deep-ocean ecosystems (Almada & Bernardino, 2017; Ban et al., 2014; Danovaro, Snelgrove, & Tyler, 2014). However, vertical zoning of marine conservation and management may not be always advisable or relevant (e.g. in areas with strong benthic–pelagic

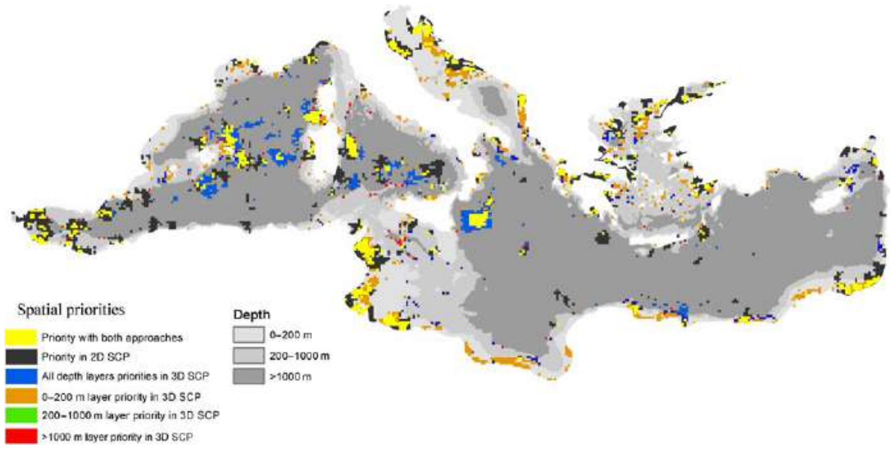


FIGURE 7 Comparison of spatial priorities obtained through a 3D and a 2D spatial conservation prioritisation

coupling or with important diel vertical migrations, all depth layers will be required for conservation). Hence, incorporating connectivity considerations for marine conservation planning in 3D would be important (Grober-Dunsmore et al., 2008).

We acknowledge that prioritising actions in 3D presents an additional challenge when compared to 2D prioritisation, which is the need for datasets with a depth component. Although such data are still somewhat limited, characterisation of the 4-D (including time) variability of the ocean is rapidly advancing (Kavanaugh et al., 2016). Obtaining information about the location and dive behaviours of marine animals is possible due to biologging (Carter, Bennett, Embling, Hosegood, & Russell, 2016) and satellite telemetry (Hart & Hyrenbach, 2009). Echosounders can detect aggregations of fish and zooplankton at different depths, improving understanding of pelagic structure (Proud, Cox, & Brierley, 2017). There are also important advances in the amount of global marine environmental data with a depth component, through the World Ocean Atlas (Boyer et al., 2013). All this information with a 3D component can be used to create species distribution models (Duffy & Chown, 2017) and ecological units (Sayre et al., 2017) in 3D, although this is still not common practice. Scientists are now able to better map cumulative anthropogenic impacts in the ocean, estimate whether these impacts are increasing or decreasing (Halpern et al., 2015), and how they can affect different stakeholders (Klein et al., 2010). Apart from data availability, another challenge for vertical zoning of ocean activities is the enforcement of regulations. Managing authorities will need to make better use of technologies such as Vessel Monitoring Systems (Game et al., 2009), as well as actively predicting occurrence of illegal activities in space and time (Arias, Pressey, Jones, Álvarez-Romero, & Cinner, 2016). While challenging, vertical zoning is possible and is already used in certain marine protected areas in New Zealand (Helson et al., 2010) and Australia (Fitzsimons & Wescott, 2008) for protecting benthic habitats, although those areas were not designated using an explicit 3D framework of systematic conservation planning.

In conclusion, 3D conservation planning and prioritisation can deliver more efficient conservation plans compared to 2D conservation planning. The 3D approach presented here helps to target conservation actions to specific locations of the water column. Thus, it provides a platform for integrating systematic conservation planning into the wider ecosystem-based and marine spatial planning process. Marine spatial planning needs to address the heterogeneity of marine ecosystems in a practical manner, to identify opportunities for shared space that can help resolve conflicts (Douvere, 2008). To our knowledge, this is the first explicit attempt to make spatial conservation prioritisation in 3D. We recommend that further steps to evaluate the feasibility of using this approach should include carrying out an analysis in which trade-offs to different stakeholders is assessed. A multi-sectoral and integral ocean planning framework which takes into account the needs of different sectors and the intrinsic spatial dimension in which the marine realm sits is critical for effective marine conservation planning and action (Ban et al., 2014; Maxwell, Ban, & Morgan, 2014).

ACKNOWLEDGEMENTS

This research was supported by the Australia Research Council (ARC) Centre of Excellence for Environmental Decisions (CEED). R.V.-L. is funded by an International Student Postgraduate Scholarship and supported by a Postgraduate Award from the Costa Rican Ministry of Science, Technology and Telecommunications and ARC CEED. S.K. is an ARC Future Fellow and HPP is an ARC Laureate Fellow. We thank T. Mazor, M. Carter, E. Gallo-Cajiao, R. Friedman and two anonymous reviewers for their valuable feedback on earlier versions of this manuscript.

AUTHORS' CONTRIBUTIONS

R.V.-L., N.L., H.P. and S.K. conceived the ideas; R.V.-L. and N.L. designed the methodology; and R.V.-L. analysed the data and led the writing of the manuscript. All authors contributed to ideas, edited the manuscript and gave final approval for publication.

DATA ACCESSIBILITY

The input files to run the 3D and 2D spatial prioritisation scenarios are made available through the University of Queensland's eSpace: https://doi.org/10.14264/uql.2017.782 (Venegas-Li, Levin, Possingham, & Kark, 2017).

ORCID

Rubén Venegas-Li http://orcid.org/0000-0003-2085-8269

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SUPPORTING INFORMATION

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How to cite this article: Venegas-Li R, Levin N, Possingham H, Kark S. 3D spatial conservation prioritisation: Accounting for depth in marine environments. *Methods Ecol Evol*. 2018;9:773–784. https://doi.org/10.1111/2041-210X.12896