1. Introduction

Knowledge of spatial patterns of fauna and flora is in high demand among the policy-making and management community, not least in areas where the biological value is such that conservation efforts are warranted. This type of information enables assessing the distribution of biodiversity and other resources (e.g. fisheries), monitoring habitat change and defining (scale-specific) representative and unique features, as prescribed for the design of reserve networks and, more generally, the realisation of spatial planning. From the micro-habitat scale to the scale of biogeographic provinces, geospatial ecological data alongside habitat mapping have significantly helped fill this knowledge gap by providing local and regional models that capture the spatial distribution of various user-defined or typology-derived classes (e.g. forest types) which can in turn be used to understand or predict species distributions.

Across the landscape lying beneath the water masses, limited means of access precludes the intensification of survey effort, hampering any broad-scale mapping endeavours. Pioneer benthic ecologist Petersen (1924) expressed this problem by stating that “‘botanizing’ out at sea is a very expensive affair” (Petersen 1924, p. 688). Embedded in this accurate statement is the notion of the high cost associated with acquiring survey data in the benthos that can compare in quality and quantity to those that plant ecologists have readily at their disposal. In addition, the extensive collection of remotely sensed data, which have boosted habitat mapping on land by virtue of efficiently complementing vegetation survey data, can only be extended seaward as far as the width of the narrow littoral fringe circling the land masses. Mapping of seabed, sublittoral environments was therefore for many years limited to what could be inferred from small numbers of scattered point samples, yielding maps with large gaps of information or restricted to very small scales.

The advent of acoustic technologies (namely sidescan sonar and single- and multibeam echo sounders) rendered it possible to acquire high-resolution, full-coverage imagery of the seafloor over extensive areas, beyond the limit of light penetration. As a result, the geophysical attributes of the terrain that can be derived from its acoustic properties can now form the basis for a classification of, for example, depth and seafloor texture. These advances endowed benthic researchers with the ability to carry out spatially continuous, ‘wall-to-wall’ mapping, following in the steps of terrestrial remote sensing science. Nonetheless, the
challenges of direct observation, though also lessened by the emergence of new technologies (e.g. underwater video camera systems, benthic sleds, etc.) have largely remained, just as they have in other remote areas across the globe.

With ecological data being sparse at best and remotely sensed data bearing mostly an indirect (and not fully disentangled) relationship with biological composition, in the benthos the challenge of mapping the various components of biodiversity (from genes to ecosystems) is largely a methodological one. To inform the classification and mapping of the communities supported by the different habitats, effort is geared toward developing techniques to better integrate point-source field data with remotely sensed data (e.g. Brown et al. 2002; 2004; Hewitt et al. 2004; Holmes et al. 2008; Jordan et al. 2005; Kloser et al. 2001; Kostylev et al. 2001).

In addition to the methodological challenges, the upper part of the continental shelf is considered to be the area likely to benefit the most from marine spatial planning (rather, its users) because it is where the highest biodiversity conservation values and the greatest threats overlap. Multiple economic interests compete for space on the continental shelf and upper slope, including fisheries, causing by far the most widespread impact to the megafauna and the ecosystem that it depends on, and to a lesser extent, oil and gas exploration, shipping, mining, aquaculture and tourism.

In this chapter we review the most widespread approaches to mapping the distribution of benthic fauna, limiting ourselves to the offshore circalittoral zone, because this is where all of the described challenges are being faced simultaneously, including methodological and management-related. Sessile benthic organisms are perceived as particularly useful for habitat characterisation because substrate is critical for their survival and proliferation; being spatially fixed, they also become indicative of environmental conditions of the adjacent seafloor (Kostylev et al., 2001). Therefore, we will focus on the particular mapping ‘school’ which places the emphasis on obtaining the best possible picture of variation within this subset of benthic biota. As far as mapping is concerned, the epibenthic megafauna is regarded as the vegetation of the benthic landscape.

By means of a case study taken from a Swedish Fjord, recently designated as a multiple-use marine protected area, we will show how benthic biotope mapping provides the most effective means to document and spatially manage seabed-dwelling biodiversity.

2. Selection of an appropriate mapping theme

From single species to broad ecosystems, any level of biological organisation can be described in terms of its spatial distribution patterns and hence be depicted in map form. Irrespective of the particular level of choice, units can also be defined with a varying degree of reference to the properties of the environment associated with them, ranging from these being completely absent (e.g. a given ‘assemblage of gorgonian corals’) to completely replacing any biological information (e.g. a ‘sand bank’). Typically, the higher up in the hierarchy of ecosystems one operates, the more weight is carried by the abiotic component, where classes are described on the basis of their physiography, geology or morphology rather than their biological composition, because the latter is often much harder to summarise than the former. Similarly, the area occupied by a single species is more easily characterised by referring to the presence of that species, rather than attempting to describe the habitat conditions in which the species can be found. This rule of thumb does not always hold up, like in the case of a biogenic reef or other habitat-forming species. This is a direct consequence of the way in which ecosystems are
structured. Intermediate to high-level units (i.e. broader categories) respond more strongly to changes in the environment and processes that operate at larger scales, than changes in biology (e.g. the presence of a predator), which affect the lower level classes more ostensibly.

Additionally, compositional turnover responds differently to different habitat gradients depending on the complexity and scale of the units under consideration (e.g. very detailed communities versus broad categories), with patterns that are not fully consistent across environments. Gonzalez-Mirelis et al. (2011) found that when considering biological variation at various levels of detail of taxon groups (admittedly a narrow window, within the gene-to-ecosystem continuum), classes at the coarsest end responded more strongly to substrate than any of the other gradients considered, including depth, while this effect was reversed in finer levels, discriminating regions with more homogeneous characteristics whose boundaries change at smaller spatial scales. However, Bergen et al. (2001) found a pattern where the coarsest divisions of a dendrogram of infaunal communities were strongly associated with depth and the finest divisions were better explained by sediment, with depth no longer significant. A key difference lies in the target of each study, where the former focused on epibenthic fauna of circalittoral environments, whereas the latter looked at infauna and also included infralittoral sites. All the above factors provide for a multitude of methods to classify the environment into units, including hierarchical systems, which can in turn be so with respect to faunal composition, or the relative importance of environmental factors in structuring the ecosystem, providing an ensemble of alternatives to choose from when solving different management problems.

Despite the apparent complexity of the task and lack of universally-applicable definitions of each of the categories potentially involved, in the marine realm, and especially in the applied environmental literature, researchers have gravitated towards one of the following two themes: (1) biotopes (Connor et al., 2004; CORINE, 1991; EUNIS, 2005; HELCOM, 1998) and (2) habitats (Allee et al., 2001; Greene et al., 1999; Valentine et al., 2005). We argue that this is so because they meet two crucial conditions: they are easy to map and they are biologically meaningful.

The two concepts are sometimes synonymised, but there are fundamental differences. The current meaning of ‘biotope’, which in fact became popular in the marine realm before the terrestrial, combines the "physical environment [...] and its distinctive assemblage of conspicuous species" (Olenin & Ducrotoy 2006, p. 22) where, crucially the concept incorporates geographic location, thus rendering it scale-dependent. ‘Habitat’ has been defined as a spatially recognisable area where the physical, chemical and biological environment is distinctly different from surrounding environments (Kostylev et al., 2001; Valentine et al., 2005). A review of the literature and available definitions reveals a focus that merely shifts from the biological properties in the case of biotopes to the environmental properties in the case of habitats, and indeed, a biotope can be defined as the sum of community and habitat. Also, the concept of habitat is generally more loose and has been used with a much broader array of meanings than biotopes have.

Both habitats and biotopes require that their boundaries be delineated in order to be fully characterised, so they are inherently ‘mapping units’ (Foster-Smith et al., 1999). Not only are they mappable, they are so across the scales where management and planning typically occur. Biotopes are biologically meaningful for trivial reasons, but habitats also have been shown to be adequate surrogates for patterns of species richness in marine environments (Ward et al., 1999). It is clear that any ordered system of classes with these properties, whether biotopes,
habitats or another aggregation level, can be easily translated into a suitable mapping theme and thus be incorporated in the framework that we review below.

3. Mapping the benthic landscape

The integration of data from multiple surveying techniques, typically including one or more full-coverage layers depicting features visible at medium to large spatial scales (e.g. pinnacles, canyons, etc.), and at least one dataset from some *in situ* benthic survey technique providing insight into small-scale variation occurring mostly at the biological level, nested within the former, has proven the most rewarding technique for mapping extensive areas of the seafloor. Here forth we will refer to any data obtained via an *in situ* sampling technique (e.g. video, dredge, trawl, etc.) as ‘survey data’, in contrast to ‘remotely-sensed data’ (note that we include video and photographic sampling methods within methods labelled as ‘*in situ*’, contrarily to other authors, on the grounds that the sampling device is located directly at the site that is being sampled, even if the operator of the device is not; we therefore reserve the term ‘remote sensing’ to refer to hydroacoustic techniques). Survey data delivers spatially-explicit information on the value of ecological variables and/or variables relating to the sediment or bedrock, whether quantitative (e.g. species abundance, granulometry information) or qualitative (e.g. ‘presence of sessile invertebrates’, ‘presence of mobile sediment’).

Alternatives to this integrative approach include using either only remotely-sensed data, or only survey data, as a basis for mapping, but both come with significant caveats. Using only hydroacoustic data severely limits the level of detail that can be attained by the map, as well as puts into question its validity as a means for elucidating biodiversity and biological patterns. Calibration is in any case needed for the results to be reliable, so some amount of sediment sampling must always accompany the remote sensing survey. Even in the early days studies would use at least some *in situ* information, if not systematically collected, to support the characterisation of acoustic habitats (Ferns & Hough, 2002; Kendall et al., 2003; McRea et al., 1999).

The highest possible accuracy in delineating faunal boundaries and/or depicting faunal occurrence patterns can only be achieved by obtaining survey data from as much of the area as possible, ideally, the whole of it. This, as Petersen (1924) pointed out, is prohibitively expensive. Riegl et al. (2001) and Norris et al. (1997) obtained highly accurate maps of coral reefs and seagrass beds respectively, but had to face the time and monetary costs of surveying 100% of the study area. This of course may be practicable depending on the accessibility to the area (e.g. depth range) and sampling method utilised, or in cases where large budgets are available. Stevens & Connolly (2005) used a more cost-effective method that combined a staggered array of sampled locations and a tessellation technique to draw boundaries around groups of similar stations. Increased cost-effectiveness is achieved by making use of observed spatial autocorrelation patterns to extrapolate beyond the sampled locations and thus fill in the blanks between data points, but the limitations of these approaches, whether budgetary or areal, are clear. Their extreme accuracy and the ability to discover unreported biological features, however, should not be underestimated. The merits of incorporating spatial patterns (e.g. scale of patchiness) into the mapping process, which can only be done in the design of the field sampling surveys, are not exclusive to this way of mapping, as will be discussed below.

The main benefits of data integration techniques stem from an induced ability to gain insight into the empirical relationships between biota occurrence and environmental gradients. The popularity of this approach has exploded in recent years, even producing ‘schools’, which we...
review briefly below, focusing on the differences at a very fundamental level and stressing the non-technical issues within each approach.

3.1 Approaches

Two general approaches can be distinguished on the basis of the role that survey data play in the mapping process: a ‘top-down approach’, where survey data are used merely for ground-truthing purposes and the process is driven by the acoustic patterns; and a ‘bottom-up approach’, where biotic patterns, as inferred from the survey data, drive the definition and mapping of classes. Even though the final result is equivalent, a thematic map showing the distribution of classes that echo biotic patterns of the seafloor to a greater or lesser degree, the path followed is fundamentally different, and at the most abstract level it can be described as (a) an attempt to find the attributes of polygons of (mostly) known boundaries, in the top-down case, or (b) an attempt to find the boundaries of polygons of (mostly) known attributes, in the bottom-up case. Stressing the importance of whether or not boundaries are known, the former approach is also known as ‘supervised’ and the latter as ‘unsupervised’.

In the top-down approach, first, a classification technique based on the identification of patterns in the remotely-sensed data, usually acoustic imagery, is used to derive homogeneous and distinct regions, often referred to as acoustic habitats. Techniques used range from visual interpretation to highly sophisticated classification algorithms (e.g. Lamarche et al. 2011). These are essentially used as a framework within which reference sites are defined. Samples of \textit{in situ} data are then collected from all the detected regions, or the reference sites, so as to validate the classified habitats (see Brown et al. 2002; 2004; Freitas et al. 2003; Jordan et al. 2005; Kloser et al. 2001; Kostylev et al. 2001), and classes are occasionally merged if they can be proven to have non-distinct faunas.

Remote sensing by hydroacoustics is highly effective in classifying habitats over large areas of seabed. The approach effectively reveals boundaries created by discontinuities in substrate types, which in turn give rise to sharp changes in community composition. But the more gradual changes, which may emerge in response to factors other than substrate, are wholly overlooked. A more serious issue is that assemblages may be identified from the \textit{in situ} data which have no corresponding acoustic class (Freitas et al., 2003). In fact, this is, according to Brown et al. (2005), to be expected. The problem is that the spatial detail of the map is limited by the scale at which the acoustic regions are defined, and although boundaries can be modified to a limited extent on the basis of the biotic patterns (which is possible only at a scale defined by the distance between reference sites, i.e. the same scale at which acoustic habitats are defined), the resolution can only decrease as a result of classes being dropped, but never increase.

Indeed, the question is increasingly being raised as to whether acoustically derived habitats are a good representation of the patterns of variability of epibenthic communities (Eastwood et al., 2006; Hewitt et al., 2004). Stevens & Connolly (2004) concluded that the ability of abiotic surrogates to predict patterns of biological similarity was indeed poor. Parry et al. (2003) detected a nested hierarchy of spatial structure within the megafaunal assemblage of a large, apparently homogeneous, soft-bottom habitat unit. Because the subset of biota of interest is precisely the epibenthic megafauna, dissatisfaction has led to a call for improved mapping methods.

The bottom-up approach emerged in response to this call and Field et al. (1982) summarises it as letting the species tell their story. In this approach, the mapping units are defined on
the basis of multivariate species patterns (e.g. peaks of similarity within the continuous gradient of faunal composition, Brown et al. 2002), which are in turn assumed to define sets of distinct environmental factors (Kostylev et al., 2001). Eastwood et al. (2006) compared top-down versus bottom-up approaches to classifying and mapping seabed assemblages and found that when “the seabed comprises relatively homogeneous, unconsolidated sediments and the main driver is the development of the best possible biological assemblage map, then a bottom-up, unsupervised approach is likely to arrive at a set of assemblages that are defined equally well or slightly better compared with a top-down approach” (Eastwood et al. 2006 p.1544).

The evolution of bottom-up methods has largely tracked, whether explicitly or implicitly, that of species (or communities) distribution modelling in its broadest meaning i.e. including concepts such as ‘habitat modelling’, ‘habitat suitability modelling’, ‘predictive mapping’ etc. which in turn focus on obtaining spatial predictions of an ecological phenomenon. This ecological phenomenon can be equated with the concept of mapping unit as used throughout this chapter.

The field of distribution modelling has been largely developed by plant ecologists and vegetation scientists, and it has seen explosive growth in the last decade, evidenced by the steadily increasing rate of published papers using this approach. Benthic ecologists have been able to capitalise on this growth due to (1) the advent of hydroacoustic technology and (2) the mechanistic similarities between conspicuous epibenthic fauna and vegetation. Below we describe this approach as it is applied to the benthos in detail.

### 3.2 Biotope mapping as distribution modelling of communities

Distribution modelling is by and large an extension of the habitat-association approach to ecology, by which biological populations, whether marine or terrestrial, are seen to distribute themselves in space according to habitat gradients (note that the alternative view would be randomly), leading to community zonation when taken as a whole. In distribution modelling, biota-environment relationships, as derived from a set of surveyed sites, are employed to predict biological properties of the unsurveyed intervening areas on a location-by-location basis, so that ‘wall-to-wall’ maps of biotic components can be cost-effectively generated, where predicting the presence of a single species or the presence of an entity at a higher hierarchical level, such as a community, are methodologically equivalent. Extensive reviews of community-level modelling can be found in Ferrier et al. (2002) and Ferrier & Guisan (2006).

Modelling the spatial distribution of megabenthos on the basis of empirical relationships between its biological composition and coinciding habitat properties as derived from hydroacoustic remote sensing techniques has been pioneered by Hewitt et al. (2004), Holmes et al. (2008), Buhl-Mortensen, Dolan & Buhl-Mortensen (2009) and Monk et al. (2011). The current trend includes variations on a framework that involves at a minimum: (1) biological (response) data compiled by means of underwater video footage analysis and (2) geophysical (predictor) data collected through echosounder (multibeam or single-beam) or sidescan sonar, from which various proxies can be derived (Buhl-Mortensen, Buhl-Mortensen, Dolan, Dannheim & Kröger, 2009; Holmes et al., 2008; Ierodiaconou et al., 2007; Rattray et al., 2009). Further, Ierodiaconou et al. (2007) were the first to use backscatter (an acoustic property of the seabed obtained as a by-product of multibeam data) in combination with bathymetry to predict dominant biotic categories and, as shown in the recent GeoHab (Marine Geological and Biological Habitat Mapping) 2011 Conference, this is becoming established as a branch in its own right of predictive mapping of the benthos.
Particularly, benthos distribution modelling has mostly followed the specific approach described by Ferrier & Guisan (2006) as ‘classification-then-modelling’, where biological survey data are classified into the units to be mapped prior to modelling, so that the relationships revealed by the model are indicative of the collective, aggregated response of all of the species detected during the surveys, at a chosen classification detail (e.g. a similarity cut off level).

The process consists of the following stages:

- Conceptualisation
- Data gathering and choice of data model
  - Field surveys (response data)
  - Preparation of explanatory variables (predictor data)
- Model fitting
- Model evaluation
- Spatial predictions
- Assessment of model applicability

If the sample, obtained from the field surveys, was fully representative of the distribution of the unit(s) to be modelled (e.g. a pre-specified assemblage of species) and if all biotic and abiotic phenomena surrounding and potentially interacting with it were adequately represented by the predictor variables, then the modelled overall ecological response obtained from the model would summarise all systematic variation in its aggregated performance, and the spatial predictions from the model would be in full accordance with its real distribution, except for stochastic variation (R. Halvorsen, pers. comm.). In other words, the only two prerequisite conditions for an adequate model are related to the data model, underlining the fact that the power and reliability of empirical models depend strongly on the data. The choice of options should be guided by properties of the model system (species, study area, sampling design, spatial domain, etc.) and, in equal measure, by the purpose of the mapping.

One of the most consequential choices to be made concerning the data model relates to the ‘grain size’ of the map or the level of spatial detail to be depicted by the map (and by extension, the amount of detail that will be ignored). Distribution modelling is typically conducted around a grid that is overlaid on the data layers (including survey and remotely-sensed), so that a prediction can be obtained for every grid cell outside of the surveyed ones, where naturally no in situ information on the biological composition is available and only environmental data exist, and full-coverage is thus achieved. It is assumed that each sampling unit is wholly contained within a single grid cell and that it is representative of it, and that each cell contains no more than one sampling unit. Ideally, then, either the size of the grid cells or the size of the sampling units (the surveyed sites), bears a relation to patterns of spatial heterogeneity of faunal composition, to ensure that the fraction of variation that is ignored (most notably, within-cell variation) only reflects variation that we are not interested in (e.g. stochastic).

Regarding the specific predictive model, the amount of choice available is overwhelming and only a handful have been tested by the benthic ecology community, where the field is still in its infancy. As a general rule, more complex methods produce models that fit the data more closely. The selection of method can have a profound impact on the reliability of the final outcome (see Elith et al. 2006 for a comprehensive review). Moreover, when the outcome is
intended to be used as a form of decision support for conservation it is vital that the strengths and limitations of the method are made explicit.

Arguably, following this approach can be regarded as a formal way of defining biotopes. First, the fact that classes are defined according to multispecies patterns accounts for the biotic aspect of the concept. Second, predicting the presence of classes on the basis of environmental data accounts for the abiotic aspect. And third the spatially-explicit nature of the model resolves the geographic boundaries.

3.3 Predicting the distribution of benthic biotopes: a case study from a Swedish fjord

Off the west coast of Sweden, the first marine national park of the country was designated in 2009 (Kosterhavet Nationalpark), conferring the fjord and archipelago of this unique site a new status, not without its responsibilities. Since the approval of the denomination a series of Remotely Operated Vehicle (ROV) surveys have been conducted across the area and underwater video footage amassed, resulting in a comprehensive inventory of epibenthic megafaunal species. In the spirit of taking full advantage of the existing library of video material and in view of a pressing need for further documenting the distribution of biological diversity of (the benthic portion of) the national park, a project was commissioned that would use a predictive mapping approach, using existing ROV data as a basis, to produce a map of benthic biotopes. This case study reports the achievements of that project and is currently under review for publication in a scientific journal. Our aim was to produce a map to support marine spatial planning (a biotope map), subject to being as close to the ‘truth’ as possible, while using methods as objective, automated and repeatable as possible, as well as using existing data.

3.3.1 Conceptualisation and data model

The first step was to create a grid lattice in a Geographic Information System (GIS) to bin all data so that surveyed sites and unsurveyed areas are all modelled at the same spatial scale and the coverage achieved is 100%. Following recommendations in Gonzalez-Mirelis et al. (2009) based on spatial patterns of epibenthic megafauna, the mesh size (linear scale) chosen for the grid was 15 m.

Species data was obtained from underwater video footage, recorded between 2006 and 2008 by means of a video camera mounted on a Sperre Subfighter 7500DC ROV. ROV navigation data was time-synchronised with the video signal, enabling the reconstruction of the ROV’s path for each of 52 survey sites (Figure 1), as well as the formalisation of a function linking the video footage to the path.

The grid was first used to clip the survey tracks into sampling units. Through this procedure, a sufficient (and parsimonious) number of presence/absence datapoints was obtained incurring no extra (monetary) costs.

For a grand total of 417 cells, or sites, equivalent to approximately 70 hours of footage, faunal data was then compiled. Species data comprised all epibenthic megafauna recorded at the relevant clip, including both attached and free-living lifeforms. Calcareous sponges, macrophytes and epibiontic fauna, were excluded from this study. Organisms were identified at least to genus level; otherwise they were not included. Additionally, a number of taxon complexes were used, encompassing those taxa difficult to tell apart sharing similar habitat requirements (e.g. the two species of sponge of the genus Phakellia and the species Axinella...
Fig. 1. Map of the study area showing the location of the ROV-surveyed sites (filled dots) and the bathymetry. The main trench running from north to south is known as the Koster Fjord. This fjord separates the mainland from the Koster Archipelago.

*infundibuliformis* were all part of the same complex and were thus counted as one variable. Where available, high-definition still photos were used to aid in the identification of taxa. In all, 192 taxa and taxon complexes were identified, out of which 178 were classified to species level. Bray-Curtis similarities were then calculated for all pairs of sites.

Lastly, sites were classified according to various thresholds for faunal similarity, rendering a total of nine classes (Table 1). The chosen classification was developed around a number of criteria, including class predictability (see Gonzalez-Mirelis et al. 2011), readiness to distinguish between classes solely by visual inspection (as it would be needed if the classification were to be used in future investigations) and closeness to classes in existing biotope classifications (such as that of Connor et al. 2004).

In the benthos, community composition and diversity have been found to be structured by water column processes (suspended particulate matter loading, food availability and hydrodynamic stress) as well as substrate properties, temperature and salinity. We developed a number of variables representing (rather local) geophysical processes that we assume to be proxies for one or more of the functionally relevant variables. Habitat data was derived from high-resolution multibeam data, including bathymetry and backscatter. The multibeam
| Class label | Physical habitat description | Characterising taxa |
|-------------|-----------------------------|---------------------|
| AA          | Offshore circalittoral rock  | Axinellid sponges, Terebratulina retusa, Anomids, Placostegus tridentatus, Spirorbinids |
| AB          | Lower circalittoral rock     | Flustrids           |
| AC          | Offshore circalittoral biogenic reef | Hathrometra sarsii, Lophelia pertusa, Mycale lingua, Ascidia obliqua, Filograna implexa |
| BA          | Lower circalittoral mixed sediment and rock | Pandalus borealis, Liocarcinus sp., Sabella pavonina, Munida rugosa |
| BB          | Offshore circalittoral fine sediment | Nephrops norvegicus, Cerianthids |
| BC          | Offshore circalittoral mixed sediment and rock | Spirontocaris lilljeborgii, Lithodes maja |
| BD          | Lower circalittoral sediment | Kophobelemnon stelliferum, Pachycerianthus multiplicatus |
| C           | Near-shore lower circalittoral sediment | Pennatula phosphorea |
| D           | Near-shore lower circalittoral coarse sediment including shell hash | Gobids, Pecten maximus |

Table 1. Description of biotopes

surveys were conducted in 2005 with a Simrad Multibeam EM 1002, at 95 kHz frequency. The set of predictor, abiotic variables included the following:

3.3.1.1 Depth

Depth has been found to be the primary habitat factor organising benthic communities, although its importance may be contingent upon spatial extent and subset of biota considered. In exposed habitats, depth can have a substantial effect on the amount of near-bed stress. Data on depth was obtained directly from 5 m resolution multibeam bathymetry data. It was resampled to the required resolution (15 m) using the mean of all (9) node values encompassed by each grid cell. Depth ranged from 30 to 262 m.

3.3.1.2 Substrate

The link between substrate type and biological composition of the benthos is robustly established, both regarding sediment type or granulometry (particularly important for infauna) and the availability of hard surfaces for organisms to settle on, like bedrock (important for epifauna). Along with depth, it represents a widely recognised driving factor of biological communities of the seabed. A classification of surficial geology (substrate type) was made available to us by the Swedish Geological Survey, who derived the classes from multibeam backscatter data. Categories are clay, gravel, rock and sand.

3.3.1.3 Surface area

Surface area refers to the total amount of available surface in the landscape and it is a function of the ruggedness of the terrain. It directly determines the amount of living space available,
thus potentially influencing emergent macro-ecological properties, such as species richness, 
that do not retain explicit information about composition. It can however also be related 
to the presence of microscale features, such as overhangs and ledges, that are home to highly 
habitat-specific species, like in the case of the lamellibranch *Acesta excavata*. Here we measured 
total surface area of the grid cell in m² using the Surface Areas and Ratios from Elevation 
Grids v. 1.2 ArcView extension (Jenness, 2002). It was calculated using the 5 m resolution 
bathymetry raster and resampled to 15 m resolution using bilinear interpolation. It ranged 
from 225 to 900 m².

3.3.1.4 Aspect
The orientation of the slope may affect, in combination with other topographic attributes, 
current velocity and bed shear stress. Aspect was derived from the 15 m bathymetry, using a 
standard 3-by-3 running window. We used the standard eight compass directions, plus a class 
for horizontal areas.

3.3.1.5 Landform
The effect of geomorphology on biological composition is unclear (Howell, 2010), although for 
some species and over some spatial scales it may be significant. The causal link is thought to 
be related with current speed and habitat availability, as well as susceptibility to sediment 
accumulation (Ierodiaconou et al., 2011). We included geomorphological attributes in the 
form of landform categories. Landform can be calculated by classifying the landscape using 
Topographic Position Index (TPI) values at two different scales, where the TPI is the difference 
between a cell’s elevation and the average elevation of a neighbourhood around that cell. It 
is a way of expressing jointly convexity and concavity. We used the Topography Toolbox for 
ArcGIS 9.2 developed by (Jenness, 2006), with a smaller rectangular neighbourhood of 5-by-5 
cells, and a larger one of 11-by-11. Upland drainages were reclassified as shallow valleys and 
upper and open slope were lumped together. Categories were as follows: canyon, shallow 
valley, U-valley, plain, slope, local ridge, midslope ridge and high ridge.

GIS layers were obtained from the multibeam data sets and then their values were assessed, 
by spatial overlay, for the grab of 417 cells for which there was biological data available, thus 
constituting the sample base for the model. Note that every data point was made up of five 
values corresponding to the predictor variables and one value for the response, which was in 
turn taken from a 9-level response variable.

3.3.2 Fitting the model and evaluating its spatial predictions
Once a specific modelling method is selected, the most commonplace procedure is to split 
the sample base into two separate datasets, both comprising complete (predictor + response) 
data points. One is used for fitting the model and the other is reserved for evaluating model 
predictions. These are referred to as ‘training set’ and ‘testing set’. The model, as induced 
by patterns in the training set, is used to make predictions for every single grid cell across 
the study area, typically involving a very large number of predictions and a potentially long 
computing time, contingent on the grid cell size:study area size ratio.

The particulars of this case study involved a restricted amount of data of unknown 
representativeness of the distribution of benthic diversity, potentially biased and noisy. 
Therefore, the model was chosen with great care that it would be capable of handling a 
challenging dataset and produce robust predictions. We fitted a Conditional Inference (CI) 
Tree-based forest which was found to outperform other decision tree-based models both in
terms of classification accuracy and the ability to discriminate between classes. CI trees have been developed recently by Hothorn et al. (2006) (the reader should refer to this study for details of how the algorithm works). Here we will only point out that the framework uses a combination of machine learning principles and hypothesis testing that renders it robust and powerful, albeit computationally demanding. A split was implemented randomly within each level of the response variable to ensure the possibility of calculating a measure of accuracy for all classes.

A map of benthic biotope classes was produced by assigning the most likely class, as determined by the model, to every single grid cell across the modelling area (Figure 2). The area of the smallest polygon is, accordingly, 225m$^2$ (one single cell) and is therefore not visible to the naked eye at the scale of the map. Tested against the known class of a reserved set of 104 sites, the model yielded an error rate of 28%. In other words, the model did significantly better than classifying every cell as the most prevalent class. A more accurate measure of error could have been attained using independently collected data, as well as understanding the spatial patterns of misclassified cases, but this was considered adequate for the purpose of this project.

Strictly, the output from our model should be regarded as a map of polygons similar in their environmental conditions, which are in turn defined on the basis of shared expected biological composition, where emphasis is added to draw attention to the fact that both can be measured in terms of (conditional) probabilities. Put differently, the model outputs are formally-defined biotopes. The good model fit and the achieved spatial resolution create an optimal scenario for addressing conservation planning questions.

### 3.3.3 Applications to marine spatial planning

The *Kosterhavet* area was designated a national park in 2009 with the conservation-related objective of long-term preservation of the marine ecosystems, habitats and species occurring naturally in the region, while ensuring the sustainable use of local biological resources, among other goals, less directly related to conservation.

Notably, the park is one where multiple uses are allowed. Various kinds of commercial and recreational fisheries have a stake in the area, alongside tourism, and to a lesser extent, shipping. There is a well established trawl fishery for shrimp (*Pandalus borealis*), and Norway lobster (*Nephrops norvegicus*), comprising around 30 boats, mostly under 12 m, as well as an additional small fleet of local fishermen targeting lobster (*Homarus gammarus*). The area is also important for recreation, with many hundreds of yachts and motor boats staying in the area over the summer. Tourism has increased 50% over the last decade with around 80,000 people visiting, mainly in July and August. In light of this, a pressing need has emerged to lay out, and ensure mechanisms of enforcement of, a management system within which competing demands inside the multiple-use park are adequately accommodated, while not compromising the conservation goals of the park.

This can only be achieved by means of adequate spatial planning, a tool now widely recognised to be suited for implementing an ecosystem-based approach to the management of ecosystems. Marine spatial planning involves the practice of zoning (to spatially and temporally designate areas for specific purposes), with the aim of reducing conflict both among different users competing for the same space, and more importantly, between users and the environment (Douvere, 2008), ensuring that the capacity of the ocean to provide goods and services remains undiminished. Far from being a straightforward task, the main challenge
that conservation spatial planning faces today is undoubtedly whether goals are perceived to be achieved in a way that minimizes, as far as possible, forgone opportunities for production (Margules & Pressey, 2000).

The zoning system currently in place involves three co-occurring management regimes (see Figure 3). Three sites are afforded the highest degree of protection by being designated as Seabed Protection Areas (SPAs) with a full trawl ban in place and where anchoring and use of other equipment that can damage the seafloor are prohibited. The remainder of the area of the national park is divided into two zones on the basis of depth, where areas above 60 m benefit from partial restrictions (partial protection zone, in Figure 3) with no commercial fisheries allowed, and areas deeper than 60 m are open for a specially-regulated fishery (see below).
The only commercial fishery that takes place inside the boundaries of the national park is a shrimp fishery, regulated by a special agreement between fishermen, researchers, fisheries organisations and authorities at different levels, in place since 2000, and is concentrated in the southern half of the fjord. Trawls must be of a specific size, lightweight and equipped with a sorting grid that allows escape of fish bycatch. Remarkably, education and sharing of knowledge are given special consideration in this agreement. Under its auspices, courses in marine ecology for fishermen, as well as courses in commercial fishing and fishery technology for researchers and officials, have been arranged in recent years. The fishery yields about 200 tonnes of shrimp per year.

Recreational lobster fishing by creels also takes places in the national park causing negligible impact. Immediately outside of the boundary to the west, trawling is allowed only for prawns and Norwegian lobster. Here too, species-specific sorting grids are required on the trawls. Further to the west, beyond the trawl limit, no trawling restrictions apply.

Given the goal set for the park, and the array of stakeholders involved, it is imperative to address the question: 'how much of each biotope is being afforded effective protection?', where a leap is taken from the idea of 'including all biotopes under some sort of protection'.
level’ to ‘preserving ecosystems, habitats and species’ (as stated in the management plan of the park) which we will, for the purpose of this chapter, assume to be possible.

3.3.3.1 Assessment of representation

The biotope map generated by the model enabled an assessment of the level of representativity of each managed zone within the park, also known as a gap analysis. As shown in Table 2, the partial protection zone includes mostly biotopes of type AB (98%) and C (89%), with no representation at all of any of the soft sediment biotopes (BA-BD); the most represented biotopes within SPAs are AC, Lophelia reefs (3%), which, it should be noted, are contributed by one single SPA, and AA (2%). Some of the biotopes not represented in the partially protected zone are indeed encompassed by the SPAs (BB, BC).

| Class | Park (km²) | Partial protection (%) | SPA (%) |
|-------|-----------|------------------------|---------|
| AA    | 117.8     | 37.3                   | 2.1     |
| AB    | 90.5      | 98.0                   | 0.6     |
| AC    | 1.9       | 0.6                    | 3.1     |
| BA    | 0.5       | 0                      | 0       |
| BB    | 23.3      | 0                      | 1.9     |
| BC    | 7.2       | 0                      | 0.5     |
| BD    | 0.1       | 0                      | 0       |
| C     | 14.7      | 89.1                   | 0       |
| D     | 3.6       | 27.7                   | 0       |

Table 2. Quantitative assessment of representation of biotopes within different conservation zones within the national park

It thus emerges that a zoning system based on depth alone is guaranteed to return a biased set of managed zones, because all soft sediment biotopes occur deeper than 60 m. This is a particularly acute issue in this area, where anthropogenic pressure is very unevenly distributed over biotopes, with BB and BC areas getting the bulk of it (compare fishing effort shown in Figure 4 and the biotope map, Figure 2). Therefore, not only are B type biotopes underrepresented in protected zones, but they are also the only ones at risk. Additionally, they are not afforded any conservation interest from the European Union, so the responsibility for the long-term preservation of the communities associated to this biotope rests solely with the national park. On the grounds of our analysis, increasing their representation in at least partially protected zones should be a priority.

The absence from the park as a whole of biotope BA is explained by the fact that a very small amount of it was predicted by the model overall (it amounted to less than 1 km²). More importantly, the sites classified as BA were deemed to be heavily fished, and they featured only sparse epifauna. Careful examination of the classification and spatial predictions suggests that this class should be merged with either BB or BD.

One of the biggest gaps that has emerged through this analysis relates to class BD, an uncommon class in the region (<1 km² contained in the park, see Table 2), completely absent from any type of conservation zone. To make matters worse, the biotope is strongly associated with the seapen Kophobolemon stelliferum, a species with conservation priority within Sweden.

3.3.3.2 An example implementation of systematic conservation planning

The above analysis has raised an important question: ‘is seabed biodiversity adequately represented inside priority areas?’ The answer of course depends on what is meant by
'adequate', which in turn raises more questions, namely: 'how much of each biodiversity surrogate (i.e. biotope) needs to be protected?', 'how should the protected sites be distributed so as to minimize conflict with users?' In general terms it is apparent that the management system in place, which was driven largely by depth and uniqueness (e.g. the coral reef SPA), has some drawbacks and can be improved.

Systematic conservation planning (SCP) involves finding cost-efficient sets of areas to protect biodiversity. SCP is a process that comprises, at a minimum, the following stages: (1) compile data on the biodiversity, or biodiversity surrogates, of the planning region; (2) identify conservation goals for the planning region, preferably in the form of quantitative, operational targets; and (3) select a set of conservation areas that collectively meet the representation targets assigned to the biodiversity features incurring the lowest possible cost. These are embedded in a larger process that includes the possibility of implementing conservation actions on the ground, as well as revisiting and adapting zoning plans based on monitoring data. The approach is highly effective because it is efficient in using limited resources to achieve conservation goals, it is defensible and flexible in the face of competing uses, and it is accountable in allowing decisions to be critically reviewed. Stage 3, probably the most critical of all, can be tackled by use of algorithms that can efficiently solve what has been called the "minimum-set problem" (Possingham et al., 2000): Minimize overall cost, subject to the constraint that all biodiversity targets are met (e.g. 20% of each biodiversity feature), where cost can be expressed as total size of the reserved area, revenue loss, etc. Kosterhavet provides for an optimal test case for a SCP approach, where biodiversity features can be readily formulated on the basis of the modelled biotopes.

Under this systematic framework, conservation planning becomes a data-driven process. Spatial data are required on all features that need to be considered, both those that contribute to achieving targets (which are, typically, biodiversity-related) and those requiring regulations, so that the true cost of allocating areas to a reserved zone can be accurately computed. The latter mainly refers to data on socioeconomic activities. When the same kind of information is available at the same level of detail throughout an area, it becomes possible to quantify the advantages and disadvantages of various zoning options and therefore legitimately compare these.

To demonstrate the possibilities of SCP we compiled fishing effort data from Vessel Monitoring System records for years 2007-2010. The fishing data were provided by the former Fisheries Board of Sweden, which is now the Swedish Agency for Marine and Water Management. Fishing positions were gridded to 1 ha cells and the maximum number of pings out of the whole period was used as an estimate of fishing effort for the location.

The software used to generate conservation networks was Marxan. Marxan (Ball et al., 2009), a decision support system designed to solve the minimum set problem, finds a number of near-optimal solutions using a heuristic algorithm called 'simulated annealing'. A planning unit layer (regular grid) comprising over 30,000 units (1 ha cells) was used. Planning units are the building blocks of reserve systems that are overlaid on maps of biodiversity features for conservation planning. Building from the amount of every feature in every planning unit, computed by spatial overlay, Marxan generated 100 different solutions to the problem of selecting the minimum number of planning units (with a spatial configuration constrained by a parameter that modifies overall boundary length) which achieves a total of at least 10% representation of all conservation features. The target amount used of 10% was arbitrary, though it is a commonly used figure. Note that the target does not have to be the same across all features, but importantly, in this approach it can be controlled by the user to prevent
the inevitable imbalance that results from non-systematic approaches, as above. Cost was included as the fishing intensity layer described above so that the algorithm strived to avoid using cells located in important fishing grounds. Here we present only one possible solution (Figure 4).

![Systematic Conservation Planning Solution](image)

**Fig. 4.** Systematic conservation planning solution obtained with Marxan encompassing 10% of every biotope, as well as minimizing the use of areas heavily targeted by fishing.

Whether or not the implementation on the ground of these areas as a conservation network is feasible is the next question that should be addressed, and one which, importantly, will get a negotiation process started.

### 4. Conclusions and future research

If planning for conservation in the sense of designing networks of protected areas is usually a practice of hope, in the marine realm, where areas are prioritised at best on the basis of scant information and more or less questionable estimates of species occurrence to fill in the blanks, it is almost a practice of faith. A lack of robustness in the process of marine conservation and spatial planning not only jeopardises the efficacy of conservation areas, but also reduces vital societal support. While it will never be possible to make conservation planning decisions based on complete knowledge of the distribution of the full complement of biodiversity, from genes to ecosystems, a degree of robustness can be achieved, as we have shown, by means of
(1) selecting a level in the biodiversity hierarchy to operate in, (2) mapping the distribution of its units, and (3) applying spatial planning principles.

One question that we have not touched upon is to what extent the level of operation selected, in our case, biotopes, is a good surrogate for biodiversity at other levels, e.g. species, where management provisions and intergovernmental mandates apply, and this should be addressed in future research on the distribution of seabed biodiversity.

We have seen that two main approaches are possible for mapping the geographic distribution of ecological patterns on the seabed. The top-down approach is driven by geophysical attributes, relies heavily on hydroacoustic, remotely-sensed data and is highly effective for mapping the distribution of habitats, in the narrowest sense of the word. If the target, however, is to reproduce patterns of epibenthic megafauna, the most conspicuous organisms living attached to the seabed which characterise the landscape, the top-down approach may be suboptimal, and an alternative is being rapidly developed. In the bottom-up approach the process is driven by patterns of occurrence of benthic communities, which are then extrapolated using observed biota-environment relationships, by means of full-coverage, hydroacoustic (usually multibeam) data. This approach draws heavily from the field of distribution modelling of species and/or communities, particularly in the framework that involves a classification of communities based on survey data first, and the modelling of the obtained units later. The outcome from this process is not only a map, but a formal definition of biotopes.

Marine spatial planning and particularly systematic conservation planning make the most of thus generated maps of habitats or biotopes. It is the tacit convention that diversity at the species level (e.g. species richness) is the most appropriate target of conservation, even if the focus is placed on a subset of this (e.g. species at risk). Notwithstanding, ecosystem diversity per se has also been used as the target of conservation, and other types of ecological patterns or even processes, could also be suitable targets within an appropriate framework. Methods for mapping dynamic processes are particularly needed in the marine environment, including the pelagic environment, so that areas that fulfil an important role in the functioning of marine ecosystems (e.g. areas of upwelling, corridors for larval transport, etc., acting as sort of ‘keystone spaces’) can be incorporated in the process of marine spatial planning.

The issue at the core is unravelling the factors that explain the distribution of species, whether benthic or otherwise. We have focused on methodological issues, but the role that ecological theory plays within this process cannot be understated. A stronger footing on ecological theory will help develop better distribution models that produce more reliable spatial predictions, and it has been called for (Austin, 2007). Distribution modelling methods have usually been developed within the field of vegetation science and only later have they been adopted by benthic ecologists, causing a delay in the progress of benthic mapping science and in the development of tools to address questions of benthic biogeography, conservation planning, etc. A closer collaboration between benthic ecologists and vegetation scientists in the field of distribution modelling and biotope predictive mapping should help overcome the lag that has so far characterised the marine relative to the terrestrial science, and improve access to knowledge of distribution of biological diversity for all ecologists.

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Marine ecosystems, a very wide topic, includes many different processes, groups of organisms and geographical peculiarities. The objective of this book is to present various topics of great importance for understanding the marine ecosystems, what they are, how they work and how we can model them in order to forecast their behaviour under changing conditions. They have been thoroughly reviewed and accepted for publication. The chapters cover aspects such as: Threats to ultraoligotrophic marine ecosystems (Ch. 1); Modelling the pelagic ecosystem dynamics: the NW Mediterranean (Ch. 2); The marine ecosystem of the Subantarctic, Prince Edward Islands (Ch. 3); meiofauna as a tool for marine ecosystem biomonitoring (Ch. 4); Chemical interactions in Antarctic marine benthic ecosystems (Ch. 5); An Interdisciplinary Approach on Erosion Mitigation for Coral Reef Protection- A Case Study from the Eastern Caribbean (Ch. 6); A revisit to the evolution and ecophysiology of the Labyrinthulomycetes (Ch. 7); Seabed mapping and marine spatial planning: a case-study from a Swedish marine protected area (Ch. 8); Management strategies to limit the impact of bottom trawling on VMEs in the High Seas of the SW Atlantic (Ch. 9); Hydrocarbon contamination and the swimming behavior of the estuarine copepod Eurytemora affinis (Ch. 10), and Interactions between marine ecosystems and tourism on the Adriatic and Mediterranean (Ch. 11).

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