Review

Benthos distribution modelling and its relevance for marine ecosystem management

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Marine benthic ecosystems are difficult to monitor and assess, which is in contrast to modern ecosystem-based management requiring detailed information at all important ecological and anthropogenic impact levels. Ecosystem management needs to ensure a sustainable exploitation of marine resources as well as the protection of sensitive habitats, taking account of potential multiple-use conflicts and impacts over large spatial scales. The urgent need for large-scale spatial data on benthic species and communities resulted in an increasing application of distribution modelling (DM). The use of DM techniques enables to employ full spatial coverage data of environmental variables to predict benthic spatial distribution patterns. Especially, statistical DMs have opened new possibilities for ecosystem management applications, since they are straightforward and the outputs are easy to interpret and communicate. Mechanistic modelling techniques, targeting the fundamental niche of species, and Bayesian belief networks are the most promising to further improve DM performance in the marine realm. There are many actual and potential management applications of DMs in the marine benthic environment, these are (i) early warning systems for species invasion and pest control, (ii) to assess distribution probabilities of species to be protected, (iii) uses in monitoring design and spatial management frameworks (e.g. MPA designations), and (iv) establishing long-term ecosystem management measures (accounting for future climate-driven changes in the ecosystem). It is important to acknowledge also the limitations associated with DM applications in a marine management context as well as considering new areas for future DM developments. The knowledge of explanatory variables, for example, setting the basis for DM, will continue to be further developed: this includes both the abiotic (natural and anthropogenic) and the more pressing biotic (e.g. species interactions) aspects of the ecosystem.

While the response variables on the other hand are often focused on species presence and some work undertaken on species abundances, it is equally important to consider, e.g. biological traits or benthic ecosystem functions in DM applications. Tools such as DMs are suitable to forecast the possible effects of climate change on benthic species distribution patterns and hence could help to steer present-day ecosystem management.

Keywords: ecosystem approach, environmental monitoring, habitat suitability modelling, macrofauna, mapping, marine spatial planning (MSP), predictive modelling, species distribution modelling.

Introduction

The marine ecosystem is known to be influenced by a combination of physical, chemical, and biological components, which has a direct influence on the integrity of species and habitats. The successful management of these systems require information from all its ecological levels. This need for ecological knowledge, the increased anthropogenic pressures on the marine environment (Halpern *et al.*, 2008; Ban *et al.*, 2010) and the potential for multiple-use conflicts, have led to an increased interest in sea-use planning with particular emphasis placed on marine spatial planning (MSP; European Commission, 2008; Douvere and Ehler, 2009). Ecosystem management is often confronted with fragmented information on the spatial distribution of marine species and habitats, mainly this is because the marine environments are more difficult to access, and to monitor, when compared with terrestrial ecosystems (Robinson *et al.*, 2011).

Recent developments in marine habitat mapping using remote sensing tools have resulted in an increased availability of environmental data (Brown *et al.*, 2011). The seabed features of marine habitats can now be characterized and mapped on relatively large spatial scales. In addition, satellite-based observation of the oceans and physical models provide information on a variety of physical parameters such as sea surface temperature or primary production on a global scale. The ability to visualize the seabed and the overlying water column has led to an increased interest in the use of habitat maps for marine nature conservation, economic exploitation and development, and resolving conflicts of multiple uses on the seabed (e.g. in support of MSP; Birchenough *et al.*, 2010).

Monitoring the biotic components of the ecosystem is prohibitively expensive and requires an enormous effort to collect with point source data of species distributions over large spatial scales. Therefore, predictive methods have become important tools to overcome these issues when looking at biotic aspects of the ecosystem components (Guisan and Zimmermann, 2000; Guisan and Thuiller, 2005). Distribution modelling (DM), which is also known as, for example, species DM, habitat suitability modelling, ecological niche modelling, or bioclimatic envelopes, mainly refer to correlative approaches that use full spatial coverage data of environmental variables to explain and predict patterns of species distribution (Elith and Graham, 2009). These predictive modelling methods have been mainly used in terrestrial ecology to study general patterns of species distributions (Hengl *et al.*, 2009), as well as for addressing conservation- and ecosystem management-related issues such as the delineation of protected areas (Valavanis *et al.*, 2008; Elsäßer *et al.*, 2013), the risk for species invasions (Gormley *et al.*, 2011), and the prediction of distribution changes in response to climate change (Cheung *et al.*, 2009). See also Guisan *et al.* (2013) for a comprehensive overview on the use of DMs in support of environmental management for terrestrial systems. The use of DMs in marine ecosystems is still in its infancy (Degraer *et al.*, 2008), when compared with the vast number of studies applying DM in the terrestrial realm. Most of the existing DM studies in the marine environment have shown their application on conservation

planning, method evaluation, theoretical ecology, climate change, species invasions, phylogeography and impact assessment (Robinson *et al.*, 2011). Commercial fish were especially targeted by recent studies using DM in marine ecosystems (Venables and Dichmont, 2004; Maxwell *et al.*, 2009; Moore *et al.*, 2010; Lenoir *et al.*, 2011; Jones *et al.*, 2012). Benthic invertebrates have also been subject to DM, although their distribution is primarily modelled over local scales (Ysebaert *et al.*, 2002; Thrush *et al.*, 2003; Ellis *et al.*, 2006; Degraer *et al.*, 2008; Meißner *et al.*, 2008; Willems *et al.*, 2008; Galparsoro *et al.*, 2009; Valle *et al.*, 2011). There are some examples from larger scales, e.g. Baltic Sea (Gogina and Zettler, 2010; Gogina *et al.*, 2010b), North Sea (Reiss *et al.*, 2011), Icelandic waters (Meißner *et al.*, 2014), and worldwide (Ready *et al.*, 2010; Wei *et al.*, 2010; Davies and Guinotte, 2011). The results of the above-mentioned applications of DMs in the marine realm rendered insight into the correlative relationships between environmental drivers and benthos species distribution, allowing for full-coverage predictions of species and community occurrence. These outputs can be used to guide management decisions.

Nonetheless, ecosystem management and MSP have to incorporate information on a variety of aspects ranging from the natural environmental conditions to anthropogenic pressures (Galparsoro *et al.*, 2013; Stelzenmüller *et al.*, 2013), of which the distribution of benthos will be only one aspect of many layers of information. Thus, this information could be the most useful in a management context, as the information derived from DM should ideally represent simple, easily interpretable results preferably with little or at least quantified uncertainty. DM performance has been shown to depend on a variety of factors such as the modelling approach (e.g. Elith *et al.*, 2006; Elith and Graham, 2009; Reiss *et al.*, 2011), ecological niche width of species (e.g. Kadmon *et al.*, 2003; Tsoar *et al.*, 2007), and dispersal range, species interactions, and mobility of species (McPherson and Jetz, 2007). Thus, although highly valuable, caution and expert guidance indeed is needed when using DM results in an ecosystem management context. Furthermore, most DM approaches only provide species occurrence probabilities; this without informing on species abundance or biomass. Scientific expert guidance will hence remain indispensable to correctly encompass these limitations and uncertainties when applying DM in an ecosystem management context. Therefore, the main objectives of this review are: (i) to provide an overview of DM applications in the marine benthic environment and (ii) to discuss their applications and limitations as a tool to support marine ecosystem management.

This review follows the consecutive steps in DM, discussing critical assets of using biological and environmental input data and their incorporation into the different DM methods (Figure 1). This paper does not intend to provide a complete overview of the different modelling methods, but rather is seeking to emphasize some general applications and limitations of the models when used for marine benthic environments. We also present several examples where the applications of DM are relevant to marine ecosystem management, highlighting their general applicability, but also their limitations in applicability to management-related
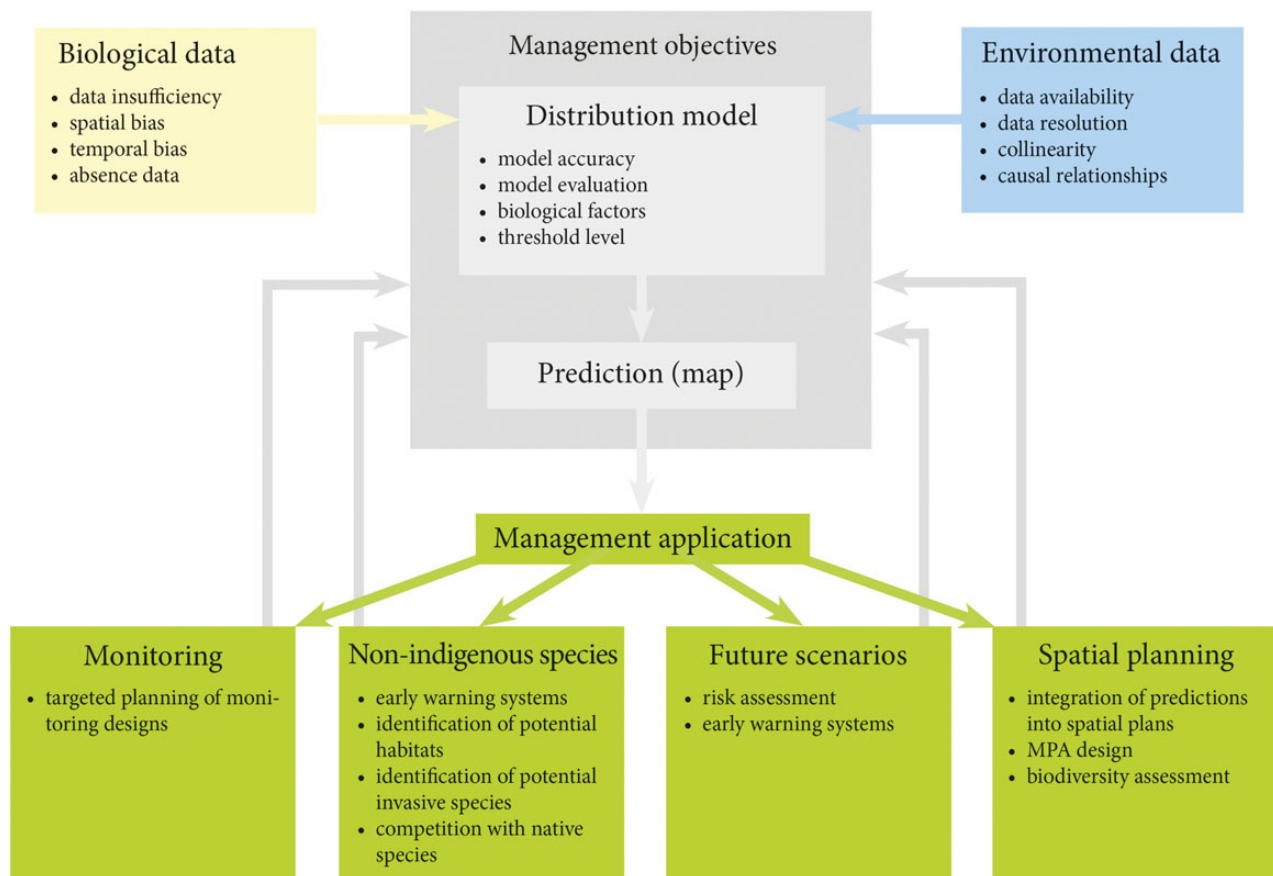
Figure 1. Conceptual diagram showing the components of statistical DM and the overall linkages for the management applications. The arrows indicate the direction of input of data/information, while the limitations and problematic issues for the biological input data, the environmental predictors, and the DM procedure are listed in the consecutive boxes. The management objectives in this figure provide the overarching framework on which the selection of DM method and prediction attributes is depending on.

issues, e.g. monitoring and spatial planning, as well as their potential for future use (e.g. early warning systems).

DM methods and data requirements
Modelling methods and associated uncertainty

There is a rapidly growing variety of methods used for marine benthic species and community DM, including both already widely applied and merely tested techniques. Detailed descriptions and more explicit lists can be found in advanced subject-specific text books (e.g. Legendre and Legendre, 1998; Zuur *et al.*, 2012), reviews, and object-specific comparative research papers (e.g. Guisan and Zimmermann, 2000; Guisan and Thuiller, 2005; Franklin, 2010; Robinson *et al.*, 2011). Three major approaches have been used to predict species distribution patterns: (i) statistical (or correlative) stochastic models that estimate parameters based on empirical or phenomenological relationships between current distribution and environmental conditions, (ii) mechanistic (or structural dynamic) models that incorporate explicit ecological relationships independent of current distribution, with mechanistic components defined by physiological relevance, and (iii) Bayesian belief networks (BNs; Table 1; Guisan and Zimmermann, 2000; Sagehashi, 2008; Buckley *et al.*, 2010; Stelzenmüller *et al.*, 2010).

Statistical approaches are probably most often used for DM and a large number of methods are now available, of which several were successfully applied to marine benthos (Table 1). Comparative studies showed that the performance of the different models can vary considerably, but it is also clear that no single model could be equally appropriate for all applications (e.g. Reiss *et al.*, 2011; Valle *et al.*, 2013). When deciding on the model selection, this needs to be adjusted according to the (management) objectives (Figure 1). Applications of statistical modelling in marine context include testing hypotheses in relation to the ranges of species distribution along environmental gradients, generating habitat suitability maps that predict the specific ecological potential of a habitat (with limitations defined by the data analysed), and assessing the possible consequences of habitat changes (either natural or anthropogenic), as part of MSP and conservation management (Degraer *et al.*, 2008; Robinson *et al.*, 2011).

The main advantage of statistical DM is that they are conceptually simple, descriptive, and require relatively few data on the modelled species, as often species occurrence data may be sufficient. This simplicity however also entails a higher risk of misinterpretation when it comes to its application in an ecosystem management context, where the desired information ideally is a single prediction with little uncertainty (Jones *et al.*, 2013). This uncertainty originates from various sources inherent to the modelling process, including the biological and environmental input data (see below), the modelling technique and the prediction itself (Beale and Lennon, 2012). While in principle the reliability of the prediction

Table 1. Common methods used for DM ("p", presence-only data; "p/a", presence/absence data; "++", known application for management in marine settings; "+", known application in marine benthos; "−", no published relevant applications).

Modelling technique	Description	Data requirements	Pros and cons	Marine application	Exemplary references
GLM, Generalized Linear Model	Based on analysis of variance and covariance; various distributions and link functions used subject to the distribution features of both predictors and response variables (binomial for binary, Poisson for count data, negative binomial for overdispersed count data, logit for probability of binary response, etc.); from simple to multivariate regression	p/a; both categorical and continuous predictors	Variety of handled distributions, common, straightforward interpretation, high predictive power; model selection uncertainty and autocorrelation should be accounted for; the greater the flexibility (e.g. number of polynomials), the higher is the risk to overfit the data	++	Ysebaert et al. (2002), Valavanis et al. (2008), Gogina et al. (2010b)
GAM, Generalized Additive Model	Straightforward extension of GLM where scatterplot smoothing functions (locally weighted mean) are used to build a sum of a set of arbitrary functions	p/a	Overfitting risk, complexity of interpretation suggests the use of sequence of non-parametric GAM to determine the dominant relationships and then apply parametric GLM for fine model fitting and prediction	++	Valavanis et al. (2008), Bergström et al. (2013)
MARS, Multivariate Adaptive Regression Splines	Non-parametric regression technique combines linear regression, mathematical construction of splines and binary response cursive partitioning to model (non-)linear relationships between environmental variables and species occurrence, coefficients differ across levels of predictor variables	p/a; continuous and categorical data	Flexible, easy to interpret, automatically models non-linearities and interactions between variables, do not give as good fits as boosted trees methods	++	Meißner et al. (2008), Reiss et al. (2011)
MAXENT, Maximum Entropy	Estimates the target probability by finding the probability distribution of maximum entropy (of minimum information content) under the constrains that the expected value of each predictor matches its empirical average	p	Superior performance among presence-only algorithms	++	Phillips et al. (2009), Reiss et al. (2011)
BIOCLIM Envelop models	Finds mean and standard deviation for each environmental variable to calculate bioclimatic envelopes	p	Output is the categorical probability of occurrence, often shows poor performance	++	Reiss et al. (2011)
Quantile regression	Serves to model the function for the depicted quintile of the response, e.g. to estimate the factors constraining the population, without strict distributional assumptions and specifications on link between the variance of response and its mean	p/a	Alternative to ordinary least-square regression methods able to reveal hidden bias and existing important processes not covered by measured variables	−	Cade and Noon (2003), Vaz et al. (2008)
ANN, Artificial Neural Networks	Non-linear mapping structures based on hundreds of simulated neurons connected together as brain's neurons, learn from experience (not programming), behaviour is defined by the way its individual computing elements are connected and by the strength of those connections (weights); can be trained to recognize patterns, classify data, and forecast future events	p/a	Largely universal and assumption-free approach for any data; however, this is a "black box" approach; therefore, it is difficult to interpret ecological relationships	−	Lek and Guegan (1999), Valavanis et al. (2008)

GARP, Genetic Algorithm for Rule-set Prediction	Uses a machine-learning genetic algorithm such as regression adaptation and range specification to select a set of rules that best predicts the distribution of species	p/a	Argued to give accurate assessment of distribution for organisms capable of dispersal; "black box" algorithm, no way to analyse contributions of individual predictors to the model, hard to interpret	+	Stockwell and Peters (1999), Reiss *et al.* (2011)
GDM, Generalized Dissimilarity Modelling	Designed to model spatial turnover in community composition, combines matrix regression and generalized linear modelling, allowing it to model non-linear responses to the environment that capture ecologically realistic relationships between dissimilarity and ecological distance	p/a	Community-modelling method—based on that, important subtle environmental trends may only be apparent in the response of multiple species and rare species are hard to model otherwise	−	Elith *et al.* (2006)
ENFA, Ecological Niche Factor Analysis	Compares statistical distributions of predictors for presence locations with that of wider geographic area. Factors are successively extracted by maximizing ratio of the variance of the global distribution to that of species distribution	p	Resulting factors have ecological meaning of "marginality" and "specialization". Requires good survey coverage for accurate prediction	−	Valavanis *et al.* (2008), Galparsoro *et al.* (2009), Valle *et al.* (2011)
CART, Classification and Regression Tree	Non-parametric decision tree learning technique based on recursive binary partitioning; a set of nodes expressed in terms of predictors defines the predicted value of the response variable at the end of the leaf. Splits are determined by minimizing the sum of squared residuals or the misclassification rate within the resulting groups	p/a	Appropriate for all types of variables, minimum assumptions about the model form; but erroneous near region boundaries, small data change may lead to significant model change, data fragmentation	++	Pesch *et al.* (2008)
RF, Random Forest	Uses collection of decision tree models to achieve top predictive performance	p/a		+	Wei *et al.* (2010), Reiss *et al.* (2011)
BRT, Boosted Regression Trees	Boosting algorithm uses iterative forward stage wise modelling. Final model is developed by progressively adding simple CART trees by re-weighting data to emphasize cases poorly predicted by previous trees	p/a	Ability to handle different types of variables and missing values, fitting interactions between predictors, immunity to extreme outliers	+	Leathwick *et al.* (2008)
BNs, Bayesian Belief Networks	Estimates the probability that a hypothesis is true given the data, and defines that probability as the degree of belief in the likelihood of an event. Classical statistical approaches estimate the probability of the data given a hypothesis, and the probability is defined as the relative frequency of an observation	p/a; all kinds of data (nominal, ordinal, continuous), e.g. multiple sets of geospatial data	Probabilities can be combined and quantified using empirical data, statistical associations, mathematical representations, and probabilistic quantities derived from expert knowledge	−	McCann *et al.* (2006), Stelzenmüller *et al.* (2010)
Mechanistic models	Translate environmental conditions into biologically relevant metrics, capture environmental sensitivities of survivorship and fecundity and use energetic to link environmental conditions and demography (i) incorporating models of species migration—ability of a species to occupy suitable habitat in new locations; (ii) linking models of landscape disturbance and succession to models of habitat suitability; (iii) fully linking models of habitat suitability, habitat dynamics and spatially explicit population dynamics	p/a	Integration of information from mechanistic models has the potential to improve the reliability of correlative predictions, e.g. in the context of range-shifting/invasive species; approach is only feasible if the life history parameters and habitat requirements of the species are well understood	−	Elith *et al.* (2006), Buckley *et al.* (2010), Franklin (2010)

Table 1. *Continued*

Modelling technique	Description	Data requirements	Pros and cons	Marine application	Exemplary references
Ordination methods	Detect interrelationships in species/communities and environmental data; unconstrained ordination methods for the analysis of community data based on Euclidean distance PCA (principal component analysis), DCA (detrended correspondence analysis), RDA (redundancy analysis), methods that perform weighted linear mapping based on χ^2 distances between predictors and dependent (species) variables, e.g. CCA canonical correspondence analysis; (n)MDS multidimensional scaling	p/a, community data, environmental data	Not strictly used for SMD, but provides knowledge of how environmental factors shape benthic habitats and communities	++	Buhl-Mortensen et al. (2009), Gogina et al. (2010a), Moore et al. (2010)

can be assessed by using, e.g. the AUC (area under the receiver characteristic curve), κ, or the true skill statistic, the validity of these commonly used performance measures is still arguably (e.g. Lobo et al., 2008). The measures are influenced *inter alia* by the quality and nature of absence data, the testing data and simply by the spatial extent of the modelled area (Guisan and Thuiller, 2005). For example, a distribution model for a stenotypic species with a restricted distribution range is bound to get a higher performance index when built on a large spatial scale with widely ranging environmental gradients (including the narrow range of environment where this species is thriving) than when built on a smaller spatial scale. However, the large-scale model is not better than the small-scale one. Thus, extending the study area by including non-suitable areas will inevitably result in better performance indicators without improving the actual distribution predictions (Lobo et al., 2008).

A central aspect of uncertainty during the modelling procedure is to which extent the realized or the fundamental niche is modelled. Statistical models are using the actual occurrence, which represents the realized niche at a given time, but do not necessarily perform well when predicting the fundamental niche. The occurrence of sink populations, for example, where the species cannot establish a stable population and only survives for a limited time span due to recruitment from other source populations, may further contribute to the uncertainty of describing the realized niche (Pulliam, 2000; Hansen, 2011). While the knowledge concerning the realized niche can satisfactorily be used in, for example, management approaches with a goal to ensure for an immediate protection of endangered species, the knowledge concerning the fundamental niche may be essential when predicting future changes in distribution. Besides the dispersal limitations, the main process that defines the realized niche of a species is the interaction with other species in the ecosystem. At present, there are only few methods available to include species interactions in DM. These range from relatively simple qualitative linkages between species to more complex quantitative linkages including resource stocks (see examples limited to plant and terrestrial species reviewed in Kissling et al., 2012).

Caution is also needed when the predictions of distribution probability need to be transferred into a simple binary distribution map to differentiate between modelled absence and presence of a species as often required by ecosystem management. In this case, a threshold probability level can be applied to set the cut-off value beyond which a feature is expected to be present. The common procedure of simply using a probability of 0.5 as a threshold was often found to be a less suitable choice, while alternative methods can give more reliable results (Liu et al., 2005; Freeman and Moisen, 2008). The ultimate choice of thresholds should always be based on the specific management objective, e.g. using a threshold with low sensitivity, if the actual presence of the species is more important than identifying the full range of potential habitats (e.g. for delineation of marine protected areas, MPAs). Freeman and Moisen (2008) therefore suggested that the DM outputs should initially be provided as continuous probability maps enabling the application of those threshold levels suitable for the specific management objectives.

Despite some limitations and the consequent need for cautiousness, statistical DM can provide essential information regarding the spatial distribution together with a correlative insight into the environmental drivers restricting the distribution, although it needs to be emphasized that statistical relationships cannot reveal any causality. Thus, the major assumption of statistical models that limits an accurate prediction of range dynamics is that processes setting the limits of the range remain fixed in space and time—and that

assumption will probably not hold when making dynamic predictions (Dormann, 2007; Sinclair *et al.*, 2010).

Most DM studies in the marine environment focused on the presence/absence, but a more quantitative approach by mapping modelled densities (abundance or biomass) would be considerably more informative (Bučas *et al.*, 2013). "Factor ceiling" (Thrush *et al.*, 2003), quantile regression (Cade and Noon, 2003; Vaz *et al.*, 2008), and machine-learning methods recently introduced for DM such as random forest and boosted regression trees (Table 1) are also considered here. Generally, regression methods such as GLM potentially provide predictive capability and machine-learning methods such as those using regression trees are often more useful for mapping and description of patterns. While statistical DM can already be applied in (marine) management, a future coupling of the results of such modelling exercises with species ecological attributes (e.g. filtration rates, bioturbation modes, etc.), via biochemical or sediment transport models, would allow assessing the benthic ecosystem functioning, thereby providing better knowledge for sustainable ecosystem management.

Furthermore, mechanistic models will provide more accurate distribution predictions (Buckley *et al.*, 2010). Generally, such models include those that translate environmental conditions into biologically relevant metrics, capture environmental sensitivities of survivorship and fecundity, as well as using energetics to link environmental conditions and demography (Table 1). The integration of information from mechanistic models has the potential to improve the reliability of correlative predictions when used in the context of range-shifting non-indigenous species (Elith *et al.*, 2010). Up to now, the application of DM based on a mechanistic approach that explicitly capture hypothetical biological processes is rare in the marine realm and their representation in the benthic environment is limited (Saraiva *et al.*, 2011; Sara *et al.*, 2013). The main reasons here are that there is still relatively poor knowledge of species interactions among benthic organisms (e.g. Ordonez *et al.*, 2013). Even trophic interactions can often not be quantified at the detailed level needed for DM, because benthic invertebrate diet is hardly studied and knowledge on the predation of benthos by demersal fish often only contains information with low taxonomic resolution. This strongly promotes the development and expansion of applications of such models and supports the need for enhanced research into the basic ecology of benthic organisms.

Bayesian BNs can be classified as the third approach (Stelzenmüller *et al.*, 2010). BNs differ basically from classical statistical DM methods. BNs estimate the probability that a hypothesis is true given the data, and defines that probability as the degree of belief in the likelihood of an event to occur (Table 1). Classical statistical approaches estimate the probability of the data given a hypothesis, where the probability is defined as the relative frequency of an observation (Franklin, 2009). BNs are models that graphically and probabilistically represent correlative and causal relationships among variables, and the most clear strength is that probabilities in the model can be combined and quantified using empirical data, statistical associations, mathematical representations, and probabilistic quantities derived from expert knowledge (McCann *et al.*, 2006). Within such frameworks, uncertainty can be accounted for to a large extent and the assessment of "what if" scenarios for planning objectives makes these a promising tool for marine ecosystem management.

In conclusion, while widely applied statistical methods have indeed been successfully applied in marine management, DM tools such as mechanistic models and Bayesian BNs are at the brink of taking DM in a marine management setting to a next step in DM performance and power.

Biological data

Most studies focus on single species, but also functional traits (e.g. filter-feeders), indices of biodiversity (e.g. species richness, rarefaction), global community descriptors (e.g. overall biomass or abundance), or community distributions. All of these faunal characteristics are possible response variables for DM. Single-species modelling already proofed to be useful in a management context by predicting the distribution of key species (e.g. Galparsoro *et al.*, 2012; Rengstorf *et al.*, 2012).

Besides its input as response variable, biological data may however also function as a predictor variable to construct statistical models, which is far less explored in the marine environment. This section focuses on the three most prominent issues associated with the performance of DM in the marine environment. The main issues are associated with: (i) data sufficiency, (ii) spatial and temporal bias, and (iii) spatial and temporal scale.

Adequate spatial coverage for modelling species distributions calls for a sufficient biological sampling. The sampling effort of biological data still is time and costly in the marine context when compared with the terrestrial realm. As a consequence, sampling effort of marine biological data generally has a relatively low spatial resolution and is often biased towards shallow sites close to the coast (Phillips *et al.*, 2009; Robinson *et al.*, 2011) and driven towards politically, socially, and economically interesting areas (e.g. important fishing grounds, MPAs). Most shortcomings in the model quality are based on paucity of data, spatial inaccuracy, and lack of valid absences (Guisan *et al.*, 2006a). There has been evidence that predictions based on few records do not perform equally well when compared with those predictions undertaken on a large dataset. This can be explained mainly because: (i) the uncertainty levels are dependent on parameter estimates (means, medians, etc.) and hence increase with decreasing sample size, (ii) the outliers gain more importance, (iii) the species ecological niches are highly complex in dimensions and small sample sizes are insufficient to allow for a description of a species niche over various environmental and biological gradients, particularly because (iv) species niches are often skewed or multimodal shaped (Wisz *et al.*, 2008 and references therein). Further, data sufficiency depends on the purpose/complexity of the model (Guisan *et al.*, 2006a; Wisz *et al.*, 2008). Qualitative sampling as often is the case in marine benthos research (e.g. trawling for epibenthos) restricts the type of the response to the presence/absence or presence-only, unavoidably resulting in the prediction of the probability of occurrence. Responses such as abundance or biomass reveal more information than occurrence predictions only (see above), but they have higher requirements on data quality that are less frequently met in the marine realm (Vierod *et al.*, 2014).

The spatial bias is particularly problematic if presence-only or pseudo-absence/background data are used for modelling (Wisz and Guisan, 2009; Lobo *et al.*, 2010). This may result in an environmental bias which may lead to inaccurate models because of the difference in the observed occurrence of species and background sampling (Robinson *et al.*, 2011). Real absence data are often lacking in the marine environment, although they would contribute to model accuracy (Phillips *et al.*, 2009) and would allow an evaluation of the predictions, i.e. standard measures for model evaluation (e.g. κ, AUC) do not work for presence-only data (*sensu* Guisan *et al.*, 2006b). Especially for benthic systems, the use of presumed absence data (i.e. the species was not found in the sample) can

also be misleading, since often the standard benthos sampling does not allow drawing final conclusions about the absence of a species because of limited sample sizes, lack of appropriate replication, or limited efficiency of the sampling gear. However, techniques to evaluate the goodness-of-fit for presence-only-based prediction such as the Boyce index (Boyce *et al.*, 2002) are under development (see Hirzel *et al.*, 2006; Skov *et al.*, 2008). Besides the spatial bias, data often contain a temporal bias too. Marine data are difficult to gather and DM input data are hence often taken from varying data sources over different years and sampling seasons. According to Guisan *et al.* (2006b), models using spatially and temporally heterogeneous samples contain an unknown level of bias and error.

Detailed knowledge on species-specific biological characteristics is basic for DM as these too may affect model accuracy (Reiss *et al.*, 2011). Predictors for spatial distribution differ as large-scale environmental predictors such as hydrography, current regime, and climate are more important for the mobile megafauna (e.g. Guisan and Thuiller, 2005) or large and sessile filter-feeders (e.g. Buhl-Mortensen *et al.*, 2010), while local environmental predictors with a more pronounced small-scale heterogeneity (e.g. sediment characteristics) might be of greater importance for smaller sedentary infaunal or less mobile species. There is further evidence that biological factors and interactions might become more important locally than on larger scales (e.g. landscape scale; Gogina *et al.*, 2010a; Nyström Sandman *et al.*, 2013). As introduced in the Modelling methods and associated uncertainty section, biological predictor variables are mostly not or insufficiently taken into account in DM (Elith and Graham, 2009). However, distribution of habitat forming species, migratory behaviour, dispersal range, species aggregation, and interactions are of specific importance in modelling the distribution of a species (Guisan *et al.*, 2006b; Kissling *et al.*, 2012). The use of biological predictors alongside the classically used physico-chemical variables is likely to increase DM performance. Compared with the terrestrial ecosystem, most marine species either have mobile adult stages (megafauna, fish) or mobile early life stages (pelagic larvae) and their dispersal ranges can be large, given the major physical continuity in the marine ecosystem (Guisan *et al.*, 2006b; Reiss *et al.*, 2011; Robinson *et al.*, 2011). Consequently, the role of environmental factors determining the distribution may even change during the life history of a species (e.g. De la Moriniere *et al.*, 2003). During the pelagic larval phase, hydrographic parameters of the water column might be most important, while the benthic phase might be more influenced by parameters acting more directly on the seabed. The inclusion of such dispersion features, influencing species distribution patterns by neighbouring spatial dependencies, i.e. spatial autocorrelation, will again add to the DM performance (Legendre, 1993; Guisan *et al.*, 2006b; Gogina *et al.*, 2010a; Robinson *et al.*, 2011).

DM performance would further profit from the incorporation of species interactions (Soberón, 2007), constituting the biological base of ecological functioning (May, 1983). Hence, species distributions are not solely shaped by the environmental setting but to a large extent by biological factors. Besides environmental conditions, particularly trophic interactions are the main forcing factors for the occurrence, distribution, and behaviour of organisms (MacArthur, 1955; Cohen, 1978; Pimm, 1982). The lack of knowledge on marine benthic interactions (e.g. trophic interactions) however hampers their incorporation into DMs. The fact that most marine benthic species feed on a variety of different food sources or prey species (omnivory; Link, 2002), as such hampering an unequivocal quantification of trophic linkages, further complicates its incorporation

into DM; this is in contrary to, for example, species-specific pollinator–plant interactions in terrestrial systems.

Finally, the biological factors themselves may affect environmental predictors, as species may change their own and the other species habitat as "ecosystem engineers" (Jones *et al.*, 1994; Pulliam, 2000). For example, species that occur gregariously or colonially may significantly change the surrounding habitat and associated species (e.g. Buhl-Mortensen *et al.*, 2010; Rabaut *et al.*, 2010; Quattrini *et al.*, 2012). Hence, DM of life history or biological traits such as, for example, reproduction, mobility, maturity, bioturbation, and feeding modes, deserves more attention as these traits are significant determinants of ecological functioning of benthic systems, and consequently important descriptors for a sustainable management of marine services and goods (Tillin *et al.*, 2006; Bremner, 2008; Braeckman *et al.*, 2014).

Environmental data and anthropogenic pressures

Environmental data constitute the fundamental basis of DM. For marine ecosystems, the availability of large-scale environmental data has significantly improved in the last decade, because of increasing research activities by using habitat mapping and remote sensing techniques, for example, to develop seabed habitat classifications based on the relation between benthic organisms and the seabed environment such as EUNIS (Davies *et al.*, 2004; Galparsoro *et al.*, 2012). These environmental predictors however tend to be temporally more dynamic in the marine realm compared with terrestrial systems, with a significant short-term (e.g. currents) or seasonal variability (e.g. temperature, primary production), which makes their application in DM challenging (Franklin, 2009).

To be useful in a modelling context, the selected environmental predictors should ideally represent limiting factors, resources, or disturbances (natural or anthropogenic) causally linked to the species and its habitat (Guisan and Zimmermann, 2000; Guisan and Thuiller, 2005; Elith and Leathwick, 2009). Causal predictors used to model benthos distribution are, for example, temperature, salinity, or primary production (Table 2), whereas others rather represent surrogate factors such as, for example, water depth or in some cases substratum, which may be indirect proxies integrating several predictor variables. The causality of the relationships between benthos and the marine environment are however often not understood in detail, mainly because most of our understanding is based on correlative approaches and experimental studies are scarce, which may reflect the poor representation of mechanistic DM in the marine environment (see the Modelling methods and associated uncertainty section). DM, especially those based on statistical approaches, should hence be considered an indicator of possible causalities rather than an identifier of such cause–effect relationships, and should hence trigger further basic research on cause–effect relationships.

When zooming into environmental predictors, substratum or bottom type is one of the key features driving the presence of benthic marine organisms and it has therefore often been used to predict the distribution of bottom fauna. For soft bottom sediments, grain size composition is commonly used (e.g. Ysebaert *et al.*, 2002; Degraer *et al.*, 2008), while more specific sediment parameters such as sediment sorting, porosity, or cohesiveness are rarely measured in the field and are consequently not often used in marine DM. For hard bottoms such as bedrock, boulder, and gravel fields, the fraction of gravel or boulders based on visual inspection and size and orientation of rocks or the space available between rocks are more relevant descriptors. Several techniques ranging from direct observations to

Table 2. Environmental variables relevant for DM of marine benthos.

Environmental variable	Common types of measurement	Remarks
Substratum	(i) Swathe techniques	(i) Reliability depends on ground-truth sampling density
	(a) Backscatter from multibeam echosounder	(ii) Can be used in a stand-alone way to provide interpolated maps (e.g. grain size distribution)
	(b) Sidescan sonar mosaics	(iii) Used to ground-truth swathe techniques rather than *per se* (hard to discriminate fine sediment categories)
	(ii) Samples: point measurements (grab or corer)	
	(iii) Visual mapping: camera/video	
Sea surface temperature	(i) Satellite, point measurements, hydrodynamic models	(i) Seldom relevant to bottom fauna except in shallow waters
		(ii) Used to identify major biogeographic regions
Bottom temperature	(i) Hydrodynamic models validated by point measurements	(i) Resolution in space and time is often coarse; however, new detailed models have been developed
		(ii) Many observations needed to cover variability
Salinity	(i) Hydrodynamic models	(i) Coarse resolution often not relevant to benthos
	(ii) Point measurements	(ii) Many observations needed to cover seasonal variability in shallow coastal areas
Depth	(i) Point measurements	(i) DTM (Digital Terrain/Elevation Model) obtained from assembling raster and point clouds sources
	(ii) Swathe bathymetry (see "Substratum")	
Light energy	(i) Satellite imagery	(i) Two parameters can be retrieved:
	(ii) Point measurements (e.g. Secchi depth)	(a) Fraction of incident light
		(b) Energy in mol photons reaching seabed
Primary production (water column)	(i) Satellite imagery	(i) Only surface waters covered by satellite imaging
	(ii) Hydrodynamic models	(ii) Coarse resolution in space and time of model output
Hydrodynamics	(i) Hydrodynamic models [e.g. (tidal) currents, bottom shear stress]	(i) Often coarse resolution in space and time of model output
	(ii) Acoustic Doppler Current Profiler (ADCP)	(ii) Local application only for ADCP

remote sensing, including acoustic techniques, may be used to qualify the substratum type (Brown *et al.*, 2011). Shallow sediments in areas experiencing high water dynamics or ice scouring may change after storms or the winter season. Below 100 m depth, sediments are normally stable. However, the hydrographic conditions around underwater canyons and seamounts as well as strong tidal-driven currents or internal waves may still generate sediment transportation also in deep waters. Except for local studies where substratum data can be collected, modelling large sea expanses requires collating and harmonizing data from various studies undertaken at different times. A key requirement of such data assemblages is hence to provide users with a confidence map, which enables them to use the data with full awareness of its reliability.

The characteristics of soft bottom substrates are often closely related to the local hydrodynamic regime and as such might rather act as an indirect proxy for the hydrodynamic predictors than being a truly independent predictor. On a larger scale, the bathymetry is an essential predictor for the composition of bottom communities. The bathymetry however also has a direct bearing on physical parameters acting on the seabed such as substratum, light, wave energy, salinity, and temperature. Depth can hence also be used as an indirect proxy for causal drivers. Thus, the selection of functionally more relevant predictors should be prioritized over indirect proxies (Elith and Leathwick, 2009), but especially in marine environments, DM is often by necessity driven by those predictors, which are readily available.

Bathymetry derivates, i.e. seabed morphological characteristics such as slope, aspect, or rugosity, further include crucial environmental descriptors that have proven useful to identify suitable habitats (Buhl-Mortensen *et al.*, 2009; Galparsoro *et al.*, 2009). The value of these derivates is however highly dependent on the spatial resolution of the bathymetric information (Rengstorf *et al.*, 2012).

Other major oceanographic drivers for marine species distribution comprise, for example, light energy, hydrodynamic energy, salinity and temperature, and of more local importance variables such as the oxygen concentration, nutrients, etc. The impact of light onto the benthos is particularly straightforward as it determines the depth to which benthic macrophytes (kelp, seaweeds, seagrass) can grow or photosynthetic primary production can occur (Carlström *et al.*, 2009; Knudby *et al.*, 2013; Saulquin *et al.*, 2013). The same goes for salinity, which is particularly important in shallow and estuarine environments where freshwater input may be substantial. The salinity gradient within the Baltic Sea is a good example of how salinity steers the distribution of species (Zettler *et al.*, 2014). The effect of hydrodynamic energy from waves and currents exerted on the seabed and benthos is more complex (Galparsoro *et al.*, 2013), yet basic to the seabed stability and substratum composition (including deposited and suspended food particles for benthic organisms). While extreme events can substantially modify the seabed (e.g. heavy storms), they usually act on the seabed by a regular action, which is best characterized by parameters computed on long time spans (Dolbeth *et al.*, 2007). The inclusion of hydrodynamics into

DM is most relevant to rocky substrata, since the composition of mobile sediments typically reflect the local hydrodynamic regime and can be considered as a surrogate variable for hydrodynamics. Seabed energy parameters are derived from hydrodynamic models. Although they are often of low spatial resolution with respect to seabed heterogeneity, especially in the coastal-zone, a lot of progress is currently being made (e.g. Chen *et al.*, 2009). Unfortunately, information on currents and particle transport in the benthic boundary layer—most relevant to benthic organisms—is poor and highly demanding to map and monitor. Temperature finally takes a special position because of its large-scale structuring relevance (Glémarec, 1973) combined with its central position within the ecological impact of climate change. Together with salinity, it defines the hydrographic setting which is used to define different water masses and depth zones. It further strongly affects oxygen concentration and consumption in the benthic environment where hypoxia is often related to year maxima in bottom water temperature (Quiñones-Rivera *et al.*, 2010). From a DM perspective, sea surface temperature may be a good proxy for the entire column where the water column can be considered homogenous, i.e. mixed waters (Méléder *et al.*, 2010). Other factors which may be relevant locally such as the oxygen conditions at the seabed (Reijonen *et al.*, 2008) or the influence of pelagic environment variables such as primary production (Holt *et al.*, 2012) in the surroundings of the benthic samples locations may also be examined where appropriate.

Anthropogenic impacts may also be considered environmental predictors in a DM context, although many impacts are relevant mainly on a local scale. The use of DM to map and monitor animal and plant distributions has become increasingly important in the context of awareness of environmental change (natural and anthropogenic) and its ecological consequences (Miller, 2010). Key activities which can have a significant impact on marine ecosystems at the regional or local scale include (recreational) fisheries, dredging, renewable energy developments, industrial and sewage effluents, hypersaline water discharge from desalination plants, aquaculture, diseases, coastal engineering (habitat alteration), and point-source pollution (Halpern *et al.*, 2008). Many of these activities primarily affect intertidal and nearshore ecosystems rather than offshore or deep-sea ecosystems, which suggests that predictive modelling and cumulative estimates of impacts are often conservative particularly for nearshore areas. The analytical process of DM provides flexible tools for regional and global efforts to allocate conservation resources, to implement ecosystem-based management, and to inform MSP, education, and basic research (Halpern *et al.*, 2008). Among the impacts with a large spatial extent, acidification (or climate change), fisheries, and eutrophication are probably the most important ones. Bottom trawling is one of the most widespread sources of physical disturbance on habitats and organisms on continental shelves throughout the world (Jackson *et al.*, 2001; Kaiser *et al.*, 2002). Vessel Monitoring Systems (VMS), introduced for fisheries recording and control, is now widely implemented and increasingly used as a proxy for fisheries activity and hence impact from bottom gears. Yet, several approaches have been developed to analyse VMS data, all having their strengths and weaknesses (Lee *et al.*, 2010; Lambert *et al.*, 2012). The lack of freely accessible VMS data, e.g. across state boundaries, however currently hampers its applicability within DM (Hintzen *et al.*, 2012).

Application of DM

The potential applications of DM in an ecosystem management context are manifold, ranging from MPA delineation to incorporation into complex marine spatial management frameworks (Gimpel *et al.*, 2013; Stelzenmüller *et al.*, 2013). This review focuses on four main applications where DM already plays an important role in marine systems or provides promising new management applications (Figure 1).

Marine spatial planning

As shown in the introduction, the incorporation of the ecosystem-based approach into, for example, MSP requires that all aspects of value associated with marine biodiversity are incorporated into the decision-making process (Rees *et al.*, 2010), which is called ecosystem-based marine spatial management (EB-MSM, *sensu* Katsanevakis *et al.*, 2011). A key goal of EB-MSM is to maintain the delivery of ecosystem services, which must be based upon ecological principles that articulate the scientifically recognized attributes of healthy functioning ecosystems (Foley *et al.*, 2010). These authors have proposed four main ecological principles: maintaining or restoring native species diversity, habitat diversity and heterogeneity, key species, and connectivity. Hence, it is critical to understand the heterogeneity of biological communities and their key components (e.g. most important predators, habitat-forming species), and key processes (e.g. population connectivity, interaction webs, biogeochemistry) that maintain them, as well as human uses (Crowder and Norse, 2008). The successful development and implementation of EB-MSM hence necessitates the use of best available science. As stated by Katsanevakis *et al.* (2011), new tools, such as, for example, geospatial analysis, remote sensing, and molecular techniques, have broadened the understanding of the linkages between marine habitats and population dynamics, and between spatio-temporal dynamics and the functioning of marine ecosystems (Crowder and Norse, 2008). Hence, DM does play and will continue playing a key role in MSP and EB-MSM.

The spatially explicit nature of the DM makes this approach of special interest for different aspects of the MSP. Scientific knowledge obtained from DM approaches could be applied in different ways in the MSP process, as it has been used to map the potential distribution of biological resources (see examples for habitat suitability of lobster from Wilson *et al.*, 2007; Galparsoro *et al.*, 2009), fish habitat modelling and evaluation (Koubbi *et al.*, 2006; Monk *et al.*, 2011), species of special interest for conservation, such as gorgonians (Bryan and Metaxas, 2007; Etnoyer and Morgan, 2007), marine mammals (Panigada *et al.*, 2008) or seabirds (Skov *et al.*, 2008), selection of suitable areas for aquaculture and farming (Cho *et al.*, 2012), and conservation of biodiversity by providing information on the ecological requirements of species at risk (Hare *et al.*, 2012; Millar and Blouin-Demers, 2012). DM and mapping hence support conservation planning, MPA selection and management plan development, mapping suitable sites for reintroductions, and restoration (Bos *et al.*, 2005; Bekkby *et al.*, 2008; Valle *et al.*, 2011). The most extended application of DM in marine systems most probably is in planning for MPAs and designating essential fish habitats (see examples in Leathwick *et al.*, 2008; Valavanis *et al.*, 2008; Maxwell *et al.*, 2009). When combined with climate change scenarios, DM results can further reveal estimations of the expected changes in protection efficiency of designated MPAs (Gormley *et al.*, 2013). Hence, DM results can be used to estimate (or have an approximation of) the potential impact of certain human activities to provide advice for an ecologically sound allocation of these activities (considering also the type of impact: habitat physical destruction, hydrological or temperature regime modification, etc.). DM may thus facilitate minimizing environmental

impact and maximizing the socio-economic benefit of marine goods and services (Salomidi *et al.*, 2012); aspects that are basic to the MSP.

DM greatly assists in defining management objectives and improving the understanding of species ecology (Robinson *et al.*, 2011). Their applications provide highly useful information (Guisan and Thuiller, 2005), among others: ecological hypotheses to be tested (Leathwick *et al.*, 2008), unsurveyed sites of high potential occurrence for rare species to be determined (Engler *et al.*, 2004; Guisan *et al.*, 2006a), and species invasion and proliferation to be assessed (Beerling *et al.*, 1995; Peterson, 2003). Their output, the habitat suitability map, could support conservation planning and MPA selection and support management plans for species recovery by mapping suitable sites for reintroduction, as mentioned before.

Monitoring designs

The main purpose of DM is to inter- or extrapolate from point observations in space and time to predict the occurrences in an area where no survey data are available or the coverage is limited. DM predictions hence complement the monitoring, but equally, the predictions can also be used to guide the monitoring strategy development (Bijleveld *et al.*, 2012; Crall *et al.*, 2013; Van Hoey *et al.*, 2013). The latter is especially important for marine environments, where the logistical effort and the costs for monitoring are substantially higher compared with monitoring in terrestrial environments. The monitoring data used for DM in marine waters are often based on heterogeneous data sources, where no specific design could be set up before the sampling (Degraer *et al.*, 2008). In such cases, there is a higher risk of predictions, biased particularly towards sites which were sampled more intensively (local project-based sampling) or logistical easily accessible (coastal areas). In other cases, the number of samples is limited because monitoring programmes often have multiple objectives, each with their own data needs and hence possibly compromising the optimal sampling design. Bijleveld *et al.* (2012) demonstrated that combining grid and random sampling is the most effective design in addressing a multitude of management applications including mapping of species distributions.

The benthic fauna and flora are monitored for various purposes, e.g. to detect general patterns of distribution with surveillance monitoring or to assess the effects of specific anthropogenic usages with operational monitoring (Gray and Elliott, 2009). In recent years, monitoring programmes on an appropriate spatial and temporal scale became specifically needed for the implementation of ecosystem-oriented management regulations such as the European Marine Strategy Framework Directive (MSFD), in which the central aim is to achieve Good Environmental Status for marine ecosystems (European Commission, 2010). The concerned biodiversity assessment criteria are largely related to, for example, species populations and habitat spatial extent, population structure, and benthic habitat condition (Rice *et al.*, 2012). When monitoring of species population dynamics, sampling effort can be reallocated to distribution "hot spots" identified with DM based on a regular sampling strategy, as illustrated for the bivalve *Ensis directus* (Houziaux *et al.*, 2011). DM predictions of species are furthermore useful to monitor the difference between the potential distribution area and the currently occupied area, which is essential for the evaluation of species/habitat area extent (Galparsoro *et al.*, 2009; Maxwell *et al.*, 2009). While DM cannot replace the actual monitoring, its predictions can be used to construct time- and cost-effective marine monitoring strategies for impact and ecological status assessments (Van Hoey *et al.*, 2013).

Such knowledge is essential to determine the locations and amount of samples needed to efficiently evaluate the ecological status. One central aspect of assessing the ecological status is defining reference conditions or baselines, which can be very difficult for marine benthic communities in regions with elevated and varied anthropogenic pressures. Although modelling approaches for hindcasting to a time before the impact were suggested as alternative methods when pristine areas are not available (Borja *et al.*, 2013), DM has probably only little to contribute to baseline definition, since necessary historical environmental data are not available usually. However, for those species which are used as indicators for baseline conditions, DM can be applied to forecast the changes in distribution in relation to large-scale environmental changes such as global warming (Hering *et al.*, 2010). This knowledge is especially important since management action would be unsuccessful, if the cause of change is related to these large-scale climatic effects, which cannot be targeted by local management.

However, most monitoring programmes in marine benthic environments are tasked with assessing benthic habitat condition [e.g. within Water framework Directive (WFD) and MSFD] and ascertaining benthic changes over time. In conclusion, although the use of DM can help directing monitoring effort towards *inter alia* important habitats or species or designing efficient monitoring programmes, it is clear that the DM will never be able to replace the actual monitoring programmes (Valle *et al.*, 2013).

Non-indigenous species

The introduction of non-indigenous species is of specific concern for marine ecosystem management, because these species can considerably affect marine ecosystems and biodiversity by, for example, altering native communities, and may even cause severe economic damage when the species become invasive (Olenin *et al.*, 2011). The non-indigenous green algae species of the genus *Caulerpa*, for example, have now spread throughout major parts of the Mediterranean Sea (Meinesz *et al.*, 2001). The non-indigenous and invasive Pacific oyster (*Crassostrea gigas*) has been shown to affect blue mussel (*Mytilus edulis*) beds in the Wadden Sea and elsewhere (Diederich, 2005; Markert *et al.*, 2010; Jones *et al.*, 2013). Once established, it is difficult, if not impossible, to extirpate or manage the spread of non-indigenous species. Therefore, early warning systems are currently in the focus of marine management strategies and suitable monitoring schemes for non-indigenous species in the marine ecosystems need to be implemented. Non-indigenous species-targeted DMs may play an important role here.

A common approach to the risk of invasion is to model the ecological niche of a species based on the occurrence within its native distribution and then to apply this model in other regions to identify potential (vulnerable) habitats. In the terrestrial environment, Thuiller *et al.* (2005) have used climate niche modelling results of endemic species from Africa to predict the potential global distribution of introductions of these species. Thus, the vulnerable habitats can be determined even before the potentially invasive species are invading the region. Monitoring schemes within an early warning system could use this information to focus the monitoring effort on these vulnerable habitats. However, such approach only poorly accounts for the early phases of introduction into marine environments, which are often associated with the major shipping pathways (e.g. harbours). Next to precautionary management measures, this might be the only stage (in marine environments) where management action can be successful in regulating the introduction of non-indigenous species.

Given the vast number of potential invaders in marine ecosystems, DMs may further serve as a tool to distinguish species with little potential from those with higher potential to invade a specific region and to prioritize management and monitoring efforts (Simberloff *et al.*, 2005). This might be an unrealistic approach for marine environments, because the availability of environmental data on a global scale still is a problem for a wide application of DMs in marine benthic environments. Thus, the lack of sufficient environmental data hampers the potential use in early warning approaches, for which environmental data are not only needed for the invaded, but also for the native region. To our knowledge, no case study on marine benthos using DMs in such a context was carried out so far.

Although species distribution models calibrated for the native range of a species and extrapolated to regions where the species occur as an invasive species is common practice in terrestrial environments, it is based on the assumption that the invasive species conserve their ecological niche in the invaded region. Usually, this might be a reasonable assumption, but it was already shown that a shift of the climate niche occurred between native and non-native ranges of plant species (Broennimann *et al.*, 2007). In this case, only the earliest colonization pattern was predicted correctly, which at least highlights the value of DMs for early warning systems.

The spatial spreading of non-indigenous species can also be modelled using occurrence data of the invaded ecosystem. Of course, this approach can only be applied when the species already colonized the ecosystem and, thus, cannot be used within early warning strategies. It can however still provide valuable information about the ecological niche of the non-indigenous species and hence its possible future spatial extent (Verween *et al.*, 2007; Azzurro *et al.*, 2013; Jones *et al.*, 2013; Neumann *et al.*, 2013). Although such approach may successfully predict the distribution of the invader, one should be cautious because of the inherent violation of the basic assumption of DMs that the species is in equilibrium with its environment (Václavík and Meentemeyer, 2012). On the one hand, the invasive species might not have colonized all the suitable habitats simply because of a lack of time for a wide dispersal, which would lead to an underestimation of the potential distribution. On the other hand, the current species distribution might have been supported by unusual environmental conditions for a short period. Thus, under "normal" conditions, the species might not be able to survive in these regions and the model outputs would result in an overestimation of distribution.

Future scenario predictions

Another major challenge for ecosystem management is to account for possible future changes of the environment in the management strategies. Climate scenario effects, for example, are currently in the focus of research efforts (e.g. Richardson *et al.*, 2012). The physical effects of climate change in marine environments mainly comprise shifts in temperature and salinity, alteration of hydrodynamics, sea level rise, and ocean acidification (IPCC, 2013). Benthic systems are directly or indirectly affected by these changes, which may result in changes in spatial distribution of species (Birchenough *et al.*, 2011; Valle *et al.*, 2014). Especially, the implementation of long-term ecosystem management measures, e.g. MPA designations, may benefit from a DM-based estimate of future changes in the ecosystem.

DMs provide a useful tool to predict the spatial distributional consequences of expected environmental changes such as climate change. In the terrestrial realm, different IPCC scenarios of climate change have been widely used to predict the future

distribution of several species and the consequences for ecosystem functioning and environmental management (e.g. Heikkinen *et al.*, 2006; Pompe *et al.*, 2008; Richardson *et al.*, 2010; Falk and Mellert, 2011). Future climate scenarios were also recently used to predict distribution shifts of marine benthic species (Cheung *et al.*, 2012; Jones *et al.*, 2013). Predictions of environmental changes based on IPCC scenarios are now indeed widely accessible for terrestrial and partly for marine environments, even on a global scale (Tyberghein *et al.*, 2012). Nevertheless, the dominant environmental factors influencing the benthos are acting on the seabed, for which large-scale data on the effects of climate change are still meagre. Especially for deep sea habitats, the conditions at the seabed differ substantially from the surface water and detailed hydrographic models focusing on the seabed or entire water column parameters are often restricted in their spatial extent (e.g. Ådlandsvik, 2008; Holt *et al.*, 2010). The same however also holds true, yet to a lower extent, for shallower habitats where especially the effects of changes in hydrodynamics (e.g. storminess) and sea level rise onto the benthic physical conditions are less straightforward, as such hampering large-scale applications of DM in predicting climate change-driven distribution shifts of benthic species (see Ready *et al.*, 2010).

With an increasing use of DMs in predicting consequences of climate change, a growing concern has emerged to improve the knowledge of uncertainty factors and to increase the reliability of predictions (Thuiller *et al.*, 2004; Botkin *et al.*, 2007). This is even more important in the context of climate change since an additional source of variability arises with the use of modelled climate scenarios. Widespread disagreement in the distribution predictions were found between DM methods when applied to extreme climate change scenarios (Elith *et al.*, 2010). Furthermore, major uncertainties related to prognostic species DM are that relevant processes such as species interactions, habitat change, and rapid evolutionary changes are not included in most of the modelling approaches (see above). Using DM for predicting future changes is associated with an unavoidable degree of uncertainty (Wenger *et al.*, 2013) and should always be done with precaution in an ecosystem management context: they should be interpreted as indications of possible future changes. These uncertainties may however partly be addressed by using multi-model procedures where the predictions of a variety of different models are taken into account to improve the robustness of the prediction. These methods are relevant both in DM and in modelling of climate change scenarios (Araujo and New, 2007; Jones *et al.*, 2013). The further incorporation of dispersal dynamics and species interactions into DMs will be specifically important to improve the robustness and reliability of climate change impact predictions (e.g. Cheung *et al.*, 2008).

Despite their relatively high level of uncertainty, DMs are among the best available tools to forecast the possible effects of climate change on benthic species distribution patterns and hence to steer present-day ecosystem management. Predictions of the expected changes in species distribution can be used *inter alia* to focus monitoring programmes towards the most sensitive regions or to identify key indicator species for long-term climate change monitoring (Cheung *et al.*, 2012).

Recommendations

Distribution models provide valuable full-coverage information on the distribution of marine benthic species, communities, and related entities inhabiting an environment that is usually difficult to assess and enable the prediction of distribution changes. On the

one hand, DM enables ecosystem managers to utilize spatial information that cannot be generated otherwise to a similar level of spatial resolution. On the other hand, the level of uncertainty is correspondingly high, and large-scale data for quality control are often insufficient. Thus, although DM is considered to increasingly constitute an essential tool for current and future ecosystem management, careful usage and interpretation are essential when applying the DM outputs in a management context.

1. Management approaches can only be successful if there is a causal link between the management objective and the implemented measure. However, the most commonly used statistical DM does not necessarily identify cause–effect relationships, which are crucial in a management context. Bayesian BNs is a promising method which considers both correlative and causal relationships, and provides good estimate of model uncertainty, (Stelzenmüller *et al.* 2010). Its application to the marine benthic realm is however rare up to now.

2. The statistical approaches used in DM are particularly effective in spatial interpolation, where proxy environmental predictors can be suitable to predict the present distribution patterns. However, for spatio-temporal extrapolation, e.g. predicting species distributions in a new area (e.g. early warning systems for invasive species) or time (e.g. climate change studies), cause–effect relationships need to be better understood. Therefore, corresponding predictions from correlative DMs have to be used with precaution, and multi-modelling approaches that incorporate models of species migration, combinations of correlative DM with dynamic ecosystem models, and spatially explicit population dynamics models will need to be developed (Franklin, 2010).

3. Potential causal environmental predictors are often not even included in correlative DMs due to mainly the lack of data availability. Especially for marine benthic ecosystems, some relevant predictors are often only available at a local scale (e.g. bottom water temperature, sediment characteristics), which hampers the large-scale application of DM. The early warning approaches for the assessment of the potential spread of non-indigenous species are specifically data demanding and large-scale environmental data are essential for these approaches. Initiatives such as Bio-ORACLE (Tyberghein *et al.*, 2012), MyOcean (Buongiorno Nardelli *et al.*, 2013), and MARSPEC (Sbrocco and Barber, 2013) are providing the first step towards the availability of large-scale environmental predictors, which are necessary for marine DM applications and will undoubtedly enable further developments.

4. Often, mechanistic models are used to predict the physico-chemical nature of the area that is then used as explanatory variable(s) in statistical DM (or in cases used as expert judgement) to describe or predict the biological response. The development of mechanistic DM approaches based on functional traits, physiological constraints, and dispersal capacity is particularly appropriate to address issues such as long-term sustainability of exploitation activities, evaluation of alternative rearing and management strategies, risk of dystrophic crises and algal blooms, effects of range-shifting and species, or even forecasting the impact of future climate (Buckley *et al.*, 2010; Elith *et al.*, 2010), although costly to design, calibrate, and validate. The prior use of correlative modelling techniques can in turn guide and optimize the application of the mechanistic models by suggesting particular traits or processes to consider and suggesting spatial limits of necessary runs (Vincenzi *et al.*, 2011).

5. One major drawback in using correlative DM is with regard to the missing incorporation of biological factors (such as feeding interactions, dispersal range, and migratory behaviour) into the modelling procedure. Although some methods are available to account for these factors, e.g. trophic interactions (Kissling *et al.*, 2012), the major scope for an increased knowledge of marine benthic ecosystems is delaying a further progress in marine DM. It is clear that more efforts including basic autecological research are required to sufficiently cover the biological factors in DMs.

6. Biological Traits Analysis recently facilitated assessing the functional diversity and roles of benthic species in marine ecosystems (e.g. Bremner, 2008; Darr *et al.*, 2014b). This type of approaches uses the information on selected ecological traits expressed by species to characterize the ecological functioning of the assemblages, and has been highlighted as a valid approach in the assessment and management of marine benthic systems (Bremner, 2008; Frid *et al.*, 2008). The combination of distinct relationships between species and both abiotic and biotic predictors with species autecological capacity (e.g. filtration rates) could help to model temporal and spatial ecosystem functioning with high resolution accuracy. This approach assumes that modelled distribution of benthic assets is expressed not only as probability of occurrence but rather as quantitative predictions (e.g. abundance or biomass). Recent studies (Wei *et al.*, 2010; Vincenzi *et al.*, 2011; Darr *et al.*, 2014a) have demonstrated that the combination of multivariate predictors and machine-learning algorithms (e.g. Random Forest) is better when compared with conventional regression models, especially when the aim is to model quantitative response variable (species abundance, biomass, or certain biological traits expressed in these units, potential yield of aquaculture, etc.). Generally, these models are most useful for purposes of spatial planning and identification of areas with different degree of suitability, e.g. for farming or endangered species. New case studies from different environments with application of these methods are urgently needed, which will help to obtain more technical experience and improve model performance and efficiency for management purposes.

In this review, it should be clear that despite the uncertainties and limitations mentioned, DM plays an important role in marine ecosystem management and its potential applications are manifold. DM is already very useful, will become even more useful in the future as current weaknesses will be tackled with new technical developments, but the application of DM in marine management will always require scientific expert advice. Thus, generic standardization and automated applications of DM for management purposes cannot be recommended as the choice of DM methods and prediction attributes need to be aligned with the specific management objectives and applications (Figure 1). DM results should of course be used with caution in decision-making by environmental managers. Despite the increasing number of applications and the improvement of the methods used, DMs still have their limitations (Guisan and Thuiller, 2005), especially in bridging between the managerial quest for simplicity and the integration of ecological theory (Austin, 2002). This actually may stimulate further development of DM to minimize this gap between management requirements and scientific integrity.

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