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## Benthos distribution modelling and its relevance for marine ecosystem management

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### Abstract:

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

68 **1. Introduction**

69 The marine ecosystem is known to be influenced by a combination of physical, chemical and  
70 biological components, which has a direct influence on the integrity of species and habitats.

71 The successful management of these systems require information from all its ecological  
72 levels. This need for ecological knowledge, the increased anthropogenic pressures on the  
73 marine environment (Halpern et al., 2008, Ban et al., 2010) and the potential for multiple use  
74 conflicts, have led to an increased interest in sea-use planning with particular emphasis placed  
75 on marine spatial planning (MSP) (European Commission, 2008, Douvere and Ehler, 2009).

76 Ecosystem management is often confronted with fragmented information on the spatial  
77 distribution of marine species and habitats, mainly this is because the marine environments  
78 are more difficult to access, and to monitor, when compared with terrestrial ecosystems  
79 (Robinson et al., 2011).

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

89 Monitoring the biotic components of the ecosystem is prohibitively expensive and requires an  
90 enormous effort to collect with point source data of species distributions over large spatial  
91 scales. Therefore, predictive methods have become important tools to overcome these issues

92 when looking at biotic aspects of the ecosystem components (Guisan and Zimmermann, 2000,  
93 Guisan and Thuiller, 2005). Distribution modelling (DM), which is also known as e.g. species  
94 distribution modelling, habitat suitability modelling, ecological niche modelling or  
95 bioclimatic envelopes, mainly refer to correlative approaches that use full spatial coverage  
96 data of environmental variables to explain and predict patterns of species distribution (Elith  
97 and Graham, 2009). These predictive modelling methods have been mainly used in terrestrial  
98 ecology to study general patterns of species distributions (Hengl et al., 2009), as well as for  
99 addressing conservation- and ecosystem management-related issues such as the delineation of  
100 protected areas (Valavanis et al., 2008, Elsäßer et al., 2013), the risk for species invasions  
101 (Gormley et al., 2011), and the prediction of distribution changes in response to climate  
102 change (Cheung et al., 2009). See also Guisan et al. (2013) for a comprehensive overview on  
103 the use of DMs in support of environmental management for terrestrial systems. The use of  
104 DMs in marine ecosystems is still in its infancy (Degraer et al., 2008), when compared to the  
105 vast number of studies applying DM in the terrestrial realm. Most of the existing DM studies  
106 in the marine environment have shown their application on conservation planning, method  
107 evaluation, theoretical ecology, climate change, species invasions, phylogeography and  
108 impact assessment (Robinson et al., 2011). Commercial fish were especially targeted by  
109 recent studies using DM in marine ecosystems (Venables and Dichmont, 2004, Maxwell et  
110 al., 2009, Moore et al., 2010, Lenoir et al., 2011, Jones et al., 2012). Benthic invertebrates  
111 have also been subject to DM, although their distribution is primarily modelled over local  
112 scales (Ysebaert et al., 2002, Thrush et al., 2003, Ellis et al., 2006, Degraer et al., 2008,  
113 Meißner et al., 2008, Willems et al., 2008, Galparsoro et al., 2009, Valle et al., 2011). There  
114 are some examples from larger scales e.g. Baltic Sea (Gogina et al., 2010b, Gogina and  
115 Zettler, 2010), North Sea (Reiss et al., 2011), Icelandic waters (Meißner et al., 2014) and  
116 worldwide (Ready et al., 2010, Wei et al., 2010, Davies and Guinotte, 2011). The results of

117 the above mentioned applications of DMs in the marine realm rendered insight into the  
118 correlative relationships between environmental drivers and benthos species distribution,  
119 allowing for full-coverage predictions of species and community occurrence. These outputs  
120 can be used to guide management decisions.

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

139 This review follows the consecutive steps in DM, discussing critical assets of using biological  
140 and environmental input data and their incorporation into the different DM methods (Fig. 1).

141 This paper does not intend to provide a complete overview of the different modelling

142 methods, but rather is seeking to emphasise some general applications and limitations of the  
143 models when used for marine benthic environments. We also present several examples where  
144 the applications of DM are relevant for marine ecosystem management, highlighting their  
145 general applicability, but also their limitations in applicability to management-related issues,  
146 e.g. monitoring and spatial planning, as well as their potential for future use (e.g. early  
147 warning systems).

148

## 149 **2. Distribution modelling methods and data requirements**

### 150 2.1 Modelling methods and associated uncertainty

151 There is a rapidly growing variety of methods used for marine benthic species and community  
152 distribution modelling, including both already widely applied and merely tested techniques.  
153 Detailed descriptions and more explicit lists can be found in advanced subject-specific text  
154 books (e.g. Legendre and Legendre, 1998, Zuur et al., 2012), reviews and object-specific  
155 comparative research papers (e.g. Guisan and Zimmermann, 2000, Guisan and Thuiller, 2005,  
156 Franklin, 2010, Robinson et al., 2011). Three major approaches have been used to predict  
157 species distribution patterns: (i) statistical (or correlative) stochastic models that estimate  
158 parameters based on empirical or phenomenological relationships between current distribution  
159 and environmental conditions, (ii) mechanistic (or structural dynamic) models that incorporate  
160 explicit ecological relationships independent of current distribution, with mechanistic  
161 components defined by physiological relevance, and (iii) Bayesian belief networks (see Table  
162 1; Guisan and Zimmermann, 2000, Sagehashi, 2008, Buckley et al., 2010, Stelzenmüller et  
163 al., 2010).

164 Statistical approaches are probably most often used for DM and a large number of methods  
165 are now available, of which several were successfully applied to marine benthos (Table 1).

166 Comparative studies showed that the performance of the different models can vary  
167 considerably, but it is also clear that no single model could be equally appropriate for all  
168 applications (e.g. Reiss et al., 2011, Valle et al., 2013). When deciding on the model selection,  
169 this needs to be adjusted according to the (management) objectives (Fig. 1). Applications of  
170 statistical modelling in marine context include testing hypotheses in relation to the ranges of  
171 species distribution along environmental gradients, generating habitat suitability maps that  
172 predict the specific ecological potential of a habitat (with limitations defined by the data  
173 analysed) and assessing the possible consequences of habitat changes (either natural or  
174 anthropogenic), as part of MSP and conservation management (Degraer et al., 2008, Robinson  
175 et al., 2011).

176 The main advantage of statistical DM is that they are conceptually simple, descriptive and  
177 require relatively few data on the modelled species, as often species occurrence data may be  
178 sufficient. This simplicity however also entails a higher risk of misinterpretation when it  
179 comes to its application in an ecosystem management context, where the desired information  
180 ideally is a single prediction with little uncertainty (Jones et al., 2013). This uncertainty  
181 originates from various sources inherent to the modelling process, including the biological  
182 and environmental input data (see below), the modelling technique and the prediction itself  
183 (Beale and Lennon, 2012). While in principle the reliability of the prediction can be assessed  
184 by using e.g. the AUC (Area under the Receiver Characteristic Curve), Kappa or the true skill  
185 statistic, the validity of these commonly used performance measures is still arguably (e.g.  
186 Lobo et al., 2008). The measures are influenced *inter alia* by the quality and nature of absence  
187 data, the testing data and simply by the spatial extent of the modelled area (Guisan and  
188 Thuiller, 2005). For example, a distribution model for a stenotypic species with a restricted  
189 distribution range is bound to get a higher performance index when built on a large spatial  
190 scale with widely ranging environmental gradients (including the narrow range of

191 environment where this species is thriving) than when built on a smaller spatial scale.

192 However, the large-scale model is not better than the small-scale one. Thus, extending the

193 study area by including non-suitable areas will inevitably result in better performance

194 indicators without improving the actual distribution predictions (Lobo et al., 2008).

195 A central aspect of uncertainty during the modelling procedure is to which extent the realised

196 or the fundamental niche is modelled. Statistical models are using the actual occurrence,

197 which represents the realised niche at a given time, but do not necessarily perform well when

198 predicting the fundamental niche. The occurrence of sink-populations for example, where the

199 species cannot establish a stable population and only survives for a limited time span due to

200 recruitment from other source populations, may further contribute to the uncertainty of

201 describing the realised niche (Pulliam, 2000, Hansen, 2011). While the knowledge concerning

202 the realised niche can satisfactorily be used in e.g. management approaches with a goal to

203 ensure for an immediate protection of endangered species, the knowledge concerning the

204 fundamental niche may be essential when predicting future changes in distribution. Besides

205 the dispersal limitations, the main process that defines the realised niche of a species is the

206 interaction with other species in the ecosystem. At present, there are only few methods

207 available to include species interactions in DM. These range from relatively simple qualitative

208 linkages between species to more complex quantitative linkages including resource stocks

209 (see examples limited to plant and terrestrial species reviewed in Kissling et al., 2012).

210 Caution is also needed when the predictions of distribution probability need to be transferred

211 into a simple binary distribution map to differentiate between modelled absence and presence

212 of a species as often required by ecosystem management. In this case, a threshold probability

213 level can be applied to set the cut-off value beyond which a feature is expected to be present.

214 The common procedure of simply using a probability of 0.5 as a threshold was often found to

215 be a less suitable choice, while alternative methods can give more reliable results (Liu et al.,



216 2005, Freeman and Moisen, 2008). The ultimate choice of thresholds should always be based  
217 on the specific management objective, e.g. using a threshold with low sensitivity, if the actual  
218 presence of the species is more important than identifying the full range of potential habitats  
219 (e.g. for delineation of marine protected areas). Freeman and Moisen (2008) therefore  
220 suggested that the DM outputs should initially be provided as continuous probability maps  
221 enabling the application of those threshold levels suitable for the specific management  
222 objectives.

223 Despite some limitations and the consequent need for cautiousness, statistical DM can  
224 provide essential information regarding the spatial distribution together with a correlative  
225 insight into the environmental drivers restricting the distribution, although it needs to be  
226 emphasised that statistical relationships cannot reveal any causality. Thus, the major  
227 assumption of statistical models that limits an accurate prediction of range dynamics is that  
228 processes setting the limits of the range remain fixed in space and time – and that assumption  
229 will probably not hold when making dynamic predictions (Dormann, 2007, Sinclair et al.,  
230 2010).

231 Most DM studies in the marine environment focused on presence/absence, but a more  
232 quantitative approach by mapping modelled densities (abundance or biomass), would be  
233 considerably more informative (Bučas et al., 2013). ‘Factor ceiling’ (Thrush et al., 2003),  
234 quantile regression (Cade and Noon, 2003, Vaz et al., 2008), and machine-learning methods  
235 recently introduced for DM such as random forest and boosted regression trees (Table 1), are  
236 also considered here. Generally regression methods such as GLM potentially provide  
237 predictive capability and machine-learning methods such as those using regression trees are  
238 often more useful for mapping and description of patterns. While statistical DM can already  
239 be applied in (marine) management, a future coupling of the results of such modelling  
240 exercises with species ecological attributes (e.g. filtration rates, bioturbation modes, etc.) via

241 biochemical or sediment transport models, would allow assessing the benthic ecosystem  
242 functioning thereby providing better knowledge for sustainable ecosystem management.

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

259 Bayesian Belief Networks (BNs) can be classified as the third approach (Stelzenmüller et al.,  
260 2010). BNs differ fundamentally from classical statistical DM methods. BNs estimate the  
261 probability that a hypothesis is true given the data, and defines that probability as the degree  
262 of belief in the likelihood of an event to occur (Table 1). Classical statistical approaches  
263 estimate the probability of the data given a hypothesis, where the probability is defined as the  
264 relative frequency of an observation (Franklin, 2009). BNs are models that graphically and  
265 probabilistically represent correlative and causal relationships among variables, and the most

266 clear strength is that probabilities in the model can be combined and quantified using  
267 empirical data, statistical associations, mathematical representations, and probabilistic  
268 quantities derived from expert knowledge (McCann et al., 2006). Within such frameworks  
269 uncertainty can be accounted for to a large extent and the assessment of “what if” scenarios  
270 for planning objectives makes these a promising tool for marine ecosystem management.

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

275

## 276 2.2 Biological data

277 Most studies focus on single species, but also functional traits (e.g. filter feeders), indices of  
278 biodiversity (e.g. species richness, rarefaction), global community descriptors (e.g. overall  
279 biomass or abundance) or community distributions. All of these faunal characteristics are  
280 possible response variables for DM. Single species modelling already proofed to be useful in  
281 a management context by predicting the distribution of key species (e.g. Galparsoro et al.,  
282 2012, Rengstorf et al., 2012).

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

288 Adequate spatial coverage for modelling species distributions calls for a sufficient biological  
289 sampling. The sampling effort of biological data still is time and costly in the marine context  
290 when compared to the terrestrial realm. As a consequence, sampling effort of marine  
291 biological data generally has a relatively low spatial resolution and is often biased towards  
292 shallow sites close to the coast (Phillips et al., 2009, Robinson et al., 2011) and driven  
293 towards politically, socially and economically interesting areas (e.g. important fishing  
294 grounds, marine protected areas). Most shortcomings in the model quality are based on  
295 paucity of data, spatial inaccuracy and lack of valid absences (Guisan et al., 2006a). There has  
296 been evidence that predictions based on few records do not perform equally well when  
297 compared to those predictions undertaken on a large dataset. This can be explained mainly  
298 because: (1) the uncertainty levels are dependent on parameter estimates (means, medians,  
299 etc.) and hence increase with decreasing sample size, (2) the outliers gain more importance,  
300 (3) the species ecological niches are highly complex in dimensions and small sample sizes are  
301 insufficient to allow for a description of a species niche over various environmental and  
302 biological gradients, particularly because (4) species niches are often skewed or multi-modal  
303 shaped (Wisz et al., 2008 and references therein). Further, data sufficiency depends on the  
304 purpose/complexity of the model (Guisan et al., 2006a, Wisz et al., 2008). Qualitative  
305 sampling as often is the case in marine benthos research (e.g. trawling for epibenthos),  
306 restricts the type of the response to presence/absence or presence-only, unavoidably resulting  
307 in the prediction of the probability of occurrence. Responses such as abundance or biomass  
308 reveal more information than occurrence predictions only (see above), but they have higher  
309 requirements on data quality that are less frequently met in the marine realm (Vierod et al.,  
310 2014).

311 The spatial bias is particularly problematic if presence-only or pseudo-absence/background  
312 data are used for modelling (Wisz and Guisan, 2009, Lobo et al., 2010). This may result in an

313 environmental bias which may lead to inaccurate models because of the difference in the  
314 observed occurrence of species and background sampling (Robinson et al., 2011). Real  
315 absence data are often lacking in the marine environment although they would contribute to  
316 model accuracy (Phillips et al., 2009) and would allow an evaluation of the predictions, i.e.  
317 standard measures for model evaluation (e.g. Kappa, AUC) do not work for presence-only  
318 data (sensu Guisan et al., 2006b). Especially for benthic systems, the use of presumed absence  
319 data (*i.e.* the species was not found in the sample) can also be misleading, since often the  
320 standard benthos sampling does not allow drawing final conclusions about the absence of a  
321 species because of limited sample sizes, lack of appropriate replication or limited efficiency  
322 of the sampling gear. However, techniques to evaluate the goodness of fit for presence-only-  
323 based prediction such as the Boyce index (Boyce et al., 2002) are under development (see  
324 Hirzel et al., 2006, Skov et al., 2008). Besides the spatial bias, data often contain a temporal  
325 bias too. Marine data are difficult to gather and DM input data are hence often taken from  
326 varying data sources over different years and sampling seasons. According to Guisan et al.  
327 (2006b), models using spatially and temporally heterogeneous samples contain an unknown  
328 level of bias and error.

329 Detailed knowledge on species-specific biological characteristics is fundamental for DM as  
330 these too may affect model accuracy (Reiss et al., 2011). Predictors for spatial distribution  
331 differ as large-scale environmental predictors such as hydrography, current regime and  
332 climate are more important for the mobile megafauna (e.g. Guisan and Thuiller, 2005) or  
333 large and sessile filter feeders (e.g. Buhl-Mortensen et al., 2010), while local environmental  
334 predictors with a more pronounced small-scale heterogeneity (e.g. sediment characteristics)  
335 might be of greater importance for smaller sedentary infaunal or less mobile species. There is  
336 further evidence that biological factors and interactions might become more important locally  
337 than on larger scales (e.g. landscape scale) (Gogina et al., 2010a, Nyström Sandman et al.,

338 2013). As introduced in section 2.1, biological predictor variables are mostly not or  
339 insufficiently taken into account in DM (Elith and Graham, 2009). However, distribution of  
340 habitat forming species, migratory behaviour, dispersal range, species aggregation and  
341 interactions are of specific importance in modelling the distribution of a species (Guisan et al.,  
342 2006b, Kissling et al., 2012). The use of biological predictors alongside the classically used  
343 physico-chemical variables is likely to increase DM performance. Compared to the terrestrial  
344 ecosystem, most marine species either have mobile adult stages (megafauna, fish) or mobile  
345 early life stages (pelagic larvae) and their dispersal ranges can be large given the major  
346 physical continuity in the marine ecosystem (Guisan et al., 2006b, Reiss et al., 2011,  
347 Robinson et al., 2011). Consequently, the role of environmental factors determining the  
348 distribution may even change during the life history of a species (e.g. De la Moriniere et al.,  
349 2003). During the pelagic larval phase hydrographic parameters of the water column might be  
350 most important, while the benthic phase might be more influenced by parameters acting more  
351 directly on the seafloor. The inclusion of such dispersion features, influencing species  
352 distribution patterns by neighbouring spatial dependencies, i.e. spatial autocorrelation, will  
353 again add to the DM performance (Legendre, 1993, Guisan et al., 2006b, Gogina et al., 2010a,  
354 Robinson et al., 2011).

355 DM performance would further profit from the incorporation of species interactions (Soberón,  
356 2007), constituting the biological base of ecological functioning (May, 1983). Hence, species  
357 distributions are not solely shaped by the environmental setting but to a large extent by  
358 biological factors. Besides environmental conditions, particularly trophic interactions are the  
359 main forcing factors for the occurrence, distribution and behaviour of organisms (MacArthur,  
360 1955, Cohen, 1978, Pimm, 1982). The lack of knowledge on marine benthic interactions (e.g.  
361 trophic interactions) however hampers their incorporation into DMs. The fact that most  
362 marine benthic species feed on a variety of different food sources or prey species (omnivory)

363 (Link, 2002), as such hampering an unequivocal quantification of trophic linkages, further  
364 complicates its incorporation into DM; this in contrary to e.g. species-specific pollinator-plant  
365 interactions in terrestrial systems.

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

375

### 376 2.3 Environmental data and anthropogenic pressures

377 Environmental data constitute the fundamental basis of DM. For marine ecosystems the  
378 availability of large scale environmental data has significantly improved in the last decade,  
379 because of increasing research activities by using habitat mapping and remote sensing  
380 techniques e.g. to develop seabed habitat classifications based on the relation between benthic  
381 organisms and the seabed environment such as EUNIS (Davies et al., 2004, Galparsoro et al.,  
382 2012). These environmental predictors however tend to be temporally more dynamic in the  
383 marine realm compared to terrestrial systems, with a significant short-term (e.g. currents) or  
384 seasonal variability (e.g. temperature, primary production), which makes their application in  
385 DM challenging (Franklin, 2009).

386 To be useful in a modelling context, the selected environmental predictors should ideally  
387 represent limiting factors, resources or disturbances (natural or anthropogenic) causally linked  
388 to the species and its habitat (Guisan and Zimmermann, 2000, Guisan and Thuiller, 2005,  
389 Elith and Leathwick, 2009). Causal predictors used to model benthos distribution are e.g.  
390 temperature, salinity or primary production (Table 2), whereas others rather represent  
391 surrogate factors such as e.g. water depth or in some cases substratum, which may be indirect  
392 proxies integrating several predictor variables. The causality of the relationships between  
393 benthos and the marine environment are however often not understood in detail, mainly  
394 because most of our understanding is based on correlative approaches and experimental  
395 studies are scarce, which may reflect the poor representation of mechanistic DM in the marine  
396 environment (see 2.1). DM, especially those based on statistical approaches, should hence be  
397 considered an indicator of possible causalities rather than an identifier of such cause-effect  
398 relationships, and should hence trigger further fundamental research on cause-effect  
399 relationships.

400 When zooming into environmental predictors, substratum or bottom type is one of the key  
401 features driving the presence of benthic marine organisms and it has therefore often been used  
402 to predict the distribution of bottom fauna. For soft bottom sediments, grain size composition  
403 is commonly used (e.g. Ysebaert et al., 2002, Degraer et al., 2008), while more specific  
404 sediment parameters such as sediment sorting, porosity or cohesiveness are rarely measured in  
405 the field and are consequently not often used in marine DM. For hard bottoms such as  
406 bedrock, boulder and gravel fields, the fraction of gravel or boulders based on visual  
407 inspection and size and orientation of rocks or the space available between rocks are more  
408 relevant descriptors. Several techniques ranging from direct observations to remote sensing,  
409 including acoustic techniques, may be used to qualify the substratum type (Brown et al.,  
410 2011). Shallow sediments in areas experiencing high water dynamics or ice scouring may



411 change after storms or the winter season. Below 100 m depth, sediments are normally stable.  
412 However, the hydrographic conditions around underwater canyons and seamounts as well as  
413 strong tidal driven currents or internal waves may still generate sediment transportation also  
414 in deep waters. Except for local studies where substratum data can be collected, modelling  
415 large sea expanses requires collating and harmonising data from various studies undertaken at  
416 different times. A key requirement of such data assemblages is hence to provide users with a  
417 confidence map, which enables them to use the data with full awareness of its reliability.

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

428 Bathymetry derivatives, i.e. seafloor morphological characteristics such as slope, aspect or  
429 rugosity, further include crucial environmental descriptors that have proven useful to identify  
430 suitable habitat (Buhl-Mortensen et al., 2009, Galparsoro et al., 2009). The value of these  
431 derivatives is however highly dependent on the spatial resolution of the bathymetric information  
432 (Rengstorf et al., 2012).

433 Other major oceanographic drivers for marine species distribution comprise e.g. light energy,  
434 hydrodynamic energy, salinity and temperature, and of more local importance variables such

435 as the oxygen concentration, nutrients, etc. The impact of light onto the benthos is particularly  
436 straightforward as it determines the depth to which benthic macrophytes (kelp, seaweeds,  
437 seagrass) can grow or photosynthetic primary production can occur (Carlström et al., 2009,  
438 Knudby et al., 2013, Saulquin et al., 2013). The same goes for salinity which is particularly  
439 important in shallow and estuarine environments where freshwater input may be substantial.  
440 The salinity gradient within the Baltic Sea is a good example of how salinity steers the  
441 distribution of species (Zettler et al., 2014). The effect of hydrodynamic energy from waves  
442 and currents exerted on the seabed and benthos, is more complex (Galparsoro et al., 2013), yet  
443 fundamental to the seabed stability and substratum composition (including deposited and  
444 suspended food particles for benthic organisms). Whilst extreme events can dramatically  
445 modify the seabed (e.g. heavy storms), they usually act on the seabed by a regular action  
446 which is best characterised by parameters computed on long time spans (Dolbeth et al., 2007).  
447 The inclusion of hydrodynamics into DM is most relevant for rocky substrata, since the  
448 composition of mobile sediments typically reflect the local hydrodynamic regime and can be  
449 considered as a surrogate variable for hydrodynamics. Seabed energy parameters are derived  
450 from hydrodynamic models. Although they are often of low spatial resolution with respect to  
451 seabed heterogeneity, especially in the coastal zone, a lot of progress is currently being made  
452 (e.g. Chen et al., 2009). Unfortunately, information on currents and particle transport in the  
453 benthic boundary layer – most relevant for benthic organisms – is poor and highly demanding  
454 to map and monitor. Temperature finally takes a special position because of its large scale  
455 structuring relevance (Glémarec, 1973) combined with its central position within the  
456 ecological impact of climate change. Together with salinity, it defines the hydrographic  
457 setting which is used to define different water masses and depth zones. It further strongly  
458 affects oxygen concentration and consumption in the benthic environment where hypoxia is  
459 often related to year maxima in bottom water temperature (Quiñones-Rivera et al., 2010).

460 From a DM perspective, sea surface temperature may be a good proxy for the entire column  
461 where the water column can be considered homogenous, i.e. mixed waters (Mélédér et al.,  
462 2010). Other factors which may be relevant locally such as the oxygen conditions at the  
463 seabed (Reijonen et al., 2008) or the influence of pelagic environment variables such as  
464 primary production (Holt et al., 2012) in the surroundings of the benthic samples locations,  
465 may also be examined where appropriate.

466 Anthropogenic impacts may also be considered environmental predictors in a DM context,  
467 although many impacts are relevant mainly on a local scale. The use of DM to map and  
468 monitor animal and plant distributions has become increasingly important in the context of  
469 awareness of environmental change (natural and anthropogenic) and its ecological  
470 consequences (Miller, 2010). Key activities which can have a significant impacts on marine  
471 ecosystems at the regional or local scale include (recreational) fisheries, dredging, renewable  
472 energy developments, industrial and sewage effluents, hypersaline water discharge from  
473 desalination plants, aquaculture, diseases, coastal engineering (habitat alteration) and point-  
474 source pollution (Halpern et al., 2008). Many of these activities primarily affect intertidal and  
475 nearshore ecosystems rather than offshore or deep-sea ecosystems, which suggests that  
476 predictive modelling and cumulative estimates of impacts are often conservative particularly  
477 for nearshore areas. The analytical process of DM provides flexible tools for regional and  
478 global efforts to allocate conservation resources, to implement ecosystem-based management  
479 and to inform MSP, education, and basic research (Halpern et al., 2008). Among the impacts  
480 with a large spatial extent, acidification (or climate change), fisheries and eutrophication are  
481 probably the most important ones. Bottom trawling is one of the most widespread sources of  
482 physical disturbance on habitats and organisms on continental shelves throughout the world  
483 (Jackson et al., 2001, Kaiser et al., 2002). Vessel Monitoring Systems (VMS), introduced for  
484 fisheries recording and control, is now widely implemented and increasingly used as a proxy

485 for fisheries activity and hence impact from bottom gears. Yet, several approaches have been  
486 developed to analyse VMS data, all having their strengths and weaknesses (Lee et al., 2010,  
487 Lambert et al., 2012). The lack of freely accessible VMS data e.g. across state boundaries,  
488 however currently hampers its applicability within DM (Hintzen et al., 2012).

489

### 490 **3. Application of distribution modelling**

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

496

#### 497 3.1 Marine spatial planning

498 As shown in the introduction, the incorporation of the ecosystem-based approach into e.g.  
499 MSP requires that all aspects of value associated with marine biodiversity are incorporated  
500 into the decision-making process (Rees et al., 2010), which is called ecosystem-based marine  
501 spatial management (EB-MSM, *sensu* Katsanevakis et al. (2011)). A key goal of EB-MSM is  
502 to maintain the delivery of ecosystem services, which must be based upon ecological  
503 principles that articulate the scientifically-recognised attributes of healthy functioning  
504 ecosystems (Foley et al., 2010). These authors have proposed four main ecological principles:  
505 maintaining or restoring native species diversity, habitat diversity and heterogeneity, key  
506 species, and connectivity. Hence, it is critical to understand the heterogeneity of biological  
507 communities and their key components (e.g. most important predators, habitat-forming

508 species), and key processes (e.g. population connectivity, interaction webs, biogeochemistry)  
509 that maintain them, as well as human uses (Crowder and Norse, 2008). The successful  
510 development and implementation of EB-MSM hence necessitates the use of best available  
511 science. As stated by Katsanevakis et al. (2011), new tools, such as e.g. geospatial analysis,  
512 remote sensing and molecular techniques have broadened the understanding of the linkages  
513 between marine habitats and population dynamics, and between spatio-temporal dynamics  
514 and the functioning of marine ecosystems (Crowder and Norse, 2008). Hence, DM does play  
515 and will continue playing a key role in MSP and EB-MSM.

516 The spatially explicit nature of the DM makes this approach of special interest for different  
517 aspects of the MSP. Scientific knowledge obtained from DM approaches could be applied in  
518 different ways in the MSP process, as it has been used to map the potential distribution of  
519 biological resources (see examples for habitat suitability of lobster from Wilson et al., 2007,  
520 Galparsoro et al., 2009), fish habitat modelling and evaluation (Koubbi et al., 2006, Monk et  
521 al., 2011), species of special interest for conservation, such as gorgonians (Bryan and  
522 Metaxas, 2007, Etnoyer and Morgan, 2007), marine mammals (Panigada et al., 2008) or  
523 seabirds (Skov et al., 2008), selection of suitable areas for aquaculture and farming (Cho et  
524 al., 2012), conservation of biodiversity by providing information on the ecological  
525 requirements of species at risk (Hare et al., 2012, Millar and Blouin-Demers, 2012). DM and  
526 mapping hence support conservation planning, marine protected area selection and  
527 management plan development, mapping suitable sites for re-introductions and restoration  
528 (Bos et al., 2005, Bekkby et al., 2008, Valle et al., 2011). The most extended application of  
529 DM in marine systems most probably is in planning for MPAs and designating essential fish  
530 habitats (see examples in Leathwick et al., 2008, Valavanis et al., 2008, Maxwell et al., 2009).  
531 When combined with climate change scenarios, DM results can further reveal estimations of  
532 the expected changes in protection efficiency of designated MPAs (Gormley et al., 2013).

533 Hence, DM results can be used to estimate (or have an approximation of) the potential impact  
534 of certain human activities and hence to provide advice for an ecologically-sound allocation  
535 of these activities (considering also the type of impact: habitat physical destruction,  
536 hydrological or temperature regime modification, etc.). DM may thus facilitate minimizing  
537 environmental impact and maximizing the socio-economic benefit of marine goods and  
538 services (Salomidi et al., 2012); aspects that are basic to the MSP.

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

547

### 548 3.2 Monitoring designs

549 The main purpose of DM is to inter- or extrapolate from point observations in space and time  
550 to predict the occurrences in an area where no survey data are available or the coverage is  
551 limited. DM predictions hence complement the monitoring, but equally, the predictions can  
552 also be used to guide the monitoring strategy development (Bijleveld et al., 2012, Crall et al.,  
553 2013, Van Hoey et al., 2013). The latter is especially important for marine environments,  
554 where the logistical effort and the costs for monitoring are substantially higher compared to  
555 monitoring in terrestrial environments. The monitoring data used for DM in marine waters are  
556 often based on heterogeneous data sources, where no specific design could be set up prior to

557 the sampling (Degraer et al., 2008). In such cases, there is an increased higher risk of  
558 predictions, biased particularly toward sites which were sampled more intensively (local  
559 project-based sampling) or logistical easily accessible (coastal areas). In other cases, the  
560 number of samples is limited because monitoring programmes often have multiple objectives,  
561 each with their own data needs and hence possibly compromising the optimal sampling  
562 design. Bijleveld et al. (2012) demonstrated that combining grid and random sampling is the  
563 most effective design in addressing a multitude of management applications including  
564 mapping of species distributions.

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

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

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

600

### 601 3.3 Non-indigenous species

602 The introduction of non-indigenous species is of specific concern for marine ecosystem  
603 management, because these species can considerably affect marine ecosystems and  
604 biodiversity by e.g. altering native communities, and may even cause severe economic  
605 damage when the species become invasive (Olenin et al., 2011). The non-indigenous green



606 algae species of the genus *Caulerpa* for example have now spread throughout major parts of  
607 the Mediterranean Sea (Meinesz et al., 2001). The non-indigenous and invasive Pacific oyster  
608 (*Crassostrea gigas*) has been shown to affect blue mussel (*Mytilus edulis*) beds in the Wadden  
609 Sea and elsewhere (Diederich, 2005, Markert et al., 2010, Jones et al., 2013). Once  
610 established it is difficult if not impossible, to extirpate or manage the spread of non-  
611 indigenous species. Therefore, early warning systems are currently in the focus of marine  
612 management strategies and suitable monitoring schemes for non-indigenous species in the  
613 marine ecosystems need to be implemented. Non-indigenous species-targeted DMs may play  
614 an important role here.

615 A common approach to the risk of invasion is to model the ecological niche of a species based  
616 on the occurrence within its native distribution and then to apply this model in other regions  
617 to identify potential (vulnerable) habitats. In the terrestrial environment, Thuiller et al. (2005)  
618 have used climate niche modelling results of endemic species from Africa to predict the  
619 potential global distribution of introductions of these species. Thus, the vulnerable habitats  
620 can be determined even before the potentially invasive species are invading the region.

621 Monitoring schemes within an early warning system could use this information to focus the  
622 monitoring effort on these vulnerable habitats. However, such approach only poorly accounts  
623 for the early phases of introduction into marine environments, which are often associated with  
624 the major shipping pathways (e.g. harbours). Next to precautionary management measures,  
625 this might be the only stage (in marine environments) where management action can be  
626 successful in regulating the introduction of non-indigenous species.

627 Given the vast number of potential invaders in marine ecosystems, DMs may further serve as  
628 a tool to distinguish species with little potential from those with higher potential to invade a  
629 specific region and to prioritize management and monitoring efforts (Simberloff et al., 2005).  
630 This might be an unrealistic approach for marine environments, because the availability of

631 environmental data on a global scale still is a problem for a wide application of DMs in  
632 marine benthic environments. Thus, the lack of sufficient environmental data hampers the  
633 potential use in early warning approaches, for which environmental data are not only needed  
634 for the invaded, but also for the native region. To our knowledge no case study on marine  
635 benthos using DMs in such a context was carried out so far.

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

644 The spatial spreading of non-indigenous species can also be modelled using occurrence data  
645 of the invaded ecosystem. Of course, this approach can only be applied when the species  
646 already colonised the ecosystem and, thus, cannot be used within early warning strategies. It  
647 can however still provide valuable information about the ecological niche of the non-  
648 indigenous species and hence its possible future spatial extent (Verween et al., 2007, Azzurro  
649 et al., 2013, Jones et al., 2013, Neumann et al., 2013). Although such approach may  
650 successfully predict the distribution of the invader, one should be cautious because of the  
651 inherent violation of the basic assumption of DMs that the species is in equilibrium with its  
652 environment (Václavík and Meentemeyer, 2012). On the one hand, the invasive species might  
653 not have colonised all of the suitable habitats simply because of a lack of time for a wide  
654 dispersal, which would lead to an underestimation of the potential distribution. On the other  
655 hand, the current species distribution might have been supported by unusual environmental

656 conditions for a short time period. Thus, under ‘normal’ conditions the species might not be  
657 able to survive in these regions and the model outputs would result in an overestimation of  
658 distribution.

659

#### 660 3.4 Future scenario predictions

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

670 DMs provide a useful tool to predict the spatial distributional consequences of expected  
671 environmental changes such as climate change. In the terrestrial realm different IPCC  
672 scenarios of climate change have been widely used to predict the future distribution of several  
673 species and the consequences for ecosystem functioning and environmental management (e.g.  
674 Heikkinen et al., 2006, Pompe et al., 2008, Richardson et al., 2010, Falk and Mellert, 2011).  
675 Future climate scenarios were also recently used to predict distribution shifts of marine  
676 benthic species (Cheung et al., 2012, Jones et al., 2013). Predictions of environmental  
677 changes based on IPCC scenarios are now indeed widely accessible for terrestrial and partly  
678 for marine environments, even on a global scale (Tyberghein et al., 2012). Nevertheless, the  
679 dominant environmental factors influencing the benthos are acting on the sea floor, for which

680 large scale data on the effects of climate change are still meagre. Especially for deep sea  
681 habitats, the conditions at the sea floor differ substantially from the surface water and detailed  
682 hydrographic models focusing on the sea floor or entire water column parameters are often  
683 restricted in their spatial extent (e.g. Ådlandsvik, 2008, Holt et al., 2010). The same however  
684 also holds true, yet to a lower extent, for shallower habitats where especially the effects of  
685 changes in hydrodynamics (e.g. storminess) and sea level rise onto the benthic physical  
686 conditions are less straightforward, as such hampering large scale applications of DM in  
687 predicting climate change driven distribution shifts of benthic species (see Ready et al., 2010).

688 With an increasing use of DMs in predicting consequences of climate change, a growing  
689 concern has emerged to improve the knowledge of uncertainty factors and to increase the  
690 reliability of predictions (Thuiller et al., 2004, Botkin et al., 2007). This is even more  
691 important in the context of climate change since an additional source of variability arises with  
692 the use of modelled climate scenarios. Widespread disagreement in the distribution  
693 predictions were found between DM methods when applied to extreme climate change  
694 scenarios (Elith et al., 2010). Furthermore, major uncertainties related to prognostic species  
695 distribution modelling are that relevant processes such as species interactions, habitat change,  
696 and rapid evolutionary changes are not included in most of the modelling approaches (see  
697 above). Using DM for predicting future changes is associated with an unavoidable degree of  
698 uncertainty (Wenger et al., 2013) and should always be done with precaution in an ecosystem  
699 management context: they should be interpreted as indications of possible future changes.

700 These uncertainties may however partly be addressed by using multi-model procedures where  
701 the predictions of a variety of different models are taken into account to improve the  
702 robustness of the prediction. These methods are relevant both in DM and in modelling of  
703 climate change scenarios (Araujo and New, 2007, Jones et al., 2013). The further  
704 incorporation of dispersal dynamics and species interactions into DMs will be specifically

705 important to improve the robustness and reliability of climate change impact predictions (e.g.  
706 Cheung et al., 2008).

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

713

#### 714 **4. Recommendations**

715 Distribution models provide valuable full-coverage information on the distribution of marine  
716 benthic species, communities and related entities inhabiting an environment that is usually  
717 difficult to assess and enables the prediction of distribution changes. On the one hand, DM  
718 enables ecosystem managers to utilise spatial information that cannot be generated otherwise  
719 to a similar level of spatial resolution. On the other hand, the level of uncertainty is  
720 correspondingly high and large scale data for quality control are often insufficient. Thus,  
721 although DM is considered to increasingly constitute an essential tool for current and future  
722 ecosystem management, careful usage and interpretation are essential when applying the DM  
723 outputs in a management context.

724 1. Management approaches can only be successful if there is a causal link between the  
725 management objective and the implemented measure. However, the most commonly used  
726 statistical DM does not necessarily identify cause-effect relationships, which are crucial in  
727 a management context. Bayesian Belief Networks is a promising method which considers

728 both, correlative and causal relationships, and provides good estimate of model uncertainty,  
729 (Stelzenmüller et al. 2010). Its application to the marine benthic realm is however rare up to  
730 now.

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

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

750 4. Often, mechanistic models are used to predict the physico-chemical nature of the area that  
751 is then used as explanatory variable(s) in statistical DM (or in cases used as expert judgement)

752 to describe or predict the biological response. The development of mechanistic DM  
753 approaches based on functional traits, physiological constraints and dispersal capacity, are  
754 particularly appropriate to address issues such as long-term sustainability of exploitation  
755 activities, evaluation of alternative rearing and management strategies, risk of dystrophic  
756 crises and algal blooms, effects of range-shifting and species, or even forecasting the impact  
757 of future climate (Buckley et al., 2010, Elith et al., 2010), although costly to design, calibrate  
758 and validate. The prior use of correlative modelling techniques can in turn guide and optimise  
759 the application of the mechanistic models by suggesting particular traits or processes to  
760 consider and suggesting spatial limits of necessary runs (Vincenzi et al., 2011).

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

768 6. Biological Traits Analysis (BTA) recently facilitated assessing the functional diversity and  
769 roles of benthic species in marine ecosystems (e.g. Bremner, 2008, Darr et al., 2014b). This  
770 type of approaches uses the information on selected ecological traits expressed by species to  
771 characterise the ecological functioning of the assemblages, and has been highlighted as a valid  
772 approach in the assessment and management of marine benthic systems (Bremner, 2008, Frid  
773 et al., 2008). The combination of distinct relationships between species and both abiotic and  
774 biotic predictors with species autecological capacity (e.g. filtration rates) could help to model  
775 temporal and spatial ecosystem functioning with high resolution accuracy. This approach  
776 assumes that modelled distribution of benthic assets is expressed not only as probability of

777 occurrence but rather as quantitative predictions (e.g. abundance or biomass). Recent studies  
778 (Wei et al., 2010, Vincenzi et al., 2011, Darr et al., 2014a) have demonstrated that the  
779 combination of multivariate predictors and machine-learning algorithms (e.g. Random Forest)  
780 is better when compared to conventional regression models, especially when the aim is to  
781 model quantitative response variable (species abundance, biomass or certain biological traits  
782 expressed in these units, potential yield of aquaculture etc.). Generally, these models are most  
783 useful for purposes of spatial planning and identification of areas with different degree of  
784 suitability e.g. for farming or endangered species. New case studies from different  
785 environments with application of these methods are urgently needed, which will help to  
786 obtain more technical experience, improve model performance and efficiency for  
787 management purposes.

788

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



801 stimulate further development of DM to minimise this gap between management requirements  
802 and scientific integrity.

803

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810

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1330 **Figures**

1331 Figure 1: Conceptual diagram showing the components of statistical distribution modelling  
1332 and the overall linkages for the management applications. The arrows indicate the direction of  
1333 input of data/information, while the limitations and problematic issues for the biological input  
1334 data, the environmental predictors and the distribution modelling procedure are listed in the  
1335 consecutive boxes. The management objectives in this figure provide the overarching  
1336 framework on which the selection of DM method and prediction attributes is depending on.

1337

Table 1: Common methods used for distribution modelling (\* ‘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
<b>GLM</b> Generalized Linear Model	Based on analysis of variance and co-variance; 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)
<b>GAM</b> 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 suggest 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)
<b>MARS</b> 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)



<b>MAXENT</b> Maximum Entropy	Estimates the target probability by finding the probability distribution of maximum entropy (of minimum information content) under the constraints 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)
<b>BIOCLIM</b> 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)
<b>Quantile regression</b>	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)
<b>ANN</b> Artificial Neural Networks	Non-linear mapping structures based on hundreds of simulated neurons connected together as brain's neurons, learn from experience (not programming), behavior 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)
<b>GARP</b> 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 analyze contributions of individual predictors to the model, hard to interpret.	+	(Stockwell and Peters, 1999, Reiss et al., 2011)

<b>GDM</b> 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)
<b>ENFA</b> 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)
<b>CART</b> 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)
<b>RF</b> Random Forest	Uses collection of decision tree models to achieve top predictive performance	p/a		+	(Wei et al., 2010, Reiss et al., 2011)
<b>BRT</b> 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)

<b>BNs</b> 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 estimates 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)
<b>Mechanistic models</b>	Translate environmental conditions into biologically relevant metrics, capture environmental sensitivities of survivorship and fecundity and use energetic to link environmental conditions and demography (1) incorporating models of species migration - ability of a species to occupy suitable habitat in new locations; (2) linking models of landscape disturbance and succession to models of habitat suitability; (3) 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)
<b>Ordination methods</b>	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 $\chi^2$ 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 about how environmental factors shape benthic habitats and communities.	++	(Buhl-Mortensen et al., 2009, Gogina et al., 2010a, Moore et al., 2010)

Table 2: Environmental variables relevant for DM of marine benthos

<b>Environmental variable</b>	<b>Common types of measurement</b>	<b>Remarks</b>
<i>Substratum</i>	<ul style="list-style-type: none"> <li>• Swath techniques:               <ul style="list-style-type: none"> <li>- Backscatter from multibeam echosounder</li> <li>- Side scan sonar mosaics</li> </ul> </li> <li>• Samples: point measurements (grab or corer)</li> <li>• Visual mapping: camera/video</li> </ul>	<ul style="list-style-type: none"> <li>• Reliability depends on ground truth sampling density</li> <li>• Can be used in a stand-alone way to provide interpolated maps (e.g. grain size distribution)</li> <li>• Used to ground truth swath techniques rather than per se (hard to discriminate fine sediment categories)</li> </ul>
<i>Sea surface temperature</i>	<ul style="list-style-type: none"> <li>• Satellite, point measurements, hydrodynamic models</li> </ul>	<ul style="list-style-type: none"> <li>• Seldom relevant to bottom fauna except in shallow waters</li> <li>• Used to identify major biogeographic regions</li> </ul>
<i>Bottom temperature</i>	<ul style="list-style-type: none"> <li>• Hydrodynamic models validated by point measurements</li> </ul>	<ul style="list-style-type: none"> <li>• Resolution in space and time is often coarse, however new detailed models have been developed</li> <li>• Many observations needed to cover variability</li> </ul>
<i>Salinity</i>	<ul style="list-style-type: none"> <li>• Hydrodynamic models</li> <li>• Point measurements</li> </ul>	<ul style="list-style-type: none"> <li>• Coarse resolution often not relevant to benthos</li> <li>• Many observations needed to cover seasonal variability in shallow coastal areas</li> </ul>
<i>Depth</i>	<ul style="list-style-type: none"> <li>• Point measurements</li> <li>• Swath bathymetry (see 'Substratum' above)</li> </ul>	<ul style="list-style-type: none"> <li>• DTM (Digital Terrain/Elevation Model) obtained from assembling raster and point clouds sources</li> </ul>
<i>Light energy</i>	<ul style="list-style-type: none"> <li>• Satellite imagery</li> <li>• Point measurements (e.g. Secchi depth)</li> </ul>	<ul style="list-style-type: none"> <li>• Two parameters can be retrieved:               <ul style="list-style-type: none"> <li>- Fraction of incident light</li> <li>- Energy in mol photons reaching seabed</li> </ul> </li> </ul>
<i>Primary production (water column)</i>	<ul style="list-style-type: none"> <li>• Satellite imagery</li> <li>• Hydrodynamic models</li> </ul>	<ul style="list-style-type: none"> <li>• Only surface waters covered by satellite imaging</li> <li>• Coarse resolution in space and time of model output</li> </ul>
<i>Hydrodynamics</i>	<ul style="list-style-type: none"> <li>• Hydrodynamic models (e.g. (tidal) currents, bottom shear stress)</li> <li>• Acoustic Doppler Current Profiler (ADCP)</li> </ul>	<ul style="list-style-type: none"> <li>• Often coarse resolution in space and time of model output</li> <li>• Local application only for ADCP</li> </ul>

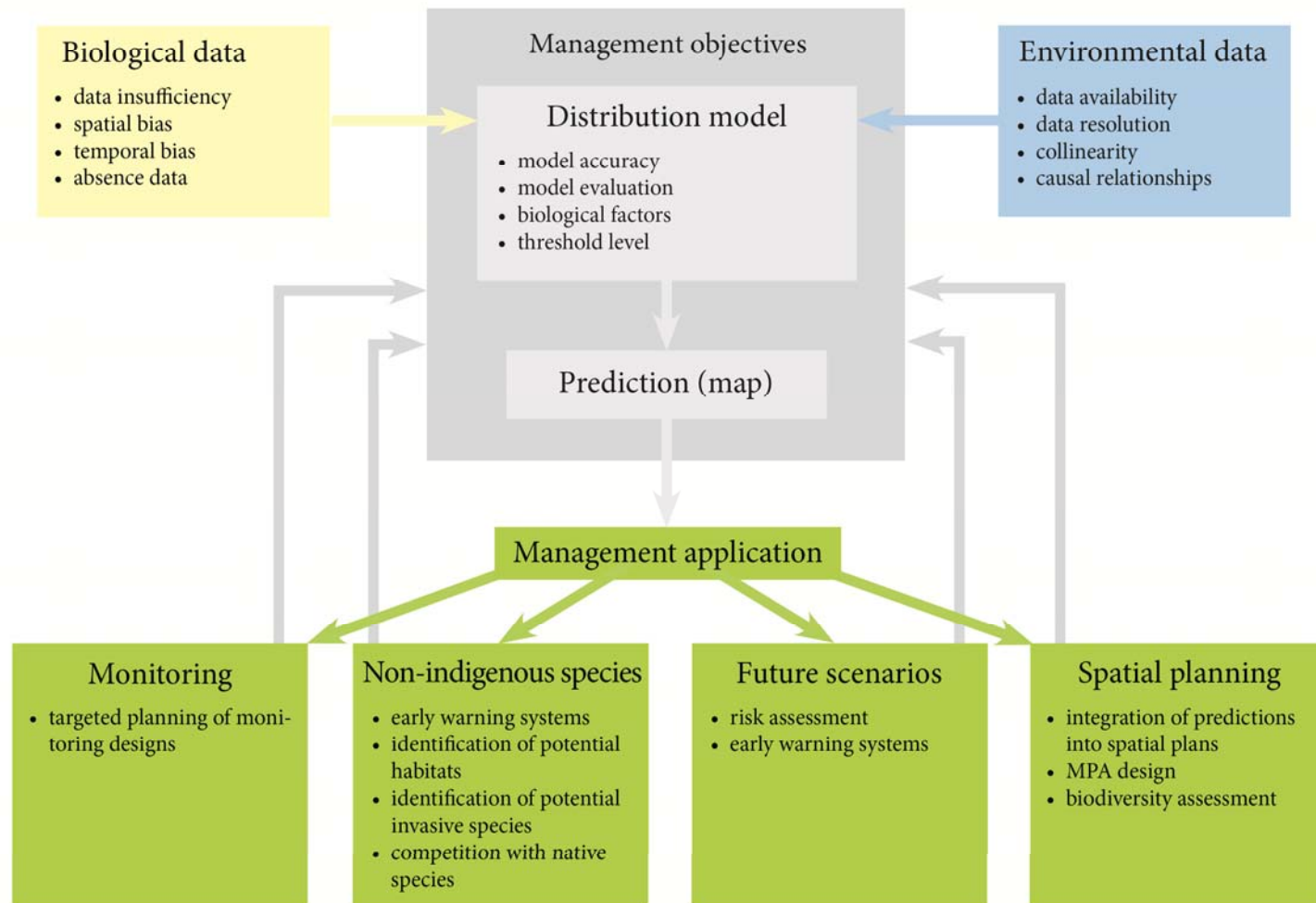


Figure 1