

*This is a pre-copy-editing, author-produced PDF of an article accepted for publication in ICES Journal of Marine Science following peer review. The definitive publisher-authenticated version is available online at :
<http://dx.doi.org/10.1093/icesjms/fsu107>*

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

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 e.g. species distribution modelling, 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 to 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 et al., 2010b, Gogina and Zettler, 2010), 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

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 derivates, 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 derivates 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 (Méléder 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

804 **Acknowledgements**

805 This publication was initiated and facilitated by the Benthos Ecology Working Group
806 (BEWG), which is an expert group of the International Council for the Exploration of the Sea
807 (ICES). We thank the Working Group on Marine Habitat Mapping (WGMHM) of ICES for
808 their valuable contribution. We would wish to thank the three anonymous reviewers for their
809 valuable comments to improve our manuscript.

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
GLM 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)
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 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)
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	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)
BIOCLIM	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	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)
GARP	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)

GDM	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	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 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)
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 (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)
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 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

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

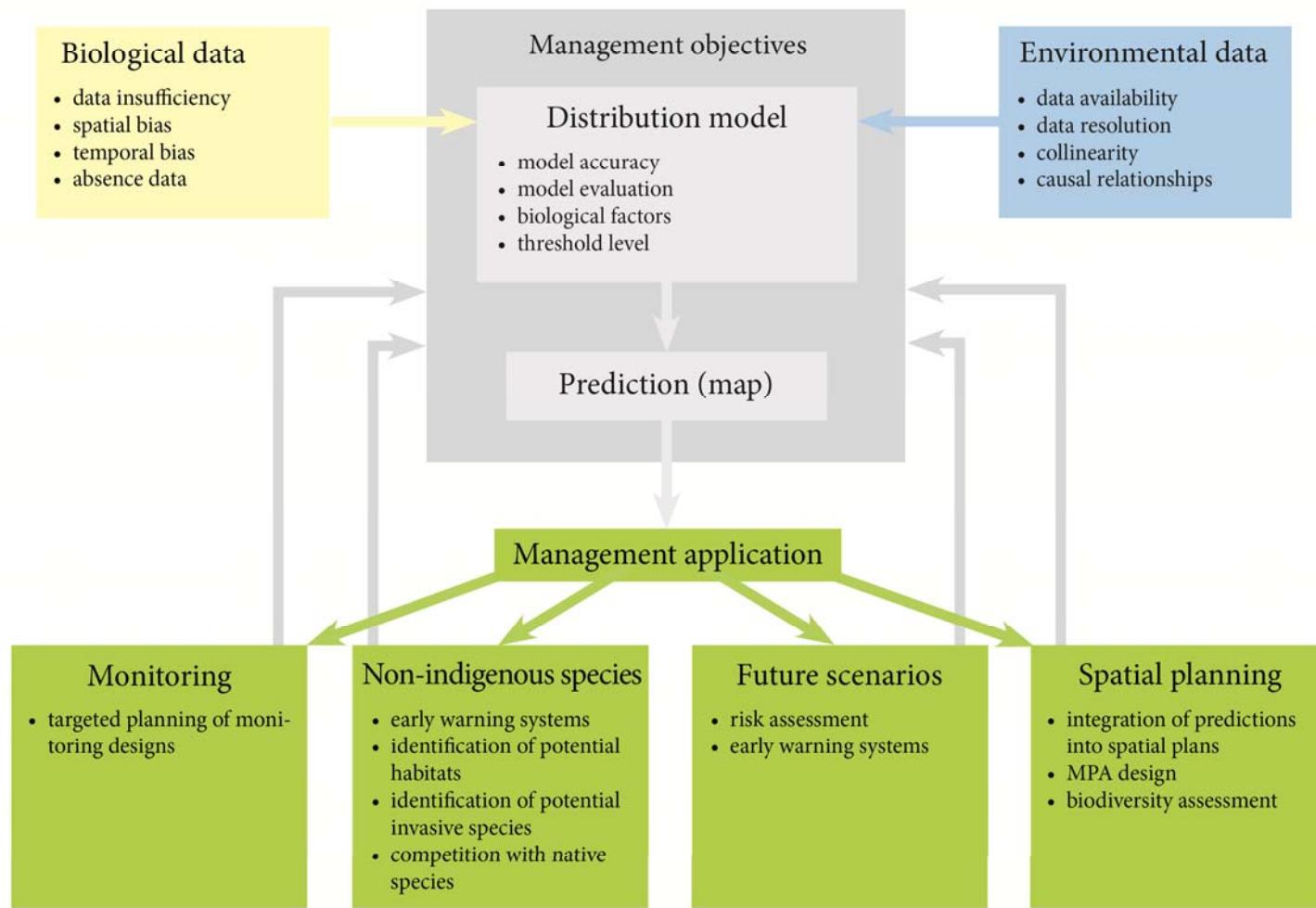


Figure 1