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Species–environment relationships and potential for distribution modelling in coastal waters

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ABSTRACT

Due to increasing pressure on the marine environment there is a growing need to understand species–environment relationships. To provide background for prioritising among variables (predictors) for use in distribution models, the relevance of predictors for benthic species was reviewed using the coastal Baltic Sea as a case-study area. Significant relationships for three response groups (fish, macroinvertebrates, macrovegetation) and six predictor categories (bottom topography, biotic features, hydrography, wave exposure, substrate and spatiotemporal variability) were extracted from 145 queried peer-reviewed field-studies covering three decades and six subregions. In addition, the occurrence of interaction among predictors was analysed. Hydrography was most often found in significant relationships, had low level of interaction with other predictors, but also had the most non-significant relationships. Depth and wave exposure were important in all subregions and are readily available, increasing their applicability for cross-regional modelling efforts. Otherwise, effort to model species distributions may prove challenging at larger scale as the relevance of predictors differed among both response groups and regions. Fish and hard bottom macrovegetation have the largest modelling potential, as they are structured by a set of predictors that at the same time are accurately mapped. A general importance of biotic features implies that these need to be accounted for in distribution modelling, but the mapping of most biotic features is challenging, which currently lowers the applicability. The presence of interactions suggests that predictive methods allowing for interactive effects are preferable. Detailing these complexities is important for future distribution modelling.

Contents

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1. Introduction

With today's pressure on the coastal environment, there is a fundamental need to understand the existence, strength and consequences of species–environment relationships (Crowder and Norse, 2008; Halpern et al., 2009). The main challenge lies in understanding how patterns in the variation of biotic and abiotic factors together influence the distribution of species and assemblages in time and space (Mitchell, 2005). In spatial planning of e.g. sea areas there is a general call for management initiatives that require spatial data and knowledge of ecosystem processes and habitat dynamics (Foley et al., 2010). Efforts are being made to address these data requirements, via the use of Geographical Information Systems and species distribution models, to produce regional coverage maps of the distributions of species and habitats (Pittman and Brown, 2011). The ecological relevance of these analyses should be assessed, and the opportunities and limitations of existing data determined (Elith and Leathwick, 2009). Thus, efforts on predictive modelling of species distributions need to incorporate the best available scientific knowledge about the relationships between the spatial distribution of species and habitats (Kissling et al., 2012; Wisz et al., 2012), and relevant environmental predictors that can be used to predict such distribution patterns.

The Baltic Sea region has been extensively studied with respect to the large-scale horizontal and vertical environmental gradients. These studies have revealed basin-wide differences in diversity and function of species assemblages caused by large-scale environmental gradients in salinity and coastal morphology (e.g. Bonsdorff, 2006; Ojaveer et al., 2010). For example, the salinity gradient affects species composition as the number of marine species decreases towards the less saline northern parts of the Baltic Sea. In this sense, the sea to some degree resembles a large estuary with clear gradients and species turnover (Heck et al., 1995; Rakocinski et al., 1992).

Studies of local and regional patterns show that a variety of environmental predictors, e.g. temperature, salinity, depth and vegetation are important in structuring coastal benthic species at these scales (Eastwood et al., 2001; Lehmann, 1998). Nevertheless, a comprehensive view of the relevance of predictors is often lacking concerning the mechanistic and correlative species–environment relationships.

In this case-study, we synthesised species–environment relationships focusing on benthic organisms in a well-studied sea, the Baltic Sea region. Our main purpose was to explore the generality and relevance and nature (main or interaction effect) of encountered environmental variables (predictors) on benthic organisms in different parts of the sea by compiling published analyses of significant relationships between organism groups and predictors. Although the present approach to use the number of significant relationships in studies as a measure of the importance of predictors has potential shortcomings, such as that significant results are more easily accepted for publication than are negative results (Sutton et al., 2000), it may still be used as a measure of the accumulated scientific knowledge and data availability, given that the published records reflect ecologically relevant relationships. With this approach, an applied meta-analysis for field studies (Fernandez-Duque and Valeggia, 1994) was not applicable because the frequency of encountered significant predictors was uneven and some were found in only a few significant relationships. The study setup of the reviewed studies showed high variability in terms of varying objectives of the studies. Instead the focus of this study was put on presenting an overview regarding the present knowledge concerning species–environment relationships, which may form a basis for species distribution modelling. As species distribution modelling requires large spatial datasets for training and validation, the significant relationships in field-studies also provides information of the potential availability of relevant predictors across the studied sea, which is important considering any efforts of pooling local and regional datasets and scaling up predictions. Thus, we wanted to find out if relationships between benthic species and predictors are equally common throughout the sea, and how the importance of predictors differs among subregions and organism groups, thus having implications for the success of species distribution models at these subregional scales, i.e. tens to hundreds of kilometres.

2. Material and methods

2.1. Literature search

The search of studies covered a 30-year period from 1979 to February 2010 (with about two thirds published in 2000 and afterwards). Peer-viewed studies from the Baltic Sea region, including Kattegat and partly Skagerrak, were searched from the database Aquatic Sciences and Fisheries Abstracts. The Baltic Sea was divided into six subregions (Fig. 1) based on HELCOM's Baltic Sea subdivisions and Bonsdorff et al. (2002). Potential papers were identified using the keywords 'Baltic Sea' (AND) 'Fish*' (OR) 'Macroinvertebrate*' (OR) 'Macrofauna*' (OR) '*benthos' (OR) 'Macrophyte*' (OR) 'Macroalga*' (Macrovegetation), which were the three major response group levels. Thus, we assured that studies with alternative regional or local sea names were covered by the search. Each paper was then sorted according to the six subregions by refining the search result using each of the subregion names, and manually by screening the studies. Fish papers were additionally screened so that only studies with a benthic focus were included, excluding studies on pelagic species. The results of the sorted papers were searched for a) significant empirical species- or assemblage–environment relationships in field studies (not field experiments), resulting in a database of field studies presenting at least one significant relationship (as no paper was found presenting a study with statistical analysis without at least one significant result). Non-significant relationships were noted. In case a paper included significant results for more than one species, the paper was regarded as two separate studies only if the species were tested individually. Otherwise >1 species were regarded as assemblages. Only studies with b) spatial replication, i.e. including more than one study site, ranging from 5 m to tens of kilometres apart were included in the database. Time series or seasonal studies were included c) only if both a) and b) were true, i.e. a significant response was spatially linked to one or several environmental predictors and this relationship was separated from the temporal one in the results. It is important to note that the database of studies does not provide an exhaustive list of all field studies on significant species-environment relationships in the regions of the Baltic Sea since late 1970s, but a representative sample based on the criteria mentioned above, i.e. spatially replicated field study of one or several benthic species with a significant response to one or several environment predictors. The database did not include descriptive studies with no statistical analysis.

2.2. Data analysis

The search identified a total of 17 predictors that showed a significant relationship with a species/assemblage in at least one study. The 17 predictors were pooled into six general categories, including bottom topography (water depth and slope), biotic features (biological processes such as predator–prey relationships, macrovegetation cover and cover of filamentous algae), hydrography (pH, nutrient content, oxygen, salinity, Secchi depth, sedimentation and water temperature), exposure (wave exposure), substrate (sediment type and substrate) and spatiotemporal variability (site and time), e.g. differences between two or more geographical locations or differences between two or more sampling dates (Table 1). The latter of these categories incorporates effects of an unknown number of deterministic or stochastic environmental gradients and is not particularly well suited for predictive purposes. The magnitude of spatiotemporal variability is informative for how patterns of biological assemblages are analysed in contemporary research, and for how frequently effects of various environmental factors may interact with spatial and temporal components. For macrovegetation, macrovegetation cover and cover of filamentous algae were excluded as predictors. For each of the individual predictors we summed the number of studies with