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REVIEW

Spatial scale and geographic context in benthic habitat mapping: review and future directions

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ABSTRACT: Understanding the effects of scale is essential to the understanding of natural ecosystems, particularly in marine environments where sampling is more limited and sporadic than in terrestrial environments. Despite its recognized importance, scale is rarely considered in benthic habitat mapping studies. Lack of explicit statement of scale in the literature is an impediment to better characterization of seafloor pattern and process. This review paper highlights the importance of incorporating ecological scaling and geographical theories in benthic habitat mapping. It reviews notions of ecological scale and benthic habitat mapping, in addition to the way spatial scale influences patterns and processes in benthic habitats. We address how scale is represented in geographic data, how it influences their analysis, and consequently how it influences our understanding of seafloor ecosystems. We conclude that quantification of ecological processes at multiple scales using spatial statistics is needed to gain a better characterization of species–habitat relationships. We offer recommendations on more effective practices in benthic habitat mapping, including sampling that covers multiple spatial scales and that includes as many environmental variables as possible, adopting continuum-based habitat characterization approaches, using statistical analyses that consider the spatial nature of data, and explicit statement of the scale at which the research was conducted. We recommend a set of improved standards for defining benthic habitat. With these standards benthic habitats can be defined as 'areas of seabed that are (geo)statistically significantly different from their surroundings in terms of physical, chemical and biological characteristics, when observed at particular spatial and temporal scales'.

KEY WORDS: Spatial scale · Benthic habitat mapping · Multiscale · Spatial statistics · Marine ecology · Spatial analysis · Surrogacy · Species distribution modelling

INTRODUCTION

The volume of space that can host life on Earth is at least 150 times greater in the oceans than on land (Gjerde 2006). However, scientific knowledge about marine environments is still sparse compared to terrestrial environments due to difficulties to access, observe, and sample most places in the marine realm (Solan et al. 2003, Robinson et al. 2011). The oceans, which cover 70% of our planet's surface, are esti-

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mated to be 90% unexplored (Gjerde 2006). Ocean research led by several international initiatives and groups (e.g. Census of Marine Life and the International Council for the Exploration of the Sea [ICES]) has increased significantly over the last decade (Heyman & Wright 2011, Borja 2014), driven by efforts by many nations to better manage and protect marine resources. In the ocean realm, benthic ecosystems provide important services (Thurber et al. 2013, Galparsoro et al. 2014) but are also increasingly impacted by human activities (e.g. bottom-contact fishing, oil and gas extraction) (Halpern et al. 2008, Williams et al. 2010, Harris 2012). Research on near-bottom environments and their associated biota has become essential to support effective monitoring and management strategies (Thrush & Dayton 2002, Ramirez-Llodra et al. 2011). Anthropogenic impacts on the seafloor alter benthic biodiversity (Cook et al. 2013, Grabowski et al. 2014), habitats (Jones 1992, Puig et al. 2012), and modify ecosystem structures and functions (Koslow et al. 2000, Olsgard et al. 2008). Ramirez-Llodra et al. (2011) noted that exploration, scientific research, monitoring, and conservation measures are essential to ensure that exploitation of resources does not lead to massive destruction of ecosystems. To protect benthic species from such threats, distribution patterns and ecological dynamics must be better understood (Ramirez-Llodra et al. 2011, Mengerink et al. 2014). Managers need accurate, quantitative and spatially explicit information, at scales relevant to their objectives, in order to support protection and management plans (Anderson et al. 2008, Davies & Guinotte 2011). Marine habitat mapping has become mandatory in some countries and contexts, such as the 1996 amendment to the United States Magnuson-Stevens Fishery Conservation and Management Act regarding the description and identification of essential fish habitats (Benaka 1999). To ensure that these efforts are as representative as possible, species distributions should be mapped at multiple scales (Lourie & Vincent 2004, Smith & Brennan 2012, Shucksmith & Kelly 2014). Mapping seafloor based on species' habitat requirements is essential and is the first step in implementing scientific management, monitoring environmental change, and assessing the impacts of anthropogenic disturbance on benthic habitats (Roff et al. 2003, Cogan & Noji 2007, Harris & Baker 2012a).

Habitats can be defined as physical spaces characterized by a combination of variables of different types in which species can survive (Whittaker et al. 1973). Several definitions of benthic habitats have been proposed. Harris & Baker (2012a, p. 8) define them as being 'physically distinct areas of seabed that are associated with the occurrence of a particular species'. A more comprehensive definition of benthic habitats could include the chemical environment and water properties known to influence benthic faunal distribution (Kostylev et al. 2001, Cogan & Noji 2007, Brown et al. 2011a). A benthic habitat can hence be defined as an area of the seabed that is distinct from its surrounding in terms of physical, biological, and chemical variables. Brown et al. (2011a) provide a comprehensive review of types of benthic habitat maps, techniques of data collection, and methods that can be used to create habitat maps. Habitat-based approaches to estimate organism response to landscape heterogeneity have been used for decades in landscape ecology (Turner et al. 2001, Robinson et al. 2011). Because species have a range of environmental preferences and requirements (Hutchinson & MacArthur 1959), many of these approaches focus on the structure and quantity of potential habitats, either instead of, or in addition to, the distribution of biological populations at the time of sampling.

Habitat maps must be placed in context with the appropriate spatial, temporal, and thematic scales (Cogan & Noji 2007). Scale is considered to be 'one of the most critical aspects in habitat mapping, as well as one of the most misunderstood' (Greene et al. 2007, p. 145). As Boyce (2006, p. 274) stated: 'Ecologists are still at a fairly naïve pattern-documentation phase in understanding the importance of scale.' Despite the well-known importance of spatial scale in benthic habitat mapping (Brown et al. 2011a), the topic is only briefly mentioned in texts (e.g. Todd & Greene 2007, Harris & Baker 2012b) and only a few publications address the implications of scale for benthic habitat mapping. Brown et al. (2011a) includes a complete section on spatial scale in benthic habitat mapping. Other publications have addressed spatial resolution (e.g. Anderson et al. 2008), the impact of scale in management and surrogacy assessment (e.g. McArthur et al. 2009, 2010), and its impact in shallow water monitoring (e.g. Van Rein et al. 2009).

Scale is only briefly acknowledged in the extensive literature on benthic habitat mapping, often with little or no treatment of the role of spatial scale in the production of benthic maps and the interpretation of research results. This lack of treatment likely indicates little awareness and understanding of the importance and role that spatial scale plays in benthic habitat mapping. Fig. 1 illustrates the increase in publications on benthic habitat mapping for the

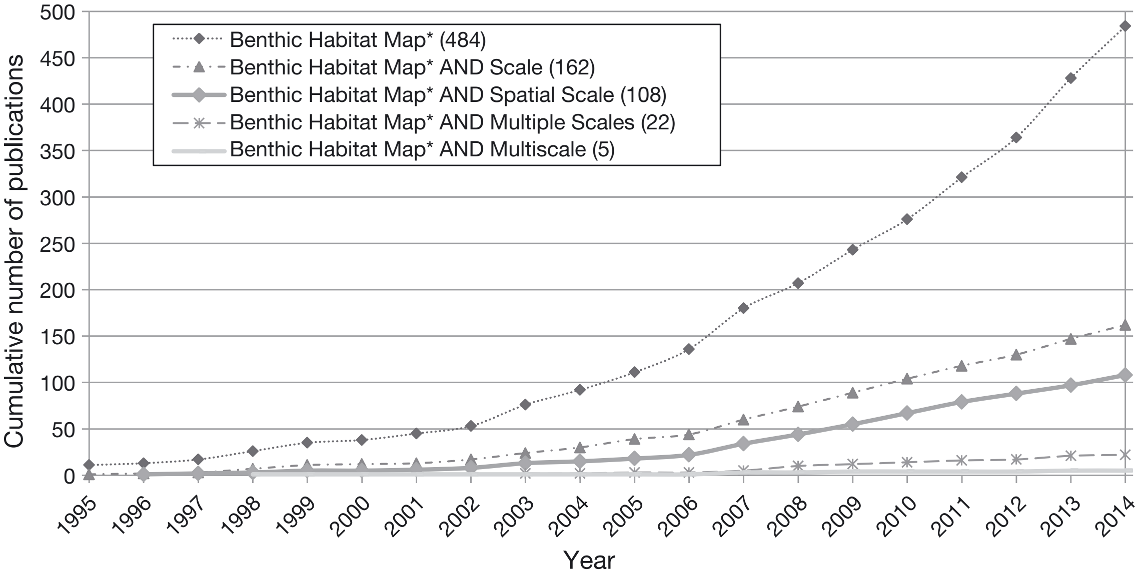

Fig. 1. Cumulative number of publications (articles or reviews) listed in the Scopus database mentioning specific keywords (see key) in their title, abstract or keywords, by the end of 2014

period 1995–2014, and the number of cases that address scale. Approximately a third of the articles and reviews used the term 'scale' in the title, abstract or keywords, with 22% for 'spatial scale', less than 5% for 'multiple scales' and 1% for 'multiscale'; these numbers are much lower than in landscape ecology-related publications, where scale is still considered as being insufficiently described (Lechner et al. 2012a).

The aims of this contribution are (1) to review existing knowledge on spatial scale in benthic habitats and their mapping, including the related practices of surrogacy assessment and species distribution modelling, and (2) identify ways to improve benthic habitat mapping practices. The paper is organized as follows. We first review knowledge of scale in ecology, including the difference between scales of phenomenon, observation and analysis. We then introduce the concepts of benthic habitat mapping, including the natural characteristics that can influence marine species distribution, the basis of their representation as spatial data and of their analysis, and the importance of characterizing habitat at multiple scales. Thirdly, we emphasize the need to consider the spatial nature of data in analyzing species' relationships with their environment. Fourth, we discuss current needs and future directions in habitat mapping, and propose a new standard for defining benthic habitat that includes the explicit statement of scale. Finally, we make recommendations regarding the integration of ecological scaling and geographical theories in habitat mapping.

SCALE IN ECOLOGY

Three types of scale are typically recognized in the ecological literature: spatial, temporal, and thematic. Several definitions of spatial scale have been given depending on the contexts (Schneider 1994, 2001a, Dungan et al. 2002, Lechner et al. 2012b). Spatial scale commonly refers to the spatial characteristic of an object or process, including both its spatial resolution (i.e. level of detail) and geographic extent (Schneider 1994, Gustafson 1998). Like spatial scale, temporal scale is characterized by both resolution (e.g. days vs. minutes) and extent (i.e. range of time) (Schneider 1994). Space and time are intrinsically linked and often depicted in joint space–time diagrams (Stommel 1963, Steele 1978, Delcourt et al. 1983). Thematic scale, also called level of organization, organizational scale, or ecological organization, is linked to the level at which objects of study are described, for instance taxonomic resolution (Levin 1992, Larsen & Rahbek 2005). Thematic scale is important because the observed relationships of any 2 variables can vary across thematic scales (Pearson 2002, Larsen & Rahbek 2005, Brown et al. 2011a, 2012). For instance, grouping species with different habitat requirements can result in conclusions that differ from when species are studied individually (e.g. Grober-Dunsmore et al. 2007, Lecours et al. 2013). Understanding the effects of spatial, temporal, and thematic scale is challenging but essential, as many important ecological processes are scale-dependent (Turner et al. 2001, Schneider 2009, De

Knegt et al. 2010). Changes in pattern with changes in scale have been recognized in ecology since the 1950s (Greig-Smith 1952), but the importance of scale only became widely acknowledged in the 1980s (Meentemeyer 1989, Schneider 2001a). Research on scale, on methods to scale-up and scale-down across scales, and on the problem of relating phenomena across scales is fundamental and remains an important focus in many sciences (Wiens 1989, Levin 1992, Schoch & Dethier 1996). According to Turner et al. (2001, p. 330): 'The effects of scale are now well recognized, but the need for improved quantitative understanding remains critical.'

Lechner et al. (2012a,b) distinguish the scale at which a pattern or process occurs from the scale of observation and the scale of analysis. The scale at which a pattern or process occurs is often referred to as intrinsic, operational, or ecological scale. The observational scale relates to the data that are used to describe natural phenomena (e.g. the pixel size, or spatial resolution, on gridded bathymetric data), while the analysis scale relates to the method used to analyze these data (e.g. the size of the analytic window used to perform focal statistics in spatial analysis).

Issues can arise when there is a mismatch between ecological, observational, and analytical scales: appropriate detection of species–habitat relationships and ecological patterns is dependent on the chosen observational and analysis scales (García & Ortiz-Pulido 2004, Gambi & Danovaro 2006). For instance, using a 1 km resolution bathymetric dataset would likely not allow the understanding of how bathymetry relates to species distribution in a coral reef, as knowledge of smaller changes in depth would be required. Observational and analytic scales are often arbitrarily chosen in ecological studies (Levin 1992), due to financial, technical or time constraints (Meentemeyer 1989) and are typically not reported in sufficient details (Pittman & McAlpine 2003). Wheatley & Johnson (2009) reviewed the use of multiple scales in terrestrial wildlife-habitat studies, finding that 70% of the articles used arbitrarily chosen scales, with no consideration of the scales relevant to wildlife or to environmental variables. They mentioned that when such choices are made, 'published results may reflect scale artefacts' and scale-dependent processes may be missed 'by examining irrelevant or redundant scales of observation' (Wheatley & Johnson 2009, p. 151). Scale artefacts are observations that seem to explain the studied pattern or process, but may not be causally linked or cannot be validated due to the choice of observational scale (Wheatley & Johnson 2009, Lechner et al. 2012b). In order to avoid scale artefacts and missing important patterns or processes, data and analysis need to capture the essential elements of the habitat, meaning that the observational and analytic scales should encompass the ecological scales of the biological or environmental phenomenon being studied (Hobbs 2003, Mayor et al. 2009, Goodchild 2011). Habitat structure must then be measured at spatial scales relevant to the organism of interest (Pearson 2002, Gallucci et al. 2009, De Knegt et al. 2010). For instance, the habitat of a wide-ranging shark would not be measured at the same scales as the habitat of a small cavity-dwelling reef fish, even if they are found within the same geographic area.

No single scale, be it spatial, temporal or thematic, is appropriate for the study of all ecological problems, and all scales do not have similar explanatory powers (Clark 1985, Wiens 1989, Levin 1992, Willis & Whittaker 2002). For instance, coarse-scale data can help understand regional patterns of terrestrial and marine species biogeography (e.g. Rahbek & Graves 2001, Davies et al. 2008) but may be insufficient for identifying specific conservation areas (Davies & Guinotte 2011). Models created with coarse-scale data to predict a species' geographic distribution can be improved using better knowledge of its habitat requirements gained from finer-scale information (Bryan & Metaxas 2007, Etnoyer & Morgan 2007, Davies & Guinotte 2011, Ross & Howell 2013). However, saying that no single scale is appropriate does not mean that all scales serve a purpose equally well or that scaling laws or patterns cannot be defined (Levin 1992).

Spatial scale is an important consideration when studying organism and habitat structure interactions (McCoy et al. 1991, Pearson 2002). Habitat selection by a particular species can occur and be measured at some scales and not necessarily at others (Owen 1972, Boyce 2006). For instance, Anderson et al. (2005) found that elks select their habitat based on broad-scale spatial distribution of wolves in conjunction with fine-scale selection of forage areas. In a marine context, the associations of infaunal (De Leo et al. 2014), sessile (Schneider et al. 1987), and mobile epibenthic species (Grober-Dunsmore et al. 2007, Kendall et al. 2011) with their environment were all found to vary with spatial scale. The concept of habitat is both scale-dependent (Pearson 2002) and species-specific (Pandit et al. 2009). For instance, habitat specialists, such as coral reef gobies (Munday et al. 1997), live in a very specific habitat characterized by a narrow range of environmental conditions and respond to more fine-scale processes. On the other hand, habitat generalists, such as the copepod *Nitocra spinipes* (Pandit et al. 2009), can tolerate a broad range of environmental conditions and respond to more broad-scale processes. More generally, Schneider et al. (1987) found that mobile species often show decoupling from the environment at finer scales, and habitat association at coarser scales, compared to finer-scale coupling with habitat by sessile species. Meyer & Thuiller (2006) reported that the majority of species respond to habitat characteristics at more than one scale at the same time. Despite that, a response measured at one particular scale cannot always be used to predict habitat use at another scale (VanderWerf 1993, Apps et al. 2001).

SCALE IN BENTHIC HABITAT MAPPING

Review of concepts and methods

Habitat mapping

The complex interactions between biological, physical, chemical, and behavioural elements of the marine environment can make benthic habitats difficult to map (Zajac 2008, Rigby et al. 2010). The integration of data representing these elements at multiple scales is especially challenging (Brown et al. 2011a). Traditional data-acquisition techniques can be limited by varying factors, including depth (as with optical remote sensing that only captures data in shallow waters), visibility (as with cameras), and time (as with SCUBA diving) (Dunn & Halpin 2009, Costa et al. 2014). Whilst some techniques can help delineate benthic habitats at some specific scales, they present challenges when trying to delineate benthic habitats at other scales. For instance, seafloor acoustic mapping from the surface and sparse ground-truthing in deeper waters provide information at a scale that Davies et al. (2008) considered regional, but lack the capacity to characterize finer-scale patterns and processes (Stone 2006, Davies et al. 2008, Tittensor et al. 2009). On the other hand, SCUBA diving allows the collection of fine-scale data in shallow waters but cannot generate a broader characterization of ecosystem pattern (Costa et al. 2014). The use of bathymetric LiDAR (in shallow waters) and acoustic remote sensing (in deeper waters) can help reduce these sampling gaps, by providing continuous and high-resolution data necessary for mapping over greater areas, and thus at scales that may be more relevant for understanding pattern and process in these habitats (Kenny et al. 2003). Despite their strengths, these techniques have their own limitations, as they do not necessarily provide data of sufficient resolution to understand very fine ecological processes. However, combining acoustic or LiDAR data with *in situ* observations, high-resolution geoscientific and environmental information, and spatial analytical techniques does allow for more accurate quantitative characterization of habitat at multiple scales, in addition to providing a framework for mapping the distribution of benthic species and interpreting spatial patterns in biodiversity (Whitmire et al. 2007, Wedding et al. 2008, Brown et al. 2011a, Harris & Baker 2012a).

Brown et al. (2011a) identified 3 of the most common approaches to benthic habitat mapping: abiotic surrogate mapping that does not consider biological data, and unsupervised (top-down approach) and supervised (bottom-up approach) classifications that integrate biological data in different ways (see Fig. 4 in Brown et al. 2011a). These methods correspond to what the 'Review of Standards and Protocols for Seabed Habitat Mapping' published by MESH (Mapping European Seabed Habitats) identified as the general approach to benthic habitat mapping: the spatial integration of different datasets, usually within a geospatial environment (Coggan et al. 2007). While a number of studies (e.g. Brock et al. 2004, Wedding & Friedlander 2008) mapped benthic habitats in shallow environments using bathymetric LiDAR, optical remote sensing, or SCUBA diving, this approach often focuses on the use of acoustic remote sensing (e.g. multibeam echosounders, side-scan sonars) to collect spatial information on the characteristics of the seafloor (Brown et al. 2011a); most of the 57 case studies presented in Harris & Baker (2012b) used either backscatter or bathymetric data, or both. For example, Copeland et al. (2012) combined information extracted from bathymetric and backscatter data with biota in a sub-Arctic fjord to determine 6 types of benthic habitats and to identify patterns of biodiversity. All the techniques used to map both shallow and deeper waters influence or determine the scale of data collection and analysis. For instance, the spatial resolution and extent of acoustic bathymetric data depends on the sensor-to-seafloor distance (e.g. Lecours & Devillers 2015) and the systems used (Kenny et al. 2003): the shorter the distance, the higher the resolution and the lower the extent.

In parallel, approaches from terrestrial ecology are increasingly used in marine ecology to represent environmental heterogeneity as habitat maps. Seascape ecology draws on techniques from landscape ecology, using spatial pattern metrics to quantify the seascape structure and delineate patch-based models of habitat type (see Boström et al. 2011, Pittman et al. 2011, Wedding et al. 2011). The size of habitat patches can be an indicator of the spatial scale at which species use an environment when linked to species distribution and behaviour (Pittman & McAlpine 2003, Pittman et al. 2007). For instance, Hitt et al. (2011) tracked fish movements, linking them to seascape structures to study habitat use in relation to patch types and connectivity, which allowed quantifying the extent of the environment that the fish were using. The literature on seascape ecology is however still scarce (Pittman et al. 2011). Applications are mostly in coastal shallow environments, using optical remote sensing (i.e. aerial photography or satellite remote sensing) (e.g. Kendall & Miller 2010) or bathymetric LiDAR data (e.g. Purkis & Kohler 2008), and are often applied to reef fishes (e.g. Kendall et al. 2011). Despite its potential to explain marine ecological patterns and processes at multiple scales (Schoch & Dethier 1996), seascape ecology has yet to be implemented in deeper water using acoustic bathymetric data. Habitat maps developed in a seascape ecology context also involve the consideration of spatial scale, as the spatial pattern metrics are dependent on the resolution and extent of the input data that influence the minimum mapping unit (MMU) (Saura 2002, Fassnacht et al. 2006, Kendall et al. 2011). MMU is the size of the smallest area to be mapped as a discrete unit, and its selection determines the scale at which patches are defined in a seascape: as the MMU increases, rare and smaller features tend to not be considered by the analysis, which can lead to erroneous interpretation (see Kendall & Miller 2008).

Significant progress has been made in the understanding of benthic habitats in the last decade (see Todd & Greene 2007, Harris & Baker 2012b) despite the difficulties associated with their mapping, modelling, and management (Diaz et al. 2004). Much work remains to be done to gain an adequate understanding of these complex ecosystems at relevant scales. For instance, very little work has been done on infaunal benthos (see De Leo et al. 2014). Not only is most benthic diversity infaunal, but the rate of release of nutrients into the water column, a key benthic variable, is driven mostly by infaunal activity. Mapping benthic diversity to the species level is not possible in the absence of continuously mappable surrogates (see next subsection) for any one species. However, with sufficiently fine-scale data, it would be possible to map evidence of biogenic flux, such as castings or burrow diameters, through the sediment surface. For instance, acoustic reflectivity (backscatter) can capture fine-scale information of the sediment surface, which can then be combined with *in situ* groundtruthing in a benthic modelling approach (e.g. Brown et al. 2011b, Freitas et al. 2011, Copeland et al. 2012). Another issue that constrains complete understanding of benthic ecosystems is the species-specific relation to habitat as a function of scale, which in turn complicates the study of species assemblages (Grober-Dunsmore et al. 2007, Howell et al. 2010, 2011; see also Brennan et al. 2002, Brown et al. 2011a). For example, Schneider et al. (1987) found that the scale-dependent association between population density and substrate differed between mobile and sedentary fauna.

Surrogacy

As in terrestrial ecology, the challenges associated with sampling marine organisms in relation to their environment has led to an increasing use of surrogates, also known as 'proxies' (McArthur et al. 2009, 2010, Anderson et al. 2011). A surrogate can be defined as 'a measurable entity that will represent, or substitute for, a more complex element of biodiversity that is more difficult to define or measure' (Harris & Baker 2012b, p. 899). Surrogates can be any measurable characteristic of the environment, sampled either *in situ* at specific locations (e.g. sediment pH), or provided as continuous or near-continuous coverage, such as bathymetry derivatives (e.g. seabed roughness or slope). Before mapping habitats, surrogate variables for a particular species first need to be identified, together with the strength of covariation in the study, and the establishment of a biological basis for the covariation. For instance, the selection of surrogates to be tested and the scale at which they should be tested may be based on knowledge gained from previous observations, experimental work or some evidence of causal connection (Brennan et al. 2002). Surrogates may be relevant only at particular scales (Urban et al. 1987, Gambi & Danovaro 2006). For instance, Tong et al. (2013) found aspect (the geographic orientation of the slope) to be a good surrogate of the cold-water coral *Paragorgia arborea*'s presence over areas of 30 × 30 m and 90 × 90 m, but not at a broader scale. They linked this result to the presence of finer-scale bottom currents in the study area that bring food to the corals, which is not the case for broader-scale currents (Tong et al. 2013).

Once defined, surrogates can be used to map habitats, predict or estimate species distribution, and build habitat suitability models (e.g. Lucieer et al. 2013, Hill et al. 2014). The use of surrogates for these purposes cannot be trusted at spatial scales other than the scale at which the surrogate was defined.

Species distribution modelling

Combining georeferenced species occurrence data with environmental variables to develop habitat suitability and predictive distribution models is an important approach increasingly used in the marine environment (Heyman & Wright 2011, Robinson et al. 2011, Brown et al. 2012, Hill et al. 2014, Vierod et al. 2014), especially for protection and management purposes (Ross & Howell 2013). These models build on existing knowledge of species–environment relationships, either directly or via surrogates, to predict the location and extent of potential habitat in areas where only environmental information is available (see Elith & Leathwick 2009, Zimmermann et al. 2010 for general reviews; and Robinson et al. 2011, Vierod et al. 2014 for specific reviews for the marine environment). The criteria (Brennan et al. 2002, Franklin 2009) to consider in the selection of a model for a particular application are (1) species characteristics, (2) data availability, (3) the observational and analysis scales, (4) stability in time (e.g. bathymetry compared to temperature), and (5) the biological and physical underpinnings (if any) of the model. As in terrestrial ecology, few marine studies address the issues of choosing an appropriate range of spatial scales at which to identify surrogates of species habitat or identify the appropriate scales at which to develop predictive models (Franklin 2009). A coarser scale model may underrepresent the area of suitable habitat since the finer-scale habitat features that drive species distribution are not captured by the data (Seo et al. 2009, Vierod et al. 2014) (see also Fig. 2). The scale (extent) of the study area also has a direct impact on the quality of the models (VanDerWal et al. 2009, Hijmans 2012), and Meyer & Thuiller's (2006) meta-analysis of species distribution modelling studies found that the use of environmental variables at more than one scale tends to give more accurate predictions. In the deep sea, the implementation of effective habitat suitability models is limited by the resolution and extent of environmental data (Vierod et al. 2014), and will only be possible if high-resolution data become globally available (Davies et al. 2008). Some data may not be available for an area, or may be available at an inappropriate scale. Often, certain variables (e.g. temperature, bottom current speed) are only available at a coarser resolution than other variables (e.g. slope and rugosity, measured using acoustic remote sensing techniques). Downscaling or improved spatial measurement of the former to a level in line with the latter is needed to free models from errors in cross-scaling and to put knowledge of species distribution relative to habitat on a sound basis.

Ecological scale: benthic species and their environment

Environmental and biological surrogates

Several environmental variables were found useful in characterizing marine habitats, with differing degrees of importance depending on species (e.g. Freeman & Rogers 2003), locations (e.g. Georgian et al. 2014), settings (e.g. submarine canyons) (e.g. De Leo et al. 2014), and spatial scales (e.g. Gambi & Danovaro 2006, Henry et al. 2013). This diversity in use of environmental variables highlights the difficulties in quantifying the distribution of benthic organisms in relation to habitat. Reviews of potential surrogates of marine benthic biodiversity can be found (e.g. McArthur et al. 2009, Howell 2010, Harris & Baker 2012b) but only McArthur et al. (2010) discuss the usefulness of surrogates in relation to spatial scale.

In addition to physical and chemical factors, biological factors and ecological interactions likely explain the distribution of benthic organisms at different scales (Robinson et al. 2011). For example, reproduction strategies can influence species distribution, following spatial patterns in which organisms expect to disperse gametes over greater areas to reduce aggregation (Gage & Tyler 1999). Ecological interactions can also be used as surrogates; if predation or commensalism is observed between 2 species (e.g. between structure-forming species and fishes), the presence of one could predict the other (Ward et al. 1999, Tissot et al. 2006, Mumby et al. 2008, Baillon et al. 2012). Both intraspecific and interspecific interactions vary with scale on land (Wiens et al. 1986b, Sherry & Holmes 1988) and in the ocean (Haury et al. 1978). Mellin et al.'s (2011) meta-analysis of the effectiveness of biological surrogates in marine studies showed that biological surrogates tend to be more effective at finer spatial scales (i.e. smaller spatial extent). According to Leaper et al. (2012, p. 858), 'the need for effective biological surrogates is especially critical in the marine realm, where a large number of species remain undescribed'. Yet biological surrogates are rarely used in habitat mapping as they are difficult to assess at meaningful (often fine) spatial scales (Muotka et al. 1998, Mellin et al. 2011, Snickars et al. 2014). The addition of biological surrogates to species distribution models can potentially improve predictions (Austin 2002, Robinson et al. 2011).

Combined environmental influence and multicollinearity

Environmental variables identified as surrogates can act together to influence species distribution. For instance, the combination of topography and currents influences the levels of connectivity among populations for reproduction at different scales (Adams & Flieri 2010, Rex & Etter 2010). On seamounts, millimetre-scale colonization patterns are affected by coarser-scale flow patterns, however the motion of the fine-scale benthic boundary layer is also a determining factor (Gage & Tyler 1999, Young 2009). On continental slopes, rough seafloors interact with meso-scale currents to create complex circulation patterns that could potentially lead to the isolation of populations (Rex & Etter 2010). Such relationships complicate data analysis because multicollinearity among variables occurs within and across scales (Rengstorf et al. 2012, Laffan et al. 2014). Multicollinearity occurs when 2 or more explanatory variables (e.g. water depth and temperature) are highly correlated (see Tabachnick & Fidell 2013), obscuring the influence of each variable (Hengl & MacMillan 2009, Tabachnick & Fidell 2013). Multicollinear explanatory variables are common in marine ecology but rarely considered in analyses (Wedding et al. 2011): multicollinearity should systematically be tested (Pittman et al. 2009). Statistical methods to address the problem can be found in Dormann et al. (2013) and Tabachnick & Fidell (2013).

That explanatory variables covary raises a question: how many and which variables are necessary to best characterize a habitat? In the past, a single surrogate was often used, but it is now widely accepted that biogeographic patterns are best explained by a combination of multiple variables (Hagberg et al. 2003, McArthur et al. 2009). Too few covariates can result in an overly general habitat characterization (Barry & Elith 2006, VanDerWal et al. 2009). The opposite, too many variables, can result in model overfitting (Peterson & Nakazawa 2008). According to Peterson et al. (2011), the number of variables will depend on the studied species, the complexity of the habitat, the availability of data, and the observational and analysis scales. Mateo Sánchez et al. (2014) argue that it is as important to identify the relevant environmental factors as to identify the scales at which these drive species distributions. Selecting relevant variables and at relevant scales is essential to the quality of habitat maps and the performance of predictive models (Austin 2002, Williams et al. 2012). The choices of variables and observational and analysis scales need to be based on their ecological relevance as these choices can impact the measurements of relationships between fauna and environmental variables (Araújo & Guisan 2006, Synes & Osborne 2011). Austin & Van Niel (2011) however report that assumptions made in the literature about the ecological relevance of variables vary among publications, are sometimes inconsistent, and so need to be revisited with a consideration of spatial scale.

Observational scale: representing nature with spatial data

Adequacy of spatial data

When expressed as ecogeographical data (i.e. ecological variables with a geographic component), surrogates have a spatial dimension defined by their latitude, longitude, and depth (or altitude for terrestrial applications). A measure derived from these 3 spatial variables is geographical distance, an important predictor of fish species distributions in coral reefs (Pittman & Brown 2011) and hard-bottom habitats (Dunn & Halpin 2009). These spatial variables define the spatial scale (resolution and extent) of ecogeographical data and can themselves be used as surrogates (McArthur et al. 2009). For instance, small changes in depth can better explain changes in populations than larger changes in latitude and longitude (Rex & Etter 2010). However, their ecological meaning is arguable (Pittman & Brown 2011). Depth for instance may itself be a surrogate of a causal variable such as light or temperature. A strong relation between a biological variable and non-causal surrogate (e.g. depth) can therefore obscure the relation to an underlying causal variable (e.g. light or temperature), reducing the predictive power of important covarying environmental variables (e.g. Araújo & Williams 2000, Clarke & Lidgard 2000, Hothorn et al. 2011).

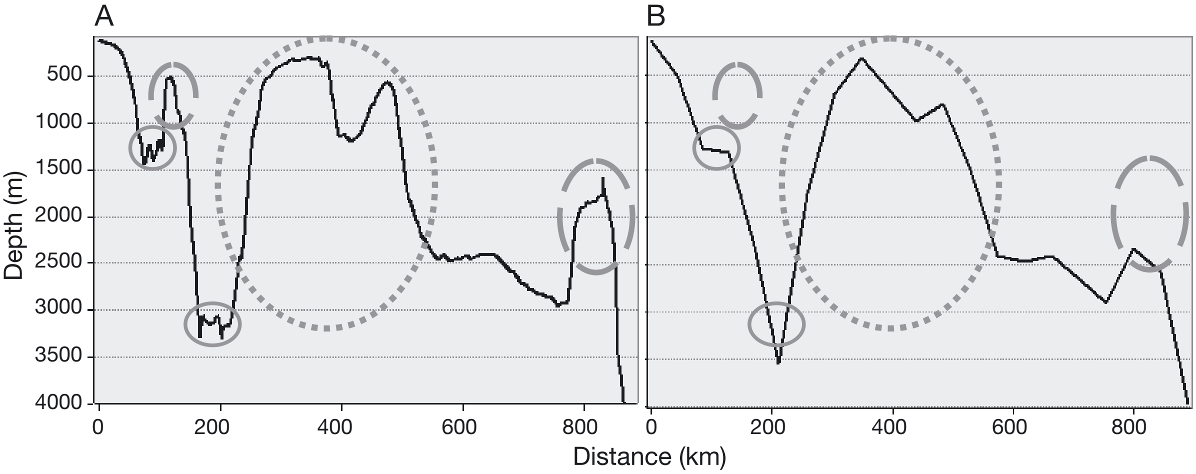

Fig. 2. Seabed profiles (black lines) showing fine-scale (solid gray ellipses), intermediate-scale (dashed gray ellipses) and broad-scale (dotted gray ellipses) topographic features delineated using (A) finer-scale and (B) coarser-scale bathymetric data. By using only a coarse observational scale, information on potentially ecologically important finer-scale features is not captured. (Conceptual figure shows bathymetric profiles derived from the General Bathymetric Chart of the Oceans [GEBCO] dataset; www.gebco.net/)

All data are not equally good at capturing the relevant information. Fig. 2 illustrates this idea with the example of bathymetry: if one finds that only broad-scale bathymetric features, such as a large seamount (dotted ellipses), drive species distribution, then finer-scale data are not needed. On the other hand, if intermediate-scale features (e.g. smaller pinnacles or banks; dashed ellipses in Fig. 2) influence species biogeography, finer-scale data would be required. If the detailed topography (e.g. single boulder; solid ellipses in Fig. 2) represent ecologically important habitats, even finer-scale data would then be essential to capture the important information.

The role of spatial scale has never been formally assessed in marine habitat mapping, despite repeated calls for an improved scientific understanding of benthic habitats at finer scales to allow better prediction of the geographic distribution of benthic species (Etnoyer & Morgan 2007, Davies et al. 2008, Davies & Guinotte 2011, Rengstorf et al. 2013). This lack of assessment makes it difficult to define which observational scales are 'fine enough' and which ones represent the upper limit of usefulness (Wilson et al. 2007). In terrestrial environments, local biological interactions often complicate the observation of the relationships between species and abiotic variables; the opposite occurs at coarser scales (Levin 1989, Sarkar et al. 2005), which makes fine-scale studies more appropriate to investigate details of biological mechanisms and broad-scale studies for generalizations (Wiens 1989). Wiens (1989) suggested that these patterns were likely to be the same in the marine realm but Steele (1991) showed that biological and physical phenomena do not scale in the same way in the ocean as on land. Planktonic life stages, the ability of some pelagic larvae to remain in an undeveloped stage until they find a suitable location to settle, and ocean fluid dynamics allow broad-scale dispersal into fine-scale suitable environments, which is not comparable to the finer-scale dispersal of many terrestrial species (Gray 1966, Carr et al. 2003, Kinlan & Gaines 2003). In benthic habitat mapping, it is possible that an intermediate observational scale finer than the current coarse-scale studies (although not too fine) could provide more useful information (cf. dashed ellipses in Fig. 2). For instance, Roberts et al. (2008) investigated communities at a local scale and concluded that intermediate-scale mapping might be useful to improve their results.

Data quality and spatial scale

Several factors, including multicollinearity, autocorrelation (see 'Adding geographic context: Spatial autocorrelation'), and spatial and thematic scales, can influence the accuracy of habitat maps (see Fig. 4 in Wedding et al. 2011). Despite recommendations to investigate and map variable uncertainty and error propagation when mapping habitats and species distribution (Rocchini et al. 2011, Beale & Lennon 2012, Vierod et al. 2014), uncertainty and quality issues associated with spatial and non-spatial data are rarely addressed in habitat mapping (Lechner et al. 2012a). Spatial data quality directly impacts the reliability of habitat maps, predictive models, and statistical description of species–habitat relationships (Menke et al. 2009, Moudrý & Šímová 2012). Data quality is conceptually related to spatial scale (Zhang et al. 2014, Lecours & Devillers 2015, Pogson & Smith 2015). For instance, the finer the data resolution, the more that uncertainty and poor positional accuracy influence relationships between variables (Hanberry 2013). Spatial matching between ecogeographical variables is particularly important: the positional error on biological data should always be smaller than the spatial resolution of the environmental data (Moudrý & Šímová 2012, Lecours & Devillers 2015) to avoid the emergence of false relationships between species and the environment, or the overestimation of a variable's range of values associated with a species (Guisan & Thuiller 2005, Guisan et al. 2007).

In habitat mapping and predictive modelling, a trade-off between data quality (i.e. accuracy and precision), sample size, and spatial scale (i.e. resolution and extent) must be considered (Brennan et al. 2002, Lecours & Devillers 2015). Despite attempts to address this challenge (e.g. Braunisch & Suchant 2010), it is still unclear which characteristics should be given a higher priority in sampling strategy. Fine resolution data arguably yields better predictive models if the data quality is adequate, even if the sample size of biological data is smaller (Huston 2002, Engler et al. 2004, Kaliontzopoulou et al. 2008, Reside et al. 2011, Williams et al. 2012), but this conclusion is not unanimous (Braunisch & Suchant 2010). Some authors suggest using uncertainty to weight the variables in modelling and statistical analyses; information with less positional error can increase precision and thus improve models (Beale & Lennon 2012, Moudrý & Šímová 2012).

Analysis scale: influence on analyzing ecogeographical data

Statistical relationships depend on the scale of analysis and results can vary as a function of it (Greig-Smith 1952, Rahbek & Graves 2001, Dungan et al. 2002). An example is given in this sub-section using surrogate variables derived from bathymetry, which are among the most sensitive to the scale of analysis. Bathymetric data have proven their potential to advance understanding of seafloor ecosystems and their value for habitat mapping (Anderson et al. 2008, Brown et al. 2011a), and can be used in geomorphometry (i.e. terrain analysis) to quantify seafloor topography and complexity (Lecours et al. 2015). In the last decade, a range of terrain attributes (e.g. slope, curvature) were found to have a relationship to marine biodiversity (McArthur et al. 2009), thus inducing an increase in the application of geomorphometric techniques in marine habitat mapping (e.g. Wedding et al. 2008, Zieger et al. 2009, Rengstorf et al. 2012, Tong et al. 2013, Dolan & Lucieer 2014). The relationship between spatial scale and terrain attributes has become an important research focus in geomorphometry (e.g. Florinsky & Kuryakova 2000, Schmidt & Andrew 2005, Deng et al. 2007, Li 2008), but a good understanding of scaling methods is still missing from geomorphometric analysis (Drăgut et al. 2009). Terrain attributes vary with scale (Evans 1972) and so their computation does not result in only one true, real fixed value, but in a range of possible values that depend on the resolution of the data and the extent of the analysis window (Shary et al. 2002, Hengl 2006). In the marine environment, coarse-scale geomorphometric analyses may not be adequate to resolve smaller features important for benthic biodiversity (Rengstorf et al. 2012, Lecours et al. 2013). The effects of the spatial resolution of bathymetry and terrain attributes on habitat suitability models are discussed in more detail by Rengstorf et al. (2012). Issues related to scale in geomorphometric analysis are similar to those in ecology and habitat mapping: it is widely accepted that a single scale (fixed resolution and window size) cannot completely describe a surface and capture all features of interest in an area (cf. Fig. 2) (MacMillan & Shary 2009, Goodchild 2011). Yet many applications use a single scale, with an arbitrary choice of spatial resolution for the input surface and a single neighbourhood size (MacMillan & Shary 2009). This limits analysis to those features that are observable at a single scale, which can have a significant impact on habitat maps and consequently on the resulting conclusions on species–habitat relationships. Similar scaling issues arise in the analysis of environmental data other than bathymetry.

Multiscale and multi-design approaches

Multiple scales and the MAUP

It has long been argued that ecology and geography would benefit from the adoption of a multiscale perspective in research, applications, and management (e.g. Stone 1972, Legendre & Demers 1984, Wiens et al. 1986a, Addicott et al. 1987, Meentemeyer 1989, Conroy & Noon 1996, Brennan et al. 2002, Pittman & McAlpine 2003). According to Wiens

(1989, p. 394), 'studies conducted at several scales or in which grain and extent are systematically varied independently of one another will provide a better resolution of domains, of patterns and their determinants, and of the interrelationships among scales.' The implementation of multiscale analysis is, however, challenging and thus remains sporadic (Wheatley & Johnson 2009) due to various difficulties including objective choice of sampling scales, simultaneous sampling of multiple scales (Addicott et al. 1987, Brennan et al. 2002), and the modifiable areal unit problem (MAUP) (Gehlke & Biehl 1934, Openshaw 1984, Marceau 1999), also known as change-of-support (COS) in spatial statistics (Cressie 1993, Cressie & Wikle 2011). MAUP is defined by Harvey (2008, p. 284) as 'the assumption that a relationship observed at one level of aggregation holds at another' and by Heywood et al. (2006, p. 416) as a 'problem arising from the imposition of artificial units of spatial reporting on continuous geographic phenomena resulting in the generation of artificial spatial patterns.' Combining data from 2 observational scales (e.g. when developing a habitat map) is invalid due to MAUP, and results from 2 different analytic scales (e.g. results of the quantification of species–habitat relationships at different scales) are not comparable: the aggregation of information taking place across changing spatial resolution or extent modifies the statistical properties (e.g. means, variances, and covariances) of the data, possibly resulting in distorted relationships between variables. Thematic scales can be very sensitive to MAUP. MAUP is related to Goodchild's (2011) concept of cross-scale inference, which occurs when inferences made at a coarser scale are transferred to a finer scale. Cross-scale inference is directly related to the concepts of ecological and atomistic fallacies (Robinson 1950, Cressie & Wikle 2011, see Lloyd 2014). The action of inferring across scales without checking for MAUP or cross-scale inference may lead to misinterpretation of results (Openshaw & Taylor 1979, Meentemeyer 1989) and unfounded conclusions. However, methods exist to deal with MAUP: Zhang et al. (2014, p. 147) elaborate on multivariate geostatistics 'to facilitate multisource and multiscale data integration', a relevant method for habitat mapping where data are often collected at different scales and with different sensors.

Multiscale and multi-design frameworks

Wheatley & Johnson (2009) distinguish multiscale from multi-design sampling. The former is characterized by 2 elements: (1) the same environmental variables must be analyzed across scales and (2) there needs to be a change in only one of the 2 elements of spatial scale (i.e. resolution or extent). When both the spatial extent and resolution are changed, a study is multi-designed rather than multiscale (see Fig. 2 in Wheatley & Johnson 2009). Fig. 3 illustrates the difference between the 2 approaches. In a number of studies, the term 'multiscale' is inappropriately used to characterize the independent use of multiple scales, thus corresponding to a 'multi-design' approach (e.g. Brennan et al. 2002, Anderson & Yoklavich 2007, Georgian et al. 2014). The distinction is important as multi-designed studies cannot allow

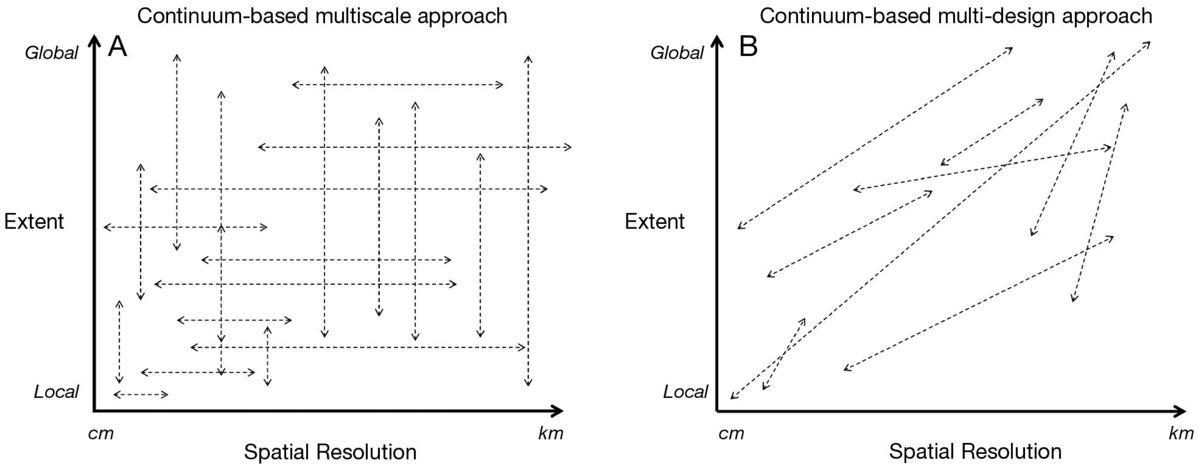

Fig. 3. (A) Multiscale and (B) multi-design continuum-based approaches. Both extent and resolution vary in a multi-design approach, while only one of these 2 scale characteristics is modified in a multiscale survey; each dotted line illustrates an example of how a single study could be framed

generalization and comparison of results between the different scales due to MAUP (Jelinski & Wu 1996, Wu et al. 1997, Nelson 2001; see Lechner et al. 2012b for MAUP in multiscale studies). Despite potential errors of interpretation caused by MAUP, comparisons between scales are often performed in the literature without exploring its effects.

Studying benthic habitats at multiple scales

Benthic habitat studies at multiple scales were first performed along transects (e.g. Schneider et al. 1987, Schneider & Haedrich 1991). Extending knowledge gained from this type of study to 2-dimensional mapping is challenging in terms of logistics, data volume, and analytic complexity. Recent work has begun to meet these challenges by looking at the differences between local and regional settings, and showing the importance of observing and mapping seafloor habitats at more than one scale (Wilson et al. 2007, Davies et al. 2008, Wedding et al. 2008, Zieger et al. 2009, Tong et al. 2013). In species distribution modelling, combining data from different scales has improved model reliability and performance (Wu & Smeins 2000, Store & Jokimäki 2003, Mateo Sánchez et al. 2014).

Benthic habitat studies at multiple spatial scales have generated several insights. For instance, some variables (substrates, food supply) were found to best explain species distribution at relatively fine scales (Davies & Guinotte 2011, Edinger et al. 2011). Conversely, other variables (e.g. productivity) were found to have a stronger influence at relatively coarse scales (Davies et al. 2008). Still other variables (e.g. depth) were found to be important at both finer and coarser scales. However, these conclusions are constrained by the observational and analysis scales used in these studies, which did not cover a broad continuum of spatial scales. For instance, fine-scale ocean chemistry could also be found to be locally important if studied within an appropriate range of fine scales.

ADDING GEOGRAPHIC CONTEXT BY CONSIDERING THE SPATIAL NATURE OF DATA

When mapping habitats, it is important to consider the spatial attributes of measurements. Beyond the questions of spatial scale, considering spatial properties of the data is vital in understanding ecological complexity in benthic habitats (Brown et al. 2011a) and in supporting management decisions about these habitats (Katsanevakis et al. 2011, Galparsoro et al. 2014). Spatial heterogeneity (spatial nonstationarity) and spatial autocorrelation (spatial dependence) are properties of most ecogeographical data: spatial heterogeneity refers to the level of variation of a property across space, i.e. if an observed variable varies locally or globally (Miller 2012), while spatial autocorrelation (SAC) is ‘the correlation of a variable with itself’ (Lloyd 2014, p. 13) and quantifies the observation that spatially closer objects tend to be more similar than spatially distant objects (Tobler 1970). These 2 properties can strongly affect observed relationships and predictive models (Foody 2004, Hothorn et al. 2011, Hijmans 2012). Finley (2011) compared predictive statistical models that account for spatial heterogeneity and SAC to regular regression models. This comparison showed that models accounting for both properties performed better than non-spatial models or models accounting for SAC alone. Spatial heterogeneity and SAC are also strongly scale-dependent, varying with both resolution and extent (Meentemeyer 1989, Legendre 1993, Dutilleul & Legendre 1993, Lloyd 2014). Zhang et al. (2014, p. 67) stated that ‘the interactions between spatial dependence and spatial heterogeneity have been shown previously to alter local definitions of scales.’ Consequently, standard statistics based on the assumptions of independent and identically distributed (IID) variables, while used in many ecological studies, should not be used if they violate these statistical assumptions (Meentemeyer & Box 1987, Marceau & Hay 1999, Brennan et al. 2002, Goodchild 2004, Beale et al. 2010, Windle et al. 2010). Demšar et al. (2013) identify the need to promote ‘spatially aware’ statistical methods, and other authors advocate for ‘the need to move beyond potentially misleading global regression models which can obscure the space-varying nature of relationships between the outcome variable of interest and covariates’ (Finley 2011, p. 149, based on Foody 2004). Nevertheless, standard IID statistics are still often used (Austin 2002, Brennan et al. 2002, Fortin et al. 2005).

Spatial autocorrelation

While rarely considered in marine habitat mapping studies, SAC is a well-known scale-dependent phenomenon in geography and ecology (Legendre & Fortin 1989, Legendre 1993) that should always be assessed before conducting spatial analysis (Dormann et al. 2007, Moudrý & Šímová 2012, Laffan et al. 2014, Vierod et al. 2014). SAC can be present even when samples are collected using random sampling schemes (Lecours et al. 2013). Samples presenting SAC are not statistically independent, which can influence standard statistical tests (Moran 1948, Cressie 1993), introducing redundancy into the analyses, and often can induce cross-scale correlation among the variables (Battin & Lawler 2006, Kristan 2006, Rigby et al. 2010). In species distribution models, SAC of environmental covariates can increase the influence of positional uncertainty in species occurrence data (Moudrý & Šímová 2012), and artificially increase the performance of models (Veloz 2009, Hijmans 2012). Segurado et al. (2006) demonstrated that SAC inflated the significance estimates of their species distribution models up to 90-fold.

Several tools can be used to measure and handle SAC (see Zhang et al. 2014). The spatial scale at which SAC occurs needs to be identified to deal with SAC effects. Techniques to identify this scale include spectral analysis (e.g. Legendre & Demers 1984), study of the 3-term local quadrat variance metric (e.g. Boyce 2006), and neutral landscape models (e.g. With & King 1997). SAC has a strong potential to help resolve ecological complexities. Legendre (1993) indicates that it should be considered as one of the structural attributes of the landscape that needs to be understood, and not considered only as nuisance. SAC can be an indicator of spatial variability, and can be used to study patchiness as a function of scale across a landscape or seascape (Sokal & Oden 1978, Sokal 1979). The exploration of the structure of SAC in occurrence data can help improve predictive models by presenting information on the dispersal potential of the organisms (Smith 1994, Araújo & Williams 2000, Keitt et al. 2002), even more when this is done at multiple scales (Václavík et al. 2012). De Oliveira et al. (2014) showed that accounting for SAC in environmental variables prevents over-fitting of models whilst improving accuracy. Despite its importance, Dormann (2007) found that less than 20% of species distribution modelling studies accounted for SAC, and most of them focused on trying to remove it, something that cannot be done (Mizon 1995, see discussion in Fortin & Dale 2009). According to Vierod et al. (2014), none of the species distribution modelling work performed in the deep sea has explicitly considered SAC (e.g. Ross & Howell 2013). Failure to account for SAC can result in the selection of predictors with the greatest level of autocorrelation (Lennon 2000), the selection of broad-scale predictors over finer-scale ones (Diniz-Filho et al. 2003), and selection of models with too many predictors (Hoeting et al. 2006, Latimer et al. 2006). Beale et al. (2007) showed that precision tends to rapidly decrease when SAC increases when using standard non-spatial models. Dormann et al. (2007), Miller et al. (2007), Veloz (2009) and Miller (2012) review SAC in a context of species distribution modelling.

The spatial structure of species distribution is influenced by the autocorrelation among environmental variables (exogenous autocorrelation) and by the autocorrelation among biological variables (endogenous autocorrelation) (Miller 2012). Failing to consider SAC in the analysis and interpretation of data can lead to misinterpretation and incorrect conclusions about spatial structure and the variables that influence it (Lennon 2000, Keitt et al. 2002, Segurado et al. 2006). Incorporating SAC into modelling effort allows additional knowledge to be gained from the analysis, allowing for habitat characterizations that are closer to reality (Hothorn et al. 2011, De Oliveira et al. 2014). Physical and biological processes can be used to generate testable hypotheses concerning change in SAC in benthic habitat structure and benthic fauna (Schneider & Haedrich 1991). Developments in geostatistical theory now allow prediction of changes in SAC and adaptation of standard statistics for use with spatial data, without violating any IID assumptions. These adaptations often result in better performance than standard statistics when compared on the same datasets (e.g. Brunsdon et al. 1996, Fotheringham et al. 2002, Jombart et al. 2008).

Using spatial statistics to account for spatial heterogeneity

The interpretation of species–environment relationships and predictive models can be influenced by the choice of statistics used to perform the analysis (Dormann et al. 2007, Finley 2011). Most habitat mapping studies have relied on simple statistics to test species–environment relationships (e.g. Pearson's correlation) before the application of multivariate statistics (Brown et al. 2011a). Multivariate techniques such as linear discriminant function (e.g. McLeod et al. 2007) or principal components analysis (PCA) (e.g. Anderson et al. 2011) allow the inclusion of correlation structure in models and are now more common. With these techniques, the independent variables correspond to the values of environmental covariates at certain point locations corresponding to species occurrences. Often, geographical effects are not considered when statistical analyses are performed on these points and their associated environmental values, and results are represented non-spatially in tables (e.g. Antunes et al. 2008, Preston 2009). Other works use raster-based statistical analyses where each pixel is considered a sample point (e.g. Maina et al. 2008, Verfaillie et al. 2009). However, despite the fact that pixels are georeferenced, the geographical effects are not taken into consideration in the calculations, but only in the representation of the output maps (Demšar et al. 2013).

Current developments in statistical sciences extend traditional methods to include the spatial component. Locally and geographically weighted statistical methods that account for spatial heterogeneity are becoming increasingly common (Lloyd 2014), particularly in social sciences (e.g. Lloyd 2010a,b), helped by the development of tools for implementation (e.g. the R package GWmodel) (Lu et al. 2014b). Rare examples of their use in marine ecology come from Windle et al. (2010, 2012), who demonstrated that the use of Geographically Weighted Regression (GWR) could improve the detection of interspecies relationships (cod and invertebrates) and species–environment relationships, with identification of the scale(s) at which these relationships were relatively strong. In addition to these methods that consider spatial effects, future developments in geostatistics will likely improve capacity to detect patterns of variations across spatial scales (see Atkinson & Tate 2000, Zhang et al. 2014). For instance, Pardo-Igúzquiza & Dowd (2002) introduced a geostatistical technique (namely a factorial cokriging) to identify how cross-correlation between variables varies with scale.

FUTURE DIRECTIONS — INTEGRATING SPATIAL CONCEPTS IN HABITAT MAPPING

Past, current and future trends in benthic habitat mapping

Studies of species–environment relationships often use a limited number of surrogates at either one scale or at multiple arbitrarily chosen scales (Lechner et al. 2012b). Studies of habitats at multiple scales tend to be multi-designed rather than multiscale. While such studies can contribute to our knowledge of marine ecosystems, they may produce results that are not comparable among scales and studies (e.g. because of MAUP) (Mayor et al. 2009, Lechner et al. 2012b). Also, the lower and upper limits of ‘useful’ scales at which to study benthic habitats are unknown: while there is a belief in the benthic habitat mapping community that finer-scale data will improve the understanding of benthic ecosystems, such an assumption is not necessarily correct as fine-scale data do not always reveal associations present at coarser spatial scales (Schneider et al. 1987).

As highlighted in this review, a multiscale perspective needs to be adopted in benthic habitat mapping (Nash et al. 2014), using objective and non-arbitrary methods to select observational and analytic scales (Wiens 1989, Lechner et al. 2012b). Data collection should be planned to characterize as much as possible of the physical, chemical, and biological environment, with emphasis on those variables relevant to the purpose of the survey. Over the past 10 yr, bathymetric LiDAR, acoustic remote sensing, and underwater vehicles have revolutionized how the seafloor environment can be mapped and studied. There are, however, some fundamental technical limitations, such as the footprint size (the size of the area of seafloor surveyed at a particular moment), that will dictate the scale at which the data are available (Kenny et al. 2003, Diaz et al. 2004). These considerations should be integrated in the scale assessment of given studies even though they are often neglected or ignored once the data enter the realm of geographic information systems (GIS) for analysis and map production (Brown et al. 2011a).

The importance of identifying changes in spatial pattern on a continuum has long been recognized in physical and biological oceanography (e.g. Stommel 1963, Steele 1978), and in ecology (Wiens 1989, Levin 1992, Brennan et al. 2002). In terrestrial ecology, Mayor et al. (2009) recommended using a spatial, continuum-based approach to identify the ranges of scales over which organisms associate with their habitat. Advances in spatial statistics (Cressie 1993) put continuum-based analysis on a sound mathematical basis. A continuum-based approach, using coarse-graining, has been applied to benthic transect data (Schneider et al. 1987), but has yet to be implemented in 2-dimensional benthic habitat mapping due to the lack of available data covering a substantial range of scales. The computational power needed to analyze and store such data (Vierod et al. 2014) further limits the application of such approach to quantify the strength of association with habitat as a function of scale. Hierarchical data models could eventually be used to map habitats at multiple scales and implemented in GIS environments so that one habitat map can be represented in different ways depending on the intended application or question.

The idea of identifying the 'best' or 'right' scale to study habitat association and habitat selection has proven elusive. A logical candidate for 'best' scale is that at which variance in either density or a habitat variable reaches a maximum. However, spectral analyses show no peaks in variance in physical and biological variables in either the pelagic (Horne & Schneider 1997) or benthic realms (Schneider et al. 1987). Similarly, peaks in the scale at which organisms are associated with habitat are another logical candidate for 'best scale'. Peaks in covariance were not found for any epibenthic species in a study on the outer continental shelf of Newfoundland (Schneider et al. 1987) and have yet to be reported in subsequent studies. Competing with the idea of 'right' scale, Wiens (1989) introduced the concept of scale domains, which he defined as ranges of continuous scales for which there is no change (or a constant change) in the observed pattern or process and separated by 'chaotic' transitions (see Fig. 4 in Wiens 1989). He argued that these domains were key to understanding ecological systems and could define the limits of generalizations (i.e. the bounds within which it is possible to scale-up or scale-down). Scale domains, as defined graphically by Wiens (1989), have not yet been confirmed by empirical data. Graphic representations of patterns and processes as a function of resolution scale in a benthic context (Schneider et al. 1987, Schneider & Haedrich 1991) show a variety of patterns, with no evidence of transitions as depicted by Wiens (1989). The term 'scale domain' has however been used by other authors to characterize levels in hierarchical theory and modelling frameworks (e.g. Wu 1999, Pearson & Dawson 2003, Muñoz-Reinoso 2009). The concept of 'scale-dependent pattern and process' is arguably of more utility in habitat mapping than attempts to 'detect the right scale' or identify 'scale domains'. Scaling manoeuvres (Schneider 2001b), in either the distance domain (e.g. lagging) or frequency domain (e.g. coarse-graining) are available for characterizing the association of benthic biota with habitat, and quantifying habitat association as a function of scale. Fig. 4 illustrates how such techniques can be implemented by quantifying the association between a species and several characteristics of its environment at multiple scales.

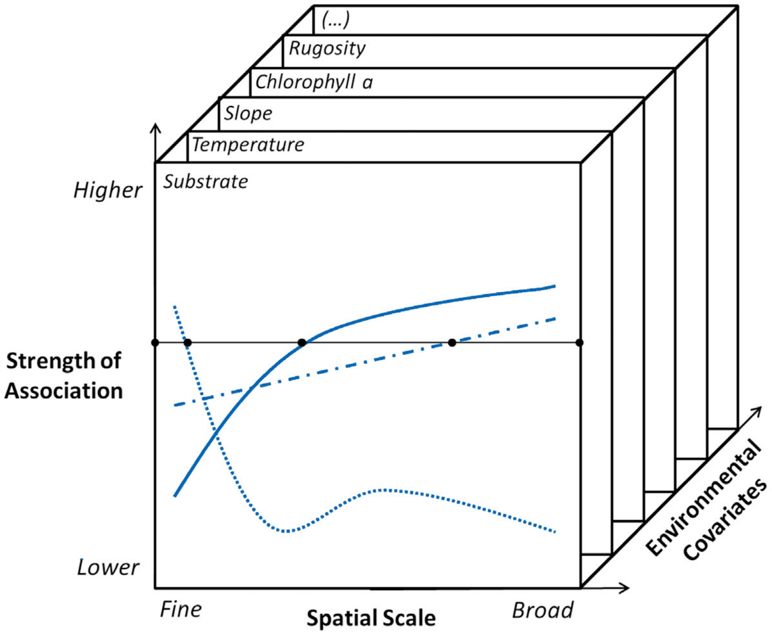

Fig. 4. Conceptual representation of the implementation of a continuum-based multiscale approach to explore scale-dependency of species–environment relationships. By sampling several environmental characteristics (*z* axis) at multiple spatial scales (*x* axis), it is possible to quantify the strength of association (*y* axis) between a species and its habitat as a function of scale (blue curves). The black horizontal line represents a given significance threshold. Note that if a coefficient of correlation was to be used to measure significance, there would be 2 significance thresholds: one for strongly positive correlations and one for strongly negative correlations. Curves are hypothetical and inspired by results from Horne & Schneider (1997) (pelagic species), and Schneider et al. (1987) and Kendall et al. (2011) (benthic and epibenthic species)

Because benthic habitats are being altered or destroyed at a faster pace than we discover and understand them (Ramirez-Llodra et al. 2011), it becomes urgent to make effective use of resources to map benthic habitats. Identifying useful surrogates will become possible as this field shifts from studies at multiple scales that only tell part of the story, to continuum-based multiscale approaches. When studying species–habitat relationships, it is as important to identify the scales at which environmental factors drive species distributions as to identify the relevant environmental factors (Williams et al. 2012, Mateo Sánchez et al. 2014). Sampling should be planned with a full combination of efforts to survey as many characteristics of the environment as possible and at as many scales as possible. Because all species cannot be studied, species assemblages (e.g. Howell et al. 2010) or those species that interact strongly with other species (e.g. Buhl-Mortensen et al. 2010, Baker et al. 2012), or that modify/create habitats (engineer species) (e.g. Howell et al. 2011), or that serve as umbrella species in a conservation context (Larsen & Rahbek 2005), should be targeted. Techniques such as bivariate scaling (e.g. Mateo Sánchez et al. 2014), spectral analysis (e.g. Schneider et al. 1987), or scalewise variance (e.g. Detto & Muller-Landau 2013) could then be used to identify the strength of association of a particular species with habitat variables at multiple scales. Muotka et al. (1998) demonstrated how geostatistics can be efficiently used to characterize the spatial associations between lotic fish and macroinvertebrate species and their habitat at multiple scales while avoiding MAUP effects. Geostatistics and spatial analysis also include methods to deal with the concept of fuzzy boundaries, which are characteristic of many habitats (Dale & Fortin 2014). The problem is rarely acknowledged in the practice of habitat mapping, which typically imposes sharp boundary delineation.

Benthic ecosystem research often lacks sufficiently extensive datasets at several scales, particularly in the deep sea where sampling is limited and sporadic (Benn et al. 2010). Current data acquisition techniques often cannot capture biological and environmental patterns and processes at a fine resolution over extensive areas (Wilson et al. 2007, Huang et al. 2012), resulting in the need to identify tools to fill the gap. Ongoing improvements in bathymetric LiDAR and multibeam echosounders data analysis are generating some of the most extensive and accurate seafloor data available (Costa et al. 2009, Schimel et al. 2010). Development of remotely operated vehicles (ROV) and autonomous underwater vehicles (AUV) has increased both the range and extent of seafloor data (Wright 1999, Heyman & Wright 2011) at ever decreasing costs per megabyte. ROV- and AUV-mounted sensors have the capacity to sample the chemical, physical, and biological environment at fine spatial scales. These new technologies allow biological, geological, chemical, and physical observations to be situated in an accurate multiscale and geospatial context, allowing identification of surrogate variables (e.g. Costa et al. 2014, see Van Rein et al. 2009). Metadata are essential to improve the use of geospatial data and to build what Devillers et al. (2007) call a 'quality-aware' community: all collected datasets will need to be associated with complete metadata files reporting scale information, error and uncertainty quantification, the species or environmental variables that were targeted, the other species that were observed, and other information relevant to further use of the datasets.

Technological developments will continue to drive progress in benthic habitat mapping. Of interest are developments in automatic species detection and analysis on video data (e.g. Purser et al. 2009, Lüdtke et al. 2012, Seiler et al. 2012, Tanner et al. 2015), in methods for generating photo-mosaics of the seafloor for accurate georeferencing (e.g. Prados et al. 2012, Kwasnitschka et al. 2013, Marsh et al. 2013), in spatial statistics (e.g. Harris et al. 2011, Lu et al. 2014a,b), in computationally fast algorithms capable of processing high-dimensional datasets (e.g. Mumby 2006, Filzmoser et al. 2008, Bermejo et al. 2011, Oyana et al. 2012), in species distribution models that consider spatial autocorrelation, non-stationarity, and scale (e.g. Miller & Hanham 2011, Robinson et al. 2011, Beale et al. 2014, Vierod et al. 2014), and in geomorphometry (Gessler et al. 2009, Guth 2013). Analyses at multiple scales with many datasets require substantial computational time and effort, and tools that can iterate analyses at multiple scales will become necessary. Surveying multiple characteristics of an area at multiple scales generates immense amounts of data. As in satellite remote sensing (Turner et al. 2015), adequate software and institutional arrangements are needed to realize the potential for these data to be used for purposes other than habitat mapping, to become a valued repository (Borja 2014), and to notify stakeholders of their existence. This resource-sharing philosophy is important to implement (Turner et al. 2015) if marine scientists are to make effective use of the data and to understand benthic ecosystems before they become substantially altered (Vierod et al. 2014). In some cases, data have been stored for decades waiting for the development of appropriate analytical tools (Knobles et al. 2008). Conversely some researchers might have developed tools applicable to more than their own application, but lack the platform to share these tools with the relevant communities.

Improving standards for defining benthic habitats

In the previous sections we review the ways that scale and the spatial nature of data influence the way we perceive, measure, analyze, and interpret the environment and species–habitat relationships in benthic habitats. We found that information on scale is not always clearly reported in published works, that a quantitative understanding of habitats and scale is needed, and that results depend on the geographic context of habitat mapping. We thus propose a better standard for defining benthic habitat, one that builds upon the habitat definition of Harris & Baker (2012a). With these standards benthic habitats can be defined as 'areas of seabed that are (geo)statistically significantly different from their surroundings in terms of physical, chemical and biological characteristics, when observed at particular spatial and temporal scales′. This revised definition of benthic habitat addresses some of the critiques discussed in the previous sections. First, it addresses the growing realization that habitats must be quantitatively delineated and that what constitutes the description of a habitat is dictated by the scale of the techniques employed (Diaz et al. 2004). Then, it addresses the argument for considering the chemical environment in the characterization of benthic habitats (Kostylev et al. 2001, Brown et al. 2011a). Finally, it addresses the case made by Cogan & Noji (2007) that habitats be placed in context with the appropriate spatial, temporal and thematic scales when being mapped. The reference to geostatistics encompasses the consideration of the spatial nature of data and the concepts of fuzzy boundary delineation, while the biological characteristics relate to thematic scale and allow the study of species assemblages as much as individual species, and the mention of spatial and temporal scales makes habitats explicit about scale. Being explicit about temporal scale is important when studying migratory species that do not inhabit the same space through time.

Recommendations

The previous section on trends in benthic habitat mapping highlighted some of the main issues currently encountered in benthic habitat mapping, proposed some solutions and gave an insight on what the future developments might bring to the field. Based on this discussion, it is possible to identify 3 elements in the habitat mapping process that can be improved: project planning and data collection, data analysis and interpretation, and communication/dissemination of research results and data. Project planning and data collection can be improved from a biological, environmental and/or approach point of view. For the biology, we recommend focusing on the study of ecosystem engineer or umbrella species that would indirectly allow collecting data on other species. For the environment, we recommend sampling as many environmental variables as possible to aim for a comprehensive understanding of the environment and its dynamics. In terms of approach, we recommend adopting continuum-based multiscale methods, which involves sampling the environment over an extensive range of spatial scales. To improve data analysis and interpretation, we recommend using spatial statistical analyses that consider spatial heterogeneity and autocorrelation of data, rather than standard statistics based on the assumptions of IID, to establish results on a sound inferential basis. We also suggest always quantifying errors and spatial uncertainty. Finally, to improve communication and dissemination of research and data, we recommend making available metadata in which the results from the quantification of errors would be reported together with the spatial scales at which the data was collected (observation scale), at which the research was intended to be conducted (ecological scale), and at which the analysis was performed (analysis scale). In terms of dissemination, we suggest developing and automating tools (e.g. GIS, statistical, ecological) for processing or analyzing data and make them available, together with datasets and complete metadata, to maximize research and application potential.

CONCLUSIONS

Organisms inhabit a space that suits their needs. Understanding what controls benthic species distribution requires understanding the physico-chemical properties and dynamics within the water column, and at the seafloor interface (Clark et al. 2012, Vierod et al. 2014). The structure and spatial arrangement of habitats constrain, and can potentially become predictors of, species distribution, abundance, and richness. The cost and difficulties associated with sampling the marine environment highlight the need for better predictions of species distributions and improvement in sampling strategies. This will become possible with a better understanding of ecological patterns and processes as a function of scale, and should bring an overall improvement to benthic research efficiency. Using appropriate surrogates at appropriate scales is likely to be more effective than the use of opportunistic or arbitrarily chosen variables and scales. Generating habitat maps is a complex process that requires multidisciplinary efforts (Heyman & Wright 2011). Technological advances will help marine scientists address the current challenges of their field and develop new approaches to understand and so protect benthic habitat structure and function (Ramirez-Llodra et al. 2011). Geospatial data and techniques from geomatics and geostatistics show potential to tackle core issues in spatial ecology (Skidmore et al. 2011, Laffan et al. 2012) and in the marine sciences (Wright & Goodchild 1997, Heyman & Wright 2011).

The need for fundamental ecological and conservation theory, including explicit treatment of spatial scale has been noted repeatedly (e.g. Guisan & Thuiller 2005, Levin & Dayton 2009). Spatial scale is central to understanding habitat use, to selecting a sampling method, and to statistical analysis. Despite being recognized as a central issue, scales are often arbitrarily chosen, and studies regularly fail to report the scale(s) investigated and how the results depend on spatial scale. As stated by Dungan et al. (2002, p. 632): 'If ecologists are explicit about all of the components and dimensions of scale so that the spatial characteristics of the quantities measured can be correctly interpreted, there will be new opportunities to gain experience and improve understanding of the effects of observations and analysis scale changes.' Evidence-based scaling functions, which link pattern to process as a function of scale, are needed to identify reliable surrogates of species distribution, to scale-up and scale-down relevant information, and for improved quantitative understanding of benthic habitats.

Based on this review, we provide 8 recommendations that could lead to more efficient practices in benthic habitat mapping: (1) umbrella species' habitats should be prioritized for mapping and prediction; (2) sampling should be conducted to obtain data covering an extensive range of spatial scales and as many environmental variables as possible; (3) continuum-based habitat characterization approaches should be adopted; (4) statistical methods that consider the spatial nature of data should systematically be used; (5) errors and spatial uncertainty should be quantified at every step of habitat mapping (i.e. data collection, surrogacy testing, predictive modelling); (6) existing tools should be automated and new tools (e.g. GIS, statistical, ecological) should be developed for processing data and defining surrogates of species distribution and habitat at multiple scales; (7) data, complete metadata, and tools should be made available to maximize research and applications potential; and (8) the spatial extent and resolution (scale) at which the research was intended to be conducted, at which the data was collected, and at which predictive or monitoring aims were directed should always be clearly reported. We further recommend that benthic habitat be defined to the following standards: (1) explicit statement of observational scale (i.e. spatial resolution and extent); (2) inclusion of chemical variables along with physical and biological variables; and (3) placement in context with the appropriate spatial, temporal and thematic scales when being mapped.

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