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Is substrate composition a suitable predictor for deep-water coral occurrence on fine scales?

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ABSTRACT

Species distribution modelling can be applied to identify potentially suitable habitat for species with largely unknown distributions, such as many deep-water corals. Important variables influencing species occurrence in the deep sea, e.g. substrate composition, are often not included in these modelling approaches because high-resolution data are unavailable. We investigated the relationship between substrate composition and the occurrence of the two deep-water octocoral species *Primnoa resedaeformis* and *Paragorgia arborea*, which require hard substrate for attachment. On a scale of 10s of metres, we analysed images of the seafloor taken at two locations inside the Northeast Channel Coral Conservation Area in the Northwest Atlantic. We interpolated substrate composition over the sampling areas and determined the contribution of substrate classes, depth and slope to describe habitat suitability using maximum entropy modelling (Maxent). Substrate composition was similar at both sites - dominated by pebbles in a matrix of sand (> 80%) with low percentages of suitable substrate for coral occurrence. Coral abundance was low at site 1 (0.9 colonies of *P. resedaeformis* per 100 m^2) and high at site 2 (63 colonies of *P. resedaeformis* per 100 m^2) indicating that substrate alone is not sufficient to explain varying patterns in coral occurrence. Spatial interpolations of substrate classes revealed the difficulty to accurately resolve sparsely distributed boulders (3–5% of substrate). Boulders were by far the most important variable in the habitat suitability model (HSM) for *P. resedaeformis* at site 1, indicating the fundamental influence of a substrate class that is the least abundant. At site 2, HSMs identified cobbles and sand/pebble as the most important variables for habitat suitability. However, substrate classes were correlated making it difficult to determine the influence of individual variables. To provide accurate information on habitat suitability for the two coral species, substrate composition needs to be quantified so that small fractions (< 20% contribution of certain substrate class) of suitable substrate are resolved. While the collection and analysis of high-resolution data is costly and spatially limited, the required resolution is unlikely to be achieved in coarse-scale interpolations of substrate data.

1. Introduction

The deep sea is the least explored ecosystem on earth with only ~0.01% of the deep seabed having been investigated in detail (Ramirez-Llodra et al., 2010). Unique ecosystems such as hydrothermal vent communities and deep-water coral reefs and gardens have been discovered over the last decades (Ramirez-Llodra et al., 2010) but detailed biogeographical patterns of most deep-sea taxa are still largely unknown. Sampling effort is often very localised and limited to areas around industrialised countries that are comparably well investigated as seen in the Northeast Atlantic (Roberts et al., 2006). Distribution modelling is a powerful tool applied to meet the need for prediction of species distribution on a coarse scale (Reiss et al., 2014). These modelling techniques use known environmental data over the sampling areas to predict species distribution (Reiss et al., 2014) and identify potentially suitable conditions for species occurrence. Environmental data such as temperature, salinity and primary production can be estimated over coarse scales, e.g. using satellite data and hydrodynamic models (Reiss et al., 2014). Acoustic sensing approaches can yield information on terrain variability, slope and orientation of the seafloor which are important for benthic habitat mapping (Brown et al., 2011). Precision of these models strongly depends on the accuracy and resolution of environmental data and species records (Rengstorf et al., 2013).

Among the unique habitats found in the deep sea are deep-water coral communities that have received increasing scientific interest since the 1990s (Roberts et al., 2009). Deep-water corals can form potentially vulnerable marine ecosystems (VMEs) such as coral reefs and coral

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gardens (FAO, 2009) that provide habitat for a diverse associated fauna (Henry and Roberts, 2007; Mastrototaro et al., 2010; De Clippele et al., 2015). Vulnerability to disturbance e.g. by fisheries is considered to be highest for ecosystems that are disturbed easily and show slow recovery rates (FAO, 2009). Since both are assumed for deep-water coral habitats, multiple conservation measures were established in the past two decades to protect these ecosystems from human impacts (Breeze and Fenton, 2007; Davies et al., 2007; Brock et al., 2009). However, detailed distribution of deep-water corals is still largely unknown since sampling effort is often highly localised (Roberts et al., 2006). Predictive habitat modelling or habitat suitability modelling can be applied to identify areas with suitable conditions for the occurrence of coral habitat and can thus aid marine spatial planning (Ross and Howell, 2013).

Studies that have used habitat suitability modelling have identified drivers of deep-water coral distribution on global (Tittensor et al., 2009; Davies and Guinotte, 2011; Yesson et al., 2012; Yesson et al., in press), regional (Bryan and Metaxas, 2007; Rengstorf et al., 2013) and local (Dolan et al., 2008; Tong et al., 2013) scales. Globally, 17% of the oceans were considered to potentially provide habitat for at least one suborder of Octocorallia and suitable habitat was influenced by temperature, salinity, oxygen, productivity, broad-scale slope (over radius of 100 km) and calcite saturation (Yesson et al., 2012). However, global studies likely overestimate suitable habitat, particularly because of the lack of high-resolution (10 s of metres) data on bathymetry, currents and substrate (Davies and Guinotte, 2011; Anderson et al., 2016). This effect can be mediated in regional models that incorporate higher resolution terrain variables derived from multibeam data (Rengstorf et al., 2013). In regional models of the Northwest Atlantic continental margin, distribution of two octocoral families, Paragorgiidae and Primnoidae, was best explained by factors including temperature, slope and chlorophyll *a* concentration (Bryan and Metaxas, 2007). On a local scale (10s to 100s of metres), suitable habitat of *Primnoa resedaeformis* and *Paragorgia arborea* was mainly characterized by topographic highs on the Norwegian margin (Tong et al., 2013).

The availability of suitable substrate is considered to play an important role in the distribution of deep-water corals (Freiwald et al., 2004). The requirement of hard substrate for attachment makes it a basic prerequisite for the occurrence of gorgonian corals, such as *P. resedaeformis* and *P. arborea* (Breeze et al., 1997; Mortensen and Buhl-Mortensen, 2004; Watanabe et al., 2009). The incorporation of high resolution substrate data is assumed to improve habitat suitability predictions because missing variables that influence species distribution can lead to overestimation of suitable habitat and generally poor prediction accuracy of habitat suitability models (HSMs) (Guinotte and Davies, 2014; Anderson et al., 2016). In one of the few studies that included substrate data into HSMs for deep-water corals, substrate was found to be the most important variable to describe suitable habitat (Howell et al., 2011). However, most often it is not included in HSMs because detailed information on substrate composition is not available. Substrate data can be extracted directly from video observations (m^2 to km^2) or on a coarser scale (100s of km^2) as interpretation from acoustic data (Rooper and Zimmermann, 2007). Direct observations are spatially limited to the video transects but interpretations of acoustic data also require extensive groundtruthing (Rooper and Zimmermann, 2007). Instead of high-resolution substrate data, roughness of the seafloor and areas of high slope are often used as proxies indicating hard substrate (Bryan and Metaxas, 2007; Dunn and Halpin, 2009). The trade-off between time-consuming substrate analysis and the actual gain in accuracy of habitat predictions by including these parameters remains uncertain (Howell et al., 2011).

This study investigates the relationship of substrate composition and the abundance of the two octocorals *P. resedaeformis* and *P. arborea* on a fine scale of metres and 10s of metres at two sites (site 1: 438–462 m depth; site 2: 471–489 m depth) in the Northeast Channel Coral Conservation Area (NECCCA), located on the Canadian Atlantic continental margin between the Gulf of Maine and the North Atlantic Ocean (Fig. 1). The dominant species, *P. resedaeformis* and *P. arborea*, occur in dense aggregations at some locations inside the NECCCA (Mortensen and Buhl-Mortensen, 2004; Bennecke and Metaxas, 2017), but patterns regulating fine-scale variations in coral distribution are unknown. We used HSMs to investigate whether high-resolution substrate composition can be used to predict coral occurrences on local scales and identify the substrate classes that contribute most to the identification of suitable habitat. We explored whether the distribution of small colonies (< 10 cm) is driven by different variables than the distribution of colonies from all size classes.

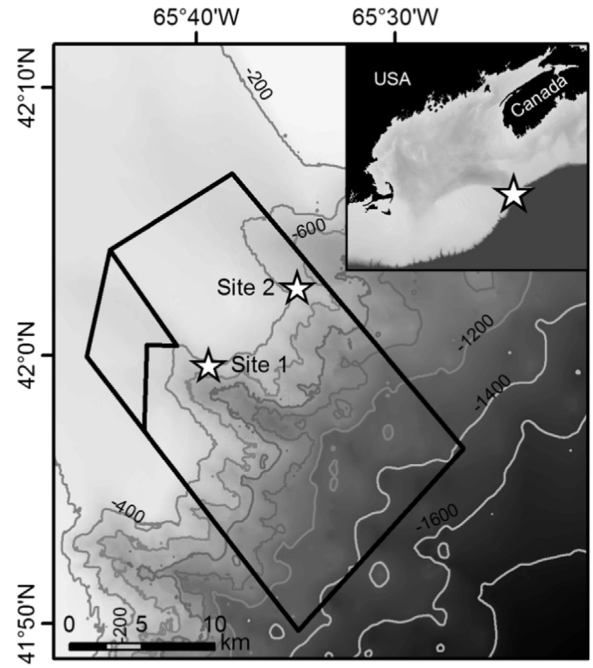

Fig. 1. Sampling locations (white stars) for substrate composition in the Northeast Channel Coral Conservation Area (black polygon) at the entrance to the Gulf of Maine. A 3-arcsecond bathymetry grid was provided by the U.S. Geological Survey (Twomey and Signell, 2013). Maps are displayed in a projected coordinate system (WGS 1984 UTM 20 N).

We can use these fundamental fine-scale data on the relationship of coral abundance and substrate composition to evaluate the necessity of incorporating substrate data into HSMs. Since the intention of many marine species distribution models (SDMs) is their application to conservation planning and management (Howell et al., 2011; Robinson et al., 2011; Rengstorf et al., 2013; Ross and Howell, 2013; Ardron et al., 2014), SDMs can be used to identify VMEs such as coral gardens. We evaluate whether information on high-resolution substrate composition is likely to improve the predictive accuracy of SDMs.

2. Materials and methods

2.1. Video/image analysis

Substrate composition was analysed from HD video sequences (Insite Pacific Mini-Zeus HD Camera) collected during two dives with the ROV ROPOS in the NECCCA on 26 June 2014 (dive number R1703, site 1) and 26–27 June 2014 (R1704, site 2) (Fig. 1). At each location, we ran 10 parallel video transects 100 m in length and spaced 10 m apart. Along each transect, an image was extracted from the video taken by a downward-oriented camera every 10 m, using the Ocean Floor Observation Protocol 3.3.5.i (OFOP). Laser beams projected on the image and spaced 10 cm apart provided scale. Average altitude of the ROV at the image locations was 2.6 ± 0.4 (mean ± SD, n = 103) m at site 1 and 3.0 ± 0.4 m (n = 102) at site 2.