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Hard substrate in the deep ocean: How sediment features influence epibenthic megafauna on the eastern Canadian margin

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ABSTRACT

Benthic habitats on deep continental margins (> 1000 m) are now considered heterogeneous – in particular because of the occasional presence of hard substrate in a matrix of sand and mud – influencing the distribution of megafauna which can thrive on both sedimented and rocky substrates. At these depths, optical imagery captured with high-definition cameras to describe megafauna can also describe effectively the fine-scale sediment properties in the immediate vicinity of the fauna. In this study, we determined the relationship between local heterogeneity (10–100 sm) in fine-scale sediment properties and the abundance, composition, and diversity of megafauna along a large depth gradient (1000–3000 m) in a previously-unexplored habitat: the Northeast Fan, which lies downslope of submarine canyons off the Gulf of Maine (northwest Atlantic). Substrate heterogeneity was quantified using a novel approach based on principles of computer vision. This approach proved powerful in detecting gradients in sediment, and sporadic complex features (i.e. large boulders) in an otherwise homogeneous environment because it characterizes sediment properties on a continuous scale. Sediment heterogeneity influenced megafaunal diversity (morphospecies richness and Shannon-Wiener Index) and community composition, with areas of higher substrate complexity generally supported higher diversity. However, patterns in abundance were not influenced by sediment properties, and may be best explained by gradients in food supply. Our study provides a new approach to quantify fine-scale sediment properties and assess their role in shaping megafaunal communities in the deep sea, which should be included into habitat studies given their potential ecological importance.

1. Introduction

Habitat heterogeneity on deep continental margins, which extend from the shelf break to the base of the continental slope and rise (i.e. depths of ~200 to ~3–4000 m), is an important driver of patterns in benthic invertebrate communities at multiple spatial scales (reviewed in Levin and Dayton, 2009; Levin and Sibuet, 2012). Vertical gradients in light, pressure, temperature, oxygen, and food availability lead to depth zonation in fauna, with the most-reported faunal change occurring at ~1000 m depth (Carney, 2005). Within these large-scale gradients, the role of finer-scale environmental factors, such as sediment characteristics, in influencing habitat heterogeneity in the deep ocean and their effect on biological patterns is less clear.

In the deep-sea, a positive relationship exists between sediment heterogeneity (particle size spectra) and deep-sea macrofauna and meiofauna in soft-sediment habitats (Gray, 1974; Etter and Grassle, 1992; Levin et al., 2001; Leduc et al., 2012; De Leo et al., 2014). However, the effect of sediment heterogeneity on benthic megafauna (i.e. organisms > 2–3 cm) may depend on a greater range of particle grain sizes than in these groups. It is expected that the local diversity of megafauna increases with an increasing range of substrate types, since specific adaptations are required for organisms to cement themselves to hard substrates (Taylor and Wilson, 2003). Indeed, differences in megafaunal communities were observed with a wide particle size spectrum (i.e. silt/mud to boulders; Jones et al., 2007; Meyer et al., 2014; Durden et al., 2015), but not with a restricted particle size spectrum (only silt; Soltwedel et al., 2009). At shallower depths (< 1000 m), differences in megafaunal communities were also observed among areas with different substrate types (‘hard’ vs. ‘soft’) in the Canadian Arctic (Roy et al., 2014), on the continental shelf west of the island of Svalbard (Bergmann et al., 2011), and in submarine canyons (Schlacher et al., 2007). Further, the sporadic presence of coarse sediment and/or hard substrate has been reported as influencing megafaunal communities, in particular on deep-water rocky reefs (Meyer et al., 2014), exposed bedrock on vertical walls and overhanging cliffs in submarine canyons (Huvenne et al., 2011; Johnson

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et al., 2013; Robert et al., 2014), and at a finer spatial scale, on stones, boulders and anthropogenic debris (Schulz et al., 2010; Meyer et al., 2016).

On deep continental margins, habitat heterogeneity due to variable sediment properties can be the consequence of a glacial legacy, accentuated by the presence of submarine canyons. 'Glacial till' ('glacial-marine sediment') consists of poorly-sorted, unconsolidated sediment deposited by glaciers during the last ice age, and is composed of coarse-grained sediment - such as gravel and boulders – interspersed in a matrix of finer-grain sediment. This surficial geology is typically present in high-latitude continental margins, particularly in the Arctic, sub-Arctic, and Antarctic, but can also be found at lower latitudes due to the extent of the ice margin. At the glacial terminus, meltwater flow deposited sediment loads ('outwash') that formed submarine 'fans'. These fans are thus often found at the mouth of important subglacial tunnels and submarine canyons. Glacial till causes variability in particle grain size on the seafloor at fine to local scales (< 1 m to 10–100 s m), likely resulting in increased habitat heterogeneity for benthic organisms.

While deep-water benthic megafaunal communities are now commonly assessed with optical imagery captured by cameras on remotely-operated vehicles and automated underwater vehicles, characterizing the habitat of this faunal group remains challenging due to the limited field of view of the cameras. Despite this limitation, optical imagery has also been used to describe fine-scale sediment properties (< 1–5 m; i.e. *substrate complexity*) in the proximity of megafauna, and their local variability (10 s to 100 s m; i.e. *substrate heterogeneity*; McCoy and Bell, 1991; Sebens, 1991), using grid-based approaches with a simplified scale of particle grain size (Jones et al., 2007; Sameoto et al., 2008; Meyer et al., 2014, 2015). Here, we used a novel approach based on principles of computer vision (Lacharité et al., 2015) with optical imagery captured by a ROV that allows to determine substrate properties along a continuous scale providing a significant improvement over the spatially limiting discontinuous grid-based scale. Our approach had the advantages of: 1) limiting bias due to human visual assessment, 2) producing reproducible and comparable results, and 3) describing gradients and boundaries in substrate characteristics, as well as sporadic features. More specifically, we: 1) characterized megafaunal communities, substrate complexity and heterogeneity using optical imagery along a large depth gradient (1000 m −3000 m) in the 'Northeast Fan', a previously-unexplored area adjacent to the Gulf of Maine downslope of submarine canyons on the eastern Canadian margin; and 2) assessed the relationship between substrate features at fine to local scales (1–100 s of m) with the abundance, composition, and diversity of epibenthic megafaunal communities. Although we used the approach in the deep-sea setting, it can be broadly applicable to any other remote (e.g. Arctic) or accessible marine habitat with significant substrate heterogeneity.

2. Materials and methods

2.1. Study area

The Gulf of Maine (northwest Atlantic) is a relic of the last glaciation event in northeastern North America (Schnitker et al., 2001; Shaw et al., 2006). Deep basins in the Gulf proper are bordered at the edge of the continental shelf by the shallow Georges Bank and Browns Bank, separated by the deep Northeast Channel (Fig. 1a). At the shelf edge of the channel, submarine canyons cut across the continental slope to a depth of ~900–1000 m, where the seafloor levels off on the continental rise (Fig. 1b, the 'Northeast Fan'). The surficial geology in the submarine canyons is typical of glaciated continental margins: a mixture of ice-contact sediment (pebbles, cobbles, boulders) amidst a matrix of sand and/or mud (Edinger et al., 2011). In the Northeast Fan, at the floor of the Middle Canyon, the presence of large boulders has been reported (Lacharité and Metaxas, 2013), but a comprehensive description of the surficial geology of the area is still lacking.

2.2. Video transects in the Northeast Fan

Video transects were performed with the ROV ROPOS at 5 locations in the Northeast Fan of the Gulf of Maine (continental slope and rise) across a depth gradient (962–2956 m) in August 2010 aboard the *CCGS Hudson* (Fig. 1, Table 1). Transect length varied between locations from 973 m (R1355; mean depth: 2091 m) to 2983 m (R1359; mean depth: 1086 m), with an overall combined length of 10,475 m surveyed on the seafloor. The speed above ground of the ROV was maintained constant at ~0.3 knots. Most transects were performed along isobaths, except the shallowest dive at a mean depth of 1086 m (dive R1359), which was performed upslope. For all transects, a constant heading was maintained, but paths in transects often deviated from a straight line due to local currents. Therefore, position is reported as 'Distance along transect', which was treated as a path. Some transects were separated into 2 contiguous segments (dives R1358, R1356) performed with a different heading. These segments were pooled for analyses. ROPOS was equipped with 2 high-definition cameras: one facing downward perpendicular to the seafloor (Insite Pacific Mini Zeus 1080i HD), and one facing forward of the vehicle at an oblique angle (Insite Pacific Zeus-Plus 1080i HD). Each camera was equipped with lasers 16.5 cm and 10 cm apart, for the downward-facing and forward-facing cameras, respectively. Along transects, the altitude of the ROV varied within and between dive locations due to sporadic strong currents and local changes in the shape of the seafloor. Portions of transects considered too far or too close off bottom were removed for analysis (details are outlined below for each camera). ROPOS is equipped with a USBL responder allowing precise positioning on the seafloor, and a CTD profiler (SBE 19plusV2).

2.3. Video data processing

Epibenthic megafaunal communities in the deep ocean are formed of relatively large protruding organisms (e.g. deep-water corals, sponges), with smaller and less conspicuous organisms, such as echinoderms, lying flat on the seafloor. In this study, we processed video from both cameras independently to examine changes in epibenthic megafaunal community composition between locations and evaluate differences in the community components captured between the two cameras. However, robust quantitative analyses are only possible with communities captured with the downward-facing camera since surface area can be accurately measured. Given the large depth gradient – and the diversity of communities encountered in the survey – we also describe communities captured by the forward-facing camera (standardized with method described below) as large organisms (e.g. deep-water corals at the shallowest location) were not optimally captured by the downward-facing camera, introducing a bias in the description of the communities.

2.3.1. Downward-facing camera

Along each transect, frame grabs (static images) were extracted from the downward-facing camera every 10 s to avoid overlap in the fields of view. Since we aimed to capture the unknown spatial variability in fine-scale substrate features in unexplored habitats, the frequency of sampled images depended on the observed variability: changes in substrate complexity, the presence of sporadic features (e.g. large boulders), and the presence of conspicuous fauna. To be consistent across depths, subsequent images were sampled at a maximum distance of 10 m apart even when no variability was observed on the seafloor. Images with poor luminosity, with an obstructed field of view (e.g., presence of fish), and/or showing blurriness were omitted. Additionally, given the objective of standardizing images to a surface area of 1 m^2, images with an original field of < 1 m^2 or > ~3 m^2 were not considered. This upper limit was adequate to not bias estimates of epibenthic megafauna, and avoid losing the needed resolution in the images for the computer vision analysis to be reliable (detailed below).