



# Environmental drivers of epibenthic megafauna on a deep temperate continental shelf: A multiscale approach

Myriam Lacharité\*, Anna Metaxas

Department of Oceanography, Dalhousie University, Halifax, NS, Canada

## ABSTRACT

Evaluating the role of abiotic factors in influencing the distribution of deep-water (> 75–100 m depth) epibenthic megafaunal communities at mid-to-high latitudes is needed to estimate effects of environmental change, and support marine spatial planning since these factors can be effectively mapped. Given the disparity in scales at which these factors operate, incorporating multiple spatial and temporal scales is necessary. In this study, we determined the relative importance of 3 groups of environmental drivers at different scales (sediment, geomorphology, and oceanography) on epibenthic megafauna on a deep temperate continental shelf in the eastern Gulf of Maine (northwest Atlantic). Twenty benthic photographic transects (range: 611–1021 m; total length surveyed: 18,902 m; 996 images; average of  $50 \pm 16$  images per transect) were performed in July and August 2009 to assess the abundance, composition and diversity of these communities. Surficial geology was assessed using seafloor imagery processed with a novel approach based on computer vision. A bathymetric terrain model (horizontal resolution: 100 m) was used to derive bathymetric variability in the vicinity of transects (1.5, 5 km). Oceanography at the seafloor (temperature, salinity, current speed, current direction) over 10 years (1999–2008) was determined using empirical (World Ocean Database 2013) and modelled data (Finite-Volume Community Ocean Model; 45 vertical layers; horizontal resolution: 1.7–9.5 km). The relative influence of environmental drivers differed between community traits. Abundance was enhanced primarily by swift current speeds, while higher diversity was observed in coarser and more heterogeneous substrates. In both cases, the role of geomorphological features was secondary to these drivers. Environmental variables were poor predictors of change in community composition at the scale of the eastern Gulf of Maine. This study demonstrated the need for explicitly incorporating scales into habitat modelling studies in these regions, and targeting specific drivers for community traits of interest.

## 1. Introduction

On deep continental margins (> 75–100 m depth) at mid to high latitudes, the distribution of epibenthic megafaunal (organisms > 2–3 cm in size) communities is influenced in part by abiotic factors, including the geological features of the seafloor (substrate composition and geomorphological features) and oceanographic properties both at the seafloor and in the water column (Beaman et al., 2005; Jones et al., 2007; Dolan et al., 2008; Buhl-Mortensen et al., 2012; Mosch et al., 2012; Rengstorff et al., 2012; Tong et al., 2012; Jones et al., 2013; Mohn et al., 2014; Navas et al., 2014; Robert et al., 2014; Jørgensen et al., 2015; Tong et al., 2016). At these latitudes, glacial history has yielded distinct geological features, such as diverse geomorphological features - deep basins, trenches and channels dug by subglacial flow - overlain by unconsolidated surficial sediment or 'glacio-marine debris', consisting of mixtures of coarse and soft sediment (Benn and Evans, 2010).

Additionally, seasonality in hydrographic conditions (temperature, salinity, water chemistry) and current patterns can affect benthic ecosystems, for example via the delivery of food particles to the seafloor. Evaluating the relative strength of these abiotic factors in driving the distribution of fauna is necessary to assess accurately the potential impacts of environmental change and support marine spatial planning, since abiotic proxies of biotic patterns can be effectively mapped (reviewed in McArthur et al., 2010).

Integrating the different abiotic factors influencing the distribution of deep-water epibenthic megafauna is challenging, since they act at varying spatial and temporal scales. For geological features in space, a multiscale description of substrate (e.g. sub-meter substrate composition to local heterogeneity) can be coupled to neighborhood analyses of geomorphology (Wilson et al., 2007), and integrated within broader divisions of the marine environment at local to regional scales (Williams et al., 2010; Huang et al., 2011). In addition to the

\* Corresponding author at: Applied Oceans Research Group, Nova Scotia Community College, Dartmouth, NS, Canada.  
E-mail address: [myriam.lacharite@nsc.ca](mailto:myriam.lacharite@nsc.ca) (M. Lacharité).

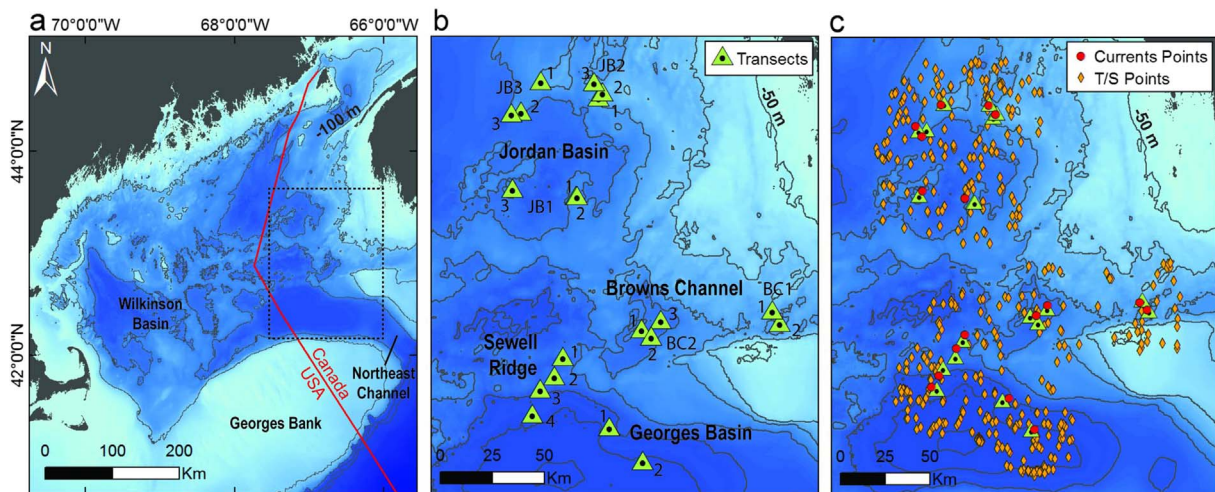


Fig. 1. (a) Gulf of Maine (northwest Atlantic). Depth contours shown: 100 m, 200 m, 300 m, 500 m, 1000 m. Study area in the eastern Gulf of Maine is indicated with the rectangular box. (b) Locations of benthic photographic transects ( $n = 20$ ) in 4 regions: Jordan Basin, Browns Channel, Sewell Ridge and Georges Basin. Subregions and transect numbers are indicated. (c) Locations of CTD casts extracted from the World Ocean Database ('T' = Temperature, 'S' = Salinity) and modelled currents ( $u$  and  $v$  components at the seafloor as monthly means) extracted from hindcasts of the ocean model FVCOM (Chen et al., 2003) for each transect from 1999 to 2008. 50-m depth contours are shown in (b) and (c).

hierarchical spatial heterogeneity of geological features, seafloor faunal patterns are influenced by multiscale variability in oceanographic properties defined in space (Mosch et al., 2012; Pitcher et al., 2012; Henry et al., 2013; Navas et al., 2014; Murillo et al., 2016), and time. For example, finer temporal variability (minutes to days; Davies et al., 2009) occurs within seasonal to multidecadal (i.e. oscillations) patterns in water column dynamics. However, because of cooler temperatures at depth, deep-water epibenthic megafauna are often assumed to be long-lived, slow-growing organisms, and hence 'integrate' environmental conditions over long periods of time. Describing oceanographic properties over similarly long periods (e.g. years) may thus be appropriate to assess their relationship with megafauna. Therefore, in addition to determining the relative strength of abiotic factors in driving the distribution of epibenthic megafauna, assessing the spatiotemporal scales (s) at which these relationships are strongest is necessary.

The Gulf of Maine is a semi-enclosed temperate basin delimited by the coasts of the United States and Canada (northwest Atlantic) with important commercial offshore benthic fisheries (Parker, 2012). In that context, knowledge of non-commercial benthic megafauna and their environmental drivers in the Gulf stems mostly from studies evaluating the impacts of mobile fishing gear on epifauna (Auster et al., 1996; Collie et al., 1997), assessing the beneficial effects of areas closed to bottom fishing in the western Gulf of Maine (US waters) for recovery and/or refuge (Grizzle et al., 2009), or determining the environmental conditions driving epifaunal patterns on commercial fishing grounds (Thouzeau et al., 1991). Few studies have assessed directly patterns of non-commercial benthic megafauna and the environmental factors influencing their distribution in the Gulf proper (Rowe et al., 1975; Kostylev et al., 2001; Watling and Skinder, 2007), and along the continental break and slope (Mortensen and Buhl-Mortensen, 2004; Watanabe et al., 2009; Quattrini et al., 2015; Bennecke and Metaxas, 2017b).

Launched in 2004 as part of the Census of Marine Life, the 'Discovery Corridor' Initiative covered an onshore-offshore axis from shallow to deep habitats in the eastern Gulf of Maine along the US-Canada border, and aimed to improve knowledge on biodiversity patterns and drivers in the Gulf (Incze et al., 2010). In deep benthic habitats, abiotic drivers of epifauna within and downslope of submarine canyons at the mouth of Northeast Channel have been assessed (Watanabe et al., 2009; Lacharité and Metaxas, 2013; Girard et al., 2016; Bennecke and Metaxas, 2017b; Lacharité and Metaxas, 2017). The present study examines these drivers in deep shelf waters of the Gulf proper.

The main objective of this study is to determine the relative influence of environmental drivers on traits of megafaunal communities (abundance, composition, and diversity quantified with morphospecies richness) in 4 regions of the eastern Gulf of Maine. We first describe 3 groups of environmental drivers important for benthic megafauna at increasing spatial and temporal scales: (1) substrate features ( $< 1$  m) and heterogeneity (variability within 100s m), (2) geomorphological features inferred with bathymetric patterns (100–5 km), and (3) oceanographic properties (hydrography and hydrodynamics) of near-sea-floor waters over a 10-year period. We then determine the relative influence of these environmental drivers on traits of epibenthic megafaunal communities.

## 2. Materials and methods

### 2.1. Study area

The Gulf of Maine (northwest Atlantic Ocean) is a relic of the last glaciation event in northeastern North America, when the Laurentide ice sheet extended to the current continental break. The Gulf proper is a semi-enclosed basin encompassing complex geomorphological features, in particular the presence of 3 deep basins (Jordan, Georges and Wilkinson), ridges and channels. In the eastern Gulf of Maine, 2 deep channels - Northeast Channel (between Browns Bank and Georges Bank) and Browns Channel (between German Bank and Browns Bank) - form connections to the open ocean and Scotian Shelf, respectively (Fig. 1a).

Surface circulation in the Gulf of Maine flows counter-clockwise and is influenced by seasonality. In the eastern Gulf, the Labrador Current flows from the Scotian Shelf along the coast of Nova Scotia (Canada), feeding into the Eastern Maine Coastal Current southwest of the Bay of Fundy. Inflow into the Gulf is also present on the northeast flank of Northeast Channel, with an outflow on the southwest flank. In addition to these broad circulation patterns, the seasonal formation of counter-clockwise gyres has been observed over Jordan and Georges Basins, and a strong eastward circulation from Northeast Channel through Browns Channel along Browns Bank (modelled in Xue et al., 2000, and supported by unpublished empirical observations).

Properties of bottom waters in the Gulf of Maine are influenced by three processes (reviewed in Mountain and Jessen, 1987): sources of inflow, density-driven vertical convection, and tidally-induced turbulent mixing. Most of the deep inflow consists of warm and salty (salinity  $> 34.0$ ) slope water into the Northeast Channel, which forms the

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