



The distribution of benthic biomass in hadal trenches: A modelling approach to investigate the effect of vertical and lateral organic matter transport to the seafloor



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ABSTRACT

Most of our knowledge about deep-sea habitats is limited to bathyal (200–3000 m) and abyssal depths (3000–6000 m), while relatively little is known about the hadal zone (6000–11,000 m). The basic paradigm for the distribution of deep seafloor biomass suggests that the reduction in biomass and average body size of benthic animals along depth gradients is mainly related to surface productivity and remineralisation of sinking particulate organic carbon with depth. However, there is evidence that this pattern is somewhat reversed in hadal trenches by the funnelling of organic sediments, which would result in increased food availability along the axis of the trenches and towards their deeper regions. Therefore, despite the extreme hydrostatic pressure and remoteness from the pelagic food supply, it is hypothesized that biomass can increase with depth in hadal trenches. We developed a numerical model of gravitational lateral sediment transport along the seafloor as a function of slope, using the Kermadec Trench, near New Zealand, as a test environment. We propose that local topography (at a scale of tens of kilometres) and trench shape can be used to provide useful estimates of local accumulation of food and, therefore, patterns of benthic biomass. Orientation and steepness of local slopes are the drivers of organic sediment accumulation in the model, which result in higher biomass along the axis of the trench, especially in the deepest spots, and lower biomass on the slopes, from which most sediment is removed. The model outputs for the Kermadec Trench are in agreement with observations suggesting the occurrence of a funnelling effect and substantial spatial variability in biomass inside a trench. Further trench surveys will be needed to determine the degree to which seafloor currents are important compared with the gravity-driven transport modelled here. These outputs can also benefit future hadal investigations by highlighting areas of potential biological interest, on which to focus sampling effort. Comprehensive exploration of hadal trenches will, in turn, provide datasets for improving the model parameters and increasing predictive power.

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1. Introduction

1.1. The effect of organic matter input on benthic biomass in the deep-sea

The main structuring factor for benthic diversity and biomass in the deep sea is believed to be food availability (Rex and Etter, 2010; Rex et al., 2006) while depth related hydrostatic pressure is likely a limiting factor for some fauna (Laxson et al., 2011; Yancey et al., 2014).

Abbreviations: LTM, Lateral Transport Model; ΔS , slope difference; B, burial; c, 50% transport efficiency threshold

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Studies of the effects of food availability on deep-sea life typically rely on inferring relationships between measures of benthic biomass and organic matter. This organic matter is mostly synthesised in the euphotic zone, and subsequently exported by gravity to deeper waters. The export mainly takes place through three processes: (1) the vertical sinking of particulate organic carbon (POC, or marine snow), produced through photosynthesis in the euphotic zone (e.g., Sweetman and Witte, 2008); (2) the delivery of dissolved organic material through currents and other water movements (Bendtsen et al., 2002); and (3) the transfer of large amounts of organic matter through sinking of animal carcasses (Higgs et al., 2014; Lebrato et al., 2012; Smith and Baco, 2003). Furthermore, inorganic carbon can be fixed through chemosynthesis both on the seafloor (Olu et al., 1997) and in the water column (Middelburg, 2011). As particulate organic matter sinks to the seafloor, it is gradually re-mineralized (Martin et al., 1987; Suess, 1980) and POC fluxes decrease exponentially with depth; as a consequence, deeper parts of the ocean generally support lower levels of benthic biomass (Rex et al., 2006).

Food availability in the deep sea also varies spatially with latitude (Honjo et al., 2008) and distance from shore (Johnson et al., 2007), and temporally, via seasonality (Fabiano et al., 2001), inter-annual climate variation (Smith et al., 2013), upwelling of nutrient-rich waters (McGillicuddy et al., 1998) and natural iron fertilization (Venables et al., 2007). Benthic biomass is higher, and dominated by larger size classes, in areas of the deep-sea overlain by temperate waters than in those overlain by tropical seas (Galeron et al., 2000; Thurston et al., 1998). Similarly temporal reductions in food supply have also been observed to relate to smaller body sizes (Ruhl et al., 2008) and lower biomass (Ruhl et al., 2014).

Bathymetric characteristics may play an additional role in driving regional and local scale patterns in food availability. In areas of complex hydrodynamic activity, such as the summit of seamounts, the community structure can be dominated by suspension feeders and their predators, resulting in a biomass that is higher than might be expected from vertical fluxes alone (Rowden et al., 2010; Thresher et al., 2011). These observations suggest that, in these areas, input of organic matter through lateral advection, rather than vertical deposition of marine snow, may be the most important factor in determining standing stock (Clark et al., 2010; Duineveld et al., 2004).

1.2. Patterns of benthic biomass in hadal trenches

Hadal trenches are the deepest parts of the ocean. They are formed at subduction zones of oceanic plates, and they can extend to depths approaching 11,000 m (Gardner et al., 2014). While they make up a relatively small part of the ocean seafloor area (~1–2%), they account for 45% of the oceanic depth range (Jamieson et al., 2010). Hadal trenches are usually shaped as long and narrow valleys, and often run parallel to coastlines (e.g., Peru-Chile and Japan trenches) or an island arc (Philippine and Aleutian trenches). They are among the least studied habitats on the planet, and the factors that control the distribution and variation of their communities over time are poorly understood (Jamieson et al., 2010).

For more than 60 years, hadal explorations have mostly used grabs and trawls (Belyaev, 1989; Vinogradova et al., 1993), and these have only provided a qualitative description of the hadal ecosystem (Belyaev, 1989). Existing data suggest that hadal macro- and megafauna communities are dominated by beard worms (Family Sibligonidae), spoon worms (Order Echiuroidea), sea cucumbers (Order Holothuroidea) and pericarid crustaceans (Order Isopoda and Amphipoda). Other taxa, such as tunicates, cirripeds, bryozoans and sponges, are rarely collected in hadal samples. Furthermore, evidence from hadal explorations (Wolff, 1961), as well as from research on osmolytes (Kelly and Yancey, 1999; Yancey et al., 2014), suggests that fish cannot live deeper than ~8200 m (Jamieson and

Yancey, 2012; Yancey et al., 2014). Depth appears also to limit the distribution of decapod crustaceans: these have been found in the Kermadec, Mariana and Japan trenches (Jamieson et al., 2009) at a maximum depth of 7703 m.

The general trends of decreasing biomass with increasing depth observed at bathyal and abyssal depths (Rex et al., 2006) are reduced and, in some cases, reversed in hadal trenches, where biomass appears to increase with greater depth (Danovaro et al., 2002; Wolff, 1970). This pattern can be spatially variable within a trench, as suggested by research in the Puerto Rico Trench where contrasting trends with depth occur in different areas (George and Higgins, 1979; Richardson et al., 1995; Tietjen et al., 1989), likely related to trench topography. The typical V-shape cross section of trenches may act as a funnel, and could convey the sediments laterally towards the axis (Itoh et al., 2011; Itou et al., 2000), and perhaps even along the axis towards the deepest points. More recent investigations, using benthic oxygen flux data, support the theory of higher deposition along the trench axis, as higher bacterial respiration has been recorded in trench sediments than in the surrounding abyssal plain (Glud et al., 2013).

In this paper we describe a modelling tool that could improve our understanding of benthic biomass in hadal trenches by accounting for the lateral transport of organic matter. The model is applied to the Kermadec Trench and the results can be used to make testable predictions about the relative distribution of benthic biomass within trenches which can be ground-truthed by future trench surveys. Moreover, any differences between model predictions and ground-truthed estimates could help constrain the degree to which other factors, such as currents, need to be taken into account.

2. Materials and methods

2.1. Modelling approach

A numerical model (Lateral Transport Model, LTM) was developed to estimate the benthic biomass of preselected benthic size classes in hadal trenches, as a function of both vertical and lateral down-slope transport of organic matter to the seafloor (Fig. 1). The model, written with the R language (R Core Team, 2012), had physical and biological compartments. In the physical compartment, fluxes of organic matter between cells were calculated

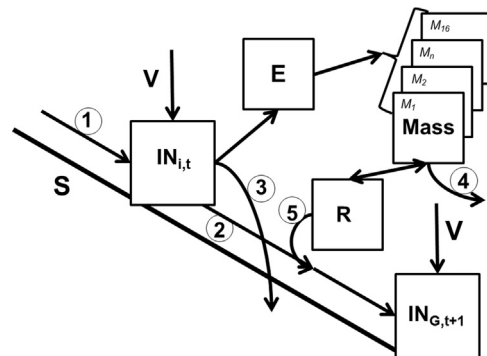


Fig. 1. Schematic diagram of the Lateral Transport Model (LTM). S = seafloor slope. V = vertical input of organic matter, obtained from Lutz et al. (2007) in this model application. 1 = lateral input of organic matter from shallower cells. $IN_{i,t}$ = total input flux in cell 'i' at time 't'. 2 = lateral output flux towards deeper cells (G), which depends on slope steepness. 3 = burial, or flux of organic matter into the sediment. This depends on the parameter B , which is the yearly burial rate. E = flux of organic matter available for consumption by benthic fauna. $Mass$ = benthic biomass stock from 16 size classes (from M_1 to M_{16}) comprising macro- and megafauna. R = stock of organic matter resulting from mortality and defecation of benthic biomass ($Mass$). 4 = loss of organic matter through respiration towards the water column. 5 = flux of dead and defecated material towards deeper cells, depending on slope steepness. $IN_{G,t+1}$ = total input flux in the deeper cells (G) at time 't+1'.

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