ARTICLE IN PRESS

Deep-Sea Research I ∎ (∎∎∎∎) ∎∎∎–∎∎∎

Contents lists available at ScienceDirect

Deep-Sea Research I

journal homepage: www.elsevier.com/locate/dsri

Comparison between infaunal communities of the deep floor and edge of the Tonga Trench: Possible effects of differences in organic matter supply

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ARTICLE INFO

Article history:
Received 17 September 2015
Received in revised form
15 November 2015
Accepted 18 November 2015

Keywords:
Southwest Pacific
Hadal
Meiofauna
Food availability
Community structure
Biodiversity
Bioturbation

ABSTRACT

Hadal trenches are characterised by environmental conditions not found in any other environment, thereby providing new opportunities to understand the processes that shape deep-sea benthic communities. Technological advances have led to an increase in the number of investigations in hadal trenches over the last two decades. However, more quantitative samples including the deepest parts of trenches is needed to better understand trends in benthic diversity, abundance, biomass and community structure in these extreme habitats, and how these may be shaped by environmental and/or evolutionary factors. In this study, we describe and compare the abundance, biomass, vertical distribution in the sediment, diversity, and community structure of nematodes and other infauna in sediments from the Horizon Deep (~10 800 m) in the Tonga Trench and a site on the edge of the trench (~6250 m). Mean nematode abundance was six times greater at the Horizon Deep site (387 ind. 10 cm^{-2}) than at the trench edge site (65 ind. 10 cm^{-2}). A similar pattern was observed for biomass (15 vs 2 μgDW 10 cm^{-2}, respectively), which likely resulted from elevated organic matter supply at the Horizon Deep site. There was no significant difference in nematode species richness between the two sites, but diversity measured using rarefaction was significantly greater at the trench edge site than at the Horizon Deep site [ES(20); 13.8 vs 7.8]. Dominance was much more pronounced in the Horizon Deep, which may be due to competitive exclusion by a small number of opportunistic species. Nematode community structure differed significantly both between sites and among sediment depth layers. The presence of subsurface peaks in pigment concentrations, bacteria abundance, and nematode abundance at the Horizon Deep site is consistent with a recent turbidite event, and may also reflect high rates of bioturbation by larger fauna resulting from high food availability. Determining the relative influences of different environmental factors on hadal trench benthic communities will require further investigation based on quantitative samples encompassing the trench axis as well as the oceanic and continental slopes.

1. Introduction

The hadal zone (> 6000 m depth) represents ~1–2% of the total seafloor area, but accounts for almost half of the ocean's depth range. Oceanic trenches are the dominant habitat within this bathymetric zone, yet quantitative studies of their benthic communities and the environmental forces that shape them are relatively rare (Jamieson et al., 2010). Trenches have often been described as depocentres of organic matter based mainly on observations of high abundance and biomass of infauna, deposit feeders, and/or mobile scavenging fauna in the deepest parts of trenches relative to shallower areas of the trench or the abyssal plain (e.g., Belyaev, 1972; Jumars and Hessler, 1976; Tietjen et al., 1989; Blankenship et al., 2006; but see Shirayama (1984a) and Itoh et al. (2011)). A recent investigation in the Challenger Deep, the world's deepest point in the Mariana Trench, provided direct evidence for elevated deposition of organic matter and intensified

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http://dx.doi.org/10.1016/j.dsr.2015.11.003
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Please cite this article as: Leduc, D., et al., Comparison between infaunal communities of the deep floor and edge of the Tonga Trench: Possible effects of differences in organic matter supply. Deep-Sea Res. I (2015), http://dx.doi.org/10.1016/j.dsr.2015.11.003

microbial metabolism at the axis of the trench relative to the edge of the trench (Glud et al., 2013). Together, these separate lines of evidence suggest a link between elevated food supply and high faunal standing stock at the greatest depths of hadal trenches.

Whilst benthic communities in hadal trenches are generally rich in terms of abundance and biomass, their species richness is low. The early analyses of trawl samples obtained mainly during the *Vityaz* and *Galathea* expeditions prior to 1960 led Wolff (1960) and Belyaev (1972) to conclude that the benthic communities of hadal trenches show trends of decreasing species richness with depth, a pattern associated with increased dominance of a small number of species (Belyaev, 1972). Since then a number of studies conducted on the diversity of hadal trench benthic communities have provided support for a trend of decreasing diversity with depth. An investigation of nematodes in Puerto Rico Trench and neighbouring abyssal plain and continental slope showed that richness was lowest in the deepest part of the trench, a pattern that was ascribed to low food availability (i.e., concentration of phytodetritus in the sediments) and homogeneous fine sediments in the trench (Tietjen, 1989). Decreasing food availability was also considered the most likely factor explaining a pattern of decreasing species richness of bait-attending amphipods in both the Peru–Chile and Kermadec trenches from ca. 6000 to 8000 m depth (Fujii et al., 2013). A similar bathymetric pattern was found for nematode diversity in the Peru–Chile Trench by Gambi et al. (2003). In this case, high food availability was suggested as the most likely factor leading to low diversity in the trench (Danovaro et al., 2002), even though measures of food availability did not differ markedly between the trench and adjoining continental slope study sites. Similarly, no obvious differences in food availability were observed between bathyal and hadal environments in the Kuril Trench region where harpacticoid genus richness declined from 2000 to 7000 m depth (Kitahashi et al., 2013). Instead diversity was correlated with sediment sorting, a measure of habitat heterogeneity (Kitahashi et al., 2013). The available evidence therefore suggests that low diversity at the deep trench floor is not necessarily dependent on food availability, and may be influenced by the physical characteristics of the sediment (Tietjen 1989; Kitahashi et al., 2013) as well as other factors such as physical disturbance and low regional diversity (Gambi et al., 2003) which have not yet been investigated directly.

Benthic communities of hadal trenches are distinct from those of the abyssal plain (Jamieson et al., 2011; Fujii et al., 2013; Kitahashi et al., 2013; Gallo et al., 2015). The transition in community structure between the two environments was originally thought to be gradual (Wolff, 1970), but more recent evidence from an analysis of scavenging amphipod data from the Kermadec Trench region suggests the presence of an ecotone at the abyssal-hadal boundary (Jamieson et al., 2011). Data for harpacticoid copepods from the Kuril Trench region also suggests that trench floor communities are substantially different from those at sites on the trench slope and abyssal plain (3030–5730 m) (Kitahashi et al., 2013), and Gallo et al. (2015) have observed differences in community structure between abyssal and hadal mega-fauna in the New Britain Trench. This shift in community structure is thought to be associated with environmental variables (e.g. habitat heterogeneity, food availability) that change with the relatively sharp transition from shallow-sloping abyssal plain to the steep and unstable topography of trenches (Jamieson et al., 2011; Gallo et al., 2015). Because of the complex and varied topography of trenches, and differences in their geographical location and associated environmental setting, the precise depth at which this transition occurs is expected to be trench-specific (Fujii et al., 2013; Schmidt and Martinez-Arbizu, 2015), and may vary within trenches.

Despite some emerging hadal paradigms for biodiversity patterns, more evidence, based on quantitative samples including the deepest parts of trenches, is needed to better understand benthic diversity, abundance, biomass and community structure trends in these extreme habitats, and how these may be shaped by environmental and/or evolutionary factors (Jamieson, 2015). Meiofauna constitute the most abundant group of metazoans in marine sediments (Giere, 2009), and become increasingly dominant in deeper waters as organic matter availability decreases, whereas the larger macro- and megafauna become relatively less abundant (Rex et al., 2006). Meiofauna are therefore ideal organisms for the study of benthic community trends across all deep-sea environments (Vanreusel et al., 2010). Diverse nematode communities have been found in the Puerto Rico Trench (Tietjen, 1989), Peru–Chile Trench (Gambi et al., 2003), and South Sandwich Trench (Vanhove et al., 2004) between 6316 and 8380 m depths, and nematodes were encountered in a trawl sample at 10 415-10 687 m in Tonga Trench during the *Vityaz* expedition in 1957 (Belyaev, 1972), suggesting that they thrive in the deepest parts of the oceans.

The vertical distribution of meiofauna in the sediments is affected by a variety of factors, including food availability, oxygen and sulphide concentrations, and macrofaunal activity (Giere, 2009). Meiofauna are typically concentrated in the top few centimetres of sediment where food is usually most abundant and oxygen levels relatively high (Meyers et al., 1987); this kind of distribution is common in abyssal sediments (Shirayama, 1984b; Alongi, 1992; Radziejewska, 2002). Data from the deepest parts of the Ogasawara, Kuril, Ryuku, and Puerto Rico trenches indicate that a similar distribution pattern is also present for meiofauna at hadal depths (Shirayama, 1984b; Tietjen et al., 1989; Itoh et al., 2011). However among the meiofauna, nematodes appear to be least affected by low oxygen concentrations and their distribution often extend to hypoxic layers where they can presumably exploit available food resources (Moodley et al., 2000; Nomaki et al., in press). Nematodes may also be transported deep into the sediments by the bioturbation activity of macrofauna (Moodley et al., 2000), or through physical disturbance (Leduc and Pilditch, 2013). The vertical distribution of nematodes in the sediment may therefore provide an indicator for the degree of vertical sediment mixing and burial of organic matter occurring as a result of bioturbation or physical processes (such as turbidite flow) thought to be relatively common in trenches (Lambshead et al., 2001; Oguri et al., 2013).

The Horizon Deep in the Tonga Trench is the second deepest point after the Challenger Deep in the Mariana Trench (Belyaev, 1989). Recent work on the Challenger Deep and other 'deeps' within the Mariana Trench has led to the recognition of the deepest points of the trenches as potentially unique, important, and well-defined ecological habitats, thereby justifying detailed study of these extreme ecosystems in the context of the wider trench environment (Jamieson, 2015). Whilst Horizon Deep has been sampled using trawls (Belyaev, 1989) and baited traps (Blankenship 2006), no quantitative benthic sampling has yet been conducted. As part of the QUELLE (Quest for the Limit of Life) around-the-world voyage in 2013, the Tonga Trench was sampled to "shed light on the habitable limits of life and its unique survival strategies" (https://www.jamstec.go.jp/quelle2013/e/pdf/brochure.pdf). The main objectives of the present study were to describe and compare the abundance, biomass, vertical distribution in the sediment, diversity, and community structure of nematodes and other infauna between the Horizon Deep and a site on the edge of Tonga Trench based on quantitative sediment core samples. We test two hypotheses: that elevated food availability at the Horizon Deep site, compared to the trench edge site, would lead to an infaunal community characterised by high abundance and biomass, low diversity and distinct community structure; and secondly that differences in sediment granulometry or higher levels of