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Habitat heterogeneity of hadal trenches: Considerations and implications for future studies

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A B S T R A C T

The hadal zone largely comprises a series of subduction trenches that do not form part of the continental shelf-slope rise to abyssal plain continuum. Instead they form geographically isolated clusters of deep-sea (6000–11,000 m water depth) environments. There is a growing realization in hadal science that ecological patterns and processes are not driven solely by responses to hydrostatic pressure, with comparable levels of habitat heterogeneity as observed in other marine biozones. Furthermore, this heterogeneity can be expressed at multiple scales from inter-trench levels (degrees of geographical isolation, and biochemical province), to intra-trench levels (variation between trench flanks and axis), topographical features within the trench interior (sedimentary basins, ridges, escarpments, 'deeps', seamounts) to the substrate of the trench floor (seabed-sediment composition, mass movement deposits, bedrock outcrop). Using best available bathymetry data combined with the largest lander-derived imaging dataset that spans the full depth range of three hadal trenches (including adjacent slopes); the Mariana, Kermadec and New Hebrides trenches, the topographic variability, fine-scale habitat heterogeneity and distribution of seabed sediments of these three trenches have been assessed for the first time. As well as serving as the first descriptive study of habitat heterogeneity at hadal depths, this study also provides guidance for future hadal sampling campaigns taking into account geographic isolation, total trench particulate organic matter flux, maximum water depth and area.

1. Introduction

The hadal zone (water depths exceeding 6000 m) differs somewhat from shallower marine environments (littoral; < 200 m, bathyal; 200–2000 m and abyssal; 2000–6000 m; Gage and Tyler, 1991) because it is not a direct continuation of the preceding biozones *per se,* but rather the descending continuum from the coasts over the continental slopes and rises onto the abyssal plains eventually fragment into clusters of often vastly isolated hadal areas of varying size, depth, length, latitude and seismicity. These areas combined total over 800,000 km^{-2} and represents the deepest 45% of the global ocean (Jamieson et al., 2010). While the term 'hadal' refers to areas deeper than 6000 m (or 6500 m; Watling et al., 2013), this is largely a convenient nomenclature that does not reflect the complexity of habitats across the 5000 m depth range that it represents. The hadal zone is comprised largely of deep trenches formed by subduction at tectonic convergence zones, with additional representation in hadal troughs, which are non-seismic deep basins within abyssal plain interiors, and trench faults formed by the fracturing of mid-ocean ridge spreading centres perpendicular to the ridge axis. There are 27 subduction trenches, 13 troughs and seven trench faults (Jamieson, 2015); Table 1 and see supplementary material Fig. S1); i.e. 47 individual habitats between 6000 m and full ocean depth (10,984 m ± 25; Gardner et al., 2014).

The hadal frontier still challenges scientific endeavour as the great distances below the sea surface and immense hydrostatic pressure at depth has resulted in an almost notorious underrepresentation in marine science. In the pursuit of long-term sustainability of the oceans (Mengerink et al., 2014; Danovaro et al., 2017) it appears logical to treat the ocean in its entirety and not simply focus on the near and easily accessible areas. Although the last 10–15 years has seen a revival in hadal exploration, progress still lags behind that of coastal and inshore research (Jamieson and Fujii, 2011), and the diminishing grasp of biodiversity with increasing depth (Webb et al., 2010) is omnipresent despite the realisation that mankind is already impacting the deepest communities that we scarcely understand (Shimanaga and Yanagi, 2016; Jamieson et al., 2017). Furthermore, despite a range of diverse deep-sea technological capabilities that are now possible (Danovaro et al., 2014), full ocean depth rated instruments and vehicles are

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relatively few in numbers (Jamieson, 2015; 2018).

Hadal biology and ecology has however progressed somewhat from simple cataloguing of species from great depths, as was the trend in the 1950s, to making the first attempts at ecological and evolutionary theory using large, statistically more robust data sets, and modern genetic and biochemical approaches (Yancey et al., 2014; Ritchie et al., 2015; Nunoura et al., 2015; Lacey et al., 2016; Tarn et al., 2016; Linley et al., 2017; Gerringer et al., 2017). Many of these studies are the first to pull comparative sampling from multiple trenches to challenge the idea that everything deeper that 6000 m is the same and any variation from abyssal communities is likely attributed to depth alone. However, as more sampling is undertaken there is a growing realisation that not everything is explained purely by pressure and in fact the habitats which support hadal fauna are as heterogenic as in any other marine biozone. Furthermore, this heterogeneity can be expressed at multiple scales from inter-trench levels (degrees of geographical isolation, and biochemical province), to intra-trench levels (variation in trench flanks and axis), topographical features within the trench interior (sedimentary ponds, ridges, escarpments, 'deeps', and seamounts) to the substrata of the trench floor (seabed sediment composition, mass movement deposits, bedrock outcrop).

In other more accessible marine habitats such as cold seeps (e.g. Levin et al., 2016), hydrothermal vents (e.g. Van Dover, 2000), submarine canyons (e.g. Amaro et al., 2016; Fernandez-Arcaya et al., 2017) and seamounts (e.g. Rowden et al., 2005), there is an established longstanding appreciation of the heterogeneity in substrata, structure, formation, connectivity and community composition, yet despite the hadal zone far exceeding these other environments in terms of depth range and footprint, virtually nothing is currently published on habitat heterogeneity on any scale smaller than inter-trench comparisons (and often only depth therein). This is in part due to so few exploratory vehicles having performed substantial seafloor imaging surveys, and those that have rarely publish. Science on the hadal frontier is therefore in a similar scenario to where more conventional deep-sea science was 50 or 60 years ago. However, a valuable resource that was capitalised on during that time is rarely found nowadays; publishing descriptive reports on images on the seafloor.

It was in the 1940s and 50s when underwater photography became an integral part of seafloor investigations (Ewing et al., 1946; Hahn, 1950; Emery, 1952; Pratt, 1962; Emery et al., 1965). The first scientifically useful images from hadal depths came from the Atlantic Ocean, in the Puerto-Rico and Romanche trenches (Pratt, 1962; Heezen et al., 1964; Heezen and Hollister, 1971), then from the South Sandwich Trench (Heezen and Johnson, 1965), and the New Britain and New Hebrides trenches (Heezen and Hollister, 1971). In 1962, ~4000 images of the hadal seafloor were taken by simple drop-cameras between 6758 and 8930 m on the American PROA expedition to the Palau, New Britain and New Hebrides trenches. Lemche et al. (1976) published the biological descriptions of these images in a well-illustrated report which is arguably still the best written reference as to what the hadal seafloor actually *looks* like, which is still an essential resource for scientists planning sampling campaigns to hadal trenches. These hard-won images provided the first glimpse at habitat heterogeneity in the hadal zone, but, unfortunately, after the 30 year hiatus in hadal exploration following the *Galathea, Vitjaz* and PROA expeditions to the introduction of the ROV *Kaikō*, the culture of publishing collections of seafloor images ceased. With the current lack of piloted vehicles operational at hadal depths, most studies rely on deploying free-fall systems and are thus jeopardising sampling success, quality of data interpretation and risk damage or loss of equipment by having literally no idea about the nature of the seafloor on which the equipment is to be deployed. In addition, cabled instruments are also easily damaged when deployed in unknown territory. Therefore any information of habitat heterogeneity at trench depths is invaluable in both the pursuit of establishing hadal ecological theory and in associated sampling operations.

This study serves as a review and reference guide for future hadal studies, taking into consideration greatly contrasting levels of hadal heterogeneity, ranging from geographic location and degrees of isolation between any given hadal zone and all others, through contrasting areas within a trench (adjacent flanks and trench axis) including complex topographical features within the trench interior. All to a backdrop of varying depths, sizes and food supply. All of these factors must be considered alongside the great water depths when planning research and interpreting results. We also report on the largest lander-derived imaging dataset that spans the full depth range of three hadal trenches (including adjacent slopes); the Mariana, Kermadec and New Hebrides trenches (Fig. 1). While the images were taken (and published) for biological and ecological studies, each deployment photographed or filmed an area of seafloor with often highly contrasting or surprising results, and therefore would serve as a crude seafloor survey of a largely inaccessible ecosystem on which to provide some guidance for current or forthcoming sampling campaigns at similar depths. This analysis also serves as the first descriptive documentation of habitat heterogeneity at hadal depths as the nature of the seafloor substratum has a profound effect on the composition of the benthic communities and biogeochemical processes (Thistle, 2003).

2. Materials and methods

2.1. Location and isolation of hadal zones

The analysis of broadscale trench topography was undertaken in ArcGIS. The trench boundaries were selected manually across contours superimposed on bathymetry of the trench derived from the General Bathymetric Chart of the Oceans (GEBCO www.gebco.net). The maps were projected to the cylindrical equal area projection with a central meridian 180° and a standard parallel 30° S, with a sub-kilometre spatial resolution. The location of each trench was identified using the position of the deepest point (Table 1). The topographic analysis was focussed further by slicing the bathymetry into 500 m depth bins. This approach also permitted the extraction of habitat size (km^{-2}) with depth.

To provide a measure for trench isolation, a geographic distance matrix was calculated in kilometres, for each point, for all pairwise combinations, from a database of deepest points of the 47 hadal zones between 6000 m water depth and full ocean depth. The Geographic Distance Matrix Generator used the semi-major axis of the WGS84 reference system as the default radius of the earth (Ersts [Internet]).

All statistical analysis was produced using R (R Development Core Team, 2005), figures were produced using ggplot2 (Wickham and Chang, 2007). The relationships between how isolated hadal zones are geographically from every other hadal zone was examined by first undertaking K-means clustering using euclidian distance and average linkage which revealed that a five cluster solution was best for determining a value of 'isolation' using the distance matrix data. This information was used in hierarchical agglomerative cluster analysis with bootstrapped p-values to determine whether the clusters were strongly supported by the data. Four of the clusters have a confidence of ≥80% with a confidence value of 67% assigned to the final cluster.

2.2. The study areas

The Kermadec Trench is formed by the subduction of the Pacific Plate below the Australian Plate resulting in a trench 1500 km in length and 60 km wide on average (Angel, 1982); Fig. 1B). The trench forms a