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Submersible- and lander-observed community patterns in the Mariana and New Britain trenches: Influence of productivity and depth on epibenthic and scavenging communities

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ABSTRACT

Deep-sea trenches remain one of the least explored ocean ecosystems due to the unique challenges of sampling at great depths. Five submersible dives conducted using the *DEEPSEA CHALLENGER* submersible generated video of undisturbed deep-sea communities at bathyal (994 m), abyssal (3755 m), and hadal (8228 m) depths in the New Britain Trench, bathyal depths near the Ulithi atoll (1192 m), and hadal depths in the Mariana Trench Challenger Deep (10908 m). The New Britain Trench is overlain by waters with higher net primary productivity (~3-fold) than the Mariana Trench and nearby Ulithi, and receives substantially more allochthonous input from terrestrial sources, based on the presence of terrestrial debris in submersible video footage. Comparisons between trenches addressed how differences in productivity regime influence benthic and demersal deep-sea community structure. In addition, the scavenger community was studied using paired lander deployments to the New Britain (8233 m) and Mariana (10918 m) trenches. Differences in allochthonous input were reflected in epibenthic community abundance, biodiversity, and lifestyle representation. More productive locations were characterized by higher faunal abundances (~2-fold) at both bathyal and hadal depths. In contrast, biodiversity trends showed a unimodal pattern with more food-rich areas exhibiting reduced bathyal diversity and elevated hadal diversity. Hadal scavenging communities exhibited similar higher abundance but also ~3-fold higher species richness in the more food-rich New Britain Trench compared to the Mariana Trench. High species- and phylum-level diversity observed in the New Britain Trench suggest that trench environments may foster higher megafaunal biodiversity than surrounding abyssal depths if food is not limiting. However, the absence of fish at our hadal sites suggests that certain groups do have physiological depth limits. Submersible video footage allowed novel in situ observation of holothurian orientation, jellyfish feeding behavior as well as lifestyle preferences for substrate, seafloor and overlying water. This study documents previously unreported species in the New Britain Trench, including an ulmariid scyphozoan (8233 m) and an acrocirrid polychaete (994 m), and reports the first observation of an abundant population of elpidiid holothurians in the Mariana Trench (10908 m). It also provides the first megafaunal community analysis of the world's deepest epibenthic community in the Mariana Trench Challenger Deep, which was composed of elpidiid holothurians, amphipods, and xenophyophores.

1. Introduction

Historically, information about the ecology of the deep sea has been gained through the specimens recovered (frequently damaged) from bottom trawls and grab samples (Belayev, 1989), and through seafloor photographs taken by underwater cameras (Heezen and Hollister, 1971; Lemche et al., 1976). The advent of new imaging technologies (Solan et al., 2003) and the use of submersibles allowed us to progress from snapshot views of the deep sea to a more holistic study of undisturbed deep-sea communities. Few deep submergence vehicles (DSVs) can reach full ocean depths, but those that can allow unique access to the world's deepest ecosystems. Previously published

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studies on trench biology using submersible-obtained video surveys have focused on either the ecology of individual taxa such as amphipods (Hessler et al., 1978) or on hadal chemosynthetic communities (Fujikura et al., 1999; Ohara et al., 2012). It is now possible to use DSV-obtained video surveys and a comparative approach to analyze deep-sea trench megafaunal community structure. The wealth of HD video footage and still images collected by the *DEEPSEA CHALLENGE* Expedition (2012) to the New Britain Trench and the Mariana Trench made such an analysis possible.

Deep-sea trenches compose the majority of the hadal zone, defined as being deeper than 6500 m (Watling et al., 2013). They represent the deepest biozone in the world but make-up only 0.24% of the entire ocean (Jamieson, 2011). Trenches are unique deep-sea ecosystems and remain one of the least understood habitats on Earth (Jamieson et al., 2010). They are characterized by high levels of species endemism (Wolff, 1960), high hydrostatic pressure, low temperatures, the absence of light, sufficient oxygen content, high sedimentation rates, and limited food supply (Jamieson, 2011). However, recent studies suggest they may trap more particulate organic matter (POM) than previously appreciated (Glud et al., 2013). Deep-sea trenches occur at tectonic convergence zones and 26 trenches deeper than 6500 m have been described worldwide, with the majority occurring in the Pacific (Jamieson, 2011).

The study of deep-sea trenches has a long history (Heezen and Hollister, 1971; Belyaev, 1989; Gage and Tyler, 1991) with much of the foundational knowledge attributed to the extensive sampling efforts of the Danish *Galathea* and the Soviet *Vitiaz* expeditions during the mid-1900s. Studies of underwater photographs of trench benthic communities (Lemche et al., 1976; Belyaev, 1989) have also added to our knowledge of trench fauna. These studies revealed that metazoan life was present in all sampled trenches and that species endemism in trenches was high, with the total degree of endemism for benthic metazoans increasing with depth (Belyaev, 1989). Due to these early sampling efforts, several important trends were established that shape how we understand deep-sea communities today. These include recognition that megafaunal biodiversity declines rapidly from 2 to 6 km, a gradual transition zone is reached between the abyssal and hadal zone at 6 to 7 km (Belyaev, 1989), and then diversity decreases much more slowly in the hadal zone below 7 km (Vinogradova, 1962). Wolff (1960, 1970) identified several distinctive features that characterize hadal communities including a) dominance of certain groups like the actinians, polychaetes, isopods, amphipods, echiurids, and holothurians, b) lower representation of non-holothurian echinoderms, c) insignificance or lack of fish and decapod crustaceans and d) mass-occurrence of holothurians at maximal trench depths. Deposit-feeding holothurians in the genus *Elpidia* and scavenging lysianassoid amphipods in the genus *Hirondellea* are recognized as common trench-floor inhabitants (Jamieson et al., 2010).

The deep sea is an organic-carbon limited system with a high fraction of refractory compounds reaching the deep-sea floor (Gage, 2003; Jamieson et al., 2010). However, recent biogeochemical/respiration studies (Glud et al., 2013) and the high abundance of deposit-feeding organisms found in trenches (Belyaev, 1989) suggest that trenches may differ from the surrounding abyssal plain by being regions of resource accumulation. Many authors have noted the importance of the overlying primary productivity regime and the amount of organic matter exiting the euphotic zone in influencing the density and composition of different trench communities (Wolff, 1960; Longhurst, 1995; Jamieson, 2011). Additional food sources for deep-sea trench communities include allochthonous marine and terrestrial sources due to the proximity of trenches to land (Gage, 2003). Sinking carcasses of euphausiids from the upper water column are an important food source for abyssal ophiuroid communities in the Orkney Trench (Sokolova, 1994). Allochthonous organic input from nearby landmasses also positively influence the faunal abundance in trenches (Belyaev, 1989), with a greater quantity of animals corresponding to trenches where abundant plant debris is present, such as the Philippine Trench, where coconut husks and bamboo have been recovered (Bruun, 1956).

The Challenger Deep in the Mariana Trench (MT) is the deepest spot in the ocean (Nakanishi and Hashimoto, 2011), with pressures reaching 1100 bar or approximately 1.1 tonnes per cm^2 (Jamieson, 2011). The Mariana Trench is overlain by oligotrophic waters with annual rates of primary production estimated to be ~ 59 g C m^{-2} y^{-1} (Jamieson et al., 2009b). Maximum bottom currents (8.1 cm s^{-1}) occur at the deepest point of the trench but are of short duration, with typical current velocities being < 1.5 cm s^{-1} for 22.9–63.8% of the time (Taira et al., 2004).

Submersible exploration of the Challenger Deep has a rich history, starting with the successful descent of the Trieste in 1960, piloted by Don Walsh and Jacques Piccard. Following that historic descent, no manned submersible dives occurred over the next 50 years, and exploration was based on the descents of the remotely operated vehicles, ROV Kaiko in the 1990s and early 2000s and the hybrid ROV (HROV) Nereus in 2009. These expeditions offered new insight into some of the specific organisms that live at the bottom of the Challenger Deep. Sediment cores obtained by Kaiko in the Challenger Deep revealed high-density assemblages of non-calcareous foraminifera (Todo et al., 2005), including a number of new taxa (Gooday et al., 2008). Researchers studying Kaiko images reported very sparse life on the seabed (Barry and Hashimoto, 2009) and HROV Nereus test dives revealed a seabed dominated by small amphipods and scarce polychaete worms, with a single small holothurian observed (Bowen et al., 2009; P. Fryer pers. comm., 2014). In 2009, a drop camera deployed by National Geographic and Scripps Institution of Oceanography researchers recovered imagery from the Sirena Deep at 9970 m in the MT, revealing many xenophyophores and a rhopalonematid jellyfish (unpublished observation). However, no quantitative megafaunal community analyses have been published from these expeditions.

The New Britain Trench (NBT) is a 840 km-long curved trench in the northern Solomon Sea, close to the landmass of Papua New Guinea (Davies et al., 1987). The deepest point is the Planet Deep at 9140 m (Davies et al., 1987). The New Britain Trench has received limited biological attention (Heezen and Hollister, 1971; Lemche et al., 1976) with the majority of published studies focusing instead on its geology (Tiffin et al., 1984; Davies et al., 1987), since the sharp bend of the trench has one of the highest rates of seismic activity in the world (Tiffin et al., 1984). Wolff (1960) notes that the New Britain Trench is particularly difficult to trawl due to bottom configuration, which likely also contributed to the lack of previously collected data. There is also confusion with nomenclature within the deep-sea biological literature in that the eastern component of the trench near Bougainville Island has occasionally been referred to as the Bougainville Trench even though there is no shallow sill separating it from the western part, which is referred to as the New Britain Trench (Tiffin et al., 1984). To avoid confusion, we will refer to the entire trench as the New Britain Trench, but believe that published historical trawl results from the Bougainville Trench (Belyaev, 1989) can be used for comparison with the findings of this study. The New Britain Trench presents an interesting contrast to the Mariana Trench because it receives more allochthonous input from both terrestrial and marine sources.

In this study, we utilized the images and videos obtained by the *DEEPSEA CHALLENGE* submersible and the landers to provide a novel look at the ecology of deep-sea ecosystems. This paper focuses on megafauna, operationally defined as organisms readily visible in photographs (Solan et al., 2003) or video. Benthic megafaunal assemblages, composed of benthic and demersal community members, were characterized with respect to their relative abundance, composition, diversity, and lifestyles. The variable productivity regimes