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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.

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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 *Vityaz* 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 cm² (Jamieson, 2011). The Mariana Trench is overlain by oligotrophic waters with annual rates of primary production estimated to be $\sim 59 \text{ g C m}^{-2} \text{ y}^{-1}$ (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 $< 1.5 \text{ cm s}^{-1}$ 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

associated with the locations and depths of the *DEEPSEA CHALLENGER* submersible dives and lander deployments allowed us to test the following hypotheses: (1) food availability as represented by allochthonous marine and terrestrial input to the sea floor is reflected in hadal community structure, (2) differences in food availability have similar effects on community abundance, biodiversity, and lifestyle representation at bathyal as at hadal depths, and (3) hadal epibenthic and scavenging communities show similar functional responses to food availability. Based on previous literature we hypothesized that sites with higher organic carbon input would have higher organismal abundance, higher percentage of demersal fauna in the epibenthic community, and higher biodiversity.

2. Materials and methods

2.1. DEEPSEA CHALLENGE Expedition

In early 2012, the *DEEPSEA CHALLENGER*, a single occupant submersible, undertook a series of dives leading up to a full-ocean-depth dive to the Challenger Deep (CD) in the Mariana Trench (MT). The *DEEPSEA CHALLENGE* Expedition consisted of thirteen submersible dives. Five of these were selected for analysis based on their value in addressing questions about trench ecology. Three dives of progressively increasing depth (994 m, 3755 m, 8228 m) were undertaken in the New Britain Trench (NBT) by the *DEEPSEA CHALLENGER* (Table 1, Fig. 1). Following their success, the *DEEPSEA CHALLENGER* dove to full ocean depth in the MT CD, and reached a maximum depth of 10908 m (Table 1, Fig. 1). One additional dive was conducted near the Ulithi atoll at bathyal depths (1192 m) (Table 1, Fig. 1). Additionally, baited landers capable of descending to full-ocean depth were deployed on this expedition in the NBT (8233 m) and MT (10918 m) (Table 2, Fig. 1).

Unlike traditional submersibles built with a horizontal structural plan, the innovative vertical attitude of the *DEEPSEA CHALLENGER* (Fig. 2) was designed to maximize its descent and ascent rates thereby increasing time available for seafloor exploration. The bulk of the 7.3 m tall submersible is made up of a now-patented syntactic foam. The foam provides flotation and a strong structural core designed to counter the buoyancy and extreme pressure demands of operating from sea surface to 1100 bar pressure at the bottom of the Mariana Trench. The pilot sits upright in a 1.09 m diameter, 6.35 cm thick, steel sphere attached to the bottom of the foam beam (Fig. 2). Beneath the pilot sphere is an array of scientific equipment including push-core sediment samplers, a payload bay with space for a suction sampler, and a hydraulic manipulator arm. The submersible has both a Seabird CTD and a Paroscientific Digiquartz pressure sensor, and depths were derived using the UNESCO pressure to depth equation (Fofonoff and Millard, 1983). Inside the sphere, a Red Epic camera, mounted directly in the small viewport, captured IMAX-quality '5K-rav' images. External to the sub were four cameras, each one-tenth the size of previous deep ocean HD cameras— a 3D pair on the boom arm, and wide-angle and macro cameras on the manipulator arm. Like the syntactic foam, the cameras and their titanium housings, the

batteries, thrusters and LED lights were all designed specifically for the submersible (Hardy et al., 2014b).

Baited landers were also developed and deployed to allow for additional comparisons of hadal scavenging communities. The *DEEPSEA CHALLENGE* "landers" are untethered, unmanned vehicles (4.27 m tall by 0.76 m wide by 0.91 m deep) (Fig. 2) that free fall from the sea surface to the seafloor, slowed by water drag to an acceptable terminal velocity. Syntactic foam provided primary buoyancy. Large hollow glass spheres were used for instrument housings and supplemental buoyancy. The landers are metacentrally stable in all conditions. They can remain in situ for great lengths of time with samplers and sensors, until acoustically commanded to release their iron anchor weight and rise to the surface. The DSC lander was equipped with camera and light arms, Niskin water samplers, sediment corers, and a drop arm with two baited animal traps (Hardy et al., 2014a).

2.2. Sampling design of submersible-obtained video and identification of megafauna

All available camera footage from each dive was examined. Megafauna that could clearly be seen with the naked eye in the Red Epic or boom camera footage were recorded and still images were extracted from the video. The best representative image of each observed taxon was then compiled into a key for each of the dives. With the help of deep-sea taxonomic experts, these still images were then used to identify observed organisms to the lowest taxonomic level possible. Due to the limitations of using imagery to identify species, counts of these taxa represent minimum species numbers (as in Fodrie et al., 2009) and certain taxa may encompass several cryptic species.

Identified taxa were quantified at each dive site using 2-minute samples of the Red Epic camera footage, chosen because it provided continuous coverage of each dive, had the highest resolution, and reduced the camera-specific bias between dives. Bottom footage from each dive was split into 10-minute sections spanning the entire time at the bottom. The first 2 minutes of each 10-minute segment was extracted as a separate clip using Final Cut Pro and was used for quantification of megafauna, as well as terrestrial plant detritus, lebensspuren (animal-generated structures in sediments), large protozoans, and the presence/absence of hard substrate. Two-minute samples were excluded from the analysis if it was apparent that the location overlapped with the prior 2-minute sample, resulting in <20% bottom time quantified for certain dives (Table 1). Since these overlapping samples were excluded, we assume no overlap between 2-minute samples and consider them to be replicates for the specific dive. However, because only one transect was made at a given depth in each trench, the 2-minute samples are technically pseudoreplicates.

2.3. Quantification of fauna from submersible dives

Megafauna were quantified within the 2-minute samples to the lowest taxonomic level possible. For some smaller taxa like amphipods, it was not possible to distinguish species. Even for taxa where

Table 1

Location, depth range, bottom time and information for two-minute video clips analyzed from the five submersible dives in the W. Pacific Ocean. NBT=New Britain Trench, MT CD=Mariana Trench Challenger Deep. Depth range represents the maximum and minimum depths traversed along the seafloor during each dive and the error margin is ± 3 m.

Dive	Locality	Depth range (m)	Total bottom time	# of 2 min samples	bottom time quantified	Date
D04 NBT	5°35'54" S, 151°36'53" E	884–994	4 h 30 min	17	13%	23-Feb-12
D05 NBT	5°49'48" S, 151°42'36" E	3712–3755	4 h 24 min	25	19%	28-Feb-12
D08 NBT	5°52'48" S, 152°22'48" E	7984–8228	3 h 04 min	18	20%	7-Mar-12
D10 MT CD	11°22'12" N, 142°35'24" E	10876–10908	2 h 34 min	15	19%	26-Mar-12
D11 Ulithi	9°52'48" N, 139°33'36" E	1130–1192	4 h 10 min	20	16%	1-Apr-12

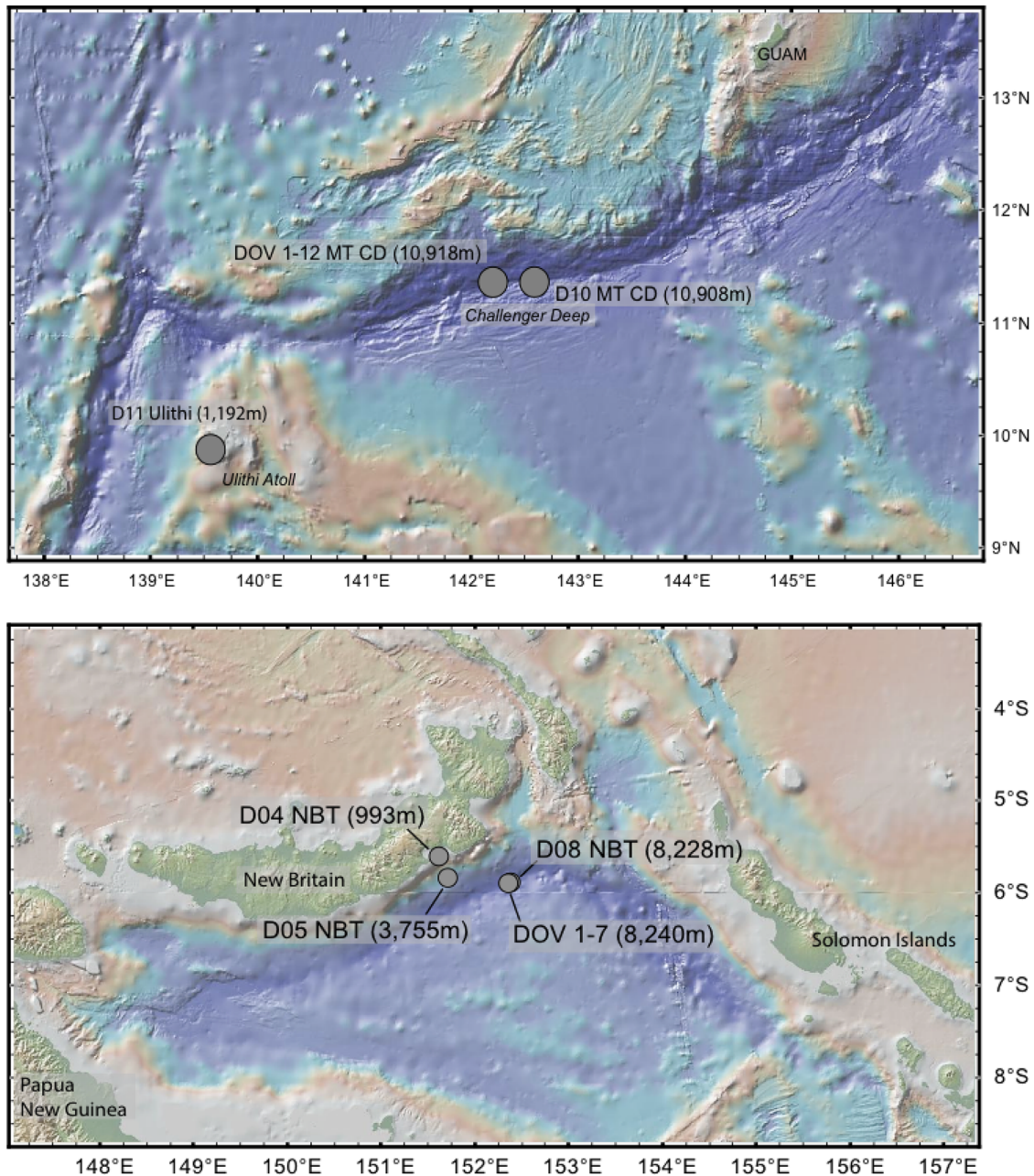


Fig. 1. Map displaying locations for the five *DEEPSEA CHALLENGER* submersible dives (D04, D05, D08, D10, D11) and the two lander drops (DOV1-7 and DOV1-12). Upper panel map shows the Mariana Trench and nearby Ulithi atoll and bottom panel map shows the New Britain Trench, near the island of New Britain. Depths indicate maximum depth reached during each dive.

Table 2

Location, depth, bottom time and information for still images analyzed from two trench lander deployments in the W. Pacific Ocean. NBT=New Britain Trench, MT CD=Mariana Trench Challenger Deep. Pressure was determined using an RBR pressure sensor and depths were derived using the UNESCO pressure to depth equation (Fofonoff and Millard, 1983).

Dive	Locality	Depth (m)	Bottom time	Images	Images quantified	Date
DOV1-7 NBT	5°53'18" S, 152°21'21" E	8233	~7h	1 image every 5-6 min	70	3-Mar-12
DOV1-12 MT CD	11°22'8" N, 142°25'58" E	10918	~5.5 h	2 images every 10 min	68	3-Apr-12

species-level identifications were made – they may include cryptic species. All distinct taxa observed during the sampled video segments of the five dives are listed in [Appendix A](#) and a key used for identification is available as [Appendix B](#). Use of the key ([Appendix B](#)) increased consistency of counts between 2-minute samples and across dives. Small epiphytic organisms such as zoanthids observed growing

on the stalks of sponges at the Ulithi dive site were not counted because they were too small to consistently identify and count. Echiuran-generated lebenspurren were counted by the number of star-shaped feeding traces (Ohta, 1984) observed, but were not included in the community analyses because one star-shaped trace cannot be assumed to equal one live echiuran (Bett et al., 1995).

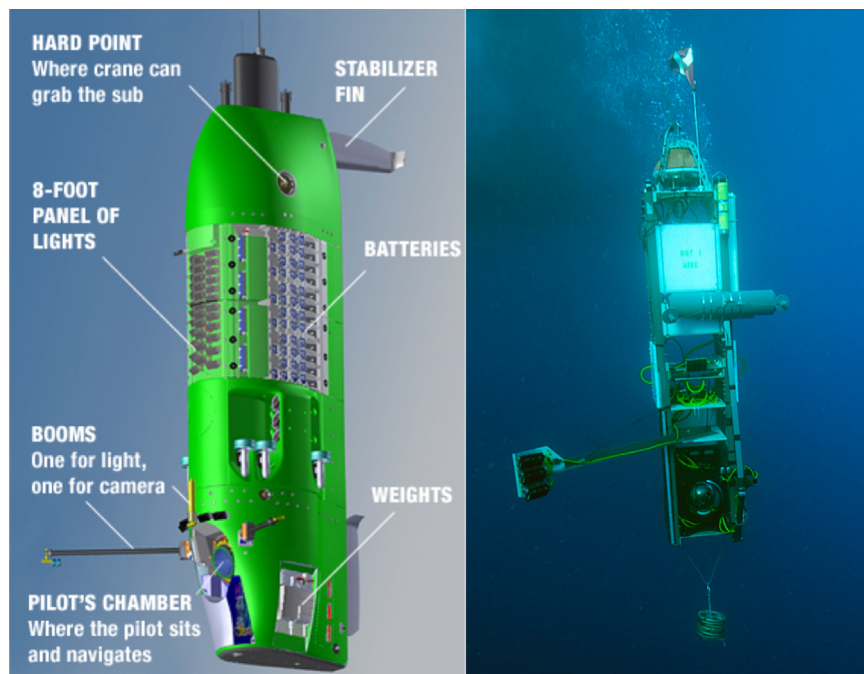


Fig. 2. Illustration of the *DEEPSEA CHALLENGER* on the left and a photograph of the *DEEPSEA CHALLENGE* lander descending through the water column on the right. Photo by Charlie Arneson, used with permission.

Xenophophores were also counted but not included in the community analyses, since we do not know which contain living protoplasm. Counts of echiuran lebenspurren and xenophophores are reported in [Appendix A](#). Terrigenous plant material visible on the seafloor surface was also quantified in each 2-minute sample. Because the submersible speed, orientation, and altitude were variable throughout the dive, quantification per 2-minute sample is the most consistent measure of abundance possible for this study.

For subsequent analysis, species recorded in the 2-minute samples were also grouped using an intermediate taxonomic designation and into a phylum-level designation (both specified in [Appendix A](#)). Community and diversity analyses were conducted at species, intermediate, and phylum-level taxonomic groupings to ensure that the conclusions of the study were robust despite the challenges of species-level identification. Epibenthic community composition was also analyzed across dive sites by lifestyle (demersal or benthic). For the lifestyle analysis, demersal organisms were characterized as all those that were either observed in the water column (while the submersible was near the bottom) or swimming up from the seafloor for an extended period of time (designation specified in [Appendix A](#)), however some may be benthic-pelagic. Most holothurians observed were characterized as benthic due to the fact that they were consistently observed on the seafloor. *Eynpniastes eximia* was characterized as demersal for the lifestyle analysis, but is acknowledged to be benthic-pelagic.

Diversity at dive sites was assessed using several metrics assuming that all species numbers represent minimums, and true diversity is likely higher. Shannon-Wiener diversity index (H') (\log_2), Pielou's evenness index (J'), Berger Parker index for rank-1 dominance, total species richness per site, and rarefaction diversity $E(S_{100})$ were calculated using the distinct taxa identified ([Appendix A](#)). Diversity metrics were calculated using all species observed during a dive across all 2-minute samples. All diversity indices were calculated in PRIMER 6 ([Clarke and Gorley, 2006](#)). Diversity was also assessed at the phylum level using these same metrics. This taxonomic level is less sensitive to errors in species-specific identification, but also may provide information about higher-order evolutionary adaptations to extreme pressure and food limitation.

2.4. Quantification of scavengers from lander images

The scavenging community of the NBT and MT CD was characterized and compared to the epibenthic community using lander images obtained from one autonomous baited lander deployment each in the NBT (8233 m) and the MT CD (10918 m) ([Table 2](#)). The NBT lander was deployed ~2.8 km from the submersible dive site and used chicken as bait, and the MT CD lander was deployed ~17.2 km away from the submersible dive site and used skipjack tuna as bait. Photographs from the landers were visually inspected and all blurred images were removed. For the NBT deployment, one photograph was quantified every ~5–6 minutes. For the MT CD deployment, two photographs were quantified every ~10 minutes. All scavenging fauna approaching the lander and visible in the images were counted for the entire deployment time. Relative amphipod abundance was assessed by counting the number of visible amphipods in each frame throughout the duration of the deployment.

2.5. Statistical analyses

Univariate analyses were performed using JMP Pro 11.0. Differences in average abundance, biodiversity (Shannon's H' \log_2), and percent benthic fauna in the epibenthic community were computed using counts from the 2-minute samples and tested for significant difference between the two upper bathyal sites (NBT 1 km VS Ulithi 1.1 km) and the two hadal sites (NBT 8.2 km VS MT CD 10.9 km). To increase robustness of the data set, counts for 2-minute samples were first bootstrapped 100 times, and the bootstrapped dataset was tested for normality and equal variance. Welch's ANOVA was used to test for significant difference between the means when the data were normally distributed but variances were unequal. When the dataset did not meet the assumptions of normally distributed data, as was the case for the abundance analysis for NBT 8.2 km and MT CD 10.9 km, the non-parametric Median and Kolmogorov Smirnov tests were used.

All multivariate statistical analyses were conducted using PRIMER 6 ([Clarke and Gorley, 2006](#)). Total minimum species observed in the 2-minute samples were included in the biodiversity estimates and rarefaction curves were created with untransformed data. Differences

in community composition at dive sites were assessed using non-parametric multidimensional scaling plots (MDS) of Bray-Curtis similarity matrices, generated from fourth root-transformed abundance data. Additional MDS plots were generated using untransformed counts and presence/absence to assess the relative importance of abundance in generating the observed patterns. ANOSIM was used to conduct pairwise tests of significance and SIMPER was used to evaluate within- and between-assemblage similarities and to assess contributions of specific taxa.

3. Results

3.1. Variability in allochthonous organic input and hard substrate

The Mariana Trench underlies oligotrophic waters that have a reported low annual primary production rate of $59 \text{ g C m}^{-2} \text{ y}^{-1}$

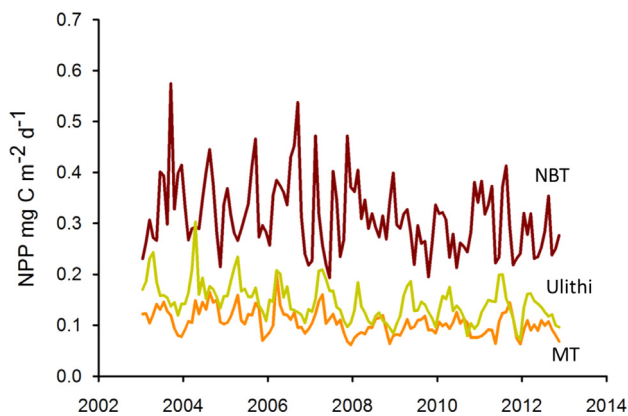


Fig. 3. Differences in net primary productivity (NPP) ($\text{mg C m}^{-2} \text{ d}^{-1}$) between the three areas visited by the DEEPSEA CHALLENGE Expedition: the New Britain Trench (NBT) (red), Ulithi (green), and the Mariana Trench (MT) (orange). Figure shows NPP monthly averages over a ten-year period (2003–2012) approximated using the standard Vertically Generalized Production Model using MODIS-Aqua Chl data downloaded from the Oregon State University Primary Productivity website. (For interpretation of the references to color in this figure, the reader is referred to the web version of this article).

(Jamieson et al., 2009b). In contrast, the New Britain Trench is located beneath less oligotrophic waters. Data on net primary production (NPP) are not published for the northern Solomon Sea for the waters overlying the NBT, so an approximation was calculated using the standard Vertically Generalized Production Model (VGPM, Behrenfeld and Falkowski, 1997) using MODIS-Aqua Chl data downloaded from the Oregon State University Primary Productivity website based on methods described in Kahru et al. (2009). The calculated ten-year average (2003–2012) of NPP for the waters overlying the NBT (latitude -5.667 to -6 , longitude 152 to 152.333) was $\sim 115 \text{ g C m}^{-2} \text{ y}^{-1}$. For consistency of comparison, the same analysis was performed for the Mariana Trench and the Ulithi location. The calculated ten-year NPP average (2003–2012) for the waters overlying the Mariana Trench (latitude 11.200 – 11.600 , longitude 142.000 – 142.950) was $\sim 39 \text{ g C m}^{-2} \text{ y}^{-1}$, or approximately one third the value of the NPP calculated for the NBT (Fig. 3). The ten-year NPP average for Ulithi (latitude 9.517 – 10.167 , longitude 139.000 – 139.567) was $\sim 53 \text{ g C m}^{-2} \text{ y}^{-1}$. Ulithi NPP was higher than the Mariana Trench NPP, but still considerably lower than the NBT NPP (Fig. 3).

The NBT also receives substantial allochthonous organic input from the nearby island of New Britain. This was evidenced at bathyal (1 km), abyssal (3.7 km), and hadal (8.2 km) depths in the NBT by the presence of leaves, sticks, palm fronds, and coconuts (Fig. 4); this has previously been documented by Lemche et al. (1976). Organisms were frequently seen interacting with this plant material, but direct consumption was never observed. Terrestrial detritus declined in the NBT with depth following a power function of $y = 58122x^{-1.15}$ with a high coefficient of determination ($R^2 = 0.994$). This attenuation was likely due both to distance from land, as well as increasing depth. In contrast, the Ulithi bathyal (1.1 km) site and the MT CD hadal (10.9 km) site are situated far from large land masses. This is reflected both in the limited quantity of terrestrial detritus observed at Ulithi and the absence of terrestrial detritus observed in the MT CD (Fig. 4).

While this analysis focuses on the influence of allochthonous food input including surface NPP (Fig. 3) and terrestrial organic detritus (Fig. 4) on structuring communities in the deep sea, it does not include large carrion falls or chemosynthetic food sources. It should be noted that several large bones, likely from marine mammals, were observed

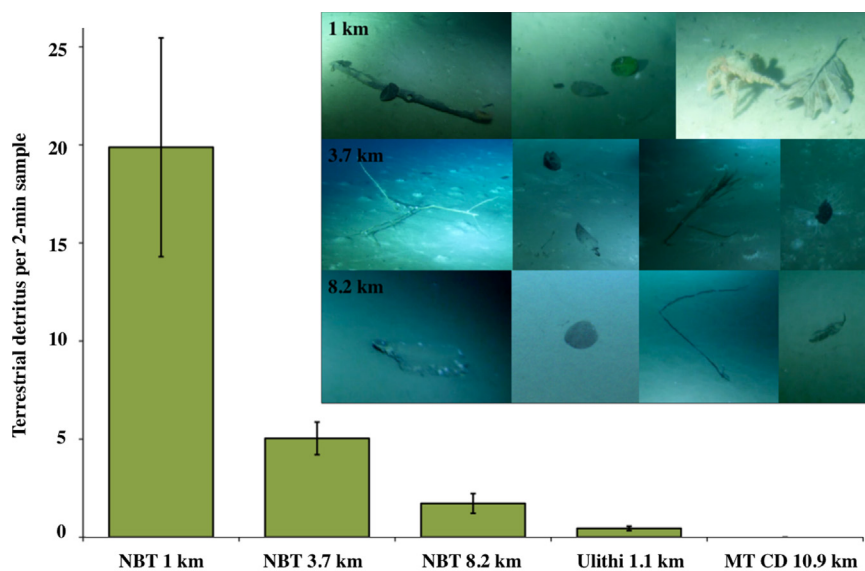


Fig. 4. Observations of terrestrial organic detritus on the seafloor. Mean counts of individual pieces of terrestrial organic detritus observed in the 2-minute video samples from the five dives in the New Britain Trench (NBT), Ulithi, and Mariana Trench Challenger Deep (MT CD). Error bars are standard error of the mean. Right panel shows examples of terrestrial organic detritus, including sticks, leaves, palm fronds, and coconuts, observed at different depths within the NBT. All images in the row correspond to the indicated depth.

at 8.2 km in the NBT and were colonized by benthic organisms, suggesting that carrion falls are an additional contributing food source.

Along with differences in marine and terrestrial allochthonous organic input, the dive sites differed based on the presence and abundance of hard substrate. Rocky outcrops and hard substrates were observed in 100% of the 2-minute samples at the Ulithi bathyal (1.1 km) site, compared to only 24% of the bathyal (1 km) NBT samples, 4% of samples at the abyssal (3.7 km) NBT site, and 44% at the hadal (8.2 km) NBT site. The hard substrates observed at the hadal (8.2 km) NBT site were composed of pillow basalts and steep rocky ledges. No hard substrates were observed during the MT CD hadal (10.9 km) dive.

3.2. Epibenthic community composition

The epibenthic communities at each of the dive sites differed significantly from each other (Figs. 5 and 6) (ANOSIM, Global $R=0.79$, $p < 0.01$), and each had different dominant taxa (Appendix A, Fig. 6). Because MDS patterns generated from untransformed counts and from presence/absence (data not shown) show the same community differences as the fourth-root transformed counts (Fig. 5A), and all communities differ significantly from each other (ANOSIM, $p < 0.01$), we infer that differences in community structure between dive locations are related primarily to community composition rather than abundance patterns. Among the five dive sites, the MT CD hadal (10.9 km) site had the greatest community homogeneity with 61% average similarity in community composition among the 2-minute samples at the species level and 75% at the phylum level. In contrast, epibenthic communities at the two bathyal sites and at the NBT hadal (8.2 km) site were more heterogeneous (Fig. 5). Patchiness of the abiotic environment at the two bathyal sites and at the NBT hadal (8.2 km) site likely increased community heterogeneity. Our findings are robust independent of the challenges of species identification because community patterns at a higher taxonomic grouping (phylum-level) show the same community-specific patterns as those at the species-level (Fig. 5) (Sommerfield and Clarke, 1995).

The Ulithi bathyal (1.1 km) community included sessile animals (sponges and corals) with amphipods and fish contributing to the demersal assemblage. In contrast, the NBT bathyal (1 km) community contained more mobile fauna, including decapods, amphipods, and fishes, with crinoids dominating the sessile fauna (Fig. 6). Comparisons of the two bathyal sites revealed significant differences in community composition ($p < 0.01$), with 83% average dissimilarity at the species level and 44% average dissimilarity at the phylum level. The abundance of decapods and holothurians at the NBT (1 km) site and the abundance of sponges, hexacorals, and

octocorals at the Ulithi (1.1 km) site (Fig. 6) contributed 62% of the community dissimilarity between the two bathyal sites (SIMPER).

Pairwise comparisons between bathyal (1 km), abyssal (3.7 km), and hadal (8.2 km) dive sites within the NBT showed that these communities differed significantly from each other (ANOSIM, $p < 0.01$). The average dissimilarity between the bathyal (1 km) and abyssal (3.7 km) NBT sites was 70% at the species level and 46% at the phylum level. The NBT abyssal (3.7 km) and hadal (8.2 km) dive sites also had high dissimilarity (87% at the species level and 59% at the phylum level). The abundance of holothurians, actinarians, and polychaetes at the hadal (8.2 km) site contributed to the high degree of dissimilarity between the abyssal (3.7 km) and hadal (8.2 km) communities.

The hadal epibenthic communities studied here consisted of both benthic species observed consistently resting or moving on the sea floor and demersal species that swim or drift just above the sea floor. Among the 560 benthic community members observed at the hadal NBT (8.2 km) site and the hadal MT CD (10.9 km) site, 44% were the cnidarian *Galatheaanthemum* sp. and 43% were holothurians; enteropneusts, small caymenostellid asteroids, actinarians, and unknown infaunal organisms accounted for another 13% of the observations. Of the 334 demersal observations at the two hadal sites, the most common taxa were scale worms (Polynoidae 46%), amphipods (26%) and a number of unidentified gelatinous swimming forms, likely belonging to the phylum Cnidaria (27%). Common taxa at bathyal depths (sponges, corals, crinoids and vertebrates) were absent in the hadal video imagery (Fig. 6).

Similar to the two bathyal communities, the two hadal communities differed significantly from each other with 85% average dissimilarity at the species level and 64% average dissimilarity at the phylum level. Both hadal communities were characterized by the presence of elpidiid holothurians and amphipods (Fig. 6). The presence of polychaetes, actinarians, enteropneusts, and unidentified gelatinous swimming forms at the NBT hadal (8.2 km) site contributed to the high degree of dissimilarity between these two hadal communities. Xenophophores were commonly observed in the hadal MT CD community and counts are given in Appendix A, however since we do not know which contain living protoplasm, they were not included in the community analysis.

3.3. Community abundance, biodiversity, and lifestyle representation

The Ulithi and MT CD sites were considered to be more food limited than the NBT sites, and thus we compared the organismal abundance, biodiversity, and lifestyle representation of the benthic communities at bathyal and hadal depths. The NBT bathyal (1 km)

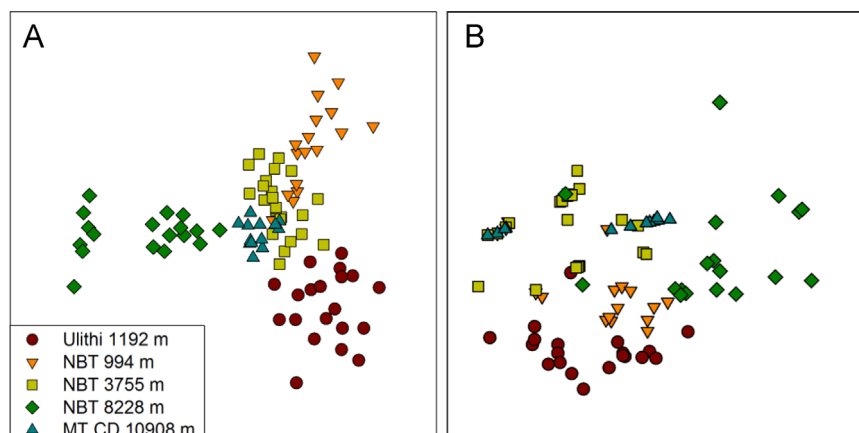


Fig. 5. Multidimensional scaling plot based on a Bray-Curtis similarity matrix of fourth root-transformed abundance data at the species level (A) and at the phylum level (B) for megafauna at the five dives sites. Each point represents a 2-minute sample and icon shape and color indicate dive location and depth. For A, 2D stress is 0.16, ANOSIM (Global $R=0.83$, $p < 0.01$), and for B, 2D stress is 0.20, ANOSIM (Global $R=0.73$, $p < 0.01$). NBT=New Britain Trench, MT CD=Mariana Trench Challenger Deep.

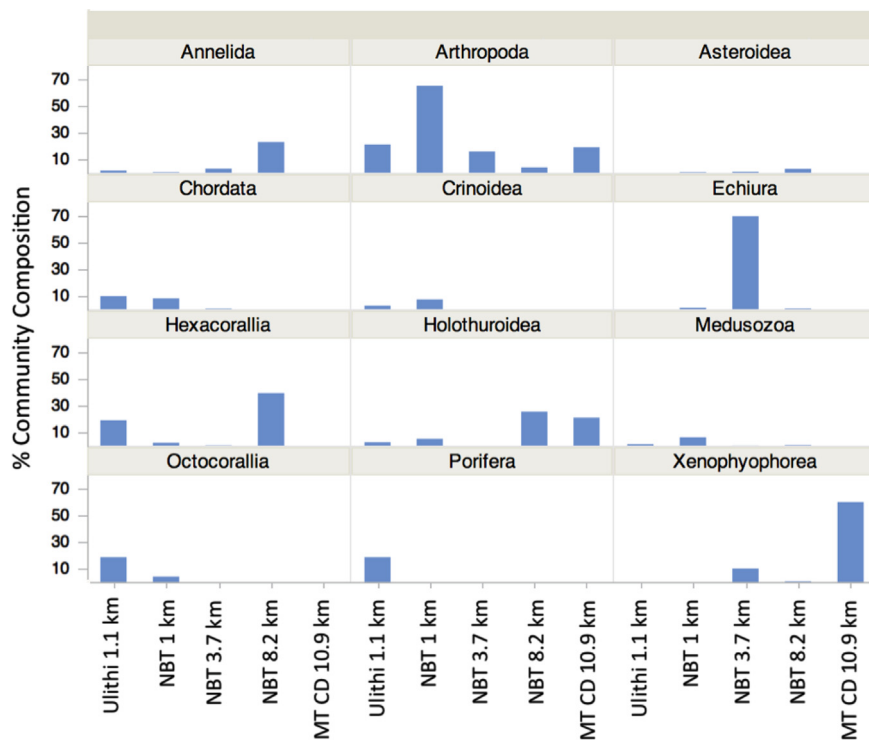


Fig. 6. Comparison of total epibenthic community composition based on intermediate taxonomic grouping at each of the five dive sites visited. Percent community composition is based on summed totals of each group counted using all 2-minute samples from each dive. NBT=New Britain Trench, MT CD=Mariana Trench Challenger Deep. Additional taxa observed but not shown in this figure, due to their minor contribution to the community, include: Ulithi 1.1 km unidentified anthozoan (5%), NBT 3.7 km cephalopod (< 1%), and NBT 8.2 km ctenophore (< 1%) and enteropneust (4%). Counts of echiuran lebenspuren and xenophyophore tests are included in this figure, however, are not included in the univariate and multivariate community analyses.

dive site had higher organismal abundance than the Ulithi bathyal (1.1 km) dive site ($F_{1,147}=239.39$, $p < 0.0001$) (Fig. 7A) and the NBT hadal (8.2 km) dive site had higher organismal abundance than the MT CD hadal (10.9 km) dive site (Median Test, K-S Test, $p < 0.0001$) (Fig. 7B). Rarefaction biodiversity did not follow the same trend (Fig. 8), and the more oligotrophic Ulithi bathyal (1.1 km) community was characterized by higher biodiversity than the NBT bathyal (1 km) dive site ($F_{1,131}=142.10$, $p < 0.0001$) (Fig. 7C), whereas the more oligotrophic MT CD hadal (10.9 km) community had lower diversity than the NBT hadal (8.2 km) site ($F_{1,179}=1755.57$, $p < 0.0001$) (Fig. 7D). Comparison of lifestyle representation reveals that the more oligotrophic Ulithi bathyal (1.1 km) community was composed of a higher proportion of benthic fauna compared to the NBT bathyal (1 km) community ($F_{1,196}=5218.98$, $p < 0.0001$) (Fig. 7E). In contrast, the NBT hadal (8.2 km) community was composed of a higher proportion of benthic fauna compared to the more oligotrophic MT CD hadal (10.9 km) community ($F_{1,198}=274.14$, $p < 0.0001$) (Fig. 7F). When xenophyophore test counts were included in this analysis (results not shown), the pattern for the hadal sites was reversed, with higher benthic lifestyle representation in the MT CD (10.9 km) site than the NBT (8.2 km) site, but the patterns of the abundance and diversity analyses were unchanged.

3.4. Biodiversity trends with depth

For the megafaunal analysis at the species level, there was no clear trend in biodiversity with depth (Table 3, Fig. 8). Within the NBT, the bathyal (1 km) site had the highest biodiversity, with 35 species observed and an H' of 3.50. Biodiversity was lowest in the NBT at the abyssal (3.7 km) site ($H'=2.06$), but then increased again at the hadal (8.2 km) site ($H'=2.64$). Across the five sites visited, the MT CD hadal (10.9 km) site had the lowest biodiversity as revealed by all diversity metrics (Table 3, Fig. 8).

Analysis of biodiversity at the phylum level revealed different trends in biodiversity with depth (Fig. 8B). Within the NBT, phylum-level biodiversity declined slightly between the NBT bathyal (1 km) ($H'=1.54$) and abyssal (3.7 km) sites ($H'=1.08$), but this decline was smaller than that observed for species-level biodiversity (Fig. 8A). Surprisingly, the NBT hadal (8.2 km) site had very high phylum-level biodiversity ($H'=1.93$; Fig. 8B) with representatives of 6 phyla observed in the hadal community (Cnidaria, Ctenophora, Annelida, Arthropoda, Echinodermata, and Hemichordata) and high evenness ($J'=0.74$) (Table 3).

3.5. Observation of potentially new taxa

Several previously unreported taxa were seen in the DEEPSEA CHALLENGE dive and lander imagery. A pelagic polychaete in the family Acrocirridae, genus *Teuthidodrilus* (squidworm) was observed at 1 km in the NBT (Fig. 9A and B). The hadal trench-floor community in the NBT revealed three new taxa and may extend the depth limit for caymenostellid asteroids to ~8.2 km. The largest organisms present in the NBT hadal community were ulmarid jellyfish that had previously not been described from this trench or from similar depths elsewhere. The observed species tentatively belongs to the subfamily Poraliinae and appeared to be feeding on the sediment surface in the NBT (Fig. 9C). Three individuals were observed during the intensively surveyed 36 minutes of bottom time (2 min samples), and nine were observed during the whole 3-hour bottom time. Crustaceans thought to be either penaid shrimp or mysids were also observed in the lander imagery from the NBT at 8.2 km (Fig. 9D). They were observed approaching the baited lander but did not approach or feed on the bait. Twenty-two individuals were observed in 70 images taken by the baited lander over a 7-hour deployment time, but it is not possible to know if these were all distinct individuals or the same individuals returning over that time period. The NBT trench floor (~8.2 km) also

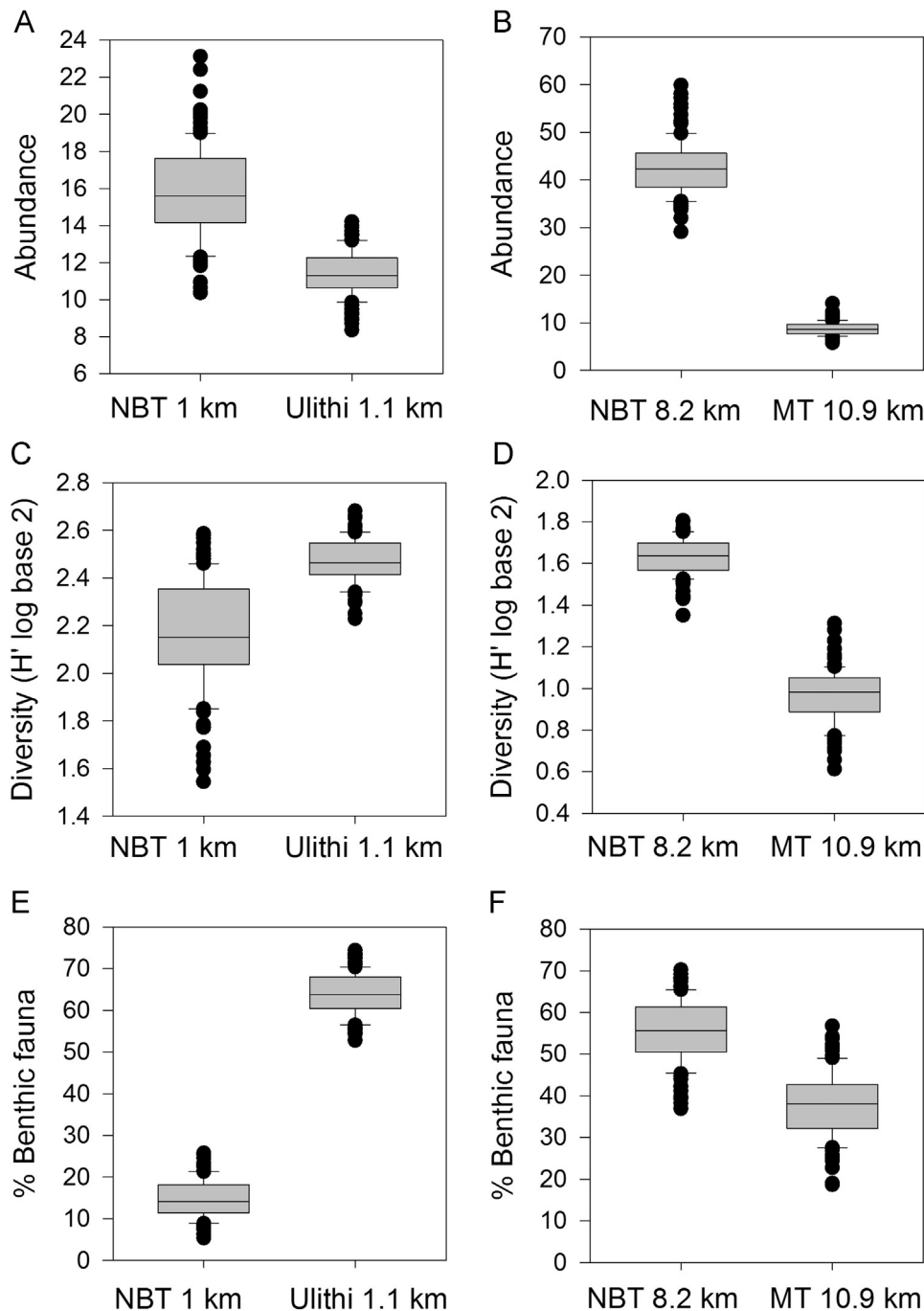


Fig. 7. Differences in abundance (A and B), diversity (C and D), and percent of seafloor benthic versus demersal lifestyles (E and F) in the epibenthic communities between two bathyal (A, C, and E) and two hadal (B, D, and F) sites. NBT=New Britain Trench, MT=Mariana Trench Challenger Deep. % benthic refers to the percent of fauna in the community consistently observed on the sea floor. Of the two bathyal sites, Ulithi 1.1 km is considered more food-limited and, of the two hadal sites, MT CD 10.9 km is considered more food-limited. Data shown have been bootstrapped 100 times and all differences were determined to be statistically significant ($p < 0.0001$). Box and whisker plots show median, upper and lower quartiles, maximum and minimums, and outliers for each bootstrapped dataset.

had large pieces of wood debris, as well as marine mammal bones, which were colonized by what appeared to be small caymenostellid asteroids (Fig. 9E and F).

The submersible dive to the Challenger Deep (10.9 km) revealed sixty-five individual elpidiid holothurians at depths between 10876–10908 m in the 2-minute video samples. These holothurians are thought to be a previously unreported species and had elongate semi-transparent bodies, extended oral tentacles (between 3–5 commonly observed in the videos), and were always observed on top of the sediment with no evidence of burrows, fecal coils, and rarely any evidence of trails. Whenever more than one holothurian was observed

in a single frame, the holothurians were always oriented in the same direction. We tentatively suggest that these individuals belong to *Peniagone* (Fig. 9G and H), a genus that is known to exhibit orientation behavior.

3.6. New Britain Trench and Challenger Deep hadal scavenging communities

Amphipods were the dominant fauna visible in the autonomous baited lander images. The NBT trench-floor scavenging community (8233 m) was more diverse and had more abundant scavengers than

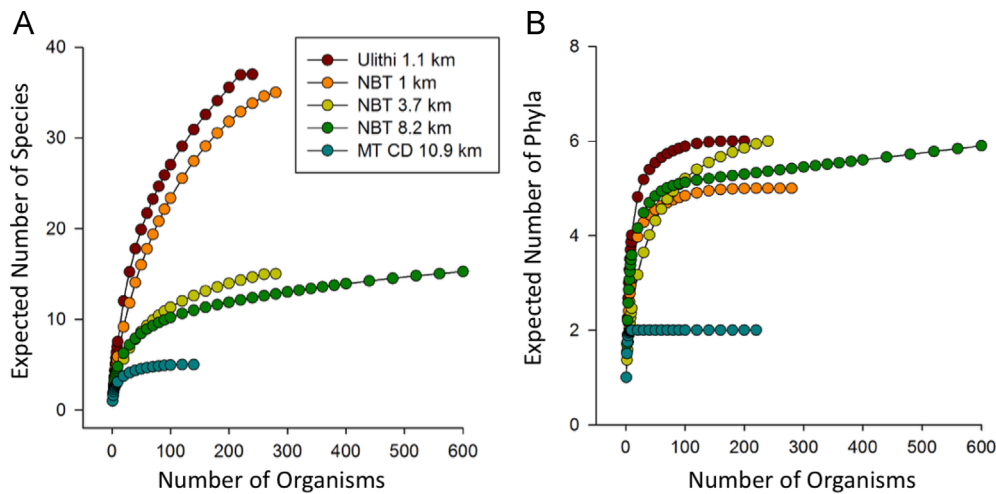


Fig. 8. Rarefaction curves for distinct taxa (A) and distinct phyla (B) observed for the five different dive sites visited on the *DEEPSEA CHALLENGER* expedition. NBT=New Britain Trench, MT CD=Mariana Trench Challenger Deep. (For interpretation of the color key in this figure, the reader is referred to the web version of this article).

Table 3
Epibenthic diversity indices for phylum and species-level epibenthos for the 5 dive sites.

	Ulithi 1.1 km		NBT 1 km		NBT 3.7 km		NBT 8.2 km		MT CD 10.9 km	
	Phylum	Species	Phylum	Species	Phylum	Species	Phylum	Species	Phylum	Species
Shannon's H' (\log_2)	2.09	4.28	1.54	3.50	1.08	2.07	1.93	2.64	1.00	1.62
Pielou's J'	0.81	0.82	0.66	0.68	0.42	0.53	0.74	0.66	1.00	0.70
Berger Parker	0.44	0.15	0.65	0.35	0.78	0.63	0.40	0.32	0.52	0.50
$E(S_{100})$	5.89	27.01	4.84	23.34	5.21	11.3	5.13	10.18	2	4.95
Total No. Species	6	37	5	35	6	15	6	16	2	5
Total No. Individuals	194	221	272	272	234	264	667	763	124	131

Diversity indices were calculated using the sum of all quantified individual species or phyla using all 2-minute samples from each dive. Counts of xenophyophore tests and echinuran-generated traces were not included. All diversity indices represent minimum values, as cryptic species may exist.

the MT CD hadal scavenging community (10918 m). The abundance of amphipods in each image was greater in the NBT for the majority of the lander deployment until about 325 minutes after landing, at which point the number of amphipods attending the bait leveled off (Fig. 10). In contrast, the abundance of amphipods attending the bait in the MT CD showed no asymptote throughout the duration of the deployment (Fig. 10). Lander imagery and unpublished molecular sequencing results from lander-collected amphipods (Cytochrome oxidase subunit 1, G. Rouse, unpubl.) revealed 5 amphipod species in the NBT, including *Alicella gigantea*, whereas only 2 amphipod species were detected in the MT CD. Image analysis also revealed the presence of holothurians and crustaceans (decapods or mysids) in the NBT hadal scavenging community, which were not present in the MT CD hadal scavenging community. Results from image analysis combined with CO1 sequencing (G. Rouse, unpubl.) suggest that the NBT hadal site, with seven distinct taxa, had a more diverse scavenging community than the MT CD community with only two distinct taxa.

4. Discussion

4.1. Strengths and challenges of video-derived submersible data

Recent advances in technology have enhanced hadal research by providing time lapse or continuous photographs and video that offer behavior information (Jamieson et al., 2009a, 2009b, 2011b). However, in trenches these have often been associated with landers, which have a fixed domain of study. This study pairs manned submersible footage from the *DEEPSEA CHALLENGER* with still images from baited landers to provide a holistic description of hadal epibenthic communities using video imagery. The video

imagery offers information about ecological patterns that might not be evident in trawl samples, as well as information about spatial heterogeneity that is not evident in imagery from fixed locations.

While the use of video for analyzing community patterns has many strengths, one of the principal challenges is identifying species consistently and accurately. To reduce bias resulting from the difficulties of species identification we (1) extracted from the video the best view of each distinct taxon observed and sent it to deep-sea experts to obtain the lowest taxonomic identification possible (Appendix A) and (2) conducted analyses of community composition and diversity at several taxonomic levels, including an intermediate taxonomic grouping and a phylum-level grouping (specified in Appendix A). Similar patterns in community composition, community heterogeneity, and community diversity at the phylum-, intermediate-, and species-level taxonomic grouping, suggest that the conclusions of this study are robust and not biased by the challenges of taxonomic resolution from video imagery (Sommerfield and Clarke, 1995). All diversity indices likely represent species minima, as there may be small, cryptic individuals that cannot confidently be identified to species level from video. Specifically, diversity of the amphipods, demersal annelids, and demersal gelatinous taxa are almost certainly underestimated by this analysis, whereas larger and more easily differentiated megafauna such as fish, echinoderms, and some cnidarians represent more accurate diversity estimates. Although highly mobile species may have avoided the submersible, most individuals observed in the video did not seem to react to the presence of the submersible, and deep-submergence vehicles have previously been used to study mobile, deep-sea animals (Barham et al., 1967).

A strength of using video footage was that it allowed us to witness the feeding behaviors of the recently recognized ulmariid

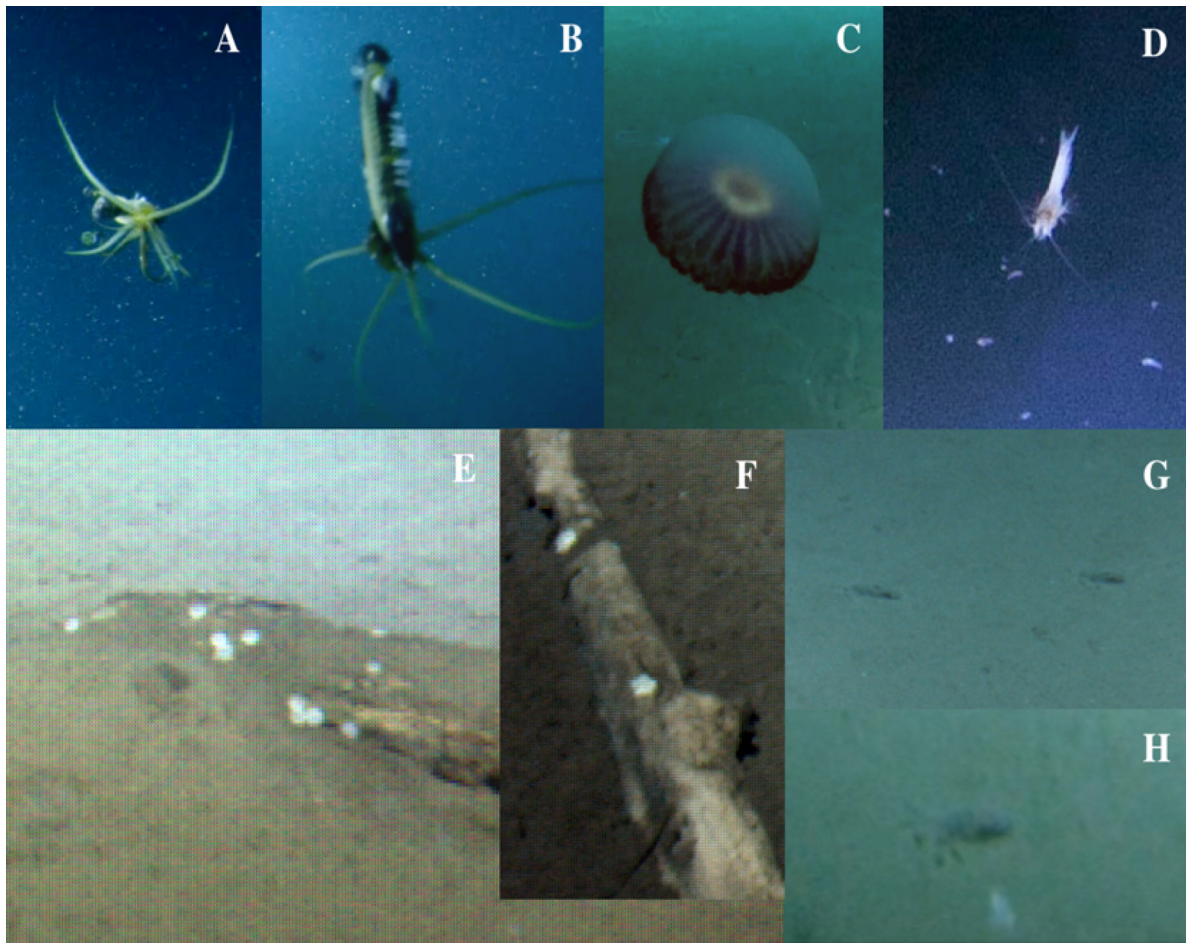


Fig. 9. Images of epibenthic and benthopelagic taxa, some of which are believed to be previously unreported, that were observed during the DEEPSEA CHALLENGE submersible and lander dives. A and B: *Teuthidodrilus* polychaete species from 1 km in the NBT. C. Large hadal ulmarid cnidarian observed at 8.2 km in the NBT. D. Crustacean (decapod or mysid) observed during baited lander deployments at 8.2 km in the NBT. E and F. Caymenostellid asteroids observed on wood debris and bones at 8.2 km in the NBT. G and H. Eplidiid holothurians observed at 10.9 km in the MT CD. NBT=New Britain Trench, MT CD=Mariana Trench Challenger Deep.

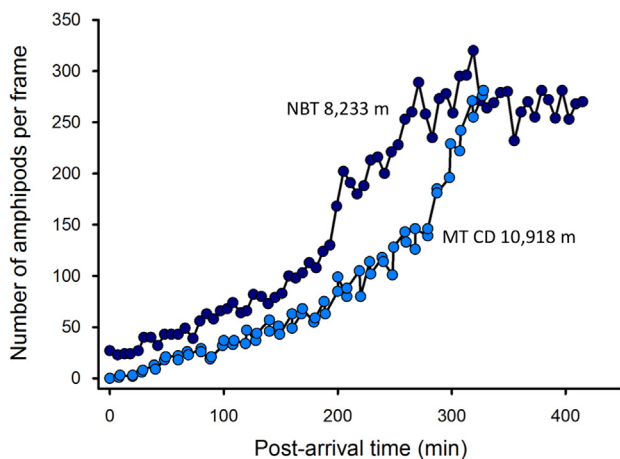


Fig. 10. Number of amphipods observed in each frame in the hadal scavenging community of the New Britain Trench (NBT) and Mariana Trench Challenger Deep (MT CD) over the deployment time of the lander.

jellyfish in the NBT and the eplidiid holothurians in the MT CD (Fig. 9). The ulmariid jellyfish at 8.2 km in the NBT was observed feeding on particulates on the sediment surface by skimming the sediment, leaving the sediment surface when disturbed by the submersible. Previous studies have described the important role jellyfish play both as members of epipelagic, deep-sea communities

(Miyake et al., 2002; Lindsay and Pagès, 2010), and as vectors of carbon transport to the deep sea following jellyfish blooms in surface waters (Sweetman and Chapman, 2011). This study reveals that jellyfish are also important members of the hadal community in productive trench environments.

In the MT CD at 10.9 km, video footage allowed us to observe that the eplidiids were oriented uniformly (Fig. 9G), suggesting they are utilizing currents for feeding. This is consistent with previous observations of eplidiid holothurians in the genus *Peniagone* utilizing bottom currents for orientation and/or feeding (Ohta, 1985; Okada and Ohta, 1993). While this behavior is not novel, this is the first description of an abundant population of epibenthic eplidiids at the bottom of the CD. Observations of eplidiid behavior in the Peru–Chile Trench made with time-lapse video (Jamieson et al., 2011a) provide another example of the value of video for increasing our knowledge of the behaviors of hadal species.

4.2. Epibenthic community patterns in the bathyal compared to the hadal zone

We tested the hypothesis that increased food has similar effects on community structure at bathyal as at hadal depths by examining nearby bathyal epibenthic communities. This hypothesis was supported for abundance (Fig. 7A, B), but not for Shannon species diversity (Fig. 7C, D) and representation of benthic lifestyles (Fig. 7E, F). The presence of hard substrate at the Ulithi bathyal (1.1 km) site and the NBT hadal (8.2 km) site may also have

contributed to the higher diversity and higher proportion of benthic fauna observed at these sites.

The diversity results are consistent with a unimodal response of deep-sea diversity to food availability (Levin et al., 2001), wherein more food gives rise to higher diversity at hadal depths, but decreased diversity at bathyal depths, where ambient food supply is higher. Most data for deep-sea diversity trends with depth in the benthos exhibit a unimodal pattern with maximum values at mid slope depths (Rex and Etter, 2010; Menot et al., 2010). However, few extend to full-ocean depth. The results presented here indicate that diversity below abyssal depths will vary significantly depending on overlying productivity regime and proximity to sources of terrestrial organic matter (Fig. 7C and D). This is consistent with current understanding that food supply is a primary driver of hadal community structure (Bruun, 1956; Jamieson, 2011). Another interesting observation is that phylum-level biodiversity may actually increase with depth (Fig. 8). This finding should be tested in other trenches, since the conclusion is based on three depths sampled in the NBT.

4.3. Similar responses in hadal scavenging and epibenthic communities

The use of paired baited lander deployments and submersible dives to the bottom of the NBT and MT CD, allowed us to assess if hadal epibenthic communities showed similar patterns of abundance and diversity as scavenging communities. Both communities exhibited greater abundance (Fig. 10) and higher diversity in the NBT than the MT CD at hadal depths. These trends were largely driven by amphipods in the scavenging assemblage, but also reflect the presence of elpidiid holothurians and decapod or mysid crustaceans at 8.2 km in the NBT. Lander imagery reveals a more complex food web in the hadal scavenging community of the NBT; crustaceans (decapods or mysids) and one amphipod species that attended the bait without feeding may be carnivores that consume the bait-attending scavengers. The observed amphipods may belong to the genus *Princaxelia*, which are carnivorous bait-attending amphipods found at hadal depths in Pacific Ocean trenches (Kamenskaya, 1984; Jamieson et al., 2011a, 2011b). In contrast, the MT CD scavenging community was only composed of two amphipod species, which both appeared to be scavengers.

This study reports higher diversity in the amphipod scavenging community at these depths than has been described in previous papers in the Philippine Trench (Hessler et al., 1978), the Kermadec Trench (Jamieson et al., 2011c), and in the Tonga Trench (Blankenship et al., 2006). In the Tonga and Kermadec trenches, 4 species of lysianassid amphipods were found to partition the trench vertically with the younger stages often occurring at shallower depths (Blankenship et al., 2006). In the NBT – 5 species co-occurring at 8.2 km may be a record for hadal depths, and suggests a more complex food web in the NBT.

4.4. Influence of geological differences on community patterns

Previous studies have explored the effects of habitat heterogeneity due to geological characteristics on macrobenthic community structure and species richness (e.g., Fodrie et al., 2009; De Leo et al., 2014). The Puerto Rico, Kermadec, Tonga, Peru-Chile, New Hebrides, West Solomon, and the New Britain trenches are known to have masses of rubble, talus slopes, and fragmented outcrops (Heezen and Hollister, 1971), which increase habitat heterogeneity in these trenches. While our analysis focused on differences in food supply as the main factor giving rise to the differences in community patterns observed, habitat heterogeneity due to geological differences likely also influenced our results. One line of evidence for this is that the sites with the greatest community heterogeneity across 2-minute samples (Ulithi 1.1 km

and NBT 8.2 km) (Fig. 5) were also sites that had rocky substrates observed in more than 40% of the samples. Thus, the lower diversity observed at the NBT abyssal (3.7 km) site and the MT CD hadal (10.9 km) site may additionally be due to the homogeneous, fine silty substrate observed at these sites. Even in the MT CD, evidence of community patchiness and habitat heterogeneity were also apparent, with higher densities of xenophyphore tests observed where there were shallow sediment troughs.

The NBT and MT subduction zones are similar with respect to the degree of seismic activity (see Fryer et al., 2003 for the MT; Yonishima et al., 2005 and Benz et al., 2010 for the NBT) but they differ in the type and degree of deformation, which could yield distinct ecological disturbance regimes for the biota. The forearc of the NBT slopes relatively gently from sea level to ~7000 m depth, then steepens within 5.5 km of the trench axis. There are a few narrow channels offshore of river mouths that broaden into swales to depths of 4,000 m in the forearc area, but little in the way of features that suggest significant faulting or wide-spread crustal deformation. By contrast with the NBT forearc, that of the southern MT area is highly deformed, with numerous fault lineaments and multiple fault-controlled canyons that feed sediment from the inner forearc slope into the trench axis (Fryer et al., 2003). Thus in addition to the southern MT axis having essentially no allochthonous organic input, it likely suffers from a greater frequency of resurfacing. This greater disturbance may reduce animal densities, inhibit subsurface, bioturbation-dependent lifestyles, and reduce fitness of benthic taxa.

The 2.7 km depth difference between the two hadal sites compared in this study (MT CD 10.9 km and NBT 8.2 km) may also have contributed to the lower abundances, lower diversity and altered lifestyles documented in the MT CD. Epibenthic diversity (Vinogradova, 1962) and scavenging amphipod diversity (Blankenship et al., 2006) is known to decrease with increasing depth in the hadal zone and certain groups such as decapod crustaceans and fishes are absent below 8.3 km (Jamieson et al., 2009a, 2009b; Fujii et al., 2010; this study), possibly due to physiological limitations (Yancey et al., 2014). It would be beneficial to conduct an additional study in a trench of similar bottom depth to the NBT, that is overlain by oligotrophic waters (similar to the MT CD), in order to tease apart the influence of depth, compared to the influence of allochthonous input, on observed differences in the epibenthic and scavenging communities.

4.5. Observations of importance

Despite limitations on level of identification, this study contributes polychaete, crustacean, cnidarian, and echinoderm observations of note for their depth records or evolutionary significance. The genus *Teuthidodrilus* was first described in 2010 (Osborn et al., 2011) and is currently monotypic with the only known species (*Teuthidodrilus samae*) occurring in the Western Celebes Sea at 2000–2900 m; a similar midwater polychaete had previously been observed off of western India at 1500 m by the SERPENT project (<http://archive.serpentproject.com/231/>) but was never collected. Based on differences in appearance, depth of observation, and distance from the Celebes Sea, the individual observed at 1 km in the NBT (Fig. 9A and B) likely represents a new species in this genus, and may be of particular interest for future study due to its location. This genus is of evolutionary interest because it is thought to be transitional between benthic and pelagic polychaetes and is a sister group to the 'bomb'-bearing clade (Osborn and Rouse, 2011).

Prior to the recent discovery of decapod crustaceans at hadal depths in the Japan and Kermadec Trenches (Jamieson et al., 2009a), it was thought that decapod crustaceans were unable to survive at hadal depths. If our NBT crustacean observations (Fig. 9D) were actually a decapod crustacean, they would extend the maximum depth of decapod crustaceans from 7703 m to 8233 m. Whether

decapod or mysid, their abundance suggests that they may be an important part of the food web in carbon-rich hadal trenches.

Prior to this expedition, the deepest known holothurian in the published literature was *Myriotrochus brunni*, which was collected by trawl from 10710 m in the Mariana Trench (Wolff, 1970; Belyaev, 1989). Our observation of elpidiid holothurians in the MT CD at 10.9 km (Fig. 9G and H) extends the depth range for elpidiids to maximum ocean depth, making them the deepest known deuterostome taxon. Taken together these findings make clear that the hadal zones remain a fertile area for extending the known depth ranges of invertebrate life forms.

We saw largely soft-bodied taxa at hadal depths, with few organisms having calcareous or siliceous skeletons. The prevalence of soft-bodied organisms at hadal depths is hypothesized to be due to the difficulties of biomineralization below the calcium compensation depth (CCD) at 4000–5000 m (Jamieson et al., 2010). Despite this, some organisms with calcareous skeletons do exist at hadal depths, such as serpulid polychaetes that inhabit calcareous tubes (Kupriyanova et al., 2014) and limpets reported from wood and seagrass in the Puerto Rico Trench (Leal and Harasweych, 1999). At 8.2 km in the NBT, we observed caymenostellid asteroids and holothurians in the genus *Elpidia*, which have calcareous endoskeletons or microspicules. The unique mineral structure of echinoderm skeletons is composed of high-magnesium calcite and confers high strength properties with minimal amounts of material (Weber et al., 1969). This structure may allow for hadal echinoderms, such as holothurians, to produce skeletal structure below the CCD.

The complete absence of fish in both the images from the baited landers and the submersible videos from both the bottom of the NBT and the MT, supports the hypothesis that fish have a physiological depth limit (Yancey et al., 2014). While our results suggest that the MT food web would be less likely to support fish taxa, the high abundance and diversity of potential prey items in the NBT suggests that the absence of fish at the base of the NBT is not due to food limitation. During the dive of the *Trieste* to the Challenger Deep, Jacques Piccard and Don Walsh observed a “flatfish” at 10916 m through the viewport of the submersible. This would be the deepest fish sighting known to man, but this sighting has been denounced as erroneous by the scientific community (Wolff, 1961; Jamieson and Yancey, 2012). The deepest published fish observation is the liparid *Pseudoliparis amblystomopsis*, observed at 7703 m in the Japan Trench (Jamieson et al., 2009a, 2009b; Fujii et al., 2010). Deep-sea bony fishes utilize the osmolyte trimethylamine N-oxide (TMAO) to stabilize protein structure against distortion by hydrostatic pressure (Kelly and Yancey, 1999; Samorette et al., 2007). It is thought that deep-sea fishes become isosmotic at 8200 m due to TMAO accumulation, and thereby are physiologically excluded from living at greater depths (Yancey et al., 2014). The absence of fish observed at 8.2 km in the NBT and at 10.9 km in the MT (Fig. 6) supports this teleost depth limit. However, during manuscript proof preparation the media reported lander-based (unpublished) observations of snailfish living at 8145 m. (<http://schmidtocean.org/story/show/3584>).

4.6. Heterogeneity of deep-sea epibenthic communities

Each of the sites examined had a distinct appearance with different faunal dominance (Fig. 6, Appendix A). While echinuran-generated lebensspuren were not included in the quantitative analyses, they were abundant at the abyssal (3.7 km) NBT site (Fig. 6). Other regions with high echinuran density have also been described including the Kaikoura canyon of New Zealand (De Leo et al., 2010) and the base of the southern Chile margin (T. Shank, A. Thurber, L. Levin, unpubl.). These observations suggest that echinurans may dominate in abyssal mid-slope regions that receive considerable allochthonous input.

At the base of the slope, the trench floor of the NBT at 8.2 km was dominated by hadal anemones in the genus *Galatheanthemum*, elpidiid holothurians in the genus *Elpidia*, and enteropneusts (Fig. 6). The observed community composition in the NBT was similar to that observed in eutrophic trenches such as the Puerto Rico Trench (George and Higgins, 1979). In contrast, amphipods and elpidiid holothurians dominated the oligotrophic MT CD megafaunal community, and protozoan xenophyophore tests were also abundant (Fig. 6). The dominant taxa present at our hadal sites have been reported from other trenches (Belyaev, 1989; Blankenship-Williams and Levin, 2009), but we did not expect to see such a large number of holothurians in the MT CD. High densities of deposit-feeding holothurians and amphipods in the trench axis may reflect accumulation of food (Belyaev, 1989; Jamieson et al., 2010).

5. Conclusions

In summary, the combined DEEPSEA CHALLENGE dives and lander deployments offer a rare glimpse into the seafloor and demersal assemblages of two very different trenches. Our observations support a key role for allochthonous productivity in shaping abundance and diversity and the relative importance of demersal lifestyles. High putative 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. As hypothesized, hadal and bathyal assemblage abundances responded similarly to greater food availability, but diversity and lifestyle representation did not. Also (as hypothesized), scavenging and non-scavenging benthic assemblages exhibited similar responses to food availability. Since climate change and near-trench deep-sea mining efforts may alter allochthonous input to trenches, changes in trench community structure, abundance, and biodiversity should be considered and studied. In this study, possible new species were seen, novel behaviors were observed, and new depth records set. Although the lander recovered amphipods, most of the taxa we observed were not sampled; retrieval would potentially have allowed the description of new species and the confirmed identification of others. We suggest multiple observation and sampling approaches are needed to maximize knowledge of these extreme and mysterious trench communities.

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Appendix A

All quantified taxa from the five *DEEPSEA CHALLENGE* submersible dives. Counts indicate the total number of individuals observed during each dive using all 2-minute video samples. Column titled “B/D” indicates which taxa were characterized as benthic (B) or demersal (D) for the lifestyle analysis. Columns titled “IntTaxGroup” and “Phylum” indicate intermediate taxonomic and phylum classifications used for the community and biodiversity analyses. NBT=New Britain Trench, MT CD=Mariana Trench Challenger Deep.

Appendix B

Image-based key with all taxa quantified from the five *DEEPSEA CHALLENGE* submersible dives. Order and names correspond to names and counts in Appendix A. Images represent the best still of each taxon extracted from the *DEEPSEA CHALLENGE* videos.

Appendix C. Supporting information

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.dsr.2014.12.012>.

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