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Comparisons of three deep-sea wreck communities in the Gulf of Mexico

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ABSTRACT: Artificial hard substrates such as shipwrecks and large debris can impact biodiversity, especially in the deep sea where hard substrate is limited. A potential complex interplay occurs where wrecks provide surfaces for recruitment of epibenthic organisms and structured habitat for mobile invertebrates and fish but may also inhibit successional processes due to the presence of oil and other toxins. Here, we examined the interplay of these dynamics using remotely operated vehicle (ROV) surveys of the wrecks of the oil rig *Deepwater Horizon*, the SS 'Robert E. Lee,' and the USS 'Peterson.' Megafauna were identified to the lowest possible taxonomic unit using the high-definition video captured by ROV. Comparisons of the 3 wrecks revealed communities with unique compositions, but that did not vary significantly in total abundance, density, richness, evenness, or diversity. Furthermore, while species identities varied between wreck sites, the functional roles they fulfilled based on motility, tiering, and feeding mode largely did not. We posit wreck age, depth, and the presence of oil as potentially interacting factors influencing the assembly of these artificial hard substrate communities. As industrial activities continue to introduce more artificial substrates into the deep sea, our findings suggest that these structures may not support the diverse, thriving ecosystems typically expected, which has important implications for deep-sea restoration and conservation efforts focused on enhancing biodiversity through artificial habitats.

KEY WORDS: Deep sea · Deep-sea environments · Shipwrecks · Oil contamination · Marine ecology

1. INTRODUCTION

Hard substrate is rare in the deep sea, making up less than 10% of the total seafloor, and less than 5% of the seafloor in the Gulf of Mexico (Glover & Smith 2003, Jenkins 2011). Despite its scarcity, hard substrate serves as crucial habitat for many species. With increasing human activities, anthropogenically derived hard substrates have become more commonplace in the deep sea and have the capacity to attract species that exhibit a preference for, or dependence on, hard substrates. These substrates may include, but are not limited to, plastic waste, lost fishing gear, energy infrastructure (including oil rigs), and shipwrecks (Jambeck et al. 2015, Cressey 2016, Richardson et al. 2022).

The biodiversity dynamics on artificial hard substrates in the deep sea, while not completely understood, appear to be complex. Biodiversity may be bolstered if the substrates provide either a physical habitat or nutritional source. For example, certain metals can be metabolized by specific bacterial communities, and wood-based substrates can provide nutrients and carbon, particularly to xylophagous species. However, these artificial substrates may predominantly function as scaffolding upon which marine communities, including some foundation species, can establish themselves (Glover & Smith 2003, Ramirez-Llodra

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et al. 2011, Taylor et al. 2014, McDermott et al. 2023). In contrast, diversity may be suppressed because some of these structures may release oil and/or other toxins into the surrounding aquatic environment (Thiel et al. 2001, Rogowska et al. 2010, Amezcua-Linares et al. 2014, Ndungu et al. 2017), posing a protracted threat to deep-sea ecosystems and the communities that may establish on these structures, potentially causing enduring harm. While the positive and negative impacts of anthropogenic hard substrate are still debated, they are recognized as complex biological habitats (Macreadie et al. 2011, Ramirez-Llodra et al. 2011, Ramos et al. 2021). These artificial hard substrates can host abundant and diverse communities, but these are often different from communities on natural hard substrate (Monroy-Velázquez et al. 2020). Investigations of a shipping container lost in the deep sea uncovered a community that experienced significant shifts in dominant taxa over 13 yr, but the community on the container lacked large corals on nearby hard substrates in the nearby canyon (Taylor et al. 2014, McDermott et al. 2023). Studies on communities developing on shipwrecks, sunken rigs, and other anthropogenic structures (Zintzen et al. 2008, Brooks et al. 2012, Larcom et al. 2014, Meyer et al. 2017, Meyer-Kaiser et al. 2022a,b) have demonstrated that in the deep sea, anthropogenic hard substrate communities also often differ from their natural hard substrate counterparts (Smith & Rule 2002, Zintzen & Massin 2010, Monroy-Velázquez et al. 2020, McDermott et al. 2023). The ecological implications of anthropogenic hard substrates become even more complex when considering catastrophic events such as the *Deepwater Horizon* (DWH) oil spill, which not only introduced significant amounts of oil into the marine environment but also deposited a substantial amount of hard substrate in the form of the wreck of the mobile offshore drilling unit and debris associated with the superstructure on the deep-sea floor. Clearly, many questions remain about the assembly and variability in ecological dynamics of ecological communities on anthropogenic hard substrates in the deep sea.

One of the largest introductions of artificial substrate to the deep oceans was the DWH. On 20 April 2010, an explosion on the DWH oil rig started a fire that would burn for 2 d before the rig sank on 22 April. All the while (continuing until 15 July), approximately 3.19 million barrels of oil spilled out into the ocean from a depth of 1500 m (Fisher et al. 2016), making the DWH oil spill the largest unintentional spill in history (United States National Commission on the BP Deepwater Horizon Oil Spill and Offshore Drilling 2011, US v. BP et al. 2015, Deepwater Horizon Natural Resource Damage Assessment Trustees 2016). The impacts of the DWH oil spill on the soft sediment habitat near the DWH wellhead are well documented (Valentine & Benfield 2013, McClain et al. 2019, Nunnally et al. 2020), as are the effects of the spill on specific species, especially vulnerable taxa such as octocorals, foraminifera, and microbes (White et al. 2012, Fisher et al. 2014, Kimes et al. 2014, Lamendella et al. 2014, Mason et al. 2014, Schwing et al. 2015, 2020, Girard & Fisher 2018). While studies have focused on soft sediment communities near the wreck (Valentine & Benfield 2013, McClain et al. 2019, Nunnally et al. 2020), none have explicitly focused on the wreckage and debris of the DWH as hard substrate. The DWH represents a significant influx of hard substrate to an otherwise soft-bottom habitat, including the rig structure (measuring 121 × 78 m), on-board equipment, and the riser pipe that connected the rig to the wellhead (measuring approximately 1500 m in length) (US Navy 2011). The resulting massive field of oiled debris extends more than 500 m to the north of the wellhead at a depth of approximately 1505 m (Valentine & Benfield 2013). However, this massive debris field is not the only source of anthropogenic hard substrates in the deep sea.

The Gulf of Mexico is home to thousands of shipwrecks (Church et al. 2009, Mugge et al. 2019). Many of these shipwrecks may not be contaminated by hydrocarbons, but nevertheless function distinctly from natural hard substrates, possessing properties that can engender patterns of colonization and ecological succession distinct from those observed on natural hard substrates (Church et al. 2009, Meyer et al. 2017, Meyer-Kaiser et al. 2022a,b). Wrecks in the deep sea behave as habitat islands analogous to artificial reefs with unique communities compared to those of the surrounding sediment (Hamdan et al. 2021). Wreck size and depth appear to be the primary drivers of turnover in community composition and the associated distribution of functional traits (Meyer et al. 2017, Meyer-Kaiser et al. 2022a). Furthermore, the physical structure of wrecks may contribute to the organization and distribution of organisms within a community. For example, sessile filter feeders are more likely to be found either high on a wreck where currents are more accessible, or under an overhanging structure that provides protection from sediment deposition (Meyer-Kaiser et al. 2022b).

Here, we provide the first quantitative assessment of the fauna colonizing the DWH wreckage and debris. We then compare these communities to those on 2 nearby shipwrecks, which, while not perfect analogs in terms of age and depth, serve as useful benchmarks for identifying ecological processes driving community dynamics on the DWH site. Finally, we apply a range of ecological metrics and analyses to disentangle patterns in community structure, including abundance, species richness, species composition, and functional diversity, to reveal key differences in community assembly among these sites. Specifically, we examined the associated megafaunal communities on the wrecks of the DWH mobile offshore drilling unit, the SS 'Robert E. Lee' (hereafter the 'Lee'), and the USS 'Peterson' (hereafter the 'Peterson') (Fig. 1, Table 1). Both of the latter wrecks are located in the relative vicinity of the DWH wreckage. According to projections of the DWH oil spill, the 'Lee' is inside of the impact zone, west of the wellhead, while the 'Peterson' is located far enough southeast as to likely be outside of the impact zone (Kujawinski et al. 2011, Montagna et al. 2013, Beyer et al. 2016, Reuscher et al. 2020). As no perfect analog exists to determine whether the hard substrate community on the DWH is typical of the Gulf of Mexico at that depth and time scale, we compared the communities of the DWH to those found on the 'Lee' (similar depth, but on a longer time scale) and the 'Peterson' (located deeper but observed on a similar time scale).

2. MATERIALS AND METHODS

2.1. Wreck selection

The shipwrecks included in this study were selected based on their location relative to the DWH, their similar sizes and orientation (upright and largely intact), primary material type (metallic), and the availability of HD video (provided by the Ocean Exploration Trust and Nautilus Exploration Program). The 'Lee,' a steam-powered passenger ship used to transport freight during World War II, sank on 30 July 1942 (Church et al. 2009). It measures 114 m long and 16 m at its widest and is located west of the DWH wellhead, at a depth of approximately 1500 m, within the well assessed zone of impact from the oil spill (exact locations of the wrecks are not provided here in accordance with Ocean Exploration Trust and federal regulations) (Kujawinski et al. 2011, Montagna et al. 2013, Beyer et al. 2016, Reuscher et al. 2020). In addition to the assessed impact zone (Kujawinski et al. 2011, Montagna et al. 2013, Beyer et al. 2016), it is known that the sediment surrounding the German submarine 'U-166' (not included in this study), which is located 2 km from the wreck of the 'Lee,' was considered heavily impacted by the 2010 oil spill when surveyed in 2014 (Hamdan et al. 2018, Mugge et al. 2019). Thus, we believe the presence of oil at the wreck of the 'Lee' is highly probable. The USS 'Peterson' (DDG-969) was a Spruance-class destroyer that was retired from service in 2002 and subsequently sunk as a target on 16 February 2004 (US Navy 2009). It measures 172 m long and 16.8 m at its widest and is located southeast of the DWH at a depth of approximately 2400 m, farther away from the DWH wellhead than the 'Lee' and potentially outside of the deep-sea area impacted by the spill (Kujawinski et al. 2011, Montagna et al. 2013, Beyer et al. 2016, Reuscher et al. 2020).

2.2. Remotely operated vehicle (ROV) video observations

On 10–14 June 2023, we collected high-definition video of the wreck of the DWH using Oceaneering's ROV 'Global Explorer' operated from RV 'Point Sur.' The ROV was equipped with a 4K UHD video camera and high-intensity LED lights. The debris field formed by the DWH explosion is primarily located near the soft sediment survey site known as 500-N, 500 m due north of the DWH wellhead (Valentine & Benfield 2013). A total of 16 distinct pieces of the wreck (herein 'sites') were selected for study based on size (surface area of at least 0.2 m^2), with an attempt to select similar sized sites at each wreck (Table 2), material (a site needed to be primarily comprised of anthropogenic materials, i.e. metal, concrete, or plastic), and confidence that the piece of the wreck originated from the DWH). Sites were discovered opportunistically near the riser pipe using sonar to detect pieces of the wreck. The surface areas of DWH sites were measured when possible in ImageJ, using ROV lasers set to 30 cm as a reference.

High-definition video surveys of the 'Peterson' and the 'Lee' were provided by the Ocean Exploration Trust and Nautilus Exploration Program, collected using a dual-body ROV system comprised of ROVs 'Hercules' and 'Argo' operated from EV 'Nautilus.' The ships were surveyed on 14 July 2014 as a part of the joint National Geographic and 'Nautilus' expedition NA044. We identified 16 distinct sites on each wreck to study. In both cases, the ROVs collected video of the starboard side of the ships, as well as from above and behind the wrecks. The sites on each shipwreck were selected based on size (sites similar in size to those found in the DWH debris field), material (sites needed to be primarily comprised of anthropogenic materials; metal, concrete, or plastic), and non-

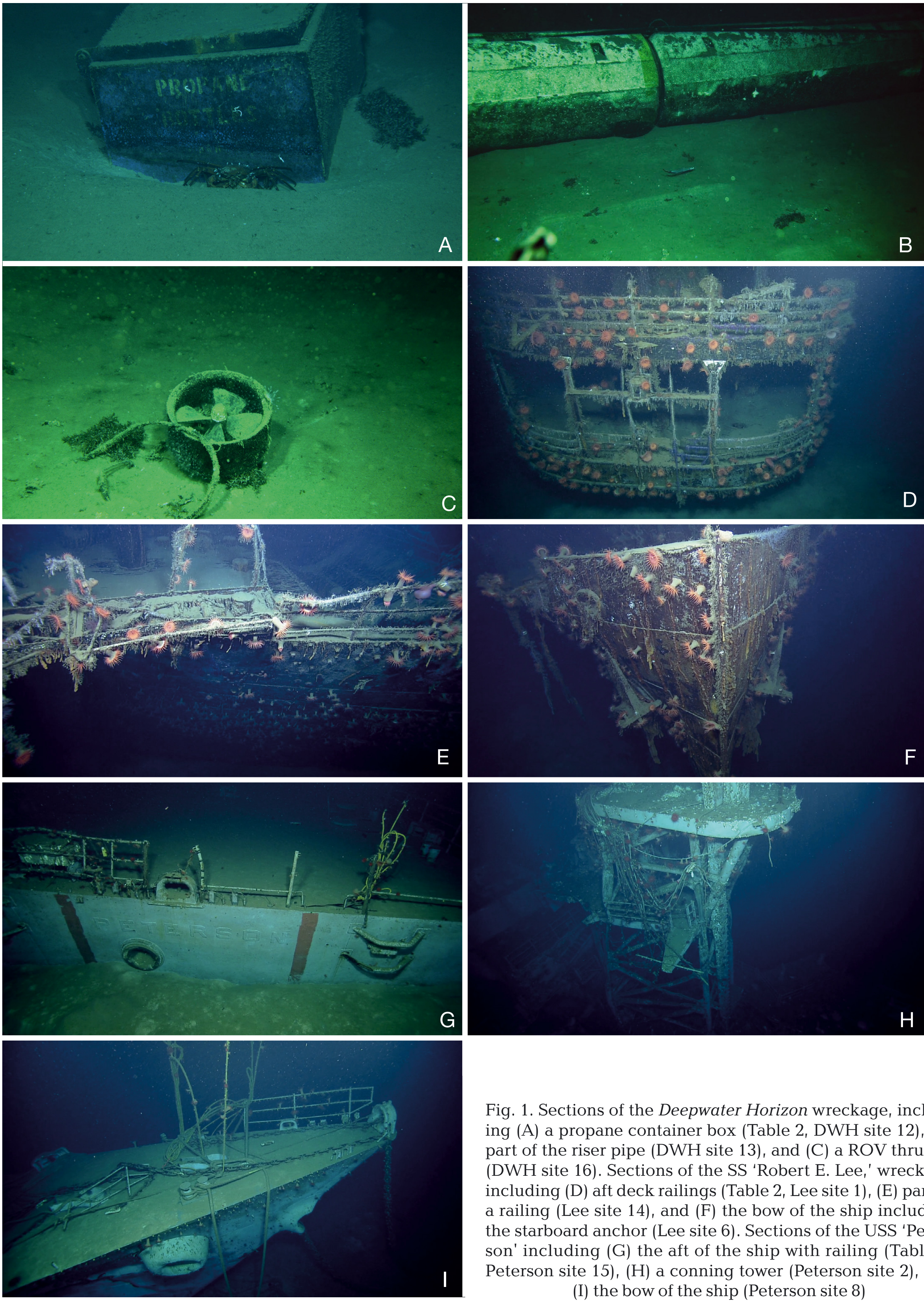

Fig. 1. Sections of the *Deepwater Horizon* wreckage, including (A) a propane container box (Table 2, DWH site 12), (B) part of the riser pipe (DWH site 13), and (C) a ROV thruster (DWH site 16). Sections of the SS 'Robert E. Lee,' wreckage including (D) aft deck railings (Table 2, Lee site 1), (E) part of a railing (Lee site 14), and (F) the bow of the ship including the starboard anchor (Lee site 6). Sections of the USS 'Peterson' including (G) the aft of the ship with railing (Table 2, Peterson site 15), (H) a conning tower (Peterson site 2), and (I) the bow of the ship (Peterson site 8)

Table 1. Wreck information

Wreck	Depth (m)	Year sunk	Year surveyed	Age at survey (yr)	Hydrocarbon contaminants	Total video survey length (min)
Deepwater Horizon	1505	2010	2023	13	Inside predicted area of impact	106
USS 'Peterson'	2400	2004	2014	10	Outside predicted area of impact	81
SS 'Robert E. Lee'	1500	1942	2014	72	Inside predicted area of impact	83

continuity (while the DWH sites are scattered, the 2 shipwrecks are mostly whole, so no selected site was closer than 2 m to any other site on the shipwrecks). The surface area of the sites were approximated in ImageJ using schematics and images of the ships before they were sunk as references.

Megafauna at each site were identified to the lowest possible taxonomic level from the video surveys using taxonomic guides (Moretzsohn & Benfield 2014, Benfield & Kupchik 2020), and consulting with taxonomic experts. Mobile organisms were counted if they were observed in close proximity (within approximately 1 m) to a site and showed strong associating behavior to that site based on the typical habitat of the observed taxon, even if they were not in direct contact. Organisms that could not be identified to a satisfactory level were assigned a distinct morphospecies ID.

2.3. Analysis

For each site, abundance and richness were defined as the number of individuals and species present, respectively. Species abundance was then transformed using $\log_{10}$. Density was calculated by dividing abundance by the approximate surface area of a site. Megafaunal diversity was calculated using the Shannon diversity index ($H = -\Sigma p_i \times \ln(p_i)$, where p_i is the proportion of the community made up of species i). Megafaunal evenness was calculated using Pielou's evenness index ($J' = H'/H'_{max}$), where $H'_{max} = \ln(S)$, S is the total number of species, and H'_{max} is the maximum possible value of H' if every species was proportional). All analyses were performed using R version 4.4.1 (R Core Team 2024). The alpha diversity metrics were calculated using the 'vegan' package (Oksanen et al. 2025). ANOVAs comparing each of the aforementioned metrics between wrecks were run with the 'aov' function in the 'stats' package in R with $\alpha = 0.05$ (R Core Team 2024).

The wreck communities were visualized in multivariate space using a principal coordinates analysis. We used a fuzzy clustering approach to explore compositional differences among the sites and between the wrecks. Rather than classifying a given object to a single cluster, fuzzy clustering associates object membership values into multiple clusters. An object that is clearly linked to a given cluster has a strong membership value for that cluster and weak (or null) values for the other clusters. The membership values add up to 1 for each site. We set the membership exponent to $r = 1.5$, as $r = 1$ gives crisper clustering but often fails to converge on clusters, and values of 2 and greater can lead to complete fuzziness. Fuzzy clustering was conducted in the 'cluster' package in R (Maechler et al. 2013). We viewed silhouette plots to select the number of clusters that led to the fewest misclassifications; in this case, $k = 6$ clusters were used. These figures plot silhouette widths, a measure of the degree of membership of an object to its cluster, based on the average distance between the object and all objects of the cluster to which it belongs, compared with the same measure computed for the next closest cluster. Silhouette widths range from −1 to 1. The greater the silhouette width is, the better the object is accurately clustered, with negative values suggesting misclassification or wrongly assigning a site to a group. Indicator species (those that contributed significantly to the distribution and clustering of sites within the multivariate space) were determined with the 'multipatt' function in the 'indicspecies' package in R ($\alpha = 0.05$) (De Cáceres & Legendre 2009).

Finally, we used the ecological mode framework outlined by Nunnally et al. (2020), modified from the principles of functional morphology developed by Bambach et al. (2007) and Bush et al. (2007). We define the ecological mode of a species by 3 axes: tiering (bathydemersal/benthopelagic, demersal, and benthic), motility (swimming, crawling, and sedentary), and feeding (benthic forager, surface deposit feeder, predatory, scavenger, filter feeder, and benthopelagic forager) (Table 3). Ecological modes were assigned to each species or morphospecies. Multivariate analysis of variance (MANOVA) tests were performed with the 'manova' function in the 'stats' package in R to determine whether there were significant differences between the wreck communities based on the 3 functional trait axes (R Core Team 2024).

Table 2. Description of sites (i.e. distinct pieces of the wrecks) at each wreck location. Four *Deepwater Horizon* sites could not be measured with remotely operated vehicle (ROV) lasers and thus have no surface area measurements (NA: data not available). All sites had defined limits and were found at least 2 m away from any other site. Sites with similar construction (railings, pipes, etc.) were selected from non-continuous sections of the wrecks

Site	Description	Approximate surface area (m^2)
Deepwater Horizon		
1	Deck container	13.4
2	Metallic debris	NA
3	Railing	NA
4	Pipe	NA
5	Cylindrical tank	1.12
6	Metallic debris	0.228
7	Cage	3.59
8	Pipe	4.05
9	Plastic debris	NA
10	Metallic debris	2.235
11	Frame	4.008
12	Propane container box	0.81
13	Riser pipe	23.56
14	Superstructure section	11.538
15	Plastic debris	0.35
16	ROV thruster	2.235
USS 'Peterson'		
1	Starboard side	10.512
2	Conning tower	29.351
3	Satellite platform	4.765
4	Raised hatch	2.654
5	Railing	2.498
6	Railing with netting	2.29
7	Mk-29 missile launcher	4.68
8	Bow section	16.652
9	Door area	3.747
10	Railing	1.977
11	Hawsehole	2.466
12	Hatch	5.163
13	Starboard side	0.864
14	Railing with netting	0.204
15	Railing	0.468
16	Cleat	0.364
SS 'Robert E. Lee'		
1	Aft deck railings	46.781
2	Mast	8.08
3	Anchor mechanism	10.84
4	Smoke stack	2.04
5	Turret	4.414
6	Starboard anchor	2.83
7	Davit	4.127
8	Hatch	2.799
9	Vent	0.641
10	Porthole	0.221
11	Cleat	1.16
12	Bow section	0.348
13	Intact top of bridge	1.104
14	Railing with ropes	7.542
15	Railing gate	2.609
16	Railing	1.221

3. RESULTS

Individual univariate metrics did not vary significantly between the 3 wreck sites (Fig. 2). Similar values for abundance ($F_{2,46}$ = 1.409, p = 0.255), density ($F_{2,45}$ = 0.026, p = 0.974), richness ($F_{2,45}$ = 0.279, p = 0.758), evenness ($F_{2,45}$ = 0.580, p = 0.564), and Shannon's diversity ($F_{2,45}$ = 0.866, p = 0.428) were found for each wreck. However, the species responsible for those metrics varied between wrecks. All 3 wrecks were dominated by different species of cnidarians. The most abundant species for the DWH wreck was a small, unidentified hydrozoan (approximately 1 cm in length), found in highest abundance on a section of the riser (0–1000 ind. site^{-1} or 0–438.6 ind. m^{-2}) (Table 4). The most abundant species on the 'Lee' was a soft coral (Alcyonacea sp. 2), found in highest abundance on the aft railings of the ship (0–1000 ind. site^{-1} (polyps 2–5 cm in length) or 0–132.6 ind. m^{-2}) (Table 4). The 'Peterson' did not have any species with outlying abundances as high as the other 2 wrecks, but the most abundant were 2 species of anemone, both in highest abundances on the conning tower (*Actinoscyphia aurelia:* 0–37 ind. site^{-1} or 0–34.3 ind. m^{-2}, 8–15 cm across; and Actinostolidae*:* 2–74 ind. site^{-1} or 0.5–29.6 ind. m^{-2}, 3–7 cm across) (Table 4).

We utilized a multivariate approach incorporating both the species present and the abundances of those species to address the community composition on each wreck as a whole. The sites from the different wrecks clustered into 6 groups, with 2 clusters of sites for each wreck (Fig. 3). Of the 16 DWH sites, 10 displayed almost complete similarity to each other, as evidenced by the pie charts showing almost completely solid light grey in Fig. 3. These sites had very little similarity to any other cluster, even the cluster containing only the 6 remaining DWH sites (dark grey). Other sites, such as those observed on the 'Lee' (Fig. 3), showed some similarities to other clusters, including those representing the other 2 wrecks. Broadly, the wrecks are separated along the 2 principal coordinate axes, with the DWH sites showing primarily negative scores along dimension 1, separating them from the 'Lee' and 'Peterson' sites, the majority of which have positive dimension 1 scores (1 out of 16 'Peterson' sites and 5 out of 16 'Lee' sites fall at or below 0 along the dimension 1 axis). The 2 shipwrecks then separate across the dimension 2 axis, with largely positive values for the 'Lee' and negative for the 'Peterson.'

Based on *k*-means clustering and the indicator species analysis (α = 0.05), 6 significant species were responsible for these multivariate patterns. Those

Table 3. Functional traits that describe the ecological mode of the megafauna based on 3 axes: tiering (physical space occupied within ecosystem), motility level (means of movement), and feeding mechanism (strategy utilized to secure food resources). Adapted from Nunnally et al. (2020)

Functional trait	Definition
Tiering	
(1) Bathydemersal/benthopelagic	Living in the water column, free of the bottom
(2) Demersal	Benthic, extending into the water mass
(3) Benthic	Benthic, not extending significantly upwards
Motility	
(1) Swimming	Regularly moving, unencumbered (walking, swimming)
(2) Crawling	Regularly moving, intimate contact maintained with substrate
(3) Sedentary/sessile	Moving only when necessary, free-lying or non-motile
Feeding mechanism	
(1) Benthic forager	Strictly foraging for food on the seafloor
(2) Surface deposit feeder	Capturing loose particles from a substrate
(3) Predatory	Capturing prey capable of resistance
(4) Scavenger	Subsisting on dead animals or plant material
(5) Filter feeder	Capturing food particles from the water
(6) Benthopelagic forager	Foraging both in water column and along seafloor

species were an unidentified hydrozoan (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m760p001_supp.pdf), Alcyonacea sp. 1 (Fig. S2), Alcyonacea sp. 2 (Fig. S2), Serpulidae sp. 1 (Fig. S3), the halosaur *Aldrovandia* sp. (Fig. S4), and *Actinoscyphia aurelia* (Fig. S5). Additionally, 3 of those species were the most abundant species found on each wreck (unknown hydrozoan on the DWH, Alcyonacea sp. 2 on the 'Lee,' and *Actinoscyphia aurelia* on the 'Peterson'). The DWH was the only wreck to host the highly abundant, unidentified hydrozoan ($p = 0.001$) and the eel-like halosaur *Aldrovandia* sp. ($p = 0.025$), although one additional halosaur that could not be identified to the genus level was present at the 'Peterson.' The DWH community also contained Serpulidae sp. 1 ($p = 0.004$) and *Actinoscyphia aurelia* ($p = 0.001$). Individuals of the 4 species other than the hydroid and eel were observed on the 'Lee' wreck. Furthermore, 3 of those species (Alcyonacea sp. 1, Alcyonacea sp. 2, and *Actinoscyphia aurelia*) were observed in the highest abundance on the wreck of the 'Lee.' The 'Peterson' community contained only one of the indicator species, *Actinoscyphia aurelia*, which was one of the most abundant species on that wreck.

In relation to functional diversity, the 3 wrecks displayed significant overlap in general. In terms of tiering, the vast majority of megafaunal abundance was concentrated in the benthic category across all of the wrecks, with no significant difference between the wrecks for any of the tier levels (bathydemersal/benthopelagic: $F_{2,45} = 0.878$, $p = 0.423$; demersal: $F_{2,45} = 1.300$, $p = 0.283$; benthic: $F_{2,45} = 1.348$, $p = 0.270$) (Fig. 4). With regards to motility, most megafauna fell into the sedentary/sessile category ($F_{2,45} = 1.319$, $p = 0.278$). The DWH and 'Lee' both had significantly more crawling organisms ($F_{2,45} = 4.761$, $p = 0.0133$) in comparison to the 'Peterson,' which in turn had more swimming organisms, though not significantly more ($F_{2,45} = 1.456$, $p = 0.244$). We acknowledge that the use of ROVs could have caused highly mobile fauna to flee as the surveys were performed, and while we did not find a significant difference in the abundance of swimming organisms between the 3 wrecks, the video collection could have resulted in bias against fast-moving mobile fauna. The DWH and 'Lee' communities contained several species of crabs (classified as crawling organisms) which were absent from the 'Peterson' community. Conversely, the 'Peterson' community contained *Enypniastes eximia* (swimming sea cucumber), a species of Halosauridae, and *Aldrovandia* sp. (deep-sea fish), which were all classified as swimming organisms and were all absent from the DWH and 'Lee' communities. The largest variance in ecological modes can be attributed to feeding mechanisms. All 3 wrecks were dominated by filter feeders ($F_{2,45} = 1.319$, $p = 0.278$), with some scavengers present in each of the communities ($F_{2,45} = 0.262$, $p = 0.771$). The DWH and 'Lee' had significantly more benthic foragers than the 'Peterson' ($F_{2,45} = 5.891$, $p = 0.005$), which can again be attributed to the presence of crabs. In turn, the 'Peterson' had more deposit feeders ($F_{2,45} = 1.714$, 0.192) in the form of sea cucumbers (Holothuroidea), which were absent from the other 2 wrecks. The DWH and 'Lee' communities both contained a single Macrouridae grenadier which was the only benthopelagic foraging species present in this study ($F_{2,45} = 0.500$, $p = 0.610$). Lastly, the DWH

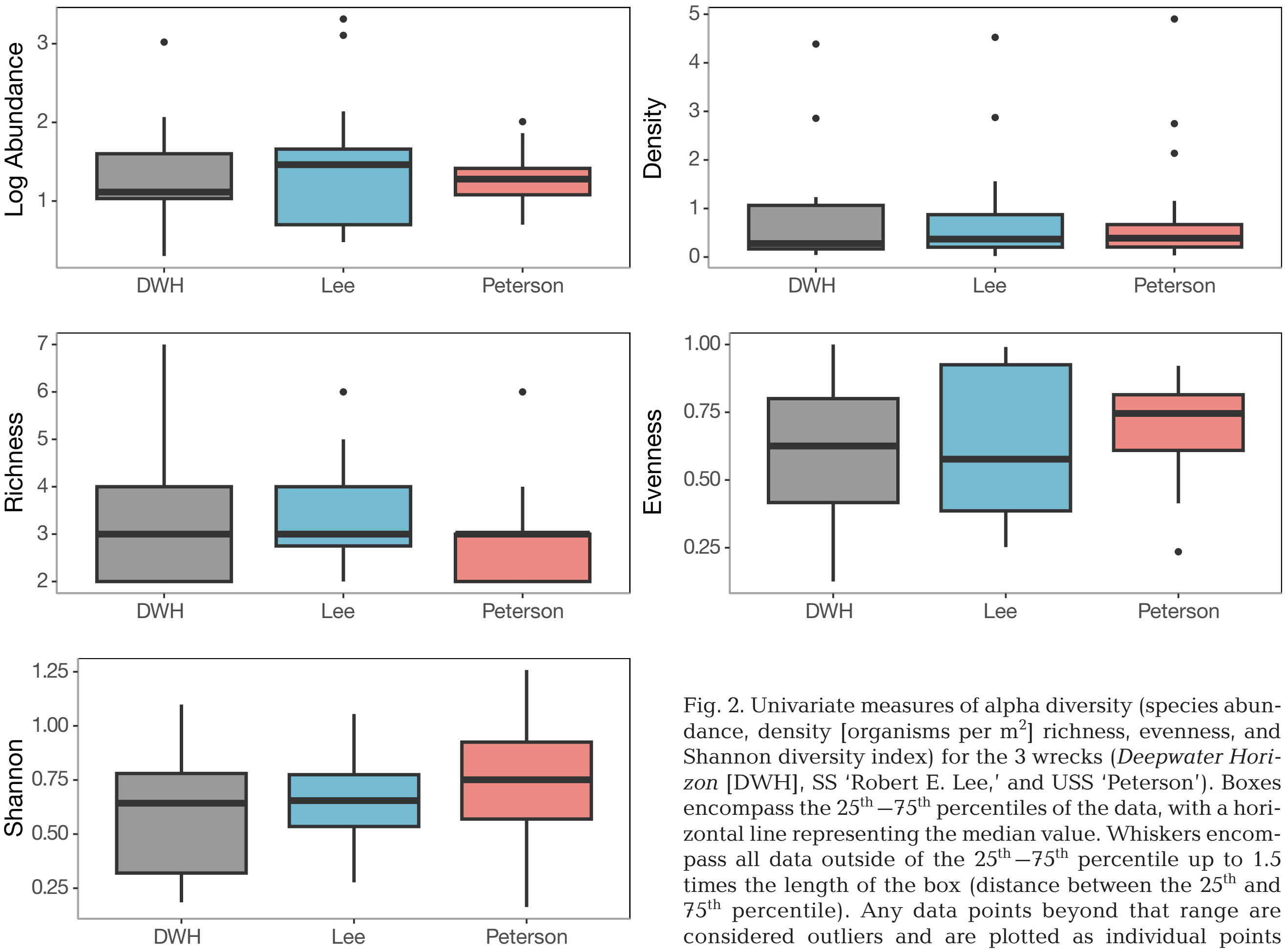

Fig. 2. Univariate measures of alpha diversity (species abundance, density [organisms per m^2] richness, evenness, and Shannon diversity index) for the 3 wrecks (*Deepwater Horizon* [DWH], SS 'Robert E. Lee,' and USS 'Peterson'). Boxes encompass the 25th–75th percentiles of the data, with a horizontal line representing the median value. Whiskers encompass all data outside of the 25th–75th percentile up to 1.5 times the length of the box (distance between the 25th and 75th percentile). Any data points beyond that range are considered outliers and are plotted as individual points

and 'Peterson' communities contained predatory fish in the family Halosauridae (n = 2 *Aldrovandia* sp. at the DWH, n = 1 unidentified Halosauridae at the 'Peterson') ($F_{2,45}$ = 2.053, p = 0.140).

4. DISCUSSION

While the areas surrounding the DWH oil spill site are known to be biologically degraded with little observed recovery (McClain et al. 2019), the wreck itself remained unstudied for 13 yr while a community developed on the hard substrate. Surveys of the soft sediment within the debris field have thus far ignored the hard substrate (Valentine & Benfield 2013, McClain et al. 2019, Nunnally et al. 2020). As there is no control system for comparison against the DWH wreck community, we also described the communities found on 2 shipwrecks in the Gulf of Mexico at either a comparable depth ('Lee') or comparable time scale ('Peterson'). Univariate measures of species abundance, density, richness, evenness, and diversity were not significantly different between the 3 wrecks. Additionally, there were similarities in the distribution of functional groups within each wreck community. However, the species present and filling those functional roles varied significantly at each wreck. This suggests that despite the similarity in univariate measures and major functional groups, each wreck hosts a largely unique community.

Differences in the wreck assemblages may be due to size differences as seen in Meyer-Kaiser et al. (2022a). The 'Lee' and 'Peterson' are similarly sized vessels, and the DWH sites were selected to represent similar surface areas, despite the larger size and fragmented nature of the wrecked structure. While the size of the different sites at the 3 wrecks varied from <1 to almost 50 m^2, there was no indication that site size impacted community assemblage in unexpected ways. Larger sites did host more organisms, but a supplemental NMDS plot showed that the sites clustered by wreck rather than size (Fig. S6). We acknowledge

Table 4. Total abundance, total relative abundance, and total density given in ranges from minimum to maximum for each species across all of the sites for each of the wrecks of the *Deepwater Horizon* (DWH), the USS 'Peterson,' and the SS 'Robert E. Lee.' Abundance was calculated as the number of individuals of a given species at each wreck. Relative abundance was calculated as the number of individuals of a given species at a site, divided by the total number of individuals at that wreck. Density was calculated by dividing the abundance for a given species at a site by the approximate surface area at that wreck. Five DWH sites are excluded from the density calculations as they could not be measured

Species	*Deepwater Horizon*			USS 'Peterson'			SS 'Robert E. Lee'		
	Abundance (ind.)	Relative abundance	Density (ind. m^{-2})	Abundance (ind.)	Relative abundance	Density (ind. m^{-2})	Abundance (ind.)	Relative abundance	Density (ind. m^{-2})
Actinoscyphia aurelia	0–5	0–0.091	0–0.250	0–37	0–0.762	0–34.314	1–158	0.026–0.938	1.724–21.569
Actinostolidae	0–20	0–0.650	0–16.049	2–74	0.2–0.962	0.476–29.624	0–12	0–0.200	0–2.908
Actiniaria 3	0–1	0–0.091	0–2.857	0	0	0	0	0	0
Actiniaria 4	0	0	0	0–4	0–0.167	0–3.472	0	0	0
Alcyonacea 1	0–10	0–0.769	0–28.571	0	0	0	0–1000	0–0.725	0–132.591
Hydrozoa	0–1000	0–0.962	0–438.596	0	0	0	0	0	0
Alcyonacea 2	0	0	0	0	0	0	0–1000	0–0.783	0–132.591
Serpulidae	0–22	0–0.759	0–14.286	0	0	0	0–2	0–0.500	0–9.050
Acanthephyra sp.	0–1	0–0.333	0–0.247	0–2	0–0.200	0–0.377	0–1	0–0.023	0–0.227
Chaceon quinquedens	0–2	0–0.100	0–2.469	0	0	0	0–2	0–0.074	0–0.707
Galathedidae	0–4	0–0.286	0–1.235	0	0	0	0–17	0–0.444	0–11.494
Zoroaster sp.	0	0	0	0–1	0–0.032	0–1.157	0	0	0
Enypniastes eximia	0	0	0	0–2	0–0.027	0–0.068	0	0	0
Benthothuria funebris	0	0	0	0–1	0–0.014	0–0.034	0	0	0
Benthodytes sp.	0	0	0	0–1	0–0.059	0–0.210	0	0	0
Halosaurus sp.	0	0	0	0–1	0–0.100	0–4.902	0	0	0
Aldrovandia sp.	0–2	0–0.333	0–0.247	0	0	0	0	0	0
Hexactinellida	0–9	0–0.900	0–1.996	0–15	0–0.387	0–13.889	0	0	0
Gastropoda	0–5	0–0.172	0–0.373	0	0	0	0	0	0
Macrouridae	0–1	0–0.034	0–0.075	0	0	0	0–1	0–0.033	0–0.092
Nematocarcinus sp.	0–1	0–0.250	0–4.386	0	0	0	0	0	0
Neolithodes agassizii	0	0	0	0	0	0	0–1	0–0.0004	0–0.133

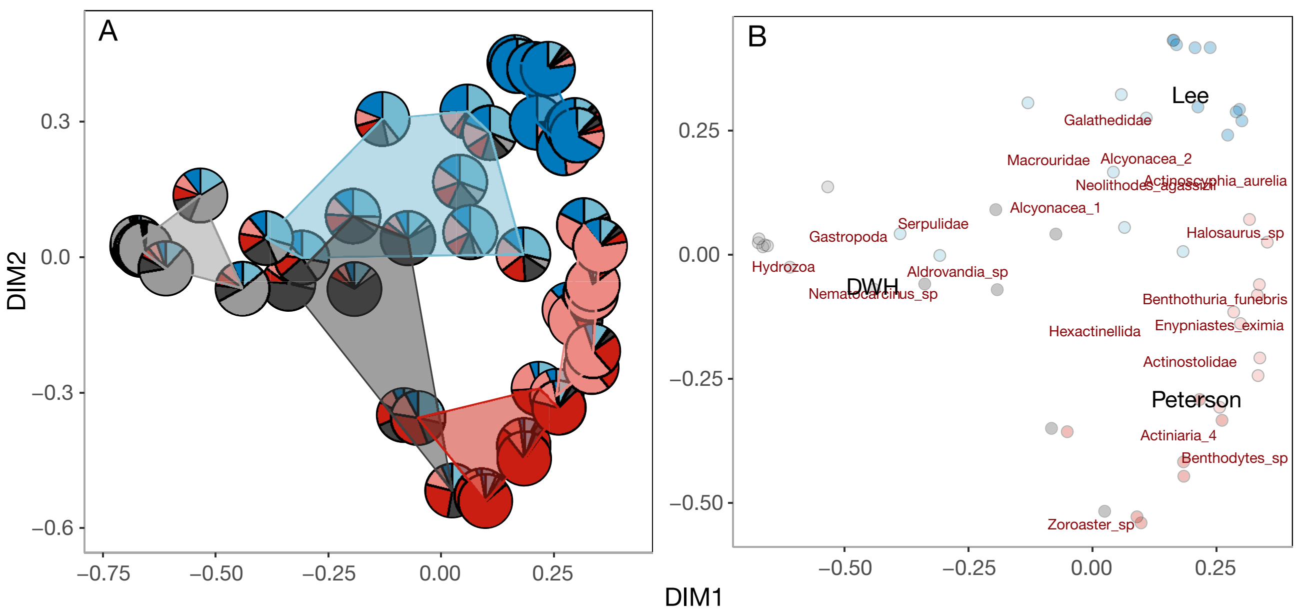

Fig. 3. Principal coordinates analysis of the wrecks. (A) Fuzzy clustering of wrecks. Each site on the 3 wrecks is associated with a pie chart with wedges proportional to its membership coefficient in that cluster. Convex hull polygons link the 6 clusters together. Shades of gray indicate the *Deepwater Horizon*, shades of blue indicate the SS 'Robert E. Lee,' and shades of red indicate the USS 'Peterson.' (B) Species loadings for all species with centroids for each wreck. Dimension 1 explains 32.8% and dimension 2 explains 22.1% of the total variance in community composition

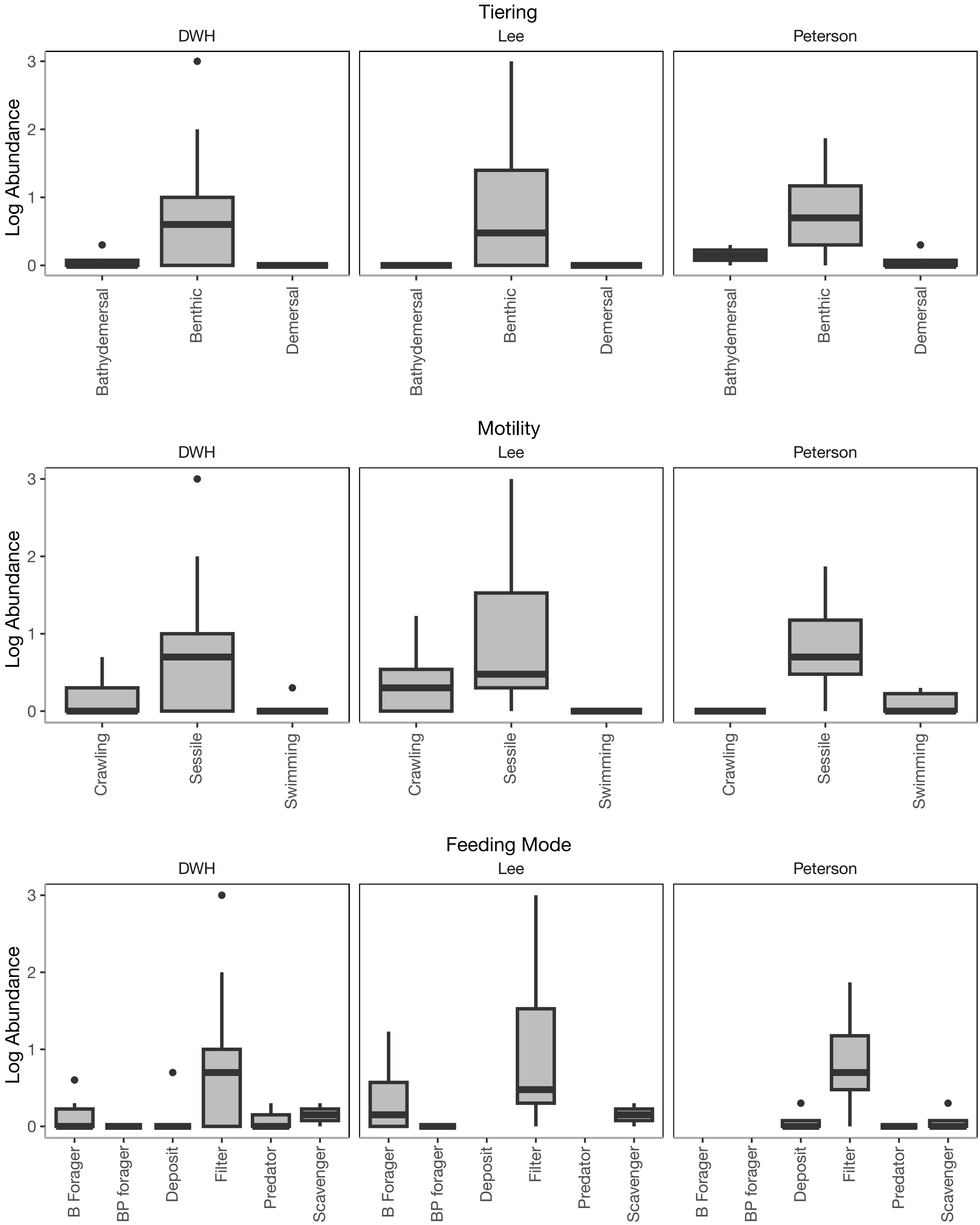

Fig. 4. Log abundance (number of individuals) for the 3 functional trait categories, i.e. tier, motility, and feeding mechanism (see Table 3) for the *Deepwater Horizon* (DWH), SS 'Robert E. Lee,' and USS 'Peterson.' B Forager: benthic forager; BP forager: benthopelagic forager. Box plot parameters as in Fig. 2

that shape could potentially play a role; however, given the complexity of the wreck profiles, quantifying this factor is challenging. Previous research has indicated that shipwrecks with complex, high-relief structures and overhanging features tend to support more abundant communities than those with simpler, low-relief habitats near the seafloor (Meyer-Kaiser et al. 2022b). While the 'Lee' and the 'Peterson' exhibit similar relief and overhang characteristics, the DWH wreckage examined in this study consists of lower-relief structures with variable overhang. Given findings from previous research (Meyer-Kaiser et al. 2022b), we might then anticipate lower abundance and diversity on the DWH. However, no significant difference in either metric was found among the shipwrecks (Fig. 2). Whether the lack of expected differences may result from intentional site selection that buffered the effects of complexity, relief, and overhang remains unclear.

Four additional factors may contribute to the differences observed between the 3 wrecks: stochastic settlement, time, depth, and presence of hydrocarbon contaminants. Larval recruitment, characterized by random and unpredictable settlement, could lead to significant differences in community composition and diversity among the 3 shipwrecks. The arrival of larvae is influenced by various factors such as ocean currents, larval availability, and environmental conditions like water temperature and food supply (Young et al. 2012, Hilário et al. 2015). These factors can vary spatially and temporally, resulting in different species colonizing each shipwreck. Additionally, the timing of larval settlement and competition for space can further amplify disparities in species composition and abundance between the wrecks. Over time, this variability can lead to unique ecological assemblages on each shipwreck, even in the absence of other driving factors.

The 'Lee' is by far the oldest wreck, having been on the seafloor for 72 yr before it was observed, and thus may have a more developed successional community as deep-sea organisms tend to establish, develop, and turnover slowly, on the scale of years to decades (Levin & Smith 1984, Smith & Hessler 1987, McClain et al. 2012, McClain & Schlacher 2015). While abundance was not significantly different between the wrecks, the community on the 'Lee' was dominated by large anemones (particularly *Actinoscyphia aurelia* or flytrap anemones) and small corals, compared to the smaller anemones on the 'Peterson' and the hydrozoans on the DWH. Those same large anemones were also present on the 'Peterson' and the DWH, just in much lower abundances (Table 4). While the exact lifespan of this species is not known, other deep-sea anemones of comparable sizes are predicted to take between 4 and 11 yr to reach maturity, indicating that temporal dynamics may be responsible for the disparity in the number and size of anemones on the 'Peterson' and DWH (Mercier & Hamel 2009, Mercier et al. 2017).

The 'Peterson' is located approximately 900 m deeper than the other 2 wrecks. Depth plays a direct role in the formation and diversity of deep-sea communities due to the physiological demands of living in high pressure environments, as well as an indirect role through its relation to temperature and productivity that influence the turnover of species (though metabolic rates are largely temperature mediated, rather than directly related to depth) (McClain et al. 2012, McClain & Schlacher 2015, McClain & Rex 2015). We would therefore expect to see similarities between the DWH and 'Lee' communities, with the 'Peterson' hosting its own distinctive community. We did see some overlap in the species present between the shallower 2 wrecks, with some of those overlapping species missing entirely from the 'Peterson' community (e.g. *Chaceon quinquedens*, Alcyonacea sp. 1, and Serpulidae), though not all of those species have been observed at the depth of the 'Peterson,' which could explain some of the differences seen in the community of the 'Peterson' compared to the other 2 wrecks. Furthermore, we observed unique species on all 3 wrecks (for example, the unidentified hydrozoan on the DWH, Alcyonacea sp. 2 on the 'Lee,' and several species of Holothuroidea on the 'Peterson,' Fig. 3). These results suggest that while depth may play an important role in the communities that have formed on these wrecks, it cannot yet be disentangled from the other factors driving community development and composition.

The presence of hydrocarbon contaminants (estimated based on predicted area of impact; Montagna et al. 2013, Berenshtein et al. 2020, Diercks et al. 2021) at each wreck may have also played a significant role in the species present in each community. One of the differences in functional trait diversity between the wrecks is the number of benthic, crawling, surface deposit feeders versus the number of benthic, crawling, benthic foragers among the 3 wrecks. The former represents holothurians (sea cucumbers), and the latter represents malacostracan crustaceans (crabs). Holothurians were exclusively found at the 'Peterson' wreck, while malacostracan crustaceans were found at both the DWH and the 'Lee' but not the 'Peterson.' A second indicator analysis at the class level (indicator classes rather than indicator species) determined that malacostracans were significant drivers of the observed distribution of sites within the multivariate space (p = 0.001), while holothurians were not (p = 0.64), potentially due to their low abundance. However, the unique functional role (benthic, crawling, surface deposit feeder) of holothurians and presence at only 1 wreck merits further consideration and investigation.

We propose 2 complementary theories. First, that as seen in laboratory studies (Li et al. 2020, 2021), exposure to hydrocarbon contaminants may have been fatal to any holothurian species that may or may not have been present at the wrecks prior to the DWH oil spill. Holothurians are found at the depths of each wreck, and do not require significant time to mature, thus the previous 2 factors are likely not responsible for the incongruity in holothurian presence (Pequegnat et al. 1990). Instead, as the DWH and 'Lee' wrecks are both within the predicted area of impact of the DWH oil spill, and the 'Peterson' is outside of that area, we posit that hydrocarbon contamination may be a major contributing factor that explains the presence or absence of holothurians. Benthic holothurians are primarily soft substrate organisms; however, several were observed on the wreck of the 'Peterson' as well as on the surrounding substrate, and 1 species of swimming holothurian (*Enypniastes eximia*) was seen in the water column around the 'Peterson.' While 3 dead benthic holothurians and several living pelagic holothurians (*E. eximia*) were observed near the DWH wreck shortly after the oil spill, no living benthic individuals have been observed in the repeated transects over the past 14 yr at the 500-N site near the DWH wreck (Valentine & Benfield 2013, McClain et al. 2019). Furthermore, no holothurians were observed on the wrecks of the DWH or the 'Lee.'

In conjunction with this theory, we also propose that the degradation of hydrocarbons originating from the oil spill may serve as a chemical attractor for malacostracan crabs, as various crustaceans have shown affinities for hydrocarbons (Kittredge 1973, Caskey et al. 2009). Additionally, the same species of crabs (*Chaceon quinquedens* and *Neolithodes agassizii*) have been observed in high abundances at the DWH soft substrate transect sites (Valentine & Benfield 2013, McClain et al. 2019, Nunnally et al. 2020). The lack of *C. quinquedens* at the 'Peterson' may also be due to the wreck being near the maximum depth range for the species ('Peterson': 2400 m, *C. quinquedens*: 2000 m) (Kilgour & Shirley 2008). However, previous work has noted the increased presence of the species at the site compared to similar depths elsewhere in the Gulf of Mexico (McClain et al. 2019, Nunnally et al. 2020).

While many additional shipwrecks occur in the Gulf of Mexico, these may not provide adequate comparisons to the DWH wreckage. For example, some studies have examined wrecks potentially affected by the DWH oil spill (Brooks et al. 2012, Larcom et al. 2014) but are not directly comparable to the 3 wrecks in this study due to differences in depth, age, size, and primary material composition. For instance, the *Lophelia* II deep-water coral research expeditions investigated several wrecks, but only one — the 7000 Foot Wreck — was at a depth similar to the DWH, 'Peterson,' and 'Lee.' However, the 7000 Foot Wreck predates the 'Lee' by at least 20 yr, is only about 25% the length of the intact shipwrecks in this study, and is a wooden wreck, introducing a potential food source for xylophagous organisms alongside its role as a hard substrate. Other studies have focused on sediments surrounding wrecks in the region, but to date, no information is available on the megafaunal communities inhabiting those sites (Hamdan et al. 2018, Mugge et al. 2019, Hamdan et al. 2021).

5. CONCLUSIONS

Overall, our findings suggest that there may not be a 'typical' wreck community in the deep sea of the Gulf of Mexico. Univariate alpha diversity metrics were invariant across the wrecks, but the organisms that made up those communities varied between the wrecks. Furthermore, many of the same functional roles were filled between the wrecks, with the majority of variation found in feeding guilds. An observation that may be of particular interest for future work and management is the low abundance of coral on the wreck of the DWH compared to the other 2 wrecks, as many of the studies of the surrounding area have focused on coral recovery (White et al. 2012, Fisher et al. 2014, Girard & Fisher 2018, Montagna & Girard 2020). Given the increasing presence of artificial substrates in the deep sea due to industrial activities, our findings suggest that these structures may not provide the rich, diverse habitats often assumed (Zintzen & Massin 2010, Macreadie et al. 2011, Monroy-Velázquez et al. 2020). This has implications for deep-sea restoration and conservation efforts, particularly in projects aimed at enhancing biodiversity through artificial habitats.

Continued monitoring of the wrecks in this study, especially the wreck of the DWH, over time is critical to inform understanding of the long-term successional processes operative on the development of megafaunal communities in an area where massive anthropogenic hard substrates have been introduced concurrent with heavy hydrocarbon contaminant loads. Additionally, further monitoring efforts on other anthropogenic hard substrates deposited in the deep sea, especially in the Gulf of Mexico, would inform expectations related to communities that should form on anthropogenic hard substrates, and the processes driving development of those communities. The megafaunal communities that form on these structures appear largely unique, and additional data concentrated in the Gulf of Mexico would assist in disentangling the effects of time, depth, and the presence of hydrocarbon contaminants on the development of deep-sea hard substrate communities.

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