



Structural drivers of biodiversity on shipwrecks and natural hard-bottom reefs in the mesophotic zone

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ABSTRACT: Hard-bottom habitats at mesophotic depths have the potential to serve as refuges from climate change, but they are understudied. Anthropogenic structures, including shipwrecks, provide critical habitats for hard-bottom-obligate invertebrates and structure-oriented fishes. A key question in marine ecology and the emerging interdisciplinary field of Maritime Heritage Ecology is how the structure of a shipwreck influences the biological community inhabiting it. To answer this question, we analyzed video recordings from 4 shipwrecks and 3 naturally occurring hard-bottom reefs in the mesophotic zone in the northern Gulf of Mexico/Gulf of America. We tested the influences of habitat size, distance between sites, and type (shipwreck or natural reef) on species richness, community composition, and functional composition of invertebrates and fishes. For both shipwrecks and natural hard-bottom reefs, our results showed a significant influence of habitat size on species richness for invertebrates but not for fishes. All factors had significant relationships with community composition and functional composition. Larger shipwrecks provided vertical relief and overhangs, which were rare on natural reefs and supported pelagic predators and sessile invertebrates, respectively. Shipwrecks hosted the non-native sun coral *Tubastraea coccinea* and regal demoiselle *Neopomacentrus cyanomos*, likely because of the microhabitats they provided. Our study demonstrates the important role that shipwrecks play in supporting biodiversity in the mesophotic zone but also highlights the possibility that they could facilitate the spread of non-native species.

KEY WORDS: Mesophotic ecosystems · Maritime Heritage Ecology · Gulf of Mexico/Gulf of America · Underwater cultural heritage

1. INTRODUCTION

Underwater cultural heritage (UCH) includes the remnants of human activities at sea — shipwrecks, plane wrecks, middens, seawalls, industrial infrastructure, and much more. Modern litter is generally not considered UCH, although perceptions are subject to change as time goes on. These anthropogenic structures become colonized by organisms and constitute integral components of the marine ecosystem (Meyer-Kaiser & Mires 2022). They also change over time, as factors including wave action, chemical reac-

tions, and fishing activities alter the physical structure of the habitat (Muckelroy 1998). Climate change impacts such as rising temperatures, declining pH, and more frequent and intense storms have the potential to accelerate the degradation of important historical structures (Wright 2016). Structural changes, in turn, influence the biological communities inhabiting UCH (Mires & Meyer-Kaiser 2023). A central question in the interdisciplinary field of Maritime Heritage Ecology is understanding how the structural elements of UCH influence biological communities (Meyer-Kaiser & Mires 2022).

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As shallow-water habitats are impacted by climate-related stressors, habitats at greater depths could serve as refuges for shallow-water taxa. In particular, mesophotic coral ecosystems are considered refuges for hermatypic corals and many associated taxa because they are buffered from high temperatures, acidification, and storms that affect shallow coral reefs (Slattery et al. 2011). Some studies suggest that mesophotic habitats could re-seed shallow reefs after disturbance (Goodbody-Gringley et al. 2021, Sturm et al. 2022). Mesophotic reefs are important sources of coral reef fish larvae, and under specific oceanographic conditions, these larvae can disperse to and repopulate shallow reefs (Goldstein et al. 2016, Vaz et al. 2016). While there have been calls for the protection of mesophotic ecosystems, they remain understudied (Soares et al. 2020a).

In the Gulf of Mexico/Gulf of America (GoM/GoA), hard-bottom habitats at mesophotic depths (30–150 m) are less continuous than their shallow counterparts, thus increasing the importance of anthropogenic structures for connectivity. Shipwrecks tend to be isolated and island-like, surrounded by plains of sand or mud. Therefore, both naturally occurring and anthropogenic mesophotic habitats may follow patterns commonly observed in island-like communities (Meyer 2017). The size of a habitat is an important factor influencing species richness, community composition, and functional composition. In general, larger habitats provide greater heterogeneity and niche space and can support a broader range of species than smaller habitats (Matthews et al. 2015).

The distance between island-like habitats influences community composition (MacArthur & Wilson 1967). A combination of oceanographic currents, species' pelagic larval durations (PLDs), and swimming behaviors influence larval dispersal (Young 1995). Temporal variations in flow, including tidal currents, internal waves, and interannual cycles such as El Niño, impact the distance traveled by larvae (Pineda et al. 2007). Furthermore, differences in the size or behavior of larvae lead to variations in dispersal within a population or cohort (Nanninga & Berumen 2014). If a species has restricted dispersal, it may be unable to reach an isolated, island-like habitat (Meyer 2017). Many marine species have dispersal ranges of <1 km (Shanks 2009). For species with long PLDs (i.e. weeks to months), swimming behaviors and small-scale oceanographic factors such as eddies can lead to localized retention of larvae (Pineda et al. 2007). This, in turn, can alter connectivity patterns and lead to strong similarities between adjacent communities.

Furthermore, the type of habitat (boulder reef or shipwreck) can influence community composition. Shipwrecks feature unique microhabitats that do not occur on natural hard-bottom reefs and can provide niches for species that would otherwise be rare (Meyer-Kaiser et al. 2022b). For example, trace metals released by shipwrecks can infiltrate the surrounding water and sediments and be taken up by fauna (Rogowska et al. 2015, Hartland et al. 2019). Variations in the chemical environment can subsequently influence community composition on and around a shipwreck (Caporaso et al. 2018, Mancini et al. 2019). As a result, anthropogenic structures that have been in place for many years host communities that differ from nearby naturally occurring reefs (Perkol-Finkel et al. 2005).

In this study, we investigated how structural factors including size, distance, and type of habitat (naturally occurring hard-bottom reef or shipwreck) influence invertebrate and fish communities in the mesophotic zone. We analyzed video imagery from 7 sites in the GoM/GoA, including 4 shipwrecks and 3 naturally occurring hard-bottom reefs, to test the hypotheses that species richness, community composition, and functional composition of the community would be driven by habitat size (Hypothesis 1), distance between habitats (Hypothesis 2), and habitat type (Hypothesis 3).

2. MATERIALS AND METHODS

2.1. Study design

We selected 4 shipwrecks (SW1, SW2, SW3, and SW4) and 3 natural hard-bottom reefs (HB1, HB2, and HB4) in the mesophotic zone for study (Table 1, Fig. 1). Sites were chosen from a database of 175 known or suspected shipwreck sites based on geophysical and visual surveys from the Bureau of Ocean Energy Management (BOEM). All sites were located in the north-central GoM/GoA, south of the Louisiana coast (28° N, 91–92° W). Shipwrecks were selected based on their similarity in depth (upper-mid mesophotic, ~40–80 m), range of sizes, and, due to concurrent archaeological research objectives, their potential historical significance. All shipwrecks were primarily composed of steel and sank in the 20th century. For each shipwreck, we identified the nearest naturally occurring hard-bottom reef based on geophysical data collected during oil and gas lease block surveys (BOEM unpubl. data). Distances between shipwrecks and the nearest natural hard-bottom reef ranged from

Table 1. Shipwreck (SW) and natural hard-bottom (HB) sites surveyed in the mesophotic zone. Dimensions of each site are based on side-scan imagery (see Fig. 2) (Redmayne & Lavery 2021). Shipwreck identifications are based on historical research conducted by the authors. 'No. of reps' indicates the number of rarefied pseudo-replicates used in statistical analysis. Coordinates (latitude and longitude) are not provided because shipwrecks are protected sites

Site	Description	Dimensions (m)	Depth (m)	Video (min)	No. of reps. (invertebrate)	No. of reps. (fish)
SW1	'CP Baker'; early drilling rig, sank on 30 June 1964	102 × 55 × 5.5	58	203	16	7
SW2	'Hamlet'; Norwegian freighter, sank on 27 May 1942 during World War II	152 × 21 × 4.0	60	216	21	12
SW3	Unidentified modern shrimp trawler or offshore supply vessel	27 × 7.0 × 3.3	42	118	7	2
SW4	Small unidentified hull	18 × 5.8 × 4.3	79	16	1	1
HB1	Low-lying boulder reef	145 × 58.5 × 1	51	78	26	3
HB2	Highly turbid reef with boulders and consolidated mud	81 × 57 × 1	50	55	3	1
HB4	Low-lying boulder reef	19 × 46 × 1	76	48	6	3

~100 m to 21 km. HB1 was the closest natural reef to both SW1 and SW3.

2.2. Data collection and image analysis

Side-scan sonar imagery of each site selected for this study was collected in 2021 by David Evans and Associates (Fig. 2) (Redmayne & Lavery 2021). Sonar data allowed the dimensions (length, width, and height off the seafloor) for each site to be calculated (Table 1). Ultra-high-definition (4K) videos were recorded from SW1 and SW2 in 2021 by technical SCUBA divers from Marine Imaging Technologies. In 2022, additional video recordings were made from each site using a 4K camera (Marine Imaging Technologies) mounted to a Reliant Robotics SeaRoVer remotely operated vehicle (ROV) deployed from the Aqueos multi-purpose support vessel 'Sea Scout'. Recordings served a dual purpose for archaeological and biological investigations; therefore, diver and vehicle flight paths followed key features and observer curiosity rather than set transects. Video quality, including altitude, lighting, and clarity of fauna, was comparable between the recordings.

Fish were counted directly from video recordings. For shoals or schools, the maximum number of individuals visible in the frame at one time was counted. Frame grabs of representative individuals were captured to enable the identification of each species by reference to taxonomic guides (Humann & DeLoach 2014). In order to quantify invertebrates, frame grabs were collected from video any time the habitat (shipwreck or hard-bottom reef) was in clear view and invertebrate fauna could be clearly discerned (Fig. 3). Invertebrates were then counted from frame grabs

and identified by reference to taxonomic guides (Humann & DeLoach 2013, Humann et al. 2013).

We characterized the functional traits of each invertebrate and fish species. For invertebrates, we characterized traits (and corresponding modalities) following Bremner et al. (2003) and Meyer et al. (2015). These included morphology (flat or encrusting, mounding, oblong, body with legs, upright and simple, upright

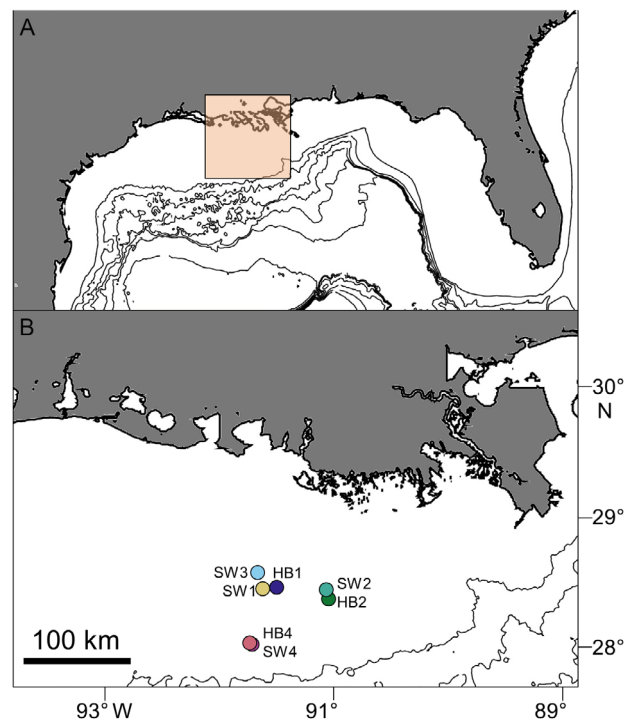


Fig. 1. Study sites, (A) within the regional context of the southeastern USA and Gulf of Mexico/Gulf of America, (B) off the coast of Louisiana. Site locations have been altered using random perturbation within a fixed radius (Smith 2020). SW: shipwreck; HB: hard bottom reef. Depth contours: 500 m

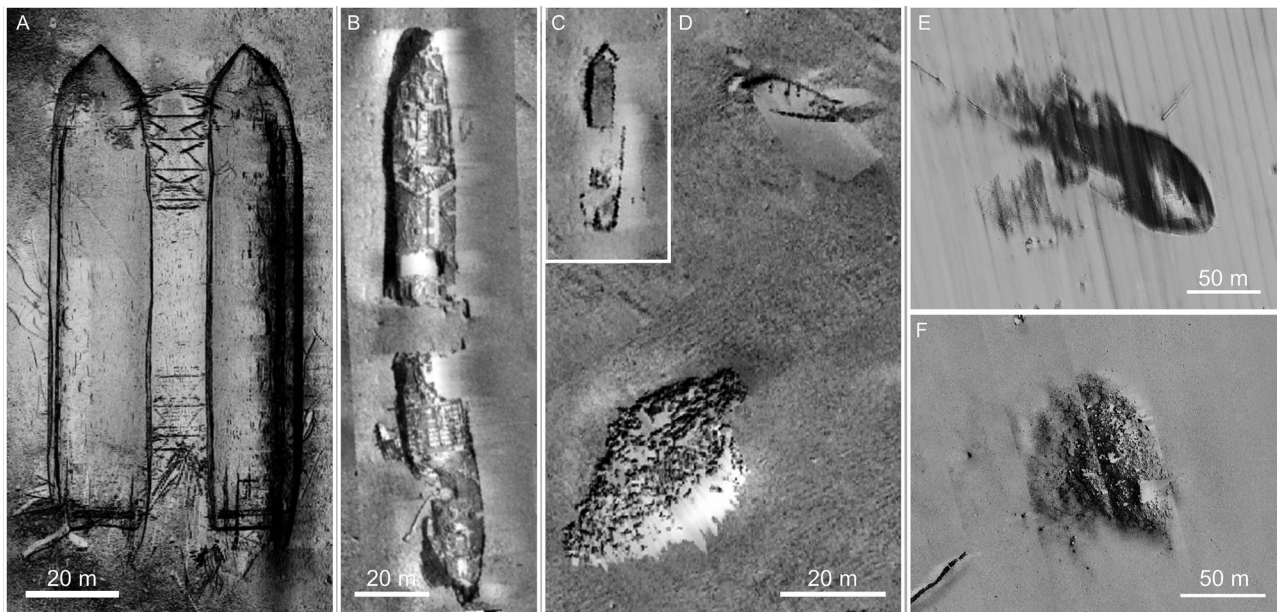


Fig. 2. Side-scan sonar images of each study site. (A) Shipwreck SW1, (B) SW2, (C) SW3, (D) SW4 and hard bottom HB4, (E) HB1, and (F) HB2. Scale bar for (D) also applies to (C). Images courtesy of David Evans and Associates

and branched), mobility (sessile, swimming, crawling), coloniality (clonal, ambiguous or sponge, solitary individual), feeding mode (photosynthetic, suspension feeder, deposit feeder, predator), and symbiosis (none, facultative, obligate). For fishes, traits and trait modalities for each species were selected following Stuart-Smith et al. (2013) and Ford & Roberts (2020). These included maximum body size (small: 10–20 cm; medium: 21–75 cm; large: >76 cm), feeding mode (herbivore, planktivore, benthic carnivore, general carnivore, omnivore, gelatinous prey specialist, piscivore), water column position (bottom or coral, structure-oriented, or pelagic), gregariousness or schooling behavior (always, sometimes, or never), and tail type (truncate, rounded, forked, lunate). Most trait modalities could be identified from video, and additional information was drawn from literature (Hayse 1989, Howe 2001, Ellis & Musick 2007, Humann & DeLoach 2013, Humann et al. 2013, Cardozo et al. 2018, Etnoyer et al. 2020).

Each trait was denoted in a functional trait matrix with a '1' for modalities expressed by a given species and a '0' for modalities not expressed by that species. Only one modality was expressed for each trait for a given species. Scleractinian corals feed both heterotrophically and autotrophically, so the feeding mode was denoted as '0.5' under the photosynthetic modality and '0.5' for the suspension feeding modality. The functional trait matrix was multiplied by the abundance of each species at each site to generate a

matrix of trait abundances. Trait abundances were then used in statistical analysis following Bremner et al. (2003).

2.3. Statistical analysis

A number of factors led to variations in the data quality and coverage between sites. Video surveys served a dual purpose for archaeological and biological investigations and did not follow standardized transects because of conflicting survey requirements. Some sites had high turbidity during dives, which severely restricted visibility. No lasers were mounted on the camera or ROV (to avoid interference with the construction of photogrammetric models), so the surface area of each frame grab could not be calculated. Furthermore, the treatment of video segments or frame grabs as replicate sampling units would have resulted in a high number of replicates with very low abundances in each (invertebrates) or a small number of replicates with high abundances (fish) and obscured patterns between sites.

In order to standardize data and enable statistical analysis of invertebrate and fish communities between sites, we used rarefaction. All data were summed for a given site, and we randomly sub-sampled the community without replacement using the 'rrarefy' function in the 'vegan' package (Oksanen 2013) in R (version 4.1.2; R Core Team 2021). Each sub-sample contained

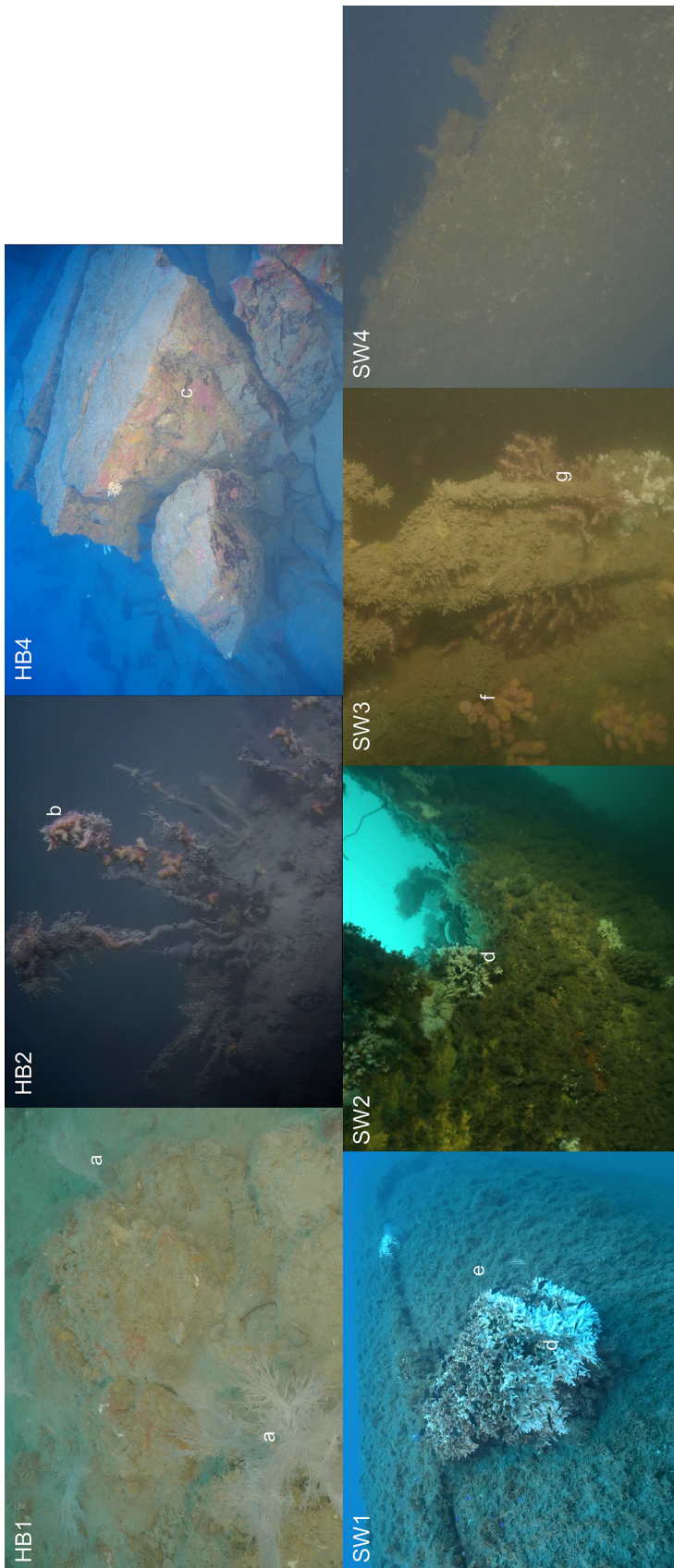


Fig. 3. Example frame grabs showing invertebrate communities at each study site. Lowercase letters indicate common species: a: bushy black coral *Antipathes* sp.; b: bearded fireworm *Hermodice carunculata*; c: crustose coralline algae; d: delicate ivory bush coral *Oculina tenella*; e: regal demoiselle *Neopomacentrus cyanomos*; f: sun coral *Tubastraea coccinea*; g: colorful sea rod *Diodogorgia nodulifera*

50 individuals and was treated as a pseudo-replicate for statistical tests. If more than 50 individuals were observed at a given site, then the raw data were used as a single pseudo-replicate.

As our data analysis was based on randomized pseudo-replicates, we could not use parametric statistical tests. Instead, we relied on non-parametric and permutational statistics, which make minimal assumptions about the data. Spearman correlations were used to test for correlations between species richness and the size of each site. Mann-Whitney U -tests were used to test for differences in species richness between shipwrecks and natural hard-bottom reefs. Mantel tests were used to test for spatial auto-correlation in species richness, community composition, and functional composition. PERMANOVA was used to test for differences in community composition and functional composition between shipwrecks and natural hard-bottom sites using the 'adonis2' function in the vegan package in R. SIMPER analysis using the 'simper' function in the vegan package showed which species or functional traits contributed the most to differences between shipwrecks and natural hard-bottom sites. We used distance-based redundancy analysis (dbRDA) to test for the influence of site size and distance between sites (calculated using latitude, longitude, and depth) on community composition of invertebrates and fishes using the 'capscale' function in the vegan package in R. For all tests, distance matrices for biological data (i.e. species abundances) were based on a Bray-Curtis method using untransformed values, and matrices for other metrics (i.e. size, distance, species richness, functional traits) were based on Euclidean distance. ANOVAs were used to test for the significance of each best-fit dbRDA model.

3. RESULTS

Not all rarefaction curves reached asymptotes, indicating that sampling was not sufficient to capture all species in the community for some habitats (Fig. 4). The best-sampled habitats were HB1, SW1, and SW2. Curves for these 3 habitats reached clear asymptotes for both invertebrates and fishes. Invertebrate and fish curves for HB4 as well as invertebrate curves for HB2 and SW3 barely reached asymptotes, indicating sampling was just sufficient. No asymptotes were reached by the rarefaction curves for SW4 invertebrates or HB2, SW3, or SW4 fishes (Fig. 3). Sites HB2, SW3, and SW4 had the lowest organismal abundances.

3.1. Species richness

Hypothesis 1 (size): there was a significant correlation between the species richness of invertebrates and the log of site size (Spearman correlation, $\rho = 0.38$, $p < 0.001$). The shape of this relationship follows the classical model (Fig. 5). For fishes, on the other hand, the relationship was not significant (Spearman correlation, $\rho = 0.17$, $p = 0.37$) (Fig. 5). Thus, Hypothesis 1 was supported for species richness of invertebrates but not for fishes.

Hypothesis 2 (distance): there was no significant relationship between a distance matrix of species richness and the distance between habitats for invertebrates (Mantel test, $r = 0.10$, $p = 0.07$) or for fishes (Mantel test, $r = 0.24$, $p = 0.06$). Thus, there was no tendency for sites closer together to have similar species richness, and Hypothesis 2 was not supported for invertebrates or fishes.

Hypothesis 3 (type): there was no significant difference in rarefied species richness of invertebrates between sites with different types (shipwreck or natural hard-bottom reef; Mann-Whitney, $U = 859$, $p = 0.47$) (Fig. 6). For fishes, there was also no significant difference in species richness between shipwrecks and natural hard-bottom reefs (Mann-Whitney, $U = 94.5$, $p = 0.36$). This hypothesis was not supported for species richness of either invertebrates or fishes.

3.2. Community composition

Hypotheses 1 and 2 (size and distance): for invertebrates, the best dbRDA model included all factors (size, latitude, longitude, depth), was statistically significant (ANOVA, $F_{4,75} = 31.7$, $p < 0.001$), and explained 62% of the community composition ($R^2 = 0.62$). In addition, there was a significant relationship between the community composition of invertebrates and the distance between our study sites (Mantel test, $r = 0.55$, $p < 0.001$). Similarly, the best dbRDA model for the fish community included all tested factors (size, latitude, longitude, depth), was statistically significant (ANOVA, $F_{4,24} = 20.7$, $p < 0.001$), and explained 77% of the community composition ($R^2 = 0.77$). There was also a significant relationship between fish community composition and distance between our sites (Mantel test, $r = 0.80$, $p < 0.001$). Hypotheses 1 and 2 were supported for community composition of both fishes and invertebrates.

Hypothesis 3 (type): there was a significant difference in invertebrate community composition based on site type (shipwreck or natural reef; PERMANOVA,

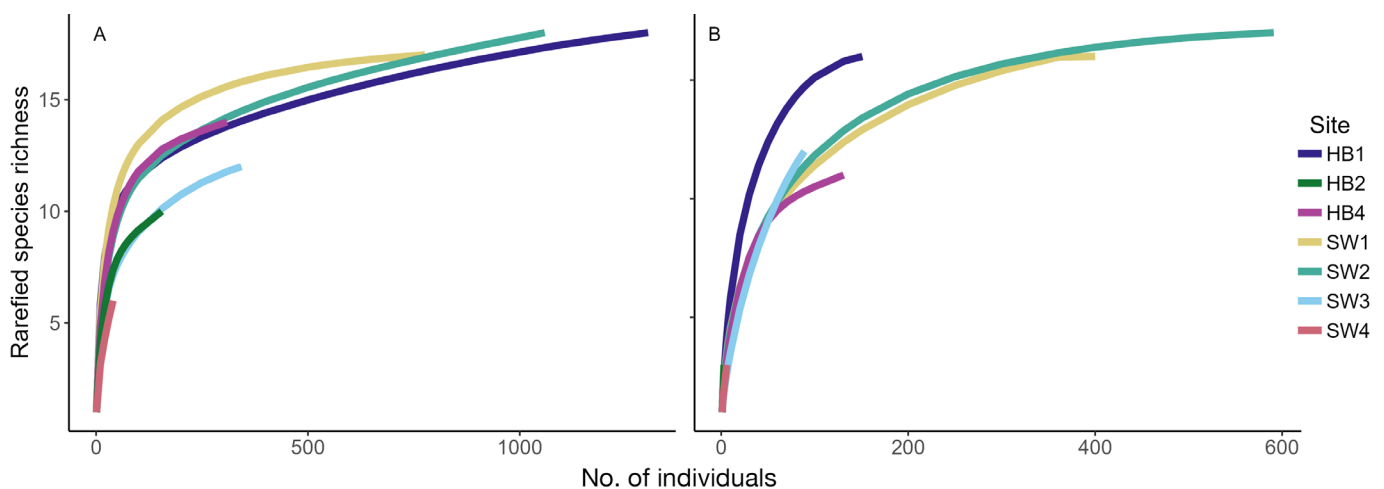


Fig. 4. Rarefaction curves for (A) invertebrates and (B) fishes at each site. Curves that reach asymptotes indicate sampling was sufficient to characterize the community at that site. Site codes as in Fig. 2 and Table 1

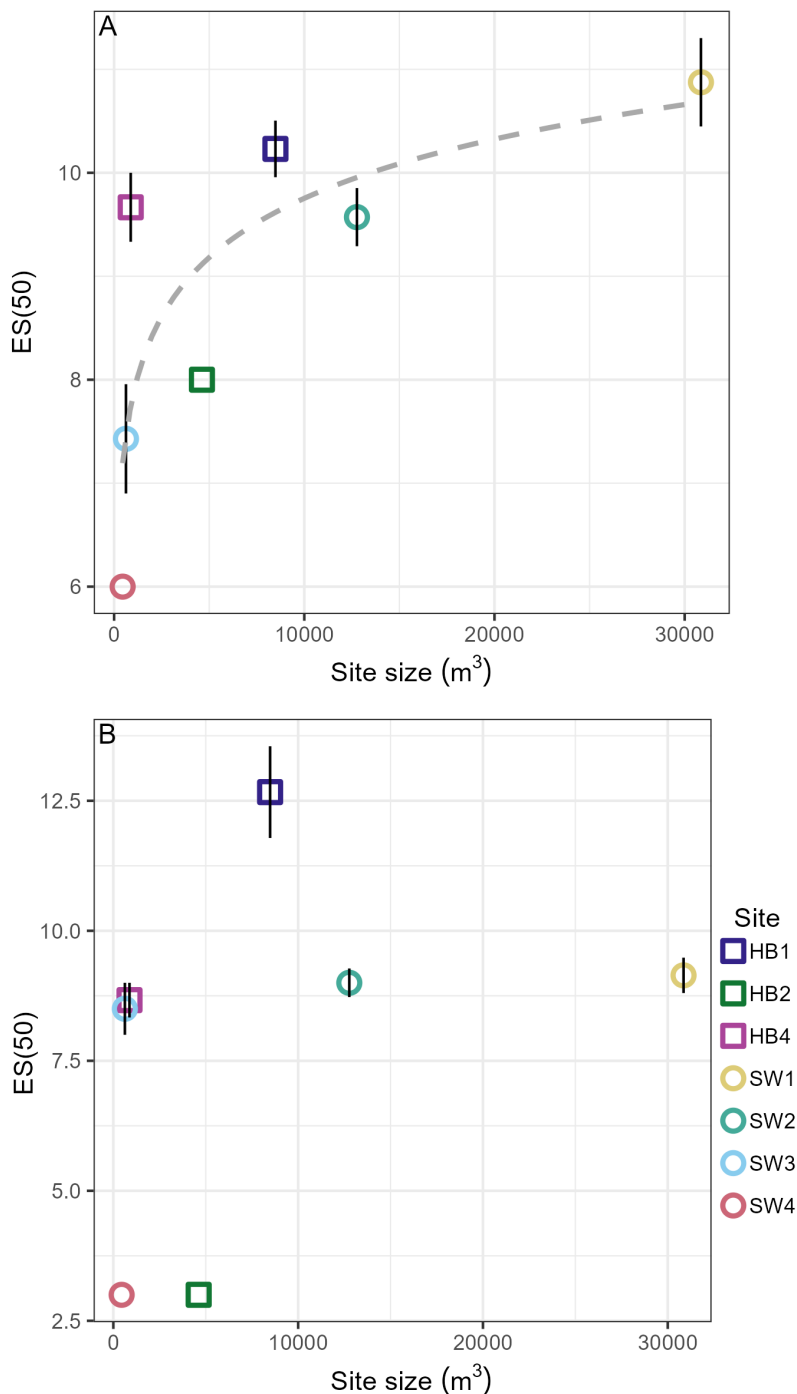


Fig. 5. Correlation between species richness (rarefied to 50 individuals) of (A) invertebrates and (B) fishes and the size of a site. Statistically significant logarithmic trendline for invertebrates is shown. Error bars represent standard error. Site codes as in Fig. 2 and Table 1

pseudo- $F_{1,78} = 29.8$, $p < 0.001$) (Fig. 7). Species driving the dissimilarity between shipwrecks and natural hard-bottom reefs were the sun coral *Tubastraea coccinea* (SIMPER, contribution: 0.13), hydroids (0.13), the feather black coral *Plumapathes pennacea* (0.10), and the white

encrusting morphotype, which is most likely a sponge (0.09). Hydroids and *T. coccinea* were more abundant on shipwrecks, while *P. pennacea* and the white encrusting morphotype were more abundant on natural hard-bottom reefs. There was a significant difference in fish community composition between shipwrecks and natural hard-bottom reefs (PERMANOVA, pseudo- $F_{1,27} = 9.32$, $p < 0.001$) (Fig. 7). Species driving the dissimilarity between site types were the regal demoiselle *Neopomacentrus cyanomos* (SIMPER, contribution: 0.26), pigfish *Orthopristis chrysoptera* (0.16), and red snapper *Lutjanus campechanus* (0.15). Of these, *N. cyanomos* and *L. campechanus* were more abundant on shipwrecks, and *O. chrysoptera* was more abundant on natural hard-bottom reefs. Hypothesis 3 was supported for community composition of both invertebrates and fishes.

3.3. Functional composition

Hypotheses 1 and 2 (size and distance): the best dbRDA model for the functional composition of invertebrates included all factors (size, latitude, longitude, depth), was significant (ANOVA, $F_{4,75} = 24.7$, $p < 0.001$), and explained 56% of the functional composition ($R^2 = 0.56$). There was a significant relationship between the functional composition of invertebrates and the distance between our study sites (Mantel test, $r = 0.50$, $p < 0.001$). Similarly, the best model for the fish community included all tested factors (size, latitude, longitude, depth), was statistically significant (ANOVA, $F_{4,24} = 21.1$, $p < 0.001$), and explained 77% of the community composition ($R^2 = 0.77$). There was also a significant relationship between fish community composition and distance between our sites (Mantel test, $r = 0.77$,

$p < 0.001$). Hypotheses 1 and 2 were supported for the functional composition of both fish and invertebrates.

Hypothesis 3 (type): there was a significant difference in invertebrate functional composition based on site type (shipwreck or natural reef; PERMANOVA,

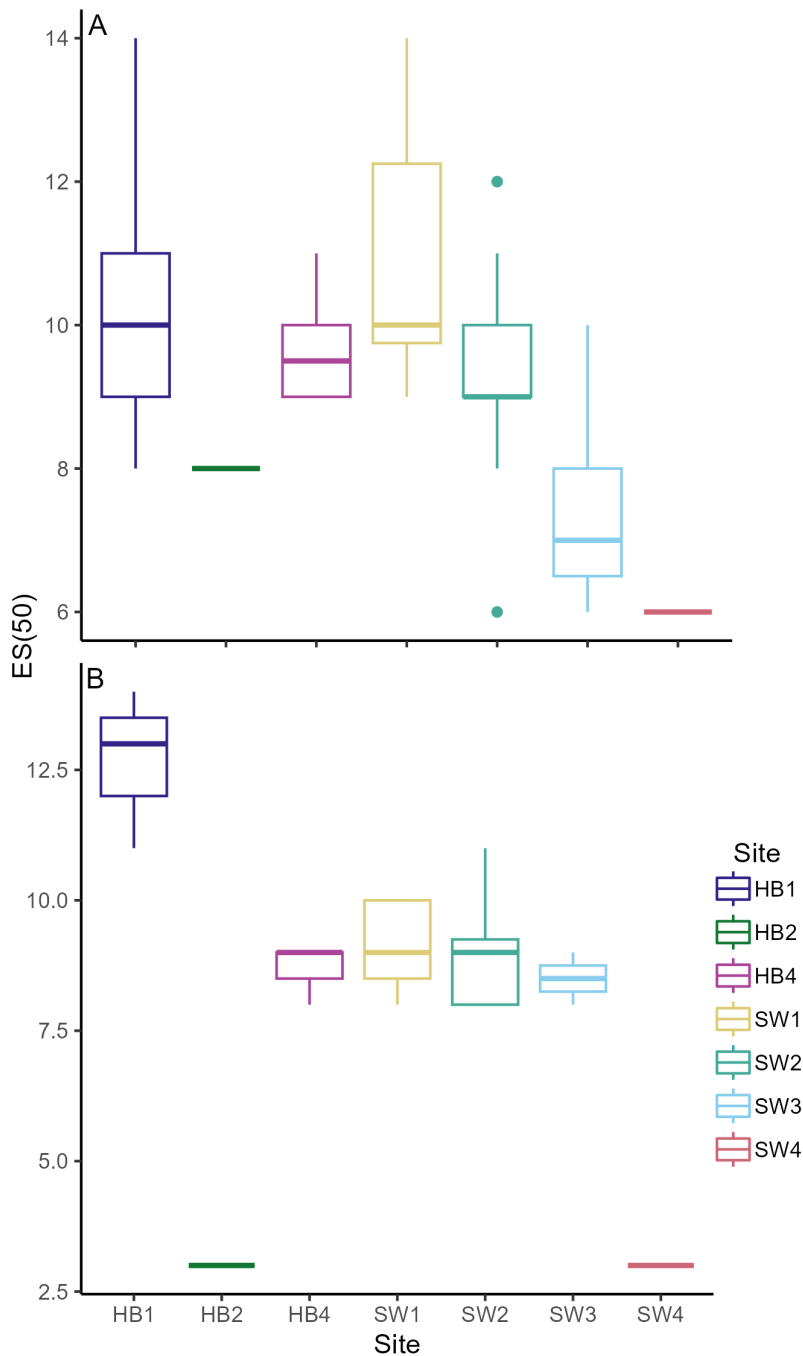


Fig. 6. Species richness (rarefied to 50 individuals) for (A) invertebrates and (B) fishes at each site. Horizontal line: median; box limits: first and third quartiles; whiskers: $1.5 \times$ the interquartile range; dots: outliers. Site codes as in Fig. 2 and Table 1

pseudo- $F_{1,78} = 44.2$, $p < 0.001$) (Fig. 8). The trait modalities most associated with the difference between shipwrecks and natural reefs were ambiguous or sponge coloniality (SIMPER, contribution: 0.12), flat morphology (0.10), and lack of symbionts (0.08). All 3 of these traits were more associated with natural hard-bottom

reefs than shipwrecks. There was a significant difference in fish functional composition between shipwrecks and natural hard-bottom reefs (PERMANOVA, pseudo- $F_{1,27} = 12.9$, $p < 0.001$) (Fig. 8). The functional traits most associated with the difference between site types were always schooling (SIMPER, contribution: 0.11), forked tail (0.08), small body size (0.08), and bottom or coral habitat (0.07). Each of these traits was more associated with shipwrecks than natural hard-bottom habitats. Hypothesis 3 was supported for the functional composition of both invertebrates and fishes.

4. DISCUSSION

Overall, we found that the community composition and functional composition of invertebrates and fishes were significantly influenced by the size, distance between sites, and type of habitat (shipwreck or natural hard-bottom reef) for our sites in the mesophotic zone. However, species richness was much less explained by the factors we tested. Low organismal abundances and insufficient sampling at some sites (as indicated by non-asymptotic species-accumulation curves) may have biased our results to show lower species richness and greater differences in community composition and functional composition than is accurate. Nevertheless, the broad-scale patterns in our data provide important insights for shipwrecks and hard-bottom reefs in the mesophotic zone.

4.1. The influence of habitat size

Species richness of invertebrates had a significant logarithmic relationship with habitat size, but no significant relationship was present for fishes. Other studies on shipwrecks have reported varied results, with a significant relationship for sessile species but not mobile species (Meyer et al. 2017) or a complete lack of significant relationships (Meyer-Kaiser et al. 2022a). Other factors, such as strong gradients in environmental conditions,

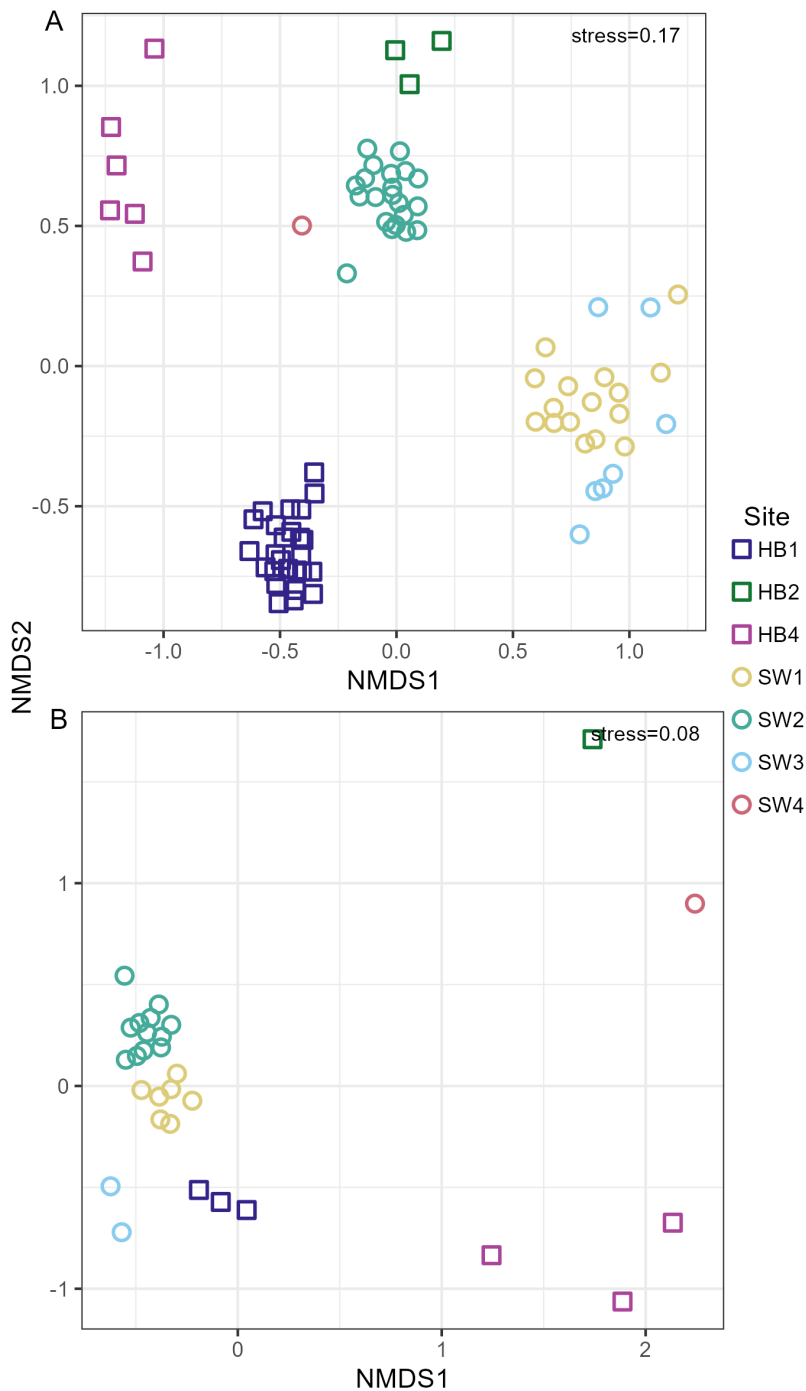


Fig. 7. Non-metric multidimensional scaling plots showing differences in community composition between sites for (A) invertebrates and (B) fishes. Each point represents one rarefied pseudo-replicate; points that are closer together have more similar community composition. Site codes as in Fig. 2 and Table 1

can be the primary driver of species richness on shipwrecks in some cases (Meyer-Kaiser et al. 2022a).

There are numerous hypotheses that attempt to explain species–area relationships. For sessile invertebrates, limited 2-dimensional space can lead

to strong intra- or interspecific competition (Sebens 1986). However, our study sites had large swaths of empty space with no invertebrate fauna, indicating competition was not likely the primary driver of species–area dynamics. Studies in other systems have also found classical species–area relationships in the absence of strong interspecific competition (Meyer et al. 2016, 2017). The hypotheses for species–area relationships that are most pertinent to shipwrecks include the sampling hypothesis — that larger habitats are larger targets for settling propagules and support more species from the regional pool (Connor & McCoy 1979) — and the principle that larger habitats have greater heterogeneity (Williams 1943, Kallimanis et al. 2008). Our invertebrate data supports both hypotheses, and they are not mutually exclusive.

Habitat size was significantly related to community composition and functional composition for both invertebrates and fishes. The largest habitats in our study were both shipwrecks, SW1 and SW2, and were characterized by high vertical relief. Elevated substrata expose sessile suspension feeders, such as corals, sponges, and octocorals, to swifter currents and higher food supply in the benthic boundary layer (Vogel 1996). Indeed, high densities of suspension feeders on elevated substrata is a near-ubiquitous pattern in the ocean (Rogers 1993, Gass & Roberts 2006, Baco 2007). Shipwrecks that are surrounded by soft sediments offer the only vertical relief in the local area and tend to host dense populations of suspension feeders and/or zooplankton predators on the upper portion of the shipwreck (Meyer-Kaiser et al. 2022b).

Vertical relief of a habitat also influences fish communities, with pelagic predators being more abundant on

tall artificial structures (Bryan et al. 2013, Paxton et al. 2020, 2024). We observed a sandbar shark *Carcharhinus plumbeus* at SW1 and high abundances of the pelagic species greater amberjack *Seriola dumerili* and red snapper *Lutjanus campechanus* around ship-

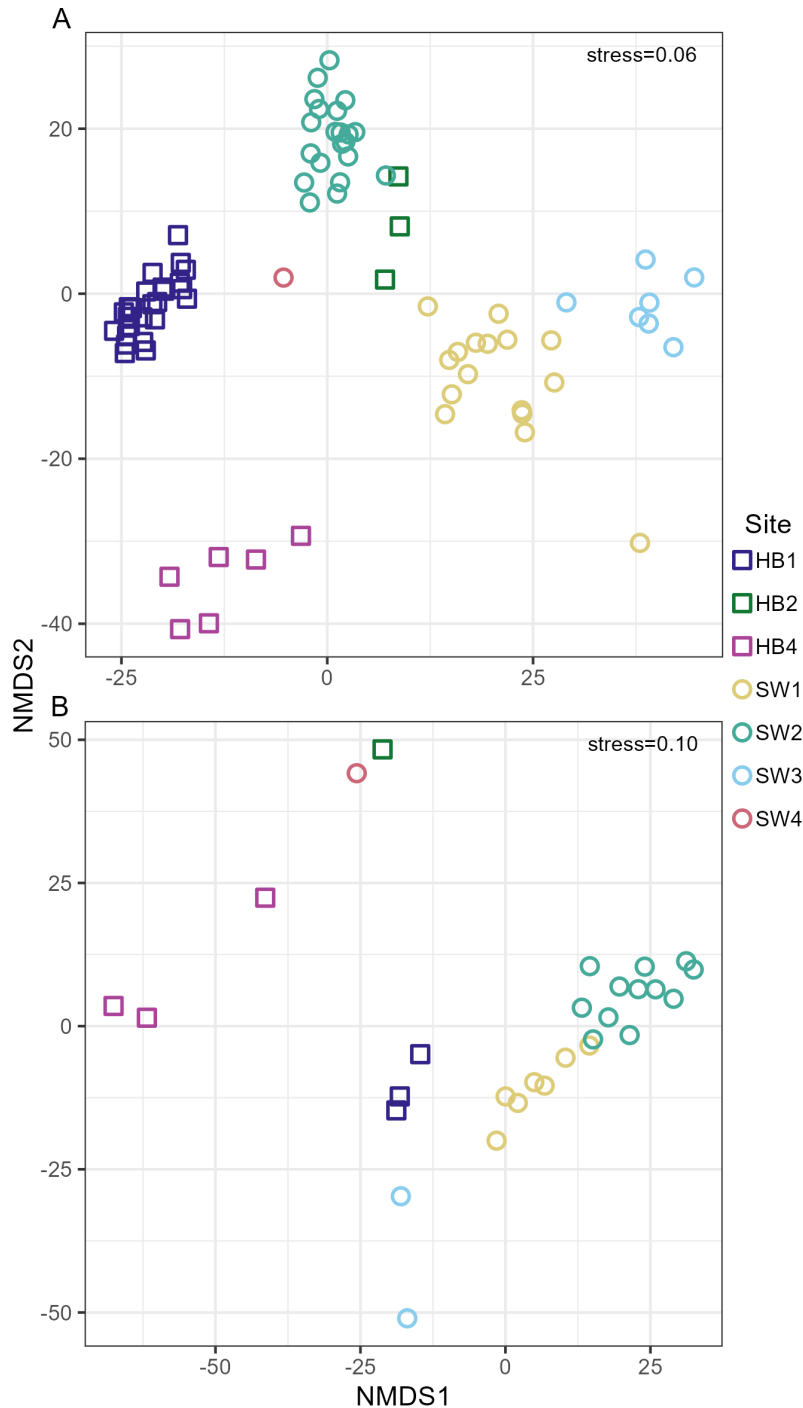


Fig. 8. Non-metric multidimensional scaling plots showing differences in functional composition between sites for (A) invertebrates and (B) fishes. Each point represents one rarefied pseudo-replicate; points that are closer together have more similar functional composition. Site codes as in Fig. 2 and Table 1

wrecks. Indeed, red snapper and the affiliated traits of schooling and a forked tail were strong contributors to the differences between shipwreck and natural hard-bottom communities. Large pelagic predators may be drawn to shipwrecks because of the availability

of prey or because of the relative ease of finding a large habitat (Paxton et al. 2020). Given the high turbidity observed at our study sites and the vertical relief provided by shipwrecks in the benthic boundary layer, we also suggest that these large structures may facilitate visual predation by hosting prey species in relatively clearer waters than low-lying natural reefs. Shipwrecks serve as island-like hotspots for fish aggregations (Paxton et al. 2021).

The natural hard-bottom sites in this study were selected based on their proximity to shipwrecks, but elsewhere in the GoM/GoA, natural hard-bottom reefs with high vertical relief can be found in the Flower Garden Banks (Gardner et al. 1998). These isolated banks support stable coral communities and fishes, including many of the same pelagic predators we observed at shipwreck sites (Johnston et al. 2016, Sanchez et al. 2023). Differences in community composition between shipwrecks and natural hard-bottom reefs in this study were strongly influenced by contrasts in habitat size and vertical relief.

4.2. The influence of distance between sites

The distance between sites had a significant relationship with community composition and functional composition for both invertebrates and fishes. Shipwrecks form island-like habitats that host unique communities and have a sphere of influence on the surrounding flora and fauna (Bałazy et al. 2019, Hamdan et al. 2021). Community composition can be controlled by larval dispersal, with only a subset of species in the regional pool able to disperse to the shipwreck's location (Walker & Schlacher 2014, Meyer 2017, Pinto et

al. 2021). The sites in this study were island-like; however, the distances between shipwrecks and natural hard-bottom reefs (i.e. 20 km or less) suggest that dispersal may not be limiting. Marine invertebrate species with PLDs of days to weeks have dispersal

ranges on the order of the distances between sites in this study (Shanks 2009). Furthermore, the GoM/GoA is home to thousands of artificial structures associated with offshore industry (Sammarco et al. 2004). Industrial infrastructure provides habitat for obligate hard-bottom species and can serve as stepping-stones for the dispersal of corals (Sammarco et al. 2004, Gass & Roberts 2006, Macreadie et al. 2011). In addition, anthropogenic structures including active and decommissioned oil rigs form important habitats for structure-oriented and pelagic fishes (Ajemian et al. 2015, Streich et al. 2017).

While the distances between our sites may not have prevented species from colonizing, dispersal dynamics likely had an influence on community composition. The larval development of many mesophotic species is poorly understood, but previous research suggests short PLDs (hours to days) and limited dispersal for black corals (Miller 1998) and sponges (Malonado 2006). Some species in our study, particularly *Tubastraea coccinea*, have longer and highly plastic PLDs (up to 69 d) (Luz et al. 2020). Modeling has shown that a PLD of 10–20 d results in high connectivity among mesophotic habitats in the GoM/GoA (Garavelli et al. 2018). However, larval behaviors, particularly swimming downward or remaining near the bottom, can restrict dispersal for species with long PLDs (Spoungue et al. 2002). Most coral reef fishes tend to recruit back to their natal populations (Swearer et al. 2002), but plastic PLDs and variable oceanographic conditions lead to variations in dispersal distance (Hogan et al. 2012). Rising ocean temperatures driven by climate change also reduce PLD in fishes and lead to more localized recruitment (Raventos et al. 2021). Restricted dispersal, even for some species, would explain the correlation between distance and both community composition and functional composition in our data. A hard-bottom species is most likely to colonize the nearest shipwreck and may recruit back to the same shipwreck in subsequent generations (Appelqvist et al. 2015, Meyer et al. 2017).

Depth is an important factor in mesophotic habitats. Declining light and lower temperatures lead to a near-universal shift in community composition at ~60 m depth (Lesser et al. 2019). The absence of many hermatypic corals and herbivorous fishes from habitats deeper than 60 m provides niche space for sponges, octocorals, and planktivorous and piscivorous fishes (Semmler et al. 2017). Our study sites spanned ~40–80 m depth, with HB4 and SW4 being the deepest sites. SW4 was the most sparsely colonized site. The patterns we observed in community composition and functional composition corroborate previous depth-

driven patterns in abundance and community composition for mesophotic invertebrates and fishes.

4.3. The influence of habitat type

The 2 species with the greatest contribution to the difference between natural hard-bottom sites and shipwrecks in our study were *T. coccinea* and the regal demoiselle *Neopomacentrus cyanomos*—both non-native species in the GoM/GoA. By providing high-relief structures and unique microhabitats, shipwrecks tend to increase regional biodiversity (Perkol-Finkel et al. 2006, Church et al. 2009). However, these habitats can also support invasive species or species at the edge of their geographic ranges (Work et al. 2008, Paxton et al. 2019). Shipwrecks can facilitate the spread of non-native species, which colonize anthropogenic habitats readily (Hoeksema et al. 2023).

T. coccinea is native to the Indo-Pacific but has spread throughout the Caribbean, GoM/GoA, and northern coast of Brazil (Fenner & Banks 2004, Paula & Creed 2005). It is a highly opportunistic species that thrives on artificial habitats (Sammarco et al. 2004, Rezek et al. 2018, Luz et al. 2020). *T. coccinea* larvae tend to settle on the undersides of surfaces, where they are protected from sedimentation (Mizrahi et al. 2014). Overhanging habitats are rare on naturally occurring boulder reefs but common on shipwrecks (Meyer-Kaiser et al. 2022b). The undersides of overhangs also provided preferred habitat for the black coral *Antipathes pennacea* on a Caribbean shipwreck (Oakley 1988). Because of the habitats they provide, shipwrecks serve as key stepping stones for the dispersal of *T. coccinea* (Soares et al. 2020b, Hoeksema et al. 2023).

N. cyanomos is another Indo-Pacific species introduced to the GoM/GoA (Robertson et al. 2021a). A second population has been observed in Trinidad, potentially from a different introduction event (Robertson et al. 2021b). *N. cyanomos* prefers artificial habitats, and indeed, multiple lines of evidence suggest the species was introduced along with oil drilling platforms from the Indo-Pacific (Robertson et al. 2018, Tarnecki et al. 2021). Similar to *T. coccinea*, it thrives on shipwrecks, suggesting that these structures may facilitate its spread throughout the GoM/GoA.

We observed lionfish *Pterois volitans* on shipwrecks and natural reefs. Mesophotic habitats, below the depth limit of recreational diving, represent a refuge for lionfish and undermine removal efforts in shallow water (Andradi-Brown et al. 2017). Lionfish also occur in much higher densities (2 orders of magnitude) on

artificial than natural reefs in the northern GoM/GoA (Dahl & Patterson 2014).

4.4. Conclusions

Shipwrecks and other UCH are integral to the marine ecosystem (Meyer-Kaiser & Mires 2022). Large shipwrecks present high-relief, heterogeneous habitats that enhance regional biodiversity. In the mesophotic zone, the effect of artificial structures on biodiversity is enhanced by the sparse availability and low-lying nature of naturally occurring hard-bottom reefs (Bryan et al. 2013). An unfortunate by-product of the unique microhabitats provided by shipwrecks is the facilitation of non-native species. While the detrimental impacts of lionfish are clearly documented (Andradi-Brown et al. 2017), it is unclear to what extent *N. cyanomos* or *T. coccinea* could displace native species (Almeida Saá et al. 2020, Tarnecki et al. 2021). Shipwrecks can also release trace metals or other contaminants into the surrounding environment, leading to complex positive and negative environmental impacts (Renzi et al. 2017, Hartland et al. 2019). Our study highlights the role of shipwrecks in supporting biodiversity in the mesophotic Gulf of Mexico/Gulf of America.

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