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Invertebrate communities on shipwrecks in Stellwagen Bank National Marine Sanctuary

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ABSTRACT: Shipwrecks serve as island-like habitats on the seafloor and can be conceptualized as unplanned, unprepared, and unintentional artificial reefs. Most artificial reef studies have been restricted in scope and duration, but we have leveraged a dataset of 18 shipwrecks ranging from 15 to 155 yr old and at 24 to 140 m depth in Stellwagen Bank National Marine Sanctuary (SBNMS; Massachusetts, USA) to investigate the factors influencing benthic invertebrate communities on shipwrecks. Classical ecological relationships between species richness and composition and shipwreck size and age (e.g. a log-linear relationship between species richness and shipwreck size) were not observed. Our hypotheses for turnover in species composition with shipwreck age and a significant influence of shipwreck material (i.e. metal, wood) on species composition were also not supported. Rather, our results showed turnover in species composition with shipwreck size, as larger shipwrecks supported dense populations of sessile species such as sponges and anemones. We also observed a high level of patchiness and a significant influence of depth on shipwreck invertebrate communities. These results highlight the importance of shipwrecks as habitats in SBNMS. High-profile shipwrecks in particular support dense invertebrate populations, but the degradation of wooden shipwrecks reduces this effect over time. Our study has implications for future artificial reef management, showing that larger shipwrecks are more valuable habitats, and that reef placement has a strong influence on the resulting species composition.

KEY WORDS: Benthic · Underwater cultural heritage · Image analysis · Island biogeography · Recruitment

1. INTRODUCTION

Shipwrecks are anthropogenic structures that can become colonized by invertebrates and fish and increase biodiversity in marine environments. The vast majority of ships that come to rest on the seafloor are unplanned losses, with the estimated 3 million shipwrecks worldwide far outnumbering planned artificial reefs (UNESCO 2002). Unplanned losses are more likely to carry contaminants than planned artificial reefs and are less likely to be located in areas with high colonization potential. Shipwrecks serve as imperfect yet useful parallels for intentional structures and present prime opportunities for ecological research. Most shipwrecks are isolated and island-like, surrounded by sand or mud. Only a sub-set of species may be able to disperse to an island-like shipwreck (Meyer 2017), leading to unique patterns in the resulting communities and pairwise species interactions (Pawlik et al. 2008). The structure of a shipwreck may be more complex and heterogeneous than surrounding substrata, altering the assemblage of organisms that can settle and augmenting the biodiversity of a region (Mallefet et al. 2008, Amaral et al. 2010, Lira et al. 2010). Shipwrecks serve as island-like habitats and host unique communities of microbes (Price et al. 2020, Hamdan et al. 2021), invertebrates (Meyer et al. 2017), and fish (Paxton et al. 2019). Those organisms in turn form an integral part of the shipwreck's site formation processes and may influence natural changes occurring at the site over time (Muckelroy 1998).

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Most artificial reef studies are limited in scope, typically involving 1–5 structures (e.g. Walker et al. 2007, Harrison & Rousseau 2020, and references above). The few studies involving multiple shipwrecks in the same region have found variations in community composition across spatial scales, which are driven by environmental and biological factors (Church et al. 2009, Meyer et al. 2017). Most studies on shipwreck communities have also been limited in duration, with data being collected over just a few years. However, insights into temporal dynamics in artificial reef communities can be gained by comparing community composition among structures with different ages. Such studies have shown low species richness on young artificial reefs (a few years old) (Walker & Schlacher 2014), followed by changes in community composition over time as the community undergoes succession (Perkol-Finkel & Benayahu 2005, Perkol-Finkel et al. 2005, Toledo et al. 2020). However, artificial reef communities do not necessarily come to resemble natural reefs even a century after installation (Perkol-Finkel et al. 2006).

Centuries of seafaring have deposited >200 shipwrecks on the seafloor in Stellwagen Bank National Marine Sanctuary (SBNMS; Massachusetts, USA) (Lawrence et al. 2015). In this study, we capitalized on the large number of shipwrecks in SBNMS to study the factors driving the community composition on these anthropogenic structures. We focused specifically on benthic invertebrate assemblages. Video recordings made in 2003–2012 present a unique dataset encompassing 18 shipwrecks spanning 15–155 yr in age. These shipwrecks also spanned nearly the entire range of water depths in SBNMS (24–140 m). The broad scope of this dataset allows for discernment of the factors driving shipwreck community structure.

Two factors that are likely to influence species richness (alpha diversity) in shipwreck communities are size and age. A relationship between species richness and habitat size is considered one of the few true laws in ecology (Lawton 1999). This species–area relationship is typically expressed using the power function model ($S = cA^z$, where S is species richness, A is area, and c and z are constants) or its log transformation, which yields a linear equation ($\log(S) = z[\log(A)] + c$) (Scheiner 2011). One prominent hypothesized explanation for this relationship is the 'sampling hypothesis': larger habitats are larger targets for settling propagules and can support more individuals, which will inevitably include more species (Connor & McCoy 1979, Bartha & Ittzés 2001, Catano et al. 2021). We hypothesized that the relationship between species richness and shipwreck size would fit the power function model (H_1).

There may also be differences in species richness over time (a species–time relationship). While investigations of species–time relationships are rare, the form of the relationship varies from linear to logarithmic and may increase or decrease over time (Hadly & Maurer 2001, Adler & Lauenroth 2003, White 2004). For marine invertebrates, species richness would be expected to increase over time as species recruit to the community (Osman 1977, Bram et al. 2005). However, interactions between established fauna and new recruits can exclude some species from late-succession communities (Osman et al. 1992, Bullard et al. 2004, Osman & Whitlatch 2004, Cifuentes et al. 2010). We therefore hypothesized an inverse second-order polynomial relationship between species richness and shipwreck age, with the highest species richness occurring at intermediate ages (e.g. ~80 yr old) (H_2).

Changes in community composition (beta diversity) over time may be expected as a result of successional dynamics. Many marine habitats are first colonized by generalist or opportunistic species with high dispersal, while less-dispersive, slower-growing species become more abundant over time (Perkol-Finkel et al. 2005, Edwards & Stachowicz 2010). In particular, colonial invertebrates or those with asexual reproduction may be better able to hold space in a community and dominate late succession (Jackson 1977). We hypothesized that there would be turnover in community composition among shipwrecks with different ages both in terms of species and in terms of their traits: younger shipwrecks were expected to be dominated by solitary species or those with planktotrophic development (e.g. barnacles), with older shipwrecks being dominated by colonial species with lecithotrophic development (e.g. ascidians) (H_3).

The material from which a shipwreck is constructed can potentially impact the community inhabiting it. For example, metal hulls may be toxic to some fauna and inhibit recruitment. Areas of the shipwreck covered in toxic metals such as copper sheathing are unavailable for colonization, resulting in a smaller effective habitat size. The effects of heavy metals from ship hulls or anti-fouling paints can even extend beyond the shipwreck itself to the surrounding benthos (Ballard 1987, Walker et al. 2007, Work et al. 2008). On the other hand, wooden shipwrecks serve as settlement substrata for hard-bottom fauna and also provide an organic energy source. Organic matter on shipwrecks can lead to unique and patchy benthic communities with burrowing and wood-boring invertebrates or species with chemosynthetic symbionts (Dando et al. 1992, Ballard et al. 2000, Gambi et al. 2011, Caporaso et al.

2018). Wooden shipwrecks degrade over time, so the only structures remaining above the sediment surface for some older shipwrecks may be cargo or a pile of ballast rocks. Parts of a shipwreck may be buried, but to date, the impact of buried shipwreck components on benthic communities has not been investigated. Shipwrecks that have only low-lying hard structures such as ballast rocks remaining above the sediment surface form the closest analog to natural reefs consisting of boulders and may have different species composition than intact ships. We hypothesized that material would also be an important factor structuring invertebrate communities on SBNMS shipwrecks (H_4).

Our study explored the influences of shipwreck size, shipwreck age, material, and location on alpha and beta diversity of shipwreck communities in SBNMS. Our findings reveal insights for community assembly on artificial reefs.

2. MATERIALS AND METHODS

2.1. Video and still image collection

Data used in this study were collected in 2003–2012 and were accessed for this study by the present authors through the SBNMS archives in 2020. We aimed to include as many shipwrecks across the sanctuary as possible in our analyses. In this study, we focused on a set of 18 shipwrecks that had (1) video data of sufficient quality to characterize the benthic invertebrate community on the shipwreck, (2) precise location data, (3) estimates of their size *in situ*, and (4) age estimates based on archaeological data.

Video footage was recorded using the remotely operated vehicles (ROVs) 'Hela' and 'Kraken II', operated by the Northeast Underwater Research, Technology, and Education Center (NURTEC) aboard the RV 'Connecticut'. Shipwrecks are complex environments with irregular surfaces. Within SBNMS, many shipwrecks have entangled fishing gear; currents are strong, and turbidity can be high. Video data used in this study were originally collected for archaeological exploration rather than biological analysis. Therefore, ROV flight paths were irregular and images were not recorded in smooth transects. We circumvented these difficulties by converting ROV video to still images, following Meyer et al. (2017). A frame grab was collected from the video any time shipwreck components or artifacts were in clear view. Frame grabs were removed from analysis if they were too bright, too dark, at an anomalous distance from the shipwreck, or had overlapping content with another frame grab. Parallel lasers mounted on the ROVs served as a distance scale and were used to calculate the area represented by each frame grab. Altogether, 11–117 frame grabs per shipwreck were analyzed, depending on shipwreck size and ROV video quality (Table 1). Frame grabs represented 1.26 ± 0.12 m^2 (mean ± SE). This study in-

Table 1. Surveyed shipwrecks. Inverted commas indicate official names; all others are working names

Wreck	Year surveyed	No. unique frame grabs	Wreck size (m^3)	Water depth (m)	Primary material	Most likely sinking date
'Portland'	2003	117	5525	137	Wood	1898
Eastern Rig Dragger	2003	24	2232	95	Wood	1930–1970
STB-008	2004	18	420	140	Wood	1930–1970
STB-016	2004	28	1112	90	Rock	1800–1900
'Paul Palmer'	2005	72	1638	24	Wood	1913
STB-007	2005	29	546	50	Wood	1898
STB-013	2005	26	240	64	Rock	1800–1900
STB-015	2005	23	32	90	Coal	1800–1900
'Palmer/Crary'	2006	62	12024	97	Wood	1902
Mystery Collier	2006	65	720	129	Metal	1850–1920
NF Hang	2006	24	510	107	Wood	1930–1970
NF 2006 Target 1	2006	12	480	130	Metal	1970–2005
STB-011	2006	38	136	110	Rock	1860–1920
'Josephine Marie'	2007	15	504	29	Metal	1992
STB-024	2009	47	540	105	Wood	1964
STB-025	2009	11	6255	82	Wood	1984
STB-027	2009	16	1485	80	Wood	1890–1910
STB-005	2012	36	855	37	Wood	1935

cludes a total of 663 frame grabs from 18 shipwrecks (Fig. 1, Table 1).

Invertebrates were counted in each frame grab (Fig. 2). For colonial species such as hydroids, tunicates, and sponges, each colony was counted as 1 individual. All invertebrate species were identified by comparison to relevant literature (Weiss 1995, Martinez 1999, Moen & Svensen 2004).

2.2. Structural and environmental factors

We analyzed shipwreck biological communities with reference to location, size, age, and primary material. Shipwreck locations were obtained from the SBNMS maritime heritage site database. Because shipwrecks in SBNMS are protected sites, the exact locations of the wrecks are not published here. Shipwreck size was determined based on side-scan sonar data in the SBNMS archives, which showed the footprint (plan area) of the shipwreck. Estimates of maximum altitude (relief) above the seafloor for each shipwreck were made using side-scan sonar data or size scales in the ROV video. In a few cases, historical records were consulted to estimate the altitude of a shipwreck for which no sonar data were available; however, this method was only considered reliable for shipwrecks that were relatively intact on the seafloor. We calculated shipwreck size as plan area × maximum altitude (Table 1).

Shipwreck age was calculated as the year sampled minus the sinking date. For shipwrecks with a range of possible sinking dates, the mid-point of the range was chosen for age calculation. Sinking dates were determined based on archaeological data including ship identity, pertinent artifacts, hull construction, and means of propulsion. Information used in this study was gleaned from the SBNMS shipwreck database as well as archived notes and reports (see Acknowledgements).

The primary material (e.g. wood, metal) for each shipwreck was determined from ROV video, archived notes, and reports. In some cases, the hull of the ship was degraded or absent, leaving behind only a pile of ballast rocks or cargo (e.g. coal). For these shipwrecks, rock or coal was considered the primary material. Shipwreck characteristics and biological data are available in the Supplement at www.int-res.com/articles/suppl/m685p019_supp.xlsx.

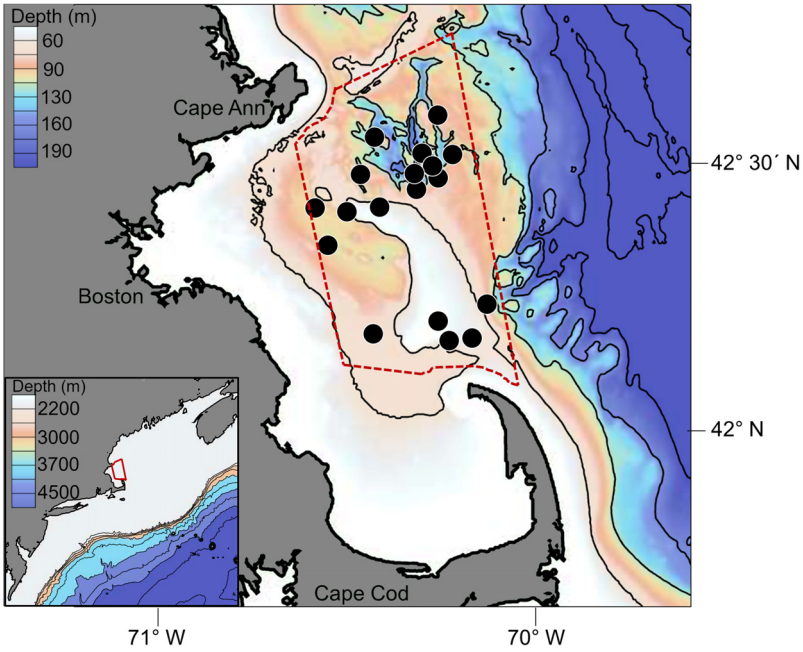

Fig. 1. Shipwreck sites included in this study. Depth contours are 50 m. Dashed red line marks the boundary of Stellwagen Bank National Marine Sanctuary (SBNMS). Inset shows SBNMS location in broader geographic context. Shipwrecks in SBNMS are protected sites, so their locations have been altered using a random perturbation within a fixed radius (Smith 2020)

Fig. 2. Example frame grab from the shipwreck 'Paul Palmer,' sampled in 2005, showing the anemone *Metridium senile* (a) and the sponges *Haliclona oculata* (b) and *Halichondria panicea* (c)

2.3. Statistical analysis

All analyses in this study were conducted on an inter-shipwreck scale. Species richness and abundance values were totaled for each shipwreck, so the unit of replication was a shipwreck. We constructed species-accumulation curves for the whole study area and for each shipwreck individually using permutations of the raw data in Primer v7. Some species-accumulation curves did not reach an asymptote, indicating that not all species had been sampled. Therefore, we used rarefaction to standardize species richness to 100 individuals for each shipwreck in Primer. Linear and non-linear regressions were used to test for significant relationships between rarefied species richness (alpha diversity) and shipwreck size and age. Regressions were conducted in Matlab R2020b.

It is possible that our survey methodology missed portions of some shipwrecks (i.e. coverage was <100%) and may have underestimated abundances of some uncommon species. Therefore, analyses of species composition (beta diversity) were conducted with and without presence–absence transformation. Analysis of abundance data allows patterns to be discerned that are driven by the common species in an assemblage, while a presence–absence transformation heavily weights the influence of rare species (Clarke & Gorley 2006). We tested for a spatial autocorrelation in species composition using a Mantel test in the 'Fathom' toolbox in Matlab (Jones 2014). Species composition on each shipwreck was used to construct a Bray-Curtis similarity matrix, and shipwreck locations (latitude, longitude, and depth) were used to construct a Euclidean distance matrix for the Mantel test. Additional multivariate statistics based on a Bray-Curtis similarity matrix (PERMANOVA, DISTLM) were conducted in Primer.

We explored differences in shipwreck communities with regard to functional traits of each species. Traits included mobility (sessile or mobile), trophic mode (suspension feeder, predator, or omnivore/detritivore), growth form (colonial/encrusting or solitary), and developmental mode (planktotrophic larva, lecithotrophic larva, or brooding). For this analysis, a matrix containing the total abundances of each species on each shipwreck was multiplied by a matrix of zeroes and ones indicating traits expressed by each species to yield a matrix of abundances of each trait on each shipwreck. We then conducted a multivariate analysis using trait abundances, similar to our analysis of species composition above.

3. RESULTS

3.1. Data verification

A species-accumulation curve for all analyzed frame grabs reached a clear asymptote, indicating that all species in the regional pool had been found (Fig. 3A). However, species-accumulation curves for some individual shipwrecks were not asymptotic (Fig. 3B). This indicates that reported species richness values for each shipwreck should be treated as minimum values. There were no significant differences in community composition among shipwrecks sampled in different years (Table 2). Therefore, we analyzed all shipwrecks together regardless of sampling year.

3.2. Patterns in alpha diversity

We tested for relationships between species richness (rarefied to 100 individuals) and shipwreck size

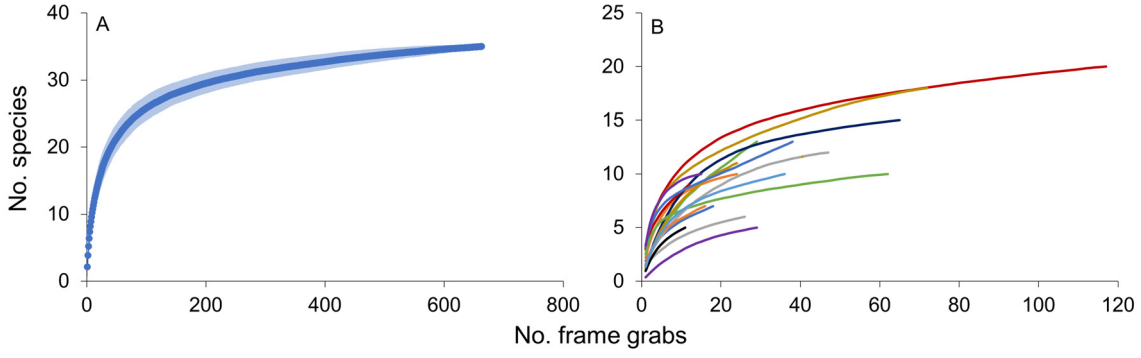

Fig. 3. Species-accumulation curves for (A) all frame grabs (shaded area indicates standard deviation) and (B) individual shipwrecks. Colors differentiate wrecks but have no specific meaning

Table 2. Statistical results for analyses in this study. P/A: presence–absence transformation applied. Significant p-values (<0.05) shown in **bold**. Some statistical tests included multiple explanatory factors, . Comp: composition; rich.: richness; rare.: rarefied; reg.: regression

Dependent variable	Independent variable	Test	Test statistic	p	R^2
Species composition	Year sampled	PERMANOVA	0.92	0.66	–
Species comp. (P/A)	Year sampled	PERMANOVA	1.44	0.13	–
Species rich. (rarefied)	Wreck size	Logarithmic reg.	10.1	**<0.001**	–0.22
Log(rare. species rich.)	Log(wreck size)	Linear regression	0.81	0.42	0.03
Species rich. (rarefied)	Wreck age	Polynomial reg.	3.89	**0.001**	3.61
Species rich. (rare.) (n = 8)	Wreck age (n = 8)	Polynomial reg.	2.77	**0.02**	–4.9
Species composition	Material	PERMANOVA	1.10	0.26	–
Species composition	Wreck location	Mantel test	0.34	**0.04**	–
Species composition	Latitude	DISTLM	1.50	0.10	0.08
	Longitude	DISTLM	1.04	0.40	0.06
	Depth	DISTLM	1.36	0.17	0.07
	Size	DISTLM	1.92	**0.005**	0.10
	Age	DISTLM	1.13	0.30	0.06
	Material	DISTLM	0.57	0.90	0.03
Species comp. (P/A)	Latitude	DISTLM	4.26	**0.001**	0.21
	Longitude	DISTLM	0.94	0.47	0.05
	Depth	DISTLM	2.51	**0.02**	0.13
	Size	DISTLM	1.55	0.18	0.08
	Age	DISTLM	2.68	**0.01**	0.14
	Material	DISTLM	0.90	0.50	0.05
Functional traits	Latitude	DISTLM	0.52	0.73	0.03
	Longitude	DISTLM	1.07	0.36	0.06
	Depth	DISTLM	0.61	0.66	0.03
	Size	DISTLM	4.15	**0.007**	0.20
	Age	DISTLM	0.45	0.82	0.02
	Material	DISTLM	1.35	0.25	0.07

and age. A logarithmic regression for species richness and shipwreck size was significant, but the negative R^2 value indicated that the logarithmic model was a poor fit for the data (Table 2, Fig. 4). A linear regression using log-transformed species richness and shipwreck size was not significant (Table 2, Fig. 4). These results did not support our hypothesis of a log-linear species–area relationship (H_1). Species richness had a significant relationship to shipwreck age, as shown by a second-order polynomial regression

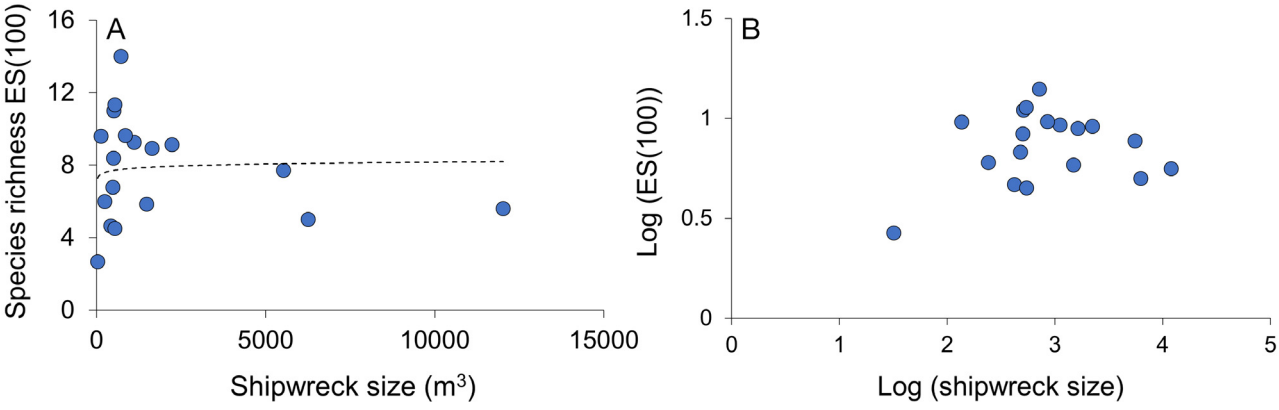

Fig. 4. Relationships between species richness (rarefied to 100 individuals; ES(100)) and shipwreck size for (A) untransformed data (best-fit logarithmic trendline shown) and (B) log-transformed species richness versus log-transformed shipwreck size

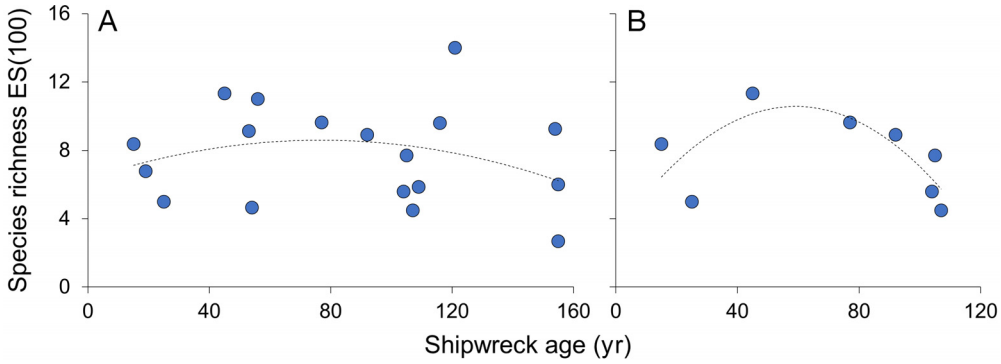

Fig. 5. Species richness (rarefied to 100 individuals) versus shipwreck age, with best-fit second-order polynomial trendlines, for (A) the full dataset and (B) shipwrecks with known sinking dates (n = 8)

(Table 2, Fig. 5). However, the R^2 value again indicated a very poor fit of the model to our data (Table 2, Fig. 5). Many of the shipwrecks in our dataset had a wide range of possible sinking dates, so we also conducted a polynomial regression using only those shipwrecks with known sinking dates (n = 8; Table 1). Similar to the full dataset, the results revealed a significant second-order polynomial relationship between rarefied species richness and shipwreck age, but the negative R^2 value indicated that the polynomial model was a poorer fit to our data than the null hypothesis of a horizontal line (Table 2, Fig. 5). Our hypothesized species–time relationship was thus not supported (H_2).

3.3. Factors driving beta diversity

A total of 32 species and 3 unidentified morphotypes of benthic invertebrates were found on SBNMS shipwrecks. The most common taxa were sponges (8 species), cnidarians (7 species), echinoderms (6 species), and tunicates (5 species). Species composition was patchy. Only 9 out of 35 taxa occurred on half or more of the shipwrecks, and 11 out of 35 occurred on only 1 shipwreck. There was a significant spatial autocorrelation for species composition on shipwrecks, indicating that shipwrecks located closer together had more similar species composition (Table 2).

DISTLM analysis revealed a significant relationship of species composition on shipwrecks with shipwreck size but not with other factors (Table 2). The best model included all 6 structural factors and explained 42% of the variation in composition (R^2 = 0.42). When a presence–absence transformation was applied, the factors of latitude, depth, and shipwreck age were significantly related to species composition (Table 2). The best model for presence–absence data included all 6 structural variables and explained 56% of the variation in the species composition (R^2 = 0.56). Material did not emerge as a strong factor in either DISTLM model, and a PERMANOVA test also

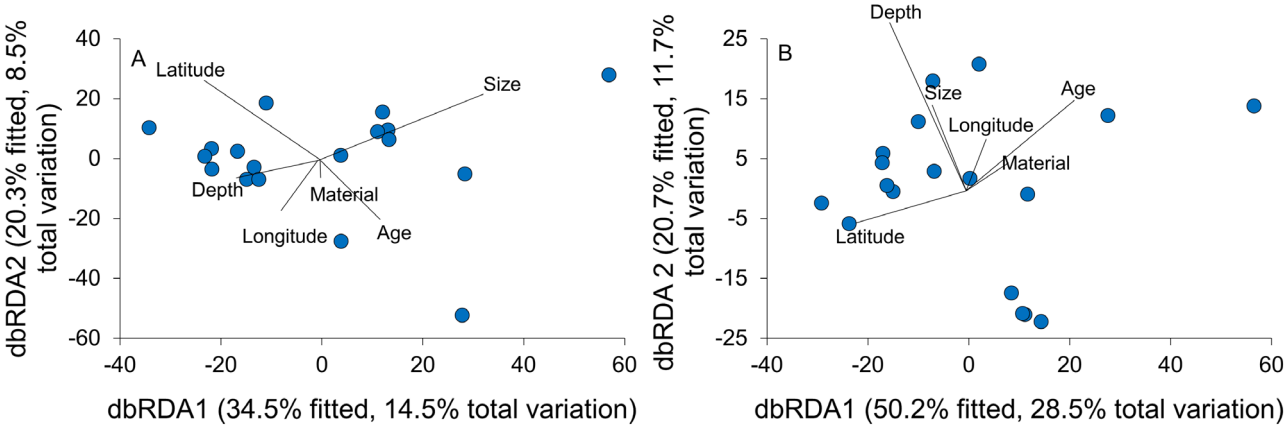

Fig. 6. Distance-based redundancy analysis (dbRDA) plots showing relationships between shipwreck species composition and structural parameters. Each point represents 1 shipwreck. (A) Untransformed species composition data; (B) presence–absence transformation applied

showed no significant differences in species composition based on shipwreck material (Table 2). Therefore, our hypothesis H_4 was not supported.

Relationships between species composition and structural factors are shown visually in dbRDA (Fig. 6). Each point represents 1 shipwreck, and the alignment of points with the axes shows their relationships with each factor. For the untransformed species composition data, points align roughly with the axis for shipwreck size (Fig. 6A). For the presence–absence transformed data, points representing most shipwrecks separate along the axes for latitude and age. There is also a cluster of points at the bottom of the plot that is separated from the other shipwrecks in a direction that is parallel to the depth axis (Fig. 6B). Species composition on these shipwrecks is most strongly influenced by depth, and in fact, this cluster represents the shallowest shipwrecks in our dataset, which are located in the southern end of SBNMS: STB-005, STB-007, 'Paul Palmer', and 'Josephine Marie' (Fig. 6B, Table 1).

Some species had distributions that were depth-stratified: the sponges *Polymastia robusta*, *P. mamillaris*, and *Axinella infundibuliformis* only occurred on shipwrecks at >90 m depth, and the cnidarian *Cerianthus borealis* was only found on shipwrecks >80 m depth. Patterns of species composition with latitude followed depth patterns, since depth and latitude were auto-correlated in our dataset (depth increases south to north in SBNMS). There were also some differences in species composition between shipwrecks with different ages. The polychaete *Myxicola infundibulum* and the scallop *Placopecten magellanicus* only occurred at shipwreck sites >100 yr old.

There was no significant relationship between shipwreck age and species traits such as mobility, trophic group, or reproductive mode. This result did not support the hypothesized difference in species traits on shipwrecks with different ages (H_3). Rather, there was a significant relationship between shipwreck size and species traits (Table 2). Larger shipwrecks had higher abundances of sessile organisms such as sponges and the anemone *Metridium senile*.

4. DISCUSSION

In this study, we investigated the environmental and structural factors influencing benthic invertebrate populations on shipwrecks in SBNMS. Our results did not fit expectations for any of our 4 hypotheses. Instead, our results revealed significant relationships of species composition (beta diversity) with shipwreck size, age, latitude, and depth that provide insights for community assembly on artificial reefs.

One significant finding of this study is the difference in species composition on shipwrecks with different sizes. These patterns were apparent in analyses using untransformed abundance data, which indicates they were driven by variable abundances of the most common species in the dataset. Sessile organisms such as anemones, sponges, and tunicates were very common on large shipwrecks and could occur at high densities (>100 m^{-2}). Large shipwrecks have high-relief structures that allow sessile organisms to live elevated above the seafloor. High densities of sessile organisms on elevated structures is a common pattern in marine environments, and it is driven by the physics of flow (Genin et al. 1986, Rogers 1994, Leichter & Witman 1997). Currents are slower in the benthic boundary layer near the seafloor, so elevated structures provide exposure to faster currents that facilitate feeding (Vogel 1996). For suspension feeders or species that rely on planktonic food (e.g. anemones that consume copepods), exposure to faster currents may allow the populations to reach high densities. The high-relief structures provided by large shipwrecks have no parallel in natural hard-bottom habitats. Most of the seafloor in SBNMS is sand or mud, and natural hard substrata include gravel or low-lying boulder reefs (Bullard et al. 2007, Tamsett et al. 2010). The same is true more broadly in the western Atlantic, although there are a few high-relief rock walls in the Gulf of Maine (Leichter & Witman 1997, Steimle & Zetlin 2000). Shipwrecks form important high-relief structures for sessile invertebrates in SBNMS.

Over time, wooden shipwrecks degrade, which reduces the elevation they provide to fauna. Shipwrecks that have lost their wooden hulls can still provide hard substrata for settlement in the form of ballast rocks or cargo, but they are unlikely to support high densities of sessile organisms. They become, functionally, like low-lying natural boulder reefs. While we did find a significant influence of shipwreck age on species composition, this was not the result of colonial, lecithotrophic species dominating older shipwrecks as we expected. Rather, the 2 species that only occurred at shipwreck sites >100 yr old were soft-bottom species (*Myxicola infundibulum*, *Placopecten magellanicus*) that we observed living in the interstitial areas between ballast rocks.

In some systems, species richness increases over time as resources accumulate, habitat heterogeneity increases, or species recruit (Hadly & Maurer 2001, Adler & Lauenroth 2003). However, habitats that

degrade over time have different dynamics. Wooden shipwrecks are closer analogs to other organic-matter falls in the ocean, such as wood falls and whale falls. These habitats are colonized by a unique assemblage of fauna and experience turnover in community composition over time (Turner 1973, Smith & Baco 2003, McClain & Barry 2014). However, while wood and whale falls ultimately disappear, wooden shipwrecks are more likely to reach an environmental equilibrium with buried or non-organic components remaining.

One potential reason why we may not have found the expected species–time relationship in our dataset is because shipwreck age is a poor predictor of colonization time. A shipwreck that lands on the seafloor, particularly a wooden shipwreck, may undergo rapid change at first as components are carried away, degrade, or become buried and then reach an environmental equilibrium (Muckelroy 1998). Time since equilibrium is likely a better indicator of colonization time than shipwreck age. In fact, for a wooden shipwreck with rock ballast, succession may not functionally begin until the hull has disappeared. We would expect the ballast to undergo succession similar to a natural boulder reef beginning from this equilibrium point. Unfortunately, our dataset was based on a single time-point measurement for each shipwreck and did not allow for estimates of time since equilibrium. The dynamics of shipwreck site formation processes, their interactions with biological colonization, and differences between types of shipwrecks are key questions for future studies.

The dynamics of wooden shipwrecks compared to metal shipwrecks makes it surprising that we found no significant influence of material on SBNMS shipwreck communities. Toxic heavy metals in ship hulls and anti-fouling materials have previously been found to impact shipwreck communities (Work et al. 2008). We also observed the effectiveness of anti-fouling materials on one shipwreck (Mystery Collier in Table 1), which did not have any organisms living on the copper-clad hull. Nevertheless, exposed wooden structures on this shipwreck were inhabited by anemones, sponges, and other sessile fauna. While localized variations may be present, our data show that on the scale of a whole shipwreck, material does not significantly impact benthic invertebrate communities in SBNMS.

A much stronger factor influencing shipwreck communities in SBNMS is the patchiness of species distributions. The level of patchiness in our data could be slightly overestimated, as shown by the species-accumulation curves. The regional species pool was well-characterized, but some curves for individual shipwrecks did not reach an asymptote. This means that more frame grabs would have revealed additional species in the regional pool on some shipwrecks and decreased the level of apparent patchiness. Nevertheless, the restriction of some species (*Polymastia robusta*, *P. mamillaris*, *Axinella infundibuliformis*, *Cerianthus borealis*) to shipwrecks >80–90 m depth is unlikely to be the result of undersampling. The Gulf of Maine (which includes SBNMS) is influenced by different water masses at shallow and deep depths and has a strong thermocline at 70–100 m (Townsend et al. 2015). Above this depth, cold, relatively fresh Scotian Shelf Water flows into the Gulf of Maine from the Nova Scotia Shelf, and below this depth, warmer, saltier, and denser slope water enters through the Northeast Channel (Townsend et al. 2015). Differences in temperature between these 2 water masses could restrict species to living at certain depths. The 2 water masses could also deliver larvae of different species to settle on habitats at their respective depths.

Some of the patchiness in shipwreck communities could be driven by recruitment patterns. Meyer et al. (2017) hypothesized that island-like shipwreck communities could be colonized by just a few individual larvae that proliferate in the new habitat in the absence of their normal predators or competitors. While this hypothesis remains untested, previous studies have found that recruitment is an important driver of community composition on artificial reefs (Perkol-Finkel & Benayahu 2007, 2009, Meyer et al. 2018). A more complete understanding of artificial reef communities in SBNMS will involve investigations of larval dispersal and recruitment dynamics.

The data used in this study were opportunistic. Video recordings were originally made for archaeological reconnaissance rather than biological analysis, so coverage was highly variable among shipwrecks. In addition, sinking date estimates based on archaeological data were imprecise and led to large potential age ranges for some shipwrecks. Close archaeology–biology collaborations and careful planning of field operations could prevent these limitations in future studies. Imagery should be collected in regular transects with as high a coverage as possible for each shipwreck. Size scales such as ROV-mounted lasers are indispensable. The limited data quality in this study restricted our analyses to an inter-shipwreck scale. Following best practices for data collection in future studies will enable more precise analyses, such as examination of intra-shipwreck patterns.

Shipwrecks in SBNMS feature diverse benthic invertebrate communities that vary over time and space. Future artificial reef management efforts could protect or enhance large elevated structures to maximize the abundance of sessile invertebrates. Our findings also demonstrate that stable structures that do not degrade over time are the most valuable invertebrate habitats, although wooden shipwrecks can provide habitat heterogeneity for >100 yr. Reef location has a strong impact on species composition of the resulting community, so the depth range, dispersal range, and thermal tolerance of desirable species should be carefully considered.

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