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Invertebrate communities on historical shipwrecks in the western Atlantic: relation to islands

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ABSTRACT: Shipwrecks can be considered island-like habitats on the seafloor. We investigated the fauna of 8 historical shipwrecks off the US east coast to assess whether species distribution patterns on the shipwrecks fit models from classical island theory. Invertebrates on the shipwrecks included both sessile (sponges, anemones, hydroids) and motile (crustaceans, echinoderms) species. Invertebrate communities were significantly different among wrecks. The size and distance between wrecks influenced the biotic communities, much like on terrestrial islands. However, while wreck size influenced species richness (alpha diversity), distance to the nearest wreck influenced community composition (beta diversity). Alpha and beta diversity on the shipwrecks were thus influenced by different abiotic factors. We found no evidence of either nested patterns or non-random co-occurrence of morphotypes, suggesting that the taxa on a given shipwreck were randomly selected from the available taxon pool. Species present on the shipwrecks generally had 1 of 2 reproductive modes: most motile or solitary sessile species had long-duration planktotrophic larvae, while most encrusting or colonial sessile species had short-duration lecithotrophic larvae and underwent asexual reproduction by budding as adults. Short-duration larvae may recruit to their natal shipwreck, allowing them to build up dense populations and dominate the wreck surfaces. A high degree of dominance was indeed observed on the wrecks, with up to 80% of the fauna being accounted for by the most common species alone. By comparing the shipwreck communities to known patterns of succession in shallow water, we hypothesize that the shipwrecks are in a stage of mid-succession.

KEY WORDS: Island biogeography · Assembly rules · Artificial reef · Succession · Benthic fauna · Continental shelf · Remotely operated vehicle · Video analysis

INTRODUCTION

There are an estimated 3 million shipwrecks worldwide, only a small fraction of which have been investigated for archaeology or biology (UNESCO 2002). A good understanding of the communities that colonize shipwrecks can inform important ecological questions, such as how habitat heterogeneity affects communities. Wooden wrecks demonstrate the impact of allochthonous organic material on the benthic fauna. If the sinking date of a wreck is known, it may be used to observe succession or estimate how quickly succession proceeds (Perkol-Finkel et al. 2005). Shipwrecks can be used as models for studies of connectivity, larval dispersal, and recruitment (Perkol-Finkel & Benayahu 2007, Amaral et al. 2010, Lira et al. 2010). Wrecks composed of heavy metals and synthetic paints also demonstrate the long-term effects of these materials on benthic communities (Walker et al. 2007, Work et al. 2008).

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Metal shipwrecks constitute islands of hard substratum on a seafloor that is mostly mud. They can provide habitat for algae (dos Santos et al. 2010), invertebrates (Pawlik et al. 2008, Lira et al. 2010), fish (Mallefet et al. 2008, Ross et al. 2016), and mobile benthic species (Kilgour & Shirley 2008). Even siboglinid tube worms, typically found in chemosynthetic habitats, have been discovered on degrading organic matter (paper, cotton, pineapple, twine) in Mediterranean and Atlantic shipwrecks (Dando et al. 1992, Hughes & Crawford 2008, Gambi et al. 2011). Shipwreck communities vary based on age, distance from natural hard-bottom habitats, and depth (Perkol-Finkel & Benayahu 2005, 2007, Perkol-Finkel et al. 2005, 2006, Church et al. 2009, Amaral et al. 2010, dos Santos et al. 2010, Lira et al. 2010). Some wrecks can have profound effects on the surrounding benthos, including the establishment of an entirely different community several meters beyond the physical structure of the wreck (Work et al. 2008).

In this study, we focused on a series of 8 shipwrecks at the edge of the continental shelf, located at ~100 m depth off the US Atlantic coast. The present analysis concerns the invertebrate fauna on the shipwrecks only; fish communities were analyzed by Ross et al. (2016).

We discuss 5 elements of classical island theory, derived from MacArthur & Wilson's (1967) equilibrium theory of island biogeography and Diamond's (1975) assembly rules. These elements are outlined by Meyer (2017), and in each case, we test the hypothesis that shipwreck fauna show the same distribution patterns as fauna on terrestrial islands (areas of land surrounded by ocean). These 5 distributional patterns include (1) a log-linear relationship between species richness and island (= shipwreck) size ($S = cA^z$, where S = richness, A = area, and c and z are constants); (2) 'incidence functions,' or the presence of different sets of species on shipwrecks of varying size; (3) isolation-by-distance, that wrecks closer together have more similar communities; (4) nested distribution patterns of the fauna, in which ever-smaller sub-sets of fauna are found on ever-smaller wrecks; and (5) non-random co-occurrence, meaning some pairs of species are found together less often (negative non-random co-occurrence) or more often (positive non-random co-occurrence) than expected by random chance.

Some of the above patterns have been applied to island-like marine substrata (Abele & Patton 1976, Schoener & Schoener 1981, Thiel & Vásquez 2000, Huntington & Lirman 2012, Meyer et al. 2016), but our dataset presents a rare opportunity to test these hypotheses without the compounding factor of island (= shipwreck) age. All of the investigated shipwrecks were underwater for approximately the same amount of time (88–91 yr at the time of sampling).

The degree of isolation of the shipwrecks (hypothesis 3 above) deserves further clarification. MacArthur & Wilson (1967) discussed both the effect of isolation from a mainland and the role of islands as 'stepping-stones,' facilitating connectivity between other islands in the surrounding area. For marine hard-bottom habitats, these concepts have been reinterpreted in the 'island model,' which states that colonists on isolated substrata are selected from a well-mixed larval pool, and the 'stepping-stone model,' which states that larvae disperse among substrata, resulting in a positive correlation between genetic and geographic distances (Vrijenhoek 1997). These 2 models have been described for marine hard substrata as diverse as coral reefs (Palumbi 2003) and hydrothermal vents (Vrijenhoek 2010). In the present analysis, we expect that shipwreck fauna produce larvae that disperse to the surrounding wrecks, so we tested the hypothesis that wrecks closer to one another on the seafloor have more similar communities (the 'stepping-stone' or 'isolation-by-distance' model; Vrijenhoek 1997).

In addition to the 5 patterns described above, we discuss the life-history traits of each of the shipwreck species and the roles they may play in succession. In classical island literature, MacArthur & Wilson (1967) and Diamond (1975) each described a shift in the life-history traits of island fauna in the course of succession, from long-distance-dispersing, fast-growing generalist species to short-distance-dispersing, slow-growing superior competitors. This shift has also been observed in succession on artificial marine hard substrata (Perkol-Finkel et al. 2005, 2006, Edwards & Stachowicz 2010). In this study, we used what is known about the life-history traits and dispersal mechanisms of the shipwreck fauna to infer 2 mechanisms of colonization on the wrecks. We also compare our data to known patterns of succession on shallower substrata at similar latitude to infer the wrecks' present stage of succession.

MATERIALS AND METHODS

Study area

The shipwrecks in this study are located near the continental shelf break, east of Chesapeake Bay (Fig. 1). They include 7 ships that were sunk in a

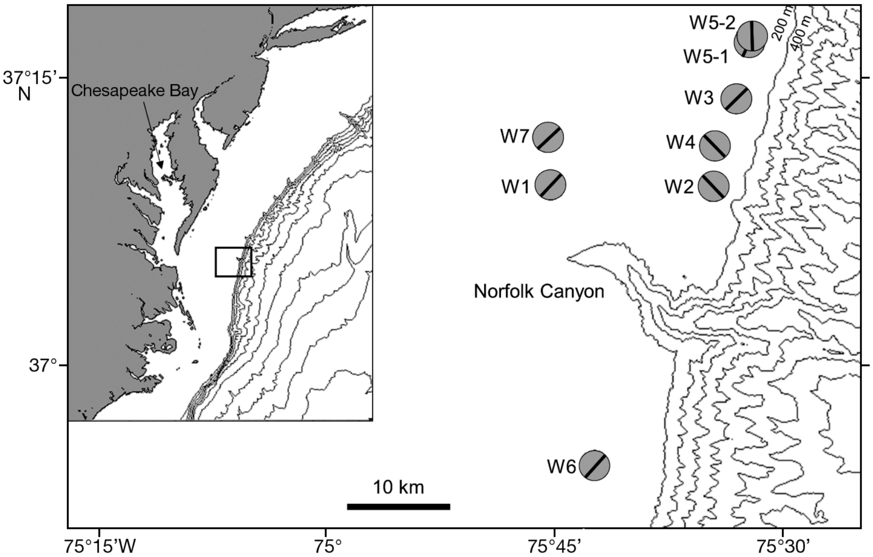

Fig 1. Shipwreck sites east of Chesapeake Bay, USA. Black lines indicate orientation of the major axis of each shipwreck

series of bombing experiments in June and July 1921 and belong to the 'Billy Mitchell fleet' (Wildenberg 2014). The eighth ship was sunk in artillery tests in 1924. The identity of each shipwreck is known, but in order to protect the historical integrity of the shipwrecks until they can be fully cataloged, the names will not be published here. Instead, the shipwrecks will be referred to by numbers, following the nomenclature of Ross et al. (2016) (Table 1).

Sample collection

In 2012, the remotely operated vehicle (ROV) 'Kraken II' (University of Connecticut), a 1000 m rated science-class vehicle, was deployed from NOAA Ship 'Nancy Foster.' A Kongsberg OE14-502 high-definition digital camera was mounted on the ROV during dives to collect video. The ROV's path of motion during the dives was driven by archaeological objectives rather than prescribed transects for analysis of benthic fauna. Thus, videos were recorded with no consistent speed or distance from the wreck, and the ROV's lasers (used for distance calibration) remained off for the majority of each dive. In order to analyze the ROV videos, frame grabs were obtained from each video whenever the surface of the shipwreck was in clear view and the invertebrate megafauna could be clearly discerned. Only frame grabs in a narrow visual range (apparent distance from the wreck) were considered eligible for analysis. The few frame grabs for which the lasers were switched on were used to calculate the average size of analyzable frame grabs of the shipwreck surface (mean ± SE = 1.45 ± 0.13 m^2, n = 29). Thirty eligible frame grabs were then randomly sub-selected from each wreck and analyzed as described below. Voucher specimens of the most common species were collected using the ROV's manipulator arm.

In order to estimate the percent cover of sessile invertebrates, 200 random points were overlain on each frame grab, and the number of points meeting each species or morphotype was counted. Mobile invertebrates were also recorded from each frame grab by simple count. To estimate habitat heterogeneity, the percentage of points belonging to the same plane was calculated, and this value was subtracted from 100. This metric is here referred to as 'surface complexity' (surface complexity = 100 − points in same plane/total number random points). Morphotypes (putative species based on morphology), were designated for those organisms of unknown identity for which no voucher specimen could

Table 1. Shipwrecks on the US Atlantic margin surveyed in September 2012. ROV: remotely operated vehicle

Shipwreck number	Date sampled (Sep 2012)	Dive ROV-2012-NF-	Latitude (N)	Longitude (W)	Shipwreck length (m)	Maximum altitude above seafloor (m)	Depth (m)
W1	22	22	37° 09.44'	74° 45.25'	45	6	90
W2	23	23	37° 09.39'	74° 34.56'	167	18	113
W3	24	24	37° 13.96'	74° 33.03'	141	7	125
W4	26	26	37° 11.51'	74° 34.46'	92	3	105
W5-1	26	27	37° 16.91'	74° 32.16'	64	3	117
W5-2	26	27	37° 17.23'	74° 32.03'	53	2	117
W6	27	29	36° 54.79'	74° 42.37'	150	14	85
W7	28	30	37° 11.93'	74° 45.43'	72	3	68

be collected. Once the fauna had been quantified, we noted the dominant taxa for each wreck, defined as those species or morphotypes with a cumulative abundance at least 1 order of magnitude greater than other rarer taxa present on the wreck.

One morphotype, called the 'brown tube complex,' consisted of proteinaceous tubes with multiple species living on them. The tubes resemble similar structures made by chaetopterid polychaetes, although no living individuals were found in the 'brown tube complex' voucher specimen collected from wreck W1. Multiple species were epibionts on the tubes, including at least 4 species of hydroids (*Lafoea dumosa* [Fleming, 1820], *Halecium* sp. Oken, 1815, *Modeeria rotunda* [Quoy & Gaimard, 1827], *Nemertesia americana* [Nutting, 1900]), 2 species of bryozoans, a caprellid amphipod, a pycnogonid, the ophiuroid *Ophiocomina* sp. Koehler, 1920, several errant polychaetes, a serpulid polychaete, and a chiton, all living on or around one another. Because each of the epibionts was too small to be seen without magnification, it was impossible to visually differentiate among the many species in ROV video. 'Brown tube complex' was thus treated as 1 morphotype for the purposes of this analysis.

Data analysis

Dominance plots and multivariate statistics were calculated using Primer v6 (Clarke & Gorley 2006). A $\log(x + 1)$-transformation was used to reduce the effect of overly dominant species for an analysis of similarity (ANOSIM) to test for differences in the biotic communities among wrecks, and a multidimensional scaling plot (MDS) to visualize these differences.

In order to determine whether a log-linear relationship existed between species richness and area (hypothesis 1), we graphed the total species richness on each wreck against the relative surface area of the wreck. It was impossible to find the absolute surface area of each wreck, given the complex nature of the wreck surfaces. Therefore, relative surface area was found by multiplying the total length of the wreck, its height (maximum altitude above the seafloor of the wreck's highest point), and its average surface complexity (surface complexity was calculated for each frame grab as described above).

We used a DISTLM procedure in the PERMANOVA+ add-on to Primer (Anderson et al. 2008) to discern the abiotic factors with the strongest influence on the biotic data. Alpha diversity (S, taxonomic richness on each wreck) was used as the dependent variable for a univariate test, and beta diversity (differences in log-transformed abundances of all species and morphotypes on each wreck) was used as the dependent variable matrix for the multivariate test. A multivariate test was also conducted using a presence–absence transformation of the biotic data to understand what factors influenced community composition on the shipwrecks. Abiotic factors tested included wreck relative surface area (hypothesis 2), surface complexity alone (a measure of habitat heterogeneity), and distance to the nearest wreck (hypothesis 3).

We tested for nested patterns of the fauna (hypothesis 4) in the program Nestedness (Ulrich 2006) using a fixed-fixed null model and the BR and N_1 indices according to the recommendations of Ulrich & Gotelli (2007). Finally, we tested for non-random co-occurrence patterns of the fauna (hypothesis 5) in the program EcoSim (Entsminger 2014) using a fixed-fixed null model and the C-score index according to the recommendations of Gotelli (2000).

RESULTS

A total of 34 invertebrate morphotypes were observed on the 8 shipwrecks. Of these morphotypes, 21 were identified at least to genus. All morphotypes with >2 individuals observed on the wrecks are depicted in Fig. 2.

Table 2 lists the invertebrate fauna present at each shipwreck and indicates the dominant taxa on each wreck. On 4 of the wrecks (W1, W5-1, W5-2, and W7), the most dominant taxon alone accounted for 60 to 80% of the fauna present on the wreck, and up to 85% of the fauna was accounted for by the 2 most dominant taxa (Fig. 3). The other 4 wrecks (W2, W3, W4, and W6) had more even communities, with only 20 to 40% of the fauna being accounted for by the most dominant taxon (Fig. 3).

ANOSIM revealed significant differences among the invertebrate communities on the 8 shipwrecks (Global $R = 0.612$, $p = 0.001$). These differences are shown graphically in an MDS plot (Fig. 4). An analysis of the sessile species also showed significant differences among wrecks ($R = 0.577$, $p = 0.001$); less extreme but still significant differences were found for the mobile species ($R = 0.275$, $p = 0.001$).

Larger shipwrecks, with greater relative surface area, had higher taxonomic richness (alpha diversity; hypothesis 1; Fig. 5). There was a logarithmic relationship between taxon richness and wreck rel-

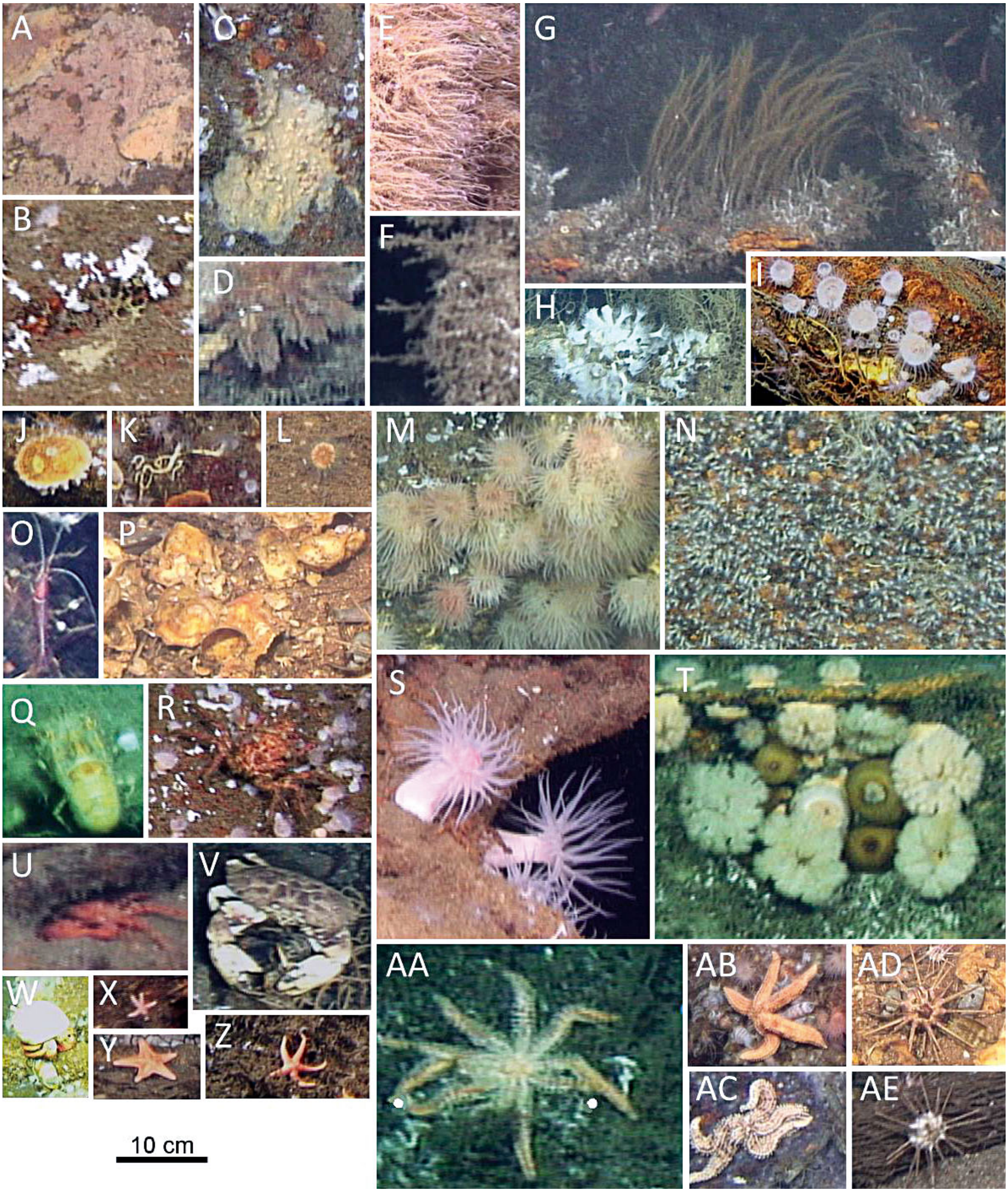

Fig. 2. Morphotypes observed in remotely operated vehicle video from 8 shipwrecks on the US Atlantic margin (surveyed in September 2012). (A) Pink encrusting sponge; (B) white didemnid ascidian; (C) yellow encrusting sponge; (D) pine hydroid; (E) cf. Corynidae; (F) brown tube complex; (G) *Plumularia setacea*; (H) white zoanthid; (I) small white anemone; (J) *Diodora tanneri*; (K) cf. *Serpula* sp.; (L) *Paracyathus pulchellus*; (M) cf. Hormathiidae; (N) *Corynactis delawarei*; (O) red shrimp; (P) *Crassostrea virginica*; (Q) *Munida* sp.; (R) *Rochinia crassa*; (S) *Halcurias pilatus*; (T) *Metridium dianthus*; (U) *Euchirograpsus americanus*; (V) *Cancer borealis*; (W) *Paguristes lymani*; (X) *Henricia* sp.; (Y) *Odontaster hispidus*; (Z) *Henricia oculata*; (AA) *Coronaster briareus*; (AB) *Sclerasterias tanneri*; (AC) *Sclerasterias* sp.; (AD) *Stylocidaris affinis*; (AE) *Stylocidaris lineata*. Size scale is relative but not precise

Table 2. Species and morphotypes present at 8 shipwrecks on the US Atlantic margin surveyed in September 2012. 'x' indicates presence; 'D' indicates a dominant species on that particular wreck; dash (–) indicates absence. See Fig. 1 for photos of species and morphotypes

Species or morphotype	Wreck							
	W1	W2	W3	W4	W5-1	W5-2	W6	W7
White didemnid ascidian	x	x	x	x	x	x	x	x
Yellow encrusting sponge	x	x	x	D	x	x	D	D
Pink encrusting sponge	–	–	–	–	–	–	x	–
Metridium dianthus	D	–	–	–	–	–	x	–
cf. Hormathiidae	x	D	x	x	x	x	x	–
Halcurias pilatus	–	–	x	–	x	x	–	–
Small white anemone	–	x	D	–	D	D	x	–
Giant purple anemone	–	–	–	x	–	–	–	–
White zoanthid	x	D	x	x	x	x	D	x
Corynactis delawarei	–	D	–	–	–	–	x	–
Brown tube complex	D	x	–	D	x	–	x	D
Plumularia setacea	x	–	–	x	–	–	x	x
cf. Corynidae	–	D	x	–	x	x	x	–
Pine hydroid	–	–	x	x	–	x	–	–
Paracyathus pulchellus	x	x	x	x	–	–	x	–
Crassostrea virginica	–	x	x	–	–	–	–	–
Diodora tanneri	–	x	x	x	x	–	–	–
Red shrimp	–	–	–	–	–	D	–	–
Rochinia crassa	–	x	x	x	D	x	x	–
Euchirograpsus americanus	–	x	–	x	–	–	–	–
Cancer borealis	–	–	–	x	–	–	–	–
Paguristes lymani	–	x	–	–	x	x	–	–
Munida sp.	–	x	–	x	–	–	–	–
cf. *Serpula*	–	x	x	x	x	x	x	–
Henricia oculata	D	–	–	–	–	–	D	D
Henricia sp.	–	–	–	x	–	–	–	–
Sclerasterias tanneri	–	D	D	x	x	D	x	–
Sclerasterias sp.	–	–	–	x	–	–	x	–
Coronaster briareus	x	–	–	x	x	–	–	–
Odontaster hispidus	–	x	x	x	x	x	–	–
Ophiocomina sp.	–	–	x	x	–	–	–	–
Stylocidaris lineata	–	x	–	D	–	x	–	–
Stylocidaris affinis	–	x	x	D	–	x	–	–
Coelopleurus floridanis	–	x	–	–	–	–	–	–

ative surface area for the sessile fauna (R^2 = 0.54) and for all taxa together (R^2 = 0.25); mobile fauna showed a general increase in taxon richness with relative surface area (Fig. 5). A DISTLM procedure revealed that species richness on the wrecks was not significantly related to distance to the nearest wreck (R^2 = 0.13, p = 0.36) or surface complexity (R^2 = 0.01, p = 0.84). Relative surface area had the strongest relationship to species richness, although its influence was still non-significant in the DISTLM test (hypothesis 1; R^2 = 0.41, p = 0.07). A distance-based redundancy analysis (dbRDA) plot shows points belonging to the different wrecks widely spaced with respect to the *x*-axis and roughly parallel to the axis of relative surface area, showing this factor's influence on the species richness on each wreck (Fig. 6A).

Variation in the biotic community (abundances on each wreck, beta diversity) was best explained by distance to the nearest wreck (hypothesis 3; DISTLM, R^2 = 0.17, $p < 0.001$). Relative surface area and surface complexity each explained much lower proportions of variation in the species abundance data (R^2 = 0.08, R^2 = 0.07, respectively; $p < 0.001$). When a presence–absence transformation of the species abundance data was used, DISTLM revealed that the community composition of each wreck

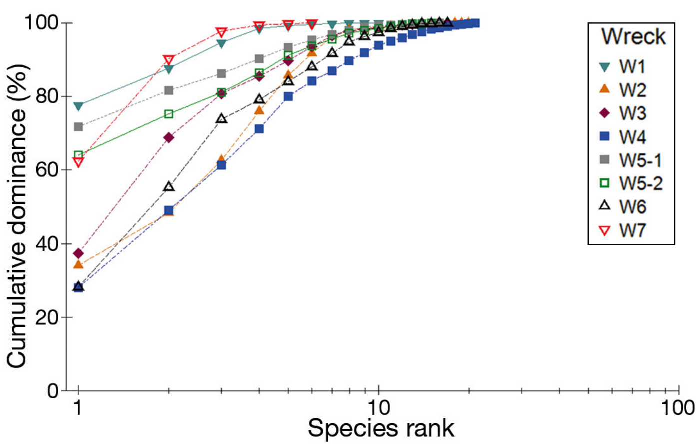

Fig. 3. Dominance plot showing cumulative percent community composition of fauna observed at 8 shipwrecks on the US Atlantic margin

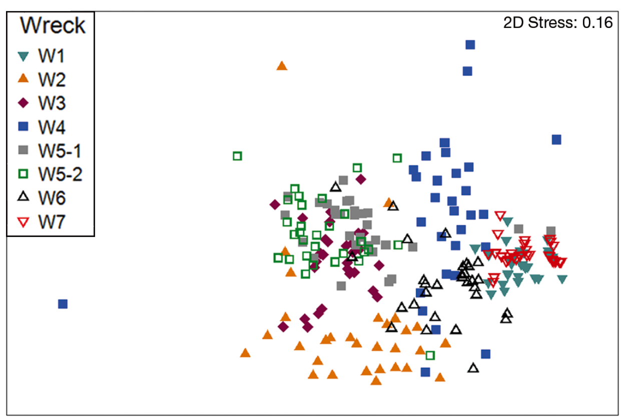

Fig. 4. Non-metric multi-dimensional scaling (nMDS) of the invertebrate communities observed at 8 shipwrecks on the US Atlantic margin. Each point represents 1 frame grab obtained from remotely operated vehicle video

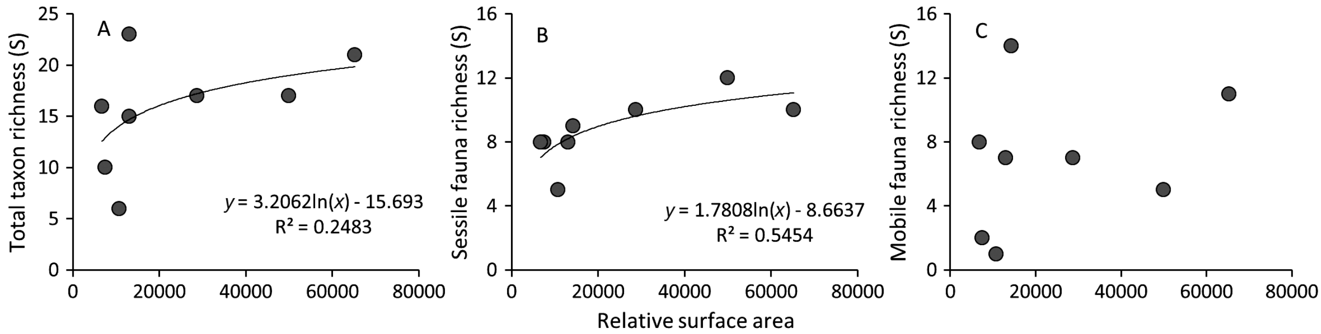

Fig. 5. Logarithmic relationships between richness of (A) all fauna, (B) sessile fauna, and (C) mobile fauna and relative surface area (height × length × surface complexity) of 8 shipwrecks on the US Atlantic margin

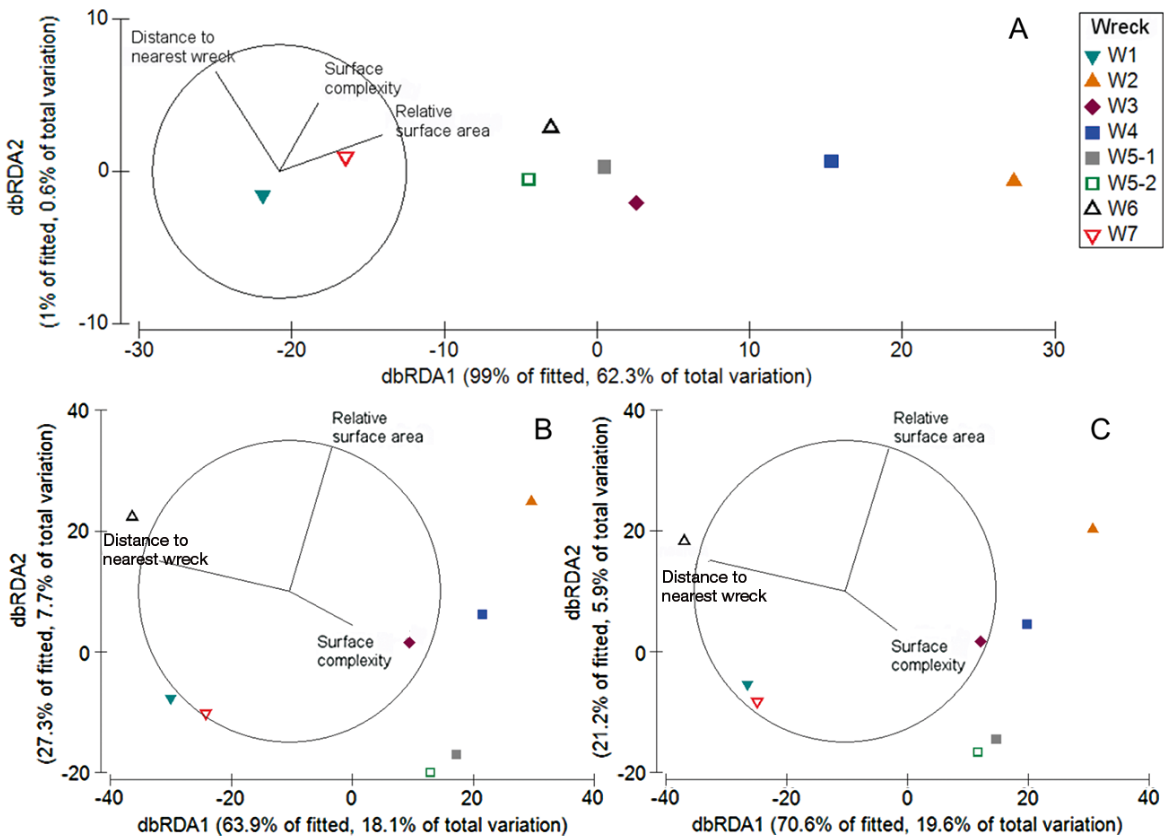

Fig. 6. Distance-based redundancy analysis plots showing how abiotic factors influence invertebrate communities on 8 shipwrecks on the US Atlantic margin. Biotic response variables include (A) species richness on each wreck, (B) log-transformed abundances of each species on each wreck, and (C) presence or absence of each species on each wreck

was again best explained by distance to the nearest wreck (R^2 = 0.17, p < 0.001). Relative surface area and surface complexity explained much less variation in the community composition (R^2 = 0.07, 0.05, respectively; p < 0.001). dbRDA plots for log- and presence–absence-transformed biotic data were nearly identical and show the influence of each of the abiotic factors on beta diversity on the wrecks (Fig. 6B,C).

No evidence of nested faunal distribution patterns was found for the shipwreck fauna (hypothesis 4); the BR and N_1 indices (30 and 46, respectively) fell within the 95% confidence interval ranges generated by the null model (27–33 and 40–58, respectively). In addition, the data showed no evidence of non-random co-occurrence patterns (hypothesis 5, p = 0.07), indicating that taxa were randomly distributed among the shipwrecks.

DISCUSSION

Species–area relationship

Higher taxonomic richness was found on larger wrecks, as predicted by MacArthur & Wilson (1967) (hypothesis 1). The function $S = cA^z$ yields a linear relationship when both axes are log-transformed but a logarithmic relationship between taxonomic richness and island area when left untransformed. This may reflect the finite nature of the species pool or a maximum carrying capacity for each wreck. In fact, each of the 8 investigated shipwrecks was inhabited by sub-sets of the same 34 species or morphotypes.

On terrestrial islands, the species–area relationship has been explained by a variety of proposed factors. These include habitat diversity, primary productivity, resistance to disturbance, equilibrium achieved through a balance of immigration and extinction, clumped distributions of species, and successional development (MacArthur & Wilson 1967, Connor & McCoy 1979, Hill et al. 1994, Gotelli & Graves 1996). However, for island-like substrata in deep water, these explanations are not satisfactory (Meyer 2017). No primary producers were observed on the shipwrecks in this study, and differences in successional development can be excluded because all wrecks are approximately the same age. Habitat diversity certainly varies for large marine island-like habitats such as seamounts, but less so for smaller island-like marine hard substrata that have been studied, such as coral heads (Abele & Patton 1976, Huntington & Lirman 2012), kelp holdfasts (Thiel & Vásquez 2000), artificial substrata (Schoener & Schoener 1981), and dropstones (stones released by melting icebergs; Meyer et al. 2016). In the case of these shipwrecks, habitat heterogeneity (quantified as surface complexity) was not significantly related to the total taxonomic richness on each wreck. The higher taxonomic richness on larger shipwrecks can be explained by the 'passive sampling hypothesis' (Connor & McCoy 1979), which states that larger substrata are merely larger targets for larval dispersal (Huntington & Lirman 2012, Meyer et al. 2016). Larger substrata have higher immigration rates and 'fill up' more slowly, allowing more species to accumulate over time (Schoener & Schoener 1981).

Beta diversity, or variation in the biotic communities among wrecks, was most strongly influenced by distance between the wrecks, not wreck size. This result does not support 'incidence functions,' or the presence of different sets of organisms on different-size wrecks (hypothesis 2). 'Incidence functions' have also not been found for other island-like marine hard substrata that have been studied (Abele & Patton 1976, Schoener & Schoener 1981, Meyer et al. 2016) and may not be important for island-like habitats in the marine environment.

Our finding that the biotic community composition was most strongly related to distance between shipwrecks leads to another interesting conclusion. Variation in the biotic community among wrecks is defined as beta diversity. By contrast, alpha diversity, or the species richness on each wreck, was most strongly influenced by wreck size (relative surface area). Thus, alpha and beta diversity on the shipwrecks appear to be influenced by different factors: the size of a wreck influences the number of species that can inhabit it, while the proximity of a wreck to others influences which species inhabit it. Shipwrecks located closer together could seed one another with larvae, causing them to have increasingly similar communities. Our data thus support the 'stepping-stone' / 'isolation-by-distance' model (hypothesis 3) for shipwreck communities (but see below).

Faunal distribution patterns among wrecks

Our data showed no evidence of either nested faunal patterns or non-random co-occurrence of taxa (hypotheses 4 & 5). In other words, the set of taxa present on a given wreck did not appear to be selected from the available taxon pool according to any 'assembly rule' (used here in the general sense following Belyea & Lancaster 1999). Rather, the taxa inhabiting a particular wreck seemed to be selected randomly from the available taxon pool. This result is in line with the 'island model' for larval dispersal among isolated marine habitats. It must therefore be considered that the 'island' and 'stepping-stone' / 'isolation-by-distance' models are not mutually exclusive — larvae may settle randomly on shipwrecks initially, but then subsequent dispersal among close wrecks can cause their communities to become increasingly similar. Succession, if it is deterministic, may also cause wreck communities to become more similar over time. The 'island' and 'stepping-stone' models are not actually the best way to conceptualize colonization of isolated marine habitats; a better understanding of larval dispersal and recruitment among these island-like habitats will be brought about by considering the life-history and dispersal capabilities of each individual species (Shank & Halanych 2007, Meyer 2017).

For island-like dropstones, Meyer et al. (2016) concluded that taxa were randomly selected from the available pool, similar to the present shipwrecks. However, they found evidence of non-random co-occurrence among dropstones, whereas we found only random co-occurrence on shipwrecks. It should be noted that individual dropstones were inhabited by a smaller fraction of the available taxon pool than the present shipwrecks, i.e. 26 of 56, or 46% of the available morphotypes (Meyer et al. 2016), whereas up to 67% of the available 34 taxa were found on a single shipwreck. Thus, the investigated shipwrecks may have only random co-occurrence because they are large enough to be inhabited by most of the available taxa. Non-random co-occurrence patterns may be less common on large, taxon-rich substrata.

Life-history traits and succession

Taxa observed on the present shipwrecks generally had 2 modes of larval dispersal: the motile fauna and solitary sessile species generally had long-duration (pelagic larval duration: months to >1 yr) planktotrophic larvae, while the encrusting or clonal fauna generally had short-duration (pelagic larval duration: days to weeks) lecithotrophic larvae but were also capable of asexual reproduction as adults (Table 3 and references therein). For example, *Stylocidaris lineata* Mortensen, 1910 has planktotrophic larvae with a pelagic duration of >3 mo (Young et al. 1998, 2012), while *Metridium dianthus* has short-duration planula larvae and also reproduces by budding or fragmentation when well-fed as an adult (Bucklin & Hedgecock 1982, Bucklin 1987).

Of the taxa observed on the wrecks, those with lecithotrophic larvae and asexual reproduction by budding as adults tend to be dominant species on the wrecks (Table 2). 'Yellow encrusting sponge' was dominant on W4, W6, and W7; *M. dianthus* dominated W1. 'Small white anemone' dominated W3, W5-1, and W5-2, while 'cf. Hormathiidae' dominated W2. Short larval life and restricted dispersal range make it less likely that a species with lecithotrophic larvae would reach an isolated shipwreck. However, successfully recruiting individuals of a lecithotrophic species could generate a dense population on the wreck through philopatry. Eight of the 13 suspected or known taxa with lecithotrophic larvae and asexual reproduction as adults were dominant on at least 1 wreck.

On the other hand, a planktotrophic larval stage would allow for colonization of shipwrecks by long-range dispersal from other hard-substratum habitats and larval dispersal among the shipwrecks. Solitary organisms would require many recruitment events and/or migration of adults from the surrounding area to generate a large population on a wreck. Only 3 of the 19 solitary or motile species (with planktotrophic larvae) were dominant on any wreck: *S. lineata*, *Rochinia crassa* (Milne-Edwards, 1879), and *Henricia oculata* (Pennant, 1777) (Tables 2 & 3).

Given the tendency for encrusting fauna with lecithotrophic larvae to dominate the shipwrecks, we hypothesize that the wrecks were each initially colonized by a small number of individuals that built up dense populations through philopatry and asexual budding as adults. In fact, 4 of the wrecks showed a high degree of dominance, with 60 to 80% of the fauna belonging to the most common taxon alone. These 4 wrecks are the smallest in our study, which have the least surface area and can therefore be most easily covered by asexually-reproducing encrusting species. The remaining 4 wrecks, the largest ships, also had 20 to 40% of the fauna accounted for by the most common species, but this lesser degree of dominance may be merely a result of the greater surface area on these wrecks and the finite growth rates of encrusting organisms.

Only 1 species found on the shipwrecks, *H. oculata*, is likely to brood its young to a crawl-away stage. Two congeners of *Henricia*, *H. sanguinolenta* and *H. pumila*, are known to brood their young (Chia 1970, Eernisse et al. 2010).

MacArthur & Wilson (1967) and Diamond (1975) both discussed a shift from long-distance-dispersing, fast-growing generalist species (such as the planktotrophic larval species above) to slow-growing superior competitors with restricted dispersal (such as the lecithotrophic larval species above) in the course of succession on islands. To explore the idea of succession, the invertebrate community composition on the shipwrecks would need to be compared to that of a natural (older) hard-bottom habitat with similar depth and similarly high relief. Unfortunately, the area surrounding the shipwrecks features mostly sand or gravel habitats, with some low-relief boulders (Steimle & Zetlin 2000, S. D. Brooke unpubl. data). A direct comparison is therefore impossible.

Nevertheless, it is evident from other studies that shipwreck communities undergo a shift in life history characteristics of the fauna with time. Shallow (<30 m) shipwrecks in the Red Sea, California, and Florida were each characterized by opportunistic species with far-dispersing larvae when young (<20 yr underwater), but older artificial reefs (>100 yr) in each location were characterized by long-lived species with restricted dispersal and spe-

Table 3. Reproductive strategies of fauna observed at 8 shipwrecks on the US Atlantic margin surveyed in September 2012. PLD: pelagic larval duration; see Fig. 1 for photos of species and morphotypes

Species or morphotype	Reproductive strategy	Source
White didemnid ascidian	Suspect lecithotrophic larva, asexual reproduction by budding as adult	
Yellow encrusting sponge	Suspect lecithotrophic larva, asexual reproduction by budding as adult	
Pink encrusting sponge	Suspect lecithotrophic larva, asexual reproduction by budding as adult	
Metridium dianthus	Planula larva, asexual reproduction by budding as adult	Bucklin (1987), Bucklin & Hedgecock (1982)
cf. Hormathiidae	Larva unknown, suspect asexual reproduction by budding as adult	
Halcurias pilatus	Unknown	
Small white anemone	Larva unknown, suspect asexual reproduction by budding as adult	
Giant purple anemone	Unknown	
White zoanthid	Suspect lecithotrophic larva, asexual reproduction by budding as adult	
Corynactis delawarei	Congener *C. californica* has large planula larva, asexual reproduction by budding as adult	Holts & Beauchamp (1993), Chadwick & Adams (1991)
Brown tube complex	Not applicable — species complex	
Plumularia setacea	Lecithotrophic planula, asexual reproduction by budding as adult	Carlton (2007)
cf. Corynidae	Suspect medusa stage, asexual reproduction by budding as adult	
Pine hydroid	Suspect medusa stage, asexual reproduction by budding as adult	
Paracyathus pulchellus	Congener *P. stearnsii* has large feeding planula, PLD: 4 wk	Fadlallah & Pearse (1982)
Crassostrea virginica	Broadcast spawner, high fecundity	Buroker (1983)
Diodora tanneri	*Diodora* spp. can broadcast spawn or lay eggs on substrata	Carlton (2007)
Red shrimp	Suspect planktotrophic larva	
Rochinia crassa	Congener *R. vesicularis* has planktotrophic larva	Pohle & Marques (2003)
Euchirograpsus americanus	Planktotrophic larva	Fransozo et al. (1998)
Cancer borealis	Planktotrophic larva, PLD: 4 mo	Hines (1991)
Paguristes lymani	Planktotrophic larva	Fransozo et al. (1998)
Munida sp.	Planktotrophic larva	Wenner (1982)
cf. *Serpula* sp.	*S. vermicularis* has feeding trochophore, nectochaete larva, PLD: 41–50 d	Young & Chia (1982)
Henricia oculata	Congeners *H. sanguinolenta* and *H. pumila* brood young to crawl-away juvenile stage	Chia (1970), Eernisse et al. (2010)
Henricia sp.	Congeners *H. sanguinolenta* and *H. pumila* brood young to crawl-away juvenile stage	Chia (1970), Eernisse et al. (2010)
Sclerasterias tanneri	Bipinnaria, PLD > 2 yr, juveniles capable of fission	Young et al. (2012), Fisher (1925)
Sclerasterias sp.	Congener *S. tanneri* has bipinnaria, PLD > 2 yr, juveniles capable of fission	Young et al. (2012), Fisher (1925)
Coronaster briareus	Ecologically similar species in same family, *Labidiaster annulata*, has bipinnaria, brachiolaria	Janosik et al. (2008)
Odontaster hispidus	Congener *O. validus* has planktotrophic, demersal, bipinnaria larva, PLD: 7–9 mo	Pearse (1965), Chiantore et al. (2002)
Ophiocomina sp.	Congener *O. nigra* has ophiopluteus larva, PLD: ~2 mo	Lönning (1976)
Stylocidaris lineata	Echinopluteus larva, planktotrophic, PLD: 3.5 mo	Young et al. (1998, 2012)
Stylocidaris affinis	Congener *S. lineata* has feeding echinopluteus	Young et al. (1998, 2012)
Coelopleurus floridanis	Small eggs, planktotrophic larva	George et al. (1997)

cies that were superior competitors (Carter et al. 1985, Perkol-Finkel & Benayahu 2005, Perkol-Finkel et al. 2005, 2006, Pawlik et al. 2008). Similarly, a 112 yr old shipwreck at 23 m off the coast of Brazil was covered in sponges and corals, resembling a natural reef (Lira et al. 2010).

Our data constitute a single time-point, so we are not able to observe the process of succession on the shipwrecks. However, we can compare our data to studies of succession at shallower depths in the same region to infer the stage of succession. Shallow hard substrata at temperate latitudes undergo succession in 3 stages: early colonizers such as acorn barnacles and serpulid polychaetes are followed by intermediate colonizers (ascidians, bryozoans, hydroids) and climax species that may outcompete or simply outlive earlier colonists (Osman 1977, Dean & Hurd 1980, Chalmer 1982). The order of succession can also depend on seasonal recruitment (Pacheco et al. 2011).

We speculate based on the fauna present that the shipwrecks are in the second successional stage described above, because they are dominated by a variety of encrusting species and morphotypes — ascidians, sponges, and hydroids. *Crassostrea virginica* and a serpulid polychaete were present on 2 and 6 wrecks, respectively, but were never dominant; these fauna may be the last remnants of the early-successional (typically calcareous) fauna. Three soft coral colonies were also observed on W2, in frame grabs not randomly sub-selected for analysis; this slow-growing taxon could be the first of the late-successional colonists.

It is possible that the present shipwrecks' isolated location makes it less likely that short-duration larvae will reach the wrecks. Short-duration larvae are typical of late-successional species, so their absence may cause succession to proceed slowly (Meyer 2017). Studies on deep-water isolated hard substrata are typically limited to single time-point observations (Church et al. 2009, Taylor et al. 2014), but this study can serve as an effective baseline for characterizing succession in the Billy Mitchell shipwreck communities in the future.

This study had some logistical limitations, all stemming from the fact that no intentional transects along the shipwrecks were recorded for the biotic analysis. Nevertheless, our results show important differences in the biotic communities among the wrecks and provide insights for the ecology of island-like habitats on the seafloor.

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