

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

3

4 Running head: Shipwrecks as islands

5

6 Kirstin S. Meyer^{1+*}, Sandra D. Brooke², Andrew K. Sweetman³, Maya Wolf¹, and Craig M.
7 Young¹

8

9 ¹Oregon Institute of Marine Biology, Charleston, OR 97420, USA

10 ²Florida State University Coastal and Marine Laboratory, St. Teresa, FL 32358, USA

11 ³The Lyell Centre, Heriot Watt University, EH14 4AP, Edinburgh, UK

12 ⁺Current address: Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA

13 ^{*}Corresponding author, e-mail: kimeyer@alumni.nmu.edu

14

15 **ABSTRACT**

16 Shipwrecks can be considered island-like habitats on the seafloor. We investigated the
17 fauna of eight historical shipwrecks off the east coast of the U.S. to assess whether species
18 distribution patterns on the shipwrecks fit models from classical island theory. Invertebrates on
19 the shipwrecks included both sessile (sponges, anemones, hydroids) and motile (crustaceans,
20 echinoderms) species. Invertebrate communities were significantly different among wrecks. The
21 size and distance between wrecks influenced the biotic communities, much like on terrestrial
22 islands. However, while wreck size influenced species richness (alpha diversity), distance to the

23 nearest wreck influenced community composition (beta diversity). Alpha and beta diversity on
24 the shipwrecks were thus influenced by different abiotic factors. We found no evidence of either
25 nested patterns or non-random co-occurrence of morphotypes, suggesting that the taxa on a given
26 shipwreck were randomly selected from the available taxon pool. Species present on the
27 shipwrecks generally had one of two reproductive modes: most motile or solitary sessile species
28 had long-duration planktotrophic larvae, while most encrusting or colonial sessile species had
29 short-duration lecithotrophic larvae and underwent asexual reproduction by budding as adults.
30 Short-duration larvae may recruit to their natal shipwreck, allowing them to build up dense
31 populations and dominate the wreck surfaces. A high degree of dominance was indeed observed
32 on the wrecks, with up to 80% of the fauna being accounted for by the most common species
33 alone. By comparing the shipwreck communities to known patterns of succession in shallow
34 water, we hypothesize that the shipwrecks are in a stage of mid-succession.

35

36 **KEYWORDS**

37 Island biogeography, assembly rules, artificial reef, succession, benthic fauna, continental shelf,
38 ROV, video analysis

39

40 **INTRODUCTION**

41 There are an estimated three million shipwrecks worldwide, only a small fraction of
42 which have been investigated for archaeology or biology (UNESCO). A good understanding of
43 the communities that colonize shipwrecks can inform important ecological questions, such as
44 how habitat heterogeneity affects communities. Wooden wrecks demonstrate the impact of
45 allochthonous organic material on the benthic fauna. If the sinking date of a wreck is known, it

46 may be used to observe succession or estimate how quickly succession proceeds (Perkol-Finkel
47 et al. 2005). Shipwrecks can be used as models for studies of connectivity, larval dispersal, and
48 recruitment (Perkol-Finkel & Benayahu 2007, Amaral et al. 2010, Lira et al. 2010). Wrecks
49 composed of heavy metals and synthetic paints also demonstrate the long-term effects of these
50 materials on benthic communities (Walker et al. 2007, Work et al. 2008).

51 Metal shipwrecks constitute islands of hard substratum on a seafloor that is mostly mud.
52 They can provide habitat for algae (Santos et al. 2010), invertebrates (Pawlik et al. 2008, Lira et
53 al. 2010), fish (Mallefet et al. 2008, Ross et al. 2016), and mobile benthic species (Kilgour &
54 Shirley 2008). Even siboglinid tube worms, typically found in chemosynthetic habitats, have
55 been discovered on degrading organic matter (paper, cotton, pineapple, twine) in Mediterranean
56 and Atlantic shipwrecks (Dando et al. 1992, Hughes & Crawford 2008, Gambi et al. 2011).
57 Shipwreck communities vary based on age, distance from natural hard-bottom habitats, and
58 depth (Perkol-Finkel and Benayahu 2005, 2007; Perkol-Finkel et al. 2005, 2006; Church et al.
59 2009, Amaral et al. 2010, Lira et al. 2010, Santos et al. 2010). Some wrecks can have profound
60 effects on the surrounding benthos, including the establishment of an entirely different
61 community several meters beyond the physical structure of the wreck (Work et al. 2008).

62 In this study, we focus on a series of eight shipwrecks at the edge of the continental shelf,
63 located at ~100 m depth off the U.S.A. Atlantic coast. The present analysis concerns the
64 invertebrate fauna on the shipwrecks only; fish communities were analyzed by Ross et al. (2016).

65 We discuss five elements of classical island theory, derived from MacArthur & Wilson's
66 (1967) equilibrium theory of island biogeography and Diamond's (1975) assembly rules. These
67 elements are outlined by Meyer (2016), and in each case, we test the hypothesis that shipwreck
68 fauna show the same distribution patterns as fauna on terrestrial islands (areas of land surrounded

69 by ocean). These five distributional patterns include: (1) a log-linear relationship between
70 species richness and island (=shipwreck) size; (2) “incidence functions,” or the presence of
71 different sets of species on shipwrecks of varying size; (3) isolation-by-distance, that wrecks
72 closer together have more similar communities; (4) nested distribution patterns of the fauna, in
73 which ever-smaller sub-sets of fauna are found on ever-smaller wrecks; and (5) non-random co-
74 occurrence, meaning some pairs of species are found together less often (negative non-random
75 co-occurrence) or more often (positive non-random co-occurrence) than expected by random
76 chance.

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

82 The degree of isolation of the shipwrecks (hypothesis 3, above) deserves further
83 clarification. MacArthur & Wilson (1967) discussed both the effect of isolation from a mainland
84 and the role of islands as “stepping-stones,” facilitating connectivity between other islands in the
85 surrounding area. For marine hard-bottom habitats, these concepts have been reinterpreted in the
86 “island model,” which states that colonists on isolated substrata are selected from a well-mixed
87 larval pool, and the “stepping-stone model,” which states that larvae disperse among substrata,
88 resulting in a positive correlation between genetic and geographic distances (Vrijenhoek 1997).
89 These two models have been described for marine hard substrata as diverse as coral reefs
90 (Palumbi 2003) and hydrothermal vents (Vrijenhoek 2010). In the present analysis, we expect
91 that shipwreck fauna produce larvae that disperse to the surrounding wrecks, so we test the

92 hypothesis that wrecks closer to one another on the seafloor have more similar communities (the
93 “stepping-stone” or “isolation-by-distance” model (Vrijenhoek 1997)).

94 In addition to the five patterns described above, we discuss the life-history traits of each
95 of the shipwreck species and the roles they may play in succession. In classical island literature,
96 MacArthur & Wilson (1967) and Diamond (1975) each described a shift in the life-history traits
97 of island fauna in the course of succession, from long-distance-dispersing, fast-growing
98 generalist species to short-distance-dispersing, slow-growing superior competitors. This shift has
99 also been observed in succession on artificial marine hard substrata (Perkol-Finkel et al. 2005,
100 2006; Edwards & Stachowicz 2010). In this study, we use what is known about the life-history
101 traits and dispersal mechanisms of the shipwreck fauna to infer two mechanisms of colonization
102 on the wrecks. We also compare our data to known patterns of succession on shallower substrata
103 at similar latitude to infer the wrecks’ present stage of succession.

104

105 **METHODS**

106 **Study area**

107 The shipwrecks in this study are located near the continental shelf break, east of
108 Chesapeake Bay (Fig. 1). They include seven that were sunk in a series of bombing experiments
109 in June-July 1921 and belong to the “Billy Mitchell fleet” (Wildenberg 2014). The eighth was
110 sunk in artillery tests in 1924. The identity of each shipwreck is known, but in order to protect
111 the historical integrity of the shipwrecks until they can be fully cataloged, the names will not be
112 published here. Instead, the shipwrecks will be referred to by numbers, following the
113 nomenclature of Ross et al. (2016) (Table 1).

114

115 **Sample collection**

116 In 2012, the remotely operated vehicle (ROV) *Kraken II* (Univ. Connecticut), a 1000 m-
117 rated science-class vehicle, was deployed from NOAA Ship *Nancy Foster*. A Kongsberg OE14-
118 502 high-definition digital camera was mounted on the ROV during dives to collect video. The
119 ROV's path of motion during the dives was driven by archaeological objectives rather than
120 prescribed transects for analysis of benthic fauna. Thus, videos were recorded with no consistent
121 speed or distance from the wreck, and the ROV's lasers (used for distance calibration) remained
122 off for the majority of each dive. In order to analyze the ROV videos, frame grabs were obtained
123 from each video whenever the surface of the shipwreck was in clear view and the invertebrate
124 megafauna could be clearly discerned. Only frame grabs in a narrow visual range (apparent
125 distance from the wreck) were considered eligible for analysis. The few frame grabs for which
126 the lasers were switched on were used to calculate the average size of analyzable frame grabs of
127 the shipwreck surface (mean = 1.45, SE = 0.13 m², n = 29). Thirty eligible frame grabs were then
128 randomly sub-selected from each wreck and analyzed as described below. Voucher specimens of
129 the most common species were collected using the ROV's manipulator arm.

130 In order to estimate the percent cover of sessile invertebrates, two hundred random points
131 were overlain on each frame grab, and the number of points meeting each species or morphotype
132 was counted. Mobile invertebrates were also recorded from each frame grab by simple count. To
133 estimate habitat heterogeneity, the percentage of points belonging to the same plane was
134 calculated, and this value was subtracted from 100. This metric is here referred to as "surface
135 complexity" (surface complexity = 100 – points in same plane/total number random points).
136 Morphotypes (putative species based on morphology), were designated for those organisms of
137 unknown identity for which no voucher specimen could be collected. Once the fauna had been

138 quantified, we noted the dominant taxa for each wreck, defined as those species or morphotypes
139 with a cumulative abundance at least one order of magnitude greater than other rarer taxa present
140 on the wreck.

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

152

153 **Data analysis**

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

158 In order to determine whether there was a log-linear relationship between species
159 richness and area (hypothesis 1), we graphed the total species richness on each wreck against the
160 relative surface area of the wreck. It was impossible to find the absolute surface area of each

161 wreck, given the complex nature of the wreck surfaces. Therefore, relative surface area was
162 found by multiplying the total length of the wreck, its height (maximum altitude above the
163 seafloor of the wreck's highest point), and its average surface complexity (surface complexity
164 was calculated for each frame grab as described above).

165 We used a DISTLM procedure in the PERMANOVA+ add-on to Primer (Anderson et al.
166 2008) to discern the abiotic factors with the strongest influence on the biotic data. Alpha
167 diversity (S, taxonomic richness on each wreck) was used as the dependent variable for a
168 univariate test, and beta diversity (differences in log-transformed abundances of all species and
169 morphotypes on each wreck) was used as the dependent variable matrix for the multivariate test.
170 A multivariate test was also conducted using a presence-absence transformation of the biotic data
171 to understand what factors influenced community composition on the shipwrecks. Abiotic factors
172 tested included wreck relative surface area (hypothesis 2), surface complexity alone (a measure
173 of habitat heterogeneity), and distance to the nearest wreck (hypothesis 3).

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

179

180 **RESULTS**

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

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

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

195 Larger shipwrecks, with greater relative surface area, had higher taxonomic richness
196 (alpha diversity) (hypothesis 1; Fig. 5). There was a logarithmic relationship between taxon
197 richness and wreck relative surface area for the sessile fauna ($R^2 = 0.52$) and for all taxa together
198 ($R^2 = 0.53$); mobile fauna showed a general increase in taxon richness with relative surface area
199 (Fig. 5). A DISTLM procedure revealed that species richness on the wrecks was not significantly
200 related to distance to the nearest wreck ($R^2 = 0.13$, $p = 0.36$) or surface complexity ($R^2 = 0.01$, p
201 $= 0.84$). Relative surface area had the strongest relationship to species richness, though its
202 influence was still non-significant in the DISTLM test (hypothesis 1; $R^2 = 0.41$, $p = 0.07$). A
203 dbRDA plot shows points belonging to the different wrecks widely spaced with respect to the x-
204 axis and roughly parallel to the axis of relative surface area, showing this factor's influence on
205 the species richness on each wreck (Fig. 6A).

206 Variation in the biotic community (abundances on each wreck, beta diversity) was best
207 explained by distance to the nearest wreck (hypothesis 3; DISTLM, $R^2 = 0.17$, $p < 0.001$).
208 Relative surface area and surface complexity each explained much lower proportions of variation
209 in the species abundance data ($R^2 = 0.08$, $R^2 = 0.07$, respectively; $p < 0.001$). When a presence-
210 absence transformation of the species abundance data was used, DISTLM revealed the
211 community composition of each wreck was again best explained by distance to the nearest wreck
212 ($R^2 = 0.17$, $p < 0.001$). Relative surface area and surface complexity explained much less
213 variation in the community composition ($R^2 = 0.07$, 0.05 , respectively; $p < 0.001$). dbRDA plots
214 for log- and presence-absence-transformed biotic data were nearly identical and show the
215 influence of each of the abiotic factors on beta diversity on the wrecks (Fig. 6B, C).

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

221

222 **DISCUSSION**

223 **Species-area relationship**

224 Higher taxonomic richness was found on larger wrecks, as predicted by MacArthur &
225 Wilson (1967) (hypothesis 1). The function $S = cA^z$ yields a linear relationship when both axes
226 are log-transformed but a logarithmic relationship between taxonomic richness and island area
227 when left untransformed. This may reflect the finite nature of the species pool or a maximum

228 carrying capacity for each wreck. In fact, each of the eight present shipwrecks were inhabited by
229 sub-sets of the same 34 species or morphotypes.

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

248 Beta diversity, or variation in the biotic communities among wrecks, was most strongly
249 influenced by distance between the wrecks, not wreck size. This result does not support
250 “incidence functions,” or the presence of different sets of organisms on different-size wrecks

251 (hypothesis 2). “Incidence functions” have also not been found for other island-like marine hard
252 substrata that have been studied (Abele & Patton 1976, Meyer et al. 2016, Schoener & Schoener
253 1981) and may not be important for island-like habitats in the marine environment.

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

264

265 **Faunal distribution patterns among wrecks**

266 Our data showed no evidence of either nested faunal patterns or non-random co-
267 occurrence of taxa (hypotheses 4 & 5). In other words, the set of taxa present on a given wreck
268 did not appear to be selected from the available taxon pool according to any “assembly rule”
269 (used here in the general sense following Belyea & Lancaster (1999)). Rather, the taxa inhabiting
270 a particular wreck seemed to be selected randomly from the available taxon pool. This result is in
271 line with the “island model” for larval dispersal among isolated marine habitats. It must therefore
272 be considered that the “island” and “stepping-stone”/“isolation-by-distance” models are not
273 mutually exclusive – larvae may settle randomly on shipwrecks initially, but then subsequent

274 dispersal among close wrecks can cause their communities to become increasingly similar.
275 Succession, if it is deterministic, may also cause wreck communities to become more similar
276 over time. The “island” and “stepping-stone” models are not actually the best way to
277 conceptualize colonization of isolated marine habitats; a better understanding of larval dispersal
278 and recruitment among these island-like habitats will be brought about by considering the life-
279 history and dispersal capabilities of each individual species (Shank & Halanych 2007, Meyer
280 2016).

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

290

291 **Life-history traits and succession**

292 Taxa observed on the present shipwrecks generally had two modes of larval dispersal: the
293 motile fauna and solitary sessile species generally had long-duration (pelagic larval duration
294 months – > 1 year) planktotrophic larvae, while the encrusting or clonal fauna generally had
295 short-duration (pelagic larval duration days – weeks) lecithotrophic larvae but were also capable
296 of asexual reproduction as adults (Table 3 and references therein). For example, *Stylocidaris*

297 *lineata* Mortensen, 1910 has planktotrophic larvae with a pelagic duration of > 3 months (Young
298 et al. 1998, 2012), while *Metridium dianthus* has short-duration planula larvae and also
299 reproduces by budding or fragmentation when well-fed as an adult (Bucklin & Hedgecock 1982,
300 Bucklin 1987).

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

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

317 Given the tendency for encrusting fauna with lecithotrophic larvae to dominate the
318 shipwrecks, we hypothesize that the wrecks were each initially colonized by a small number of
319 individuals that built up dense populations through philopatry and asexual budding as adults. In

320 fact, four of the wrecks in fact showed a high degree of dominance, with 60 – 80% of the fauna
321 belonging to the most common taxon alone. These four wrecks are all the smallest wrecks, which
322 have the least surface area and can therefore be most easily covered by asexually-reproducing
323 encrusting species. The remaining four wrecks, the largest ships, also had 20 – 40% of the fauna
324 accounted for by the most common species, but this lesser degree of dominance may be merely a
325 result of the greater surface area on these wrecks and the finite growth rates of encrusting
326 organisms.

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

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

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

343 location were characterized by long-lived species with restricted dispersal and species that were
344 superior competitors (Carter et al. 1985, Pawlik et al. 2008, Perkol-Finkel & Benayahu 2005,
345 Perkol-Finkel et al. 2005, 2006). Similarly, a 112-year-old shipwreck at 23 m off the coast of
346 Brazil was covered in sponges and corals, resembling a natural reef (Lira et al. 2010).

347 Our data constitute a single time-point, so we are not able to observe the process of
348 succession on the shipwrecks. However, we can compare our data to studies of succession at
349 shallower depth in the same region to infer the stage of succession. Shallow hard substrata at
350 temperate latitude undergo succession in three stages: early colonizers such as acorn barnacles
351 and serpulid polychaetes are followed by intermediate colonizers (ascidians, bryozoans,
352 hydroids) and climax species that may outcompete or simply out-live earlier colonists (Osman
353 1977, Dean & Hurd 1980, Chalmer 1982). The order of succession can also depend on seasonal
354 recruitment (Pacheco et al. 2011).

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

362 It is possible that the present shipwrecks' isolated location makes it less likely that short-
363 duration larvae will reach the wrecks. Short-duration larvae are typical of "late-succession"
364 species, so their absence may cause succession to proceed slowly (Meyer 2016). Studies on
365 deep-water isolated hard substrata are typically limited to single time-point observations (Church

366 et al. 2009, Taylor et al. 2014), but this study can serve as an effective base-line for
367 characterizing succession in the Billy Mitchell shipwreck communities in the future.

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

372

373 **ACKNOWLEDGEMENTS**

374 This material is based upon work supported by the National Science Foundation Graduate
375 Research Fellowship Program under Grant No. DGE-0829517. Funding for this project was
376 supplied by the Bureau of Ocean Energy Management (BOEM), under contract to CSA Ocean
377 Sciences, Inc. (contract M10PC00100) in partnership with the National Oceanographic
378 Partnership Program. We thank Greg Boland (BOEM) and Steve Viada (CSA) for support during
379 the development of the cruise and the overall project. NOAA ship *Nancy Foster* and *Kraken II*
380 ROV were provided by the NOAA Office of Ocean Exploration and Research. The U.S.
381 Geological Survey contributed equipment and personnel to this project. We thank the officers,
382 crew, and ROV team for their assistance at sea. Stephen Cairns (Smithsonian Institution) and
383 Lea-Anne Henry (Heriot Watt Univ.) assisted with taxonomic identification of voucher
384 specimens. Roderick Mather (Univ. Rhode Island) consulted on the identity and history of each
385 shipwreck. Comments from Katherine Dunlop (International Research Institute of Stavanger),
386 Michelle Wood (Univ. Oregon), Alan Shanks (OIMB), Craig McClain (Duke Univ.), and 2
387 anonymous reviewers improved previous versions of this manuscript.

388

389 **References**

- 390 Abele LG, Patton WK (1976) The size of coral heads and the community biology of associated
391 decapod crustaceans. *J Biogeogr* 3:35–47
- 392 Amaral FD, Farrapeira CMR, Lira SMA, Ramos CAC (2010) Benthic macrofauna inventory of
393 two shipwrecks from Pernambuco coast, northeast of Brazil. *Rev Nord Zool*:24–41
- 394 Anderson MJ, Gorley RN, Clarke KR (2008) PERMANOVA+ for PRIMER: guide to software
395 and statistical tools. Primer-E, Plymouth.
- 396 Belyea LR, Lancaster J (1999) Assembly rules within a contingent ecology. *Oikos* 86:402–416
- 397 Bucklin A (1987) Growth and asexual reproduction of the sea anemone *Metridium*: comparative
398 laboratory studies of three species. *J Exp Mar Bio Ecol* 110:41–52
- 399 Bucklin A, Hedgecock D (1982) Biochemical genetic evidence for a third species of *Metridium*
400 (Coelenterata: Actinaria). *Mar Biol* 66:1–7
- 401 Buroker NE (1983) Population genetics of the American oyster *Crassostrea virginica* along the
402 Atlantic coast and the Gulf of Mexico. *Mar Biol* 75:99–112
- 403 Carlton JT (2007) *The Light and Smith manual: Intertidal invertebrates from central California*
404 *to Oregon*, Fourth edi. University of California Press
- 405 Carter JW, Carpenter AL, Foster MS, Jessee WN (1985) Benthic succession on an artificial reef
406 designed to support a kelp-reef community. *Bull Mar Sci* 37:86–113
- 407 Chadwick N, Adams C (1991) Locomotion, asexual reproduction, and killing of corals by the
408 corallimorpharian *Corynactis californica*. *Hydrobiologia* 216-217:263–269
- 409 Chalmer PN (1982) Settlement patterns of species in a marine fouling community and some
410 mechanisms of succession. *J Exp Mar Bio Ecol* 58:73–85
- 411 Chia F-S (1970) Some observations on the histology of the ovary and RNA synthesis in the
412 ovarian tissues of the starfish, *Henricia sanguinolenta*. *J Zool* 162:287 – 291
- 413 Chiantore M, Cattaneo-Vietti R, Elia L, Guidetti M, Antonini M (2002) Reproduction and
414 condition of the scallop *Adamussium colbecki* (Smith 1902), the sea-urchin *Sterechinus*
415 *neumayeri* (Meissner 1900) and the sea-star *Odontaster validus* (Koehler 1911) at Terra
416 Nova Bay (Ross Sea): different strategies related to inter-annual . *Polar Biol* 25:251–255
- 417 Church RA, Warren DJ, Irion JB (2009) Analysis of deepwater shipwrecks in the Gulf of
418 Mexico: artificial reef effect of six World War II shipwrecks. *Oceanogr* 22:50–63.
- 419 Clarke K, Gorley R (2006) *Primer v6: user manual/tutorial*. Primer-E, Plymouth
- 420 Connor EF, McCoy ED (1979) The statistics and biology of the species-area relationship. *Am*
421 *Nat* 113:791–833
- 422 Dando PR, Southward A, Southward EC, Dixon DR, Crawford A, Crawford M (1992)
423 Shipwrecked tube worms. *Nature* 356:667–667

- 424 Dean TA, Hurd LE (1980) Development in an estuarine fouling community: the influence of
425 early colonists on later arrivals. *Oecologia* 46:295–301
- 426 Diamond JM (1975) Assembly of island communities. In: Cody ML, Diamond JM (eds) *Ecology*
427 *and Evolution of Communities*. Belknap Press of Harvard University Press, Cambridge and
428 London, p 342–444
- 429 Edwards KF, Stachowicz JJ (2010) Multivariate trade-offs, succession, and phenological
430 differentiation in a guild of colonial invertebrates. *Ecology* 91:3146–3152
- 431 Eernisse DJ, Strathmann MF, Strathmann RR (2010) *Henricia pumila* sp. nov.: a brooding
432 seastar (Asteroidea) from the coastal northeastern Pacific. *Zootaxa* 2329:22–36
- 433 Entsminger G (2014) EcoSim Professional: null modeling software for ecologists, version 1.
434 Acquired Intelligence Inc., Kesey-Bear and Pinyon Publishing, Montrose, Colorado, USA
- 435 Fadlallah YH, Pearse JS (1982) Sexual reproduction in solitary corals: synchronous
436 gametogenesis and broadcast spawning in *Paracyathus stearnsii*. *Mar Biol* 71:233–239
- 437 Fisher WK (1925) Asexual Reproduction in the Starfish, *Sclerasterias*. *Biol Bull* 48:171–175
- 438 Fransozo A, Cuesta JA, Negreiros-Fransozo ML (1998) The first zoal stage of two species of
439 Grapsidae (Decapoda, Brachyura) and a key to such larvae from the Brazilian coast.
440 *Crustaceana* 71:331–343
- 441 Gambi MC, Schulze A, Amato E (2011) Record of *Lamellibrachia* sp. (Annelida: Siboglinidae:
442 Vestimentifera) from a deep shipwreck in the western Mediterranean Sea (Italy). *Mar*
443 *Biodivers Rec* 4:e24
- 444 George SB, Young CM, Fenaux L (1997) Proximate composition of eggs and larvae of the sand
445 dollar *Encope michelini* (Agassiz): the advantage of higher investment in planktotrophic
446 eggs. *Invertebr Reprod Dev* 32:11–19
- 447 Gotelli NJ (2000) Null model analysis of species co-occurrence patterns. *Ecology* 81:2606–2621
- 448 Gotelli NJ, Graves GR (1996) *Null models in ecology*. Smithsonian Institution Press,
449 Washington and London
- 450 Hill JL, Curran PJ, Foody GM (1994) The effect of sampling on the species-area curve. *Glob*
451 *Ecol Biogeogr Lett* 4:97–106
- 452 Hines AH (1991) Fecundity and reproductive output in nine species of *Cancer* crabs (Crustacea,
453 Brachyura, Cancridae). *Can J Fish Aquat Sci* 48:267–275
- 454 Holts LJ, Beauchamp KA (1993) Sexual reproduction in the corallimorpharian sea anemone
455 *Corynactis californica* in a central California kelp forest. *Mar Biol* 116: 129-136.
- 456 Hughes DJ, Crawford M (2008) A new record of the vestimentiferan *Lamellibrachia* sp.
457 (Polychaeta: Siboglinidae) from a deep shipwreck in the eastern Mediterranean. *Mar*
458 *Biodivers Rec* 1:1–3
- 459 Huntington BE, Lirman D (2012) Species-area relationships in coral communities: evaluating
460 mechanisms for a commonly observed pattern. *Coral Reefs* 31:929–938

- 461 Janosik AM, Mahon AR, Scheltema RS, Halanych KM (2008) Life history of the Antarctic sea
462 star *Labidiaster annulatus* (Asteroidea: Labidiasteridae) revealed by DNA barcoding.
463 *Antarct Sci* 20:563
- 464 Kilgour MJ, Shirley TC (2008) Bathymetric and spatial distribution of decapod crustaceans on
465 deep-water shipwrecks in the Gulf of Mexico. *Bull Mar Sci* 82:333–344
- 466 Lira SM de A, Farrapeira CMR, Amara FMD, Ramos CAC (2010) Sessile and sedentary
467 macrofauna from the Pirapama Shipwreck, Pernambuco, Brazil. *Biota Neotrop* 10:155–165
- 468 Lønning S (1976) Reproductive cycle and ultrastructure of yolk development in some
469 echinoderms from the Bergen area, western Norway. *Sarsia* 62:49–72
- 470 MacArthur RH, Wilson EO (1967) The theory of island biogeography. Princeton University
471 Press, Princeton, New Jersey
- 472 Mallefet J, Berghe M vanden, Vincx M, Massin C, Norro A, DeMaerschalck V, Steyaert M,
473 Degraer S, Cattijssse A (2008) Belgian shipwreck - hotspots for marine biodiversity
474 (BEWREMABI).
- 475 Meyer KS (2016) Islands in a sea of mud: insights for community assembly on isolated marine
476 hard substrata from terrestrial island theory. *Adv Mar Biol* 76: 1–40.
- 477 Meyer KS, Young CM, Sweetman AK, Taylor J, Soltwedel T, Bergmann M (2016) Rocky
478 islands in a sea of mud: biotic and abiotic factors structuring deep-sea dropstone
479 communities. *Mar Ecol Prog Ser* 556: 45–57
- 480 Osman RW (1977) The establishment and development of a marine epifaunal community. *Ecol*
481 *Monogr* 47:37–63
- 482 Pacheco AS, Laudien J, Thiel M, Oliva M, Heilmayer O (2011) Succession and seasonal onset of
483 colonization in subtidal hard-bottom communities off northern Chile. *Mar Ecol* 32:75–87
- 484 Palumbi SR (2003) Population genetics, demographic connectivity, and the design of marine
485 reserves. *Ecol Appl* 13:146–158
- 486 Pawlik J, Henkel T, McMurray S, López-Legentil S, Loh T, Rohde S (2008) Patterns of sponge
487 recruitment and growth on a shipwreck corroborate chemical defense resource trade-off.
488 *Mar Ecol Prog Ser* 368:137–143
- 489 Pearse JS (1965) Reproductive periodicities in several contrasting populations of *Odontaster*
490 *validus* Koeler, a common Antarctic asteroid. *Antarct Res Ser* 5:39–85
- 491 Perkol-Finkel S, Benayahu Y (2005) Recruitment of benthic organisms onto a planned artificial
492 reef: Shifts in community structure one decade post-deployment. *Mar Environ Res* 59:79–
493 99
- 494 Perkol-Finkel S, Benayahu Y (2007) Differential recruitment of benthic communities on
495 neighboring artificial and natural reefs. *J Exp Mar Bio Ecol* 340:25–39
- 496 Perkol-Finkel S, Shashar N, Barneah O, Ben-David-Zaslav R, Oren U, Reichart T, Yacobovich
497 T, Yahel G, Yahel R, Benayahu Y (2005) Fouling reefal communities on artificial reefs:

- 498 Does age matter? *Biofouling* 21:127–140
- 499 Perkol-Finkel S, Shashar N, Benayahu Y (2006) Can artificial reefs mimic natural reef
500 communities? The roles of structural features and age. *Mar Environ Res* 61:121–135
- 501 Pohle G, Marques FPL (2003) Zoeal stages and megalopa of *Leucippa pentagona* H. Milne
502 Edwards, 1833 (Decapoda: Brachyura: Majoidea: Epialtidae) obtained from laboratory
503 culture and a comparison with other epialtid and majoid larvae. *Invertebr Reprod Dev*
504 43:55–70
- 505 Ross SW, Rhode M, Viada ST, Mather R (2016) Fish species associated with shipwreck and
506 natural hard-bottom habitats from the middle to outer continental shelf of the Middle
507 Atlantic Bight near Norfolk Canyon. *Fish Bull* 114:45–57
- 508 Santos DHC dos, Silva-Cunha M da GG, Santiago MF, Passavante JZ de O (2010)
509 Characterization of phytoplankton biodiversity in tropical shipwrecks off the coast of
510 Pernambuco, Brazil. *Acta Bot Brasilica* 24:924–934
- 511 Schoener A, Schoener TW (1981) The dynamics of the species-area relation in marine fouling
512 systems 1. Biological correlates of changes in the species-area slope. *Am Nat* 118:339–360
- 513 Shank TM, Halanych KM (2007) Toward a mechanistic understanding of larval dispersal:
514 insights from genomic fingerprinting of the deep-sea hydrothermal vent tubeworm *Riftia*
515 *pachyptila*. *Mar Ecol* 28:25–35
- 516 Steimle FW, Zetlin C (2000) Reef habitats in the Middle Atlantic Bight: abundance, distribution,
517 associated biological communities, and fishery resource use. *Mar Fish Rev* 62:24–42
- 518 Taylor JR, DeVogelaere AP, Burton EJ, Frey O, Lundsten L, Kuhnz LA, Whaling PJ, Lovera C,
519 Buck KR, Barry JP (2014) Deep-sea faunal communities associated with a lost intermodal
520 shipping container in the Monterey Bay National Marine Sanctuary, CA. *Mar Pollut Bull*
521 83:92–106
- 522 Thiel M, Vásquez JA (2000) Are kelp holdfasts islands on the ocean floor? – indication for
523 temporarily closed aggregations of peracarid crustaceans. *Hydrobiologia* 440:45–54
- 524 Ulrich W (2006) Nestedness - a FORTRAN program for calculating ecological temperatures.
525 www.uni.torun.pl/~ulrichw
- 526 Ulrich W, Gotelli NJ (2007) Null model analysis of species nestedness patterns. *Ecology*
527 88:1824–1831
- 528 Vrijenhoek RC (1997) Gene flow and genetic diversity in naturally fragmented metapopulations
529 of deep-sea hydrothermal vent animals. *J Hered* 88:285–93
- 530 Vrijenhoek RC (2010) Genetic diversity and connectivity of deep-sea hydrothermal vent
531 metapopulations. *Mol Ecol* 19:4391–4411
- 532 Walker SJ, Schlacher TA, Schlacher-Hoenlinger MA (2007) Spatial heterogeneity of epibenthos
533 on artificial reefs: fouling communities in the early stages of colonization on an East
534 Australian shipwreck. *Mar Ecol* 28:435–445

- 535 Wenner EL (1983) Invertebrate communities associated with hard bottom habitats in the South
536 Atlantic Bight. *Estuar Coast Shelf Sci* 17:143–158
- 537 Wildenberg T (2014) Billy Mitchell’s war with the Navy: the interwar rivalry over air power.
538 Naval Institute Press, Annapolis, Maryland
- 539 Work TM, Aeby GS, Maragos JE (2008) Phase shift from a coral to a corallimorph-dominated
540 reef associated with a shipwreck on Palmyra Atoll. *PLoS One* 3:e2989
- 541 Young CM, Chia FS (1982) Ontogeny of phototaxis during larval development of the sedentary
542 polychaete, *Serpula vermicularis* (L.). *Biol Bull* 162:457–468
- 543 Young C, Ekaratne SUK, Cameron JL (1998) Thermal tolerances of embryos and planktotrophic
544 larvae of *Archaeopneustes hystrix* (A. Agassiz) (Spatangoidea) and *Stylocidaris lineata*
545 (Mortensen) (Cidaroidea), bathyal echinoids from the Bahamian Slope. *J Exp Mar Bio Ecol*
546 223:65–76
- 547 Young CM, He R, Emlet RB, Li Y, Qian H, Arellano SM, Gaest A Van, Bennett KC, Wolf M,
548 Smart TI, Rice ME (2012) Dispersal of deep-sea larvae from the intra-American seas:
549 simulations of trajectories using ocean models. *Integr Comp Biol* 52:483–496
- 550
- 551
- 552
- 553
- 554
- 555
- 556
- 557
- 558
- 559
- 560
- 561
- 562

563 Fig 1. Map of shipwreck sites east of Chesapeake Bay. Black lines indicate orientation of the
564 major axis of each shipwreck.

565
566 Fig. 2. Morphotypes observed in ROV video from shipwrecks (September 2012). A, pink
567 encrusting sponge; B, white didemnid ascidian; C, yellow encrusting sponge; D, pine hydroid; E,
568 cf. Corynidae; F, brown tube complex; G, *Plumularia setacea*; H, white zoanthid; I, small white
569 anemone; J, *Diodora tanneri*; K, cf. *Serpula* sp.; L, *Paracyathus pulchellus*; M, cf.
570 Hormathiidae; N, *Corynactis delawarei*; O, red shrimp; P, *Crassostrea virginica*; Q, *Munida* sp.;
571 R, *Rochinia crassa*; S, *Halcurias pilatus*; T, *Metridium dianthus*; U, *Euchirograpsus*
572 *americanus*; V, *Cancer borealis*; W, *Paguristes lymani*; X, *Henricia* sp.; Y, *Odontaster hispidus*;
573 Z, *Henricia oculata*; AA, *Coronaster briareus*; AB, *Sclerasterias tanneri*; AC, *Sclerasterias* sp.;
574 AD, *Stylocidaris affinis*; AE, *Stylocidaris lineata*. Size scale is relative but not precise.

575
576 Fig. 3. Dominance plot showing cumulative percent community composition of fauna on
577 shipwrecks on the U.S. Atlantic margin.

578
579 Fig. 4. Non-metric multi-dimensional scaling (nMDS) of the invertebrate communities observed
580 at eight shipwrecks on the U.S. Atlantic margin. Each point represents one frame grab obtained
581 from ROV video.

582
583 Fig. 5. Logarithmic relationships between richness of all fauna (A), sessile fauna (B), and mobile
584 fauna (C) and relative surface area (height x length x surface complexity) of each shipwreck.

585

586 Fig. 6. dbRDA plots showing how abiotic factors influence invertebrate communities on eight
587 shipwrecks on the U.S. Atlantic margin. Biotic response variables include species richness on
588 each wreck (A), log-transformed abundances of each species on each wreck (B), and presence or
589 absence of each species on each wreck (C).

590

591

592

593

594

595

596

597

598

599

600

601

602

603

604

605

606

607

608

609 Table 1. Shipwrecks surveyed in September 2012.

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'	301	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	118
W7	28	30	37° 11.93'	74° 45.43'	72	3	79

610

611

612

613

614

615

616

617

618

619

620

621

622

623

624

625

626 Table 2. Species and morphotypes present at each shipwreck in September 2012. An x indicates
 627 presence; D indicates a dominant species on that particular wreck.

Species or morphotype	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	
<i>Metridium dianthus</i>	D						x	
cf. Hormathiidae	x	D	x	x	x	x	x	
<i>Halcurias pilatus</i>			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
<i>Corynactis delawarei</i>		D					x	
Brown tube complex	D	x		D	x		x	D
<i>Plumularia setacea</i>	x			x			x	x
cf. Corynidae		D	x		x	x	x	
Pine hydroid			x	x		x		
<i>Paracyathus pulchellus</i>	x	x	x	x			x	
<i>Crassostrea virginica</i>		x	x					
<i>Diodora tanneri</i>		x	x	x	x			
Red shrimp						D		
<i>Rochinia crassa</i>		x	x	x	D	x	x	
<i>Euchirograpsus americanus</i>		x		x				
<i>Cancer borealis</i>				x				
<i>Paguristes lymani</i>		x			x	x		
<i>Munida</i> sp.		x		x				
cf. <i>Serpula</i>		x	x	x	x	x	x	

<i>Henricia oculata</i>	D					D	D
<i>Henricia</i> sp.				x			
<i>Sclerasterias tanneri</i>		D	D	x	x	D	x
<i>Sclerasterias</i> sp.				x			x
<i>Coronaster briareus</i>	x			x	x		
<i>Odontaster hispidus</i>		x	x	x	x	x	
<i>Ophiocomina</i> sp.			x	x			
<i>Stylocidaris lineata</i>		x		D		x	
<i>Stylocidaris affinis</i>		x	x	D		x	
<i>Coelopleurus floridanis</i>		x					

628

629

630

631

632

633

634

635

636

637

638

639

640

641

642

643

644

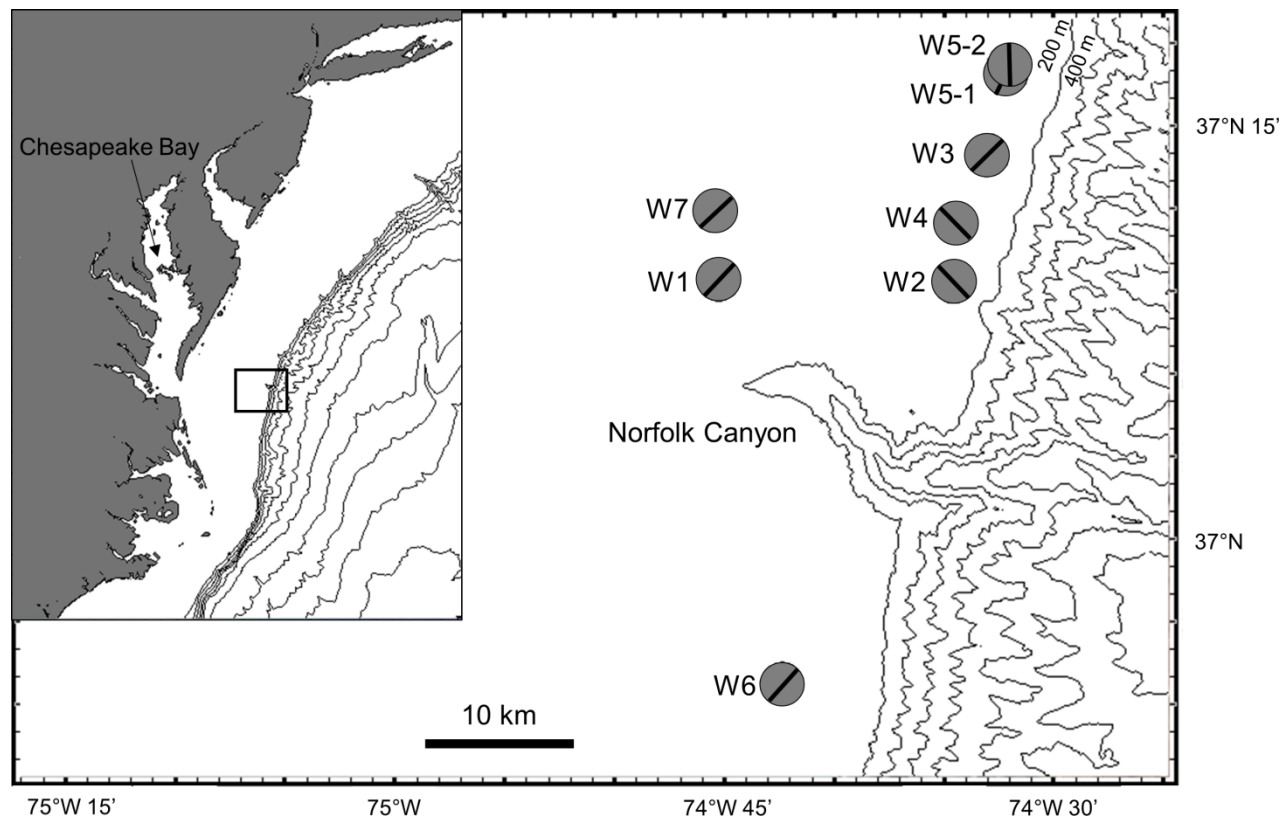
645

646 **Table 3.** Reproductive strategies of the shipwreck fauna. PLD, pelagic larval duration

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	
<i>Metridium dianthus</i>	Planula larva, asexual reproduction by budding as adult	Bucklin 1987, Bucklin & Hedgecock 1982
cf. Hormathiidae	Larva unknown, suspect asexual reproduction by budding as adult	
<i>Halcurias pilatus</i>	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	
<i>Corynactis delawarei</i>	Congener <i>C. californica</i> has large planula larva, asexual reproduction by budding as adult	Holts & Beauchamp 1993, Chadwick & Adams 1991
Brown tube complex	Not applicable – species complex	
<i>Plumularia setacea</i>	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	
<i>Paracyathus pulchellus</i>	Congener <i>P. stearnsii</i> has large feeding planula, PLD 4 weeks	Fadlallah & Pearse 1982
<i>Crassostrea virginica</i>	Broadcast spawner, high fecundity	Buroker 1983

<i>Diodora tanneri</i>	<i>Diodora</i> spp. can broadcast spawn or lay eggs on substrata	Carlton 2007
Red shrimp	Suspect planktotrophic larva	
<i>Rochinia crassa</i>	Congener <i>R. vesicularis</i> has planktotrophic larva	Pohle & Marques 2003
<i>Euchirograpsus americanus</i>	Planktotrophic larva	Fransozo et al. 1998
<i>Cancer borealis</i>	Planktotrophic larva, PLD 4 months	Hines 1991
<i>Paguristes lymani</i>	Planktotrophic larva	Fransozo et al. 1998
<i>Munida</i> sp.	Planktotrophic larva, long PLD	Wenner 1983
cf. <i>Serpula</i> sp.	<i>S. vermicularis</i> has feeding trochophore, nectochaete larva, PLD 41-50 days	Young & Chia 1982
<i>Henricia oculata</i>	Congeners <i>H. sanguinolenta</i> and <i>H. pumila</i> brood young to crawl-away juvenile stage	Chia 1970, Eernisse et al. 2010
<i>Henricia</i> sp.	Congeners <i>H. sanguinolenta</i> and <i>H. pumila</i> brood young to crawl-away juvenile stage	Chia 1970, Eernisse et al. 2010
<i>Sclerasterias tanneri</i>	Bipinnaria, PLD > 2 years, juveniles capable of fission	Young et al. 2012, Fisher 1925
<i>Sclerasterias</i> sp.	Congener <i>S. tanneri</i> has bipinnaria, PLD > 2 years, juveniles capable of fission	Young et al. 2012, Fisher 1925
<i>Coronaster briareus</i>	Ecologically similar species in same family, <i>Labidiaster annulata</i> , has bipinnaria, brachiolaria	Janosik et al. 2008
<i>Odontaster hispidus</i>	Congener <i>O. validus</i> has planktotrophic, demersal, bipinnaria larva, PLD 7-9 months	Pearse 1965, Chiantore et al. 2002
<i>Ophiocomina</i> sp.	Congener <i>O. nigra</i> has ophiopluteus larva, PLD ~2 months	Lönning 1976
<i>Stylocidaris lineata</i>	Echinopluteus larva, planktotrophic, PLD 3.5 months	Young et al. 1998, 2012
<i>Stylocidaris affinis</i>	Congener <i>S. lineata</i> has feeding echinopluteus	Young et al. 1998, 2012
<i>Coelopleurus floridanis</i>	Small eggs, planktotrophic larva	George et al. 1997

648 Fig. 1



649

650

651

652

653

654

655

656

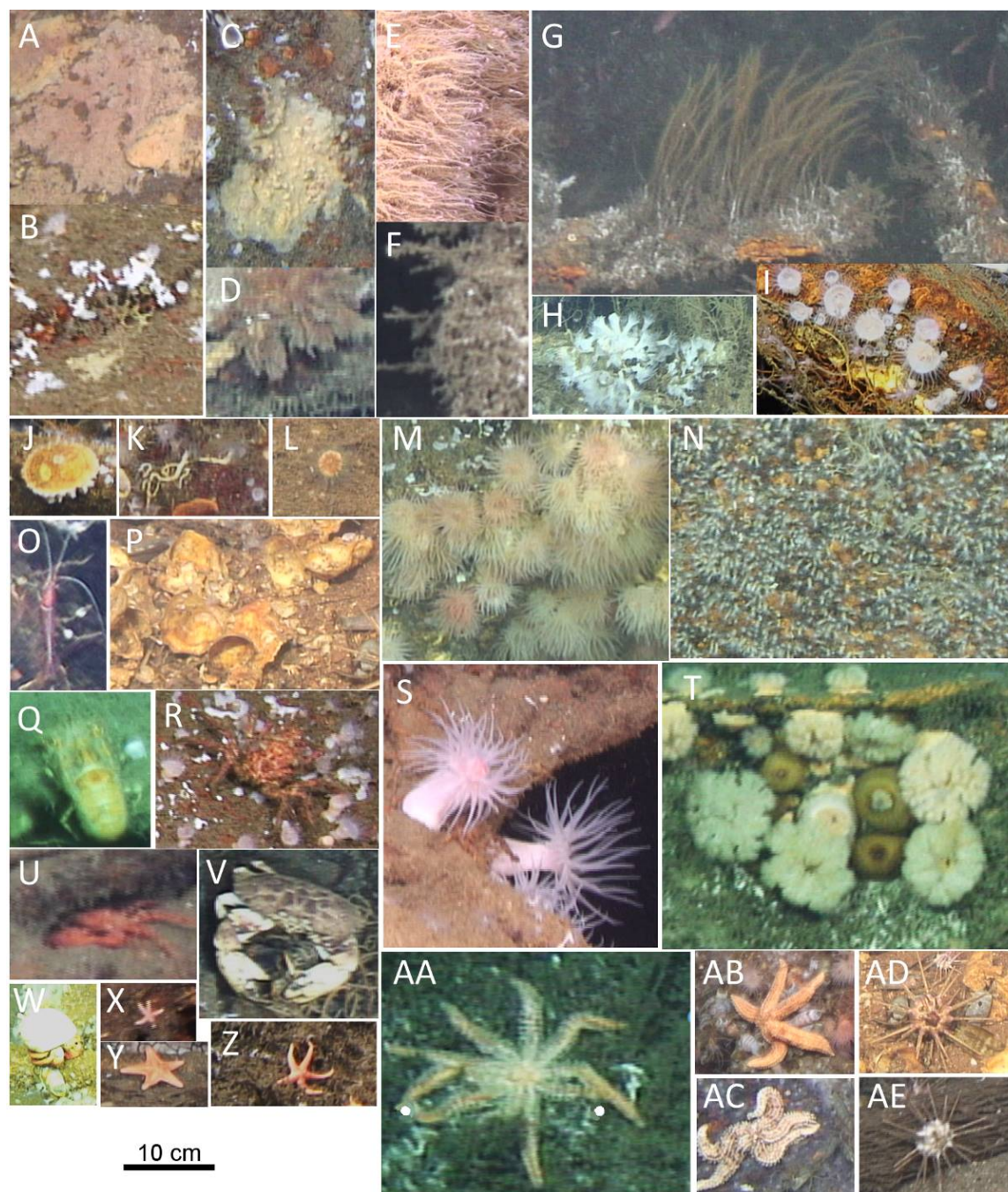
657

658

659

660

661 Fig. 2



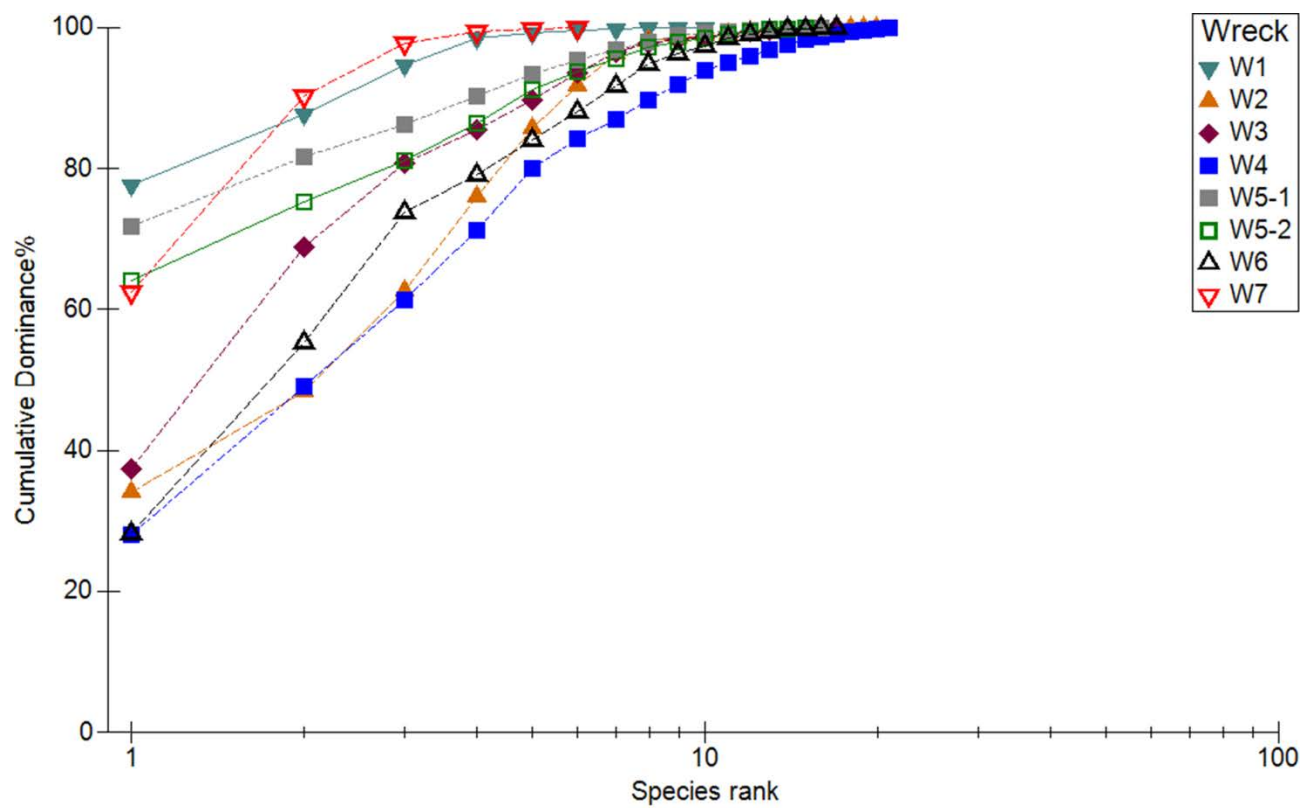
662

663

664

665

666 Fig. 3



667

668

669

670

671

672

673

674

675

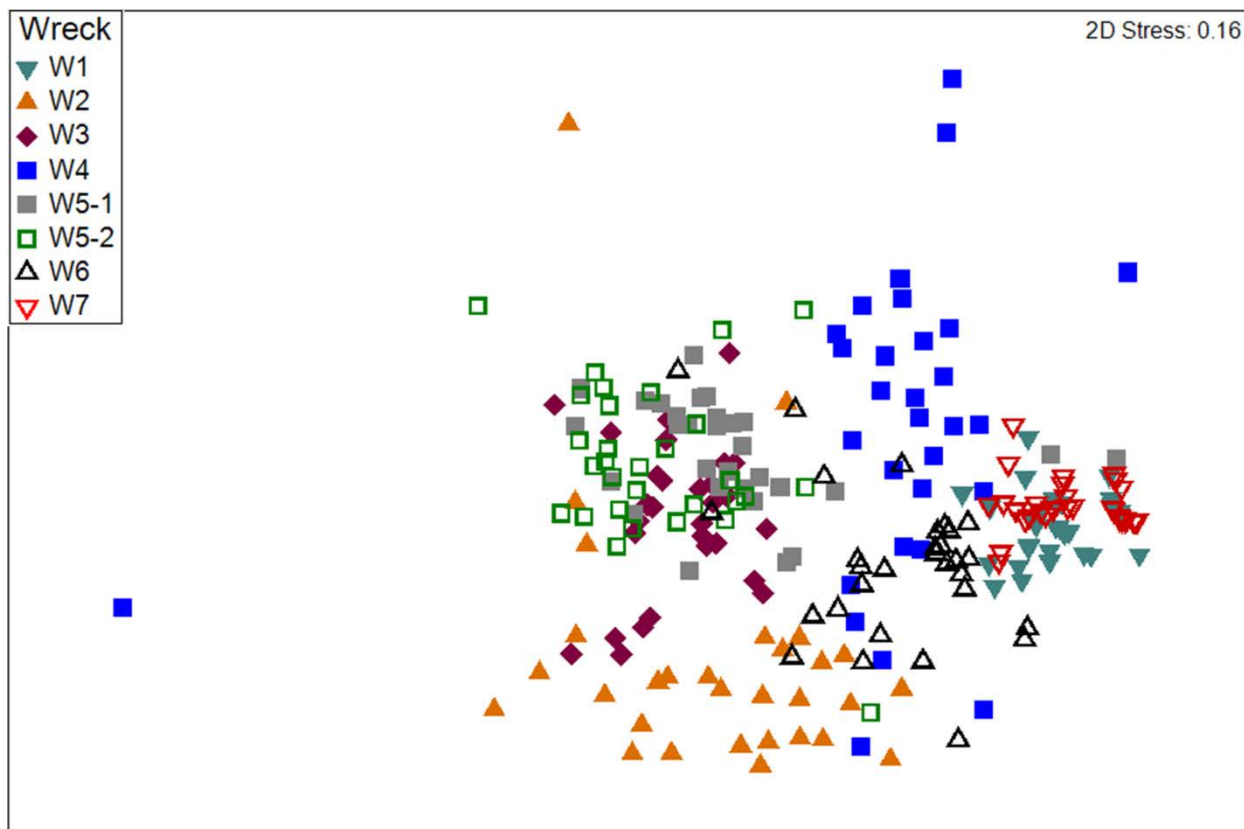
676

677

678

679

680 Fig. 4



681

682

683

684

685

686

687

688

689

690

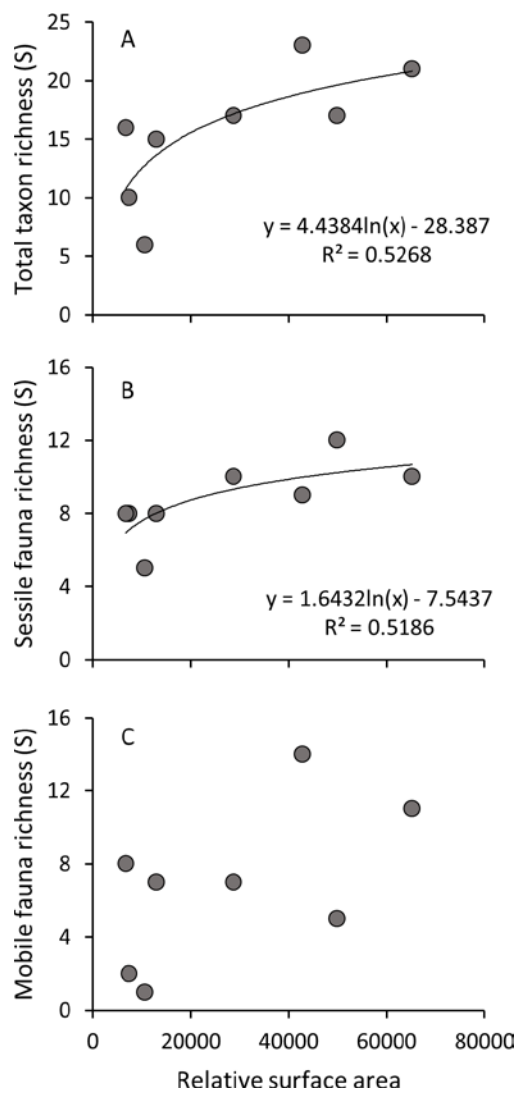
691

692

693

694

695 Fig. 5



696

697

698

699

700

701

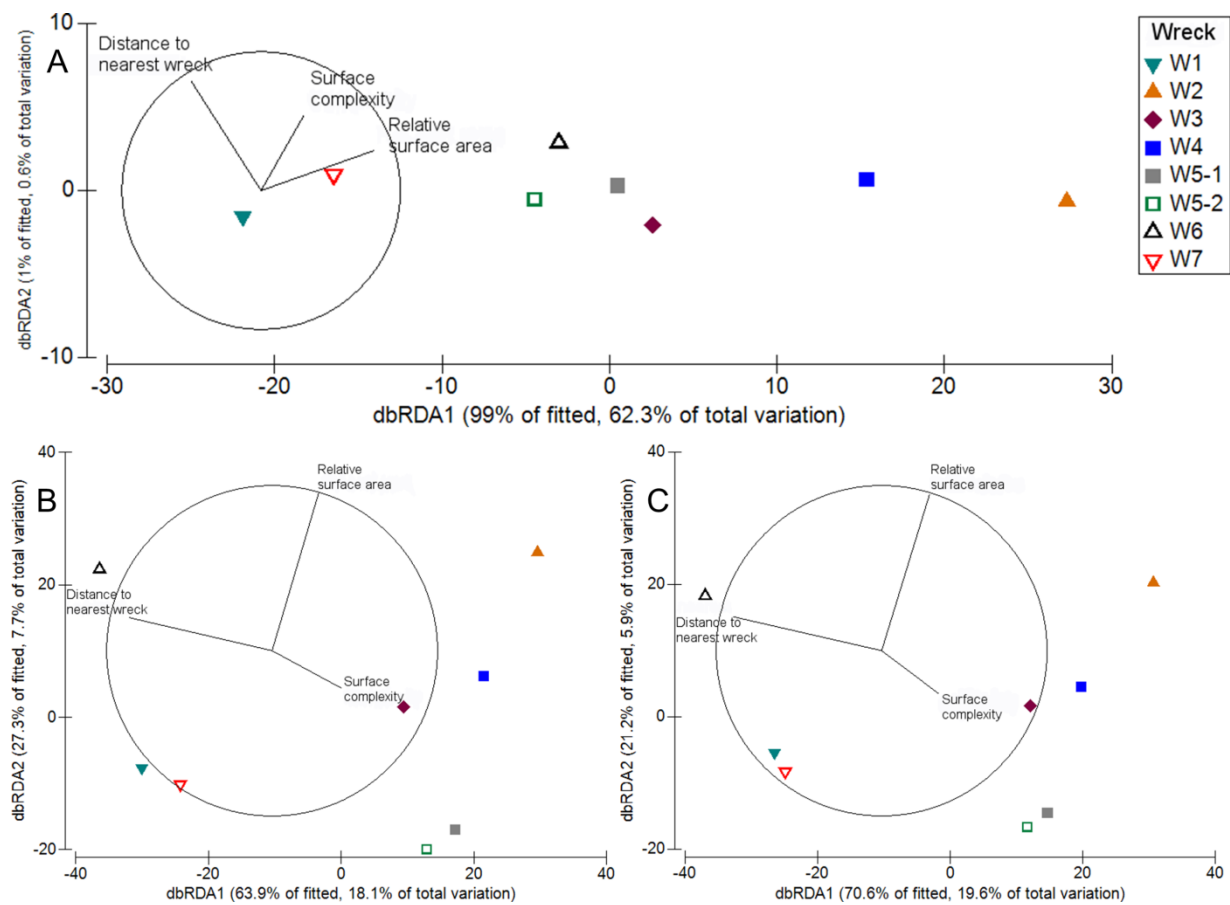
702

703

704

705

706 Fig. 6



707