

1 Title: Underwater cultural heritage is integral to marine ecosystems

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9 **Abstract (50/50 words):** Underwater cultural heritage (UCH) supports marine biodiversity and  
10 influences connectivity. UCH structure, colonizing organisms, and anthropogenic stressors  
11 interact to shape sites over time, but these interactions are poorly understood. We express the  
12 urgent need for biology-archaeology collaborations to address interdisciplinary questions. We  
13 codify the emerging field of Maritime Heritage Ecology.

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15 **Main text (1608/1500 words):**

16

17 *Underwater cultural heritage role in the ecosystem*

18 **Underwater cultural heritage** (UCH, see Glossary) constitutes the long-term remains of  
19 anthropogenic activities in the ocean. Shipwrecks, sunken aircraft, paleolithic middens,  
20 submerged settlements, and other artifacts are irreplaceable historical resources that also  
21 constitute habitats for microbes, flora, and fauna [1]. On a local scale, UCH provides the primary  
22 hard-bottom habitat and can be isolated and island-like. In places with a long history of seafaring  
23 and/or favorable conditions for preservation, such as the Mediterranean, UCH can be particularly

24 abundant. UCH introduces novel ecosystem functions to the seafloor, including microbial  
25 communities [2,3] and obligate hard-bottom invertebrates and fish where there was previously  
26 only sand or mud [4].

27         The physical structure of UCH and the biological community inhabiting it undergo  
28 parallel changes over time (i.e., **site formation processes**). If exposed to a dynamic marine  
29 environment, wooden shipwrecks degrade quickly, leaving parts of the hull and a **ballast reef**.  
30 This process is influenced by shipworm colonization and closely parallels other organic matter-  
31 falls in the ocean. Limestone artifacts are particularly susceptible to bioerosion from a range of  
32 **boring species** [5]. Metal and fiberglass structures also degrade, but more slowly. Metal  
33 corrosion is strongly influenced by chemical conditions of the surrounding water and burial in  
34 sediment. Composite sites with multiple materials undergo complex transformations and  
35 heterogenous degradation. There is almost no understanding of how site formation processes and  
36 ecological **succession** influence one another, although understanding this **reciprocal influence**  
37 will be key for management of UCH sites and the biological communities inhabiting them  
38 (Figure 1).

39         UCH exhibits a **sphere of influence** on biodiversity beyond the physical bounds of its  
40 structure. In one case study, a shipwreck in the Line Islands caused a phase shift from a coral-  
41 dominated to a corallimorph-dominated community that persisted after the shipwreck was  
42 removed [6]. The *Costa Concordia* shipwreck in the Mediterranean similarly impacted the  
43 seafloor, causing regression of endemic habitats and a surge of opportunistic species (e.g., the  
44 bryozoan *Reteporella* sp.) [7]. Such far-reaching impacts of shipwrecks are likely mediated by  
45 the availability of trace metals such as copper and iron and the microbial biofilms that assimilate

46 them [8]. However, interactions between UCH structure, microbial communities, and eukaryotic  
47 communities that drive **community assembly** are extremely poorly understood.

48         One key impact of UCH is on species distributions. By creating hard-bottom habitats  
49 where there was previously sand or mud, UCH can act as stepping-stones for **larval dispersal**.  
50 UCH in the western Atlantic hosts tropical fishes at the edge of their geographic ranges [9].  
51 WWII shipwrecks in Brazil facilitated the spread of the invasive cup coral *Tubastraea coccinea*  
52 along that country's northern coast [10]. Such undesirable impacts of UCH present a challenge  
53 for management, which must balance historical preservation with ecological goals.

54         Like other marine habitats, UCH sites are impacted by anthropogenic stressors. Climate-  
55 related acidification, erosion, and intense storms accelerate the degradation of UCH. Fishing,  
56 especially bottom trawling, damages UCH and leads to the entanglement of ghost gear [11].  
57 Eutrophication alters the community structure on otherwise similar shipwrecks [12]. The  
58 ecological disaster of the Deepwater Horizon oil spill altered microbial communities and  
59 accelerated corrosion of metal on historically-important shipwrecks in the Gulf of Mexico [13].

60

### 61 ***Research challenges***

62         The dual objectives of protecting biodiversity and preserving cultural heritage necessitate  
63 a clear understanding of the processes impacting UCH sites and their biological communities.  
64 Managers in particular need to have a deep understanding and appreciation of UCH as historical  
65 and ecological resources. There is an urgent need for collaborative biology-archaeology research  
66 to fill knowledge gaps.

67         Recent years have seen a rise in studies on biological colonization of UCH, which is a  
68 promising trend. However, marine ecologists and maritime archaeologists rarely encounter one

69 another in professional circles – they sit in different departments, attend different conferences,  
70 and publish in different journals. Furthermore, researchers are unlikely to take courses outside  
71 their home field beyond the undergraduate level. We have noticed an interest among biology and  
72 archaeology researchers in designing studies outside disciplinary boundaries, but a mutual  
73 ignorance of the vocabulary and research framework in each other’s fields can lead to time-  
74 consuming diversions. Put succinctly, there is no need to re-invent the wheel when one can  
75 collaborate with the patent owner.

76           One challenge for biology-archaeology collaborations is the difference in cultural norms  
77 between fields, particularly surrounding study design. Research studies can take place at three  
78 theoretical levels. Low-level theory involves observations of the physical features, artifact  
79 assemblages, and/or biological communities at a given site. Mid-level theory includes  
80 generalizations that attempt to account for patterns between variables and among sites. High-  
81 level theory is a set of abstract rules that explain major phenomena.

82           Many archaeological studies constitute in-depth site descriptions (low-level theory).  
83 Descriptive studies may be ignored by ecologists, who place higher value on quantitative studies  
84 at the mid- and high- levels. Currently, a high-level theory for understanding UCH in an  
85 ecological context is lacking. Low- and mid- level studies constitute a valuable foundational  
86 database for the formation of high-level theory. Existing high-level ecological theories such as  
87 Island Biogeography Theory should be applied to UCH sites [14].

88

### 89 ***Framework for interdisciplinary research***

90           Addressing these research challenges will require ecologists and archaeologists to work  
91 in strong interdisciplinary teams. Frequent, genuine dialogue and good-faith cooperation can

92 mitigate cultural and training barriers. There is especially ripe opportunity for investigations of  
93 mid-level theory. For example, a study of UCH structure and community composition  
94 highlighted the value of shipwrecks as habitats and demonstrated the effects of fishing gear  
95 entanglement [15]. Likewise, there is a real opportunity for researchers and managers to bring  
96 knowledge of ecological succession and site formation processes (both mid-level theories) into  
97 policy considerations.

98         Here, we codify the emerging interdisciplinary field of **Maritime Heritage Ecology** by  
99 proposing a common vocabulary, framework, and identifying key overarching questions for  
100 collaborative study (Figure 1). Most of the examples provided in this review focus on shipwrecks  
101 because they are the best-studied UCH sites for ecological processes; however, the framework of  
102 Maritime Heritage Ecology can and should be applied to all UCH, including those in transitional  
103 environments, such as intertidal shipwrecks, wharfs, lighthouses, decommissioned oil rigs, and  
104 artifacts. It is our genuine hope that this framework will facilitate intentional interdisciplinary  
105 collaboration and address UCH management challenges.

106

107 Overarching question 1: How do site formation processes and succession influence one another?

108         UCH deterioration does not happen linearly. For shipwrecks, there is a wrecking event,  
109 which causes rapid change, followed by an **environmental equilibrium**. Shipwrecks that remain  
110 largely intact during wrecking (i.e., closed systems) degrade more slowly than open systems and  
111 present novel environmental conditions in the shipwreck interior. Simultaneously, **recruitment**  
112 of organisms to a UCH site depends on a suite of environmental and biological factors and may  
113 be stochastic. UCH structure undoubtedly influences the succession of microbes, flora, and  
114 fauna, but the reciprocal influence of UCH structure and biology over time has never been

115 studied. How does the structure of UCH influence the species that colonize it, and how do those  
116 species influence the UCH structure in turn? How do subsequent **natural and cultural**  
117 **transformations** affect colonization by removing organisms from the community or revealing  
118 new surfaces for colonization? How do the time scales of ecological succession and site  
119 formation compare and interact?

120

121 Overarching question 2: What is the net effect of UCH on biodiversity?

122 As UCH becomes colonized and undergoes succession, the community may come to  
123 resemble a natural reef and host desirable species such as corals. UCH can also facilitate the  
124 spread of invasive species. Low-level studies on local and regional scales will be necessary to  
125 unravel the complex interactions of UCH structure and biodiversity. To what extent can UCH  
126 communities resemble natural reefs, and if so, how long does that process take? How can the  
127 efforts to preserve and restore natural reefs affect colonization and preservation of UCH? What  
128 are the long-term impacts of stepping-stone UCH sites on species distributions and larval  
129 dispersal/connectivity? How does the system change if these sites are removed or destroyed?

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131 Overarching question 3: How do anthropogenic stressors impact UCH structure and biological  
132 communities?

133 Anthropogenic stressors range from micro-events such as SCUBA diving and fishing to  
134 macro-events including climate change, high-impact storm events, pollution, and ocean  
135 acidification. While the influence of rising temperatures and acidification on marine organisms  
136 has been extensively studied, understanding of these stressors on UCH structure and site  
137 formation processes is extremely limited. Anthropogenic stressors are overlaid and interact with

138 other natural and cultural processes, but feedback cycles between these factors are poorly  
139 understood. On what time scales do different anthropogenic stressors impact UCH structure and  
140 communities? How does the spatial scale of a stressor control the extent or severity of impact?  
141 How can controls on human activities preserve historical and biological resources on UCH?

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### 143 *A path forward*

144 In the Anthropocene, it is inappropriate to view anthropogenic structures as separate from  
145 naturally-occurring ecosystems and vice versa. Yet, this is the common view among many  
146 audiences and stakeholder groups. UCH constitutes integral and impactful seafloor habitats  
147 which influence biodiversity beyond the physical bounds of the site. Effective and genuine  
148 biology-archaeology collaborations are absolutely essential for future research. We have  
149 proposed a framework and questions for the emerging field of Maritime Heritage Ecology in  
150 order to launch interdisciplinary investigations. We call upon maritime archaeologists and  
151 marine ecologists alike to learn from one another and pursue answers to the broad-scale  
152 questions proposed here.

153

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161 **References**

- 162 1 Gravina, M.F. *et al.* (2021) First report on the benthic invertebrate community associated  
163 with a bronze naval ram from the First Punic War: a proxy of marine biodiversity. *Front.*  
164 *Mar. Sci.* 8, 772499
- 165 2 Hamdan, L.J. *et al.* (2021) Deep-sea shipwrecks represent island-like ecosystems for  
166 marine microbiomes. *ISME J.* 15, 2883–2891
- 167 3 Price, K.A. *et al.* (2020) A shallow water ferrous-hulled shipwreck reveals a distinct  
168 microbial community. *Front. Microbiol.* 11, 1897
- 169 4 Bałazy, P. *et al.* (2019) Shipwrecks and underwater objects of the southern Baltic – hard  
170 substrata islands in the brackish, soft bottom marine environment. *Estuar. Coast. Shelf*  
171 *Sci.* 225, 106240
- 172 5 Perasso, C.S. *et al.* (2022) The bioerosion of submerged archaeological artifacts in the  
173 Mediterranean: an overview. *Front. Mar. Sci.* 9, 888731
- 174 6 Work, T.M. *et al.* (2018) Managing an invasive corallimorph at Palmyra Atoll National  
175 Wildlife Refuge, Line Islands, Central Pacific. *Biol. Invasions* 20, 2197–2208
- 176 7 Casoli, E. *et al.* (2020) *Reteporella* spp. success in the re-colonization of bare  
177 coralligenous reefs impacted by Costa Concordia shipwreck: the pioneer species you did  
178 not expect. *Mar. Pollut. Bull.* 161, 111808
- 179 8 Hartland, A. *et al.* (2019) Aqueous copper bioavailability linked to shipwreck-  
180 contaminated reef sediments. *Sci. Rep.* 9, 1–13
- 181 9 Paxton, A.B. *et al.* (2019) Artificial reefs facilitate tropical fish at their range edge.  
182 *Commun. Biol.* 2, 168
- 183 10 Soares, M. de O. *et al.* (2020) Shipwrecks help invasive coral to expand range in the



- 184 Atlantic Ocean. *Mar. Pollut. Bull.* 158, 111394
- 185 11 Brennan, M.L. *et al.* (2016) Quantification of bottom trawl fishing damage to ancient  
186 shipwreck sites. *Mar. Geol.* 371, 82–88
- 187 12 Jimenez, C. *et al.* (2017) Epibenthic communities associated with unintentional artificial  
188 reefs (modern shipwrecks) under contrasting regimes of nutrients in the Levantine Sea  
189 (Cyprus and Lebanon). *PLoS One* 12, e0182486
- 190 13 Mugge, R.L. *et al.* (2019) Deep-sea biofilms, historic shipwreck preservation and the  
191 Deepwater Horizon spill. *Front. Mar. Sci.* 6, 48
- 192 14 Meyer-Kaiser, K.S. *et al.* (2022) Invertebrate communities on shipwrecks in Stellwagen  
193 Bank National Marine Sanctuary. *Mar. Ecol. Prog. Ser.* 685, 19–29
- 194 15 Meyer-Kaiser, K.S. *et al.* (2022) Structural factors driving benthic invertebrate community  
195 structure on historical shipwrecks in a large North Atlantic marine sanctuary. *Mar. Pollut.*  
196 *Bull.* 178, 113622
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- 198

199 **Glossary (422/500 words):**

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201 Ballast reef: a reef formed by the remains of a ship's cargo or ballast rocks after the wooden hull  
202 has degraded and disappeared. It is the closest analogue of natural boulder reefs.

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204 Community assembly: the process by which a biological community becomes established,  
205 including interactions among species and the structure of the habitat they occupy.

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207 Cultural transformations (c-transforms): site formation process stemming from human activities  
208 and behaviors that modify archaeological sites over time including artifact removal, fishing  
209 damage, and litter.

210

211 Boring species: species that chemically and physically alter UCH to create cavities in the  
212 material, resulting in degradation or erosion. The best-known example is the shipworm *Teredo*  
213 *navalis*, but boring species span a wide taxonomic range, including cyanobacteria, fungi, algae,  
214 and invertebrates.

215

216 Environmental equilibrium: a state in which the slope of the rate of change for an underwater  
217 cultural heritage site is zero. This does not imply that the rate of change is zero – the site may  
218 still be changing, but at a constant rate.

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220 Larval dispersal: the process by which the early life-history stages of invertebrates and fish  
221 spread through the marine environment, carried by oceanographic currents.

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Maritime Heritage Ecology: an emerging interdisciplinary field of study integrating maritime archaeology, community ecology, and biological oceanography to understand how maritime heritage and underwater cultural heritage function as habitats.

Natural transformations (n-transforms): site formation processes stemming from environmental conditions such as wave action, chemical reactions, and biological colonization.

Reciprocal influence: the concept that the physical structure of a UCH site and the species that colonize it influence one another and together determine the transformations of the site over time.

Recruitment: the process of a larva transitioning from its pelagic to its benthic life-stage and establishing itself in a benthic community. Recruitment is defined as the survival of an individual until counted by a researcher.

Site formation processes: the causal mechanisms that move artifacts and structures from their use context to their archaeological context and lead to further transformations over time.

Sphere of influence: the three-dimensional space surrounding a UCH site with some observable impact on biodiversity. Examples include changes in species composition in the sediments and schools of reef fish or swarms of zooplankton in the water column.

245 Stabilizing species: species that have a net effect of preserving or preventing the erosion of  
246 UCH. The concept of a stabilizing species is largely theoretical, though some studies have  
247 suggested that metabolic by-products from certain species could preserve textiles or paper, and  
248 sessile reef-building invertebrates could shield artifacts from erosion.

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250 Succession: the process of change in community structure over time as the result of  
251 environmental conditions or species interactions.

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253 Underwater cultural heritage: the remains of sea-going vessels and anthropogenic activities in a  
254 submerged environment.

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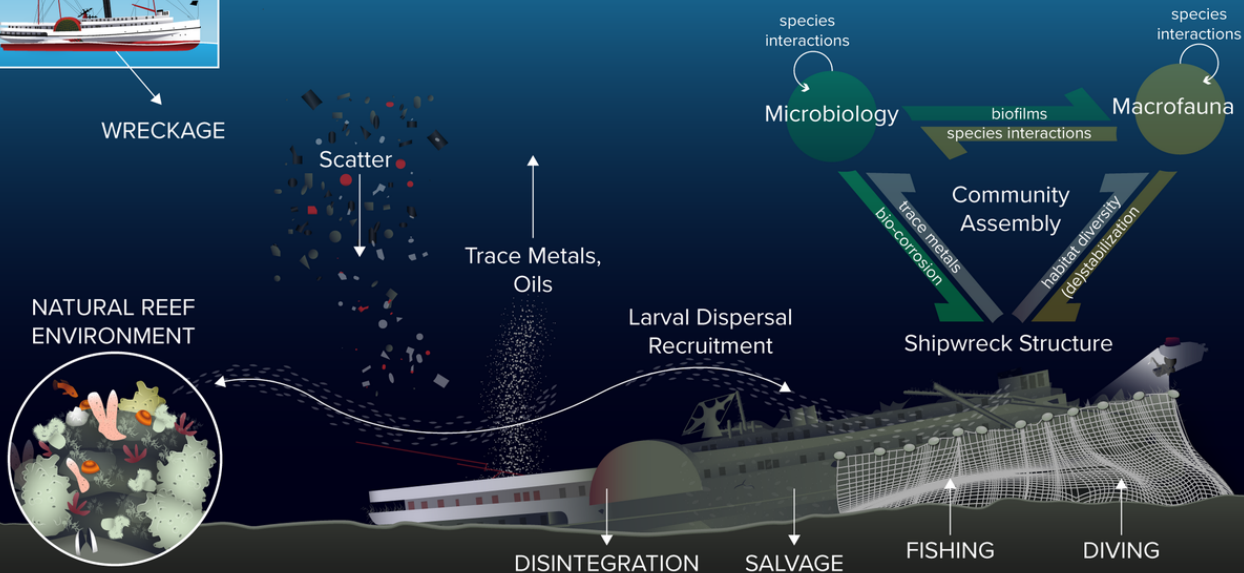
258 Figure 1: Intellectual framework for Maritime Heritage Ecology. A ship or other structure is  
259 transferred from its use context to its archaeological or environmental context via wrecking.  
260 Scattered materials, trace metals, and oil affect the surrounding environment. Disintegration and  
261 salvage remove material or contribute to the fragmentation of the shipwreck, but fishing and  
262 diving introduce material such as nets to the system. The UCH site is colonized by larval  
263 dispersal and recruitment of organisms from surrounding natural hard-bottom reefs and can serve  
264 as a stepping-stone for dispersal in turn. Interactions between microbes, macrofauna, and UCH  
265 structure shape the community. Succession of species, natural transformations, and cultural  
266 transformations of the site reciprocally influence one another over time.

## Use Context



WRECKAGE

## Environmental/Archaeological Context



Time

Succession

Natural Transformation

Reciprocal Influence

Cultural Transformation

