



First Report on the Benthic Invertebrate Community Associated With a Bronze Naval Ram From the First Punic War: A Proxy of Marine Biodiversity

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Historical traces of organisms on the seafloor, such as shells and tubes, constitute the ecological memory of ancient benthic assemblages and serve as an important resource for understanding the assembly of modern communities. Archeological shipwrecks are particularly interesting submerged substrata for both their archeological and biological implications. For the first time, we studied the species composition and life-history traits of dominant organisms in the benthic assemblage on a bronze Carthaginian naval ram, which sank more than two thousand years ago in the Southern Tyrrhenian Sea. By comparing the species composition of the ram assemblage with those of the surrounding habitats, we inferred possible colonization patterns for the ram and discussed the informative role of the shipwreck as a proxy of marine biodiversity. The ram assemblage was rich in species, including both sessile (bryozoans, serpulid polychaetes, and few bivalves) and motile (gastropods) species. Sexual reproduction with free-spawning fertilization and long-duration larvae characterized most species. The long submersion time of the ram, together with the reproductive strategies, growth forms, and motility of the dominant species were key factors shaping the community of the ram. The ram itself offers an archeological artifact of inestimable value, but our analysis revealed it to be an effective collector of fauna from the surrounding seabed. The ram community hosted species from a range of nearby natural habitats (mostly coralligenous, detritic bottoms, and zoosteracean meadows) and thus served as a proxy for marine biodiversity on the surrounding seabed. We conclude that the presence of many species on the ram that commonly occur in adjacent habitats of great environmental value was informative and highlight the important marine biodiversity in the area of the Aegadian archipelago.

Keywords: underwater cultural heritage, historical shipwrecks, submerged archeological artifacts, benthic community, marine biodiversity, Aegates archipelago, Mediterranean Sea

INTRODUCTION

Paleontological investigations of geological remains primarily aim at reconstructing ancient communities (i.e., tanatocenosis). However, the traces of more recent ecosystems offer further valuable consideration in neontological investigations. In fact, such ecological memory provides not merely a passive legacy but rather as a primary driver in the assembly of modern communities (Balaguer et al., 2014). Given that the time-scales for limestone degradation greatly exceed those for sedimentation, the accumulation of calcified remains such as skeletons and shells in marine sediments preserves the remnants of organisms that previously lived on a substratum. On the one hand, the analysis of historical traces of organisms trapped within a substratum provides the opportunity to describe ancient benthic assemblages over time (Bertolino et al., 2014). On the other hand, calcareous remains of organisms accumulated on a substratum have been used to study biodiversity over spatial scales (Albano and Sabelli, 2011).

Shipwrecks provide one type of substrata for the growth of benthic organisms that also hold interesting information on the development and dynamics of benthic communities. Archeological shipwrecks, the wreckages of ships sunk in the past, are considered highly valuable for both their archeological and biological implications. Most shipwreck studies have focused on archeological questions (for example, see Bass et al., 1989; Pulak, 2008; Foley et al., 2009; Petriaggi and Davidde, 2010; Leidwanger et al., 2021). In contrast, our study addresses ecological questions and focuses on the biological colonization of these substrata. Few published studies consider benthic communities colonizing shipwrecks. Some of them focus on ships sunk less than 100 years ago (Costa, 2016; Meyer et al., 2017), whereas others focus on archeological remains and the epilithic bioencrustations of ships' cargos (e.g., the marble statues from Antikythera, Greece, and the bronze statue of Satyrus of Mazara del Vallo, Sicily, Italy) (Ricci and Bartolini, 2005; Davidde et al., 2017; Ricci et al., 2019). Studies in the last decade have reported on the biodeterioration of underwater remains on stone and organic materials, in particular epilithic and endolithic assemblages and their role in the biodeterioration of archeological submerged artifacts (Ricci et al., 2013, 2015, 2016a,b; Antonelli et al., 2015; Sacco Perasso et al., 2015; Calcinai et al., 2019; Casoli et al., 2019a; Gravina et al., 2019).

Ours is the first study on the benthic assemblage associated with a bronze artifact and offers a novel contribution to the assessment of biodiversity on the seabed surrounding the archeological shipwreck. The ram 13 sank with a punic ship in 241 BC during the Aegates battle between the Romans and the Carthaginians (Tusa and Royal, 2012). We analyze the calcified zoobenthic organisms, including gastropod and bivalve mollusks, serpulid polychaetes, and bryozoans, accumulated in the sediment inside the naval ram during the prolonged period lying on the seabed in order to: (i) document species composition of the benthic assemblage collected in the ram; (ii) compare the observed assemblage with those of other Mediterranean communities and recognize biocenotic affinities; (iii) hypothesize possible colonization patterns of the ram by the benthic biota; and

(iv) infer the role of the wreck as “ecological memory” of marine biodiversity in the Aegates archipelago region.

MATERIALS AND METHODS

Study Area

The Battle of the Aegates Islands marked the end of the First Punic War and took place on March 10th 241 BC, when the Carthaginian relieving fleet was defeated off of western Sicily.

The environmental context of the area off-shore of Trapani, Marsala, and Mazza del Vallo (west and southwest of Sicily) that comprises the Aegates islands is a good example of a shelf affected by marine abrasion of a rocky, tectonized substratum, where scarce recent sediment deposits are mainly composed of bioclastic fragments (Colantoni et al., 1993).

The ram on which our study focuses work was discovered on the inner continental shelf that joins the islands of Favignana and Levanzo with the mainland (**Figure 1**). The shelf has a gentle slope with several shallow banks and minor islets that rise from the seafloor as erosional remnants. Depth minima occur on the shoals of Secca del Toro, 6 m; Secca dei Pesci, 21 m; and NW of Levanzo, 29 m (Colantoni et al., 1993).

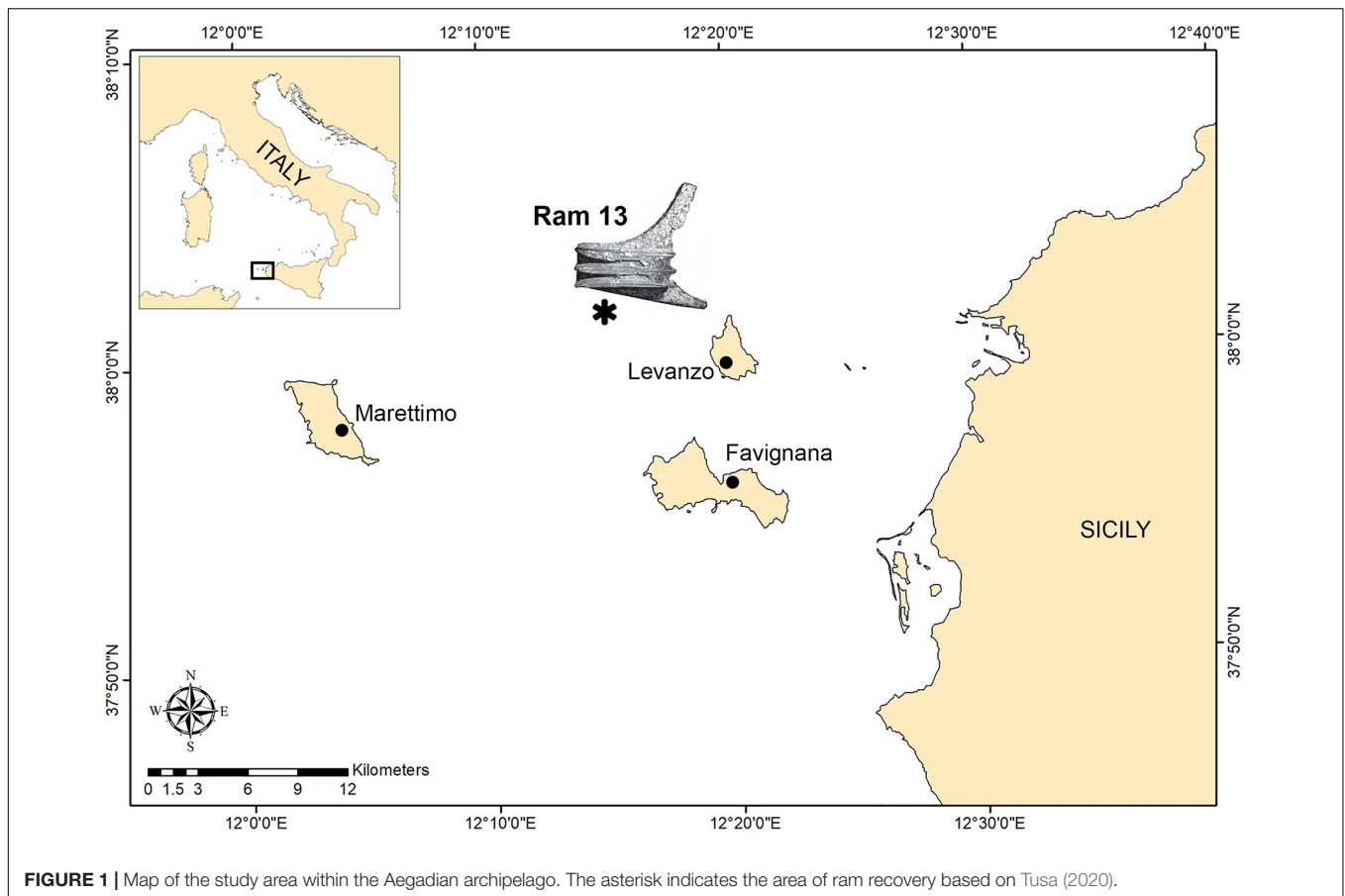
The Ram Egadi 13

A naval ram (*rostrum* in Latin) is a breakthrough thrusting weapon that was fitted to the bow of ancient galleys to break the hull framing of enemy ships. The rams found in the Aegates Islands weigh 170 kg on average and vary in thickness from about 1.5 cm in the laminar region to 5 cm in the front. The artifact examined in this study, referred to as ram 13, is a trident rostrum characterized of three sharp and blunt cuts (**Figure 2A**). This type of ram was common among the main Mediterranean warships beginning in the 4th century BC (Tusa and Royal, 2012). Ram 13 is of great importance because since it shows a Punic inscription on the upper sheath. This is the second rostrum with a Punic inscription discovered to date (the other was the Egates 3) (Tusa, 2020).

The discovery of these remains of significant scientific value occurred during several research campaigns as part of the Egadi Project. Exploration was carried out by the Soprintendenza del Mare della Regione Sicilia in collaboration with technical SCUBA divers from the organization GUE (Global Underwater Explorers). The project was conceived and directed through the cooperative efforts of Prof. Sebastiano Tusa and Jeffrey Royal and their institution, the Soprintendenza del Mare, Regione Siciliana, and the RPM Nautical Foundation, from 2005 to 2018. The ram in this study was recovered in October 2017 between 75 and 95 m depth, about 7 km north-west of the island of Levanzo, together with rostrum 12 and 10 bronze Montefortino helmets (Tusa, 2020).

Sampling Analysis

The ram was restored in 2019 using metals and alloys by Stefano Ferrari and Antonella Di Giovanni of the ICR Restoration Laboratory. The first stage of restoration involved sampling and documentation of the sediment blocks and biogenic materials



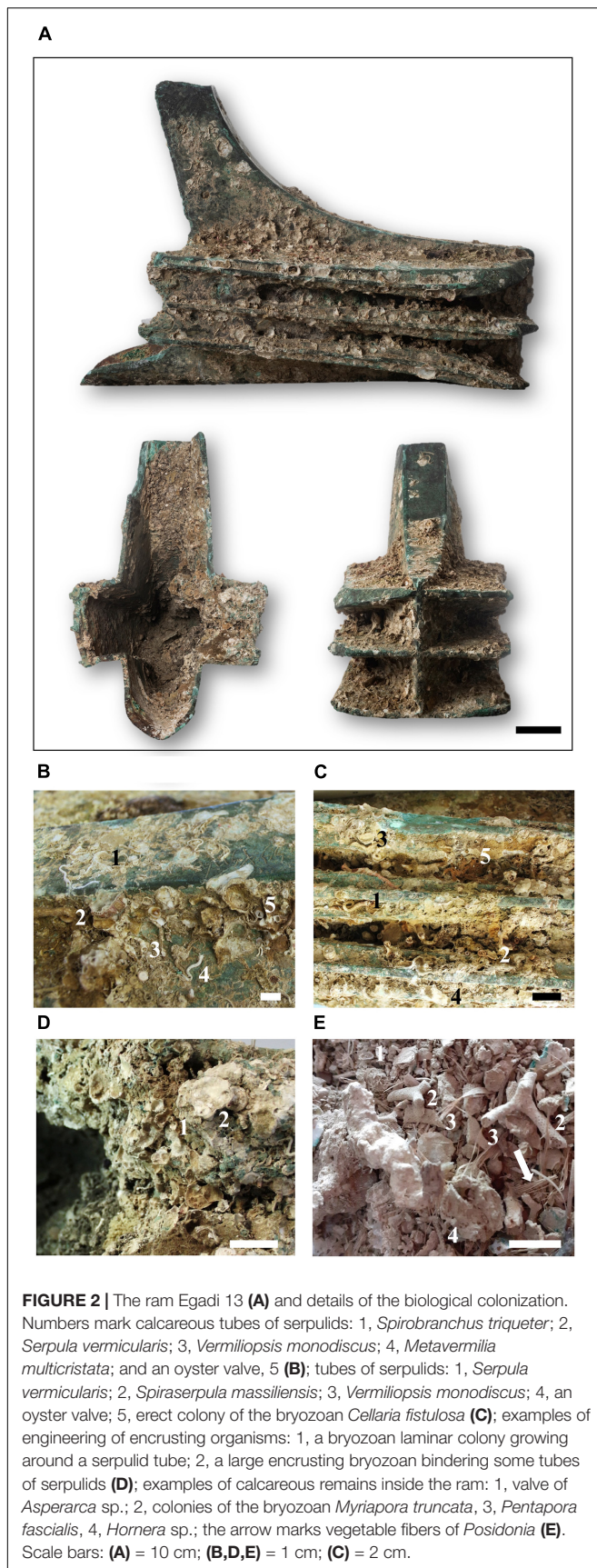
collected inside the inlet of the artifact. Images of the concretions and the material accumulated in the ram were collected using a digital camera. The sediment blocks compacted with *Posidonia* fibers and bioconcretions were separated from the sandy sediment. Every block was wetted with water, cleaned with a brush to remove the sediment, dried, and sieved with a 0.5 mm mesh. Subsequently, samples were observed under a stereomicroscope. All the biogenic fragmented remains, shells and tubes, were sorted by higher taxon and preserved in Petri dishes.

Data Analysis

Benthic specimens collected inside the entire ram were identified to species level whenever possible, and all data were used to construct a binary presence/absence matrix. The species richness of total benthos and of mollusks, polychaetes, and bryozoans, respectively, was considered a measure of α -diversity. All faunal data were analyzed by means of multivariate ordination technique non-metric multidimensional scaling (nMDS) using the Jaccard index. A clustering analysis based on Ward's minimum variance method compared the similarity between the faunal assemblage found in the ram and those of common shallow (infralittoral) and deep (circalittoral and bathyal) habitats. Analysis of similarities (ANOSIM) based on Bray–Curtis similarity matrix assessed significant differences between grouping of

habitats. A non-parametric SIMPER (Similarity Percentage) test identified those species that contributed most to the distinction among groups of habitats. Published literature sources provided information on species composition in each natural habitat and functional traits of each species on the ram (Table 2).

To infer possible colonization patterns of the artifact, we considered the main functional traits (Table 2) of the dominant species associated with the ram. We considered seven traits to describe the species' niches: (1) reproductive mode (sexual, asexual), (2) development strategy (brooding, free spawning, eggs laid in capsules or masses), (3) larval type (planktotrophic or lecithotrophic, for species with pelagic larvae), (4) modularity (solitary, aggregation, aggregation of a few individuals, colonial), (5) adult motility (sessile, motile), and (6) engineering (primary constructor, binder, dweller), (7) size (large, medium, small, according the details described in the caption of Table 1). Information on the engineering role of each species was based on Fagerstrom (1988). Specifically, primary constructors refer to erect well-skeletonized builders that provide volume and rigidity to the concretion; binders are encrusters that expand and connect the organic structures; and dwellers are mostly motile (rarely sessile) organisms that are not strictly builders but inhabit cavities and crevices of the concretion. Moreover, the ecological affinity of each species was assigned by combining personal observations and literature data reported in Table 2.



RESULTS

Species Composition, Ecology, and Life-Traits

The faunal assemblage in the ram included 114 species, including 58 species of mollusks (51%), 33 species of gastropods, 25 species of bivalves, 33 species of polychaetes (29%), and 23 species of bryozoans (20%). **Table 1** provides a complete list of species identified from the ram and their functional traits and ecological affinities. Sessile species, i.e., bryozoans, serpulids, and a few bivalves, colonized the ram surface extensively and grew in epibiosis on calcareous surfaces of other organisms. Motile species, mostly mollusks, occupied the inside of the ram in large numbers together with the remains of sessile species (colony fragments, tubes) (**Figures 2B–E**). The percentage of the species sharing each of the functional traits is reported in **Figure 3**.

Sexual reproduction, pelagic spawning, and extended pelagic larval duration characterized most of the mollusks. Embryonic development in masses or capsules with short pelagic larval duration characterized about half of the gastropods, e.g., *Alvania* spp., *Bittium reticulatum*, *Chauvetia giunchiorum*, *Jujubinus exasperates*, and *Turritella turbona*. Almost all of the species were solitary and motile. A few bivalves were sessile and primarily contributed to the concretion, such as *Chama gryphoides* and Ostracidae. In contrast, other sessile bivalves, i.e., *Acar clathrata*, *Arca tetragona*, *Asperarca secreta*, *Pteria hirundo*, and *Striaca lactea*, and all the motile mollusks were concretion dwellers. As for polychaetes, all species reproduced sexually, except for *Filograna* sp., *Filogranula* spp., and *Josephella marenzelleri*, which reproduced asexually. Most polychaetes were pelagic spawners with external fertilization and planktotrophic larvae and long pelagic duration, while only *Filograna* sp. and five Spirorbinae species were brooders that produced lecithotrophic, short-duration larvae. All polychaetes were sessile in the adult stage, and most were solitary. Among the serpulids, only *Filograna* sp., *J. marenzelleri*, and *Spiraserpula massiliensis* formed aggregations: *Filograna* sp. formed dense aggregations of small tubes in the ram. Spirorbid species occurred in a specific epibiotic association on mollusk shells, bryozoans, and tubes of other serpulids. Gregarious settlement occurred in the spirorbid *Janua*. Based on the tube size and their role in building the concretion, we considered serpulids important encrusting species that played the role of binders. This group included 20 species with medium and large tubes. We considered an additional 11 small-sized species from the genera *Filogranula* and *Semivermilia* and subfamily Spirorbinae as dwellers because they colonized crevices and interstices among calcareous surfaces and settled on top of shells and skeletons of other organisms. Bryozoans on the ram included species with sexual and asexual reproduction. Their colonies grew by asexual fragmentation and budding. Lecithotrophic larvae produced by sexual reproduction developed into new colonies. In the identified species, individuals placed eggs either into external brood chambers or retained them in the body cavity. Almost half of the bryozoan species grew on the substrate with

TABLE 1 | List of the identified species and their life-history traits and ecological affinities.

	Species	Life traits						Size	Ecological affinity
		Reproduction mode	Development strategy	Larval type	Modularity	Adult motility	Engineering		
Mollusk Bivalves									
1	<i>Abra prismatica</i> (Montagu, 1808)	Sex	FS	Plankto	S*	Motile	DW	l	DET
2	<i>Acar clathrata</i> (Defrance, 1816)	Sex	FS	Plankto	S	Sessile	DW	m	COR
3	<i>Arca tetragona</i> Poli, 1795	Sex	FS	Plankto	S*	Sessile	DW	l	COR, DET
4	<i>Asperarca nodulosa</i> (O. F. Müller, 1776)	Sex	BR	Lecitho/plankto	S*	Sessile	DW	l	COR, DET, CAV, BAT
5	<i>Asperarca secreta</i> La Perna, 1998	Sex		Plankto	S	Sessile	DW	s	SPH, COR
6	<i>Astarte sulcata</i> (da Costa, 1778)	Sex	FS	Plankto	S*	Motile	DW	l	DET
7	<i>Cardiomya costellata</i> (Deshayes, 1835)	Sex	FS	Plankto	S*	Motile	DW	l	DET
8	<i>Centrocardita aculeata</i> (Poli, 1795)	Sex	FS	Plankto	S*	Motile	DW	l	SPH, DET
9	<i>Chama gryphoides</i> Linnaeus, 1758	Sex	FS	Plankto	S	Sessile	PC	l	SPH, PZM, COR, DET
10	<i>Globivenus effossa</i> (Philippi, 1836)	Sex	FS	Plankto	S	Motile	DW	l	COR, DET
11	<i>Limaria loscombi</i> (G. B. Sowerby I, 1823)	Sex		Lecitho	S*	Motile	DW	l	PZM, DET
12	<i>Manupecten pesfelis</i> (Linnaeus, 1758)	Sex	FS	Plankto	S	Motile	DW	l	COR
13	<i>Mimachlamys varia</i> (Linnaeus, 1758)	Sex	FS	Plankto	S*	Motile	DW	l	SPH, COR, DET
14	<i>Nucula nucleus</i> (Linnaeus, 1758)	Sex	FS	Plankto	S*	Motile	DW	m	BAT
15	<i>Nucula nitidosa</i> Winckworth, 1930	Sex	FS	Plankto	S/A	Motile	DW	l	PZM, DET
16	<i>Ostreidae</i> ind.	Sex	FS	Plankto	S/A	Sessile	PC	l	
17	<i>Palliolium incomparabile</i> (Risso, 1826)	Sex	FS	Plankto	S*	Motile	DW	l	SPH, COR, DET
18	<i>Papillicardium papillosum</i> (Poli, 1791)	Sex	FS	Plankto	S/A	Motile	DW	l	SPH, PZM, COR, DET
19	<i>Pecten jacobaeus</i> (Linnaeus, 1758)	Sex	FS	Plankto	S	Motile	DW	l	DET
20	<i>Pododesmus squama</i> (Gmelin, 1791)	Sex	FS	Plankto	S	Motile	DW	l	
21	<i>Pteria hirundo</i> (Linnaeus, 1758)	Sex	FS	Plankto	S	Sessile	DW	l	COR
22	<i>Striarca lactea</i> (Linnaeus, 1758)	Sex	FS	Plankto	S/A	Sessile	DW	m	SPH, PZM, COR, DET, CAV
23	<i>Timoclea ovata</i> (Pennant, 1777)	Sex	FS	Plankto	S/A	Motile	DW	l	SPH, PZM, DET
24	<i>Venus nux</i> Gmelin, 1791	Sex	FS	Plankto	S	Motile	DW	l	COR, DET, BAT
25	<i>Venus verrucosa</i> Linnaeus, 1758	Sex	FS	Plankto	S*	Motile	DW	l	SPH, PZM, COR, DET
Mollusk Gastropods									
26	<i>Alvania cimicoides</i> (Forbes, 1844)	Sex	EC	Lecitho	S*	Motile	DW	s	BAT
27	<i>Alvania hispidula</i> (Monterosato, 1884)	Sex	EC	Lecitho	S*	Motile	DW	s	SPH, PZM, COR, DET
28	<i>Alvania subareolata</i> Monterosato, 1869	Sex	EC	Lecitho	S*	Motile	DW	s	COR
29	<i>Alvania weinkauffi jacobusi</i> Oliverio, Amati and Nofroni, 1986	Sex	EC	Lecitho	S*	Motile	DW	s	SPH
30	<i>Anatoma umbilicata</i> (Jeffreys, 1883)	Sex			S*	Motile	DW	s	BAT
31	<i>Bittium</i> sp. (Juvaniles)	Sex	EC	Lecitho	S*	Motile	DW	m	
32	<i>Bittium reticulatum</i> (da Costa, 1778)	Sex	EC	Lecitho	S*	Motile	DW	m	SPH, PZM, COR, DET
33	<i>Bolma rugosa</i> (Linnaeus, 1767)	Sex	FS	Plankto	S	Motile	DW	l	SPH, PZM, COR, DET

(Continued)

TABLE 1 | (Continued)

	Species	Life traits						Ecological affinity	
		Reproduction mode	Development strategy	Larval type	Modularity	Adult motility	Engineering		Size
34	<i>Calliostoma conulus</i> (Linnaeus, 1758)	Sex	FS	Plankto	S	Motile	DW	l	SPH, PZM, COR
35	<i>Cancellaria</i> sp.	Sex			S	Motile	DW	l	BAT
36	<i>Cerithiopsis</i> sp.	Sex	EC	Plankto	S	Motile	DW	l	
37	<i>Cerithium</i> sp. (Juveniles)	Sex			S	Motile	DW	l	
38	<i>Chauvetia giunchiorum</i> Micali, 1999	Sex	EC	Lecitho	S	Motile	DW	s	DET
39	<i>Chauvetia</i> sp.	Sex	EC	Lecitho	S	Motile	DW	s	
40	<i>Danilia tinei</i> (Calcara, 1839)	Sex	FS	Plankto	S	Motile	DW	m	PZM, COR, BAT
41	<i>Emarginula adriatica</i> O. G. Costa, 1830	Sex	FS	Plankto	S	Motile	DW	l	PZM, COR, DET
42	<i>Emarginula huzardii</i> Payraudeau, 1826	Sex	FS	Plankto	S	Motile	DW	l	SPH, COR
43	<i>Epitonium tiberii</i> (de Boury, 1890)	Sex	EC	Lecitho	S	Motile	DW	s	BAT
44	<i>Homalopoma sanguineum</i> (Linnaeus, 1758)	Sex	FS	Plankto	S	Motile	DW	m	PZM, COR
45	<i>Jujubinus exasperatus</i> (Pennant, 1777)	Sex	EC	Lecitho	S*	Motile	DW	m	PZM, COR
46	<i>Jujubinus</i> sp.	Sex	EC	Lecitho	S*	Motile	DW	m	
47	<i>Marshallora adversa</i> (Montagu, 1803)	Sex	FS	Plankto	S	Motile	DW	m	PZM, COR
48	<i>Metaxia metaxa</i> (Delle Chiaje, 1828)	Sex	FS	Plankto	S	Motile	DW	m	SPH, PZM, COR, DET
49	<i>Monophorus thiriota</i> Bouchet, 1985	Sex	FS	Plankto	S	Motile	DW	m	SPH, COR
50	<i>Murexsul aradasii</i> (Monterosato, 1883)	Sex	EC	Lecitho	S	Motile	DW	l	PZM, COR, BAT
51	<i>Pyrrunculus hoernesii</i> (Weinkauff, 1866)	Sex	FS	Plankto	S	Motile	DW	s	SPH, BAT
52	<i>Raphitoma pseudohystrix</i> (Sykes, 1906)	Sex	FS	Plankto	S	Motile	DW	m	BAT
53	<i>Raphitoma</i> sp.	Sex		Plankto	S	Motile	DW	m	
54	<i>Similiphora similior</i> (Bouchet and Guillemot, 1978)	Sex	FS	Plankto	S	Motile	DW	m	SPH, COR
55	<i>Sticteulima jeffreysiana</i> (Brusina, 1869)	Sex	FS	Plankto	S*	Motile	DW	s	COR, BAT
56	<i>Talassia dagueneti</i> (de Folin, 1873)	Sex	FS	Plankto	S	Motile	DW	s	BAT
57	<i>Turritella turbona</i> Monterosato, 1877	Sex	EC	Lecitho	S/A	Motile	DW	l	SPH, PZM, COR, DET
58	<i>Volvarina mitrella</i> (Risso, 1826)	Sex	FS	Plankto	S	Motile	DW	m	COR, DET
Annelida Polychaetes									
59	<i>Bathypermillia eliasoni</i> (Zibrowius, 1970)	Sex			S	Sessile	BN	m	MRH, BAT
60	<i>Filograna</i> sp.	Sex/asex	BR	Lecitho	S/A	Sessile	BN	s/m/l	
61	<i>Filigranula annulata</i> (O. G. Costa, 1861)	Sex/asex	FS	Plankto	S	Sessile	DW	s	CAV, MRH, BAT
62	<i>Filigranula calyculata</i> (O. G. Costa, 1861)	Sex/asex	FS	Plankto	S	Sessile	DW	s	MRH, CAV, BAT
63	<i>Filigranula gracilis</i> Langerhans, 1884	Sex/asex	FS	Plankto	S	Sessile	DW	s	MRH, BAT
64	<i>Hyalopomatus marenzelleri</i> Langerhans, 1884	Sex			S	Sessile	BN	m	BAT, MRH
65	<i>Janua</i> ind.	Sex	BR	Lecitho	S/A	Sessile	DW	s	
66	<i>Janua heterostropha</i> (Montagu, 1803)	Sex	BR	Lecitho	S/A	Sessile	DW	s	SPH, PZM, DET, COR, MRH, CAV
67	<i>Josephella marenzelleri</i> Caullery and Mesnil, 1896	Sex/asex	FS	Plankto	S/A	Sessile	BN	m	SPH, COR, MRH, CAV
68	<i>Metavermillia multicristata</i> (Philippi, 1844)	Sex	FS	Plankto	S	Sessile	BN	m	COR, MRH, CAV, BAT

(Continued)

TABLE 1 | (Continued)

	Species	Life traits						Ecological affinity	
		Reproduction mode	Development strategy	Larval type	Modularity	Adult motility	Engineering		Size
69	<i>Pileolaria endoumensis</i> (Zibrowius, 1968)	Sex	BR	Lecitho	S	Sessile	DW	s	SPH
70	<i>Pileolaria militaris</i> Claparède, 1870	Sex	BR	Lecitho	S	Sessile	DW	s	SPH, MRH
71	<i>Placostegus crystallinus</i> Zibrowius, 1968	Sex	FS	Plankto	S	Sessile	BN	m	DET, COR, MRH, CAV
72	<i>Placostegus tridentatus</i> (Fabricius, 1779)	Sex	FS	Plankto	S	Sessile	BN	l	BAT, MRH
73	<i>Protula tubularia</i> (Montagu, 1803)	Sex	FS/EC	Plankto	S	Sessile	BN	l	SPH, PZM, COR, MRH, CAV, BAT
74	<i>Semivermilia agglutinata</i> (Marenzeller, 1893)	Sex	FS	Plankto	S	Sessile	DW	s	BAT, MRH
75	<i>Semivermilia crenata</i> (O. G. Costa, 1861)	Sex	FS	Plankto	S	Sessile	DW	s	COR, MRH, CAV
76	<i>Semivermilia cribrata</i> (O. G. Costa, 1861)	Sex	FS	Plankto	S	Sessile	DW	s	PZM, COR, DET, MRH, CAV
77	<i>Serpula cavernicola</i> Fassari and Mollica, 1991	Sex			S	Sessile	BN	l	MRH, CAV
78	<i>Serpula concharum</i> Langerhans, 1880	Sex	FS	Plankto	S	Sessile	BN	m	SPH, DET, COR, MRH, CAV
79	<i>Serpula lobiancoi</i> Rioja, 1917	Sex	FS	Plankto	S	Sessile	BN	l	COR, MRH
80	<i>Serpula vermicularis</i> Linnaeus, 1767	Sex	FS	Plankto	S/A	Sessile	BN	l	SPH, PZM, COR, DET, MRH, CAV, BAT
81	<i>Spiraserpula massiliensis</i> (Zibrowius, 1968)	Sex	FS	Plankto	S/A	Sessile	BN	m	MRH, CAV, COR
82	<i>Spirobranchus</i> sp.	Sex	FS	Plankto	S	Sessile	BN	l	
83	<i>Spirobranchus lima</i> (Grube, 1862)	Sex	FS	Plankto	S	Sessile	BN	l	DET, COR, MRH
84	<i>Spirobranchus polytremata</i> (Philippi, 1844)	Sex	FS	Plankto	S	Sessile	BN	m	SPH, PZM, COR, MRH, CAV
85	<i>Spirobranchus triqueter</i> (Linnaeus, 1758)	Sex	FS	Plankto	S	Sessile	BN	l	SPH, PZM, COR, DET
86	<i>Spirorbis (Spirorbis) infundibulum</i> Harris and Knight-Jones, 1964	Sex	BR	Lecitho	S	Sessile	DW	s	SPH
87	<i>Vermiliopsis infundibulum</i> (Philippi, 1844)	Sex	FS	Plankto	S	Sessile	BN	l	COR, DET, MRH, CAV
88	<i>Vermiliopsis labiata</i> (O. G. Costa, 1861)	Sex			S	Sessile	BN	l	SPH, COR, MRH, CAV
89	<i>Vermiliopsis monodiscus</i> Zibrowius, 1968	Sex			S	Sessile	BN	l	MRH, CAV, BAT
90	<i>Spiochaetopterus typicus</i> M. Sars, 1856	Sex				Sessile			
91	<i>Spiochaetopterus solitarius</i> (Rioja, 1917)	Sex				Sessile			
Bryozoans									
92	<i>Adeonella pallasii</i> (Heller, 1867)	Sex/asex	BR	Lecitho	C	Sessile	PC	m	COR, CAV
93	<i>Aplousina filum</i> (Jullien and Calvet, 1903)	Sex/asex	BR	Lecitho	C	Sessile	BN	m	DET, CAV
94	<i>Cellaria fistulosa</i> (Linnaeus, 1758)	Sex/asex	BR	Lecitho	C	Sessile	PC	m	SPH, DET, MRH
95	<i>Celleporina caliciformis</i> (Lamouroux, 1816)	Sex/asex	BR	Lecitho	C	Sessile	BN	s	PZM, COR, CAV
96	<i>Celleporina caminata</i> (Waters, 1879)	Sex/asex	BR	Lecitho	C	Sessile	BN	s	SPH, PZM, COR, MRH, CAV
97	<i>Celleporina lucida</i> (Hincks, 1880)	Sex/asex	BR	Lecitho	C	Sessile	BN	s	SPH, COR, DET, MRH, BAT
98	<i>Cribellopora trichotoma</i> (Waters, 1918)	Sex/asex	BR	Lecitho	C	Sessile	BN	s	SPH, DET
99	<i>Criblaria hincksii</i> (Friedl, 1917)	Sex/asex	BR	Lecitho	C	Sessile	BN	l	BAT
100	<i>Criblaria setiformis</i> Harmelin and Aristegui, 1988	Sex/asex	BR	Lecitho	C	Sessile	BN	m	COR, DET, MRH, CAV
101	<i>Diporula verrucosa</i> (Peach, 1868)	Sex/asex	BR	Lecitho	C	Sessile	PC	m	COR, DET, CAV
102	<i>Escharella variolosa</i> (Johnston, 1838)	Sex/asex	BR	Lecitho	C	Sessile	BN	l	COR, DET, MRH

(Continued)

TABLE 1 | (Continued)

Species	Life traits				Ecological affinity		
	Reproduction mode	Development strategy	Larval type	Modularity	Adult motility	Engineering	Size
103 <i>Escharina vulgaris</i> (Moll., 1803)	Sex/asex	BR	Lecitho	C	Sessile	BN	m
104 <i>Escharoides mamillata</i> (Wood, 1844)	Sex/asex	BR	Lecitho	C	Sessile	BN	s
105 <i>Fron dipora verrucosa</i> (Lamouroux, 1821)	Sex/asex	BR	Lecitho	C	Sessile	PC	m
106 <i>Hippellozoon mediterraneum</i> (Waters, 1895)	Sex/asex	BR	Lecitho	C	Sessile	PC	m
107 <i>Hornera frondiculata</i> (Lamarck, 1816)	Sex/asex	BR	Lecitho	C	Sessile	PC	m
108 <i>Hornera lichenoides</i> (Linnaeus, 1758)	Sex/asex	BR	Lecitho	C	Sessile	PC	m
109 <i>Myriapora truncata</i> (Pallas, 1766)	Sex/asex	BR	Lecitho	C	Sessile	PC	m
110 <i>Onychocella marioni</i> Julien, 1882	Sex/asex	BR	Lecitho	C	Sessile	BN	l
111 <i>Palmiskenea skenei</i> (Ellis and Solander, 1786)	Sex/asex	BR	Lecitho	C	Sessile	BN	l
112 <i>Pentapora fascialis</i> (Pallas, 1766)	Sex/asex	BR	Lecitho	C	Sessile	PC	l
113 <i>Schizoretopora imperati</i> Busk, 1884	Sex/asex	BR	Lecitho	C	Sessile	PC	l
114 <i>Smittina cervicornis</i> (Pallas, 1766)	Sex/asex	BR	Lecitho	C	Sessile	PC	m

Reproductive mode: sex, sexual; asex, asexual. Development strategy: BR, brooding; FS, free (pelagic) spawning; EC, egg capsules/masses. Larval type: Plankto, planktotrophic larvae; Lecitho, lecithotrophic larvae. Modularity: S, solitary; S', solitary/few individuals; S/A, solitary/aggregation; C, colonial. Adult motility: Motile, motile; Sessile, sessile. Engineering: PC, primary constructors; BN, binders; DW, dwellers. Size: s, small; m, medium; l, large (for mollusks, s ≤ 5 mm, m = 6–10 mm, l > 10 mm; for serpulids and bryozoans colonies, s < 10 mm, m = 10–20 mm, l > 20 mm). Ecological affinity: SPH, Shallow Shelf Photophilic habitat; PZM, Posidonia and Zoosteraceae Meadows; DET, Detritic bottoms; COR, Coralligenous; MRH, Mesophotic Reef Habitat; CAV, Caves; BAT, Bathyal habitats.

erect-rigid colonies: *Myriapora truncata*, *Pentapora fascialis*, and *Schizoretopora imperati* with large colonies (more than 20 mm), and *Adeonella pallasii*, *Cellaria fistulosa*, *Diporula verrucosa*, *Fron dipora verrucosa*, *Hippellozoon mediterraneum*, *Hornera frondiculata*, *H. lichenoides*, and *Smittina cervicornis* with medium-sized colonies (11–20 mm). These bryozoans formed new colonizable substrata and increased habitat heterogeneity with their three-dimensional structures. The other half of the bryozoan species formed monolaminar and multilaminar colonies encrusting the substratum, such as *Cribilaria hinckinsii*, *Escharella variolosa*, *Onychocella marioni*, and *Palmiskenea skenei*, firmly attached to the substratum with their large multilaminar colonies. Other species, e.g., *Celleporina* spp., formed celleepoliform colonies and, together with species with small-sized (less than 10 mm) monolaminar encrusting colonies, e.g., *Cribellopora trichotoma* and *Escharoides mamillata*, colonized mostly fissures and interstices.

Faunal Assemblage of Ram and Similarity With Other Habitats

The nMDS ordination analysis (Figure 4A) highlighted differences between benthic assemblages in three groups. The ram assemblage most closely resembled the assemblages in coralligenous and detritic habitats in group 1. This group separated from shallow photophilic habitats and zoosteracean meadows (group 2) on one side of the nMDS plot and deeper mesophotic and bathyal habitats and caves (group 3) formed a second group on the other side of the nMDS plot (Figure 4A). The cluster analysis (Figure 4B) supported the nMDS ordination by yielded three main clusters. The assemblage on the ram grouped together with coralligenous and detritic habitats in group 1, while the shallower habitats and the deeper habitats in groups 2 and 3 formed separate clusters. The distinction between groups occurred at about 82% similarity. A total of 67 and 54 species on the ram, respectively, had affinities for coralligenous reefs (COR) and detritic bottoms (DET); meanwhile, bathyal habitats were less represented on the ram, with 30 species (Figure 4C).

A between-habitat ANOSIM comparison confirmed significant differences among these groups (Global R = 0.857, mean rank within group = 5.5, mean rank between groups = 17.5, and p < 0.005). Simper identified the species contributing most (>50%) to dissimilarity among habitats, including 22 species responsible for separating groups 1 and 2 (average dissimilarity 59%) and another 28 species that separated groups 1 and 3 (average dissimilarity 67.8%) (Table 3). A mostly sessile group of 12 species of bryozoans, eight species of serpulids, and two species of gastropods differentiated groups 1 and 2; bryozoans that form erect rigid colonies (66.7% of the species) contributed 54.5% to dissimilarity, with encrusting species comprising the remaining 33.3%. Large- or medium-sized serpulids (except *S. crenata*) accounted for 36% of dissimilarity. In contrast, 16 species of mollusks, all gastropods, were primarily responsible for the dissimilarity between groups 1 vs. 3 (57.2%). Different shell sizes and a wide range of ecological affinities

TABLE 2 | List of the references providing information on the functional traits and ecological affinities of each species of mollusks, polychaetes, and bryozoans found in the ram; species are marked in brackets with the same numbers as **Table 1**.**Mollusks:**

Lebour, 1937a	(11)
Lebour, 1937b	(32, 34, 36, 45)
Pérès and Picard, 1964	(1, 3, 7, 11, 21)
Meloni and Sabelli, 1980	(28)
Hughes, 1986	(57)
Webb, 1986	(1)
Dauvin and Gentil, 1989	(1)
Fish and Fish, 1989	(20)
Micali, 1998	(38)
Palazzi and Villari, 2001	(40)
Covazzi Harriague et al., 2002	(6, 23)
Allen, 2004	(11)
Castriota et al., 2005	(9, 18, 23, 58)
Oliver and Holmes, 2006	(2, 3, 4, 5, 22)
Crocetta and Spanu, 2008	(5, 17, 21, 34, 41, 45, 50)
Mazziotti et al., 2008	(4, 9, 18, 19, 22, 23, 25, 32, 33, 41, 48)
Morton, 2009	(23)
Rueda et al., 2009	(11, 15, 18, 23)
Rueda et al., 2016	(4, 40)
Scaperotta et al., 2009–2018	(1–5, 7–10, 12–19, 22, 23, 27, 32–34, 40–43, 45, 47–49, 51, 52, 55–58)
Albano and Sabelli, 2012	(27, 34, 47, 48)
Popović et al., 2013	(25)
Donnarumma et al., 2018a	(2, 9, 13, 27, 47, 54)
Donnarumma et al., 2018b	(3)
Donnarumma et al., 2018c	(45)
Giacobbe and Renda, 2018	(5, 8, 9, 17, 18, 22, 27, 29, 34, 42, 48, 49, 51, 54, 57)
Macri, 2018	(8, 10, 13, 14, 15, 17, 24, 33, 34, 57)
Casoli et al., 2019b	(3, 4, 9, 18, 22, 32, 47, 48).

Polychaetes:

Bianchi, 1981	(60, 61, 62, 64, 66, 67, 69, 70, 71, 72, 73, 75, 77, 82, 85, 86, 87)
Belloni and Bianchi, 1982	(60, 61, 62, 66, 67, 68, 74, 76, 79, 82, 85, 87, 88, 89)
Martin, 1987	(70, 88)
Smriglio et al., 1987a	(89)
Smriglio et al., 1987b	(68, 72, 75, 89)
Balduzzi et al., 1989	(66, 67, 70, 76, 77, 81, 85, 87, 88, 89)
Smriglio et al., 1989	(61, 68, 72, 89)
Sanfilippo and Mòlica, 2000	(78)
Antonoli et al., 2001	(81)
Boury-Esnault et al., 2001	(88)
Bianchi and Sanfilippo, 2003	(61, 62, 63, 66, 67, 68, 69, 70, 71, 72, 73, 74, 77, 78, 79, 80, 81, 82, 84, 85, 86, 87, 88, 89)
Rosso and Sanfilippo, 2005	(60, 66, 79, 82)
Ballesteros, 2006	(60, 71, 73, 74, 79, 85)
Rosso and Sanfilippo, 2009	(66, 71, 73, 76, 79, 80)
Mastrototaro et al., 2010	(59, 60, 63, 68, 85, 89)
Rosso et al., 2010	(59, 61, 63, 68, 75, 82, 89)
Rosso et al., 2013b	(67, 70, 74, 76, 81)
Taviani et al., 2015	(82)
Casoli et al., 2016	(60, 66, 67, 68, 70, 73, 74, 76, 77, 79, 80, 81, 82, 85, 86, 87, 89)
Sanfilippo et al., 2017	(60, 66, 67, 70, 74, 76, 77, 79, 82, 85, 88)
Corriero et al., 2019	(60, 63, 68, 71, 76, 78, 79, 81, 82, 87, 88)

(Continued)

TABLE 2 | (Continued)

Polychaetes:

Taviani et al., 2019	(59, 82)
Cardone et al., 2020	(59, 60, 61, 62, 63, 64, 66, 67, 68, 70, 71, 72, 73, 74, 75, 76, 77, 78, 79, 80, 81, 84, 85, 87, 89)
Gravina et al., 2021	(59, 60, 61, 62, 63, 66, 67, 68, 70, 71, 72, 73, 74, 75, 76, 77, 78, 79, 80, 82, 84, 85, 87, 88, 89).

Bryozoans:

Harmelin, 1985	(96)
Pisano and Boyer, 1985	(98)
Harmelin and Aristegui, 1988	(100)
Zabala et al., 1993	(111)
Rosso, 1996	(93)
Rosso, 1999	(110)
Harmelin, 1997	(93)
Rosso and Di Geronimo, 1998	(101, 108, 111)
Morri et al., 1999	(97, 103)
McKinney and Jaklin, 2000	(94)
Cocito et al., 2002	(112, 114)
Kocak et al., 2002	(96, 103)
Novosel et al., 2004	(95, 109, 113)
Novosel, 2005	(94, 112)
Novosel et al., 2019	(92, 97)
Harmelin et al., 2009	(114)
Rosso et al., 2010	(111)
Rosso et al., 2013a	(96, 103, 107, 110)
Rosso et al., 2013b	(101, 104)
Souto et al., 2010	(98)
Janssen et al., 2013	(100)
Madurell et al., 2013	(94, 102, 104, 105, 110)
Chimenz Gusso et al., 2014	(92, 94, 96, 97, 98, 102, 103, 104, 106, 109, 110, 112, 113, 114)
Gili et al., 2014	(100)
Harmelin, 2017	(103, 109)
Rosso et al., 2019	(92, 96, 97, 105, 106, 110)
Rueda et al., 2019	(99)
Casoli et al., 2020	(112, 114)
Giampaoletti et al., 2020	(94, 96, 97, 100, 102, 103, 105, 109, 112, 114).

characterized these gastropods, including sciaphilic circalittoral and photophilous infralittoral habitats (except for *Volvarina mitrella*, *Alvania subareolata*, and *C. giunchiorum*, which show specific preference for coralligenous and detritic habitats). Ten species of bryozoans contributed to the dissimilarity (35.7%), half of which form erect colonies and the other half form encrusting colonies.

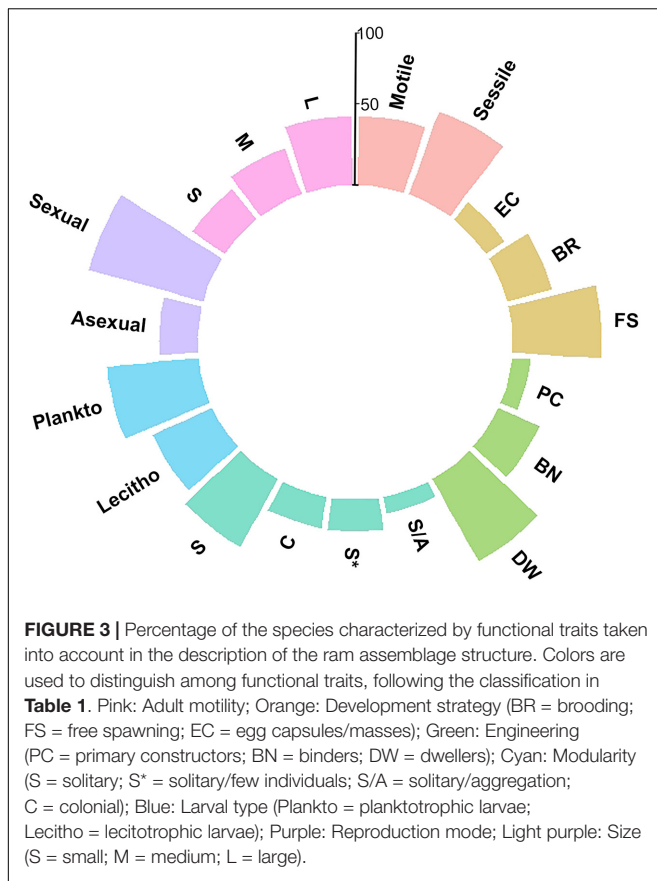
DISCUSSION

Ours is the first study on the macrobenthic assemblage that colonized an artifact of cultural interest that remained submerged for two millennia in the Mediterranean Sea. The bronze naval ram, from a Carthaginian ship sunk during the battle of Aegates in 241 BC, collected colonizing fauna from surrounding habitats over a 2000-year period. The marine organisms settled, overgrew, and encrusted all available surfaces and, given the long time of immersion, we infer that this cultural artifact has

become a suitable substratum for the development of a benthic community with ecological connectivity to natural communities in adjacent habitats. Indeed, duration of submersion and functional traits of the dominant species play major roles in shaping community structure on artificial reefs and their similarities (or dissimilarities) with natural reefs (Perkol-Finkel et al., 2005, 2006).

Faunal Assemblage Associated With Ram

The benthic fauna associated with the ram included a highly diverse assemblage primarily dominated by mollusks and secondarily dominated by polychaete serpulids and bryozoans. The analysis of functional traits revealed that the majority of species in the assemblage were large, sessile, solitary, or colonial invertebrates, i.e., all the bryozoans, the serpulids, and only nine bivalves. Among them, the bryozoans with erect colonies played the role of primary constructors. This

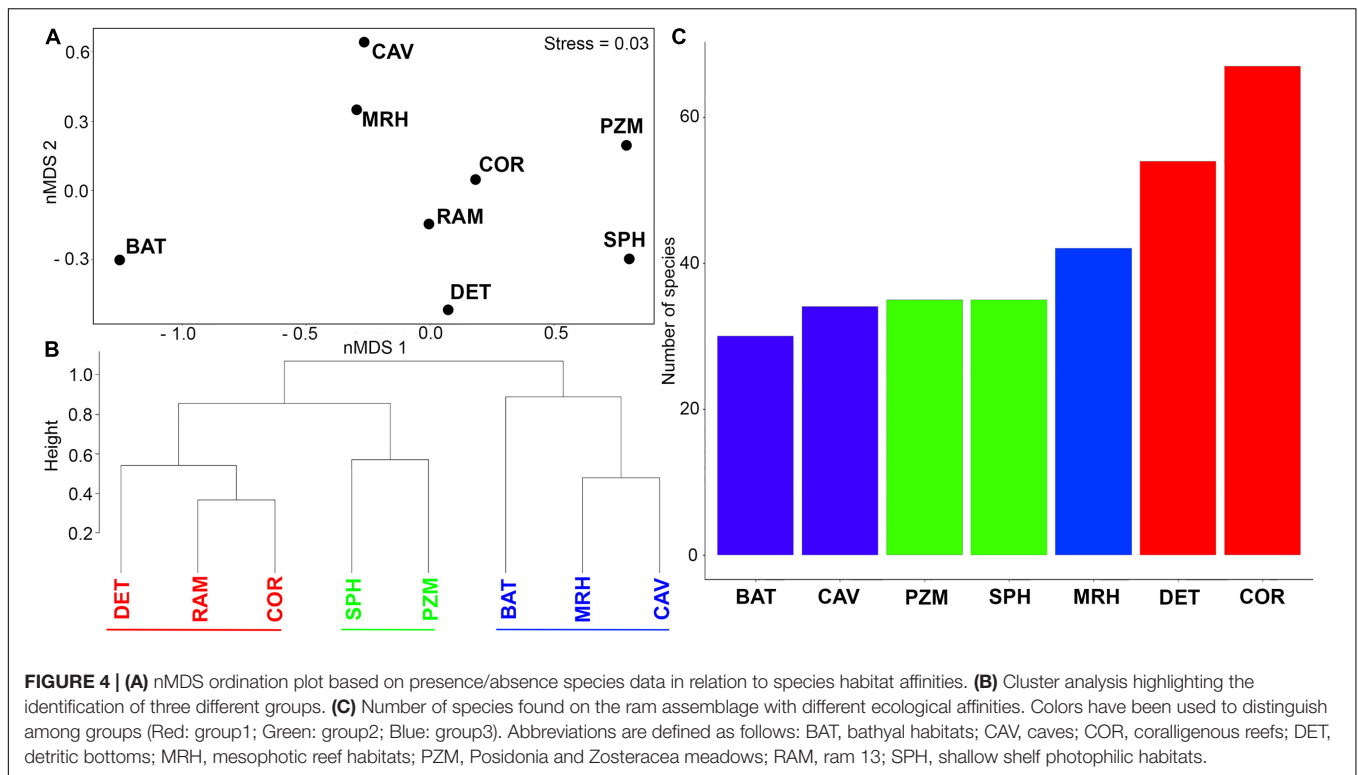


role was filled by very few species (*H. mediterraneum*, *M. truncata*, *P. fascialis*, and *S. cervicornis*), similar to what occurs on hard substrata in shallow photophilic and deeper habitats, as well as on coralligenous reefs, semi-dark caves, and mesophotic bioconstructions. Bryozoans often act as frame builders with erect colonies resulting in distinct conditions, such as the facies of large arborescent bryozoans on coastal detritic bottoms or structures built by just a few species (Cocito, 2004; Bianchi, 2009). In contrast, in many bioconcretions, bryozoans play a role as secondary constructors (encrusters) and produce crusts rather than erect layers (Cocito, 2009). The ram exhibited this latter colonization pattern, where the bryozoans largely encrusted the substratum and played the role of binders. Species such as *Escharina vulgaris*, *Onyhecella marioni*, *E. variolosa*, *Cribrilaria setiformis*, *Cribrilaria hincksii*, and *P. skenei*, as well as other small-sized colonies, e.g., *Celleporina caminata*, *Celleporina lucida*, and *C. trichotoma* bound together the concretion as well as detrital material. They expanded their mineralized colonies both on the ram (as primary substratum) and on organic calcareous surfaces (as secondary substrata), overgrowing colonies, shells, and tubes of other organisms. They cemented the underlying species and, in turn, were colonized by epibiotic organisms. Similarly, several medium- to large-sized serpulids (e.g., *Serpula vermicularis*, *Serpula concharum*, *Protula tubularia*, *Spirobranchus triqueter*, *Vermilipsis labiata*, *Vermilipsis infundibulum*, *Vermilipsis monodiscus*, and *Placostegus tridentatus*) contributed to build

the basal framework of the concretion, settling with their calcareous tubes directly on the bronze substrate. Many serpulids grew as epibionts on calcareous skeletons and valves of other sessile organisms, thus acting as secondary constructors together with the bryozoans. In this way, serpulids and bryozoans enhanced the small-scale spatial heterogeneity and increased the three-dimensionality of the ram's surface. They created new microhabitats, from laminar crusts to massive crusts rich in interstices, pits, and crevices. These microhabitats provided cryptic refuges that served as high-quality habitat for many dweller species.

The engineering category of dwellers constituted the majority of the ram assemblage, including the inhabitants of the interstitial spaces of the concretion and of the detritus collected inside the ram. Small-/medium-sized species formed a conspicuous component of this functional group because of their small dimensions, an effective adaptation to cryptic habitats. Serpulids (*Semivermilia cribrata*, *Semivermilia crenata*, *Filigranula annulata*, *F. calyculata*, *F. gracilis*, *Janua eterostropha*, and *Pileolaria militaris*) with their small tubes and bryozoans (*Celleporina* spp., *C. trichotoma*, and *Escharoides mamillata*) with small-sized colonies both settled in clusters on interstitial surfaces. Similarly, many small gastropods typically occur in shaphilic coralligenous (*Alvania subaereolata*, *Stricteulima jeffreysiana*, and *Volvarina mitrella*) and bathyal habitats (*Anatoma umbilicata*, *Epitonium tiberii*, *Raphitoma pseudohystrix*, and *Talassia degueneti*) and colonize interstices and crypts where they find refuge from currents, irradiance, and predation. In contrast, most mollusks of medium to large size colonized both the concretion and the detritus accumulated inside the ram. Here, many bathyal and cave-dwelling species (*Asperarca nodulosa* and *Venus nux*) co-occurred with other species typical of shaphilic detritic and coralligenous habitats (*Abra prismatica*, *Astarte sulcata*, *Cardiomya costellata*, *Pecten jacobaeus*, *Mimachlamys varia*, *Palliolium incomparabile*, *Papillicardium papillosum*, and *S. lactea*).

Our analysis of the reproductive and life-history traits of the species in the ram supports conclusions from previous studies on the colonization of artifacts. Most species (60%) reproduced sexually through pelagic fertilization and produced larvae with long pelagic durations that may undergo long-range dispersal in the intense deep currents in our study area (Suriano et al., 1992). Thus, we consider the ram an island-like habitat (Meyer et al., 2017) of solid substrate surrounded by a soft seabed. In fact, the ram interrupted the continuity of the soft seafloor and offered a surface suitable for larval settlement of hard-bottom species as well as adequate elevation above the bottom to expose organisms to stronger bottom currents and associated particulate food sources. Moreover, planktonic larvae advected by oceanographic currents were not the only dispersal mechanism for the ram fauna. The presence of a remarkably high percentage (40%) of brooding species on the ram (i.e., all the bryozoans, a few serpulids, and half of the gastropods with embryonic development inside attached capsules) suggested that recruitment on the ram also took place *via* short-dispersal planktonic propagules, small-sized adults, and fragments of colonies arriving from source populations in the area by passive drift. Moreover, we



hypothesize the arrival of some species by migration from nearby habitats, particularly for large-sized motile gastropods from coralligenous habitats (e.g., *Murex sul aradasii* and *Calliostoma conulus*) and detritic bottoms (e.g., *T. turbona* and *Bolma rugosa*).

Ram Assemblage and Relationship With Surrounding Habitats

Based on the ecological affinity of the species, the benthic assemblage on the ram differed in similarity from those in infralittoral, circalittoral, and bathyal habitats. All these habitats used as comparisons have been reported in the waters of the Aegadian archipelago. The Aegates Islands seabeds represent an area of great ecological value, with several endemic habitats protected by EU regulations and effectively managed through the designation of the largest Italian MPA (Aegates Islands MPA). Nevertheless, knowledge gaps remain regarding the distribution, biodiversity, and ecological status of benthic communities in the area. Uniformly distributed *Posidonia oceanica* meadows in the infralittoral zone cover the sandy seabed to depths over 30 m. Conversely, algae-dominated (i.e., brown algae belonging to the genus *Cystoseira*) belts develop at shallow depths and characterize photophilic rocky floors (Catra et al., 2006). The presence of the *Cystoseira* spp. thalli shapes environmental features and creates suitable conditions for invertebrate settlement (Sanfilippo et al., 2017). Coralligenous reefs occur mainly on steep walls, hard bottoms below 40 m depth, and shoals around the whole archipelago and represent the most attractive seascape for diving tourists (Cocito et al., 2014). Among the 200 Rhodophyta species

reported in the algal checklist of the area (Catra et al., 2006 and the references therein), widespread distributions across all islands of the archipelago characterize the Corallinales and Peyssonneliales that form the basal layer of coralligenous reefs. Recent distribution patterns of encrusting red algae likely reflect the spread of coralligenous reefs in the study area. The carbonatic lithology of the islands supports several submerged caves that originated through karstic phenomena (Gerovasileiou and Bianchi, 2021). Furthermore, organogenic detritus composed of animal debris enriches the carbonate sandy bottom sediments of the Aegadian archipelago, likely stemming from the erosion of coralligenous reefs and marine cave communities. Recent work described deep and cold-water coral assemblages in seamounts and banks surrounding the Aegean islands between 240 and 300 m depth (Bo et al., 2014; Angiolillo et al., 2021). Although this previous work reported Porifera and Cnidaria as the most frequent taxa, our study did not find them. Angiolillo et al. (2021) highlighted the importance of hard bottoms (sparse boulders and wrecks) for the richness and diversity of the megabenthic assemblages, resulting in high ecological value and conservation interest for the whole area.

All of these factors play a key role in understanding the composition of the ram assemblage. Indeed, the distribution and bathymetric range of the benthic communities in the region explain the higher affinity in species composition of the ram assemblage with coralligenous reefs and detritic bottoms, which form the group 1 in the nMDS plot and in the cluster analysis. On the one hand, both coralligenous and detritic habitats thus represent the main source populations that would have provided the larval supply necessary for colonization of the ram; in

TABLE 3 | Results of SIMPER analysis for identification of species contributing the most to faunal dissimilarity between habitats.

Group 1 vs. Group 2 (Overall dissimilarity 59%)	Av. dissimilarity	Contrib.%	Cumulative%
<i>Volvarina mitrella</i> (M)	1,48	2,51	2,51
<i>Smittina cervicornis</i> (B)	1,48	2,51	5,03
<i>Schizoretepora imperati</i> (B)	1,48	2,51	7,54
<i>Spirobranchus lima</i> (S)	1,48	2,51	10,05
<i>Escharoides mamillata</i> (B)	1,48	2,51	12,56
<i>Fron dipora verrucosa</i> (B)	1,48	2,51	15,08
<i>Palmiskenea skenei</i> (B)	1,48	2,51	17,59
<i>Escharella variolosa</i> (B)	1,48	2,51	20,1
<i>Cribrilaria setiformis</i> (B)	1,48	2,51	22,61
<i>Hippellozoon mediterraneum</i> (B)	1,48	2,51	25,13
<i>Diporula verrucosa</i> (B)	1,48	2,51	27,64
<i>Myriapora truncata</i> (B)	1,48	2,51	30,15
<i>Placostegus crystallinus</i> (S)	1,48	2,51	32,66
<i>Vermiliopsis infundibulum</i> (S)	1,48	2,51	35,18
<i>Metavermilia multicristata</i> (S)	1,12	1,9	37,08
<i>Alvania subareolata</i> (M)	1,12	1,9	38,98
<i>Serpula lobiancoi</i> (S)	1,12	1,9	40,88
<i>Semivermilia crenata</i> (S)	1,12	1,9	42,78
<i>Vermiliopsis labiata</i> (S)	1,12	1,9	44,68
<i>Spiraserpula massiliensis</i> (S)	1,12	1,9	46,59
<i>Hornera lichenoides</i> (B)	1,03	1,75	48,34
<i>Hornera frondiculata</i> (B)	1,03	1,75	50,09
Group 1 vs. Group 3 (Overall dissimilarity 67,8%)	Av. dissimilarity	Contrib.%	Cumulative%
<i>Escharoides mamillata</i> (B)	1,622	2,392	2,392
<i>Alvania hispidula</i> (M)	1,622	2,392	4,784
<i>Bolma rugosa</i> (M)	1,622	2,392	7,175
<i>Schizoretepora imperati</i> (B)	1,622	2,392	9,567
<i>Volvarina mitrella</i> (M)	1,622	2,392	11,96
<i>Metaxia metaxa</i> (M)	1,622	2,392	14,35
<i>Emarginula adriatica</i> (M)	1,622	2,392	16,74
<i>Monophorus thiriota</i> (M)	1,24	1,829	18,57
<i>Emarginula huzardii</i> (M)	1,24	1,829	20,4
<i>Alvania subareolata</i> (M)	1,24	1,829	22,23
<i>Similiphora similior</i> (M)	1,24	1,829	24,06
<i>Calliostoma conulus</i> (M)	1,24	1,829	25,89
<i>Homalopoma sanguineum</i> (M)	1,24	1,829	27,72
<i>Jujubinus exasperatus</i> (M)	1,24	1,829	29,54
<i>Cribellopora trichotoma</i> (B)	1,14	1,682	31,23
<i>Chauvetia giunchiorum</i> (M)	1,14	1,682	32,91
<i>Palmiskenea skenei</i> (B)	1,124	1,658	34,57
<i>Onychocella marioni</i> (B)	1,116	1,646	36,21
<i>Diporula verrucosa</i> (B)	1,116	1,646	37,86
<i>Hippellozoon mediterraneum</i> (B)	1,116	1,646	39,5
<i>Spirobranchus triqueter</i> (S)	1,003	1,48	40,98
<i>Turritella turbona</i> (M)	1,003	1,48	42,46
<i>Smittina cervicornis</i> (B)	1,003	1,48	43,94
<i>Spirobranchus lima</i> (S)	1,003	1,48	45,42
<i>Escharella variolosa</i> (B)	1,003	1,48	46,9
<i>Bittium reticulatum</i> (M)	1,003	1,48	48,38
<i>Pentapora fascialis</i> (B)	1,003	1,48	49,86
<i>Murexsul aradasii</i> (M)	0,984	1,451	51,31

M = mollusks, B = bryozoans, S = serpulids.

fact, pelagic spawning species with long-lived pelagic larvae dominated. On the other hand, the strong regional hydrodynamic regime, which presumably promoted the transport of both propagules and fragments or mineralized remains inside the ram, can partially explain the presence of species whose affinity links shallow habitats, such as *Posidonia* meadows. In support of this hypothesis, the facies dominated by *Laminaria rodriguezii* reported in the region (Suriano et al., 1992; Araújo et al., 2016) indicate the presence of high-speed bottom currents on the surrounding seabed.

These results offer insights regarding the expected timeframe for a submerged wreck to match natural habitats. Previous research showed that the benthic invertebrate communities on shipwrecks up to more than a century old do not match the background community (Perkol-Finkel and Benayahu, 2004; Perkol-Finkel et al., 2005, 2006). Indeed, wrecks generally have lower functional diversity than natural habitats and are dominated by species with long pelagic larval duration and/or asexual reproduction by fission. Our study showed that a ram that has accumulated biota over many centuries hosts a community with high functional diversity and species that occur in a range of surrounding natural habitats.

CONCLUSION

Ram 13, which remained on the sedimentary seafloor for more than 2000 years, has had sufficient time to establish a long-term stable community composed of both hard- and soft-bottom benthic organisms. The ram has trapped mineral structures and fragments (i.e., tubes and shells) of species living in the surrounding habitats transported by bottom current. Therefore, together with its inestimable value as an archeological artifact, the ram represents a novel and effective sampling tool. The ram highlights the dynamics of biological colonization on a large spatial scale and serves as a relevant proxy for the study of marine biodiversity.

Our study highlighted the high species richness of the benthic assemblage associated with the ram, whose composition showed strong similarity with coralligenous reefs and detritic circalittoral habitats, with *Posidonia* beds and photophilic rocky bottoms, and to a lesser degree with the deeper bathyal habitats and caves. All these habitats have great environmental value and are considered hotspots of biodiversity in different depth ranges. Thus, the presence of species in the ram assemblage that are common to

different habitats serves as “ecological memory” of the occurrence of such habitats in the surrounding seabed and highlights the high marine biodiversity in the Aegadian archipelago region. In this way, the benthic assemblage of the ram served as a remarkable proxy for marine biodiversity over a large spatial scale. The present study may act as a crucial baseline for future investigations in the Battle of the Aegates Islands region, which is of great interest in ecology and in archeology.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

MG: supervision, conceptualization, data curation, investigation, taxonomical and formal analysis, methodology, writing—original draft, and writing—review and editing. EC: data curation, investigation, formal analysis, methodology, and writing—review and editing. LD and JG: data curation, investigation, taxonomical and formal analysis, methodology, and writing—review and editing. FA and CS: data curation, investigation, laboratory and formal analysis, methodology, and writing—review and editing. SR: supervision, conceptualization, data curation, investigation, formal analysis, writing—original draft, and writing—review and editing. All authors contributed to the article and approved the submitted version.

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