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Effects of substrata and environmental conditions on ecological succession on historic shipwrecks

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A B S T R A C T

An understanding of the interactions between biological, chemical and physical dynamics is especially important for the adequate conservation of the Underwater Cultural Heritage. However, while physical and chemical processes are relatively well-investigated, the biological communities associated with these habitats are poorly studied. We compared the sessile community developed on panels of different materials placed on two historical shipwrecks, the *Fougueux* and the *Bucentaure*, from the Battle of Trafalgar (October 1805). Six materials used at the construction of vessels at the 18th and 19th centuries were selected: copper, brass, cast iron, carbon steel, pine and oak. The sessile community developed on the panels was studied two and 15 months after their immersion at the water to determine the effects of materials and environmental conditions (sediments, waves, hydrodynamic conditions, temperature and salinity) on ecological succession and the possible implications at the conservation of historical shipwrecks. On the *Fougueux*, the environmental conditions more strongly influenced the biological succession than the material type, with pioneer colonisers dominating the communities in both sampling periods. On the *Bucentaure*, exposed to more stable environmental conditions, the sessile community showed differences between sampling periods and among materials at the end of the experiment. Under these more stable environmental conditions, the material type showed a higher influence on the sessile community. Species that produce calcareous concretions developed on metallic panels, but were absent on wood panels, where the shipworm *Teredo navalis* was more abundant. The relationship between environmental conditions, sessile organisms and material type can influence the conservation status of the archaeological sites.

1. Introduction

In recent decades, underwater archaeology has highlighted that site formation is a complex process and involves a variety of physical, chemical and biological phenomena (Fernández-Montblanc et al., 2016; López-Garrido et al., 2015; Ruuskanen et al., 2015). Thus, for adequate conservation of the Underwater Cultural Heritage (UCH), an understanding of the interactions between biological, chemical and physical dynamics is especially important (Zintzen et al., 2008). To assess the impacts of such dynamics on site formation, it is necessary to consider certain physico-chemical variables such as temperature, salinity, intensity and direction of currents and waves, etc. (Bergstrand and Godfrey, 2007; Richards, 2009). However, while physical and chemical processes are relatively well-investigated, the biological communities associated with UCH sites are poorly studied (Massin et al., 2002; Zintzen et al., 2006).

Historic shipwrecks and other UCH sites can play important

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roles in marine ecosystems, constituting a substratum for the colonisation by marine organisms and the development of a stable community over time (Zintzen et al., 2006, 2007, 2008). Shipwrecks can act as artificial reefs and hotspots of biodiversity, providing shelter and nursery zones for some species (Lengkeek et al., 2013; Walker et al., 2007). Artificial substrata provide a unique opportunity to study the colonization patterns into new habitats by faunal communities (García-Sanz et al., 2012). Indeed, several authors highlight that artificial reefs, such as shipwrecks, are good model systems to assess the colonization of artificial substrata in the sea (Boaventura et al., 2006; Walker et al., 2007).

The study of the biological communities associated to the UCH (Massin et al., 2002; Zintzen et al., 2008, 2006; among others) is also important as such communities can have positive or negative effects on the conservation and integrity of the site and the individual artefacts that comprise it, that is, a given biological community may influence their preservation or deterioration. The detrimental effects of micro- and macroorganisms that comprise the biofouling community may have both mechanical (consequence of their attachment to substratum) and metabolic origin (physical-chemical changes induced at materials). For example, bacterial activities may lead to the biodegradation of some materials (Wheeler, 2002), and boring species are especially destructive towards wood (Cragg et al., 1999; Wheeler, 2002). On the other hand, the sessile community can provide protection from physical and chemical degradation (Bethencourt et al., 2010; López-Garrido et al., 2015; Wheeler, 2002). In this regard, the presence of some species on wood could prevent the action of boring organisms (Pournou et al., 2001) or the abrasive effect due to sediment transport (Camidge, 2009). One of the most obvious influences of the sessile community is the formation of bio-concretions, at particular over iron objects, both cast and wrought (López-Garrido et al., 2015; Wheeler, 2002). Unlike concretions formed on terrestrially recovered artefacts, marine concretions are almost exclusively formed of calcium carbonate. These concretions, developed by sessile marine species (such as coralline algae, bivalve, calcareous sponges, bryozoans or corals), can provide a protection against degradation (López-Garrido et al., 2015), reducing the rate of oxygen-dependent corrosion of iron in seawater by allowing metal reaching the passivity zone in the Pourbaix diagram (Gregory, 1999; MacLeod, 2006, 1995).

This paper determines the way in which artificial habitats, such as historic shipwrecks, influence the processes of colonization and ecological succession of the sessile community. We studied the effect of different substrata and environmental condition on recruitment and community development. To this end, two historic shipwrecks of the French Navy related to the Battle of Trafalgar and sunk at the same time (October 1805) were studied. The sessile biological communities developed on panels made of different materials were analysed at both sites. The development of the sessile community at the early stage of the ecological succession and 15 months after the immersion of the panels was assessed to test if the recruitment selection differed in terms of material and time. Additionally, the environmental conditions at the two shipwrecks were characterised in order to understand how the marine environment and material type could influence ecological succession. This work provides baseline information to better predict how the artificial habitats may be colonized, the interaction among environmental conditions, substratum type and biological community development, and their possible implications in the conservation of UCH.

2. Materials and methods

Two shipwrecks from the Battle of Trafalgar, close to the coast of Cádiz (Southern Spain), were selected: the *Bucentaure* and the *Fougueux* (Fig. 1a). The *Bucentaure*, at a depth of 12 m (Fig. 1b), was sunk on 23 October 1805 and the *Fougueux*, at a depth of around 7 m (Fig. 1c), on 22 October 1805. The *Bucentaure* represents a dispersed shipwreck comprising 22 iron cannons, an anchor and other metallic artefacts, but no wood was preserved. This shipwreck is located on a mixed rocky-sandy bottom. In contrast, the *Fougueux* has a portion of the hull structure preserved with metallic elements but mainly wood, and 32 cannons and an anchor. The *Fougueux* is seated on a sandy-bottom with isolated natural rocky reef outcrops.

To assess the development of the sessile community on different materials, panels of 20 $\times$ 30 cm were placed on trestles on the shipwreck areas. The trestles were randomly placed on the centre of each archaeological site. Preliminary studies carried out at the studied zones showed as horizontal panels were completely cover by sediment and vertical panels were often lost or broken due to currents. For these reasons the panels were placed 1.5 m above the sea floor, with an inclination of 45° and facing prevailing currents (See supplementary content). Six different materials employed in the construction of vessels in the 18th to the 19th centuries were chosen: copper, brass, cast iron, carbon steel and two kinds of wood, pine and oak. The sessile community associated to them was studied at two (August 2012) and 15 months (September 2013) after their immersion in the water. Four panels of each material were used. Photoquadrat images of the panels were collected by scuba diving using a Canon PowerShot S100 digital camera. The photoquadrat apparatus was constructed from PVC and attached to the underwater housing camera following other studies (Preskitt et al., 2004; Van Rein et al., 2011). Specimens were identified to maximum level of taxonomic resolution possible, in most cases to species level. Abundance estimates were performed by calculating the percentage cover by 100 fixed point-interception (Van Rein et al., 2012, 2011) using the image analysis software NIS-Elements Advanced Research v.3.10. Additionally, to assist with species identification, samples were collected for subsequent analysis in the laboratory and species were preserved in 70% ethanol.

2.1. Data analysis of sessile community on panels

The sessile community on the panels was analysed using a distance-based permutational multivariate analysis of variance (PERMANOVA, Anderson, 2001; McArdle and Anderson, 2001). A repeated measures PERMANOVA was run considering the factors 'Time' (fixed, with two levels: two and 15 months after the immersion of the panels); 'Shipwreck' (random, with two levels: *Fougueux* and *Bucentaure*), and 'Material' (fixed). The original design included six levels for 'Material'. However, after 15 months, no macro-benthic organisms were present on the copper panels. For this reason, the results exposed here consider only five levels for the factor 'Material': brass, cast iron, carbon steel, pine and oak. 'Panel' was included in the design, identifying it as the repeated measure (Anderson et al., 2008).

The multivariate analysis was based on the Bray-Curtis similarity matrix of square root-transformed data (Bray and Curtis, 1957). The homogeneity of multivariate dispersion among the groups of each factor of interest was tested by PERMDISP (Anderson, 2006). When the number of total possible permutations was low, the P values were estimated by Monte Carlo sampling (Anderson and Robinson, 2003). The dissimilarities among samples were represented by non-metric multidimensional scaling ordinations (nMDS, Clarke, 1993). Similarity percentages analysis (SIMPER) (Clarke, 1993) was used to identify the contribution that each taxon made to the measures of similarity within (or dissimilarity among) the different levels of the factors. Multivariate

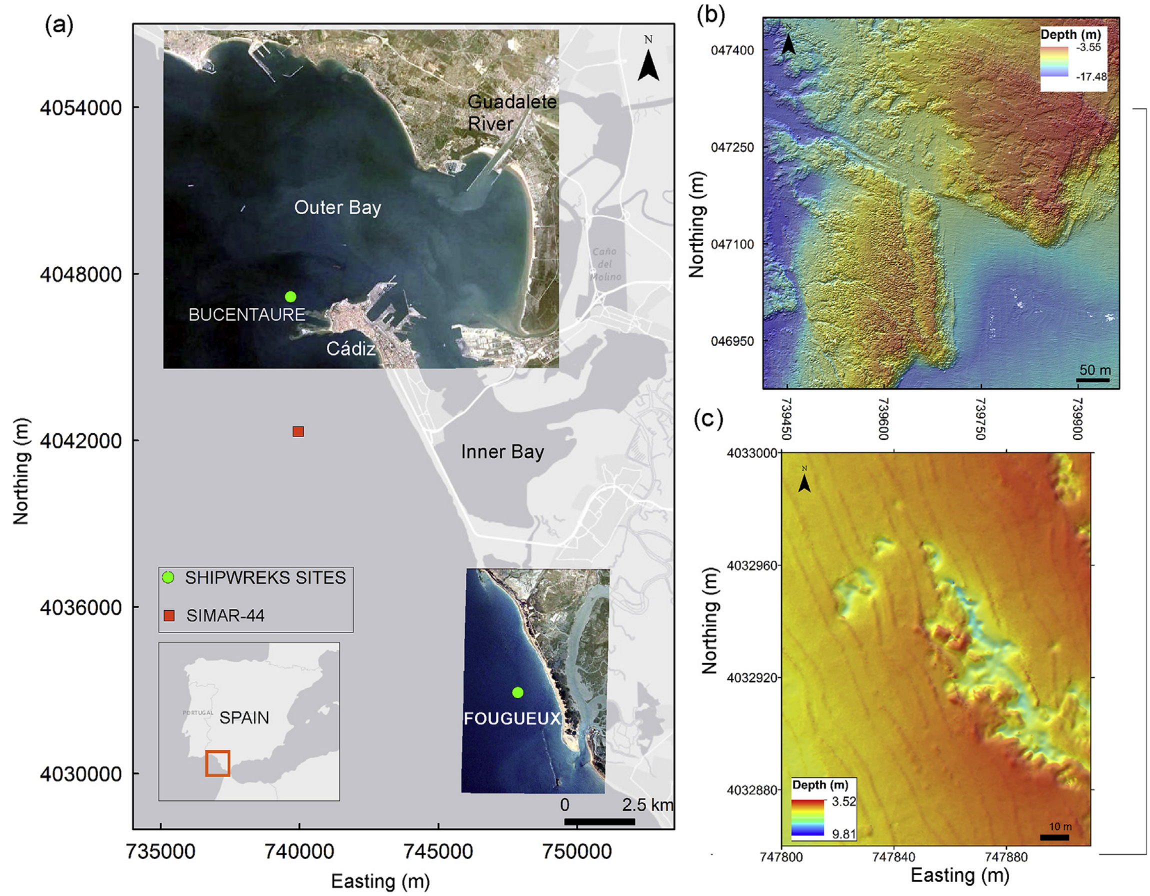

Fig. 1. (a) Overview of location of the study area. Location of shipwreck site and location of historical wave hindcast 44-year-long hourly time series (SIMAR-44) (b) Detailed map of the *Bucentaure* shipwreck site from multibeam echo sounder bathymetric (MBES) survey. (c) Detailed map of the *Fougueux* shipwreck site derived from MBES bathymetric survey.

analyses were performed using the software PRIMER v6.1.11 & PERMANOVA + v1.0.1 statistical package (Clarke and Gorley, 2006).

Additionally, the number of species on the panels over time (two and 15 months after immersion of the panels) was assessed using repeated-measurement analysis of variance (ANOVA). Newman-Keuls test (Underwood, 1997) was used for *a posteriori* comparison of the means. This analysis was performed with STATISTICA v6.0 computer package (Statsoft Inc, 2001).

2.2. Data analysis of environmental conditions

2.2.1. Sediment characterisation

To characterise the sediment grain size, scuba divers manually collected five random sediment samples of 1000 cm^3 on each shipwreck site. After drying and homogenizing 200 g were subsampled from each sample to perform the granulometric analysis following the standard dry sieving procedure. Subsequently, particle size distributions were computed using the Folk and Ward (1957) method within the GRADISTAT software developed by Blott and Pye (2001).

2.2.2. Waves and hydrodynamic conditions

A bottom-mounted Acoustic Doppler Current Profiler was used to characterise current conditions in the whole water column by recording the three components of the current velocity vector. Measurements were gathered simultaneously at the *Fougueux* and *Bucentaure* sites from 03/07/2013 to 09/09/2013. The data obtained were processed using statistical and harmonic analyses (Munk and Cartwright, 1966) to characterise the wind- and tidal-induced dynamics.

2.2.3. Numerical wave modelling

To avoid restrictions of the field measurement, such as extreme wave conditions, and to obtain a sufficient time series length for satisfactory statistical analysis, a wave propagation model was used to reproduce the characteristic wave climate at the studied shipwrecks, taking into account the near shore processes (shoaling, breaking, diffraction, etc.) that modify the wave characteristics. The wave climate regimes at the *Fougueux* site and the *Bucentaure* site were modelled by propagating a historical wave hindcast 44-year-long hourly time series (SIMAR-44) (Fig. 1a) to the shipwreck locations using the Oluca-SP model (GIOC, 2001). SIMAR-44 data provided the offshore wave spectral characteristics (significant wave height, Hs_0, peak period, Tp_0, wave direction, θ_0, and seawater level [SWL]). These deep-water spectral waves were propagated to the site, and the local sea state parameters (Hs_i,Tp_i,θ_i, SWL) were obtained for each of the 385704 hourly (44 years) offshore sea states. Once the time series had been reconstructed at the sites the scalar wave climate regime of significant wave height (Hs) and bottom orbital velocity (Uw) were calculated.

2.2.4. Physico-chemical characteristics of the water column

During a monitoring program from December 2011 to December 2014, seawater temperature and salinity profiles were acquired monthly using a multiparametric probe (Hidronaut 305). The data collected were used to characterise the annual cycles of temperature and salinity at the studied areas.

3. Results

3.1. Sessile biological community

The nMDS plot (Fig. 2) shows the different distribution of the samples based on the sessile community developed on the panels. This figure presents the two sampling periods as two different groups. Furthermore, two months after immersion of the panels, the samples show a separation between the two shipwrecks studied. However, at 15 months after the immersion of the panels, there was no clear separation between the shipwrecks. The results of the multivariate analyses using PERMANOVA showed significant differences in the sessile community between 'Shipwreck' and 'Time' [PERMANOVA 'Shipwreck': Pseudo-F = 7.25, P(perm) = 0.001; 'Time': Pseudo-F = 14.00; P(perm): 0.016], but not among materials. However, the interactions among these factors were significantly different [PERMANOVA 'Shipwreck x Time': Pseudo-F = 2.70, P(perm) = 0.016]. The multivariate dispersion within levels of the different factors tested by PERMANOVA did not show significant differences [PERMDISP 'Shipwreck': $F_{1,63}$ = 7.97E-2, P(perm) = 0.83; 'Material': $F_{4,63}$ = 0.72, P(perm) = 0.69; 'Time': $F_{1,63}$ = 4.49; P(perm): 0.06].

Given the significant interactions, the analyses were conducted by sampling period (Table 1). For the first sampling period (two months after the immersion of the panels), the results of the PERMANOVA (Table 1), showed significant differences in the developed community on panels between shipwrecks, but not among materials. At the end of the experiment, 15 months after immersion, PERMANOVA indicated significant interactions between 'Shipwreck' and 'Material' (Table 1), implying that the differences among materials were not homogeneous across levels of the factor 'Shipwreck'. The multivariate dispersion within levels of the factors did not show significant differences two months [PERMDISP 'Shipwreck': $F_{1,28}$ = 3.87; P(perm) = 0.09)] or 15 months after the immersion of the panels [PERMDISP 'Shipwreck': $F_{1,29}$ = 1.94, P(perm) = 0.27; PERMDISP 'Material': $F_{4,26}$ = 3.54; P(perm) = 0.07].

The SIMPER analysis identified six species that contributed most to the differences between the shipwrecks two months after the immersion of the panels (Average dissimilarity [DISS] = 52.18%) (Table 2). With the exception of the algae *Dictyota dichotoma*, the average cover percentage of the species was extremely low at both shipwrecks. Only the algae *Colpomenia peregrina* and *Laurencia obtusa* showed higher values at the *Fougueux* (average similarity [SIM] = 48.50%). The algae *D. dichotoma* and *Halopteris scoparia*, the hydroid *Orthopyxis* sp. and the polychaete *Spirobranchus triqueter*, showed higher values at the *Bucentaure* (SIM = 66.69%).

In the second sampling period (15 months after the immersion of the panels), analysis of the interaction by PERMANOVA Pairwise test (see supplementary content), did not show significant differences in the community developed on the panels at the *Fougueux* among materials [P(perm) > 0.05]. However, the sessile community at the *Bucentaure* were significantly different among materials, with no differences between pine and oak. The species that contributed most to the quantitative characterisation of the community on each material at the *Bucentaure* in this period are provided in Table 3. Only the turf algae formed by *Ceramium diaphanum* + *Scagelia* sp. characterised the brass panels (SIM = 76.46%). The barnacle *Balanus* sp. and the polychaetes *Filograna implexa* and *S. triqueter* were species characteristic of the community developed on cast iron panels (SIM = 55.42%). *C. diaphanum* + *Scagelia* sp., *D. dichotoma* and *F. implexa* were most common on the carbon steel panels (SIM = 68.02%). The pine (SIM = 56.42%) and oak panels (SIM = 87.55%) were mostly colonised by *C. diaphanum* + *Scagelia* sp.; *D. dichotoma* and the mollusc *Teredo navalis*. Conversely, at the *Fougueux*, 15 months after the immersion of the panels, SIMPER analysis only identified *C. diaphanum* + *Scagelia* sp. (SIM = 25.58) and *D. dichotoma* (SIM = 4.13) as the species that characterised all the materials, with the addition of *T. navalis* (SIM = 3.38) on the wood panels.

From a qualitative point of view (see supplementary content), two months after the immersion of the panels, six species were sampled at the *Fougueux* and eight species at the *Bucentaure*. Three and six were species of algae, respectively. Fifteen months after the immersion of the panels, the number of detected species increased to 13 at *Fougueux* (five of them were algae) and 10 at *Bucentaure* (only two species of algae). At this shipwreck, the number of algae species was greatly reduced and the algae were replaced by other biological groups, such as bryozoans, crustaceans, molluscs,

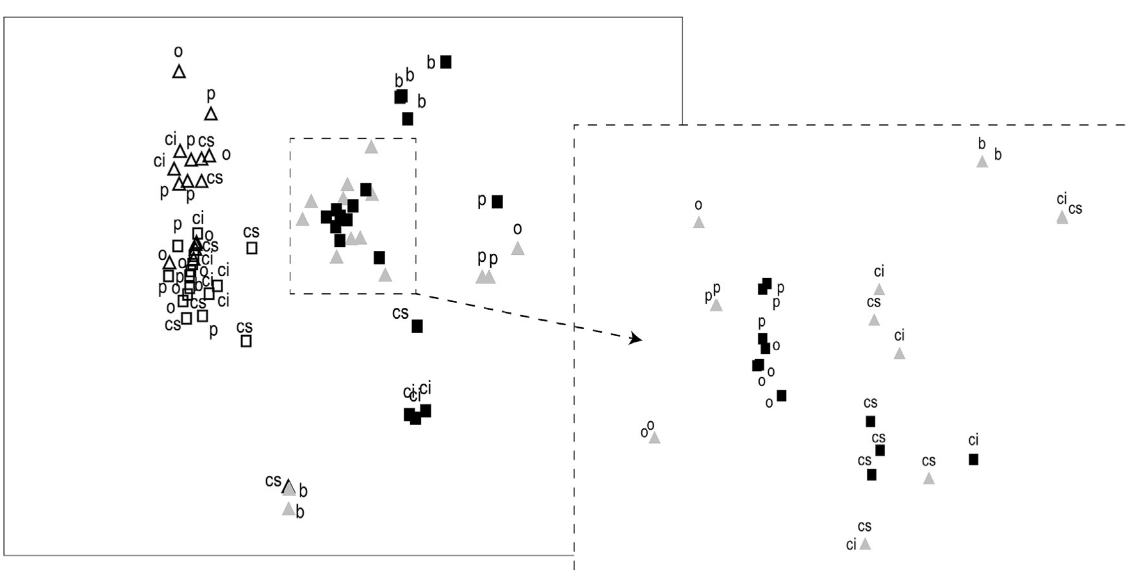

Fig. 2. Non-metric Multidimensional Scaling ordination of the sessile community of the experimental panels, on the basis of the Bray–Curtis dissimilarity. Hollow symbols = August 2012; filled symbols = September 2013; triangles = *Fougueux*; squares = *Bucentaure*; b = brass; ci = cast iron; cs = carbon steel; p = pine; o = oak. (Stress = 0.1).

Table 1
Results of PERMANOVA tests performed on Bray–Curtis similarity matrix based on abundance of sessile organisms two (August 2012) and 15 months (September 2013) after the immersion of the panels. * = significant differences

Month	Source	df	SS	MS	Pseudo-F	P(perm)
August 2012	Shipwreck	1	7850.9	7850.9	11.474	0.001*
	Material	4	5158.3	1289.6	1.343	0.303
	Shipwreck x Material	3	3047.3	1015.8	1.485	0.117
	Residual	23	14369	684.26		
	Total	31	30323			
September 2013	Shipwreck	1	2074.3	2074.3	2.568	0.080
	Material	4	24147	6036.8	2.332	0.055
	Shipwreck x Material	4	10355	2588.8	3.205	0.006*
	Residual	21	16961	807.65		
	Total	30	60859			

Table 2
SIMPER analysis. Species significantly contributing to differentiate between shipwrecks two months after the immersion of the panels. F = *Fougueux*, B = *Bucentaure*.

	Average similarity		Average dissimilarity
Species	F	B	F *vs* B
Colpomenia peregrina	–	–	3.26
Dictyota dichotoma	42.98	61.59	24.09
Halopteris scoparia	–	–	8.69
Laurencia obtusa	4.12	–	6.02
Orthopyxis sp.	–	–	2.21
Spirobranchus triqueter	–		2.97

Table 3
SIMPER analysis. Species significantly contributing to characterising each material at the *Bucentaure*, 15 months after the immersion of the panels.

	Average similarity				
Species	brass	cast iron	carbon steel	pine	oak
Balanus sp.	–	9.52	–	–	–
C. diaphanum + *Scagelia* sp.	73.46	–	41.27	21.09	50.89
D. dichotoma	–	–	9.23	–	17.04
F. implexa	–	29.20	15.16	–	–
S. triqueter	–	16.70	–	–	–
T. navalis	–	–	–	32.35	18.06

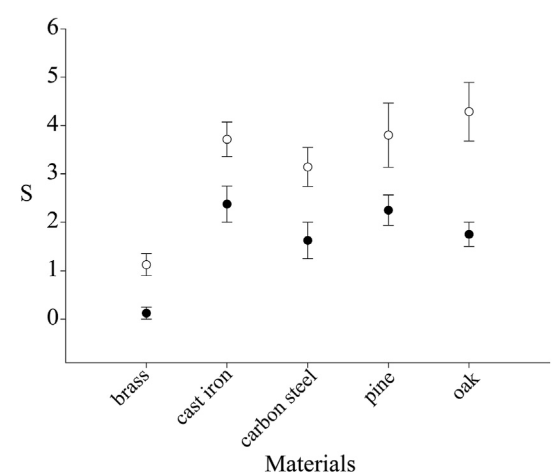

Fig. 3. Results of the Newman-Keuls post hoc test for significant differences in 'Time' and 'Material'. Black circles = two months after immersion of the panels; white circles = 15 months after immersion of the panels. S = mean of the number of species per panel; error bars = Standard Error.

polychaetes and tunicates.

Univariate analysis of the number of species per panel suggested significant differences among materials and between sampling periods. Analysis by *a posteriori* Newman–Keuls test confirmed that the number of species was significantly lower two months after the immersion of the panels. Furthermore, in the two sampling periods, the brass panels showed the lowest number of species with respect to the rest of the materials that could not be statistically distinguished among them on each period. All materials increased their number of species 15 months after the immersion of the panels (Fig. 3).

3.2. Environmental variables

3.2.1. Sediment

Grain size analysis showed differences between shipwrecks. While at the *Bucentaure*, the sediment can be classified as moderately sorted coarse sand ($D_{50} = 1.095$ mm), at the *Fougueux*, it is categorised as well-sorted fine sand ($D_{50} = 0.177$ mm). Accordingly, the combined wave-current bed shear stress should be larger than 0.55 N m^{-2} to initiate the sediment motion at the *Bucentaure* site, whereas at the *Fougueux* values of bed shear stress of 0.15 N m^{-2} would be sufficient.

3.2.2. Waves

Fig. 4 depicts the scalar wave climate at the *Fougueux* and *Bucentaure* sites, achieved from the wave propagation model. The log-normal distribution of significant wave height (Hs) (Fig. 4a) shows that at both sites, significant wave height is < 1 m for 50% of the time during an average year. However, the *Fougueux* presented higher values of Hs during 78% of the time over an average year. In addition, at the *Fougueux* during extreme storm conditions (Hs > 3.85), wave breaks occur, supplying additional energy to near-bottom dynamics. Near-bottom orbital velocities (Fig. 4b), at the *Fougueux* were higher than at the *Bucentaure* during the average year, with differences increasing during stormy conditions.

3.2.3. Currents

The depth-averaged current velocity roses (Fig. 5) show a typical

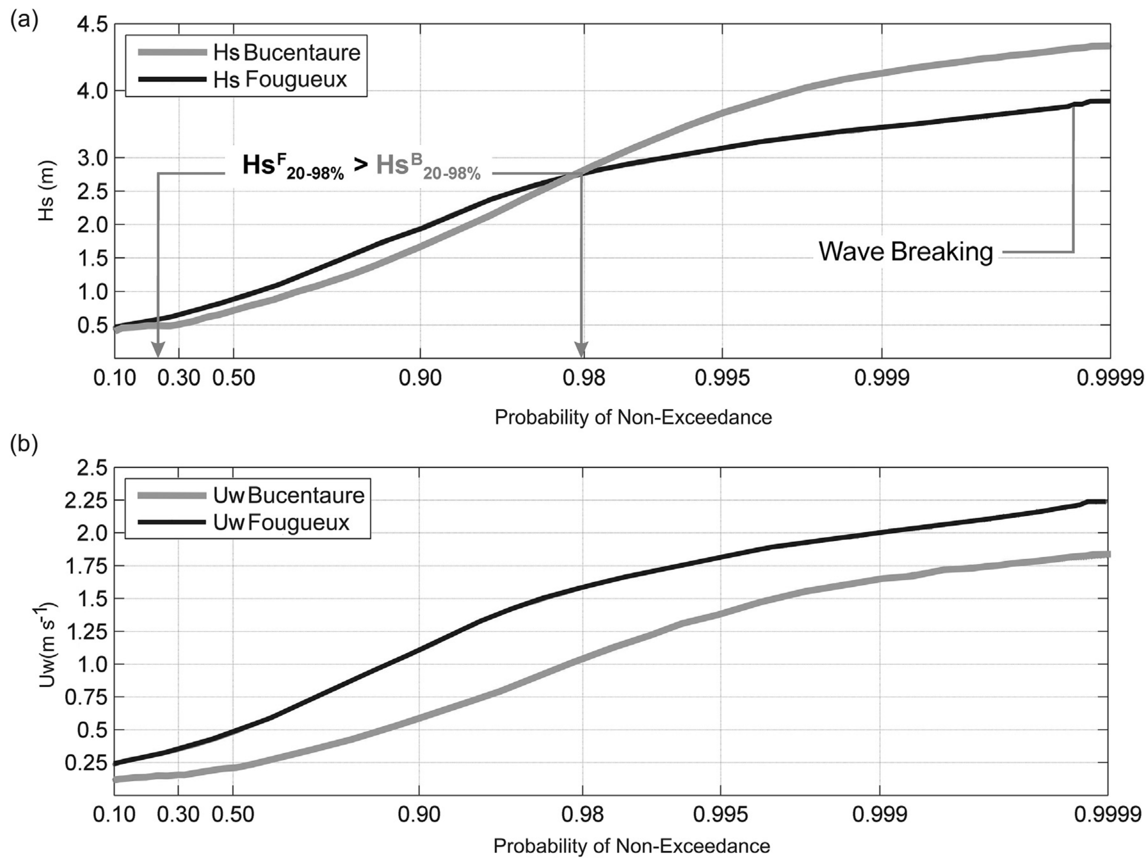

Fig. 4. Scalar wave climate. (a) log-normal distribution of significant wave height. (b) Log-normal distribution of near bottom orbital velocity calculated using linear theory. Hs = wave height; Uw = bottom orbital velocity; F = *Fougueux*; B = *Bucentaure*.

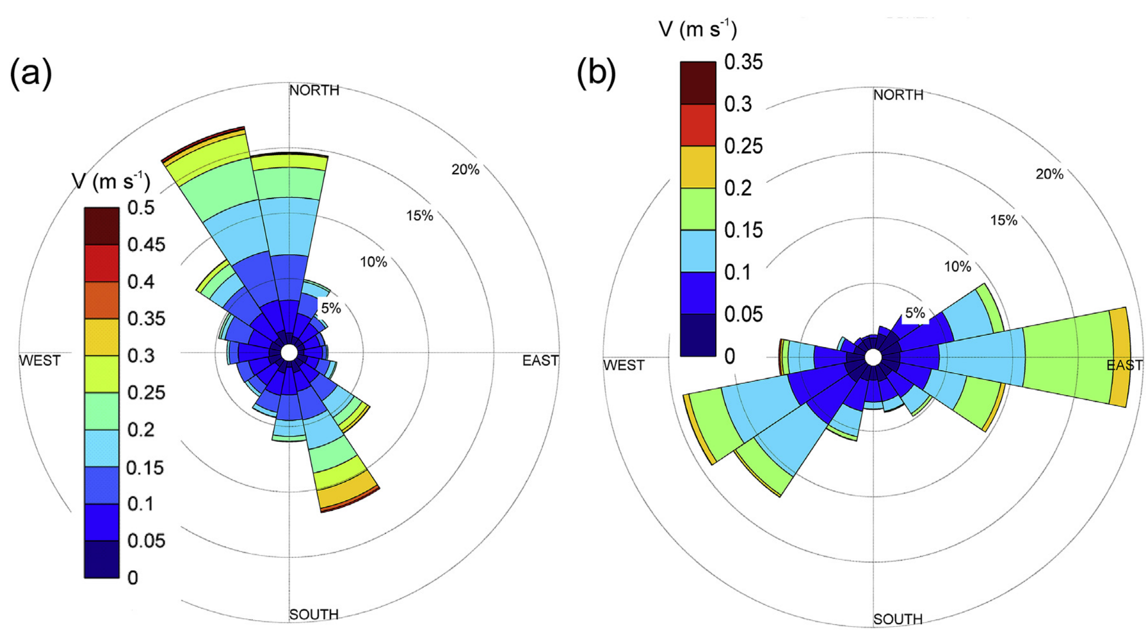

Fig. 5. (a) Depth-averaged current velocity rose corresponding to the *Fougueux* site. (b) Depth-averaged current velocity rose corresponding to the *Bucentaure* site.

semidiurnal tidal variability. At the *Fougueux* (Fig. 5a), the mean current velocities were 0.15–0.25 m s^{-1}, with a preferred orientation parallel to the coast and isobaths. Higher velocity values, directed NNW, correspond to SE winds and reach up to 0.5 m s^{-1}, while current velocities greater than 0.25 m s^{-1}, directed SSE, are linked to a west wind event registered during the field experiment. The mean current velocities at the *Bucentaure* ranged between 0.10 and 0.25 m s^{-1} (Fig. 5b), with a dominant WSW orientation for flood and E for ebb tide conditions. Wind-driven currents increase the current velocities directed to W up to 0.35 m s^{-1}during an east wind event.

3.2.4. Temperature

Fig. 6a presents the annual temperature cycle at the *Fougueux*. Seawater temperature ranged from 14 °C recorded in March to 23.7 °C recorded in September. The vertical orientation of the isotherms revealed a well-mixed water column during all seasons. The annual variation of temperature at the *Bucentaure* site (Fig. 6b) behaves similar to that at the *Fougueux* site, with changes of 13 to 23 °C from February to September. Well-mixed waters were recorded from January to June, indicated by the vertical isotherms. From July to December, a strong thermal stratification takes place in the near-bed layer, with the vertical temperature gradient peaking at 4 °C during August and September. At this stratified period, the surface temperature changed from 19 to 24 °C, whereas in the near-bed layer, it remained below 20 °C most of the time.

3.2.5. Salinity

Fig. 7a shows the salinity variation at the *Fougueux* site with vertical isohalines, indicating no stratification, with the exception of a superficial stratification that did not penetrate beyond 1 m at depth. Seasonal values ranged between 35.5 (April) and 36.5 (September). Fig. 7b illustrates the seasonal variation at the *Bucentaure*, showing a surface stratification between January and April. The decrease in the surface salinity (35) penetrates down to 7 m at depth and is possibly associated to the proximity of the Guadalete River. From July to December, a slight decrease of salinity with depth takes place in the near-bed layer.

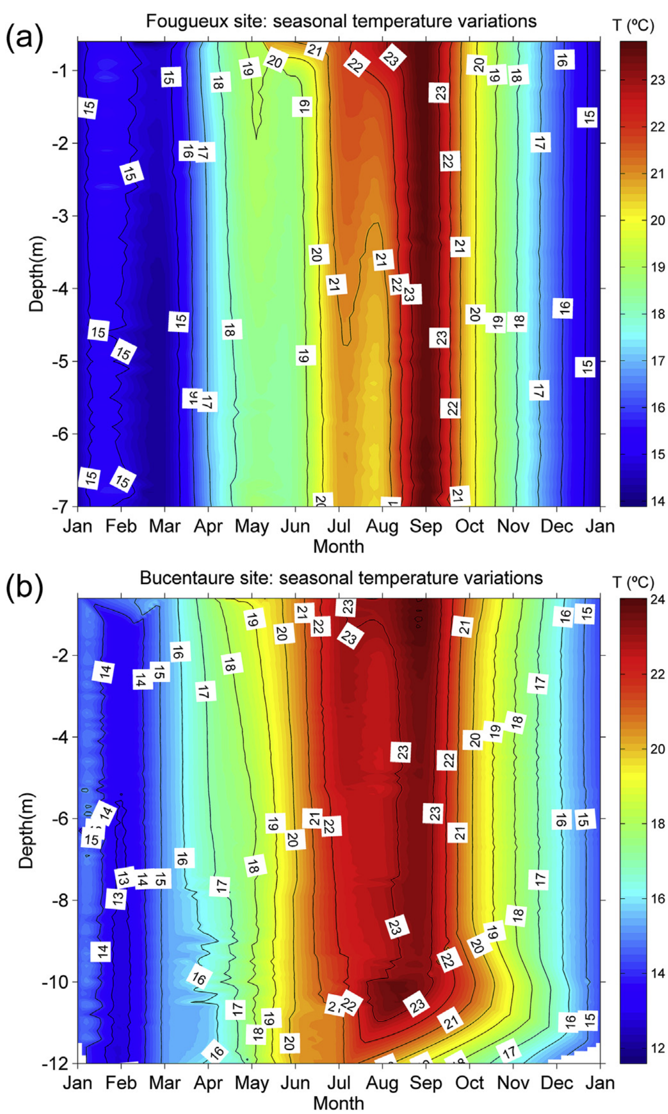

Fig. 6. Annual cycle of temperature measured at the *Fougueux* (a) and *Bucentaure* sites (b).

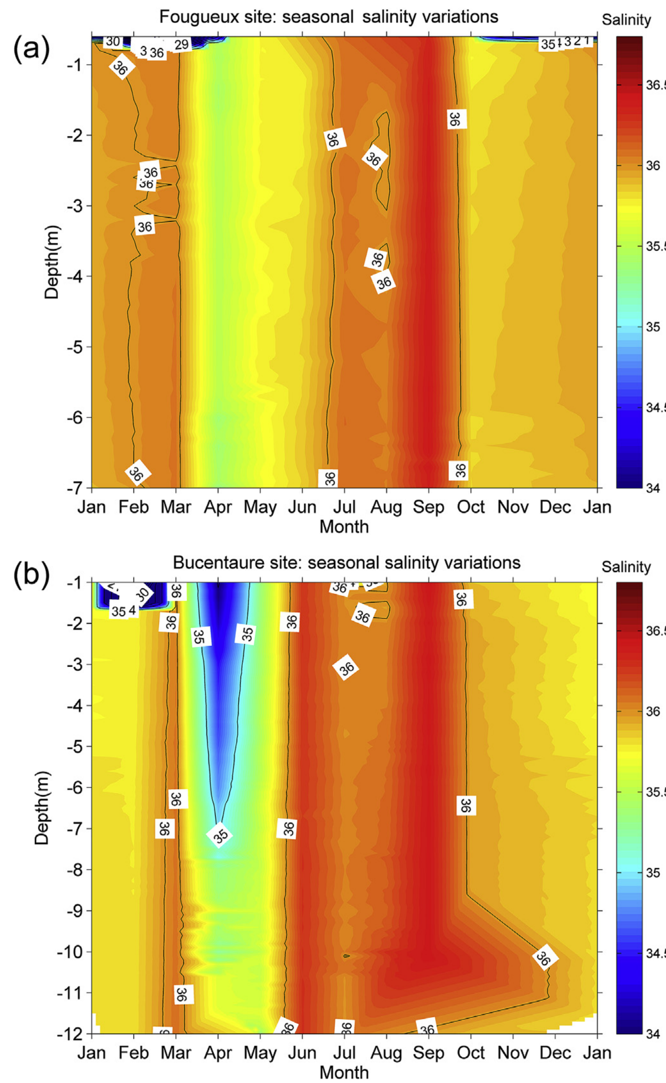

Fig. 7. Annual cycle of salinity measured at the *Fougueux* (a) and *Bucentaure* sites (b).

4. Discussion

There are thousands of shipwrecks in the coastal areas of Europe (Consoli et al., 2014; Wheeler, 2002) and millions around the world (UNESCO, 2017). Nevertheless, studies about the ecological succession at historic shipwrecks and the influence of the material type and the environmental conditions are still scarce (López-Garrido et al., 2015; Zintzen et al., 2006), although these factors can strongly affect the conservation of the UCH (López-Garrido et al., 2015). However, such knowledge is especially important in order to comply with the principles of the UNESCO 2001 Convention for the Protection of the Underwater Cultural Heritage

(UNESCO, 2001), indicating the need to protect the UCH *in situ* through knowledge of the physical, chemical and biological conditions of the environment.

The observations of sessile community on panels showed significant differences between the two shipwrecks and periods considered that are correlated with the environmental conditions. After two months of the immersion of the panels, the communities were in the initial stages of ecological succession. The number of species growing was low and all the species showed a low cover percentage on both shipwrecks. All taxa were algae and hydroids, with the exception of the polychaete *S. triqueter* (Table 2). Many hydroids and algae could be considered as opportunistic and pioneer species and are able to adapt to a wide range of environmental conditions, such as different depths, currents, light intensities, different substrata, etc. (Airoldi and Bulleri, 2011; Megina et al., 2013; Perkol-Finkel et al., 2012). Some studies of artificial habitats recorded that algae appeared in the early stage of ecological succession (Bulleri and Airoldi, 2005; Moschella et al., 2005; Svane and Petersen, 2001). On the other hand, the hydroids are common components of fouling communities (Boero, 1984; Megina et al., 2016, 2013), and benthic hydroids are among the first to colonise virgin substrata (Boero, 1984; Gili and Hughes, 1995; Zintzen et al., 2007). Some hydroid species with small-size colonies and a free-swimming medusa stage have been described as typical r-strategist species and common components on artificial habitats (Megina et al., 2016, 2013; Ralston and Swain, 2014).

After 15 months of the immersion of the panels, the number of species recorded and the cover percentage of the panels were higher at both shipwrecks compared to after two months. At the *Fougueux*, the panels did not show differences among materials from a quantitative point of view (species identified by SIMPER analysis). Furthermore, qualitatively, algae were important components of the sessile community at this shipwreck. Previous studies on artificial substrata in temperate regions have demonstrated the dominance of sessile invertebrates such as bryozoans, sponges or barnacles at more advanced successional stages (Antoniadou et al., 2010; Pacheco et al., 2011; Watson and Barnes, 2004). This scenario, however, does not seem to occur at the *Fougueux*, where algae were a main component of the sessile community of the panels in both sampling periods. The *Fougueux* is placed in a shallow zone, with higher light intensity than at the *Bucentau*re. This can facilitate the proliferation of algae (Svane and Petersen, 2001; Terlizzi et al., 2000). Furthermore, at the *Fougueux*, a higher frequency of disturbances due to environmental conditions, with larger variability in dynamic and physico-chemical conditions, may limit the settlement of other organisms (Cangussu and Altvater, 2010; Canning-Clode et al., 2013; Floerl and Inglis, 2005).

The *Fougueux* had higher values of Hs and bottom orbital velocity (Uw) (Fig. 4). Therefore, the combined wave-current bed shear stress is markedly larger at the *Fougueux* site, especially during autumn and winter periods when storms are more frequent (Rangel-Buitrago and Anfuso, 2013). This can represent a stress factor for sessile organisms (Railkin, 2004). In addition, the larger bed shear stress during high wave energy periods, combined with the presence of smaller grain size sediment ($D_{50} = 0.177$ mm) measured at the *Fougueux* site, could produce an easier resuspension and transport of sandy sediment than at the *Bucentaure*. This marked seasonality in bed shear stress produces alternate periods of erosion and deposition (Fernández-Montblanc et al., 2016), which can greatly change the characteristics of benthos and promote the periodic reburial of sessile organisms, therefore impeding the ecological succession of the benthic community (Figurski et al., 2016; Storlazzi et al., 2013). Indeed, the stratification of the water column did not take place at the *Fougueux* site, unlike at the *Bucentaure* site (Fig. 6). The environmental conditions, rather than the substratum type, play an important role in the development of the biological community at this shipwreck. At a shipwreck with these characteristics, where the sessile community does not reach the climax state, the components of the biological community would have no significant effect on the conservation of the shipwreck.

The *Bucentaure* site is exposed to a lower variability of environmental conditions. This shipwreck is in a deeper zone with lower current velocity and a stronger stratification near the bottom during the end of summer and the beginning of autumn. This stronger stratification reduces the levels of turbulence (Monin and Yaglom, 2007) and thus, the turbulence dynamics have a lower effect on the biological community and materials at the *Bucentaure*. The sessile community on the panels of this shipwreck showed differences between the two sampling periods and among materials at the end of the experiment. Under these more stable environmental conditions, material type showed a higher influence on the composition and the abundance of the sessile community. An important point is whether the sessile marine communities, together with the environmental conditions, could influence the conservation of the UCH (López-Garrido et al., 2015; Ruuskanen et al., 2015; Wheeler, 2002). Some species, mainly on the metallic panels at the *Bucentaure*, have developed calcareous concretions. *F. implexa* and *S. triqueter* are serpulid polychaetes which construct calcareous tubes that they inhabit (Nelson-Smith and Gee, 1966). The barnacle *Balanus* sp. also constructs a calcareous shelf (Anderson, 1994). Such organisms could provide protection from physical and chemical degradation of the shipwrecks since they represent a physical barrier that decreases the biocidal effects of chemical substances (López-Garrido et al., 2015; Wheeler, 2002). Barnacles and serpulids have been described as typical components of sessile communities on shipwrecks (Boaventura et al., 2006; Walker et al., 2007). An important point in the conservation of a shipwreck could be whether these organisms persist over time or whether they are replaced by other organisms, such as sponges (Boaventura et al., 2006). At the *Bucentaure* site, the predominance of these organisms may promote the preservation of metallic archaeological materials acting as an oxygen barrier, in agreement with the lower corrosion rates and the wider bio-concretion layer measured at the *Bucentaure* site (Bethencourt and Fernández-Montblanc, 2011). On the other hand, on the wood panels, species such as *T. navalis* can be particularly destructive. The abundance and type of boring species influence wood deterioration and the conservation of the shipwrecks (Pournou et al., 2001). Bivalves of the family Teredinidae (shipworms) are considered one of the principal organisms responsible of the biodegradation of artificial wooden substrata in the sea, causing significant economic damage (Pimentel et al., 2005; Singh and Sasekumar, 1996). Erosion due to hydrodynamical process, such as sediment abrasion, in conjunction with boring organisms, can contribute to the relatively rapid deterioration of the parts of the shipwreck not covered by sediment (Gregory et al., 2012). In this study and at both shipwrecks, the pine panels seem to be more susceptible to degradation by *T. navalis* than oak panels.

The orientation of the substratum is a relevant factor in the processes of colonization and settlement (Chapman and Clynick, 2006; Glasby, 2000; Oganjan et al., 2017; Perkol-Finkel et al., 2006; Railkin, 2004). In general, algae show more cover and diversity on horizontal surfaces (Chapman and Clynick, 2006) and many invertebrates are more common at vertical surfaces (Chapman and Clynick, 2006; Dafforn et al., 2012). Nevertheless, there are exceptions, and some invertebrate taxa do not show a clear pattern of cover in relation to the surfaces or covered a larger area on horizontal (Knott et al., 2004). For example, Oganjan et al.

(2017) revealed that mussels preferred horizontal surfaces, while barnacles were more abundant on vertical surfaces. All panels in this study had the same orientation (45°) and, hence, similar exposure to current or light intensity, however, this orientation could have conditioned the recruitment of some species with a strong preference for horizontal or vertical surfaces.

In both periods analysed in this study, the average number of species that colonised the panels was relatively low and there were no clear differences among materials on any shipwreck (with the exception of brass). The antifouling characteristics of the copper are well known (Dafforn et al., 2011; Piola et al., 2009), and brass is an alloy made of copper and zinc. This could explain the lower species numbers on brass panels (López-Garrido et al., 2015).

5. Conclusions

This study is one of the few works dealing with the ecological succession on shipwrecks and its relation with different substrata and environmental conditions. This work indicates that environmental conditions, biological communities and substratum type are related, and this relationship could play an important role in UCH conservation. The variability of dynamic and physico-chemical conditions determines the ecological succession of the sessile communities associated to UCH. In addition, the different materials potentially impact the sessile community developing on a shipwreck. In turn, the organisms colonising a shipwreck can influence the conservation status of the UCH. The environmental conditions, the sessile organisms and their effects on different materials are especially important aspects and need to be further elaborated in the evaluation of strategies to conserve UCH. Continuous monitoring of underwater archaeological sites is necessary, even in supposedly stable sites. Monitoring is the key to ensure that suitable environmental conditions and positive biological effects persist over time and that negative biological effects (e.g. boring species) do not increase.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.ecss.2017.11.014.

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