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GIULIO FRANZITTA, ALEESIO MARRONE, ADAM GAUCI, JOHANN GALDIES, MARIA CRISTINA MANGANO, GIANLUCA SARA, ALAN DEIDUN

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Bridging the knowledge gap on the distribution and typology of vermetid bioconstructions along the Maltese coastline: an updated assessment

Giulio FRANZITTA[1], Alessio MARRONE[2], Adam GAUCI[2], Johann GALDIES[2], Maria Cristina MANGANO[3], Gianluca SARA[4] and Alan DEIDUN[2]

[1] Department of Research Infrastructures for Marine Biological Resources (RIMAR), Stazione Zoologica Anton Dohrn, Naples, Italy
[2] Department of Geosciences, Faculty of Science, University of Malta, Msida, Malta
[3] Department of Integrative Marine Ecology (EMI), Stazione Zoologica Anton Dohrn, Sicily Marine Centre, Palermo, Italy
[4] Department of Earth and Marine Sciences (DISTEM), University of Palermo, Palermo, Italy

Corresponding author: Alan DEIDUN; alan.deidun@um.edu.mt

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Abstract

In the Maltese Islands, insufficient attention has been paid to vermetid reefs, endemic Mediterranean bioconstructions widely distributed along the southern part of the basin. As a result, this is a largely-overlooked coastal ecosystem despite the multitude of ecosystem services it provides. The perennial urban development in the Maltese Islands calls for the adoption of urgent action to protect coastal habitats, in particular bioconstructions that increase biodiversity and contribute to mitigating the effects of climate change. The objective of our study was to extensively document the presence and typology of the vermetid reef ecosystems along the coast of Malta and Gozo, assessing the occurrence of putative anthropogenic threats on the same ecosystem. Quantitative measurements were additionally taken to morphologically characterize the recorded bioconstructions. Furthermore, we tested the human pressure effect on the density of vermetid individuals and associated biodiversity. "True" *trottoirs* were only documented along the south-east coast of Malta, where unfortunately land reclamation projects are expected to be implemented. Although no direct relation between a number of assessed human activities and the density of vermetid individuals was reported in the current study, we suggest the conduction of further studies to investigate the influence of specific disturbances on the conservation status of this ecosystem. This study expands the existing knowledge on the status of vermetid reefs in the Maltese Islands and calls for management and conservation actions to preserve this bioconstruction.

Keywords: vermetid trottoirs; coastal ecology; ICZM; Maltese Islands; central Mediterranean.

Introduction

The high level of marine biodiversity that typifies the Mediterranean Sea is supported by various bioconstructions that modify the primary substrate, increase the habitat heterogeneity and enhance ecosystem functioning (Ingrosso *et al*., 2018). Among the Mediterranean bioconstructions, vermetid reefs develop in the intertidal zone of many temperate coastal areas (Milazzo *et al.*, 2016). These biogenic reefs are elevated structures composed of calcareous outer skeletons of marine tube-secreting gastropods belonging to the family Vermetidae and associated with the encrusting red alga *Neogoniolithon brassica-florida* (Harvey) Setchell & Mason (1943) (Calvo *et al.*, 1998; Chemello & Silenzi, 2011). *Dendropoma cristatum* (Biondi, 1859) is the main vermetid reef-builder species in the central Mediterranean (Templado *et al*., 2016). This species is the Sicilian-Tyrrhenian lineage of the *Dendropoma petraeum*-complex (Mollusca: Caenogastropoda) which includes four cryptic species with non-overlapping distributions within the Mediterranean Sea (Calvo *et al*., 2009).

The structure and the morphology of vermetid reefs are influenced by several factors, including the geomorphology of the coast, hydrodynamic condition and the main builder species (Schiaparelli *et al.*, 2003; Milazzo *et al.*, 2016). Calcarenitic geological substrates, high wave exposure and a coastal slope between 15° and 40° favour the development of wide vermetid reef platforms that extend laterally for several kilometers of coastline, as observed along extensive stretches of the north-western and south-eastern Sicilian coastline (Chemello *et al.*, 2000; Chemello, 2009). Alternatively, when the substrate is less subject to physical erosion (e.g., dolomite, basaltic, granitic, flysch), the slope is flatter (0-15°) or sub-vertical (>40°) and the water turbulence is limited, vermetid reefs can take the form of narrow (extending for 1-2 m at most) encrustations on geogenic abrasion platforms or even form a narrow fringe covering rock surfaces just a few centimetres below mean sea level (Azzopardi & Schembri, 1997; Antonioli *et al.*, 1999; Milazzo *et al.*, 2016). In the Mediterranean, these structures are particularly frequent in the warmest water areas, typically above the 14°C winter isotherm (Chemello *et al.*, 2000), but are also reported from more northerly waters (Chemello & Silenzi, 2011; Milazzo *et al.*, 2016).

Vermetid reefs provide an array of ecosystem services, such as protection of the shoreline from coastal erosion and regulation of sediment transportation. In addition, they are carbon sinks and are habitats for fish and invertebrates, thus greatly enhancing marine biodiversity (Ben-Eliahu & Safriel, 1982; Chemello *et al.*, 1998; Chemello, 2009; Chemello & Silenzi, 2011; Gordo-Vilaseca *et al.*, 2021). The more developed the structure of a reef is, the more ecosystem functions it can sustain (Sarà *et al.*, 2021); indeed, the inner edge, cuvette and outer edge areas of a vermetid bioconstruction can host different communities (Ape *et al.*, 2018), creating new habitats and refuges for subtidal species and acting as nursery areas for fish (Consoli *et al.*, 2008). Vermetid reefs can be extensively used as bio-indicators (e.g., for biodiversity) (Safriel & Ben-Eliahu, 1991; Chemello *et al.*, 2000).

To date, vermetid reefs are not adequately protected by international environmental legal frameworks, an exception being the European Habitat Directive (92/43/ECC, code1170), which broadly protects biogenic reefs; in addition, *D. petraeum* (*D. cristatum* is still often listed under this former scientific name) and associated algal species are included under the annexes of the Bern Convention as well as under Annex II (Endangered or Threatened Species) of the Protocol for Specially Protected Areas in the Mediterranean (SPAMI Protocol of the Barcelona Convention). However, less than 30% of the Mediterranean vermetid reefs are protected through inclusion within designated boundaries of MPAs (Chemello *et al.*, 2014) which, coupled with their vulnerability to several anthropogenic threats, such as pollution, climate change (Sarà *et al.*, 2021), the spread of invasive species (Mannino & Balistreri, 2021), ocean acidification (Milazzo *et al.*, 2014) and urban development along rocky shores, may cause the regression of these assemblages along the entire Mediterranean basin (Galil, 2013). The degree of protection remains remarkably low even in some regions, such as the Levantine basin, where most collapses of the biological community associated with vermetid formations have been reported (Gordo-Vilaseca *et al.*, 2021). In the Mediterranean, the vermetid reef is considered as an ideal indicator of human impacts on coastal ecosystems by virtue of its ecological relevance and vulnerability to anthropogenic pressures (Relini, 2000).

Among the most extensive vermetid reefs within the Mediterranean basin are those built by *D. cristatum* along the coasts of Sicily, in the central Mediterranean (Antonioli *et al.*, 1999; Calvo *et al.*, 2009). Little is still known about these bioconstructions along the Maltese coastline. Vermetid bioconstructions were described for Malta by Richards (1983) and by Azzopardi & Schembri (1997), with both studies mainly assessing the occurrence of crusts. More recently, Calvo *et al.* (2009) have determined that the main bioconstructive species in Malta is *D. cristatum*. Maltese national environmental legislation provides for the protection of this bioconstructive species: *D. cristatum* (ex *petraeum*) is listed under Schedule III of Subsidiary Legislation SL 549.44, which lists all animal and plant species whose conservation requires the designation of Special Areas of Conservation (SACs). Despite this, recent management measures for Malta's eighteen designated MPAs released by the Environment and Resources Authority (ERA) for public consultation on July 2021 do not make any references to vermetid reefs.

The rationale for the current study is framed within the following context: (i) the considerable urban transformation and alteration that the coastline of the Maltese islands has been subjected to in recent years and (ii) the lack of updated distribution maps for these biogenic formations along the Maltese coastline. The aims of the current study include (i) a characterization of the morphology and structure of vermetid bioconstructions through qualitative observations and quantitative measurements; (ii) an identification of the potential anthropogenic threats affecting the same bioconstructions and (iii) an evaluation of the potential effect of human pressures on the density of vermetid bioconstructions and supported biodiversity.

Materials and Methods

Study area

This study was carried out along the coast of the Maltese archipelago, located in the central Mediterranean (eastern flank of the Strait of Sicily, approximately 96 km from Sicily and 290 km from the north African coast of Libya, at a latitude of 36.4077778 - 36.0833333 °N and a longitude of 14.1844444 - 14.5769444 °E). The total area of the archipelago is 316 km^2, with the island of Malta having the largest surface area (246 km^2), followed by the island of Gozo (67 km^2) and the minor island of Comino (3 km^2), in addition to a small number of uninhabited islets and rocks. The coastline of the island of Malta is 196 km long and dominated by vertical cliffs, indented bays, cliffy coves and inlets, which are etched within sedimentary rock (primarily limestone) formations (Biolchi *et al.*, 2016). The western and south-western coasts generally consist of either Lower or Upper Coralline Limestone and are dominated by the steep profile of sheer cliffs. In contrast, outcrops of the friable Globigerina Limestone formation (Biolchi *et al.*, 2016), which extend predominantly along the eastern and south-eastern coasts, favour the development of extended shore platforms. Mobile sediment beaches (shingle and sandy) are rare, constituting just 2.4% of the total coastline of the archipelago (Schembri, 1990) and mainly occur in the northern part of Malta.

Sampling procedures

The survey, carried out during summer 2019 under calm water, covered most of the coastal area of the island of Malta, which was accessed either on foot or through swimming. On the island of Gozo, observations were made at voucher sites only, pre-selected on the basis of coastal morphology and topography considerations. The survey aimed to detect the presence of vermetid bioconstructions, their characterization as morphotypes and the identification of operational anthropogenic pressures. The recorded vermetid bioconstructions were classified either as '*trottoir*' or as 'crust'. The former forms the 'platform' or 'true reef' and so represent the more complex morphotype where the typical outer edge, inner edge and cuvette are clearly distinguishable. The latter does not produce a true *trottoir* but appears as an encrustation on the abrasion platform made by a thin layer of *Dendropoma* spp. shells or, alternatively, with a thicker ledge (usually 20-30 cm) extending from the rocky substrate (Antonioli *et al.*, 1999; Milazzo *et al.*, 2016).

Multiple types of anthropogenic factors are recognized as being threats responsible for negative impacts on vermetid reefs (Graziano *et al.*, 2007; Di Franco *et al.,* 2011; Galil, 2013; Milazzo *et al.*, 2002; 2014; 2016; Badreddine *et al.*, 2019). Among these, one can consider (i) the potential exposure of the bioconstructions to urban and infrastructural development, (ii) the ease of access to the site and therefore exposure to potential human trampling and (iii) the occurrence of invasive species within the bioconstruction. Ultimately, all the sampled sites were included in a map using QGIS (https://www.qgis.org/en/site/). In addition, for each location, a quantitative description of the vermetid bioconstruction was done by measuring its length (linear extension of the reef along the coastline) and width (linear extension from the inshore towards the open sea; 0.1 m) at five randomly-placed replicates.

The quantitative analysis to test the potential influence of human pressures on vermetid bioconstructions considered as variables the density of *D. cristatum* individuals and the benthic biodiversity associated with the bioconstructions. The density of individuals was assessed using the photographic method. Six photos (i.e. replicates) were taken by means of a digital camera, within a 100 cm^2 quadrat randomly placed with respect to the outer edge of the bioconstruction. The composition of the associated algal community was assessed by an *in situ* visual census within a 400 cm^2 quadrat placed within the same bioconstruction, with five replicates being taken for each site, and was expressed in terms of percentage cover for each identified algal taxon. Data consisted of estimates of percentage cover for algal species. Percentage cover estimates were visually obtained by dividing each quadrat into 25 sub-quadrats and assigning to each of these a score from 0 (absence) to 4 (when an identified taxon totally covered a subquadrat) and adding up the 25 estimates (as per Dethier *et al.*, 1993). Organisms filling <1/4 square were given an arbitrary value of 0.5. Final values were expressed as percentages (as per Dethier *et al.*, 1993).

The visual censuses of the benthic communities allowed us to identify seven Operational Taxonomic Units (OTUs) of algae for subsequent multivariate analysis: AC - Articulated Corallinae, GFA - Green Filamentous Algae, DFA - Dark Filamentous Algae, ECR - Encrusting Coralline Rodophytes, CB - Coarsely-Branched Algae, *Cystoseira* spp., *Padina pavonica* (L.) Thivy, 1960) (cf. Di Franco *et al.*, 2011 for reference to the OTUs and corresponding species).

The intensity of human pressures acting at each site supporting a vermetid bioconstruction was characterized through the computation of the Land Use Simplified Index (LUSI; Flo *et al.*, 2011). The LUSI index integrates several pressures (i.e. urbanization, agricultural and industrial activities, sewage outfalls, commercial harbours, aquaculture and freshwater input). Subsequently, scores were assigned to each type and level of pressure and summated to produce a final LUSI value for each site (Flo *et al.*, 2011; Badreddine *et al.*, 2019).

As applied by Flo *et al.* (2011), the LUSI index calculated for this study follows equation (1):

LUSI = (U + A + I) * coastal correction factor

where: U = urban score; A = agricultural score; and I = industrial score. The urban, agricultural and industrial scores were assigned as follows using GIS software and a land cover map:

Urban Score
- < 33% of the area is built up: 1
- 33% to 66% of the area is built up: 2
- > 66% of the area is built up: 3

Agriculture Score
- < 10% of the area is agricultural land: 0
- 10% to 40% of the area is agricultural land: 1
- > 40% of the area is agricultural land: 2

Industrial Score
- < 10% of the area is industrialised: 0
- > 10% of the area is industrialised: 1

The area considered for each site extended for a maximum of 1.5 km inland from the vermetid reef. The coastal correction factor was assigned as 1.25 when the coastline morphology was concave, 0.75 when the coastline morphology was convex and 1.00 when the coastline morphology was straight.

Unlike Flo *et al.* (2011), riverine pressure was not factored in this study, since, following the equation presented by Flo *et al.* (2011), the riverine score would be assigned to 0 for all the Maltese coast since salinity values are always above 37.5.

Two groups of sites were distinguished on the basis of their LUSI index scores - "medium disturbance" and "high disturbance" ones, segregated by a LUSI index threshold value of 5. Given that no site registered LUSI index values close to 0, "low disturbance" and "no disturbance" categories were not designated.

Data analysis

In order to test potential differences between sites supporting different typologies of vermetid bioconstruction subject to the influence of human pressure, a two-way orthogonal experimental design was adopted, with Pressure (fixed; two levels: Medium and High) and Typology (fixed; two levels: Trottoir and Crust) included as factors. Among the several sites identified during the survey, we randomly selected two sites per each factor combination for a total of eight sites considered for the subsequent statistical analysis. Statistical differences between densities of *Dendropoma* individuals were tested by univariate PERMANOVA based on the Euclidean distance matrix of untransformed data. Additionally, differences in the algal OTUs relative abundance were tested by a multivariate PERMANOVA based on the Bray-Curtis distance matrix of square-root transformed data. For all the PERMANOVAs, P-values were obtained from 9999 permutations. Monte Carlo tests were also considered in case of low numbers of unique permutations. These analyses were conducted using the Primer v. 6 statistical package with the PERMANOVA+ extension (Clarke & Gorley, 2006; Anderson *et al.*, 2008).

Results

The survey conducted along the coast of the Maltese archipelago allowed us to identify 15 sites on the island of Malta, 6 sites on Gozo Island and 1 site on the islet of Comino, supporting the presence of vermetid bioconstructions. The location of these sites is given in Figure 1, with the vast majority being distributed along the northern and eastern flanks of the island of Malta, with only three sites being located along the south-western coast of the island. In fact, the southern flank of the island, being characterized by cliffs, is not congenial for the development of vermetid bioconstructions. Along the south-eastern flank, the prevailing identified morphotype was the *trottoir* one, in which the inner, outer and cuvette edges could be distinguished, especially at sites 6-9, whilst the south-west coastal bioconstructions were characterized mainly by the crust typology. This is coherent with the nature of the substrate and slope of the coast which in the various coastal sectors favours the different typologies of vermetid reef. At other sites, vermetid concretions developing on the natural abrasion platform were recorded. A further six sites were identified on the island of Gozo, where additional presence/absence and typology observations have been conducted on the recorded vermetid bioconstructions (Table 1). "Għajn Żejtuna", located along the southern flank of Mellieħa Bay, supports a narrow vermetid *trottoir* (Site 1, Table 1), but the presence of a slipway at this site suggests that urban development could be a relevant factor of disturbance. At "Qawra", at the northern extremity of Qawra Point, a relatively large extent of vermetid bioconstruction was found in highly fragmented form, although the site is not heavily frequented due to its difficult access (Site 2, Table 1). "Qalet Marku" site supports vermetid bioconstructions in the form of the crust typology, apparently not highly impacted by anthropogenic threats (Site 3, Table 1). "Pembroke" area supports the crust typology of vermetid bioconstructions and hosts a desalination plant. "Exiles" is characterised by a vermetid reef in the form of a *trottoir,* with amplitude of about 3 meters (Site 5, Table 1). This site lies in a popular touristic area which is subject to intense bathing and trampling pressure due to its ease of

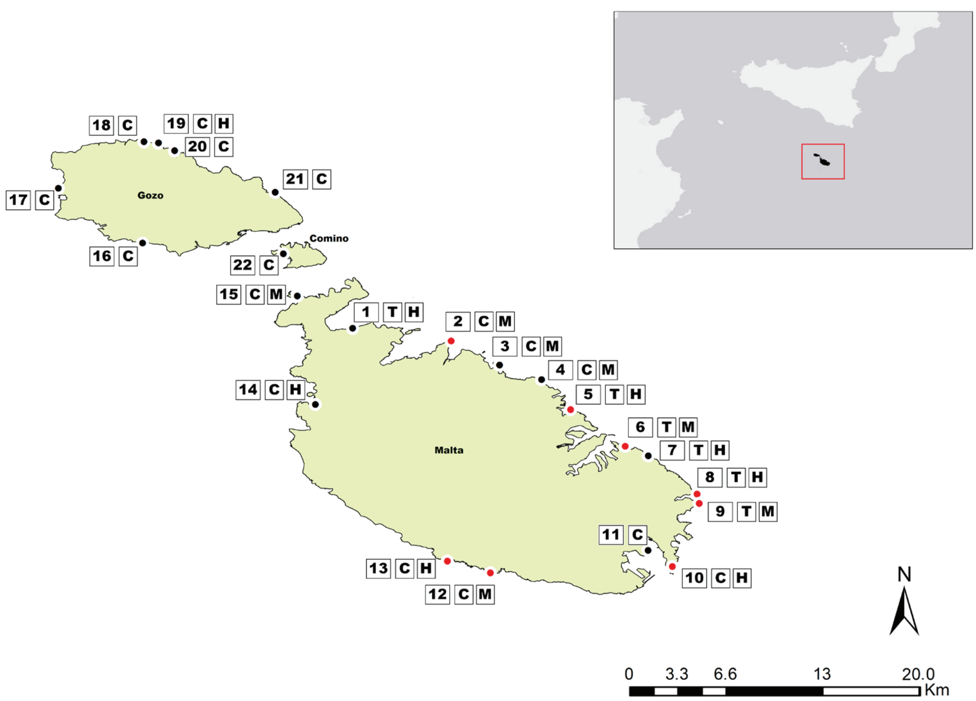

Fig. 1: Distribution map for the vermetid bioconstructions investigated in this current study. Vermetid reef typologies and putative human pressures are displayed for each study site. Sites marked with a red dot are those included in the experimental design for subsequent statistical analysis.

Table 1. Attributes of the vermetid bioconstructions along with the corresponding LUSI index values recorded at each of the sampled sites. The sites marked with asterisks are those selected for the following statistical analysis. 'Length' is the linear extension of the vermetid bioconstruction at the given site expressed in centimetres. 'Width' is the mean amplitude of the bioconstruction expressed in cm (± Standard Deviation). "Density" is reported as number of individuals/100 cm^2 (±SD). The "Typology" column synthesizes the attribution of Trottoir (T) and Crust (C) morphotypes at each site.

Label	Localities	Length	Width	Density	Typology	LUSI
Site 1	Għajn Żejtuna	400	173,5 (±22,91)	136,83 (±99,98)	T	5,00
Site 2*	Qawra	600	292,5 (±78,72)	95,83 (±41,79)	C	3,75
Site 3	Qalet Marku	2300	284,17 (±87,49)	107,33 (±38,28)	C	3,75
Site 4	Pembroke	2300	566,67 (±215,21)	79,83 (±28,46)	C	4,00
Site 5*	Exiles	1360	348,33 (±143,59)	199 (±50,91)	T	6,25
Site 6*	Malta Film Studios	4400	155,67 (±79,36)	152,83 (±57,35)	T	3,00
Site 7	Dawrett ix-Xatt	3900	217,5 (±58,12)	346,33 (±236,94)	T	5,00
Site 8*	Żonqor	2050	173,83 (±72,57)	43,6 (±21,12)	T	5,00
Site 9*	Jerma	3200	744,17 (±443,78)	127,50 (±35,44)	T	3,75
Site 10*	Kalanka	21000	170 (±33,29)	83,17 (±53,91)	C	6,25
Site 12*	Żurrieq	700	64,67 (±32,12)	47,5 (±14,87)	C	4,00
Site 13*	Għar Lapsi	680	188,33 (±108,47)	93,17 (±22,33)	C	5,00
Site 14	Ġnejna	2220	434 (±101,71)	82,83 (±29,44)	C	5,00
Site 15	Ċirkewwa	325	98,17 (±69,75)	65,83 (±16,94)	C	3,00
Site 19	Marsalforn	1670	488,33 (±255,59)	150 (±21,62)	C	6,25

access. The "Malta Film Studios" site is located along the south-east flank of Malta, in close proximity to the Malta Film Studios. The accessibility to this site is limited by a fence around the perimeter of the studios. This site presents a true vermetid *trottoir* (according to Antonioli *et al.*, 1999) where the inner edge, outer edge and cuvette are clearly distinguishable (Fig. 2A). Nonetheless, this is a narrow *trottoir*, ranging between 76 cm and 235 cm in width (Site 6, Table 1). "Dawrett ix-Xatt" along the southern coastline of the island of Malta, supports a narrow vermetid *trottoir* morphotype, subject to moderate anthropogenic threats due to the absence of formal touristic infrastructure (Site 7, Table 1, Fig. 2B). "Żonqor" presented a *trottoir* typology, located along the south-eastern coast of the island of Malta (Site 8, Table 1, Fig. 2C). The invasive species *Brachidontes pharanoins* (Fisher, 1870) was recorded within this same *trottoir*, which is located within an urbanized coastline popular with tourists and for bathing purposes. "Jerma", located along the eastern extremity of St. Thomas Bay along the south-eastern coast of Malta, presents the typical vermetid platform (Site 9, Table 1, Fig. 2D). This formation extended seaward up to a maximum of 12 m away from the shoreline and exhibited the presence of *B. pharaoinis*. "Kalanka" Bay, situated along the south-eastern extremity of the island of Malta, is characterized by a relatively large vermetid *trottoir*, being putatively threatened by considerable human trampling due to its ease of access (Site 10, Table 1, Fig. 2E). "Fossa", sited within Marsaxlokk Bay, specifically at Il-Fossa, was characterized by a localized concretion of vermetids described as crust. The formation does not form an emergent structure and is presumably threatened by the considerable urbanization and industrial activity ongoing within the same bay. Given its very limited physical extension, this site was not included for further qualitative and quantitative measurements (Site 11, Table 1). "Żurrieq" is located close to the jetty deployed by tourist boat operators and supports a narrow vermetid crust, which is not threatened by trampling pressures due to its inaccessibility from land. In this site the presence of *B. pharanonis* in the vermetid crust was detected (Site 12, Table 1). "Għar Lapsi" located along the south-west coast of the island of Malta, supports a vermetid crust and is relatively popular with bathers (Site 13, Table 1)."Ġnejna" is characterised by an abrasion platform located eastward of the beach at Ġnejna Bay, populated by vermetids which form a crust extending over a width in excess of 4 meters. This site, located along the north-western coast of the island of Malta, is potentially exposed to trampling due to its popularity for bathing activities (Site 15, Table 1). "Ċirkewwa" is in close proximity to the Gozo ferry terminal and supports narrow crusts of vermetids (Site 15, Table 1), with formal tourism infrastructure (e.g., hotels) being located nearby.

Fig. 2: Photos of the vermetid typology *trottoir* recorded at sites 6 "Malta Film Studios" (A), 7 "Dawrett x-Xatt" (B), 8 "Żonqor" (C) and 9 "Jerma" (D), crust at sites 10 "Kalanka" (E) and 19 "Marsalforn" (F).

On Gozo, vermetid bioconstructions were recorded at six sites,specifically at "Xatt l-Aħmar", "Dwejra", "Reqqa", "Marsalforn", "Daħlet Qorrot" and "Xwejni Beach" (Fig. 1). "Marsalforn" was the only Gozitan coastal site selected for further qualitative measurement and quantitative analysis. At the northeast extremity of Marsalforn Bay, an abrasion platform colonized by crusts of vermetids was recorded, extending over a maximum width of 7 meters and being subjected to seasonal trampling disturbance due to its popularity for bathing (Fig. 2F).

To date, no comprehensive census of the occurrence of vermetid bioconstructions on the island of Comino has been conducted. In the current study, we record the occurrence of a small-scale vermetid crust in close proximity to the Blue Lagoon in Comino (36°00'46.4"N 14°19'27.5"E; Fig. 1). Despite the popularity of contiguous areas for tourism, this vermetid crust showed few signs of anthropogenic disturbance.

Human pressure and typology effects

To evaluate the putative influence of human pressures and different morphology of bioconstruction on the density of *D. cristatum* individuals (Table 1) and on the percentage cover of different algal OTUs (Table 2), we selected the following sites: 2 (pressure: Medium; typol-

Table 2. OTUs values (% cover ± standard deviation) for the sites included in the experimental design. AC: Articulated Corallinae, GFA: Green Filamentous Algae, DFA: Dark Filamentous Algae, ECR: Encrusting Coralline Rodophytes, CB: Coarsely-Branched algae.

Site	AC	GFA	DFA	ECR	CB	*Cystoseira* spp.	*P. pavonica*
2	38 (±23,15)	8,8 (±9,63)	3,6 (±8,05)	6,4 (±7,83)	39,6 (±27,95)	0	1,2 (±2,17)
5	13,4 (±8,2)	0	0	4,6 (±5,37)	30 (±13,36)	4,2 (±5,5)	39,6 (±8,96)
6	21,6 (±20,66)	10,4 (±5,03)	0,6 (±1,34)	0	9,2 (±5,89)	15 (±18,6)	11,2 (±4,87)
8	46 (±24,72)	26,8 (±30,42)	0,6 (±1,34)	2,8 (±1,3)	7,2 (±8,64)	0,6 (±1,34)	0
9	15,8 (±9,98)	8,6 (±4,67)	0	7,6 (±3,85)	54,2 (±17,11)	0,4 (±0,89)	0
10	1,6 (±2,61)	0,4 (±0,89)	0	8,8 (±9,01)	19,4 (±16,99)	9,8 (±18,63)	8,4 (±0,89)
12	2 (±2,83)	0,6 (±1,34)	0	12,8 (±12,44)	24,8 (±8,11)	9 (±9,27)	13 (±10,84)
13	2,6 (±2,79)	0,2 (±0,45)	0	15,6 (±21,13)	52,2 (±41,7)	11,8 (±25,28)	1,4 (±2,19)

Table 3. Results of the univariate two-way PERMANOVA analysis conducted with the density of *Dendropoma cristatum* individuals and of the multivariate two-way PERMANOVA analysis conducted with algal composition (OTUs) as a Factor. The table also reports the pairwise comparisons for pairs of levels of the factor "Typology" within levels "High" and "Medium" of factor "Pressure".

PERMANOVA table of results					
DENSITY					
Source	df	SS	MS	Pseudo-F	P(perm)
Pressure	1	208,33	208,33	5,82E-02	0,8105
Typology	1	27456	27456	7,6757	**0,0076**
PrxTy	1	5125,3	5125,3	1,4328	0,2399
Res	44	1,57E+05	3577,1		
Total	47	1,90E+05			
OTU					
Pressure	1	972,59	972,59	0,78213	0,5324
Typology	1	6204,3	6204,3	4,9893	**0,0024**
PrxTy	1	2641,4	2641,4	2,1241	0,0989
Res	36	44767	1243,5		
Total	39	54585			

ogy: Crust); 5 (High; Trottoir); 6 (Medium; Trottoir); 8 (High; Trottoir); 9 (Medium; Trottoir); 10 (High; Crust); 12 (Medium; Crust); 13 (High; Crust). Results show a similar trend in the sites' segregation pattern, both in terms of *D. cristatum* population density and in terms of the percentage coverage of different algal OTUs (Table 3). Indeed, for both the univariate and the multivariate analysis, significant differences were detected between sites with a different typology but not with respect of different level of human pressure. Indeed, a subsequent pairwise test was not performed because the non-significance of the interaction Pressure x Typology (Table 3).

Discussion

Vermetid reefs are bioconstructions of high conservation value by virtue of the services they provide to intertidal marine ecosystems within the Mediterranean. It is of no surprise that a number of international agreements establish the need to protect these ecosystems. But, despite the fact that these bioconstructions are included, for example, in the SPA/BIO Protocol of the Barcelona Convention and in the Habitats Directive 92/43/EEC, Chemello *et al.* (2014) estimated that the management measures prescribed to protect the same assemblages extend over less than 30% of all known vermetid bioconstructions in the Mediterranean basin.

Whilst in the central Mediterranean region Sicilian vermetid-associated bioconstructions are the most studied, similar bioconstructions in the Maltese archipelago still deserve greater scientific and management attention given the existing knowledge gaps concerning these formations and the conservation challenges facing their integrity. Previous studies have reported the presence of vermetid-associated crusts along the north-east coast of the island of Malta (Azzopardi & Schembri, 1997). Our study extends existing knowledge on these bioconstructions to the entire coast of the island of Malta and also reports, for the first time, the occurrence of vermetid reefs on the island of Gozo and on the islet of Comino. The current study also demonstrates that Maltese vermetid reefs may even develop into true *trottoirs* (*sensu* Antonioli *et al.*, 1999), which typically include a *cuvette* lodged between the inner and the outer edge, as observed at the 'Malta Film Studios' coastal stretch and at other sites along the south-eastern coast of Malta. Given the relative lack of public access, this vermetid *trottoirs* site was characterized by a reasonably good conservation status, although the same coastal stretch having been earmarked for potential future land reclamation efforts and despite the fact that the LUSI index value for the same stretch is high. Additional vermetid *trottoirs* were recorded at additional sites, including at the 'Exiles' and 'Żonqor' ones. However, these sites, unlike the 'Malta Film Studios' one, are apparently subject to potential anthropogenic threats given that they are easily accessible and are located within popular touristic spots, which might warrant the adoption of additional management measures for these sites.

Vermetid bioconstructions along the western side of the island of Malta are less extensive than those settled along the eastern side, although the former sites are less accessible to human visitors. A relevant - but still not quantified and well-studied - threat to the conservation status of vermetid reefs appears to be the presence of marine non-indigenous species (e.g., *B. pharaonis*) whose impact on the vermetid reefs is not yet clear and which thus requires further specific study (Milazzo *et al.*, 2009).

The interaction between vermetids and this alien species needs to be further investigated seening that recent mechanistic modelling efforts (Sarà *et al*., 2013) predict an increasing performance of *B. pharaonis* in the central Mediterranean Sea, especially within the Strait of Sicily. This exotic bivalve is widely distributed along the Maltese (Cilia & Deidun, 2012) and Sicilian (Sarà *et al*., 2008; 2018) coastlines and hence this prediction is a plausible one. Nevertheless, the direct impact of *B. pharaonis* on vermetid bioconstruction-associated biodiversity and on the goods and services these provide has yet to be studied in detail along the Maltese coastline. Climate change-related stressors impact vermetid bioconstructions not only through the pressure represented by non-indigenous species, but also through direct mortality induced by higher temperatures (Rilov *et al*., 2020) as well as by a higher degree of ocean acidification which suppresses recruitment (Milazzo *et al*., 2014).

In Gozo, the distribution of vermetid bioconstructions was observed to be more disparate and less continuous, with existing bioconstructions being isolated from each other.

In this study, statistical differences emerge between vermetid reef typologies, both in terms of individual density and associated biodiversity. On the other hand, the absence of a discriminating human pressure effect (i.e. no significant differences in LUSI values) might be due to the high degree of anthropogenic pressure itself. In fact, since extensive swathes of the Maltese coastline are heavily disturbed by ongoing human activity, the segregation of different coastal sites on the basis of pressure intensity does not emerge. The homogenous human disturbance operating along the Maltese coastline does not allow for the identification of “control” (i.e. relatively pristine) sites since no sampled sites had a low LUSI index value.

The average vermetid individual density recorded in this study is that of 120 individuals/100 cm^2. This value falls within the range recorded along the Sicilian coasts, extending between 31 individuals/100 cm^2 in an impacted site up to more than 650 individuals/100 cm^2 in pristine sites (Di Franco *et al*., 2011; Fine *et al*., 2017). Schembri *et al.* (2005) reported a corresponding average density of 36 individuals/100 cm^2 for a smaller number of Maltese coastal sites concentrated along the north-east swathe of the island of Malta. Vermetid *trottoirs* have been recorded along the south-east coast of Sicily and even within the Pelagian Islands MPA (Chemello, 2009), located circa 100 km to the south-west of the Maltese archipelago. Given the geological congruence between the south-east coast of Sicily, the island of Lampedusa within the Pelagian Islands MPA and the Maltese archipelago, the latter vermetid bioconstructions represent potentially useful sites for future comparative studies involving Maltese vermetid reefs. Further research in this field could also benefit from a greater deployment of Remotely Piloted Aircraft Systems technology which can deliver an effective mapping and description of the complexity of these marine bioconstructions (Donnarumma *et al*., 2018; 2021).

The observed differences in the composition and structure of the algal community suggest an increase in terms of complexity from the crust to the *trottoir* typology. Specifically, the sites characterized by the crust typology presented a low coverage of erect algae (specifically, in the coverage by the Articulated Corallinae and by the Green Filamentous Algae), while the coverage by the Encrusting Coralline Rodophytes was higher than in the *trottoir* sites. The erect macroalgae associated with vermetid reefs offer meio- and macrofaunal species good conditions for colonization, refuge from predators and shelter from vigorous hydrodynamic activity and other abiotic factors (Chemello & Milazzo, 2002; Ape *et al*., 2018). Therefore, the greater the architecture of the fronds, the greater the complexity of the habitat (Chemello & Milazzo, 2002).

Although largely overlooked, Maltese vermetid bioconstructions are distributed over extensive swathes of the Maltese archipelago’s coastline, whilst being exposed to a plethora of anthropogenic threats, including trampling, climate change and associated impacts (e.g., the establishment of non-indigenous species), coastal urbanization, coastal runoff and vessel-originating pollution. Incorporating vermetid bioconstructions into future coastal management strategies and promoting a greater engagement of local citizens, stakeholders and policy makers is key to fostering a greater public awareness of the ecological role played by these often-overlooked assemblages. Echoing the appeal made by Gordo-Vilaseca *et al.* (2021) for a greater effort to protect this key ecosystem, we also underscore the need to formulate and to adopt policies and legislation which safeguard and improve the conservation status of vermetid bioconstructions within future Maltese MPA management plans.

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