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Vermetid crusts from the Maltese Islands (Central Mediterranean)

Faciès à vermets des îles maltaises (Méditerranée centrale)

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ABSTRACT

Azzopardi L., P.J. Schembri, 1997 - Vermetid crusts from the Maltese Islands (Central Mediterranean). Mar. Life, **7** (1-2): 7 - 16.

The vermetid crusts on 11 gently sloping rocky shores on the island of Malta were investigated. Crusts were formed by two species of vermetid gastropods, Dendropoma petraeum *(Monterosato, 1884) and* Vermetus triquetrus *Ant. Bivona, 1832, together with the rhodophyte* Neogoniolithon notarisi *(Dufour) Setchell and Mason.* Dendropoma *and* Vermetus *co-occurred on eight shores studied, one shore had a monospecific* Dendropoma *crust, while two shores had monospecific* Vermetus *crusts. Overall,* Dendropoma *was much commoner than* Vermetus *(2105.1 individuals per m², as against 115.5 individuals per m²). The mean width of the vermetid crust was of 0.67 m (range: 0.4 m to 1.2 m), extending from a mean of 0.51 m upshore from sea-level to a mean of - 0.12 m below the water line (range: 0.8 m to - 0.4 m). Crusts were between 0.1 cm and 10 cm thick, maximum thickness being reached just above mean sea-level. It is suggested that crust development is limited by climatic factors rather than by geology or geomorphology. For adult* Dendropoma, *crowding resulted in shells with smaller apertures, and crowding was at a maximum, and hence individuals were smallest, a small distance above mean sea-level. For monospecific* Vermetus *crusts, mean shell aperture diameter was more or less constant irrespective of position on the shore.*

RÉSUMÉ

Azzopardi L., P.J. Schembri, 1997 - [Faciès à vermets des îles maltaises (Méditerranée centrale)]. Mar. Life, **7** (1-2) : 7 - 16.

L'étude porte sur les encroûtements à vermets de onze estrans rocheux en pente douce de l'île de Malte. Les encroûtements sont formés par deux espèces de gastéropodes vermetidae, Dendropoma petraeum *(Monterosato, 1884) et* Vermetus triquetrus *Ant. Bivona, 1832, associés à l'algue rhodophycée* Neogoniolithon notarisi *(Dufour) Setchell et Mason. Les deux espèces* Dendropoma petraeum *et* Vermetus triquetrus *coexistent sur huit des estrans considérés, tandis que trois faciès sont monospécifiques ; un faciès présente* Dendropoma petraeum *seule et les deux autres sont formés par* Vermetus triquetrus. *Dans l'ensemble,* Dendropoma *est beaucoup plus abondant que* Vermetus *(2105,1 individus par m² contre 115,5 individus par m²). La largeur moyenne du faciès à vermets est de 0,67 m (variation de 0,4 m à 1,2 m), tandis qu'il s'étend d'une moyenne de 0,51 m au-dessus du niveau de la mer à une moyenne de - 0,12 m au-dessous (variation de 0,8 à - 0,4 m). L'épaisseur des encroûtements varie entre 0,1 et 10 cm, le maximum d'épaisseur étant atteint juste au-dessus du niveau de la mer. Il est suggéré que le développement de l'encroûtement est limité par les facteurs climatiques plutôt que par la géologie ou la géomorphologie. En ce qui concerne les adultes de* Dendropoma petraeum, *l'entassement entraîne une réduction de la taille de l'ouverture. A ce propos, l'entassement maximum, et donc la taille réduite des individus, est atteint juste au-dessus du niveau de la mer. Par contre, sur les faciès monospécifiques à* Vermetus triquetrus, *la taille moyenne de l'ouverture est plus ou moins constante, indépendamment de la position des individus sur l'estran.*

INTRODUCTION

According to the most recent catalogue of Mediterranean marine molluscs (Sabelli *et al.*, 1990), nine species of vermetid gastropods, belonging to four genera, occur in the Mediterranean. Of these, two species, *Vermetus triquetrus* and *Dendropoma petraeum*, have been implicated in the formation of characteristic biogenic constructions variously called vermetid platforms, reefs, or rims (Safriel, 1975; Barash, Zenziper, 1985), but also commonly referred to by their French name of *'trottoir'* (Pérès, Picard, 1964). These structures are formed when aggregations of vermetid shells on rocky shores are embedded in a calcareous matrix formed primarily by the coralline alga *Neogoniolithon notarisi* accompanied by other epilithic and endolithic species (Molinier, Picard, 1953; Safriel, 1975).

Such constructions take various forms (Laborel, 1987), but all develop more or less at mean sea-level and indeed have been used as biological markers of past shorelines (Fevret, Sanlaville, 1966, Thommeret *et al.*, 1983; Pirazzoli *et al.*, 1991). Vermetid *trottoirs* are characteristic of the warmer parts of the Mediterranean, particularly the central region and the East Basin (Safriel, 1966; 1974; Barash, Zenziper, 1985; Laborel, 1987). In many parts of the Mediterranean, these and other biogenic constructions are being negatively impacted by anthropic activities (Laborel, 1987) and for this reason vermetid trottoirs have been listed as threatened in the Red Data Book for the Mediterranean (anon., 1990), while the main trottoir former, *D. petraeum*, has recently been included in Appendix II (strictly protected fauna) of the Berne Convention (Council of Europe).

Both *Vermetus triquetrus* and *Dendropoma petraeum* have been recorded from the Maltese Islands (Cachia *et al.*, 1993), however, while vermetid *trottoirs* are known to exist (Paskoff, Sanlaville, 1978; Fenech, 1980; Richards, 1983), these structures and the species which form them have never been systematically studied. In this paper we report on a study of the vermetid formations of Maltese gently sloping rocky shores and the gastropods which construct them.

MATERIAL AND METHODS

Fieldwork was carried out in the period July to September. Accessible rocky shores on the northern, north-eastern, eastern and south-eastern coasts of Malta were surveyed and 11 shores with relatively large stretches of vermetid crusts were selected for detailed study (figure 1). Details of these stations are given in table I.

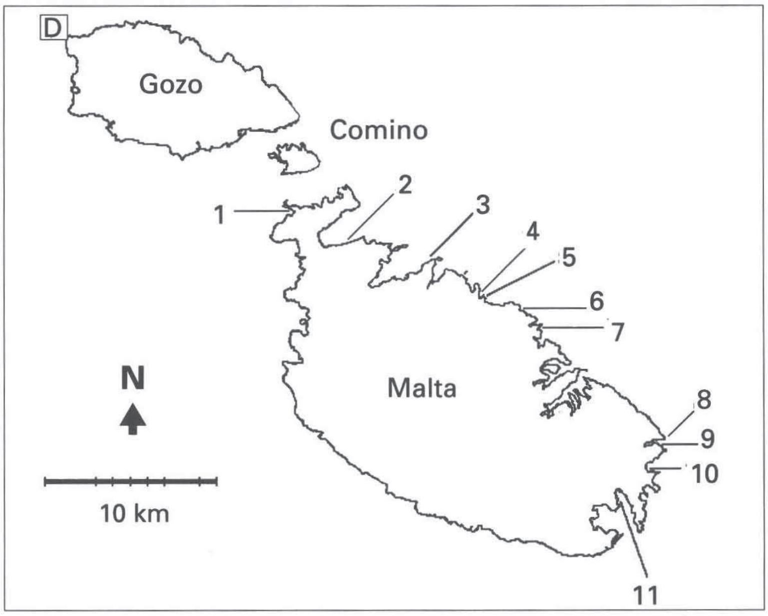

Figure 1- Map of the Maltese Islands showing the location of the shores studied. San Dimitri Point, the most exposed shore in the Maltese Islands, is also shown (D). / *Carte des îles maltaises présentant les estrans étudiés. Le cap San Dimitri, point le plus exposé, est aussi indiqué (D).*

1 - Cirkewwa; 2 - Ghajn Zejtuna; 3 - Qawra; 4 - Bahar ic-Caghaq; 5 - White Rocks; 6 - Pembroke; 7 - Il-Qaliet; 8 - Zonqor Point; 9 - Marsascala Bay (Il-Kappara); 10 - St.Thomas Bay (Tal-Munxar); 11 - Marsaxlokk Bay (Il-Qrajten).

Table I - Characteristics of the shores and the vermetid crusts studied. / *Caractéristiques des estrans et des encroûtements à vermets étudiés.*

Locality	Rock type[a]	Thomas Exposure Index	Transect[b]	Length of vermetid zone (m)	Maximum thickness of vermetid crust (mm)	Population density of vermetids (individuals per m²)		
						Dendropoma	*Vermetus*	Juveniles
Cirkewwa	UCL	11.3	A1	1.2	80	4391.7	0	852.3
			A2	0.7	100	3428.6	14.3	757.1
Ghajn Zejtuna	UCL	15.6	B1	0.4	40	2075	0	2475
			B2	0.5	40	1720	0	2600
Qawra	LCL	11.9	C1	0.7	15	4028.6	42.9	2257.1
			C2	0.7	—	857.1	0	14.3
Bahar ic-Caghaq	LCL	13.9	D1	0.7	30	2214.3	128.6	671.4
			D2	0.5	50	2860	80	160
White Rocks	GL	9.5	E1	0.8	80	1300	100	200
			E2	0.5	15	1720	40	180
Pembroke	LCL	7.7	F1	1.0	6	3360	0	0
			F2	0.5	7	5120	20	0
Il-Qaliet	LCL	11.2	G1	1.0	10	2740	100	60
			G2	0.8	9	3550	12.5	0
Zonqor Point	GL	9.8	H1	0.7	18	0	728.6	1385.7
			H2	0.4	15	0	105	2400
Marsascala Bay	GL	3.6	I1	0.6	8	0	450	0
(Il-Kappara)			I2	0.6	8	0	633.3	0
St.Thomas Bay	GL	3.7	J1	0.5	12	1975	0	0
(Tal-Munxar)			J2	0.6	11	1966.7	16.7	0
Marsaxlokk Bay	GL	5.2	K1	1.0	6	1030	70	0
(Il-Qrajten)			K2	0.4	6	1975	0	0

(a) Key to rock types: GL, Globigerina Limestone; LCL, Lower Coralline Limestone; UCL, Upper Coralline Limestone.
(b) Two transects were taken on each shore.

Exposure was estimated by the method of Thomas (1986) which assigns a numerical value for the wave action on a shore. This method estimates the magnitude of wave action on a shore from information on the velocity, direction and duration of the wind, as modified by the direction, shape and angle of impact on the shore, the wind fetch, and the distribution of shallow water both close to and away from the shore within the fetch. For the Maltese Islands, where there is no water less than 6 m deep not adjoining the shore within the fetch, Thomas' formula reduces to:

$$EI = \sum \log W \times \log(1 + F / CS)$$

where *EI* is Thomas' exposure index, *W* is the wind energy, *F* is the fetch in nautical miles (100 nautical miles maximum), and *CS* is the extent in nautical miles of water < 6 m deep adjoining the shore. The terms *W, F* and *CS* are determined separately for each of the twelve 30° sectors of the compass centred on the exact point of the shore whose exposure is to be determined. Only these sectors which were at least 50 % unobstructed by adjacent shorelines were used for the calculation of the exposure index, as recommended by Thomas (1986). The wind energy for each sector was determined using data on the percentage time the wind blows in each sector, the wind strength and the duration, obtained from the Meteorological Office of the Department of Civil Aviation, Luqa, Malta. To put the calculated exposure indices of the shores studied in perspective, the exposure of the most exposed shore in the Maltese Islands, that at San Dimitri Point on the northwestern coast of Gozo (figure 1), which is exposed to the prevailing Northwesterly wind with no sheltering landmass for at least 100 nautical miles, was also calculated; *EI* for San Dimitri Point was 34.54.

On each shore, two transects, situated approximately 5 m apart, were laid down perpendicular to the waterline. Transects were sited where the rock was relatively flat and areas with ridges, depressions and rockpools were avoided. The position of the 'vermetid zone' within each transect was determined by locating the highest (*i.e.* up the shore, relative to sea-level) and lowest individual vermetid tubes. The lowest tubes always occurred close to, or below, water level and to locate these, a face mask was used. The position of the 'biological zero point' (the upper limit of phaeophyceans of the genus *Cystoseira*; Boudouresque, Cinelli, 1976) was determined and this was taken to represent mean sea-level (Mallia, Schembri, 1996). A 10 x 10 cm quadrat was placed such that its upper edge coincided with the upper limit of the 'vermetid zone'. All vermetids occurring in the quadrat were identified and counted. Vermetids with a shell aperture of < 0.1 mm could not be identified in the field and were counted as 'juveniles'. Contiguous quadrats were analysed in this way until the lower limit of the 'vermetid zone' was reached. Abundance data were standardised as number of individuals per square meter. For measurements of shell aperture diameter, 10 individual adult vermetids were picked at random from each quadrat and the maximum diameter of the tube aperture was measured with vernier callipers. Samples of rock encrusted by vermetids were collected using a hammer and chisel and transported to the laboratory for detailed examination.

RESULTS

All specimens examined belonged to two species: *Dendropoma petraeum* (Monterosato, 1884) and *Vermetus triquetrus* Ant. Bivona, 1832. In the field, adults of these two species could be told apart by examination of the operculum: reddish brown and fitting the shell aperture completely in *Dendropoma*, and yellow and less than half the diameter of the shell aperture in *Vermetus* (Keen, 1961; Barash, Zenziper, 1985).

Dendropoma and *Vermetus* co-occurred on eight (72.7 %) of the 11 shores studied; *Dendropoma* was the sole vermetid at Ghajn Zejtuna, while *Vermetus* was the sole vermetid at Zonqor Point and at Marsascala (table I). In terms of abundance, *Dendropoma* was much commoner than *Vermetus*, reaching a mean population density of 2105.1 individuals per m^2 on the 11 shores as a whole, as against 115.5 individuals/m^2 reached by *Vermetus*. In general, the population density of *Dendropoma* tended to increase with exposure (figure 2), although this correlation was not significant. Similarly, there was no significant correlation between the population density of *Vermetus* and the exposure as measured by the Thomas index.

On all the shores studied, the vermetids formed a crust over the underlying bedrock, which was either Coralline Limestone or Globigerina Limestone (table I). This crust was composed predominantly of closely juxtaposed dead vermetid tubes cemented together by the calcareous rhodophyte *Neogoniolithon notarisi* (Dufour) Setchell and Mason; living vermetids occurred only on the surface of this crust. The width of the vermetid crust (defined as the linear distance between the uppermost and lowermost individual vermetids on the shore) varied from a maximum of 1.2 m at Cirkewwa, to a minimum of 0.4 m at Ghajn Zejtuna, Zonqor Point and Marsaxlokk (table I). The mean width of the vermetid crust on the 11 shores taken together was of 0.67 m. In relation to mean sea-level, the crust extended a maximum distance of 0.8 m upshore at Cirkewwa, Qaliet and Pembroke, and a maximum distance of -0.4 m below the water line at Cirkewwa. For the 11 shores taken together, the corresponding mean values are 0.51 m and - 0.12 m.

The submerged lower edges of the vermetid crust were usually riddled by rock-boring organisms. In places, there were gaps in the crust, probably caused by collapse of the original continuous crust.

Some of these gaps were heavily settled by juvenile vermetids, suggesting that the eroded crust was being re-built. Apart from gaps, the highest population densities of juveniles occurred on mediolittoral rock devoid of macroalgae, or, where algal cover was substantial, on the adult vermetid shells. In general, juveniles appeared to settle preferentially in small pits or irregularities in the substratum. On some shores, juvenile vermetids were present in high abundance; however, on others no juveniles at all were present (table I). There is a significant positive correlation ($r = 0.5881$; $0.001<P<0.01$)between population density of juveniles and exposure index (figure 2). The mean abundance of juveniles for the 11 shores taken together was 637 individuals per m^2.

The vermetid crust was between 0.1 cm and 10 cm thick. Maximum thickness was reached just above mean sea-level and the crust thinned out in either direction, with the submerged portion of the crust thinning out much more rapidly than the exposed portion. The crust thus assumed the aspect of a raised ridge or rim running parallel to the shore just above mean sea-level.

Where the two vermetids co-occurred, they were differentially distributed within the crust. *Dendropoma* formed the bulk of the crust and exclusively built the raised rim just above mean sea-level. *Vermetus* occurred on the flattened portion of the crust behind the raised rim, as well as below the water line. For the eight shores where the two species co-occurred in the same crusts, the ratio of *Den-*

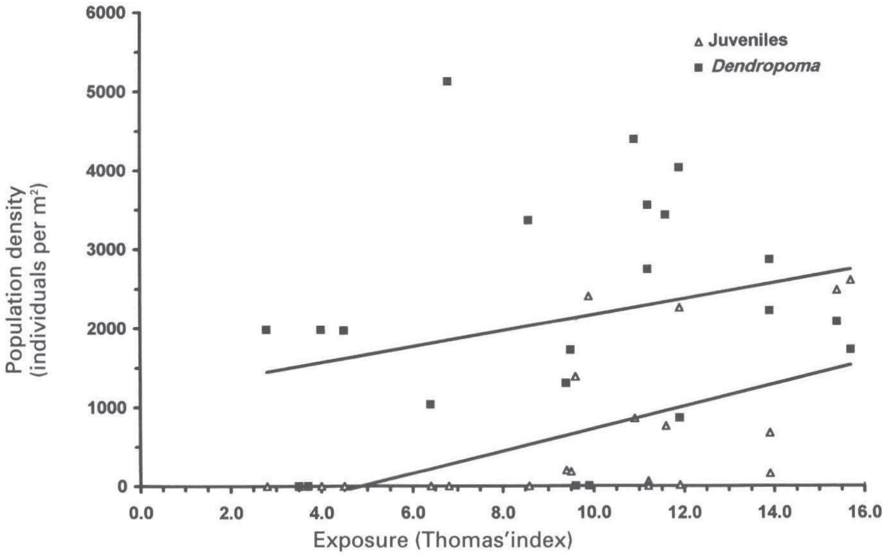

Figure 2 - The correlation between population density of adult *Dendropoma petraeum* (upper regression line) and of juvenil vermetids (lower regression line) within each transect and exposure. / *Corrélation entre les densités de population de* Dendropoma petraeum *adultes (ligne de régression supérieure) et de vermets juvéniles (ligne de régression inférieure) dans chaque transect et indice d'exposition.*

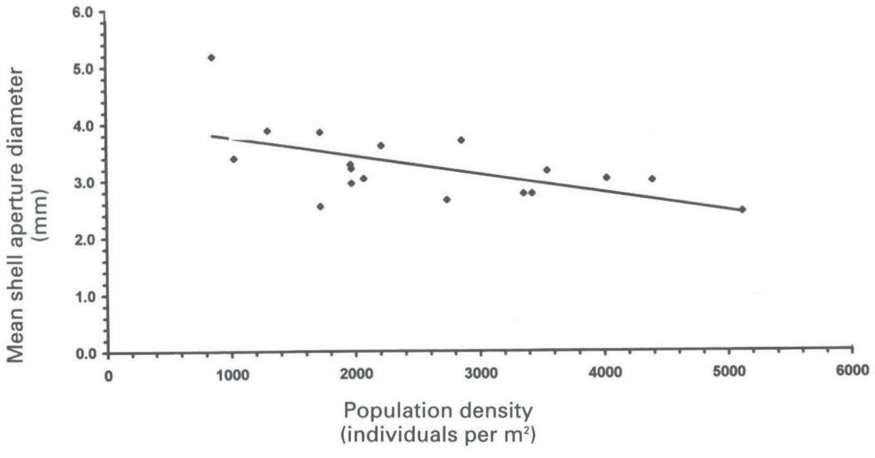

Figure 3 - The correlation between the mean shell aperture diameter and the population density of adult *Dendropoma petraeum* within each transect. / *Corrélation entre le diamètre moyen de l'ouverture de coquille et la densité de population de* Dendropoma petraeum *dans chaque transect.*

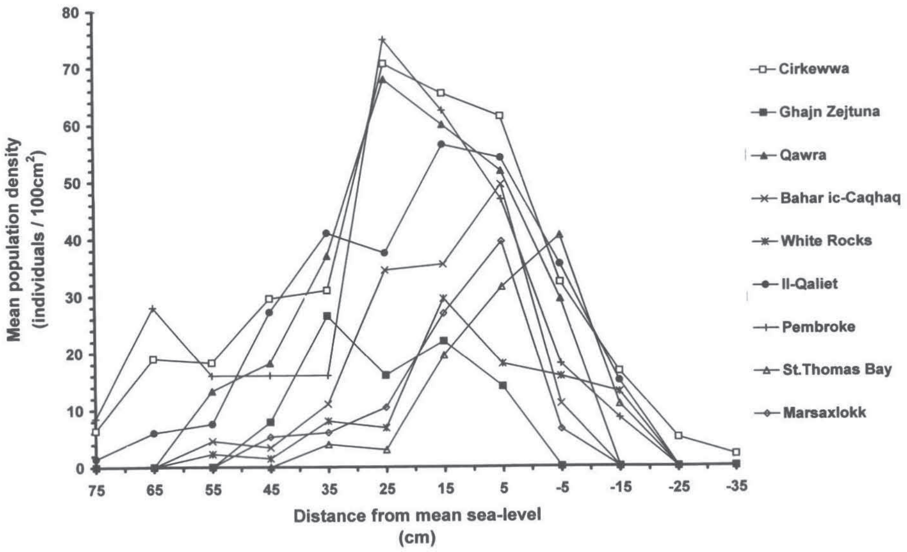

Figure 4 - The variation in the mean population density of adult *Dendropoma petraeum* with distance from mean sea-level (at 0 cm) for the nine shores on which this species occurred. / *Variation de la densité de population moyenne de* Dendropoma petraeum *adultes en fonction de la distance au niveau moyen de la mer (à 0 cm) pour les neuf estrans où cette espèce est présente.*

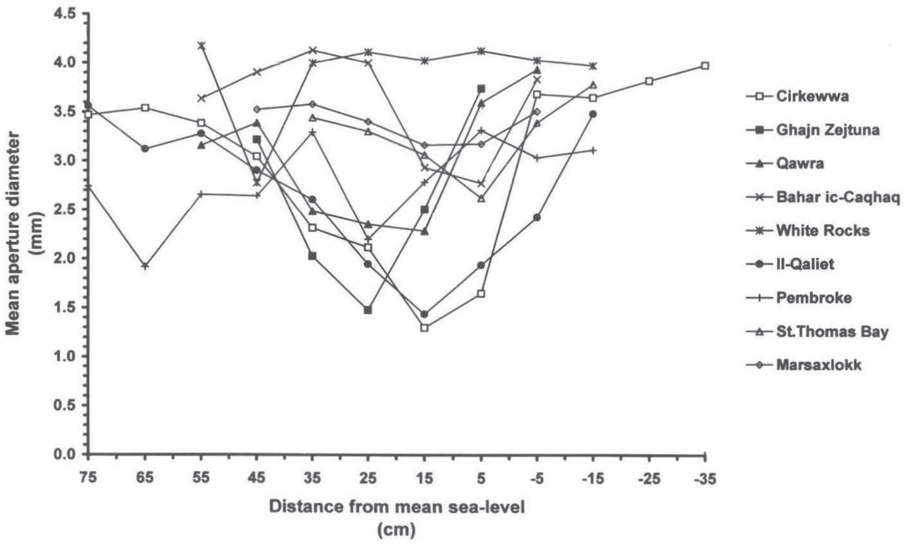

Figure 5 - The variation in the mean shell aperture diameter of adult *Dendropoma petraeum* with distance from mean sea-level (at 0 cm) for the nine shores on which this species occurred. / *Variation du diamètre moyen de l'ouverture de coquille des* Dendropoma petraeum *adultes en fonction de la distance au niveau moyen de la mer (à 0 cm) pour les neuf estrans où cette espèce est présente.*

dropoma to *Vermetus* on the surface of the crust varied between 559:1 for Cirkewwa and 22:1 for White Rocks; the mean ratio for all eight shores taken together was 185:1.

Where the crusts were formed exclusively by *Vermetus* (at Zonqor Point and at Marsascala), the gastropods occurred on rock encrusted by coralline algae in a loose aggregation, with each tube being an average of 5 to 10 mm from its neighbours. Solitary individuals of *Vermetus triquetrus* also occurred on the bottom of shallow (10-30 cm) lowershore rockpools on many of the shores studied, particularly if the edges of these pools were 'built up' into a raised rim by *Dendropoma* crusts.

At Qaliet, Ghajn Zejtuna, St. Thomas Bay and Marsaxlokk, the vermetid crust was completely overgrown by *Neogoniolithon notarisi*, such that only the apertures of the vermetid tubes were visible as minute black holes in the overlying algal layer. In many cases, the tube apertures were severely constricted by the encrusting alga to tiny round or elliptical pinholes.

For adult *Dendropoma*, there is a significant negative correlation (r = 0.5954; 0.001<P<0.01) between the population density estimate for each of the transects considered, and size, as measured by the shell aperture diameter (figure 3). Crowding thus appears to result in shells with smaller apertures. The same analysis could not be made for *Vermetus* since the numbers occurring in most transects were too low.

The relationship between population density of adult *Dendropoma* and position on the shore was explored by plotting the mean population density along the shore, against the distance from mean sea-level, for all shores with *Dendropoma* (figure 4). In most cases, the highest population densities occurred just above mean sea-level, at a distance of between + 5 cm and + 35 cm (mean 13.5 cm), however, for the shore at St. Thomas Bay, the peak popu-

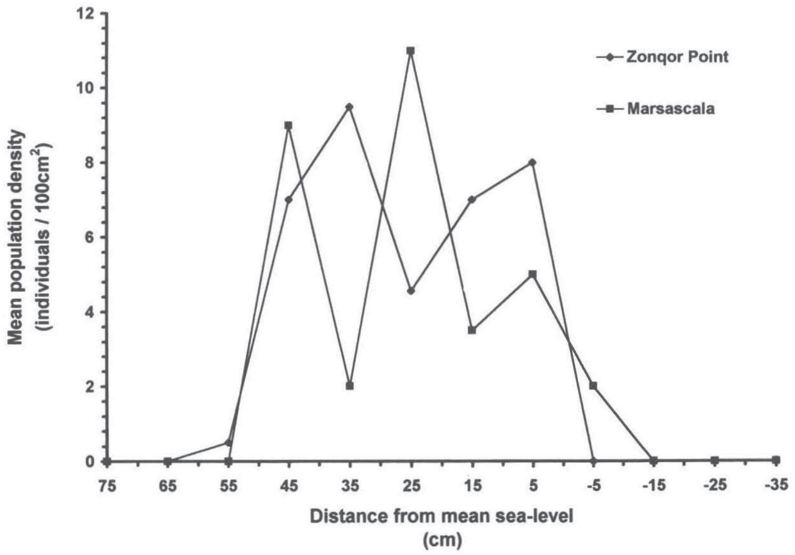

Figure 6 - The variation in the mean population density of adult *Vermetus triquetrus* whith distance from mean sea-level (at 0 cm) for the two shores where this species was the only vermetid present. / *Variation de la densité de population moyenne de* Vermetus triquetrus *adultes en fonction de la distance au niveau moyen de la mer (à 0 cm) pour les deux estrans où cette espèce est l'unique vermet présent.*

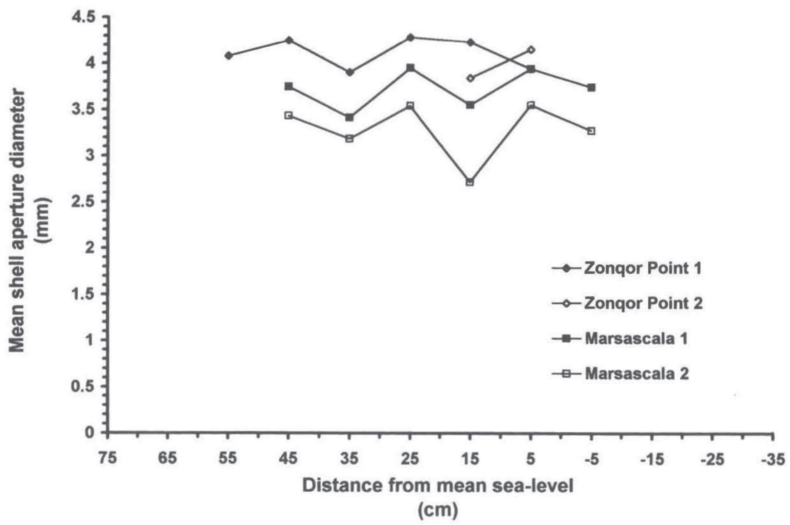

Figure 7 - The variation in the mean shell aperture diameter of adult *Vermetus triquetrus* with distance from mean sea-level (at 0 cm) for the two shores where this species was the only vermetid present. Two transects were taken on each shore. / *Variation du diamètre moyen de l'ouverture de coquille des* Vermetus triquetrus *adultes en fonction de la distance au niveau moyen de la mer (à 0 cm) pour les deux estrans où cette espèce est le seul vermet présent. Deux transects ont été réalisés sur chaque côte.*

lation density was at - 5 cm below mean sea-level, while for the shore at Pembroke there was a second, minor peak, higher upshore at a distance of + 65 cm (figure 4). Since crowding results in smaller sized individuals, the smallest individuals are expected to occur where the population density peaks. This was explored by plotting the mean shell aperture diameter for each quadrat in a transect, against the distance of the quadrat from mean sea-level (figure 5). As expected, the resulting patterns mirrored those for population density, with the minimum occurring at a distance of between + 5 cm and + 45 cm from mean sea-level (mean 12.3 cm), except for Pembroke where there were two minima at + 25 cm and at + 65 cm (figure 5).

The same analyses were made for *Vermetus*, using the data for the transects from Zonqor Point and Marsascala, the two localities where this species was the only vermetid present. Although population density was very low on both shores, peak densities were recorded at a distance of between + 25 cm (Marsascala) and + 35 cm (Zonqor Point) from mean sea-level (figure 6). In both localities, the mean shell aperture diameter was more or less the same in all quadrats, irrespective of their position on the shore (figure 7).

DISCUSSION

Dendropoma petraeum is the principal crust-forming vermetid on Mediterranean shores, and in many cases, the only such species. Where *Vermetus triquetrus* occurs, it normally occupies shallow water-filled holes and depressions within and behind the *Dendropoma* aggregations, where conditions are less turbulent (Safriel, 1966; 1975). This is also the situation on those Maltese shores where the two species co-occur, however, a significant number of shores have crusts composed only of *Vermetus triquetrus*. In both the *Dendropoma* and the *Vermetus* crusts, the matrix filling the spaces between the vermetid tubes is produced mainly by the coralline alga *Neogoniolithon notarisi*, however, the *Vermetus* crusts differ from the *Dendropoma* ones in that the tubes are more spaced out from each other, tube density is less, while the crust is usually much thinner. Very few reports of monospecific *Vermetus triquetrus* crusts appear to have been published; Safriel (1975) describes uninterrupted *Vermetus* crusts 2-4 cm thick, cemented by *Neogoniolithon notarisi*, however, these are apparently always rimmed by *Dendropoma* crusts.

Chemello (1989) describes how a third species of vermetid, the sublittoral *Serpulorbis arenaria*, may grow along the submerged lower edge of the mediolittoral crusts and extend these into deeper water. Although this species also occurs in the Maltese Islands (Fenech, 1980), no such extended crusts were encountered.

Laborel (1987) has described three types of vermetid trottoirs from the Mediterranean: the bench or platform type, the atoll type and the cornice type. The first consists of a more or less wide platform at sea-level covered with depressions each a few centimetres deep. The atoll type takes the form of raised circular rim surrounding a central depression, reminiscent of a miniature atoll. The cornice type consists of a small horizontal ledge growing out from steep or vertical rock-faces. The Maltese vermetid crusts are closest to the platform type in morphology, however, they are much less developed than the vermetid platforms described from parts of Sicily, where they can be up to 10 m wide and more than 5 cm thick (Molinier, Picard, 1953; Chemello *et al.*, 1990), or from those of the eastern Mediterranean which may be up to 30 m across and 3 to 25 cm thick (Safriel, 1966, 1975).

Where growth of the vermetids is not limited by the cold winter temperatures, platform development seems to be related to the nature of the substratum, the tidal range and the degree of wave action. Vermetid platforms are best developed where marine erosion of soft rock results in a horizontal or subhorizontal platform at sea-level which becomes colonised by a crust of vermetids embedded in a coralline algal matrix (Safriel, 1975). The greater the tidal range and the exposure to wave action, the greater the width of the vermetid crust, since the Mediterranean crust-forming species are strictly water-line species, at least in their gregarious form. The limited width of the Maltese vermetid crusts relative to Sicilian and Israeli ones is probably related to the less exposed nature of Maltese shores and the reduced tidal range [maximum exposure during spring tides c.20 cm in Malta (Drago, Xuereb, 1993) as compared to 25-30 cm in Israel (Safriel, 1975)], rather than to topography; Maltese rocky shores are all made of limestone, which erodes into more or less horizontal platforms at sea-level where the coast is not cliffs (Paskoff, Sanlaville, 1978). Nonetheless, the effect of hydrodynamism on the degree of development of vermetid trottoirs is well demonstrated by the Maltese crusts where there is generally a direct relationship between exposure and width of the vermetid zone (table I).

The different niches occupied by the two Mediterranean crust-forming vermetids are well documented (Safriel, 1966; 1974; 1975; Barash, Zenziper, 1985). *Dendropoma petraeum* thrives where there is considerable wave action and frequent subaerial exposure, while *Vermetus triquetrus* occupies more sheltered situations in holes and depressions or in the shelter provided by the raised *Dendropoma* rims (Safriel, 1966; 1975). This is also the situation in the Maltese Islands. Here, generally, the lowest population densities of *Vermetus* were recorded from the more exposed shores, and the most exposed shore studied (Ghajn Zejtuna) had no *Vermetus* at all. However, it is interesting to note that while the shores with monospecific *Vermetus* crusts have a low exposure, as is to be expected, certain Maltese shores with a similar or even lower exposure than those with the monospecific *Vermetus* crusts have crusts formed mainly by *Dendropo-*

ma. In such cases, it is likely that microclimatic conditions result in turbulence or frequent episodes of emergence (or both) which favour *Dendropoma* over *Vermetus.*

The observation of gaps in the Maltese vermetid crusts and the heavy settlement of juveniles in them suggests that these structures are quite dynamic. As already suggested by Safriel (1974; 1975) once a crust grows to the maximum thickness permitted by the prevailing environmental conditions, further growth takes place at the edges. As the crust extends further under water, it becomes invaded by borers whose galleries weaken the structure, making it susceptible to erosion by waves. Once a gap appears, this exposes fresh rock at sea-level which is colonised by juvenile vermetids and the cycle repeats. The positive correlation between exposure and population density of juveniles on Maltese shores supports this hypothesis since the more exposed a shore, the more severe the erosion is expected to be.

No studies appear to have been made on the exact relationship between the Mediterranean gregarious vermetids and the organisms which make up the matrix filling the spaces between their shells, principally the coralline alga *Neogoniolithon notarisi.* The observation that on a number of Maltese shores the vermetid shells were completely overgrown by this alga, to the extent that the apertures were all but occluded, suggests that this relationship might involve elements of competition for space. It would appear that the final vermetid-algal composite is maintained by a dynamic balance between growth of the alga and the gastropods, and the inhibitory effects of subaerial exposure, once the crust reaches a certain thickness and lateral expansion.

There are also indications that there is intraspecific competition for space amongst the vermetids. Thus, in *Dendropoma,* the higher the population density within the vermetid zone as a whole, the smaller the mean size of the individuals, an effect which has already been noted by Hopper (1981) for *Dendropoma gregaria* in Hawaii and by Smalley (1984) for the non-gregarious *Dendropoma maxima* in Guam. Similarly, within a crust, the mean size of *Dendropoma* reached a minimum where there was maximum crowding, that is, at around mean sea-level. Hopper (1981) reported a similar phenomenon for *Dendropoma gregaria* in Hawaii. In monospecific *Vermetus* crusts, maximum crowding occurred just above mean sea-level, however, this effect was much weaker than in the *Dendropoma* crusts. Unlike the latter, monospecific *Vermetus* crusts did not show any pronounced differences in the size of individuals with position on the shore, presumably because tube density is much lower than in the *Dendropoma* crusts.

From the above it follows that for *Dendropoma* crusts at least, measuring the point where tube density is at a maximum and tube size at a minimum will provide an approximate position for mean sea-level. This is applicable to both living and fossil crusts.

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