

Associated fauna of the fan shell *Pinna nobilis* (Mollusca: Bivalvia) in the northern and eastern Tunisian coasts

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SUMMARY: Epifaunal communities associated with the fan shell *Pinna nobilis* Linnaeus, 1758 along the Tunisian coastline were investigated. Both univariate and multivariate analysis were done at different spatial scales within five populations located at different localities, three from northern and two from eastern Tunisia. The size of *Pinna* did not appear as the main factor affecting the structure of the associated biota, which seemed to be more influenced by (a) marine-lagoon and (b) biogeographic gradients. Patterns of similarity of sessile sclerobionts and motile epifauna were clearly different. The former assemblage best replied to lagoon-sea gradient and to locality, with three real clusters at 40%, whereas the latter assemblage scattered widely in a non-metric MDS plane, with two real clusters only at 20% similarity. The spatial turnover of motile species was ten times higher than that of sessile species at a small spatial scale, being less affected by *Pinna* size, and three times higher though invariant at a large geographic scale. On the other hand, β -diversity of sessile species appeared to be more influenced by latitudinal (climatic) gradient at a large scale, being higher in the northern than in the eastern communities. Analysis of taxonomic (dis)similarity of the whole community detected these two sources of environmental (lagoon-sea gradient) and biogeographic (lati-longitudinal gradient) variation, although each phylum showed its peculiar pattern. In terms of Dajoz's constancy index the majority of associated communities were dominated by rare species, and within the majority of epifaunal assemblages, the most abundant sessile epizobiont was a bivalve mollusc. The sessile epifauna was dominated by active filterers, which led to a possible existence of trophic competition between the host and the sedentary epizoites, since both basibionts and sclerobionts occupy the same trophic niche. The fan shell played an important ecological role, providing new hard substrate to colonise, increasing the spatial heterogeneity for the surrounding soft-bottom communities, and contributing to the overall increase of the local biotope complexity level.

Keywords: *Pinna nobilis*, epifauna, assemblages, β -diversity, spatial scale, Tunisian coasts.

RESUMEN: FAUNA ASOCIADA A LA NACRA *PINNA NOBILIS* (MOLLUSCA: BIVALVIA) EN LA COSTA NORTE Y ESTE DE TÚNEZ. – Se investigaron las comunidades de la epifauna asociadas a la nacra *Pinna nobilis* Linnaeus, 1758 a lo largo de la costa de Túnez. Se realizaron análisis univariantes y multivariantes a diferentes escalas espaciales en cinco poblaciones situadas en diferentes localidades, tres del norte y dos del este de Túnez. La talla de *Pinna nobilis* no fue el factor que más afectó la estructura de los organismos asociados, que parecieron más influenciados por (a) lagunas marinas y (b) gradientes biogeográficos. Los patrones de similitud de los esclerobiontes sésiles y la epifauna móvil fueron claramente distintos. La primera asociación respondió mejor al gradiente laguna-mar así como a la localidad, con tres grupos reales a 40% de similitud, mientras que el último grupo se repartió ampliamente en el plano no métrico (MDS), con sólo dos grupos reales a 20% de similitud. La renovación espacial de especies móviles fue diez veces más alta que la de las sésiles a pequeña escala espacial, estando menos afectada respecto a la talla de *Pinna nobilis*, y tres veces más alta a pesar de ser invariante a mayor escala geográfica. Al contrario, la diversidad- β de especies sésiles estuvo más influenciada por el gradiente latitudinal (climático) a gran escala, siendo más alto en las comunidades del norte que en las del este. El análisis de (di)similitud taxonómica de toda la comunidad detectó estas dos fuentes de variación ambiental y biogeográfica, aunque cada phylum mostró su peculiar patrón. En términos del índice de constancia de Dajoz la mayoría de comunidades agrupadas estuvieron dominadas por especies raras, y dentro de la mayoría de agrupaciones de la epifauna, los epibiontes sésiles más abundantes fueron los moluscos bivalvos. La epifauna sésil estuvo dominada por filtradores activos, lo que lleva a la existencia de

una posible competencia trófica entre el huésped y los epizoites sedentarios, ya que tanto basibiontes como esclerobiontes ocupan el mismo nicho trófico. La naera juega un importante papel ecológico proporcionando un sustrato nuevo y duro para colonizar, incrementando la heterogeneidad espacial para las comunidades de fondos blandos y contribuyendo al incremento global de la complejidad del biotopo local.

Palabras clave: *Pinna nobilis*, epifauna, agrupaciones, diversidad- β , escala espacial, costa Tunecina.

INTRODUCTION

In marine ecosystems the survival of many sessile macro-invertebrate species is highly dependent on a suitable substrate in which to settle; the colonising taxa and the structure of the epifaunal community are determined by the structure and dynamics of the substratum (Sebens, 1991). However, because of the scarcity of rocky substrata in sandy and muddy habitats, colonisation of the body surface of other marine animals becomes a valuable strategy for the survival of sessile as well as motile organisms. In this context, some crustacean and mollusc species play an important role as hard living substrata which can host epibiontic assemblages of varying complexity (Conover, 1979; Warner, 1997; Parapar *et al.*, 1997; Silina and Ovsyannikova, 1998; Fernández *et al.*, 1998). In Mediterranean marine ecosystems, the fan shell *Pinna nobilis* is one of the most evident examples of this phenomenon. It is described as a considerable centre of species aggregation and it is known as being a very important biological substratum for many epizoobionts (Zavodnik, 1963, 1967). Several studies about the associated communities of *P. nobilis* have shown that this basibiont plays an important role in providing a hard substratum for a complex epizoobiontic community (Corriero and Pronzato, 1987; Giacobbe, 2002; Cosentino and Giacobbe, 2007). However, these studies concerned one taxon only (molluscs or sponges) and did not take into account the possible modifications of the epifaunal community in terms of habitat type, and also at increasing spatial scale. In the present study, the fauna associated with *P. nobilis* was investigated within five populations located on the northern and eastern coasts of Tunisia. Five epifaunal communities were compared, analysing their variability according to the habitat type and the spatial turnover of the associated species. The aims of the study were therefore: (i) to assess the structure and variability of the associated community respect to the basibiont size and the habitat where it lives; and (ii) to evaluate the epifaunal similarity and diversity, with a particular focus on species turnover (β -diversity) at increasing spatial scales as a function of environ-

mental and biogeographic gradients, also assessing the differential contribution of each phylum to the taxonomic (dis)similarity.

MATERIAL AND METHODS

During a study of the growth of *Pinna nobilis* in Tunisia (Rabaoui *et al.*, 2007), thirty specimens of *P. nobilis* were collected from each of five populations located along the northern and eastern Tunisian coastline, two in Bizerta Lagoon (N1 at Echaâra; N2 at Njila), one in the Gulf of Tunis (N3 at Sidi Rais) and two in Monastir Bay (E1 at Stah Jaber and E2 at Teboulba) (Fig. 1). N1 is located in the channel which joins Bizerta Lagoon and the Mediterranean Sea (lagoon-sea population), N2 is located inside Bizerta Lagoon (strictly lagoon population), and N3, E1 and E2 are strictly marine populations. All samples were taken by free diving in shallow areas at a depth that did not exceed 3 m. Seagrass meadows (mainly *Cymodocea nodosa*, with or without *Posidonia oceanica*) were present at all sampling sites, and the main environmental features are reported in Table 1. Epifauna was collected by scraping off and washing out the valvar surface of each basibiont over a 0.5 mm sieve. The associated species were sepa-

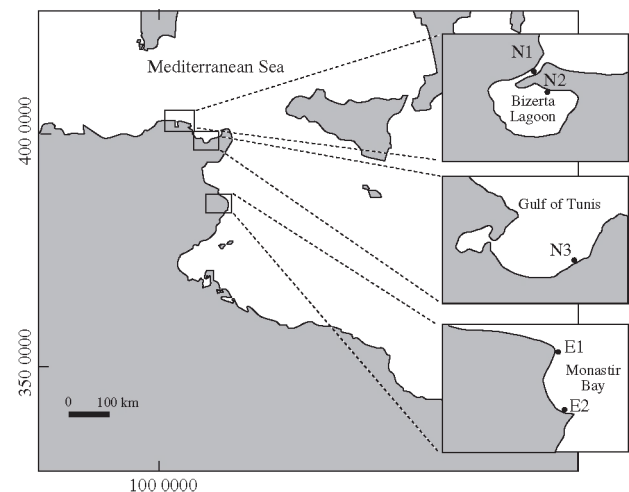


FIG. 1. – The location of the five sampling sites of *Pinna nobilis* specimens. N1, Echaâra; N2, Njila; N3, Sidi Rais; E1, Stah Jaber; E2, Teboulba.

TABLE 1. – Environmental characteristics assessed during the sampling period for the five sites.

Environmental features	N1 - Echaâra (Bizerta Lagoon)	N2 - Njila (Bizerta Lagoon)	Sampling site N3 - Sidi Rais (Gulf of Tunis)	E1 - Stah Jaber (Monastir Bay)	E2 - Teboulba (Monastir Bay)
Habitat type	Lagoon-Sea	Lagoon	Sea	Sea	Sea
Sediment typology	Sand-Mud + biodetritrus	Mud	Sand-Mud	Sand-Mud	Sand-Mud + biodetritrus
Season (temperature)	Summer (28.8°C)	Autumn (17.6°C)	Winter (9.0°C)	Winter (10.3°C)	Summer (29.7°C)
Salinity	39.2 psu	37.3 psu	37.3 psu	37.2 psu	38.8 psu
Hydrodynamism / exposure	Currents in the channel / Moderately exposed	Weak currents / Sheltered	Waves, littoral currents/ Moderately exposed	Waves, littoral currents / Moderately exposed	Strong waves and currents / Exposed
Vegetation	<i>Cymodocea nodosa</i>	<i>Cymodocea nodosa</i>	<i>C. nodosa</i> - <i>Posidonia oceanica</i>	<i>Cymodocea nodosa</i>	<i>C. nodosa</i> - <i>Posidonia oceanica</i>
Depth	3 m	2 - 3 m	1.5 - 3 m	2 m	2 - 3 m

rated into the major taxonomic groups, preserved in 5% buffered formalin solution and classified at the highest possible level. Sessile taxa were separated from motile taxa. Abundance of colonial species of Porifera and Bryozoa was assessed in terms of cover percentage for each valve, ordered in the following categories: absence (0%), less than 10%, from 10 to 50%, from 51 to 90%, more than 91%; the average cover percentage was then calculated for each *Pinna* specimen. Abundances (percentages and counts) of both sessile and motile taxa were therefore standardised per sample total ($N_{\text{species}} / N_{\text{total}} \times 100$). Number of species *S*, Shannon-Wiener's diversity H' (\log_e) and Pielou's evenness J' were calculated for each fan shell and for the five populations. To determine the most common epizoites of each *Pinna* population, Dajoz's (1971) constancy index was used, $CA1 = nA1 / n1 \times 100$, where *nA1* was the number of shells where the species *A* was present and *n1* the total number of shells examined ($n1 = 30$). According to this index, epifaunal taxa were classified as rare (less than 12%), not very common (13-24%), common (25-49%), very common (50-74%), and constant (75-100%).

To test the variability among the five associated assemblages and their multivariate spatial arrangement, non-metrical Multi-Dimensional Scaling (2-d nmMDS) ordination joined with sample cluster classification were performed separately for sessile and motile assemblages. In order to reduce differences of abundance due to sample size and to remove differences of counts with regard to colonial or individual sessile sclerobionts, the data matrix was converted to presence/absence. Six samples of *Pinna* with a very low occurrence of species were considered as outliers and excluded from ordination of motile epifauna. One-way Analysis of Similarity (ANOSIM) was performed to test for the following factors:

i. Habitat type (lagoon; lagoon-sea; sea); ii. Shell size class (small: less than 25 cm; medium: from 25 to 40 cm; large: more than 40 cm). Moreover, two-way nested ANOSIM was computed to test for differences or similarities at a larger spatial scale, between (a) *Pinna* population (N1, N2, N3, E1, E2) nested within (b) Locality (Bizerta Lagoon, Gulf of Tunis, Monastir Bay), and between factor (b) and (c) Geographic Location (north, east). Similarity Percentage Analysis (SIMPER) was computed to assess the patterns of species which most contributed to differentiating the three localities. The original data matrix was reduced to the sixty-five epizoic species which contributed at least 3% to sample abundance, and abundances were converted to presence/absence.

Spatial turnover of species was investigated by computing two different indices: traditional Whittaker's β_w -species diversity and the new taxonomic (dis)similarity Γ^+/Δ_s . The former index was computed according to the ratio of the total species found in the whole investigated area (the so called γ -diversity) to the average "sample" species richness at (i) the small-scale level (*Pinna* specimens, α -point-diversity), (ii) each site (α -sample-diversity) and (iii) each locality (α -regional-diversity) (Whittaker, 1960; Gray, 2000; Magurran, 2004). This measure allowed us to evaluate the changing of motile and sessile species as a function of geographic and environmental gradients. Non-parametric Spearman's ρ was employed to assess the rank correlation between this diversity and environmental or large-scale geographic gradients. The other two indices were employed in order to evaluate a) the changing diversity among sites in terms of taxonomic relationships and b) the differential contribution of each taxon (phylum-level) to the spatial modification of the fauna. Taxonomic Distance (Γ^+) and Taxonomic Similarity (Δ_s) were computed on presence/absence data ac-

ording to Clarke and Gorley (2006) and to Izsák and Price (2001), respectively, for each phylum. The relative triangular matrices were obtained and elaborated by means of cluster classification and multi-dimensional scaling. Statistical and multivariate analyses were performed by means of the PRIMER-E 6 (Clarke and Warwick, 2001) and STATISTICA v.5 (StatSoft Italia) packages.

RESULTS

Associated community: spatial distribution and relation to *Pinna* size and habitat

A total of 146 species were found on *Pinna nobilis*, divided into 76 sessile and 70 motile associated taxa. Molluscs were better represented (39.73%), followed by annelids (16.44%), crustaceans (15.07%), ascidians (7.53%), sponges (6.85%), cnidarians (6.16%), echinoderms (4.79%) and bryozoans (3.42%). Five mollusc species (*Arca noae*, *Pinctada radiata*, *Modiolus barbatus*, *Anomia ephippium* and *Pisania striata*), one ascidian (*Pyura dura*), one polychaete (*Neanthes cf. virens*) and one echinoderm (*Paracentrotus lividus*) were present at all the sampling sites. The cnidarian *Actinia equina*, the annelids *Sabella pavonina* and *Sabellaria alveolata* and the crustacean *Pilumnus hirtellus* were encountered at all the sampling sites except for E2. However, other species were very localised or patchily distributed, and were exclu-

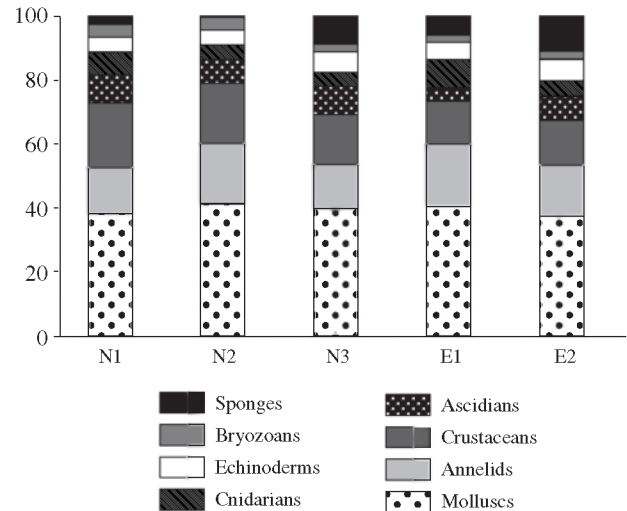


Fig. 2. – Bar plot of cumulated percentages of species for each phylum, which was found associated with the five populations of *Pinna*. Localities are shown in Fig. 1.

sively found at one locality only, as was the case of the cnidarians *Sagartiogetum undatum*, *Sagartia elegans*, *Cereus pedunculatus* and *Telmatactis forskali*, the sponges *Dysidea avara*, *Dysidea tupa*, *Ircinia variabilis*, *Spongia officinalis* and *Polymastia mammillaris* and the bryozoan *Flustra foliacea*. Sites E1 and E2 showed the highest species richness (67 and 64 species respectively), while N1, N2 and N3 showed the poorest (44, 43 and 44 species, respectively). It is worth noting that molluscs were the most dominant taxon in terms of species richness at all five sites (Fig. 2). The majority of associated species for each site

TABLE 2. – Percentages of *Pinna* size and species categories, phyla, species richness and total species numbers recorded at the five study sites. N1 Echaara, N2 Njila, N3 Sidi Rais, E1 Stah Jaber, E2 Teboulba.

	E2	E1	N3	N2	N1
Size class structure of <i>Pinna nobilis</i>					
Small (%)	6.67	23.33	50.00	10.00	10.00
Medium (%)	26.67	76.67	46.67	73.33	66.67
Large (%)	66.67	0.00	3.33	16.67	23.33
Number of associated species (S)	64	67	44	43	44
Molluscs (%)	37.54	0.30	40.00	41.86	38.64
Annelids (%)	15.63	19.40	13.33	18.60	13.64
Crustaceans (%)	14.06	13.43	15.56	18.60	20.45
Ascidians (%)	7.81	4.48	8.89	6.98	9.09
Cnidarians (%)	4.69	8.96	4.44	4.65	6.82
Echinoderms (%)	6.25	4.48	6.67	4.65	4.55
Bryozoans (%)	3.13	2.99	2.22	4.65	4.55
Sponges (%)	10.94	5.97	8.89	0.00	2.27
Total species abundance (N)*	730	928	507	636	944
Rare species (%)	60.94	55.22	34.09	46.51	9.09
Not very common species (%)	12.50	16.42	22.73	23.26	27.27
Common species (%)	9.38	7.46	25.00	16.28	45.45
Very common species (%)	0.00	4.48	4.55	4.65	6.82
Constant species (%)	17.19	16.42	13.64	9.30	11.36

* considering only countable species

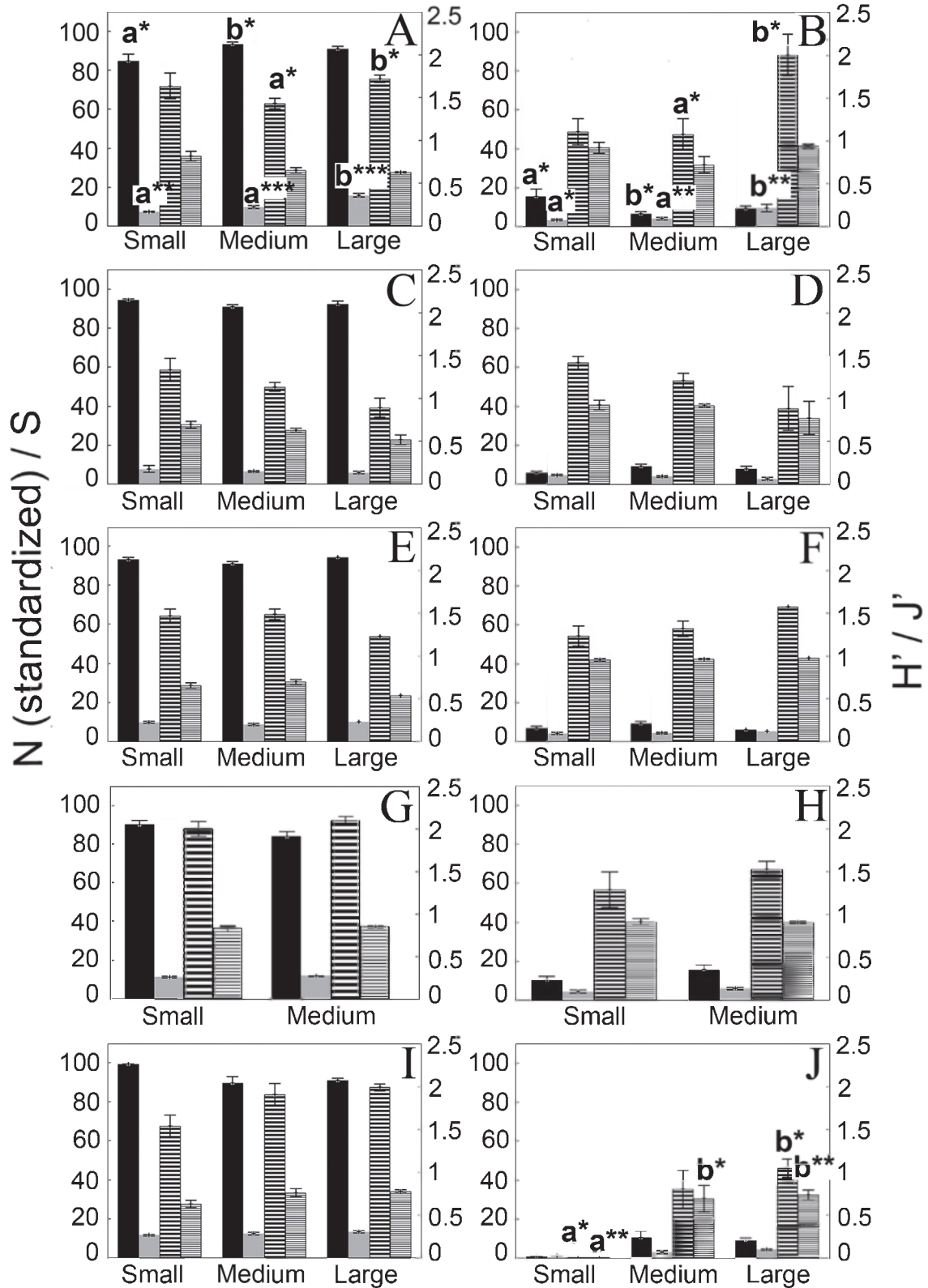


FIG. 3. – Bar diagrams of standardised abundance (black bars), number of species (grey bars), biodiversity (thick-lined bars) and evenness (thin-lined bars) of the sessile (left panes) and motile epifauna (right panes), which was found on the five sampled populations of *Pinna nobilis*. Data have been grouped for each size class of the basibiont (means ± SE): small < 25 cm; medium > 25, < 40 cm; large > 40 cm; Tukey's honest significant differences of means are indicated by letters on the top at a *p*-level of 0.05 (*) and 0.001 (**). A-B. Echaâra, N1. C-D. Njila, N2. E-F. Sidi Rais, N3. G-H. Stah Jaber, E1. I-J. Téboulba, E2.

(Table 2) belonged to the “Rare” category except for N1, where “Common” species represented the most dominant category. “Constant” epizoites belonged to Spongia, Bryozoa, Mollusca, Annelida and Crustacea and were dominated especially by colonial taxa i.e. Spongia and Bryozoa. It is worth mentioning that if we consider only the sedentary countable taxa, the most abundant species in each of the five epifaunal communities was a filter-feeding bivalve, except at N1, where the crustacean *Balanus sponsicola* was the most dominant species. Total species abundances ranged between 507 specimens in N3 (mean = 12.67; SD = 18.81) and 944 in N1 (mean = 23.02; SD = 57.48). The lowest total species abundance was observed at N3, where small *Pinna* shells showed the highest percentage. In contrast, the highest abundances were noted at the localities where medium-size shells represented the dominant categories, i.e. N1 and E1. Considering the whole sample, most of the associated taxa were not very common (58.91%; 86 species); common taxa represented 18.5% (27 species), followed by very common (13.01%; 19 species) and constant (9.58%; 14 species) taxa. The percentages of species categories varied among the sites. Rare species dominated at N2, N3, E1 and E2, whereas at N1 common species dominated.

At the local scale (each *P. nobilis* shell), variations of abundance, richness, biodiversity and evenness were stressed in Figure 3. Sessile fauna prevailed sharply at all five sites in terms of N and S, whereas indices H' and J' were broadly similar to those of motile epifauna, except at the easternmost site. ANOVA highlighted significant differences of means only at N1 for both motile and sessile fauna (Fig. 3A-B), and at E2 for motile epifauna only

(Fig. 3J). At N1 species richness significantly increased in accordance with shell size for sessile (F-test_[0.05; 27] = 11.43, p-level<0.001) and motile epizoites (F-test_[0.05; 27] = 6.89, p-level<0.01); the abundance of sessile species increased moderately between small and medium shells (F_[0.05; 27] = 5.03, p<0.05), whereas it decreased in the same size categories for the motile assemblage (F_[0.05; 27] = 5.03, p<0.05); finally, H' of sessile and motile species increased between medium and large-sized shells (F_[0.05; 27] = 3.79 and F_[0.05; 27] = 4.08, p<0.05 respectively). H' and J' comparisons were different at E1 for the motile epifauna, between small and large basibionts (F_[0.05; 27] = 4.04, p<0.05) and between all the three categories (F_[0.05; 27] = 5.26, p<0.05). At N2 S, H' and J' showed a decrease for both sessile and motile fauna (Fig. 3C-D) with respect to almost constant N values. At N3 H' and J' of sessile fauna were slightly reduced with *Pinna* size (Fig. 3E), against the increase of H' and the constancy of J' for motile fauna (Fig. 3F). Notwithstanding the absence of large basibionts in E1 samples, the similar pattern to E2 showed the moderate decrease in N for sessile species in comparison with motile species (Figs. 3G-I and H-J), the increase in H' for the motile fauna and the almost constant values of S and J' for both categories. These data highlighted the variability of these univariate indices among different locations and showed that the size of the basibiont was not the sole factor that may explain such variability. Sessile epifauna was dominant in the younger *Pinna* specimens; its prevalent coverage determined the reduction of abundance and species richness of motile taxa, but did not imply the curtailing of their average Shannon diversity and evenness of individuals among species.

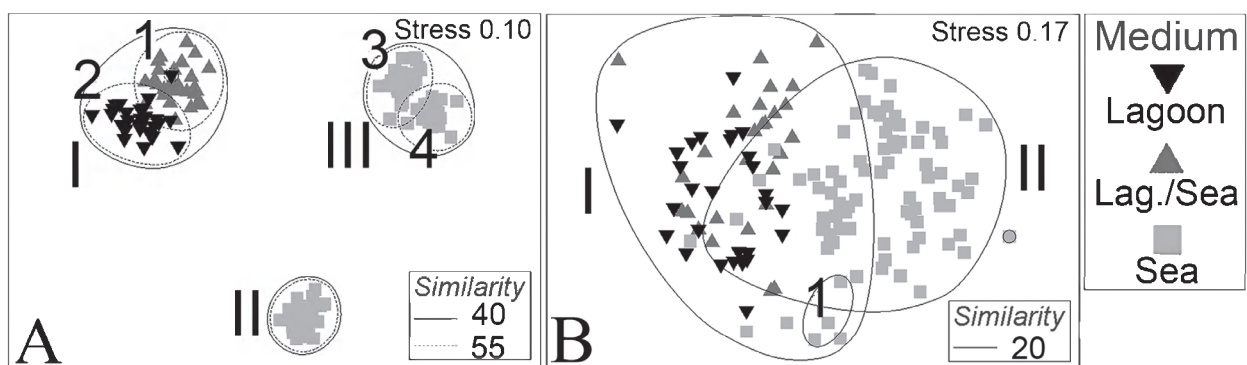


FIG. 4. – Multivariate ordinations with overlying clusters of sites in accordance with Bray-Curtis species similarity of individual communities of *Pinna nobilis*. **A.** Sessile epifauna on 150 sampled shells. **B.** Motile epifauna on 144 samples (six outliers excluded). Two opposite patterns are displayed, with sessile assemblage best discriminating samples in terms of geographic location/habitat type (clusters I, II, III) and, secondarily, in terms of sampling site (from cluster 1 to 4). Motile assemblage is more ubiquitous among *Pinna* shells and is roughly discriminated by the large geographical scale (cluster I and II, plus sub-cluster 1 and one sample apart. “Lag.”, lagoon).

TABLE 3. – One-way and two-way nested analysis of similarity test (ANOSIM) sessile and motile assemblages. Habitat type discriminates sessile epifauna better than motile epifauna, whereas the size of the basibiont shows no influence. Both site and locality are significantly more discriminant for the former group than for the latter (see Materials and Methods for explanation of the tested factors).

	Sessile epifauna				Motile epifauna			
ANOSIM one-way	Habitat type	p-level	Size class	p-level	Habitat type	p-level	Size class	p-level
Global R	0.63	0.01	0.06	ns	0.44	0.01	0.00	ns
ANOSIM two-way nested								
Nested Factor: Size class	between "habitat type"		between "size class"		between "habitat type"		between "size class"	
Global R	0.85	0.04	0.14	0.01	0.96	0.04	0.08	ns
Nested Factor: Site	between "locality"		between "site"		between "locality"		between "site"	
Global R	1.00	ns	0.82	0.01	1.00	ns	0.28	0.01
Nested Factor: Locality	between		between "locality"		between		between "locality"	
Global R	"geographic location"				"geographic location"			
	-1.00	ns	0.99	0.01	0.00	ns	0.40	0.01

Sampling design was established in order to encompass at least three main steps of increasing spatial scale, from the community settled on one individual shell (surface order of cm²) to the community of one population (order of m²), up to the meta-community of one locality or one region (order of km²). Non-metrical scaling with superimposed clusters (Fig. 4) clearly displayed two opposite patterns of sessile and motile associated fauna, more or less strictly reflecting the change of scale. Sessile assemblage (pane A) was best differentiated in terms of location and habitat type. The 40% similarity level gathered samples into three main clusters, which coincided perfectly with the three sectors of Bizerta Lagoon (cluster I), Gulf of Tunis (cluster II) and Monastir Bay (cluster III); the 55% level gathered samples in accordance with the five populations of *Pinna* at different sites of N1 (sub-cluster 1), N2 (sub-cluster 2, except for one sample), N3 (cluster II), E1 (sub-cluster 3) and E2 (sub-cluster 4). The SIMPROF test showed that both clusters at 40% (lowest similarity $S' = 19.61$; π statistic = 13.32, p-level < 0.001) and sub-clusters at 55% ($S' = 51.63$; π statistic = 6.37, p-level < 0.001) constituted real groups. Motile epizoids appeared to be distributed more uniformly across different sites and locations, thus increasing the sample similarity up to the large-scale level (pane B). The only true two clusters were highlighted at 20% (lowest $S' = 9.26$; π statistic = 1.69, p-level < 0.001), with cluster I grouping almost all Bizerta Lagoon samples, plus five samples in the Gulf of Tunis and two in Monastir Bay, and cluster II (plus the sub-cluster 1 of only three samples) grouping most of the two latter localities. These results demonstrated the limited dispersion ability of the sessile taxa (modular as well as individual) and of adult as well as larval stages in comparison with

motile taxa. The response to the environmental constraints, primarily to the lagoon-sea gradient, was best mirrored in the former assemblage, whereas the latter reflected the widespread distribution in the available colonising space, thus increasing the inter-sample heterogeneity. One-way ANOSIM (Table 3) attributed the greatest Global R value to the "habitat type" factor for sessile epifauna, with the pairwise R statistic discriminating most between marine and lagoon habitats (pairwise $R = 0.79$, p-level < 0.001), secondarily between lagoon-sea and marine habitats ($R = 0.66$, p < 0.01) and finally between lagoon-sea and lagoon habitats ($R = 0.63$; p < 0.01). Motile fauna showed a lower R statistic, with sea and lagoon being inhabited by the most different assemblages ($R = 0.50$; p-level < 0.001), in comparison with the sea vs. lagoon-sea community ($R = 0.49$; p < 0.001) and the almost identical lagoon-sea and strictly lagoon community ($R = 0.16$; p > 0.05). By contrast, size-class groups of the basibiont did not significantly discriminate motile and sessile epifauna, whether tested as a single factor or nested within the habitat. Similarity comparisons at a higher spatial scale were tested through two-way nested factors. With regard to sessile sclerobionts, population (site) groups were discriminated if nested within localities and, similarly, the different localities were discriminated if nested within the wider geographic location. As expected for the motile assemblage, no statistical distinction emerged at the local scale, whereas a slight discrimination emerged at the higher spatial scale of locality nested within the geographic location.

The dissimilarity percentage contribution of 65 out of 146 epizoids (97.16% of total abundance) among the three localities (Table 4) confirmed the assemblages established in the Gulf of Tunis and in Monastir Bay as being the least dissimilar, with

TABLE 4. – Dissimilarity percentage analysis of the epifaunal communities living on *Pinna nobilis* at three different localities. Sixty-five out of 146 species (at least 3% of species abundance per sample) are considered; cut-off for low contributions 90%. Bold face names indicate the most contributing species in among-locality comparisons (δ). Asterisk on δ /SD ratio indicates the most significant species for discriminating the different localities in terms of $\delta\%$ (nd, not detectable value). Habit (SE, sessile; MO, motile) and constancy index is also reported for every epizoite.

SIMPER Comparison between Localities	Habit	Bizerta - Tunis			Tunis - Monastir			Bizerta - Monastir		
		Bizerta	Lagoon = 54.21	%	Gulf of Tunis = 65.31	%	%	Monastir Bay = 61.75	%	%
Average dissimilarity (δ)		δ	δ /SD		δ	δ /SD		δ	δ /SD	
Within-group similarity										
PORIFERA										
<i>Cacospongia scalaris</i> Schmidt, 1862	SE	nd	nd	nd	3.52	3.08*	4.56	3.65	2.86*	4.29
<i>Dysidea avara</i> (Schmidt, 1862)	SE	nd	nd	nd	1.88	0.99	2.43	1.94	0.97	2.28
<i>Dysidea fragilis</i> (Montagu, 1818)	SE	2.01	0.90	2.36	3.78	5.7*	4.90	2.27	1.05*	2.66
<i>Dysidea tupa</i> (Martens, 1824)	SE	nd	nd	nd	1.98	0.99	2.56	2.05	0.97	2.41
<i>Hymeniacidon sanguinea</i> (Grant, 1826)	SE	4.75	5.16*	5.57	3.85	8.57*	4.99	nd	nd	nd
<i>Ircinia fasciculata</i> (Esper, 1794)	SE	nd	nd	nd	3.85	8.57*	4.99	4.00	5.91*	4.69
<i>Ircinia muscarum</i> (Schmidt, 1826)	SE	4.75	5.16*	5.57	1.88	0.99	2.43	2.05	0.97	2.41
<i>Ircinia variabilis</i> (Schmidt, 1862)	SE	4.60	3.68*	5.39	3.73	4.53*	4.83	nd	nd	nd
<i>Polymastia mamillaris</i> (Müller, 1806)	SE	nd	nd	nd	1.98	0.99	2.56	2.05	0.97	2.41
<i>Spongia officinalis</i> Linnaeus, 1758	SE	nd	nd	nd	1.91	0.95	2.48	1.99	0.94	2.33
CNIDARIA										
<i>Actinia equina</i> (Linnaeus, 1758)	SE	1.52	0.72	1.79	nd	nd	nd	1.18	0.68	1.39
MOLLUSCA										
<i>Anomia ephippium</i> Linnaeus, 1758	SE	1.80	0.82	2.11	1.66	0.87	2.15	1.74	0.89	2.04
<i>Arca noae</i> Linnaeus, 1758	SE	3.91	1.85*	4.58	3.48	2.81*	4.51	0.96	0.58	1.13
<i>Bittium reticulatum</i> (Da Costa, 1778)	MO	2.11	0.91	2.47	1.66	0.88	2.15	1.68	0.87	1.97
<i>Gibbula umbilicalis</i> (Da Costa, 1778)	MO	nd	nd	nd	0.76	0.51	0.98	nd	nd	nd
<i>Lunatia poliana</i> (Della Chiaje, 1826)	MO	1.20	0.59	1.41	0.99	0.60	1.28	nd	nd	nd
<i>Modiolus barbatus</i> (Linnaeus, 1758)	SE	2.01	0.81	2.36	1.12	0.62	1.45	1.60	0.78	1.88
<i>Musculus costulatus</i> (Risso, 1826)	SE	nd	nd	nd	nd	nd	nd	0.93	0.59	1.09
<i>Mytilus galloprovincialis</i> Lamark, 1819	SE	4.75	5.16*	5.57	nd	nd	nd	4.00	5.91*	4.69
<i>Ostrea edulis</i> Linnaeus, 1758	SE	1.12	0.61	1.32	nd	nd	nd	1.00	0.63	1.18
<i>Pinctada radiata</i> (Leah, 1814)	SE	1.72	0.73	2.01	2.13	1.11*	2.76	2.54	1.32*	2.98
<i>Pisania striata</i> (Gmelin, 1791)	MO	nd	nd	nd	1.68	0.90	2.18	1.68	0.87	1.97
ANNELIDA										
<i>Eupolymnia nebulosa</i> (Montagu, 1818)	SE	2.13	0.91	2.49	1.84	0.96	2.38	1.07	0.62	1.25
<i>Hediste diversicolor</i> (O.F. Müller, 1776)	MO	nd	nd	nd	nd	nd	nd	1.04	0.59	1.22
<i>Neanthes cf. virens</i> (Sars, 1835)	MO	2.64	1.07*	3.10	1.58	0.84	2.05	2.47	1.23*	2.90
<i>Sabella pavonina</i> Savigny, 1818	SE	2.34	0.97	2.74	1.92	0.99	2.48	1.85	0.92	2.18
<i>Sabellaria alveolata</i> (Linnaeus, 1776)	SE	2.20	0.93	2.57	0.95	0.58	1.23	1.90	0.95	2.23
ARTHROPODA										
<i>Athanas nitescens</i> (Leach, 1814)	MO	nd	nd	nd	nd	nd	nd	0.67	0.46	0.79
<i>Balanus spongicola</i> Brown, 1844	SE	2.18	0.95	2.56	nd	nd	nd	1.86	0.96	2.18
<i>Catapaguroides timidus</i> (Roux, 1830)	MO	1.18	0.60	1.39	nd	nd	nd	0.93	0.57	1.10
<i>Cymodoce truncata</i> Leach, 1814	MO	2.50	1.03*	2.93	1.86	0.95	2.41	3.17	1.88*	3.72
<i>Elasmopus rapax</i> Costa, 1853	MO	1.77	0.80	2.07	1.95	1.01*	2.53	2.12	1.08*	2.49
<i>Paracercis sculpta</i> (Holmes, 1904)	MO	1.66	0.76	1.95	nd	nd	nd	1.42	0.76	1.66
<i>Pilumnus hirtellus</i> (Linnaeus, 1761)	MO	1.33	0.63	1.56	nd	nd	nd	1.09	0.62	1.27
<i>Pisidia longicornis</i> (Linnaeus, 1767)	MO	1.82	0.77	2.13	1.31	0.70	1.69	nd	nd	nd
LOPHOPHORATA										
<i>Diastopora patina</i> (Lamarck, 1816)	SE	nd	nd	nd	3.78	5.74*	4.89	3.92	4.69*	4.60
<i>Flustra foliacea</i> Linnaeus, 1758	SE	4.75	5.16*	5.57	3.85	8.57*	4.99	nd	nd	nd
<i>Micropora coriacea</i> (Johnston, 1847)	SE	nd	nd	nd	3.85	8.57*	4.99	4.00	5.91*	4.69
<i>Myriapora truncata</i> (Pallas, 1766)	SE	4.75	5.16*	5.57	nd	nd	nd	4.00	5.91*	4.69
<i>Schizobrachiella sanguinea</i> (Norman, 1868)	SE	4.75	5.16*	5.57	nd	nd	nd	4.00	5.91*	4.69
ECHINODERMATA										
<i>Paracentrotus lividus</i> (Lamarck, 1816)	MO	1.90	0.80*	2.23	1.03	0.60	1.33	1.49	0.76	1.75
<i>Phylloporus urna</i> Grube, 1840	MO	1.75	0.74	2.05	1.44	0.76	1.86	nd	nd	nd
TUNICATA										
<i>Clavelina lepadiformis</i> (Müller, 1776)	SE	nd	nd	nd	0.84	0.52	1.09	0.87	0.52	1.03
<i>Pyura dura</i> (Heller, 1877)	SE	1.87	0.82	2.19	1.91	0.99	2.48	1.98	0.97	2.33

the Gulf of Tunis and Bizerta Lagoon, and Bizerta Lagoon and Monastir Bay equally the most dissimilar. Greater within-group similarity was shown by the Gulf of Tunis in comparison with the other localities, probably due to the more recently settled population of basibionts and the less numerous sam-

ples of *Pinna*. Thirty-three associated species made the greatest contribution to comparisons in terms of percentage contribution and δ /SD ratio (Clarke and Warwick, 2001), and accounted for an average of 77.11% cumulative dissimilarity. Modular epizoobionts such as Porifera and Lophophorata accounted

for most of the significant species in comparisons, due to their predominant percent coverage, but other non-colonial sessile species, mainly Mollusca and Polychaeta, contributed substantially to discriminating the localities. The sponges *Dysidea fragilis*, *Ircinia muscarum* and *Anomia ephippium*, the molluscs *Mytilus galloprovincialis* and *Pinctada radiata*, the annelids *Sabella pavonina* and *Sabellaria alveolata* and the ascidian *Pyura dura* were distinctive in almost all the similarity comparisons. Because of their wider spatial distribution, very few motile species contributed to dissimilarity, and *Neanthes* cf. *virens*, *Cymodoce truncata*, *Elasmopus rapax* and *Bittium reticulatum* were the most significant species. With respect to within-group similarity, *M. galloprovincialis*, *Myriapora truncata*, *Schizobrachiella sanguinea*, *N. cf. virens*, were the most characterising species within Bizerta Lagoon (average similarity $S' = 34.67$; cumulative similarity 63.95%), thus showing an assemblage with some euryhaline traits. *Arca noae*, *Hymeniacidon sanguinea*, *I. muscarum*, *Flustra foliacea*, *Ircinia variabilis* and *Modiolus barbatus* made the greatest contribution to similarity in the Gulf of Tunis (average $S' = 50.29$; cumulative 77.02%). Finally, the populations of Monastir Bay were best characterised by *Ircinia fasciculata*, *Micropora coriacea*, *D. fragilis*, *Diastopora patina*, *Cacospongia scalaris*, *M. barbatus*, *C. truncate* and *Pinctada radiata*, which amounted to an average S' of 44.02 and a cumulative one of 71.31%.

Spatial and taxonomic species turnover. The contribution of each Phylum

The change in species composition according to both lagoon to sea and north to east geographical gradients showed three different patterns from the small to large-scale view (Fig. 5). Sample-to-sample variation (pane A) was ten times lower for sessile than for motile species, with different trends at different sites and with significant statistics limited only to site N1 or to site E2 for sessile and motile assemblages, respectively. The former assemblage was more variable in the strictly lagoon population of N2, with an increase in species turnover according to *Pinna* shell size. The other sites showed a less variant β_w -diversity, which generally decreased with increasing shell size; ANOVA showed meaningful differences in means at N1 ($F_{[0.05; 27]} = 7.69$, $p < 0.01$) between small, medium and large-sized basibionts. By contrast, the spatial turnover of motile species

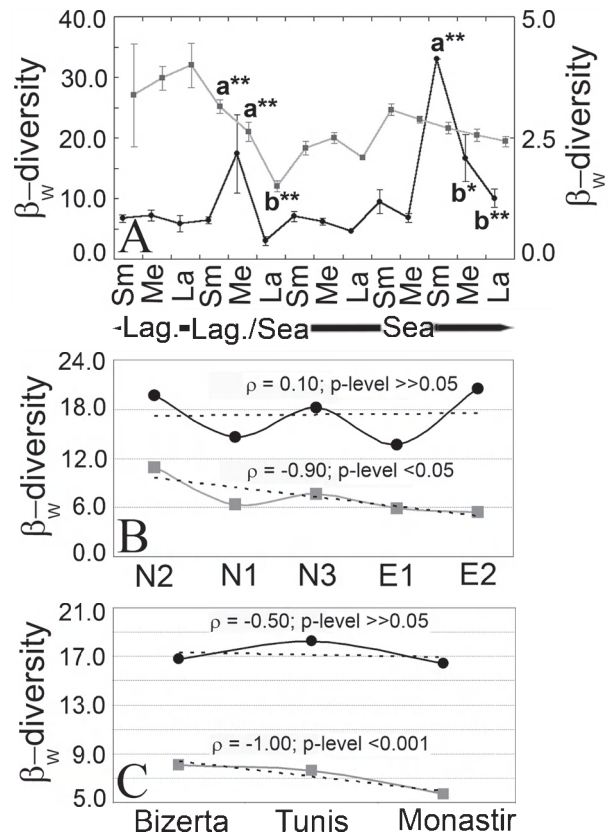


FIG. 5. – Line-plot of turnover of motile- and sessile-associated species at three increasing spatial scales. Sites and localities are primarily arranged according to lagoon-sea environmental gradient and secondarily to the north-east geographic gradient. A. beta-diversity at the small-scale level between the total richness of the investigated area and richness of *Pinna* individuals; means (\pm SE) are scaled separately for sessile (right) and motile (left) epifauna. ANOVA and Tukey's HSD test highlighted differences of means (letters on the top) at a p -level of 0.05 (*) and 0.01% (**). B. beta-diversity at the site level between the total richness and the average richness for each site. C. beta-diversity at the regional level between the total richness and the average richness at each locality. Spearman's rank correlation (ρ) is calculated for habitat gradients (B) and biogeographic gradients (C). Black circles: motile species; grey squares: sessile species (see the text for abbreviations: "Lag.", lagoon).

was more variant at N1, for medium shells in particular, and at E2 for larger basibionts. No general trend was observed, except at the easternmost site E2, which showed a significant decrease in β_w -diversity in comparison with small and medium-large basibionts ($F_{[0.05; 27]} = 8.76$, $p < 0.01$). At the intermediate scale of locality (pane B), the lagoon-sea gradient became clearer, with the most enclosed station of Njila (N2) showing the highest turnover of species in contrast to the lagoon-sea site N1 and the true marine sites N3, E1, E2. At the largest spatial scale of the region (pane C), the previous pattern was confirmed, the motile epifauna being almost invariant to the large-scale geographic gradient in contrast to the

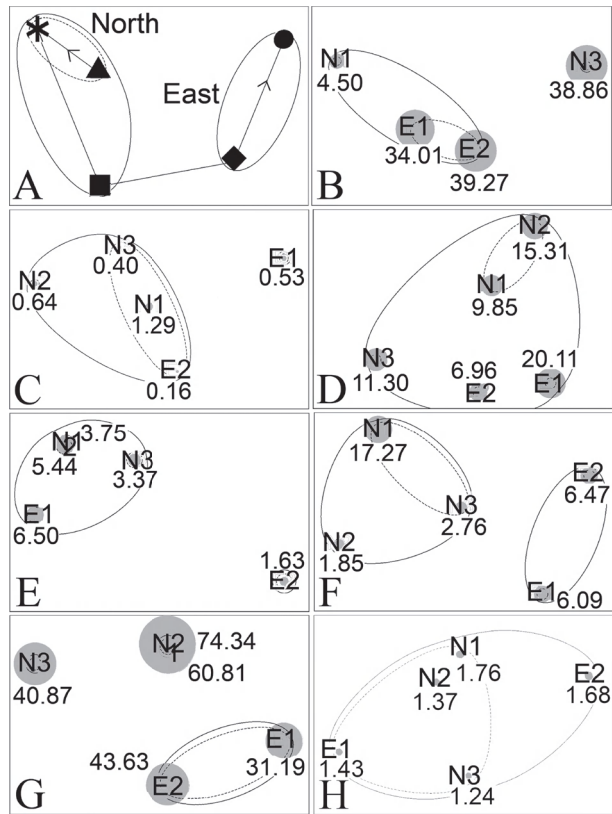


FIG. 6. – MDS plots built up using measures of taxonomic dissimilarity index (Γ^+) between pairwise "Site" comparisons (presence/absence data); 2d-stress is equal to zero in all pictures. Clusters at 20% (dashed contour) and at 30% dissimilarity (continuous contour) are overlaid. Standardised taxon abundances and scaled bubbles were also superimposed. None-detectable sclerobiontic sponges were found at N2. A. total epifauna on *Pinna nobilis*; trajectory line joins sites according to N-NE-E geographic gradient. B. Porifera. C. Cnidaria. D. Mollusca. E. Annelida. F. Arthropoda. G. Lophophorata. H. Tunicata. The species-poor phylum Echinodermata is not shown. Legend: triangle, Echaâra (N1); asterisk, Njila (N2); square, Sidi Rais (N3); rhomb, Stah Jaber (E1); circle, Téboulba (E2).

decreasing trend of the sessile assemblage, although this latter variation at this spatial step was probably tied to the summation of both local environmental features and biogeographic gradients.

Turnover of the whole epibiota expressed as taxonomic variation (Γ^+) among the five sites (Fig. 6A) showed the highest taxonomic similarity (lowest β -diversity) within Bizerta Lagoon and the highest distance (highest β -diversity) within the bay of Monastir. The habitat features at the local spatial scale as well as the latitudinal/climatic gradient at a large geographic scale were therefore also reflected through the taxonomic structure of the whole community, even though each phylum displayed its own peculiar pattern of variation. Bryozoa showed the greatest average taxonomic dissimilarity (mean Γ^+ = 42.78; SD = 22.63), followed by Porifera (mean Γ^+ = 32.60; SD = 13.63), Echinodermata (mean Γ^+ = 32.01;

SD = 17.42) and Arthropoda (mean Γ^+ = 31.35; SD = 9.16), in contrast to Annelida (mean Γ^+ = 27.70; SD = 5.84), Mollusca (mean Γ^+ = 25.85; SD = 3.85), Cnidaria (mean Γ^+ = 23.37; SD = 10.00) and Tunicata (mean Γ^+ = 18.23; SD = 6.87), which showed the lowest dissimilarity. Though no macroscopic colony of sclerobiontic sponges was detected at the lagoon site N2 (Njila), Porifera (pane B) was taxonomically more similar within the eastern sector, although the threshold of 30% dissimilarity included the northernmost site N1 (Echaâra). The less abundant and species-poor phylum of Cnidaria (pane C) showed a different pattern, which was not clearly related to any particular faunistic or environmental gradient. Except for *Actinia equina*, this sessile taxon was not constantly present as an epizooibiont on *Pinna*, and its more clumped distribution may be the possible answer for such peculiar patterns of taxonomic similarity. Mollusca (pane D) were the richest taxon in species composition and showed a greater similarity in Bizerta Lagoon than at the other sites, though they were all grouped at a 70% level of taxonomic similarity. Annelida Polychaeta (pane E) and mainly Arthropoda Crustacea (pane F) and Lophophorata Bryozoa (pane G) showed a more stressed dissimilarity between the northern and eastern sectors, which was probably related to significant changes in the taxonomic composition of the assemblages in comparison with the latitudinal biogeographic gradient. Bryozoa, in particular, showed a distinction between the (semi-)lagoon habitat of Bizerta and the true marine habitat of Tunisia, with a possible response of selected sessile sclerobionts to confined vs. open sea environments. The pattern of Tunicata was roughly similar to that of Mollusca (pane H), but with lower Γ^+ , all sampling sites being clustered between a 70 and 80% taxonomic similarity level and without a clear habitat or geographic location distinction.

DISCUSSION

As has been observed for several macro- and mega-benthic faunal taxa (Vance, 1978; Karlson and Shenk, 1983; Gili *et al.*, 1993; Davis and White, 1994; Barnes and Clarke, 1995; Wahl, 1996; Key *et al.*, 1996; Thompson *et al.*, 1996; Parapar *et al.*, 1997; Fernandez *et al.*, 1998; Olabarria, 2000), shells of *Pinna nobilis* represent no more than available space for a typical epibenthic community of hard substrata

(Zavodnik, 1963, 1967; Corriero and Pronzato, 1987; Giacobbe and Rinelli, 1992). However, the intimate nature of the living vertical surface and the neighbouring soft sediment habitat may influence the contingent of associated species, constituting potential factors of selection for the epibiota (Cosentino and Giacobbe, 2008). In the present study, the clear influence of shell size was demonstrated only for the mature population N1 (Echaâra), while the other epizoic assemblages showed a moderate to low correlation, thus confirming that the dimensions of *Pinna* did not play a prominent role in structuring the associated biota (Cosentino and Giacobbe, 2007). Such observation can be explained by an early settlement of the epifauna upon the juvenile or sub-adult *Pinna* individuals, as demonstrated by Munguia (2004) for the fan shell *Atrina rigida*. Other environmental features seemed to play a major role in characterising the biota at different spatial scales. The marine-lagoon gradient was the most significant, although not strictly in terms of salinity or temperature of seawater. At the other site, the biogeographic gradient seemed to play another important role in distinguishing northern from eastern assemblages, thus representing a further source of variability at greater scale. The clear discrimination of N1 (Echaâra) and N2 (Njila) from true marine locations, especially for sessile-associated assemblage, was probably tied to the peculiar habitats, the former population being located at the ecotone lagoon-sea, the latter being located in a strictly lagoon habitat. The occurrence of euryhaline species such as *Balanus spongicola*, *Mytilus galloprovincialis* and *Hediste diversicolor* at both sites confirmed this hypothesis. The true marine communities became more heterogeneous in species composition from northern to eastern sites, providing some evidence that other underlying environmental or biogeographic factors may operate. The presence of the warm-water species *Pinctada radiata*, which was almost restricted in the eastern samples, supported the influence of a biogeographic gradient of species.

Changing of species across the spatial (environmental/biogeographic) gradient, generally termed as β -diversity, has been widely reviewed (Loreau, 2000; Gray, 2000; Magurran, 2004; Loreau and Mouquet, 1999). In the present study, patterns of β_w -diversity were clearly different according to the considered spatial scale and were very informative for distinguishing adult motile or sessile species. In general, motile species had higher species turnover at all spa-

tial steps. In particular, this functional assemblage was probably more influenced by factors at the small scale level (tens of cm^2 or m^2), such as the available shell surface. By contrast, the sessile contingent of epizoites had a lower turnover of species, probably linked to their limited dispersion abilities, and being more variant at intermediate (many hundreds of m^2) and larger scales (tens to hundreds or thousands of km^2). These species could be more sensitive towards the brackish to sea water gradient than the motile fauna. The greater environmental (climatic-habitat) variability of northern sites than eastern ones may therefore be reflected in the higher species turnover at an intermediate and larger spatial scale. Differences in life-history patterns, such as larval dispersion, recruitment and substrate selection, may also influence the differential spatial diffusion and spatial “perception” between sessile and motile organisms (Giangrande *et al.*, 1994; Bhaud, 2000).

During the adult stage, motile fauna is relatively able to re-localise itself and to actively select the surface to occupy. Moreover, the dispersion may involve adult/juvenile specimens as well as larval forms (Davidson *et al.*, 2004). As a consequence, the distribution of motile species is more subject to the “sorting” effect. The total richness to sample richness ratio may therefore be more sensitive to patch size (shell surface of *Pinna*) at small scale, whilst no trend of large-scale β -diversity is detectable as a consequence of the “local” versus “regional” diversity saturation (Munguia, 2004). Sessile species, on the other hand, disperse mainly at larval or propagule stages and their distribution is more subject to the so-called “priority” effect. Several studies have demonstrated the highly variable distribution of sessile species on hard substrata, last but not least affected by stochastic events (Butler and Connolly, 1999). The spatial turnover of such species is therefore more insensitive to patch size, whereas it decreases at larger scale as a possible consequence of the unsaturated “local” vs. “regional” space. In general the contingent of species found in Bizerta Lagoon accounted for fewer taxa in comparison with the regional richness as a consequence of the local habitat constraints (“lagoon” effect). Moreover, the influence of the biogeographic lati-longitudinal gradient due to the colder near-Atlantic versus the warmer near-Levantine faunistic contingent can also increase the faunal variability and widen the taxonomic breadth (higher β -diversity; Price *et al.*, 1999; Izsák and Price,

2001). These aspects can lead to a higher β -diversity in terms of both numbers of registered taxa and increased taxonomic dissimilarity at the regional scale, as is best observed in the patterns of colonial sclerobiotic sponges and bryozoans. By contrast, associated taxa with prevalent individual motile habits, such as molluscs, polychaetes and arthropods, showed a lower taxonomic distance (lower β -diversity) among N2 (Njila), N1 (Echaâra) and N3 (Sidi Rais). The greater taxonomic similarity of the lagoon and lagoon-sea mollusc and polychaete assemblages was probably more related to the selective environmental features of the brackish habitat (Gravina *et al.*, 1988; Piraino and Morri, 1990), which may conversely reduce the breadth of the taxonomic tree at the local scale. For the Tunisian epizoic community on *P. nobilis* the taxonomic similarity generally decreased by increasing the spatial scale, apparently in contradiction to what Izsák and Price (2001) stated for the Echinodermata assemblage alone, although up to the province/oceanic scale. The greater the species richness of a taxon for a particular habitat, the greater its sensitivity to changes in biological or environmental gradients. However, results have also demonstrated that each taxon (phylum level) might respond very differently to the others as consequence of its local representativeness, its relative composition of motile or sessile forms, its evolutionary history for that habitat and the potential breadth of its taxonomic/phylogenetic tree (Arvanitidis *et al.*, 2002; Glasby, 2005).

The notable occurrence of sessile filter-feeding species upon the shells of *Pinna* can support the possible existence of competition for nutrients, since the two parts belong to the same trophic guild. The competition between the epibionts and the host when they both occupy the same trophic niche has also been postulated in other studies (Novak, 1984; Bronmark, 1985). At the E1 sampling site, the dominant species was the alien mollusc *Pinctada radiata*, with more than 10 specimens on some *Pinna*. The trophic structure of *Pinna nobilis* epifauna was similar to that described for neogastropod Muricidae shells by Olabarria (2000), who reported the dominance of sedentary filter-feeding epizoobionts and explained that these epibionts were favoured by the currents generated by the movement of the host, which guaranteed the availability of food. However, there was no competition for food because of the different trophic behaviour of the host (carnivore) and most

epibionts (filter-feeders). By contrast, Cosentino and Giacobbe (2007, 2008) found a low abundance of suspension-feeders in a current-exposed habitat (Strait of Messina), and a non-balanced trophism of mollusc epifauna, as a consequence of food supply limitation and possible alimentary competition exerted by the basibiont.

In conclusion, the present study has shown that the community associated with *Pinna nobilis* was influenced by both lagoon-sea and biogeographic gradients, and therefore by the environmental features of the habitat where fan shells were settled. The structure of the epifauna was more diversified and balanced in the open sea than in lagoon and lagoon-sea habitats for both motile and sessile species. Factors linked to the confinement of shallow sublittoral bottoms, such as thermo-haline seasonal variations, hydrodynamics and water exchanges, and food availability were probably the main environmental constraints that can affect the structure of the associated sessile and motile assemblages at a local scale. On the other hand, the biogeographic gradient of motile and sessile taxa, which was the expression of long-term (climate) and large-scale (region) biotic processes, exerted its main influence towards patterns of taxonomic and functional diversity. It is worth mentioning that the motile fauna was more diversified and balanced than the sessile fauna. Moreover, many motile species seem to be dependent on sessile ones in particular sponges which appear to serve as a habitat for many crustaceans and annelids, thus increasing the biodiversity of the fan shell-associated fauna. *P. nobilis* hosts very complex and well-characterised epifaunal communities consisting of sessile and motile species and it contributes to the biotope complexity. Further studies are needed to quantify this contribution and to understand how this Mediterranean bivalve helps the surrounding communities at local and regional scales.

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