



Aspects of epizoobiotic mollusc assemblages on *Pinna* shells.

I. Composition and structure

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Abstract: From populations of *Pinna nobilis* and *P. rudis* in the Strait of Messina (Central Mediterranean), 11 individuals per species were sampled and the epizoobiotic molluscs investigated. Univariate indices of richness, biodiversity and equitability were assessed and compared with multivariate analyses to single out the epizoic patterns, their different specific composition and the biotic/abiotic factors potentially affecting them. Bathymetric level, species/size of basibionts, conch sculpture patterns and other secondary factors, such as the occurrence of shell fractures and algal covering, were investigated and/or tested as potentially discriminating agents. At last, rank-based matrices joined to functional guilds were employed to evaluate the species redundancy in these assemblages, and their trophic structure. Univariate diversity indices did not detect any evident discrimination but showed the early settlement of zoobiontic molluscs on *Pinna* individuals. Multivariate analyses supported the hypothesis of a gradual multi-species differentiation between the two basibionts, with *P. nobilis* zoobionts more abundant and less variant in species composition. Feeding guilds of the *P. nobilis* assemblage were in accordance with ephemeral epizoophytes, whilst *P. rudis* zoobionts showed a wider trophic spectrum in accordance with enduring epizoophytes.

Résumé : *Mollusques épibiontes sur les coquilles du genre Pinna. I. Composition et structure.* A partir de deux populations de *Pinna nobilis* and *P. rudis*, provenant du Détroit de Messine (Méditerranée centrale), 11 individus de chaque espèce ont été prélevés. Afin d'étudier les mollusques épizoobiontes chez les deux espèces et les facteurs abiotiques qui peuvent potentiellement les affecter, les indices univariés traditionnels ont été comparés à des analyses multivariées. Les indices univariés de diversité n'ont pas permis de détecter de discrimination évidente mais ils ont pu montrer la fixation précoce des mollusques zoobiontes sur les spécimens de *Pinna*. En revanche, les analyses multivariées ont prouvé l'hypothèse de l'existence d'une différenciation multi-espèce graduelle entre les deux basibiontes. En effet, les zoobiontes sont plus abondants et moins diversifiés chez *P. nobilis*. Le niveau bathymétrique ainsi que, indirectement, la morphologie coquillière affectent le couvert algal et donc l'épifaune des mollusques. Par ailleurs, l'association trophique de la communauté de *P. nobilis* est composée essentiellement d'épizoophytes éphémères, alors que les zoobiontes de *P. rudis* montrent un spectre trophique plus large en faveur des épizoophytes durables.

Keywords: Pinnidae • Associated assemblages • Multi-species patterns • Mollusc epizoites • Mediterranean

Introduction

Colonization of body surface on behalf of other organisms represents a widespread natural phenomenon, which has been widely investigated in marine ecosystems. Although space competition is primarily involved (O'Connor et al., 1980, Brooks & Mariscal, 1986), complex relationships develop between basibiont and zoobiont *sensu* Taylor & Wilson (2002) (D'Antonio, 1985; Barnes & Clarke, 1995; Wahl & Mark, 1999). The role of the basibiont in providing a hard substratum to colonize has been pointed out, especially in benthic assemblages (Keough, 1984; Olabarria, 2000), and some implications of the dynamic properties of living substrates, such as the response of zoobionts to spatial complexity increase (Koukouras et al., 1996), and to the behavioural (Fernandez et al., 1998) and physiological characteristics of the basibiont (Gili et al., 1993) have been stressed. Typological characterizations of the established community, in relation to temporal and spatial scales, have been dealt with (Seed, 1996), and also compared in congeneric basibiont (Iwasaki, 1995). In this regard, the biggest Mediterranean bivalve, *Pinna nobilis* L., 1758, hosts complex and well-characterized taxocoenosis (Giacobbe, 2002), whose settlement can be affected by shell morphology and sculpture, recently described in comparison with the congeneric *P. rudis* L., 1758 (Cosentino & Giacobbe, 2006).

The present investigation aims at:

- Comparing the distribution patterns of the most recurrent epizoic mollusc species, as well as dissimilarity which characterizes the mollusc assemblages tied to both *P. nobilis* and *P. rudis*,
- Verifying how these patterns are influenced by small-scale spatial differences due to different shell sculptures,
- Describing the respective trophic guild patterns of the two epizoic assemblages,
- Evaluating the possible higher accuracy of the multi-species approach than traditional univariate population/diversity measures to describe ecological trends and multi-factorial processes, which affect small-scale biodiversity.

Materials and Methods

Samples of *P. nobilis* and *P. rudis*, were collected in the Strait of Messina (Sicily, Italy), from 10-20 m and 25-50 m depth respectively, according to their prevalent bathymetric distribution (Cosentino & Giacobbe, 2006). All animals and algae adhering to the shell surface of each specimen were removed and washed together over a 0.5 mm mesh size sieve. Afterwards, living molluscs were sorted, stored in 70% ethanol, and subsequently determined. Abundance N, number of species S, Margalef's richness d, Shannon-

Wiener's diversity (ln-based) H', and Pielou's evenness J were calculated for the mollusc assemblages associated with each specimen, and for the two *Pinna* groups.

Given the high variability of mollusc epifauna with aggregated or sporadic epizoobionts, which is also affected by stochastic components, abundances were standardized for each sample total, and square root transformed to reduce skewness and stabilize variance (Clarke & Warwick, 2001); the Bray-Curtis similarity index was employed. Principal components analysis (PCA) ordination was performed to evaluate how extrinsic (depth, damages) or intrinsic (species of basibiont, size classes, shell morphologies) factors may contribute to discriminate the basibionts. PC axes were obtained by means of linear combination (Euclidean distance) of the following abiotic parameters: depth level, scar number, main axis length (mm), total emergent surface (TES) (mm²), roughness ratio (RR), percentage roughness (R%), and spine density (Cosentino & Giacobbe, 2006); such variables were normalized to convert them into a dimensionless scale. Other variables such as partial length, maximum width, emergent plane surface (EPS), total spine surface (TSS), expected spine number (ESN), were not included in the PC ordination due to high collinearity with the above-mentioned parameters (Pearson's $r \geq 0.80$). Finally, BIO-ENV analysis was carried out to assess some possible causal correspondences between the abiotic (Euclidean distance of normalised data) and the biotic (non transformed data of all epizoobionts) matrices.

Sample-Cluster analysis together with non-metric multi dimensional scaling (nm-MDS) ordination (group-average linkage) and multivariate dispersion (MVDISP) were employed to single out the multivariate dispersion of basibionts as a function of associated assemblages. Analysis of similarities (ANOSIM) permutation test allowed assessing the influence of single or nested factors (bathymetric level, species/size of basibiont). Similarity percentage analysis (SIMPER) joined with species-Cluster analysis (including only those epizoobionts that contribute at least to 3%, standardised and square root transformed abundances) was subsequently employed to identify the mollusc epizoic patterns in the two pen-shell species. Stepwise procedure (BVSTEP) to search best explaining subsets of mollusc species respect to the whole taxo-community matrix (BIO-BIO analysis) was employed (Clarke & Warwick, 1998); this procedure singled out the subsets of epizoic species best matching ($r > 0.90$) the patterns of the two basibionts and allowed us to postulate on the redundancy of mollusc epifauna (Loreau et al., 2002). These subsets of species were therefore turned into functional guilds (trophism/motility) and the triangular matrices were compared with the total *Pinna* assemblage or with the two assemblages apart (RELATE procedure). All

Figure 1. Bar-graphs of the structural univariate indices for each basibiont specimen, arranged according to size classes and for each basibiont species total. **A.** Number of species *S* and abundance *N*. **B.** Richness *D*, diversity *H'* and equitability *J*. Box & Whisker plots with mean and SD for each index are shown below. Major axis length is reported in mm; small specimens *s* ≤ 250 mm; medium specimens *m* > 250 mm and ≤ 350 mm; large specimens *l* > 350 mm. **Nb**, *Pinna nobilis*; **Rd**, *P. rudis*.

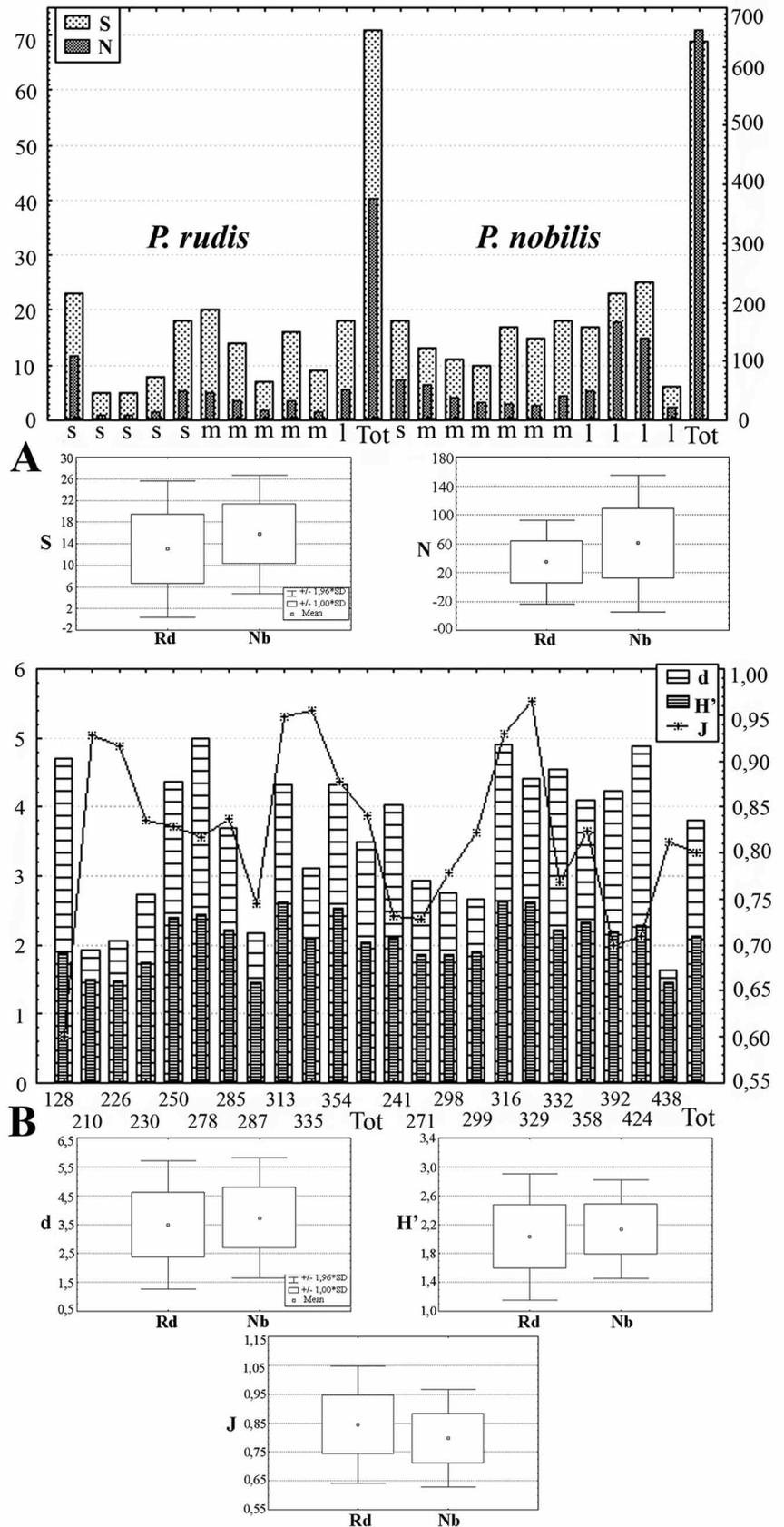
Figure 1. Indices de structure univariés pour chaque exemplaire-hôte, ordonnés selon les classes de taille et pour la totalité des spécimens de chaque espèce-hôte. **A.** Nombre d'espèces *S* et abondance *N*. **B.** Richesse *d*, diversité *H'*, équitabilité *J*. Diagrammes Box & Whisker avec valeurs moyennes et écart-types pour chaque indice. La longueur du grand axe est indiquée en mm ; petits exemplaires *s* ≤ 250 mm) ; exemplaires moyens *m* > 250 mm et ≤ 350 mm ; grands exemplaires *l* > 350 mm. **Nb**, *Pinna nobilis* ; **Rd**, *P. rudis*.

these analyses are available in PRIMER 6 routine (Clarke & Warwick, 2001).

Results

A regular occurrence of erected turfs of brown macroalgae (mainly *Cystoseira* spp.), noticed in shells of *P. nobilis* more than 25/30 cm length, showed an average density of 2/3 thalli for each specimen. By contrast, *P. rudis* showed less conspicuous algal epigrowth, most of which consisting of incrusting Rhodophyceae and other low epizoic algae.

Extraction of fauna from shell surface and attached epizoophytes provided 105 species of epizoic molluscs, 71 of which



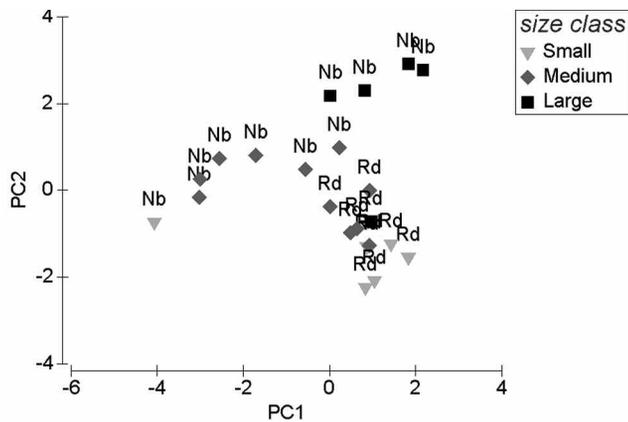


Figure 2. Principal Component ordination of the two *Pinna* basibionts based on main morphometric (intrinsic) and environmental (extrinsic) parameters. The wider scattering of *P. nobilis* specimens indicates the higher abiotic variability of this pen-shell compared to its co-generic *P. rudis* (for abbreviations see caption of Figure 1).

Figure 2. Analyse en composantes principales des deux espèces-hôtes de *Pinna*, basée sur les principaux paramètres morphométriques (intrinsèques) et environnementaux (extrinsèques). La vaste dispersion des exemplaires de *P. nobilis* indique la plus grande variabilité “abiotique” de ce bivalve par rapport à son congénérique *P. rudis* (pour les abréviations voir légende de la Figure 1).

(mean = 13.00, SD = 6.43) were found on *P. rudis*, while 69 species (mean = 15.70, SD = 5.27) were found on *P. nobilis*; 36 epizoobionts were exclusively found in the former basibiont, 34 in the latter and 35 shared species. Abundances amounted to 376 specimens (mean = 34.18, SD = 29.54) in *P. rudis*, while it reached 662 specimens (mean = 60.18, SD = 48.41) in *P. nobilis*. Richness showed a similar range of values in the two basibionts, from 1.92 to 4.99 (mean = 3.49, SD = 1.14) in *P. rudis* and from 1.64 to 4.91 (mean = 3.74, SD = 1.06) in *P. nobilis*. Similarly, H' diversity varied from 1.45 to 2.62 (mean = 2.03, SD = 0.45) in the former basibiont and from 1.45 to 2.63 (mean = 2.13, SD = 0.35) in the latter; evenness ranged from 0.45 to 0.95 (mean = 0.84, SD = 0.10) in *P. rudis* and from 0.70 to 0.95 (mean = 0.80, SD = 0.09) in *P. nobilis*. A comparison of the above-discussed indices for all *Pinna* individuals, ordered according to length (Fig. 1), did not show any correlation between the four structural indices and the species of basibiont as well as their size. None of these indices discriminated the two groups significantly ($p > 5\%$). S and N did not correlate to depth level (*P. nobilis*: Pearson's $r = 0.51$ and 0.44 , $p > 5\%$; *P. rudis*: $r = 0.06$ and -0.18 , $p \gg 5\%$) nor to the total colonising surface (*P. nobilis*: $r = -0.04$ and 0.28 , $p \gg 5\%$; *P. rudis*: $r = -0.07$ and -0.30 , $p \gg 5\%$). d , H' and J were substantially unrelated with the assessed abiotic (intrinsic/extrinsic) variables.

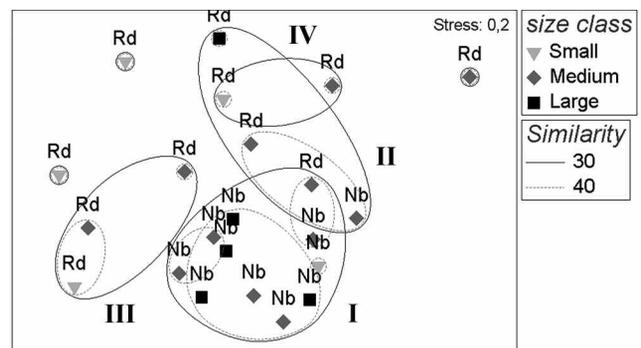


Figure 3. Non-metric MDS of the *Pinna* associated mollusc fauna, with superimposed clusters at 30% (continuous line) and 40% (dotted line) similarity. The closer dispersion of *P. nobilis* pattern reveals the more homogeneous assemblages in terms of species composition and frequency (for abbreviations see caption of Figure 1).

Figure 3. MDS non métrique de la faune de mollusques associés à *Pinna*, montrant les groupes dormés à une similarité de 30% (ligne continue) et de 40% (ligne en tirets) de similarité. La dispersion moins accentuée des individus de *P. nobilis* met en évidence un peuplement plus homogène en termes de composition spécifique et de fréquence (pour les abréviations voir légende de la Figure 1).

According to extrinsic/intrinsic factors (Cosentino & Giacobbe, 2006), a different multivariate dispersion of the two *Pinna*-groups was observed in PC ordination (Fig. 2). PC1 axis (eigenvalue = 3.07, variation = 43.90%) ordered the basibionts according to the reduction of spine number (eigenvector = -0.46), relative roughness (-0.52), percentage roughness (-0.39) and total emergent surface (-0.53); *P. nobilis* specimens were preferentially ordered according to these parameters. PC2 axis (eigenvalue = 2.29, variation = 32.70%) ordered the basibionts in relation to bathymetric level (-0.48), the increase of linear length (0.56), number of scars (0.38), and spine density (0.30); *P. rudis* dispersion was mainly consistent to this axis.

Non-metric multi dimensional scaling (stress = 0.2) showed the two assemblages only tendentially discriminated (Fig. 3); *P. rudis* showed a wider 2-d dispersion and, therefore, a greater within-group dissimilarity compared to the co-generic species. Breakdown of similarity (30% level) singled out one main cluster (I), formed by 10 out of the 11 *P. nobilis* and a single *P. rudis*. Fewer specimens of both basibionts and one large shell apart (cluster II), or of *P. rudis* only (cluster III and IV), formed the other three clusters, while three other specimens of *P. rudis* did not cluster. At this similarity level, therefore, the factor “species” seemed to play a role in affecting epibiotic assemblages. Moreover, at 40% similarity, a separation within cluster I of medium-sized basibionts (two sub-clusters) in respect to one further group of prevalent large-

sized ones, and one small-sized basibiont apart is recognizable. Cluster II, similarly, showed a single sub-cluster with two medium-sized basibionts, while cluster III showed one sub-cluster with small and medium specimens and one medium specimen apart. Notwithstanding the close relationships existing between abundance/species and area (e.g. Underwood & Chapman, 1996), in particular for bi-dimensional hard substrata (Thompson et al., 1996), the above-reported multivariate discrimination could determine only a relative influence of “size” factor on this assemblages constitution.

One-way ANOSIM test (“species” factor) gave a Global R value of 0.37 ($p < 0.1\%$), which did not support a sharp discrimination of the two assemblages, while the “depth level” factor better distinguished the assemblages (Global R = 0.47, $p < 0.1\%$). Two-way analysis (“size class” nested within “species” factor) did not produce significant results for either the “species” factor, with Global R value of 0.92, but with $p > 5\%$, or for the “size class” factor (Global R = -0.09, $p \gg 5\%$). MVDISP (“species” factor) quantified the tighter cluster of *P. nobilis* (dispersion factor = 0.61) in respect to the co-generic bivalve (dispersion factor = 1.40). Index of multivariate dispersion (IMD) was equal to 0.80, thus indicating the greater variability of the *P. rudis* associated assemblage in terms of densities as well as species occurrences. In contrast, BIOENV procedure on the whole assemblages did not highlight significant rank correlations ($r_s = 0.25$) for the best subset of variables: total length, width, spine density. Similarly, no significant higher correlations were found in *P. rudis* ($r_s = 0.39$, total length and spine density) and in *P. nobilis* ($r_s = 0.27$, depth level and estimated spine number). Conch shape and roughness therefore did not play a direct role in influencing all the associated mollusc epifauna or in differentiating the patterns of each *Pinna* species.

Species-Cluster analysis (“inverse analysis”, Field et al., 1982) highlighted the patterns of shared epizoites, together with the most recurrent epizoites in the two basibionts separately. These clusters have been compared with results of similarity/dissimilarity percentage analysis (SIMPER, “species” 1-way factor). Table 1 shows the epizoites of *P. nobilis* grouped in four main clusters (I-IV; 40% similarity) and eight sub-clusters (1-8; 50% similarity), although sub-clusters 6, 7, 8 must be considered as “pseudo-clusters”, because they consisted mainly of species found on a single basibiont. In particular, cluster IV and sub-clusters 3 and 4, grouped some of the associated species which mostly contributed to within group similarity of *P. nobilis*, but also to the differentiation from the other associated assemblage. *Rissoella inflata* Locard, 1892, *Bittium reticulatum* (Da Costa, 1778), *Arca noae* (L., 1758) and, secondarily, *Omalogyra atomus* (Philippi, 1841) and *Ammonicera fischeriana* (Monterosato, 1869) were the most recurrent

epizoites. Notwithstanding the fact that these species, together with *Vitreolina philippi* (De Rayneval & Ponzi, 1854), *Columbella rustica* (L., 1758), *Gibbula turbinoides* (Deshayes, 1835) and *Gibberula philippi* (Monterosato, 1868) were common in both basibionts (except for *A. fischeriana* and *O. atomus* found on *P. nobilis* only), they discriminated the basibiont well in terms of abundance and frequency, as these species were prevalent in *P. nobilis*. By contrast, *P. rudis* hosted a more heterogeneous assemblage (Table 2), even though with some recurrent species. Similarity breakdown singled out five main clusters (I-V), each one divided into two sub-clusters, along with four other small clusters, two of which mainly had epizoites present on a single specimen (“pseudo-clusters” 12 and 13). Also in this case, the most recurrent epibiotic mollusc was *B. reticulatum*, followed by *Tricolia deschampsi* Gofas, 1993, which prevailed on *P. rudis*. Other differentially distributed epizoites were the commensal or ecto-parasite Pyramidellidae *Odostomia* and *Vitreolina* species, for which species higher basibiont/epizoobiont specificity may be involved (Powell et al., 1987).

Discrimination between the mollusc epifauna of the two fan-shell species reached an average dissimilarity value δ of about 76.74%. According to δ/SD ratio, as a measure of each species contribution to the total inter-group δ (Clarke, 1993), the most discriminating species were *R. inflata*, *B. reticulatum*, *A. noae*, *A. fischeriana*, *V. philippi*, *O. atomus*, *T. deschampsi*, *C. rustica*, *G. turbinoides*, *Pisinna glabrata* (Von Muehlfeldt, 1824), *G. philippi* (41.53% cumulative contribution) and, secondarily, *Sinezona cingulata* (Costa O.G., 1861), *Crepidula gibbosa* Defrance, 1818, *Microsetia ochroleuca* (Brusina, 1869), *Hiatella rugosa* (L., 1767), *Monophorus perversus* (L., 1758), *Ocenebrina aciculata* (Lamarck, 1822), *Musculus costulatus* (Risso, 1826), *Anomia ehippium* L., 1758, *Chauvetia brunnea* (Donovan, 1804), and *Jujubinus striatus* (L., 1758) which amount to 59.15% of total dissimilarity. In particular, the widespread gastropod *B. reticulatum* was the most important species for intra-group similarity in both basibionts, but it was also a good-discriminating species ($\delta/SD = 1.45$) in inter-group comparison. The abundance and spatial distributions of these species were responsible for most of the discrimination between the two groups, by comparing both the average values and each pair of values. Therefore, more than ten associated species made the two patterns tendentially different, testifying that many epizoites partly and gradually contributed to total inter-group dissimilarity.

The main guilds found were browsers/grazers (feeding on algal or bacterial microfilms), omnivores (non-selective macrophages and scavengers), carnivores (predators), parasites, suspension/filter feeders, motile and sessile

Table 1. Sample-clusters compared with dissimilarity percentage values of 3% most recurrent mollusc epizoites on *Pinna nobilis*; less recurrent and sporadic species are not shown.

Roman number: 40% similarity clusters. Arabic number: 50% similarity clusters. Av. S': average similarity within each basibiont-group. Av. d: average dissimilarity between the two basibiont-groups. Points on the left of species name: number of nodes in the dendrogram. Vertical bar after dash: species present on one single basibiont. Underline: epizoites occurring in one basibiont species only. (*) Significant species in within basibiont-group similarity. (**) Highly significant species in within basibiont-group similarity. (°) Significant species in among basibiont-group dissimilarity. (°°) Highly significant species in among basibiont-group dissimilarity.

Tableau 1. Groupes comparés aux pourcentages de dissimilarité rapportés aux mollusques épizoobiontes les plus abondants (au moins 3% d'abondance) associés à *Pinna nobilis*; les espèces les moins abondantes ou sporadiques ne sont pas montrées.

Chiffres romains: groupes à 40% de similarité. Chiffres arabes: groupes à 50% de similarité. Av. S': similarité moyenne de Bray-Curtis dans chaque groupe hôte. Av. d: dissimilarité moyenne entre les deux groupes-hôtes. Points à gauche de l'espèce: nombre des noeuds du dendrogramme. Barre verticale: espèces présentes sur un seul exemplaire hôte. Soulignement: espèce présente seulement sur une espèce de bivalve hôte. (*) Espèce à similarité significative dans le groupe-hôte. (**) Espèce à similarité très significative dans le groupe-hôte. (°) Espèce discriminante entre les deux hôtes. (°°) Espèce très discriminante entre les deux hôtes.

		<i>Pinna nobilis</i> (L.)	Av. abn.	Av. S'	S'/SD	S'%	Av. δ	δ/SD	δ%
		[group av. S' = 38.38]							
Increasing cluster similarity	I	1 .. <i>Microsetia ochroleuca</i>	0.51	—	—	—	1.29	0.81 °	1.68
		.. <i>Tricolia deshampsi</i>	0.29	—	—	—	3.10	1.03 °°	4.04
	2	.. <i>Odostomia turruta</i>	0.40	—	—	—	0.77	0.59	1.00
		.. <i>Anomia ephippium</i>	0.23	—	—	—	1.48	0.68	1.93
	II	.. <i>Odostomia carrozzai</i>	0.45	—	—	—	0.71	0.56	0.92
		.. <i>Fasciolaria lignaria</i>	0.15	—	—	—	0.43	0.44	0.56
	III	.. <i>Vitreolina anteflexa</i>	0.35	—	—	—	0.56	0.45	0.73
		.. <i>Lamellaria perspicua</i>	0.14	—	—	—	0.53	0.44	0.69
	3	.. <i>Ocenebrina aciculata</i>	0.39	—	—	—	0.80	0.72 °	1.04
		.. <i>Vitreolina philippi</i>	1.61	1.95	0.68	5.07	3.04	1.18 °°	3.96
	4	... <i>Columbella rustica</i>	0.84	0.98	0.59	2.56	1.46	1.09 °°	1.90
	 <i>Gibberula philippi</i>	1.61	1.89	0.57	4.93	2.71	1.02 °°	3.53
	5 <i>Arca noae</i>	2.06	3.36	1.00 **	8.75	2.84	1.29 °°	3.70
	 <i>Bittium reticulatum</i>	4.20	9.40	1.81 **	24.49	3.56	1.45 °°	4.64
	6	... <i>Cerithiopsis minima</i>	0.15	—	—	—	0.66	0.53	0.86
	 <i>Gibbula turbinoides</i>	1.67	1.93	0.56	5.04	2.64	1.06 °°	3.44
	7 <i>Jujubinus striatus</i>	0.46	—	—	—	0.79	0.65	1.04
	 <i>Musculus costulatus</i>	0.70	—	—	—	1.92	0.62	2.50
	8 <i>Ammonicera fischeriana</i>	1.15	1.62	0.77 *	4.23	1.70	1.24 °°	2.21
	 <i>Hiatella rugosa</i>	0.54	—	—	—	1.10	0.78 °	1.44
9 <i>Omalogyra atomus</i>	1.47	2.04	0.73 *	5.31	2.26	1.16 °°	2.94	
 <i>Rissoella inflata</i>	4.45	10.30	2.69 **	26.83	5.51	1.67 °°	7.18	
10	.. <i>Alvania scabra</i>	0.45	—	—	—	0.78	0.50	1.02	
	.. <i>Haminoea navicula</i>	0.19	—	—	—	0.29	0.31	0.38	
11	.. <i>Sinezona cingulata</i>	0.82	—	—	—	1.35	0.88 °	1.76	
	.. <i>Monophorus perversus</i>	0.37	—	—	—	1.43	0.74 °	1.86	
12	.. <i>Pseudochama gryphina</i>	0.33	—	—	—	0.50	0.47	0.65	
	.. <i>Melanella microstoma</i>	0.44	—	—	—	0.63	0.46	0.82	
13	.. <i>Calliostoma conulus</i>	—	—	—	—	—	—	—	
	.. <i>Cerithium vulgatum</i>	—	—	—	—	—	—	—	
14	.. <i>Chauvetia brunnea</i>	0.25	—	—	—	1.73	0.60	2.25	
	.. <i>Circulus striatus</i>	—	—	—	—	—	—	—	
15	.. <i>Muricopsis cristata</i>	0.18	—	—	—	0.48	0.44	0.62	
	.. <i>Modiolus barbatus</i>	0.26	—	—	—	0.37	0.42	0.49	
16	.. <i>Anisocycla pointeli</i>	—	—	—	—	—	—	—	
	.. <i>Crepidula gibbosa</i>	0.26	—	—	—	1.63	0.86 °	2.12	
17	.. <i>Gibberula oryza</i>	—	—	—	—	—	—	—	
	.. <i>Raphitoma linearis</i>	—	—	—	—	—	—	—	
18	<i>Chrysallida emaciata</i>	0.24	—	—	—	0.79	0.54	1.03	
	<i>Pollia dorbignyi</i>	0.17	—	—	—	0.54	0.53	0.70	
19	<i>Thracia distorta</i>	0.17	—	—	—	0.29	0.31	0.37	

Table 2. Sample-clusters compared with dissimilarity percentage values of 3% most recurrent mollusc epizoites on *Pinna rudis*; less recurrent and sporadic species are not shown (for symbols see legend of Table 1).

Tableau 2. Groupes comparés aux pourcentages de dissimilarité rapportés aux mollusques épizoobiontes les plus abondants (au moins le 3% d'abondance), associés à *Pinna rudis*; les espèces moins abondantes ou sporadiques ne sont pas montrées (pour les symboles voir légende du Tableau 1).

		<i>Pinna rudis</i> (L.) [group av. S' = 22.22]	Av. abn.	Av. S'	S' / SD	S' %	Av. δ	δ / SD	δ %	
Increasing cluster similarity	I	<i>Musculus costulatus</i>	0.73	—	—	—	1.92	0.62	2.50	
		... <i>Hiatella rugosa</i>	0.36	—	—	—	1.10	0.78 °	1.44	
		... <i>Microsetia cossuræ</i>	0.59	—	—	—	1.12	0.54	1.46	
		... <i>Alvania scabra</i>	0.13	—	—	—	0.78	0.50	1.02	
		... <i>Pisinna glabrata</i>	0.13	—	—	—	1.44	1.06 °°	1.88	
		... <i>Tubiola nitens</i>	—	—	—	—	—	—	—	
	II	2	... <i>Rissoella inflata</i>	1.10	0.88	0.44	3.94	5.51	1.67 °°	7.18
		... <i>Arca tetragona</i>	0.75	0.34	0.22	1.53	1.19	0.54	1.55	
		... <i>Chrysalida emaciata</i>	0.34	—	—	—	0.79	0.54	1.03	
		3	... <i>Coralliophila squamosa</i>	—	—	—	—	—	—	—
			... <i>Fasciolaria lignaria</i>	0.16	—	—	—	0.43	0.44	0.56
			... <i>Haliotis tuberc. lamellosa</i>	—	—	—	—	—	—	—
	... <i>Columbella rustica</i>		0.43	—	—	—	1.46	1.09 °°	1.90	
	4	... <i>Diodora gibberula</i>	0.40	—	—	—	0.58	0.58	0.76	
... <i>Crepidula gibbosa</i>		0.99	0.97	0.43	4.37	1.63	0.86 °	2.12		
III	5	... <i>Gibberula philippi</i>	0.77	0.31	0.22	1.41	2.71	1.02 °°	3.57	
		... <i>Vitreolina philippi</i>	1.45	0.96	0.34	4.33	3.04	1.18 °°	3.96	
	6	... <i>Ammonicera rota</i>	0.31	—	—	—	0.43	0.46	0.57	
		... <i>Sinezona cingulata</i>	0.34	—	—	—	1.35	0.88 °	1.76	
		... <i>Vitreolina curva</i>	0.43	—	—	—	0.67	0.45	0.88	
		... <i>Chauvetia turritellata</i>	0.47	—	—	—	0.66	0.44	0.86	
IV	7	... <i>Cerithiopsis tubercularis</i>	0.28	—	—	—	0.39	0.31	0.51	
		... <i>Lamellaria perspicua</i>	0.25	—	—	—	0.53	0.44	0.69	
		... <i>Modiolarca subpicta</i>	0.22	—	—	—	0.31	0.31	0.40	
	8	... <i>Pollia dorbignyi</i>	0.22	—	—	—	0.54	0.53	0.70	
		... <i>Chauvetia brunnea</i>	1.03	0.35	0.18	1.60	1.73	0.60	2.25	
		... <i>Muricopsis cristata</i>	0.19	—	—	—	0.48	0.44	0.62	
9	... <i>Oodostomia turrita</i>	0.14	—	—	—	0.77	0.59	1.00		
	... <i>Ocenebrina aciculata</i>	0.27	—	—	—	0.80	0.72	1.04		
	... <i>Oodostomia conoidea</i>	0.52	—	—	—	0.77	0.55	1.00		
V	10	... <i>Microsetia ochroleuca</i>	0.60	0.30	0.24	1.33	1.29	0.81 °	1.68	
		... <i>Mitrolumna crenipicta</i>	0.36	—	—	—	0.51	0.45	0.67	
	11	... <i>Cerithiopsis minima</i>	0.31	—	—	—	0.66	0.53	0.86	
		... <i>Jujubinus striatus</i>	0.09	—	—	—	0.79	0.65	1.04	
		... <i>Tricolia deschampsii</i>	2.14	2.56	0.73 *	11.53	3.10	1.03 °°	4.04	
		... <i>Bittium reticulatum</i>	4.17	10.15	1.69 **	45.66	3.56	1.45 °°	4.64	
12	... <i>Gibbula turbinoides</i>	0.76	0.53	0.34	2.38	2.64	1.06 °°	3.44		
	... <i>Monophorus perversus</i>	0.74	0.41	0.24	1.83	1.43	0.74 °	1.86		
	... <i>Oodostomia nitens</i>	0.52	—	—	—	0.80	0.56	1.04		
	... <i>Willamia gussoni</i>	1.07	0.64	0.32	2.89	1.81	0.55	2.36		
	... <i>Anomia ephippium</i>	0.80	0.50	0.24	2.24	1.48	0.68	1.93		
	... <i>Arca noae</i>	1.24	1.32	0.41	5.93	2.84	1.29 °°	3.70		
	13	... <i>Mitrolumna olivoidea</i>	0.34	—	—	—	0.53	0.40	0.69	
		... <i>Barleeia rubra</i>	0.25	—	—	—	0.40	0.31	0.52	
	14	... <i>Jujubinus sequenzæ</i>	0.36	—	—	—	0.57	0.31	0.74	
		... <i>Gregariella subclavata</i>	0.25	—	—	—	0.42	0.31	0.55	
		... <i>Jujubinus montagui</i>	0.25	—	—	—	0.42	0.31	0.55	
		... <i>Sinum bifasciatum</i>	0.25	—	—	—	0.42	0.31	0.55	
	15	... <i>Barleeia unifasciata</i>	0.41	—	—	—	0.65	0.44	0.85	
		... <i>Chama gryphoides</i>	0.16	—	—	—	0.55	0.52	0.71	

Table 3. Functional guilds analysis of the whole epibiotic mollusc fauna and of the main subsets of epizoites on each basibiont species, based on Spearman's rank correlation (r_s) of the relating matrices. Trophic guilds are specified in the text. (*) $p < 5\%$. (**) $p < 1\%$. (***) $p < 0.1\%$. n.d., not detectable.

Tableau 3. Analyse des groupes fonctionnels de l'ensemble des mollusques et des principaux groupes d'épizoobiontes associés à chaque espèce hôte, basée sur la corrélation de rang de Spearman (r_s) des matrices correspondantes. Groupes trophiques spécifiés dans le texte. (*) $p < 5\%$. (**) $p < 1\%$. (***) $p < 0.1\%$. n.d., non décelable.

Trophic guild Motility	Browsers	Omnivores	Carnivores	Parasites	Suspension	Motile	Sessile
Both basibionts							
RELATE Rank correl. (r_s)	0.73***	0.44***	0.22*	0.31*	0.45***	0.94***	0.46***
<i>Pinna rudis</i>							
RELATE	0.63***	0.43*	0.30*	0.26	0.30	0.90***	0.32*
1 st subset							
BVSTEP	0.59***	n.d.	0.43**	0.18	0.49**	0.91***	0.49**
2 nd subset							
BVSTEP	0.37**	n.d.	n.d.	0.28*	0.44**	0.48***	0.44**
<i>Pinna nobilis</i>							
RELATE	0.48***	0.65***	0.22	0.06	0.2	0.93***	0.22
1 st subset							
BVSTEP	0.58**	0.61***	0.25	n.d.	0.18	0.84***	0.18
2 nd subset							
BVSTEP	0.54***	n.d.	n.d.	0.01	n.d.	0.76***	n.d.

forms. RELATE procedure (Table 3) applied to the whole mollusc epifauna showed that browsers/herbivores best characterized the associated mollusc fauna, followed by suspension feeders and omnivores; motile epizoites were more prevalent than sessile fauna. Nevertheless *P. rudis* was best characterized by motile browsers, whereas the *P. nobilis* assemblage was constituted by motile omnivores and, secondarily, by motile browsers. On the former basibiont, the BVSTEP (BIO-BIO) procedure identified a subset of 15 species ($r_s = 0.95$), a second best subset which amounted to 11 epizoites ($r_s = 0.68$), and the third subset amounted to one species only ($r_s = 0.34$). The same procedure carried out on *P. nobilis* showed a first best subset of 16 species ($r_s = 0.94$), a second subset of 10 species ($r_s = 0.77$) and a third residual subset of 4 species ($r_s = 0.53$). Taking into account the limited number of samples and the analysis restricted to mollusc taxon, both basibionts showed two representative subsets of almost 15/10 associated epizoites. These results may suggest a certain redundancy/coexistence of species, in particular for *P. nobilis*. As regards functional guilds, only the first *P. rudis* subset showed a well-structured trophism with motile browsers and carnivores, followed by sessile suspension feeders, whilst motile browsers and sessile suspension feeders alone were representative of the second subset. The first subset of *P. nobilis* was characterized by omnivores and, secondarily, by motile browsers, whilst only this latter guild was significantly representative of the second subset.

Discussion

Epizotic mollusc assemblages described in this paper denote a high variability degree in the number of species, as well as in abundance, in both fan-shells. Notwithstanding the fact that a clear discrimination of the two basibionts has been highlighted in terms of bathymetric distribution as well as morphologic characterization, epizotic assemblages are not distinguishable from the traditional univariate structural indices. The weak influence of size factor to regulate these assemblages could indicate an early settlement of mollusc epifauna upon the juvenile or sub-adult individuals of both *Pinna* species, as also demonstrated by Munguia (2004) for the west-Atlantic fan shell *Atrina rigida* (Lightfoot, 1786).

Among extrinsic factors, the permutation test supported the primary influence of bathymetry and the related processes, such as wave action disturbance and light irradiance, to the epizotic algal canopy (Ramus et al., 1976). From another point of view, breakdown of multivariate similarity, with singling out of multi-specific patterns, allows us to observe the tendential typological differentiation of the two *Pinna* basibionts and the constitution of two patterns, which tend to differentiate mainly in terms of density and frequency of several associated molluscs. The *P. rudis* assemblage seems to be more influenced by a stochastic component with lower frequencies of species, but with a better trophic structure, whilst the *P. nobilis* assemblage is less variant concerning both species/

frequency composition and related functional guilds. One of these discriminating species is certainly the small generalist Cerithiidae *Bittium reticulatum*, which occurs all over the *P. nobilis* specimens with a higher average density than in *P. rudis*.

If we compare multivariate ordinations based upon morphometric/abiotic variables or upon associated assemblages, it is possible to note the contrasting wide scattering of *P. nobilis* individuals of the PC plane compared to the closer distribution of the same individuals on MDS, and vice versa for *P. rudis*. In addition, if we consider the shallower distribution and the higher occurrence of damages in the former bivalve, a greater exposure to physical disturbance of *P. nobilis* and its epizoic assemblage may be inferred. Due to stochastic recruitment of epifauna from adjacent patch assemblages (Kay & Keough, 1981; Nalesso et al., 1995), a direct influence of the different algal assemblages on associated molluscs could be suggested (Williams & Seed, 1992). The prevalence of erected thallii of *Cystoseira* spp. upon *P. nobilis* compared to *P. rudis* may have a structuring effect on the associated community (Gee & Warwick, 1994) and, therefore, on the mollusc fauna. On the other hand, the different algal covering could be related to the different shell sculpture, which affects the hydrodynamic flow at micro and meso-scale. *P. nobilis* sculpture, with more numerous and denser spines, may facilitate the deposition and settlement of epizooxymytes, thus determining a cascade effect (Guichard & Bourget, 1998) up to the establishment of well-developed vertical turfs. The consequent conspicuous algal covering implements the 3-d colonizing space, thus increasing the diversity of micro-habitats as well as small-scale complexity (Stoner & Lewis, 1985); it also supplies important food resources (Bologna & Heck, 1999), reducing micro-currents and enhancing the shelter-effect (aspects overviewed by Orth, 1992; Vadas & Elner, 1992) even when most of the spines are eroded in the adult/senescent stage of shell. The greater availability of small hollows on small to medium *P. nobilis* shells may also favour early settlements of crevice-dwelling zoo-benthos, as Olabarria (2000) demonstrated for some Muricidae gastropods. Due to the lower density of spines, these processes occur in *P. rudis* to a lesser extent, determining the prevalence of incrusting algae. The lower occurrence of erected thallii would imply the reduction of shelter, sediment trapping and food supply. These aspects make *P. rudis* basibionts a more exposed substratum, which determines, together with the wider bathymetric distribution, the more stochastic settlement of species, mainly in terms of abundance and frequency, and favours a more variant assemblages. Therefore, the mollusc epifauna associated with *P. nobilis* has to be interpreted as best selected and more specialized in its trophic/habitat

requirements than *P. rudis*. Moreover, the prevailing motile epizooxymytes on *P. nobilis* may indicate the ephemeral character of algal canopy compared to the congeneric species, where long-lived encrusting algae may favour a more structured associated assemblage, with a non negligible occurrence of sessile species. Similarly, small-scale spatial and temporal variability of *Pinna* as substrate may favour the co-occurrence of several species with a similar trophic role, suggesting the specific/functional redundancy of associated assemblages (Loreau et al., 2002). Nevertheless, the coexistence of functionally equivalent species, supported by a higher cyclic variability, could be also explained by the alternative hypothesis of niche partitioning and species complementarity (Loreau & Hector, 2001), particularly for the shallower *P. nobilis*, more exposed to seasonal variability than *P. rudis*.

The observed prevalence of selective browsers, non-selective grazers and low abundance of suspension feeders, could indicate a non well-balanced trophism of mollusc epifauna. An interesting comparison is possible with the data given by Olabarria (2000) on Muricidae as basibionts, regarding the more abundant sedentary filter-feeding epizooxymytes on the motile carnivorous molluscs, in contrast to the prevalence of motile grazers on the sessile filter-feeders. Thus the motility and feeding strategy of the basibiont probably influence the prevalent motility and trophism of the associated epifauna.

In conclusion, analysis of the mollusc fauna associated on *Pinna* showed the substantial inadequacy of the traditional structural and diversity univariate indices to describe these assemblages. By contrast, multi-species analyses identified the two patterns, which appeared only tendentially differentiated. Many species contributed to the characterization of these patterns, in terms of density and frequency per sample of basibiont. Both assemblages settled early on pen-shells, but *P. nobilis* epifauna appeared more abundant and less variant in species composition. The contrasting dispersion of basibionts in PC and MDS ordinations inferred the apparent discordance between the conch morphology and each epizoic pattern. The primary influence of bathymetry combined with the indirect role of conch sculpture to affect algal assemblages and related mollusc fauna, may therefore be postulated. The structuring effect of algal covering has also been highlighted by the functional differentiation of the two patterns. The lower balanced trophism of *P. nobilis* assemblage, with the prevalence of motile specialized micrograzers and opportunistic epizoites, was more adapted to seasonality and to ephemeral algae, whilst the *P. rudis* assemblage was more functionally diversified in accordance with an enduring phytocoenosis.

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