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Biodiversity associated with *Sabellaria alveolata* (Polychaeta: Sabellariidae) reefs: effects of human disturbances

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Infauna diversity is reported from the *Sabellaria alveolata* reefs in the bay of Mont Saint-Michel in France, known as the greatest European reef formation. Polychaetes dominate the fauna, but other species also play a role in terms of reef functioning. Species richness of the associated infauna is much higher than that of the surrounding sediments and is concentrated mainly on the reef surface. Species richness clearly varied according to the three stages of reef evolution: the 'degraded' reef stage is different from the 'ball-shaped structure' and 'platform' stages. Multivariate analyses indicate that three species communities can be distinguished, each corresponding to a different stage of reef development. The number of species is very high, but only a few species are restricted to a particular reef stage. Variations of surface topography and spatial heterogeneity can explain unusual associations of species that make infauna associated with *S. alveolata* reefs very unique.

Moreover, the high densities of *S. alveolata* (up to 60,000 ind m^{-2}) raise questions regarding the role of the reefs in the ecosystem of the bay. Anthropogenic influences, notably mechanical disturbances due to fishing activity, show a steady increase and may have a serious impact on the assemblage diversity and the ecological stability of the reef, even though recolonization of *S. alveolata* is possible in degraded reef areas. An important question that must be addressed is whether human activities could influence the role of *S. alveolata* reefs in the bay of Mont Saint-Michel.

INTRODUCTION

Corals are not the only organisms to build reefs. Some polychaetes of the family Sabellariidae build formations reaching several kilometres in length (Pawlick, 1988). In temperate climes, the species *Sabellaria alveolata* (L.) is present from the Bristol Channel (Wilson, 1971, 1974) to the south of the Moroccan coast (Rullier, 1958; Rullier & Amoureux, 1970). The bioconstructions of *S. alveolata* are found in two major forms. The first are colonies built as structures adhering to rocks ('veneers'), which are very common at the mid level of the intertidal zone. The second developed structures, much more rare, are 'reefs' spread over several acres on sandflats at the lower level of the intertidal zone (Gruet, 1982). Reefs are structured in banks whose size and extent on the sandy beaches of Mont Saint-Michel Bay and are the greatest European reef formations known.

Sabellariid constructions are known all over the world as the habitat for numerous benthic invertebrates: India (Achary, 1969, 1974), South America (Fausto-Filho, 1970), the Mediterranean (Molinier & Picard, 1953; Rivosecchi, 1961; Bellan, 1964; Porras, 1996); western American coast (Posey, 1984), and Portugal (Sousa Dias, 2001). On the French coast, we have an in-depth understanding of reef dynamics and macrofauna inventories (Gruet, 1970, 1972a,b, 1977, 1982, 1986). However, there is a lack of data concerning the link between physical structures—i.e. different stages of the reef evolution—and associated species.

In this study, the differences between the types of physical structures and their associated infaunal species are assessed in order to define assemblages and understand how the communities are structured by reef evolution.

In the same way as coastlines all around the world (Viles & Spencer, 1995), the French coast is more and more frequented by humans and its resources exploited. *Sabellaria* reefs are known for their abundance of commercial species—shrimps, oysters, mussels, crabs, fishes—(Vorberg, 2000 for *Sabellaria spinulosa*; Legendre, 1992 for *S. alveolata*). In the bay of Mont Saint-Michel, *S. alveolata* reefs have always been exploited for oysters and mussels, which caused authorities to restrict fishing activities after a very strong decline of the reef in 1970. Fishing activity is always combined with trampling, which is seriously damaging these reefs, as demonstrated by Eckrich (2000) for sea grass assemblages. Patches of reef are broken-off, turned-over and stamped on. Directly because of destructive manual fishing methods or indirectly through shellfish aquaculture, degraded areas are more and more widespread in *S. alveolata* reefs in the bay of Mont Saint-Michel. We try in the present study to assess and understand the consequences of such degradation for a reef. The problem is also to know how the communities associated with reef evolution stages maintain their populations on the reef and how degradation of the reef affects them.

MATERIALS AND METHODS

Study area

The *Sabellaria alveolata* reefs reach their maximum size in the bay of Mont Saint-Michel where two main formations are present in the intertidal zone. We chose to sample the southern section of the north formation because it typifies all stages and aspects of the reef dynamic. The reef studied stands on the east coast of the bay of Mont Saint-Michel (France) (Figure 1) at 48°43′971″N 01°33′176″W. The general orientation of the reef is parallel to the coast and to the prevailing tidal currents (i.e. north west–south east). The examination of numerous formations by Gruet (1972a–1986) has provided the basis for distinguishing the different stages in the evolution of the reef. The natural evolution of the reef begins with the settlement of young recruits to ball-shaped structures which then fuse as they grow to form barriers and then platforms. Through natural or anthropogenic disturbance, the reef can be degraded. Thus, a reef extending over several hectares as in the bay of Mont Saint-Michel is composed of all these evolution stages in varied proportions.

In this study, three key stages of the reef dynamic have been chosen as representative of the entire reef evolution: ball-shaped structures, platforms, and degraded reef. Evolution stages are easily distinguished in the field because of their morphology (Gruet, 1982). The sampling site was chosen to include all stages of the reef evolution within a restricted area in order to avoid being in different environmental conditions (hydrodynamism and sedimentation). Personal communications with occasional or professional beachcombers, review of local newspaper articles, and field observations provide evidence that anthropogenic disturbances are obviously responsible for the degraded reef we studied here.

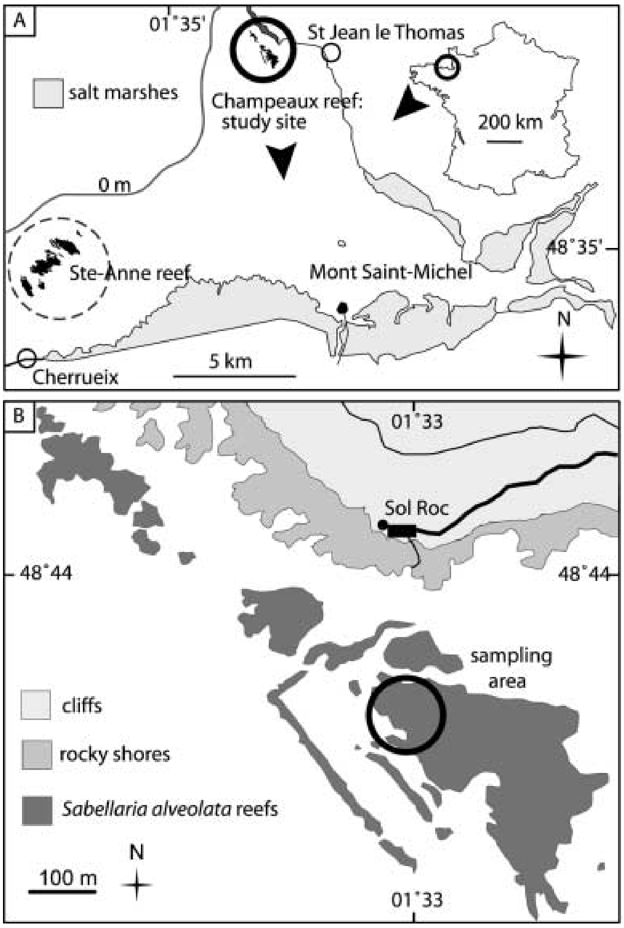

Figure 1. (A) Localization of the bay of Mont Saint-Michel on the French coast and general overview of the studied reef in the bay of Mont Saint-Michel; (B) the studied site in detail.

Sample collection and processing

Winter sampling was carried out during March 2000 to avoid coinciding with the reproductive period of most polychaete species (Bhaud, 1972). Cores were extracted from the reef with a 15 cm side corer (225 cm^2) to a depth of 60 cm. Each core was cut into four slices of 15 cm each. The first slice (0–15 cm) corresponds to the level where *S. alveolata* lives (Gruet, 1972b). Each core was extracted randomly on each evolution stage studied, with a distance among cores from 2 to 30 m, and at the same distance from the reef edges to avoid a possible biodiversity gradient from edge to inside. A total of 24 cores (eight per evolutionary stage) were collected and preserved in a 4.5% formaldehyde solution.

In the laboratory, the *S. alveolata* tubes were dismantled in seawater, and the fauna retained on a 500-m mesh were sorted, counted and identified. Thus, assessment of the level of density and abundance was more precise than studies carried out before on *S. alveolata* reefs by Gruet (1982), who used 1-mm mesh. The sorting method may damage species and make identification to the specific level sometimes impossible. Nematodes and oligochaetes were abundant but were excluded from analysis because the sorting method—i.e. mesh size—was unsuitable.

Data analysis

Infaunal species diversity was estimated using Hill's indices (Hill, 1973): where N0=SR=Species Richness, N1=exp(H) where H is Shannon–Wiener diversity (Shannon, 1948), N2=1/SI where SI is Simpson's index (Simpson, 1949). N1 is an index of the number of abundant species and N2 the number of very abundant species.

One-way analysis of variance (ANOVA) was used to test for differences between each evolutionary stage and for differences between depth levels within each evolutionary stage. The parameters tested were computed in the PRIMER (Plymouth Routines In Multivariate Ecological Research) software package: species richness, diversity indices, and species abundances. Bartlett's test was used to determine whether variances were homogenous or not and whether the data required transformation. In that case, data were $\log_e$ transformed. When parametric ANOVA testing was acceptable, least significant difference (LSD) test was used to multiple comparisons. A significance level of $P < 0.05$ was used in all tests.

Size-class frequencies of *S. alveolata* were based on the measurement of the opercular crown and thus are linked to the age of individuals according to a biometrical relationship (Gruet, 1982).

Dominance curves were plotted for each physical structure and associated species only—i.e. with exclusion of

S. alveolata—were ranked in order of importance in terms of abundance.

Multivariate analysis followed methods of Clarke & Warwick (1994), using the PRIMER software package. Data analysis was performed by using non-metric multidimensional scaling ordination (MDS), and clusters were created using group average linking with the Bray–Curtis similarity measure. Log-transformed data were used to down-weight the importance of the very abundant species. Species occurring in only one sample with only one individual were excluded for a more interpretable outcome. In order to characterize each physical structure by species assemblage, it appears here biologically more relevant to define two samples as being similar when they have the same percentage composition of species and that is the reason why multivariate analysis was carried out using standardized data. To identify within two different sample groups which species primarily accounted for the observed assemblage difference, SIMPER (similarity percentage) routines were performed using a decomposition of Bray–Curtis dissimilarity on standardized and log-transformed abundance data. By looking at the overall percentage contribution of each species to the average dissimilarity between two sample groups, species were listed in decreasing order of their importance in discriminating the two sets of samples (Clarke & Gorley, 2001).

Table 1. *Mean abundances (number of individuals m^{-2}) of infauna associated with* Sabellaria alveolata *reef. Total abundances is sum of all samples of all evolution stages. '%' represents the dominance of each group or each species (*Sabellaria alveolata *excluded) among the groups classified according to the number of species.*

Species	MA	±SD	%
Sabellaria alveolata	22001.85	13807.35	
Polychaeta: 40 spp.			64.32
Fabricia stellaris	3577.78	7422.10	28.63
Pygospio elegans	1551.85	2957.53	12.42
Pomatoceros lamarckii	1090.74	1838.39	8.73
Capitomastus minimus	705.56	1076.31	5.65
Goniadella bobrezkii	461.11	1166.19	3.69
Perinereis cultrifera	231.48	190.82	1.85
Syllis gracilis	77.78	96.53	0.62
Odontosyllis ctenostoma	48.15	110.37	0.39
Eulalia ornata	44.44	93.60	0.36
Polydora ciliata	35.19	75.26	0.28
Phyllodoce laminosa	24.07	61.44	0.19
Eumida sanguinea	22.22	39.32	0.18
Perinereis marionii	18.52	41.27	0.15
Brania pusilla	18.52	47.10	0.15
Terebellidae sp1	16.67	38.91	0.13
Lumbrineris tetraura	11.11	23.63	0.09
Eteone longa	11.11	30.03	0.09
Protodorvillea kefersteini	9.26	32.05	0.07
Sthenelais boa	7.41	21.40	0.06
Cirratulidae sp1	7.41	21.40	0.06
Sphaerosyllis ovigera	7.41	16.92	0.06
Pholoe synophthalmica	7.41	21.40	0.06
Eulalia viridis	7.41	16.92	0.06
Kefersteinia cirrata	5.56	19.93	0.04
Terebellidae sp2	5.56	19.93	0.04
Phyllodoce mucosa	3.70	12.55	0.03
Eusyllis blomstrandi	3.70	18.14	0.03
Phyllodoce maculata	3.70	12.55	0.03
Marphysa sanguinea	1.85	9.07	0.01
Phyllodoce lineata	1.85	9.07	0.01
Lumbriconereinae sp1	1.85	9.07	0.01
Ensyllis lamelligera	1.85	9.07	0.01
Leptonereis glauca	1.85	9.07	0.01
Aphroditidae sp1	1.85	9.07	0.01
Capitella capitata	1.85	9.07	0.01
Pholoe inornata	1.85	9.07	0.01
Cirratulidae sp2	1.85	9.07	0.01
Exogone gemmifera	1.85	9.07	0.01
Drilonereis filum	1.85	9.07	0.01
Lysidice ninetta	1.85	9.07	0.01
Crustacea: 9 spp.			8.62
Corophium volutator	377.78	576.81	3.02
Porcellana platycheles	324.07	727.29	2.59
Melita palmata	138.89	575.52	1.11
Sphaeroma monodi	79.63	141.75	0.64
Carcinus maenas	64.81	113.49	0.52
Gnathia maxillaris	48.15	123.58	0.39
Balanus balanoides	35.19	107.26	0.28
Gammarus sp.	7.41	21.40	0.06
Leucothoidae sp.	1.85	9.07	0.01
Mollusca: 4 spp.			0.68
Mytilus edulis	38.89	39.99	0.31
Cerastoderma edule	31.48	94.03	0.25
Venerupis saxatilis	11.11	19.66	0.09
Crepidula fornicata	3.70	18.14	0.03
Insecta/Arachnids: 4 spp.			10.49
Axelsonia littoralis	792.59	888.47	6.34
Hydrogamasus sp.	509.26	721.66	4.08
Collembola sp2	5.56	27.22	0.04
Acarina sp2	3.70	12.55	0.03
Pycnogonida: 1 sp.			
Achelia echinata	33.33	60.42	0.27
Nemertean: 1 sp.			
Lineus sp.	412.96	315.49	3.30
Anthozoa: 1 sp.			
Cereus pedunculatus	44.44	58.61	0.36
Echinodermata: 1 sp.			
Amphipholis squamata	1.85	9.07	0.01
Sipuncula—1 sp.			
Golfingia vulgaris	1492.59	1108.51	11.94

MA, mean abundance; SD, standard deviation; sp., species.

RESULTS

Characteristics of the fauna

In addition to the 11,881 individuals of *Sabellaria alveolata*, a total of 6750 individuals belonging to 63 species were identified from the 24 samples (Table 1). Polychaetes were the principal component of fauna associated with *S. alveolata* reef, dominating both in terms of number of species and individuals. Other groups with a lower number of species (Sipuncula, Nermertea, Insecta), were also very abundant.

Whatever the reef state, *S. alveolata* was the dominant species: up to 45,000 ind m^{-2} on platforms (mean 35,150 ±10,923 ind m^{-2}) down to 2500 ind m^{-2} on the degraded reef (mean 6522 ±4000 ind m^{-2}) (Figure 2A). *Sabellaria alveolata* was less abundant on the degraded reef than on ball-shaped structures (P=5.2×10^{-5}) and platforms (P=10^{-6}). On the other hand, other species were more abundant on the degraded reef than on ball-shaped structures (P=3.6×10^{-4}) or platforms (P=10^{-6}). Platforms and ball-shaped structures were also different concerning *S. alveolata* density (P=5.8×10^{-3}) but not for the density of other species. The density ratio of *S. alveolata* to other species (Figure 2B), reveals differences at each evolutionary stage, showing an inverse relationship between the density of *S. alveolata* and the density of other species. But differences between evolutionary stages do not only concern densities. Size-class frequencies of *S. alveolata* clearly show deep contrast between ball-shaped structures and platforms where adults dominated and the degraded reef where almost all individuals were juveniles (Figure 3).

Species richness showed significant differences between degraded reef and other evolution stages (P=0.038), but there were no significant variations in the two Hill's indices (N1 and N2) among stages (Figure 4A). With respect to the vertical levels within the reef, none of the three indices revealed significant variation on ball-shaped structures (Figure 4B). The surface level (0–15 cm) on the degraded reef contrasted clearly with other levels (Figure 4D) (SR, N1, N2: $P<0.001$). On platforms, according to Hill's indices, there were more abundant species in the surface level than in the others (N1, N2: $P<0.05$).

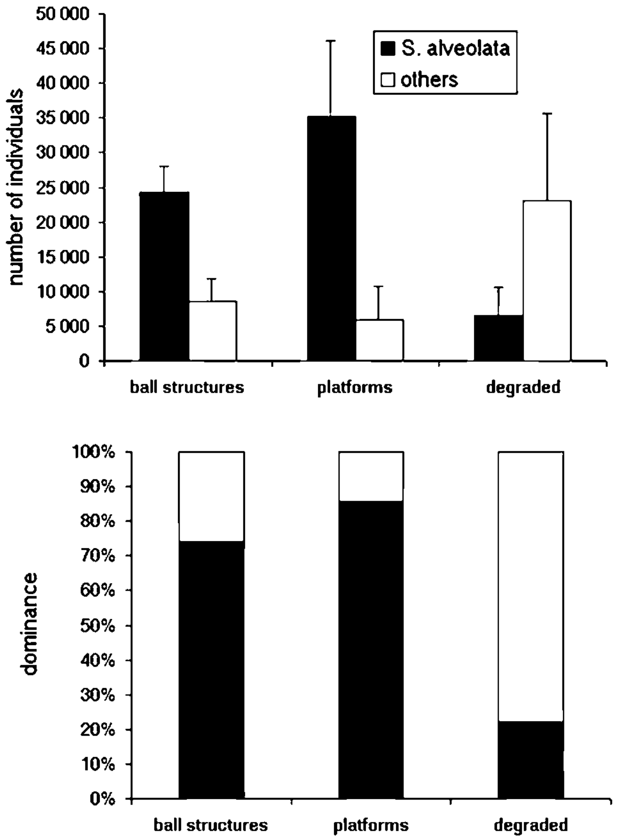

Figure 2. (A) Variations of *Sabellaria alveolata* density and other species (number of individuals m^{-2}) according to the evolution stage. SD are represented on histograms; (B) relative percentage of the density of *Sabellaria alveolata* and other species according to each evolution stage.

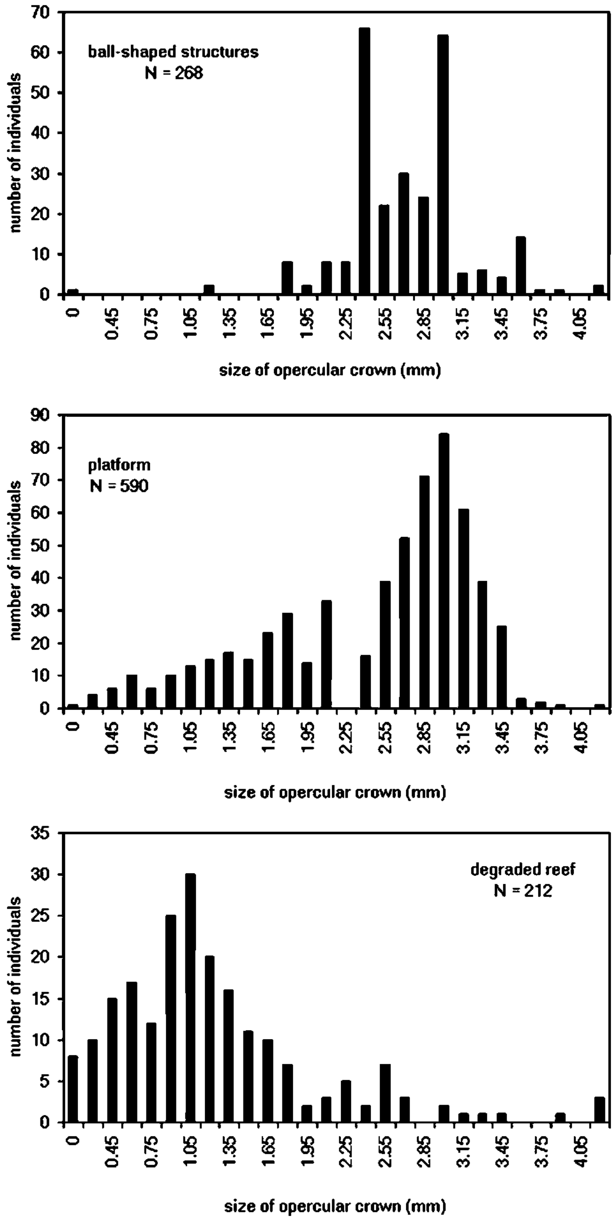

Figure 3. Size-class frequency based on the measurement of the opercular crown according to each evolution stage. N, number of individuals measured.

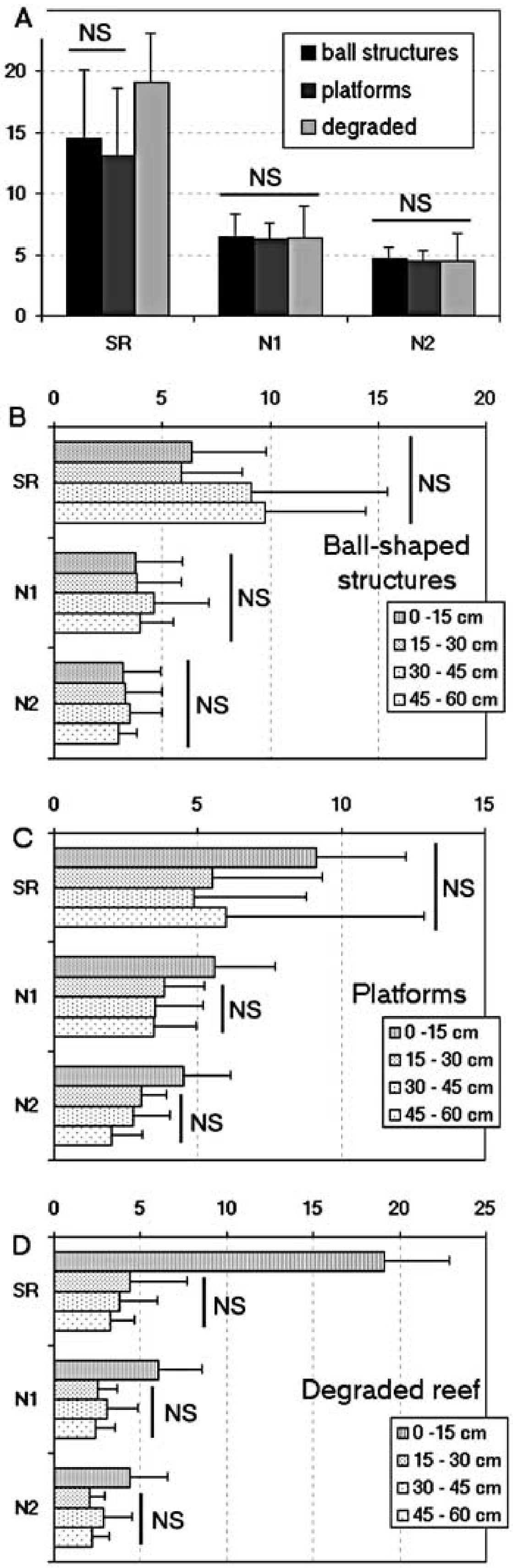

Figure 4. (A) Variations of the species richness (SR) and Hill's indices (N1, N2) according to the evolution stage; (B–D) variations SR, N1 and N2 on each evolution stage according to the vertical level within the reef. In all histograms, SE is represented. NS, variation non-significantly different at a P-level=0.05.

Species assemblages

Non-multi dimensional scaling (nMDS) revealed four clusters at a similarity level of 50% (Figures 5 & 6). The evolution stages of the reef were separated, showing that the degraded reef was very different in community composition from both ball-shaped structures and platforms. Figure 6 clearly shows the transition between ball-shaped structures and degraded reef. The possible separation of samples extracted from ball-shaped structures and platforms can be confirmed by the one-way layout analysis of similarities (ANOSIM) on these two reef stages (r=0.781; P=0.001).

Figure 7 displays the result of a cluster analysis on the species similarity matrix. At the similarity level of 25%, three clusters can be separated. Cluster I is composed of species whose abundance is much more higher on the ball-shaped structures than on the others (*Goniadella bobrezkii*), or by species exclusive to or preferentially found on this stage (*Cerastoderma edule*, *Sthenelais boa*, *Phyllodoce laminosa*). Species in cluster III are difficult to associate with any evolution stage because of their occurrence in a very small number of samples, even if *Gnathia maxillaris* and *Melita palmata* are much more abundant on platforms than on other evolution stages. Cluster II can be separated into two subgroups. Subgroup IIa is distinguished by species very abundant in degraded reef samples (*Pygospio elegans*, *Fabricia stellaris*) or preferentially found on this evolution stage (*Corophium volutator*, *Brania pusilla*, *Perinereis marionii*), while subgroup IIb comprised the majority of the species, with no clear distinction for any evolution stage (*Lineus* sp., *Hydrogamasus* sp., *Axelsonia littoralis*, *Golfingia vulgaris*). The SIMPER analysis shows the results of breaking down the dissimilarity between samples extracted from platforms and ball-shaped structures into species contributions (Table 2). Many species play some part in determining the dissimilarity between these two groups of samples but some species typify a group because they are found at higher abundance and at a more consistent abundance throughout a group of samples.

Thus, we can define each evolution stage as a sub-set of the *S. alveolata* assemblage (Figure 8) with species typifying each evolution structure. The two sub-assemblages defined on ball-shaped structures and platforms are probably a variation of the same sub-community, and more precisely the platform sub-assemblage is an impoverished state of the ball-shaped structure assemblage.

k-dominance curves for species abundance (Figure 9)—*S. alveolata* excluded—of each evolution stage show additional differences in structure community. Curves for platforms and ball-shaped structures show a more even distribution of numbers of individuals among species than does the degraded reef. The curve for the degraded reef, typically found in the case of disturbance, shows that reef community becomes dominated by one or two species.

DISCUSSION

A valid assessment of biodiversity and variations in *Sabellaria alveolata* assemblages according to the reef dynamic is necessary for further investigations of this ecological system. Although the link between biodiversity and ecosystem functioning is strongly debated, ecosystem

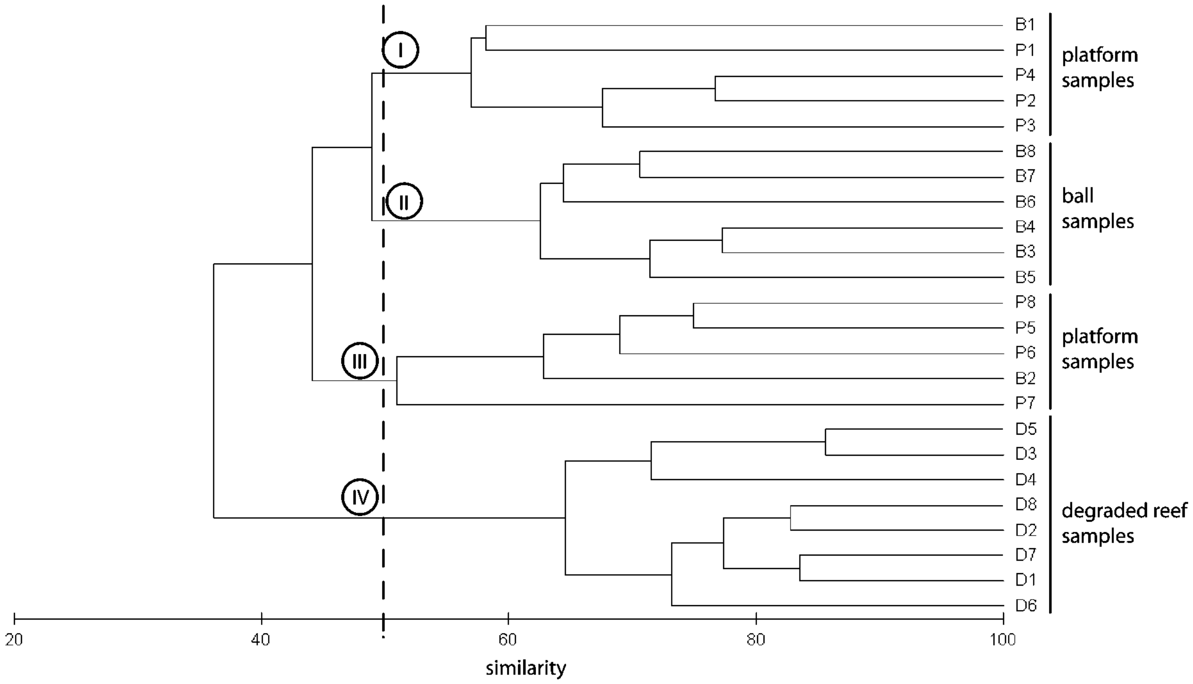

Figure 5. Dendrogram for hierarchical clustering of the 24 samples, using group average linking of Bray–Curtis similarity on standardized and log-transformed abundances data. The four groups of samples separated at 50% similarity threshold are indicated.

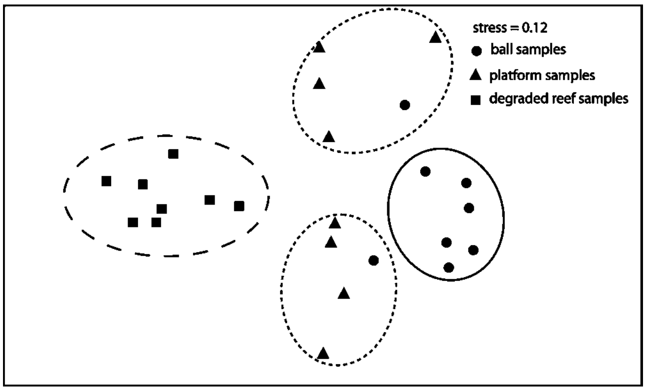

Figure 6. The MDS ordination of the 24 samples based on standardized and log-transformed abundances and Bray–Curtis similarities (stress=0.12).

function seems to be positively correlated with biodiversity (Schwartz et al., 2000). Degraded areas, where biodiversity is clearly higher, are becoming more and more widespread in reefs of the bay of Mont Saint-Michel and are probably playing a different role than other evolution stages in reef functioning. That is why the consequences of human activities have to be examined, and the present study is part of a larger research design to understand how the *S. alveolata* reefs are integrated into the local ecosystem.

The higher species richness on degraded reef (especially the first level) can be explained by several factors like habitat fragmentation associated with change in surface topography. The first few centimetres of the reef are damaged by destructive methods of collecting oysters, and this activity is clearly the most harmful to the health of the reef. Human activities create disturbed areas and irregular surface features with lower densities of *S. alveolata* tubes, thus affecting hydrodynamics, flow environments (Nowell & Jumars, 1984) and the trapping of sediment, larvae, and postlarvae (and *S. alveolata* size-class histograms support this view). Modification of flow regimes by physical structure is known to occur for polychaete tubes (Eckman, 1983; Qian et al., 1999), eelgrass meadows (Eckman, 1987), and mussel beds (see references in Snover & Commito, 1998; Commito & Rusignuolo, 2000).

The increase of sedimentation on the degraded reef may also explain the presence of many polychaete species typically found in mud-bottom communities (*Fabricia stellaris*, *Pygospio elegans*, *Polydora ciliata*). Most of the species found on ball-shaped structures or platforms are typically found on hard substrata (*Perinereis cultrifera*, *Eulalia viridis*, *Phyllodoce laminosa*) or sand bottoms (*Capitomastus minimus*, *Goniadella bobrezkii*, *Pholoe synophthalmica*) (Fauvel, 1923, 1927; Glynne-Williams & Hobart, 1952; Richoux, 1972; Walker, 1972). In fact, the unique nature of the assemblages found on *S. alveolata* reefs in the bay of Mont Saint-Michel is not related to the presence of one particular species—even if the species *Eulalia ornata* may be found in large numbers especially in *S. alveolata* reefs (Pleijel & Dales, 1991). Rather, it is due to very uncommon assemblages created by the juxtaposition of species belonging to surrounding communities. Some species found on *S. alveolata* reefs probably have their origins in the subtidal muddy sand gravel community (*Sthenelais boa* or *Pomatoceros lamarcki*) or in the *Macoma balthica* community (*Fabricia stellaris*, *Pygospio elegans*), widely distributed in the bay of Mont Saint-Michel (Thorin, 2001). Nevertheless, *Goniadella bobrezkii* has never been recorded or mentioned in the bay of Mont Saint-Michel, nor in the English Channel, probably because of misidentification.

Many species are common between ball-shaped structures and platforms, leading to the conclusion that the

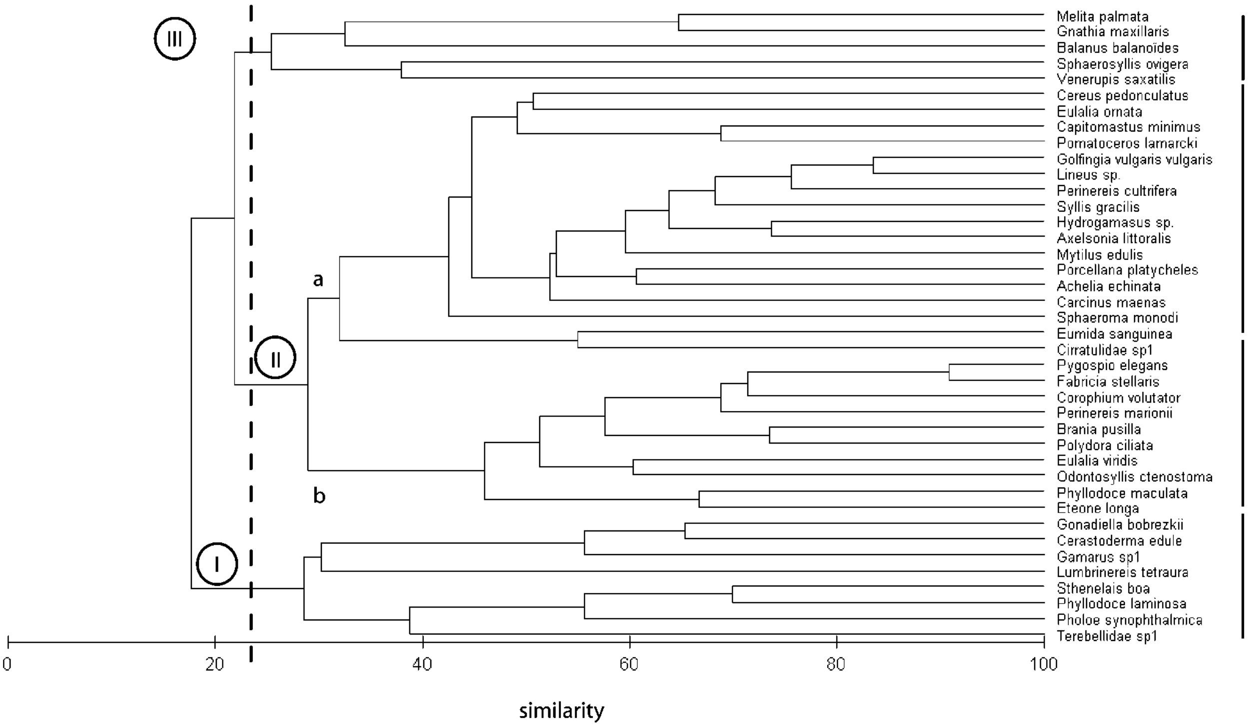

Figure 7. Dendrogram for most abundant species from Bray–Curtis similarities computed for standardized and log-transformed species abundances.

platform assemblage is actually an evolution of the ball-shaped structure assemblage due to similarities in surface complexity. Nevertheless, we can observe a decrease in free spaces and microenvironments due to an increased number of individuals of *S. alveolata*. That may explain why the platform sub-assemblage is an impoverishment state of the ball-shaped structure sub-assemblage.

In terms of biodiversity, the obvious contrast between *S. alveolata* reefs, a biodiversity hot-spot, and the *Macoma balthica* community edging these reef formations in the bay of Mont Saint-Michel and known for its low species richness (Meziane, 1997; Thorin, 2001) is an argument to support the idea that these reefs are not only a biological inheritance built by a polychaete species. The link between these reefs and the surrounding sediment and effects on adjacent soft-bottom communities is still to be assessed, following the example of studies carried out on smaller subtidal *Sabellaria* reefs (Mettam, 1992) or rocky reefs

Table 2. *Breakdown of average dissimilarities between samples from platforms and ball-shaped structures into contribution from each species. Species—until 80% contribution—are ordered in decreasing contribution. Average abundances have been calculated with standardized and log-transformed data (in number of individuals* m^{-2}*). Average dissimilarity between ball-shaped structures and platforms: 53.18.*

Species name	Platforms (MA)	Balls (MA)	av. δi	av. δi/SD(δi)	av. δi(%)	sum av. δi (%)
Goniadella bobrezkii	–	1333	5.22	1.79	9.82	9.82
Pomatoceros lamarckii	1188	2061	4.59	1.48	8.63	18.46
Capitomastus minimus	133	1827	3.86	1.79	7.26	25.71
Axelsonia littoralis	800	583	3.70	1.32	6.95	32.66
Lineus sp.	400	227	3.11	1.35	5.85	38.51
Perinereis cultrifera	327	144	3.09	1.25	5.82	44.33
Hydrogamasus sp.	405	72	2.76	1.12	5.18	49.51
Porcellana platycheles	644	33	2.52	1.00	4.74	54.25
Corophium volutator	66	5	2.26	0.83	4.24	58.50
Sphaeroma monodi	33	144	2.22	0.98	4.18	62.68
Carcinus maenas	72	88	1.89	1.23	3.55	66.23
Golfingia vulgaris	966	1233	1.70	1.32	3.21	69.43
Melita palmata	411	5	1.55	0.59	2.92	72.36
Cereus pedunculatus	16	66	1.45	0.92	2.74	75.09
Syllis gracilis	50	55	1.36	1.19	2.55	77.65
Gnathia maxillaris	127	5	1.25	1.25	2.36	80.00

MA, mean abundance; av. δi, average dissimilarity; SD(δi), standard deviation; sum av.δi, total average dissimilarity.

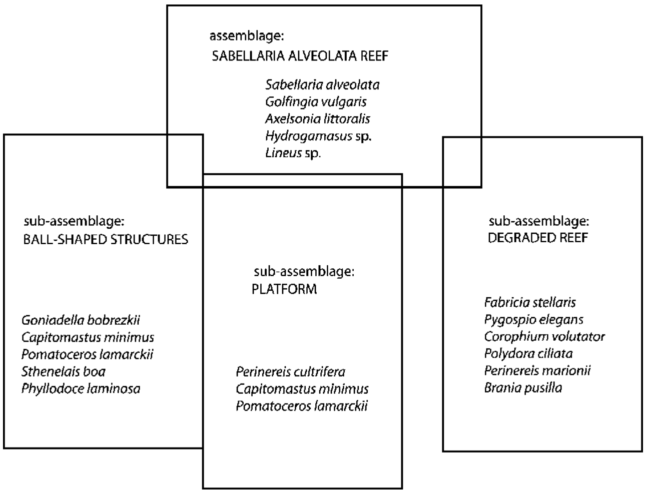

Figure 8. Species sub-assemblages defined within the *Sabellaria alveolata* reef in the bay of Mont Saint-Michel.

(Ambrose & Anderson, 1990; Cusson & Bourget, 1997; Barros et al., 2001). They showed the influence of topographic heterogeneity on biodiversity, biomass, and spatial variation in structure of species assemblages.

Looking at the density reaching by *S. alveolata* and the surface area covered by these reef formations in the bay of Mont Saint-Michel—300 ha (Gruet, 1982)—it is possible to think about these reefs in terms of a super-organism. Even if the species *S. alveolata* is not an endangered species, the function of filtration or matter production in the bay-ecosystem can be seriously damaged if the number of individuals is not enough to allow reef renewal. The recognition of human pressure is highly dependent on the scale of the sampling. We can here conclude that on a small scale (evolution reef stage scale), human pressure increases species richness and abundances in general by increasing surface heterogeneity. But on a larger scale (whole reef), it leads to a simplification of the 'landscape' by extending the degraded reef and therefore decreasing the biocoenotic diversity.

Anthropogenic impacts raise also the question of the reversibility of the modifications for the reef itself and for associated fauna. The degraded reef is not a dead reef and the size-class histograms suggest that degraded structures could be the preferential substratum for *S. alveolata* larvae. Like other gregarious Sabellariid polychaetes, *S. alveolata* is known to have larvae that settle and metamorphose preferentially on the tubes of conspecific adults (Wilson, 1968; Pawlick, 1988). Pawlick (1988) demonstrated in the laboratory that the metamorphosis-inducing capacity of sand from recently cemented natural tubes was not different from that of sand from older natural tubes. Therefore, the degraded reef and remnants of structures, where free-spaces are larger than on other stages, are likely to stimulate settlement, a proposition recently supported by field observations.

Moreover, more information is required about reproduction in the bay of Mont Saint-Michel of the most abundant species of each reef stage in order to understand mechanisms of recruitment on the reef and the preservation of assemblages. We can nevertheless notice that species dominating ball-shaped structures and platforms—*Goniadella bobrezkii*, *Capitomastus minimus*, *Pomatoceros lamarcki* and *Perinereis cultrifera*—have a bentho-planktonic life cycle with pelagic larvae (Schroeder & Collins, 1975; Castric-Fey, 1984; Marty, 1997) allowing a more or less large

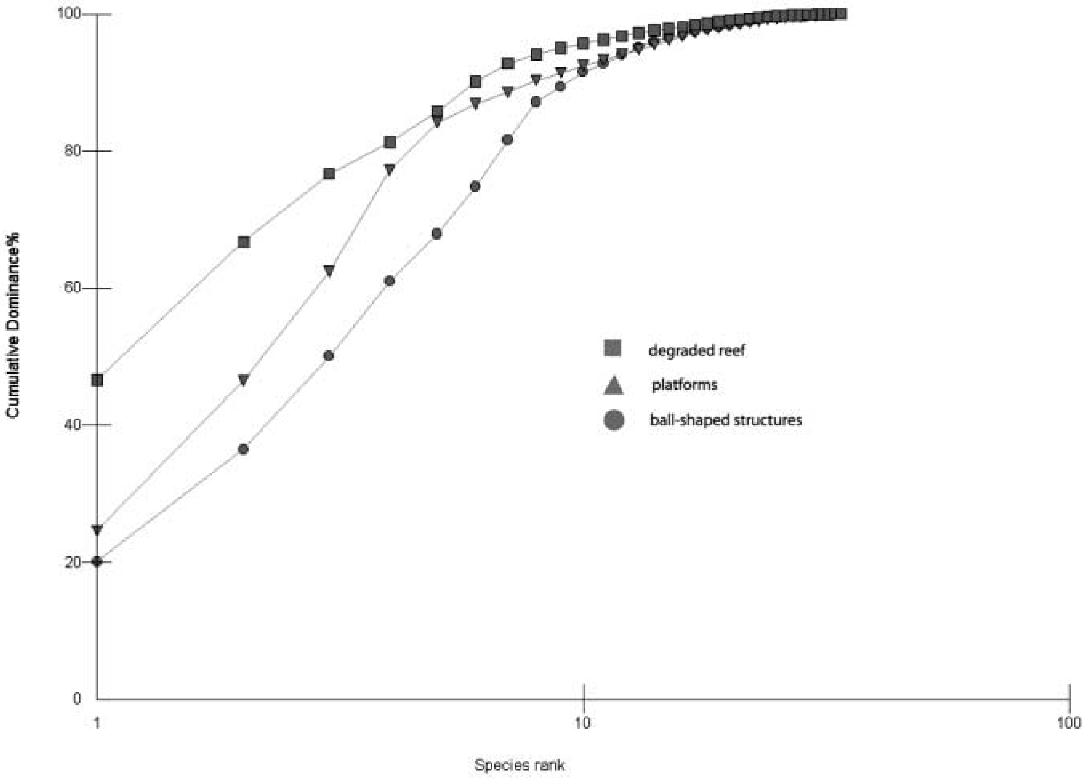

Figure 9. *k*-dominance curves from each evolution stage of the reef (x-axis logged).

dispersion of larvae and are influenced by hydrodynamic processes and topography of the environment. Thus, recolonization of these species after perturbation (destruction, erosion) is very dependant on hydrodynamics. On the degraded reef, *Fabricia stellaris* spawn eggs in capsules in tubes of mucus (Lewis, 1961; Rasmussen, 1973; Knight-Jones & Bowden, 1984), and *Pygospio elegans* exhibits both sexual and asexual reproduction (Rasmussen, 1973; Anger, 1984). Both are adapted to a small dispersion and thus, a rapid colonization of degraded areas.

In the bay of Mont Saint-Michel, the *S. alveolata* reefs can be seen as a unique community with very high species richness. Their role and function in the marine ecosystem is still to be fully appreciated and studies are in progress. However, increasing environmental degradation linked to anthropogenic impacts on the reef is presently raising questions concerning the conservation of this biological inheritance.

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