

Sublittoral hard substrate communities of the northern Adriatic Sea

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Abstract: In the northern Adriatic Sea there is a high number of rocky outcrops (of which a census has not yet been taken) with dense and diversified benthic communities that have not been studied until now. We studied two of these communities, as well as two other ones, which live on artificial substrata (a naval wreck and a barrier of concrete blocks), by collection of several samplings taken by SCUBA diving. A total of 116 species were identified, 67.6% of which were suspension feeders: ascidians, bivalves and poriferans, in decreasing order of frequency. Classification and ordination analysis, based on biomass values (ash free dry weight, AFDW), distinguished the communities on artificial structures from those on outcrops. Such a distinction is not due to the nature of the substratum but to an interaction between 1. the slope, almost horizontal in outcrops, and subvertical in artificial structures, 2. the water turbidity and 3. the consequent rate of sedimentation. An outcrop near the coast, with hydrological conditions similar to those present at stations with artificial substrata, has a lower biomass. These three environmental factors act on the relative percentage of species, of which some may become strongly dominant. They have no effect on the number of species in the community except for Porifera of which the number of species decreases as the turbidity increases. Where the slope of substrata does not exalt the negative effect of sedimentation, the biomass values (as g AFDW m⁻²) are very high, ranging from 346 to 436 at stations with a high water turbidity, to around 195 for the station farthest from the coast, where there is both lower turbidity and sedimentation.

Résumé : *Communautés sublittorales de substrats durs du nord Adriatique.*

Dans le nord de la mer Adriatique, une grande quantité de roches sublittorales (dont le nombre est encore inconnu) hébergent des peuplements benthiques riches et diversifiés. Deux communautés ont été étudiées et comparées avec deux autres vivant sur des substrats artificiels : une épave de navire et une barrière en blocs de béton. Plusieurs échantillonnages ont été effectués en scaphandre autonome. Cent seize espèces ont été identifiées, dont 67,6 % sont représentées par des espèces suspensivores : ascidies, bivalves et spongiaires, par ordre de fréquence décroissant. L'analyse statistique multivariée pratiquée avec les valeurs de biomasse (poids sec sans cendres, AFDW) distingue les communautés établies sur des structures artificielles de celles vivant sur les roches. Une telle distinction ne dépend probablement pas de la nature du substrat, mais de l'interaction entre 1. la pente du substrat, 2. la turbidité des eaux et 3. l'intensité de la sédimentation. Dans des conditions hydrologiques similaires, la biomasse sur les roches presque horizontales près de la côte est inférieure à celle des substrats artificiels subverticaux. Ces trois facteurs du milieu ont un effet sur la composition en pourcentage des espèces, parmi lesquelles quelques-unes sont notablement dominantes, mais non sur le nombre d'espèces dans les communautés sauf pour les spongiaires où ce nombre décroît avec l'augmentation de la turbidité. Les valeurs de biomasse (g AFDW m⁻²) atteignent environ 195 en condition de faible turbidité et en l'absence de sédimentation, à la station la plus éloignée de la côte, mais peuvent atteindre 346 à 436 aux stations de forte turbidité, lorsque la pente du substrat atténue les effets négatifs de la sédimentation.

Keywords : northern Adriatic Sea, hard substrates, benthic communities, species composition, biomass, multivariate analysis.

Introduction

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The northern Adriatic sea is characterized by a strong thermal range, generally greater than 20°C, with winter and

summer temperatures of about 5°C and 26°C respectively (Zore-Armanda, 1963). This thermal situation and the fresh water input from the Po River causes, in summer, a difference in water densities between the northern and southern Adriatic, which is so strong as to generate the water circulation of the whole basin (Vucetic, 1973; Franco et al., 1982; Mosetti, 1983). But, during summer in the northern Adriatic, the high temperature and the low salinity due to the plume of the Po River also causes a strong stratification in the water column (Franco, 1983), with a drop in dissolved oxygen near the bottom. These two hydrological characteristics, together with high water turbidity due to phytoplankton and organic and inorganic debris transported by the river, make this marine area biologically particularly interesting.

The northern Adriatic, an alluvial plain that was flooded by the sea after the last glacial period, is characterized by depths shallower than ca. 30 m and was for a long time believed to be exclusively sedimentary, though some areas with a hard bottom were already reported by Olivi in his *Zoologia Adriatica* (1792). It was only in late 1960s that many previously unreported zones, with a rocky bottom, were found off Italian beaches (Stefanon, 1969a). These outcrops turned out to be beachrocks, formed in the intertidal zone during the period of sea water flooding 3,000-4,000 years ago (Stefanon, 1969b; 1972), although some of these formations are probably exclusively bioconstructed. At present, these structures, which may range in size from less than 1 m² to over 100,000 m², are generally covered by an upper layer of biogenic rock (Newton & Stefanon, 1975; Boldrin et al., 1980) and are colonized by a dense community of benthic organisms. However, almost nothing is known about these communities. The present article would help to fill this gap. It refers to a quantitative study of the benthic communities living on two of such outcrops and compares the results with those obtained from two artificial hard substrata present in the same area.

Materials and methods

I. Sampling stations and operations

The location of the four stations studied is shown in Fig. 1.

TCH: This is an outcrop ~ 3.5 miles off Chioggia (45° 13' 15" N, 12° 23' 03" E) at a depth of 21 m; it is ~ 70 m long and ~ 30 m wide. The relief ranges from 1 to 3 m, its surface is almost horizontal, irregularly cut by deep fissures and covered by a muddy layer. The visibility was generally lower than 2 meters. This station was sampled seven times: July, August and October 1994; January, April, June and August 1995.

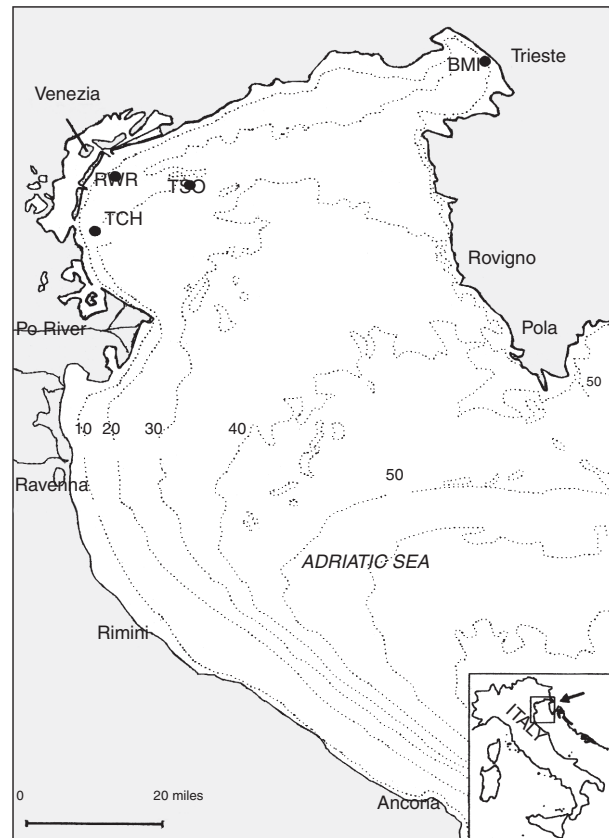


Figure 1. Location of sampling stations in the northern Adriatic sea. BMI: artificial concrete reef; depth, ca. 15 m. RWR: naval wreck ca. 3.8 miles from Venice; depth, ca. 17 m. TCH: outcrop ca. 3.5 miles off Chioggia; depth, ca. 21 m. TSO: outcrop ca. 13 miles off Venice; depth, ca. 23 m.

Figure 1. Localisation des stations d'échantillonnage dans le nord de l'Adriatique. BMI: barrière artificielle; profondeur, ca. 15 m. RWR: épave à environ 3,8 miles de Venise; profondeur, ca. 17 m. TCH: formation rocheuse à environ 3,5 miles au large de Chioggia; profondeur, ca. 21 m. TSO: formation rocheuse à environ 13 miles au large de Venise; profondeur, ca. 23 m.

TSO: This outcrop is located ~ 13 miles off Venice (45° 20' 15" N, 12° 43' 30" E) at a depth of ~ 23 m. It has an oblong shape with the major axis ~ one hundred m and the minor ~ 30 m. It has a lower relief than TCH, the surface is almost horizontal and the visibility was good: more than six meters. The station was sampled four times: July and October 1995; May and November 1996.

RWR: This is a naval wreck which sank in 1963, located ~ 3.8 miles off Venice (45° 21' 52" N, 12° 26' 30" E) at a depth of ~ 17 m; the sloping hull is ~ 50 m in length and rises up to 5 m from the sea floor. The surface is subvertical and the visibility was generally lower than 2 meters. Five samplings were done: June, September and November 1994; June and September 1995.

BMI: This is an artificial concrete reef, immersed in 1978, located on the border of the Marine Park of Miramare (Trieste), ~ 150 m off the coastline and at a depth of ~15 m. The reef is ~ 2 m high and is widely covered by a muddy layer. The surface is subvertical and the visibility was lower than 2 meters. The station was sampled five times: March, June and October 1995; January and March 1996.

The mean current strength in the considered area was 2.8 cm sec⁻¹ at -25 m and 4.4 cm sec⁻¹ at -15 m and the prevailing wave exposure was from SE (unpublished data of Istituto di Biologia del Mare, CNR; Dr. Rabitti: personal communication).

A total of 21 samplings were carried out by SCUBA diving from June 1994 to November 1996. The organisms present in squares of 50 by 50 cm were carefully scraped off the surface; at least 3 randomly chosen squares were sampled each time; in stations TCH and TSO they were horizontal while in RWR and BMI they were subvertical. The collected organisms were carried alive to the laboratory in refrigerated seawater containing menthol and novocaine to obtain their relaxation. At every sampling, cores (2 cm diameter) of the sediment surrounding the outcrops or the artificial structures were collected to determine granulometry (Buchanan, 1984) and organic matter content (Gaudette et al., 1974) (Table 1).

Table 1. Characteristics of sediments surrounding the sampling stations. Mean values and standard deviations (in brackets) are given.

Tableau 1. Caractéristiques du sédiment aux stations d'échantillonnage. Les moyennes et l'écart type (entre parenthèses) sont indiqués.

Stations	TSO (n = 4)	TCH (n=7)	RWR (n=5)	BMI (n = 5)
Depth	23 m	21 m	17 m	15 m
Sand (%)	95.3 (3.2)	65.9 (25.8)	28.3 (28.6)	8.1 (3.5)
Silt (%)	2.1 (1.9)	24.0 (18.0)	46.0 (36.9)	42.0 (9.7)
Clay (%)	2.6 (1.7)	10.0 (10.8)	25.7 (27.3)	49.9 (13.0)
Particle Ø (µm)	241 (21.8)	138 (98.7)	45.0 (40.6)	11.1 (5.3)
Organic matter (%)	0.2 (0.1)	0.99 (0.7)	1.1 (1.0)	2.5 (0.4)

II. Biomass estimation

The biomass of the organisms is expressed in ash free dry weight (AFDW). The animals were dried in an oven at 80°C until they reached a constant weight and then ashed in a muffle furnace at 550°C for 5 hours as recommended by Crisp (1984). To avoid the tedious determination of ash content, for some of the most abundant organisms, the AFDW values were obtained by means of conversion

factors that allow these values to be calculated from wet weight (Gabriele et al., 1997). The energy content (J) was obtained by multiplying the AFDW by the corresponding conversion factor obtained from the literature (Wacasey & Atkinson, 1987; Brey et al., 1988; Gabriele et al., 1997).

III. Statistical analysis

Data were handled by means of both univariate (ANOVA) and multivariate statistical techniques. The latter were employed to assess similarities between stations; the Bray-Curtis similarity index, calculated on biomass and presence/absence data, was used for all computations since it is not affected by "joint absences" (Clarke & Warwick, 1994). An ordination method, multidimensional scaling (MDS), was used to evaluate the group separation derived by cluster analysis. Similarity percentages, calculated on presence/absence data for each station after excluding species present in fewer than 3% of samples, were used to estimate the average similarity within a station to determine the «typical species» (those found most frequently in the replicates). Because a species may be typical in more than one station, a more analytical way to characterize stations is to compute the average dissimilarity between each pair of stations using the SIMPER procedure of Clarke (1993). That allows the "discriminant species" to be defined, i.e. the species responsible for the differentiation between pairs of stations. In practice, in a comparison between stations, the contribution of each species to the discrimination is estimated by calculating its average contribution ($\bar{\delta}_i$) to the average total dissimilarity $\bar{\delta}$. Because there are many pairs of samples making up the $\bar{\delta}_i$, a useful measure to quantify the contribution of a species to $\bar{\delta}$ is the standard deviation ($SD\bar{\delta}_i$) for the dissimilarity of that species. Thus, if $\bar{\delta}_i$ is large and $SD\bar{\delta}_i$ is small, their ratio is high and the species is called the "discriminating species". Multivariate analyses were performed by means of the PRIMER programs package (Clarke & Warwick, 1994). The Shannon diversity index was calculated from biomass values of each replication on a log₂ basis.

For the determination of the species, the following books and articles have been used: Brunetti, 1979, 1987, 1994; Lafargue, 1977; Monniot, 1962, 1972; Riedl, 1991.

Results

I. Community structure

Although depth was never > 24 m, because of the high water turbidity algae were represented only by a few specimens of Rhodophyta. Moreover the animal communities were dominated by suspension-feeders. A total of 111 macrobenthic animal species were recorded (Table 2) of which ascidiacea comprised 27.03%, bivalvia 14.41%,

Table 2. List of the species found in the four sampled stations. Trophic categories (tc): c/s = canivorous or scavenger; p = photosynthetic; l = limivorous; as = active suspension feeder; ps = passive suspension feeder. The number in brackets after the indication of presence (+) refers to the number of unspecified species. In Ascidiacea asterisks indicate the colonial species.

Tableau 2. Liste des espèces trouvées dans les quatre stations échantillonnées. Catégories trophiques (tc) : c/s = prédateurs ou nécrophages ; p = photoautotrophes ; l = limivores ; as = suspensivores actifs ; ps = suspensivores passifs. Le nombre entre parenthèses qui suit l'indication de présence (+) indique le nombre d'espèces non déterminées. Pour les ascidies, l'astérisque indique les espèces coloniales.

	tc	TSO	TCH	RWR	BMI		tc	TSO	TCH	RWR	BMI
RHODOPHYTA						ANNELIDA					
<i>Pseudolithophyllum</i> sp.	p	+	+	-	-	<i>Lagisca extenuata</i>	c/s	-	-	-	+
<i>Peysonnellia</i> sp.	p	+	+	-	-	<i>Harmothoe imbricata</i>	c/s	-	+	-	-
<i>Chrysimenia uvaria</i>	p	-	+	-	-	<i>Eunice aphroditois</i>	c/s	-	+	+	-
<i>Rhodomenia</i> sp.	p	+	+	+	-	<i>Eunice torquata</i>	c/s	-	-	-	+
<i>Anthitamnion</i> sp.	p	-	+	+	-	<i>Eunice vittata</i>	c/s	-	-	-	+
Total		3	5	2	0	<i>Nereis</i> sp.	c/s	-	-	-	+
PORIFERA						<i>Chaetopterus variopedatus</i>	as	-	+	-	+
<i>Chondrosia reniformis</i>	as	+	-	-	-	<i>Serpula concharum</i>	ps	-	+	+	-
<i>Cliona celata</i>	as	-	-	-	+	<i>Serpula vermicularis</i>	ps	+	+	+	+
<i>Tethya</i> sp.	as	+	+	-	-	<i>Pomatoceros lamarckii</i>	ps	-	-	-	+
<i>Axinella verrucosa</i>	as	-	-	+	-	<i>Pomatoceros triqueter</i>	ps	+	+	+	+
<i>Hemimycale columella</i>	as	-	-	-	+	<i>Hydroides dianthus</i>	ps	-	-	-	+
<i>Mycale massa</i>	as	+	-	-	-	<i>Sabella</i> sp.	ps	-	-	-	+
<i>Dysidea</i> sp.	as	+	+	+	+	Total		2	6	4	11
<i>Ircinia</i> sp.	as	+	-	-	-	CRUSTACEA					
<i>Sp. p. (7)</i>	as	+(5)	+(2)	+(2)	+(2)	<i>Verruca stroemia</i>	as	-	+	-	-
Total		10	4	4	5	<i>Balanus</i> sp. p. (2)	as	+(2)	+(2)	+(2)	+(2)
HYDROZOA						<i>Galathea</i> sp.	c/s	-	-	-	+
<i>Eudendrium racemosum</i>	c/s	-	-	+	-	<i>Pisidia</i> sp.	c/s	+	+	+	+
Total		0	0	1	0	<i>Ethusa mascarone</i>	c/s	+	-	-	-
ANTHOZOA						<i>Pinnotheres pinnotheres</i>	c/p	-	-	-	+
<i>Epizoanthus arenaceus</i>	c/s	-	+	+	+	<i>Pinnotheres pisum</i>	c/p	-	-	-	+
<i>Calliactis parasitica</i>	c/s	-	-	-	+	Total		4	4	3	6
<i>Sagartia elegans</i>	c/s	-	-	+	-	BRYOZOA					
<i>Sp.p. (3)</i>	c/s	-	+(3)	-	+(3)	<i>Schizoporella errata</i>	as	-	-	+	+
Total		0	4	2	5	Total		0	0	1	1
GASTROPODA						ECHINODERMATA					
<i>Diodora gibberula</i>	c/s	-	-	-	+	<i>Holothuria tubulosa</i>	l	+	-	+	-
<i>Diodora graeca</i>	c/s	-	-	+	-	<i>Cucumaria planci</i>	ps	+	+	-	-
<i>Diodora italica</i>	c/s	-	-	+	-	<i>Ophiotrix</i> sp.(2)	ps	+(2)	+(2)	+(2)	+(2)
<i>Calliostoma conulum</i>	c/s	-	+	-	-	Total		4	3	3	2
<i>Barleëia rubra</i>	c/s	-	-	+	-	ASCIDIACEA					
<i>Bitium reticulatum</i>	c/s	-	+	-	-	<i>Clavelina lepadiformis</i> *	as	-	-	-	+
<i>Aporrhais pespelecani</i>	c/s	-	-	-	+	<i>Distaplia</i> sp. *	as	+	-	-	-
<i>Murex trunculus</i>	c/s	-	-	+	+	<i>Diplosoma listerianum</i> *	as	-	-	+	+
<i>Muricopsis cristatus</i>	c/s	-	+	-	-	<i>Diplosoma</i> sp. *	as	-	-	-	+
<i>Ocenebra erinacea</i>	c/s	-	-	+	-	<i>Lissoclinum perforatum</i> *	as	-	-	-	+
<i>Hinia costulata</i>	c/s	-	-	-	+	<i>Lissoclinum</i> sp. *	as	-	-	+	+
<i>Hinia incrassata</i>	c/s	-	+	+	+	<i>Didemnum</i> sp. *	as	+	-	+	-
<i>Hinia reticulata</i>	c/s	-	-	+	+	<i>Polycitor adriaticus</i> *	as	+	+	-	-
<i>Fusinus rostratus</i>	c/s	-	+	-	-	<i>Cystodytes dellechiaiei</i> *	as	+	-	-	-
<i>Cythara albida</i>	c/s	-	+	-	-	<i>Eudistoma mucosum</i> *	as	+	-	-	-
Total		0	6	6	6	<i>Aplidium conicum</i> *	as	+	-	-	-
BIVALVIA						<i>Aplidium elegans</i> *	as	-	-	-	+
<i>Modiolus barbatus</i>	as	-	+	+	-	<i>Aplidium</i> sp. *	as	+	+	-	-
<i>Mytilaster minimus</i>	as	-	-	+	-	<i>Phallusia fumigata</i>	as	+	-	+	-
<i>Modiolarca subpicta</i>	as	+	+	-	-	<i>Phallusia</i> sp.	as	-	-	+	-
<i>Modiolula phaseolina</i>	as	-	-	+	-	<i>Ascidiaella aspersa</i>	as	-	+	-	+
<i>Musculus costulatus</i>	as	-	-	+	-	<i>Perophora</i> sp. *	as	+	-	-	-
<i>Mytilus galloprovincialis</i>	as	-	-	+	+	<i>Styela plicata</i>	as	-	-	+	-
<i>Arca noae</i>	as	+	+	+	-	<i>Styela</i> sp.	as	-	-	-	+
<i>Striarca lactea</i>	as	-	-	-	+	<i>Polycarpa</i> sp.	as	-	+	-	-
<i>Aequipecten opercularis</i>	as	-	-	-	+	<i>Metandrocarpa</i> sp. *	as	-	+	+	-
<i>Chlamys multistriata</i>	as	-	+	-	+	<i>Botryllus</i> sp. *	as	+	-	-	-
<i>Chlamys varia</i>	as	-	-	+	+	<i>Pyura squamulosa</i>	as	-	+	-	+
<i>Proteopecten glaber</i>	as	-	-	-	+	<i>Pyura microcosmus</i>	as	-	+	-	+
<i>Ostrea edulis</i>	as	-	+	+	+	<i>Pyura dura</i>	as	-	+	+	+
<i>Chama gryphoides</i>	as	-	-	+	-	<i>Pyura</i> sp.	as	+	-	-	-
<i>Hiatella arctica</i>	as	+	+	+	+	<i>Microcosmus vulgaris</i>	as	+	+	+	+
<i>Rocellaria dubia</i>	as	+	+	+	+	<i>Microcosmus polymorphus</i>	as	-	-	+	+
Total		4	7	12	9	<i>Microcosmus sabatieri</i>	as	-	-	-	+
SIPUNCULIDA						<i>Molgula</i> sp.	as	-	-	+	+
<i>Physcosoma granulatum</i>	l	+	-	-	+	Total		12	9	11	15
<i>Phascolosoma vulgare</i>	l	-	+	-	-	% of solitary species		25	67	64	60
Total		1	1	0	1	Total number of species: 116					

gastropoda 13.51%, porifera 13.51%, annelida 11.71% and the remaining taxa 19.82% (Fig. 2). A faunal summary based on the 64 samples from the various stations is shown in Table 3. Most species occurred in the artificial concrete reef (BMI) station and the least number in the offshore outcrop (TSO). However, the BMI station was characterized by the lowest Shannon diversity index and the TSO station by the highest. This is explained by the k-dominance curves for biomass shown in Fig. 3. At BMI, the community was greatly dominated by a single species (*Ostrea edulis*) and that lowers the diversity index.

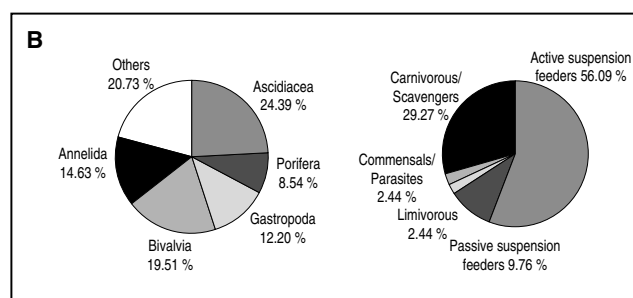
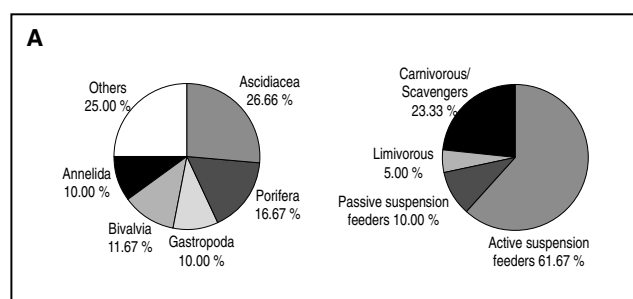


Figure 2. Distribution of the organisms among the main taxonomic groups (left) and the trophic categories (right). (A) natural substrate; (B) artificial substrate.

Figure 2. Distribution des organismes selon les principaux groupes taxonomiques (à gauche) et les catégories trophiques (à droite). (A) substrats naturels ; (B) substrats artificiels.

Table 3. Summary of the faunal characteristics of the four stations.
Tableau 3. Résumé des caractères faunistiques des quatre stations.

Stations	TSO	TCH	RWR	BMI
number of replicates	13	21	15	15
total number of species	40	50	50	62
number of site endemic species	11	9	12	26
mean number of species per replicate	23,7	16,5	23,5	24,3
standard deviation	3,5	2,5	3,0	5,1
Shannon diversity index	2,34	1,26	2,00	1,24
standard deviation	0,53	0,54	0,47	0,45

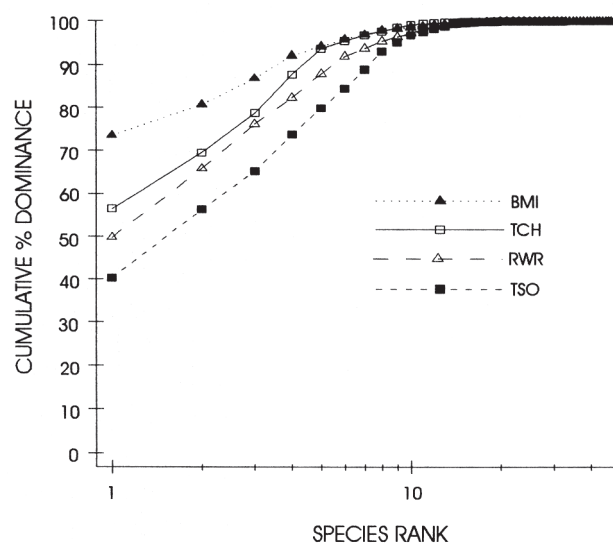


Figure 3. K-dominance curves for species biomass at each site.

Figure 3. Courbes de K-dominance construites avec les valeurs de biomasse des espèces présentes dans les différentes stations.

II. Biomass

The average values of total biomass in the four stations (TCH = 74.69; TSO = 194.83; RWR = 346; BMI = 436.16) were highly significantly different from each other (Fig. 4, Table 4, Fig. 8A). Observation of the contributions to the biomass values of the three main groups, ascidians, sponges and bivalves, shows that the differences are due to high biomass of bivalves at RWR and BMI, of sponges at TSO and of ascidians at TSO and RWR stations (Fig. 8B).

III. Clustering and ordination

From the cluster analysis, based on presence or absence data in the 64 replicate sampling events (Fig. 5A), four main groups could be distinguished, corresponding to the four stations. At a similarity level of about 36% the cluster analysis was able to distinguish the TCH and TSO stations from RWR and BMI; these latter two stations appear to separate at a similarity level of ~ 44% while the analysis did not distinguish between the TCH and TSO stations. This situation is better illustrated by the MDS plot which shows the above groupings graphically (Fig. 5B). However, the relatively high stress (0.14) suggested that more thorough analyses should be performed. Hence, we decided to repeat the same analysis using the average biomass values obtained by the three replicates per sample; in this case the cluster analysis showed strong differentiation among the four stations (Fig. 6A). In particular, at a Bray-Curtis index level of 22%, the TCH and TSO stations are separated from

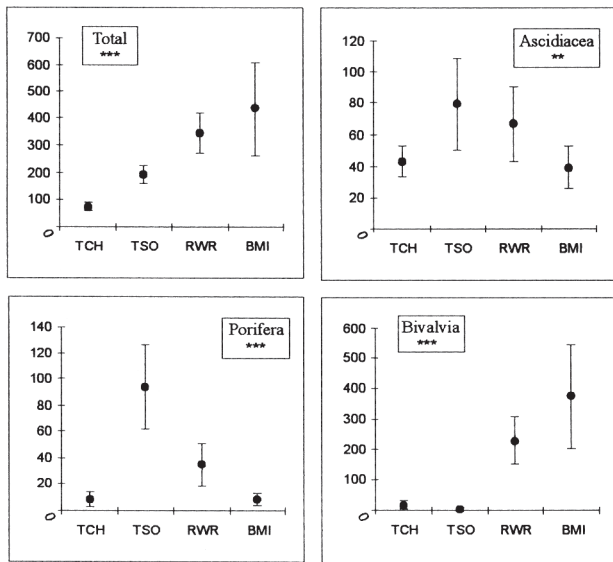


Figure 4. Values of biomasses, at each site, for the main taxonomical groups, as well as total values (means, as g AFDW m⁻², and 95% confidence intervals). Asterisks indicate the statistically (ANOVA) significant difference: ** = P < 0.01; *** = P < 0.001.

Figure 4. Valeurs des biomasses, aux différent sites, pour les principaux groupes taxonomiques ainsi que valeurs totales (moyenne en g AFDW m⁻², et intervalles de confiance à 95 %). L'astérisque indique une différence statistiquement significative : ** = P < 0.01 ; *** = P < 0.001.

RWR and BMI, and all stations are differentiated at a similarity level of ~ 43%. The MDS plot based on these data clearly displays the above groupings and the low value of stress (0.05) indicates the good quality of the representation (Fig. 6B). The same analysis performed on the average biomass of ascidians, which presents the highest number of

species, provide similar results with increased discriminating power (Fig. 7). In fact, the separation between TCH, TSO and RWR, BMI occurred at a similarity level of 7%, while all four stations are distinct groups at a value of 39%. Also in this case, the MDS plot gives a clear image of the above groupings with low stress (0.08).

IV. Typical and discriminant species

In light of the results of multivariate analyses, we tried to better distinguish the stations by determining the typical and discriminant species. The results of these analyses are shown in Table 5. The highest values of similarity within a group were shown by RWR and TSO and the lowest by BMI (Table 5A). *Polycitor adriaticus* (see Fig. 9) is a typical species in both TCH and TSO while *Ostrea edulis* is typical in RWR and BMI. It is interesting to note that *Polycitor adriaticus* also is a discriminant species in four comparisons out of six (Table 5B). This is because this colonial ascidian is able to live, on natural substrata, in both clear and cloudy waters. Table 5B shows that the highest dissimilarity resulted from comparisons between stations with natural and artificial substrata. The most dissimilar stations were TSO and BMI, and those display the highest and lowest turbidity and Shannon diversity indices. In the two stations with a bioconstructed bottom, TCH and TSO, the discriminant species belong to porifera and ascidiacea, and are present only at TSO (Fig. 9).

Discussion

Our data clearly separate the communities on the natural substrata (TCH and TSO) from those on artificial ones (RWR and BMI). However, this separation in two groups is probably not exclusively due to the nature, age or slope of

Table 4. Biomass (Ash Free Dry Weight, AFDW) and energy values in the four stations. Mean values ± 95% confidence intervals are given.

Tableau 4. Biomasse (poids sec sans cendres, AFDW) et valeurs énergétiques dans les quatre stations. Les moyennes ± les limites de confiance (95 %) sont données.

Stations Taxa	TSO (n = 13)		TCH (n = 21)		RWR (n = 15)		BMI (n = 15)	
	g AFDW m ⁻²	kJ m ⁻²	g AFDW m ⁻²	kJ m ⁻²	g AFDW m ⁻²	kJ m ⁻²	g AFDW m ⁻²	kJ m ⁻²
Porifera	95.45 ± 32.13	2183.00 ± 735.00	8.52 ± 5.31	194.90 ± 121.50	35.10 ± 16.21	802.70 ± 370.8	8.34 ± 4.98	190.7 ± 113.8
Anthozoa	0	-	0.80 ± 1.35	-	2.55 ± 1.24	-	0.77 ± 0.81	-
Gastropoda	0.05 ± 0.08	1.15 ± 1.83	0.07 ± 0.09	1.56 ± 2.17	6.83 ± 5.41	159.00 ± 125.9	9.98 ± 10.47	232.2 ± 243.8
Bivalvia	4.55 ± 3.57	103.70 ± 81.33	16.78 ± 13.31	382.40 ± 303.20	228.40 ± 77.92	5205.00 ± 1776.0	375.30 ± 170.4	8553.0 ± 3884.0
Annelida	0	-	0.55 ± 0.34	-	0.39 ± 0.30	-	1.39 ± 0.73	-
Crustacea	0.16 ± 0.19	3.71 ± 4.36	0.11 ± 0.10	2.55 ± 2.42	0.02 ± 0.02	0.42 ± 0.46	0.83 ± 0.64	19.0 ± 14.4
Echinodermata	15.32 ± 6.97	348.50 ± 158.60	4.99 ± 2.39	113.40 ± 54.30	5.32 ± 6.55	121.00 ± 149.3	0.03 ± 0.06	0.6 ± 1.3
Ascidiacea	79.19 ± 29.52	1780.00 ± 671.00	42.87 ± 9.22	998.90 ± 215.40	66.97 ± 23.80	1317.00 ± 468.0	39.25 ± 13.13	71.7 ± 257.8
Others	0.08 ± 0.12	-	0.01 ± 0.014	-	0.32 ± 0.68	-	0.03 ± 0.04	-
Total	194.80 ± 32.04	4420.00 ± 730.00	74.70 ± 16.68	1694.00 ± 382.00	345.90 ± 72.60	7605.00 ± 1644.0	435.90 ± 172.30	9767.0 ± 3917.0

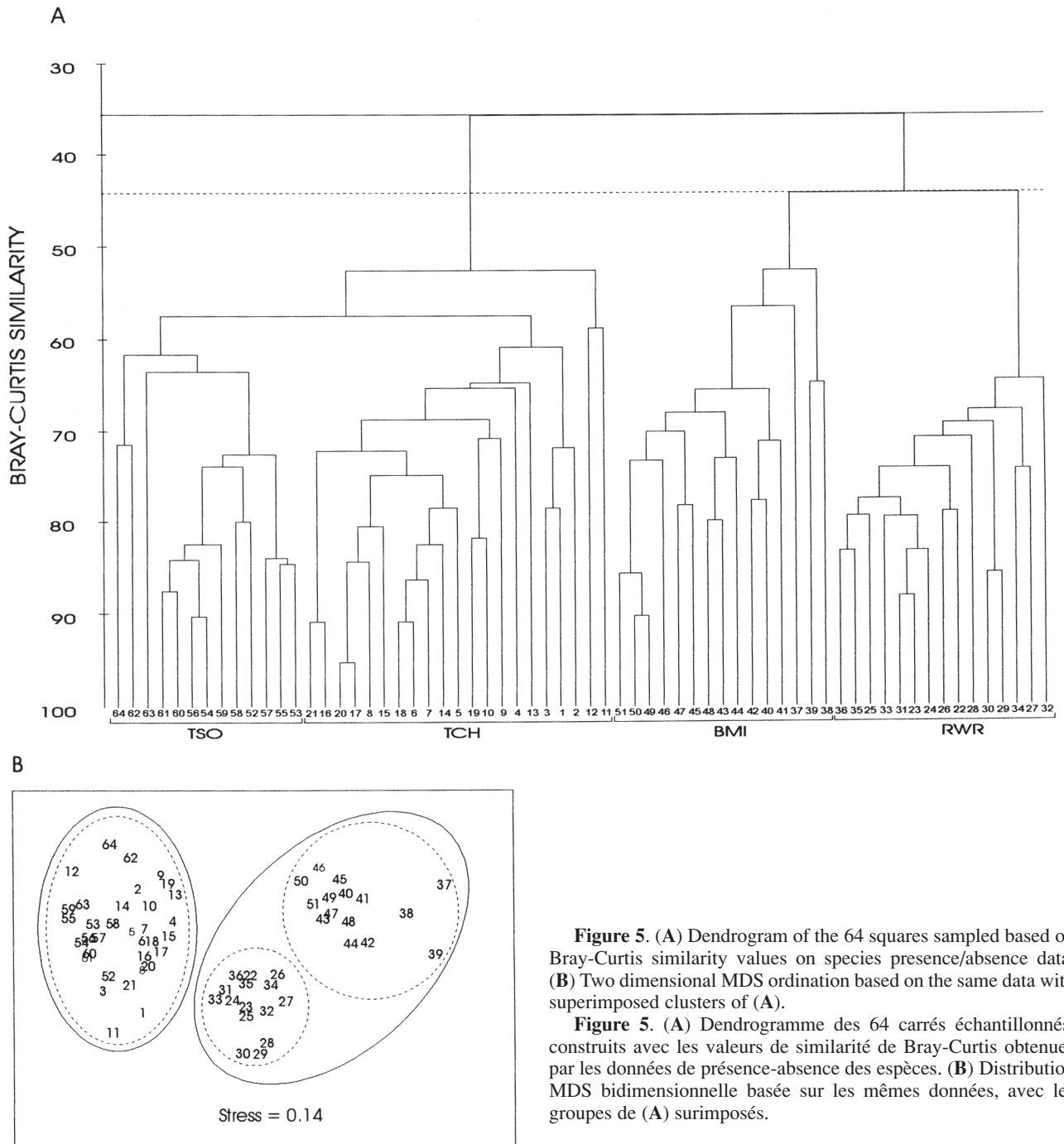


Figure 5. (A) Dendrogram of the 64 squares sampled based on Bray-Curtis similarity values on species presence/absence data. (B) Two dimensional MDS ordination based on the same data with superimposed clusters of (A).
Figure 5. (A) Dendrogramme des 64 carrés échantillonnés, construits avec les valeurs de similarité de Bray-Curtis obtenues par les données de présence-absence des espèces. (B) Distribution MDS bidimensionnelle basée sur les mêmes données, avec les groupes de (A) surimposés.

the substrata but to other environmental factors. At the RWR station, organisms live on a naval wreck. Relini & Relini Orsi (1971-72) showed that the settlement of a biotic community on ferrous scrap is not limited by the toxicity of the metal but rather by the desquamation of the scrap itself as a consequence of oxidation. However, these authors underlined that processes on these substrata may be more rapid than in naval wrecks which were built to resist marine

corrosion. Indeed, in these latter cases the growing of a biotic community may slow down the destructive process. The fact that the substrata were artificial was even less important in the case of BMI which was represented by concrete structures, generally regarded as non-toxic and, on the contrary, are considered one of the best substrates for colonization by hard substrate flora and fauna (Leewis et al., 1989). From Table 1 we can see that our stations were

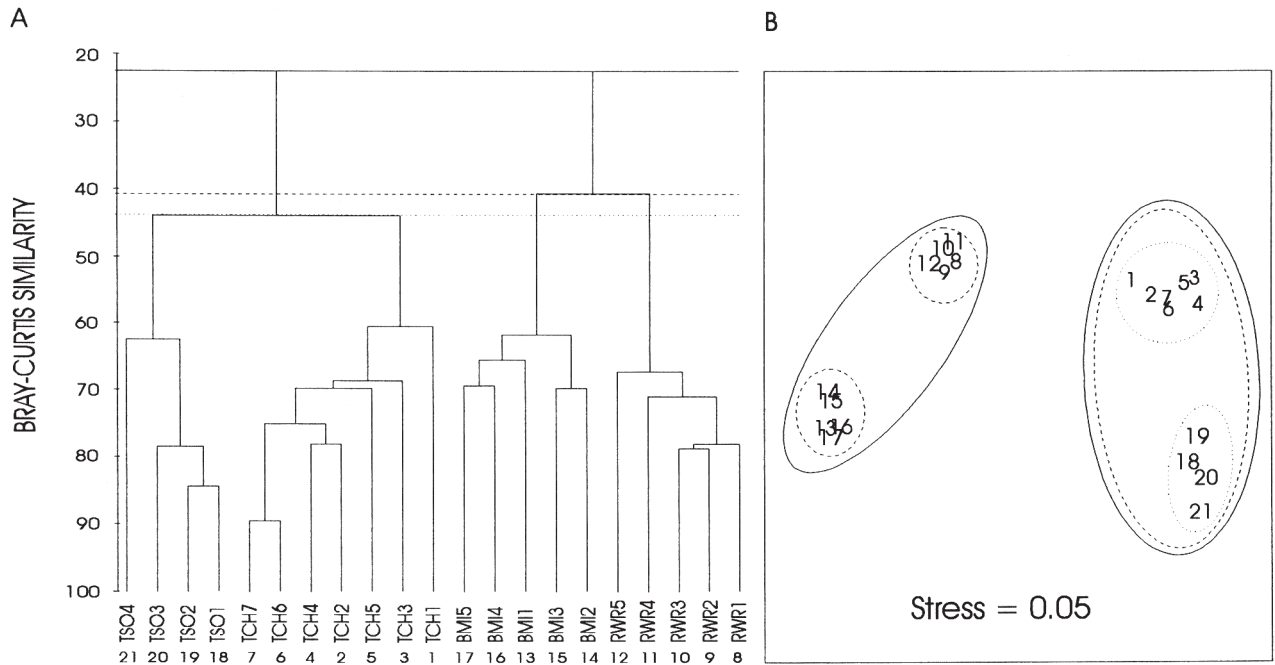


Figure 6. (A) Dendrogram for hierarchical clustering of the 21 samplings, using Bray-Curtis similarities, calculated on double root transformed mean biomass values. (B) Two dimensional MDS ordination based on the same data with superimposed clusters of (A).

Figure 6. (A) Dendrogramme des 21 échantillonnages, basé sur les valeurs de similarité de Bray-Curtis établies avec les moyennes de biomasse transformées en double racine carrée. (B) distribution MDS bidimensionnelle basée sur les mêmes données, avec les groupes de (A) surimposés.

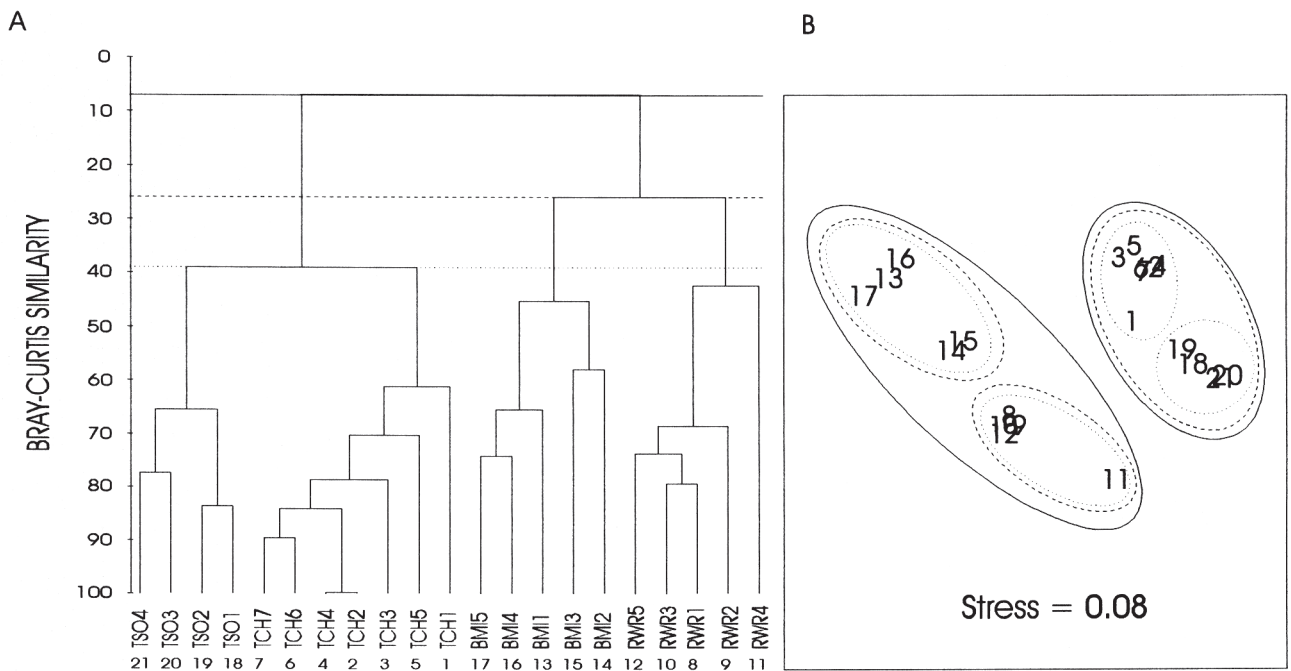


Figure 7. (A) Dendrogram for hierarchical clustering of the 21 samplings, using Bray-Curtis similarities, calculated on double root transformed mean biomass values of ascidians. (B) Two dimensional MDS ordination based on the same data with superimposed clusters of (A).

Figure 7. (A) Dendrogramme des 21 échantillonnages, basé sur les valeurs de similarité de Bray-Curtis établies avec les moyennes de biomasse des ascidies transformées en double racine carrée. (B) distribution MDS bidimensionnelle basée sur les mêmes données, avec les groupes de (A) surimposés.

Table 5. (A) Breakdown of average similarity (\bar{S}) within individual stations and contributions (\bar{S}_i) from each species. **(B)** Breakdown of average dissimilarity ($\bar{\delta}$) between pairs of stations and contributions ($\bar{\delta}_i$) from each species. The list of species is only partly given. In the last column, on the right, the station in which the discriminant species is present or more abundant is indicated.

Tableau 5. (A) Répartition de la similarité moyenne (\bar{S}) entre les stations individuelles et contributions (\bar{S}_i) des espèces dans les diverses stations. **(B)** Répartition de la dissimilarité moyenne ($\bar{\delta}$) entre couple de stations, et contributions ($\bar{\delta}_i$) des espèces. La liste des espèces n'est donnée qu'en partie. Dans la colonne de droite, la station où l'espèce discriminante est présente, ou plus abondante, est indiquée.

A	Typical species	\bar{S}_i	\bar{S}_i SD(S_i)	$\Sigma \bar{S}_i$ %	
_ TCH (S = 66.15)	<i>Rocellaria dubia</i>	9.2	7.63	14.0	
	<i>Polycitor adriaticus</i>	9.2	7.63	27.9	
	<i>Pomatoceros triqueter</i>	9.2	7.63	41.9	
	<i>Ophiotrix sp.</i>	7.3	2.03	52.9	
	<i>Serpula vermicularis</i>	6.9	1.59	63.4	
_ TSO (S = 70.49)	<i>Hiatella artica</i>	6.5	1.59	73.3	
	<i>Polycitor adriaticus</i>	6.9	8.15	9.8	
	<i>Rocellaria dubia</i>	6.9	8.15	19.6	
	<i>Balanus sp.</i>	6.9	8.15	29.4	
	<i>Serpula vermicularis</i>	6.9	8.15	39.2	
_ RWR (S = 71.39)	<i>Pomatoceros triqueter</i>	6.9	8.15	49.0	
	<i>Hiatella artica</i>	5.7	2.25	57.0	
	<i>Ostrea edulis</i>	5.7	12.09	7.9	
	<i>Arca noae</i>	5.7	12.09	15.9	
	<i>Pomatoceros triqueter</i>	5.7	12.09	23.8	
_ BMI (S = 63.50)	<i>Ophiotrix sp.</i>	5.7	12.09	31.7	
	<i>Balanus sp.</i>	5.7	12.09	39.6	
	<i>Dysidea</i>	5.7	1.67	45.5	
	<i>Aplidium elegans</i>	4.7	2.37	7.4	
	<i>Ostrea edulis</i>	4.7	2.37	14.8	
B	<i>Balanus sp.</i>	4.6	2.38	22.1	
	<i>Eunice aphroditois</i>	4.6	2.42	29.3	
	<i>Pomatoceros triqueter</i>	4.0	1.65	35.5	
	<i>Hinia incassata</i>	4.0	1.63	41.7	
RWR vs TCH ($\bar{\delta}$ = 54.03)	<i>Polycitor adriaticus</i>	3.5	2.69	6.49	TCH
	<i>Ostrea edulis</i>	3.0	2.37	12.1	RWR
	<i>Sagartia elegans</i>	3.0	2.45	17.6	TWR
	<i>Microcosmus vulgaris</i>	2.9	2.16	23.0	RWR
	<i>Shizoporella errata</i>	2.84	1.95	28.3	RWR
	<i>Mytilus galloprovincialis</i>	2.55	1.62	33.0	RWR
BMI vs TCH ($\bar{\delta}$ = 54.03)	<i>Polycitor adriaticus</i>	3.42	6.94	4.9	TCH
	<i>Aplidium elegans</i>	3.07	2.62	9.3	BMI
	<i>Mytilus galloprovincialis</i>	2.94	2.36	13.5	BMI
	<i>Microcosmus polymorphus</i>	2.93	2.36	13.7	BMI
	<i>Ophiotrix sp.</i>	2.91	2.26	21.9	TCH
	<i>Rocellaria dubia</i>	2.82	1.91	25.9	TCH
BMI vs RWR ($\bar{\delta}$ = 55.71)	<i>Arca noae</i>	2.77	8.53	5.0	RWR
	<i>Ophiotrix sp.</i>	2.61	3.42	9.7	RWR
	<i>Aplidium elegans</i>	2.59	3.39	14.3	BMI
	<i>Modiolus barbatus</i>	2.38	2.43	18.6	RWR
	<i>Sagartia elegans</i>	2.38	2.43	22.8	RWR
	<i>Hinia incassata</i>	2.13	1.77	26.7	BMI
TSO vs TCH ($\bar{\delta}$ = 43.36)	<i>Chondrosia reniformis</i>	3.34	2.21	7.7	TSO
	<i>Phallusia fumigata</i>	2.69	1.46	13.9	TSO
	<i>Distaplia sp.</i>	2.66	1.46	20.0	TSO
	<i>Mycale massa</i>	2.31	1.24	25.4	TSO
	<i>Cystodites dellechiaiei</i>	2.13	1.06	30.3	TSO
	<i>Aplidium conicum</i>	2.12	1.07	35.1	TSO
TSO vs RWR ($\bar{\delta}$ = 61.28)	<i>Ostrea edulis</i>	3.11	9.54	5.1	TWR
	<i>Polycitor adriaticus</i>	3.11	9.54	5.1	RWR

<i>Modiolus barbatus</i>	2.67	2.45	14.5	RWR	
<i>Sagartia elegans</i>	2.67	2.45	18.9	RWR	
<i>Chondrosia reniformis</i>	2.63	2.25	23.1	TSO	
<i>Schizoporella errata</i>	2.52	1.94	27.3	RWR	
TSO vs BMI ($\bar{\delta}$ = 74.91)	<i>Polycitor adriaticus</i>	3.04	7.27	4.1	TSO
	<i>Aplidium elegans</i>	2.85	3.28	7.9	BMI
	<i>Ostrea edulis</i>	2.84	3.28	11.6	BMI
	<i>Eunice aphroditois</i>	2.79	3.37	15.4	BMI
	<i>Mytilus galloprovincialis</i>	2.62	2.37	18.9	BMI
	<i>Microcosmus polymorphus</i>	2.61	2.37	22.3	BMI

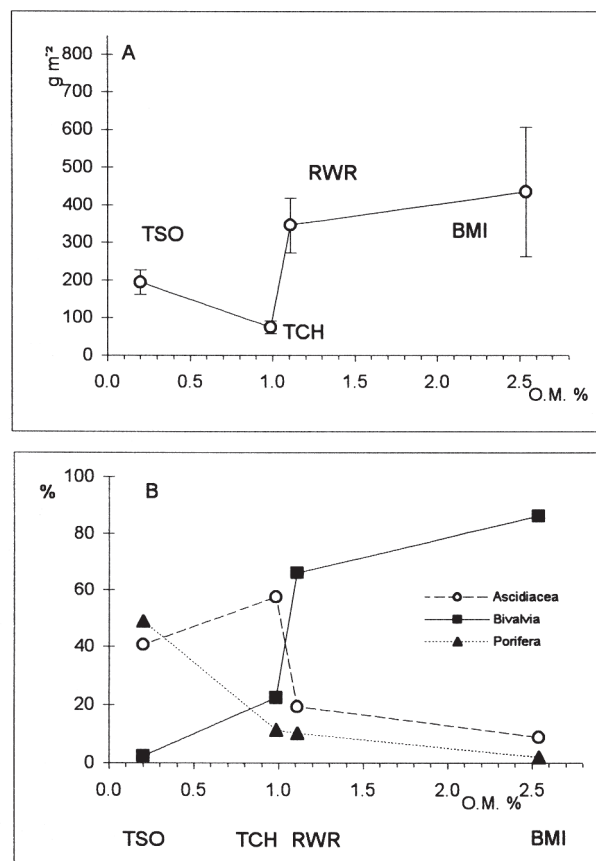


Figure 8. (A) Biomasse totale dans les quatre stations (g AFDW m⁻²); les moyennes sont indiquées en fonction de la teneur en matière organique des sédiments (les barres verticales indiquent les intervalles de confiance à 95 %). **(B)** contribution en pourcentage des principaux taxons à la biomasse totale en fonction de la teneur en matière organique (O.M.) des sédiments.

Figure 8. (A) Biomasse totale dans les quatre stations (g AFDW m⁻²); les moyennes sont indiquées en fonction de la teneur en matière organique des sédiments (les barres verticales indiquent les intervalles de confiance à 95 %). **(B)** contribution en pourcentage des principaux taxons à la biomasse totale en fonction de la teneur en matière organique (O.M.) des sédiments.

surrounded by different kinds of sediment: TSO was sandy with relatively low organic content, BMI was muddy with a high percentage of organic matter and TCH and RWR were intermediate. Such differences may be due to different

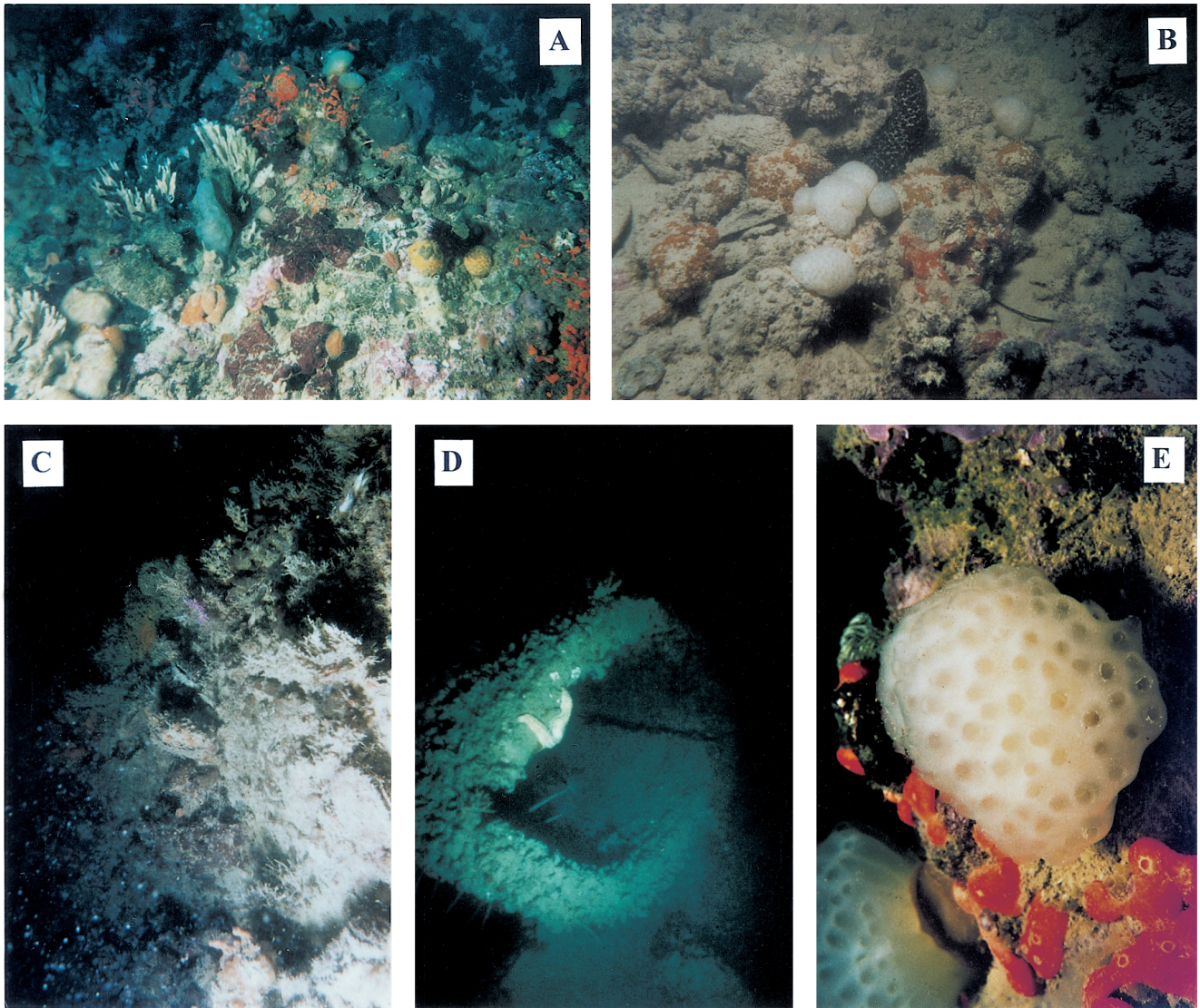


Figure 9. (A) TSO station (ca. 23 m depth), view of the outcrop in relatively clear water. (B) TCH station (ca. 21 m depth), note the surface of the outcrop largely covered by a muddy layer. The white roundish bodies are colonies of the ascidian *Polycitor adriaticus*. In the middle, the black body of *Holothuria tubulosa*. (C) RWR station (ca. 17 m depth), subvertical wall of the hull with abundant presence of bivalves. (D) BMI station (ca. 15 m depth), a concrete element making up the barrier. (E) macrophotograph of colonies of *P. adriaticus*, the dominant species at the TCH station; the encrusting orange colonies belong to another ascidian genus *Didemnum*.

Figure 9. (A) : station TSO (profondeur ca. 23 mètres), une roche sublittorale dans une eau relativement claire. (B): station TCH (ca. 21 mètres). On remarque la surface de la roche couverte d'une couche vaseuse ; les corps blancs et ronds sont des colonies de l'ascidie *Polycitor adriaticus*. Au milieu, le corps noir d'*Holothuria tubulosa*. (C) station RWR (ca. 17 mètres), paroi presque verticale de la coque de l'épave avec plusieurs bivalves. (D) station BMI (ca. 15 mètres), un élément de béton constituant la barrière. (E) macrophotographie de colonies de *P. adriaticus*, l'espèce dominante dans la station TCH; l'autre colonie encroûtante de couleur orange appartient à l'ascidie du genre *Didemnum*.

hydrodynamic conditions, however, as the strength of the current was not very different in the four stations, fluctuating around a mean value of 10 cm sec⁻¹ (Mosetti, 1983), they must be ascribed to the sedimentation rate. This was obviously related to the water turbidity and to the wave exposure and the two factors can exert a strong influence on

the biotic communities. The high turbidity at RWR and BMI had a strong positive influence on the biomass (Fig. 4), since the suspended particles are an energy input to the environment. In particular, turbidity (represented in Fig. 8 by the percentage of organic matter in the sediment) increased the percentage of the biomass of bivalvia while

the effect is opposite on porifera and ascidiacea. These variations in biomass were generally due to a change in relative abundance more than in diversity (Table 2). At RWR and BMI *Mytilus galloprovincialis* and *Ostrea edulis* were dominant and, as a consequence of their large size, responsible for the high biomass values of bivalvia. For ascidiacea, increases in turbidity resulted in an increase in the number of solitary species to the detriment of colonial ones. This was probably due to the delicacy of the filter of the colonial species in comparison with the solitary ones. Among porifera, *Chondrosia reniformis* was exclusively present in the relatively clear waters of the TSO station and *Cliona celata* in the cloudy ones at BMI, however for this taxon we could also observe a reduction in diversity with increasing turbidity rates. This confirms the observations of Leewis & al. (1994) of a decrease in sponges in a Dutch estuary as a consequence of increased sedimentation due to the construction of a storm-surge barrier. Obviously these differences are related to specific anatomical and physiological differences.

In Fig. 8, the standing crop at TCH was lower than both at RWR, which had a very similar energetic input, and at TSO where turbidity was clearly much lower. To explain this situation we must consider another factor, the slope of the substrate. At RWR and BMI, the communities were settled on subvertical surfaces. On the contrary, the outcrops at TSO and TCH were almost horizontal. Clearly under these different conditions the sedimentation rate's effect on the community structure is fundamental. On a horizontal surface, a high sedimentation rate can both bury the organisms and prevent settlement. Hence, the most important feature modelling the communities was a combination of sedimentation and the inclination of the substrate. A particular example for such a situation is that of the ascidian population at TCH, where high sedimentation is associated with horizontal substrata. Here the number of species (9) was not much smaller than in other stations (from 11 to 15), but a single species, *Polycitor adriaticus*, represented 97% of the biomass.

Lastly we would like to compare the recorded biomass value with those reported for other similar environments. Concerning the area studied, we have to compare our values with the biomass values of infauna plus epifauna measured in the Gulf of Trieste by Orel & Mennea (1969) and with those of the macro-epibenthic communities measured in the Adriatic Sea by Fedra et al. (1976) on soft bottoms defined "fonds sablo-détritiques plus ou moins envasés" by Gamulin-Brida (1974). The mean biomass values recorded by these authors amounted to 166 and 370 g m⁻² of wet weight, respectively. These are much lower values than ours which ranged from 1295 to 3352 g m⁻² (in this computation of wet weight we applied to the shells of heavy molluscs the same correction factor of one-third as done by Fedra et al.

(1976)). It is more interesting to compare the results of the present work with those obtained by Leewis & Waardenburg (1990) and Leewis et al. (1994) who, in the Oosterschelde estuary (SW Netherlands), found on a storm surge barrier represented by irregular concrete blocks a mean value of 327 g AFWD m⁻². This is a much higher value than those in TCH and TSO but lower than those obtained in RWR and BMI (Table 4). The Oosterschelde estuary and the northern Adriatic are comparable in depth, but in the case of the Dutch site, turbidity is probably less than in our area, as indicated by the high number of algae (30% of the total species) and the prevalence of sponges over ascidians (Leewis & Waardenburg, 1990).

In short, the hard bottom communities of the northern Adriatic Sea were characterized by a high biomass of filter-feeding organisms, but, for natural substrata (which are the majority), paradoxically the highest values were present where the input of suspended organic matter was lower. That is due to the slight slope of the substratum which facilitates the sedimentation of particles and, as a consequence, prevents larval settlement. Because of the high number of ecological niches, these communities provide protection and nursery sites for many animals, some with a particular commercial value (i.e. *Homarus gammarus*). The number of the outcrops in the basin considered is still unknown but from a preliminary survey we have carried out among fishermen and divers, we believe that they may be more than a few thousand. The dominance in these communities of filter-feeding, among species of medium and large size (i.e. *Tethya* sp., *Dysidea* sp., *Ostrea edulis*, *Polycitor adriaticus*, *Microcosmus vulgaris*), made them strong energy storers able to transfer this energy as detritus, during periods of minor energetic input, to the surrounding environment. This concept of a "buffer" already proposed by Fedra et al. (1976, p. 144) for the epibenthic communities of filter-feeding animals of soft bottoms is, in our opinion, even more valid for the hard bottom communities which show higher biomass values. Moreover, these communities may have another function in addition to that of "buffer". Such a large quantity of filter-feeding animals is able to produce a lot of faecal pellets which in terms of size are intermediate between the suspended (and then sedimented) particles used by limivores and those used by macrofaunal invertebrates. This is an interesting hypothesis which should be analysed further.

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