Quantitative sampling of soft-bottom macroepifauna for assessing the benthic system in the Bay of Brest (France)

Epibenthos
Sampling method
Quantitative distribution
Microhabitats
Trophic web

Épibenthos
Méthode d'échantillonnage
Distribution quantitative
Microhabitats
Réseau trophique

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ABSTRACT

Macroepifauna of mixed sediments was quantitatively studied at three stations in the Bay of Brest. Samples were collected with the quantitative video dredge *Aquareve II*. Sampling performance varied from 6.1 to 55.6 m^2 according to the mesh diameter of the net (10, 40, and 70 mm) and the quality and quantity of the hard structures lying on the bottom. The efficiency of the different sampling options is tested. The ecological analysis shows differences between epifaunal assemblages, which are mainly explained by the characteristics of the ruggedness in each station. Ruggedness is defined in terms of quality and quantity of hard structures (pebbles, gravels, shells, coraline algae and macroalgae) lying on the sediment surface. Hard substrates act as microhabitats to the epifauna, providing sites for settlement to many suspension feeders and shelter to vagile predators, particularly brachyuran decapods. The contribution of quantitative epifaunal data to overall modelling of benthic trophic food webs is later discussed.

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RÉSUMÉ

Échantillonnage quantitatif de la macroépifaune des sédiments meubles pour comprendre le fonctionnement du système benthique en rade de Brest (France)

La macrofaune épibenthique des sédiments hétérogènes a été étudiée dans trois stations de la rade de Brest. Les échantillons ont été prélevés avec le traîneau-drague quantitatif *Aquareve II*. Les surfaces échantillonnées varient de 6,1 à 55,6 m^2 selon la maille utilisée sur le filet de la drague et la nature et l'abondance des substrats durs dispersés à la surface du sédiment (galets, graviers, coquilles, maërl, macrophytes). L'efficacité des différentes options d'échantillonnages est testée. L'analyse écologique met en évidence des différences faunistiques entre les trois stations, expliquées essentiellement par les caractéristiques de la rugosité du sédiment à chaque station. La notion de rugosité est définie par plusieurs paramètres tels que la nature des substrats durs (coquilles, graviers, algues...), la hauteur, la surface couverte ou l'abondance de ces microépibiotopes. Ceux-ci jouent un rôle de support pour de nombreuses espèces suspensivores et un rôle d'abri pour les prédateurs vagiles (notamment les crustacés brachyoures). L'apport de données quantitatives sur l'épifaune des substrats meubles dans les modèles de réseau trophique benthique est discuté.

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INTRODUCTION

Ecological studies of the macrozoobenthos are classically divided in two categories based on the habitat type: hard bottom or soft bottom. Generally, the mixture of hard microsubstrates on a soft-bottom sediment surface has escaped benthic investigations. These microhabitats are generally created by biogenic structures such as shells or coralline algae, but also by cobbles and boulders. They are used as supports by sessile fauna (sponges, ascidians, molluscans) and as refuges by vagile fauna (crustaceans, polychaetes, echinoderms; Hily, 1989; Hily and Le Foll, 1990). A trophic web can be identified which enhances the links between epifauna and infauna of soft sediments. Many epifaunal vagile taxa prey on infaunal organisms (Feder and Pearson, 1988). Many epifaunal sessile taxa are suspension feeders which produce faecal pellets exploited by infaunal deposit feeders. The primary aim of this paper is to study the ecological role of epifauna in soft-bottom ecosystem. First, a definition of a methodology for the quantitative study of epifaunal habitats and organisms is provided. Next, the ecological variability of epifauna and infauna, and the environmental factors, were studied in three sites of the Bay of Brest. Finally, the consequences of the results for our understanding of soft-bottom trophic webs are discussed.

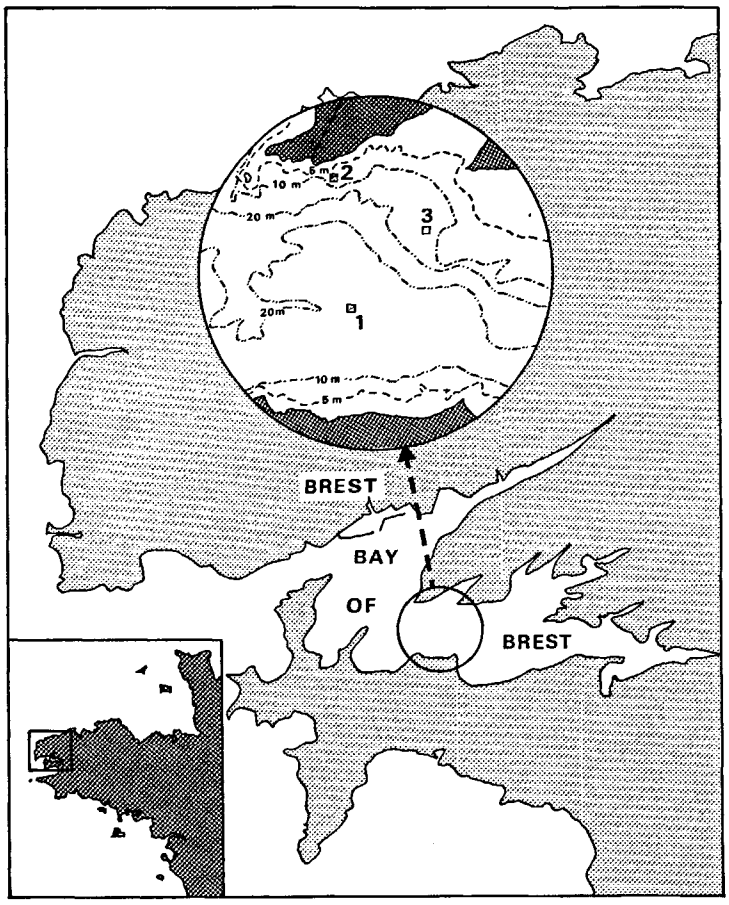


Figure 1

Location of the sampling stations in Bay of Brest.

Localisation des stations d'échantillonnage en rade de Brest.

Until recently, technical problems of sampling prevented the consideration of epifauna in most quantitative soft-bottom benthic studies (McIntyre *et al.*, 1970). Most of macrofaunal epibenthic taxa belong to the large macrofauna (> 10 mm) as defined by Grassle *et al.* (1975). These taxa generally show high individual biomass, and low abundances (often < 1 individual per square metre), and cannot be sampled quantitatively by grabs, *i.e.* the Smith-McIntyre grab (0.1 m^2 sampling unit) or the Baird grab (0.5 m^2 sampling unit). Since the size of sampling units should be adjusted to the spatial distribution of organisms (Elliott, 1977), a method capable of sampling more than 5 m^2 would have to be employed. Previous studies of soft-bottom epifauna are rare and most of them were qualitative or semi-quantitative studies using dredges or small beam trawls such as the Agassiz trawl (Pearson and Eleftheriou, 1981; Feder and Pearson, 1988; Basford *et al.* 1989). Photography and video recording are useful methods to estimate abundances but are limited by the size of organisms (Cabioch, 1967; Rice *et al.*, 1979); 25 to 30 mm is the lower size of organisms which can be quantitatively counted on video tapes (Mason *et al.*, 1983). The *Aquareve* sampling technique (Thouzeau and Hily, 1986) permits the quantitative sampling of replicates larger than 1 m^2. This method associates dredging and underwater video-taping. The dredging function is monitored with a video system, to avoid overfilling of the dredge collector. The towed distance is measured by an odometric wheel.

The *Aquareve II* system has been previously used to study the ecology of juveniles of the scallop *Pecten maximus* (Thouzeau and Lehay, 1988; Thouzeau, 1989); the method had to be adapted to the aims of that work. For the present study, some technical questions had to be adressed, *i.e.* what was the best mesh size to quantitatively sample the large epifauna of soft-bottom sediments partially covered with various types of coarse epibiotopes? Was this sampling really complementary to classical sampling by, *e.g.*, the Smith-McIntyre grab, in describing the soft-bottom community?

Study site

The Bay of Brest (48°20'N - 4°30'W) is a sheltered area of 180 km^2 in the extreme west of Europe (Fig. 1), in which fertilization by nutrient inputs from the land induces high levels of primary production (Tréguer and Quéguiner, 1989). The high energetic flow from pelagic production is exploited by the benthic system and particularly by suspension-feeding taxa which attain high biomass (Hily, 1991). This author has described the extensive development of epibenthic fauna on soft-bottom sediments in the area. In the present study, three stations were selected, in three types of mixed sediments which occupy most of the surface of the bay (Hily, 1989).

Station 1 was located in one of the deepest areas of the bay (22 m). The sediment there was of coarse sand-shell (median grain size ≈ 500 µm), poorly sorted and containing 15 to 20 % silt (fraction < 63 µm) and 3 to 4 % organic matter. At the sediment surface, scattered empty shells and gravels (percentage cover = 30 to 40 %) provided many refuges and supports for benthic macrofaunal taxa. The bivalve *Glycymeris glycymeris* was the main species providing shells as habitats, both because of its abundance and because for years after the death of the animal, the two valves remain half opened and fixed by the hinge (Hily, 1989). In this zone, tidal currents ranged between 0.2 and 1 $m.s^{-1}$.

Station 2 was located at the edge of a muddy bank and slope (7 m). The sediment there was mixed sand (median grain size ≈ 300 µm), poorly sorted, and containing 15 to 20 % silt, and about 7 % organic matter. Tidal currents ranged from 0.1 to 1.5 $m.s^{-1}$; the bottom was partly overlaid by beds of the coralline algae *Lithothamnion corralioides* (% cover = 80 %) and by scattered empty molluscan shells which supported numerous erected macroalgae (% cover = 95 %).

Station 3 was located at the top of a slope (12 m) where the sediment was of sandy heterogeneous mud (median grain size ≈ 250 µm), poorly sorted, containing biogenic chips, 40 % pelitic fraction and 5 to 8 % organic matter. Tidal currents ranged between 0 and 2 $m.s^{-1}$. On this sediment, dead and living *Crepidula fornicata* shells of % cover = 50 % were the only supports and refuges for sessile fauna and vagile epibenthic taxa respectively (Hily, 1989).

MATERIAL AND METHODS

Sampling

Epifauna

The *Aquareve II* technique has been previously described in several studies (Thouzeau and Hily, 1986; Thouzeau and Lehay, 1988; Thouzeau, 1989). The *Aquareve II* is a video-monitored sled-dredge which collects epifauna and the first centimetres of sediment. The gear can be fitted with various collecting bags. An odometer gives a precise estimate of the tow length. The camera, connected to a video monitor on board, is oriented towards the opening of the bag, allowing control of dredging efficiency during the tow.

The *Aquareve II* sled-dredge was successively equipped with three bags of different mesh size (net with 10 mm square mesh and steel bags with 40 and 70 mm rings) to define the best size fitted to the structure of the sediment surface and associated epifauna in each station. Different mesh sizes led to different sample sizes, the latter inducing variations in quality and quantity of the retained fraction (alive or not) in the net of the dredge. In March 1989, three random samples were collected with each mesh size at each station. On board, samples were sieved on a 10 mm mesh. The retained material was fixed in a 7 % formalin-seawater mixture. In the laboratory, animals were sorted, identified to the highest possible taxonomic level, and counted and weighted, thus permitting an estimation of species richness (S) abundance (A) and biomass (B). Samples obtained with a Smith-McIntyre grab (sampling surface = 0.1 m^2) were used for grain analysis and determination of silt/clay content.

Infauna

During the same cruise at each station, ten 0.1 m^2 Smith-McIntyre grab samples were collected (Benabid, unpublished) to study the infauna of the three stations.

Data processing

Distinction between taxa sampled quantitatively and qualitatively

The *Aquareve II* system samples only the first centimetres of the sediment; consequently it does not sample the infauna quantitatively. Thus, infaunal taxa were first removed from the total list of fauna used in the quantitative analysis. For epibenthic taxa, the decision was made to eliminate the smallest species which should have escape the dredge because of their small adult size (< 10 mm), *i. e.* inferior to the smallest mesh opening used in this study. A total list of 68 large epibenthic taxa was then obtained (Tab. 3).

Abundance, biomass and diversity

Abundance ($ind.m^{-2}$) and biomass ($g.m^{-2}$) per sample were estimated for each taxon. Biomass ($g.m^{-2}$) is the total dry weight (DW; precision of 0.01 g), after the organisms were dried 48 h at 60°C. Except for *Porcellana longicornis*, the biomasses of all decapod crustaceans were grouped together.

Diversity was calculated from abundance data, using the Shannon-Wiener index (H'; Daget, 1979).

In order better to define the energetic contribution of each group to the total community structure, biomasses were then expressed in carbon equivalents ($g\ C.m^{-2}$) using conversion factors from Rumohr *et al.* (1987) and Steele (1974). Taxa of the same trophic group were then grouped together, allowing the elaboration of a global trophic web diagram of the benthic system.

Assessment of the influence of mesh size and sampling surface on specific abundances and biomass

In order to detect a significant influence of the mesh size, abundances of taxa between samples were compared using a two-way ANOVA (F test). An *a posteriori* Newman-Keuls test was used when a significant difference was detected.

Ecological analysis

The matrix of abundances was processed through multivariate analysis [Correspondence Analysis (CA),

Lebart *et al.*, 1982]. The CA is an ordination analysis carried out from the centre of gravity (chosen as origin) of the points (Chardy *et al.*, 1976) and which can locate each sample and taxa in relation to all the others.

Indexed environmental factors (Hily, 1989) characterizing each station were additional lines of the matrix and identified on the CA graph: percentage of the sediment surface covered by dead and living *Crepidula fornicata* shells (code from 0 to 5: 1 = 1 to 20 %..., 5 = 81 to 100 %); pelitic fraction of the sediment surface (code 0 to 4); height of epibiotic and abiotic structures raised off the sediment surface [code from 0 to 6: 1 = 1 to 5 cm..., 6 > 20 cm (large macrophytes)]; percentages of the sediment surface respectively covered with coralline algae *Lithothamniom corallioides*, erected algae, gravels and/or pebbles (diameter: 2 to 20 cm) were coded from 0 to 5 (1 = 1 to 20 %..., 5 = 81 to 100 %).

RESULTS

Samples size

Structural variability of the sediment surface in each station can explain the observed differences of the sampled surface between stations and between mesh sizes (average sampled surface varied from 6.1 to 46.8 m^2; Tab. 1).

- With mesh 10 mm, no significant difference (Newman-Keuls test; $p > 0.05$) was observed between stations. The collectors were filled up rapidly with gravels/pebbles + *Glycymeris* shells in station 1, *Lithothamniom* + Macroalgae in station 2 and *Crepidula fornicata* shells in station 3.

- For mesh 40, no significant difference (Newman-Keuls test; $p > 0.05$) was observed between stations 1 and 2. In station 3 most of the *Crepidula fornicata* chains did not pass the mesh and the dredge was filled rapidly.

- For mesh 70, the surface sampled was maximum at station 3 because almost all the *Crepidula fornicata* chains passed the mesh, while there were not enough pebbles and cobbles to fill up the dredge. In contrast, the surface quantitatively sampled in station 2 was reduced because macroalgae progressively jammed the steel bag rings.

Sampling efficiency

Each station can be considered as being sampled with four types of samplers: *Aquareve II* mesh 10, *Aquareve II* mesh 40, *Aquareve II* mesh 70, and Smith-McIntyre grab (mesh 1). The total number of collected taxa varied considerably from one type of sampler to the other (Tab. 2). Using mesh 70, the number of taxa collected was much smaller than with the meshes 40 and 10 (less than 50 %), though the sample size was greater. Using mesh 70, most of the epibionts, gravels, shells and sediment in the three studied stations passed the mesh. Consequently, the data obtained with this mesh size have not been used for the further ecological analysis of the areas studied.

Likewise, the Smith-McIntyre grab is a suitable sampler for the infauna but is not suited to global sampling of the soft-bottom communities, even when ten samples were collected per station. Data obtained with the *Aquareve II* sampler (meshes 10 and 40) have been used only for the quantitative analysis of large epibenthic communities, and infaunal and small epibenthic (< 10 mm) organisms have been discarded. Sixty-eight taxa were finally considered for the quantitative analysis of the epifaunal assemblages, 63 others in the quantitative analysis of the infaunal assemblages, and 27 taxa were discarded in the epifaunal analysis, because they were too small or were not sampled by the grab.

Table 1

Sampling performances of Aquareve II *according to mesh diameter of the net in the three stations, sediment grain size, and surface sediment characteristics. In brackets: abbreviations and code of these parameters as mentioned in CA (see text and Fig. 2).*

Performances d'échantillonnage de l'*Aquareve II* selon la maille de filet utilisée dans les trois stations, nature granulométrique du sédiment et caractéristiques de la surface sédimentaire. Entre parenthèses, abréviations et valeurs codées de ces paramètres utilisées pour l'A.F.C. (*voir* texte et fig. 2).

		Station 1		Station 2		Station 3	
Sampled surface (m^2)		x	σ_n	x	σ_n	x	σ_n
Mesh 10 mm		7.30	0.50	6.45	0.35	6.05	0.00
Mesh 40 mm		11.70	1.14	11.31	1.41	7.85	1.60
Mesh 70 mm		36.70	3.70	20.17	8.50	46.79	8.50
Sediment characteristics							
Mediane (µm)	(med)	500 (7)		300 (6)		250 (5)	
Pelitic fraction (%)	(pel)	18 (2)		12 (1)		40 (3)	
Surface sediment characteristics							
Height of epibiotopes (cm)	(hei)	10 (2)		20 (4)		5 (1)	
Shell cover (%)	(she)	30 (3)		10 (1)		0 (0)	
Gravel cover (%)	(gra)	30 (2)		0 (0)		0 (0)	
Macrophytic cover (%)	(mac)	0 (0)		50 (4)		0 (0)	
Lithothamnion cover (%)	(lit)	0 (0)		70 (4)		0 (0)	
Crepidula fornicata cover (%)	(cre)	0 (1)		0 (0)		50 (3)	

From one station to another, abundances were not affected by mesh size (two-way ANOVA, F-test - mesh 10 and 40). Among the 68 epibenthic taxa, only three showed significant difference (two-way ANOVA - $p \leq 0.05$): the bivalve *Chlamys opercularis*, the fish *Gobius minutus* and the polyplacophora molluscs. Therefore either of the two mesh sizes might be used to sample the epifauna quantitatively. For each station it was possible to calculate average taxa abundances (and biomass) from six samples: three obtained with the 10 mm mesh and three obtained with the 40 mm mesh. This composite definition of abundance decreased standard deviation, thus improving the precision of the estimates. Consequently, the abundance matrix used in the CA included 18 samples (3 stations x 3 samples x 2 mesh sizes - 10 and 40 mm).

Ecological analysis by station

Station 1

Total surface sampled with the *Aquareve II* was 46.8 m^2. Species richness (49 species) and diversity (H' = 3.88) were highest at station 1; abundance reached 41.3 ± 22.1 ind.m^{-2}. When pooled together, carnivorous decapods (ten species), the suspension feeder *Porcellana longicornis*, chitons, *Anomia ephippium*, *Ophiothrix fragilis* and the filter-feeding gastropod *Crepidula fornicata*, accounted for 63 % of the organisms collected (Tab. 3). In terms of biomass, only the latter two species were well represented, together with two scallop species (*Chlamys opercularis* and *Pecten maximus*), the urchin *Echinus esculentus* and *Asterias rubens*. This assemblage included a high proportion of filter feeders, distributed among bivalves, echinoderms, decapods and gastropods. These species are characteristic of the fairly compacted coarse sands, mixed with shell fragments, found in the deep central area of the Bay of Brest.

Station 2

Total surface sampled was 53.2 m^2. Although species richness (39 species) and total abundance (10.7 ± 4.1 ind.m^{-2}) were the lowest at this station, the assemblage was diversified (H' = 3.84). Decapods (nine species) accounted for 40 % of the organisms collected, the carnivorous crab *Liocarcinus arcuatus* representing 30 % of total abundance. Other abundant species were *Morchellium argus* (ascidian), *Crepidula fornicata*, *Gibbula magus* (herbivorous gastropod) and the polychaete *Hermione hystrix*, together accounting for 33 % of total abundance. Total biomass was only 14.36 g DW.m^{-2}. In terms of biomass, the urchins *Sphaerechinus granularis* and *Echinus esculentus* and the gastropod *Gibbula magus* were dominant (71 % of total biomass). These herbivores are characteristic of beds of *Lithothamnion corralioides* (Hily *et al.*, 1992).

Station 3

At station 3, total surface sampled was 41.8 m^2 and total abundance was 26.9 ± 16.1 ind.m^{-2}. Species richness reached 46 species, but the assemblage was less diverse (H' = 3.52) than at the two other stations. The gastropod *Crepidula fornicata* (11.88 ind.m^{-2}) alone accounted for 44 % of the organisms collected. *Liocarcinus arcuatus*, *Hermione hystrix* (two carnivores), the scallop *Chlamys varia* and the holoturid *Thyone fusus* (both suspension feeders) all together accounted for 23 % of the epibenthos abundance. Because of their large individual weight, *Chlamys opercularis* and *C. varia* balanced the dominance of *Crepidula fornicata* by biomass. These three filter-feeding species accounted for 74 % of total biomass. Dominances of *Crepidula fornicata* and deposit-feeding species, either by abundance or by biomass, are characteristic of muddy sediment in the shallow banks of the southern Bay of Brest.

Ecological analysis between stations

Species. Abundance. Biomass

Each station had exclusive species (station 1: seven; station 2: four; station 3: seven), all of them being present in low densities (Tab. 3).

- Only 13 of the 68 taxa showed significant differences in terms of abundances from one station to another (two ways ANOVA; $p \leq 0.05$).

- Considering the five dominant species by weight at each station, eleven different species were represented in the three stations (Tab. 4). The distribution of seven species was significantly different from one station to another ($p \leq 0.05$). *A posteriori* Newman-Keuls tests showed that only one species (*Chlamys opercularis*) presented a significant difference at each station.

Correspondence analysis

In terms of abundance, most of the dominant species contributed poorly to axes 1 and 2 and scattered close to the origin of these axes (Fig. 2). *Porcellana longicornis* and *Liocarcinus arcuatus* were the two major contributors to the inertia explained by axis 1 (respectively 16.8 and

Table 2

Total number of species collected with the different samplers. Numbers are cumulated in the n *samples* (Aquareve II, *n = 3; grab, n = 10).*

Nombre total d'espèces collectées avec les différents engins d'échantillonnage. Chiffres cumulés pour *n* réplicats (*Aquareve II*, n = 3; benne, n = 10).

	Station 1	Station 2	Station 3
AQUAREVE mesh 10 mm	105	84	106
AQUAREVE mesh 40 mm	114	92	104
AQUAREVE mesh 70 mm	36	52	61
AQUAREVE mesh 10 + 40 mm	153	108	130
AQUAREVE mesh 10 + 40 +70 mm	158	115	136
Smith McIntyre grab 1mm	43	51	58

	CODE	TAXA	ABUNDANCE (ind . m-2) STATION 1	STATION 2	STATION 3	BIOMASS (g . m-2) STATION 1	STATION 2	STATION 3
CARNIVORES								
Anthozoa	CAP	*Calliactis parasitica*	-	0.12	0.11	-	0.05	0.03
	EDH	*Edwardsia halcampa*	0.01	-	0.01	-	-	0.00
	HAS	*Halcampa sp.*	0.03	0.14	0.23	0.01	0.00	0.01
Polychaeta	APA	*Aphrodite aculeata*	0.02	0.03	0.52	0.01	0.14	0.50
	HEH	*Hermione hystrix*	0.91	1.29	1.56	0.39	0.81	0.65
Gastropoda	BUU	*Buccinum undatum*	0.05	0.06	-	0.07	0.88	-
	NAA	*Natica alderi*	0.08	0.01	0.10	0.07	0.02	0.09
	NAI	*Nassarius incrassatus*	0.85	-	0.08	0.14	-	0.01
	NAR	*Nassarius reticulatus*	-	0.37	0.13	-	0.25	0.10
	OEE	*Oecenebra erinacea*	0.10	-	0.13	0.06	-	0.35
Crustacea	ANC	*Anapagurus curvidactylus*	0.04	0.06	-	-	-	-
	EBB	*Ebalia tuberosa*	0.18	-	0.03	-	-	-
	EBM	*Ebalia tumefacta*	0.04	-	-	-	-	-
	EUA	*Eurynome aspersa*	1.63	0.11	0.37	-	-	-
	EUB	*Eupagurus bernhardus*	0.15	0.41	0.46	-	-	-
	IND	*Inachus dorsettensis*	0.15	0.05	0.28	-	-	-
	LIA	*Liocarcinus arcuatus*	0.02	3.19	1.70	-	-	-
	LID	*Liocarcinus depurator*	-	-	0.05	-	-	-
	LIP	*Liocarcinus pusillus*	0.79	0.23	0.15	-	-	-
	LIU	*Liocarcinus puber*	-	0.03	-	-	-	-
	MAL	*Macropodia linaresi*	-	0.01	-	-	-	-
	MAR	*Macropodia rostrata*	-	0.24	0.16	-	-	-
	PIH	*Pilumnus hirtellus*	0.35	-	-	-	-	-
	XAP	*Xantho pilipes*	0.02	-	-	-	-	-
	CRG	TOTAL DECAPODS	3.37	4.33	3.20	0.82	0.86	0.99
Echinodermata	ANP	*Anseropoda placenta*	2.08	0.05	0.25	0.57	0.02	0.10
	ASR	*Asterias rubens*	0.07	0.14	0.06	1.87	0.34	0.04
Osteichthyes	CTR	*Ctenolabrus rupestris*	0.02	-	-	0.01	-	-
	GOM	*Gobius minutus*	0.07	0.19	0.16	0.01	0.03	0.05
DEPOSIT-FEEDERS								
Gastropoda	APP	*Aporrhais pespelecani*	0.03	-	0.08	0.12	-	0.45
	TUC	*Turritella communis*	0.06	0.01	0.25	0.02	0.01	0.12
HERBIVORES								
Gastropoda	AKB	*Akera bullata*	-	-	0.26	-	-	0.11
	APU	*Aplysia punctata*	-	-	0.03	-	-	0.06
	GIC	*Gibbula cineraria*	0.05	-	-	0.01	-	-
	GIM	*Gibbula magus*	-	1.03	0.79	-	1.33	1.28
Polyplacophora	CHI	*Chiton ind.*	3.78	0.33	0.55	0.07	0.01	0.13
Echinodermata	ECE	*Echinus esculentus*	0.27	0.12	0.07	3.32	0.97	0.25
	ECP	*Echinocyamus pusillus*	0.01	0.05	-	0.00	0.01	-
	PSM	*Psammechinus miliaris*	2.67	-	0.62	2.22	-	1.01
	SPG	*Sphaerechinus granularis*	0.02	0.15	-	0.22	8.00	-
	PAL	*Paracentrotus lividus*	0.06	-	-	0.31	-	-
SUSPENSION-FEEDERS								
Porifera	ADS	*Adocia simulans*	0.11	0.01	0.19	1.10	0.01	0.08
	DYF	*Dysidea fragilis*	-	-	0.10	-	-	0.05
	TEA	*Tethya aurantium*	-	-	0.08	-	-	0.12
Anthozoa	ALD	*Alcyonium digitatum*	0.23	-	-	0.08	-	-
Gastropoda	CAC	*Calyptrea chinensis*	1.02	0.17	-	0.03	0.02	-
	CRF	*Crepidula fornicata*	9.00	0.74	11.88	5.67	0.36	11.87
Bivalvia	ANE	*Anomia ephippium*	2.59	-	0.26	0.20	-	0.51
	CHD	*Chlamys distorta*	0.07	-	-	0.13	-	-
	CHO	*Chlamys opercularis*	0.63	-	0.47	5.41	-	3.30
	CHV	*Chlamys varia*	0.41	0.19	1.19	2.10	0.95	7.76
	MOB	*Modiolus barbatus*	0.04	-	0.29	0.00	-	0.46
	PEM	*Pecten maximus*	0.04	0.01	0.03	4.92	0.02	0.92
Crustacea	POL	*Porcellana longicornis*	8.04	0.11	0.23	0.37	0.01	0.01
Echinodermata	CUA	*Cucumaria elongata*	-	-	0.31	-	-	0.05
	HOI	*Holothurie ind.*	0.02	-	-	0.00	-	-
	THF	*Thyone fusus*	0.77	0.42	1.87	0.07	0.09	0.47
	OPF	*Ophiothrix fragilis*	3.34	0.04	-	1.86	0.02	-
	OPL	*Ophiocomina nigra*	0.10	-	-	0.02	-	-
Ascidiacea	ASA	*Ascidiella aspersa*	-	0.04	-	-	0.01	-
	ASM	*Ascidia mentula*	-	-	0.05	-	-	0.02
	ASV	*Ascidia virginea*	0.03	0.03	0.10	0.01	0.02	0.01
	CII	*Ciona intestinalis*	0.12	0.03	-	0.01	0.00	-
	DRO	*Distaplia rosea*	-	-	0.03	-	-	0.00
	MOR	*Morchellium argus*	-	0.43	0.63	-	0.01	0.11
	MOS	*Molgula sp.*	0.03	-	0.06	0.05	-	0.03
	PMA	*Phallusia mammillata*	-	-	0.03	-	-	0.00
	PYM	*Pyura microcosmus*	0.05	0.02	-	0.04	0.00	-
	STP	*Styela partita*	-	0.01	-	-	0.00	-
TOTAL			41.25	10.68	26.99	31.57	14.36	31.12

◀ Table 3

Abundance and biomasses (g DW.m^{-2}) of the 68 selected taxa in the three stations. Abbreviations of taxa names refer to Figure 2.

Abondance et biomasse (g DW.m^{-2}) des 68 taxons sélectionnés dans les trois stations. Les abréviations des noms de taxa font références à la figure 2.

28.4 %). *P. longicornis* was associated with samples from station 1, while *L. arcuatus* was associated with samples from station 2. *Crepidula fornicata* cover (cre) and pelitic fraction (pel) were the main environmental factors contributing to the inertia explained by axis 1 (respectively 0.63 and 0.60 %). Along this axis, these two factors separated station 1 samples from samples at the two other stations. *C. fornicata* and *L. arcuatus* were the only major contributors to the inertia explained by axis 2 (38.2 and 11.1 %). Gravel cover index (gra) and mean height of hard substrata (hei) were the main environmental factors defining axis 2 (respectively 0.24 and 0.22 % of total inertia). Along this axis, samples from station 2 were associated with two environmental factors (Lithothamnion corralioides and epiphytic macroalgae) and were separated from samples of stations 3 and 1.

Trophic structure in terms of biomass

Epifaunal trophic structure is illustrated in Figure 3. Suspension feeders clearly dominated in biomass at station 1; their biomass was significantly lower at stations 2 and 3 ($F = 9.416$; $p = 0.003$; *see* Tab. 5). Biomasses of other trophic groups were not significantly different between stations.

Only carnivore biomass was significantly affected by the size of the mesh used for sampling (Tab. 5; $F = 13.437$; $p = 0.003$). Biomasses of other trophic groups were not significantly different regarding the mesh size.

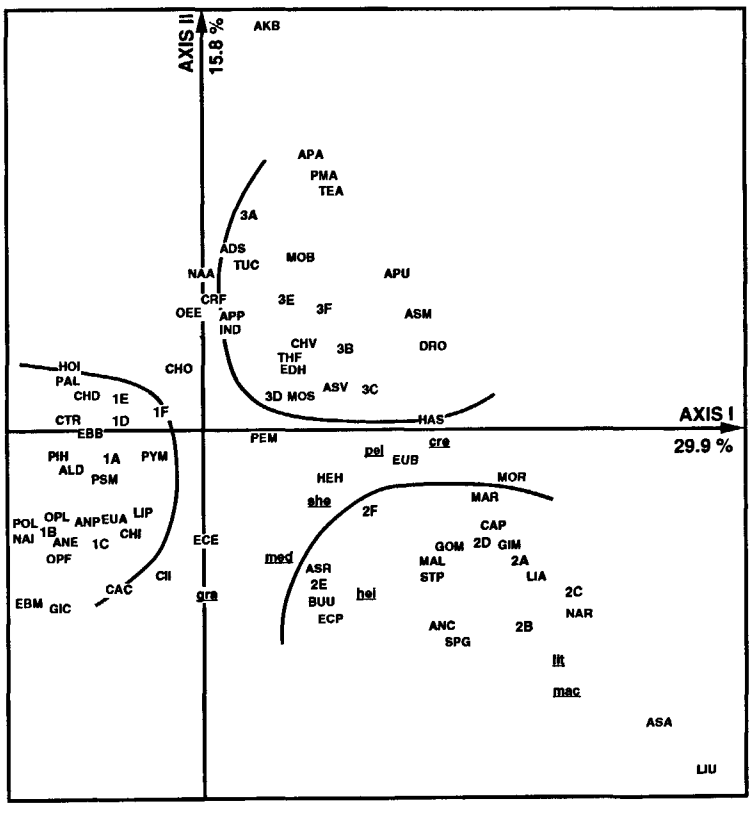
Infauna

Ecological analysis of the infauna was not the objective of this study. However, to interpret the results of the epibenthic analysis, it was necessary to define the main features of the infaunal assemblages. The global parameters species, abundance and diversity are shown in Table 6. A CA carried out on the thirty samples emphasized the homogeneity of infauna at the three stations. The stations could only be differentiated by variability in the abundance of dominant species: *Notomastus latericeus*, *Eunice vittata* and *Heterocirrus bioculatus*. Thus the three stations can be regarded as one assemblage or community for which a progressive increase of the pelitic fraction (from station 1 to station 3) induced local development of some species, *e. g.*, *Nucula turgida* and *Clymena modesta* in station 1 (two species dominant in the sandy muds of the east Atlantic coastal waters; Hily, 1976), *Nucula nucleus* and *Pista cristata* in station 2 (two species characterizing mixed muddy sands; Hily, 1976) and *Glycymeris glycymeris* in station 1 (a large-size bivalve which presents dense populations in coarse sands of the Bay of Brest; Hily, 1989). This last species largely dominated the assemblage in terms of biomass in station 1 (98 %). Because *G. glycymeris* presented high individual weight and abundance, the suspension-feeding biomass was significantly higher in station 1 than in the two other stations (ANOVA: $p < 0.05$; Fig. 4). Biomass of other trophic groups was not significantly different between the three stations.

Figure 2

Plane 1-2 correspondence analysis (CA) performed on abundances of the 68 taxa in the eighteen samples of the three stations. Location of the environmental factors used as additionnal variables in the CA. Sets of samples of each station are identified with lines. Identification of species: three capital letters (see Tab. 3). Identification of samples: number of the station (1, 2, 3) followed by the number of the sample (A to F). Environmental variables are identified by three underlined small letters (see Tab. 1).

Analyse factorielle des correspondances (CA) : projection simultanée dans le plan des axes 1 et 2 des abondances des 68 taxa dans les dix huit échantillons des trois stations. Localisation des facteurs environnementaux rentrés dans l'analyse en variables supplémentaires. L'ensemble des échantillons de chaque station est identifié par un trait. Les espèces sont identifiées par trois lettres majuscules (*voir* tab. 3) ; les échantillons sont identifiés par deux caractères : le premier correspond à la station (1,2,3), le second au numéro d'échantillon (A à F). Les facteurs environnementaux sont identifiés par trois lettres minuscules soulignées (*voir* tab. 1).



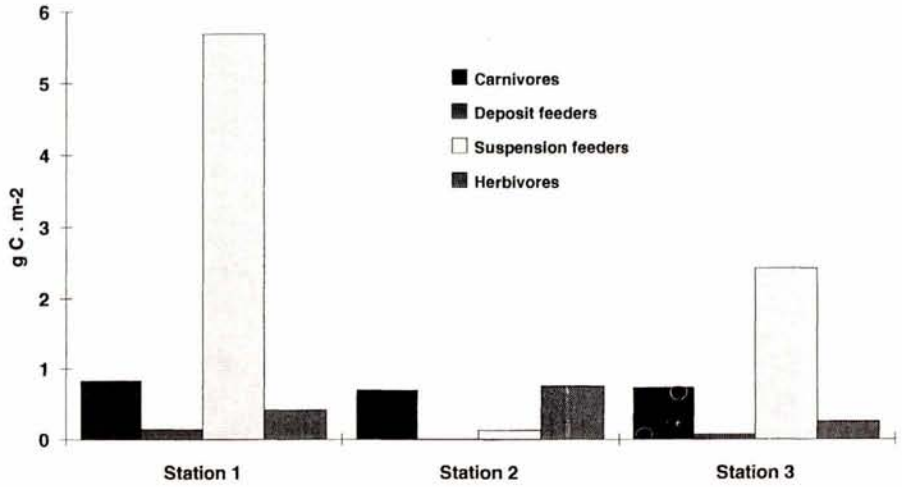


Figure 3

Trophic structure by weight of the epibenthic assemblages in the three stations (g C.m^{-2}).

Structure trophique en terme de biomasse des assemblages d'espèces épibenthiques dans les trois stations (g C.m^{-2}).

DISCUSSION

Quantitative sampling of the epibenthos

Results from this study make it possible to propose a methodology suited to quantitative sampling of the epibenthos associated with the microhabitats at the sediment surface:

Sampler

The *Aquareve II* sampler appeared well adapted to sample quantitatively the surface of coarse sediments partially covered by pebbles and cobbles, large shells, dense *Crepidula fornicata* populations and coralline algae beds.

The specificity of the *Aquareve II* as a better collector of epibenthic macrofauna compared to grabs is partly due to the greater areas sampled. However, the use of different samplers and different mesh sizes, inducing variations of the sampled surface, precludes any quantitative comparisons of species richness referring to different sampling methods, as pointed out by Maciolek and Grassle (1987) and Steimle (1987).

Mesh size

The mesh size can be 10 or 40 mm: no statistical difference emerged from the ecological analysis between these two options. Most of microhabitats had surface sizes > 40 mm and the sessile species remained fixed on them; furthermore, many vagile species remained hidden (and

Table 4

Dominant species by weight (g DW.m^{-2}) in the three stations. Species underlined in one station have significantly higher biomass (ANOVA: p ≤ 0.05) than in the two others.

Espèces dominantes en biomasse (g DW.m^{-2}) dans les trois stations. Les espèces soulignées dans une station ont une biomasse significativement supérieure (ANOVA: p ≤ 0.05) à celles des deux autres stations.

Station 1	Station 2	Station 3
Chlamys opercularis	*Sphaerechinus granularis*	*Crepidula fornicata*
5.41	8.00	11.87
Pecten maximus	*Gibbula magus*	*Chlamys varia*
4.92	1.33	7.76
Asterias rubens	*Echinus esculentus*	*Chlamys opercularis*
1.87	0.97	3.30
Echinus esculentus	*Chlamys varia*	*Psammechinus miliaris*
3.22	0.95	1.01
Psammechinus miliaris	*Buccinum undatum*	Σ Decapods
2.22	0.88	0.99

Table 5

Two-way ANOVA between biomasses (g DW.m^{-2}) of epifaunal trophic groups. p is in bold italics when a significant difference is detected between stations (p ≤ 0.05).

ANOVA à deux facteurs sur les biomasses (g DW.m^{-2}) des différents groupes trophiques de l'épifaune. p est indiqué en italiques gras lorsqu'une différence significative est détectée entre les stations (p ≤ 0,05).

Trophic group	Varying parameter	F	p	Newman-Keuls test
Carnivores	Station	0.223	0.804	-
	Mesh opening	13.437	***0.003***	10 mm ≠ 40 mm
	Interaction	0.683	0.527	-
Deposit	Station	1.584	0.224	-
Feeders	Mesh opening	0.018	0.890	-
	Interaction	0.040	0.961	-
Herbivores	Station	3.099	0.081	-
	Mesh opening	3.166	0.097	-
	Interaction	0.319	0.736	-
Suspension	Station	9.416	***0.003***	(St2=St3) ≠ St1
feeders	Mesh opening	3.368	0.088	-
	Interaction	1.054	0.380	-

Figure 4

Trophic structure by weight of the infaunal benthic assemblages in the three stations (g C.m^{-2}).

Structure trophique en terme de biomasse des assemblages d'espèces endobenthiques dans les trois stations (g C.m^{-2}).

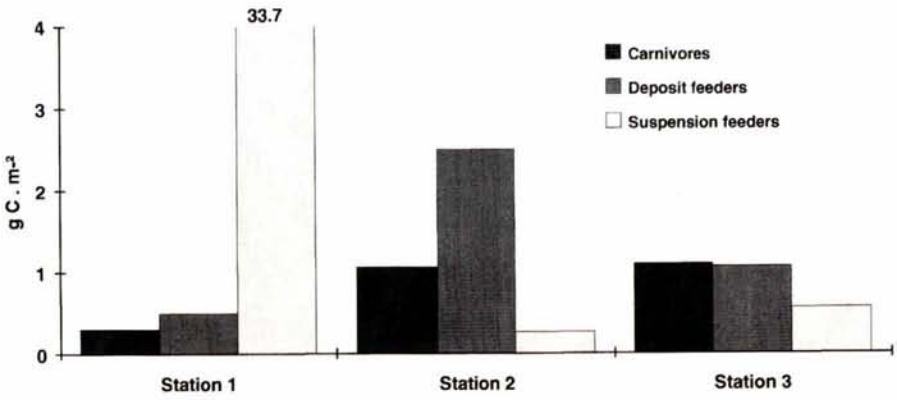


Table 6

Abundance and diversity (H' Shannon-Wiener index) of infauna in the three stations.

Abondance et diversité (indice H' de Shannon-Wiener) de l'endofaune dans les trois stations.

Station	Abundance (ind.m^{-2})	H' Shannon
1	732	4.42
2	1408	4.41
3	1605	4.45

were trapped) in the holes and cavities of these substrata. Considering epifauna larger than 10 mm, the first mesh size is theorically more satisfying; in practice, the sieving of samples through a 40 mm size occurs more rapidly, and for a given sampling period it could be possible to increase the number of replicates.

A sampling unit varying from 5 to 10 m^2 appeared well adapted to statistical estimation of abundances (from 10 to 0.1 individuals per square metre for most species). These surfaces can be sampled without dredge clogging, using either the 10 and 40 mm mesh, even when soft bottoms are covered with dense hard microhabitats.

A 70 mm mesh size was too large and inefficient, while a mesh size smaller than 10 mm would give too small samples as demonstrated by Thouzeau in the Bay of Saint-Brieuc (1989; sampled surface: 1.3 to 2.4 m^2, with 2 mm mesh size).

Number of replicates

Logistic constraints and the time-consuming sieving process (large sample volume) restrict the number of samples at each station. Because of the aggregative distribution of the microhabitats and organisms (Hily and Le Foll, 1989) in this area, standard errors frequently remained high even with six samples for each station (Tab. 1). Three replicates for each station could be sufficient in a general ecological survey of a large area, however five or six samples are recommended.

Ecology of micro-epi habitats of soft-bottom sediments

Historic evolution of the topic

Thorson (1957) emphasized the multitude of "microenvironments" and "microlandscapes" formed by stones and shells which define different conditions for life, support large numbers of species "sitting and crawling on the substratum" and have a wide range of ecological requirements. Subsequently, most benthologists did not take these microstructures into account in assessing the quantitative ecology of soft-bottom ecosystems. The sample size was not adapted to the spatial distribution of those microhabitats and of large epifauna. The latter were not taken into account, either because they were not sampled adequately by the grabs used, or because the data obtained were not quantitative. Pearson (1970; 1971) described the epifauna and associated biotopes before by adapting its results on the study of infauna. At present, developments in the modelling of benthic ecosystems, such as steady state models and predictive (simulation) models, are widely used to help understand the functioning of marine ecosystems (Chardy, 1987; Herman and Scholten, 1990). To assess state variables accurately, energy budgets require a precise estimate of the relative importance of each compartment; studies on epibenthic assemblages are consequently a priority for future improvement in ecosystem modelling.

An integrated food web

Combining data of the infauna with those of epifaunal trophic groups permits us to propose a conceptual model of an integrated food web (Fig. 5). Mean values for the three stations were considered in this diagram because of the absence of significant differences between stations when using ANOVA testing. Our results show that, in terms of abundance and biomass (in g C.m^{-2}), the trophic structures of epifauna and infauna were very different in the same area. Thus, food webs based on infaunal data only are likely to distort the real trophic structure of some communities. The epi- and infaunal subsystems overlap in terms of ecosystem functioning. Epibenthic carnivores are predators of many infaunal species (Feder and Pearson,

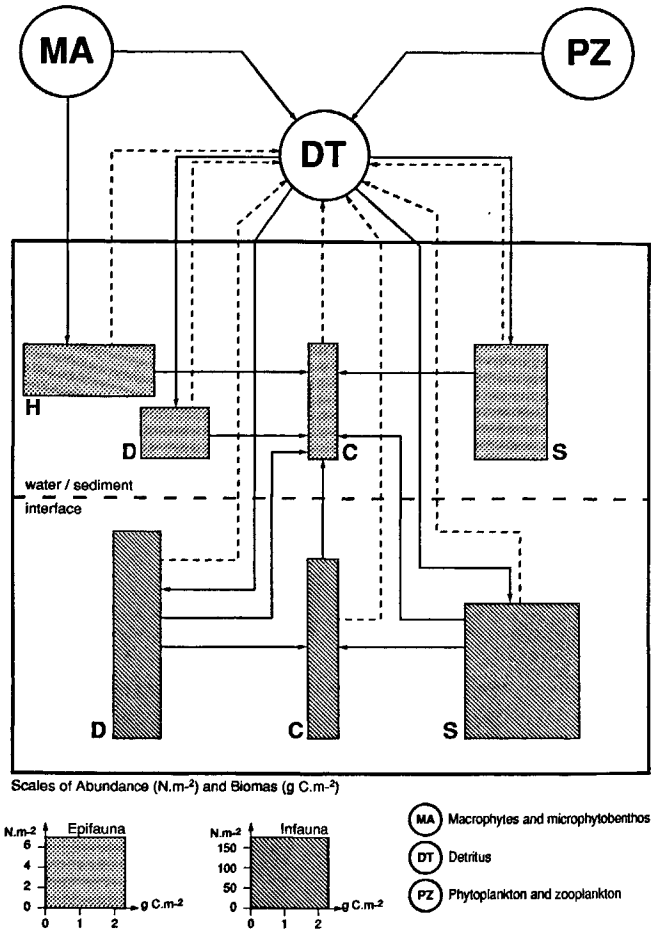


Figure 5

Benthic macrofaunal food web diagram in the coarse soft-bottoms in the Bay of Brest: Data of the three stations were averaged. Area of boxes depends on abundance (vertically) and on biomass (horizontally) of the considered trophic groups. Note the difference in scale of abundance between epifauna and infauna. C: carnivores; S: suspension feeders; D: deposit feeders; H: herbivores. Plain lines: sedimentation and ingestion. Dashed lines: faeces and natural mortality. Arrow: direction of energy fluxes.

Modèle conceptuel du réseau trophique de la macrofaune des sédiments hétérogènes de la rade de Brest. Moyennes des données des trois stations. La surface des boîtes dépend de l'abondance (en ordonnée), et des biomasses (en abscisse). Noter la différence d'échelle des abondances entre l'épifaune et l'endofaune. C : carnivores ; S : suspensivores ; D : déposivores ; H : herbivores. Traits continus : sédimentation et ingestion. Traits pointillés : faeces et mortalité naturelle. Flèches : sens des principaux flux d'énergie.

1988). In the areas studied, the high abundance and diversity of carnivorous crabs and gastropods suggest favourable biotopes providing refuges (hard microhabitats) and prey (numerous infaunal deposit feeders, essentially polychaetes). Valderhaug and Gray (1984) and Ambrose (1984) have shown the key function of epifaunal carnivores in controlling benthic community structure. The trophic pattern in Figure 5 reveals an energetic balance between infaunal deposit feeders and epibenthic suspension feeders. Herbivores were confined to epibenthic motile species such as chitons, gastropods and echinoids. High complexity of the trophic food web, when integrating epi- and infauna, may explain community dynamics. Margalef (1963) emphasized that the relative amount of energy necessary for maintaining an ecosystem (*i. e.* stability-resiliency) was related to the degree of structure or organisation of that ecosystem: "less energy is necessary for a more complex ecosystem". Integrating the epifaunal food loop to trophic patterns and mathematical models is of paramount importance to benthic ecosystem energetics.

The epifaunal biomass of invertebrates is particularly vulnerable to predation by carnivorous fishes which can strongly interact with these epibionts.

Originalities of the fauna associated with hard microhabitats

For several species, the abundance and biomass values reported in Table 3 are probably the first quantitative data available from the literature. Particular attention should be paid to three taxa:

Decapoda

Fifteen species of small crabs were sampled in the three stations, of which 14 were active predators. Together, they represented more than 4 ind.m^{-2} and more than 1 g.m^{-2} of organic matter. In each station one species was strongly dominant: *Eurynome aspera* in station 1; and *Liocarcinus arcuatus* in stations 2 and 3. All were strictly dependent on the presence and quality of the hard microsubstrates; for example *Eurynome* and *Ebalia* (short appendices) were strongly linked to the shells of *Glycymeris* lying on sediments at station 1, while *Macropodia* and *Inachus* (very long appendices) were linked to the presence of erected filamentous algae at station 2. Little information is available on the ecology of these species, and their abundance and diversity are surprisingly high in such environments.

Bivalvia

Among the six species three were pectinids (*Chlamys opercularis*, *Chlamys varia* and *Pecten maximus*) which are commercially exploited. As shown previously, the *Aquareve II* system can be used in invertebrate fisheries management providing information either on juveniles (Thouzeau, 1989; 1991; Thouzeau *et al.*, 1988; 1991) or adults (Hily and Thouzeau, 1987). Quantitative data of this type are useful for fishery management because they provide information on the biomasses of the different cohorts of exploited species, as well as on predators and trophic competitors.

Ascidiacea

Not surprisingly, shells, gravels and cobbles appeared to be very favourable substrata to the solitary ascidians. Because of the annual life cycle of most of the ten species encountered, frequent winter disturbances of their substrata by waves (Hily *et al.*, 1992) should not be a limiting factor to their development. Those species, which are commonly described in rocky areas, may also extend their spatial distribution area to the hard microbiotopes.

In other latitudes, Meesters *et al.* (1991) adopted a similar approach on the sub-rubble communities of the Curaçao and Bonaire coral reefs. These authors enhanced the

exceptional species richness and diversity of theses coral rubbles. They showed the function of refuge to the sessile cryptobionts and their predators and the role in maintaining coral reef diversity.

Environmental factors explaining epifaunal variability

Correspondence analysis clearly shows that the three stations belong to a single community, the common species accounting for most of the abundance or/and the biomass. This situation corresponds to the definition of a "facies" in a community (Picard, 1965). Sampling sites were characterized by secondary species associated with specific environmental factors. Environmental factors which induced structural variability within the community are identified on the CA graph. They are gravel cover and shells (*Glycymeris*) at station 1, erected algae and *Lithothamnion* cover at station 2, and slimper limpet (*Crepidula fornicata*) cover and pelitic fraction at station 3. All these factors are linked to the epibiotopes. It can be concluded that the nature of the hard microepibiotopes and their relative abundance modifies the structure of the whole community. Although each station had several exclusive species, major faunal differences are observed in terms of dominance (abundance and biomass). Thus, the effects of these structuring factors should be maximized when considering the variability in terms of energy flux. It should be noted that the infaunal analysis also demonstrated the existence of one community and three different "facies" which can be explained by modification of sediment grain size. Proportion of fine particles in sediment and sediment heterogeneity are parameters linked to characteristics of the benthic boundary layer, hence linked with epibiotopes. Shells and coralline algae are progressively buried in the sediment, the coarse fraction being essentially biogenic. Thus, the whole system is self maintained by the fauna and flora of those areas. One species can be simultaneously the dominant epifaunal taxa and the main substrate for settling of other epifaunal species (*e. g., Crepidula fornicata*). In another case, one infaunal species provides the main habitat for the epifaunal assemblage (*e. g., Glycymeris glycymeris*). It can be concluded that the whole system is maintained over the long term by the population dynamics of those species. The exceptional biomass of such monocohort-monospecific beds was also noted in coastal waters of South Brittany for *Spisula ovalis* (Berthou and Glémarec, 1988); these authors observed negative interactions between recruitment and adult density. This phenomenon could be an additional factor explaining the mosaic distribution of *Glycymeris* shells on sediments.

Ruggedness of the sediment surface: a determining factor of the epifaunal assemblage structure

Our findings indicate that the surficial sediment structure should be considered more often in soft-bottom ecological studies. For lack of a better term we shall use "ruggedness" to describe the aspect of the sediment surface. Ruggedness of the sediment surface should be defined by the quality and abundance of the components which raised above the sediment, and the type (biotic and/or abiotic), size (mean individual height and surface), density and spatial distribution should be described. This type of surface can be considered as a habitat for epifauna and a physical factor modifying hydrodynamism close to the bottom. Clearly more work needs to be done in this field to advance our understanding of epibenthic subsystems and their relations with the infaunal subsystems. Our own current research is at present directed towards extending this analysis, particularly to modelling the benthic ecosystem of the Bay of Brest where the suspension feeding organisms which colonize those hard microhabitats strongly influence the pelagos/benthos exchanges.

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