Meiobenthos of the Bay of Saint-Brieuc (North Brittany, France).
II: Harpacticoid copepod diversity and species assemblages

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ABSTRACT

Harpacticoid copepods (Crustacea) of the Bay of Saint-Brieuc (Western Channel, France) were collected in winter and late spring 1988, at five intertidal and six subtidal sites. 140 species (many new and some rare) were identified, and several diversity indices (Shannon; Fisher *et al.*; Margalef) were calculated for the different sites: very high values were obtained at some of them, specially in heterogeneous sediment (H' = 5.26). Pearson's correlation coefficients show that diversity was positively correlated with TOM and depth. Correspondence factorial analyses applied to dominant species suggested the existence of an intertidal fine sand assemblage, with a low salinity "facies" (*sensu* Bodin, 1977), and a subtidal heterogeneous muddy sand assemblage, with several facies related to the sediment structure. These assemblages more or less correspond to the macrofauna communities of the bay and are compared with other harpacticoid copepod assemblages worldwide.

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RÉSUMÉ

Le méiobenthos de la baie de Saint-Brieuc (Côtes d'Armor, France). II : Peuplements et diversité des copépodes harpacticoïdes

Les copépodes harpacticoïdes (crustacés) de la baie de Saint-Brieuc (Manche Ouest, France) ont été récoltés en hiver et fin de printemps 1988, à cinq stations intertidales et six stations subtidales. 140 espèces (dont beaucoup sont nouvelles et quelques unes rares) ont été identifiées et plusieurs indices de diversité (Shannon ; Fisher *et al.* ; Margalef) ont été calculés pour les différents sites : des valeurs très élevées ont été obtenues pour certains d'entre eux, en particulier dans les sédiments hétérogènes (H' = 5.26). Les coefficients de corrélation de Pearson montrent une relation positive entre la diversité et la MOT, ainsi qu'avec la profondeur. Une analyse factorielle des correspondances appliquée aux espèces dominantes suggère l'existence d'un peuplement de sable fin intertidal, avec un faciès (*sensu* Bodin, 1977) de dessalure, et d'un peuplement de sable envasé hétérogène subtidal, avec plusieurs faciès dépendant de la structure du sédiment. Ces peuplements correspondent plus ou moins aux communautés macrobenthiques de la baie et sont comparés à d'autres peuplements d'harpacticoïdes de par le monde.

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INTRODUCTION

Following a quantitative study of the meiofauna densities and biomass in the Bay of Saint-Brieuc (North Brittany, France), as part of the "Euphorbe" programme (Le Guellec and Bodin, 1992), the harpacticoid copepod species (which have not been examined previously in this area) were identified and their distribution analysed in relation to the different sediment types of the bay. Meiofauna sites were chosen to represent the ecosystem structural entities first defined by the Institut Français de Recherche pour l'Exploitation de la Mer (IFREMER) based on sediment characteristics and macrofaunal assemblages (Gros and Hamon, 1988), in an effort to compare meiofaunal and macrobenthic community structures. Moreover, the search for "isocommunities" (i. e. assemblages with the same genera, but with different species) was carried out.

Beside the "stability-time" hypothesis of Sanders (1968), another theory on possible causes of biodiversity gradient relates to latitude: in many marine macrobenthic groups so far studied, species richness increases from the polar latitudes toward the equator (Fischer, 1960). Surprisingly high diversities recorded in the Bay of Saint-Brieuc question these hypotheses discussed in some well-known or recent papers (Fischer, 1960; Pianka, 1966; Sanders, 1968; Boucher, 1990).

MATERIAL AND METHODS

Sampling sites are shown on Figure 1. Measurement of environmental variables and methods of fauna sampling and extraction have been described in a previous paper (Le Guellec and Bodin, 1992). In addition to our own measurements (in March 1988), environmental data given by Gros and Hamon (1988), Thouzeau (1991) and Gros et al. (1990) have also been used.

Harpacticoid copepod diversity has been calculated using the Shannon-Weaver index (H', log base 2), the species richness (SR) of Margalef (1957), the diversity index (a) of
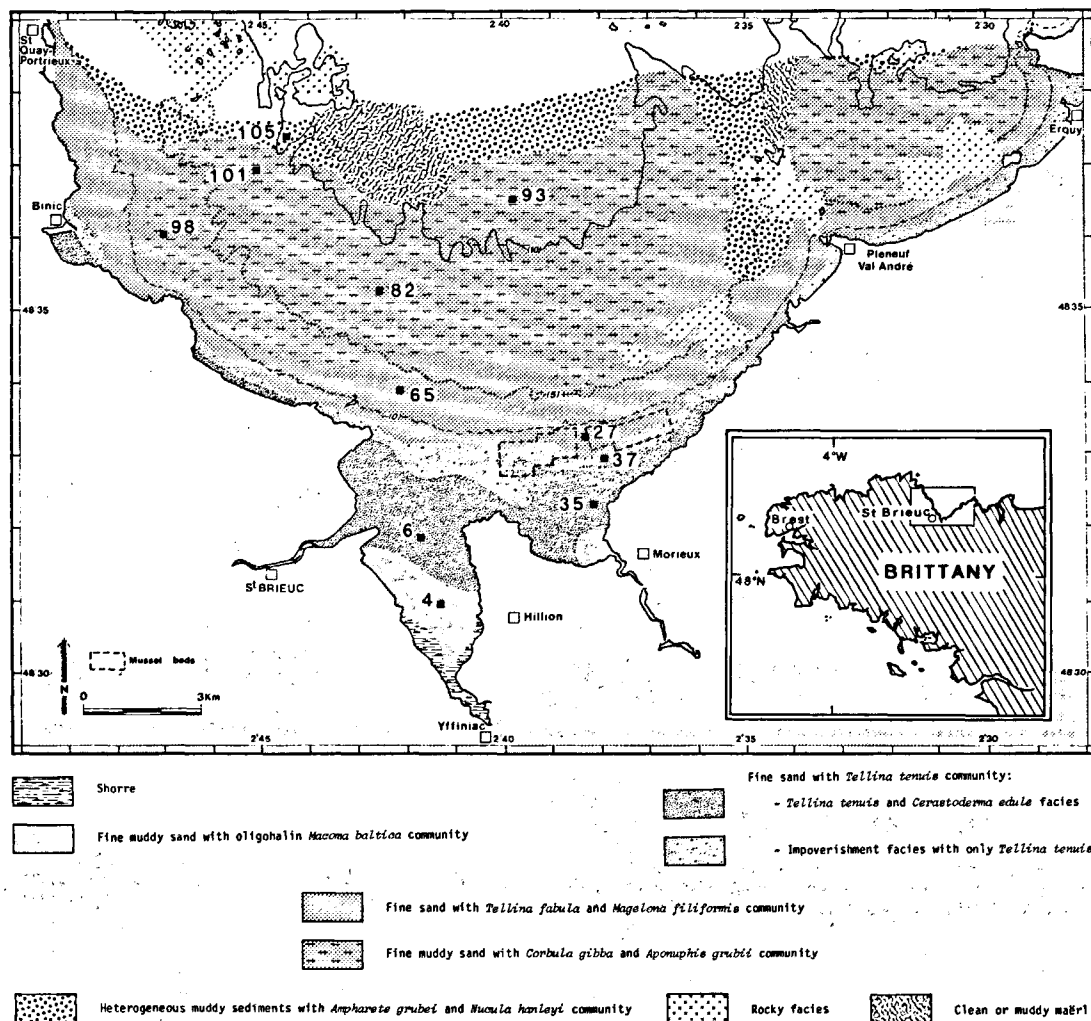

Figure 1

Biosedimentary structure of the Bay of Saint-Brieuc, with location of the study sites (modified from Gros and Hamon, 1988 and Thouzeau and Hamon, 1992).

Carte biosédimentaire de la baie de Saint-Brieuc, avec emplacement des stations (modifiée d'après Gros and Hamon, 1988 et Thouzeau and Hamon, 1992).

Table 1

List of recorded species, with their abbreviation on CFA graphs (Abbr.), their winter + spring mean dominance (%) in the intertidal (Int.) or/and subtidal (Subt.) zone (+ for a dominance < 0.1 %), and the ecological group (E.G.) they are supposed to belong to (S = sandy, Sm = mesopsammic, M = muddy, MS = muddy sand, estu. = estuarine, E = eurytopous, Ph = phytophylous).

Species	Abbr.	Int.	Subt.	E. G.
LONGIPEDIIDAE				
Longipedia scotti	Lsc		0.9	S
Longipedia helgolandica			0.1	S
CANUELLIDAE				
Canuella perplexa	Cpe	87.1	0.4	S
ECTINOSOMATIDAE				
Ectinosoma normani	Eno		1.3	S, Ph
Ectinosoma melaniceps	Eme		1.0	S, Ph
Ectinosoma reductum	Ere		0.2	S
Ectinosoma tenuipes	Ete		0.2	S
Ectinosoma dentatum			0.2	S
Halectinosoma propinquum	Hpr		1.1	S
Halectinosoma herdmani	Hhe	1.3	8.4	S
Halectinosoma pterinum	Hpt	0.2	0.1	S
Halectinosoma cooperatum	Hco		1.7	M
Halectinosoma paraspinicauda	Hpa		0.2	S
Halectinosoma similidistinctum	Hsi		0.1	S
Halectinosoma sp. 1			+	
Halectinosoma sp. 2			+	
Halectinosoma sp. 3			+	
Halectinosoma sp. 4	Hs4		0.3	
Halectinosoma sp. 5	Hs5		0.3	
Halectinosoma sp. 6			0.1	
Halectinosoma sp. 7			0.1	
Pseudobradya minor	Pmi	0.4		MS, estu.
Pseudobradya similis	Psi		0.2	S
Pseudobradya hirsuta			+	
Pseudobradya beduina	Pbe		0.5	S
Pseudobradya sp.			+	
Sigmatidium kunzi	Sku		0.7	M
Halophytophilus sp.	Has		0.9	MS
Arenosetella tenuissima	Ate	0.3		Sm
Hastigerella leptoderma	Hle		0.2	Sm
Hastigerella grandimandibularis			0.1	Sm
Hastigerella bozici	Hbo		0.5	Sm
Hastigerella sp. 1			0.2	Sm
Hastigerella sp.2			0.1	Sm
Lineosoma sp.	Lis		0.1	Sm
TACHIDIIDAE				
Tachidius discipes	Tdi	1.3		E
Thompsonula hyaenae	Thy	5.5		S
HARPACTICIDAE				
Harpacticus gracilis			+	Ph
Harpacticus flexus	Hfl		0.6	S
Harpacticus littoralis			0.1	Ph
TISBIDAE				
Tisbe tenera (?)	Ttt		0.3	Ph
Tisbe perplexa			0.2	Ph
Tisbe sp.		+	0.1	Ph
Idyella exigua			0.1	
Tachidiella minuta	Tmi		0.6	MS
PELTIDIIDAE				
Alteutha interrupta		+		
THALESTRIDAE				
Rhynchothalestris rufocincta	Rru		0.5	Ph
Diarthrodes nanus	Dna		0.3	E
Diarthrodes andrewi	Dan		3.1	E
Dactylopusia tisboides	Dti		0.3	E
Dactylopusia vulgaris s. str.	Dvu		0.1	Ph
Dactylopodella flava	Dfl		0.5	Ph
DIOSACCIDAE				
Stenhelia (D.) palustris bispinosa	Spb	0.9		M, estu.
Stenhelia (D.) giesbrechti	Sgi		1.4	E
Amphiascus varians	Ava		0.4	Ph
Amphiascus propinqvus	Apr		2.0	Ph
Amphiascus longarticulatus	Alo		1.2	S
Haloschizopera pygmaea	Hpy		10.0	E
Amonardia normani			0.1	Ph
Bulbamphiascus imus	Bim		0.3	E
Typhlamphiascus confusus	Tco		0.3	M
Rhyncholagena pestai			0.1	Ph
Rhyncholagena spinifera			+	
Amphiascoides subdebilis			+	Ph
Amphiascoides neglectus			+	E
Amphiascoides nanoides (?)			+	
Helmutkunzia (?) sp.			0.1	
AMEIRIDAE				
Ameira parvula s. str.	Apa		0.6	E, Ph
Ameira parvula nana	Apn		1.4	E
Ameira scotti			0.3	E

Species	Abbr.	Int.	Subt.	E. G.
Ameira pusilla	Apu		4.5	E, MS
Ameira brevipes pestae	Abp		0.6	E, MS
Ameira divagans	Adi		0.1	S
Ameira parasimulans (?)			0.1	
Ameira longifurca			+	
Ameira (?) sp.			0.1	
Proameira signata	Prs		0.1	M
Proameira thetiensis (?)			+	M
Proameira sp.			0.7	M
Psyllocamptus (P.) minutus s. str.	Ppm		0.1	S
Ameiropsis brevicornis			0.1	
Ameiropsis nobilis			0.1	
Pseudameira crassicornis	Pcr		1.5	S, SM
Sarsameira parva			0.1	M
Sarsameira longiremis			0.1	M
Sarsameira propinqua			0.1	
Sarsameira sp. 1			0.1	
Sarsameira sp. 2			+	
Sicameira leptoderma	Sle		0.3	MS
Parevansula sp.	Pas		1.2	S
Ameiropsyllus monardi			+	
Ameiridae gen. et sp. ?			+	
PARAMESOCHRIDAE				
Paramesochra helgolandica			+	Sm
Paramesochra (?) helgolandica M75			+	Sm
Leptopsyllus (L.) harveyi			+	Sm
Leptopsyllus (L.) celticus			+	Sm
Leptopsyllus (L.) sp.			0.1	Sm
Apodopsyllus littoralis	Ali		1.3	Sm
Kliopsyllus sp. 1	Kl1		5.0	Sm
Kliopsyllus sp. 2	Kl2		0.2	Sm
Kliopsyllus sp. 3	Kl3		0.2	Sm
Scottopsyllus (Sc.) langi	Ssl		0.1	Sm
Scottopsyllus (Sc.) robertsoni (?)	Ssr		0.7	Sm
Scottopsyllus (I.) intermedius	Sin		0.2	Sm
Scottopsyllus (W.) sp.		+		Sm
Diarthrodella secunda (?)			0.1	Sm
TETRAGONICIPITIDAE				
Tetragoniceps malleolatus			0.1	Ph
Phyllopodopsyllus bradyi	Pbr		0.1	MS
CANTHOCAMPTIDAE				
Mesochra pygmaea	Mpy		3.5	E
Heteropsyllus curticaudatus	Hcu		0.3	S, estu.
Mesopsyllus atargatis	Mat		0.1	MS
Psammocamptus axi	Pax		0.6	MS
Canthocamptidae gen. et sp. 1			+	
Canthocamptidae gen. et sp. 2			+	
CYLINDROPSYLLIDAE				
Stenocaris minor			0.1	
Leptastacus laticaudatus	Lel		6.8	Sm
Paraleptastacus espinulatus			0.2	Sm
Arenotopa sp.	Ars		7.6	Sm
Notopontia (?) sp.	Nos	0.6		Sm
CLETODIDAE				
Cletodes limicola	Cli		1.5	M
Cletodes tenuipes	Cte		3.7	M
Cletodes spinulipes	Csp		0.8	M
Enhydrosoma propinquum	Epr		1.9	M
Enhydrosoma curvirostre	Ecu		0.4	M
Enhydrosoma longifurcatum			+	M
Stylicletodes longicaudatus			+	M
HUNTEMANNIIDAE				
Huntemannia jadensis	Hja	0.2		M, estu.
RHIZOTHRICIDAE				
Rhizothrix minuta	Rmi	1.8	1.1	S
Rhizothrix wilsoni	Rwi		0.6	S
Tryphoema porca	Tpo		0.3	MS
Tryphoema bocqueti			0.1	MS
LAOPHONTIDAE				
Asellopsis intermedia	Ain	0.4	0.6	MS
Asellopsis hispida	Ahi	+	2.0	S
Esola longiremis			0.1	
Pseudolaophonte glemareci			+	
Laophontina sp.			+	
Laophontopsis lamellifera	Lla		0.6	Ph
Normanella incerta	Nin		2.6	Ph
Normanella mucronata	Nmu		1.0	E
Normanella tenuifurca			+	
ANCORABOLIDAE				
Laophontodes bicornis	Lbi		0.3	M

Liste des espèces récoltées, avec leurs abréviations sur les diagrammes AFC (Abbr.), leur dominance moyenne hiver + printemps (%) dans la zone intertidale (Int.) et/ou subtidale (Subt.) (+ indique une dominance < 0.1 %), et le groupe écologique (E.G.) auquel elles sont supposées appartenir (S = sabulicole, Sm = mésopsammique, M = vasicole, MS = mixte, estu. = typique d'estuaire, E = eurytope, Ph = phytophile).

Fisher *et al.* (1943) and "evenness" (equitability) index (J') of Pielou (1975).

Pearson's correlation coefficients were calculated and linear regression diagrams were plotted to estimate the relationships between diversity and some environmental variables (Total Organic Matter (TOM), depth, Sorting index (So), % silt/clay). In this purpose, depth real figures were replaced with their rank (depth increasing from 1 towards 11) because of the negative (subtidal) and positive (intertidal) values.

Species abundance values are the mean of the four cores (10 cm^2 each) from each station (but only two at station 105 in winter) expressed as a percentage of the total harpacticoid abundance at each station (= dominance in %). Dominant species (Bodin, 1977) are species with a relative abundance > 1 % in at least one station.

After a log transformation (y = $\log_{10}$ [x + 1]) of relative abundance data of the dominant harpacticoid species, a correspondence factorial analysis (CFA, *cf.* Chardy *et al.*, 1976) was applied to the winter and spring data from both intertidal and subtidal zones together and separately.

Table 2

Diversity and evenness indices at each zone, each season, and combinations of both. INW = intertidal (winter); INS = intertidal (spring); INT = intertidal (winter + spring); SUW = subtidal (winter); SUS = subtidal (spring); SUBT = subtidal (winter + spring); WIN = winter (intertidal + subtidal); SPR = spring (intertidal + subtidal); GEN = general index (intertidal + subtidal, winter + spring).

Indices de diversité et d'équitabilité à chaque zone, chaque saison, et aux deux combinés. INW = intertidal (hiver) ; INS = intertidal (printemps) ; INT = intertidal (hiver) ; SUW = subtidal (hiver) ; SUS = subtidal (printemps) ; SUBT = subtidal (hiver + printemps) ; WIN = hiver (intertidal + subtidal) ; SPR = printemps (intertidal + subtidal) ; GEN = indice général (intertidal + subtidal, hiver + printemps).

	INW	INS	INT	SUW	SUS	SUBT	WIN	SPR	GEN
Diversity	0.68	0.96	0.91	5.05	5.39	5.45	3.44	3.83	3.79
Evenness	0.19	0.24	0.23	0.8	0.79	0.78	0.53	0.55	0.53

RESULTS

Species diversity and distribution

A total of 8,790 harpacticoid copepods were identified belonging to 140 species distributed in 19 families and 72

WINTER *Intertidal zone*	Station 4 18-03-88	Station 6 18-03-88	Station 27 18-03-88	Station 35 18-03-88	Station 37 18-03-88	
X/10 cm2	16.0	13.9	12.4	308.6	7.7	
N	63	55	49	1234	30	
S	9	4	8	3	6	
H'	2.81	1.59	1.71	0.04	1.78	
J'	0.89	0.79	0.66	0.03	0.69	
SR	1.93	0.75	1.28	0.28	1.47	
a	3.0	1.0	1.9	0.5	2.3	
Subtidal zone	Station 65 08-03-88	Station 82 08-03-88	Station 93 08-03-88	Station 98 08-03-88	Station 101 08-03-88	Station 105 08-04-88
X/10 cm2	10.8	54.0	36.3	23.0	106.5	35.8
N	43	211	145	92	426	138*
S	17	33	28	18	20	27*
H'	3.89	4.28	3.73	3.34	3.44	3.93
J'	0.95	0.85	0.78	0.80	0.80	0.83
SR	4.25	5.95	5.42	3.76	3.14	5.27
a	10.2	10.3	10.4	6.8	4.2	10.5
SPRING *Intertidal zone*	Station 4 01-07-88	Station 6 01-07-88	Station 27 01-07-88	Station 35 01-07-88	Station 37 10-06-88	
X/10 cm2	14.2	59.8	36.5	690.4	55.2	
N	56	238	145	2761	220	
S	6	8	7	4	7	
H'	1.66	1.53	0.53	0.06	1.73	
J'	0.64	0.51	0.19	0.03	0.62	
SR	1.24	1.28	1.21	0.38	1.11	
a	1.7	1.5	1.6	0.6	1.5	
Subtidal zone	Station 65 10-06-88	Station 82 10-06-88	Station 93 10-06-88	Station 98 10/27-06-88	Station 101 10-06-88	Station 105 10-06-88
X/10 cm2	14.8	173.5	65.8	61.0	232.3	172.3
N	59	675	254	243	928	674
S	9	46	34	26	25	73
H'	2.39	4.14	4.22	3.16	3.32	5.26
J'	0.75	0.75	0.83	0.67	0.72	0.85
SR	1.96	6.88	5.92	4.55	3.51	11.02
a	3.0	11.0	11.0	7.2	4.8	21.2

Table 3

Diversity and evenness indices at each station. X = mean density (/10 cm^2); N = number of identified copepods; S = number of species; H' = Shannon-Wiener index; SR = Margalef index; a = Fisher et al. index; J' = Pielou evenness index. Using different parameters and logarithm bases, the order of diversity values can differ from an index to the other.

Indices de diversité et d'équitabilité pour chaque station. X = densité moyenne (/10 cm^2) ; N = nombre de copépodes déterminés ; S = nombre d'espèces ; H' = indice de Shannon-Wiener ; SR = indice de Margalef ; a = indice de Fisher *et al.* ; J' = indice d'équitabilité de Piélou. En raison de l'utilisation de bases logarithmiques et de paramètres différents, l'ordre des valeurs de la diversité peut varier d'un indice à l'autre.

Stations	Intertidal zone					Subtidal zone					
	4	6	27	35	37	65	82	93	98	101	105
Total number of species	9	8	9	4	8	22	50	52	32	29	82
	16					131					
	141										
Nb. of peculiar sp.	1	0	1	0	1	1	7	12	4	4	36
	9					124					
Nb. of shared sp.	2					3					
	7										

Table 4

Peculiar and shared number of species in the different sites.

Nombre d'espèces communes et propres aux différentes stations.

genera (of which 6 could be new to science); at least 30 species are new to science and the status of 7 is uncertain (Tab. 1). Thus the overall Shannon diversity was 3.79, but with a much lower diversity in the intertidal zone (0.91) than in the subtidal zone (5.45). Winter and spring had similar diversities: 3.44 and 3.83 respectively, and similar evenness: 0.53 and 0.55 (Tab. 2). In samples, species richness ranged from 0.28 to 11.02 and Shannon diversity from 0.04 to 5.26; evenness ranged from 0.03 to 0.95 (Tab. 3).

Sixteen species were present in the intertidal zone and 131 in the subtidal zone (Tab. 4). Nine species (*Pseudobradya minor*, *Arenosetella tenuissima*, *Tachidius discipes*, *Thompsonula hyaenae*, *Alteutha interrupta*, *Stenhelia (D.)*

Table 5

*Pearson's correlation coefficients (for 9 degree of freedom, $r_{0.05}$ = 0.6021 and $r_{0.01}$ = 0.7348). Significance level: * = $p < 0.05$, ** = $p < 0.01$.*

Coefficients de correlation de Pearson (pour 9 degrés de liberté, $r_{0.05}$ = 0.6021 et $r_{0.01}$ = 0.7348). Degré de signification : * = $p < 0.05$, ** = $p < 0.01$.

	T.O.M.	depth	% silt/clay	median grain size	Sorting index
Diversity					
H' winter	+0.6160 *	+0.7329 *	+0.5778	+0.3111	+0.2222
H' spring	+0.8505 **	+0.8345 **	+0.6326 *	+0.5734	+0.2272

Figure 2

Significant linear regression graphs (least squares method) of diversity H' versus T.O.M., depth and % silt/clay (solid triangles: winter data; solid circles: spring data).

Droites de régression linéaire significatives (méthode des moindres carrés) de la diversité H' en fonction de la M.O.T., de la profondeur et du pourcentage de pélites (triangles pleins : données hivernales ; cercles pleins : données du printemps).
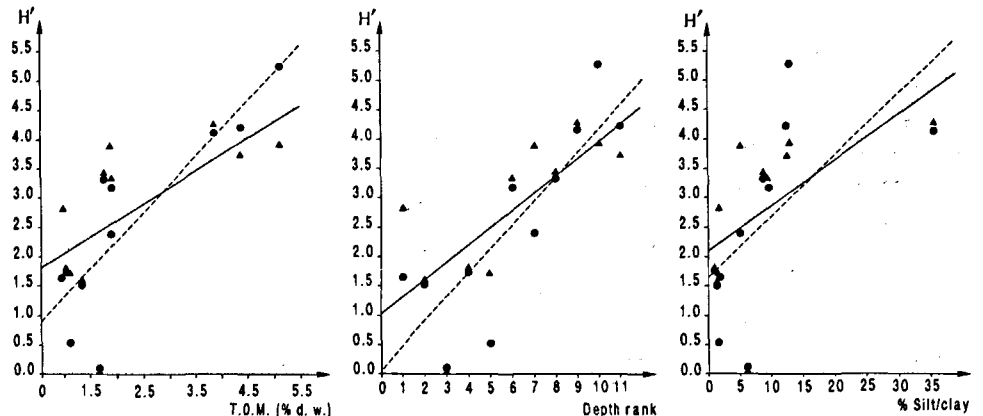
palustris bispinosa, *Scottopsyllus (W.)* sp., *Notopontia* (?) sp. and *Huntemannia jadensis*) were peculiar to the intertidal zone and 124 to the subtidal zone, with only seven species (5 %) present in both zones. No species was found at all stations, but *Halectinosoma herdmani* was missing only from station 105 (in both winter and spring). *Canuella perplexa* and *H. herdmani* were found at all the intertidal stations (the latter in 100 % of the intertidal samples); *Longipedia scotti*, *Haloschizopera pygmaea* and *Mesochra pygmaea* were found at all the subtidal stations (the two latter being absent only at station 65 in spring). In the subtidal zone, *Typhlamphiascus confusus* was missing only from station 101, *Pseudameira crassicornis* and *Asellopsis hispida* from station 82 and *Cletodes tenuipes* and *Normanella incerta* from station 65.

Shannon's diversity indices were positively correlated with TOM and depth (p < 0.05 in winter and p < 0.01 in late spring). Late spring diversity is positively correlated (p < 0.05) with the silt/clay content (Tab. 5; Fig. 2). A rather good positive correlation was also observed between

spring H' and median grain size, but samples in coarse sand were not numerous enough to conclude on this point. On the other hand, diversity was poorly correlated with sorting indices, but there were only two heterogeneous stations sampled.

Species assemblages

Intertidal and subtidal zones

The correspondence factorial analysis (CFA) was first applied to 84 dominant species of both intertidal and subtidal zones for winter and spring (Fig. 3 and 4). The contribution to the total inertia (4.683) of the first three axes is only 41.04 %, distributed as follows:

1st axis	2nd axis	3rd axis
17.28 %	12.16 %	11.60 %

Major absolute contributors to the inertia explained by axis 1 are, in decreasing order: *Canuella perplexa*, *Tachidius discipes* and *Stenhelia (D.) palustris bispinosa*. For axis 2,
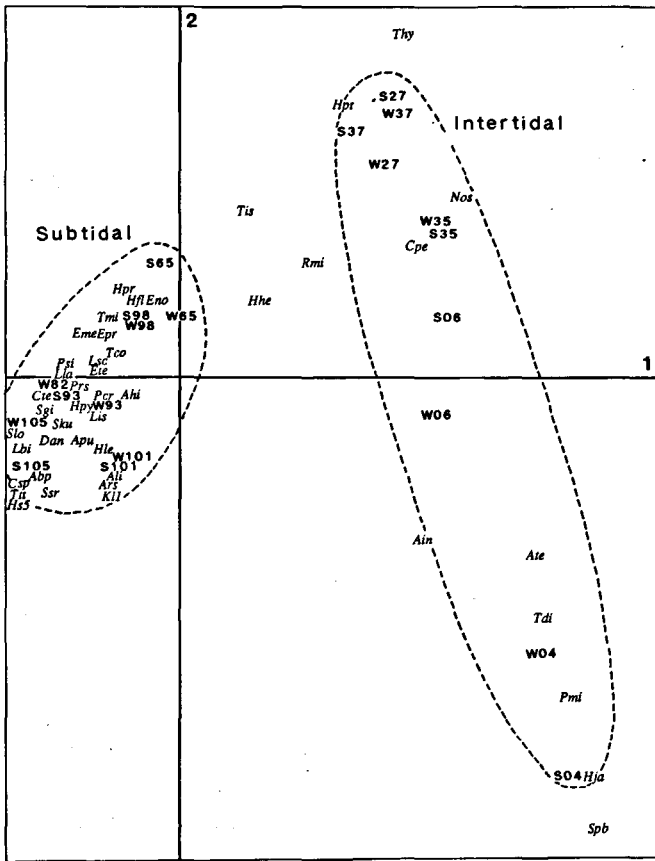
Figure 3

Correspondence factorial analysis graph for intertidal and subtidal zones (plane 1-2). Each sample is represented by a letter (W = winter, S = spring) followed by the station number. Species are usually represented by initials of the genus name and the first two letters of the species name (e. g. Cpe = Canuella perplexa; see Tab. 1). Ellipses roughly delimit assemblages and facies described in the text. S82, Hco and Cli are hidden by W82; Nin, Apa, Dti, Apn, Mat and Has are hidden by W105; Sle, Ava, Apr, Alo, Pax, Kl2, Kl3 and Sin are hidden by Hs5; Hs4 is hidden by Lsc; Hbo is hidden by Ttt; Ecu and Dna are hidden by Rru; Rru, Bim and Dfl are hidden by Sgi; Pbe, Dvu, Tpo, Ppm, Pbr and Adi are hidden by S98; Hpa is hidden by W65; Ssl is hidden by Lis; Prs is hidden by Mpy; Hsi and Hcu are hidden by Cte; Lel is hidden by Ali; Pas is hidden by Ars; Nmu is hidden by Hle; Psi is hidden by Lla; Rwi is hidden by Epr.

Diagramme de l'Analyse Factorielle des Correspondances pour les zones intertidale et subtidale (plan 1-2). Chaque prélèvement est représenté par une lettre (W = hiver, S = printemps) suivie du numéro de la station. Les espèces sont représentées par l'initiale du nom de genre et les deux premières lettres du nom d'espèce (ex. Cpe = Canuella perplexa, voir tabl. 1). Les ellipses délimitent approximativement les peuplements et faciès décrits dans le texte. S82, Hco et Cli sont masqués par W82 ; Nin, Apa, Dti, Apn, Mat et Has sont masquées par W105 ; Sle, Ava, Apr, Alo, Pax, Kl2, Kl3 et Sin sont masquées par Hs5 ; Hs4 est masquée par Lsc ; Hbo est masquée par Ttt ; Ecu et Dna sont masquées par Rru ; Rru, Bim et Dfl sont masquées par Sgi ; Pbe, Dvu, Tpo, Ppm, Pbr et Adi sont masquées par S98 ; Hpa est masquée par W65 ; Ssl est masquée par Lis ; Prs est masquée par Mpy ; Hsi et Hcu sont masquées par Cte ; Lel est masquée par Ali ; Pas est masquée par Ars ; Nmu est masquée par Hle ; Psi est masquée par Lla ; Rwi est masquée par Epr.

major absolute contributors are *Thompsonula hyaenae*, *Stenhelia (D.) palustris bispinosa* and *Huntemannia jadensis*; for axis 3: *Arenotopa* sp., *Leptastacus laticaudatus* and *Kliopsyllus* sp. 1.

Projections of the observations (*i. e.* samples) on the different CFA planes are obviously correlated with those of
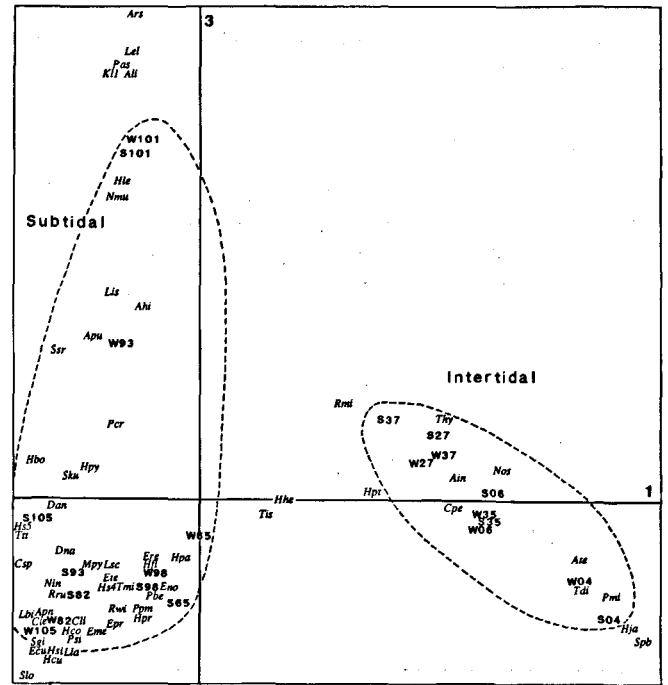

Figure 4

Correspondence factorial analysis graph for intertidal and subtidal zones (plane 1-3); see legend Figure 3. Kl2, Kl3, Sin, Pax, Sle, Ava, Apr and Alo are hidden by Hs5; Bim is hidden by Dti; Tco is hidden by Tmi; Apa is hidden by Dan; Has is hidden by Apn; Abp is hidden by Hbo; Pbr and Adi are hidden by Dvu; Prs is hidden by S82; Ssl is hidden by Lis; Mat and Dti are hidden by Sgi; Dfl is hidden by Cte; Tpo and Dvu are hidden by Ppm.

Diagramme de l'Analyse Factorielle des Correspondances pour les zones intertidale et subtidale (plan 1-3), voir légende figure 3. Kl2, Kl3, Sin, Pax, Sle, Ava, Apr et Alo sont masquées par Hs5 ; Bim est masquée par Dti ; Tco est masquée par Tmi ; Apa est masquée par Dan ; Has est masquée par Apn ; Abp est masquée par Hbo ; Pbr et Adi sont masquées par Dvu ; Prs est masquée par S82 ; Ssl est masquée par Lis ; Mat et Dti sont masquées par Sgi ; Dfl est masquée par Cte ; Tpo et Dvu sont masquées par Ppm.

variables represented here by species. Intertidal and subtidal populations are clearly separated on the 1-2 plane graph (Fig. 3). Consequently axis 1 represents the stability gradient of physico-chemical factors according to depth, station 65 being on the axis 2, at the turning-point of the two systems (intertidal/subtidal). However, winter and spring samples were not distinct. Intertidal station 4 is clearly isolated at the negative extremity of axis 2, with typical estuarine species (*Stenhelia (D.) palustris*, *Huntemannia jadensis*, *Pseudobradya minor*). Stations 27 and 37, less influenced by freshwater input, are grouped at the other side of this axis 2, whilst intertidal station 6 and all subtidal stations are grouped around axis 1. Thus, axis 2 seems to represent salinity.

On the 1-3 plane (Fig. 4), station 101 is isolated at the positive end of axis 3, with numerous mesopsammic species such as *Arenotopa* sp., *Leptastacus laticaudatus* or *Apodopsyllus littoralis*. At the opposite side are grouped muddy or tolerant species such as *Sarsameira longiremis*, *Enhydrosoma curvirostre*, *E. propinquum*, *Cletodes limicola*, *Halectinosoma cooperatum* and *Laophontodes bicor-*

nis. Axis 3 represents the gradient of the silt/clay fraction, much more emphasized in the subtidal zone than in the intertidal one.

Intertidal zone

The CFA was then applied to thirteen dominant species of the intertidal zone, *Tisbe* sp. being eliminated as an outler (Fig. 5 and 6). The contribution to the total inertia (1.421) of the first 3 axes is 79.2 %, distributed in the following manner:

1st axis	2nd axis	3rd axis
42.84 %	23.53 %	12.87 %

Major absolute contributors to the inertia explained by axis 1 are, in decreasing order: *Stenhelia (D.) palustris bispinosa*, *Thompsonula hyaenae*, *Tachidius discipes* and *Huntemannia jadensis*. For axis 2, major absolute contributors are *Canuella perplexa* and *Thompsonula hyaenae*, and for axis 3: *Notopontia* (?) sp., *Arenosetella tenuissima* and *Rhizothrix minuta*.

On the 1-2 plane graph (Fig. 5) again station 4, with typical estuarine or tolerant species, is clearly isolated at the positive end of axis 1, while stations 27 and 37, closer to the subtidal zone, are grouped at the opposite side, as they are in the field. Therefore, axis 1 appears to represent salinity. For the lower stations 27 and 37, winter and spring samples are clearly distinct along axis 2, which may represent seasonal factors (temperature or hydrodynamism, or both). On this 1-2 plane, an antagonism (competition ?) between *Canuella perplexa* and *Thompsonula hyaenae* is also emphasized, as well as different ecological position
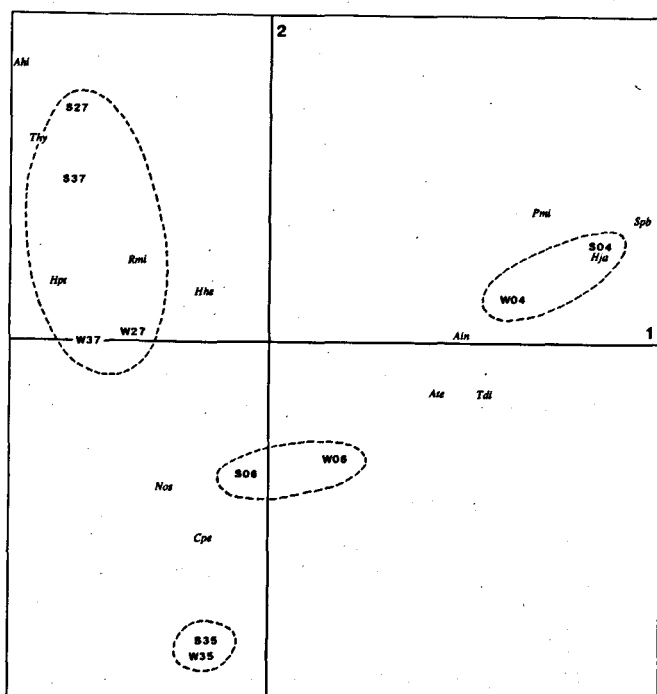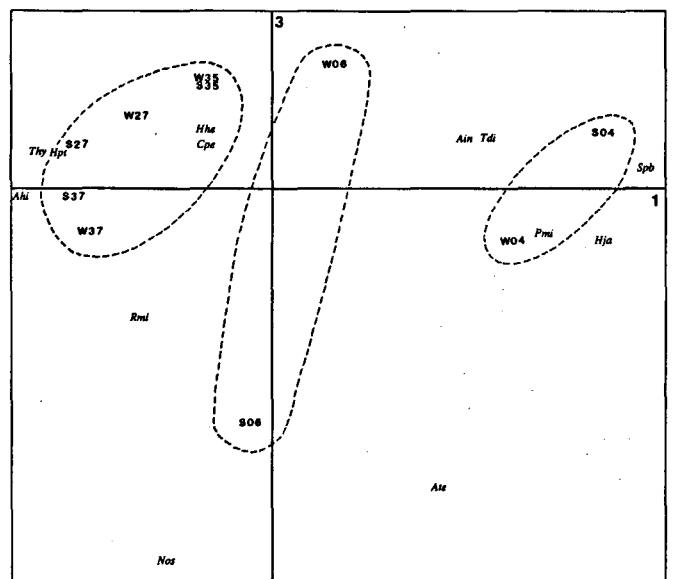

Figure 6

Correspondence factorial analysis graph for intertidal zone (plane 1-3); see legend Figure 3.

Diagramme de l'Analyse Factorielle des Correspondances pour la zone intertidale (plan 1-3), voir légende figure 3.

for *Asellopsis intermedia* and *A. hispida*. Furthermore, station 6 and 35 are each clearly isolated along the negative side of axis 2.

On the 1-3 plane (Fig. 6), station 4 is still isolated at the positive end of axis 1, with estuarine muddy species, while stations closer to the subtidal zone are grouped at the opposite site with euhaline sandy species. This confirms that axis 1 represents the salinity. In the middle, station 6 shows a clear separation between winter and spring samples, the latter being characterized by mesopsammic species. Thus, axis 3 probably represents a seasonal factor such as hydrodynamic conditions, settlement of mesopsammic species becoming easier in more calm conditions at this station 6 at the end of June 1988.

Subtidal zone

A CFA was applied to the 75 dominant species in subtidal samples. The contribution to the total inertia (2.787) of the first 3 axes is 52.26 % distributed as follows:

1st axis	2nd axis	3rd axis
20.32 %	17.85 %	14.09 %

Major absolute contributors to the inertia explained by axis 1 are, in decreasing order: *Arenotopa* sp., *Leptastacus laticaudatus*, *Kliopsyllus* sp. 1 and *Apodopsyllus littoralis* (all mesopsammic species). For axis 2, major absolute contributors are *Halectinosoma herdmani*, *Amphiascus propinqvus*, *Amphiascus longarticulatus* and *Cletodes spinulipes*; and for axis 3: *Amphiascus propinqvus*, *A. longarticulatus*, *Stenhelia (D.) giesbrechti* and *Cletodes tenuipes*.

The 1-2 plane graph (Fig. 7) shows 4 groups of stations and species. Station 101 is clearly isolated and constitutes a first group on the negative side of axis 1, with several mesopsammic species such as *Arenotopa* sp., *Leptastacus*
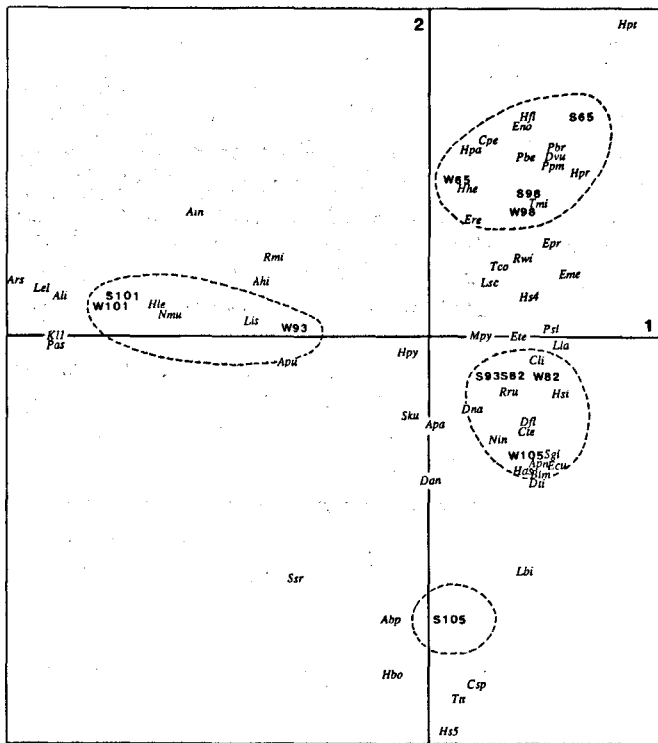

Figure 5

Correspondence factorial analysis graph for intertidal zone (plane 1-2); see legend Figure 3.

Diagramme de l'Analyse Factorielle des Correspondances pour la zone intertidale (plan 1-2), voir légende figure 3.

Figure 7

Correspondence factorial analysis graph for subtidal zone (plane 1-2); see legend Figure 3. Apr, Alo, Sin, Kl2, Kl3, Sle, Ava and Pax are hidden by Hs5; Ssl is hidden by Lis; Hco is hidden by W82; Adi is hidden by Dvu; Hcu is hidden by Hsi; Mat is hidden by Apn; Tpo is hidden by Pbr.

Diagramme de l'Analyse Factorielle des Correspondances pour la zone subtidale (plan 1-2), voir légende figure 3. Apr, Alo, Sin, Kl2, Kl3, Sle, Ava et Pax sont masquées par Hs5 ; Ssl est masquée par Lis ; Hco est masquée par W82 ; Adi est masquée par Dvu ; Hcu est masquée par Hsi ; Mat est masquée par Apn ; Tpo est masquée par Pbr.

laticaudatus, *Apodopsyllus littoralis*, *Kliopsyllus* sp. 1 and *Hastigerella leptoderma*. Sediment of this station 101 is the most heterogeneous, with a sorting coefficient around 2.5. Despite a median grain size < 180 μm, an important silt/clay fraction, and a good sorting coefficient, winter samples of station 93 can be incorporated in this first group with some other mesopsammic species (*Lineosoma* sp., *Scottopsyllus (Sc.) langi*), perhaps because of the presence of maërl which make the sediment more heterogeneous.

At the other side of axis 1, we find almost all the other stations which fall into three further groups. One group, at the negative end of axis 2, contains only the spring samples of station 105, where the sediment is also heterogeneous and badly sorted. Despite an important silt/clay fraction (13 %) and likely due to the very large median grain size (1510 μm) and the presence of maërl, several mesopsammic species were observed at this station in spring (*Kliopsyllus* sp. 2 and sp. 3, *Scottopsyllus (I.) intermedius*, *Hastigerella bozici*), mixed with some typical muddy species (*Laophontodes bicornis* and *Cletodes spinulipes*) and some phytophilous and sandy species.

Around the centre of the graph, another group encompasses the winter samples of stations 82 and 105 and spring samples of stations 82 and 93, with many eurytopous (*i. e.* non significant) species such as *Haloschizopera pygmaea*,

Mesochra pygmaea, *Diarthrodes nanus*, *D. andrewi*, *Ameira parvula*, *Bulbamphiascus imus* and *Dactylopusia tisboides*. Some muddy (station 82 contained more than 30 % of silt/clay) and phytophilous species were mixed in with previous ones: *Cletodes limicola*, *Proameira* sp., *Enhydrosoma curvirostre*, *Rhynchothalestris rufocincta*, *Dactylopodella flava*, *Normanella incerta*. At the upper part of the group, some sandy species are observed: *Halectinosoma similidistinctum*, *Ectinosoma tenuipes*, *Pseudobradya similis*.

The last group, on the positive side of axes 1 and 2, contains the winter and spring samples of near-intertidal stations 65 and 98 (fine grained sediments), with typical sandy species (*Canuella perplexa*, *Harpacticus flexus*, *Pseudobradya beduina*, *Halectinosoma propinquum*, *H. herdmani*, *Ectinosoma reductum*, *Psyllocamptus (P.) minutus*).

From the composition of these different groups of stations and species, we can deduce that axis 1 probably represents the silt/clay content, which is low on the negative side and increases towards the positive side, and axis 2 may represent the heterogeneity of the sediment, with well sorted sands on the positive side and heterogeneous sediments on the negative side.

The 2-3 plane graph (Fig. 8) again shows the originality of station 105 spring samples which are, moreover, clearly distinct from the winter ones, with many mesopsammic species. However, it is difficult to attribute a signification to axis 3 (perhaps hydrodynamic conditions ?).
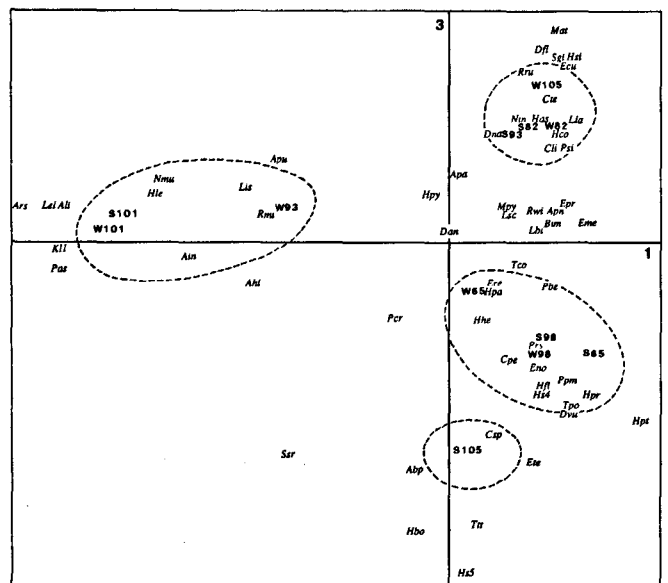

Figure 8

Correspondence factorial analysis graph for subtidal zone (plane 1-3); see legend Figure 3. Apr, Alo, Sin, Kl2, Kl3, Sle, Ava and Pax are hidden by Hs5; Pbr and Adi are hidden by Dvu; Hcu is hidden by Hsi; Ssl is hidden by Lis; Sku is hidden by Hpy; Dti is hidden by Cte; Tmi is hidden by Pbe.

Diagramme de l'Analyse Factorielle des Correspondances pour la zone subtidale (plan 1-3), voir légende figure 3. Apr, Alo, Sin, Kl2, Kl3, Sle, Ava et Pax sont masqués par Hs5 ; Pbr et Adi sont masqués par Dvu ; Hcu est masqué par Hsi ; Ssl est masqué par Lis ; Sku est masqué par Hpy ; Dti est masqué par Cte ; Tmi est masqué par Pbe.

DISCUSSION

Dominance

As expected, intertidal and subtidal populations were clearly different. In the first biotope, as all along the northern Brittany coast (Bodin, 1988), *Canuella perplexa* overwhelmingly dominated (more than 85 %, *cf.* Tab. 1), followed by *Tachidius discipes* and *Halectinosoma herdmani* in winter and by *Thompsonula hyaenae* and *Rhizothrix minuta* in spring. In the subtidal zone, dominances were much lower; *Haloschizopera pygmaea* was generally dominating (around 10 %), followed by *Arenotopa* sp. and *Halectinosoma herdmani* in winter and the same, in reverse order, in spring. Probably as a result of the silt/clay fraction being higher than 5 % in all subtidal stations, *C. perplexa* was never dominant in this zone (0.7 % in winter and 0.3 % in spring). This species was not more dominant in fine clean sands of the Bay of Douarnenez (Bodin, 1984). In this bay, *H. herdmani* had almost the same dominance in fine muddy sands (4.2 %) where *H. pygmaea* (named *H. junodi*) was rare; but other secondary species cited above were not collected.

Biodiversity

"Despite the handicap of insufficient ecological data, or perhaps because of it, theorization and speculation as to the possible causes of diversity gradients has been frequent and varied" (Pianka, 1966). For instance, the widespread hypothesis of a decreasing species richness from high latitudes towards the equator (Klöpfer, 1959; Fischer, 1960) can be explained by numerous components of the diversity (Pianka, *op. cit.*), and was demonstrated for several marine macrobenthic groups (Fischer, 1960; Sanders, 1968). Such gradients are however not universal and, in the marine environment, are questionable, especially for meiofauna. In a revision of published data on species diversity of marine nematode assemblages, Boucher (1990) found significantly higher values in temperate coastal sediments than in tropical open sea and lagoonal sublittoral sediments of similar depth. But tropical and equatorial data on harpacticoid diversity are still scant, and it is always difficult to interpret overall values, especially for diversity indices which depend more or less on the sample size and on logarithmic transformations of data (Hicks, 1980). Despite these limitations, an attempt was made to compare our results with those of the literature (Tab. 6). In the temperate Bay of Saint-Brieuc, we found some of the highest harpacticoid copepod diversities ever recorded in the subtidal zone; only Soyer (1971) recorded higher values in the Mediterranean Sea, around Banyuls-sur-Mer. Moore (1979 *b*) also recorded similar diversity (H'= 5.21) in coarse muddy sands of the Irish Sea. This contradicts Hicks and Coull's assertion (1983) that "in shallow-water sedimentary habitats, harpacticoid diversity appears similar worldwide".

Generally speaking, heterogeneous sediments and coarse sands are favourable conditions for high meiofauna biodiversity and evenness in shallow sites, especially in spring-summer season and in stable zones (McIntyre and Murison, 1973; Soyer and Bodiou, 1974; Heip and Decraemer, 1974; Wolf, 1974; Moore, 1979 *b*; Hicks, 1982; Willems *et al.*, 1982; Bodin, 1984; Vanosmael *et al.*, 1985). Current explanations are either limited predation due to the complex structure of these biotopes (Menge and Sutherland, 1976), or a greater input of nutrients and more diverse feeding patterns due to the higher permeability of coarse sediments (Williams, 1972), while Marcotte (1986) put forward the hypothesis that the hydrodynamic stability of these sediments, and their capacity to accommodate mesopsammic species fostered higher diversity. Finally, mechanisms controlling biodiversity can operate simultaneously or separately, and correlation does not mean necessarily causation (Pianka, 1966).

According to Cancela da Fonseca (1966), an evenness frequently higher than 0.80 is an indication of a balanced population: here it is the case for 8 samples out of 22, only one of them being in the intertidal zone. Due to the instability of physico-chemical factors, mainly the salinity (Coull, 1970; van Es *et al.*, 1980; Govaere *et al.*, 1980; Bouwman, 1981; Kondalarao, 1984; Radziejewska, 1984; Castel, 1986), the lowest diversities and evenness were recorded in this intertidal zone. Such low values were also recorded in the intertidal fine muddy sands of North-Finistère (Bodin and Jackson, 1989), and in the intertidal fine sands of the Isle of Man (Moore, 1979 *a*).

The silt/clay content, sometimes high in the Bay of Saint-Brieuc, is not necessarily a factor unfavourable to biodiversity. Moore (1979 *b*) recorded values up to 4.4 in sandy muds and 5.1 in pure muds of the Irish Sea, and we also recorded here high values in muddy sands of station 82 (Tab. 3).

Biogeography

The Bay of Saint-Brieuc harpacticoid fauna presents a real originality. As already stated above, at least thirty species and probably six genera are new to science and will be described later. Moreover, males of three species (*Halectinosoma similidistinctum* Lang (1965), *Halophytophilus* sp. and *Diarthrodes andrewi* (T. Scott)) were discovered here for the first time. Furthermore, ten species are reported for the first time in the Atlantic Ocean: *Halectinosoma similidistinctum* Lang (1965), *Hastigerella grandimandibularis* Wells (1967), *Sigmatidium kunzi* Mielke (1979), *Amphiascus propinqvus* Sars, *Sarsameira propinqua* (T. Scott), *Paramesochra (?) helgolandica* Kunz, *Scottopsyllus (Sc.) langi* Mielke (1984), *Mesopsyllus atargatis* Por (1960), *Psammocamptus axi* Mielke (1975) and *Cletodes spinulipes* Por (1967). Lastly, seven species are new for the French harpacticoid fauna: *Tisbe perplexa* Volkmann (1979), *Diarthrodes andrewi* (T. Scott), *Rhyncholagena spinifera* (Farran), *Ameira divagans* Nicholls (1940), *Apodopsyllus littoralis* (Nicholls, 1939), *Heteropsyllus curticaudatus* T. Scott and *Esola longiremis* (T. Scott). Thus, despite the great number of new species, the harpacticoid fauna of this bay seems to be cosmopolitan. Although all sediment types were not sampled, the high diversity found in the Bay of Saint-Brieuc, as well as

Table 6

Compared data on harpacticoid copepod diversity and evenness (see legend Tab. 3). sed. = sediment, s = sand, f = fine, c = coarse, med. = medium, int. = intertidal, subt. = subtidal, n = north, w = west, e = east, AO = Atlantic Ocean, PO = Pacific Ocean, IO = Indian Ocean, α = Fisher, Corbet and Williams diversity index, SR = Margalef diversity index.

Données comparées sur la diversité et l'équitabilité des copépodes harpacticoïdes (voir légende du tab. 3). sed. = sédiment, s = sable, f = fin, c = grossier, med. = moyen, int. = intertidal, subt. = subtidal, n = nord, w = ouest, e = est, AO = Océan Atlantique, PO = Océan Pacifique, IO = Océan Indien, α = indice de diversité de Fisher, Corbet and Williams, SR = indice de diversité de Margalef.

Sediment	Location	Nb. species	H'(or *H)	α	SR	J'(ou J)	References
salt marsh	N-Inlet estuar. (AO)	23	1.5-1.61		11-11.5	0.63-0.68	Bell, 1979
fine muddy sand	Douarnenez Bay (AO)	38	4	8		0.76	Bodin, 1984
fine sand	idem	16	2.9	3.5		0.72	idem
coarse sand	idem	49	4.1	14		0.73	idem
int. ± muddy FS	n-Finistère, Channel	57	0.04-2.76			0.02-0.65	Bodin & Jackson, 1989
idem	w-Ireland (AO)	31	1.13-3.15			0.38-0.81	idem
int. fine sand	S. Brieuc B., Channel	3-9	0.04-2.81	0.5-3.0	0.28-1.93	0.03-0.89	} Bodin & Le Guellec
subt. f.- c. sand	idem	9-73	2.39-5.26	3.0-21.2	1.96-11.0	0.67-0.95	} (present study)
infr. fine sand	Mediterr. (10-20 m)		3.67-4.88	6.2-12.9			Bodiou, 1982
mud to fine sand	Ems estuary (N-Sea)	26					Bouwman, 1981
mud to muddy sand	Gironde estuar. (AO)	17-18	1.82-2.35			0.51-0.76	Castel, 1986
heter. muddy sand	Arcachon marsh (AO)	26	3.36			0.74	idem
muddy sands	Arcachon reservoirs	7-22	2.06-2.81			0.65-0.73	idem
muddy sands	Arcachon reservoirs	4-19	0.4-1.9				Escaravage & Castel, 1989
fine to c. sand	Bermuda platform (AO)	22-40	1.6-3.1				Coull, 1970
mud and FS to CS	Bermuda platform (AO)		1.19-4.54			0.42-0.87	Coull, 1972
mud	N-Inlet estuar. (AO)	8.5-11.1	1.47-1.58			0.53-0.55	Coull & Fleeger, 1977
sand	idem	10.3-12.5	1.44-1.69			0.43-0.57	idem
int. marsh	N-Inlet estuar. (AO)	19	1.50			0.63	Fleeger, 1980
subt. mud	idem	17	1.44-1.69			0.66-0.70	idem
subt. sand	idem	10	1.47-1.58			0.58-0.74	idem
subt. muddy sand	South. Bight, N. Sea	10-54	0.18-2.73				Govaere et al., 1980
subt. coarse sand	Virgin Islands (AO)	7-15	0.9-3.3				Hatzband & Hummon, 1974
subt. coarse sand	W-Norway, North Sea	total	1.7				Drzycimski, 1969
subt. muddy FS		=	2.5				idem
bathyal muds		156	3.3				idem
muddy sands	West. Scheldt estuary	7-11	*0.43-0.87				Heip et al., 1984
mud to fine sand	W-Ostend, North Sea	5-26	*0.13-1.30				Herman et al., 1985
estuar. medium S	River Ythan, N. Sea	99		3.27-6.84			Hockin, 1982
coarse sand	N-Inlet estuar. (AO)	7-15	0.91-1.23			0.34-0.51	Ivester, 1980
medium sand	idem	5-14	0.77-2.10			0.43-0.88	idem
muds	idem	7-12	0.95-1.97			0.43-0.79	idem
ñ polluted sed.	Marseille, Medit. Sea	1-15	0.0-3.47		0.0-4.12	0.0-0.91	Keller, 1986
int. sands	L-Angeles L-Beach, PO	38					Knatz, 1986
estuar. sediments	E-coast India (IO)	22					Kondalarao & Ramana Murty, 1988
int. sands	Isle of Man (Channel)	1.0-12.6	0.1-3.4			0.09-0.98	Moore, 1979a
muddy gravel	Irish Sea	22	3.56			0.80	Moore, 1979 b
coarse sand	idem	33	5.13-5.19			0.91-0.93	idem
coarse muddy sand	idem	23-32	4.12-5.21			0.79-0.87	idem
shallow fine sand	idem	6-7	1.97-2.08			0.74-0.76	idem
deep fine sand	idem	9-20	2.35-3.94			0.74-0.88	idem
fine muddy sand	idem	20-25	3.91-4.28			0.73-0.80	idem
muddy sand	idem	28	4.79			0.88	idem
sandy mud	idem	24-26	4.23-4.56			0.78-0.81	idem
pure mud	idem	20-34	4.01-5.14			0.83-0.94	idem
Macrocyst. pyrif. fronds	Argentine (AO)	34	0.20-2.05			0.01-0.57	Pallares & Hall, 1974a,b
plankton		65	1.90-4.72			0.38-0.93	idem
mud to gravel	Elat Gulf, Red Sea	15					Por, 1979
org. enrich. sed.	Pomer. Bay, Balt. Sea		0.04-0.74				Radziejewska, 1984
int. fine to coarse sand	Andaman and Nicobar Islands (IO)	70					Rao, 1980
f. sand to gravel	Lakshadweep (IO)	35					Rao & Misra, 1983
mud to gravel	W-Mediterran. Sea	63-129		13.5-29.0			Soyer, 1971
med. to c. sand	Kwinte bank, N. Sea	16-42					Vanosmael et al., 1985
estuar. sediments	English Channel	25	0.40-2.41				Warwick & Gee, 1984
faecal mounds of *Streblosom. bairdi*	Oslofj., Norweg. Sea	13					Warwick et al., 1986
subt. f.- c. sand	Kwinte bank, N. Sea	5-37	*1.24-3.15			0.49-0.86	Willems et al., 1982
fine sand	Grevelingen, N. Sea	4-14	*0.75-2.8				Willems et al., 1984

in the Bay of Douarnenez (Bodin, 1984), suggests that the real biodiversity of the European coasts is still far from being known.

Comparing harpacticoid populations (intertidal + subtidal), the Bay of Saint-Brieuc had 36 species (26 %) in common with Douarnenez Bay (Bodin, 1984) and 24 % if only subtidal zones are compared. The best correlation is with fine muddy sands: 23 shared species (16.4 %) and even 24 (17.1 %) if intertidal species of Saint-Brieuc are taken into account. In the latter case, there are still 14 species (10 %) in common with coarse dunar sands of the Bay of Douarnenez, and 12 (8.6 %) in common with fine clean sands.

With the whole intertidal populations of La Rochelle (Bodin, 1977), the Bay of Saint-Brieuc shared 46 species (33 %), 33 species (24 %) being in common with the fine clean sands population, 28 species (20 %) with the sandy muds population, and 19 species (13.6 %) in common with pure intertidal muds population.

Surprisingly, the population of the Bay of Saint-Brieuc had 57 species (41 %) in common with Mediterranean populations surrounding Banyuls-sur-Mer (Soyer, 1971), and 28 species (20 %) in common with populations surrounding Marseille (Bodin, 1964), but with no clear similar assemblage.

Harpacticoid copepod assemblages

As expected, CFA graphs (Fig. 3 and 4) show an obvious separation between harpacticoid populations of the intertidal zone (with *Canuella perplexa*, *Thompsonula hyaenae*, *Rhizothrix minuta*, *Halectinosoma herdmani*, *Tachidius discipes* and *Stenhelia (D.) palustris bispinosa* as main species, dominance and frequency taken into account) and the subtidal zone (with *Haloschizopera pygmaea*, *Halectinosoma herdmani*, *Leptastacus laticaudatus*, *Mesochra pygmaea*, *Ameira pusilla*, *Cletodes tenuipes*, *Diarthrodes andrewi*, *Normanella incerta* and *Enhydrosoma propinquum* as main species).

In each zone, influence of some important ecological factors was highlighted, particularly the influence of the salinity gradient in the intertidal zone; and the influence of sediment heterogeneity, grain size and silt/clay content (varying seasonally) in the subtidal zone.

Thus, in the Bay of Saint-Brieuc, the intertidal zone could be considered as a single fine sand assemblage in which a low salinity facies (*i. e.* a special aspect of the fauna induced by the dominance of an environment factor, here the low salinity at station 4) can be distinguished with typical estuarine species such as *Stenhelia (D.) palustris bispinosa*, *Tachidius discipes*, *Huntemannia jadensis*, and *Pseudobradya minor*, *Asellopsis intermedia* being well represented. Curiously, station 35 is closer to station 6, situated in a different cove, than to station 37 which was very close; but they belong to the same bio-sedimentary entity.

As for the subtidal sites, the species could be distributed in two sets:

- a shallow fine sand assemblage (stations 65 and 98) with *Ectinosoma normani*, *Halectinosoma herdmani*, *Tryphoema porca*, *Harpacticus flexus*, *Halectinosoma*

propinquum, but also *Tachidiella minuta*, *Enhydrosoma propinquum*, etc.;

- a large heterogeneous more or less muddy-sand assemblage, where several facies can be distinguished:

1) a medium badly sorted muddy-sand facies (station 101 and winter samples of station 93), with *Arenotopa* sp., *Leptastacus laticaudatus*, *Kliopsyllus* sp. 1, *Apodopsyllus littoralis*, *Halectinosoma herdmani*, *Haloschizopera pygmaea*, *Normanella mucronata*, *Parevansula* sp., *Asellopsis hispida*, etc.;

2) a very muddy-sand facies (station 82, winter samples station 105 and spring samples station 93) with eurytopous, muddy and phytophilous species such as *Haloschizopera pygmaea*, *Cletodes tenuipes*, *Enhydrosoma propinquum*, *Normanella incerta*, *Dactylopodella flava*, *Stenhelia (D.) giesbrechti*, *Mesochra pygmaea*, *Halectinosoma cooperatum*, etc.;

3) a very heterogeneous coarse muddy-sand (with maërl) facies (spring samples station 105) with *Amphiascus propinqvus*, *A. longarticulatus*, *Cletodes spinulipes*, *Diarthrodes andrewi*, *Psammocamptus axi*, *Haloschizopera pygmaea*, but also mesopsammic species such as *Scottopsyllus (I.) intermedius*, *Sc. (Sc.) robertsoni* (?), *Hastigerella bozici*, *Kliopsyllus* sp. 2. The importance of phytophilous species in this station 105 can be explained by the proximity of rocks to the northwest.

Although it is clearly shown for some stations (6, 105), no obvious seasonal difference between populations was demonstrated. Perhaps the low gap between winter and spring temperatures (about 10 to 12° C) does not allow such a difference? Even for winter/spring differences at stations 6 and 105, it seems that sediment factors are more involved than temperature.

Comparing harpacticoid assemblages highlighted by CFA analysis with those of macrofauna defined by Gros and Hamon (1988) and by Thouzeau and Hamon (1992), a good correlation is found:

- station 4 is well individualized in the "intertidal oligohalin fine muddy sands" with *Macoma balthica*, *Nereis diversicolor* and *Hydrobia ulvae* described by Gros and Hamon and corresponds to a low salinity facies;

- stations 6 and 35 clearly belong to the "intertidal fine sands" with *Tellina tenuis* and *Cerastoderma edule*.

- station 37 is closely correlated with station 27 due to their field proximity, although they are supposed to belong to different macrofauna assemblages: respectively an "impoverishment facies of intertidal fine sands" with *T. tenuis* but without *C. edule*, and "subtidal fine sands" with *Tellina fabula* and *Magelona filiformis*;

- station 65 clearly belongs to the subtidal zone but is grouped with station 98 on the 1-2 plane subtidal graph (Fig. 7), although they are supposed to belong respectively to the "fine clean sands" with *Tellina fabula* and *Magelona filiformis* and to the "fine muddy sands" with *Corbula gibba* and *Aponuphis grubii* (after Thouzeau and Hamon, 1992). Their common sediment structure and situation near the zero level subjects them to the same biological consequences, then to approximately the same species composition.

There are some differences between other subtidal macrofauna assemblages of Gros and Hamon (1988) and Thouzeau and Hamon (1992), those of the latter being somewhat more detailed. According to the first authors, stations 82, 93 and 101 belong (with sation 98) to "fine more or less muddy sands" with *Hyalinoecia bilineata* and *Corbula gibba*, while station 105 belongs to "heterogeneous muddy sands" with *Tapes rhomboides*. According to Thouzeau and Hamon, station 82 belongs to a "muddy facies of the fine muddy sands" with *Corbula gibba*, *Aponuphis grubii*, *Ampelisca tenuicornis*, *Ampharete grubei* and *Crepidula fornicata*, while stations 93, 101 and 105 are supposed to belong to a "lower muddy facies" with more *Ampelisca tenuicornis*, *A. brevicornis*, *Aponuphis grubii* and *Clymene oerstedii*. Actually, harpacticoid copepod assemblages did not overlap exactly any of these macrofauna communities.

Por (1959; 1960; 1964 *a* and *b*) and Soyer (1971) defined "isocommunities", *i. e.* assemblages with the same families and genera but possibly different species. Compared with other European harpacticoid copepod assemblages, only the intertidal zone as a whole is similar to the fine "Brandungssand" described from the North Sea *Bathyporeia*-zone by Noodt (1957), except for the scarcity of *Harpacticus flexus*, never dominant here, and different dominances for other species. Moreover, despite the important percentage of common species with Banyuls-sur-Mer fauna described by Soyer (1971), no real "isocommunity" with this area of the Mediterranean Sea was found in the Bay of Saint-Brieuc.

Diversity can be considered as a measurement of the "health" and stability of a biotope: it varies inversely with pollution (Wilhm and Dorris, 1968 and Orciari and Hummon, 1975, cited in Legendre and Legendre, 1984). Considering the high harpacticoid copepod diversity found here, at least in subtidal zone, the Bay of Saint-Brieuc seems far from being eutrophicated. However, if we consider this area as an "eutrophicated coastal ecosystem" as Gros et al. (1990) did, then the copepod community could be situated near a "stimulation" phase sometimes described for macrofauna in unbalanced ecosystems (Pearson and Rosenberg, 1978; Glémarec, 1986), characterised by a large number of species and moderate abundance and biomass.

The sediment structure of the subtidal zone, both muddy and heterogeneous, permits a coexistence of mesopsammic and muddy species and great diversification in the harpacticoid fauna of this bay. Thus, importance of the heterogeneity factor in the species diversity is supported.

In addition to a clear difference between populations of intertidal and subtidal zones, it is possible to highlight distinct assemblages and facies in both: a) intertidal fine sand assemblage, with a low salinity facies; b) subtidal shallow fine sand assemblage; c) large subtidal heterogeneous more or less muddy-sand assemblage, with three facies: medium badly sorted muddy sand, finer muddy sand and very heterogeneous and coarse muddy sand.

These assemblages and facies more or less mirror macrofauna communities defined previously in the Bay of Saint-Brieuc, but only the intertidal zone has a clear isocommunity in the Bathyporeia-zone of the North Sea.

CONCLUSIONS

The harpacticoid copepod assemblage of the Bay of Saint-Brieuc is characterized by an exceptional diversity, with many new species and some others rare and described from faraway sites (Pacific and Indian Oceans), which gives a cosmopolitan character to this fauna. A similar peculiarity has already been reported (Bodin, 1984) from the Bay of Douarnenez (South-Finistère, Brittany). These bays represent precious reserves of harpacticoid copepod species.

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REFERENCES

Bell S.S. (1979). Short- and long-term variation in a high marsh meiofauna community. *Estuar. coast. mar. Sci.*, 9, 331-350.

Bodin P. (1964). Recherches sur la systématique et la distribution des Copépodes Harpacticoïdes des substrats meubles des environs de Marseille. *Recl Trav. Stn mar. Endoume*, 51, 35, 107-183.

Bodin P. (1977). Les peuplements de Copépodes Harpacticoïdes (Crustacea) des sédiments meubles de la zone intertidale des côtes charentaises (Atlantique). *Mém. Mus. natn. Hist. nat., Paris, Zool.*, 104, 1-120.

Bodin P. (1984). La méiofaune et les peuplements de Copépodes Harpacticoïdes de la baie de Douarnenez (Finistère). *Annls Inst. océanogr., Paris*, 60, 1, 5-17.

Bodin P. (1988). Results of ecological monitoring of three beaches polluted by the "Amoco Cadiz" oil spill: development of meiofauna from 1978 to 1984. *Mar. Ecol.-Prog. Ser.*, 42, 105-123.

Bodin P. and D.F. Jackson (1989). A comparison of the intertidal harpacticoid copepod assemblages of sandy beaches in Galway Bay (Ireland) and Northern Brittany (France). *J. mar. biol. Ass. U.K.*, 69, 573-588.

Bodiou J.-Y. (1982). Copépodes Harpacticoïdes (Crustacea) des sables fins infralittoraux de Banyuls-sur-Mer. II: Variations saisonnières qualitatives du peuplement. *Vie Milieu*, 30, 3-4, 269-274.

Boucher G. (1990). Pattern of nematode species diversity in tempe-rate and tropical subtidal sediments. *Pubbl. Staz. zool. Napoli, Mar. Ecol.*, 11, 2, 133-146.

Bouwman L.A. (1981). The meiofauna of the Ems estuary. *Mar. Zool.*, 4, 153-157.

Cancela da Fonseca J.P. (1966). Théorie de l'information et diversi-té spécifique. *Bull. Mus. natn. Hist. nat., Paris, sér. II*, 38, 961-968.

Castel J. (1986). Facteurs de distribution des peuplements de copé-podes méiobenthiques dans les écosystèmes eutrophes littoraux (côte atlantique). *Cah. Biol. mar.*, 27, 441-455.

Chardy P., M. Glémarec and A. Laurec (1976). Application of inertia methods to benthic marine ecology: practical implications of the basic options. *Estuar. coast. mar. Sci.*, 4, 179-205.

Coull B.C. (1970). Shallow water meiobenthos from the Bermuda Platform. *Oecologia*, 4, 325-357.

Coull B.C. (1972). Species diversity and faunal affinities of meio-benthic Copepoda in the deep sea. *Mar. Biol.*, 14, 1, 48-51.

Coull B.C. and J.W. Fleeger (1977). Long-term temporal variation and community dynamics of meiobenthic copepods. *Ecology*, 58, 1136-1143.

Drzycimski I. (1969). Harpacticoida (Copepoda) wod morskich oko-lic Bergen (zachodnie wybrzese norwegii) i ich ekologia. *Rozpr. Wyzs. Szk. Roln. Szczecinie*, 17, 1-72.

van Es F.B., M.A. van Arkel, L.A. Bouwman and H.G.J. Schröder (1980). Influence of organic pollution on bacterial, macro-benthic and meiobenthic populations in intertidal flats of the Dollard. *Neth. J. Sea Res.*, 14, 3/4, 288-304.

Escaravage V. and J. Castel (1989). Application de la notion de confinement aux peuplements méiobenthiques des lagunes endiguées du bassin d'Arcachon (côte atlantique). *Acta Oecologica, Oecol. gen.*, 10, 1, 1-17.

Fischer A.G. (1960). Latitudinal variations in organic diversity. *Evolution*, 14, 64-81..

Fisher R.A., A.S. Corbet and C.B. Williams (1943). The relation between the number of species and the number of individuals in a random sample of an animal population. *J. Anim. Ecol.*, 12, 42-58.

Fleeger J.W. (1980). Community structure of an estuarine meioben-thic copepod assemblage. *Estuar. coast. mar. Sci.*, 10, 107-118.

Glémarec M. (1986). Ecological impact of an oil spill: utilisation of biological indicators. *Wat. Sci. Tech.*, 18, 203-211.

Govaere J., D. van Damme, C. Heip and L. de Coninck (1980). Benthic communities in the Southern Bight of the North Sea and their use in ecological monitoring. *Helgoländer Meeresunters.*, 33, 507-521.

Gros P. and D. Hamon (1988). Typologie biosédimentaire de la baie de Saint-Brieuc (Manche Ouest), et estimation de la biomasse des catégories trophiques macrozoobenthiques. Rapport IFREMER/DERO-88-27 EL, 1-153.

Gros P., M. Blanchard, P. Chardy, P. Gentien, D. Hamon and Y. Monbet (1990). Euphorbe project: quantifying energy and matter fluxes through the benthic trophic web in an eutrophicated coastal ecosystem. *Rapport de l'Atelier franco-suédois sur l'Environnement, Chambéry, 30 September-3 October 1990*, 1-18.

Hartzband D.J. and W.D. Hummon (1974). Sub-community struc-ture in subtidal meiobenthic Harpacticoida. *Oecologia*, 14, 37-51.

Heip C. and W. Decraemer (1974). The diversity of nematode communities in the Southern North Sea. *J. mar. biol. Ass. U.K.*, 54, 251-255.

Heip C., R. Herman and M. Vincx (1984). Variability and produc-tivity of meiobenthos in the Southern Bight of the North Sea. *Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer*, 183, 51-56.

Herman R., M. Vincx and C. Heip (1985). Meiofauna of the Belgian coastal waters: spatial and temporal variability and producti-vity, in: Biological processes and translocations, Actions de Recherches concertées, C. Heip and P. Polk, editors. Action Interuniversitaire, Océanologie, Rapport final, 3, 41-63.

Hicks G.R.F. (1980). Structure of phytal harpacticoid copepod assemblages and the influence of habitat complexity and turbidity. *J. expl mar. Biol. Ecol.*, 44, 157-192.

Hicks G.R.F. (1982). Habitat structure, disturbance, and equili-brium in crustacean communities. *Pubbl. Staz. zool. Napoli, Mar. Ecol.*, 3, 1, 41-51.

Hicks G.R.F. and B.C. Coull (1983). The ecology of marine meioben-thic harpacticoid copepods. *Oceanogr. mar. Biol. a. Rev.*, 21, 67-175.

Hockin D.C. (1982). The harpacticoid copepod fauna of the River Ythan and its estuary, Aberdeenshire, Scotland. *J. mar. biol. Ass. U.K.*, 62, 3, 729-736.

Ivester M.S. (1980). The distribution of meiobenthic copepods along a sediment gradient: factor and niche analyses. *Bull. mar. Sci.*, 30, 3, 634-645.

Keller M. (1986). Structure des peuplements méiobenthiques dans le secteur pollué par le rejet en mer de l'égout de Marseille. *Annls Inst. océanogr., Paris*, 62, 1, 13-36.

Klöpfer P.H. (1959). Environmental determinant of faunal diversity. *Am. Naturalist*, 93, 337-342.

Knatz G. (1986). Temporal distribution and reproductive patterns of harpacticoid copepods from Los Angeles-Long Beach harbors. *J. crustacean Biol.*, 6, 1, 79-88.

Kondalarao B. (1984). Distribution of meiobenthic harpacticoid copepods in the Gautami-Godavari estuarine system. *Indian J. mar. Sci.*, 13, 80-84.

Kondalarao B. and K.V. Ramana Murty (1988). Ecology of interti-dal meiofauna of the Kakinada Bay (Gautami-Godavari estuarine system), east coast of India. *Indian J. mar. Sci.*, 17, 40-47.

Lang K. (1965). Copepoda Harpacticoidea from the Californian Pacific coast. *K. svenska vetensk. Akad. Handl.*, 10, 2, 1-566.

Legendre L. and P. Legendre (1984). *Écologie numérique. 1: Le traitement multiple des données écologiques*. Masson, éditeur, Paris, 335 pp.

Le Guellec C. and P. Bodin (1992). Meiobenthos of the Bay of Saint-Brieuc (North Brittany, France). I: Quantitative distribution in subtidal and intertidal zones. *Oceanologica Acta*, 15, 6, 661-671 (this issue).

Marcotte B.M. (1986). Sedimentary particle sizes and the ecological grain of food resources for meiobenthic copepods. *Estuar. coast. Shelf Sci.*, 23, 3, 423-427.

Margalef D.R. (1957). Information theory in ecology. *Gen. Syst.*, 3, 36-71.

McIntyre A.D. and D.J. Murison (1973). The meiofauna of a flat-fish nursery ground. *J. mar. biol. Ass. U.K.*, 53, 1, 93-118.

Menge B.A. and J.P. Sutherland (1976). Species diversity gra-dients: synthesis of the role of predation, competition, and temporal heterogeneity. *Am. Naturalist*, 110, 351-369.

Mielke W. (1975). Systematik der Copepoda eines Sandstrandes der Nordseeinsel Sylt. *Mikrofauna Meeresbodens*, 52, 1-134.

Mielke W. (1979). Interstitielle Fauna von Galapagos. XXV. Longipediidae, Canuellidae, Ectinosomatidae (Harpacticoida). *Mikrofauna Meeresbodens*, 77, 1-107.

Mielke W. (1984). Interstitielle Fauna von Galapagos. XXXI: Paramesochridae (Harpacticoida). *Microfauna Mar.*, 1, 63-147.

Moore C.G. (1979 a). The zonation of psammolittoral harpacticoid copepods around the Isle of Man. *J. mar. biol. Ass. U.K.*, 59, 3, 711-724.

Moore C.G. (1979 b). Analysis of the associations of meiobenthic Copepoda of the Irish Sea. *J. mar. biol. Ass. U.K.*, 59, 4, 831-849.

Nicholls A.G. (1939). Some new sand-dwelling copepods. *J. mar. biol. Ass. U.K.*, 23, 2, 327-341.

Nicholls A.G. (1940). Marine harpacticoids and cyclopids from the shores of the St. Lawrence. *Fauna Flora Laurent.*, 2, 241-316.

Noodt W. (1957). Zur Ökologie der Harpacticoidea (Crust. Cop.) des Eulitorals der deutschen Meeresküste und der angrenzenden Brackgewässer. *Z. Morph. Ökol. Tiere*, 46, 149-242.

Orciari R.D. and W.D. Hummon (1975). A comparison of benthic oligochaete populations in acid and neutral lentic environments in southeastern Ohio. *Ohio J. Sci.*, **75**, 44-49.

Pallares R.E. and M.A. Hall (1974 *a*). Analisis bioestadistico-ecologico de la fauna de copepodos asociados a los bosques de *Macrocystis pyrifera*. *Physis*, **33A**, 86, 275-319.

Pallares R.E. and M.A. Hall (1974 *b*). Analisis bioestadistico-ecologico de la fauna de copepodos asociados a los bosques de *Macrocystis pyrifera*. Conclusion. *Physis*, **33A**, 87, 409-432.

Pearson T.H. and R. Rosenberg (1978). Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanogr. mar. Biol.*, **16**, 229-311.

Pianka E.R. (1966). Latitudinal gradients in species diversity: a review of concepts. *Am. Naturalist*, **100**, 33-46.

Pielou E.C. (1975). *Ecological diversity*. John Wiley and Sons, Wiley Interscience Publ., New York, USA.

Por F.D. (1959). *Harpacticoide noi (Copepoda, Crustacea) din mîlurile Mǎrii Negre*. Acad. Republ. Pop. Romine, 11, 347-368.

Por F.D. (1960). *Mesopsyllus atargatis*, n. g., n. sp., ein neuer Harpacticoide (Copepoda, Crustacea) aus dem Schwarzen Meer. *Trav. Mus. Hist. nat. Gr. Antipa*, **2**, 177-181.

Por F.D. (1964 *a*). A study of the Leventine and Pontic Harpacticoida (Copepoda, Crustacea). *Zoologische verh.*, **64**, 1-128.

Por F.D. (1964 *b*). Les Harpacticoïdes (Copepoda, Crustacea) des fonds meubles du Skagerak. *Cah. Biol. mar.*, **5**, 3, 233-270.

Por F.D. (1967). Level bottom Harpacticoida (Crustacea, Copepoda) from Elat (Red Sea); Part I. *Israel J. Zool.*, **16**, 101-165.

Por F.D. (1979). The Copepoda of Di Zahav pool (Gulf of Elat, Red Sea). *Crustaceana*, **37**, 1, 13-30, 4 pl.

Radziejewska T. (1984). Meiofauna communities in organically enriched estuarine environment. *Limnologica*, **15**, 2, 425-427.

Rao G.C. (1980). On the zoogeography of the interstitial meiofauna of the Andaman and Nicobar islands, Indian Ocean. *Rec. zool. Surv. India*, **77**, 153-178.

Rao G.C. and A. Misra (1983). Meiofauna from Lakshadweep, Indian Ocean. *Cah. Biol. mar.*, **24**, 51-68.

Sanders H.L. (1968). Marine benthic diversity: a comparative study. *Am. Naturalist*, **101**, 925, 243-282.

Soyer J. (1971). Bionomie benthique du plateau continental de la côte catalane française. III: Les peuplements de Copépodes Harpacticoïdes (Crustacea). *Vie Milieu*, **21**, 2B, 337-511.

Soyer J. and J.-Y. Bodiou (1974). Diversité spécifique inter et intra-communautaire dans les peuplements de Copépodes Harpacticoïdes de substrats meubles. *2nd International Conference on meiofauna, York*, 11 pp.

Thouzeau G. (1991). Déterminisme du pré-recrutement de *Pecten maximus* (L.) en baie de Saint-Brieuc : processus régulateurs de l'abondance, de la survie et de la croissance des post-larves et juvéniles. *Aquat. Liv. Res.*, **4**, 2, 77-99.

Thouzeau G. and D. Hamon (1992). Carte des peuplements benthiques de la baie de Saint-Brieuc (Manche). Special Publication IFREMER/UBO/Région Bretagne, 29 pp.

Vanosmael K., K. Willems, M. Vincx, D. Clayes and C. Heip (1985). Benthos of the Kwinte bank (an exploited sandbank in the Southern Bight), in: Biological processes and translocations. Actions de Recherche concertées, C. Heip and P. Polk, editors. Action Interuniversitaire, Océanologie, Rapport final, 3, 65-80.

Volkmann B. (1979). A revision of the genus *Tisbe* (Copepoda, Harpacticoida). Part I. *Archo Oceanogr. Limnol., suppl.*, **19**, 121-284.

Warwick R.M. and J.M. Gee (1984). Community structure of estuarine meiobenthos. *Mar. Ecol.-Prog. Ser.*, **18**, 97-111.

Warwick R., J.M. Gee, J.A. Berge and W. Ambrose Jr. (1986). Effects of the feeding activity of the polychaete *Streblosoma bairdi* (Malmgren) on meiofaunal abundance and community structure. *Sarsia*, **71**, 11-16.

Wells J.B.J. (1967). The littoral Copepoda (Crustacea) of Inhaca Island, Mozambique. *Trans. R. Soc. Edinb.*, **67**, 7, 189-358.

Wilhm J.L. and T.C. Dorris (1968). Biological parameters for water quality criteria. *Bioscience*, **18**, 477-481.

Willems K., M. Vincx, D. Clayes, C. Vanosmael and C. Heip (1982). Meiobenthos of a sublittoral sandbank in the Southern Bight of the North Sea. *J. mar. biol. Ass. U.K.*, **62**, 3, 535-548.

Willems K.A., Y. Sharma, C. Heip and A.J.J. Sandee (1984). Long-term evolution of the meiofauna at a sandy station in lake Grevelingen, The Netherlands. *Neth. J. Sea Res.*, **18**, 3/4, 418-433.

Williams R. (1972). The abundance and biomass of the interstitial fauna of a graded series of shell-gravels in relation to the available space. *J. Anim. Ecol.*, **41**, 623-646.

Wolf W.J. (1974). Benthic diversity in the Rhine-Meuse estuary. *Hydrobiol. Bull.*, **8**, 242-252.