Results of ecological monitoring of three beaches polluted by the 'Amoco Cadiz' oil spill: development of meiofauna from 1978 to 1984

P. Bodin

Université de Bretagne Occidentale, Faculté des Sciences, Laboratoire d'Océanographie Biologique, U.A. 711 du C.N.R.S.,
6 Avenue Le Gorgeu, F-29287 Brest Cedex, France

ABSTRACT: Following the 'Amoco Cadiz' oil spill, time-series sampling of the meiofauna was carried out from 1978 to 1984 in the intertidal zone of 3 sandy beaches on the northern Finistère coast (Brittany, France). Quantitative analysis documented 2 principal phases in the development of the main taxa (Nematoda and Copepoda). First came a degradation phase leading to impoverishment in density and diversity of the populations. This first phase could be subdivided into several stages corresponding mainly to the toxicity period and, on one beach (Kersaint), to a summer 'bloom'. Then came a recovery phase corresponding to a quantitative and qualitative reconstitution of the meiofauna. Each phase lasted a greater or lesser time according to station exposure and the considered taxon. A qualitative analysis of harpacticoid copepods illustrated the development of population diversity and 'ecological groups'. During the first phase, replacement of the original population by a substitute fauna was observed. Correspondence factorial analysis on the development of harpacticoid communities allowed a better understanding of the main pollution and recovery factors such as toxicity, organic matter, hydrodynamism and zoological groups. Meiofauna, particularly harpacticoid copepods, are significant bioindicators of ecological disturbances.

INTRODUCTION

Few long-term studies on meiofauna exist, particularly any dealing with the consequences of oil pollution (Feder et al. 1976, Boucher 1983, 1985, Elmgren et al. 1983).

Following the wreck of the oil tanker 'Amoco Cadiz' (16 March 1978), time-series sampling of the meiofauna was carried out from 1978 to 1984 in the intertidal zone of 3 sandy beaches on the northern Finistère coast (Brittany, France). Two of these beaches (Brouennou and Corn ar Gazel) are situated on either side of the mouth of the Aber Benoit river; the third (Kersaint) about 4 km south of the wreckage point, near Portsall (Fig. 1). Preliminary results of this ecological monitoring were presented in 2 previous papers (Bodin & Boucher 1981, 1983) and several reports. The aim of the present paper is to synthesize the final results. Special attention is paid to the 2 principal zoological groups involved: nematodes and harpacticoid copepods.

MATERIAL AND METHODS

Study sites. Brouennou is a fine-sand beach (median grain size 127 to 160 μm), poorly sorted, containing 1.7 to 6.6 % silt/clay and 0.2 to 0.3 % organic carbon (Table 1, Fig. 2). It faces west, but a rocky point and several small islands shelter it from open sea swells. Its 'morpho-sedimentary vulnerability index' is 6 (Berné & D'Ozouville 1979). On this vulnerability scale, ranging from 1 to 10, low figures mean greater exposure to wave and current action.

Corn ar Gazel is a fine-sand beach (median grain size 122 to 150 μm), well sorted, containing 0.9 to 2.2 % silt/clay and 0.3 to 0.4 % organic carbon. It faces northeast and is under the influence of strong tidal currents as well as wave action. Its morpho-sedimentary vulnerability index is 2.

Kersaint has coarser sand (median grain size 191 to 210 μm), well sorted, containing 0.9 to 2.4 % silt/clay and about 0.1 to 0.3 % organic carbon. It faces north-northwest and, consequently, is exposed to the strong

Fig. 1. Location of study sites on the northern Finistère coast, Brittany, France

winds blowing from this sector in winter. Its morpho-sedimentary vulnerability index is also 2. A modification of the grain structure took place in April 1984: for unknown reasons, the median grain size decreased to between 155 and 165 μm , and persisted at this level until at least June 1984.

In general, a 'gradient' of increasing exposure and granulometry was observed from Brouennou to Kersaint.

Fauna sampling and extraction. Monthly samples were taken from October 1979 (March 1978 in Kersaint) to November 1980, then bimonthly (between March and June) from 1981 to 1984. The period covering March to June was chosen as representative of the whole year: it theoretically includes the winter minimum and the spring maximum. At Corn ar Gazel, samples were taken on 17 March 1978, the day after the accident: these were used as a reference for this station.

Samples were taken in the midlittoral zone, between mean tide level (MTL) and mean low water neaps (MLWN) level. Each sample consisted of 3 separate cores of 10 cm^2 by 10 cm depth, spaced several meters apart on a line running parallel to the shore.

Cores were preserved in 5 % formalin, then elutriated and filtered (Bodin 1977) on a sieve column with 1 mm, 100 μm and 40 μm mesh size. Animals were sorted under a binocular microscope ($\times 25$) and indi-

viduals of the different taxa constituting the meiofauna (except Foraminifera) were counted. The nematode/copepod ratio (N/C) was evaluated. Harpacticoid copepods were identified to species (Table 2), thus permitting an estimate of species richness (SR) and a study of their community structure.

Ecological parameters. Complementary samples were used for data collection for the main ecological factors.

Granulometry, silt/clay content (<63 μm) and interstitial water temperature were measured by means of conventional methods (Hulings & Gray 1971). Salinity was measured using a 'Guildline-Autosal 8400' salinometer. These parameters are summarized in Table 1 and Fig. 2. At Brouennou, the silt/clay fraction was generally low but not negligible.

The degree of sediment oxygenation, which is directly linked to hydrodynamism, was estimated by measuring the thickness of the oxidized layer (Le Moal 1981). Lowest values were found at Brouennou (1 to 2 cm) and highest at Corn ar Gazel and Kersaint (5 to 20 cm); this confirms the greater instability of the latter stations.

Salinity values varied between 25 and 34 ‰. The presence of a brook on Kersaint beach and freshwater springs on Corn ar Gazel beach probably contributed to the low values found at these 2 sites (Table 1).

Interstitial water temperature (recorded between

Table 1. Minimum and maximum values of granulometric parameters, silt/clay fraction, organic carbon content and salinity during the study period

	Brouennou		Corn ar Gazel		Kersaint	
	Min	Max	Min	Max	Min	Max
Median grain size (μm)	127	160	122	150	191	200
Sorting coefficient	1.40	1.53	1.14		1.08	1.14
Silt/clay (%)	1.73	6.60	0.87	2.17	0.90	2.36
Org. carb. (%)	0.17	0.30	0.32	0.42	0.10	0.30
Salinity (‰)	32.5	33.7	30.8	33.8	24.8	32.8

Fig. 2. Cumulative granulometric curves for sand from the 3 sites

10:00 and 14:00 h) during the study ranged from 4.7°C (minimum) to 17.3°C (maximum). Air temperatures (35 yr daily mean) fluctuated approximately between 7 and 16°C, with unusually high values being recorded throughout 1982 and in summer 1983 and 1984.

Total hydrocarbon content was measured from 1978 to 1981 by infrared spectroscopy. On the most polluted beach (Brouennou), values ranged from 3500 ppm in November 1978 to about 50 ppm in 1980 (Le Moal 1981, Morel 1981, Bodin & Boucher 1983).

Total organic matter was initially determined by incineration at 600°C, but was later used only as supplementary information since these values were of low accuracy due to the low levels present (<5%). In Brittany, one source of organic matter is the permanent input from intensive agriculture (fertilizers, liquid manure, etc.). This could have somewhat enhanced the organic pollution during 1978 to 1980, but it is unlikely that its effect could have masked the succession induced by pollution from the 'Amoco Cadiz'. From 1983, organic carbon content was measured by gas chromatographic analysis, using a 'Carlo Erba-Ana 1500' analyser (Hily et al. 1986). Results, expressed as percentage of sediment dry weight, are presented in

Table 1. Since 1984, organic carbon content appears to be normal for this type of beach. The slightly higher rates found at Corn ar Gazel can probably be explained by frequent inputs of stranded algae to this beach.

Data processing. Among data, quantitative (i.e. zoological group overall densities) and qualitative (i.e. species and ecological group densities) parameters are distinguished. For each zoological group, abundance is expressed as numbers present per 10 cm² surface area (density). For harpacticoids, density was also calculated relative to the total abundance at each station (dominance). In order to allow comparisons, values given here (Tables 2 and 4) represent means for the period March to June, the only period surveyed from 1981 to 1984. Mean dominance of a species is the percentage of the species compared to the total mean density of all species. Dominant species (Bodin 1977) are species which show at least one mean dominance $\geq 1\%$ during monitoring (Table 4).

After a log transformation ($y = \log [x + 1]$) of the mean dominances of only the dominant harpacticoid species, a correspondence factorial analysis (CFA) was applied to the data gathered from all 3 stations and also to the data from each individual station. The CFA is an inertia analysis carried out from the centre of gravity (chosen as origin) of the points. The χ^2 distance is used, and points are unequally weighted, which makes possible the symmetry between observations (= samples here) and variables (= species here). Further details are given, among others, by Chardy et al. (1976). This method allows a graphic representation of the time-space development of samples and species. In this way, the main ecological parameters contributing to the community structure can be assessed.

Harpacticoid copepod diversity was calculated using the Shannon-Wiener index (H' of Pielou 1975), and 'evenness' (or equitability) with the Pielou (1975) index (J).

In order to facilitate comparisons from year to year, harpacticoid species showing a similar behaviour and sensitivity to a given ecological factor (granulometry, organic matter, etc.) were arranged in 'ecological groups' using literature data and my own observations. Development of the mean dominance of these different groups was determined in the successive phases indicated by this long-term ecological monitoring.

RESULTS

Quantitative fluctuations of meiofauna

Beside data on nematodes and harpacticoid copepods, tables giving quantitative variations of 'minor taxa' and temporary meiofauna (juveniles of

Table 2 (continued)

Species	EG	Brouennou					Corn ar Gazel					Kersaint								
		1979	1980	1981	1982	1983	1984	1979	1980	1981	1982	1983	1984	1978	1979	1980	1981	1982	1983	1984
<i>Leptopsyllus</i> (L.) <i>paratypicus</i>	SM				0.6														2.1	0.6
<i>Leptopsyllus</i> (L.) <i>celticus</i>	SM					<0.05													<0.05	
<i>Leptopsyllus</i> (L.) sp.	SM					<0.05					0.1			34.4	31.8	9.8	54.0	10.1	26.2	18.2
<i>Apodopsyllus arenicolus</i>	SM			0.1										262.8	8.2	0.3	159.6	4.2	150.3	7.7
<i>Kliopsyllus constrictus</i> s. str.	SM					<0.05								47.4	0.2				0.1	
<i>Intermedopsyllus intermedius</i>	SM																			
<i>Mesochra pygmaea</i>	E													0.2						0.4
<i>Itunella muelleri</i>	M				0.2		<0.05													
<i>Evansula incerta</i>	SM													0.8						
<i>Stenocaris pontica</i>	SM																0.1			
<i>Stenocaris</i> sp.	SM				0.1															
<i>Leptastacus laticaudatus</i>	SM													23.4						
<i>intermedius</i>																				
<i>Paraleptastacus spinicauda</i>	SM																0.2			
<i>Paraleptastacus espinulatus</i>	SM							1.0						104.8	82.8	71.3	134.9	16.2	9.6	1.9
<i>Psammastacus confluent</i>	SM																0.7			<0.05
<i>Leptopontia curvicauda</i>	SM													0.4						
<i>Arenopontia subterranea</i>	SM																0.9			
<i>Arenopontia</i> sp.	SM									1.0							1.7			
<i>Cylindropsyllidae</i> gen. et sp.	SM													0.2				0.1		1.9
<i>Enhydrosoma propinquum</i>	M	25.8	0.3	1.2	0.1		<0.05			0.1										
<i>Rhizothrix minuta</i>	S			0.2	0.1	0.6	5.3	2.8	4.5	0.1			<0.05	8.2	2.0	1.0	3.3	0.1	5.1	37.2
<i>Rhizothrix wilsoni</i>	S						0.2	1.5												
<i>Huntemannia jadensis</i>	M			1.0		0.6		0.5												
<i>Tryphoema porca</i>	S	1.0												0.2						
<i>Tryphoema bocqueti</i>	S																0.1	0.1		
<i>Heterolaophonte stroemi</i> s. str.	Ph	23.3	20.8	5.6	19.7	1.6	12.1													
<i>Heterolaophonte minuta</i>	Ph	0.5																		
<i>Paronychocamptus curticaudatus</i>	S	0.5		0.1												0.3				
<i>Paronychocamptus nanus</i>	S																0.1			
<i>Asellopsis intermedia</i>	S	83.3	1.8	3.4	4.1	58.6	480.0	275.5	14.8	0.4	0.2	0.3	0.3	4.8	12.8	10.8	0.1	0.1	14.5	64.5
<i>Klieonchocamptus</i> sp.	S			0.1																
<i>Laophontopsis lamellifera</i>	Ph			0.1	0.1															
Unspecified		85.5		0.2	0.5	0.2		0.5		0.1								0.1	0.2	0.1
Total		447.8	403.5	121.8	174.3	290.6	935.7	328.0	221.8	231.5	141.9	341.9	146.7	506.8	139.4	98.0	386.6	32.1	213.3	219.3

Table 3. Meiofauna mean densities (no. 10cm⁻²); nematode/copepod (N/C) ratio; species richness (SR), diversity (H') and evenness (J) of harpacticoid copepods. 'Diverse' = Rotifera, Acania, cyclopoids, nauplii, etc. In 1978 and 1979, this item also included Turbellaria and temporary meiofauna. + : group present but at very low density

	Brouennou					Corn ar Gazel					Kersaint								
	B79	B80	B81	B82	B83	B84	C79	C80	C81	C82	C83	C84	K78	K79	K80	K81	K82	K83	K84
Meiofauna	10 473	8 840	13 764	13 529	12 071	14 700	6 088	1 513	2 949	6 634	8 340	5 773	2 060	1 179	1 530	2 344	1 523	2 170	2 770
Nematodes	8 758	7 054	12 951	12 621	11 326	12 631	3 276	1 067	2 526	6 112	6 897	4 302	797	318	240	797	943	1172	1 525
Harpacticoids	447.7	403.5	121.8	174.3	290.6	935.7	328.0	221.8	231.5	141.9	341.9	146.7	506.8	139.4	98.0	386.7	32.1	213.3	219.3
N/C	19.5	17.5	106.2	72.5	38.9	13.5	10.0	4.8	10.9	43.0	20.2	29.3	1.6	2.3	2.4	2.1	29.5	5.5	7.0
SR	15	13	28	25	26	23	9	6	7	5	9	7	22	7	10	15	13	16	19
H'	2.52	1.85	2.49	2.65	2.29	2.07	0.95	0.56	0.05	0.04	0.12	0.18	2.19	1.66	1.38	1.90	1.75	1.58	2.76
J	0.64	0.50	0.52	0.57	0.49	0.46	0.30	0.22	0.02	0.02	0.04	0.06	0.49	0.59	0.42	0.49	0.47	0.39	0.65
Tardigrades	73	186	142	9	89	79	128	12		1	+	1	26	37	44	25	16	63	304
Gastrotichs		+	16	6	6	8	935	98	44	82	620	1028	49	97	57	490	72	216	175
Ostracods		+	167	67	56	128	35	21	60	50	26	36	31	116	212	316	213	206	163
Turbellarians		179	29	30	30	37	22	22	3	146	68	236			426	56	47	26	54
Annelids		137	88	105	40	125	28	26	12	1	1	6			+	2	6	4	5
Tanaids							9	1							17	4	5	6	4
Amphipods			4	+	2	2		5	16	2	1					3	7	4	1
Cumaceans									11	9	1	1			+	+	2	3	1
Molluscs		+	1	8	+			1	14	+	+	+	650	472	436	264	241	257	319
Diverse	1194	880	244	509	261	754	1386	29	29	64	384	16							

macrofauna) between 1978 and 1980 were previously presented (Bodin & Boucher 1981, 1983). Further data on all these groups were regularly collected between 1981 and 1984: they are averaged in Table 3. As several inexperienced sorters were involved in this study, we cannot be absolutely confident in the data concerning Rotifera, Tardigrada, Turbellaria and Gastrotricha. This could partially explain some important variations recorded between years, but general trends are clear and can be summarized as follows:

- These 'minor taxa' were relatively more important in Kersaint than at other stations, which is probably related to the granulometry.

- Nauplii frequently constituted the main part of these so-called 'other groups', particularly in 1979, 1982 and 1984 at Brouennou, in 1979 at Corn ar Gazel, and in 1978, 1979, 1980 and 1984 at Kersaint. They were very rare in 1984 at Corn ar Gazel.

- Tardigrades were abundant at Kersaint, mainly in 1984, and at Brouennou, except in 1982. They were also abundant in 1979 at Corn ar Gazel, but later became very scarce.

- Gastrotrichs were always abundant at Corn ar Gazel and Kersaint, and rare at Brouennou.

- Ostracods were particularly abundant at Kersaint. Low figures recorded in 1978 at Kersaint and in 1979–80 at Brouennou could reflect their sensitivity to hydrocarbon pollution already mentioned by some authors (Bonsdorff 1981, Elmgren et al. 1983).

- Turbellarians were especially abundant at Corn ar Gazel and Kersaint.

- Among the other species ('diverse' in Table 3), rotifers were generally abundant at Kersaint and particularly numerous in 1983 at Corn ar Gazel.

- Annelids were regularly abundant only at Brouennou, which seems normal for this sheltered station where the anoxic layer is very close to the surface.

- Tanaids and amphipods were totally absent from Brouennou and rare at the other sites.

- Molluscs (gastropods and bivalves) were very scarce at all 3 sites.

Thus, densities of these groups were often too irregular and dependent on the site to provide significant comparisons; therefore, this study deals essentially with nematodes and harpacticoid copepods.

One major observation stands out: the 'Amoco Cadiz' disaster did not result in total destruction of the meiofauna on the northern Finistère coast, as occurred in other cases (Spooner 1977). This resistance to the 'Arabian light' petroleum carried by the 'Amoco Cadiz' was also noticed by Renaud-Mornant & Goubault (1980) on Roscoff beaches (Brittany).

Brouennou. The meiofauna at this station was principally composed of nematodes (generally more than 80 %; Fig. 3). Few harpacticoid copepods were present

Table 4. Mean dominances (% of mean total of all species) of harpacticoid copepod dominant species

	Brouennou				Corn ar Gazel				Kersaint										
	B79	B80	B81	B82	B83	B84	C79	C80	C81	C82	C83	C84	K78	K79	K80	K81	K82	K83	K84
<i>Canuella perplexa</i>	Cpe	1.0	5.3	25.4	34.4	18.4	5.8	5.8	90.6	99.6	99.6	98.7	97.9		0.3	0.1	0.3	0.4	2.1
<i>Halectinosoma herdmanni</i>	Hhe		0.1	0.5	0.2	0.8	1.8					<0.05							2.9
<i>Arenosetella tenuissima</i>	Ate			0.1		0.6	<0.05					<0.05				7.9	2.2	1.2	<0.05
<i>Tachidius discipes</i>	Tdi	0.8	1.3	1.0	0.1	0.1	0.5	1.8	<0.05	0.1	0.3	0.6	0.05	1.1	4.1	<0.05	0.9	0.5	<0.05
<i>Microarthridion reductum</i>	Mre	0.1			1.1														
<i>Microarthridion perkinsi</i>	Mpe			1.1	2.1	1.0												0.1	
<i>Thompsonula hyaenae</i>	Thy						6.6					<0.05						0.1	13.8
<i>Harpacticus flexus</i>	Hfl	1.9	3.2	11.3	11.0	46.5	2.9	0.2			0.8	1.2	<0.05		0.3		<0.05	20.1	
<i>Stenhelia (D.) palustris bispinosa</i>	Spb		0.5	1.9	4.4	1.2	2.6												
<i>Robertsonia celtica</i>	Rce	19.7	27.8	4.5	4.7	0.1													
<i>Amphiascoides debilis</i> s. str.	Ade	23.1	55.1	43.3	26.5	5.3	5.7						<0.05			0.3			
<i>Amphiascoides debilis limicolus</i>	Adl	3.9	0.6	0.7	0.2	3.3	27.2												
<i>Schizopera</i> sp.	Scs												2.2						
<i>Ameira pusilla</i>	Apu												1.1						
<i>Leptopsyllus (L.) celticus</i>	Lce																	1.0	0.3
<i>Apodopsyllus arenicolus</i>	Aar			0.1		<0.05				0.1			6.8	22.8	10.0	14.0	31.5	12.3	8.3
<i>Kllopsyllus constrictus</i> s. str.	Kco					<0.05							51.9	5.9	0.3	41.3	13.1	70.5	3.5
<i>Intermedopsyllus intermedius</i>	lin												9.4	0.1				<0.05	
<i>Leptastacus laticaudatus intermedius</i>	Lli												4.6						
<i>Paraleptastacus espinulatus</i>	Pes							0.5	<0.05				20.7	59.4	72.8	34.9	50.5	4.5	0.9
<i>Cylindropsyllidae</i> gen. et sp.	Cys												<0.05				0.3		0.9
<i>Enhydrosoma propinquum</i>	Epr	5.8	0.1	1.0	0.1		<0.05												
<i>Rhizothrix minuta</i>	Rmi			0.2	0.1	0.2	0.6	0.9	2.0	<0.05		<0.05	<0.05	1.6	1.4	1.0	0.9	0.3	2.4
<i>Heterolaophonte stroemi</i> s. str.	Hst	5.2	5.2	4.6	11.3	0.6	1.3												
<i>Asellopsis intermedia</i>	Asi	18.6	0.4	2.8	2.4	20.2	51.3	84.0	6.7	0.2	0.1	0.1	0.2	0.9	9.2	11.0	0.1	<0.05	6.8
																			29.4

Fig. 3. Development of mean annual densities of nematode and harpacticoid copepod for each station. Standard error indicated for copepods (broken bars) and for total meiofauna (continuous bars)

(Table 3), but these were well diversified. Up to 1980 the meiofauna remained abundant, but average spring densities decreased noticeably. This reduction was greater for nematodes than for harpacticoids. In 1981, there was a definite rise in total population density (to an average of 13 700 ind 10cm⁻²). This increase was mainly due to nematodes, as harpacticoids continued to decrease and even showed their lowest mean density that year. After 1981, the overall meiofauna density had stabilized, the nematode population fluctuating around 12 000 ind 10cm⁻². The harpacticoid copepod population very slowly regained normal density for this type of biotope (940 ind 10cm⁻² in 1984). The N/C ratio was 19.5 in 1979 and 13.5 in 1984, and reached a maximum of 106.2 in 1981 (Table 3).

Corn ar Gazel. Meiofauna density here was approximately half of that at Brouennou (Fig. 3). The proportion of nematodes varied between 40 and 90 %. Few harpacticoids were present and were poorly diversified: their community was often almost monospecific (Table 3). Overall densities decreased until spring 1980. This was mainly due to a pronounced reduction in nematodes; the copepod density remained relatively stable throughout the study. From 1981, there was a steady recruitment to the meiofauna (up to more than 8000 ind 10cm⁻² in 1983), but harpacticoids never exceeded 350 ind 10cm⁻² (1983). Therefore, by 1983 harpacticoid mean density had already returned to the level initially observed in the reference sample of March 1978; but the year 1984 was characterized by a new density loss which reduced the average to the level of 1982. The N/C ratio ranged between 4.8 (1980) and 43.0 (1982) (Table 3).

Kersaint. Meiofauna density here was, on average, one-third of that at Corn ar Gazel and, therefore, about

6 times less abundant than at Brouennou (Fig. 3). Due to the grain structure of the sediment here, important proportions of harpacticoid copepods (up to 25 %) can be sustained (Table 3). Among these were found a large number of typically interstitial forms (mesopsammic species), which increased the diversity compared to Corn ar Gazel. Kersaint is the only beach monitored monthly since 17 March 1978; thus it gives the only example of meiofaunal development for this area during the first months of pollution (Fig. 4). Up to the end of May 1978, an important decrease in numbers was observed, especially among harpacticoids, with a reversal of the N/C ratio in May. This was followed by a population explosion in June 1978. This 'bloom', which affected nematodes as well as harpacticoids and other meiofauna groups, led to a mean density of 2000 ind 10cm⁻² during that year of maximum pollution. Afterwards, the population decreased and stabilized at around 1200 to 1500 ind 10cm⁻² until 1980. A first major recolonization by both nematodes and copepods took place in 1981. It reached 1978 levels but, in 1982, harpacticoid density fell again to an extremely low level (32 ind 10cm⁻²). Nematodes, however continued to increase. The latter reached a maximum of 1525 ind 10cm⁻² in 1984, but that year harpacticoids did not exceed 220 ind 10cm⁻². The N/C ratio was 1.6 in 1978 and 7.0 in 1984, with a maximum of 29.5 in 1982 (Table 3).

Qualitative development of meiofauna

Study of the qualitative development was based on the identification of harpacticoid copepod species and the constitution of different ecological groups.

Species richness

Variation of the number of harpacticoid species (Fig. 5) was similar for the 3 stations. First, a drastic reduction in species richness was observed until 1980, except at Kersaint where an increase had begun by

Fig. 4. Details of the meiobenthos development (total, nematodes, harpacticoids) at Kersaint during the first year after the oil spill

Fig. 5. Development of the harpacticoid species number for the 3 stations

1980. The number of species then increased, with a peak in 1981, particularly well defined at Brouennou. At Corn ar Gazel, the total number of species was generally low and variations were not very obvious. Table 3 shows a high diversity at Brouennou, medium diversity at Kersaint and very low diversity at Corn ar Gazel. Corn ar Gazel was a nearly monospecific station where an extremely low evenness index, particularly from 1981, characterized an unstable site.

Development of ecological groups

Despite numerous uncertainties which remain in the autecology and feeding habits of many species, harpacticoid copepods can be divided into several 'ecological' groups. Thus, we can distinguish 'sandy', 'muddy', 'phytophilous' and 'eurytopous' species. Among sandy species, we distinguish 'epipsammic' forms which generally remain at the surface of the sand, 'endopsammic' forms whose appendages, armed with strong spines, allow them to dig through the sand by shifting the grains, and 'mesopsammic' forms whose size and structure (vermiform, simplified appendages, reduced number of seta and eggs, etc.) allow them to move between sand grains without any need to shift the grains. Some 'muddy' species are also characteristic of estuarine muds, i.e. they tolerate both lower salinity and higher organic matter content. 'Phytophilous' species usually live among algae or are linked to the presence of stranded algae and plant detritus. 'Eurytopous' species can develop in most biotopes. They are generally euryhaline, eurythermal and tolerant to the silt/clay fraction and to the organic matter content (Remane 1952, Soyer 1971, Bodin 1977).

Brouennou. All 4 main ecological groups were found at this station and appeared in the following order (Fig. 6a): After the oil spill, and until 1980, sandy species diminished and were progressively replaced by eurytopous and phytophilous species. In 1981, these last 2 groups decreased although eurytopous species remained numerous. In that year, the proportion of sandy species increased again and became almost as important as the eurytopous species, regaining by 1983 a large preponderance, followed by a decline in 1984. This development allows us to consider sandy species as the normally prevailing characteristic group at this station. Muddy species (with typical estuarine species as *Stenhelis (D.) palustris bispinosa*, *Enhydrosoma propinquum*, *Amphiascoides debilis limicolus*) reached 10 % in 1979, then stabilized at around 5 to 7 % until 1983, when they began to increase, reaching 30 % in 1984.

Corn ar Gazel. Here the harpacticoids present were virtually all sandy species, and an alternation of 2 species, *Canuella perplexa* (epipsammic) and *Asellop-*

Fig. 6. Mean dominance development of (a) the 4 ecological groups at Brouennou; (b) *Canuella perplexa* and *Asellopsis intermedia* at Corn ar Gazel; (c) the 3 ecological groups at Kersaint, and dominance development of *Kliopsyllus constrictus*

sis intermedia (endopsammitic) was observed. The latter almost completely replaced *C. perplexa* in 1979, but later regained its original dominance (Fig. 6b).

Kersaint. Here, as at Corn ar Gazel, the harpacticoid fauna consisted almost entirely of sandy species. However, 3 other ecological groups were distinguished: (1) mesopsammitic forms, (2) epi- or endopsammitic species, and (3) different eurytopous and phytophilous species considered together as a single group: the 'diverse' group. Mesopsammitic forms largely predominated up to 1983, but they gradually decreased during the 2 yr following the oil spill (94 % in 1978, 88 % in 1979, 84 % in 1980). Simultaneously, an increase of other sandy species was recorded. Meanwhile, in 1981, mesopsammitic species had peaked and other sandy species were almost absent. However, from 1981, an increase of epi- and endopsammitic species was observed to the detriment of mesopsammitic forms, the abundance of the latter collapsing in 1984 (13.8 %) (Fig. 6c).

One of the mesopsammitic species at Kersaint, *Kliopsyllus constrictus*, showed a very interesting development (Fig. 6c): largely predominant (more than 50 %) in 1978, it decreased drastically in 1979 and almost completely disappeared in 1980, but re-appeared in 1981 with 41.3 %. This first peak was followed by a second sharp increase (>70 %) in 1983. However, because of the change to finer grain structure on the beach, the species decreased drastically in 1984 and, although still frequent, represented only 3.5 % of the harpacticoid copepods.

Development of harpacticoid copepod communities

The correspondence factor analysis (CFA) applied to annual mean dominances of the sample set of 'domi-

nant species' confirmed that the 3 stations had very different populations (Fig. 7). Samples are well grouped in 3 different sectors of the 1–2 plane, and a time development can be seen in each station. Thus, Axes 1 and 2 represent graphically the role played by abiotic factors (granulometry, hydrodynamism, etc.) which characterized each station. This analysis was also applied to the data from each station, which highlighted a temporal development that corroborates the results of the ecological groups study.

Brouennou. Here, samples are clearly grouped in year order on the 1–2 plane graph (Fig. 8), and years are distributed along a trajectory following a chronological progression which illustrates a 'Guttman effect'. This development was initially slow: years 1979 and 1980 are partly superposed. Only the year 1981 (B09 to B14), which is centred on the intersection of the Axes, is out of this trajectory. Plane 2–3 (Fig. 9) shows the same chronological development along Axis 2, with a reversal of the progression starting from 1982. Moreover, another temporal gradient, seasonal this time, is visible along Axis 3. This 'seasonality' is particularly obvious in 1982 and 1983, when samples are arranged almost chronologically from March towards June (i.e. from winter to summer), from the negative towards the positive sector of Axis 3, in the upper part of the graph. Except in a few cases, the interstitial water temperatures recorded during the monitoring were >7°C in the positive sector and <7°C in the negative sector of Axis 3.

The contribution to the total inertia (0.687) of the first 3 axes is 67.2 %, distributed in the following way:

1st axis	2nd axis	3rd axis
35.49 %	21.40 %	10.36 %

Major absolute contributors to the inertia explained by Axis 1 are, in decreasing order, *Asellopsis inter-*

Fig. 7. Correspondence factorial analysis graph for Brouennou, Corn ar Gazel and Kersaint (Plane 1-2). Each sample (= observation) is represented by a letter (K = Kersaint, B = Brouennou, C = Corn ar Gazel) and the last 2 figures of the year. Each species (= variable) is represented by the initial of the genus name and the first 2 letters of the species name (e.g. Cpe = *Canuella perplexa*)

media, *Robertsonia celtica*, *Amphiascoides debilis limicolus* and *Heterolaophonte stroemi*. For Axis 2, major absolute contributors are *Enhydrosoma propinquum*, *Canuella perplexa*, *R. celtica* and *Stenhelix (D.) palustris bispinosa*; for Axis 3, *Harpacticus flexus*, *Microarthridion reductum* and *C. perplexa*.

Projections of the observations (samples) on the different CFA planes are, naturally, correlated with those of variables represented here by species. Distribution of the latter equally describes the general development of the population at Brouennou, with eurytopous and phytophilous species characterizing the first years, sandy species regrouped in the year 1983, and a recurrence of muddy or, at least, tolerant species (*Asellopsis intermedia*) in 1984.

Corn ar Gazel. The 1-2 plane graph (Fig. 10) shows a very asymmetrical distribution: samples of years 1979 (C01 to C04) and 1980 (C05 to C08) are easily distinguished, those of June (C08) tending already towards a confused set where all samples of years 1981 (C09 to C14) to 1983 (C21 to C26) are concentrated, as well as the first samples of 1984, a much more dispersed year. This progression is roughly situated along Axis 1 with,

at the beginning, the reference sample of March 1978 (C00). June samples for 1983 (C27) and 1984 (C34) are very isolated on the positive side of Axis 2. Other planes do not provide more information on the development of the community structure at Corn ar Gazel. In particular, there is no clear seasonal gradient.

The contribution to the total inertia (1.017) of the first 3 axes is 82.6 %, distributed in the following way:

1st axis	2nd axis	3rd axis
43.77 %	24.05 %	14.78 %

Major absolute contributors to the inertia explained by Axis 1 are, in decreasing order, *Asellopsis intermedia*, *Thompsonula hyaenae* and *Canuella perplexa*. For Axis 2, major absolute contributors are *Harpacticus flexus* and *Rhizothrix minuta*; for Axis 3, *R. minuta*, *H. flexus* and *T. hyaenae*. The species *A. intermedia* characterizes well the year 1979, as was seen in the qualitative development (Fig. 6b), while *C. perplexa* is in the center of the compact group of the other years.

Kersaint. The 1-2 plane graph (Fig. 11) shows a distribution for the total samples and species along Axis 1, except for the sample of June 1978 (K05) which is situated towards the lower part of the negative sector

Fig. 8. Correspondence factorial analysis graph for Brouennou (Plane 1-2)

Fig. 9. Correspondence factorial analysis graph for Brouennou (Plane 2-3)

Fig. 10. Correspondence factorial analysis graph for Corn ar Gazel (Plane 1-2). Samples C15, C18, C21, C22 and C29 are hidden by Sample C12; Samples C16 and C17 are hidden by Sample C13; Sample C20 is hidden by Sample C26; Samples C23, C28 and C31 are hidden by Sample C10; Sample C24 is hidden by Species *Cpe*; Sample C25 is hidden by Sample C19

Fig. 11. Correspondence factorial analysis graph for Kersaint (Plane 1-2). Samples K08 and K22 are hidden by Sample K21; Sample K11 is hidden by Sample K04; Samples K12 and K33 are hidden by Sample K07; Samples K15, K27 and K32 are hidden by Sample K25; Samples K17 and K22 are hidden by Sample K18; Sample K24 is hidden by Sample K03; Samples K29 and K34 are hidden by Sample K28; Sample K31 is hidden by Sample K38; Sample K33 is hidden by Sample K26; Sample K35 is hidden by Sample K30

of Axis 2 with its 4 characteristic species. This distribution is also visible on Plane 2–3, with some grouping of observations towards the intersection of the axes, these latter being therefore not very discriminant. The 1–3 plane graph (Fig. 12) shows a distribution of observations and variables along a parabola. Years are poorly distinguishable, except for the period between 13 April and 29 June 1984 (K36 to K40), i.e. after the change of grain structure at Kersaint. However, on closer examination, we can distinguish a chronological graduation along Axis 1 from the negative towards the positive sector. It passes successively from 1978 to 1979 and to 1980; then regresses in 1981 (to the 1978 level), to start again the progression towards the positive pole in 1982, 1983 and, particularly, in 1984, the latter 2 being largely spread out along the parabola. As at Corn ar Gazel, there is no clearly distinct seasonal gradient.

The contribution to the total inertia (1.816) of the first 3 axes is 65 %, distributed in the following way:

1st axis	2nd axis	3rd axis
29.24 %	22.82 %	12.97 %

Major absolute contributors to the inertia explained by Axis 1 are, in decreasing order, *Thompsonula hyaenae*, *Harpacticus flexus* and *Asellopsis intermedia*. For Axis 2, major absolute contributors are *Intermedopsyllus intermedius*, *Leptastacus laticaudatus intermedius*, *Schizopera* sp. and *Ameira pusilla*; for

Axis 3, *H. flexus* and *Kliopsyllus constrictus*. Starting from April 1984 (K36), non-mesopsammic sandy species (*H. flexus*, *Halectinosoma herdmani*, *T. hyaenae*) characterized the community.

DISCUSSION

The factorial analysis applied to the 3 stations for the 6 yr surveyed showed that each station's community is distinct. In fact, these stations were chosen precisely because they represented 3 different types of intertidal sandy biotopes. At Kersaint, observations would have been even better grouped in the '–/+ ' sector of the 1–2 plane (Fig. 7) had there been no change in granulometry in 1984 (K84).

Quantitatively, the data permit the following tentative interpretation. Overall, 2 principal phases in the meiofauna development can be observed: Phase 1, which can be termed degradation, resulted in a quantitative and qualitative impoverishment of the population which continued for variable periods of time according to sites and to zoological groups. Generally, this phase lasted until 1980, particularly for nematodes, which constituted by far the most abundant group. However, this phase lasted until 1981 for the harpacticoids of Brouennou. Phase 2, corresponding to a

Fig. 12. Correspondence factorial analysis graph for Kersaint (Plane 1–3). Sample K07 is hidden by Sample K15; Sample K24 is hidden by Sample K03; Sample K35 is hidden by Sample K18; Species Asi is hidden by Species Cpe

reconstitution of the meiofauna, appeared suddenly in 1981 at Brouennou (for nematodes) and at Kersaint (for harpacticoids), and more progressively at Corn ar Gazel.

When examined in detail, it was seen (Bodin & Boucher 1983) that the first phase could be subdivided into several stages (Fig. 4):

At Kersaint, during the first 3 mo there was drastic fall in densities, particularly among harpacticoid copepods, and this led to an increase of the N/C ratio: values were <1 until late April 1978, when they became >1 . It was the only clear change in this ratio that could be observed during the whole monitoring. This first stage probably corresponds to direct effects of hydrocarbon and dispersant toxicity. Thus, harpacticoids seem particularly sensitive to this toxicity, which confirms previous results (Elmgren et al. 1983).

Following this period, an extraordinary 'bloom' was observed, from which repercussions were felt for about 4 mo (during the summer). Such blooms have been observed in intertidal as well as in subtidal zones, at Roscoff in 1978 (Boucher 1980), at Hong-Kong (Spooner 1977), on the Spanish coast (Giere 1979) and even in algae species (Chassé & Morvan 1978). They could correspond to a phase of stimulation occurring after an exceptional enrichment of the environment with different nutrients (phytal detritus, bacteria, diatoms, protozoa, small metazoa). This dystrophy would be followed by accumulation of organic matter in the sediment during the calm summer (decay accelerated by temperature): this accumulation itself appears to be correlated to hydrocarbon pollution (Renaud-Mornant & Gourbault 1980, Glémarec & Hussenot 1981). This phenomena was also observed (but to a lesser degree) in July 1979 at Corn ar Gazel.

Such population explosions require, especially for harpacticoids, a good oxygenation of the environment, which was perhaps still the case in June–July 1978. Within a few months after the oil spill, we observed a process initiated by organic pollution previously described for macrofauna by Pearson & Rosenberg (1978). In the present case, following the massive disappearance of herbivores, there was an excessive load of stranded algal detritus, whose bacterial decay into simple molecules (nitrogen, carbon, mineral salts) required a large amount of oxygen. Also, bacterial degradation of hydrocarbons accumulated in sediments consumes much oxygen. Thus, the whole environment showed an increasing deficit in the oxygen balance, particularly augmented by the sheltered nature of the biotope. The oxygen impoverishment could explain the decrease in meiofauna (Elmgren 1975), which continued until 1980 in the most exposed zones (Corn ar Gazel and Kersaint) and until 1981 for harpacticoids in a sheltered zone (Brouennou).

Recovery to a balanced phase also depends on the zoological group considered. As also noted by other authors (Mielke 1976, Coull & Bell 1979, Renaud-Mornant & Gourbault 1980, Hicks & Coull 1983), it was seen that harpacticoid copepods are more sensitive than nematodes to the lack of oxygen: at Brouennou, after the minimum of 1981, harpacticoid density began to increase again very slowly, regaining its initial density only in 1984, while nematodes reached their equilibrium level as early as 1981. The peak of harpacticoids recorded in 1981 in Kersaint can be considered as a first recolonization of the original fauna, an attempt perhaps favored by a temporary disorganization of trophic relations (absence of usual predators), as was suggested by Glémarec (1986). However, as is often the case with macrofauna after an abnormally high peak which exceeds the 'load capacity' of the environment, this recolonization was followed a year later by a decline which can be likened to an 'ecotone', a well-known phase in the development of macrofauna populations on these same beaches.

To our knowledge, none of the 3 monitored stations was subjected to special cleaning measures. On the other hand, large quantities of various oil spill dispersants were utilized to treat hydrocarbon slicks off the coast and to clean beach rocks. Through the action of winds and currents, a significant quantity of these products certainly reached the beaches. The exact effects of dispersants are of course difficult to determine. However, a study carried out at another station showed short-term noxious effects of an oil spill remover on meio- and macrofauna (Bodin & Le Moal 1982). These effects must certainly delay recovery of the original fauna.

The differences noticed here in the quantitative development of the main meiofauna groups are also perceptible in the 'ecological groups' distinguished among harpacticoid species. This prompted a study of the development of these groups during ecological monitoring. During the first phase (degradation), replacement of the original population by a substitute fauna was observed.

At Brouennou, in spite of the lack of data on the initial state of the community, it seems that sandy species were simultaneously replaced by a set of phytophilous and, above all, eurytopous species, which peaked in 1980. Then, owing to decontamination, this group of 'opportunistic species' (*sensu* Elmgren et al. 1983), was progressively replaced by the sandy species group originally thought to inhabit the site. The abundance of muddy (or estuarine) species recorded in 1984 could be due to the installation, over a fairly large area at the site, of clam beds, although trapping of fine particles inherent to this

aquaculture activity had not yet affected the silt/clay fractions recorded that year (Table 2). Perhaps the importance of the muddy species group in 1984 constitutes a normal aspect of the community for this station which is situated at the mouth of a river (Aber Benoît) and is relatively sheltered.

At Corn ar Gazel, the replacement of *Canuella perplexa* by *Asellopsis intermedia* in 1979 can be explained by a higher tolerance of the latter to an excess of organic matter and fine particles (Bodin 1977). Greater exposure here than elsewhere allowed for an almost complete return to normal by 1980. Thus, on this beach, competition between harpacticoid ecological groups was limited to substitution within the same group, i.e. to interspecific competition within the sandy species group.

At Kersaint, the degradation phase was expressed by a reduction in the dominance of mesopsammic species to the benefit of epi- and endopsammic sandy species. From this point of view, the year 1981 was marked by a return to normal. However, this biotope can experience sudden changes in grain structure, which led in 1984 to a drastic reduction of mesopsammic forms to less than 14 %. The unexplained changes in grain structure induced a qualitative change in the community structure rather than an important change in the N/C ratio (7 instead of 5.5). This confirms how problematic it is to utilize the N/C ratio without assessing the impact of a perturbation (Coull et al. 1981, Raffaelli 1981, 1982, Raffaelli & Mason 1981, Warwick 1981, Hennig et al. 1983).

At Kersaint, the development of *Kliopsyllus constrictus* suggests that this species is particularly sensitive to the pollution and could be considered, for this type of biotope, as a 'test species', i.e. a bioindicator. Unfortunately, owing to the change in grain structure (1984), a return to the level of 1978 after the 1983 peak could not be confirmed.

These substitution and stimulation phenomena were well described for the macrofauna of this area and, when compared with groups determined by Glémarec & Hily (1981), the sandy harpacticoid species correspond to the 'sensitive' species of macrofauna Group I, phytophilous harpacticoids to the 'opportunistic species' of Group IV that can intervene during a temporary substitution, and eurytopous harpacticoids to 'tolerant species' of Group III, regularly present but in low densities, and stimulated here by an enrichment of the environment with organic matter. Moreover, a relationship between the development of meiofauna and macrofauna appeared during this long-term monitoring.

Development of harpacticoid copepod ecological groups is also a good indicator of the 2 phases in the effects of the pollution, already apparent from the

overall quantitative study. Moreover, the harpacticoid species study permitted a better understanding of the succession of these phenomena. In particular, the sudden appearance, then progressive disappearance, of phytophilous species is an indication of the plant (algal) origin of the greatest part of the organic matter which had contaminated the sediments, in addition to the hydrocarbons themselves.

The factorial analysis allows a better understanding of the importance of the main ecological factors for the community structure. Thus, the development of harpacticoid copepod populations at Brouennou is clearly evident from graphs and shows that 1981 was an exceptional year. Going upwards chronologically on Axis 2 (Fig. 9), one changes from muddy species, tolerant to an excess of organic matter (*Enhydrosoma propinquum*), to eurytopous species (*Tachidius discipes*, *Amphiascoides debilis* s. str.) and finally to sandy species (*Canuella perplexa*). Thus, Axis 2 should represent the organic matter content of the environment. Axis 1 separates phytophilous species, on the negative side, from several sandy and 2 muddy species on the positive side of the axis. One passes chronologically from one to the next, with a reversal in 1982. Thus, Axis 1 could represent the plant detritus content of the sediment. More obviously (particularly for 1982 and 1983), Axis 3 probably represents the 'seasonality' of temperature-dependent species, which is visible in progressing chronologically towards summer from the negative to the positive sector along this axis (Fig. 9).

The CFA graphs for Corn ar Gazel also correspond to the results of the qualitative analysis. The year 1979, which was marked by a brief predominance of *Asellopsis intermedia* over *Canuella perplexa*, is isolated from the others and stands close to the reference of March 1978 (Fig. 10). 1980 samples (C05 to C08) become closer to the compact set formed by the samples of 1981 to 1983 and the beginning of 1984. The grouping of all these points at the negative extremity of Axis 1 marks a pause in the development of the population and signifies a greater stability of the fauna during this period. Thus, Axis 1 could reflect the stage of pollution in the environment.

The grouping of most of the Kersaint observations close to the intersection of Axes 1 and 2 (Fig. 11) signifies a high temporal stability for the whole community from 1979. Samples taken after 2 April 1984 (K36 to K40) are isolated from the others in the positive sector of Axis 1, with the 6 non-mesopsammic sandy species (*Canuella perplexa*, *Asellopsis intermedia*, *Rhizothrix minuta*, *Thompsonula hyaenae*, *Halectinosoma herdmani* and *Harpacticus flexus*). This suggests that Axis 1 could represent a granulometric factor. Finally, due to the disparity in

ecological groups represented by the species of Sample K05 (June 1978) (*Ameira pusilla*, *Schizopera* sp., *Intermedopsyllus intermedius* and *Leptastacus laticaudatus intermedius*), the significance of Axis 2 cannot be determined. The dispersion of observations in the 1–3 plane (Fig. 12) confirms the representation of granulometry by Axis 1 and faithfully reflects the fluctuations of the species *Kliopsyllus constrictus*, observations of which are grouped on the negative side of this axis.

CONCLUSIONS

The above discussion suggests that all the methods utilized in this study are complementary and lead to coherent conclusions, which allows the extraction of some lessons for the future.

For the meiofauna, the effects of the 'Amoco Cadiz' oil spill pollution resulted in a succession of 2 main phases, the first of which can be subdivided into several stages (at Kersaint). These phenomena, already observed by several authors, highlight the importance of the time of the year in which the pollution occurs on the subsequent development of the communities. For example, the pollution would perhaps have been much more disastrous for the meiofauna if it had occurred in June–July.

The toxicity of the hydrocarbons was probably felt by meiofauna only during the first weeks. Thereafter the major pollution came from excess organic matter that induced oxygen impoverishment in the environment. In the intertidal zone of the northern Finistère coast, when considering only overall densities, it appears that harpacticoid copepods are more sensitive than nematodes both to hydrocarbon toxicity and to the lack of oxygen. Thus, it seems that for an ecological survey it may be sufficient to study only harpacticoid copepods. This confirms Heip's (1980) conclusions, although even the use of harpacticoid copepods as indicators of environmental quality can remain sometimes 'problematic' (Hockin 1983). However, overall quantitative study is always insufficient; it is necessary to add a qualitative study at the species level in order to be able to follow the development of the ecological groups (Hockin 1982). Among harpacticoid copepods, as in macrofauna (Glémarec et al. 1982), 'test' species and groups (sensitive, tolerant, opportunistic, etc.) can be distinguished which represent bioindicators for an imbalance caused by perturbations due to excess organic matter. For future studies, it seems desirable to specify ethological behaviour and ecological preferences for as many species as possible, in order to improve this 'biological tool' and to perfect a biotic index system such as the one obtained from the mac-

rofauna (Hily et al. 1986). On the other hand, it seems that, for such an ecological survey, the sampling period can be restricted, in Brittany, to the 4 mo including both the winter minimum and the main annual density peak, i.e. March to June.

The nematode/copepod ratio does not appear to be very useful here. It could be utilized as a pollution index only after determination of the role played by abiotic factors in the perturbation, especially grain structure. Even in this case, the N/C ratio can remain relatively stable while the harpacticoid species composition can be very different (e.g. at Kersaint, 1984).

A 'turning-point year', 1981, roughly separates the 2 principal phases of the meiofauna development. The first phase – 'degradation' and 'impoverishment' of the fauna – lasted 2 or 3 yr according to the taxon studied and the exposure of the site considered. The length of the second phase – 'recovery' or 'reconstitution' of the original fauna – also depends on the faunal groups recorded and on the site. Moreover, quantitative and qualitative parameters must be considered separately.

Despite the lack of references prior to 1978 for this coastal sector, we can consider, after this long-term study, that the return to 'normal' of the meiofauna (for this type of biotope) took place approximately in 1983. However, if we wish to assess the exact 'recovery time', i.e. the length necessary to return to the initial balance of the populations (known at Corn ar Gazel and Kersaint), it is also necessary to consider each station separately.

On the whole, population variations seem to occur more suddenly, but to last for a shorter period, at exposed sites ('high energy'), while variations are more progressive, and last longer, at sheltered sites. At Brouennou, we could observe both group stimulation and substitution during the period monitored, while at Corn ar Gazel we recorded only a sudden and brief (1979) substitution of 2 species within a group. At Kersaint, the sudden group substitution observed in 1984 was due to a perturbation irrelevant to the oil spill.

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LITERATURE CITED

- Berné, S., D'Ozouville, L. (1979). 'AMOCO CADIZ', cartographie des apports polluants et des zones contaminées. Rapp. contrat CNEXO/Ministère de l'Environnement et du Cadre de Vie, Brest, France

- Bodin, P. (1977). Les peuplements de Copépodes Harpacticoides (Crustacea) des sédiments meubles de la zone intertidale des côtes charentaises (Atlantique). *Mém. Mus. natn. Hist. nat., Paris, sér. A, Zool.* 104: 1–120 + 31 tables
- Bodin, P., Boucher, D. (1981). Évolution temporelle du méio-benthos et du microphytobenthos sur quelques plages touchées par la marée noire de l'AMOCO CADIZ. In: CNEXO (Brest, France) (ed.) AMOCO CADIZ, conséquences d'une pollution accidentelle par les hydrocarbures. Actes Coll. Int., Brest, 19–22 November 1979, p. 327–345
- Bodin, P., Boucher, D. (1983). Évolution à moyen terme du méio-benthos et des pigments chlorophylliens sur quelques plages polluées par la marée noire de l'Amoco Cadiz. *Oceanologica Acta* 6 (3): 321–332
- Bodin, P., Le Moal, Y. (1982). Effets à court terme, sur la méiofaune et la macrofaune, du nettoyage d'une plage polluée par les hydrocarbures, avec utilisation d'un dispersant. *Acta Oecologica, Oecol. Applic.* 3 (3): 263–280
- Bonsdorff, E. (1981). The Antonio Gramsci oil spill. Impact on the littoral and benthic ecosystems. *Mar. Pollut. Bull.* 12 (9): 301–305
- Boucher, G. (1980). Impact of 'Amoco Cadiz' oil spill on intertidal and subtidal meiofauna. *Mar. Pollut. Bull.* 11 (4): 95–101
- Boucher, G. (1984). Évolution du méio-benthos des sables fins sublittoraux de la baie de Morlaix de 1972 à 1982. *Oceanol. Acta (vol. spéc.)*: 33–37
- Boucher, G. (1985). Long-term monitoring of meiofauna densities after the AMOCO CADIZ oil spill. *Mar. Pollut. Bull.* 16: 328–333
- Chardy, P., Glémarec, M., Laurec, A. (1976). Application of inertia methods to benthic marine ecology: practical implications of the basic options. *Estuar. coast. mar. Sci.* 4: 179–205
- Chassé, C., Morvan, D. (1978). Six mois après la marée noire de l'Amoco Cadiz, bilan provisoire de l'impact écologique. *Pen ar Bed* 11 (93): 311–338
- Coull, B. C., Bell, S. S. (1979). Perspective of marine meiofaunal ecology. In: Livingston, R. J. (ed.) *Ecological processes in coastal and marine systems*. Plenum Publ. Corp., New York, p. 189–216
- Coull, B. C., Hicks, G. R. F., Wells, J. B. J. (1981). Nematode/Copepod ratios for monitoring pollution: a rebuttal. *Mar. Pollut. Bull.* 12 (11): 378–381
- Elmgren, R. (1975). Benthic meiofauna as indicator of oxygen conditions in the Northern Baltic Proper. *Merentutkimuslait. Julk./Havsforskningsinst. Skr.* 239: 265–271
- Elmgren, R., Hansson, S., Larsson, U., Sundelin, B., Boehm, P. D. (1983). The 'Tsesis' oil spill: acute and long-term impact on the benthos. *Mar. Biol.* 73: 51–65
- Feder, H. M., Cheek, L. M., Flanagan, P., Jewitt, S. C., Johnston, M. H., Naidu, A. S., Norrell, S. A., Paul, A. J., Scarborough, A., Shaw, D. (1976). The sediment environment of Port VALDEZ, Alaska: the effect of oil on this ecosystem. Rep. Off. Res. Develop. U.S. Environ. Protec. Agency. Ecol. Res. Ser., EPA-600/3-76-086: 1–332
- Giere, O. (1979). The impact of oil pollution on intertidal and subtidal meiofauna. Field studies after the La Coruña-spill, May, 1976. *Cah. Biol. mar.* 20: 231–252
- Glémarec, M. (1986). Ecological impact of an oil spill: utilisation of biological indicators. *Wat. Sci. Tech., Plymouth* 18: 203–211
- Glémarec, M., Hily, C. (1981). Perturbations apportées à la macrofaune benthique de la baie de Concarneau par les effluents urbains et portuaires. *Acta Oecologica, Oecol. Applic.* 2 (2): 139–150
- Glémarec, M., Hussenot, E. (1981). Définition d'une succession écologique en milieu meuble anormalement enrichi en matières organiques à la suite de la catastrophe de l'AMOCO CADIZ. In: CNEXO (Brest, France) (ed.) AMOCO CADIZ, conséquences d'une pollution accidentelle par les hydrocarbures Actes Coll. Int., Brest, 19–22 November 1979, p. 499–512
- Glémarec, M., Hussenot, E., Le Moal, Y. (1982). Utilization of biological indicators in hypertrophic sedimentary area to describe dynamic process after the 'AMOCO CADIZ' oil spill. *Int. Symp. Util. Coast. Ecosyst., Rio Grande, RS Brazil* 1982: 1–18
- Heip, C. (1980). Meiobenthos as a tool in the assessment of marine environmental quality. *Rapp. P.-v. Réun. Cons. int. Explor. Mer* 179: 182–187
- Hennig, H. F.-K. O., Eagle, G. A., Fielder, L., Fricke, A. H., Gledhill, W. J., Greenwood, P. J., Orren, M. J. (1983). Ratio and population density of psammolittoral meiofauna as a perturbation indicator of sandy beaches in South Africa. *Environ. Monit. Assess.* 3 (1): 45–60
- Hicks, G. R. F., Coull, B. C. (1983). The ecology of marine meiobenthic harpacticoid copepods. *Oceanogr. mar. Biol. A. Rev.* 21: 67–175
- Hily, C., Le Bris, H., Majeed, S., Glémarec, M. (1986). Surcharge du milieu côtier en matière organique. Actes Coll. Océanographie côtière, 'BORDOMER', oct. 1985: 214–228
- Hockin, D. C. (1982). The effects of sediment particle diameter upon the meiobenthic copepod community of an intertidal beach: a field and a laboratory experiment. *J. Anim. Ecol.* 51: 555–572
- Hockin, D. C. (1983). The effects of organic enrichment upon a community of meiobenthic harpacticoid copepods. *Mar. environ. Res.* 10: 45–58
- Hulings, N. C., Gray, J. S. (1971). A manual for the study of meiofauna. *Smithson. Contr. Zool.* 78: 1–83
- Le Moal, Y. (1981). Ecologie dynamique des plages touchées par la marée noire de l'Amoco Cadiz. 3rd Cycle thesis, Université de Bretagne Occidentale, Brest
- Mielke, W. (1976). Ökologie der Copepoda eines Sandstrandes der Nordseeinsel Sylt. *Mikrofauna Meeresboden* 59: 1–86
- Morel, G. (1981). Évolution des hydrocarbures biogènes et fossiles dans un site confiné de la côte nord du Finistère, l'Aber Benoît, fortement perturbé par la pollution pétrolière de l'AMOCO CADIZ. 3rd Cycle thesis, Université de Bretagne Occidentale, Brest
- Pearson, T. H., Rosenberg, R. (1978). Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanogr. mar. Biol. A. Rev.* 16: 229–311
- Pielou, E. C. (1975). *Ecological diversity*. Wiley Interscience Publ., J. Wiley & Sons edit., New York
- Raffaelli, D. (1981). Monitoring with meiofauna – a reply to Coull, Hicks and Wells (1981) and additional data. *Mar. Pollut. Bull.* 12 (11): 381–382
- Raffaelli, D. (1982). An assessment of the potential of major meiofauna groups for monitoring organic pollution. *Mar. environ. Res.* 7 (2): 151–164
- Raffaelli, D., Mason, C. F. (1981). Pollution monitoring with meiofauna, using the ratio of nematodes to copepods. *Mar. Pollut. Bull.* 12 (5): 158–162
- Remane, A. (1952). Die Besiedlung des Sandbodens im Meere und die Bedeutung der Lebensformtypen für die Ökologie. *Verh. dt. zool. Ges.* 1951–1952: 327–359
- Renaud-Mornant, J., Goubault, N. (1980). Survie de la méiofaune après l'échouement de l'Amoco Cadiz (chenal de Morlaix, grève de Roscoff). *Bull. Mus. Hist. nat., Paris, 4e Ser., 2, Sect. A*, 3: 759–772

-
- Soyer, J. (1971). Bionomie benthique du plateau continental de la côte catalane française. III. Les peuplements de Copépodes Harpacticoïdes. *Vie Milieu* 21 (2-B): 337–511 + maps
- Spooner, M. F. (1977). Oil spill in Hong Kong. *Mar. Pollut. Bull.* 8 (3): 62–65
- Warwick, R. M. (1981). The nematode/copepod ratio and its use in pollution ecology. *Mar. Pollut. Bull.* 12 (10): 329–332

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