Benthic recovery following cessation of fish farming: a series of successes and catastrophes

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ABSTRACT: After the removal of fish cages at an intensive aquaculture site, the sedimentary environment was monitored over 23 mo for redox potential, total organic carbon and nitrogen, total phosphorus, algal pigments and macrofauna. Three sampling stations were established: one under the previous location of the cages (R-0), a second one (R-10) at 10 m distance from the edge of the cages and a control site (R-c) at >1 km distance. At both stations near the farming site the sediment was initially found to be anoxic and overlain by a highly organic black layer. Most geochemical variables at Stn R-10 attained values close to those at Stn R-c within 11 mo. Large fluctuations in the values of most variables were observed at Stn R-0 over the 23 mo, indicating that the environment had not fully recovered before the end of the observations. Similar results were obtained from the macrofaunal analysis, which revealed that after 23 mo a high proportion of benthic fauna at Stn R-0 was still composed of opportunistic species; abundance biomass and species composition showed marked successive changes in the direction of succession. This regression was attributed to a secondary disturbance due to a benthic algal bloom, caused by the seasonal release of nutrients from the farm sediment. It is concluded that the recovery process of heavily enriched benthos in a dynamic coastal environment is subject to the influence of different factors, resulting in progress and regression, and therefore the succession model proposed by Pearson & Rosenberg (1978; Oceanogr Mar Biol Annu Rev 16:229–311) may not be applicable in the early stages of succession.

KEY WORDS: Fish farms · Aquaculture · Benthic recovery · Redox · Organic carbon · Nitrogen · Phosphorus · Pigments · Macrofaunal succession · Abundance-Biomass Comparison curves

INTRODUCTION

Organic enrichment, usually resulting from sewage discharge, is the most widely encountered type of marine pollution (Gray 1981), and given the constantly increasing human settlement along the coast it could be seen as the most important threat for the marine environment globally (McIntyre 1995). The coastal zone is the most important part of the marine environment in terms of productivity, as well as in terms of biodiversity (Ray & Grassle 1991, Gray et al. 1997). During the last few years there has been an attempt to value the environment (Navrud 1991), and to assess its importance as a provider of goods and services (Costanza et al. 1997) to human society. Despite rea-

sonable doubts, as to the accuracy of the estimates and the efficiency of the assumptions behind this concept, it would be important to assess the value of public goods, such as the marine environment, assigned to private use. In this context perhaps the most relevant information needed is the potential, and the time needed, for recovery after the exploitation or the disturbance of a particular resource.

Among the different types of environmental impact caused by aquaculture, the effects on benthos are the most commonly found throughout the world (Gowen & Bradbury 1987, Iwama 1991). The sedimentation of organic material results in an anoxic sediment layer on the sea bed beneath the farm cages (Hall et al. 1990, Holmer 1991) with specific geochemical properties such as negative redox values (Hargrave et al. 1993), high organic content (Hall et al. 1990, Holmer 1991, Karakassis et al. 1998) and accumulation of nitrogen-

ous and phosphorous compounds (Holby & Hall 1991, Hall et al. 1992). Several studies addressing the effects of fish farming on macrobenthos (Brown et al. 1987, O'Connor et al. 1989, Weston 1990, Kupka-Hansen et al. 1991) revealed similarities with the empirical succession model of Pearson & Rosenberg (1978) in terms of spatial distribution of macrofauna. However, little is known regarding the temporal succession of biogeochemical processes prevailing in the sediment after the cessation of fish farming. To our knowledge the only relevant published information comes from a study in a Scottish sea loch (Gowen et al. 1988), while limited seasonal recovery has been reported in terms of geochemical processes without removal of the farms (Holmer & Kristensen 1992, Karakassis et al. 1998).

It has been suggested that the rotative use of sites available for fish farming (fallowing) could be employed in order to minimize effects on the environment and to avoid the effects of souring on the farmed stocks (Iwama 1991, Munday et al. 1992). However in order to use such a means for the abatement of pollution it is essential that recovery processes are well understood so that a site could be left vacant over sufficient time before being used again. Gowen et al. (1988) have suggested that cages should be left in position for 6 mo to 1 yr and then farming should cease for 1 to 2 yr. For the microtidal coastal environment in the Mediterranean it is quite difficult to suggest such a guideline since information on the environmental impacts of aquaculture is rather limited (Munday et al. 1994).

In the present study, after the removal of a fish farm situated in a microtidal Mediterranean coastal bay, geochemical variables and macrofauna were monitored for a period of 2 yr. During this period it was found that the recovery in benthic conditions was influenced by a combination of geochemical factors, resulting in a complicated temporal pattern, and therefore, due to a secondary disturbance, the overall succession seemed to deviate from the known paradigm of community succession in relation to organic enrichment (Pearson & Rosenberg 1978). Disturbance has been defined as 'a process which occurs when any physical or biological agent acts to reduce population size, either by a direct biocidal action or by some indirect effect on population growth rates' (Platt & Lambshead 1985). In this paper the term catastrophe (significant result) is used as opposed to disturbance (process). The term 'opportunist' is used as by MacArthur (1960, cited in Pearson & Rosenberg 1978), i.e. 'species whose reproductive and growth characteristics fit them to take immediate advantage of a sudden environmental change providing them with a favourable unexploited niche'.

MATERIALS AND METHODS

Sampling strategy. Sampling was carried out in Cephalonia Bay, Greece, after the cessation of fish farming in August 1995. The farm unit comprised 10 cages (2 rows of 5) and had been in production for more than 6 yr, with an average annual production of 140 t of sea bream and sea bass during the preceding 2 yr. Two sampling stations were established, one below the previous position of the cages (R-0) and a second (R-10) at 10 m distance from the edge of the cages at 19 m depth. The positions of the stations were relatively easy to find after the cages had been removed due to the accidental sinking of a large cage corridor which was left there during the entire monitoring period. The substrate at both Stns R-0 and R-10 was silty (72 and 71 % respectively) with median grain diameter (MD) of 0.026 and 0.075 mm respectively. Samples were also taken from a control site (R-c) which was selected at a distance of 1.2 km from the cages, but with a similar depth (21 m) and sediment type (MD = 0.017 mm, silt and clay content 87 %), and upstream from the main current direction. Photosynthetically active radiation (PAR) measured using a CTD profiler (SEABIRD-19) during July and November showed that during the 2 periods PAR at the bottom was 14 and 7 %, respectively, of that measured at the surface; PAR measured at the bottom during autumn was lower by a factor of 3 than that measured during summer.

Seven visits to the site were carried out during November 1995, April, June and October 1996, and February, May and July 1997, henceforth referred to as t_3, t_8, t_{11}, t_{14}, t_{17}, t_{21} and t_{23} respectively, named after the time interval (in months) between cessation of aquaculture and the sampling cruise. At each of the stations the sea bed was sampled for geochemical variables (total organic carbon [TOC] and nitrogen [TON], and algal pigments) by means of a plastic core tube (2.5 cm diameter). Following retrieval, cores were sliced into horizontal layers (2 cm thick) and kept deep frozen (–20°C) until subsequent analysis. Redox potential (Eh) was measured in larger core samples at 2 cm intervals from the water-sediment interface by means of an electrode standardized with Zobell's solution (Zobell 1946).

Macrofauna samples were taken by SCUBA divers using sampling cores of 9.5 cm internal diameter and 15 cm depth of sediment from the water-sediment interface. Five replicates were taken for each sampling station in order to determine the variability within samples. In the first 2 sampling cruises (t_3 and t_8) 3 replicate samples were taken from the control station by means of a Smith McIntyre grab (0.1 m²).

During cruises t_{14}, t_{17}, t_{21} and t_{23} samples in vertical sediment profiles were collected from Stn R-0 and

analysed for chlorophyll, sediment water content (SWC), and organic material (LOI: loss on ignition). These samples were taken by SCUBA divers, using 20 cm long core tubes of 5 cm internal diameter. Immediately after sampling, cores were deep frozen (at −20°C) until subsequent analysis. Data on the vertical distribution of sediment variables from the control site have been reported previously (Karakassis et al. 1998).

Chemical analyses. TOC and TON were determined in the sediment samples by means of a Perkin Elmer 2400 CHN Elemental Analyzer following the procedure of Hedges & Stern (1984). Sediment contents in chlorophyll and phaeopigments were determined according to the method described by Yentsch & Menzel (1963) using a Turner fluorometer (model 112) and 90% acetone to extract pigments. SWC was determined as the weight loss after drying at 80°C until constant weight (approximately 20 to 30 h). Total phosphorus was determined in the dried samples, which were homogenized by grinding and digested with a mixture of perchloric and nitric acid (Burton & Riley 1956, Sturgeon et al. 1982). The concentration of phosphorus was determined colorimetrically as molybdate reactive phosphorus (Strickland & Parsons 1972). Organic material (LOI) was determined as the weight loss of the dried sample after combustion for 6 h at 500°C (Kristensen & Andersen 1987).

Macrofauna analyses. Macrofauna samples were sieved *in situ* through a 500 µm mesh. The retained sediment containing the macrofaunal organisms was preserved in 10% buffered formalin. Rose Bengal was added to stain the organisms and to facilitate sorting. Samples were sorted by hand into major taxa and specimens were identified to species level. Macrofauna wet biomass (g m^{-2}) was determined separately for each species and each sample.

Data analysis. Abundance-Biomass Comparison (ABC) curves were plotted according to the method proposed by Warwick (1986) and the associated *W*-statistic (Clarke 1990) was calculated for each station and for each sampling cruise using the average values over all the replicates in each station. This technique has been considered as a tool for analyzing disturbance, combining information on abundance and biomass for all the species in the community. Diversity was calculated by means of the (log$_2$) Shannon-Wiener index (Shannon & Weaver 1949), as was also calculated in Pearson & Rosenberg (1978). Multidimensional scaling (MDS) ordination analysis (Field et al. 1982) was performed using the Bray-Curtis similarity index (Bray & Curtis 1957) in order to obtain a 2-dimensional plot of the macrofaunal temporal

Table 1. Coefficient of variation (%) for geochemical variables determined in replicated samples taken at the control site (Stn R-c) during 3 sampling cruises in Cephalonia Bay, Greece. nd: not determined

Sampling period	Sediment layer	Number of replicates	Chl a	Phaeopigments	TOC	TON	Eh
Nov 1995 (t_3)	0–2	5	23	9	2	4	40
	2–4	5	24	12	4	3	45
Apr 1996 (t_8)	0–2	3	50	35	31	36	10
	2–4	3	61	27	15	31	4
Jul 1997 (t_{23})	0–2	3	15	1	6	nd	26
	2–4	3	52	20	6	nd	13

succession at the 3 stations; in order to normalize the data and to avoid skew a fourth root transformation was applied to the abundance data prior to cluster analysis (Field et al. 1982).

RESULTS

Sediment chemistry

In order to obtain a measure of the natural variability among samples in the geochemical variables determined, replicated samples were taken at Stn R-c during 3 sampling cruises (t_3, t_8 and t_{23}) corresponding to autumn, spring and summer (Table 1). During the first sampling cruise (t_3) the redox regime (Fig. 1) was highly reducing at the stations under (R-0) and near (R-10) the abandoned fish farming site, with Eh values lower than −100 mV at −2 cm and lower than −110 mV at −4 cm from the sediment surface, whereas at Stn R-c Eh was found to be +30 and +12 mV for the respective depths. During subsequent cruises Eh at Stn R-c was found to fluctuate between +30 and
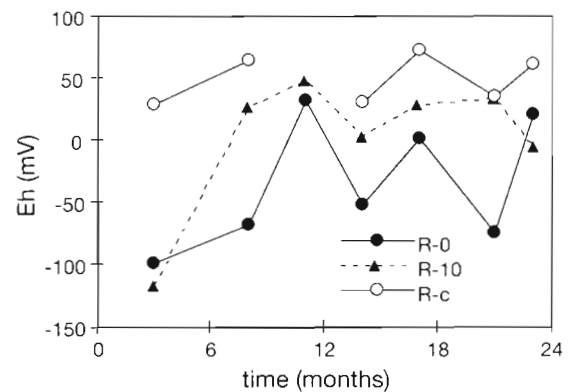

Fig. 1. Temporal variation in redox potential at −2 cm from the water-sediment interface at Stns R-0 (previously under the farming site), R-10 (at 10 m distance) and R-c (control site) after the cessation of fish farming activities
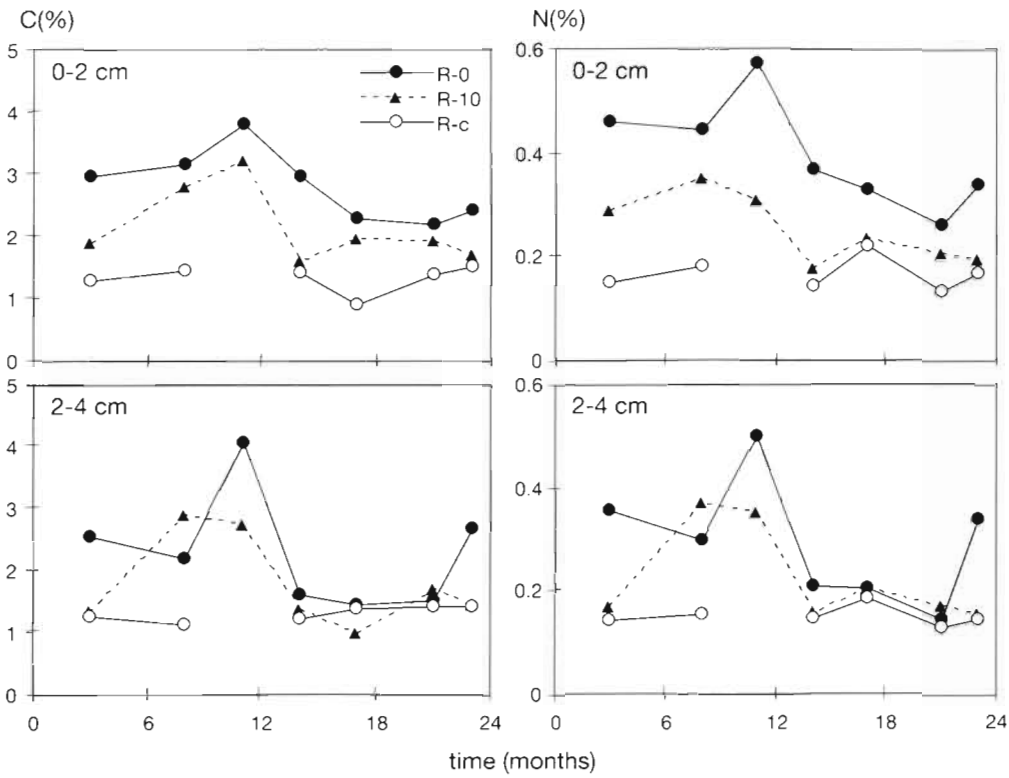
Fig. 2. Temporal variation in organic carbon and nitrogen content at the surface (0 to 2 cm) and the subsurface (2 to 4 cm) sediment layers at Stns R-0, R-10 and R-c
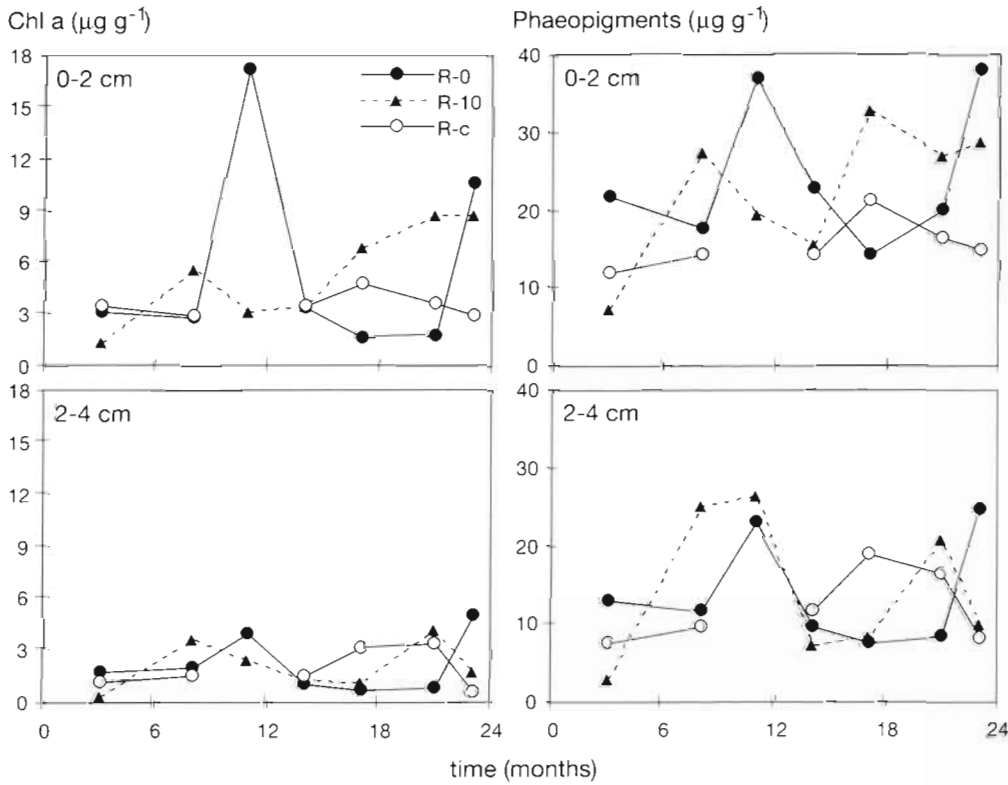

Fig. 3. Temporal change in concentrations of chlorophyll and phaeopigments at the surface (0 to 2 cm) and the subsurface (2 to 4 cm) sediment layers at Stns R-0, R-10 and R-c

+64 mV at the −2 cm sediment layer. Redox at Stn R-10 increased rapidly reaching positive values 5 mo later (cruise t_8) and remained close to levels at Stn R-c thereafter. Redox at Stn R-0 had increased to positive values by sampling cruise t_{11}, but in subsequent cruises was found to fluctuate between −7 and −100 mV. A similar pattern was found for the sediment layer at −4 cm from the water-sediment interface.

TOC and TON (Fig. 2) showed increases in concentration which reached maximal values 11 mo after the cessation of fish farming for Stn R-0 both at the surface (0 to 2 cm) and the subsurface (2 to 4 cm) sediment layer. At Stn R-10, TOC and TON concentrations determined during the t_8 and t_{11} cruises were higher than those determined in the samples taken during the first (t_3) cruise. The concentrations of these variables at the surface layer of both Stns R-0 and R-10 remained higher than those at Stn R-c (by a factor of 2) until the end of the survey, although after the t_{11} cruise the levels at Stn R-10 approached the levels at the control site.

Chlorophyll concentration in the sediment (Fig. 3) at Stn R-0 peaked at the surface layer during the t_{11} cruise (July 1996) and again during t_{23} (July 1997), showing a similar temporal distribution to concentrations of TOC and TON. During the peaks the concentration of phaeopigments was 2.1 and 3.6 times higher than chlorophyll for t_{11} and t_{23} respectively, whereas at other times phaeopigment concentration exceeded chlorophyll by a factor of 6 to 11. Similar temporal patterns were also found for chlorophyll, TOC and TON at the surface layer at Stn R-10. At the subsurface sediment layer the differences between Stn R-c and Stns R-0 and R-10 were less noticeable.

The results of Spearman rank correlation analysis among chemical variables (Table 2) indicated that organic nitrogen decreased significantly with time at both the impacted sites. The strong correlations between C, N, chlorophyll and phaeopigments indicated that a large proportion of the variation in organic material is related to the biomass of autotrophs. The positive correlation between Eh and pigments at Stn R-0 indicates that during high pigment concentration the organic material is in fairly good condition (bound in living cells), and therefore during this period the redox is not adversely affected by decomposition processes. Finally the significant positive correlation between Eh values at Stns R-0 and R-c could be attributed to similar seasonal patterns in geochemical processes, although these patterns were not detected at the same level of significance at Stn R-10.

The results obtained from 2-way ANOVA (Table 3) indicated that there were significant differences between the impacted stations (R-0 and R-10) and Stn R-c regarding redox and TOC. Concentrations of TOC and TON at Stn R-0 were significantly higher than at Stns R-c and R-10. These differences were not evenly distributed over time, the most conspicuous differences being detected during t_{11} for TOC. Despite the conspicuous differences between Stns R-0 and R-c in terms of chlorophyll a and phaeopigments (Fig. 3) during t_{11} and t_{23} ANOVA did not show significant results since these differences were not maintained over the entire period (as with TOC and TON) but were manifested only during certain periods of the year.

Vertical profiles

The vertical distribution of sediment variables during the second half of the experiment (Fig. 4), i.e. from

Table 2. Rank correlation coefficients between time and chemical variables at all sediment layers. Significant values: $p < 0.05$; $p < 0.01$

Stn	Variable	Month	R-0 Eh	R-0 TOC	R-0 TON	R-0 Chl	R-0 Phaeo.	R-10 Eh	R-10 TOC	R-10 TON	R-10 Chl	R-10 Phaeo.	R-c Eh	R-c TOC	R-c TON	R-c Chl
R-0	Eh	0.37														
	C	−0.45	0.34													
	N	−0.52*	0.34	0.98**												
	Chl	−0.01	0.52*	0.79**	0.77**											
	Phaeo.	0.15	0.58*	0.73**	0.72**	0.96**										
R-10	Eh	0.24	0.51	0.04	0.02	−0.02	0.07									
	C	−0.28	0.27	0.50	0.48	0.46	0.37	0.43								
	N	−0.52*	0.21	0.44	0.46	0.25	0.14	0.26	0.82**							
	Chl	0.43	0.24	−0.02	−0.08	0.21	0.29	0.40	0.55*	0.27						
	Phaeo.	0.35	0.43	0.10	0.03	0.21	0.29	0.49	0.64*	0.47	0.91**					
R-c	Eh	0.27	0.67*	0.11	0.08	0.22	0.22	0.43	0.63*	0.63*	0.66*	0.85**				
	C	0.47	0.24	0.24	0.15	0.43	0.42	0.04	−0.07	−0.23	0.35	0.25	0.11			
	N	−0.09	0.66*	0.09	0.14	0.01	−0.04	0.20	0.26	0.53	0.12	0.38	0.75**	−0.17		
	Chl	0.03	0.13	−0.05	−0.01	−0.17	0.03	0.51	0.41	0.46	0.45	0.45	0.32	−0.11	0.11	
	Phaeo.	0.42	0.47	−0.41	−0.39	−0.37	−0.18	0.74**	0.20	0.28	0.53	0.60*	0.54	0.12	0.34	0.77**

Table 3. Results of 2-way ANOVA for geochemical variables for all sampling cruises. $^*p < 0.05$, $^{**}p < 0.01$, ns: not significant

Variable	Source of variability	F	df	p	Tukey post hoc test								
						R-0	R-10		t_3	t_8	t_{11}	t_{14}	t_{17}	t_{21}
Redox	Station	12.481	2	0.001	R-10	ns		t_8	ns					
	Time	3.825	6	0.026	R-c	**	*	t_{11}	*	ns				
								t_{14}	ns	ns	ns			
								t_{17}	*	ns	ns	ns		
								t_{21}	ns	ns	ns	ns	ns	
								t_{23}	ns	ns	ns	ns	ns	ns
TOC	Station	31.286	2	0.000	R-10	**		t_8	ns					
	Time	6.686	6	0.003	R-c	**	**	t_{11}	*	ns				
								t_{14}	ns	ns	*			
								t_{17}	ns	ns	**	ns		
								t_{21}	ns	ns	**	ns	ns	
								t_{23}	ns	ns	**	ns	ns	ns
TON	Station	27.616	2	0.000	R-10	**		t_8	ns					
	Time	4.075	6	0.029	R-c	**	ns	t_{11}	ns	ns				
								t_{14}	ns	ns	ns			
								t_{17}	ns	ns	ns	ns		
								t_{21}	ns	ns	*	ns	ns	
								t_{23}	ns	ns	ns	ns	ns	ns
Chl a	Station	0.236	2	ns										
	Time	0.944	6	ns										
Phaeo.	Station	1.830	2	ns										
	Time	1.000	6	ns										

Macrofaunal community structure

A total of 4749 individuals were identified to belong to 145 macrofaunal species. The macrobenthic community at Stn R-c was a mixture of the biocoenoses of the terrigenous mud (VTC) and the muddy detritic bottoms (DE) as described by Pérès (1967). Some of the 'characteristic species' (sensu Pérès 1967) of the VTC were among the most abundant species at Stn R-c (Table 4), such as *Mysella bidentata*, *Nephtys hystricis*, *Sternaspis scutata*, while *Abra nitida* and *Labidoplax digitata* were also consistently present at Stn R-c although at a lower percentage. With the exception of *M. bidentata* (which attained high abundance towards the end of the survey), these species were found only sporadically at Stn R-10, while they were completely absent from Stn R-0 throughout the survey. Some of the preferential species of the DE biocoenose, such as the bivalve *Corbula gibba* and the polychaete *Glycera rouxi*, were found at Stns R-c and R-10 whereas they were found only once in the samples taken at Stn R-0.

October 1996 (t_{14}) to July 1997 (t_{23}), showed that in terms of SWC the surface sediment at Stn R-0 was not different from the sediment at Stn R-c. The phosphorus content however indicated that the surface layer of the sediment (0 to 4 cm) contained a considerable proportion of waste material 2 yr after the cessation of the fish farming activity, although the amount of phosphorus at the surface sediment was considerably lower (by 50%) than that measured at an active farming site in the same bay (Karakassis et al. 1998). Chlorophyll and phaeopigment content showed pronounced differences with season, reaching maximal values during spring and early summer. In all cases the concentration of phaeopigments was higher than chlorophyll, by a factor of 5, and, in general, the concentrations of phaeopigments and chlorophyll at the surface layers of Stn R-0 were higher than the respective concentrations at Stn R-c. Below 5 cm depth from the water-sediment interface pigment concentration, as well as all other variables measured, did not show any noticeable difference from Stn R-c. The vertical distribution of organic content of the sediments, determined by LOI, presented a similar pattern, with chloroplastic pigments (Fig. 4) indicating that during the second year after the cessation of the farming activity new carbon is fixed in the sediment as a consequence of primary production.

The macrofaunal abundance (Fig. 5) measured at both Stns R-0 and R-10 started at values lower than the values first measured at Stn R-c and lower than the minimum abundance measured at Stn R-c throughout the survey. The fauna during the first cruise (t_3) was dominated by polychaetes of the *Capitella capitata* complex by 70 (R-10) to 84% (R-0). During later stages of the succession (t_8 onwards) the range of abundance measured at Stn R-10 (2200 to 6500 ind. m^{-2}) was found to be within the range measured at Stn R-c (900 to 7400 ind. m^{-2}) and the percentage of opportunistic species at Stn R-10 decreased progressively to 0% during the t_{14} and t_{17} cruises. However, throughout the survey macrofaunal abundance at Stn R-0 fluctuated beyond the range measured at Stn R-c, showing either extremely high values during summer (t_{11} or t_{23}) or very low during autumn (t_{14}). The cumulative abundance of opportunistic species at Stn R-0 exceeded 50% throughout the survey, with the exception of the samples taken during February 1997 (t_{17}), when the *C. capitata* complex accounted for only 1% of the total abundance at that station.

Biomass data (Fig. 5) exhibited a similar pattern, with biomass estimates at Stn R-10 approaching and remaining close to the range of levels recorded at Stn R-c. Biomass at Stn R-0 showed pronounced fluctu-
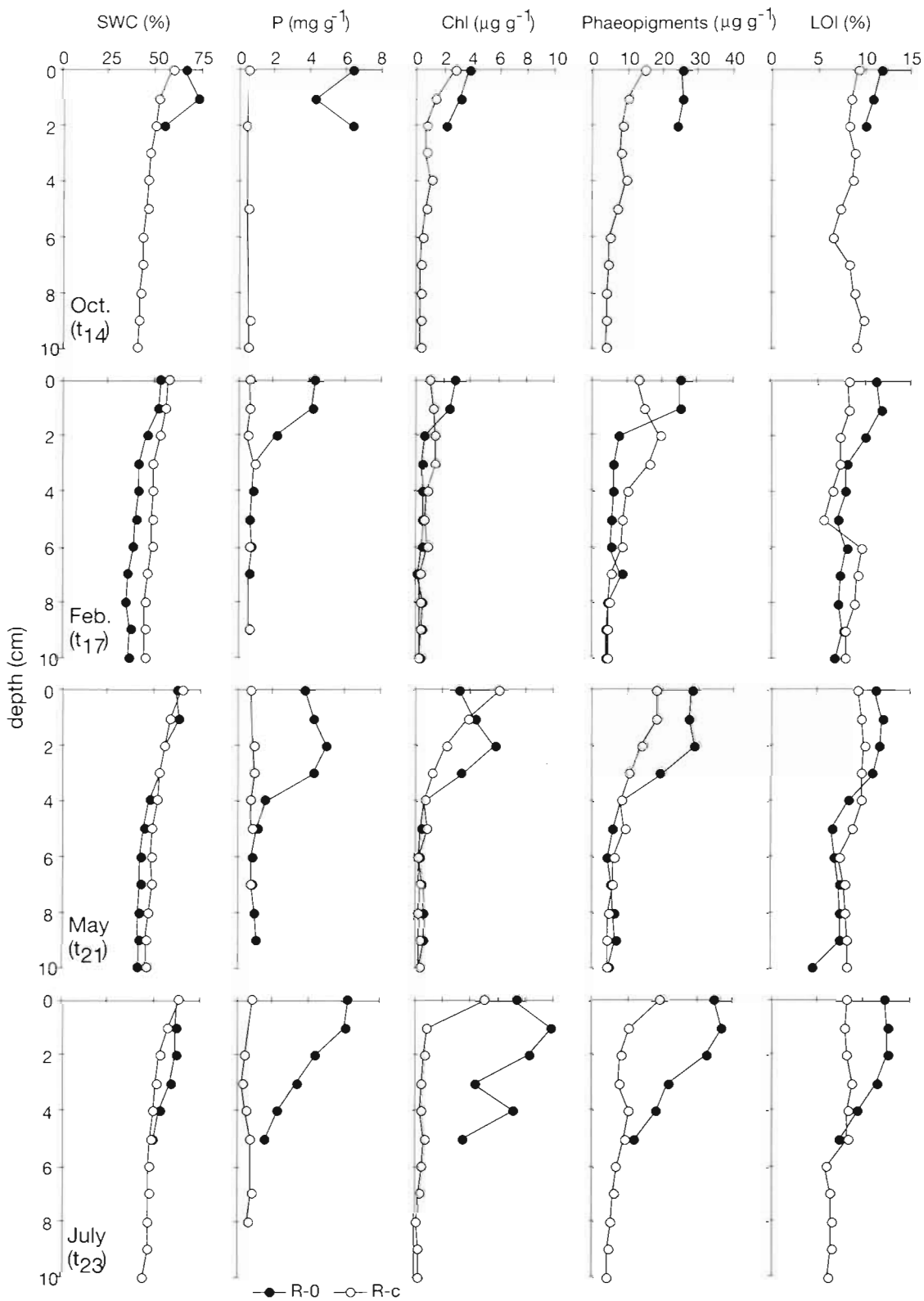
Fig. 4. Vertical distribution of sediment variables in core profiles at Stns R-0 and R-c during the last 4 sampling cruises. SWC: sediment water content; LOI: organic material

Table 4. Macrofaunal species comprising more than 4% of the total abundance at any one station and sampling cruise (values are %). +: presence at a percentage <1%. (C: Crustacea, E: Echinodermata, M: Mollusca, N: Nemertinea, P: Polychaeta, Ph: Phoronida). Species in the list were arranged by decreasing average abundance at Stn R-0 and increasing average abundance at Stn R-c

Species (taxon)	R-0							R-10							R-c					
	t_3	t_8	t_{11}	t_{14}	t_{17}	t_{21}	t_{23}	t_3	t_8	t_{11}	t_{14}	t_{17}	t_{21}	t_{23}	t_3	t_8	t_{14}	t_{17}	t_{21}	t_{23}
Capitella cf. capitata (P)	84	93	86		+	91	99	70	45	4			3	37						+
Poecilochaetus serpens (P)			33									+			1					
Pseudoleiocapitella fauveli (P)				9					+	7	7									
Scolelepis fuliginosus (P)					5															
Aricidea fragilis (P)	3									11	16	18					+			
Iphinoe serrata (C)		+	+				+	3	2			3	31				+			
Prionospio fallax (P)		+		2					+	3	5	1	3							
Glycera rouxi (P)				+				+	+		4	1	+		+				+	
Spio filicornis (P)													7			+				
Sigambra tentaculata (P)				+								+		6						
Phaxas pellucidus (M)									5						+				1	
Tubulanus sp. (N)									1	4	3				+		2			+
Abra alba (M)		+		2	+			5	5		1	10	3			1	+		1	+
Amphiura chiajei (E)	3			15				20	4			+	1		+	1		+	1	
Nucula sulcata (M)									5	2		1			1	3	+			+
Apseudes elisae (C)																			8	
Heteromastus filiformis (P)							+		4	2		8			3	+	+	+	3	+
Putilla alleryana (M)				33					+		3	5		+	+	2	+	4	1	2
Leucothoe incisa (C)		+		3											+	+	2	+	4	2
Ampelisca typica (C)								2	6					1	2	4	1	3		5
Phoronis sp. (Ph)										9	6	3			2	7	2	4	10	+
Levinsenia gracilis (P)				+						7	2	5			1	2	6	7	9	4
Lumbrineris gracilis (P)	6	+	+	33	8			5	5	17	23	8	2		2	1	13	18	2	2
Sternaspis scutata (P)												+			2	11	+	14	12	5
Corbula gibba (M)		+						11	11	+	3	15	3		17	14	12	4	3	4
Nephtys hystricis (P)												+			19	23	4	8	14	4
Mysella bidentata (M)		+		25				7	22	10	10	3		8	30	8	32	20	8	50
Total number of individuals	31	224	855	13	182	58	1104	10	107	219	123	148	79	230	421	270	216	106	92	261

ations throughout the survey, with biomass twice that at Stn R-c during the last sampling cruise.

The Shannon-Wiener diversity (Fig. 5) index at Stn R-c fluctuated between 3.4 and 4.3 throughout the survey. After the t_8 cruise the species diversity in the samples taken at Stn R-10 was found to be within this range (with a slight decrease during t_{23}), while the diversity in the samples taken at Stn R-0 was consistently lower than 2.0 throughout the survey, with the exception of t_{17}, when diversity at Stn R-0 peaked reaching 4.2 bits. The shape of the curve at Stn R-0 was similar to the general pattern described in Pearson & Rosenberg (1978), and indeed during the peak of diversity the macrobenthic assemblage was found to be a mixture of species from various stages of the organic enrichment succession. However, the subsequent decrease in diversity was not due to a lack of opportunists but to excessive dominance of these species, indicating that macrofauna regressed towards the polluted stage of the succession.

ABC curves

According to the ABC method introduced by Warwick (1986), in undisturbed communities the biomass curve always lies above the abundance curve, with the reverse being true for grossly disturbed communities. In moderately disturbed areas the 2 curves may coincide or cross each other. This pattern is reflected by the W-statistic (Clarke 1990), which takes values in the range (–1,1), approaching 1 for equal abundances across species but for a biomass dominated by 1 species. Using these criteria the community at Stn R-c (Fig. 6) was found to be undisturbed throughout the survey with the exception of the t_{23} cruise, when the 2 lines crossed as a consequence of the recruitment of young individuals of a small-size bivalve (Mysella bidentata). Stn R-10 was found to be moderately disturbed during the first 3 cruises (t_3, t_8 and t_{11}) while during the next 3 cruises it was found to be undisturbed. Stn R-0 was found to either be disturbed or have a very low number
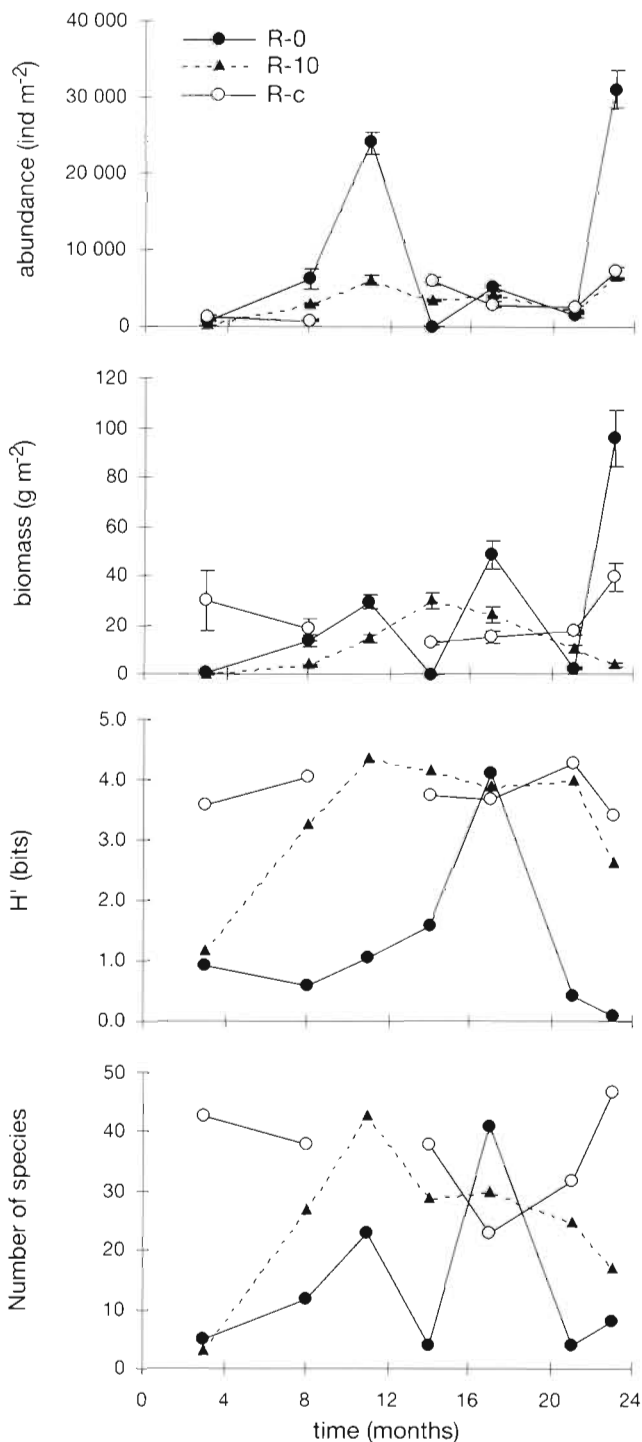
Fig. 5. Macrofaunal abundance and biomass (± standard error), Shannon-Wiener diversity (H') and number of species at Stns R-0, R-10 and R-c

Multivariate analysis

Combined inspection of the dendrogram produced through cluster analysis (Fig. 7) and the MDS ordination plot (Fig. 8) revealed a well-defined group of samples corresponding to Stn R-c with 45% similarity which remained relatively stable in terms of species-abundance structure over the 2 yr period of the survey. At Stns R-0 and R-10 during the first sampling cruise the macrofaunal community structure was very dissimilar to the reference site. Similarity to the 'normal conditions' increased rapidly at Stn R-10, conditions there approaching the Stn R-c community structure during t_{14}, t_{17} and t_{21}. However, the general pattern for both stations located near the previous fish farming site, particularly Stn R-0, showed strong fluctuations between the initial conditions and the typical structure of Stn R-c. Among the samples taken from Stn R-0, only those taken during t_{11} (July 1996) and t_{17} (February 1997) clustered with the Stn R-c and Stn R-10 samples in the classification dendrogram.

DISCUSSION

Bonsdorff & Blomqvist (1993) discussing the post-catastrophe recovery of zoobenthos in the microtidal, low-salinity Northern Baltic emphasized that the pattern of community succession in these species-poor systems follows the generalizations proposed for marine ecosystems by Pearson & Rosenberg (1978), although in some cases this pattern may be altered by secondary disturbances caused by the initial stress factor. As an example, Bonsdorff & Blomqvist (1993) mentioned reduced oxygen conditions in the near-bottom water following dredging activities. In the present paper there is a clear indication of secondary disturbance induced by factors different (although related) to the initial stressor. The nutrients, particularly phosphate, which do not induce stress on macrofauna during fish farming, triggered benthic algal production after the cessation of aquaculture activities. This enhancement of primary production had maximal values during summer, when light availability on the sea bed is higher, particularly after removal of the cages and the consequent elimination of shading due to the floating structures and the dust from the fish feed. The farm sediment is a rich source of phosphorus as indicated by the sediment profiles in the present paper and as has been found for trout farms in Northern Europe (Holby & Hall 1991). Phosphate is particularly important for primary production in Cephalonia Bay, where N:P molar ratio ranges between 23 and 34 throughout the year (Karakassis unpubl. data). The flux of phosphorus from the sediment to the boundary layer is particularly
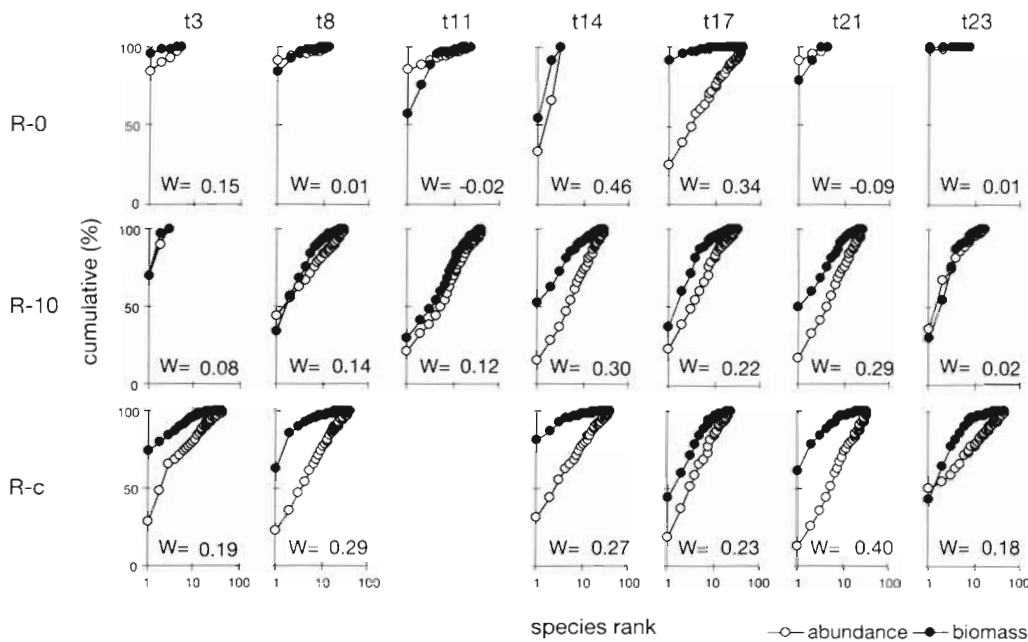
of species for most of the time, except for the t_{17} cruise (February 1997) when it showed a pattern indicative of an undisturbed community. For all the stations the W-statistic was found to be positive, except for Stn R-0 during July 1996 (t_{11}) and May 1997 (t_{21}).

Fig. 6. ABC curves (Warwick 1986) and the corresponding values of the W-statistic (Clarke 1990) for the macrobenthos species data at Stns R-0, R-10 and R-c during all the sampling cruises
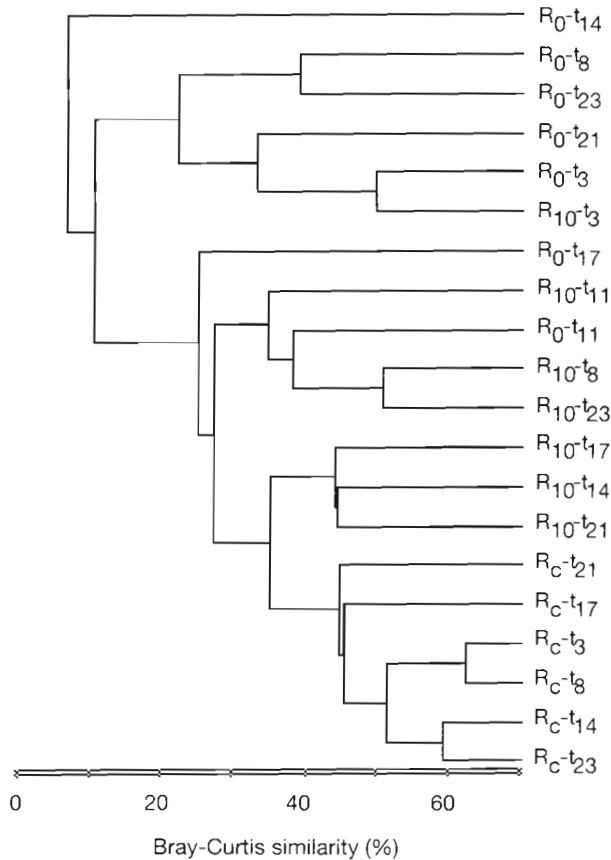

Fig. 7. Classification dendrogram of the samples taken from Stns R-0, R-10 and R-c during all the sampling cruises (t_3 to t_{23}) based on species-abundance data

favoured under reduced conditions (Sundby et al. 1992). Under oxidized conditions the surface sediment layer acts as a trap for phosphate (Mortimer 1971). Consequently, intense redox fluctuations between reduced and oxidized conditions (as at Stn R-0) could result in pulses of P release which could favour benthic algal production during part of the year. This relation between redox, phosphorus and chlrorophyll could explain the much more pronounced fluctuations in chlorophyll at Stn R-0 than at Stn R-10. This new source of carbon resulted in an increase in organic carbon and nitrogen content at the surface of the sediment after the cessation of fish farming, i.e. after the supply of exogenous organic material had stopped. However, this type of silty environment, previously described by Pérès (1967) as 'terrigenous mud' (VTC), is known to have high sedimentation rates and a complete absence of algae. As a consequence of the burial of the algal biomass in the sediment, the concentration of degrading organic material increased in the period after the peak in pigments and the oxygen and redox decreased. Therefore conditions in the sediment become adverse for macrofauna, at least for part of the year, and consequently the community regresses towards the polluted end of the succession, where macrofauna consists, almost exclusively, of opportunistic species and macrobenthic biomass decreases dramatically.

Pearson & Rosenberg (1978) related the redox regime to the presence or absence of macrofauna and since then several other studies have also done so. Oxidized (Eh > 0) and oxic (presence of molecular oxy-
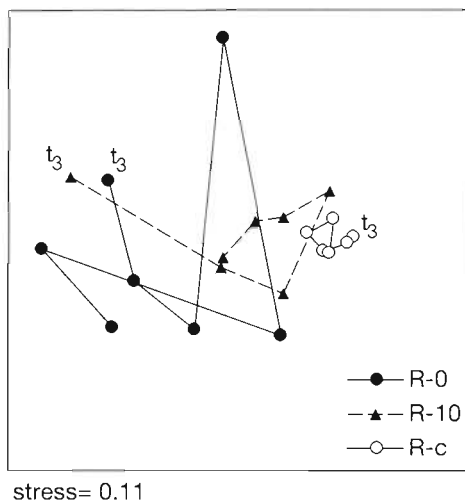
stress= 0.11

Fig. 8. MDS plots of macrofauna data for Stns R-0, R-10, R-c sampled during all the sampling cruises (t_3 to t_{23}). For each station the point corresponding to the first cruise is indicated with the cruise name (t_3). Points corresponding to successive sampling cruises for each station are linked with a line

gen) were no longer identical terms after Jørgensen & Revsbech (1989) showed, by means of oxygen micro-electrodes, that the oxygen penetrates the sediment up to 6 mm whereas the redox can be positive up to 70 mm from the sediment surface. A clear connection between oxygen supply, redox and macrofauna has been demonstrated in an experimental study by Nilsson & Rosenberg (1994), who found reduced survival of macrofauna in severe hypoxia compared to in moderate hypoxia or normoxia. Nilsson & Rosenberg (1994) also found that under normoxia redox increased by >100 mV at 1 to 2 cm depth in the sediment, which they attributed to the increased activity of macrofauna pumping oxygen-rich water into the sediment. In non-impacted areas of the coastal environment, the geo-chemical variables show seasonal fluctuations, related to seasonal patterns in water column stratification or to seasonal variability in precipitation. Both these factors result in high nutrient availability during winter and spring and consequently in higher primary production from phytoplankton and benthic algae. This increase in primary production can result in a strong pulse of organic carbon towards the sea bed and consequently in a decrease in oxygen concentration at the water-sediment interface due to increased microbial activity. In other words there is a seasonal pattern in the supply of electrons to the benthic environment. In a non-impacted environment this decrease in oxygen concentration and Eh is usually small while the increase in food availability induces an increase in benthic biomass. But, when the system is on the margin of recovery, the Eh being already very low, the natural pulse

could be expected to result in a 'small catastrophe' for the succession process inducing low survival of macrofauna. This was the case in Cephalonia Bay, where similar patterns of redox fluctuation (in terms of direction of change) were found between the control and the heavily impacted site and, although the benthic assemblages at the former site showed no signs of degradation, at the latter the effect was dramatic in terms of species composition and diversity.

Gowen et al. (1988) conducted a similar study in a Scottish sea loch, where they monitored a station close to (although not underneath) a farming site for 14 mo after removing the fish. The cages remained in position for part of the experiment (10 mo). They also found that the site, having been stocked for 3 yr, had not entirely recovered at the end of the experiment. The redox and the carbon content at the impacted Scottish site varied considerably with time, and so did macrobenthic abundance, biomass and diversity. After removal of the cages (June 1986) there was an increase in organic content by a factor of 2 with a simultaneous increase in Eh (July 1986) and during the following month carbon decreased by 50% and Eh decreased by 56 mV. Although Gowen et al. (1988) did not monitor chlorophyll content in the sediment during their experiment, and despite the difficulties they had in positioning the sampling boat accurately after the removal of the cages, their results are consistent with those presented in the present paper and perhaps they could be explained using the same scheme.

Recovery processes may vary considerably depending on the type of stressor and the spatial and temporal scales of the disturbance. Moore & Rodger (1991) investigating the recovery process in the Firth of Clyde (Scotland) found that after 14 yr from the cessation of sewage sludge disposal there were still signs of disturbance, such as high abundance of Capitella cf. capitata and low diversity, although the situation at most stations had improved considerably. A rather slow benthic recovery process (more than 12 yr) has also been found in respect of colliery spoil dumping (Johnson & Frid 1995), although in this case the stressor (smothering effect due to a wide range of particle size) did not seem to induce secondary degradation. Rosenberg (1976; cited in Gowen et al. 1988) found that a site enriched by discharge from a sulphite pulp mill took 5 to 8 yr to recover, while there was no sign of recovery during the first 3 yr after the pollution abatement. Ferraro et al. (1991), investigating the recovery from sewage and industrial wastewater discharge, also found a regression in the sediment conditions and macrofauna, which was attributed to a secondary disturbance due to natural phenomena. Compared with these studies the recovery of sediments impacted by fish farming is more rapid since the spatial scales of

impact are smaller and the sedimenting material (fish feed and faeces) is more labile than most types of industrial or sewage waste, as has also been suggested by Gowen et al. (1988). However, the recovery succession in the case of the farm waste is not necessarily simple or monotonic since a complex of factors seem to affect recovery and different biogeochemical processes could be involved. Bonsdorff et al. (1995) identified 10 different factors, ranging from hydrodynamic processes to intraspecific interactions, potentially affecting settling success and early survival of macroinfaunal invertebrates. The role of macrofauna in these processes is relatively small during the initial stages of the succession but becomes increasingly important with time, since bioturbation induces further remineralization of the organic material, release of nutrients and changes in the redox regime of the sediment. As has been recently demonstrated (Gilbert et al. 1998), the presence of macrofauna increases denitrification rates by 160 to 280%.

The ABC technique has been tested in a wide range of disturbance types, suggesting it could be used for the analysis of such impacts (Warwick 1986, Warwick et al. 1987, Gray et al. 1988), and it has been used as a standard criterion for assessing disturbance (Tuck et al. 1998). In the present study the ABC technique produced in some cases results inconsistent with the other sources of information on macrofauna, as has been also reported by Weston (1990), who used it in a study on fish farming impacts, and by Reizopoulou et al. (1996), who studied the physical disturbance in Mediterranean lagoons. In particular, none of the samples at Stn R-0 was found to be disturbed under the ABC criterion (Fig. 6) although for most of the time there was a clear dominance by capitellids (Table 4). The macrofaunal assemblage at Stn R-c was only once (during the t_{23} sampling cruise) misclassified as moderately disturbed under the ABC criterion due to the excessive abundance of new recruits of *Mysella bidentata*, while during all other periods was found to be undisturbed. The MDS results and the dominance of capitellids in faunal abundance (Table 4) provided a much clearer pattern of the succession. The catastrophic collapse of macrofaunal abundance during t_{14}, the consequent recovery during t_{17} and finally the regression towards the polluted side of the succession during the last sampling cruises (t_{21} and t_{23}) were consistent with the geochemical results obtained and particularly with the fluctuations of the redox regime, which is in turn explained by the temporal variation in carbon content. The latter is affected by the initial source of sedimented material but also by the new carbon fixation through benthic algal production.

To our knowledge there is no universal criterion for deciding whether a site has recovered or not. Azoic sediments, increased numbers of opportunistic species and increased similarity with the control site are 3 obvious stages in the recovery succession (Pearson & Rosenberg 1978). The high percentage of capitellids at Stns R-0 and R-10 indicated that the system remained disturbed 23 mo after the cessation of fish farming, although the sediment was not azoic and therefore it could be expected that the potential for recovery is high. However our results indicate that macrofaunal assemblages were not stabilized since the 'best' conditions were encountered at 17 mo, when the benthic assemblages at Stn R-0 approached the composition at Stn R-c but subsequently benthic conditions deteriorated again. The benthic conditions at Stn R-10 were found to be intermediate between those at Stns R-0 and R-c. The high percentage of capitellids (37%) found during t_{23} and the fluctuations in macrofaunal composition (Fig. 8) indicate that this station had not reached the end of the recovery succession either.

Although the biocoenoses described by Pérès (1967) are not always applicable to the Mediterranean benthos (Karakassis & Eleftheriou 1997) they have been traditionally used for the classification of benthic assemblages, and a large amount of empirical information has confirmed the presence of the characteristic and preferential species in the sediment types described. Among the species described by Pérès (1967) as preferential for the (undisturbed) biocoenose of the muddy detritic bottoms (DE) was *Corbula gibba*. However, this species has also been considered as a 'characteristic species in subnormal zone' or a 'species present on the edge of the afaunal zone' or an 'important secondary species in polluted zones' by several authors reviewed in Pearson & Rosenberg (1978). In Cephalonia Bay the densities of *C. gibba* were high at both Stns R-10 and R-c. It is not clear, however, whether this high abundance at Stn R-10 indicates a second phase of succession (transitory zone according to Pearson & Rosenberg 1978) or an indication of recovery. Perhaps it is worth noting that most of the species included in the inventory of species relevant to organic enrichment (Pearson & Rosenberg 1978) are species encountered in silty substrates. This is not surprising since the potential for the accumulation of sedimenting organic material is higher in this type of sea bed than in coarse highly flushed sediments.

The sea bed in Cephalonia Bay is not a typical site for aquaculture in the Mediterranean. As has been shown in comparative studies (Hatziyanni et al. 1997, Karakassis et al. 1997) coarse sediments below fish farms showed little effect in terms of geochemical variables and macrofauna in comparison to the silty substrate in Cephalonia Bay. It could be expected that coarse sediment sites will show different recovery rates, depending on the initial conditions of enrich-

ment and the local hydrodynamic processes. Coarse sediment sites surveyed by divers in the coastal waters of Greece (Papoutsoglou et al. 1996) and Israel (Angel et al. 1995) showed very little effect on the sea bed even under the fish cages. Furthermore, it should be noted that the type of disturbance described here was highly localized and did not result in azoic conditions in respect of macrofauna.

The empirical model presented by Pearson & Rosenberg (1978) is robust in respect of the spatial characteristics of succession as well as in respect of the long-term evolution of enriched benthic communities. This model parallels spatial distance from a pollution source to temporal distance from a pollution event. However, short-term temporal processes may vary considerably in coastal environments: the succession towards recovery proceeds through regressions, small-scale catastrophes, complex interactions between deposit feeders and predators and seasonal variability. In this context it would be rather strange if the long-term pattern were reflected on each short-term interval of the succession. Although our data do not falsify the basic attributes of the macrofaunal response to organic enrichment described by Pearson & Rosenberg (1978), there is evidence that the temporal pattern of succession may differ from the spatial, the former being more fragmented due to secondary disturbance such as the increase in organic material due to exploitation of sedimented nutrients by algal production. The decomposition of this organic material results in deterioration of the sediment conditions and consequently in a regression of the composition of macrofaunal assemblages towards the polluted stage of the succession. Therefore, monitoring of the recovery succession needs to be based on several variables and adequate time scales, since the interplay of different processes could result in considerable deviations from the expected improvement in benthic conditions.

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