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Seasonal changes in macrophyte and macrozoobenthos assemblages in three coastal lagoons under varying degrees of eutrophication

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The dynamics of macrophytic and macrozoobenthic communities were studied during two consecutive years in three French lagoons with differing degrees of eutrophication: (1) Arcachon Bay, a macrotidal lagoon on the Atlantic coast; (2) the fishponds of Certes, an almost enclosed system adjacent to Arcachon Bay; and (3) the Etang du Prévost, a highly eutrophic Mediterranean lagoon experiencing summer dystrophic crises. Two stations were sampled seasonally in each system. The intertidal area of Arcachon Bay was covered by a dense, stable seagrass (*Zostera noltii*) bed. In terms of abundance, macrofauna were dominated by oligochaetes, which could be related to the high below-ground plant biomass, including slow-decaying debris; faunal biomass remained relatively constant, throughout the study period. In the Certes lagoons, which were intermediate between the other two systems in terms of eutrophication, vegetation was dominated by another rooted phanerogam (*Ruppia cirrhosa*) with fairly constant biomass, while sporadic development of green macroalgae occurred in spring; both biomass and species richness of macrofauna were low. In the Prévost lagoon, macrophytes were opportunistic macroalgae that first proliferated and then disappeared over a short period in summer; this seasonal crisis resulted in a marked decrease in both biomass and abundance of macrozoobenthos. Macrobenthic dominance shifted after the first summer from suspension-feeding bivalves to subsurface deposit-feeding annelids. The differences in structure and seasonal dynamics of benthos in the three systems may have significant effects on higher trophic levels.

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Key words: coastal lagoons, eutrophication, macrophytes, macrozoobenthos.

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Introduction

Eutrophication has been defined by Nixon (1995) as an increase in the rate of supply of organic matter to an ecosystem. In marine environments, moderate nutrient inputs generally result in increased growth rates for both phytoplankton and macroalgae and thus are almost exclusively regarded as "positive" factors (Gray, 1992). Because more food becomes available for the primary consumers during the initial enrichment phase, it is assumed that zoobenthos responds to the better feeding conditions by faster rates of growth and higher productivity. This has been demonstrated, for example, in the Dutch Wadden Sea where, during a 15-year period of increasing eutrophication, both biomass and annual production of the intertidal macrozoobenthos doubled (Beukema and Cadée, 1986). If amounts of nutrients added are increased further, eutrophication may have more "negative" effects on benthic fauna and flora (Gray, 1992; Heip, 1995): changes in species composition (Pearson and Rosenberg, 1978; Reise *et al.*, 1989; Beukema, 1991); changes in the behaviour of species sensitive to reduced oxygen concentrations (Baden *et al.*, 1990); and mass growth of macroalgae (Sfriso *et al.*, 1988; Piriou *et al.*, 1991). During the ultimate phase of eutrophication, dystrophic events

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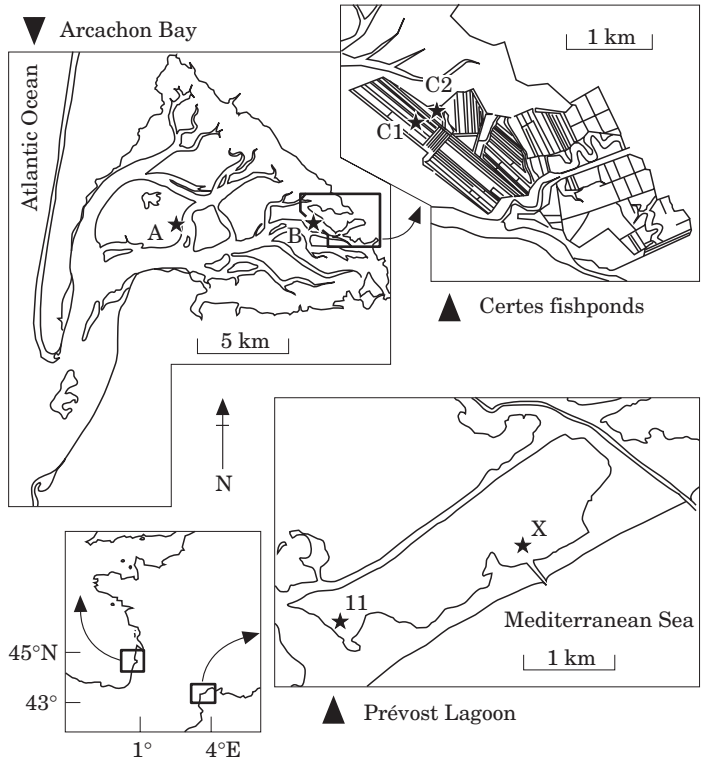


Figure 1. Location of the three lagoons and the sampling stations.

may occur, characterized by oxygen depletion, release of toxic hydrogen sulphide, and mass mortality of zoobenthos (Amanieu *et al*., 1975; Rosenberg and Loo, 1988; Olive and Cadnam, 1990; Desprez *et al*., 1992; Fallesen, 1992; Peterson *et al*., 1994; Rybarczyk *et al*., 1996).

As a consequence of their location between land and sea, most lagoons receive large amounts of organic and mineral nutrients derived from urban, agricultural, and industrial effluents. In addition, owing to their shallow depth and their relatively weak exchange with the open sea, lagoons are amongst the marine environments most sensitive to eutrophication. They also are amongst the most productive ecosystems and provide natural food resources, such as oysters, shrimps, and fish. We compare the dynamics of benthic communities in three French coastal lagoons that differ in level of eutrophication (Caumette *et al*., 1996): (1) Arcachon Bay, a mesotidal lagoon on the southwestern Atlantic coast; (2) the Etang du Prévost, a highly eutrophic Mediterranean lagoon which experiences summer dystrophic crises; and (3) the fishponds of Certes, an almost enclosed system on the eastern coast of Arcachon Bay, which may be considered as intermediate between the other two lagoons in terms of eutrophication. Our hypothesis was that, because of the different degrees of eutrophication prevailing in each system, the seasonal evolution of macrophytes and zoobenthos assemblages would be different in each lagoon. In particular, assemblages were hypothesized to remain quite stable throughout the year in Arcachon Bay, whereas more significant changes were expected for both plant and animal populations in the inner parts of Prévost and Certes lagoons following summer dystrophic crises.

Material and methods

Study sites

In each lagoonal system two stations were selected (Fig. 1), one close to the channel through which water exchange takes place (the outer station), and one distant from the marine entrance of the lagoon (the inner station). A brief account of the environmental setting is given below for the three coastal lagoons and the sampling stations. More detailed information on these systems can be found in Castel *et al*. (1996).

The Bay of Arcachon (44°40′N, 1°10′W) is a triangular-shaped mesotidal lagoon with a total area of 156 km^2 and a maximum water depth of 20 m at low tide. The largest part (115 km^2) of the lagoon is intertidal, with beds of widgeon grass (*Zostera noltii*) and oyster parks occupying 70 and 10 km^2, respectively. The lagoon is connected to the Atlantic Ocean by a narrow

Table 1. Annual flux of total phosphorus and nitrogen ($t\ 10^6\ m^{-3}\ yr^{-1}$) during the 1990s and summer values of dissolved nitrate and ammonia (µM) in the three lagoon systems under study (data from Castel *et al.*, 1996).

Lagoon system	Input of P	Input of N	NO_3^-	NH_4^+
Arcachon Bay	0.1	3.0	0.3–2.0	1.5–2.5
Certes fishponds	—	—	0.7–1.0	4.6–8.3
Prévost Lagoon	4.3	24.6	1.2–4.9	5.7–10.5

channel (2–3 km wide), through which important water exchange occurs at each tide ($370 \times 10^6\ m^3$ on a spring tide and $130 \times 10^6\ m^3$ on a neap tide). Most of the primary production is due to *Zostera noltii*. Since the 1970s, agriculture in the region has intensified, resulting in an increase of more than 50% in the annual flux of total nitrogen. Some evidence of eutrophication is now visible, such as massive summer development of the green alga *Monostroma obscurum* (Kützing) since 1988. However, nutrient concentrations are still low (Table 1), and Arcachon Bay is the least eutrophic of the three systems studied. The outer station (A) was located in a dense seagrass bed on an intertidal flat in the eastern part of the Ile aux Oiseaux. Although this location is in the centre of the system, Bachelet and Dauvin (1993) showed that, owing to the hydrology of the bay, its zoobenthos community is similar to those living near the marine entrance. The tidal amplitude ranges from 4.9 m at spring tide to 1.5 m at neap tide. Annual surface water temperature and salinity ranges are 6–22.5°C and 27–35 (Bouchet, 1968; Robert *et al.*, 1987). The sediment consisted of muddy sand (median grain size, Md = 170 µm; 23–32% silt and clay; POC = 0.7–1.9%). The inner station (B) was situated in the intertidal area on the eastern side, where there is little water exchange with the coastal area. The tidal range is 3.0 m on a spring tide and 1.0 m on a neap tide. Water temperature fluctuates annually between 1 and 25°C, and salinity between 22 and 32. This station was located in a very sparse *Z. noltii* bed. The sediment was a very muddy fine sand (Md = 50–83 µm; 35–62% silt and clay; POC = 2.4–3.5%).

The fish ponds of Certes are semi-enclosed and shallow (0.2–2.0 m in depth) lagoonal impoundments designed for extensive aquaculture. These man-made enclosures are flooded twice a month (at spring tide) from April to October with sea water from the adjacent Bay of Arcachon, through the action of sluice gates distributed around sea embankments. Several species of euryhaline fish are farmed in these ponds (Labourg, 1976): grey mullets (*Chelon labrosus, Liza ramada*), sea bass (*Dicentrarchus labrax*), gilt head bream (*Sparus aurata*), and eel (*Anguilla anguilla*). However, the ponds have progressively gone into decline because of the relatively low yield (50 kg ha^{-1}) and high labour costs. The most important primary producers are seagrasses (*Ruppia cirrhosa*) and filamentous green algae. Because of the shallowness of these ponds and the low rate of water renewal from the bay, dystrophic crises may occur during some warm summers, with the formation of white waters due to the precipitation of carbonates (Castel *et al.*, 1996) and fish mortalities (Labourg, 1975). However, such dramatic events do not occur every year, and the fishponds of Certes may be considered moderately eutrophic systems (Table 1). The salinity may range from almost freshwater to 60; our measurements varied from 9 (March 1994) to 43 (September 1993). The outer station (C2) was located close to a sluice, at 1.5 m depth, in an access channel distributing the incoming marine water to the ponds. Sediment was an unvegetated muddy sand mixed with greyish clay (POC = 1.5–5.6%). The inner station (C1) was situated in a shallow polyhaline reservoir at 0.3 m-depth within a loose mat of *R. cirrhosa*. The sediment was similar to Stn C2 (Md = 100 µm; 36–58% silt and clay; POC = 4.0–5.1%).

The Etang du Prévost (43°30′N, 3°54′E) is a rectangular, shallow lagoon covering an area of 3.8 km^2. Depths range from 0.3 m on the periphery to 1.5–2.0 m in the middle. The water is slowly renewed *via* a narrow (12 m wide) channel (“grau”) communicating with the Mediterranean Sea. The tidal range may attain 0.3 m, but water renewal mainly results from wind forcing. Water temperature ranges from 5°C in winter to 27°C in summer. This lagoon is extremely eutrophic owing to agricultural and urban run-off (Table 1). Dystrophic crises, locally called “malaïgues”, occur every year during the warm summer months for a period of 2–3 weeks. These crises begin in spring with a bloom of green macroalgae (*Ulva rigida*). In summer, the algal biomass is degraded by aerobic heterotrophic bacteria; oxygen production then decreases, leading to anoxia and the predominance of anaerobic processes. Coloured waters (white waters occurring before red waters) can invade most of the lagoon and disappear within a few days (Amanieu *et al.*, 1975; Caumette and Baleux, 1980). Such dystrophic crises generally have dramatic effects on aquaculture, especially oyster farming. The outer station (X) was situated on a small tidal flat near the “grau”. Salinity varies between 25 during winter and 42 during dry summer periods. Sediment was a homogeneous, clean medium sand (Md = 165 µm; POC = 0.1–0.2%). The inner station (11) was located at 50 cm water depth in the western, sheltered part of the lagoon. Annual salinity range is 11–42. Sediment was a shelly mud mixed with some sand (60–80% particles <40 µm; POC = 2.9–3.4%).

Sampling methods and treatment of samples

Macrophytes and macrozoobenthos were quantitatively surveyed for two years on a seasonal basis. Samples were

collected in March, June, September, and December 1993, and in March, June, and September–October 1994. Sampling at Stn X was impossible in September 1994 because the sand bank had been dredged by fishermen some days before to enhance water exchange. Because of the between-site heterogeneity (intertidal/subtidal; benthos abundance) sampling methods could not be identical at all stations. A preliminary survey was conducted in March 1993 to determine the number of replicates of a given size required for a tolerance of a 20% error on the mean abundance (Bachelet *et al.*, 1993).

Macrophytes were sampled within a 400 cm^2 metal frame at the intertidal and shallow Stns A, B, Cl, and X; with a 216 cm^2 Ekman grab at Stn C2; within a 2500 cm^2 by 1 m high enclosure at Stn 11. Four to five replicates were taken randomly at each station. In the laboratory, plant material was washed through a 0.5 mm sieve and sorted to the species level within 24 h. Biomass was determined as dry weight (DW, 80°C for 48 h). For *Z. noltii*, above and below-ground living biomass as well as buried dead parts were determined separately.

In Arcachon Bay, macrofauna samples were taken using a 79 cm^2 PVC corer penetrating about 15 cm deep into the sediment. Five replicates were taken randomly at Stn A, and 4 at Stn B. Additionally, four 2500 cm^2 quadrats were searched by hand at Stn A for large molluscs and crustaceans. At the Certes and Prévost stations, macrozoobenthos was collected using a 216 cm^2 Hydro-Bios-Ekman grab (penetration depth, 15 cm). Three replicates were taken at Stns C1 and C2, 10 at Stn X, and five at Stn 11. Samples were washed on a 0.5 mm sieve, fixed in 4% buffered formalin and stained with Rose Bengal. The organisms were identified to the lowest possible taxon and counted. Biomass was determined as ash-free dry weight (AFDW), after oven-drying to constant weight at 80°C and combustion at 550°C for 2 h. This was determined for each of four major groups: annelids, molluscs, arthropods, and minor or miscellaneous phyla. All data were standardized to 1 m^2 and are presented as mean values ± standard error.

Each species was assigned a feeding strategy, based on literature data and own observations (Table 2). Six major trophic groups were distinguished: suspension feeders, surface-deposit feeders, subsurface-deposit feeders, predators (including scavengers), herbivores, and omnivores (Fauchald and Jumars, 1979). Species that feed by different methods (e.g., spionid polychaetes, several amphipods) were evenly distributed amongst the trophic groups assigned.

Macrobenthic community diversity was analysed by Shannon's diversity index (H′). A correspondence analysis was performed on abundance data to determine similarity (using chi-squared distance) among sampling dates, following the recommendation by Legendre and Legendre (1984) for the ordination in reduced space of a data matrix containing a high number of zeros.

Results

Arcachon Bay (Fig. 2)

The seagrass bed at Stn A was typical of the *Z. noltii* populations in the median part of the bay (Auby and Labourg, 1996): high density of shoots, relatively small size of leaves, and high development of roots and rhizomes compared with the above-ground parts (ratio of biomass of living above-ground parts to biomass of living below-ground parts = 0.29–0.87). The above-ground biomass (living leaves and sheaths) was minimum in winter (12 g DW m^{-2} in March 1994); it remained relatively constant throughout the rest of the year, reaching a maximum value of 51 g DW m^{-2} in October 1994. Similarly, the biomass of the below-ground parts (dead leaves + living and dead roots and rhizomes) was minimum in March 1994 (95 g DW m^{-2}) and relatively constant at the other sampling dates (133–173 g DW m^{-2}). Several species of macroalgae were found at this station: *Monostroma obscurum, Enteromorpha* sp., *Ulva* sp. (green algae), *Gracilaria verrucosa, Caulacanthus ustulatus* (red algae). However, their biomass exceeded 0.5 g DW m^{-2} only on a single occasion (4.9 g DW m^{-2} in December 1993).

Total abundance of macrozoobenthos at Stn A was high and underwent relatively few variations (between 37 000 ind. m^{-2} in March 1993 and 70 370 ind. m^{-2} in September 1993). Annelids were always dominant in terms of numbers, especially the oligochaetes *Tubificoides benedeni* and an undetermined species (Sp. A), which together represented between 36 and 54% of the total abundance (Table 2). Other abundant annelids were the polychaetes *Manayunkia aestuarina, Tharyx marioni, Heteromastus filiformis*, and, in seasonal pulses, the spionids *Pygospio elegans* and *Streblospio shrubsolii*. Molluscs (mainly *Hydrobia ulvae* and *Abra tenuis*) were the second most abundant phylum, while crustaceans occurred in small numbers.

The total biomass, also dominated by annelids, was moderate and relatively constant (7–15 g AFDW m^{-2}). A notably higher number of species was collected in 1993 (39–46 per date) than in 1994 (26–29 per date). Shannon's diversity index remained quite stable and high (H′ = 3.0).

The trophic structure of the macrozoobenthos assemblage, based on numbers, did not change greatly during the two years: the deposit feeders were always dominant, especially the subsurface-deposit feeders (45–63%).

The silty Stn B was located in the eastern part where *Monostroma obscurum* usually initiates its seasonal development. This green alga was always present at

Table 2. Average densities (m^{-2}) of macrozoobenthic species/taxa over the six (Stn X) or seven (other stations) sampling dates.

Taxon	Type	Arcachon Bay		Certes fishponds		Prévost lagoon	
		Stn A	Stn B	Stn C2	Stn C1	Stn X	Stn 11
Anthozoa	F	25	5	—	—	—	—
Turbellaria	P	30	23	—	—	1	—
Nemertea	P	693	231	—	—	8	2
Oligochaeta							
Tubificoides benedeni Udekem	SSD	**18 118**	**121 046**	22	—	—	—
Unidentified spp.	SSD	**7614**	**9332**	**937**	—	1	293
Polychaeta							
Serpulidae	F	142	—	—	—	—	4
Manayunkia aestuarina (Bourne)	F/SD	**5034**	**7545**	—	—	—	2
Polydora cornuta Bosc	F/SD	157	304	**724**	**619**	**755**	**6275**
Prionospio malmgreni Claparède	F/SD	**360**	—	—	—	—	—
Pygospio elegans Claparède	F/SD	1796	92	2	—	**1210**	—
Spio filicornis (O. F. Müller)	F/SD	—	—	—	—	**466**	—
Streblospio shrubsolii (Buchanan)	F/SD	**1020**	**6869**	1537	—	—	—
6 other F/SD spp.	F/SD	298	234	15	—	337	13
Melinna palmata Grube	SD	**499**	—	—	—	—	—
Tharyx marioni (Saint-Joseph)	SD	**3565**	487	—	—	—	—
9 other SD spp.	SD	73	9	—	—	21	44
Capitella spp.	SSD	444	6736	256	—	**5076**	**1539**
Heteromastus filiformis (Claparède)	SSD	**2708**	27	—	—	231	—
5 other SSD spp.	SSD	345	—	—	—	11	—
Hediste diversicolor (O. F. Müller)	O	46	75	197	13	**89**	**897**
2 other O spp.	O	11	—	—	—	2	—
1 O/P spp.	O/P	14	—	—	—	—	—
Parapionosyllis gestans (Pierantoni)	P	**987**	—	—	—	—	—
9 other P spp.	P	236	429	2	—	45	15
Phoronidea (1 sp.)	F	157	—	—	—	—	—
Mollusca							
Cerastoderma glaucum (Bruguière)	F	—	24	—	70	**303**	**521**
Donax trunculus L.	F	—	—	—	—	**39**	—
Ruditapes decussatus (L.)	F	11	—	—	—	**188**	—
Venerupis aurea (Gmelin)	F	2	—	—	—	**240**	4
7 other F spp.	F	385	10	—	—	94	1
2 H spp.	H	18	—	2	—	—	—
Bittium reticulatum (da Costa)	SD	**182**	—	—	—	—	—
Gibbula umbilicalis (da Costa)	SD	**109**	—	—	—	—	—
Hydrobia acuta (Draparnaud)	SD	—	—	—	—	**3194**	**7476**
Hydrobia ulvae (Pennant)	SD	**3118**	**14 095**	—	—	—	—
Hydrobia ventrosa (Montagu)	SD	—	—	379	**2315**	—	—
Abra ovata (Philippi)	SD	158	**1161**	20	—	14	**400**
Tellina tenuis (da Costa)	SD	—	—	—	—	**86**	—
2 other SD spp.	SD	2755	38	—	—	5	—
3 P spp.	P	—	14	—	—	113	11
2 P/SD spp.	P/SD	4	5	—	—	3	—
Pycnogonida (1 sp.)	P	7	—	—	—	—	—
Crustacea							
Corophium insidiosum Crawford	F/SD	—	—	**11 420**	18	**1487**	**8094**
3 other F/SD spp.	F/SD	205	—	—	—	16	120
Gammarus insensibilis Stock	H/SD	—	—	—	—	52	**1773**
2 other H/SD spp.	H/SD	7	—	141	—	—	—
Cyathura carinata (Kröyer)	SD	**1978**	5	—	—	—	—
Lekanesphaera hookeri (Leach)	SD	7	—	**1065**	626	4	2
10 other SD spp.	SD	428	299	4	—	58	—
3 P spp.	P	9	—	—	—	5	4
5 O spp.	O	81	19	55	320	61	303
Insecta (larvae)							
Chironomus salinarius Kieffer	SD	**594**	**2611**	**7773**	6572	6	**2625**
2 other SD spp.	SD	137	14	—	333	—	—
2 P spp.	P	—	—	—	276	—	—

Numbers in bold characters refer to species collected on every date at a given station. Irregularly observed species were grouped by trophic type: F, suspension feeder; H, herbivore; O, omnivore; P, predator; SD, surface-deposit feeder; SSD, subsurface-deposit feeder.

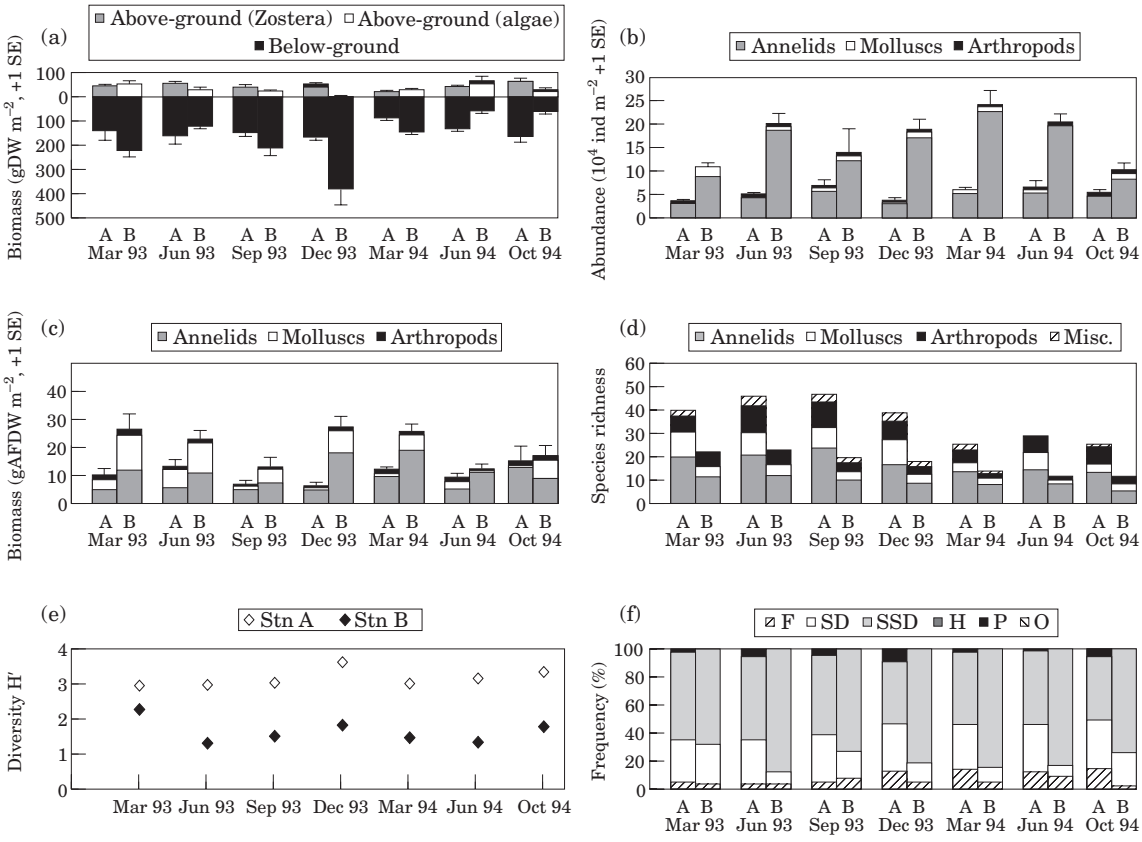


Figure 2. Arcachon Bay. Seasonal variations in (a) above-ground (upper graph) and below-ground (lower graph) biomass of macrophytes, (b) abundance, (c) biomass, (d) species richness (5 replicates at Stn A, 4 at Stn B), (e) Shannon's index of diversity, and (f) trophic group composition of macrozoobenthos (see Table 2 for abbreviations). Left bars: Stn A; right bars: Stn B.

Stn B, with a peak of biomass in spring (44 g DW m^{-2} in March 1993). Although no living *Z. noltii* was collected in significant amounts, a high biomass of dead leaves and rhizomes (123–383 g DW m^{-2}) was present in the sediment at all depths.

Macrozoobenthos densities at Stn B were the highest of the six stations investigated (range: 104 000–247 000 ind. m^{-2}), without a clear seasonal pattern. This assemblage was strongly dominated in numbers by the oligochaete *T. benedeni*, which represented between 50 and 79% of the total abundance (Table 2). Other top-ranked species were another oligochaete (Sp. A), the polychaetes *M. aestuarina, S. shrubsolii*, and *Capitella* spp., and the mudsnail *H. ulvae*. Biomass also was relatively high and fluctuated between 13 (June 1994) and 28 g AFDW m^{-2} (December 1993), without a consistent pattern from year to year. Species richness reached about half the value of Stn A and decreased steadily from June 1993 (23 species) to October 1994 (12 species). Shannon's diversity index decreased in June 1993 and in March–June 1994 because of the increased dominance of *T. benedeni*.

The trophic structure of macrozoobenthos assemblages was remarkably constant. Nearly all macrofauna were deposit feeders, especially subsurface-deposit feeders (68–87%).

Certes fishponds (Fig. 3)

No vegetation was found at Stn C2, except debris of *R. cirrhosa* in the sediment. Macrofauna densities were relatively low (usually <30 000 ind. m^{-2}), but showed a high temporal variability (between 6127 ind. m^{-2} in June 1994 and 80 509 ind. m^{-2} in March 1994). Arthropods were the dominant phylum in all seasons, especially the amphipod *Corophium insidiosum* (responsible for the peaks of total abundance in June 1993 and March 1994) and the larvae of the dipteran *Chironomus salinarius* (Table 2). Spionid polychaetes (*S. shrubsolii, Polydora cornuta*) were present in lower numbers. Molluscs were almost absent. Macrofauna biomass was very low (1–9 g AFDW m^{-2}).

Species richness at Stn C2 fluctuated between 8 and 18 species per sampling date. The assemblage was

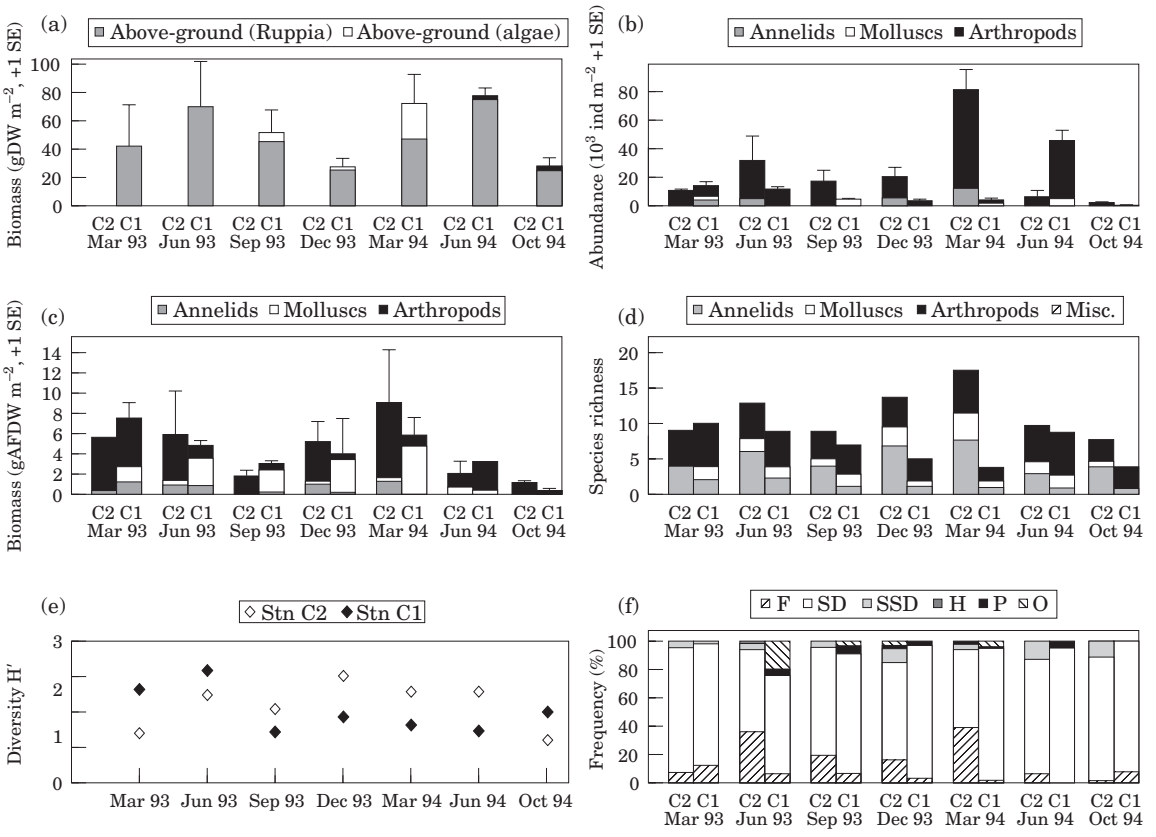


Figure 3. Certes fishponds. Seasonal variations in (a) biomass of macrophytes, (b) abundance, (c) biomass, (d) species richness (3 replicates at each station), (e) Shannon's index of diversity, and (f) trophic group composition of macrozoobenthos (see Table 2 for abbreviations of trophic groups). Left bars: Stn C2; right bars: Stn C1.

dominated by surface-deposit feeders (57–90%), while subsurface-deposit feeders accounted for only 2–12% of the total abundance. Suspension feeders were relatively abundant (up to 37% in June 1993 and March 1994).

At Stn C1, a clear seasonal trend was observed in the biomass (including both above and below-ground living parts) of *R. cirrhosa*, with the highest values recorded in June of both years and the lowest biomass occurring in December 1993. *Ulva* sp. was also collected from September 1993 to October 1994, with a peak of biomass in March 1994.

Total abundances of macrozoobenthos were the lowest of the six stations, decreasing from 12 731 ind. m^{-2} in March 1993 to 370 ind. m^{-2} in October 1994; however, a peak of 45 711 ind. m^{-2} occurred in June 1993, owing to larvae of *C. salinarius*. This dipteran and *Hydrobia ventrosa* were the top-ranked species in densities; other occasionally abundant taxa were *P. cornuta*, the isopod *Lekanesphaera hookeri* and the shrimp *Palaemonetes varians* (Table 2). Total biomass followed a seasonal pattern, with the highest values in March (7.6 and 5.8 g AFDW m^{-2} in 1993 and 1994, respectively) and the lowest value in October 1994 (0.3 g AFDW m^{-2}).

The number of species (4–10) was the lowest of the six stations. Shannon's diversity index fell in September 1993, owing to the strong dominance of a single species (*H. ventrosa*), and did not recover till the end of study. The benthic assemblage existed almost exclusively of surface-deposit feeders (72–97%).

Prévost Lagoon (Fig. 4)

Stn X was located on a sandy, unvegetated bank. Only the June 1993 and March 1994 samples contained some *Enteromorpha* spp. and *Ulva rigida* flowing from the inner parts of the lagoon.

Macrofauna densities at Stn X were rather low. After a first maximum in June 1993, total abundance declined until March 1994 and then increased in June 1994. The taxonomic composition was highly variable. Crustaceans were dominant in numbers in March 1993, owing to local proliferation of the amphipod *Corophium insidiosum*. From June 1993 to March 1994, molluscs

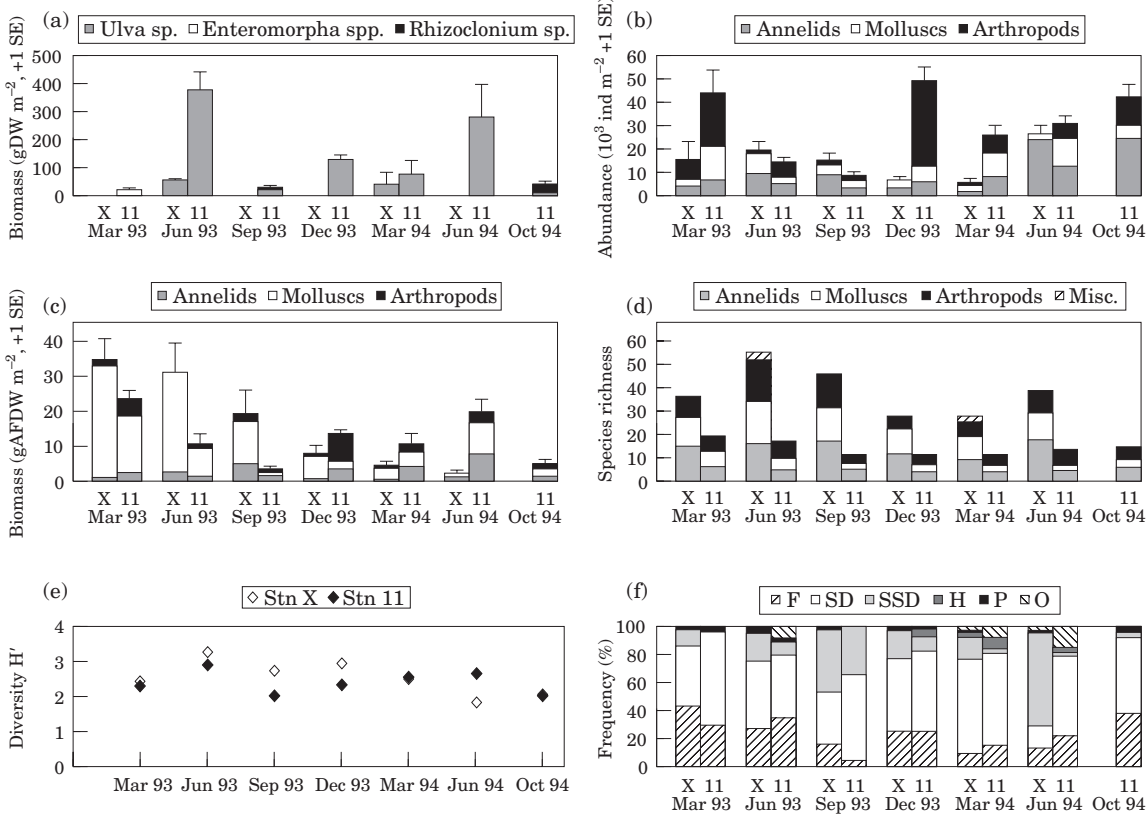


Figure 4. Prévost Lagoon. Seasonal variations in (a) biomass of macrophytes, (b) abundance, (c) biomass, (d) species richness (10 replicates at Stn X, 5 replicates at Stn 11), (e) Shannon's index of diversity, and (f) trophic group composition of macrozoobenthos (see Table 2 for abbreviations of trophic groups). Left bars: Stn X; right bars: Stn 11.

(*Hydrobia acuta* and several bivalves) and polychaetes (spionids and capitellids) were almost equally dominant. Annelids became highly abundant in June 1994 because of a dense recruitment of *Capitella* spp. Owing to the abundance of large suspension-feeding bivalves (*Donax trunculus, Venerupis aurea, Ruditapes decussatus, Chamelea gallina, Cerastoderma glaucum*), which represented more than 90% of the total biomass, extremely high biomass values (>30 g AFDW m^{-2}) were found in March and June 1993. The biomass then markedly decreased till June 1994 (2.2 g AFDW m^{-2}), when most bivalve populations collapsed.

A high number of species was recorded at Stn X, with maxima in June 1993 (55 species) and June 1994 (39), and a drop during the winter 1993/1994 (28 species). Shannon's index also decreased markedly after a maximum in June 1993. Suspension feeders were abundant (41%) at the onset. Their importance in numbers progressively declined, reaching only 12% in June 1994, while subsurface-deposit feeders increased from 12 to 68%.

In March 1993 the samples at Stn 11 contained a small amount of *Enteromorpha flexuosa* and *E. intestinalis* (15.5 g DW m^{-2}). These filamentous algae disappeared in June 1993 when they were replaced by proliferating *U. rigida*, which filled the whole water layer and probably induced anoxia for the benthos. In September 1993, algal biomass (*Enteromorpha*+*Ulva*) had decreased to a low value. A new development of *U. rigida* occurred in December 1993 and again in June 1994. In June of both years lots of isopods and amphipods were seen swimming amongst the floating leaves of *Ulva*.

Macrozoobenthos abundance at Stn 11 decreased dramatically in 1993 from March to September, but recovered in December to reach the original densities (49 000 ind. m^{-2}). The seasonal evolution in 1994 was quite different, with an increasing trend from March to September. The two highest values in 1993 were due to the amphipod *C. insidiosum*, which represented 40 and 43% of the total abundance in March and December, respectively. Polychaetes remained moderately abundant in 1993, but increased in 1994 because of the contribution of *P. cornuta*.

Macrofauna biomass at Stn 11 also fell from March 1993 to September 1993. Molluscs (mainly the bivalves

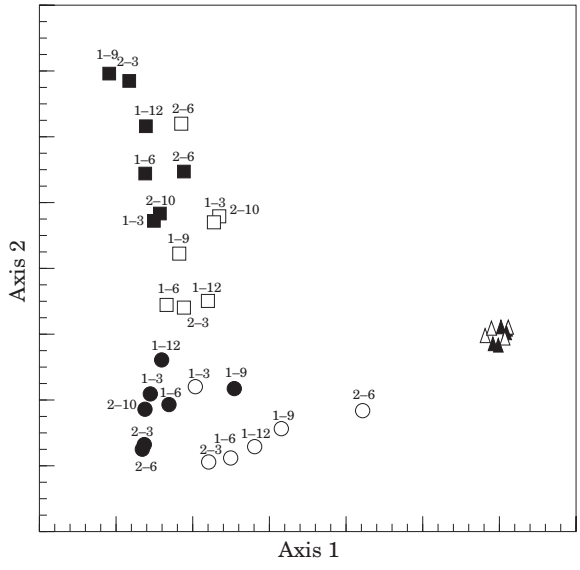


Figure 5. Correspondence analysis on macrozoobenthos abundance in the six stations (Arcachon Bay: open triangles, Stn A; black triangles, Stn B; Certes fishponds: open squares, Stn C2; black squares, Stn C1; Prévost Lagoon: open circles, Stn X; black circles, Stn 11). Sampling dates are numbered using a year-month code (year: 1=1993, 2=1994; month: 3=March, 6=June, 9=September, 10=October, 12=December).

Abra ovata and *C. glaucum*) were deeply affected by the summer events. After recovery during winter, biomass increased till next June, followed by another decline. Species richness was much lower (11–19 species) than at Stn X. Shannon's diversity index decreased between June and September in both years. On the whole, surface-deposit feeders were the main trophic group (47–70%); the proportion of suspension feeders was relatively constant (14–38%), except in September 1993 (3%), when subsurface-deposit feeders increased to 33%.

Multivariate analysis

The first two axes of the correspondence analysis accounted for 20.7% and 13.7%, respectively, of the total inertia (Fig. 5). The points representative of the three coastal lagoons are clearly distinct in the plane F1 × F2, with axis 1 separating Arcachon Bay from the other two lagoons and axis 2 separating the Certes fishponds from the Prévost Lagoon. The two stations of Arcachon Bay (Stn A and Stn B) display a high temporal stability in the structure of their macrozoobenthos community in terms of abundance. In the fishponds of Certes (Stn C1 and Stn C2) and in the inner site of Prévost Lagoon (Stn 11), the trajectory of seasonal samples is quite unstable, especially between March and June or between June and September of both years, showing that the zoobenthos community is affected by summer events; however, in these three stations, the samples of October 1994 return close to those of March 1993 in the plane F1 × F2. The community structure of Stn X in Prévost Lagoon appears to be strongly disturbed between March and September 1993, and again between March and June 1994. The sample of June 1994 is completely opposite to the sample of March 1993 along axis 1, indicating that the assemblage did not recover one year after the summer dystrophic crisis of 1993.

Discussion

Lagoons differ considerably from one another in size, morphology, degree of isolation, water depth, salinity, etc. (Barnes, 1980). Such a range of environmental characteristics applies to the three systems studied here. In addition, the three lagoons differ in their input of nutrients. According to their eutrophication status, the lagoons may be ranked as Prévost lagoon>Certes fishponds>Arcachon Bay (Table 1). Besides eutrophication, other parameters (e.g. water renewal rate, presence of seagrass) may influence the patterns observed in the benthos. However, these factors only strengthen the effects of the input of nutrients: seagrass is present only at Arcachon and Certes, and water renewal is the lowest in the Prévost. As a consequence of the degree of eutrophication, great differences have been found in the dynamics of the benthic communities in these systems.

Arcachon Bay is relatively large, and its water is renewed twice a day by the tides. In spite of a significant increase in the annual flux of nitrogen to the bay during the last three decades (Auby *et al.*, 1994) and recent sporadic blooms of macroalgae, phytoplankton production is rather low (Robert *et al.*, 1987), as are nutrient concentrations (Table 1). Stal *et al.* (1996) postulated that ferric iron, which is abundant in the sediments of the bay, could control primary productivity and algal growth. The high biomass of suspension-feeding oysters could also be one of the mechanisms reducing the effects of eutrophication, as demonstrated in other shallow marine environments (Cloern, 1982; Hily, 1991).

One of the main characteristics of Arcachon Bay is the occurrence of dense meadows of *Z. noltii*. At the outer station, the biomass of macroalgae was extremely low compared with the biomass of phanerogams, and the only significant biomass of green macroalgae was found at the inner station. Although there was some seasonal trend in the biomass of above-ground parts of *Z. noltii*, the total living biomass at the outer station did not fluctuate greatly throughout the year because of slow growth (Auby and Labourg, 1996; Viaroli *et al.*, 1996). Similarly, the abundance and biomass of macrozoobenthos was relatively constant. A small range of

seasonal variation was also found by Castel *et al.* (1989) at a neighbouring station.

Arcachon Bay, especially the inner station, had the highest levels of macrozoobenthos abundance of the six stations investigated. The dominant taxa in terms of both abundance and biomass were annelids, and the high densities were mainly due to a single species, *T. benedeni*. This species is a deep-living worm, occurring as deep as 15–20 cm in the sediment and preferring muddy substrates with a high content of plant remnants or organic matter (Rasmussen, 1973). According to Brinkhurst (1982), tubificids derive the bulk of their nutrition from bacteria and perhaps from algae. Bourguès *et al.* (1996) found that the anaerobic decomposition of *Z. noltii* resulted in a rapid release of inorganic nitrogen and phosphorus. The enrichment of the deep layers of the sediment with decaying plant material is probably responsible for the extremely high abundance and constant dominance of subsurface-deposit feeders in Arcachon Bay.

In the small reservoirs of Certes, water from the adjacent Arcachon Bay is allowed to enter only every fortnight at best. The most important macrophyte is *R. cirrhosa*, the biomass of which was fairly constant throughout the year at the outer station. Sporadically, green algae (*Ulva* sp.) also developed, which is a sign of eutrophication. Although abundance, biomass, and species richness of macrozoobenthos were generally low, the assemblages were dominated by arthropods, with spring proliferations of *C. insidiosum* at the inner station and larvae of *C. salinarius* at the outer station. Labourg (1980) observed marked changes in the structure of benthic assemblages in July–August, with mortalities of bivalves and migrations of *C. salinarius* on *Ruppia* leaves, caused by a series of short dystrophic crises. The correspondence analysis indicated some instability in the structure of benthic communities over the two years of study. However, no catastrophic mortalities such as those reported by Labourg (1980) were observed in 1993–1994. The summer decay of *R. cirrhosa* due to the massive development of epiphytes (Viaroli *et al.*, 1996) might have resulted in a high flux of fresh organic matter to the bottom fauna, which were continuously dominated by surface-deposit feeders.

The waters of Prévost Lagoon receive high inputs of nutrients and are renewed mainly during periods of easterly winds. Every summer is characterized by dystrophic crises caused by a combination of high temperatures, high oxygen consumption, prolonged periods of calm winds, and subsequent reduction in water exchange. A clear sign of these events was the proliferation of opportunistic macroalgae (mainly *U. rigida*) in June of both years.

The species composition of macrozoobenthos in the Étang du Prévost is similar to those previously observed (Guelorget and Michel, 1979*a*, *b*) and to those in other western Mediterranean lagoons (Gravina *et al.*, 1989; Arias and Drake, 1994; Lardicci *et al.*, 1997). In all these systems, the rapid macrophyte decomposition during warm periods leads to a marked decrease in dissolved oxygen concentrations and to fluxes of free sulphide from the bottom (Viaroli *et al.*, 1996). These crises usually have dramatic consequences for the benthic fauna, such as the total disappearance of macrozoobenthos in July–August (Amanieu *et al.*, 1977, 1980; Guelorget and Michel, 1979*a*; Lardicci *et al.*, 1997; Tagliapietra *et al.*, 1998). Although we did not observe such dramatic events, the seasonal variation of macrozoobenthos followed different patterns at the two stations.

Correspondence analysis on the abundance data indicated a stressed situation at the inner station, especially between June and September 1993 when densities decreased markedly as *Ulva* proliferated. Densities increased during 1994 owing to the recruitment of *P. cornuta*, which is known as one of the most opportunist species in shallow areas (Grassle and Grassle, 1974). Biomass of bivalves fell during the summer months. Surface-deposit feeders were the dominant trophic group at all seasons.

Although the huge development of green algae was sustained in the greater part of the lagoon (including the inner station), the area close to the "grau" remained relatively free of algae. Paradoxically, correspondence analysis suggests that the benthic fauna has been more affected at the outer than at inner station. The most striking feature at the outer station is the decline in bivalve biomass after the dystrophic crisis of June 1993. Most of these bivalves were long-lived and the populations did not recover until the final sampling in June 1994. In terms of abundance, surface-deposit feeders dominated till March 1994. However, the proportion of suspension feeders progressively decreased, whilst subsurface-deposit feeders (*Capitella* spp.) increased and even became dominant in June 1994. These observations underline the profound changes that may occur in the trophic structure of the benthic system near the inlet.

As hypothesized, the least eutrophic lagoon with high water exchange, Arcachon Bay, exhibited a high stability in both the structure of macrozoobenthic assemblage and in plant biomass. In Certes fishponds, characterized by intermediate eutrophication, a seasonal stress occurred every year in both macrophyte (summer development of green algae) and zoobenthic assemblages, followed by a recovery phase. In the highly eutrophic Prévost Lagoon, the seasonal pattern in the structure of the macrofaunal community at the inner station was similar to that of the Certes fishponds while the most stressed zoobenthic assemblage was found at the outer station. However, the original presence of long-lived bivalves indicates that dramatic events do not occur each year.

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