

Eutrophication gradients in coastal lagoons as exemplified by the Bassin d'Arcachon and the Étang du Prévost

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Abstract

The conditions of eutrophication are described in three lagoon systems differing by their structure, their catchment area and their connection with the sea: the Bassin d'Arcachon on the Atlantic coast, SW France, the semi-artificial fish ponds of the Bassin d'Arcachon, and the Étang du Prévost on the Mediterranean. The Bassin d'Arcachon is a shallow semi-enclosed bay, strongly influenced by climatic factors and tidal currents. The Bassin receives significant inflow of freshwater and the waters are only partially renewed. The greatest part of the primary production is due to the seagrass *Zostera noltii*. Although the ecosystem remains on the whole in steady state, some evidence of potential eutrophication are visible. For instance, the flux of nitrogen into the Bassin d'Arcachon has increased by more than 50% during the last 25 years. The most significant change among primary producers is the massive development since 1988 of the green alga *Monostroma obscurum*. The fish 'réservoirs' of the Bassin d'Arcachon are man-made enclosures designed for extensive aquaculture and where the water renewal is only possible during certain periods of time. Thus, because of the shallowness and the confined nature of these fish ponds, acute eutrophication is sometimes observed in summer. The Étang du Prévost is extremely eutrophic due to agricultural and urban run-off. Red waters occur periodically during the warm summer months as a consequence of ecological events beginning in the early spring with a bloom of green macroalgae (*Ulva* sp.). In summer, the algal biomass is degraded by aerobic heterotrophic bacteria; the oxygen demand encompasses the oxygen production, leading to the predominance of anaerobic processes and dystrophic crisis. From the comparison of the selected sites, three stages of eutrophication are recognized according to the conceptual model of Nienhuis (1992) describing the relation between the relative dominance of primary producers connected to the availability of nutrients. Such macroscopic observations should, now, be explained by the study of microbiological processes including meiofauna, protozoa, bacteria and all the components of the microbial loop.

Introduction

Littoral ecosystems such as lagoons, estuaries, and salt marshes are highly productive environments but how they function is still not fully understood (Lasserre, 1979a; Lasserre & Postma, 1982). Most of them are subjected to continuous natural modifications. Lagoons, in particular, may undergo periods of disorder due to excessive eutrophication which can lead to dystrophic crisis, the so-called malaïgue in Mediterranean lagoons (Caumette & Baleux, 1980). The control of production and consequently the control of

eutrophication are amongst the major problems faced by those responsible for the management of these sensitive ecosystems.

Lagoons have been historically important as sites for human settlement providing access to both the land and the sea. Not only they are important for transportation, they also provide natural food resources, such as oysters, clams, shrimps, fish, as well as providing a convenient place to dump urban and industrial waste. Some of these multiple uses are compatible; others are not. It is a key objective of the management of these systems that the maximum benefit can

Table 1. Comparison of the characteristics of seawater and lagoonal water. Example from the Bassin d'Arcachon, SW France (August 1986, after Escaravage, 1990). Seawater = open water in the Bassin d'Arcachon, fish ponds = shallow lagoonal enclosures.

	Seawater	Fish ponds
PO ₄ ($\mu\text{mol l}^{-1}$)	0.25	1
NH ₄ ($\mu\text{mol l}^{-1}$)	0.78	5.62
NO ₃ ($\mu\text{mol l}^{-1}$)	1.14	0.30
NO ₂ ($\mu\text{mol l}^{-1}$)	0.26	0.15
pH	8.5	7.3
O ₂ (% saturation)	87	35

be derived from these exploitations without jeopardising their long-term future.

Ecological structure and biogeochemical cycles of eutrophic coastal lagoons

Basic model of lagoon ecosystem

Coastal lagoon ecosystems are directly related to the physical and chemical environment, i.e. coastal lagoons are dynamic, open systems where functions are dominated and controlled by physical processes (Figure 1).

The driving forces of these systems are characterized by:

- flux vectors (currents, tide, solar energy, rain),
- marine inputs (sediment, coastal waters and associated elements such as nutrients, plankton),
- continental inputs (rivers, groundwater, nutrients, sediment, organic matter).

Because of their position as an interface between the terrestrial and marine environments, they are subject to both continental and marine influences. Thus they are highly dynamic environments.

The lagoon ecosystem receives from the marine environment oxidized forms of inorganic nitrogen and phosphorus which are restored as reduced compounds. Ammonia is a preponderant form of nitrogen (Table 1). Its concentration in the sediment is high, due to the mineralization of large amount of organic matter. In contrast, nitrate concentrations are generally low. Low phosphate concentrations recorded in lagoon waters are related to adsorption by particulate matter and the sediments. However, frequent release of PO₄ leads to high variation in the measured concentrations.

The continental inputs in the coastal lagoons are mainly characterized by river waters and, sometime, by ground water or rain water that drain the surrounding soils. These waters not only carry large amounts of particulate material in the form of clay particles and organic detritus but also dissolved material in the form of dissolved organic matter and nutrients arising from human activity in the vicinity of the lagoons (fertilizers, domestic and industrial effluents...). Most of these materials are deposited and concentrate in the lagoons.

Nutrient and organic inputs, together with shallow water conditions, good light penetration and good mixing, lead to high primary production. It is widely accepted that the rates of primary production in coastal lagoons are among the highest measured for natural ecosystems (Lasserre, 1979a). The bulk of the primary production is due to macrophytes: phanerogams (*Ruppia*, *Zostera*) and macroalgae (*Enteromorpha*, *Ulva*). However, significant production by microphytes (epiphytic and/or epibenthic) have also been recorded.

The pelagic compartment (phyto- and zooplankton) is not the most important component in lagoon ecosystems. The shallowness of the water column associated with the stagnation of the water normally does not allow the planktonic community to develop to any great extent. Most of the micro-invertebrates encountered in the water column are phytophilous or epibenthic.

In lagoons, the benthic compartment largely controls the functioning of the ecosystem. The superficial film of sediment on the lagoon bed is generally covered by a blanket of unicellular organisms (cyanobacteria, peridinians, dinoflagellates, diatoms). Through the intense browsing action of herbivorous fauna such as small gastropods and crustaceans, this vegetal material is converted into increasingly fine debris (Figure 2) which is quickly colonized by a large number of microorganisms (microalgae, bacteria) and small-sized invertebrates (meiofauna, crustaceans, annelids). This colonized detritus constitutes an important food source for higher trophic levels (shrimps, fish, especially mullet).

The excessive primary production leads to high rates of production in the rest of the biological food web in these ecosystems. Thus eutrophication is characteristic of many coastal lagoons which should be considered as frontal ecosystems, which whilst very productive are unstable and sensitive to changes in physical and chemical conditions. Recent research, however, suggests that their biological communities are well adapted to such perturbations and are able to function as apparently stable ecosystems.

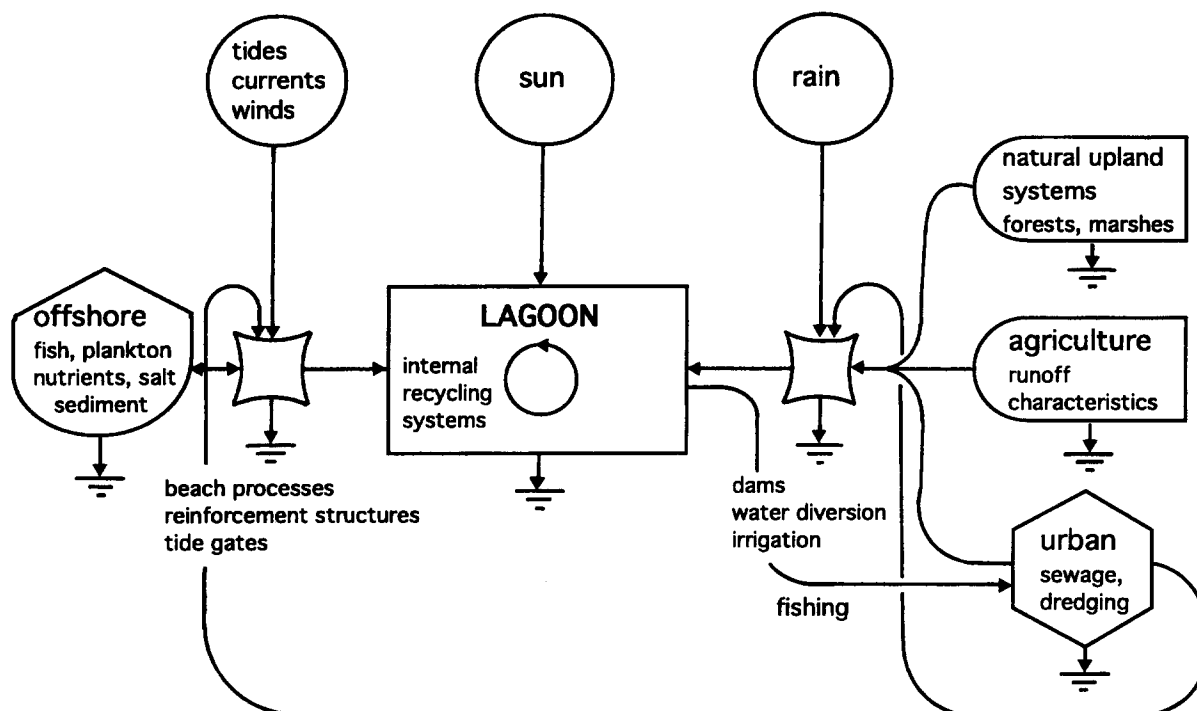


Figure 1. The lagoon as concentrating mechanism and controllable interface between land and sea (redrawn from Lasserre, 1979a).

Microbial communities in coastal lagoons

Many shallow coastal lagoons exhibit well defined salinity gradients from seawater salinity near the connection with the sea to low salinity in the continental areas of the lagoon receiving river inputs, or to brines in solar evaporation lagoons. Such variable conditions of salinity have a very important impact on the distribution and the selection of the components of the biological communities of coastal lagoons.

In the water column bacterial communities are dominated by aerobic heterotrophic bacteria, either with strictly oxidative metabolism or facultatively fermentative metabolism. These bacteria are halotolerant organisms and are mainly of terrestrial origin (Carmouze & Caumette, 1985). The distribution of marine bacteria depends on the influence of tides (Erchenbrecker & Stevensen, 1975). Although many authors have reported on their distribution and physiology (see references in Caumette, 1989a), little is known about their activity and role in coastal lagoons. They mineralize organic material either in free living conditions, or associated with clays or particulate organic matter. They contribute to the release of inorganic nutrients. It is known that fast growing plants such as phytoplank-

ton, filamentous algae and *Ulva* sp. benefit from the increased levels of nutrients and will grow in volume and dominance at the expense of flowering plants and other algae. They commonly dominate in many coastal lagoons.

In the sediment, the microbial community is more complex depending on the gradients of oxygen penetrating the sediment and subsequently on the interface between oxic and anoxic phases. This interface is generally found within the first 2 mm of the sediment. Therefore many different kinds of semi-aerobic and anaerobic bacteria coexist, living by fermentation or anaerobic respiration. In most coastal lagoons, it is known that the anaerobic bacterial community is dominated by sulphate-reducing bacteria that can transform up to 50% of the organic material (Jørgensen, 1983) but produce H_2S , a toxic compound that accumulates as FeS_2 (pyrite) in the anoxic environment. If light reaches the anoxic layers, phototrophic sulphide-oxidizing bacteria can grow and sometimes populate these environments by forming dense purple to brown colored masses (Caumette, 1989b; Van Gernerden, 1983). In addition to sulphur bacteria, anoxic layers of coastal lagoons are densely populated by nitrogen bacteria and methanogenic bacteria (Caumette, 1989a). However,

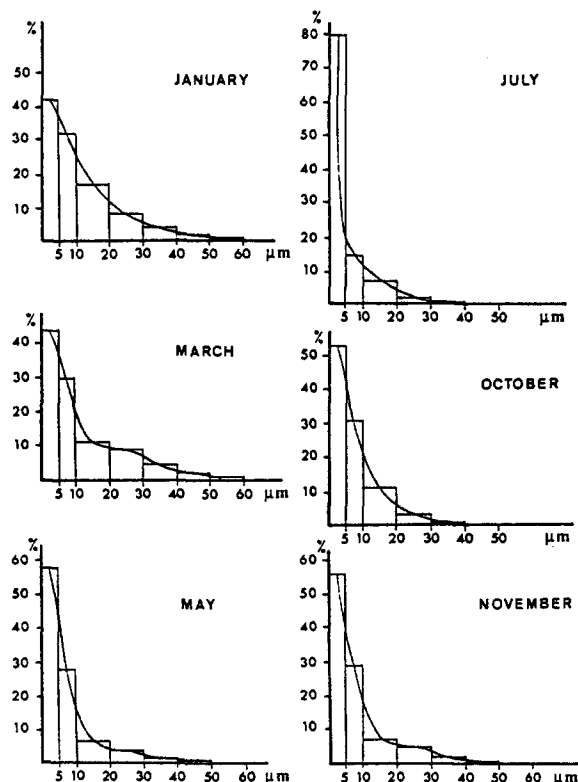


Figure 2. Seasonal variation of the particle size (first mm of the sediment) in a semi-enclosed lagoon ecosystem: the fish ponds of the Bassin d'Arcachon (Castel, unpublished).

although many papers describe these bacteria and their role in marine or coastal estuarine environments (Herbert, 1975; McFarlane & Herbert, 1984; Marty et al., 1990), little is known on their distribution and role in coastal lagoons.

Lagoon environments display very high densities of meiofauna composed mainly of nematodes, harpacticoid copepod, oligochaetes, ostracods, turbellarians, and polychaetes (Castel, 1992). These meiofauna components may consume much more energy in the form of organic matter (detritus + microflora + bacteria) than do the macrofauna (Lasserre et al., 1976). Furthermore respiration rates when related to biomass are very high, indicating the importance of the micro- and meiofaunal communities in coastal lagoons (Table 2). One gram of meiofauna respire a rate at least ten times greater than an equivalent macrofaunal biomass. In shallow eutrophic areas, the ratio macrofauna, meiofauna, microfauna, in term of biomass is approximately 100, 10, 1; whereas from a metabolic point of view it is 4, 2, 1.

In coastal lagoons, the trophic structure is characterized by a number of different primary food types and a highly connected food web of generalist feeders. Much of the emergent and submergent plant material enters the food web as detritus. Because of the net nutrient uptake which occurs during the fermentation of detritus, this material may have a higher nutritional value than the original plant material. For both detritus and epiphytes, it is not just plant material, but an entire community which is consumed, including bacteria, fungi, microalgae and protozoans.

The increased pool of autochthonous particulate matter results in intense microbial activity in the surface sediment. This might be further enhanced by benthic-pelagic coupling in the topmost layer of the sediment. Due to the good light conditions, the high primary production resulting from eutrophication exceeds the capacity of the heterotrophic decomposers to completely mineralize the biomass. As a consequence, the pool of particulate organic matter in the sediment is increasing due to the imbalance between production and mineralisation.

In coastal lagoons, the excess detritus is accumulated from late autumn through winter. The eutrophic conditions prevailing in spring and summer contribute to a rapid decomposition of detritus. As a result decomposer production and the microbial loop are also stimulated. This provides an abundant food source on which luxurious development of the meiofauna can occur. In this case, the ratio of detritus to biomass results in an imbalance if the energy released from the detritus by the meiofauna is dissipated too rapidly. These high decomposition rates result in an increased oxygen demand and may lead to a temporary disappearance of dissolved oxygen in the water column (Lasserre et al., 1976). This phenomenon causes mass mortality of the benthic macrofauna and fish.

These summer dystrophic crises lead to the formation of high bacterial biomasses in the lagoons as a consequence of high bacterial activity involved in mineralization (both aerobic and anaerobic bacteria). Such biomass can further be used as a food source by the meiofauna. In many coastal lagoons, particularly at the sediment surface, bacteria play an important role as a food source for higher organisms via the detritic food chain (Coull, 1973). However the quantitative importance of bacteria was not appreciated until relatively recently (Fenchel & Jørgensen, 1977) although some early studies (see Zobell, 1946) emphasized the importance of bacteria in marine food chains.

Table 2. Total *in situ* oxygen consumption and relative uptake by micro- and meiofauna (in percent) in man-made lagoons (fish ponds) and salt marshes in the Bassin d'Arcachon (from Lasserre et al., 1976 and Lasserre, 1979b).

Biotope	Compartment	Oxygen consumption (ml O ₂ m ⁻² h ⁻¹)		% Micro- and meiofauna	
		July	December	July	December
Fish ponds	Phytal	218	44	17.9	20.5
	Benthos	108	28	58.3	42.9
Salt marshes	Phytal	99	23	11.1	21.7
	Benthos	81	16	16.0	25.0

Recent studies have shown very high bacterial productivity in coastal lagoons (references in Torretton, 1991) but few describe accurately the interrelationships between such biomass and the consumers in the water column and benthos (Gophen et al., 1974; Caumette et al., 1983; Rieper, 1982; Carman & Thistle, 1985; Decho & Castenholz, 1986; Souza-Santos et al., 1996). Fenchel & Jørgensen (1977) calculated that bacteria in the detritic food chain provided between 60–80% of the diet of the meiofauna. On average, meiofauna graze at a rate of 1% of the standing stock of both heterotrophic bacteria and autotrophic microalgae per hour (Montagna, 1995). Meiofauna grazing is therefore broadly in equilibrium with microbial production. However, new more accurate data are now required to clarify our understanding of the functioning of coastal lagoons, in terms of carbon turnover, organic matter fluxes via the biogeochemical cycles, and the mineralization and the production of organic material through the food chain.

Biogeochemical nitrogen and sulphur cycles in coastal lagoons

The nitrogen and sulphur cycles include a diverse range of oxidation and reduction reactions (Figures 3 & 4). These can be divided into two categories: dissimilatory reactions that are found principally amongst prokaryotes and assimilatory reactions that occur in both prokaryotes and eucaryotes (Ferguson, 1988).

In both cycles, the production of reduced compounds such as NH₃, NO₂⁻, H₂S, S⁰ are either the end products of dissimilatory anaerobic respiration or derive from aerobic and anaerobic degradation of organic material (Herbert, 1982; Caumette, 1986; Herbert & Nedwell, 1990). These compounds accumulate in the anoxic layers mainly in the sediment of eutrophic coastal lagoons. Their oxidation is dependent on the

redox state of the sediments and overlaying water column. It is well established that their oxidation is mainly mediated by chemotrophic prokaryotes that use oxygen as terminal electron acceptor.

Such organisms live around the redoxcline of the lagoon ecosystem, depending on reduced compounds from the anoxic layer and oxygen from the overlying oxic layer. Thus reduced nitrogen compounds are generally oxidized via the activity of ammonia- or nitrite-oxidizing bacteria. In contrast, reduced sulphur compounds can be oxidized under anoxic conditions. Chemotrophic bacteria that perform anaerobic respiration such as *Thiobacillus denitrificans* generate a proton electrochemical gradient as electron flow from reduced sulphur compounds to nitrate, nitric or nitrous oxides. Moreover, in the upper part of the anoxic layers reached by light, phototrophic sulphur oxidizing bacteria are able to oxidize reduced sulphur compounds to sulphate as a consequence of their anoxygenic photosynthesis. Thus, in coastal lagoons, both cycles are functioning in similar conditions: reduction of nitrogen or sulphur compounds occurs under anoxic conditions whereas oxidation of the reduced compounds mostly occur at the interface between oxic and anoxic zones, i.e. the redoxcline. Almost all eutrophic shallow water coastal lagoons have a redoxcline occurring at the sediment surface. Therefore most of these metabolic processes coexist within the first millimeters of the sediment. In eutrophic coastal lagoons, ammonia is the major nitrogen compound produced in anoxic layers (Koike & Hattori, 1978; Nishio et al., 1982, 1983; Marty et al., 1990). However, production of reduced nitrogen compounds is lower compared to that of reduced sulphur compounds which are derived from sulphate reduction which is the most important anaerobic respiratory process occurring in coastal lagoons (Caumette, 1986) and coastal marine environments (Jørgensen,

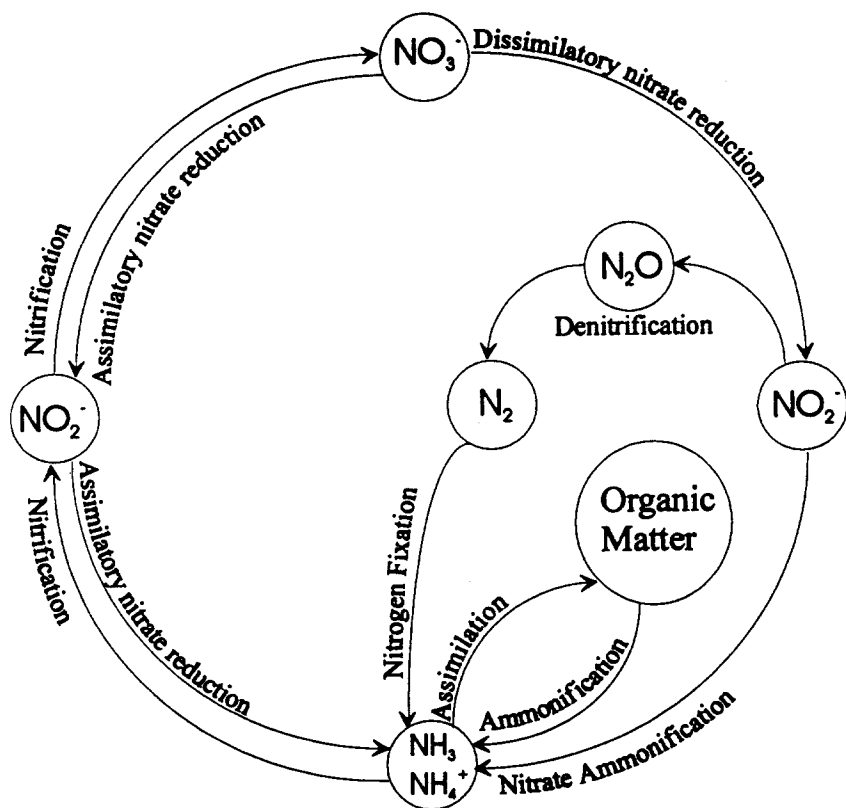


Figure 3. Nitrogen cycle.

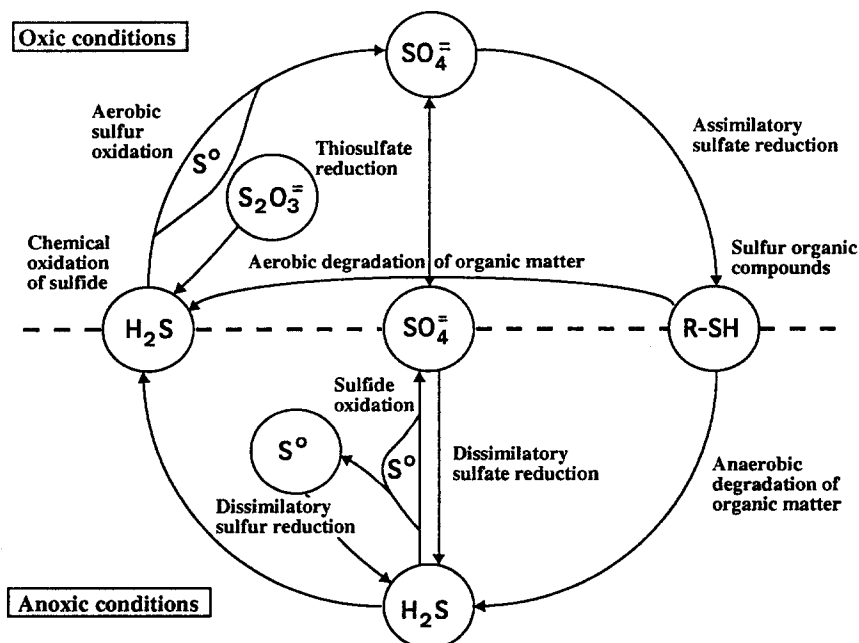


Figure 4. Sulphur cycle.

1982, 1983). The bacterial oxidation of reduced nitrogen or sulphur compounds at the sediment surface prevents their diffusion into the overlying oxic layer (the water column). Little is known on the oxidation of nitrogen compounds in coastal lagoons and field work as well as laboratory work are required to determine and quantify the oxidative pathways of reduced nitrogen compounds. In contrast, it is established that in most of the coastal sediments studied so far, between 50 to 95% of the H_2S produced is reoxidized, at the interface between the oxic and anoxic zones. However, sulphide does not usually reach the oxic zone unless sulphate reduction is very intensive.

Thus, it appears that the abiotic and biotic equilibrium in coastal lagoons is primarily dependent on the balance between oxidation and reduction activities in the biogeochemical cycles. When reduction of nitrate or sulphate in the anoxic layers is enhanced, the reduced compounds produced can diffuse into the oxic layers leading to the establishment of anoxic conditions and the release of reduced nitrogen and/or sulphur compounds to the atmosphere. In recent years, attention has been paid to volatile methylated sulphur compounds and their metabolism at the sediment surface of coastal environments. In coastal lagoons, their intensive production and transformations may have important consequence on the global sulphur cycle and the atmospheric behaviour of sulphur. It is known that these conditions develop when organic matter accumulates and the subsequent activity of mineralization processes are stimulated in the water column and sediments. However, detailed field experiments on the oxidation and reduction processes taking place in both cycles at the sediment surface are required in order to understand the development of such drastic events in coastal lagoons.

In many shallow coastal lagoons, much of the surface light irradiance reaches the sediment surface leading to the development of photosynthetic benthic communities which in turn may lead to the development of microbial mats. These mats, which are characteristics of many coastal lagoons, are composed of different laminated layers of oxygenic and anoxygenic phototrophic bacteria (cyanobacteria and different kinds of purple or green sulphur oxidizing bacteria) depending on oxygen and sulphide microgradients in the upper sediment. It has been recently shown that methylated sulphur compounds are very important in the sulphur cycle that takes place in microbial mats, at the oxygen sulphide interface (Visscher et al., 1991).

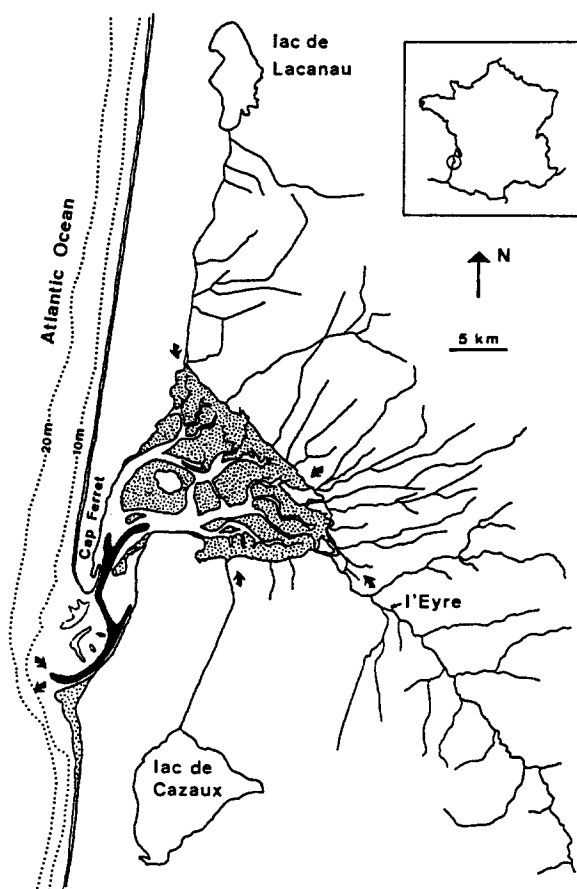


Figure 5. Location of the Bassin d'Arcachon along the Atlantic coast, showing the drainage basin and the most important inputs of freshwater.

Examples of eutrophication gradients in coastal lagoons

The Bassin d'Arcachon, a moderately eutrophic lagoon

General hydrography

The Bassin d'Arcachon (44° 40' N, 1° 10' W) is a triangular shaped embayment on the South-West Atlantic coast of France (Figure 5). Channels and intertidal areas cover 155 km² but only 40 km² of the bay are subtidal. Seventy percent of the lagoon is composed of intertidal flats called 'crassats' which are used for oyster farming. The intertidal areas, especially in the eastern half of the Bay are covered by *Zostera noltii* Hornem. whilst *Zostera marina* L. is found in the channels. The oyster beds cover an area of 10 km². The decaying eelgrass and detritus from the oysters pro-

vides a rich supply of organic nutrients for the intertidal sediments leading to an enhancement of the abundance of the small invertebrate fauna (Castel et al., 1989). The Bassin d'Arcachon is connected to the Atlantic Ocean at the South-West end by two narrow channels (4–5 m deep at low water). The presence of sandbanks at the entrance to the lagoon have a major effect on water exchange between the bassin and the Atlantic. On a spring tide $370 \times 10^6 \text{ m}^3$ of water are exchanged whilst on a neap tide this is reduced to $130 \times 10^6 \text{ m}^3$. These volumes are similar to those calculated by Caspari in 1863 (*cit. in* Labourg, 1985). This shows how stable the tidal influence has been over more than a century. The exchange of such large volumes of water induces considerably high water flow: the mean discharge through the channels is $17 \times 10^3 \text{ m}^3 \text{ s}^{-1}$ (comparable to the average discharge of the St Lawrence). These waters carry a great amount of sand in suspension particularly on the ebb during spring tides. Sediment transport has been estimated to be as much as 11 500 t through the channels on a spring tide. In contrast, in the inner bay, resuspension is much less; on average the concentration of suspended matter is around $3\text{--}7 \text{ mg l}^{-1}$. At Arcachon Eyrac, the tidal range is 4.9 m on a spring tide and 1.1 m on a neap tide. Tidal currents are strong, reaching velocities of 2 m s^{-1} in the channels.

The oceanic water entering the bassin is diluted by freshwater inflow, mainly from the northern and eastern parts of the bassin ($1.8 \times 10^6 \text{ m}^3 \text{ d}^{-1}$). Furthermore, ground waters provide approximately $10^6 \text{ m}^3 \text{ d}^{-1}$. As a consequence, salinity and temperature variations are directly proportional to the distance 'upstream' from the inlet. In summer the water temperature reaches $21\text{--}22^\circ \text{C}$ in August, falling to $6\text{--}8^\circ \text{C}$ in mid-winter. Salinity ranges from $30\text{--}33\text{‰}$ at high water but occasionally decreases to 20‰ after periods of heavy rain. In spring and summer the temperatures are notably higher in the inner bay than in the outer channels: the converse is observed in autumn and winter. Temperatures are uniform in the bassin in February-March and in September-October. During these periods water temperatures of the Bassin d'Arcachon and the Bay of Biscay tend to be similar. This has strong ecological implications, especially in spring when migrating species (cephalopods, fish) enter the bassin.

Three distinct water masses have been recognised in the Bassin d'Arcachon (Bouchet, 1968; Figure 6):

- External neritic waters: temperature: $9.5\text{--}21^\circ \text{C}$, salinity: $34\text{--}35\text{‰}$
- Intermediate neritic waters: temperature $6\text{--}22.5^\circ \text{C}$, salinity: $26.8\text{--}33.2\text{‰}$

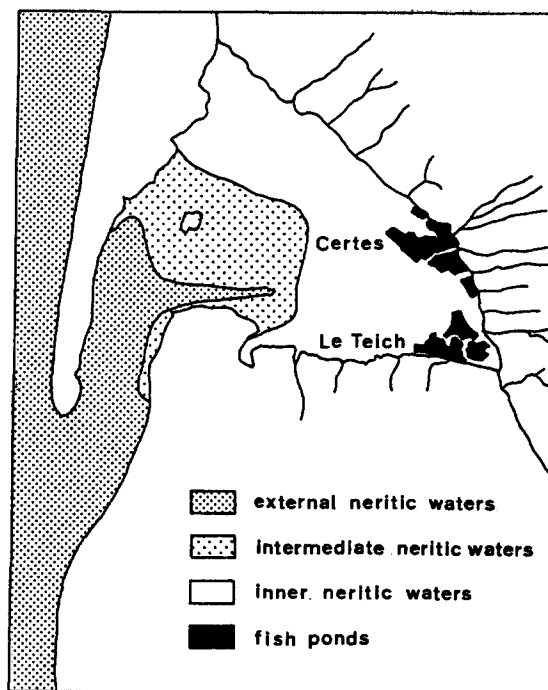


Figure 6. Distribution of the water masses in the Bassin d'Arcachon according to salinity (modified from Bouchet, 1968). Fish ponds are shallow brackishwater enclosures.

- Inner neritic waters: temperature: $1\text{--}25^\circ \text{C}$, salinity: $22\text{--}32\text{‰}$

These water masses move according to the tidal state and their renewal is only partial. In the North-East and eastern sectors of the lagoon, water exchange with the Atlantic is occasional, probably once or twice a year. The inner waters are eliminated from the Bassin as a laminar flow or nappes at the surface. The intermediate body of water oscillates and tend to mix with the inner waters whilst the water mass associated with the deep channel is well mixed with Atlantic water during each tidal cycle.

Whilst the Bassin d'Arcachon is continuously changing, the system as a whole remains in a steady-state. The lagoon is subject to erosion but this is balanced by sedimentation. The most important changes occur near the inlet and the adjacent coast area:

- slow advance and sporadic erosion of the Cap Ferret spit
- migration of the navigation channel and associated sand banks to the South
- erosion of the southern coast.

These changes tend to reduce exchange between the Bassin and the Atlantic. In the inner bay the sed-

Table 3. Annual flux of mineral nitrogen (in tonnes) originating from the drainage basin in the Bassin d'Arcachon (Auby et al., 1994).

Origin	Years		
	1970	1980	1990
Forests	263	257	252
Agriculture	281	415	575
Lakes	17	66	27
TOTAL	561	738	854

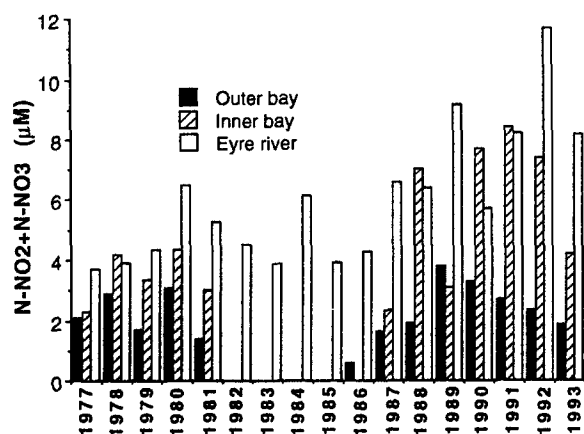


Figure 7. Long-term distribution of nitrite + nitrates in the Bassin d'Arcachon (outer and inner water masses) and in the river Leyre (modified from Auby et al., 1994).

imentation rate is quite low (10 cm per century today cf. 1 m per century 1700 years ago).

Evidence of eutrophication

The catchment of the Bassin d'Arcachon covers an area of 4140 km² (Figure 5). Approximately a quarter of the catchment can be considered to indirectly contribute nutrients to the Bassin through coastal lakes. Since the 1970's intensive agriculture in the region (especially maize) has increased. In 1970 agriculture was responsible for 50% of the annual flux of nitrogen to the Bassin d'Arcachon; at present it is responsible for 66% of this flux (Table 3). The annual flux of total phosphorus remains quite stable (25–30 t yr⁻¹). Urban sewage has significantly decreased during the last twenty years (from 127 t total N yr⁻¹ to 40 t total N yr⁻¹).

Most of the freshwater flux comes from the river Leyre (see Figure 5) thus it is not surprising that nutrient concentrations have increased during in recent years (Figure 7). Although there is a dilution effect

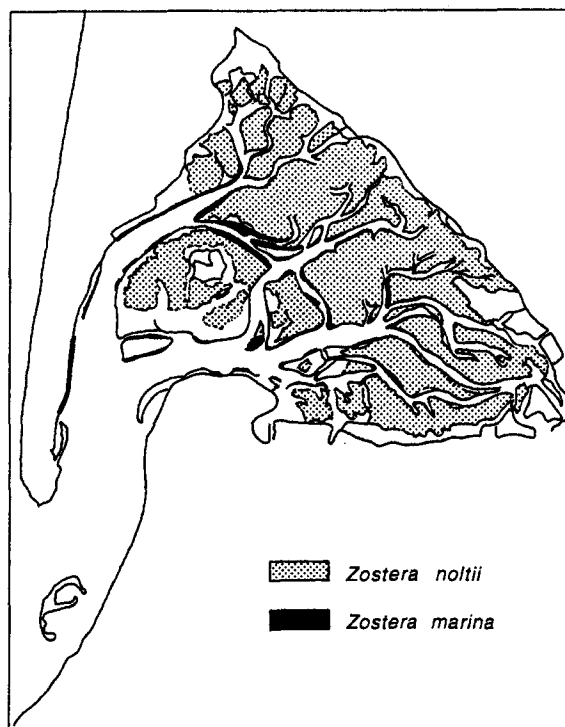


Figure 8. Location of the seagrass beds of *Zostera noltii* and *Z. marina* in the Bassin d'Arcachon (redrawn from Auby, 1993).

from the river input to the outer region of the Bassin, the nutrient concentrations have clearly increased in a large part of the Bassin d'Arcachon (by a factor 2 in the inner Bassin from 1977–1981 and 1990–1993). Such increases could have stimulated the primary production and thus eutrophication. Measurements made since 1976 (Castel, unpublished; Robert et al., 1987) indicate however that the standing stock of phytoplankton (expressed in chlorophyll *a*) is not particularly high and remains at a relatively constant level from one year to another: the baseline value is around 2 µg l⁻¹ and the spring bloom does not exceed 15 µg l⁻¹.

The most abundant primary producer in the Bassin d'Arcachon is the seagrass *Zostera noltii* (Table 4). The seagrass beds occupy 7000 ha in the intertidal zone (Figure 8) which represents the largest area in Europe. In contrast to other places in Europe where the biomass of *Z. noltii* has declined in recent years, the seagrass meadows in Arcachon have remained almost constant over the last 30 years. Mean annual biomass is 70–100 g DW m⁻² for the leaves and 70–160 g DW m⁻² for the roots and rhizomes (Auby, 1991).

Table 4. Estimated annual production of the different primary producers in the Bassin d'Arcachon (from Auby et al., 1993).

Taxa	Total production (t d.w. yr ⁻¹)	Carbon (t yr ⁻¹)	Nitrogen (t yr ⁻¹)	Phosphorus (t yr ⁻¹)
Halophilous phanerogams	7612–9098	3045–3636	537–686	73–93
<i>Zostera noltii</i>	30, 790–43,700	9275–13,300	660–960	70–100
<i>Zostera marina</i>	6213	2003	157	15
<i>Monostroma obscurum</i>	7600	2508	342	23
Other macroalgae	unknown	unknown	unknown	unknown
Microphytobenthos		4930–12,270	860–2140	120–290
Phytoplankton		3540	625	85

The subtidal eelgrass *Zostera marina* occupies 4.26 km² in the channels (Figure 8). It constitutes a unique refuge for invertebrates as well as fish.

The most significant change among primary producers is the development, since 1988, of the green alga *Monostroma obscurum* (= *Ulvaria obscura* Kützinger). This species was first described in 1843 on the Basque coast. It is a cosmopolitan species found in Northern Europe as well as in the Pacific. Since the early 1980's, fishermen from Arcachon have exploited the natural deposits of oysters near the Adour estuary, close to the site where this species was first described. The oysters were transported to Arcachon for growth, without cleaning the shells. It is probable that some thalli were imported together with the oysters. The rapid development of *Monostroma* shows that this alga finds environmental conditions in the Bassin ideal for growth. Although no causal relationship can be demonstrated, it is interesting to note that the development of *Monostroma* coincided with the increased nutrient input into the Bassin d'Arcachon. In spring, the total biomass of *Monostroma* has been estimated to be between 18 000 to 21 000 t. The alga mainly colonizes the inner region of the Bassin, in the intertidal zone as well as in the channels (Figure 9). The maximum density is around 6 kg W W m⁻², which is comparable to other macroalgal blooms (Étang du Prévost, *Ulva*: 5 kg W W m⁻²; Baie of St Brieuc, *Ulva*: 8 kg W W m⁻²) although it is less than the massive development of *Enteromorpha* and *Ulva* observed in the lagoon of Venice (30 kg W W m⁻²). Arcachon is the only place in the world where a bloom of *Monostroma* has been observed.

Changes in animal populations and other algae have also been observed (Labourg, 1985). It is not always possible to differentiate between the impact of natural variation of the environment and the effect of

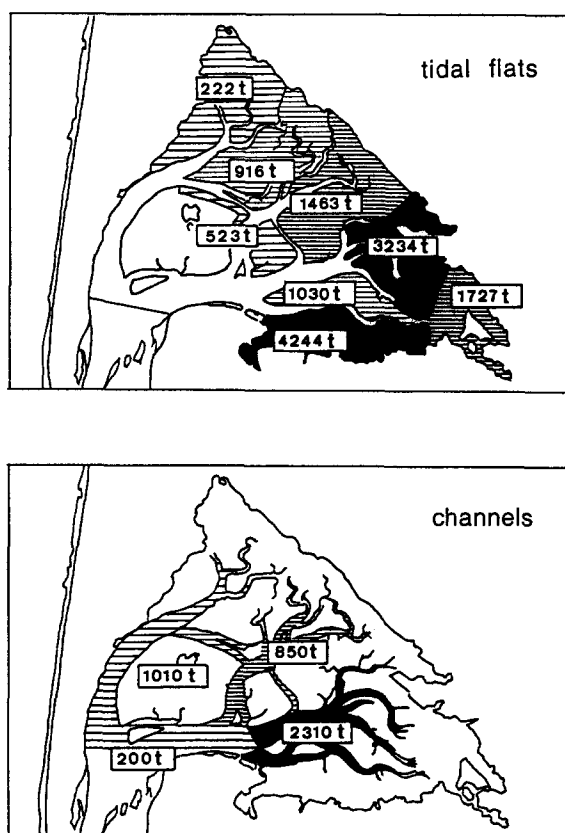


Figure 9. Total biomass (tonnes wet weight) of the green alga *Monostroma obscurum* in the Bassin d'Arcachon in June 1993 (redrawn from Auby et al., 1994).

the human activities, however, it is clear that some species have disappeared and some appeared during the last century. The barnacle *Elminius modestus* Darwin, originating from Australia, after colonizing the Mediterranean coasts, appeared in Arcachon in 1960. The Mediterranean balist *Balistes capriscus* L. was

reported in the bassin in 1962. These are example of species having extended their area of distribution. Other species have appeared since 1968 as a consequence of the importation of the Pacific oyster *Crassostrea gigas* Thunberg, including the tunicate *Styella clava* Herdman, some Bryozoans and Annelids. More recently, the large brown alga *Sargassum muticum* (Yendo) Fensholt accidentally introduced in Great Britain with the Pacific oyster, invaded the coast of Brittany and appeared some years ago in Arcachon. Even small organisms (< 1 mm) such as the Harpacticoid Copepod *Stenhelia latioferculata* Itô (originally from Japan) are likely to have been introduced with oysters. Conversely, some species have disappeared due to either modifications of hydrological conditions (e.g. the clam *Venus verrucosa* Linné) or to overexploitation (e.g. the bivalve *Chlamys varia* Linné).

Fish ponds of the Bassin d'Arcachon, a moderately eutrophic lagoon system

General description

The 'fish reservoirs' of the Bassin d'Arcachon (Figure 10) are man-made enclosures created in the lagoonal marshes (wetlands) and where a number of euryhaline fish are farmed: grey mullet (*Chelon labrosus* Risso, *Liza ramada* Risso), sea bass (*Dicentrarchus labrax* Linné), eels (*Anguilla anguilla* Linné) and gilt head bream (*Sparus aurata* Linné). Such fish reservoirs are also known from the Charente and Vendée along the Atlantic coast. These structures, designed for traditional extensive (without food supply) aquaculture, are comparable to the 'valli', situated along the Adriatic coast, and also to the tropical 'tambaks' in Indonesia. They constitute mixohaline and shallow (0.2–1.5 m depth) environments where the rich input of detritus plays a prominent role in the food chain. Originally they were salt-pans exploited since the end of the Middle Ages. Progressively, during the late eighteenth century the exploitation of the salt decreased and the salt-pans were converted into fish ponds. These fish reservoirs schemes flourished all through the nineteenth century up to the end of the Second World War but they have since gone into decline because of the labour costs and the relatively low yield (50 kg ha⁻¹) of this type of extensive aquaculture. These semi-enclosed lagoonal systems cover a surface area of approximately 940 ha in the Bassin d'Arcachon. The old salt-evaporation areas and the salt-pan runoff ditches are separated by embankments from the sea and through which inflow

and outflow are regulated by sluice gates (Figure 11). The fish ponds or fish reservoirs have a characteristic shape: channels or ditches, 1.5 to 2 m in depth, feed large expanses known as 'flats', each of which covers an area ranging from 1000 to 10 000 m². In the canals the fish are 'penned' during the winter months to counteract the colder temperatures prevailing in the shallow areas. These flats, 20–50 cm deep, are separated from each other by ridges formed from the mud removed during the digging of the ditches. All inflows and outflows can be regulated by sluices located at intervals along these embankments.

At high tide, the sluices are manoeuvred in such a way that a current is created and the fish, both immature and adults, are drawn into the reservoirs. The fish are prevented from returning to the sea by a system of mesh frames. These operations are usually carried out during the cooler seasons, from March to November. Every two weeks, when high tides occur at the time of the full or new moon, water from the sea is allowed to flow into the reservoir through the sluices. This operation lets in the young fish and natural mineral salts, and replenishes the reservoir by exchanging the water held in the ponds and fresh seawater. This operation is carried out at low tide. The young fish are free to move and to grow inside the complicated network of basins, in which the salinity may vary from very dilute brackish water to full seawater.

Because of the shallowness and the confined nature of the fish ponds, the salinity regime is extremely variable both in time and space. The salinity ranges from almost freshwater to hypersaline (60‰). The salinity regime of the fish reservoirs is strongly linked to (1) the relative location of the ponds between the sea and the continental freshwater inputs, and (2) the renewal of the water through the sluices. The man-induced renewal of water is supposed to maintain salinity compatible with biological activities. However, the maintenance of a given salinity requires a careful and periodic operating of the sluices since, due to the shallowness of the ponds, the salinity tends to vary widely (Figure 12) between periods of renewals. The same situation can also be observed for nutrients (Escaravage, 1990). In such ponds, the greatest part of the regulation of nutrient concentrations is controlled by *in situ* biochemical processes, especially at the benthic level. These mechanisms are hardly affected by the renewal of the overlaying water.

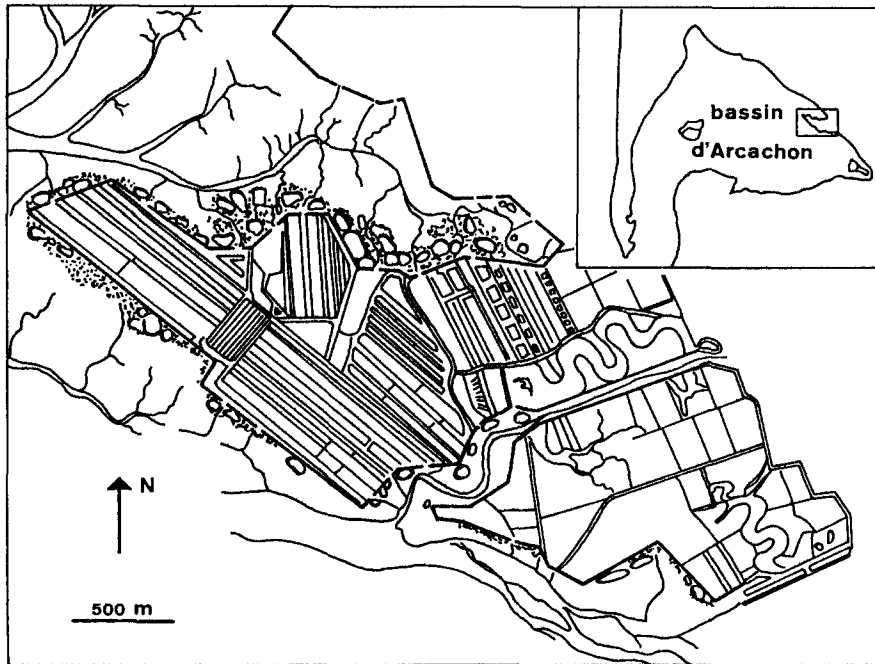


Figure 10. Map of the fish ponds of the Bassin d'Arcachon (Certes reservoirs).

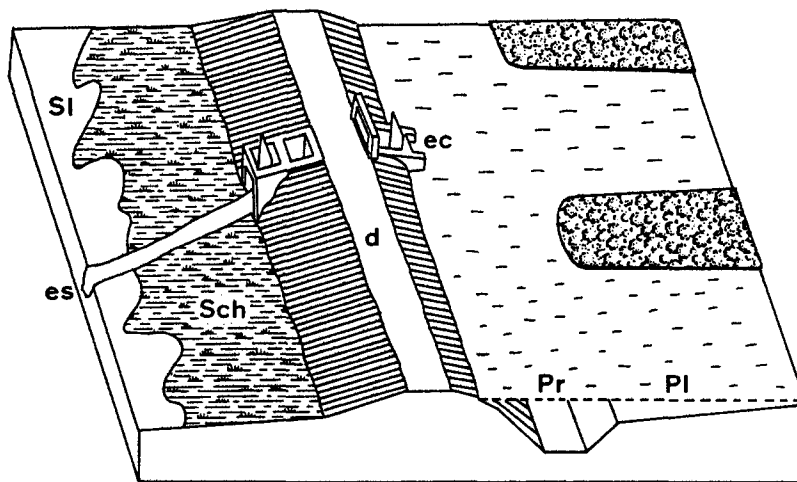


Figure 11. Schematic diagram of the fish ponds of the Bassin d'Arcachon. Left: salt marsh comprising the 'slikke' (SI) = mudflat, the 'schorre' (Sch) = high marsh and 'estey' (es) = small channel. The ponds are separated from the salt marsh by a dyke (d) along which a sluice (ec) is established. Right: typical structure of the reservoirs, Pr = channel (width: 3–4 m, depth: 0.8–1.5 m), Pl = shallow basins (width: 10–40 m, length: 100–800 m, depth: 0.2–0.5 m). Redrawn from Lasserre (1979a) and Castel (1989).

From eutrophy to dystrophy

As in many inshore areas, the rich input of detritus, organic matter, bacteria and benthic microflora play a prominent role in the food chain of the fish ponds. The most important primary producers are sea grasses (*Ruppia cirrhosa* Petag), and filamentous green algae:

Cladophora vadorum (Aresch.) Kütz at the water surface, and mats of green algae (*Lamprothamnium papulosum* J. Groves, *Chaetomorpha aerea* (Dillwyn) Kütz, or cyanobacteria at the sediment surface. The biomass of *Ruppia cirrhosa* has been estimated to 126 g W W m⁻² for the above-ground and to 51 g W W m⁻² for the

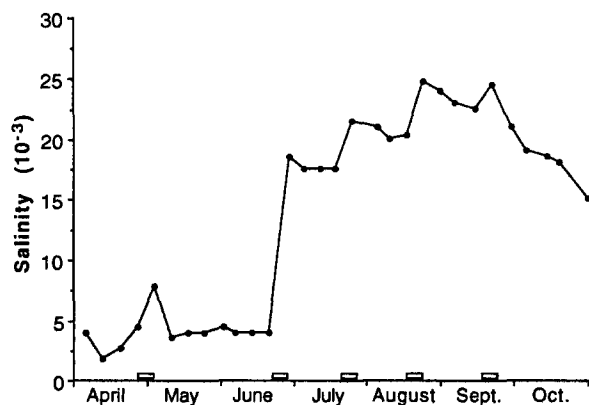


Figure 12. Temporal variation of salinity in a fish pond of the Bassin d'Arcachon (Le Teich in Figure 6, April–October 1974). Measurements were made 100 m far from a sluice. The bars on the x-axis indicate the periods of water renewal (Castel, unpublished).

below-ground structures (Soriano-Sierra, 1988). This biomass appears to be relatively stable from year to year and has on average standing stock of $149\text{--}186\text{ g W W m}^{-2}$ (Labourg, 1979). Green macroalgae are strongly dominated by *Chaetomorpha area* with an average biomass of 79 g W W m^{-2} . Macro-epiphytes (*Cladophora vadorum*, *Rhizoclonium kernerii* Stockmayer) are found on the stalks and blades of *R. cirrhosa*. Their average biomass has been estimated at 68 g W W m^{-2} (Soriano-Sierra, 1988).

Temperature is probably one of the principal factors conditioning the eutrophication processes and further the dystrophic crisis. In the fish ponds, the variations in temperature depend both on the sun light and renewal of the waters. Each time seawater is allowed to enter the pond the temperature significantly decreases (Figure 13). In contrast, on a neap tide, when there is no entry of seawater, the temperature rapidly increases, reaching sometimes values close to $30\text{ }^{\circ}\text{C}$. Generally, production of hydrogen sulfide is observed for temperature reaching $24\text{--}25\text{ }^{\circ}\text{C}$, at the end of the neap tide period, when the water is stagnant. Concurrently (even before the production of H_2S) the oxygen concentration drops to very low values. pH values also tend to decrease due to a hyper production of acids (organic acids, sulfate, sulphur). A biological indication of eutrophication is the presence of Peridinians in the plankton, usually dominated by diatoms in the fish reservoirs (Castel, 1978).

In some years, during warm summer, true dystrophic crises may occur, with the formation of white waters due to the precipitation of carbonates. During such periods, high mortalities of fish may be observed

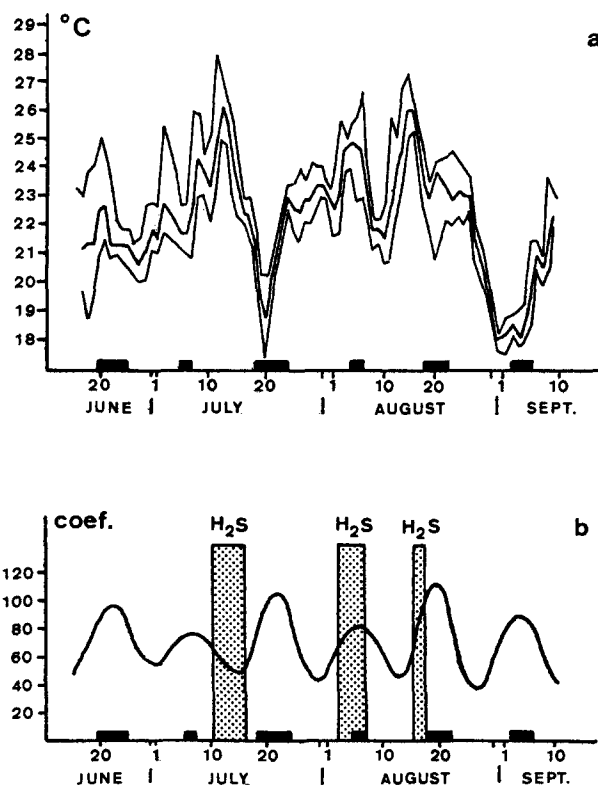


Figure 13. a) Daily variation of temperature (mean, maximum, minimum) during the period 19 June – 11 September 1974 in a fish pond of the Bassin d'Arcachon (Certes in Figure 6). Measurements were made 20 m far from a sluice at 0.40 m depth. b) Daily variation of the tide coefficient (proportional to the height of water) during the same period. Periods of H_2S production are indicated by vertical shaded bars. The horizontal bars on the x-axis indicate the period of water renewal (redrawn from Castel, 1978).

(Labourg, 1975; Castel, 1978). Several tonnes of dead fish have been collected during particularly acute crises. However, such dramatic events do not occur every year. Generally, dystrophic crises in the fish ponds of the Bassin d'Arcachon are less acute and less extensive in space than in the Mediterranean lagoons.

The Étang du Prévost, a strongly eutrophic lagoon

General hydrography

The Prévost Lagoon ($43^{\circ}30'\text{ N}$, $3^{\circ}54'\text{ E}$), located on the French Mediterranean coast, belongs to a lagoon system that extends along the coast, between Sète and Montpellier. This littoral zone is formed by a succession of coastal brackish ponds ('étangs'), surrounded by marsh and separated from the sea by a low, sandy beach allowing only limited amount of

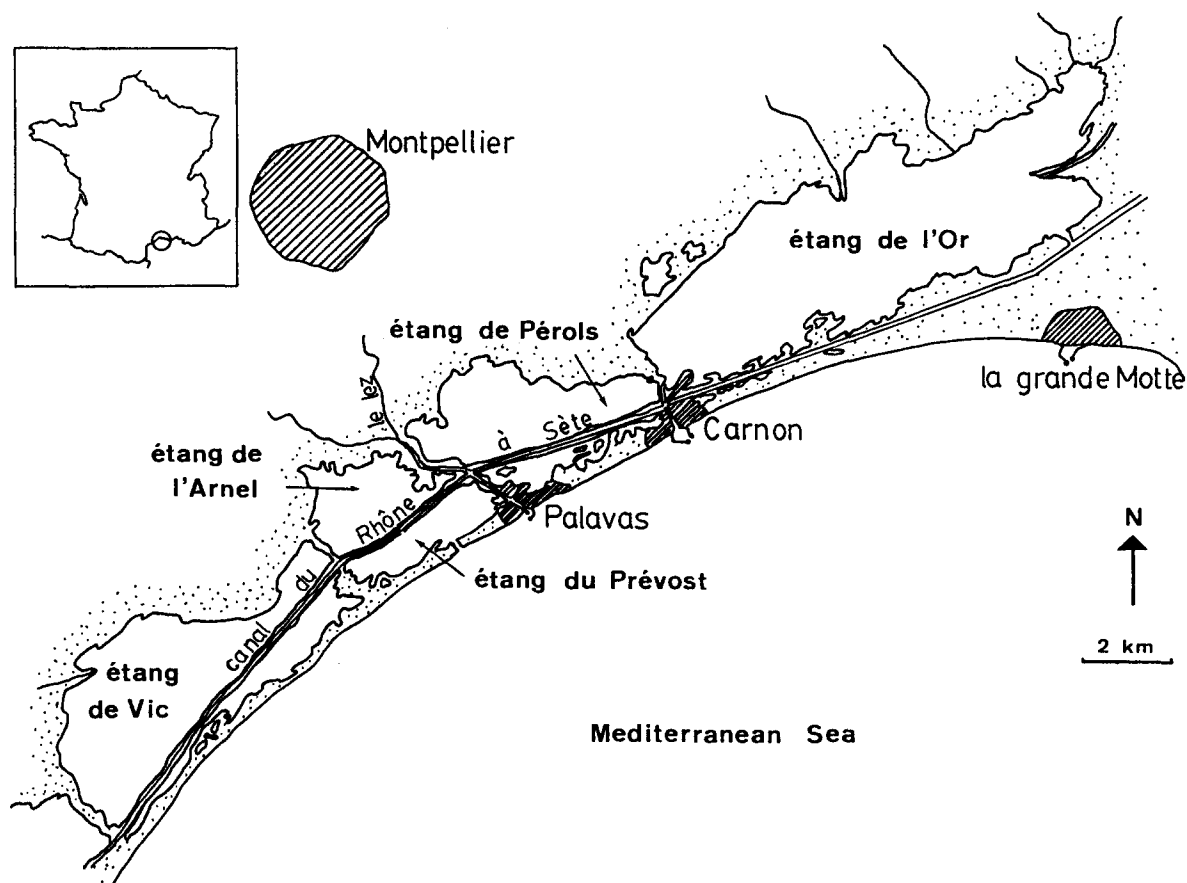


Figure 14. Location of the principal lagoons along the Languedocian Mediterranean coast.

water exchanges. The Étang du Prévost is situated in a lagoonal complex delimited to the South-West by the Étang de Thau and the Sète promontory and to the North-East by the wetlands of the Camargue and Rhône delta (Figure 14). These ponds are of recent geological formation. The sandy and detrital zones in this region explain their continental formation. The creation by the currents of offshore bars ('cordons littoraux') has allowed the transformation of the coastline and the formation and evolution of these coastal lagoons since the quaternary period.

The water in these lagoons is slowly renewed, via small channels ('graus') communicating with the Mediterranean sea. These shallow bodies of water are subjected to continental inputs. They are directly influenced by urban or industrial effluents.

In contrast to the Bassin d'Arcachon, the Étang du Prévost is a shallow lagoon with an average depth of about 0.8 m and a surface area of 380 ha (Figure 14). It receives fresh water and sewage carried by a small river

'Le Lez', and seawater through the only connection with the sea 'Le Grau du Prévost'. Although the lagoon is situated in a nontidal zone, the water level can vary from -0.30 m to $+0.40$ m relative to the mean level because of the strong winds. In the meantime, the current speed can reach 0.40 m s^{-1} in the lagoon and 0.80 m s^{-1} in the 'grau'. When the wind is blowing, 20 to 25% of the water can be renewed in one day. In contrast, during calm periods, the water remains stagnant. This is particularly true in summer. The wind action may induce very strong and rapid variations of the salinity (Figure 15). In summer, because of the evaporation, the salinity can reach 40‰.

The system is extremely eutrophic due to agricultural and urban run-off. For the Étang du Prévost, 85–90% of the input of N and P are of domestic origin (Table 5). The input per volume unit of lagoonal water is approximately $24.6 \text{ t } 10^6 \text{ m}^{-3}$ for the total nitrogen and $4.3 \text{ t } 10^6 \text{ m}^{-3}$ for the total phosphorus (Anony-

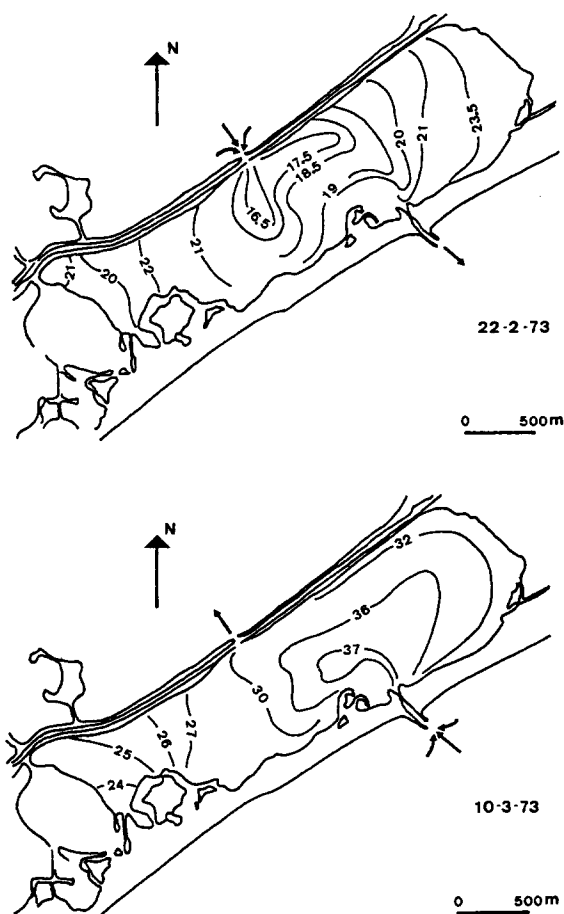


Figure 15. Salinity fields (‰) in the Prévost lagoon during two different climatic conditions: wind blowing from the Northeast (22.02.1973) and wind blowing from the Southwest (10.03.1973) (redrawn from Guélorget & Perthuisot, 1992).

Table 5. Annual input and stocks of nitrogen and phosphorus, expressed in tonnes, in the Étang du Prévost (anonymous, 1991).

Origin	Nitrogen	Phosphorus
Domestic input	60.2	11.1
Agriculture	5.5	0.5
Industry	1.4	0.2
Sediment stock (10 cm)	475	140
Annual flux in sediment	22	2.4
<i>Ulva</i> stock	20.6	1.8

mous, 1991). As a comparison, the input of nitrogen in the Bassin d'Arcachon is only $3 \text{ t } 10^6 \text{ m}^{-3}$.

Such large inputs of nutrients lead to the development of high biomass of primary producers in the

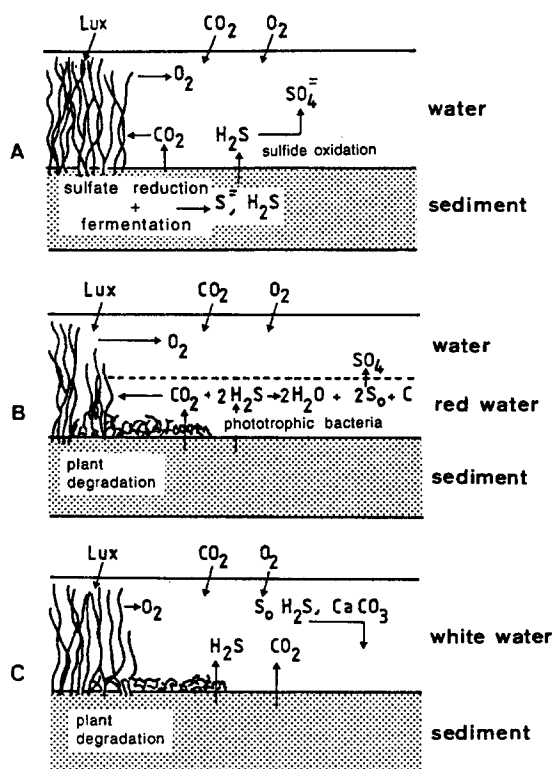


Figure 16. Schematic description of the biogeochemical processes occurring during a dystrophic crisis (redrawn from Baleux et al., 1979). A: Equilibrium state of the sulphur cycle, B: Dystrophic crisis with formation of 'red waters', C: Dystrophic crisis with formation of 'white water'.

Étang du Prévost. Its flora is essentially composed of green algae (*Ulva* and *Enteromorpha* spp.). The biomass of these algae may reach 5 kg W W m^{-2} and sometimes accumulates at densities up to 30 kg W W m^{-2} . In summer, this biomass is rapidly degraded by aerobic heterotrophic bacteria whose numbers and activities increase rapidly. During this period the water turns anoxic and becomes rich in sulphide, which leads to severe dystrophic crisis.

The dystrophic crisis

The Étang du Prévost is regularly subject to dystrophic crises, locally called the 'malaïgues'. Such dramatic events appear every year during the warm summer months for a period of about 15 days. They have a dramatic consequence for aquaculture, particularly oyster culture that takes place in the lagoon. Macroscopically, the dystrophic crises are characterized by coloured waters (white, red or black waters). They originate from a perturbation of the sulphur cycle.

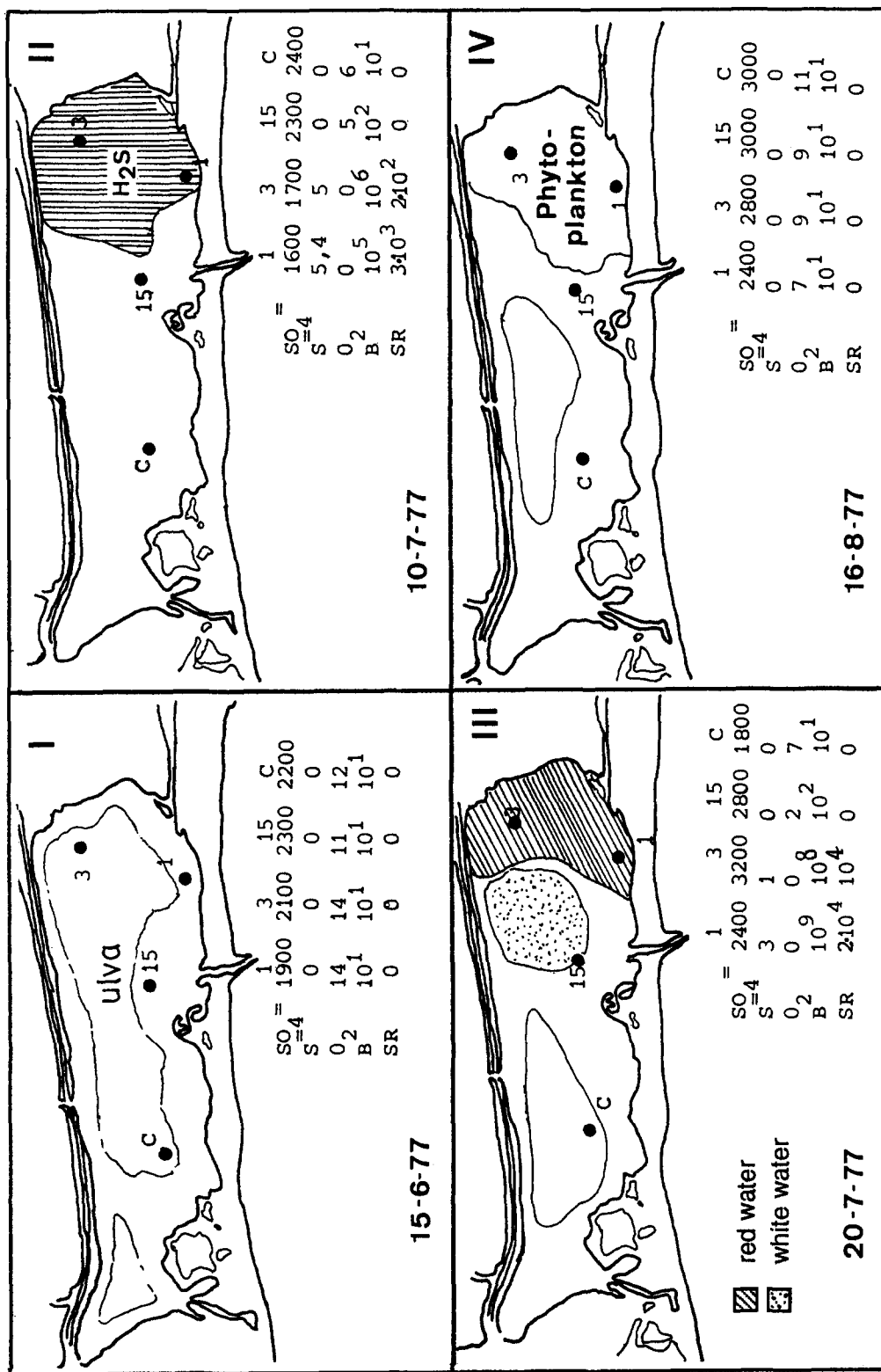


Figure 17. The Prévost lagoon during a dystrophic crisis (June–August 1977). I: before the dystrophic crisis, II: appearance of anoxic water with presence of sulfide, III: appearance of red and white waters, IV: after the dystrophic crisis. 1, 2, 3 and C refer to sampling stations. SO₄²⁻, S²⁻ and O₂ are expressed in mg l⁻¹. B = phototrophic bacteria, SR = sulfate reducers. Bacterial counts are expressed in numbers ml⁻¹.

In normal conditions, there is a steady-state at the benthic level between sulfate-reducing bacteria producing hydrogen sulfide and bacteria oxidizing this reduced sulphur compounds or elemental sulphur (Figure 16). The reactions of sulphate reduction lead to the production of hydrogen sulfide which is then rapidly oxidized to sulphate in the presence of oxygen. After an increase in organic load these oxido-reduction reactions accelerate. The SO_4/Cl ratio increases considerably indicating a solubilization of the sulphate. This ratio, which is typically around 11–12, can exceed 16 during a period of eutrophication. Under anoxic conditions white waters can be observed together with the production of H_2S . They usually occur when the light intensity is low. Concentrations of sulphur and carbonates are high which imparts a white colour to the water. The pH is generally low (< 7.5) due to the presence of considerable quantities of sulphur. This induces precipitation of carbonates in the form of white suspension (Figure 16).

Under certain conditions, red waters can be observed. They are due to the development of phototrophic sulphur oxidizing bacteria (e.g. *Thiocapsa*). The conditions for their development are: a sufficient light intensity, a pH value near 8 and a H_2S concentration < 1 ppm. In anoxic conditions, in the light, only phototrophic bacteria are able to oxidize sulfide and to use it as an electron donor for reducing carbon dioxide.

Chronologically, white water is observed before red water. In favourable conditions, phototrophic bacteria metabolize the toxic compounds generated by anaerobic bacteria during fermentative processes and reduction of sulfate. In a reduced environment, rich in hydrogen sulfide, they are able to induce a new steady-state of the sulphur cycle by oxidizing the sulphur, under anaerobic conditions, using light energy. In the Étang du Prévost lagoon a succession of such events is commonly observed in summer (Amanieu et al., 1975; Caumette & Baleux, 1980). Coloured waters can invade most of the lagoon within a few days and disappear almost as quickly (Figure 17). In contrast to the Étang du Prévost, in the fish ponds of Arcachon only white waters have been observed. This is probably due to a lower light intensity, and the absence of complete anoxia in the water column (some *Ruppia* are always present).

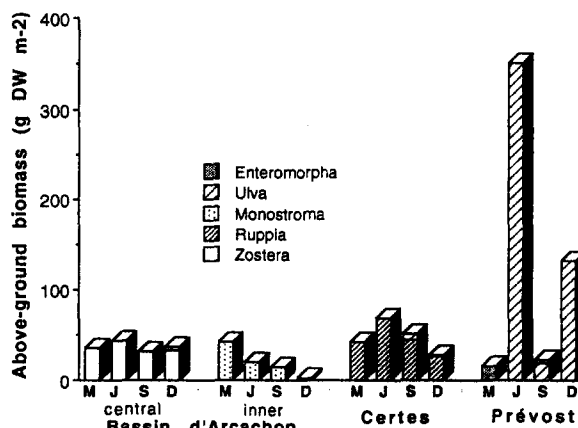


Figure 18. Biomass of living, above-ground parts of macrophytes in the Bassin d'Arcachon (central and inner parts), fish ponds of the Bassin d'Arcachon and Prévost lagoon, in March, June, September and December 1993 (modified from Auby et al., 1993 and Bachelet et al., 1994).

Conclusions: the eutrophication gradient

The three lagoon systems: Bassin d'Arcachon, fish réservoirs and étang du Prévost clearly differ by their degree of eutrophication. An evidence of eutrophication gradient is the increase in nutrient concentrations between the Bassin d'Arcachon and the Étang du Prévost (Table 6). As a consequence, the biomass of primary producers also increases.

This is shown by a recent study (Auby et al., 1993) where species composition and biomass of macrophytes have been studied in spring and summer 1993. One station (station A) was located in a seagrass bed (*Zostera noltii*) on a sandy mudflat in the central part of the Bassin d'Arcachon. Total living biomass (leaves + roots + rhizomes) of seagrass amounted to 141–167 g AFDW m^{-2} (173–211 g DW m^{-2}), which is close to values reported in an earlier study (Auby, 1991) in the Bassin d'Arcachon (140–260 g DW m^{-2}). The above-ground biomass did not show any clear seasonal trend (Figure 18). In the inner part of the Bassin d'Arcachon (station B) living biomass was dominated by the green alga *Monostroma obscurum*. It declined from March to September (29–13 g AFDW m^{-2} , or 43–15 g DW m^{-2}) and never reached the high values found for other Ulvaceae in the Étang du Prévost (Figure 18). A high biomass of *Zostera* debris was measured in the sediments (92–186 g AFDW m^{-2}). The shallow fish ponds of Certes (station C1) were colonized by *Ruppia cirrhosa*. There was a clear seasonal trend with the highest biomass (63 g AFDW m^{-2}) occurring in

Table 6. Dissolved nitrate and ammonia in the water of the Bassin d'Arcachon (central and inner parts), fish réservoirs of Certes and Étang du Prévost. Values are given for the summer 1993 (Sloth et al., 1993) except for the fish réservoirs (summer 1985, Castel, unpublished).

Lagoon system	NO_3^- (μM)	NH_4^+ (μM)
Bassin d'Arcachon, central part (station A)	0.32 – 2.0	2.0 – 2.4
Bassin d'Arcachon, inner part (station B)	0.32 – 1.3	1.5 – 2.5
Fish réservoirs (station C1)	0.7 – 1.01	4.6 – 8.3
Étang du Prévost (station 11)	1.2 – 4.9	5.7 – 10.5

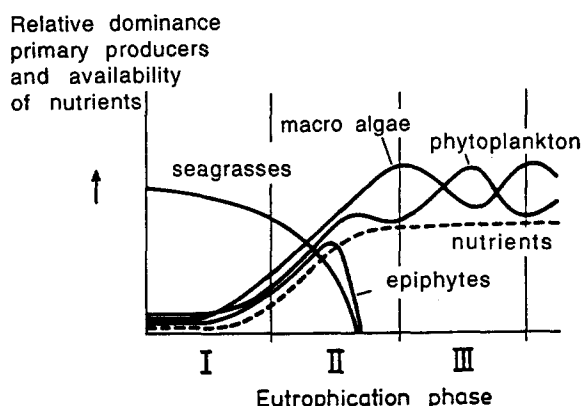


Figure 19. Tentative model depicting the relation between primary producers and nutrients, and the successive stages in the process of eutrophication (after Nienhuis, 1992).

June. Some *Monostroma* were also collected in September. In the Prévost lagoon (Station 11) the March samples contained a small amount of *Enteromorpha flexuosa* (Wulfen ex Roth) J. Agardh and *E. intestinalis* (Linn.) Link (12 g AFDW m^{-2}). These algae disappeared in June when they were replaced by *Ulva* sp. (270 g AFDW m^{-2}) which filled the whole water column and induced anoxia in the benthos. In September algal biomass (*Enteromorpha* + *Ulva*) decreased to a low value (19 g AFDW m^{-2}). From these observations it appears that macrophytes did not show any seasonal trend in the Bassin d'Arcachon. Some evidence of eutrophication were visible in the Certes lagoons. The most obvious changes in macrophyte biomass occurred in the Prévost lagoon, especially in its inner part, with a massive development of green algae in June, followed by their complete disappearance in September.

A tentative model has been developed by Nienhuis (1992) describing the relation between the relative dominance of primary producers connected to the availability of nutrients and the successive phases in the process of increasing eutrophication (Figure 19).

This model applies to the three types of lagoon environments described here. In 'healthy' lagoons seagrasses dominate. Nitrogen load and concentrations are low and the relative importance of phytoplankton in the shallow seagrass beds is insignificant. The Bassin d'Arcachon is an example of phase I. In brackish waters where eutrophication increases, revealed by higher nitrogen loads and nitrogen concentrations and generally lower, unstable salinities, seagrasses are out-competed by macroalgae. Epiphyte growth on seagrass and algae increases considerably together with the relative dominance of phytoplankton. The fish ponds of the Bassin d'Arcachon are an example of phase II. In hypereutrophicated systems (phase III) nutrient concentrations are continuously high. Dense uncontrolled phytoplankton blooms alternate with mass growth of macroalgae and rooted plants have completely disappeared. Bottom sediments suffer from permanent anoxia. The Étang du Prévost is an example of phase III.

Such macroscopic observations should, now, be explained by the study of microbiological processes including meiofauna, protozoa, bacteria and all the components of the microbial loop.

Acknowledgements

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