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PARALIC ECOSYSTEMS

Biological organization and functioning

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ÉCOSYSTÈMES PARALIQUES
LAGUNES
BASSIN MÉDITERRANÉEN
ORGANISATION BIOGÉOLOGIQUE
CONFINEMENT

RÉSUMÉ – Les milieux aquatiques paraliques, situés entre le domaine marin et le domaine continental, sont extrêmement variés quant à leur taille, leur morphologie et leur genèse. En outre, les conditions climatiques et hydrographiques régionales et les caractéristiques hydrologiques locales y induisent une grande variété et une grande variabilité des paramètres physiques et chimiques ainsi que des dépôts sédimentaires. Au contraire, les peuplements biologiques se caractérisent par la présence d'espèces strictement inféodées à ce type de milieu, une organisation zonale qualitative et quantitative commune, indépendante des salinités et relativement stable dans chaque bassin. Ces caractéristiques biologiques originales autorisent à considérer l'ensemble des milieux aquatiques paraliques comme constituant un domaine écologique autonome. Le paramètre qui semble gérer pour l'essentiel la distribution des organismes et les caractéristiques des peuplements, peut s'exprimer comme le temps de renouvellement des éléments d'origine marine en un point donné et a été appelé le confinement (par rapport à la mer). Il en est proposé une échelle à partir des données biologiques pour l'ensemble du sous-domaine où persistent les formes thalassoïdes (proche paralique). Au-delà, le paralique lointain se caractérise par l'apparition d'espèces dulçaquicoles ou au contraire évaporitiques et l'on passe sans transition marquée au domaine continental. A la lumière de ces conceptions nouvelles, il apparaît que loin d'être marginal, le domaine paralique a joué un rôle essentiel dans l'histoire de la biosphère et de la lithosphère de notre planète. Enfin, sa haute productivité organique et ses caractéristiques sédimentologiques font du domaine paralique une source considérable de richesses économiques. Le confinement est la principale clé de la mise en valeur rationnelle de ses potentialités.

PARALIC ECOSYSTEMS
LAGOON
MEDITERRANEAN
BIOGEOLOGICAL ORGANIZATION
CONFINEMENT

ABSTRACT – The paralic aquatic ecosystems which are situated between the marine and continental domains are extremely different as far as their size, morphology and genesis are concerned. Furthermore, the regional climatic and hydrographic conditions, along with the local hydrological patterns, induce a great variety and variability of the physical and chemical parameters and of the sedimentary deposits. On the contrary, the biological populations are characterized by species strictly bound to that kind of environments; their common qualitative and quantitative zonal organization is independent of salinity and/or salinity gradients, and they are relatively stable in spite of variations of the environment. These original biological features allow the paralic ecosystems to be considered together as an autonomous ecological domain : it is proposed to call it the « paralic domain ». The parameter which appears largely to control the distribution of organisms and the features of living populations may be described as the time of renewal of the elements of marine origin at any given point, and is referred to as « confinement » (by comparison with the sea). A confinement scale is proposed from biological data, which essentially concerns the seaward part of the paralic domain, where thalassoid species still persist (Near Paralic). Further from the sea, the Far Paralic is characterized by the appearance of freshwater, or on the contrary, evaporitic associations, and changes gradually towards the continental domain. Lastly, given the high organic productivity and original sedimentological features of the paralic domain, it appears that paralic basins are a considerable source of economic richness. Confinement may be in many cases the key to a rational exploitation of their economic potentialities

INTRODUCTION

It is common practice to divide hydrobiosphere into a marine domain and a continental domain each possessing its own features, its original populations, its sedimentary processes, and its distinct geochemical characteristics.

Bordering these two great domains, there exist a number of environments apparently very different from one another described by an extensive terminology. They are very rich from an economic point of view, and have been and still are the object of many applied studies, either with a view toward their exploitation or their development.

The generic terms used to qualify these environments are as imprecise as they are unsatisfactory and show the perplexity of the authors faced with their « mixed » aspect and their diversified geochemistry : one can find in literature (biological as well as geological) terms such as : transition areas, mixing zones, intermediary environments, variable salinity areas, coastal fringing zones, brackish environments. Here they are termed paralic (from Nauman, 1854 and Perthuisot, 1975). The adjective « paralic » applied to an area, a basin or an ecosystem simply means that it possesses a certain relationship with the sea.

One can wonder whether the morphological variety and geochemical diversity of paralic environments found today in nature entail an equivalent diversity in their populations and their biological dynamics.

I. MORPHOLOGICAL, GEOCHEMICAL AND SEDIMENTARY DIVERSITY OF PARALIC ENVIRONMENTS

A. Morphological and genetic diversity of paralic basins

The shape and size of natural paralic basins, and those of the channel communicating with the sea, depend on various factors which all belong to a sometimes complex geological history. It is not aimed to give here any classification but rather to single out the main types.

The « estuary » type situated more or less perpendicularly to the coast correspond to portions of valleys (either recent or fossil) flooded by the sea. To this type belong rias, fjords, deep creeks, etc. In some cases the river mouths are cleared by fluvial currents and/or tides, while in other cases the mouth may be partially or totally obstructed by a barrier of sedimentary or other origin.

The basins of the « laguna » (*sensu lato*) (or lagoon) type, are generally more isodiametrical

(circular in shape), or stretch parallel to the coast. Among them can be mentioned :

« **Lagunas.** » (*sensu stricto*) which correspond to the isolation of certain portions of the maritime domain by one or several recent soft coastal bars. There usually remains a communication link with the sea, more or less permanent thanks to one or several « graus » (more or less fixed, sometimes maintained by man). Generally, in this type of basin the water depth is low in relation to the surface area.

In arid countries intermittent stretches of water may alternate with « coastal » sebkhas (Perthuisot, 1975).

Delta areas often have lagoons whose formation is aided by a massive inflow of detrital debris, the progradation of sedimentary bodies and coastal transit.

« **Bahira** » (small sea in Arabic), diversely shaped, correspond to land-locked continental depressions of complex and various origin (river, wind, tectonic, etc.) developed or completed during the Quaternary era and flooded by the sea during the Holocene transgression. They communicate with the sea by permanent passages. The water depth varies but may be considerable in relation to the surface area.

To this type belong the Bahiret el Biban (Medhioub, 1979, 1984) in the southeast of Tunisia, the Etang de Diana in Corsica, etc.

Recent tectonic movements (subsidence and/or uplift) occurring in the vicinity of the waterline may lead to the isolation of a paralic stretch of water : in this case alone the term « **tectonic laguna** » can be used. Example are few; however one could mention the saltwater lake of Guemsah, Gulf of Suez (Ibrahim *et al.*, 1982; Ibrahim, 1983, 1886; Ibrahim *et al.* 1985, 1986).

It is obvious that the above-mentioned types represent only the different extremes of typology. There exist a great number of intermediary types : thus the laguna of Nador in Morocco or the Etang d'Urbino in Corsica fall between the « laguna » type and the « bahira » type.

Lastly, there exist artificial stretches of paralic water corresponding to the development of natural paralic zones (salt marshes for example) or harbour structures (Perthuisot and Guelorget, this issue).

B. Hydrochemical gradients

1. Mediterranean examples

a. *Three standard examples* : the Etang du Pré-vost (France), the Etang d'Urbino (Corsica) and the Bahiret el Biban (Tunisia).

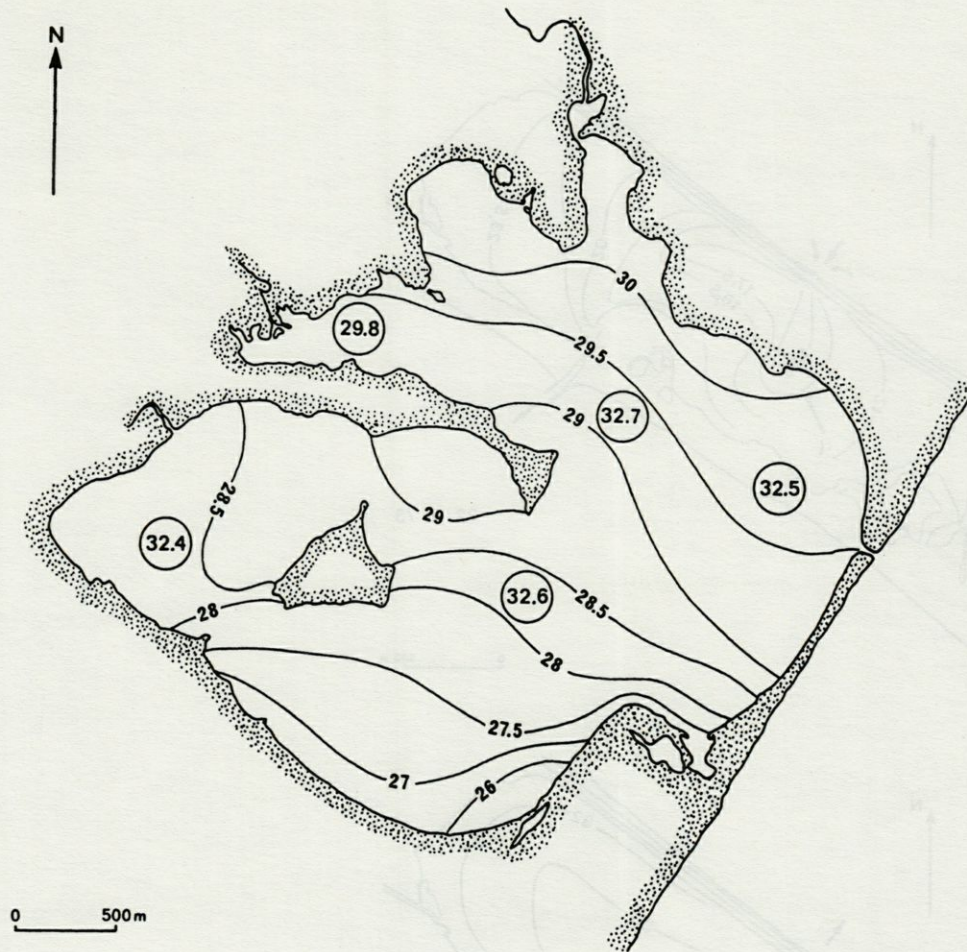


Fig. 1. – Map of isohalines in the Etang d'Urbino in February 1978 by northerly wind. The encircled figures correspond to the salinity averages (in ‰) calculated over 1978 and 1979.

The hydrochemical diversity of the paralic systems appears when considering only a few examples taken around the Mediterranean: the Etang du Prévost on the Languedoc coast (Guelorget and Michel, 1976), the Etang d'Urbino in western Corsica (Frisoni *et al.*, 1982) and the Bahiret el Biban in southeast Tunisia (Medhioub, 1979, 1984; Medhioub and Perthuisot, 1977, 1981).

These three basins of very different sizes correspond to different morphologies and origins. The Etang du Prévost (3.8 km², 1m depth) is a laguna in the strict sense of the word, i.e., a stretch of water progressively separated from the sea by a sandbar and still communicating with it through a « grau » (communication link). The Bahiret el Biban (230 km², 6.5 m depth) is a Würmian continental depression flooded by Flandrian transgression; it communicates with the Gulf of Gabes through a series of channels the larger of which is a former transverse valley. The Etang d'Urbino (7.9 km², 9 m depth) is a continental depression of a complex origin covered by and then separated

from the sea by a sandbar intermittently sectioned by a grau.

If the Etang d'Urbino maintains a salinity close to that of the sea (Fig. 1), the other two basins are very different, one tending towards hypohaline (Fig. 2), the other towards hyperhaline conditions (Fig. 3). In both cases, there exists a salinity gradient, variable according to the seasons, progressing from the channel communicating with the sea to the continental margins of the basins. The salinity gradient is negative in the Etang du Prévost and positive in the Bahiret el Biban. Naturally these differences in direction and value of the salinity gradients are related to the intensity of the exchange with the sea on the one hand, and on the other, with the total quantity of freshwater received by each basin (direct rainfall, continental inflows as opposed to evaporation). Moreover, the outermost edges are subject to local variations: inflows from tributaries, exchanges with supratidal waters.

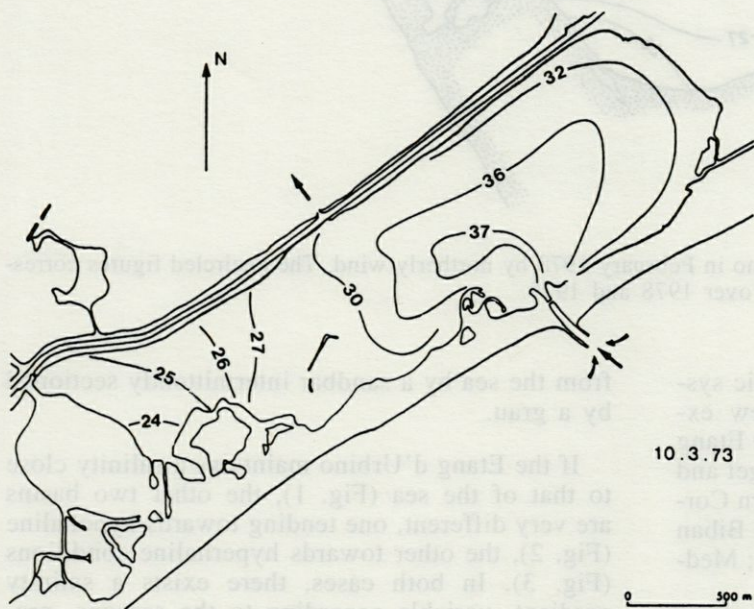
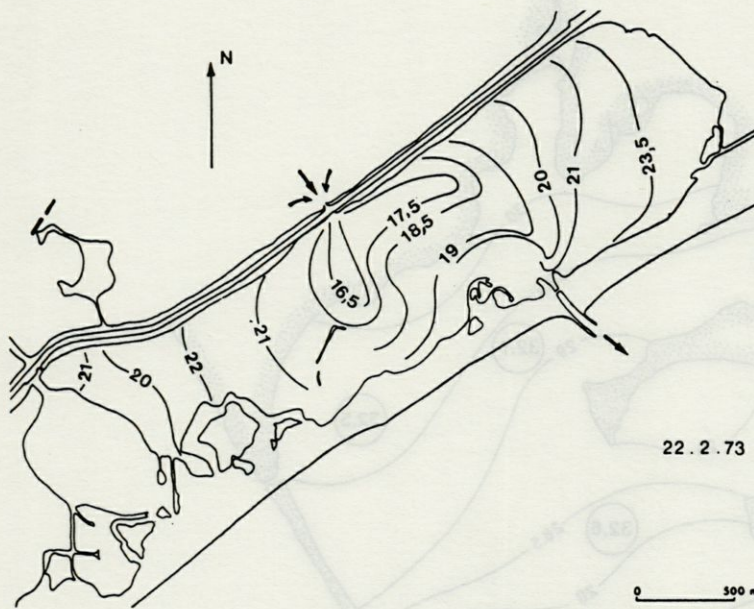


Fig. 2. — Salinity levels (in ‰) in the Etang du Prévost at ebb-tide and by northerly wind at flow-tide by southerly wind. From Guélorget and Michel (1976).

b. Etang de Biguglia (Fig. 4)

This lagoon on the western Corsican plain lies parallel to the sea, from which it is separated by a thin sandbar. The communication link with the sea is situated in the north at the end of a long narrow channel. To the south this lagoon communicates with the mouth of a small coastal river, the Golo, through a system of canals. It has a surface of 1450 ha, and a depth of about 1 m. Its average salinity varies between 5 and 26 ‰; however, values below 1 ‰ may be observed in the southern zone which is subject to continental inflows. Near-normal values are to be found in the

northern part of the basin where the influence of the sea is constant (Burelli *et al.*, 1979).

c. Others

The study of other Mediterranean basins, unnecessary to describe here in detail, confirms the generality of salinity gradients in paralic ecosystems. The following can be mentioned: — Lagoon of Nador (Mar Chica) (Frisoni *et al.*, 1982, Guélorget *et al.*, 1987). — Bermuda Triangle (Spain) (Perthuisot *et al.*, 1983); — Lagoons of the Louros Delta: Tsoukalio, Rodia, Logarou (Greece) (Frisoni *et al.*, 1982; Guélorget *et al.*,

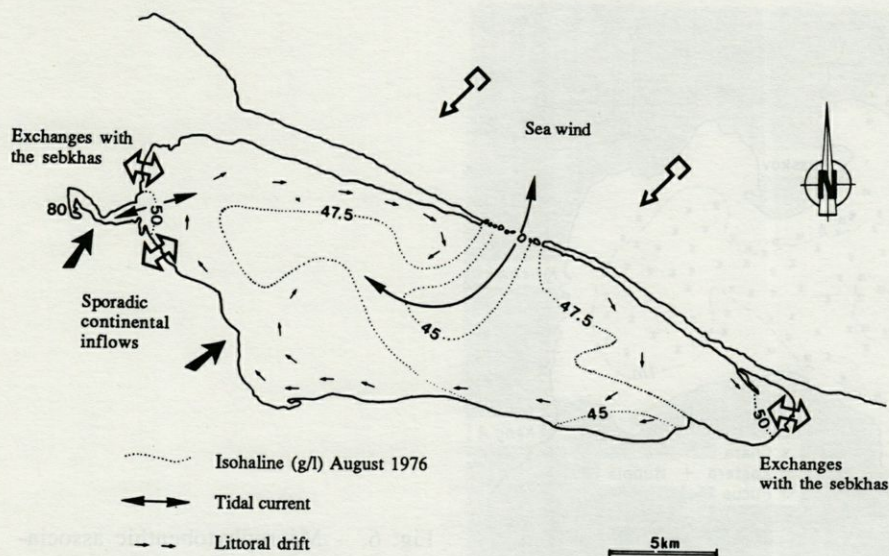


Fig. 3. - Total concentrations (in g/l) in the surface waters of the Bahiret el Biban, in August 1976. From Medhioub (1979), modified.

1986). - Lagoons of Mesologhi (Greece) (Nicolaidou *et al.*, 1988) - Lake Melah (Algeria) (Guelorget *et al.*, 1989)

2. Examples outside the Mediterranean

Several further examples of paralic systems, in very different climatic contexts, are discussed below :

a. Danish fjords

The lagoon of the Dypsø Fjord was described by Muus (1967) in an outstanding study dealing with the entire system of Danish lagoons and estuaries. The Dypsø Fjord is a lagoon opening onto the Baltic Sea in the south of the Danish Sjaelland; it has a surface area about 1 700 ha and an average depth of 1.50 m. The fjord communicates with the sea through a narrow channel, 3-4 m deep, opening to the west onto the lagoon. In spite of several small tributaries, there is no salinity gradient, with values remaining relatively stable around an average of 10 ‰ (Figs. 5 and 6).

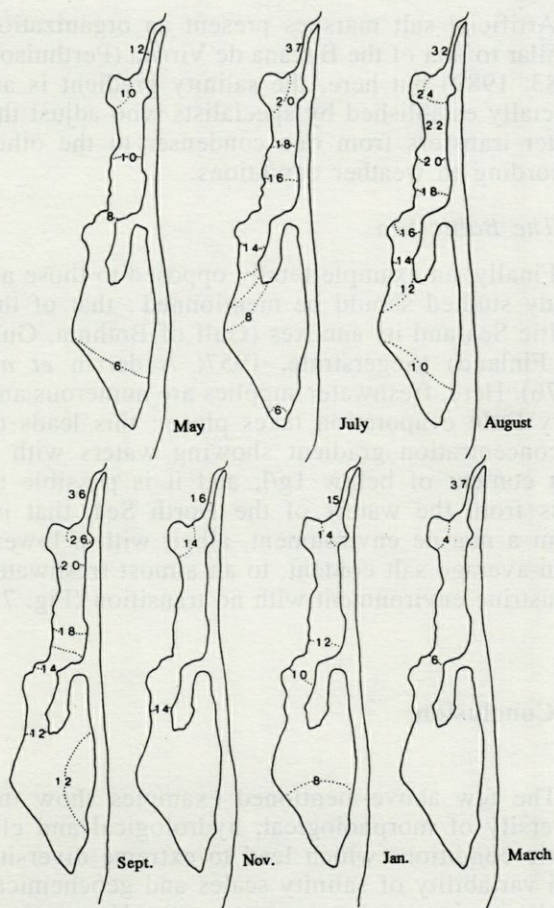


Fig. 4. - Salinity levels (‰) in the Etang de Biguglia, from May 1978 to March 1979.

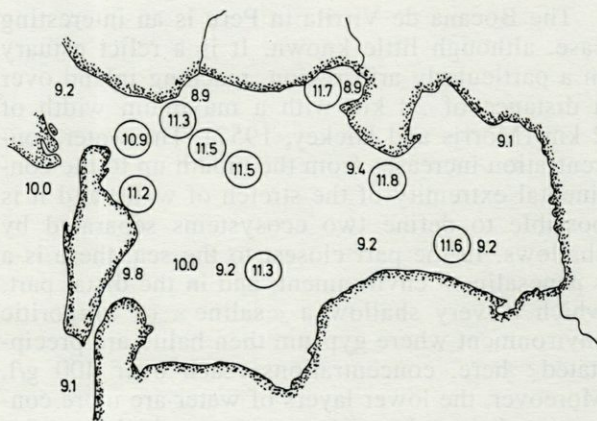


Fig. 5. - Salinity levels (in ‰) of the Dybsø Fjord in May 1955 (Figures not in circles) and Aug. 1955 (Figures in circles). From Muus (1967).

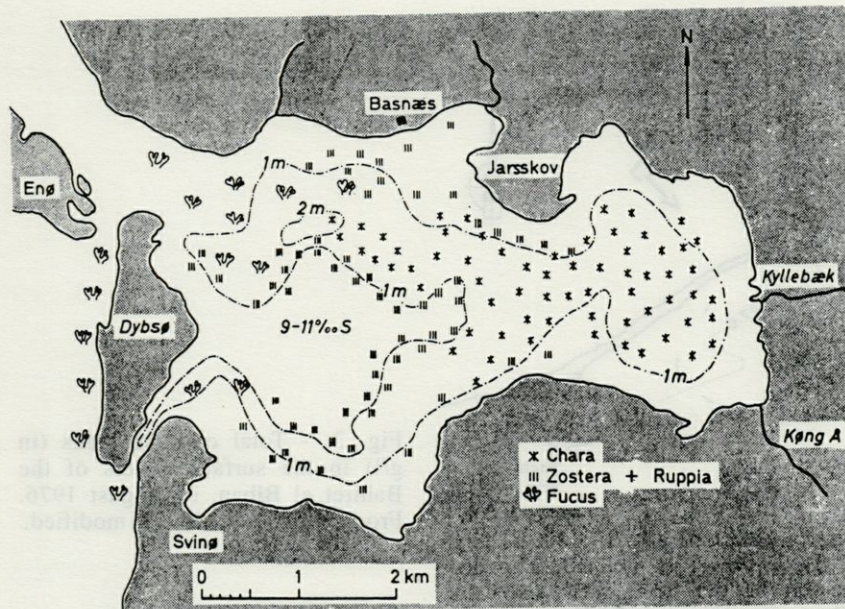


Fig. 6. – Macrophytobenthic associations in the Dybsø Fjord. From Muus (1967).

b. A lagoon in the Persian Gulf

The Khour el Aadid with a surface area of around 100 km² is situated between the Emirates of Qatar and Abu Dhabi. It is a Flandrian « bahira » progressively reduced by a sandy spit which leaves only a long narrow channel between the Gulf and the first of a succession of three basins. The rarity of rain results in a salinity gradient with levels of salts reaching over 110 g/l in the distal basin which, moreover, is totally covered by a thick microbial mat (Perthuisot and Jauzein, 1978).

3. Extreme examples

When paralic basins stretch inland far from the open sea, or when climatic conditions become extreme, the tendencies described above are intensified.

a. Bocana de Virrila

The Bocana de Virrila in Peru is an interesting case, although little known. It is a relict estuary in a particularly arid region, reaching inland over a distance of 20 km with a maximum width of 2 km (Morris and Dickey, 1957). The water concentration increases from the mouth up to the continental extremity of the stretch of water and it is possible to define two ecosystems separated by shallows. In the part closest to the sea, there is a « penesaline » environment, and in the distal part, which is very shallow a « saline » or evaporitic environment where gypsum then halite are precipitated: here, concentrations reach over 400 g/l. Moreover, the lower layers of water are more concentrated than the surface waters, which reveal a certain stratification.

At present the Bocana de Virrila seems to be the only paralic stretch of water in direct com-

munication with the sea where halite can precipitate (Perthuisot, 1980, 1989).

b. Example of salt-marsh : Salin de Giraud (Camargue)

Artificial salt marshes present an organization similar to that of the Bocana de Virrila (Perthuisot, 1983, 1989) but here, the salinity gradient is artificially established by specialists who adjust the water transfers from one condenser to the other according to weather conditions.

c. The Baltic Sea

Finally, an example totally opposed to those already studied should be mentioned: that of the Baltic Sea and its annexes (Gulf of Bothnia, Gulf of Finland) (Segerstråle, 1957; Andersin *et al.* 1976). Here, freshwater supplies are numerous and very little evaporation takes place: this leads to a concentration gradient showing waters with a salt content of below 1g/l, and it is possible to pass from the waters of the North Sea, that is, from a marine environment, albeit with a lower-than-average salt content, to an almost freshwater lacustrine environment with no transition (Fig. 7).

4. Conclusion

The few above-mentioned examples show the diversity of morphological, hydrological and climatic conditions which lead to extreme diversity and variability of salinity scales and geochemical gradients in paralic environments. However, a general characteristic of these salinity fields seems to emerge: that is their longitudinal organization from the communication link (on the zone of

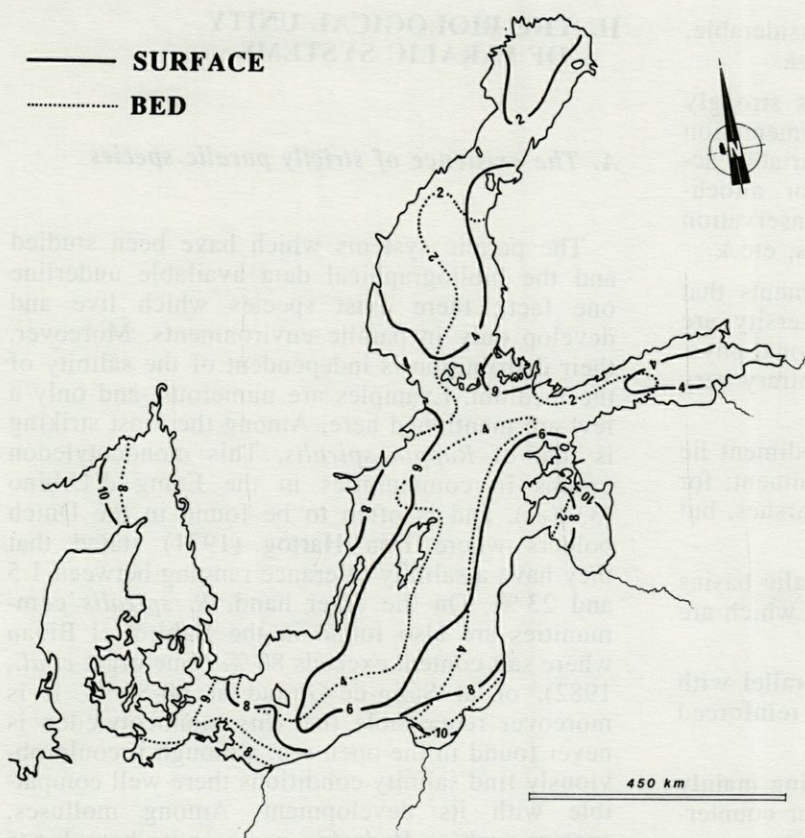


Fig. 7. - The Baltic Sea and its salinity levels (‰) in May (average over several years). From Bock (1971).

marine supply) towards the continental margins. This organization, particularly obvious in very elongated basins, supplied by the sea at one of their ends, is less schematically obvious in the more isodiametric basins where it assumes more concentric shapes. It should also be noted that, locally, longitudinal gradients may be accompanied by vertical gradients which tend to establish a true stratification of the waters (a phenomenon well known in the Black Sea, for example) with appearance of clines (haline, thermic, etc.).

This tendency to a stratification of the waters, however shallow, is a common characteristic of the paralic environments; the lateral co-existence of water masses of varying chemical compositions and therefore varying densities, which tend to overlap when they come into contact, contribute greatly to this stratification.

This wide geochemical diversity - which does not affect salinity alone, but all the mineral components of water - is the most striking aspect of paralic environments: it has led many authors to propose classifications based on salinities. Their complete description will be found in Petit (1953), D'Ancona (1954), Aguesse (1957), Petit and Schachter (1959), Segerstråle (1959), Mars (1966), Amanieu (1967), Arnaud and Raimbault (1969), and Marazanof (1972).

The Venice Symposium (1958) adopted a fairly simple classification known as the « Venice System », which defines a series of standard waters

characterized by an average salinity varying from 0.5 ‰ for limnic waters to over 40 ‰ for hyperhaline waters. Geochemical gradients (essentially salinity, but also other scales such as ionic concentrations, or hydrochemical parameters) depend not only upon the hydrodynamic parameters of each basin, but also local climatic and hydrographic characteristics.

C. The sedimentological diversity of paralic systems

This diversity is apparent by a simply considering the difference between estuaries where sedimentation is low and the deltas which are characterized by a rapid deposition of large quantities of detrital matter. In lagoons, sedimentation may vary considerably from one basin to another, according to local conditions: in the Etang du Prévoist, for example, the detrital fraction of the sand class predominates along the maritime shore; the opposite occurs in the Bahiret el Biban because of wind-borne deposits on the continental margin. Therefore, their qualitative importance, the nature and the granulometry of the detrital phase, depend upon local or regional transport agents, the importance of the winnowing of the peripheral zones of the basins, the lithological characteristics of the adjacent region, etc.

The biodetrital phase is often considerable, especially in the zones closest to the sea.

The biochemical carbonated phase is strongly modified by bioclimatic conditions; sedimentation of organic matter is also extremely variable according to its origin (autochthonous or allochthonous) and the conditions of its conservation (presence of reducing systems or brines, etc.).

It is in the extreme paralic environments that the best examples of sedimentary diversity are seen, since, depending on local and regional physiography either evaporites or on the contrary very coarse detrital debris can be found.

It may even be that both types of sediment lie side by side in the same paralic environment; for example, the Camargue with its salt marshes, but also its quasi-lacustrine basins.

In general, the sedimentology of paralic basins is a result of two types of organization which are more or less superimposed :

— a longitudinal organization in parallel with geochemical gradients, in some cases reinforced by the distribution of affluents;

— a concentric organization depending mainly on depth; this too may be reinforced or counteracted by the disposition of the tributaries.

According to local conditions either organization can prevail, but all types of intermediary situations exist between purely longitudinal organization and purely concentric ones (Perthuisot, 1975, 1980, 1989; Busson and Perthuisot, 1977).

D. Conclusion

Thus, to the geochemical diversity of the paralic environments can be added the extreme variability of the sedimentary deposits they contain : both are examples of the variability of climatic hydrological and morphological conditions.

However, it is possible to differentiate schematically two types of paralic ecosystems or areas :

— In the basins or the portions of basins closed to the sea, the biogenic phases –biodetrital and/or biochemical– prevail; the geochemistry is moderately different from that of sea water.

In the portions of basins furthest away from the sea, the abiogenic mineral phases become predominant whether one considers the hyperhaline systems where evaporites deposits, or the heavily hypohaline quasi freshwater systems where terrigenous deposits –associated or not with vegetal debris– constitute practically the totality of the sediment.

II. THE BIOLOGICAL UNITY OF PARALIC SYSTEMS

A. The existence of strictly paralic species

The paralic systems which have been studied and the bibliographical data available underline one fact : there exist species which live and develop only in paralic environments. Moreover, their distribution is independent of the salinity of the medium. Examples are numerous, and only a few are mentioned here. Among the most striking is that of *Ruppia spiralis*. This monocotyledon groups in communities in the Etang d'Urbino (33 ‰), and is often to be found in the Dutch polders where Den Hartog (1971) stated that they have a salinity tolerance ranging between 1.5 and 23 ‰. On the other hand, *R. spiralis* communities are also found in the Bahret el Biban where salt content exceeds 80 ‰ (Guelorget *et al.*, 1982), or at Salin-de-Giraud at 60-80 ‰. It is moreover remarkable that this monocotyledon is never found in the open sea, although it could obviously find salinity conditions there well compatible with its development. Among molluscs, species such as *Hydrobia acuta* or its homologue *Pirenella conica* can be cited, or again *Cerastoderma glaucum* found only in lagunar environments –whether hypo– or hyperhaline. Such examples could be enlarged from Protozoa to Tunicata, from Cyanobacteria to Monocotyledons. These paralic species are generally « thalassoïd » species. « Thalassoïd » refers to species which both morphologically and genetically are akin to maritime stock without necessarily issuing from the maritime domain, and totally independent of continental stock. « Thalassic » implies species of entirely maritime stock likely to colonize the lagunar regions which are in immediate contact with the sea. Therefore, thalassoid species include both thalassic and paralic species.

In the zones furthest from the sea, there is a more or less clear-cut transition between original communities which will be different from each other depending on whether the evaporitic environment or systems with a freshwater tendency are being considered :

— in the evaporitic environments the macrofauna often consists of only 1 or 2 species (such as *Artemia salina*), as does the microfauna either benthic or planktonic (Bacteria, Cyanobacteria, *Dunaliella salina*). However, the importance should be mentioned, at least qualitatively, of the meiofauna (Rotifera, Nematodes, etc.) to be found even within the salt deposits (Busson *et al.*, 1977). One should note that these species occur all over the world, and also inhabit the continental evaporitic lakes.

— In the environments with a freshwater tendency, as the sea becomes more distant, typically continental species appear (insects, Pulmonata, Oligochaeta, etc.), without it being possible to define precisely the transition into a freshwater medium.

There are, however, some rare species capable of passing from evaporitic environments into freshwater, such as the common Eel, but its presence in these extreme environments seems only transitory. Nevertheless, this shows a remarkable capacity of osmotic regulation. Some Rotifera seem to be totally insensitive to the concentration of the milieu since the same species can be found from 1‰ up to 350‰ (Ruttner-Kolisko, 1971).

Thus, the more qualitative examination of the flora and fauna of paralic systems shows their originality in comparison with the continental and maritime domains, particularly owing to the presence of species particular to that kind of environment, i.e., strictly paralic.

B. Biological zoning of paralic environments

A notable property of paralic systems is their biological zoning particularity in the regions not far from the sea.

This characteristic is obvious for benthic communities which sooner or later integrate the minor fluctuations of the medium (Guelorget *et al.*, 1983; Guelorget and Perthuisot 1983; Guelorget, 1985). However, it will be seen that the other links in the trophic chains behave in a comparable way.

1. The distribution of benthic species

The distribution of species in paralic environments is generally longitudinal—leaving aside the local anomalies linked to the bathymetry or to the nature of the substratum—and roughly identical whether considering hypohaline or hyperhaline ecosystems.

a. Plant communities

The above-mentioned property is obvious with the distribution of macrophytic species. In the Etang de Biguglia for instance, *Zostera noltii* is confined to the vicinity of the grau, directly under marine influence. Further south, a *Ruppia spiralis* community has developed, then a *Potamogeton pectinatus* / Characeae association where Chlorophyceae develop (*Cladophora vagabunda*, *Chaetomorpha linum*).

A similar distribution can be observed in the lagoons of the Louros delta (Logarou, Tsoukalio, Rodia) where *Z. noltii* prevails in the zones close to the sandbars; *R. spiralis* dominates the central zones, sometimes constituting mixed communities

with *Chara sp.* in the zones further from the sea. The lagunar confines are colonized either by little-developed cyanobacterial fields or by Chlorophyceae (*Ulva sp.*, *Enteromorpha sp.*).

The bottom of the Bahiret el Biban is carpeted with a vast *Cymodocea nodosa* community, often associated with *Caulerpa prolifera*. The latter, in the marginal fringes, gives way to a *R. spiralis* community with fibrous Chlorophyceae (*Chaetomorpha linum*, *Cladophora sp.*), which in its turn is superseded by cyanobacterial fields.

In the same way, at Salin-de-Giraud, the association of *R. spiralis* with *Enteromorpha gr intestinalis* which characterizes the first condensers gives way in the more concentrated enclosures, to *Lyngbya aestuarii* and *Microcoleus chthonoplastes* microbial mats, and beyond, to *Oscillatoria laetevirens*, *Phormidium sp.*, and *Spirula subsalsa* (Thomas and Geisler 1983; Perthuisot, 1982).

A very interesting case is that of the Dypso Fjord where a longitudinal zoning of the benthic macroflora can be noted in spite of the absence of any salinity gradient, which shows that the latter plays no part in the distribution of the macrophytic species in paralic environments (Fig. 6).

b. The invertebrate macrofauna

The study of a considerable number of paralic basins shows, **whatever the salinity gradient**, the following horizontal succession as the distance increases from the communication link with the sea :

— a pelecypod-dominated region, with a few echinoderms, i.e., associations which still have a « stenobionte » (thalassic species) tendency;

— a transitional region still dominated by pelecypods, but from which the echinoderms have disappeared. In this case, the marine influence is too slight to allow an optimal development of species with marine affinities, but still too strong for paralic species to flourish fully. Local variations can however be introduced in cases of « organic pollution ». Then the number of pelecypods decreases to the advantage of crustaceans and detritivorous annelids. It is in this zone that the « mixed » species which are also present in the sea are found;

— a third region where strictly paralic species abound (*Cerastoderma glaucum*, *Abra ovata*, *Nereis diversicolor*, *Gammarus gr locusta*, *Sphaeroma hookeri*, Chironomidae).

— a typical fourth region, common in hyperhaline ecosystems, less clearly so in hypohaline ecosystems (particularly in cold climates), is characterized by the presence of cyanobacterial mats or stromatolitic structures, mono- or paucispecific, associated with a small number of animal species (*Hydrobia acuta*, *Sphaeroma rugi-*

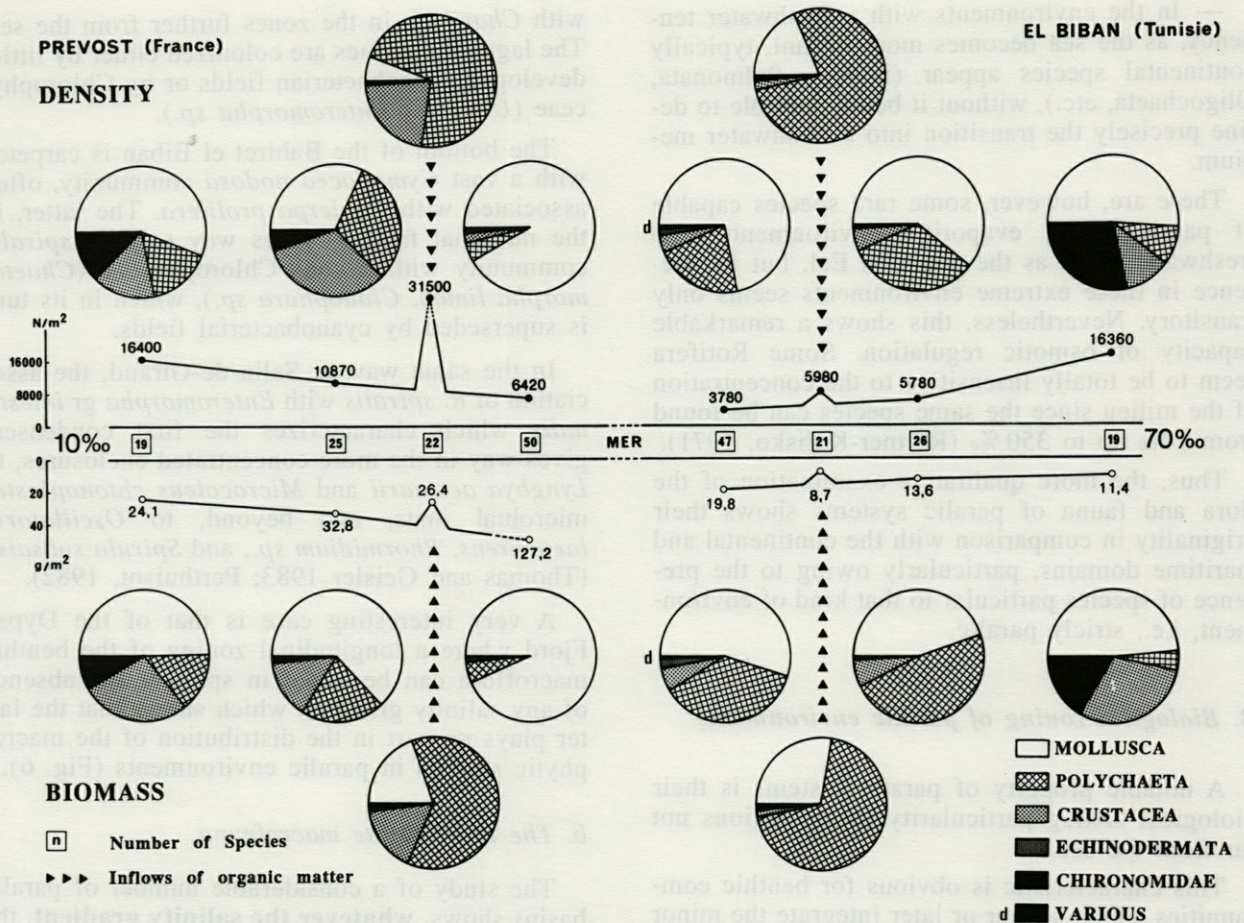


Fig. 8. — Quantitative variations of benthic macrofauna in the Etang du Prévost (France) and the Bahiret el Biban (Tunisie). From Guélorget and Perthuisot (1982).

N.B. Local deposits of organic matter (contact between marine waters and lagunar waters, hydraulic umbilicus, zones of intense biosedimentation, inflows of pollution effluents) influence the benthic communities by transforming their qualitative and quantitative features: increase of detritivorous species to the detriment of suspension feeders, appearance of species indicative of « organic pollution ».

cauda, *Pirenella conica*, *Ammonia beccarii* var. *tepidi*).

Beyond these, are the extreme environments. There, no zoning is obvious, neither in the almost freshwater media, nor in the evaporitic environments which remain little known. Perhaps the biological zoning continues at the level of the meiofauna but, for instance in a salt marsh, no notable qualitative difference can be observed between the communities in gypsum areas and those of the crystallizers, despite considerable differences in salinity between those two environments.

2. Biological gradients

As far as the benthic communities (macrofauna) are concerned, the distinctive scales (variety of species, density, biomass, production), can be observed to form gradients from the communication link(s) with the sea, towards the edges of the lagoon. Independently of the salinity field and the

value of its gradient, the comparison between the Etang du Prévost and the Bahiret el Biban is highly significant in this respect (Fig. 8) (Guélorget and Perthuisot, 1982). Nevertheless, as explained in detail later, in all the cases studied, and according to bibliographical data, the following can be observed progressively from the communication link with the sea:

- a significant decrease in variety or diversity of species;

- a progressive increase in the density of the invertebrate macrofauna, followed by a pronounced decrease near the freshwater pole, while the benthic macrofauna disappears completely in the vicinity of the evaporitic pole;

- a progressive decrease in biomass, for the increase in density accompanies a decrease in size (lagunar « dwarfism »);

- a drastic decrease in the overall production (calculated from the malacofauna which predominates in paralic systems) falling from a maximum

situated in the zones directly influenced by the sea (Guelorget *et al.*, 1982);

— a parallel can be drawn with specific scales of the phytoplanktonic and ichthyological communities which present similar patterns.

C. The influence of salinity upon marine species

There are cases where marine organisms reputedly stenohaline, such as echinoderms, live in saline concentrations obviously different from those of the sea.

This is the case in the Gulf of Salwa situated between Saudi Arabia and the Qatar peninsula (Basson *et al.*, 1977), where at least three species of stelleroides (*Astropecten phragmosus*, *A. polyacanthus* and *Asterina burtoni*) « tolerate » salinities in excess of 60 ‰. In the same places live stonebass fish (*Epinephelus tauvina*), a common gastronomical species of the Persian Gulf, found at over 70 ‰.

Another similar case is the Vonitza Bay, in the Gulf of Amvrakikos, Greece, where a curious association of snakes and sea-urchins (*Paracentrotus lividus*) have been observed by authors, at salinities which, measured in January and June 1982, do not exceed 5 ‰.

These two examples show that « osmotic regulation » is not a particular problem, even for species considered as not being among the most « stenohaline ».

D. The stability of paralic communities

Another property of paralic ecosystems is their extreme stability, when compared to marine or freshwater ecosystems. It is even possible to say that the more paralic an ecosystem is, and therefore situated in an unstable environment, the more stable it is itself. This is obvious when one considers the margins of paralic basins (e.g., the Bahiret el Biban), which can be subjected, according to the seasons, to considerable variations in the salt content, and change from a generally hyperhaline system into a highly desalinated one. In the case of the Bahiret el Biban, pluri-annual floodings do not affect at all the communities in the most marginal zones.

« Dystrophics crises » (« malaigues » = « bad waters ») which affect the lagoons of the Languedoc coastline should also be mentioned: although they destroy instantly great numbers of individuals — especially those which enter the lagoon to feed — they do not destroy the ecosystem which recovers very quickly as soon as the crisis is over.

All things considered, this stability of paralic ecosystems is logical, since the species living in

these environments have hardly any regulatory problems — particularly osmotic ones — since they live in conditions (of salinity for example) which are both varied and variable.

E. Conclusion

The panorama of the paralic environments outlined above shows that beyond the morphological, geochemical and sedimentological diversities, these environments present an undeniable biological unity: an originality and specificity of the communities, an independence of the qualitative and quantitative biological gradients with respect to salinity fields, and stability of their ecosystems. They are not « mixtures » of flora and fauna, some marine and others freshwater, but original communities having their own logic which is different from the marine or inland water logics.

Therefore a paralic environment exists as an autonomous entity, distinct from the marine and inland water ones, having its own structure and its own dynamics. The limit between the marine domain and the paralic domain is not always exactly the shoreline: for example, all seas do not belong to the marine domain. The Baltic, the Black Sea and the Caspian Sea are paralic basins. Moreover, there are zones of the marine domain with abnormal salinities (Salwa Gulf, Vonitza Bay). Therefore, the totality of paralic environments is different from the totality of « variable salinity » environments (Plaziat, 1982), as well as from the totality of « marginal-coastal » environments (Levy, 1970).

According to geological and biological data, two sub-systems can be observed:

— the sub-domain closest to the sea (Near paralic) is characterized by a geochemistry little different from that of the sea, by the large quantities of sediment involved in the biogenic phases (carbonates, organic matter), by essentially « thalassoid » communities, and by pronounced biological gradients;

— the sub-domain farthest from the sea (Far paralic) is characterized by a geochemistry radically different from that of the sea with two poles that are also found in the continental domain: the evaporitic pole and the freshwater pole. The abiogenic sedimentary phases are dominant. The communities are « specialized », original, and the biological gradients not very pronounced (unless proved to be the contrary by future studies).

The limit between these two domains is approximately in the microbial mats area; when leaving the sea, this limit also corresponds to the disappearance of Foraminifera (Zaninetti, 1982).

The above-mentioned affirmations are not intended as dogma, but can be regarded as suffi-

ciently innovative to be used in the following sections as the basis for certain deductions.

III. CONFINEMENT : THE FUNDAMENTAL PARAMETER OF THE PARALIC DOMAIN

There is a natural zoning, biological and geological, in every sizable portion of the hydrosphere. In the marine domain, depth is undoubtedly the leading parameter responsible for zoning. The decisive influence can be only modulated by other parameters. In the continental domain (aquatic or otherwise), latitude, which affects temperature and photoperiodicity, seems to be the fundamental parameter. Is there a dominant parameter in the paralic domain, and if so, what is it ?

A. The reasons for a mistaken approach

Until recently, salinity has generally been considered as the fundamental ecological parameter of the distribution of the communities in paralic environments (Kiener, 1978; Remane and Schlieper, 1956; Petit, 1962; Sacchi, 1967; Vatova, 1963), and it is on a salinity scale that the usual classification rests: euryhaline, mesohaline, poikilohaline systems, etc. A simple observation of the natural surroundings which leads to the considerations mentioned in the previous chapter, shows that salinity (along with the major ionic relations, etc.) as a fundamental ecological parameter of the paralic domain is a mistaken notion.

It is likely that the main reason is the variability, but also the accessibility of this parameter, the presence in paralic environments of « abnormal salinities » (with relation to the sea which is considered « normal ») is an inducement to consider this parameter as paramount. It is true, moreover, that for a given basin, the biological zoning can generally correspond with the local geological zoning; on a regional scale, if the correspondence is less clearcut, it can be ascribed to local differences and other parameters.

Hyperhaline paralic environments are rare and to date little studied. Therefore few scientists have studied both hyper - and hypohaline environments: only comparison between the two, together with the revelation of an identical zoning for both could cast doubts and lead to the discarding of a mistaken idea (Guelorget and Perthuisot, 1982).

Finally, another error accepted by many authors is the chemical stability of seawater (in composition and concentration) in the course of geological

time. This would imply that the marine domain is the fundamental original one, from which most aquatic stocks issue, and that those which « adapt » to « abnormal » media must « solve problems of osmotic regulation ». Now, there are firm doubts regarding the chemical stability of seawater (Perthuisot, 1980, 1989), and on the fundamental or original quality attributed to the marine domain.

B. The search for the fundamental parameter of the paralic domain

It is established that the biological zoning organizes itself roughly according to the distance from the open sea, as do the geochemical gradients (whatever their values). In fact, this is only an estimate. In more detail, it is noted that the weaker the exchange of water with the sea the more « typically paralic » the communities become, i. e., they are composed of eurybiontic species, not numerous, with a strong density, etc. Conversely, the nearer to the zones where the movements of the water allow a regular **renovation** of the medium, the richer in species the communities are and the lower the density becomes (Guelorget *et al.*, 1981, 1982 (a) and (b); Perthuisot, 1983; Perthuisot et Guelorget 1982 (a) and (b).

The most adequate term to qualify the value which organizes the biological zoning of the paralic ecosystems would appear to be « **confinement** ». This term, used in a both empirical and intuitive way in various disciplines of natural science is ambiguous: for example, it is sometimes used to mean « anoxia ».

This word is used to imply « with relation to the sea »; first, because the lagunar ecosystems are arranged in relation with the communication link with the sea, and second, because of the initial concept that in the smaller, even restricted basins where most of the life-giving elements (mineral salts, trace elements, vitamins, etc.) come from the outside (like oxygen in a nearly closed room); the communities organize themselves, according to the rarity of these elements, rarefaction which they themselves are mostly responsible for. This idea (which will be developed later) is based, for instance, on the amazing capacity of molluscs to fix certain trace elements (Cu, Pb, etc.), within their tissues.

Obviously, in the marine domain, the situation is otherwise, since it can be considered infinite, or at least inexhaustible, if equated to the biomass it contains with the available volumes of water elements.

Thus, confinement at a given point in a paralic ecosystem would correspond to the lack of « vital elements » of marine origin at that same point.

Since this deficiency is essentially linked schematically, confinement is a function of the **time** it takes water coming from the sea to reach the point in question.

Further, it can be said that the marine domain is the main communication agent between the different fractions of an apparently very fragmentary domain. This is without doubt a determining factor in the dissemination of paralic species, and of the completion of their biological cycles. On the other hand, many marine species, particularly fish, use paralic environments to feed.

The confinement of a specific zone of a given paralic ecosystem is the outcome of various factors such as the size of the communication link, the force of the tide, the currentology of the basin, the continental inflow, etc. Thus, at Salin-de-Giraud, for instance, in the zones where the water flow is great (near the sluice valves, in the by-pass channels), the biological associations show a confinement lower than the totality of the condensers where they belong. It is therefore essentially hydrodynamic. In this connection, it must be mentioned that depth can play a fundamental role when it leads to the presence of a deep stable water mass: it then creates a very large local confinement that can bring about the almost total disappearance of the benthos, and the appearance of facies of a euxinic type (Perthuisot, 1975, 1980, 1989).

Finally, when the confinement becomes very widespread (in the Far paralic), its leading role in the dynamics of the communities diminishes, and biological logic tends to depend upon other factors.

What is the relationship between confinement and salinity (or concentration)? Climatic and hydrographic data must be examined: it is clear that in any given basin, salinity at a given point depends both on the renewal of the medium, hence of the confinement, and on the local freshwater supply (by convention, that algebraic value of the difference between evaporation and freshwater supplies is termed « hydrous deficit »). If the hydrous deficit is positive, the basin is hyperhaline, if the hydrous deficit is negative, the basin is hypohaline. In each basin, hyper- or hypohalinity increases with confinement at a given value (not nil) of the hydrous deficit provided the latter is constant for the whole of the basin being considered.

This proposition has been formalized mathematically in a paper belonging to the present issue (Perthuisot and Guelorget, 1992). It shows that granted an equal confinement, two points from a same basin or from different basins in similar climatic conditions, have closely related salinities. Conversely, in very different climates, two points of equal confinement have very different salinities. In all cases, as confinement increases, the

difference in salinity (or concentration) from the sea increases, except when the hydrous balance is close to zero: in that case, the salinity remains close to that of the sea, whatever the confinement. It is clear that in nature, the more confined a milieu is – hence enclosed within the continental domain – the less likely it is to belong to an environment with a balanced hydrous value; except if it is a bathymetric confinement: in the case of stratified basins, the lowest body of water is characterized by a zero hydrous deficit. Lastly, if the confinement is nil, the point in question belongs to the marine domain.

While there is an apparent concordance in each basin of the biological gradients and the chemical gradients, there is a total obliquity of the geochemical zoning over the biological zoning on the scale of the entire paralic domain since this biological zoning depends largely on confinement alone.

In spite of present inability to quantify either the confinement or the « hydrous deficit » in natural environments, this concept seems to account for the situations encountered in the field better than an ecological classification of the paralic systems according to their salinity.

Thus, to each of the three domains which constitute the hydrobiosphere corresponds a fundamental parameter: depth in the marine domain, latitude in the continental domain, confinement in the paralic domain. All have something to do with time.

D. The establishment of a confinement scale

As emphasized before, confinement is a complex and abstract value, which cannot be measured in the present state of knowledge. Not having a unit of measurement, a qualitative scale is proposed (comparable for example, to Moh's hardness scale or Mercalli's scale for the intensity of earthquakes). This attempt cannot rely on either geochemistry or sedimentology: it is therefore necessary to use the peculiar features of the biological zoning, and in this connection, benthos proves convenient: apart from the fact that it is relatively easy to harvest, that it allows an easy direct observation, and in addition to its autochthonous species, it integrates in the short term, minor variations of the environment, and reflects the latter's global conditions.

In comparing various Mediterranean paralic basins, it is possible to establish 6 degrees of confinement starting from the particular features of the distribution of benthic species on a soft bottom (Fig. 9). This scale, valid for the Mediterranean, concerns only the portion of the paralic domain close to the sea (Near paralic) (Perthuisot and Guelorget, 1982; Guelorget *et al.*, 1982, 1983).

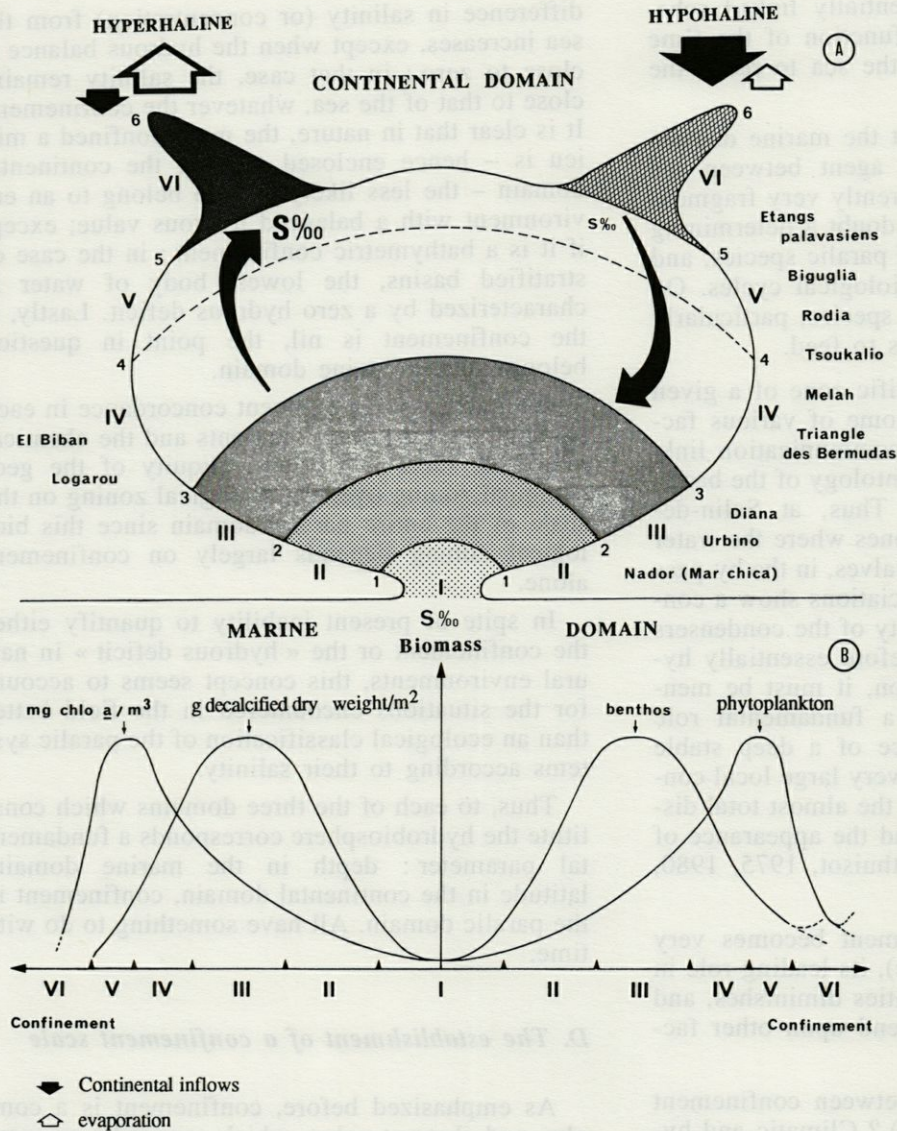


Fig. 9. - A, A diagrammatic representation of the biological zoning (Roman figures) defining the scale of confinement (in Arabic figures) in the model of the Mediterranean paralic ecosystem. B, Variations showing the phytoplanktonic and benthic biomass in relation to the confinement scale. The single points of the diagram (maximum, curve crossings) remain fixed in relation to the biological zoning. The corresponding values of the biomass can vary according to the overall productivity of each basin.

Zone I - This zone falls between degrees 0 and 1. In this zone situated in the immediate vicinity of the communication links with the sea and which is simply a continuation of the marine domain, the macrofauna consists of many strictly thalassic species generally belonging to the fauna of the marine biocenoses described by Pérès and Picard (1964).

Zone II - This zone falls between degrees 1 and 2 : from degree 1, the penetration into the paralic domain can be considered effective. The benthic macrofauna is characterized by the loss of the sensitive strictly marine species, the most « stenohaline ». Molluscs can still be found : *Macra corallina*, *M. glauca*, *Tellina tenuis*, *Donax semistriatus*, *D. trunculus*, *Acanthocardia echinata*, *Dosinia exoleta*, the polychaeta : *Audouinia tentaculata*, *Magelona papillocornis*, *Owenia fusiformis*, *Phyllodoce mucosa*, *Pectinaria koreni*, the crustaceans : *Portunus latipes*, and the echinoderms : *Asterina gibbosa*, *Holothuria polii*, *Paracentrotus lividus*. Lastly, the presence should

be mentioned of *Branchiostoma lanceolatum* in the sandy facies devoid of « organic pollution ».

The phanerogamic macroflora loses the *Posidonia oceanica*; and small phanerogams predominate such as *Zostera marina*, *Cymodocea nodosa*, *Zostera noltii* and *Caulerpa prolifera*.

The limit of this zone (degree 2) is marked by the total disappearance of echinoderms.

Zone III - This zone falls between degrees 2 and 3 : it is dominated by « mixed species » (*Venerupis decussata*, *V. aurea*, *Scrobicularia plana*, *Corbula gibba*, *Loripes lacteus*, *Gastrana fragilis*, *Akera bullata*, *Nephtys hombergii*, *Armandia cirrosa*, *Glycera convoluta*, *Upogebia littoralis*) as far as the benthic macrofauna is concerned.

Zone IV - Zone falling between degrees 3 and 4 : at degree 3, all thalassic fauna disappears, and the species found are strictly paralic : *Abra ovata*, *Cerastoderma glaucum*, *Hydrobia acuta*, *Nereis*

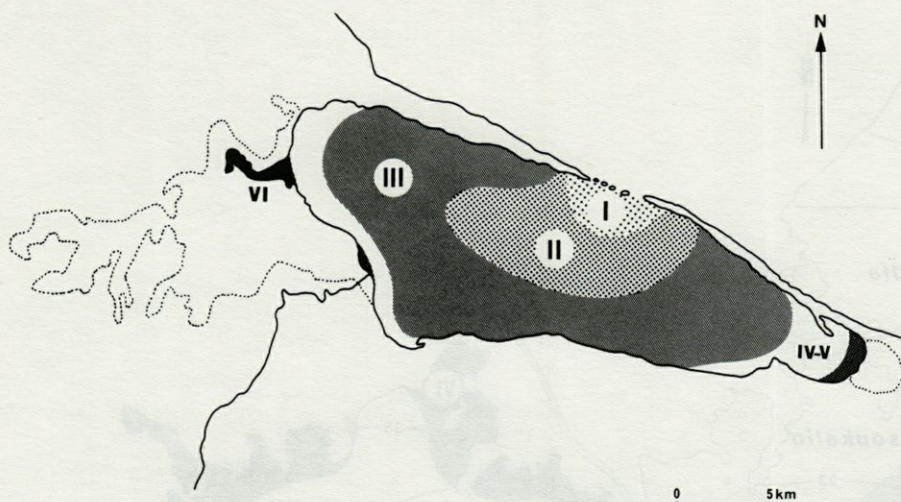


Fig. 10. – Diagrammatic map of confinement zones in the Bahiret el Biban. From Guélorget *et al.*, 1982.

diversicolor, *Gammarus insensibilis*, *G. aequicauda*, *Corophium insidiosum*).

The macrofauna is characterized by the appearance of *Ruppia spiralis*.

Zone V – Zone falling between degrees 4 and 5: in this zone, the phytoplanktonic production (pinnated diatoma, Cyanobacteria) is at its maximum. The surface of the sediment is in the process of being colonized by the Cyanobacteria. Thus the sedimentation is essentially organic, and the interstitial system is highly reducing.

The community consists essentially of vagile fauna with detritivorous crustaceans (*Sphaeroma hookeri*, *S. rugicauda*, *Corophium insidiosum*, *Idothea balthica*), browsing gastropods (*Hydrobia acuta*, *Pirenella conica*), polychaetes such as *Nereis diversicolor*, and larvae of Chironomidae in the uppermost stratum of the sediment (a few millimeters). In this zone, and most particularly in very hypohaline ecosystems, elements of freshwater fauna appear (Tricoptera, Oligochaeta, Odonata). Further, in hyperhaline ecosystems elements of evaporitic fauna (*Artemia salina*) can be found.

The plant communities – if any – are dominated either by *Potamogeton pectinatus*, or by the Characeae. They can also be mixed.

Zone VI – Zone falling between degrees 5 and 6. It represents the passage into Far paralic, either freshwater or evaporitic, and is usually characterized by an almost total colonization of the substratum by Cyanobacteria which form microbial mats or stromatolithic structures. The passage into freshwater is marked by the appearance of strictly freshwater species. The sub-evaporitic system is characterized by the absence of benthic macrofauna, except browsers which momentarily visit that zone for trophic reasons (browsing of the microbial mats).

The far edges of this zone are the outer limit of the Near paralic. Foraminifera disappear, which coincides, around the evaporitic pole, to a considerable extension.

Beyond this, in the Far paralic, the role of confinement seems to decrease, as far as present knowledge indicates.

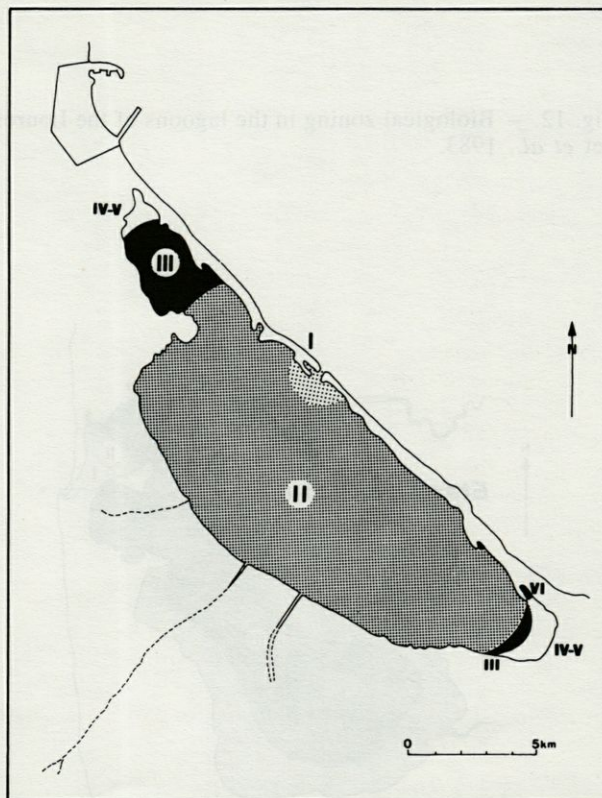


Fig. 11. – Diagrammatic map of confinement zones in the Nador lagoon (Mar Chica or Sebkhia bou Areg). From Guélorget *et al.*, 1983.

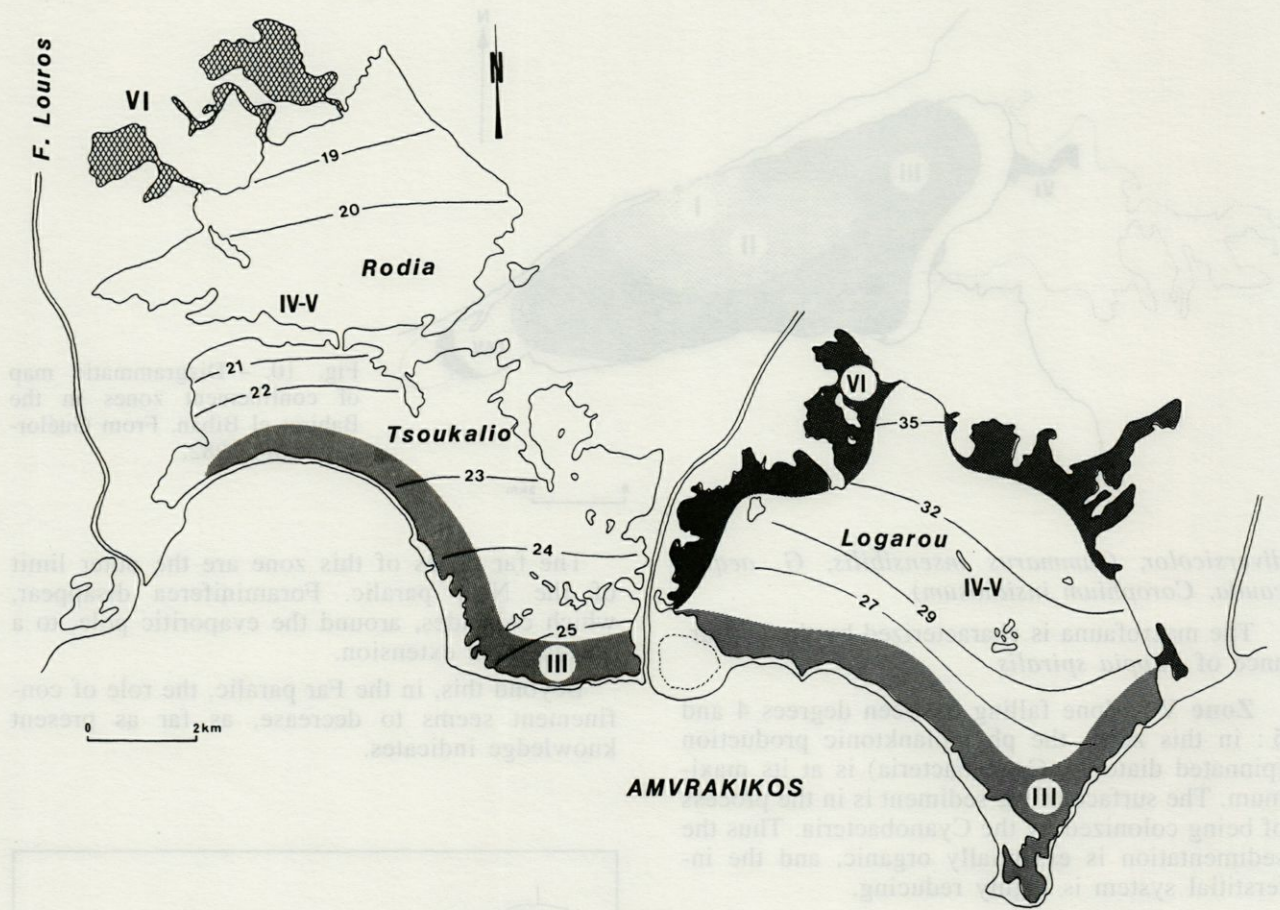


Fig. 12. - Biological zoning in the lagoons of the Louros Delta (Amvrakikos, Greece), Isohalines in ‰. From Guélorget *et al.*, 1983.

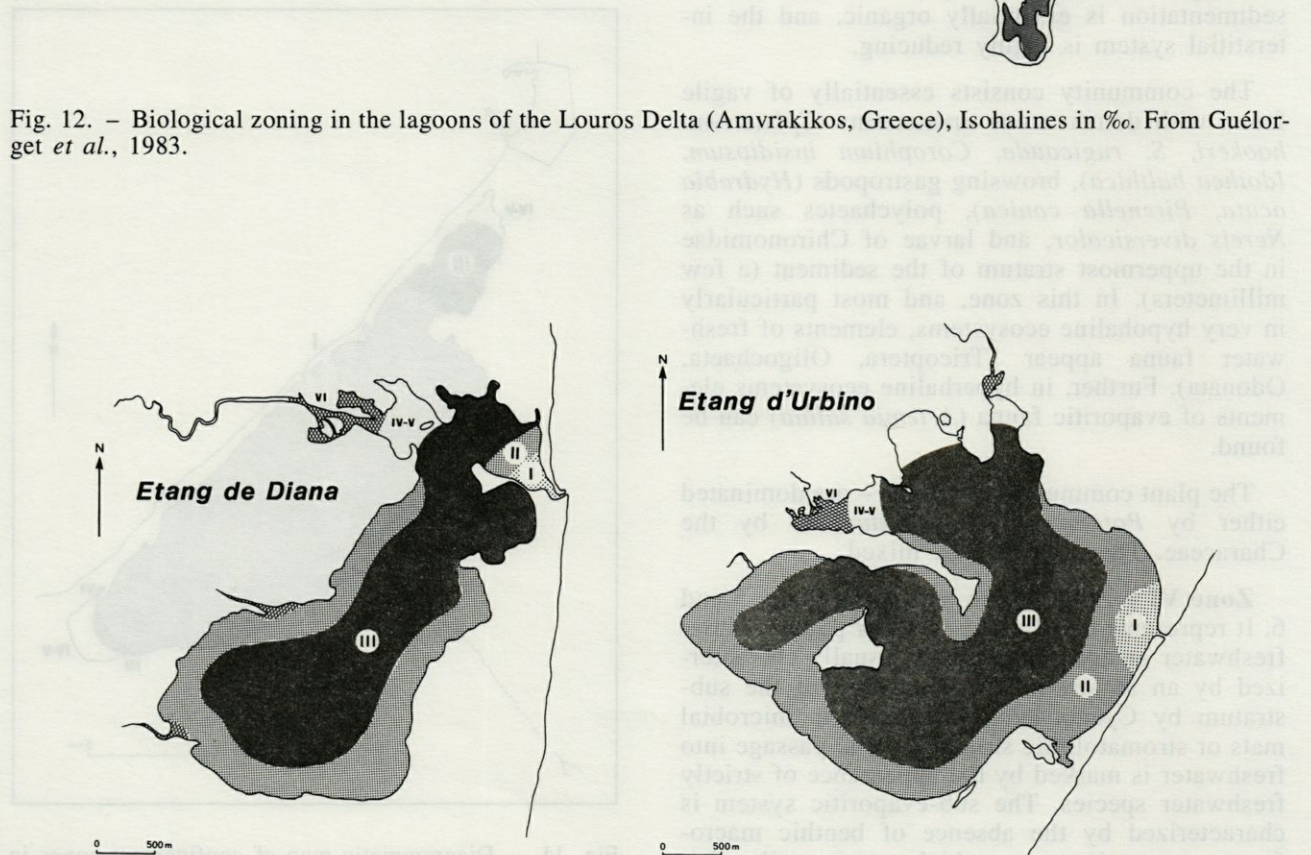


Fig. 13. - Biological zoning in the lagoons of the eastern plain of southern Corsica. From Guélorget *et al.*, 1983.

E. The position of several Mediterranean basins on the confinement scale

According to the confinement scale proposed, the organization of a peri-Mediterranean type lagoon can be illustrated (Fig. 9). This graph shows the zoning of the ecosystem according to its confinement. With regard to this standard diagram, the lagoons in question can either spread over the entire scale, or occupy only a portion of it.

1. Bahiret el Biban (Tunisia) (Fig. 10)

Bahiret el Biban, a hyperhaline lagoon, covers the entire confinement scale; however, the largest portion is situated in zones II and III, thus showing low confinement due to sizable and regular exchanges with the sea (wide pass, strong tidal currents) (Guelorget *et al.*, 1983).

2. Mar Chica of Nador (Morocco) (Fig. 11)

This basin, which has a complex history, is little confined at present, because it communicates extensively with the sea. Only a few small marginal areas can suddenly become confined, thus leading to the development of microbial mats (Frisoni *et al.*, 1982; Guelorget *et al.*, 1987).

3. Lagoon of Logarou (Greece) (Fig. 12)

Almost completely situated in zones IV and V, this lagoon—of deltaic formation—hyperhaline in summer, reaches the cyanobacterial zone in its northern part (Frisoni *et al.*, 1982). Only a narrow strip along the lido indicates some influence of the marine domain.

4. Lagoons of Tsoukalio and Rodia (Greece) (Fig. 12)

These lagoons, close to that of Logarou and belonging to the same deltaic formation, have the same pattern of confinement, but with a negative salinity gradient (Frisoni *et al.*, 1982; Guelorget *et al.*, 1986).

5. Lagoons of Diana and Urbino (Corsica) (Fig. 13)

These two lagoons are very similar. The marine influence prevails. However, the hydrological originality of Diana has permitted the establishment of a little-confined zone (II) around the sides furthest from the communicating link with the sea. Due to the great depth (9-10 m) in relation to the surface area (500-700 ha), the central zones of these lagoons, little renewed, are submitted to a bathymetric confinement linked to a « hydrological remoteness » from the sea, and above all, to

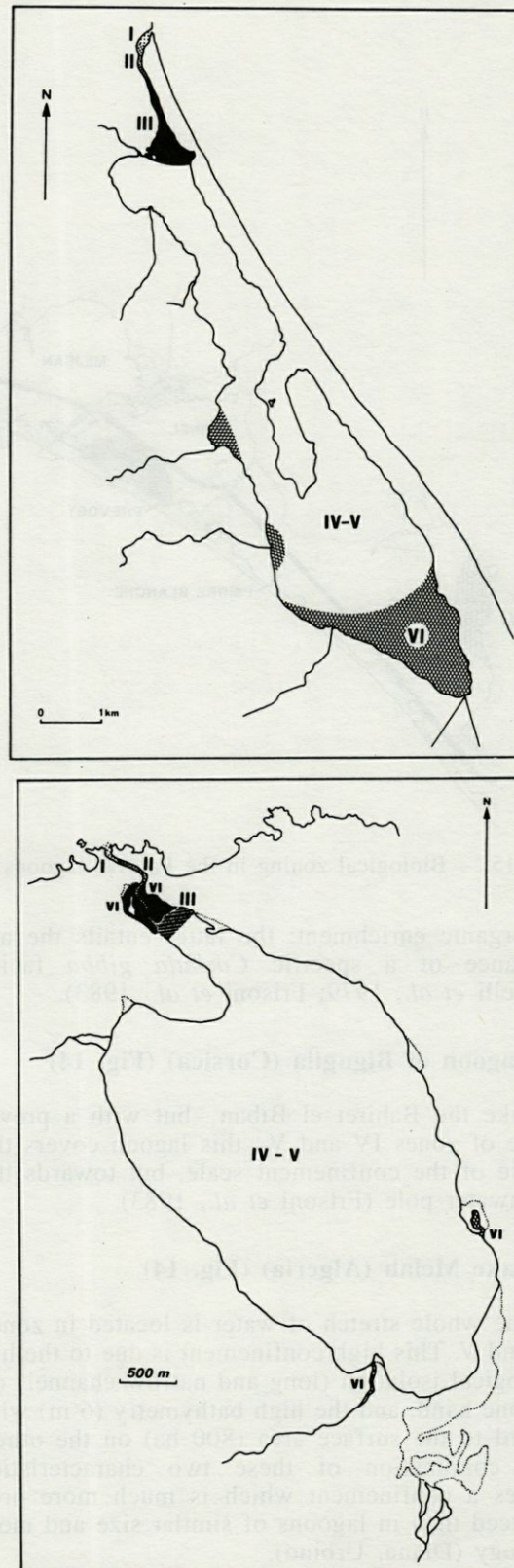


Fig. 14. — Above, biological zoning in the Etang de Biguglia in the northern part of the eastern Corsican plain. From Guélorget *et al.*, 1983. Below, biological zoning in « Lake » Melah (Algeria). From Guélorget *et al.*, 1983.

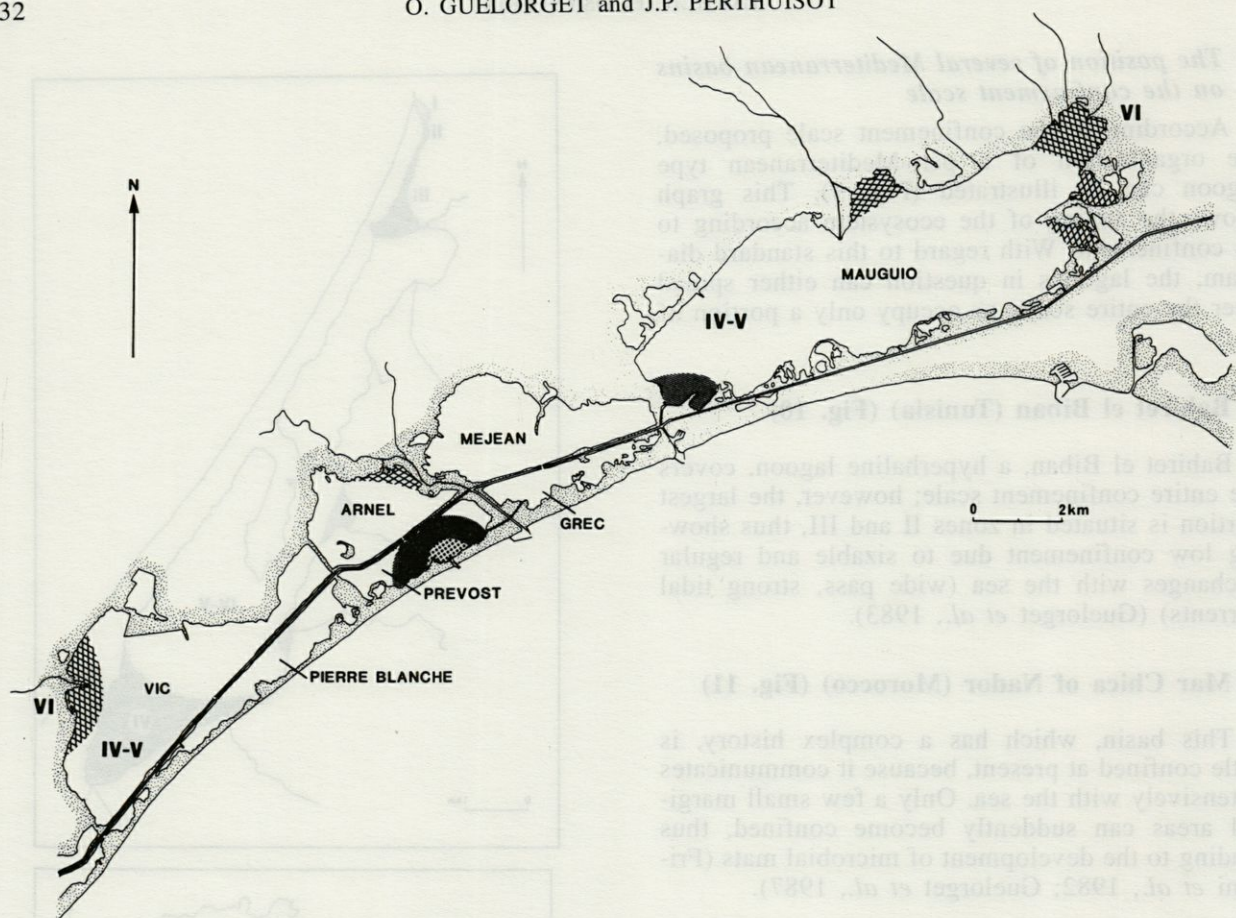


Fig. 15. – Biological zoning in the Palavas lagoons (France). From Guélorget *et al.*, 1983.

an organic enrichment; the latter entails the appearance of a specific *Corbula gibba* facies (Burelli *et al.*, 1979; Frisoni *et al.*, 1983).

6. Lagoon of Biguglia (Corsica) (Fig. 14)

Like the Bahiret el Biban –but with a prevalence of zones IV and V– this lagoon covers the whole of the confinement scale, but towards the freshwater pole (Frisoni *et al.*, 1983).

7. Lake Melah (Algeria) (Fig. 14)

The whole stretch of water is located in zones IV and V. This high confinement is due to the hydrological isolation (long and narrow channel) on the one hand, and the high bathymetry (6 m) with regard to the surface area (800 ha) on the other. The conjunction of these two characteristics causes a confinement which is much more pronounced than in lagoons of similar size and morphology (Diana, Urbino).

This lagoon offers a particular originality with the presence of microbial mats (zone IV) in the vicinity of the communicating link with the sea: those regions contiguous to the embanked channel are isolated from marine currents and undergo a high confinement (Guelorget *et al.*, 1983, 1989).

8. Palavas lagoons (France) (Fig. 15)

This entire lagunar system with a few communicating links with the sea (2 graus) is almost entirely situated in zones IV and V, except for the regions of the graus which allow implementation of thalassic communities.

The prevailing influence of the catchment area leads to the appearance of freshwater zone VI at the periphery of the complex.

9. Bermuda Triangle (Santa Pola, Spain) (Fig. 16)

This former salt production condenser (Perthuisot *et al.*, 1983) is an annex of hypohaline paralic marsh. More confined and saltier than the latter, the entire basin is situated at the upper end of the confinement scale (IV, V, VI).

F. Adjustment of other biological compartments into the confinement scale

With regard to the biological characterization of benthic macroflora and macrofauna, the biological zoning of these characteristics is sufficiently clear and stable as to define a confinement

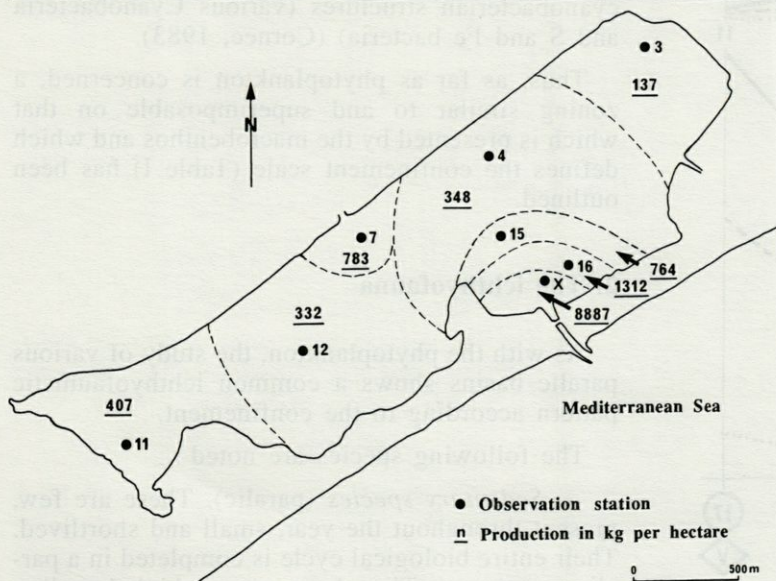
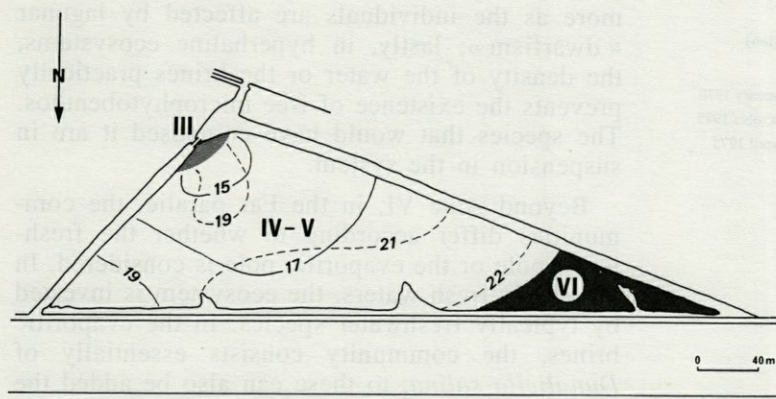


Fig. 16. - Above, biological zoning in the Bermuda Triangle (Santa Pola, Spain). From Guélorget *et al.*, 1983, Perthuisot *et al.*, 1983. Isohalines en g/l. Unbroken line: June 1981. Dotted line: October 1981. Below, situation of the stations and levels of total malacological production (in kg/ha/year) in the different parts of the Etang du Prévost. From Guélorget *et al.*, 1983.

scale. This is not the case for the other links of the trophic chain which, composed as they are of more mobile species reacting more strongly to the minimum variation in the system, present a less obvious, more fluctuating zoning pattern.

1. The Phytoplanktonic Communities of Paralic Ecosystems

Although they are, in most of the paralic basins studied, pronounced and significant gradients concerning the phyto-planktonic biomass and the chlorophyll production, it seems that the phytoplanktonic communities are relatively homogeneous in each basin. This is probably due to the fact that the major part of each basin spreads over a limited number of confinement zones (usually one or two). Thus only the comparison of a considerable number of paralic basins can trace the outline of a specific zoning of paralic phytoplankton (Frisoni, 1984).

a. Taxonomic resources

Finally, it should be noted that an increase in confinement results in a decrease of the taxonomic

resources; however, the basins strongly influenced by continental inflows gain in freshwater taxa.

b. Specific composition of the phytoplanktonic communities

The zones directly under reviving marine influence (I, II, III), are characterized by the presence of typically neretic plankton essentially composed of centric diatoma -up to more than 25 % on relative average- (*Skletonema costatum*, *Melosira sp.*, *Coscinodiscus sp.*, *Chaetoceros sp.*, *Rhizosolenia sp.*, *Thalassiosira sp.*) along with pinnated diatoma (*Nitzschia closterium*, *Thalassiothrix frauenfeldi*) and with some peridiniens (*Ceratium furca*) and various nannoplanktonic forms (Chlorophyceae, Cryptophyceae, Cyanobacteria-ceae).

In the typically paralic zones (IV, V) centric Diatoma are very rare; pinnated diatoma, although always present, are rarely plentiful (*Navicula sp.*, *Gyrosigma sp.*, *Amphora sp.*, *Striatella sp.*). The community is generally dominated by peridiniens and the nannoplankton groups.

Among the peridiniens can be noted the frequent and abundant presence of *Exuviella com-*

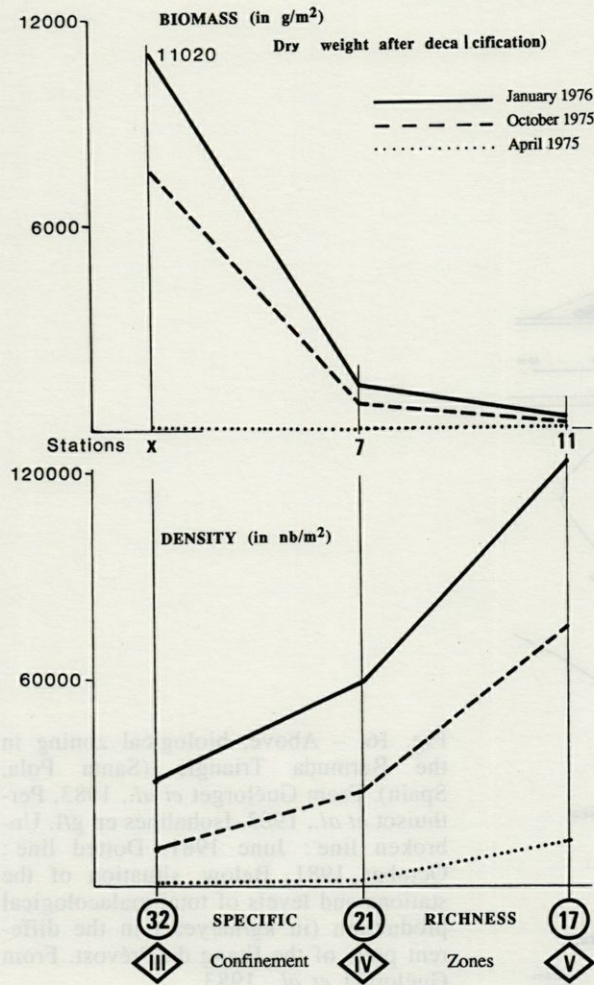


Fig. 17. — The biological gradients (specific richness, density, biomass) of the hard substrate macrobenthofauna in the Etang du Prévost. The stations concerned (X, 7, 11) are shown in Fig. 8). The biomass measured in January 76 corresponds to an annual production.

pressa and *Prorocentrum scultellum* which can represent up to 99 % of the community (Lake Melah). These species can also be observed all through the annual cycle in the same basin (Etang de Biguglia) (Frisoni, personal communication). Among the peridinians, it can be noted that *Exuviella marina* and *Prorocentrum micans*, « mixed » species of notable size, are to be found especially in zones II and III, whereas their paralic homologues, the smaller *Exuviella compressa* and *Prorocentrum scultellum*, colonize mainly zones IV and V.

In the most confined zones of the Near paralic (zone VI), the phytoplanktonic communities are dominated by species which are usually periphytic or benthic. In this connection it should be noted that in these usually very shallow media, the microphytobenthos easily regains a state of suspension, that sample taking can perturb the system and affect the element of the phyto-benthos all the

more as the individuals are affected by lagunar « dwarfism »; lastly, in hyperhaline ecosystems, the density of the water or the brines practically prevents the existence of free microphytobenthos. The species that would have composed it are in suspension in the system.

Beyond zone VI, in the Far paralic, the communities differ according to whether the fresh-water pole or the evaporitic pole is considered. In the nearly fresh waters, the ecosystem is invested by typically freshwater species. In the evaporitic brines, the community consists essentially of *Dunaliella salina*; to these can also be added the cyanobacterian structures (various Cyanobacteria and S and Fe bacteria) (Cornee, 1983).

Thus, as far as phytoplankton is concerned, a zoning similar to and superimposable on that which is presented by the macrobenthos and which defines the confinement scale (Table I) has been outlined.

2. The ichthyofauna

As with the phytoplankton, the study of various paralic basins shows a common ichthyofaunistic pattern according to the confinement.

The following species are noted :

— *Sedentary species* (paralic). These are few, present throughout the year, small and shortlived. Their entire biological cycle is completed in a paralic ecosystem. They have a very high breeding potential and are present in large numbers. As far as Mediterranean basins are concerned, *Atherina boyeri*, *Aphanius fasciatus*, *Potamoschistus marmoratus*, *Syngnathus abaster* should be mentioned.

— *Migrant species*, often larger than the sedentary ones, with a longer life-span and whose biological cycle comprises a necessary reproductive phase at sea (or of ill-defined type). Within this group are to be distinguished :

The **regular** migratory species (« mixed » species) whose fry and juveniles (0+) enter a paralic system to spend a compulsory (trophic) period of their biological cycle : these include mullet, some Sparidae (*Sparus aurata*, *Diplodus sargus*, *Pagellus mormyratus*), sea bass (*Dicentrarchus labrax*), sole (*Solea vulgaris*), plaice (*Pleuronectes platessa*), eels (*Anguilla anguilla*). Some adult or juvenile (1+) individuals of these species are liable to return occasionally to the lagoon to feed.

The **occasionally or accidentally** migratory species (usually thalassic) are sometimes found by chance in a paralic milieu. Among the more frequent are : Labridae, Gobiidae, garfish (*Belone belone*), anchovy (*Engraulis encrassicolus*), red mullet, Rajidae (*Myliobatis aquilla*), *Coecula coeca*...

Table I. - Above, taxonomic resources of the phytoplankton in various Mediterranean paralic basins. Below, number of species and diversity of the ichthyological populations of the lagoons of the eastern plain of Corsica. From Frisoni *et al.*, 1983.

Basin	Taxonomic resources		Prevailing confinement zones			
Étang de Diana	41		II (III)			
Mar Chica	29		II			
Étang de Mauguio	13		IV (V)			
Lac Melah	10		IV - V			
Triangle des Bermudas	8		IV - V (VI)			
Étang de Biguglia	27		V - VI			
(freshwater influences)						
	BIGUGLIA		DIANA		URBINO	
	mouth	centre of lagoon	south	north	north	south
Sedentary	78 %		82,0 %		94 %	
Migrant	21 %		10,4 %		4 %	
Occasionals (% of the captures*)	1 %		7,6 %		2 %	
In numbers						
M/S * Ratio (numbers) (1981)	0,31	0,07	0,09	0,15	0,03	0,02
Number of species* (Migrant + sedentary) (numbers)	16	11	23	20	20	18
ESH (numbers)	Maximum 0,659 (Spring)		0,716 (Summer)		0,558 (Summer)	
	Minimum 0,463 (Winter)		0,304 (Winter)		0,342 (Winter)	

* All periods taken together

Hereafter all individuals belonging to sedentary species will be referred to as « sedentary », and the fry and juveniles (0+) of the regularly migratory species as « migrant ». The term « occasional » will be applied to all the others.

The study of the three largest lagoons of the eastern plain of Corsica (Biguglia, Diana and Urbino)

(Frisoni *et al.*, 1983) outlines the relative connection of the ichthyofaunistic communities to the confinement scale, both from a qualitative, and a quantitative point of view. The diagram thus proposed can be applied to all the paralic basins having been similarly studied (Frisoni *et al.*, 1982; Guelorget *et al.*, 1983; Quignard and Zaouali, 1981).

Table II. - Above, « sedentary » species : percentages of captures (over one year). Below, quantity of Molluscs in the Etang du Prévost. N = Density in number of individuals per m²; B = Biomass in grammes of decalcified dry weight per m².

(year)	BIGUGLIA		DIANA		URBINO					
	Mouth	Centre	North	South	Mouth	North	South			
(year)	81	81	81 (79)	81 (79)	81	81	81			
Athérine	26	61	83 (87,8)	68 (71,3)	38	65	72			
Aphanius	36	20	13 (2)	17 (13)	59	29	25			
Syngnathe	1	18	2 (3,6)	9 (2,3)	1	4	1,5			
Mottled Goby	38	1	2 (6,6)	6 (13,2)	2	2	1,5			
weight										
Athérine	58	81,5	89	87	51,5	75	75			
Aphanius	24	15	9	12	47,5	20	23			
Syngnathe	0,5	2,5	1	0,5	0,5	2,5	1,5			
Mottled Goby	18	1	1	1	0,5	2,5	0,5			
	Fine sands St. X		Muddy sands St. 15 et 16		Lagunar muds					
					North. emis. St. 7		West. bas.		East. bas.	
	N	B	N	B	N	B	N	B	N	B
Molluscs	9052	401,3	3083	33,8	1083	15,7	4031	8,4	919	8,3
Total fauna	9716	415,4	4010	44,9	6282	22,6	7331	16,9	2851	14,9

Table III. – Average values of density and biomass, annual production of the main Pelecypod Molluscs at different stations in the Etang du Prévost. N : Number of individuals per m². B : Weight of dry organic matter in g/m²; P : Production of dry organic matter in g/m²/year.

A	Station X				Station 16				Station 15				Station 7			
	N	B	P	P/B	N	B	P	P/B	N	B	P	P/B	N	B	P	P/B
<i>Venerupis decussata</i>	641	56,7	221,7	3,9	427	8,6	30,4	3,5	139	0,7	2,2	3,1				
<i>Venerupis aurea</i>	2705	54,6	190,9	3,5	1546	39,8	65,4	1,6	1301	13,5	45,3	3,3				
<i>Scrobicularia plana</i>	4901	122,9	451,9	3,7	1952	6,3	34,3	5,4	1162	5,1	16,2	3,2	322	9,6	29,1	3,0
<i>Cerastoderma glaucum</i>	189	7,4	24,2	3,3	68	1,3	0,1	0,1	234	2,6	8,4	3,2	428	9,8	43,9	4,5
<i>Abra ovata</i>					312	0,5	1,0	1,9	561	1,6	4,3	2,7	506	1,4	5,3	3,8
TOTAL	8436	241,6	888,7		4305	56,5	131,2		3397	23,5	76,4		1256	20,8	78,3	

B	Station 12				Station 11				Station 4				Station 3			
	N	B	P	P/B	N	B	P	P/B	N	B	P	P/B	N	B	P	P/B
<i>Venerupis decussata</i>									11	0,2	0,6	3,0				
<i>Venerupis aurea</i>									30	0,5	1,4	2,8				
<i>Scrobicularia plana</i>									22	1,1	4,4	4,0				
<i>Cerastoderma glaucum</i>	2401	11,0	26,8	2,4	6071	8,0	38,2	4,8	613	9,4	22,3	2,4	260	4,4	10,9	2,5
<i>Abra ovata</i>	503	1,2	6,4	5,3	1220	0,8	2,5	3,0	492	2,6	6,1	2,3	199	0,7	2,8	4,1
TOTAL	2904	12,2	33,2		7291	8,8	40,7		1168	13,8	34,8		459	5,1	13,7	

In the Corsican lagoons, migrant and sedentary species constitute more than 90 % of the stock collected.

a. Number of species and diversity

In the three lagoons, the same annual evolution of the number of species can be observed with one peak in spring in one in autumn, each corresponding to the two propitious periods for the « lagoon-ward movement » of the migrant fry and juveniles.

Taking these seasonal variations into consideration, the overall number of species in Biguglia is much lower than that in Diana and Urbino. Moreover, whereas the last two are very homogeneous (Table II), at Biguglia a decrease in the number of species can be observed between the center of the lagoon and the grau: this again corresponds to migrant movement and can be shown by the study of the proportion of migrant stock to sedentary stock (M/S). At Urbino, the ratio is very low because of the poor communication with the sea. At Diana, the opening of the basin allows a better stocking with fry. However, as the edges are generally only slightly confined, the migrants spread themselves evenly throughout the basin. At Biguglia (a much more confined lagoon), the migrants, although numerous, are mainly localized in the vicinity of the grau and seldom penetrate the « occasionals » which are more numerous at Diana than in the two other lagoons (Table I).

The diversity of the resident species, measured by the equitability of the Shannon coefficient (ESH) also shows (1981) a cycle with a spring maximum at Biguglia, and a summer one at Diana and Urbino. The minimum diversity occurs in

winter, a period when stocking with young fish is low: it therefore characterizes the sedentary populations.

At Biguglia, the rather high minimum diversity can be explained by the presence of a large range of the sedentary ichthyic populations. On the other hand, the relatively low maximum diversity shows that the influence of the migrants upon the resident populations remains moderate (except in the vicinity of the grau), and affects only a small number of species: the migrants do not greatly favour highly confined zones.

At Diana and Urbino, the very low minimum diversities are in keeping the high homogeneity of both the basins. At Diana, the maximum diversity is high because stocking with young fish is easy, and moreover, as the basin is on the whole little confined, the migrants spread throughout the basin. On the contrary at Urbino there is a low maximum diversity because of the small number of migrant arrivals related to the uncertainty of communication with the sea.

b. Sedentary species

Table II gives the average annual percentages of the captures of the various sedentary species in various zones of the lagoons studied, and the corresponding weights.

Considering only *Aphanius* and *Atherina*, it is noted that the former predominates in the vicinity of the graus in the low confinement zones, while *Atherina* predominates in the more confined zones. This is also the case at Diana whose northern basin, although near the mouth, is on the whole more confined than the southern basin.

The mottled goby seems to behave like the *Aphanius* as far as its distribution is concerned,

except at Urbino where it is evenly distributed, but low in numbers.

The syngnathid, very dependent on the plant communities, is seldom seen in the zones near the mouths.

c. Migrant species

They are 20 species of fry and juvenile migrants listed in three lagoons. They can be divided into three groups :

- Mulletts (5 species) present in three lagoons,
- Sparidae : *Diplodus* (5 species), *Puntazzo* (1 species), *Boops* (1 species), *Lithognathus* (1 species)
- Other species : Sea-bass (*Dicentrarchus labrax*), Soles (*Solea vulgaris* and *Solea sp.* at Urbino), Eel (*Anguilla anguilla*), Garfish (*Belone belone*), Anchovy (*Engraulis encrassicolus*), Red mullet (*Mullus barbatus*)

At Biguglia, the fry belongs mostly to eurybiotic species (garfish, eels, sea-bass). On the other hand, there are very few Sparidae (only 3 species), and no soles, red mullets or anchovies. At Diana and Urbino, the migrant species are more diversified and include more specifically marine species. This is also the case for the « occasionals ».

The specific composition of the migrant populations varies according to the season : if the mullets are present all the year round, due to successive arrivals of the different species, the Sparidae and the sea-bass appear mostly in spring, and the other species in late summer and in autumn.

The distribution of the different species is not uniform. The mullets are concentrated in the grau regions (Diana and Urbino) where they often pass through in shoals. The other species are more evenly distributed. Moreover, the stocking with young fish is very irregular : at Diana, for example, in May 1978, 16 % mullets, 59 % Sparidae and 25 % other species were counted; in May 1979, 97 % mullets, 2 % Sparidae, 1 % other species. Obviously, the state of the grau influences the stocking with fry : at Urbino, it remained practically nil for several years while the grau was closed. Its recent opening and maintenance have allowed a better stocking, and a proportion of migrants more in keeping with the position of this lagoon on the confinement scale.

d. Diets and coefficient of condition

The species of the paralic environments are essentially carnivorous or omnivorous, and very few microphagous. Therefore, the fish consume directly very little phytoplankton.

As far as the sedentary species *Atherina boyeri* is concerned, the highest average weights and sizes of the captured individuals are to be found

at Biguglia, taking the year as a whole. Again at Biguglia is noted the highest monthly average coefficient of condition. *A. boyeri* reaches the maximum coefficient of condition in the spring, i.e., during the reproduction period.

The coefficient of condition is given by the formula :

$Kc = W.L^{-3}$ where W is the weight in grammes and L the length in centimeters.

With regards to mullet (*Liza saliens*), a regular migrant species, a similar evolution is found according to seasons; but the individuals reach their maximum coefficient of condition towards the end of summer, before migrating towards the sea. This coefficient is even higher at Biguglia than the two other basins.

Thus, the Biguglia lagoon seems to be more favourable for the growth of individuals, especially sedentary ones, than the other lagoons. This is likely to be related to the heavy phytoplanktonic biomasses which characterize this highly confined lagoon, and which result in the presence of great numbers of primary consumers.

e. Conclusions

Unlike the relatively fixed benthic communities which settle in stable zones, according to the confinement range of each basin, the ichthyological populations are much more mobile. Therefore, their organization systems is of a more global type, and depends upon the totality of the characteristics of each basin and particularly on the relative surface areas occupied by the various zones of confinement, on the type of communication with the sea, etc. Thus, the qualitative and quantitative characteristics of the ichthyological fauna of the paralic ecosystems account for the originality of each of them, and for the place each occupies on the confinement scale.

Certain data suggest, however, that within the ichthyological population biological gradients exist, which are identical from one basin to another (the *Atherina / Aphanis* population, for example), which further studies may perhaps specify more accurately.

G. Quantitative biological gradient

Biological study of the peri-Mediterranean lagoons shows that the quantitative variations in the phytoplanktonic and benthic communities (macrofauna of invertebrates) differ according to confinement.

1. Phytoplanktonic Biomass and Biomass of the Benthic Macrofauna (soft bottom)

The chlorophyll biomass (expressed in mg of chlorophyll *a* per m³ fluorimetric analysis) increases regularly from the marine waters (values close to 1) up to zone V. Thus, the lagoons of Diana, Thau, el Biban and Nador, have a biomass of between 1 and 4; the lagoon of Biguglia reaches values of about 20; the lagoon of Mauguio (subject to urban and agricultural pollutions) has biomass values of about 1 000.

Beyond this zone V, the shape of the curve will depend on which pole (freshwater or evaporitic) is approached. In a freshwater medium, either the persistence of a high biomass (eutrophic system), or a decrease of this biomass (oligotrophic system) is noted. In a sub-evaporitic environment, in all cases a drastic decrease can be observed in the phytoplanktonic biomass. In this extreme zone, the primary link is hardly represented except by the microphytobenthos (microbial mats).

The biomass of benthic macrofauna (expressed in grammes of dry decalcified weight per m²) shows a similar curve. However, this curve shifts in relation to the preceding one: the position of the maximum moves into zone III (Fig. 9). However, as with the primary link, this diagram can show vertical fluctuations (maximum values) according to seasonal, interannual variations of the enrichment of the ecosystem by organic pollution.

The following values should be kept in mind:

— Around 1 g in zone I, about 10 g in zone II, about 50 g in zone III subject to few organic deposits (el Biban), reaching as much as 500 g in highly enriched zones (Prévost).

Beyond zone III, the curve shows a decrease of the values as far as zone VI where, as with the primary link, two possibilities arise:

— increase of biomass through contamination of the freshwater fauna when in hypohaline aquatic ecosystem;

— disappearance of benthic macrofauna when moving towards the evaporitic pole, which is the limit of the passage into the terrestrial domain.

Thus, at the level of zone IV, the decrease of benthic biomass and the increase of phytoplanktonic biomass are demonstrated by a crossing of the two curves.

Insofar as the majority of the peri-Mediterranean lagoons are located within zones III, IV, and V, this phenomenon is shown by a quantitative antagonism in the ecosystem between benthic macrofauna and phytoplankton. Thus, at the Bahiret el Biban, the confinement gradient results in phytoplanktonic biomass increase, and a benthic biomass decrease (Guelorget *et al.*, 1981). This is also the case at Biguglia, for instance,

where the inverse evolution of these two gradients is obvious (Frisoni *et al.*, 1983). On the contrary, Diana and Urbino, not highly confined and less rich in chlorophyll than Biguglia, possess a greater weight of macrofaunistic communities. The single point made by the crossing of the two curves is likely to correspond to a characteristic (as yet not explained) of the organization and the working of the paralic domain. However, considering this single point, it is obvious that the very high primary biomass (essentially phytoplankton and microphytobenthos) shows a large excess with respect to what is consumed by the low biomass benthic populations where the filter-feeders have disappeared and only browsers and detritivorous species remain. Thus, the major part of the chlorophyll biomass is unutilized. Besides, within these zones situated at the hydrological limits, the masses of water move extremely slowly, thus creating conditions which contribute to the accumulation of organic matter. The highly « abnormal » salinity of these zones contributes to the stratification of the water, the generalization of the reducing systems, and the diagenetic preservation of this organic matter. Zones V and VI therefore create sediments liable to become « mother-rocks » for hydrocarbons.

2. Production of soft bottom Pelecypoda. Example of the Etang du Prévost

The evaluation of benthic macrofauna production could only be approached with respect to pelecypods which have been the subject of a particular study in the Etang du Prévost (Guelorget and Michel, 1976; Guelorget *et al.*, 1982).

This restriction to one zoological group is due to the impossibility of assessing the production of all the benthic species present in a lagoon, even though there are fewer species present than in the marine domain. It is impossible, with a reasonably workable sampling system, to collect enough individuals of each species to be able to access their production. A great number of pelecypods, which are largely dominant in the Near paralic, appear in every sample of sediment and they offer reliable, easily measurable biometrical criteria, which is not the case for other groups, especially Polychaeta. It should also be remembered that pelecypod populations integrate the various factors of the ecosystem on a more or less long-term basis, owing to their relative immobility dependent on their connection with the bottom; they achieve this much better than the more mobile Polychaeta and Crustaceans.

The study of the production curves (Table III) is based on the study of five species which alone constitute almost the whole of the benthic macrofauna (*Venerupis decussata*, *Scrobicularia plana*, *Abra ovata*, *Venerupis aurea*, *Cerastoderma glau-*

cum) (Guelorget *et al.*, 1980; Guelorget and Mayere, 1981 a and b, 1983 a and b).

The samples of sediment, taken monthly with a suction pump over an area of 0.5 m², are sifted through a 1mm grid. The measurements of the pelecypods (maximum antero-posterior diameter) are taken with callipers to the nearest millimetre. The biomass is measured in dry weight after decalcification. Production is expressed in g/m²/year (Table III).

Within the malacological fauna, three groups of species can be distinguished :

— « Thalassic » species only found in the sea and in the vicinity of the grau which, because of their density and their biomass, represent only a minor fraction of the total macrofauna. They are not taken into consideration in the present study.

— « Paralic » species (*Abra ovata* and *Cerastoderma glaucum*) whose distribution follows the general rule of the increase in density and the decrease in the size in conjunction with the rising gradient of confinement.

— « Mixed » species (*Venerupis aurea*, *V. decussata*, *Scrobicularia plana*) present both in the marine ecosystem and in the lagunar ecosystem. Here can be noted a decrease in density and size as the confinement increases, but they have a high or very high biomass, considering the size of the individuals.

After having compared the result obtained by various methods, preference was given to the Bojzen-Jensen method (1919) adapted by Masse (1968) to short time-intervals (a month). This simple method allows the comparison of different ecosystems and takes migratory phenomena into consideration.

The profiles of annual production show the extent of the exchange zone of the mouth from where the total production descends from 890 g/m²/year down to 75 g/m²/year within only 200 m (Station 15). Moving away from this zone, annual output stabilizes or decreases more slowly, for the paralic species begin to take over from the mixed species. Finally, towards the lagunar confines (Station 11), whereas the production of mixed species is practically nil, that of paralic species increases distinctly, but here the pronounced « dwarfism » of the individuals reduces the effect of the increase in density, and the yearly production remains moderate (40 g/m²).

This general pattern is valid when considering the seasonal variations in output : particularly the vivified zone of the mouth remains the main producer all year-round. Winter and spring correspond to the maximum outputs (respectively 60 and 54 g/m²/year on average), for both the mixed species in the vivified zone and the paralic species in the lagunar confines. Production decreases considerably in summer and autumn (respectively 19

and 13 g/m²/year on average) because of the dystrophic crises (« malaigues ») which affect mainly the paralic populations which are less soil-dwelling than the mixed species. In autumn, production is minimal, for it is the period of juvenile recruitment for all the pelecypod species, which yield only very little organic matter despite their high density.

The total annual output of the Etang du Prévost represents 171 000 kg of decalcified dry organic matter, which corresponds to a « marketable » quantity of around 1 700 t.

Further, the cartography of the annual overall production shows the economic advantages of the medium confinement zones (Zones II and III, Guelorget *et al.*, 1982). Here, the malacological communities consist mainly of young individuals undergoing a phase of exponential weight increase, explained no doubt by the local concentration of larvae and the flow of nutriment originating in both the marine domain and the lagoon itself (Fig. 15).

Thus, the paralic domain shows capacities of production which are considerably superior to those of the marine ecosystem. Another fundamental characteristic is the small number of species constituting this production, which is moreover limited to a specific zone in the confinement area (moderate confinement zone where mixed species flourish).

H. Qualitative and quantitative biological zoning of the paralic macrobenthos on hard substrate

The study of the soft-bottom benthic settlement of several Mediterranean lagunar systems gave an insight into the biological organization of the paralic domain. Is the qualitative and quantitative biological zoning, established according to confinement and which applies to other biological compartments such as phytoplankton and ichthyofauna, also valid for benthic communities on hard substrate ? The question is all the more important as hard substrates are rare or absent in the natural paralic ecosystems – especially in the lagunar ecosystems – and most of the lagoon-bred species are fixed species of considerable economic importance (oysters, mussels). Because of this lack of hard substrates in the paralic ecosystems, the authors followed the establishment and the qualitative and quantitative evolution of the benthic communities on bare artificial surfaces, immersed in the lagoons of Diana and Urbino, and the Etang du Prévost : a general organization system of the fixed communities appears both with regard to the specific composition and to the characteristic values of macrobenthofauna.

1. Biological Zoning

This is an exact parallel with the zoning calculated for the benthic populations of the sediment.

Zone I includes most of the thalassic species of the infracoastal communities of the Mediterranean rocky coastlines (Peres and Picard, 1964).

In **Zone II**, the taxonomic diversity is considerably reduced and comprises only just over fifty thalassic and mixed species. Among these, the more commonly found are: *Hydroides elegans*, *Serpula vermicularis*, *Bowerbankia imbricata*, *Bugula stolonifera*, *Anomia ephippium*, *Modiolus barbatus*, *Botryllus schlosseri*. The plant communities are dominated by *Bangia fuscopurpurea*, *Ceramium rubrum*, *Padina pavona*, *Cystoseira* (various species), *Acetabularia mediterranea*, *Codium vermilara*, *Halimeda tuna*. In the vicinity of the boundary between zones II and III reef structures with *Neogoniolithon notarisii* may appear (Denizot *et al.*, 1981).

In **zone III**, mainly the mixed suspension-feeding species develop: *Mytilus galloprovincialis*, *Ostrea edulis*, *Avicula hirudo*, *Pinctada radiata* (Bahiret el Bou Grara), *Ciona intestinalis*, *Styella plicata*, *Phalusia mamillata*, *Bugula neritina*, *Membranipora membranacea*, *Balanus eburneus*, represent most of the fixed fauna. In the flora, various species of *Enteromorpha* and *Ulva lactuca* appear.

Zones IV and V are characterized by a small number of paralic species, and the community is dominated by the Cirripedia *Balanus amphitrite amphitrite* (associated with *B. eburneus*), the pelecypod *Brachydontes marioni* and the Polychaeta *Mercierella enigmatica* (Vuillemin, 1965), which is liable to produce reef-type structures, as for example in the northern lagoon of Tunis. The flora is almost exclusively composed of Chlorophyceae *Enteromorpha gr intestinalis* and *Ulva lactuca* locally associated with *Gracilaria verrucosa*.

All fixed macrofauna disappears in **zone VI** to give way to a cyanobacterial covering (*Lyngbya confervoides*, *Callotrix eruginea*, *C. scopulorum*, *Anabaena sp.*, *Oscillatoria nigro-viridis*).

2. Biological gradients

These were analysed from data collected in the Etang du Prévost (Fig. 17) and were confirmed by studies on other Mediterranean lagoons, the Venice lagoon (Barbaro and Francescon, 1976; Francescon and Barbaro, 1976) and lagoons of eastern Corsica.

From the communicating link with the sea towards the confines of the lagoon, these can be observed:

- a significant decrease in number of species
- a considerable increase in density

a decrease in biomass, despite the increase of density, with regard to the small size of the individuals (lagunar dwarfism).

This pattern, identical to that of soft-bottom communities remains the same whatever time the colonization of the immersed areas takes. However, it is obvious that both biomass and density increase with time at a given point.

As with the soft-bottom communities, the paucity of species, counter-balanced by a high density, generates an incomparably greater biomass than in the marine domain, especially in zone III where mixed species thrive. In this zone, after a year's immersion, at the Etang du Prévost can be collected a biomass of 11 000 g/m² (in dry weight after decalcification), 96 % of which consists of *Mytilus galloprovincialis*.

This shows how well-founded the empirical methods are, based on an ancestral knowledge of the environment. They allowed the development of conchyliculture in the paralic domain, whereas random trials, often carried out for political reasons without any previous knowledge of the host ecosystem, have never led to profitable production because they were situated in zones of inadequate confinement. The economic interest of the zoning of the paralic ecosystems can be understood in terms of confinement, since it allows the definition of optimal zones of conchylicultural – or even aquacultural – activity. It is even possible to envisage, through development work on the passes, the modification of a given basin with regard to the confinement scale.

I. Conclusions regarding the confinement parameter

Because confinement appeared to be the fundamental parameter of the organization of the paralic domain, the authors thought it necessary to propose an explanation and define its main levels. On the basis of the qualitative biological zoning of the benthic macrofauna, they have established a scale of confinement on which are expressed the various qualitative and quantitative parameters which describe the biological organization.

The arrangement proposed for the dynamics and the biological structure of the ecosystems of the Mediterranean paralic domain appears to apply to each of them, taking into consideration its morphological and hydrological particularities. Thus the different zones defined can vary as to their surface area and localization, but in all cases the zoning is respected.

The study of other biotic (meiofauna, microfauna) and abiotic parameters will permit to re-

fine, and indeed perhaps enlarge towards the Far paralic, the zoning which has been established for the Near paralic Mediterranean domain.

However, the knowledge of extra-Mediterranean paralic systems such as the Caribbean mangrove swamps (Belle Plaine and Manche à Eau; Guelorget *et al.*, 1990), the Red Sea lagoons (Guemsah; Ibrahim *et al.*, 1982, 1985) and the Persian Gulf lagoons (Khour el Aadid lagoon; Perthuisot and Jauzein, 1978), and bibliographical data confirm the general nature of the proposed model.

IV - HYPOTHESES CONCERNING THE INFLUENCE OF CONFINEMENT ON PARALIC COMMUNITIES

A. Confinement in time, stabilization of the gradient, the role of depth

There are at present certain basins having poor communication with the sea but which do not have the special biological characteristics for high confinement: this is the case of the Gulf of Amvrakikos in Greece. In this respect, it can be noted that the volume of water it contains (8 km^3) is high with regard to its surface area (460 km^2). Moreover, it is of recent formation, since the Amvrakikos depression has been flooded by sea for a relatively short time, 8.000-10.000 years at the most. It can therefore be assumed that the initial stock of marine water has not yet had time to become sufficiently impoverished, bearing in mind its communication with the open sea. The rarefaction of certain species (according to local fishermen) and the dwarfish of species such as *Parocentrotus lividus* is however perhaps the indication of the beginning of confinement.

Other examples are even more striking. The Caspian « Sea » (77.000 km^3 and 436.000 km^2) has been cut off from the marine domain since the end of the Tertiary, i. e., for several million years. However, it still contains 60 % of thalassoid forms (Zenkevitch, 1957), and therefore has not yet shifted into the continental domain (apparently most of the basin is situated in zones III and IV as defined above), in spite of the great time-lapse since it was cut off from the sea. Moreover, the maps of biomass distribution established by Zenkevitch from 1935 onwards show that the upper layer of the deep southern basins is less confined than the shallow northern basin.

Therefore, the depth parameter plays an important part in the speed of confinement of a basin in the process of being cut off from the sea; it may also be deduced that the deeper a paralic

basin is, the slower its biological response to a diminishing exchange with the sea will be.

It was suggested earlier that confinement influences the communities through an impoverishment of the ecosystem in certain « vital » elements of marine origin – or, at least, coming essentially from the sea – consumed and immobilized by the living beings themselves, whose activity (with regard to the solar energy available) is at most proportional to the surface area of each basin, whereas the initial reserves of « vital » elements are proportional to the volume of the basin. Thus, in extremely shallow paralic basins, the confinement gradient very quickly reaches its state of equilibrium. In deep basins, on the contrary, the impoverishment of the medium and the stabilization of the confinement gradient are much slower and, if ever they become completely cut off from the sea, a considerable lapse of time is needed for their total « continentalization » to occur.

B. Intracontinental « paralic » basins

Mention has already been made of the Caspian which today is an intracontinental basin but which, once was in communication with the sea.

This is not the case with some smaller basins –fossil or present-day– of North Africa and the Sahara, which contain or have contained in a recent past, typically paralic flora and fauna: for example, the chotts of pre-Saharan Tunisia (Coque, 1962; Levy, 1982) the Pleistocene lake of Shati, in Libya (Petit-Maire *et al.*, 1982), Birkat Karun in Egypt, which is the outlet of a branch of the Nile and where a typically paralic fauna thrives 300 km away from the sea (*Cerastoderma glaucum*, *Bittium reticularium*, *Brachydontes marioni*) (Perthuisot *et al.*, 1990).

Finally, there is the Sebkhia Mellala near Ouar-gla, in Algeria, where Boye *et al.*, (1978) described associations of *Cardium*, *Melania*, *Hydrobia*, *Melanopsis*, with Foraminifera (*Ammonia*, Nubeculariidae, Discorbidae) and oogonia of Characea, in sediments dated between 8.000 and 10.000 years ago.

These were paralic communities which could imply:

— on the one hand, that the continental waters which fed the endoreic basin were re-creating a biochemistry close to that of the paralic domain.

— on the other hand, that the ecosystem had been inseminated by paralic species, and therefore that there was a relationship with the sea, via the usual paralic domain.

This second phenomenon is easily explained: perhaps air-borne transportation by paralic birds or by waterspouts, etc.

The first opens up strange horizons, and it is possible to imagine the fortuitous existence of endoreic basins whose catchment area is such as to allow the creation of biochemical conditions compatible with the development of thalassic species.

C. Importance of trace elements in the biological expression of confinement

In the preceding sections, it has already been suggested that confinement should correspond to an impoverishment of the ecosystem in « vital elements » coming essentially from the sea, and consumed or trapped by the living beings themselves. Among these elements are vitamins and trace elements which include the heavy metals.

In the marine domain, numerous studies have shown that indeed a great many of these elements are « limiting » as far as their concentrations and above all their « bio-availability » are concerned. Obviously, the critical values vary according to the species (Provasoli, 1963; Belser, 1963). Moreover, it is likely that these « vital elements » include inconspicuous compounds as yet unknown.

Considering only the heavy metals, many studies have shown the accumulation of certain of these in the tissues of benthic animals and, consequently, *pro parte* in the sediments. In this respect, molluscs, especially Lamellibranchia and Gastropoda, and also Polychaeta, seem particularly efficient.

Thus, the zones of the paralic domain where molluscs predominate (zones II, III, IV) constitute a trap for heavy metals, and a screen for the populations of the more confined zones. It is possible to consider that in these zones, it is the species whose requirements in heavy metals are lower, or species which cannot tolerate them in very high concentrations which develop. For example, according to a study on the *Nereis diversicolor* of the Humber estuary (Jones *et al.*, 1976) it seems that these polychaeta lose their osmoregulatory capacity when the medium is too rich in Cu. This seems to be true for other paralic species, particularly crustaceans.

D. Conclusions regarding the influence of confinement

It can be supposed that if confinement indeed corresponds to an impoverishment of the waters in « vital elements » its influence is two-fold :

— it sets limits to the extension of species for which there is a minimal threshold, for one or several elements

— it contributes to the development of species for which there is maximal threshold beyond which one or several elements would act as poisons.

In detail, the situation is likely to be more complex and, there may be an interaction (synergy) between several inconspicuous chemical variables of the medium. However, schematically, the first type of action could apply to mixed species, and the second to strictly paralic species.

Thus, the biological zoning of the paralic ecosystems would be controlled by all the biohydrochemical gradients of the « vital elements », each playing a positive, neutral or negative part, according to the species.

In this discussion, the following comments extracted from a study by Amanieu *et al.* (1978) should be considered :

« From a historical point of view, the « i » ecosystems are presumed to have preceded the « s » ecosystems, in order of evolution. From a geographical point of view, the « i » strategies are presumed to have been preserved in those regions of the globe where the factors of the milieu show great fluctuations, whereas the « s » strategies are presumed to have developed in the sites with a stable environment. » The i-type cenotic strategies (Blandin *et al.*, 1976) concern ecosystems which are poor in species but rich in individuals (typical case of paralic communities). The s-type strategies concern ecosystems with high diversity and rich in species (thalassic communities).

« We were discussing... the reputation of the lagunar ecosystems of being fragile, juvenile and highly productive. Here we have not broached the subject of productivity which is indeed very high; but then, we have stated why the term juvenile seemed to us inadequate. Lastly, as far as « fragility » is concerned, we consider that it cannot be disassociated from the stability which we have discussed. Indeed, the coastal lagoons are fragile and vulnerable, both to natural disturbances and to the inconsiderate behaviour of man. But, on what time scale and to what extent ? Even since Strabon and Pliny has it not been common knowledge that the « malaigues » ruin our lagoons and that excessive fishing depletes them ? Thus, for over two thousand years, our fragile lagoons have been in the process of dying. Yet how many « stable » peaks have for ever disappeared in the meantime ? All through the cyclic vicissitudes from malaigues to « martegades » (winter freezing-over), through years good and bad, it may be that these everlasting swings of pendulum, these

steps forward hesitating between the worst which never happens and an ever-hoped-for improvement, are not accidents of the ecosystems, an ecosystem into which nearly 100 generations of local fishermen have been integrated, but its very nature. It is true that « *Homo economicus* » now has the means, with sea-front developments, motorways, stabilized shores and « lagooning », to stabilize and « valorize » once and for all these great coastal ponds which will soon survive only as a memory. »

Amanieu *et al.*, 1978

V. THE SCIENTIFIC IMPORTANCE OF THE PARALIC DOMAIN

If the paralic domain is seen as an autonomous entity, in terms of the Earth and its history, it takes on a dimension other than that of a mere contact (or exchange) zone between the land and the sea.

A. From a biological and paleontological point of view

The sediment associated with the first traces of life on Earth (« *Sensu lato* » stromatoliths) along with various considerations (concentration of nutritive elements, indications of shallow or intermittent water levels) imply that it was truly in a paralic environment that life first appeared on our planet, about 4 000 million years ago (Cloud, 1968). In this respect, it is indeed the paralic rather than the marine domain which appears as the original one (Fig. 16).

The paralic domain is an obligatory transit channel for anadromous and catadromous species. Moreover, because of its high productivity, it represents a place of growth for many species which breed at sea, and is probably indispensable for the completion of the reproductive cycles of many marine species.

A remarkable property of strictly paralic stocks is their slow almost non-existent evolution. This is the case of the « lagunar » molluscs whose shape has hardly changed since the Tertiary, or certain Foraminifera, which have remained identical since the Cretaceous (*Ammonia tepida*). *Lingula* are an example of a paralic « panchronic » form. By comparison, the rapid evolution of marine or continental stocks is clearly revealed by stratigraphy (cephalopods, echinoderms, branchiopods, mammals, etc.). There is an obvious reason for the stability of paralic stocks : the species are adapted to a certain physical and chemical variability of the environment and, if confinement is the essential parameter of the distribution of the species, there is always a zone in the paralic

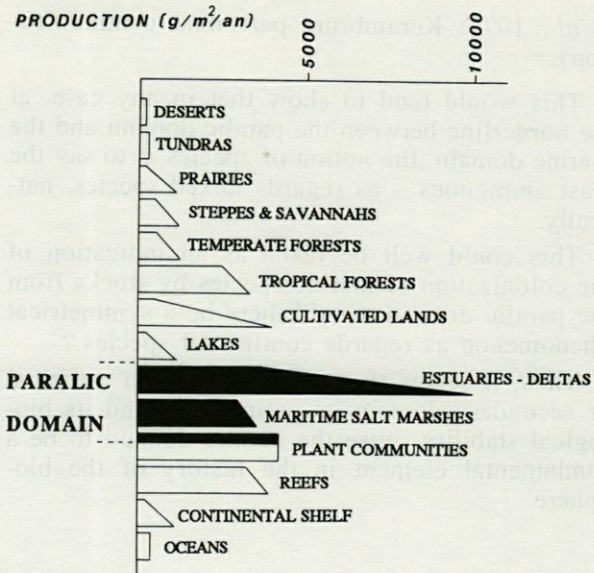


Fig. 18. – Comparative production of some terrestrial and aquatic systems (adapted from Basson *et al.*, 1977 and Allen *et al.*, 1979).

domain where an adequate degree of confinement allows them to survive. Thus, the physical or chemical variations of the environment exercise only a low or indeed non-existent « selective pressure » on the paralic stocks, and the genetic shift is extremely weak. Conversely, in the marine or continental aquatic domains, the stability of the abiotic parameters of the environment is greater and their variations slower : there, the species are much more specialized and unable to adapt to sudden changes should they occur : these stocks are therefore condemned to evolve or disappear in case of « crisis » in the domain (variation of the salinity, temperature, currentology, etc.).

One may even wonder whether the paralic domain does not constitute some sort of potential reservoir for stocks capable of replacing the marine or continental stocks in case of a crisis leading to the disappearance of the latter.

The problem arises of the species that are hitherto referred to as « mixed » i. e., species which colonize both the marine and the paralic domain, in spite of the obvious differences in the biological dynamics of these domains. It should be noted that many mixed « species » have an ambiguous taxonomic status, with duplications of specific nomenclature or an adventitious nomenclature (a variety of the form referred to, or « endemic »).

Moreover, recent research in population genetics (electrophoretic spectral analyses of the inner system) detects notable differences within a same mixed species, between the marine and the paralic populations (Worms and Pasteur, 1982; Buroker

et al., 1979; Kerambrun, personal communication).

This would tend to show that in any case, at the borderline between the paralic domain and the marine domain, the notion of species is to say the least ambiguous – as regards mixed species, naturally.

This could well be taken as an indication of the colonization of marine species by stocks from the paralic domain. Could there be a symmetrical phenomenon as regards continental species ?

Thus, it seems that far from being a marginal or secondary domain its permanence and its biological stability cause the paralic domain to be a fundamental element in the history of the biosphere.

B. From a geological point of view

The various types of sedimentary deposits in the paralic domain have been considered, and also the importance of the biogenic carbonates in the Near paralic, that of the evaporites and of the « deltaic » structures in the Far paralic. The main characteristics of these deposits is their high speed of sedimentation (the highest in present-day natural conditions) by comparison with the oceanic domain where the rate of sedimentation is minimal, and with the continent where erosion predominates. The paralic ecosystems make a leading contribution to the accumulation of sediments on the continental shelves.

The importance of the sedimentation of organic matter should also be remembered. The high intrinsic productivity. (Fig. 19) of the paralic domain is combined with its ability to conserve organic matter, owing to the prevalence of reduc-

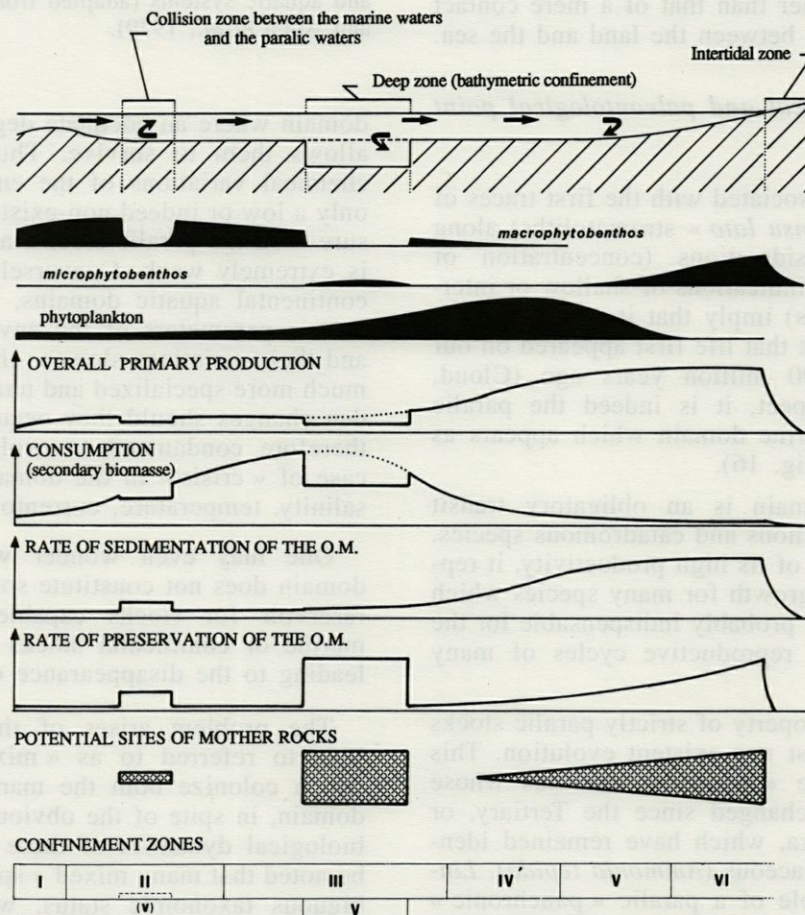


Fig. 19. – The potentialities of the Near paralic in the genesis of hydrocarbons in relation to confinement. In parallel, with an idealized section of a paralic basin, a diagrammatic representation of the various values which control the accumulation of potential mother rocks.

It is noticed that, with regard to an increasing confinement, there are relay points between the various links in the chain of the primary production. Moreover, the organic matter, a consequence of the biological activity of all the consumers (dead bodies, various secretions, faeces), contributes to the organic sedimentation : it has been shown that the recent development of intensive aquacultural activities speeds up the enrichment of paralic sediments in organic matter.

ing zones, hyperhaline or otherwise. Here the shift in the curves of the benthic biomass and the phytoplanktonic biomass with regard to an increasing confinement (Fig. 9) should be remembered. It implies that, in high confinement zones (IV and V), the primary production shows a large surplus with regard to consumption: this surplus of organic matter will be deposited and form *in fine* a mother rock, if the conditions of conservation of that organic matter during the diagenesis are favorable. The coincidence of the frequent proximity of mother rocks, detrital or carbonated deposits (possibly dolomized under the influence of magnesian brines) liable to constitute reservoirs, and muddy or evaporitic sediments able to produce excellent covering, explain the presence of a great number of hydrocarbon deposits in the paralic series. Coal seams, for a large part, also belong to the paralic domain (Barrabe and Feys, 1965). However, whereas with petroleum and natural gas the organic matter is essentially autochthonous, the continent makes a large contribution in the case of coal.

The observation of present-day nature offers only an incomplete idea of the geological importance of the paralic domain (Perthuisot, 1980). The Baltic is one of the largest paralic basins in the world today, with a surface area of 420 000 km², and a length of 1 500 km. The study of the sedimentary series of the great platforms of the past shows that at certain periods in time, particularly outside the « orogenic phases », the paralic ecosystem could spread considerably, over a region several thousands of kilometres wide (Busson, 1972).

These few considerations show the fundamental role, too often ill-known, played by the paralic domain in the geological and biological history of our planet.

VI. THE ECONOMIC IMPORTANCE OF THE PARALIC DOMAIN

A. Mineral production

The paralic domain supplies fossil energy resources, coal and oil and the fossil or present-day evaporitic areas abundantly supply minerals and elements indispensable for human activities:

— halite (NaCl) comes almost exclusively from the paralic domain; world production was 143 million t in 1971.

— gypsum (CaSO₄, 2H₂O) is mainly used for making plaster but is also a constituent of cements.

— potassium salts, sylvite (KCl) and carnallite (KMgCl₃, 6H₂O), essential constituents of fertilizers (world production in 1971: 17 million t.).

— elements extracted from connate brines or from the mother-waters of salt marshes (Mg, Br, K, etc.)

There seem to be genetic connections (which are incidentally variable) between the confined environments and certain metal-bearing deposits, particularly of lead, zinc, copper, magnesium (Routhier, 1980; Lagny, 1980; Quemeneur, 1974)). As seen before, the processes of biological concentration of some of these elements are probably closely related to the notion of confinement.

B. Food production

The rich biological resources and the high productivity of paralic ecosystems explain their having been exploited since antiquity and probably even since long-distance prehistoric times.

1. Gathering of « Sea Food »

This is, of course, the first form of exploitation, and can be intensive, for —unlike the very fragile marine ecosystems which can be seriously perturbed by over-harvesting (even to the extent of a possible disappearance of certain species) and furthermore highly sensitive to « pollution »— the paralic domain, because of its biological stability and high productivity, appears to be practically inexhaustible; for example, the conchylicultural yield of the lagoons of Diana, Thau and Urbino is around 15t./ha/year of marketable products.

2. Halieutic (fish) Production

Amanieu and Lasserre (1981) demonstrated the production levels of the Mediterranean coastal lagoons and their contribution to the enrichment of demersal fishing. The lagoon fishing-groups represent an 8-10% contribution to the entire Mediterranean catch (the Black Sea excluded). The overall production of Mediterranean fishing is relatively well known, around 1 200 000 t/year (Statistical Bulletin, GFCM, n° 3, 1980). According to Levi and Troadec's figures (1974), the exploitation of the totality of the lagoons represents a third of the demersal fishing in the Mediterranean. It must also be emphasized that lagoons represent feeding nurseries for young fish during their first years of life; later these same fish will be found in the marine fishing-grounds.

a. Levels of halieutic production in the Mediterranean lagunar sites

After analysis of data collected from 46 peri-Mediterranean lagunar sites, Amanieu and

Lasserre (1981) demonstrate « the extreme disparity of the outputs which vary from 6 kg/ha/year (Nador lagoon, Morocco), to 149 kg/ha/year (Venice lagoon, Italy) or even 172 Kg/ha/year (the Ebro estuary, Spain); therefore, an average figure would be meaningless. On the contrary, it would be useful to have a better knowledge of the Mediterranean lagoons' production potentialities. A preliminary estimate would be different from the above, the variations noted at present being largely due to the conditions of exploitation. If the true potentiality is equal to the highest yield of the Spanish or Italian lagoons, i. e., around 150 Kg/ha/year and by extrapolating to the 883.720 ha of available lagoons around the Mediterranean, a potential annual production is obtained of 125.000 t, more than twice the present yield. However, such an estimate remains speculative and artificial.

b. Contribution of the lagunar sites for the enrichment of demersal fishing

According to Amanieu and Lasserre (1981): « The lagunar sites are very irregularly distributed along the coast of the Mediterranean. The level of inshore captures also varies considerably and, so it seems, in relation to the proximity of lagoons likely to contribute to trophic supplies, or indeed recruitment. Thus, the lagunar ecosystems of the Adriatic and the Gulf of Lion, which cover around 280.000 ha, i. e., nearly 34 % of the totality of the mediterranean lagoons, are themselves among the most prolific sites (between 80 and 150 Kg/ha/year). They furthermore run parallel with the coastline where the production of demersal fishing grounds is particularly high, about 35-50 t/km of coast. On the contrary, such regions as the French Riviera, the south of the Peloponnese in Greece, or the Libyan coast, are characterized both by a low rate of productivity (between 0 and 5 t/Km of coast) and by the absence of coastal lagoons. Such an estimate can only remain rough insofar as it does not take sufficiently into account the surface areas of the fishing grounds, which depend on the local width of the continental shelf ».

Thus, compared with the sea coast, the lagoons contribute largely to the increase of the halieutic demersal potential: the zones of high demersal production correspond to the zones where the lagoons are large and productive. The paralic domain appears here again as a highly productive ecosystem which exports a good deal of its excess energy towards the sea.

3. Aquaculture

As confinement contributes to the reduction of species and simultaneously the increase in their density, it is clear that the paralic environments are propitious for mono- or pauci-specific culture,

provided that the species chosen are adequate: it is from this point of view that aquaculture has developed, first empirically, and now more rationally. Today, most aquaculture takes places in paralic ecosystems.

C. Future prospects

1. Biomass

The considerable productivity of the paralic domain can no doubt be used for the creation of energy if, for instance, the production of organic matter by phytoplankton or by the microbial mats of Cyanobacteria, or again the amazing rate of growth of certain algae such as the *Ulva* and the *Enteromorpha* are considered.

A reasonably long-term exploitation of such a potential resources can therefore be envisaged.

2. A strategy for the development of the Paralic Domain

Given that the hypotheses concerning the paralic domain and its dynamics continue to be proved correct through observed facts, an overall strategy for the development of these ecosystems is proposed.

First, the place of each basin on the confinement scale and the shape of the various confinement zones it includes determine its biological potentialities (species likely to develop, productivity rate, location of the beds, etc.). The ecological characterization in terms of confinement of these stretches of water (Guelorget *et al.*, 1983) is then an essential phase of their development, without modifying the initial natural environment (Guelorget and Perthuisot, 1984; Guelorget *et al.*, 1983).

However, if, in the marine or continental domain, man has only limited means of action over the fundamental parameters of the environment, the situation is different in the paralic domain, since it is possible, often quite cheaply, to influence the confinement. This is exactly what salt-producers do in the salt marshes, when they adjust the inflow of seawater and the displacement speed of the brines, according to meteorological variations and, with a specific aim, the production of salt.

It is therefore possible to envisage, for each paralic basin, the regulation of the confinement, and possibly its gradient values, to the quantitative and qualitative requirements of a coherent economic policy. Thus, the present effort to develop the coast must necessarily be accompanied by the study of the paralic environments.

CONCLUSION

The existence of a fully fledged ecological domain has been confirmed, this term being understood in the widest and most multidisciplinary sense, which has its own dynamics: the paralic domain.

Its principal originality lies in its obvious geographical dispersion at the present time and in the spacial and temporal variability of its abiotic parameters. Paradoxically but logically, these two fundamental characteristics lead to both a deep biological unity and biological stability.

The geographical dispersion of the paralic domain is only apparent, since every coast, even that most open to the sea, has its more or less extensive paralic fringe, if only because there is always an intertidal fringe (Perthuisot, Guelorget and Calvario 1986; Ponthoreau-Granet, 1987). Moreover, there are many transfer agents between the different basins, the sea itself, the living beings it contains, sea birds, etc.

The variability of the abiotic parameters results incomparably greater hydrochemical gradients than those found in the other domains of the hydrobiosphere, even if one considers endoreic basins, which are often highly homogeneous at a given moment of the seasonal cycle.

The biological unity of the paralic domain appears in a qualitative and quantitative zoning common to the entire sub-domain close to the marine domain (the Near paralic). This zonal organization, which affects the species (mainly thalassoid) depends on the confinement (relative to the sea), an inconspicuous but obligatory parameter in any paralic system. Beyond this, in the Far paralic, the communities very rapidly become richer in freshwater species, or in species characteristic of the evaporitic ecosystems: confinement becomes too great and appears therefore to lose its leading biological role. However, perhaps later studies may prove the contrary.

In order to be able to compare the spatial and temporal variations of the different biotic and abiotic parameters which, in each basin of the Near paralic or within the sub-domain as a whole, describe the confinement field (and gradient), is a scale proposed based on the communities of benthic invertebra which best assimilate the minor fluctuation of the environment. The other links of the trophic chain, along with the quantitative variations of the different biological parameters (number of species, biomass, density, production, productivity), can satisfactorily and logically be incorporated in this scale.

The exact way in which confinement affects the distribution of the paralic living beings still remains unclear, but various reasons allow the sup-

position that confinement results in an impoverishment of the ecosystem in « vital » elements of essentially marine origin, trace elements, small organic components (vitamins, alkaloids, etc.), around which the communities are organized.

These different considerations lead to a qualification of the paralic domain as a biological cross-roads between the marine and continental domains (evaporitic and freshwater), to abandon the marginal status it was hitherto conceded, and on the contrary to grant it a key position in the history of the biosphere. The paralic domain is moreover a preferential place for the accumulation of biogenic sediments (deltaic series, evaporites) and organic matter on the surface of the Earth, and, in this respect, plays a fundamental part in the history of the lithosphere.

To conclude, the various original characteristic features of the paralic domain – both biological and geological – open up considerable economic possibilities, incomparably superior to those of the Oceans, both in the present and in the fossil realms. In this respect, the study of confinement and its various mineral and biological expressions appears as an effective, reliable, and inexpensive instrument for the development and the survival of the paralic domain.

One of the most remarkable features of confinement is that it can be applied to all the spatial scales (Perthuisot, 1989). Compare, for example, the tiny Bermuda Triangle passing from zone III into zone IV in the space of a few hundred metres with the great Baltic Sea, where zones III to V stretch over more than 1 500 km. This is because, in every paralic basin, confinement depends on the effectiveness of the communication with the sea and of the currents within the basin with regard to its size and volume. Thus, the large paralic basins are similar – in the geometrical sense of the word – to the smaller ones, as far as their biological zoning is concerned. In this respect, it should be remembered that the intertidal zoning on rocky surfaces is simply the transposition over several metres – or indeed centimetres – of sub-vertical wall, of the horizontal zoning of the lagunar ecosystems which can stretch over several kilometres.

Apart from the biological zoning, confinement controls the hydrochemical zoning (for a given freshwater balance), and one notes the similarity of the large paralic basins of the past and the smaller basins of today: for example, the Vosgian sandstones and the Rhone Delta, the Silurian formation of Salina, Michigan and the Sebkh el Melah, the evaporitic Trias of the Saharan shelf and the salt marsh of Salin-de-Giraud.

All this, in spite of the space/time scale differences separating the knowledge of the Earth's past which man is trying to acquire from the present-

day knowledge of nature, justifies the study of the present to better understand past.

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