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Mediterranean Lagoons and Estuaries

Coastal areas provide the majority of the biosphere's current economic wealth. They account for 38% of the value of all services rendered by its ecosystems, representing over 12,600 billion dollars per year out of a total value of services rendered by natural ecosystems of 33,300 billion dollars per year (Costanza *et al.*, 1997). Among the coastal ecosystems, the paralic domain only covers just over 6% of the globe's surface, but produces 26% of the biosphere's total food resources, representing around 366 billion dollars a year (Figure 1.1).

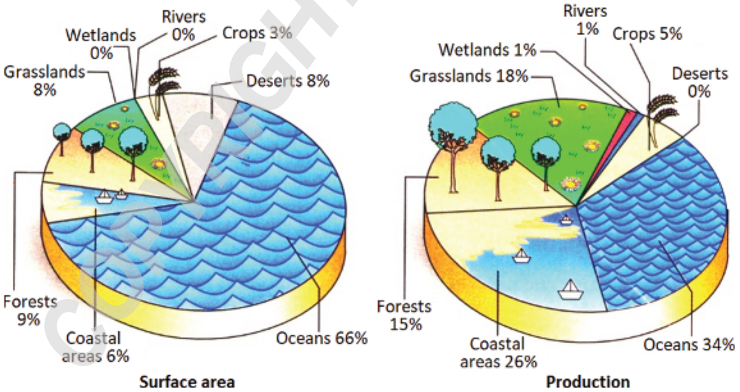

Figure 1.1. *Surface area and production of the Earth's various ecosystems (Guelorget* et al.*,1998). For a color version of this figure, see www.iste.co.uk/kara/fishes1.zip*

Guelorget and Perthuisot (1983, 1984, 1992) define the paralic domain as "permanent or temporary bodies of water that are closely or less closely (and/or intermittently) connected to the sea". In the Mediterranean, these water bodies, known as "transitional", are classified from a hydrogeological point of view into three physiographic types: river mouths (estuaries and deltas), lagoons and salt marshes. They are defined by Kjerfve (1986) as follows: "shallow aquatic environments, located in the transitional zone between terrestrial and marine ecosystems (marginal shoreline aquatic systems), which span from freshwater to hypersaline".

1.1. What is a lagoon and what is an estuary?

Lagoons and estuaries account for around 13% of the world's shoreline (Lasserre, 1979). These two features occur at all latitudes (Kiener, 1978); more abundantly in some coastal regions than others (Table 1.1). On the land–sea border, they are characterized by steep physicochemical gradients, very variable ionic relationships (Kiener, 1978) and environmental fluctuations that necessitate physiological and ecological adaptations on the part of the species that live there. These environmental gradients are fundamental in the processes of shaping species composition (Sanders, 1992). Their common characteristics mean that they share, within a given biogeographic sector, the same basic species, and that we can talk about "lagoon/estuarine guilds".

Continent	Length (in km) of lagoon shoreline	Lagoon shoreline (%)	Global lagoon coast (%)
North America	10,765	17.6	33.6
Asia	7,126	13.8	22.2
Africa	5,984	17.9	18.7
South America	3,302	12.2	10.3
Europe	2,693	5.3	8.4
Australia	2,168	11.4	6.8
Total	32,038	–	–

Table 1.1. *World distribution of the coastal lagoon barrier (Cromwell, 1971)*

The Mediterranean estuaries and certain lagoons correspond to the definition of transitional water bodies given in the DCE[1], but a number of

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[1] Directive 2000/60/EC of the European Parliament and of the Council of 23 October 2000 establishing a framework for community action in the field of water, Official Journal L327 of December 22, 2000.

lagoons do not correspond exactly with the given description, since they have no freshwater inflow. In fact, according to this definition, “transitional waters are bodies of surface water in the vicinity of river mouths which are partly saline in character as a result of their proximity to coastal waters but which are substantially influenced by freshwater flows”.

According to Pritchard (McLusky, 1999), “an estuary is a semienclosed coastal body of water, which has a free connection with the open sea, and within which sea water is measurably diluted with fresh water derived from land drainage”. According to Fairbridge (McLusky, 1999), an estuary is the part of a fluvial valley that is subject to tidal influences (estuary, from the Latin *aestus*, tide). These definitions are not without controversy. The mouths of Mediterranean rivers are commonly called estuaries, even if the tidal influence is very slight and sometimes non-existent. Traditionally, coastal lagoons have been considered as transitional systems between the continental and marine domains (Bianchi, 1988). Barnes’ definition (1980), according to which “coastal lagoons are areas of salt or brackish water separated from the adjacent sea by a low-lying sand or shingle barrier” do not allow for them to be clearly differentiated from estuaries that can in some cases be briefly cut off from the sea. Tagliapietra *et al.* (2009) seek to clarify the scientific, historical and geographic context of the terms used to define estuaries and lagoons, but conclude that currently no commonly accepted term or common definition exists for the whole of the semienclosed coastal environment and, more importantly, the crucial question – whether they can be considered as one functional ecological group – remains unclarified.

Pérez-Ruzafa *et al.* (2011) produced a summary (Figure 1.2) of different types of water bodies and aquatic assemblages in lagoons based on three main factors: ionic composition (from limnogenic to thalassogenic), saline concentration and confinement. The ionic composition of the water can be a determining and destabilizing factor in cellular osmotic balances, the regulation of which calls for physiological adaptations, requiring significant energy expenditure. Limnogenic waters contain mostly HCO_3^-, Ca^{2+} and SO_4^{2} ions, but with substantial differences in the relative proportion (rapic or rhopic factor) and composition of the ions depending on the origin, then the salt composition of the soils in the catchment area. In contrast, thalassogenic waters have a homogeneous ionic composition and stable ionic relationships, unconnected to saline concentration, and are dominated by Cl^- and Na^+ ions. In coastal lagoons, salinity varies from below 0.5‰ to above 140‰ in ß-hypersaline waters and above 300‰ in δ-hypersaline lagoons, according to Por (1980). Although estuaries have a generally fairly stable saline gradient going from fresh water to brackish water and then saline, lagoons are exposed to a far wider range of situations, inter- and intralagoon, depending on the "fresh water versus seawater" influence and the "precipitation versus evaporation" balance, and also on other factors such as the localization of fresh water and sea water inflows, hydrodynamics, vertical zoning and input of nutritional salts. Thus, in lagoons there is not necessarily a clear unidirectional salinity gradient.

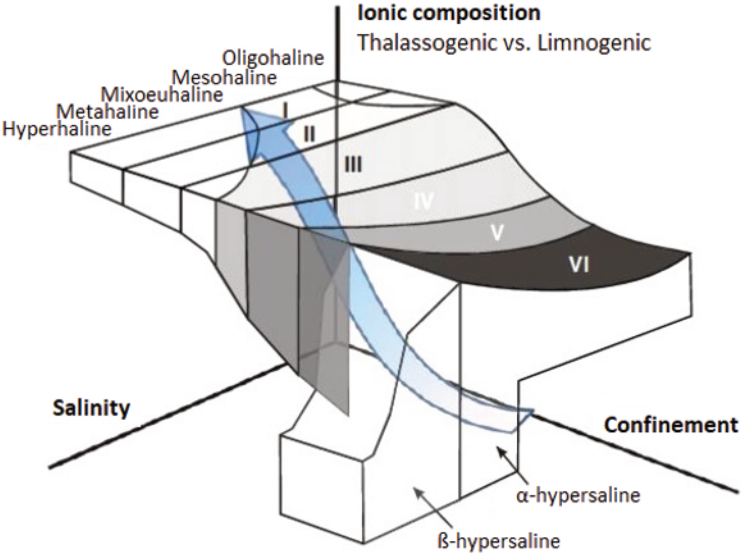


Figure 1.2. *Conceptual model of the different types of water bodies and aquatic assemblages in lagoons (in black) and estuaries (blue arrow) according to three main structural factors (ionic composition, salinity and confinement) (Pérez-Ruzafa* et al.*, 2011). For a color version of this figure, see www.iste.co.uk/kara/fishes1.zip*

"Confinement", defined as being the inverse of the rate of colonization by marine organisms, leaving aside the factors mentioned earlier, and the renewal time for elements of marine origin at a given point in the lagoon, leads to a "sea–continent" horizontal zoning model (Guelorget and Perthuisot, 1983; Frisoni *et al.*, 1983) (Figure 1.3).

It should be noted that Guelorget and Perthuisot's model has been reinterpreted in line with other concepts such as that of "saproby" (the state of an aquatic system resulting from additions, decomposition and renewal of the organic matter and its catabolites) (Tagliapietra and Sigovini, 2012) and in line with the speed, the rate of colonization and the dispersion processes of the organisms (Pérez-Ruzafa and Marco-Diego, 1992). Taken altogether, these factors determine the final complexity of the trophic network or networks and their capacity to develop homeostatic mechanisms in the face of environmental stress and anthropic impacts, such as eutrophication.

Thus, according to Pérez-Ruzafa *et al.* (2011), the specific composition models and the structure of communities (biocenosis) may be the principal characteristics that differentiate estuaries from lagoons.

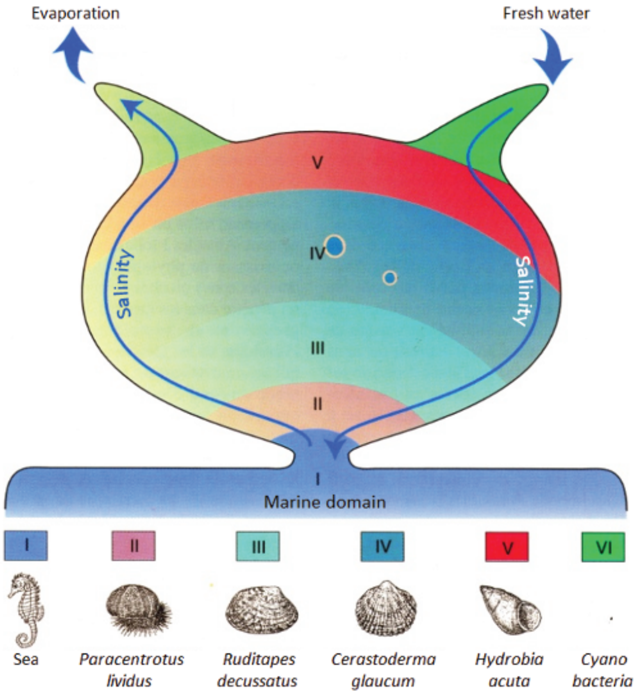
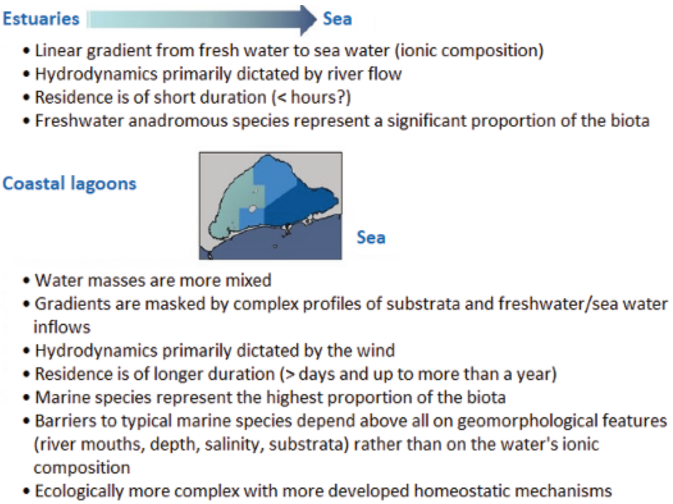


Figure 1.3. *The biological organization of a paralic ecosystem. Between the marine domain (at the bottom of the graphic) and the continental domain (at the top of the graphic), six zones are defined in increasing order of confinement. Each zone includes environments with varying levels of salinity, going from brackish water when inflows of fresh water are significant (darker colors) to saline water when the evaporation rate is high (paler colors). Each zone is identified from its characteristic species, according to biogeographic region – this example relates to the Mediterranean ecosystems (Guelorget* et al.*, 1998). For a color version of this figure, see www.iste.co.uk/kara/fishes1.zip.*

Although estuaries show a longitudinal gradient (one dimension) in species composition, i.e. limnic biocenosis to thalassic biocenosis, the assemblages (biocenosis) of lagoons are the result of complex local interactions that are multidimensional, environmental and biological, and not simply a response to extreme physicochemical conditions or to a single horizontal gradient. Figure 1.4 summarizes the principal differences between structure and functioning of estuaries and lagoons.



- Linear gradient from fresh water to sea water (ionic composition)
- Hydrodynamics primarily dictated by river flow
- Residence is of short duration (< hours?)
- Freshwater anadromous species represent a significant proportion of the biota

- Water masses are more mixed
- Gradients are masked by complex profiles of substrata and freshwater/sea water inflows
- Hydrodynamics primarily dictated by the wind
- Residence is of longer duration (> days and up to more than a year)
- Marine species represent the highest proportion of the biota
- Barriers to typical marine species depend above all on geomorphological features (river mouths, depth, salinity, substrata) rather than on the water's ionic composition
- Ecologically more complex with more developed homeostatic mechanisms

Figure 1.4. *Principal differences between the structure and functioning of estuaries and lagoons (Pérez-Ruzafa* et al.*, 2011). For a color version of this figure, see www.iste.co.uk/kara/fishes1.zip*

Some authors (Albaret, 1994a; Albaret, 1994b) suggest bringing estuaries and lagoons together in a larger category of “estuarine and lagoon environments”, located at the interface of the continental and the marine domains. In some ways, we subscribe to this point of view, in spite of the differences we have just mentioned, to which can be added (Joyeux and Baker Ward, 1998) that estuaries, because they are widely open to the sea, are certainly more important than lagoons for migratory amphidromous fish. In the Mediterranean, there are five major estuaries, which are of the “delta” type: Ebro (Spain), Rhone (France), Medjerda (Tunisia), Po (Italy, Adriatic) and Nile (Egypt).

It should be noted that geomorphology, especially the length and width of the pass (grau, channel), is taken into consideration to distinguish between lagoons and enclosed bays (Lasserre, 1979). Nevertheless, the degree of connection to the sea does not depend solely on geomorphology and the amplitude of the lagoon-to-sea connection; it is also linked to the tidal ranges and the general hydrological regime (Newton *et al.*, 2013).

For the purposes of this work, we will regard lagoons as separate entities from “wetlands”, that is, “habitats in which the salt or freshwater body is located on the soil surface or close to this surface” (Cuenca and Gauthier, 1987). These wetland environments, often called marshes, swamps or mudflats, are “relatively independent” of the catchment areas and of the sea. They are marked, in terms of their hydrodynamics and thus their existence, by the irregularity and the seasonality of the flows (Bonnet *et al.*, 2005), which cause them to alternate, rapidly and frequently, between “aridity and flooding by fresh or salt waters”. Also, these wetlands are not exploited as fisheries.

Throughout the rest of this work, we will use the term “lagoon” to designate marginal coastal environments, in other words permanent water bodies with varying salinity, measuring more than 50 ha and with a depth of more than 50 cm, relatively “continentalized” and which are visibly of fisheries interest. With a more or less permanent connection to the sea via passes (inlets, canals, channels) and, in the case of barrier beaches, via percolation, they can receive atmospheric and superficial continental fresh water either at surface level (precipitation) or at a deeper level (springs, resurgences). These environments were created as a result of tectonic activity, folds, collapses or when part of the marine domain was cut off as a consequence of displaced unconsolidated sediments (lidos) attaching themselves to anchorage points (islands, peninsulas, headlands).

Additionally, and possibly “improperly”, we include under the term “estuary” some very different river outflows into the sea, these being deltas and estuaries. Estuaries are actually river mouths to the sea which form a deep indentation in the coastline. In the Mediterranean, these are created by the numerous small rivers in rocky areas. Deltas are river mouths that divide into several arms separated by deposits of the sediments they carry, forming an open space, triangular in shape. The latter are few in number and are connected to the major Mediterranean rivers (Nile, Po, Rhone, Ebro). The waters in deltas, like those in estuaries, are subject to tidal influence and present a very clearly defined salinity gradient and stratification. It should be underlined that many lagoons are connected to deltas.

1.2. Lagoons and estuaries of the Mediterranean: characteristics, inventory and classification

In the Mediterranean, 290 lagoons of more than 50 ha have been counted, covering an area of approximately 600,000 ha (see Appendix, section A1). The brackish lagoons are situated on the northern coast, while the southern lagoons are for the most part marinized with salinity levels close to those of the sea or even higher due to negligible run-off and high evaporation (with the exception of deltaic lagoons). The distribution of these environments between various countries is shown in Figure 1.5. They occur most frequently in Italy (104), Greece (84), Turkey (46) and France (27), but from the point of view of surface area, they are particularly well represented in Italy (155,000 ha), Egypt (135,000 ha), Tunisia (102,000 ha), France and Greece (53,000 ha each), Turkey (32,000 ha on the Mediterranean coasts), Spain (21,000 ha), Morocco (11,500 ha) and Albania (11,200 ha), but there is only one lagoon (Mellah) of 860 ha in Algeria.

Most of the lagoons have a surface area below 1,000 ha (Figure 1.6); only a few exceed 15,000 ha: Bardawil (59,500 ha), Venetian (55,000ha), Boughrara (50,000 ha), Burullus (42,000 ha), El Biben (30,000 ha), Mar Menor (17,000 ha), Messolonghi (16,000 ha), Marano Grado (15,800 ha) and Berre and Bizerte (both 15,000 ha). These alone account for 52% of the total surface area of Mediterranean lagoons. Lake Skaddar (53,000 ha and with a level of 6 m below sea level) is not taken into account, even though is directly connected to the Adriatic Sea via a 32 km canal known as the “River Bojana”.

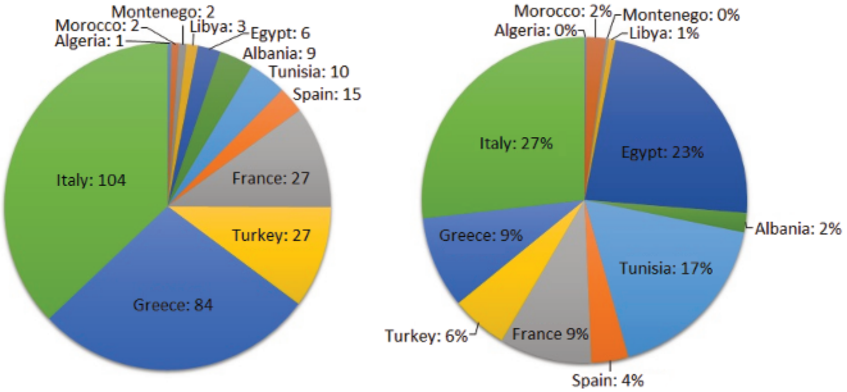


Figure 1.5. *(a) Number of lagoons per country. (b) Lagoon surface area of each country as a proportion of the total surface area of Mediterranean lagoons. For a color version of this figure, see www.iste.co.uk/kara/fishes1.zip*

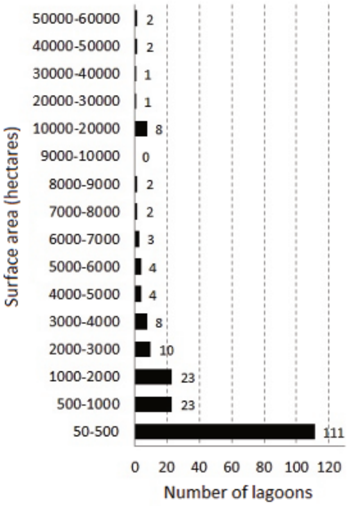


Figure 1.6. *Numerical distribution of Mediterranean lagoons by surface area*

Most of the lagoons are shallow (1–2 m, see Figure 1.7), but some are deeper (4 m or more), such as the Nador lagoon in Morocco (8 m), Bahiret el Biben in Tunisia (6.8 m), the Diana and Urbino lagoons in Corsica (15 m) and the Thau lagoon in France (9 m).

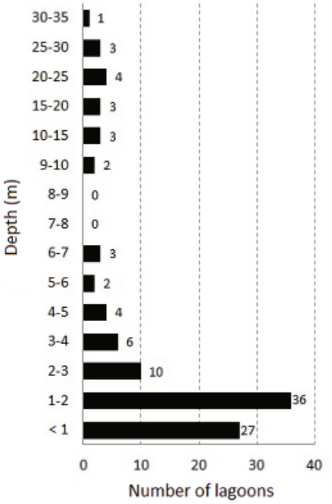


Figure 1.7. *Numerical distribution of Mediterranean lagoons by depth*

Tides range from weak to very weak (1 m maximum in the Gulf of Gabès and the Central Adriatic), but nonetheless they do induce alternating sea–lagoons interactions via passes (canals, inlets). However, generally speaking the tide is only perceptible in the immediate vicinity of these passes. In some geographical sectors, it is primarily wind-generated currents that determine the direction and magnitude (duration and volume) of hydraulic interaction. Additionally, heavy precipitation during storms (local Mediterranean conditions), inducing a surfeit of water in the lagoons, triggers brief, intense "evacuations" of excess water to the sea. Likewise, strong marine inflows during tempestuous storms trigger a rise in the water level in lagoons, followed by an evacuation when the storm stops. Vertical water circulation in each basin is almost exclusively a function of wind cycles and sometimes of water density. The sedimentation pattern is dependent on marine and continental inputs, the bathymetry, the environment's physical and chemical characteristics and its biological activity (Perthuisot and Guelorget, 1987). Lagoons can be the site of major bioconstructions: "mats" of *Mytilus galloprovincialis* and *Mytilus minimus* mussels, and "reefs" of *Ficopomatus* (*Mercierella*) *enigmaticus* tubeworms that contribute to the structure of the environment and the deposits of fine and coarse calcareous sands.

The Mediterranean's lagoons are relatively young ecosystems. The majority of them were formed during the periods of *Holocene marine transgression* between 5,000 and 1,000 years BCE. Irrespective of the mechanisms that gave rise to the various coastal lagoons, all share the characteristic of changing shape and dimensions in time and space, due to natural processes and their nature as ephemeral ecosystems (De Wit *et al.*, 2011b). Barnes (1980) states that the typical lifespan of a lagoon is around 1,000 years, but a number of lagoons manage to survive for longer. The Venetian lagoon in the Adriatic Sea was formed 5,000 years ago, as, probably, was the Tunis lagoon, while some lagoons have been in existence since Roman times and others were formed during the medieval period (De Wit *et al.*, 2011a). Nevertheless, the lifespan of coastal lagoons is also linked to human intervention, manipulating their morphology by earthworks, dredging and other structural modifications that, very often, give rise to progressive fragmentation of the original water body. The lagoons in their current form are thus the result of robust interaction between the coastal dynamic and human intervention.

The various usages of lagoons areas and the surrounding land for agriculture, industry and urban development have contributed to the contraction of the overall surface area of many lagoons. The first interventions date back to 5,000 years BCE in Mesopotamia and Ancient Egypt. To give an idea of the magnitude of the loss of lagoon surface area, one only needs to consider that in Italy the wetlands that used to cover more than 3 million ha in the pre-Roman era had diminished to 1.3 million ha by 1865 and now cover 160,000 ha (Rossi-Doria and Bevilacqua, 1984).

Many coastal lagoons have survived due to programs of safe-keeping, because fish production there was of social and economic interest. Several would not have survived without the ongoing management by local communities with the objective of maintaining navigability or improving fish production, thus assisting not only the physical preservation of these environments, but also the protection of their biodiversity. In fact, human activities that imitate natural processes and dynamics enable the survival of ecological communities, and also economic activities.

Lagoons bear little resemblance to each other (Figure 1.8) in their climatogeographic situations, differences relating to their surface area, their depth and their hydrologic pattern that depends both on the extent of their catchment area, their tributaries and how well connected they are to the sea.

However, they all share the characteristic of variable (unstable or unpredictable, according to some writers) physicochemical parameters, a positive (evaporation lagoons) or negative (dilution lagoons) haline gradient from their sea mouth toward the continent, and significant sedimentation related to lower hydrodynamics than the sea (Guélorget and Perthuisot, 1983, 1984; Lasserre 1979, 1989; Quignard, 1984a; Cognetti and Matagliati, 2000; Nicolaidou *et al.*, 2005). From a bioecological point of view, the lagoon environment is often considered to be an "ecotone", a contact zone at the interface between two different, adjacent ecosystems, one continental and the other marine, whose biodiversity consists of species distinctive to each of the ecosystems in contact, along with its own distinctive species. This concept is far from being applicable to the whole of the lagoon domain, since its heterogeneity is so great. The term "continental species" can, for example, be meaningless in the case of concentration lagoons such as Bardawil (Egypt) and the term "distinctive species" is often contested. If we accept that the ecotone is a place of production and above all of exchanges of energy between ecosystems (Sacchi, 1995; Cognetti and Maltagliati, 2000), the lagoon system in its entirety can be seen as one vast “fragmented ecotone”.

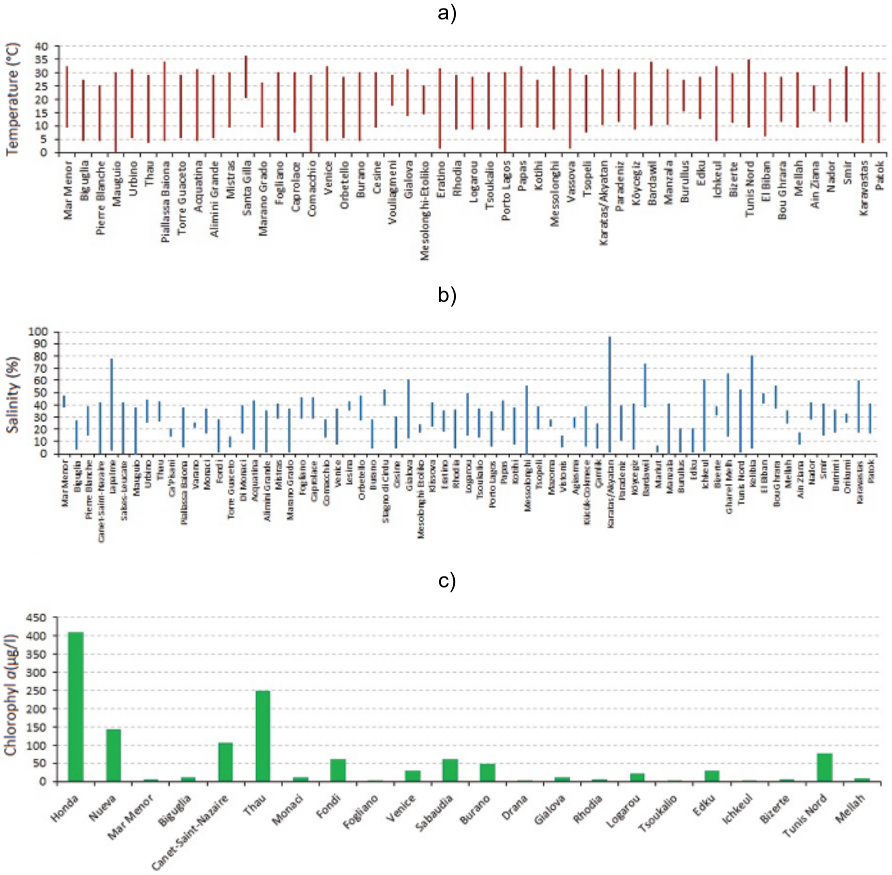


Figure 1.8. *Interlagoon differences in (a) temperature, (b) salinity and (c) chlorophyll in the Mediterranean. For a color version of this figure, see www.iste.co.uk/kara/fishes1.zip*

Attempts at an ecological classification of lagoons have been relatively numerous (Nisbet *et al.*, 1958; Nisbet and Schachter, 1961; Schachter and Casabianca, 1964; Casabianca, 1967–1980, etc.), but the one most frequently used to describe and characterize lagoon waters is the one advanced at the Venice Symposium (Battaglia, 1959). Known as “the Venice System”, this classification, based on salinity, recognizes five categories of lagoon based on this factor: oligohaline (salinity <5 psu), mesohaline, polyhaline, euhaline and hyperhaline (salinity >40 psu).

Subsequently, another approach was proposed by Guelorget and Perthuisot (1983) based on the concept of "confinement". These authors take into account how long the waters remain and propose intralagoon zonation from an area of rapidly renewed waters (close to the lagoon entrance with a strong marine influence) to a very enclosed area (a long way from the lagoon entrance) that can be either oligohaline or hyperhaline, according to climate and connection to continental waters. According to their degree of confinement, Kjerfve (1986, 1994) classifies these ecosystems as:

– open lagoons, connected to the sea by numerous entrances and characterized by excellent water exchanges:

– semiopen lagoons, that are connected to the sea by no more than two canals;

– very "restricted" lagoons connected to the sea by one or several shallow, narrow entrances, allowing only a small amount of water exchange with the open sea.

More recently, the European Framework Directive (DCE 2000/60/EC) stressed the need to develop a more effective typology for aquatic ecosystems including transition zones, of which lagoons form a part (Basset and Abbiati, 2004; Basset *et al.*, 2006; Tagliapietra and Ghirardini, 2006).

With regard to ownership of Mediterranean lagoons, they can be privately owned, but generally speaking they form part of the state-owned continental and maritime domain; a state-owned lagoon can sometimes have privatized sectors. When they are extensively used for pisciculture, these lagoons are often managed by local authorities or rented to groups of local fishermen, cooperatives or private business that may or may not have exclusive fishing rights and management obligations. In Italy, many of the Venetian "valli" are privately owned. In France, more than 10% of the lagoons have been purchased by the Conservatoire du Littoral, an institution dedicated to the protection of coastal areas. In Algeria, Albania, Greece and Tunisia, all the lagoons are in the public domain. In Algeria, the Mellah lagoon has been granted on concession for a period of 33 years. In Albania, 10-year fishing licenses have been granted to fishing cooperatives and private fishermen. In Tunisia, there is a licensing system for private businesses and private fishermen. In Egypt, four lagoons belong to the public domain and one belongs to a public corporation.

1.3. Some recurrent preconceived ideas and problems concerning lagoons

We will here set out for the reader a few phrases that have been found regularly over the decades and even a century and more, in written works about lagoons:

– lagoons are aquatic areas, cut off from the sea to a greater or lesser extent, are heterogeneous, are fragile and unstable concentration basins;

– lagoons are "transitional" zones between ocean and continent;

– the habitation potential of a lagoon is determined by variations in salinity and temperature, in particular by their extremes (pre-lethal, Petit, 1953);

– the living creatures that inhabit lagoons are euryvalent, mainly eurytherm and euryhaline, and display strong genetic polymorphism;

– for the most part, lagoon populations only survive due to the continuous and seasonal influx (recruitment) of marine larvae, juveniles and adults (migrants), since sedentary species are relatively few;

– sea–lagoon migrations are essentially driven by trophic needs and to avoid predators (entering), and for thermic and reproductive reasons (leaving);

– the specific richness of the lagoon is dependent on the biodiversity of the adjacent marine area, modulated by the quality of reception provided by the lagoon and the "threshold" effect produced by the channel connecting the lagoon to the sea;

– the biodiversity of a lagoon is considerably less than that of the adjacent marine area and decreases from the sea mouth toward the continent (filter effect, selection). The flora and fauna supplied by continental waters do not fully compensate for the depletion of the marine elements;

– although biodiversity is relatively low overall, there is high density in the number of species and individuals (biomass) per surface unit;

– lagoons are first-rate nurseries (trophic riches), conducive to strong growth of hatchlings and juveniles compared with that of individuals that remain in the sea;

– lagoons are considered to be "havens from predators" for larvae and juveniles, or "refuges";

– lagoons are sites where a high level of production, transformation and recovery of organic matter takes place, but they are subject to climatic and dystrophic crises that can have catastrophic (or regulatory) consequences;

– marine migrants do not reproduce in lagoons;

– migrant fish leaving lagoons exit in successive waves, relatively homogeneous from the point of view of both sex and size;

– fish production is higher than that achieved in the sea.

Most of these statements are inadequately or poorly substantiated and only in a few cases does the data at our disposal make it possible to confirm or rebut them.

1.4. Geological, geographic and physicochemical types of lagoon

A number of types of lagoon can be recognized according to their geological origin, their connection with the sea, their physicochemistry, their haline system or their geographical position relative to the sea.

1.4.1. *According to their geological origin*

Four major categories of lagoon can be identified (Quignard, 1984a; Brambati, 1988; Quignard and Zaouali, 1980):

1) *potamic-thalassic lagoons*, lido resulting from the combination of sediments deposited by rivers and their transfer by coastal marine currents (the majority of the lagoons in the Gulf of Lion, France). These are generally shallow (–1 to –3 m maximum) and lie parallel to the coastline. These lagoons are linked to a watercourse and to a gently sloping continental shelf, as in the Gulf of Lion. They are generally divided into two categories:

– *intra-deltaic lagoons* such as the lagoons of the Rhone (Vaccarès), Po and Nile (Borullus, etc.);

– *para-deltaic or para-estuarine lagoons* formed on both sides of river mouths by “sand spits” (lidos), which have developed parallel to the shore from coastal anchor points (islands, peninsulas, etc.), such as most of the lagoons of Languedoc-Roussillon (France);

2) *tectonic lagoons* linked to geological events (Berre, Urbino, Diana in France; Bizerte, Ichkeul in Tunisia; Mellah in Algeria; Vistonis in Greece, etc.). They are deep (>5 m) and vary in shape. The barrier beach that cuts them off from the sea is relatively small;

3) *mixed tectonic–potamic-thalassic lagoons*, of which one section is essentially of tectonic origin and another is the result of a body of marine water being cut off by a potamic-thalassic sand spit (Thau in France);

4) *bay-head lagoons* such as the “Lake” of Tunis.

1.4.2. *According to their connections with the sea*

Lagoons are connected to the sea via one or more permanent or temporary “passes” (graus, channels):

1) *perennial, live lagoons, known as open*, whose inlets (graus) can be either natural (Ayrolles) or artificial (Lake of Tunis, Thau lagoon etc.); they are fed by the tide and certain climatic events (heavy rainfall, winds, exceptional marine or human inflows);

2) *dead or closed lagoons* that are no longer connected to the sea (lagoons in the process of dulcification and sometimes extinction), such as the Bagnas lagoon in the Gulf of Lion. They can, however, have hydrological interactions with the sea via “percolation” through the sand barrier;

3) *mixed lagoons with an intermittent connection to the sea*, whose “passes” can be blocked for periods of varying duration, usually a few months. This blockage is caused either by sedimentary inputs carried by longshore currents as in the case of the lagoons in the Gulf of Lion, or by a strong input of sediment from rivers flowing into the lagoon, or else as a consequence of a temporary drying up of the tributary rivers and evaporation resulting in a drop in water level, as in the case of the lagoons in the Gulf of Setubal in Portugal. The reopening of mixed lagoons occurs at the “weakest” points of the lido through its destruction by storms or through the “flushing effect” under the pressure of the lagoon water mass, following an overload resulting from heavy rainfall on the lagoon and its catchment area.

Lasserre (1979) proposes a variant on this classification of lagoons:

– with a strong tidal range (type a);

– open (type b);

– partly closed (type c);

– closed or blocked (type d).

However, no matter what the type of a lagoon, they all have a tendency to disappear naturally through becoming clogged, and most lagoons are kept permanently connected to the sea due to works designed to stabilize the natural passes.

1.4.3. *According to their physical chemistry*

Three types of lagoons are recognized:

1) *submarine lagoons,* which have fairly stable salinity (stenohaline lagoons) and constant ionic relationships, of the marine type (Thau, France is of this type);

2) *brackish lagoons* with variable salinity and ionic relationships (euryhaline) across the intralagoon area and over time, the majority of shallow lagoons (Mauguio, France is of this type);

3) *sublimnic lagoons* whose salinity is weak (oligohaline) and variable (sometimes substenohaline) (Ichkeul, Tunisia is of this type).

1.4.4. *According to their haline system*

Two types of lagoons are recognized:

– *dilution lagoons* that show a negative haline gradient from a marine-influenced area, at the entrance of the “pass” (grau), up to an area under a continental potamic influence at the tributaries’ exit that can equate to fresh water. In these lagoons, inflows of marine water contribute to “salting” them, while the fresh waters of the tributaries and rain water “desalt” them; the continental inputs of nutrient salts are often greater than the nutrient salts of marine origin. These lagoons correspond to the “estuarine lagoon” type described by Boudouresque (2013). This author puts great emphasis on water stratification according to their source: fresh water at the surface, which flows to the sea, and salt sea water, which introduces itself at depth;

– *concentration lagoons* whose haline gradient is the inverse of the latter. These are located in semiarid or arid regions, such as Bahiret El Biben in southern Tunisia and the Bardawil lagoon in Egypt. They can also be found in temperate Mediterranean areas, such as the Doul lagoon in the Gulf of Lion (Boutière, 1974). These lagoons have a tendency to become “hypersaline” relative to the sea: 39–50‰ and above in the El Biben lagoon (Bouhlal, 1981); 53–57‰ in Doul (Boutière, 1974); 45–55‰ and as high as 70‰ in Bardawil (Pisanty, 1981). In these lagoons, the inflows of sea water dilute the oversalted waters in the lagoon after high evaporation and a shortfall in inflows of continental fresh water and/or rain water. The elimination of these excess salts occurs via an outflow of lagoon water or via the deposit of evaporites around the edges of the lagoon. This type of lagoon corresponds to that described by Boudouresque (2013) under the name “antiestuarine lagoon”, where stratification is characterized by the presence of a deep, very salty layer of “lagoon water”, above which is a layer of incoming sea water that is less salt-laden.

All these lagoons display a *confinement gradient* between the marine and continental domains (Guélorget and Perthuisot, 1984–1992; Frisoni *et al*., 1983).

1.4.5. *According to their nutrient content*

Three types of lagoons are recognized:

– *oligotrophic lagoons*, such as the Bardawil lagoon (Egypt), which are low in nutrient salts essentially supplied by the incoming sea waters; continental inputs being virtually non-existent in an arid environment with little urban development;

– *mesotrophic lagoons*, such as the lagoons of Salses-Leucate (France) and Messolonghi (Greece) where external inputs are relatively insignificant; where urban development is limited and the catchment areas not very active (typical Mediterranean climate). In addition, the renewal of the water in the lagoon by marine inflows is balanced (well-regulated inlets), avoiding any excessive confinement or marinization;

– *eutrophic to hypertrophic lagoons*, such as the Mauguio and Prévost lagoons (France) where the level of nutrient salts is excessive due to urban development, the presence of urban waste discharge, leaching from farmland and possibly poor water circulation. Consequently, we see a strong growth of benthic (*Ulva enteromorpha*) or planktonic algae, the source of devastating dystrophic crises (anoxia, H_2S), especially in summer.

1.4.6. *According to their geographic position and connection with the sea*

Taking into account their position in relation to the sea and their locations in relation to each other, four types of lagoon can be recognized:

– *marginal shoreline lagoons* largely open to the sea, with a wide, short canal (grau) (Prévost, Salses-Leucate in France);

– *continentalized lagoons*, with a long, narrow canal (grau) (Mauguio in France, Mellah in Algeria);

– *primary lagoons with a direct connection to the sea* via one or more passes (canals, graus). The majority of the Mediterranean lagoons are of this type;

– *secondary lagoons connected to a primary lagoon* via one or more passes upon which they depend in terms of their marine characteristics. “Natural” lagoons of this type are rare (Lake Ichkeul which flows into the Bizerte lagoon in Tunisia; the Trichonis lagoon which flows into the Lysimachia lagoon; the Vistonis connected to the Porto-Lagos lagoon in Greece; the Olivier and Bolmon lagoons which flow into the Berre lagoon in France). The “secondary lagoon” status can result, as in the case of six lagoons in Languedoc-Occitanie (France), from the fragmentation of large lagoons at the time of the construction of the Rhone-Sète canal.

1.5. Lagoon hydroclimate and hydrodynamics

Lagoons are generally considered “unstable environments” in terms of their hydroclimate. This kind of instability is relative. In fact, we should differentiate between:

1) “predictable” changes, mostly seasonal, which depend upon the laying periods, the recruitment of hatchlings and where appropriate the migration of spawning adults;

2) "unpredictable" changes, triggered by exceptional climatic events (dystrophia, anoxia, thermal crises of heat or cold and wind, floods, etc.), which are responsible for limiting reproductive success in sedentary species or high mortality levels (Bouchereau *et al.*, 1989).

All lagoons present a stronger or less strong gradient of abiotic factors (salinity, temperature, O_2 concentration, pH, oxydoreduction potential), from the sea toward the continent, and wide temporal variations in these factors (Guélorget and Perthuisot, 1983; Sacchi, 1985; Quignard, 1984a; Tournoud, 2000–2001; Wilke, 1998–2002). In addition, in calm weather they can present a bathymetric stratification (Boudouresque, 2013) and gradient, even in the case of shallow lagoons (Chenereau and Scerci, 2000–2001).

The width of variation in abiotic factors is linked to the depth of the lagoon. The so-called laminar lagoons have lower "inertia" than deep lagoons, and because of this are subject to wider and more rapid variations than deep lagoons. Haline variations can also be very great: from 5‰ in winter to >20‰ in summer in the Ichkeul lagoon and from 5‰ to 70‰ in the Hergla lagoon in Tunisia (Bouhlal, 1981). Day-to-day thermal variations can also be very great; the same applies between the summer and winter seasons: from –2°C to +30°C in the laminar lagoons of Palavas (France).

Hydraulic interactions between the lagoon and the sea, in the form of "incoming currents" and "outgoing currents" in the "passes", under the influence of tides (even in areas of very weak tides) and/or winds, ensure, together with inflows of fresh water from tributaries and precipitation, the renewal of the lagoon waters. Interaction with the sea via "percolation" through the sand barrier contributes to the water balance. Freshwater inflows from groundwater and "upsurges" in karstic regions, such as in Salses-Leucate (France), can also contribute to a local reduction in salinity.

Lagoons often act as "sedimentation basins" that concentrate fine sediments of continental or marine origin, which along with indigenous biosediments contribute to the progressive infill of these water bodies. In effect, they are natural receptacles of catchment areas, where dissolved and solid matter transported by rivers and wadis is stored and sedimented.

Being relatively enclosed, lagoons are more sensitive than coastal waters to inflows of fresh water and are characterized by wide spatial and temporal variations in their physical properties (temperature), chemical properties (salinity, nutrients) and biological properties (food chain). Although salinity, along with the depth and nature of the substrata, are the major structural factors of fish populations, local impacts such as silting and a change or disappearance in vegetation, as well as more general impacts such as water stratification or changes to the connection with the sea, also play an important role. Salinity depends simultaneously on the quantity of water coming from the catchment areas, rainfall, groundwater, industrial and urban effluents, marine inflows and evaporation. The effects of quantitative variations in these inflows can be illustrated by examples of certain French lagoons: an increase in salinity in the Vaccarès lagoon (4–8 g/L between 1952 and 1979, to 20–30 g/L between 1982 and 1989; Heurteaux, 1992) or alternatively, as a consequence of the discharge of fresh water from the River Durance used by the hydroelectric stations at Salon and Saint-Chanas, a sharp fall in the salinity in the Berre lagoon (30–32 g/L before 1966, to 10–15 g/L after 1966) (Schachter, 1954; Le Corre and Garcia, 1989) led, respectively, to a change in the number of migrant marine species and to an increase in the number of freshwater species with, in general, no change in the total number of fish species but a decrease in benthic diversity (Stora and Arnoux, 1983; Crivelli and Ximenes, 1992b). The reduction in inflows of fresh water coming from the hydroelectric station at Saint-Chanas as from 2005 once again changed the characteristics of this lagoon ecosystem (GIPREB, 2013).

1.6. Some features of lagoon ichthyoecobiology

Lagoons are ecosystems with fluctuating physicochemical properties, especially those that are shallow (winter chilling, waters that are sometimes rough, overheated in summer, anoxia, H_2S, etc.). Lagoons are often classed among “extreme environments”. For this reason, the survival of species in these environments calls for the ability to adapt, in the case of both migratory and sedentary species. To explain the presence of the latter, it is necessary to take into consideration the prevailing margin of variation in salinity (and in temperature) during the reproduction period of the species (Chassany de Casabianca, 1980). Be that as it may, it follows that lagoons are inhabited by biocenosis composed of few species, but sometimes excessive numbers of individuals (Chauvet, 1986); however, basing their work on a study concerning the physicochemical and ecological aspects of the Corsican lagoons, Casabianca *et al.* (1972–1973) take a more nuanced view: the most stenohaline lagoons are more species rich than euryhaline lagoons.

The highly productive character of lagoon environments is recognized by many authors (Sacchi, 1967, 1973; Labourg *et al.*, 1985). For example, in a number of Greek lagoons, the chlorophyll α-concentration is higher than that of the unpolluted coastal regions of the Eastern Mediterranean (Friligos and Gotsis-Skretas, 1987; Asimakopoulou and Gotsis-Skretas, 1997; Kormas, 1998; Kormas *et al.*, 2001) and is comparable to that of other Mediterranean lagoons (Vaulot and Frisoni, 1986). The exploitation of the "quite exceptional" trophic resources (Mathias and Jalvy, 1958) of these rich "pastures" (Gourret, 1907) by fish (at least groups aged 0 and 0^+) enables them to achieve growth rates well above those of their counterparts who remain in the sea (Gourret, 1897; Petit, 1953; Amanieu, 1973a; Chauvet, 1979, 1981; Lasserre, 1979, 1989; Isnard, 2015). These trophic factors, in combination with favorable thermal factors, constitute an advantage of lagoon waters over sea waters (Amanieu, 1973a). Conversely, other researchers (Albertini-Berhaut, 1973; Lasserre and Labourg, 1974b; Labourg *et al.*, 1985) express doubts about the very advantageous nature of the lagoon environment. Some go as far as denouncing the "trap"-like (Quignard *et al.*, 1984b, Cambrony, 1984; Bruslé and Cambrony, 1992) nature of these enclosed environments, even likening it to a "death trap" (Boutière, 1974) or "a place of death" (Chauvet, 1986). In fact, from the time they arrive in the lagoon, fish can fall victim to climatic variations (winter and/or summer crises) and also to environmental disturbances of anthropic origin (eutrophization causing phytoplanktonic blooms that can be toxic, dystrophic crises, pollutions from various effluents, etc.). The very special case of massive fish mortality, observed in 1990 in the Etolikon lagoon (Leonardos and Sinis, 1997), shows very clearly the importance of local geohydrological conditions. In fact, hydrobiological studies suggest that this mortality was due to a high concentration of H_2S, an extremely toxic gas, in the hypolimnion, resulting in the water becoming enriched in this element from gypsum deposits present in the catchment area, at an anaerobic period caused by the accumulation of organic matter.

In the temperate regions, certain cohorts, particularly those with summer–fall recruitment such as *Liza aurata* and *Chelon labrosus*, benefit from quite favorable conditions, with the exception of "summer crisis" periods (thermo-anoxic, dystrophic crises). However, those with autumn–winter recruitment, such as *Liza saliens* and *Mugil cephalus* which are confronted upon arrival by the rigors of winter's climatic conditions, suffer heavier penalties, at least in years when the winters are harsh.

Furthermore, for the same cohort, growth rates can present an interlagoon spatiotemporal variation; for example, between the Bourdigou lagoon and the Lapalme lagoon (France) for the mullet *Liza ramada* (Figure 1.9, Bruslé and Cambrony, 1992). The same applies to the bream *Sparusaurata* in the Gulf of Lion (Cambrony, 1983; Quignard *et al*., 1984b; Mosconi and Chauvet, 1990; Isnard, 2015) (Figure 1.10).

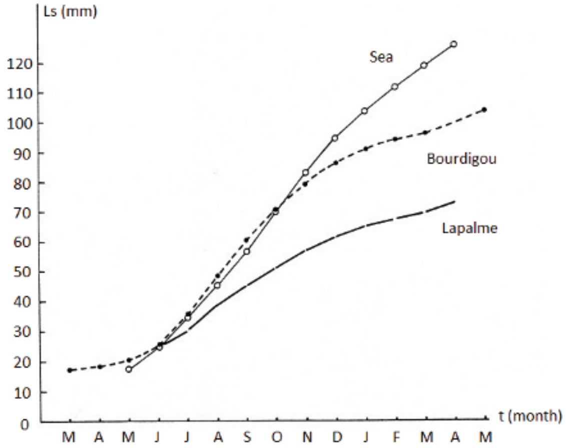


Figure 1.9. *Comparison of linear growth curves of* Liza ramada *in the sea and in the Bourdigou and Lapalme lagoons (Bruslé and Cambrony, 1992)*

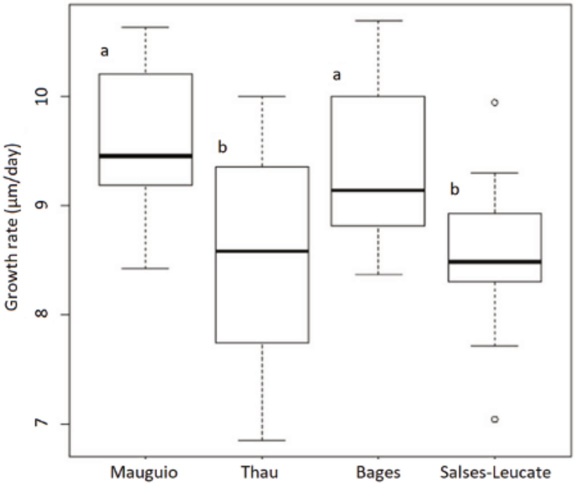


Figure 1.10. *Growth rate of* Sparus aurata *juveniles in the four lagoons in the Gulf of Lion, France (Isnard* et al.*, 2015)*

Within the same lagoon, such as the Mauguio lagoon (France), Escalas *et al.*, (2015) observed differences in growth between the Eastern and Western sectors of the lagoon (Figure 1.11) that they attributed to the quality and quantity of specific organic matter; the matter of continental origin (CPOM) in the Eastern sector was more favorable to good somatic condition and good growth in sea bream and doubtless in fish in general than the more marinized matter of the Western sector.

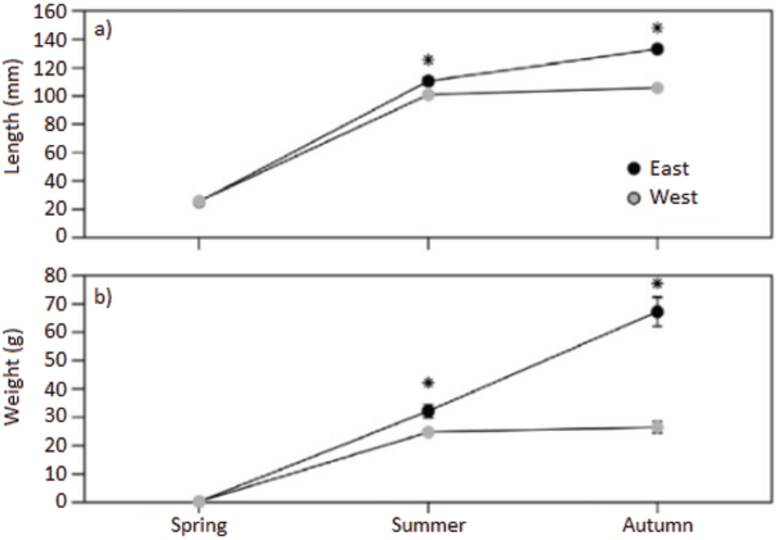


Figure 1.11. *Development of the corporeal size (a) and mass (b) of* Sparus aurata *juveniles during their period of residence in the Mauguio lagoon (France) according to their location in the continentalized Eastern sector or the marinized Western sector (Escalas* et al.*, 2015)*

Thus, bearing in mind the “adaptive strategies” (Amanieu and Lasserre, 1982) deployed by the species that inhabit lagoon ecosystems, the chances of survival and strong growth, and likewise the risk of mortality and poor growth, vary considerably according to lagoon, intralagoon positioning and year (Amanieu, 1973a). For this reason, it is not possible to chart a “uniform” scenario and the “advantage of lagoons” relating to individual growth cannot always be accepted. Comparative lagoon–sea data, collected at the same time (same period, same year), at marine and lagoon sites close to each other, are very little documented or missing. However, it can be accepted that certain lagoons or certain intralagoon areas, especially those rich in continental (CPOM) inputs, can provide postlarvae and juveniles with somatic conditions favorable to their survival and later development, and give them “a good start in life”, according to Isnard *et al.* (2015).

In lagoons, fish mortality varies according to species, environment, year, and also the age and size of individuals. An interpretation of the results, relating to natural mortality, should take all these factors into account. Thus, in the Tunis lagoon, *Mugil cephalus* seems, when adult, to have a natural mortality rate three times lower than in the marine environment, while juveniles a few months old suffer drastic mortality in the same lagoon (Chauvet, 1984). Bearing in mind the fact that lagoons are home to populations with a marked numerical predominance of young, the average mortality rates calculated are overall higher in a lagoon than in the sea. The natural mortality of juveniles and adults would probably be higher in a lagoon due to predation by avifauna (Chauvet, 1984), which is probably facilitated in shallow lagoons. In fact, on the north-west shore of the Mediterranean, around 14 bird species come to feed in Languedoc-Roussillon’s lagoons: five all-year round (gray heron, little egret, yellow-legged gull, black-headed gull and sandwich tern) and nine seasonally, five from autumn to spring (great crested grebe, cormorant, gray heron, red-breasted merganser and Caspian tern) and four in spring/summer or autumn (purple heron, osprey, common tern and little tern) (Blondel and Isemann, 1981; Larrey *et al*., 2005). Also, the impact of piscivorous birds, in particular the great cormorant *Phalacrocorax carbo*, should be taken into account as an example of the interaction in lagoons between fishing and the environment.

In Lake Tunis, the winter colony of cormorants comprised 1,500 individuals in 1977 and remained in this environment for three months; in 1980, it comprised 5,000 and stayed for five months (October to March). Their predation, estimated by counts and a study of stomach contents, amounted to 200 tons (Chauvet, 1984)

Twenty-eight species overwinter in the complex lagoon of Messolonghi (Greece), and the number of individuals showed an upward trend between 1982 and 2012 (Liordos *et al*., 2014), which would impact on fish stocks. In Greece, Liordos and Goutner (2007) show that the mullet *Liza aurata* is the major prey for these birds in the Axios Delta, both in number and in weight, whereas in the Evros Delta, the Crucian carp *Carassius gibelio* is dominant. In the Messolonghi lagoon, the silverside fish *Atherina boyeri* are dominant in number and the grey mullet in weight. In these three environments, fish of high commercial value make a small contribution to the cormorant's diet (at most 22.4% in number and 11.5% in weight in Messolonghi), which indicates little competition with commercial fishing.

In Sardinia's lagoons (Cabras and Mistras), the cormorant principally eats the mullet *Liza ramada* (Index of Relative Importance = 75.28) and *Liza saliens* (IRI = 17.78). The number taken during their overwintering period (October 2010–March 2011) has been assessed at 422 tons, while fishing took 189.4 kg/ha during the same period (Buttu *et al*., 2013). In the Venice lagoon, *Atherina boyeri* and gobies together accounted for 86.3% of these birds' food while mullet contributed only 6.4% (Cherubini *et al*., 1997).

The ecological interest of lagoons in terms of flora and fauna (avifauna in particular) justifies certain lagoons being internationally designated Ramsar sites (the Petite Camargue lagoons in France) or Biosphere Reserves (Mellah lagoon in Algeria). Others hold a national classification, such as ZNIEFF (natural areas of ecological, faunal and floral interest) in France, and nature reserves and nature parks in a number of Mediterranean countries.

1.7. Production in lagoons and trophic chains

Mediterranean lagoons are oligotrophic and mesotrophic ecosystems in arid regions and generally eutrophic in temperate regions. Besides favorable thermal and energy conditions (sunshine), dilution lagoons in temperate regions have the benefit of continental inflows, via runoff and via tributaries, of nutrient salts (nitrates, phosphates, silicates, etc.), unlike concentration lagoons in which the only nutrient inputs are of marine origin**.** These nutrient salts tend to accumulate in the lagoon's sediments that become "nutrient reservoirs".

The inert organic elements (excrement, corpses) brought into, or produced in, the lagoon decompose into byproducts, which are mineralized and also gasified. If these elements are not quickly reintegrated into the primary and/or secondary production cycle, they can be removed directly into the atmosphere or into the sea by outgoing currents or onto the land by the combined action of wind and waves (spray).

Inert particulates (living or nonliving) can exit the lagoon system, borne away to the sea by the outflows, or can be deposited on the banks (lagoon foreshore). Finally, reduction in organic load can result from the voluntary active movement (swimming) of creatures in the lagoon toward the sea or the tributaries, or involuntary movements toward other ecosystems induced by fishing by various predators including birds and humans.

Nowadays, in addition to the "natural" nourishing inputs there are also inputs of anthropic origin linked to farming (fertilizers) and urban (water from water treatment plants) activities, which contribute to creating a eutrophication of the lagoon waters, which is often harmful. In fact, an excess of nutrients simulates the production in the lagoon of organic material by photosynthesis. This overproduction is at the origin of "dystrophic crises" resulting from significant bacterial decomposition of this organic matter (Cahet, 1974; Amanieu *et al.*, 1975; Boutière *et al.*, 1982; Mazoyer, 2000-2001), with a deficit of O_2 (anoxia) and the production of toxic hydrogen sulfide H_2S. The resultant mortality of aquatic organisms is often massive and catastrophic. However, these *malaigues* (or "unhealthy water") crises contribute to ensuring the "self-cleansing" of the lagoon water by discharging the excess sulfur, phosphorus, nitrogen etc., into the atmosphere and into the sea.

It should be noted an excessive opening of passes or "graus" not controlled by gates or valves can, through the massive inflow of salt water, induce "marinization" of the waters and, by intensifying the currents, a "washing" of the lagoon bed, leading to impoverishment in nutrient salts and weaker primary production, for example in the case of the Salses-Leucate lagoon, France (Bourquard and Quignard, 1984). By contrast, purposeful "subnatural" management (Tunis north lagoon, the Italian *valli*) can improve water quality and productivity in the lagoon.

While "primary production" is often very high, "secondary production" is (or has been) also significant, as shown by fish production (Amanieu and Lasserre, 1981; Quignard, 1984; Quignard *et al.*, 1983b; Lasserre, 1989) which in Mediterranean lagoons that have not suffered degradation can be as high as 100–150 (maximum 279) kg/ha/year. Highly marinized and hyperhaline lagoons are less productive: 7 kg/ha/year in the El Biben lagoon in Tunisia (Bouhlal, 1981); 14–24 kg/ha/year in 1969 and 1971 (S‰ = 5–70‰) and 32–35 kg/ha/year in 1974–1978 (S‰ = 45–55‰) in Bardawil in Egypt (Pisanty, 1981). A comparison of these catch data is difficult because of the differences that exist in the methods and the fishing gear used (Gourret, 1897; Petit and Doumenge, 1955; Angelis, 1959; Quignard and Autem, 1982; Quignard and

Farrugio, 1981a), and also in the application of species selection for commercial purposes.

The trophic network structure of lagoons is complex. To simplify, we could say there are three trophic chains (bacteriophagic, detritivore and herbivore) according to the primary nutrient: bacteria, detritus and living plants, planktonic or benthic:

a) *the bacteriophagic chain* corresponds to the use of the "proteobacterial film" covering the sedimentary substrata, following decomposition of the organic matter. This is also referred to as the "decomposer chain". Certain invertebrates and fish such as mullets (*Liza ramada*, *Liza aurata*, etc.) consume this bacterial film;

b) *the detritivore chain* is dominant in shallow meso- and eurotrophic lagoons. The organisms that use dead organic matter are essentially invertebrates, mainly crustaceans, and rarely fish (such as mullets):

c) *the herbivore chain* corresponds to invertebrates, phytoplanktonophagic fish and those that "graze on" living benthic plants, such as the salema *Sarpa salpa* (sea bream), the only herbivorous fish that visits lagoons, principally marinized deep lagoons.

Trophic networks in the lagoon environment are complex, due to the large number of primary producers, the prominence of the detrital food chain and the high level of connectivity (Knoppers, 1994; Alongi, 1998). This makes it difficult to assign a consumer to a particular trophic level and to assess the relative role of each source of organic matter. With a view to describing the trophic network in the Sabaudia lagoon (Italy), the ratios of stable carbon and nitrogen isotopes ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) of primary producers and consumers were analyzed on a seasonal basis during 1999 (Vizzini and Mazzola, 2003). Particulate organic matter (POM) and algal matter (plant and macroalgae epiphytes) appear to constitute the main food source of the primary consumers (zooplankton and benthic invertebrates), while meadows of *Cymodocea nodosa* appear to play a negligible trophic role. With regard to ichtyofauna, stable carbon isotopes differentiate planktivore fish from benthivores. However, a benthic–pelagic pairing appears to occur, with certain fish at a high trophic level feeding on both benthic and pelagic matter. Sarà *et al.* (2002) contradict the generally accepted notion of uncoupling between pelagic and benthic consumers (France, 1995a, 1995b), observed in a number of aquatic ecosystems. Using isotopic markers ($\delta^{13}C$ and $\delta^{15}N$), these authors analyzed the trophic differentiation between two lagoon-dwelling fish: one benthic consumer (*Gobius niger*) and one pelagic consumer (*Atherina boyeri*) in the same lagoon in winter and summer. The fact that these two species live in different spatial niches leads us to suppose that they are dependent on the corresponding trophic resources. However, although *Gobius niger* feeds exclusively, as expected, on benthic prey (harpacticoids and amphipods) during both seasons, *A. boyeri* consumes planktonic prey (calanoid larvae and decapods) as well as benthic prey. Thus, the atherine exploits sources belonging to different trophic compartments according to availability.

Persic *et al*. (2004) attempted a quantitative analysis of the trophic status of the Vaccarès lagoon (Camargue, France) using stable carbon and nitrogen isotopes. The biota distribution in the four trophic compartments (deposit feeders, zooplanktivore, predator and superpredator) was confirmed. The isotopic signatures of the species analyzed in this work showed an increase in ^{15}N with the trophic level. The lowest values were found among copepods (5.6‰) and the highest among the three superpredator fish: *Stizostedion lucioperca*, *Anguilla anguilla* and *Lepomis gibbosus* (around 13‰). Conversely, the same profile was not found for ^{13}C. The relative trophic position of members of the aquatic community of Vaccarès (France) shows annual stability. In spite of variations in fishes' feeding strategies and in the specific composition of the environment, mysids and gammarids are in a constantly dominant position in the diet of fish and remain their principal prey. Sander and pumpkinseed sunfish occupy the highest trophic level, above the European eel, which is common in the Camargue.

The impact of dystrophic crises on the structure and functioning of the trophic network in lagoons has also been studied. In the Canet lagoon (France), suspended organic matter and the organic matter in the sediment appear to constitute the principal food source for the majority of primary consumers (*Mytilus galloprovincialis*, *Cerastoderma glaucum*, *Abra ovata* and *Scrobicularia plana*) (Carlier *et al*., 2008). Despite significant eutrophication of this environment, this food chain structure has been preserved, but it has been simplified and reduced to one single trophic dynamic leading from sedimentary organic matter to the higher predators. In the Santa Giusta lagoon (Sardinia), Magni *et al*. (2008) indicate that the base level of food chain for the majority of consumers is composed essentially of macroalgae and sedimentary organic matter, and that the quantities before and after a dystrophic event (e.g. in summer 2004) do not differ significantly one from the other. These authors show that certain effects of this phenomenon triggered a drastic reduction in macrozoobenthos and massive fish mortality. In three lagoons in the Ebro Delta, subject to contrasting salinity regimes (polyhaline in the Tancada lagoon, mesohaline in Encanyissada and oligohaline in Clot), Prado *et al.* (2014) suggest that changes in salinity could alter the trophic dynamics of the lagoon system, causing it to evolve from benthic to planktonic.

Finally, we can identify three primary trophic sources according to the source of the POM available to and consumed by the fish: autochtone, continental and marine. These three sources can co-exist in dilution lagoons (substantial inflow of fresh water), whereas in concentration lagoons, only marine and autochtone sources are present. The origin of food resources has a not insignificant impact on biodiversity and on the growth and condition of the fish. Continental POM is, for some species, a food conducive to better growth than marine POM (Isnard *et al.*, 2015; Escalas *et al.*, 2015, see also Chapter 3, section 3.4).

1.8. Lagoon habitats

A lagoon's richness in habitats is primarily linked to its surface area, its depth, the diversity of its substrata and the type of relationship it has with continental and marine water bodies. Be that as it may, each lagoon is composed of a "mosaic of habitats" whose hydrologic parameters, the nature of the substrata, vegetation coverage and extent determine the nature of the biocenosis and the intercohort variability of the species in them (Cambrony, 1984; Quignard *et al.*, 1984b; Escalas *et al.*, 2015). The bottom of a lagoon is generally characterized by a certain impoverishment in hard substrata (less rocky). However, the biotopes composed of fine sediments (movable sediments) of telluric and biological origin are well represented. Shell sands are relatively rare. Phanerogam meadows (eelgrass, *Cymodocea*, *Zostera*, etc.) and plots of erect or low-lying algae develop on the movable sediments, and these are very significant in eutrophic lagoons. In addition to these, there are often "neo-biotopes" of anthropic origin: rockfill along the banks, installations for fish farming (rearing cages) and shellfish farming (Loste, 2000–2001) on the floor in the open water (Nador in Morocco, Mar Menor in Spain, Thau in France, etc.). Some lagoons have been extensively "remodeled" not only morphologically and hydrologically but also edaphically (Tunis north and south lakes, the Italian *valli* to the north of the Adriatic, the Languedoc-Roussillon lagoons in France, Mar Menor in Spain).

It should be noted that the typological tests related to "transitional"[2] aquatic habitats are difficult to use as a benchmark for the Mediterranean, given the uniqueness of its coastal waters in terms of hydrodynamics. However, Pihl *et al.* (2002) recognize that Mediterranean lagoon-estuarine systems (Ebro, Messolonghi) correspond to Type 6 (movable subtidal substrata) of their own classification.

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[2] Sources: Corine Biotope 1991, 1993; European Council Directive, 1992 (92/43/EEC); European Council Directive, 2000 (2000/60/EC); A Classification of Palearctic Habitats, 1996; Classification of Pihl *et al.*, 2002, EUNIS, available at: http://eunis.eea.europa.eu/habitats.jsp.