Fish communities in estuaries and lagoons

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Estuaries and lagoons, along with mangroves and maritime marshes, occupy a considerable area along the coast of the African continent. Often subjected to strong marine influence, both in terms of their physical structure and their bio-ecological functioning, lagoon and estuarine environmental systems (abbreviated later as LEE) are nonetheless generally attached to the field of continental waters. In fact, the diversity of situations makes it difficult, if not impossible, to classify them as either marine or continental, and the term "interface environment" perfectly captures their nature and environmental functioning.

Introduction

Dufour *et al.* (1994) point out that the plethora of definitions proposed to express the concept of "lagoon" indicates that there are no universally-accepted criteria for differentiating them from bays, estuaries, coastal marshes, and other parts of the coastal landscape (Mee, 1978). According to the outline proposed by Davies (1973), there is a continuum within the broad category of estuarine environments (figure 22.1). One end of the spectrum contains lagoons of marine origin (wave action), sheltered behind a sedimentary belt formed by

FIGURE 22.1.

Schematic representation of the continuum from lagoons to deltas (adapted from Davies (1973).
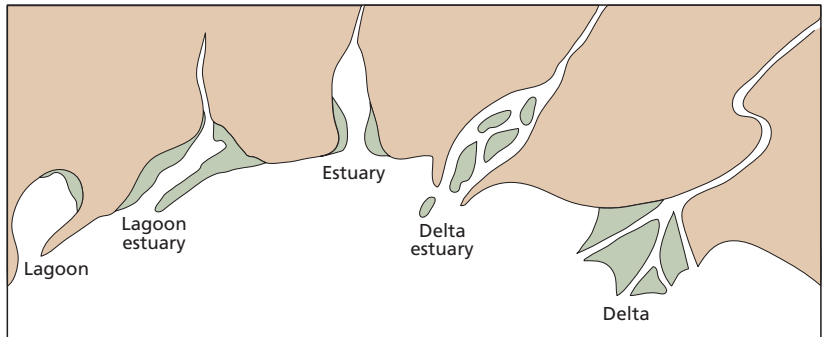
relatively large-sized particles (sand). On the other end of the spectrum can be found deltas, resulting from the action of rivers rather than marine activity, and characterized by the small size of sedimentary particles (silt). Between these two, there are different types of environments that display a mix and a gradation of the two extremes of coastal environments. A large number of type classifications of lagoon and estuarine environmental systems have been proposed, each favouring a specific approach: geological, morphological, hydrodynamic, physico-chemical (water quality, particularly salinity levels), bio-ecological. A typology of LEEs can thus not claim to be either exhaustive or multipurpose. To give an example of a morphological and hydrodynamic approach, we can mention the classification proposed by Lankford (1977) which prioritises the dynamics of formation, with sub-classes taking partly into account a given system's opening to the marine environment (figure 22.2), and that of Nichols and Allen (1981) which distinguishes two main dynamic factors that determine both the evolution and the function of lagoons (figure 22.3):

• the effect of tidal currents and continental discharge;

• the effect of waves and coastal current.

Based on the dominant influence of each of the two factors, lagoons can be classified into four principal types (Nichols & Allen, 1981) (figure 22.3).
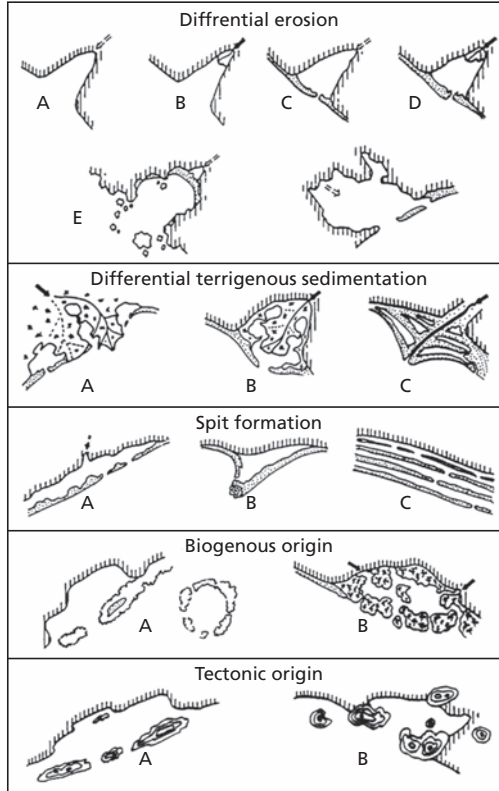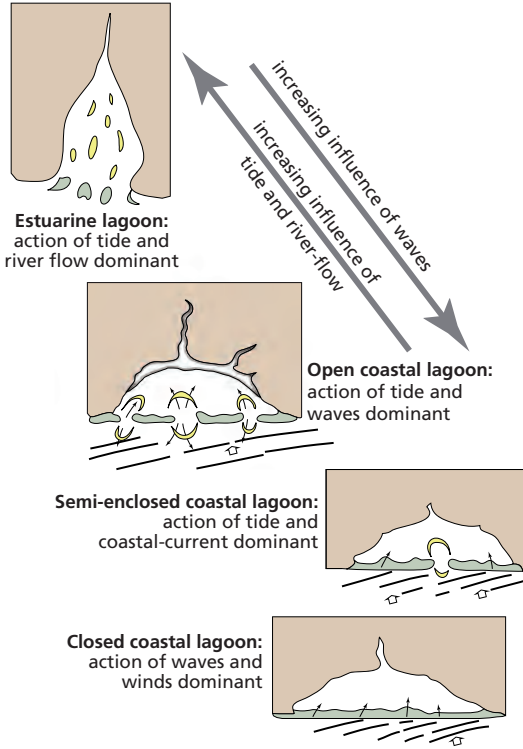
FIGURE 22.3.
Four lagoon types based on the importance of dynamic and energetic factors (from Nichols & Allen, 1981).

Estuarine lagoon: action of tide and river flow dominant

increasing influence of waves

increasing influence of tide and river-flow

Open coastal lagoon: action of tide and waves dominant

Semi-enclosed coastal lagoon: action of tide and coastal-current dominant

**Closed coastal lagoon:** action of waves and winds dominant

For various reasons that essentially have to do with their apparent complexity (if only for the mixture of fauna of different origins) but also the difficulty of defining and demarcating these fluctuating systems in space and time, the study of these systems as ecosystems in their own right is relatively recent, particularly in the intertropical area. Moreover, available information remains fragmented and often sparse. Nonetheless, in recent years LEEs have become the focus of growing scientific interest, tied in large part to the development of multiple human activities that are performed within or near them, such as fishing, aquaculture, tourism, urban and port planning. In addition, their generally small dimensions (compared with oceans and large fluvial basins), the intensity of physical and biological gradients, and the diversity and scope of hydro-climatic variations make them desirable sites for the application of ecological methods and theories.

Because of its halieutic and aquacultural applications, ichthyology has been one of the most frequently-tackled scientific fields.

Two large areas that are particularly rich in LEEs, West Africa and Southern Africa (sometimes referred to as sub-continents), have been the subject of extensive ichthyological investigations and will provide most of the information and bibliographical elements mentioned in this chapter (figures 22.4 and 22.5). It can be noted that in both cases, the scientific approach and reasoning were essentially the same. Initially research focused on the systematic inventory and
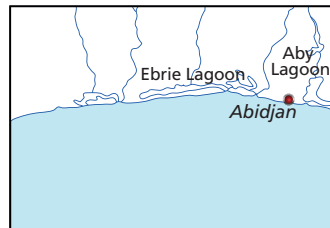
West Africa
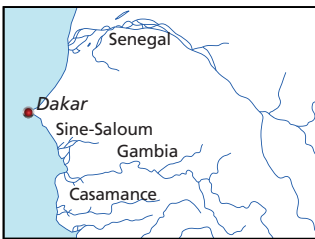
Z1: Senegal

Z2: Guinea-Bissau

Z3: Guinea

Z4: Côte d'Ivoire

taxonomy of species, which sometimes allowed a biogeographical approach. Studies on the biology and ecology of the major species developed at the same time. Subsequently, synecological research developed, as scientists attempted to describe and sometimes explain the ecological functioning of the communities of specific systems: the Ébrié lagoon, Casamance, Lake Togo, Sine Saloum, Fatala estuary for West Africa; St Lucia System, Lake Nhlange (Kosi System), Poelela Lagoon for Southern Africa. The acquisition of this body of knowledge, which will be referred to extensively in this chapter, now allows a twofold comparative approach – firstly geographic, with the comparative analysis of faunistic and functional characteristics of several systems, but also

FIGURE 22.5.
Coastal lagoons of
south-east Africa
(based on Blaber,
1985).
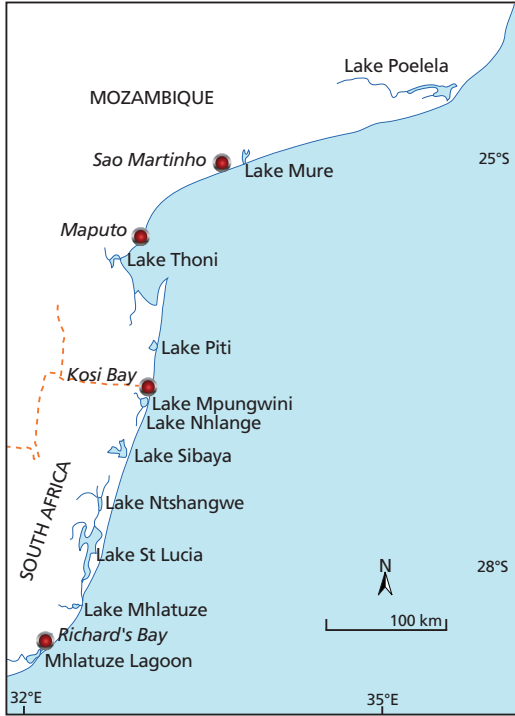
diachronic, making it possible to follow and understand the evolution of an estuary system subjected to considerable changes (particularly climate-related) to which it is sometimes possible to make a connection with changes in the composition and structure of communities. In this chapter, we will attempt to provide the elements that explain what an estuarine species is, what its origin may be, how ichthyological communities are formed and organized and to point out the essential factors (biotic or physical) that influence their structure. We will examine the vital strategies used by species to take the greatest advantage of these supposedly stressful and inhospitable environments. Some pressing current issues regarding LEEs will also be discussed, particularly the debate regarding their biodiversity (is it high or not?) and the vital question – as their survival sometimes depends on it – of the ecological and economic role of these systems. We will conclude by discussing the concepts of the fragility and sturdiness of these environments and the threats that face them.

General characteristics of fish communities

By definition, LEEs are found at the interface of continental and marine areas. Like the physical system, the fauna and flora of these environments are influenced by the adjacent systems based on an equilibrium that varies according

to situation. The question then arises whether the faunistic compositions that occupy these ill-defined environments present a certain degree of structure and meet some general organizational principles, or if on the contrary they are simple, more or less random aggregates of opportunistic fish originating from either the adjacent continental plateau or from continental tributaries.

Lagoon or estuarine environments: strong biodiversity or species-poor systems?

Depending on the author, lagoon and estuarine environments are presented as species-poor environments (Remane & Schlieper, 1971; Kiener, 1978; Day & Yañez-Arancibia, 1985) or as ecosystems that are rich in species (Albaret, 1994; Albaret & Diouf, 1994; Baran, 1995). The main cause of this divergence is the absence of a consensus on the definition of estuarine ichthyofauna during species inventories (what is an estuarine species; what are the limits of the estuary; what should be counted?). In the first case, generally the only species taken into account are those that complete their entire life cycle in estuaries and lagoons, species that are exclusively confined to brackish environments. Species of marine or continental origin that are found temporarily in LEEs, or those that can complete their life cycles in or out of the estuary environment are excluded from inventories. Yet for some of these species, lagoons and estuaries serve an extremely important function ("nursery" role) that is sometimes indispensable for the completion of the life cycle (Wootton, 1992; Beckley, 1984; Ross & Epperly, 1985; Day *et al.*, 1989). Moreover, the interactions (predation, competition) of these migratory species with resident ichthyofauna are an important contributor to the structure of fish populations (Monteiro *et al.*, 1990; Blaber, 1985). If we are to study how these systems function, it thus seems necessary – going beyond inventory and classification – to include migratory and amphibiotic species in estuarine ichthyofauna and discuss the notion of species richness in LEEs while taking them as open systems.

An examination of the structure of fish communities in estuaries and lagoons around the world shows that, in general, only a few species contribute to most of the biomass of these otherwise species-rich systems (table 22.I and 22.II) (Kennish, 1990; Yañez-Arancibia *et al.*, 1985; Chao *et al.*, 1985; Horn & Allen, 1985; Whitfield, 1994a; Kromer *et al.*, 1994; Albaret, 1987; Baran, 1995; Diouf, 1996).

TABLE 22.I.
Species richness of ichthyofauna in different countries of West Africa (adapted from Baran, 1995).

Senegal River	Senegal Gambia River	Gambia Fatala River	Guinea Comoé River	Côte d'Ivoire Niger River	Nigeria
Number of freshwater species	111	96	41	96	193
Number of estuarine species	133	89	102	153	79
Number of marine species	292	337	158	103	-

TABLE 22.II.

Species richness of ichthyofaunal of some LEEs around the world (Diouf, 1996).

	Environment type	Country	Specific richness	Source
Africa				
Senegal	estuary	Senegal	111	Reizer, 1988; Diouf *et al.*, 1991; Kébé *et al.*, 1992
Sine Saloum	inverse estuary	Senegal	114	Séret, 1983
Gambia	estuary	Gambia	89	Daget, 1960; Dorr *et al.*, 1985
Casamance	inverse estuary	Senegal	86	Pandaré & Capdeville, 1986; Pandaré, 1987; Albaret, 1987; Pandaré & Niang, 1989; Badji, 1990
Rio Buba	ria	Guinea-Bissau	92	Kromer *et al.*, 1994
Fatala	estuary	Guinea	102	Baran, 1995
Ébrié lagoon	lagoon	Côte d'Ivoire	153	Albaret, 1994
Aby lagoon	lagoon	Côte d'Ivoire	82	Charles-Dominique, 1994
Lagos lagoon	lagoon	Nigeria	79	Fagade & Olanyan, 1974
Niger	delta	Nigeria	52	Boeseman, 1963
Ogowe	estuary	Gabon	66	Loubens, 1966
Santa Lucia	lagoon	South Africa	108	Blaber, 1988
Poelela	lagoon	South Africa	12	Blaber, 1988
Nhlange (Kosi)	lagoon	South Africa	37	Blaber, 1988
Sibaya	lagoon	South Africa	18	Blaber, 1988
Swarvlei	lagoon	South Africa	25	Blaber, 1988
Richard's Bay	lagoon	South Africa	74	Blaber, 1988
Morrumbene	estuary	Mozambique	114	Day, 1974
Pangalanes	8 small lagoons	Madagascar	10 to 43	Lasserre, 1979
America				
Teacapan-Agua Brava	lagoon	Mexico	75	Flores-Verdugo *et al.*, 1960
Terminos Lagoon	lagoon	Mexico	122	Yañez-Arancibia *et al.*, 1980
Santa Lucia	estuary	Mexico	83	Chavez, 1979
Nichupte	lagoon	Mexico	37	Chavez, 1979
Tuxpan	lagoon	Mexico	126	Chavez, 1979
Alvarado	lagoon	Mexico	71	Chavez, 1979
Laguna Madre	lagoon	Mexico	111	Chavez, 1979
Tamiahua	lagoon	Mexico	49	Chavez, 1979
Mandinga	lagoon	Mexico	24	Chavez, 1979
La Mancha	lagoon	Mexico	42	Chavez, 1979
Tabasco	lagoonal system	Mexico	62	Resendez-Medina, 1979
Tamiahua	lagoon	Mexico	56	Resendez-Medina, 1979
Zontecopopan	lagoon	Mexico	50	Resendez-Medina, 1979
Nicoya Gulf	coastal mangrove	Costa Rica	61	Philips, 1983
Punta del Este	coastal mangrove	Cuba	55	Valdes-Muñoz, 1983
Laguna Joyuda	lagoon	Puerto Rico	41	Stoner
Belle-Plaine	lagoon	Guadeloupe	25	Louis *et al.*, 1985
Mancha à Eau	lagoon	Guadeloupe	24	Louis *et al.*, 1985
Fort-de-France bay	coastal mangrove	Martinique	87	Louis *et al.*, 1985
Cayenne River	estuary	French Guiana	59	Tito de Morais & Tito de Morais, 1994
Barrier reef complex of Belize	reef	Belize	87	Sedbery & Carter, 1993
Jaguaribe	estuary	Brazil	86	Oliveira, 1976
Huizache-Caimanero	lagoon	Mexico	44	Warbuton, 1978
Tijuana estuary	estuary	USA (South California)	21	Nordby & Zedler, 1991
Los Penasquitos Lagoon	lagoon	USA (South California)	13	Nordby & Zedler, 1991
Wells estuary	estuary	USA (Maine)	24	Ayvazian et al., 1992
Waquoit Bay	Bay	USA (Massachusetts)	46	Ayvazian et al., 1992

	Environment type	Country	Specific richness	Source
Asia				
Pagbilao	coastal mangrove	Philippines	128	Pinto, 1988
Klang-Langat	delta	Malaysia	119	Chong *et al.*, 1990
Oceania				
Labu Estuary	estuary	Papua New Guinea	38	Quinn & Kojis, 1986
Moreton Bay	coastal mangrove	North Australia	112	Weng, 1988
Trinity inlet system	estuary	North Australia	91	Blaber, 1980
Dampier Bay	coastal mangrove	North Australia	113	Blaber, 1980
Leanyer Swamp	coastal mangrove	North Australia	38	Davis, 1988
Alligaror Creek	estuary	North Australia	128	Robertson & Duke, 1990
Embley estuary	estuary	North Australia	197	Blaber *et al.*, 1989
Botany Bay	coastal mangrove	North Australia	46	Bell *et al.*, 1984
Swan River	estuary	West Australia	71	Loneragan *et al.*, 1989
Deama	coastal mangrove	New Caledonia	75	Thollot, 1989
Europe				
Ria Aveiro	estuary	Portugal	55	Rebelo, 1992
Ria Formosa	estuary	Portugal	67	Monteiro, 1989
Étang de Thau	lagoon	France	53	Bach, 1985
Mauguio	lagoon	France	71	Bouchereau, 1994

The diversity in the definition of limits both upstream and downstream of LEEs (Caspers, 1954; Rodriguez, 1975; Fairbidge, 1980; Day, 1981; Baran, 1995), is also a source of controversy regarding the species richness of these systems.

In a given biogeographic province, the species richness of LEEs in West Africa is comparable to that of rivers and never less than a third of the number of species found at sea on the neighbouring continental plateau (Baran, 1995) (table 22.I). At the global level, we can note that the richness of Africa's estuaries and lagoons is greater overall compared with other LEEs (table 22.II).

Factors influencing or regulating diversity

The LEEs of West Africa thus play temporary or permanent host to a large number of species. This richness can be traced to certain characteristics of these ecosystems.

Size of the system

In the ecology of aquatic systems, it is common for scientists to describe the species richness of an ecosystem according to its extent (see chapter *Species richness of fish communities*). The main condition for the application of this model stipulates that ecosystems should form isolated ensembles such that on their borders, their fauna does not undergo any pressure from neighbouring fauna. Yet one of the fundamental characteristics of LEEs is, indeed, to allow the integration of elements from adjacent systems into the animal communities that they host. Another essential characteristic of these ecosystems is that they rely primarily on exchanges (of matter, energy, and biomass) with adjacent systems. While their dimensions have an influence on their species richness, the area/species richness model does not apply to LEEs.

Extent, number, diversity, and permanence of interfaces

The reasons for the extent of species richness in a lagoon or estuary must be treated as having more to do with the extent, diversity, and permanence of its interfaces with adjacent systems (Albaret, 1994). The moment and duration of their connection with the ocean also play an essential role on the diversity and abundance of fish in a given lagoon or estuarine system. LEEs that have a permanent connection to the ocean show greater species richness compared with systems that have temporary connections (Whitfield & Kok, 1992).

Diversity of available habitats

The morpho-edaphic (shape of water body, depth, nature of bottom) and bankside vegetal variety, heightened by the diversity of hydrological and hydro-climatic situations, leads to a great diversity of habitat types available to fish communities in the LEEs. (Blaber, 1974; Branch & Grindley, 1979; Marais 1982; Whitfield, 1983; Cyrus & Blaber, 1987a, b, c; Albaret 1987; Diouf 1996.).

Population potential (diversity of colonization sources)

This high "hosting capacity" also corresponds to very high colonization potential from coastal marine, estuarine, and continental species.

A large proportion of the fish species making up the neritic communities of the African coasts is liable to penetrate into neighbouring estuaries and lagoons for varying periods and at different life stages.

Estuarine species, which are euryhaline and have generally low endemicity, can (little by little, and at another time scale) also colonize new LEEs via the sea.

Continental species, generally less numerous than the others, come from rivers that are tributaries of the LEEs.

The species of the first two groups have a vast biogeographic distribution whereas the majority of continental species have a more restrained area of distribution. This contributes to the regional, even local (endemic species) specificity of estuarine communities.

Biogeography

Biogeography also plays an important role in determining the "availability" of species for recruitement in a given estuary (Blaber, 1981).

Whitfield (1994a, b) notes that in general, tropical and sub-tropical estuaries have more species richness than temperate systems owing mainly to the greater richness of fauna associated with habitats that are close to the equator, be they marine or riverine. In South Africa, Wallace and van der Elst (1975) have shown that there is a decrease in ichthyological diversity when one moves from the sub-tropical estuaries of the Natal (Indian ocean) to the "temperate-warm" ones of the Cape's coast then the "temperate-cold" ones of the Atlantic shoreline.

Other factors that may influence species richness

Other factors, often interdependent, can be mentioned: the strength and duration of floods, (Marais, 1982), physico-chemical characteristics of water and their spatio-temporal variations (Blaber, 1974; Whitfield *et al.*, 1981; Cyrus & Blaber,

1987a, b, c; Albaret, 1987; Diouf, 1996), trophic richness and resource avail-ability (Marais, 1984; Whitfield, 1988); presence, abundance, and health state of mangroves (Diouf, 1996). The composition of LEE communities is also modified, sometimes considerably, by human interventions such as the construction of engineering works (ports, dikes, dams, etc.), creation of connections to the ocean, halieutic and aquacultural activities, pollution from urbanisation and industrialization as well as agricultural activities (Blaber *et al.,* 1984; Plumstead, 1990; Albaret & Diouf, 1994).

Finally, we should note the essential role of historical factors (at various time scales) in the creation of fish communities as we know them today. How, indeed, would it be possible to understand the current organization of the highly saline Casamance and Sine Saloum estuaries (Senegal) if we were not aware of past climate evolution and the recurrent rainfall deficits typical of this Sahelian region?

On another scale, it can be useful to remember that the existence of LEEs, tied to major climatic changes and ocean level fluctuations, have existed for a relatively short time compared with lakes, rivers, seas, and oceans. To a certain extent we can thus think of them as being ephemeral (on a case-to-case basis, as there will always – more or less – be lagoons and estuaries regardless of sea level) on a geological (and evolutionary process) time scale. This is probably one of the reasons for the low level of speciation in LEEs (as indicated by the low number of species per family) compared with other aquatic systems and, consequently, the relatively low number of true, uniquely estuarine species.

As an example, the Ébrié lagoon, with more than 150 species, is one of the LEEs with the greatest species richness, and combines many factors that encourage population diversity (Albaret, 1994). Located near the equator (5° North), it is the largest lagoon system in West Africa (566 km^2), possessing interfaces with a wide range of aquatic ecosystems: forest rivers, Sudanese-Sahelian river, other lagoons, mangrove, marshes, a continental shelf with over 300 fish species. The connection with the ocean occurs mainly through the Vridy canal, an artificial permanent opening (width: around 300 m, average depth: 15 m) allowing the transit of considerable water masses (annual entry 38.10^9 m^3, annual discharge 50.10^9 m^3) (Varlet, 1978). The extreme variety of landscapes and the diversity of hydro-climatic situations round out the list of factors encouraging the temporary or permanent hosting of many species from different origins, and showing a wide range of ecophysiological adaptations and biological cycles.

Classification of species in ecological categories

Undoubtedly more than for any other type of aquatic system, specialists have run into the problem of defining and classifying estuarine and lagoon commu-nities, an essential step for describing and comparing communities, then for investigating certain aspects of their functioning. Typologies based in the main on the osmoregulatory capacities of species have been proposed (Kiener, 1978) but these have turned out to be largely unsatisfactory when put in practice. A classification that takes not only the degree of euryhalinity into account, but also the characteristics of each species' bio-ecological cycle (distribution and

regularity, breeding sites and conditions, place in the trophic network, abundance and location of ecophases), makes it possible to gain a better grasp of the origin, nature, and certain functional aspects of ichthyological communities. Such classifications, undergirded by the concept of estuarine dependence and adapted to the study of vast regions, have been proposed for the subtropical and temperate estuaries of southern Africa (Whitfield, 1994a, b) and the LEEs of West Africa (Albaret, 1994; Albaret & Diouf, 1994). The Whitfield classification has five main categories, three of which are subdivided, for a total of nine categories or sub-categories. The one proposed by Albaret (figure 22.6) includes eight bio-ecological categories, which from a central point of strictly estuarine species, splits unevenly on two gradients of continental and marine affinities. Four of these groups (strictly estuarine, estuarine of marine origin, estuarine of continental origin, marine-estuarine species), composed of largely euryhaline and eurybiotic species, make up the basic elements of the ichthy-ocenosis of the LEEs of West Africa. About thirty of these species constitute the core of communities owing to their ubiquity, their abundance (or at least their regularly), and the essential role they play in the halieutic economy and ecology of these systems (table 22.III). The other groups comprise species that are variously referred to in literature as "complementary", "accessory", "rare", or "occasional" species. They are found on the extreme ends of the marine and continental axes, their number and diversity varying according to type, size, and hydrological and hydroclimatic characteristics of the system in question.

Arius latiscutatus	*Gerres nigri*
Citarichthys stampflii	*Porogobius schlegelii*
Caranx senegallus	*Pomadasys jubelini*
Chloroscombrus chrysurus	*Liza dumerili*
Trachinotus teraia	*Liza falcipinnis*
Hemichromis fasciatus	*Liza grandisquamis*
Sarotherodon melanotheron	*Mugil curema*
Tilapia guineensis	*Galeoides decadactylus*
Ethmalosa fimbriata	*Ilisha africana*
Sardinella maderensis	*Pseudotolithus elongatus*
Cynoglossus senegalensis	*Pseudotolithus senegalensis*
Dasyatis margarita	*Scomberomorus tritor*
Elops lacerta	*Sphyraena afra*
Eucinostomus melanopterus	*Monodactylus sebae*

Different types of estuarine communities

In the diverse and varied LEEs of West Africa, the different ecological categories described are more or less well-represented (figure 22.6) and we can schematically describe the theoretical evolution of fish populations based on hydroclimatic characteristics (Diouf, 1996) (figure 22.7).
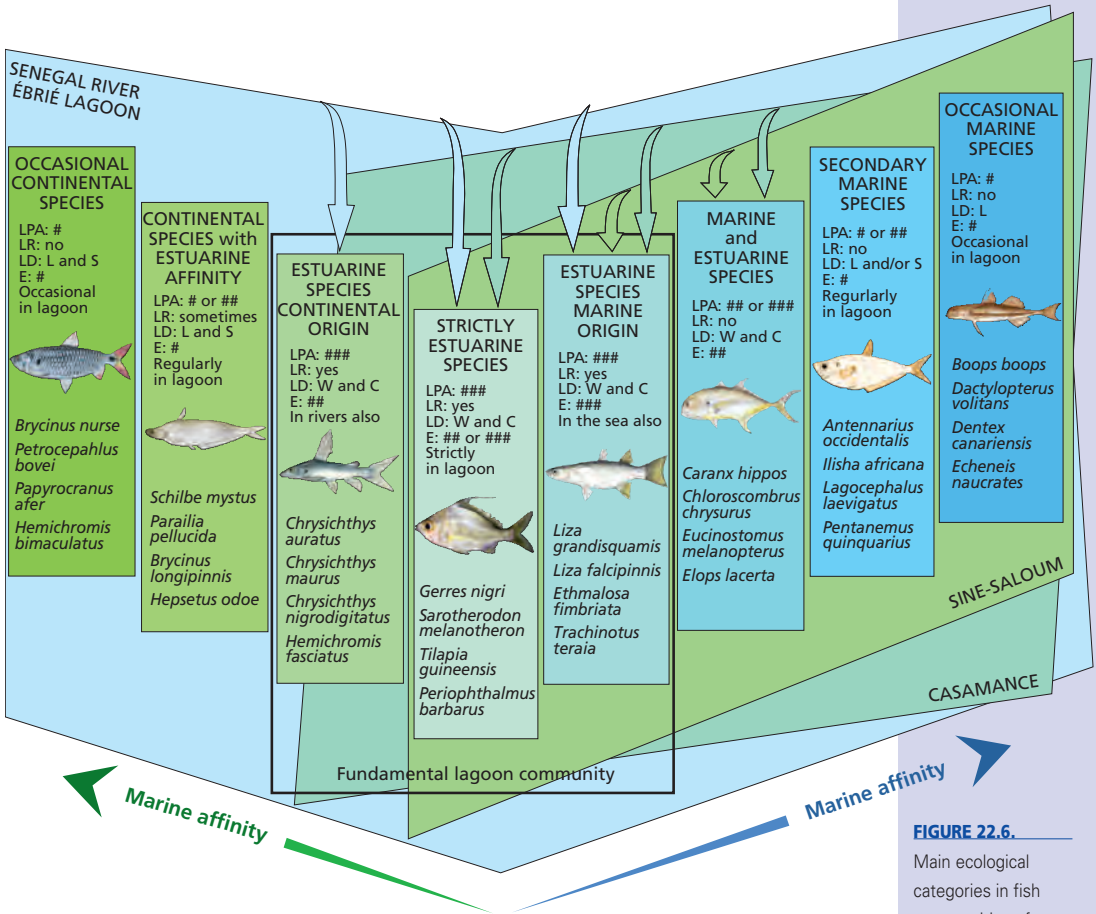
FIGURE 22.6.

Main ecological categories in fish communities of West African LEEs. LPA : lagoonal populations abundance (# rare, ## abundant, ### very abundant); LR: lagoonal reproduction; LD: lagoonal distribution; W: wide; L: limited; S: seasonal; C: continuous; E: euryhalinity (# low, ## high, ### quasi-total)

All the ecological categories are represented in certain LEEs, largely open to both marine and continental domains (type E). This is the case of the Ébrié lagoon, of the Senegal River estuary before the commissioning of the Diama dam, and of the estuaries of the Gambia and the Niger Rivers. Type M is characterized by the reduction of continental influence and the predominance of oceanic influence. This situation is seen in the Rio Buba in Guinea-Bissau, for example. In the inverse estuaries (type I) of Casamance and Sine Saloum (Senegal), the "centre of gravity" of the population shifted towards the marine side with a near-disappearance of the continental component (one or two species of group E.c. can remain). In the case of certain lagoons or certain lagoonal estuaries, the shift occurred in the other direction and the categories of the marine affinities axis are absent (M.o., M.a., M.E.) or hardly represented (E. m). Lake Togo during its closed-off period (Laë, 1992a) and the Potou and Aghien lagoons in Côte d'Ivoire (Albaret, 1994) are good examples of this type of situation (type C).
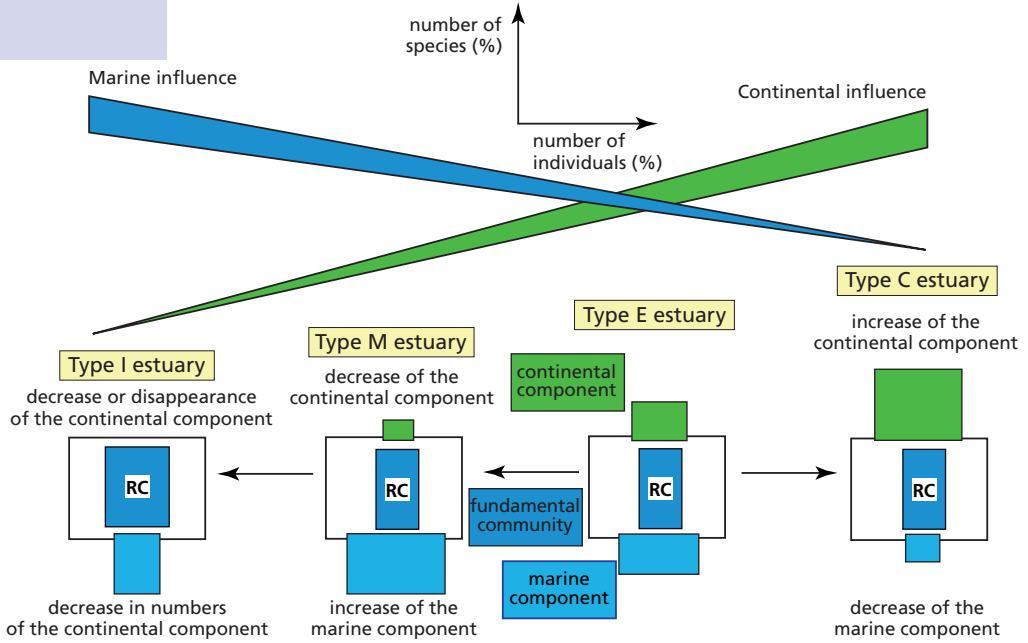
Organization of communities

The recruitment of fish in LEEs has three distinct sources: marine species and continental species that penetrate the estuarine area at a more or less advanced stage of their development, and juvenile forms of species that reproduce there obligatorily, regularly, or occasionally. From these different population sources, fish communities organize themselves according to the bio-ecological cycles of species (first of all in terms of their eco-physiological aptitudes), the biotic capacity of the system (in particular trophic availabilities), and interspecific relationships (spatial competition, trophic competition, predation, etc.).

The great diversity and extreme variability of LEEs corresponds to very uneven degrees of organization and stability. Some communities are characterized by high species richness but highly unequal abundance distributions. These types of communities are characterized by the marked dominance of a very small number of species (or even a single species, generally a pelagic Clupeiform one, *Ethmalosa fimbriata* or *Sardinella maderensis* in West Africa) and correspond to juvenile communities undergoing constant renewal and with high biological activity (production, life cycles, energy transfer). Conversely, other communities with often lower species richness but a more even distribution of abundance reflect greater environmental stability and a higher degree of maturity and structure of the communities in place.

Factors for community structuring

The species composition and structure of fish populations in a given location is a result of the action of a series of ecological filters (Wootton, 1992). The most obvious and striking characteristic of LEEs is without a doubt the high spatio-temporal variability of the aquatic environment. Therefore among these

filters, environmental factors are generally considered to play a crucial role in the organization of fish communities in these systems that are considered highly "physically controlled". When interspecific relationships have been studied, this was most often owing to their intrinsic interesting nature and not for the purpose of understanding the structure of communities. Hence, in some cases, an overestimation of the role of physico-chemical parameters (particularly salinity) and an erroneous or incomplete identification of factors that structure the ichthyocenosis have been achieved. It is thus important, in the quest for explanatory hypotheses accounting for the structure of fish communities in LEEs, to take into account the roles of the hydrobioclimate and of inter-species relationships simultaneously.

Structuring role of environmental factors

Salinity, temperature, turbidity, and dissolved oxygen concentration have a strong influence on the composition, distribution, and abundance of communities in estuarine waters (Kennish, 1990). Diouf (1996) points out that for some fifty studies carried out in estuarine waters, turbidity (in 75% of cases) is one of the most frequently mentioned structuring factors for populations, followed by salinity (58%) and temperature (40%). Other factors are trophic richness (30%), nature of sediments (24%), depth (12%), current (11%) and finally oxygen (10%). However, while a wide variety of structuring factors are generally taken into account, a closer examination of their correlations show that the main ones are turbidity, salinity, and temperature; other factors are often no more than co-variables (McLusky, 1993).

Importance of interspecific relationships

Sedentary and migrant (adult and juvenile) fish species living in LEEs may reach very high densities, which often results in strong intraspecific competition (Wootton, 1992). In extreme cases, the youngest stages are cannibalized.

As juveniles of many large species have the same dietary requirements as adults of small species, LEEs are the venue for strong interspecific competition. However, the spatial heterogeneity and temporal variability of the environment may limit such competition as a result of habitat segregation (Wootton, 1992; Blaber & Whitfield, 1977).

The intensity of predation is tied in large part to turbidity (Cyrus & Blaber, 1987b; Deegan & Thompson, 1985) since prey is hunted by sight for many species (Nikolsly, 1963; Hyatt, 1979; Wootton, 1992). As turbidity is often high in estuaries, predation there generally tends to be low. In some conditions, clear and deep waters, predation may increase (Blaber *et al.*, 1985).

In estuaries and lagoons, it has been shown that predators rarely specialize in a single species (dietary opportunism). As soon as prey populations decline, predators select a closely-related species (Sykes & Manooch, 1978).

Stability-instability

Fish communities in LEEs are often described as heterogeneous and unstable. This presumed instability (which sometimes earns them a reputation for fragility) must be revised after the findings of studies in West and Southern

Africa. Granted, the level of structural organization is never very high in LEEs (primarily in zones that are close to connections with the ocean) and seasonal variations are very marked, in terms of both composition and structure of communities). Yet, in the Ébrié lagoon, Albaret & Écoutin (1990) have shown that at the scale of the annual cycle as well as at an interval of nearly twenty years, a group of species, mainly estuarine (E.c., E.s., E.m.) but also marine-estuarine (M.E.), is constantly present, which thanks to their ecophysiological performance constitute a remarkably stable base community in an environment that displays extreme variability at different levels. Moreover, it is interesting to note that these species are essentially the same as the ones forming the base community for all the LEEs of West Africa mentioned earlier. Beyond the stability of the base community, we can also note an evolution described as the "marinization" of the population which is seen as a consequence of the general rainfall deficit in the region during the period under study (Albaret & Écoutin, 1990). This heightened importance of the marine component within the populations can be felt more in the structure of the community (rank and frequency of species with an oceanic affinity in abundance distributions) than in their species composition which, aside from the inclusion of a few "accidental" marine species, fundamentally remains the same. The highly-marked seasonal variations of the community are induced by the changes in the environment, with the abundance and distribution of fresh water inputs at the fore. The cycle appears to be stable from one year to another, although modulated by the modalities of these inputs: degree and precocity of the rainy season locally, and of the flood of the Comoé river determined by rains in the Sudanian region.

Whitfield (1994a, b) points out that despite the instability or rather, the strong physical variability of the Southern African estuaries at various temporal and spatial scales, the species composition of ichthyologic communities of these environments is relatively stable, and fishes there have more or less predictable distribution and abundance patterns (Day *et al.,* 1981). Moyle & Cech (1982) attribute this stability to four main conditions that apply to all Southern African estuaries (Whitfield, 1994a, b) and to West African LEEs:

- regular distribution of populations throughout the gradients of the environment;
- seasonal migrations of fishes in and outside the estuary;
- dominance of only a few species within communities;
- robust nature of food webs inside estuaries.

A fifth condition that seems essential can be added: the great physiological and ecological tolerance of species "using" estuaries (Whitfield, 1994b).

He also underscored the fact that LEEs differ from some other continental systems in that they have a low tendency to shift towards more mature animal and vegetal communities. In Lake Malawi, for example, the fish community is characterized by a growing proportion of specialized forms with progressively stronger interdependent relationships between species (Bruton, 1989). Meanwhile, the estuaries of South Africa, and African LEEs in general, are characterized by wide variations of abiotic conditions, the constant reorganization of biological communities and homeostatic mechanisms, and the frequent resetting of ecological successions to an earlier stage (Whitfield & Bruton, 1989).

Owing to the structural and functional complexity of LEEs, the stability and organization of fish communities, in the sense of the permanence of their species composition and structure, is subjected to two processes (Baran, 1995):

• mobility of species that affects the degree of organization of biocoenoses,

• ecophysiological plasticity of sedentary species that allow them to tolerate environmental variations and which encourage stability.

In the short term, that is at a seasonal level, the outcome of these two processes with antagonistic effects tends to encourage instability.

But, from year to year, the cyclical nature of climatological, hydrological, and hydrochemical factors that directly or indirectly determine the organization of communities through inter-species competition (Guiral, 1992) encourages a certain stability.

At the scale of one or two decades, this stability is also seen (Livingston, 1976; Whitfield, 1994a; Albaret & Écoutin, 1990) except in cases of rapid anthropogenic and/or natural changes in the environment (Albaret, 1987; Albaret & Écoutin, 1989; Albaret & Diouf, 1994).

Biology and adaptive strategies

In fishes as in other organisms living in LEEs, physiological (Vernberg & Vernberg, 1976) and behavioural (Smith *et al.*, 1966; McDowall, 1976; Day & Yañez-Arancibia, 1985; Day *et al.*, 1989) adaptations have been developed to deal with the stress generated by the degree and speed of fluctuations in physico-chemical factors (McHugh, 1985; Deegan & Thompson, 1985; Day & Yañez-Arancibia, 1985; Whitefield, 1994a).

The strategies in play can be outlined in three broad categories: breeding strategies, space occupation strategies, and resource use strategies (Lévêque, 1994).

Reproduction and breeding strategies

LEEs are often viewed solely as transit areas, "nurseries" for juvenile stages of fish whose adult life and reproduction occur in adjacent ecosystems, notably the marine environment. Only a few sedentary species, of small size and little ecological or economic significance, were believed to be capable of completing their full biological cycle in these systems whose strong variability and unpre-dictability are sometimes considered physiological obstacles to the reproductive process. In fact, studies conducted in West Africa (Albaret, 1987; Albaret, 1994; Diouf, 1996; Baran, 1995) show that lagoons and estuaries are the site of intense reproductive activity for a very wide range of species (table 22.IV). Reproductive activity is generally very widely spread out over time and space with, however, peaks of activity around the dry or rainy seasons depending on the marine or continental affinity of species. Environmental requirements, particularly for salinity, are generally low. The euryhalinity of most estuarine species at the time of reproduction is remarkable (Albaret & Diouf, 1994).

Reproduction in lagoon	Advanced maturation in lagoon	Early stage of maturation in lagoon
Brycinus longipinnis	*Antennarius occidentalis*	*Brachydeuterus auritus*
Aplocheilichthys spilauchen	*Apogon imberbis*	*Drepane africana*
Chrysichthys auratus	*Chromidotilapia guntheri*	*Eucinostomus melanopterus*
Chrysichthys maurus	*Chrysichthys nigrodigitatus*	*Galeoïdes decadactylus*
Dasyatis margarita	*Eleotris senegalensis*	*Marcusenius bruyerei*
Citarichthys stampflii	*Fodiator acutus*	*Plectorhynchus macrolepis*
Arius parkii	*Hemiramphus balao*	*Pomadasys incisus*
Arius latiscutatus	*Heterobranchus isopterus*	*Sardinella maderensis*
Cynoglossus senegalensis	*Hyporamphus picarti*	*Scomberomorus tritor*
Eleotris daganensis	*Liza dumerili*	*Sphyraena afra*
Eleotris vittata	*Mugil curema*	
Ethmalosa fimbriata	*Petrocephalus bovei*	
Gerres nigri	*Pseudotolithus senegalensis*	
Gobionellus occidentalis	*Schilbe mystus*	
Hemichromis fasciatus		
Liza falcipinnis		
Liza grandisquamis		
Monodactylus sebae		
Parailia pellucida		
Pellonula leonensis		
Pseudotolithus elongatus		
Pomadasys jubelini		
Porogobius schlegelii		
Sarotherodon melanotheron		
Schilbe mandibularis		
Strongylura senegalensis		
Tilapia guineensis		
Tilapia mariae		
Trachinotus teraia		
Trichiurus lepturus		
Tylochromis jentinki		
Yongeichthys thomasi		

TABLE 22.IV.

List of species engaging in sexual activity in the LEEs of West Africa (Albaret & Diouf, 1994).

In the LEEs, reproductive strategies are aimed on one hand at minimizing the negative effects of environmental instability and on the other hand on combatting the dispersion of eggs, larvae, and embryos outside the estuary. Oviparous species have developed two "tactical choices" (Wootton, 1989). The first is based on maximizing the number of eggs released, and increases the probability that at least a fraction of the population will be transported to a favourable site in order to ensure recruitment (*Liza* spp., *Ethmalosa fimbriata*). The second tactic attempts to maximize the survival rate of eggs, larvae, and fry by limiting the number of eggs released and engaging in sometimes intensive parental care and/or seeking zones that are ecologically favourable to development. This, for instance, is the case of *Arius* spp, *Sarotherodon melanotheron,* and *Tylochromis jentinki* which practice mouth brooding, *Chrysichthys* spp whose clutches are attached and hidden in crevices or hollow pieces of wood, or *Tilapia guineensis* which build nests and guard the clutch and the fry (McKaye, 1989; Albaret & Diouf, 1994).

Viviparous (*Clinus superciliosus* in Southern Africa and *Dasyatis margarita* and *D. margaritella* in West Africa, for example) and ovoviviparous species (such as *Syngnathus acus* in Southern Africa and *Enneacampus kaupi* in West Africa) also have low fecundity. Embryos often reach a large size before hatching or release. Because of their large size, juveniles are less susceptible to predation or being carried away by currents (Whitfield, 1994a).

To reduce the risk of egg dispersal, groups with high estuarine affinity such as Atherinidae, Hemiramphidae and Gobiidae produce adhesive benthic eggs (Breder & Rosen 1966; Neira *et al.*, 1988; Potter *et al.*, 1990; Whitfield, 1990). Some species (mainly viviparous and ovoviviparous), sharply decrease or eliminate the initial larval stages and give birth to larvae that can swim well. It thus appears that the "precocial" reproductive strategy of some estuarine species can be traced to the fact that these fishes are attempting to limit the mortality risks associated with the uncontrolled dispersion of eggs and early larval stages (Whitfield, 1990). Other species such as *Amniataba caudavittata*, *Nematalosa vlaminghi* and *Gilchristella aestuaria* (species from southwestern Australia and Southern Africa), spawn far from the river mouth, very high upstream in the estuary, thus reducing the risk that eggs are transported out to sea (Talbot, 1982; Chubb & Potter, 1984; Potter *et al.*, 1990).

In most of the species reproducing in the estuary, the period of sexual activity is long if not continuous. This spread of the reproductive season can be interpreted as the guarantee of sufficient recruitment in all eventualities (Wallace, 1975; Baran, 1995).

The "eco-reproductive" plasticity of most strictly estuarine species (E.s.) and estuarine species of marine or continental origin (E.m. and E.c.) is the reason for the high variability in reproductive modalities and energy allocation for reproductive activity depending on changes in the environment (Pauly, 1975) and biological interactions (Barbault, 1981; Legendre, 1992). This is the case in particular of *Ethmalosa fimbriata* and *Sarotherodon melanotheron* which display reduced size at first maturity when the environmental conditions become extreme: pollution (Albaret & Charles-Dominique, 1982), hypersalinity (Albaret, 1987); life in a confined system (Legendre & Écoutin, 1991).

Space occupation strategies

Heterogeneity, which increases the diversity of ecological niches, plays a fundamental role in the organization of communities (Barbault, 1992). It allows the maintenance of predator-prey systems by increasing the probability of survival of a fraction of the prey population which can colonize habitats that are not accessible to predators (Barbault, 1990).

Thus, in LEEs, many shoals, silt and sand bars, mangrove channels, as well as the root network of mangroves (stilt roots of *Rhizophora* and respiratory roots of *Avicennias*) are shelters that are accessible only to juveniles.

Moreover, the spatial segregation of species, related to heterogeneity, helps decrease the phenomena of inter-species competition (Blaber & Whitfield, 1977; Gorman, 1987; Wootton, 1992).

Species that use LEEs during their biological cycle demonstrate two occupation strategies to exploit to their advantage these nutrient-rich environments where predation is often low: migration and eco-physiological plasticity.

Migration is the solution adopted by a very large number of opportunistic species of marine origin and (to a lesser degree) species with a continental affinity that temporarily exploit the trophic richness of LEEs when the physico-chemical (Guiral, 1992) and biological (Sykes & Manooch, 1978; Day & Yañez-Arancibia, 1982) conditions are favourable. The space occupation strategies of these migratory species aim in many cases to reduce the distances between marine breeding areas and estuarine and lagoonal nursery zones (Whitfield, 1990).

The second strategy is adopted by sedentary species (at the scale of one lagoon or one estuary) that adapt to the variability of the system owing to their strong adaptability and great eco-physiological tolerance. In the case of very significant environmental stress, representatives of this category are capable of surviving, thriving, and in some cases proliferating. The extreme abundance of *Sarotherodon melanotheron*, the only species present in the hyperhaline upstream section of the Casamance during periods of rainfall deficit is one of the most spectacular examples of this ability to adapt (Albaret, 1987).

Food webs and resource use strategies

Fish diets and food webs have been the target of numerous investigations in both West Africa (Longhurst, 1957; Fagade & Olanyian, 1973; Pauly, 1975; Albaret 1994; Baran 1995; Diouf 1996.) and Southern Africa (Whitfield & Blaber, 1978a, b; Whitfield, 1980a, b).

LEEs are very productive ecosystems (Correll, 1978; Horn & Allen, 1985; Day & Yañez-Arancibia, 1982; Day *et al.*, 1989). Among aquatic systems, only coral reefs are generally seen as being more productive (Whittaker & Likens, 1973; Whitfield, 1993). This productivity, which is reflected in the great availability of nutrients for fishes, stems from the number and diversity of nutrient sources (Day & Yañez-Arancibia, 1982): runoff (Day & Yañez-Arancibia, 1985), fluvial (Yañez-Arancibia *et al.*, 1985) and marine (Cecchi, 1992) waters, remineralization of organic matter from river and submerged vegetation (William & Eric, 1972; Odum & Head, 1975; Twilley *et al.*, 1986; Day *et al.*, 1989; Alongi, 1988). In addition to all these advantages encountered by young fishes in estuarine systems, tropical zones are also characterized by the high production of mangrove formations (Odum & Head, 1975; Dor & Levy, 1984; Rodelli *et al.*, 1984). While tree production is not directly consumed by fish, it allows the creation of a rich and complex microbial network (Guiral, 1994). This bacterial and fungal biomass, which mineralizes litter, as well as the algal, phytobenthic and epiphytic production occurring on mangrove roots (Rodriguez & Stoner, 1990) that stem partially from that biomass, make up particularly rich and varied nutrient resources owing to their zooplanktonic, micro-, meio-, and macro-benthic communities (Alongi, 1989). Trophic chains in LEEs are thus characterized by the diversity of primary producers (Day

& Yañez-Arancibia, 1985; Flores-Verdugo *et al.*, 1990), which ensures abundant production throughout the year (Day & Yañez-Arancibia, 1982; Whitfield, 1980b). Phytoplankton is not the sole primary producer, nor is it necessarily the most important. Mangrove leaves, marsh vegetation, grasses, and the phytobenthos also play an important role.

In tropical LEEs, these resources display significant variability in time and space (Barett *et al.*, 1978; Deegan & Thompson, 1985). Adaptations developed by species living in these ecosystems are mainly intended to adjust to the unpredictable nature of food availability. Many migratory species, whether marine or continental in origin, optimize the use of lagoonal and estuarine trophic richness by synchronizing their reproduction and migration with periods of nutrient abundance (Yañez-Arancibia *et al.*, 1980; Day & Yañez-Arancibia, 1982).

There is little available information on food competition in LEEs. In general, it is believed that the absence of trophic specialization is an efficient way of preventing competition for resources that are abundant but of variable nature and quantity. However, in Southern Africa where detritivores are numerous, it has been shown that competition can be reduced by different mechanisms leading to a certain dietary segregation (Whitfield & Blaber, 1978b). This nonetheless seems to be very rare in many Mugilidae species (Blaber, 1977), which Whitfield (1996) interprets as an indicator that detritivores have access to extremely abundant nutrient resources in estuaries.

The most successful trophic strategy in these systems is based on low special-ization and strong dietary opportunism. Omnivores (Deegan & Thompson, 1985) and unspecialized predators that can include fishes, crustaceans, molluscs, and insects in their diet are consequently the most numerous species (up to 80%, Albaret, 1994). Crustaceans, particularly Peneidae and Mysidacae shrimp, represent a crucial dietary source for estuarine fishes, particularly young predators (Albaret, 1994).

Although they are represented by a relatively low number of species (15 to 30% depending on the case), opportunistic filter-feeders such as *Ethmalosa fimbriata* that can feed on phytoplankton, zooplankton, and even microbenthos depending on the supply in the ecosystem, often make up the bulk of fish biomass in the LEEs of West Africa (Albaret, 1994).

Whitfield (1996) points out the absence of phytoplanktivorous fishes in the estuaries of South Africa where he notes, along with authors such as Blaber (1977), the importance of the detrital path also highlighted by Albaret & Diouf (1994) for the LEEs of West Africa which, according to Diouf (1996), is an addition to primary production-based trophic chains that are usually seen in aquatic systems.

We should still note the rarity of linear food chains and of exclusive or highly-determined predator/prey relationships in these ecosystems where, on the contrary, species show low dietary specialization, high adaptability, and even great trophic opportunism.

Functional role
of lagoon and estuarine ecosystems

Exportation of organic matter and energy

The influence of LEEs on the halieutic production of coastal marine areas is well established (Moore *et al.*, 1970; Sutcliffe, 1973; Yañez-Arancibia *et al.*, 1980; Baran, 1995). One of the main paradigms of the ecology of coastal lagoons and estuaries these past three or four decades is that these systems produce an excess of organic matter and nutrients, a good part of which is exported out to sea. This is the so-called "outwelling hypothesis" (Darnell, 1967; Day *et al.*, 1973; Odum *et al.*, 1974).

Some studies call this hypothesis into question and suggest on the contrary that organic carbon may be imported into certain LEEs (Hains & Dunstran, 1976; Woodwell *et al.*, 1977). In fact, the direction of the net flow of exchanges between an estuarine environment and a marine coastal zone may depend on local conditions (Day & Yañez-Arancibia, 1982; Day & Yañez-Arancibia, 1985).

Fishes in the LEEs play an important role in the flow of energy and nutrients. As secondary consumers, they can constitute energy and nutrient reserves, thus limiting the exportation of nutritional elements. Moreover, through their migrations, they can allow nutrient and energy exchanges with coastal marine systems (Yañez-Arancibia & Nugent, 1977; Kitchell *et al.*, 1979). The exportation of juveniles after growing in lagoon and estuarine environments corresponds to a loss of energy for these systems and an energy gain for the ecosystems receiving them (Thollot, 1992). This energy loss can be considerable. In effect, juveniles migrating out to sea may have multiplied their individual weight by 2,000 during their stay in estuaries and lagoons (Wagner, 1973; Hinchee, 1977). This good growth is also accompanied by high survival rates for these juveniles in lagoon and estuarine ecosystems owing to food abundance and relatively low predation (Day *et al.*, 1989).

Nursery

The importance of estuaries as nurseries for the juvenile forms of many fish species has been seen in diverse latitudes (Johannes, 1978; Beckley, 1984; Ross & Epperly, 1985; Day *et al.*, 1989). In many cases, breeders spawn in coastal areas (Yañez-Arancibia, 1985; Whitfield 1990), then larvae arrive in the estuary through passive transport among plankton or through active swimming. The interpretations put forth to explain the adaptive advantage of this migration generally refer to water turbidity (suspension of mineral and organic particulate matter of a planktonic or detrital nature) and high trophic availability observed in LEEs. Post-larval and juvenile fishes in the estuary thus find favourable trophic conditions that are diverse and suited to their filtration and capture capacities (May, 1974; Miller & Dunn, 1980; Mann, 198; Legett, 1986). The aggregating behaviour of fry with limited swimming and escape capacities, combined with the frequent turbidity of LEE waters that reduce a predator's distance of perception, increases the probability of escape for prey and thus the overall survival rate for the population. Such a mechanism has been verified

experimentally by several authors (Viniyard & O'Brien, 1976; Cyrus & Blaber, 1987a, b, c; Gregory, 1993). Moreover, the abundance of shoals in LEEs restricts the access of large ichthyophagic predators, thereby contributing to less predation pressure on juveniles and small species (Blaber, 1980; Blaber & Blaber, 1980; Kneib 1987). Finally, compared with the marine system, the diversity and structural complexity of habitats in LEEs encourages the concentration and retention of juvenile forms (Fraser & Cerri, 1982; Cowder & Cooper, 1982; Nelson & Bonsdorff, 1990).

Such favourable conditions for the nutrition and survival of juvenile forms, combined with the relatively high temperatures often found in LEEs, encourage rapid growth (Potter *et al.*, 1990; Lenanton & Hodgkin, 1985).

However, to benefit from these advantages, these forms must have acquired certain ecophysiological adaptations that allow them to thrive in a variable and often unpredictable environment. Thus, the metabolic effort associated with temperature and ion regulation in these tolerant, opportunistic species in the juvenile stage may remain two to three times less than the energy they would consume by actively swimming out of estuaries (Miller *et al.,* 1985).

There is broad scientific consensus about the role of LEEs as systems favourable to hosting, survival, and growth of juveniles of many coastal fish species, but many questions remain as to the qualitative aspect of the relationships connecting these species to LEEs and the existence of alternative habitats and nurseries in the coastal environment (Baran *et al.*, 1999).

Many species of continental origin also spend part or all of their lives in an estuarine ecosystem. Some, such as *Schilbe mandibularis* (with a large lagoonal distribution), *Parailia pellucida* and *Schilbe mystus* (limited to low salinity and freshwater sectors) can be observed as being notably abundant there (Albaret, 1994). The relationships between fluvial and lagoonal "populations" remain poorly understood, and the nursery role of the estuarine zone is still hypothetical as far as they are concerned.

Conclusions

Contrary to many preconceptions, the composition and general structure of estuarine fish communities display a high degree of stability and robustness at certain time scales (periods of 10 years or more). A connection must be made between this stability and the adaptability of species comprising these communities, the diversity and efficiency of the vital strategies deployed, as well as the existence within these communities of compensatory mechanisms for species (replacement over time of certain species by others that occupy a similar place and role without altering the general structure of the community). The constant availability of varied trophic resources and the sturdiness of food webs (Moyle & Cech, 1982) also constitute a factor contributing to the stability of fish communities. Such long-term stability and robustness nonetheless has limits, which were seen after monitoring the changes that occurred in certain brackish water systems: hypersalinization of the Casamance (Albaret, 1987),

isolation of Togolese lagoons from the sea (Laë, 1992a) or, conversely, an increase in exchanges following the opening of a new channel in the Ébrié lagoon (Albaret & Écoutin, 1989), construction of a dam in the upstream section of the Senegal River estuary, etc. These studies show that communities then undergo major changes in species richness, structure, and the mechanisms that govern their functioning. Baran (1995) stresses that tolerance and adaptability are written in the genes of estuarine species (Schachter, 1969; Battaglia & Fava, 1982), but only within the limits of the "natural" environmental variations encountered during the evolution of the species. The example shows that such tolerance and adaptability do not allow species to adapt to disturbances of an anthropogenic nature when these are of unusual scope, duration, or nature (Livingston, 1984).

Found at the interface of the continent and the ocean, LEEs are among the environmental systems most affected by anthropogenic activity and global changes. They have been sites of human occupation since prehistoric times. Today, with population growth, these systems are under heavy demand from all directions, often in contradictory ways: fishing, aquaculture, transport, protection of fauna and flora, urbanisation, tourism, various exploitations (e.g. mangrove wood, sand), hydro-agricultural works, etc.

While human activities are most often behind the deterioration of LEEs, natural events or changes may also lead to a more or less significant erosion of biological diversity. In fact, quite often the most delicate situations are the result of the combination of the two types of factors and their mutual aggravation. In West Africa, the chronic rainfall deficit in the Sahelian area enters in combination with multiple human interventions, profoundly modifying the biocenoses of estuarine systems without making it possible, at least in the current state of knowledge, to determine the exact degree of "responsibility" of the offending factors.

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The Inland Water Fishes of Africa

Diversity, Ecology and Human Use

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The inland water fishes of Africa

Diversity, ecology and human use