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African Shads, with Emphasis on the West African Shad *Ethmalosa fimbriata*

Emmanuel Charles-Dominique[1] and Jean-Jacques Albaret
Institut de Recherche pour le Développement, 213 rue Lafayette, 75480, Paris Cedex 10, France

Abstract.—Four shad species are found in Africa: twaite shad *Alosa fallax* and allis shad *A. alosa* (also known as allice shad), whose populations in North Africa can be regarded as relics; West African shad *Ethmalosa fimbriata* (also known as bonga), an abundant tropical West African species; and kelee shad *Hilsa kelee*, a very widely distributed species present from East Africa to the Western Pacific. *Ethmalosa fimbriata* has been the most studied species in this area. The concentrations of *E. fimbriata* are found only in estuarine waters of three types: inland, coastal, and lagoon estuaries. The species is rare in other habitats. Distribution thus appears fragmented, with possible exchanges between adjacent areas. In all populations, juveniles, subadults, and mature adults have different habitat preferences. These groups are distinguished by local people and can be considered as ecophases. The older group has a preference for the marine environment, and the intermediate one is more adapted to estuaries, with a large plasticity within its reproductive features. Information regarding population dynamics is poorly documented, but the populations appear generally resilient except when the estuarine environment deteriorates. West African shad has been exploited for many years and carries great cultural value for the coastal people of West Africa. The catches are marketed cured in the coastal zone, sometimes far from the fishing areas. It is a locally important, cheap, and much-appreciated food fish. The fisheries are intensive and developing (175,000 metric tons/year at present) and are entirely artisanal, and some reliable fisheries data do exist for certain areas. The main threats to the West African shad populations are overfishing and the deterioration of the environment. *Hilsa kelee* has the widest distribution of any alosine and is relatively important for fisheries (comparable to *E. fimbriata*). It is a microfeeding, marine pelagic fish entering estuaries. Very little information is available on this species.

Introduction

Shads depend upon different types of habitats: the sea, freshwater, and estuaries (McDowall 1988). These habitats have been surveyed individually in Africa (Chaboud and Charles-Dominique 1991), leading to an underestimation of the importance of overlapping species. The African shads' economic and cultural importance was revealed, among other resources, due to the development of artisanal fisheries (in West Africa; Chauveau et al. 2000). In addition, their ecological importance was recognized with the growing environmental concerns for the coastal zone and estuarine water bodies among the more populated areas.

Four shad species (Clupeidae, subfamily Alosinae) are found in Africa (Whitehead 1985). Twaite shad *Alosa fallax* (Lacépède, 1803), and allis shad *A. alosa* (Linnaeus, 1758; also known as allice shad) occurred in North Africa where they were at their southernmost limit of distribution (Figure 1). They have now almost disappeared from Morocco and other countries due to habitat degradation and overfishing (Baglinière and Elie 2000).

The last two species are West African shad *Ethmalosa fimbriata* (also known as bonga) (S. Bowdich, 1825) and kelee shad *Hilsa kelee* (Cuvier, 1829). They are of equal importance as fisheries (annual landings about 150,000 metric tons) but differ in the extent of their distribution area (much larger in the kelee shad) and the information available. The literature on West African shad is more abundant, especially when local publications and sources are considered. In the African context, local information (written or from traditional ecological knowledge) is difficult to find but worth collecting, as this review and an earlier one (Charles-Dominique 1982) attempt to show.

Ethmalosa fimbriata

Ethmalosa fimbriata is a tropical species, distributed between 24°N (Lozano-Rey 1950) and 12°S (Poll 1953) latitude. It is a species of marine ori-

[1] Corresponding author: charldom@ird.fr

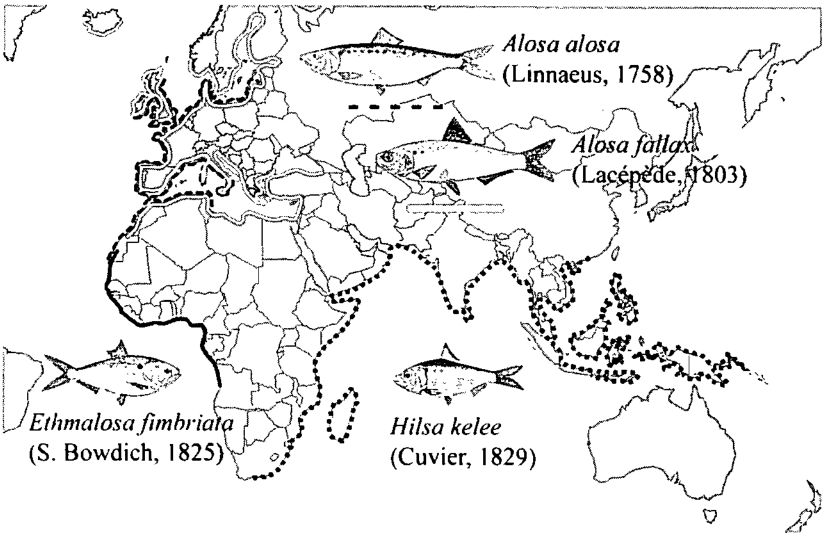

Figure 1.—Distribution of African shads.

gin but has marked affinities for estuaries, deltas, and lagoons.

Systematics and Identifying Characteristics

Ethmalosa fimbriata (Figure 2) belongs to the family Clupeidae (subfamily Alosinae). The species was first described as *Clupea fimbriata* by Sarah Bowdich (Sarah Lee at that time, the widow of the naturalist Thomas Edward Bowdich; to eliminate any confusion, some authors, such as Monod [1961], recommend adding her first initial before her last name.). The main morphometric and meristic characteristics of the species are given in Charles-Dominique (1982). *Ethmalosa fimbriata* is distinguished from other close Clupeidae by its upper jaw that has a distinct median notch into which the tip of the lower jaw fits.

Ethmalosa fimbriata has many local names in different languages of West Africa. One of them, bonga, is often used for the species common name. Bonga is actually used in most English-speaking countries, but it is little used or unknown elsewhere. Thus, it is preferable to retain West African shad, as used by several authors, as the most universal common name.

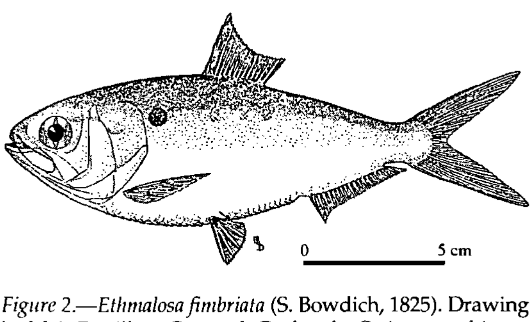

Figure 2.—*Ethmalosa fimbriata* (S. Bowdich, 1825). Drawing by Maja Devillers, Centre de Recherche Océanographique.

The Estuarine Habitat of Ethmalosa fimbriata

In this section, the different types of estuarine environments encountered in the distribution area are described, as related to specific climatic and hydroclimatic conditions. This characterization defines the extent of the estuarine habitats, which is correlated with the abundance of *E. fimbriata* populations. Also, the habitat characteristics are necessary to understand the differences among the biology of the different populations (next section).

The Notion of Estuarine Environment

From an ecological point of view, the term "estuary" applies to aquatic environments with variable salinity or turbidity at different time scales (from days to years). This variation can be due to the mixing of freshwater and saltwater or concentration by evaporation, with salinity varying from near 0‰ to hyperhaline (>40‰) waters. Other typical characteristics of estuaries are shallowness, presence of silt sediment, and, in the tropical zone, relatively warm and steady temperatures. Biogeographic aspects must also be considered. Some fish communities are typically associated with estuarine environments, for example, the "estuarine sciaenid community" (Longhurst 1963) or the benthic "margino-littoral" communities (Le Loeuff 1999) in West Africa. These communities can persist when the climate changes and estuarine conditions disappear, as in Banc d'Arguin, Mauritania (Le Loeuff 1999) or Angola (Costa et al. 2002) where *E. fimbriata* occurs.

The Three Types of Estuarine Environments in West Africa

Three types of estuarine environments within the distribution range of *E. fimbriata* will be distinguished according to their hydrodynamics (Figure 3). An "inland estuary" is comprised of flat river valleys that are seasonally drowned successively by the intrusion of marine water, sometimes hundreds of kilometers inland, and by floodwater; the diffusion of freshwater at sea is limited. This type of estuary is found from the Senegal River to Guinea-Bissau (Figure 4). In a "coastal estuary," marine water penetrates inland only to a maximum of 30–40 km, and freshwater discharge into the sea is abundant, making long coastal strips of freshwater (hundreds of km, 0–20 m in depth). This type of estuarine environment is found in two regions, from Guinea to Sierra Leone and from Nigeria to Cameroon (Figure 4). In a "coastal lagoon," estuarine (brackish) waters are mostly limited to inland water bodies with openings toward the sea (open or semienclosed lagoons) and may expand a very short way inland or at sea. This type is found mainly in the Gulf of Guinea from the Ivory Coast to West Nigeria (Figure 4).

The Hydroclimatic and Climatic Conditions

The marine environment, coastal hydrodynamics, the climate (rainfall and runoff), and the geomorphology (river slope, shelf width, etc.) determine the hydrodynamics of the estuaries.

In the "inland estuary" region, rainfall is low (400–1,600 mm/year from north to south) and seasonal (Nicholson 2000). Freshwater runoff depends on the size of the drainage areas, but the seasonal patterns are similar, with very little or no runoff at low water. The slight slope of the rivers allows the marine water to penetrate the rivers far upstream. From Mauritania to Guinea-Bissau, the marine environment shows strong seasonal fluctuations in temperature (16–28°C) due to seasonal coastal upwellings, producing destratification of waters. Thus, the warm, estuarine, low-salinity coastal waters are localized near river mouths and do not last throughout the year.

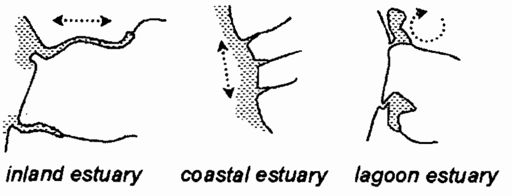

Figure 3.—Hydrodynamic types of estuaries in West Africa.

The "coastal estuaries" are found in the two highest rainfall (2,000–4,000 mm/year) regions of West Africa where runoff is also very high. The marine environment in these areas is typical tropical (Le Loeuff and von Cosel 1998), characterized by permanently stratified waters with low seasonal variations in sea surface temperature and high seasonal variations in salinity near the coast. Salinity of the surface layer (20–30 m) can decrease to 18‰ during the wet season on the continental shelf of Cameroon (Mahé 1993) and to 10‰ along the Guinea coast at a depth of 0–10 m (Baran 1995; Pezennec 2000). The large supply of freshwater and the permanent stratification of marine water produce estuarine conditions on the continental shelf (with regard to salinity, turbidity, sediment, and estuarine benthic and fish communities). This has been called the "coastal estuary" for Guinea and Sierra Leone (Baran 2000) or the "estuarization" phenomenon (Longhurst 1983). The coastal estuary, as defined above, expands and shrinks but persists throughout the year despite seasonal interruption of freshwater supplies. In these environments, the penetration of marine waters inland is often limited to a few tens of kilometers (because of different factors, e.g., large flows, coastal morphology, and stratification of coastal waters). Few direct studies confirm this point (Tetsola and Egborge 1991; Baran 1995), but confirmation can be found by observation of the distribution of true freshwater fishes found in the lower reaches near the coast (Lévêque and Paugy 1999).

The third type of estuary is the "coastal lagoon," found in the central Gulf of Guinea and in the southern distribution area from south Gabon to Angola. Off these coasts, there are alternating hydroclimatic seasons, with destratification of marine waters due to seasonal upwellings, variable temperatures (from 20–22°C to 29–30°C), and steady salinities, except seasonally and locally near the river mouths. The rainfall (800–2,000 mm/year) is lower than in the previous area, but the runoff of some large rivers may be important (the Congo River alone supplies 50% of the global freshwater runoff of West Africa; Mahé 1993).

In these conditions, the permanent estuarine environment is limited to the lagoons themselves. Their morphology hampers the penetration of seawater into the rivers, and coastal estuarization can

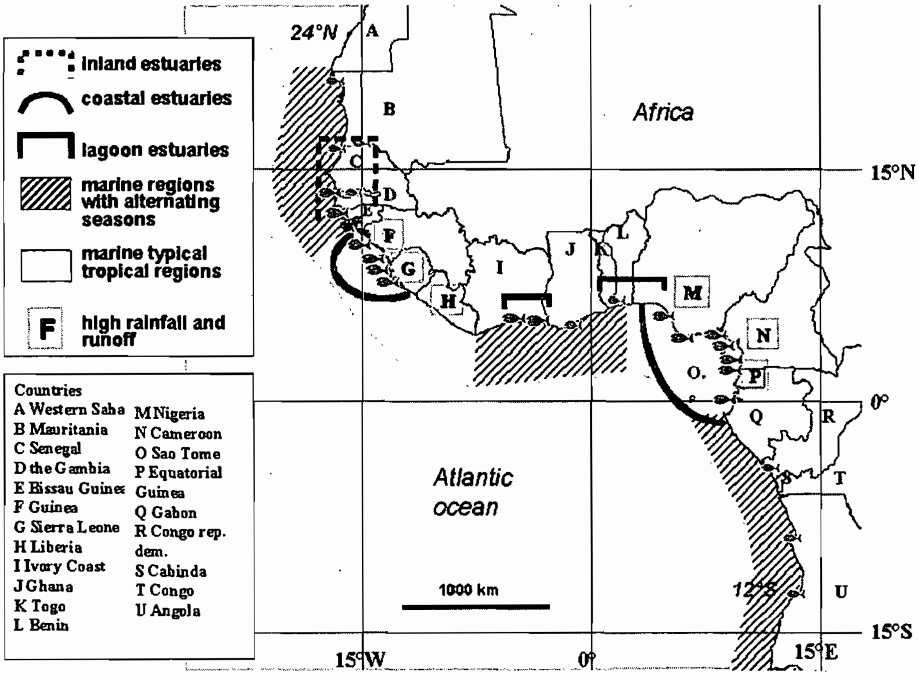

Figure 4.—The global distribution of *Ethmalosa fimbriata* in West Africa, from 24°N to 12°S latitude. Fish symbolize the main areas of concentration. The main types of estuaries are shown, with the hydroclimatic areas according to Le Loeuff and von Cosel (1998); mean annual rainfall from Nicholson (2000).

occur but is limited by the seasonal destratification (off Abidjan, Ivory Coast, during the flood season, the inshore salinity can decrease to 29–24‰; Colin et al. 1993).

Main Concentrations of Ethmalosa fimbriata

The concentrations of *E. fimbriata* are found only where estuarine areas, as defined above, are present. An approximate index of abundance is the annual landings by artisanal fisheries, since these are well developed and occur almost everywhere along the West African coast (Table 1). The main concentrations are found in Senegal, the Gambia, Guinea, Sierra Leone, Nigeria, and Cameroon. Among them, smaller concentrations are found in smaller estuaries and lagoons. At a distance from the estuarine areas, there are no significant landings.

Eleven estuarine areas were estimated (see Table 1 for details), and the relationship between area and annual catch of West African shad was plotted (Figure 5). A linear regression was fitted through the origin (r^2 = 0.7). As a first approximation, productivity of West African shad was roughly comparable among the different areas (mean productivity = 46 kg/ha), whatever the type of estuary and the geographical situation.

Presence Outside Estuaries

Some elements suggest a possible fragmentation of *E. fimbriata* populations (e.g., the discontinuity of estuarine habitats and the absence of large-scale migrations between the main concentration areas).

Ethmalosa fimbriata is rare at sea except at places near direct estuarine influence. For example, in the "lagoon estuaries" area on the Ivory Coast, though a high abundance is found in the lagoons (catches equal about 7,500 metric tons), the species is very rarely found at sea. A careful sorting of the pelagic catches at sea in 1987 revealed 50 metric tons of *E. fimbriata* caught of a total of 50,000 metric tons (Pezennec et al. 1993). In Togo, Faggianelli and Faggianelli (1984) did not find any *E. fimbriata* despite a detailed sorting of the 13,000 metric tons of fish caught in that year by the marine artisanal fishery.

Ethmalosa fimbriata is, however, probably present everywhere near the shore, albeit rarely or sporadically; occurrences are reported in all the distribution areas (Froese and Pauly 2001). Thus, interchanges probably exist between concentration areas.

Differences between distant populations were sought, but not found, by several authors (genetic

Table 1.—Estuarine areas and annual catches (metric tons) of *Ethmalosa fimbriata*. The bold data are used for the catch–area relationship (Figure 5).

Country	Area	Size (km^2)	Production (kg/ha)	Catch per year	Sources	Notes
Mauritania	Sea			0	Hatti and Worms (1998)	
Senegal	**Senegal River**	**270**	**22**	**600**	**Authors' planimetry; Scheffers (1973)**	**Annual average of inland estuarine area; probably not exceeded since this 1972 figure**
	Sine-Saloum and the Gambia	**4,040**	**88**	**35,700**	**Authors' planimetry**	**Annual average of inland estuarine area; for size calcuation**
	Sine-Saloum estuary	**540**		**6,700**	**Bousso (1996)**	**1992 catches**
	Gambia River	**700**		**22,000**	**FishStat (2000)**	**1996–1998 catches**
	Coastal strip (10 km wide)	**2,800**		**7,000**	**CRODT (1994)**	**1982–1993 catches; "petite côte" between Dakar and the Sine–Saloum estuary**
	Casamance	**500**	**58**	**2,900**	**Authors' planimetry; Diadhiou et al. (1986)**	**1984–1985 catches**
Guinea	**Sea**	**5,300**	**48**	**26,000**	**Chavance and Domalain (2000a)**	**1989 catches; coastal strip 0–10 m deep, 18 km wide**
Sierra Leone	**Sea**	**3,800**	**56**	**21,500**	**FishStat (2000)**	**1982–1998 catches; coastal strip 10 km wide**
Liberia	Sea			26	FishStat (2000)	1990–1998 catches
Ivory Coast	Grand Lahou Lagoon	190			Authors' planimetry; Laë (1992)	*Ethmalosa fimbriata* estimated to be 9% of the total fish abundance
	Ebrie Lagoon	**566**	**37**	**2,100**	**Durand et al. (1994); Laë (1992)**	**1978–1982 catches**
	Aby Lagoon	**484**	**105**	**5,100**	**Durand et al. (1994); Charles-Dominque (1994)**	**1979–1990 (except 1981) catches**
	Sea			50	Pezennec et al. (1993)	1978 catches
Ghana	Sea			920	FishStat (2000)	1975-1996 catches
Togo	Togo Lake	52	4.4	23	Laë (1992)	1983–1984 catches
Benin	**Nokoue Lake**	**146**	**205**	**3,000**	**Texier (1983)**	**By 1959–1970, the total fish catch was 5,000-15,000 metric tons; extremely large production value of 700 kg/ha due to the enhancement of productivity by brush parks; proportion of *E. fimbriata* was 30%, annual catch of 1,500–4,500 metric tons**
Nigeria	**Sea and estuaries**	**14,000**	**33**	**47,000**	**Marcus (1984b)**	**Estimates in Nigeria have varied widely**
					FishStat (2000)	**Reports large and questionable year-to-year variations from 5,000–45,000 metric tons**
					Federal statistics from 1980	**25,000 metric tons globally**
					FAO (1981)	**30,000 metric tons globally**

Table 1.—Continued.

Country	Area	Size (km²)	Production (kg/ha)	Catch per year	Sources	Notes
Nigeria	**Western region**			**8,000**		
	Niger Delta region			**10,000**		
	Cross River estuary area			**17,000–41,000**	**Moses (2001)**	**1973–1991 catches**
	Coast			**35,000–60,000**	**Marcus (1984b)**	**22-30% of the total catches; FAO maximum sustainable yield estimate is 60,000 metric tons**
Cameroon	**Sea and estuaries**	**3,600**	**49**	**17,700**	**FishStat (2000); also Njifonjou (1998)**	**1980–1994 catches; coastal strip 10 km wide**
Gabon	**Sea, lagoons, and estuaries**	**5,000**	**25**	**12,500**	**FishStat (2000); Fréon et al. (2000)**	**1985–1997 catches**
	Sea	**800**				
	Estuaries	**4,200**				
	Rio Muni Bay	**1,600**				
	Gabon estuary	**865**				
	Nkomi Lagoon and Ogooué Estuary	**1,000**				
	Ngobé Lagoon	**208**				
	Ngodo Lagoon	**389**				
	Mbanio Lagoon	**142**				
Republic of Congo	Sea	1,500	2.0	300	Gobert (1985)	1981–1983 catches; *E. fimbriata* only fished in important quantities at Matombi, 200-300 metric tons
					Fréon et al. (2000)	Total artisanal landings 10,000 metric tons in 1983; coastal strip 10 km wide
Angola	Sea			1,800	Fréon et al. (2000)	
Subtotal[a]		**37,706**	**46**	**174,000**		
Total catch (rounded)				180,000		

[a] Subtotal of bold data used for the catch–area relationship.

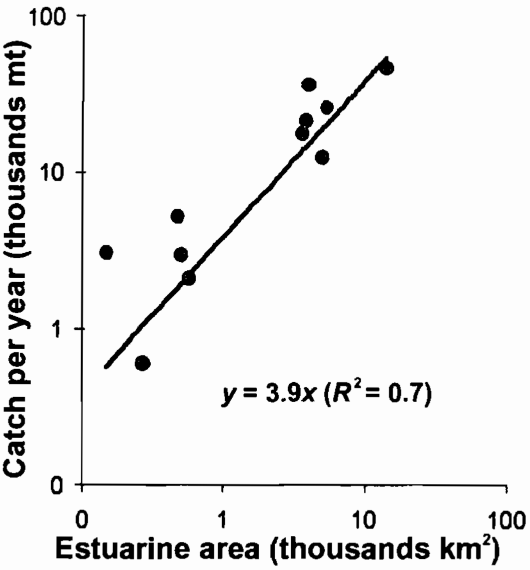

Figure 5.—Annual catch of *Ethmalosa fimbriata* versus estuarine area relationship (data from Table 1). Linear regression through the origin; mt = metric tons.

comparison, Gourène et al. 1993; biological comparison, Scheffers and Conand 1976), although Fréon (1979) found significant morphometric differences between the Mauritanian and Senegambian populations. Yet, these morphometric differences in clupeids may depend more on environmental conditions than genetic differences in populations.

Though tolerant of low salinities and even freshwater, *E. fimbriata* does not stay completely in freshwater. It is always absent from closed water bodies that have no connection with the sea.

Comparative Biology of Different Populations of Ethmalosa fimbriata

In this section, some life history case studies of *E. fimbriata* are presented, taking into account the specificity of West African shad environments and their typical changing behavior through successive developmental phases.

Ecophases.—One of the more striking features of the biology of *E. fimbriata* is its changing ecological preferences through successive phases, from juveniles to preadults and young adults to large adults. These different groups have been recognized and named by local people in several countries and agreed to by biologists (Sierra Leone, Salzen 1958; Lagos Lagoon, Nigeria, Fagade and Olaniyan 1972; Aby Lagoon, Ivory Coast, Charles-Dominique 1994; Cameroon, Njifonjou et al. 1999). The movements and reproduction of *E. fimbriata* from five areas (two inland estuaries, two coastal estuaries, and one lagoon estuary) are presented.

Inland Estuaries: Senegal River, Sine-Saloum Estuary and Gambia River, and Casamance River.—The Senegal River (Figure 6) has a seasonal flood (September–December) and a flat profile that allows seawater to penetrate upriver during the dry season. Its hydrodynamics has been entirely modified by the construction of a dam 50 km from the mouth at Diama in 1986. The estuarine area in the dry season is now restricted to about 70% of its previous natural area. Hyperhaline conditions are found seasonally in some parts of the estuary, for example, the Diawling Park, Mauritania, where *E. fimbriata* is found.

Two studies of *E. fimbriata* in the Senegal River before the dam was constructed (Scheffers et al. 1972; Scheffers 1973) showed that *E. fimbriata* was present in the lower reaches all year and moved upstream only during the dry season (January–May), as also evidenced by seasonal fishing activity. In July 1972, *E. fimbriata* was found 140 km upstream where salinity was 5‰. During the dry season, reproduction occurred everywhere in the brackish waters of the river. In the river, maximum larval density was found upriver at 5–10‰ salinities. Thus, movements characteristic of anadromous fishes seemed to occur but involving only a fraction of the population at most. A more likely hypothesis is the accompanying movement of fish (possibly up and down) within an expanding estuarine area.

During flood conditions (September–December), immature fish take refuge in the shallow water downstream. At this time, the adults are rarely in the lower reaches, although at sea, *E. fimbriata* appear in set gill nets and beach seines (Scheffers 1973).

The total landings (sea and river) were 600 metric tons in 1972. The population of the Senegal River is thus a small one, with possibly few interactions with the nearer populations of Mauritania and Sine-Saloum estuary–Gambia River (each about 3–400 km apart). The landings at sea from 1982 to 1993 (50–200 metric tons; CRODT 1994) did not show a collapse after the dam was built. Further studies will be necessary to assess the viability of this small population in a highly modified environment.

The Sine-Saloum estuary and Gambia River (Figure 7) form a composite area where separate studies of the biology of *E. fimbriata* have been un-

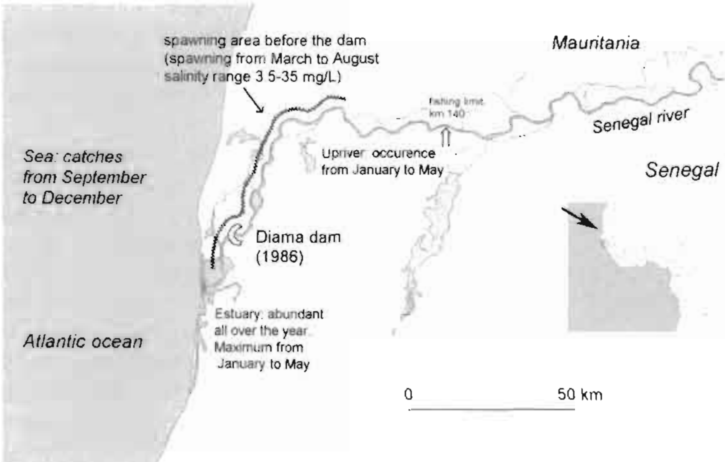

Figure 6.—Life history of *Ethmalosa fimbriata* in the Senegal River.

dergone. The specific sites include the Gambian coast and river (Scheffers and Conand 1976; Lesack 1986), the Sine-Saloum estuary (Bousso 1996; Diouf 1996), and the Senegalese coast (Blanc 1951; Lopez and Fréon 1981).

Estuarine conditions are very different in these subareas. The Sine-Saloum estuary (540 km^2) receives very low freshwater supplies and shows inverse estuary conditions seasonally or year-round during dry years. In 1991, the salinities were rather steady seasonally and increased from 37‰ to 40‰ in the lower part and 60‰ to 100‰ upstream (Diouf 1996). *Ethmalosa fimbriata* was found at salinities up to 90‰ in February 1992.

The Gambia River has a very flat lower basin (0.5-m elevation at 500 km from the mouth) and a discharge of zero during the dry season from December to June, allowing marine waters to penetrate as far as 250 km upriver (Lesack 1986), where salinity is 1‰ in June. The flood, typically tropical with high waters from July to November, pushes down the 1‰ salinity limit to 80 km from the mouth, where salinity can decrease below 25‰ (Scheffers and Conand 1976).

The West African shad drift gill net fisheries of the Sine-Saloum estuary were studied by Bousso (1996) by a thorough survey of the fisheries. The fishing season lasted from February to May (the cold season at sea) and was based upon the 18–30-cm (fork length; FL) size-group (the selectivity range of the mesh). Length measurements for *E. fimbriata* given throughout the text have been con-

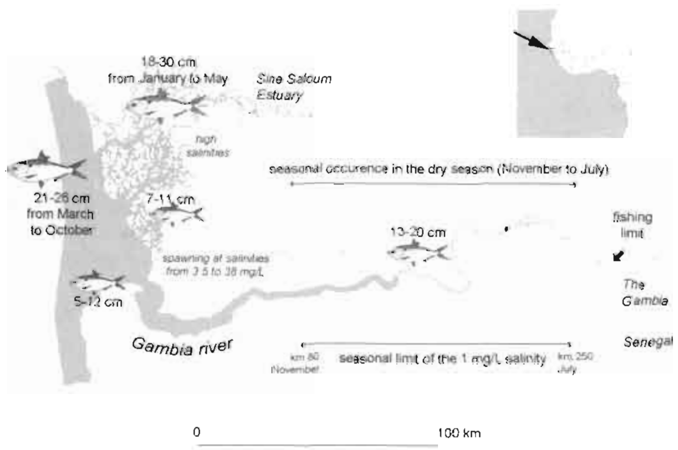

Figure 7.—Life history of *Ethmalosa fimbriata* in the Sine-Saloum–The Gambia area. The main distribution area is shaded.

verted to FL using the following equations: from total length (TL), FL(cm) = 0.81 TL(cm) + 0.21 (Gerlotto 1979), and from standard length (SL), FL(cm) = 1.008 SL(cm) + 0.215 (Moses 1988). The seasonal abundance of this size-group was confirmed by research surveys (RAP 2001), forming 12% of the numbers from February to May but only 0.4% from June to December.

Along the Senegalese coast south of Dakar, long fisheries data series are available (CRODT 1994). The main fishing methods are encircling nets, set gill nets, and purse seines, all resulting in catch sizes of 21–26 cm (Fréon et al. 1978; Lopez and Fréon 1981). The encircling nets and set gill nets have a higher catch per trip during the warm season from May to October (also noted by Blanc 1948), while the purse seines have higher yields during the cold season from January to July. Thus, there are probable seasonal movements of big adults between the sea and the estuary, but they are not well documented in the Sine-Saloum or elsewhere.

In the Gambia River and estuary (Figure 7), *E. fimbriata* penetrates seasonally up to 180 km following the penetration of saltwater, as observed by Lesack (1986). Reproduction in the Gambia River was studied using larval surveys (Scheffers and Conand 1976). It occurred throughout the year at the river mouth in salinities of 18–38‰ but only during the dry season upriver with salinities above 10‰. The larval abundance index (larvae/100 m^3) was high but irregular at the river mouth (0–150), low in the middle reaches (<10), and seasonally as high upstream as at the river mouth. Most of the reproduction probably occurred downstream, as the spawning area upstream was much smaller than the downstream one. Furthermore, some immature fish (13–17 cm; less than the estimated size at first maturity for females of 18.5 cm) also moved upriver. As in the Senegal River, only a fraction of the population, made up from the intermediate class of young adults, moved upstream for spawning (Figure 8).

Analysis of the different size distributions (Figure 8) demonstrates that *E. fimbriata* probably moves between the subareas of the Sine-Saloum estuary and the Gambia region. In the Sine-Saloum, small fish (5–10 cm) are well represented and middle sizes (10–18 cm) are underrepresented. It is the reverse in the Gambia River. Adults (>18.5 cm) are found in different areas. These possible migrations between adjacent areas and the possibility of a single population still remain hypotheses because of the heterogeneity of the data available.

The Casamance estuary is the third inland estuary in the region. It has a weak runoff and inverse estuary conditions during dry years. *Ethmalosa fimbriata* was found in abundance as far as 218 km from the mouth, at salinities of up to 82‰ (Albaret 1987). Below 66‰, the abundance and even the reproduction did not seem to be affected. These observations increase the previously known limits of salinity tolerance for this species.

Coastal Estuaries: Guinea, Sierra Leone, Nigeria, and Cameroon.—The Guinea and Sierra Leone coastlines make up 8% of the total area and contribute to 27% of the total catch. The environmental conditions in this area include high rainfall and runoff from small rivers producing an estuarization effect on the coastal area (Longhurst 1983; Baran 1995). The shelf is broad except in the south of Sierra Leone. In Guinea, the 0–20-m depth strip is between 20 and 90 km wide.

In Guinea, *E. fimbriata* is the main target species for the artisanal fisheries, which have developed rapidly during the last 20 years. Accurate estimates of catches of *E. fimbriata* were made for 1989 at 26,000 metric tons (50% of the total catch; Chavance and Domalain 2000a). The main fishing techniques are encircling nets and drift gill nets (Chavance and Domalain 2000a). The fishing areas at sea are mapped for 1995 (Chavance and Domalain 2000b); they lie on the coastal strip at depths from a few meters to 15–20 m and from inshore to 35–50 km offshore. The catches per trip show seasonal variations related to environmental changes (Figure 9). As the dry season progresses, the yields of the surrounding nets fishing further offshore decrease while the yields of the gill nets fishing onshore are maximal. *Ethmalosa*

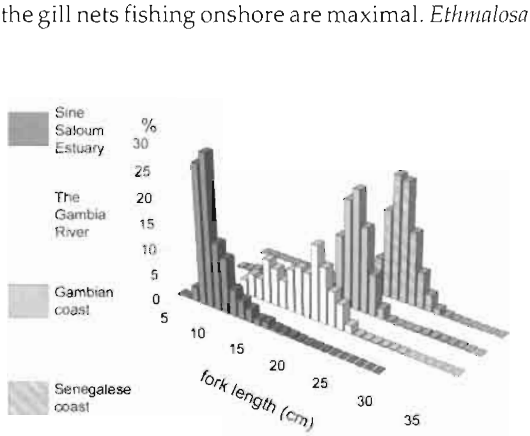

Figure 8.—Size distributions of *Ethmalosa fimbriata* in the Sine-Saloum–The Gambia area.

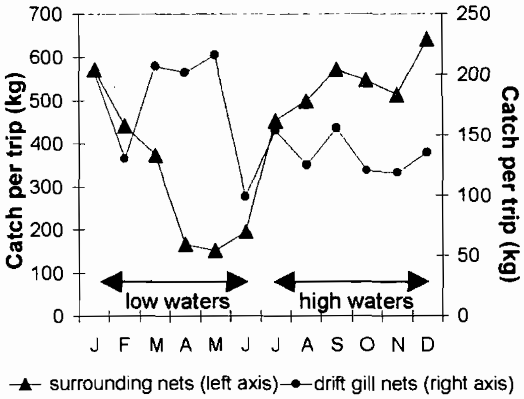

Figure 9.—Abundance indices of *Ethmalosa fimbriata* at sea on the Guinean coast by two fishing techniques (after Chavance and Domalain 2000a). Capital letters are abbreviations for the months of the year, chronologically, starting with January.

fimbriata seems to concentrate or spread out depending on the shrinkage and expansion of estuarine waters.

Annual landings of *E. fimbriata* in Sierra Leone were estimated to be 21,500 metric tons/year in 1972–1998 (FishStat 2000), about 50% of the total catches, as was the case in Guinea. Fish are caught both onshore and in the lower reaches of the rivers. *Ethmalosa fimbriata* moves up the Sierra Leone River as the dry season progresses and moves down toward the sea during the wet season. The marine fishing area of pelagic species (*Sardinella* spp. and *E. fimbriata*), as mapped by Marcus (1984a), is a narrow coastal strip of 10–20 km. The local nomenclature distinguishes three size-groups: awefu, 0–12 cm FL; bonga, 12–23 cm FL; and bonji, 23–32 cm FL (Salzen 1958). The first group was not found at sea and was restricted to the shallow waters of the estuary (2–4 m). The last group was found mostly at sea where the sizes caught ranged from 15 to 32 cm (Salzen 1958) and rarely occurred in the estuary where they were restricted to depths of over 11 m.

Bah et al. (1991) studied the reproduction in Guinea which occurred throughout the year, and multiple spawnings were observed within a spawning season. Size at first maturity was 18–20 cm both in Guinea and Sierra Leone (Table 2).

The Nigeria–Cameroon coastline comprises 16% of the total area, and the estimated annual catch is 37% of the total. Ssentongo et al. (1986) synthesized the available information on the hydroclimatic conditions off the Niger delta. The major discharge of the Niger River occurs in the central area near the Niger delta (Figure 10). To the east of the delta, the freshwater discharge is much smaller and the waters are more saline. Saltwater intrusion reaches upstream to a distance of over 80 km from the mouth in the Bonny River estuary where the salinities range from 10‰ to 32‰ (Anonymous, Nigerian Institute for Oceanography, unpublished abstract) and reaches 75 km in the Wari River (Tetsola and Egborge 1991). *Ethmalosa fimbriata* tends to be more abundant in the estuaries during the dry season from October to April. Juveniles are "definitely more abundant in rivers and estuaries," while young spawners and adults can be found both in estuaries and at sea (Ssentongo et al. 1986).

At sea, *E. fimbriata* is rarely caught in areas with depths below 20 m and prefers warm and relatively turbid waters. It seems less abundant in the area influenced by the Niger discharge, but its actual abundance in this area is questionable and possibly underestimated due to low fishing effort. Kusemiju and Onadeko (1990) studied West African shad abundance at sea off Aiyetoro, Nigeria (150 km from Lagos Lagoon). Sampling was performed efficiently with a trawl at 10–20-m depths. The authors got high catches during the dry season and nothing during the wet season (July–November). The same gap in apparent abundance at sea during the wet season has been observed at different places off the Nigerian coast (Marcus 1984b). This author hypothesizes a migration further offshore of the larger fish during the wet season. If so, the distribution at sea could be less coastal in Nigeria than in other areas (Guinea, etc.).

The overall landings of *E. fimbriata* in Nigerian waters are uncertain, probably ranging from 30 to 60,000 metric tons; in Cameroon, the catches are about 20,000 metric tons (Table 1).

Lagoon Estuaries of the Gulf of Guinea.—These large lagoons stretch over about 1,000 km from the Ivory Coast to Nigeria (Figure 11). They form two distinct areas separated in Ghana by a string of small coastal lagoons (tens of small lagoons of a few km² each).

The ecology and exploitation of some of these lagoons have been comprehensively studied (see reviews by Texier and Kapetsky 1984; Laë 1992; Charles-Dominique 1994; Durand et al. 1994).

The hydrodynamics of the coastal lagoons is complex and highly variable, depending on runoff (that can be affected by dams) and the interconnections between the lagoon and the sea (that can undergo natural or man-made changes). The Ebrie Lagoon, Ivory Coast, has a varied set of hydrody-

Table 2.—First maturity size (fork length, cm) of *Ethmalosa fimbriata* from different studies. L50 = size at which 50% of the fish sampled were mature.

	First maturity size					
Area	Male	Female	Not stated	Estuary type	Notes	Source
Senegal River	16	17		Inland	L50	Scheffers et al. (1972)
Sine-Saloum estuary	17.5	18		Inland	L50, maturation stages ≥ 3	Diouf (1996)
Gambia River		18.5		Inland	L50	Scheffers and Conand (1976)
Rio Grande de Buba	14.4	15		Inland/coastal		Kromer (1994)
Coast of Guinea	18	19		Coastal		Bah et al. (1991)
Fatala River			21	Coastal	L50, maturation stages ≥ 3	Baran (1995)
Sierre Leone River			18-20	Coastal	Size at which 50% of individuals are mature	Salzen (1958)
Ebrie Lagoon	13	14		Lagoon	Mean size at spawning	Albaret and Gerlotto (1976)
Ebrie Lagoon	12	13		Lagoon	L50, maturation stages ≥ 3	Albaret (1994)
Ebrie Lagoon	11.5	12.5		Lagoon	L50, maturation stages ≥ 3	RAP (2001)
Ebrie Lagoon	8.1	8.4		Lagoon	L50, maturation stages ≥ 3, polluted area	Albaret and Charles-Dominique (1982)
Aby Lagoon	9.6	9.9		Lagoon		N'Goran Ya (1991)
Coast of Ghana			17		Small area, length frequency of mature fishes	Blay and Eyeson (1982b)
Nokoue Lake			<10	Lagoon	Mean size at spawning	Gras (1958)
Lagos Lagoon	10	14		Lagoon	Size at which fish are sexually mature	Fagade and Olaniyan (1972)
Niger delta			15.5	Coastal		Longhurst (1965)

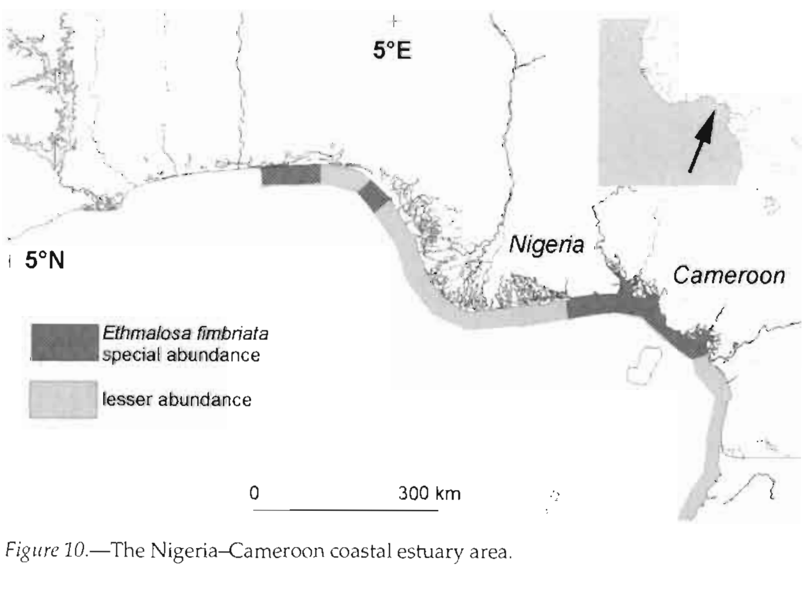

Figure 10.—The Nigeria–Cameroon coastal estuary area.

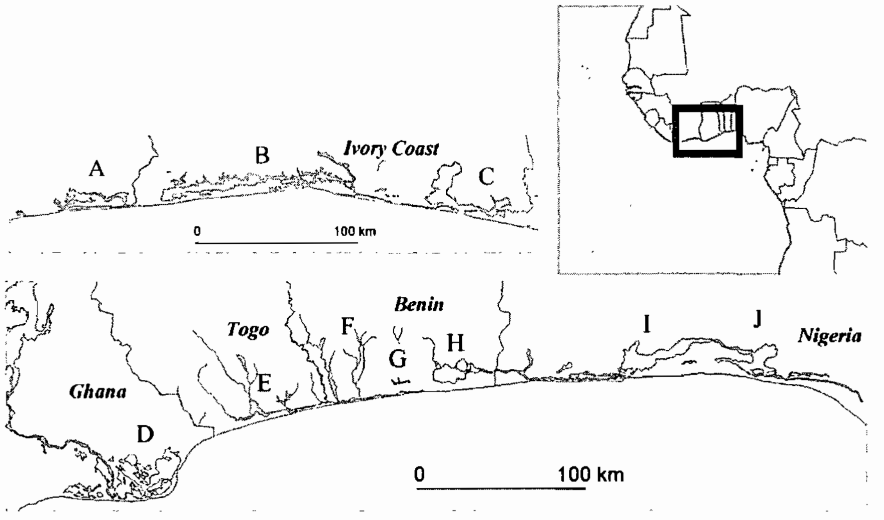

Figure 11.—The lagoons of the Gulf of Guinea: (A) Grand Lahou Lagoon, (B) Ebrie Lagoon, (C) Aby Lagoon, (D) Anlo-Keta Lagoon complex, (E) Togo Lake, (F) Aheme Lake, (G) Togougba Lagoon, (H) Nokoue Lake, (I) Lagos Lagoon, and (J) Lekki Lagoon.

namic conditions: large freshwater supply and seasonally turbid waters on the east, more stable waters on the west, and an artificially enlarged inlet. West African shad biology was studied using data from the fisheries and experimental fishing over several years (e.g., Gerlotto 1976, 1979). The information was reviewed by Ecoutin et al. (1994). Reproduction occurs at salinities higher than 10‰ from December to April (dry season) near the inlet. Juveniles stay in the area for 4 months after reproduction until they attain a size of 6 cm. They then spread out in the lagoon, attaining a size of 12 cm at 9–10 months, and return subsequently for spawning near the inlet. The size at first maturity is close to 12–13 cm, depending on the sex. The one exception to this was an 8.3-cm size at first maturity (the lowest for the species) for fish caught in a polluted area of the lagoon (Table 2). It has not been possible to state whether this resulted from nanism (slow growth) or early maturity. The second hypothesis is preferred since the size at maturity appears to vary much more in the species than does size at age.

After the first spawning, occurring at about age 1, adults (16–21 cm) are found in some parts of the lagoon, but only occasionally; they become extremely rare after reaching 21 cm in length (about 2 years old).

An emigration to the sea is suspected to occur for large adults, but it has never been directly observed. *Ethmalosa fimbriata* occurs at sea on the Ivory Coast but very rarely as mentioned before; the only analyzed sample of fish caught at sea consisted of mature fish 18–30 cm in length (Charles-Dominique 1994).

The Aby and Ebrie lagoon inlets are 80 km apart, a distance smaller than the range of reported occurrences at sea. Thus, some fish possibly move from one lagoon to another and perhaps reach the more remote regions of the distribution area.

The Aby Lagoon receives the runoff from two large rivers: the Bia in the north, regulated by a dam, and the Tanoé in the east. The surface salinity is between 0‰ and 2‰ during the wet season and 5–10‰ in the dry season, less in the eastern part. *Ethmalosa fimbriata* is abundant only in the more stable and saline western part of the lagoon and absent in the totally freshwater eastern end.

A systematic survey of the fisheries of this lagoon has been carried out for the period 1979–1990 (Charles-Dominique 1994). The whole lagoon area was fished from the shallow banks near the shore to the central basin using different fishing methods with known selectivity.

Reproduction occurred essentially from February to May when the salinities were high (5–10‰; N'Goran Ya 1991). The smaller juveniles (<9 cm) stay in the shallow areas and creeks during the first months of their life. Preadults and adults from 10 to 16 cm remain abundant throughout the year in the western part of the lagoon. Adults larger than 20 cm leave the lagoon during the wet season (June–November) and come back during the dry season.

Size at first maturity was low (9.6 cm for males and 9.9 cm for females). During the first months of their life, the juveniles stay out of reach of fishing gear in very shallow waters. Afterwards they spread out in the western part of the lagoon, avoiding the shore area during the flood season.

An analysis of size distribution clearly shows a regular emigration of small numbers of big fish from the Aby Lagoon (19–30 cm). It coincides with the flood around June 15. A return migration into the lagoon is observed at a period around November 15 when flood waters and turbidity begin to decrease but salinities are still very low.

It is worth noting that emigrating fish find upwelling conditions at sea from July to September (i.e., good trophic conditions and also cooler waters of 20–21°C). In Sine-Saloum, as already mentioned, upwelling occurs during the dry season, and fish penetrating into estuaries seem to be avoiding the cooler waters (16–17°C). The supposed preference of *E. fimbriata* for warm waters is unclear and will need to be re-examined in different areas for different size-groups.

The Lagos Lagoon is a small part of a large web of lagoons (Figure 11, H–J). Fagade and Olaniyan (1972) found that the salinity in the lagoon varied seasonally from near 0‰ to 20‰ and that turbidity varied according to the same seasonal pattern. West African shad reproduction occurred from January to May in waters with salinities greater than 10‰. Size at first maturity was 10 cm for males and 14 cm for females, close to the observations in the Ebrie Lagoon. The other features of the life cycle were similar between this study and those of the Ivory Coast lagoons. Different behavior patterns were observed between the three size-groups, the very young fish staying in shallow waters near the shore during the first months of their life, intermediate-sized fish inhabiting the lagoon throughout the year, and the larger fish leaving the lagoon during the flood, exactly as in the Aby Lagoon.

Opening of Inlets.—The variable opening of inlets can change lagoonal hydrodynamics markedly and may be followed by the colonization of estuarine species. In the eastern sector of the Ebrie Lagoon, which has the lowest salinity, *E. fimbriata* were rare or absent before an artificial inlet was opened in 1987. The salinity increased markedly and *E. fimbriata* rapidly became very abundant (Albaret and Ecoutin 1989), probably due to the migration of the resident lagoon population. Other cases of rapid recolonization of water bodies after salt intrusion have been reported. The Aby Lagoon was mostly freshwater before a natural opening in the bar in 1942; the actual population of *E. fimbriata* would have colonized at this time (Charles-Dominique 1994:105). Togo Lake had an irregular inlet that opened and closed; its fishing communities thus changed accordingly, for example, after the 1988 opening (Laë 1992).

Atypical Distribution Areas and Margins of the Distribution Area

In these areas, the estuarine conditions can differ from the three types already presented. No important concentrations of *E. fimbriata* have been found.

Guinea-Bissau.—This country has a very large network of indented estuaries, receiving little freshwater runoff. The salinity rarely falls below 20‰ (Kromer 1994). This environment does not appear unfavorable to *E. fimbriata*; for some unknown reason, the species is not very abundant and is secondary in the catches. It was, however, relatively abundant in the Rio Buba in the catches of the minor artisanal fisheries nearby, and reported from the Bijagos Islands, mostly during the wet season (Lafrance 1992, cited in Kromer 1994).

Liberia.—Despite favorable climatic (freshwater supplies) and oceanographic (stable tropical waters) conditions comparable to those of Guinea and Sierra Leone, *E. fimbriata* is rare in Liberia. No specialized artisanal fishery exists for the species, and annual landings of *E. fimbriata* are only a few tens of metric tons (Table 1). Further information will be necessary to assess the habitats of *E. fimbriata*, which are possibly restricted by the coastal morphology (straight coast with few coastal lagoons and estuaries; narrow shelf).

Ghana.—The coast of Ghana is edged with numerous very small lagoons receiving moderate freshwater runoff. *Ethmalosa fimbriata* has been reported and studied from a small estuary near the Cape Coast and nearby at sea by Blay and Eyeson (1982a, 1982b); however, these authors gave no indication of the species distribution and abundance elsewhere in Ghana. According to the fisheries data (Table 1), 920 metric tons have been caught at sea in Ghana where the maritime artisanal fisheries are among the most developed of West Africa. These quantities are important with regard to the scarcity of the species at sea from the Ivory Coast to Benin but are possibly inaccurate.

Atypical conditions are also found in the northern and southern limits of the distribution area. South of Gabon (4°S), the rainfall decreases sharply

(Nicholson 2000) from 1,500 to 3–400 mm/year at the southernmost recorded occurrence of *E. fimbriata* (12°S in Angola; Poll 1953). The inland estuaries are limited in this region (see Daget and Stauch 1968, for Congo). Despite its considerable runoff, the Congo River does not appear to have a marked effect on the coastal estuarization due to its hydrodynamic pattern; the primary production in the plume is low (Cadee 1979), and the salinity at the coast remains high (it rarely falls below 30‰ near the coast of the Congo). *Ethmalosa fimbriata* occurs in the small estuaries of the Congo but is found mainly at sea. All size-classes from 3 to 30 cm are caught at sea by different fishing methods (Gobert 1985). The annual landings of *E. fimbriata* in the Congo are 300 metric tons (Table 1).

Further south, *E. fimbriata* is found on the seagrass beds of the Mussulo Lagoon (9°S; Costa et al. 2002). The climate is arid (340 mm/year), and the salinity is steady at 39‰ throughout the year. The abundance is very low, only 0.7% of the total number of fish caught. However, *E. fimbriata* seems not rare at sea in Angola, since 1,759 metric tons were reported from the small-scale fishery catches (Fréon et al. 2000).

The northernmost significant concentration of *E. fimbriata* seems to be that of Banc d'Arguin, Mauritania (20°N latitude; Hatti and Worms 1998), situated in the most arid environment of the distribution area (100–200 mm/year rainfall). As noted before, this area was an estuary in an earlier period and preserves some traces of it, for example, the presence of estuarine species of invertebrates (Le Loeuff 1999). This limited information on the distribution of *E. fimbriata* suggests that there are only small concentrations of the species in these arid areas where estuarine waters are quite absent.

Reproduction and Ecophases

The sexes are well differentiated in *E. fimbriata*, and observations of increasing proportions of females with size are not attributable to sex inversion (Albaret 1999). As already stated, reproduction takes place both inland and at sea, with a very large tolerance to variations in salinity, from fresh to hyperhaline. The tolerance range is wider for maturation than for spawning and larval development; the latter two occur in a narrower environmental window, excluding freshwater and very high salinities. Figure 12 summarizes the ecological features observed for the three ecophases from all the case studies and also reported by traditional ecological knowledge. Size at first maturity is highly variable for the species, ranging from 8.3 to 18.5 cm depending on the area. First maturity and spawning always occur during the intermediate ecophase in those environments with higher variability.

Fecundity was estimated to be 300–500 oocytes/g ripe female (Fagade and Olaniyan 1972; Albaret and Gerlotto 1976) but about 200 oocytes/g by Blay and Eyeson (1982b). Because multiple within-season spawning can occur for individuals (Bah et al. 1991), the annual fecundity is probably higher than these instantaneous measurements.

Growth

The maximum size for the species was recorded by Postel (1950) in the Sine-Saloum estuary (total length = 47 cm, FL = 38.5 cm, weight = 1,150 g); Cadenat (1950) found ripe females at Saint-Louis, Senegal, measuring 46 cm FL and weighing 1 kg. The information available on growth is reported in Figure 13.

The nine growth studies available were split into two groups, one of six upper estimates and one of three distinctly lower estimates. The observations in the first group come from different types of estuaries and different geographical areas and

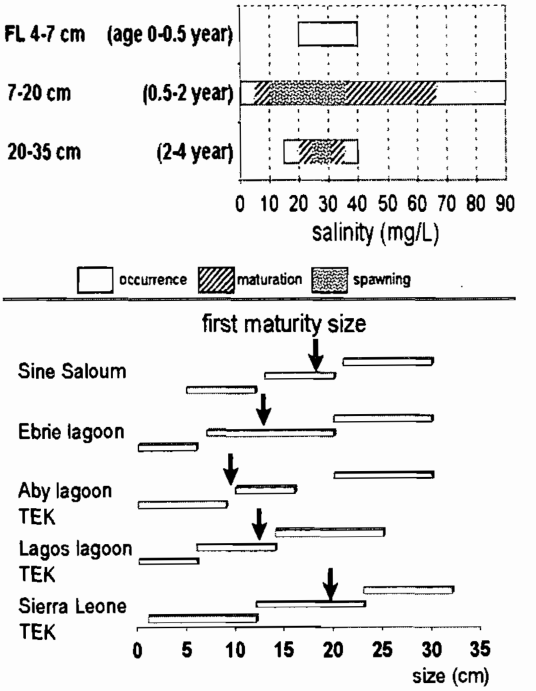

Figure 12.—Summary of ecophases in *Ethmalosa fimbriata* (above) and their variability in different areas (below). FL = fork length; TEK = Traditional Ecological Knowledge confirmations.

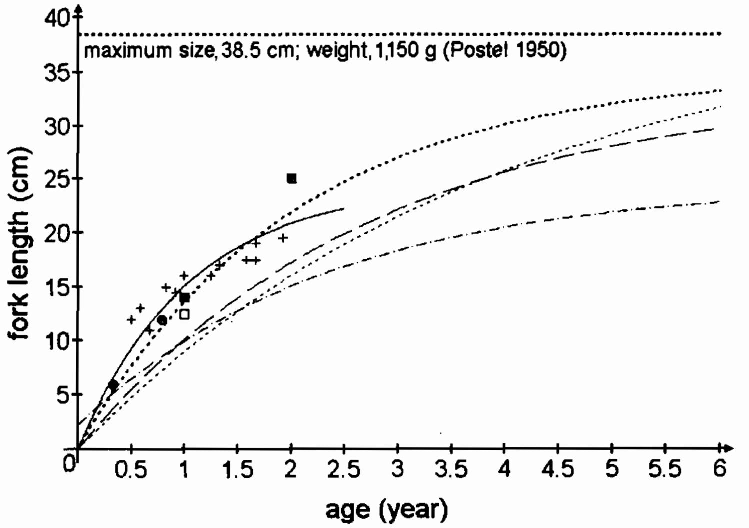

Figure 13.—Growth curves and observations of *Ethmalosa fimbriata* from locations in Nigeria (Longhurst 1965, heavier dotted line) and other nearby countries, including Lagos Lagoon, Nigeria (Fagade and Olaniyan 1972, solid squares); Ebrie Lagoon, Ivory Coast (Gerlotto 1976, solid line; Ecoutin et al. 1994, solid circles); Senegal River, north Senegal (Scheffers 1973, plus signs); Aby Lagoon, Ivory Coast (Charles-Dominique 1994, open squares); Niger delta, Nigeria (Essen 1995, long dashes; east of the delta, Moses 1988, dashed line); and locations in Sierre Leone (Showers 1996, dotted line).

were made using different methods. A similar growth pattern thus appears for at least a majority of the studies. Contrary to the opinion of some authors, there is no evidence of larger sizes of *E. fimbriata* in the northern part of the distribution area. Insufficient information is available to assess the status of the three lower estimates. With that exception, growth is much less variable than size at first maturity. This argues for the possibility of precocious reproduction (with little variations of growth) rather than nanism (marked variation of growth) in populations where first maturity occurs at smaller sizes.

It is likely that differential growth exists between the sexes, as sexual differences were noticed in size at first maturity and in most of the size distributions (males being smaller). It is important that sex should thus be determined in any subsequent growth studies. Species longevity is probably 4–5 years.

Food and Feeding Habits

Ethmalosa fimbriata is planktivorous, and its diet changes from zooplankton feeding in young fish to a more microphagous diet (with more phytoplankton) in adults (see summary of diet in Blay and Eyeson 1982a; Charles-Dominique 1982; Lazzaro 1987; Ikomi 1992; Adite and Winemiller 1997). Fagade and Olaniyan (1972) observed that gill filtration of *E. fimbriata* changes as the fish grows. They concluded that the gill filter mesh size diminished, explaining the change in diet. A study from the Ebrie Lagoon, however, refutes this reduction in gill filter mesh size. The changes in diet could also be due to food availability because the species is an opportunistic feeder (Charles-Dominique 1982).

Lazzaro (1987) considered *E. fimbriata* a passive plankton filter feeder. This result fits with observations of fishing yields in the Aby Lagoon purse seine fishery: higher when the fish is feeding and more vulnerable (Charles-Dominique 1994); high yields were obtained in low-light conditions (night, no moonlight, maximal turbidity), indicating a probable passive feeding behavior in the species. However, high yields were also observed in brighter conditions (moonlight), and *E. fimbriata* may also feed visually.

The fine filtering mechanism of *E. fimbriata* could fill with suspended material carried by turbid waters, and this may explain the avoidance of such waters, particularly by bigger fish. In the Ebrie Lagoon, yields decreased sharply in a sector swept by floods, but there was no decrease in a more stable, though lower salinity, sector (Charles-Dominique 1982).

Population Dynamics

The population dynamics of *E. fimbriata* are relatively unknown as few time series of catch and effort exist. Some comparisons of abundance can, however, be made between areas (see mean catches/ha in Table 1). In the Ebrie Lagoon, the catch of *E. fimbriata* made up 33% of the total fish caught (Laë 1992). The year-to-year variability was high, ranging from 1–7. In the Aby Lagoon, the proportion was 70% in 1986 (Charles-Dominique 1994), and the year-to-year variability of catch of *E. fimbriata* varied from 1 to 7.8. In the Grand-Lahou Lagoon, abundance of *E. fimbriata* was only 9% of the total catch as estimated by using the set gill nets catch per unit effort. In Togo Lake, catches of *E. fimbriata* were 2.4% of the total in 1983–1984 (23 metric tons out of 960 total metric tons; Laë 1992). These rank differences among communities are not well understood. They seem to be less related to salinities than to some kind of instability of the waters (Grand-Lahou Lagoon receiving the largest amount of river water and having the smallest volume, Aby Lagoon having more stable waters). The gear type or mesh size used in the different regions may also explain these differences.

Moses (2001) found no correlation between the annual catch of *E. fimbriata* and either the rainfall or the flood index in a large area of southeastern Nigeria, where peak recruitment occurred in both wet and dry years. This confirms the adaptability of the species in general and the resilience of large populations within these highly variable estuarine environments.

The hydroclimatic parameters can nevertheless affect the population sizes in some critical situations. The year-to-year variations of West African shad population size in the Aby Lagoon were analyzed for a period of 11 years (Charles-Dominique 1994). The annual catches varied from 1,200 to 9,500 metric tons (1979–1990, except 1981). Fishing effort varied from 1 to 4, explaining only a limited part of the variability. A further explanation was looked for within the environmental conditions during the critical spawning season (February–April), a dam upstream releasing large quantities of water during this period. The runoff during this time varied from 1 to 3.6 and was used as a variable in a Pella and Tomlinson model using both the fishing effort and a climatic variable (Fréon 1991). The model explained 86% of the variance.

Fishing and Cultural Importance

Ethmalosa fimbriata is one of the most exploited West African fishes. It has been exploited for many years due to its easy accessibility to both offshore and inland water fisheries and also its abundance and eating qualities. The coastal estuaries, with their sheltered and rich environments (mangrove forest, salt marshes, etc.) have been among the most ancient human settlement areas (Cormier-Salem 1999). In the 1950s, *E. fimbriata* was the most commonly exploited clupeid fish. Cadenat (1950) wrote that "*Ethmalosa fimbriata* ... is by far the most abundant clupeid along the West African coast," inferring the abundance of the species from fisheries landings at that time (*Sardinella* spp. are actually the major clupeid species.).

Ethmalosa fimbriata is essentially exploited by artisanal fisheries. These fisheries are made up of numerous family or community-based exploitation units, where fishing is often shared with other activities (agriculture, trade, fish processing, etc.). Although artisanal, these fisheries are intensive and operate often on a large spatial scale due to the migrations of fishermen. They have been developing at a rapid rate since the 1950s, faster than the industrial fisheries, notwithstanding the stagnation or recession of the global economy (Chaboud and Charles-Dominique 1991; Chauveau et al. 2000). According to FishStat (2000) the catches of 175,000 metric tons of *E. fimbriata* caught today are twice what they were 30 years ago.

In most countries, fish are processed near the landing sites, usually smoked, and marketed locally, but sometimes also at a distance from the fishing areas (from Senegal to Guinea, for instance). *Ethmalosa fimbriata* is much appreciated locally as an important low-cost food but not so much outside these areas.

The principal fishing techniques for *E. fimbriata* are encircling gill nets (mesh sizes 36–40 mm), drift gill nets (sometimes used alternatively as drift and encircling nets), set gill nets (Senegalese coast), beach seines (Ivory Coast lagoons, etc.), surrounding nets (Guinea, Cameroon), and purse seines (Senegal; accessory target). The fisheries are generally selective, due to either the mesh size (gill nets) or the differential accessibility of ecophases.

Hilsa kelee

Hilsa kelee (Figure 14) has the largest distribution in the subfamily Alosinae by far. Globally, its importance for fisheries is not negligible and is comparable to that of *Ethmalosa fimbriata*. Nevertheless, the literature available is limited and no synthesis exists for the species. Thus, this section is a first attempt to synthesize the available information. Whitehead

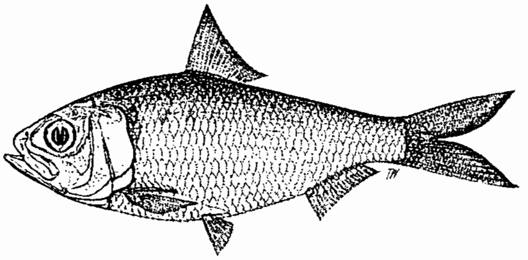

Figure 14.—Hilsa kelee (Cuvier, 1829). From Whitehead (1985).

(1985) gives the diagnostic features for the species, which make reference to most authors.

Distribution and Fisheries

Hilsa kelee is probably present all along the coasts of the Indian Ocean and on the West Pacific coasts (27°N to 35°S, 21°E to 155°E) and occurs occasionally in some other areas (Oman Sea, Somalia). The Food and Agriculture Organization of the United Nations (FAO) landing statistics (1992–1998) give a total of 100,000 metric tons/year taken solely by India. The details of the catch by area are 43,000 metric tons from the Bay of Bengal, Indian Ocean, and only 3,300 metric tons from the West Pacific coast, other catches (46,000 metric tons) being reported from continental waters.

No catches of *H. kelee* are reported by the FAO for Africa, although the species is locally abundant on the eastern coast of Africa, particularly in Mozambique. For instance, Sousa (1987) describes the gill net fishery for *H. kelee* as an important one in Maputo Bay, south Mozambique. The total catches in the bay were estimated at 4,600 metric tons in 1986. Thousands of fishermen work in hundreds of fishing centers in the country, where pelagic fish species are abundant. The main fishing techniques used are beach seines, gill nets, and handlines. The artisanal fisheries of Mozambique have just begun to be studied; in the Zambezia province (Baloi et al. 1999), *H. kelee* showed strong spatio-temporal variations, reaching 30–60% of the catches in some months and places.

Life History

Hilsa kelee is a marine pelagic species entering estuaries. According to Whitfield (1996), kelee shad inhabits the deepest areas of estuaries with salinities ranging from 3‰ to 35‰. It was studied in Lake St-Lucia, South Africa, a large and shallow lake with varying salinity (1–35‰) and only a narrow connection with the sea (Blaber 1979). Juvenile *H. kelee* spend their first months in the lake. On the eastern coast of Madagascar, Amanieu and Lasserre (1982) reported that *H. kelee* were found only near the inlets of lagoons in relatively small numbers (0.5–4.5% of the sampled biomass). Their mean weight was 16 g to 47 g (10.8 cm and 14.7 cm). At sea, *H. kelee* apparently do not form large schools (Whitehead 1985).

Spawning

Spawning usually occurs at sea, although running-ripe specimens have been recorded in the Durban Bay estuary (Wallace 1975). In Maputo Bay, spawning takes place mainly during October–January, with a peak in December. There is also some evidence that spawning takes place during June–July (Gjosaeter and Sousa 1983). After spawning, juveniles remain in the lower parts of estuaries for 2–3 months before returning to sea.

Food

In the Godavari estuary, India, *H. kelee* feeds chiefly on phytoplankton (mainly diatoms and dinoflagellates) but also on copepods, molluscan and crustacean larvae, prawns, amphipods, and polychaetes (Whitehead 1985; quoting Babu Rao 1964). Caddy and Garibaldi (2000) consider that the species should, however, be classified as an herbivore because of its numerous and fine gill rakers (van der Elst 1988).

Growth

Growth has been estimated from reading otoliths and size-frequency distributions (Gjosaeter and Sousa 1983; Gjosaeter et al. 1984; Sousa and Gjosaeter 1987).

The von Bertalanffy growth curve parameters (quoted in FishBase; Froese and Pauly 2001) are: L_{inf} = 17.7 cm, K = 1.100, and t_0 = -0.44 (Figure 15).

Some other growth data can be compared with this equation. According to van der Elst (1988), the sexual maturity is attained after 1 year, at a size of 12.3 cm (Figure 15). Blaber (1979) gives an estimate of juvenile sizes at age. He found juveniles of 4.1 cm during February 1978 in the St-Lucia Lake; they grew approximately 10 mm per month to reach a length of 11.3 cm by August 1978. These data are reported in Figure 15. The maximum recorded length is 25.0 cm (SL = 24.4 cm in Whitehead [1985]). Froese and Pauly (2001) give a larger maximum size of 28.8 cm (conversion relationship between sizes given in FishBase; Froese and Pauly 2001).

A rough fit taking into account these other data (L_{inf} = 24 cm, K = 0.75, t_0 = 0; dotted line) is made in

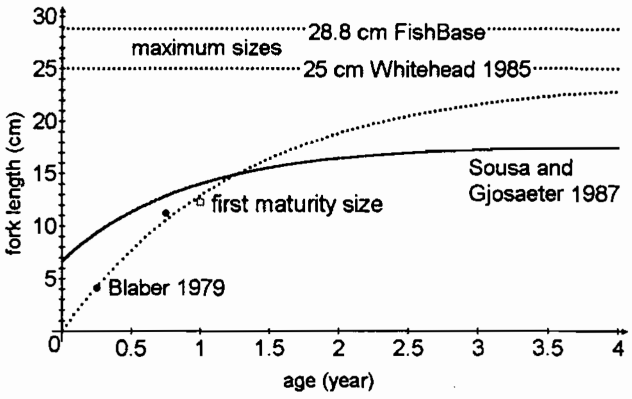

Figure 15.—Growth curves and observations in *Hilsa kelee*.

Figure 15. It shows that large discrepancies persist among the growth estimations.

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