

Effects of salinity on fish assemblage structure: An evaluation based on taxonomic and functional approaches in the Casamance estuary (Senegal, West Africa)

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ABSTRACT

The utility of taxonomic and functional approaches in assessing the structure of fish communities is tested in the hypersaline estuary of the Casamance river using data from surveys of commercial fisheries conducted between April and July of 2005. Both taxonomic and functional diversity decrease from downstream to upstream regions of the estuary. In terms of species composition, marine-estuarine species (33.3–46.3%, depending on the site) and estuarine species of marine origin (29.3–41.7%) dominate the exploited population in the Casamance estuary. In contrast, the proportion of strictly estuarine species observed upstream is twice that observed downstream.

Quantitative analysis based on biomass landed distinguishes two groups in the population: (1) a group of species that is dominant downstream, containing primarily terminal predators and secondary consumers categorised as marine species that are occasional or accessory in estuaries, estuarine marine species, and estuarine species of marine origin; and (2) a group of species characteristic of the upstream region, dominated by a few species (*Sarotherodon melanotheron*, *Tilapia guineensis*, and *Mugil cephalus*) mainly of strictly estuarine and/or herbivorous categories and *Elops lacerta*, a carnivore fish. The outcomes of the two approaches are similar, and both indicate that the fish community in this estuary is under the influence of strong environmental disturbance. However, the scales at which the specific and functional approaches most reliably reflect environmental conditions are different. The taxonomic approach, i.e., the use of specific biomass is more appropriate at the ecosystem scale and therefore more accessible to local human communities, whereas the functional approach is better suited to regional and sub-regional studies because of the change in species composition from one environment to another.

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1. Introduction

The importance of estuarine ecosystems is widely acknowledged throughout the world. Estuaries are transitional ecosystems between the sea and the mainland, are highly variable and support a rich biodiversity, of which fish (larvae, juveniles, and adults) are one of the most important components (Yáñez-Arancibia et al., 1993; Whitfield, 1994, 1999). Estuaries play an important role in the bioecology of fish species, serving as nursery areas that are crucial for the renewing of stocks (Cowley et al., 2001; Mumby et al., 2004; Barletta et al., 2005). They also support a major fishing industry and contribute to meeting the animal protein

needs of human populations (Houde and Rutherford, 1993; Blaber, 1997).

As estuarine ecosystems are located in coastal areas, they are subjected to increasing pressures from industrial and/or domestic pollution, resource exploitation, dam construction, and climate change (Vitousek et al., 1997; Scheren et al., 2002; Mumby et al., 2004; Lotze et al., 2006). The importance of estuarine environments and the threats to which they are exposed have resulted in increased scientific interest in these environments, as shown by the growing number of studies in these areas since the 1980s (Faunce and Serafy, 2006).

Many studies of estuarine ecosystems have been based on the taxonomic approach, i.e., the use of specific biomass or abundance to describe the patterns of biotic communities and elucidate their structuring variables (Elliott et al., 2007). Alongside this approach, a new functional approach has been developed in recent years. This

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approach involves separating species into functional groups based on life history traits such as reproductive mode, diet, and degree of dependence on the estuary (Nordlie, 2003; Elliott et al., 2007; Mouillot et al., 2007; Franco et al., 2008; Lobry et al., 2008). The use of functional groups facilitates both the simplification of the complex biotic communities and ecosystems studied (Potter et al., 1986; Albaret et al., 2004; Elliott et al., 2007) and the comparative analysis of communities across ecosystems whose species compositions vary widely (Harrison and Whitfield, 2006, 2008; Barletta and Blaber, 2007; Franco et al., 2008). The use of functional groups to diagnose the impact of a disturbance in an ecosystem implies that more or less homogeneous (functionally similar) units respond similarly to environmental conditions and respond differently from other functionally distinct groups (Gowns, 2004; Franco et al., 2008; Olden et al., 2010).

The taxonomic and functional approaches are not incompatible, and they have been used in combination in some studies to understand the dynamics of estuarine ecosystems at different spatial and/or temporal scales (Harrison and Whitfield, 2004; Simier et al., 2004; Vega-Cendejas and de Santillana, 2004; Hoinghaus et al., 2007; Ecoutin et al., 2010). However, questions remain about the complementarity of the two approaches, the benefits of using one over the other, and the applicability of each approach (Devictor et al., 2010).

This study addresses these questions by combining the taxonomic and functional approaches to assess the effects of prolonged drought on the health of fish communities in the Casamance estuary in Senegal, West Africa (Fig. 1), using data from scientific monitoring of the landings of artisanal fisheries. The transformation of this ecosystem into an inverse hypersaline estuary is thought to have begun in 1973 (Mikhailov and Isupova, 2008) and to have become complete during the drought period from 1977 to 1981 (Savenije and Pagès, 1992). Since the environmental disruption of this ecosystem and its transformation into an 'inverse' estuary (Pitchard, 1967), the Casamance River has been the subject of many studies. These have focused on both abiotic and biotic components including geomorphology (Saos et al., 1987), hydrology (Savenije and Pagès, 1992; Pagès et al., 1995; Thiam and Singh, 2002), phytoplankton (Pagès et al., 1987, 1995; Pagès, 1994), foraminifera and zooplankton

(Debenay and Pagès, 1987), shrimps (Le Reste, 1987, 1992) and the fish population (Albaret, 1987). study aims to assess the extent to which taxonomic and functional approaches reveal the changes caused by hypersalinisation, using both historical and recent data on the fish population of the Casamance estuary. This estuary, in which extreme salinities are sometimes observed in the upstream region (172 in June 1986 at about 220 km from the sea; Pagès, 1986) and in which an inverse salinity gradient has existed for over 30 years, is well suited for this type of investigation. The hypothesis underlying this work is that different fish species and functional groups react differently to salinity, leading to differences in fish community structure determined mainly by environmental differences between the upstream and downstream regions of the estuary.

2. Study area

Located in southwestern Senegal, the Casamance River is formed by the confluence of several small rivers that dry up during the dry season (Thiam and Singh, 2002). It is 350 km long (with 260 km of permanent river) and drains a watershed of 14 000 km² (Saos et al., 1987). In the southern part of Senegal, the climate is sudano-guinean, characterised by the alternation of two seasons (Thiam and Singh, 2002): a wet season from mid-May to mid-September and a dry season during the rest of year.

The relief of the Casamance River basin is flat, with the highest point (75 m) located 400 km from the sea. The slope is generally very weak in the upper region (0.5 m km⁻¹) and almost zero on the last 200 km of river (Marius, 1985; Pagès, 1986; Pagès et al., 1987).

The river flow is remarkably low, with an average annual discharge of 3 m³ s⁻¹ (Pagès, 1986). The freshwater inputs into the river are seasonal and occur mainly between the onset of the rainy season and November (Thiam and Singh, 2002). In the years 1960–1980, the annual water balance in the river was negative, with shortfalls of freshwater estimated to be between 300 and 800 mm (Pagès, 1986, 1994).

The salinity of the Casamance shows an increasing longitudinal profile from downstream to upstream. Salinity increases throughout the river during the dry season, with maxima that vary across years.

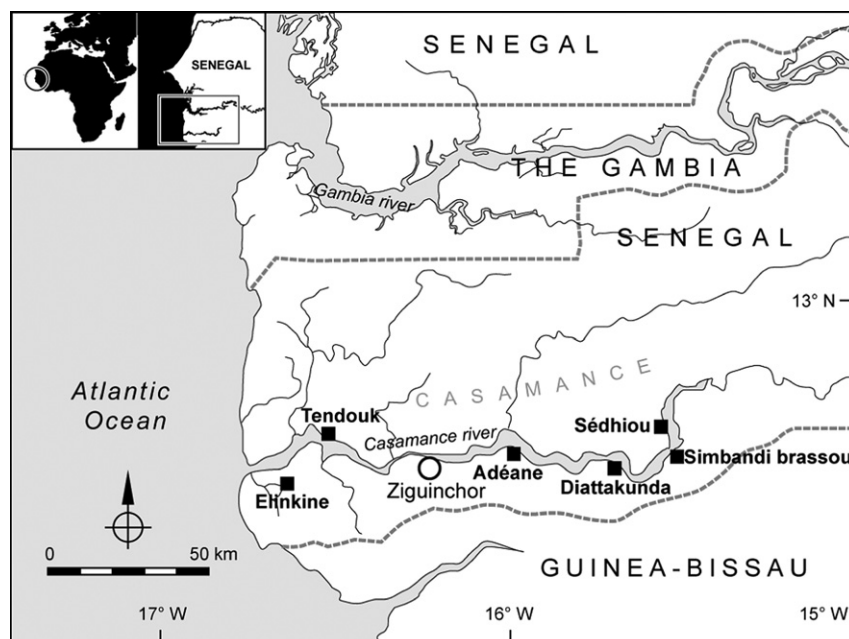


Fig. 1. Geographic location of the Casamance River and the sampled villages (open circle = regional capital and meteorological station; black points = sampled villages).

The salinity of the river is influenced by evaporation and rainfall of both the current year and previous years (Savenije and Pagès, 1992). High salinities have been recorded in the Casamance estuary as a result of a persistent decline in rainfall that began in the late 1960s and has caused decreased river flow and saltwater intrusion (Thiam and Singh, 2002). The cumulative annual rainfall in the 1960s was 1470 mm versus 1600 mm in the 1950s (Fig. 2). The rate of decline in rainfall increased thereafter, and the cumulative annual rainfall reached 1060 mm in the 1980s. During the 1990s, rainfall increased slightly to an average of 1250 mm yr⁻¹.

3. Materials and methods

3.1. Sampling design

Artisanal fisheries in the Casamance estuary were monitored by studying six fishing villages. Surveys were conducted monthly between April and July of 2005. The villages were investigated for a period of about 15 days each month. The sampling strategy was adapted from Laë et al. (2004) and Kantoussan et al. (2007). Each survey was composed of three operations: (1) counts of active fishing units (one fishing unit = one canoe) to assess the fishing potential in each surveyed location; (2) surveys of landings to determine the species composition and size structure of fish; and (3) surveys of the fishing activity performed by all active fishing units each evening during the survey period to estimate the fishing effort. During the survey period, as well as during pilot sampling, the salinity was measured once a month in each village.

Fisheries in the Casamance estuary are characterised by the use of several types of fishing gear, which can be categorised based on fishing technique and mesh size. For gillnets, three categories of mesh sizes were distinguished in our surveys: small (<30 mm), medium (30–50 mm) and large (>50 mm). Fourteen fishing techniques were observed at Elinkine, 11 at Tendouk, 10 at Adéane and only 4 or 5 in each of the three villages located further upstream. The fish landed were identified to species, the total number or weight of each species was calculated for each catch, and the fork lengths (cm) of 20 individuals of each species landed were recorded.

3.2. Data processing

3.2.1. Diversity index

Species diversity in the catches was estimated by coupling the conventional diversity index of Shannon–Wiener (H' , Shannon and Weaver, 1949) and the Pielou evenness index (J' , Pielou, 1966) with the taxonomic diversity index (Warwick and Clarke, 1995).

The indices H' and J' are estimated by

$$H' = - \sum_{i=1}^S p_i \log(p_i)$$

$$J' = H' / \log(S)$$

where p_i is the proportion of species i (or of functional group i) in the catch, and S is the total number of species (or functional groups) observed in the catch.

Two taxonomic diversity indices (Warwick and Clarke, 1995) were also used to estimate the diversity in the landed catch, taking into account taxonomic relationships. The first index (Δ , the taxonomic diversity index) is based on the classic Shannon diversity index with an added component of taxonomic separation and is estimated as

$$\Delta = \frac{\sum_{i < j} w_{ij} x_i x_j}{\sum_{i < j} x_i x_j + \sum_i x_i (x_i - 1) / 2}$$

where w_{ij} is the weight given to the path length linking species i and j in the hierarchical Linnean tree, and x_i represents the catch of the i th species.

The second index (Δ^* , the taxonomic distinctness index) is an index of taxonomic distinctness expressed without regard for the contribution of each species to diversity. It is expressed as

$$\Delta^* = \frac{\sum_{i < j} w_{ij} x_i x_j}{\sum_{i < j} x_i x_j}$$

Taxonomic indices are less sensitive to sample size or sampling effort than in the Shannon diversity index (Magurran, 2004; Roberts and Connell, 2008). Here, species were ranked according to the taxonomic classification used in FishBase (Froese and Pauly, 2011) at the levels of species, genus, family, order, class and phylum. Taxonomic indices were estimated from catches transformed by the function $\log(x + 1)$ to reduce the weight of dominant species (Clarke and Warwick, 1998).

3.2.2. Functional categories

Species observed in the catches (Table 1) were assigned to estuarine bioecological categories according to the classification defined by Albaret (1999) for West African estuaries. This

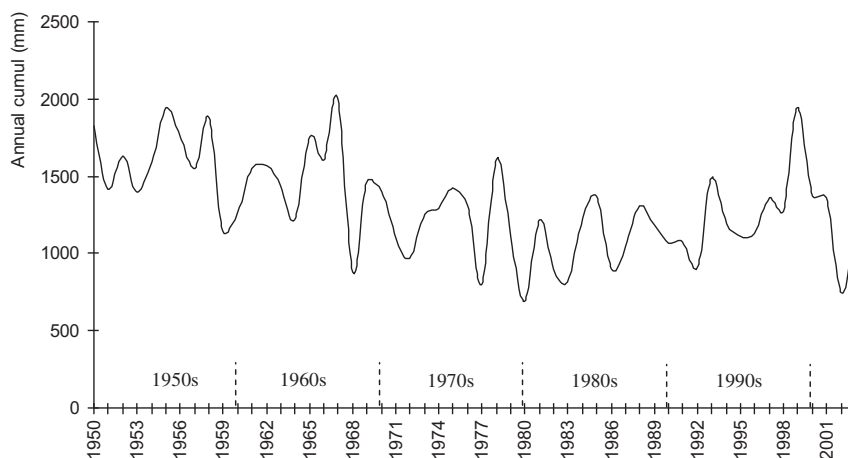


Fig. 2. Rainfall recorded at the Ziguinchor meteorological station (one-way ANOVA on data per decade transformed by $\log(x + 1)$ from 1950s to 1990s; $p < 0.05$).

classification consists of 8 categories: strictly estuarine species (Es), three categories of species with continental affinity (Co: continental species occasional in estuaries, Ce: continental species with estuarine affinities, and Ec: estuarine species of continental origin), and four categories of species with marine affinity (Em: estuarine species of marine origin, ME: marine-estuarine species, Ma: marine species accessory in estuaries, and Mo: marine species occasional in estuaries).

Designation of trophic categories was adapted from Paugy and Lévêque (1999). These authors identified three major trophic categories: (1) primary consumers (PC), which are detritivores or herbivores that graze and/or feed on phytoplankton or microphytes; (2) secondary consumers (SC), which are first-level predators including benthivores (which feed on molluscs and annelids), zooplanktivores, and first-level generalists (which feed on crustaceans and insects); and (3) terminal predators (TP), which are

Table 1

List of the fish species recorded in the total catch landed in the Casamance estuary. EC: ecological category (Ec: estuarine species of continental origin; Es: strictly estuarine species; Em: estuarine species of marine origin; ME: marine-estuarine species; Ma: marine species accessory in estuaries; Mo: marine species occasional in estuaries); TC: trophic category (PC: primary consumers; SC: secondary consumers, TP: terminal predators); +: observed species. Distance (km) from the mouth is shown in parentheses.

Specie	Specie code	EC	TC	Elinkine (13 km)	Tendouk (42 km)	Adéane (93 km)	Diattakunda (130 km)	Simbandi brassou (158 km)	Sédhiou (170 km)
<i>Arius latiscutatus</i>	Aga	ME	TP	+	+	+		+	+
<i>Arius parkii</i>	Arp	ME	TP	+	+	+			
<i>Brachydeuterus auritus</i>	Bau	ME	SC			+			
<i>Caranx crysos</i>	Ccr	Mo	TP		+				
<i>Caranx hippos</i>	Chi	ME	TP	+	+				
<i>Caranx senegallus</i>	Cas	ME	TP	+	+	+	+		
<i>Carcharhinus</i> spp.	Cch	Mo	TP	+					
<i>Chaetodipterus goreensis</i>	Chg	Mo	SC	+	+	+	+		
<i>Chaetodipterus lippei</i>	Cli	Ma	SC			+			
<i>Chloroscombrus chrysurus</i>	Chl	ME	SC	+	+				
<i>Citharichthys stampflii</i>	Cst	Em	TP		+	+	+		
<i>Cynoglossus monodi</i>	Cym	Mo	SC	+					
<i>Cynoglossus senegalensis</i>	Cys	Em	SC	+	+				
<i>Dasyatis margarita</i>	Dma	Em	SC	+					
<i>Dasyatis margaritella</i>	Dam	Em	SC	+					
<i>Drepane africana</i>	Daf	ME	SC	+	+	+			
<i>Echeneis naucrates</i>	Ena	Mo	SC	+					
<i>Elops lacerta</i>	Ela	ME	TP	+	+	+	+	+	+
<i>Ephippion guttifer</i>	Egu	ME	SC	+	+				
<i>Epinephelus aeneus</i>	Eae	ME	TP	+	+				
<i>Ethmalosa fimbriata</i>	Efi	Em	PC	+	+	+	+	+	+
<i>Eucinostomus melanopterus</i>	Gme	ME	SC	+	+	+	+	+	+
<i>Galeoides decadactylus</i>	Gde	ME	TP	+	+				+
<i>Gerres nigri</i>	Gni	Es	SC	+	+	+	+	+	+
<i>Hemichromis fasciatus</i>	Hfa	Ec	TP	+	+	+	+	+	+
<i>Hemiramphus balao</i>	Hba	Em	TP			+	+		
<i>Hyporhamphus picarti</i>	Hpi	Ma	TP						+
<i>Ilisha africana</i>	Iaf	Em	SC	+	+				
<i>Lichia amia</i>	Lia	Ma	TP	+	+				
<i>Liza bandialensis</i>	Lba	Em	PC	+					
<i>Liza dumerili</i>	Ldu	Em	PC	+	+	+	+	+	+
<i>Liza falcipinnis</i>	Lfa	Em	PC	+	+	+	+	+	+
<i>Liza grandisquamis</i>	Lgr	Em	PC	+	+	+	+		+
<i>Lobotes surinamensis</i>	Lsu	Mo	TP	+					
<i>Lutjanus agennes</i>	Lag	Mo	TP	+	+				
<i>Monodactylus sebae</i>	Psb	Es	TP	+	+	+		+	+
<i>Mugil bananensis</i>	Mba	ME	PC	+	+	+	+	+	+
<i>Mugil cephalus</i>	Mce	ME	PC	+	+	+	+	+	+
<i>Mugil curema</i>	Mcu	Em	PC			+	+		+
<i>Plectorhinchus macrolepis</i>	Plm	Em	TP	+	+	+			
<i>Polydactylus quadrifilis</i>	Poq	ME	TP	+	+	+	+	+	+
<i>Pomadasys jubelini</i>	Pju	Em	SC	+	+	+	+	+	+
<i>Pomadasys perotai</i>	Ppe	Em	SC	+	+	+	+	+	+
<i>Psettodes belcheri</i>	Pbe	Mo	TP	+					
<i>Pseudotolithus brachygnathus</i>	Pbr	ME	TP	+	+	+	+	+	+
<i>Pseudotolithus elongatus</i>	Pel	Em	TP	+	+	+		+	
<i>Pseudotolithus typus</i>	Pty	ME	TP	+	+				
<i>Rhinobatos</i> spp.	Rhi	Mo	TP	+					
<i>Sardinella aurita</i>	Sau	Ma	SC	+	+				
<i>Sardinella maderensis</i>	Seb	ME	SC	+	+				
<i>Sarotherodon melanothron</i>	The	Es	PC	+	+	+	+	+	+
<i>Scomberomorus tritor</i>	Ctr	Ma	TP	+	+				
<i>Sphyraena afra</i>	Spi	ME	TP	+	+	+	+	+	+
<i>Strongylura senegalensis</i>	Bes	Em	TP	+	+				
<i>Synaptura lusitanica</i>	Slu	Ma	SC			+	+	+	+
<i>Tilapia guineensis</i>	Tgu	Es	PC	+	+	+	+	+	+
<i>Trachinotus teraia</i>	Tfa	Em	SC	+	+	+	+	+	+
<i>Trichiurus lepturus</i>	Tle	ME	TP	+	+				
<i>Tylosurus crocodilus</i>	Tcr	Mo	TP			+			

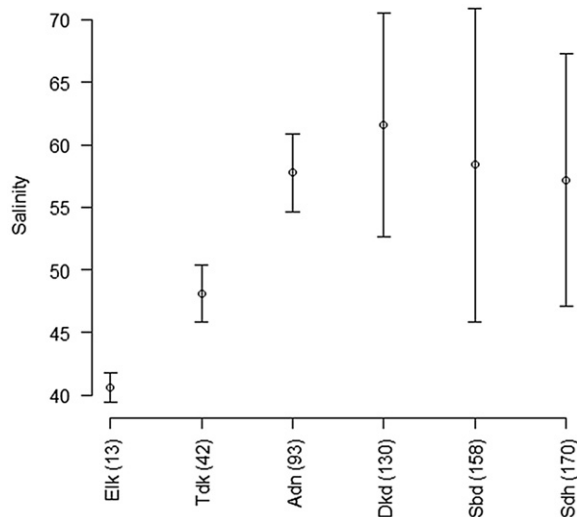


Fig. 3. Mean monthly salinity at the six sampled villages in the Casamance estuary (Elk: Elinkine; Tdk: Tendouk; Adn: Adéane; Dkd: Diattakunda; Sbd: Simbandi Brassou; Sdh: Sédhio; the distance (km) of each village from the mouth is shown in parentheses).

second-level piscivorous or generalist predators (which feed on fish and other prey).

3.2.3. Statistical analyses

Statistical tests were used to determine whether any differences observed between the samples could be considered significant at $p \leq 0.05$. The distribution of salinity across locations or months was tested using one-way ANOVA (Chambers and Hastie, 1992). A linear regression was applied to the per-species catch data versus salinity to determine species dynamics across the salinity gradient. Both catch and salinity data were log-transformed to approximate normality. The results of this linear regression (not significant relationship, significant relationship with a positive slope, significant relationship with a negative slope) were used as a proxy to classify the species into 3 groups respectively, species indifferent – tolerant – sensitive to salinity. In order to determine the hierarchical structure of the species in the estuary, a Correspondence Analysis (CA, Greenacre, 1984) was performed on the per-species catch weight per village per month, transformed by $\log(x + 1)$ to reduce the relative contribution of dominant species. An Ascending Hierarchical Classification (Euclidean distance, average linkage agglomeration method, Sneath and Sokal, 1973) was then performed using the coordinates of each species on the two most significant axes of the CA, which were found to explain 72.7% of the total variability. The species included in the analysis were those whose contribution to the total catch yielded $\log(x + 1) \geq 1$.

A Between-Class Principal Component Analysis (PCA, Dolédec and Chessel, 1987) was performed on the landings of each

species, using $\log(x + 1)$ -transformed biomass per village per month for each category of fishing gear. Data were analysed using the R software (R Development Core Team, 2009) with the ade4 package for multivariate analysis (Dray and Dufour, 2007).

4. Results

4.1. Salinity

For the three downstream villages, the mean monthly salinity increased from about 40 at Elinkine village (13 km from the mouth) to 57 beyond the village of Adéane (93 km from the mouth; Fig. 3). In this region of the estuary, the monthly salinity exhibited low variability compared to that observed at the three villages further upstream. The maximum mean monthly salinity (62) was observed at Diattakunda (130 km from the mouth), followed by a slight decrease at the remaining two villages. The longitudinal variations in salinity differed significantly across the sampled villages ($p < 0.05$). However, the effect of month on salinity was not significant across the estuary ($p > 0.05$) during the survey period.

4.2. Species richness and diversity

A global richness of 59 species was observed during the 2005 survey. The local richness observed at the downstream sites was twice that observed at the upstream sites (50 species at 13 km, 21 species at 158 km, and 24 species at 170 km from the mouth; Table 2).

The composition of catches in terms of the number of species in each bioecological category (Fig. 4) was dominated at all sites by the ME (33.3–46.3%) and Em (29.3–41.7%) categories. The proportion of Mo was three times higher at Elinkine (12% at 13 km) than at Adéane (4.2% at 130 km). This category was not observed in the villages located at 158 km (Diattakunda) and 170 km (Sédhiou) from the mouth. The proportion of Es in the landings at 170 km (16.7%) was twice that at 13 km (8.0%).

The representation of each trophic category in terms of the number of species was well balanced across the landings of all surveyed villages (Fig. 5). However, terminal predators predominated at the three downstream villages, representing between 42.4 and 51.2% of the species recorded at these sites. At the upstream villages, except for Simbandi Brassou at 158 km, primary consumers dominated, representing 37.5% of the species recorded at 130 km and 170 km.

Globally, the species diversity indices (H' and J' as estimated by species) decreased from downstream to upstream sites (Table 2). However, high values of both diversity indices were observed at the village of Diattakunda (130 km) due to a more even distribution of catches between species. The lowest species diversity index values were observed at the villages of Adéane (93 km) and Simbandi Brassou (158 km). The decrease in diversity from downstream to upstream regions of the estuary was also reflected in the taxonomic

Table 2
Species richness, Shannon diversity index (H'), evenness (J'), taxonomic diversity (Δ), taxonomic distinctness (Δ^*) and species dominance at the six sampled villages in the Casamance estuary (D = distance from the mouth in km).

Village	Species								Ecological categories	
	D. (km)	Species number	H'	J'	Δ	Δ^*	Species dominance (50% biomass)	Species dominance (90% biomass)	H'	J'
Elinkine	13	50	1.19	0.71	3.69	3.74	4	17	0.41	0.53
Tendouk	42	43	0.35	0.22	3.49	3.56	1	3	0.15	0.20
Adéane	93	33	0.24	0.16	3.43	3.54	1	2	0.14	0.18
Diattakunda	130	24	0.52	0.38	3.38	3.52	1	4	0.36	0.52
Simbandi Brassou	158	21	0.24	0.18	3.39	3.56	1	2	0.09	0.13
Sédhiou	170	24	0.30	0.22	3.49	3.67	1	2	0.13	0.19

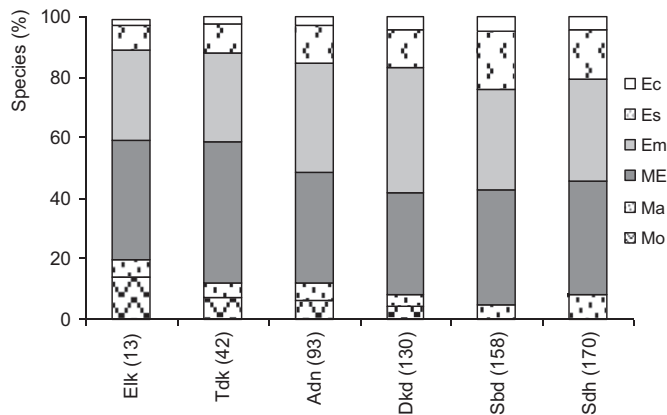


Fig. 4. Species richness by functional estuarine category at the six sampled villages in the Casamance estuary (Elk: Elinkine; Tdk: Tendouk; Adn: Adéane; Dkd: Diattakunda; Sbd: Simbandi Brassou; Sdh: Sédhio; the distance (km) of each village from the mouth is shown in parentheses). Es: strictly estuarine species; Ec: estuarine species of continental origin; Em: estuarine species of marine origin; ME: marine-estuarine species; Ma: marine species accessory in estuaries; Mo: marine species occasional in estuaries).

diversity indices Δ and Δ^* . However, these two indices, particularly Δ^* , showed that the species caught at the two villages furthest upstream have relatively high mean positions on the hierarchical classification tree even though the number of species observed at these two localities was low.

The functional diversity indices (H' and J' as estimated by bio-ecological categories) showed trends similar to those based on species but exhibited lower values at all localities. This was particularly true of H' . The lowest functional diversity indices were observed at the village of Simbandi Brassou (158 km).

4.3. Species abundance and salinity

The regression analysis of species abundances in each catch in relation to salinity revealed three distinct groups of species (Table 3). The first group consists of species for which abundance was negatively influenced by salinity. This group contains the largest number of species, including *Arius latiscutatus*, *Caranx senegalensis*, *Drepane africana*, *Pseudotolithus elongatus*, and other species. The second group consists of species that seem unaffected

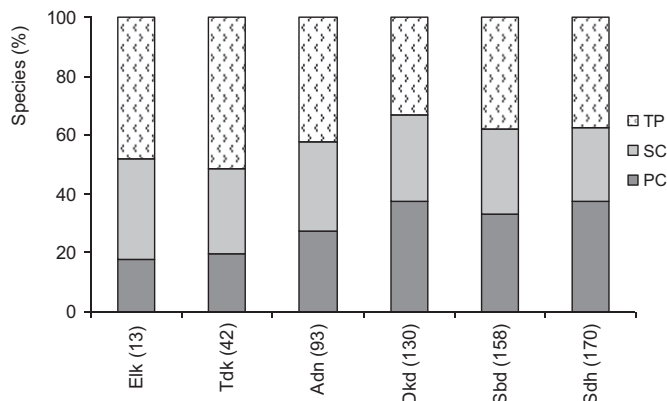


Fig. 5. Species richness by trophic category at the six sampled villages in the Casamance estuary (Elk: Elinkine; Tdk: Tendouk; Adn: Adéane; Dkd: Diattakunda; Sbd: Simbandi Brassou; Sdh: Sédhio; the distance (km) of each village from the mouth is shown in parentheses). PC: Primary consumers; SC: Secondary consumers; TP: Terminal predators).

Table 3

Relationship between landed catch by species and salinity in the Casamance estuary; species are grouped according to the results of the linear regression (N = number of observations; a and b = parameters of the linear regression $y = ax + b$; r^2 = coefficient of regression; p = probability level: ns = not significant; * significant at probability level 0.05; ** significant at probability level 0.01; *** significant at probability level 0.001).

Sensitivity to salinity	Species	N	a	b	r^2	F-statistic	p
Species sensitive to salinity	Aga	24	-11.79	21.62	0.82	97.32	***
	Cas	24	-4.90	8.93	0.59	32.56	***
	Chg	24	-5.56	10.03	0.69	49.04	***
	Chi	24	-4.77	8.60	0.53	25.05	***
	Chl	24	-1.64	2.96	0.44	17.6	***
	Cyn	24	-3.56	6.38	0.54	26.03	***
	Daf	24	-8.11	14.62	0.68	45.98	***
	Eae	24	-1.68	3.03	0.41	14.99	***
	Egu	24	-5.59	10.07	0.62	35.61	***
	Gde	24	-5.07	9.14	0.74	62.58	***
	Gme	24	-10.71	19.51	0.79	86.42	***
	Iaf	24	-1.45	2.66	0.17	4.578	*
	Lgr	24	-9.92	18.55	0.48	20.45	***
	Lia	24	-1.59	2.86	0.48	20.18	***
	Mba	24	-8.57	16.36	0.39	14.04	**
	Pbr	24	-4.63	9.13	0.24	6.751	*
	Pel	24	-8.02	14.59	0.66	43.13	***
	Pju	24	-6.16	11.19	0.68	47.12	***
	Plm	24	-8.18	14.88	0.59	32	***
	Poq	24	-8.55	16.19	0.36	12.52	**
	Pty	24	-5.20	9.33	0.72	56.68	***
	Spi	24	-9.59	17.78	0.55	26.81	***
	Tle	24	-2.11	3.78	0.47	19.39	***
Species indifferent to salinity	Efi	24	2.09	-0.24	0.07	1.759	ns
	Hfa	24	0.92	-1.13	0.02	0.4824	ns
	Ldu	24	2.52	-3.08	0.09	2.337	ns
	Lfa	24	-0.31	2.92	0.004	0.08476	ns
	Ppe	24	0.17	0.17	0.001	0.01331	ns
	Psb	24	-0.53	1.06	0.06	1.384	ns
Species tolerant to salinity	Tfa	24	2.72	-3.33	0.11	2.808	ns
	Ela	24	8.01	-11.61	0.62	35.76	***
	Gni	24	5.88	-8.66	0.35	11.71	**
	Mce	24	8.16	-12.59	0.52	23.86	***
	Slu	24	1.42	-2.33	0.19	5.159	*
	Tgu	24	9.54	-13.87	0.46	18.92	***
	The	24	13.55	-19.87	0.71	54.56	***

by salinity, with non-significant variations in abundance. Species in this group include *Ethmalosa fimbriata*, *Hemichromis fasciatus*, *Liza dumerili*, *Pomadasy perotaei*, and others. The last group contains species for which abundance was positively influenced by salinity, including *Elops lacerta*, *Gerres nigri*, *Mugil cephalus*, *Tilapia Guineensis*, and *Sarotherodon melanotheron*. The remaining species in Table 1 that are not listed in Table 3 were observed mainly in the villages further downstream or sporadically in some of the upstream villages.

4.4. Fish species assemblage structure inferred from catches

The Ascending Hierarchical Clustering performed on the Correspondence Analysis coordinates of the 22 most abundant species by weight (99.7% of the total landings) shows that the exploited assemblage in the Casamance estuary is structured into three groups (Fig. 6). The first group, Group 0, contains only one species, *P. perotaei*. This species was always observed at all surveyed villages throughout the estuary. Group I consists of 10 species, including three, *S. melanotheron*, *E. lacerta* and *T. guineensis*, that were particularly closely associated. These three species were caught at all villages, and always in high abundances at the four villages furthest upstream. These three species were associated strongly with *Trachinotus teraia*, *E. fimbriata*, and *Liza falcipinnis* and

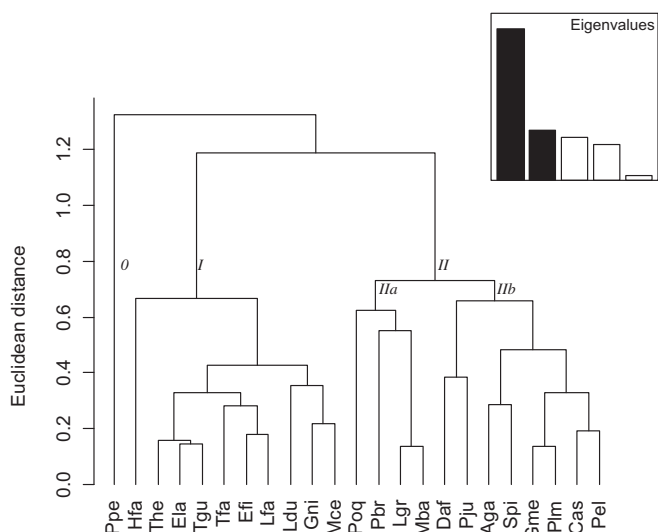


Fig. 6. Dendrogram of the cluster analysis of the biomass per species in the Casamance estuary (based on the coordinates on the first two Correspondence Analysis axes, which explained 72.68% of the variance; species codes: Ppe = *P. perotaei*, Hfa = *H. fasciatus*, The = *S. melanotheron*, Ela = *E. lacerta*, Tgu = *T. guineensis*, Tfa = *T. teraia*, Efi = *E. fimbriata*, Lfa = *L. falcipinnis*, Ldu = *L. dumerili*, Gni = *G. nigri*, Mce = *M. cephalus*, Poq = *P. quadrifilis*, Pbr = *P. brachygnathus*, Lgr = *L. grandisquamis*, Mba = *M. bananensis*, Daf = *D. africana*, Pju = *P. jubelini*, Aga = *A. latiscutatus*, Spi = *S. afra*, Gme = *E. melanopterus*, Plm = *P. macrolepis*, Cas = *C. senegallus*, Pel = *P. elongatus*).

less strongly with *L. dumerili*, *G. nigri*, and *M. cephalus*. These latter species were captured at every village, with maximum abundances at the two villages located at 93 km (Adéane) and 130 km (Diatlakunda). *Hemichromis fasciatus*, the only estuarine species of freshwater origin, was also associated with this group, but much more weakly than the other species. Group II can be differentiated into two subgroups. The four species *Polydactylus quadrifilis*, *Mugil bananensis*, *Liza grandisquamis* and *Pseudotolithus brachygnathus* form Subgroup IIa. These species were present at almost all villages, and their abundances were highest at the three downstream villages. Subgroup IIb includes *P. elongatus*, *A. latiscutatus*, *Sphyræna afra*, and *C. senegallus*, which were always present at the three downstream villages, with maximum abundance at the village of Elinkine. In the downstream landings, the species of Subgroup IIb were often associated with *D. africana* and *Pomadasys jubelini*, which had generally low abundances.

4.5. Sampled villages and functional structure inferred from total catches

Between-class PCA based on the landed catches by species (Fig. 7) showed that the main structuring axis (axis 1, which explained 38.4% of the total variance) corresponded to the upstream–downstream gradient. Villages differed with respect to the species composition of landings. The two villages furthest downstream were the most distinct from the others in catch composition and very similar to each other in this parameter. The three villages furthest upstream were also very similar to each

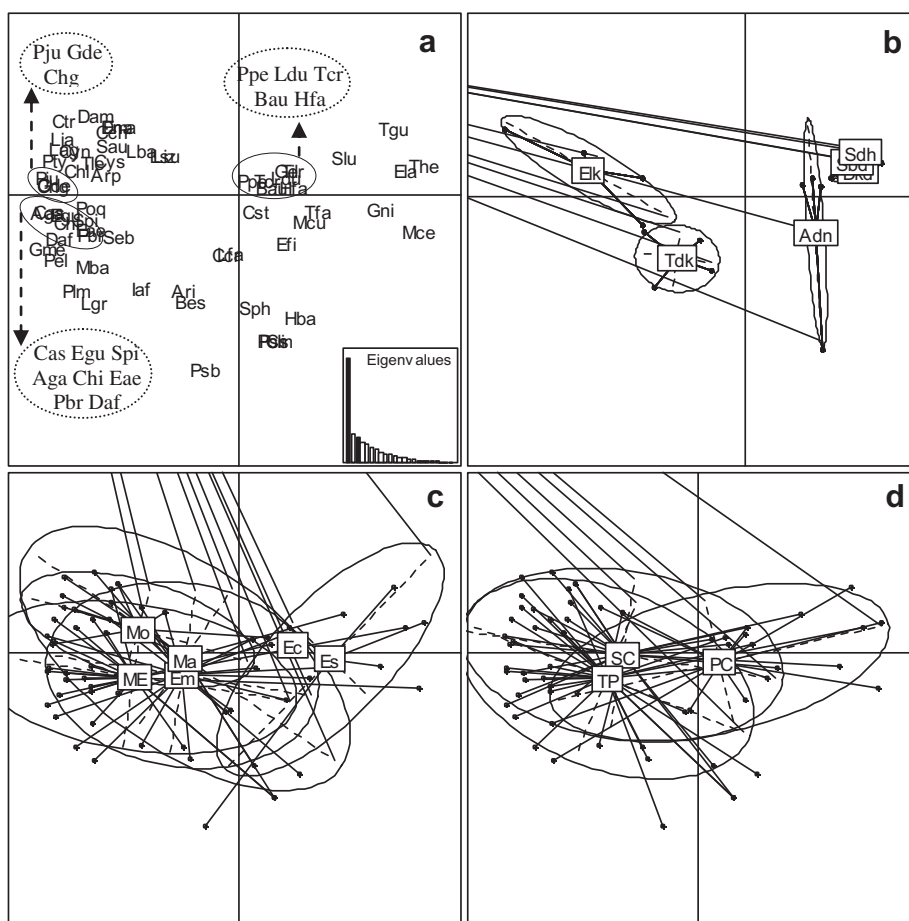


Fig. 7. Between-class PCA of the landed catch biomass in the Casamance estuary: (a) projection of sampled species; (b) projection of means for each sampled village (Elk: Elinkine; Tdk: Tendouk; Adn: Adéane; Dkd: Diattakunda; Sbd: Simbandi Brassou; Sdh: Sédhiou); (c) projection of means for each functional estuarine category; (d) projection of means for each trophic category. Solid lines connect the points of observation to the mean points; dotted lines indicate the axes of symmetry of the ellipses. For codes refer to Table 1.

other in species composition. Adéane was closer in species composition to the upstream villages than to the downstream villages. Axis 3 separated groups of species that were characteristic of the downstream portion of the river in different months. Together, axes 1 and 3 explained 47.7% of the total variance. Axis 3 (9.3%) was preferred over axis 2 (10.2%), which explained a similar percentage of the variance, because the distribution of points on axis 3 was easier to interpret than that obtained using axis 2.

The catches at the two villages furthest downstream, Elinkine (13 km) and Tendouk (42 km), were dominated by species with marine affinities (Fig. 7c). At the four villages further upstream, Adéane (93 km), Diattakunda (130 km), Simbandi Brassou (158 km), and Sédhiou (170 km), catches were dominated by Es and Ec species. This last category was represented by a single species, *H. fasciatus*.

Regarding the trophic categories of fish (Fig. 7d), the catches were dominated by terminal predators and secondary consumers at the downstream villages, Elinkine and Tendouk, whereas at the four villages further upstream the catches were dominated by primary consumers. This last category was also fairly well represented at the downstream sites, which explains why the ellipse in Fig. 7d includes some of the negative area on axis 1. The species belonging to the estuarine category were mostly primary consumers, whereas those with marine affinities were mostly secondary consumers or terminal predators.

5. Discussion

The total fish species richness observed in the catches landed during the surveys conducted in 2005 in the Casamance estuary was 59 species. This richness was distributed across six of the eight bioecological categories previously described in West African estuaries (Albaret, 1999). The two categories Co and Ce were absent, and Ec was represented by a single species. The richness observed in the downstream region of the estuary was twice that observed in the upstream region. This decrease in richness upstream agreed with previous investigations conducted in the Casamance estuary by Albaret (1987) and with the observations by Whitfield et al. (2006) of the St. Lucia estuarine system in South Africa. The pattern of variation in species richness observed in Casamance might be explained by one or both of the following possibilities. Firstly, in the permanent exchange between the estuary and the sea, the penetration of most marine species is restricted to the downstream portion of the estuary where the mean salinity, between 41 and 48, is relatively low. In contrast, the increased salinity upstream (up to 61 on average) significantly reduces the presence of species with low tolerance for salinity because of the adaptative capacity needed in this constraining environment (Deegan et al., 1997; Cabral et al., 2001; Mouillot et al., 2007). According to Sosa-López et al. (2007), the area of highest richness in normal estuaries occupies a narrow range of salinities between 5 and 10. Similarly, Cognetti and Maltagliati (2000) suggest that within the range of salinities from 10 to 30, fish communities are most highly structured in terms of different functional groups. Both of these salinity ranges are below those currently observed in the Casamance estuary.

Secondly, the diversity of fishing gear and techniques recorded downstream facilitates the exploitation of a greater variety of habitats, and so might enable the catching of more species. However, the different fishing techniques used in the different regions of the estuary reflect those methods that are successful, rather than a difference in fishing effort, and these methods are likely to be less diverse upstream because the population in that area is little diversified due to an unfavourable environment. Indeed, it has been observed in other ecosystems that increased

fishing effort is accompanied by a diversification of the gear considered most efficient (Laë et al., 2004; Kantoussan et al., 2007).

Dominance was very high in the upstream portion of the estuary (except at Diattakunda), where most of the landings were composed of a small group of species, almost all of which belonged to the strictly estuarine/herbivore category. This is a sign of a stressed environment (Warwick, 1986; Blanchard et al., 2004). Simplification of the taxonomic structure, due to both the absence and the reduced abundance of several species, was observed in areas of high salinity in the upstream region of the Casamance estuary. Additionally, species at the upstream sites are positioned on the hierarchical tree at a functional level generally lower than was observed downstream, as was suggested by Warwick and Clarke (1995) and Clarke and Warwick (1998) to occur in stressful situations. This result emphasises the relevance of taxonomic indices as indicators of environmental condition and corroborates the findings of other studies conducted in the waters of north-western Europe (Rogers et al., 1999), the Terminos Lagoon in Mexico (Miranda et al., 2005) and the lagoons of the Languedoc-Roussillon in France (Mouillot et al., 2005).

5.1. Fish assemblage structure

The fish community of the Casamance estuary, as observed through the catches documented here, is strongly dominated by species in the categories ME and Em. However, quantitative analysis based on species biomass revealed significant differences in the composition of populations in different regions of the estuary, with two major groups. Most of the species that are characteristic of the exploited population in the downstream region of the estuary, which include *A. latiscutatus*, *P. elongatus*, *P. macrolepis*, and *E. melanopterus*, belong to the categories ME and Em. In the upstream region, this group of species is replaced by species of the strictly estuarine category including *S. melanothron* and *T. guineensis*, which are widely prevalent in hypersaline areas, and *E. lacerta* and *M. cephalus*, both of the ME category. The species in this second group were found to be widely distributed throughout the estuary, and their catches were either positively correlated with or independent of salinity, reflecting their high tolerance for salinity (Hotos and Vlahos, 1998; Charles-Dominique and Albaret, 2003). The fish assemblage organisation observed in the upstream region of the Casamance estuary is comparable to the observation done by Whitfield et al. (2006) in the St. Lucia estuarine system where Cichlidae (*Oreochromis mossambicus*), Elopidae (*Elops machnata*), Mugilidae (*M. cephalus*) are among the species capable to withstand the highest salinity. The organisation of the fish community along a downstream–upstream gradient in the Casamance estuary suggests that the inversion of the salinity gradient that has resulted from a continued decline in freshwater inputs since the late 1960s (Thiam and Singh, 2002) is the main structuring force in the Casamance estuary. The habitat of species with continental affinities appears to be particularly affected by the inverse salinity gradient, and in fact this group is represented in this estuary by only one species, *H. fasciatus*, which is not very abundant.

Despite the importance of salinity in structuring fish communities in estuarine environments (Marshall and Elliott, 1998; Barletta et al., 2005, 2008; Cardona, 2006; Vivier et al., 2010), it is difficult to attribute the current structure of the fish population of the Casamance estuary to this factor alone. The combined analyses of bioecological categories and trophic categories show that in this estuary, strictly estuarine species are typically primary consumers with a diet dominated by phytoplankton or microphytes. In contrast, species with marine affinities (Mo, ME, Ma, and Em) are typically terminal predators or secondary consumers. The

abundance of primary consumers in the upstream region of the Casamance estuary might be explained not only by the salinity tolerance of most of these species, but also by biological and trophic interactions. Indeed, the mean positions of species of the different trophic categories (Fig. 7d) suggest weak competition for habitat between primary consumers and species of higher trophic levels as well as a low rate of predation by terminal predators on primary consumers.

Biotic interactions such as these are powerful determinants of the structure of communities and ecosystems (Daskalov, 2003; Cardona et al., 2008; Casini et al., 2008, 2009). Moreover, in the Casamance estuary, chlorophyll concentrations are positively correlated with salinity, with values of 2–10 $\mu\text{g l}^{-1}$ in the central and downstream regions and 50 $\mu\text{g l}^{-1}$ in the upstream region (Pagès, 1994). The higher amounts of chlorophyll in the upstream region of the Casamance estuary could be explained by a weak flow and a longer residence time of the water in this region (Lane et al., 2007). Despite an increasing trend in rainfall recorded in recent years, the flow of freshwater remains low, as reflected in the salinity gradient in the estuary. The residence time of the water in the upstream region remains significant and continues to maintain a high level of primary production, which is conducive to the development of primary consumers. Both top-down and bottom-up processes therefore are likely to contribute to the structure of the fish community observed in the Casamance estuary.

5.2. Comparison of the taxonomic and functional approaches

The taxonomic and functional approaches used in this study yielded similar descriptions of the fish populations exploited in the Casamance estuary. Both approaches revealed: (1) lower diversity in the upstream region of the estuary than in the downstream region; and (2) an upstream population dominated by a small group of highly adaptable species, most of which are strictly estuarine and/or primary consumers. In a study of the effects of changes in freshwater inputs into the East Bay (Florida), Livingston et al. (1997) found a marked increase in the proportion of herbivorous species in times of drought. A similar observation was made by Khalaf and Kochzius (2002) in the Gulf of Aqaba (Jordan), in locations subjected to different anthropogenic pressures. The dominance of species of these two categories (strictly estuarine and primary consumers) is an indicator of the degradation of environmental conditions in the Casamance estuary.

The assessment of the condition of the Casamance community based on the two approaches shows that both approaches are relevant and complementary, allowing interpretation at both taxonomic and functional levels. However, the taxonomic approach has limited applicability in more comprehensive studies that include multiple ecosystems, because of the variation in species composition at different scales (Harrison and Whitfield, 2006; Franco et al., 2008). Thus, the use of functional groups is more appropriate in regional studies such as those designed to compare sub-regional structures of populations or to define estuary typology (Potter et al., 1990; Nordlie, 2003; Franco et al., 2008; Harrison and Whitfield, 2008). Conversely, the functional approach may be less suitable for application at the ecosystem scale. Changes within a community take place primarily at lower levels of organisation (Adams, 2002), and the population level may first reflect a change that would remain unseen at higher levels of biological organisation including functional categories. In terms of management, monitoring the health of ecosystems using indicator species is probably more feasible for local populations than are approaches based on ecological categories. The establishment of functional categories requires knowledge of the ecology and biology of the

species, and these data are still lacking for many species in the tropics.

In conclusion, the taxonomic and functional approaches used in this study to evaluate the status of the Casamance estuary yielded similar images of a community strongly affected by environmental degradation. The two approaches are complementary, and their combination allows both taxonomic and functional interpretation. The hypothesis that environmental disturbance, in particular the increased salinity in the upstream region of the Casamance estuary, is the main factor structuring fish communities in this estuary is largely supported by the indicators tested in this study.

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