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A multimetric-index approach using fisheries data to assess fish assemblage structure in relation to salinity gradient in a tropical West African estuary

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This study examines the effects of increasing salinity on fish assemblage structure in the Casamance Estuary, Senegal, using a series of indices. The study data were derived from commercial fishery surveys conducted between April and July 2005. Analysis of within-trophic-group diversity in the Casamance Estuary shows a significant drop in the diversity of apex predators in the upper, more saline reaches of the estuary. By contrast, primary consumers adapted well to salinity changes and exhibited higher taxonomic diversity in the upper reaches of the estuary than in the lower reaches. The findings also indicate decreases in average sizes of the landed species and the trophic levels among fish catches in the direction of the upper reaches. However, the catch per unit effort (CPUE) was globally higher in the upstream area of the estuary as compared with the downstream area. This increasing CPUE trend from the lower towards the upper reaches is attributed to (i) the high primary productivity in the upper Casamance Estuary; (ii) the increasing abundance of euryhaline fish species in an upstream direction; and (iii) 'telescoping' of the food chain through the presence of mostly herbivorous fishes in the upper reaches. Such a situation likely facilitated high fish production in the upstream area of the estuary, though multimetric indices indicated unfavourable living conditions for many fish taxa in this area.

Keywords: biological indicators, Casamance Estuary, ecosystem monitoring, fishery statistics, inverse hypersaline estuary, Senegal, taxonomic diversity

Introduction

Estuaries are transitional ecosystems, the ecological dynamics of which are subject to both marine and continental influences (Elliott and Whitfield 2011). Estuaries are characterised by complex physical processes and high productivity, and play an important role in the life cycles of many coastal fish species (Cardoso et al. 2011; Wasserman and Strydom 2011; Whitfield et al. 2012). Fishes in tropical estuaries are often subject to subsistence and commercial exploitation to meet the food requirements of local populations (Blaber 1997, 2013; Pérez-Ruzafa and Marcos 2012; Saintilan and Wen 2012).

Although the ecological importance of estuaries is largely acknowledged, these ecosystems are increasingly affected by various types of disturbance, such as pollution, eutrophication, habitat modification, overfishing and climate change, the combined effects of which seriously affect their structure and functioning (Scheren et al. 2002; Simier et al. 2004; Champalbert et al. 2007; Kantoussan et al. 2012). These forcing factors have direct and/or indirect negative effects on the quality of aquatic ecosystems for biota. These factors also affect the biological processes occurring in estuaries and threaten biodiversity, and thus may reduce the goods and services provided to local populations (Panfili et al. 2004; Miranda et al. 2005; Sosa-López et al. 2007; Gueye et al. 2012; Walsh et al. 2013).

To improve the diagnosis of various threats, tools based on indices measuring the ecological status of aquatic ecosystems have been widely developed during the last two decades (Harrison and Whitfield 2006; Borja et al. 2009; Coll et al. 2016). Thus, many indicators have been devised at different levels of biological organisation, with varying results depending on the systems studied (Gislason and Rice 1998; Adams 2002; Rochet et al. 2005; Dauvin 2007). Preliminary findings suggest that these indicators are very sensitive to the nature of the disturbance and to the tools chosen for investigation (Jennings et al. 2002; Laë et al. 2004; Rochet et al. 2005; Harrison and Kelly 2013). It is therefore important to extend their use to monitoring disturbances of various origins, including anthropogenic (e.g. pollution and overexploitation) and natural (climate variability), and to adapt their computation to available data sources, including commercial fishery statistics.

The relevance of testing indicators from commercial fisheries data is justified by the fact that in developing countries it is often difficult to organise scientific monitoring of ecosystems for lack of means, and data from commercial fisheries are often more accessible in many of these countries. Previous indicator studies of estuarine fishes have avoided the use of commercial fisheries data, hence

it is important to assess the suitability of such data as diagnostic tools to assist with the management of aquatic ecosystems. In terms of disturbance levels and threats to aquatic ecosystems, estuaries have received considerable research attention (Deegan et al. 1997; Harrison and Whitfield 2004; Hallett et al. 2012), often with reference to the difficulty of separating assessments of natural stress (as generated by normal environmental fluctuations) from those of anthropogenic stress (Elliott and Quintino 2007).

This study was carried out in the Casamance Estuary in Senegal, West Africa (Figure 1), to assess the effects of salinity gradients on fish assemblages. Data used are from scientific monitoring of the catch landed by artisanal fisheries. Since the transformation of the Casamance River into an inverse, hypersaline estuary, first noted in the early 1970s (Mikhailov and Isupova 2008), few studies have examined the fish assemblage structure in this ecosystem (Albaret 1987; Kantoussan et al. 2012). Nonetheless, these studies have revealed differences in the species composition and structure of fish assemblages between upstream and downstream sites, and noted a decrease in taxonomic diversity associated with increasing hypersalinity in an upstream direction. The present study uses commercial fishery data to analyse the estuary's within-trophic-group taxonomic diversity, fish size-structure, trophic-level variation and yield per fishing trip. The information is also used to determine whether the decrease in river flow and modification to the salinity gradient associated with climate change could impact (i) within-trophic-group diversity; (ii) the size structure of fish assemblages, trophic levels, and yield by fishing trip; and (iii) the indices that best reflect changes in functional relationships within this tropical estuary.

The hypothesis underlying this work was that fish assemblage structure along a salinity gradient could be evaluated using indices based on artisanal commercial fishery data. The Casamance Estuary was chosen for this study because, since the 1970s, this ecosystem has been subjected to a prolonged drought and a significant long-term decline in riverine input, leading to a persistent reversed salinity gradient (Conchedda et al. 2008, 2011; Sambou et al. 2014).

Study area

Located in southwestern Senegal, the Casamance River is formed by the confluence of several small rivers that cease flowing during the dry season (Thiam and Singh 2002). The system is 350-km long (approximately 260 km of permanent river) and drains a watershed of approximately 14 000 km² (Saos et al. 1987). In the southern part of Senegal, the climate is Sudano-Guinean, characterised by an alternation between two seasons: a wet season from mid-May to October, and a dry season during the rest of the year (Thiam and Singh 2002; Carney et al. 2014).

The relief of the Casamance River basin is predominantly flat, with its highest point (75 m) located 400 km from the sea. The slope is generally very gentle in the upper part of the river (0.5 m km⁻¹) and almost zero for the last 200 km of the river (Marius 1985; Pagès 1986; Pagès et al. 1987). Data from the meteorological station at Ziguinchor shows an overall decrease in annual precipitation in the area since the 1950s, when it was 1 614.5 mm; mean rainfall was 1 475.4,

1 226.5 and 1 066.8 mm, respectively, during the 1960s, 1970s and 1980s, increasing during the 1990s to an average of 1 254.3 mm (Figure 2a); but, between 2000 and 2003, the average annual precipitation declined again, to 1 164.3 mm.

The river's flow rate is remarkably low, with an annual average of 2.7 m³ s⁻¹ (Binet et al. 1995). Freshwater inputs from the river into the estuary are seasonal and occur mainly between June and November (Thiam and Singh 2002).

Salinity values recorded for the Casamance system reflect hypersaline conditions (>40) downstream of the Maka anti-salt dam, located approximately 200 km from the river mouth (Albaret 1987; Debenay et al. 1989; Binet et al. 1995; Kantoussan et al. 2012). This dam was built to stop the advance of the saline waters upstream of the dam wall and to avoid the salinisation of agricultural lands in the area above the dam. Observations by Ndour et al. (2011) indicated salinity values falling to zero in the upstream part of the dam between October and February. Salinities in the Casamance Estuary are strongly influenced by evaporation and rainfall from both past and present years (Savenije and Pagès 1992). Human use of water from the estuary is very low due to prevailing salinities, and family (subsistence) farming is based mainly on direct rainfall onto the land.

During the study period, the salinity increased from the village of Elinkine, located 13 km from the estuary mouth (40.6 [SD 1.1]), to Diattakunda, 130 km upstream of the mouth (61.6 [SD 9.0]), and then decreased slightly at the two most-upstream villages, Simbandi Brassou (58.9 [SD 10.9]) and Sédhiou (57.2 [SD 10.1]) (Figure 2b).

Materials and methods

Sampling design

Artisanal fisheries in the Casamance Estuary were monitored at six fishing villages: Elinkine and Tendouk in the downstream area, Adéane and Diattakunda in the middle reaches, and Simbandi Brassou and Sédhiou in the upstream area. At each village, the surveys were conducted monthly between April and July 2005, for approximately 15 days each month. The sampling method was adapted from Laë et al. (2004) and Kantoussan et al. (2007). Each survey was composed of three operations: (i) monthly counts of active fishing units (one fishing unit = one canoe) to assess the fishing potential of each surveyed location; (ii) surveys of the landings, conducted to determine the species composition and size of the fish; and (iii) information on fishing trips to estimate the fishing effort (e.g. fishing site, distance from village, fishing time, gear used, number of nets set, number of people involved in fishing), collected by interviewing fishers every evening during the survey period.

The fishery in the Casamance Estuary makes use of multiple types of fishing gear. In the present study, the fishing gear was classified into major categories based on the fishing technique and mesh size of the net used. For gillnets, three categories of mesh sizes (knot to knot) were distinguished: small mesh (<30 mm), medium mesh (30–50 mm) and large mesh (>50 mm).

Fish that were landed were identified to species level, catches were estimated as mass of each species, and the fork length (FL, cm) of twenty individuals of each species landed was recorded.

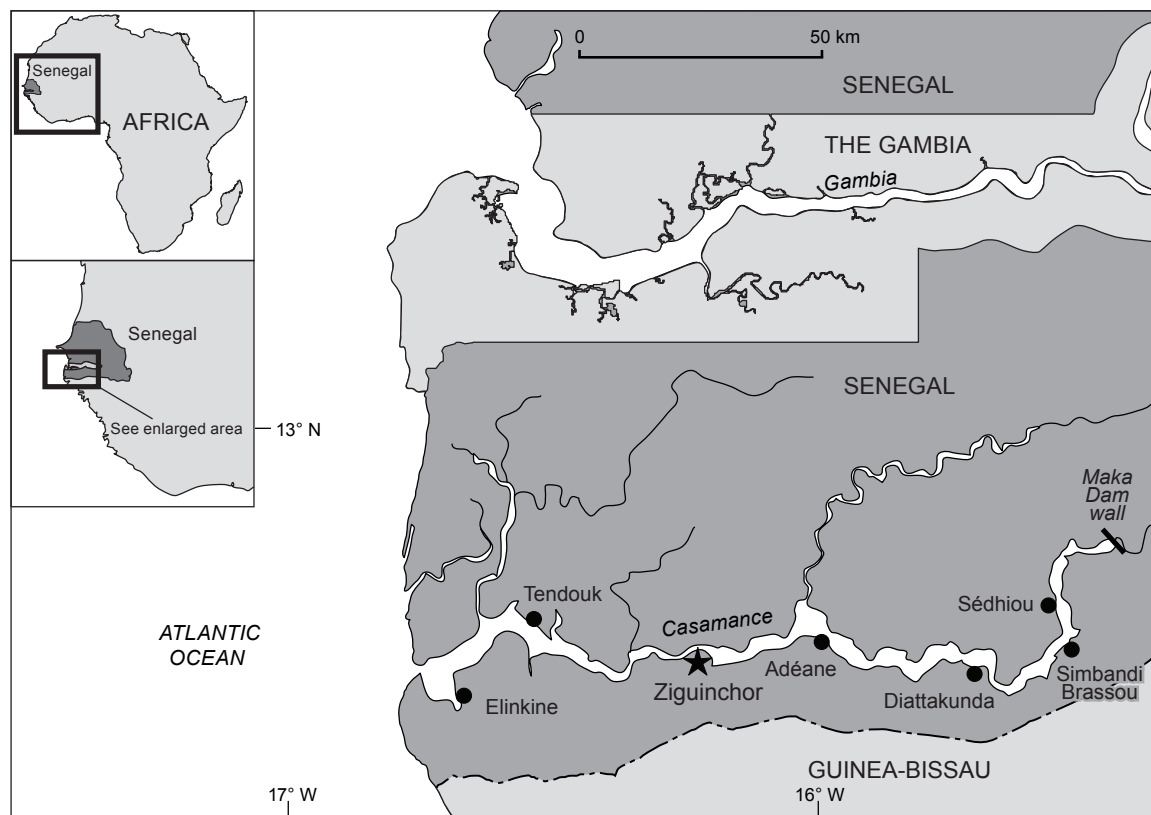


Figure 1: Geographic location of the Casamance Estuary system, Senegal, and the sampled villages (dots); star = regional capital and location of meteorological station

Data processing

Diversity indices

Two taxonomic diversity indices (Warwick and Clarke 1995) were used to estimate the within-trophic-group taxonomic diversity in the landed catch, using the identity of the landed species. The first index (taxonomic diversity index, Δ) is based on the classic Shannon diversity index, with an added component of taxonomic separation. This index is estimated as:

$$\Delta = \frac{\sum \sum w_{ij} x_i x_j}{\sum \sum x_i x_j + \sum x_i (x_i - 1) / 2}$$

where w_{ij} is the weighting given to the path length linking species i and j in the Linnean hierarchy, and x_i represents the catch in mass of the i th species. The second index (taxonomic distinctness index, Δ^*) is purely an index of taxonomic distinctness (i.e. taxonomic distance), expressed without considering the contribution of the species to diversity. This index is expressed as:

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

Taxonomic indices are less sensitive to the sample size or sampling efforts than the Shannon diversity index (Magurran 2004; Roberts and Connell 2008). The species were ranked according to their classification in FishBase (www.fishbase.org).

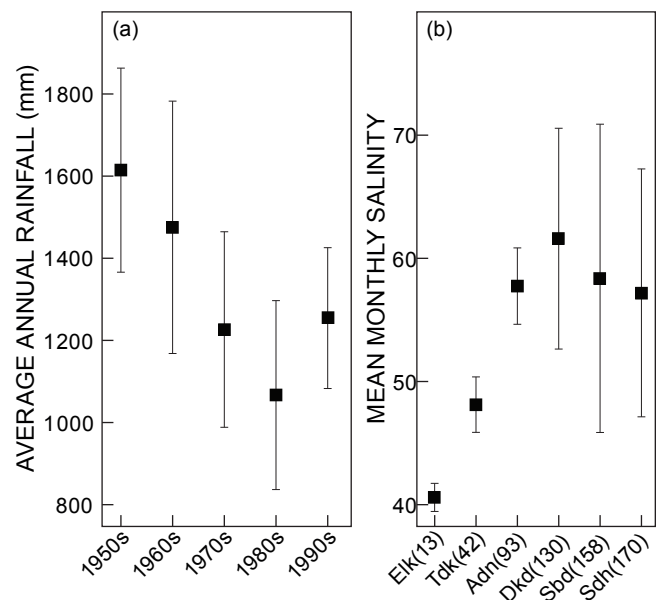


Figure 2: (a) Average annual rainfall by decade, from data collected by the meteorological station at Ziguinchor; (b) mean monthly salinity at the six locations along the Casamance Estuary (Elk = Elinkine; Tdk = Tendouk; Adn = Adéane; Dkd = Diattakunda; Sbd = Simbandi Brassou; Sdh = Sédhiou). The distance (km) of each village from the estuary mouth is shown in parenthesis (modified from Kantoussan et al. 2012)

org). Taxonomic indices were estimated from the $\log(x+1)$ transformed catches to reduce the weighting of the dominant species (Clarke and Warwick 1998).

Trophic categories

The recorded fish species (Table 1) were assigned to trophic categories adapted from an earlier classification system devised by Paugy and Leveque (1999). Those authors identified three major trophic categories: (i) mainly primary consumers (PC), which are herbivorous or predominantly phytoplanktivorous, microphytophagous, detritivorous or grazer species; (ii) mainly secondary consumers (SC), which are predominantly zoobenthivorous (feeding on molluscs, annelids, etc.), first-level predators or first-level generalists (feeding on crustaceans, insects, etc.), or predominantly zooplanktivorous species; and (iii) terminal predators (TP), which are second-trophic-level generalist predators (fish and other prey) or predominantly piscivorous species.

Size structure

Indicators derived from various fish size-spectra, namely average size, modal class, proportions of large (>50 cm) and small (<10 cm) individuals, mean maximum observed length, and slope and intercept of the size distributions, were used to detect the possible effects of salinity on these various population parameters. The mean maximum observed length was calculated from the maximum observed sizes for each species, and each size class was represented by the median value of the size class. Logarithmic transformation was applied to the number of individuals (y variable) in each size class (x variable), in order to normalise fish size distributions. Linear regression was performed on the size classes larger than or equal to (\geq) the first modal size class. In principle, an increase in disturbance in the form of salinity should result in a steeper slope and a higher intercept upstream of the location where the abundance of large individuals is expected to decrease—as these fish should be more sensitive to hypersalinity as a forcing factor—and where the abundance of smaller individuals is expected to increase (Rice and Gislason 1996; Gislason and Rice 1998).

Trophic level

Information on the trophic level of each species was obtained from FishBase (www.fishbase.org). The mean trophic level (TL_m) of the catches was estimated by weighting the TL_i using the mass of each species, according to the formula:

$$TL_m = \frac{\sum_{i=1}^S (Y_i TL_i)}{\sum Y_i}$$

where Y_i is the yield for the species i ; TL_i is mean trophic level of species i ; and S is the total number of species.

Statistical analyses

The differences observed between samples were compared using statistical tests with a significance level $\alpha = 0.05$ (Scherrer 1984). The Kruskal–Wallis test for independent

samples was used to compare the mean sizes and average maximum sizes observed between villages from the surveyed sizes. An analysis of covariance (ANCOVA) was applied to the $\log(x+1)$ transformed numbers of individuals according to size class to test the slopes and intercepts between the villages. Catch per unit effort (CPUE) data were analysed based on the three most-representative gears for the sampled villages, namely castnets, small-mesh gillnets (<30 mm) and medium-mesh gillnets (30–50 mm). CPUE values, according to gear, were compared between the landings of the different villages using the Kruskal–Wallis test followed by a pairwise test using Holm's method for p -value adjustment.

Results

Taxonomic diversity according to trophic category

The most dominant fish species (based on catch mass) in the Casamance Estuary as a whole were the primary consumers *Sarotherodon melanotheron* (71.4%), *Ethmalosa fimbriata* (12.6%) and *Tilapia guineensis* (10.0%). These species also dominated catches in the upstream region of the estuary, with *S. melanotheron* (83.6%), *T. guineensis* (10.7%) and *E. fimbriata* (3.7%) making up 98% of the fish mass harvested in this area. By contrast, certain species which are all terminal predators or secondary consumers, namely *Arius latiscutatus*, *A. parkii*, *Caranx hippos*, *Cynoglossus senegalensis*, *Dasyatis margarita* and *Trichiurus lepturus*, were very scarce and comprised <1% of the total catch.

The within-trophic-group taxonomic diversity showed that the primary-consumer category was least impacted by the hypersalinisation of the Casamance Estuary (Table 2). Indeed, this category had higher taxonomic diversity indices in the upper reaches than in the lower reaches of the estuary. The diversity indices at 13 km were $\Delta = 2.85$ and $\Delta^* = 3.08$, and at 170 km they were $\Delta = 3.17$ and $\Delta^* = 3.64$. The pattern of variation of the diversity indices was less clear for the secondary consumers. In this category, the least diversified catches ($\Delta = 2.65$) were landed 130 km from the mouth. The catches of the terminal consumers were more diversified downstream, with $\Delta = 3.52$ at 13 km, which was greater than upstream, where $\Delta = 3.05$ at 158 km and at 170 km.

Size distribution of the catches

The distributions of the size spectra differed significantly in the surveyed localities (Kruskal–Wallis test, $p < 0.05$). The widest size spectrum was observed in the catches 13 km from the mouth, with a modal class of approximately 19–20 cm, 2.8% individuals with a size >50 cm, and almost 0% small individuals (Table 3). At other localities, the size spectra were narrower, with a significant proportion of small individuals and lower modal classes: 11–12 cm at 93 km and at 158 km, 7–8 cm at 130 km, and 9–10 cm at 170 km from the mouth.

The mean sizes of the fish decreased from Elinkine, 13 km from the mouth (22.9 cm [SD 16.4]), to Diattakunda, 130 km from the mouth (12.2 cm [SD 9.5]) (Table 3). The mean sizes showed a slight increase at Simbandi Brassou (16.2 cm [SD 9.9]) and at Sédhieu (14.7 cm [SD 7.3]),

Table 1: List of fish species and their occurrence (%) in artisanal catches at villages along the Casamance Estuary, Senegal, from April to July 2005. Occurrence indicates the percentage of the total landings at each village that contained each species. The maximum salinity in which the species has been recorded, either in the Casamance Estuary or elsewhere, is taken from Albaret (1987) or Panfili et al. (2006). Trophic categories: PC = primary consumer, SC = secondary consumer, and TP = terminal predator

Species	Species code	Trophic category	Location (distance from estuary mouth)						Maximum salinity
			Elinkine (13 km)	Tendouk (42 km)	Adéane (93 km)	Diattakunda (130 km)	Simbandi Brassou (158 km)	Sédhiou (170 km)	
<i>Arius latiscutatus</i>	Aga	TP	47.30	18.25	14.89	0	3.74	0.39	48
<i>Arius parkii</i>	Arp	TP	3.04	0.24	1.53	0	0	0	45
<i>Brachydeuterus auritus</i>	Bau	SC	0	0	1.15	0	0	0	–
<i>Caranx crysos</i>	Ccr	TP	0	0.71	0	0	0	0	–
<i>Caranx hippos</i>	Chi	TP	7.77	2.61	0	0	0	0	49
<i>Caranx senegallus</i>	Cas	TP	4.73	7.11	1.53	0.33	0	0	–
<i>Carcharhinus</i> spp.	Cch	TP	1.35	0	0	0	0	0	–
<i>Chaetodipterus goreensis</i>	Chg	SC	12.84	5.92	1.15	0.33	0	0	–
<i>Chaetodipterus lippei</i>	Cli	SC	0	0	0.76	0	0	0	56
<i>Chloroscombrus chrysurus</i>	Chl	SC	5.41	1.66	0	0	0	0	58
<i>Citharichthys stampflii</i>	Cst	TP	0	0.95	2.29	0.65	0	0	–
<i>Cynoglossus monodi</i>	Cym	SC	0.34	0	0	0	0	0	–
<i>Cynoglossus senegalensis</i>	Cys	SC	1.01	0.24	0	0	0	0	48
<i>Dasyatis margarita</i>	Dma	SC	1.01	0	0	0	0	0	40
<i>Dasyatis margaritella</i>	Dam	SC	1.69	0	0	0	0	0	–
<i>Drepane africana</i>	Daf	SC	22.64	2.84	0.76	0	0	0	56
<i>Echeneis naucrates</i>	Ena	SC	0.34	0	0	0	0	0	–
<i>Elops lacerta</i>	Ela	TP	22.30	21.33	38.17	53.75	80.61	84.38	83
<i>Ephippion guttifer</i>	Egu	SC	6.08	0.71	0	0	0	0	>46
<i>Epinephelus aeneus</i>	Eae	TP	4.39	0.47	0	0	0	0	–
<i>Ethmalosa fimbriata</i>	Efi	PC	33.78	75.59	45.04	65.15	88.78	89.06	97
<i>Eucinostomus melanopterus</i>	Gme	SC	31.42	18.48	9.16	1.95	0.68	1.56	66
<i>Galeoides decadactylus</i>	Gde	TP	22.64	2.84	0	0	0	0.78	66
<i>Gerres nigri</i>	Gni	SC	4.39	2.61	60.69	53.42	53.06	28.13	79
<i>Hemichromis fasciatus</i>	Hfa	TP	2.36	1.66	3.82	7.82	5.10	3.13	>56
<i>Hemiramphus balao</i>	Hba	TP	0	0	1.15	0.65	0	0	–
<i>Hyporhamphus picarti</i>	Hpi	TP	0	0	0	0	0	0.39	–
<i>Ilisha africana</i>	Iaf	SC	5.41	4.50	0	0	0	0	48
<i>Lichia amia</i>	Lia	TP	3.38	0.24	0	0	0	0	–
<i>Liza bandialensis</i>	Lba	PC	4.73	0	0	0	0	0	–
<i>Liza dumerili</i>	Ldu	PC	13.51	4.03	38.93	39.41	15.31	13.28	83
<i>Liza falcipinnis</i>	Lfa	PC	29.73	21.09	55.73	43.97	56.46	34.77	73
<i>Liza grandisquamis</i>	Lgr	PC	32.77	22.51	48.85	3.58	0	0.39	45
<i>Lobotes surinamensis</i>	Lsu	TP	0.34	0	0	0	0	0	–
<i>Lutjanus agennes</i>	Lag	TP	4.73	0.47	0	0	0	0	–
<i>Monodactylus sebae</i>	Psb	TP	2.03	3.55	0.38	0	1.02	1.17	57
<i>Mugil bananensis</i>	Mba	PC	27.70	25.36	43.13	17.26	2.04	0.78	66
<i>Mugil cephalus</i>	Mce	PC	3.04	2.84	42.37	38.11	17.69	15.63	66
<i>Mugil curema</i>	Mcu	PC	0	0	0.38	0.98	0	0.78	–
<i>Plectorhinchus macrolepis</i>	Plm	TP	17.57	5.45	3.82	0	0	0	66
<i>Polydactylus quadrifilis</i>	Poq	TP	25.68	4.27	9.16	0.98	1.70	0.39	56
<i>Pomadasys jubelini</i>	Pju	SC	21.62	1.90	3.05	2.61	2.04	2.34	56
<i>Pomadasys perotaei</i>	Ppe	SC	2.36	0.24	33.59	7.49	1.36	1.56	–
<i>Psettodes belcheri</i>	Pbe	TP	0.68	0	0	0	0	0	–
<i>Pseudotolithus brachygnathus</i>	Pbr	TP	35.47	9.95	11.83	4.89	1.70	2.34	48
<i>Pseudotolithus elongatus</i>	Pel	TP	22.97	26.78	2.67	0	0.68	0	48
<i>Pseudotolithus typus</i>	Pty	TP	12.84	0.95	0	0	0	0	56
<i>Rhinobatos</i> spp.	Rhi	TP	0.68	0	0	0	0	0	–
<i>Sardinella aurita</i>	Sau	SC	2.36	0.47	0	0	0	0	–
<i>Sardinella maderensis</i>	Seb	SC	7.09	0.71	0	0	0	0	68
<i>Sarotherodon melanotheron</i>	The	PC	11.15	8.53	79.01	95.77	99.66	100	134
<i>Scomberomorus tritor</i>	Ctr	TP	6.08	0.71	0	0	0	0	56
<i>Sphyræna afra</i>	Spi	TP	22.64	17.77	4.96	0.33	1.36	1.56	66
<i>Strongylura senegalensis</i>	Bes	TP	0.34	0.95	0	0	0	0	–
<i>Synaptura lusitanica</i>	Slu	SC	0	0	1.15	5.54	5.44	8.59	–
<i>Tilapia guineensis</i>	Tgu	PC	10.81	7.35	67.56	81.76	99.32	100	>80
<i>Trachinotus teraia</i>	Tfa	SC	3.38	4.98	14.12	14.01	22.45	19.53	58
<i>Trichiurus lepturus</i>	Tle	TP	4.73	0.47	0	0	0	0	42
<i>Tylosurus crocodilus</i>	Tcr	TP	0	0	0.38	0	0	0	–
Total number of landings			296	422	262	307	294	256	

Table 2: Species richness (count), index of taxonomic diversity (Δ), and index of taxonomic distinctness (or distance) (Δ^*) for each trophic category of fishes recorded in catches at six village sites along the Casamance Estuary, Senegal, April to July 2005; distance from the estuary mouth is given in parenthesis

Trophic category	Indicator	Elinkine (13 km)	Tendouk (42 km)	Adéane (93 km)	Diattakunda (130 km)	Simbandi Brassou (158 km)	Sédhiou (170 km)
Primary consumer	Species count	9	8	9	9	7	9
	Δ	2.85	2.90	2.90	2.88	3.00	3.17
	Δ^*	3.08	3.22	3.20	3.18	3.50	3.64
Secondary consumer	Species count	17	13	10	7	6	6
	Δ	3.76	3.27	2.69	2.65	2.75	2.70
	Δ^*	3.85	3.44	2.94	3.05	3.21	3.21
Terminal predator	Species count	24	22	14	8	8	8
	Δ	3.52	3.21	3.64	3.19	3.05	3.05
	Δ^*	3.63	3.31	3.75	3.64	3.48	3.48

Table 3: Variation between downstream and upstream salinity and the fish size-spectrum parameters for catches at each village site, with distances from the estuary mouth given in parentheses. FL = fork length; MOL = maximum observed length of the species

Location	Elinkine (13 km)	Tendouk (42 km)	Adéane (93 km)	Diattakunda (130 km)	Simbandi Brassou (158 km)	Sédhiou (170 km)	<i>p</i>
Salinity (SD)	40.6 (1.1)	47.9 (2.0)	57.3 (2.9)	61.6 (9.0)	58.9 (10.9)	57.2 (10.1)	***
FL < 10 cm (%)	0	0	21.7	47.7	5.6	14.6	
Modal class (cm FL)	19–20	19–20	11–12	7–8	11–12	9–10	
Mean size (cm FL) (SD)	22.9 (16.4)	20.6 (13.7)	12.7 (11.1)	12.2 (9.5)	16.2 (9.9)	14.7 (7.3)	***
FL ≥ 25 cm (%)	31	24.2	2.7	2	0.6	0.8	
FL ≥ 50 cm (%)	2.8	0.1	0	0	0	0	
Mean MOL (cm FL) (SD)	50.4 (23.7)	40.8 (21.6)	32.6 (17.2)	33.7 (18.6)	32.0 (16.5)	25.2 (11.0)	***

*** $p < 0.001$

situated 158 km and 170 km from the mouth, respectively. All the differences in the mean landed sizes between the villages were significant ($p < 0.05$).

The mean maximum observed length (MOL) was 50.4 cm at 13 km from the river mouth. The MOL showed a decreasing profile upstream, declining by 19.1% at 42 km, 36.5% at 158 km, and 50% at 170 km from the mouth. The MOL was similar at 93 km and 158 km. However, the MOL differed significantly between the villages surveyed.

The linear models (Table 4) fitted from the size distributions of the total catches at the sampled villages showed that the slopes were steeper for upstream than for downstream sites (ANCOVA, $p < 0.05$). The intercept values of the size distributions were higher upstream than downstream.

Mean trophic level

The mean trophic level (TL_m) estimated for the total catch in the Casamance Estuary was 2.16. The TL_m of the catches by location were 3.17 at 13 km, 2.39 at 42 km, and 2.07 at 93 km from the mouth (Figure 3); TL_m of the catches at 158 km and at 170 km were very similar, at 2.15 and 2.12, respectively.

Catch per unit effort (CPUE)

CPUE data showed that the average yield per trip was mostly higher upstream (Figure 4). The highest fishing yields were recorded at 158 km and 170 km from the mouth. The differences in fishing yields were significant

for the same gear between villages (Kruskal–Wallis test, $p < 0.05$). However, CPUE for each category of fishing gear presented in Figure 4 was not significantly different between Elinkine, Tendouk and Adéane (pairwise test, $p > 0.05$). For castnet catches, CPUE was different between Sédhiou and Elinkine, and Tendouk and Diattakunda, whereas the CPUE for catches in drift gillnets with medium mesh at Elinkine, Adéane and Diattakunda was each significantly different from that recorded at Sédhiou. The CPUE in drift gillnets with small mesh at the three most downstream villages, Elinkine, Tendouk and Adéane, differed significantly from that at Simbandi Brassou and Sédhiou in the upstream part of the estuary (pairwise test, $p < 0.05$).

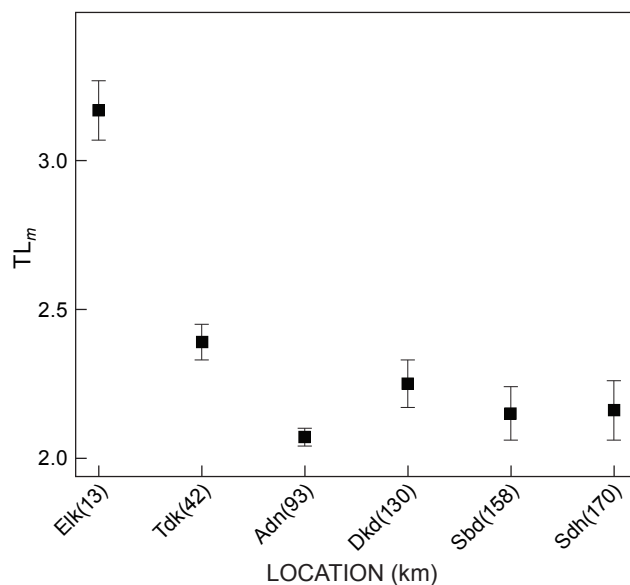
Discussion

Fish assemblages in relation to salinity

In the Casamance Estuary, the most diverse upstream catch category comprised primary consumers, dominated by *Sarotherodon melanotheron* (83.6%), *Tilapia guineensis* (10.7%) and *Ethmalosa fimbriata* (3.7%). These three species have a wide distribution in hypersaline environments, as they may occur in areas with salinity values reaching or exceeding 134, 80 and 97, respectively (Albaret 1987; Panfilii et al. 2006). By contrast, several other of the recorded species, such as *Arius latiscutatus*, *A. parkii*, *Caranx hippos*, *Cynoglossus senegalensis*, *Dasyatis margarita* and *Trichiurus lepturus*, have relatively limited

Table 4: Linear regression with slope (S) and intercept (I) of the fish size-spectra for catches at each village site along the Casamance Estuary, Senegal; distance from the estuary mouth is given in parenthesis. ANCOVA test: ns = not significant; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

S / I	Elinkine (13 km)		Tendouk (42 km)		Adéane (93 km)		Diattakunda (130 km)		Simbandi Brassou (158 km)		Sédhiou (170 km)	
	S	I	S	I	S	I	S	I	S	I	S	I
	-0.04	4.40	-0.07	5.87	-0.08	5.87	-0.08	5.89	-0.10	6.73	-0.14	7.64
Elinkine	S	—	—	***	***	***	***	***	***	***	***	***
	I	—	—	ns	ns	ns	*	***	***	***	***	***
Tendouk	S	—	—	—	ns	ns	ns	ns	*	***	***	***
	I	—	—	—	ns	ns	ns	ns	*	***	***	***
Adéane	S	—	—	—	—	—	ns	ns	ns	ns	***	***
	I	—	—	—	—	—	ns	ns	ns	ns	ns	ns
Diattakunda	S	—	—	—	—	—	—	—	ns	ns	***	***
	I	—	—	—	—	—	—	—	ns	ns	ns	ns
Simbandi	S	—	—	—	—	—	—	—	—	—	***	***
Brassou	I	—	—	—	—	—	—	—	—	—	—	*

**Figure 3:** Monthly variation of the mean trophic level (TL_m) among the landings at each sample site (for x-axis codes, see Figure 2)

distributions and become rare in estuaries when the salinity exceeds approximately 48–50 (Panfili et al. 2006). The abundance of blackchin tilapia *S. melanotheron* in the upper Casamance Estuary was highlighted by Albaret (1987) and is comparable to the dominance of Mozambique tilapia *Oreochromis mossambicus* in Lake St Lucia (South Africa) when that system experiences hypersaline conditions (Whitfield et al. 2006). The same observation was made in Sine Saloum Estuary (Senegal) where *S. melanotheron* dominated the fish assemblage in the upstream area, where the salinity sometimes reached 110 (Baran 2000).

The upstream increase in the diversity of primary consumers can be explained not only by their tolerance of hypersalinity but also by high food availability due to high primary production in the upstream area. In fact, phytoplankton biomass greatly increases from downstream to upstream, from 2–10 $\mu\text{g l}^{-1}$ in the downstream and middle areas to 50 $\mu\text{g l}^{-1}$ in the upstream area of the Casamance

Estuary (Pagès 1994). This substantial productivity can be explained by low rainfall and insufficient inputs of freshwater to repel the entry of seawater downstream and thus counter the phenomenon of evaporation responsible for the noted hypersalinity. The normal flow of water from the upstream portion to the downstream portion is no longer ensured, as evidenced by the reverse salinity gradient in the estuary. A causal relationship between the residence time of water and high primary production in estuaries was established by Lane et al. (2007).

Size structure of the fish populations

The fish size-spectrum from the landings in the Casamance Estuary showed a significant decline, from downstream to upstream, in the number of individuals from the large size classes. This decline in larger fish (>24 cm) in the catches was most prevalent in the areas adjacent to the four most upstream villages, resulting in a significant decrease in the mean size and landed MOL. These large individuals appear to be more sensitive to degradation of the environmental conditions, especially salinisation, which limits their penetration into the upstream part of the Casamance Estuary. This size distribution according to salinity is consistent with the observations of Panfili et al. (2004, 2006) in the Sine Saloum and Gambia estuaries, where smaller individuals have higher occurrences in high-salinity areas. Hence, the structure of the exploited fish populations in Casamance Estuary results in a steeper slope in the size spectrum at the upstream locations.

Analysing the size structure of the fish populations in another inverse hypersaline estuarine system, the Sine Saloum Estuary, Ecoutin et al. (2010) observed a steeper slope and higher intercept at the end of a 10-year period, reflecting deterioration in the environmental conditions during those years due to both hypersalinity and fishing pressure. The findings of our study are likewise consistent with those of other studies based on detection of the impacts of fishing pressure as a structuring factor of the size spectra of fish communities (e.g. Rice and Gislason 1996; Enin et al. 2004; Ault et al. 2005).

In addition to the limited number of large individuals in the upstream region of the Casamance Estuary, due to their greater vulnerability to hypersalinity as a forcing

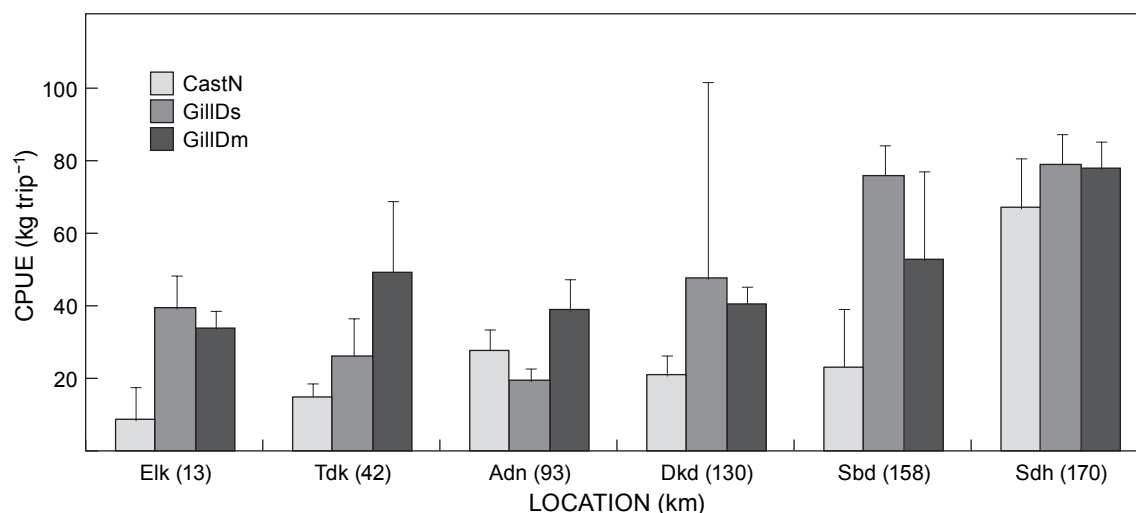


Figure 4: Variations in CPUE at each sample site by fishing-gear category (for x-axis codes, see Figure 2). The distance (km) of each location from the estuary mouth is shown in parenthesis. CastN = castnets; GillDs = drift gillnets with small mesh (<30 mm); GillDm = drift gillnets with medium mesh (30–50 mm)

factor (Jennings et al. 1998), the decline in average fish sizes along the salinity gradient might also be linked to physiological demands. Under hypersaline conditions, the amount of energy required to osmoregulate becomes increasingly important and comes at the expense of growth (Boeuf and Payan 2001). This results in a decline in the physical growth rate of fish that are otherwise adapted to adverse environmental conditions. Thus, in the case of juvenile *E. fimbriata* from the Casamance Estuary, Labonne et al. (2009) showed that the growth rate of this species was lower in hypersaline areas. Similarly, Alava (1998) experimentally demonstrated that the growth of milkfish *Chanos chanos* decreases with increasing salinity. This adaptive response of fish appears to be more important upstream than downstream in the Casamance Estuary, due to a more challenging environment in the former region, and could partly explain the lower mean sizes landed by the upstream villages.

Trophic level of fish catches

The mean trophic levels of the fish catches were lower in the Casamance villages located in the middle and upstream area of the estuary than those located in the downstream area. This decrease detected in the mean trophic level of the catches suggests that apex predators are rare in the former two areas, and that landings in the middle and upstream regions of the estuary essentially comprised primary consumers. The increase in the diversity of this trophic category upstream shows that these species are better adapted to the environmental conditions than other species. In this trophic category, *S. melanotheron* ($TL_i = 2.0$) and *T. guineensis* ($TL_i = 2.8$) were typical of the population exploited in the upstream area and were responsible for much of the mean trophic level of catches in that area. In contrast, the mean trophic level downstream at Elinkine was elevated due to the increased abundance of fish species such as *A. latiscutatus* ($TL_i = 3.3$), *Polydactylus quadrifilis* ($TL_i = 4.0$), and *Sphyræna afra* ($TL_i = 4.1$); these three species combined

represented 54.7% (by mass) of the total catch landed at this village (Kantoussan et al. 2012).

In the Casamance Estuary, three mostly herbivorous species, namely *S. melanotheron*, *T. guineensis* and *E. fimbriata* ($TL_i = 2.5$), dominated the total catch mass. The consequence of the overwhelming dominance of these species in the ecosystem is an overall decrease in the mean trophic level of the landed catches ($TL_m = 2.16$). Fish species composition in the Casamance Estuary was different from that of the Gambia Estuary (Gambia) which is not affected by strong environmental change and human disturbance (Simier et al. 2006). Indeed in that West African estuary, cichlids are poorly represented in the fish assemblage. For instance, *S. melanotheron*, which represented 83.6% of the total landed biomass in the Casamance Estuary, was ranked 26th in the upstream portion of the Gambia Estuary and constituted only 0.05% of total fish biomass. Also in that estuary, several fish species, such as *Pseudotolithus elongatus*, *E. fimbriata*, *Ilisha africana* and *Sardinella maderensis*, were abundant and distributed over a large part of the estuary, from upstream to downstream, in the dry season (November–May) (Albaret et al. 2004). This finding was consistent with the observation made by Baran (2000) that the clupeids *E. fimbriata* and *S. maderensis* were the dominant fishes in the Gambia Estuary.

Catch rates and productivity

The CPUE of fish in the Casamance Estuary was generally higher upstream than downstream, which might be a consequence of several factors. First, mangroves are more abundant downstream in the estuary, which makes fishing conditions more difficult for some gear types. Second, higher primary production has been recorded upstream in the estuary as compared with downstream (Debenay et al. 1989; Pagès 1994). Finally, the abundance of species with a short biological cycle (e.g. *S. melanotheron*: Pauly 1976; Lowe-McConnell 1982; Legendre and Ecoutin 1996), and hence whose biomass can be quickly renewed, is higher upstream.

Senegal has been marked by drought and a decrease in coastal river flows since the early 1960s. This decline in freshwater input has resulted in the emergence of inverse hypersaline estuarine systems due to the salinity increase in upstream areas, as documented for the Sine Saloum (Pagès and Citeau 1990; Gueye et al. 2013) and Casamance systems (Thiam and Singh 2002). In parallel with the physicochemical changes recorded in the Casamance Estuary, primary production per biomass unit has increased in the upstream area as compared with in the middle and downstream areas (Pagès 1994). High primary production upstream is due, in large part, to increased water residence time in this portion of the estuary. Tidal exchange with the sea has become increasingly weak upstream and, at the same time, riverine flow has significantly declined due to drought and the construction of the Maka Dam (Albaret 1987; Ndour et al. 2011). These conditions favoured the emergence of a relatively stagnant body of water in the upper reaches, which was subject to high net evaporation rates and increasing salinity.

Fish population diversity appears to have been strongly affected by the above changes, with only highly euryhaline species capable of surviving in the hypersaline areas (Kantoussan et al. 2012). Thus, a small number of euryhaline fishes, mostly species with high productivity and a herbivorous or detritivorous feeding behaviour, have increased in abundance due to the high primary productivity of this environment. In addition, reduced predation due to the decline in abundance of secondary consumers and piscivorous predators supports high fish production in the estuary's upstream area.


Conclusions

Ultimately, an extended period of climate change, marked by a significant reduction in freshwater inflows from the Casamance River, has strongly impacted the overall functioning of the estuarine environment. The effects on fish populations are reflected in the loss of biodiversity, a decrease in fish size-structures, and changes in the trophic dynamics associated with declines in the mean trophic level. The paradoxical increase in upstream CPUE is a consequence of the development of a fish population dominated by mainly euryhaline species with a short life cycle and high secondary productivity. The indices used in this study have been shown to be relevant as a tool for assessing environmental conditions and have also shown that commercial fisheries data collected in a scientific manner can assist with the monitoring of aquatic ecosystems.

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