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Ecological zonation of the hyperhaline estuary of the Casamance River (Senegal): Foraminifera, zooplankton and abiotic variables

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Abstract

Due to a long-lasting drought afflicting the Sahel, the Casamance River has been transformed into a hyperhaline estuary, with salinities up to 170‰ at a distance of 210 km from the sea.

Foraminifera and zooplankton populations both show a marked decrease in the number of species in increasingly confined water, the distribution of species being closely related to the evolution of abiotic variables. Our three-prong study allowed us to identify six zones, upwards from the sea. The uppermost ones are characterized by drastic conditions which considerably reduce the number of species. Therefore, the populations of Foraminifera, zooplankton and even fish become oligo or mono specific.

The Casamance River appears to fit quite well into the general rules concerning hyperhaline environments. However, it shows some peculiar features which are: the large dimensions of the hyperhaline estuary (over 230 km long and over 5 km wide in the lower course); peak salinities among the highest known for a permanently open estuary (up to 170‰); and water remaining trapped inside the river for several years.

Introduction

Salinity is one of the most tangible characteristics of a water body, and has often been considered as the main factor in ecological zonation. A rich array of studies has described and classified the aquatic ecosystems along a salinity scale (Por, 1972); the various coastal lagoons in the arid belt provided a rich experimental field of study for the distribution of biological communities as a function of salinity. A unifying concept has been provided by the confinement at work in 'paralic' systems (Guelorget & Perthuisot, 1983), salinity being only one of the many consequences of confinement. Nevertheless, salt content is still a useful factor for describing an aquatic system. Most thalassic waters have salinities of 35‰ to 50‰ (Butler, 1969; Krumgalz *et al.*, 1980), occasionnally reaching 100‰ (Hedgpeth, 1967); some isolated parts may reach gypsum or even halite saturation (Morris & Dickey, 1957). Hypersaline estuaries are more seldom, or at least less known (Wolanski, 1986).

During the recent years, the Casamance River, flowing along the southern margin of the Sahel countries, has reached a hyperhaline level which threatens the resources of the region, such as fishing or rice growing. We describe here some consequences of the salt regimen in terms of ecological zonation, as deduced from several distinct biological and abiological variables.

Background and general setting

The Casamance region is located in the south of Senegal (West Africa), at about 13° N (Fig. 1).

Climate

The sub-Guinean climate characteristically has one rainy season; in the Casamance, the rains fall between June and October (Fig. 2). The cool, dry season lasts from November to May; evaporation is highest around February. The yearly water balance is negative. The climate gets warmer and dryer from W-SW (Ziguinchor) towards E-NE (Kolda).

The most prominent long-term feature has been a long rain deficit since 1968 (Fig. 3). Yearly

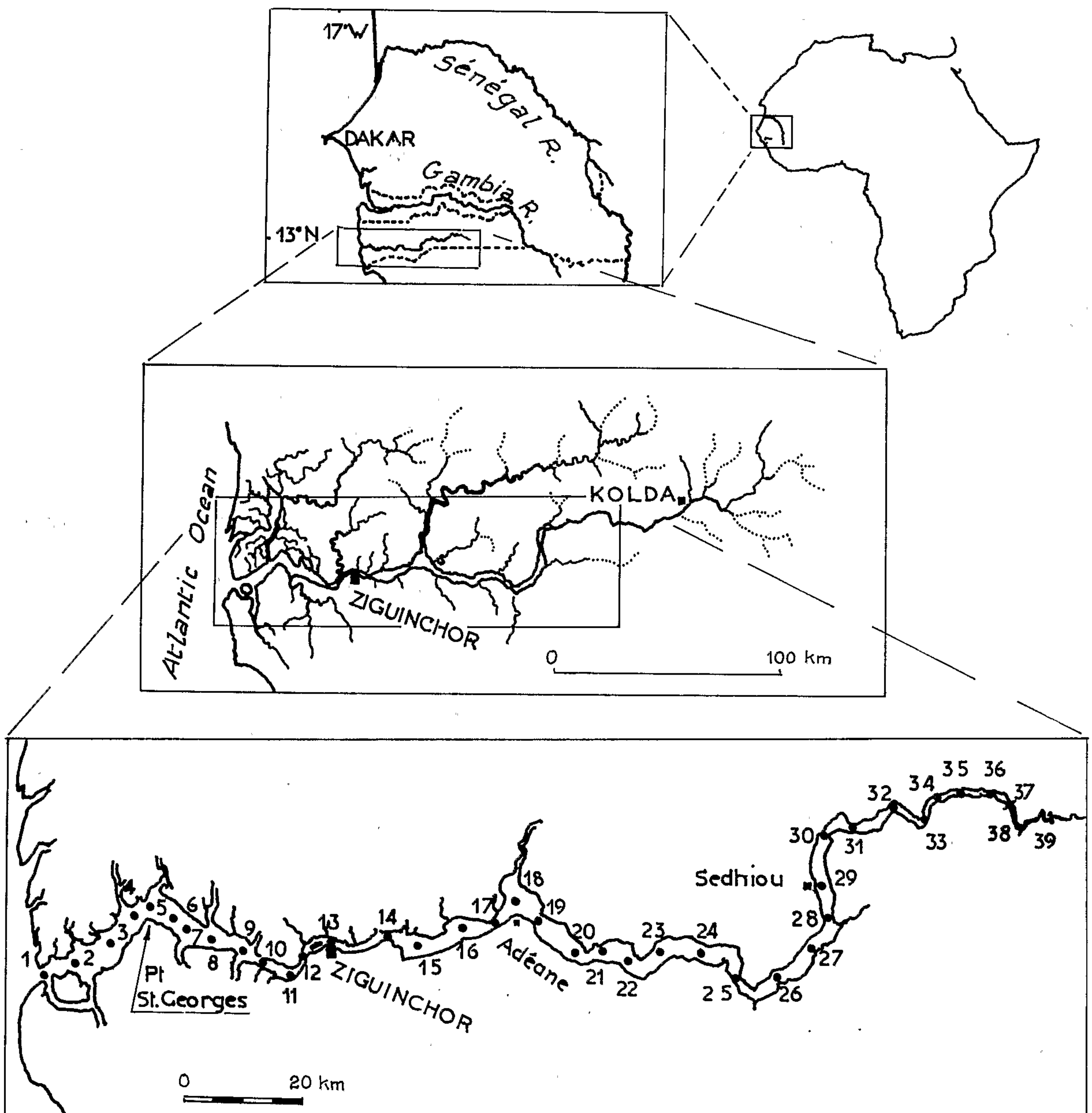

Fig. 1. Location map.

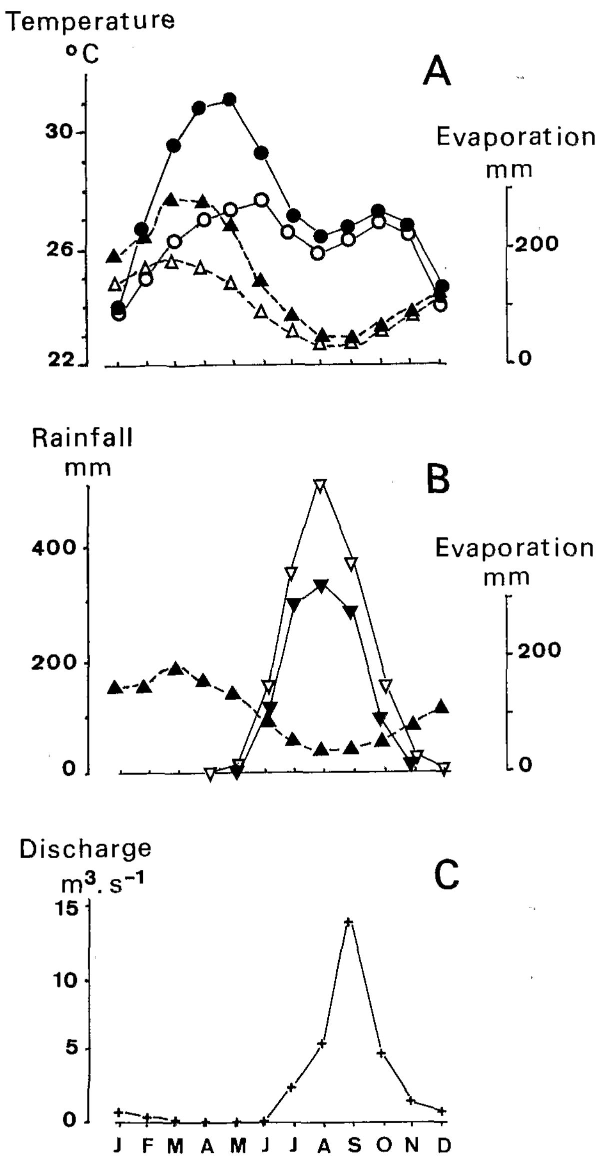

Fig. 2. Average annual climate in the Casamance region. A: air temperatures (o) and monthly evaporation (△) at Ziguinchor (light) and Kolda (dark); 1954–1979 mean. B: Water balance at Ziguinchor: average monthly rainfall, 1940–1960 (▽) and 1975–1985 (▼), and evaporation, 1975–1985 (▲). C: Discharge of the Casamance River at Kolda; 1968–1983 mean.

averages for the region shrank from 1400 mm to some 1050 mm; this decrease of about 25% has brought the average rainfall well below the average evaporation (1560 mm).

Hypsometry and bathymetry

The Casamance River drains some 14000 km^2; the permanent course of the river is about 260 km long, with a negligible slope. Even the upper reaches, mostly temporary streams, are only slighly inclined. Thus, the run off coefficient is low (5% to 8%), especially in the dryer years. The lower reaches are mostly flat mangrove swamps with meandering and branching channels (the '*bolons*'). Numerous mud banks choke the main course. The width of the wetted section is between 2 km and 5 km along most of the course. The average water depth decreases from 5 m at the mouth to some 0.2 m at station 39, 240 km from the sea. There, *Phragmites* swamps may be many times broader than the river itself (a study using SPOT satellite data is currently under way on this point).

Methods

A multi-disciplinary program on the Casamance River was launched in February 1984 by the C.R.O.D.T. (Centre de Recherches Océanographiques de Dakar-Thiaroye). Forty stations were agreed upon, and surveyed during field trips made from Ziguinchor with a 8 m open hull. Samples were taken back to Dakar for analysis.

Hydroclimate and chlorophyll (J. P).

Twenty-one field trips were made between February 1984 and March 1987. Most results reported here stem from the period February, 84-November, 85. Field measurements were carried out for salinity (hand refractometer, Atago S-20), temperature (mercury thermometer), dissolved oxygen (YSJ O_2 probe, kept on 'freshwater'; corrections for temperature and salinity were calculated), pH (field pH meter, Cole-Parmer Digisense) and underwater light (LICOR quantum meter and Secchi disk).

Samples for chlorophyll were filtered at once on Whatman GF/C filters and kept at 0 °C in the dark. Subsequently, methanol extracts were analyzed by fluorometry (Turner 111. fluorometer). Dissolved organic matter was determined from

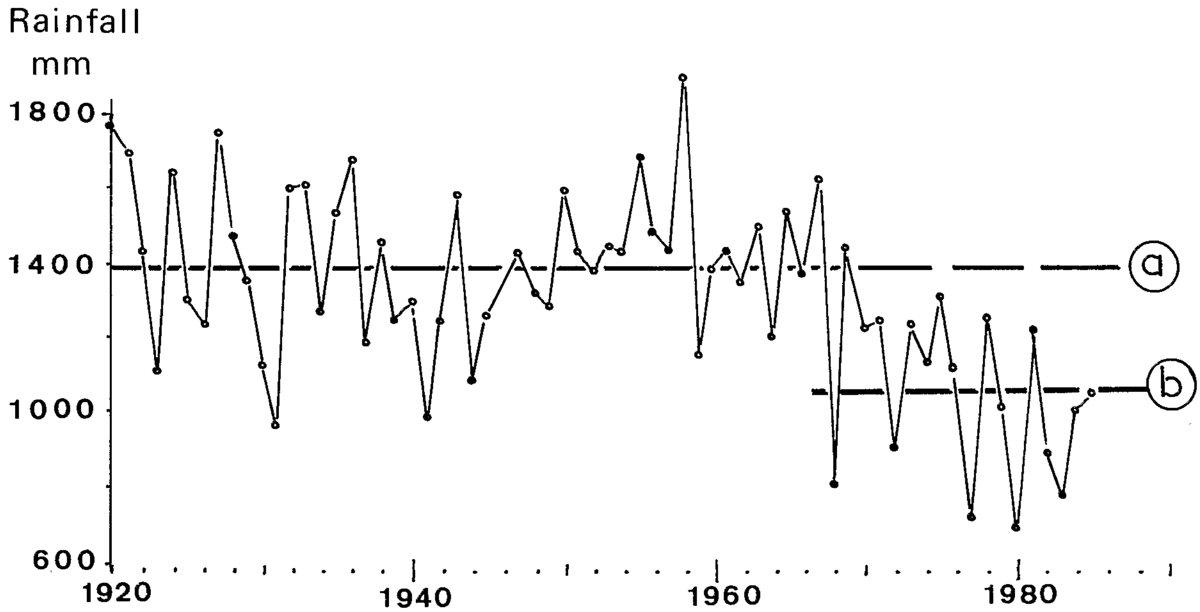

Fig. 3. Variation of the annual rainfall over the Casamance region, from 1920 to the present. Averaged data from Ziguinchor, Sedhiou and Kolda. a: 1920–1967 mean (1 380 mm) b: 1968–1985 mean (1 057 mm).

optical density of filtered water at 254 nm (Gadel & Texier, 1986). Dissolved inorganic carbon was determined by gas chromatography.

Foraminifera (J-P. D.)
Depth profiles were obtained with an echo-sounder in March 1984 (Debenay, 1984) and used to define the three to five sampling locations at each station. Fifteen surveys were made in 1984 and 1985. Fifty cm^3 of the top-most 5 mm layer of sediment were scraped off a grab sample, and kept in neutralized formaline. The microfauna was then washed on a 50 μm sieve, stained with a 2% rose Bengal solution and separated on carbon tetrachloride.

Zooplankton (P. S. D.)
Sampling was done with a 200 μm W.P.2 net of 53 cm diameter. The net is equiped with a cod-end of the Tregouboff type and a T.S.K. flowmeter. Three minutes hauls were made near the bottom, at a constant speed of approximatively 2 knots. The mean sample for each station was calculated from 5 samples taken at 8 A.M., 11 A.M., 2 P.M., 5 P.M. and 8 P.M. Each station was sampled monthly from February 1984 to December 1986 downstream from station 18, and from December 1985 to December 1986 upstream from this station. The abundance of zooplancton is represented using a Log^2 transformation, which reduces the amplitude of large variations, without giving too much importance to variations of low numbers, such as a simple logarithm transformation does (Frontier, 1974). Diversity index is calculated after Shannon & Weaver (1949) and expressed as bits/individuals.

Hydroclimate and chlorophyll

The distribution of the variables along the river varies according to the season, but a general pattern exists throughout the year (Fig. 4.).

Salinity
The few measurements carried out before or around 1968 show a 'normal' longitudinal profile, with a decrease in salinity toward the continent (Brunet-Moret, 1970). The scattered data available before 1982 show a slow but steady

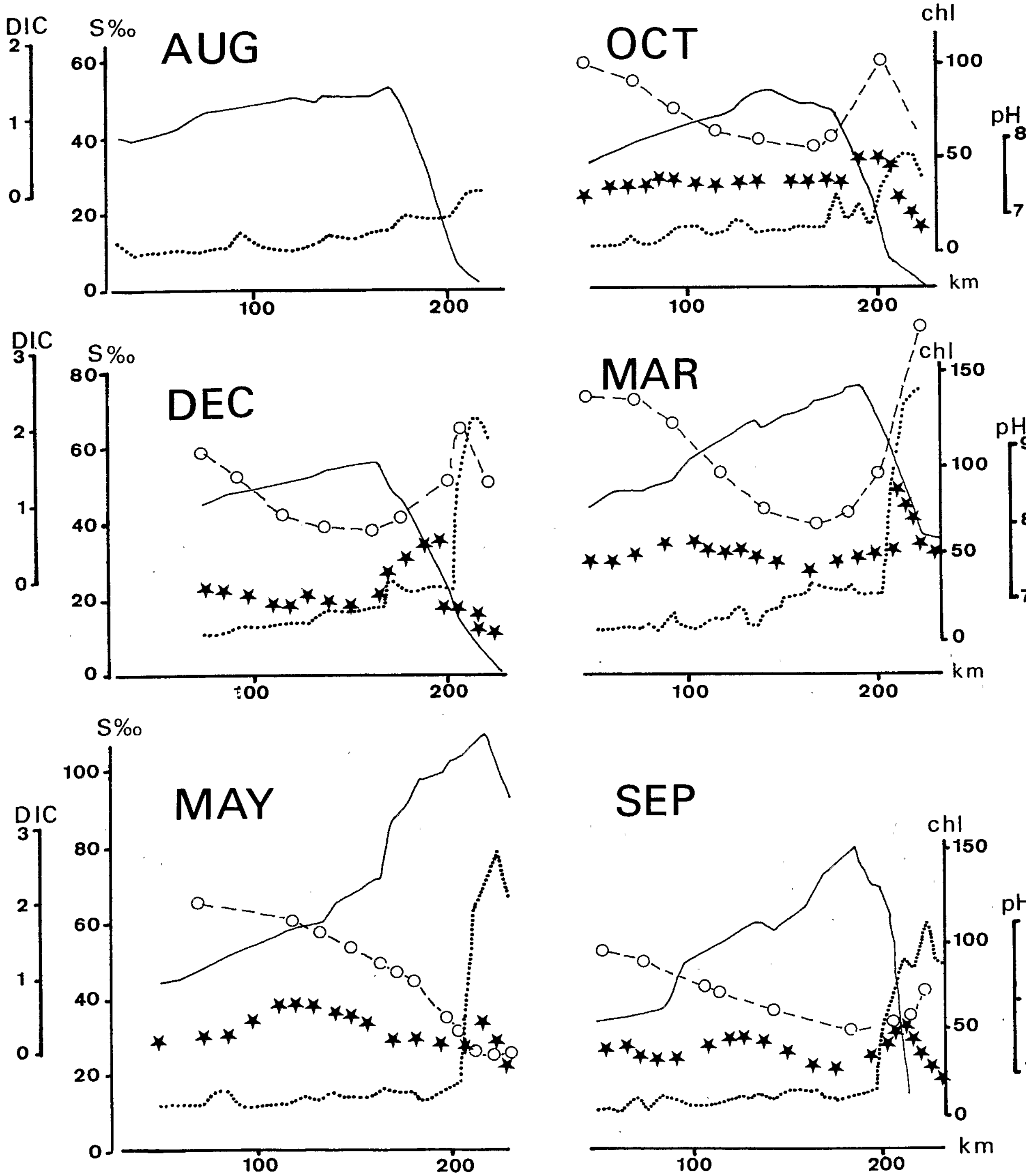

Fig. 4. Geographical distribution of several parameters along the river at different seasons between August 1984 and September 1985: Salinity (——), pH (★), dissolved inorganic carbon (D.I.C.: -o-o-) and chlorophyll (-----).

worsening, by the invasion of concentrated seawater (Le Reste, 1984).

Throughout our study, a 'salinity plug' (Wolanski, 1986) was always found along the river. After the end of the rainy season, in November, when the overall salinity is as its lowest, salinity still peaks at about 50‰ around stations 25–26. Freshwater (less than 1‰) was found only upstream from stations 34–35. During the dry season, the salinity plug moves upriver (about 30 km in 100 days) while its salinity increases; salinity thus peaked at 124‰ at station 37 in June 1985. The decrease in salinity during the rainy season is rather slow; flooding (as measured at Kolda) seems to have a limited role during that period; direct dilution by rain appears more important (Pages & Debenay, 1987). Seasonal salinity variations are thus wider at the upstream stations (Fig. 5).

Similar cycles were observed throughout the four years of our study. The long-term, interannual, variations appear to be gradual, owing to a 'memory effect' (Nemec, 1983; Le Reste, 1984). No significant layering ('salt wedge') was observed in this 'well mixed' estuary.

Other abiotic variables

a) Currents. Tidal currents are prevalent throughout the year, even during flooding. No net discharge of freshwater could be measured (Brunet-Moret, 1970; Le Reste, 1984; Millet *et al.*, 1987). Tide amplitude decreases upstream and becomes negligible at station 39, although slow tidal currents (0.10 to 0.15 $m.s^{-1}$) still exist there.

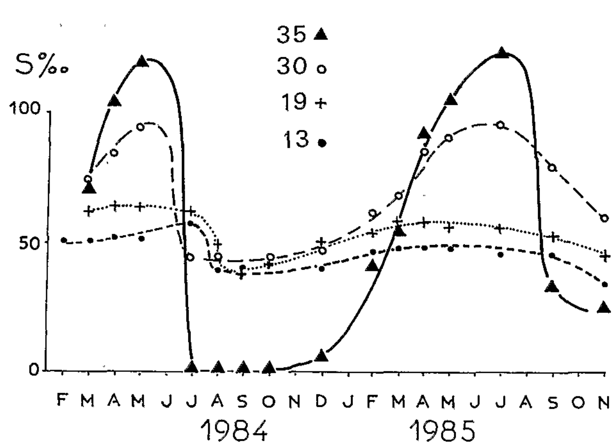

Fig. 5. Seasonal variation of salinity at four stations along the river.

b) Water temperature. The average temperature varies from 21 °C in January-February to 30 °C between June and October. The daily variation in surface temperature can exceed 5 °C. Vertical stratification is quickly destroyed by the frequent winds.

c) Dissolved oxygen. Apart from daily variations due to photosynthesis, concentrations are generally close to saturation, except in the bottom waters of some upstream stations (40% at stations 37–39 before sunrise).

d) pH. Taken over the whole course of the river, average values vary between 7,25 and 7,75, with some daily variations due to photosynthesis. No significant seasonal pattern could be identified. It appears that even concentrated seawater can retain its buffer capacity.

e) Dissolved inorganic carbon. D.I.C. concentrations reflect the salinity pattern: calcite precipitation occurs in the concentrated seawater, while (presumably autochthonous) organic matter liberates D.I.C. in the upstream portion.

f) Nutrients. No significant seasonal pattern could be identified. Ammonium is the main nitrogen form; its concentration increases upstream. Dissolved organic matter concentrations are high in the mangrove waters, and still higher (about 200 μgat $C.l^{-1}$) in the upstream portion (stations 30 to 39), where the *Phragmites* swamps are –or were– located.

Chlorophyll

No taxonomic study has been carried out. 'Total chlorophyll' concentrations throughout a yearly cycle show a distinct geographical pattern:

- an area downstream from station 17 has relatively low concentrations (2–4 $\mu g \cdot l^{-1}$) comparable to those of the coastal marine waters off the Casamance mouth (Dia, 1983);

- an intermediary area stretching between station 18 and stations 24–25, with moderatly high concentrations (5 to 10 $\mu g \cdot l^{-1}$) tending to decrease during the rainy season;
- an 'upriver' area where biomass is high (> 10 $\mu g \cdot l^{-1}$) and increases to a peak. Values at peak are lowest (35 to 50 $\mu g. l^{-1}$) in the rainy season; high concentrations (100 to 200 $\mu g \cdot l^{-1}$) are reached in December and stay high until the next rainy season is well established.

The chlorophyll peak appears to be located upriver from the salinity peak; this correspondence hints at a positive relationship between salinity and biomass. This relationship becomes obvious on a plot of chlorophyll *vs* morphoedaphic index (M.E.I.) (Fig. 6). This M.E.I., quotient of conductivity through average depth, has been defined and used for lakes. Hydrodynamical reasons have prompted us to apply this index to the Casamance River, which appears to consist of discrete compartments with few longitudinal exchanges (Pages & Debenay, 1987). Such increases in chlorophyll concentration with increasing salinity have been described in other highly saline or hyperhaline water bodies (Melack & Kilham, 1974; Javor, 1983).

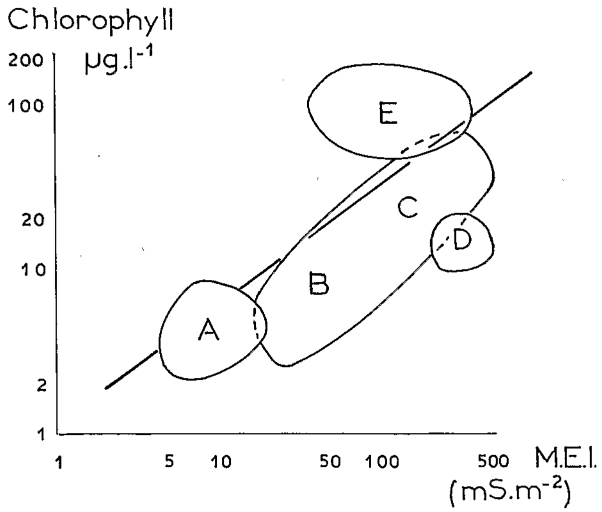

Fig. 6. Relationship between chlorophyll and morphoedaphic index, pooling all available data between March 1984 and May 1985. Several regions are delineated: A: downstream from st. 13; B: st. 17 to 27; C: st. 28 to 31; D: st. 32 and 33 at the end of dry season; E: upstream from st. 34. The straight line shows the relation found in Lake Chad (Lemoalle, 1979).

Conclusions

Long term salinity variations. The Casamance estuary has been an 'inverse estuary' (Pritchard, 1967) for several years. The 'salinity plug' (Wolanski, 1986) which is found in the main course was described, with much lower salinities (43‰) as early as 1968 (Brunet-Moret, 1970). In small tributaries, hyper salinity (more than 45‰) was observed in 1970 (Vieillefon, 1977). Unfortunately, no data is available – especially for the upper reaches – from before 1968, date of the onset of the present drought. We are, thus, unable to ascertain whether the 'salinity plug' was a customary feature of this tropical estuary before the drough; the presumably small excess of salinity at that time would not have been felt by fishermen, so historical sources are silent. Modelling, by numerical simulation, appears to be only solution.

Geographical zonation of the estuary. The variables considered here determine several zones (Fig. 7):

- from salinity profiles, it can be seen that the upriver mixing zone between hypersaline water and freshwater never extends below stations 28–29;
- the variability in salinity throughout the year increases markedly around station 31;
- C.I.D. concentrations are lowest around stations 28–29;
- chlorophyll concentrations indicate two limits, at stations 17–18 and at station 25; the chl *vs* M.E.I. plot enables five zones to be distinguished, with limits at stations 13, 17, 27 and 33.

We shall see that most of these limits are found again, independently, from other, biotic, variables. The overall feature is an upriver increase in the variability and in the spatial gradients.

distance (km from the sea)	0	63	90	140	170	180	200	230
station n°	1	13	17-18	25	28	31	33	39
S‰ - profiles	increasing			hypersaline		mixing zone	fresh	
S‰ - variability				low		increase		high
C.I.D.		decrease			minimum			increase
chl conc^on	low		medium	high				
chl M.E.I.	A			B		C + D		E

Fig. 7. Main zones determined according to some abiotic parameters.

Foraminifera

About 40 species, 14 of them with living specimens, have been found in the Casamance estuary. This microfauna is thus richer and more diversified than that described for the Senegal River (Ausseil-Badie, 1983). It is very similar to that of marshes and mangrove along the Brasil coast (Zaninetti *et al.*, 1977, 1979), mangrove swamps in Trinidad (Todd & Bronnimann, 1957; Saunders, 1958), marshes in Mexico (Phleger & Lankford, 1978), and bays in Texas (Parker *et al.*, 1953; Phleger, 1960), Puerto Rico (Culver, pers. comm.) and Indonesia (Margerel, pers. comm.). Three sub-orders, Textulariina, Rotaliina and Miliolina are unequally represented (Table 1). A detailed systematic study is being carried on, using the samples collected monthly in 1984 and 1985.

Table 1. List of foraminiferal species from the estuary of Casamance river.

– Textulariina:
Ammoastuta salsa Cushman et Bronnimann
Ammobaculites exiguus Cushman et Bronnimann
Ammotium salsum (Cushman et Bronnimann)
Arenoparella mexicana (Kornfeld)
Asterotrochammina sp.
Eggerelloides scabrum (Williamson)
Gaudryina exillis Cushman et Bronnimann
Happlophragmoides wilberti Andersen
Miliammina fusca (Brady)
Reophax nana Rhumbler
Siphotrochammina lobata Saunders
Textularia sp.
Trochammina inflata (Montagu)
Trochammina sp.
Trochamminita salsa (Cushman et Bronnimann)

– Miliolina:
Quinqueloculina spp.
Triloculina spp.

– Rotaliina:
Ammonia tepida Cushman
Ammonia parkinsoniana (d'Orbigny)
Bolivina pseudoplicata (Heron-Allen et Earland)
Bolivina striatula Cushman
Bolivina spp.
Cibicides lobatulus (Walker et Jacob)
Discorbis sp.
Elphidium gunteri (Cole)
Elphidium poeyanum (d'Orbigny)
Elphidium spp.
Fissurina spp.
Lagena spp.
Nonion sp.
Nonionella atlantica Cushman

Distribution of total populations

The number of calcareous species decreases progressively from the mouth (11 species in station 2) to the upper course of the river. The number of arenaceous species found in each station is low and relatively stable up to the uppermost stations. Between the mouth and Pointe Saint Georges (station 5), the microfauna is quite diversified (almost every species is present) and attests the marine influence. However, *Ammonia tepida* and *Elphidium gunteri* represent more than 50% of the tests.

At Pointe Saint Georges, the course of the river bends sharply to the SE. Arenaceous tests rapidly become preponderant, and *Ammotium salsum* is found for the first time. Most of the calcareous tests desappear, except *A. tepida* and *E. gunteri*. However, their proportion decreases up to station 10, before increasing again upstream from this station. They represent about 50% of the tests between stations 14 and 18 (Fig. 8 B). Upstream from Adeane (station 18), where the course of the river bends to the SE, the relative abundance of *A. tepida* and *E. gunteri* decreases rapidly. *E. gunteri* disappears completely after station 20. Upstream from station 25 the occurence of *A. tepida* is exceptional and more than 90% of the tests are from *A. salsum*. The total number of tests in 50 cm^3 of sediment is almost always higher than 1 000 up to station 30. A sudden decrease occurs after this station, and only scattered tests are observed up to station 38.

Calcareous tests are found to be quite small (rarely more than 0,3 mm) upstream from Pointe Saint Georges. This dwarfism is probably a consequence of the restricted character of the medium, which modifies the metabolism of the organisms. For instance, the growth of *A. tepida* is known to be inhibited when salinity exceeds 60‰ (Bradshaw, 1957). The progressive increase in the relative abundance of arenaceous tests (Fig. 8B) is probably in relation with the increasingly restricted character of the medium (Murray, 1973; Zaninetti *et al.*, 1977). The effects of the restricted character of this hyperhaline medium are the same as those observed in the hypohaline medium of normal estuaries. However, another factor seems to influence the disappearance of calcareous tests. In fact, if the ratio of living specimens relative to empty tests is very low for arenaceous species, it often reaches about 50% for the calcareous species. This fact, added to the frequent observation of basal organic layers, proves that calcareous tests are rapidly destroyed, whereas the arenaceous tests are preserved.

Distribution of living specimens

The number of living species is highest downstream from Pointe Saint Georges (Station 5) with 11 species. Some of them (*Arenoparella mexicana, Trochammina inflata, Trochammina* sp., *Ammonia parkinsoniana, Bolivina* spp., *Discorbis* sp., and *Nonion* sp.) are restricted to this zone which stays under marine influence and where salinity never exceeds 40‰. Other species (*Eggerelloides scabrum* and *Asterotrochammina?* sp.) are to be found a little further upstream. The most tolerant species are *Gaudryina exilis, Reophax nana, Ammonia tepida*, and mainly *Ammotium salsum*. A test of *A. salsum* containing cytoplasm (alive?) was observed in a station where salinity reached 105‰ at the time of sampling (Fig. 8C).

On account of the very few living specimens, it was impossible to observe a possible gradient in their distribution as it has been done with the total population. However, the survey of the foraminiferal populations during 2 years showed that thanatocoenoses change rapidly when the environment changes (Debenay & Pages, 1987). Therefore thanatocoenoses themselves can be considered good medium indicators.

Conclusion

On the basis of the distribution of foraminiferal tests, it is possible to divide the course of the river into five zones. The first zone is under strong marine influence from the mouth to Pointe Saint Georges, and under progressively decreasing marine influence up to stations 10 and 11. It is succeeded by an intermediate zone up to stations 18 to 20, where *A. tepida, E. gunteri* and *A. salsum* prevail. The third zone, from station 20, is hyperhaline. It is dominated by *A. salsum*, whose tests

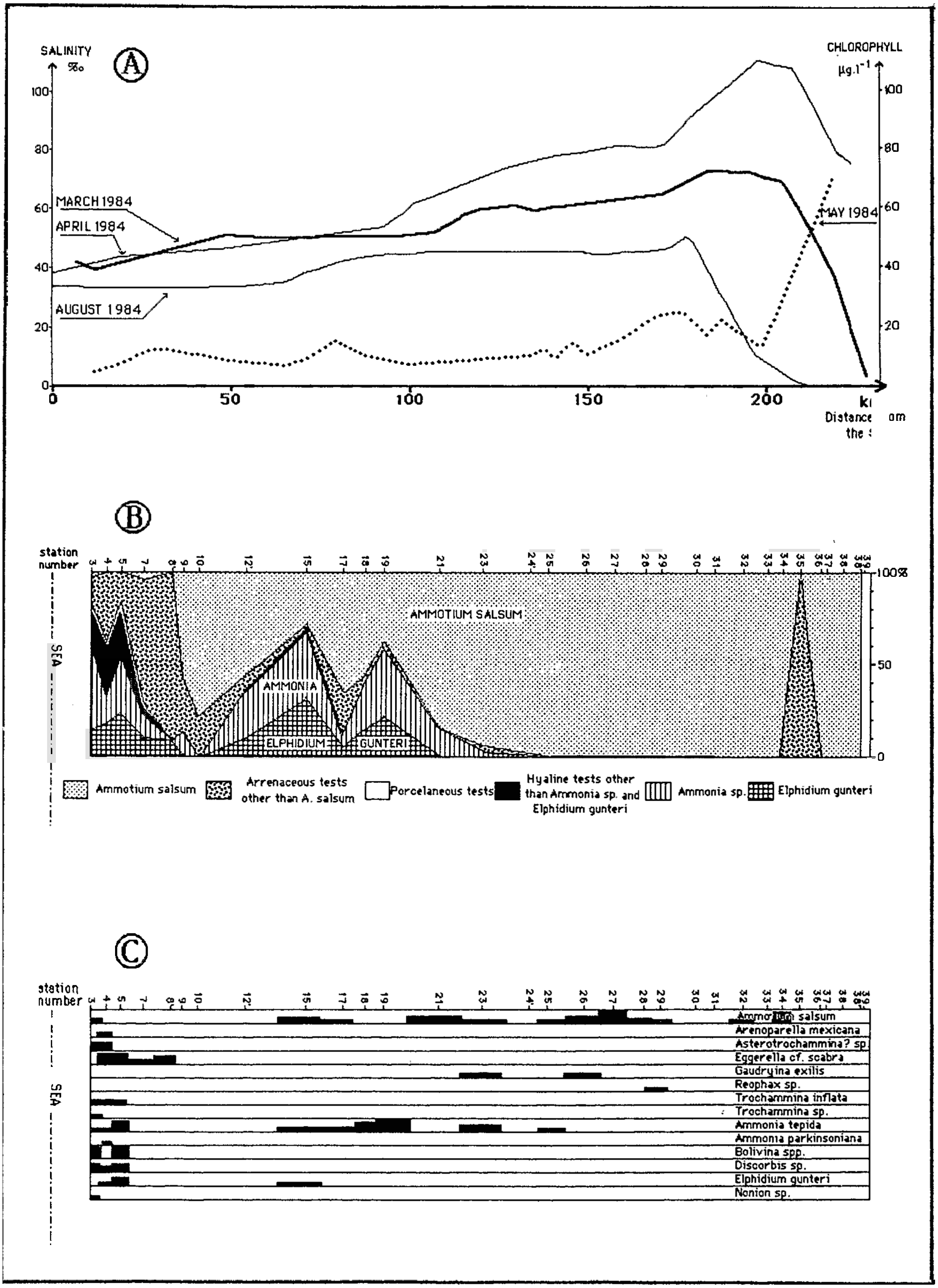

Fig. 8. Distribution of the Foraminifera along the Casamance River. A: Salinity and chlorophyll about the period of sampling. B: Distribution of the thanatocoenoses. C: Distribution of the living specimens.

are very abundant up to station 30. Their abundance then suddenly decreases while Thecamoebians, typical of this upper zone, appear. Meanwhile, foraminiferal tests are present up to station 38, where the continental area begins.

Finally, the river course can be divided into five main areas, with boundaries roughly corresponding to stations 11–18 to 20–30 and 38. Limits of minor importance can also be observed at stations 5 (Pointe Saint Georges) and 25. Four main foraminiferal populations are distributed along the 230 km studied. Their distribution is closely related to the evolution of abiotic characteristics.

Table 2. Inventory of zooplankton from the Casamance estuary.

COELENTERA
Aglaura hemistosoma Kramp
Muggia sp.

CHAETOGNATA
Sagitta friderica Ritter-Zohony
S. inflata Grassi

MOLLUSCA
Limacina inflata (d'Orbigny)
L. bulimoides (d'Orbigny)
Limacina sp.
Creseis acicula Rang
C. virgula Eschscholtz

CLADOCERA
Evadne tergestina (Claus)
Penilia avirostris (Dana)
Moina dubia De Guerne et Richard

OSTRACODA
Cyprideis sp. 1
Cyprideis sp. 2
Neomonoceratina sp.

COPERODA
Eucalanus pileatus Giesbrecht
E. monachus Giesbrecht
E. crassus Giesbrecht
Paracalanus scotti Grucht
P. parvus (Claus)
Clausocalanus jobei Fros-Fleminger
Temora turbinata (Dana)
Pseudodiaptomus serricaudatus (T. scott)
Labidocera scotti Giesbrecht
L. nerii (Kroyer)
Pontella gabonensis T. scott
P. securifer Brady
Acartia (Acanthacartia) plumosa T. scott
A. (Paracartia) grani Sars
A. clausi Sars
Centropages chierchiae Giesbrecht
C. furcatus Dana
Corycaeus giesbrechti F. Dahl
Oithona nana Giesbrecht
O. plumifera Braid
Afrocyclops doryphorus (Kieffer)
Ectocyclops sp.
Caligus sp.
Pontella sp.
Microsetella norvegica Boeck
M. rosea (Dana)
Cletocampus sp.
Euterpina acutifrons (Dana)
Euterpina sp.

MYSIDACEA
Mesopodopsis slabberi (Van Beneden)
Rhopalophthalamus africana Tattersall
R. longicauda Tattersall

AMPHIPODA
Hyperia latissima Bovalius
H. schizogeneios Stebbing
Gammarus sp.

DECAPODA
Lucifer sp.

PROTOCHORDATA
Oikopleura dioica Fol
O. longicauda Vogt

LARVAE
Polychaete larva
Cirripede cypris larva
Copepod nauplius
Lepas nauplius
Balanus nauplius
Porcellana zoea
Brachyuran zoea
Others Decapod larva
Insect larva (chronomidae)
Chaoborus larva
Gastropod larva
Lamellibranch larva
Fish larva

Distribution of zooplankton

Specific composition
Fifty five species have been identified in the Casamance estuary, 55% of them belonging to the Copepods (Table 2). Moreover, 40 types of larvae have been found. One of the more striking characteristics of faunal composition is the scarcity of typically continental species and the abundance of marine species. This phenomenon is usual in hyperhaline paralic environments (Hedgpeth, 1967; Parker, 1955).

Distribution of abundance (Fig. 9) and specific diversity
From the mouth of the estuary to Pointe Saint Georges (station 5 included), the zooplankton is abundant and diversified. The diversity index varies from 3.5 to 2. This area contains practically nothing but marine species, the dominant one being *Paracalanus scotti* (Copepod) during most of the year. However, Lamellibranch larvae (mainly *Ostrea*) are very abundant and even dominant during the rainy season, especially in July and August.

From station 5 to station 13, the stenohaline marine species desappear and only euryhaline species remain. *Limacina* sp. is dominant in this area during most of the year, except from September to November, when salinity is lowest. *Paracalanus scotti* then becomes dominant. Zooplankton is still relatively rich and diversified, the diversity index being about 3 to 2.

From station 13 to station 18, lies an intermediate community dominated by *Acartia grani* (Copepod), a coastal marine and estuarine species (Gaertner, 1985; Seret, 1985; Diouf & Diallo, 1987). Zooplancton is almost as abundant as in the previous zone. The diversity index ranges from 2 to 1.3.

From station 18 to station 29 lives the extremely euryhaline community of the middle estuary. The bulk of this community is constituted by *Acartia grani, Cyprideis* sp., *Cletocampus* sp. and insect larvae (Chironomidae). Related species have been found in hyperhaline environments throughout the world. Hedgpeth (1967) mentioned the presence of *Acartia tonsa* at salinities of about 80‰ in the Laguna Madre (Texas) – We found living *Acartia grani* in the Casamance

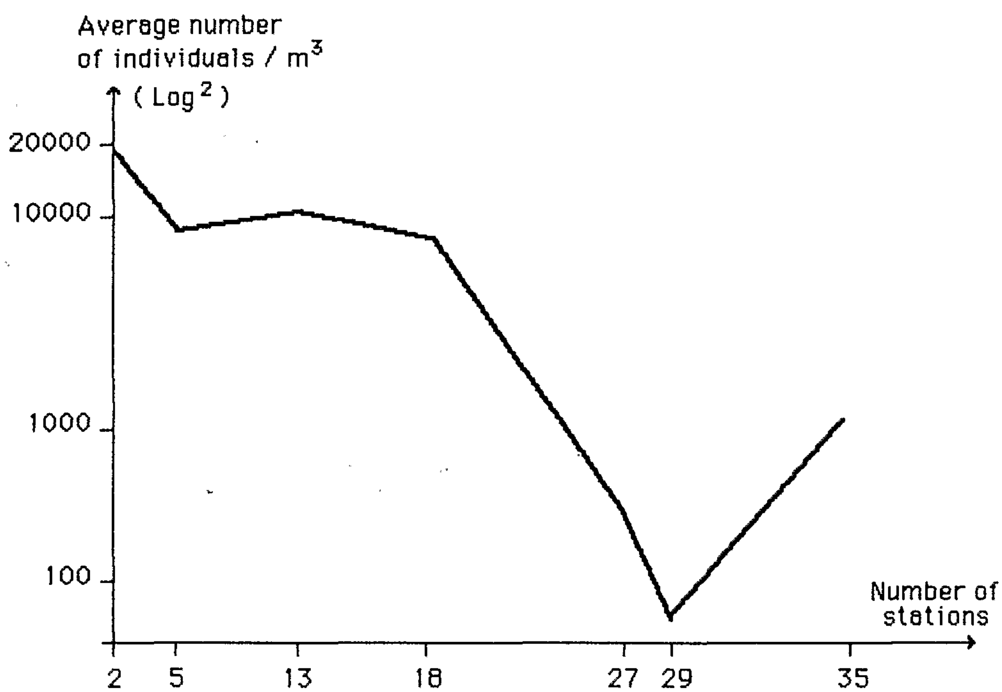

Fig. 9. Decrease of the zooplankton abundance from the sea to the uppermost stations.

estuary at salinity of 101‰ –. *Cletocampus retrogressus* bears salinities of about 140‰ (Löffler, 1961), which is markedly higher than the maximum recorded for *Cletocampus* sp. in the Casamance estuary (78‰). *Cyprideis mandviensis* has been found at salinities of about 60‰ by Carbonnel (1985) in the Sine-Saloum estuary and Chironomidae larvae have been reported in hyperhaline environments by Hedgpeth (1957). In this area, the abundance of the zooplankton is much lower and the diversity index ranges from 1.2 to 0.

Upstream from station 29, the abundance increases again while the diversity decreases and from station 35 the diversity index is very low (0.2 to 0), corresponding to an impoverished continental fauna, especially during the months of highest salinity (June and July), when only a few insect larvae can develop.

Conclusion

Refering to zooplankton, the Casamance estuary can be divided into five zones:

- a marine zone up to station 5;
- a zone under marine influence from station 5 to stations 11 to 13 (Ziguinchor);
- an intermediate zone from station 13 to station 18;
- an hyperhaline zone from station 18 to station 29;
- a zone under continental influence, upstream from station 29.

There is a great similarity between the zooplankton of the Casamance and that of the Sine-Saloum, and neighbouring estuary with a rather identical hydrological evolution in its salinity (Seret, 1985). On the other hand, the zooplanktonic faunas of the Casamance and the Gambia, a normal salinity gradient estuary located to the north of the Casamance, are quite different (Page, 1984).

It seems that confinement (Guelorget & Perthuisot, 1983) acts differently on the spatial distribution of zooplankton according to whether continental outflow or oceanic inflow is dominant.

Discussions and conclusions

Ecological zonation

Each of our studies showed, independently, a partition of the estuary. Grouping these results, it is possible to identify six zones, upstream from the sea (Fig. 10):

- a marine zone up to station 5;
- a zone under marine influence (mixohaline zone) between stations 5 and 11–13;
- an intermediate, metahaline zone from stations 11–13 to stations 18–20;

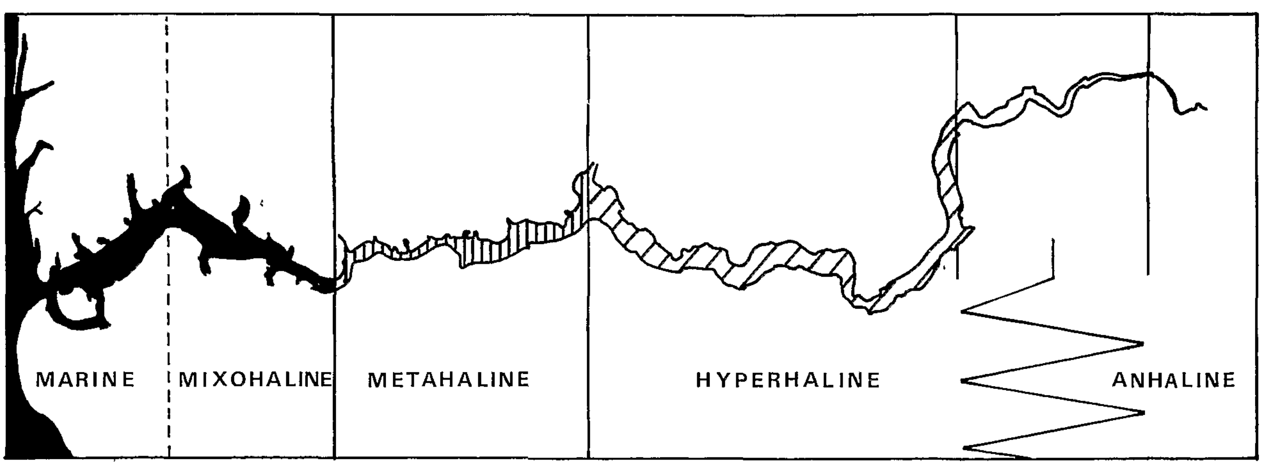

Fig. 10. Main ecological zones along the Casamance River.

- a permanently hyperhaline zone between stations 18–20 and 30;
- a zone of widely varying salinity in a closely confined environment, between stations 30 and 38;
- the continental anhaline area, under fresh water most of the year, upstream from station 38.

These limits have been reidentified during other studies carried out on the Casamance River (Fig. 11). Mangrove forest is tall and healthy up to station 11, then more sparce till stations 18–20 (Badiane, pers. comm.). Died out remains of large *Rhizophora* are found up to station 25; some dead *Avicennia* still stand at station 30. *Phragmites* turions are still found in small number at station 25, and in dense formations at station 30. Living reeds are found above station 37. The tidal currents decrease abruptly above 18 (Millet, pers. comm.), probably in relation with river morphology and bathimetry (the broad shallow expanse of station 18 acts as a muffler).

Specific diversity in the ecosystem

We have seen that zooplankton and foraminifera populations both show a marked decrease in the number of species in increasingly confined water. Although we have no taxonomic study of phytoplankton, the high proportion of carotene in upper reaches hints at a population dominated by *Dunaliella salina* (Ben Amotz & Avron, 1980, 1983). Other studies on the Casamance River have shown that other taxa disappear with increasing salinity: the fish fauna becomes monospecific (*Sarotherodon melanopteuron*) above 75‰ (Albaret, pers. comm.).

Such decreases in species diversity in relation to salinity have been described for other hyper-

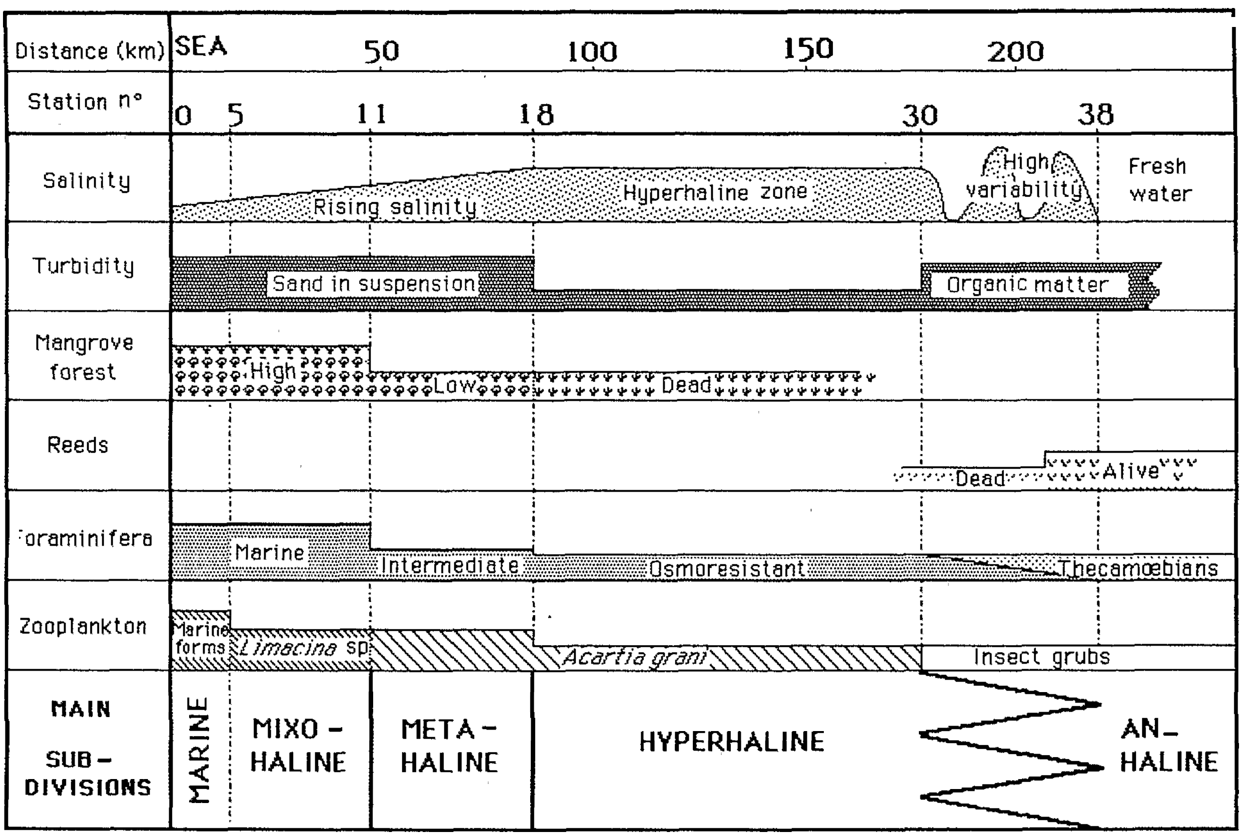

Fig. 11. Distribution of some biotic and abiotic parameters along the Casamance River.

haline environments (Phleger, 1960; Hedgpeth, 1967; Por, 1972; Baily, 1972; Kushner, 1978; De Deckker & Geddes, 1980; Rodriguez-Valera *et al.*, 1981; Rushforth & Felix, 1982). Several diagrams have expressed the effect of salinity on the number of species (Remane & Schlieper, 1958 in Hedgpeth, 1967; Day, 1981 in Hodgkin & Kendrick, 1984). The simultaneous increase in population numbers has been stressed (i.g. Guelorget & Perthuisot, 1983). In this respect, the Casamance River appears to fit quite well into the general rules.

Salinity regime

A part of the uppermost reaches (at Kolda and above) may dry up at the end of the dry season; this would put this portion in the type B of Williams's classification (1985). Other parts, in the small tributaries, would fit in Williams's type C, since the drying up of both environments is more or less predictable. The main part of the river is none the less permanent and falls into Baily's 'hypersaline class'; although the upper portion (stations 36 to 41) may swing to 'athalassic fresh' characters during certain months.

Several other water-bodies throughout the world may exhibit such salinity range and some hyperhaline sebkhas reach zero salinity during the rains (Kerambrun, 1986). Here, the peculiarfeatures are that: i) the peak salinities (170‰) are among the highest for a permanently open estuary (Hodgkin & Lenanton, 1981); ii) the decrease in salinity remains limited in its geographical extent. It appears plausible that at least part of the water remains trapped inside the river for more than one year; Wolanski (1986) evoked such a possibility in the case of a 'salinity plug'. Its chemistry, and nutrient cycling in particular, will be peculiar.

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