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## **Complexity in trophic structure and stability in a modelled West African estuary**

### ***Complexité de la structure trophique et stabilité d'un estuaire ouest-africain modélisé***

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**KEY WORDS.** — Biodiversity ; Coastal Ecosystem ; Ecopath ; Estuary ; Omnivory ; Senegal ; System Stability ; West Africa.

**MOTS-CLÉS.** — *Afrique de l'Ouest ; Biodiversité ; Ecopath ; Ecosystème côtier ; Estuaire ; Omnivorie ; Sénégal ; Stabilité des systèmes.*

**ABSTRACT.** — An Ecopath model of the Sine Saloum estuary (Senegal) with a total of 37 functional groups is used in this study to determine the key features of this aquatic system. The high fish species biodiversity in the ecosystem may play a role of ensuring its integrity, especially in the presence of stress, though it was observed that this is not entirely the case. Results show that another mitigating factor is the level of interaction strengths between functional groups. Stability is improved by weaker connectance as well as shorter and fatter pyramids. Though differing issues arise with respect to questions driving a system's stability, methods and approaches should consider placing results in the context of a broader ecological theory.

**RÉSUMÉ.** — Un modèle Ecopath de l'estuaire du Sine-Saloum (Sénégal) comportant au total 37 groupes fonctionnels a été appliqué dans la présente étude en vue de déterminer les faits essentiels de ce système aquatique. La grande biodiversité spécifique des poissons de l'écosystème peut y jouer un rôle en assurant son intégrité, spécialement en présence de facteurs de stress, bien qu'il

ait été observé que ce n'est pas entièrement le cas. Les résultats montrent qu'un autre facteur de mitigation est le niveau des forces d'interaction entre les groupes fonctionnels. La stabilité est accrue par des relations plus faibles et des pyramides plus courtes et plus larges. Bien que différentes questions se posent concernant les facteurs conduisant à la stabilité d'un système, les méthodes et les façons de les approcher devraient envisager d'en situer les résultats dans le contexte d'une théorie écologique plus large.

### Introduction

Sine Saloum estuary ( $13^{\circ} 35'$  and  $14^{\circ} 10'$  N,  $16^{\circ} 50'$  and  $17^{\circ} 00'$  W) is located on the coast of Senegal. It has an area of approximately 543 km<sup>2</sup> (Fig. 1) opening into the Atlantic Ocean (DIOUF 1996, VILLANUEVA 2004). It is an inland type, deltaic system characterised by flat river valleys with varying water levels depending on seasonal floods (September-December) from adjacent marine ecosystems extending. Three distinct seasons are observed : dry and cold from November to March, dry and hot from April to June and a wet season from July to October. Outflow of continental waters to the sea is usually rare as the hydrological regime is characterised by a deficit of freshwater inflow from January to September (PAGÈS & CITEAU 1992, CHARLES-DOMINIQUE & ALBARET 2003).

The watershed comprising the Sudanian-Sahelian rivers have been greatly altered by the early 1970s drought during which the freshwater inputs decrease considerably in certain coastal zones. A distinction of this estuary is the development of saline gradients opposing "normal" trends compared to other coastal systems. Saline concentrations follow an inverse pattern where an elevated value of up to 130 psu was observed along upstream areas (J.-J. ALBARET, IRD, unpublished data). Despite these severe environmental conditions, the system has a high fish species richness (114 species), mainly of marine origin (SIMIER *et al.* 2004), compared to the Gambia estuary (70 species) (ALBARET *et al.* 2004). Density, however, declines from the estuarine mouth to the upstream area as a function of the increase in saline concentration (SIMIER *et al.* 2004). Although estuarine species demonstrate considerable tolerance to salinity variations, this factor influences development and growth of organisms that impinges biomass production (BŒUF & PAYAN 2001).

Ecosystem diversity depends on biotic processes and abiotic constraints. Complex and seasonal environmental conditions consequently influence biotic communities' distribution and interactions. Compositional changes can evoke significant responses as much as changes in

**FIGURE MANQUE !**

Fig. 1. — A general map of the Sine Saloum estuary

diversity (DOWNING & LEIBOLD 2002). Species richness and abundance have been observed to have considerable effects on trophic structure (PETCHEY *et al.* 2004) and system productivity (KAUTZINGER & MORIN 1998). Species extinction following exposure to stress may affect system functioning, lowering its resistance against environmental stress (COGNETTI & MALTAGLIATI 2000, BŒUF & PAYAN 2001).

The significance of understanding how interaction strength patterns influence both structure and dynamics in food webs is crucial in elucidating several obstacles to production (ELLIOT *et al.* 2002). System productivity and nutrient cycling depend on the diversity of functional traits of biota. The paper aims to describe some ecosystem properties of the Sine Saloum estuary using the Ecopath software, especially that pertaining to how ecological communities in this system are structured. An advantage of using this model is that it considers prey-predator links and

does not outcast the potential significance of non-trophic interactions, such as competition, facilitation and biotic disturbance which are often neglected by typical non-dynamic food web community structures. Although this software offers much more functionality than what is tackled in this paper, interest has been focused mainly on food web topology and some characteristics that indicate system resistance and resilience to stress.

### Materials and Methods

For this study, we considered a previously mass-balanced model of the Sine Saloum estuary for the year 1991-1992 (VILLANUEVA 2004). The Ecopath software is used to describe the trophic interactions of functional groups such as foraging rates, body size, metabolic rate, biomass distribution, and other species traits occurring in this ecosystem are considered. Fish group biomasses were estimated from experimental fishing data from SIMIER *et al.* (2003) while non-fish groups were adopted from SAMB & MENDY (2003). The detritus biomass is estimated from multiple regression analysis suggested by PAULY *et al.* (1993) as a function of primary production and the depth of the euphotic zone.

In addition to balancing the model, other parameters such as omnivory index (*OI*) and connectance index (*CI*) are computed to describe network structure complexity and predator-prey ratio (CHRISTENSEN *et al.* 2000, CHRISTENSEN & WALTERS 2004).

Group-specified *OI* pertains to the variance of the trophic level of each predator's prey groups (CHRISTENSEN & PAULY 1993) while system *OI* indicates the allocation of predator-prey interactions linking each trophic level (CHRISTENSEN & WALTERS 2004). Both ranges from 0 to 1, where a value close to 0 indicates high predatory specialization and 1 indicates feeding versatility on several trophic levels.

The *CI* is the ratio between the number of definite trophic associations among all the groups and the theoretical possible number of connections,  $(N-1)2$  for  $N$  groups, including consumptions of detritus (CHRISTENSEN *et al.* 2000, CHRISTENSEN & WALTERS 2004).

### Results and Discussion

A total of 37 functional groups were considered based on similarities of species properties (YODZIS & WINEMILLER 1990). This includes 29 fish groups, 5 invertebrate groups, 2 groups of primary production and a

detritus group. Table 1 shows the estimated biomass and some results of the balanced Ecopath model for the Sine Saloum estuary during the early 90s. The total computed fish biomass is 9.1 tons.km<sup>-2</sup>. This value is similar to that estimated in the Gambia estuary and slightly low compared to that of Ébrié lagoon (9.5 tons.km<sup>-2</sup>). Biomass estimated for exploited invertebrates (shrimps and crabs) is 4.7 tons.km<sup>-2</sup> (Table 1).

Groups with highest computed biomasses are the blackchin tilapia (*Sarotherodon melanotheron*) and madeiran sardinelle (*Sardinella maderensis*) representing respectively 30 and 27 % of the total biomass estimated by the model. Considerable abundance of the tilapia has already been observed in other West African estuaries and lagoons, especially in highly stressed ones, due to its “opportunistic” capacities under different environmental stress (BARAN 2000, PAULY 2002, LALÈYÈ *et al.* 2003, VILLANUEVA *et al.* 2003).

The TL of consumer groups ranges from 2 to 3.8 indicating a short food web and that most populations are composed of juveniles and that the ecosystem functions as a nursery or refuge zones (MANICKCHAND-HEILEMAN *et al.* 1998).

In Sine Saloum, certain fish assemblages considered here consume a wide variety of food resources ranging from detritus, algae, mollusks and fish. Several groups, mostly in TLs 2.5 to 3.2, have an *OI* higher than 0.2 (Table 1). In general, high *OI* values are observed in lower TLs which indicate more complexity in this part of the food web (ZETINA-REJÓN *et al.* 2003). For some groups, high *OI* values were observed : *Arius* spp (sea catfishes), *Polydactylus quadrifilis* (giant African threadfin), *Pseudotolithus* spp (croakers), madeiran sardinelle, shrimps and crabs. This is partly due to ontogenic feeding changes and migration of these species in or out of the estuary according to their environmental requirements for optimal growth and reproduction. The system *OI* for Sine Saloum estuary is low (0.137) indicating that most functional groups exhibit a certain degree of diet specialisation. This indicates that weak and strong interactions are observed among species in the estuary (Table 1). According to QUINCE *et al.* (2002) this is common in matrix analyses of food webs especially in competitive communities. The co-existence of these 2 types of interactions is evident though the stability in an ecosystem is a balance of these links.

For this model, the *CI* value obtained is 25 % which is slightly lower than that observed in Celestun lagoon and Huizache-Caimanero lagoon complex (VEGA-CENDEJAS & ARREGUÍN-SÁNCHEZ, 2001 ; ZETINA-REJÓN *et al.* 2003) or in other coastal shelves (SÁNCHEZ & OLASO 2004).

**Table 1**

*Input values and estimates (in parenthesis) of some parameters for the 37 functional groups of the balanced trophodynamic model of 1991-1992.*

*TL : trophic level, B : biomass (t.km<sup>2</sup>) and OI : omnivory index*

	<b>Ecopath Group</b>	<b>CODE</b>	<b>TL</b>	<b>B (fw)</b>	<b>OI</b>
1	<i>Sphyraena afra</i> *	SGU	(3.7)	0.030	(0.082)
2	<i>Scomberomorus tritor</i>	CTR	(3.8)	0.049	(0.083)
3	<i>Polydactylus quadrifilis</i>	POQ	(3.6)	0.026	(0.126)
4	<i>Galeoides decadactylus</i> *	GDE	(3.4)	0.363	(0.079)
5	<i>Pseudotolithus elongatus</i> *	PEL	(3.5)	0.241	(0.085)
6	<i>Pseudotolithus brachygnathus</i>	PBR	(3.6)	0.092	(0.057)
7	<i>Elops lacerta</i> *	ELA	(3.6)	0.056	(0.101)
8	<i>Arius laticutatus</i> *	AGA	(3.4)	0.090	(0.132)
9	<i>Pomadasys jubelini</i> *	PJU	(3.2)	0.174	(0.123)
10	<i>Chloroscombrus chrysurus</i>	CHL	(3.2)	0.154	(0.209)
11	<i>Caranx hippos</i> *	CHI	(3.5)	0.019	(0.051)
12	<i>Trachinotus teraia</i> *	TFA	(3.3)	0.045	(0.081)
13	<i>Citarichthys stampflii</i>	CST	(3.6)	(0.029)	(0.013)
14	<i>Cynoglossus senegalensis</i> *	CYS	(3.3)	(0.039)	(0.093)
15	<i>Eucinostomus melanopterus</i> *	GME	(3.0)	0.098	(0.257)
16	<i>Drepane africana</i> *	DFA	(2.8)	0.143	(0.308)
17	<i>Dasyatis margarita</i> *	DMA	(3.2)	0.069	(0.139)
18	<i>Ilisha africana</i>	IAF	(3.0)	0.426	(0.271)
19	<i>Brachydeuterus auritus</i>	BAU	(2.7)	0.188	(0.233)
20	<i>Epinephelus aeneus</i> *	EAE	(3.2)	(0.191)	(0.150)
21	<i>Hemiramphus brasiliensis</i> *	HBR	(2.3)	0.035	(0.242)
22	<i>Pellonula leonensis</i>	PEF	(3.3)	(0.259)	(0.071)
23	<i>Trichiurus lepturus</i>	TLE	(3.2)	0.027	(0.073)
24	<i>Monodactylus sebae</i>	PSB	(3.2)	0.024	(0.064)
25	<i>Ethmalosa fimbriata</i>	EFI	(2.6)	0.630	(0.268)
26	<i>Sardinella maderensis</i> *	SEB	(2.7)	2.413	(0.227)
27	<i>Liza grandisquamis</i> *	LGR	(2.7)	0.426	(0.244)
28	<i>Sarotherodon melanotheron</i>	THE	(2.0)	2.719	(0.076)
29	<i>Tilapia guineensis</i>	TGU	(2.0)	0.073	(0.043)
30	Shrimps	CREV	(2.5)	(2.815)	(0.284)
31	Crabs	CRAB	(2.7)	(1.858)	(0.232)
32	Macrobenthos	MACR	(2.0)	93.000	(0)
33	Meiobenthos	MEIO	(2.1)	19.600	(0.053)
34	Zooplankton	ZOOP	(2.1)	20.636	(0)
35	Phytoplankton	PHYTOP	(1.0)	82.000	(0)
36	Phytobenthos	PHYTOB	(1.0)	(32.158)	(0)
37	Detritus	DETR	(1.0)	1.000	(0.286)

Fig. 2 shows that the Sine Saloum is characterised by a short and fat pyramid. NEUTEL *et al.* (2002) demonstrated that the organization of strong and weak linkages in food webs seem to be reflected in the shape of the trophic flow pyramid itself. This is based on the energy conversion efficiencies where the body size depends on trophic levels. This explains

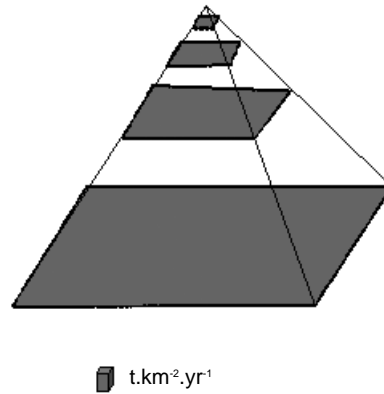


Fig. 2. — The flow pyramid of Sine Saloum showing flows by TL. The volume of each compartment is proportional to its flow throughput ( $\text{t.km}^{-2}.\text{yr}^{-1}$ ).

why large, long-lived animals with higher energy efficiencies (i.e. carnivores) are found in higher trophic levels of the pyramid. This indicates that the slope of the side of the pyramid may be a good indicator of web stability : Webs that give tall, thin pyramids are less likely to be stable than those with shorter, more stout pyramids.

The salinity-stress had already been indicated in other brackish ecosystems to contribute on the decline of species diversity (COGNETTI & MALTAGLIATI 2000). PANFILI *et al.* (2004) observed that although vital processes such as reproduction and growth occur for blackchin tilapia, salinity-stress affects negatively its growth and age-at-maturity. This species had been observed to adapt well in other ecosystems with extreme conditions with life-cycle trade-offs (PAULY 2002, LALÉYÈ *et al.* 2003).

According to SIMIER *et al.* (2004), the estuary is divided into 3 major habitats based on the salinity gradients and where fish faunas differed significantly in total biomass and density between areas and seasons. This may have lead to the formation of “biotic discontinuities” (RAY 1996) in the ecosystem where the development and organization of estuarine biota differ from the mouth to the hypersaline zone. The regrouping of distinct sub-assemblages among populations depending on their ability to tolerate salinity-stress can affect and alter the energy community budgets and transfer efficiencies due to loss in efficiency of biological communities, thereby limiting the potential productivity of the system (GONZÁLEZ-OREJA & SAIZ-SALINAS 1999). Due to the ecosystem’s elevated species diversity, energy transfers may have been ensured by tolerant species

when extreme conditions chase out the less tolerant ones. According to PETCHEY *et al.* (2004), a higher biodiversity can act as an insurance to continued ecosystem functioning through species replacement by other species with similar properties.

According to VILLANUEVA (2004), however, the level of stress is more pronounced along the transition zones contrary to what might be expected in an inverse hypersaline estuary. This may be due to short-term, extremely varying hydrologic conditions, acting as multiple stressors which can lead to biodiversity loss and, consequently, to biotic community structure shifts. These can lead to fragmentations between marine-estuarine habitats (LAYMAN *et al.* 2004) following fluctuating environmental conditions that can impinge efficient energy fluxes and may explain the presence of pronounced stress along the estuarine mouth. The high temporal and spatial variations within communities with high richness mediate negative effects of species loss such that another species' tolerance to several stressors can compensate for loss of sensitive taxa and maintain ecosystem functioning (PETCHEY *et al.* 2004).

The decline to a complete absence of freshwater flows along the upstream area of the Saloum meander leads to habitat condition stabilization advantageous for hypersaline-tolerant species. The effects of salinity-stress declined over time due to low fluctuating hydrologic conditions. Positive relationship is reflected by high variations among communities of low species richness. High energy cost of adaptation to stress is compensated by increased survival rates (less competition and predation) and thus enhancing trophic capacities. GORDON (2000) indicated that such condition may have evolved into a sort of "conservation habitat" for tolerant species as it limits competitive interactions while enlarging the species' ecological niche.

### Conclusion

In Sine Saloum, the drought which has endured for 30 years had completely blocked freshwater inputs into the estuary and modified hydrologic conditions and trophic functioning of biologic communities. The seasonal salinity fluctuations in the estuary appeared to be a significant factor in structuring fish and other biologic assemblages, as well as affecting their metabolisms. The mouth and, in certain cases, the intermediate zones of the estuary continues to function as a nursery and refuge areas for juveniles as observed by the short food web. In the hypersaline zone, the shortening of food chain seems to be due to the decline in



species diversity and proliferation of hypersaline-tolerant, mainly detritus feeders, such as *Sarotherodon melanotheron*.

The effect of species loss due to stress on system's total biomass depends on the food web organization (i.e. species distribution among trophic levels and feeding versatility) and how loss of less tolerant species is compensated by more tolerant species in ensuring the system's significant properties (i.e. total biomass). A combination of strong (i.e. less plasticity in diet) and short (i.e. abundance of detritus feeders) predator-prey links making up the complex food chain of the estuarine biota mitigate stress impacts on the ecosystem's trophic functioning while ensuring its stability. Less seasonal fluctuations along the upstream (hypersaline) area may have contributed to the quasi-stable trophic relationships existing among species inhabiting this zone.

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