
Contrasting tropical estuarine ecosystem functioning and stability: A comparative study

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Abstract :

A comparative study of the Sine-saloum (Senegal) and Gambia (The Gambia) estuaries was performed based on trophic model outputs that describe the system structure and functioning. These trophic models were constructed such as to differentiate main energetic flows in the systems and express how climate change may have impacted ecosystem resilience to change. Estuarine fish assemblages are highly resilient despite exposure to vast hydrodynamic variations and stress. Coupled with strong anthropogenic-driven stresses such as fisheries and climate change, ecosystems may undergo severe regime shifts that may weaken their resilience and stability. Taxonomically related and morphologically similar species do not necessarily play similar ecological roles in these two ecosystems. Biomass and production in the Sine-saloum are concentrated at trophic levels (TLs) 2 and 3, while for the Gambia, both are concentrated at TL3. Higher TL biomasses in Gambia compared to Sine-Saloum may be explained by the latter ecosystem being characterized by inverse hypersalinity. Higher TL of production in Sine-Saloum is due to higher exploitations compared to Gambia where fishing activities are still less developed. High production and consumption rates of some groups in both ecosystems indicate high system productivity. Elevated productivity may be due to higher abundance of juvenile fishes in most groups that utilize the latter as refuge and/or nursery zones. Both ecosystems are phytoplankton-driven. Differences in group trophic and ecological roles are mainly due to adaptive responses of these species to seasonal and long-term climate and anthropogenic stressors. System indicators suggest different levels of ecosystem resilience and stability as a function of biodiversity. Relevance of other observations on ecosystem functioning and indicators in relation to perturbation is discussed.

Keywords : complex adaptative systems, climate change, food web models, regime shifts, ecosystem resilience, trophic ecology

Introduction

Tropical estuaries are considered as biogeochemical hotspots due to high levels of primary production, large reserves of organic matter and habitat diversity that offer optimal niches for numerous aquatic species which utilize these areas as refuge and/or nursery grounds and anthropogenic pressures on ecosystems ([Baran 2000](#); [Cloern et al. 2013](#)). Production in estuaries and coastal lagoons tend to be 10-15 times higher than those of other continental shelves ([Duarte 1995](#)).

As transitional areas with intense fluctuations of environmental conditions, these ecosystems influence multi-species dynamics and impose physiological constraints on biota ([Baran 2000](#)). Estuaries are often shallow with highly varying hydrological regimes and are structured by marine-freshwater inflows and bio-geographic regions ([Whitfield et al. 2012](#)). Biodiversity varies as a function of marine and/or continental water flows into these 'intermediate' systems ([Blaber 2002](#); [Deegan and Garritt 1997](#)). Species abundance trends tend to decrease as salt marshes increase ([Ferreira et al. 2005](#); [Struyf et al. 2004](#)). Changes in environmental conditions generally provoke diverse biological responses, allowing only tolerant species to persist ([Glaser 2003](#); [Taylor et al. 2014](#)).

Drivers to ecosystem changes include natural and anthropogenic processes. Due to their location, and the multitude of ecological services they provide, estuarine areas often attract large human populations, and thus the risks of environment degradation are

1 also high (Glaser 2003; Lotze et al. 2006). In developing countries, development of
2 artisanal/traditional and industrialized fisheries and aquaculture in these ecosystems have
3
4 also been growing, to meet increasing demand for local consumption and export (Lalèyè
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6 et al. 2007; Welcomme 2002). However, fisheries usually target not only highly
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8 commercial stocks, but also impacts forage species, consequently impacting the
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10 dynamics of the entire ecosystem (Sadovy 2001).
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14 Apart from fisheries, another human-related threat to coastal wetlands is climate
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16 change. Five estuarine environmental factors can be impacted as a response to climate
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18 change: sea level, intensity and frequency of rainfall, salinity, freshwater-sediments-
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20 nutrients inputs and water circulation (Kennedy 1990). Negative impacts of seasonal
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22 hydrologic regimes (Ponce Campus et al. 2013; Taylor et al. 2014) and global climate
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24 change (Alongi 2008; James et al. 2013; Kennedy 1990) on estuaries are well
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26 documented. Changes affect individual bio-ecological processes (i.e., osmoregulation,
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28 growth, reproduction) and community abundance and distribution. These eco-
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30 geomorphological alterations can have negative impact on biodiversity that can disrupt
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32 system integrity, leading to changes in structure, functioning, dynamics and productivity
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34 (Ferreira et al. 2005; Roessig et al. 2004).
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41 In this study, two West African estuaries are considered and compared. As
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43 transitional ecosystems, they are noted for their high taxonomic richness due to a
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45 succession of species utilizing these environments as nurseries and refugia. Due to the
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47 limited geographical distance between these estuaries, close similarities of marine and
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49 estuarine fish faunas have been observed (Baran 2000). However, differences in
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51 hydrological regimes have led to contrasting observations on fish ecology and utilization
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53 of these environments (Diouf 1996; Panfili et al. 2006; Vidy 2000; Vidy et al. 2004;
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55 Villanueva 2004).
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As highly productive and complex ecosystems, knowledge on the biological and ecological functioning of fish faunas utilizing, as well as, the environmental forces contributing to geographic specificities of these environments is vital for sustainable management and conservation of these ecosystems. Recognizing that anthropogenic activities impact not only on the environment, but the dynamics and functioning of its living resources, untangling ecosystem processes can increase understanding on its current health and resilience to change. An ecosystem-based approach that can synthesize multi-specific analyses and the combined influence of their characteristics (i.e., production, mortality, trophic interactions, physiological adaptation, etc.) following environmental changes can be valuable to understand and manage such fragile ecosystems (Imperial and Hennessey 1996).

This study attempts to summarize and integrate existing data and to draw a larger picture of interactions among biological components and how abiotic conditions mould the structure and functioning of these ecosystems. This is also a comparative study of two systems with severely contrasting hydrological regimes: a ‘normal’, less exploited estuary (The Gambia) and an ‘inverse hypersaline’, highly exploited system (Sine-Saloum). Trophic models of these ecosystems are constructed in order to quantify energetic flows, trophodynamic links and transfer efficiencies among trophic levels (*TLs*) and identify differences in the species ecological functioning and ecosystem structure as adaptive response to contrasting hydrological regimes. Modelling ecological systems can be valuable in describing how an ecosystem is organized and how changes can affect system internal processes (Berlow et al. 2004). Modelling can also provide indicators to assess risks on ecosystem stability and biodiversity through the complex, but tractable depictions of energy transfers, trophic fluxes, assimilation efficiencies and dissipation (Rambouts et al. 2013). Results can provide critical insights that can be

1 further utilized to evaluate the impacts of changes in biodiversity (Balvanera et al. 2006;
2 Christian et al. 2005), ecosystem structure and functioning (Roessig et al. 2004;
3 Villanueva et al. 2006) and verify multi-species management decisions and conservation
4 (Brando et al. 2004; Imperial and Hennessey 1996).
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9 **Methods**

10 *Study sites*

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14 The Sine-Saloum estuary (Figure 1a) is 100 km south of Dakar, Senegal, 13°55'
15 and 14°10' N and 16°03' and 16°50' W. It has a total area of approx. 543 km² opening
16 into the Atlantic Ocean. As an inland type, deltaic system, it is characterized by flat river
17 valleys with varying water levels depending on seasonal floods from adjacent marine
18 ecosystems. It consists of three main branches from north to south: Saloum, Diomboss
19 and Bandiala. At the western end of these branches are characterized by a network of
20 fine creeks (locally called 'bolongs') dominated by dense mangrove trees. The Saloum
21 extends up to 180 km with water depths from 25 m (mouth) to 13 m (upstream), while
22 Diomboss and Bandiala have maximum water depths of 10 m. Water hypersalinity was a
23 result of a perennial 'El Niño phenomenon' that had completely cut-off freshwater
24 inputs (Pagès and Citeau 1990; Simier et al. 2004). Aside from the system
25 geomorphology, the inverse hypersalinity effect is due to small freshwater inflows, not
26 compensating for a high evaporation. Water salinity in upstream areas can reach over
27 130 psu during the dry season (November -June) and remain between 45-50 psu during
28 the rainy season (July-October). The average water temperature is 25°C (Diouf 1996).
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50 *Figure 1 here*

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53 The Gambia River Estuary (Figure 1b) has a total catchment area of 78,000 km²
54 (13°28'N;16°34'W-13°41'N;15°08'W). It originates in the Fouta-Djalón plateau and
55 flows through Guinea. The estuary zone, considered in this study, has a total area of 654
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km². Average depth varies from 3-15 m. The average water temperature is 27°C and the average annual precipitation is 1,500 mm. This ecosystem has a ‘normal’ decreasing down-to-upstream salinity gradient (Figure 1a). Maximum river flow ranges from 4.5-1,500 m³·s⁻¹. Water salinity at the mouth of the estuary varies between 38 and 45 psu (Villanueva 2004).

Ecosystem models

The Ecopath software implements an ecosystem model based on a set of simultaneous linear equations for each entity considered. It assumes mass-balance, i.e., group production is equal to the sum of all predations, non-predatory losses and exports (Christensen et al. 2005). In order to minimize information loss and taxonomic biases, biological components are pooled according to similarities of species trophic properties (i.e., diets, predators and metabolism) and distribution (Yodzis and Winemiller 1999). Each trophic group has an energy balance expressed as:

$$B_i \left(\frac{P}{B_i} \right) = \sum_{j=1}^n B_j \left(\frac{Q}{B_i} \right) - DC_{ji} + (B_i) \left(\frac{P}{B_i} \right) (1 - EE_i) + EX_i \quad (1)$$

where B_i is the biomass of group i ; P/B_i is the production rate of i equal to the total mortality coefficient (Z) (Allen 1971); Q/B_i is the relative consumption rate; B_j is the biomass of the predating group j ; DC_{ji} , the proportion of the predated group i in the diet of the predating group j ; EE_i is the ecotrophic efficiency representing the part of the total production transferred to higher TLs through predation or captured in the fisheries; EX_i export or catch in fisheries of group i , assumed exploited in fisheries.

A total of 37 and 41 compartments were considered for the Sine-Saloum and Gambia models, respectively (Tables 1 and 2). The lower number of fish groups in Sine-Saloum is due to the absence of freshwater fishes caused by the inverse hypersalinity of the system following the Sahelian drought in the late 1960s as well as the lower species

richness of euryhaline fishes. The input data were mainly primary data collected by (Simier et al. 2003), complemented by literature data (Albaret et al. 2004; Diouf 1996; Écoutin et al. 2005; Guillard 1998; Guillard et al. 2004; Healey et al. 1985; Laë et al. 2004; Panfili et al. 2004a; Panfili et al. 2004b; Simier et al. 2004; Simier et al. 2006). The choice of the study period was based on the availability and abundance of data for each ecosystem and on periods marked by considerable fishing and hydrologic variations: 1991 for Sine-Saloum and 2001 for Gambia. For trophic groups with several species, estimates were derived from properties of the dominant species. Biomasses were expressed and standardized as annual average in $t \cdot km^{-2}$. Flows between compartments are given in $t \cdot km^{-2} \cdot yr^{-1}$.

B , P/B and Q/B per functional group (Tables 1 and 2) were estimated using several empirical equations (De Mérona 1983; Froese and Palomares 2000; Gayanilo et al. 2002; Lévêque et al. 1977; Palomares and Pauly 1998; Pauly et al. 1993) using parameters obtained from several databases (Froese and Pauly 2014; N'Diaye et al. 2003; Simier et al. 2003) and information from the literature (Abarca-Arenas and Valero-Pacheco 1993; Albaret 1987; Arreguín-Sánchez et al. 1993; Bah et al. 2010; Chávez et al. 1993; FAO 1997; Guillard et al. 2004; Healey et al. 1985; Lhomme and Garcia 1984; Manickchand-Heileman et al. 1998; Mendy 2003; Mendy 2005; Njai 2000; Pagano and Saint-Jean 1994; Pauly 1982; Samb and Mendy 2003; Ziegler et al. 2011). DCs were initially summarized and compiled by Villanueva (2004). Complementary information were obtained from Diouf (1996), Ngouda (1997), Kone and Teugels (2003), Gning et al. (2008), Le Loc'h (2013) and Fishbase (Froese and Pauly 2014).

The Sine-Saloum catch data were from unpublished estimates provided by Dème (pers. comm., CRODT, Senegal) and complemented by artisanal catches (Simier et al. 2003). Here, high fish catches were recorded until the end of the 1970s. Reizer (1974)

1 indicated annual catches of 18,500 to 25,900 tonnes. Others indicated twice these values,
2 reaching up to 49,000 t-yr⁻¹ (Ba et al. 2006; Bousso 1996; FAO 2006; Lesack 1986). A
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4 common observation, however, is that catches greatly declined by 50-80% (~10,000 t-yr⁻¹
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7¹) mainly due to the 20-year drought, which caused salinity levels 3-5 times higher
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9 (>100 psu upstream) than that of the adjacent sea, combined with a growing fishing
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11 effort.. A slight increase of annual fish catches has been observed recently (Niang 2009).
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14 The fishery sector in Gambia still appears to operate at low-moderate levels
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16 (FAO 2006; Laë et al. 2004; Mbye 2005; United Nations 2014). Annual catches (fish,
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18 mollusks and shrimps) was estimated at 4,360 tonnes and the fishery is mainly artisanal
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20 (73-93%). Mean annual shrimp catches during the early 1990s was estimated at 334 t,
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22 contributing \$600,000 per year to the economy of The Gambia. Despite 'normal',
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24 seasonal marine-freshwater inflow dynamics, it has one of the lowest annual fish yields
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26 compared to adjacent West African brackish waters (Lalèyè et al. 2007) and other
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28 tropical estuaries (Marten and Polovina 1982).
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34 The Ecoranger routine of Ecopath was used to test for model sensitivity and to
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36 limit possible technical errors as it adjusts accordingly possible input parameters that can
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38 be modified depending on the data source and calculates the resulting impact. This is
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40 useful in refining less accurate data, common for most qualitative data on diet
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42 compositions (Christensen et al. 2005). Pedigree indices estimated through a quasi-
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44 Bayesian re-sampling technique were also implemented to quantify model uncertainties
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46 for reliable parameterization of Ecopath models (Kavanagh et al. 2004).
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51 ***Network analysis***

52 *A. structural analyses*

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56 The Omnivory index (*OI*) quantifies the variations of the TL of different preys
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58 consumed by a predator (Pauly et al. 1993). *OIs* near 0 indicate highly specialized
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1 predators. Group aggregations into discrete *TLs* were carried out based on approach
2 suggested by Ulanowicz (1995). This simplifies the food-web into discrete sums of
3 input-output flows in one *TL* to the next. This concept is a useful abstraction to organize
4 energy transfers in ecosystems and overcome bias from varying species abundance when
5 comparing ecosystem state and functioning.
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11 *B. Network analyses*

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14 Fishery gross efficiency (*GE*) is computed as the ratio between the total catch
15 (plus discards) and the total primary production (*TPP*) in the system. The *GE* value is
16 higher for systems with a fishery relying on low-*TL* species. This index tends to increase
17 with fisheries ‘development’ (Pauly et al. 1998). Total system throughput (*TST*) is
18 defined as the sum of all flows in a system. It represents the ‘size of the entire system in
19 terms of flow’ (Ulanowicz 1986). Total system biomass to the total system throughput
20 ratio, *B/TST*, (Christensen 1995) is directly proportional to system maturity, where
21 estimated value tends to be low during the ecosystem development phase and increases as
22 a function of maturity. Energy is conserved through component energy stocking (Odum
23 1971; Ulanowicz 1986). The ratios of net primary production to total respiration (*PP/TR*)
24 and *TPP* to production respiration (*TPP/PR*) are system maturity indices (Christensen
25 1995; Odum 1969). Here, values close to 1 indicate an ecosystem approaching maturity.
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44 System net primary production less total respiration (*NPP-TR*) is another index of
45 system maturity (Odum 1969) and should zero-out in a truly balanced ecosystem
46 (Christensen 1995). System omnivory index (*SOI*) is computed as the average *OI* of all
47 consumers weighted by the logarithm of each consumer food intake (Christensen et al.
48 2005). The Connectance index (*CI*) for a given food web is the ratio of the number of
49 actual links between groups to the number of theoretically possible links. Detrivory is
50 included in the count, but the opposite links are disregarded. This index is correlated with
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1 system maturity because a trophic structure changes from linear to web-like as a system
2 matures (Odum 1969).
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4 Finn's cycling index (*FCI*) is a quantitative importance of cycles in an ecosystem
5 or the proportion of system recycled *TST* (Finn 1976). It is considered as an important
6 indicator of ecosystem integrity through positive feedback (Allesina and Ulanowicz
7 2004) and can be used as stress (Ulanowicz 1986) or system maturity indicators
8 (Vasconcellos et al. 1997). This is similar to predator cycling index (*PCI*), calculated by
9 excluding the cycling through detritus. Disturbed systems are characterized by short-fast
10 cycles while complex trophic structures have long and slow ones (Kay et al. 1989).
11 Length of each cycle is quantified using Finn's mean path length, which accounts for the
12 number of groups involved in a flow. Finn's straight-through path length (excluding
13 detritus) is another ecosystem health indicator, wherein a low value translates a stressed
14 ecosystem and a short food chain controlled by bottom-up forces (Christensen et al.
15 2005).
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33 Macro-descriptors are typically applied for large and complex ecosystems whose
34 aim is to present ecosystem growth and development. Ascendancy, *A*, (Ulanowicz 1997)
35 and mutual information, *I*, (Hirata 1995) are examples of quantitative descriptors that
36 differ from those used in classical food webs. Ascendancy is a measure of system growth
37 (i.e., age, size) and development (i.e., organization) of network links, or simply, of
38 ecosystem performance (Patrício et al. 2004; Ulanowicz 2000). The fraction of a system's
39 capacity not considered as *A* is considered as the systems overhead (*O*), which is the
40 energy in reserve of an ecosystem, useful in case of perturbations. The relative
41 ascendancy (*A/C*) is the fraction of possible organization that is actually realized and it is
42 negatively correlated with maturity (Ulanowicz 1986).
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58 **Results**

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Models sensitivity

Basic parameterization results for the Sine-Saloum and Gambia models are shown in Tables 1 and 2, respectively. Pedigree sensitivity indices obtained were 0.81 and 0.78 for Sine-Saloum and Gambia models, respectively. Both values conform with the gauge of overall quality of an Ecopath model (Christensen et al. 2005). The Ecoranger routine was then used for each model to assess their viability. For Sine-Saloum, 165 acceptable runs out of 10,000 were obtained with a least sum of deviation equal to 10.08. A higher number of acceptable runs (188/10,000) were obtained for Gambia with a least sum of deviation equal to 9.23. These values indicated that both models are tightly fitted. The initial inputs-outputs based on field data were very close to the mean values generated by Ecoranger. Respiration to assimilation (R/A), production to respiration (P/R) ratios and estimated EEs for all considered group are less than 1.

Tables 1 and 2 here

Structural analyses

Group TLs varied between 1.0 and 3.8 in Sine-Saloum and Gambia ecosystems. In the former, highest values corresponding to groups 1-3, 6-7 and 13 and where most fish groups (72 %) is at TLs 2-3 (Table 1). In Gambia, highest value corresponds to group 1 followed by groups 4-5 and 12 and where most fish groups (82%) is at $TL3$ (Table 2). Cumulative biomass of major fish groups is almost similar: Sine-Saloum (9.13 t km^{-2}) and Gambia (9.07 t km^{-2}). However, the fraction of fish groups belonging to $TL3$ is higher in the Gambia estuary (71%) compared to that in Sine-Saloum (27%).

Based on estuarine fish ecological categories (Figure 2I) suggested by Albaret (1994), most fish populations in terms of species occupying Sine-Saloum have strong marine water affinities (Figure 2II). The presence of an elevated number of strictly marine species is mainly due to the elevated salinity. Simier et al. (2004) identified 73

1 species in their study, which is 40% lower than the value (123) indicated by Baran
2 (2000). Species number and diversity vary, but were related to salinity stratification,
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4 with lowest values observed in upstream areas where hypersalinity of >70 psu was
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6 recorded. In general, hypersaline waters impose additional physiological challenges (i.e.,
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8 greater osmotic and ionic stresses) on fishes which limit growth and production. Despite
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10 such extreme environments, fish assemblages have acclimatized to this ecosystem and
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12 actually characterized by a remarkably high biodiversity. Hypersaline areas, however, do
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14 not serve as nurseries (Vidy 2000) and are mainly inhabited by stunted estuarine fish
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16 species (e.g., *Sarotherodon melanotheron*). High fish species richness and biodiversity
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18 were also observed in other estuaries like in Casamance (Kantoussan et al. 2012), Mar
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20 Menor (Verdiell-Cubedo et al. 2013) and Rio Lagartos (Vega-Cendejas and Hernandez
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22 de Santillana 2004).
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29 *Figure 2 here*
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31 In Gambia, taxonomic richness is also elevated due to habitat diversity (Baran
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33 2000). Seasonal inflows of fresh- and marine waters provide environment conditions to
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35 fish species with differing affinity to water salinity (Figure 2II). Contrary to Sine-
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37 Saloum, trophic structure is highly unstable as species display a strong seasonal
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39 variability. Seasonal cycle variations of phytoplankton and nutrient in estuaries cascade
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41 towards higher *TLs* in food web (Deegan and Garritt 1997). Variations in temperature
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43 and freshwater inputs would ultimately drive ecological changes and overall ecosystem
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45 structure and functioning.
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51 *OIs* obtained are higher for most fish groups in Gambia than in Sine-Saloum
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53 (Tables 1 and 2). Lower *OIs* may be due to increased prey specialization of some fish
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55 groups depending on environmental conditions and availability of prey in each
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57 ecosystem. Higher group *OIs* in Gambia indicate fish groups with more diversified prey
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1 preferences as a response to seasonal environmental and biodiversity changes. It is
2 interesting to note that seven functional groups in Gambia have *OIs* greater than 0.25,
3 compared to only four groups in Sine-Saloum. Among these are mobile epibenthos
4 which consume plankton, benthos, crustaceans and organic materials.
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10 *Figure 3 here*

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12 *Network analyses*

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14 Fish and crustacean biomasses and ecological production at *TL2* is higher than at
15 *TL3* in Sine-Saloum. Biomass and catch are highest at *TL3* in Gambia. The production at
16 lower *TLs* are higher in Sine-Saloum compared to Gambia (Figure 3). *TEs* decline at
17 higher *TLs* in both ecosystems (Figure 4), which is similar to observations in other
18 tropical coastal ecosystems (Haputhantri et al. 2008; Van et al. 2010; Villanueva et al.
19 2006). *TEs* are higher in Sine-Saloum than in Gambia for *TLs* 2-3, but the trend reversed
20 itself for *TLs* 4-5, due to the difference of fish community roles in both ecosystems
21 (Figure 2). The geometric mean *TEs* are 8.2 and 15.8% for Sine-Saloum and Gambia,
22 respectively. The percentage of total flow originating from the detritus is similar for both
23 estuaries: 43% in Sine-Saloum and 42% in Gambia.
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39 *Figure 4 here*

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41 Trophic interspecific responses for Sine-Saloum and Gambia are shown in figure
42 4. For Sine-Saloum, the total consumption is estimated at 5,273 tkm⁻²yr⁻¹ (Table 3)
43 where 76% of flow from *TLs* 1-2 originates from primary producers, whereas detritus
44 contribute only 24%, with a detrivory: herbivory ratio (*D:H*) of 1:3.1. Most
45 phytoplanktonic production is incorporated into the food web by macrobenthos. The *TE*
46 is highest at *TL3* (9.0%) and decreases at higher *TLs*. In Gambia, the total food
47 consumption is lower and estimated at 1,317 tkm⁻²yr⁻¹ (Table 3). Energy transferred
48 from *TL1* is accessed mainly from the primary production (58%) by zooplankton and
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benthic organisms as compared to that coming from detritus (41%) with a $D:H$ ratio of 1:1.4. TE rate is highest in $TL2$ (19%) and decreases as TL increases. The mean catch TL is 2.59 in Sine-Saloum and is 3.10 in Gambia (Figure 3). Catch GE is lower in Sine-Saloum (0.001) than in Gambia (0.005). TST for each ecosystem (Table 3) is higher in the former than the latter.

The highest flow back to detritus is observed from autotrophs ($8,118 \text{ t km}^{-2} \text{ yr}^{-1}$) in Sine-Saloum and from $TL2$ ($376 \text{ t km}^{-2} \text{ yr}^{-1}$) in Gambia (Figure 4). Total ecosystem flow back to detritus in Sine-Saloum ($10,855 \text{ t km}^{-2} \text{ yr}^{-1}$) is 20 times higher than that observed in Gambia ($530 \text{ t km}^{-2} \text{ yr}^{-1}$). Exploitation flows are highest in $TL3$ in both ecosystems (5.8 and $2.0 \text{ t km}^{-2} \text{ yr}^{-1}$, respectively). The SOI value is slightly lower in Sine-Saloum (0.137) compared to Gambia (0.152). However, CI in Sine-Saloum (0.245) is almost twice that estimated for Gambia (0.192) which indicates a more complex, web-like feature of trophic structure in the former.

Table 3 here

In this study, Sine-Saloum is less mature than Gambia due to lower TPP/PR and B/TST values. Considering other attributes of ecosystem maturity and stability such as $PP-TR$ and PP/B , values obtained for Sine-Saloum are higher than those in Gambia which indicate that the latter is reaching a mature stage *sensu* Odum (1969).

Discussion

Estuarine biodiversity and species ecological roles

Similarities in hypo-halobic and cosmopolitan species are mainly due to close biogeographic location of both systems. Dissimilarities in species occurrence and abundance may be due to specific hydrologic regimes occurring in each ecosystem (Baran 2000) and on their capacities of adaptation (Milton 2009). Both models show several common functional groups that occupy differing TL in each ecosystem (Tables 1

1 and 2) which may imply differences in ecological roles and ecosystem utilization. High
2 biodiversity in estuaries can be attributed to various productive ecotones that can
3 accommodate different biological populations (Cognetti and Maltagliati 2000). Resource
4 utilization and ecological interactions are highly dependent on habitat heterogeneity and
5 may explain deviation in trophic guilds and behaviors of similar taxonomic groups in
6 different ecosystems (Villanueva et al. 2006).
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14 Estuarine processes and lifecycles of estuarine organisms are strongly influenced
15 by physiochemical, hydrological and seasonal variations, thus, making these ecosystems
16 highly unstable and 'stressful'. Variations may either be naturally- or anthropogenically-
17 induced, or both, leading to either positive or negative changes in biological assemblages.
18 Seasonal marine and freshwater inflows are natural sources of variability and play
19 significant roles in the various aspects of an organism's life cycle. Species usually have a
20 higher capacity for adaptation due to exposure to constantly varying hydrologic
21 conditions (Blaber 2002; James et al. 2013).
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33 Sine-Saloum, where a severe and long-term hydroclimatic change occurred, is
34 mainly inhabited by species of marine affinity (Figure 2b). Most hypersaline waters are
35 associated with low biodiversity since, for most species, such extreme environments
36 impose additional biological and physiological challenges (Brauner et al. 2013).
37 Estuarine species of freshwater origin (i.e., *Chrysichthys* spp) have disappeared and the
38 estuary is occupied by euryhaline fish assemblages (Baran 2000; Simier et al. 2004).
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48 Taxonomic changes usually lead to structural and functional diversities (Villéger
49 et al. 2010). Despite species diversity alterations, constant water hypersalinity conditions
50 in Sine-Saloum seems to offer stabilized habitats/conditions for tolerant biological
51 communities and has stabilized fish populations. High diversity, productivity and
52 resilience of fish species to hypersalinity stress may also be driven by the presence of
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'belongs' (Guèye et al. 2012), which are suitable places for refuge, limiting fish predation and niche competition (Vidy et al. 2004). In Gambia, these creeks function mainly as conduits that facilitate fish movements on and off the floodplain (Louca et al. 2008).

Fish biodiversity in Gambia is lower (89) compared to that observed in Sine-Saloum (Albaret et al. 2004). Overall species richness (Figure 2), however, is higher due to seasonal incursions of both marine and freshwater fish populations. These incursions, however, may be limited by dispersal opportunities depending on hydrodynamic conditions (Baran 2000). In Gambia, diversity and production are positively correlated where differences in distribution and eco-physiological characteristics increase efficiency of energy utilization. In Sine-Saloum, in contrast, a negative correlation can be observed due to the strong spatial zonation which may limit access and efficient use of available resources. High diversity can enhance ecosystem reliability through increase in redundant species per functional group. Some groups occupying a specific *TL* maintain ecosystem functioning by compensating for temporary loss of other groups performing similar roles or occupying the same *TL* (Naeem and Li 1997). This might explain higher *SOI* in Gambia despite seasonal temperature and fluvial inflow changes.

In both ecosystems, species belonging to three families Clupeidae (*Ethmalosa fimbriata*, *Ilisha africana*, *Sardinella aurita* and *S. maderensis*), Mugilidae (*Liza* spp and *Mugil* spp) and Cichlidae (*S. melanotheron* and *Tilapia guineensis*) are most abundant (Tables 1 and 2). In Sine-Saloum, these species appear to have developed adaptive mechanisms in order to persist under such stress. Their acclimatization is highly facilitated by their elevated capacity for osmoregulation, plasticity (Güner et al. 2005; Lorin-Nebel et al. 2012; Prunet and Bornancin 1989), which enables wide-range distributions (Guyonnet et al. 2003).

1 Clupeids abundance and distribution are significantly different in these estuaries.
2 In Gambia, they are abundant along the mouth with relatively large seasonal oscillation,
3 and decreasing abundance further upstream (Guillard et al. 2004). In Sine-Saloum,
4 clupeids and cichlids are the most dominant fish species. *S. maderensis* has been
5 observed to dominate areas with salinities >60 psu (Guillard 1998; Simier et al. 2004),
6 showing that high water salinity does not limit their distribution.
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14 The high versatility of *S. melanotheron* especially with regard to diet and habitat
15 plasticity is well documented (Adité and Winemiller 1997; Gnohossou et al. 2013; Pauly
16 et al. 1988), as well as its high tolerance of stress (Duponchelle and Panfili 1998;
17 Duponchelle et al. 1998; Guèye et al. 2012; Panfili et al. 2004b). Tilapias are able to
18 adapt and occupy hypersaline zones (>100 psu) in Sine-Saloum (Villanueva 2004).
19 Guèye et al. (2012) reported threshold hypo- or hypersaline conditions beyond which
20 stunted growth and precocious reproduction occur. Successful acclimatization to highly
21 perturbed systems has been observed in Sakumo (Pauly 2002), Ébrié (Konan-Brou and
22 Guiral 1994), Muni (Koranteng et al. 2000) and Toho-Todougba lagoons (Adité and
23 Winemiller 1997). In Gambia, tilapias are present, though less abundant, and have a
24 higher probability of occurrence along stenohaline and euryhaline zones (Guillard et al.
25 2004). Here, abundance and occurrence may be influenced by river discharges which
26 increases availability of food (Amogu et al. 2010; Louca et al. 2008) similar to
27 observations in South African estuaries (Whitfield and Harrison 2003). In both
28 ecosystems studied, tilapias consume detritus and bacteria, especially in degraded
29 habitats, as reported from other West African brackish waters (Gnohossou et al. 2013;
30 Pauly 2002; Villanueva et al. 2006).
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1 Ecosystem functioning can be better viewed in terms of biomass fluxes between
2 *TLs*. Predators and resource availability can cause direct changes of diversity from one
3 *TL* to the next (Nielsen 2001). This suggests that flow rates between predators and preys
4 may vary as a function of limiting conditions or variables (Powers et al. 2003; Taylor et
5 al. 2014). Higher biomasses were estimated for most functional groups in Gambia.
6 Despite their higher abundance in Sine-Saloum, biomasses are low, as individual fish size
7 are smaller than those inhabiting Gambia (Panfili et al. 2006). Fishes inhabiting
8 hypersaline waters usually have a metabolic rate 40% lower than those found in seawater.
9 Possible trade-offs with fish performance traits can include osmo-respiratory compromise
10 in gill size, muscle fibre size, trait maintenance of energetic costs and gene expression
11 modifications (Johnston et al. 2005; Lorin-Nebel et al. 2012; Sardella and Brauner 2007).

12 Estuaries have either a detritus- or phytoplankton-based food chain (Gearing et al.
13 1984; Maier et al. 2011). Primary producers and detritus are energy sources that play
14 differing roles and significance in the diet of groups of higher *TLs* in these ecosystems.
15 Results showed that phytoplankton is the key food source in both ecosystems (Figures 4).
16 Elevated biomasses at *TL1* in both ecosystems show its significant role in supporting
17 species at higher *TLs*. Phytoplankton productivity is usually low in euryhaline waters as
18 tidally imported seawaters have limited nutrient loading (Adams 1994). Productivity,
19 however, is maintained in water salinities <40 psu (Schlacher and Wooldridge 1996).
20 Lower utilization of primary production by zooplankton in Sine-Saloum may be due to
21 the hypersalinity and temperature limiting effects on phytoplankton productivity and
22 impose species composition changes. Microorganisms (halophilic algae and bacteria) can
23 proliferate under such stress (Gunde-Cimerman et al. 2000). Deficiencies may also be
24 complemented by productions from dense mangrove forests fueling grazing pathways
25 similar to Orbetello (Brando et al. 2004) and Terminos lagoons (Rivera-Monroy et al.

1998). Zooplankton density and species richness are lowest in hypersaline areas of Sine-Saloum, as also reported from the Casamance (Debenay et al. 1989) and in Bardawil (Mageed 2006). Zooplankton communities (copepods, protozoa and mollusks) in these areas are strongly impacted and physiological constraints limit their abundance and distribution. Rotifer abundance seems low compared to other highly degraded West African brackish waters (Villanueva et al. 2006). In the Casamance estuary, zooplankton abundance and distribution decreased significantly in areas where salinity reached 70 psu (Diouf and Diallo 1987) and impacted zooplanktivores distribution (Debenay et al. 1989).

High primary productivity in estuaries may also be due to intense bacterial remineralization of organic matters and the continuous circulation of water and sediment nutrients which directly or indirectly regulate primary to secondary production (Sorokin et al. 1996), which is essentially the case in Gambia. In addition to nutrient loadings, seasonal river inflows lead to larger floodplains and diversified ecotones (Deegan and Garritt 1997; Louca et al. 2008). Freshwater inputs have positive effects on phytoplankton biomass and production (Adams 1994) in that fluvial hydrodynamics lead to vertical stratifications that retain system phytoplankton population. This process also releases the bulk of allochthonous or inorganic nutrients to estuarine primary producers.

In Sine-Saloum, poor utilization of *TL1* by *TL2* is indicated by the low phytoplankton transfer efficiency coupled with large flows back to detritus (Figures 4a). Primary link of *TL1* to *TL2* is mainly by epibenthos and herbivorous fish instead of zooplankton (Ngouda 1997). Zooplankton are rarely present in the diet of most planktivores, e.g., *E. fimbriata*. This visual-filtering clupeid has been observed in other estuaries as feeding mainly on zooplankton (Blay and Eyeson 1982). Stomach contents in Sine-Saloum contain large amounts of phytoplankton, especially in areas where salinity is <50 psu. Shrimps, crabs and some euryhaline fish tolerate such extreme conditions due to

1 their efficient osmoregulation capacity and may participate in *TL2* transfer to higher *TLs*
2 (Deegan et al. 2010; Guerin and Stickle 1992; Lin et al. 2002). However, other less
3 tolerant organisms may be inefficiently transferred to higher *TLs* due to hypersalinity
4 limitations. The transfer efficiencies from *TL2* may also be reduced by dense mangroves,
5 used as refuge zones that limit predation.
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11 In Gambia, zooplankton is the primary link of *TL1* to *TL2*, as in Ebrié (Villanueva
12 et al. 2006) and Huizache-Caimanero lagoons (Zetina-Rejón et al. 2003). Here, clupeids
13 consume mainly zooplankton with a slight tendency of herbivory during the rainy season,
14 which may explain lower flows back to the detritus (Figure 4b). Shift to a more
15 phytoplankton- or detritus-based feeding behaviour may be an adaptive response to
16 resource limitation. Substantial shift towards detritivory in other ecosystems coincide
17 mainly to strong river run-offs (Charles-Dominique 1982; Gnohossou et al. 2013) and
18 water salinities >50 psu (Villanueva 2004). Environmental degradation induced changes
19 in species' diets have already been observed in other ecosystems such as the Terminos
20 Lagoon (Villéger et al. 2010).
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36 The importance of herbivory in both ecosystems is high, in accordance with
37 Ngouda (1997), who demonstrated that even clupeid species such as the *S. maderensis*,
38 *E. fimbriata* and *I. africana* consume large amount of phytoplankton. Clupeids in these
39 ecosystems consume zooplankton in lower proportions compared to other West African
40 brackish waters (Adité and Winemiller 1997; Charles-Dominique 1982).
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49 Aside from physiological and biochemical mechanisms, fish tolerance to
50 environmental stress is high for omnivores which are able to feed on a larger range of
51 prey types and are important predators in highly unstable systems (Villanueva et al.
52 2006). Omnivory in a food web structure is of primary importance, as it can either
53 contribute to ecosystem stability or instability (Vandermeer 2006). This can take the form
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1 of top-down control mechanism through strong predation, or via fishery (Bascompte et al.
2 2005) and may prevent species extinction by providing a wider range of prey choice to
3 predators (Strong 1992). In other estuaries, trophic shifts from omnivory to grazing or
4 detritivory have been observed as an adaptive response to severe resource limitations (Fox
5 et al. 2009; Villanueva et al. 2006).

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11 A greater interspecific resource partitioning seems to occur in Gambia than in
12 Sine-Saloum. In Sine-Saloum, fish species with strong marine water affinities (Em and
13 ME) have the highest *OIs*, while strictly estuarine and accessory fish species (Es and
14 Ma) have more specialized feeding habit (Table 1). In Gambia, at least one fish
15 functional group, usually with a high biomass, per ecological category has high *OI*
16 (Table 2) which may explain slightly higher *SOI*. Similar results were observed in Ebríe
17 Lagoon (Villanueva et al. 2006) and Shoalhaven River (Taylor et al. 2014). Low *CI*
18 coupled with a slightly elevated *SOI* may indicate an ecosystem less dependent on
19 detritus as energy source (Heymans et al. 2004). Here, mangroves and terrestrial
20 vegetation contribute to organic material productions complementing ecosystem
21 phytoplankton production deficiencies (Bouillon et al. 2008).

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39 Estuaries are very dynamic, and change and disturbance can be seen as natural
40 features of these ecosystems (Bengtsson et al. 2000); thus, it seems paradoxal to describe
41 them as stable systems (Mikkelsen 1999). However, quantifying ecosystem changes and
42 dynamics as a response to stress can be a gauge to evaluate ecosystem stability observed
43 in mature systems (Odum 1969). Ecosystem interaction strength can be measured based
44 on connectance (weighted number of nonzero entries in the flow matrix), such that more
45 complex energetic flow network means higher ecosystem stability (Grimm et al. 1992).
46 Length (absence or presence of predators) and strength (connectivity) of trophic links
47 can also affect ecosystem stability. Higher *CI*s and *SOI* estimated in Sine-Saloum
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1 indicate that it is more stable and has a higher resilience to stress than Gambia, despite
2 similarly high biodiversity. Shorter, but stronger interaction strengths in Sine-Saloum
3 may explain ecosystem stability despite strong environmental degradation coupled with
4 overexploitation compared to other West African brackish water ecosystems (Villanueva
5 et al. 2006). Ecosystem *TLs* is high along the estuary mouth due to high biological
6 diversity which decreases exponentially in hypersaline areas. Villanueva (2004)
7 indicated that food web structure in this estuary become shorter and less complex in
8 areas where salinity values exceed 60 psu. In these hypersaline zones, very few species
9 exist (Simier et al. 2004). Among fish species, only *S. melanotheron* is observed
10 throughout the year. An ecosystem adaptive response under stress may lead to shorter,
11 but stronger trophic interaction strengths among species. Simplification of trophic links
12 (fewer predator-prey links) had been observed in highly stressed aquatic ecosystems
13 (Moreau et al. 2001; Villanueva et al. 2006). Higher omnivory and
14 shortening/strengthening of food chain lengths seem to increase in ecosystem stability
15 (Long et al. 2011).
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36 The *TPP/TR* ratio in Sine-Saloum is high where total system respiration
37 approaches its production, which is a common feature in highly stressed systems.
38 According to Pagés et al. (1995), dissolved inorganic carbon concentrations decrease in
39 hypersaline estuaries due to phytoplankton sedimentation, biological calcification or
40 carbon loss from fish exportation leading to overall system high respiration rates. This is
41 not, however, the case in Gambia. The estimated *TST* in Sine-Saloum (27,938 tkm⁻²yr⁻¹)
42 is considerably higher than that estimated in Gambia (2,585 tkm⁻²yr⁻¹). *TST* estimates in
43 this study are comparable to values obtained by Christensen and Pauly (1993) for coastal
44 ecosystems, while lower than that obtained by Villanueva et al. (2006) in Lake Nokoué
45 (57,967 tkm⁻²yr⁻¹) and Lin et al. (1999) in Chiku lagoon, China.
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System *A* and *TST* can be used as an indicator of degradation in an ecosystem (Patrício et al. 2004). This is characterized by an increased value in *A*, as a function of elevated *TST* parallel to a decline in *I* (Ulanowicz, 1986). In Sine-Saloum, an elevated *A* is compensated by a low value of *I* indicating higher degradation in the system, in contrast to Gambia, where *A* and *I* are low (Table 3).

Energy and matter recycling is considered as an important process in ecosystem functioning (Odum 1969) and is measured as *FCI*. According to Heymans and Baird (2000), value of this index is between 4-15% for coastal ecosystems. Estimated *FCI* value in Gambia is much higher than in Sine-Saloum (Table 3). It is, however, relatively low compared to that obtained by Villanueva et al. (2006) in other West African lagoons. Slightly higher value of Finn's straight-through path length (excluding detritus) in Sine-Saloum (2.82) suggests a shorter food chain perhaps due to shifting of diets of other groups towards detritivory, especially in hypersaline zones where primary production is strongly limited.

TEs from one *TL* to the next are generally lower in Sine-Saloum compared to the Gambia estuary (Figures 4). A large bulk of energy from *TL1* is not effectively transferred to higher *TLs*. According to Lindeman (1942), only 10% of net production from lower *TL* is generally transferred to higher *TL*. Instead of being consumed, a significant amount of energy is lost due to non-predatory processes such as egestion, respiration and mortality. Most energy in Sine-Saloum is significantly lost either in respiration and flows back to detritus. In Gambia, on the other hand, energy losses per *TL* transfer are proportionally lower. This may explain the higher *GE* value calculated in Gambia compared to Sine-Saloum (Table 3). *GEs* are lower than the values obtained by Lin et al (1999) in Chiku lagoon.

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Apart from various industrialized and agricultural activities, over-fishing is responsible for a wide variety of impacts on fish communities, including modification of population composition and ecosystem adaptations to a changing environment due to stress conditions. In both estuaries, fisheries are mainly artisanal (Bouso 1996; Laë et al. 2004). Despite severe hydrologic changes due to climate change, annual catches are almost 4 times higher in Sine-Saloum (12.057 tkm²) than in Gambia (3.359 tkm²). Higher fish production in more degraded brackishwater ecosystems has already been observed by in Lake Nokoué where annual fish production can reach up to 102 tkm² (~85% of this is the acadja-grown *S. melanotheron*) despite strong degradations (Villanueva et al. 2006).

In Sine-Saloum, catches are highest in *TLs* 2 and 3 estimated at 5.7 and 5.8 tkm⁻²yr⁻¹, respectively (Figure 3a). *E. fimbriata* dominates by 80% the total landings followed by mullets (6%). Other target species include mollusks (2,601 t·yr⁻¹) such as *Arca senilis*, murex, oysters and cymbium (Ba et al. 2006). In Gambia, catch is highest in *TL3* (Figure 3b) mainly due to significant fish and shrimp artisanal fisheries by foreign/migrating fishermen from Senegal, Mali and Guinea. Recent estimates indicate that annual catch is 2,350 tonnes (77% fish and 23% shrimps). Fifty-five fish species were captured mainly using selective gears in this estuary but only 1/3 of these accounted for 90% of the annual catch (Laë et al. 2004). *Polydactylus quadrifilis* and *Arius* spp. are the two main targeted fish species representing 26 and 20% of total fish landings, respectively.

Tropical estuaries and brackish ecosystems are constantly exposed to both long-term trends and rapid environmental changes. Biological organisms inhabiting these ecosystems have evolved under these changing environmental conditions while less tolerant species have become extinct (Baran 2000; Blaber 2002; Diouf 1996; Guèye et al. 2012). These ecosystems are often characterized by complex food webs and inhabiting

1 biological communities have high eco-physiological capacities against extremely varying
2 environmental conditions, in both space and time (Albaret et al. 2004; Villanueva et al.
3 2006). Levels of fish structure organizations in these ecosystems can be complex
4 although frequent food web restructuration occurs due to seasonal variations, prey
5 limitations and habitat modifications (Cloern and Jassby 2012; Fox et al. 2009;
6 Winemiller and Jepsen 1998).

14 **Conclusions**

16 Global climate change and continued anthropogenic-driven environmental
17 degradations contribute to biodiversity loss coupled with species extinctions (Sala et al.
18 2000; Stork 2009). Fishes and macroinvertebrates are very good environmental indicators
19 to track environmental health and ecological changes as adaptive response to stress,
20 especially in estuaries and lagoons (Elliot and Quintino 2007; Whitfield and Elliot 2002).
21 Ecosystem-level indicators include several structural attributes such as food web
22 complexities, energetic transfer efficiencies, species trophic links, system omnivory,
23 maturity and interaction length just to enumerate some. Such food web properties have
24 been proposed as determinants in ecosystem stability (Rambouts et al. 2013).

25 Debates on how biodiversity contributes to ecosystem stability exist in several
26 literatures (Mooney 2002; Naeem 2002). Some indicate that high biodiversity ensures
27 ecosystem stability through the multiplication of trophic roles by different species. In
28 ecosystems where frequent seasonal species migrations or stress may occur, ecological or
29 functional redundancy may ensure ecosystem stability through functional replacement of
30 a particular species or community by another (Rosenfeld 2002). A negative effect of high
31 biodiversity on ecosystem integrity can also be observed in other ecosystems. In highly
32 unstable environments, biodiversity reduces variability in ecosystem productivity through
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1 compensatory effects where species abundance may increase as a response to a decrease
2 of another (Naeem and Li 1997; Thébault and Loreau 2006).
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5 Often, low species biodiversity can be observed in highly degraded ecosystems.
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7 This was not the case for the Sine-Saloum estuary where biodiversity remains elevated
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9 despite severe hydrodynamic changes. High biological diversity may largely contribute to
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11 ecosystem stability despite the regime shift as a response to climate change (Folke et al.
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13 2004). System integrity may have been weakened due to extinctions and restructuration
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15 following freshwater inputs cutoff as other inhabiting species learned to adapt over time.
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17 Ecosystem stability seems maintained in highly stressed areas through further
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19 simplification of food web structure and increased recycling of organic matter. Coupled
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21 with strong anthropogenic degradation, Villanueva et al. (2006) reported when comparing
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23 two West African lagoons that ecosystem adaptation takes the form of a simplification of
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25 energetic links among biological communities under stressed conditions. In the Gambia
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27 estuary, on the other hand, biodiversity seems to promote production by maintaining
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29 ecosystem integrity through ecological/functional role redundancies of some groups
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31 occupying the same *TL* (i.e., marine or estuarine fish predators by freshwater predators)
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33 against seasonal hydrodynamic and anthropogenic stresses coupled with high *FCI*.
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41 Both ecosystems are phytoplankton-based as primary production showed a
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43 positive effect in supporting groups in higher *TLs*. Fish species in both estuaries showed
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45 wider niche diversifications and high structural organization of biological communities.
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47 Commercially important top fish predators were more sensitive to short-term pulsed
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49 events compared to lower level fish species. Most fish species in both ecosystems have
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51 opportunistic and omnivorous feeding habits that increase their survival and tolerance in
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53 such highly unstable environments.
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1 Both estuaries have complex food webs due mainly to numerous species utilizing
2 these ecosystems for food, shelter and reproduction. Food web snapshots in this study
3 indicate that both ecosystems are resilient to environmental stress and change, allowing
4 maintenance of a functional ecosystem across seasonally-driven changes in
5 environmental conditions and species assemblages and biomass. Biodiversity contributes
6 by increasing trophic structure complexity in both estuaries but compared to Sine-
7 Saloum, trophic links in Gambia seem more fragile due to seasonal trophic
8 restructuration.
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10 This study has also shown how regime shifts due to climate change and fisheries
11 can impact ecosystem health and stability in a tropical estuary. A severe regime shift
12 occurred in Sine-Saloum following the El Niño drought leading to marked shifts in trend,
13 profoundly changing estuarine fauna and dynamics. Although the occurrence of
14 freshwater forms completely disappeared, taxonomic richness and biodiversity in the
15 estuary is as rich as in adjacent estuaries. Acclimatized species undergo drastic
16 physiological and genetic adaptations (i.e., stunted sizes, higher osmoregulation, delayed
17 reproduction, diet shifts) to survive and multiply. These, however, are not sufficient
18 compensations for loss of freshwater biological diversity. At the ecosystem level,
19 structure and internal ecological processes have evolved. Water hypersalinity in Sine-
20 Saloum impose severe additional stress on biological assemblages leading to unfavorable
21 system energetic flows. Results show that despite the regime shift, this estuary has
22 evolved and dynamics have reached another level of system integrity. Based on
23 ecosystem indicator results, Sine-Saloum seems slightly more stable mainly due to the
24 'long-term' abundance of highly adapted species that drive recovery processes under
25 severe hydrodynamic perturbation. Due to short-term and seasonal marine-freshwater
26 inflow shocks, Gambia undergoes seasonal food web restructuration that may impose
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1 decreasing resilience to recurring stress. Ecosystem ecological indicators considered in
2 the study have already been used on other brackish water ecosystem health comparative
3 and quality assessments
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7 Anthropogenic stressors in West Africa are projected to increase due to
8 exponential human population increase. This analysis illustrates the significance of sound
9 estuarine structure description is crucial in understanding its dynamics and functioning.
10 Understanding how the loss or reduction of a predator or prey, as well as, energetic links
11 connecting them may affect ecosystem functioning is relevant especially on providing
12 knowledge on the likely impact of anthropogenic related activities on ecosystem health.
13 Such information is useful for refining future environmental management plans for
14 estuarine biodiversity conservation.
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Table 1. Basic inputs and estimated outputs (bold) of the Sine-Saloum estuary model. For fish groups with more than one species, a key species is considered and is indicated by (*). *EC*: Ecological category; *TL*: Trophic level; *B*: biomass; *P/B*: Production rate; *Q/B*: Consumption rate; *Y*: landings and *OI*: Omnivory index

	Group name	Code	EC	TL	<i>B</i> (tkm ²)	<i>P/B</i> (tkm ² yr ⁻¹)	<i>Q/B</i> (tkm ² yr ⁻¹)	<i>Y</i> (tkm ² yr ⁻¹)	<i>OI</i>
1	<i>Sphyraena guanchancho</i> *	SPI	ME	3.7	0.030 ^a	1.700 ^d	8.645 ^j	0.034 ^o	0.082
2	<i>Scomberomorus tritor</i>	CTR	Ma	3.8	0.049 ^a	0.650 ^e	6.821 ^j	0.015 ^o	0.084
3	<i>Polydactylus quadrifilis</i>	POQ	ME	3.6	0.026 ^a	1.540 ^d	9.272 ^j	0.002 ^o	0.126
4	<i>Galeoides decadactylus</i> *	GDE	ME	3.4	0.363 ^a	3.280 ^e	16.820 ^j	0.461 ^o	0.079
5	<i>Pseudotolithus elongatus</i>	PEL	Em	3.5	0.241 ^a	0.750 ^e	6.944 ^j	0.075 ^o	0.085
6	<i>Pseudotolithus brachygnathus</i> *	PBR	ME	3.6	0.092 ^a	1.280 ^e	7.294 ^j	0.057 ^p	0.057
7	<i>Elops lacerta</i> *	ELA	ME	3.6	0.056 ^a	1.820 ^e	13.877 ^j	0.048 ^o	0.101
8	<i>Arius latiscutatus</i> *	AGA	ME	3.4	0.090 ^a	2.655 ^e	7.530 ^j	0.201 ^p	0.132
9	<i>Pomadasys jubelini</i> *	PJU	ME	3.2	0.174 ^a	1.350 ^d	12.064 ^j	0.171 ^o	0.123
10	<i>Chloroscombrus chrysurus</i>	CHL	ME	3.2	0.154 ^a	2.490 ^e	19.696 ^k	0.194 ^p	0.209
11	<i>Caranx hippos</i> *	CHI	ME	3.5	0.019 ^a	1.585 ^f	16.969 ^j	0.002 ^o	0.051
12	<i>Trachinotus teraia</i> *	TFA	Em	3.3	0.045 ^a	0.611 ^f	8.445 ^j	0.001 ^o	0.081
13	<i>Citarichthys stampflii</i>	CST	Em	3.6	0.029	1.649 ^f	14.284 ^j	0.017 ^p	0.014
14	<i>Cynoglossus senegalensis</i> *	CYS	Em	3.3	0.039	1.210 ^f	10.346 ^j	0.017 ^p	0.093
15	<i>Eucinostomus melanopterus</i> *	GME	ME	3.0	0.098 ^a	1.590 ^e	12.883 ^j	0.067 ^o	0.257
16	<i>Drepane africana</i> *	DAF	ME	2.8	0.143 ^a	1.680 ^e	9.291 ^j	0.073 ^p	0.308
17	<i>Dasyatis margarita</i> *	DMA	Em	3.2	0.069 ^a	0.733 ^f	4.613 ^j	0.007 ^p	0.139
18	<i>Ilisha africana</i>	IAF	Em	3.0	0.426 ^a	1.510 ^e	16.059 ^k	0.221 ^o	0.271
19	<i>Brachydeuterus auritus</i>	BAU	ME	2.7	0.188 ^a	4.680 ^e	20.509 ^j	0.577 ^o	0.233
20	<i>Epinephelus aeneus</i> *	EAE	ME	3.2	0.191	0.748 ^f	6.992 ^k	0.004 ^p	0.150
21	<i>Hemiramphus brasiliensis</i> *	HBR	ME	2.3	0.035 ^a	1.117 ^f	13.250 ^k	0.005 ^p	0.242
22	<i>Pellonula leonensis</i>	PEF	Ec	3.3	0.259	3.080 ^f	28.994 ^j	0.000 ^o	0.071
23	<i>Trichiurus lepturus</i>	TLE	Ma	3.2	0.027 ^a	0.420 ^e	4.163 ^j	0.002 ^p	0.073
24	<i>Monodactylus sebae</i>	PSB	Es	3.2	0.024 ^a	1.910 ^e	16.724 ^k	0.007 ^p	0.064
25	<i>Ethmalosa fimbriata</i>	EFI	Em	2.6	0.630 ^a	2.510 ^e	13.971 ^j	0.922 ^o	0.268
26	<i>Sardinella maderensis</i> *	SEB	ME	2.7	2.413 ^a	3.050 ^e	18.975 ^j	4.549 ^o	0.227
27	<i>Liza grandisquamis</i> *	LFA	Em	2.7	0.426 ^a	1.080 ^e	11.464 ^j	0.092 ^o	0.244
28	<i>Sarotherodon melanotheron</i>	THE	Es	2.0	2.719 ^a	2.480 ^e	32.467 ^j	3.086 ^o	0.022
29	<i>Tilapia guineensis</i>	TGU	Es	2.0	0.073 ^a	2.400 ^e	35.264 ^k	0.101 ^p	0.043
30	Shrimps	SHR	Em	2.5	2.815	4.605 ^g	22.000 ^l	1.050 ^q	0.284
31	Crabs	CRA	Em	2.7	1.858	2.500 ^h	8.500 ^l	-	0.232
32	Macrobenthos	MAC		2.0	93.000 ^b	1.200 ^b	10.000 ^b	-	0.010
33	Meiobenthos	MEI		2.1	19.600 ^b	4.000 ^b	50.000 ^m	-	0.110
34	Zooplankton	ZOO		2.1	20.636 ^b	50.000 ⁱ	150.000 ⁿ	-	0.053
35	Phytoplankton	PPL		1.0	82.000 ^b	138.189 ^h	-	-	-
36	Phytobenthos	PBE		1.0	32.158	15.000 ^b	-	-	-
37	Detritus	DET		1.0	1.000 ^c	-	-	-	-

(a) Estimated from experimental fishing (Diouf 1996 ; Simier *et al.* 2003); (b) From Samb and Mendy (2003) ; (c) Based on a primary production multiple regression predictive model and euphotic zone depth (Pauly *et al.* 1993) ; (d) Estimated from Lévêque *et al.* (1977) ; (e) From Albaret (1987) and (Simier *et al.* 2003) using FiSAT (Gayaniilo *et al.* 2002) ; (f) Estimated from de Merona (1983) and Frøese and Binohlan (2000) ; (g) Average P/B values obtained by Lhomme and Garcia (1984) of 4.2 and by Pauly (1982) of 5.01 ; (h) From Abaca-Arenas and Valero-Pacheco (1993) ; (i) From Pagano and Saint-Jean (1994) ; (j) Food consumption obtained using the predictive model of Palomares and Pauly (1998) from estimated aspect ratio values ; (k) Obtained from the predictive model of Palomares and Pauly (1998) using aspect ratio values obtained from Fishbase (Frøese et Pauly 2014) ; (l) Q/B adopted from Arreguín-Sánchez *et al.* (1993) ; (m) From Chavez *et al.* (1993) ; (n) From Browder 1993 ; (o) Unpublished data from CRODT/ISRA; (p) Estimated as a function of biomass and fishing mortality coefficient (*F*), $Y=B/F$; and (q) From Bah *et al.* (2010) and Ziegler *et al.* 2011.

Table 2. Basic inputs and outputs (bold) of the Gambia estuary model. For fish groups with more than one species, a key species is considered and is indicated by (*). *EC*: Ecological category; *TL*: Trophic level; *B*: biomass; *P/B*: Production rate; *Q/B*: Consumption rate; *Y*: landings and *OI*: Omnivory index.

	Group name	Code	CE	TL	B (t km^{-2})	P/B (t $\text{km}^{-2}\text{yr}^{-1}$)	Q/B (t $\text{km}^{-2}\text{yr}^{-1}$)	Y (t $\text{km}^{-2}\text{yr}^{-1}$)	OI
1	<i>Sphyraena afra</i> *	SPI	ME	3.8	0.095	1.110 ^d	11.900 ⁱ	0.053 ^k	0.173
2	<i>Polydactylus quadrifilis</i>	POQ	ME	3.3	1.509 ^a	0.850 ^e	4.519 ⁱ	0.688 ^l	0.114
3	<i>Galeoides decadactylus</i> *	GDE	ME	3.4	0.181 ^a	2.390 ^e	16.465 ⁱ	0.142 ^l	0.062
4	<i>Pseudotolithus elongatus</i>	PEL	Em	3.5	0.257 ^a	1.630 ^e	9.053 ⁱ	0.236 ^l	0.128
5	<i>Pseudotolithus senegalensis</i> *	PSN	Ma	3.6	0.405 ^a	0.680 ^e	4.495 ⁱ	0.134 ^k	0.081
6	<i>Elops lacerta</i> *	ELA	ME	3.3	0.104	0.860 ^e	9.109 ⁱ	0.019 ^k	0.080
7	<i>Arius latiscutatus</i> *	AGA	ME	3.4	1.613 ^a	1.140 ^f	10.117 ⁱ	0.534 ^l	0.071
8	<i>Pomadasy jubelini</i> *	PJU	Em	3.4	0.105	0.953 ^f	10.409 ⁱ	0.069 ^k	0.034
9	<i>Chloroscombrus chrysurus</i>	CHL	ME	3.1	0.005	3.950 ^e	25.291 ⁱ	0.005 ^k	0.175
10	<i>Caranx hippos</i> *	CHI	ME	3.5	0.040 ^a	0.700 ^e	10.449 ⁱ	0.008 ^l	0.081
11	<i>Trachinotus teraia</i> *	TFA	Em	3.3	0.039 ^a	0.760 ^e	6.185 ⁱ	0.012 ^l	0.326
12	<i>Citarichthys stampflii</i>	CST	Em	3.5	0.005	2.413 ^f	17.988 ⁱ	0.000 ^k	0.034
13	<i>Cynoglossus senegalensis</i> *	CYS	Em	3.3	0.463 ^a	0.570 ^e	5.768 ⁱ	0.100 ^l	0.155
14	<i>Eucinostomus melanopterus</i> *	GME	ME	3.1	0.066	1.643 ^f	15.621 ⁱ	0.001 ^k	0.155
15	<i>Drepane africana</i> *	DAF	ME	2.8	0.042 ^a	1.170 ^f	7.880 ⁱ	0.016 ^k	0.384
16	<i>Dasyatis margarita</i> *	DMA	Em	3.4	0.107 ^a	0.706 ^f	7.122 ⁱ	0.022 ^l	0.080
17	<i>Ilisha africana</i>	IAF	Em	3.1	0.032 ^a	3.400 ^e	18.436 ⁱ	0.067 ^l	0.146
18	<i>Brachydeuterus auritus</i>	BAU	ME	3.1	0.016	2.340 ^f	19.684 ⁱ	0.001 ^k	0.020
19	<i>Hemichromis fasciatus</i> *	EAE	Ec	3.3	0.212 ^a	0.800 ^f	8.668 ⁱ	0.058 ^l	0.072
20	<i>Schilbe intermedius</i> *	SIN	Ce	3.1	0.003	1.690 ^f	16.093 ⁱ	0.000 ^k	0.199
21	<i>Strongylura senegalensis</i> *	BES	Em	3.2	0.005	0.725 ^f	12.307 ⁱ	0.000 ^k	0.117
22	<i>Hydrocynus forskalii</i> *	HOD	Co	3.3	0.381 ^a	0.737 ^e	7.824 ⁱ	0.008 ^l	0.175
23	<i>Pellonula leonensis</i>	PEF	Ec	3.2	0.010	2.716 ^f	29.505 ⁱ	0.000 ^k	0.066
24	<i>Chrysichthys auritus</i> *	CNI	Ec	3.3	0.203 ^a	0.730 ^e	6.548 ⁱ	0.041 ^k	0.022
25	<i>Trichiurus lepturus</i>	TLE	Ma	3.2	0.079	0.440 ^f	4.368 ⁱ	0.003 ^k	0.288
26	<i>Synodontis gambiensis</i> *	SYG	Ce	2.8	0.007	4.170 ^f	21.508 ⁱ	0.003 ^k	0.314
27	<i>Monodactylus sebae</i>	PSB	Es	3.1	0.079 ^a	1.660 ^e	15.348 ⁱ	0.011 ^k	0.027
28	<i>Ethmalosa fimbriata</i>	EFI	Em	2.7	1.094	1.400 ^e	9.063 ⁱ	0.106 ^k	0.281
29	<i>Sardinella maderensis</i> *	SEB	ME	3.0	0.268	5.260 ^f	27.707 ⁱ	0.001 ^k	0.123
30	<i>Liza grandisquamis</i> *	LGR	Em	2.4	0.591 ^a	1.660 ^f	14.523 ⁱ	0.152 ^l	0.251
31	<i>Tylochromis jentinki</i>	TJE	Es	3.0	0.130	1.738 ^f	11.724 ⁱ	0.000 ^k	0.300
32	<i>Sarotherodon melanothron</i>	THE	Es	2.1	0.640	1.740 ^e	22.616 ⁱ	0.042 ^k	0.080
33	<i>Tilapia guineensis</i>	TGU	Es	2.0	0.284	1.902 ^e	43.794 ⁱ	0.001 ^k	0.024
34	Shrimps	SHR	Es	2.6	1.436	3.000 ^b	22.000 ^b	0.821 ^m	0.373
35	Crabs	CRA	Es	2.8	5.794	2.000 ^b	8.000 ^j	0.006 ^k	0.404
36	Macrobenthos	MAC		2.4	9.016	5.000 ^b	20.000 ^b	-	0.239
37	Meiobenthos	MEI		2.0	6.073	10.383 ^g	48.763 ⁱ	-	0.001
38	Zooplankton	ZOO		2.1	5.500 ^b	30.000 ^g	120.000 ^b	-	0.111
39	Phytoplankton	PPL		1.0	6.000 ^c	96.853 ^h	-	-	-
40	Phytobenthos	PBE		1.0	10.500 ^b	15.000 ^b	-	-	-
41	Detritus	DET		1.0	1.832 ^c	-	-	-	-

- (a) Estimated from Guillard et al. 2004 and Mendy 2005 ; (b) From Mendy (2003) ; (c) Based on a primary production multiple regression predictive model and euphotic zone depth (Pauly *et al.* 1993) ; (d) From Ndiaye *et al.* 2003 using predictive model of Fröese and Binohlan (2000) ; (e) Value estimated from Ndiaye *et al.* 2003 using FiSAT (Gayanilo *et al.* 2002) ; (f) Value from Simier *et al.* 2003 ; (g) Manickchand-Heileman *et al.* (1998) ; (h) Healey *et al.* (1985) ; (i) Obtained using the predictive model of Palomares and Pauly (1998) from estimated aspect ratio values ; (j) Arreguín-Sánchez *et al.* (1993) ; (k) FAO 1997 and Mendy 2005 ; (l) FAO 1997 and Njai 2000 complemented with unpublished data; and (m) From Laë *et al.* (2004) and Mbye 2005.

Table 3. Summary statistics and network flow indices of the two ecosystems considered.

Parameter	Value	
	Sine-Saloum	Gambia
<i>Ecosystem theory indices</i>		
Sum of all consumption ($\text{t km}^2\text{yr}^{-1}$)	5273.320	1317.033
Sum of all exports ($\text{t km}^2\text{yr}^{-1}$)	9677.043	81.547
Sum of all respiratory flows ($\text{t km}^2\text{yr}^{-1}$)	2138.531	657.071
Sum of all flows into detritus ($\text{t km}^2\text{yr}^{-1}$)	10855.340	529.494
Total system throughput (TST. $\text{t km}^2\text{yr}^{-1}$)	27938.000	2585.000
Sum of all production ($\text{t km}^2\text{yr}^{-1}$)	13074.000	1036.000
Mean trophic level of the catch	2.59	3.10
Gross efficiency (GE. catch/net p.p.)	0.001020	0.004548
Calculated total net primary production ($\text{t km}^2\text{yr}^{-1}$)	11815.570	658.511
Total primary production/total respiration (TPP/TR)	5.525	1.124
Net system production (PP-TR. $\text{t km}^2\text{yr}^{-1}$)	9677.043	81.547
Total primary production/total biomass (PP/B. yr^{-1})	45.278	13.834
Total biomass/total system throughput (B-TST. yr^{-1})	0.009	0.021
Total biomass (excluding detritus) (t km^2)	260.957	53.390
Total catches ($\text{t km}^2\text{yr}^{-1}$)	12.057	3.359
Connectance Index (CI)	0.245	0.192
System Omnivory Index (SOI)	0.137	0.152
<i>Cycling indices</i>		
Throughput cycled excluding detritus ($\text{t km}^2\text{yr}^{-1}$)	164.65	66.32
Throughput cycled (including detritus) ($\text{t km}^2\text{yr}^{-1}$)	22.01	17.12
Finn's cycling index (FCI. %)	2.68	14.99
Predatory cycling index (PCI. %)	2.64	4.35
Finn's mean path length	2.368	3.500
Finn's straight-through path length (excluding detritus)	2.819	2.210
Finn's straight-through path length (including detritus)	2.301	2.975
<i>Information indices</i>		
Ascendancy (A. flowbits)	30892.50	2730.70
Overhead (\emptyset . flowbits)	51491.4	9091.7
Capacity (C. flowbits)	82383.9	11822.4
Information (I)	1.106	1.056
A/C	0.375	0.231

Legends of figures:

Figure 1. The Sine-Saloum estuary in Senegal (A, above) and the Gambia River-Estuary in Gambia (B, below). Graphs show monthly salinity variations at different zones of each estuary. Values encircled are maximum values recorded for each zone. Salinity gradient from the mouth to the upstream area of each estuary (b).

Figure 2. (I) Fish population ecological categories in Estuarine-Lagoon Systems (ELS). The population abundance is noted as: * rare, ** abundant or *** very abundant; R indicates reproduction in brackishwaters; D indicates distribution in ELS: V-vast, L-limited, S-seasonally or P-permanent and E euryhalinity (modified from Albaret 1994). (II) Species abundance per ecological category in the two ecosystems considered (Source: Villanueva 2004).

Figure 3. Detailed trophic structure of biomass ($t\ km^{-2}$, left) and ecologic production ($t\ km^{-2}\ yr^{-1}$, right), of fish groups as summarized using Ecopath: (A) Sine-Saloum and (B) Gambia.

Figure 4. Simplified trophic flow models of Sine-Saloum (a) and Gambia (b) estuaries showing discrete trophic levels. Detritus (part of TL I) has been separated to show its significance as energy source in each ecosystem. Percentage (%) values indicate trophic efficiencies per trophic level. Numbers on arrows indicate flow of energy expressed in $t\ km^{-2}\ yr^{-1}$.

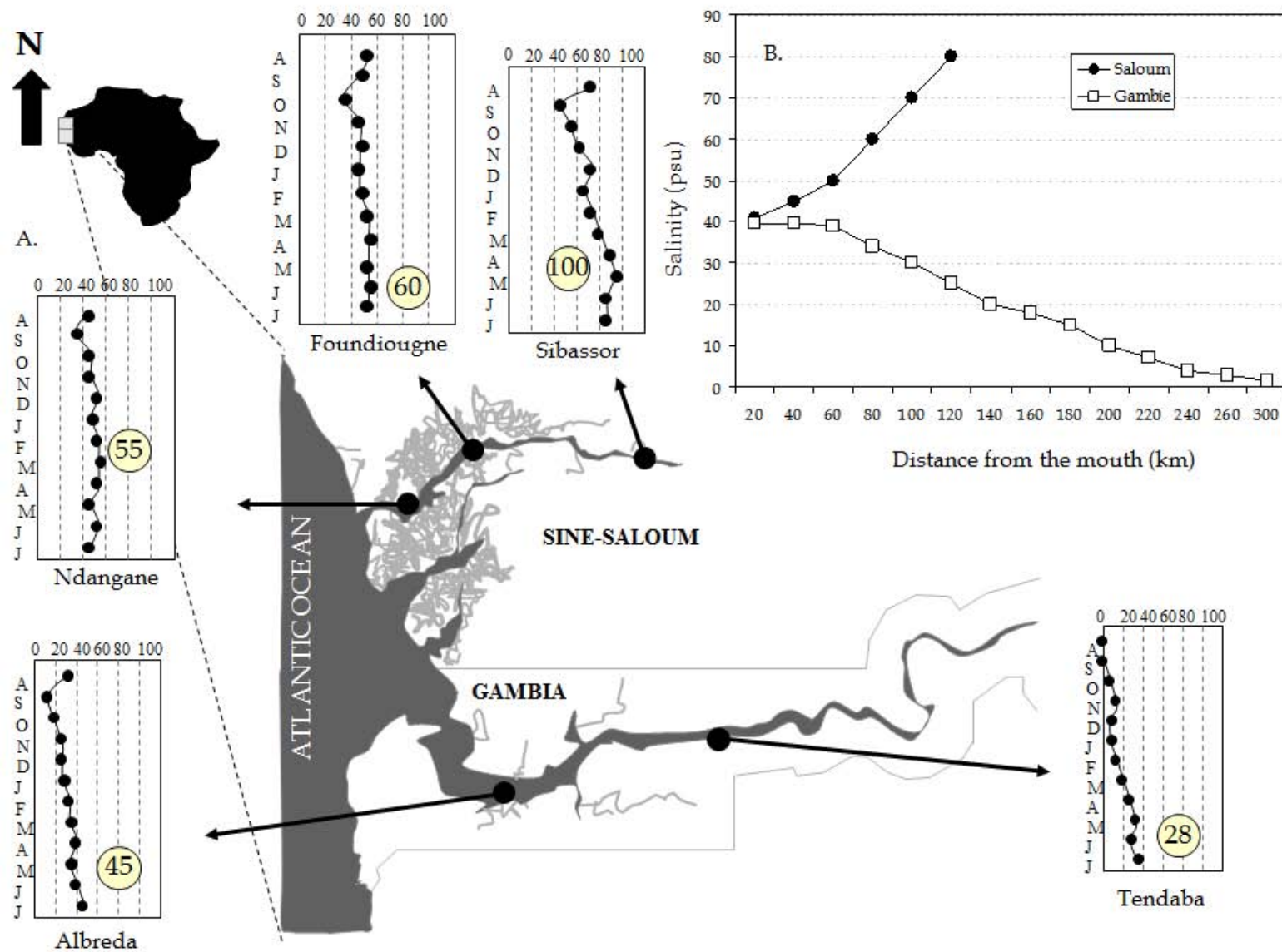


Figure 1
Villanueva

I.

Populations with freshwater affinity			FUNDAMENTAL POPULATIONS OF ESTUARINE-LAGOON SYSTEMS				Populations with marine affinity	
Continental species (C)	Occasional continental species (Co)	Continental with estuarine affinity species (Ce)	Estuarine of continental origin species (Ec)	Strict Estuarine Species (Es)	Estuarine of marine origin species (Em)	Marine-estuarine species (ME)	Marine Accessory Species (Ma)	Occasional marine species (Mo)
A *	A *	A * or **	A ***	A ***	A ***	A ***	A *(*)	A *
R no	R no	R at times(+)	R yes	R yes	R yes	R no	R no	R no
D L & S	D L & S	D ± L & S	D V & P	D V & P	D V & P	D ± V & P	D L & (or) S	D L
E low	E low	E low	also in rivers	also in lagoons	also in seas	E strong	E low	E low
E strong			E strong	E strong to quasi total	E quasi total	E strong		
Occasionally in ELS	Occasionally in ELS	Regularly in ELSL					Regularly in ELS	Occasionally in ELS

II.

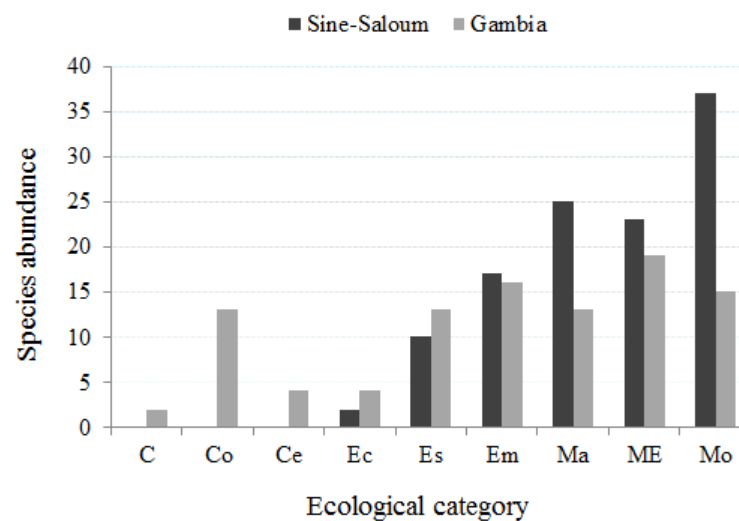


Figure 2
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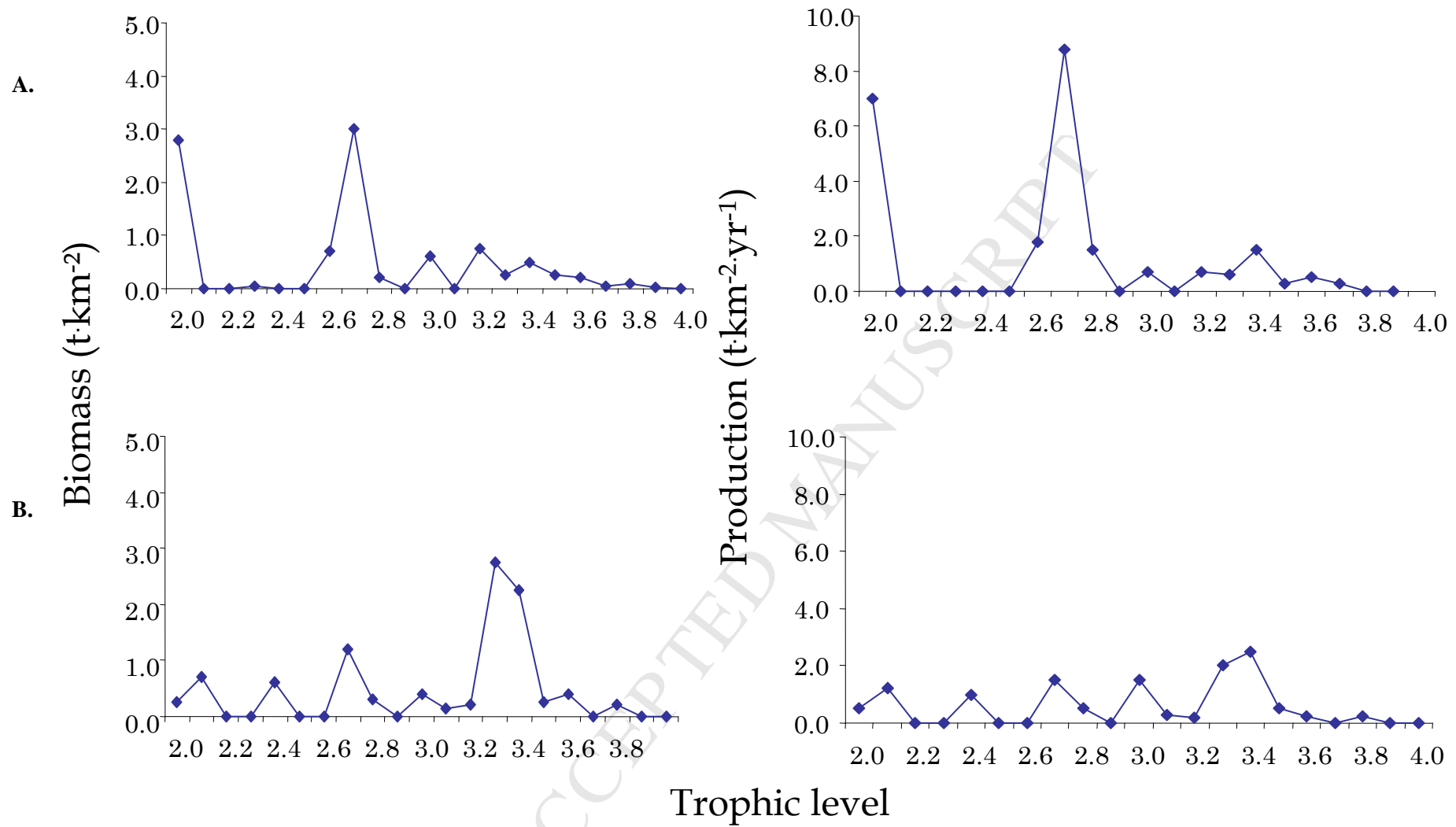


Figure 3
Villanueva

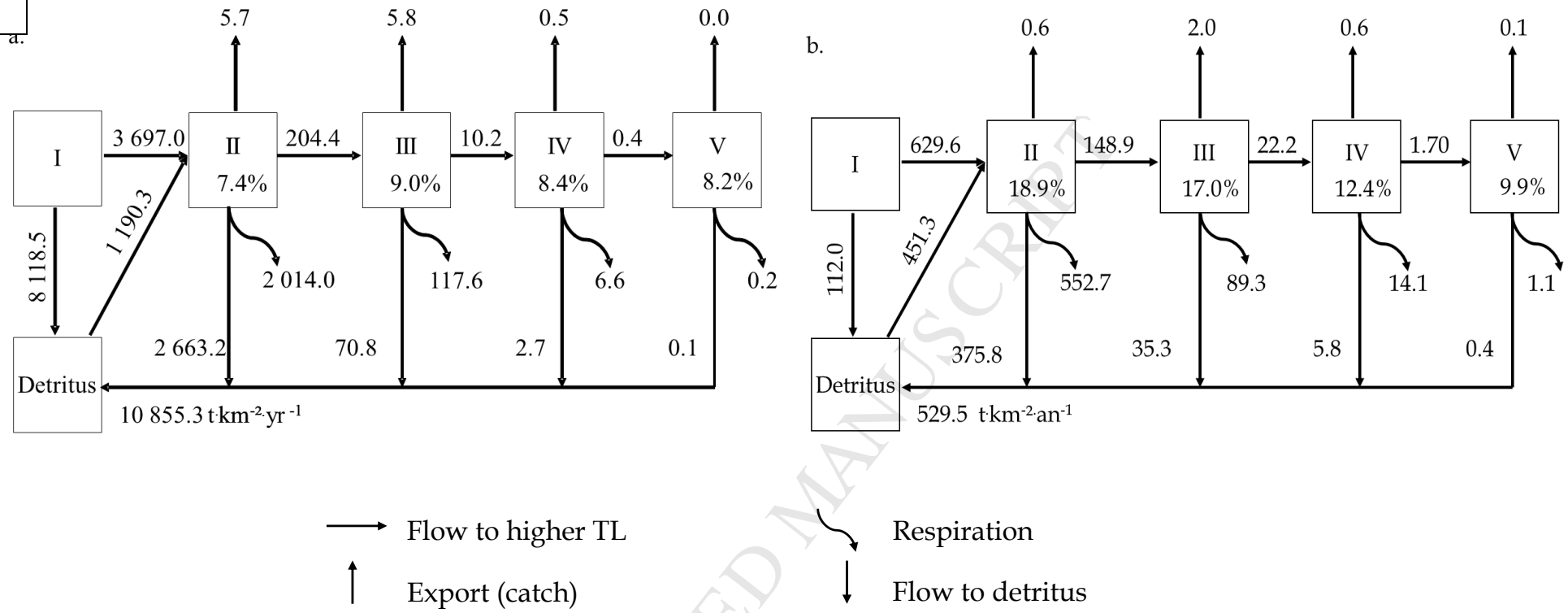


Figure 4
Villanueva