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Trophic flow structure of a neotropical estuary in northeastern Brazil and the comparison of ecosystem model indicators of estuaries

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Abstract :

We developed an Ecopath model in the Estuary of Sirinhaém River (SIR), a small-sized system surrounded by mangroves, subject to high impact, mainly by sugar cane industry and other farming industries in order to describe the food web structure and trophic interactions. In addition, we compared our findings with those of 20 available Ecopath estuarine models for tropical, subtropical and temperate regions, aiming to synthesize the knowledge on trophic dynamics and provide a comprehensive analysis of the structures and functioning of estuaries. Our model consisted of 25 compartments and its indicators were within the expected range for estuarine areas around the world. The average trophic transfer efficiency for the entire system was 11.8%, similar to the theoretical value of 10%. The Keystone Index and MTI (Mixed Trophic Impact) analysis indicated that the snook (*Centropomus undecimalis* and *Centropomus parallelus*) and jack (*Caranx latus* and *Caranx hippos*) are considered as key resources in the system, revealing its high impact in the food web. Both the species have a high ecological and commercial relevance, despite the unregulated fisheries. As result of the comparison of ecosystem model indicators in estuaries, differences in the ecosystem structure from the low latitude zones (tropical estuaries) to the high latitude zones (temperate system) were noticed. The structure of temperate and sub-tropical estuaries were based on high flows of detritus and export, while tropical systems have high biomass, respiration and consumption rates. Higher values of System Omnivory Index (SOI) and Overhead (SO) were observed in the tropical and subtropical estuaries, denoting a more complex food chain. Globally, none of the estuarine models were classified as fully mature ecosystems, although the tropical ecosystems were considered more mature than the subtropical and temperate ecosystems. This study is an important contribution to the trophic modeling of estuaries,

which may help to knowledge of the role of key ecosystem processes in the SIR.

Highlights

► Sirinhaém estuary, Northeast Brazil, is an immature and resilient ecosystem. ► The jack and, mainly, snook were key species in the Estuary of Sirinhaém River. ► Tropical estuaries were based in high biomass, respiration and consumption rates. ► The System Overhead Index was higher in tropical estuaries than in the other systems. ► TPP/TR was lower in tropical estuaries than in the other systems.

Keywords : Tropical estuary, Ecopath, Food web, Global comparison of ecological indicators

1. Introduction

Ecosystem models attempt to represent the entire ecological system by considering the interactions between its components. They have been increasingly developed worldwide as tools for evaluating the impact of climate change and fishing pressure in coastal areas (Bentorcha et al., 2017; Ruzicka et al., 2016). In addition, they can simulate scenarios that support the Ecosystem Approach to Fisheries (EAF) (Corrales et al., 2015; FAO, 2003). The EAF is an effective framework for ecosystem management that considers “the knowledge and uncertainties about biotic, abiotic, and human components of ecosystems and their interactions and applying an integrated approach to fisheries within ecologically meaningful boundaries” (FAO, 2003).

In the family of ecosystem models, energy balance models (Pikitch et al., 2004) have arisen as promising management advice tools for decision makers. They allow the evaluation of the energetic fluxes between biological compartments, the description of their functional roles and the assessment of the maturity of the ecosystem (Christensen and Pauly, 1993). This family of models may also simulate scenarios like overfishing (Cáceres et al., 2016; Wang et al., 2016) and have been used to evaluate the mechanisms that regulate the trophic controls of food webs (e.g., resource limitation, bottom-up and top-down controls) (Angelini et al., 2010; Ruiz et al., 2016). Ecopath mass-balance models are most commonly used to investigate marine trophic networks worldwide (Colléter et al., 2015). They simplify the complexity of marine ecosystem dynamics through a mass balance approach that considers trophic flows between biological compartments, thus allowing the investigation of the possible responses of the ecosystem to anthropogenic impacts such as habitat degradation and/or fishing. However, very few Ecopath models have been built for estuarine ecosystems.

Estuaries are productive ecosystems providing valuable benefits to human populations (Costanza et al., 2014), such as raw materials, food, coastal protection, erosion control, water purification, fisheries resources, carbon sequestration, and tourism and recreation services (Barbier et al., 2011; Boerema and Meire, 2016). In addition, they are considered to be essential habitats for the feeding, reproduction and growth of many aquatic organisms (Cloern et al., 2014; Odum and Barret, 2007). However, increasing anthropogenic pressures, such as urban development, threaten vegetated estuarine ecosystems, often degrading water quality, eroding aquatic biodiversity and disturbing the functioning of these ecosystems (Hooper et al., 2005). In the northeast of Brazil, urbanization, mangrove degradation and overfishing have negatively affected estuarine areas (Lessa et al., 2009; Viana et al., 2012). Elfes et al. (2014) applied the Ocean Health Index framework (Halpern et al., 2012) to Brazilian coastal ecosystems and found low scores in Pernambuco State (score of 55 out of 100), northeast Brazil. In the Sirinhaém

estuary, southern Pernambuco State, the huge impacts of the sugar cane industry and other farming industries (Mello, 2009) have degraded rivers and estuarine areas, which probably affects both the whole aquatic system and small-scale fisheries that have economic and food security implications for the local population (Tischer and Santos, 2003).

In this study, we developed an Ecopath model for the Sirinhaém River estuary to describe the estuary food web structure and the trophic interactions among its biological compartments, thus improving the current knowledge on the role of key ecosystem processes in order to help the development of decision support tools necessary for effective management (Crowder and Norse, 2008; Murawski et al., 2010). In addition, we compared our findings with those of 20 available Ecopath estuarine models for tropical, subtropical and temperate regions, aiming to synthesize the knowledge on trophic dynamics and provide a comprehensive analysis of the structures and functioning of estuaries. To the best of our knowledge, a comparison of the ecological indicators of estuarine Ecopath models has never been performed before (Coll and Libralato, 2012; Colléter et al., 2015).

2. Material and methods

2.1 *Sirinhaém Ecopath model*

Study area

The Sirinhaém River Estuary (SIR) is a small shallow coastal plain estuary 9.5 km long and 350 m wide, increasing up to 800 m at the river mouth. Its depth varies between 1.2 and 4.5 m (Silva et al., 2011). Located between the Marine Protected Area of Guadalupe and the Marine Protected Area of Sirinhaém, the SIR is characterized by a high density of mangrove, occupying 18 km² (Maia et al., 2006) (Fig. 1). The climate is tropical, with a rainy season occurring between May and October. The rainfall ranges from 20 to 450 mm·yr⁻¹, the mean water temperature is 29 °C, and the pH and salinity range between 5.8 - 8.5 and 0 - 36, respectively (APAC, 2015; Silva, 2009). The spatial extent of the model is the permanent wet area of the SIR, including the river and marine areas (hachured area in Fig. 1), totaling 1.7 km².

Mass-balanced modeling approach

The Ecopath with Ecosim (EwE) approach (www.ecopath.org) was used to quantify the trophic flows among a given number of biological compartments of the SIR. The Ecopath model (Christensen and Walters, 2004) is based on a set of linear equations that quantify the trophic flows among species and/or functional groups and that guarantee the mass balance in the ecosystem. The flow to and from each compartment is described by

the main Ecopath equation representing the production of each group (Christensen and Pauly, 1992):

$$B_i \times PB_i \times EE_i - \sum_j (B_j \times QB_j \times DC_{ji}) - EX_i = 0 \quad (1)$$

where B_i is the biomass of group (i); PB_i is the production/biomass ratio of (i), which is equal to total mortality (Z) or natural mortality (M) (Allen, 1971); EE_i is the ecotrophic efficiency of (i), which varies from 0 to 1 and represents the part of the production of the group that is transferred to higher trophic levels and/or removed by fishing; B_j is the biomass of the predators (j); QB_j is the food consumption per unit of biomass of the predators (j); DC_{ji} is the fraction (%) of (i) in the diet of (j); EX_i is the export of (i) and refers to the biomass that is caught by fishing and/or migrates to other environments. In this case, as for other Ecopath models (Coll et al., 2006; Han et al., 2016; Patrício and Marques, 2006), we considered migration to be equal to immigration, given the difficulty of estimating the movements of individuals.

For n groups (compartments), the Ecopath model solves a system of n linear equations. At least three out of four of the input parameters B_i , PB_i , QB_i and EE_i must be fixed to parameterize an Ecopath model. By connecting the production of one group with the consumption of the others, the missing parameter can be estimated based on the assumption that the production of one group is utilized by another group inside the system (Christensen and Pauly, 1992). The biomasses and flows were expressed in $t \cdot km^{-2}$ and in $t \cdot km^{-2} \cdot year^{-1}$, respectively.

Fig 1

2.2 Model components

The Sirinhaém model is based on 25 trophic groups: three primary producer groups, one zooplankton compartment, six groups of macrobenthos, 14 fish groups and one detritus group (Table 1). Fish were selected given the importance of their biomass, landings relevance, and position in the water column (pelagic, demersal, benthic). Species were grouped on the basis of trophic guilds (Elliott et al., 2007; Mourão et al., 2014). Four compartments were allocated to represent one single fish species (Table 1).

Table 1

Fish

Fish were captured quarterly, between March of 2013 and May of 2014, with a beach seine that was 250 m long and 2.5 m high and had a mesh size of 25 mm. Three replicates were carried out for each sample. For each set, the sampled area was obtained by GPS tracking using the open source image processing software *ImageJ*.

The biomasses for the fish compartments were estimated through the sum of the individual weights of each group divided by the total dragged area, expressed in t·km⁻². To minimize problems related to the underestimation of biomass due to gear selectivity, a catchability model (Lauretta et al., 2013) was applied to each fish species:

$$p = q \times E \times A^{-1} \quad (2)$$

$$N = C \times p^{-1} \quad (3)$$

where p is the mean proportion of the population captured, q is the catchability coefficient (see below), E is the fishing effort (total area sampled- km²), A is the model area (1.71 km²), C is the catch of the experimental samples (t·km⁻²) and N is the biomass corrected with the catchability model (t·km⁻²).

The catchability coefficients (q) of Lauretta et al. (2013) were used, taking into account the genus, the body shape and/or the fin profile of our species (see supplementary material Table S1).

The production/biomass rate (P/B) can be estimated under mass-balance conditions as total mortality (Z) (Allen, 1971), which is the sum of the fishing mortality (F) and natural mortality (M). Here, Z was estimated by linearized length converted catch curves (Chapman and Robson, 1960; Pauly, 1983) (see Figure S2.1). For the species that were not fished, P/B was equal to M , which was computed in accordance with Pauly (1980):

$$M = k^{0.65} \times L_{\infty}^{-0.279} \times T^{0.463} \quad (4)$$

where M is the natural mortality (year⁻¹), k is the growth coefficient (year⁻¹), L_{∞} is the asymptotic length (cm) and T is the mean water temperature (°C). The parameters k and L_{∞} were obtained from the literature or using the empirical equations of Le Quesne and Jennings (2012) and Froese and Binohlan (2000), respectively. T was measured *in situ* and considered to be the mean annual temperature, 27.8 °C (see Table S2.2).

The consumption/biomass rate (Q/B) was estimated according to the following equation (Palomares and Pauly, 1998):

$$\log Q/B = 7.964 - 0.204 \times \log W_{\infty} - 1.965 \times T' + 0.083 \times Ar + 0.532 \times H + 0.398 \times D \quad (5)$$

where W_{∞} is the asymptotic weight (g), T' is the temperature in Kelvin ($T' = 1000/(T^{\circ}\text{C}+273.15)$), and Ar is the aspect ratio of the caudal fin. W_{∞} was estimated by the

equation $W_{\infty} = a \times L_{\infty}^b$, where a and b were based on Viana et al. (2016). Photographic records of the caudal fin were taken for each species with the *ImageJ* software (see Table S1). Ar was calculated as $Ar = h^2 / s$, where h is height of the caudal fin and s is the surface area of the fin, extending to the narrowest part of the caudal peduncle (Palomares and Pauly, 1998). H and D represent the feeding type ($H = 1$ for herbivores; $D = 1$ for detritivores; $H = D = 0$ for other feeding habits). See Table S3 for the parameters used to calculate the consumption/biomass rate (Q/B).

Diet composition

The diet information for each fish compartment was primarily estimated from stomach content analyses carried out in the study area or, when data from a stomach content analysis was not available, the literature (see Table S4 for sources). For phytoplankton feeders, the excretion/egestion physiological rate was fixed at 40% in accordance with the recommendation of Heymans et al. (2016).

Other compartments

The phytoplankton biomass estimate was obtained from a study conducted in our area (Silva, 2009), and the epiphyton biomass was estimated from studies developed in an estuarine area near our study site (Baltar et al., 1996). The zooplankton, microphytobenthos and macrobenthos biomasses were estimated by fixing the EE (Table S4).

The macrobenthos (including the fiddler crab, polychaete, and gastropod compartments) P/B values were estimated based on the equation of Brey (1999), considering the maximum age for each group obtained from the literature and the maximum body mass for each group based on our database. The Q/B value was based on the equation proposed by Nichols (1974). All information on the P/B and Q/B values estimated in the model were obtained from the literature (see Table S4 for the parameters, equations and references).

For phytoplankton, epiphyton, microphytobenthos, zooplankton, bivalves, blue crabs and shrimp, the P/B and Q/B were obtained from the literature. The detritus compartment of the ecosystem was estimated by the equation of Pauly et al. (1993).

2.3 Fishery landings

Data on the SIR fishery landings were based on the Brazilian official statistics for the period from 2000 to 2007 (IBAMA, 2017) (for details, see Table S5).

2.4 Validation, sensitivity and balancing of the model

The pedigree index was calculated to quantify the uncertainty related to each input value (B, P/B, Q/B, diet and catch) in the model (Christensen et al., 2005), ranging from 0 (low precision information) to 1 (data and parameters fully rooted in local data).

Additionally, in accordance with Heymans et al. (2016) and Link (2010), we analyzed the confidence of our model by observing a set of criteria and assumptions using the pre-balanced (PREBAL) diagnostics routine (Link, 2010). The EE values had to be lower than 1.0. If this assumption was not reached, we adapted the diet matrix based on the literature and/or scientific advice. The production/consumption ratios (P/Q) had to range from 0.1 to 0.3; the respiration/assimilation and respiration/production ratios had to be lower than 1.0. The respiration/biomass ratios had to range between 1 and 10 for fish and 50 to 100 for groups with higher values of P/B and Q/B. A significant and negative relationship of the biomass, production and consumption with the trophic levels was also a required assumption for the model.

2.5 Ecopath outputs

The Ecopath model estimates several ecosystem attributes related to the resilience, maturity, stability (sensu Odum, 1969) and dynamics of the ecosystem. Some of these attributes were selected based on Christensen (1995) to explain the ecosystem bioenergetics, community structure, system recycling and balance (Gubiani et al., 2011). To analyze the direct and indirect impacts of a single compartment on the others, we performed the Mixed Trophic Impact (MTI) analysis (Ulanowicz and Puccia, 1990), which allows the identification of key groups of the system quantified by the Keystonness index developed by Valls et al. (2015).

2.6 Comparison of estuarine Ecopath models

The Sirinhaém estuary model (SIR model) was compared to the outputs of 20 other estuarine Ecopath models found in the EcoBase models repository and the literature (Table 2 and Table S6). Each model was classified according to three geographic zones: tropical (nine models, including Sirinhaém), subtropical (five models) and temperate (seven models). We selected thirteen ecosystem attributes (Table 3) related to the characterization and structure (five attributes – TST; TC; TE; TR and TD), maturity (six attributes – TPP/TR; TPP/TB; SOI; CI; H/D; AC), resilience and stability (two attributes – SO; FCI) of the ecosystems to investigate the differences and similarities among the estuaries and zones. Based on the methods proposed by Fulton et al. (2005) and Heymans et al. (2014), eight attributes were selected for the subsequent multivariate analysis - TC, TR, TE, TD, FCI, SO, SOI and CI. Collinearity was not observed between those attributes. TC, TR, TE and TD do not depend on the number of functional groups or the trophic links, according to Heymans et al. (2014). However, SOI, SO and CI, despite their robustness, may be

strongly dependent on the number of functional groups or the trophic links of the food web models (Fulton et al., 2005). In our case, this dependence was tested, and it was not significant; hence, these indicators were considered important since they were related to the trophic characterization and maturation degree of the system. Data were normalized using a square root transformation and TC, TR, TE and TD were divided by TST to standardize for the ecosystem size (Heymans et al., 2014; Selleslagh et al., 2012).

Table 2

Table 3

To synthesize multiple attributes and search for groupings of similar models, we applied a Principal Components Analysis (PCA) followed by an ascendant Hierarchical Clustering Analysis (AHC). In addition, the attributes of the models were compared across a Nonparametric multivariate permutational analysis of variance (PERMANOVA) with a significance level of 5%, with cluster groups obtained with AHC as factors. Statistical and multivariate analyses were performed with the R software (Core Team, 2017).

3. Results

3.1 Basic estimation

To balance the model, we adapted the diet matrix for some groups like croakers, grunts and mojarras (*Eucinostomus* spp.), which initially presented $EE > 1$. In relation to the criteria and assumptions applied to evaluate the confidence of the model, the production/consumption, respiration/assimilation and respiration/biomass ratios reached the accepted ranges (see Table S7.1). Based on the PREBAL routine, the relations between B, P/B and Q/B showed significant negative correlations with the trophic level (TL) (see Figure S7.2).

The values of the B, P/B, Q/B, EE and landings for all groups (Table 4) showed that the invertebrates represented more than half of the total biomass, while the biomass of the fish represented 26% of the total biomass, with catches of approximately 31% this amount. High EE values were reported for most groups (e.g., sardines, *Eucinostomus* spp., grunts, and croakers), mainly due to the high predation by predators (e.g., pemecou sea catfish, snook, and *Diapterus* spp.). However, the EE values of the snapper and jack were considerably lower than those of other groups, since they are neither heavily predated nor fished (Table 4). Table 5 shows the final diet matrix used in the balanced model. The EE values of the five groups targeted by fishing activities (snook, pemecou sea catfish, other catfish, *Diapterus* spp. and mullet) ranged between 0.36 and 0.58. The pedigree index for the SIR model was 0.43.

Table 4

Table 5

3.2 Food web structure and trophic analysis

Trophic structure

Piscivore fish such as jack (TL = 3.31), grunt (TL = 3.27), snook (TL = 3.26), snapper (TL = 3.21) and drum (TL = 3.20) showed the highest estimated trophic levels of the food web (Fig. 2). Although top predators (snook and jack) had a larger number of trophic pathways, their Omnivory Index (OI) values were lower than those observed for *Diapterus* spp. and puffers (TL = 2.72).

Fig 2

Transfer efficiencies

The herbivore/detritivore rate (H/D) was 1.02, indicating that the energy flowed, with similar efficiency, in equal amounts from the primary producers and the detritus to the second trophic level in the Sirinhaém food web (Table 6).

Mixed trophic impacts (MTI) and keystone species

The MTI included both direct and indirect impacts of all groups of the system. For example, an increasing snook biomass would have negative effects (red blocks) on most of the groups in the SIR ecosystem, but positive effects (blue blocks) on the snapper and polychaets (Fig. 3). An increase in the capture rate would cause relatively strong negative effects on the snook and mullet but, through trophic cascade, would increase the biomass of lower trophic levels groups (Fig. 3).

Fig 3

The jack and snook had a lower relative biomass and a higher impact in the food chain compared to other groups (Fig. 4). These groups were considered as the main keystone species of the SIR (see Table S8). Other groups, despite lower total impact values, were important nodes for the transfer of energy from the base of the trophic chain

to the top predators. These groups were fiddler crabs ($509 \text{ t}\cdot\text{km}^{-2}\cdot\text{y}^{-1}$), gastropods ($204 \text{ t}\cdot\text{km}^{-2}\cdot\text{y}^{-1}$), mullet ($139 \text{ t}\cdot\text{km}^{-2}\cdot\text{y}^{-1}$) and shrimp ($114 \text{ t}\cdot\text{km}^{-2}\cdot\text{y}^{-1}$).

Fig 4

3.3 Ecosystem properties and indicators

The Total System Throughput (TST) was $5598 \text{ t}\cdot\text{km}^{-2}\cdot\text{y}^{-1}$, with 28% due to consumption and 14% due to respiratory processes. The rates of the TPP/TR and TPP/TB were 2.59 and 32.59, respectively, while the Finn's Cycling Index (FCI) was low and the system overhead was high (71%).

Table 6

3.4 Multivariate analysis

Based on the indexes matrix of the 21 estuarine models (Table 2 and Table S6), the PCA and cluster analysis showed two groups differentiating the tropical and temperate models (Fig. 5). The total amount of variability explained by the first two principal components was 79.8%: the first axis (PC1) accounted for 61.6% of the variation (influenced by the consumption, respiration, exports and detritus), while the System Omnivory Index (SOI) and Connectance Index (CI) were highly correlated with the second principal component (Table 7).

Fig 5

Table 7

Significant differences were observed between the two cluster groups (PERMANOVA, d.f. = 1; pseudo-F = 14.37; $p = 0.003$). The tropical cluster, including Sirinhaém, showed a positive correlation with TC/TST and TR/TST and negative correlation with TE/TST and TD/TST. This cluster presented higher values of SO, TC/TST and TR/TST (Fig. 6). The SIR values were similar to those of other tropical ecosystems, which displayed intermediate attribute values (Figs. 5 and 6). The subtropical/temperate cluster presented

higher values of TE/TST and TD/TST and lower values of FCI, CI and System Overhead (SO) than the tropical cluster. High total export (TE/TST) and low FCI values were observed in two tropical systems (the Ogun coastal estuary, Nigeria, and the Sine-Saloum estuary, Senegal), which were also classified as cluster 1.

Fig.6.

4. Discussion

Estuaries are complex interfaces between marine and continental ecosystems, characterized by their high ecological and economic relevance (Sheaves et al., 2014). However, the trophic functioning of these systems has been poorly documented. Colleter et al. (2015) compiled the largest metadata of Ecopath and Ecosim applications and, of the 434 models described, only 4.3% were carried out in estuarine ecosystems. In this study, we developed a mass-balanced Ecopath model to describe the trophic interactions and fluxes in a small tropical estuary of northeast Brazil. We compared our model with 20 other estuary models from across the world using ecological network analysis indicators (Heymans et al., 2014), investigating how the comparison of the network indicators increased our knowledge on the trophic functioning of the Sirinhaém River Estuary and of estuaries in general.

Sirinhaém River Estuary Ecopath model

The estuary of the Sirinhaém River (SIR) is a small system surrounded by mangroves with a total surface area of 20.6 km². However, we delimited the modeled area to focus on the “wet” part of the estuary, 1.7 km², where most of the interactions among the aquatic compartments occur. In the absence of information on the movement of organisms in/from the continental part of the river or in/from the adjacent marine area, we neglected any immigration/emigration processes and biomass accumulations (Coll et al., 2006), and an assumption of no net migration was presumed here, as it is in other Ecopath models (Coll et al., 2006; Han et al., 2016; Patrício and Marques, 2006).

The model developed in the Sirinhaém River was, to the greatest possible extent, based on local studies, the diet of the main consumers and fishery statistics (snook, *Diapterus* spp., pemecou sea catfish, other catfish and mullet). We also conducted specific sampling in the area to estimate the biomass of several groups (all fish, with exception of mullet, fiddler crab and polychaete groups). We applied the catchability coefficient of Lauretta et al. (2013) to balance the gear selection bias in the fish biomass assessment. We adapted this coefficient q for species of the same genus and for species with similar body and/or fin shapes. The confidence of our model was evaluated through the PREBAL

routine, which identifies possible inconsistencies of the input data (Heymans et al., 2016). Overall, our input data respected the general rules/principles of ecosystem ecology (Link, 2010), similar to other studies (Bentorcha et al., 2017; Piroddi et al., 2017), except for the observed positive relationship between the production/consumption and trophic level. In our case, this effect was mainly caused by four compartments: the gastropod, mullet, sardine, and snook. The gastropods, mullet, and sardine, primary consumers with low TL values, had high consumption rates and low P/Q values. In contrast, the snook had a high TL and an elevated production value (high fishery exploitation) compared to other groups with a high TL and a low P/Q (Figure S7.2).

Given the absence of data for some compartments (zooplankton, microphytobenthos and macrobenthos), we decided to use the EE values of other estuarine models (Villanueva, 2015; Wolff et al., 2000) (Table S4). Considering that those components have low TL and provide energy to the top of the pyramid, the biomass estimates based on the chosen EE values were acceptable for balancing the food-web model. Hence, the fragilities of our model were reflected in a pedigree index value (0.43) with inferior (0.78-0.81; Villanueva, 2015) or higher (0.36; Abdul and Adekoya, 2016) values compared to other estuarine models, but it was considered acceptable and within the expected range for models of medium to high quality (0.137- 0.743; Colléter et al., 2015; Morissette et al., 2006).

Invertebrates (mainly fiddler crabs) encompassed most of the biomass in the SIR, followed by fish (mainly mullet, catfish and snook). Invertebrates in tropical systems, particularly in estuaries, are important components as supporters of the food web, providing links between the primary producers and higher trophic levels (McQuaid and Griffiths, 2014; Sheaves et al., 2016). Some groups considered to represent top predators (jack – *Caranx* spp. and snapper - *Lutjanus* spp.) had low values of EE. The low predation rates on those groups and the lack of targeted fishing efforts (they were juveniles with no commercial value) may explain this result.

The 11.8% mean Transfer Efficiency (TE) between trophic levels was similar to the theoretical value of 10% assumed by Lindeman (1942) and comparable to those of other estuarine trophic models: Yangtze Estuary, China, TE = 10% (Han et al., 2016); Río de la Plata Estuary, Uruguay, TE = 9.4% (Lercari et al., 2015) and Caeté Estuary, Brazil, TE = 9.8% (Wolff et al., 2000). In Sirinhaém, the relatively higher level of TE in the system is probably because there were fewer pathways between the trophic levels, which can be associated with low species diversity in ecosystems (Tomczak et al., 2009). Silva-Júnior et al. (2016) observed that, in Sirinhaém, the lowest diversity occurred among the estuaries of Pernambuco. Systems such as lagoons, estuaries and bays often have more species at the lower trophic levels (detritivores, suspension feeders, etc.), which can reduce the mean transfer efficiency (Heymans et al., 2014).

The Omnivory Index in the SIR was lower in comparison to those of temperate estuarine systems, such as the Seine estuary, France (Tecchio et al., 2015); however, it was similar to those of tropical systems, such as the Sine-Saloum and Gambia estuary in Senegal (Villanueva, 2015), with several groups specialized in low prey numbers. Usually, in tropical environments (e.g., estuaries), most fish species tend to be generalist or opportunist (Kroetz et al., 2016; Pereira et al., 2017), a consequence of the high biodiversity in these systems (Pereira et al., 2012). However, in the SIR, the reduced diversity (Silva-Júnior et al., 2016) may be causing the reduction of the Omnivory Index.

Considering the MTI and the Keystonness index, the jack and, mainly, the snook were considered keystone species in Sirinhaém due to their high impact on the food web. Usually, keystone species are mainly composed of large organisms with high trophic level, such as sharks, marine mammals and top predatory fish (Heymans et al., 2014). In estuarine ecosystems, larger fish, mostly pre-adult and adults, are considered to be top predators (Kroetz et al., 2016; Matich et al., 2017) that provide a predation pressure on forage species through top-down control in the food web (X. Du et al., 2015; Wasserman et al., 2013). In our model, the snook group mainly contained pre-adult individuals, and they drove a top-down control of the system, a type of control where top predators determine the bulk of the lower TLs through direct and indirect effects (Dineen and Robertson, 2010; Testa et al., 2016). Snook is considered to be an important species in estuarine tropical systems (Boucek et al., 2017; Greenwood, 2017), and, in Sirinhaém, its trophic role is the predation of fish and crustaceans (Lira et al., 2017; Merigot et al., 2016; Silva-Júnior et al., 2016). Anthropogenic-induced changes (e.g., fishing) on the biomass of key groups could be transferred through a trophic cascade effect within the food web. Snook in the SIR has a high commercial importance (IBAMA, 2008), and its fishery remains unregulated and unreported.

Indicators of the ecosystem structure in the SIR model were similar to those of the others tropical models, with values of respiration and consumption that were larger than the values exports and detritus and a low TPP/TR value. The SIR model had a high Overhead and low values of FCI, similar to the values of other tropical ecosystems, such as the Mamanguape Estuary, Brazil (Xavier, 2013), the Gambia Estuary, Senegal (Villanueva, 2015), and the temperate Somme Estuary, France (Rybarczyk et al., 2003). The high system overhead value in the SIR, and the results reported for other indicators (TPP/TR; TPP/TB; AC and FCI), suggest that the SIR is an ecosystem in the process of development with an acceptable degree of resilience, similar to other estuarine systems (Senegal, Colléter et al. (2012); Nigeria, Abdul and Adekoya (2016); France, Tecchio et al. (2015); and Uruguay, Lercari et al. (2015)). Given their high dynamics, as in the case of other coastal ecosystems (i.e., bays, reefs, lagoons and shelves), estuaries are considered to be

immature or developing systems (John and Lawson, 1990) that require particular strategies to maintain the equilibrium state, such as ecosystem-based management that integrates the river basins and the coastal and marine areas, considering the functional limits of the systems (Pallero Flores et al., 2017).

Comparison of estuarine Ecopath models

All the data analyzed in our comparison were derived from the available EwE models. However, detailed information was sometime missing, which prevented us from using the whole collection of metadata as initially envisaged. The great difficulty of standardizing models for a large-scale analysis, such as our study, has already been addressed in Heymans et al. (2014). Thirteen indicators (Fulton et al., 2005) were compared among 21 estuarine Ecopath models (including Sirinhaém model) in different climatic zones (tropical, subtropical and temperate).

Overall, differences in the ecosystem structure from the low latitude zones (tropical estuaries) to the high latitude zones (temperate system) were noticed. The food web structures in subtropical and temperate estuaries were more based on detritus (Lin et al., 2007), with greater exports rates, than those in tropical estuaries. However, tropical estuaries showed higher respiration and consumption rates. Heymans et al. (2014) showed that the high respiration and consumption rates in East Atlantic ecosystems are due to their high production and flow values. Higher rates of primary production per unit biomass and respiration flow (TPP/TB and TPP/TR) were noticed in basically all systems, revealing that the majority of the ecosystems were immature. However, the tropical estuaries had higher resilience (overhead values) than the temperate ones. Usually, in mature systems, the Primary Production rate (TPP) is similar to the respiration flow, while the total biomass of the ecosystem is larger than the TPP (Christensen et al., 2005), causing an accumulation of biomass within the system compared to the productivity (Corrales et al., 2017).

Higher values of the System Omnivory Index were observed in the tropical and subtropical estuaries, denoting a more complex food chain (Chen et al., 2015) compared to temperate systems, with a linear food web pattern (Raoux et al., 2017). The low SOI value may also be influenced by the number of aggregations in the models (Pinnegar et al., 2005); for example, of the seven temperate models analyzed, four had compartment aggregations with less than 20 groups, which can cause a reduction in the number of trophic paths and consequently a decrease in the SOI. Some indicators, such as the Connectance Index and Finn's Cycling Index, did little to explain differences between the climatic zones. These indicators are partly a function of the structure of the models and are considered to be good indexes of the food web robustness and, indirectly, of the ecosystem maturity and stability (Christensen and Pauly, 1992; Saint-Béat et al., 2015). However, they

often do not reflect the structure of the ecosystem with accuracy (Christensen et al., 2005; Finn, 1976).

Some models (e.g., the Loire estuary in western France) were outliers, as they differed the general patterns, with a very high Ascendency value (AC) and a lower Overhead due to a high primary production. High AC values can be derived by eutrophication (due to nutrient enrichment), which causes an increase in the total system throughput (Ulanowicz, 1986). Two other tropical systems, Sine-Saloum and Ogun State (Africa), had similar flows as those of temperate and subtropical ecosystems, which could be attributed to their high production of organic matter and lower consumption values (Abdul and Adekoya, 2016). Moreover, the Seine Estuary (temperate) showed a similar flow as that of tropical estuaries.

5. Conclusions

Although it may be a simplified representation, our SIR model respected the general rules/principles of ecosystem ecology, and its indicators were within the expected ranges for estuarine areas around the world, showing that, regardless of the model fragilities, we can reasonably have confidence on our main findings. Jack and, mainly, snook were key species in the SIR and were ecologically and commercially relevant, as is the case in several other tropical estuaries. However, the SIR was subject to high levels of anthropogenic impacts, mainly because of sugar cane and other agribusiness industries, despite its location within two marine protected areas; furthermore, it has no management plan. The snook fishery in the SIR is also unregulated and unreported. Compared to other tropical estuaries, the SIR is a complex and immature ecosystem, and its degradation may heavily affect its ecological functioning and local fishery.

The comparison of the estuarine ecosystems was useful to integrate available ecological data into a concrete framework, providing a comprehensive analysis of the estuarine functioning. The structures of the temperate and subtropical estuaries were based on high primary production and flows of detritus and export, while the tropical systems had high biomass, respiration and consumption values. Globally, none of the estuarine models were classified as fully mature ecosystems, although the tropical ecosystems were considered more mature than the subtropical and temperate ecosystems.

This study is an important contribution to the trophic modeling of estuaries, improving the knowledge of the role of key ecosystem processes. In Sirinhaém, the approach of this study should be further improved with complementary and more accurate local information, mainly for the base of the trophic chain, landings and fishing effort time series, which could help to identify impact of fishing on the ecosystem. However, input

data (such as data on biomass, diet and landings) and, consequently, many indicators were also lacking for many models in temperate, subtropical and tropical systems, reinforcing that there is still an overall fragility of the estuarine models. Considering this scenario, the use of stable isotope analyses to validate some of the main findings (i.e., the trophic levels) derived from the Ecopath model should be used in future research (Dame and Christian, 2008; J. Du et al., 2015). Additionally, incorporating additional tools to the current model, such as Ecospace (which allows a spatial evaluation of the model, Walters et al., 1999; Abdou et al., 2016) and “Value-Chain” (an economical “chain” of the resources, Christensen et al., 2011; Halouani et al., 2016), would enable useful insights on the effects of various management policies and possible trade-offs at the ecosystem level.

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Captions figures

Fig. 1. Estuary of Sirinhaém River, Northeastern Brazil, the area of model (1.7 km²) and the sampling points (black) carried out between 2013 and 2014.

Fig. 2. Food web of the Estuary of Sirinhaém River model. The gray lines are the trophic paths. B is biomass in t·km⁻². Sources of drawings: fish and macroinvertebrates (our drawings); exceptions: zooplankton (ecoanalystis.com), polychaeta (Copyright 2013 Denis Riek), phytoplankton (seahack.org) and epiphyton (Copyright Daniel Sullivan's).

Fig. 3. Mixed Trophic Impact (MTI) of the Estuary of Sirinhaém River model. The color boxes show negative (red) or positive (blue) impacts and the intensity is proportional to the degree of the impacts.

Fig. 4. Relationship between relative total impact and relative biomass of each compartment of the Estuary of Sirinhaém River model. Circle size is proportional to relative biomass for each group. * Conceptual identification of keystone species in food-web (Valls et al., 2015).

Fig. 5. Principal Component Analysis for 21 estuarine Ecopath models described by ecosystem attributes. Blue, red and yellow correspond the Cluster 1, Cluster 2 and the Estuary of Sirinhaém River model respectively. TR: total respiration; TC: total consumption; TD: total detritus; TE: total Export; TST: total system throughput; SOI: System Omnivory Index; CI: Connectance Index; FCI: Finn's Cycling Index; SO: System Overhead. ●: Sub tropical; ▲: temperate; +: Tropical ecosystems. GAM: Gambia; MAM: Mamanguape; CAM: Cameroon; SIR: Sirinhaém; BOL/ BOL2: Bamboung; CAE: Caeté; SEI: Seine; PEA/PEA2: Pearl River; OGU: Ogun; GIR: Gironde; SOM: Somme; STM: St Michel; LOI: Loire. See Table S6 for model details.

Fig. 6. Boxplot of ecosystems indicators of 21 estuary Ecopath models divided by climate zone (Temperate; Sub tropical; and Tropical). The horizontal line and box represent median value and interquartile range respectively, while the vertical line is the upper limit (25% of the data). SIR: The Estuary of Sirinhaém River model is highlighted on the graphs. TR: Total respiration; TC: Total consumption; TD: Total detritus; TE: Total Export; TST: Total system throughput; TB: Total biomass; SO: System Sverhead; TPP: Total primary production; TB: Total biomass, SOI: System Omnivory Index; CI: Connectance Index; FCI: Finn's Cycling Index.

Table 1 Taxonomic composition and trophic guilds of each compartment of the Estuary of Sirinhaém River Ecopath model. %Relative fish sample is the composition of fish, expressed in % in weight; captured with manual beach seine in the Estuary of Sirinhaém River, Northeast Brazil.

	Group name	Family	Scientific name	Guilds	%Relative fish sample
1	Phytoplankton	-	-	Primary producer	-
2	Zooplankton	-	-	Filter-feeder	-
3	Epiphyton	-	-	Primary producer	-
4	Microphytobenthos	-	-	Primary producer	-
5	Fiddler crab	Ocypodidae	<i>Uca</i> spp.	Deposit-feeder	-
6	Polychaeta	-	-	Several guilds	-
7	Bivalve	Veneridae	<i>Anomalocardia brasilliana</i>	Filter-feeder	-
8	Gastropod	Neritidae	<i>Neritina virginia</i>	grazer	-
9	Blue crab	Portunidae	<i>Callinectes</i> spp.	Zoobenthivore	-
10	Shrimp	Peneidae	<i>Farfantepenaeus</i> spp.	Detritivore	-
11	Sardine	Clupeidae Engraulidae	<i>Opisthonema oglinum</i> <i>Cetengraulis edentulus</i> <i>Anchoa spinifer</i>	Zooplanktivore	2.19
12	Mullet	Mugilidae	<i>Mugil</i> spp	Detritivore	5.37
13	Flatfish	Achiridae	<i>Achirus lineatus</i> <i>Trinectes paulistanus</i>	Zoobenthivore	5.02
14	Puffer	Tetraodontidae	<i>Sphoeroides testudineus</i>	Omnivore	5.30
15	<i>Eucinostomus</i> spp.	Gerreidae	<i>Eucinostomus argentus</i> <i>Eucinostomus gula</i>	Zoobenthivore	0.25
16	<i>Diapterus</i> spp.	Gerreidae	<i>Diapterus auratus</i> <i>Diapterus rhombeus</i>	Omnivore	8.61
17	Snapper	Lutjanidae	<i>Lutjanus jocu</i>	Piscivore/Zoobenthivore	0.33
18	Pemecou sea catfish	Ariidae	<i>Sciades herzbergii</i>	Zoobenthivore	24.14
19	Others Catfish	Ariidae	<i>Aspistor luniscutis</i> <i>Aspistor quadriscutis</i>	Omnivore	14.35
20	Drum	Sciaenidae	<i>Bairdiella ronchus</i> <i>Menticirrhus americanus</i>	Zoobenthivore	1.16
21	Grunt	Haemulidae	<i>Conodon nobilis</i> <i>Pomadasys crocro</i>	Piscivore/Zoobenthivore	0.68
22	Croaker	Sciaenidae	<i>Micropogonias furnieri</i>	Omnivore	2.56
23	Snook	Centropomidae	<i>Centropomus undecimalis</i> <i>Centropomus parallelus</i>	Piscivore/Zoobenthivore	21.64
24	Jack	Carangidae	<i>Caranx hippos</i> <i>Caranx latus</i>	Piscivore	2.41
25	Detritus	-	-	-	-

Table 2. Characterization of the different estuarine systems compared with our model. For more details of

Ecosystems	Code	Area (km ²)	Country	Number of groups	Geographic zone	Reference
Sirinhaem	SIR	1.7	Brazil	25	Tropical	Present study
Mamanguape estuary	MAM	-	Brazil	24	Tropical	Xavier (2013)
Caete estuary	CAE	220	Brazil	19	Tropical	Wolff et al. (2000)
Sine-Saloum estuary	SIN	543	Senegal	37	Tropical	Villanueva (2015)
Gambia River estuary	GAM	654	Senegal	41	Tropical	Villanueva (2015)
Cameroon estuary	CAM	1750	Cameroon	26	Tropical	Simon and Raffaelli (2016)
Ogun State coastal estuary	OGU	26	Nigeria	14	Tropical	Abdul and Adekoya (2016)
Bamboung Bolong*	BOL BOL2	4.7	Senegal	31	Tropical	Colléter et al. (2012)
Río de la Plata estuary	RÍO	70500	Uruguay	37	Sub-Tropical	Lercari et al. (2015)
Pearl River estuary*	PEA PEA2	72600	China	24	Sub-Tropical	Duan et al. (2009)
Danshuei River estuary	DAN	2726	Taiwan	16	Sub-Tropical	Lin et al. (2007)
Yangtze estuary	YAN	-	China	17	Sub-Tropical	Han et al. (2016)
Breton Sound estuary	BRE	1100	United States	39	Temperate	de Mutsert et al. (2012)
Canche estuary	CAN	7.8	France	15	Temperate	Selleslagh et al. (2012)
Somme estuary	SOM	50	France	9	Temperate	Rybarczyk et al. (2003)
Seine estuary	SEI	188.7	France	15	Temperate	Rybarczyk and Elkaïm (2003)
St Michel estuary	STM	250	France	25	Temperate	Arbach Leloup et al. (2008)
Loire estuary	LOI	239	France	-	Temperate	Selleslagh et al. (2012)
Gironde estuary	GIR	625	France	18	Temperate	Lobry et al. (2008)

models and systems, see SOM 7. * Two models of same ecosystem in different periods.

Table 3. Statistic and ecological indicators used for the comparison of the estuaries.

Code	Ecosystems Attributes	Description	Goal	Units
TST	Total System Throughput	Sum of all the flows through the ecosystem	Represent the size of the entire system in terms of flow	$\text{tkm}^{-2}\text{y}^{-1}$
TC/TST	Total Consumption/TST	Total consumption over the sum of all the flows	Characterization of the system	$\text{tkm}^{-2}\text{y}^{-1}$
TR/TST	Total Respiration/TST	Total respiration over the sum of all the flows	Characterization of the system	$\text{tkm}^{-2}\text{y}^{-1}$
TE/TST	Total Exports/TST	Total exports from the system over the sum of all the flows	Characterization of the system	$\text{tkm}^{-2}\text{y}^{-1}$
TD/TST	Flows to detritus/TST	Flows to detritus over the sum of all the flows	Characterization of the system	$\text{tkm}^{-2}\text{y}^{-1}$
TPP/TR	TPP/Total Respiration	Ratio between Total Primary Production and Total Respiration in a system	Represent the maturity of an ecosystem. In mature systems, the ratio should approach 1	-
TPP/TB	TPP/Total Biomass	Ratio between Total Primary Production and Total Biomass in a system	Represent the maturity of an ecosystem. In mature systems, the TPP/TB should be low	-
SOI	System Omnivory Index	Variance mean of trophic levels in the diet composition	Description of the trophic amplitude associated to maturity. SOI should increase with mature systems	-
CI	Connectance Index	Ratio of the number of actual links to the number of possible links in food web	Description of the trophic links associated to maturity. In mature system, the high CI value indicate a food web with large number of trophic links	-
AC	Ascendency	Index of the optimization of a food web opposed to Overhead (%)	In mature systems, the percentage of AC should be high	%
SO	System Overhead	Reserve energy of the ecosystem and opposed to Ascendency (%; $AS+SO=100\%$)	In resilient systems, the percentage of SO should be high	%
FCI	Finn's Cycling Index	Quantifies the of flows in of recycling process	Description of the system maturity, resilience and stability. Higher values indicate more mature and resilient systems	%TST
H/D	Herbivore/Detritivore rate	Relation between the flows of the grazing and Flows from grazing/ Flow to detritus path to food web	Characterization of the system. In mature systems, the contribution from detritus is high	-

Table 4. Basic inputs and estimated outputs (in bold) of the groups of the Estuary of Sirinhaém River model. TL: trophic level; B: biomass; P/B: production–biomass ratio; Q/B: consumption–biomass ratio; EE: ecotrophic efficiency; Y: landings; OI: Omnivory Index.

	Group name	TL	B (t.km ⁻²)	P/B (year ⁻¹)	Q/B (year ⁻¹)	EE	OI	Y (t.km ⁻²)
1	Phytoplankton	1.00	2.220	652.71	-	0.215	-	-
2	Zooplankton	2.11	1.845	50.21	150.65	0.900	0.111	-
3	Epiphyton	1.00	1.370	153.31	-	0.717	-	-
4	Microphytobenthos	1.00	2.084	209.61	-	0.501	-	-
5	Fiddler crab	2.00	16.000	7.30	31.89	0.509	0.004	-
6	Polychaeta	2.19	4.284	2.91	17.26	0.950	0.173	-
7	Bivalve	2.00	6.339	2.00	-	0.950	-	-
8	Gastropod	2.00	5.270	2.65	38.83	0.950	-	-
9	Blue crab	2.55	3.740	2.00	8.00	0.760	0.325	-
10	Shrimp	2.32	4.257	2.81	26.90	0.950	0.243	-
11	Sardine	2.56	0.305	2.11	56.86	0.824	0.309	-
12	Mullet	2.02	3.237	1.88	43.15	0.550	0.019	2.98
13	Flatfish	2.99	0.912	3.16	13.43	0.556	0.257	-
14	Puffer	2.78	0.871	3.17	11.06	0.528	0.337	-
15	<i>Eucinostomus</i> spp.	2.95	0.028	1.33	12.84	0.814	0.249	-
16	<i>Diapterus</i> spp.	2.78	1.612	2.90	10.61	0.356	0.295	0.91
17	Snapper	3.21	0.074	0.33	6.42	0.060	0.076	-
18	Pemecou sea catfish	2.83	4.573	1.38	9.94	0.537	0.149	2.75
19	Others Catfish	2.90	1.799	1.13	12.50	0.580	0.221	0.51
20	Drum	3.20	0.150	1.73	9.43	0.469	0.089	-
21	Grunt	3.27	0.117	0.93	8.78	0.869	0.079	-
22	Croaker	2.21	0.431	0.21	6.90	0.966	0.201	-
23	Snook	3.26	2.574	1.68	5.70	0.556	0.273	2.40
24	Jack	3.31	0.226	0.466	6.66	0.149	0.196	-
25	Detritus	1.00	2.760	-	-	0.344	-	-

Table 5. Diet composition matrix of the Estuary of Sirinhaém River model.

	Prey	Predator																						
		2	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24		
1	Phytoplankton	0.800		0.109	0.600			0.144	0.500	0.154														
2	Zooplankton	0.100	0.003	0.152			0.016	0.201	0.500	0.015	0.006	0.023	0.227	0.413			0.063		0.007	0.057	0.086			
3	Epiphyton		0.150			0.037	0.037			0.462			0.042	0.059										
4	Microphytobenthos		0.003	0.326	0.200	0.594	0.267	0.150		0.231	0.152		0.042	0.059										
5	Fiddler crab							0.018			0.040	0.050			0.423	0.817	0.651	0.404	0.01		0.250	0.164		
6	Polychaeta						0.150	0.005			0.260		0.460	0.200				0.007						
7	Bivalve			0.011			0.200	0.027				0.181							0.01	0.052	0.015	0.020		
8	Gastropod			0.011			0.105	0.045			0.060	0.228	0.022	0.001	0.002	0.002	0.023	0.001	0.01	0.050	0.028	0.006		
9	Blue crab										0.017	0.192	0.084		0.176	0.003	0.042	0.051			0.157	0.033		
10	Shrimp						0.005				0.417		0.059	0.360	0.001	0.050	0.400	0.884	0.078	0.100	0.393			
11	Sardine														0.007	0.001			0.03		0.031	0.004		
12	Mullet																				0.025			
13	Flatfish						0.020										0.056	0.009		0.055	0.072			
14	Puffer																	0.049	0.003	0.017	0.065			
15	<i>Eucinostomus</i> spp.																			0.003	0.002	0.001		
16	<i>Diapterus</i> spp.														0.009						0.049	0.020		
17	Snapper																					0.001		
18	Pemecou sea catfish																					0.043		
19	Others Catfish																					0.045		
20	Drum															0.005			0.001		0.006	0.015		
21	Grunt																				0.004	0.022		
22	Croaker																				0.005	0.010		
23	Snook																							
24	Jack																					0.001		
25	Detritus	0.100	0.844	0.391	0.200	0.370	0.200	0.410		0.138	0.048	0.326	0.122	0.209	0.017	0.177	0.184	0.018	0.04	0.813	0.089	0.045		
26	Import																					0.021	0.043	
	Total	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Table 6. Ecosystem attributes, ecological and flow indicators of the Estuary of Sirinhaém River model.

Parameters	Value	Units
Ecosystem properties		
Sum of all consumption (TC)	1554.63	t km ⁻² ·y ⁻¹
Sum of all exports (TE)	1286.96	t km ⁻² ·y ⁻¹
Sum of all respiratory flows (TR)	809.27	t km ⁻² ·y ⁻¹
Sum of all flows into detritus (TD)	1947.44	t km ⁻² ·y ⁻¹
Total system throughput (TST)	5598.30	t km ⁻² ·y ⁻¹
Sum of all production (TP)	2394.22	t km ⁻² ·y ⁻¹
Mean trophic level of the catch (TLc)	2.68	-
Gross efficiency (catch/net p.p.)	0.0046	-
Calculated total net primary production (TNPP)	2095.88	t km ⁻² ·y ⁻¹
Net system production (NSP)	1286.61	t km ⁻² ·y ⁻¹
Total biomass (excluding detritus) (TB)	64.32	t.km ⁻²
Total catch (Tc)	9.57	t km ⁻² ·y ⁻¹
Ecosystem maturity		
Total primary production/total respiration (TPP/TR)	2.59	
Total primary production/total biomass (TPP/TB)	32.59	
Total biomass/total throughput (TB/TST)	0.01	y ⁻¹
Food web structure		
Connectance Index (CI)	0.27	
System Omnivory Index (SOI)	0.16	
Finn's Cycling Index (FCI)	5.61	% TST
Finn's mean path length (FML)	2.67	-
Ascendancy (AS)	29.00	%
System Overhead (SO)	71.00	%
Herbivore/Detritivore rate (H/D)	1.02	
Model reability		
Ecopath pedigree index	0.43	
Transfer efficiency total	11.58	%

Table 7. Results of the principal components analysis (PCA) used to summarize eight ecosystem attributes for 21 estuarine Ecopath models. Eigen-vectors (correlation) for each variable and percentage of explanation (%) for each axis are also presented.

	PC1	PC2
Eigenvalue	2.22	1.20
Variance (%)	61.65	18.24
Cum. Variance (%)	61.65	79.89
Contribution on axes		
TC/TST	-0.889	0.028
TE/TST	0.851	0.035
TR/TST	-0.850	0.364
TD/TST	0.820	-0.427
SO	-0.725	-0.252
SOI	-0.246	1.330
FCI	-0.650	-0.749
CI	0.275	1.134

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Abstract

We developed an Ecopath model in the Estuary of Sirinhaém River (SIR), a small-sized system surrounded by mangroves, subject to high impact, mainly by sugar cane industry and other farming industries in order to describe the food web structure and trophic interactions. In addition, we compared our findings with those of 20 available Ecopath estuarine models for tropical, subtropical and temperate regions, aiming to synthesize the knowledge on trophic dynamics and provide a comprehensive analysis of the structures and functioning of estuaries. Our model consisted of 25 compartments and its indicators were within the expected range for estuarine areas around the world. The average trophic transfer efficiency for the entire system was 11.8%, similar to the theoretical value of 10%. The Keystone Index and MTI (Mixed Trophic Impact) analysis indicated that the snook (*Centropomus undecimalis* and *Centropomus parallelus*) and jack (*Caranx latus* and *Caranx hippos*) are considered as key resources in the system, revealing its high impact in the food web. Both the species have a high ecological and commercial relevance, despite the unregulated fisheries. As result of the comparison of ecosystem model indicators in estuaries, differences in the ecosystem structure from the low latitude zones (tropical estuaries) to the high latitude zones (temperate system) were noticed. The structure of temperate and sub-tropical estuaries were based on high flows of detritus and export, while tropical systems have high biomass, respiration and consumption rates. Higher values of System Omnivory Index (SOI) and Overhead (SO) were observed in the tropical and subtropical estuaries, denoting a more complex food chain. Globally, none of the estuarine models were classified as fully mature ecosystems, although the tropical ecosystems were considered more mature than the subtropical and temperate ecosystems. This study is an important contribution to the trophic modeling of estuaries, which may help to knowledge of the role of key ecosystem processes in the SIR.

Key-words: Tropical estuary, Ecopath, Food web, Global comparison of ecological indicators

Highlights

- Sirinhaém estuary, Northeast Brazil, is an immature and resilient ecosystem.
- The jack and, mainly, snook were key species in the Estuary of Sirinhaém River.
- Tropical estuaries were based in high biomass, respiration and consumption rates.
- The System Overhead Index was higher in tropical estuaries than in the other systems.
- TPP/TR was lower in tropical estuaries than in the other systems.

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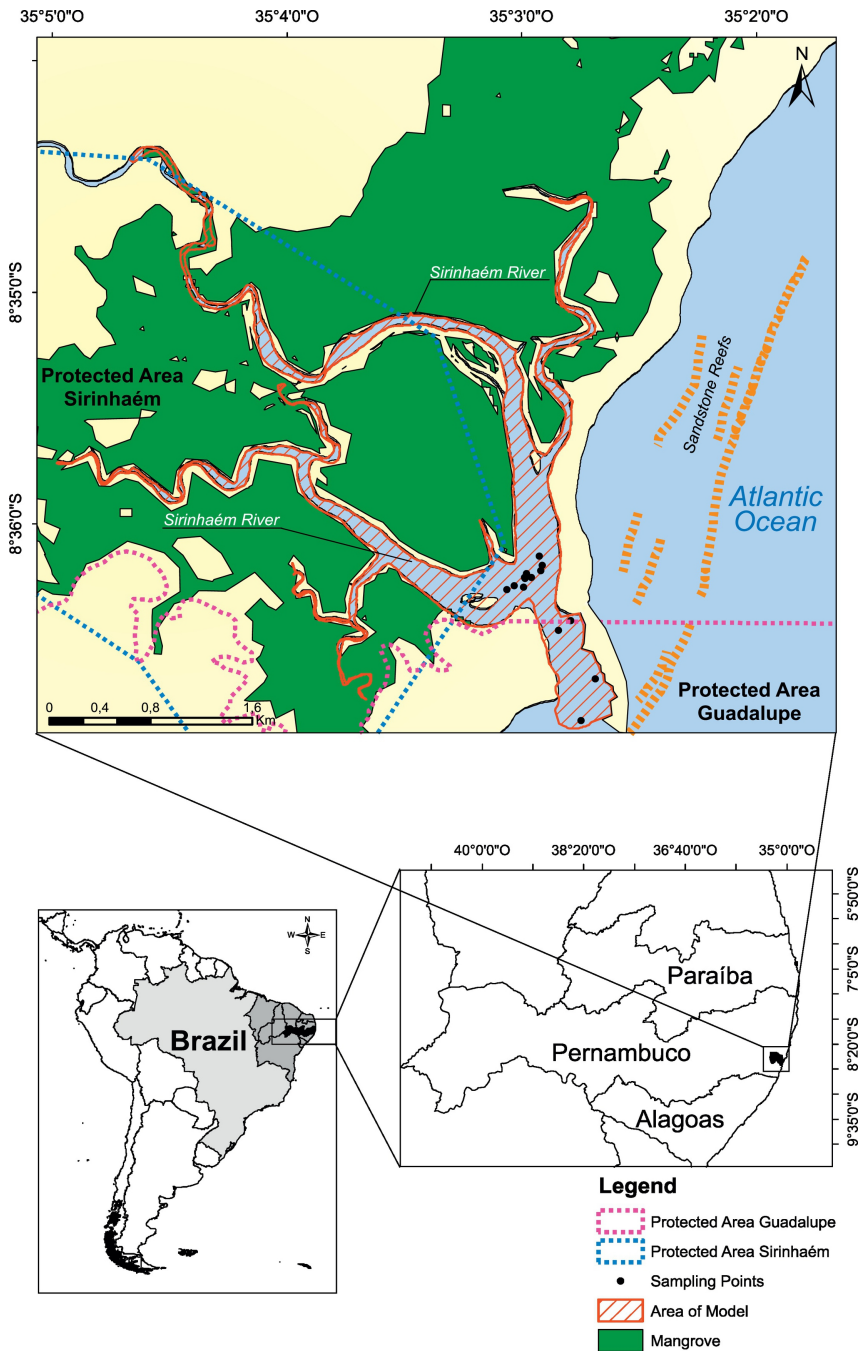


Figure 1

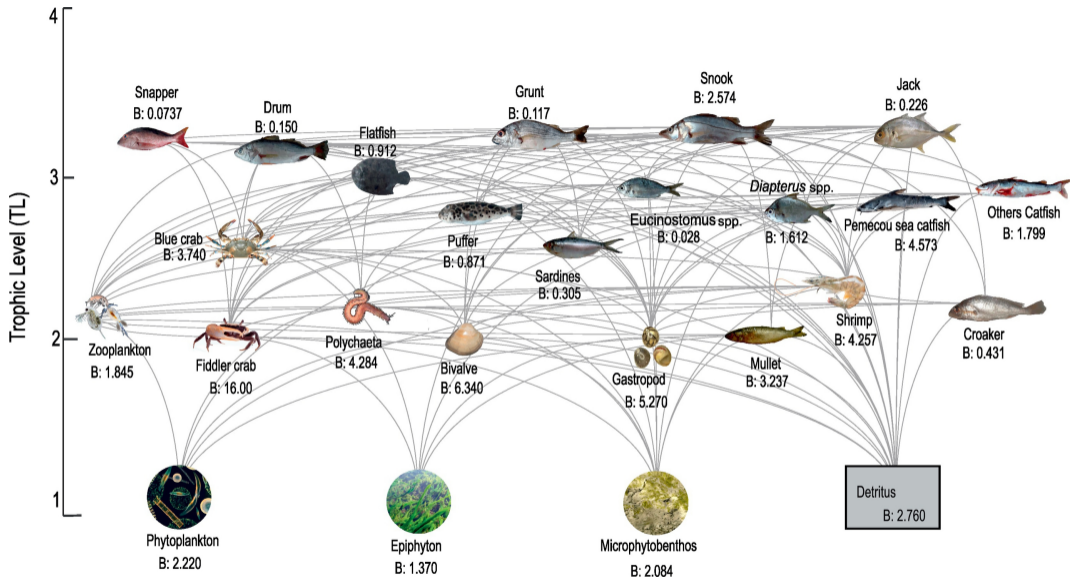


Figure 2

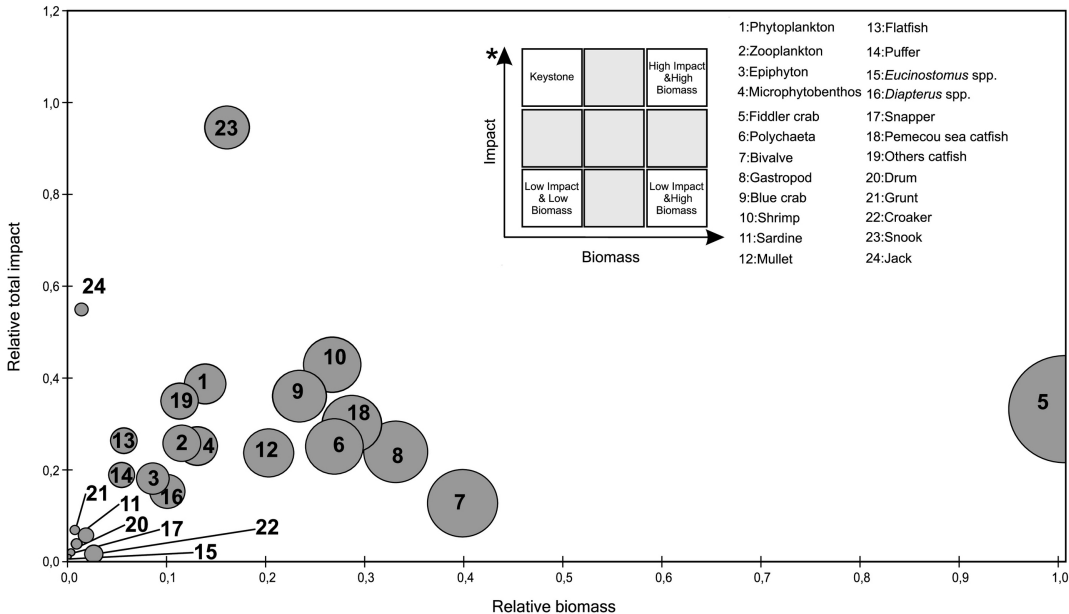


Figure 4

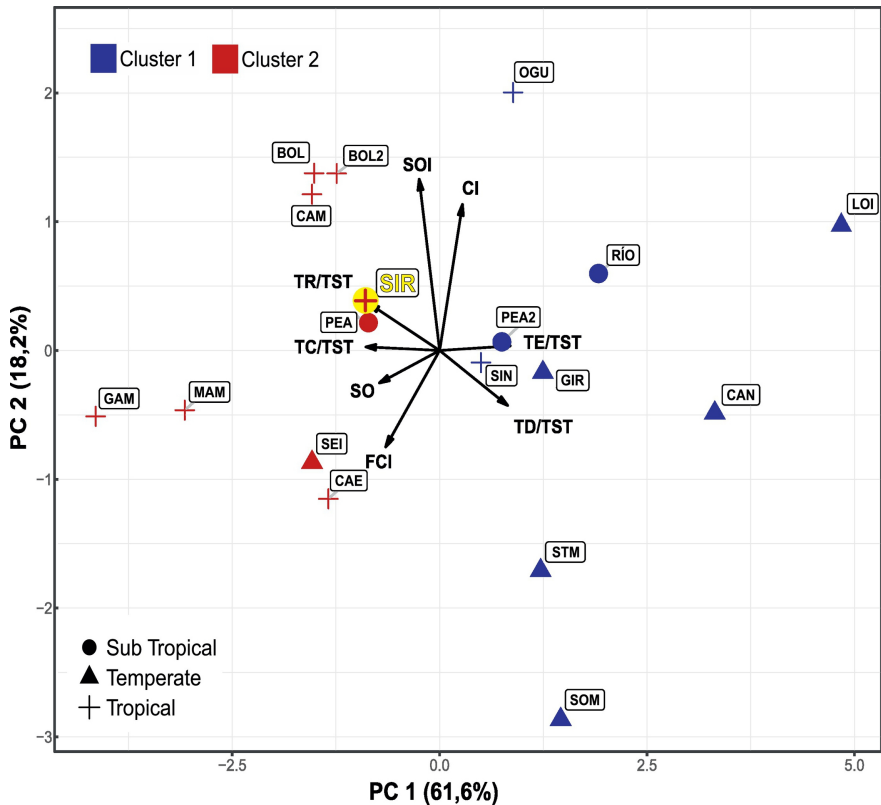


Figure 5

Geographic zone

Temperate

Sub Tropical

Tropical

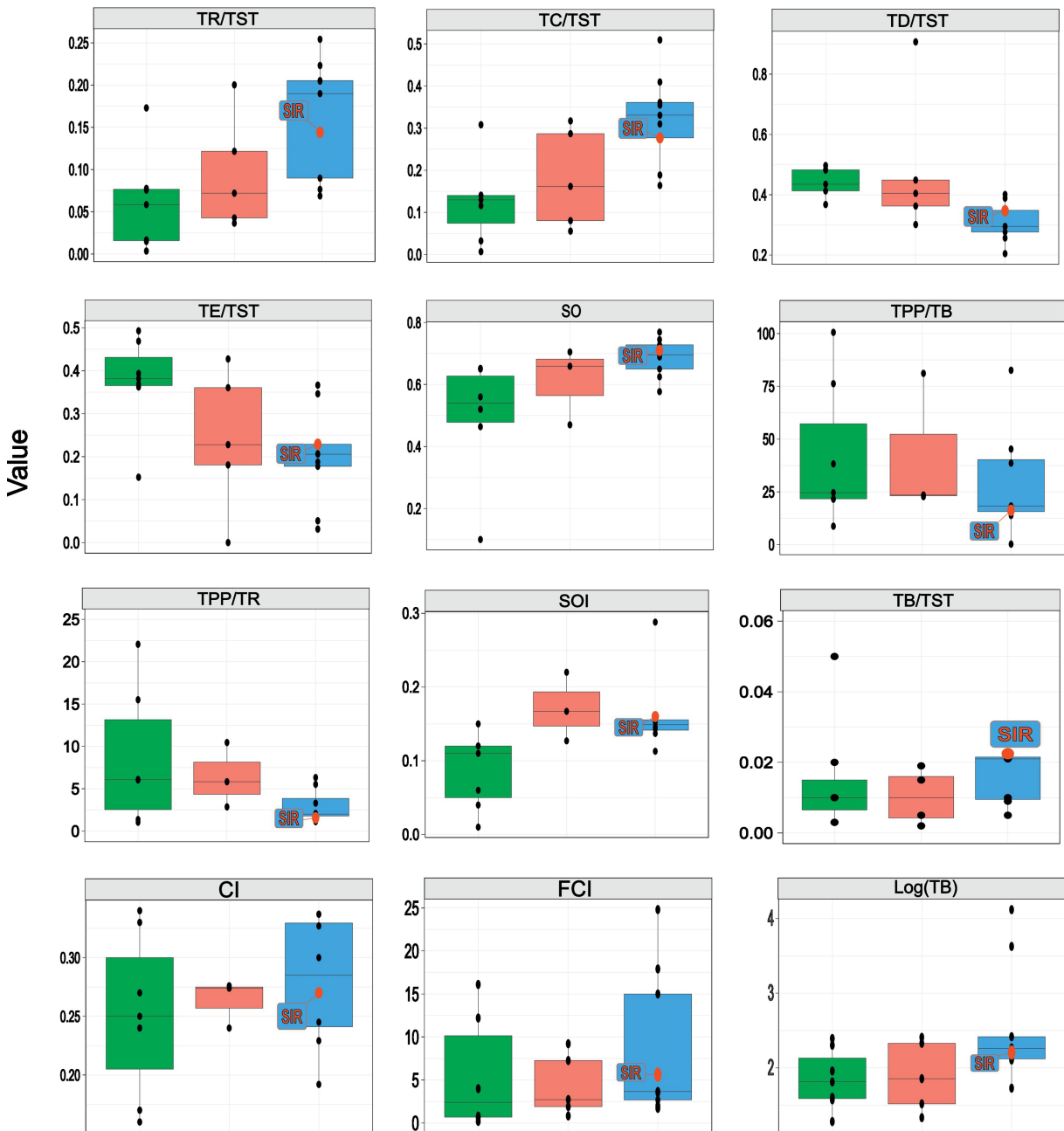


Figure 6