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Effect of fishing effort on the trophic functioning of tropical estuaries in Brazil

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A trophic web is a network of complex interactions and energy links between species. These interactions can be simplified into trophodynamic models, such as Ecopath (EP) and EcoTroph (ET), important tools providing the holistic view needed for the ecosystem approach to fisheries. We described food web structure and trophic interactions by developing an EP model for the Santa Cruz Channel (SCC), a large tropical estuarine system in northeastern Brazil, surrounded by mangroves and highly subject to the impacts of domestic pollution, industry, artisanal fisheries, and aquaculture. In addition, considering ecological and fisheries perspectives, we developed ET models in three neighboring Brazilian estuaries (SCC; Sirinhaém – SIR and Mamanguape – MAM) to explore levels of exploitation that affect their trophic functioning. Our EP and ET models consisted of 32 compartments (three primary producers, six invertebrates, 22 fish, and detritus). Keystone Index and Mixed Trophic Impact analysis pointed that several groups of commercial relevance are also ecologically relevant and lack fishing regulations, such as Snooks (*Centropomus* spp.), Jacks (*Caranx* spp.) and Barracudas *(Sphyraena* spp). Fishery impacts across the trophic level spectrum differ between ecosystems, which causes top-down effects depending on the exploitation dynamics of each system. The fishing pressure affects mainly the low and intermediate Trophic Level (TLs) in MAM and SCC and high TLs in the SIR estuary. Consequently, a decrease of biomass for low and high TL was found with the increasing of fishing effort, respectively. These findings are an important contribution to the trophic modelling of tropical estuaries, indicating that both EP and ET approaches can be effective tools to improve the understanding of the trophic functioning and fishery effect on estuarine ecosystems. Additionally, increasing the knowledge of key ecosystem processes in estuarine systems may help to enhance conservation initiatives for sustainable use of the ecosystem, such as protected areas, temporal control of fishing, and the catch size limit.

1. Introduction

Food webs consist of interactions and energy links among species and the environment (Thompson et al., 2012). It creates ecosystems, complex systems whose overall functioning is difficult to comprehend. Models attempt to replicate the major characteristics of the original systems to be realistic but also need to be simple enough to be understood as they are crucial for the clarification and understanding of this complexity (Brown et al., 2004).

Among ecosystem models, Ecopath with Ecosim (EwE) and EcoTroph (Christensen et al., 2005; Gascuel, 2005) are relevant tools for modelling aquatic food webs rather than ecosystems in the sense that

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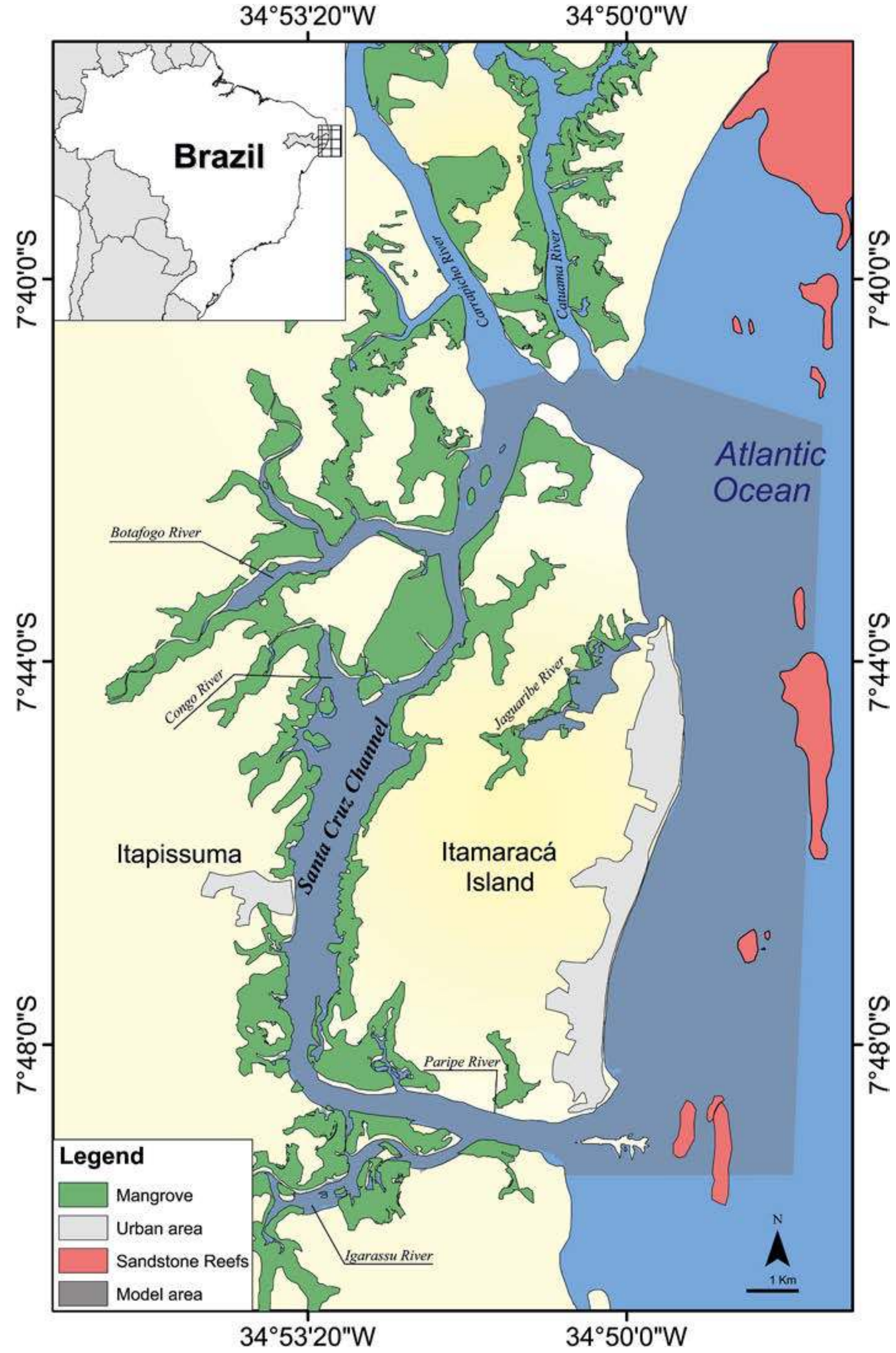

Fig. 1. Santa Cruz Channel estuary, northeastern Brazil, sampling stations and model area. The model area covers 56.2 km^2.

they do not represent direct interactions with the environment (Colléter et al., 2015). The EwE approach describes the food web resources and interactions among different ecological groups, identifying and quantifying major energy (biomass) flows in the food web accounting for fisheries (Colléter et al., 2012; Gasche and Gascuel, 2013; Rakshit et al., 2017). EwE has been recognized as one of NOAA's (National Oceanic and Atmospheric Administration) top ten scientific breakthroughs (Heymans et al., 2016). In complement, the EcoTroph approach (linked to the Ecopath model) quantifies the continuous distribution of the model biomass as a function of trophic level (Gascuel, 2005; Gascuel and Pauly, 2009), corroborating the theory that most marine animals feed on more than one TL (Odum and Heald, 1975). Both models are useful for evaluating the direct and indirect effects of fisheries (Freire et al., 2007; Halouani et al., 2015, 2016; Lercari et al., 2015; Natugonza et al., 2016; Rehren and Gascuel, 2020). This is especially crucial in coastal and estuarine zones where fishing and other anthropogenic perturbations are more severe (Colléter et al., 2012; Jackson et al., 2001).

Estuaries play an essential role in developing several species that use these systems for spawning, feeding, or completing their life cycles (Elliott et al., 2007; Potter et al., 2015). Many researchers have contributed to the increasing knowledge about the biological and ecological aspects of these ecosystems (Blaber, 2013; Elliott et al., 2007; Mclusky and Elliott, 2004), including areas where studies on trophic web interactions are still scarce, such as the coastline of Brazil (Campos et al., 2015; Claudino et al., 2015; Dolbeth et al., 2016; Lira et al., 2018; Paiva et al., 2017).

In the northeast of Brazil, the State of Pernambuco has 14 estuaries, including the Santa Cruz Channel estuary (SCC), one of the country's largest estuarine systems and integrates the Santa Cruz Environmental Preservation Area (CPRH, 2010). The SCC is the most productive estuarine complex in Pernambuco, with high fish biodiversity (Merigot et al., 2016) and essential small-scale fishery activity crucial for the local economy (Andrade and Silva, 2013; CPRH, 2010). SCC has a complex trophic web supported by high energy and biomass flows between estuarine and marine organisms (Figueiredo et al., 2006; Pelage et al., 2021; Vasconcelos Filho et al., 2003, 2010). As elsewhere, this estuarine system is affected by human occupation and has gradually become altered due to anthropogenic activities (Blaber and Barletta, 2016), which may change its productivity, biodiversity, and, consequently, its trophic interactions.

The increasing anthropic impacts caused by the multiple uses of estuaries are worrisome. Food-web models may help to understand the temporal energy flows within these ecosystems and how they respond to distinct anthropogenic impacts (Heymans et al., 2014). Changes in trophic flow may indicate, for example, seasonal change or intense catch of apex predators. In other cases, it can indicate negative impacts at the base of the trophic web since fisheries also target lower trophic level species (e.g., oysters, shellfish, and shrimps). We, thus, focus on two points. Firstly, develop EcoTroph models to explore the potential effect of different levels of exploitation on tropical estuaries. We focused on three neighboring Brazilian estuaries with diverse anthropogenic uses and an artisanal fishery of high socio-economic importance. Secondly, we provided key information for developing management actions in a Brazilian estuary of relevant socio-economic importance through the characterization of the food-web structure and its trophic flows based onan Ecopath model.

2. Materials and methods

2.1. Study area

The Santa Cruz Channel Estuary (SCC) is the largest estuarine system in the State of Pernambuco (Fig. 1), subject to intensive fishing and habitat degradation resulting from high levels of domestic pollution and industrial, touristic, and aquaculture activities (CPRH, 2010). The channel bottom consists of quartz sand and muddy banks dominated by *Rhizophora mangle*, *Laguncularia racemosa*, and *Avicennia* sp. (Neumann-Leitão et al., 2001). The Catuama, Carrapicho, Botafogo, Congo, Igarassu, and Paripe streams flow into the SCC, which communicates with the Atlantic Ocean through the Catuama and Orange River mouths, to the north and south of Itamaracá Island, respectively (Fig. 1). The channel, from north to south, is approximately 22 km long, a width of up to 1.5 km, and an average depth of 5 m. The surface water temperature varies between 25 and 31 °C, and salinity between 18 and 34 °C (Lacerda et al., 2004). The model of SCC covers a total area of 56.2 km^2 (Fig. 1). The site was chosen due to its high biodiversity and the state's largest landing area (IBAMA, 2008), considered crucial for the local economy.

2.2. Ecopath model

The Ecopath model was proposed by Polovina (1984) and further developed by Christensen and Pauly (1992). The model allows to estimate the trophic flows, production and consumption rates in a food web that describe the trophic structure by quantifying the energy flows within the ecosystem (Christensen et al., 2008). The main equation Eq. (1) of the Ecopath model (Christensen and Pauly, 1992; Christensen and Walters, 2004) is:

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

where B is the biomass of prey ($_i$) and predators ($_j$); PB$_i$ is the production/biomass ratio of i, equivalent to the total mortality coefficient (Z) or natural mortality rate (M; Allen, 1971) in an equilibrium state; QB$_j$ is the food consumption per unit biomass of group j; DC$_{ji}$, the proportion of the prey i in the diet of the predator j; EE$_i$ is the Ecotrophic Efficiency, representing the part of the total production transferred to higher trophic levels or captured by fisheries, ranging from 0 to 1; and EX$_i$ is the export of (i) and refers to the biomass that is caught through fishing and/or that migrates to other environments. Biomasses and flows are expressed in t.km^{-2} and t.km^{-2}.year^{-1}, respectively.

The calibrated model included 32 functional groups chosen according to relevance in terms of biomass estimated based on our samples, importance in landing considering the official statistics (2000–2007) (IBAMA, 2008), and different ecological guilds (Ferreira et al., 2019): three primary producers, six invertebrates, 22 fish compartments and one detritus group. Twelve among the 22 fish compartments were represented by more than one species grouped by ecological similarity and feeding habitats.

2.2.1. Data sampling and data input for each compartment

Biological fish data (e.g., abundance, length, and weight) were obtained monthly, from October 2013 to September 2014, with a seine net (67.5 m in length with a mesh size of 10 mm). Three replicates were carried out for each sample. Fish were identified and weighed. The stomach contents were analyzed for some species and used as input for the diet matrix (Supplementary Table S1). The sampled area was obtained by GPS tracking using the open-source image processing software ImageJ (Schneider et al., 2012). Landing data for this area, considering 2000 to 2007, were obtained from official Brazilian statistics (IBAMA, 2008) (See Supplementary Table S2).

Biomass values for fish groups were estimated by the sum of the individual weights of each group divided by the total trawled area (t. km^{-2}). The catchability model proposed by Lauretta et al. (2013) was used to correct the biomass values (Eqs. (2) and (3)), which are underestimated due to gear selectivity (Supplementary Table S3).

$$p = q \times E \times A^{-1} \tag{2}$$

$$N = \mathrm{C} \times p^{-1} \tag{3}$$

where p is the mean proportion of the population captured, q is the catchability coefficient, E is the fishing effort (total area sampled - km^2), A is the model area, 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 S3). Some species that only occupy part of the model area (Heymans et al., 2016) had their biomass values prorated by area, for example, in the gobiids group that is restricted to the channel area (9.12 km^2; Vasconcelos Filho and Oliveira (1999)), its biomass was prorated by a coefficient 9.12/56.2.

Biomass values of phytoplankton, epiphyton, and bivalves were obtained from the literature (Baltar, 1996; El-Deir, 2009; Figueiredo et al., 2006), while microphytobenthos, zooplankton, gastropod, worm, blue crab, and shrimp biomass were estimated by the Ecopath model. Considering the lack of information of EE values for these groups, we chose to use EE obtained from other models applied on nearby tropical estuaries (Lira et al., 2018; Villanueva, 2015; Wolff et al., 2000). When unavailable, information from estuaries models of more distant areas were used.

Production refers to increased living tissue within a functional group over a given period. The production/biomass rate (P/B) can be estimated under steady-state conditions as total mortality Z, which is the sum of fishing mortality (F) and natural mortality (M). This study estimated Z by linearized length-converted catch curves (Chapman and Robson, 1960; Pauly, 1983) using data from the study area (Supplementary Fig. S1). For species not fished, P/B ($year^{-1}$) is equal to M, computed as Pauly (1980) by Eq. (4):

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

where M is natural mortality ($year^{-1}$), k is the growth coefficient ($year^{-1}$), L_{∞} (cm) is the asymptotic length, and T is the mean water temperature (°C). The parameters k and L_{∞} are from the Von Bertalanffy Growth Function (VBGF) and were obtained from the literature or using the empirical equations of Le Quesne and Jennings (2012) and Froese and Binohlan (2000), respectively (Supplementary Table S4). The estimated mean annual temperature value was 29 °C.

Consumption is food intake by a group over a given interval of time. The annual consumption/biomass rate (Q/B; $year^{-1}$) for fish was estimated according to the following equation Eq. (5) (Palomares and Pauly, 1998):

$$Log\, Q/_{B} = 7.964 - 0.204 \times \log W_{\infty} - 1.965 \times T' + 0.083 \times Ar + 0.532 \times H + 0.398 \times D \tag{5}$$

where W_{∞} is the asymptotic weight (g), T′ is the temperature in Kelvin (T’ = 1000/(T°C + 273.15)), and Ar is the aspect ratio of the caudal fin (See details in Table S5). H and D represent the feeding type (H = 1 for herbivores; D = 1 for detritivores; H = D = 0 for other feeding habits). For the producers and invertebrate functional groups, P/B and Q/B values were obtained from the literature, using information from similar estuarine systems (Supplementary Table S5).

The Diet Composition matrix (DC) was constructed using information from stomach content analyses for several species from the study area or found in the literature (e.g., Lira et al., 2017; Vasconcelos Filho et al., 2010). All information and the sources thereof are given in Supplementary Table S6.

The Ecopath model is considered ecologically and thermodynamically balanced when: (i) EE < 1 for all functional groups; (ii) values of P/Q (Production/Consumption rate) are between 0.1 and 0.35, except for some fast-growing groups (Guenette, 2014); (iii) R/A (Respiration/Food assimilation) < 1; (iv) R/B (Respiration/Biomass) is between 1 and 10 for fishes and higher values for small organisms, (v) NE (Net efficiency of food conversion) > P/Q; and (vi) P/R (Production/Respiration) < 1 (Christensen et al., 2008; Heymans et al., 2016). The validation process also verified the negative relationship between Trophic Level and three main input values, B, PB, and QB (PREBAL routine; Link, 2010). Each model input value received a pedigree value between 0 (low precision information) and 1 (high precision information) to quantify model uncertainties for reliable parameterization of the Ecopath model (Christensen et al., 2005).

Additional nitrogen stable isotope data ($\delta^{15}N$) collected for several species (see details in Table S7) was used as a new validation criterion in terms of the accuracy of the diet matrix. Correlation (Spearman's coefficient) of the Trophic Level (TL) estimated by Ecopath with the nitrogen stable isotope composition ($\delta^{15}N$), considered a proxy of TLs, were examined, taking into account 17 functional groups of the SCC model. This approach has been used in previous studies (Deehr et al., 2014; Lira et al., 2018, 2021; Milessi et al., 2010; Navarro et al., 2011). The isotope data collection and analysis are detailed in Supplementary Material Table S7.

2.2.2. *Ecological Network Analysis (ENA)*

We used several ecosystem indicators and ENA indices to describe the energetic flows, community structure, and recycling (Christensen, 1995; Gubiani et al., 2011; Kones et al., 2009; Safi et al., 2019; Saint-Béat et al., 2015; Ulanowicz, 2004) (see Supplementary Table S8). We also used the Matrix Trophic Impacts (MTI) (Ulanowicz and Puccia, 1990), to assess the direct and indirect trophic impact through the trophic food web. This analysis allows the identification of key groups of the system quantified by the Keystone Index (KS3; Valls et al., 2015).

2.3. *EcoTroph model*

2.3.1. *The modelling approach*

In the EcoTroph model, the biomass considered in TL I is generated by the photosynthetic activity or recycled from the detritus and transferred to TL II by grazing processes on primary producers and biomass recycling by the microbial loops (Gascuel, 2005; Gascuel and Pauly, 2009). The biomass at trophic levels higher than II is distributed along a continuum of TL, based mainly on predation (Gascuel, 2005; Halouani et al., 2015).

In steady-state conditions, the biomass in trophic classes is derived from Eq. (6):

$$B_{\tau} = \frac{\varphi_{\tau}}{K_{\tau}} \times \Delta_{\tau} \tag{6}$$

where B_{τ} is the biomass of the trophic class [τ, $\tau+\Delta_{\tau}$], Φ_{τ} is the mean flow of biomass passing through that trophic class, and K_{τ} is the mean flow speed through that class. The flow of biomass (Φ_{τ}), which changes as a function of TL through natural mortality or losses from metabolism (excretion, egestion, and respiration) and fishing, is calculated as Eq. (7):

$$\varphi_{(\tau+\Delta\tau)} = \varphi_{\tau} \times \quad \exp[-(\mu_{\tau} + \varphi_{\tau}) \times \Delta_{\tau}] \tag{7}$$

where μ_{τ} is the net natural loss rate of biomass flow and φ_{τ} is the rate of fishing loss. The fishing loss rate ($\varphi\tau$) estimates the rate of fished production caught each year. This parameter can more accurately reflect fisheries' impacts on the ecosystem by TL, given that the effects (e.g., natural mortality and fishing mortality) on a species depend on its productivity.

The biomass transfer speed through the food chain (K_{τ}) is associated with changes in life expectancy caused by fishing and changes in predator abundance (Gascuel et al., 2008). Thus, the speed of the flow (K_{τ}) is expressed as Eq. (8):

$$K_{\tau} = \left[K_{ref,\tau} - F_{ref,\tau}\right] \times \left[1 + \alpha_{\tau}\frac{B^{\gamma}_{pred} - B^{\gamma}_{ref,\ pred}}{B^{\gamma}_{ref,\ pred}}\right] + F_{\tau} \tag{8}$$

where $K_{ref,\tau}$ is the speed of the flow at TLτ in the current state of the ecosystem, fishing mortality is $F_{ref,\tau}$; B_{pred} is the predator biomass of trophic groups from TLτ + 1; α determines the level of natural mortality (between 0 and 1) at TLτ that is dependent on predator abundance; and γ is a shape parameter (varying between 0 and 1) that defines the functional relationship between prey and predators. A value of γ = 1 results in the abundance of predators having a linear effect on flow kinetics, while smaller values reflect non-linear effects due to competition between predators. Additionally, the indirect effects of fishing and top-down control in the ecosystem can be observed when performing simulations (see details in Gascuel et al., 2011).

2.3.2. *Comparison of estuarine EcoTroph models*

We constructed an EcoTroph model based on the Ecopath model from the Santa Cruz Channel estuary (SCC model) and compared it with two other Ecopath models on Brazilian estuaries (Sirinhaém –SIR and Mamanguape – MAM) (Lira et al., 2018; Xavier, 2013). These estuaries are different in type, size, fishing intensity, and anthropogenic stressors (see details in Supplementary Table S9). Each model was calibrated using *EcoTroph* R package 1.6 developed by Colléter et al. (2013). EcoTroph is based on trophic level, biomass, catch, production, and Omnivory Index for each group from the balanced Ecopath models. Sensitivity analyses conducted by Halouani et al. (2015) showed that

Table 1

Basic inputs (in normal font) and estimated outputs (in bold) of the functional groups of the Santa Cruz Channel estuary model, northeastern Brazil. TL = trophic level, B ($t.km^{-2}$) = biomass, P/B ($year^{-1}$) = production per unit biomass, Q/B ($year^{-1}$) = consumption rate per unit biomass, EE = Ecotrophic Efficiency, OI = Omnivory Index, Y ($t.km^{-2}$) = landings. Values in bold were estimated by Ecopath.

	Functional group	TL	B	P/B	Q/B	EE	OI	Y
1	Epiphyton	**1.00**	1.37	153.31	–	**0.53**	–	–
2	Microphytobenthos	**1.00**	**2.06**	209.61	–	0.90	–	–
3	Phytoplankton	**1.00**	6.40	652.71	–	**0.33**	–	–
4	Zooplankton	**2.11**	**10.10**	50.21	150.65	0.90	**0.11**	–
5	Bivalve	**2.12**	**11.28**	2.00	9.00	**0.99**	**0.12**	8.32
6	Gastropod	**2.00**	**9.32**	2.65	38.83	0.90	–	–
7	Worms	**2.12**	**11.13**	2.91	17.26	0.95	**0.12**	–
8	Blue crab	**2.69**	**9.91**	2.00	8.00	0.8	**0.46**	4.89
9	Shrimp	**2.30**	**10.96**	2.81	26.90	0.95	**0.25**	2.29
10	Herring	**2.89**	**9.59**	2.01	19.36	0.82	**0.20**	11.55
11	Clupeiformes	**2.74**	3.39	2.28	26.46	**0.60**	**0.27**	–
12	Anchovies	**2.92**	0.30	1.58	18.92	**0.85**	**0.82**	–
13	Batrachoididae	**2.72**	1.21	1.11	8.37	**0.04**	**0.47**	–
14	Mullet	**2.03**	1.24	2.20	33.68	**0.90**	**0.03**	2.37
15	*Hyporhamphus unifasciatus*	**2.02**	0.38	1.13	4.50	**0.02**	**0.03**	–
16	Snook	**3.21**	0.15	1.96	6.00	**0.85**	**0.16**	0.25
17	Jack	**2.96**	0.24	0.48	6.95	**0.85**	**0.22**	0.07
18	*Oligoplites* spp.	**3.16**	0.05	0.98	15.95	**0.98**	**0.24**	–
19	Snapper	**2.61**	0.16	0.34	6.92	**0.55**	**0.45**	–
20	*Lutjanus* spp.	**2.64**	0.26	0.34	6.10	**0.98**	**0.49**	–
21	*Diapterus* spp.	**2.57**	0.77	4.09	12.10	**0.54**	**0.37**	0.07
22	*Eucinostomus* spp.	**2.43**	2.59	1.35	11.92	**0.49**	**0.33**	–
23	*Archosargus rhomboidalis*	**2.51**	1.92	1.01	8.11	**0.82**	**0.41**	–
24	*Sparisoma radians*	**2.09**	0.12	1.00	29.12	**0.99**	**0.09**	1.16
25	*Gobionellus stomatus*	**2.05**	9.27	1.18	33.34	**0.96**	**0.05**	–
26	*Gobionellus oceanicus*	**2.05**	4.56	1.45	30.65	**0.94**	**0.05**	–
27	Gobiidae	**2.05**	0.55	1.33	31.25	**0.84**	**0.05**	–
28	*Sphyraena* spp.	**3.23**	0.15	0.42	6.47	**0.28**	**0.12**	–
29	*Citharichthys spilopterus*	**2.50**	0.51	1.34	13.19	**0.72**	**0.37**	–
30	Flatfish	**2.57**	0.60	1.42	13.05	**0.78**	**0.39**	–
31	Puffer	**2.71**	5.74	1.56	6.15	**0.10**	**0.40**	–
32	Detritus	**1.00**	2.62	–	–	**0.25**	**0.29**	–

some of these parameters (mainly the α parameter) changed the magnitude of the result but not the observed trend. Hence, the default values, as recommended, were used for the parameters α and γ (0.4 and 0.5, respectively; details in section 2.3) (Bentorcha et al., 2017; Colléter et al., 2013). Thus, we focused on evaluating the distributions of the four attributes (biomass, catch, fishing mortality, and fishing loss rate) along the trophic spectrum related to the characterization and fishing impacts on the food web, to investigate the differences and similarities among estuaries.

In addition, the ET-Diagnosis routine simulated the fishing mortality multiplier for all trophic classes (mE from 0 to 5.0) to evaluate the effect of changing fishing mortalities along with the trophic spectrum (Colléter et al., 2013; Gasche and Gascuel, 2013). In this method, the current state is defined as mE = 1, while an unexploited ecosystem is represented by mE = 0, values between 0 and 1 represent a decrease in fishing mortality, and values above 1 represent an increase in fishing mortality. To evaluate the change in the biomass and catch, we compared the outputs of simulations with the current state where mE = 1.

A Generalized Additive Model (GAM) was made to indicate the profiles of biomass, catch, fish mortality, and fishing loss estimated by the EcoTroph model, described as follows Eq. (9):

$$\mathrm{B\ \ or\ \ C\ \ or\ \ F\ \ or\ \ F_{loss}} = \mathrm{s(TL,\ \ by:\ \ est) + est} + \varepsilon \tag{9}$$

where B is Biomass; C is the Catch; F is Fish Mortality; F_{loss} is Fishing Loss; TL is Trophic Level; est corresponds to the different estuaries, and (ε) is the residual error of the Gaussian model.

An additive model incorporates smooth functions of one or more covariates and is thus able to model non-linear relationships between covariate and response (See method details in Wood, 2003; Rose et al., 2012). To observe the differences among the estuary profiles, the fitted smooth functions were then compared with confidence intervals (95%) by pairs of ecosystems (SCC–SIR, SCC–MAM, SIR–MAM) via the use of a prediction matrix related to the fitted values of the response. When the confidence intervals do not overlap with the x-axis in 0, the values are considered significantly different, indicating significant slope changes. Statistical analyses were performed in R software (R Core Team, 2020) with the *MGCV* package, version 1.8–31 (Wood, 2003, 2004, 2011, 2017; Wood et al., 2016).

3. Results

3.1. Model balancing

The balanced Santa Cruz Channel Estuary (SCC) model reached an adapted predation rate in the diet matrix for some groups like *Gobionellus stomatus, Gobionellus oceanicus*, *Sparisoma radians, Oligoplites* spp., *Lutjanus* spp., and bivalves, which initially presented EE > 1. Thus, accepted ranges of production/consumption (P/Q), respiration/biomass (R/B), and respiration/assimilation ratios were obtained, which are considered important criteria to evaluate the balance of the model (see Supplementary Table S10). PREBAL diagnostics also confirmed that the SCC model agrees with biological reality since there are negative correlations between TL and B, P/B, and Q/B (Fig. S2). The pedigree index value (0.44) and the significant correlation between TL estimated by Ecoapth and $\delta^{15}N$ in the SCC ($r = 0.85$; $p < 0.05$) indicated acceptable accuracy of the input parameters (see Supplementary Table S7 and Fig. S3).

3.2. Basic estimates

The values of B, P/B, Q/B, EE, and landings for all groups (Table 1) revealed that benthic invertebrates represented half of the animal biomass, highlighting the bivalve and shrimp groups at 11.28 t km^{-2} and 12.38 t km^{-2}, respectively. The fish biomass represented 41% of the

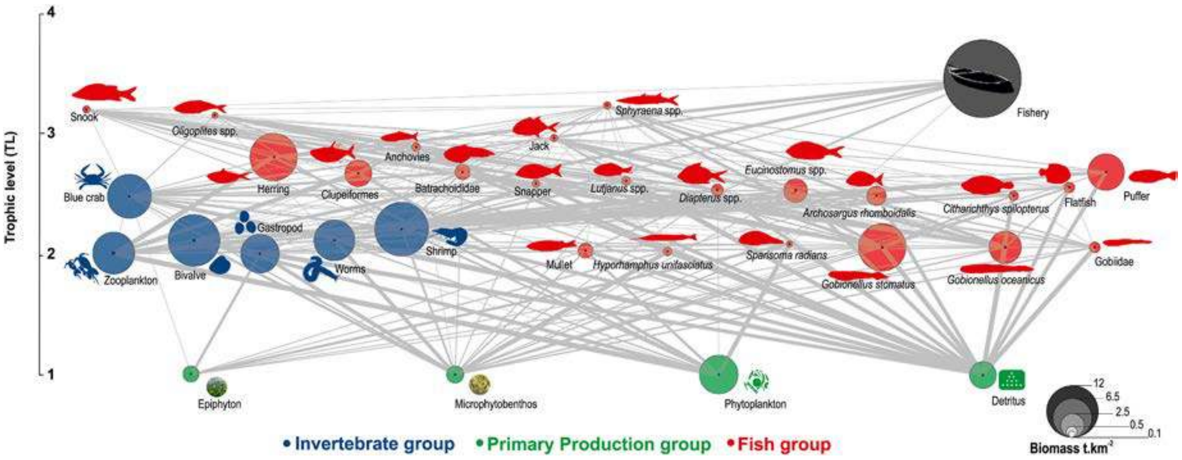

Fig. 2. Flow diagram of the Santa Cruz Channel estuary food web, northeastern Brazil.

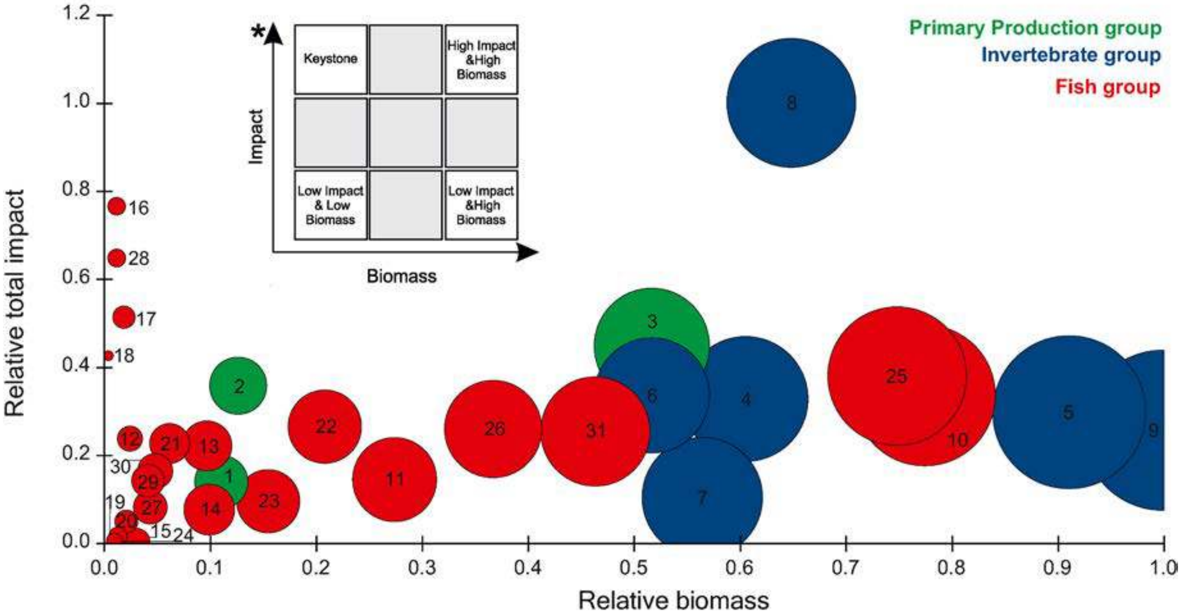

Fig. 3. Functional groups plotted against relative total impact and relative biomass for the Santa Cruz Channel estuary, northeastern Brazil. The numbers identify the functional groups of the model (listed in Table 1). The size of each circle is proportional to the biomass of the functional group. *Conceptual identification of keystone species in the food web (Valls et al., 2015).

animal biomass, with catches of approximately 36%. High EE values (0.8–0.99) were reported for some fish groups (e.g., Mullet, *Gobionellus oceanicus*, *Sparisoma radians,* and Herring), mainly due to high predation and capture by fishing activities. However, the EE values of the Batrachoididae, *Diapterus* spp., and puffer were considerably lower than those of other groups, since they are neither heavily predated nor fished (Table 1). The Omnivory index of SCC groups was low, indicating diet specialization, except for anchovies (OI = 0.82), which have high food plasticity (Table 1).

3.3. Food-web structure and trophic analysis

The mean trophic level of the SCC ecosystem was 2.23 (Table 1), and the highest TL value was 3.2 for snook and *Sphyraena* spp. (Fig. 2) The food web base is sustained by the high biomass of phytoplankton, microphytobenthos, and detritus. Invertebrates and fish (e.g., *G. stomatus, G. oceanicus*, *Eucinostomus* spp., puffer) were the functional groups with the highest biomass contribution in TL 2 (Fig. 2).

Most of the fish biomass and ecological production takes place at around TL II, as shown in Fig. 2, and the herbivore pathway is twice as high as the detritivore one (1545 vs. 796 t km^{-2}.year^{-1}), indicating that the energy flows mainly from the primary producers to the second trophic level. The transfer efficiency (TE) for TL II was 15%, decreasing to the highest trophic levels. The mean trophic level of the catch (TLc) was 2.44 and filter-feeders and invertebrates (e.g., bivalves, shrimps, *Sparisoma radians*, sardines, and mullets) were the groups most frequently caught (Table 1).

The Matrix Trophic Impacts revealed that increased blue crab biomass would negatively impact *Eucinostomus* spp., *Archosargus rhomboidalis,* and flatfish. Similarly, increasing *Gobionellus stomatus* biomass would negatively impact worms and gastropods. A rise in fishing, however, may cause an increase in *Sphyraena* spp. biomass and adverse effects on *Sparisoma radians*, mullet, snook, and jack (Supplementary Fig. S4).

Invertebrates generally had high biomass and low impact in the SCC model, except blue crab, which had high impact. The top predators,

Table 2

Summary of the morphology, anthropogenic impacts, fishing description, Ecopath and EcoTroph indicators, and current management actions for the three estuarine systems considered in this study. Fish.B and Inver.B: proportion of fish and invertebrates in the total biomass, respectively; TLc: Tropic level of the catch; TPP/TR: Ratio between Total Primary Production and Total Respiration in a system; A/C: relative ascendency; B flows: Main biomass flows across trophic levels; Catch flows: Main catch fluxes across trophic levels; Fishing mortality: Main fishing mortality across trophic levels.

Estuarine system	Morphology	Anthropogenic impacts	Fishing description	Main Ecopath Indicators	Main Ecotroph outputs	Current management actions	Sources
Mamanguape (MAM)	Type: Coastal plain Estuary (km^2):164 Vegetated area (km^2):54 Mean depth (m):2 Max. depth (m):9.8 Mouth width (km):3.4 Temperature (°C, annual mean): 26 Salinity (mean): 25.9	Aquaculture; industrial and domestic waste; and fishing.	Small-scale mainly targeting shrimps, shellfish, and crab.	Fish.B: <1% Inver.B: >80% Tlc:2.42 TPP/TR:1.22 A/C: 30.8% Key species: Sardines, crabs, shrimps, macroalgae	B flows: TL 2 to 2.5 Catch flows: TL 2.2 to 2.5 Fishing mortality: TL 2.2 to 2.8 and > 3.5	Protected area without management plan.	1
Santa Cruz Channel (SCC)	Type: Ria Estuary (km^2):49.8 Vegetated area (km^2):35.2 Mean depth (m): 7.5 Max. depth (m):20 Mouth width (km):1.3 Temperature (°C, annual mean ± SD): 26.6 ± 0.79 Salinity (annual mean ± SD): 28.5 ± 1.18	Aquaculture; industrial and domestic waste; and fishing.	Small-scale mainly targeting sardines, blue crabs, oysters, mussels, shellfish and shrimps.	Fish.B: 41% Inver.B: >50% Tlc:2.44 TPP/TR:3.10 A/C: 32.4% Key species: Jack and Barracuda	B flows: TL 2 to 3 Catch flows: TL 2 and 2.5 to 2.8 Fishing mortality: TL 2.5 > TL > 3.5	Protected area without management plan.	2; 3; 4
Sirinhaém (SIR)	Type: Coastal plain Estuary (km^2):18.7 Vegetated area (km^2):17 Mean depth (m):2.6 Max. depth (m):5 Mouth width (km):0.4 Temperature (°C, annual mean ± SD): 27.24 ± 2.47 Salinity (annual mean ± SD): 9.57 ± 3.69	Aquaculture; fishing; sugarcane production and other agribusiness industries	Small-scale mainly targeting snooks, catfish, mullet, oyster, and shellfish.	Fish.B: 26% Inver.B: >50% Tlc:2.68 TPP/TR:2.59 A/C: 29% Key species: Jack and Snook	B flows: TL > 2.5 Catch flows: TL 2 and 2.5 to 2.9 Fishing mortality: 3.0 > TL > 4.0	Protected area without management plan.	4; 5; 6; 7; 8

1. Xavier (2013); 2. Guimarães et al. (2010); 3. Medeiros and Kjerfve (1993); 4. Gonzalez et al. (2019); 5. CPRH (2001); 6. Silva (2009); 7. Lira et al. (2018); 8. Pelage et al. (2019).

snook, jack, and *Sphyraena* spp., were considered key groups with low biomass and high impact within the SCC trophic web (Fig. 3).

3.4. Statistics and ENA

In the SCC, the total system throughput (TST) was 10,794 t $km^{-2}.y^{-1}$ and the TPP/TR and TPP/TB were 3.10 and 46.84, respectively (Supplementary Table S11). The Connectance Index was 0.25, relative Ascendancy (A/C) was 32.46%, and Finn's cycling index was 2.71%, with a Transfer Efficiency Total value of 9.1%, close to the theoretical value of 10% (Supplementary Table S11).

3.5. EcoTroph models

Overall, the Mamanguape, Santa Cruz Channel, and Sirinhaém estuaries differed in fishery targets, composition, abundance, and food-web structure between ecosystems (Table 2), and consequently, they differed in terms of biomass and catch structure along the trophic spectrum (Table 2).

The largest proportions of total biomass and catch for the SSC model were found to be between TL II and III, decreasing at higher TLs (Fig. 4). Sirinhaém (SIR) showed biomass flows similar to SSC; however, the catch increased at higher TLs (Fig. 4). The Mamanguape estuary (MAM) had the highest proportions specifically between TL 2 and 2.5. In the SSC model, species with TL comprised between 2.5 and 3.5 were the main fisheries targets, with fishing mortalities higher than 0.4 $year^{-1}$. A decreasing trend appeared for higher trophic levels (Fig. 4). Low TLs (around 2.0) were characterized by low fishing mortality values (about 0.1 $year^{-1}$), except in the Santa Cruz Channel estuary, where F is close to 0.3 $year^{-1}$.

Groups with TLs from 3 to 4 were more affected by fishing pressure (maximum fishing loss rate, $\varphi\tau = 40\%$), indicating that 40% of the species production is caught annually, mainly in SCC and SIR estuaries. The exception was in the MAM estuary, where, although the fishing loss rates were lower than in other ecosystems, they were constant at TLs higher than 4.0 with $\varphi\tau = 25\%$ (Fig. 4).

The additive model also shows the difference in fitted trends for biomass, catch, fishing mortality, and fishing loss between the estuaries (SCC, MAM, SIR) (Fig. 5), where positive or negative slopes different from zero were observed. All relations between TL and biomass, catch, fishing mortality, and fishing loss for each estuary were significant (Supplementary Table S12). For SCC–SIR, a positive slope identified from TL 2.1 to 2.6 in biomass, and catch (Fig. 5) indicates significantly higher values (different from zero) in SCC compared with SIR. Both SCC

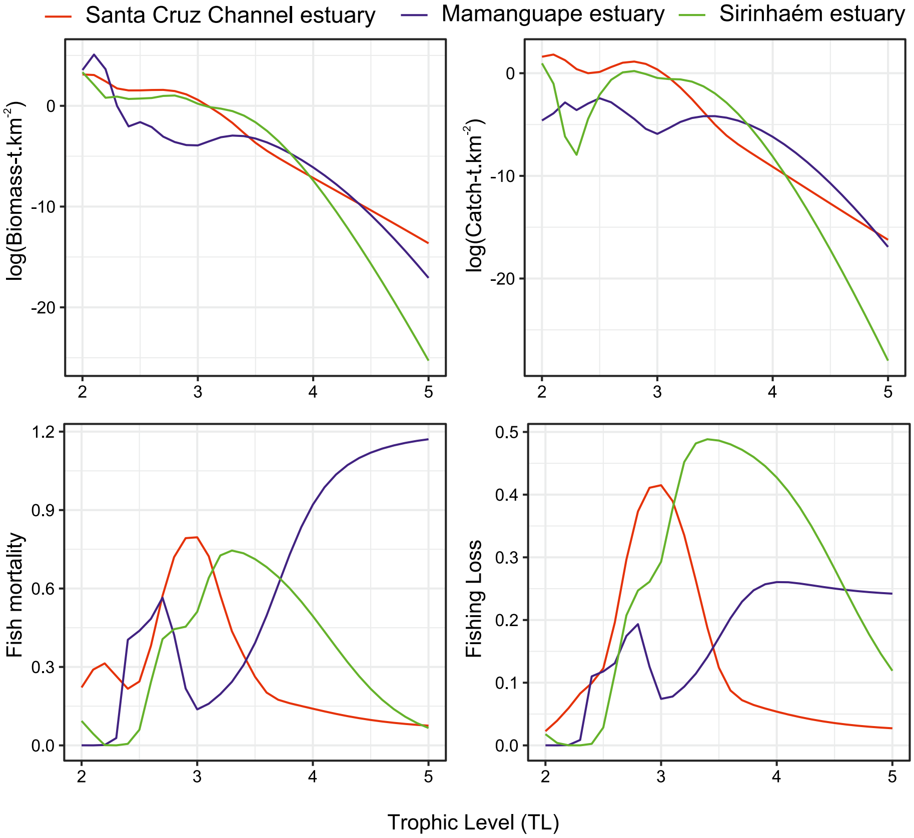

Fig. 4. The trophic spectra of biomass, fisheries catch, fishing mortality, and fishing loss for the three Brazilian estuarine ecosystems examined. Note: to obtain a better graphical representation of the biomass, spectra for TLs 1 and 2 were omitted.

and SIR ecosystems have greater biomass and positive trends between TL 2.3 and 3.4 compared with the MAM estuary (Fig. 5). Yet, the SIR estuary showed a significant negative slope, above TL 3.5 for biomass, catch, and fishing (mortality and loss), contrasting with MAM, which had higher values for this range of TL (Fig. 5).

The evolutions in the shape of the catch and biomass trophic spectra with changes in the fishing mortality were very similar among the estuaries. However, the biomass trophic spectra in the MAM estuary were less affected by the simulated fishing effort than in the SCC and SIR ecosystems, mainly due to high biomass in lower trophic levels (Fig. 6). In contrast, the total fisheries catch for all ecosystems increased as fishing mortality increases. In particular, in the SIR estuary, the catch changes were limited between trophic levels of 2.5 and 3.5, while for the other two simulated ecosystems, the catches were more greatly modified below TL 2.5 (Fig. 6).

Simulating the effect of an increase in fishing mortality on trophic spectra indicated that the biomass ratio (B/B_{ref}: simulated biomass/current biomass) at TLs > 3 decreased in all the ecosystems, but most markedly in the SCC estuary (Fig. 7). However, a simulation with no fishing (mE.0) revealed that, in SIR and MAM, TLs above 3.5 were positively affected (increases the biomass) by the reduction of fishery compared with the current scenario but, in SCC, this effect was more evident between TL 2.5 and 3 (Fig. 7).

The current state catches were compared with the simulated catches for each TL (Fig. 7). The three ecosystems showed differences in the catch trophic spectrum structure with increased fishing. In the SIR estuary, the simulated catches decreased as fishing effort intensified for TLs above 3.5, while the catches of species with low TL increased with fishing pressure. For the SCC and MAM estuaries, the increased fishing led to an increased catch throughout the trophic spectrum, except above TL3 in SCC and above 4.5 in MAM.

4. Discussion

4.1. Santa Cruz Channel Estuary Ecopath model

Here we developed an Ecopath model for the most productive estuary of Pernambuco State, the Santa Cruz Channel, in northeastern Brazil (Merigot et al., 2016; Vasconcelos Filho et al., 2010). The functional groups generally had low Omnivory Indexes, indicating a specialist diet, except for some groups, such as anchovies, that consume prey from multiple trophic levels (Pauly et al., 1993). The P/Q values in the SCC ranged from 0.03 to 0.33. High production and consumption rates of some fish groups indicate high productivity, which may be due to the high abundance of juveniles using the area as a refuge and nursery grounds (Villanueva, 2015). The SCC is a highly productive ecosystem (CPRH, 2010; Figueiredo et al., 2006), and many species, mainly marine migrants (Ferreira et al., 2019), are known to use this area as a nursery and for growth and feeding (Vasconcelos Filho and Oliveira, 1999).

The transfer efficiencies for TL II were compatible with that proposed by Testa et al. (2016), Ryther (1969), within the range of 10–20% suggested by Odum (1971). The highest biomass of primary consumers (e.g., invertebrates and fish) was observed in the SCC, given the dominance of fish at the lower trophic level (Vasconcelos Filho et al., 2003). Direct and indirect trophic interactions highlighted that blue crab, for example, has high biomass and could impact the overall trophic web (Araújo and Bundy, 2012) despite its high exploitation in the area (CPRH, 2010). Detritivore fish (e.g., gobiids and mugilids) widely impact the invertebrate functional groups, highlighting the importance of these groups in the ecosystem (Paiva et al., 2005). A decrease in biomass of the detritivore fish (e.g., Mullets) could be induced by an increase in fishing mortality, and it negatively would affect several other groups, such as snooks. In contrast, this positively impacted *Sphyraena* spp., possibly due to top-down effects or trophic cascades caused by the

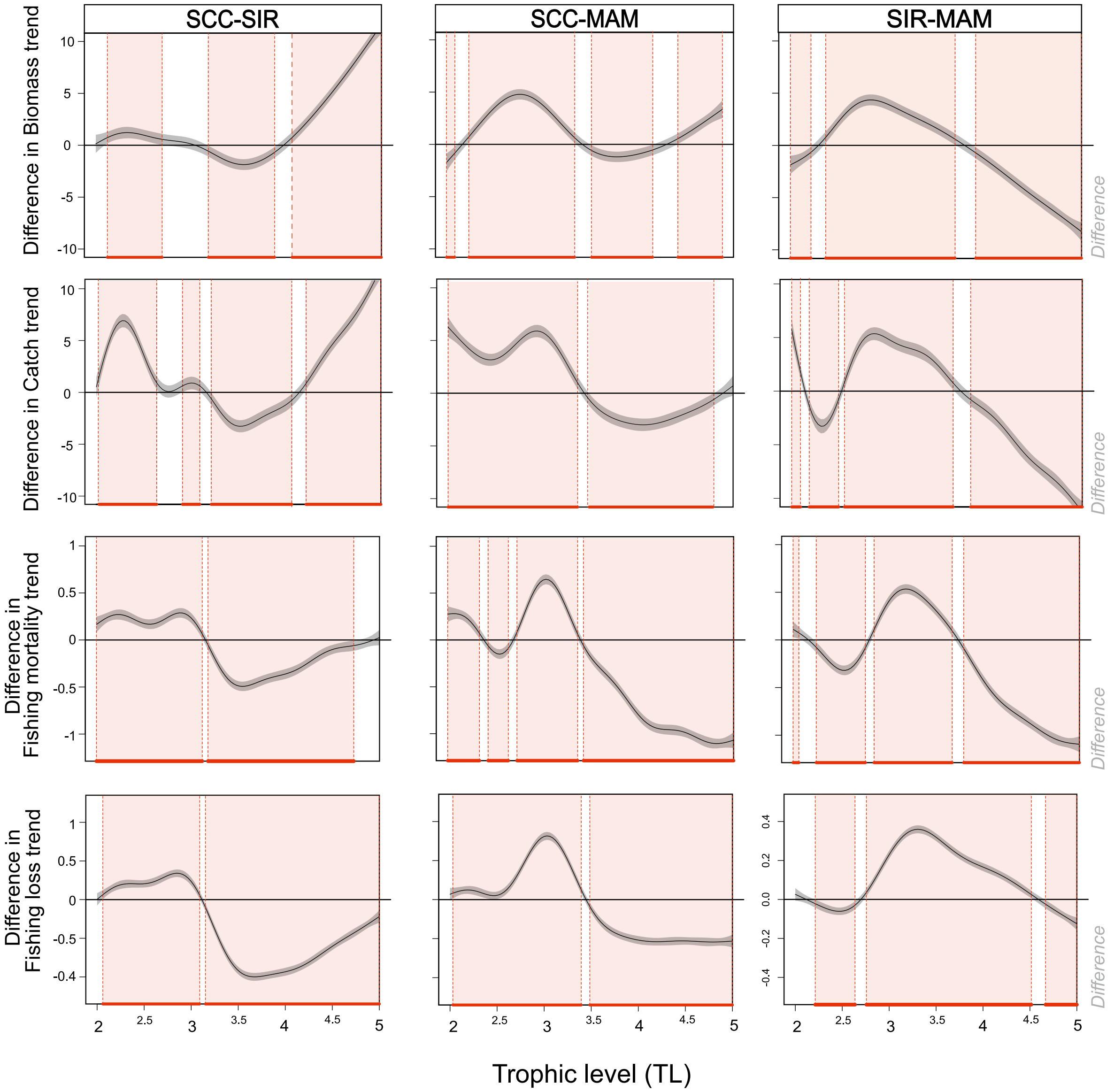

Fig. 5. Differences between fitted smooth functions from a Generalized Additive Model (GAM) (difference in trends; solid lines) and approximate, 95% confidence intervals on this difference for biomass, catch, fishing mortality, and fishing loss in pairs of estuaries (SCC = Santa Cruz Channel, SIR = Sirinhaém, MAM = Mamanguape). When the confidence interval does not overlap with the x-axis in zero, the value is significantly different, this is indicated by the transparent red box. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

removal of predators (Christensen et al., 2005).

The keystone species (snook, jack, and *Sphyraena* spp.) in the SCC include keystone species in the Sirinhaém estuary (snook, jack) (Lira et al., 2018), revealing their strong influence on these estuarine ecosystem food webs. Despite the unregulated fisheries, these species have a high ecological and commercial relevance. Therefore, they need to be better understood and monitored due to their essential role in controlling the food web in SCC. In addition, key species are crucial to the ecosystem balance (Bornatowski et al., 2017; Perry, 2010; Valls et al., 2015) and need to be closely considered by managers because of their potential impact to modify the trophic interactions in the food-web.

Ecological Network Analysis (ENA) is a valuable tool for understanding ecosystems and plausible future scenarios while evaluating environmental status (Coll and Steenbeek, 2017). In the SCC, the ENA implies that the environment is not a mature ecosystem, probably due to the continuous influence of the rivers, which maintain it in a constant state of perturbation. The low values of TST, TPP/TB, and TPP/TR were similar to those of other estuaries in northeastern Brazil (Lira et al., 2018; Xavier, 2013). The low values of SOI, CI, and AC may indicate that the trophic web of SCC is typical of an immature system. The low SOI of SCC was also found in other estuarine tropical systems (Lira et al., 2018; Villanueva, 2015), indicating that predators feed predominantly on the prey of low trophic levels, as observed by Vasconcelos Filho et al. (2003, 2009, 2010). The ENA indices in the SCC can be considered standard, as for those reported in other tropical estuaries (Lira et al., 2018): low Ascendency (A/C) and FCI values indicate a low level of organization of the food webs, characteristics of ecosystems in development (Heymans et al., 2014; Ulanowicz, 1986). While the SOI, CI, and A/C index indicated that SCC is immature, the SO suggests an intermediate-to-high level of potential resilience (capacities) (SO = 67%).

Furthermore, the high overhead (SO) of the network reflects a high proportion of parallel pathways in the system (Allesina et al., 2005), suggesting a high "energy reserve" (Heymans et al., 2014; Ulanowicz and Puccia, 1990) and thus high potential resilience (capacities). However, the definition of maturity and resilience based on ecological indicators

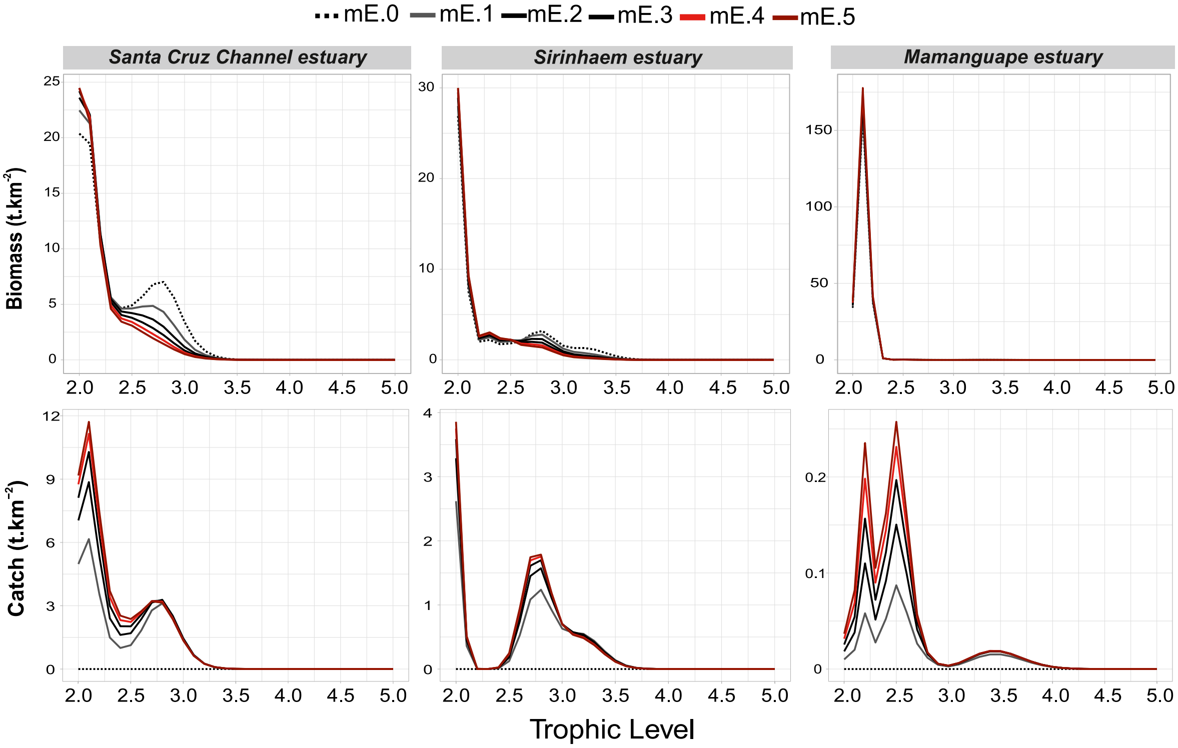

Fig. 6. The simulated biomass and catch for trophic spectra for fishing mortality multipliers (mEs; range: 0–5) in each Brazilian estuary examined.

(ENA) alone can be uncertain and lead to different conclusions (Christensen, 1995). For instance, in our analyses some indices indicated an immature ecosystem, while others point towards a developing stage. In general, estuaries and other coastal ecosystems (i.e., bays, reefs, lagoons, and shelves) are considered systems immature or developing due to their high dynamics (John and Lawson, 1990). Therefore, these environments require particular strategies to maintain the equilibrium state, such as ecosystem-based management considering the functional limits of the systems and integrating for instance river basins and marine coastal areas (Pallero Flores et al., 2017).

4.2. *Fishing impact on the trophic level spectrum for tropical estuaries*

The data used for this first comparison between EcoTroph models in Brazil were derived from the present study and two available EwE models of Brazilian estuaries (Lira et al., 2018; Xavier, 2013). Overall, the invertebrates (shrimps, blue crabs, and bivalves), small pelagic fish (herrings, anchovies), and piscivorous fishes (snooks, jacks, barracudas) are the main targets of the fisheries in the northeast Brazilian estuaries (Guebert-Bartholo et al., 2011; Silva-Cavalcanti and Costa, 2009; Vasconcellos et al., 2011).

The three estuaries considered here differed in biomass and catch structure along the trophic spectrum. These differences are mainly due to differences in fishery targets, abundance, and food-web structure among ecosystems. The high productivity of the benthic fauna that characterizes tropical estuaries (Bissoli and Bernardino, 2018) may explain the increased flow of biomass assessed between trophic levels 2 and 3.5. For example, in the Mamanguape estuary (MAM), the highest values of biomass and catches were estimated between TL 2.0 and 2.5. Target species in the MAM estuary mostly have low TLs, such as zooplanktivorous fishes (e.g., *Opisthonema oglinum* and *Mugil curema*), shellfish (*Anomalocardia brasiliana*), and oysters (*Crassostrea Rhizophora*) (Pimentel Rocha et al., 2008; Xavier et al., 2012).

Particularly in the SCC estuary, the high abundance of detritivore species, mainly fishes of the Gobiidae family (e.g., *Gobionellus stomatus*) (Ferreira et al., 2019; Merigot et al., 2016), is also reflected by the highest biomass values being between TL 2.0 and 2.5. Otherwise, in SCC, the fishing pressure on low and intermediate TLs, is associated with the exploitation of filter-feeders and invertebrates (bivalves, shrimps, Sparisoma radians, sardines, and mullets) (Lima and Andrade, 2018; Lira et al., 2010; Silva-Cavalcanti and Costa, 2011). This drives the system to a higher biomass reduction for TLs 2.5 to 3.0 with increasing fishing effort. These resources are often caught manually or by small boats with limited sailing range and are responsible for most of the landings in this region (Oliveira et al., 2019).

For the Sirinhaém estuary, the largest proportions of total biomass were found between TL 3 and 4, which is related to the high biomass of snook species (e.g., *Centropomus undecimalis* and *C. paralellus*) (Lira et al., 2018), commonly exploited by beach trawling and block net (Lira et al., 2017). In this estuary, low catches were found around TL 2–2.5, precisely due to the small number of target species fished. Consequently, with the increased simulated fishing effort, biomass increased for low TLs and a reduction for high TLs. Similar trends to the Sirinhaém estuary were observed in other marine ecosystems, such as in the Gulf of Gabes and the Adriatic Sea (Halouani et al., 2015). Therefore, it suggests an ecological aspect where the decrease in predation rate for the lower TLs is a result of the reduced abundance of higher TLs predators. Additionally, there is a second aspect associated with the nature of the local fisheries, which is mainly focused on high TLs. Since low TL species often have a high production/biomass ratio and they are not the main targets of fisheries and consequently are less sensitive to fishing pressure than higher TLs. In this type of trophic control, top predators determine the bulk of the biomass fluxes in lower TLs through direct and indirect effects (Dineen and Robertson, 2010; Testa et al., 2016). In terms of fishing, this process is also known as “fishing down the food web.” A gradual transition of landings starts on long-lived and high trophic level fishes to on short-lived, low trophic level invertebrates and planktivorous pelagic fish (Pauly et al., 1998; Pauly and Palomares, 2005). The top-down control has already been observed in large ecosystems of northeast Brazil, including the Pernambuco and Paraiba states, where the Santa Cruz Channel, Sirinhaém, and Mamanguape estuaries are located (Freire and Pauly, 2010).

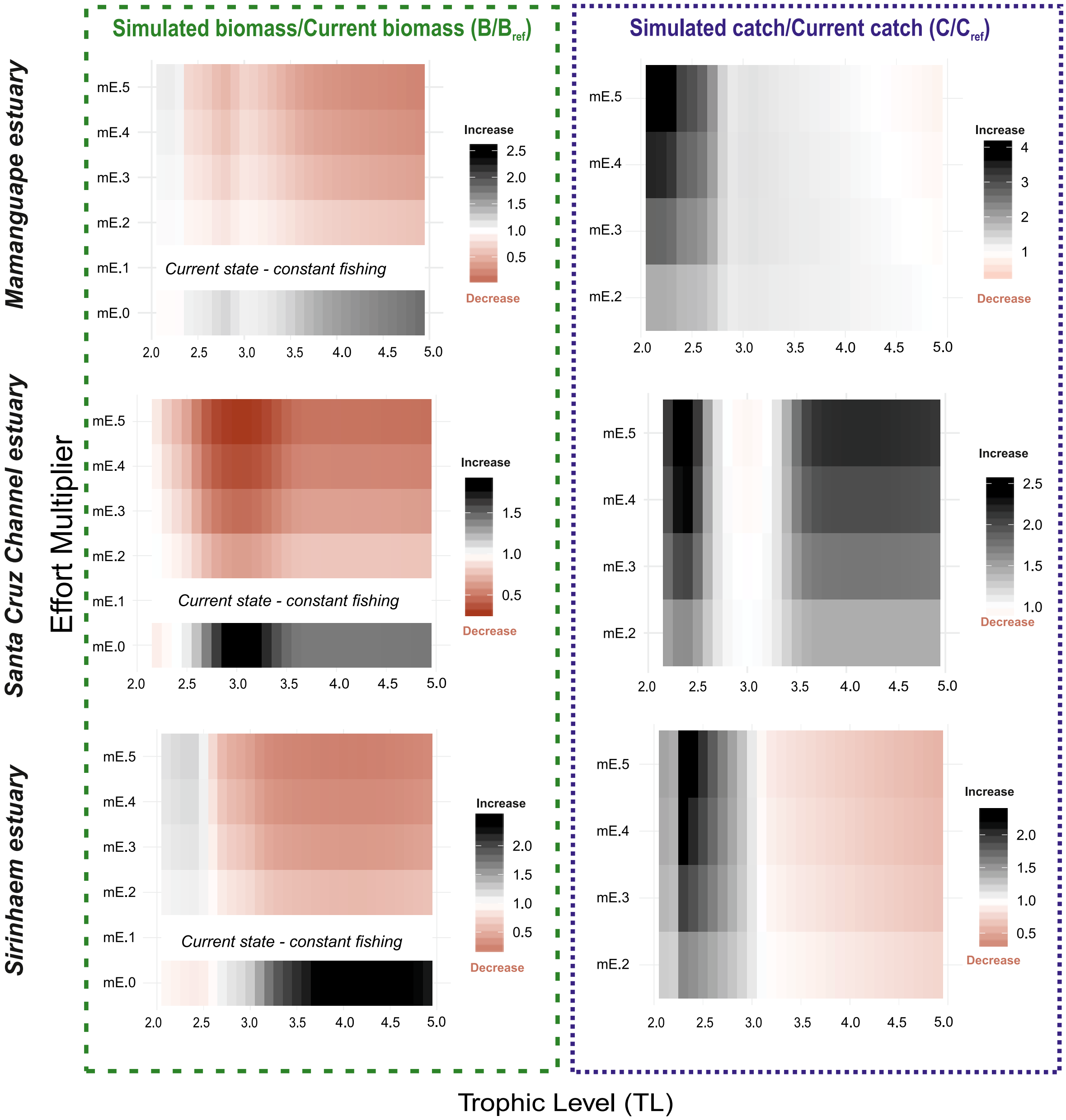

Fig. 7. The simulated relative fisheries catches (C/C$_{\text{ref}}$: simulated catch/current catch) and relative biomass (B/B$_{\text{ref}}$: simulated biomass/current biomass) for fishing mortality multipliers (mEs) ranging from 1 to 5 for each of the three Brazilian estuaries. To achieve a better graphical representation of the simulation, spectra for TLs <2 were omitted.

4.3. *Caveats of the SCC model*

Overall, our model followed the general rules/principles recommended by Darwall et al. (2010) and Heymans et al. (2016) and was consistent with the recommendations of Link (2010), available within the PREBAL routine. Information about organism movements in our study area is limited. Therefore, immigration/emigration processes, biomass accumulations, and thus net migration were not considered, as in other Ecopath models (Coll et al., 2006; Han et al., 2016; Patrício and Marques, 2006). Moreover, due to the lack of information discriminated by life stages (e.g., Biomass, life traits and etc.), we were unable to include multi-stanza groups, which could address this issue, to evaluate the ontogenetic effect in the model. In addition to the lack of data for some compartments (microphytobenthos, zooplankton, gastropod, worm, blue crab, and shrimp), we decided to use the EE values of other estuarine models (Lira et al., 2018; Villanueva, 2015; Wolff et al., 2000). Considering that those components have low TL and provide energy to the top of the trophic pyramid, the biomass estimates based on the chosen EE values were acceptable for balancing the food-web model. While fixing EE is not ideal, it is an overall process in balancing EwE models (Bornatowski et al., 2017; Chea et al., 2016; Zetina-Rejón et al., 2015) but can lead to problems of under-or overestimation of biomass, especially for primary producers (Heymans et al., 2016). In our case, we believe that fixing EE for a few groups (7 out of 32 groups) was not a problem for the model since much local information was used for most of the groups with high TL, including biomass and the diet of the main consumers and fishery statistics. Even considering the potential fragility of our choices, a clear correlation between the TLs assessed by Ecopath and δ^{15}N values were observed, indicating that the model may be reliable in predicting, with reasonable accuracy, the shifts and changes in trophic level and diet as assessed by stable isotopes (Deehr et al., 2014; Milessi et al., 2010; Navarro et al., 2011).

An Ecotrophic Efficiency (EE) with a value just above zero indicates that the trophic group is neither consumed by any other group in the system nor fished. Conversely, a value close to, or equal to, 1 indicates that the group is being heavily preyed upon and/or fished, preventing individuals to grow old (Ullah et al., 2012). EE values of top predator are expected to be low when not fished (Christensen and Walters, 2004). However, the high values for the predators snook and jack in our study may indicate the predominance of juveniles in the estuary, which are predated by other species in the SCC. The high EE of *Lutjanus* spp. and *G. oceanicus* revealed that these groups are highly predated and exploited in the SCC, mainly by fishing (IBAMA, 2008). The high EE of invertebrates (worms, gastropods, and shrimp) could be due to the dominance in the SCC of benthivores and detritivores that predate these groups (Ferreira et al., 2019; Vasconcelos Filho et al., 2003, 2010), as well as fishing targeting shrimps in this estuary (IBAMA, 2008).

4.4. Concluding remarks

As in other tropical estuaries, despite their economic, ecological, and social importance and inclusion in marine protected areas, the ecosystems analyzed here, have no official statistics or management proposition. In addition, the fisheries and other anthropogenic activities related to mangrove use (Pelage et al., 2021) are poorly regulated and reported, hampering ecosystem conservation and activity management. The structure in biomass flow and fishing along the trophic spectrum differed among the ecosystems studied. The decision-makers should consider the differential impact of fishing over the trophic structure under the Ecosystem Approach to Fisheries (EAF). In SIR, snooks and jacks (higher trophic levels) are key species (Lira et al., 2018) with no management regulation. As marine migrants, these species are also caught by other gears in the coastal zone (e.g., gillnet, hook and line), which increases their vulnerability given the multiple sources of anthropogenic impacts. SCC is one of the most productive estuaries in northeast Brazil, with high mortality in the lower trophic levels. These levels consist primarily of estuarine species such as bivalves, gobiids, and small pelagic fish, often used as the primary source of income by local communities. However, this estuary is subject to high tourism, agricultural, aquaculture levels, fishing activities, and the discharges of domestic and industrial effluents (CPRH, 2010). The latter have increased mercury concentrations beyond environmentally acceptable levels (Araújo et al., 2021) and reduced mangrove coverage in this area by 10% over the last three decades (Pelage et al., 2021). In this case, habitat degradation (Pelage et al., 2021) mainly affects the low trophic levels composed of the main target species of the multiple gears used in the estuary (Ferreira et al., 2019). This could lead to considerable changes in the exploitation of these resources and, consequently, the trophic spectrum of the catch. Likewise, MAM is a crucial estuarine system under substantial anthropogenic pressure with high catches at the lower trophic levels. Although it is in a protected area (MPA Mamanguape) and the region suffers similar impacts to the SSC area, some co-management actions have been reported (Soares et al., 2018). These measures could greatly help the conservation and sustainable use of aquatic resources, such as crabs and bivalves, whose exploitation is crucial as a local source of food and income (Nascimento et al., 2016; Rocha et al., 2012).

Therefore, despite their morphological differences, all the estuarine systems considered here have high socio-ecological importance, a high degree of connectivity with adjacent environments, and are part of protected areas where no management plans are being applied. Hence, it is imperative to consider the vulnerable key species highlighted here (such as snooks and jacks) and the high level of impact that may affect the trophic dynamics as a whole and, consequently, the sustainability of local fisheries essential for food security.

CRediT authorship contribution statement

Alex Souza Lira: Conceptualization, Formal analysis, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Flávia Lucena-Frédou:** Conceptualization, Formal analysis, Writing – original draft, Writing – review & editing. **Carlos Henrique Figueiredo Lacerda:** Formal analysis, Writing – original draft. **Leandro Nolé Eduardo:** Writing – original draft, Writing – review & editing. **Valdimere Ferreira:** Formal analysis, Writing – original draft. **Thierry Frédou:** Writing – original draft, Writing – review & editing. **Frédéric Ménard:** Writing – original draft, Writing – review & editing. **Ronaldo Angelini:** Conceptualization, Writing – original draft, Writing – review & editing. **François Le Loc'h:** Conceptualization, Formal analysis, Methodology, Writing – original draft, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The authors are unable or have chosen not to specify which data has been used.

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