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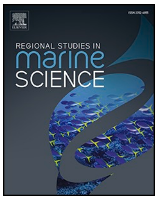

Trophic web structure and ecosystem attributes of a coastal lagoon system in the southwest Atlantic

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ABSTRACT

A comparative study of the lagoons that form the coastal lagoon system of Maricá-Guarapina (Southeast Atlantic, Brazil) was carried out based on the results of trophic models that describe the structure and functioning of each system. Two models were constructed using ECOPATH program to differentiate the main biomass fluxes in the systems. The model developed for Guarapina Lagoon considered 32 functional groups while that of Maricá Lagoon was developed with 29 that included primary producers to top predators, in addition to artisanal lagoon fisheries. The results indicated that biomass and production are concentrated at trophic levels 2 and 3 and the detritivore is more relevant than the grazing chain in both lagoons. This highlights the bottom-up control of our food webs despite the high trophic level of key groups. Otherwise, the increasing detritus could also reduce oxygen and influence most fish species, including mortality mass events reducing the fishery and the water quality. Ecosystem attributes suggest that both lagoons are in the intermediate stages of development. The low value of the Finn cycling index shows that Maricá Lagoon cannot recycle the organic matter, mainly because of the high input of nutrients. The importance of an ecosystem-based assessment, as presented here, constitutes an important tool for anticipating possible impacts from environmental disturbances on ecosystem functions, including the associated socio-economic challenges.

1. Introduction

Coastal lagoons have long been recognized as some of the most productive aquatic systems in the world (*e.g.*, Bueno-Pardo et al., 2018; López-Vila et al., 2019). They are large reservoirs of organic matter, within which critical biogeochemical processes cycle nutrients on a highly variable and dynamic regime (Knoppers and Kjerfve, 1999; Pérez-Ruzafa et al., 2019a). They constitute transition zones between the continental runoff from rivers and the sea, where marine and freshwater species may coexist. Wetlands, mangroves, salt marshes, and seagrass meadows within lagoons are important shallow water habitats harboring rich biodiversity, including, mollusks, crabs, fishes, and birds (Newton et al., 2018). Fishes and invertebrates may inhabit these biotopes permanently, cyclically, or occasionally, taking advantage of the constantly changing environment. Therefore, many of these species have particular physiological adaptations, allowing them to tolerate environmental extremes occurring at different scales in these ecosystems (Day et al., 2012). Estuarine-resident, estuarine-dependent, opportunistic marine, and occasional marine, freshwater fishes, shrimps, and crabs use coastal lagoons for food, shelter, and reproduction (Monteiro-Neto et al., 2008; Fortes et al., 2014).

Beyond nutrient processing, coastal lagoons also provide essential ecosystem services and goods, including water regulation, sediment retention, food provision (through fisheries and aquaculture), recreation, and aesthetic value (López-Vila et al., 2019). Unsurprising that coastal lagoons harbor a large part of the human population that may depend directly on these ecosystems (Newton et al., 2018). Yet, notwithstanding their relevance and the fact that coastal lagoons are

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among the most studied ecosystems in the world (Pérez-Ruzafa et al., 2011a), they are also one of the most threatened aquatic environments on the planet due to tremendous human pressure. Anthropogenic activities, such as sewer pollution, eutrophication, draining of wetlands, overfishing, urban development, oil and gas exploration, and modifications on the natural flow of rivers, may directly or indirectly affect biodiversity, ecology, function, and structure of coastal lagoons (Day et al., 2013; Ruiz et al., 2012; Raposo et al., 2018).

Understanding how human-induced effects may change ecosystem structure must use environmental monitoring and analytical tools to validate reasonable predictions. Under these circumstances, mathematical models are valuable tools for studying aquatic ecosystems' structure and functioning, performing ecosystem comparisons, deriving emergent properties, and assessing human activities. While species within ecosystems are organized through their trophic interactions, modeling food webs integrate information on population dynamics, community structure, species interactions, biodiversity, ecosystem productivity, and community stability (Rooney and McCann, 2012). Under such premises, the Ecopath with Ecosim (EwE) software is one of the most recognized tools, with worldwide acceptance (López-Vila et al., 2019), that provide an overview of the ecosystem's trophic state using few data requirements (Christensen et al., 2008). Designed to evaluate energy flow through trophic linkages under mass balance (Christensen and Pauly, 1992), it provides information on system growth and development and its resilience capacity. Such models may be used as a common framework for comparative studies, with the advantage of assessing biomass response as a function of ecosystem changes derived from natural or anthropic pressures (Christensen et al., 2008).

This study used the Ecopath with Ecosim mass-balanced modeling software (Christensen and Pauly, 1992; Christensen et al., 2008) to describe the trophic structures of two interconnected lagoons, Maricá and Guarapina. These lagoons are part of a regional complex system of coastal lagoons on the southeastern coast of Brazil (Knoppers and Kjerfve, 1999), which are of substantial social, economic, and ecological value. We aimed to gather and integrate existing data and represent in a comparative way between the two primary components of the system, Maricá, and Guarapina lagoons, providing a broader picture of interactions between biological components and how abiotic conditions shape their structure, metabolism, and ecosystem function.

Considering that the Guarapina Lagoon is permanently connected to the sea by a channel and that its salinity is higher than the other lagoons that make up the Maricá-Guarapina Lagoon System, the following hypotheses have been formulated to be tested. Is the composition and abundance of fish species in the Guarapina Lagoon different from the other lagoons that form the Maricá-Guarapina Lagoon System? Consequently, this composition makes the trophic structure of the Guarapina Lagoon distinct from the other lagoons that make up the Maricá-Guarapina Lagoon System.

2. Methods

2.1. Study area

The Maricá-Guarapina Lagoon System (MGSL) is located on the southeastern coast of Brazil, between 22º52’ - 23º00’ S and 43º00’ - 42°45’ W (Fig. 1) and is part of a set of coastal lagoons that extend along a narrow plain, with approximately 120 km of coastline formed approximately at 5500 years ago, in the last marine regression in the Holocene (Knoppers and Kjerfve, 1999). The MGSL has a circular shape and a total area of 37.25 km^2. It includes four interconnected lagoons, the lagoons of Maricá, Padre, Barra, and Guarapina (Machado and Knoppers, 1988). The drainage basin comprises the Vigário and Ubatiba rivers, both flowing into the Maricá Lagoon, and the Caranguejo river, which flows into the Guarapina Lagoon (Cruz et al., 1996; Laut et al., 2019). Regional climate is humid to semi-humid tropical with annual rainfall between 1100 and 1500 mm, average temperature of 23.2°C, and humidity of around 80 % (Laut et al., 2019).

The Guarapina lagoon has an area of 6.50 km^2 and depths varying between 2.0 and 5.0 m (Knoppers et al., 2004). It is permanently connected to the sea by the Ponta Negra Channel, built-in 1951. The average water temperature is 28.4°C and the salinity is 17.2 (Laut et al., 2019). The Maricá Lagoon has a typical morphology, with narrow bottlenecks that forming semi-enclosed compartments locally called Maricá, Barra, and Padre lagoons, covering an area of 30.75 km^2. This set of interconnected compartments will be called from now on the Maricá Lagoon (the largest of all three). Depth varies between 0.5 and 1.5 m, average water temperature is 29.8°C and salinity 1.6 (Laut et al., 2019). To one side, the Maricá Lagoon is connected to the sea by the Brejo Channel, which is about 30 km long and has very limited water circulation. To the other, is connected to the Guarapina Lagoon by a narrow and shallow channel, thus forming the Maricá-Guarapina Lagoon System. The intrusion of salt water through the Ponta Negra channel, the discharge of

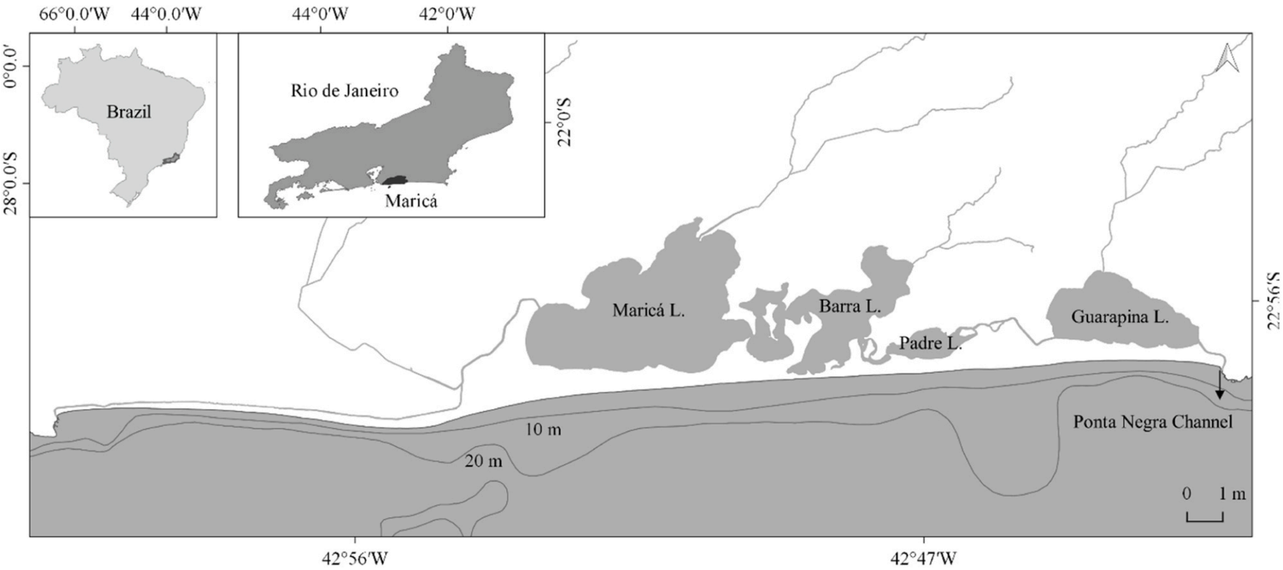

Fig. 1. The Maricá-Guarapina Lagoon System, with four interconnected lagoons, the lagoons of Maricá, Padre, Barra, and Guarapina. The Ponta Negra Channel is indicated with the black arrow.

rivers and the input of domestic sewage are the main factors influencing the entry of nutrients into the system (Carmouze et al., 1991; Knoppers et al., 1991; Knoppers and Kjerfve, 1999).

The fishing activity within the Maricá-Guarapina lagoons has socioeconomic importance for the population, contributing to the fish supply in local and regional markets. There are 12 fishing communities with about 120 fishermen working daily, and generating an estimated annual production of 128 tons in Maricá lagoon. On the other hand, the Guarapina lagoon is less intensively exploited and captures are concentrated mainly along the channel connecting the sea (Costa et al., 2022).

2.2. Field work

Between July 2013 and June 2014, a systematic program of bimonthly biological sampling was carried out at 15 points distributed throughout the lagoons. Fish samples were obtained using three different fishing gears: a) otter trawl, with a net 120 m high and 840 m wide, towed at constant speed for ten minutes; b) beach seine with 8.5 m wide and 2.6 m high, with 5 mm mesh on the bag, and 13 mm on the wings, hauled by two people over a 20 m beach stretch at each sampling station; c) a circular cast net, with a perimeter of 12 m and, mesh size of 7 mm, thrown three times randomly at each sampling station. Crustaceans were collected in the beach seine (crabs and blue crabs) and the cast net (shrimps). Benthic organisms were collected using a Van Veen grab sampler (area 0.048 m^2) in three replicates launches.

2.3. Modelling approach

The food webs of the Maricá and Guarapina lagoons were constructed using the ecosystem trophic modeling software Ecopath with Ecosim (EwE) 6.6.5 (Christensen et al., 2008). This program allows the elaboration of static models of mass balance, integrating energy fluxes and biomass information between functional groups of one or more species sharing similar life history parameters and ecological functions in the ecosystem.

For the elaboration of the trophic models, four input parameters are needed for each functional group: biomass (B); biomass production (B/P); consumption by biomass (Q/B), and ecotrophic efficiency (EE). If one of these parameters is not provided, it is estimated by the program itself, based on the consumption of the other groups, based on the assumption that the production of one group is used by the others within the system (Christensen and Pauly, 1992). These data are complemented with a predator-prey matrix that indicates which fraction of each functional group is part of the diet of all other groups. Along with these input parameters, information about the species' diet is applied to the basic linear equation of the Ecopath, in which the predator's consumption causes the mortality of its prey (Christensen and Pauly, 1992). EwE models are developed based on a set of linear equations, one for each functional group as prey (*i*) and as a predator (*j*), representing the biomass fluxes in the ecosystem, which is assumed to be in equilibrium. The master equation of EwE is:

$$\mathrm{B_i} * \left(\frac{P}{B}\right)_i * \mathrm{EE}_i = \mathrm{Y}_i + \mathrm{B}_i * \left(\frac{P}{B}\right)_i * (1 - \mathrm{EE}_i) + \sum_{j-1}^{n} \mathrm{B_j} * \left(\frac{Q}{B}\right)_j * \quad \mathrm{DC}_{ji}$$

where, *B* is the biomass, *P/B* and *Q/B* are the production/biomass and consumption/biomass ratios respectively, *EE* is the ecotrophic efficiency, DC*ji* is the fraction of prey *i* in the diet of predator *j*, and Y*i*, the total fishery catch rate of *i* (Christensen et al., 2008).

2.4. Functional groups

Thirty-two functional groups were considered for the construction of the Guarapina Lagoon model and twenty-nine for the Maricá Lagoon (Table 1). The composition of the functional groups was defined based on the criteria of taxonomic similarity and life history parameters of the species, especially in relation to their diets, abundance in biomass, and importance for local fisheries.

Table 1
Functional groups of the Guarapina (GL) and Maricá (ML) lagoons and their constituent species. Compartments and species with one * were present only in the GL model, and species with double * * were present only in ML.

N°	Compartment	Species
1	Aquatic birds	_Nannopterum brasilianus, Ardea_ spp., _Egretta thula, Platalea ajaja_
2	_Centropomus_ spp.	_Centropomus parallelus, C. undecimalis_
3	Carangidae*	_Carangoides bartholomaei_*, _Trachinotus falcatus_*
4	Flatfishes	_Achirus lineatus, A. declivis_*, _Symphurus diomedianus_*, _S. tessellatus_*
5	_Genidens genidens_	_Genidens genidens_
6	Gerreidae	_Diapterus rhombeus, Eucinostomus argenteus, E. gula, E. melanopterus, Eugerres brasilianus_**
7	_Hoplias malabaricus_	_Hoplias malabaricus_*
8	Ladyfish	_Albula vulpes, Elops smithi_
9	_Pogonias cromis_	_Pogonias cromis_
10	_Anchoa_ spp.	_Anchoa januaria, A. filifera_
11	_Micropogonias furnieri_	_Micropogonias furnieri_
12	Sardines*	_Cetengraulis edentulus_*, _Harengula clupeola_*, _Ophistonema oglinum_*
13	_Atherinella brasiliensis_	_Atherinella brasiliensis_
14	_Brevoortia aurea_	_Brevoortia aurea_
15	Gobiidae	_Gobionellus oceanicus, Ctenogobius boleosoma, C. stigmaticus, C. shufeldti_*
16	_Mugil_ spp.	_Mugil curema, M. liza_
17	_Geophagus brasiliensis_	_Geophagus brasiliensis_
18	_Coptodon rendali_	_Coptodon rendali_
19	Poeciliidaes	_Phalloptychus januarius, Poecilia reticulata, P. vivipara_
20	Crabs	_Neohelice granulata, Acantholobulus schmitti_**
21	Blue crabs	_Callinectes sapidus, Arenaeus cribarius_*
22	Shrimps	_Farfantepenaeus_ spp., _Litopenaeus schmitti_
23	Bivalve molluscs	_Tagelus plebeius, Anomalocardia brasiliensis_*
24	_Heleobia australis_	_Heleobia australis_
25	Benthic microcrustacea	Tanaidacea, Gammaridea, Isopoda
26	Polychaeta	_Alitta_ sp., _Capitella_ sp., _Heteromastus_ sp., _Laeonereis_ sp., Polydora, _Sigambra_ sp., _Streblospio_ sp.
27	Oligochaeta	Oligochaeta
28	Nematoda	Nematoda
29	Zooplankton	Appendicularia, Chaetognatha, Cladocera, Coelenterata, Copepoda, _Ctenophora_, Euphausiaceae, Mysidaceae, Pteropoda, Rotifera, Thaliacea, Turbellaria, Amphipoda
30	Phytoplankton	Chlorophyta, Cryptophyceae, Diatomophyceae, Euglenophyceae, Xantophyceae
31	Macrophytes	_Thypha domingensis_
32	Detritus	Organic matter

2.5. Input data

The biomass per area of many functional groups was estimated from primary data obtained during the sampling program. Thus, we used three fishing gears: otter trawl, beach seine, and cast net. The otter trawl has 0.84 m of width, and 555.5 m was the mean distance covered by the boat, resulting in a trawled area of 466.62 m^2 by sampling. The beach seine has 9 m of the width with 20 m of the covered distance, resulting in a trawled area of 180 m^2 by sampling. The cast net has a radius of 1.91 m and an area of 11.45 m^2 by casting. The total area was calculated by multiplying the area of each fishing gear by the number of times it was used.

For fishes, in Guarapina the total area dragged from each fishing gear (15,703.92 m^2) was multiplied by the biomass of each species (g). For species that were grouped such as “Sardines” a proportion was made on the area of fishing gear used, so that there would not be an underestimation/overestimation of values. In Maricá the values were calculated by dividing the total biomass of each compartiment by the total area dragged (109,544.64 m^2).

For crabs and blue crabs compartments, the biomass per area was calculated in the same way, considering only the beach seine sampling (180 m^2 in Guarapina and 24,480 m^2 in Maricá) (Appendix A. Supplementary material). The shrimps biomass per area values were generated based on the samples obtained with the cast net (11.45 m^2 and 706.9 m^2 Guarapina and Maricá, respectively) (Appendix A. Supplementary material). The benthic organisms were collected from 132 samples obtained with a Van Veen grab sampler, totaling an area of 6.34 m^2 in Maricá. These values were also applied to the Guarapina model. The zooplankton, Nematoda and Macrophytes compartments had their biomass values estimated by the EwE program in both models.

The biomass values per area for phytoplankton of the two models were calculated from the data of Chl.a (g/m^3), available in Knoppers et al. (1999). In Guarapina the Chl.a value was 43 $g/WW/m^3$, it was transformed into g/m^2 and multiplied by the euphotic zone of the lagoon 0.64 m, resulting in a value of 27.52 g/m^2, which was used in the model. For Maricá, an average was made between the maximum (190 g/m^3) and minimum (87 g/m^3 values, obtaining a value of 138.5 g/m^3. This Chl.a value of 138.5 g/m^3 was multiplied by its Maricá euphotic zone (0.54 m) resulting in a value of 74.79 g/m^2, which was used in the model. The total values were divided by the areas of each modeled lagoon. An estimate of aquatic bird biomass was obtained from a model developed for the Araruama Lagoon (Almeida-Silva, 2015), a nearby system located within the same coastal plain of the present study.

To respect the physiological characteristics of the species, the values of the other input parameters (production per biomass - P/B, and consumption per biomass - Q/B) were the same in both models (Table 2). Such values were obtained in ecosystem models of other coastal lagoons or similar environments. The P/B and Q/B parameters for each functional group were obtained from several sources. For fishes, we used the life history tool available on the FishBase website (Froese and Pauly, 2021). This tool uses a set of information on the characteristics of different populations made available in FishBase site. For other groups, these parameters were adapted from other published models developed for similar coastal lagoons, and if possible, geographically close. When the functional groups included two or more species, the values were calculated as a weighted average respecting the participation of each one.

Diet composition is one of the essential input parameters for the elaboration of the trophic web to determine trophic level and additional attributes of functional groups (Pauly and Christensen, 2000). To build the predator-prey matrix, information on the feeding habits of the species that make up each functional group was used. This information was generated from the analysis of the stomach contents of fish species found in the lagoons, added to data available in the literature for other groups (see Supplementary materials).

In order to verify the effects of fishing on the studied ecosystems, we incorporated biomass values from the captures carried out over an annual cycle (2019) into the trophic model (Table 2). Information on fisheries production was obtained through a program of systematic monitoring of landings carried out in the various artisanal fishing communities that operate in and around the lagoons. Among the fishing gears that operate in the lagoons, our study defined four fishing gears. Three to Marica lagoon (seine net, gillnet, puça trap and casting net) and one to Guarapina lagoon, in which we bring together the two most frequent fleets (seine net and casting net). The production values obtained in each lagoon for each fishing gear and target species were measured by their areas, generating estimates of annual fishing production per area. These estimates were included in the models.

2.6. *Balancing the model*

To evaluate the input parameters, biomass, and vital rates, the prebalancing diagnostic routine (PREBAL) was applied (Link, 2010). We followed the balancing routines of Ecopath models proposed by Heymans et al. (2016) in which the balanced model must have Ecotrophic Efficiency (EE) values lower than 1.0. In cases where this value was greater than 1.0, the diet matrix was adapted. The Production by Consumption (PQ) values must vary between 0.1 and 0.3; the values of respiration rate by assimilation must present values lower than 1.0; and values of the Biomass Respiration rate between 1 and 10 for the fish compartments and between 50 and 100 for the groups with the highest renewal rates. The quality of the trophic model was validated by using the Pedigree Index, which goes from 0 to 1; values closer to one indicate a model of better quality. This index depends on the relative use of direct and local vs. indirect and removed information. Values above 0.4 are considered reliable models (Christensen et al., 2008).

2.7. *Ecosystem’s traits*

To better understand the organization and activity of the modeled systems, we use some ecological indices provided by EwE that allow us to assess the degree of maturity and organization of ecosystems (*sensu* Odum, 1969). Macro-descriptors are typically applied for large and complex ecosystems whose aim is to present ecosystem growth and development (Ulanowicz, 1997).

For this, we considered the Finn Cycling Index (ICF), responsible for indicating the recycled fraction of ecosystem transfer, also determining its resilience stability (Vasconcellos et al., 1997); Finn’s mean path length, parameters related to system recovery time; the Total Primary Production/Total Respiration Rate (PPT/RT), which indicates ecosystem maturity, in mature ecosystems, this value tends to 1 (Odum, 1969); the Connectance and Omnivory Indexes (CI and IO, respectively), which measure system complexity in different ways. The total Throughput, is a parameter that indicates the size of the system in terms of flow (Ulanowicz, 2004). And finally, Overhead (O) and Ascendancy (A), is a measure of system growth (i.e. age, size) and development (i.e. organization) of network links, ecosystem attributes that are correlated with system maturity (Christensen, 1995), being inversely proportional. Overhead is also seen as a measure of ecosystem stability and resilience (Bueno-Pardo et al., 2018).

In addition, we used Lindeman Spine to verify the transfer efficiency between trophic levels and the contributions of primary producers and detritus to sustain the food chain (Bueno-Pardo et al., 2018). The trophic impact matrix was used to identify direct and indirect relationships between compartments (Ulanowicz and Puccia, 1990; Pace et al., 1999). The key species were identified in each model from the combination of the trophic impact matrix and the relative biomass of each group (Libralato et al., 2006).

3. Results

The two models were parametrized and balanced after integrating all the basic inputs (Table 2). Both food web models have similar trophic levels range. Top predators were the Aquatic birds and *Centropomus* spp. (TL = 4.1), whereas primary consumers were mugilids, poeciliids, and polychaetes (Fig. 2). Zooplankton and benthonic invertebrates have TL lower than 2.5. In Guarapina, most of the biomass was found in the benthic and planktonic invertebrates corresponding to 71.3 %, followed by phytoplankton and macrophytes (24.7 %). Overall, 4.0 % of the total biomass was fish’s compartments. In Maricá, 52.9 % of biomass corresponds to phytoplankton and macrophytes. According to the system Omnivore Index, both models showed similarity (OI 0.136–0.149). OI was high for *Micropogonias furnieri* in both models since it is a generalist species (Fig. 2).

Even catch trophic levels are very similar in both models (~2.5),

Table 2
Basic inputs and estimated outputs (in bold) of Ecopath models for Guarapina Lagoon (GL) and Maricá Lagoon (ML). F is the fishing mortality, and F/Z represent the exploitation rate. Compartments with * were only present on GL model.

N°	Compartment	Trophic level		Biomass (t/km^2)		Production/ Biomass		Consumption/ Biomass		Ecotrophic Efficiency		Omnivory Index		Landing (t/km^2/year)		F		F/Z	
		GL	ML	GL	ML	GL	ML	GL	ML	GL	ML	GL	ML	GL	ML	GL	ML	GL	ML
1	Aquatic birds	**3.59**	**3.55**	0.005	0.005	0.1		60.9		**0.000**	**0.000**	**0.20**	**0.19**						
2	*Centropomus* spp.	**3.64**	**3.43**	0.004	**0.708**	0.3	0.5	8.4		**0.750**	0.990	**0.37**	**0.22**	0.001	0.347	**0.23**	**0.49**	0.75	0.98
3	Carangidae*	**3.51**		0.001		0.5		7.6		**0.169**		**0.19**							
4	Flatfish	**3.39**	**3.35**	0.141	0.004	1.4		12.5		**0.480**	**0.769**	**0.19**	**0.21**						
5	*Genidens genidens*	**3.24**	**3.32**	0.169	0.005	1.0		25.3		**0.180**	**0.306**	**0.12**	**0.14**						
6	Gerreidae	**3.09**	**2.96**	0.054	0.460	2.4	2.7	15.5		**0.743**	**0.981**	**0.12**	**0.24**		0.005		**0.01**		0.01
7	*Hoplias malabaricus**	**3.16**		0.001		0.9		5.7		**0.000**		**0.29**							
8	Ladyfish	**3.13**	**3.13**	0.073	0.036	0.7		11.0		**0.333**	**0.604**	**0.24**	**0.11**						
9	*Pogonias cromis*	**3.13**	**3.18**	0.037	**0.037**	1.2		4.1		**0.069**	0.900	**0.07**	**0.10**		0.040		**1.08**		0.90
10	*Anchoa* spp.	**3.01**	**3.16**	0.309	0.300	3.8		26.2		**0.114**	**0.870**	**0.12**	**0.07**						
11	*Micropogonias furnieri*	**2.85**	**2.76**	0.008	**0.939**	0.9		5.9		**0.569**	0.900	**0.37**	**0.48**	0.001	0.722	**0.12**	**0.77**	0.13	0.86
12	Sardines*	**2.73**		0.015		3.6		11.0		**0.826**		**0.30**							
13	*Atherinella brasiliensis*	**2.63**	**2.67**	0.736	0.490	1.8		15.9		**0.181**	**0.983**	**0.35**	**0.43**						
14	*Brevoortia aurea*	**2.61**	**2.57**	0.050	**0.013**	1.7		28.9		**0.899**	0.900	**0.37**	**0.45**						
15	Gobiidae	**2.62**	**2.62**	0.100	0.030	1.3		37.2		**0.703**	**0.375**	**0.31**	**0.33**						
16	*Mugil* spp.	**2.36**	**2.31**	0.450	3.000	1.3		14.6		**0.286**	**0.477**	**0.31**	**0.32**	0.132	1.844	**0.29**	**0.62**	0.23	0.47
17	*Geophagus brasiliensis*	**2.25**	**2.17**	0.006	0.080	1.3		35.0		**0.958**	**0.370**	**0.22**	**0.15**		0.008		**0.10**		0.08
18	*Coptodon rendali*	**2.15**	**2.51**	0.072	0.057	1.4		28.0		**0.151**	**0.407**	**0.13**	**0.33**		0.002		**0.04**		0.03
19	Poeciliids	**2.04**	**2.04**	2.317	1.685	3.4		13.8		**0.007**	**0.013**	**0.04**	**0.04**						
20	Crabs	**2,96**	**2.98**	0.310	0.214	1.4		19.1		**0.818**	**0.867**	**0.11**	**0.13**						
21	Blue crabs	**2.85**	**2.87**	0.330	0.060	2.3		9.1		**0.944**	**0.779**	**0.18**	**0.20**	0.004	0.041	**0.01**	**0.68**	0.01	0.30
22	Shrimps	**2.00**	**2.00**	0.200	0.150	7.8		26.7		**0.988**	**0.807**	**0.00**	**0.00**		0.012		**0.08**		0.01
23	Molluscs bivalves	**2.00**	**2.00**	0.800	0.040	55.2		402.0		**0.078**	**0.815**	**0.00**	**0.00**						
24	*Heleobia australis*	**2.00**	**2.00**	16.27	16.27	12.3		65.0		**0.015**	**0.016**	**0.00**	**0.00**						
25	Microcrustacea benthonic	**2.21**	**2.36**	2.500	2.500	70.0		354.0		**0.798**	**0.132**	**0.18**	**0.27**						
26	Polychaeta	**2.10**	**2.00**	17.35	17.35	70.0		354.0		**0.003**	**0.006**	**0.10**	**0.00**						
27	Oligochaeta	**2.00**	**2.00**	0.521	0.521	5.2		50.0		**0.142**	**0.005**	**0.00**	**0.00**						
28	Nematoda	**2.00**	**2.00**	**0.238**	**0.380**	11.4		45.4		0.900	0.900	**0.00**	**0.00**						
29	Zooplankton	**2.05**	**2.11**	**41.500**	**31.233**	18.6		74.6		0.990	0.900	**0.05**	**0.11**						
30	Phytoplankton	**1.00**	**1.00**	27.520	74.790	365				**0.124**	**0.036**	**0.00**	**0.00**						
31	Macrophytes	**1.00**	**1.00**	**0.149**	**11.187**	8.2				0.100	0.100	**0.00**	**0.00**						
32	Detritus	**1.00**	**1.00**	-	-					**0.633**	**0.280**	**0.29**	**0.17**						

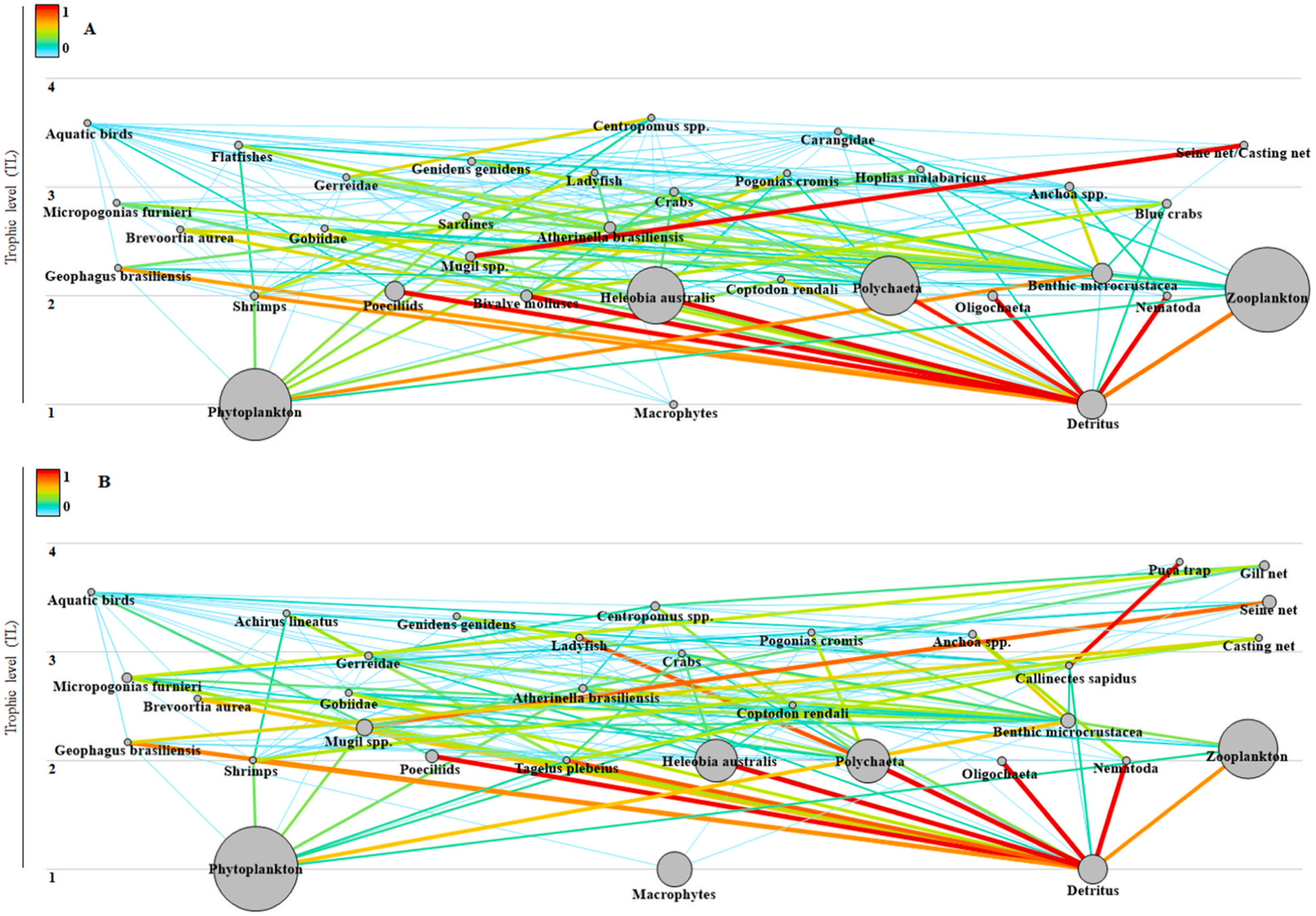

Fig. 2. Food network and energy flow diagrams for the Guarapina (A) and Maricá (B) lagoons. The size of the nodes is proportional to the biomass of each functional group. The width and color intensity of the lines is proportional to the energy flow. The ordinate axis shows the trophic level occupied by the compartments.

regarding catch in Maricá is higher than Guarapina (3.02 and 0.14 t/km^{-2}*year, respectively). The *Mugil* spp. represents 95 % of the total catch in Guarapina and 65 % of the total catch in Maricá, being the most captured species in both lagoons. Fishing mortality (F) showed the highest values in Marica lagoon, highlighting *Pogonias cromis* (1.08) and *Micropogonias furnieri* (0.77). The Exploitation rates (F/Z) ranged from 0.004 to 0.98 in Maricá and 0.005–0.75 in Guarapina, with the highest value in both lagoons being for *Centropomus* spp. Furthermore, it is worth highlighting that half of Marica's fleets had relatively high F/Z ($>$ 0.3) (Table 2).

The detritus chain is more relevant than the grazing chain in both models. Herbivory:Detritivore rates have similar values, 1:7.5 and 1:9.1 for Guarapina and Maricá, respectively (Fig. 3). The detritus-based chain seems an essential energy source in coastal lagoons (Albaret, 1999; De Sylva, 1985, Villanueva et al., 2006).

The Mixed Trophic Impact (MTI) from Guarapina Lagoon shows that Aquatic birds' biomass increment negatively impacts their prey (*Pogonias cromis*, *Geophagus brasiliensis*, *Genidens genidens*, and Poeciliids). However, simultaneously and indirectly, this impact can increment Blue crab, Shrimp, and Crab biomass values (Appendix A. Supplementary material). Another huge impact is that Microcrustacea benthonic positively affects predators (*B. aurea*, *A. brasiliensis*, and Gerreidae). Otherwise, flatfish affects negatively directly and indirectly on six compartments. Detritus could positively affect many compartments reinforcing its fundamental role in this food web. Fishing in Guarapina lagoon can especially affect *Mugil* spp. and *Centropomus* spp. (Appendix A. Supplementary material).

The MTI of the Maricá model also shows Aquatic birds impacting their prey negatively and benefiting Oligochaeta (Appendix A. Supplementary material). However, it also indicates more impacts (positive and negative) from compartments with lower trophic levels than the Guarapina's MTI. This higher sensitivity on basal compartments could demonstrate a direct bottom-up control in this lagoon. In this model, fisheries are detailed, showing that seine net fishing activity could negatively affect *Mugil* spp. and *P. cromis*, while gill net affects *M. furnieri* and *Centropomus* spp.

Aquatic birds and catfish (*G. genidens*) are the main key groups in both models (Table 3). The other three crucial key groups are quite different, but their trophic levels are similar, indicating similar ecosystem functioning on the food web.

The Maricá lagoon model has total flows almost two times higher than the Guarapina Lagoon (Table 4), reflecting the total system biomass and the PPT/RT rate, which is more elevated in Maricá. Maricá had a higher PPT/BT rate and lower Finn`s Cycling Index, with the other values indicating that Maricá is probably less resilient (*sensu* Odum, 1969) than Guarapina (Table 4). The transfer efficiency is higher in Maricá (4.5 %) than in the Guarapina (2.4 %) ecosystem.

4. Discussion

Coastal lagoons are among the world's most productive ecosystems (Behera et al., 2020) with physical and ecological characteristics that support several ecosystems' services to human populations (Pérez-Ruzafa et al., 2011b). However, a lack of their trophic structure prevents better management actions. We hope to fill this gap in this work by building ecosystem models for two tropical coastal lagoons

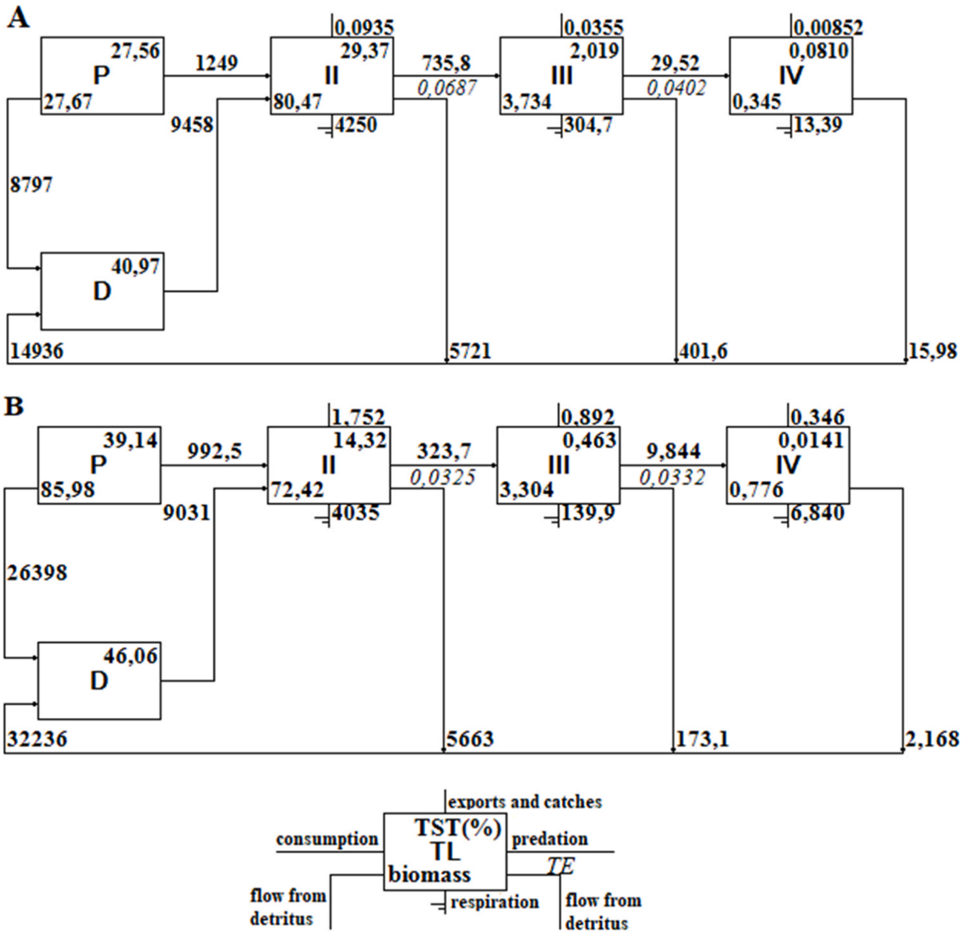

Fig. 3. Lindeman spine. (A) Guarapina Lagoon and (B) Maricá Lagoon. Arrows indicate the direction of biomass flow. P = Primary producers; D = Detritus; I, II, III and IV = Trophic level (TL); TST (%) = Total system throughput and TE = Transfer efficiency.

Table 3
Ranking of the main keystones groups of Guarapina Lagoon (GL) and Maricá Lagoon (ML) indicated in bold, and their respective trophic levels.

N°	Compartment	Trophic Level		Ranking of keystones	
		GL	ML	GL	ML
1	Aquatic birds	3.7	3.5	**1°**	**1°**
2	*Genidens genidens*	3.4	3.3	**2°**	**2°**
3	Ladyfish	3.2	3.1	**3°**	22°
4	Flatfish	3.5	3.4	**4°**	10°
5	Gerreidae	3.3	3.0	**5°**	9°
6	*Pogonias cromis*	3.2	3.2	28°	**3°**
7	*Centropomus* spp.	3.7	3.4	11°	**4°**
8	*Anchoa* spp.	3.2	3.2	7°	**5°**

(Guarapina and Maricá) in Rio de Janeiro State (Brazil).

These two studied lagoons have similar features, such as species composition and richness. The food webs are relatively short (TL mean = 2.5) with high biomass of producers' and invertebrates' groups, but with top predators. This pattern has already been observed in other coastal lagoons, such as Chilika and Alvorado lagoons in Mexico (Behera et al., 2020; Cruz-Escalona et al., 2007) and Mar Menor Lagoon in Spain (Pérez-Ruzafa et al., 2019b). Otherwise, there are differences between Guarapina and Maricá. The latter has higher biomass and flows supporting a high capture from the small-scale fishery (Prestrelo and Monteiro-Neto, 2016) on some species, such as *Mugil* spp., *M. furnieri*, and *Centropomus* spp., due to its high primary production.

The high fishing mortality rates, particularly in the Maricá Lagoon, for species such as *Pogonias cromis*, *Mugil liza*, *M. furnieri* and snook, associated with relatively high exploitation rates, suggest that stocks may be close to their carrying capacity. Similar results were found by Malfatti et al. (2023) in the Garzón Lagoon (Uruguay). The fact that the Maricá Lagoon is more isolated than the Guarapina Lagoon causes the species to remain there for longer periods of time, making them more susceptible to constant fishing pressure. Although high fishing mortality rates indicate a potential risk of overexploitation of certain species, such as *Mugil* spp., uncertainty in input values makes it essential to conduct species-specific stock assessments. Such assessments are important for estimating biomass, maximum sustainable yield, and other indicators commonly used in fish stock management.

Indeed, this environment is hypereutrophic, caused by the sewage release that increases the concentration of nutrients (phosphorus and nitrogen), sometimes causing an algal boom (Bernardino et al., 2019). Despite this, the system does not effectively use macrophytes as a source of primary production for the food web (Bernardino et al., 2019). Although Guarapina has lower fishery production, its ecosystem is more resilient and able to optimize the flows, including higher recycling, possibly because of its constant connection to the sea. Independently of these differences, the detritivore is much more relevant than the grazing chain in both lagoons.

Notwithstanding the differences, both models have similar main key groups able to influence the food webs, such as the Aquatic birds, which could indirectly reduce their prey and other components. In Guarapina, three of the five main key groups are exclusively marine organisms (Flatfish, Ladyfish, and Gerreidae), due to a constant connection between the lagoon to the sea, increasing the salinity (Laut et al., 2019), and favoring the presence and role of these species (Sánchez-Botero

Table 4
Ecosystem indicators calculated by Ecopath, describing Guarapina (GL) and Maricá (ML) Lagoons. ML/GL values lower than 1 (in italic), means a higher value in Guarapina Lagoon.

Parameters	Guarapina Lagoon	Maricá Lagoon	ML/GL	Units
Ecosystem properties				
Total system throughput	36608.33	70216.11	1.91	t/km^2/year
Total net primary production	10046.02	27390.08	2.72	t/km^2/year
Mean trophic level of the catch	2.38	2.56	1.07	
Total biomass (excluding detritus)	112.23	162.54	1.44	t/km^2
Net system production	5477.89	23208.2	4.23	t/km^2/year
Total catch	0.14	3.02	21.57	t/km^2/year
Total biomass				
Fish biomass	4.54	7.84	1.73	t/km^2
Invertebrate biomass + zooplankton	80.01	68.71	*0.85*	t/km^2
Producers biomass + phytoplankton	27.67	85.98	3.11	t/km^2
Ecosystem maturity				
Total primary production/total respiration	2.19	6.55	2.99	
Total primary production/total biomass	89.51	168.52	1.88	t/km^2
Total biomass/total throughput	0.003	0.002	*0.66*	t/km^2/year
Food web structure				
Connectance Index	0.180	0.188	1.04	
System Omnivory Index	0.136	0.149	1.09	
Ascendancy	28.99	42.89	1.47	%
Finn's Cycling Index	21.12	9.04	*0.42*	% of total throughput
Finn'n mean path length	3.64	2.56	*0.70*	
Model reability				
Pedigree Index	0.81	0.76		
Total transfer efficiencies	2.4	4.5	1.87	%

et al., 2009; Sosa-López et al., 2007; Gómez-González, 2011).

Detritus is the main abiotic component in coastal lagoons' ecosystems (Zetina-Rejon et al., 2003) with a relevant role in the diet of several species (Villanueva et al., 2006). We could show that detritus in both ecosystems could increase almost all the component's biomass. This reinforces the bottom-up control of our food webs despite the high trophic level of key groups. Otherwise, increasing detritus input could also reduce oxygen and impact most fish species, including mortality mass events reducing the fishery and the water quality (Domingos et al., 2012), an effect that our models are unable to preview.

The primary source of detritus in Maricá Lagoon is the phytoplankton, which concentrates 46 % of the total biomass of this food web. However, in Guarapina, macrophytes (especially, *Thypha dominguensis*) are the most abundant component, with biomass flows directly to detritus as the lack of any consumers (Ricevuto et al., 2013).

Total System Throughput values are high in both lagoons when assessing other coastal environments, such as the Carretas-Pereyra lagoon system (López-Vila et al., 2021) and Chilika Lagoon (Behera et al., 2020). Maricá Lagoon, a hypereutrophic environment, has the highest value since it is isolated from the sea and with high detritus accumulation (Flores-Verdugo et al., 1987). The low value of the Finn cycling index shows that ML cannot recycle organic matter, mainly because of the high input of nutrients from an urban river and sewage released (Bernardino et al., 2019; Mendes and Soares-Gomes, 2013).

It should be noted that both lagoons are connected by a meandering channel, with laminar flow regulated by tides and that they present distinct physical characteristics. GL is deeper and maintains a constant connection with the sea. At the same time, ML is shallow, hypereutrophic and choked most of the time (eventually connection with the sea via the nearby Barra Lagoon) and with urbanized surroundings. In this case, there are two leading management solutions: sewage treatment (an expensive procedure) and action to artificially open the lagoon and connect it to the sea to increase its water quality.

The option of artificially connecting to the sea to improve the water quality of ML tends to reduce phytoplankton (Suzuki et al., 1998; Perissinotto et al., 2010), changing the community structure (Santangelo et al., 2007), which could also reduce the fisheries catches. Thus, the managers face the dilemma: to increase the water quality of Maricá Lagoon, preventing algal blooms with cyanobacteria which are unhealthy for people (Vanderley et al., 2021), nevertheless, at the same time, reducing the fish catch and the food security for at least, more than 120 fishers. An alternative could be to make a slow and constant reduction in sewage input could increase the water quality and guarantee fishers enough time to adapt to lower levels of primary production. Furthermore, fishermen could benefit from the increase in tourists in the lagoons and add value to the production chain associated with fishing, with catches of top predators at sustainable levels. At the same time, the Maricá ecosystem, which has low resilience, could reach a sustainable alternative state. Nevertheless, its ecosystem difference from Guarapina could remain because this late continues with a direct connection to the sea.

The input data for constructing the two models were sampled locally and complemented with local scientific information. This kind of information resulted in a high Pedigree Index (~0.78) if compared to other models for other coastal lagoons, such as Carretas-Pereyra (López-Vila et al., 2021); Chantuto-Panzacola (López-Vila et al., 2019); Ria de Aveiro (Bueno-Pardo et al., 2018), and Tapog bay (Lin et al., 2006). However, we have a lack of information in both ecosystems, such as the zooplankton and data-poor fisheries data from GL, and the deficiency is fish biomass value for some species from ML. The latter, the Ecopath had estimated and could be filled by appropriate environmental monitoring.

5. Conclusions

This study is essential to the trophic modeling of lagoon environments, improving the knowledge of the relationships between different biological compartments and revealing the role of the main ecosystem processes. The structural patterns of food webs in the Maricá-Guarapina lagoon system shown in this study represent an initial step towards expanding comparative studies with other adjacent coastal lagoons, constituting a necessary reference. The results generated here should provide a basis for direct users of the system to recognize the likely impact of their actions on the environment and help managers make management decisions. The approach of this study should be improved with historical fishing series and other parameters that allow the dynamic simulation of the trophic network based on scenarios of interest, such as an increase or decrease in fishing effort and variation in organic load in the system, among others. In addition, implementing a monitoring program could fill the lack of data and make the mode more realistic and able to create simulations.

The relationship discussed between organism functions, environments, and responses to stress have implications for understanding environmental perturbations on ecological communities. Ecosystem changes cause a profound restructuring of local communities, which cannot be predicted without a clear understanding of the mechanisms that retain species' assemblages and functions. As elucidated here, the value of an ecosystem-based evaluation should be significant not only for fundamental science but for anticipating the likely impacts of environmental perturbations on ecosystem functions and socio-economic challenges they may involve.

CRediT authorship contribution statement

Marcus Costa: Writing – review & editing, Writing – original draft, Investigation, Funding acquisition. **Cassiano Monteiro-Neto:** Writing – review & editing, Writing – original draft, Investigation, Funding acquisition, Conceptualization. **Acácio Tomás:** Writing – review & editing, Writing – original draft, Investigation, Data curation. **Ronaldo Angelini:** Writing – review & editing, Writing – original draft, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Marianna Bello:** Writing – original draft, Investigation, Formal analysis, Data curation. **Rafael Tubino:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Letícia Monteiro:** Writing – review & editing, Writing – original draft, Formal analysis, Data curation.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Rafael de Almeida Tubino reports financial support was provided by Carlos Chagas Filho Foundation for Research Support of Rio de Janeiro State. Marianna Montenegro Bello reports financial support was provided by Coordination of Higher Education Personnel Improvement. Cassiano Monteiro-Neto reports financial support was provided by National Council for Scientific and Technological Development. Acacio Ribeiro Gomes Tomas reports financial support was provided by National Council for Scientific and Technological Development. Leticia Fernandes Alvarenga Monteiro reports financial support was provided by Project Pesquisa Marinha e Pesqueira (TAC Frade. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.rsma.2024.103950.

Data availability

Data will be made available on request.

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