

Ecological role and historical trends of large pelagic predators in a subtropical marine ecosystem of the South Atlantic

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Received: 1 February 2017 / Accepted: 25 July 2017
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Abstract Large pelagic predators occupy high positions in food webs and could control lower trophic level species by direct and indirect ecological interactions. In this study we aimed to test the hypotheses: (1) pelagic predators are keystone species, and their removals could trigger impacts on the food chain; (2) higher landings of pelagic predators could trigger fishing impacts with time leading to a drop in the mean trophic level of catches; and (3) recovery in the pelagic predators populations, especially for sharks, could be achieved with fishing effort reduction. We performed a food web approach using an Ecopath with Ecosim model to represent the Southeastern and Southern Brazil, a subtropical marine ecosystem, in 2001. We

then calibrated the baseline model using catch and fishing effort time series from 2001 to 2012. Afterwards, we simulated the impact of fishing effort changes on species and assessed the ecological impacts on the pelagic community from 2012 to 2025. Results showed that the model was well fitted to landing data for the majority of groups. The pelagic predators species were classified as keystone species impacting mainly on pelagic community. The ecosystem was resilient and fisheries seem sustainable at that time. However, the temporal simulation, from 2001 to 2012, revealed declines in the biomass of three sharks, tuna and billfish groups. It was possible observe declines in the mean trophic level of the catch and in the mean total length of landings. Longline fisheries particularly affected the sharks, billfish and swordfish, while hammerhead sharks were mostly impacted by

Electronic supplementary material The online version of this article (doi:10.1007/s11160-017-9492-z) contains supplementary material, which is available to authorized users.

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gillnet fishery. Model simulations showed that large sharks' biomasses could be recovered or maintained only after strong fishing effort reduction.

Keywords Ecopath with Ecosim · Fishing simulations · Fishing down food web · Istiophoridae · Sharks · Brazil

Introduction

Several characteristics of Large Pelagic Predators (LPP), such as long generation times, slow growth rates and low reproductive rates (Camhi et al. 1998; Collette et al. 2011) make them especially susceptible to overexploitation (Hall 1999) and local extinction (Dulvy et al. 2014). As a consequence, there is evidence of population declines for large pelagic fish worldwide (Jackson et al. 2001; Myers and Worm 2003; Heithaus et al. 2008; Worm et al. 2013).

Fisheries, climate change, habitat destruction, introduction of non-native species and pollution are factors that threaten the overall biodiversity (Burrows et al. 2011; Harnik et al. 2012; Pimm et al. 2014). However, overfishing is considered the primary threat to many marine organisms (Jackson et al. 2001) and recent studies suggest that populations of LPP are showing a sharp decline in some regions (Myers and Worm 2003; Collette et al. 2011; Dulvy et al. 2014). As large-bodied species are more susceptible to extinction due to high market value and/or low production rates, these declines have turned LPP such as large sharks, billfishes (Istiophoridae spp.), swordfish (*Xiphias gladius*) and tunas (*Thunnus* spp.) into some of the most threatened groups of marine animals worldwide (Lucifora et al. 2011; Collette et al. 2011; Britten et al. 2014; Dulvy et al. 2014; McClenachan et al. 2016).

LPP occupy high positions in marine food webs and therefore act as important regulators of lower trophic level species, playing a fundamental role in marine ecosystems through direct (predation) and indirect (competition) ecological interactions (Heithaus et al. 2008; Ferretti et al. 2010; Bornatowski et al. 2014a; Navia et al. 2016). These organisms could exert top-down effects on marine food webs and their reductions could alter the ecosystem structure and functioning (Myers et al. 2007; Baum and Worm 2009; Ritchie and

Johnson 2009; Heithaus et al. 2010; Ferretti et al. 2010).

Ecological indicators, such as trophic level (TL) and size-based indicators, are important tools to assess fishing impacts on marine ecosystems (Shannon et al. 2014; Coll et al. 2016). The Convention on Biological Diversity (CBD, 2004) selected the mean TL of the catch as one of its eight indicators of ecosystem health (Pauly and Watson 2005), because reductions of large predators with high TL have been widely documented, forcing fisheries to target smaller organisms with lower TLs (Pauly et al. 1998). This is known as 'fishing down marine food webs' and has been described in several marine ecosystems worldwide (e.g. Pauly et al. 2001; Arancibia and Neira 2005; Sibert et al. 2006; Coll et al. 2010; <http://www.fishingdown.org/>). Fishing also leads to substantial modifications in the size structure of exploited communities, and some studies used size-based indicators, such as the mean length of the fish, to assess fishing impacts on size of individuals (Shin et al. 2005).

The industrial longline fisheries in the South Atlantic have shown large changes in the last three decades in terms of effort and target species (Freire et al. 2014). These changes include the introduction of new technologies, commercial preferences, and management actions (Hazin et al. 2008; Barreto 2015; Barreto et al. 2016). LPP such as large sharks, swordfish and tunas have been fished in the South Atlantic since 1950; however between 1998 and 2012 the catches of these LPP showed a large increase (Barreto 2015; Barreto et al. 2016). Nevertheless, the impacts of these catches on large predators of the South Atlantic remain largely unknown.

Most studies of LPP declines have been concentrated in the Northern Hemisphere, and several overexploited tropical ecosystems remain poorly understood (Worm et al. 2009). In this study we explored the ecological role of LPP in southeastern and southern Brazil (SSB), a subtropical ecosystem, and the impact of catch increases on LPP and other species. To do so, a food web model using the Ecopath with Ecosim approach (EwE) (Christensen and Walters 2004) was developed to represent the ecosystem in 2001 and to characterize the food web structure of the SSB area. Such ecosystem modeling tools can provide the basis for testing several scenarios of fishing effort change and evaluating the capability of LPP to support

certain levels of fishing pressure and the ecosystem impacts of their population changes (Coll et al. 2006).

We used our model to examine the trophic relationships of three pelagic sharks on the food web: blue, mako, and hammerhead sharks (*Prionace glauca*, *Isurus oxyrinchus*, and *Sphyrna* spp., respectively), and three groups of large teleosts: tunas (*Thunnus* spp.), billfish (Istiophoridae spp.), and swordfish (*Xiphias gladius*). Afterwards, the baseline model was calibrated using the catch and fishing effort time series from 2001 to 2012 and the Ecosim temporal dynamic model. Therefore, the present study aimed to test the hypotheses that: (1) Large pelagic predators are keystone (defined as species that play an important role in a community's structure despite its low abundance), and their removals provoke impacts on the food chain; (2) higher landings of large pelagic predators trigger fishing impacts reducing the Mean Trophic Level of catches; and (3) recovery in the large predators populations, especially for large sharks, could be achieved with a fishing effort reduction.

Methods

Study area

The study area is located in the Southeastern and Southern Brazil (SSB) area from Cabo Frio City, Rio de Janeiro (23° S) to Rio Grande do Sul States (34° S), with depths between 100 and 600 m (Fig. 1). The total area comprises ~140,000 km² and corresponds to the Exclusive Economic Zone (EEZ) of SSB. In this region there is moderate upwelling between October and April (the rainy season), especially nearby Cabo Frio City (Fahrbach and Meincke 1979).

Food web modeling using the Ecopath approach

A food web model was constructed using Ecopath with Ecosim software (EwE, version 6.5) (Christensen and Walters 2004). The model represented the year 2001 as a baseline reference point. In the basic equation of the Ecopath model the consumption by a predator (or group) leads to the mortality of its prey (or group) due to predation. This is mathematically described by a system of linear equations (Christensen and Walters 2004):

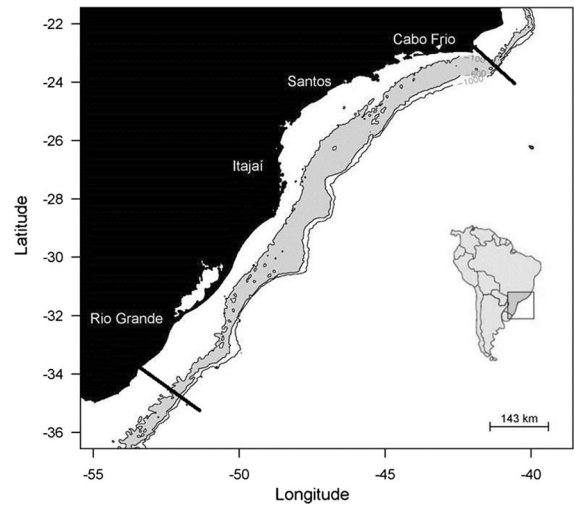


Fig. 1 Study area: Southeastern and Southern of Brazil (SSB) (depth between 100 and 600 m). Area limits are indicated by black lines between the states of Rio de Janeiro and Rio Grande do Sul. The map indicates the main coastal cities (Cabo Frio, Santos, Itajaí and Rio Grande) where catches are landed

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

where B_i is the biomass of group i ; PB_i is the Production/Biomass rate of i , which is equal to the total mortality Z (Allen, 1971); EE_i is the Ecotrophic Efficiency of i , which varies from 0 to 1 and represents the fraction of the production of the group that is used within the system or exported from the system; B_j is the biomass of predator j ; QB_j is the food consumption per unit of biomass for predator j ; DC_{ji} is the fraction of i in the diet of j ; and EX_i is the export of i and represents the biomass that is caught through fishing and/or that migrates to other ecosystems. A detailed introduction of the EwE approach and description of main features, data requirements and limitations can be found in the literature (Christensen and Walters 2004; Link 2010; Steenbeek et al. 2016; Heymans et al. 2016).

Parameterization of the SSB Ecopath model

We used two previous EwE models developed in the region (Gasalla et al. 2007; Nascimento et al. 2010) to develop the SSB model (see Online Resource 1 for more details). However, our food web model was constructed by selecting functional groups based on

relative abundance of species in total landings during the last 10 years, and on their relevance as prey or commercial value. Most traded species were defined as compartments into the model, since fishing activity is the main impact to be evaluated and likely to have high influence upon these species. Some species were grouped, while others remained as single species due to our main goals.

Our new food web model has some original elements, including separating three species of large sharks as individual functional groups: blue (*Prionace glauca*), mako (*Isurus oxyrinchus*) and hammerhead sharks (*Sphyrna* spp.), which were grouped together as “shark” in previous models. Also, *Thunnus* spp. species were grouped into a tuna group, the billfish group is composed of *Istiophorus platypterus*, *Makaira nigricans*, and *Kajikia albida*, and *Xiphias gladius* is called the swordfish group (Online Resource 2; Table 1). Thus, a total of 44 functional groups were used in SSB EwE model, with 26 groups of teleosts, 10 groups of invertebrates, five shark groups, one ray group, a phytoplankton group, and Detritus (Online Resource 2; Table 1). The definition of the functional groups for the SSB model was also based on biological and ecological characteristics of the species such as feeding habit, size, biology, habitat and depth distribution of the main landed species.

To parameterize the model, biomass estimates ($t\ km^{-2}$) were obtained from the Evaluation of the Sustainable Potential of Living Resources process in the Exclusive Economic Zone (REVIZEE—South Score) that evaluated the fishing stocks in the area between 2001 and 2002 (Amaral and Rossi-Wongtschowski 2004; Madureira and Rossi-Wongtschowski 2005; Rossi-Wongtschowski et al. 2006; Haimovici et al. 2008, 2009), and from other previous EwE models developed in some marine Brazilian regions (e.g. Velasco and Castello 2005; Gasalla et al. 2007; Freire et al. 2008; Nascimento et al. 2010). Biomass of blue shark was estimated according to Carvalho et al. (2015), hammerhead shark according to Hayes et al. (2009), swordfish according to Kell et al. (2014), and tuna according to Velasco and Castello (2005). When not available, biomass values were estimated from EwE through Ecotrophic Efficiency (EE) collected from the literature regarding similar groups and, when possible, close by regions and similar ecosystems (see Online Resource 1).

The Production/Biomass ratio (P/B , $year^{-1}$) was calculated using the Pauly (1980) equation or was obtained from the literature (Cox et al. 2002; Gasalla and Rossi-Wongtschowski 2004; Gasalla et al. 2007; Freire et al. 2008; Griffiths et al. 2010; Nascimento et al. 2010). The Consumption/Biomass ratio (Q/B , $year^{-1}$) was estimated using Palomares and Pauly (1998) empiric equation and from FishBase (Froese and Pauly 2015). When obtained from the literature, data were thoroughly selected according to similar species and environments (see Online Resource 1).

The diet composition (DC) matrix was obtained by retrieving data from the literature, prioritizing those studies coming from the study area or similar areas (Online Resource 3, Section 1 and 2, with all specific references).

The model was considered balanced when estimated EE values were all lower than 1 and were high (~ 0.95) for exploited species and more preyed ones (small fish species, e.g. sardines), and low for unexploited top predators ($EE < 0.5$). In addition, values of production/consumption (P/Q) for functional groups were between 0.1 and 0.35 with the exception of some fast growing species, and values of net efficiency were < 1 (Christensen et al. 2008). The criteria from the Pre-Balance (PREBAL) approach was also used to analyse the relationship between biomass, P/B , and Q/B values with increasing trophic levels (Link 2010; Heymans et al. 2016).

EwE model outputs

EwE estimates overall indicators and properties of each functional group useful for the ecological analysis. In particular, we used the Omnivory Index (OI, Christensen et al. 2008) to investigate the strategy of feeding for each functional group and the System Omnivory Index (SOI) for the general ecosystem. We also analyzed a series of overall ecosystem attributes such as the Total Primary Production/Total Respiration (TPP/TR), Total System Throughput (TST), Total Primary Production/Total Biomass (TPP/TB), Total Biomass/Total System Throughput (TB/TST), overall Connectance Index (CI), Finn's Cycling Index (FCI), and Overhead (O). These attributes quantify an overall development status for the ecosystem sensu Odum (1969) considering that “mature” environments are more resilient than “immature” ecosystems (for more details about these attributes see Angelini et al. 2013).

The Mixed Trophic Impact (MTI) analysis was used to quantify the relative impact of biomass change within a component (impacting group) on each of the other components (impacted groups) in the food web, including fishing fleets (Ulanowicz and Puccia 1990, based on Leontief 1951). The MTI provides two estimated parameters: the trophic impact component (ε_i) and the relative biomass component (p_i), which are used to estimate keystone species indices. Parameter ε_i represents the overall direct or indirect trophic effect of group i on all the other groups in the food web:

$$\varepsilon_i = \sqrt{\sum_{j \neq i} m_{ij}^2} \quad (2)$$

where ε_i is expressed as the sum of the squared values of m_{ij} of group i , paired with each of the other living group j and m_{ij} is the effect of group i on j , which could be positive (if the impacted group's biomass increases) or negative (if it decreases). The m of group i on itself (m_{ii}) is excluded, as well as the m on non-living groups such as detritus (Libralato et al. 2006).

Parameter p_i corresponds to the contribution of group i to the total biomass in the food web:

$$p_i = \frac{B_i}{\sum_{k=1}^n B_k} \quad (3)$$

where B_i is the biomass of group i , and B_k the biomass of each one of the n living groups in the food web (Power et al. 1996; Libralato et al. 2006).

A keystone species is defined as a species with low relative biomass but which plays an important role in the food web (Paine 1995). We estimated the three keystone species indices (KS) provided by EwE: KS1 (Libralato et al. 2006) and KS2 (adapted from Power et al. 1996) indices were obtained by combining ε_i and p_i for each group i , such as:

$$KS_{1i} = \log[\varepsilon_i \times (1 - p_i)] \quad (4)$$

$$KS_{2i} = \log[\varepsilon_i \times (1/p_i)] \quad (5)$$

Using the same approach, Valls et al. (2015) proposed a third index (KS3):

$$KS_3 = IC_L \times BC_0 \quad (6)$$

where: IC_L (Impact Component) is estimated from Eq. 1 (ε_i) and BC_0 (the Biomass Component) is estimated from Eq. 2 (p_i), where BC_0 is the biomass in a descending order ranking (see Valls et al. 2015 for more details).

Finally, in order to understand the influence of large predators on the pelagic SSB community, we used feeding overlap values between large sharks and other large pelagic predators provided by EwE.

Fisheries data and ecological indicators

We analyzed landing data derived from fishing monitoring systems, developed as part of a scientific cooperation program established between the Ministry of Agriculture (Brazilian Government) and the University of Vale do Itajaí (UNIVALI) (Perez and Wahrlich 2005). The Santa Catarina Industrial Landing Statistics Program provided information on catch and fishing operations obtained from log books, markets, and skipper interviews at the main Santa Catarina harbors (<http://gep.acad.univali.br>). Landing and fisheries data were compiled from fisheries bulletins from 2000 to 2012 (Online Resource 4).

Due to the large number of licensing arrangements in Brazil (78 different types of licenses for fishing) data were analyzed using broad categories. Because otter trawls, pair trawls and double rig trawls may have the same impact on fishes, for example, all boats using trawls were included in the category 'trawlers'. The 'gillnets' category, similarly, comprised all boats using pelagic and bottom gillnets. Demersal and pelagic longliners were separated because the target different resources. Bait and purse seiners were grouped in the "Others" category.

We estimated the Mean Trophic Level of the catch Index ($MTLI_k$) using the above landing data and TL values obtained from the EwE model for those species occurring in the landings (Online Resource 4). The $MTLI_k$ was calculated as:

$$MTLI_k = \frac{\sum_{i=1}^m Y_{ik} TL_i}{\sum_{i=1}^m Y_{ik}}, \quad (7)$$

where Y_{ik} are landings of species i in year k , and m is the number of species or group of species caught in year k (Pauly et al. 2001). A $MTLI_k$ using a cut-off at TL 3.25 ($MTLI_{\geq 3.25}$) was also calculated as:

$$MTLI_{\geq 3.25} = \sum_{i=1}^n Y_{TLi \geq 3.25} \cdot TL_i / Y_{L(TLi \geq 3.25)}, \quad (8)$$

where Y_L is total landings of organisms with $TL \geq 3.25$, Y_i is the landing of species i , and TL_i is the trophic level of species i . We calculated the $MTLI_{\geq 3.25}$ to exclude lower TL species such as forage fish and smaller organisms (Pauly and Watson 2005).

A $MTLI_k$ using a cut-off at TL 4.0 ($MTLI_{\geq 4.0}$) was also calculated as:

$$MTLI_{\geq 4.0} = \sum_{i=1}^n Y_{TLi \geq 4.0} \cdot TL_i / Y_{L(TLi \geq 4.0)}, \quad (9)$$

where Y_L is total landings of organisms with TL > 4.0, Y_i is the landing of species i , and TL_i is the trophic level of species i . We calculated the $MTLI_{\geq 4.0}$ with to examine changes within the top predator community, while excluding small and medium pelagic fish species (Pauly and Watson 2005; Shannon et al. 2014).

The impact of fisheries on total length of species also was estimated. In this study, we estimated the Maximum Total Length ($MaxT_k$) of the catch using:

$$MaxT_k = \frac{\sum_{i=1}^m Y_{ik} \cdot MaxT_i}{\sum_{i=1}^m Y_{ik}}, \quad (10)$$

where m is the number of species or group of species, Y_{ik} are landings of species i in year k , and $MaxT_i$ is the maximum total length (cm) of species i caught in year k . $MaxT_i$ values were obtained from FishBase for those species occurring in the landings (Froese and Pauly 2015; see Online Resource 4).

We also estimated the Loss in secondary production (L index) due the fishing and the associated probability of sustainability (Psust; Libralato et al. 2006) to evaluate the fisheries sustainability in the SSB ecosystem.

Food web time-dynamic modelling with Ecosim

The temporal-dynamic model of EwE, the Ecosim model (Walters et al. 1997; Christensen and Walters 2004), uses the baseline Ecopath model as the initial conditions to dynamically represent prey-predator interactions. Specifically, the system of linear equations is transformed into a system of ordinary differential equation as follows (Walters et al. 1997, 2000):

$$\begin{aligned} dB_i/dt = & g_i \times \sum_j Q_{ji} - \sum_j Q_{ij} + I_i \\ & - (MO_i + F_i + e_i) \times B_i \end{aligned} \quad (11)$$

where dB_i/dt is the change in B of group i over time t , g_i is the net growth efficiency, Q_{ji} is the consumption of group j by group i , n is the number of prey groups, Q_{ji} is the consumption of group I by group j , m is the number of predator groups, I_i is the extent of immigration of group i , MO_i is the non-predation rate

of natural mortality of group i , F_i is the fishing mortality of group i , and e_i is the emigration of group i . Ecosim represents prey-predator interaction by ‘vulnerability’ settings (v_{ij}), which captures the degree to which an increase in predator biomass will cause an increase in mortality for its prey. This parameter expresses how far a group is from its carrying capacity (Christensen and Walters 2004; Walters and Christensen 2007).

The quantification of prey i consumed by predator j (Q_{ji}) is a nonlinear relationship based on the “foraging arena concept” acting on the consumption rates of predators and prey (Walters et al. 2000; Walters and Christensen 2007; Ahrens et al. 2011):

$$Q_{ij} = \frac{a_{ij} \times v_{ij} \times B_i \times B_j}{2 \times v_{ij} \times a_{ij} \times B_j} \quad (12)$$

where a_{ij} is the effective search rate of predator j feeding on prey i , B_i is the biomass of the prey, B_j is the predator biomass, and v_{ij} is the vulnerability of prey i to predator j . The “foraging arena concept” implies that the prey biomass is divided into vulnerable and non-vulnerable components and the transfer rate between these two components is the vulnerability rate (v_{ij}), which determines whether the flow control is top-down ($v_{ij} > 2$), bottom-up ($v_{ij} < 2$), or mixed ($v_{ij} = 2$; the defaults values in EwE).

In this study, we used a time series of relative fishing effort (computed as number of fishing trips) as the driving factor to fit the model to catch data from 2001 to 2012 for the main exploited species (see Online Resource 5). The model fitness was assessed through the sum of squared deviations (SS) that was calculated using the disparity between the log of observed catches and the log of predicted catches (Christensen et al. 2008). We used the EwE traditional method to fit the models, which changes on vulnerability values matrix by searching automatically for smaller SS values and best fits for the evaluable time series (Heymans et al. 2016). Vulnerability parameters were estimated using an optimization search routine (based on Davidson–Fletcher–Powell nonlinear optimization procedure) which reduces the sum of squares difference between the predicted and observed data (Scott et al. 2016). This procedure tests a combination of hypotheses to assess the top-down and bottom-up controls using the time series analysis. A total of 17 time series of catch was used for estimating the SS, and therefore 15 parameters were estimated as vulnerability.

Temporal simulations of fishing effort using Ecosim

After model calibration, we performed simulations from 2012 to 2025, changing fishing effort (FE) and assessing its influence on the food web. The experimental modeling design had eight levels: Simulation 1, keeping all fishing effort (FE) constant from 2012 to 2025; Simulation 2, increasing the gillnet FE by twofold; Simulation 3, decreasing the gillnet FE by 50%; Simulation 4, excluding gillnet FE; Simulation 5, increasing the longline FE by twofold; Simulation 6, decreasing the longline FE by 50%; Simulation 7, excluding longline FE; Simulation 8, excluding trawler FE.

Results

Ecopath model of SSB

Ecopath estimated the biomass values for seven fish compartments (Table 1), and just a few input values were modified to balance the model (Online Resource 1). The final diet composition matrix, for example, differed from the input matrix only for some species/groups and these changes were not higher than 20% of the original input values (Online Resource 3, Section 3).

The balanced model showed that the organism with the highest TL was the blue shark, $TL = 4.6$, while mako and hammerhead sharks showed $TL = 4.5$. Billfish and swordfish had $TL = 4.3$, and tuna $TL = 3.1$ (Fig. 2; Table 1). Invertebrate groups showed low trophic levels because they have a diet based on detritus, phytoplankton and/or zooplankton (Fig. 2; Table 1).

The food web model of the SSB ecosystem showed high complexity ($SOI = 0.40$). TST was $4939.2 \text{ t/km}^2/\text{year}$, TPP/TR was $2.4 \text{ t/km}^2/\text{year}$, TPP/TB was $32.8 \text{ t/km}^2/\text{year}$, TB/TST per year was 0.01, and FCI was 1.9% with an overhead value of 65%. The L index was 0.003, and $Psust$ was 95%. In general, all these values suggest that the SSB ecosystem in 2001 had a high potential for adaptation and resilience capacity, and that fishery activity was overall sustainable.

The ecological role of large pelagic predators (LPP)

The three large sharks had different effects on other ecosystem components according to MTI analysis.

Blue shark showed high negative impact on swordfish, and mako shark (Fig. 3), while mako shark had a reduced negative impact on swordfish (Fig. 3). Hammerhead shark had small negative impacts on tuna and positive ones on red-porgy fish (Fig. 3).

Blue shark was negatively impacted by surface longline fishery, medium pelagic fishes, and tuna, and was positively impacted by cephalopods, skipjack tuna and large pelagic fish (Fig. 3). Mako shark was negatively impacted by pelagic longline, gillnets and blue shark and was positively impacted by large pelagic fish (Fig. 3). Hammerhead shark was negatively impacted by gillnets and pelagic longline. This group was positively impacted by cephalopods and phytoplankton (Fig. 3).

Within the large teleosts, Tuna showed high negative impact on red-porgy, smaller negative impact on blue and mako sharks, and no important positive impacts (Fig. 3). Billfish had a high negative impact on tuna and flyfish, and a positive impact on red-porgy (Fig. 3). Swordfish showed a slight negative impact on tuna as well as blue, mako and hammerhead sharks (Fig. 3).

Tuna was negatively impacted by billfish, large pelagic fish, and skipjack tuna (Fig. 3) and positively impacted by dolphinfish, cephalopods and medium pelagic fish (Fig. 3). Billfish was negatively impacted by dolphinfish, medium pelagic fish, and the “other” category of fishing gears, and were positively impacted by large pelagic fish and skipjack tuna (Fig. 3). Swordfish were negatively impacted by blue shark, and were positively impacted by cephalopods and medium pelagic fish (Fig. 3).

The LLP had slight to moderate trophic effects on other functional groups of the food web (Fig. 3). Main trophic impacts were due to indirect effects, and slightly impacts were shown on direct preys. For example, tuna has a highly negative impact on red porgy, so an increase in tuna biomass reduces red porgy biomass, because tuna is a predator on red porgy. Conversely, billfish has a negative impact on tuna (billfish is a predator on tuna) and consequently, by reducing tuna, billfish has a positive impact on red porgy (indirect impact) (Fig. 3). Besides, the connection between trophic components occurs through many pathways. The connection between Hammerhead sharks and phytoplankton occurs, for instance, along pathways such as phytoplankton to zooplankton to small pelagic fishes to Hammerhead sharks or

Table 1 Basic input and output (in bold) parameters for the Ecopath model of the southeastern and southern Brazil (SSB) ecosystem

Code	Group name	TL	B	PB	QB	EE	PQ	OI	Total catches
1	Flyfish	3.0	0.012	1.60	17.0	0.95	0.09	0.02	
2	Blue shark	4.6	0.003	0.24	2.75	0.60	0.09	0.50	0.00043
3	Mako shark	4.5	0.001	0.09	5.02	0.75	0.02	0.24	0.00004
4	Hammerhead sharks	4.5	0.002	0.12	2.0	0.61	0.06	0.26	0.00014
5	Angel sharks	4.3	0.030	0.29	3.2	0.06	0.09	0.69	0.00042
6	Demersal sharks	4.3	0.060	0.35	1.89	0.37	0.19	0.86	0.00004
7	Rays	3.7	0.050	0.28	4.4	0.09	0.06	0.20	0.00097
8	Large pelagic fish	4.1	0.266	2.90	7.9	0.20	0.37	0.65	0.00000
9	Medium pelagic fish	3.1	1.251	1.90	8.7	0.95	0.22	0.84	0.00256
10	Small pelagic fish	2.8	0.441	0.60	2.8	0.95	0.21	0.38	
11	Dolphinfish	4.2	0.007	4.36	20	0.70	0.22	0.77	0.00015
12	Tuna	4.1	0.010	0.82	8.0	0.51	0.10	0.39	0.00107
13	Billfish	4.3	0.005	0.70	4.0	0.40	0.18	0.34	0.00001
14	Swordfish	4.3	0.002	0.43	3.4	0.74	0.13	0.39	0.00017
15	Monkfish	4.4	0.081	0.40	2.3	0.12	0.17	0.34	0.00289
16	Hake fish	3.9	0.797	0.95	2.7	0.99	0.35	0.41	0.00134
17	Cutlassfish	3.4	1.000	0.91	3.1	0.30	0.29	0.71	0.00010
18	Cephalopode	3.4	0.340	6.70	36.5	0.96	0.18	0.44	0.00064
19	Skipjack tuna	3.6	0.500	1.35	20.0	0.02	0.07	0.70	0.00812
20	Brazilian codfish	4.4	0.146	0.70	2.5	0.19	0.28	0.87	0.00287
21	Rosefish	4.1	0.016	0.80	4.8	0.45	0.17	0.58	0.00001
22	Maurolucus	3.0	3.900	1.30	20.1	0.25	0.06	0.00	
23	Flatfish	3.6	0.032	1.30	5.17	0.49	0.25	0.21	0.00074
24	Bluewing searobin	3.7	0.035	0.38	2.5	0.22	0.15	0.17	0.00224
25	Sciaenidae	3.6	0.070	0.60	4.3	0.70	0.14	0.39	0.01362
26	Small bento-pelagic fish	3.0	0.170	0.55	6.5	0.95	0.08	0.09	0.00012
27	Clupeidae and Engraulidae	2.9	4.400	1.34	10.2	0.96	0.13	0.09	0.01906
28	Other benthopelagic fish	3.9	0.160	0.73	4.1	0.98	0.18	0.88	
29	Synagrops spp.	3.9	0.300	1.11	5.6	0.35	0.20	0.26	
30	Large demersal fish	4.1	0.038	1.08	4.2	0.05	0.26	0.41	0.00038
31	Large benthopelagic fish	3.8	0.477	0.30	2.0	0.61	0.15	0.18	0.00011
32	Demersal fish	3.5	0.447	1.14	3.9	0.10	0.29	0.57	
33	Red-porgy	3.7	0.007	0.89	3.5	0.03	0.25	0.41	0.00003
34	Predator molluscs	3.6	0.288	4.50	20.0	0.61	0.23	0.75	
35	Omnivory invertebrates	3.1	4.495	5.50	12.0	0.99	0.46	0.42	
36	Predator invertebrates	3.5	0.980	3.50	20.0	0.48	0.18	0.22	
37	Detritivorous invertebrate	2.9	4.215	4.50	12.2	0.58	0.37	0.83	
38	Infauna	2.0	4.350	14.60	40.0	0.99	0.37	0.00	
39	Crabs	2.4	2.100	3.17	19.0	0.96	0.17	0.23	0.00017
40	Shrimps	2.9	2.790	6.00	20.0	0.64	0.30	0.43	0.00159
41	Polychaeta	2.4	7.709	3.50	20.82	0.85	0.17	0.36	

Table 1 continued

Code	Group name	TL	B	PB	QB	EE	PQ	OI	Total catches
42	Zooplankton	2.0	3.600	104.00	248.0	0.47	0.42	0.00	
43	Phytoplankton	1.0	9.970	182.96	0	0.53		0.00	
44	Detritus	1.0				0.18		0.42	

TL Trophic level, B biomass (t km^{-2}), PB production/biomass (year^{-1}), QB consumption/biomass (year^{-1}) EE Ecotrophic efficiency, PQ production/consumption, OI Omnivory Index, Total catches ($\text{t km}^{-2} \text{ year}^{-1}$)

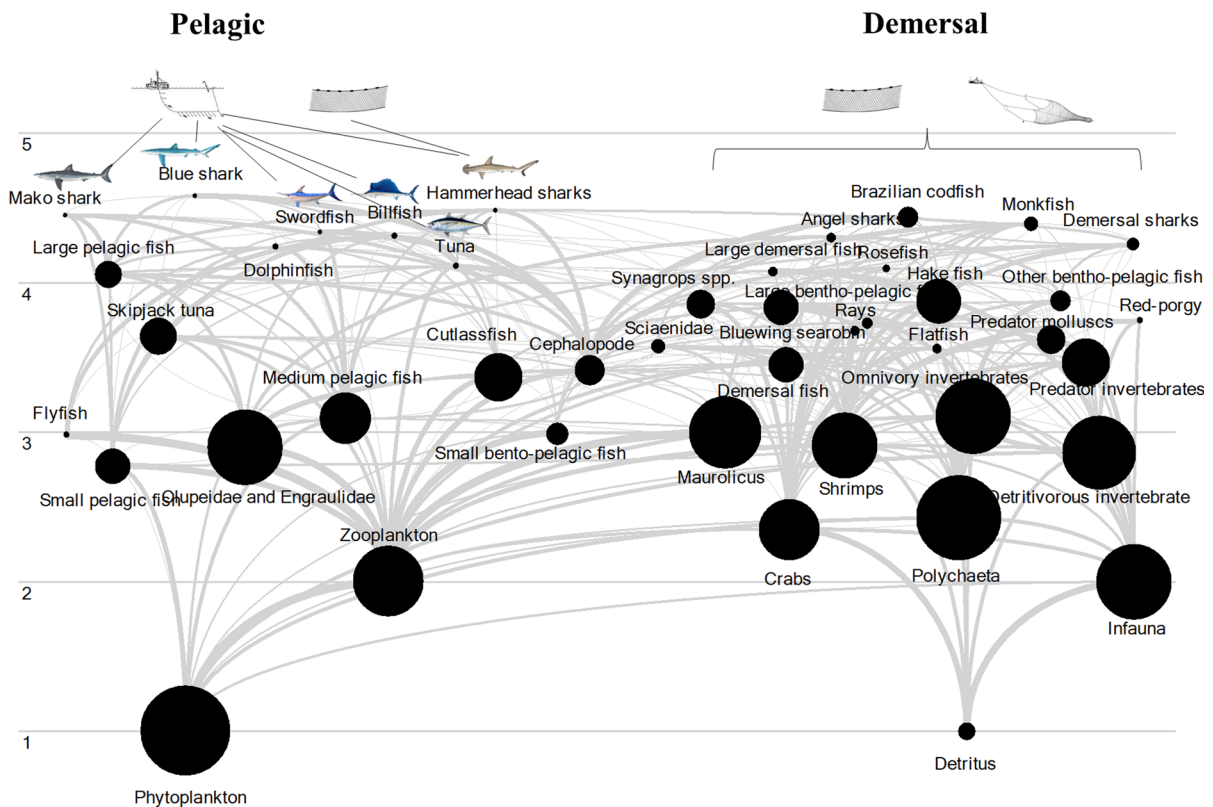


Fig. 2 Flow diagram of the SSB ecosystem separated by pelagic and demersal habitats. Dots are scaled by the log of the biomass value with trophic level varying on the y axis. Trophic interaction widths are proportional to consumption flows. Main

fisheries (longline and gillnet) interactions are shown for large pelagic predators. Gillnets and trawlers interact with demersal groups

phytoplankton to small pelagic fishes to Hammerhead sharks.

Regarding keystone species, the species or groups with high KS1 scores (Libralato et al. 2006) were large pelagic fish, followed by medium pelagic fish, skipjack tuna, and dolphinfish (Online Resource 2; Table 2). LPP were ranked as keystone species or groups according to the KS2 index, which ranked the blue shark in the first position. Blue sharks, Billfish and Tuna were keystones for both KS2 and KS3

(Online Resource 2; Table 2). The dolphinfish group had the highest value in the KS3 index and was the only one group appointed as a keystone species by all three indexes. In summary, the keystone species in the SSB ecosystem have high TL, with the exception of the KS1 index that recorded cephalopods and omnivorous invertebrates in the fifth and sixth positions, respectively (Online Resource 2; Table 2).

Pelagic predators had high trophic overlap among themselves and with other groups (Online

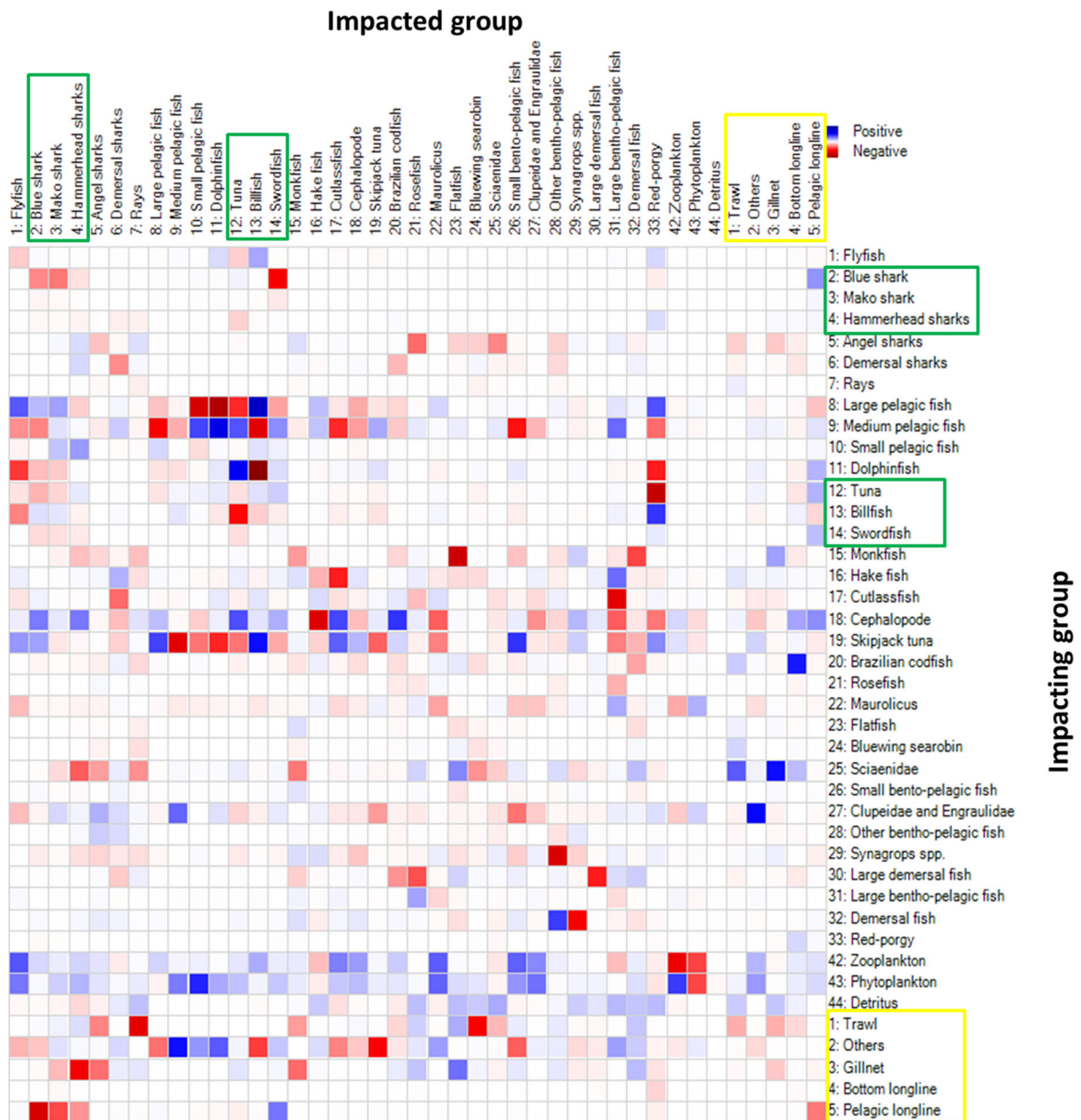


Fig. 3 Mixed trophic impact (MTI) analysis of large pelagic predators (LPP) (green rectangles) and functional groups of the southeastern and southern Brazil food web as impacting (how an increase of biomass of species would impact on other

components, m_{ji}), and as impacted (how species would be impacted by biomass increasing in other components, m_{ij}). The fishing gears are highlighted in yellow rectangles. Some groups were omitted for better visualization

Resource 2; Table 3). Blue sharks showed trophic overlap with swordfish and tuna groups. Mako sharks overlapped with dolphinfish, tuna and swordfish groups. Hammerhead sharks also presented high overlap with swordfish, tuna, and large

pelagic fish groups (Online Resource 2; Table 2). Only Billfish did not show any overlap. These results highlight that LPP could have indirect effects on other groups besides their usual predator–prey relationships.

History of southern Brazilian fisheries

Landings in the SSB area show a significant increase ($p < 0.001$) over the past 12 years (Online Resource 2; Fig. 1a): in 2012, the last year of the time series, landings were 119,756 ton, or almost double that of 2000. For 2012, the main caught species or groups were sardines (Engraulidae and Clupeidae, 46% of total catch), skipjack (*Katsuwonus pelamis*, 17%), Brazilian codfish (*Urophycis brasiliensis*, 5%), Sciaenidae fish (*Umbrina canosai* and *Cynoscion* spp., 4%), bluewing searobin (*Prionotus punctatus*, 3%), flatfish (*Paralichthys* spp., 1%), and rays (Rajidae, 1%) (See details in Online Resource 2; Fig. 1). The results also indicate that there has been a drop in shark landings (Online Resource 2; Fig. 1b–d), and declines of billfish (Online Resource 2; Fig. 1e); however, tuna (Online Resource 2; Fig. 1f) and swordfish (Online Resource 2; Fig. 1g) landings showed an increase in the last years of the time series.

All TL-based indicators ($MTLI_k$, $MTLI_{\geq 3.25}$, $MTLI_{\geq 4.0}$) showed a significant decline ($p < 0.01$, Fig. 4), which is in line with the drop in MaxT (Fig. 4d, $p = 0.001$).

Ecosim time-dynamic fitting and simulation

We use the fit to time series routine and accomplish to reach the best fitting with some changes on vulnerabilities individually, producing minimum values of sums of squares (SS). The LPP showed vulnerabilities >10 , suggesting top-down control in SSB ecosystem (Online Resource 6 shows the final vulnerability matrix). Results from the fitted model to observed trends of landings for the main commercial groups showed a decrease in the catch of blue, mako and hammerhead sharks, and also of billfish and demersal sharks (Fig. 5).

Management simulations

Simulation 1 (Fishing Effort constant from 2012 to 2025), resulted in declines in the biomass of blue shark (80%), hammerhead shark (54%), Mako shark (42%), Tuna (40%), and billfish (5%), angel sharks (2.4%) and hakefish (1.5%) (Online Resource 2; Fig. 2). In contrast, swordfish showed an increase of 280% of relative biomass. Increases in the biomass of flatfish (14%), bluewing searobin (13%), Rays (4%) and

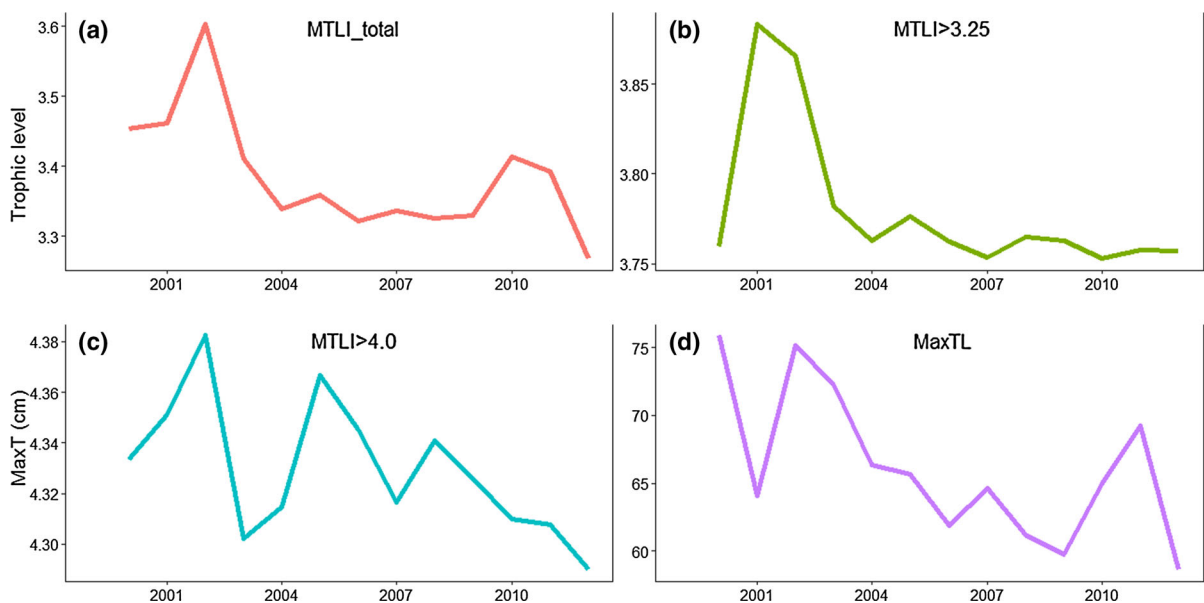


Fig. 4 Fishery indicators: **a** Mean Trophic Level Index (MTLI) of total catches ($r^2 = 0.38$; $p < 0.01$), **b** MTL of cut-off ≥ 3.25 total length (TL) ($r^2 = 0.34$; $p < 0.01$), **c** MTL of cut-off ≥ 4.0 TL ($r^2 = 0.31$; $p < 0.01$), and **d** Mean maximum TL (MaxT) of

catches ($r^2 = 0.41$; $p < 0.01$). TL for species was estimated from the Ecopath with Ecosim model for southeastern and southern Brazil (see Table 2); Maximum length (cm) was estimated from literature values (see Supplementary Material 3)

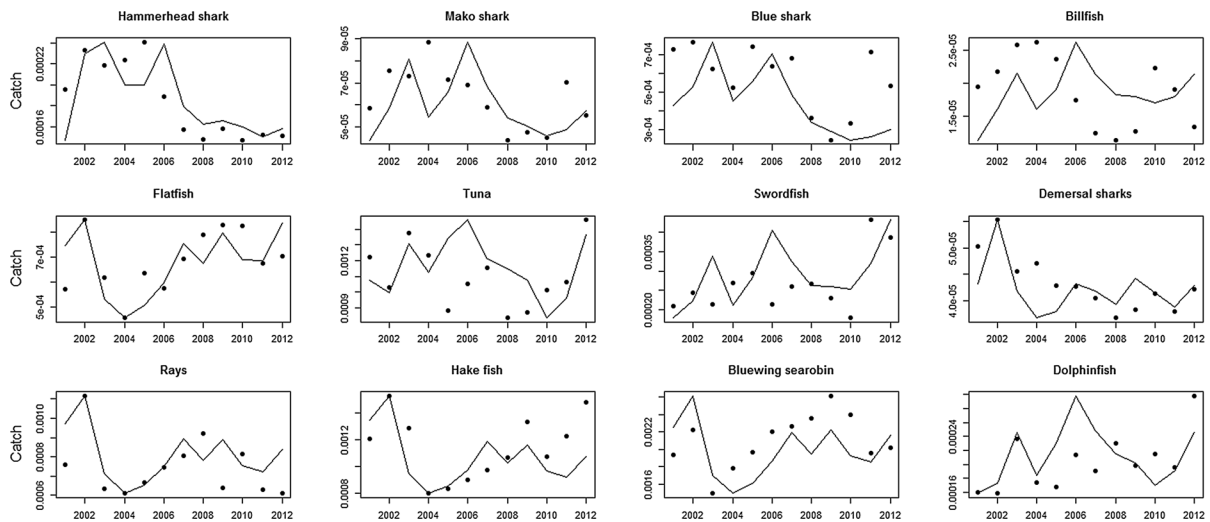


Fig. 5 Landing time series trends for three large sharks and other main fish resources estimated (line) by the Ecosim time-dynamic model of southeastern and southern Brazil (SSB) for

the period from 2001 to 2012 and observed landings data (dots). Units: tonnes·km⁻²·year⁻¹

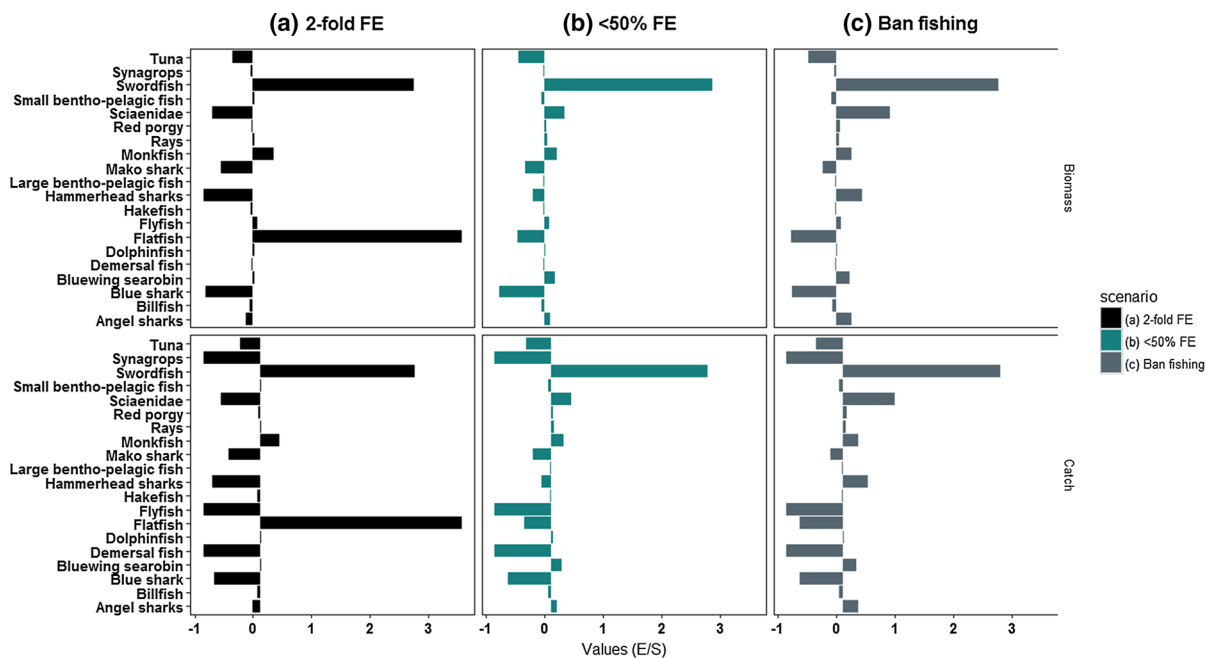


Fig. 6 Relative changes in the biomass and catches (End/Start) of species in SSB ecosystem after reducing or increasing gillnet fishery effort: **a** a twofold increase in fishing effort from 2012 to

2025, **b** a 50% reduction over the same period, and **c** a fishing ban over this period

dolphinfinh (1%) were also predicted (Online Resource 2; Fig. 2). Other species did not reveal representative changes.

The Simulation 2 scenario (increasing the gillnet FE by twofold), resulted in a reduction of large sharks,

tuna, billfish and Sciaenidae fish (Fig. 6a). Flatfish, swordfish and monkfish, on the other hand, increased in biomass by 356, 274, and 35%, respectively. In the Simulation 3 scenario (reduction in gillnet FE by 50%), we there was a lower decline in hammerhead

sharks compared to Simulation 2, an increase in Sciaenidae, monkfish, and angel shark biomass by 34, 21, and 9%, respectively, and a decrease in flatfish biomass (Fig. 6b). Finally, in Simulation 4 (ban gillnet FE), the biomass of hammerhead sharks showed a recovery of 44% (Fig. 6c). Angel sharks and Sciaenidae showed increases in their biomass, while monkfish declined. Swordfish showed an increase in biomass in all three simulations, while blue and mako sharks declined by more than 50% of relative biomass from 2012 (Fig. 6a–c).

In Simulation 5 (increase the longline FE by twofold), we observed a reduction in the biomass of the three large sharks, and also in swordfish, tuna and billfish (Fig. 7a). In Simulation 6 (reducing the longline FE by 50%), we observed a recovery of blue and mako shark biomass (Fig. 7b). Swordfish showed an extraordinary increase, while tuna and billfish declined (Fig. 7b). Billfish and tuna declined more than in Simulation 5, probably due the large increase of swordfish (see Fig. 7a). In Simulation 7 (ban the longline FE), the biomass of blue and mako sharks showed an impressive recovery (Fig. 7c). Swordfish also increased in biomass, however less so than in Simulation 6 (Fig. 7b). billfish and tuna remained in

decline. In Simulation 8 (ban of trawlers), the biomass of large sharks and tuna declined, while the biomass of swordfish increased (Online Resource 2; Fig. 3). This fishery inflicted changes in demersal groups, where a drop in biomass could be observed for flatfish, resulting in increases in the biomass of bluewing searobin fish, rays, and Sciaenidae (Online Resource 2; Fig. 3).

These results highlight the influence of large sharks on large teleosts, evidencing the complex influences among pelagic fishes by both feeding overlap and direct predation (see MTI in Fig. 3). Overall, results revealed that only ceasing the fishing activity, the biomass of the three large sharks could recover or at least be maintained. Blue and mako sharks, billfish, and swordfish would be particularly affected by longline fisheries, while hammerhead sharks would be mostly impacted by gillnet fishery.

Discussion

This work represents the first attempt to assess the ecological role of Large Pelagic Predators (LPP) in the South Atlantic ecosystem of Brazil and to estimate

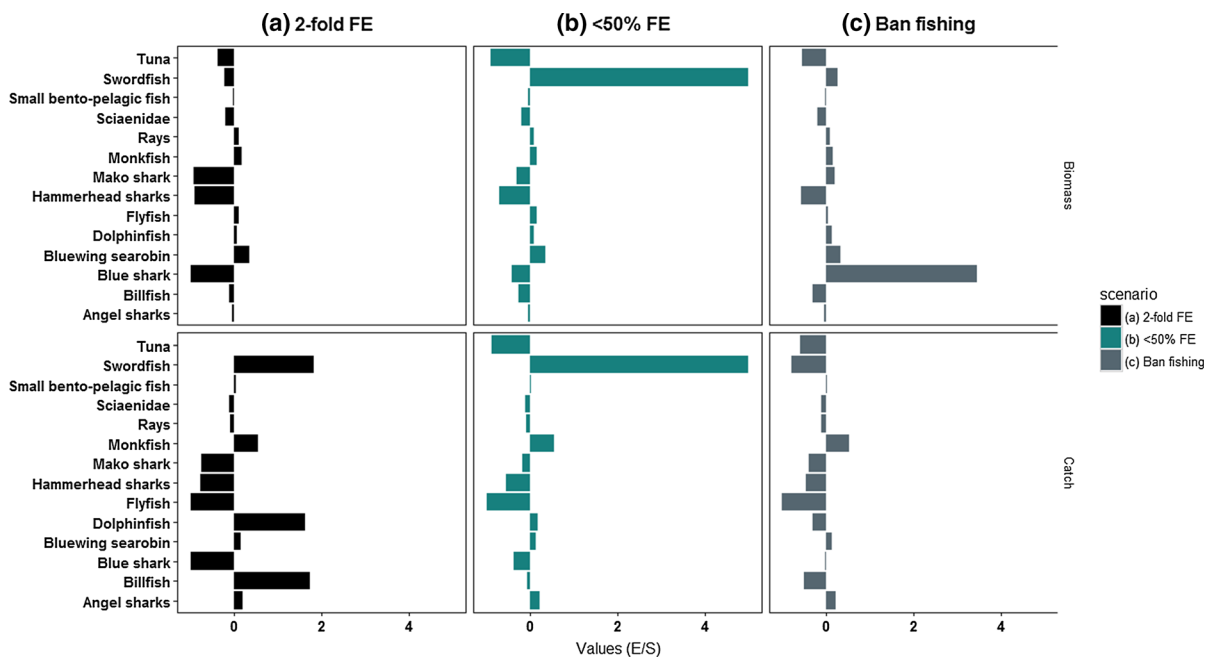


Fig. 7 Relative changes in the biomass and catches (End/Start) of species in the SSB ecosystem after reducing or increasing longline fishery effort: **a** a twofold increase in fishing effort from

2012 to 2025, **b** a 50% reduction over the same period, and **c** a fishing ban over this period

fishing impacts on the marine ecosystem. The baseline food web model developed to represent the ecosystem in 2001 showed a high resilience and high probability of fishery sustainability. All predators groups were classified as keystone species according to one of the keystone species indices used (KS2). The ecological role of LPP is greater on pelagic community, where changes in biomass of groups lead to changes on other organisms. Landings time series from 2001 to 2012 showed a large increase of total catches in the SSB, however decreases in landings of LPP were observed. We detected a reduction of all trophic level-based indicators and also of mean total length. During the period simulation (2012–2025), with exception of swordfish, the biomass of the LPP declined strongly. Simulations also showed that the stocks of sharks, billfish, and tuna no longer support the current fishing effort. Moreover, recovery (or maintenance) in the LPP populations, especially for large sharks, could be only achieved with a strong fishing effort reduction.

A “keystone species” is defined as species that play an important role in a community’s structure despite its low abundance (Mills et al. 1993; Paine 1995; Libralato et al. 2006), and some studies have focused on the key role of LPP in ecosystems (e.g. Heithaus et al. 2008; Navia et al. 2010; Coll et al. 2013a; Bornatowski et al. 2014b, 2016). We used three indexes (KS1, KS2, and KS3) to assess keystone-ness in the SSB model. The blue shark was found to be the first keystone species according to KS2 (*sensu* Power et al. 1996), and other LPP appear in sequence in the KS2 index. Blue sharks and billfish also were within the seventh position in KS3 (Valls et al. 2015). These two indexes (KS2 and KS3) tend to emphasize groups with high TL values and rare species, while KS1 tends to emphasize the key role of abundant species (Valls et al. 2015). Dolphinfinch (TL = 4.2) was considered a keystone species according all three indices, which makes sense because dolphinfinch impact (negatively or positively) all LPP groups. Otherwise blue sharks had a strong influence on swordfish biomass.

The MTI analysis was used to detect indirect impacts through trophic cascades or competition, and also allowed identification of pelagic-demersal relationships (Corrales et al. 2015). The LLP had influences basically on pelagic organisms through top-down control, with minor effects on the demersal community. The pelagic-demersal relationship, while small, illustrates the complexity within the food web

due to interactions between components by direct influence in addition to intra- and interspecific interactions with other species (Coll et al. 2013b; Corrales et al. 2015; Bornatowski et al. 2016). Therefore, the existence of these links reinforces the need to understand fishing effects on SSB food web.

The Marine Trophic Level Index (MTLI) is a powerful indicator of marine ecosystem integrity and of sustainability of fisheries (Pauly et al. 1998), and decreases in MTLI of landings (‘fishing down marine food webs’) have been reported for several regions (e.g. Pauly et al. 2001; Arancibia and Neira 2005; Sibert et al. 2006; Baeta et al. 2009; Freire and Pauly 2010, and see www.fishingdown.org). We also observed this effect according to all indicators analyzed, which was confirmed by reduction of landed species length (MaxT). This phenomenon could show the depletion of bigger species, including sharks and other large pelagic teleosteans in the South Atlantic (e.g. Barreto et al. 2016 for sharks), with a subsequent shift toward targeting smaller fishes (Shannon et al. 2014).

Understanding the effects of top predator removal on marine ecosystems has proven to be a great, complex challenge (Hussey et al. 2014, 2015). While studies have shown that removals of sharks and large teleosteans produces profound impacts on the food chain (e.g. Stevens et al. 2000; Kitchell et al. 2006; Myers et al. 2007; Ferretti et al. 2010; Britten et al. 2014), others have indicated that effects, after shark species loss, were not so persistent on trophic relationships (e.g. Kitchell et al. 2002; Griffiths et al. 2010). Some authors have stated that systems with large numbers of high trophic level species with similar trophic positions (functional similarity) can make food webs more resistant to exclusions of top predators (Walker 1991; Naem 1998; Okey et al. 2007; Griffiths et al. 2010). Our simulations outputs diverge it, because changes on predator biomass, affected other high trophic level species at pelagic environment without spreading through the trophic network. For instance, exclusion of longline fisheries caused large increases in the biomass of blue and mako sharks, and declines in swordfish, billfish and tunas. These unexpected result draw attention, especially because LPP are high-value species (Collette et al. 2011; McClenachan et al. 2016), and there is no control on pelagic shark fishing, especially in tropical areas (Barreto 2015).

The intense fishing effort on large pelagic sharks is persistent because of the relatively high profitability of

the target species (billfish, tuna, and fins of large sharks), in addition to a lack of interest in managing sharks (Dulvy et al. 2008, 2014). In the Atlantic Ocean, swordfish (*Xiphias gladius*) have been the main target by longline fisheries since the 1990s, but some vessels have been targeting large sharks (mainly the blue shark - *Prionace glauca*) since the early 1980s (Hazin et al. 2008; Barreto et al. 2016). The interest on blue sharks has risen progressively due to the demand for shark meat and fins in the domestic and international market (Amorim et al. 1998; Hazin et al. 2008; Domingo et al. 2014).

The gillnet fishery (driftnet), on the other hand, started in 1986 in Brazil and mainly targeted hammerhead sharks (*Sphyrna lewini* and *S. zygaena*) for the commercial sale of fins and meat to Asian and domestic markets (Zerbini and Kotas 1998; Kotas et al. 2008). There is no regulation on Blue and mako sharks catches in SSB ecosystem turning them in the main target for longline pelagic fishing markedly under lower catches of other species (such as tuna and billfish). Worryingly, tuna, swordfish and blue sharks, have considerably lower abundances than the target species.

This intense fishing pressure on LPP has led to depletion of some populations in South Atlantic (Barreto 2015; Barreto et al. 2016), including threatened species such as mako shark (VU), hammerhead sharks (*S. lewini*-EN and *S. zygaena*-VU), Istiophoridae fish (*M. nigricans* and *K. albida* both VU) (IUCN 2016). The present study confirmed this situation: shark biomass has declined in the observed time series and in the fishing effort simulations. Shark population just recovers after a ten-year period, with reducing of longline by 50% and banning gillnet effort. Therefore, is urgent to establish an effective plan to manage these populations because Brazil has been identified the world's largest importer of shark meat (Dent and Clarke 2015), with suspicion of its acting a global flow channel for shark carcasses.

Following the concept of humans acting as “super predators” (see Darimont et al. 2015; Worm 2015), fishing fleets are classified as “top-predators” in some ecosystem models (e.g. Coll et al. 2006; Kitchell et al. 2006; Tsagarakis et al. 2010; Corrales et al. 2015). In this study, outputs from fishing effort simulations indicated that the fleets are top predators, with pelagic longlines impacting on three large sharks (billfish, tuna, and swordfish) and gillnets impacting on

hammerhead sharks. By viewing the fishing fleets as top-predators, our results show a trophic cascade whereby fishing reduces blue and mako sharks, leading to an increase of swordfish biomass, and similar fishing “predation” on tuna and billfish leads to an increase of dolphinfish and flyfish. Further reinforcing the “top-down force” of fisheries activities on stocks, removal of the fishing effort is the only option to recover or preserve biomass for LPP groups. These results are consistent to Barreto et al. (2016), who also indicated that shark populations in South Atlantic might recover if fishing effort would be reduced accordingly. Still, it should be noted that Brazil must reorganize its fisheries monitoring programs (which have been interrupted since 2012) to provide a basis for science-based management (Bornatowski et al. 2013, 2014b). In recent years, Brazilian monitoring has been manifest by a deconstruction of the basic elements necessary for fisheries management (Dario et al. 2015; Barreto et al. *in prep.*).

A considerable number of local shark species in Brazil have declined in recent decades and several species were recently assessed as threatened (Barreto 2015; Barreto et al. 2016). While in the past, tuna and swordfish were major targets for oceanic industrial fisheries, recently sharks have gained more prominence because of the demand for fins and the rapid increase in meat consumption by Brazilian citizens (Bornatowski et al. 2017). This was reflected in declines in the Mean Trophic Level of the Catch and the Mean Total Length of landings. Therefore, our fishing simulations become very important to drive attention toward requiring fisheries management and monitoring programs in Brazil.

Conclusion

Contemporary marine food webs have become less diverse, less robust, and more unstable due to over-exploitation by human populations (Yeakel and Dunne 2015). The Southeastern and Southern Brazil (SSB) food web model showed a high resistance to perturbations in 2001, and large pelagic predators (LPP) were considered as keystone species that exhibit diverse impacts on pelagic fishes of high trophic level (TL). Therefore, losses of LPP, by fishing pressure, could trigger unexpected effects on the community. Landings data already indicate that LPP have declined

over time due to increased fishing effort. Our simulations revealed that shark biomass species may recover (or be maintained) only after strong reductions in longline and gillnet effort. The fisheries impacts into the pelagic community can lead to the collapse of the LPP populations, which is comprised of long-lived and high-valuable species, jeopardizing the economy and maintenance of ecosystem services. There is therefore an urgent need to establish recovery plans both for large sharks and large pelagic teleosts and to reorganize fisheries monitoring programs.

Acknowledgements We thank Dr. Jeffrey Muehlbauer for English reviewing, the São Paulo Research Foundation (FAPESP—2013/25930-0) and the Coordination for the Improvement of Higher Education Personnel (CAPES) for scholarships to HB, and the National Counsel of Technological and Scientific Development (CNPq) for a research grant to RB. CAPES supported M. Coll (Proc. PVE A063/2013, Ed.71/2013). Thanks also to Ministry of Agriculture (Brazilian Government) and University of Vale do Itajaí (UNIVALI) for organizing the dataset of the Landing Statistics Program. Two anonymous reviewers contributed to increase quality of this paper.

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