Aquatic food webs of the oxbow lakes in the Pantanal: A new site for fisheries guaranteed by alternated control?

Ronaldo Angelini [a,*], Ronny José de Morais [b], Agostinho Carlos Catella [c], Emiko Kawakami Resende [c], Simone Libralato [d]

[a] Departamento de Engenharia Sanitária e Ambiental, Universidade Federal do Rio Grande do Norte, UFRN, BR-101, Campus Universitário, Natal, RN 59078-970, Brazil
[b] Mestre em Ecologia e Evolução, Universidade Federal de Goiás, Goiânia, GO, Brazil
[c] Centro de Pesquisa Agropecuária do Pantanal, EMBRAPA, Corumbá, MS, Brazil
[d] Istituto Nazionale di Oceanografia e di Geofisica Sperimentale – OGS, Trieste, Italy

ARTICLE INFO

ABSTRACT

Flood pulse and biotic interrelationships control the food web dynamics of river floodplain systems. The Pantanal Plain in the Paraguay River Basin (Brazil) occupies 140,000 km² of periodically flooded areas and is divided into 12 subregions with different characteristics related to the flood pulse duration, the vegetation, the type of soil, and the resources used in activities, particularly fishing. In this study, we used Ecopath with Ecosim (EwE) to model three oxbow lakes in the South Pantanal Plain, where there is no fishing activity, to test the similarity of the ecosystems, to identify the keystone species and the types of food web controls, and to determine whether these environments can support moderated fishing pressure. We found that the food webs of the oxbow lakes are similar to each other because, although they depend mainly on the presence or absence of predators, flood pulses similarly homogenize the lakes. The results highlight the importance of detritus in these food webs. In addition, the highest values of the keystoneness species index in the three models highlight the role of top predators (*Hoplias malabaricus*, *Serrasalmus* spp., *Pseudoplatystoma reticulatum*, birds, and mammals). Therefore, we suggest that the food webs in the three systems are subjected to an alternated control process: detritus controls the food web during the flood season and by the top predators during the dry season. The simulation outputs indicate that these oxbow lakes can sustain only moderate fishing because increasing the fishing pressure reduces the biodiversity and can negatively impact the top predators.

© 2013 Elsevier B.V. All rights reserved.

1. Introduction

The hydrological regime in river floodplain systems is considered the key factor that determines the structure and functioning of the communities in these areas (Junk et al., 1989; Jepsen and Winemiller, 2002; Agostinho et al., 2007). This assumption is true because the flood pulse determines the exchange of nutrients among the terrestrial and the aquatic environments, and this exchange influences the productivity, allows the migration of species, and thus increases the possibility of interactions between species (Zeug and Winemiller, 2008; Alho, 2008; Hamilton, 2010).

In addition to the flood pulse, the biotic interrelationships also regulate the dynamics of the communities of river floodplain systems (Thomaz et al., 2007; Luz-Agostinho et al., 2008), and the food web may be affected by different food web controls (Hunter and Price, 1992; Pace et al., 1999; Cury et al., 2000; Hunter, 2001; Hunt and McKinnell, 2006; Yaragina and Dolgov, 2009).

In a top-down control system, the higher trophic levels (TLs) determine the bulk of the lower TLs through direct and indirect effects (Carpenter et al., 1985; Leibold et al., 1997; Dyer and Letourneau, 2003; Moore et al., 2003; Dinnen and Robertson, 2010). In a bottom-up control system, the basis of the food chain (producers or detritivores) regulates the productivity and abundance of the higher TLs (Nielsen, 2001; Lorentsen et al., 2010). The species in the intermediate TLs may exert a type of control called wasp-waist, in which changes in the abundances of these species affects both their predators and their prey (Cury et al., 2000; Shannon et al., 2004). However, the dynamics of some communities are determined through a mixed control, i.e., with some influence from both the producers and the predators (Achá and Fontúrbel, 2003; Hunt and McKinnell, 2006).

The species that most influence these types of controls are considered key species because they play a dominant role in the development of the ecosystem. This role is independent of the biomass (Mills et al., 1993; Piraino et al., 2002; Libralato et al., 2006;

* Corresponding author. Tel.: +55 8487433020.
E-mail addresses: ronangelini@yahoo.com.br (R. Angelini), ronnybio@hotmail.com (R.J. de Morais), catella@cpap.embrapa.br (A.C. Catella), emiko@cpap.embrapa.br (E.K. Resende), slibralato@ogs.trieste.it (S. Libralato).

Gasalla et al., 2010) or *TL* of the key species (Paine, 1995; Power et al., 1996; Bond, 2001; Davic, 2003; Jordan et al., 2007).

Through a quantitative analysis of food webs and, in particular, of the interactions of key species, it is possible to predict the stability of food webs that face various impacts, such as fishing (Travers et al., 2010). This information can support the management of fishing activities (Angelini et al., 2006; Angelini and Velho, 2011) to ensure the sustainability and conservation of the ecosystem productivity (Coll et al., 2008a).

The High Paraguay River Basin occupies an area of 496,000 km^2 in the midwestern region of Brazil and comprises 140,000 km^2 of periodically flooded areas of the Pantanal Plain at its center and surrounding non-flooded areas (Junk et al., 2006). More than 270 fish species are found in this area (Britski et al., 2007), and the fishing of mainly a few large species is an important economic and social activity that is practiced under professional, non-professional, sport, and subsistence modalities (Catella et al., 2008). The fishing activity takes place predominantly in the southern and northern areas of Pantanal. Thus, it is of interest to improve the spatial distribution of the fishing effort to avoid overfishing and to ensure the presence of species and environments that are currently underused or have low commercial value (Catella, 2003).

This study aims to quantify the trophic interactions and the energy/matter flows of three oxbow lakes that are situated in the basins of the Miranda and Aquidauana Rivers in the Pantanal floodplain. There is currently no fishing activity in these lakes. In addition, this study investigates the following ecological issues:

(a) These environments present similar ecosystem attributes. Our proposition is that these studied environments are very similar systems because they have the same physical characteristics (e.g., river distances and depths).
(b) The food web is alternatively controlled, i.e., by both top predators and detritus. Despite the flood pulse being a fundamental controlling factor in the wet season, the premise for this supposition is that the biotic control by the top predators (key species) also contributes to the structuring of the communities in these areas, particularly during the dry season.
(c) These environments can support moderate fishing pressure. Pantanal fishing is mainly concentrated on large species and top predators. Thus, there are unexploited species in the studied environments that have not been previously explored, and food web modeling simulations permit the evaluation of the potential effects of fishing on these oxbow lakes.

2. Materials and methods

The Pantanal is characterized by complex drainage due to the different types of rivers, lakes, temporary streams, and marshland that are found in the area. This region is composed of 12 subregions with different characteristics related to the flood pulse duration, the vegetation, and the type of soil (Súarez et al., 2004). The average fishing catch recorded between 2000 and 2005 in the South Pantanal was equivalent to 667 t: 40% was captured through professional fishing and 60% was obtained through sports fishing. In 2005, the eight most captured species represented 82% of the catch: six were top chain carnivores (*Pseudoplatystoma corruscans*, *Pseudoplatystoma reticulatum*, *Paulicea luetkeni*, *Salminus brasiliensis*, *Pygocentrus nattereri*, and *Pinirampus pirinampu*) and two were omnivore species (*Piaractus mesopotamicus* and *Leporinus macrocephalus*) (Albuquerque and Catella, 2009). Neto and Mateus (2009) compared professional and sport fishing in the North Pantanal and showed that these same species were responsible for 95% of the total catch. Two species represented 50% of the catch obtained through professional (*P. corruscans* and *P. reticulatum*) and sport
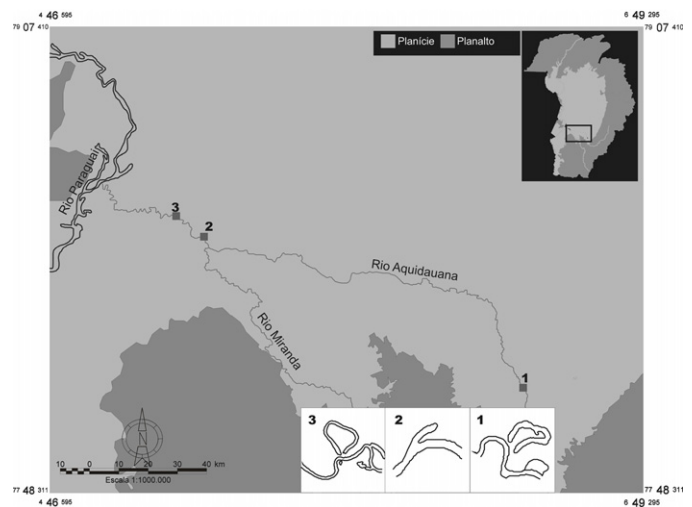

Fig. 1. Map of region and localization of three oxbow lakes (in details): (1) Baía da Onça (ONC model); (2) Braço Morto Acima (MAB); (3) Braço Morto Abaixo (MAC).

fishing (*P. corruscans* and the omnivore "pacu-peva", which is a group of three species of the Mileynae family).

The three oxbow lakes investigated in this study (Baia da Onça, Braço Morto Acima, and Braço Morto Abaixo) are situated south of the Pantanal in Mato-Grosso do Sul State (Brazil). As shown in Fig. 1, these are oxbow lakes of the Miranda River and of its largest tributary, the Aquidauana River. Both of these rivers exhibit meandering courses and are associated with approximately 260 marginal lakes, which are locally referred to as "*Baias*", along the last 353 km of their courses.

The Baia da Onça (with an area of 0.153 km^2) joins the Aquidauana River during flooding periods (December–January) and is disconnected April through May. It has a maximum depth of 3 m and includes no aquatic macrophytes because it is surrounded by a long-term semi-deciduous riparian forest (Catella and Petrere, 1996). The Braço Morto Acima (with an area of 0.2875 km^2) and the Braço Morto Abaixo (with an area of 0.3365 km^2) are situated near the Miranda River and join the river in January and are disconnected from it in months of drought. The depth of these systems varies between 1 m (drought) and 3 m (flood), and there is a predominance of riparian forest and aquatic macrophytes (Resende, 2000). The average water temperature in the three water bodies is approximately 26 °C and exhibits little annual variability. These environments were chosen due to their permanent pattern, the fact that they are equally distant from rivers, and their relatively easy access, i.e., these lakes are easier to study because the approach to most of the aquatic ecosystems in the Pantanal floodplain is quite difficult, regardless of the season. Moreover, these systems represent unexploited lakes of the Pantanal and thus represent potential new areas for fishery activities.

2.1. Model

Ecopath with Ecosim (EwE, versions 6.0 and 5.2 for preliminary balancing processes), which is based on the mass-balance assumption, was used for the elaboration and quantification of models of the three environments. In the basic equation, the consumption by a predator (or group) leads to the mortality of its prey (or group) due to predation. This is mathematically described by linear equations (Christensen and Pauly, 1992):

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

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 ecotropic efficiency of i, which varies from 0 to 1 and represents the fraction of the production of the group that is transferred to higher TLs 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. The species of the investigated lakes are not involved in reproductive migrations or fishing; thus, the value of EX_i of all fish species was initially set to very low values (1% of biomass) to represent occasional fishing. The biomasses were expressed as tww km^{-2} (metric tons of wet weight per square kilometer), and the flows in the food web were expressed in tww km^{-2} year^{-1}.

For an ecosystem with n groups (compartments), the model will have a system of n linear equations. In the development of an EwE model, it is necessary to include at least three of the four main input parameters (B_i, PB_i, QB_i, and EE_i) because it is possible to estimate the missing parameter by connecting the production of one group with the consumption by the other groups based on the assumption that the production of one group is utilized by another group inside the system (Christensen and Pauly, 1992). In the three models developed for the oxbow lakes of the Pantanal, EE_i was the parameter that was estimated by EwE, with few exceptions (see below).

2.2. Dataset

2.2.1. Fish compartments

The samplings of the ichthyofauna in the three environments were conducted using seining nets. Nine collections were performed at the Baia da Onça between 1988 and 1989 (Catella and Petrere, 1996), whereas 15 collections were conducted in the other two systems between 1998 and 2000 (Resende and Pereira, 1998; Resende et al., 1998, 2000a,b). All of the fish samples collected in the three ecosystems were standardized through the use of a 66-m wide trawling net (stretched mesh size = 13.3 mm, net height = 4 m). In Baia da Onça, the samples were collected once a month from September to December. In September, two trawling per day were conducted to sample the ichthyofauna (in the morning and in the afternoon). In the following months, three hauls per day (morning, midday, and afternoon) were conducted. The trawling was performed using a running canoe (0.5 m s^{-1}) and encircling a total area of approximately 4845 m^2 (Catella and Petrere, 1996). Similar procedures and mesh sizes were used in the three hauls that were performed each day in Braço Morto Abaixo and Braço Morto Acima during the 1 week of sampling that was conducted in October and November; the sampling areas comprised a total area of 4500 m^2 for each system. The swept area was assumed to have the shape of half of an ellipse (Ellipse Area = $\Pi \times a \times b$, where a is 1/4 of the length of the trawling net (16.5 m) and b is the distance (m) between the start position of trawling and the end position). Therefore, assuming a constant and even catchability among the species, the biomass (B) value was calculated as the sum of the individual weights of fish divided by the swept areas, which gave the corresponding densities (biomass per unit of area).

During the sampling period of this study (1988–2000), Pantanal flooding was higher than the historical means (Junk et al., 2006 and Fig. 3). In the second sampling period (1998–2000), the river level was slightly lower than in 1988, although the inundation patterns in the Pantanal remained relatively constant (Hamilton, 2002) despite the ENSO events in this period, which did not influence the Pantanal hydrologic dynamics (Clarke et al., 2003). Thus, during both periods and in the years between samplings, the three lakes were regularly flooded to a similar extent and remained isolated from the rivers during the same time periods. Therefore, we could safely assume that the location and the temporal differences did not indicate dissimilar ecosystem dynamics, which permits the comparison of these modeled environments.

Of the approximately 270 fish species found in the Pantanal (Britski et al., 2007), 75, 90, and 80 fish species were collected in the Baia da Onça, the Braço Morto Acima, and the Braço Morto Abaixo, respectively. All of these species belong to 20 families. All of the species sampled in Braço Morto Abaixo were also caught in Braço Morto Acima. In Baia da Onça, only two different species were sampled. Thus, the sampling revealed a high similarity among the three oxbow lakes.

In each model, the main fish species and the most important species in the biomass were represented by a single compartment: there were 31 fish species in the Baia da Onça (ONC model), whereas 29 fish species were found in the Braço Morto Acima (MAC) and in the Braço Morto Abaixo (MAB). The 29 species that were found in both the MAC and the MAB were also found in the ONC; *Cynopotamus kincaidi* and *Hypophthalmus edentatus* were only found in the Baia da Onça. The species that constituted the ONC, MAC and MAB models represented at least 97% of the total fish biomass in each system.

The Production/Biomass (PB) was calculated using the Pauly (1980) equation; the equation parameters were obtained from studies on tropical fish (Cunha et al., 2007; Angelini and Agostinho, 2005a; Capistrano-Santana et al., 2004; Vazzoler et al., 1997) or from FishBase (Froese and Pauly, 2009). Palomares and Pauly (1998) equation was used to determine the Consumption/Biomass ratio (QB) using parameters that were estimated based on our samplings, including the caudal fin area index.

The diet composition matrix was determined through an analysis of the stomach contents of the collected individuals (Resende and Pereira, 1998; Resende et al., 1998, 2000a,b). Novakowski et al. (2008) estimated the diet of a fish community in this same region and found very similar values. Although seasonality is a discernible characteristic in the Pantanal region, negligible seasonal differences were observed in the diet composition of the studied species; this similarity supported the development of only one annual model for each environment. The diet composition of the models is shown in the supplementary materials (Annex A).

2.2.2. Non-fish compartments

The non-fish compartments used in the three models were phytoplankton, zooplankton, aquatic insects, terrestrial insects, birds, caimans, mammals, and detritus. Aquatic macrophytes were used only for the models of the MAC and the MAB because these organisms are not found in the Baia da Onça (Catella and Petrere, 1996).

The B and PB values for caimans (*Caiman crocodilus yacare*) were estimated according to the method suggested by Campos et al. (2006), who studied the movement of caimans in another region of the Pantanal. The diet composition used was obtained from Borteiro et al. (2009), who studied caimans of the same basin (Uruguay), and the QB value was obtained from African crocodiles in Villanueva et al. (2006a). The value of B for the birds (including *Ardea alba*, *Egretta thula*, *Phalacrocorax brasilianus*, and *Sterna superciliaris*) was estimated according to the research performed by Figueira et al. (2006), who studied the birds in the entire Pantanal region; the values of PB and QB were obtained from the study conducted by Villanueva et al. (2006a), who studied freshwater lakes in Africa and found that the composition of the diet of birds was generally distributed among small fish species. The value of B for mammals was estimated based on the study by Desbiez et al. (2010), whereas the PB, QB, and DC values were estimated according to the research conducted by Waldemarin et al. (2007), who studied *Pteronura brasiliensis* and *Lontra longicaudis* in the Pantanal.

Due to the lack of local information for the other compartments (phytoplankton, macrophytes, zooplankton, and invertebrates), the values of B for these groups were estimated using the PB Ecopath inputs, which were obtained from Angelini and Agostinho (2005b), who modeled a floodplain near the site of this study. The EE values for these groups were obtained from Angelini et al. (2006), who quantified a food web in the Amazonas River, which has a similar hydrological regime as the one in the Pantanal. The B value for detritus was estimated using the following empirical regression:

$$\log detritus = 0.954 \times \log primary\ production$$
$$+ 0.863 \times \log euphotic\ zone - 2.41 \qquad (2)$$

where the Primary Production unit is $gC\,m^{-2}$ (values were estimated from Cole et al., 1988) and the units for the euphotic zone are meters (2 m, Catella and Petrere, 1996).

2.2.3. Balance and validation of models

The Pedigree Index (IPdgr) was calculated to determine the quality associated with the input values of each parameter (B, PB, QB, and the diet matrix elements; Christensen et al., 2005). In EwE, the user attributes a quality value between 0 (low) and 1 (high) for each parameter according to the source of the information (low for general model-based input values and high for values obtained through experimental data). Then, the average of the quality values of all of the parameters in all of the groups is calculated to obtain a general synthetic index of the model input data quality (Christensen et al., 2005; Morissette et al., 2006).

The Ecoranger routine (EwE version 5.2) was used to test the consistency of the model outputs because it allows an evaluation of the quality of the input data using the Pedigree Index. The Ecoranger routine considers the input values the mean of a normal distribution with a user-defined confidence interval (Christensen et al., 2005). Thus, Ecoranger re-samples these input values, runs the models, and tests the reliability of the model outputs, which reduces the inherent imprecision of the input values using a least-squares criterion to obtain the model with the minimum residual. Consequently, when the data are not completely accurate, EwE helps find the model that best fits the most robust set of available data (Pauly et al., 2000).

2.2.4. Output models

The EwE model calculates the series of indicators and properties of each functional group that are useful for the ecological analysis of the food web. In particular, EwE calculates the fractional trophic level (TL_i) of each component based on its diet composition (Christensen and Pauly, 1993) and the variance of prey across TLs, which is called the Omnivory Index (OI; Christensen et al., 2005).

Moreover, using the Mixed Trophic Impact (MTI) matrix, which is used to assess the direct and indirect interactions between the species in a food web, Libralato et al. (2006) developed a keystoneness species index (KS_i):

$$KS_i = \log[e_i(1 - p_i)] \qquad (3)$$

where e_i is equal to $\sqrt{\sum m_{ij}^2}$ (m_{ij} represents the interaction between the impacting group i and the impacted group j; this measure is calculated based on the MTI); therefore, e_i is a measure of the effects of each group on all of the other groups of the food web (including the indirect ones). The effect of the change on the group biomass itself (i.e., m_{ii}) is not included; p_i is equal to (B_i/total B), where B_i is the biomass of the impacted group and total B is the total biomass (excluding detritus). Through the evaluation of the positive and negative contributions to the value of e_i, it is possible to make inferences regarding the type of control that governs the analyzed ecosystem (Libralato et al., 2006).

Global properties of ecosystems were used to describe the state of development of the environments and to support the comparisons among them (Odum, 1969): (a) Total System Throughput (TST), which is the sum of all flows in the system (consumption, exports, respiration, and flows to detritus); (b) Total Primary Production/Total Respiration (PPT/RT), which describes the maturity of systems, i.e., it increases to values close to 1 as the systems becomes more mature; (c) Biomass/Total System Throughput (B/TST), which was used to evaluate the biomass maintained by a unit of flow in the system and is expected to increase with maturity (Christensen, 1995); (d) Finn Cycling Index (Finn%), which represents the proportion of recycled flows in the system (Finn, 1976) and can be used as a measure of resilience (Vasconcellos et al., 1997); (e) the path length (PL), which is calculated as the total system flows divided by the sum of the total export and the total respiration flows and is directly connected to the maturity of the ecosystem (Christensen and Pauly, 1993); (f) the Connectance Index (CI), which is the ratio of the number of actual links to the number of possible links in the modeled food web such that a greater connectivity tends to indicate a higher system maturity (Christensen and Walters, 2004a; Christensen et al., 2005); (g) the System Omnivory Index (SOI), which aggregates the variations between the diets of the components and is not affected by the aggregation method (Libralato, 2008), i.e., values of SOI close to 0 indicate a dominance of specialist consumers, whereas values close to 1 indicate a dominance of groups with high food plasticity (Pauly et al., 1993; Christensen et al., 2000); and (h) ascendancy and overhead, which are emergent properties (Ulanowicz, 2009) that correspond to a measure of system maturity and a measure of ecosystem stability, respectively (Christensen, 1995).

EwE also aggregates the biomasses and flows into integer TLs, thereby representing the system using the "Lindeman Spine" (Libralato et al., 2010), which allows the estimation of the Transfer Efficiency (TE) as the ratio between the productions obtained at two consecutive integer TLs. The Lindeman Spine allows a better understanding of the effectiveness of energy transfer in the system (Lindeman, 1942) because it separately takes into account the detritus-based and the grazing food chains and allows the performance of biomass analysis by TL.

2.2.5. Fisheries-related outputs and derived measures

Another EwE output is the Primary Production Required (PPR) to sustain the biomass production of the food web organisms. This measure was mainly used to quantify the pressure of fishing on the ecosystems by calculating the PPR to sustain catches (Pauly and Christensen, 1995). Based on the PPR, Libralato et al. (2008) developed the loss of secondary production index (L index):

$$L = \frac{-1}{P1 \times \ln TE} \times \sum (PPR_i \times TE^{TL_i - 1}) \qquad (4)$$

where P1 = PP (Calculated Net Primary Production) + FLDET (Flows to Detritus) and indicates the autotrophic production and detritus production by the food web ($t\,km^{-2}\,year^{-1}$), TE is the average efficiency of transfer between the TLs (%), PPR_i is the Primary Production Required for component i ($t\,km^{-2}\,year^{-1}$), and TL_i is the TL of component i.

Libralato et al. (2008) used the trophic level of the catches (TLc) in Eq. (4) and developed the L index to measure the loss of secondary production due to fishing. The authors also calculated the L index in 51 marine ecosystems that were classified as sustainably and not sustainably exploited by fishing. Based on the frequency distribution of the L values, these researchers proposed reference levels to classify the probability of the sustainability of fishing (psust). Therefore, the reference values for the L index that indicates a sustainability (psust) between 75% and 95% would be $L75\% = 0.021$ (standard deviation (s.d.) = 0.013) and $L95\% = 0.007$ (s.d. = 0.007)

(Coll et al., 2008a). The L index of the three models investigated in this study was estimated considering a very small catch in the base models, which was equivalent to 1% of the biomass of each fish species ($F = 0.01$), and successively increasing the catch in each additional set of simulations (see below).

The Total Primary Production Required (TPPR) depends on the cycles that occur between the higher TLs that magnify the production that affects TL 1. Therefore, it is important to compare TPPR with P1 to obtain an estimate of the system's autocatalysis potential (sensu Ulanowicz, 2009), i.e., to measure the positive feedbacks that help the system develop on its own through recycling cycles. Therefore, the index $[1 - (P1/TPPR)]$, which varies from 0 to 1, was estimated: values close to unity indicate that the system maintains itself through high autocatalysis with a low production (P1), whereas values close to zero indicate that the higher TLs are not exerting positive feedback on the system, which thus tends to be unable to unfold itself, i.e., in low autocatalysis conditions, all production is used in the upper TLs and only a small amount of material is recycled.

The Kempton index (Q) includes species or functional groups at a TL 3 or higher (Kempton and Taylor, 1976). Q is a relative index of biomass diversity that was derived from Kempton's $Q75$ index, which was also developed as an indicator of biodiversity evenness (Ainsworth and Pitcher, 2006). A lower value of Q implies a low evenness and richness and higher group dominance. The Kempton Q index is automated in EwE as a dynamic output in the simulations (Christensen and Walters, 2004b).

2.2.6. Fisheries and simulations

The trophodynamic module of EwE (i.e., Ecosim) uses settings from the mass-balance module (i.e., Ecopath) as the initial conditions and parameter definitions (Christensen and Walters, 2004b). Namely, the system equation (Eq. (1)) is transformed into a system of ordinary differential equation as follows (Walters et al., 1997, 2000):

$$dB_i/dt = g_i \times \sum_j Q_{ij} - \sum_j Q_{ij} + I_i - (MO_i + F_i + e_i) \times B_i \qquad (5)$$

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_{ij} 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.

In Eq. (5), the quantity of prey i consumed by predator j (Q_{ij}) is a nonlinear relationship based on the "foraging arena concept" (Walters et al., 2000; Walters and Christensen, 2007; Ahrens et al., 2011):

$$Q_{ij} = \frac{a_{ij} \times v_{ij} \times B_i \times B_j}{2 \times v_{ij} \times a_{ij} \times B_j} \qquad (6)$$

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 foundation of Eq. (6) is the "foraging arena concept", in which 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).

A system of differential equations, such as Eqs. (5) and (6), permits the simulation of food web dynamics and can be used to investigate fisheries under several management scenarios.

To answer our third ecological issue (i.e., whether these environments can support moderate fishing pressure), we performed a set of fishing simulations on the oxbow lakes to assess the ecosystem changes induced by fishing and to verify the performance of the Kempton and L indexes. With each of the three models, we performed 20 simulations, each of which represented 30-year scenarios with increasing fishing mortality for all fish species. The simulations were performed using the Ecosim routine (Christensen and Walters, 2004a) and maintaining the initial Ecopath fishing mortality ($F_0 = 0.01$, i.e., 1% of the initial Ecopath biomass) for the first 4 years of the simulation, then linearly increasing the fishing mortality in years 5–13 from F_0 to $F = F_0 \times f$ (where f is a multiplier), and then maintaining the last value of F for the last 13 years of the simulation. A total of 20 simulations were performed for values of f equal to 10, 20, 30, 40, 50, 60, 70, 80, 90, 100, 200, 300, 400, 500, 600, 700, 800, 900, and 1000. Thus, the simulations explored the effects of fishing mortality (F) ranging from 0.01 to 10.

The Ecosim vulnerability parameters are usually determined through the best fit with the observed time series (see, for example, Freire et al., 2008). However, no time-series data were available in the present study to perform an authentic calibration; thus, we used the Ecosim default vulnerability parameters (Christensen and Walters, 2004a; $v = 2$, which indicates a mixed food web control), and only the fishing mortality was changed in the different simulations. The phytoplankton production was maintained constant during the simulations ("max rel P/B" = 1). If the biomass of a compartment decreased to less than 20% of the original biomass, the compartment was not considered in the analysis of the model outputs. The outputs of the 30-year simulations were used to compare the Kempton Q indexes, the numbers of compartments that remained in the system (S), the TL dynamics, and the L index between the three models.

3. Results

3.1. Basic estimates and Pedigree Index

Of the three proposed models, the Baia da Onça (ONC) and the Braço Morto Acima (MAC) were balanced without the need to change the original input values. Five components (Psectrogaster curviventris, Moenkhausia spp., Trachydoras paraguayensis, Curimatella spp., and Pimelodella spp.) of the Braço Morto Abaixo (MAB) model had EE values higher than 1, which indicates that the flows were not balanced (the consumption flows of a group were higher than its production flows). The model was balanced using the automatic mass balance routine (Christensen et al., 2005; Kavanagh et al., 2004), which, through a series of iterative runs, minimizes the changes in the input values for those parameters with a low contribution to the Pedigree Index to produce a model with EE values less than 1.0.

The global Pedigree Indexes were 0.71, 0.61, and 0.59 for the ONC, MAC, and MAB models, respectively. These values indicate that the quality of the input data for the models is generally good for ecosystem analysis (Christensen et al., 2000). Through the Ecoranger routine, the ONC model showed a larger number of acceptable executions (200/10,000), with a minimum residual sum of 159.07. The MAC had 85 acceptable executions out of 10,000, with a minimum residual sum of 172.38, whereas the MAB had 27 acceptable executions out of 10,000, with a minimum residual sum of 202.46. These values are considered acceptable for the purposes of this study (Villanueva et al., 2006b).

The values of Production/Biomass (PB) and Consumption/Biomass (QB) for the fish species were the same in the three models (Tables 1–3). However, the values of B for the phytoplankton, macrophytes, aquatic, and terrestrial insects compartments that were calculated by EwE varied. The matrix of the diet composition in each system is shown in Tables A1–A3 of Appendix A;

Table 1

Basic inputs parameters and outputs (in bold) for Ecopath of the Baía da Onça (ONC model). *TL*, trophic level (*TL*); *B*, biomass (t km^{-2}); *PB*, Production/Biomass (t km^{-2} year^{-1}); *QB*, Consumption/Biomass (t km^{-2} year^{-1}); *EE*, Ecotrophic Efficiency; OI, Omnivory Index; PN, Path Number.

	Compartimentos	TL	B	PB	QB	EE	OI	PN	Catch
1	Phytoplankton	**1.00**	**3.82**	250.00		0.334			
2	Mammals	**4.08**	0.41	1.50	3.65	**0.000**	**0.306**	**2085**	
3	Caymans	**4.16**	0.10	0.25	0.80	**0.000**	**0.243**	**2023**	
4	Birds	**3.62**	0.10	0.30	47.20	**0.000**	**0.275**	**155**	
5	Zooplankton	**2.00**	**3.03**	55.00	250.00	0.530	**0.000**	**2**	
6	Aquatic insects	**2.00**	**4.28**	10.40	40.00	0.620	**0.096**	**1**	
7	Terrestrial insects	**2.00**	**2.42**	25.00	250.00	0.620	**0.128**	**1**	
8	*Schizodon borellii*	**2.17**	0.66	3.47	55.99	**0.315**	**0.324**	**1**	0.006
9	*Sturisoma robustum*	**2.00**	0.40	1.19	55.78	**0.982**	**0.007**	**1**	0.004
10	*Tetragonopterus argenteus*	**2.94**	0.11	3.20	18.73	**0.996**	**0.062**	**5**	0.001
11	*Chaetobranchopsis australis*	**2.57**	0.27	1.90	15.71	**0.922**	**0.241**	**5**	0.002
12	*Pseudoplatystoma reticulatum*	**3.43**	0.74	2.82	10.00	**0.228**	**0.444**	**798**	0.007
13	*Hemiodus orthonops*	**2.10**	0.28	1.46	69.66	**0.774**	**0.205**	**4**	0.003
14	*Hypostomus* spp.	**2.00**	1.33	2.46	33.20	**0.641**	**0.000**	**1**	0.013
15	*Psectrogaster curviventris*	**2.00**	3.63	1.40	62.81	**0.998**	**0.009**	**1**	0.036
16	*Pseudoplatystoma corruscans*	**3.50**	0.10	2.82	10.00	**0.062**	**0.483**	**489**	0.001
17	*Moenkhausia* spp.	**2.99**	5.36	5.00	25.84	**0.432**	**0.180**	**6**	0.053
18	*Loricaria* spp.	**2.00**	0.15	4.50	26.06	**0.212**	**0.013**	**1**	0.001
19	*Potamorhina squamoralevis*	**2.00**	1.08	1.24	40.28	**0.994**	**0.001**	**1**	0.010
20	*Auchenipterus nuchalis*	**2.98**	0.29	3.00	14.56	**0.398**	**0.023**	**5**	0.003
21	*Leporinus* spp.	**2.04**	0.17	2.60	20.00	**0.324**	**0.043**	**3**	0.001
22	*Plagioscion ternetzi*	**3.31**	0.32	1.41	8.77	**0.993**	**0.270**	**108**	0.003
23	*Acestrorhynchus pantaneiro*	**3.41**	0.15	2.20	24.64	**0.401**	**0.390**	**248**	0.001
24	*Hemisorubim platyrhynchos*	**3.34**	0.11	1.30	10.32	**0.465**	**0.191**	**108**	0.001
25	*Hypophthalmus edentatus*	**2.25**	0.73	1.85	8.14	**0.298**	**0.184**	**3**	0.007
26	*Cynopotamus kincaidi*	**3.14**	0.26	1.75	14.54	**0.939**	**0.286**	**66**	0.002
27	*Trachydoras paraguayensis*	**2.65**	0.10	2.35	25.67	**0.816**	**0.222**	**6**	0.001
28	*Hoplias malabaricus*	**3.50**	1.23	2.67	8.53	**0.411**	**0.388**	**358**	0.012
29	*Serrasalmus* spp.	**3.30**	0.58	1.62	14.64	**0.995**	**0.413**	**68**	0.006
30	*Gymnogeophagus balzanii*	**2.56**	0.12	1.94	17.63	**0.985**	**0.242**	**6**	0.001
31	*Pimelodus* spp.	**2.74**	1.78	1.99	11.70	**0.397**	**0.269**	**5**	0.017
32	*Loricariichthys* spp.	**2.00**	0.80	1.17	25.51	**0.991**	**0.006**	**1**	0.008
33	*Roeboides* spp.	**3.20**	1.06	2.12	21.48	**0.947**	**0.424**	**11**	0.010
34	*Steindachnerina* spp.	**2.00**	1.82	1.30	52.78	**0.988**	**0.000**	**2**	0.018
35	*Curimatella dorsalis*	**2.00**	5.83	1.48	18.43	**0.998**	**0.001**	**1**	0.058
36	*Triportheus* spp.	**2.72**	0.79	2.11	14.30	**0.960**	**0.325**	**6**	0.008
37	*Pimelodella* spp.	**2.93**	0.42	1.40	12.73	**0.943**	**0.241**	**32**	0.004
38	*Astyanax sp*	**2.59**	0.12	2.40	15.27	**0.855**	**0.313**	**4**	0.001
39	Detritus	**1.00**	30.00			**0.966**	**0.391**		

these matrices are evidence of the similarity of the diet of the species in the three environments.

3.2. Output models

In the ONC model (Table 1), the highest *TL* was obtained for caimans (4.16). Among the fish species, the highest *TL* values were obtained for *Hoplias malabaricus* (3.50), *P. corruscans* (3.50), and *P. reticulatum* (3.43). In the MAC model (Table 2), the highest *TL* value was 4.31 (mammals); among the fish species, the highest *TL* values were obtained for *P. reticulatum* (3.33), *P. ternetzi* (3.33), and *H. malabaricus* (3.32). Mammals were also the group with the highest *TL* (4.32) in the MAB model (Table 3); the four fish species with the next highest *TL* values were the following: *H. malabaricus* (3.47), *P. ternetzi* (3.41), *Acestrorhynchus pantaneiro* (3.33) and *Serrasalmus* spp. (3.33).

In general, the top predators have the larger number of paths that lead to them. Among the groups with a *TL* > 3, nine, six, and three of the groups in the ONC (Table 1), MAB (Table 2), and MAC (Table 3) models, respectively, exhibited an Omnivory Index (OI) greater than 0.25. In the three models, the species *Astyanax altiparanae*, *Triportheus* spp., *Pimelodus* spp., *Pimelodella* spp., *Roeboides* spp., and *H. edentatus* from the intermediate *TL*s (between 2 and 3) had an OI greater than 0.25 due to a highly diversified diet despite the low number of paths.

The zero *EE* value for the caimans, birds, and mammals compartments in the three models reflects the absence of predation on these groups because these are considered top predators in the

system (Christensen et al., 2005). The *EE* values in the other compartments were high, demonstrating the importance of all of these groups as prey and/or predators. The estimated values of the zooplankton biomass (between 2.24 and 3.62) are comparable to those that were observed in the Pantanal floodplain by Fantin-Cruz et al. (2010).

In general, the values of the ecosystem attributes (Table 4) are very similar among the three environments, which show a high overhead, high recycling flows (Finn index), and likely a high maturity (PPT/RT close to 1), although the ascendancy values are low. The MAB and MAC models have a higher total biomass than the ONC model due to the presence of aquatic macrophytes. The biomass of the fish groups in the ONC model is smaller (30.79 t km^{-2}) than in the MAB (36.03 t km^{-2}) and the MAC (43.97 t km^{-2}) models, but these biomass differences do not significantly alter the values of the attributes of the ecosystems.

The geometric average of the energy transfer among the *TL*s (Table 4) is higher in the MAB (9.4%) model compared with the ONC and MAC models (8.1% in both). These values are similar to each other and close to those obtained with other environments (Christensen et al., 2005; Villanueva et al., 2006b).

The Transfer Efficiency (*TE*) between *TL*s 2 and 3 is higher in a grazing food chain than in a detritus-based food chain for the ONC model (Fig. 2), which is the oxbow lake with a significantly lower biomass of primary producers (without a macrophytes compartment). For the other *TL*s, the efficiency of the grazing food chain was higher than the corresponding efficiency of the detritus-based chain. In addition, there are differences in the magnitude of the

Table 2

Basic inputs parameters and outputs (in bold) for Ecopath of the Braço Morto Acima (MAC model). *TL*, trophic level (*TL*); *B*, biomass (t km^{-2}); *PB*, Production/Biomass (t km^{-2} year^{-1}); *QB*, Consumption/Biomass (t km^{-2} year^{-1}); *EE*, Ecotrophic Efficiency; *OI*, Omnivory Index; *PN*, Path Number; Catch, 1% of biomass.

	Compartments	TL	B	PB	QB	EE	OI	PN	Catch
1	Phytoplankton	**1.00**	**4.17**	250.00		0.401			
2	Macrophytes	**1.00**	**133.23**	10.00		0.300			
3	Mammals	**4.31**	0.43	1.50	3.65	**0.000**	**0.005**	**1526**	
4	Caymans	**4.16**	0.10	0.25	0.80	**0.000**	**0.156**	**1569**	
5	Birds	**3.52**	0.02	0.30	47.20	**0.000**	**0.105**	**122**	
6	Zooplankton	**2.00**	**3.80**	55.00	250.00	0.536	**0.000**	**2**	
7	Aquatic insects	**2.00**	**12.08**	10.40	40.00	0.570	**0.096**	**2**	
8	Terrestrial insects	**2.00**	**2.85**	25.00	250.00	0.616	**0.147**	**1**	
9	*Schizodon borellii*	**2.17**	1.91	3.47	55.99	**0.302**	**0.214**	**3**	0.019
10	*Sturisoma robustum*	**2.00**	0.52	1.21	55.78	**0.943**	**0.007**	**1**	0.005
11	*Tetragonopterus argenteus*	**2.93**	0.30	3.16	18.73	**0.966**	**0.064**	**7**	0.003
12	*Chaetobranchopsis australis*	**2.57**	0.50	1.95	15.71	**0.996**	**0.241**	**6**	0.005
13	*Pseudoplatystoma reticulatum*	**3.33**	2.26	2.82	10.00	**0.102**	**0.339**	**490**	0.022
14	*Hemiodus orthonops*	**2.03**	0.59	1.46	69.66	**0.904**	**0.029**	**6**	0.006
15	*Hypostomus* spp.	**2.00**	2.59	2.46	33.20	**0.643**	**0.000**	**1**	0.026
16	*Psectrogaster curviventris*	**2.00**	3.14	1.40	62.81	**0.985**	**0.006**	**1**	0.031
17	*Pseudoplatystoma corruscans*	**3.07**	0.34	2.82	10.00	**0.121**	**0.189**	**39**	0.003
18	*Moenkhausia* spp.	**2.76**	**3.32**	5.00	25.84	0.944	**0.184**	**8**	0.033
19	*Loricaria* spp.	**2.00**	0.27	4.50	26.06	**0.280**	**0.007**	**1**	0.002
20	*Potamorhina squamoralevis*	**2.00**	2.33	1.23	40.28	**0.975**	**0.001**	**1**	0.023
21	*Auchenipterus nuchalis*	**2.98**	**0.20**	2.71	14.56	**0.944**	**0.023**	**6**	0.002
22	*Leporinus* spp.	**2.03**	0.21	2.60	12.72	**0.473**	**0.033**	**5**	0.002
23	*Plagioscion ternetzi*	**3.33**	0.47	1.40	8.77	**0.996**	**0.194**	**378**	0.004
24	*Acestrorhynchus pantanaeiro*	**3.29**	0.14	2.22	24.64	**0.429**	**0.108**	**42**	0.001
25	*Hemisorubim platyrhynchos*	**3.27**	0.27	1.30	10.32	**0.643**	**0.122**	**345**	0.002
26	*Trachydoras paraguayensis*	**2.65**	**3.70**	2.35	25.67	**0.870**	**0.222**	**7**	0.037
27	*Hoplias malabaricus*	**3.32**	3.02	2.67	8.53	**0.105**	**0.297**	**590**	0.030
28	*Serrasalmus* spp.	**3.24**	0.43	1.58	14.64	**0.994**	**0.367**	**407**	0.004
29	*Gymnogeophagus balzanii*	**2.56**	0.58	1.94	17.63	**0.999**	**0.242**	**7**	0.006
30	*Pimelodus* spp.	**2.54**	1.56	1.99	11.70	**0.397**	**0.250**	**6**	0.015
31	*Loricariichthys* spp.	**2.00**	2.51	1.16	25.51	**0.972**	**0.006**	**1**	0.025
32	*Roeboides* spp.	**3.02**	1.05	2.09	21.48	**0.996**	**0.301**	**32**	0.010
33	*Steindachnerina* spp.	**2.00**	3.17	1.33	52.78	**0.969**	**0.000**	**2**	0.031
34	*Curimatella dorsalis*	**2.00**	**6.74**	1.47	18.43	**0.987**	**0.000**	**2**	0.067
35	*Triportheus* spp.	**2.73**	1.46	2.11	14.30	**0.830**	**0.210**	**7**	0.014
36	*Pimelodella* spp.	**2.84**	**4.18**	1.40	12.73	**0.988**	**0.212**	**42**	0.042
37	*Astyanax sp*	**2.62**	0.40	2.43	15.27	**0.991**	**0.266**	**6**	0.004
38	Detritus	**1.00**	30.00			0.638	**0.317**		

flows from the food chains: the energy that arrives at the *TL* 2 in the ONC model arises from detritus (1224.0 tww km^{-2} year^{-1}) and producers (318.7 tww km^{-2} year^{-1}), resulting in a detritivore:herbivore ratio (D:H) of 3.8:1. In the MAC model, this ratio is smaller (D:H = 1.9:1) and similar to that of the MAB model (D:H = 1.82:1). These ratios decreased at higher *TLs* and exhibited mean values of 3.06, 1.4, and 1.46 in the ONC, MAC, and MAB models, respectively (Fig. 2).

The mammals, birds, and top-predator fish compartments (*H. malabaricus*, *P. reticulatum*, *Serrasalmus* spp., and *Pimelodella* spp.) had the highest *KS$_i$* (Table 5) in the three environments.

3.3. Quantification and analysis of fishing effects

The Total Primary Production Required (TPPR) surpassed P1 (energy available at *TL* 1), which is the sum of Calculated Net Primary Production (PP) with Flows to Detritus (FLTED) (Table 6). The differences between TPPR and P1, which is estimated by the [1 − (P1/TPPR)] index (Table 6), show values close to 0.5 for the MAC and MAB models and 0.66 for the ONC model.

The *L* index values were small and similar between the three environments (Table 6). This finding indicates that fishing is a sustainable activity in the steady-state models. The increased fishing mortality in the simulations raised the *L* index values, but these increased *L* index values indicated a high probability of fishery sustainability (Fig. 3).

The simulations of the models of the three lakes indicated that an increase in the fishing effort reduced the Q index and the number of compartments (Fig. 4). For the ONC model (Fig. 4a and b), an

"optimum Kempton" was found at *f* = 7, i.e., at this value, the fishing activity is likely to improve the biodiversity evenness. For *f* > 70 with the ONC model (Fig. 4b) and *f* > 50 with the MAC and the MAB models (Fig. 4d and f), the Kempton values tended to infinity and cannot be used to evaluate the food web structure. To maintain the Kempton index value close to its initial value (without fishing mortality), the *f* values have to remain at less than 7 for the ONC model and at less than 4 for the MAC and the MAB models.

In general, the simulations with high fishing pressure resulted in the removal of the highest *TL* species/group (Table 7), such as *Hemisorubim platyrhynchos* (TL = 3.34), mammals (TL = 4.32), *A. pantaneiro* (TL = 3.33), and caimans (TL = 4.16). Most of the removals were registered in the simulation with *f* = 20 (13–14 compartments). The *TLs* of the compartments for the community (excluding *TL* = 1) decreased (Fig. 5a) as the *TL* of the remaining fish compartments increased (Fig. 5b) to greater than 2.5 (Table 7): *Moenkhausia* spp. (TL = 2.76), *Triportheus* spp. (TL = 2.59), and *Tetragonopterus argenteus* (TL = 2.93). *Auchenipterus nuchalis* (2.98) and *Pimelodus* ssp. (TL = 2.74) also persisted in the ONC model, whereas *T. paraguayensis* (TL = 2.65) remained in the MAC model and *Gymnogeophagus balzanii* (TL = 2.56) remained in the MAB model.

4. Discussion

The models (ONC, MAC, and MAB) of the three oxbow lakes integrated different biological information and sources of data, including some that are available only in the gray literature. The good quality of the input values, particularly the biomass estimates for the fish and their diet compositions, were reflected in the high

Table 3
Basic inputs parameters and outputs (in bold) for Ecopath of the Braço Morto Abaixo (MAB model). *TL*, trophic level (*TL*); *B*, biomass (t km^{-2}); *PB*, Production/Biomass (t km^{-2} year^{-1}); *QB*, Consumption/Biomass (t km^{-2} year^{-1}); *EE*, Ecotrophic Efficiency; *OI*, Omnivory Index; *PN*, Path Number; Catch, 1% of *B*.

	Compartments	*TL*	*B*	*PB*	*QB*	*EE*	*OI*	*PN*	Catch
1	Phytoplankton	**1.00**	**2.88**	250.00		0.400			
2	Macrophytes	**1.00**	**123.26**	10.00		0.300			
3	Mammals	**4.32**	0.09	1.50	3.65	**0.000**	**0.019**	**2892**	
4	Caymans	**3.82**	0.02	0.25	0.80	**0.000**	**0.384**	**2774**	
5	Birds	**3.54**	0.02	0.30	47.20	**0.000**	**0.104**	**137**	
6	Zooplankton	**2.00**	**2.66**	55.00	250.00	0.535	**0.000**	**2**	
7	Aquatic insects	**2.00**	**12.98**	10.40	40.00	0.627	**0.096**	**2**	
8	Terrestrial insects	**2.00**	**2.18**	25.00	250.00	0.626	**0.144**	**1**	
9	*Schizodon borellii*	**2.17**	0.83	3.40	55.99	**0.227**	**0.214**	**3**	0.009
10	*Sturisoma robustum*	**2.00**	0.22	1.22	55.78	**0.926**	**0.002**	**1**	0.002
11	*Tetragonopterus argenteus*	**2.93**	0.39	3.12	18.73	**0.988**	**0.064**	**7**	0.004
12	*Chaetobranchopsis australis*	**2.54**	0.44	1.91	15.71	**0.996**	**0.242**	**6**	0.004
13	*Pseudoplatystoma reticulatus*	**3.20**	1.31	2.82	10.00	**0.050**	**0.539**	**591**	0.013
14	*Hemiodus orthonops*	**2.03**	0.36	1.46	69.66	**0.956**	**0.029**	**6**	0.003
15	*Hypostomus plecostomus*	**2.00**	0.43	2.46	33.20	**0.009**	**0.000**	**1**	0.004
16	*Psectrogaster curviventris*	**2.00**	**4.53**	1.40	62.81	0.916	**0.001**	**1**	0.045
17	*Pseudoplatystoma corruscans*	**3.14**	0.04	2.82	10.00	**0.094**	**0.455**	**119**	0.000
18	*Moenkhausia* spp.	**2.76**	**1.28**	5.00	25.84	0.904	**0.184**	**8**	0.012
19	*Loricaria* spp.	**2.00**	0.50	4.50	26.06	**0.278**	**0.002**	**1**	0.005
20	*Potamorhina squamoralevis*	**2.00**	1.70	1.24	40.28	**0.992**	**0.001**	**1**	0.017
21	*Auchenipterus nuchalis*	**2.98**	**0.74**	2.71	14.56	0.901	**0.023**	**6**	0.007
22	*Leporinus* spp.	**2.03**	0.79	2.60	12.72	**0.347**	**0.030**	**5**	0.008
23	*Plagioscion ternetzi*	**3.41**	0.43	1.46	8.77	**0.998**	**0.290**	**465**	0.004
24	*Acestrorhynchus pantaneiro*	**3.33**	**0.05**	2.22	24.64	0.880	**0.196**	**1014**	0.005
25	*Hemisorubim platyrhynchos*	**3.20**	0.32	1.30	10.32	**0.559**	**0.096**	**428**	0.003
26	*Trachydoras paraguayensis*	**2.65**	**3.25**	2.35	25.67	0.906	**0.222**	**7**	0.032
27	*Hoplias malabaricus*	**3.47**	1.17	2.67	8.53	**0.266**	**0.501**	**1451**	0.011
28	*Serrasalmus* spp.	**3.30**	1.89	1.59	14.64	**0.978**	**0.354**	**731**	0.019
29	*Gymnogeophagus balzanii*	**2.56**	0.38	1.95	17.63	**1.000**	**0.242**	**7**	0.004
30	*Pimelodus* spp.	**2.48**	1.57	1.99	11.70	**0.382**	**0.242**	**6**	0.015
31	*Loricariichthys* spp.	**2.00**	2.06	1.26	25.51	**0.920**	**0.006**	**1**	0.020
32	*Roeboides* spp.	**2.74**	0.94	2.08	21.48	**0.999**	**0.256**	**32**	0.009
33	*Steindachnerina* spp.	**2.00**	0.85	1.33	52.78	**0.985**	**0.000**	**2**	0.008
34	*Curimatella* spp.	**2.00**	**2.04**	1.47	18.43	0.917	**0.000**	**2**	0.020
35	*Triportheus* spp.	**2.59**	1.65	2.11	14.30	**0.999**	**0.235**	**7**	0.016
36	*Pimelodella* spp.	**2.85**	**4.53**	1.40	12.73	0.902	**0.205**	**42**	0.045
37	*Astyanax sp*	**2.52**	**1.34**	2.40	15.27	0.903	**0.245**	**6**	0.013
38	Detritos	**1.00**	30.00			**0.603**	**0.304**		

Table 4
Ecosystem attributes values for three models: Baía da Onça (ONC), Braço Morto Acima (MAC), Braço Morto Abaixo (MAB).

Attributes	ONC	MAC	MAB
Total System Throughput (t km^{-2} year^{-1})	5333	9075	7210
Total Primary Production/Total Respiration (dimensionless)	0.60	1.05	1.12
Total biomass/total throughput (year)	0.008	0.023	0.025
Total biomass (excluding detritus) (t km^{-2})	44.94	204.83	180.14
Connectance Index (CI; dimensionless)	0.146	0.151	0.164
Total catches simulated (t km^{-2} year^{-1})	0.304	0.471	0.355
Mean trophic level of simulated catches (dimensionless)	2.51	2.49	2.52
System Omnivory Index (SOI; dimensionless)	0.170	0.126	0.144
Throughput cycled (including detritus) (t km^{-2} year^{-1})	494.51	547.68	417.97
Transfer Efficiency (%)	8.1	8.10	9.40
Finn's Cycling Index (%)	9.27	6.03	5.80
Ascendency (%)	26.40	26.90	27.10
Overhead (%)	73.60	73.10	72.90
Path length [Tf/(TEx + TRe)] (dimensionless)	3.25	2.88	2.85
Path Number (dimensionless)	6621	5671	10,765

Table 5
Top five species with higher keystoneness species index (KS_i) in the three oxbow lakes: Baía da Onça (ONC), Braço Morto Acima (MAC) and Braço Morto Abaixo (MAB).

Rank	ONC	MAC	MAB
Oxbow lakes (KS_i)			
1	Birds (0.194)	Mammals (0.139)	*Serrasalmus* spp. (0.374)
2	*H. malabaricus* (0.108)	*H. malabaricus* (0.122)	*H. malabaricus* (0.345)
3	*P. reticulatum* (0.105)	*P. reticulatum* (0.0375)	Mammals (−0.002)
4	Mammals (0.094)	*Serrasalmus* spp. (−0.0122)	Aquatic insects (−0.0462)
5	Aquatic insects (−0.060)	Aquatic insects (−0.0328)	*Pimelodella* spp. (−0.0477)
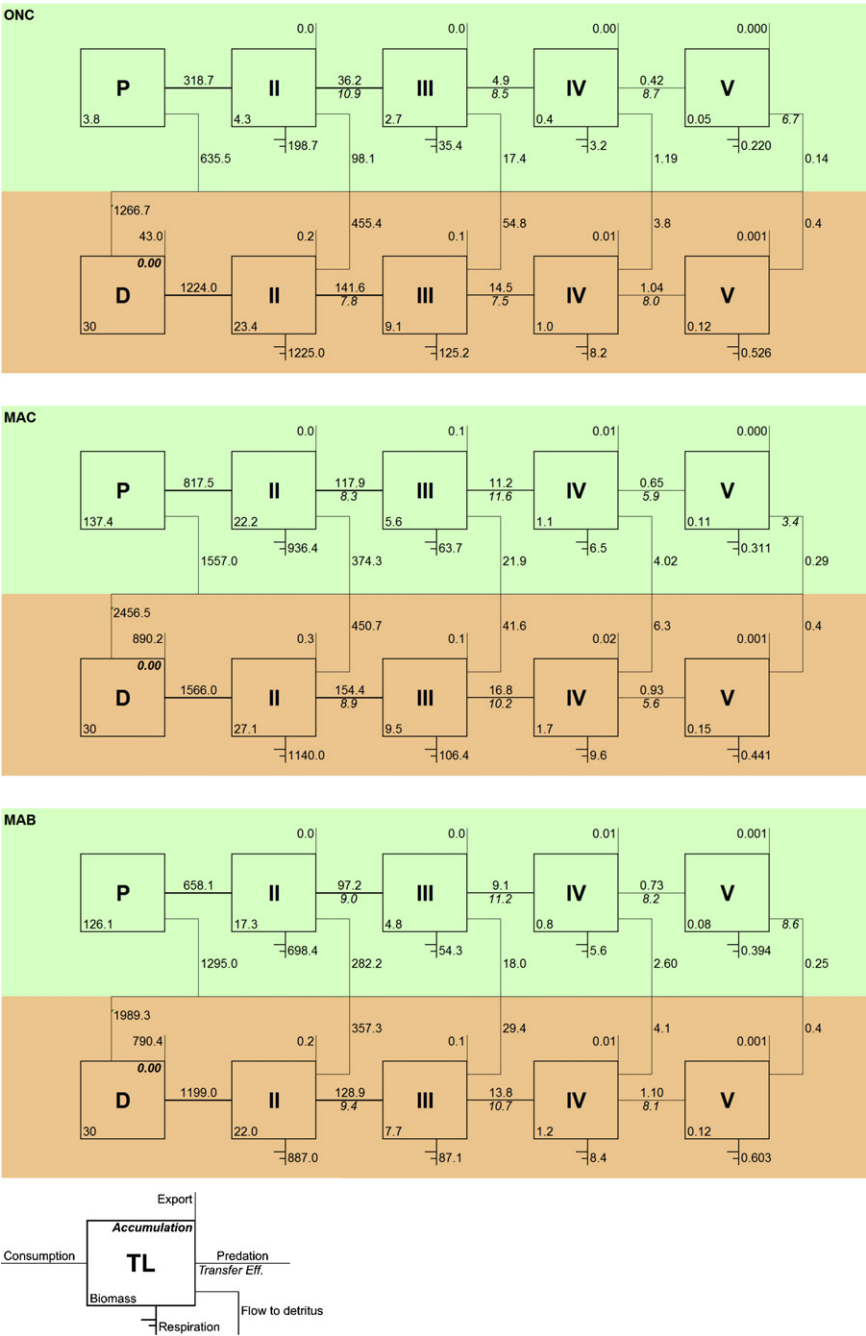
Fig. 2. Modified Lindeman Spine of three oxbow lakes in Pantanal (Brazil): Baía da Onça – ONC, Braço Morto Acima – MAC and Braço Morto Abaixo – MAB. *P* for primary producers and *D* for detritus identify, respectively, detritus-based and grazing food chains for each model. Roman numbers stand for integer trophic level. Transfer Efficiency in percentage. Flows in tww km^{-2} year^{-1} and biomass in tww km^{-2}.

Table 6
Estimates to calculate *L* index for three oxbow lakes in Brazilian wetland Pantanal: Baía da Onça (ONC), Braço Morto Acima (MAC) and Braço Morto Abaixo (MAB).

Attributes	ONC	MAC	MAB
Primary Production – PP (t km^{-2} year^{-1})	954.25	2374.19	1953.58
Flow to Detritus (t km^{-2} year^{-1})	1267	2456	1990
P1 = PP + Flow to Detritus	2221.25	4830.19	3943.58
Total Primary Production Required – TPPR (t km^{-2} year^{-1})	6652.08	9521.24	7696.99
1 − (P1/TPPR)	0.666	0.493	0.488
P1/TPPR (%)	33.39	50.73	51.24
PPR from Prim. Prod. (t km^{-2} year^{-1})	1521.06	3415.56	2867.38
PPR from detritus (t km^{-2} year^{-1})	5131.01	6105.63	4829.61
L' index (for catch of 1% of initial biomass)	0.000075	0.000084	0.000052
Fishery sustainability – psust	~1	~1	~1

Table 7
Number of the compartments (see Tables 1–3) extinct and respective mean trophic levels by simulations with increasing of fishing mortality (F).

F	ONC		MAC		MAB	
	No. of the extinct comp.	Mean TL	No. of the extinct comp.	Mean TL	No. of the extinct comp.	Mean TL
4					24	3.33
5						
6	24	3.34	3	4.31	3	4.32
7	2	4.08	25	3.27	25	3.20
8	9; 13; 16	2.53	4; 24	3.72	4	3.82
9	3	4.16	17	3.07	23	3.41
10	12; 29	3.37			10	2.00
20	11; 15; 19; 22; 23; 25; 26; 28; 32; 34; 35; 37	2.59	10; 12; 13; 14; 20; 21; 23; 27; 28; 29; 31; 33; 34	2.57	12; 13; 14; 15; 16; 17; 20; 21; 27; 28; 30; 31; 33; 34	2.51
30	4; 8; 14; 21; 27; 30; 33	2.61	3; 9; 15; 16; 22; 30	2.38	5; 9; 22	2.58
40	1	1	32	3.02	32; 36	2.66
50	38	2.59			19; 37	2.26
60			36	2.84		
70	18	2	19; 37	2.31	26	2.65
Comp. remaining	5; 6; 7; 10; 17; 20; 31; 36; 39	2.54	1; 2; 6; 7; 8; 11; 18; 26; 35; 38	2.44	1; 2; 6; 7; 8; 11; 18; 29; 35; 38	2.32

values of the Pedigree Indexes, which were similar to those found by Villanueva et al. (2006b), Pedersen et al. (2008), Tsagarakis et al. (2010), and Gubiani et al. (2011). The low sum of squares difference between the reference models and the successful runs of the Eco-ranger routine showed that the models realistically describe the food webs of these environments (Christensen et al., 2005).

However, the lack of local and quantitative information for the non-fish compartments restricts the models built in this study. For example, the parameters for the caimans (PB and QB) were based on information obtained with crocodiles, and the biomass was estimated by tuning the MAB model. Nevertheless, the integration of all of the ecosystem information highlighted the compartments and regions for which more detailed and quantitative studies are needed. Indeed, although it is one of the largest floodplains in the world, the Pantanal still requires the accumulation of basic information to provide insights that would prove useful to its management (da Silva et al., 2001; Junk et al., 2006).

Furthermore, the lack of time-series data (group biomass and landing) that might have allowed the calibration of the ecosystem dynamics against observed values represents a limitation of the model results. Therefore, the consistency of the model outputs using the Ecoranger routine represented the best possible test of the

Fig. 3. L index dynamics with different values of fishing mortality (F) simulated for the three models ONC, MAC and MAB.

available information. Thus, our simulations need to be considered with caution and will certainly require additional data.

Notably, these oxbow lakes have the same distances, depths, and times of isolation as the river; these are the abiotic variables that most influence the fish species richness in the lakes of the Pantanal (Súarez et al., 2004). Accordingly, the three lake models serve as a good basis for the comparison of these environments.
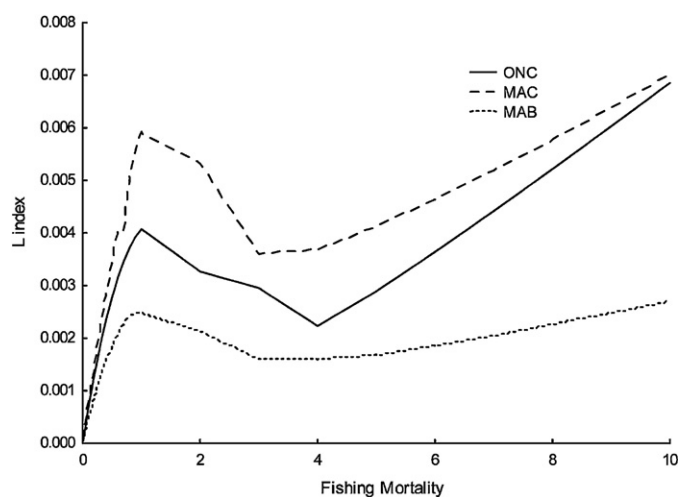
Although there is similarity among the species compositions, some species occupy different TLs in each environment; for example, the TL of $P. corruscans$ is 3.5 in the ONC, 3.07 in the MAC, and 3.14 in the MAB. This finding indicates that, despite the similarity of the habitats and diets, there is still a considerable small-scale spatial variability (Girard et al., 2010), which indicates that the species act more in a trophic continuum than in constant TLs (Wantzen et al., 2002) and highlights the need for site-specific evaluations.

The range in species diets may also favor their coexistence and increase the tolerance to environmental stress (Mérona and Mérona, 2004; Pouilly et al., 2006). In the studied lakes, the variance in the diets across TLs, i.e., the OI, was low compared to that obtained in other systems (Angelini and Agostinho, 2005b). This variability is an unusual situation in tropical environments, where most of the fish species are generalists (Hahn et al., 2004), and may be an effect of the aggregation of functional groups with lower TLs (zooplankton, insects, and primary producer compartments), which consequently reduces the OI of their predators.

The low global values for SOI and CI result from systems that are more dependent on detritus as a source of energy (Heymans et al., 2004); systems that are less dependent on detritus have higher CI and SOI values because the organisms need to diversify their energy sources (Christensen, 1995; Vasconcellos et al., 1997). Thus, the high dependence of the organisms on the detritus food chain simplifies the food webs.

The importance of detritus is confirmed by the higher energy flow from detritus (Fig. 2) to TL 2, which demonstrates the high degree of dependence of the system on the hydrological seasonality that brings the detritus (Silva et al., 2010). This result is supported by the ecological theory for tropical lakes, in which the main energy flow path in shallow waters flows through detritus (Bowen, 1983). Mature ecosystems are more dependent on detritivory than on herbivory (Odum, 1969), and the D:H ratio (detritivory:herbivory) in the models (Fig. 2) that were developed in this study was always high, particularly in the ONC model.

The role of detritus from flood pulses could be even larger because it maintains the energy flow; stabilizes the food web
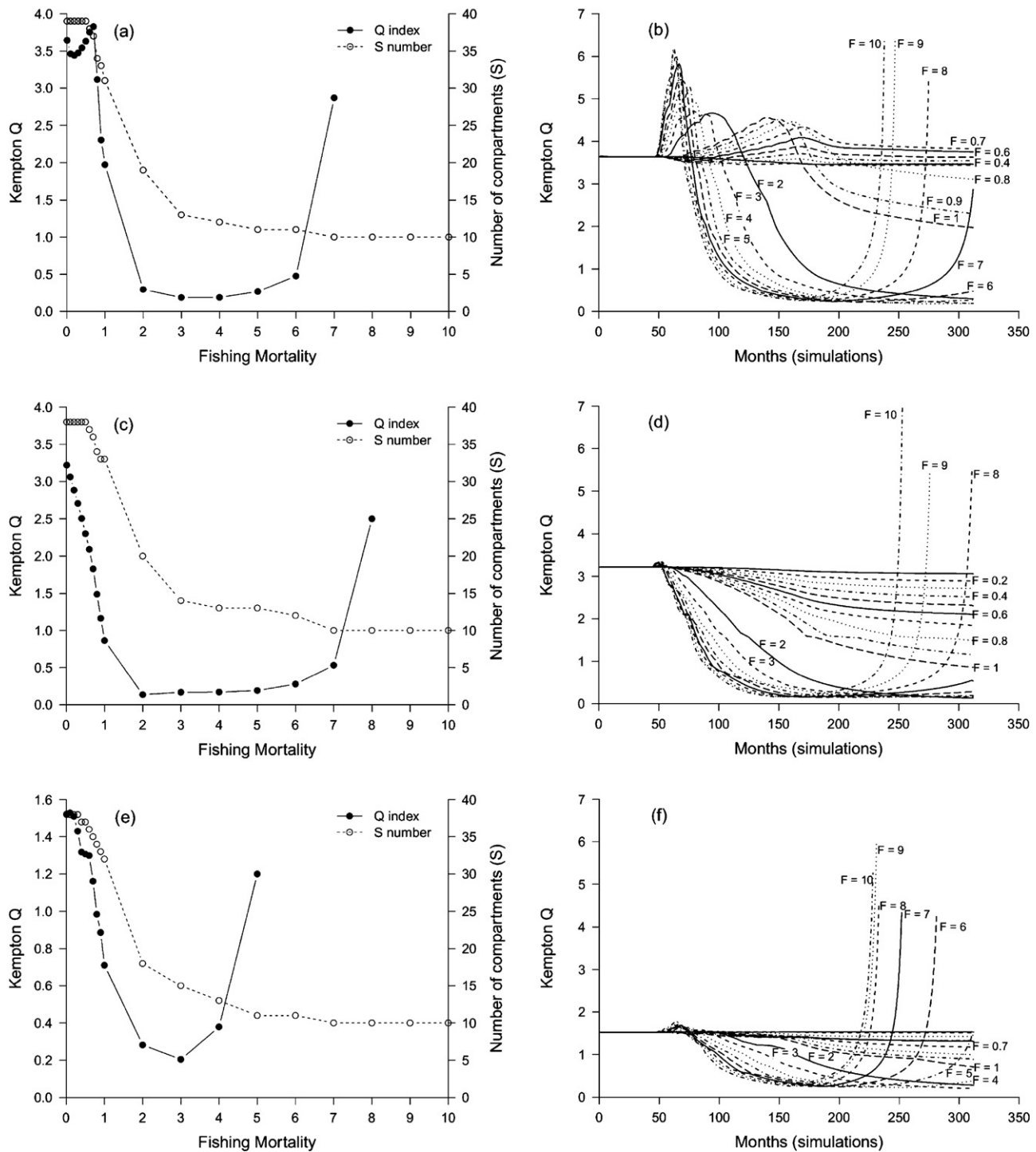
Fig.4

Fig. 4. Kempton Q index and number of compartments simulated with fishing increasing for three models. Left panels represent the Kempton Q and the number of species at the end of 30 years simulations for ONC (a), MAC (c) and MAB (e). Right panels represent Kempton Q index monthly dynamics during the simulations with different values of fishing mortality (F) simulated (see text), for models ONC (b); MAC (d) and MAB (f).

(Moore et al., 2004) when the physical modification of the habitat and of its variables, such as dissolved oxygen, pH, water clarity, and water speed are induced (Silva et al., 2010; Williamson et al., 1999); and plays a fundamental role in the organization and maintenance of ecosystems (Cyr and Pace, 1993; Junk et al., 2006; Luz-Agostinho et al., 2008; Hamilton, 2010). Fish consumption on the Baia da

Onça shows that detritus and algae are the main food items that are converted into fish biomass (46.5%), and they are followed by fish (8.4%), insects (6.5%), and microcrustaceans (3.9%). This finding shortens the food web and increases the effectiveness of the community (Catella and Petrere, 1996) despite the fact that the values of trophic Transfer Efficiency (TE) were lower (8.1% for the ONC and
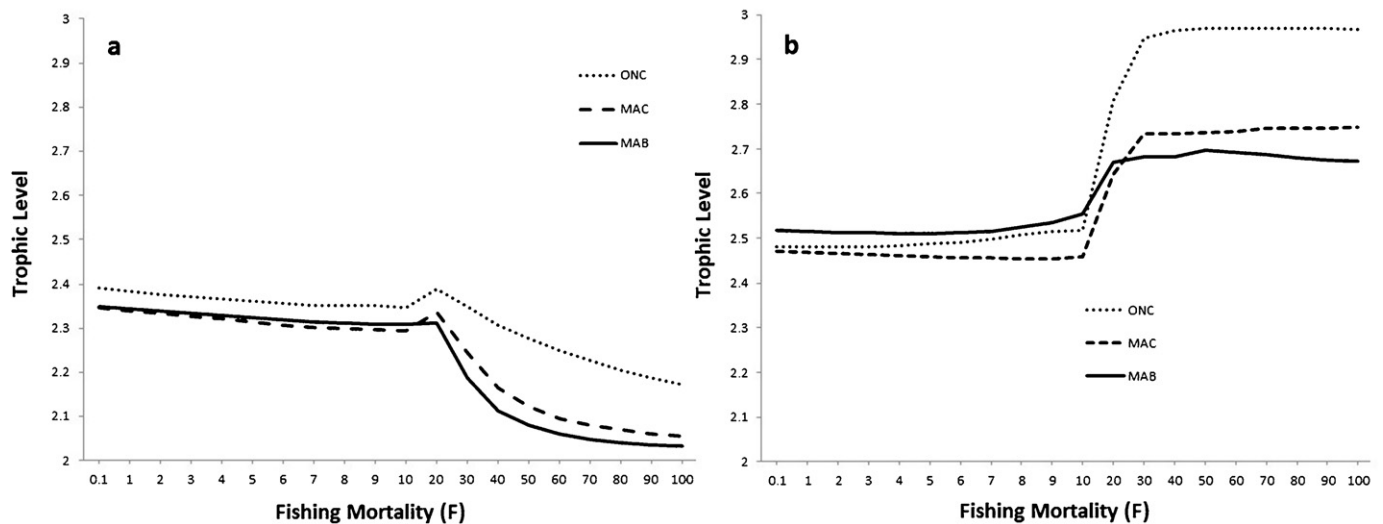
Fig. 5. Trophic level (*TL*) dynamics during the simulations with different values of fishing mortality (*F*) simulated (see text) for models ONC, MAC and MAB. (a) *TL* for all species remained; (b) *TL* for fish species remained.

the MAC models and 9.4% for the MAB model) than expected (10%; Pauly and Christensen, 1995).

The dependence on detritus maintains the resiliency of the system by providing a high source of reserved energy because the overhead values are high (Christensen, 1995) and maintains the flexibility and likely the maturity of the system because the PPT/RT values are close to one. The ONC model has a PPT/RT smaller than one because no aquatic macrophytes are included in this model. As a result, the detritus is supplied through the flood pulses, and its internal cycling, which is estimated by the Finn index, is higher than that in the other models, regardless of the smaller flow of detritus. The similar outputs among the oxbow lakes confirm that the food webs of the lakes are analogous to each other; although the lakes follow distinct paths in times of drought, which depend on the presence or absence of predators, the lakes are homogenized by the high-tide flood pulse (Thomaz et al., 2007), which likely causes an intermediate disturbance that limits the maturing process of the lakes (models have low ascendancy values).

The high values of the keystoneness species index in the three models highlight the important role of the top predators (*H. malabaricus*, *Serrasalmus* spp., *P. reticulatum*, birds, and mammals). Therefore, in addition to the detritus (bottom-up processes), the top predators also tend to be very influential in the configuration of the food web, which suggests that an emerging feature of the three systems is the action of a mixed or alternated control system. In fact, the separation of top-down and bottom-up processes becomes particularly difficult in a flooding-prone environment, which does not necessarily induce the predominance of any of these processes. The strong relationship between biotic (predators) and abiotic components (detritus) in the determination of the fish communities in the Pantanal, has also been stressed by Silva et al. (2010). It is likely that the top predators have a higher level of action in the dry season (Wantzen et al., 2002; Thomaz et al., 2007) and that detritus has a higher level of action during floods. This explains and supports the proposition that an alternated control system determines the ecosystem processes in the Pantanal lakes. The fact that the models used in this study represent annual budgets does not allow the full confirmation of this suggestion, which appears quite plausible, and provides a topic for future studies and analyses.

An important fraction of the Total Primary Production Required (TPPR) returns to detritus and enhances the recycling caused by the predatory species in the higher *TL*s, which results in values of TPPR that are higher than twice the P1 (sum of Primary Production (PP)

with Flow to Detritus). The difference between TPPR and P1 indicates that the higher *TL*s created a high level of positive feedback in these systems, especially in the ONC model, which has a lower biomass of primary producers. Therefore, the top predators create an effective set of positive parallel feedbacks that generate an indetermination of flows and enrich the system, thereby allowing it to grow, to be flexible, and to withstand disturbances (Ulanowicz, 2009).

Increasing the effect of fishing in the simulations resulted in an increase in the *L* index values (Fig. 3). However, the highest values of the *L* index that were obtained were not sufficient to modify the probability of sustainable fishery, which was very close to 1, regardless of the fishing pressure. This result implies the sustainability of fisheries (Libralato et al., 2008). The Kempton index exhibited different trends depending on the system (Fig. 4). In the ONC model the *Q* index reached an "optimum value" at *f* = 7, which indicates that the loss of *H. platyrhynchos* and mammals likely increased the evenness of the remaining species. In contrast, the Kempton *Q* index for the MAC and the MAB models decreased before the first removals from the ecosystem (Fig. 4), likely because increasing the fishing mortality (*F*) decreases the evenness among the compartments. The Kempton index for the models of the three oxbow lakes confirmed that the fishing activity could considerably modify the fish community, as has been observed in other ecosystems (Coll et al., 2008b). In addition, when many compartments became locally extinct, the Kempton values tended to increase notably (note that EwE limits the computation for the Kempton *Q* when its value is higher than twice its initial Ecopath value) in response to a substantial change in the food web.

The simulated average value of the trophic level of the community (TLco) at increasing values of *f* showed two opposite patterns: the TLco decreased for all species (excluding *TL* = 1) and increased for fish species as the fishing pressure increases. In all models, the zooplankton, aquatic, and terrestrial insects (*TL* = 2.0) compartments remained and exhibited increased biomass when the weighted *TL* decreased. When it was calculated only for the fish compartments, the TLco increased because all of the fish compartments with *TL* = 2.0 were removed, particularly when *F* = 20 (Table 7). At the end of the simulation, only those fish compartments with *TL* > 2.5 remained in the three models (Table 7).

The mammals' compartment was the only key species (Table 5) that were first removed in the MAC and the MAB models (Table 7; compartment 3). In general, these removals could be

considered local extinctions. The compartments (or species) that rapidly became locally extinct can be called "non-impacted-food-web-dependent" (sensible to impacts). Moreover, these species generally have similar TLs compared with the key species. However, with the exception of mammals and *P. reticulatum* in the ONC model, which became extinct with $F = 10$, the other key species were extinct only when $F > 20$, which is a very high value for the communities in these areas. This result indicates that the key species have a high capacity to remain in impacted environments and attempt to maintain their interaction strengths with the components of another system even under impact. However, this assumption requires future investigation.

The main ecological role of these oxbow lakes is to provide a habitat for the growth of many small species, which are preyed on by the species that are the main targets of fishing. However, some of those species that are not the main targets of fishing (e.g., *Hoplias* sp., *Hypostomus* sp., and *Potamorrhyna* sp.) have a high potential to be directly used in the productive sector (non-professional and even industrial) as long as value is added to them during the fish processing (Lara et al., 2008). Nevertheless, the results also indicate that only moderate fishing can be sustained because the reduction of the biomass of these species negatively impacts the top predators and increases their probability to become locally extinct. This finding is in accordance with the importance of "forage fish" in supporting larger piscivores (Walters et al., 2005).

5. Conclusion

Considering that there are approximately 260 oxbow lakes in the studied region, which have a total water surface area of 14.05 km^2 and on average 37.4 t of fish per km^2 (Tables 1–3), one could expect the total fish biomass in the oxbow lakes to be approximately 525 t. A fishing mortality of 3, which would correspond to catching almost 10 t year^{-1} in the three systems simulated in this study or close to 140 t year^{-1} in all of the oxbow lakes, would not affect the fish stock or local biodiversity. This fishing amount corresponds to half of the annual professional fishing average of 270 t that was recorded in the entire Pantanal in the period between 2000 and 2005 (Albuquerque and Catella, 2009). Our result agrees with the guidelines proposed by Catella (2003) for the local fishing policy to increase the utilization of underexploited species that are present in these environments and to simultaneously reduce the fishing effort on large target species in the Pantanal, which does not currently occur in the environments analyzed in this study. The use of these underexploited fishes by professional fishermen could even contribute to a reduction in the conflicts of interest regarding the use of fishing resources that exist among non-professional fishermen and the touristic fishing sector in the Pantanal (Catella et al., 2008). An improved and more cautious approach toward the fish stock and the Pantanal biodiversity would use an adaptive management approach (Marttunen and Vehanen, 2004; Walters, 1986), which implies a gradual increase of fishing: for the first 5 years, the fishing mortality should be $F = 1$, and if the fishing and population monitoring show results that are in agreement with our findings, the managers could increase the catches. However, it would be necessary to define, together with the users and the regulatory agencies, the rules for exploitation: (a) permitted gears and mesh size (only the hook is currently allowed), (b) community-based data monitoring (Carvalho et al., 2009), and (c) suitable processing technologies to avoid discards and supply the market demand.

The results of the exploratory simulation analysis presented here should be considered with appropriate caution. The models developed highlighted the input data that require local estimates for the biomass and parameters of some groups. Similarly, the lack of time-series data did not allow a proper model calibration.

Nevertheless, the models developed include the best available information and have been checked for consistency. Moreover, the model results substantiate known ecological features. The issues investigated indicate the potential for ecosystem modeling in this biome and identified areas in which further investigation and the collection of additional data would allow filling the gaps identified in this study to ultimately improve both the ecological knowledge and the modeling approach. It is worth mentioning that these are the first quantified food web aquatic models elaborated for the Pantanal oxbow lakes: the models highlight the ecological importance of this approach and provide insights for future studies that would help understand the effect of the fishery on the environments of the Pantanal through ecosystem modeling.

The EwE approach provided an understanding of the aquatic food webs of three marginal lakes in the Pantanal, which are supposed to be structurally characterized by alternated control, through the use of basal compartments: detritus, which enters the system through flood pulses (wet season), and top predators, such as *H. malabaricus*, *Serrasalmus* spp., *P. reticulatum*, birds, and mammals (dry season). The oxbow lakes may be considered resilient systems due to their ecosystem attributes and are able to sustainably withstand a low fishing pressure, particularly of species that are not currently exploited, because this fishery would be monitored and evaluated with the outputs from our models.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolmodel.2013.01.001.

References

Achá, D.C., Fontúrbel, F.R., 2003. La diversidad de una comunidad, ¿está controlada por top-down, bottom-up o una combinación de estos? La revista 13, 1–15.
Agostinho, A.A., Pelicice, F.M., Petry, A.C., Gomes, L.C., Júlio Jr., H.F., 2007. Fish diversity in the upper Paraná River basin: habitats, fisheries, management and conservation. Aquatic Ecosystem Health & Management 10 (2), 174–186.
Ahrens, R., Walters, C., Christensen, V., 2011. Foraging arena theory. Fish and Fisheries 13, 41–49.
Ainsworth, C.H., Pitcher, T.J., 2006. Modifying Kempton's species diversity index for use with ecosystem simulation models. Ecological Indicators 6 (3), 623–630.
Albuquerque, F.F., Catella, A.C., 2009. Fishery monitoring system of Mato Grosso do Sul. Sistema de Controle da Pesca de Mato Grosso do Sul SCPESCA/MS-12, 2005. Corumbá, MS: Embrapa Pantanal/Campo Grande: SEMAC-IMASUL (Embrapa Pantanal. Boletim de Pesquisa, 94), 57 p. (in Portuguese).
Alho, C.J.R., 2008. Biodiversity of the Pantanal: response to seasonal flooding regime and to environmental degradation. Brazilian Journal of Biology 68 (4 Suppl.), 957–966.
Allen, R.R., 1971. Relation between production and biomass. Journal of the Fisheries Research Board of Canada 28, 1573–1581.
Angelini, R., Agostinho, A.A., 2005a. Parameter estimates for fishes of the Upper Paraná River floodplain and Itaipu Reservoir (Brazil). NAGA, The WordFish Center Quarterly, Manila 28, 53–57.
Angelini, R., Agostinho, A.A., 2005b. Food web model of the Upper River Floodplain: description and aggregation effects. Ecological Modelling, Amsterdam 181, 109–121.
Angelini, R., Velho, F.V., 2011. Ecosystem structure and trophic analysis of Angolan fishery landings. Scientia Marina 75 (2), 309–319.
Angelini, R., Fabré, N.N., Silva Jr., U.L., 2006. Trophic analysis and fishing simulation of the biggest Amazonian catfish. African Journal of Agricultural Research 1, 151–158.
Bond, W., 2001. Keystone species: hunting the snark? Science 292, 63–64.

Borteiro, C., Gutierrez, F., Tedros, M., Kolenc, F., 2009. Food habits of the Broad-snouted Caiman (Caiman latirostris: Crocodylia, Alligatoridae) in northwestern Uruguay. Studies on Neotropical Fauna and Environment 44 (1), 31–36.

Bowen, S.H., 1983. Detritivory in neotropical fish communities. Environmental Biology of Fish 9, 137–144.

Britski, H.A., Silimon, K.Z.S., Lopes, B.S., 2007. Peixes do Pantanal – Manual de identificação. Embrapa Informação Tecnológica, Brasilia, DF, 227 pp.

Campos, Z., Coutinho, M., Mourão, G., Bayliss, P., Magnusson, W.E., 2006. Long distance movements by Caiman crocodilus yacare: implications for management of the species in the Brazilian Pantanal. Herpetological Journal 16, 123–132.

Capistrano-Santana, A., Almeida, R.S., Ávila, R.W., Catella, A.C., 2004. Parameters estimates for growth of R. paraensis. Estimativa dos parâmetros de crescimento de Roeboides paranensis: diferentes respostas para uma mesma pergunta. IV Simpósio sobre recursos naturais e socioeconômicos do Pantanal Corumbá/MS. CPAP – Pantanal, Corumbá – MS, 6 p.

Carpenter, S.R., Ktchell, J.F., Hodgson, J.R., 1985. Cascading trophic interactions and lake productivity. Bioscience 35, 634–639.

Carvalho, A.R., Williams, S., January, M., Sowman, M., 2009. Reliability of community-based data monitoring in the Olifants River estuary (South Africa). Fisheries Research 96, 119–128.

Catella, A.C., 2003. South Pantanal Fishery: nowadays and perspectives. A Pesca no Pantanal Sul: situação atual e perspectivas. Documento 48. Editora da Embrapa. Corumbá/MS. 43 p.

Catella, A.C., Petrere Jr., M., 1996. Feeding patterns in a fish community of Baia da Onça, a floodplain lake of the Aquidauana River, Pantanal, Brazil. Fisheries Management and Ecology 3, 229–237.

Catella, A.C., Mascarenhas, R.O., Albuquerque, S.P., Albuquerque, F.F., Theodoro, E.R.M., 2008. Fisheries Statistics For Pantanal: politics and technical support. Sistemas de estatísticas pesqueiras no Pantanal, Brasil: aspectos técnicos e políticos. Panamjas 3 (3), 174–192.

Christensen, V., 1995. Ecosystem maturity—towards quantification. Ecological Modelling, Amsterdam 77, 3–32.

Christensen, V., Pauly, D., 1992. ECOPATH II—a software for balancing steady-state ecosystem models and calculating network characteristics. Ecological Modelling, Amsterdam 61, 169–185.

Christensen, V., Pauly, D.,1993. Trophic models of aquatic ecosystems. In: ICLARM Conference Proceedings, IL, No. 26. ICLARM/International Council for the Exploration of the Sea; Danish International Development Agency, Metro Manila/Copenhagen, 374 p.

Christensen, V., Walters, C.J.,2004a. Ecopath with Ecosim: methods, capabilities and limitations. Ecological Modelling, Amsterdam 172, 109–139.

Christensen, V., Walters, C.J., 2004b. Trade-offs in ecosystem-scale optimization of fisheries management policies. Bulletin of Marine Science 74 (3), 549–562.

Christensen, V., Walters, C.J., Pauly, D., 2000. Ecopath with Ecosim: A User's Guide. October 2000 edition. Fisheries Centre, University of British Columbia/ICLARM, Vancouver, Canada/Penang, Malaysia, 130 p.

Christensen, V., Walters, C., Pauly, D., 2005. Ecopath with Ecosim: A User's Guide. Fisheries Centre of University of British Columbia, Vancouver, Canada, Available at: http://www.ecopath.org

Clarke, R.T., Tucci, C.E.M., Collischonn, W., 2003. Variabilidade temporal do regime hidrológico da Bacia do rio Paraguai. Revista Brasileira de Recursos Hídricos 8 (1), 201–211.

Cole, J.J., Findlay, S., Pace, M.L., 1988. Bacterial production in fresh and salt water ecosystems: a cross-system overview. Marine Ecology Progress Series 4, 1–10.

Coll, M., Libralato, S., Tudela, S., Palomera, I., Pranovi, F., 2008a. Ecosystem overfishing in the ocean. PLoS ONE 3 (12), e3881.

Coll, M., Palomera, I., Tudela, S., Dowd, M., 2008b. Food-web dynamics in the South Catalan Sea eco system (NW Mediterranean) for 1978–2003. Ecological Modelling 217, 95–116.

Cunha, N.L., Catella, A.C., Kinas, M.A., 2007. Growth parameters estimates for a small fish of the Pantanal, Brazil: Moenkhausia dichroura (Characiformes, Characidae). Brazilian Journal Biology 67 (2), 631–637.

Cury, P., Bakun, A., Crawford, R.J.M., Jarre, A., Quinones, R.A., 2000. Small pelagics in upwelling systems: patterns of interaction and structural changes in "wasp-waist" ecosystems. ICES Journal of Marine Science 57 (3), 603–618.

Cyr, H., Pace, M.L., 1993. Magnitude and patterns of herbivory in aquatic and terrestrial ecosystems. Nature 361, 148–150.

da Silva, C.J., Wantzen, K.M., Nunes da Cunha, C., Machado, F.de.A., 2001. Biodiversity in the Pantanal wetland, Brazil. In: Gopal, B., Junk, W.J., Davis, J.A. (Eds.), Biodiversity in Wetlands: Assessment, Function and Conservation, vol. 2. Backhuys Publishers b.V., Leiden, pp. 187–215.

Davic, R.D., 2003. Linking keystone species and functional groups: a new operational definition of the keystone species concept. Conservation Ecology 7 (1), r11.

Desbiez, A.L.J., Bodmer, R.E., Tomas, W.T., 2010. Mammalian densities in a neotropical wetland subject to extreme climatic events. Biotropica 42 (3), 372–378.

Dinnen, G., Robertson, A.L., 2010. Subtle top-down control of a freshwater meiofaunal assemblage by juvenile fish. Freshwater Biology 55, 1818–1830.

Dyer, L.A., Letourneau, D., 2003. Top-down and bottom-up diversity cascades in detrital vs. living food webs. Ecology Letters 6, 60–68.

Fantin-Cruz, I., Pedrollo, O., Bonecker, C.C., Motta-Marques, D., Loverde-Oliveira, S., 2010. Zooplankton density prediction in a flood lake (Pantanal – Brazil) using artificial neural networks. International Review of Hydrobiology 95 (4–5), 330–342.

Finn, J.T., 1976. Measures of ecosystem structure and function derived from analysis of flows. Journal of Theoretical Biology 56, 363–380.

Figueira, J.E.C., Cintra, A.R., Viana, L.R., Yamashita, C., 2006. Spatial and temporal patterns of bird species diversity in the Pantanal of Mato Grosso, Brazil: implications for conservation. Brazilian Journal of Biology 66 (2A), 393–404.

Freire, K.M.F., Christensen, V., Pauly, D., 2008. Description of the East Brazil large marine ecosystem using a trophic model. Scientia Marina 72 (3), 477–491.

Froese, R., Pauly, D. (Eds.), 2009. FishBase. World Wide Web electronic publication. www.fishbase.org, version (10/2009).

Gasalla, M.A., Rodrigues, A.M., Postuma, F.A., 2010. The trophic role of the squid Loligo plei as a keystone species in the South Brazil Bight ecosystem. ICES Journal of Marine Science 67, 1413–1424.

Girard, P., Fantin-Cruz, I., Loverde de Oliveira, S.M., Hamilton, S.K., 2010. Small-scale spatial variation of inundation dynamics in a floodplain of the Pantanal (Brazil). Hydrobiologia 638, 223–233, http://dx.doi.org/10.1007/s10750-009-0046-9.

Gubiani, E.A., Angelini, R., Gomes, L.C., Agostinho, A.A., 2011. Trophic models in neotropical reservoirs: testing hypotheses on the relationship between aging and maturity. Ecological Modelling 222, 3838–3848, http://dx.doi.org/10.1016/j.ecolmodel.2011.10.007.

Hahn, N.S., Fugi, R., Andrian, I.F., 2004. Trophic ecology of the fish assemblages. In: Thomaz, S.M., Agostinho, A.A., Hahn, N.S. (Eds.), The Upper Paraná River and its Floodplain: Physical Aspects, Ecology and Conservation. Backhuys Publishers, Leiden, pp. 247–269, 393 p.

Hamilton, S.K., 2002. Human impacts on hydrology in the Pantanal wetland of South America. Water Science and Technology 45, 35–44.

Hamilton, S.K., 2010. Biogeochemical implications of climate change for tropical rivers and floodplains. Hydrobiologia 657, 19–35.

Heymans, J.J., Shannon, L.J., Jarre, A., 2004. Changes in the northern Benguela ecosystem over three decades: 1970, 1980 and 1990. Ecological Modelling 172, 175–195.

Hunt Jr., G.L., McKinnell, S., 2006. Interplay between top-down, bottom-up and wasp-waist control in marine ecosystems. Progress in Oceanography 68, 115–124.

Hunter, M.D., 2001. Multiple approaches to estimating the relative importance of top-down and bottom-up forces on insect populations: experiments, life tables, and time-series analysis. Basic and Applied Ecology 2, 295–309.

Hunter, M.D., Price, P.W., 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. Ecology 73, 724–732.

Jepsen, D.B., Winemiller, K.O., 2002. Structure of tropical river foof webs revealed by stable isotope ratios. Oikos 96, 46–55.

Jordan, F., Benedek, Z., Podani, J., 2007. Quantifying positional importance in food webs: a comparison of centrality indices. Ecological Modelling 205, 270–275.

Junk, W.J., Bayley, P.B., Sparks, R.E., 1989. The flood pulse concept in river-floodplain systems. Canadian Special Publication – Fisheries and Aquatic Sciences 106, 110–127.

Junk, W.J., Nunes da Cunha, C., Wantzen, K.M., Petermann, P., Strüssmann, C., Marques, M.I., Adis, J., 2006. Biodiversity and its conservation in the Pantanal of Mato Grosso, Brazil. Aquatic Sciences 68, 278–309.

Kavanagh, P., Newland, N., Christensen, V., Pauly, D., 2004. Automated parameter optimization for Ecopath ecosystem models. Ecological Modelling 172, 141–149.

Kempton, R.A., Taylor, L.R., 1976. Models and statistics for species diversity. Nature 262, 818–820.

Lara, J.A.F., Resende, E.K., Delbem, A.C.B., Garbelini, J.S., 2008. Agro industry technologies: products of fish's species (Pantanal). Tecnologias para a agroindústria: produção de farinha e produto tipo caviar de peixes do Pantanal. Corumbá: Embrapa Pantanal (Embrapa Pantanal, Circular Técnica, 83), 5 p. (in Portuguese).

Leibold, M.A., Chase, J.M., Shurin, J.B., Downing, A.L., 1997. Species turnover and the regulation of trophic structure. Annual Review of Ecology 28, 467–494.

Libralato, S., 2008. System omnivory index. In: Jørgensen, S.E., Fath, B.D. (Eds.), Encyclopedia of Ecology. Elsevier, Oxford, pp. 3472–3477.

Libralato, S., Christensen, V., Pauly, D., 2006. A method for identifying keystone species in food web models. Ecological Modelling 195, 153–171.

Libralato, S., Coll, M., Tudella, S., Palomera, I., Pranovi, F., 2008. Novel index for quantification of ecosystem effects of fishing as removal of secondary production. Marine Ecology Progress Series 355, 107–129.

Libralato, S., Coll, M., Tempesta, M., Santojanni, A., Spoto, M., Palomera, I., Arneri, E., Solidoro, C., 2010. Food-web traits of protected and exploited areas of the Adriatic Sea. Biological Conservation 143, 2182–2194.

Lindeman, R., 1942. The trophic-dynamic aspect of ecology. Ecology (Washington, DC) 23, 399–418.

Lorentsen, S.-H., Sjotun, K., Grémillet, D., 2010. Multi-trophic consequences of kelp harvest. Biological Conservation 143, 2054–2062.

Luz-Agostinho, K.D.G., Agostinho, A.A., Gomes, L.C., Júlio Jr., H.F., 2008. Influence of flood pulses on diet composition and trophic relationships among piscivorous fish in the upper Paraná River floodplain. Hydrobiologia 607, 187–198.

Marttunen, M., Vehanen, T., 2004. Toward adaptive management: the impacts of different management strategies on fish stocks and fisheries in a large regulated lake. Environmental Management 33 (6), 840–854, http://dx.doi.org/10.1007/s00267-003-3021-7.

Mérona, B., Mérona, J.R., 2004. Food resource partitioning in a fish community of central Amazon floodplain. Neotropical Ichthyology 2 (2), 75–84.

Mills, L.S., Soulé, M.E., Doak, D.F., 1993. The keystone-species concept in ecology and conservation. Bioscience 43, 219–224.

Moore, J.C., McCann, k., Setälä, H., de Ruiter, P.C., 2003. Top-down is bottom-up: does predation in the rhizosphere regulate above ground dynamics? Ecology 84, 846–857.

Moore, J.C., Berlow, E.L., Coleman, D.C., de Ruiter, P.C., Dong, Q., Hastings, A., Collins Johnson, N., Mc Cann, K.S., Melville, K., Morin, P.J., Nadelhoffer, K., Rosemond, A.D., Post, D.M., Sabo, J.L., Scow, K.M., Vanni, M.J., Wall, D., 2004. Detritus, trophic dynamics and biodiversity. Ecological Letter 7, 584–600.

Morissette, L., Hammill, M.O., Savenkoff, C., 2006. The trophic role of marine mammals in the Northern Gulf of St Lawrence. Marine Mammal Science 22, 74–103.

Neto, S.L., Mateus, L.A.F., 2009. Comparing fishing professional, artisanal and sporting in Pantanal. Comparação entre a pesca profissional-artesanal e pesca amadora no Pantanal de Cáceres, Mato Grosso, Brasil. Boletim do Instituto de Pesca, Sao Paulo 35 (3), 373–387 (in Portuguese).

Nielsen, K.J., 2001. Bottom-up and top-down forces in tide pools: test of a food chain model in an intertidal community. Ecological Monographs 71, 187–217.

Novakowski, G.C., Hahn, N.S., Fugi, R., 2008. Diet seasonality and food overlap of the fish assemblage in a pantanal pond. Neotropical Ichthyology 6 (4), 567–576.

Odum, E.P., 1969. The Strategy of ecosystem development. Science (Washington, DC) 164, 262–270.

Pace, M.L., Cole, J.J., Carpenter, S.R., Kitchell, J.F., 1999. Trophic cascades revealed in diverse ecosystems. Trends in Ecology and Evolution 14, 483–488.

Paine, R.T., 1995. A conversation on refining the concept of keystone species. Conservation Biology 9, 962–964.

Palomares, M.L.D., Pauly, D., 1998. Predicting food consumption of fish populations as functions of mortality, food type, morphometrics, temperature and salinity. Marine and Freshwater Research, Collingwood 49 (5), 447–453.

Pauly, D., 1980. On the interrelationships between natural mortality, growth parameters and mean environmental temperature in 175 fish stocks. Journal du Conseil International pur l'Exploration de la Mer, Copenhagen 39 (3), 175–192.

Pauly, D., Christensen, V., 1995. Primary production required to sustain global fisheries. Nature 374, 255–257.

Pauly, D., Soriano, M.L., Palomares, M.L., 1993. Improved construction, parametrization and inerpretation of steadystate ecosystem models. In: Chrisntensen, V., Pauly, D. (Eds.), Trophic Models of Aquatic Ecosystems. ICLARM Conference Proceedings No. 26. , pp. 1–13.

Pauly, D., Christensen, V., Walters, C., 2000. Ecopath, Ecosim and Ecospace as tools for evaluating ecosystem impact of fisheries. ICES Journal of Marine Science 57, 697–706.

Pedersen, T., Nilsen, M., Nilssen, E.M., Berg, E., Reigstad, M., 2008. Trophic model of a lightly exploited cod-dominated ecosystem. Ecological Modelling 214, 95–111.

Piraino, S., Fanelli, G., Boero, F., 2002. Variability of species' roles in marine communities: change of paradigms for conservation priorities. Marine Biology 140, 1067–1074, http://dx.doi.org/10.1007/s00227-001-0769-2.

Pouilly, M., Barrera, S., Rosales, C., 2006. Changes of taxonomic and trophic structure of fish assemblages along an environmental gradient in the Upper Beni (Bolívia). Journal of Fish Biology 68, 137–156.

Power, M.E., Tilman, D., Estes, J.A., Menge, B.A., Bond, W.J., Mills, S., Daily, G., Castilla, J.C., Lubchenco, J., Paine, R., 1996. Challenges in the quest for keystones. Bioscience 46 (8), 609–620.

Resende, E.K., 2000. Trophic structure of fish assemblages in the lower Miranda river, Pantanal, Mato Grosso do Sul State, Brazil. Revista Brasileira de Biologia 60 (3), 389–403.

Resende, E.K., Pereira, R.A.C., 1998. Detritivorous fishes from Miranda river floodplain. Peixes detritívoros da planície inundável do rio Miranda, Pantanal, Mato Grosso do Sul, Brasil. Corumbá, MS: EMBRAPA-CPAP, 50 p. (EMBRAPA-CPAP. Boletim de Pesquisa, 12) (in Portuguese).

Resende, E.K., Pereira, R.A.C., Almeida, V.L.L., 1998. Herbivores fishes from Miranda river floodplain. Peixes herbívoros da planície inundável do rio Miranda, Pantanal, Mato Grosso do Sul, Brasil. Corumbá, MS: EMBRAPA-CPAP, 24 p. (EMBRAPA-CPAP. Boletim de Pesquisa, 10) (in Portuguese).

Resende, E.K., Pereira, R.A.C., Almeida, V.L.L., Silva, A.G., 2000a. Insectivores and Zooplanktivores fishes from Miranda river floodplain. Peixes insetívoros e zooplanctófagos da planície inundável do rio Miranda, Pantanal, Mato Grosso do Sul, Brasil. Corumbá, MS: EMBRAPA-CPAP, 40 p. (EMBRAPA-CPAP. Boletim de Pesquisa, 17) (in Portuguese).

Resende, E.K., Pereira, R.A.C., Almeida, V.L.L., 2000b. Onivores fishes from Miranda river floodplain. Peixes onívoros da planície inundável do rio Miranda, Pantanal,

Mato Grosso do Sul, Brasil. Corumbá, MS: EMBRAPA-CPAP, 44 p. (EMBRAPA-CPAP. Boletim de Pesquisa, 16) (in Portuguese).

Shannon, L.J., Field, J.G., Moloney, C.L., 2004. Simulating anchovy-sardine regime shifts in the southern Benguela ecosystem. Ecological Modelling 172, 269–281.

Silva, H.P., Petry, A.C., da Silva, C.J., 2010. Fish communities of the Pantanal wetland in Brazil: evaluating the effects of the upper Paraguay river flood pulse on baía Caiçara fish fauna. Aquatic Ecology 44, 275–288, http://dx.doi.org/10.1007/s10452-009-9289-9.

Súarez, Y.R., Petrere, M., Catella, A.C., 2004. Factors regulating diversity and abundance of fish communities in Pantanal lagoons, Brazil. Fisheries Management and Ecology 11, 45–50.

Thomaz, S.M., Bini, L.M., Bozelli, R.L., 2007. Flood increase similarity among aquatic habitat in river-floodplain systems. Hydrobiologia 579, 1–13.

Travers, M., Watermeyer, K., Shannon, L.J., Shin, Y.J., 2010. Changes in food web structure under scenarios of overfishing in the southern Benguela: comparison of the Ecosim and OSMOSE modelling approaches. Journal of Marine Systems 79, 101–111.

Tsagarakis, K., Coll, M., Giannoulaki, M., Somarakis, S., Papaconstantinou, C., Machias, A., 2010. Food-web traits of the North Aegean Sea ecosystem (Eastern Mediterranean) and comparison with other Mediterranean ecosystems. Estuarine, Coastal and Shelf Science 88, 233–248.

Ulanowicz, R.E., 2009. A Third Window: Natural Life Beyond Newton and Darwin. Templeton Foundation Press, Pennsylvania, 196 p.

Vasconcellos, M.S., Mackinson, K., Sloman Pauly, D., 1997. The stability of trophic mass-balance models of marine ecosystems: a comparative analysis. Ecological Modelling 100, 125–134.

Vazzoler, A.E.S.M., Agostinho, A.A., Hahn, N.S. (Eds.), 1997. A planície de inundação do Alto Rio Paraná: aspectos físicos, biológicos e socioeconômicos (High Paraná River Floodplain: physical, biological and socioeconomics aspects). Ed. da Universidade Estadual de Maringá, Maringá/PR, 460 p. (in Portuguese).

Villanueva, M.C., Ouedraogo, M., Moreau, J., 2006a. Trophic realtionships in the recently impounded Bagré reservoir in Burkina Faso. Ecological Modelling 191, 243–259.

Villanueva, M.C., Laléye, P., Albaret, J.-J., Laë, R., Tito de Morais, L., Moreau, J., 2006b. Comparative analysis of trophic structure and interactions of two tropical lagoons. Ecological Modelling 197, 1–17.

Waldemarin, H., Rico, M., Muanis, M., 2007. Seasonality effects on habitat of Pteronura brasiliensis e Lontra longicaudis in the Pantanal, MS. In: Workshop Research and Conservation for Pteronura brasiliensis (giant otters) in Brazil, Manaus (in Portuguese).

Walters, C.J., 1986. Adaptive Management of Renewable Resources. McGraw Hill, New York, NY.

Walters, C., Christensen, V., 2007. Adding realism to foraging arena predictions of trophic flow rates in Ecosim ecosystem models: shared foraging arenas and bout feeding. Ecological Modelling 209, 34–350.

Walters, C., Christensen, V., Pauly, D., 1997. Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. Reviews in Fish Biology and Fisheries 7, 139–172.

Walters, C., Pauly, D., Christensen, V., Kitchell, J.F., 2000. Representing density dependent consequences of life history strategies in aquatic ecosystems: Ecosim II. Ecosystems 3, 70–83.

Walters, C.J., Christensen, V., Martell, S.J., Kitchell, J.F., 2005. Possible ecosystem impacts of applying MSY policies from single-species assessment. ICES Journal of Marine Science 62, 558–568, http://dx.doi.org/10.1016/j.icesjms.2004.12.005.

Wantzen, K.M., Machado, F.A., Voss, M., Boriss, H., Junk, W.J., 2002. Seasonal isotopic shifts in fish of the Pantanal wetland, Brazil. Aquatic Sciences 64, 239–251.

Williamson, C.E., Morris, D.P., Pace, M.L., Olson, A.G., 1999. Dissolved organic carbon and nutrients as regulators of lake ecosystems: resurrection of a more integrated paradigm. Limnology and Oceanography 44, 795–803.

Yaragina, N.A., Dolgov, A.V., 2009. Ecosystem structure and resilience—a comparison between the Norwegian and the Barents Sea. Deep-Sea Research II 56, 2141–2153.

Zeug, S.C., Winemiller, K.O., 2008. Evidence supporting the importance of terrestrial carbon in a large-river food web. Ecology 89, 1733–1743.