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Persistence of fish populations in the upper Paraná River: effects of water regulation by dams

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Abstract – River–floodplain systems present intense temporal variations in physical, chemical and biological factors. These variations are closely related to alterations in water levels, which have been attributed to the flood pulse. As several species are strictly related to the flood pulse to fulfil their life cycle, the pulse may be seen as a dispersal mechanism of species onto a floodplain. In this study, we determine how dam construction influenced the persistence of *Prochilodus lineatus* population, a large migratory fish species from the upper Paraná River floodplain. Data used were collected in two distinct periods, from April 1992 to March 1993 and from January 1999 to December 2001. Fish were collected using seining nets in six (monthly in the first period) and seven (quarterly in the second period) isolated lagoons. The fraction of occupied lagoons was high in the first period (higher than 0.65), when flood was intense. However, in the second period, when the flood pulse did not happen or was short, the fraction of occupied lagoons sharply decreased over time (from 0.85 to 0.22). For the first period, no model fitted to data, but for the second period, a negative linear model (named drought-dependent model) presented good fit ($r^2 = 0.97$). Therefore, it is possible to infer that long and intense flood pulses are important to maintain the persistence of *P. lineatus* populations in the floodplain. The artificial control of water levels prompted by dams disrupts this dynamic, reducing persistence to critical levels.

É. A. Gubiani[1], L. C. Gomes[1,2], A. A. Agostinho[1,2], E. K. Okada[2]
[1]Graduate Course in Inland Aquatic Environments, Department of Biology, [2]Nucleus of Research in Limnology, Ichthyology and Aquaculture (Nupélia), Maringá State University, Avenida Colombo, Maringá, Paraná, Brazil

Key words: floodplain; flood pulse; persistence

É. A. Gubiani, Graduate Course in Inland Aquatic Environments, Department of Biology, Maringá State University, Avenida Colombo, 5790 Maringá, Paraná 87020-900, Brazil;
e-mail: eagubiani@nupelia.uem.br

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Introduction

Natural populations are subject to random fluctuations, because environmental conditions vary stochastically, influencing birth and death rates, and thus, populations have a non-zero probability of extinction at all times. Distribution of organisms in natural landscapes (usually a mosaic of habitats) is rarely homogeneous and a population may be divided in subpopulations (Karieva 1990) or a metapopulation, which means in the simplest sense, population of populations (Levins 1969; Hanski & Gilpin 1996; Hanski 1999). Therefore, even if a local population goes extinct, the metapopulation can persist on a regional scale. The ability of a population surviving for many generations is defined as persistence (Hixon et al. 2002).

The spatial dynamics of interconnected subpopulations may vary from little to complete isolation. In addition, because of extinction or migration of local populations along the landscape, not all available habitats are occupied, which will certainly influence persistence of a population in a regional scale. Some factors influencing these are distance among occupied areas, geographic barriers and ability of dispersion (Harrison & Taylor 1996). However, there are few studies dealing with populations in floodplain.

Floodplains are particular forms of landscapes, which present high temporal variations on physical, chemical and biological properties, mainly related to oscillations in water level. These oscillations play a central role in the interpretation of ecological processes of these systems, what motivated the formulation of the flood pulse concept (Junk et al. 1989; Neiff

1990). Nevertheless, impoundments usually modify the original river water regime, leading to diminished flooded area downriver, decreasing connectivity, and, consequently, biodiversity of isolated habitats (lagoons) may be severely threatened by the absence of floods. Therefore, the flood pulse can be considered a mechanism that maintains population persistence because it disperses individuals among the several floodplain habitats, especially for species closely dependent on the pulse, such as long distance migratory species (Agostinho et al. 2003, 2005).

Dams constructed upstream from the upper Paraná River floodplain control river discharge, limiting floods, altering the dispersal mechanism of several species. Thus, as flood decreases, the dispersion of various populations also decreases with consequences on the maintenance of local and regional biodiversity. Therefore, the understanding of the effects of flood regulation on extinction and colonisation rates is fundamental to solve several questions in ecology and conservation of floodplains (*sensu* Hanski & Gilpin 1996; Levin et al. 1997; Hixon et al. 2002). Considering this scenario, the present work evaluates the influence of dam construction on the persistence of *Prochilodus lineatus* (Valenciennes, 1836) population, a large migratory fish species, in the upper Paraná River floodplain. Specifically, we intend to answer the following question: how did the construction of a large dam (Porto Primavera in 1998) influence the persistence of the species in the stretch below, where the plain is located?

Material and methods

Study area and sites

The upper Paraná River floodplain is located between Porto Primavera Dam and Itaipu Reservoir (Fig. 1). This is the last stretch of the Paraná River within the Brazilian territory without dams. In this area (230 km long), marginal lagoons (temporary or not) are abundant, usually fed by groundwater, local rains, channels connected with the main river or by seasonal floods. Water reduction during dry periods contributes to create several pools. Therefore, the flood pulse is considered the main force driving floodplain functioning (Agostinho et al. 2004), and it varies in intensity over time, or sometimes it does not happen. However, after the construction of several dams in the upper Paraná, water level became less variable and it may be absent more frequently. Then, in this study, two periods of different water levels are considered. The first period (April 1992 to March 1993) was characterised by an intense flood whereas the second period (January 1999 to December 2001), the flood pulse was absent or short.

Lagoons sampled in the first period (group 1) are located in two islands of the upper Paraná River: Porto Rico (Canal do Meio and Pontal lagoons) and Mutum (Porto Rico, Pau Véio, Três Irmãos and Mutum lagoons) (Fig. 1). These lagoons are old channels of the Paraná River and are, in general, long shaped with high water flow during floods. However, these lagoons may fragment (except Porto Rico) during periods of receding water level and drought, they get isolated, forming smaller pools that may dry out completely.

Lagoons sampled in the second period (group 2) are spread over the plain, in the rivers Ivinheima (Zé do Paco, Ventura and Capivara lagoons), Baia (Jacaré, Fechada and Pousada das Garças lagoons) and Parana (Osmar Lagoon) (Fig. 1). These lagoons present varied shapes (rounded to longed), sizes and depths, and they are disconnected from the main river channel.

Water level and samplings

Water levels of the Paraná River were obtained in the 'Posto Hidrometereológico de Porto São José (PR)', supplied by DNAEE (Departamento Nacional de Água e Energia Elétrica). We opted to present historical data (from 1964 to 2001) to show the influence of dams in the upper Paraná River water level and detailed data of the studied periods, before and after the construction of Porto Primavera Dam (completely closed in 1998).

In the first period (April 1992 to March 1993), *P. lineatus* was collected monthly using seining nets (30 m long and 0.5 cm mesh size). In the second period (January 1999 to December 2001), isolated lagoons were quarterly sampled, using seining nets (20 m long and 0.8 cm mesh size).

Data analysis

Trends in water level were identified graphically. To better determine the historical influence of dams in the hydrograph, water level data were divided into phases. Phase I represents water level of the upper Paraná River main channel without dams. Every phase after that (II, III and IV) corresponds to the period immediately after the closure of a large dam (Jupiá: main channel of the Paraná River; Rosana: Paranapanema River, a tributary on the east side of the Paraná River, just above the plain; and Porto Primavera, main channel of the Paraná River, just below Jupiá and above the plain). Water level before and after the closure of Porto Primavera Dam (phase IV) was analysed in detail, to show trends related to the sampled periods.

Abundance of fish was expressed in number of individuals per 100 m^2 of seined area. This abundance was also analysed graphically, to identify trends over time. In addition, to evaluate persistence, abundance

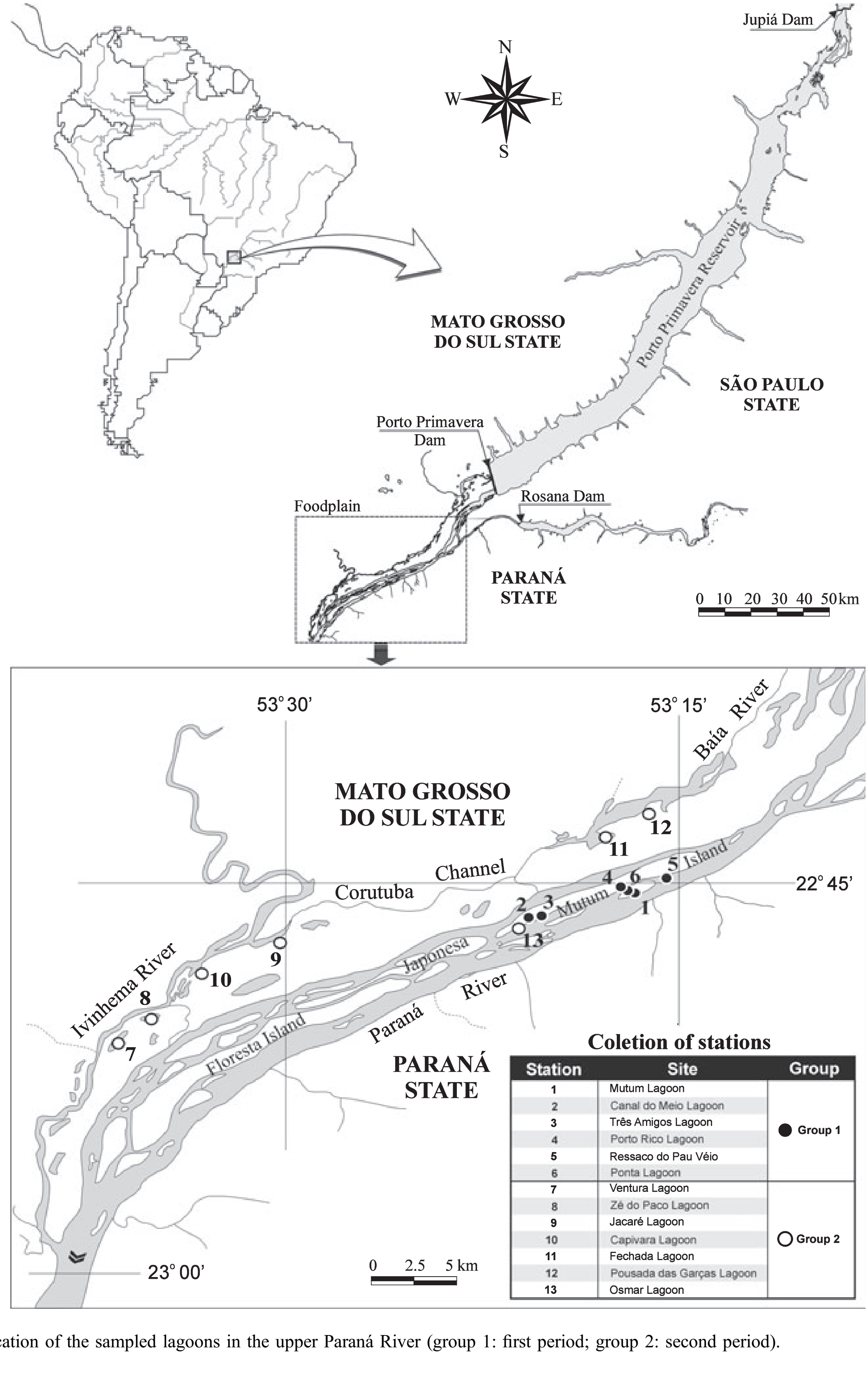

Fig. 1. Location of the sampled lagoons in the upper Paraná River (group 1: first period; group 2: second period).

data of *P. lineatus* (lagoons and months, separated by periods) were transformed in presence (1) and absence (0). The fraction of occupied lagoons by the population (*f*) was calculated dividing the number of occupied lagoons in a given month by the total number of lagoons sampled in the same month.

Values of *f* were plotted against time and persistence was modelled using linear regression. To meet assumptions, the regressor variable (*t*) was ln transformed. All calculations were made using the software Statistica™ for Windows 7.1.

Results

Dam construction in the Paraná River altered water levels in the studied region (Fig. 2). During phase I, there were few reservoirs above the floodplain and none in the main channel of the Paraná River. For every large reservoir filled just above the studied area (Jupiá before phase II; Rosana before phase III and Porto Primavera before phase IV), the hydrograph was altered. Then, after the closure of Porto Primavera Dam, mean water levels decreased about 40% when compared with those registered in phase I. These alterations, therefore, severely impacted the biota in the region, including long distance migratory species, such as *P. lineatus*.

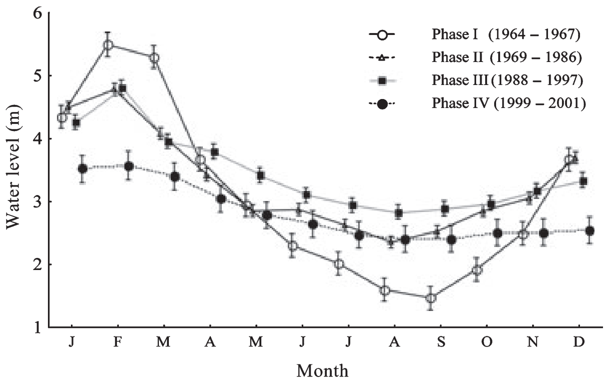

Fig. 2. Changes in water level in the upper Paraná River. Each phase corresponds to a period immediately after a closure of a large dam above the studied area, except phase I (natural discharge) (after Agostinho et al. 2007).

Considering the studied periods, in the first, the flood pulse occurred between April and May 1992 and between November 1992 and February 1993 (Fig. 3a). In the second period, from January 1999 to December 2001, there was not a conspicuous flood. Only in the beginning of 1999 and in May 2002 occurred pulses (Fig. 4a); however, they reached low levels and they were short.

Abundances of *P. lineatus* in the area presented high variability (Fig. 5). Two patterns are of relevance: (i) abundances were higher in the first period (Fig. 5a) and (ii) for both periods, there were a tendency of decreasing abundances over time. However, the reduction in abundance in the first period occurred, probably, because *P. lineatus* abandoned lagoons with the next flood.

Persistence was measured by the fraction of occupied lagoons, and it was higher in the first period, with values always above 0.65. In addition, fraction of occupied lagoons reached 100% during 4 months (Fig. 3b). In the second period, there was a tendency of exponential decrease in the fraction of occupied lagoons over time. When sampling started, this fraction was approximately 0.85 (1999; when a fast, but low-intensity pulse occurred), decreasing to 0.22 at the end of the period (Fig. 4b).

Therefore, the 1999 flood had an intensity and duration that worked as a dispersion mechanism of individuals to lagoons of the floodplain. Conversely, in the following years, the flood pulse presented lower intensity and duration, and, therefore, colonisation

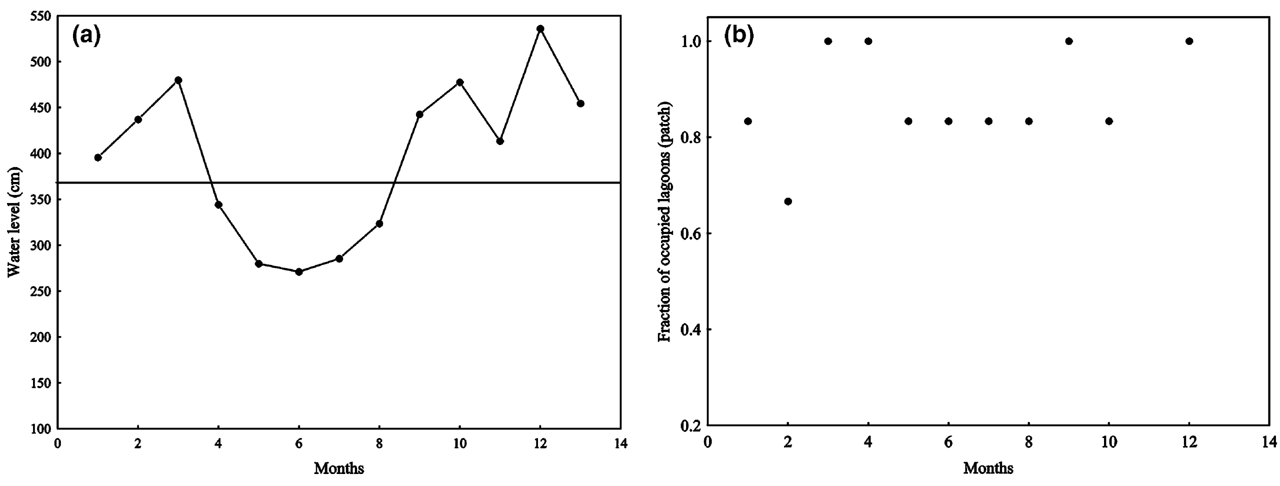

Fig. 3. Mean water levels (cm; a) of the upper Paraná River measured near the city of Porto Rico, between April 1992 and March 1993. Continuous line indicates the minimum water level (370 cm) necessary to characterise a flood. The fraction of occupied lagoons by *P. lineatus* in the period is presented in (b).

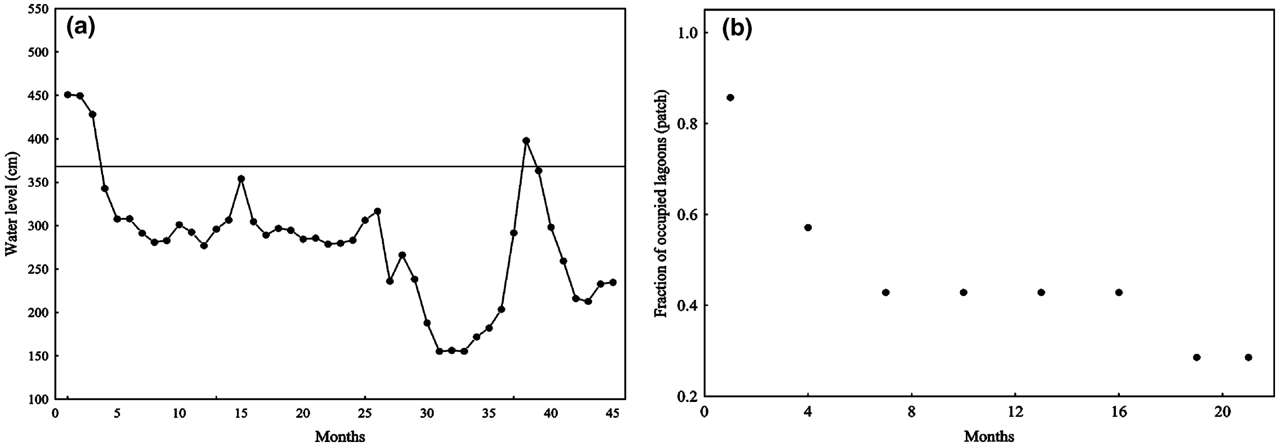

Fig. 4. Mean water levels (cm; a) of the upper Paraná River measured near the city of Porto Rico, between January 1999 and March 2002. Continuous line indicates the minimum water level (370 cm) necessary to characterise a flood. The fraction of occupied lagoons by *P. lineatus* in the period is presented in (b).

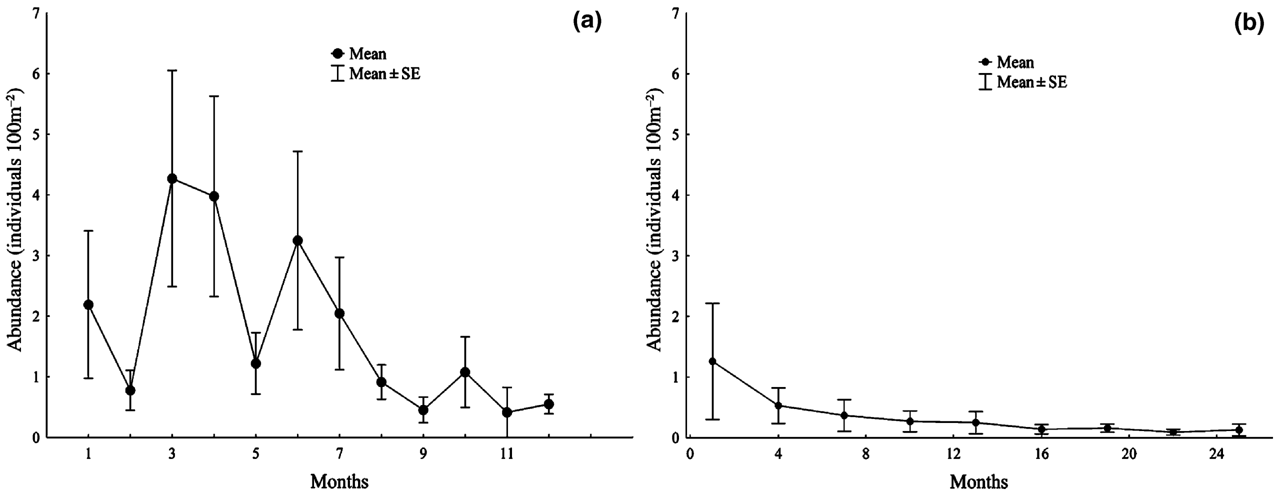

Fig. 5. Abundances of *Prochilodus lineatus* in the upper Paraná River floodplain in the studied periods [(a) April 1992 to March 1993; (b) January 1999 to December 2002).

decreased, what reinforces the influence of the flood on the persistence of *P. lineatus* in the floodplain.

For the first period, it was not possible to fit a model to data (Fig. 3b). Persistence was influenced by the flood pulse. When flood inundated the plain, fraction of occupied lagoons reached 100%. This means that all sampled lagoons where occupied, and then, the plain was saturated by *P. lineatus*. In the second period, however, it was observed a clear exponential decrease in the fraction of occupied lagoons (Fig. 4b) which allowed to fit a linear model: $f = \mathrm{pe}\ \ln(t) + a$ ($r^2 = 0.97$), herein named drought-dependent model, where *pe* is the velocity of persistence decrease (extinction rate), and *a* is defined by the initial condition of the model. In this period, there were no relevant flood pulses. Then, the species was not dispersed onto the plain and also, migration was not possible because of reduced connectivity.

Apparently, the decay in the fraction of occupied lagoons is dependent on the time between flood events. Longer the time between floods, more intense will be the decrease in the fraction of occupied lagoons, with reflex on the persistence of *P. lineatus*.

Discussion

Prochilodus lineatus is one of the most studied fish species in the Paraná River basin (Sverlij et al. 1993). It is a long-distance migratory species that depend on the flood pulse to complete its life cycle. Juveniles inhabit lagoons of the plain for 1–2 years, where they find food and shelter, returning to the main river after a flood (Agostinho et al. 1993; Gomes & Agostinho 1997; Agostinho et al. 2003). Biological events of migratory species, such as gonad maturation, migration, spawning, larval development and growth are strictly related to floods. In addition, recruitment success is dependent on the timing and duration of the floods (Gomes & Agostinho 1997; Agostinho et al. 2003, 2005).

In the upper Paraná River floodplain, juveniles of *P. lineatus* may represent more than 70% of the fish biomass in lagoons after a long flood. However, if a flood is short, the species may be completely absent in the region (Agostinho & Zalewski 1995). In lagoons of the same studied area, Agostinho et al. (2004) observed that *P. lineatus* accounted for 65% of the total fish biomass, what corroborated the results shown by Agostinho et al. (1997) and Ferreti et al. (1998). Cunico et al. (2002) also discussed the importance of flood duration for lagoons colonisation, noticing, in 1998, an expressive increase in the abundance of *P. lineatus* in isolated lagoons, after a significant flood. We found similar results, with greater abundance of *P. lineatus* in the first period, when the flood pulse was intense.

During flood events, the higher connectivity among floodplain habitats (including the main river channel) allows movement of several fish species. Fish disperse throughout the area, and after water retraction, the landscape becomes again a mosaic of fragmented habitats, similarly what occurs on the mainland–island metapopulation model (Gotelli 1991, 2001; Hanski 1991, 1999). In this case, the river works as the 'mainland' and lagoons as the 'islands', and the flood pulse is the dispersal mechanism that intensifies colonisation, as reproduction of migratory fish species occurs during high water periods, as in the case of *P. lineatus*.

The fraction of occupied lagoons (persistence) in the upper Paraná River, for *P. lineatus*, is totally dependent on the flood pulse. During the first period, no model fitted the data reinforcing the importance of the flood pulse on maintaining the persistence of *P. lineatus*. When the flood pulse was considered 'normal', colonisation rate was completely at random and close to saturation. When inundation fails to happen (or it has short duration), colonisation becomes impossible and an expressive decrease on the fraction of occupied lagoons is observed. Under this condition, *P. lineatus* population is condemned to extinction, as showed by our drought-dependent model.

Floods with a short duration can affect negatively *P. lineatus* reproduction success and recruitment, ultimately conducting to a total failure, leading to decreased number of occupied lagoons. We noted a high probability of extinction during the second period, and during the 2 years with no floods, fraction of occupied lagoons by *P. lineatus* was close to zero, again, demonstrated by our drought-dependent model.

Other factors may be related to the persistence of the species. For example, extinction rate should be higher in small populations than large ones (Shaffer 1981; Lande 1993), then, the occurrence of a species is more likely to happen in large habitats. In addition, colonisation should be greater in well-connected habitats when compared with isolated ones. These factors may also influence the persistence of *P. lineatus*, but it was clear that the abundance of the species was lower in the second period. Area of the lagoons and connection were not considered in this study.

For fish in creeks, Koizumi & Maekawa (2004) demonstrated that habitat size, type and degree of isolation influenced the occurrence of Dolly Varden in tributaries of the Shiisorapuchi River (upper and middle stretches). Other studies have demonstrated the effects of these factors on the persistence of fish species in creeks. In addition, anthropogenic actions, especially those related to agriculture, construction of roads and dams have influence on persistence of fish species in creeks (Koizumi & Maekawa 2004).

Predictions cited above are valid for rivers in a continuum, where distance and size of habitats have important consequences for colonisation and extinction. In floodplains, the distance between the lagoon and the main river may be considered the essential aspect, because when floods are of low intensity and duration, lagoons may not be reached, decreasing the persistence of a species. According to our drought-dependent model, absence of long floods is the key factor for the persistence of *P. lineatus* in the upper Paraná River floodplain.

Other factors, not mentioned here, may also contribute to increase local extinctions of *P. lineatus* in isolated lagoons, such as abiotic factors, predation and competition (Okada et al. 2003; Agostinho et al. 2004; Thomaz et al. 2004; Piana et al. 2006). However, for them to influence persistence, a species must first reach the lagoons, what is only possible when floods occur, which was more conspicuous in the first period. Therefore, the artificial control of the hydrological cycle prompted by dams seems to be more serious than considered so far, especially when floodplains are located at the end of a cascade of reservoirs, as the case of the upper Paraná River.

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