ORIGINAL RESEARCH

Flooding effects on abundance of an exploited, long-lived fish population in river-floodplains of the Amazon

Leandro Castello · Peter B. Bayley · Nidia N. Fabré · Vandick S. Batista

Abstract Flooding regulates the amount and quality of habitat available for fish populations in river-floodplains. Although previous studies assessed fish population responses to river hydrology, the processes by which flooding affects fish abundance and catch remain unclear. Here, we investigated whether degree of flooding affects abundance and catch of *Colossoma macropomum,* a long-lived, overexploited fish population of the central Amazon Basin. We computed the degree of flooding corresponding to the feeding area of young-of-the-year *C. macropomum* as the annual magnitude of the moving littoral zone (ML). We estimated abundance of age classes one, two, and three of *C. macropomum* using a modeling program based on catch, fishing effort, and fish length frequency data from the principal commercial fishery. We found that flooding positively and non-linearly affected abundance of the age-one cohort but not of older age classes. ML data corresponding to a late rising water phase in which zooplankton, seeds, and fruits dominated the diet provided the strongest effect on age-one abundance. However, flooding effects on total catch were not found, likely due to catches comprising several age classes. These results provide support to existing evidence that the magnitude of the moving littoral zone regulates abundance of juvenile fish. Because the ML quantifies food and habitat availability for various other fish species, it may constitute an important control of fish abundance in these systems. Management of these fisheries may be improved by adjusting fishing effort based on hydrology. More generally, the information also serves to assess the impacts of hydrological alterations (e.g., dams) on fish recruitment.

Keywords *Colossoma macropomum* · MULTIFAN-CL · Fisheries · Flood pulse · Young-of-the-year · Várzea

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Introduction

Seasonal water level changes, known as flood pulses, regulate the amount and quality of habitat available for fish populations in river-floodplain systems (Junk et al. 1989). Of the two phases of the hydrological cycle, flooding exerts a major role prompting fish inhabiting river channels and floodplain lakes to spawn and migrate laterally on to the advancing 'moving littoral' zone (Castello 2008a, b; Fernandez 1997; Gomes and Agostinho 1997). The moving littoral allows fish of all ages to feed on abundant food sources (i.e., detritus, insects, fruits seeds) found in vegetated floodplain habitats (Bayley 1988; Goulding 1980). As the flooded area increases, fish density decreases and mortality rates by predation can be reduced (Agostinho et al. 2004; Caraballo et al. 2014; Junk 1985; Lagler et al. 1971). By affecting fish production and mortality processes, flooding can influence the amount of fish biomass available for harvesting as well as associated catches (Castello et al. 2015; Welcomme 1985). However, the processes by which flooding affects fish biomass and catch remain unclear (e.g., Linhoss et al. 2012).

Most studies have inferred flooding effects on indices of fish population magnitude based on statistical relationships. Early studies modeled river-floodplain fish catch in a given year as a function of hydrological indexes of high or low waters (e.g., minimum stage) 1 or 2 years before (de Mérona and Gascuel 1993; Lagler et al. 1971; Welcomme 1985). More recently, fish catch in a given year was modeled as a function of fishing effort and hydrological indexes 1, 2, and 3 years before. The results from such studies show that fish biomass available for harvesting tends to vary with hydrological indices, and that effort responds positively to changes in fish biomass, thereby amplifying hydrological effects on fish catch (Castello et al. 2015). The interannual lags of such hydrological effects tend to be similar to mean age of capture, suggesting that hydrological conditions during the early life or juvenile stages influence fish biomass available for harvesting (Isaac et al. 2016). Despite this body of knowledge, however, the effects of flood pulses on fish biomass (or abundance) have only rarely been assessed explicitly in natural flowing river-floodplains. Because fish catch is affected by fishing effort in addition to hydrological conditions (Castello et al. 2015), there is a need to investigate mechanistic

relationships between natural river hydrology and fish abundance while independently accounting for effort effects.

To our knowledge, there have been only a few mechanistic studies of fish population responses to flooding in river-floodplains. Welcomme and Hagborg (1977) used data for several species and fisheries to develop a generalized model of fish populations and fisheries for African rivers, showing that fish biomass and catches are positively related to the amount of water in the system. More recently, Linhoss et al. (2012) used aggregated catch per unit effort data for tilapia species (*Oreochromis andersonii, Tilapia rendalli,* and *Oreochromis macrochir*) to develop a density-dependent model that tracked age cohorts over time. In line with expectations, they found that recruitment variation induced by the magnitude of the flood was a key driver of fish population dynamics in the Okavango Delta. Building on previous studies, Bayley et al. (2018) used a range of biological, ecosystem, and fisheries data for *Prochilodus nigricans* in the central Amazon to fit an age-structured population model to test the effect of interannual variation in the littoral zone on age-class abundance. They found that age-two abundance of *P. nigricans* was positively related to the magnitude of the littoral zone, and suggested the population may be regulated by density-dependence with respect to its principal feeding habitat.

A quantitative understanding of hydrological effects on fish abundance can lead to predictions of fishery yields. Given that fish production processes in tropical river-floodplains with monomodal flood pulses are generally associated with the magnitude of flooding or the moving littoral zone, it is likely that fish population abundance increases with flooding extent. The effect of the flooding cycle on abundance of young-of-the-year individuals may, in turn, vary during different phases of the flooding period (i.e., early rising vs late rising), as fish diets often change during their first year and tend to vary with habitat quality and quantity (Fuiman and Werner 2002). However, any flooding effect on fish catch can be expected to depend on population age-structure. Whereas flooding effects on the catch of short-lived species can be observed within one or a couple of years (de Graaf 2003a, b), such effects may not always be observed in long-lived populations. In long-lived populations, two or more cohorts contributing to fish

catch are likely affected by different year-specific hydrological effects when they are younger, thus tending to attenuate hydrological signals when they recruit to the fishery (Welcomme 1985).

There is great need to understand flooding effects on abundance and catch of river-floodplain fish populations. River-floodplain fisheries underpin food security in many tropical and sub-tropical countries (Lynch et al. 2016), but are poorly studied, poorly managed, and widely affected by overfishing and hydrological alterations (Allan et al. 2005). Long-lived fish populations are among the most overexploited and depleted (Welcomme 1999). Yet, their management rarely accounts for life history characteristics or hydrological variation.

Here, we investigated whether flooding affects abundance and catch of a long-lived fish population in river-floodplains of the central Amazon Basin. We asked: Does flooding extent of the moving littoral affect fish population abundance? If flooding extent affects young-of-the-year abundance, are there flooding phases corresponding to specific diets that account for more of the variation in abundance? And, does flooding extent affect catch? We addressed these questions based on an analysis of *Colossoma macropomum*, a widely distributed fish species of the Amazon Basin that is long-lived by tropical standards. *Colossoma macropomum* depend on floodplains to feed. During the first 3 years of life, when they grow to maturity at about 58 cm long, they depend on a diet which changes with size (Araujo-Lima and Goulding 1997). Young-of-the-year *C. macropomum* feed primarily on zooplankton, insects, and wild rice seeds (*Oryza* spp.); juveniles and adults feed mainly on fruits and seeds when they inhabit the floodplains during high waters, though they also feed on zooplankton (Carvalho 1981; Goulding and Carvalho 1982; Honda 1974). Adults are highly fecund and migrate out of the floodplains into river channels and then up to several hundred kilometers upstream in whitewater river channels to spawn between November and December; after spawning, they migrate seasonally to floodplain flooded forests to feed (Araujo-Lima and Goulding 1997). *Colossoma macropomum* has sustained important fisheries in the Amazon and is highly priced nowadays, having been found to suffer growth overfishing in the central and lower Amazon regions (Isaac and Ruffino 1996; Petrere 1983). In addition to overfishing, this and many other floodplain-dependent fishes of the Amazon Basin are increasingly vulnerable to a broad suite of alterations that threaten the maintenance of the annual flood pulse and quality of floodplain habitats (Castello et al. 2013). If a predictive relationship of age-class abundance can be established based on flooding extent, flooding effects on resulting fish catches could potentially be predicted in the future using typical mortality rates. Such information could guide the implementation of controls of fishing effort based on river hydrology and be used to assess the likely impacts of hydrological alterations.

Methods

We investigated the effects of flooding on catch and abundance of *C. macropomum* using two approaches, both based on estimates of the moving littoral zone as a predictor variable. The 'direct' approach attempted to predict total catch of *C. macropomum* on the basis of the moving littoral magnitude during the same or in previous years. In this direct approach, the factors responsible for causing or compromising the detectability of a hydrological effect include fishing effort, gear efficiency, and ecological effects on age class abundance. The 'indirect' approach attempted to predict age class abundance of *C. macropomum* on the basis of moving littoral magnitude earlier in the same year or during a previous flood. A relationship between age class abundance and moving littoral magnitude has the advantage of implicating a limited set of ecological mechanisms without direct fishery effects.

To implement these approaches, we calculated the magnitude of the moving littoral zone for the central Amazon Basin for each hydrological year during a 14-year period based on river stage, inundation area, and distribution of young-of-the-year *C. macropomum* within the moving littoral. We computed total annual catch (of all age classes) based on fishery landing data. We estimated abundance of age classes of *C. macropomum* using a length-based, age-structured population modeling program that we fit using catch, fishing effort, and fish length frequency data. We assessed the potential effects of flooding on catch and age-class abundance by evaluating regression models that predicted catch and age-class abundance as a function of the moving littoral zone magnitude.

Study area and fishery

Our study area comprised the central Amazon region, including the Madeira, Purus, and Amazon-Solimões rivers, as defined by the area exploited by the fishing fleet of Manaus city in Amazonas State, Brazil (Fig. 1). Here, the ecosystem is a river-floodplain system. The floodplain comprises a complex mosaic of seasonally inundated rain forests and other vegetation types, lakes, swamps, and connecting channels. A large part of the floodplain, called the várzea, is maintained by the seasonal, monomodal, and predictable flooding of river whitewaters stemming from the Andes Mountains (Irion et al. 1997), while smaller parts are maintained by low-sediment blackwater rivers (e.g., Rio Negro) or direct rainfall. Much of the floodplain, including most of the floodplain habitats, is connected hydrologically and reflect the stage variation in the main river most of the year (Hess et al. 2015). On average, river water levels begin to rise around December, reaching their maximum level in June, at which time they begin to drop, reaching their lowest level in October, with an average amplitude of 12 m. The fishing fleet of Manaus (Fig. 1)

comprised about 2500 boats $\sim$ 14 m in length that typically were operated by 8–12 fishers in fishing trips lasting between 10 and 28 days; the main gears used were lampara seines and gill nets (Batista and Petrere 2007).

Moving littoral magnitude

We defined and quantified the magnitude of the moving littoral and described how to obtain annual estimates for our study area in a companion paper (Fig. 2; Bayley et al. 2018). The moving littoral was first proposed as the inshore zone that traverses the floodplain during the seasonal advance of the flood pulse (Bayley 1991; Junk et al. 1989), representing the feeding habitat available for many fishes and other aquatic organisms within a given depth range. Our previous data from 409 individuals caught in 86 samples during two and a half hydrological cycles in floodplains of the central Amazon Basin (Bayley 1983) indicated that young-of-the-year and older *C. macropomum* select for a depth range of 0–3 m (Fig. 3a, b), especially during the rising water period when growth of fishes in these systems is faster on

Fig. 1 Study area in the central Amazon Basin. The rectangle delineates the area comprising the bulk of fishing sites, and circles of different sizes denote the relative catch contribution of *C. macropomum* to fishery landings in the city of Manaus (denoted with a star) in Amazonas State, Brazil, between 1993 and 2006
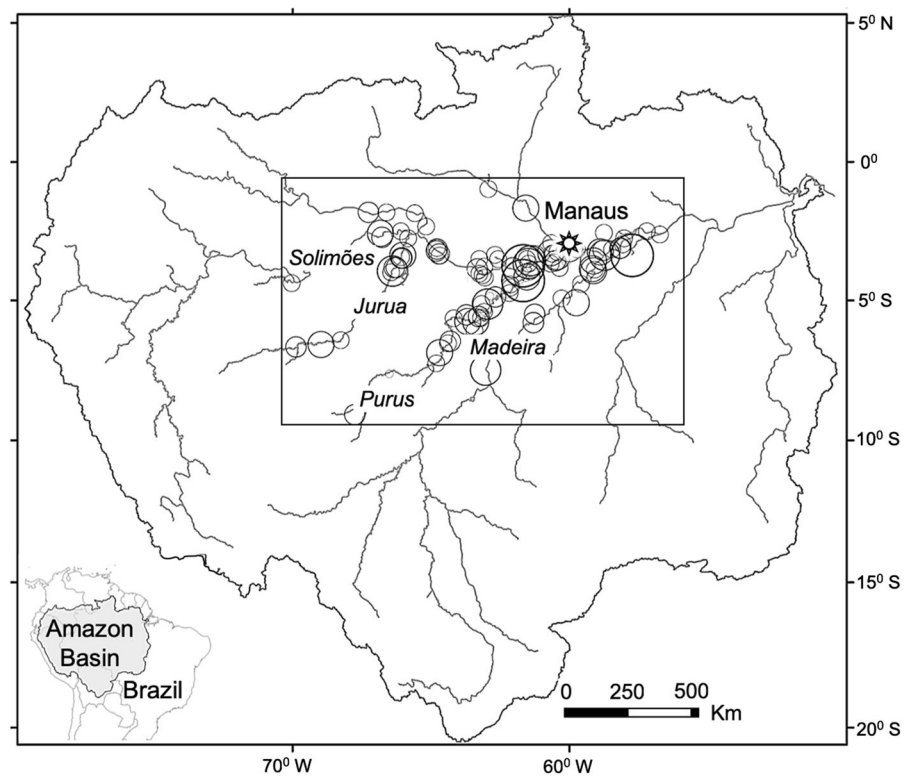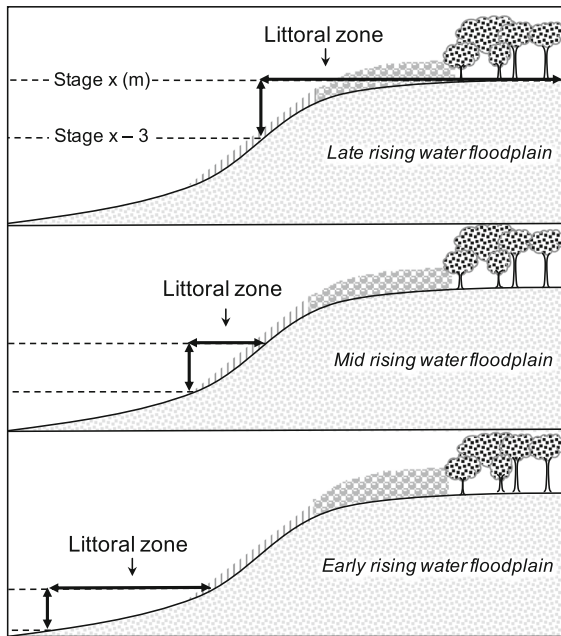
Fig. 2 Schematic of the littoral zone (vertically exaggerated) at three points in time during the flooding process, depicting the calculation of the magnitude of the moving littoral zone. The area of the littoral zone was defined here as inundated floodplain area in the study area with depth of 3 m or less. It was calculated as the difference between the estimated total flooded area at stage x and the corresponding area at stage x − 3 (m) for a given date. The moving littoral (ML) was quantified as the sum of daily littoral areas during the annual rising water period. Typical vegetation forms found in the várzea floodplains are illustrated

Fig. 3 Depth range and size over time of *C. macropomum* in floodplains of the central Amazon region during two and a half hydrological cycles. Data are from a previous study that collected 160 25-m seine samples of floodplain fish and habitat (Bayley 1983). **a** River stage during the 1977–1979 period (ANA 2017). **b** Habitat depth for 409 individuals of *C. macropomum* collected in 89 of the samples where they were present, showing strong use of 0–3 m ML habitat. Most (n = 407) of those individuals were under 22 cm FL (i.e., young-of-the-year). **c** Fork lengths by date of young-of-the-year *C. macropomum* based on 398 individuals. Data points for young fish caught in months 2–5 (1977 year) represent the 1977 cohort, those between month 11 (1977 year) and month 1 (1978 year) represent the 1978 cohort, and those in months 1–2 (1979 year) represent the 1979 cohort. A growth function, FL = − 12.78 + 9.62*sqrt(month) (R^2 = 0.88, n = 64), was fitted to 1977 cohort data and plotted with 95% confidence range. In b, c symbol sizes are proportional to fish density after being corrected for catchability (Bayley and Herendeen 2000)

average than during the receding period (Bayley 1988). Therefore, we defined the magnitude of the moving littoral (ML) for *C. macropomum*, as the sum of daily littoral areas within 0–3.0 m water depth during the rising water period.

To estimate ML, we derived a predictive relationship of total flooded area based on river stage for our study area from data provided by a study of passive microwave data from the Nimbus-7 satellite (Sippel et al. 1998). Daily river stage data were obtained from ANA (2017) for the station at Manacapuru, which reflects river hydrology for the bulk of the area where the fisheries data for *C. macropomum* analyzed here came from (Fig. 1). For each day during the annual rising water periods, the littoral surface area was estimated by subtracting the total flooded area predicted at stage three meters lower from that corresponding to the current stage (Fig. 2). The magnitude of the ML was computed by summing the daily littoral area estimates during the rising water period in each
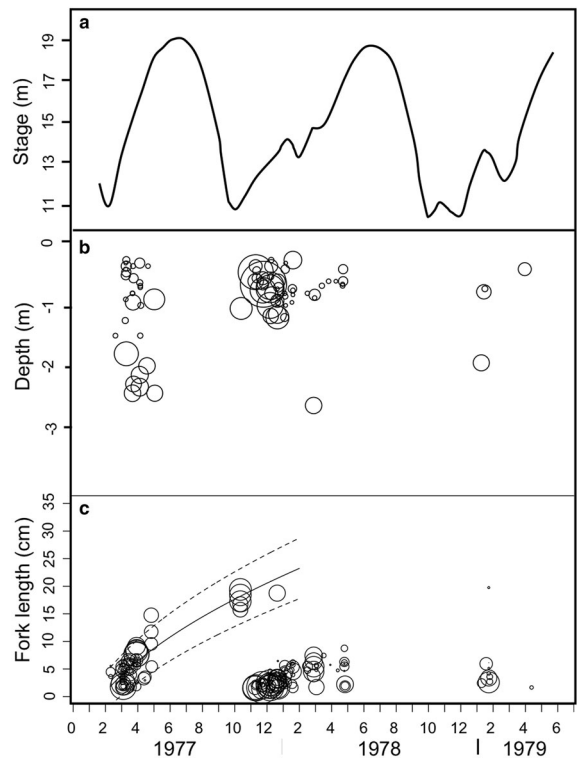
hydrological year. Variants of ML, corresponding to different life stages and a descending water level period were also investigated.

Catch and abundance estimates

We computed catch and estimated abundance of age classes one, two, and three of *C. macropomum* based
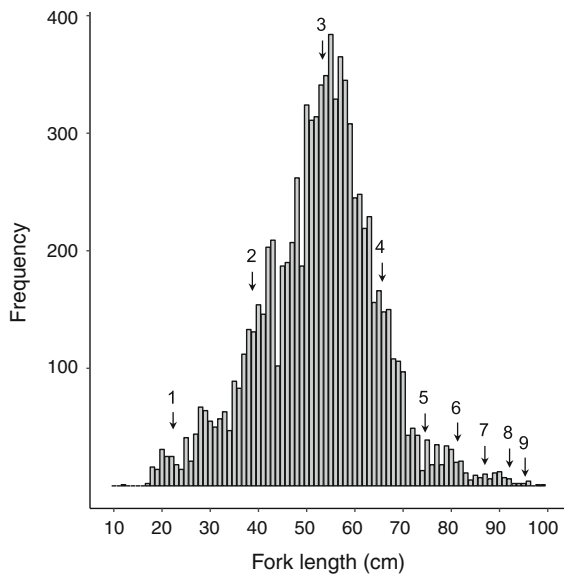
Fig. 4 Length frequency distribution of the catch and corresponding mean length-at-age (numbers with arrows). Length measurements were done on a total of 8752 *C. macropomum* specimens to the nearest whole centimeter down by trained data collector at Manaus, between 1993 and 2006. Length-at-age estimates are based on the growth model estimated by this study (Fig. 5)

on landing surveys of 30,702 fishing trips done between July 1993 and March 2006, including catch (kg), dates of departure and arrival, number of days spent fishing, number of fishers, types of gears used, and subsamples of length-frequencies totaling 8752 *C. macropomum* specimens (Fig. 4). These landing surveys allowed us to record catch and effort, modified due to minor corrections of unrecorded boats and days (Bayley et al. 2018), and to estimate age-class population abundance by year using MULTIFAN-CL, which is a program that models a multi-age exploited fish population over time (Fournier et al. 1990). MULTIFAN-CL requires catch, fishing effort, and fish length frequency data that describe an age-structured fish population. Parameters are estimated based on catch equations used in conventional fish population dynamics models (Fournier et al. 1998; Kleiber et al. 2014). Key outputs estimated include growth rate (using a relative form of the von Bertalanffy model), instantaneous rates of natural and fishing mortality, and age-class abundance over time.

We assumed that *C. macropomum* constituted a single population, based on Santos et al. (2018), with no significant net-migration outside the study area. In our model, that population was exploited by three 'fisheries' defined by their gears (lampara seine net, gill net, and mixed seine and gill net) and their respective catchability and selectivity characteristics. The data were summed within quarterly periods in each year (called 'fishing events'; Jan.–Mar., Apr.–Jun., etc.) that corresponded to typical hydrological periods associated with catches by the three fisheries (Table 1). To model recruitment, we considered that the smallest harvested individuals were 18 cm FL (Fig. 4), and used absolute age-at-size estimates from the literature and independent data on *C. macropomum* individuals collected in the natural environment to fit a growth function on size of post-larval *C. macropomum* (Fig. 3c). By experimenting with MULTIFAN-CL, we found that the youngest age class determined by MULTIFAN-CL (i.e., age-one) was likely of individuals born in the previous mid-November and averaged 10.5 months old when their population size was estimated by MULTIFAN-CL for October 1. Maturity was assumed to occur at age three, as per previous studies (Araujo-Lima and Goulding 1997; Vieira et al. 1999; Villacorte-Correa and Saint-Paul 1999). The growth model was based on narrow priors from previous studies (Table 2). Finally, we assumed that natural mortality was 0.42, based on Barthem and Fabre (2004). Further methodological details of our modeling of *C. macropomum* population using MULTIFAN-CL are provided in the Supplementary Information.

Data analyses

We assessed our research question, of whether flooding extent of the ML affects population abundance, by evaluating the significance of regression models that predicted abundance of age classes one, two, and three in a given year (e.g., age-one$_{-0}$) as a function of the ML magnitude earlier in the same year (i.e., ML$_{-0}$). Visual inspection of the count response suggested overdispersion, so we tested for it using the QCC function of the Qcc package in R (Scrucca 2004). We tested the fit of a generalized linear model appropriate for overdispersion, the Negative Binomial. We assessed the assumptions of that model based on Cook statistics (D_i), based on residual plots of jackknife deviance residuals against the linear predictor as well as normal scores of standardized deviance residuals, using the glm.diag.plot function of the Boot package in R (Canty and Ripley 2017).

Table 1 Total catch of *C. macropomum* recorded in 153 fishing events by periods of the year and gear-defined fisheries in the central Amazon

Period	Gill net (kg)		Gill net & Lampara (kg)		Lampara seine (kg)		Total (kg)	
Jan–Mar	419,779	3%	297,874	2%	18,475	0%	736,128	6%
Apr–Jun	1,152,859	9%	841,942	7%	1,479,517	12%	3,474,318	28%
Jul–Sep	2,324,070	19%	2,300,074	19%	574,820	5%	5,198,964	42%
Oct–Dec	1,875,075	15%	749,229	6%	286,331	2%	2,910,635	24%
Total	5,771,783	47%	4,189,119	34%	2,359,143	19%	12,320,045	100%

Table 2 Parameter coefficients of three von Bertalanffy growth models for *C. macropomum* in the Amazon Basin

Source	K (year^{-1})	L_∞ (cm)
Petrere (1983)	0.227	107.3
Isaac and Ruffino (1996)	0.228	121.2
This study	0.227	119.5

Table 3 Coefficients of models testing for relationships between the moving littoral magnitude at varying time lags and abundance (1000's) or catch (kg) of *C. macropomum* in the central Amazon

Response	Predictors	Estimate	SE	*p* value
Age-one$_0$	ML$_0$	1.99E−03	6.21E−04	0.003
Age-two$_0$	ML$_0$	− 3.14E−04	7.12E−04	1.977
Age-three$_0$	ML$_0$	1.49E−03	7.58E−0.4	0.147
Catch$_0$	ML$_0$	− 2.02E−10	4.59E−10	2.013
Catch$_0$	ML$_{-1}$	2.32E−09	1.40E−09	0.391
Catch$_0$	ML$_{-2}$	5.030E−10	8.60E−10	1.719
Catch$_0$	ML$_{-3}$	− 1.17E−09	7.65E−10	0.474

The effect of moving littoral (ML) magnitude on age class abundance was tested using a negative binomial model with the response as 1000 s of fish; on catch it was tested using simple linear models. *p* values are Bonferroni corrected

We assessed if there were flooding phases corresponding to specific diets that account for more of the variation in abundance. We did this by running regression models as above but with the ML magnitude recomputed to correspond to four flooding phases associated with diet-related phases of *C. macropomum*. Using results from our empirical growth function and literature diet data for young-of-the-year, we defined the following four flooding phases based on length-at-age estimates that approximately matched diet-related phases: Early rising, Mid rising, Late rising, and Declining (Table 3).

Finally, we assessed if flooding extent affects catch using regression models that predicted (total) annual catch of all age classes in weight in a given year (e.g., catch$_0$) as a function of ML magnitude in the same and 1, 2, and 3 years before (e.g., ML$_{-1}$). These possible lag effects were determined because recruitment to the fisheries occur through age-classes one, two, and three (Fig. 4). We used the Box-Cox transformation (lambda = − 1) to achieve normality in the catch data and used simple linear regression to assess the effects of flooding. We assessed the assumptions of the linear regression models with respect to normality of residuals (Q–Q Plots), constant variance in residuals and linearity of association between predictors and outcome (plots of Residuals vs Fitted Values), and leverage of certain observations (Residuals vs Leverage plots) using the plot function. We analyzed the data using R (version 1.0.143), and results reported as non-significant used type I error $\alpha = 5\%$.

Results

Growth model

The growth model we obtained from MULTIFAN-CL was consistent with previous information. MULTI-FAN-CL's mean estimate of 22 cm FL for age-one individuals (i.e., the youngest age class detected in the catches) was encompassed by the 19 ± 5 cm FL mean length-at-age interval for 10.5 month-old individuals predicted by field data (Figs. 3c, 5). In addition, MULTIFAN-CL's estimates of length-at-age varied by only − 0.8 and 7.2 cm on average for all 13 age classes, relative to those estimated by Isaac and Ruffino (1996) and Petrere (1983), respectively (Fig. 5). This congruence was expected because the
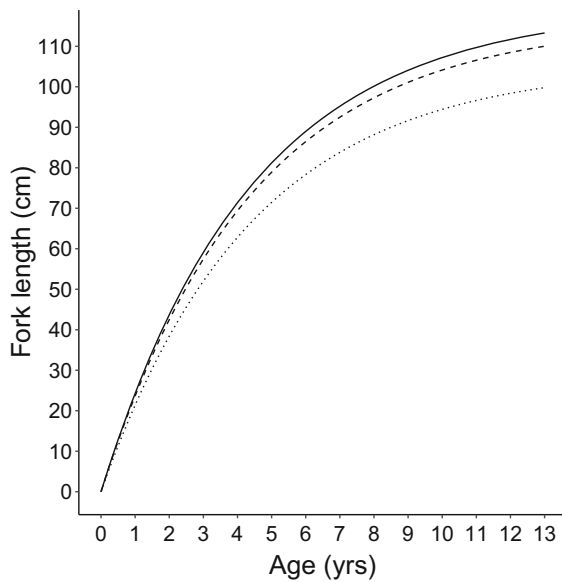
Fig. 5 Growth curves for *C. macropomum* based on the results of MULTIFAN-CL in this study (solid line), Isaac and Ruffino (1996; dashed line), and Petrere (1983; dotted line). Total length estimates from Isaac and Ruffino (1996) and Petrere (1983) were converted to FL based on Binohlan et al. (2011)

priors used in MULTIFAN-CL's growth model were influenced by those two studies (Table 2).

Flooding effects on abundance of ages one, two, and three

Flooding positively affected abundance of the age-one cohort but not of the older age classes. Whereas ML_{-0} was positively related to abundance of age-one at $p = 0.003$, there was no relationship detected with abundance of age classes two or three (Fig. 6; Table 3). The age-one relationship was maintained ($p = 0.001$) even when the highest observation of age-one abundance and ML magnitude (Fig. 6) was excluded from the dataset. The magnitude of the positive effect of ML on age-one abundance of *C. macropomum* increased with increasing ML values (Fig. 6). The relationship predicts that an increase in 500 km^2-days from 2500 to 3000 km^2-days increases age-one abundance by ~ 100 million while a similar increase from 3500 to 4000 km^2-days increases age-one abundance by ~ 750 million. This relationship resulted as ML_{-0} varied by 2.9 times, from 1751 km^2-days in 1992 to 5108 km^2-days in 1994 while age-one abundance varied widely by 15,000 times, from

438,011 individuals in 1999 to as much as 6597,786,164 individuals in 1994 (Fig. 6a). Cook's statistics indicated absence of influential data points ($D_i < 0.6$); a plot of residuals against the predictor showed no patterns; and scores of standardized deviance residuals fell approximately on a straight line.

Flooding phase effects on abundance of age-one individuals

The MLs of the Early and Late rising flooding phases were positively related to abundance of age-one at the end of the same year, whereas no relationship was detected for Mid rising and Declining phases (Table 4). However, MLs of the Early and Mid rising phases were mildly correlated ($r = 0.6$), and the Mid rising and Declining phases were strongly correlated ($r = 0.84$). Therefore, results for each of these two pairs of flooding phases cannot be considered to be independent from each other. The Late rising phase was uncorrelated to any other flooding phase and had the highest significance and greatest effect (see "Discussion" section) on the response, so it is likely the flooding phase most influential of abundance of age-one individuals.

Flooding effects on catch

Although flooding affected abundance of age-one individuals, it did not affect total catch (of all age groups; Fig. 7). In contrast to the enormous interannual variability in age-one abundance, annual catch (comprising individuals from various age classes, but mostly ages two, three, and four) varied by only 18 times. There was no evidence of a relationship between $catch_{-0}$ and ML at 1-, 2-, and 3-year lags (p values > 0.1; Table 4). Residual plots of these models indicated normality and constant variance of residuals and linearity between predictors and response. Leverage plots indicated that one datum (for year 1992) could be influential ($D_i < 1.1$) in models of $catch_{-0}$ vs ML_{-1}, ML_{-2}, and ML_{-3}, but that observation was maintained because there was no independent evidence to question the datum.
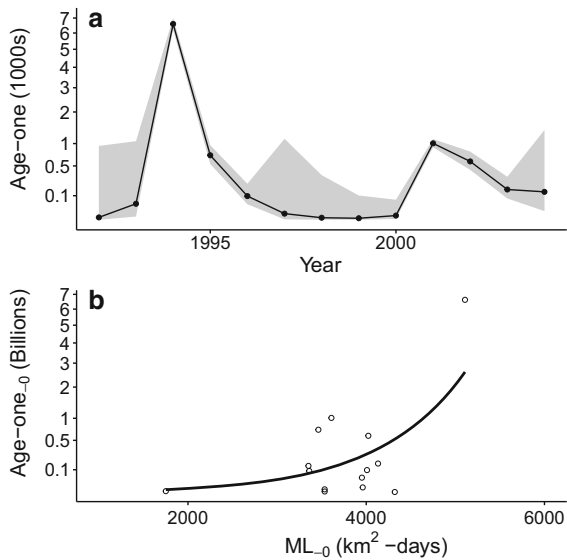
Fig. 6 a Age-one abundance of *C. macropomum* and respective 95% confidence intervals during the study period. **b** Negative binomial general linear model of abundance of age-one *C. macropomum* (at 10.5 months of age) in a given year and the moving littoral magnitude (ML) earlier in the same year. Age-one abundance of *C. macropomum* is shown in squared-root scale in (**a**) and (**b**). Similar regressions testing for relationships for age classes two and three were non-significant (Table 3)

Discussion

Our result showing that the magnitude of the ML zone positively affected the abundance of age-one individuals (Fig. 6) provides empirical evidence that flooding regulates abundance of age-one abundance of *C macropomum*. The moving littoral, as measured by ML, has a strong effect because it quantifies the habitat where food and habitat availability are determined by key interactions between flooding events, nutrient cycling, and biotic production processes. *C. macropomum* spawn during the early stages of the flooding season on the margins of river channels in areas adjacent to the floodplains, causing the larvae to be transported to shallow areas of the floodplain, near floating stands of aquatic macrophytes (Araujo-Lima and Goulding 1997). After consuming the yolk during the first 4 to 5 days, the larvae are about 5.5–6 mm long and begin feeding on zooplankton, mainly cladocera, copepods, and rotifers (Sipaúba-Tavares 1993; Zaniboni Filho 1992). Invertebrates are very abundant in aquatic macrophyte stands during this time (Junk and Robertson 1997), as the advancing ML releases nutrients from the ground that contribute to

Table 4 Tests of four distinct flooding phases on abundance of young *C. macropomum*

| Flooding phase	Mean age range (mo)	Estimated length range (cm)	Diet (%)					Diet studies length range (cm)	Model coefficients	
			Zoo-plankton	Insects	Wild rice	Fruits, seeds	Algae		Estimate (SE)	*p* value
Early rising[a]	1.5–2.7	2.0–6.5	45	20	13	0	0	2.1–4.0	1.58E−2 (5.75E−03)	0.023
Mid rising[a]	2.7–6.0	6.5–13.0	20	4	22	0	54	7.0–10.0	3.00E−03 (1.46E−03)	0.156
Late rising[a]	6.0–7.0	13.0–15.0	50	0	31	15	0	16.0–20.0[b]	4.49E−03 (1.30E−03)	0.002
Declining[a,c]	7.0–10.5[c]	15.0–20.0	60	0	30	4	0	16.0–20.0[b]	1.52E−03 (1.41E−03)	1.120

Diet data summarized from Araujo-Lima and Goulding (1997). Flooding phases were determined based on estimates of mean length (from growth analysis in Fig. 4) for corresponding length ranges observed in diet studies. Diet values measured in percent contribution by weight. For Late rising and Declining flooding phases, maximum date refers to day when water level was the highest. *p* values are Bonferroni corrected

[a]Early rising encompassed the period between Jan 3 and Feb 3; Mid rising (Feb 3–May 15), Late rising (May 15—Max date), and Declining (Max date—Oct 1)

[b]The diet data for Late rising and Declining flooding phases were reported as "high water" and "low water", respectively, and therefore do not correspond exactly to the age-related data such as length range. However, *C. macropomum* are expected to exit higher inundated areas (and the flooded forest) when water levels are declining and catch data show that young-of-the-year fish are caught in increasing numbers in the rivers during that period (Table 1). Also, note that there is a larger gap between their 7–10 and 16–20 cm ranges

[c]Retreating ML only, until the average recruitment date of October 1 when the population size response was estimated

Fig. 7 Scatterplots of (total) catch and the moving littoral magnitude (ML) in the same year (**a**) and one (**b**), two (**c**), and **d** 3 years before. Regressions testing for relationships between catch and ML were non-significant (Table 3)
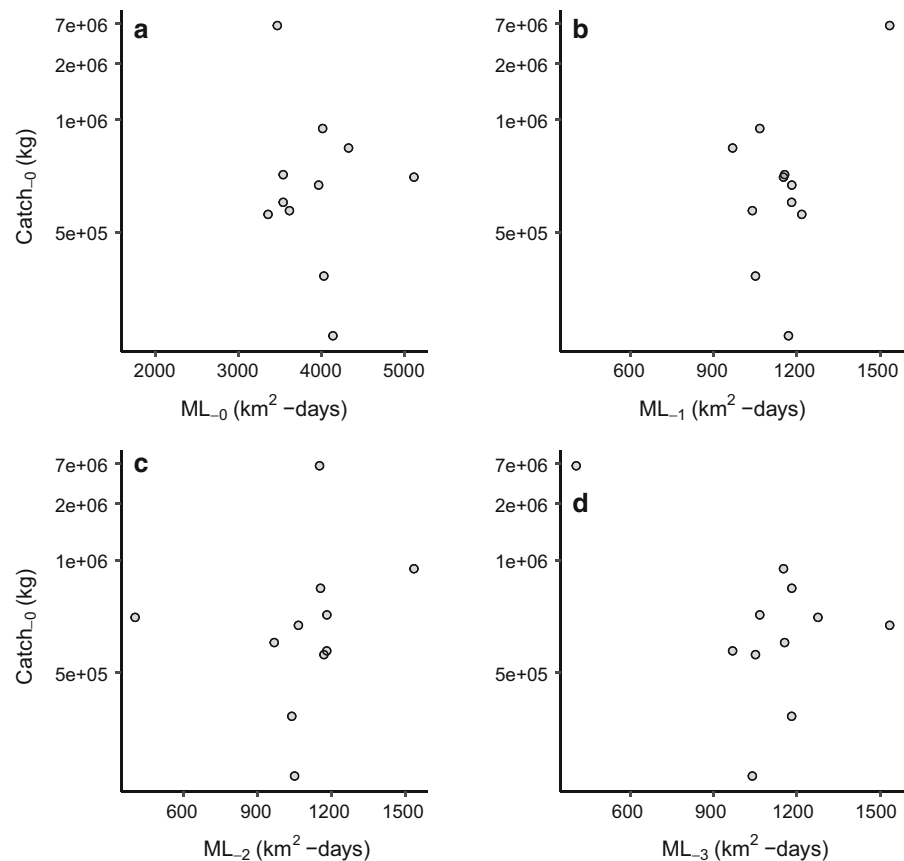
rapid growth of periphyton and aquatic macrophytes; periphyton are consumed by invertebrates, and aquatic macrophytes provide habitat for them (Junk 1973). This is in addition to the expected support of zooplankton resulting from high phytoplankton production (Melack and Fisher 1983) in this zone. As the young grow to 10 cm in length, their diets include filamentous algae, grass seeds (*Oryza* spp.), and insects, which they too find in the floating stands of aquatic macrophytes (Araujo-Lima and Goulding 1997). As the young grow, their diet becomes increasingly dependent on zooplankton while also including wild rice seeds, fruits, and other seeds (Araujo-Lima and Goulding 1997). The annual availability of this food-rich nursery habitat likely promotes feeding activity and increases in body size, as observed for *Colisa fasciatus* and *Channa punctata* in floodplains of Bangladesh (de Graaf 2003a, b), thereby lowering rates of natural mortality by starvation and predation.

The nonlinear effect of ML on age-one abundance of *C. macropomum* (Fig. 6) is consistent with the Late rising phase having a more significant effect than the Early rising phase of the flooding period. The Late rising phase differs from other phases in having zooplankton, wild rice (*Oryza* spp.) seeds, and fruits and other seeds comprise the bulk of the diet of *C. macropomum*, although that diet composition is not too different from that in the Declining phase (see below). Zooplankton is available and consumed year-round by *C. macropomum* (Carvalho 1981). However, wild rice seeds, fruits, and other plant seeds, which stem from C3 plants, have relatively high energy content (Oliveira et al. 2006) and tend to be found in higher elevation areas of the floodplain (Junk 1983). Whereas fruits and other seeds are available through most of the period when the floodplains are flooded (Araujo-Lima and Goulding 1997), wild rice seeds are mainly available from February to June (Rubim 1993).

These seasonal and spatial patterns of distribution of wild rice seeds, fruits, and other plant seeds may explain why the Late rising phase has a strong effect on age-one abundance of *C. macropomum*. In a companion paper (Bayley et al. 2018), we found a positive and non-linear effect of the magnitude of ML over the age-two abundance of the detritivore *Prochilodus nigricans*. We suggested the non-linearity of that ML effect was due to stands of C3 plants such as wild rice, which also underpin carbon sources for *P. nigricans*, being more common in higher elevation areas of the floodplains (Junk 1983). However, food quality and distribution may not be the only explanatory factors, as the Declining phase of the ML was unrelated to age-one abundance of *C. macropomum*, even though their diet during this phase was also dominated by wild rice seeds, fruits, and other plant seeds. This difference in ML effect may be because, although food for young *C. macropomum* may be present during the Declining phase, it may be unavailable for *C. macropomum* as decomposition processes during this phase increase relative to production, often decreasing dissolved oxygen levels (Bayley 1995).

Interannual variability in age-one abundance, however, did not seem to directly affect annual catches of *C. macropomum*. As expected from theoretical predictions that long-lived populations are generally less susceptible to environmental stochasticity (Winemiller 2005), possible flooding effects on catches of *C. macropomum* appear to have been dampened by the presence of as many as nine age classes in the catch. This dampening effect can be shown quantitatively: whereas the coefficient of variation of annual estimates of age-one abundance was 257%, that of annual *C. macropomum* catch was only 150%. We note, however, that a failure to find a relationship between the ML magnitude and total catch (of all age groups) of *C. macropomum* (Fig. 7) does not mean there is not an intrinsic relationship between the two. Increased age-one abundance in a given year has to affect abundance of age-two, age-three and older age classes in subsequent years, even if natural mortality variation affects total mortality in addition to the dominant fishing mortality predicted by known fishing effort. Analyses such as ours, done using a frequentist approach based on a restricted number of observations, are often affected by sample size (Stang et al. 2010). In line with expectations from this study, an analysis based on the information-theoretic approach of 12 years of data on the combined catch of two omnivorous fishes, including *C. macropomum* (which contributed with about 40% of the total weight), found they were influenced by the magnitude of floods and droughts 2 and 3 years before (Castello et al. 2015).

Management implications

The only two stock assessments done for *C. macropomum*, which found it to suffer growth overfishing (Isaac and Ruffino 1996; Petrere 1983), are from the 70s and 90s. More recent data on *C. macropomum* populations suggest further overfishing (Campos et al. 2015; Castello et al. 2011). Despite the presence of minimum size (55 cm FL) and closed season (Dec.– Feb.) limits, poor enforcement has led to widespread noncompliance and prevalence of undersized *C. macropomum* individuals in the markets (e.g., Castello et al. 2011; Cavole et al. 2015). Therefore, although the data used in this study are from 1993 to 2006, the implications of the ML effect on age-one abundance with respect to the management of *C. macropomum* fisheries deserve consideration. One output from the MULTIFAN-CL program is spawning biomass, which we assessed in relation to age-one abundance to investigate the presence of a stock-recruitment relationship. A plot of the two variables showed they were unrelated. This and the two stock analyses (Isaac and Ruffino 1996; Petrere 1983) support the interpretation that this highly fecund species suffers from growth overfishing. But that leaves open the question of how low can the spawning biomass go before a collapse. The importance of the quality and magnitude of the moving littoral on recruitment has been shown here, illustrating the need to avoid disturbances to the hydrological regime while addressing direct effects of fishing mortality on adults and juveniles.

To increase the spawning biomass of *C. macropomum* to a safer level, an obvious need is fostering compliance with catch limits of size and season, which can prevent stock collapse even at high levels of fishing mortality (Myers and Mertz 1998). Such a strategy could be combined with reductions of fishing mortality 2 or 3 years following years when the ML magnitude is smaller-than-normal. Fishing mortality could be controlled via the implementation of harvest quotas, shortening of the harvest season, or even

banning commercial harvests in certain tributaries. The latter options are probably more viable options for IBAMA, the regional management agency, which has minimal human and monetary resources to do its job in a vast area. The challenge is that enforcement of such regulations is costly, and recovery of such costs via increased future yields takes time.

Ensuring that *C. macropomum* become vulnerable to fishing gear only after having spawned once, and reducing catches subsequent to low recruitment years, will be increasingly necessary in the future to buffer the effects of escalating hydrological alterations arising from construction of dams and changes in land cover and global climate (Castello and Macedo 2016). Such hydrological alterations are expected to significantly lower the magnitude of river flooding in the Amazon Basin (Costa 2005). Our results indicate that reduced flooding would lower recruitment rates of *C. macropomum* and potentially other fishes whose recruitment is regulated by flooding. Regional management agencies can now consider the dependency of fish populations on river flooding when they make fisheries and environmental decisions.

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