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RESEARCH PAPER

Modeling population dynamics and conservation of arapaima in the Amazon

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Abstract To promote understanding of fish population dynamics in tropical river-floodplains, we have synthesized existing information by developing a largely empirical population model for arapaima (*Arapaima* sp.). Arapaima are characterized by very large bodies, relatively late sexual maturity, small clutches, and large parental investment per offspring, and their populations are overexploited and even declining due to overfishing. We used unparalleled time series data on growth, reproduction, catch-at-age, and size-class abundance estimates for a population that has increased several-fold and undergone drastic changes in fishing practices in the Amazon, Brazil. Model population numbers were close to observed numbers, with generally low mean absolute percentage errors for juveniles (16%), adults (30%), and catch (18%). In using the model to test ecological hypotheses and to investigate management strategies, we found the following: (1) Annual recruitment is directly and positively related to spawner abundance, and it appears to be density-compensatory following a Beverton–Holt relation ($R^2 = 0.85$). (2) Fishing-selectivity of arapaima caused by use of harpoons and gillnets can lower yield potentials dramatically through removal of the faster-growing individuals of the population. That is in part because fewer individuals live long enough to reproduce and survivors take longer to reach reproductive age. (3) Arapaima populations can sustain annual catches of up to 25% of the number of adults in the population the previous year if minimum size (1.5 m) and closed season (December–May) limits are met. (4) When 25% of the number of adults in the population the previous year is harvested under a 1.6 m minimum size limit of catch, catches are slightly smaller but abundance of adults in the population is considerably greater than under a 1.5 m limit. These findings can be used in ongoing management initiatives, but caution is needed because of present biological and ecological uncertainty about these fishes.

Keywords Brazil · Fishing selectivity · Floodplain · Life-history · Management · Recruitment

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Introduction

Fisheries in tropical river-floodplains are an important natural resource use activity. But they are under increasing exploitation pressure, and most of them are being degraded rapidly, threatening biodiversity and human food security (Allan et al. 2005). Much-needed policy action has been hampered so far, in part because of lack of fisheries data and poor understanding of the dynamics of floodplain fish populations (Bayley 1988; Bayley and Petrere 1989; Halls et al. 2001). We can improve our understanding of these fisheries by focusing scarce scientific efforts on fish resources with distinct life-history strategies.

Most of the existing understanding on tropical fish population dynamics in river-floodplains stems from fishes in the "opportunistic" and "equilibrium" life-history strategies of Winemiller and Rose (1992). The first comprehensive study of floodplain fish populations, by Welcomme and Hagborg (1977), was based on a composite of various tilapia species in Africa, and apparently with emphasis on species of the mouth-brooding genus *Oreochromis* Günther, which would fit within the typical "equilibrium" life-history strategy of Winemiller and Rose (1992). "Equillibrium" fishes are more like the traditional K-strategists, characterized by large eggs and parental care resulting in the production of relatively small clutches of relatively large-bodied juveniles. More recently, a study was done by Halls et al. (2001) on population dynamics of the pool barb, *Puntius sophore* (Hamilton) from floodplains in Bangladesh, a fish that probably fits in the "opportunistic" strategy of Winemiller and Rose (1992). "Opportunistic" fishes tend to have large intrinsic rate of population increase due to early sexual maturity, frequent reproduction, small eggs, and rapid larval growth.

These studies have shown the major distinction of floodplain fish population dynamics, which is the influence of flooding cycles. High water levels tend to promote their body growth and reproduction as the flooded plains typically offer abundance of food and low predator density (Agostinho et al. 2004; Dudley 1974; Gomes and Agostinho 1997; Nikolsky 1956; Welcomme 1979). Low water levels, on the other hand, tend to promote their mortality through deterioration of environmental conditions (e.g., anoxia) and increased vulnerability to fishing activity (e.g., by stranding in pools; Brinkmann and Santos 1973; Halls et al. 2000; Junk 1985).

Here, we studied the population dynamics of a floodplain fish that has characteristics mainly of "equilibrium" fishes but also shares similarities with fishes in the "periodic" strategy of Winemiller and Rose (1992). "Periodic" fishes delay maturation in order to attain a size sufficient for production of a large clutch and to allow adult survival during periods of suboptimal environmental conditions (e.g., winters, dry seasons, reduced food availability).

Arapaima (*Arapaima* sp.) are among the fishes of greatest conservation concern (Allan et al. 2005). *Arapaima gigas* (Shinz) was enlisted in the IUCN Red List as "vulnerable" in 1986, but due to lack of data it now is listed as "data deficient" (World Conservation Monitoring Centre 1996). That species is listed in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (Castello and Stewart 2010). Others have considered the arapaima present in our study area to be *A. gigas*, but recent data suggest that it may be an undescribed species (DJ Stewart unpublished data).

Arapaima have constituted historically important food fisheries in the Amazon Basin (Veríssimo 1895), and they likely play key ecosystem roles because they are top predators (Queiroz 2000). Government policies of minimum size of catch (1.5 m total length, TL) and closed season (December–May), and even total moratoria in three states in Brazil, have been established, but they have been poorly enforced (Castello et al. 2009; Castello and Stewart 2010). With most of the catch being in violation of management policies, fishing of arapaima, which is done through harpooning and gillnetting, is now believed to have led wild populations to become overexploited and even declining throughout much of the basin (see review in Castello and Stewart 2010). Most populations in the wild now are limited to local community-based management areas (Castello et al. 2011).

Population recoveries of arapaima have occurred in a management scheme developed recently based on annual population counts done at the moment of the species' aerial breathing. The counts include two size classes: Juvenile (with capital 'j', 1–1.5 m TL) and Adult (with capital 'a', >1.5 m TL), and they can be very accurate, varying by about 20% around the true value (Arantes et al. 2007; Castello 2004). In the management scheme, annual population counts done by local fishers in 1 year (before they harvest) are used to determine catch quotas for the following year. The potential effectiveness of this management scheme is evident in Jarauá, an area within the Mamirauá Reserve (Amazonas State, Brazil), where the arapaima population was overexploited and under risk of collapse (Queiroz and Sardinha 1999).

1. Compliance with the minimum size policy has increased mean TL of the captured arapaima by 53 cm, from 108 cm before the management scheme (1993–1998), to 161 cm after the management scheme was implemented (Fig. 1a).
2. The combined population of Juveniles and Adults of arapaima, and associated catch quotas, have increased several-fold (Fig. 1b; Castello et al. 2009; Viana et al. 2004, 2007).

These results in Jarauá have been largely responsible for the following wider implications.

3. Fishing of arapaima became permitted in the Brazilian States of Amazonas and Acre (in 2004 and 2008, respectively, encompassing ~26% of the Amazon basin) only to fishers that present population counts and follow catch quotas.
4. The number of communities using the management scheme in the State of Amazonas alone increased from four in 1999 to more than 100 now, making it the fastest expanding participatory fisheries conservation approach in the basin (Castello et al. 2009, 2011).

One of the main contributions of this management scheme to resource conservation is creating the conditions for fishers to actively participate in the management process, something that tends to improve compliance with management policies, although poor enforcement of management policies by government authorities remains a problem (see Castello et al. 2009, 2011). Another key contribution of the management scheme is allowing restrictions of annual harvests according to population size. However, catch quotas in that management scheme have been determined by trial-and-error, because of lack of understanding about the population dynamics of arapaima. There is only one estimate of sustainable arapaima fishing (0.3 kg ha^{-1} year^{-1}; Sánchez 1969) and some information on their biology and ecology.

The arapaima in Jarauá have been found to migrate among all floodplain habitats every year (Castello 2008a, b). They inhabit lakes, rivers and connecting channels during low water levels, at which time the adults form pairs and subsequently reproduce (Queiroz 2000). The adults build their nests in the margins of water bodies during rising water levels, and there are reports that they exhibit territorial behavior (Fontanele 1948). Nest building, hatching of the young, and parental care all take about 3 months (Fontanele 1948; Isaac et al. 1993), and in Jarauá there is a one-to-one sex ratio (Queiroz and Sardinha 1999). As water levels decline, they migrate back to connecting channels and lakes, where they are generally fished.

Body growth of arapaima in Jarauá has been found not to follow density-compensatory theory (e.g., Rose et al. 2001), which is not unusual in Amazonian river-floodplains (Bayley 1988). Arapaima in Jarauá grow to 70–90 cm TL in 1 year, and mature at about 160 cm in 3–5 years (Arantes et al. 2010). But they were found to grow faster (by an average of 27 cm in median length-at-age) in the high population densities now observed in Jarauá than in the low population densities of the un-managed situation (Fig. 1a, b, Table 1; Arantes et al. 2010). Because age-at-first-reproduction depends mainly on body biomass, as it was shown by a meta analysis of 235 fish populations (He and Stewart 2001), the average female arapaima matured at age 3 in high population densities, and at age 5 in low population densities (Arantes et al. 2010). Arantes et al. suggested that those growth patterns could reflect size-selectivity effects during the low population density (un-managed) situation, when fishers targeted the young individuals, in violation of the minimum size limit (compare size structures in Fig. 1a).

We used the above data and information on arapaima to develop a population model to explore the effects of fishing strategies. In doing this, we tested four hypotheses: (1) population recruitment is not density-dependent; (2) compliance with minimum size limit has no effect on yield potential; (3) current catch rates cannot be increased without causing adverse population effects in the long-term; and (4) a minimum size limit of catch of 1.6 m TL has no

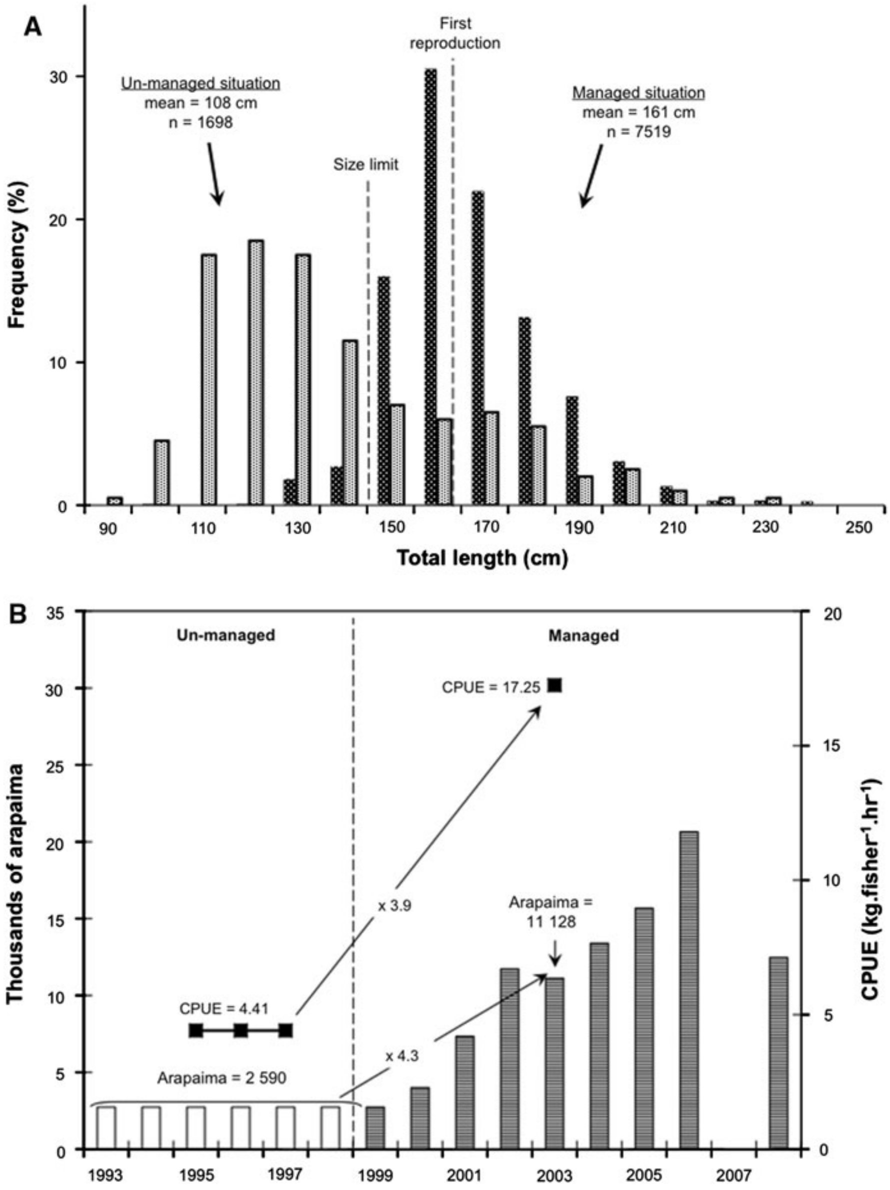

Fig. 1 **a** Size structure of the catch of arapaima in Jarauá (an area of the Mamirauá Sustainable Development Reserve) for the periods before and after the management scheme was implemented, 1993–1998 and 1999–2008. Data provided by the Mamirauá Institute were divided into 10-cm total length intervals. Note that not all arapaima below the minimum size limit of catch (1.5 m) necessarily are illegal as the law allows up to 10% of the catch to be below that limit. **b** Time-series data on counts of arapaima (> 1 m TL) in Jarauá. Abundance data shown for 1993–1998 are estimated based on the assumption that they are identical to that for 1999 (see Section “Data sources and interpretations”)

effect on yield potential compared to the current 1.5 m TL policy.

Methods

Study area and modeling approach

The study area is the Jarauá sector (562 km^2 of floodplain area) of the Mamirauá Sustainable Development Reserve with about 85 lakes and many connecting channels (about 2°50′S and 64°59′W). The reserve was created to protect biodiversity via sustainable and participatory natural resource use. Jarauá is formed by relatively pristine ‘várzea’ of the Amazon, which are floodplains formed by a complex mosaic of forests, lakes, and channels. Annual water-levels vary by about 13 m, flooding the entire area during high water, and leaving it mostly dry during low water (Junk 1997).

The population model developed is age-based, with age 5–6 assumed to be maximum age class. Removals from the population in each time step are

Table 1 Median total length-at-age of the arapaima population in Jarauá for the un-managed (1993–1998, low density) and managed (2005–2006, high density) situations

Age	Un-managed situation				Managed situation			
	Median length (cm)	Count class	*H*	*A*	Median length (cm)	Count class	*H*	*A*
1	67.3		0.00	0	88.3		0.00	0
2	96.8	Juvenile	0.27	0	123.6	Juvenile	0.06	0
3	119.6	Juvenile	0.51	0	154.4	Adult	0.52	0.29
4	144.4	Juvenile	0.14	0.19	174.9	Adult	0.29	0.85
5	166.3	Adult	0.04	0.64	188.9	Adult	0.13	0.91
6	172.7	Adult	0.04	0.86				

The count classes equivalent to the age classes, and age-specific proportion of arapaima harvested (*H*, see Eq. 1), and age-specific proportion of Adult arapaima ready to spawn (*A*, Eq. 3), also are shown

based first on fishing mortality, after which natural mortality is applied. Reproduction is then assumed to occur, with resulting recruitment occurring at age 2. The model runs on annual time steps with discrete difference equations implemented in a Microsoft Office Excel® spreadsheet. It is a deterministic model in which an initial set of parameters are established for the first year of the run and kept constant throughout a given run, producing only two results for each modeling run: annual population numbers and catch. As the model makes an annual time step, five features change dynamically (Fig. 2):

1. total abundance, because of the net effects of recruitment and mortality processes;
2. abundance in each age class, and hence proportional distribution of numbers among ages;
3. abundance of spawners in each sexually mature age class, and thus total number of spawners;
4. number of recruits for the time step, as a result of change in number of spawners 2 years previously;
5. catch quota (in numbers), because it is a proportion of Adult abundance the previous year (except in modeling of the un-managed situation, where catch quotas are a fixed total number, see Section "Model description"); however, proportional age structure of the catch remains constant.

The model is run for two periods, one before and one after 1999. That year represents an intermediate situation, as it was the first year under the new management scheme but the population still was low due to overexploitation in previous years (Fig. 1b; see Section "Data sources and interpretations"). The period between 1993 and 1998 represents the un-managed situation, when the fishery was overexploited (Queiroz and Sardinha 1999) and influenced by lack of compliance with minimum size policies (Fig. 1a, b). The period between 1999 and 2008 represents the managed

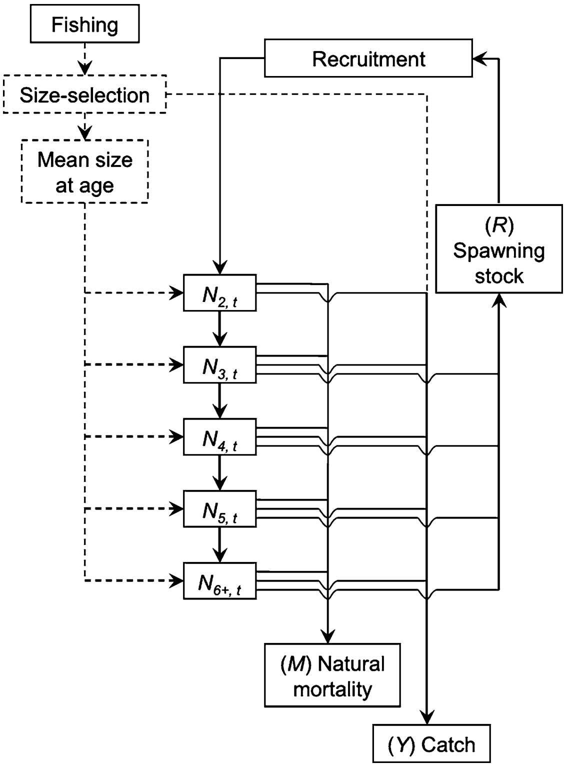

Fig. 2 Diagram of the age-specific population model of arapaima developed and applied herein for the Jarauá. *Solid lines* indicate 'flows' of individual fish; *dotted lines* indicate controlling factors. As explained in the text, recruitment occurs at age 2, and age 1 is integrated into the stock-recruitment relation

situation when local fishers complied with size, season, and quota policies (Fig. 1a), and the population recovered from overexploitation (Fig. 1b). Each of these two modeling periods is based on notably distinct model inputs, although all but one of the model equations are identical.

The model is based on five major assumptions, all based on best-available information.

1. Natural mortality rates are density- and age-independent (excluding age-0, which is pre-recruitment and not explicitly modeled). Although there are published age-specific estimates of *M* for arapaima (=0.26–0.31, Queiroz and Sardinha 1999), they are likely to be biased given they are based on fished populations (Pauly 1980), with Juveniles being heavily exploited. They also were markedly different from estimates of *M* between age classes within the same year in the last few years in Jarauá, when it was closer to unfished conditions for individuals under 1.5 m.
2. Growth and age-at-first-reproduction are density-independent, as observed by Arantes et al. (2010) at least for the range of densities observed to date.
3. Male arapaima mature sexually at the same age as females. Maturity of females from Jarauá has been quantified (Arantes et al. 2010), but not males. If males are actually maturing earlier than females (e.g., Godinho et al. 2005; Tocantins basin population), then our model as configured with a Beverton–Holt stock-recruitment function will generate conservative predictions of recruitment rate. That is because more fishes would reach maturity than what we presently are estimating.
4. Annual recruitment is independent of inter-annual variation in water levels. Several hydrological indices have been correlated to recruitment and mortality of several other floodplain fish populations (Welcomme 1979). But an analysis of annual recruitment of arapaima in Jarauá and several indices of the flood cycle of the várzea floodplain found no relation (Castello 2007), perhaps because of the short time series of data available and/or the intense parental care done by male arapaima (e.g., Agostinho et al. 2004).
5. Net migration in and out of the area is negligible, so the population is closed or nearly so. The home range of arapaima is small, involving annual migrations of about 10 km (Queiroz 2000; Castello 2008a), and the population in Jarauá has increased dramatically while adjacent populations have remained stable at relatively low levels (see Castello et al. 2009).

Data sources and interpretations

Abundance data stem from counts of Juvenile and Adult arapaima in Jarauá. Previous detailed descriptions of the procedures used in censusing arapaima populations have shown that the count data for arapaima in Jarauá are relatively reliable (Castello 2004; Castello et al. 2009, 2011). Count data were collected by local fishers who had their counts validated by concurrent total seine catches or mark-recapture estimates of abundance (Arantes et al. 2006, 2007; Castello 2004). Also, the Mamirauá Institute monitors the accuracy of the counts through the use of field observers and crosschecks of counts in certain lakes. However, count data for 2004 were underestimated, because unusually high water levels during the low-water period allowed the arapaima to be dispersed in the floodplain rather than concentrated in lakes as in most years. We corrected the 2004 data by interpolating data for 2003 and 2005. Count data for 2007 were disregarded because of suspicion about data accuracy (i.e., exaggerated counts).

Population abundance for the years during the un-managed situation (1993–1998) was estimated using count data for 1999, which was assumed to represent the mean population abundance for that period. This is reasonable, as the 1999 count data represents the typical population of the un-managed situation before the new management regulations took effect (e.g., counts done before fishing). Also, there is close agreement between population counts and catch per unit effort (CPUE) data available for both the un-managed and managed situations (Fig. 1b). Mean CPUE of arapaima in Jarauá increased 3.9-fold from 1995–1997 to 2003, and counts of arapaima increased 4.3-fold from 1999 to 2003 (Castello et al. 2009).

Observed catch-at-length (±5 cm) data during the managed situation stem from relatively accurate recording of the harvested fishes at a single check point location, Jarauá community. However, recorded catch data during the un-managed situation were biased due to under-reporting of the catch, which back then was mostly illegal. To account for under-reporting of the catch during the un-managed situation, data for that situation were corrected by a factor of 2.5 for all age classes. This correction factor is based on estimates of underreporting of the catch provided by the Jarauá fishers based on recollections of their own fishing activities during the un-managed situation (Viana et al. 2004).

Estimates of catch-at-age and abundance-at-age were obtained using growth data. We used the median length-at-age data of Arantes et al. (2010, Table 1) to derive intervals of length-at-age by assuming that the mean between two consecutive medians of length-at-age (Table 1) were the limits between age classes. Based on data of growth of the studied population, this procedure determined five age classes for the managed situation, and six age classes for the un-managed situation. Two previous studies in Jarauá found that arapaima older than 5- or 6-years old are rare (Table 1), so they are not included in the model (Arantes et al. 2010; Queiroz 2000). The inclusion of age 6 in the modeling of the un-managed situation reflects their greater proportional representation in the population compared to the managed situation, and that is in part an artifact of young age classes being depleted by heavy fishing in the un-managed situation. That also may reflect the difficulty of catching large arapaima with gillnets designed to catch smaller, under-sized, individuals. However, in terms of absolute numbers, age six fishes are more abundant in the managed than in the un-managed situation.

The length-at-age intervals were used to convert count data of Juveniles and Adults into abundance-at-age data by fitting an assumed decline with age class (Table 2). We estimated abundance-at-age using negative exponential equations that accurately predicted (±1%) numbers of individuals in the age classes included in each of the two count size-classes (Table 1). For example, size-class count data for 1999 indicated there were a total of 2,590 individuals, 2,000 Juveniles and 590 Adults (Table 2). The Juvenile size-class comprises age 2, and Adult size-class comprises ages 3–5 (Table 1). Fitting a negative exponentially declining abundance-at-age for all age-classes yielded an estimate of 2,031 individuals age-2 for the Juvenile size-class, and 439 age-3, 103 age-4, and 23 age-5 for the Adult size-classes (Table 2).

Model description

Field and published data were incorporated in the model as follows.

Growth

In the model, every year the individuals of a given age-class (e.g., $N_{2,1}$) that survive to the following year have their body length increased to that of the next older age-class (e.g., $N_{3,2}$, Fig. 2). This procedure used data of the management situation in question (Table 1).

Natural mortality

In the model, every year, the number of arapaima surviving to the next year is reduced by a constant rate of natural mortality (M, Fig. 2). $M = 0.45$ was obtained using Cubillos (2003) theoretical approach based on one parameter of the Von Bertalanffy growth model ($K = 0.25$, Arantes et al. 2010). $M = 0.45$ is close to values calculated using Pauly's (1980) approach ($M = 0.4$), which is based on water temperature and parameters of the Von Bertalanffy growth model (temperature = 27.5°C, $K = 0.25$, and $L_\infty = 244$ cm; Arantes et al. 2010).

Fishing mortality

In the model, every year, the number of arapaima is reduced due to fishing, following the rationale of the management scheme during the managed situation. Modeling of annual harvests of arapaima depends on: (1) a catch quota Q, which is the number of individuals to be harvested in a given year, and which is based on a proportion, i.e., catch rate (C), of the Adult abundance (ages 3–5) in the previous year; and (2) the age structure of the catch, which determines catch-per-age. For the managed situation, C was estimated using a simple linear regression between Adult abundance in 1 year and the Q in the following year (where the intercept is zero). The

Table 2 Estimates of age-specific abundance and catch for the population

Data type	Age/size class	Jarauá										
		1993–1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008
Abundance	1											
	2	1,104	2,031	3,041	5,822	7,570	7,171	8,689	8,460	11,983		7,604
	3	669	439	750	1,187	2,771	2,638	3,165	4,159	5,283		3,091
	4	406	103	185	242	1,014	970	1,153	2,045	2,329		1,257
	5	246	23	46	49	371	357	420	1,005	1,027		511
	6	149										
	Adults		590	950	1,441	4,120	4,091	4,998	7,111	8,596		4,878
	Juveniles		2,000	3,050	5,901	7,611	7,037	8,402	8,564	12,054		7,593
	Total		2,590	4,000	7,342	11,731	11,128	13,401	15,675	20,650		12,471
Catch	1	0	0	0	0	5	0	0	0	0		0
	2	409	48	11	0	32	4	53	213	1		0
	3	764	132	228	242	326	500	608	487	566		605
	4	209	45	36	99	136	291	234	304	652		757
	5	64	31	8	35	79	74	63	201	306		332
	6	59										
	Total	1,505	120	120	200	500	879	2,500	1,250	1,500		1,694

Catch and count data were observed, and values shown have been corrected for under-reporting or biases as noted in the text. Abundance-at-age data for all years were estimated based on the count data. The number of age classes included in the abundance and catch data depends on growth data of the management regime in question (managed or un-managed, Table 1). Abundance-at-age data for 1993–1998 were estimated using count data for 1999 and length-at-age data for the un-managed situation from Table 1 (see text)

value of C was estimated to be 0.228 ($R^2 = 0.89$, $p < 0.05$), indicating that Jarauá fishers have had catch quotas of about 23% of the Adult abundance the previous year. However, because the catch in Jarauá was unregulated during the un-managed situation, the catch rate during the un-managed situation was assumed to be constant throughout that period and equal to the mean annual catch estimate reported for that period (i.e., 1,505 fishes, Table 2). Thus for any given year, Q was modeled as:

$$\begin{aligned} Q_t &= C \sum_{i=3}^{5} N_{i,t-1} \text{ if managed;} \\ &= 1505 \text{ if un-managed} \end{aligned} \quad (1)$$

where N is the number of individuals of each age class in the population; i the age class; and t is the time, year.

In the context of initializing the modeling simulation for the managed situation, the value of Q for 1999 was set to 120 fishes, the empirically observed harvest in that year. An empirically observed value of 1,505 (Table 2) was used to initialize the simulation for the un-managed situation.

The age structure of the catch (Y) was determined by calculating mean frequency distributions of catch-at-age, one for the managed and another for the un-managed situation, using the observed catch-at-age data shown in Table 2 and Fig. 1a. Thus, in the model, compliance (or lack of compliance) with the minimum size limit changes the structure of the catch when modeling managed and un-managed situations.

$$Y_{i,t} = Q_t H_i \quad (2)$$

where Y is the catch per age class (in numbers of individuals); H is the proportion of fish harvested per age class (Table 1).

Recruitment

In the model, every year the number of individuals that survive fishing activity and natural mortality and that are ready to spawn is used to compute the number of recruits that will be added to the population 2 years later. Modeling recruitment for arapaima required developing an alternative approach to conventional matrix population models (e.g., Caswell

2001), because existing data on early life stages (e.g., Fontanele 1948; Lowe-McConnell 1964; Lüling 1964) are unclear for use in such models. To model recruitment, we first derived a stock-recruitment function based on empirical data, and then used it in the model to predict number of recruits. We derived a stock-recruitment function based only on data for the managed situation by relating observed numbers of annual recruitment with observed numbers of spawner stock 2 years earlier. We defined recruits as arapaima >1 m TL, at which length they are included in the counts of Juveniles and are about 2 years old (Table 1). Observed numbers of recruits were assumed to be equal to our estimates of abundance-at-age 2 given in Table 2. Observed numbers of spawners (R_t) were obtained by multiplying our annual estimates of abundance-at-age given in Table 2 by age-specific estimates of proportion of sexually mature fishes given in Table 1 (from Arantes et al. 2010):

$$R_t = \sum_{i=2}^{f} [N_t A_i] \tag{3}$$

where f is the final age class and A_i are the proportions of Adults by age that are ready for spawning, assuming maturity of males is similar to that of females.

To test the hypothesis that population recruitment is not density-dependent, we followed the approach of Needle (2002) of first determining the shape of the curve based on biological knowledge and then using linear or non-linear regression to estimate model parameters (Statistica, Statsoft®). There are various stock-recruitment models, but many of those have several variables and require much longer data sets than that available for this arapaima population. We used non-linear regression methods to assess the fit of the Beverton–Holt model (Eq. 4, from Needle 2002), which applies to situations where recruitment is limited by lack of habitat in territorial organisms (Beverton and Holt 1957). The resulting Beverton–Holt model, fitted to the data in Table 2, was used in our modeling to predict $N_{2,t}$

$$N_{2,t} = \frac{\alpha R_{t-2}}{R_{t-2} + k} \tag{4}$$

where α, k are the parameters (empirical constants) of the Beverton–Holt model.

In the context of initializing the modeling of the managed situation, N_2 was set to the empirically observed value (for 1999, Table 2) of 2,031 for both 1999 and 2000; subsequent years used Eq. 4. To model recruitment during the un-managed situation, we used the best-fit model of the managed situation (Eq. 4), with estimates of body growth and spawner abundance for the un-managed situation; N_2 in the first 2 years was set to 1,104 (Table 2). Finally, the abundance-at-age of arapaima 3 years old and older in any given year depends on the abundance of the previous age class and year, on age-specific catch rate, and on annual rate of natural mortality (M):

$$N_{i,t} = \left[\left(N_{i-1,t-1} - Y_{i-1,t-1}\right) * (1 - M)\right] \tag{5}$$

Fishing selectivity hypothesis

Because the 27 cm difference in median length-at-age of arapaima in the managed and un-managed situations (Table 1) contradicts ecological theory, we investigated if that difference could be due to selectivity associated with fishing of under-sized arapaima (<1.5 m TL; Fig. 1a). Fishing selectivity of the faster-growing individuals of younger age-classes during the un-managed situation potentially could lower the length-at-age estimates compared to those observed during the managed situation (Fig. 1b). This is reasonable, because gillnetting naturally selects the faster-growing individuals, and harpooning is very selective given that fishers benefit from catching the larger individuals (Castello 2004).

To test the hypothesis that compliance with minimum size limit has no effect on yield potential, we modeled the body growth of arapaima under situations with and without fishing, each representing the managed and un-managed situations, respectively. First, we initiated our modeling with a cohort of 1-year-old arapaima using a normal frequency distribution with 20 length intervals and with mean following the data in Table 1. Then, we modeled the growth of this cohort in the following years. We applied the annual rate of natural mortality and added the difference in length between ages 1 and 2, 2 and 3, etc. (Table 1) to the length of the individuals of each of the 20 length intervals of the cohort. Finally, we modeled the effects of size-selection on apparent body growth by applying size-dependent rates of mortality to the 20 length intervals of each cohort.

Size selection of gillnets tends to follow a normal distribution (Jennings and Kaiser 1998), and harpooning by experienced fishers selects the larger individuals (Queiroz and Sardinha 1999). We attempted to model size-dependent fishing mortality of arapaima using both linear and logistic equations across the 20 length intervals of each cohort, in both cases with greater mortality rates in the larger length intervals. But only the logistic model provided a close approximation to observed values; for that relation, proportion caught (P_j) from each length interval was modeled as follows:

$$P_j = \frac{e^{c+dj}}{1 + e^{c+dj}} \tag{6}$$

where j is the length interval; e the base of natural logarithm; and c, d are the empirical constants.

We manually adjusted the parameters of the logistic model until the modeled mean length of each age class was close to the observed length-at-age data for the un-managed situation (Table 1). And we assessed the accuracy of these model estimates using a Mann–Whitney U-test calculated based on predicted and observed values of mean length-at-age with and without size-selective fishing for all age classes.

Model assessment

To assess the accuracy of the model, we calculated mean absolute percentage errors using observed numbers of Juvenile, Adult, and catch of arapaima for the managed situation and respective modeled numbers. Mean absolute percentage error is a measure of the accuracy, in this case, of modeled numbers of Juveniles and Adults relative to observed data; it is expressed as a percentage, allowing for ease of interpretation (Mayer and Butler 1993). Based on criteria normally used in stock assessments, a mean absolute percentage error of up to about 30% is reasonable. The model was initialized using the estimates of abundance-at-age for 1999 (Table 2), and run until 2008 using $C = 0.228$ (Eq. 2). However, even though the model is run for the two situations, the modeling of the un-managed situation was not assessed quantitatively, because of the lack of monitoring data characteristic of such situations (i.e., under-reported illegal fishing).

Sensitivity analysis

An individual parameter perturbation analysis of sensitivity was done to evaluate the relative importance of input parameters for Adult abundance output. We assessed the sensitivity of the model's output to changes of ±10% in the values of the parameters for: catch rate (C), recruitment model (α, k), reproduction (L_{50}, r; see Arantes et al. 2010), and natural mortality (M). A sensitivity of 10% means that a change in the parameter in question by 10% causes a resultant 10% change in modeled abundance of Adults in year 2008. The resultant % change is calculated relative to the modeling run to assess the model (as in Section "Model assessment"), which was initialized in 1999 using the estimates of abundance-at-age for 1999 (Table 2), and run until 2008 using $C = 0.228$ (Eq. 2).

Exploring management strategies

To test the hypothesis that current catch rates cannot be increased without causing adverse population effects in the long-term, we assessed the effects of various catch rates on abundance of Adults. To do this, we initialized the model of the managed situation in 1999 using that year's estimate of abundance-at-age, and ran it until 2016 under various catch rates between 0 and 1. To test the hypothesis that a minimum size policy of catch of 1.6 m TL has no effect on yield potential compared to the current 1.5 m TL policy, we compared the effects of both policies on the catch and Adult populations. To do this, we ran the model as above with the difference that H (Eq. 2; Table 1) for age classes 1, 2, 3 was set as 0, and H for age classes 4 and 5 was set as 0.5. We complemented this analysis with a comparison of the yield productivity of the population in managed and un-managed situations. To do this, we initialized the model of the un-managed situation using estimates of abundance-at-age for 1999 (Table 2), and ran it from 1993 to 1998. The model of the managed situation was run as earlier but with $C = 0.23$. Catches were assessed in terms of biomass, using a length-weight relation (Martinelli and Petrere 1999).

Results

Recruitment

The Beverton–Holt model forced at the origin provided a good fit to the spawner stock-recruitment data, but one of the two parameters did not provide a statistically significant fit (Fig. 3a; Eq. 4, $R^2 = 0.85$; function parameters: $\alpha = 9611.61$, SE $\pm$ 927.06, $p < 0.001$, and $k = 94.74$, SE $\pm$ 59.35, $p = 0.16$). The density-compensatory nature of that model was supported by the reasonable but no better fit of the power model ($R^2 = 0.45$).

Fishing selectivity

The simulations of mean length-at-age of the population for situations with and without fishing were both highly correlated and not statistically different from measured medians of length-at-age for both the un-managed and managed situations, respectively (Table 1; Fig. 4; $R^2 = 1$, and Mann–Whitney *U*-tests, $n = 5$, p-value > 0.05). This shows that selective removal of the faster-growing young individuals of the population potentially can lower mean body growth rates and delay age-of-first-reproduction by almost 2 years (Fig. 4).

Model assessment

Modeled numbers of arapaima during the managed situation were close to observed numbers, except for the year 2008. Mean absolute percentage errors calculated for years 2000–2008 were 16% for Juveniles, 30% for Adults, and 18% for the catch (Fig. 3b). The modeling of the un-managed situation oscillated widely. Numbers of Juveniles increased in 1995–1996 and then decreased, and numbers of Adults were near (but not) zero in the same years and then recovered (Fig. 3b). Here, the recovery of the population was due to the strong density-compensation of recruitment.

Sensitivity analysis

The sensitivity analysis indicates that the model outputs of Adult abundances are most sensitive to the

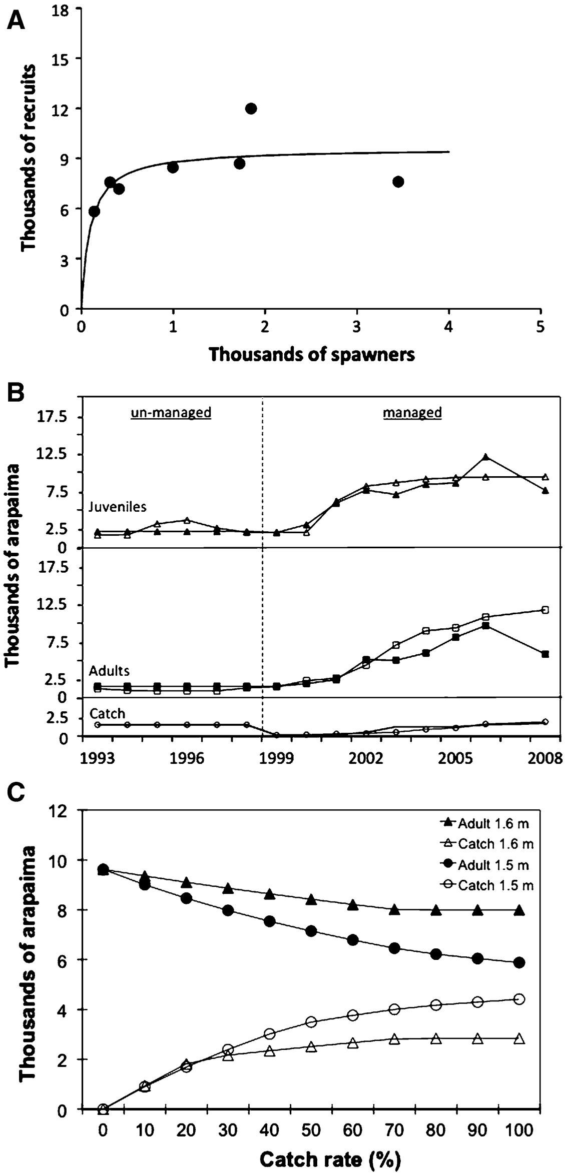

Fig. 3 (**a**) Beverton-Holt spawning stock-recruitment relation for the arapaima population in Jarauá (Eq. 4, $R^2 = 0.85$; function parameters: $\alpha = 9611.61$, SE $\pm$ 927.06, $p < 0.001$, and $k = 94.74$, SE $\pm$ 59.35, $p = 0.16$). (**b**) Modeling of the un-managed (1993–1998) and managed (1999–2008) situations of Juveniles, Adults, and catch of arapaima in Jarauá, and respective observed data also are shown. Modeled data are shown in *open markers* (*triangle*, *square*, *circle*), and observed data in *solid black markers* (*triangle*, *square*, *circle*). (**c**) Effects of various catch rates of two minimum size policies, 1.5 m TL and 1.6 m TL, on numbers of arapaima individuals harvested and numbers of Adult arapaima (>1.5 M TL) remaining in the population

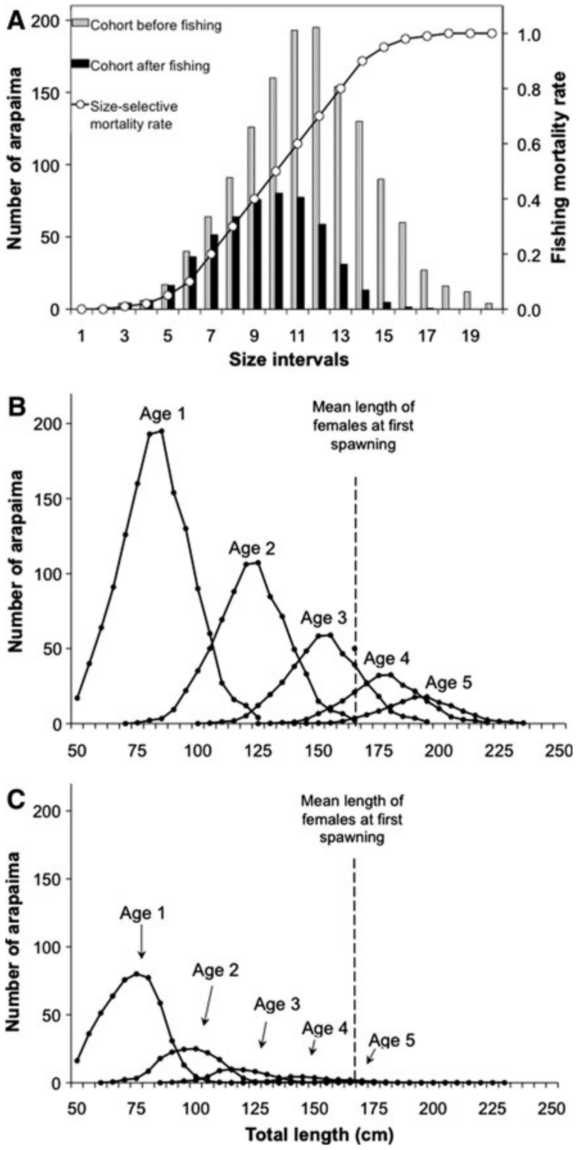

Fig. 4 (**a**) Cohort of arapaima 1 year old before and after the effects of size-selective fishing mortality following a logistic function (Eq. 6, function parameters: $c = -5.07$, $d = 0.50$ un-managed situation, and $c = 100$, $d = 100$ managed situation). Modeled length-at-age of arapaima populations in Jarauá under situations (**b**) with no-fishing, and (**c**) with un-managed size-selective fishing (as in **a**)

mortality parameter (M, 13%; Table 3). The model showed a sensitivity of 10% with respect to the parameter α of the Beverton–Holt function, but it showed low sensitivities with respect to the other parameters. Relatively higher sensitivity of the parameter α is compensated by very high statistical confidence in our estimation of that value.

Table 3 Sensitivity analysis results

Parameter	Perturbation (10%)	Output change (%)
r	+	0
	−	0
L_{50}	+	−5
	−	1
k	+	0
	−	0
α	+	−10
	−	10
C	+	−2
	−	2
M	+	−12
	−	13

The parameters k and α are from the Beverton–Holt model, r and L_{50} are from the logistic function of age of first reproduction from Arantes et al. (2010), C is catch rate from Eq. 1, and M is natural mortality from Eq. 5. Presented values correspond to percentage change in modeled number of Adults caused by a ±10% perturbation of individual input parameters

Catch rates and management strategies

The assessment of various catch rates of the (current) policy of a minimum size limit of 1.5 m TL on the Adult population showed that catches increased with increasing catch rates, but only up to about 40% (Fig. 3c). Catch rates greater than 40% appear to be undesirable as they brought only small additional returns, and catch rates above 60% extirpated the entire Adult age class five in the population (Fig. 3c). The population did not collapse even with $C = 1$, because the catch quota depends on the abundance of Adults the previous (not the same) year of harvest, allowing for Juveniles to recruit to the Adult population in that 1-year time lag (Eq. 2). When the model was run until 2016, the population reached a maximum of about 17,500 individuals total (>1 m TL) at $C = 0.25$, and 19,000 individuals at $C = 0$; these conditions represent a first approximation of maximum carrying capacity.

During the un-managed situation the population yielded about 36 t (of whole fish) of catch annually, and that catch already was near, if not above, maximum sustainable levels for a harvest dominated by immature fishes (Queiroz and Sardinha 1999). But the population yielded much more during the managed situation, when yields were about 70 t in

2006–2008. Such disparate values of catch are not observed in number of individuals, because the biomass of the catch grows exponentially with the length of the harvested fishes.

The minimum size policy of 1.6 m TL produced smaller catches and greater Adult populations than the current 1.5 m TL policy (Fig. 3c).

Discussion

Model development

The model developed here appears to be a sound tool for understanding the dynamics of the arapaima population in Jarauá. It is largely empirical, it appears to be robust to changes in individual parameters (Table 3), and it modeled numbers of Juvenile, Adult, and catch of arapaima during the managed situation relatively accurately (see Section "Model assessment"; Fig. 3b). However, the over-prediction of the model for 2008 cannot be explained with available information. In addition to possible data and modeling uncertainties, several aspects of arapaima populations remain un-studied that could explain that discrepancy, including effects of inter-annual variation in water levels on body growth or response of prey abundance to high arapaima densities. As for the un-managed situation, modeled numbers of Juveniles and Adults showed inter-annual oscillations, and modeled numbers of Juveniles accounted for 92% of the population (Table 2; Fig. 3b). Unstable population numbers and dominance of Juveniles are two features that are to be expected of an overexploited population (Queiroz and Sardinha 1999; Martinelli and Petrere 1999). Eighty-five percent of the individuals counted in 1999 were Juveniles (Table 2). However, this is a preliminary model of an unusual and poorly studied fish species inhabiting an ecologically complex ecosystem. The results herein must be interpreted carefully.

Because the model requires few data inputs, it is suitable for use in the Amazon where scientific and management resources are limited, and it can be used to guide community-based management. The model implemented in an excel spreadsheet is available from the authors upon request. Based on counts of Juveniles and Adults, fishery managers can assess the population effects of various catch rates, and they can pass the information to fishing communities. Model predictions are likely to be accurate when done for 1 year into the future.

Recruitment

The fit of the density-compensatory Beverton–Holt stock-recruitment model (Fig. 3a) is consistent with a previous finding that availability of nesting habitat could be limiting in Jarauá. Numbers of Adult arapaima in Jarauá increased 6-fold while the number of nests increased by only 1.3-fold from 2000 to 2005 (Castello 2008b). The lack of relation between annual recruitment and annual water levels previously found for this same population (Castello 2007) is consistent with a review that showed that the recruitment of fishes that do parental care in the Paraná River floodplain depends less on water levels than does recruitment of other fishes that lack parental care (Agostinho et al. 2004). This seems to be an issue of divergence between "equilibrium" fishes such as arapaima and "opportunistic fishes" (Winemiller and Rose 1992), whose annual recruitment has been shown to be highly dependent on inter-annual variation in water conditions (Halls et al. 2001). However, the available time series of data is very short, and the fit of the Beverton–Holt model had to be forced through the origin, indicating uncertainty with respect to the exact shape of the stock-recruitment function.

Fishing selectivity

Our results support the hypothesis that selective removal of faster-growing, under-sized individuals from the population potentially could have lowered length-at-age, delaying age-at-first reproduction by almost 2 years, and greatly lowering the numbers of arapaima reaching sexual maturity (Fig. 4). All of that, in turn, would have drastically lowered yield potentials of the arapaima population during the un-managed situation. Thus, lack of compliance to the minimum size policy during the un-managed situation, when the population was overexploited, appears to have constituted a positive feedback mechanism that pushed down population numbers even more. In line with this is the prediction by another study that the Jarauá population, during the un-managed situation, was going to halve in 5 years if fishing practices remained the same (Queiroz and Sardinha 1999).

Furthermore, our results indicate that lack of compliance to the minimum size policy (i.e., fishing of under-sized arapaima) appears to have greater effects on yields than very high catch rates of arapaima >1.5 m TL (Fig. 3b). Whereas yields were ~36 t annually during the un-managed situation, yields of 70 t were observed in 2006–2008 during the managed situation, and the model suggests that yields could be greater. These results emphasize the importance of minimum size policies not only in promoting recruitment through protection of the spawners, but also in preserving the natural age-at-first-reproduction of fished populations. By reproducing 2 years earlier, the population gains in capacity to recover and to sustain higher harvest levels. These results indicate that, in this particular case, how fishing is done is comparatively more important than the total amount of fishing. This is something to be considered, as many studies tend to emphasize total fishing mortality, and not so much fishing practices (e.g., Myers and Worm 2005). Unfortunately, lack of compliance with the minimum size policy is the norm in the Amazon and elsewhere in the world (Agnew et al. 2009).

However, this modeling analysis provides only circumstantial evidence of size-selection, as there are not data comparing size and age structure of the un-fished individuals against catch from the same overexploited population. Other factors potentially could explain the observed changes in length-at-age (Arantes et al. 2010), such as increased prey availability under high population density (i.e., managed situation), but we believe it is unlikely.

Studies showing the effects of fishing selectivity on key life history traits of fished populations (see review in Law 2000) have led to calls for attention to possible permanent genetic effects (Conover and Munch 2002). Arapaima in Jarauá have been exploited intensely for decades with possible effects on their gene pool. However, we have provided circumstantial evidence indicating that there were increases in length-at-age soon after fishers in Jarauá targeted older, sexually mature arapaima (Fig. 4; Table 1). This would imply that fishing selectivity effects on arapaima body growth in Jarauá have been primarily phenotypic, not genotypic. A recent meta-analysis based on 73 fish stocks found that fishing selectivity has caused little evolutionary impact in body growth rates (Hilborn and Minte-Vera 2008).

Management and conservation

There are three management implications. First and most important, complying with the minimum size and closed season policies appears to be the most effective strategy for population recovery and sustainable use of arapaima. In our deterministic model projections, the arapaima population did not collapse even with catch rates over 80% of mature Adults (Fig. 3c); this is consistent with the analysis of Myers and Mertz (1998), who showed that spawn-at-least-once policies minimize threats of stock collapse.

Second, if management policies of size and season are met, catch rates of about 25% of Adults (in the population the previous year) are close to maximum and likely to be sustainable, at least if applied with a 1-year time lag between count and fishing. At 25% catch rate, the arapaima population in Jarauá yields ~1.5 kg ha^{-1} $year^{-1}$ (of whole fish), which is five times more than Sánchez's (1969) estimate of sustainable fishing of ~0.3 kg ha^{-1} $year^{-1}$. This 25% catch rate seems reasonable given that catch rates of ~28% in three other Mamirauá communities also have led to population recoveries. Catch rates potentially could be higher (Fig. 3c), but we do not endorse such high rates because of present uncertainties (see Section "Conservation under uncertainty"). At 25% catch rate, yields are ~3% of (conservatively) predicted maximum total fish production per unit area for the Amazon basin (on the basis of 50 kg ha^{-1} $year^{-1}$; Bayley and Petrere1989).

Third, a 1.6 m TL minimum size policy would provide greater protection for spawners and produce yields nearly similar to a 1.5 m TL policy. Whereas this policy would be difficult to implement in overexploited populations, due to near-absence of large individuals, it should be viable in "healthy" populations such as that of Jarauá and many others.

Basin-wide production

On the basis of our modeling projections, we estimate that total number of arapaima (>1 m TL) in Jarauá would level off near ~19,000 in unfished conditions (i.e., the presumptive carrying capacity), ~17,500 in "well-managed" conditions ($C = 0.25$), and ~2,500 in seriously overexploited conditions (i.e., involving fishing of Juveniles) for an area of 562 km^2 (i.e., flooded area at high water). On a per hectare basis, these values are 33.8, 31.1, and 4.4 indiv. ha^{-1}, respectively, and they offer a comparative baseline to assess the health of arapaima populations elsewhere (e.g., community-based management).

The estimate of 180,360 km^2 of várzea in the whole basin (Bayley and Petrere 1989) would suggest an estimated potential population of about 6 million individuals (>1 m TL) in unfished conditions, 5.4 million in "well-managed" conditions ($C = 0.25$), and 0.8 million in seriously overexploited conditions. The latter estimate, which is valid for the current situation in the region, appears to be realistic. It is close to the generalization that large predatory fishes worldwide today are only about 10% of their pre-industrial abundance (Myers and Worm 2005); 0.8 million arapaima in seriously overexploited conditions is about 13% of 6 million individuals that we predict for unfished conditions. It also is somewhat close to that by Hrbek et al. (2005) of ~0.3 million individuals, which was derived via genetic analyses. The whole basin thus could produce ~27,000 t year^{-1} of whole fish if arapaima were "well-managed", and it could generate ~US $30 million annually, or ~US $1.6 ha^{-1} year^{-1}, assuming that fishers sell fresh (non-salted) arapaima fillets for ~US $2 per kg, and a whole fish to fillet conversion ratio is 0.56 (Martinelli and Petrere 1999). This estimate points to a potential economic value that is being lost due to overfishing.

Conservation under uncertainty

Ensuring the conservation of arapaima genetic diversity and their ecosystem roles requires care in extrapolating these results, because of present uncertainties about their biology and ecology. In this regard, the giant European skates (*Dipturus* spp.) provide a cautionary example (Iglesias et al. 2010). In the 1920s, a taxonomic analysis of the giant European skates concluded that there was a single species, but a recent re-analysis revealed that, in fact, there are two closely similar species that reach sexual maturity at markedly different sizes, 120 and 200 cm. As in life-history theory, the larger-bodied species has a lower potential rate of reproduction, and so it cannot sustain as high a rate of exploitation as can the smaller-bodied species. After 80 years of indiscriminate exploitation, the late-maturing species has been decimated and now may be "the first clear case of a fish species being brought to the brink of extinction by commercial fishing" (Dulvy and Reynolds 2009).

With arapaima, there are uncertainties with respect to size- and age-at-first-reproduction and taxonomy, as well as many other life history traits, which to complicate things further may vary geographically. For example, Godinho et al. (2005) found that arapaima in the Tocantins River basin mature sexually at a smaller size than in Jarauá. Also, the genus *Arapaima* is multi-specific, but at present we cannot map the distribution of any of the four previously described species (Castello and Stewart 2010). As with the giant skates, three species of *Arapaima* were merged with *A. gigas* (Günther 1868), so *Arapaima* has been considered monotypic for 140 years. If $M = 0.45$ for arapaima, a survivorship curve reveals that only about 3% of fishes recruiting at 1.0 m TL will live to be 7 years old; adding $C = 0.23$ to all fishes over 1.5 m TL allows only 0.3% of recruits to live to age 7. This would explain why arapaima more than 5–6 years old are very rare now in Jarauá (Arantes et al. 2010). It also suggests that if a larger-bodied, slower-growing arapaima species with age-at-first reproduction of 6–7 years ever existed, it would have been eliminated even under a seemingly "well-managed" situation.

The most useful approach to prevent undesirable outcomes in the use of the management strategies investigated here is: (1) adaptive harvesting based on best available ecological information for a given population, and (2) reliable routine monitoring of wild populations. Reducing catches can reverse eventual population declines brought about by excessive harvesting, and a 1-year time lag between counts and catches buffers effects of harvests.

Research needs

Five focal areas deserve attention: (1) Migration data are key for determining stock units, spawning habitats and appropriately scaled community-based management schemes, but detailed studies are lacking for most areas. (2) Estimates of M based on unfished populations are needed to validate theoretical estimates, as M appears to be one of the most influential parameters in the model (Table 3). (3) As the available time-series of annual data grows longer, future studies could revisit our proposed density-compensatory recruitment model, as well as possible influences of inter-annual variation in water levels. The parameter α of the Beverton–Holt function has a key influence on model outputs (Table 3), and the shape of the function needs further study. (4) The possible phenotypic effects of fishing selectivity on life-history traits need further investigation, as well as possible delayed density effects on growth (e.g., Ratikainen et al. 2008). (5) Effects of high arapaima densities upon prey fish assemblages are unknown, but might involve important trade-offs if arapaima eat the young of other commercial fishes, or if they eventually deplete their prey populations. (6) Finally, geographical variations in taxonomy, growth, mortality, and reproduction, as well as other key biological parameters need further study to allow better application of the results herein to conservation and management across the distribution range of arapaima.

Main conclusions

This study has shown that fast body growth, relatively late sexual maturity, intense parental care, and density-compensatory recruitment have allowed the arapaima population in Jarauá to grow fast in numbers and rapidly change its age composition towards an older structure. This fast population growth was realized when fishing selected individuals of sizes close to or greater than that of their first maturation (>1.5 m) and fishing was ceased during their reproductive period (December–May in Mamirauá). In marked contrast, fishing activity targeting under-sized arapaima appears to have had great effect on slowing population growth rates through delayed sexual maturation and early removal of potential spawners. These findings highlight the suitability of the arapaima for sustained harvesting and the influential effects of management restrictions.

A fishery-monitoring tale

In 1999, research on the skills and knowledge of expert fishers in Jarauá led to the development of a cost-effective method to count arapaima populations. That method was applied in a community-based management scheme conducted by the same fishers, and by allowing for adaptive harvesting, it led to a surprisingly rapid recovery of an overexploited population of arapaima. That experience was consolidated into a management model that in 2004 was incorporated into regional policy and now is being disseminated widely. The data generated in various fishing communities now are allowing for better understanding of fish population dynamics, and this, we hope, will improve arapaima management and conservation efforts in the field. This synergism between research, policy, and management can continue to make positive contributions in the future. But for that happen, it is essential to continue to collect high quality monitoring data. Here lies a message to other fisheries. Fisheries monitoring data—which are dismal in the tropics—can effectively unite the work of fishers, scientists, and policy-makers in a mutually beneficial process that works towards preserving fishery resources.

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