

Population density, growth and reproduction of arapaima in an Amazonian river-floodplain

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Abstract – Compensatory density effects are key features of fish population dynamics that remain poorly understood in tropical river-floodplains. We investigated possible compensatory growth and reproductive processes for a river-floodplain population of *Arapaima* sp., an extinction-prone fish species of South America. Body growth was studied through analysis of ring patterns on the scales, and size and age at sexual maturity was studied through analysis of female gonads. Growth and maturity were compared for unmanaged conditions with relatively low population density (in 1990s) versus managed conditions with markedly higher density (in 2005–2006); between 1999 and 2005–2006, abundance increased 7.3 fold. Results contradict theoretical expectations for slower growth and delayed reproduction at higher population density. Total lengths of arapaima at low population density were significantly shorter for age classes 1–5 compared with lengths of those age classes at high population density (ANCOVA, $P < 0.0001$ for both slopes and intercepts). Total length at 50% maturity (L_{50}) only declined about 4% with increasing density (e.g., 164 cm at low density vs. 157 cm at high density). Apparent faster growth at high density and only a slight change in size at maturity resulted in fishes spawning at an earlier age with high density conditions (age 3 vs. age 4–5). We hypothesise that these patterns reflect compliance with minimum size limits of catch during the high density (managed) situation, where there was no harvest of immature fishes. Compliance with minimum size limits, thus, may have led to faster average body growth rate and earlier reproduction, which has greatly promoted population recovery.

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Introduction

Compensatory density effects are key aspects of the dynamics of fish populations (Rose et al. 2001). They promote growth of harvested populations, allowing the populations to persist, and inhibit growth of nonharvested populations, preventing them from growing indefinitely (e.g., Schaefer 1954; Beverton & Holt 1957). These population-level effects stem from differential availability of resources per individual, leading to faster body growth in low population densities and slower growth in high densities, thus altering key life-history traits such as size-at-age and size and age of first sexual maturity (Nicholson 1933; Taylor & Taylor 1977; Lorenzen & Enberg 2002;

Vandermeer & Goldberg 2003). Compensatory density effects have been studied in many animal populations worldwide (Bohlin et al. 2002; Schuller & Hansen 2005; Simonovic & Nikolic 2007), but there are very few studies in tropical river-floodplain fisheries. This is problematic because, these fisheries are among the most overfished globally, and they occur in regions with the least developed scientific and managerial capacity (Allan et al. 2005). Information is needed to help reverse this situation.

There have been few studies of density compensatory effects on body growth and reproduction in tropical river-floodplain fishes. Dudley (1974) studied growth of three fish species in the Kafue River floodplain, Zambia, and found compensatory density

effects on adults of only one species, *Tilapia Macrochir*. Kapetsky (1974) also studied fishes of the Kafue floodplain and found seasonal variations in growth of five fish species, but attributed those variations to the seasonal hydrologic cycle. Bayley (1988) evaluated the growth of 12 fish species in the Amazon, and found weak evidence of compensatory density effects in only two. Studying these effects is difficult, because of scarcity of time-series data (Bayley & Petrere 1989).

Here, we investigate compensatory density effects for a population of the giant fish *Arapaima sp.*¹ in a river-floodplain of the Amazon. Arapaima have been a key fishing resource in the Amazon (Verissimo 1895) but now are considered to be generally over-exploited and even commercially extinct near urban centers (Castello & Stewart 2010). They are listed in the Appendix II of the Convention of International Trade of Endangered Species, which means they could become threatened with extinction if trade and associated harvests are not strictly regulated. All existing data show predominance of young in the catch largely because of widespread lack of compliance with size and season management regulations (Martinelli & Petrere 1999; Queiroz & Sardinha 1999). Community-based fishery management schemes can effectively conserve arapaima populations, and now they are the most used approach for arapaima conservation (Castello et al. 2009; McGrath et al. 2008). However, understanding of fish body growth, reproduction, and associated density effects is lacking, inhibiting management and conservation initiatives.

Fortunately, now it is possible to study density effects on an arapaima population at the Mamirauá Reserve, Brazil. Previous ecological studies have shown that arapaima is piscivores (Sánchez 1969) and their life cycle, like other river-floodplain fishes, is governed by flood pulses (Junk et al. 1989; Castello 2008a). When water levels are rising, they build nests and reproduce along the margins of the forests (Castello 2008b), guarding their offspring for about three months in the flooded plains where there is much food and few predators. When water levels lower, they migrate to the only remaining water bodies, the channels and lakes. Here, arapaima are very vulnerable to harpoon- and gillnet-specialist fishers because their obligate air-breathing behaviour makes them visible to the fishers every 5–15 min.

Fisheries management efforts at the Mamirauá Reserve have monitored abundance and aspects of body growth and reproduction over a 16-year period.

¹Taxonomic status of the studied population remains uncertain (Castello & Stewart 2010), so we use only the genus name. Our ongoing analyses suggest the species in the study area is undescribed.

In the 1990s, Queiroz (2000) studied growth and reproduction of arapaima when the population was overexploited and at relatively low population density (average 4.45 ind.·km⁻²). In this study, we re-evaluate those processes at a markedly higher density after population recovery (e.g., in 2005–2006 with about 32.3 ind.·km⁻²); population density increased about 7.3 fold (Arantes et al. 2006; Castello et al. 2009). Population abundance estimates stem from existing catch-per-unit-effort and direct census data collected during the study period and summarised in Castello et al. (2009). The reported population increase has been shown to be accurate and due to the implementation in 1999 of a new management scheme for the arapaima based on compliance with minimum size (150 cm), closed season (December–May), and total catch limits (Castello et al. 2009). Because smaller population increases in other fishes have caused density effects on body growth and reproduction (e.g., Muth & Wolfert 1986; Koslow et al. 1995), in this study we test the null hypothesis that this increase in arapaima population neither reduced body growth rates nor changed length or age-at-first-reproduction.

Materials and methods

Study area

The study was developed in the Mamirauá Sustainable Development Reserve, located in the middle of the Solimões River, Amazonas State, Brazil. The area is primarily varzea floodplain seasonally inundated by muddy or whitewaters that are rich in sediments and nutrients. This floodplain is a complex mosaic of tropical rainforests, lakes, and canals that become broadly interconnected during seasonal floods (Irion et al. 1997). The reserve was created to protect biodiversity through participative and sustainable management of the natural resources, made with the involvement of local communities, Mamirauá Institute and Brazilian governmental bodies (state and federal). The studied arapaima population is managed by the community of Jarauá, which controls an area encompassing approximately 562 km² with about 85 lakes (about 2°50' S and 64°59' W). We refer to our study area simply as Mamirauá, but it is a small part of that much larger reserve.

Population density estimates

Accurate estimates of population abundance of arapaima were made each year for 1999 through 2006, using the counting method of Castello (2004), which involves experienced fishermen counting fishes at the moment of aerial breathing. This method was

validated through experiments that showed that the visual counts made by fishermen only varied about 10% around values of abundance estimated by mark-recapture using large seines (Castello 2004; Arantes et al. 2007). Fishers involved in population censuses had the accuracy of their counts of arapaima assessed by independent observations of total seine catches of the same populations, and they also were accompanied by technicians from the Mamirauá Institute to avoid possible cheating (e.g., inflating counts; Castello et al. In Press).

Because the biological samples for the low density situation were collected during 1993–1998, and population abundance estimates are available only from 1999 on, we assumed that population densities during the 1993–1998 period were similar to that in 1999. This is reasonable for various reasons. First, that population abundance data reflected the situation in earlier years given that the results of management (which started in 1999) had not yet had effects. Second, there is close agreement between population abundance data and a stock-assessment study of the same population for that time period (Queiroz & Sardinha 1999; Castello et al. 2009), both of which found scarcity of adult individuals (i.e., growth overfishing); average total length of capture being only 121 cm, which is well below the minimum length of catch (150 cm) set by the Brazilian government (Queiroz & Sardinha 1999). Lastly, there is close agreement between assumed population abundance and catch-per-unit-effort data for 1995–1997 and 2003 (see Castello et al. 2009). These data suggest that this arapaima population was seriously overexploited during the 1990s. Thus, throughout this paper, we refer to this 1990s period as one of “low density”, and 2005–2006 is referred to as relatively “high density”.

Scale samples for studying growth

We studied growth through analysis of scales taken from two complementary sources: the commercial catch and fishes that we captured and released using large seines. Use of other calcified structures was not feasible mainly because in the study area arapaima are sold whole and it is socially problematic to harvest an endangered species for research purposes. Also, fishing of arapaima is highly dispersed with the harvest occurring in about 100 different spots and deboning occurring in urban centers. Scale samples were collected only during the dry period (between August and November), when fishes are concentrated in lakes and connecting channels and most of the commercial harvest occurs. Year-round sampling was not done because capturing arapaima during the flood in numbers adequate for growth studies is practically

impossible in the study area, when they inhabit densely forested habitats.

We sampled 270 and 274 arapaima in periods of low and high density, respectively. In a previous analysis of the low-density period, Queiroz (2000) included some samples for months other than August–November, but those samples were excluded from this study. So results in that earlier report are not strictly comparable to those presented here. We removed 6–10 scales from a standard area posterior to the pectoral girdle (usually 5–6 scale rows below the lateral line and starting 3–4 scales posterior to the pectoral girdle), and put them in plastic bags. We took scales from that area of the body because the incidence of regenerated scales seemed to be relatively lower. Higher on the body, scales are larger but more of them are regenerated, perhaps reflecting damage from harpoon strikes. We measured total length of each fish to the nearest 1 cm (from tip of lower jaw to tip of caudal fin). Our samples of live arapaima were made in lakes and canals of the study area using a large seine (140 × 5 m, 16 cm stretch mesh); for smaller fishes, we used gill nets (40 × 4 m, 9 cm stretch mesh). To minimise stress, netted fishes were held in the water during measurement and scale removal or brought into the boat for the shortest possible time; then they were released where caught. Sometimes length of large fishes being measured alive could only be taken to the nearest 5 cm. All scale samples were subsequently cleaned with water and brush, dried in the shade, labelled and stored in paper envelopes. Unlike scales of higher teleosts, arapaima scales will disintegrate in a few days if stored wet.

Readings of growth rings

From the set of scales for each arapaima, we selected one (~best) scale for reading based on definition of the border, focus and rings. Growth rings in the scales were observed using transmitted light and a magnifying glass that enlarged the image by three-fold. As with temperate fishes, the circuli change deposition rate when growth rate changes. Rapid growth leads to more widely spaced circuli resulting in translucent bands; and slow growth yields opaque zones. Only those opaque zones that went completely around the scale (or nearly so) were considered to be growth rings (Fig. 1; Bagenal & Braum 1978). Scales from the low density period were analysed by marking positions of focus, rings and distal margin on a piece of cellulose acetate laid over the flattened scale, and then taking measurements from those marks using a caliper (by H.Q.). Scales from the high density period were analysed by marking rings directly on the scale with a fine pencil using a 3× magnifying glass, and then making a high-resolution

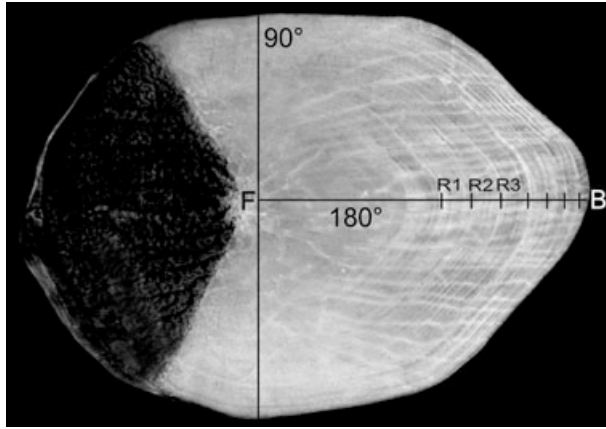


Fig. 1. Scale of an Arapaima from Mamirauá Reserve indicating focus (*F*), seven rings (*R*₁, *R*₂, etc.), distal border (*B*), and the angles of measurement (90°, 180°) for distances from the focus to each ring and the border. For this example, distance $F-B = R_t = 3.63$ cm.

digital image of the marked scale using a flatbed scanner with transmitted light (e.g., slide-scanner attachment). Dried scales tended to curl, but soaking them in water made it easier to flatten them on the scanner. Digital-imaging software was used to take measurements from enlargements of the scanned images (Fig. 1, see below).

For high-density samples, the selected scale of each arapaima was read independently by two observers without reference to length of the fish (i.e., C.A. and a technical assistant). Then observers made a third reading together to obtain a consensus in the final reading. Readings of scales taken from the low density period were made by a different observer (H.Q.). To ensure that readings from the two time periods were consistent and comparable, the two observers of the 2005–2006 scales also examined a subsample of 39 scales from the low density situation. We applied the Wilcoxon test (Snedecor & Cochran 1989) to evaluate the null hypothesis that interpretation of growth rings was similar among readers and, hence, among time periods.

We measured the distances from the focus of the scale to each ring (radius of each ring) and to the scale's distal border (radius of scale, Fig. 1). Those measurements were used to back-calculate length-at-ring of each arapaima. The best angle for scale measurements was determined by evaluating correlation coefficients between scale radius measured at different angles (i.e., 90° and 180°, Fig. 1) and total length of the fish. In the low density situation, Queiroz (2000) concluded that the lateral radius (90°, $r = 0.64$) had the best correlation, but for the high density situation we found that the longitudinal radius was best (180°, $r = 0.77$). This difference may be simply an artefact of the different methods used (i.e., acetate

over-lays vs. scanned images). To ensure comparable data for back-calculated lengths from the two sample periods, we used the following equation, which precludes the need for a body-length to scale-radius regression equation.

$$L_n = (R_n/R_t) * (L)$$

Where, L_n is total length (cm) of the fish when ring n was deposited; L is total length when the scale was obtained; R_n is radius of each ring (cm); and R_t is total scale radius (cm) from focus to border (Fig. 1). Use of this proportional relation assumes that relative growth of scales and body length is linear, not allometric. A linear regression between body length and radial diameter of the scale calculated using the high density data showed a very good fit ($R^2 = 0.75$, $P < 0.0001$; Body length = $45.69 * (\text{radial diameter}) + 29.21$). The fit of the linear regression to the data was equally good using both normal or log-transformed data, and distributions of residuals indicated homogeneous variance.

To test the null hypothesis that size-at-age trajectories were similar during periods of low and high population density, we used an analysis of covariance (ANCOVA, Systat Software 2000). For this ANCOVA, we used only the observed length-at-age data, not back-calculated values, because inclusion of the latter would violate the assumption of independence. For our estimation of median length-at-age, we used the full data set including back-calculated values, as is traditional in fisheries science.

Interpretation of growth rings

Based on preliminary results for arapaima from Mamirauá (Queiroz 2000) and related observations in this expanded analysis, it was clear that they steadily gain rings on their scales as body size increases. Given the regularity of that pattern, we infer that those rings do not involve 'false annuli' related to environmental variation, which would be more irregular, or 'spawning checks', which would only occur in mature fishes. The two most likely alternative interpretations of those rings are annuli versus biannuli (i.e., one or two rings per year). Distinguishing those two alternatives is not difficult because predictions that follow from them are markedly different. To make that distinction, we draw upon three lines of evidence: (i) our own observations on size-frequency for young-of-year fishes, (ii) published observations on lengths of arapaima at known ages compared with our observations, and (iii) growth increments for three arapaima from Mamirauá that were tagged, released and then recaptured 1–5 years later (see Results, below).

Estimating growth patterns

We evaluated possible changes in the growth trajectories for arapaima using the von Bertalanffy growth model (VBGM):

$$L_t = L_\infty * (1 - e^{-K*(t-t_0)})$$

Where, L_t is total length at age t ; L_∞ is asymptotic length; K is the VBGM growth coefficient (year^{-1}); t is age (years); and t_0 is theoretical age when length is zero (Quinn & Deriso 1999). Parameter values for the VBGM were estimated for each time period using the stage-explicit Ford-Walford plot for a body-growth trajectory and associated equations developed by He & Stewart (2002). This new approach by He & Stewart (2002) clarifies some prior ambiguities and better explains relations between a Ford-Walford plot and the VBGM. Unlike a typical Ford-Walford plot (e.g., Ricker 1958) the complete Ford-Walford plot involves plotting yearling size on the y-axis and calculating a separate yearling relative growth rate (ρ^y) for growth between ages 1 and 2. Those stage-explicit expressions of the VBGM (Fig. 2) provide a basis for comparing arapaima growth trajectories between periods of low and high population densities.

Length and age of first maturity

We collected data on total length of first sexual maturation for female arapaima from fishes commercially harvested by the Jarauá community. We determined maturity state of females by macroscopic observations of the gonads, sampling 240 arapaima in the low density situation and 168 in the high density situation. We considered fish in stages III and IV of gonad maturation to be mature (Flores 1980; Lopes & Queiroz 2009). A stage-III ovary is developed with round, large, green oocytes mixed with a few rose-coloured, yellowish or whitish oocytes, and all are immersed in a rose-coloured matrix. A stage-IV ovary is completely developed with large, round, swollen oocytes, giving the gonad a dark green colour.

We estimated total length of first sexual maturation (L_{50}) of female arapaima through nonlinear regression of the logistic curve (M_f), using Systat 10.0 software (Systat Software 2000). For that regression, we used as initial values the L_{50} and r estimated by Logit transformation (Hosmer & Lemeshow 1989).

$$M_f = 1/(1 + \exp[-r * (L - L_{50})])$$

Where, M_f is proportion of mature females in a length class L ; r is slope of the curve for rate of change in M_f ; and L_{50} is the average length of first maturation or the length where 50% of females are mature. Length classes consisted of 10 cm wide intervals starting from 70 cm TL.

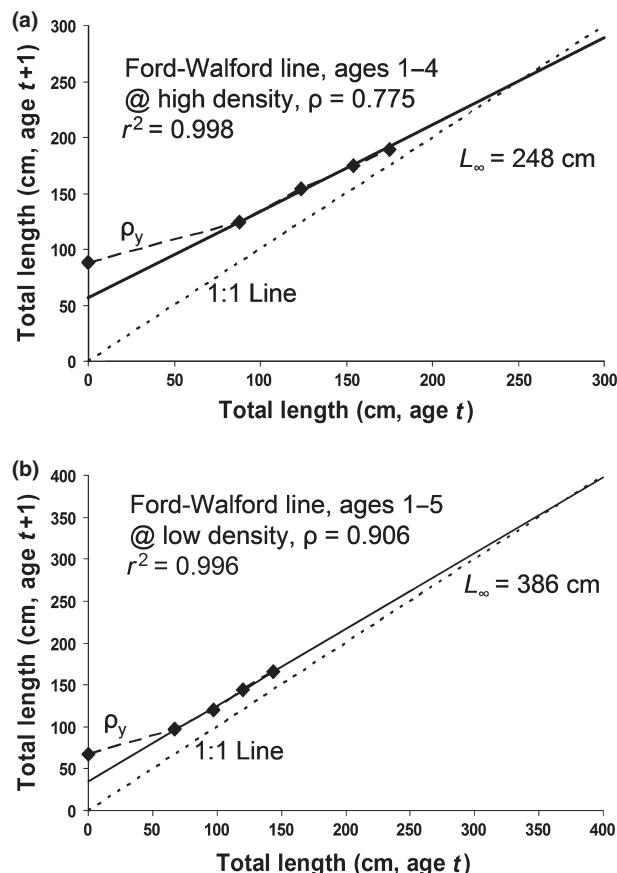


Fig. 2. Complete, stage-explicit Ford-Walford plots (He & Stewart 2002) for Arapaima from Mamirauá Reserve for situations of relatively high (a, 2005–2006) and low (b, 1990s) population densities. Parameter symbols, their definitions and values are presented in Table 3. The Ford-Walford lines are based on median total length at age from Table 1; the line in the upper plot is for ages 1–4; that in the lower plot is for ages 1–5.

Results

Interpretation of growth rings

The combination of empirical evidence and strong inference support the hypothesis that arapaima in Mamirauá form biannuli on their scales. Late in the dry season, young-of-year arapaima attain total lengths exceeding 60 cm and have grown well beyond the size where the first ring forms on scales (i.e., 50 cm TL in low density and 64 cm TL in high density). If each ring was an annulus, then lakes at that time would have to be filled with much smaller fishes together with a larger size class of about 60–80 cm, but that has never been observed in our many years in the field. In line with this is a study in Peru by Wosnitza-Mendo (1984), who found that arapaima juveniles in a closed lake grew to an average length of 80 cm in their first year of life. That size at age-1 closely agrees with our growth data (Table 1) and corresponds to a fish with two rings.

Table 1. Age key and number of rings for total lengths of arapaima in the Mamirauá Reserve during periods of low (1990s) and high (2005–2006) population densities. L_t is median total length, cm, back-calculated from scale annuli; IQR is inter-quartile range; and N is sample number. Three published observations on total lengths for fishes of known age are included for comparison.

Number of rings	Age (years)	Low density			High density			Published observations	
		L_t	IQR	N	L_t	IQR	N	TL, cm	Reference
2	1	67.3	18.6	269	88.3	24.6	269	80	Wosnitza-Mendo 1984
4	2	96.9	22.4	247	123.6	26.0	238		
6	3	119.6	27.5	172	154.4	24.0	227	120	Fontanele 1948
8	4	144.4	31.4	61	174.9	19.1	113		
10	5	166.3	29.9	16	188.9	13.5	15	170	Lüling 1964
12	6	172.7		1					

Table 2. Comparison of total length gained to predicted length gain for three arapaima that were marked and recaptured in Mamirauá Reserve during the 1990s (Queiroz 2000). Predicted range of total length gain is based on Ford-Walford regression relations for arapaima at low and high density (Fig. 2). Scale rings gained is the number of rings that we observed to correspond with those F-W predictions of length gains (i.e., two per year).

Years, mark to recapture	Starting TL, cm	Final TL, cm	Observed TL gained	F-W predicted TL gained		Range Pred. – Obs.	Rings gained
				Low Den.	High Den.		
1	127	153	26	25	28	–1 – 2	2
5	118	200	82	102	69	–13 – 20	10
4	186	220	34	64	37	3 – 30	8

Fontanele (1948) found that 19 arapaima raised in captivity in Brazil grew to an average length of 120 cm in 3 years. That is identical to average length of an age-3 fish at Mamirauá in the 1990s, and such fishes have six rings on their scales (Table 1). More recently, growth has been faster, but a fish that size would still have four rings. When a 127 cm fish at Mamirauá was tagged, released and recaptured 1 year later, it had gained 26 cm, which is nearly identical to the gains predicted by our estimated growth relations (Table 2). That annual length gain also matches a gain of two rings on the scales.

Finally, Lüling (1964) in Peru, studied growth of arapaima by analysis of vertebrae; he reported that an arapaima known to be age-5 had attained a length of 170 cm and had nine rings in the vertebrae. That length corresponds with length intervals for arapaima from Mamirauá with eight to ten growth rings (Table 1), providing further support for the biannuli hypothesis. Two other fishes from Mamirauá with lengths of 118 and 186 cm were tagged, released and recaptured 5 and 4 years later, respectively (Table 2). Observed length gains for those fishes were similar to or somewhat less than gains predicted by our growth relations but still would be accompanied by gains of 8–10 rings on the scales. Taken together, the foregoing observations lead us to infer that the typical growth pattern for arapaima in Amazonian floodplains is to form two rings per year or biannuli. The alternative of one ring per year is inconsistent with empirical evidence and related inferences.

Body growth rate

There was very good agreement in comparisons among scale readings made by observers for samples for the low and high population density situations. There was absolute agreement of growth-ring counts for more than 54% of the scale samples, another 30% differed by only one ring, and only 15% differed by two rings. Despite these errors, on average observers from both periods showed no tendency to over- or under-estimate number of rings per scale relative to one another. Furthermore, there was no statistically significant difference between the readings made by observers from the two periods, as indicated by the Wilcoxon signed-rank test ($P > 0.05$), providing assurance that growth comparisons are reliable.

Fish total lengths in our samples ranged from 52–220 cm, so we are confident that our samples included all the age classes present in the population. Arapaima larger than 220 cm were rare in our study area. That probably reflects high fishing mortality for the adults, including a strong financial incentive to catch the biggest individuals. Number of rings observed in the scales varied from 1–12, representing ages 0.5 (young-of-year) to 6 years (Table 1).

We found that median lengths-at-age of arapaima in high density situations were all significantly greater than at low population density (Table 1). The ANCOVA test for length-at-age data for both density situations showed significant differences between intercepts ($F = 19.3$, d.f. = 1, 163, $P < 0.0001$) and regression

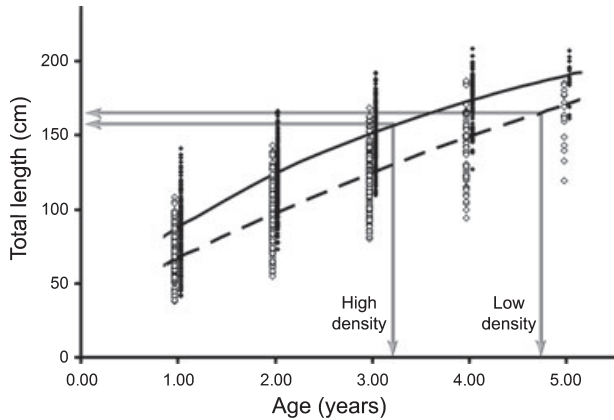


Fig. 3. Growth curves based on the von Bertalanffy growth model parameters from Table 3 compared with empirical observations of total length at age for arapaima from Mamirauá Reserve for situations of relatively low (1990s, open symbols, dashed curve) and high (2005–2006, closed symbols, solid curve) population densities. Also shown are total length (cm) and age (years) for first sexual maturity (horizontal and vertical arrows, respectively) of female arapaima for each time period.

coefficients ($F = 709.8$, d.f. = 1, 163, $P < 0.0001$). Overall median increase in lengths-at-age of arapaima between low and high density was 27 cm (Fig. 3). Those differences in lengths-at-age were reflected in parameters of the von Bertalanffy growth functions (Tables 2 and 3) and associated growth curves (Fig. 2). At high population density, Ford-Walford slope and L_{∞} were less while yearling length and t_0 were greater than under low density conditions. The predicted maximum length of 248 cm is less than the maximum that has been observed in Mamirauá in recent years (i.e., ~290 cm), but may be reasonable given natural variation in individual growth trajectories. The relation for the high density situation was based only on ages 1–4, because at age 5 the population was being subjected to heavy fishing mortality, while ages 1–3 were largely unfished. If age 5 was included in the relation, the estimate of L_{∞} would be reduced to 230 cm. At low population

Table 3. Estimated parameters for the stage-explicit expression of the von Bertalanffy growth model (He & Stewart 2002; and references therein) for situations of low and high population densities of arapaima from Mamirauá.

Parameter	Definition	Low density value	High density value
L_1	Yearling total length, cm	67.0	88.0
L_{int}	Ford-Walford intercept, cm	34.8	56.5
L_{∞}	Asymptotic total length, cm	386	248
ρ^y	Yearling relative growth rate	0.447	0.409
ρ	Ford-Walford slope	0.906	0.775
K	$-\text{Log}_e \rho$, VBGM growth coefficient	0.0986	0.2552
t_0	Age with zero body length	-0.931	-0.719

density, in contrast, Ford-Walford slope and L_{∞} were much greater while yearling length and t_0 were less than under high density conditions (Table 3). The low intercept and high slope result in a projected L_{∞} of 386 cm, which seems excessive relative to empirically observed maximum length. In the low density situation, all age classes were being harvested, and that may have affected results of the low-density Ford-Walford relation (see Discussion, below).

Applying a total length (L , cm) to wet weight (W , kg) relationship estimated by Queiroz (2000) for arapaima during the low density situation (i.e., $W = 3.788E-05 * L^{2.7045}$; $N = 885$, size range about 55–230 cm, but mostly 100–200 cm), an age-1 fish in the high density situation would weigh about 6.9 kg. A fish at size of first reproduction (157 cm) would weigh 32.9 kg, and at $L_{\infty} = 248$ would weigh 113 kg. The largest documented specimen in Mamirauá (about 290 cm TL) would weigh about 173 kg.

Length and age of first maturity

Female arapaima sampled for gonad condition included a wide range of length classes (75.5–266 cm TL). At low density, the L_{50} was 164 cm (95% C.I = 162–166 cm), and at high density, it was 157 cm (95% C.I = 156–159 cm; Fig. 4). We inferred that the length of first sexual maturation of females (L_{50}) was slightly but significantly shorter (e.g., about 7 cm or 4.3% less) at high population density compared with low density, because confidence intervals do not overlap. So with respect to our null hypothesis that population density changes would not affect L_{50} , there was a minor change.

Given our finding that length-at-age increased by an median of 27 cm (Table 1, Fig. 3), we find that many arapaima at high density are reproducing at age 3, while at low density they generally did not reproduce

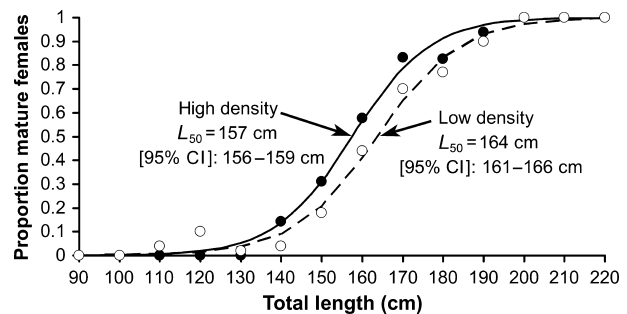


Fig. 4. Curves of total length (cm) versus proportion sexually mature females for Arapaima from Mamirauá Reserve for situations of relatively low (1990s, open circles, dashed curve) and high (2005–06, closed circles, solid curve) population densities. Sizes at first maturity (L_{50}) and 95% confidence limits of those parameters are indicated for each density condition.

until age 4 or 5 (Fig. 3). That change in age at first maturity is explained almost entirely by apparent increases in growth rate, because the slightly lower length at first maturity was not large enough to give that result. Reproduction at an earlier age but at nearly the same length again is contrary to expectations for a compensatory density effect; a marked increase in population density should result in slower growth and delayed reproduction.

Discussion

Formation of biannuli

We have provided strong inferential evidence suggesting that arapaima form biannuli. Formation of these twice-yearly rings probably relates to ecological processes involving life cycle of the species and water-level variations on the floodplains. Other species of fish from Amazonian floodplains, including *Osteoglossum bicirrhosum*, which belongs to the same family as arapaima (Osteoglossidae), also form two growth rings a year in their scales, one during low water and another during the flood, corresponding to dry-season food limitations and flood-season reproductive activities, respectively (Ribeiro 1983; Villacorta-Correa 1987; Oliveira 1996; Vieira 1999; Cutrimi & Batista 2005; Pérez & Fabré 2009). Formation of biannuli by tropical freshwater fishes also has been observed in Africa (e.g., Blake & Blake 1978; Admassu & Casselman 2000) and elsewhere in the world. However, because of the scope of our study, we have not provided conclusive evidence that the arapaima form biannuli, making it desirable to study further the mechanisms underlying formation of growth rings. The results reported here are, nevertheless, appropriate for testing the hypotheses of compensatory density effects on body growth and length and age-at-first-reproduction; conclusions about temporal changes in relation to density would be similar whether one uses each ring or every other ring to represent growth patterns.

Body growth rate

We found no evidence that increased population density led to declines in body growth rate. In fact, median size-at-age increased markedly after 7 years of consecutive increases in population density (Table 1, Fig. 3), contradicting theoretical compensatory density effects (e.g., Rose et al. 2001). We believe that these results are real because our methodological approach was sound. Furthermore, it is unlikely that environmental stochasticity influenced these results by preventing the formation of growth rings in the high density situation. For that to occur, an improbable

match between years of sampling and abnormal environmental conditions would be needed, causing the entire dataset for the high density situation to show two or more missing rings than for the low density situation.

Nevertheless, we cannot identify with certainty the fundamental cause leading to these counter-intuitive results, but they probably stem from broader natural- or human-related phenomena. There are various plausible, nonexclusive explanations. First, there was no per capita shortage of food resources for arapaima in high density, because varzea ecosystems are highly productive (Junk et al. 1989), and arapaima feed on fishes that are both abundant and near the base of the trophic web (Sánchez 1969). Also, air-breathing and lateral migration behaviours make arapaima well-adapted to exploiting the spatial and temporal heterogeneity of energy resources on these floodplains (Castello 2008b). Second, there might have been increased prey availability in the high density period created by climate variability (e.g., El Niño) affecting flooding patterns, which can affect biological production processes in the varzea (Schongart et al. 2004). Third, some density effect could be developing but cannot be detected yet because of time lags in such complex systems. Fourth, density effects were not evident because they were masked by more dramatic changes in life-history traits caused by changes in fishing practices associated with the recovery of the population, as suggested below. Finally, given that previous studies on growth of floodplain fishes (Dudley 1974; Kapetsky 1974; Bayley 1988) have generally not found compensatory density effects, it could be that such effects are less common in tropical floodplains than in other ecosystems.

Length and age of first maturity

We also found no evidence of compensatory density effects on length and age of first reproduction. There was a small (-7 cm) but statistically significant decline in L_{50} (Fig. 4) that probably is because of having different observers in the two studied periods, and is not important because the range of sizes for either time period (157–164 cm) falls in the same age class (Table 1). With respect to age of first reproduction, we found a decline from 4–5 years to about 3 years as population increased (Fig. 3). This change is the opposite of what might be expected from a compensatory density effect, so it probably was not caused by the density increase. Unlike the minor change in size of first reproduction, this change has very important implications for population dynamics, because intrinsic rate of increase in a population is strongly (negatively) related to age of first

reproduction (e.g., Vandermeer & Goldberg 2003). Spawning at an earlier age will tend to accelerate population recovery, and indeed, we have observed an exponential growth in abundance of arapaima in the study area (Castello et al. 2009).

The observed L_{50} values in Mamirauá differ from that of other regions. Godinho et al. (2005) found that female arapaima in the Tocantins River basin in Brazil matured at a smaller size of 145–154 cm, and males of that population matured even smaller at 115–124 cm. In contrast, Lüling (1964) reported 170 cm as size of first sexual maturity for arapaima in Peru.

The size-selective fishing hypothesis

Why, then, does arapaima in relatively high population density appear to grow more quickly and mature in less time than in low population densities? We suspect that the observed changes in growth and age-at-first-reproduction are the result of differential fishing selectivity on each situation, caused primarily by fishing that tends to select the faster growing fishes. In the low density situation, the arapaima harvest was unregulated and some 80% of the harvest was immature fishes with average size of only 121 cm (Queiroz & Sardinha 1999). So, most of the faster growing fishes that generally are more susceptible to gillnet and harpoon fishing tended to be fished out. However, in 1999 a new management system was implemented stipulating that fishers were allocated harvest quotas in numbers of arapaima per year, so the average size of catch increased to 161 cm, maintaining in the population a greater proportion of faster growing fishes during the high density situation (Castello 2007). Some evidence for that can be seen by comparing the growth curves for the two time periods (Fig. 3). The curve for the 1990s appears to be much straighter, and the greatest deviation between the two curves is near the modal size of harvested fishes in the low density situation. In a complementary paper, we provide data supporting this hypothesis with a modelling analysis. Castello (2007) hypothesised that those growth responses result from a relaxation of intensive removal of young and fast-growing individuals, finding that fishing selectivity can in fact explain the observed growth patterns of arapaima in Jarauá. The effects of fishing selectivity on life history traits of fishes (e.g., growth and age-at-first-reproduction) have been documented elsewhere (Law 2000; Nielsen and Pavey 2010).

Conclusions and implications

This study provides new information on variations in growth, reproduction, and age structure that is an

important foundation for modelling population dynamics and sustainable harvests (Quinn & Deriso 1999). Castello (2007) extended this analysis in that direction and considered broader implications for population rehabilitation and conservation of arapaima. We provided a first comprehensive assessment of age at first reproduction, which reveals a possible problem with existing Brazilian harvest regulations. The minimum size of capture of arapaima in Brazil, 150 cm TL, does not fully protect reproductive potential of the population, because it allows harvest of sexually immature females. For instance, about 20% of the individuals legally captured in Mamirauá between 1999 and 2006 measured between 150 and 157 cm TL. This legal harvest of sexually immature arapaima could slow recovery of overexploited populations and perhaps increase the risk of population collapse (Myers & Mertz 1998).

The Mamirauá population is unique for its 9 years of annual assessment of arapaima density in some 85 lakes, and accuracy of those counts should be high (Castello 2004; Arantes et al. 2007). We suggest that this population might serve as a model system for studies of fisheries science in general and, in particular, for understanding dynamics of a managed arapaima population. Various authors have commented on the importance and difficulty of obtaining quality, long-term data appropriate for studying density effects, and those difficulties are exacerbated in tropical floodplain systems (Bayley & Petrere 1989). In the near future, we expect the Mamirauá population to level off as energy or space becomes limiting. As we approach that situation, this study will provide a valuable benchmark for quantifying density effects and estimating sustainable harvests.

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