Viability of Natural Populations of Hypancistrus zebra (Siluriformes, Loricariidae), Xingu, Brazil

Liriann Chrisley Nascimento Da Silva (liriannns@gmail.com)  
Federal University of Para

Leandro Melo de Sousa  
Federal University of Para

Paulo De Marco Jr.  
Universidade Federal de Goiás

Thiago Bernardi Vieira  
Federal University of Para

Research Article

Keywords: Individual Based Modeling, Overfishing, Habitat loss, Ornamental fish, Volta Grande do Xingu

Posted Date: January 31st, 2022

DOI: https://doi.org/10.21203/rs.3.rs-1233118/v1

License: © ️ This work is licensed under a Creative Commons Attribution 4.0 International License.  Read Full License
Abstract

*Hypancistrus zebra* is an endemic fish species from the Middle Xingu River and recently included in the Critically Endangered (CR) category in the Red Book List of Endangered Brazilian Fauna that follows IUCN criteria. Given these impacts and the lack of information about the species, it is difficult to assume the viability of natural populations. Thus, this work aims to evaluate the effect of the variation of intrinsic parameters on the population viability of *H. zebra*. For this, an Individual Based Model (MBI) was created of the type Agent Based Modeling (MBA). To create the model, we considered “individuals” as an entity and the following variables of interest: longevity, age of sexual maturity, annual reproduction number, instant birth rate (b0), instant mortality rate (d0), interference of each individual in population growth (b1), interference of each individual in population mortality (d1), time (t), radius, richness (S), tolerance (tol) and population size (N). The model showed that natural populations today, even not taking human impacts in account, are at the limit of viability. However, any factor that causes a reduction in resource availability, even if not evident, can lead to a steep population decline, affecting the viability of the populations.

Introduction

The construction of Hydroelectric Power Plants (HPP) has become one of the main threats to the maintenance of the global ichthyofauna \(1^\text{–}3\). The dam causes the blocking of migratory fish activities (e.g. reproductive migration of *Salmo salar*), physical changes (e.g. change from lotic to lentic environment and retention in sediment transport), chemical changes (e.g. physicochemical water characteristics) and affects community (e.g. causes the process of biotic homogenization, contaminates individuals with methyl mercury, favors the increase of generalist species and the disappearance of specialist species)\(4^\text{–}13\). These impacts change the dynamics of aquatic communities and populations\(12^,14^,15\).

After damming, lotic fish communities are replaced by lentic species, since the dam reduces the water flow, transforming the natural water regime into a characteristic environment of lakes and reservoirs\(5^,7,16^,17\). Physical and chemical water change, such as flow alteration and irregular seasonal variation downstream of the reservoir\(18^,19\), causes the loss of flooded area and reduction of areas for reproduction and foraging\(12^,19,20\). The reduction of areas destined for foraging and reproduction is also observed upstream of the impoundment and causes a reduction in fish populations\(8^,12\), however, the loss of upstream areas is linked to the drowning of environments, while downstream is linked to the period of permanent drought, created by the dam. Additionally, we observed a process of discontinuity in the rivers, which hinders the access of migratory fish to the headwaters to reproduce and later return, in turn, the fish from the eggs hatched above the dam are prevented from going downstream to grow\(21^\text{–}23\). These effects lead to the loss of fish diversity, therefore, reducing the abundance of populations can be the representation of a feeding strategy\(18\) and result in changes in the fish assemblage\(5\).

We are currently seeing an advance in studies in temporal and spatial scales in an attempt to mitigate the damage caused by the construction of dams\(2^,3,14^,24^\text{–}30\). Despite these advances, the lack of information about some groups of species and environments is still scarce, especially in the neotropical region\(22,23,26^,27\). This lack of knowledge associated with the expansion of these projects increases the risk of local extinctions of endemic populations and species\(28\). Ecological modeling can be an effective method for studies with little data available and enables results in shorter time intervals\(29\). In addition, Individual-Based Models (IBM) has increasingly stood out for being a more realistic ecological analysis when compared to classical models\(30\).

IBM is mainly characterized by using individuals as a basic unit that interact and differ from each other, making the population no longer represent a continuous variable and become a set of discrete entities\(30,31\). Despite working at individual-level, the simulations can achieve results at the level of population, community and even ecosystem organization\(30,32\). Thus, the Population Viability Analysis (PVA) through extinction risk estimation performed by IBM provides a good way to access the status species of interest\(30,33^\text{–}36\).

Tropical rivers are representatives of the greatest diversity of freshwater fish in the world, only in the neotropical region there are 8000 described species\(2,37\). This region has been undergoing an accelerated process of implementation of hydroelectric plants, from small to large dams\(2\). In the Brazilian Amazon alone, 416 projects have already been implemented and 334 are being planned\(41^,14\). This region has a high potential for hydroelectric expansion, as it has large stretches of rapids and waterfalls\(33^,38^,39\), and is home to about 16% (2411 described species) of fish diversity. Due to the characteristics of the environments (presence of rapids and waterfalls) the places where these projects are implemented have fish fauna with great diversity of species, morphological and functional\(2,40\). An example of this are the hydroelectric projects on the Madeira and Xingu rivers\(2,37\). Located on the Xingu River, Belo Monte HPP may be the record holder in terms of loss of biodiversity, as it is located in a highly endemic place\(41\). Belo Monte was built in the middle Xingu River region, in a stretch known as Volta Grande do Xingu, home to populations of rare and endemic species with lithophytic and current habits\(42,43\).

Among these populations, those of *Hypancistrus zebra* Isbrucker & Nijssen, 1991, stand out, since the project covers the entire area of occurrence of the species. Currently, this species is included in the category of Critically Endangered according to the A3c criterion, which deals with a reduction \(\geq 80\%\) of the past, present or projected population, based on habitat quality and/or reduction of the occupied area (AOO) and extent of occurrence (EOO)\(44\). *Hypancistrus zebra* is a species of fish in the subfamily Hypostominae (Loricariidae, Siluriforme) known for having a black and white oblique stripe pattern on the body and fins, and a snout with an “E”-shaped “striped” pattern\(45^\text{–}47\). These characteristics allow it to be highly valued in the ornamental fish market, and the high value of acquiring the specimen has generated great demand in the clandestine market\(46,48\). However, the impact caused by the Belo Monte HPP is the main concern regarding the viability of its populations\(44\). Furthermore, there are no data, or even predictions, about the current situation of natural populations of *H. zebra*.

Therefore, we seek to understand how the variation in the intrinsic parameters of the species *H. zebra* can affect its population viability. Additionally, we intend to answer the following questions: (I) What are the combinations between the values of birth and death rates necessary to keep the population viable? (II) What are the combinations between the level of influence of habitat specialization and intraspecific competition in the persistence of this species? (III) Based on the generated scenarios, what is the viability condition of natural populations?
Results

The algorithm that describes the effect of birth and mortality rates on the population viability of *H. zebra* (MetaZebra 01) presented 137 (31%) scenarios with 100% persistence of the populations (Table 1). The remaining scenarios, 304 (69%), had some chance of extinction, ranging from 0.020 to 1.00, with 201 (45%) of the scenarios having a probability greater than 50% of extinction and 162 (36.7%) of the scenarios had 100% chances of extinction (Table 1). Based on our results, the combinations between the values of birth and death rates necessary to keep the population viable must have a birth rate greater than 0.55 and a mortality rate lower than 0.25. Otherwise, the population starts to decline, however it does not inhibit the chances of the population re-establishing itself. However, if a $b$ is less than 0.55 and $d$ greater than 0.6, the population goes into extinction.

### Table 1

Values of population survival probability in different combinations in the birth rate ($b$) and in the mortality rate ($d$) estimated by the model. Values closer to 1 represent persistence of the population, values in yellow and next to the red are scenarios between mid to low chances of persistence. While values in red represent 100% of the population remaining over a long period of time.

<table>
<thead>
<tr>
<th>Birth rate ($b$)</th>
<th>0.1</th>
<th>0.15</th>
<th>0.2</th>
<th>0.25</th>
<th>0.3</th>
<th>0.35</th>
<th>0.4</th>
<th>0.45</th>
<th>0.5</th>
<th>0.55</th>
<th>0.6</th>
<th>0.65</th>
<th>0.7</th>
<th>0.75</th>
</tr>
</thead>
<tbody>
<tr>
<td>1,000</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.05</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.15</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.25</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.3</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.35</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.5</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.55</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.6</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.65</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.7</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.75</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.8</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.85</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.9</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.95</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1,000</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

As for the algorithm used to describe the influence of the level of habitat specialization and intraspecific competition on the species’ persistence (MetaZebra 02), we had 219 (49.6%) scenarios with 100% persistence (Table 2). There were 345 (78.2%) scenarios with a greater than 50% of persistence. Our results showed that the combinations between the values of the rates of tolerance level and radius of competition necessary to maintain the persistence of the population owe the level of tolerance with a rate greater than 0.5 and a radius of competition with a rate less than 0.4. No scenario presented a 100% chance of extinction of the population (Table 2). As for the level of influence of habitat specialization and competition, the results showed that tolerance has a greater influence on population persistence than the effect generated by intraspecific competition. The competition starts to act more conspicuously on the population from radius greater than 0.4. The tolerance level is more likely to keep populations viable with tolerance rates higher than 0.5, below these rates the population starts to influence population decline.
The variation in habitat quality in the landscape (spatial variation) also affects population persistence. Stochastic variation and can make it easier to predict the actual population fate. The persistence of a population depends on the number of short-term population persistence, just as a high birth rate and low mortality do not guarantee long-term persistence of time.

### Discussion

The 441 scenarios generated by the model showed that the relationship between the intrinsic birth rate above 0.6 with the intrinsic death rate below 0.5 allows populations to remain viable for a long time (Table 1). The model also showed that the number of scenarios with some extinction risk was higher (69% of the scenarios) than the number of scenarios with a 100% chance of persistence. This may be an indication of the vulnerability of _Hypancistru zebra_ populations to events that may change the demographic stochastic process.

Stochastic birth-and-death process is probably the simplest modeling approach to predicting extinction. In simple models they are independent rates, but they can show high correlation through the years in real populations, since the temporal variation can provide years with high or low resource availability, affecting the reproduction and survival of individuals. However, not always that the value of _R_ is negative (the birth rate lower the death rate) is a guarantee of short-term population persistence, just as a high birth rate and low mortality do not guarantee long-term persistence of time. The high number of scenarios expands the view of stochastic variation and can make it easier to predict the actual population fate. The persistence of a population depends on stochastic or variation.

Generally, the persistence of a population is ensured by large, connected, suitable and close to each other habitats, high population reproductive rate and environmental conditions with variation in balanced carrying capacity. _Hypancistru zebra_ is an endemic species, restricted to about 170 km from the middle Xingu river, possibly its populations are closed and currently the environmental conditions and available resources are not favorable due to the dam.

The variation in habitat quality in the landscape (spatial variation) also affects population persistence, therefore, the feasibility presented by the model does not guarantee the real maintenance of _Hypancistru zebra_ populations. Generally, stochastic events are of concern especially for viability of small populations, as they present greater chances of extinction due to their demographic fluctuation, whether due to demographic stochasticity (internal mechanisms) or...
environmental stochasticity (external mechanisms)\textsuperscript{30,72,73}. These events are linked to birth and death rates\textsuperscript{74}. We consider that the three natural populations of *H. zebra* are represented by high population size, which could have a different result in viability if their populations go into decline, either by mortality or the removal of individuals with overfishing.

In the model, it was observed that tolerance has a greater influence on population persistence than the effect generated by intraspecific competition (competition radius; Table 2). Since the radius is less than 0.5, the tolerance force is greater. However, in scenarios with a radius greater than 0.55, competition starts to have a greater effect on populations, regardless of the high tolerance rate. Therefore, even in scenarios with a high tolerance rate, the probability of population extinction will be greater when the competition radius reaches high values in the rate. However, if both rates are low, it is possible that the population will be maintained. This indicates that intraspecific competition is an interaction that acts more visibly in the population from a radius greater than 0.4. On the other hand, the tolerance level is more likely to maintain viable populations with tolerance rates greater than 0.5, below these rates the population starts to present a greater risk of extinction.

We did not include effects of anthropogenic actions in the study. We emphasize that models that address the variation between individuals is essential to develop and study population dynamics and associate it with different life history tactics\textsuperscript{75}. The development of modeling with intrinsic parameters allows testing uncertain impacts on the life history, evaluating the demography of species\textsuperscript{76}, in addition to making it possible to identify predominant parameters in the system when well delimited\textsuperscript{77}.

Data from the life history or population growth rate are used for the functioning of the PVA, this information serve as parameters in the model projecting the population dynamics\textsuperscript{78}. As these rates vary, they influence intrinsic processes (e.g. stochasticity, genetic drift, demographic, social structure)\textsuperscript{79}, and given the fluctuation in population size and over time, random (stochastic) variation occurs. The greater the amount of information about the population, the more detailed is an MBI\textsuperscript{30}, which benefits better results, but requires a more advanced computer system\textsuperscript{80,81}. MBI is widely used to assess population dynamics through intrinsic rates\textsuperscript{82}. Individual variation is the evolutionary basis existing in all populations and organisms and this individual heterogeneity occurs in practically all characteristics, including reproduction, physical conditioning and survival\textsuperscript{75,83–85}.

Our results show a 100% probability of population viability for the three natural populations of *H. zebra*, given the combination of values of birth rate (b = 0.6) and intrinsic mortality (d = 0.3). However, the models that generated the scenarios did not include fishing pressure and habitat change caused by the Belo Monte HPP, which covers the entire area of occurrence of the species\textsuperscript{56,57}. Due to the fact that these impacts already exist in the area of occurrence of the species and already promote changes in conditions and resources, we can suggest that populations are threatened. Since a decrease in the birth rate or an increase in mortality would cause species to move from the area green (100% probability) for areas with a lower probability of viability.

The model that investigates the relationship between birth and mortality rates showed that birth rates below 0.55 and mortality rates above 0.25 can lead to extinctions. Our model populations showed little difference in these thresholds, 0.6 for birth and 0.3 for mortality, reinforcing the idea that natural populations nowadays would not be in conditions of 100% viability. Females of *Hypancistrus zebra* guarantees breed in plots and have low fertility\textsuperscript{43}. This can demonstrate that the natural behavior of the species prioritizes spending more energy for individual maintenance than for reproduction, such as spending looking for mates and investing in offspring. In the absence of a good amount of available resources, individuals tend to choose to spend more energy with reproduction (increasing the birth rate of newborns and reducing adult individuals) or avoid the risk of mortality (lower mortality of mature individuals, but low rate of newborns)\textsuperscript{86}, influencing a dynamic in population birth and mortality rates. Poor reproduction and high mortality (positive and/or negative covariance) also result in resource availability in the face of temporal variation.

Loricariidae show low tolerance in sections of reservoir formation\textsuperscript{49} and species with characteristics adaptable to fast-flowing water habitats are more vulnerable to dams\textsuperscript{2}. In addition, the model showed that natural populations of *H. zebra* are viable, but it is possible to observe that it is an intrinsically sensitive species and may be vulnerable to human disturbances. So it is also with regard to the level of specialization of the habitat. In Table 2, no scenario showed 100% extinction, however, it is possible to observe that tolerance has a greater influence on the intraspecific competition radius, demonstrating the high specialization of the species. Although these is not small populations, it is an endemic species, with high removal of specimens from nature for illegal sale\textsuperscript{48,49} and its habitat is practically all affected by the implementation of a hydroelectric plant\textsuperscript{44}. In addition, paucity of data is likely a major limitation in assessing population viability\textsuperscript{87}.

The reduction in the birth rate can be a process of response to increased mortality, fewer individuals to reproduce, or the removal of individuals from the population, either through migration or fishing, in the case of fish. Another worrying factor in population decline is overexploitation of the species. Such a decline had already been reported due to the consequent history of exploitation and habitat loss caused by mining activities\textsuperscript{88} and even after the fishing prohibition, their specimens are still being collected due to their high value and difficult inspection\textsuperscript{89}. In this way, it will promote a reduction in the population's birth rate, but the change in habitat does not only affect recruitment. Considering the paucity of studies on the niche and reproductive biology of *H. zebra*, possibly it is a kind of *k*-strategist due to its low fertility that takes time to reach sexual maturity, takes care of parents, is sedentary and has a long life cycle\textsuperscript{55–57}. Given the parameters that fed the algorithms, the tolerance level is greater than the concurrency radius effect.

Our study presents a theoretical ecological intrinsic modeling for predicting how the populations of *H. zebra* will behave with variation of the parameters, showing that a high rate of withdrawal of individuals or impacts caused by the alteration of the water flow in the natural environment can cause a reduction of population viability that will generate extinction of its populations. In addition, some authors claim that *H. zebra* is sensitive to changes in water quality\textsuperscript{88} and climate changes\textsuperscript{90}. In addition to these factors, the species is considered endemic\textsuperscript{42,47} which corroborates that it is a more specialized niche species. Their narrow tolerance range indicates that their populations are below the median tolerance level in Table 2, which should not be a concern if the current ecological condition is to contribute to greater competition between individuals for resources. In natural conditions without human alterations and capture pressure,
natural populations of *H. zebra* are viable in a delicate balance, however, according to the model, small disturbances can promote a decline in population growth, generating great probabilities of the species' extinction. Impacts such as the change in the hydrological cycle caused by the Belo Monte HPP dam, as well as the high rate of specimen withdrawal by illegal fishing, will synergistically cause irreversible damage to the population viability of this species.

**Material And Methods**

In this research, was used the IBM type Agent Based Modeling (ABM). The algorithms used (Supplementary Material I, II and III) were developed within the platform Matlab® version R2015a. The model description is structured according to the protocol ODD (Overview, Design concepts, Details) updated suggested by Grimm et al. (2010).

**Purpose**

The purpose of the models is to assess the effect of varying intrinsic parameters on the population viability of an endemic fish species. Although endemism and species unity are not a limiting feature for replicating models. Thus, the developed algorithms indicate how (i) the ratio between the birth and mortality rates (Supplementary II – MetaZebra01) and (ii) the level of specialization and competition (Supplementary III – MetaZebra02) of the specimens affect population viability.

**Entities and state variables**

The model has only one entity, specimens. The specimens are representatives of a single species of fish distributed in three populations of different sizes. Each specimen was characterized by a set of specific parameters based on information from literature and breeders of the species. Basically, we used characteristics that influence population dynamics, including the following state variables: longevity, age of sexual maturity, annual reproduction number, instant birth rate (b0), instant mortality rate (d0), interference of each individual in population growth (b1), interference of each individual in population mortality (d1), time (t), radius, richness (S), tolerance (tol) and population size (N). We consider the following assumptions for determining the values of our variables:

**Longevity.** Species of the same family (e.g. Ancistrus ssp.) can reach more than 15 years of age. According to aquarists, longevity in captivity is at least 15 years for the species under study. However, probably in a natural environment, specimens have a shorter life span when compared to individuals in good health in captivity. Therefore, in the model, we estimate that specimens can reach 12 years of life in nature.

**Age of sexual maturity.** According to breeders who produce the species in captivity, individuals reach sexual maturity at the age of three.

**Annual reproduction rate.** To determine b0, we need to know the number of individuals who enter the cohort each year by birth. Because the male copulates with more than one female, we only consider females in the calculation. We used 50% of the specimens of each hypothetical population, since the parameter is more related to the fertility of females, as the number of individuals depends more on that sex, so the sex ratio considered was 1:1. Each female spawns an average of 14 eggs per spawn. In captivity, multiple spawning are observed throughout the year. In a natural environment, reproduction can occur at any time of the year, but two reproductive peaks were observed annually. We estimate that 95% of the females in each cohort are able to reproduce. Most females spawn twice a year, possibly larger females with better nutritional performance, are more apt for a greater number of annual reproduction. We consider the following rates: 35% of females reproduce only once / year, 45% reproduce twice / year and only 15% of females reproduce three times / year.

**Mortality rate.** Regarding mortality, we arbitrarily define that in a natural environment despite parental care, the mortality of individuals under one year of age is high, around 50%, due to predation and competition for hide. Additionally, adult females are assigned a 25% mortality rate, while adult males have 20%. We consider that the behavior of the male to stay hidden and protecting its crevice (Ramon, 2011; Gonçalves, 2011) provides less vulnerability to males and consequently a lower mortality rate than females in the population.

**Intrinsic birth rate (b0).** According to the assumptions of the hypothetical natural population size and annual reproduction rate, we obtained the result of b0 = 0.6. We used only the females of each population (50% of the individuals) and the rate value was obtained through a difference equation presented in more detail in section 2.6 (sub-models).

**Intrinsic mortality rate (d0).** Following the assumptions of the hypothetical natural population size and annual mortality rate it was estimated as d0 = 0.3. We used only the females of each population (50% of the individuals) and the rate value was obtained through a difference equation presented in more detail in section 2.6 (sub-models).

**Interference of each individual in the growth (b1) and mortality (d1) of the population.** We did not consider the effect of b1 (interference of each individual on population growth) and d1 (interference of each individual on population mortality) in the models.

**Time (t).** Time was measured in years in models with t = 0 as a starting point, ending in 1,000 years.

**Radius.** The radius rate varies from 0 to 1, being 0 when there is no competition and 1 when everyone is competing with each other. There are no studies that say how competitive the species is. So, we determine an average value (0.5).

**Richness (S).** As the study deals with the population of just one species, we considered S = 1.

**Tolerance (tol).** There is also no information on the species tolerance, therefore, we determined an average value (0.5).
Initial population size \((N)\). In both modules of model execution, we considered \(n\) the initial size of the population with 100,000 individuals.

Process overview and scheduling

The processes of the models promote the simulation of the dynamics of individuals within the population in an environment without anthropic effects and interspecific interaction (Figure 1; Supplementary I – PopZebra). The process begins with the entry of a cohort with an initial number of individuals \((n = 10,000)\) in the population. Gradually, individuals are assigned to the Optimal level range (OLR) randomly determined, or to the Maximum or Minimum tolerance level range (LRMaxMin) ranging from zero to one, according to the model. Specimens included in the OLR are aged, go through the update of age and later young individuals go through the process of sexual maturity until they reach the age of sexual maturity (adult individuals), the individuals enter the reproduction process, causing the origin of a new cohort by birth.

As for the individuals that enter FNMaxMin, they are destined to the competition processes for resources (territorialism and/or food). Randomly, some individuals are classified as survivors and enter the aging process and the consecutive ones mentioned above, while the rest are removed from the model by the mortality process. Individuals who reach the age of longevity are also removed by the model through the process of natural mortality (by age).

This dynamic is generated through the PopZebra program (supplementary material I). However, to meet our objectives, two metaprograms were developed. MetaZebra 01 (supplementary material II) for objective one and MetaZebra 02 (supplementary material III) for objective two. The values of the variables used in the algorithms (shown in Table 3) are based in knowledge gathered in specialized hobbyists’ magazines, hobbyists and fishermen personal communications, as well as experiments carried out in captive breeding program in the laboratory. The MetaZebra 01 algorithm was built to create combinations of birth and mortality, thus varying \(b_0\) and \(d_0\) from zero to one in 0.05 intervals. Considering \(H.\ zebra\) as r or k strategist (depending on the tolerance rate). This procedure will build an interface of values where the x-axis will be the entire variation of the mortality rate while the y-axis will be the entire variation of the birth rate and the 441 cells (21 birth values multiplied by 21 mortality values) will represent all possible combinations between these two rates. Thus, indicating the effect of the ratio between birth and mortality rates on population viability.

<table>
<thead>
<tr>
<th>Variables</th>
<th>PopZebra</th>
<th>MetaZebra 01</th>
<th>MetaZebra 02</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maturidade sexual (year)</td>
<td>3</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Longevidade (year)</td>
<td>12</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>(b_0)</td>
<td>-</td>
<td>0.0.05:1</td>
<td>0.6</td>
</tr>
<tr>
<td>(b_1)</td>
<td>0</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>(d_0)</td>
<td>-</td>
<td>-</td>
<td>0.3</td>
</tr>
<tr>
<td>(d_1)</td>
<td>0</td>
<td>0.0.05:1</td>
<td>-</td>
</tr>
<tr>
<td>(t) (year)</td>
<td>1,000</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>(r) (year)</td>
<td>-</td>
<td>0.5</td>
<td>0.0.05:1</td>
</tr>
<tr>
<td>(t) (year)</td>
<td>-</td>
<td>0.5</td>
<td>0.0.05:1</td>
</tr>
<tr>
<td>sp ou S</td>
<td>1</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>(n)</td>
<td>100,000</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

As for the MetaZebra 02 algorithm, it was created to vary the tolerance and the radius of competition, thereafter the tol and the radius vary from zero to one in 0.05 intervals. Considering the species as generalist or specialist (depending on the tolerance rate) and little or very competitive (depending on the competition radius rate) in the face of changes. This procedure will generate an interface of values, where the x-axis will be the entire variation of the competition radius rate and the y-axis will be the entire variation of the tolerance rate and, the 441 cells (21 tolerance values multiplied by 21 radius values competition) will represent all possible combinations between these two rates. This way, it is possible to compare the effect of the species’ level of specialization (tolerance) and relate it to the influence of intraspecific competition on the persistence of \(H.\ zebra\). Each algorithm generated 441 combinations of values (scenarios) that represent the population’s probability of survival over an interval of 1,000 years. This probability was calculated from five replicates of each combination.

Design concepts

**Basic principles.** Population dynamics are maintained with the constant influence of several factors. Growth is determined by the number of entities (individuals) that enter (birth and migration) and leave (mortality and emigration) the population\(^{59}\). The population grows exponentially until it is controlled by the amount of resources available in the environment, called support capacity\(^{60}\). In addition, ecological factors within the habitat will influence the interaction between individuals (intraspecific interaction) and with the environment (Law of Tolerance), which depending on the level of specialization of the species will determine the growth and survival of this set of organisms\(^{61–63}\). We assumed, in the model under study, the population as being a closed one (entry of individuals by birth and exit by mortality), since it is an endemic species with no migratory characteristics, restricted to about 170 km of the river section.

**Emergency.** Population dynamics included an emerging result of behavior and interactions between individuals and their habitat.
Interaction. Only internal interactions are recorded in the process. Intraspecific competition is about organisms of the same species that start competing for resources when demand is greater than what the environment can offer, causing a reduction in population growth due to mortality. Another interaction that will influence the survival of individuals is the level of specificity in terms of habitat (general and specialist species). Species with a more generalized niche tend to occupy large geographical areas and are vulnerable to factors that reach large scales, while specialist species have a restricted niche, occupying small geographical areas, their populations are small and more vulnerable to extinction, usually endemic and rare species are specialists.

Initiation

Initially, the condition variables b0, b1, d0, d1, radius, time, n, S and tol generate the behavior curve of the population of the single species under study, executed through the IND function, creating the intrinsic values of the species. Then, the characteristics of the individuals are inserted, using information from the following variables: longevity, age of sexual maturity, tolerance value (ranging from tol = 1 to 0 with 0.05 intervals) and random optimal values (random numbers). Optimal values will not influence the model, as they are irrelevant when S = 1. This way, we created initial conditions to generate the first cohort with n = 10,000 individuals aged = zero (year of age). Each individual is created based on the variation of the optimum and tolerance.

Submodels

Intrinsic birth (b0) and mortality (d0) rates. For one of our models, we had to define b0 and d0 of the estimated natural populations. b0 (Equation 1) and d0 (Equation 2) were calculated using the following expressions:

\[ b = \frac{B}{N_t} \quad \text{Equation 1} \]

where B represents the number of births, and \( N_t \) represents the size of the current population.

\[ d = \frac{D}{N_t} \quad \text{Equation 2} \]

Where, D represents the number of deaths, and \( N_t \) represents the size of the current population. We considered only the females (50% of the value) of each population in the calculations.

Both b0 (0.6) and d0 (0.3) showed the same result in the three populations.

Aging of individuals and competition. Each cohort is aged by adding one year. Effective number (Ne) is calculated by the product of the radius and the population size (sum of all living individuals in the base year).

Birth. From the third year of life, when the age of sexual maturity begins, individuals start reproduction and births are calculated by individuals, following equation 3:

\[ B = b_0 + b_1 \times Ne \quad \text{Equation 3} \]

Where, \( b_0 \) represents the intrinsic birth rate, \( b_1 \) when each individual interferes with population growth and \( Ne \) the effective number.

Mortality due to the number of individuals. Depending on the radius and population growth, individuals are removed from the population, following the following equation 4:

\[ D = d_0 + d_1 \times Ne \quad \text{Equation 4} \]

Where, \( d_0 \) represents the intrinsic mortality rate, \( d_1 \) when each individual interferes in the mortality of the population and \( Ne \) the effective number.

Mortality by age. When the surviving individuals of each cohort reach 12 years of age, they are eliminated from the population by the aging mortality process.

Delimitation of natural populations and viability study

As for the third objective, to infer about the viability status of natural populations, we defined the existence of three populations of H. zebra considering the proximity of the known occurrence points and possible natural barriers (Figure 2), since there are no studies that define the size of existing natural populations. Taking into account that we do not know the location of the geographical barriers that separate the populations, we defined only three natural populations: Gorgulho da Rita (from the city of Altamira to Volta Grande), Volta Grande (from the downstream of Altamira to the upstream of Vila Belo Monte) and Belo Monte (from Vila Belo Monte to Vitória do Xingu; Figure 2).

Population sizes were defined based on literature and informal reports by fishermen and personal observations. This informal estimate was supported by the rate of offered smuggled specimens on the internet. According to some information, in 2017, around 10,000 specimens of H. zebra were removed, from nature, monthly in the dry season (July to November). It was assumed that in the high-water period, 40% (4,000 individuals/month) of this quantity was illegally collected. We assume that the number of individuals taken from nature represents 10% of the population, generating a total size of 7,800,000 distributed among three populations. The abundance of each population was estimated based on the abundance of the capture samples of Gonçalves (2011). Given the total size of the species’ metapopulation, we consider that 15% (1,170,000 individuals) belong to Gorgulho da Rita, 60% (4,680,000) are in Volta Grande and 25% (1,950,000) in Belo Monte. So, the study of the viability of the three populations was carried out through the interface that combines birth with mortality rates, using the MetaZebra 01 algorithm. We used the values that can be found in equations 1 and 2 (see Submodels) of intrinsic birth rate (b0 = 0.6) and intrinsic mortality rate (d0 = 0.3) for the three natural populations and related their viability status.
Declarations

Author Contributions

L.C.N.S. analyzed the data and results, wrote the main manuscript; L.M.S. contributed to the revision of the text; P.D.M.J. contributed to manuscript design and supervision and T.B.V. supervised the study and analyzed the data. All authors revised the text during the review process and gave approval before submission.

Funding Information
Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Finance Code 001.

Ethical statements
Not applicable

Consent to participate
Not applicable

Consent to publish
Not applicable

Competing Interests
The authors declare no competing interests.

Additional Information

Supplementary Information The online version contains supplementary material available at https://doi.org/10.5061/dryad.msbcc2g0h

Correspondence and requests for materials should be addressed to L.C.N.S.

Acknowledgments

This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Finance Code 001. We thank Rita Pelicano for revising the English.

References


34. Giacomini, H. C. A Vulnerabilidade da Ictíofauna à Invasão por Espécies Exóticas Peixes: Um Modelo Baseado no Indivíduo. (Universidade Estadual Paulista, 2006).


89. IBAMA. Diagnóstico Geral das Práticas de Controle Ligadas a Exploração, Captura, Comercialização, Exportação e Uso de Peixes para Fins Ornamentais e de Aquariologia. 217 (2008).


**Figures**

![Diagram](image_url)  
**Figure 1**

Processes that promote the dynamics of specimens in the model over an interval of 1,000 years.
Figure 2

Species occurrence area in the current overlap of the stretch: (A) Distribution of the occurrence points of the three hypothetical populations: Gorgulho da Rita, Volta Grande and Belo Monte; (B) Illustrative image of *Hypancistrus zebra*.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- SupplementaryIPopZebra.txt
- SupplementaryIIIMetaZebra01.txt
- SupplementaryIIIMetaZebra02.txt