

# Lateral migration of *Arapaima gigas* in floodplains of the Amazon

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**Abstract** – This study deduced in detail the lateral migration –those between river channels and floodplain habitats – of the pirarucu (*Arapaima gigas*), a giant, obligate air-breathing species of the Amazon Basin. Over a thousand samples of the pirarucu were taken through counts of the individuals performed at the moment of aerial breathing; these samples were taken in eight habitats of a floodplain near the Amazon River every week throughout an entire flood cycle. The lateral migration of the pirarucu accompanied water level fluctuations closely. As water levels rose, the pirarucu migrated to increasingly higher habitats in flooded forests and remained there during high water levels. As water levels declined, the pirarucu migrated first back to lower habitats of flooded forests, then to communicating channels, and, eventually, to the lakes, where they remained during low water levels. These results allow for a conceptual model of lateral migration of floodplain fishes.

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**Key words:** Brazil; flood-pulse; habitat and temporal heterogeneity; várzea

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## Introduction

Fish migration optimises the use of resources in temporally and spatially heterogeneous environments by investing energy in movements that bring larger energy returns (Hall 1972). Moreover, it ensures the survival of fish populations, and enhances the yields of fisheries and the structure and function of entire ecosystems (Harden Jones 1968; Welcomme 1979). Yet, the spatial and temporal scales of fish migration in floodplains are poorly understood (Junk et al. 1989; Winemiller & Jepsen 1998). The subject deserves attention because floodplains are among the most threatened ecosystems (Tockner & Stanford 2002), and several floodplain fishes are threatened with extinction (Allan et al. 2005).

Floodplain fishes migrate in two main ways: longitudinally, along the main river channel, and laterally, between the main river channel and the floodplain (Lowe-McConnell 1987). The understanding of the latter, the ‘lateral migration’, is so limited that a general scheme proposed in 1971 (Lagler et al. 1971) and slightly modified in 1987 (Lowe-McConnell 1987)

remains uncontested. The subject has been addressed only by a few detailed studies (Winemiller 1990; Fernandez 1997). Most studies have focussed on seasonal and temporal variations of floodplain fish assemblages and communities (Lowe-McConnell 1964; Mago-Leccia 1970; Rodriguez & Lewis 1997; Saint-Paul et al. 2000; Silvano et al. 2000; Petry et al. 2003; Galacatos et al. 2004).

The lateral migration of floodplain fishes follows closely the dynamic ‘pulsing’ of water levels (Junk et al. 1989). The ‘flood-pulse’ creates a moving littoral zone that advances into and over ‘terrestrial’ habitats when water levels rise, gradually transforming ‘terrestrial’ habitat into ‘aquatic’; the process is reversed when water levels decline (Junk et al. 1989). In river-floodplain systems, many fish species spawn during rising water levels, as inputs of nutrients and suspended solids promote maximum availability and production rates of aquatic vegetation (Bayley 1989). Young-of-the-year and predators migrate with the moving littoral, colonizing the floodplains in a timely fashion (Bayley 1988). The flooded forest generates an environment with relatively low

predation pressure upon fishes, as the great increase in flooded area lowers animal densities (Lowe-McConnell 1987). Food is generally abundant, and many fishes feed on the abundant detritus available in the newly flooded areas and on pollen, fruits, seeds, and some insects that drop into the water from the canopy forest (Goulding 1980). During high water levels, decomposition processes tend to increase relative to production, generally resulting in decreased dissolved oxygen levels (Junk et al. 1989). Many fishes possess adaptations to live in deoxygenated areas (Junk et al. 1983). During low water levels, only a few of the formerly flooded habitats contain water. Of those, the lakes and connecting channels tend to have high temperatures and low oxygen levels (Junk et al. 1983); the main river channels are exceptional in maintaining more moderate temperature and oxygen during low water levels. During declining water levels, most fish are forced to migrate out of the floodplains and into main river channels in search of conditions in which they can survive (Welcomme 1979). Only fishes with adaptations to deoxygenated environments migrate to the lakes and connecting channels, and the others go to the river channels (Lowe-McConnell 1987). During low water levels, many fishes show marked decreases in feeding activity (Junk 1985).

Despite this understanding, however, most studies on lateral migration have not analysed how fishes utilise the spatial heterogeneity of relatively pristine floodplains over an entire flooding cycle (Winemiller 1990, being an exception). This is critical because in pristine floodplains not only do water levels change daily, and sometimes dramatically, but the 'flood pulse produces and maintains a highly diverse and dynamic habitat structure' (Junk et al. 1989). Here, the lateral migration of the pirarucu (*Arapaima gigas* Shinz) in a pristine floodplain of the Amazon Basin was studied in detail. The following research questions were asked: (1) What are the main drivers of the migration of the pirarucu in floodplains? (2) What habitats are used the most? (3) To what extent and in what ways is the diversity of habitat structure of floodplains used by the pirarucu?

The pirarucu is an important fish of the Amazon and Essequibo Basins. By being piscivores (Sánchez 1969) and attaining sizes of up to 3 m in length and 200 kg in weight (Queiroz 2000), they probably play a key role in regulating energy and nutrient flows of aquatic ecosystems. As they possess tasty meat and an obligatory air-breathing system, they move to the surface to breath every 5 to 15 min, and they can be harpooned easily to develop important fisheries (Veríssimo 1895; Martinelli & Petreire Jr. 1999). Pirarucu fisheries are so important that the few data available indicate they are overfished in most of the Amazon (Isaac et al. 1998; Queiroz & Sardinha 1999), have

been extirpated in some regions (Goulding et al. 1996), and consequently are even vulnerable to extinction (World Conservation Monitoring Centre 1996).

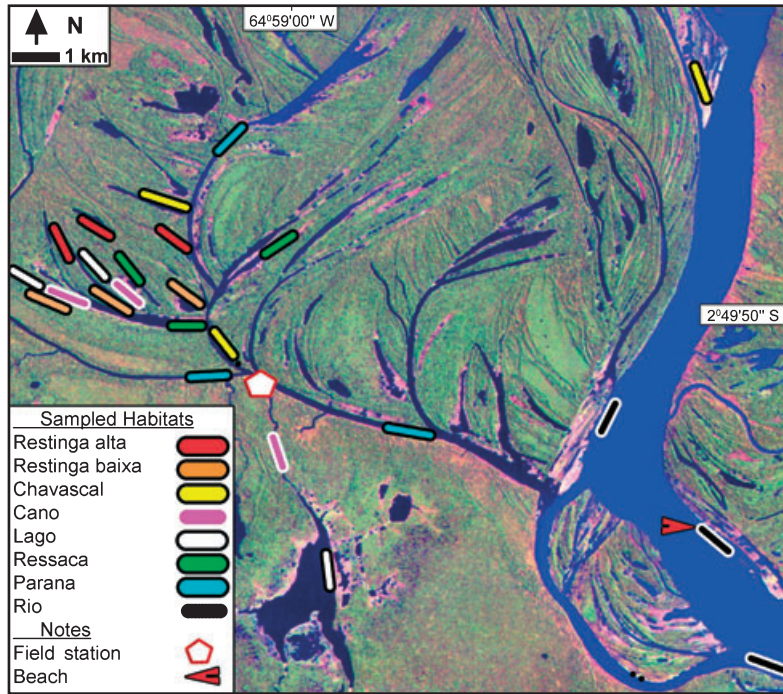
Despite this situation, virtually no information exists on the migration patterns of the pirarucu, making it difficult to assess and manage the populations. The pirarucu are characterised as being 'sedentary', meaning they do not conduct long migrations (Isaac et al. 1993). Only a very minimal outline of the lateral migration of the pirarucu was speculated from their annual cycle of events in an unpublished study (Queiroz 2000). Queiroz (2000) speculated that the pirarucu inhabit the lakes during the dry season, where they feed and the adults develop gonads, court, build nests, and mate. During rising water levels, the water previously concentrated in the lakes and some channels (including the river itself) spreads to much greater areas. The pirarucu appears to migrate to the flooded forests where males care for the offspring. During the initial and rapid declining of water levels, parental care ceases and the pirarucu migrate back to the river, connecting channels, or lakes where they are fished. The cycle then repeats itself. Little is known about the lateral migration of the pirarucu, or of other fishes, because of the practical difficulties of obtaining statistically reliable data using conventional methodologies, such as gillnets or sonar for example. During high water levels, the forested habitats of floodplains are densely vegetated, and fish population densities are low, especially when they are overexploited as the pirarucu (Queiroz & Sardinha 1999).

## Materials and methods

This study deduced the lateral migration of the pirarucu by detecting their per-effort presence periodically in all habitats of a river floodplain system throughout an entire flood cycle. For this, the presence of the pirarucu was determined by counts, performed by two fishers, of the individuals at the moment of obligate aerial breathing. Water levels, current velocity, and transparency were measured simultaneously. Sampling occurred between 29 March 1999 and 21 May 2000, yielding a total of 1035 samples of pirarucu.

### Study area and physical variables sampled

The Mamirauá Sustainable Development Reserve (State of Amazonas, Brazil) is at the confluence of the Solimões and Japurá Rivers (approximately 3°S and 65°W; Fig. 1). The reserve is formed by pristine várzea, a type of floodplain that flanks the sediment-rich white water rivers of the Amazon; it is a complex mosaic of seasonally inundated rain forests, lakes, and



*Fig. 1.* The study area and the locations of the sampled transects. This satellite image was taken a few months before the start of this study, in 1999, during the dry season. The study area represents a typical pristine section of várzea floodplain. The large (light-blue) channel is the Japurá River (rio) with its white waters. The smaller (dark blue) channels and water bodies are the paraná, cano, ressaca, and lago habitats (see Table 1 for habitat definitions and Fig. 2 for schematic descriptions); most of them containing 'black waters' at the time the image was taken because of carbon-rich humic substances. The land between these channels and water bodies are the chavascal (light green), and restinga baixa, and restinga alta forest habitats (both are dark green). In many places, floating meadows (pink) abound during both the flood and dry seasons. The image comprises an area of about 450 km<sup>2</sup> of várzea floodplain; in Brazil, this ecosystem spans over an area of 107,000 km<sup>2</sup>.

winding channels (Irion et al. 1997). The study area is of the holocenic type (Ayres 1995), being completely flooded annually. Seasonal water temperatures vary between 27 and 31 °C (Sociedade Civil Mamirauá 1996).

A total of eight habitats of the várzea were sampled (Table 1). This stratification of habitats comprises all major types and is consistent with the literature and

local knowledge. At each habitat, three transects 1 km in length were established. The specific locations of the transects (Fig. 1) depended on their representativeness of major habitat types, similarity to the characteristics described by the literature and local knowledge, and the possibility of sampling by canoe (in some places that would be impossible). Also, they had to be close enough to each other and to the field station to allow weekly visits to every site.

The specific locations of the transects depended, also, on the existing variation within the rio and chavascal habitat types. In the rio habitat, all transects were established near and parallel to the shore because, according to the fishers, the pirarucu is never found in the middle of the rio where depth and water current velocity tend to be much greater. Two of the rio transects were established in relatively fast-flowing areas, and one (indicated in Fig. 1) near a slow-flowing area where a sandy beach is exposed during low water levels. As the water level declined, the beach emerged and the rio became narrower, so that the location of this transect moved towards the middle of the rio, but it always remained near and parallel to the shore, roughly in the same position. As water levels rose, the location of this transect moved back towards its original position.

For each transect, we measured water current velocity and transparency. Current velocity was measured using a floating piece of wood attached to a line of known length. The line was attached to the canoe used for sampling work, which was attached to objects fixed on land (e.g., trees, branches). The

Table 1. Sampled habitats of the várzea floodplain and their descriptions.

Habitat type	Description
<b>Entirely or mainly aquatic</b>	
Rio	The main river channel. The rio is wide (up to 3 km), deep (up to 50 m) and swift flowing (Junk, 1984); the Japurá River was sampled.
Paraná	Channels transporting river waters and crossing sections of várzea. Both ends connect to the rio (Junk, 1984; Crampton, 1998).
Lago	Lakes of various sizes and shapes (Junk, 1984). Lagos hold water throughout the flood cycle.
Ressaca	A shallow type of lago with a large and open mouth. Most ressacas dry up during the dry season (Local classification).
Cano	Channels connecting lagos to any other water body. Canos may dry up during dry season, making lagos physically isolated (Crampton, 1998).
<b>Mainly terrestrial</b>	
Chavascal	Low swampy woodland. Usually, chavascal forests are located behind levees (Ayres, 1995).
Restinga Baixa	Silt-heightened riverbanks and bars on which grows tall forest (Ayres, 1995).
Restinga Alta	Like the restinga baixa, but riverbanks and bars are higher and the forests are taller, older, and more diverse (Ayres, 1995).

wooden piece was put in the water, and the time taken for the line to stretch was measured. Care was taken to avoid potential bias in the measurements that could be created by the canoe. This methodology measures surface flow accurately (W. G. R. Crampton, University of Central Florida, Orlando, USA, personal communication). Transparency was measured using a secchi disk. On the day in which the flood cycle reached its maximum during the study period, we took 10 measurements of the depth of all transects using a sounding line. We measured water levels daily at the field station (Fig. 1), and used the data to calculate the mean depth of each transect we ran.

### Sampling the pirarucu

To sample the pirarucu, two local fishers used a modified version of the counting method described by Castello (2004). Castello (2004) demonstrated that experienced fishers can count the number of pirarucu accurately, by comparing counts made by the fishers (of pirarucu longer than 1 m) with independent estimates of abundance (calculated using total catches and mark-recapture methods). The two fishers and the author

paddled silently along all transects every week in an aluminium canoe 5 m in length looking for breathing pirarucu. Two exceptions were made. The first was that during the dry season some habitats were dry; so obviously they were not sampled. The second regards the lago habitat. The cano habitat, which is the only type of habitat that connects the lago to any other water body during low water levels (Table 1; Fig. 2a), is shallower than the lago. So, when the cano dries up, the lago becomes disconnected from all other water bodies, making it impossible for fish to migrate in or out of the lago. This made, also, our access to some of the lago transects very difficult. Thus, during the period when the lago was physically isolated, the lago was sampled only in the first week after it became isolated. In doing this, it was assumed that the abundance of pirarucu in the lago was constant throughout that period. This is a reasonable assumption because two of the lago transects were in areas where fishing is prohibited and protected by paid guards, and the pirarucu is too large to be predated on. The third lago transect was in a lago of large size that received little fishing pressure. Sampling the lago transects was resumed in the first week when the cano transects connecting to them were flooded.

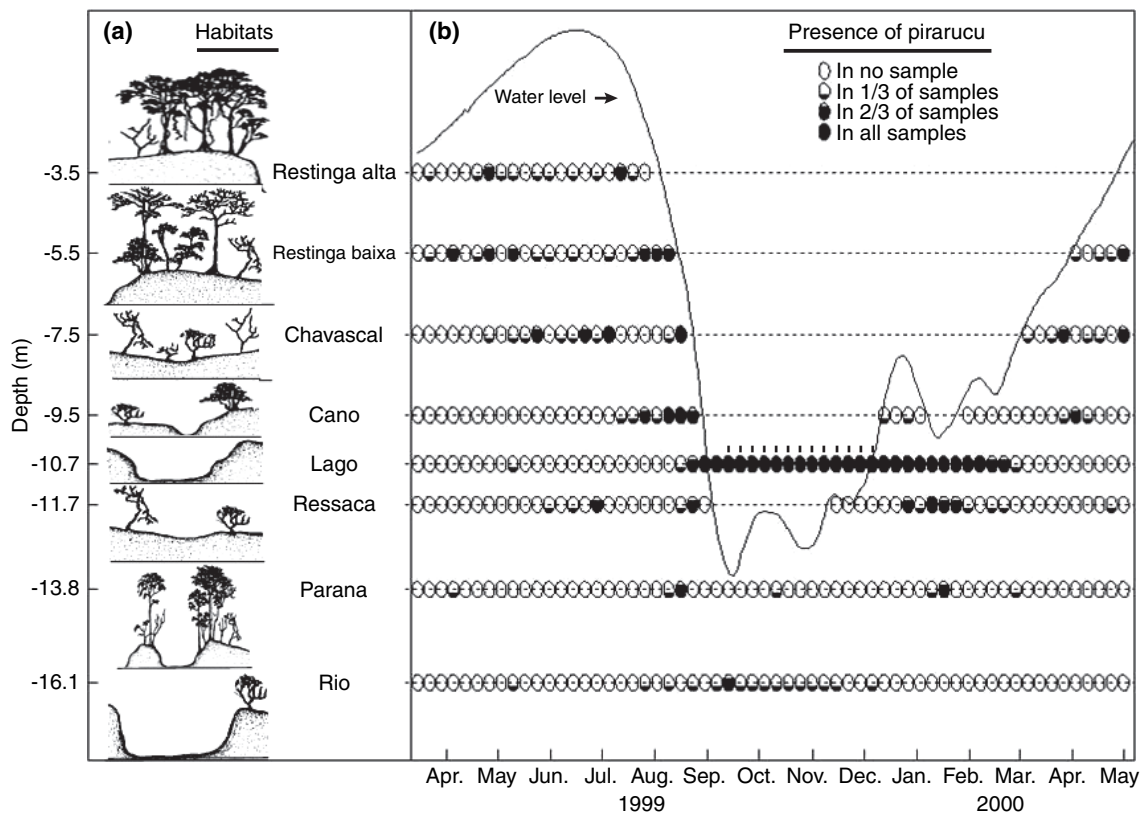


Fig. 2. (a) Schematic description of the sampled habitats of the várzea floodplain. (b) Seasonal variation of the relative abundance of the pirarucu in the sampled habitats and the pulsing water cycle. The vertical axis represents the average depth of all sampled habitats relative to the maximum level reached by the water. Daily water levels measured at the field station are indicated by the solid curve. Note that the lago habitat contained water at levels higher than the field station because it was isolated during dry season. Tick marks on lago habitat samples indicate samples that were assumed to equal the sample taken in the first week after the lago became physically isolated; see text for details.

The speed of the canoe was regulated at a nearly constant speed,  $0.3 \text{ m}\cdot\text{s}^{-1}$ , using a geographical position system. No transect was run under conditions of rain or wind. In the study area, rains tend to be heavy but short in time. Wind speeds tend to be near zero, usually less than 1 knot; stronger winds tend to accompany the rains. At every transect ran, the fishers counted the number of pirarucu they heard or observed. In this study, no size limits were applied to the counts of pirarucu. However, pirarucu smaller than 1 m are difficult to hear and observe; so the majority of pirarucu counted were longer than that length.

To analyse the collected data, four issues were considered. First, not all three replicate transects of a given habitat could be run in some weeks because one or two of the transects were dry; these transects were excluded from all analyses performed. Second, the methodology developed here assumes that the two fishers were capable of (i) detecting the presence of the individuals of pirarucu, and (ii), when more than one individual were in the area, of distinguishing among different surfacing individuals. In this regard, there is reason to believe that double- or no-counts of pirarucu are unlikely, although entirely possible. In 1999, both fishers together possessed over 50 years of professional and continual experience with the pirarucu. The experiments performed by Castello (2004) showed that the counts of the pirarucu performed by these two fishers varied 10% around the true value (compare Table 1 with Table 3 in Castello 2004). Third, in the study of Castello (2004) the fishers counted the pirarucu using the equivalent of quadrat-plots, which allow the estimation of absolute population densities. In the present study, the fishers counted the pirarucu using line-transects in which the length of the sampled area is known (1 km) but the width is not; so absolute population densities for the entire area sampled could not be estimated. Fourth, it was impossible to estimate the width of the line-transect samples, i.e., the distance reached by the senses of the fishers (vision and hearing) while running the transects. This was so because of the combined influences of: (i) differences among habitats, such as vegetation cover and floating meadows; (ii) constantly changing differences within habitats, such as sunlight intensity and noise made by moving tree branches and animals (e.g., fishes, frogs, birds); and (iii) the impossibility of determining the precise locations of most surfacing pirarucu in forested habitats (because of the dense vegetation).

These considerations imply that the collected data set would not allow determining whether one habitat was, say 50%, more densely inhabited by the pirarucu than another. Nevertheless, the data set was appropriate for deducing migration patterns of the pirarucu, if considered as an indicator of the

presence or absence, and if it was analysed with regard to temporal changes. For example, if at a given point in time the pirarucu were found only in the lago habitat and nowhere else, and if at a later point in time, the pirarucu were no longer found in the lago but only in the rio, then it would be reasonable to infer that migration occurred. An implicit assumption is that the effect of migration in and out of the entire study area was negligible in terms of migration between and among habitats. It is through the use of this qualitative analysis of the data set that this study deduced the lateral migration of the pirarucu. Thus, the counts of pirarucu performed at each of the three transects established at each habitat type were used to determine an average index of the presence of the pirarucu for each sampled week.

## Results

The main results of this study are: (i) the pirarucu were found in all of the surveyed habitats at distinct parts of the annual cycle; (ii) preferred habitats are the lago (i.e., lakes) and chavascal, restinga baixa, and restinga alta (i.e., forest habitats); (iii) the main physical drivers of the lateral migration of the pirarucu appear to be low depth and low current velocity.

### Lateral migration of the pirarucu

The lateral migration of the pirarucu accompanied water level fluctuations closely (Fig. 2a,b). As water levels rose, the pirarucu migrated to increasingly higher habitats in flooded forests, and as water levels declined, the pirarucu migrated first back to lower habitats of flooded forests, then to communicating channels, and eventually to the lakes. Between April and June 1999, virtually all pirarucu were found in the seasonally flooded forests, the habitats of chavascal, restinga baixa, and restinga alta (Fig. 2a,b). Pirarucu over 1.5 m in length were observed swimming in very shallow water (0.5 m). Eighteen pirarucu were observed caring for the young in the flooded forests, guiding the off-spring that followed them near their head. Mouth-brooding was not observed. Between July and August 1999, the pirarucu were found in the cano, ressaca, paraná, and lago (Fig. 2a,b). Between August 1999 and February 2000, when the lago remained physically isolated, most pirarucu were in the lago (Fig. 2a,b). In mid-September, however, some pirarucu were observed in that transect of the rio located near a beach where current velocity tend to be slow (Figs 1 and 2a,b). In mid-December, during a small flood pulse, some pirarucu were found in the cano and ressaca (Fig. 2a,b). After February 2000, when the lago was no longer physically isolated, the pirarucu



were found first in the chavascal and then in restinga baixa forests.

### Relation to physical variables

The relative abundance of the pirarucu in the habitats (measured in terms of the proportion of the transect samples in which the pirarucu were found, i.e., 0, 1/3, 2/3, and 1) was not related to any of the physical variables measured (Kruskal-Wallis,  $n_0 = 229$ ,  $n_{1/3} = 64$ ,  $n_{2/3} = 28$ , and  $n_1 = 13$ ,  $P > 0.1$ ). But the presence or absence of the pirarucu in any given habitat was related to current velocity and depth (Table 2). The pirarucu selected generally shallow, slow flowing habitats (Table 2). Water transparency in the samples in which the pirarucu were present during the reproductive period of the species (around 67 cm, from December to May; Queiroz 2000) was significantly lower than during the rest of the year (around 115 cm; Mann-Whitney  $U$ -test,  $n_{\text{reproductive}} = 109$ ,  $n_{\text{nonreproductive}} = 212$ ,  $P < 0.0001$ ).

### Discussion

The lateral migration of the pirarucu appears to be a very cost-effective strategy for optimising the spatial and temporal heterogeneity of resources of the várzea. The migrations to and through the habitats of chavascal, restinga baixa, and restinga alta appear to have functions related to feeding and reproduction (nest building, mating, and parental care). The migrations to and through the habitats of paraná, cano, lago, ressaca, and rio appear to have functions related to survival (i.e., avoidance of unfavourable conditions), feeding, and reproduction (courting and pairing; Fig. 2a,b). The habitats of the várzea are arranged in such a way spatially that in most instances the distances among them are very small, rarely over 1 km (the rio being an exception, Fig. 1). So, the pirarucu appear to benefit from, and fulfil the ecosystem roles of, migration with only modest investments compared with that of the longitudinal migrations of other fishes. These results

serve as a conceptual model for understanding the lateral migration of other floodplain fishes.

### Lateral migration of pirarucu

During rising and high water levels (April–June 1999), the pirarucu were found in the flooded forest habitats of chavascal, restinga baixa, and restinga alta (Fig. 2a,b). The pirarucu migrated into these habitats right after they were flooded. This was enabled by the air-breathing system of the pirarucu, which allows them to inhabit hypoxic environments of flooded forest, and by their elongated body, which allows them to swim in very shallow water (0.5 m).

There are two advantages for the pirarucu to inhabit the flooded forests and, in particular, to migrate into them immediately after they are flooded: feeding and parental care. The pirarucu aged about 1 year and older feed primarily on fish (Sánchez 1969; Queiroz 2000). Four fish families comprise about half of all ingested food in weight; these are species of the families Callichthyidae, Loricariidae, Pimelodidae, and Heptapteridae, in order of decreasing importance (Queiroz 2000). Most such fishes are detritivorous or omnivorous, and several species of Callichthyidae and Loricariidae are adapted to hypoxic conditions, tend to be nonmigratory, and inhabit these floodplains throughout their life cycles (Crampton 1999). With exception of the Callichthyidae, the three other prey groups are reported to inhabit the flooded forests during high water levels (Crampton 1999). Thus, they are likely to constitute constant food sources for the pirarucu. This is especially so early in the flood when these prey species find generally higher oxygen levels (Winemiller & Jepsen 1998).

All 18 observations of parental care occurred in the flooded forests, and half of them near floating meadows. The flooded forests offer many species of insects, fish larvae, and other small organisms (Junk et al. 1989) for the offsprings of the pirarucu to eat. Indeed, the young pirarucu has a very diverse diet (Queiroz 2000). In addition, floating meadows constitute ‘an important nursery habitat for a great number, perhaps the great majority, of fishes’ in the várzea (Winemiller & Jepsen 1998). Food-rich conditions like these help explain the fast growth of the young pirarucu, which may grow to 0.5 m in total length by the end of the flood, i.e., 3 months (personal observations).

During low water levels (August 1999–February 2000), most of the pirarucu were observed in the lago in population densities that were obviously much greater than during the rest of the year when they were dispersed in much greater forested areas (Fig. 2a,b). This is consistent with all previous reports (Veríssimo 1895; Queiroz & Sardinha 1999; Martinelli & Petrer Jr. 1999). During this time, inhabiting the lago may

Table 2. Medians and first and third quartiles (in parentheses) of the three physical variables measured, for all samples, and for samples in which the pirarucu were present and absent.

Variable	All (n=1002)	Pirarucu	
		Present (n=321)	Absent (n=681)
Depth (m)	5.8 (2.13–10.75)	3.08 (1.40–5.20)*	7.92 (4.86–11.11)*
Current velocity (m·s <sup>-1</sup> )	0.14 (0.05–0.41)	0.12 (0.04–0.18)*	0.15 (0.06–0.41)*
Transparency (cm)	103 (47–138)	120 (56–143)**	93 (39–146)**

\*  $P < 0.0001$

\*\* Non-significant

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provide the pirarucu with three advantages. The first is increasing survival rates. Low water levels are associated with higher fish mortality (Welcomme 1979). Because the lago may, and usually does, become physically isolated, inhabiting them provides safety against extreme drought, e.g., El Niño years. The second is maintaining adequate feeding rates. During low water levels, oxygen levels in the lago tend to be low (Junk et al. 1983). While most fish species in the lago are stressed, some even die, the pirarucu do fine and predate actively. The pirarucu show very small seasonal variations in fat content (Junk 1985). The third is promoting reproduction. By inhabiting a habitat in high population densities, the chances of engaging in courtship and mating activities are increased. Indeed, the end of the low water period (December–March) coincides with the reproductive period of the pirarucu (November–December; Queiroz 2000). Thus, courting activities must have occurred in the lago. Also, a study in this same area showed that preferred nesting habitats are the flooded banks of *ressaca*, *lago*, and *paraná* (Castello, in review). Thus nest building must have occurred at the time of the third and fourth flood pulses, December and February, respectively. At that time, the water levels flooded the *cano* and the banks surrounding the *lago*, *ressaca*, and *paraná* (Fig. 2a,b), allowing the pirarucu to migrate out of the lago and into the *ressaca* and *paraná*.

### Relation of migration to physical variables

Shallow depth ( $\sim 3$  m) and low current velocity ( $\sim 0.12$  m·s<sup>-1</sup>) are the best predictors of the presence of the pirarucu in any given habitat (Table 2). The relation between the migration of the pirarucu and depth is clear. Water levels varied over 13 m in the *várzea* (Fig. 2a,b); but, lateral migration maintained depth at locations where the pirarucu were between 1.4 and 5.2 m (Table 2). The relation between the migration of the pirarucu and current velocity is less clear, however. The difference between current velocity of the samples in which the pirarucu were present and those in which they were absent is small (0.12 and 0.15 m·s<sup>-1</sup>, respectively; Table 2).

The pirarucu tend to prefer the more elevated habitats (Fig. 2a,b), namely the flooded forests and the lago. There may be two reasons for their preference for shallow habitats. First, full exploration of the column of water (e.g. to inspect for prey and predators) depends on the capacity of the pirarucu to swim between the bottom and the surface to breath. Thus, deeper habitats may involve greater energy costs. Second, fish abundance is directly correlated with shallow depth in many ecosystems. In floodplains, this is evidenced by the migration of fish to flooded forests during high water levels, and to lakes and river

channels during low water levels (Lowe-McConnell 1987). In creeks, total ecosystem metabolism per unit of volume increases with decrease in depth, perhaps due to concentration of food resources and the smaller energy the fish expend searching for food (Hall 1972). In the oceans, the association of fishes with shallow depths and their high biological productivity there has been well-documented (e.g., Lindeboom 2002).

But no relation was found between water transparency and the lateral migration of a visual predator like the pirarucu (Table 2). The only relation found was seasonal: the lowest transparencies occurred during the reproductive period of the species, from December to May. Low transparency may, thus, reduce predation pressure on the offspring by birds or other fishes, for example, and increase reproductive success.

### Understanding lateral migration of other fishes

This study lends support to a conceptual model of lateral migration of floodplain fishes (Fig. 2a,b). Obviously, the validity of this model varies depending on the species in question as well as habitat structure and flooding cycles of the region. However, this model illustrates clearly the type of intricate interplay that exists in pristine floodplains between fish migrations, dynamic water levels, and heterogeneous habitat structure. For example, the omnivorous tambaqui (*Colossoma macropomum* Cuvier) migrate laterally in the *várzea* (Araújo-Lima & Goulding 1997), following among other things the ripening order of their preferred fruits and seeds. Local fishers know this order and benefit from it. This model implies that detailed understanding of lateral migration can only be obtained through careful consideration of the spatial and temporal heterogeneity of floodplains.

### Note

The author has just found out the studied fish is an un-described species.

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