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# Lateral migration of fish between an oxbow lake and an Amazonian headwater river

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Abstract – We report on lateral movements of fish between an Amazonian headwater river (Manu River in Manu National Park, Perú) and a 24-ha oxbow lake (Cocha Cashu) in the adjacent floodplain. During wet season flood pulses, or '*crecientes*,' fish can enter and exit the lake through a connecting channel that is normally dry. To investigate fish movements, we operated a bi-directional funnel trap in the connecting channel during high water interludes. We captured 4090 fish of 60 species during the 2005 and 2006 rainy seasons and sub-sampled the adults for gonadal state and stomach contents. We found that most exiting fish were gravid and that most entering fish had recently spawned, suggesting that fish were leaving the lake to spawn in the river or elsewhere. Entering fish had full stomachs more often than exiting fish and entering and exiting individuals of most species were of similar size.

Key words: Amazon; fish; lateral migration; Manu River; oxbow lake; Cocha Cashu

## Introduction

Migrations of fish within the great Amazonian fluvial system are of major biological and economic importance, determining species diversity and abundance that vary strongly by season (Goulding 1980; Fernandes 1997; Winemiller & Jepsen 1998). Best known are longitudinal migrations that most commonly run between downstream feeding areas and upstream spawning grounds. These are incompletely studied, and both the upstream and downstream destinations of many migrations remain poorly documented (Barthem & Goulding 1997). Even less well-studied are so-called lateral migrations that refer to fish movements between the deepwater channels of permanent streams and lower-order tributaries or other floodplain zones such as lakes and flooded varzea forests (Winemiller & Jepsen 1998). Reports of such lateral migrations are few and scattered geographically (Sudan – Hickley & Bailey 1987; Illinois, USA – Kwak 1988; Mali – Bénech & Peñáz 1995; Czech Republic – Hohausová et al. 2003). Studies of lateral migrations in the Amazon are similarly few and confined to the central Amazon where flooding is of high amplitude and long duration (Fernandes 1997; Castello 2008; Sousa & Freitas 2008; Fernandes et al. 2009). In the Central Amazon, Fernandes (1997) reported that gravid fish exited lakes in the low water season, apparently to spawn in the river. Here, we report data from 2 years' of monitoring a lateral migration between a floodplain lake and the Manu River in the Amazon headwaters region where the hydrological regime is distinct from that of the Central Amazon.

In contrast to the predictable, long-duration and monomodal flooding regime of the Central Amazon, the Manu River experiences unpredictable, short-duration and polymodal flood pulses. With lower predictability in the timing and intensity of flooding events compared with Central Amazon regions, fish in the Manu River may be less able to depend upon isolated floodplain lakes as part of their life history (Junk 1993). However, relative to most lakes of the

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Central Amazon, oxbow lakes of the Manu River provide high-productivity conditions as measured by chlorophyll-a, oxygen, and conductivity, among other measures (Carvalho et al. 2001; Davenport 2008; Davenport LC, J Terborgh & S Whalen, unpublished data). Little is known about how fish movements between headwater streams and oxbow lakes such as Cocha Cashu feature in the life history of the regional fish fauna (Junk & Furch 1993). High-productivity floodplain lakes could provide important seasonal feeding grounds, as do the flooded forests of the Central Amazon floodplain.

## Study area

The focus of the research was Cocha Cashu, an oxbow lake in the floodplain of the Manu River, a whitewater tributary of the Rio Madeira in south-eastern Perú. The entire watershed of the Manu River is contained within the 1.9-million-ha Manu National Park. The park's protected status ensures that the entire drainage basin is without significant anthropogenic influences as the human population density within the Manu watershed is <0.1 individual per km$^2$ (Ohl-Schacherer et al. 2007).

The Manu arises along the eastern margin of the Isthmus of Fitzcarrald and flows eastward, merging with the Río Alto Madre de Dios at Boca Manu to form the Rio Madre de Dios proper. Its right bank tributaries arise in the eastern Andes at elevations above 3000 m and flow generally northward until they join the main channel of the Manu, whereas its left bank tributaries arise in Amazonian lowlands at elevations below 500 m. The elevation at Cocha Cashu is approximately 350 m.

Located at 11°56′S and 71°24′W, Cocha Cashu experiences a dry season from May to October, when the river is low and many lowland swamps and minor tributaries dry up, and a wet season from November through April, when flood pulses, locally known as *crecientes*, pass down the Manu. Crecientes arrive at Cocha Cashu approximately 30 h after a torrential rain and seldom persist more than a day or two. Thus, the flood regime in this headwaters region is intermittent and quite distinct from that farther downstream where the flood pulse is annual, produced by a huge catchment area, and may persist for months. Accordingly, the composition of the floodplain forest that flanks the Manu River has little in common with that of varzea forests far downstream and contains few tree species known to be dispersed by fish (Terborgh & Andresen 1998).

The Manu is an actively meandering river that experiences channel avulsions at the rate of about 2 per decade (personal observation of JT). We have informally recognised two types of Manu oxbow lakes that we denote as connected and unconnected (following Tejerina-Garro et al. 1998; Davenport 2008). Connected lakes have permanent streams flowing into and out of them and are thus directly coupled to the Manu River year-round. Unconnected lakes, among them Cocha Cashu, do not have permanent streams flowing into them and for most of the year are isolated from the river, experiencing neither inflows nor outflows except during and following *crecientes*. On these occasions, river water backs up through permanent (though usually dry) drainage channels, causing unconnected lakes to rise as much as 2–3 m above their normal levels. It is only during these brief periods, amounting at most to a few weeks a year, that fish are able to move between unconnected lakes and the river.

Among Manu River oxbow lakes, Cocha Cashu is of average size, being 2.2 km long and approximately 110 m wide, giving it a surface area of roughly 24 ha. Judging from the size of successional trees along its inner margin, the lake can be estimated to be between 100 and 150 years old (Terborgh et al. 1997). The depth is quite uniformly 1.5–2.0 m in the centre during the dry season low stage. Shallows occur at the ends and along the inner margin, as is typical of the channels of meandering rivers.

Manu oxbow lakes, whether connected or unconnected, are semi-open systems (Junk 1997) that can assume alternative states of three basic kinds in which the primary productivity is dominated by phytoplankton, submerged macrophytes (*Najas spp.)* or floating macrophytes (*Pistia stratiotes*) (Scheffer et al. 2003; Scheffer & van Nes 2007). We shall not elaborate on alternative states here, but it does bear mentioning that Cocha Cashu has been in each of these three states for at least 2 years during the decade of 2000–2010, with notable changes in fish fauna and limnological measures.

The hydrological conditions of unconnected oxbow lakes, whatever their state with respect to primary producers, are drastically different from those of rivers. Unconnected lakes act as nutrient sinks, receiving nutrients from rainfall and, especially, runoff and a generous input of litterfall from the overhanging forest. Large inputs of allochthonous and autochthonous organic matter create high levels of biological oxygen demand that can, during hot, still periods, produce low oxygen levels approaching anoxia near the bottom (Junk et al. 1983; Junk 1993; Crampton 1998). The water of oxbow lakes is still and relatively free of sediment (except during incursions of river water). The bottom itself is covered by a metre or more of soft sediment containing a mix of incompletely decomposed organic matter and river sediment carried in during *crecientes*. High productivity of Cocha Cashu and other Manu River oxbow lakes is indicated by high pH, high chlorophyll and high conductivity as well as the presence of the two top aquatic predators of the headwaters region, the giant otter (*Pteronura brasiliensis*) and the black caiman (*Melanosuchus niger*) (Schenck 1999; Davenport 2008).

### Hypotheses

The high productivity of Manu oxbow lakes suggests that they should be highly attractive as feeding habitat for juvenile fish, whereas the soft bottoms and tendencies to anoxia should render them unsuitable as spawning sites for adults. If so, mature fish might opportunistically leave the lake to spawn in the river or elsewhere during periods of connectivity. This is a pattern that has been observed in other studies of lateral movements in tropical South America (Goulding 1980; Fernandes 1997; Winemiller & Jepsen 1998). Alternatively, periods of connectivity might be so brief and unpredictable in time that unconnected lakes would mainly support fish species that could complete their life cycles in the lake environment. The first of these hypotheses would be supported by the finding of gravid individuals leaving the lake and post-reproductives entering it. Alternatively, species reproducing in the lake might occur only casually in the connecting canal during periods of high water and they would not be expected to show any strong tendencies with respect to reproductive status.

## Methods

The 4-m wide, steep-sided channel connecting Cocha Cashu to the Manu River afforded an ideal situation for monitoring fish movements between the two water bodies. We constructed two removable funnel traps, 1.0 m wide, 1.0 m tall and 1.5 m long and installed them flush with the bank on one side of the channel (Fig. 1). The traps were constructed of galvanised 1-cm wire cloth stapled to a wooden frame. The funnel openings were roughly oval in shape with dimensions of 12 × 18 cm. The traps were held in place by a wooden superstructure that enabled investigators to insert or remove them from above (Fig. 2). Traps facing the river and lake ends of the channel were installed back-to-back. Angled leads made of the same 1-cm wire cloth extended across the entire channel on both sides and directed fish into the traps.

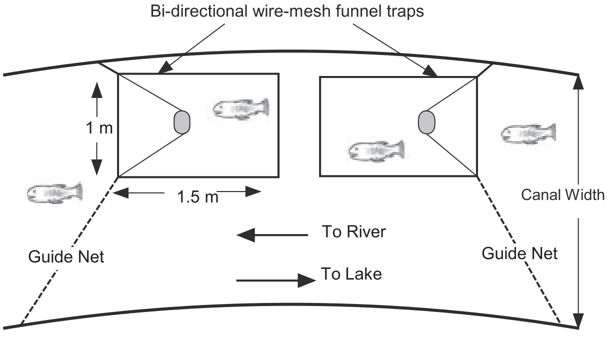

*Fig. 1.* Set-up of the bi-directional fish trap in the main canal between Cocha Cashu and the Manu River.

*Fig. 2.* Bi-directional funnel traps in the connecting channel, dry season 2004.

We operated the traps during two successive wet seasons, from November 2004 to April 2005 (107 h) and from January to April, 2006 (549 h) for a total of 656 h of operation. We sampled fish movements during suitable periods when water was either entering or exiting the lake via the channel. Sampling periods (when the traps were installed and open) varied from 3 to 24 h, depending on the level of water in the channel. Altogether, we took 12 samples in 2005 and 42, in 2006.

Fish were identified to species, whenever possible, using keys (Gery 1977; Lauzanne & Loubens 1985; Kullander 1986; Britski et al. 1999) and through comparing vouchers with specimens in the collection of the Museo de Historia Natural of San Marcos University in Lima, Perú. A fraction of the fish in each sample (approximately half of the overall total) was collected for analysis; the rest were counted and released. Collected fish were measured, weighed and dissected to assess gonadal condition and stomach contents. As the purpose of collecting was to assess reproductive condition, the sub-samples of fish selected for analysis were composed of individuals above a size (by species) thought to be capable of reproduction. This size was determined in the first sample each season, in which abdomens were assessed by inspection and palpation and ultimately dissection of possible candidates. Fish that died from crowding or low-oxygen conditions in the trap were also dissected, but these constituted <5% of any sample.

Dissected fish were classified into four categories based on gonadal characteristics adapted from Holden & Raitt (1974): Stage (I) immature, Stage (II) ripening, Stage (III) ripe and Stage (IV) spent.

We examined the stomach contents of fish that were dissected and classified them simply as empty, half-full or full. No attempt was made to identify the contents.

Prior to and during the 2005–2006 period of the research, we repeatedly sampled Cocha Cashu for the purpose of compiling an inventory of the fish species present in the lake (Osorio & Ortega 2006; Davenport 2008; Osorio 2008). We used three methods: cast net, gill net and seine net. Collectively these methods captured fish of a wide range of sizes from both the shallow and deep portions of the lake (Osorio 2008). In addition, some species of fish not captured in nets were observed to be eaten by giant otters (Davenport, unpublished) or were observed visually by the authors. For the present purpose, we use the list of all species recorded in the lake as a frame of reference to compare the list of migrating species captured in the funnel trap.

## Results

### Overview

The 2004–2005 rainy season was abnormal in that few heavy rains fell before the end of March and the lake remained unconnected until then. We took the first samples when there were light *crecientes* that brought water into the channel but not high enough to allow it to enter the lake. Consequently, we only captured inbound fish in these first samples and the first outbound fish were not registered until the end of March. In 2005–2006, the rains began prior to December with repeated periods of connection that provided a longer sampling period. As our sampling in 2006 began in January, we probably missed the earliest migration pulse, and so obtaining a similar sample size (approximately 2000 fishes) required a longer effort in 2006 (107 vs. 549 sampling hours, respectively) but resulted in capture of more species.

Despite the somewhat different sampling periods and number of hours and *crecientes* sampled, similar numbers of individual fish were captured in the 2 years: 2022 in 2004–2005 (678 individuals of 25 species entering and 1344 of 31 species exiting) and 2068 in 2006 (564 of 50 species entering and 1504 of 44 species exiting) for a grand total of 4090 fish of 60 species (Table 1). Approximately twice as many fish were caught exiting as entering in both years, although this was not necessarily reflected at the species level. The number of individuals entering exceeded the number exiting in 28 species, or 47% of the species total. In 11 species, we captured more than 100 individuals and these made up 74% of the grand total of individuals caught. Most of the remaining 49 species were caught sporadically in small numbers.

Among the common species, there were some strong asymmetries with respect to captures entering or exiting the lake (Table 1 and Fig. 3). With the majority of species, and especially in the characids, outbound individuals greatly exceeded entering individuals (e.g., *Moenkhausia dichroura, Roeboides affinis, Roeboides myersii, Serrasalmus spilopleura, Tetragonopterus argenteus*). However, a minority, mainly silurids, displayed the opposite trend, as more individuals were captured entering than exiting the lake (*Bunocephalus sp., Pimelodella gracilis, Pimelodus blochii*). The diversity of both entering and exiting cohorts was greater in 2006 than in 2005 (56 species vs. 35).

There was considerable year-to-year variation in the occurrence of some species, even after correcting for differences in sampling effort (hours) in each year (Fig. 3). For example, *Ageneiosus sp., Leporinus yophorus, Prochilodus nigricans, P. gracilis, P. blochii* and *Triportheus sp2* were more abundant in 2005, whereas *Astyanax sp1, Astyanax sp2, Loricaria sp.* and *Pygocentrus nattereri* were captured mainly or exclusively in 2006.

Of the total of 60 species captured over the two seasons, only 26 had been documented in previous systematic sampling of Cocha Cashu. An additional four species were recorded as otter prey or observed visually. Another eleven species were captured in one or more of three additional oxbow lakes surveyed by our group (Table 1). The remaining 19 species (35% of the total) had not been captured in any of the four surveyed oxbow lakes. However, these 19 species contributed only 8% of the 2-year total of individuals.

### Size cohorts of entering and exiting adult fish

During our field sampling efforts, it became clear that samples of many species represented schools of same-age (and same-size) cohorts moving in synchrony and captured together. In a few cases, involving both entering and exiting fish, the size distributions appeared bimodal in spite of the fact that we focused on sampling adult fishes, suggesting that more than 1 year class may have been included in the samples. In all such cases, except *R. affinis* and *R. myersii* one of the two size classes was represented by only a tiny number of individuals (≤5). For a majority of the species, entering and exiting cohorts were of similar length; note in Table 2 that the standard deviations around the mean lengths of entering and exiting individuals broadly overlap. *Steindachnerina bimaculata* was a possible exception, with exiting individuals predominately intermediate in size between two distinct size classes of entering individuals.

### Reproductive status of entering and exiting adult fish

Reproductive condition was determined by dissection for 394 fish in 2005 (189 entering and 205

Table 1. Fish species found from sampling in Cocha Cashu, in channel fish-trap, and in other Manu River lakes.

| | | 2005 | | 2006 | | |
|---|---|---|---|---|---|---|
| Species | Found in lakes* | Entering, No. | Exiting, No. | Entering, No. | Exiting, No. | Total per sp. |
| *Acestrorhynchus falcatus* | 1,3 | 0 | 0 | 4 | 1 | 5 |
| *Acestrorhynchus sp.* | | 0 | 1 | 6 | 2 | 9 |
| *Aequidens tetramerus* | 1,3 | 1 | 0 | 1 | 3 | 5 |
| *Ageneiosus sp.* | 2 | 4 | 39 | 4 | 1 | 48 |
| *Ancistrus sp.* | 1,3 | 0 | 3 | 3 | 1 | 7 |
| *Anodus sp.* | | 0 | 0 | 1 | 0 | 1 |
| *Aphanotorulus unicolor* | | 0 | 0 | 0 | 2 | 2 |
| *Astyanax sp. 1* | 1,3 | 7 | 29 | 158 | 96 | 290 |
| *Astyanax sp. 2* | | 0 | 0 | 7 | 38 | 45 |
| *Bujurquina sp.* | | 0 | 0 | 0 | 1 | 1 |
| *Bunocephalus sp.* | | 73 | 7 | 49 | 15 | 144 |
| *Chalceus guaporensis* | 3 | 0 | 4 | 0 | 0 | 4 |
| *Crenicichla sp.* | 1,3 | 0 | 3 | 2 | 2 | 7 |
| *Ctenobrycon sp.* | 1,3 | 0 | 1 | 2 | 13 | 16 |
| *Curimatella sp.* | 3 | 0 | 0 | 1 | 0 | 1 |
| *Cynopotamus sp.* | 3 | 0 | 0 | 10 | 2 | 12 |
| *Eigenmannia sp. 1* | 2 | 11 | 7 | 3 | 3 | 24 |
| *Eigenmannia sp. 2* | | 0 | 4 | 2 | 25 | 31 |
| *Farlowella sp.* | | 0 | 0 | 1 | 0 | 1 |
| *Gymnotus sp.* | 3 | 0 | 0 | 1 | 0 | 1 |
| *Hoplias malabaricus* | 1,3 | 0 | 3 | 4 | 3 | 10 |
| *Hypophthalmus sp.* | 2 | 1 | 2 | 19 | 2 | 24 |
| *Hypostomus emarginatus* | 1,3 | 2 | 6 | 8 | 11 | 27 |
| *Leporellus sp.* | | 0 | 1 | 0 | 0 | 1 |
| *Leporinus arcus* | | 0 | 1 | 0 | 0 | 1 |
| *Leporinus friderici* | 1,3 | 22 | 3 | 11 | 26 | 62 |
| *Leporinus trifasciatus* | 3 | 1 | 4 | 0 | 1 | 6 |
| *Leporinus yophorus* | 3 | 24 | 100 | 0 | 9 | 133 |
| *Liposarcus disjunctivus* | 1,3 | 1 | 0 | 2 | 0 | 3 |
| *Loricaria sp.* | | 0 | 0 | 23 | 14 | 37 |
| *Loricariichthys sp.* | 1,3 | 0 | 0 | 5 | 3 | 8 |
| *Moenkhausia dichroura* | 1,3 | 3 | 180 | 1 | 31 | 215 |
| *Pimelodella gracilis* | 3 | 89 | 12 | 9 | 12 | 122 |
| *Pimelodus blochii* | 1,3 | 34 | 1 | 1 | 0 | 36 |
| *Pimelodus maculatus* | 1,3 | 1 | 0 | 3 | 0 | 4 |
| *Plagioscion sp.* | 1,3 | 0 | 0 | 2 | 4 | 6 |
| *Potamorhina altamazonica* | 1,3 | 0 | 0 | 23 | 1 | 24 |
| *Prochilodus nigricans* | 1,3 | 100 | 65 | 18 | 5 | 188 |
| *Psectrogaster rutiloides* | 1 | 0 | 4 | 0 | 0 | 4 |
| *Pygocentrus nattereri* | 3 | 0 | 0 | 5 | 46 | 51 |
| *Raphiodon vulpinus* | 3 | 0 | 0 | 0 | 1 | 1 |
| *Rhamdia quelen* | | 0 | 0 | 5 | 0 | 5 |
| *Rineloricaria sp.* | | 0 | 0 | 12 | 2 | 14 |
| *Roeboides affinis* | 1,3 | 18 | 199 | 17 | 138 | 372 |
| *Roeboides myersii* | 1,3 | 1 | 65 | 11 | 387 | 464 |
| *Salminus sp.* | | 0 | 0 | 5 | 2 | 7 |
| *Schizodon fasciatus* | 1,3 | 4 | 10 | 3 | 0 | 17 |
| *Serrasalmus elongatus* | | 0 | 0 | 1 | 2 | 3 |
| *Serrasalmus rhombeus* | 1,3 | 0 | 0 | 11 | 3 | 14 |
| *Serrasalmus spilopleura* | 1,3 | 2 | 45 | 6 | 101 | 154 |
| *Serrasalmus sp.* | | 0 | 0 | 4 | 0 | 4 |
| *Steindachnerina bimaculata* | 1,3 | 27 | 77 | 35 | 49 | 188 |
| *Steindachnerina güentheri* | | 1 | 0 | 2 | 6 | 9 |
| *Steindachnerina hypostoma* | | 0 | 0 | 5 | 3 | 8 |
| *Steindachnerina sp.* | 3 | 0 | 0 | 1 | 0 | 1 |
| *Sturisoma sp.* | | 0 | 0 | 1 | 0 | 1 |
| *Synbranchus sp.* | 2 | 0 | 0 | 0 | 1 | 1 |
| *Tetragonopterus argenteus* | 1,3 | 247 | 423 | 45 | 431 | 1146 |
| *Triportheus angulatus* | 1,3 | 2 | 15 | 3 | 1 | 21 |
| *Triportheus sp.* | 3 | 2 | 30 | 8 | 4 | 44 |
| Total | | 678 | 1344 | 564 | 1504 | 4090 |
| No. species | | 25 | 31 | 50 | 44 | |
| No. species in year | | 35 | | 56 | | |

*1 = found in Cocha Cashu sampling; 2 = seen in Cocha Cashu but not in net sampling; 3 = found in other Manu River oxbow lakes.

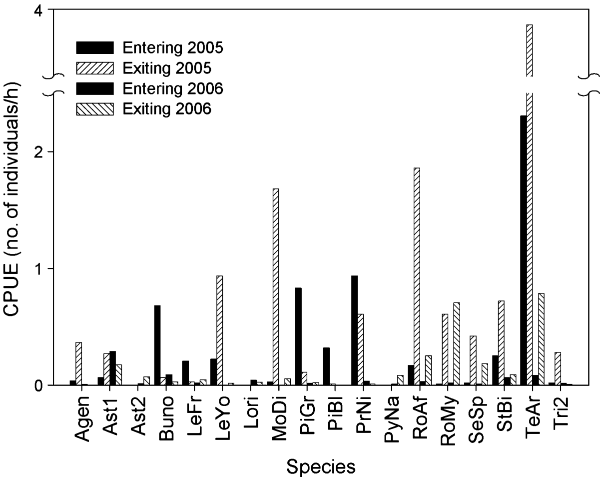

*Fig. 3.* CPUE (Catch Per Unit Effort) of some common species entering and exiting Cocha Cashu in 2005 and 2006.

exiting) and 648 fish in 2006 (206 entering and 442 exiting) (Tables 3, S1 and S2, and Figs 4 and 5). Tables S1 and S2 provide data on all species in all years, while Figs 4 and 5 depict only those species in which entering and exiting cohorts were large enough to permit within-year comparisons. While few species provided extensive numbers in all relevant classes, it was nevertheless clear that entering and exiting cohorts in both years were lopsidedly uneven with respect to reproductive condition. Overall, entering fish were roughly eight times more likely to be spent (Stage IV) than ripe (Stage III), and exiting fish were roughly five times more likely to be ripe than spent.

### Stomach contents

We examined the stomachs of dissected fish to determine whether they had recently fed. Forty-five per cent of entering fish had positive stomach contents (average for both years), whereas only 30% of exiting fish did. The proportion of piscivorous fish in the samples was negligible, largely ruling out the possibility that positive stomach contents resulted from piscivory in the confined space of the funnel traps.

## Discussion

Our first hypothesis was that the highly productive lake environment would provide a feeding ground but a poor spawning ground for many species, leading to

Table 2. Size distributions of entering and exiting cohorts of some common fish species, 2005 and 2006 samples combined.

| Species | Direction traveling | Number sampled | Range in length (mm) | Unimodal/bimodal | Mean length | Standard deviation |
|---|---|---|---|---|---|---|
| *Bunocephalus sp.* | Entering | 20 | 60–113 | uni | 92.8 | 13.8 |
| | Exiting | 0 | – | – | | |
| *Leporinus friderici* | Entering | 10 | 111–182 | uni | 142.8 | 21.2 |
| | Exiting | 0 | – | – | | |
| *Leporinus yophorus* | Entering | 6 | 121–137 | uni | 127.8 | 6.0 |
| | Exiting | 2 | 81–87 | bi | 84.0 | 4.2 |
| | Exiting | 32 | 114–161 | bi | 131.6 | 12.3 |
| *Moenkhausia dichroura* | Entering | 0 | – | – | – | – |
| | Exiting | 48 | 61–84 | uni | 70.4 | 7.4 |
| *Pimelodella gracilis* | Entering | 4 | 75–91 | bi | 84.0 | 6.8 |
| | Entering | 13 | 103–145 | bi | 119.3 | 11.6 |
| | Exiting | 9 | 99–128 | uni | 115.8 | 10.4 |
| *Pimelodus blochii* | Entering* | 30 | 132–194 | uni | 169.4 | 20.9 |
| | Exiting | 1 | 156 | uni | 156.0 | – |
| *Prochilodus nigricans* | Entering | 2 | 67–69 | bi | 68.0 | 1.4 |
| | Entering | 22 | 193–277 | bi | 228.1 | 16.3 |
| | Exiting | 26 | 210–257 | uni | 229.3 | 9.0 |
| *Roeboides affinis* | Entering | 4 | 101–126 | uni | 117.0 | 11.2 |
| | Exiting | 29 | 84–100 | bi | 92.6 | 4.5 |
| | Exiting | 22 | 102–133 | bi | 116.6 | 8.9 |
| *Roeboides myersii* | Entering | 1 | 113 | uni | 113.0 | – |
| | Exiting | 14 | 113–119 | bi | 115.4 | 2.3 |
| | Exiting | 24 | 125–158 | bi | 141.1 | 8.9 |
| *Serrasalmus spilopleura* | Entering | 2 | 36–42 | uni | 39.0 | 4.2 |
| | Exiting | 21 | 36–46 | uni | 39.7 | 2.8 |
| *Steindachnerina bimaculata* | Entering | 3 | 69–84 | bi | 78.0 | 7.9 |
| | Entering | 15 | 108–127 | bi | 117.6 | 5.9 |
| | Exiting | 23 | 82–102 | bi | 91.8 | 4.5 |
| | Exiting | 1 | 118 | bi | 118.0 | – |
| *Tetragonopterus argenteus* | Entering | 5 | 50–61 | bi | 55.4 | 4.0 |
| | Entering | 55 | 74–114 | bi | 89.5 | 8.5 |
| | Exiting | 53 | 72–109 | uni | 89.5 | 9.8 |

*Two larger outliers: 210 and 230 mm.

Table 3. Reproductive state of mature fish entering and exiting the lake in 2005 and 2006 (all species).

| Orientation | Gravid | Post-reproductive | Prob.* |
|---|---|---|---|
| Entering 2005 | 12 | 117 | $P < 0.001$ |
| Entering 2006 | 14 | 87 | $P < 0.001$ |
| Exiting 2005 | 50 | 32 | $P = 0.012$ |
| Exiting 2006 | 200 | 21 | $P < 0.001$ |

*Binomial test, 2-tailed.

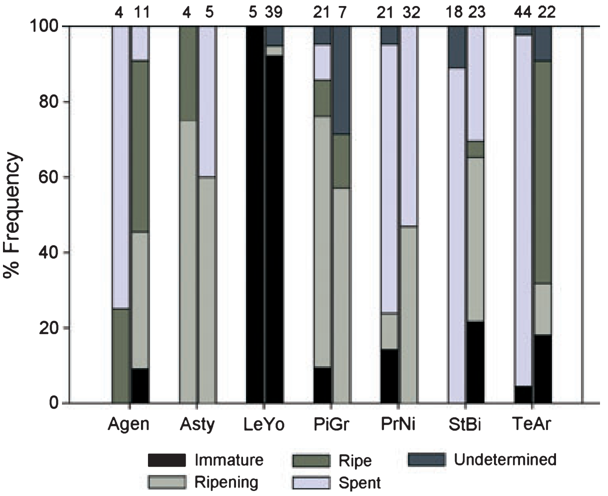

*Fig. 4.* Reproductive stage of entering versus exiting fish collected in 2005. Entering fish are represented in the left column by species, and exiting fish, in the right column. Sample size is noted above each column.

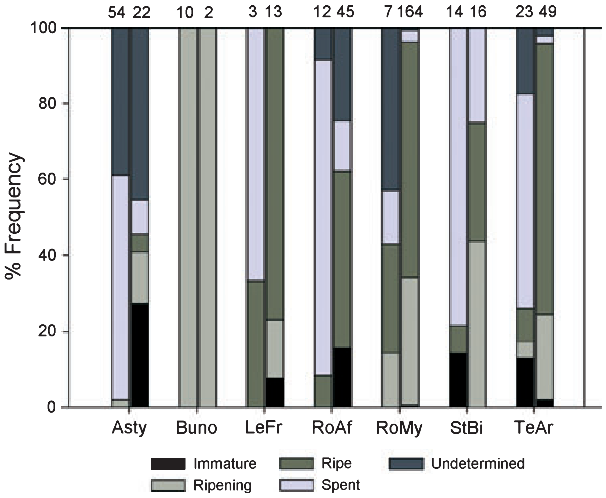

*Fig. 5.* Reproductive stage of entering versus exiting fish collected 2006. Entering fish are represented in the left column by species, and exiting fish in the right column. Sample size noted above each column.

the prediction that departing individuals would more often be gravid than entering individuals. This expectation was strongly upheld, supporting the conclusion that the most common migrating species are spawning in the river or other non-lake environments (Goulding 1980; Fernandes 1997; Winemiller & Jepsen 1998). Thus, despite the unpredictable occurrence of periods of connectivity, at least some species resident in the lake are able to spawn in other environments (Junk et al. 1989). However, contrary to the hypothesis of the lake as a productive feeding ground, entering fish had full stomachs more often than departing fish. One possible explanation for this observation is that the trap was much closer to the river (approximately 800 m) than to the lake (approximately 2000 m). If fish spent considerable time moving through the channel, digestion may have progressed further for exiting fish than entering fish.

Another unexpected result was that larger numbers of individuals of several common species were captured exiting the lake than entering it. If the lake were serving primarily as a feeding ground, then one would expect large numbers of smaller sized fish to be entering to feed and grow and a smaller number of adults to be exiting because predation in the lake is presumably intense. Instead, the entering and leaving cohorts of the relevant species were composed of individuals of about the same size. A possible interpretation of this is that gravid fish are leaving the lake to spawn. Spent fish returning in the same season could have originated from Cocha Cashu or any of a dozen other oxbow lakes on the Manu River. This is consistent with Goulding's (1980) report of the movements of migratory characins in Rio Madeira tributaries, in which he describes gravid fishes migrating to the main river channel to spawn near the confluence, and shortly thereafter returning to the tributaries. The main channel of the Manu River may similarly be the preferred spawning site of oxbow lake residents, allowing eggs and larvae to travel downstream in oxygen-rich conditions to better sites for larval development (Carvalho de Lima & Araujo-Lima 2004).

By emphasising potentially reproductive individuals, our selection of fish for gonadal analysis should have yielded a fair evaluation of reproductive condition of all adult-size fishes. Had larger fish been entering or exiting than those moving in the opposite direction, we would certainly have detected the difference, given the large sample sizes for common species. That we obtained similar results in 2 years of sampling reinforces this conclusion.

If the most common migratory species are spawning in non-lake environments, at what stage in ontogeny are juveniles entering the lake? The fact that we captured relatively few juveniles suggests that some migration into the lake may be occurring very early in ontogeny at body sizes too small to be retained by the 1-cm mesh used in the traps (Barthem & Goulding 1997).

Of the total catch of 4090 fish, 82% consisted of species known to be present in the lake. Of the 60 species captured in the trap, only 11 were represented by >100 individuals and thus captured in sufficient numbers to perhaps qualify as obligate migrants. Of these, about half were also common (>5% of individuals) in lake sampling (reported in Osorio 2008). These include *Moenkhausia dichroura, P. nigricans, R. myersii, S. spilopleura* and *S. bimaculata.* Members of the other 49 species might only have been vagrants or species inherently attracted to the moving current in the canal. There remain another 30 species known to be present in Manu oxbow lakes that failed to be captured in the trap or that were captured in small and/or sporadic numbers. It seems doubtful that many of these could be obligate migrants, but it remains to be discovered where and how most of them complete their life cycles.

Differences in lake state could have made the lake more or less attractive to certain species (Scheffer et al. 2003; Scheffer & van Nes 2007). But given that we know there were differences between 2004–2005 and 2006 in lake state, the similarities in the fish runs of the 2 years appear more remarkable than the differences.

The only comparable study of which we are aware that examined lateral migration between a floodplain lake and a major river was that of Fernandes (1997) undertaken in the Central Amazon where the water level rises and falls roughly 8 m in an annual cycle. Year-round monitoring of a connecting channel revealed a strong seasonality in fish movements, with a peak exodus of gravid individuals occurring during the period of low water (December–January). Although fish similarly appear to be leaving the lake environment to spawn, the seasonal pattern is the opposite of the one we observed in the headwaters region where connections to many floodplain lakes are intermittent and occur only at the season of high water.

The goal of our effort was to determine the degree of coupling between the fish faunas of the Manu River and Cocha Cashu, but the evidence proved to be equivocal. Some species showed evidence commensurate with a hypothesis of obligate migration, but many others did not. The highly variegated floodplain, with its lakes, seasonal pools, swamps and tributary streams, offers many possibilities for a diversity of reproductive strategies and much remains to be learned.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Table S1**. Number of individuals by species and reproductive state in 2005.

**Table S2.** Number of individuals by species and reproductive state in 2006.