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DOCUMENTATION OF THE TEMPORAL AND SPATIAL PATTERNS OF PIMELODIDAE CATFISH SPAWNING AND LARVAE DISPERSION IN THE MADRE DE DIOS RIVER (PERU): INSIGHTS FOR CONSERVATION IN THE ANDEAN-AMAZON HEADWATERS

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ABSTRACT

Catfishes (Siluriformes: Pimelodidae) in the Amazon River Basin serve important ecological and economic roles in structuring foodwebs, transferring nutrients and providing food resources for human populations. Large-scale developments such as construction of the Interoceanic Highway and associated proposed hydroelectric facilities could lead to alterations in river hydrology and aquatic ecosystems within Amazon headwater regions. We assessed temporal and spatial distribution patterns of catfish larvae to determine spawning location (highlands or lowlands) and larval drift patterns associated with rainfall events in the Andean-Amazon headwaters. We found significant differences in larval fish catch between transects with highest catches occurring in the Madre de Dios River, suggesting that the primary spawning habitats for these catfishes were in regions upstream of our sampling region within the Peruvian Andes. Highest larval catfish catches generally occurred near shore and in association with seasonal pulses in river flow. Based on our observations, we propose that this section of the Madre de Dios River is near the first identified spawning area for Pimelodidae species in the Peruvian Andes, and from this river reach larvae are transported downstream with each seasonal flood event with peak transport generally occurring in October, November and December. This research documents the important role the Madre de Dios Basin plays as spawning habitat for a key fish family in the Amazon River by serving as a corridor both for adult catfish spawning migrations and downstream larval fish transport. Given the critical role these catfishes play in structuring aquatic ecosystems in the Andean-Amazon region, their importance as a food resource for local people, and increasing threats to this riverine ecosystem associated with dam construction and channel modification, it is important to maintain and protect natural hydrologic conditions in the Madre de Dios to minimize losses of these ecosystem goods and services. Copyright © 2010 John Wiley & Sons, Ltd.

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INTRODUCTION

The Amazon Basin supports a group of ecologically and economically important catfishes (Siluriformes: Pimelodidae, the 'long whiskered' or 'giant' catfishes), some of which demonstrate long distance spawning migrations (up to 4000 km) from estuarine areas near the mouth of the Amazon, to headwaters in the Andean foothills (Barthem *et al*., 2003). Fish migrations for reproduction are considered one of the main behavioural responses to the annual hydrologic regime occurring in large tropical rivers (Lowe-McConnell, 1975; Munro, 1990; Junk and Wantzen, 2004). In Peru, the Madre de Dios River Basin represents one of the Andean-Amazon headwaters where commercial fisheries exploit these large catfish for human consumption (Cañas, 2000; Barthem *et al*., 2003). These catfishes also play critical ecological roles in the Amazon River foodweb demonstrating both top down (as apex predators) and bottom up (as dispersers of nutrients from estuaries and floodplain systems) roles (Goulding, 1979; Barthem and Goulding, 1997). While sexually mature individual catfish have been found from the commercial catch in the Made de Dios River, no larval fish collections have been made to assess whether this region is a spawning ground for these catfishes, nor have studies been done to assess how spawning patterns may relate to the annual hydrologic regime.

Viability of Amazonian large catfish populations may be dependent on annual flooding events. Timing and frequency of flows are thought to be crucial to trigger upstream adult fish migration to spawning areas and to transport larvae downstream (Welcomme and Halls, 2002; Junk and Wantzen, 2004). Adult catfish migrations from lowland to headwater regions and gonad development of these catfish are known to be synchronized with seasonal flood pulses (Munro, 1990; Cañas, 2000; Welcomme and Halls, 2002; Barthem *et al*., 2003). Flooding events are also likely important for larval development as a dispersal mechanism from incised headwater channels to large lowland floodplains which serve as nursery and rearing habitats for many catfish species (Araujo-Lima, 1994; Oliveira and Araujo-Lima, 1998; Araujo-Lima *et al*., 2001).

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In freshwater ecosystems, many fish species have evolved strategies to link reproductive cycles with environmental conditions to improve the likelihood of successful spawning and survival of larvae to adulthood (recruitment) (Bye, 1984). Day length, temperature and food availability predominate as environmental factors influencing timing of reproduction in temperate regions (Bye, 1984; Munro, 1990; Scott, 1990). Spawning activity of tropical fishes may be initiated by similar environmental cues including annual flooding events, which are thought to increase food availability and facilitate transport of larvae from spawning to rearing habitats via interaction with the floodplain (Bye, 1984).

The catfishes of the Amazon River basin represent one of the most globally diverse group of fishes and are currently the subject of several large-scale taxonomic assessments (see Sabaj *et al*., 2003–2006—the All Catfishes Inventory http://silurus.acnatsci.org/). While the taxonomic relationships of these species are being actively researched, information related to their population ecology is sparse. Fish larvae studies in the Amazon began in the 1980s, and the taxonomic characteristics needed to separate most of the commercial species, including their larvae, are known (Araujo-Lima, 1994; Araujo-Lima and Oliveira, 1998; Leite and Araujo-Lima, 2002; Leite *et al*., 2007). Key information including spawning habits, growth and exploitation rates are not available for most species and this information is critical to developing effective fishery management plans for these exploited species or in assessing possible impacts of large-scale habitat modifications such as dam construction. Relative abundance, timing and linear distance of migrations of adult Amazonian catfishes exists from monitoring commercial fishery catches to track trends in species abundance related to harvest patterns (Goulding, 1979; Cañas, 2000; Barthem and Goulding, 2007). However, little or no information exists to assess larval drift and dispersal patterns for this large group of fish species. Most freshwater fish species undergo ontogenetic habitat shifts necessitating different habitat requirements for each life stage (Scheidegger and Bain, 1995; Robinson *et al*., 1998; Leite *et al*., 2007). Larval fish distribution information provides strong inference about the location of spawning grounds and dispersal processes which are two key factors to consider in developing effective conservation and management programs for fish populations in tropical and temperate ecosystems (Oliveira and Araujo-Lima, 1998).

In this study, we used weekly field collections of pimelodid catfish larvae from the genera *Brachyplatystoma*, *Pseudoplatystoma*, *Platynematichthys* and *Sorubimichthys* based on descriptions by Leite *et al.* (2007) in the Madre de Dios Basin to examine the spatial and temporal aspects of catfish spawning and compare patterns in larval catfish abundance (as measured by weekly catches) with seasonal flow characteristics. By understanding patterns of larval occurrence and dispersal of these species, we can identify spawning areas and determine the synchrony of spawning with seasonal flooding of the Madre de Dios Basin. This study represents the first analysis of larval catfish in the Southern Peruvian Amazon and also the first larval fish research in the Andean foothill reaches of the Madeira River, the second largest tributary in the Amazon Basin. Information on the location, timing and duration of catfish spawning is important to develop conservation and management plans for these species.

MATERIALS AND METHODS

Study area

Our study area was located around the city of Puerto Maldonado, the principal urban centre in the Madre de Dios Basin in southeastern Peru. Puerto Maldonado is located at 480753 8607445 (19L UTM zone), in the confluence of the rivers Madre de Dios and Tambopata, at 256 m above sea level (Figure 1). Here the river channel is approximately 425 m wide and channel depth varies 10–13 m during the rainy season (Barthem *et al*., 2003). Physical and chemical conditions of the river vary based on these hydrologic periods, with large increases in water level, average velocity, water discharge and sediment load during the wet season (Barthem *et al*., 2003).

The Madre de Dios River is the largest river in southeastern Peru flowing from west to east with a drainage area of approximately 90 000 km^2. Nine tributaries discharge into the Madre de Dios River, through which water leaves the basin. Six tributaries drain from highlands areas over 4000 m above sea level, and three drain lowlands areas from the northern area of the basin (Goulding *et al*., 2003) (Figure 2).

Hydro-climatologically, the Amazon lies in a feedback system between rainforest that recycles almost one half of the precipitation it receives, and the Andes which act as an orographic barrier importing atmospheric water and exporting surface waters to the Amazon System (Poveda *et al*., 2006). The natural flow regime of the Madre de Dios Basin is largely influenced by the high rainfall variability caused by its proximity to the Andes (Kalliolla and Puhakka, 1993; Puhakka *et al*., 1993; Puhakka and Kalliolla, 1993; Goulding *et al*., 2003). Rainfall records obtained mostly from two Andean meteorological stations from the *Servicio Nacional de Meteorología e Hidrología del Perú* (SENAMHI), the Peruvian Weather Service Institution, indicated a high geographic variability in precipitation pattern within this basin, suggesting a rainy season between October and April and a drier season between May and September. River level variability in the Madre de Dios

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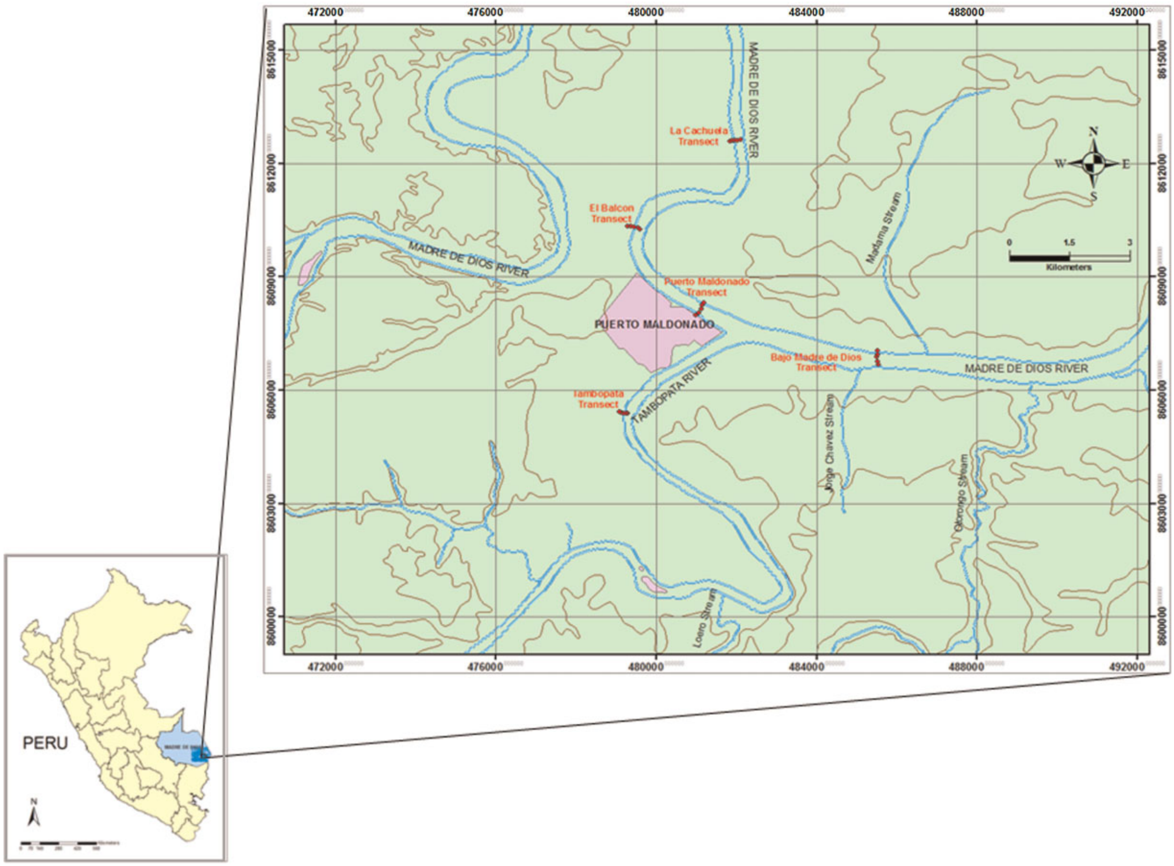

Figure 1. Location of the study area and sampling transects around Puerto Maldonado along a section of Madre de Dios River in southeastern Peru

Basin is controlled principally by rainfall as snow melt does not influence the flow regime in the Andean region (Barthem *et al*., 2003).

Sampling

During 2006 weekly larval fish sampling was conducted along five cross channel transects located on the Madre de Dios River near the city of Puerto Maldonado. All transects crossed the river from bank to bank (Figure 1). Three of them (La Cachuela, El Balcon and Puerto Maldonado) were located in the Madre de Dios River upstream of the confluence with the Tambopata River, and a fourth transect (Bajo Madre de Dios) was placed downstream of the confluence. The fifth transect (Herrera) was located in the Tambopata River, approximately 4 km upstream of the mouth (Figure 1). Transects in the Madre de Dios River were approximately 3.5 km from each other, with the most upstream transect placed 12 km from the most downstream. The Tambopata River transect was re-located 1.5 km further upstream during the dry season due to channel shallowness. For the final analysis, this new location was treated as a different transect, mostly sampled during the dry season.

Spatial location of transects is important because of the biological inferences that can be drawn from larval catches at each location. While headwater areas of the Madre de Dios River drain both highlands (in the Andes) and lowlands, headwaters of the Tambopata River only drain highlands from a different geographic region than the Madre de Dios River. Differences in larval catfish catch between these systems (i.e. differences in catch between Herrera site in the Tambopata River and La Cachuela, El Balcon, and Puerto Maldonado in the Madre de Dios River, upstream of the mouth of the Tambopata) would suggest differences in the timing and occurrence of spawning in these drainage areas.

At each transect, samples were collected at five sites representing distinct habitat categories: cutting banks (erosive areas usually with high velocities); filling banks (depositional areas with lower velocities); main channel; and zones in-between the main channel and cutting bank and main channel and filling bank. Samples at the bank habitats were taken at distances <20 m from shore. Surface samples were taken at 1 m depth, and depth samples were taken at 70% of the maximum depth at each of the five habitat categories. Physico-chemical measures were taken at the surface of each sampling station.

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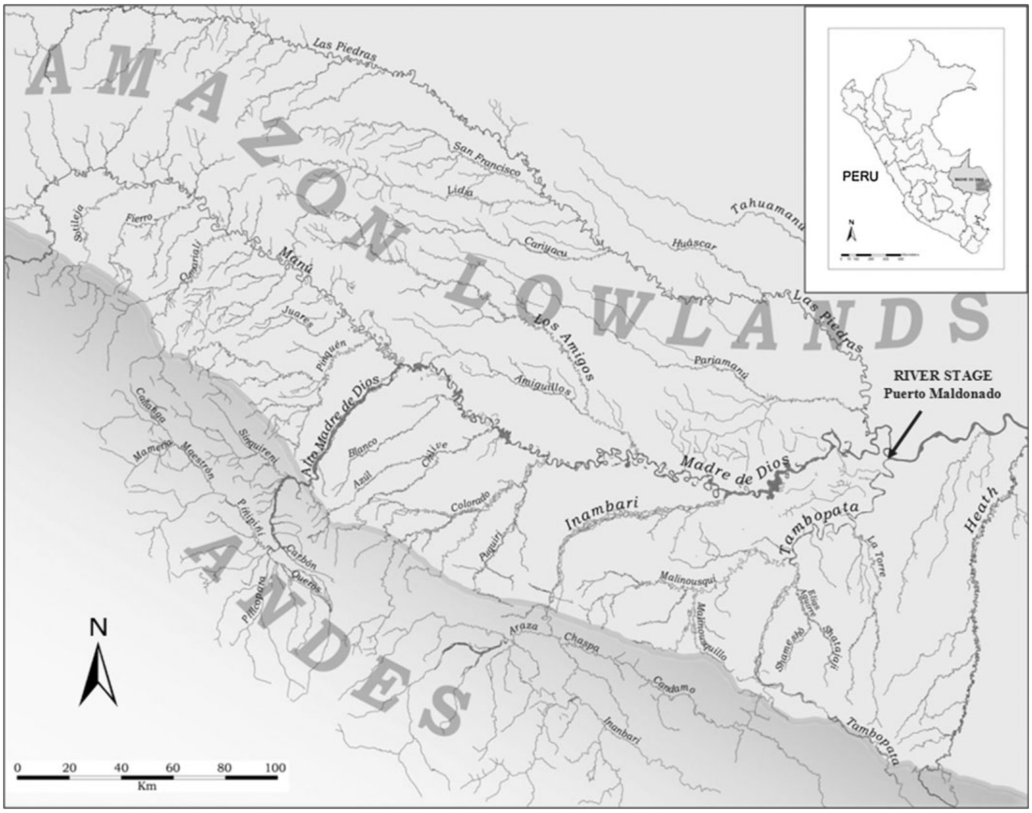

Figure 2. The Madre de Dios Basin, its andean (south) and lowland (north) tributaries, and location of Stage in Puerto Maldonado, where field work was carried out

A 365-micron ichthyoplankton net (0.47-m diameter, 1.50-m length) fitted with a removable collection bottles was used to sample larval fish. Volume of water sampled was determined by using a mechanical flowmeter in the mouth of the net (General Oceanics 2030R). Depth measurements were recorded with an electronic sounding unit (Lowrance LMS-480M), dissolved oxygen and temperature were measured using a YSI Model 550A, conductivity was assessed using a YSI 30 conductivity meter, and pH was measured with a Hanna Tester HI98130. Channel width and lateral distance between sample sites was determined using an electronic range finder (Nikon ProStaff Laser440).

Water level measurements were obtained from a gauge stage installed on the Madre de Dios River in Puerto Maldonado. Measurements were recorded twice daily (0800 and 1800 h) between 4 December 2004 and 31 December 2006. For analysis on the relationship between seasonal flow and larval transportation water level records of 2006 were used only, which included rainy season (January–March and October–December) and dry season (April–September). Channel width was also recorded with the range finder during 2006 and integrated water velocity was recorded at five equidistant points across the channel. Daily discharge of the Madre de Dios River was then estimated using the velocity–area technique by calculating discharge in individual river segments across the channel (Buchanan and Somers, 1969).

Larval fish collections were made at standardized times during daylight hours based on previous work in the central Amazon that demonstrated no difference in day and night larval fish catches (Araujo-Lima *et al.*, 2001). At each habitat site within a transect, the net was deployed from an anchored boat to the selected depth for 3 or 5 min (depending on flow conditions). All net contents were rinsed into a collection bottle and preserved in a 4% formalin solution. Samples were returned to the laboratory in Puerto Maldonado where fish larvae were sorted and identified by using Leite *et al.* (2007), who based larval identification on morphological features of homocercal fin development. Catfish larvae were counted and all biological material was archived at *Museo de Historia Natural* in Lima, Peru.

Statistical analysis

Larval fish counts were standardized by density (number of larvae per 50-m^3 of water sampled) to compare catches to time period, transect and station (habitat). A generalized linear mixed model (GLIMMIX, SAS version 9.1, SAS

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Institute, Cary, North Carolina) was used to compare larval fish densities at various temporal and spatial levels. During comparison analyses, season (two seasons, wet or dry), transects (six transects, spatial location), and station (five stations, habitat types) were all fixed effects within the GLIMMIX procedure. Because the variances were not proportional to the means (Levene's test, $p < 0.0001$), we specified within the model procedure that larval catches followed a negative binomial distribution. If larval density differed by fixed effects ($p < 0.05$) a Least Square Means (LS Means) procedure was used to determine which effects (seasons, transects or habitat station) differed ($p < 0.05$).

RESULTS

Two hydrological periods in Madre de Dios River were identified in the 2-year stage records in Puerto Maldonado: a low water period that occurred May–September (dry season), and a high water period during other months (wet season; October–April). During this time period the river stage varied over 9 m (Figure 3). A total of 44 984 catfish larvae were captured from the five sample transects. Seasonal patterns are apparent with highest catches occurring during wet seasons and lower catches during dry seasons (Figure 4).

Significant differences in larval densities were found by week (GLIMIX procedure, $F = 89.21$ $p < 0.0001$) and season (GLIMIX procedure, $F = 128.91$ $p < 0.0001$). Mean weekly catches of larval catfish declined from April to September, and increased from October to December and January to March concurrent with increases in weekly river discharge (Figure 4). Correlative patterns between river water level and larval catfish catch were apparent. For example, during weeks 41–43 (7 October–21 October 2006) the stage of the Madre de Dios increased by 3.99 m (Figure 4). And during the following weeks (beginning in week 44, 28 October) catches of larval catfish increased and remained high for the remainder of the calendar year (Figure 4). Similar patterns were observed at the beginning of the year sampling with higher catches during high water events (approximately weeks 1–14) and declining catches as water levels rapidly declined (weeks 14–22; Figure 4).

Comparisons of larval catfish catch between transects, habitat types and depth

Because the majority of the fish larvae were collected during the wet season, we used LS Means to separate differences in larval fish catch by transect during the wet season only. Catches of larval catfish were significantly different between El Balcon and Puerto Maldonado transects (both in Madre de Dios River), and between transects in the Tambopata River and Puerto Maldonado transect in the Madre de Dios River (upstream of Tambopata River mouth) (Figure 1; Table I).

During the wet season when water levels were high, LS Means comparisons of larval fish catch by habitat category found significant differences in larval density between habitat areas near shore versus areas near the main channel (Figure 5). Mean catch of larval catfish during the rainy season was significantly different between both cutting and filling bank habitats and between these habitats and those that were closer to the channel. Larval catfish catches among habitats associated with the channel were not significantly different (all $p > 0.05$, Table II). No statistical differences in larval catches were found between 1-m depth samples and those taken at greater depths in any habitat (LS Means $p = 0.36$) greater than 1 m (GLIMIX procedure, d.f. $= 2313$, $p < 0.0001$).

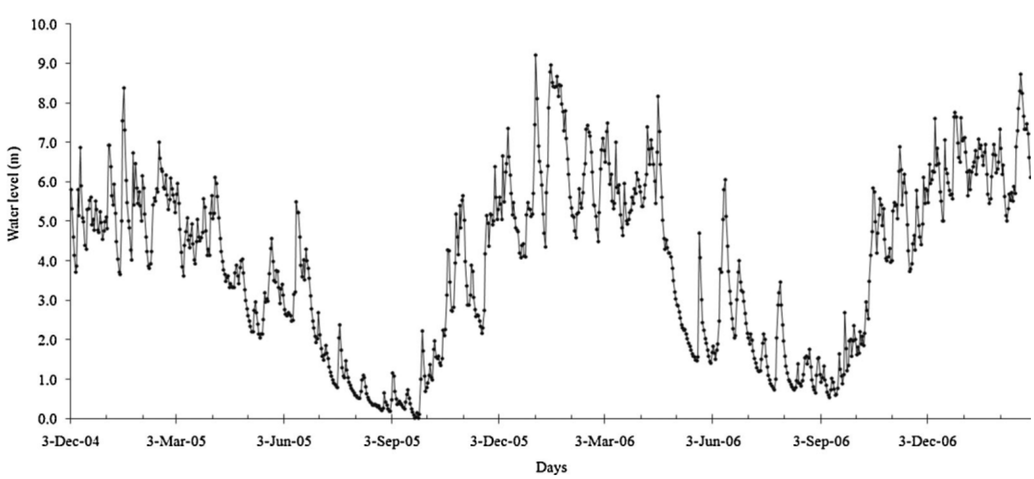

Figure 3. Daily water level variation for the Madre de Dios River in Puerto Maldonado, Peru (December 2004 to February 2007)

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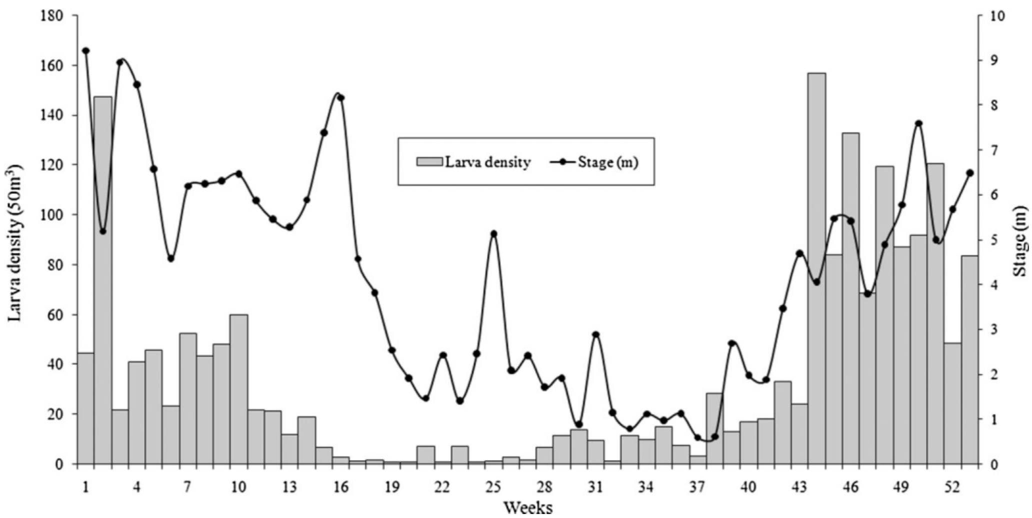

Figure 4. Average larval density (larvae per 50 m^3) and water level in Madre de Dios River during 2006

Water quality characteristics varied among transects likely due to transect location with respect to the Tambopata River, mean values of the hydrological and physico-chemical characteristics are presented in Table III. Transects above the confluence with Tambopata River showed higher conductivity values (the highest 88.814 $\mu S\,cm^{-1}$ for El Balcon during dry season), and pH values followed a similar pattern: higher during dry season than rainy season. Dissolved oxygen kept values over 6 ppm most of the year along all transects, surface temperatures kept a similar pattern, with average values above 25.4°C. Velocity and discharge got the highest values at Bajo Madre de Dios transect during rainy season (0.716 $m\,s^{-1}$ and 2502.19 $m^3\,s^{-1}$, respectively), and Tambopata River showed the lowest values during dry season with regard to discharge and velocity: 293.54 $m^3\,s^{-1}$ and 0.497 $m\,s^{-1}$, respectively (Table III). In the Madre de Dios River, conductivity was not significantly different between the three transects located above the Tambopata River, but they were different downstream at the Bajo Madre de Dios transect as well at the transect within the Tambopata River, which suggests the strong influence of Tambopata River waters into the Madre de Dios River channel (transect Bajo Madre de Dios is located about 4 km downstream from confluence). Dissolved oxygen values were not significantly different between the four transects of the Madre de Dios River but did differ with the transect in the Tambopata River. No statistical differences in temperature appeared between most of transects, with the exception of the Herrera transect that was generally warmer than other transects (Table IV).

Table I. Statistical comparisons between larval densities by transects for the high water period (Least Square Means. GLIMMIX Procedure, $p < 0.0001$, d.f. 2305)

Transect name	Transect name	$Pr > \|t\|$
La Cachuela	El Balcon	0.4524
La Cachuela	Puerto Maldonado	0.0003
La Cachuela	Bajo Madre de Dios	0.7060
La Cachuela	Herrera	0.0535
La Cachuela	Candamo Port	0.0929
El Balcon	Puerto Maldonado	<0.0001
El Balcon	Bajo Madre de Dios	0.2619
El Balcon	Herrera	0.1749
El Balcon	Candamo Port	0.3090
Puerto Maldonado	Bajo Madre de Dios	0.0012
Puerto Maldonado	Herrera	<0.0001
Puerto Maldonado	Candamo Port	<0.0001
Bajo Madre de Dios	Herrera	0.0272
Bajo Madre de Dios	Candamo Port	0.0453
Herrera	Candamo Port	0.6612

DISCUSSION

In the Amazon River, downstream dispersal of eggs and larval fish are proposed to be the key to successful recruitment in many riverine fish species where large, seasonally inundated floodplains offer juvenile rearing habitat (Araujo-Lima and Oliveira, 1998; Araujo-Lima *et al*., 2001). Seasonal increases in river flow provides fish with access to headwater spawning areas (Harrow and Schlesinger, 1980; Araujo-Lima and Oliveira, 1998; Welcomme and Halls, 2002), creating corridors for upstream passage of spawning adults and downstream passage of eggs and larvae, and provides access to floodplain rearing habitats (Goulding, 1980; Lowe-McConnell, 1987; Araujo-Lima *et al*., 2001; Humphries *et al*., 2002; Humphries, 2005). Seasonal high flow events may also influence fish community structure, decreasing the likelihood of predation

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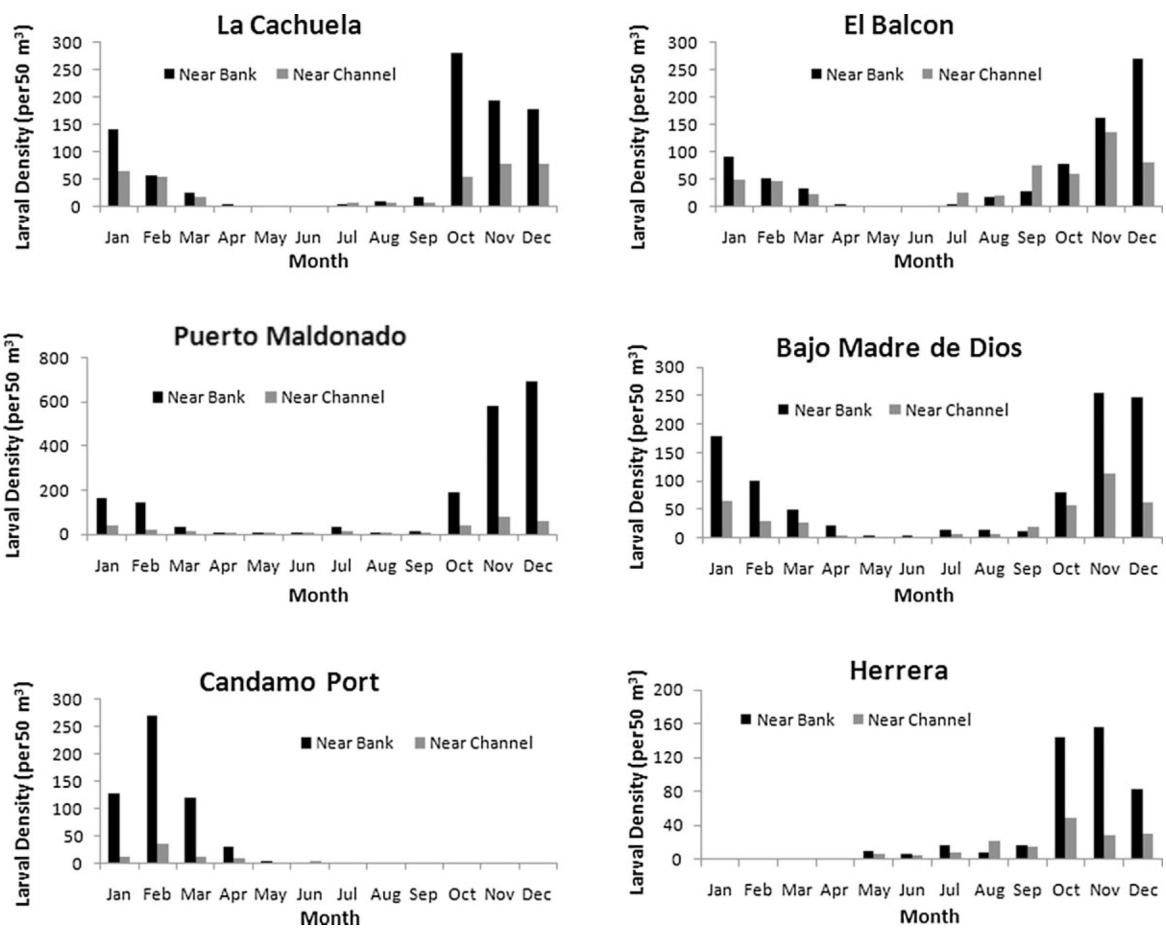

Figure 5. Average monthly larval catches at the five sampling transects by habitats: Near the bank (black bars) and Near the main channel (gray bars). Note differences in density among transects in Madre de Dios River (four on top) and Tambopata River (two on bottom)

on fish larvae as they are transported downstream (Junk and Wantzen, 2004). Fish migration, both by larvae moving downstream and adults moving upstream, are important factors to maintaining river basin productivity (Welcomme and Halls, 2002) through nutrient transport, seed dispersal and foraging opportunities for piscivores.

Table II. Statistical comparison between larval densities by habitats across the channel for the high water period (Least Square Means. GLIMMIX Procedure, $p < 0.0001$, d.f. 2307)

Habitat	Habitat	$Pr < \|t\|$
Cutting bank	Filling bank	<0.0001
Cutting bank	Middle channel	<0.0001
Cutting bank	Cutting–Middle	<0.0001
Cutting bank	Filling–Middle	<0.0001
Filling bank	Middle channel	<0.0001
Filling bank	Cutting–Middle	<0.0001
Filling bank	Filling–Middle	<0.0001
Middle channel	Cutting–Middle	0.0809
Middle channel	Filling–Middle	0.2527
Cutting–Middle	Filling–Middle	0.5458

Timing and spawning

Based on our catches of fish larvae, the Madre de Dios River Basin is an important spawning area for catfishes and other fish species. Most of the fish larvae (>95%) captured in the river channel belonged to the orders Characiformes and Siluriformes (70% and 25.2%, respectively), other orders that could be identified included Perciformes, Clupeiformes and Gymonotiformes. Densities of larval catfish collected weekly at fixed transect locations demonstrated strong seasonal patterns with highest catch rates measured during times of highest flow. Significantly higher densities of catfish larvae in the river channel between October and December indicated that spawning activity of these species was synchronized with the time of water level rising and remaining high until the end of the rainy season in March (Figure 4). Similar increases in larval fish abundance with

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Table III. Mean values of physico-chemical characteristics of the Madre de Dios River recorded at the assessed transects

Transect	Hydrologic season	Dissolved oxygen (mg L^{-1})	Temperature (°C)	pH	Conductivity (μS cm^{-1})	Velocity (m s^{-1})	Discharge ($m^3 s^{-1}$)
La Cachuela	Rainy	6.581	25.464	6.539	68.032	0.617	1812.75
	Dry	6.618	25.510	7.045	87.787	0.601	1110.51
El Balcon	Rainy	6.506	25.519	6.870	67.786	0.477	1297.97
	Dry	6.528	25.763	7.093	88.814	0.399	735.90
	Dry	6.576	25.798	7.071	87.942	0.617	1294.75
Bajo Madre de Dios	Rainy	6.430	25.764	6.718	58.817	0.716	2502.19
	Dry	6.623	25.986	7.021	79.442	0.560	1006.09
Herrea	Rainy	5.859	26.422	6.761	37.718	0.589	617.72
	Dry	6.686	26.667	6.752	49.041	0.499	293.54
Candamo Port	Rainy	6.874	25.769		31.455	0.604	917.83
	Dry	7.123	26.170	6.776	43.285	0.497	357.05

increases in discharge have been observed in other regions including Australia (Humphries and King, 2003) and North America (Robinson *et al*., 1998).

The largest numbers of larval catfish were collected the fourth week of October with larval density values increasing by factors of 5–10 compared to the previous catch in all transects (maximum average during our study = 180 individual per 50 m^3, El Balcon transect). Based on these catches, this week likely represented the peak of the spawning activity of these catfishes in this basin for 2006. Frequency of flood events during the high water period in the area is supporting this transportation and appears to be closely linked with spawning behaviour of large catfishes (Cañas, 2007). In the Central Amazon River, catfish larvae have also been collected moving downstream during the last months of the year (Araujo-Lima and Oliveira, 1998), as well as Characiform larvae (Oliveira and Araujo-Lima, 1998).

Morphological features of sampled larvae, such as yolk sac presence and absence of support structures for caudal fin ('pre-flexion larva', in Leite *et al*., 2007) could suggest additional finer scale information on the timing and location of fish spawning and be used as proxies to assess potential spawning areas for catfishes in the Madre de Dios River. We observed that most captured fish larvae had not yet absorbed their yolk sac, which indicated that most fish were collected within a few hours to days post-hatching at collection sites. Time for incubation and embryo differentiation for most of the species that disperse eggs and larvae is relatively short, 12–18 h (Nakatani *et al*., 2001). Given that the average surface velocity of the river during this period was about 0.79 m s^{-1} (Cañas, 2007) it is possibly that the spawning

Table IV. *p*-values from statistical comparison of water parameters by transects for high water period (Least Squares Means. GLIMMIX Procedure, $p < 0.0001$)

Transect name	Transect name	Conductivity (μS cm^{-1})	Oxygen (mg L^{-1})	Temperature (°C)
La Cachuela	El Balcon	0.8774	0.3156	0.7260
La Cachuela	Puerto Maldonado	0.9277	0.0623	0.3628
La Cachuela	Bajo Madre de Dios	<0.0001	0.0483	0.0501
La Cachuela	Herrera	<0.0001	<0.0001	<0.0001
La Cachuela	Candamo Port	<0.0001	0.0003	0.0968
El Balcon	Puerto Maldonado	0.9494	0.388	0.5757
El Balcon	Bajo Madre de Dios	<0.0001	0.3292	0.1072
El Balcon	Herrera	<0.0001	<0.0001	<0.0001
El Balcon	Candamo Port	<0.0001	<0.0001	0.1751
Puerto Maldonado	Bajo Madre de Dios	<0.0001	0.9068	0.2920
Puerto Maldonado	Herrera	<0.0001	<0.0001	<0.0001
Puerto Maldonado	Candamo Port	<0.0001	<0.0001	0.3843
Bajo Madre de Dios	Herrera	<0.0001	<0.0001	0.0009
Bajo Madre de Dios	Candamo Port	<0.0001	<0.0001	0.9606
Herrera	Candamo Port	0.0050	<0.0001	0.0021

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grounds would be located within approximately 51 km upstream from the sampling area, near the Andean foothills (200–400 m of elevation). This region is then likely previously unidentified spawning grounds for these ecologically and economically important fishes in the Amazon Basin.

Spatial distribution of catfish larvae

Significantly higher densities of larval catfish were collected in the Madre de Dios River than in the Tambopata River suggesting that the former offers more suitable spawning habitat conditions for these species. Most of the captured larvae were in the early post-emergent phases; and most still with the yolk sac or vestiges of the yolk sac. Moreover, within each transect larval densities differed by habitat type with higher densities along near-shore habitats, which demonstrates passive transport downstream by river currents within the main channel. These characteristics suggest that successful Amazonian catfish spawning depends on adults having access to areas with higher flooding dynamic to transport eggs and larvae to downstream floodplain rearing habitats.

CONCLUSIONS

Key findings from this study include (1) identification of the headwaters of the Madre de Dios River as spawning habitat for Pimelodidae catfishes, the first known spawning area in the Andean-Amazon basin, (2) spawning is synchronized with high flow events during the wet season and (3) the spawning window is protracted over about for 10–16 weeks. These results have conservation implications for this fish family and other aquatic organisms throughout the Amazon River basin.

Lateral connectivity drives nutrient exchange, habitat availability and dispersal of plants and animals, and is widely studied in the Amazon (Galetti *et al*., 2008). For fish, this flooding creates a suitable environment for spawning and feeding of adults, juvenile and larvae (Lowe-McConnell, 1987; Leite and Araujo-Lima, 2002; Junk and Wantzen, 2004). In Madre de Dios River, lateral inundations of the floodplain are short in duration (hours to a few days), but very frequent (Cañas, 2007). These frequent flooding events create pulsed flows that transport larvae downstream to connect spawning areas in the Andean foothills with known nursery areas downstream in the large floodplains of the central Amazon River in Brazil and further up to 4000 km downstream (Barthem and Goulding, 1997; Oliveira and Araujo-Lima, 1998; Araujo-Lima *et al*., 2001).

Two critical periods in the life history of these catfishes, upstream migration of adults to spawning grounds and downstream transport of larvae to rearing habitats, depend on the longitudinal connection of the entire river basin and the interplay between hydrology and flow events. Large development projects currently being planned in the Madre de Dios Basin associated with the Interoceanic Highway have the potential to dramatically alter flow conditions of this region through proposed development of hydropower dams within the Madre de Dios Basin (Inambari River) and within other headwaters in the Peruvian Andes (Urubamba, Ene and Apurimac Rivers). This development will alter riverine flow and create migratory barriers for larval and adult catfish, possibly causing population reductions and extirpations similar to what has occurred for most of the big river native fishes in much of western North America (Minckley, 1991) and elsewhere in the Amazon basin (Gubiani *et al*., 2009).

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