# HYDROLOGIC REGIME AND DOWNSTREAM MOVEMENT OF CATFISH LARVAE IN THE MADRE DE DIOS RIVER, SOUTHEASTERN PERU

By

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A THESIS PRESENTED TO THE GRADUATE SCHOOL
OF THE UNIVERSITY OF FLORIDA IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE

UNIVERSITY OF FLORIDA

2007

To Yrma and Carlos, my parents, for their great effort in supporting my life and education.

## ACKNOWLEDGMENTS

I am very appreciative to Dr. Peter Waylen, Dr. Bill Pine, and Dr. Joann Mossa, members of my advisory committee, for their permanent academic support on the completion of this research. I am especially grateful to Dr. Peter Waylen, for his dedication, energy and encouragement to develop more interesting questions in order to understand the hydrology of Amazonian headwaters in Peru. I want to dedicate a special gratitude and appreciation to Michael Goulding and Mimi Zarate for their warm reception and friendship during my arrival and time living in Gainesville. I am indebted to Dr. Michael Goulding, Dr. Ronaldo B. Barthem, Dr. Bruce R. Forsberg and Dr. Rosseval G. Leite for intellectual stimulation on Amazon fish ecology and limnology.

For financial support I am indebted to the Gordon & Betty Moore Foundation and The John D. and Catherine T. MacArthur Foundation, under grants awarded to Dr. Michael Goulding. Several institutions in Peru also helped with data and facilities to execute different phases of this research. In Lima, the *Servicio Nacional de Meteorología e Hidrografía* (SENAMHI) assisted with meteorological data of the region; the Ichthyology Department in the *Museo de Historia Natural* of the *Universidad Nacional Mayor de San Marcos* helped with fish larva identifications and the collection of biological samples. For field facilities and the implementation of larvae sampling in the Madre de Dios River I would also like to thank the following institutions: The Fishermen's Union, the Amazon Conservation Association (ACCA), and the *Marina de Guerra del Perú*. For logistical assistance during the field research I am especially indebted to the following fishermen from Puerto Maldonado: Carlos Saire, Genaro Apaza, Exaltación Tapara, Landers Macahuachi, and Rolando Vela. Mr. Alfredo Soza kindly allowed us to use his riverside property to place river level gauges.

Finally, I want to express my special thanks to my family in Peru, to Yrma and Carlos, my parents, for their total support and encouragement on pursuing my education goals; to my sisters Mirian, Jenny and Milagros for always being there; to Maria Luisa, my grandmother, who waits anxiously for my return; and to my dear aunt Elsa, who was next to my mom during my first years of childhood to take care of me.

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August 2007

Chair: Peter R. Waylen
Major: Geography

Seasonal flow conditions and catfish larvae production were evaluated in the Madre de Dios River (southeastern Peru) in order to understand the influence of environmental conditions on the reproductive behavior of a group of large catfishes (Siluriformes: Pimelodidae), important species in commercial fisheries, that annually arrive into this headwater region for spawning. A simple stochastic model is presented to describe the influence of the natural flow regime of this river on the downstream transportation of catfish larvae. Temporal and spatial drifting patterns of these catfish larvae were also analyzed and described within the river channel, and the significant ecological role of this region was emphasized in the completeness of life cycle of this important Amazon fish resource.

One year of daily river stage records were related to weekly larval catches to determine the association between floods and spawning events, and on the basis of hydro-climatologic characteristics of Andean-Amazon regions, available long-term historical rainfall records were employed to determine the inter-annual variability of floods within the Madre de Dios Basin. Larval catches obtained from five cross sectional transects placed in a 12 km-section of the channel of Madre de Dios River, and surface and deep samples, were employed to assess larvae drifting within the channel.

Major larval drift occurred during the high water season, and specifically they appeared to be associated with stages of over the 5 m, a level which served as a physical indicator of the river, triggering spawning responses of these species, termed a “Biologic Hydrological Significant Event” (BSE). Timing of these BSEs, estimated from the historical rainfall records, described a uniform distribution during the wet season, and their inter-arrival times were exponentially distributed. These observations provided the basis of the stochastic model describing the likelihood of larvae releases from this headwater region to the lowland Amazon. Within the channel, larval drift occurred mostly along the banks of the river, however no significant spatial differences in the numbers of fish larvae moving downstream were found along the sampled sections, which indicated that spawning habitats were located near this Andean foothill region. The permanent flood pulses during the periods of larval peaks and the limited availability of floodplain areas in the channel indicated that larvae do not stay in this region.

Analysis of hydrologic regime and catfish larvae drifting in the Madre de Dios Basin demonstrated the strong association between fish fauna and the aquatic environment, the fundamental role of the Amazon headwater regions in fish abundance and diversity, and the function of river channels on catfish spawning and migrations. It is fundamental to maintain and protect hydrologic conditions in the Andean-Amazon region in order to keep aquatic life and connectivity of the complete basin from the headwaters to the estuary.

# CHAPTER 1
# INTRODUCTION

The Andes represents one of the three principal ecological-geological zones of the Amazon System, embracing six major Amazon headwater tributaries along most of its western border (Goulding et al. 2003). Hydrologic characteristics of these tributaries are heavily influenced by local rainfall (Barthem et al. 2003; Poveda et al. 2005), which, combined with high rates of erosion, topography and land cover vegetation, create in the river channel environmental conditions to support very important ecological processes (Poff et al. 1997; Goulding et al. 2003; Junk & Wantzen 2004). Migrations for reproduction are one of the most important behavioral responses of fish to the annual natural hydrologic regime of this large basin (Lowe-McConnel 1975; Barthem & Goulding 1997; Poff et al. 1997; Junk & Wantzen 2004), and in the Madre de Dios headwater region (southeastern Peru), large catfishes (Siluriformes: Pimelodidae) have adapted and synchronized their reproductive behavior and gonad development to the seasonal flood pulses (Munro 1990; Barthem & Goulding 1997; Poff et al. 1997; Cañas 2000; Welcomme & Halls 2002; Barthem et al. 2003). After spawning, survival of catfish larvae also depends on flooding events, which enhances the connectivity of these running ecosystems and support larval drifting from this upland region to the lowlands (Araujo-Lima & Oliveira 1998; Oliveira & Araujo-Lima 1998; Araujo-Lima et al. 2001).

The “Natural Flow Regime” paradigm postulates that streamflow quantity and timing drive the distribution of aquatic fauna and the connectivity of flowing water ecosystems (Poff et al. 1997). This concept is used to describe the relationship between the downstream drift of catfish larvae and hydrologic regime of the Madre de Dios Basin, and to develop a simple stochastic model of larval releases from this Amazon-Andes headwater region to the lowlands. This research shows that the temporal variability of catfish larvae subjected to the likelihood of occurrences of Biological Hydrologic Significant Events (BSE), which herein are considered to be signified by critical river level stage associated with peaks of larval production measured in the Madre de Dios River. Partial Duration Series (PDS) analysis has been employed in the past to evaluate flood risks and related problems (Ashkar & Rouselle 1981; Waylen & Woo 1983), and this method is used to evaluate the probability of frequency and timing of BSEs during the flooding period in the Madre de Dios Basin. Given the limitation of flow information for this basin and the notable interaction between precipitation in the eastern Andes and streamflow from the headwaters of the Amazon (Poveda et al. 2006), historical rainfall records of two meteorological stations of the Madre de Dios Basin are used to predict, or "hindcast" longer term BSE records and characterize the inter-annual variability of hydrologic conditions in the basin. It is the intention of the first part of this research to introduce a simple stochastic model that describes the strong influence of the natural flow regime on the releases of larvae of the large migratory catfishes of Amazon.

The river channel is also of critical importance for the reproduction of Amazonian large catfishes, as it is the principal habitat through which fish larvae are dispersed downstream to nursery habitats, as well as being the spawning ground where breeding occurs (Goulding 1980; Oliveira & Araujo-Lima 1998; Nakatani et al. 2001). Dispersion of eggs and larvae are usually hypothesized to constitute the most fragile phase of fish natural history (Araujo-Lima & Oliveira 1998; Oliveira & Araujo-Lima 1998; Nakatani et al. 2001). Most fish species in the Amazon Basin spawn at the beginning of and/or during the high water season as a response to the physical and chemical changes associated with large rivers (Goulding 1980, 1988; Barthem & Goulding 1997; Araujo-Lima & Oliveira 1998). Floods provide favorable conditions in river channels in both upstream and downstream directions (Poff et al. 1997; Goulding et al. 2003).

Temporal and spatial distributions of catfish larvae from the Madre de Dios River were examined as a function of seasonal flow characteristics of the principal channel. Five cross section transects were established and sampled on a weekly basis during 2006. Two years of river stage records were used to characterize the annual hydrologic regime of the Madre de Dios River, and larval catches were used to determine the influence of seasonal floods on larval drift patterns, and thus indirectly on spawning times. The second part of this research highlights the importance of understanding temporal and spatial patterns of catfish larval drift in this Amazon headwater region and provides fundamental information for conservation and fishery management of migratory species in the Amazon Basin.

The construction of the Transoceanic Highway is now underway in southeastern Peru, and two dams on the Madeira River are planned near Porto Velho, Rondônia (Brazil). Both the highway and dams represent large economic development projects with probable direct impacts on the flow regime of the Madre de Dios River and some of its tributaries. These impacts in turn could negatively impact long-distance migratory catfishes. This research not only provides scientific information to aid the understanding of the close association between fish resources and flow regime in freshwater ecosystems, but also to present a baseline for future assessments in this headwater region after these large projects are completed.

# CHAPTER 2
# RELATING HYDRO-CLIMATOLOGY OF MADRE DE DIOS BASIN TO CATFISH LARVAE DRIFTING IN SOUTHEASTERN PERU

## Introduction

Natural flow regime is the principle variable driving both the distribution and abundance of freshwater aquatic fauna, and the integrity and connectivity of flowing water ecosystems (Poff et al. 1997). Flood events are strongly influenced by seasonal precipitation patterns within the Amazon headwater region, and in Madre de Dios Basin (Peru) it has been noted that they are related to the initiation of spawning migration behavior of a group of large catfishes (Barthem et al. 2003). The timing of flood events is critical ecologically in the life cycles of these species – mature adults swimming upstream to reproduce, and larvae drifting downstream to colonize new habitats– their life cycles are timed to take advantage of flood occurrences in spawning areas (Low-McConnell 1975; Barthem & Goulding 1997; Poff et al. 1997). Currently, construction of the Transoceanic Highway is underway in southeastern Peru, and two dams at Madeira River are being considered to be built near Porto Velho, Rondônia (Brazil). Both large development projects represent sources of significant land use change and potential alteration of the natural flow regime of Madre de Dios Basin. This study postulates a simple model relating basin hydro-climatologic conditions to catfish larvae production.

The concept of Partial Duration Series (PDS) of hydrologic events on the Madre de Dios River is employed to establish a stochastic flood model of catfish larvae releases from the headwaters to lowland Amazon. Two years of daily rainfall records from three meteorological stations, and daily observed stage measurements at Puerto Maldonado, are available for comparison to weekly captures of fish larvae. The derived relationship is extended to those historical rainfall records which precede the limited period of stage records in order to evaluate the inter-annual variability of the number and timing of flood events within the basin. This assessment considers a Biological Hydrologic Significant Event (BSE) to be one which equals or exceeds a critical stage associated with peaks of larval production in the Madre de Dios River. This chapter shows the relationship between temporal variability of catfish larvae production and the likelihood of such BSE events. The results provide a base line against which potential future scenarios of flow regime alterations and their associated consequences on larval production at other similar regions of the Amazon System can be compared.

## Literature Review

All river basins display a natural hydrologic signature, or regime, which exerts control over productivity of aquatic life and habitat conditions (Poff et al. 1997; Junk & Wantzen 2004; Winemiller 2005). The regime of most rivers in the Amazon System consists of high and low water periods, with a clear regional influence of seasonal precipitation as the principal generator of floods (Welcomme & Halls 2002). Spawning migration of large catfishes along major tributaries of the Amazon System is one of the main responses of aquatic fauna to natural flow regime (Low-McConnell 1975; Welcomme 1979; Goulding 1980). During high flows ideal habitat conditions are created to ensure downstream transportation of new fish generation and to avoid predator presence in the main channel (Welcomme & Halls 2002).

Long term flow records are available for some areas of the Brazilian Amazon, but the headwater regions, located among the four Andean countries of Ecuador, Colombia, Bolivia, and Peru, have received little attention, therefore the region’s hydro-climatology is poorly understood (Goulding et al. 2003). Poveda et al. (2006) point out the unique interrelationship between the climate of the Amazon Basin, precipitation on the slopes of the eastern Andes, and streamflow returning towards the lowlands, and the possibility of longer term persistence of drought/flood conditions within the system because of these feedbacks. Giving the close association between freshwater ecology and the regional hydrologic cycle, such longer term trends may also manifest themselves in ecosystems.

The limited available flow data are assessed statistically by means of a probability analysis of flood characteristics. The analysis of PDS is based on the model proposed by Todorovic & Zelenhasic in 1970, based on earlier works of Langbein (1949), and has been accomplished to evaluate flood risks and related problems (Todorovic 1978; Ashkar & Rousselle 1981; Waylen & Woo 1983; Woo & Waylen 1986; Adamowski 2000; Rémillard et al. 2004). PDS evaluates the probability characteristics of flow attributes such as frequency, duration, magnitude, and timing above some selected threshold level (Waylen & Woo 1983). The number of events surpassing this level during the flooding period follows a Poisson distribution as the threshold becomes sufficiently distant from the mean (Waylen & Woo 1983; Bras & Rodríguez-Iturbe 1985; Rasmussen & Rosbjerg 1991; Rémillard et al. 2004) and the inter-arrival time between such events exhibit an exponential distribution (Evans et al. 1993).

In large tropical rivers fish biology is synchronized to the flood cycle. Most large catfishes of the Amazon complete long distance migrations upriver to spawn in the river channel just prior to, or during, flood phase (Goulding 1980; Barthem & Goulding 1997) and the larval drift during the high water season (Araujo-Lima & Oliveira 1998; Welcomme & Halls 2002). Therefore, the occurrence of larvae in the main channel is associated, in a complex fashion, to the timing and frequency of flood events.

## Modeling Approach

Some simple assumptions controlling the expected larval counts are considered within this model: 1) the timing of BSEs and the number of adult catfish ready for spawning are uniformly distributed, and 2) the inter-arrival times between BSEs are exponentially distributed. If accumulated larvae waiting to be released in a next BSE are produced at a uniform rate, the distribution of the number of larvae associated with each BSE should itself be exponentially distributed. These assumptions can be adjusted within this simple model based on additional information that future research will generate in both the hydro-climatological and biological environments.

The rate of spawning follows a temporal distribution, S(t), which is temporally related to optimal conditions for the transport and survival of the spawn. This distribution is related to the historic characteristics of the high flow season and the number of mature fish, M, in that year (j), $M_j$. The number of mature fish which have already spawned or are ready to spawn on day t, in year j, m(t,j), is given by:

$$m(t, j) = S(t) \times M_j$$

Characteristics of floods occurrences are based on the selection of a truncation level of the river, which is determined by the nature of the flood-related problem (Waylen & Woo 1983). A BSE, defined as a particular river stage threshold related to peaks of larval production, is the basis of modeling flood characteristics and larval numbers. The number of larvae released (n) during the $k^{\text{th}}$ BSE of a year is proportional to the time since the last BSE ($k$-1).

$$n_k = m(t_k, j) - m((t_{k-1}), j) \ldots\ldots\ldots\ldots. k > 1$$
$$n_1 = m(t_1, j) \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots. k = 1$$

The number of BSE in a given high flow season is a random variable, k, which follows a Poisson probability distribution (Todorovic 1978), determined by the average number of BSE per year (Λ),

$$P(k) = \frac{e^{-\Lambda} \times \Lambda^k}{k!}$$

and, the inter-arrival times (s) between these BSEs are exponentially distributed (Evans et al. 1993).

$$F(s \le x) = 1 - e^{(-x/\gamma)}$$

where:

$\gamma$ = Average length of inter-arrival times

$x$ = Number of days between BSEs

The hydroloclimatological characteristics of the basin therefore control the number and timing of BSEs, which in part control expected larval production and release. If these propositions can be verified and parameterized then it is possible to model the likelihood of larval releases at Puerto Maldonado at various times during the high flow season.

## Study Area

The Madre de Dios Basin drains an area of approximately 90,000 $km^2$ of the eastern flank of *Cordillera de los Andes* in southeastern Peru, from over 4,000 m in elevation to the lowland Amazon at 200 m (Barthem et al. 2003). It is the most western headwater basin of the Madeira River, the largest tributary of the Amazon Basin (Goulding et al. 2003) (Figure 2-1). Puerto Maldonado is the largest city within the Madre de Dios Basin and it is the principal urban center for commercial activity and economic development of southeastern Peruvian Amazon (Cañas 2000, Goulding et al. 2003).

Field work for this study was carried out near Puerto Maldonado, located in the Amazon lowlands at 256 meters elevation on the right bank of the Madre de Dios River. Upstream of Puerto Maldonado there are nine principal tributaries of the Madre Dios Basin. Six of these tributaries rise in the south with most of their areas located in the Andes, and three flow from northern, mostly lowland, areas (Figure 2-2). Discharges from these nine tributaries control the flow behavior of the principal river. Daily water level (stage) measured at Los Amigos Research

Station between September 2001 and January 2003 is the known basis in this basin for the expected periods of high and low water, and flood events (Barthem et al. 2003).

Monthly precipitation records at Pilcopata (32 years), Quincemil (25 years) and Puerto Maldonado (50 years) obtained from the *Servicio Nacional de Meteorología e Hidrografía* (SENAMHI), indicate that the rainy season generally extends between October and April, and lower precipitation prevails during the remainder of the year (Figure 2-3). They also indicate high geographic variability arising from elevation and location with respect to the Andes, which act as an orographic barrier to the southeast trades importing atmospheric water and exporting surface waters (Poveda et al. 2006).

Hydrologic characteristics of the basin vary as a function of elevation and season. In the Andean region, channels gradients are steeper, with smaller, shallower channels, low suspended sediments, low temperatures and high levels of dissolved oxygen. The flow regime is highly sensitive to local precipitation, and no snow melt effect has been observed (Barthem et al. 2003). In lowland areas (400m and below) rivers flow over a flatter topography, with large and numerous meanders, large channel widths, and surrounded by dense forests (Goulding et al. 2003). During field observations in 2006 at Puerto Maldonado, the channel width averaged 425 m, and the stage range was 9.21 m.

## Materials and Methods

Two meteorological stations (Pilcopata and Quincemil) are located on the eastern foothills of the *Cordillera de los Andes*, within the two most important Andean headwater tributaries, the Alto Madre de Dios and Inambari Rivers, respectively (Figure 2-2). The rainfall station in Puerto Maldonado is located at 256 m, Pilcopata at approximately 900 m and Quincemil at approximately 600 m. After year 2000 precipitation in the Pilcopata area was monitored from Chontachaca rainfall station, located 50 km from the former rainfall station and at similar elevation. A total of 30 years of historical daily rainfall records were available for analysis (Table 2-1).

A system of board gauges was installed at the right bank of Madre de Dios River to register water level measurements. Recordings were taken twice daily, at 8:00 am and 6:00 pm, from which a daily average river level was obtained between December 4$^{th}$, 2004 and December 31$^{st}$, 2006. Weekly larva sampling was completed throughout 2006 using a 365 micron ichthyoplankton net with a circular mouth of 47 cm and 1.50 m of length. A General Oceanics 2030R mechanical flowmeter attached at the open section of the net permitted calculation of the volume of water filtered during the sampling. Samples were taken to the laboratory, where large catfish larvae were sorted out by using a Zeiss Stemi DV4 Stereo Microscope. Biological materials were stored at *Museo de Historia Natural* – UNMSM in Lima, Peru. Larval counts and the volume of water filtered were used to calculate larva density values (individuals per 50m$^3$) in order to relate them to variations in stage.

Larva densities and observed stage records were used to identify a threshold water level which triggered larval production in the channel. In order to consider the independence of consecutive BSEs, an arbitrary period of 3 days was established as the minimum time to separate two flood events. This criterion was based on the high frequency of short-period peaks observed in the hydrograph, on the vastness of the basin that includes several tributaries discharging independently into the main stream, and on the requirement to obtain a reasonable number of BSEs for statistical analyses.

Times of critical stage were correlated with varying periods of cumulative antecedent rainfall from each meteorological station (1 day, 2 days, etc) to determine the volumes of cumulative rainfall in the headwaters most related to the generation of BSEs at Puerto

Maldonado. Observed PDS and antecedent precipitation values from Pilcopata and Quincemil meteorological stations were related to establish a minimum rainfall value necessary in the Andean headwaters to generate an event. This criterion was then applied to the historical daily rainfall records for the two meteorological stations, to identify similar rainfall conditions and postulate the annual number and timing of BSE prior to the limited period of observed floods. Flood frequency characteristics were calculated on the basis of a water year, considered in the Madre de Dios Basin from September 1st to August 30th.

## Results

### Larvae and Stage in Puerto Maldonado

Average larval densities varied significantly between the high and low water periods (Figure 2-4 and Table 2-2). After week 43 (October 21st, 2006) larval densities increased dramatically from 24 per 50 $m^3$ to 156, the maximum larval production observed during 2006. Meanwhile, between weeks 41 and 43 (October 7th to October 21st, 2006), the 400 m channel of Madre de Dios River rose almost 4 m to 5.84 m. After this point, and until the end of 2006, larva densities remained high (values greater than 44 larvae per 50 $m^3$), but variable.

Although the relationship between stage and larval production was complex, the 5m mark seemed to approximate a "break point" between high a low values of larval production (Figure 2-5). At lower stages, most values of larva densities were at background levels, with an average of 10 larvae/50$m^3$; and over this threshold, larval production was extremely variable, with both high and low values and an average of 60 larvae/50 $m^3$.

Twenty BSEs were identified within the 2006 stage records, 18 of them occurring during the wet season. The cumulative frequency of dates of events implied a uniform distribution throughout the high water period, commencing during the second half of October and extending through the second half of March (Figure 2-6). Although the inter-arrival times of observed

BSEs followed an exponential distribution with an average of 4 days (Figure 2-7), the assumption of Poisson distributed annual numbers of BSEs could not be tested due to the very limited period of flood data. The average number of BSEs in the two years of observations was 8 for the high water period, and 1 for the dry season. A preliminary application of the stochastic model based on information obtained from the short period of observed BSEs suggested an exponential cumulative distribution of larvae during the rainy season (Figure 2-8). High values of larvae were impossible (the “infeasible zone” in Figure 2-8), during the early rainy season, as even if a BSE were to occur, an insufficient period of time has passed since the beginning of spawning to accumulate such large numbers of larvae.

**Analysis of Available Rainfall Records**

Considering the large areal extent of the basin and the lack of flow information, 30 years of daily rainfall records from two Andean meteorological stations represented a major, and perhaps unique, source of hydroclimatological information from which to extend knowledge of historic BSEs in the region. To this end, a detailed analysis of the association between observed rainfall data and the observed floods -2005 and 2006- was performed to determine whether sufficient evidence exists to forecast floods on the basis of precipitation.

BSEs were best correlated with rainfall cumulated over the prior 8 days at Pilcopata and 5 days at Quincemil (Figure 2-9; Figure 2-10). Rainfall totals cumulated over the appropriate period, were then related to starting dates of observed BSEs. A 75 mm-rainfall total appeared to be the minimum required from each of the selected stations to attain critical stage at Puerto Maldonado (Figure 2-11; Figure 2-12). An alternative approach that utilizes both stations records and entertains the possibility that rain falling in both headwater tributaries might, together, generate a BSE, indicated that BSEs in Puerto Maldonado were sustained when the sum of the two rainfalls exceed an enveloping line of about 200 mm of rainfall (Figure 2-13).

In order to test the efficiency of these graphically derived rainfall thresholds, several possible values were numerically compared to the observed (2005-2006) series of BSEs. A chi-square statistical analysis of contingency tables between observed and forecast BSEs, suggested optimal values of 75 mm at Quincemil, 125 mm at Pilcopata, and a 225 mm combined total (Table 2-3; Table 2-4). Forecasted BSEs based on the Quincemil criteria yield 70% agreement with the observed BSEs, 67% of agreement using Pilcopata, and 73% agreement for the combined totals (Table 2-5; Table 2-6; Table 2-7). These values constituted the basis to reconstruct BSE occurrences for the historical rainfall records. The combined total criterion was used when both records were available. Two possible errors in forecasting represented potential limitations of the model: 1) when a BSE is forecasted based on upstream rainfall and none is observed and 2) no BSE is forecast and one occurs.

A total of 313 potential BSEs were identified from the 30 years of available historical rainfall records, 225 during the high water period and 88 during the low water period (Table 2-8). The average number of estimated floods was 8.03 during the wet season and 2.93 in the dry – remarkably close top to the observed figures over the short period of stage records and not statistically different ($p < 0.05$) (Table 2-9). The annual number of potential events was fitted by a Poisson distribution (Figure 2-14), and their dates appeared to be reasonably uniform, but showed a slightly reduction in frequencies after day 100 (December 9$^{th}$) and again in the dry season (Figure 2-15). Inter-arrival times between potential BSEs were fitted by an exponential distribution, with an estimated mean of 9.54 days (Figure 2-16), which again was close to the observed value of 7 days, once the arbitrary minimum separation figure of 3 days is added to the observed mean inter-arrival time of about 4 days.

## Discussion

Larval presence in Madre de Dios Basin is related to the occurrence of BSEs during the high flow season, while very low values were encountered during most of the dry season, suggesting that hydrologic factors are triggering reproduction activity of large catfish populations and the release of larvae. The number of larvae associated with such events varies markedly, but appears to be represented by the simple “threshold and stochastic” model presented. While the model complements initial propositions about the arrival of long-distance migratory catfishes for spawning (Cañas 2000; Barthem et al. 2003; Goulding et al. 2003), several key issues related to the model require further discussion.

### Threshold Stage

The threshold of 5m is arbitrary, based purely on observed conditions, and could potentially be redefined to a slightly lower value (Figure 2-4; Figure 2-5). However, this stage should not be viewed as the direct “generator” of observed larval densities, but merely as an indicator that both hydrologic and biologic variables are related to a common, unobserved cause - the hydro-climatological conditions upstream in the Andean region. Therefore no stage measured at Puerto Maldonado will unambiguously define events releasing larvae completely satisfactorily

Larvae in the channel are clearly identifiable at low background levels even under the 5-meter level of the stage (Figure 2-5), indicating a reduced reproductive activity of fish fauna in the basin during the dry season and between BSEs. Larval catches during BSEs represent reproductive activity of catfishes during these events and the length of time since the previous BSE.

**Independence Criterion**

The threshold was also selected to identify a reasonably large PDS for adequate parameter estimation and modeling, while ensuring, as much as possible, independent BSEs, and excluding small hydrologic events of no biological significance during the dry season. Taesombut & Yevjevich (1978) propose a minimum number of days between two independent hydrologic events of 5 + ln(basin area, $km^2$). Application of this formula to the Madre de Dios (16 days) and its major tributaries (14 days) yield only one event per year.

The effect of precipitation on discharge in Andean tributaries is almost immediate, and it is common for rivers to experience high stage during and immediately following rainfall occurrences, and to cease as soon as rainfall ceases (Barthem et al. 2003; Goulding et al. 2003). Stage at Puerto Maldonado (Figure 2-4) exhibits high variability with frequent peaks of short duration surpassing the selected threshold - clear indication of the influence of Andean tributaries - supporting the short period used to separate consecutive floods. Numerically, independent events could be derived by increasing the truncation level, but figure 2-4 indicates that, although hydrologically and statistically reasonable, this has no biological basis. Non-independent, or clusters of events can be handled statistically (Rosbjerg 1985; Favre et al. 2002), however, in this model it is ultimately inter-arrival times which are of greatest significance to larval releases, and empirically at least, these still appear to follow an exponential distribution (Figure 2-7). Clustering of events would tend to produce a greater frequency of both shorter (within clusters) and longer (between clusters) inter-arrival times (such as figure 2-15), which still could be modeled by an exponential like a gamma distribution (Evans et al. 1993) or generalized Pareto (Waylen & Laporte 1999).

## Sampling Intervals

The selection of a critical stage is further clouded by the logistic restriction that a full sampling of larvae could only be carried out once a week. The time and resources required to properly sample at appropriate width and depth intervals, is further compounded by the time taken to identify and count larvae. Weekly sampling clearly misses the peak stages (and larval production) of several potentially large BSE events. In an effort to reduce both work load and the interval between samples in the future, an effort is being made to identify sampling points (in terms of horizontal position and depth) which are most representative of cross sectional mean larval counts at various stages. In this way, future daily measurements may be made at this point in order that biological and hydrologic processes to be sampled at the same frequency. This may lead to some loss of accuracy in larval counts, but the relationship can be continuously updated.

## Nature of Relationship when Stage exceeds Threshold

A notable feature of the relationship between larval production and stage (Figure 2-5) is that maximum observed densities of larvae appear to diminish with larger values of stages in excess of the threshold. This is explicable in terms of the joint probabilities of both peak stage levels and the distribution of larval densities, as opposed to any physical or biological process. In hydrology, the probability of the size of flood events above a threshold is commonly represented by an exponential-type distribution (Waylen & Laporte 1999). The probability distribution of larval catches has also been shown to follow an exponential distribution. Both flood size above threshold, and larval densities, are independent under the assumption that the latter is a function of the length of the time since the last BSE (Figure 2-17), rather than the size of the flood. Considering both variables, a joint probability distribution results which exhibits a pattern similar to that observed when stages exceed 5 m (Figure 2-5; Figure 2-17).

**Spawning Rates**

In terms of biological processes, an assumption of uniformly distributed of rate of spawning is generally accepted (Pine, personal communication). No estimates thus far exist of this important variable in the basin, however, if the simple PDS model holds true, then counts of larvae exported [{larval density (per 50 $m^3$) x estimated discharge ($m^3s^{-1}$)}/50] are themselves exponentially distributed with a mean of 2902 ($s^{-1}$) (Figure 2-18). This average figure results from an average inter-arrival time of approximately 7 days (4 average days + 3 days of arbitrary minimum separation) (Figure 2-7), yielding an approximate basin-wide spawning rate of 414 larvae $s^{-1}dy^{-1}$ (2902 $s^{-1}$/7dy), which is about half of the observed "background" less of larval counts when no BSE are occurring.

Observed data hint at a decline in this rate over the rainy season (Figure 2-4), but current data provide insufficient evidence to reject the most basic hypothesis of uniformity. Local fisherman have noted that sexually mature catfish migrate upstream during floods, suggesting that BSEs may have a far more complex "2-way-gate" function, not only releasing larvae from upstream, but also enabling mature adults to migrate upstream to the spawning areas. If the latter is the case, then the density of larvae released by a BSE will also be a function of the number of adults that successfully migrated during the previous BSE. The first BSE of a year would initiate upstream migration, but release no larvae. For instance, in Figure 2-4 the rising stage experienced in week 39 (September 23rd) is not associated with any larva released beyond background levels while the next high stage of week 43 (October 21st) produced the highest larval density of the year. No previous research has related adult catfishes ready for spawning and larvae being delivered during a same wet period. In the future, this information should be acquired and confirm/deny the assumption of rate of larval production within the model.

## Small Sample Sizes

The 20 observed BSEs represent a small sample size upon which to support the model. However, the larger sample provided by the estimation of potential BSEs from historical precipitation gives strong validatory information. This approach is supported geographically, as proximity to the Andes causes the rainfall pattern to be the principal variable controlling the annual hydrologic regime in Madre de Dios Basin (Barthem et al. 2003; Goulding et. al 2003); and from the perspective of data availability, as daily precipitation are more abundant than stage in the basin.

The 8-days and 5-days of cumulative rainfall periods obtained for Pilcopata and Quincemil, respectively, can be interpreted in terms of the distances involved and the topography (Figure 2-2). From Pilcopata (900 m), the Alto Madre de Dios tributary drains over gentler terrain and describes a wide, braided and shallow channel that discharges into the Madre de Dios, before flowing approximately 600 km as a wider and meandering channel to Puerto Maldonado. From Quincemil (600 m), the Araza River runs over steep terrain with rapid-flowing waters, discharging into the Inambari River, a braided river channel that enters to the Madre de Dios approximately 100 km above Puerto Maldonado. Unfortunately, there are no water level data from these two sites, or any other, headwater tributaries, which should be ideal situation to obtain PDS closer to the spawning grounds.

## Potential Sources of Errors in Forecast

Cumulative rainfalls obtained from the two Andean tributaries, potentially responsible for each BSE, performed satisfactorily when used to forecast BSEs for the period 2005-2006. However approximately 30% of the forecasts (both BSE and no BSE) did not agree with the observed data. Potential no-agreements arise when rainfall indicates a BSE, but none occur, and when BSEs occur but none are forecast. The former indicates that, either rainfall events were highly localized, or that, given the non-linear nature of the hydrologic system, basin conditions, particularly dry antecedent conditions, may not have converted this input into the anticipated flow. The latter reflects either the inadequacy of the spatial coverage of the meteorological network (2 stations in 90,000 $km^2$, the biologically significant portions of which are mountainous) or, once again, the over simplification of the proposed rainfall/runoff representation (Figure 2-19).

Cumulative frequencies of the dates of forecasted floods from the historical rainfall data (Figure 2-15) displayed a reasonably uniform distribution throughout most of the high water period, with a slightly greater frequency of floods between October and the middle of December. This hydrologic condition indicates that as soon as the rainy season starts, BSEs become frequent, which, in turn, could signal additional adult catfishes to swim upstream to spawn.

It can be argued that BSEs estimated in this way are a good estimate of hydrologic conditions in the basin. However the frequency of these potential events did not exactly fit in a Poisson distribution (Figure 2-14). Despite this, their inter-arrival times during the rainy season, the controlling factor in the number of larvae exported, are exponentially distributed (Figure 2-16).

**Inter-Annual Variability**

The inter-arrival times of BSEs, particularly during the wet season, has to this point been considered to be a simple random variable. However, BSEs can be closely linked to regional climatology, much of which in South America has been shown (Grimm et al. 2000) to be controlled at lower frequencies by the El Niño-Southern Oscillation (ENSO) phenomenon (see for example Poveda et al. (2006) with regard to the Colombian Amazon, and Garreaud et al. (2003) for the Bolivian/Peruvian Altiplano). Application of the hypergeometric probability distribution (Grimm et al. 2000) provides a simple means to identify any potential impact of

ENSO in a time series. Each forecast annual BSE is assigned to one of three mutually exclusive classifications of ENSO phase, provided, *a priori*, by the Center for Ocean-Atmosphere Prediction Studies (COAPS) at Florida State University (http://coaps.fsu.edu/jma.shtml). As various lead/lag associations exist between ENSO phase and regional climates throughout South America, the classifications are extended to consider the phase in the year prior and post to the forecast BSE count, as well as the synchronous phase.

The time series (Table 2-8) is sorted ($N = 28$) and divided into two categories, above median and below median years (n = 14 in each). A count is kept of the total number ($k$) of cold, neutral and warm phase years in the series (roughly; $k_{\text{cold}} = 8$, $k_{\text{neutral}} = 14$, $k_{\text{warm}} = 6$, although this varies slightly with the lead/lag employed), and of the number of these years, $x$, falling above/below median (Table 2-10; Table 2-11). Assuming a null hypothesis of a random sampling scheme, the probability of $x$ should follow a hypergeometric distribution as follows:

$$p(x|k,N,n) = \frac{\binom{k}{x}\binom{N-k}{n-x}}{\binom{N}{n}}$$

Tables 2-10 and 2-11 suggest that there is no association between rainfall conditions at the two Andean stations likely to generate BSEs, and the phase of ENSO. Although an association of regional drought with warm phases of ENSO (El Niño events) and excess rain during cold phase (La Niña) was found in the Altiplano (Tapley & Waylen 1990; Garreaud et al. 2003), the lead relationship precludes the use of ENSO indicators as forecasters of stream flow characteristics in this region.

## Conclusions

This simple stochastic model is presented to explain characteristics of the complex, and previously unmonitored, crucial relationship between larval production sent downstream to the lower Amazon Basin, and the stage of the Madre de Dios River. Physically, it is well based in the hydroclimatology of the region as well as both the limited biological data and anecdotal observations of local fishermen. The concept and use of PDS is well established in the field of hydrology and has a sound theoretical basis in statistics. The numbers of potential BSEs are equally likely to occur through out the wet season (time–homogeneous Poisson process); and their inter arrival times are exponentially distributed. The simple assumption of uniformly distributed timings of BSEs and spawning during the wet season appears reasonable on the basis of stage and rainfall derived records, however, a variety of non-homogeneous and seasonally varying rates of both variables could be incorporated if necessary (Todorovic 1978; Waylen & Laporte 1999; Remillard et al. 2004). The requirements of the model are fairly basic and appropriate for this part of the world. They can, however, be combined in a variety of ways to produce results which appear to emulate a complex bio-hydrologic system

This collation of hydrologic and biologic data, albeit for only a limited period of time is unique in the headwater regions of the southern Peruvian Amazon. Recording the flow regime of this huge basin was achieved by daily water level observations in Puerto Maldonado, which is well situated for flood recording purposes with respect of the major tributaries and provides a good “flooding-foot print” of the complete basin, as supported through the calibration of the rainfall-BSE to extend the period of records. The current data not only provide the basis for the parameterization of this proto-type model, but may also furnish information concerning a more efficient biological sampling scheme at a frequency more appropriate to the hydrologic processes.

This research also suggests the possibility of feedbacks between biological and climatological systems. The lack of flooding records is a common denominator in remote areas of the Amazon headwaters. Since larva modeling analysis needed long-term flooding records, this limitation was surmounted by using rainfall records, the most abundant hydrological surrogate in these regions, and they performed reasonably for forecasting the derived annual counts of BSEs. This type of association between weather conditions and aquatic biological responses, apparently not directly associated, should be included into experiment design for future research. External factors such as climate change should be considered in the potential variability of these environmental associations.

Larvae of long-distance migratory catfish observed in the Madre de Dios Basin drifting to lowlands, complemented with the upstream adult migrations previously observed in the basin, confirmed the connection of the whole Amazon System. Survival of these catfish species depends on two key displacements during different phases of their life history, which are strongly related to flood timing and the connectivity of the complete system. Any changes to flow regime or disruption on the connection of this river will not only put populations of large Amazon catfish at risk, but influence the survival of other fish species dependent upon the lateral connection between river channel and adjacent floodplains. Consideration of the migration of catfish and other species need to be incorporated into any environmental assessment of projects in the Amazon System, especially those related with the use of water resources, such as dam and reservoirs, which potentially alter the connectivity of this large basin. Increased deforestation rates in Amazon headwaters, in association with the expansion of the agriculture frontier and road construction, will also have potential effects in catfish migration by altering the nature of flow regime in these upstream regions. Adults and larvae rely on the predictability of flooding patterns, for spawning and for drifting, respectively.

Finally, the simple framework of this stochastic model, well-supported by hydroclimatological and biological concepts, is able to be improved with more detailed information about fish biology and climatology of the region, and able to be applied and adapted to similar scenarios along the eastern flank of *Cordillera de los Andes* in other countries such as Colombia, Ecuador, Peru, and Bolivia.

Table 2-1. Periods of daily rainfall record available from three meteorological stations in the Madre de Dios Basin.

| Meteorological Station | Period | Records not available |
|---|---|---|
| Pilcopata / Chontachaca | Jan 1st, 1966 – Dec 31st, 1967 | Dec 1974 |
| | Jan 1st, 1970 – Dec 31st, 1986 | Dec 1978 |
| | Jan 1st, 2001 – Dec 31st, 2006 | |
| Quincemil | Jan 1st, 1966 – Dec 31st, 1970 | Apr 1973 |
| | Jan 1st, 1973 – Dec 31st, 1976 | May 1988 |
| | Jan 1st, 1998 – Dec 31st, 2006 | |
| Puerto Maldonado | Jan 1st, 2000 – Dec 31st, 2006 | Aug 2006 |

Table 2-2. Test of Fixed Effects (SAS GLIMMIX Procedure Type III, $p < 0.0001$) showing statistical differences of larval densities between weeks and seasons.

| Effect | DF | DF | F value | Pr > F |
|---|---|---|---|---|
| Season | 1 | 10 | 128.19 | < .0001 |
| Week | 1 | 251 | 89.21 | < .0001 |
| Week * Season | 1 | 251 | 48.34 | < .0001 |

Table 2-3. Chi-square test values of contingency tables of possible estimated and observed flood events in Puerto Maldonado, considering different cumulative rainfall in each station. Highest $X^2$ is shown in bold.

| | 75 mm | 100 mm | 125 mm | 150 mm | 175 mm | 200 mm |
|---|---|---|---|---|---|---|
| Quincemil | **154.98** | 131.53 | 93.82 | 64.56 | 52.36 | 47.91 |
| Pilcopata | 69.33 | 77.11 | **84.26** | 82.88 | 54.8 | 41.07 |

Table 2-4. Chi-square test values of contingency tables of possible estimated and observed flood events in Puerto Maldonado, considering total cumulative rainfall from both stations. Highest $X^2$ is shown in bold.

| | 200 mm | 225 mm | 250 mm | 275 mm | 300 mm |
|---|---|---|---|---|---|
| Pilcopata + Quincemil | 155.33 | **167.81** | 138.28 | 141.30 | 101.39 |

Table 2-5. Percentage of agreement between forecasted and observed BSE when there is 75 mm of rain falling in Quincemil area.

| Quincemil (75 mm) | Observed No BSE | Observed BSE |
|---|---|---|
| Forecast No BSE | 304 (40%) | 41 (6%) |
| Forecast BSE | 181 (24%) | 228 (30%) |

Table 2-6. Percentage of agreement between forecasted and observed BSE when there is 125 mm of rain falling in Pilcopata area.

| Pilcopata (125 mm) | Observed No BSE | Observed BSE |
|---|---|---|
| Forecast No BSE | 319 (42%) | 82 (11%) |
| Forecast BSE | 165 (22%) | 185 (25%) |

Table 2-7. Percentage of agreement between forecasted and observed BSE when there is 225 mm of rain falling in both assessed areas.

| Quincemil + Pilcopata (225 mm) | Observed No BSE | Observed BSE |
|---|---|---|
| Forecast No BSE | 331 (44%) | 50 (7%) |
| Forecast BSE | 153 (20%) | 217 (29%) |

Table 2-8. Number of potential Biologically Significant Events forecasted from historical rainfall records in the Madre de Dios Basin. Records for wet periods for years 1986 and 2006 (**) were incomplete, and not included for comparisons.

| Year | High Water | Low Water | Year | High Water | Low Water |
|---|---|---|---|---|---|
| 1966 | 8 | 4 | 1981 | 11 | 2 |
| 1967 | 10 | 2 | 1982 | 9 | 1 |
| 1968 | 7 | 6 | 1983 | 10 | 2 |
| 1969 | 10 | 4 | 1984 | 6 | 2 |
| 1970 | 9 | 4 | 1985 | 4 | 1 |
| 1971 | 8 | 0 | 1986 | ** | 1 |
| 1972 | 4 | 0 | 1998 | 7 | 4 |
| 1973 | 7 | 3 | 1999 | 8 | 3 |
| 1974 | 9 | 2 | 2000 | 9 | 5 |
| 1975 | 8 | 3 | 2001 | 9 | 5 |
| 1976 | 9 | 5 | 2002 | 6 | 5 |
| 1977 | 6 | 3 | 2003 | 10 | 6 |
| 1978 | 6 | 2 | 2004 | 11 | 4 |
| 1979 | 8 | 1 | 2005 | 9 | 3 |
| 1980 | 7 | 2 | 2006 | ** | 3 |

Table 2-9. Chi-Square analysis ($p < 0.05$; DF=1) confirming no statistical differences between estimated floods in historical records and observed floods in the 2-years period in Puerto Maldonado.

| | High Water | Low Water |
|---|---|---|
| Estimated Floods | 8.03 | 2.93 |
| Observed Floods | 8.00 | 1.00 |

Table 2-10. Number of forecasted wet season BSEs occurring above/below median, classified according to the phase of ENSO (based on COAPS at FSU), and considering the phase in the prior, contemporary and next years.

| | ENSO Phase | Prior year | Contemporary year | Next year |
|---|---|---|---|---|
| Above median | Cold | 3 | 4 | 4 |
| | Neutral | 9 | 7 | 7 |
| | Warm | 2 | 3 | 3 |
| Below median | Cold | 4 | 3 | 2 |
| | Neutral | 5 | 8 | 7 |
| | Warm | 5 | 3 | 3 |

Table 2-11. Number of forecasted dry season BSEs occurring above/below median, classified according to the phase of ENSO (based on COAPS at FSU), and considering the phase in the prior, contemporary and next years.

| | ENSO Phase | Prior year | Contemporary year | Next year |
|---|---|---|---|---|
| Above median | Cold | 4 | 4 | 3 |
| | Neutral | 7 | 7 | 8 |
| | Warm | 3 | 3 | 3 |
| Below median | Cold | 4 | 4 | 4 |
| | Neutral | 6 | 8 | 6 |
| | Warm | 4 | 2 | 4 |

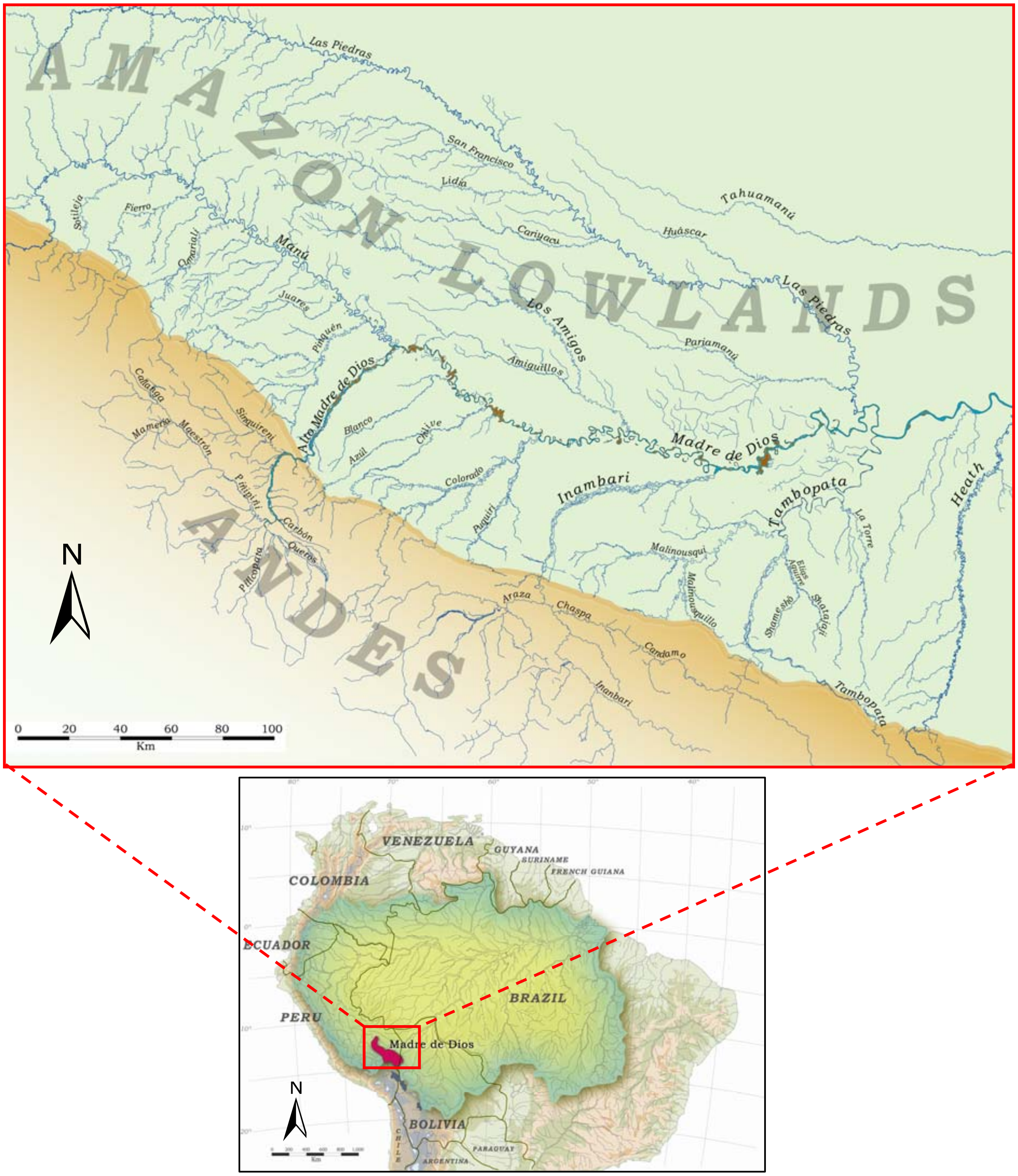


Figure 2-1. The Madre de Dios Basin. Location and its major tributaries draining from the Andes and Amazon lowlands.

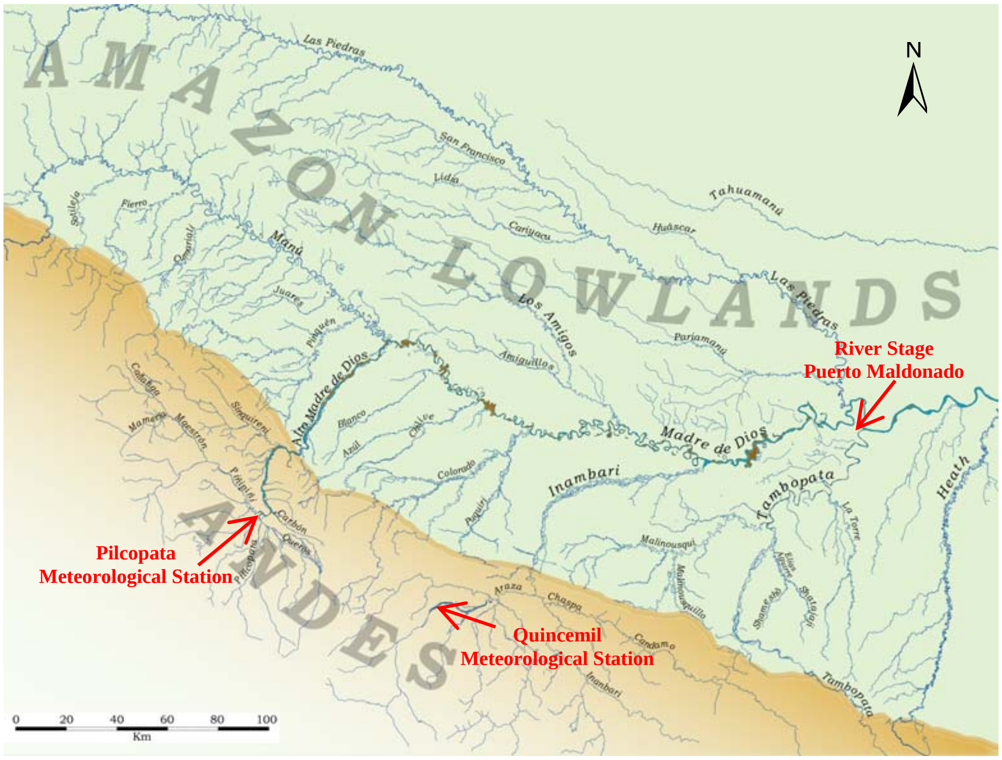


Figure 2-2. Location of meteorological stations in the Madre de Dios Basin. Pilcopata (900 m) and Quincemil (600 m) are located in the Andes. Puerto Maldonado (256 m), where river stage was placed, is located in the Amazon lowlands.

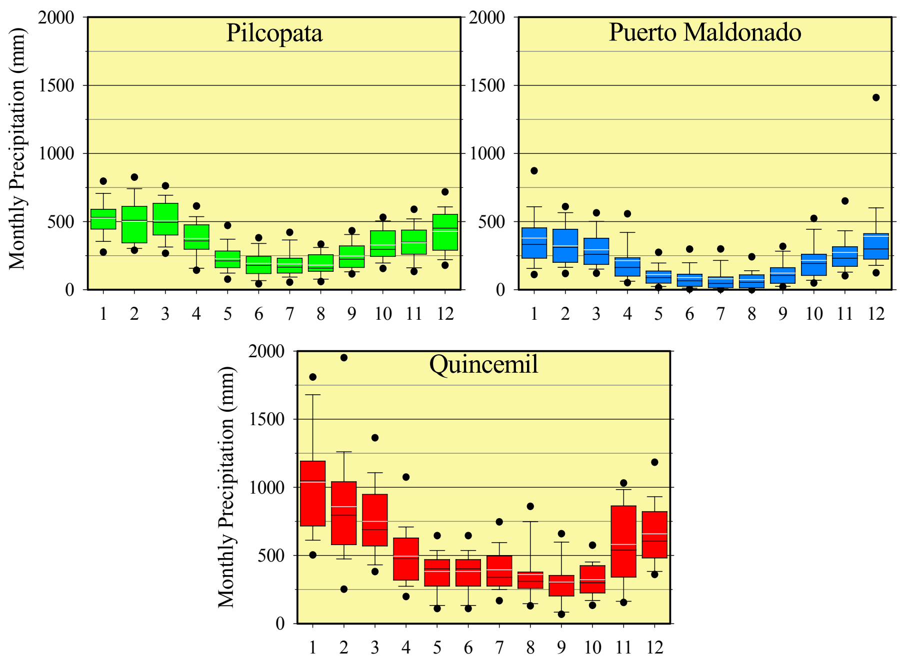


Figure 2-3. Monthly Precipitation (mm) in Pilcopata (32 years), Quincemil (25 years), and Puerto Maldonado (50 years) rainfall stations in the Madre de Dios Basin.

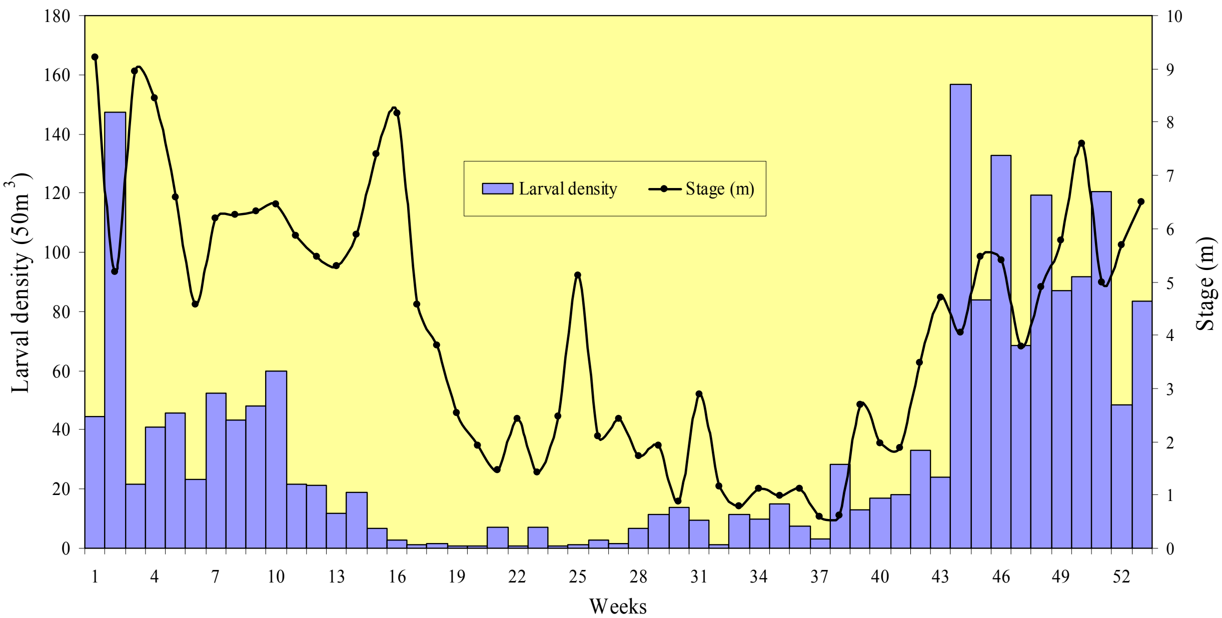


Figure 2-4. Larval density and stage records in Puerto Maldonado showing the seasonal pattern of larval production during the sampled period.

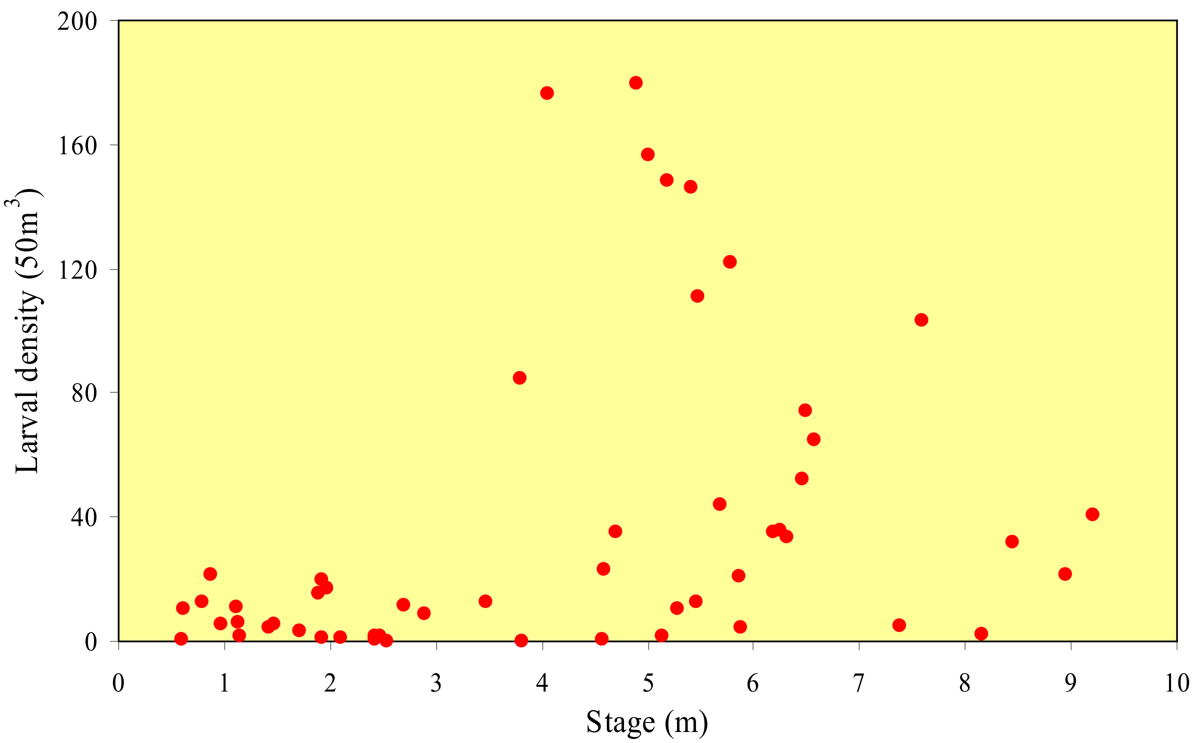


Figure 2-5. Relationship between larval density and stage records in Puerto Maldonado, 2006.

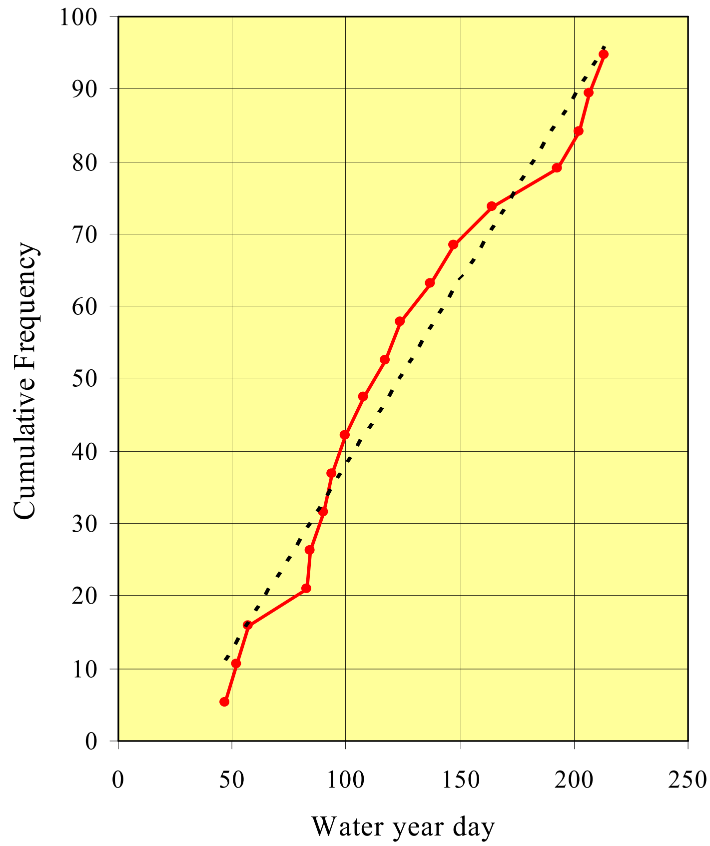


Figure 2-6. Cumulative Frequency of Biologically Significant Events during high water period in Madre de Dios River for 2005 and 2006.

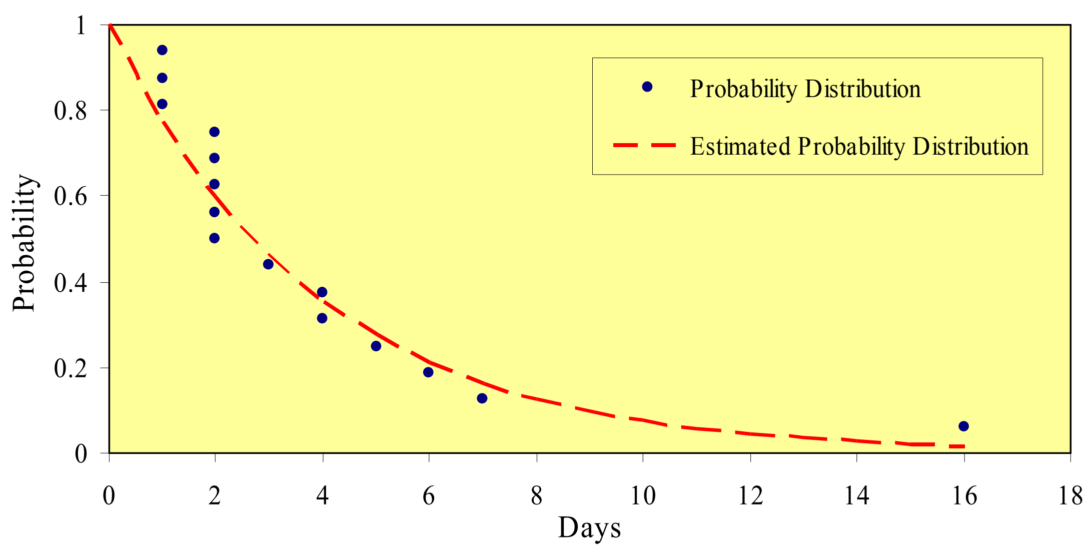


Figure 2-7. Probability Distribution of inter-arrival times of Biologically Significant Events in Puerto Maldonado during 2005 and 2006 (Average = 4 days).

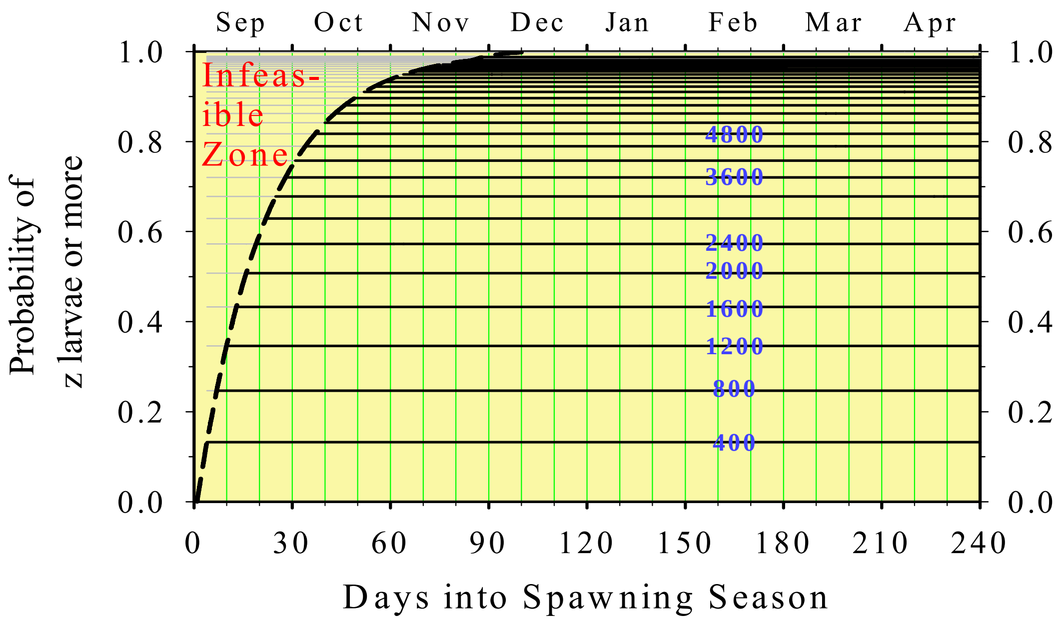


Figure 2-8. Anticipated cumulative distribution (y) of larvae (z) associated with BSE occurring at any time (x) during the spawning/rainy season. The "Infeasible" zone indicates values which will not be encountered due to the proximity of the date to the start of the spawning/rainy season.

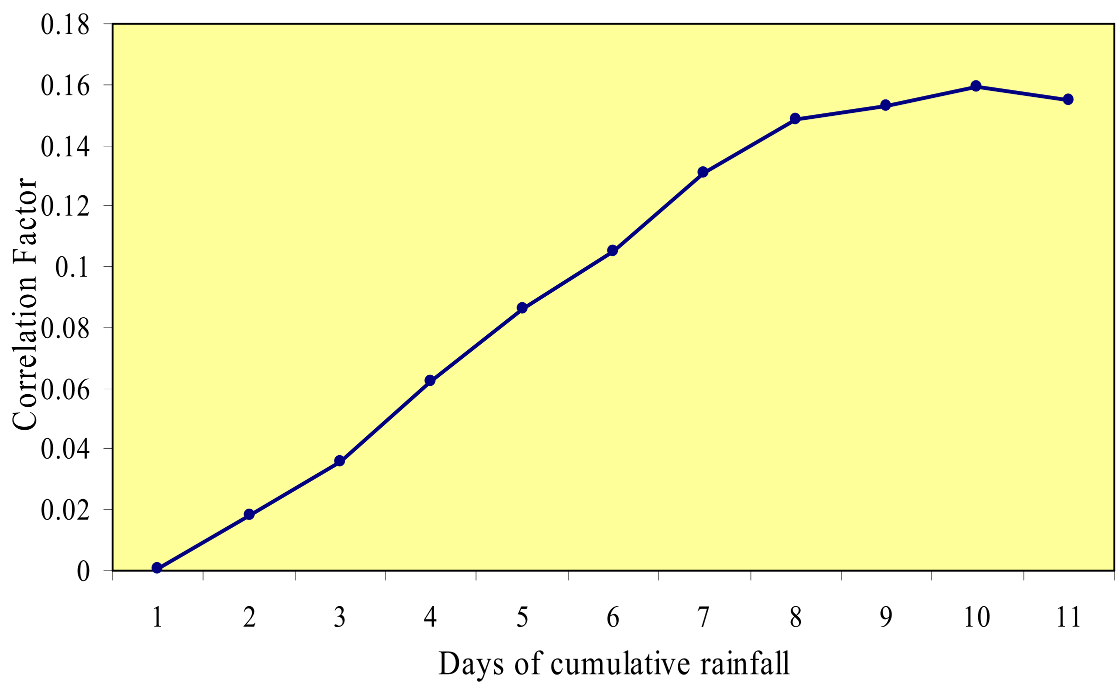


Figure 2-9. Correlation factors obtained for cumulative rainfall periods in Pilcopata and Biologically Significant Events in Puerto Maldonado.

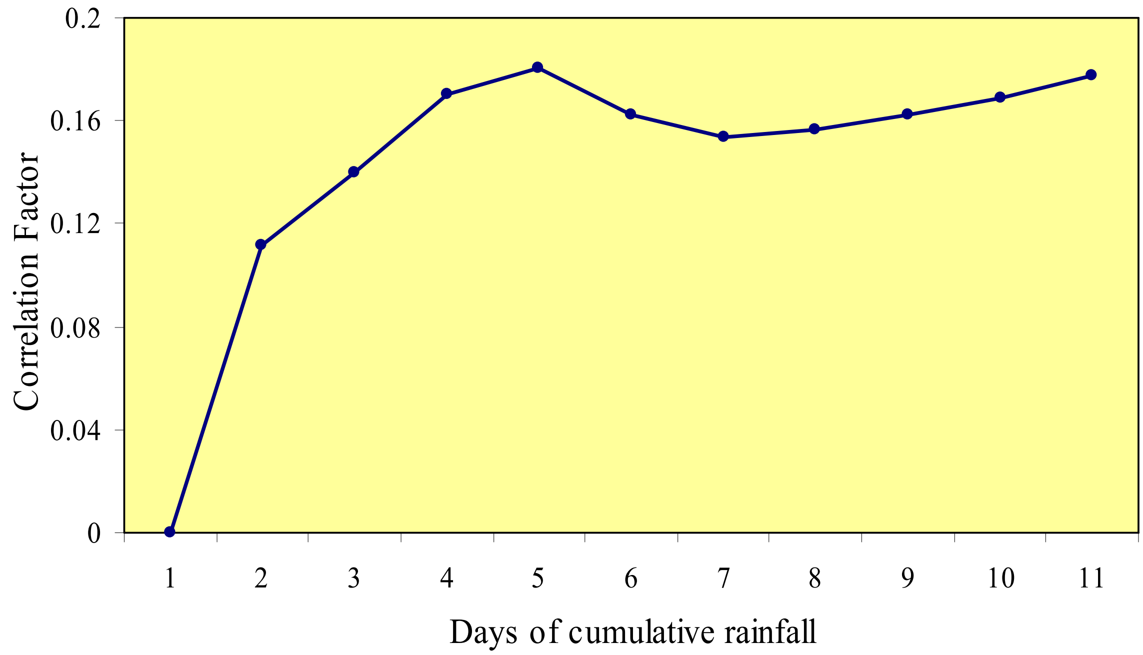


Figure 2-10. Correlation factors obtained for cumulative rainfall periods in Quincemil and Biologically Significant Events in Puerto Maldonado.

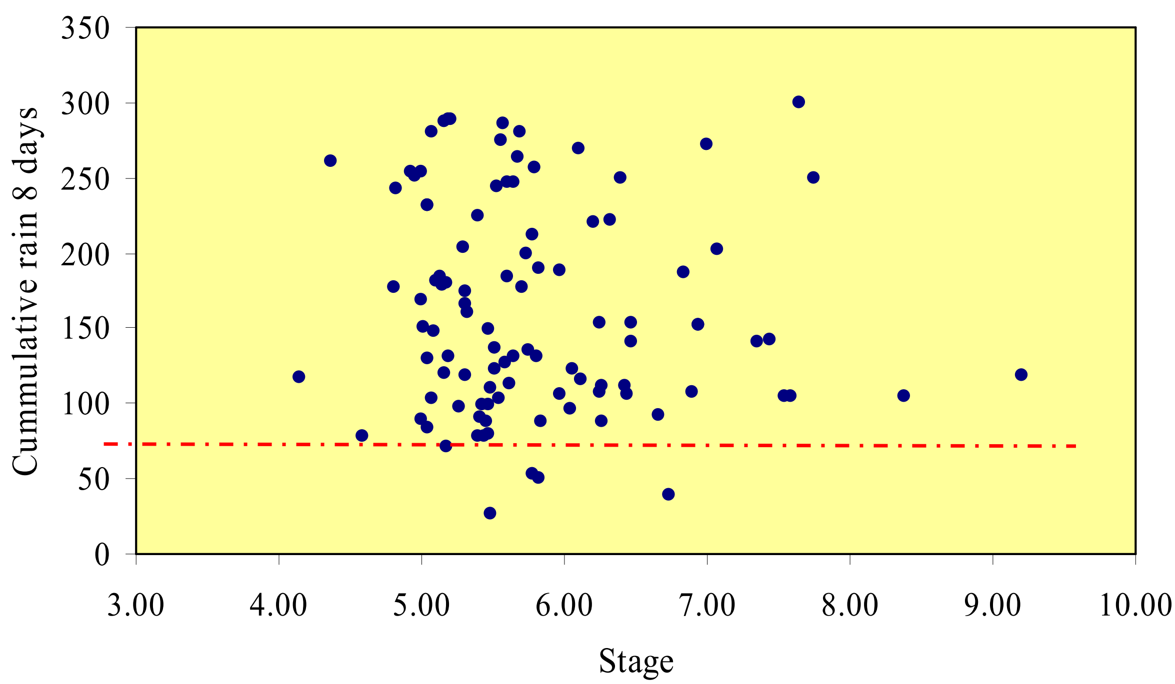


Figure 2-11. Comparison between 8-days period of cumulative rainfall in Pilcopata and Biologically Significant Events in Puerto Maldonado.

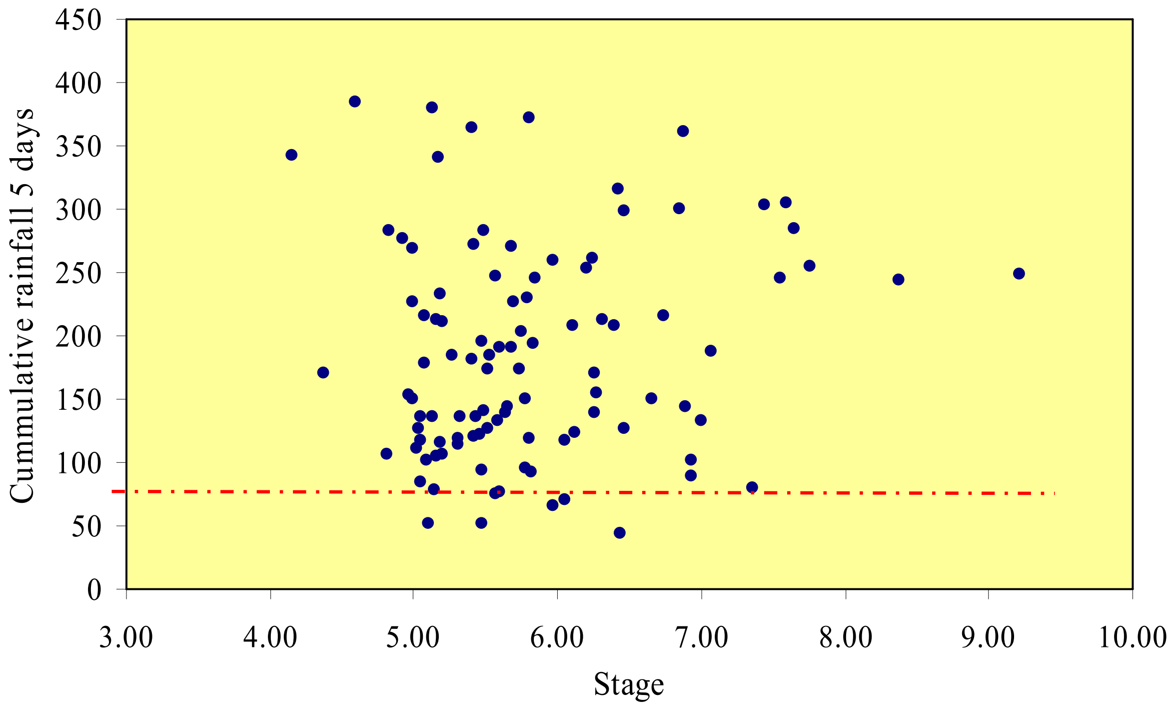


Figure 2-12. Comparison between 5-days period of cumulative rainfall in Quincemil and Biologically Significant Events in Puerto Maldonado.

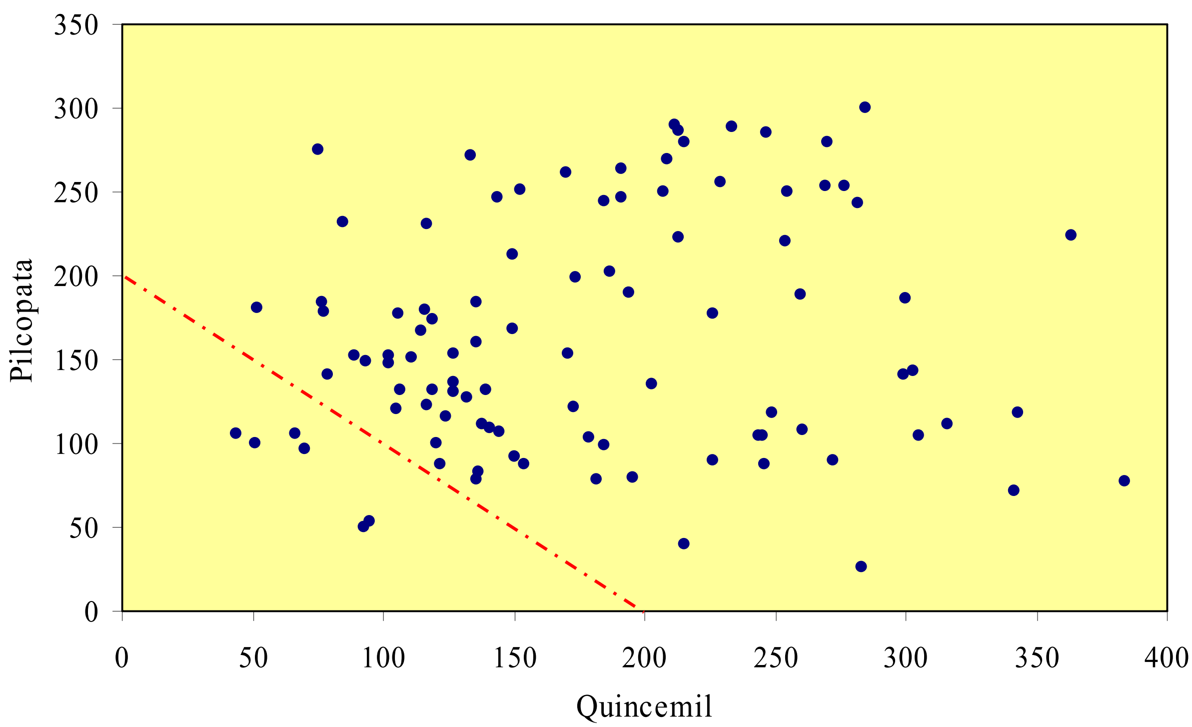


Figure 2-13. Comparison between cumulative rainfall of Quincemil and Pilcopata during Biologically Significant Events in Puerto Maldonado.

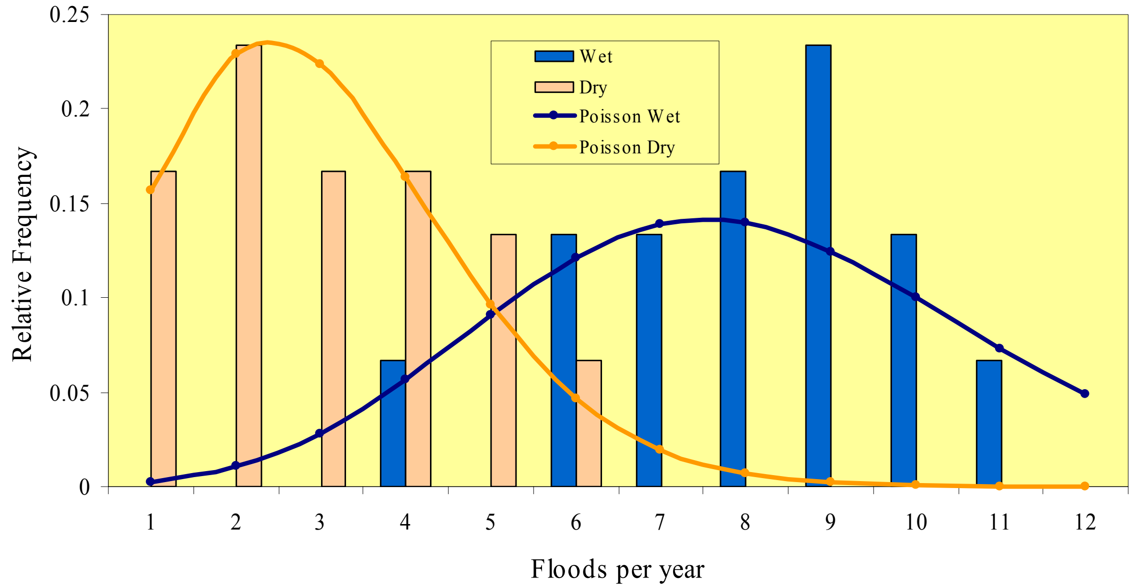


Figure 2-14. Probability and Poisson distributions of forecasted floods in the Madre de Dios Basin for wet and dry seasons (Flood average: wet season = 8.03; dry season = 2.93).

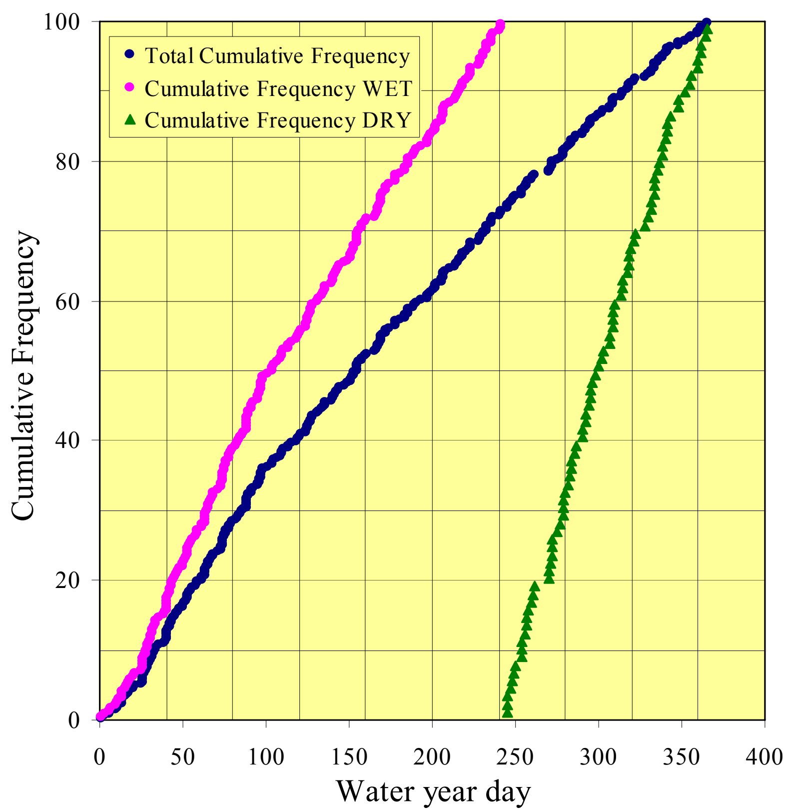


Figure 2-15. Cumulative Frequencies of Biologically Significant Events forecasted from 30 years of historical rainfall records.

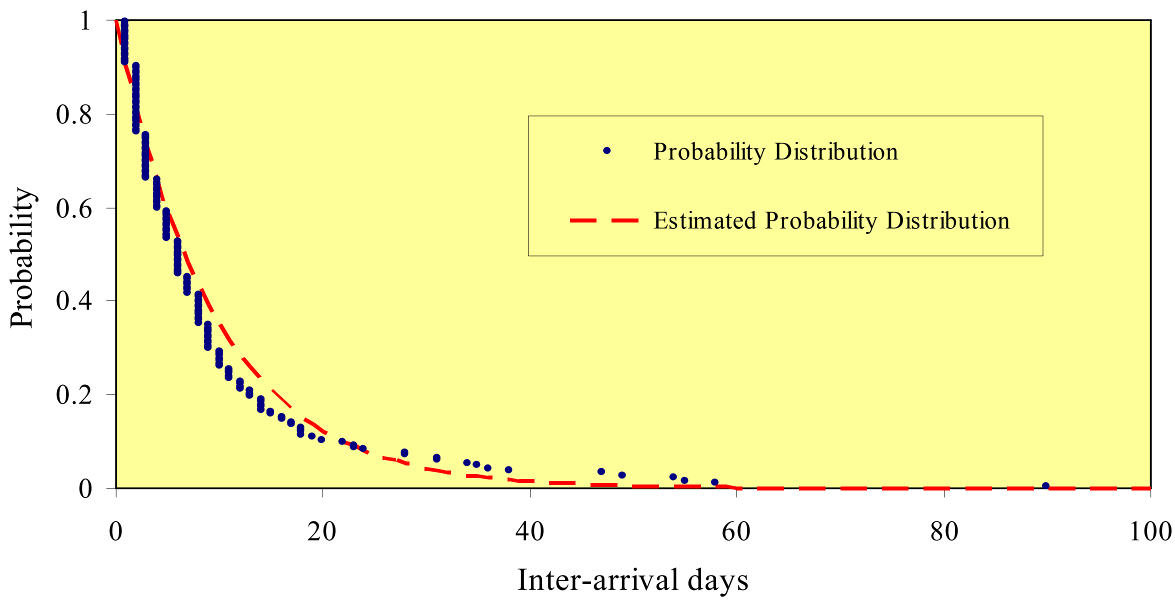


Figure 2-16. Probability Distribution of inter-arrival times between forecasted Biologically Significant Events in Puerto Maldonado.

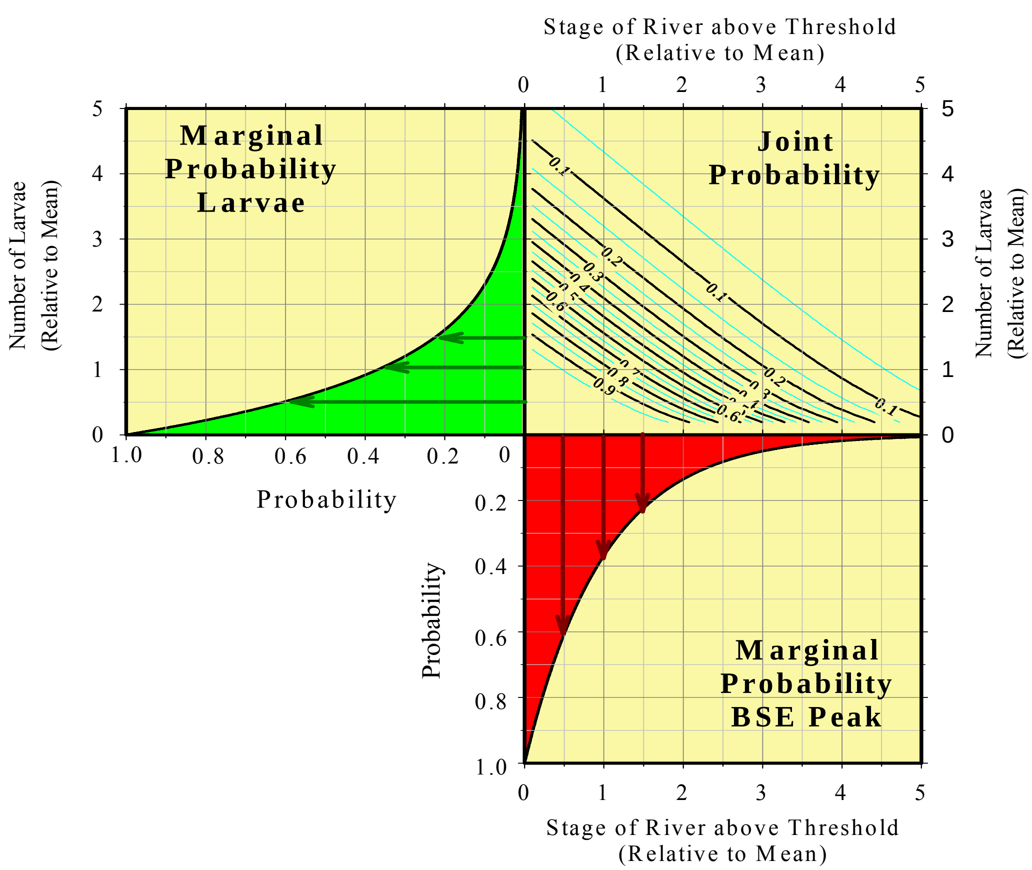


Figure 2-17. Joint Probability Distribution of larval catches when surpassing the threshold river level.

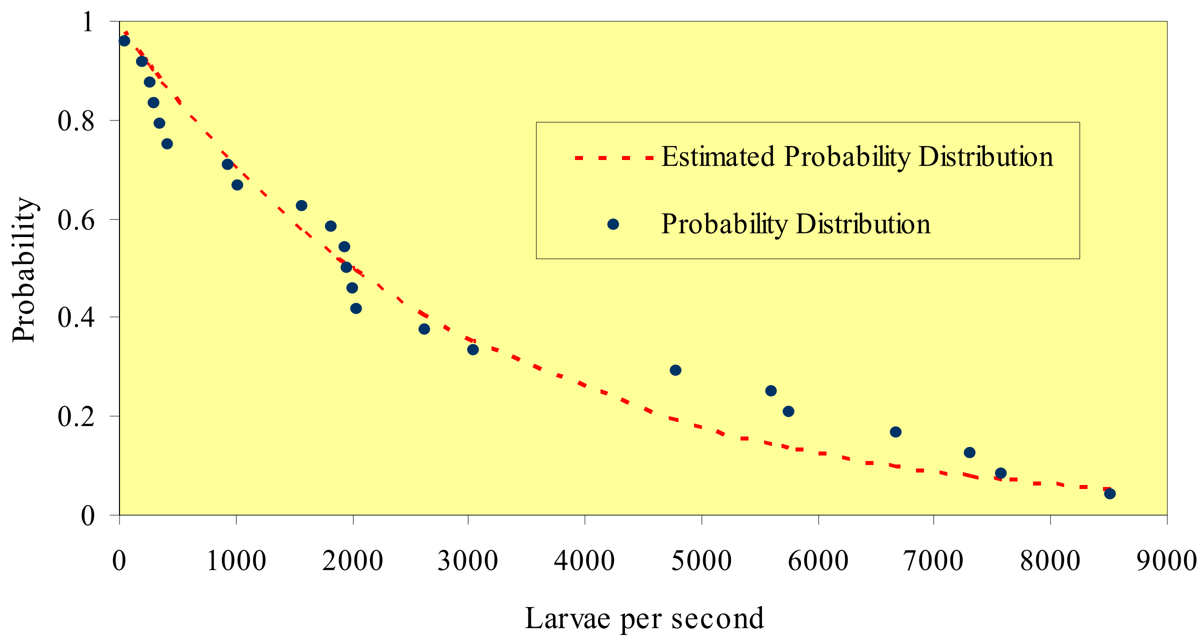


Figure 2-18. Probability Distribution of estimated larvae exported and passing Puerto Maldonado (Average = 2902 larvae per second).

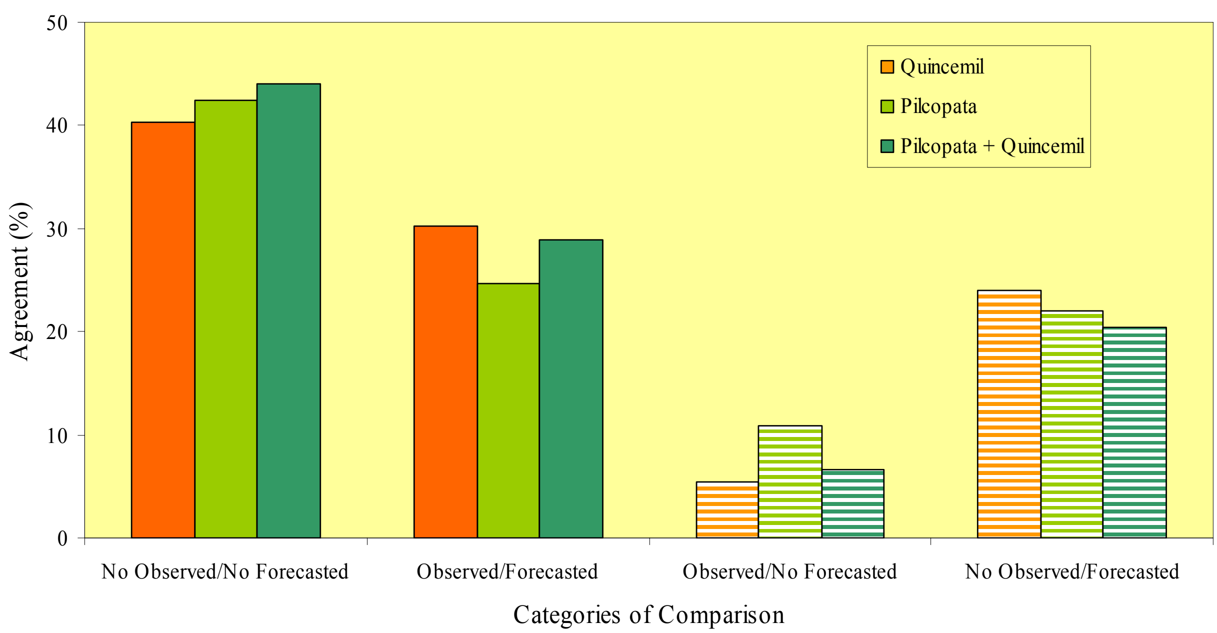


Figure 2-19. Percentage of agreement (in solid color) and no-agreement (in horizontal pattern color) between forecasted and observed Biologically Significant Events in Puerto Maldonado.

CHAPTER 3
# TEMPORAL AND SPATIAL PATTERNS OF DISPERSION OF CATFISH LARVAE IN MADRE DE DIOS RIVER, PERU

## Introduction

Fish migrations for reproduction are considered one of the main behavioral responses to the annual hydrologic regime occurring in large tropical rivers (Lowe-McConnell 1975; Munro 1990; Poff et al. 1997; Junk & Wantzen 2004). In the Amazon Basin, a group of large catfishes (Siluriformes: Pimelodidae) develop long distance longitudinal migrations for reproduction. These migrations are most evident during the rising water period but, depending on the species, may occur at other times of the annual cycle as well. Several species of migratory catfish swim upstream in the principal tributaries from lowland areas toward the headwaters in the Andean foothills (Barthem et al. 2003). In Peru, the Madre de Dios Basin represents one of the Andean-Amazon headwaters where the commercial fishery exploits large catfish (Cañas 2000; Barthem et al. 2003). While sexually mature individuals have been found, no larval fish collections have been made to determine whether this region is a spawning ground and how fish spawning may relate to the annual hydrologic regime.

Survival of Amazonian large catfishes is thought to be dependent on annual flooding events as the adult migrations and gonad development are synchronized with the seasonal flood pulses (Munro 1990; Poff et al. 1997; Cañas 2000; Welcomme & Halls 2002; Barthem et al. 2003). Flooding events are also likely important for larval development as the seasonal floods help to disperse drifting larvae from the upland region to the lowlands (Araujo-Lima & Oliveira 1998; Oliveira & Araujo-Lima 1998; Araujo-Lima et al. 2001). The purpose of this chapter is to examine the relationship between the larval production and seasonal flow characteristics of the Madre de Dios Basin. To achieve this, temporal and spatial distributions of catfish larvae in the Madre de Dios River collected during 2006 were analyzed. Five cross sectional transects were sampled on a weekly basis using an ichthyoplankton net. At each transect a known volume of water was sampled for each catch and a suite of physio-chemical parameters measured. Icthyoplankton samples were then sorted and catfish larvae were counted. Results for the Madre de Dios River showed a temporal variability with significant higher larval density values during the rainy/high water periods of the year. Larval density within the main river in this section of Madre de Dios River was not significant different by depth, but did differ laterally across the river width. River flow characteristics provided favorable conditions for fishes to spawn and for larvae to be displaced downstream and survive. By understanding patterns of larval dispersion of these species we will be able to identify their spawning areas and determine their relationship with the seasonal flooding of the Madre de Dios Basin. This study represents not only the first analysis of larvae drifting in the Southern Peruvian Amazon, but also the first larval research developed in one of the headwaters of the Madeira River, the largest tributary in the Amazon Basin. This work also provides a basis for important research on catfishes in the Amazon Basin which is fundamental for developing important conservation plans, given the importance of these species to local peoples and the continuing threats in this region from poor land use practices and proposed construction of hydroelectric facilities in the southwestern Amazon.

## Literature Review

In freshwater ecosystems, fish species have evolved strategies to regulate timing of their sexual cycles with ideal environmental conditions to ensure their reproductive success (Bye 1984). In temperate regions day length, temperature, and food availability predominate as environmental factors influencing timing of reproduction (Bye 1984). Most authors have agreed that photoperiod is the principal environmental factor controlling spawning in most Salmonids (Scott 1990). Temperature is thought to be an important ultimate factor influencing fertilization success and survival of larvae of Cyprinids (Hontela & Stacey 1990). In tropical regions, several fish species have predictable and restricted spawning periods, which are related to seasonal rains, flooding of rivers, or the monsoons (Munro 1990). Spawning activity of tropical fishes may be initiated by environmental changes such as yearly flooding events, which are associated with an increment of food availability in the aquatic ecosystem, and with a direct effect on fish larvae that ensures their displacement to areas for feeding and protection (Bye 1984).

It is commonly thought that the natural flow regime of a river is important in structuring the productivity and connectivity of riverine ecosystems (Poff et al. 1997). Hydrological conditions of tropical rivers are determined largely by annual cycles of rainfall and desiccation occurring at these regions (Lowe-McConnell 1975; Welcomme & Halls 2002), and regional variability of rainfall patterns, as well as geology, topography and land cover vegetation, influence in the final characteristics of the natural flow regime of a river (Poff et al. 1997). Five critical components including magnitude, frequency, duration, timing and rate of change of hydrologic conditions are said to control most ecological processes in river ecosystems (Poff et al. 1997). In many rivers, timing and frequency of flows are thought to be crucial to trigger adult fish migration to spawning areas and to transport larvae downstream (Poff et al. 1997; Welcomme & Halls 2002; Junk & Wantzen 2004), their spawning activity is timed with the occurrence of the flooding period (Lowe-McConnell 1975; Bye 1984; Welcomme & Halls 2002). Flooding events also drive a change of chemical contents and nutrient status of the parental river because of its lateral connection with the adjacent floodplain, where nutrient cycles, primary and secondary production, and organic matter decomposition occurs in higher levels (Goulding 1980; Junk & Wantzen 2004). This seasonal change gives the river channel the ideal conditions not only for hosting spawning grounds, but also for transporting larvae downstream.

In general, larvae drifting have received less attention than adult fish migrations in freshwater ecosystems. Abundance and migratory data of adult catfishes exist from monitoring commercial fishery catches, since this information represents the basis to detect impacts of over-fishing, one of the major concerns about fish population management (Goulding 1979; Welcomme 1979; Cañas 2000; De Resende 2004; Filho & Schulz 2004; Payne et al. 2004). Larval fish ecology represents a valuable knowledge and a major significance for the life history of most freshwater fishes, as their requirements are often different than those of adult fishes (Scheidegger & Bain 1995; Robinson et al. 1998) and their distribution often permits a good inference about spawning ground locations and dispersion processes, which are also two important conditions to consider in conservation and management of fish populations (Oliveira & Araujo-Lima 1998).

In temperate rivers of North America, larval studies have been conducted to understand the effects of navigation, flood controls, reservoirs and impoundments in the community structure of larvae and their drifting process (Harrow & Schlesinger 1980; Holland & Sylvester 1983; Brown & Coon 1994; Scheidegger & Bain 1995). In the Missouri River the complex pattern of flow between the lower portion of the river and the tributaries drives the productivity and maintenance of larval fish diversity (Brown & Coon 1994). Scheidegger & Bain (1995) suggested that flow regulation in Tallapoosa River, a tributary of Alabama River, appeared to lead degradation of microhabitats of fish larvae, and protection of these microhabitats should have priority in order to protect fish populations in this river. Flow regulation is also thought to have significantly altered the recruitment of most native fish species in Caspaspe River in Australia (Humphries et al. 2002). A variety of life history and recruitment styles of freshwater fishes have been identified in Murray-Darling Basin (Australia) based on different hydrological conditions occurring within a range of geographical zones (Humphries et al. 1999). In South America, most larval studies have been concentrated in Brazilian Amazon, and they have generated information about larval development and drifting pattern related to hydrologic conditions in the Central Amazon (e.g. in rivers Solimões and Amazon), where the presence of large floodplains is the principal feature. In such regions, larval production is strongly related to annual hydrological conditions occurring in the principal river, which is produced by the influence of upstream tributaries (Araujo-Lima & Oliveira 1998; Oliveira & Araujo-Lima 1998; Araujo-Lima et al. 2001; Nakatani et al. 2001).

Egg and larval stages constitute the most fragile and important phases on fish life, since natural fish population continuance will be based on the survival and success of recruitment during these dispersal phases (Araujo-Lima & Oliveira 1998; Oliveira & Araujo-Lima 1998; Araujo-Lima et al. 2001; Nakatani et al. 2001). Seasonal increments of water flow in most rivers are critical not only to create channel conditions where spawning process occurs (Harrow & Schlesinger 1980; Barthem & Goulding 1997; Araujo-Lima et al. 2001; Welcomme & Halls 2002), but also as the main aquatic highway through which fish larvae will reach and occupy their final habitats (Scheidegger & Bain 1995; Oliveira & Araujo-Lima 1998; Humphries et al. 2002; Humphries 2005). After spawning, downstream displacement ensures eggs and larvae drift-transportation to nursery areas, where larger amount of food and protection are available (Goulding 1980; Lowe-McConnell 1987; Araujo-Lima & Oliveira 1998; Nakatani et al. 2001; Humphries et al. 2002; Humphries 2005). Flushing condition also influences fish community structure, decreasing the likelihood of predator presence on the way downstream of most of fish larvae (Junk & Wantzen 2004). Fish migration, in any of its directions, represents one of the most important factors to maintain basin productivity and integrity in rivers (Welcome & Halls

2002) -larval fish not only grow to become adult fish, but larval and juvenile fish are also important components of the food web as prey items for many other species of fish, invertebrates, birds, and mammals related to freshwater ecosystems.

Hydro-climatologically, the Amazon lies in a feed-back between the vast rainforest, that recycles almost one half of the precipitation it receives and the Andes, which acts as an orographic barrier importing atmospheric water and exporting surface waters to the Amazon System (Poveda et al. 2006). River level variability in most of Amazon headwaters, such as the Madre de Dios Basin, is controlled principally by rainfall, snow melt does not cause influence in flow regime in the Andean region (Barthem & Goulding 1997; Barthem et al. 2003). Most of the highest annual rainfall values in the large Amazon Basin are reached in the eastern Andean foothills with records about 8000 mm (Barthem et al. 2003).

## Materials and Methods

### Study Area

The study area was located around Puerto Maldonado city, the principal urban center in the Madre de Dios Basin. Puerto Maldonado is located at 480753E and 8607445N coordinates (19L UTM zone/Datum WGS84), in the confluence of the rivers Madre de Dios and Tambopata, at 256 meters above sea level (Figure 3-1). In front of Puerto Maldonado, the river channel was approximately 425 meters wide, the deepest part of the channel varied between 10 m and 13 m, and water level variation reached 9.21 meters between 2005 and 2006 (field observations). Barthem and his research team (2003) reported that 8.9 meters was the maximum annual fluctuation of the Madre de Dios River between 2001 and 2003 near the confluence of Los Amigos River. Physical and chemical conditions of the river vary based on these hydrologic periods, with evident increment of water level, average velocity, water discharge, and sediments in suspension during the wet season (Barthem et al. 2003).

The Madre de Dios River is the largest river in southeastern Peru and one of the 10 largest rivers in the Peruvian Amazon. Flowing generally from west to east, it has a drainage area of approximately 90,000 $km^2$ (Goulding et al. 2003). Its natural flow regime is largely influenced by the high rainfall variability caused by its proximity to the Andes (Kalliolla & Puhakka 1993; Puhakka & Kalliolla 1993; Puhakka et al. 1993; Goulding et al. 2003). Nine important tributaries discharge in the Madre de Dios River, through which water leaves the basin. Six tributaries drain from highlands areas over 4000 meters above sea level, and three drains in lowlands areas and drain at the northern area of the basin (Goulding et al. 2003) (Figure 3-2). Rainfall records obtained mostly from two Andean meteorological stations from the *Servicio Nacional de Meteorología e Hidrografía* (SENAMHI), the Peruvian Weather Service Institution, indicated a highly variability in precipitation pattern within the drainage basin. These records also suggested that in general the rainiest season in the basin takes place between October and April and the drier season does between May and September.

**Sampling**

During year 2006 a weekly larva sampling was carried out along five cross channel transects located on the Madre de Dios River near the city of Puerto Maldonado. All transects crossed the channel from bank to bank, three of them (named: 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 (named Bajo Madre de Dios) was placed downstream of the confluence. The fifth transect (named Herrera) was in the Tambopata River, approximately 4 km upstream of the mouth (Figure 3-1). 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 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.

Across each transect, sampling was carried out at five designated habitats categories: Cutting banks, referred to erosive areas usually with high velocities; filling banks, included depositional areas and with lower velocities; the main channel, that included the deepest part of the channel; and zones in between the main channel to the cutting bank and main channel to the filling bank. Samples at the bank habitats were taken within distances no larger than 20 meters off shore. Surface samples were taken at one meter depth, and deep samples corresponded to 70% the total depth at each of these five habitat categories. Physical and chemical parameters of water were obtained at surface of each sampling point.

A 365-micron ichthyoplankton net with a circular mouth of 0.47 m diameter, 1.50 m long, conical shaped, and fitted with a removable collection bottle with two 365-micron mesh windows was used to perform the larva sampling. A mechanical flowmeter General Oceanics 2030R was attached at the open section of the net to calculate water filtered during each sampling. Depth measurements were obtained by using a Lowrance Fish-finding Sonar & Mapping GPS LMS-480M. Dissolved oxygen and temperature were measured with an oxymeter YSI Model 550A, conductivity was obtained with a conductivimeter YSI 30, and pH was measured with a Hanna Tester HI98130. A range finder Nikon ProStaff Laser440 was used to record channel width measurements and lateral distances between the sample points.

Water level measurements were obtained from a gauge stage installed at right bank of Madre de Dios River in Puerto Maldonado city (Figure 3-1). Daily records were taken twice a day (8:00 am and 6:00 pm) between December 4$^{th}$, 2004 and December 31$^{st}$, 2006. During all mornings of 2006, channel width was also recorded with the range finder in front of the water level stage. Integrated water velocity was recorded at five equidistant points across the channel, also in front of the river stage. Discharges of the Madre de Dios River were estimated with the velocity-area technique, which involved the calculation of discharge segments across the channel by using the mean section method.

Larva was collected at the five transects during day time hours and in the same order to standardize timing of collection at each site. Night time sampling was not included since no differences were found between day and night larval sampling (Araujo-Lima et al. 2001). At each habitat the net was placed at the selected depth and left for 3 or 5 minutes, depending on the conditions of stream velocity. A concrete block helped the net to reach deep positions and the boat was kept stopped by using an anchor. After lifting the net, all the content retained in the collection bottle was rinsed, and the sample was placed into flasks of 500 ml. and preserved in 4% formalin solution. Flasks were taken to laboratory facilities installed in Puerto Maldonado, where larvae were sorted out. Eggs were also counted, although they were not possible to differentiate into any specific fish group. A Zeiss Stemi DV4 Stereo Microscope was used to identify and count catfish larvae. Biological material was finally stored at *Museo de Historia Natural* – UNMSM in Lima, Peru.

**Statistical Analysis**

Larva counts were standardized to density units (number of larvae per 50 $m^3$) in order to make comparisons between periods, transect, and habitat catches. Statistical analyses were performed by using SAS software and all statistical significance was reported at $p < 0.05$. A non parametric method was used, the Generalized Linear Fixed Model procedure (GLIMMIX), which allowed comparing larval densities at various temporal and spatial levels. During comparison analyses, seasons (two), transects (six), and habitats (five) were the fixed effects within the GLIMMIX procedure. Because the variances were not proportional to the means, we specified within the model procedure that larval catches followed a Negative Binomial Distribution. If larval density differed by fixed effects the Least Square Means procedure was used to determine which effects (seasons, transects or habitats) differed.

## Results

A total of 44,984 catfish larvae were captured along the five transects around Puerto Maldonado city. Larval catches presented a seasonal pattern during the sampled period. High variability characterized the samples, and Levene test indicated non homogeneity of variances in the weekly larva catches, that is, the variance in each of the samples were not proportional to the respective means (Table 3-1).

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 between May and September, and a high water period for the rest of months (from January to April, and from October to December). The river fluctuated 9.21 meters, with the highest peak reached for January 3rd, 2006 and the lowest for September 22nd, 2005 (Figure 3-3).

During 2006 estimated larval densities presented significant differences between weeks and hydrological periods (Table 3-2). Lower mean values of week densities were found between April and September, and higher values occurred during the beginning and the end of the year (January to March, and October to December). The 400-meters channel of Madre de Dios River rose up in 3.99 meters between weeks 41 and 43 (October 7th to October 21st, 2006). Higher larval densities occurred during week 44 (October 28th, 2006) until the last week of the year. Lower density values appeared between weeks 17 and 41 (April 22nd and October 7th, 2006). Between January 3rd and April 17th, larval densities were also high, but with a tendency to decrease as the flood season ended after week 17 (April 22nd). A peak of larva density similar to those found at the end of the year occurred during the second week (January 9th) (Figure 3-4).

Since presence of most larvae occurred during the high water season, all comparison was focused on catches for this hydrologic period. Least Square Means procedure indicated significant differences between transects El Balcon and Puerto Maldonado (both in Madre de Dios River), and between transects from the Tambopata River and Puerto Maldonado transect in the Madre de Dios River (Table 3-3).

During the high water season larval drift was evaluated by habitats and depths identified within the cross channel transects. Statistical comparison of Least Square Means between the five arbitrary habitat categories indicated clear differences between larval densities obtained near the banks and those obtained in areas closer to the main channel. Larvae found in habitats related to the main channel did not present statistical differences. Larvae found at filling banks were significantly greater than those found at the cutting banks (Table 3-4). No statistical differences in larval catches were found between 1-meter depth samples and those taken at depths greater than 1 meter (Table 3-5).

Eggs were also captured during the sampling, and their abundances (eggs/50m$^3$) were significantly increased for weeks 42 and 43 (October 14$^{th}$ and October 21$^{st}$ 2006) in a better synchronization with rising water dates. During the beginning of the year, egg presence was detected during most of February, with a reducing pattern until week 10 (March 6$^{th}$, 2006) (Figure 3-5). We were not able to differentiate the species whose those eggs belonged, but their temporal presence, and mainly their large increment as the waters started rising, was a closer indicative to detect spawning periods and potentially, spawning grounds. No significant differences in egg densities were found between the four transects placed in the Madre de Dios River (Table 3-6).

Channel characteristics were recorded in front of the water level stage. Channel width kept fairly constant values during most of the year, between 414 and 446 meters, the maximum width was reached in January 2006. At this same point, the highest discharge was 4125.48 $m^3$/sec, and the mean surface velocity was 0.789 m/sec. Chemical characteristics of both rivers varied accordingly to the hydrologic periods. Conductivity kept higher values in the Madre de Dios River over 80 micro-Siemens/cm during most of the dry season, with the highest average value for July 2006 (93.44 micro-Siemens/cm); during the lower season values fluctuated between 62 micro-Siemens/cm and 75 micro-Siemens/cm. In the Tambopata River conductivity varied between 27.8 micro-Siemens/cm in April and 58.7 micro-Siemens/cm in September. Dissolved oxygen in the surface of the Madre de Dios River increased gradually after the dry season, from a minimum value for October (5.53 mg/litter) to a maximum value in May (7.90 mg/l). Similar pattern of oxygen variability was observed for Tambopata River, with values in the range of 5.53 mg/l in October and 7.64 mg/litter in May. Surface temperatures were higher during the dry season, their values increased from 22.2 °C reached for May to 27.6 °C for September in the Madre de Dios River. Temperatures in the Tambopata River varied in a similar pattern than those recorded in the Madre de Dios River. Values for pH were only obtained for the dry season and they followed a decreasing pattern, from a maximum 7.6 recorded in July to 6.30 in October. Madre de Dios River presented higher values of pH than the Tambopata River.

Water characteristics varied between transects, and variation was related to transect's location with respect to the tributary entrance. In the Madre de Dios River, conductivity was not significantly different between the three transects located upstream Tambopata River, but they were different than Bajo Madre de Dios transect, located downstream this tributary; and they were also different than transect placed within Tambopata River. Oxygen values were not significantly different between the four transects of Madre de Dios River, but they were with those located in Tambopata River. No statistical differences in Temperature appeared between most of transects, except for transect Herrera that kept higher values than the rest (Table 3-7).

## Discussion

### Timing and Spawning

The Madre de Dios Basin plays an important role in the recruitment of large catfishes (Family Pimelodidae) into the Amazon System. In this region, 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 it started in the middle of October for year 2006. High values of larvae were also encountered during the beginning of the year 2006 (January to March), which constituted part of the preceding spawning period of these species within the basin (2005-2006). Based on the temporal distribution of larval production observed during 2006, spawning activity of large catfishes in the Madre de Dios Basin was found to be between October and March. In other tropical regions a similar period occurs, such as in the Campaspe River (Australia) the peak time larval drift was between October and December (Humphries & King 2003). In temperate regions, spawning occurs at different period, in the Colorado River for example, most of cyprinids and catostomids spawn primarily during March to June (Robinson et al. 1998). Because the Colorado River is in the northern hemisphere the seasonal timing of spring floods is different than the other examples, however the response in the fish populations is likely the same.

The largest numbers of larva catches were sampled for the fourth week of October, larval density values went up 5 to 10 times with respect to the previous week in all transects (maximum average: 180 individual per 50 $m^3$ in El Balcon transect). This week represented the on-set of the spawning activity of these catfishes in this basin for 2006, and although we did not register larval stage, the presence of the yolk sac in most of the individuals indicates a life time of a few hours to days after hatching, which also suggests that this downstream migration of large catfish larvae represents the primary dispersion from spawning grounds in Madre de Dios River. Frequency of flood events during the high water period in the area is supporting this transportation and appears to be very linked with spawning behavior of large catfishes. In the Central Amazon catfish larvae have also been reported to be drifting the river in large quantities during the last months of the year (Araujo-Lima & Oliveira 1998), and other species such as Characiforms in the Amazon spawn also during this period (Oliveira & Araujo-Lima 1998).

Although eggs captured in the nets were not able to be identified, their presence can give a more exact time-indicator of the on-set of spawning season and potentially, location of spawning grounds in the Madre de Dios River. Time for embryo differentiation for two species of these large catfishes is known to take between 3 to 7 hours (Nakatani et al. 2001), and time from fertilization to hatching lasts up to 16 hours for many other characiforms in the Amazon (Araujo-Lima 1994). The large increment in egg densities found between October 14th and October 21st, which matches closer in time to rising water dates, confirm with another evidence that spawning period in Madre de Dios River during 2006 started with the rising of river level for the middle of October. Further, considering that both, the average surface velocity of the river during the flooding reached up to 0.789 m/sec (2.84 km/hour) and the time of embryo differentiation is less than 7 hours, then the spawning grounds could be potentially located around 20 km upstream from the sampling area. An area of rapids is located within this distance in the Madre de Dios River (Locality: La Cachuela, Madre de Dios, Peru), where the increased turbulence caused by flood events give the water a better oxygenation and velocity, potentially favorable conditions for these catfishes to spawn.

**Environmental Conditions and Spawning**

It is known that environmental factors are influencing spawning activity of most fishes in the world, and some authors consider that environmental factors are even more important in the spawning activity than biological factors (Lowe-McConnell 1987; Munro 1990; Humphries et al. 1999). In temperate zones photoperiod is considered the environmental condition best related with fish spawning, since climate and length-day vary markedly from season to season, and it can be detected by fishes (Sumpter 1990). In Kalkaveem River (Russia) downstream migration of young coho salmon (*Oncorhynchus kisutch*) was thought to be controlled by temperature (Pavlov & Maslova 2006); in the Nile River spawning of the cyprinid *Barbus bynni* coincides with the increment of water level and inundation of shallow areas (Hontela & Stacey 1980); and in the Little Colorado River it is likely that temperature and photoperiod are important spawning cues for four native fishes (Robinson et al. 1998).

The influence of precipitation from the close Andean Region in the flow regime of Madre de Dios Basin is apparent, rivers get flooded a short period after rainfall events occur and cease as soon as precipitation stops (Goulding et al. 2003). During 2006 rainfall records from two Andean foothill meteorological stations within the basin indicated that rainy season started between the first and second weeks of October, and for those dates the water level of the large Madre de Dios River rose up in almost 4 meters. In Amazon headwaters regions, such the Madre de Dios Basin, hydro-climatological conditions are controlling spawning activity of catfish larvae. Floods drive changes in the physical and chemical conditions of the river that can be the signal for catfishes that a favorable environment is ready to ensure the survival of the new fish generation. Based on the classification of fish reproductive styles suggested by Balon (1984), these large catfishes (Family Pimelodidae) would be considered pelagic spawners, non-guarders and less protective, producers of eggs in large numbers, and with a long larval period terminated by metamorphosis. Then, these characteristics suggest that successfulness of Amazonian catfish spawning depends on adults by producing and placing their larvae in optimal habitat conditions.

Chemical characteristics are also potential signals for fishes to spawn, and changes of their levels in the water are a consequence of the hydrologic periods (Lowe-McConnell 1987; Barthem et al. 2003; Junk & Wantzen 2004). Significant differences were found mostly for conductivity and dissolved oxygen values between transects located in different tributaries, and between transects placed upstream and downstream of the tributary entrance. Differences in conductivity in the Amazon are given by geology through which a basin passes, and its variability in the same river is related to the water period (Barthem et al. 2003). Between October and December, the starting of spawning period, transects in Madre de Dios River presented significantly higher values of conductivity and dissolved oxygen than Tambopata River. Interestingly, the Tambopata River presented more dissolved oxygen values previous to the first significant rising of water level (October), after which values decreased for the spawning period. This can be explained by a dam effect the larger Madre de Dios produces on the Tambopata River by this time. Regarding to larval production, no significant differences were encountered between transects upstream and downstream Tambopata, which could be indicating not only the low contribution of catfish larvae of this tributary in the basin, but also that its lower oxygen and conductivity values could be the missing potential conditions that "prepare" the river channel for spawning. Upstream of La Cachuela transect, an area of rapids exists in the Madre de Dios River, which can be contributing with oxygen conditions. Transport of sediments from tributaries upstream of the Madre de Dios River seems to be larger than sediment transportation in

Tambopata River (Barthem et al. 2003), which caused the high values of conductivity. Since temperature was not significantly different between transects and rivers, it could be said that these two chemical variables, oxygen and conductivity, signal this group of catfishes to the spawning areas.

**Spatial Distribution of Catfish Larvae**

Larva densities found in transects placed in the Madre de Dios River were significantly greater than those found in the Tambopata transects. No statistical differences were found between transects placed upstream and downstream from the entrance of the tributary Tambopata, which indicated the poor contribution in larval production from this tributary in the Madre de Dios Basin. It is likely that physical and chemical characteristics of Tambopata River did not represent the best conditions for spawning of these species.

A non-homogeneous larval distribution was advised across each transect. Significant differences in larva densities were found between the five designated habitat categories. Larval densities along side banks were significantly greater than larvae found in areas related to the middle channel. A similar larval distribution across the channel has been reported for larvae in other regions (Harrow & Schlesinger 1980; Holland & Sylvester 1983; Araujo-Lima & Oliveira 1998; Robinson et al. 1998; Humphries & King 2003). Considering only cutting and filling bank habitats, higher larval density values were found in the deposition zone (filling bank) where lower stream velocities occurred. In Madre de Dios River, catfish larvae are being transported by the currents and getting clumped at these low-velocity habitats to then occupy areas downstream for feeding and hiding. Young larvae of many other species prefer sedimentation areas of the channel, which are in general considered habitats with better conditions such as lower abrasion process of sediments and more food availability (Harrow & Schlesinger 1980; Brown & Coon 1994; Scheideggeer & Bain 1995; Oliveira & Araujo-Lima 1998; Robinson et al. 1998;

Humphries et al. 2002). Some authors have also found that high flow velocity habitats appear to increase larval mortality (Robinson et al. 1998). Most of caught larvae were in the early stages of development either with yolk sac or switching to initial phases of exogenous feeding (vestiges of yolk), which meant swimming was not their practice yet. It was stream velocity that transported them to depositional areas as the flood water increased. Some authors consider these habitats also suitable and preferred by larvae in older stages, which already possess swimming abilities, are able to avoid high stream velocities, and need to forage for food (Robinson et al. 1998).

No significant differences were found in vertical distribution of larvae in the river channel, which indicated that a massive larvae downstream displacement was occurring in most of channel sections in Madre de Dios River. A similar homogeneous vertical dispersion of fish larvae was advised in the upper Colorado River (Valdez et al. 1985). In Central Amazon, larvae of two species of Characiforms were found to be distributed significantly different in the water column, and this was attributed to a reduction of inter specific competence for space and food in the ample floodplain (Oliveira & Araujo-Lima 1998).

**Transport of Larvae to Downstream Areas**

Flooding also produces a lateral connection of running water ecosystems with the adjacent floodplain. The exchange of nutrients and energy from terrestrial phases to the main channel creates a suitable environment for spawning and feeding of adults, juvenile, and larvae (Bye 1984; Lowe-McConnell 1987; Junk & Wantzen 2004). Flooding also emphasizes the dynamic concept of connection and continuously changes of physical conditions along the river (Vannote et al. 1980). In Madre de Dios River, since lateral inundations are short in time, but very frequent, floods are more related to give the optimal conditions to the river to host spawning grounds, and also make the river to become the “highway” through which larvae will be transported downstream, connecting spawning and nursery areas of these species, geographically far away apart. Nursery areas of these species are suggested to be located in the lowlands, close to the discharge area of the Amazon River next to the Atlantic (Barthem & Goulding 1997).

When compared with lowland areas, floodplains in Madre de Dios River are very limited, and if they occur, it will be for quite a few hours. Floodplains facilitate better conditions for the development of microbenthos and zooplankton, principal food sources for fish larvae when they switch from endogenous (from yolk sac) to exogenous feeding (Humphries et al. 2002). The presence of young larvae in all the transects during the same sampling periods indicates they are moving downstream and not staying in this region since food offer is very limited, and they take advantage of high flows to reach more favorable areas downstream for feeding. Predation is another consideration in this headwater region. Large floodplains have been associated with larger number of larvae because they find places for shelter and protection from predators (Oliveira & Araujo-Lima 1998; Brown & Coon 1994). No many areas for shelter, such as vegetation at margins, exist in Madre de Dios banks, which do not offer conditions to larvae for shelter. Further, drifting during high water diminishes the mortality by predation (Araujo-Lima & Oliveira 1998). Floods in headwaters are necessary to ensure these individuals to reach areas with better conditions to survive and grow.

## Conclusions

Timing of spawning of Amazon large catfishes is driven by hydrologic regime in the Madre de Dios River. Larval production was evidenced to be significantly higher during months of high water season than in the low water season. The outstanding increment of larvae presence in the channel also corresponded with starting moments of the rainy season, which confirmed the strong link between starting time of spawning behavior of these species and the hydro-climatologic conditions of the entire basin. The period of reproduction of these species in the

Madre de Dios Basin extends from October to March, and this research actually obtained partial samples of two consecutive periods: the end of 2005-2006 and the beginning of 2006-2007.

Spatial patterns of larvae within the channel were driven by hydrologic forces of flooding events. Morphological characteristics of most captured larvae suggested they were not good swimmers, and given the significant differences in larval presence found between filling and cutting banks in all the study area, it is the floods that concentrate larvae in the depositional zones of the channel. The filling banks could act as potential floodplain areas for these larvae in this region, however, given the high variability in water levels recorded in the hydrograph, this condition will last for a short period of time, not being completely beneficial for larvae, in the case they were able to swim and select this habitat to stay and grow.

Channel conditions during high water levels, featured by temporary short flood peaks, suggest that flooding events are directly related with the transportation of larvae to downstream areas. No adequate areas for feeding and protection exist in the channel of the Madre de Dios River, since floodplain areas are short in space and time. The almost permanent flood pulses in the Madre de Dios channel, caused by the discharges of Andean headwater tributaries, will give this river the capacity of constantly transporting larvae downstream and no time to create large floodplain as those existing in the lowlands. Floodplains are thought to be the best habitats for survival of larvae, and in Madre de Dios Basin this condition was not occurring to support catfish larvae growth.

The necessity of spatial connection along the large Amazon Basin, between the spawning areas in the headwaters, such as Madre de Dios Basin, and lowland areas where larvae will survive successfully, is suggested by this research. Amazon headwater regions do not support areas for nursing larvae of these large catfishes, which are conditioned to reach, in the short term, lowland areas to survive, and it is flood events that support them to achieve this goal. This spatial connection is also necessary for adult catfishes that, during high water periods, will find the favorable conditions for swim upstream and reach the spawning areas. Two critical moments in natural life history of these catfishes depend on the longitudinal connection of the complete basin, which is controlled by the flow regime. Physical interruption of this route or alteration of the temporal pattern of hydrologic regime in Amazon Basin will put under serious risk the populations of these species, by stopping dispersion of larvae or altering the natural upstream migration of adults. Further, any detriment on these catfish populations will also affect important economic activity such as fisheries, and also protein availability for local stakeholders established along the Amazon rivers in the Madeira valley, principal consumers of these species.

Finally, natural flow regime in the Amazon headwaters is very sensitive to alteration by land use practices, and it is critical not only for survival of catfish populations, but also of other species that depend on the floodplain in the lowland Amazon. Large projects under development in Madre de Dios Basin, such as the Interoceanic Highway, have to consider their potential influence in changing flow conditions of this region; such alterations will have an effect far downstream. In a similar situation are considered large projects in Brazilian Amazon related to use of water resources, such as dams in the Madeira River. It is critical to include as potential effects of these projects the likelihood of disruption of critical routes for long distance migratory catfishes. These species consider, from the Atlantic to the Andes, their living habitat, and their natural life history is defined by achieving their principal goal of reaching both the headwaters near the Andes (in Ecuador, Colombia, Peru, and Bolivia) and the nursery areas near the estuary (in Brazil).

Table 3-1. Levene's test for Homogeneity of Larval Catches Variances (p < .0001)

| Source | DF | Sum of Squares | Mean Square | F Value | Pr > F |
|---|---|---|---|---|---|
| Season_Week | 53 | 5.7426E9 | 1.0835E8 | 3.57 | < .0001 |
| Error | 2263 | 6.862E10 | 30320552 | | |

Table 3-2. Test of Fixed Effects (SAS GLIMMIX Procedure Type III, p < 0.0001) showing statistical differences of larva densities between weeks and seasons.

| Effect | Num DF | Den DF | F value | Pr > F |
|---|---|---|---|---|
| Season | 1 | 10 | 128.19 | < .0001 |
| Week | 1 | 251 | 89.21 | < .0001 |
| Week*Season | 1 | 251 | 48.34 | < .0001 |

Table 3-3. Statistical comparisons between larval densities by transects for the high water period (Least Square Means. GLIMMIX Procedure, p < 0.0001).

| Transect name | Transect name | Degrees of Freedom | Pr > \| t \| |
|---|---|---|---|
| La Cachuela | El Balcon | 2305 | 0.4524 |
| La Cachuela | Puerto Maldonado | 2305 | 0.0003 |
| La Cachuela | Bajo Madre de Dios | 2305 | 0.7060 |
| La Cachuela | Herrera | 2305 | 0.0535 |
| La Cachuela | Candamo Port | 2305 | 0.0929 |
| El Balcon | Puerto Maldonado | 2305 | < .0001 |
| El Balcon | Bajo Madre de Dios | 2305 | 0.2619 |
| El Balcon | Herrera | 2305 | 0.1749 |
| El Balcon | Candamo Port | 2305 | 0.3090 |
| Puerto Maldonado | Bajo Madre de Dios | 2305 | 0.0012 |
| Puerto Maldonado | Herrera | 2305 | < .0001 |
| Puerto Maldonado | Candamo Port | 2305 | < .0001 |
| Bajo Madre de Dios | Herrera | 2305 | 0.0272 |
| Bajo Madre de Dios | Candamo Port | 2305 | 0.0453 |
| Herrera | Candamo Port | 2035 | 0.6612 |

Table 3-4. Statistical comparison between larval densities by habitats across the channel for the high water period (Least Square Means. GLIMMIX Procedure, p < 0.0001).

| Habitat | Habitat | Degrees of Freedom | Pr < \| t \| |
|---|---|---|---|
| Cutting bank | Filling bank | 2307 | < .0001 |
| Cutting bank | Middle channel | 2307 | < .0001 |
| Cutting bank | Cutting – Middle | 2307 | < .0001 |
| Cutting bank | Filling – Middle | 2307 | < .0001 |
| Filling bank | Middle channel | 2307 | < .0001 |
| Filling bank | Cutting – Middle | 2307 | < .0001 |
| Filling bank | Filling – Middle | 2307 | < .0001 |
| Middle channel | Cutting – Middle | 2307 | 0.0809 |
| Middle channel | Filling – Middle | 2307 | 0.2527 |
| Cutting – Middle | Filling – Middle | 2307 | 0.5458 |

Table 3-5. Statistical comparison between larval densities by depths for the high water period (Least Square Means. GLIMMIX Procedure, p < 0.0001).

| Sample depth | Sample depth | Degrees of Freedom | Pr < \| t \| |
|---|---|---|---|
| 1-meter Surface | > 1-m surface | 2313 | 0.3539 |

Table 3-6. Statistical comparison between egg densities by transects in the Madre de Dios River for the high water period (Least Squares Means. GLIMMIX Procedure, p < 0.0001).

| Transect | Transect | Degrees of Freedom | P > \| t \| |
|---|---|---|---|
| La Cachuela | El Balcon | 1868 | 0.7574 |
| La Cachuela | Puerto Maldonado | 1868 | 0.4834 |
| La Cachuela | Bajo Madre de Dios | 1868 | 0.0026 |
| El Balcon | Puerto Maldonado | 1868 | 0.6998 |
| El Balcon | Bajo Madre de Dios | 1868 | 0.0074 |
| Puerto Maldonado | Bajo Madre de Dios | 1868 | 0.0208 |

Table 3-7. Statistical comparison of water parameters by transects for high water period (Least Squares Means. GLIMMIX Procedure, p < 0.0001).

| Transect name | Transect name | Conductivity (micro-Siemens/cm) | Oxygen (mg/L) | 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 | < .0001 | 0.0483 | 0.0501 |
| La Cachuela | Herrera | < .0001 | < .0001 | < . 0001 |
| La Cachuela | Candamo Port | < .0001 | 0.0003 | 0.0968 |
| El Balcon | Puerto Maldonado | 0.9494 | 0.388 | 0.5757 |
| El Balcon | Bajo Madre de Dios | < .0001 | 0.3292 | 0.1072 |
| El Balcon | Herrera | < .0001 | < .0001 | < 0.0001 |
| El Balcon | Candamo Port | < .0001 | < .0001 | 0.1751 |
| Puerto Maldonado | Bajo Madre de Dios | < .0001 | 0.9068 | 0.2920 |
| Puerto Maldonado | Herrera | < .0001 | < .0001 | < .0001 |
| Puerto Maldonado | Candamo Port | < .0001 | < .0001 | 0.3843 |
| Bajo Madre de Dios | Herrera | < .0001 | < .0001 | 0.0009 |
| Bajo Madre de Dios | Candamo Port | < .0001 | < .0001 | 0.9606 |
| Herrera | Candamo Port | 0.0050 | < .0001 | 0.0021 |

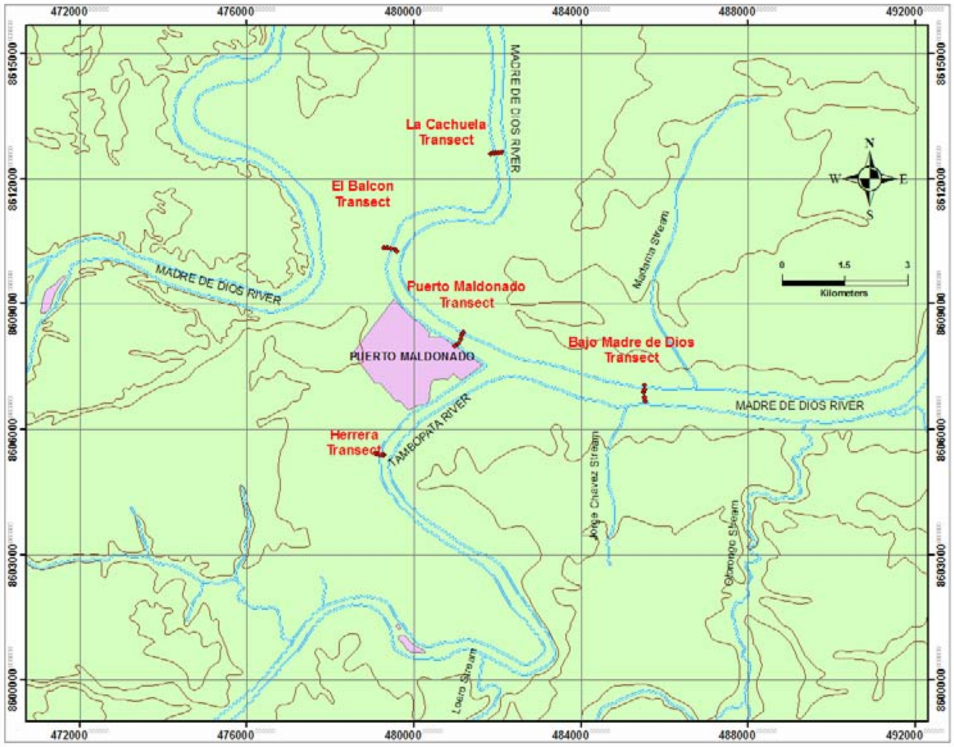


Figure 3-1. Location of the study area and sampling transects around Puerto Maldonado, Peru.

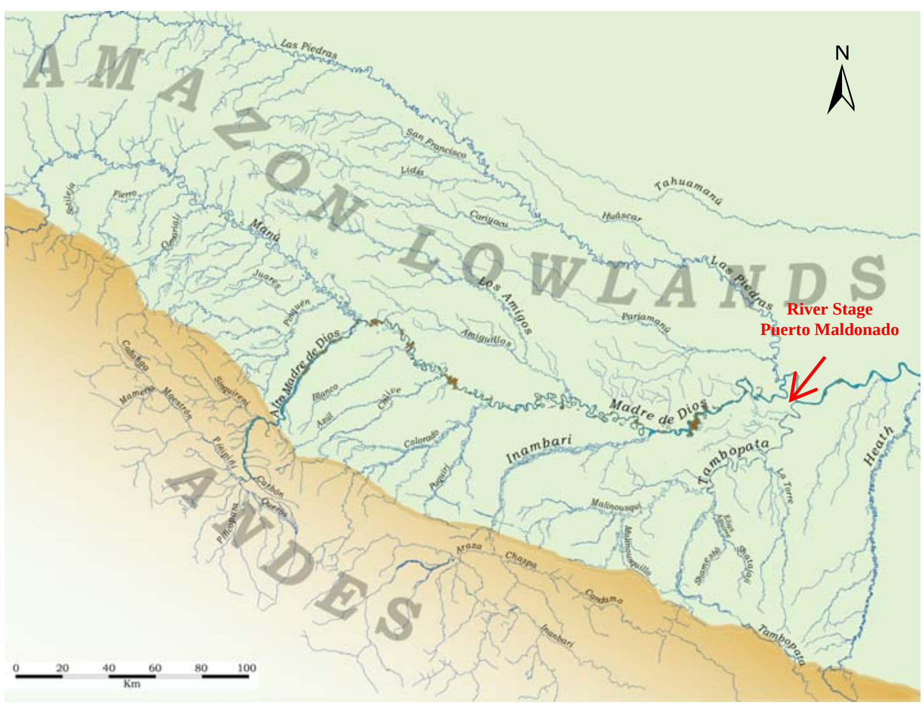


Figure 3-2. The Madre de Dios Basin, its Andean (south) and lowland (north) tributaries, and location of Stage in Puerto Maldonado, where field work was carried out.

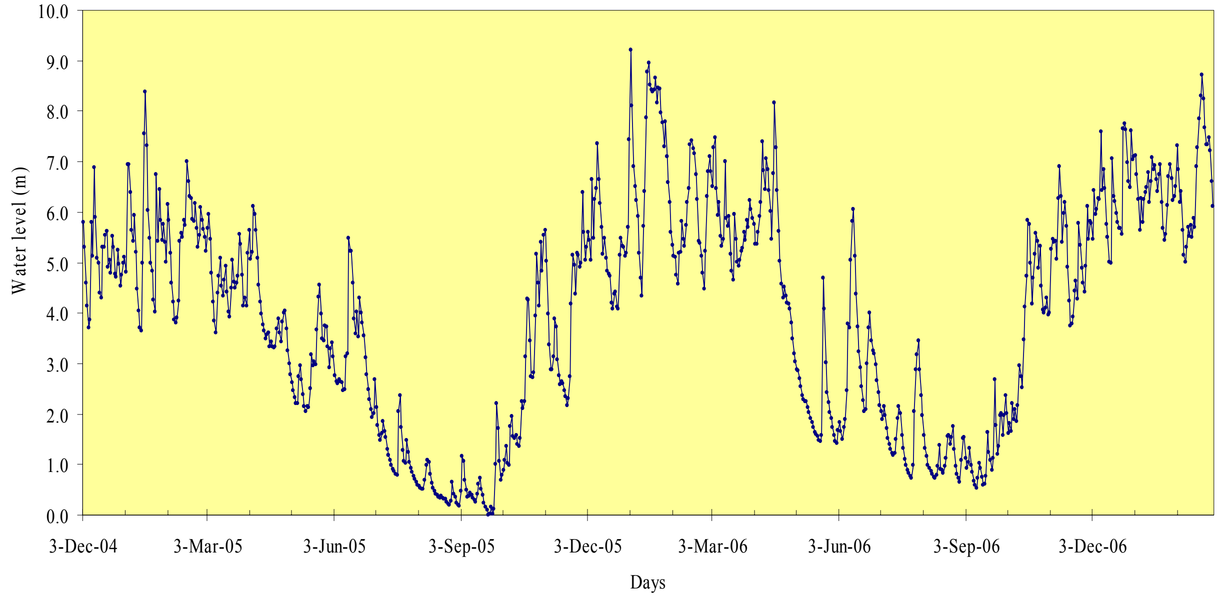


Figure 3-3. Daily water level variation for the Madre de Dios River in Puerto Maldonado, Peru (December 2004 to February 2007).

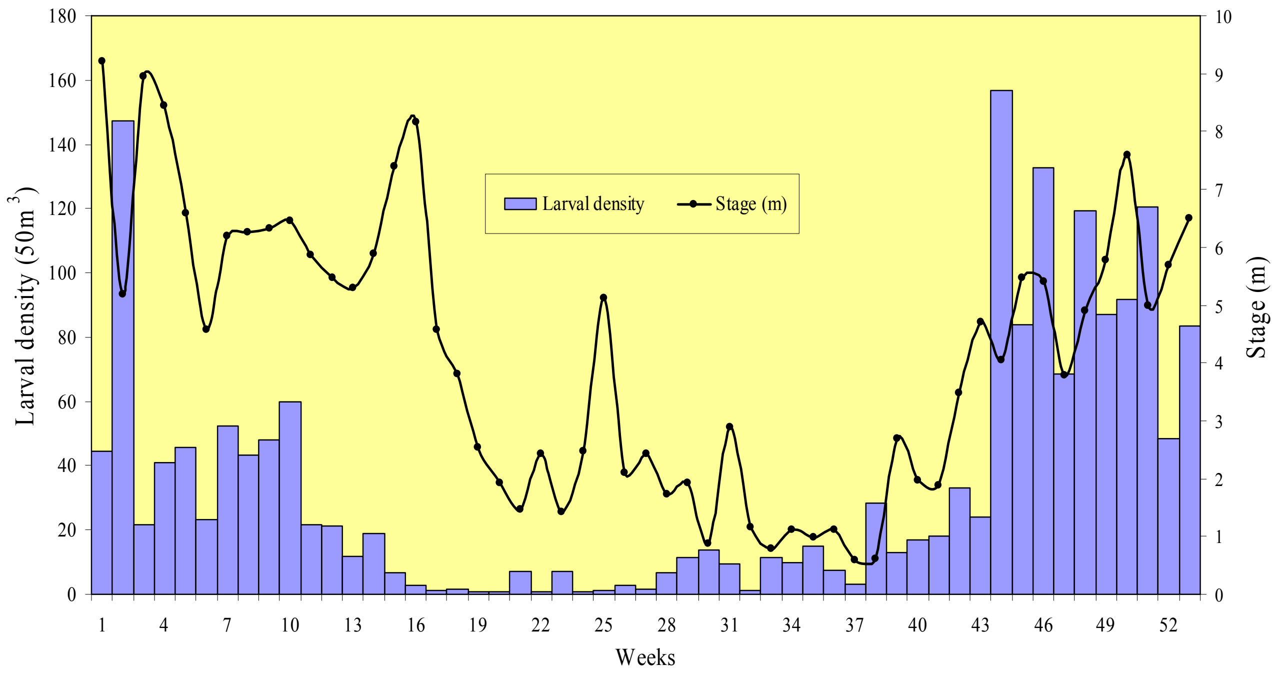


Figure 3-4. Average larval density (larvae/$50m^3$) and water level in Madre de Dios River during 2006.

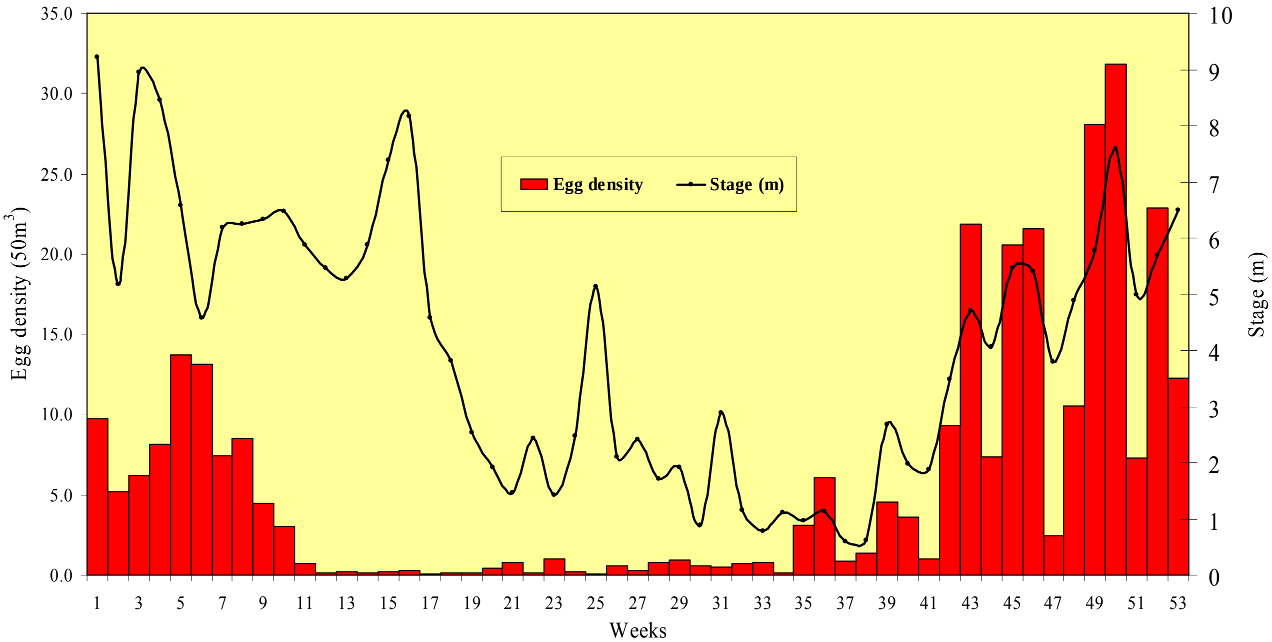


Figure 3-5. Average egg density (eggs/50m$^3$) and water level in Madre de Dios River.

CHAPTER 4
CONCLUSIONS

River dynamics and the reproductive behavior of fish are profoundly related in the Madre de Dios headwater region of the southwestern Amazon Basin in southeastern Peru. Several large catfish species – and probably many smaller species of various fish groups – have evolved to take advantage of, and now depend on, hydrologic conditions associated with the Andes-Amazon interface zone. The downstream drift of catfish larvae in the Madre de Dios River, as well as the presence of ripe adults, strongly indicates that these species spawn in this headwater region during the high water period. The nursery habitats for several of the large catfish that spawn in the Madre de Dios headwater region are found only in the Amazon River estuary, more than 3,500 km downstream. Longitudinal migrations of both adults moving upstream and newly born fish downstream, demonstrate that these species have evolved to use nearly the entire east-west extension of the Amazon Basin for their life histories.

A simple stochastic model was proposed to characterize fish larvae recruitment from the Madre de Dios headwaters to the Amazon lowland rivers. Biological and hydrological variables were employed to strengthen the model. Simple assumptions about the uniform temporal distribution of flooding events and larvae were tested with the support of the long term hydrologic data derived from historical precipitation records. This approach, of generating long term hydrologic conditions from precipitation information, is reasonable and also supported by the nature of the hydro-climatologic conditions characterizing the Andes-Amazon headwater region of the Madre de Dios Basin, where rainfall patterns are strongly associated with river dynamics. Nevertheless, considering the great spatial variation within this headwater basin, and especially the high Andes and lowland Amazon, it is necessary to also consider additional potentially important variables, other than just water level, that could produce environmental signals that determine when large migratory catfish spawn. Sediment types, pH and conductivity are among the variables considered.

The concept of a "two-way gate" is introduced to help explain the fundamental role of flooding events in the life cycles of large migratory catfishes in the Amazon Basin. Flow characteristics of the Madre de Dios headwaters during the high water period provide environmental signals that induce large catfishes to migrate upstream to seek spawning habitats in Andean foothill tributaries. These "open-gate" signals are considered biologically significant events, and they are considered as being sent randomly during the rainy season, which in turn will also determine the intensity of the next spawning based on the number of ripe adults present. In this sense the flow regime of the Madre de Dios River heavily determines when and if ripe adults migrate to the headwater region and the number of fish larvae that will be released to migrate downstream.

The model is also designed to incorporate other non-uniform variables that are expected to be derived from future research. These additional variables should improve forecasting of spawning events and also provide more detailed information on the interaction of variables and hydrologic regimes. Although there is only limited hydro-climatic information available for most of the Madre de Dios Basin and only short-term fish larvae sampling, the model presented here should nevertheless provide a basis for which to consider how headwater hydrologic regimes need to be maintained for migratory catfish life cycles.

Larva production that is released from the Madre de Dios headwater region demonstrates the importance of the Andes-Amazon interface zone in the maintenance of fish abundance and diversity over a much broader area within the Amazon Basin. Observed drifting patterns of catfish larvae indicate the importance of river channels as the principal habitat where spawning and downstream/upstream transportation take place. No significant spatial differences were found in the numbers of fish larvae moving downstream in the Madre de Dios River. This indicates that spawning habitats are near the Andes or in the Andean foothills, and probably mostly the latter. Since many of the species are important commercially the maintenance of hydrologic conditions in the Amazon-Andes headwaters has important implications for the maintenance of commercial fisheries from the headwaters to the estuary.

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## BIOGRAPHICAL SKETCH

Carlos Canas was born in 1973 in Chimbote, Ancash, Peru, where he grew up and got his elementary and high school education. In 1991 he moved to Lima, and in 1997 he obtained his bachelor's degree in biology at the *Universidad Nacional Mayor de San Marcos*, Lima, Peru, with specialization in hydrobiology and fisheries. During his years as an undergraduate student, he worked extensively on freshwater fishes in the Department of Ichthyology of the *Museo de Historia Natural Javier Prado*, Lima, Peru. In the early 1990s he also began participating in scientific expeditions to various Peruvian rivers. As a fish ecologist he has 7 years of field experience in the Amazon Basin and Andes of Peru, and has conducted aquatic research with Conservation International (CI) and the Amazon Conservation Association (ACA). In 2005 he enrolled in the Master's program of the Geography Department of the University of Florida to pursue a specialization in hydrology and freshwater ecosystems, and to gain knowledge in GIS and remote sensing. At present he is active in scientific research and conservation efforts in the Madre de Dios Region of southeastern Peru.