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Modelling production of migratory catfish larvae (Pimelodidae) on the basis of regional hydro-climatology features of the Madre de Dios Basin in southeastern Peru

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Abstract:

A simple stochastic model is presented to describe the influence of the natural flow regime of the Madre de Dios River (southeastern Peru) on the presence and downstream transportation of catfish larvae (Siluriformes: Pimelodidae), an important migratory species in commercial fisheries in the Peruvian Amazon region. One year of daily river stage records were related to weekly larval catches to determine the association between floods and spawning events, and based on the hydro-climatologic characteristics of Andean-Amazon regions, available long-term historical rainfall records were used to determine the inter-annual variability of floods within the Madre de Dios Basin. Major larval drift occurred during the high water season, specifically in association with stages of over 5 m, which served as an indicator triggering spawning responses of these species, termed a 'biologically 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. Copyright © 2011 John Wiley & Sons, Ltd.

KEY WORDS hydro-climatology; catfish larvae; Madre de Dios; rainfall; Amazon; headwaters; Peru

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INTRODUCTION

All river basins display a natural hydrologic regime, which exerts control over productivity of aquatic life and habitat conditions (Poff *et al.*, 1997; Junk and Wantzen, 2004; Winemiller, 2004). In large tropical rivers, fish biology is synchronized to the timing of flood events that are critical ecologically in the life cycle of many fish species (Lowe-McConnell, 1975). Flood events are strongly influenced by seasonal precipitation patterns within the Amazon headwater region, and in the Madre de Dios Basin (Peru), it has been noted that they are related to the initiation of spawning migration behaviour of a group of pimelodid large catfishes (Barthem *et al.*, 2003; Leite *et al.*, 2007). Most of these migratory catfishes of the Amazon complete long distance displacements upriver to spawn in the river channel just prior to, or during, flood phase (Goulding, 1980; Barthem and Goulding, 1997) and their larvae drift during the high water season (Araujo-Lima and Oliveira, 1998; Leite *et al.*, 2007). Therefore, larvae occurrence in the main channel is associated, in a complex manner, with the timing and frequency of flood events.

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, their hydro-climatology is poorly understood (Goulding *et al.*, 2003a). Poveda *et al.* (2006) point out the unique inter-relationship 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. Given the close association between freshwater ecology and the regional hydrologic cycle, such longer term trends may also manifest themselves in ecosystems.

The analysis of partial duration series (PDS), based on the model proposed by Todorovic and Zelenhasic (1970), has been used to evaluate flood risks and related problems (Todorovic, 1978; Ashkar and Rousselle, 1981; Woo and Waylen, 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. The number of events surpassing this level during the flooding period follows a Poisson distribution once the threshold becomes sufficiently distant from the mean (Rasmussen and Rosbjerg, 1991; Bras and Rodríguez-Iturbe, 1993; Rémillard *et al.*, 2004), and the inter-arrival time between such events exhibit an exponential distribution (Evans *et al.*, 1993).

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This PDS concept of hydrologic events on the Madre de Dios River is used to statistically analyse the limited available flow data in the Madre de Dios Basin to establish a stochastic flood model of migratory catfish larvae releases from the headwaters to lowland Amazon. Two years of daily rainfall records from two 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 that 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 biologically significant event (BSE) to be one that equals or exceeds a critical stage associated with peaks of larvae capture at Puerto Maldonado. Based on the relationship between temporal variability of catfish larvae production and the likelihood of such BSE events in Madre de Dios Basin, a simple stochastic model is introduced to describe the strong influence of the natural flow regime on the number and sizes of releases of larvae of these large migratory catfishes of the Amazon. The results provide a base line against which potential future scenarios of flow regime alterations and their associated consequences on larvae production in other similar regions of the Amazon System can be compared.

Currently, the Peruvian government has shown serious interest on developing dams for hydropower stations at several points along the Andean–Amazon headwaters. There is no previous experience on dam's construction in this particular region in Peruvian territory; therefore, the importance of hydrologic regime and its link with river's productivity is being underestimated (Dourojeanni *et al.*, 2009). After destruction of riverine ecosystems by deforestation and overexploitation of migratory fishes in the Amazon, construction of dams for energy power generation is now considered the most severe threat to the long-term survival of migratory fish populations (Barthem and Petrere, 1991; World Commission on Dams, 2000; Goulding *et al.*, 2011). Dams represent one of the major human modifications in rivers; they alter directly not only the morphology of channels in rivers but also the natural distribution and timing of river's natural flow regime, and these alterations lead to meaningful negative effects in river integrity and productivity (Poff *et al.*, 1997; World Commission on Dams, 2000). These migratory catfishes depend on the connectivity of the entire basin to complete their life cycle, dams in these headwater regions will interrupt the downstream drifting of larvae and eggs to nursery habitats, as well as the annual upstream displacement of adults to spawning grounds, fisheries and fish diversity will be significantly altered at both headwaters and lowlands reaches as well (Barthem and Goulding, 1997, Goulding *et al.*, 2003b).

The aim of this research is to test the relationship between the temporal variability of catfish larvae production and the temporal characteristics of the flow regime of Madre de Dios Basin in southeastern Peru. We hypothesize that the hydro-climatological characteristics of the basin 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 larvae 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 the Cordillera de los Andes in southeastern Peru, ranging in elevation from 200 m to over 4000 m (Barthem *et al.*, 2003). Field work for this study was carried out near Puerto Maldonado, the principal urban center of the southeastern Peruvian Amazon, located at 256 m of elevation on the right bank of the Madre de Dios River. Upstream of Puerto Maldonado, nine principal tributaries discharge into the Madre de Dios River and control flow characteristics, six rise in the south with the majority of their areas draining the Andes, and three flow from northern mainly over lowland areas (Figure 1).

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

Hydrologic characteristics of the basin vary as a function of elevation and season. In the Andean region, channel 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 (400 m and below), rivers flow over a flatter topography, describing large and numerous meanders with larger channel widths (425 m average in front of Puerto Maldonado) and higher values of total suspended sediments and of dissolved oxygen and temperature. During the high flow season, lowland rivers become very turbid since transportation of total suspended sediments is increased given the high erosion rate occurring in the sub-Andean piedmont region (400 m of elevation) (Goulding *et al.*, 2003b).

METHODS

Modelling approach

Some basic 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

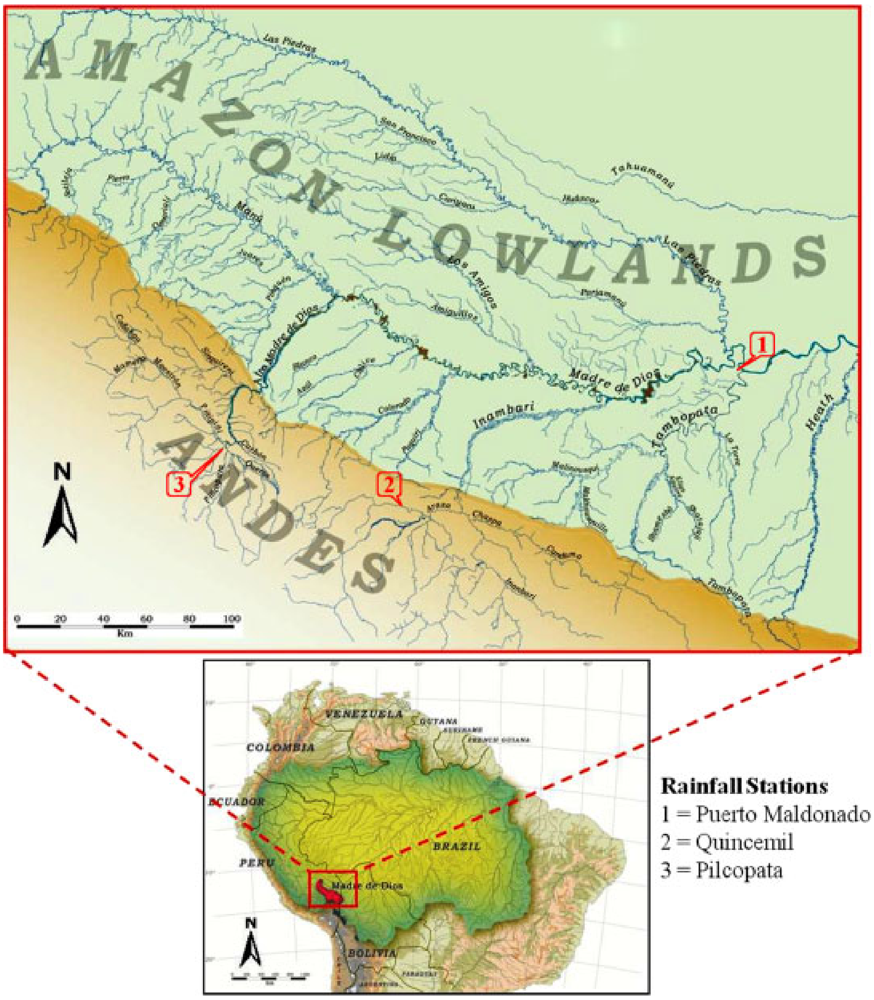

Figure 1. The Madre de Dios Basin, major tributaries, and location of rainfall meteorological stations

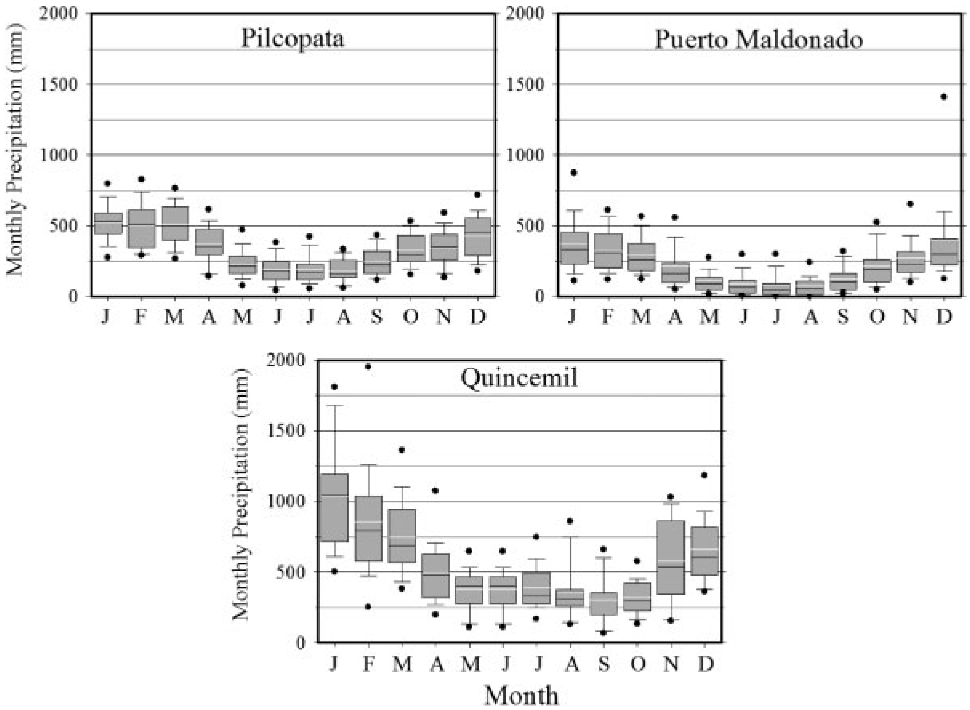

Figure 2. Monthly precipitation (in millimeters) in Pilcopata (32 years), Quincemil (25 years), and Puerto Maldonado (50 years) rainfall stations in the Madre de Dios Basin

are uniformly distributed during rainy season and (2) the inter-arrival times between BSEs are exponentially distributed. If the total amount of adult catfish ready for spawning waiting to reach the spawning grounds in a next BSE arrives in the Madre de Dios Basin at a uniform rate during the high flow season, 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 framework based on additional information that future research might generate in both the hydro-climatological and biological environments.

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

$$m(t, j) = S(t) \times M_j \tag{1}$$

Characteristics of flood occurrences are based on the selection of a truncation level of the river, which is determined by the nature of the flood-related problem. A BSE, defined as a particular river stage threshold related to peaks of larvae release, is the basis of modelling flood characteristics and larval numbers. The number of larvae released (n) during the kth BSE of a year is proportional to the time since the last ($k - 1$th) BSE.

$$\begin{aligned} n_k &= m(t_k, j) - m((t_{k-1}), j) \qquad k > 1 \\ n_1 &= m(t_1, j) \qquad\qquad\qquad\quad k = 1 \end{aligned} \tag{2}$$

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),

$$P(K) = \frac{e^{-\Lambda} \times \Lambda^k}{k} \tag{3}$$

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

$$F(s \le x) = 1 - e^{(-x/\gamma)} \tag{4}$$

where γ is the average length of inter-arrival times and x the number of days between BSEs.

Migratory catfishes

This group of 'giant' catfishes (Siluriformes, Pimelodidae) represents the most widespread predatory species along the Amazon Basin. Their exceptional migrations for reproduction, between estuarine areas near the mouth of the Amazon in the Atlantic Ocean and headwaters in the Andean foothills, are considered the main behavioural response to the annual hydrologic regime occurring in large tropical rivers (Lowe-McConnell, 1975; Barthem and Goulding, 1997; Junk and Wantzen, 2004). Ecologically, these species play a critical function, as both top down (as predators) and bottom up (as dispersers of nutrients from estuaries and floodplain systems) roles, in the river's aquatic food web, regulating rivers' productivity (Goulding, 1979; Barthem and Goulding, 1997). Although taxonomic relationships and population dynamic of these species still under active research (Lundberg and Littmann, 2003), we focused on the study of pimelodid catfish larvae from the genera *Brachyplatystoma, Pseudoplatystoma, Platynematichthys*, and *Sorubimichthys* as they were considered to spawn within the Andean–Amazon headwaters (Leite *et al*., 2007) and to have large commercial importance in the fisheries of the region (Cañas, 2000). The specific area for spawning has not yet identified, but based on the notable presence of larvae in early life stages in the Madre de Dios River during the flooding period, it is believed that spawning may take place about 200–300 m of elevation in this region (Goulding *et al*., 2003; Leite *et al*., 2007).

Larval sampling

Weekly larva sampling was completed throughout 2006 using a 365 μm ichthyoplankton net with a circular mouth of 47 cm and 1·50 m of length; the net was deployed during 5 min at each sampling point. Samples were taken from five bank-to-bank transects along a 12-km section of the Madre de Dios River. At each transect, larvae were captured at five points across the channel, and at 1-m depth and 70% of maximum depth at each point. A General Oceanics 2030R mechanical flowmeter attached at the open section of the net permitted calculation of the volume of water filtered during each sampling. Samples were taken to the laboratory, where pimelodid migratory catfish larvae were sorted out by using the methods described by Leite *et al.* (2007). Larval counts and volume of water filtered were used to calculate larval abundances, which were standardized as 'individuals per 50 m^3' for comparisons and following the method of Araujo-Lima and Oliveira (1998). A generalized linear mixed model (GLIMMIX, SAS version 9.1, SAS Institute, Cary, NC, USA) was used to compare larval fish densities by weeks and season (two seasons: wet and dry).

Estimating model parameters

Two meteorological stations (Pilcopata at 900 m and Quincemil at 600 m) are located on the eastern foothills of the Cordillera de los Andes, each one within the two most important Andean headwater tributaries, the Alto Madre de Dios and Inambari, respectively (Figure 1). Including the rainfall station at Puerto Maldonado (256 m of elevation), a total of 30 years of historical daily rainfall records, with a few missing months, represent the major source of hydro-climatological information considered for analysis to extend the knowledge of historical BSEs in the region.

A system of board gauges was installed at the right bank of Madre de Dios River to register water levels. Recordings were taken twice daily (8 : 00 am and 6 : 00 pm), from which a daily average river level was obtained between 4 December 2004 and 31 December 2006 (2 years and 27 days). Larva densities and observed stage records in Puerto Maldonado were used to identify a threshold water level associated with larva production in the channel. To secure the necessary statistical independence of consecutive BSEs (Rosbjerg, 1985), an arbitrary period of 3 days was established as the minimum time to separate two 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 pragmatic requirement of a reasonable number of BSEs for statistical analyses. Potential BSEs not separated by the requisite period are subsequently considered as constituting a single event.

Times of critical stage were plotted against antecedent rainfall cumulated over increasing numbers of days at each meteorological station to determine the minimum volumes and timings of rainfall in the headwaters most closely related to the generation of BSEs at Puerto Maldonado. This criterion was then applied to the historical daily rainfall records of the two Andean meteorological stations, to identify similar past rainfall conditions to estimate the annual number and timing of BSE prior to the limited period of observed flow records.

To test the efficacy of the various numbers of days of antecedent precipitation, several similar possible values were numerically compared with the observed (2005–2006) series of BSEs by applying simultaneous chi-square statistical analyses of contingency tables. A final chi-square analysis was also applied to test the statistical differences between final estimated floods in historical records and observed floods in the 2-year period in Puerto Maldonado.

Given the size of the basin and the source of rainfall records (two meteorological stations in 90 000 km^2), forecast attributes of dichotomous (yes/no) contingency tables, such as proportion correct, discrimination rate, and false alarm, were also measured to test the forecast performance of our predictions of BSEs for the period 2005–2006 in Puerto Maldonado (Wilks, 2006). All flow characteristics were calculated on the basis of a water year, considered in the Madre de Dios Basin from 1 September to 31 August.

RESULTS

Larvae and stage at Puerto Maldonado

Captured larvae belonged to migratory species of genera *Brachyplatystoma, Pseudoplatystoma, Platynematichthys*, and *Sorubimichthys* (Family Pimelodidae, the 'long whiskered' large catfishes) based on the descriptions by Leite *et al*. (2007). Average larva densities varied significantly between the high and low water periods (Figure 3 and Table I). After week 43 (21 October 2006), larvae densities increased dramatically from 24 to 156 per 50 m^3, the maximum larva production observed during 2006. Meanwhile, between weeks 41 and 43 (7 October 2006 to 21 October 2006), the 400-m-wide channel of Madre de Dios River rose almost 4–5·84 m mark.

Although the relationship between stage and larva production was complex, the 5-m mark seemed to approximate a 'break point' between high and low values of larvae production (Figure 4). At lower stages, most values of larva densities were at background levels, with an average of ten larvae per 50 m^3; and above this threshold,

Table I. Test of Fixed Effects (SAS GLIMMIX Procedure Type III, $p < 0{\cdot}0001$) showing statistical differences of larva densities between weeks and seasons (Num DF = Numerator Degrees of Freedom; Den DF = Denominator Degrees of Freedom)

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

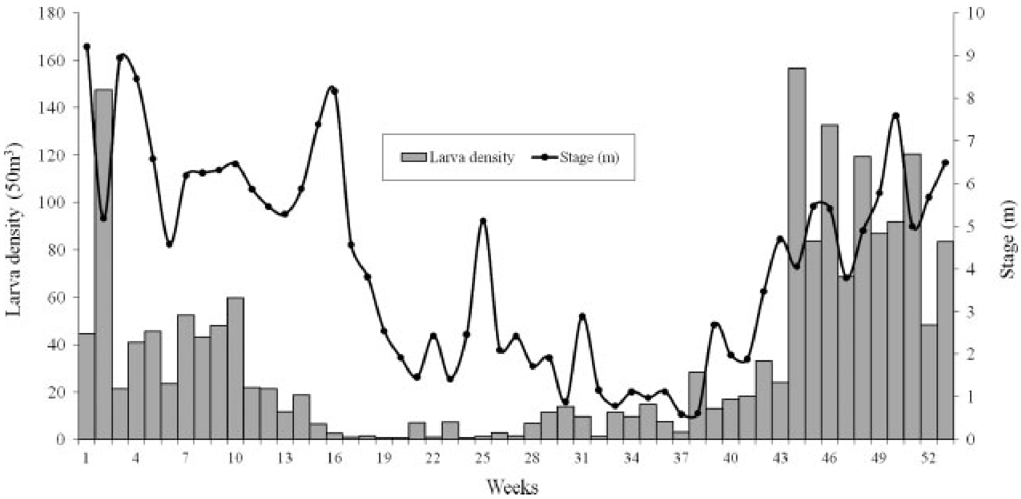

Figure 3. Larva densities and stage records in Puerto Maldonado showing the seasonal pattern of larva production during 2006

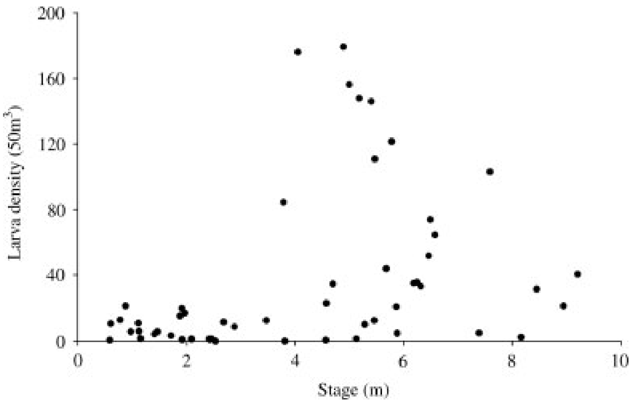

Figure 4. Larva production and stage measurements in Puerto Maldonado, 2006

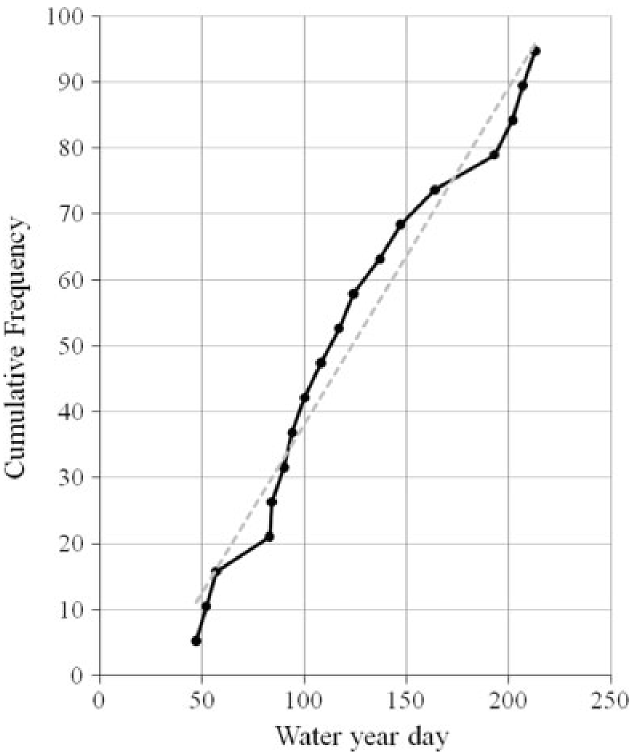

Figure 5. Cumulative frequency of observed BSEs during high water period in Madre de Dios River for 2005 and 2006

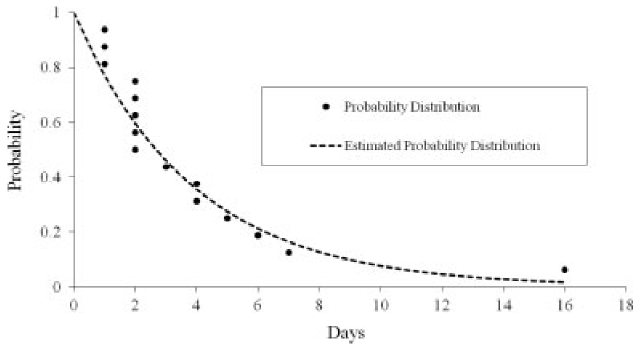

Figure 6. Probability distribution of inter-arrival times of BSEs observed in Puerto Maldonado during 2005 and 2006 (average = 4 days)

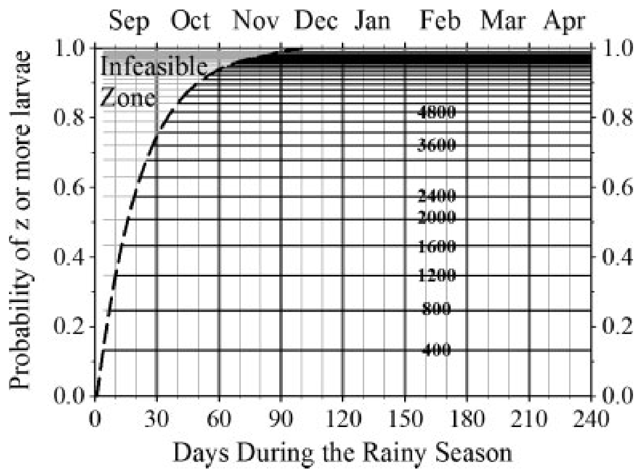

Figure 7. Anticipated cumulative distribution (y) of larvae (z) associated with BSE occurring at any time (x) during the spawning/rainy season. Assuming 400 larvae as mean daily production rate

larva production was extremely variable, with both high and low values and an average of 60 larvae per 50 m^3.

Eighteen BSEs were identified within the stage records, 16 of them occurred during wet season (11 in 2005 and 5 in 2006) and 2 during dry season (1 in 2005 and 1 in 2006). 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 5). Although the inter-arrival times of observed BSEs followed an exponential distribution with an average of 4 days (Figure 6), the assumption of Poisson-distributed annual numbers of BSEs could not be tested due to the very limited number of years of flow data. The average number of BSEs in the 2 years of observation was eight for the high water period and one for the dry season. 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 7). High values of larvae were impossible (the 'infeasible zone' in Figure 7), during the early rainy season, as even if a BSE were to occur, an insufficient period of time has passed to allow adult catfishes to reach the spawning grounds and to produce large numbers of larvae.

Analysis of available rainfall records

The magnitudes of BSE best correlated with rainfall cumulated over the prior 8 days at Pilcopata and 5 days at Quincemil (Figure 8). A 75-mm rainfall in total appeared to be the minimum required from each of the selected stations to attain critical stage at Puerto Maldonado (Figure 9). An alternative approach utilizing both stations' records entertains the possibility that rain falling in both headwater tributaries might, together, generate a BSE, indicating 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 10).

The chi-square statistical analysis of contingency tables between observed and forecast BSEs suggested optimal

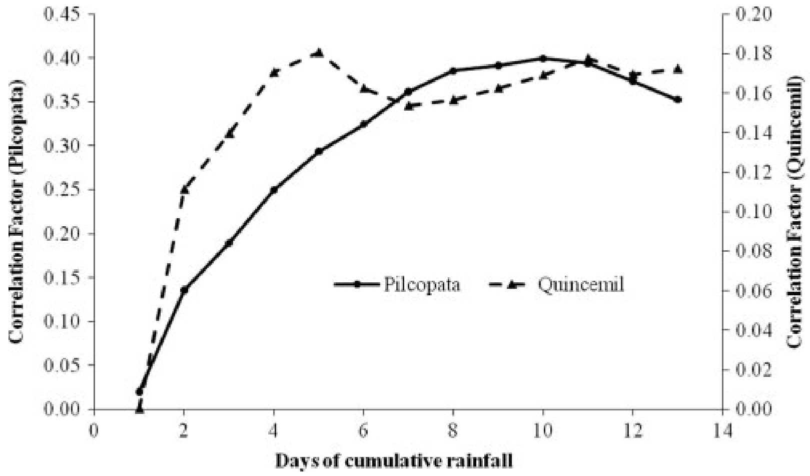

Figure 8. Correlation coefficients obtained for cumulative rainfall periods in both Quincemil and Pilcopata stations and BSEs in Puerto Maldonado

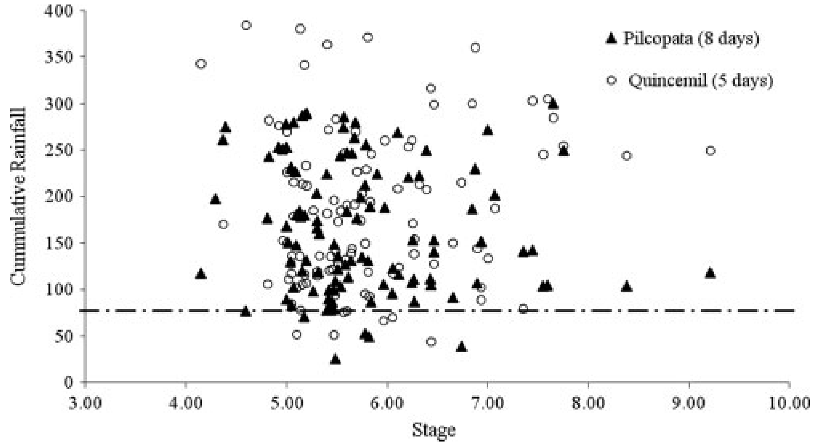

Figure 9. Comparison between cumulative rainfall in both stations Pilcopata (8-day period) and Quincemil (5-day period) with BSEs in Puerto Maldonado

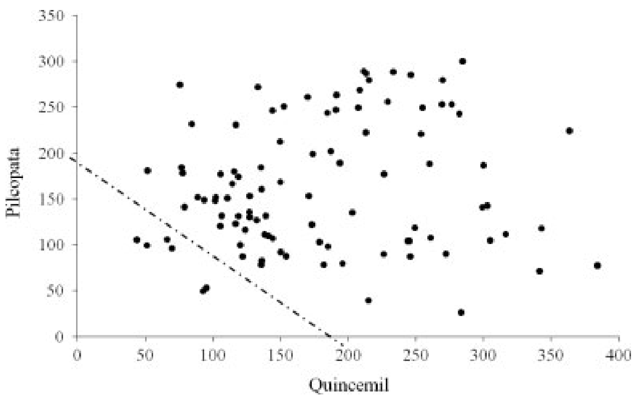

Figure 10. Comparison between cumulative rainfall of Quincemil and Pilcopata during BSEs in Puerto Maldonado

values of 75 mm at Quincemil, 125 mm at Pilcopata, and a 225 mm combined total (Tables II and III). Forecasted BSEs based on the Quincemil criteria yield 70% agreement with the observed BSEs, 67% agreement using Pilcopata, and 73% agreement for the combined totals (Tables IV and V). These values constituted the basis to reconstruct BSE occurrences from the historical rainfall records. Since two possible errors in forecasting would represent potential limitations of the model (1) when a BSE is forecast based on upstream rainfall and none is observed and (2) no BSE is forecast and one occurs, analyses of forecast skills performed for validation suggested that more than 70% of actual BSE were forecast to occur (discrimination rate or hit rate) and around 34% of no BSE were falsely warned as a BSE (false alarm) (Table V).

A total of 313 potential BSEs were identified from the 30 years of available historical rainfall records in the Madre de Dios Basin, 225 during the high water period and 88 during the low water period. Mean annual number of estimated floods was 8·03 during the wet season and 2·93 in the dry—remarkably close to, and not statistically different ($p < 0{\cdot}05$, $df = 1$) from, the figure observed over the short period of stage records (observed floods: eight for wet season and one for dry season). The annual number of potential events conformed to a Poisson distribution (Figure 11), and their dates appeared to be reasonably uniform but showed a slight reduction in frequency after day 100 (9 December) and again in the dry season (Figure 12). Inter-arrival times between potential BSEs described an exponential distribution, with an estimated mean of 9·54 days (Figure 13), which

Table II. Chi-square test values of contingency tables of possible estimated and observed BSEs at Puerto Maldonado, considering different cumulative antecedent rainfall in each station

	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

Highest χ^2 is shown in bold.

Table III. Chi-square test values for contingency tables of possible estimated and observed BSEs at Puerto Maldonado, considering total cumulative antecedent rainfall from both stations

	200 mm	225 mm	250 mm	275 mm	300 mm
Pilcopata + Quincemil	155·33	**167·81**	138·28	141·30	101·39

Highest χ^2 is shown in bold.

Table IV. Percentage of agreement between forecast (F) and observed (O) BSE when there is 75 mm of rain falling in Quincemil area, 125 mm in Pilcopata, and 225 mm falling in both assessed areas

	Quincemil		Pilcopata		Quincemil + Pilcopata	
	O no BSE	O BSE	O no BSE	O BSE	O no BSE	O BSE
F no BSE	304 (**40%**)	41 (6%)	319 (**42%**)	82 (11%)	331 (**44%**)	50 (7%)
F BSE	181 (24%)	228 (**30%**)	165 (22%)	185 (**25%**)	153 (20%)	217 (**29%**)

Table V. Forecast verification of dichotomous BSE and no BSE system of three forecast skills assessed when there is 75 mm of rain falling in Quincemil, 125 mm in Pilcopata, and 225 mm falling in both assessed areas

Station	Proportion correct (%)	Discrimination rate (%)	False alarm (%)
Quincemil	70·56	84·76	37·32
Pilcopata	67·11	69·29	34·09
Quincemil + Pilcopata	72·97	81·27	31·61

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

The export of larvae from the 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 pimelodid catfish populations and the release of larvae. A very similar relationships occurs in other large river systems, such as Mekong Basin, where the spawning season of most of migratory species are tuned up with the river hydrology and onset of monsoon season (Poulsen *et al*. 2002; Hogan *et al*., 2004).

The number of larvae associated with such events varies markedly but appears to be represented by the simple 'threshold' and stochastic model presented. The threshold of 5 m is arbitrary, based purely on observed conditions, and could potentially be redefined to a slightly lower value (Figures 3 and 4). However, this stage should not be viewed as the direct 'generator' of observed larval densities but merely as an indicator that both hydrological and biological variables are related to a common, unobserved cause: the hydro-climatological conditions upstream in the Andean–Amazon region. Therefore, no stage measured at Puerto Maldonado will unambiguously define events which are exporting larvae completely satisfactorily.

The threshold was also selected to identify a reasonably large PDS for adequate parameter estimation and modelling, while ensuring, as much as possible, independent BSEs and excluding small hydrological events of no biological significance during the dry season. Taesombut and 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) would yield a sample of 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*., 2003b). Stage at Puerto Maldonado 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 3 indicates that although hydrologically and

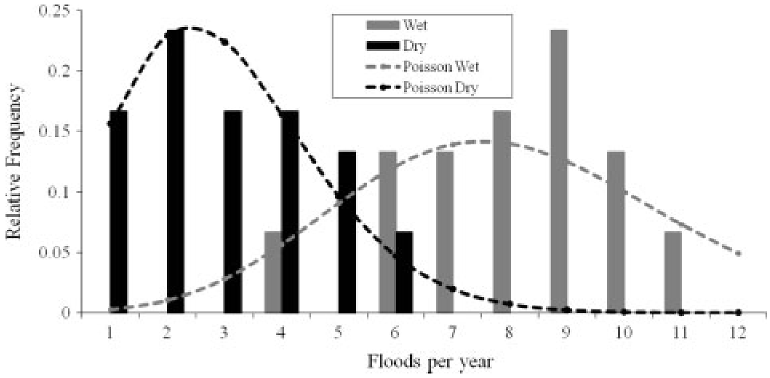

Figure 11. Probability and Poisson distributions of forecasted floods in the Madre de Dios Basin for wet and dry seasons (flood averages: wet season = 7·97; dry season = 2·93)

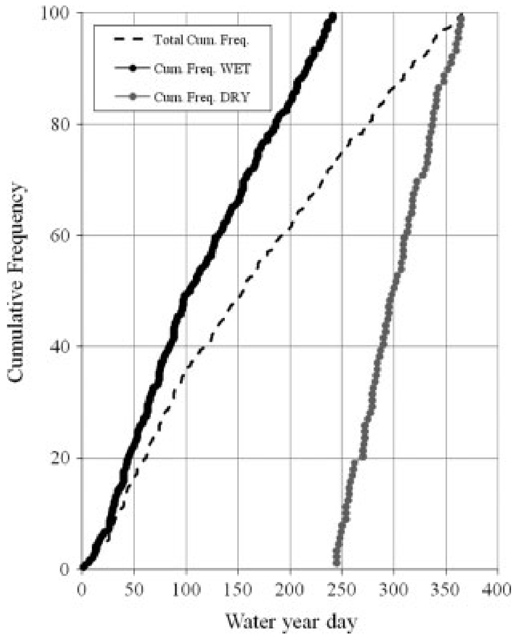

Figure 12. Cumulative frequencies of BSEs forecasted from 30 years of historical rainfall records

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 that are of greatest significance to larval releases, and empirically, at least these still appear to follow an exponential distribution (Figure 6). Clustering of events would tend to produce a greater frequency of both shorter (within clusters) and longer (between clusters) inter-arrival times (such as that shown in Figure 12), which still could be modelled by an exponential like a gamma (Evans *et al*., 1993) or generalized Pareto distribution (Waylen and Laporte, 1999).

A notable feature of the relationship between larvae production and stage (Figure 4) 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 larvae 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 and Laporte, 1999). The probability distribution of larva catches has also been shown to follow an exponential distribution. Both flood size above threshold and larvae densities are independent under the assumption that the latter is a function of the length of the time since the last BSE (Figure 14) rather than the size of the flood. Considering both variables, a joint probability distribution results that exhibits a pattern similar to that observed when stages exceed 5 m (Figures 4 and 14).

In terms of biological processes, we assume that catfish spawning occurs uniformly in time and space across the

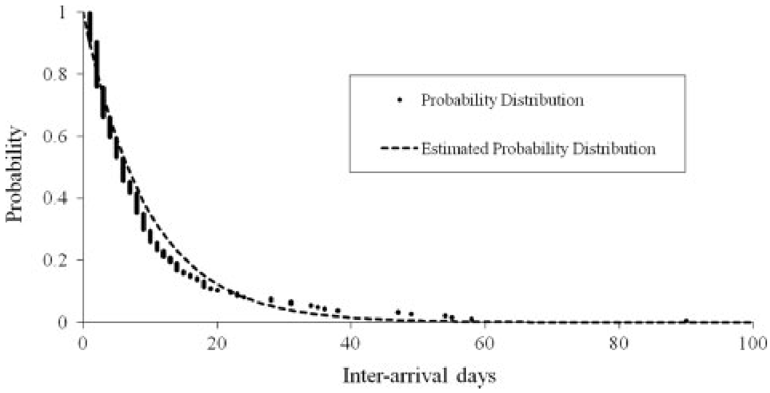

Figure 13. Probability distribution of inter-arrival times between forecasted BSEs in Puerto Maldonado

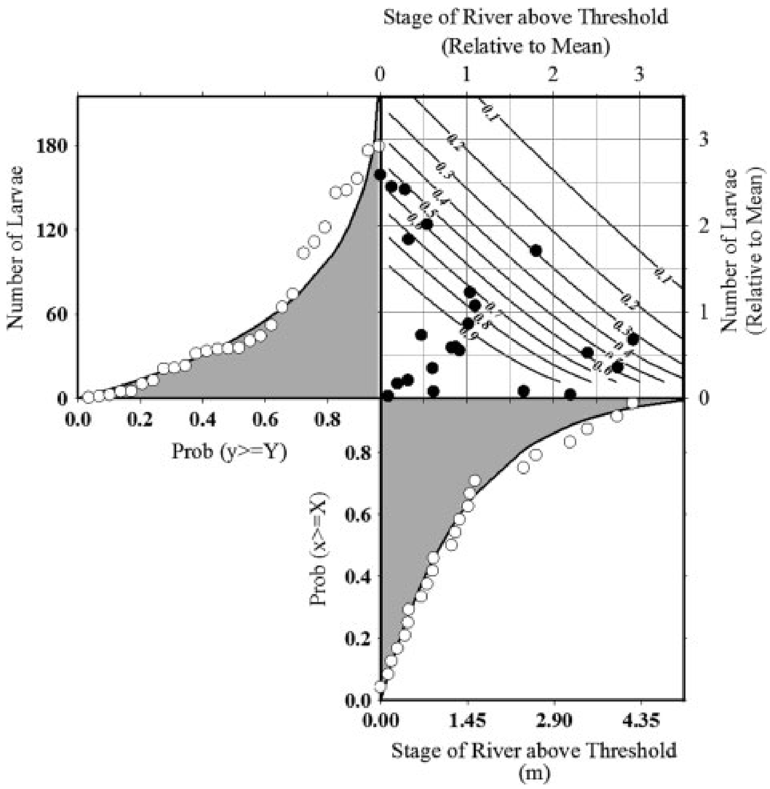

Figure 14. Joint probability distribution of larva catches when surpassing the threshold river level

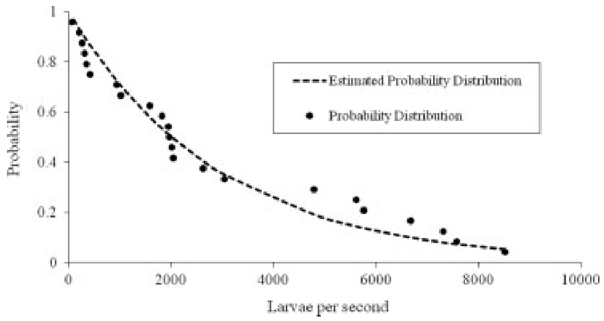

Figure 15. Probability distribution of estimated larvae exported and passing at Puerto Maldonado (average = 2902 larvae per second)

Madre de Dios Basin once flooding season starts (Goulding *et al.*, 2003b). 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) $\times$ estimated discharge (m^3 per second)] $\times$ 50^{-1}} are themselves exponentially distributed with a mean of 2902 per second (Figure 15). This figure results from an observed average inter-arrival time of approximately 7 days (4 average days + 3 days of arbitrary minimum separation) (Figure 6), yielding an approximate basin-wide spawning rate of 414 larvae per second per day (2902 larvae per second per 7 days), which is about half of the observed 'background' levels of larva counts when no BSE are occurring.

Observed data hint at a decline in this rate over the rainy season (Figure 3), 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 a far more complex '2-way-gate' function of BSEs, not only exporting larvae from upstream but also enabling mature adults to migrate upstream to the spawning areas. The first BSE of a year would therefore initiate upstream migration but release no larvae. For instance, in Figure 3, the rising stage experienced in week 39 (23 September 2006) is not associated with any larval release beyond background levels, while the next high stage of week 43 (21 October 2006) produced the highest larval density of the year. No previous research has related adult catfishes ready for spawning and larvae being delivered during the same wet period. In the future, this information should be acquired to confirm or deny the rate of larvae production assumed within the model.

The 20 observed BSEs represent a small sample size upon which to estimate the parameters of the model. However, the larger sample provided by the estimation of potential BSEs from historical precipitation gives strong, validatory information. This approach is supported, from a geographical perspective, by the dominant control of the Andes on rainfall and annual hydrologic regime of the basin and, from a perspective of data, by the numerous historic daily precipitation records.

The 8- and 5-day periods of cumulative rainfall determined at Pilcopata and Quincemil can be interpreted in terms of distances to Puerto Maldonado and topography (Figure 1). From Pilcopata (900 m of elevation), 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 of elevation), 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 only 100 km above Puerto Maldonado. Unfortunately, no water level data from these two sites or any other headwater tributaries exist to provide PDS information closer to the spawning grounds.

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 (proportion correct and hit rate); however, approximately 30% of the forecasts (both BSE and no BSE) did not agree with the observed data (false alarm) (Table V). These figures most likely reflect (1) the sparse rainfall 'network' (two stations in 90 000 km^2, significant portions of which are mountainous), (2) the nonlinear nature of the hydrologic system and basin conditions, particularly dry antecedent conditions, which may not have converted this input into the anticipated flow, and (3) the over simplification of the proposed rainfall/runoff representation.

Cumulative frequencies of the dates of forecasted floods from the historical rainfall data (Figure 12) displayed a reasonably uniform distribution throughout most of the high flow 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 provide a reasonable estimate of hydrologic conditions in the basin. However, the frequency of these potential events did not exactly fit in a Poisson distribution (Figure 11). Despite this, their inter-arrival times during the rainy season, the controlling factor in the number of larvae exported, are exponentially distributed (Figure 13).

CONCLUSIONS

This simple stochastic model explains the characteristics of the complex, previously unmonitored, crucial relationship between larvae exported downstream to the lower Amazon Basin and the stage of the Madre de Dios River. Physically, it is well based in the hydro-climatology 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, with a sound theoretical basis in statistics. The numbers of potential BSEs are equally likely to occur throughout 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 and Laporte, 1999; Rémillard *et al*., 2004). The requirements of the model are fairly basic and appropriate for this part of the world, where data are sparse. They can, however, be combined in a variety of ways to produce results that appear to emulate a complex biohydrologic 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. A record of 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 to 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 prototype 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 modelling of the larvae required long-term flooding records, this limitation was surmounted using daily rainfall records, a more abundant hydrological surrogate in these regions, which performed reasonably well in forecasting the derived annual counts of BSEs. This association between meteorological conditions and aquatic biological responses should be included in experiment design for future research. External factors such as climate change and variability can thereby 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 the lowlands, complemented with the upstream adult migrations previously observed in the basin, confirmed the interconnectivity of the whole Amazon system. Survival of these catfish species depends on two key displacements during different phases of their life history, both of which are strongly related to flood timing and the connectivity of the complete system. Any changes to the flow regime or disruption on the connection of this river will not only put populations of these catfishes at risk but also influence the survival of other fish species depending on the lateral connection between river channel and adjacent floodplains. Consideration of the migration of catfish and other species needs to be incorporated into any environmental assessment of projects in the Amazon system, especially those related with the use of water resources. Dams and reservoirs have already altered the connectivity of large rivers in Africa, Asia, and Latin America with significant effects in migratory fish fauna and fisheries productivity (McCully, 2001; Poulsen *et al*. 2002; Dugan *et al*., 2010), similar effects are expected to occur after the natural flood regime is altered in the Amazon headwaters in Peru, now being designated by the central government as 'important region' for dam construction (Dourojeanni *et al*., 2009).

Finally, the simple framework of this stochastic model, well supported by hydro-climatological and biological concepts, can 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.

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