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RELATIONSHIP BETWEEN OVIPOSITION OF *Podocnemis unifilis* AND WATER LEVEL IN PERUVIAN AMAZONIAN FLOODPLAINS

RELACIÓN ENTRE OVIPOSICIÓN DE *Podocnemis unifilis* Y EL NIVEL DEL AGUA EN LLANURAS DE INUNDACIÓN DE LA AMAZONIA PERUANA

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William Santini^{1,5} and Jean Loup Guyot^{1,6}

Abstract

In the Amazon floodplains, hydrological variability plays a crucial role by shaping the habitat, offering shelter and feeding or breeding areas. During the dry season, some fresh water turtles such as the yellow-spotted turtle (*Podocnemis unifilis* Troschel, 1848) use the sand banks at point bar areas as breeding sites, which must be available in time for the start of oviposition. In this study, we used altimetry-derived water level data from radar satellites combined with in-situ hydrological measurements to evaluate water level variations and relate them to oviposition starting dates (2003-2012) from Pacaya-Samiria National Reserve, Peru. Synchronous hydrological behavior was found between the major river stems (Ucayali and Marañón) and the inner rivers (Pacaya and Samiria), thus enabling the utilization of water level in the main river stem to correlate with oviposition in the inner rivers. Mean oviposition date was July 23rd with selection of a narrow water level range (92 masl $\pm$ 0.9 SD). Consistent shifts towards early/late oviposition were found for years with early/late dry season onset. Extreme biological shifts in terms of oviposition date onset, were identified for specific years (2004, 2010 and 2011) mainly for the extreme dry year of 2010.

Key words: hydrology, water level, radar altimetry, *Podocnemis*, oviposition, Amazon Basin.

Resumen

En las llanuras de inundación amazónicas, la variabilidad hidrológica desempeña una función esencial en dar forma al hábitat, ofreciendo refugio y zonas de alimentación o reproducción. Durante la estación seca, algunas tortugas de agua dulce, como la Taricaya (*Podocnemis unifilis* Troschel, 1848), utilizan los bancos de arena en las zonas de barras puntuales como lugares de reproducción, que deben estar disponibles temporalmente para el inicio de la oviposición. En este estudio, utilizamos datos de nivel de agua derivados de la altimetría de satélites de radar combinados con mediciones hidrológicas *in situ* para evaluar las variaciones del nivel del agua y relacionarlas con fechas de inicio de la oviposición (2003-2012) en la Reserva Nacional Pacaya-Samiria, Perú. Se encontró un comportamiento hidrológico sincronizado entre los ríos principales (Ucayali y Marañón) y los ríos interiores (Pacaya y Samiria), lo que permitió la utilización del nivel del agua de los ríos Ucayali y Marañón para correlacionarla con la oviposición en los ríos interiores. La fecha media de oviposición fue el 23 de julio, que corresponde a un rango estrecho de nivel de agua (92 msnm $\pm$ 0.9 SD). Se encontraron variaciones consistentes de la oviposición temprana/tardía durante años con el inicio de la estación seca temprana/tardía. Se identificaron cambios biológicos extremos, en términos del inicio de la fecha de oviposición, para años específicos (2004, 2010 y 2011), principalmente para el año de extrema sequía (2010).

Palabras clave: hidrología, nivel de agua, altimetría de radar, *Podocnemis*, oviposición, Cuenca Amazónica.

Introduction

Seasonal patterns among living organisms are normally aligned with the best environmental conditions in the habitat to assure that energy demanding activities (reproduction, feeding, hibernation, flowering, etc.) take place during the best favourable conditions (Visser & Both, 2005). This temporal dimension of natural history is called phenology (Forrest & Miller-Rushing, 2010). There are different interactions between abiotic parameters and phenology depending on the latitudinal location. In temperate regions, phenology is more influenced by temperature and/or photoperiodism (Edge *et al.*, 2017),

whereas in tropical latitudes, precipitation is more likely to play a significant role in phenology than temperature (Forrest & Miller-Rushing, 2010; Junk & Piedade, 2011). For fresh water organisms, biological processes are more influenced by the seasonal timing imposed by hydrological cycles such as the dry and wet season (Junk & Piedade, 2011). To explain the relation between hydrological cycle and biological processes in Amazon Basin, Junk *et al.* (1989) proposed the River Flood Pulse Concept, that is based on hydrological considerations, which considers the river and its floodplains as an indivisible unit. During an annual flood, floodplains oscillate between terrestrial and

aquatic environments, with a degree of connection with the main stem depending on water level. The complex relationship between hydrological cycles and biological processes requires the understanding of hydrological functioning in the local floodplain rivers. Unfortunately, in-situ monitoring in remote areas is uncommon, especially in protected areas far from human influence. Moreover, main and tributary rivers in a floodplain become spatially connected during periods of higher water level and potential synchronicity between small tributaries and major rivers must be assessed. In this context, spatial altimetry is an important tool to assess inland waters hydrology (Maillard & Calmant, 2013). Satellite altimetry measurements enable hydrologists to measure basin-wide of discharge, storage and water level, which are much easier than monitoring changes from in situ gauge networks. Water level time series with decimeter accuracy were obtained for Amazonian wetlands (Getirana et al., 2009; Silva et al., 2010). Turtles' species from the *Podocnemis* genus offer an interesting opportunity to study the complex relationship between hydrology and biological process, such as reproductive phenology, given that oviposition and incubation take advantage of the sandbanks appearing in the point bar areas during the dry season (Soini, 1996). Although oviposition and its linkage with the dry season is widely documented (Soini & Cópula, 1980; Carvajal et al., 2011; Yapu-Alcázar et al., 2018), few studies identify particular river stages or water level thresholds related to the onset of, and peaks in oviposition. Unravelling the role of hydrology on biotic processes is crucial to develop correct strategies to management and conservation, particularly in *Podocnemis* sp. which provides an important source of protein for human population during the dry season (Conway-Gómez, 2008; Pantoja-Lima et al., 2014) and improves the economic well-being in Peru (Gockel & Gray, 2009; Harju et al., 2018).

The aim of this study was to use spatial altimetry to evaluate the potential hydrological synchronicity between the river's main stem and its floodplain, and determine the relationship between water level variability in wetlands with *Podocnemis unifilis* Troschel, 1848 oviposition timing variations.

Methods

Study Area

This study was conducted in the Peruvian Amazon floodplains, focusing in two convergent river-floodplain systems: the Ucayali River and its plain tributary Pacaya, and the Marañon River and its plain tributary Samiria. This area is located at the Pacaya-Samiria National Reserve (PSNR) between 4°26'15"S 73°25'57"W and 6°21'26"S 75°32'01"W (Figure 1), where since 1979, due to repopulation efforts, the *P. unifilis* is currently abundant in places where management programs have been implemented.

Although *P. unifilis* is currently categorized as vulnerable by national legislation, the recovery of the species is evident in the basins where it has been managed sustainably. The management and conservation of *P. unifilis*, in the last two decades has been considered by experts as one of the most successful experiences in the recovery of endangered species. The number of hatchlings released has been increasing continuously and significantly since 1995. The participation of local communities in the conservation program is of great importance, demonstrating that the model of productive and commercial conservation, with clear benefits for local populations, has been a success.

Annual temperature ranges between 20.1 and 33.1 °C (Rodríguez et al., 1995). In the plain, precipitation reaches values of 2 744 mm·yr⁻¹ in the Ucayali at Requena gauge station (REQ, 5°02'28" S, 73°50'24" W) (HYBAM, 2018), and 2 817 mm·yr⁻¹ in the Marañon at Santa Rita de Castilla meteorological station (4°30'48" S, 73°54'24" W). The dry season occurs between June and the first days of October (Soini & de Soini, 1986).

Hydrology Data Sources

To assess water level in small rivers, we made use of spatial altimetry techniques retrieving data from different satellite missions. A set of altimetry-derived water level data retrieved from virtual stations in inner rivers (Pacaya and Samiria) vs. *in situ* hydrological data (2000-2017) in the major rivers (Ucayali and Marañon), was used to assess if behaviour in the inner rivers was similar to major rivers. *In situ* water level data were retrieved from the Critical Zone Observatory (CZO) – HYBAM database (HYBAM, 2018). Requena water level gauge station (REQ) is located in the Ucayali River downstream the river mouth of Pacaya River, whereas San Regis (SRG) is located in Marañon River downstream Samiria River mouth (Figure 1). Altimetry-derived water level data were obtained from different space agencies: Collecte Localisation Satellites (CLS, 2018) for Jason-2, Copernicus Open Access Hub de l'ESA (European Spatial Agency) (ESA, (2018) for Sentinel-3A, Satellite Data and Services Center (AVISO+, (2018) for Saral and Jason-3, Center for Topographic studies of the Ocean and Hydrosphere (CTOH, (2018) for ENVISAT. Three families of altimetry satellites (Figure 1) were used to define a set of virtual stations: Jason-2 and Jason-3 with a return cycle of 10 days, ENVISAT and Saral with a cycle of 35 days and Sentinel-3A with a return cycle of 27 days. A total of four virtual stations for Pacaya River, and seven for Samiria River, were spatially distributed so that spatial representativeness was covered (Table 1). For Samiria River, five out of the seven virtual stations happened to be located close together at the same geographical point (S3A331Sami03, env422sami03, env551sami03, srl422sami03, srl551sami03). This "multistation" was

used to obtain temporal representativeness (Aug 2002 – May 2018). More detailed information on altimetry can be found in Fu & Cazenave (2001).

Correlation graphs, with correlation coefficients (r^2), were constructed using the daily water level z-scored transformed values to account for normality and comparativeness. Firstly, an upstream-downstream spatial comparison where each virtual station in the tributary inner river was compared with the in-situ gauge station downstream in the major river. Secondly, since rivers in our study area run from west to east, comparisons between virtual stations in north/south transects (one in the inner river vs. one in the major river) were carried out to assess the influence of water lateral exchanges between the major and the inner river on water level variability. Selection of pairs was subjected to the conditions they were located either in the same satellite pathway or at similar geographical longitudinal location. Fisher statistics (F), degrees of freedom (df) and p values were also calculated.

Oviposition data sources of the freshwater turtle *Podocnemis unifilis*

P. unifilis is a medium sized freshwater turtle with a mean weight of 8.5 kg and a carapace length between 33 and 48 cm. The species reaches sexual maturity at the age of 5 or 6 years, laying eggs between July and August in our study area. The incubation time in Peru is between 55-70 days and the mean clutch size is 34.5 (Soini & Cópula, 1980; Soini & de Soini, 1986; Soini, 1996).

Daily oviposition historical data (2003-2012) of *P. unifilis* were provided by the natural resource management programme running at the PSNR (more information in Harju *et al.*, 2018). Every record corresponds to a single nest, for which the oviposition date, number of eggs, habitat substrate type, river margin and local name of the place is recorded. A set of more than 53 795 nest records were checked for data quality and reliability, and then aggregated per day to obtain daily amount of oviposition. These data were merged with the daily water level, discharge and precipitation data above mentioned and were treated using Fisher statistic. The collect effort (CE) that is the number of nests per kilometer per person was also estimated.

Oviposition data analysis

To assess the onset of oviposition for the population, we identified the Julian day at which 5% of the total nesting activity was complete (Prodon *et al.*, 2017; Wheeler *et al.*, 2018). Using a 5% threshold assures that oviposition onset reflects the population level oviposition behaviour, and is not affected by particular individuals (Palmer *et al.*, 2017). Median oviposition date was used as a thick mark against which a measure of deviance (shifts) was calculated using the absolute deviation around the median. This method has been suggested when the purpose is to detect outliers or extreme values, in this case called “extreme biological

responses” (Palmer *et al.*, 2017). The absolute deviation around the mean is defined as the median value plus two median absolute deviations (MAD). MAD is the median of the absolute differences between each data and the sample median, multiplied by a factor “b” (Formula 1).

$$MAD = b \times M_i (|x_i - M_j(x_j)|)$$

Formula 1.

Where:

x_i is the observation;

$M_j(x_j)$ is the sample median value;

M_i is the median of the absolute deviation.

Factor “b” is a constant associated to the assumption of normality and takes the value of 1.4826 (Leys *et al.*, 2013). For this work, normality was tested for all oviposition starting dates converted as Julian days.

Results

Hydrological analysis

Water levels for REQ and SRG stations are presented in Figure 2, from January 2000 until December 2017. The amplitude of the water level was larger during this period at REQ station (Ucayali) than at SRG (Marañon) (10 ± 0.5 m for REQ, 8.5 ± 0.5 m for SRG). The mean annual water level was 95 meters above sea level (masl) for REQ and 93 masl for SRG. The highest amplitude ranges were registered during 2011 and 2012 (11.9 and 11.4 for REQ, 10.4 and 10.5 for SRG, respectively). Water levels reached the lowest values for 2005 (88.6 masl for REQ and 86.9 masl for SRG) and 2010 (87.7 masl for REQ and 86.7 masl for SRG). Highest values were registered for SRG during 2012 (98.1 masl) and for REQ during 2000 (100.3 masl) and 2012 (100.0 masl). When comparing altimetry-derived data with *in situ* water level measures, a synchronic behaviour was found along time.

In Figure 3, altimetry-derived data from Jason-2 in Samiria River follows the same temporal variation of SRG located 210 km far away from the virtual station in the Marañon Basin. Similar results were obtained for virtual station S3A331_Samiria02 and the Multistation in Samiria River located upstream from SRG, with R-squared values of 0.9 and 0.75, respectively (Table 2). Synchronic behaviour was also found for Ucayali Basin between the four virtual stations in Pacaya river vs. REQ *in situ* gauging station in Ucayali River. These virtual stations (JA3191Pac_01, JA3191Paca01, S3A331Paca03, S3A310Paca04) obtained correlation values ranging between 0.84-0.93 (Table 2).

The set of north/south transects also showed synchronic behaviour for Ucayali and Marañon basins. Only one transect from Sentinel 3 was available for Marañon Basin, with correlation coefficient values of

0.78 and 0.83 (Table 2). For Ucayali Basin three transects were available, two Sentinel 3 tracks and one Jason 2 tracks. Therefore, comparisons were made between Pacaya and Puinahua Channel, and Pacaya vs. Ucayali River. These comparisons also showed water level synchronicity between virtual stations with R squared values ranging from 0.83 to 0.94.

Oviposition analysis

During 10 years of oviposition data (2003 – 2012), female *P. unifilis* nested in this area between June 22th and September 30th with mean oviposition duration of 61.5 days $\pm$ 11.7 SD for both basins (Table 3). Oviposition onset did not occur below 89 masl or above 96 masl with a constant preference of water level values around 92-93 masl (Figure 4). Across both basins and along the years the 5% of the total oviposition activity occurs at July 23th (Julian day 204) as median oviposition starting date and a mean water level of 91.8 masl $\pm$ 0.8 SD. Oviposition starting dates showed a normal distribution ($W = 0.9649$, $p: 0.497$) and hence, median absolute deviation (MAD) was set to 6.7 days. Therefore, extreme biological responses (extreme shifts towards early or late oviposition) are the oviposition starting dates 13 days far from the median oviposition date.

For Pacaya Basin years with an early start were between 2005 and 2008, and late start were registered for 2003, 2004, 2009, 2011, 2012. In Samiria Basin, years with an early start were 2005 – 2010, 2012 and a later start was registered for 2003, 2004 and 2009. Extreme biological responses were registered for 2011 in Pacaya Basin (15 days later), and 2010 for Samiria Basin (21 days earlier). A marginal extreme value of 12 days later was registered for Pacaya Basin during 2004.

Discussion

River floodplain hydrological functioning

Hydrological synchronicity in the study area was tested using altimetry-derived water level from virtual stations vs. *in-situ* water level gauge station. Synchronic hydrological functioning was found between tributaries in the floodplain, and Ucayali and Marañon rivers (Figure 3). This synchronicity might reflect a quasi-permanent water lateral exchange. Similar hydrological behaviour was observed in other Amazonian floodplain systems (Bonnet *et al.*, 2008; Alsdorf *et al.*, 2010; Moreira-Turcq *et al.*, 2013), where contribution from the main river channel to the floodplain is between 77 and 93%; while local runoff, direct precipitation and groundwater contributes with the remaining percentage (Alsdorf *et al.*, 2010; Rudorff *et al.*, 2014). Furthermore, the water exchanges between the floodplain and the main river are mainly controlled by the water levels in the main channel. Upstream-downstream comparisons in the upper Amazon Basin are especially relevant, since the majority of studies using spatial altimetry have been carried out in the lower and middle Amazon Basin,

where channel width is between 3 – 7 km. Here, channel widths range from 1 - 2.5 km for Marañon and between 0.5 – 1.3 km for Ucayali River, and Pacaya and Samiria tributaries widths ranges between 15 m (upper basin) and 130 m (river mouth, satellite image measurements). Lateral exchange influences not only water fluxes but also sediment and organic matter transportation (Moreira-Turcq *et al.*, 2013). Sediment input from the main river stem during the high-water periods, influences grain size distribution, dimensions and morphology of oviposition areas in the inner rivers during the dry season (Ferreira Júnior & Castro, 2003). This interaction is important for the turtle species under study since oviposition areas may be affected when extreme changes in water level and discharge occur/or are absent.

Relation hydrology-oviposition and extreme hydrological events

In our study, oviposition occurred at a mean water level value of 92 masl $\pm$ 0.8 SD (Figure 4 and Table 3) with a mean oviposition duration of 61.5 days $\pm$ 11.7 SD (Table 3). A comparison between the Julian day at which water level reaches 92 masl with the Julian day of oviposition onset at 5% was carried out (Figure 5). Points located very close to a 1:1 line illustrate the relationship, whereas points above this line but below the critical value of July 23th (Julian day 204) are the years with early dry season onset where turtle population made an attempt to follow these early shifts but did not succeed to be close to the 1:1 line. On the other hand, points located below the 1:1 line and later than July 23th are years with late dry season onset. In this case, points below the 1:1 reflect the attempts of turtle populations to follow these shifts. Within these shifts, there are extreme biological events that cause values to exceed the median oviposition date (July 23th) plus two median absolute deviations (13 days). Those are 2011 and a marginal value for 2004 for Pacaya Basin (15 and 12 days later respectively), and 2010 for Samiria Basin with 21 days earlier.

P. unifilis shares oviposition habitats with *P. expansa* the largest fresh water turtle in Amazonian rivers. While *P. unifilis* starts oviposition earlier and lay eggs in the middle and lower parts of the point bar, *P. expansa* starts laying eggs later using the upper areas (Soini & de Soini, 1986); thus, overlap in nest placement is rare (Ferreira Júnior & Castro, 2003). Other authors find that height of nest above water level is an important variable among all species of *Podocnemis* genus (Escalona & Fa, 1998; Pezzutti & Vogt, 1999). Both turtles have temperature-dependent sex determination (Ferreira & Castro, 2010), pointing to the importance of nest site on the resulting sex ratios and species preservation. Where incubation success is highly determined by the ambient temperature. (Rodrigues & Lima-Ribeiro). The river dynamics also significantly affect the hatching success (Leao *et al.*, 2019).

In general, oviposition starting dates have followed consistently early and late start of the dry season. Years with an early beginning of the dry season were 2005, 2006 and 2007 in Tamshiyacu (Ronchail *et al.*, 2018), and shifts towards early oviposition were identified from 2005 to 2008 for both basins. Samiria Basin registered two more years (2010 and 2012) with shifts to earlier oviposition (21 and 10 days, respectively). Furthermore, our time series contains two extreme dry years 2005 and 2010 (Espinoza *et al.*, 2011), where early oviposition starting dates occurred. This illustrates a consistent biological response facing not only dry years, but also early beginning of the dry season. Literature refers similar shifts towards earlier oviposition onset for 1988 (Soini & Correa, 1989), a year with an early beginning of the dry season (Ronchail *et al.*, 2018). Years with a late beginning of the dry season were 2004 and 2009 (Ronchail *et al.*, 2018) and in this study shifts towards later oviposition onset were 2003, 2004, 2009 and 2011 for both basins. Year 2011 showed the most important delay of 16 days for Pacaya Basin (Figure 4). This year has been catalogued as a transitional year between a dry (2010) and a flooded (2012) year (Espinoza *et al.*, 2012), where water level values peaked up to almost the same values obtained for 2012. As a consequence, the water receding process took longer reaching the critical value of 92 masl by the end of July, thus in accordance with oviposition onset delay. Although, 2011 was not an extreme year, a focus on the dry season explains this result.

Although these temporal shifts may be considered a good trait facing extreme events, extreme shifts towards late oviposition could also pose a threat for the population. Since incubation period requires a time window of 55 – 70 days, extreme delays in oviposition onset may be risky when the next rainy season starts earlier. Considering that mean oviposition duration for our database was 61.5 days $\pm$ 11.7 SD (n = 53 795 nests), 15 days of delay during 2011 represents between 22-32% of the oviposition period, thus increasing inundation risk at the end of incubation. Nest loss via inundation reached between 28 – 50% during 1980 and 1982, in the same location of this study (Soini & Soini, 1982). It has been suggested that if extreme floods return with a frequency of less than 10 years, population decline is likely to occur in few decades (Véliz Rosas, 2012). For *P. expansa* in Trombetas River (Brazil) an increase of 137 cm of water height would result in 50% of mortality (Eisemberg *et al.*, 2016). Additionally, when oviposition onset for *P. unifilis* is delayed, increased competition for space may occur due to an overlap in oviposition time with *P. expansa* which breeds later (Soini & de Soini, 1986).

Extreme hydrological events can also affect habitat quality. This was the case for 2010 (oviposition started 21 days earlier for Samiria Basin) when park rangers in the study area referred that *P. unifilis* were laying eggs

in sites covered with vegetation. Vegetation has shading effects which potentially cause poor embryological development or bias in sex ratios (Soini & Soini, 1982; Janzen, 1994). Morphology, topography and grain size in the beach are also important for nest site selection, and erosion during the flood period is an important driver shaping breeding areas with good habitat quality (Ferreira Júnior & Castro, 2003; Ferreira Júnior & Castro, 2010). Natural and anthropogenic impacts on nesting areas can negatively affect the reproductive rate of populations (Quintana Garcia, 2018). For conservation purposes, it is important to protect the nesting beaches where the species nests during the dry season, but also the flooded forest zones that are heavily used during the rainy season. (De Leão *et al.*, 2019). If the habitat offers low quality areas, productivity can also be affected. In fact, during 2010 the numbers of nests per km and per person (CE) were very low (Table 3). In this water level time series, the frequency of extreme events is higher during the last 20 years and we can identify constant shifts on the direction of change from drought to flooding and vice versa (eg. an unprecedentedly abrupt transition from the extreme drought in September 2010 to one of the four highest discharges in April 2011) (Espinoza *et al.*, 2011; 2012). Several studies have shown an increase in the frequency and intensity of extreme hydrological events, such as droughts and floods, in the Amazon Basin during the last decades (Marengo & Espinoza, 2016). We can expect that in the future, these extreme events will increase even more, as is already being observed, and that organisms that have their development directly dependent on environmental conditions (e.g. temperature and water level) will be more likely to be affected in a way that may be critical for the preservation of the species. *P. unifilis* is known for its nest-site fidelity but under adverse environmental conditions a migration to other nesting sites can be expected (Naveda-Rodriguez *et al.*, 2018). Winter *et al.* (2016) demonstrated in an extensive review paper that climate change has a strong impact on reptile and amphibian population declines.

Conclusions

This work shows the existence of a synchronous hydrological functioning between the inner rivers (Pacaya and Samiria) and the major rivers (Ucayali and Marañón). Consequently, this allows us to use the *in situ* data set as a proxy of the hydrological behaviour of small rivers. Furthermore, *Podocnemis unifilis* start laying eggs around 92 masl, show oviposition responses in accordance with dry season onset changes, and extreme biological responses for at least one extreme dry year (2010).

Synchronicity and water lateral exchange in the floodplains are topics which are not currently included in the environmental impact assessments of large infrastructure projects. Currently, dam construction in

the upper Mara  n Basin, and navigability in the Amazon waterway are major projects fostered by the government. Possible impacts like long-distance discharge regulation, river's course modifications and removal of bed sediments, have not been discussed in relation to river synchronicity found in this work and the subsequent biological impacts. In that sense, research on this topic and its relation with biota, becomes important to assess future impacts in one of the most important Peruvian wetlands and Ramsar site.

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Literature cited

Alsdorf D., Han S.C., Bates P. & Melack J. 2010. Seasonal water storage on the Amazon floodplain measured from satellites. *Remote Sensing of Environment*, 114(11): 2448–2456. DOI: 10.1016/j.rse.2010.05.020.

AVISO (Archiving, Validation and Interpretation of Oceanographic Satellite Data). 2018. Consulted between January to August 2018 directly from: <https://www.aviso.altimetry.fr/en/data/data-access/ftp.html>.

Bonnet M.P., Barroux G., Martinez J.M., Seyler F., Moreira-Turcq P., Cochonneau G., Melack J., Boaventura G., Maurice-Bourgoin L., Leon J.G., Roux E., Camant S., Kosut P., Guyot J.L. & Seyler P. 2008. Floodplain hydrology in an Amazon floodplain lake (Lago Grande de Curuai). *Journal of Hydrology*, 349(1-2): 18–30. DOI: 10.1016/j.jhydrol.2007.10.055.

Carvajal P., Miranda G. & Wallace R. 2011. Par  metros reproductivos de *Podocnemis unifilis* en el R  o Beni, Bolivia. *Revista Boliviana de Ecolog  a y Conservaci  n Ambiental*, 29: 23-32. <http://www.cesip.org.bo/rebeca/index.php/rebeca/article/view/9>.

CLS (Collecte Localisation Satellite). 2018. <https://www.cls.fr/>. Consulted between January to August 2018 directly from: <ftp://ftpsedr.cls.fr/pub/oceano/pistach/J2/IGDR/hydro/>.

Conway-G  mez K. 2008. Market integration, perceived wealth and household consumption of river turtles (*Podocnemis* spp.) in eastern lowland Bolivia. *Journal of Latin American Geography*, 7(1): 85–108. <https://www.jstor.org/stable/25765200>.

CTOH (**Error! Referencia de hiperv  nculo no v  lida**. Center for Topographic studies of the Ocean and Hydrosphere). 2018. Consulted between January to August 2018 from: <http://ctoh.legos.obs-mip.fr/data/offline-data-request>.

De Le  o S.P., Famelli S. & Vogt R.C. 2019. Home Range of Yellow-Spotted Amazon River Turtles (*Podocnemis unifilis*) (Testudines: Podocnemididae) in the Trombetas River Biological Reserve, Para  , Brazil. *Chelonian Conservation and Biology*, 18(1): 10-18 DOI: 10.2744/CCB-1273.1.

Edge C.B., Rollinson N., Brooks R.J., Congdon J.D., Iverson J.B., Janzen F.J. & Litzgus J.D. 2017. Phenotypic plasticity of nest timing in a post-glacial landscape: how do reptiles adapt to seasonal time constraints? *Ecology*, 98(2): 512-524. <https://doi.org/10.1002/ecy.1665>.

Eisemberg C.C., Machado Balestra R.A., Famelli S., Pereira F.F., Bernardes V.C. & Vogt R.C. 2016. Vulnerability of Giant South American Turtle (*Podocnemis expansa*) nesting habitat to climate-change-induced alterations to fluvial cycles. *Tropical Conservation Science*, 9(4): 1940082916667139. DOI: 10.1177/1940082916667139.

ESA. 2018. Copernicus Open Access Hub. ESA (European Spatial Agency). Consulted between January and August 2018 from: <https://scihub.copernicus.eu/dhus>.

Escalona T. & Fa J.E. 1998. Survival of nests of the terecay turtle (*Podocnemis unifilis*) in the Nichare-Tawadu Rivers, Venezuela. *Journal of Zoology*, 244(2): 303–312. DOI: 10.1111/j.1469-7998.1998.tb00034.x.

Espinoza J.C., Ronchail J., Guyot J.L., Junquas C., Drapeau G., Martinez J.M., Santini, W., Vauchel P., Lavado W., Ordonez J. & Espinoza R. 2012. From drought to flooding: understanding the abrupt 2010–11 hydrological annual cycle in the Amazonas River and tributaries. *Environmental Research Letters*, 7(2): 024008. DOI: 10.1088/1748-9326/7/2/024008.

Espinoza J.C., Ronchail J., Guyot J.L., Junquas C., Vauchel P., Lavado W., Drapeau G. & Pomposa R. 2011. Climate variability and extreme drought in the upper Solim  es River (western Amazon Basin): Understanding the exceptional 2010 drought. *Geophysical Research Letters*, 38(13): L13406. <https://agupubs.onlinelibrary.wiley.com/doi/full/10.1029/2011GL047862>.

Ferreira J  nior P.D. & Castro P. de T.A. 2003. Geological control of *Podocnemis expansa* and *Podocnemis unifilis* nesting areas in Rio Java  s, Bananal Island, Brazil. *Acta Amazonica*, 33(3): 445-468. DOI: 10.1590/S0044-59672003000300010. <https://acta.inpa.gov.br/fasciculos/33-3/PDF/v33n3a10.pdf>.

Ferreira J  nior P.D. & Castro P. de T.A. 2010. Nesting ecology of *Podocnemis expansa* (Schweigger, 1812) and *Podocnemis unifilis* (Troschel, 1848) (Testudines, Podocnemididae) in the Java  s River, Brazil. *Braz. J. Biol.*, 70(1): 85-94. <https://doi.org/10.1590/s1519-69842010000100012>.

Forrest J. & Miller-Rushing A.J. 2010. Toward a synthetic understanding of the role of phenology in ecology and evolution. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1555): 3101–3112. DOI: 10.1098/rstb.2010.0145.

- Fu L.-L. & Cazenave A. 2001. Satellite Altimetry and Earth Sciences - A Handbook of Techniques and Applications. Elsevier Inc. <https://www.sciencedirect.com/bookseries/international-geophysics/vol/69>.
- Getirana A.C.V., Bonnet M.-P., Calmant S., Roux E., Rotunno Filho O.C. & Mansur W.J. 2009. Hydrological monitoring of poorly gauged basins based on rainfall-runoff modeling and spatial altimetry. *Journal of Hydrology*, 379(3-4): 205-219. DOI: 10.1016/j.jhydrol.2009.09.049.
- Gockel C.K. & Gray L.C. 2009. Integrating Conservation and Development in the Peruvian Amazon. *Ecology and Society*, 14(2): 11. <http://www.ecologyandsociety.org/vol14/iss2/art11/>.
- Harju E., Sirén A.H. & Salo M. 2018. Experiences from harvest-driven conservation: Management of Amazonian river turtles as a common-pool resource. *Ambio*, 47: 327-339. DOI: 10.1007/s13280-017-0943-5.
- HYBAM 2018. Amazon Basin water resources observation service. Consulted between October 2017 and August 2018. <http://www.ore-hybam.org>.
- Janzen F.J. 1994. Vegetational Cover Predicts the Sex Ratio of Hatchling Turtles in Natural Nests. *Ecology*, 75(6): 1593-1599. DOI: 10.2307/1939620.
- Junk W.J. & Piedade M.T.F. 2011. An Introduction to South American Wetland Forests: Distribution, Definitions and General Characterization. In: Junk W.J., Piedade M.T.F. & Wittmann F., Schöngart J. & Parolin P. (eds) Amazonian Floodplain Forests: Ecophysiology, Biodiversity and Sustainable Management. 3-25. Ecological Studies book series (ECOLSTUD, volume 210). Springer Netherlands, Dordrecht. DOI: https://doi.org/10.1007/978-90-481-8725-6_1.
- Junk W.J., Bayley P.B. & Sparks R.E. 1989. The flood-pulse concept in river-floodplain systems. In: Dodge D.P. (Ed.) Proceedings of the International Large River Symposium (LARS). Canadian Journal of Fisheries and Aquatic Sciences, Special Publication 106. 110-127. NRC research press, Ottawa. <https://waves-vagues.dfo-mpo.gc.ca/Library/111846.pdf>.
- Maillard P. & Calmant S. 2013. Spatial processing techniques for satellite altimetry applications in continental hydrology. In: Proceedings Volume 8887: Remote Sensing for Agriculture, Ecosystems, and Hydrology XV. SPIE REMOTE SENSING 23-26 SEPTEMBER 2013, Dresden, Germany. International Society for Optics and Photonics. DOI: <https://doi.org/10.1117/12.2028371>
- Marengo J.A. & Espinoza J.C. 2016. Extreme seasonal droughts and floods in Amazonia: causes, trends and impacts. *International Journal of Climatology*, 36(3): 1033-1050. DOI: 10.1002/joc.4420.
- Moreira-Turcq P., Bonnet M.-P., Amorim M., Bernardes M., Lagane C., Maurice L., Pérez M. & Seyler P. 2013. Seasonal variability in concentration, composition, age and fluxes of particulate organic carbon exchanged between the floodplain and Amazon River. *Global Biogeochemical Cycles*, 27(1): 119-130. DOI: 10.1002/gbc.20022.
- Naveda-Rodríguez A., Cueva R. & Zapata-Ríos G. 2018. Space Use of Yellow-Spotted River Turtles (*Podocnemis unifilis*) in Yasuni National Park, Ecuador. *Chelonian Conservation and Biology*, 17(1): 37-43. DOI: 10.2744/CCB-1270.1.
- Palmer G., Platts P.J., Brereton T., Chapman J.W., Dytham C., Fox R., Pearce-Higgins J.W., Roy D.B., Hill J.K. & Thomas C.D. 2017. Climate change, climatic variation and extreme biological responses. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 372(1723): 20160144. DOI: 10.1098/rstb.2016.0144.
- Pantoja-Lima J., Aride P.H., de Oliveira A.T., Félix-Silva D. Pezzuti J.C.B. & Rebêlo G.H. 2014. Chain of commercialization of *Podocnemis* spp. turtles (Testudines: Podocnemididae) in the Purus River, Amazon basin, Brazil: current status and perspectives. *Journal of Ethnobiology and Ethnomedicine*, 10: 8. DOI: 10.1186/1746-4269-10-8.
- Pezzuti J.C.B. & Vogt R.C. 1999. Nesting ecology of *Podocnemis sextuberculata* (Testudines, Pelomedusidae) in the Japurá River, Amazonas, Brazil. *Chelonian Conservation and Biology*, 3(3): 419-424. [https://chelonian.org/wp-content/uploads/file/CCB_Vol_3_Nos_1-4\(1998-2000\)/Pezzuti_and_Vogt_1999.pdf](https://chelonian.org/wp-content/uploads/file/CCB_Vol_3_Nos_1-4(1998-2000)/Pezzuti_and_Vogt_1999.pdf).
- Prodon R., Geniez P., Cheylan M., Devers F., Chuine I. & Besnard A. 2017. A reversal of the shift towards earlier spring phenology in several Mediterranean reptiles and amphibians during the 1998-2013 warming slowdown. *Global Change Biology*, 23(12): 5481-5491. DOI: 10.1111/gbc.13812.
- Quintana Garcia I. 2018. Pressão antropogênica afeta a nidificação de Tracajás (*Podocnemis unifilis*) na Amazônia Oriental? Dissertação de Mestrado, Programa de Pós-Graduação em Ecologia, do Instituto de Biociências da Universidade Federal do Rio Grande do Sul. Porto Alegre, BR-RS. URI: <http://hdl.handle.net/10183/187239>.
- Rodrigues J.F.M. & Lima-Ribeiro M.S. 2017. Predicting where species could go: climate is more important than dispersal for explaining the distribution of a South American turtle. *Hydrobiologia*, 808: 343-352. DOI: 10.1007/s10750-017-3436-4.
- Rodriguez F., Rodriguez M. & Vasquez P.G. 1995. Realidad y perspectivas: la Reserva Nacional Pacaya-Samiria. Analyse intégrée. Pronaturaleza. Lima. <http://cdc.lamolina.edu.pe/Descargas/ANPs/RealidadPerspectivaRNPS.html>.
- Ronchail J., Espinoza J.C., Drapeau G., Sabot M., Cochonneau G. & Schor T. 2018. The flood recession period in Western Amazonia and its variability during the 1985-2015 period. *Journal of Hydrology: Regional Studies*, 15: 16-30. DOI: 10.1016/j.ejrh.2017.11.008.
- Rudorff C.M., Melack J.M. & Bates P.D. 2014. Flooding dynamics on the lower Amazon floodplain: 2. Seasonal and interannual hydrological variability. *Water Resources Research*, 50(1): 635-649. DOI: 10.1002/2013WR014714.
- Silva J.S., Calmant S., Seyler F., Rotuno Filho O.C., Cochonneau G. & Mansour J.W. 2010. Water Levels in the Amazon Basin derived from the ERS-2 and Envisat Radar Altimetry Missions. *Remote Sensing of Environment*, 114(10): 2160-2181. DOI: 10.1016/j.rse.2010.04.020.
- Soini P. & Cópula M. 1980. Estudio, reproducción y manejo de los quelonios del género *Podocnemis* (charapa, cupiso y taricaya) en la cuenca del Pacaya. Reporte Pacaya - Samiria. Investigaciones en la Estación Biológica Cahuana 1979 - 1982. Centro de Datos para la Conservación. UNALM., Lima, Perú.

- Soini P. & Correa J. 1989. Estudio y manejo de quelonios acuáticos, 1987. Informe No 26. Reporte Pacaya-Samiria. Investigaciones en Cahuana 1994. 279–287.
- Soini P. & de Soini M. 1986. Un resumen comparativo de la ecología reproductiva de los quelonios acuáticos. Reporte Pacaya-Samiria: Investigaciones en la Estación Biológica Cahuana 1979 – 1994. 215–226. Centro de Datos para la Conservación. UNALM, Lima, Perú.
- Soini P. & Soini M. 1982. Ecología reproductiva de la taricaya (*Podocnemis unifilis*) y sus implicaciones en el manejo de la especie. Informe No 9. Reporte Pacaya-Samiria. Investigaciones en Cahuana 1994. 99–128.
- Soini P. 1996. Reproducción, abundancia y situación de quelonios acuáticos en la Reserva Nacional Pacaya Samiria, Perú. *Folia Amazónica*, 8(1): 145–162. DOI: 10.24841/fa.v8i1.310.
- Troschel. 1848. Amphibien. In: Schomburgk R. (Ausgeführt) Reisen in Britisch-Guiana in den Jahren 1840-1844. Theil 3. Veblagsbucihandlung Von J. J. Weber. Leipzig, 645-661. <https://doi.org/10.5962/bhl.title.109982>.
- Véliz Rosas C. 2012. Laying eggs early or late? Modelling oviposition plasticity in the fresh water turtle *Podocnemis unifilis* for different hydrological regimes. Mg.Sc. Thesis, Wageningen Univerity, Netherlands.
- Visser M.E. & Both C. 2005. Shifts in phenology due to global climate change: the need for a yardstick. *Proceedings of the Royal Society B: Biological Sciences*, 272(1581): 2561–2569. DOI: 10.1098/rspb.2005.3356.
- Wheeler C., Lind A., Welsh Jr. H.H. & Cummings A.K. 2018. Factors that Influence the Timing of Calling and Oviposition of a Lotic Frog in Northwestern California. *Journal of Herpetology*, 52(3): 289-298. <https://doi.org/10.1670/17-103>.
- Winter M., Fieldler W., Hochachka W.M., Koehncke A., Meiri S. & De la Riva I. 2016. Patterns and biases in climate change research on amphibians and reptiles: a systematic review. *Royal Society Open Science*, 3(9): 160158. DOI: 10.1098/rsos.160158.
- Yapu-Alcázar M., Tellería L., Vaca C., García J., R. Arias & Pacheco L.F. 2018. Bases para el manejo de la tortuga de río *Podocnemis unifilis* en la Reserva de la Biosfera Estación Biológica Beni, Bolivia. *Ecología en Bolivia*, 53(1): 52-72. <https://ecologiaenbolivia.com/documents/Yapuetal.5312018.pdf>. http://www.scielo.org.bo/pdf/reb/v53n1/v53n1_a07.pdf.

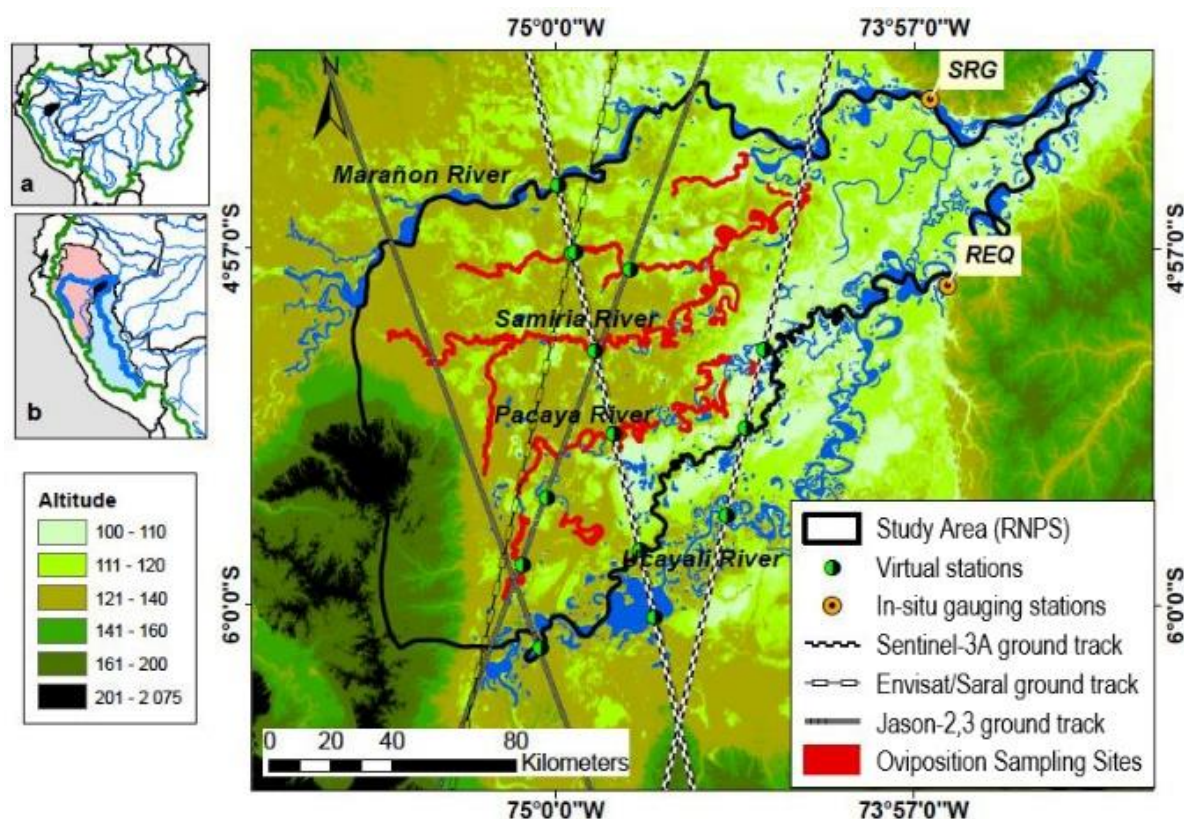


Figure 1. Study area with satellite trajectories location of virtual stations *in situ* water level gauge stations (SRG, REQ) in the Ucayali and Marañón rivers, and oviposition sampling areas. (Projection: GCS WGS 84 UTM 18S). (a) Amazon Basin in green border with the study area Pacaya Samiria National Reserve in black. (b) Peruvian Amazon Basin with the two major basins: Marañón Basin in pink with mainstem Marañón River and Ucayali Basin in blue with Ucayali River mainstem.

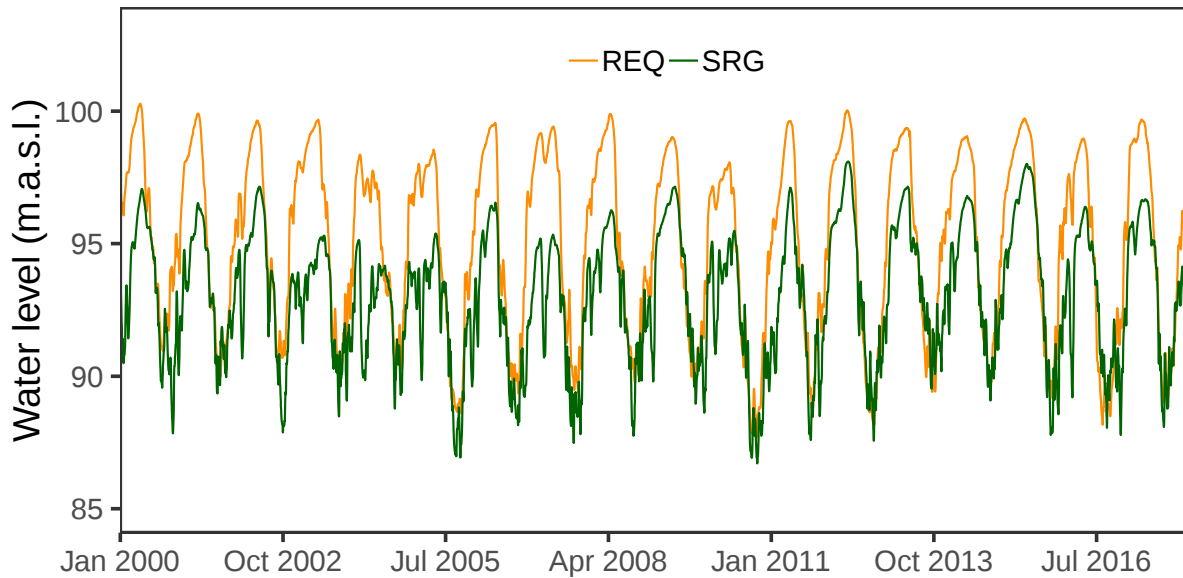


Figure 2. Water level time series for REQ (Ucayali River) and SRG (Maranon River) gauge stations from 2000 to 2017.

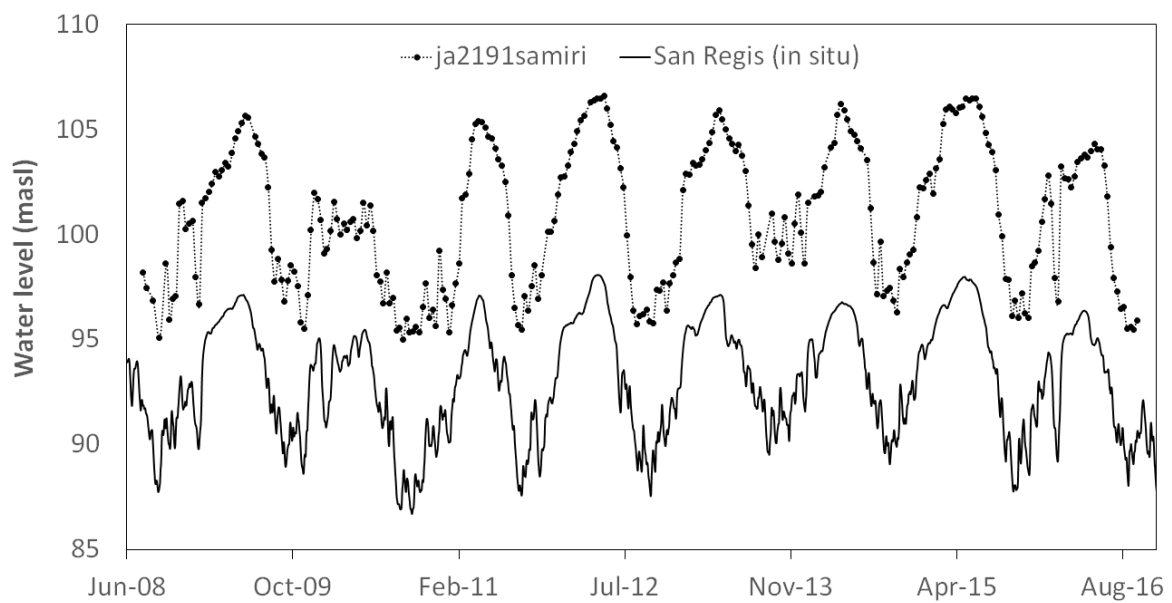


Figure 3. Temporal series of water level for SRG in-situ gauge station (black line) and water level obtained from virtual station JA2191samiri (Jason 2 pathway 191) in Samiria River (dashed line).

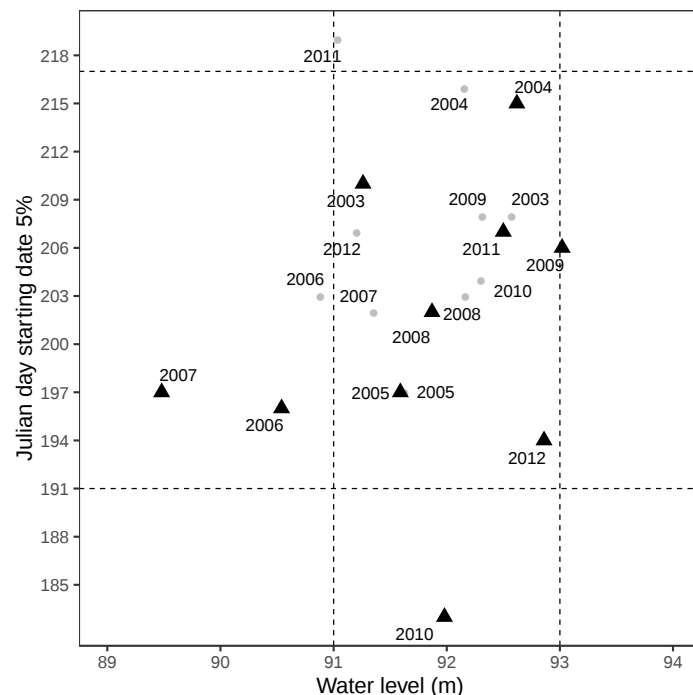


Figure 4. Water level values during the oviposition starting dates at which 5% of the total nesting activity is complete (Julian days). Pacaya Basin in grey and Samiria Basin in black. Vertical dashed lines represent one standard deviation for water level and horizontal dashed lines two median absolute deviations (12 days) for oviposition dates. Median oviposition date July 23th (Julian day 204).

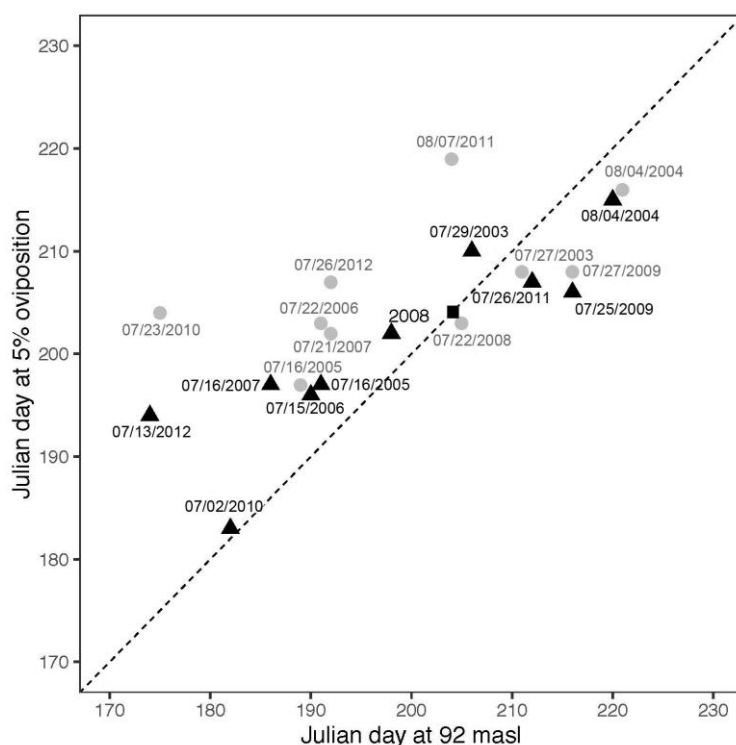


Figure 5. Julian day at which the 92 masl critical water level value occurs versus the Julian day of oviposition onset at 5% of nesting activity. Pacaya Basin in grey circles and Samiria Basin in black triangles. The black square on the line represents the Julian day 204.

Table 1. Virtual stations from different altimetric satellites and geographical coordinates used in this study.

River	Virtual Stations	Altimetric Satellite	Latitude	Longitude	Beginning date	End date	Interval (days)
Pacaya River	JA3191Pac_01	Jason-3	-5.8829	-75.0969	02/24/2016	07/26/2018	10
	JA3191Paca01	Jason-3	-5.6850	-75.0183	02/24/2016	04/18/2018	10
	S3A331Paca03	Sentinel-3A	-5.5002	-74.8296	06/25/2016	10/10/2018	27
	S3A310Paca04	Sentinel-3A	-5.2480	-74.3894	12/29/2016	04/29/2018	27
Puinahua Channel	S3A331Ucay02	Sentinel-3A	-5.8431	-74.7527	12/31/2016	12/17/2017	27
	S3A310Ucay04	Sentinel-3A	-5.4830	-74.4421	12/29/2016	12/15/2017	27
Ucayali River	JA3204JuOrel	Jason-3	-6.1305	-75.0439	02/25/2016	01/09/2018	10
	S3A331Ucay01	Sentinel-3A	-6.0390	-74.7094	12/31/2016	12/17/2017	27
	S3A310Ucay03	Sentinel-3A	-5.7366	-74.4983	12/29/2016	12/15/2017	27
Samiria River	S3A331Sami03	Sentinel-3A	-4.9681	-74.9470	12/31/2016	05/28/2018	27
	env422sami03	Envisat	-4.9663	-74.9530	08/06/2002	09/28/2010	35
	env551sami03	Envisat	-4.9640	-74.9423	08/11/2002	10/03/2010	35
	srl422sami03	Saral	-4.9663	-74.9530	03/28/2013	02/11/2016	35
	srl551sami03	Saral	-4.9640	-74.9423	04/02/2013	04/26/2016	35
	JA2191samiri	Jason-2	-5.0119	-74.7810	07/19/2008	09/30/2016	10
	S3A331sami02	Sentinel-3A	-5.2542	-74.8834	12/31/2016	05/28/2018	27
Marañon River	S3A331SanPed	Sentinel-3A	-4.7641	-74.9930	12/31/2016	05/28/2018	27

Data was retrieved between the beginning and end dates, with different time intervals.

Table 2. Correlation coefficients (r^2) from the z-scored correlations between virtual stations and *in situ* gauging stations (Upstream – Downstream), and among virtual stations (North/South transects). Values of Fisher statistics (F), degrees of freedom (df) and p values are provided.

		Paired station names	r2	F	df	p value
PACAYA RIVER	Upstream – Downstream	S3A310Paca04 vs. REQ	0.85	76.15	12	1.5E-06
		S3A331Paca03 vs. REQ	0.93	288.3	22	4.0E-14
		JA3191Paca01 vs. REQ	0.84	400.7	75	2.2E-16
		JA3191Pac_01 vs. REQ	0.85	429.7	75	2.2E-16
	North/South transects	S3A331Paca03 vs. S3A331Ucay02 (p)	0.90	113.7	11	3.9E-07
		S3A310Paca04 vs. S3A310Ucay04 (p)	0.83	55.28	10	2.2E-05
		JA3191Pac_01 vs. JA2_204_Jusante Orellana	0.89	257.6	31	2.2E-16
		S3A331Paca03 vs. S3A331Ucay01	0.94	192.2	12	9.5E-09
		S3A310Paca04 vs. S3A310Ucay03	0.88	85.96	11	1.6E-06
		Multistation vs. SRG	0.75	625.2	211	2.2E-16
		#JA2191SAMIRI vs. SRG	0.88	2131	290	2.2E-16
		#S3A_331_Samiria 02 vs. SRG	0.90	143.7	14	9.5E-09
SAMIRIA RIVER	Upstream – Downstream	#S3A331Sami02 vs. S3A331SanPed	0.83	81.53	16	1.1E-07
	North/South transects	#S3A331Sami03 vs. S3A331SanPed	0.78	57.28	15	1.7E-06

Table 3. Dates of oviposition at 5% with its correspondent water levels registered for the same day in REQ for Pacaya Basin and SRG for Samiria Basin. CE stands for collecting effort (nests per kilometer per person).

Year	Date at 5% of population oviposition	PACAYA				SAMIRIA				
		Water level at oviposition 5% (m)	Oviposition duration (days)	N° shifted days from median †	CE (nest·Km ⁻¹ ·per ⁻¹)	Water level at oviposition 5% (m)	Oviposition duration (days)	N° shifted days from median †	CE (nest·Km ⁻¹ ·per ⁻¹)	
2003	27-Jul	92.6	77	4	0.0148	29-Jul	91.3	85	6	0.0194
2004	4-Aug	92.2	53	12	0.0299	3-Aug	92.6	66	11	0.0556
2005	16-Jul	91.6	54	-7	0.0349	16-Jul	91.6	38	-7	0.0984
2006	22-Jul	90.9	55	-1	0.0419	15-Jul	90.5	69	-8	0.0999
2007	21-Jul	91.4	71	-2	0.0401	16-Jul	89.5	51	-7	0.1295
2008	22-Jul	92.2	58	-1	0.084	21-Jul	91.9	45	-2	0.0568
2009	27-Jul	92.3	59	4	0.0568	25-Jul	93.0	67	2	0.0603
2010	23-Jul	92.3	67	0	0.0338	2-Jul	92.0	70	-21	0.0205
2011	7-Aug	91.1	48	15	0.0628	26-Jul	92.5	76	3	0.0447
2012	26-Jul	91.2	63	3	0.0571	13-Jul	92.9	58	-10	0.0415

† Positive values accounts for the number of days later than July 23th, while negative values for days earlier than July 23th. Highlighted values exceed two median absolute deviations.

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