

Protection of spawning habitat for potamodromous fish, an urgent need for the hydropower planning in the Andes



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Because dams block migratory routes of potamodromous fish to their spawning areas, and energy generation changes natural flow seasonality, it is necessary to identify spawning areas and their conditions. This information will help in management decisions in the Magdalena River basin regarding the future hydropower development. We identified which characteristics of the tributaries to the Magdalena River are important for determining potamodromous fish spawning grounds, and we estimated the percentage of future loss of spawning areas because of dam development. Ichthyoplankton density is directly related to the floodplain area, and inversely related with channel slope. Low channel slopes offer adult fish a longer distance for their upstream migration and a longer time for embryo development during their drift downstream from the spawning areas to nursery habitats (floodplain lakes). These features could increase the migration distance of the adults, the time for initial embryo development, and, because of its relationship with nursery habitats access, the offspring survival. The potential loss of the actual spawning grounds in the river network was estimated to be nearly 70% because of new dams. Our findings will help to reduce conflicts between hydropower and ecological interests.

Keywords: Basin geomorphology, Conservation, Freshwater fish, Magdalena River, Reproductive migrations.

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La construcción de hidroeléctricas puede afectar la reproducción de los peces migratorios potamódromos, ya sea porque las represas bloquean las rutas migratorias a sus áreas de desove, o porque la generación de energía cambia la estacionalidad del flujo natural. Esto hace necesario generar información sobre las áreas de desove y sus características, que permitan tomar decisiones de manejo, teniendo en cuenta el desarrollo hidroeléctrico propuesto a futuro en la cuenca del río Magdalena. Identificamos qué características de algunos afluentes del río Magdalena son importantes para los desoves y estimamos el porcentaje de pérdida futura de áreas de desoves debido al desarrollo hidroeléctrico. La densidad del ictioplancton se relacionó directamente con el área de la llanura aluvial e inversamente con la pendiente del canal. Estas características aumentan la distancia de migración de los adultos maduros, el tiempo para el desarrollo inicial del embrión y la supervivencia de la descendencia debido a la proximidad y/o conectividad con los hábitats de cría. La pérdida potencial de las zonas de desove en la red fluvial se estimó en casi el 70% debido a las nuevas presas. Nuestros hallazgos ayudarán a tomar decisiones sostenibles para reducir los conflictos entre intereses de desarrollo hidroeléctrico y ecológicos.

Palabras clave: Conservación, Geomorfología de cuenca, Migraciones reproductivas, Peces dulceacuícolas, Río Magdalena.

INTRODUCTION

Reproduction is a biological process that increases the abundance of a population (Begon *et al.*, 2006). Freshwater fish present an extraordinary diversity of strategies and tactics to reproduce (Wootton, Smith, 2014). The decision on where and when fertilization will occur, and how much to invest in the care of embryos are examples of reproductive traits in fish (Welcomme *et al.*, 2006). Similarly, habitat conditions allow fish with a specific body conformation; the environment provides the conditions under which an individual spawns and its embryos survive (Matthews, 1998). Some fish species lay few eggs inside nests and care for them until the larvae feed independently. Others spawn hundreds of thousands of oocytes, fertilization occurs in open waters, and the embryos drift with the currents. Based on these and other traits in fish life strategies, Winnemiller, Rose (1992) proposed three reproductive strategies; one of them, is the periodic (or seasonal) strategy. This strategy involves fish spawning in open areas and without parental care.

Only those fish whose bodily features, food, and reproductive preferences can be satisfied by the conditions provided by a single habitat may be residents of that habitat. When not all the traits “work” within the same conditions, a fish can use different habitats that satisfy the requirements it has in each of its development periods (Matthews, 1998). Those are called periodic species and use different habitats during their life cycles (Winemiller, Rose, 1992). The movements carried out between these habitats are called migrations, and in freshwaters, they are associated with the environmental conditions imposed by the hydrological seasonality in the basins (Lucas, Baras, 2001).

The most striking migrations are those made to find places to reproduce. Several of these migrations have been described in freshwater around the world (Lucas, Baras,

2001). In tropical freshwaters, individuals travel long distances from their growth and feeding habitats in search of places within each basin that provide adequate conditions for spawning, fertilization of the oocytes, and the survival of the embryos (Carolsfeld *et al.*, 2003).

The Magdalena River basin has 234 fish species (DoNascimento *et al.*, 2018); 23 of them are recognized as migratory fish species (Usma *et al.*, 2009; Zapata, Usma 2013; López-Casas *et al.*, 2016). Half of these migratory fish species are important for the country's inland fisheries (Lasso *et al.*, 2011). These species migrate upstream twice a year from the floodplain habitats in the lowlands of the basin to the parental river and its tributaries (Jiménez-Segura *et al.*, 2016; López-Casas *et al.*, 2016) at a maximum of 1200 m.a.s.l. and spawn with the beginning of the floods (Jiménez-Segura *et al.*, 2010). Their embryos drift downstream from the spawning habitat; incubate during the drift, and lateral flooding transports larvae into floodplain lakes, which serve as their nursery habitats (Jiménez-Segura *et al.*, 2016).

In Colombia, hydropower is by far the country's largest source of energy. Colombia's hydropower system generated 57341.9 GWh, representing 86% of the total generation in the country (66667 GWh; UPME, 2018). The Magdalena River basin has a high hydropower potential because of its proximity to transmission infrastructure, and it is one of the top ten rivers that produce the largest renewable water supply in the world (<https://www.mapsofworld.com/world-top-ten/world-top-ten-fresh-water-supply-map.html>; last consulted December 21, 2020; Ledec, Quintero, 2003). The basin currently has 35 hydropower dams (~70% of the country generation), and more than 100 new dams could be installed based on the Colombian energy sector plans (Opperman *et al.*, 2017).

The most recent hydropower construction in the Magdalena River basin had been located in channels at elevations below 1000 m, breaking the migratory circuit of fish and disrupting reproduction (Jiménez-Segura *et al.*, 2014a). To facilitate evidence-based decision making for the conservation of Colombian aquatic biodiversity, we used ichthyoplankton density to identify where the migratory freshwater fish spawn in the Magdalena River Basin, which environmental characteristics determine spawning sites, and how the hydropower planning may affect those spawning areas. Our analysis tests two hypotheses: a) if environmental characteristics of tributaries influence the habitat selection for fish spawning and b) if the hydropower planning development may affect some of those tributaries as spawning areas. Our results highlight the importance of variables at geomorphological basin scale in the spawning intensity of the potamodromous fish in a tropical Andean river system and provide relevant information for decision-making in energy development planning in the Magdalena River basin, aimed at reducing the impacts of the industry on the diversity of the ichthyofauna, on the dynamics of fish populations and artisanal fisheries production.

MATERIAL AND METHODS

Study area. The Magdalena River basin is located in the north-western region of the South American continent and is the largest hydrological basin in the northern Andes. It is entirely located in Colombia and has an extension of 257,438 km², about a quarter of the country's land area. It flows from South to North between the central and

eastern Andes ranges between 3° and 11° North latitude and between 74° and 76° West longitude (Nie *et al.*, 2010). It is unique worldwide because the three Andean branches generate one of the most complex aquatic systems in South America (Restrepo *et al.*, 2020). With a 1612 km length from its source in the Andes, it discharges 7100 m³.s⁻¹ of water and 144 Mt of sediment per year to the Caribbean Sea (Kettner *et al.*, 2010). There are two main drainage areas, the Magdalena and Cauca Rivers, which each have 151 sub-basins, 42 of which are tributaries that drain directly into the Magdalena mainstream (Restrepo, Kjerfve, 2000; López-Casas *et al.*, 2016). The watershed is characterized by high tectonic activity, hillslopes commonly exceeding 45°, landslides, steep gradients, and high relief tributary basins (Restrepo *et al.*, 2006).

This basin has moderate rainfall with 2050 mm yr⁻¹ on average, and an annual bimodal hydrological cycle with two rainy and two dry seasons. Water temperature changes with the altitude and the climatic seasons (Ramírez González, Viña-Vizacaíno, 1998). At elevations between 3500 and 500 m, the temperature is within a range between eight and 26.7 °C (Herrera-Pérez *et al.*, 2019); in the main river at 135 m of elevation, the annual mean temperature is 27 °C (Jiménez-Segura, 2007) and in the floodplain lakes it can reach 37 °C (Restrepo *et al.*, 2020).

Eighty percent of the population of Colombia inhabit the Magdalena basin, which carries a high environmental impact (Galvis, Mojica, 2007). Current trends for the Magdalena drainage basin include an increase in population densities; accelerated upland erosion rates due to poor agricultural practices, widespread deforestation, and mining (Restrepo *et al.*, 2006). In addition, the Magdalena River basin has been the focus of many hydropower plants, most with dams higher than 15 m, and 32% are located between 0 and 1000 m in altitude (Jiménez-Segura *et al.*, 2014b).

Fish species. Because of the spawning characteristics of the potamodromous fish species in the Magdalena River, the density of drifting ichthyoplankton (eggs and/or larvae) can be used to measure spawning intensity (King *et al.*, 2016). Ichthyoplankton data of thirteen species were included: bocachico *Prochilodus magdalenae* Steindachner 1879, bagre rayado *Pseudoplatystoma magdaleniatum* Buitrago-Suarez & Burr, 2007, blanquillo *Sorubim cuspicaudus* Littmann, Burr & Nass, 2000, picuda *Salminus affinis* Steindachner, 1880, dorada *Brycon moorei* Steindachner, 1878, vizcaína *Curimata mivartii* Steindachner, 1878, moino *Megaleporinus muyscorum* (Steindachner, 1900), bagre sapo *Pseudopimelodus bufonius* (Valenciennes, 1840), sardina *Psalidodon cf. fasciatus* (Cuvier, 1819), arenca *Triportheus magdalenae* (Steindachner, 1878), pacora *Plagioscion magdalenae* (Steindachner, 1878) and one genera with two very similar species, difficult to identify in their first stages of life, capaz *Pimelodus grosskopfii* Steindachner, 1879 and barbudo *Pimelodus yuma* Villa-Navarro & Acero P., 2017.

Sampling design. In order to test which environmental parameters are related to the intensity of fish spawning, we selected ten tributaries of the Magdalena River based on discharge magnitude (less than 200 m³.s⁻¹, between 201 and 500 m³.s⁻¹, and more than 501 m³.s⁻¹) and accessibility. This pool of ten included five tributaries of less than 200 m³.s⁻¹ (Opón, Cesar, Boque, Espíritu Santo and Nechí rivers), four between 201 and 500 m³.s⁻¹ (Samaná, Nare, Carare and Sogamoso rivers), and one bigger than 501 m³.s⁻¹ of discharge (San Jorge River) (Fig. 1).

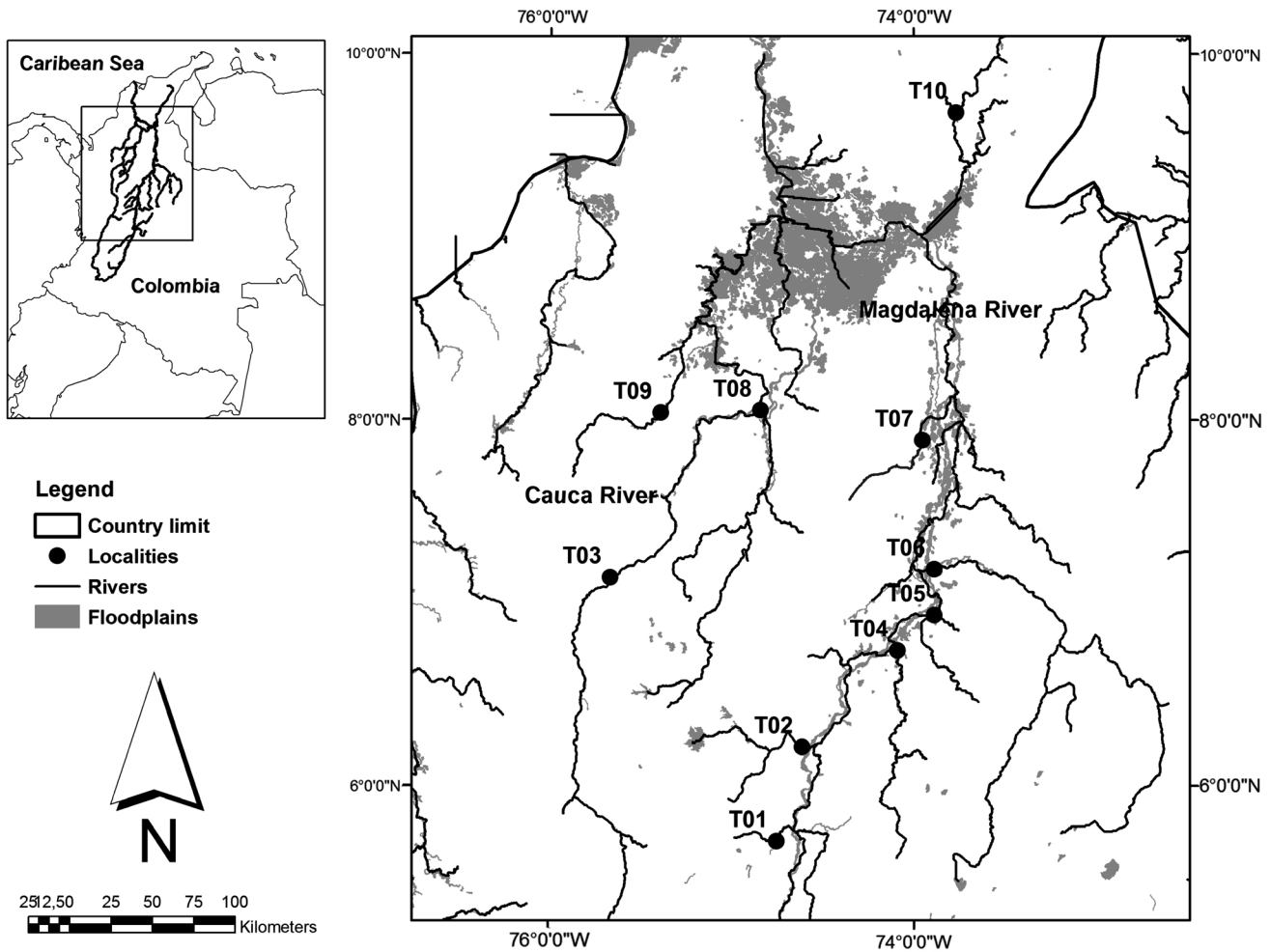


FIGURE 1 | Location of the sampling tributaries (black circles) in the Magdalena River basin. T01: Samaná River; T02: Nare River; T03: Espíritu Santo River; T04: Carare River; T05: Opón River; T06: Sogamoso River; T07: Boque River; T08: Nechí River; T09: San Jorge River and T10: Cesar River. Magdalena River runs north.

Ichthyoplankton sampling. Because spawning of potamodromous fish in the Magdalena River is highly seasonal (Barletta *et al.*, 2015), ichthyoplankton samples were taken at the beginning of the two-yearly floods of the basin. Each day before 09:00 h during twenty consecutive days in September of 2013 (spawning after the second migration of the year) and May of 2014 (spawning after the first migration). Ichthyoplankton was collected with a conical–cylindrical plankton net (1.5 m long, 0.5 m mouth diameter, 400 μm mesh net tapering to collection jar), placed horizontally to filter against the flow for one minute at the highest velocity section of the channel; longer filtering times were not possible because of clogging of the net due to the high concentration of suspended sediment. The sampled volume was measured using a General Oceanics Inc. (Florida, USA) flowmeter fixed into the net mouth. Three samples were taken each day. Ichthyoplankton density was estimated as the sum of all the individuals collected per sample by the water filtered volume and related to ten cubic meters (ind.10m^{-3}) (Tab. 1).

Ichthyoplankton samples were separated and grouped according to their development period and stage following Nakatani *et al.* (2001) in eggs, embryos, yolk sac larvae, larvae–preflexion, larvae–flexion and larvae–postflexion. Eggs and embryos were fixed in 96% alcohol for subsequent genetic identification, and the other larvae stage in a solution of buffered 4% formalin for subsequent taxonomic identification. Larval taxonomic identification was carried out using the keys of Nakatani *et al.* (2001) for neotropical groups (Order, Family, and Genera), and the key of Jiménez-Segura (2007) for Magdalena species as well as descriptions for some genera and species (Contreras, Contreras, 1989; Aristizabal-Regino *et al.*, 2004; Atencio-García, 2005; Novoa, Cataño, 2005; Arias-Gallo *et al.*, 2010; Valbuena-Villarreal *et al.*, 2012; AUNAP, 2012). Eggs were separated according to the characteristics associated with spawning eggs of migratory species (open waters) according to Godinho *et al.* (2010): eggs laid in open and current areas and synchronous total spawns during the rising waters. To identify the species of the embryos, the sequences of the COI gene of the potamodromous fish species of the basin were defined following standard protocols (Hebert *et al.*, 2003), and a coincidence analysis was carried out between the COI gene sequence of embryos and that of adult individuals, using PCR multiplex tests.

TABLE 1 | Basin-scale geomorphic variables and local physicochemical variables that were examined as a part of this study. The average median density of ichthyoplankton per tributary is also presented.

Tributary	Geomorphologic basin scale variables					Physicochemical reach scale variables				
	Density (ind.10m ⁻³)	Basin area (ha)	Channel sinuosity index	Elevation (msnm)	Floodplain area (ha)	Slope (%)	Flow (m ³ .s ⁻¹)	Conduc (µS)	Temp (°C)	Trans (cm)
Samaná River	0.00	1,153	1.40	175	0	13.04	278.4	52.8	25.3	26.5
Nare River	0.51	5,606	1.51	130	1	12.82	409.7	25.6	24.	28.4
Espíritu Santo River	0.00	572	1.72	253	0	43.55	NA	77.5	23.38	11.8
Carare River	4.65	6,556	1.42	94	515	5.82	275.7	240.6	28.7	7.7
Opón River	3.49	2,164	1.57	84	509	7.34	64.3	208.8	27.9	4.9
Sogamoso River	3.42	22,398	1.80	71	324	6.92	NA	167.0	26.0	3.2
Boque River	0.18	803	1.35	43	60	9.26	45.5	62.7	24.7	13.5
Nechí River	11.07	14,411	1.36	40	1,304	5.49	692.6	23.8	27.0	8.9
San Jorge River	13.02	4,155	1.53	36	960	6.37	309.7	46.3	26.9	5.2
Cesar River	24.66	9,617	1.64	30	1,684	3.29	171.8	165.5	28.9	9.1

Geomorphological and physicochemical characteristics of the tributary basins. Nine non-redundant geomorphological and physicochemical variables were measured at the reach and basin-wide scales (Tab. 1). Reach scale includes *in situ* variables such as transparency, conductivity and water temperature measured in the field. Basin-wide scale variables include basin area, channel sinuosity, elevation, floodplain area, average channel slope and average flow were calculated from 90-m digital elevation models (DEM) covering the Colombian Andes. Forty-two layers of the U.S. Geological Survey were downloaded from <http://gdem.ersdac.jspacesystems.or.jp> and merged for further processing. Average flow data was calculated from the serial data flow of the Colombian Hydrological Institute “Instituto de Hidrología, Meteorología y Estudios Ambientales (IDEAM)”.

To calculate the basin-wide scale variables: basin area, channel sinuosity, floodplain area, and average channel slope, we first derive the drainage paths and directions within the drainage basin using the hydrological ArcGis software tools. For this, we created a digital flow network with two derived grids for each watershed from the modified elevation model: a flow direction grid and a flow accumulation grid. To ensure the proper direction of flow across each basin, we made a hydrological correction using the function TopoGrid (Fransen *et al.*, 2006). This function modifies the DEM in areas under hydrology stream vectors to force downstream flow. It assures hydrologically conditioned digital elevation models, so they can better represent actual flow across the landscape. After that, we create vectors delineating streams from the accumulated flow grid, assuming a minimum basin area of 1.5 ha to generate a channel (Fransen *et al.*, 2006). Finally, we create 3D points for each sample site from coordinates taken in sampled localities with a Global Positioning System (GPS) Garmin Etrex 20x.

Channel sinuosity was expressed as a sinuosity index calculated by dividing the total length of the river channel between the length of a straight line between the highest and the lowest points of the river (Fukushima, 2001). For the mean floodplain extension estimation, we follow Hall *et al.* (2007) procedure, which calculates it as a function of valley topography, projecting the river height at the lowest point of the reach in the DEM and then calculating the area corresponding to that height and surrounding surfaces with low vertical relief (< 1 m) above the stream channel. This approach cannot replace *in situ* methods for providing accurate representative geometries at a single reach but can permit one to obtain the spatial variability (Beighley, Gummadi, 2011). ArcView® software was used to calculate geomorphological basin characteristics.

Location of the spawning area. To locate the reaches of the rivers used by migratory fish to spawn, we use a Tier 1 tool. The model uses the time it takes an individual (post-fertilization hours) to reach a period and stage of development as the drifting time, and average speed of the water at each stretch of the river (López-Casas *et al.*, 2018).

Reservoir locality and the change in the spawning area. The model used to predict spawning areas is sensitive to infrastructure associated with barriers in water bodies. For our analysis, we used the database incorporated in the mathematical model that identifies large dams in the Magdalena-Cauca basin under the categories of projects

in operation, projects under construction and possible future projects (López-Casas *et al.*, 2018). The database for possible future projects corresponds to the one identified in the study of the electric power sector: inventory of hydroelectric resources developed for Colombia (DNP *et al.*, 1979).

Statistical Analysis. To realize further analyses, we checked first for significant differences in ichthyoplankton density among tributaries using an ANOVA test. After that, we tested for relationships between geomorphological and physicochemical variables and the ichthyoplankton density with a squared multiple correlation analysis (SMC). Then, a multiple regression analysis, and separated simple linear regressions for significantly correlated variables were performed to evaluate the magnitude of the effect of these variables on ichthyoplankton density. To find differences in ichthyoplankton density among tributaries, the [boxplot]{boxplot} (Becker *et al.*, 1988; Murrell, 2005) and [stats]{kruskal.test} were used for the boxplot and ANOVA test (Gibbons, Chakraborti, 2011). The [lrm]{lm.test} function (Rizopoulos, 2006) was used to calculate the correlations and probabilities between variables, and the [psych]{smc} function (Revelle, 2014) to calculate the multiple correlations. The [SciViews]{panel.hist}, [SciViews]{panel.cor} and [SciViews]{panel.reg} functions (Grosjean, 2014) and [graphics]{pairs} for the graphic. To evaluate the independent variables (selected from the SMC analysis) contribution to regression model and their effect on ichthyoplankton density, the hierarchical partitioning algorithm of Chevan, Sutherland (1991) was conducted, using the [hier.part]{hier.part} function (Walsh, Mac Nally, 2013). Simple regression analyses were made with the [stats]{lmtest} function (Hothorn *et al.*, 2015). All analyses were made using R version 3.3.2, and all the tests were conducted at a significance level of 0.05.

To ensure the validity of statistical analysis results, all variables were tested for normality using the Kolmogorov–Smirnov test through the function [nortest]{lillie.test} (Gross, 2015); autocorrelation among all the variables was tested using the Durbin–Watson test by the function [lmtest]{dwtest} (Hothorn *et al.*, 2015); and Breusch–Pagan test was used to prove variance homogeneity using the function [lmtest]{bptest} (Hothorn *et al.*, 2015). When assumptions were not satisfied, variables were log-transformed with the $\text{eqnln}(\text{variable} - (\min(\text{variable}) - 1))$ equation.

RESULTS

Ichthyoplankton density was different among tributaries (Kruskal–Wallis $H = 208.29$, $df = 9$, $p < 2.2e-16$; Fig. 2). In the Cesar and San Jorge rivers we detected the highest densities of eggs and larvae.

Geomorphologic determinants of spawning migrations. Only two significant correlations were found between the measured variables and ichthyoplankton density (Multiple Correlation $R^2 = 0.92$, $F = 21.62$, $df = 6$, $p = 0.001$). A direct relation (positive correlation) was found between ichthyoplankton density and floodplain area ($R = 0.95$, $p < 0.001$) and an inverse relation (negative correlation) with the average stream slope ($R = 0.81$, $p = 0.016$) (Tab. 2; Fig. 3).

Floodplain area and channel slope explains 92% of the variability in the ichthyoplankton density in the Magdalena basin ($R^2 = 0.92$, $F = 40.4$, $p = 0.0001$, $df = 7$). However, just the floodplain area was significantly influential in the model (multiple regression, $\beta = 0.001$, $p = 0.005$). The assumptions of normality (Kolmogorov-Smirnov test $D = 0.14$, $p = 0.79$), autocorrelation (Durbin-Watson test $DW = 1.63$, $p = 0.23$) and homoscedasticity in the residuals (Breusch-Pagan test $BP = 1.13$, $p = 0.56$) were fulfilled. Simple linear regression for floodplain area and channel slope versus ichthyoplankton density were significant with a probability of 99%. Of the variability of ichthyoplankton density, 79% was explained by floodplain area ($R^2 = 0.79$, $F = 29.86$, $df = 8$, $p = 0.0005$) and 65% for the slope ($R^2 = 0.65$, $F = 14.82$, $df = 8$, $p = 0.004$). All the assumptions were fulfilled for both models (slope: K-S test $D = 0.16$, $p = 0.62$; D-W test $DW = 1.03$, $p = 0.06$; B-P test $BP = 1.03$, $p = 0.06$) (floodplain: K-S test $D = 0.23$, $p = 0.13$; D-W test $DW = 1.93$, $p = 0.42$; B-P test $BP = 0.50$, $p = 0.47$).

Location of the spawning area. According to our sampling design and the model used, potential spawning grounds for the 13 fish species analyzed accounted for a total of 7,278.8 km of rivers (Fig. 4A), including Strahler orders from three to eight (7.2 % of the 101,110 km of the total network).

Reservoir locality and the change in the spawning area. The potential spawning areas for the same 13 fish species under a scenario of full hydroelectric development in the Magdalena basin allows us to predict a loss of migratory spawning grounds of 68.3%, with just 2.3% of the rivers of the basin (2304.7 km of rivers) remaining as viable and connected spawning habitat (Fig. 4B).

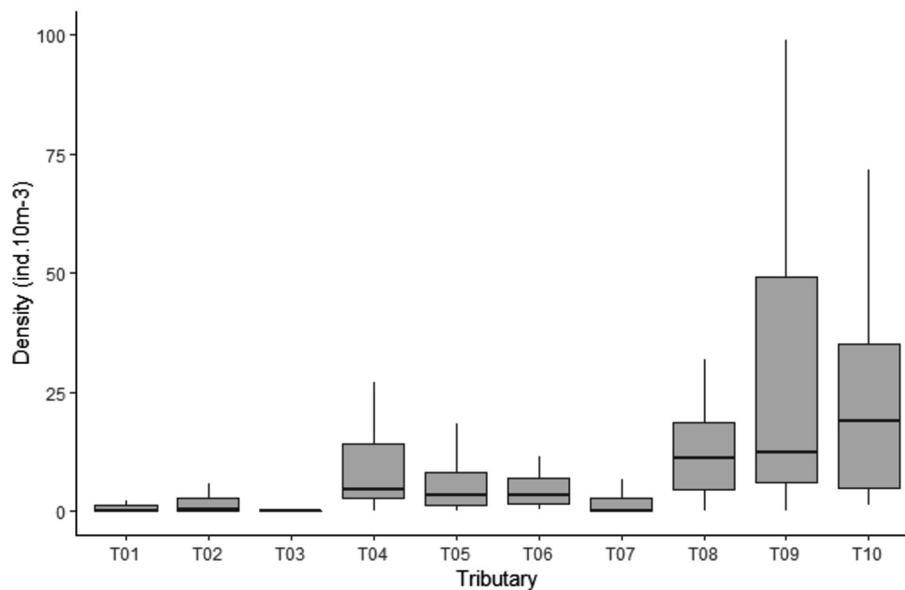


FIGURE 2 | Spatial variation in the median density of ichthyoplankton among tributaries. (Kruskal-Wallis $H = 208.29$, $df = 9$, p -value $< 2.2e-16$). T01: Samaná River; T02: Nare River; T03: Espíritu Santo River; T04: Carare River; T05: Opón River; T06: Sogamoso River; T07: Boque River; T08: Nechí River; T09: San Jorge River and T10: Cesar River.

TABLE 2 | Correlation and p-values of the Squared Multiple Correlation (SMC) analysis. Upper diagonal part contains correlation coefficient estimates and the lower diagonal part contains corresponding p-values. Significant correlated variables (listed in bold) with density were then used for the multiple regression analysis.

	Density	Basin	Sinuos	Height	Slope	Flood	Flow	Cond	Transp	Temp
Density	****	0.61	0.58	-0.66	-0.81	0.95	0.12	0.17	-0.51	0.69
Basin	0.11	****	0.02	-0.43	-0.58	0.75	0.74	-0.06	-0.26	0.45
Sinuos	0.13	0.97	****	-0.19	-0.34	0.43	-0.35	0.38	-0.23	0.44
Height	0.07	0.28	0.65	****	0.81	-0.72	0.02	-0.07	0.77	-0.43
Slope	0.02	0.13	0.41	0.01	****	-0.88	-0.02	-0.49	0.88	-0.87
Flood	<0.01	0.03	0.28	0.04	<0.01	****	0.26	0.18	-0.64	0.74
Flow	0.78	0.03	0.40	0.96	0.96	0.51	****	-0.51	0.16	-0.05
Cond	0.69	0.88	0.35	0.87	0.22	0.68	0.19	****	-0.52	0.75
Transp	0.19	0.59	0.58	0.02	<0.01	0.09	0.71	0.19	****	-0.76
Temp	0.06	0.26	0.28	0.29	<0.01	0.03	0.91	0.03	0.03	****

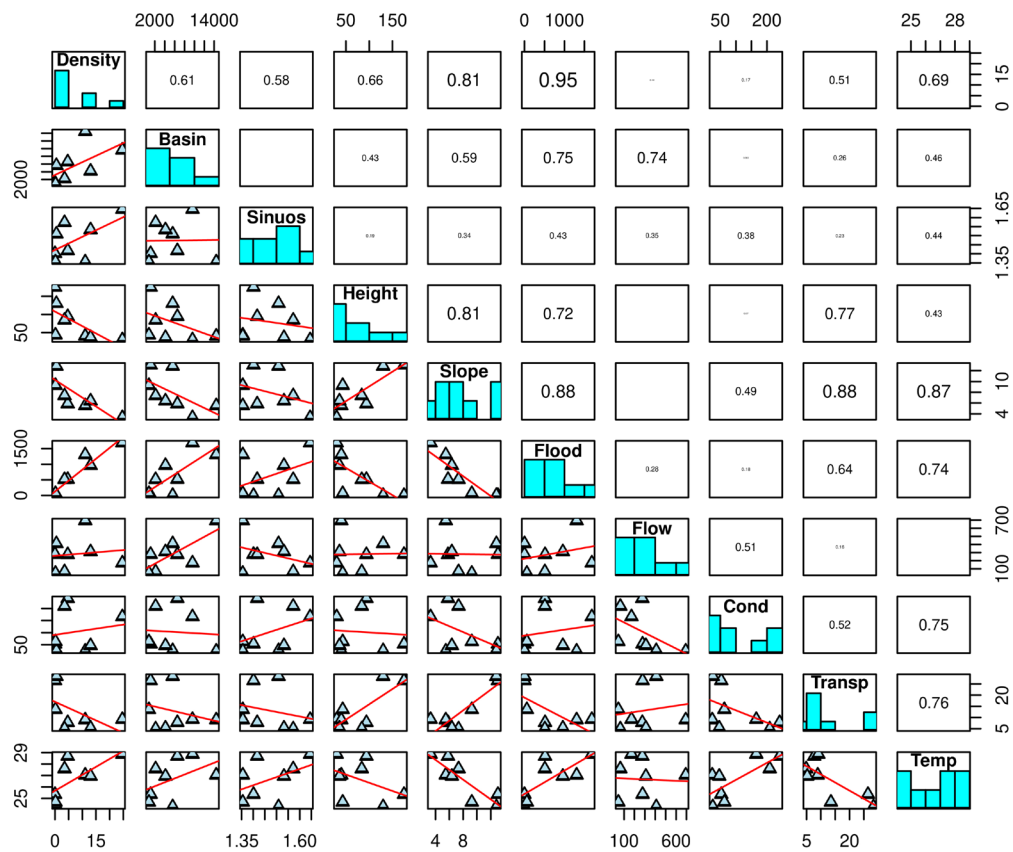


FIGURE 3 | Correlations between geomorphological and physicochemical variables, and ichthyoplankton density. Basin: basin area, Sinuous: channel sinuosity index, Flood: floodplain area, Cond: conductivity, Trans: transparency, Temp: temperature. $\alpha = 0.05$.

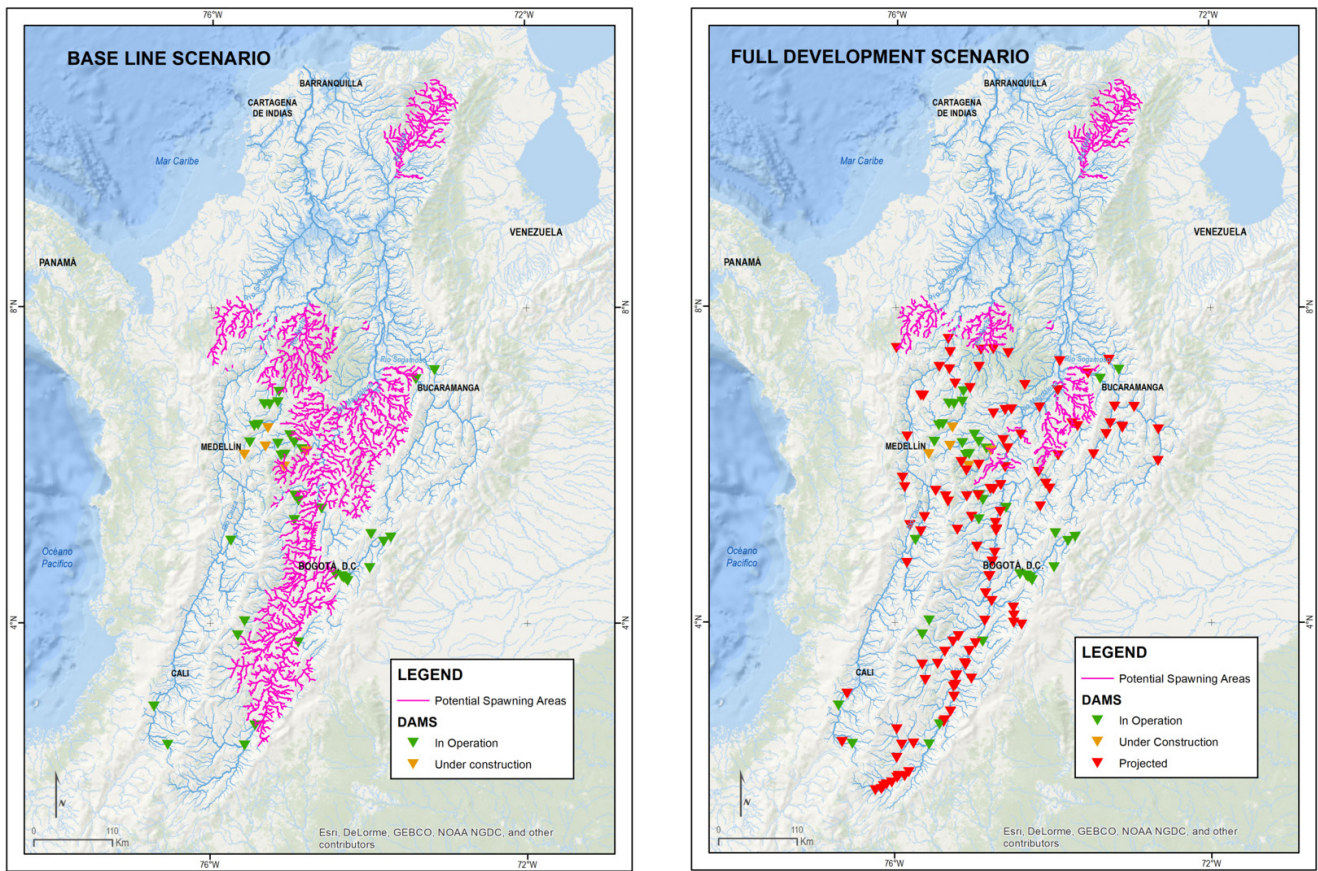


FIGURE 4 | Potential spawning grounds for 13 sampled potamodromous fish species of the Magdalena basin. **A.** Baseline (current) scenario, and **B.** Full hydroelectric projects development scenario.

DISCUSSION

Geomorphological variables were shown to be determinant for spawning site selection, while no significant relationship of ichthyoplankton density with each effluent water characteristics was found. Mature individuals of potamodromous fish lay their eggs into the open waters in the river channel without nests construction or any parental care (Winemiller, Rose, 1992). This means that the local conditions tested in this study are unimportant in the selection of tributaries for spawn. In contrast, broad-scale variables of each river basin, such as slope and nearest floodplain area, were important because they determine the drifting distance, which is mediated by water velocity and, with that, the developmental stage of the embryos when reach nursery habitats. Water direction and velocity increase connectivity between important environments for the different phases of the fish life cycle, being responsible for driving eggs and very recently hatched larvae from spawning to nursery grounds (Lopes, Zaniboni-Filho, 2019). In addition, the proximity of the floodplains in these drifting reaches, increase the chance that river floods take the larvae into the floodplain lakes.

This study aimed to develop a better understanding of the spawning ground selection and reproductive migratory behavior of potamodromous tropical fish through

the relation of local physicochemical and geomorphological basin scale variables with ichthyoplankton density. Furthermore, using a complementary tool allows analyzing hydropower development to choose project configurations at macro basin scale, we assess possibilities for minimizing impacts related to potential spawning areas in a basin. Although several studies of migratory fish spawning habitats have been made in temperate zones (Garbe *et al.*, 2016; King *et al.*, 2016; Thurow, 2016; Naus *et al.*, 2018; Zhang *et al.*, 2018; Harding *et al.*, 2019), as far as we know, this study is the first of this kind in tropics.

Floodplain ecosystems are the most productive aquatic ecosystems in the tropics and maintain a great diversity and abundance of organisms, including several species of fishes that depend on them for completion of the life cycle (Harvey, Carolsfeld, 2003; Granado-Lorencio *et al.*, 2012; White *et al.*, 2012; Górski *et al.*, 2014; Zacardi *et al.*, 2017; Ben-Hasan *et al.*, 2018). For potamodromous species, for example, the extension of floodplains and the amount of resources within them determines abundance (Gomes, Agostinho, 1997) and growth (López-Casas, 2015) for mature reproductive adults and offspring (Godinho *et al.*, 2010, Reynalte-Tataje *et al.*, 2013). This could explain why the tributaries with the most extensive floodplain areas presented higher ichthyoplankton densities. As the migrant reproductive populations live in those habitats, it is expected that tributaries connected to more extensive floodplains maintain a greater number of mature spawners and then a higher reproductive activity than those with a small, more remote floodplain area.

The habitats fish select for reproduction must be aimed to increase the survival of the offspring (Lassala, Renesto, 2007), ensuring that larvae reach the most suitable rearing habitats. For potamodromous fishes, this means spawning upstream of the greatest areas of inundated floodplains with the greatest production and abundance of food and shelter (Hamilton, 2002; Hall *et al.*, 2007). Potamodromous fish are pelagic spawners with very high fecundities, and total spawning (Godinho *et al.*, 2010). They inhabit the floodplain lakes where they feed and grow (Reynalte-Tataje *et al.*, 2013) and carry out seasonally reproductive migrations to the main river and tributaries where they spawn (Jiménez-Segura *et al.*, 2010). After spawning, both offspring and parents go downstream with the current to return to floodplains, which provide critical rearing and growth habitats (Junk *et al.*, 1989; Marmulla, 2001; Jiménez-Segura *et al.*, 2010; Reynalte-Tataje *et al.*, 2012; Barzotto *et al.*, 2015; López-Casas *et al.*, 2016).

Our results suggest that reproductive adults probably migrate to rivers closer and better connected to their growth areas, allowing their larvae to get into the closer and more connected floodplain systems. If this is true, some genetic structure and a homing signal could be expected in those species. However, still if this behavior has not been described for species in the Magdalena basin, it has been proposed for other potamodromous Neotropical species (Sivasundar *et al.*, 2001; Castro, Vari, 2004; Hatanaka *et al.*, 2006; Sanches, Galetti Jr., 2007, 2012; Pereira *et al.*, 2009; Barroca *et al.*, 2012; Aguirre-Pabón *et al.*, 2013; Berdugo, Narváez Barandica, 2014; Landínez-García, Márquez, 2016; Márquez Fernández *et al.*, 2020) and some studies in the Magdalena basin found genetic populational structure between the main river and its tributaries for the bocachico, *P. magdalenae*, the pataló, *Ichthyoelephas longirostris* (Steindachner, 1879), the capaz, *Pimelodus grosskopfii* and the barbudo, *Pimelodus yuma* (= *Pimelodus clarias*) (Márquez Fernández *et al.*, 2020) suggesting some kind of homing behavior, and

supporting the idea of migrations to closer and more connected rivers to the growth areas. It has been proposed, notwithstanding, that genetic structure can be explained by spatial or temporal reproductive isolation, given the broad geographic scales and extreme weather events. In the Magdalena basin, isolation by distance (IBD) can be caused because of natural or artificial barriers. However, in absence of geographic barriers, as happens in the medium and lower sections of the Magdalena basin, isolation by time (IBT) can explain genetic structure, because of the bimodal hydrological behavior of the basin and the presence of several reproductive peaks of the species (Márquez Fernández *et al.*, 2020).

Some studies, on the contrary, suggest that neotropical migratory freshwater fishes are panmictic populations or with a high gene flow between sub-basins or different sections of the basin (Sivasundar *et al.*, 2001; Castro, Vari, 2004; Aguirre-Pabón *et al.*, 2013, Márquez Fernández *et al.*, 2020). In this regard, López-Casas *et al.* (2016) suggest that even if potamodromous fishes can present homing behavior, some populations or at least a portion of individuals into populations can migrate long distances through the Magdalena basin for spawning in more distant rivers. This could be explicated by the IBT concept, since temporal variations in hydrological and weather events, can make or erase geographical barriers for potamodromous fishes. As could be occurring in the Momposina depression in the lower section of the Magdalena basin, which depending on the hydrological moment and the intensities of rains can join or separate Cauca and Magdalena sub-basins (Jiménez-Segura *et al.*, 2020). Hence, depending on the timing of migrations and reproductive peaks of different species will present genetic structure or not (Márquez Fernández *et al.*, 2020). There is not enough evidence to support any of these hypothesis, and further studies will need to be undertaken.

In agreement with our results, different studies show that fish in temperate zones have lower spawning activity in steeper rivers (Moir *et al.*, 1998, 2002; Montgomery *et al.*, 1999; Merz, Setka, 2004; Louhi *et al.*, 2008). The slope can be determinant for fish reproduction at different scales. At the local scale, slope influences the availability of suitable and more oxygenated places for egg deposition and successful incubation (Dauble, Geist, 2000), especially in temperate migratory fish which are nest spawners and have high requirements of habitat for their nest location (Pandian, 2010). At the basin scale, slope restrictions could be imposed for migrations itself, as steeper rivers affect the capability of fishes to reach higher places (Kruse *et al.*, 1997; Dauble, Geist, 2000; Walters *et al.*, 2003; Fransen *et al.*, 2006). As potamodromous tropical fishes are open substratum pelagic spawners and lay numerous buoyant eggs into the current (Godinho *et al.*, 2010), requirements at the local scale for parental fish or spawners are not so important as in temperate zones. The challenge for them may be the energy budget to move upstream a sufficient distance to enhance the survival of their offspring, because the longer the embryos drift, the longer time they will have to develop themselves during the downstream drift from their spawning grounds to the rearing areas. Larvae must travel the river to their nursery habitats in the floodplain before their yolk sac reserves run out. To take advantage of the food in the floodplains, the digestive system of the larvae must be already functional, and it must be sufficiently mobile to engage in foraging of available plankton and invertebrates. If fish larvae can not access the floodplain lakes in this critical developmental window, they will starve.

Channel slope seems to be a barrier and determines the fish capability to access the

tributaries (Hall *et al.*, 2007). The point at which a gradient becomes a barrier depends on the fish species. Cramer (2001) found that segments of rivers in which the gradient is greater than or equal to 20% for at least 200 m imperil Atlantic Salmon migration, but a limit of 10% in the channel slope has been found in other species as limiting to fish migration (Edds, 1993; Kruse *et al.*, 1997). There is no information related to this for migratory fishes in the Magdalena basin. However, this study shows that slopes greater than 14% limit the migratory fish upstream movements, and rivers with higher slopes are less used as spawning areas than those with gentler slopes.

Although variables such as elevation, temperature, basin area, sinuosity, and conductivity are correlated with spawning habitats and migrations in temperate rivers (Moir *et al.*, 1998, 2002; Montgomery *et al.*, 1999; Merz, Setka, 2004; Louhi *et al.*, 2008) as well as local physicochemical variables as flow, temperature and conductivity, which can act as a trigger of spawning and as a cue for fish spawning in tropics (Jiménez-Segura, 2007, Jiménez-Segura *et al.*, 2010; Baran, Guerin, 2012; Zacardi *et al.*, 2017; Rosa *et al.*, 2018; King *et al.*, 2019), no significant effect of these variables seems to exist on spawning activity in this study. We conclude that those variables do not influence migration and selection of tributaries used for reproduction. However, a significant relationship was found between elevation and temperature with the floodplain area and channel slope, so it is probable that those two variables indirectly capture the effects of other landscape-scale factors influencing the likelihood of fish presence. Streams at higher elevations tend to be steeper and colder and therefore may contain more barriers to upstream fish movements (Bozek, Hubert, 1992; Jaramillo-Villa *et al.*, 2010; Carvajal-Quintero *et al.*, 2015), and streams in lower areas tend to be in wider valleys that support bigger floodplain extensions and warmer waters (Junk, 1989).

Unlike temperate migratory fishes, spawning ground selection in tropical migratory species is not determined by physicochemical and geomorphological habitat characteristics at the spawning sites, but by the strength of the migration, which depends on the size of the migratory adult population inhabiting the floodplain lake systems connected to those rivers and on the capability of fishes to reach the tributaries, or potential barriers preventing fishes from reaching those tributaries. The species reproductive strategy determines different environmental constraints on fish in temperate systems. Most temperate migratory fish are nest constructing and need precise physical and chemical variables to ensure the development and survival of the offspring. However, tropical migratory fishes are pelagic spawners, and offspring survival depends on the favorable conditions at the nursery habitats more than in spawning ones, so those fishes need conditions to allow their offspring to reach rearing habitats in the floodplains. Even though this study was made in one basin in the tropics, we believe that these findings can be extended to other mountains' tropical floodplain-river systems; nonetheless, further studies are needed.

We applied the Tier 1 model (López-Casas *et al.*, 2018) to map the distribution of spawning grounds in the Magdalena basin in two different scenarios of hydropower development: current scenario, and full hydroelectric project development scenario. Our results of both modeling show that if the more than 100 new dams proposed in the Magdalena Basin are installed, 68.3% of the potential 7278.8 km of rivers used for our 13 studied migratory species will be lost, and a similar proportion of the spawning areas of the 10 non-studied remaining migratory species in the basin will be lost as well. This

would aggravate the already delicate situation of the fisheries resource in the Magdalena Basin, on which a large part of the riparian population depends for both, economic incomes and as a protein source (more than 157,000 people are directly associated with fishing in the basin) (Valderrama-Barco *et al.*, 2020).

We analyzed the effects of dam construction on the spawning area extension. However, it is well known that the effect of different environmental alterations is synergistic. Other alterations, such as deforestation, mining, erosion, poor agricultural practice, climate change, overfishing, non-native species introductions and eutrophication, affect the aquatic environment and its biota (Bunn, Arthington, 2002; Barletta *et al.*, 2010) and can reduce the quantity and quality of these remaining spawning areas. An assessment of hydroelectric development scenarios in the Magdalena basin is beyond the scope of this study, nevertheless, we recognize that hydroelectric development will continue in the basin. We believe the Tier 1 model could be a useful tool to evaluate project configurations at the basin scale to minimize impacts on potential spawning areas in a basin and conserve the fishing resource, which is of great ecological and social importance.

As the Tier 1 model did not consider the density of ichthyoplankton, it gives equal importance to spawning habitat lost in the entire basin. Our results indicate that spawning habitat importance varies widely between tributaries, primarily in response to flooded areas and slopes. Taking this into account, we consider that the model could be improved, including ichthyoplankton densities, slope and floodplain areas, to be more precise in the location of these critical areas for the conservation of potamodromous species.

Finally, we would like to highlight that, in addition to the findings of various authors who have found a relationship between the physical and chemical conditions of the water with spawning in Neotropical fish, we found that spawning site selection for potamodromous fish is influenced mainly by geomorphological variables that mediate the time of embryo drift and development and the entrance of larva into the floodplains (nursery habitats); information that had not been previously identified or quantified before in Neotropical systems. However, because of the particularity of the Magdalena basin hydrogeomorphology and a more homogeneous geology, compared to other neotropical hydrological systems, certain reproductive strategies linked to geomorphology but not to physicochemical characteristics are favored. This is of particular importance, since, due to the construction of dams, the geomorphology of the basins would be affected and with them the availability of spawning areas. A critical next step is the identification and conservation of the most important migratory fish habitats in the basin. Given the many pressures the fisheries resource in the Magdalena basin faces today, and the additional impacts to come from hydroelectric projects proposed in the spawning area extension, as well as the importance of this resource for a significant proportion of the population settled in the basin, we emphasize and propose to use our results for better planning of the basin, which would allow hydroelectric development without compromising the conservation of the fish resource, and the livelihoods of the communities that depend on it.

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Neotropical Ichthyology

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ETHICAL STATEMENT

The care and use of experimental animals complied with the Colombian Ministry of Environment and Sustainable Development (MinAmbiente) animal welfare laws, guidelines, and policies as approved by National Aquaculture and Fisheries Authority (AUNAP) through resolution 986 of 2013.

COMPETING INTERESTS

The authors declare no competing interests.

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