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Spawning grounds model for neotropical potamodromous fishes: conservation and management implications

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Introduction: Freshwater fish migrations are an important natural process. All main river basins in South America have potamodromous fish that migrate upstream to spawn. Therefore, these species withstand fisheries and are socially, economically, and ecologically important. Hydropower dams cause one of the main threats to these fish's survival. Hydropower is the main source of low-carbon electricity in South America, where the most diverse and endemic riverine fish fauna inhabit. However, hydropower development rarely considers spawning areas or cumulative impacts in fish migratory routes at a macro-basin scale in their environmental impact assessment (EIA) studies. In the present case study conducted in the Magdalena basin in Colombia, a distribution model of potential spawning areas of migratory fish species was developed. The objective of the current research is to demonstrate the potential use of early planning tools at the macro-basin scale to ensure that freshwater ecosystems remain functional in supporting fish migrations.

Methods: Potential spawning areas for 15 migratory fish species were determined using ichthyoplankton sampling records, embryonic and larval time development, water velocity, and average flow time estimations. Spawning distribution grounds, analyzed for species diversity and richness, were overlaid with the national hydropower projects portfolio to examine the potential loss of reproduction areas due to hydropower dam development.

Results and discussion: Our basin-wide model calculated spawning areas for all of the identified species in available ichthyoplankton samples, using available data on the duration for larval and embryonic development. The proposed model estimated the potential impacts of projected hydropower development in the Magdalena basin and revealed spawning grounds encompassing 11,370 km of rivers, spanning Strahler orders three to eight, which represented 11.2% of the entire river network. These areas overlapped with 80 hydropower projects (56.7% of the total), with a projected 45.0% loss experienced in reproduction areas for potamodromous species.

Conclusion: Management measures to promote freshwater fish species conservation must avoid river fragmentation and critical habitat loss, while

promoting habitat connectivity. This model provides a solution to analyze fragmentation impacts from hydropower dam development in data-limited basins. It supports science-based decision-making for choosing dam location arrangements that minimize impacts (connectivity and reproductive habitat loss), while ensuring that rivers continue to support migratory fish for better conservation and food security outcomes.

KEYWORDS

development by design, early planning, environmental impact assessment, freshwater migratory fish, hydrological modeling, mitigation hierarchy, species spatial modeling

1 Introduction

Inland aquatic ecosystems and their biodiversity provide irreplaceable services to both nature and people (Lynch et al., 2023). Despite being very important, the wetlands are disappearing globally, three times faster than forests, and rate of decline of populations of inland aquatic vertebrates is more than twice than that of terrestrial or marine vertebrates (Albert et al., 2021). Over the past 50 years, 30% of inland aquatic ecosystems and 83% of their species have disappeared, thereby posing a severe threat to people who depend on rivers, lakes, and tributaries for water, food, and their economic well-being (Albert et al., 2021; Almond et al., 2022; Deinet et al., 2024). This global accelerated biodiversity loss has been called by scientists as the freshwater biodiversity crisis (Albert et al., 2021).

Studies have established threats to freshwater biodiversity (Dudgeon et al., 2006), with loss of connectivity being one of the main threats (Grill et al., 2019). Furthermore, dams and other types of infrastructure have been particularly damaging in fragmenting freshwater ecosystems and disrupting movements of water, species, sediments, and nutrients (Opperman et al., 2017; Brink et al., 2018; Grill et al., 2019; Tickner et al., 2020; Angarita et al., 2021; Deinet et al., 2024). Water resource planning is not accorded prime importance in the maintenance of natural ecosystems and their constituent species in a relatively intact state (Flitcroft et al., 2019). To address this challenge, Tickner et al., 2020 developed an emergency recovery plan to reverse the loss of freshwater biodiversity. This plan proposed safeguard measures to prevent further loss and to restore river connectivity as one of its six priority actions.

Hydropower provides approximately 17% of electricity worldwide (IEA, 2021). In several countries in Latin America, hydropower provides more than 50% of the total electricity supply and remains a key source of low-carbon energy and is likely to be largest renewable source across the region in future (IHA, 2022). Though hydropower is important for achieving sustainable development and economic goals, the creation and operation of hydropower dams can cause considerable social and environmental harm (Opperman et al., 2015). These impacts include the isolation of spawning grounds from feeding and growth habitats of migratory fish species; such isolation leads to a decline in the population of these species (Asmal et al., 2000; Agostinho et al., 2007; Grill et al., 2019), as well as a reduction in freshwater ecosystem services that impoverish local fishers (Hoeinghaus et al., 2009).

Potamodromy, the predominant migration type in stream fishes (Flecker et al., 2010), is crucial for nutrient energy flows and

sustaining artisanal fisheries, especially in tropical regions, where it accounts for more than 60% of fish catches (Welcomme, 1985; Welcomme et al., 2015; Zhao et al., 2015; Barletta et al., 2016; Ainsworth et al., 2023; Deinet et al., 2024). The highest riverine fish biodiversity and the highest number of endemic species are found in South Africa (Oberdorff et al., 2011; Tedesco et al., 2017; Jézéquel et al., 2020), with at least 20% of these fish species being potamodromous (Carolsfeld et al., 2003). However, in this region, Andean rivers are the target for hydropower project development (Tognelli et al., 2016; Anderson et al., 2018). However, Environmental Impacts Assessment (EIA) studies of hydropower projects often overlook fish migratory routes and spawning grounds. Additionally, these assessments are typically conducted on a project-by-project basis rather than considering impacts at a macro-basin scale, which would take into account cumulative impacts, including those on wide-ranging migratory fish. Lack of data on the spatial distribution of migratory fish and their habitat use is one of the challenges in making EIA studies. The difficulties of observing freshwater fish significantly hinder the ability to develop an accurate understanding of these resources and to provide users with the feedback needed for effective management in the wild (Zhang et al., 2020). Identifying spawning grounds is essential for this management; however, a few studies have been documented for tropical potamodromous species (Godinho et al., 2017; Miranda-Chumacero et al., 2020; Moreno-Arias et al., 2021). To overcome this challenge, different models on species distribution are employed to predict the population responses of these species or species groups under different scenarios and identify an accompanying management strategy (Langhans et al., 2019).

Because of the economic and social importance of potamodromous fishes, the present study aims to develop and test a framework for constructing a distribution model to identify potential spawning areas for migratory fish species. We intend to use the findings of this approach to highlight the value of early planning tools in achieving a balance between hydropower dam development and the preservation of functional freshwater ecosystems that sustain migratory fish. This might minimize conflicts between fishing communities and hydropower projects while assessing fragmentation and potential critical habitat loss for various species of conservation and economic importance.

The proposed model is an innovative combination of straightforward mathematical hydraulic analysis and field-collected ichthyological data. It offers a practical solution for environmental agencies and consultants worldwide conducting EIAs in basins with limited fish distribution data. This model can be used by various stakeholders to evaluate the potential impacts of

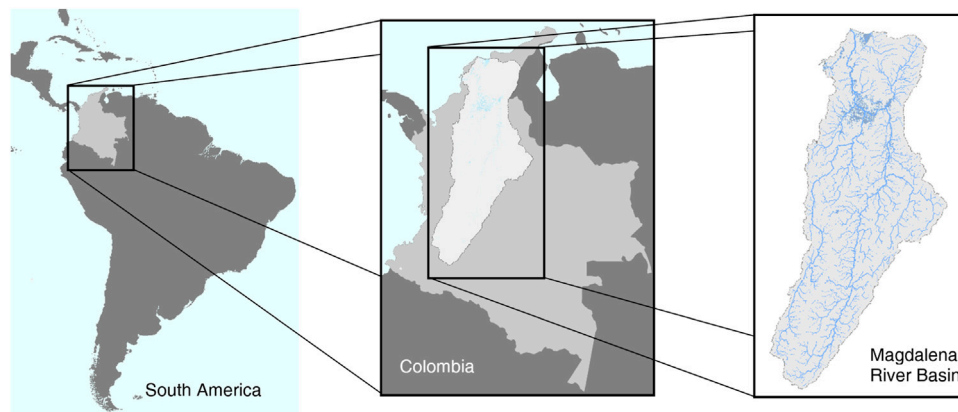


FIGURE 1
Location of the Magdalena basin (Colombia).

dam-induced habitat fragmentation and critical habitat loss by dams on freshwater migratory ichthyofauna more effectively.

2 Methods

2.1 Study area

The Magdalena River basin is located in the northwestern region of South America. It exhibits a bimodal hydrological cycle, which has two rainy and two dry seasons, annually. The basin has two primary drainage areas: the Magdalena River and the Cauca River (Figure 1). The Magdalena River flows 1,500 km from its source in the Andes mountains to the Caribbean Sea and spans approximately 273,000 km² basin area. The basin covers nearly a quarter of Colombia's land area, with a mean annual flow of 7,300 cubic meters per second, making it the fifth-largest river in South America.

The basin is densely populated, containing approximately 75% of the Colombian population (or 36 million people; Opperman et al., 2017). Due to its hydrography and proximity to existing transmission infrastructure and key water demand centers, this basin has been the target of several hydropower dam projects. These dams represent 84% of Colombia's reservoirs, with 35 operational hydropower dams, most of which exceed 15 m in height (Opperman et al., 2017). These dams generate approximately 70% of the Colombia's power (UPME, 2018) and over 100 new dams could be installed in the future to fulfill the country's needs (DNP, 1979).

The Magdalena basin is home to a diverse range of fish species, with 237 recorded so far (DoNascimento et al., 2024). Of these species, 23 are identified as migratory fish species (Usma et al., 2009; Zapata and Usma, 2013; López-Casas and Jiménez-Segura, 2015; López-Casas et al., 2016; Jiménez-Segura et al., 2020), which support artisanal fisheries and account for half of the 40 to 45 commercial species consumed in the basin (Lasso et al., 2011; The Nature Conservancy, Fundación Alma, Fundación Humedales, & AUNAP, 2016). These migratory species undertake two annual upstream migrations from their feeding and growing habitats in the floodplains of the basin to their reproductive habitats in the

upper river stretches, up to 1,200 m a.s.l., in the Cauca sub-basin (Mojica et al., 2012) and approximately 1,000 m a.s.l. in the Magdalena basin (Jiménez-Segura et al., 2016). Their catches represent approximately 50% of Colombia's inland fisheries harvest. The fishing industry in this basin supports approximately 61,000 fishers directly, without considering their families, of which 84.7% get their food from fishing (AUNAP and PNUD, 2021).

2.2 Data sets

To build the species model, different ichthyoplankton data sets were compiled and systematized in a database that contained information on the date recorded, sampling point name and coordinates, taxonomic identification, and individual development phases: early embryos and larvae classification according to their embryonic and larval stage of development. Ichthyoplankton sampling data were obtained from fieldwork conducted by The Nature Conservancy (TNC) and the University of Antioquia (UA), with data gathered from reports of the National Authority of Environmental Licensing (or Autoridad Nacional de Licencias Ambientales (ANLA) in Spanish) and ichthyoplankton monitoring of the El Quimbo hydropower plant, which was facilitated by the ENEL-EMGESA Environmental Department (Table 1).

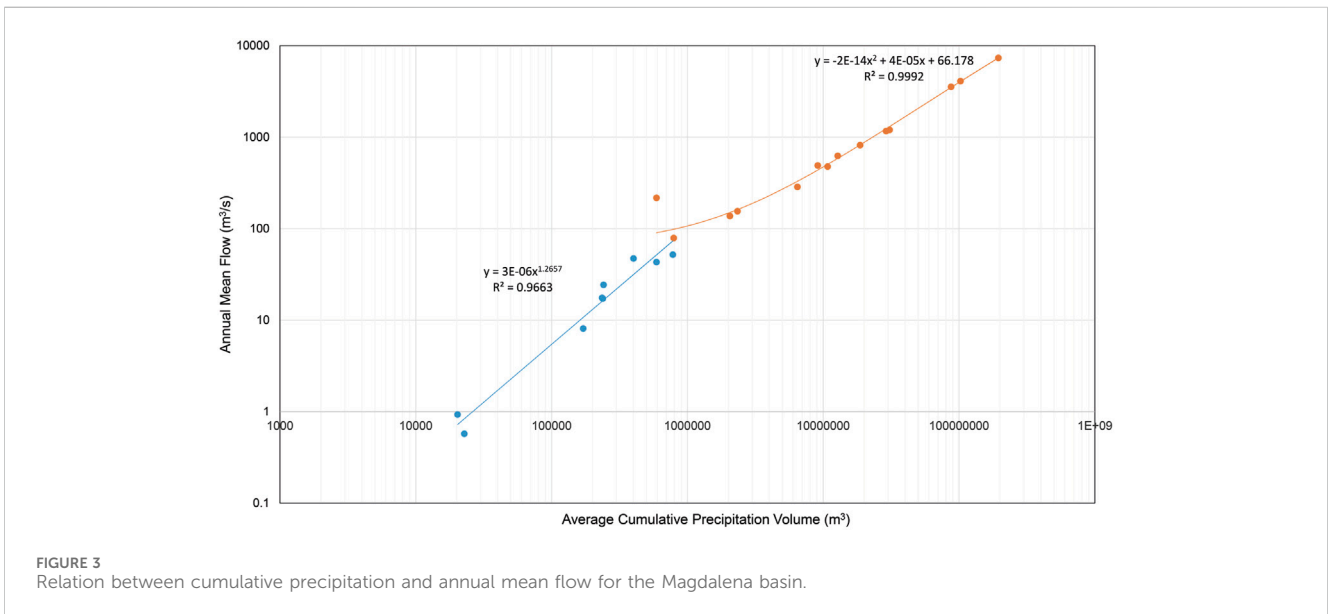
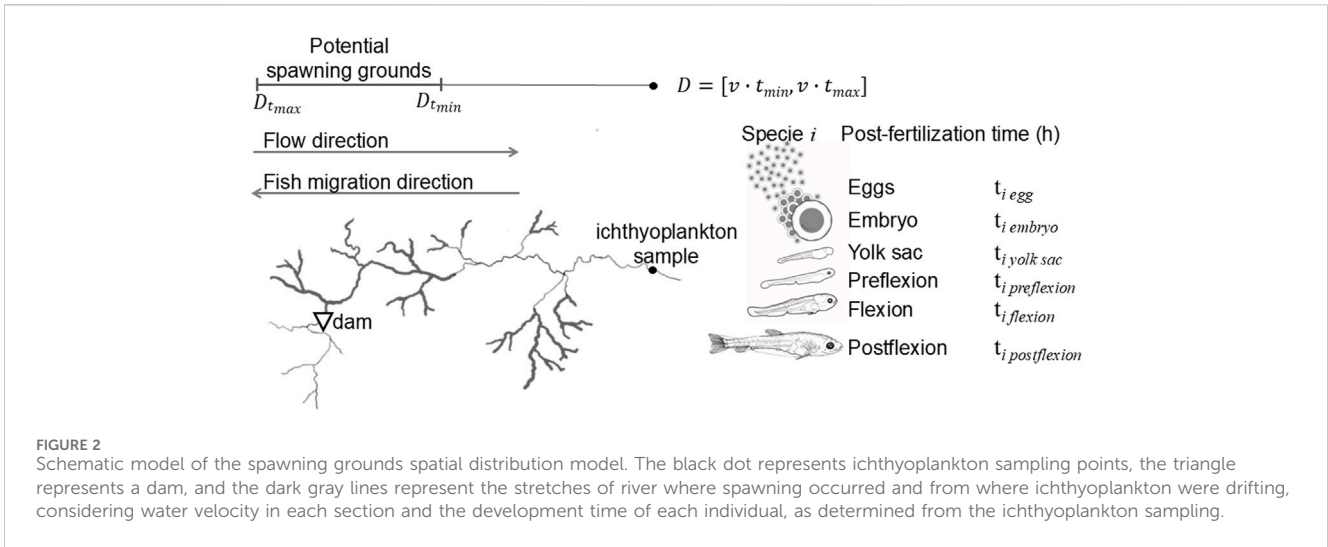
Data were collected from different projects and by different researchers, and all followed standardized ichthyoplankton sampling methods for the basin; data sampling was done daily over 15 consecutive days during at least two different reproductive seasons (Jiménez-Segura, 2007). All larvae were classified by development phases and taxonomically or genetically identified by experts in the Universidad de Antioquia, Universidad Surcolombiana, or Centro de Investigación Piscícola de la Universidad de Córdoba. Genetic identification was used in the TNC-UA data set, which allowed for the classification of species that are difficult to identify in their first stages of life, such as two species from the genus *Pimelodus* (*Pimelodus grosskopfii* and *Pimelodus yuma*).

TABLE 1 Name and location of the ichthyoplankton sample points and origin of the data sets.

ID	Sampling point	Locality (latitude; longitude)	Data origin
1	Magdalena River Main Channel I	Upstream La Miel River (5°45'37.63"N; 74°39'41.77"W)	Field work
2	Samaná Sur River	San Miguel (5°42'8.12"N; 74°44'29.66"W)	Field work
3	Magdalena River Main Channel II	Upstream Nare River (6°10'51.49"N; 74°35'2.31"W)	Field work
4	Nare River	Puerto Nare (6°12'42.56"N; 74°36'36.03"W)	Field work
5	Magdalena River Main Channel III	Puerto Berrío (6°29'18.27"N; 74°23'53.06"W)	Field work
7	Carare River	Puerto Parra (6°46'5.46"N; 74° 6'25.14"W)	Field work
9	Opon River	Yondó (6°56'48.17"N; 73°53'17.89"W)	Field work
10	Magdalena River Main Channel IV	Barrancabermeja (7°11'14.25"N; 73°56'6.05"W)	Field work
11	Sogamoso River	Barrancabermeja (7°11'57.95"N; 73°54'39.71"W)	Field work
13	Boque River	Simití (7°53'2.31"N; 73°55'53.78"W)	Field work
14	Cesar River	Puente Canoa (9°39'1.54"N; 73°38'45.19"W)	Field work
16	San Andrés River	Ituango (7° 7'52.43"N; 75°39'55.70"W)	Field work
17	Espíritu Santo River	Espíritu Santo (7°14'58.85"N; 75°26'20.01"W)	Field work
18	Cauca River Main Channel I	Valdivia (7°15'4.04"N; 75°26'30.48"W)	Field work
19	Cauca River Main Channel II	Caucasia (7°57'36.61"N; 75°11'57.85"W)	Field work
20	Nechí River	Nechí (8° 5'36.85"N; 74°45'7.75"W)	Field work
21	San Jorge River	San Jorge River at bridge autopista Cauca - Planeta Rica (8° 4'4.36"N; 75°21'30.10"W)	Field work
22	Cauca River Main Channel III	Pinillos (8°54'49.39"N; 74°28'49.47"W)	ANLA reports
23	Cauca River Main Channel IV	Cáceres (7°34'44.75"N; 75°21'23.14"W)	ANLA reports
24	Magdalena River Main Channel V	Puerto Seco (2°29'42.82"N; 75°32'36.02"W)	ANLA reports
25	Magdalena River Main Channel VI	RM (2°20'6.82"N; 75°36'56.87"W)	ANLA reports
26	Cauca River Main Channel V	Buga (3°55'3.37"N; 76°19'46.79"W)	ANLA reports
27	Cauca River Main Channel VI	La Virginia (4°53'11.03"N; 75°52'18.64"W)	ANLA reports
28	Cauca River Main Channel VII	La Pintada (5°44'44.58"N; 75°36'25.71"W)	ANLA reports
29	Cauca River Main Channel VIII	Santafe de Antioquia (6°33'31.84"N; 75°48'4.37"W)	ANLA reports
30	Cauca River Main Channel IX	La Ilusión (8° 1'0.97"N; 75° 4'57.92"W)	ANLA reports
31	Magdalena River Main Channel VIII	Bengala (2°21'18.3"N 75°35'55.6"W)	Emgesa Field work
32	Magdalena River Main Channel IX	Peña Alta (2°10'7.70"N 75°41'23.73"W)	Emgesa Field work
33	Magdalena River Main Channel X	Puerto Seco (2°29'14.2"N 75°34'05.8"W)	Emgesa Field work
34	Suaza River	Upstream from the Magdalena (2°10'22.8"N 75°40'11.5"W)	Emgesa Field work
35	Páez River	Upstream from the Magdalena (2°26'51.8"N 75°34'39.3"W)	Emgesa Field work
36	Magdalena River Main Channel XI	Bilú (2°34'56.15"N 75°29'39.10"W)	Emgesa Field work

Samples came from 36 localities across the basin. Nevertheless, the lower basin of both the Magdalena and Cauca rivers, as well as the upper Cauca River, were under-represented because a majority of the data were collected from the TNC-UA data sets, which was focused on the middle Magdalena basin, while ANLA environmental licensing reports contained data about hydropower generators, excluding significant parts of the basin.

A literature review was conducted to set up the post-fertilization time (in hours) of each development stage for each of the species reported in the data sets. During the study review period, each collected individual for a single fish species takes to reach the development phase in which it was collected. The review searched for information on the early development of migratory fish from the Magdalena Basin, or congeneric and related species of



the Magdalena or other neotropical basins, for those species with unknown development time. Most of the reports corresponded to initial development under controlled conditions at water temperature of 26°C to 28°C (Contreras and Contreras, 1989; Atencio, 2001; Nakatani et al., 2001; Aristizábal-Regino et al., 2004; Novoa and Cataño, 2005; Arias-Gallo et al., 2010; Valbuena-Villarreal et al., 2012b; Valbuena-Villarreal et al., 2012a; Stevanato, 2016; Montes-Petro et al., 2019; Arashiro et al., 2020). This time of initial development was used to determine downstream drifting time from a spawning ground.

2.3 Modeling and data analyses

The tier 1 complementary tool is a combined method using a hydraulic approximation to create the average flow velocity (flow time) and ichthyological records from embryonic and larval sampling.

First, a topological fluvial network for the Magdalena basin was created using a digital elevation model (SRTM, 90 m) and a conventional GIS procedure described by Baumbach et al. (2015). This resulted in a topological network with 34,046 river stretches with a Strahler order ranging from 1 to 8. Data from the Institute of Hydrology and Meteorology of Colombia (IDEAM, 2023) were used to determine annual mean flow for each reach and to correlate flow and cumulative precipitation.

Using aerial photographs and satellite images, and considering wide rectangular channels, the association between hydraulic radius and mean annual flow was estimated. To estimate the velocity (U) for each reach in the drainage network, the Manning equation was used:

$$U = \frac{1}{n} R_h^{2/3} S^{1/2},$$

where S denotes the slope of the reach and was calculated from the digital elevation model. R_h is the hydraulic radius and was deduced

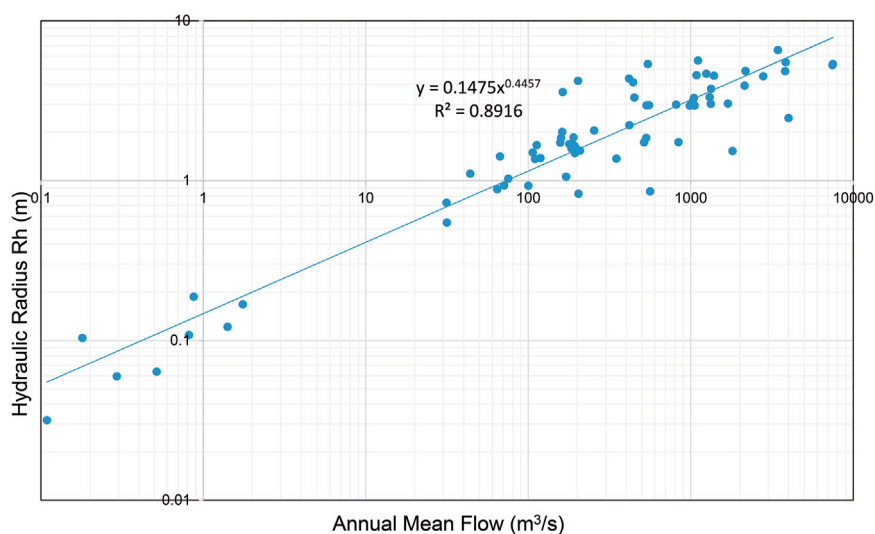


FIGURE 4
Relation between annual mean flow and hydraulic radius for the Magdalena basin.

using the relation between cumulative precipitation and annual mean flow for the Magdalena basin (Figure 3), and n represents roughness, which was estimated according to the values recommended by Bathurst (1997) based on channel slope (Manning, 1891). Using these data as a tier 1 approximation, velocity could be calculated for each reach of the system.

After determining the velocities, the flow time was calculated as

$$t = \frac{L}{U}$$

where t is the flowing time and L denotes the reach length.

After estimating the flow time for each reach, an efficient algorithm in MATLAB (MathWorks, 2017) was developed to analyze the topological fluvial network. In this code, the user must define the location of the ichthyological sample including information on the development time (embryonic or larval stage) for each collected species, i.e., the time from spawning. To delimit a river stretch, it was necessary to set up a maximum and a minimum time for each species, otherwise spawning ground would be marked as a dot. An elevation and a Strahler order limit were set to delimit the accumulation of river stretches. The algorithm accumulates the flow time through the river network from the arc (river stretch) where the collection of the sample was indicated. Based on simple time rules of embryonic or larval time development obtained from literature, the potential stretches where spawning occurred were identified for each of the analyzed fish species (Figure 2). The algorithm was also used to locate the barriers (e.g., hydropower projects) to consider the effects of infrastructure in the topological network. The hydropower project sites were used from the 1979 master plan formulated by the Colombian government with support from the German Cooperation Agency, which generated approximately 100 points on the Magdalena River main stem, as well as several of its tributaries (DNP, 1979).

In Colombia, dams are generally located in Andean regions, upstream of key feeding and growth habitats in the floodplains. As Colombian dams are typically big (>15 m in height) and lack fish

passage facilities, they act as barriers to fish reaching these critical spawning areas. Moreover, in addition to the impacts of habitat loss and isolation, even when trapped individuals might spawn in the reservoir upstream of the dam, reservoirs located between spawning grounds and floodplains can entirely block the downstream drift of eggs and larvae, thereby preventing them from reaching their critical feeding and growing habitats (Pelicice and Agostinho, 2008). Consequently, all upstream river stretches of a dam, identified in the baseline as potential spawning grounds were considered lost. In our algorithm, this type of disconnection meant that spawning drift was interrupted downstream by these barriers. To simulate this, in the special arcs where a barrier is located, the cumulative flow time is set to zero. It implies that spawning drift is completely interrupted in these arcs and travel time is reset in the arc downstream of the barrier, assuming total interruption of connectivity.

Additionally, to highlight the importance of some river basins or river sections, the richness of potential spawners in each river stretch was plotted by accumulating the number of species that potentially spawn in it.

3 Results

The ichthyoplankton samples were abundant and representative of modeling concerns. We obtained 102,303 individuals (embryos and larvae) registered in samples collected by the TNC-UA, comprising 19,748 individuals in mid-2013 and 82,555 individuals in 2014. Additionally, 2,932 larval individuals from 11 potamodromous fish species were extracted from 15 reports submitted to ANLA between 2013 and 2018. Fifteen individuals were obtained from data sets provided by ENEL-EMGESA, collected between 2014 and 2017. A final data set of 105,250 individuals and 15 fish species was used in the analysis.

In the proposed model, the river basin topological network developed consisted of 101,110 km of rivers represented in 34,046 river stretches, and mean annual flow and cumulative

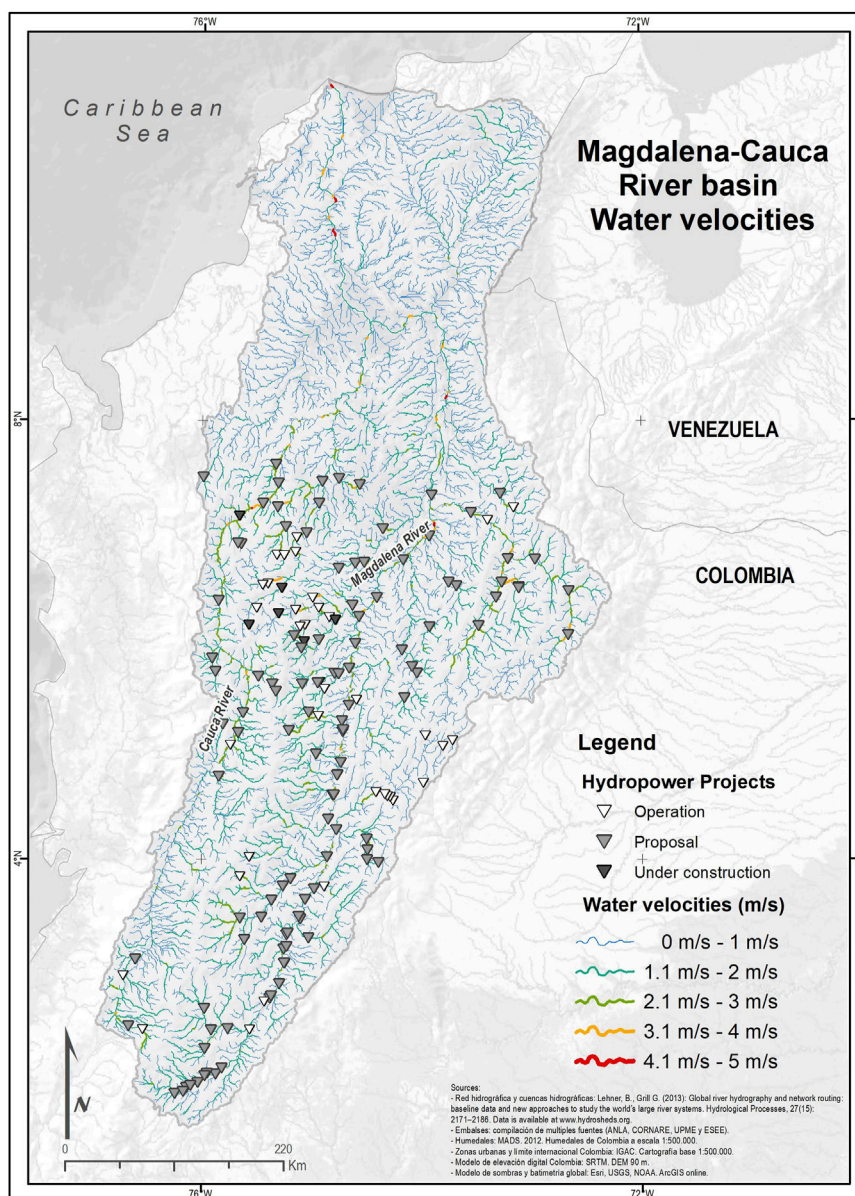


FIGURE 5
Water velocities estimated for the river network of the Magdalena basin.

precipitation in this network were both positively and significantly correlated with hydraulic radius and mean annual flow (Figures 3, 4). The relation between hydraulic radius and mean annual flow can be represented by the following:

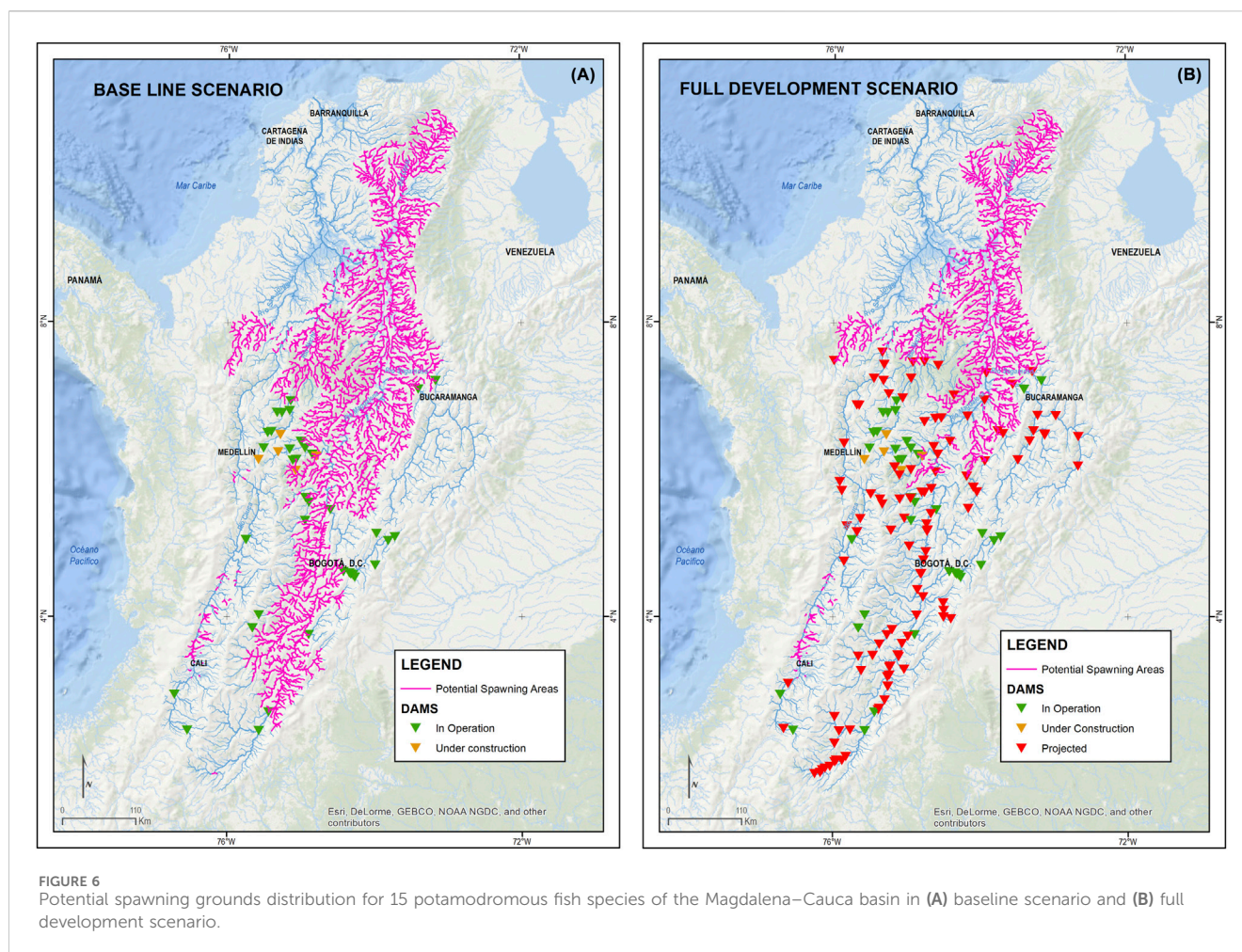
$$Rh = 0.145Q^{0.4457}.$$

The velocities obtained from the modeling process for the entire basin ranged between 0.01 m/s and 4.89 m/s (Figure 5), whereas the velocities obtained using the flowmeter for days when eggs and larvae occurred in the samples ranged between 0.20 m/s and 4.86 m/s.

Through a simple algorithm, potential spawning areas in the Magdalena–Cauca basin were delimited considering the effects of the barriers. With an elevation limit of 1,000 m a.s.l. for the accumulation of spawning areas, the potential spawning grounds

for the 15 processed species in the current (baseline) scenario accounted for 11,370 km of rivers, including Strahler order from two to eight (Figure 6A), corresponding to 11.2% of the 101,110 km of the total network) or 3656 river stretches of the basin topological network. The spawning grounds overlapped with 80 hydropower projects (56.7% of the total). Under the scenario for full development of the hydropower portfolio, spawning areas were predicted to be reduced by 45.0% for river kilometers and 45.8% for river stretches (Figure 6B; Table 2).

Total spawning area length differed by species and between the baseline and full development scenarios. Species like *Pseudoplatystoma magdaleniatum*, *M. muyscorum*, and *Prochilodus magdalenae* had a larger number of potential rivers available for spawning, ranging from 7.9% to 9.9% of the Magdalena basin river network, while other species like *S. affinis* and from the



genus *Brycon* had fewer and more restricted spawning areas, respectively, comprising 1.2% and ~2%, of the river network. Species that were difficult to identify as larvae, which may have been underestimated in samples, such as those from the genera *Pimelodus*, *Pseudopimelodus*, and *Astyanax*, had smaller areas, ranging from 0.1% to 5.7% of the river network (Table 1). Samples collected for *Pseudopimelodus atricaudus* species in the Cauca River did not have spawning areas available under the baseline scenario due to recent dam construction.

Potential habitat loss for each species differed among the analyzed fish species and was independent of the total length of respective spawning areas. Species with restricted spawning grounds and those with widely distributed spawning grounds were predicted to have significant habitat loss under the full hydropower project portfolio development scenario. Species with restricted reproductive areas, like those from the genera *Pseudopimelodus* and *Brycon*, were predicted to be worse affected, with respective losses of 73% and 65% of reproductive habitats, while species like *S. affinis* and those of the genera *Astyanax* and *Pimelodus* were potentially the least affected. Fish species with wide spawning ground distributions, like *P. magdalenae* and *M. muyscorum*, were predicted to lose approximately half (55.9% and 50.3%, respectively) of their reproductive areas (Table 1).

Spawning areas are not homogeneously distributed in the basin, and some river stretches showed higher richness of spawners species

than others. In both the baseline and full development scenario, there are some river stretches in which up to 10 species spawn, whereas in other spawning areas, one species was found (Figures 7, 8). In both hydropower scenarios, spawner species richness mode was five species (Figure 8) in the largest number of river sections. Greater habitat loss was experienced on river sections with three, nine, and ten fish spawners species (60.2%, 74.7%, and 56.2% of the cumulative spawning area, respectively), while river stretches with one or two species loss were less than 20% of its area (Figure 8). Dam projects on rivers stretch with a higher Strahler order and located in a central position of the basin, demonstrated a greater number of predicted impacts, as shown by spawning grounds loss, than those located at the headwaters of the river network (Figure 7). Due to limited data available from the upper and middle Cauca River and the lower Magdalena River basins, their potential spawning grounds could not be precisely determined for those river stretches.

4 Discussion

Species distribution models are quantitative tools that combine species occurrence data with environmental estimates, thereby offering valuable insights into ecology and evolution while predicting distributions across landscapes (Elith and Leathwick,

TABLE 2 Potential spawning grounds length (km of rivers or number of rivers stretches) for each of the analyzed fish species in the baseline and full hydropower development scenarios and potential habitat loss between the two scenarios. Knowing the migratory fish behavior, the model was restricted to river stretches between 3 and 8 Strahler order and below 1,000 m a.s.l.

Species	Spawning grounds length				Habitat loss	
	Baseline scenario		Full development scenario		(km)	(%)
	(km)	(% of total network)	(km)	(% of total network)		
<i>Astyanax</i> spp	3941.1	3.9	2493.1	2.5	1448.0	36.7
<i>Brycon</i> spp	1985.9	2.0	683.1	0.7	1302.8	65.6
<i>Curimata mivartii</i>	5624.3	5.6	3091.0	3.1	2533.3	45.0
<i>Megaleporinus muyscorum</i>	8758.1	8.7	4352.8	4.3	4405.3	50.3
<i>Pimelodus</i> spp	4223.4	4.2	2741.4	2.7	1482.1	35.1
<i>Pimelodus grosskopfii</i>	121.4	0.1	61.3	0.1	60.1	49.5
<i>Pimelodus yuma</i>	121.4	0.1	61.3	0.1	60.1	49.5
<i>Prochilodus magdalenae</i>	8011.9	7.9	3536.8	3.5	4475.1	55.9
<i>Pseudopimelodus</i> spp	5800.0	5.7	1570.6	1.6	4229.4	72.9
<i>Pseudopimelodus atricaudus</i>	300.7	0.3	280.8	0.3	19.9	6.6
<i>Pseudopimelodus magnus</i>	0.0	0.0	0.0	0.0	0.0	
<i>Pseudoplatystoma magdaleniatum</i>	9970.4	9.9	5166.0	5.1	4804.4	48.2
<i>Salminus affinis</i>	1562.0	1.5	1221.1	1.2	340.9	21.8
<i>Sorubim cuspidatus</i>	5585.1	5.5	3356.8	3.3	2228.3	39.9
<i>Triportheus magdalenae</i>	4294.0	4.2	2221.7	2.2	2072.3	48.3
Total km of rivers	11,370.2	11.2	6257.8	6.2	5112.4	45.0
River stretches (n)	3656		1982		1674.0	45.8
% of stretches of the total network	10.7		5.8			

2009). The proposed model, with its simple assumptions and calculations, and without rigid limits or data extrapolations, serves as a Tier 1 tool for rapid assessments and early planning, aiming to minimize environmental impacts. Its reliance on ichthyoplankton samples and current knowledge of embryonic and larval development enables efficient mapping of potential spawning areas at the macro-basin scale, despite its spatial and temporal limitations. Furthermore, it provides a foundation for ecosystem-based management planning (Langhans et al., 2019). Moreover, the model allows for easy improvement with the incorporation of new data.

This study has some limitations, such as gaps in sampling coverage and incomplete knowledge of developmental stages for some species, although this is the first time that a map of spawning areas has been obtained for Colombia. Notably, spawning grounds were likely underestimated due to limited data from several key sections of the river, while some species could not be modeled because of a lack of early developmental data, even among congeneric species. Similarly, inadequate sampling frequency and imprecise taxonomic identification could dramatically affect the determination of the major spawning rivers and the detection of spawning events of some migratory species (Pompeu et al., 2023). Thus, some migratory species (*Cynopotamus magdalenae*, *Cyphocharax magdalenae*, *Ichthyoelephas longirostris*, and

Pimelodus cripticus) recognized as migratory in the basin (López-Casas et al., 2016; Jiménez-Segura et al., 2020), were found absent in our samples, highlighting the need for broader temporal and spatial data collection. Taxonomic challenges in identifying species of taxonomically challenging groups of species (*Astyanax* spp, *Brycon* spp, *Pimelodus* spp, and *Pseudopimelodus* spp) at early life stages also require genetic tools for improved accuracy.

Notably, data sets were compiled from different years. Specifically, data on *Pseudopimelodus atricaudus* were collected in the Cauca River before the construction of the Hidroituango dam. Currently, the river is dammed, and the model recognizes the dam as a barrier to fish migration, resulting in no identified spawning areas in the baseline scenario. Still, to improve the accuracy of quantifying available spawning kilometers, we explored the possibility of constraining the network using the river's Strahler order and altitude. A deeper understanding of spawning ground requirements—incorporating geomorphological and hydraulic factors—could further refine this approach. Furthermore, integrating hydrodynamic models could significantly improve the spatial and temporal resolution of our analysis, offering a more comprehensive and precise understanding of spawning habitats.

Overlaying spawning grounds and hydropower projects provides a useful approach for prioritizing hydropower dam planning. With a portfolio of more than 100 planned projects in

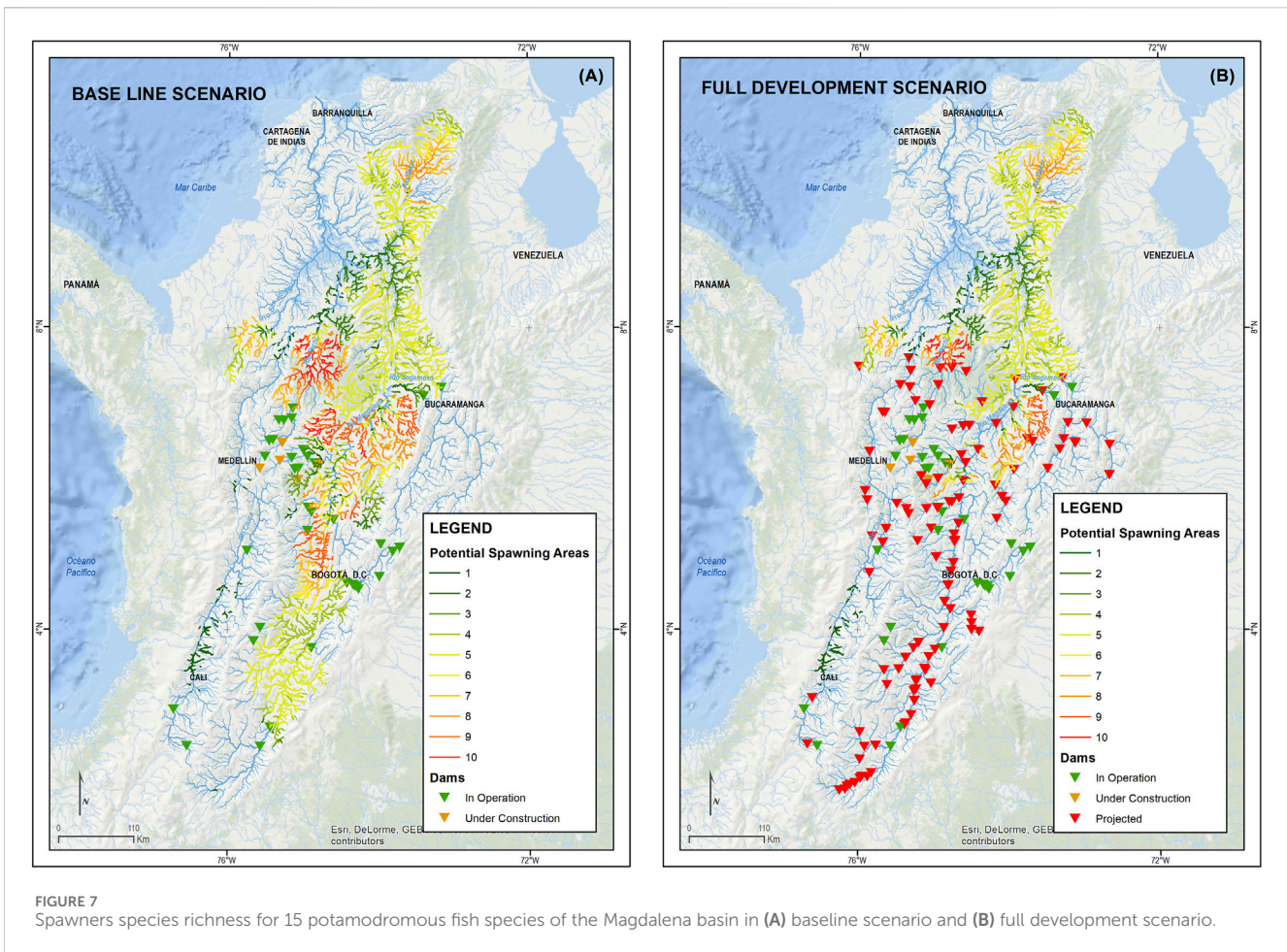


FIGURE 7 Spawners species richness for 15 potamodromous fish species of the Magdalena basin in (A) baseline scenario and (B) full development scenario.

the basin (DNP, 1979), the absence of suitable policies that address river fragmentation and conservation of potamodromous fish species underscores the importance of the current analysis. By prioritizing projects based on basin-wide planning, policymakers can better balance hydropower development with freshwater biodiversity conservation. This information can be considered in the early planning stages of a project at the macro-basin scale to eliminate or minimize environmental impacts and find optimal.

Our findings emphasize the need for integrated, basin-wide cumulative impact assessments rather than the traditional isolated project evaluations. Typically, EIAs consider the potential habitat impacts and loss associated with an individual project only. Therefore, a single project may be approved for construction, despite causing minimal habitat loss (measured in river kilometers of spawning grounds) for one or a few species. Yet, when viewed at the macro-basin scale, these river kilometers may represent critical habitats for species with limited spawning grounds (such as *Brycon* spp. and *Pseudopimelodus* spp.). Therefore, this seemingly minor loss can have far-reaching consequences, compromising the ecosystems' ability to sustain these species and their fisheries.

Prioritizing regional and basin-wide planning for dam placement is crucial for striking a balance between conflicting energy and biodiversity interests in the energy sector while ensuring that freshwater ecosystems remain functional to support migratory fish populations and the services these species and

ecosystems provide, as suggested to invigorate freshwater conservation (Flitcroft et al., 2019). Nevertheless, it is crucial not only to preserve the spawning grounds but also to feed and grow habitats (the floodplain systems) and the river stretches that connect them. This integrated approach is vital for preserving essential global freshwater ecosystem services and effectively addressing the current freshwater biodiversity crisis (Albert et al., 2021).

Our results revealed that certain river stretches and basins are more critical as spawning habitats for potamodromous fish than others, indicating that not all rivers are of equal importance for the conservation and maintenance of these species. Though it may seem intuitive to prioritize spawning areas with high species richness, such as those supporting 11 species, conservation efforts should instead focus on river stretches that encompass the entire distribution of each species. This approach aligns with the principles of systematic conservation planning. This stresses the need for comprehensive landscape management strategies that balance production and protection (Margules and Pressey, 2000), following comprehensiveness, adequacy, representativeness, and complementarity criteria.

Dam projects occupying a central position in the network have greater impacts on habitat loss for the reproduction and maintenance of potamodromous fish species. Although we could not conduct a comprehensive analysis of the Magdalena hydropower project portfolio, the maps indicated that projects

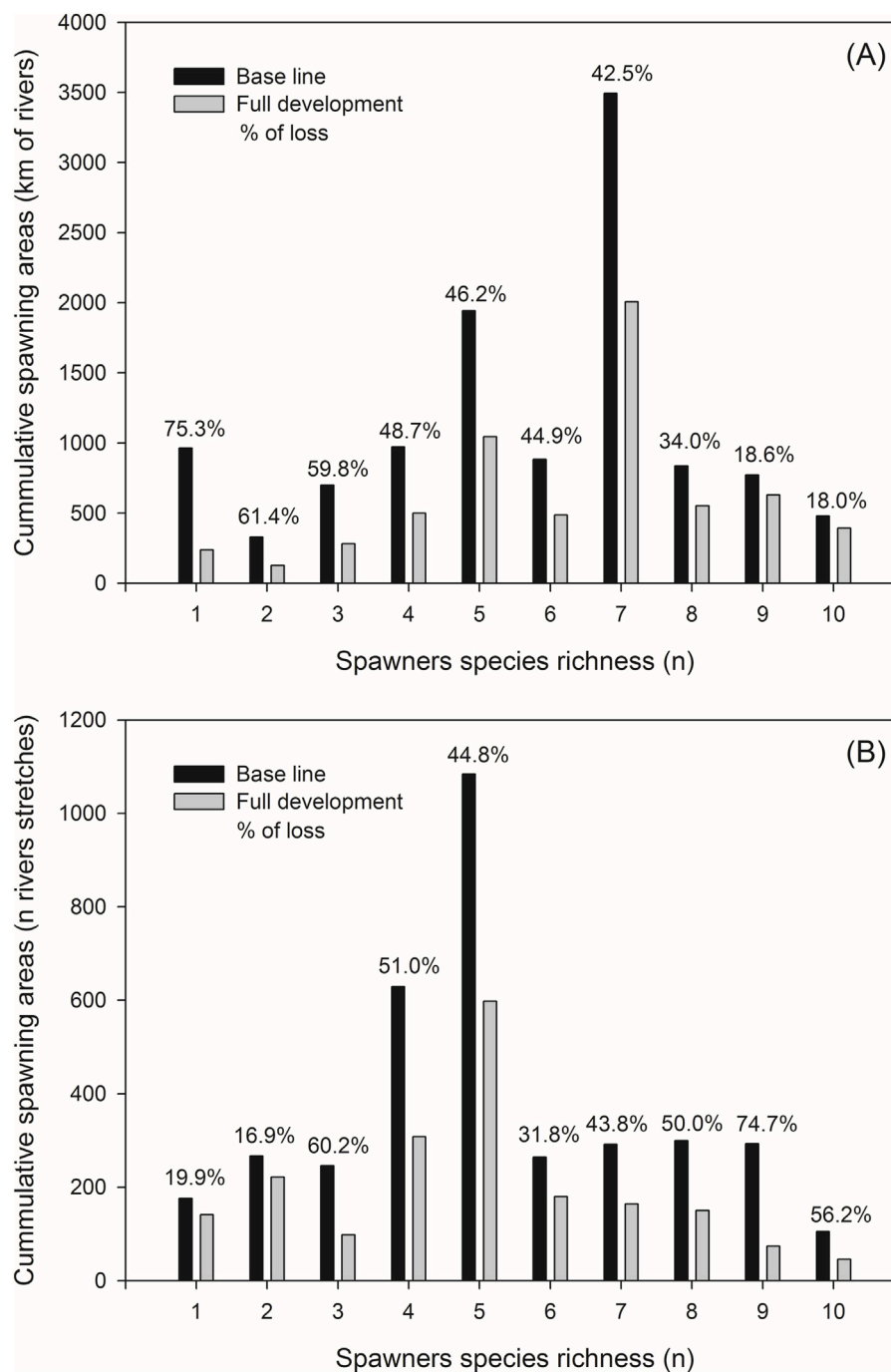


FIGURE 8 Cumulative spawning areas by species richness values calculated for 15 potamodromous fish species of the Magdalena basin in baseline scenario (dark gray) and full development scenario (light gray). (A) Length. (B) Number of river stretches.

located on major rivers (Strahler orders 8 and 7, such as the Cauca and Magdalena Rivers) tended to have more impacts and would disproportionately affect critical spawning habitats for commercially and ecologically significant potamodromous fish. Notably, even a single project can lead to the loss of critical habitats for multiple species, resulting in the elimination of spawning areas with both high and low species richness. This risk stresses the importance of maintaining connectivity within dendritic river systems for fish and fisheries conservation (Koning et al., 2020) as documented in the

emergency recovery plan to bend the curve of global freshwater biodiversity loss (Tickner et al., 2020).

5 Conclusion

The present study demonstrates the application and potential benefits of the proposed model, in minimizing habitat loss through a quantitative case study of hydropower development in the

Magdalena River basin. The results elucidate how the proposed model can help minimize environmental impacts for projects, particularly those related to the loss of critical spawning areas for potamodromous fish species and disruptions to fish migration patterns that affect fisheries, considering that projects are part of a larger system. Furthermore, we can also conclude that the model can also help identify solutions that balance economic benefits with biodiversity conservation, resulting in lower environmental and social impacts and greater economic benefits.

Data availability statement

The code associated with this paper is openly available at https://github.com/N4W-Facility/Spawning_Ground_Model.

Ethics statement

Ethical approval was not required for the study involving animals in accordance with the local legislation and institutional requirements because we used datasets of ichthyoplankton samples from different projects, so we did not handle or use live animals.

Author contributions

SL-C: conceptualization, data curation, formal analysis, methodology, supervision, visualization, writing–original draft, and writing–review and editing. CR-P: conceptualization, formal analysis, methodology, software, validation, visualization, writing–original draft, and writing–review and editing. VA-G: data curation, formal analysis, writing–original draft, and writing–review and editing. CM-Á: data curation, writing–original draft, and writing–review and editing. DA: data curation, writing–original draft, and writing–review and editing. KR-C: data curation, writing–original draft, and writing–review and editing. LJ-S: data curation, writing–original draft, and writing–review and editing.

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Conflict of interest

Author DA was employed by Integral S.A.

The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fenvs.2025.1425804/full#supplementary-material>

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