

Development of microsatellite loci and population genetics of the catfish *Pimelodus yuma* (Siluriformes: Pimelodidae)

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Pimelodus yuma (formerly *Pimelodus blochii*) is a freshwater fish, endemic to the Colombian Magdalena-Cauca and Caribbean basins that experiences habitat disturbances resulting from anthropogenic activities. Due to the lack of information about the population genetics of this species, this study developed 14 species-specific microsatellite loci to assess the genetic diversity and population structure of samples from the lower section of the Cauca River. The studied species showed genetic diversity levels higher than the average values reported for Neotropical Siluriformes and significant inbreeding levels as was described for some congeners. Furthermore, *P. yuma* comprises two coexisting genetic groups that exhibit gene flow along the lower section of the Cauca River. This information constitutes a baseline for future monitoring of the genetic diversity and population structure in an anthropic influenced sector of the Magdalena-Cauca basin.

Keywords: Freshwater fish, Genetic diversity, Gene flow, Molecular marker, Next generation sequencing.

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Pimelodus yuma (anteriormente *Pimelodus blochii*) es un pez dulceacuícola endémico de las cuencas colombianas Magdalena-Cauca y Caribe que experimenta alteraciones del hábitat como resultado de actividades antropogénicas. Debido a la falta de información sobre la genética poblacional de esta especie, este estudio desarrolló 14 loci microsatélites especie-específicos para evaluar la diversidad genética y la estructura poblacional de muestras de la sección baja del río Cauca. La especie estudiada mostró niveles de diversidad genética más altos que los valores promedio reportados para Siluriformes neotropicales y niveles de endogamia significativos como se describió para algunos congéneres. Además, *P. yuma* comprende dos grupos genéticos coexistentes que exhiben flujo de genes a lo largo de la sección baja del río Cauca. Esta información constituye una línea base para futuros monitoreos de la diversidad genética y la estructura poblacional en un sector de influencia antrópica de la cuenca Magdalena-Cauca.

Palabras clave: Diversidad genética, Flujo genético, Marcadores moleculares, Peces de agua dulce, Secuenciación de próxima generación.

INTRODUCTION

Seasonally migratory patterns may influence the gene flow or genetic structure in the natural populations of fishes of the family Pimelodidae. Since the gene flow is only possible if the fishes successfully reproduce once they have arrived at their new site (Freeland, 2020), both the migrations and reproductive cycles explain the gene flow in *Pimelodus maculatus* Lacepède, 1803 in the upper section of the Uruguay River, Tibagi River basin, or Tietê River (Almeida *et al.*, 2001; Almeida *et al.*, 2003; Ribolli *et al.*, 2012) and in *Pseudoplatystoma corruscans* (Spix & Agassiz, 1829) in the São Francisco River (Dantas *et al.*, 2013) and the Paraguay basins in Brazil (Prado *et al.*, 2017).

Despite the lack of spatial genetic structure, discrete genetic stocks that cohabitante the same river area during the migratory period has been observed in *Pseudoplatystoma reticulatum* Eigenmann & Eigenmann, 1889 in Paraná-Paraguay basin (Prado *et al.*, 2017) and *Pimelodus grosskopfii* Steindachner, 1879 in the Cauca River (Restrepo-Escobar, Márquez, accepted). Additionally, some species in the genera *Pimelodus*, *Pseudoplatystoma* and *Steindachneridion* exhibit genetic structure explained by short-distance migration range, isolation by distance, geographical accidents, disconnections among rivers, or homing behavior (Sekine *et al.*, 2002; Almeida *et al.*, 2003; Ramella *et al.*, 2006; Pereira *et al.*, 2009; Abreu *et al.*, 2009; Carvalho *et al.*, 2012; Telles *et al.*, 2014; Fonseca *et al.*, 2017; Prado *et al.*, 2017).

Pimelodus yuma Villa-Navarro & Acero, 2017 is one of the 36 valid species of the genus *Pimelodus* Lacepède, 1803 (Fricke *et al.*, 2020) distributed in Cauca, Magdalena and Sinú River drainages in Colombia (Villa-Navarro *et al.*, 2017). This species and their congener *Pimelodus crypticus* Villa-Navarro & Cala, 2017 were both considered as *Pimelodus blochii* Valenciennes, 1840 before 2017 (Villa-Navarro *et al.*, 2017). Currently, there are no reports of any risk category for *P. yuma* in the Colombian red list of threatened freshwater fishes (Mojica *et al.*, 2012) or in the red list of threatened species of the International Union for

Conservation of Nature, IUCN. Nevertheless, there is concern about the real status of the species considering the available information of fisheries in the Magdalena-Cauca basin.

Based on the bioeconomic model analysis, *P. yuma* is considered overexploited (Gutiérrez *et al.*, 2011). Additionally, fisheries and the fish production modeling data show a decline in number of captures from 17,969 tons in 1975 to 8,370 tons in 2016, indicating the high fishing pressure exerted over this catfish (Barreto Reyes, 2017). Additionally, other factors that compromise this species are the pollution of water due to disposal materials, anthropogenic disturbance of hydrodynamics of the river (hydropower stations), deforestation, and introduction of alien fish species (Jiménez-Segura *et al.*, 2016; Tognelli *et al.*, 2016). Nonetheless, studies of population genetics of *P. yuma* remain absent, although they could provide information to estimate the degree of genetic vulnerability of this species.

The use of microsatellite loci permits a high-sensitivity evaluation of the population genetic diversity due to their polymorphism levels and wide distribution in the genome (Triantafyllidis *et al.*, 2002). Additional to these advantages, considering the high mutation rates of microsatellite loci, they are also useful to examine recent events (Chistiakov *et al.*, 2006). Despite of the available microsatellite loci for three species within the genus (Paiva, Kalapothakis, 2008; Restrepo-Escobar, Márquez, 2020; Savada *et al.*, 2020) and some others within Pimelodidae (Batista *et al.*, 2010; Carvalho, Beheregaray, 2011; Saulo-Machado *et al.*, 2011; Souza *et al.*, 2012; Prado *et al.*, 2014), their use for studying the population genetics of *P. yuma* may be problematic. The limitations of cross-amplification of microsatellite loci, related to unsuccessful amplification in phylogenetically distant species (Barbará *et al.*, 2007), include low levels of polymorphism, presence of null alleles (Rutkowski *et al.*, 2009), allele size homoplasy (Estoup *et al.*, 2002), and inability to evaluate properly orthologous loci (Yue *et al.*, 2010).

Since *Pimelodus yuma* was catalogued as a medium-distance migrant (100–500 km) (Usma *et al.*, 2013) and the sampling sites in this study are separated by less than 260 km with a geography lacking slopes, rapids, cascades, the existence of gene flow in *P. yuma* was hypothesized for three sites of the lower sections of the Cauca River. Furthermore, given the anthropogenic intervention in the Magdalena-Cauca basin and the decrease of captures, it is expected a loss in genetic diversity. To test these hypotheses, we developed a set of species-specific microsatellite loci that allow the study of the population genetics for the endemic Colombian catfish.

MATERIAL AND METHODS

This study analyzed 138 muscle tissues of *Pimelodus yuma* from the main channel and floodplain lakes in the lower sections of the Cauca River. Although a sampling effort using gillnet, and cast nets was made along the eight sections of the Cauca River described by Landínez-García, Márquez (2016), this species was found only in the area that corresponds to three sampling sections (S4/5, S6, and S7/8) (Fig. 1, S1). The S4/5 section consists of sites distributed along the main channel of the river and floodplain lakes, whereas S6 and S7/8 encompass floodplain lakes in the lower section of the Cauca River. The analyzed sections were selected according to the availability of samples and geographical distance. All the samples were collected by Integral S.A. from 2011

to 2014, before the construction of the Hydroelectric Ituango Project. The samples, preserved in ethanol 96%, were provided to the laboratory by Integral S.A. through two scientific cooperation agreements (September 19th, 2013; Grant CT-2013).

We followed the methodology described by Landínez-García, Marquez (2018) to develop the species-specific microsatellite loci for *P. yuma*. The DNA isolation was performed in one individual of *P. yuma* from S8, a site of the lower section of the Cauca River. The 454 GS FLX (+) (ROCHE) technology was used for pyrosequencing the previously obtained genomic library. Sequences reads were analyzed with the PRINSEQ-LITE v0.20.4 to assess the quality of the reads and to eliminate sequences with less than 100 bp in length. Then, PAL_FINDER v0.02.03 (Castoe *et al.*, 2010) was used to identify and extract microsatellite loci with perfect di-, tri-, tetra-, penta- and hexa- nucleotide motifs. To design the primers, the flanking sequences of the microsatellite loci were analyzed using PRIMER3 v2.0 (Rozen, Skaletsky, 2000). An electronic PCR (primer-BLAST; available in <https://ncbiinsights.ncbi.nlm.nih.gov/2017/06/28/e-pcr-is-retiring-use-primer-blast/>) was carried out to evaluate the correct alignment of the selected primers.

Forty-one microsatellite loci were selected to evaluate their amplification capacity. To assess PCR conditions (Landínez-García, Márquez, 2016), DNA was extracted with the GeneJET Genomic DNA Purification Kit (ThermoScientific) following the manufacturer's instructions. The amplification capacity of the loci was tested using two random samples

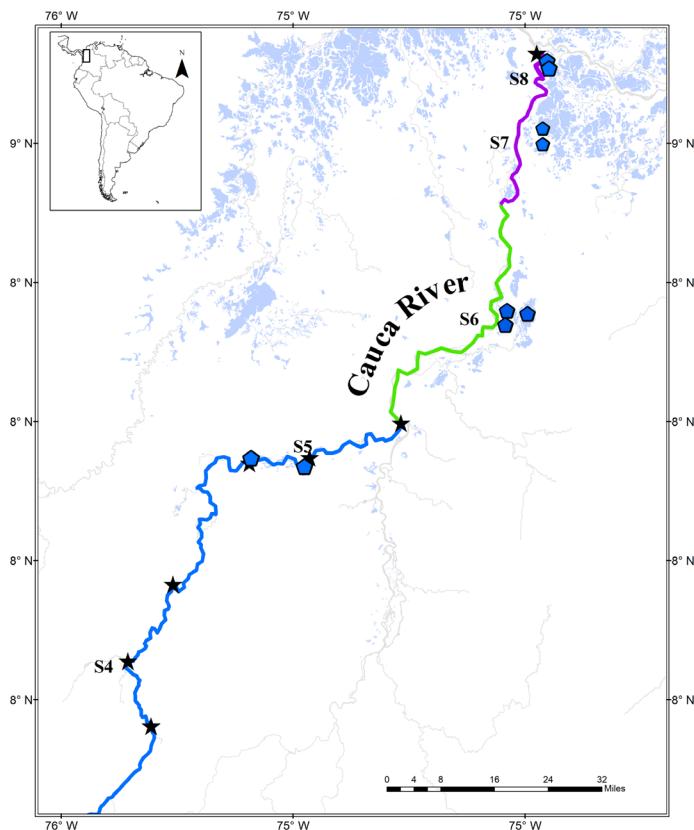


FIGURE 1 | Studied sampling sites of *Pimelodus yuma* along the lower sections (S4–S8) of the Cauca River. The pentagons indicate sampling sites in floodplain lakes and the stars indicate sites along the main channel of the river.

and the products of the amplifications were separated through electrophoresis in 10% polyacrylamide gel setting 100 volts during 45 min in a Mini-PROTEAN Tetra Cell (Bio-Rad) and visualized with silver stain. Then, 28 loci that showed amplification capacity were tested using 12 random DNA samples from the three sections analyzed. Later, 22 loci were selected due to their level of polymorphism and band resolution within 100 and 350 bp in size. A set of 14 microsatellite loci that showed well-defined peaks and absence of stutter bands were considered for population genetic analysis.

The optimal conditions and concentrations for amplification reactions were as proposed by Landínez-García, Marquez (2018) with some modifications described below. In this three-primer strategy, 0.5 pmol/ μ L was used for each of the forward primer labeled in the 5' end with each one the adapters (Blacket *et al.*, 2012), 1.0 pmol/ μ L of each reverse primer and 10–12 ng/ μ L of template DNA. Furthermore, the PCR amplifications were carried out with an initial denaturalization at 94°C for 3 min, followed by 45 cycles consisting of a denaturalization step of 90°C for 22 s and an annealing step of 56°C for 18 s without an extension step or final elongation. The products were separated by electrophoresis in an automatic sequencer ABI 3500 HD (Applied Biosystems), using the GeneScan™ 600 LIZ™ dye size standard (Applied Biosystems), and the allelic sizes were edited using GENEMAPPER ID-X v1.5. Potential genotyping errors were detected using Micro-Checker v.2.2.3 software (Van Oosterhout *et al.*, 2004).

The polymorphic information content (PIC) was calculated with CERVUS v3.0.7 (Marshall *et al.*, 1998) for each locus. The software ARLEQUIN v3.5.2.2 (Excoffier, Lischer, 2010) was used to test Hardy-Weinberg (HW) and linkage equilibrium for all the microsatellite loci. Additionally, in multiple comparisons, the statistical significance was adjusted with the sequential Bonferroni correction (Holm, 1978; Rice, 1989). The genetic diversity estimators, such as allelic diversity, expected (H_E), observed (H_O) heterozygosities, and inbreeding coefficient (F_{IS}), were calculated for each locus and across loci with ARLEQUIN v3.5 (Excoffier, Lischer, 2010).

Evidences of geographical genetic differentiation among populations were examined with the standardized statistics F'_{ST} (Meirmans, 2006), Jost's D'_{EST} (Meirmans, Hedrick, 2011), and an analysis of molecular variance (AMOVA) (Meirmans, 2006) included in GENALEX v6.503 (Peakall, Smouse, 2012). Additionally, a discriminant analysis of principal components was carried out with using the R-package ADEGENET (Jombart, 2008) considering 138 individuals and 18 retained principal components.

The above calculations were complemented with a Bayesian analysis in STRUCTURE v2.3.4 (Pritchard *et al.*, 2000; Falush *et al.*, 2002, 2007; Hubisz *et al.*, 2009). This analysis was performed with 200,000 Monte Carlo Markov Chain (MCMC) steps, 20,000 iterations as burn-in and setting the parameters admixture and non-admixture models, as well as correlated frequencies. The analysis was repeated 20 times per each simulated genetic group (K), which range between 1 and 6 groups. Finally, the web-based software STRUCTURESELECTOR (Li, Liu, 2018) was used to calculate the best estimated K, the estimators MEDMEANK, MAXMEANK, MEDMEDK, MAXMEDK (Puechmaille, 2016), and heuristic scores (Raj *et al.*, 2014). The summarized results of the runs were plotted in a co-ancestry histogram of all the individuals using STRUCTURESELECTOR and the integrated software CLUMPAK (Kopelman *et al.*, 2015). Finally, based on coancestry coefficients obtained with STRUCTURE and CLUMPP v1.1.1 (Jakobsson, Rosenberg, 2007), the individuals were rearranged by genetic stock and then were accordingly analyzed.

RESULTS

A total of 14 microsatellite loci were characterized in this study (Tab. 1); such loci did not show evidence of large allele dropout or stutter bands. Although two loci seemed to exhibit null alleles after Bonferroni correction, the departures from Hardy-Weinberg and heterozygote deficit, also observed in other loci in greater sample size, indicate a possible Wahlund effect (Tab. 2) as discussed below. The number of alleles per locus ranged between 8 and 23 with an average value of 13.071 alleles/locus. The allele sizes were in the expected range (100–350 bp) with a minimum size of 114 bp and a maximum of 347 bp. The polymorphic information content (PIC) showed values ranging from 0.508 to 0.937. Additionally, the observed and expected heterozygosities presented average values of 0.670 and 0.849, respectively. Five of the 14 developed microsatellite loci were excluded from the further genetic diversity analysis pending exploration in a greater sample size (Pyu6, Pyu7, Pyu11, Pyu22, and Pyu32).

TABLE 1 | Sequences and characteristics of 14 polymorphic microsatellite loci selected for *Pimelodus yuma*. Na: number of alleles per locus; Ra: allele size range; H_o and H_e : observed and expected heterozygosities, respectively; P: statistical significance for the tests of Hardy-Weinberg equilibrium; PIC: polymorphic information content.

Locus	Repeat motif	Sequences for forward (F) and reverse (R) primers (5'→3')	Ra	Na	H_o	H_e	P	PIC
Pyu11	(AGTG)n	F: TCGATCCAACCACTTCATCG	241–269	8	0.750	0.704	0.987	0.651
		R: ACAGCTCAGCAGCCATTAGC						
Pyu24	(ATCT)n	F: CTGTTGCTGGCAATACTGG	210–268	13	0.938	0.905	0.910	0.881
		R: TGCACACATTCCAACACCC						
Pyu29	(AAC)n	F: CACTTGTATGAACCAGCTAAAGACC	120–174	17	0.906	0.929	0.439	0.908
		R: CACTGCTGCACACAGACTAAACC						
Pyu15	(ATCT)n	F: AAAATGGCTGATTTAACAGC	156–184	8	0.781	0.859	0.171	0.827
		R: GTGGAGATTACCCATCCTGC						
Pyu03	(ATACC)n	F: CTGGATTGGTTTCACCTGCC	217–347	23	0.813	0.955	0.087	0.937
		R: CCACAGTGAGGAAGACCTGC						
Pyu32	(ATC)n	F: CTGAGCCTGGATGAGTCCC	114–173	17	0.719	0.904	0.018	0.881
		R: TTGTGATGAGGTCACTGTGTGG						
Pyu13	(AGTG)n	F: CAACATACCATATAATGCAACTAGGC	178–210	8	0.406	0.536	0.006	0.508
		R: CTITTCACTTACTCACTGATTACGC						
Pyu6	(ATTAG)n	F: GCATTTCATGGCTGTGTACC	250–285	8	0.656	0.767	0.003	0.718
		R: TGAAACGGTGTGACAGTCC						
Pyu28	(TCTG)n	F: AGAAAAGACAAGAGGCTCGG	114–174	15	0.688	0.885	0.001	0.861
		R: CTCCCCAGACATGACACAGG						
Pyu39	(ATT)n	F: ACAGAGGTTTAGTGTGCC	118–160	13	0.656	0.907	0.000	0.883
		R: TCACCTCTCACTGTACTGC						
Pyu7	(TGTGC)n	F: CATTAGCGCACACCTGTCC	160–235	12	0.656	0.876	0.000	0.849
		R: CCAAAGAGTCAGGGCAGAGC						
Pyu22	(ATCT)n	F: TGCTGAGAAAGTGAGGG	137–195	15	0.375	0.913	0.000	0.891
		R: TCCTAGCTCCTCTTACTGCC						
Pyu10	(ACTG)n	F: CTGACGGATAAGTGAATGAAAGC	200–248	11	0.438	0.875	0.000	0.846
		R: TTCGCGCTCTTAACCTCC						
Pyu02	(AATAG)n	F: TGTGTGCAGTGTCTTGTCCG	205–290	15	0.594	0.872	0.000	0.846
		R: TTTAATCAAACGTCAATAAGTACTCAGG						
Across loci				13.071	0.670	0.849	0.000	0.820

The diversity estimators (Tab. 2) showed the lowest average expected heterozygosity in S4/5 (0.832) and the highest in S7/8 (0.873). The observed heterozygosity exhibited the lowest value in S6 (0.703) and the highest in S4/5 (0.744). Additionally, S4/5 (12.556 alleles/locus) showed the lowest average number of alleles per locus while S6 showed the highest average number (15.889 alleles/locus). Only two of the nine loci were departed from HWE in the three evaluated sites and the other were in the HWE in at least one site. Additionally, the across loci values of the inbreeding coefficients for all analyzed sites showed deficit of heterozygosity ($0.109 < F_{IS} < 0.186$). These levels of genetic diversity and inbreeding were similar to those obtained for the genetic stocks (Stock1 and Stock2) supported by the genetic structure analysis.

Using the pairwise (S4/5-S6, S4/5-S7/8, S6-S7/8) standardized estimators F'_{ST} (-0.014, 0.019, -0.004) and D_{EST} (0.007, 0.011, 0.005) there was not statistical significance among the individuals of the different analyzed sites. Similarly, the AMOVA ($F'_{ST} = -0.003$; $P = 0.605$) and the DAPC (Fig. 2) also showed that there were no differences among the three sections of the river. Hence, the individuals from the three sampling sites were genetically similar.

TABLE 2 | Genetic diversity of *Pimelodus yuma* in three sections (S4/5, S6, and S7/8) of the Cauca River in Colombia. Na: number of alleles per locus; H_o and H_e : observed and expected heterozygosities, respectively; F_{IS} : inbreeding coefficient; P: statistical significance for the Hardy-Weinberg test, values in bold indicate significance after Bonferroni correction.

Sector		Pyu24	Pyu15	Pyu29	Pyu13	Pyu10	Pyu28	Pyu03	Pyu39	Pyu02	Across loci
S4/5 (26)	Na	11	9	16	6	9	13	22	12	15	12.556
	Ho	1.000	0.731	0.962	0.346	0.654	0.769	0.846	0.654	0.731	0.744
	He	0.898	0.818	0.927	0.376	0.828	0.877	0.962	0.893	0.913	0.832
	P	0.126	0.395	0.990	0.151	0.028	0.212	0.032	0.004	0.001	0.000
	F_{IS}	-0.116	0.109	-0.038	0.080	0.214	0.125	0.122	0.272	0.202	0.109
S6 (71)	Na	12	8	17	12	13	19	30	13	19	15.889
	Ho	0.859	0.690	0.859	0.549	0.704	0.662	0.690	0.648	0.662	0.703
	He	0.883	0.821	0.913	0.609	0.858	0.896	0.955	0.905	0.920	0.862
	P	0.152	0.062	0.512	0.150	0.016	0.000	0.000	0.000	0.000	0.000
	F_{IS}	0.027	0.160	0.059	0.099	0.180	0.262	0.279	0.286	0.282	0.186
S7/8 (41)	Na	13	9	17	10	10	16	23	13	17	14.222
	Ho	0.902	0.756	0.951	0.537	0.585	0.756	0.732	0.707	0.634	0.729
	He	0.878	0.828	0.933	0.664	0.889	0.897	0.956	0.904	0.911	0.873
	P	0.708	0.282	0.873	0.000	0.000	0.000	0.000	0.004	0.000	0.000
	F_{IS}	-0.028	0.088	-0.020	0.193	0.345	0.158	0.237	0.219	0.306	0.167
Stock1 (64)	Na	17	9	11	8	8	15	14	15	24	13.444
	Ho	0.891	0.703	0.891	0.453	0.594	0.719	0.703	0.625	0.688	0.696
	He	0.900	0.806	0.881	0.492	0.778	0.872	0.871	0.890	0.931	0.825
	P	0.853	0.452	0.132	0.083	0.023	0.058	0.023	0.000	0.000	0.000
	F_{IS}	0.010	0.129	-0.011	0.080	0.238	0.177	0.194	0.299	0.263	0.157
Stock2 (74)	Na	19	9	15	12	13	21	14	19	30	16.889
	Ho	0.919	0.730	0.905	0.554	0.716	0.703	0.635	0.703	0.770	0.737
	He	0.928	0.828	0.874	0.662	0.892	0.905	0.912	0.918	0.958	0.875
	P	0.776	0.199	0.829	0.001	0.003	0.000	0.000	0.000	0.000	0.000
	F_{IS}	0.009	0.120	-0.036	0.164	0.198	0.225	0.305	0.236	0.197	0.159

The analysis in STRUCTURE showed two genetic stocks that coexist in the studied area (Fig. 3, S2; DeltaK = 2; MEDMEANK, MAXMEANK, MEDMEDK = 2; Mean LnP(K) = -5944.415 and -5930.270, for admixture and non-admixture models, respectively), without evidence of geographical structure. The analysis of diversity of the two stocks found in the study area evidenced that even without a geographical arrangement of the individuals, the heterozygosity deficit (0.000; 0.000) and F_{IS} (0.157; 0.159) were statistically significant for both genetic stocks.

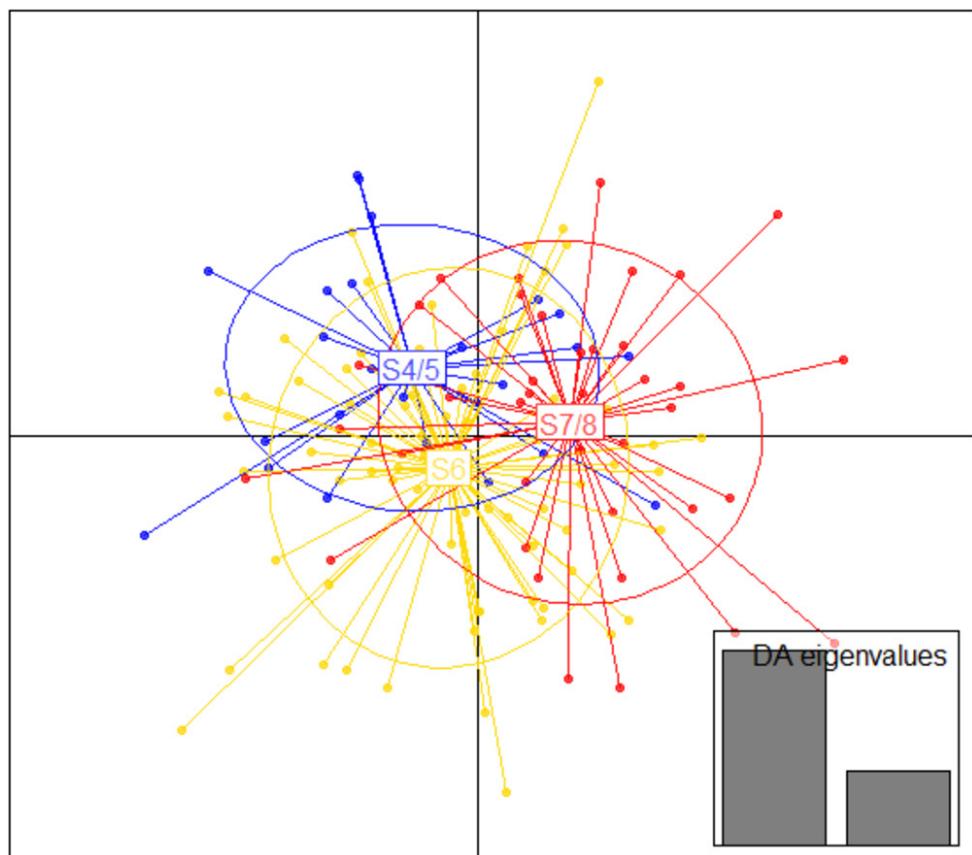


FIGURE 2 | Discriminant analysis of principal components for nine microsatellite loci and 138 individuals of *Pimelodus yuma* in three sections (S4/5, S6 and S7/8) of the Cauca River.

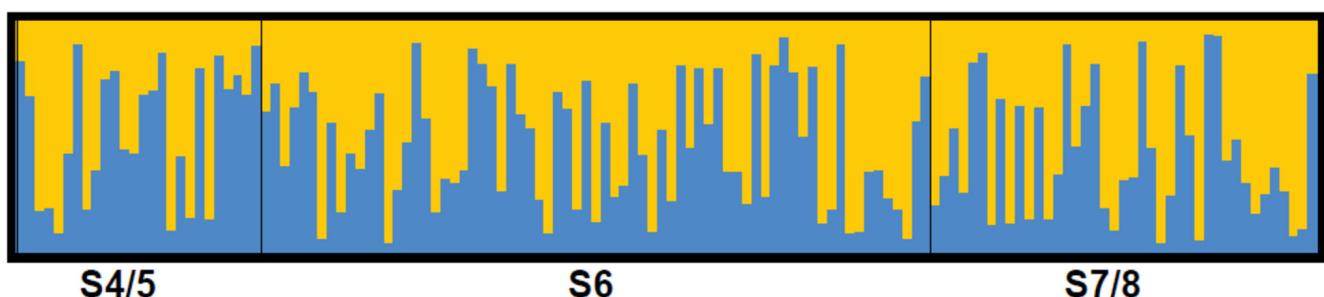


FIGURE 3 | STRUCTURE results for *Pimelodus yuma* showing K= 2 genetic stocks in three sections (S4/5, S6 and S7/8) of the Cauca River.

DISCUSSION

This study developed species-specific microsatellite loci to tests the hypothesis that *Pimelodus yuma* exhibits gene flow in three sites without geographical barriers, separated by less than 260 km in the middle and lower sections of the Cauca River. Among 41 microsatellite loci examined, 14 are considered highly informative showing values of PIC above the range proposed by Botstein *et al.* (1980). These loci exhibited values of average number alleles per locus (13.071) and expected heterozygosities (0.849) lower than those reported in the congener *P. grosskopfii* (Restrepo-Escobar, Márquez, 2020), but higher than those reported in *P. microstoma* Steindachner, 1877 (Savada *et al.*, 2020) and were similar to those reported in *P. maculatus* (Paiva, Kalapothakis, 2008). Furthermore, these values were higher than those reported in *Brachyplatystoma rousseauxii* (Castelnau, 1855) (Batista *et al.*, 2010), *Conorhynchus conirostris* (Valenciennes, 1840) (Carvalho, Beheregaray, 2011), *Pseudoplatystoma reticulatum* (Prado *et al.*, 2014), *Pseudoplatystoma punctifer* (Castelnau, 1855) (Saulo-Machado *et al.*, 2011), and *Phractocephalus hemioliopterus* (Bloch & Schneider, 1801) (Souza *et al.*, 2012).

The genetic analysis of 138 samples of *P. yuma* showed high genetic diversity comparing values of alleles per locus (17.444) and expected heterozygosity (0.861) to those described in Neotropical Siluriformes (N_a : 7.450, H_E : 0.609; Hilsdorf, Hallerman, 2017). Additionally, *P. yuma* showed similar values to those reported for the congeners *P. grosskopfii* (Restrepo-Escobar, Márquez, 2020) and *P. maculatus* (Ribolli *et al.*, 2012). In contrast, *P. yuma* showed higher diversity than the reported for some members of the family Pimelodidae such as *Brachyplatystoma rousseauxii* (Carvajal-Vallejos *et al.*, 2014), *P. coruscans* (Vaini *et al.*, 2016), and *P. reticulatum* (Prado *et al.*, 2017). A high genetic diversity is a desirable characteristic for species, since it helps them to adapt to eventual adverse events (Li *et al.*, 2017).

Despite the high genetic diversity, *P. yuma* exhibited significant deficit of observed heterozygosity that could be explained by several non-excluding alternatives. The presence of null alleles is invoked as a technical cause of the deficit of observed heterozygosity although the development of species-specific loci minimizes this possibility. As discussed below, *P. yuma* represents two genetic stocks that cohabitante the studied area, which may explain the deficit of observed heterozygosity (Wahlund effect). However, since the deficit of observed heterozygosity remained significant in the analysis by genetic stocks (not only by sampling site), other biological causes such as inbreeding may also explain this result considering the reduction in fishery production (Barreto Reyes, 2017), and the overexploitation exerted over the species since 2010 (Gutiérrez *et al.*, 2011). Besides the fishing pressure, degradation of the Magdalena-Cauca basin caused by environmental, economic and demographic factors, also contribute to the observed decline in the number of catches of this fish species (Jiménez-Segura *et al.*, 2016). Some Neotropical catfishes such as *P. grosskopfii* (Restrepo-Escobar *et al.*, 2020), *P. maculatus* (Ribolli *et al.*, 2012), and *Pseudoplatystoma reticulatum* (Abreu *et al.*, 2009), have also shown evidences of inbreeding. Following Franklin (1980) and Soulé (1980), *P. yuma* requires a rigorous management of the populations since values above 10% indicate possible adverse effects over these populations.

According to the *a priori* expectation, this study showed evidences that the populations of *P. yuma* are not genetically structured in the middle and lower sections of the Cauca

River, which is in line with the medium-range migration capacity of the species (100–500 km) and the absence of geographical barriers that facilitate the gene flow. This outcome was also found in some congeners like *P. grosskopfii* from the middle and lower sections of the Cauca River (Restrepo-Escobar *et al.*, *in press*) and *P. maculatus* from upper section of the Uruguay River (Ribolli *et al.*, 2012); although this species also showed genetic structure due to the multiple cascades in the rivers Uruguay and Paranapanema (Almeida *et al.*, 2003; Ramella *et al.*, 2006). In contrast to the study of *P. grosskopfii* (Restrepo-Escobar *et al.*, *in press*), this work did not find individuals of *P. yuma* upstream from one of the slopes of the river, suggesting that this fish species is not capable to overcome this steeped geography.

Although *P. yuma* did not show genetic differences between the evaluated sections, it comprises two genetic stocks that cohabit. A similar genetic structure was found in its congener *P. grosskopfii* in the same area (Restrepo-Escobar, Márquez, 2020). The existence of those two genetic stocks might be related to spatial or seasonal reproductive isolation. Nevertheless, it remains to explore if the reproductive isolation by season can explain these differences since it was demonstrated that *P. yuma* (as *P. blochii*) from a floodplain lake in the medium section of the Magdalena River basin only reproduces during rainfall peaks, despite maintaining a constant condition factor at different environmental conditions (Lopez-Casas, Jimenez-Segura, 2007). Although our study was not designed to test the hypothesis of temporal genetic structure, the comparisons among available samples in the rain and drought periods per year (S3) did not show any tendency to seasonal or annual genetic structure.

This study led to establish that the populations of *P. yuma* from the lower sections of the Cauca River do not exhibit spatial genetic structure, although there are two biological populations along the study area. Likewise, even though this species is affected by different anthropogenic activities, it was found that *P. yuma* shows a high genetic diversity, but with a deficit in the observed heterozygosity. The first 14 developed polymorphic microsatellite loci for this species are recommended for further studies of genetic diversity on population of *P. yuma*. Finally, these results are the baseline for future studies aiming to monitor the genetic diversity and structure of the populations of this endemic Colombian fish species in order to generate appropriate management plans.

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AUTHOR'S CONTRIBUTION

Cristhian Danilo Joya: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Validation, Visualization, Writing-original draft, Writing-review and editing.

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Edna Judith Márquez: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing-original draft, Writing-review and editing.

Neotropical Ichthyology



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The authors declare no competing interests.

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