




Review

A Synthesis of the Ecology and Conservation of *Pseudoplatystoma* Catfishes in the Neotropics

Luciana A. Pereira ^{1,*}, Leandro Castello ¹, Donald J. Orth ¹ , Fabrice Duponchelle ²  and Eric M. Hallerman ¹ 

¹ Department of Fish & Wildlife Conservation, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061, USA

² Institut de Recherche pour le Développement (IRD), MARBEC (Université Montpellier, CNRS, Ifremer, IRD), 34095 Montpellier, France

* Correspondence: lucianaa@vt.edu; Tel.: +1-(206)-696-1224

Abstract: Species of the genus *Pseudoplatystoma*, the long-whiskered catfishes, are important in commercial and recreational fisheries in South America, and some species have become key to regional aquaculture. Some species of the genus are under pressure due to overfishing and the negative impacts of dams. Six questions are asked in this review: (i) What species are in the genus, and where are they distributed? (ii) What are the life histories and ecologies of *Pseudoplatystoma* species? (iii) What are the patterns of somatic growth for these species? (iv) What is known about the biomass, production, and population dynamics of *Pseudoplatystoma*? (v) What is the geographic distribution of genetic variation within *Pseudoplatystoma* species? (vi) What are the threats to the conservation of these species? The taxonomy of the genus currently includes eight species, respectively, distributed over the Orinoco, Amazon, Paraná, and São Francisco basins. *Pseudoplatystoma* catfishes typically exhibit longitudinal migrations for reproduction and lateral migration for feeding, but these patterns may vary among populations. The size of the first maturation of these catfishes varies between 57 cm to 82 cm in total length. Five of the eight species spawn during the rising water season. *Pseudoplatystoma* species can grow to about 130 cm in total length and 100 Kg in weight and live until 30 years of age, depending upon the species. Biomass production and population dynamics of these catfishes have not yet been fully described. Their life-history characteristics indicate that they are periodic strategists with associated population recruitment dynamics. Population genetic patterning varies among *Pseudoplatystoma* species, with some degree of homing behavior and genetic differentiation among populations, indicating the need for management by applying the Management Unit and perhaps Evolutionary Significant Unit concepts. The main threats to the persistence of these catfishes are overfishing and alterations in and obstruction of river flow due to the construction of hydropower dams. After synthesizing existing information on species of the genus *Pseudoplatystoma*, we offer suggestions for future research to fill critical gaps in the knowledge of this group.



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Keywords: surubim; ecology; conservation; management

Key Contribution: This review synthesizes existing information on the ecology of species of the genus *Pseudoplatystoma* and offers suggestions for fisheries management and for research to fill critical gaps in the knowledge of the group.

1. Introduction

Freshwater fishes include diverse lineages collectively summing to over 18,000 species, representing ~51% of all fishes and ~25% of all vertebrates [1–4]. Freshwater fishes are important economically, culturally, aesthetically, scientifically, and educationally [5]. They provide the basis for human nutrition, employment, and ecosystem services, including nutrient transport within aquatic ecosystems, disease vector control, and seed dispersal [5,6]. About one-third of all freshwater species occur in the Neotropics, with an estimated

4475 species within 71 families [7], with new species being recognized regularly. This assemblage, however, faces a high level of anthropogenic pressure and is threatened by overexploitation, water pollution, river flow modification, degradation of habitat, and invasive exotic species [5,6,8]. Studies of the ecology of many Neotropical species are relatively scarce in the peer-reviewed literature, limiting the basis for science-based actions for fisheries management and conservation.

Catfishes of the Order Siluriformes include 39 families with 498 accepted genera and 4123 species [4]. More specifically, members of the Family Pimelodidae, the long-whiskered catfishes, and the genus *Pseudoplatystoma* are distributed from South America to southernmost Mexico [9]. They are a highly distinctive group of catfishes, with three pairs of barbels, maxillary barbels the length of their bodies, no scales, and well-developed adipose fins [9] (Figure 1). Many long-whiskered catfishes grow to be over 1 m in total length. The Family Pimelodidae includes 30 genera and 116 described species [4], and many valid pimelodid species have been described only recently [7]. Lundberg et al. [10] suggested that there are at least 25 undescribed living species, as well as five described and many undescribed fossil species.

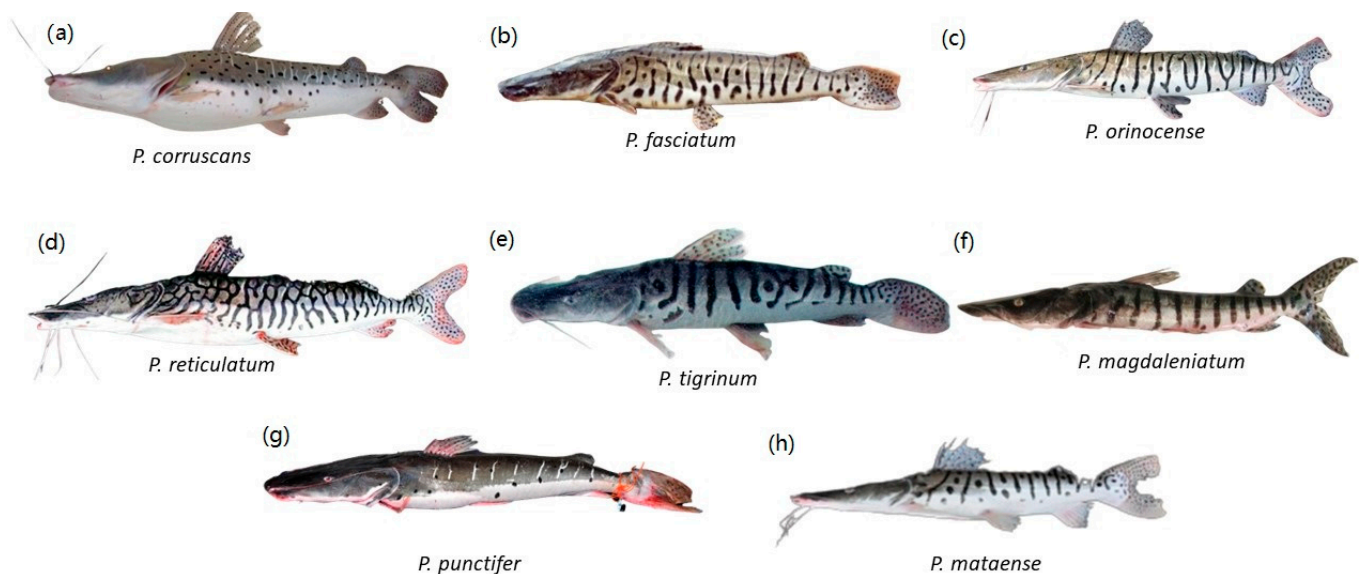


Figure 1. Eight *Pseudoplatystoma* species, members of the Family Pimelodidae; (a) *P. corruscans*; (b) *P. fasciatum*; (c) *P. orinocense*; (d) *P. reticulatum*; (e) *P. tigrinum*; (f) *P. magdaleniatum*; (g) *P. punctifer*; (h) *P. mataense*. Illustrations courtesy of Timm, C.D.; Magalhães, K.; Alvarez, F.; Sabaj Pérez; and F. Duponchelle.

Fishes of the genus *Pseudoplatystoma* support important commercial and artisanal fisheries, and some species have become important to regional aquaculture [11]. Most species of the genus are under pressure from dam construction and overfishing [12–18]. Two species are of conservation concern: *P. corruscans* is classified as Critically Endangered [13] and *P. magdaleniatum* as Endangered by IUCN [19]. Relatively few studies have focused on species of the genus *Pseudoplatystoma*, and further information on their biology, ecology, and population dynamics is needed to inform fisheries management and conservation. This review synthesizes existing information on the species of the genus *Pseudoplatystoma*. Six questions are asked: (i) What species are in the genus, and where are they distributed? (ii) What are the life histories and ecologies of *Pseudoplatystoma* species? (iii) What are the patterns of somatic growth for these species? (iv) What is known about the biomass production and population dynamics of *Pseudoplatystoma*? (v) What is the geographic distribution of genetic variation within *Pseudoplatystoma* species? (vi) What are the threats to the conservation of these species? After establishing what is known about the genus,

this review offers suggestions for future research to fill critical gaps in the knowledge of this group.

2. What Species Are in the Genus, and Where Are They Distributed?

2.1. Natural History

An understanding of the natural history of the lineage provides insights into the geographic distribution of *Pseudoplatystoma* species. The first and so-far only reported fossil record for the genus is a neurocranium recently discovered from late Pleistocene deposits of the Cacarana River of Argentina, which was assigned to the extant species *Pseudoplatystoma corruscans* [20]. The fossil record of freshwater fishes in South America is not as well studied as that of terrestrial mammals [21]. Lundberg et al. [10] present a map showing sites where fossils from the Neogene period, spanning from the end of the Paleogene Period 23 million years ago (MYA) to the beginning of the present Quaternary Period 2.6 MYA, have been found, suggesting that additional finds might be made with effort directed there.

The systematics and taxonomy of the genus *Pseudoplatystoma* can be better understood in the context of the biogeological history of South America. *Pseudoplatystoma* has diverse species because extensive geomorphological and physiographic processes have transformed South American drainages over time, allowing vicariance, divergence, and subsequent secondary contact of lineages [22,23]. Fishes of the genus *Pseudoplatystoma* are currently distributed across four of the eight zoogeographic regions of South American freshwater fishes described by Géry [24], from north to south: the Magdalenian, Orinoco, Guinea-Amazonian, and Paranean regions. Géry [24] emphasizes that there are or have been connections between some South American river systems, some permanent (e.g., the Cassiquiera Canal joining the Rio Negro of the Amazon and the Orinoco drainages), some temporary (due to flooding in the rainy season), and some historical but no longer in existence. Current patterns of species distribution reflect these biogeographical processes, including marine incursions and the uplift of paleoarches, or ancient ridges [25].

2.2. Systematics and Taxonomy

The isolation of freshwater refugia permitted allopatric speciation, and subsequent recolonization of the lowland allowed the mixing of the respective lineages. Hubert and Renno [25] showed seven putative dispersal routes that gave rise to different species' distributions. Against this background, it becomes apparent that *P. magdaleniatum*, *P. orinocense*, and *P. mataense* persisted in northern refugia, *P. corruscans* and *P. reticulatum* in southern refugia, and other *Pseudoplatystoma* species in western refugia. The model proposed by Hubert and Renno [25] could explain how four species' distributions now overlap in the Amazon basin. *Pseudoplatystoma* species are not shared between the now-connected Orinoco and Amazon basins, which may be explained by the species not dispersing readily through small river systems.

The phylogeny and distributions of species across the South American landmass are linked [10]. Until recently, three species of *Pseudoplatystoma* were recognized, *P. fasciatum*, *P. tigrinum*, and *P. corruscans*. Despite their apparent morphological homogeneity within species, the genus *Pseudoplatystoma* has cryptic species [26]. Based on morphological characteristics, Buitrago-Suárez and Burr [26] increased the number of known species to eight: *P. punctifer* and *P. tigrinum* in the Amazon basin, *P. orinocense* and *P. mataense* in the Orinoco basin, *P. corruscans* and *P. reticulatum* in the Paraná basin, *P. magdaleniatum* in the Magdalena basin, and *P. fasciatum* in the Guyana Shield. Later, using molecular genetic analyses, Torrico et al. [27] and Carvalho-Costa et al. [28] invalidated the distinction between *P. fasciatum* and *P. punctifer* made by Buitrago-Suárez and Burr [26]. Torrico et al. [27] evaluated species boundaries and biological and geographic patterns within the genus *Pseudoplatystoma* using a variation of mitochondrial cytochrome *b* and control region sequences to reconstruct phylogenetic relationships. They confirmed aspects of the morphological classification [26], but other elements were not supported. Morphology and molecular data supported the monophyly of the genus *Pseudoplatystoma*, i.e., their descent from a common

ancestor. Molecular data also showed that *P. tigrinum*, *P. corruscans*, *P. reticulatum*, and *P. magdaleniatum* were highly supported clades, validating their taxonomic status. However, there were discrepancies between morphological and molecular genetic findings regarding *P. mataense* and *P. orinocoense*, suggesting either mtDNA introgression between the two species or misidentification of samples. The absence of phylogenetic and clear morphological differentiation between *P. fasciatum* and *P. punctifer* was such that Buitrago-Suárez and Burr [26] had erroneously separated *P. fasciatum* into two distinct species, thereby invalidating the taxonomic status of *P. punctifer*. On the other hand, Lundberg et al. [29] included four species in their study of the phylogenetics of Family Pimelodidae using nuclear and mitochondrial gene sequences, omitting the species *P. punctifer*. Moreover, the species *P. fasciatum*, *P. tigrinum*, *P. magdaleniatum*, and *P. corruscans* formed a well-supported, monophyletic clade embedded within the sorubimines, a lineage of ten genera. The position of *P. tigrinum* differed from that in the analysis of Buitrago-Suárez and Burr [26]. Moreover, García-Dávila et al. [30] showed the existence of a cryptic species within *Pseudoplatystoma*, with the new species resembling what Castelnau (1855) had named *Platystoma punctifer*, a species with no black stripes and a distinct mouth (Figure 1). While becoming clearer, details of the phylogeny of *Pseudoplatystoma* are yet undefined and will become more firmly established only with further study of suitably large collections of lineages and the application of suitable phylogenetic markers.

2.3. Distributions

Developments in understanding the systematics of the genus *Pseudoplatystoma* have led to eight species being currently recognized in the taxonomy, and their distributions (Figure 2) are explained based on the natural history of South America. The Amazon basin contains three nominal species: *P. tigrinum*, *P. fasciatum* (named *P. punctifer* by Buitrago-Suárez et al. [27]), and *P. reticulatum* in the Amazon River, distributed in the mainstem Amazon and its Madeira, Solimões, Xingu, Tapajós, and Jurua tributaries. Additionally, there are the cryptic species believed to be what Castelnau (1855) described as *P. punctifer*: *P. cf. punctifer* [30]. Two species occur in the Orinoco basin: *P. mataense*, distributed in the Orinoco River in Venezuela and Colombia, and *P. orinocoense* in the Orinoco River in Venezuela. *P. magdaleniatum* is found in the Magdalena basin. *P. fasciatum* is found in the Guyana Shield in the Amazon, Corantijn, Essequibo, Orinoco, (Figure 1). Two species occur in the Paraná basin: *P. corruscans* and *P. reticulatum* in the central Amazon River and the Paraná River basin in Argentina, Bolivia, Brazil, Paraguay, and Uruguay. Only *P. corruscans* occurs in the São Francisco basin. However, because our understanding of the systematics of the respective species is still not fully defined, more studies are needed to clarify the systematics, refine the taxonomy, and explain the distributions of the respective lineages in the genus.

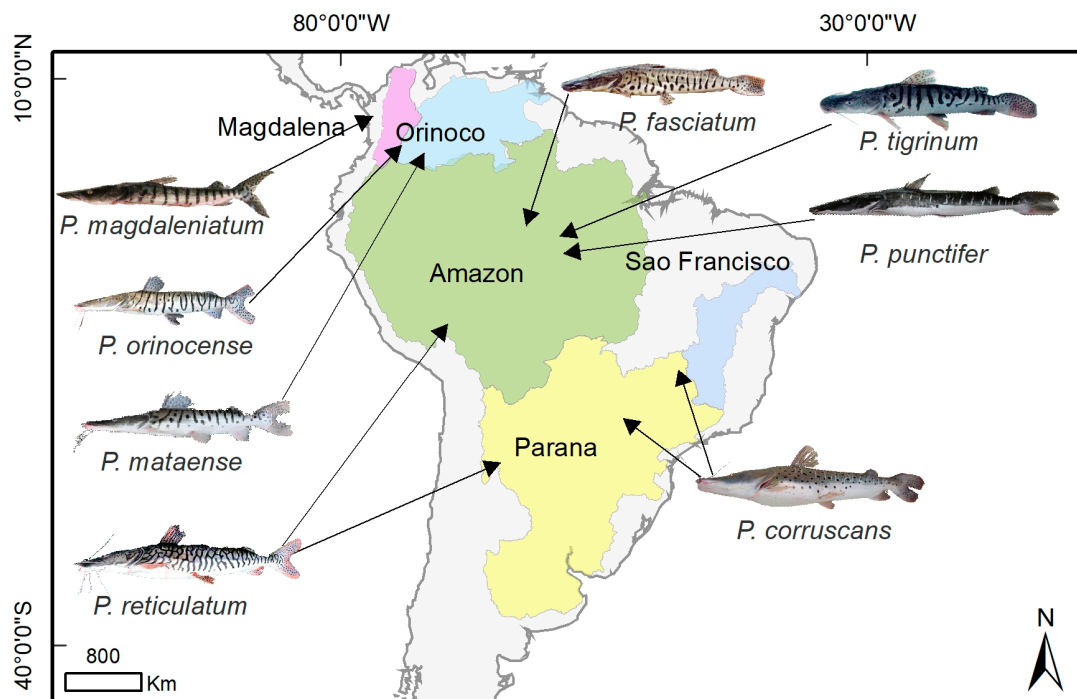


Figure 2. Distributions of species of genus *Pseudoplatystoma* from the literature review data. The Magdalena basin is (represented in purple) where *P. magdaleniatum* is distributed. The Orinoco basin (light blue) encompasses the *P. orinocense* distribution. The Amazon basin (green) where *P. fasciatum*, *P. tigrinum*, *P. reticulatum*, and *P. punctifer* are distributed. *P. corruscans* is distributed in the São Francisco basin (blue), and *P. corruscans* and *P. reticulatum* are distributed in the Paraná basin (yellow). Illustrations courtesy of Timm, C.D.; Magalhães, K.; Alvarez, F.; Sabaj Pérez, and F. Duponchelle.

3. What Are the Life Histories and Ecologies of *Pseudoplatystoma* Species?

3.1. Movement Ecology

Most *Pseudoplatystoma* catfishes exhibit ontogenetic and feeding migrations, longitudinal migration for reproduction, and lateral migration for feeding [31,32]. However, the migration patterns of certain *Pseudoplatystoma* species need to be better understood, as there have been very few studies on the topic [32,33]. In the Colombian Amazon, it is believed that *Pseudoplatystoma* spp. migrate between 300–500 km [34], but no movement data are available. Patterns of movement in *Pseudoplatystoma* have been shown to vary by sex, size, time of year, and ability of fish to cross natural barriers such as waterfalls [18,31,33,35].

While there is only a limited understanding of the movement ecology of *Pseudoplatystoma* spp., especially regarding its potential importance in demographically and genetically structuring their populations, general patterns of migration of freshwater floodplains fishes suggest insights into species-level ecology of *Pseudoplatystoma* catfishes. The eggs and larvae of pimelodid catfishes have been found drifting in currents, in both white- and black-water rivers, and in both clear and turbid waters [36,37]. Catfish larvae drift mainly near the bottom of the water column, drifting distances of up to several thousand kilometers. Fast downstream movement (averaging 250 km/d) was suggested by Barthem et al. [38] for the early life stages of some pimelodids in rain-swollen currents.

Few studies have explicitly distinguished the movement ecology of sexes and life stages of *Pseudoplatystoma* catfishes. Male *P. fasciatum* and *P. tigrinum* usually inhabit rivers, while females inhabit riverside lakes during the low-water season [31]. Adults of both species migrate upstream for spawning during the beginning of the high-water season in the Mamore River in the Beni basin, Bolivia. At the same time, juvenile individuals believed to be non-migratory remain in the floodplains [31]. Adult *P. fasciatum* that possessed undeveloped gonads moved upstream and passed through river rapids during

the low-water season in the Madeira River [35]; no fish were seen returning downstream. Juvenile *P. fasciatum* are always caught in the floodplains; other migratory behavior is unknown. Moreover, *P. fasciatum* and *P. tigrinum* migrate upstream across the rapids in the Madeira River, probably seeking prey. However, despite the incomplete and seemingly inconsistent information about the timing and the direction of migration in *P. tigrinum* and *P. fasciatum* [31,33], some studies have elucidated the migration of *P. punctifer* (*P. fasciatum*) and *P. corruscans*.

P. fasciatum performs movements both up and down river channels, and most movements occur between the dry season and the rising water period [39]. *P. fasciatum* individuals were tracked using telemetry methods in the Xingu River, where they migrated up to 164 km between the dry season and the rising water period. *P. fasciatum* was mainly detected moving upstream during the end of the rising-water period.

Migration and spawning patterns of *P. corruscans* in the São Francisco River were observed using radio telemetry [40]. Two migration patterns were exhibited, showing resident and migratory fish. According to the spawning stage, the migration was classified into pre-spawning staging and spawning migration. Female *P. corruscans* migrated among pre-spawning staging, spawning, and non-spawning sites. Godinho et al. [40] suggested that ripe females performed homing migration from feeding areas to the spawning sites, i.e., discrete sites where they returned multiple times. After spawning, most females migrated from the spawning site to other habitat units. The natural history of *P. corruscans* in the La Plata River in the Uruguay River basin was inferred using ratios of strontium isotopes ($^{87}\text{Sr}/^{86}\text{Sr}$) along a transect of the otolith [41]. *P. corruscans* was inferred to originate from the Paraná River, indicating a distinct nursery area. All *P. corruscans* individuals showed ontogenetic shifts in their isotopic signature, with strontium ratios corresponding to catchment sub-basins, suggesting that this species presents spatially bounded reproduction in the respective areas [41].

Given the lack of information about ontogenetic migration patterns for *Pseudoplatystoma* species, more studies are necessary to fully understand the life cycle of these species in the respective basins in which they are distributed. Questions that can and should be asked in future studies include, How far do the species migrate? Which habitats are used during their longitudinal and lateral migrations? Do juveniles and adults, and females and males, have the same migration patterns? Do all members of a species have the same migratory life history? Answering these questions would improve our understanding of the species' life cycles and inform fisheries management and conservation for *Pseudoplatystoma* species.

3.2. Reproduction

The reproductive biology of *Pseudoplatystoma* species is not yet well studied. The current knowledge of the reproductive ecology of *Pseudoplatystoma* indicates that five of the eight species have common characteristics. Size-at-maturity varies among species between 57 cm to 82 cm, with all three species for which data are available spawning during the rising water season via total spawning, i.e., the release of all eggs in one batch (Table 1). Larvae of *P. fasciatum* were mostly observed drifting with currents during the end of the flood pulse, while larvae of *P. tigrinum* were detected flowing during the start of the flood pulse in the Peruvian Amazon [42].

Additionally, the reproductive morphology of *Pseudoplatystoma* is like that of other Siluriformes. *Pseudoplatystoma* species have double gonads, with elongated ovaries and testicles with digitiform projections all over their extent, features that are more evident during the reproductive period. The ovaries are covered by conjunctive and muscular tissues and blood vessels [43]. The gonads converge at the caudal region and join a duct. The female gonads are cistovaries, meaning that the lumen is connected to the oviduct, through which the oocytes are released into the water [44]. The male gonads are covered by conjunctive tissue that ramifies into septa filled with seminiferous tubules [44].

The reproduction of *Pseudoplatystoma* is closely related to their migratory ecology, as their reproduction is synchronized with the flood pulse and occurs during the period

of rising and high waters [32,44–48] (Table 1). The synchronization of reproduction with the upstream migration during the period of rising water enables these species to spawn when the river's water level is favorable for the small, semi-buoyant eggs and larvae to drift with the current until they reach the inundated floodplains, which are their nursery habitats [32,36]. Consequently, an important life-history characteristic of the genus is that its species do not seem to provide parental care, given knowledge about their biology and considering the egg size and number. Females exhibit total spawning of numerous ova and high fecundity, which compensate for high early mortality [31,49,50]; however, quantitative data about the fecundity of most of these species is lacking. Embryogenesis is rapid, lasting around 16 h at an average temperature of 23.0 ± 1.0 °C [51]. For *P. fasciatum*, the hatching takes place 14 h after fertilization at 27 °C [52].

Table 1. Reproductive parameters of *Pseudoplatystoma* species.

Species	Size at First Maturation (cm)	Spawning Season	Spawning Type	Oocyte Diameter (mm)	Ref.
<i>P. corruscans</i>	62.92	Rising water	Total	0.9	[32,48]
<i>P. reticulatum</i>	57.84	Rising water	Total	-	[48]
<i>P. tigrinum</i>	69.4	Rising water	Total	-	[45,53]
<i>P. fasciatum</i>	53	Rising water	Total	0.64	[31,53]
<i>P. magdaleniatum</i>	82	Rising water	-	0.9	[47]
<i>P. tigrinum</i>	69.4	High water	-	-	[42]
<i>P. fasciatum</i>	53	Rising water	-	0.64	[42]

Current knowledge of the reproductive biology of some of the species allows managers and decision-makers to take action even in the absence of more detailed studies. Based on the current information for five species in the genus, the establishment of regulations for time and minimum size-at-capture for those species lacking information could be to restrict their fisheries during the rising and high-water periods. Managers could calculate a ratio L_{50}/L_{max} for the species with available information and recommend an average ratio for the others until new studies are done.

The reproductive biology of *Pseudoplatystoma* species is not yet well studied, so existing knowledge gaps represent opportunities for research. One question that remains unanswered in regard to their behavioral reproductive ecology is: What is the female behavior during spawning? Do females emit any pheromonal or behavioral signal prior to or during spawning? In addition to fecundity information available for *P. fasciatum* and *P. reticulatum* [54,55], another knowledge gap relates to the fecundity of these five species: what is the range of age- or size-specific fecundities? Additionally, knowledge of the characteristics of eggs and larvae is important for understanding the reproductive ecology of *Pseudoplatystoma* species. In particular, we must answer the questions: Do larvae perform vertical movement in the water column? What factors limit their recruitment to the juvenile stage? Are the respective species iteroparous or semelparous? If the former, how many spawning cycles occur during the lifetime? Do the species have broadcast spawning or other behaviors? Do juveniles have direct development or transformations? If the latter, how many inflection points? Answering these questions would enhance the current knowledge of reproductive biology, which is essential to managing fisheries and conserving these species.

3.3. Growth

The growth of six *Pseudoplatystoma* species has been studied. As noted above, these catfishes are large-bodied compared to other Neotropical species and can grow up to about 130 cm in total length and 100 kg in weight, depending on the species [56]. They can grow to 40 cm in their first year of life [14]. Females grow larger and faster than males. Von Bertalanffy growth parameters and \emptyset values for *Pseudoplatystoma* species are summarized in Table 2.

Table 2. Summary of von Bertalanffy growth parameters and \emptyset values for *Pseudoplatystoma* species.

Species	L_{∞} (cm)			K			Longevity (Years)			\emptyset			Ref.
	L_{∞}	$L_{\infty m}$	$L_{\infty f}$	k	k_m	k_f	Longevity	Male	Female	\emptyset	\emptyset_m	\emptyset_f	
<i>P. tigrinum</i>	180	-	-	0.29	-	-	-	-	-	0.97	-	-	[56]
<i>P. tigrinum</i>	-	146	170	-	0.11	0.01	25–30	-	-	-	0.49	−0.55	[51]
<i>P. tigrinum</i>	-	119.8	131.8	-	0.17	0.15	-	-	-	-	0.63	0.59	[32]
<i>P. fasciatum</i>	-	77	103.1	-	0.44	0.24	15	-	-	-	0.91	0.72	[32]
<i>P. corruscans</i>	200	-	-	0.08	-	-	10	-	-	0.47	-	-	[57]
<i>P. corruscans</i>	-	99.2	131.8	-	0.51	0.34	-	-	-	-	1.05	0.95	[58]
<i>P. reticulatum</i>	-	72.7	82.5	-	0.44	0.33	-	-	-	-	0.89	0.81	[59]
<i>P. punctifer</i>	-	99.5	97.3	-	0.16	0.2	-	-	-	-	0.54	0.63	[15]
<i>P. mataense</i>	-	108.6	119.9	-	0.19	0.17	-	12.37	15.7	-	0.64	0.62	[60]

Most studies on the growth of *Pseudoplatystoma* found a similar pattern of growth rings in calcified structures such as otoliths and vertebrae, with opaque ring formation in the hard parts of *Pseudoplatystoma*, indicating fast growth occurring during the dry season [14,31,50,58,60]. Several studies showed that one opaque ring is formed annually during the dry season and the beginning of the rainy season for *P. punctifer*, *P. tigrinum*, and *P. mataense* in the Peruvian Amazon, Orinoco, and Mamore basins [14,31,57], probably because the dry season is when prey capture is more difficult due to competition with larger catfishes and dolphins and the beginning of the reproductive stage [14,31,33]. However, studies on central and eastern Amazon tributaries are necessary to determine whether the pattern of one ring per annual cycle is consistent for *P. fasciatum* and *P. tigrinum*. Other fish species—such as gilded catfish *Brachyplatystoma rousseauxii* (Castelnau, 1855) [58], mapara catfish *Hypophthalmus marginatus* (Valenciennes, 1840) [57], piaracatinga catfish *Calophysus macropterus* (Lichtenstein, 1819) [61], and pirarucu *Arapaima* spp. [59] in the central Amazon—form two growth rings per flood cycle [14]. Validation of ring formation has been done for *P. punctifer*, *P. tigrinum*, and *P. fasciatum*, but it is lacking for *P. corruscans*, *P. reticulatum*, and *P. magdaleniatum* [14,31].

Generally, species that are distributed in tropical and temperate regions have faster growth rates in the warmer tropical waters because food availability is the main constraint for growth in tropical regions, while temperature constrains the growth in temperate regions [62,63]. For example, all species of the genus *Pseudoplatystoma* that are distributed in the tropical areas of the Amazon, Orinoco, and Magdalena basins grow faster than the *Pseudoplatystoma* catfishes distributed in the Paraná basin (references in Table 2).

4. What Is Known about the Biomass Production and Population Dynamics of *Pseudoplatystoma* Species?

Biomass production and population dynamics of *Pseudoplatystoma* species have not been properly studied. However, current knowledge about their life-history and general patterns of biomass production and population dynamics of tropical species are expected to follow general patterns common to fishes in river floodplains [64,65]. This pattern involves seasonal changes in biomass via increases during high-water months due to active feeding and reproduction activities and decreases during low-water months due to natural mortality [66].

The population dynamics of *Pseudoplatystoma* species can also be understood based on the triangular model proposed by Winemiller and Rose [67], which classifies fishes in relation to their life-history trade-offs and the adaptive response to environmental variation. According to this classification, fishes can be classified within a continuum of three strategies: (1) periodic, in which fish have high values of both fecundity and age-at-maturity and a low value of juvenile survival; (2) opportunistic, in which fish have a low value of absolute fecundity but high productivity for their size, low age-at-maturity, and juvenile survival; and (3) equilibrium, in which fishes have low values of fecundity and high values in the age-at-maturity and juvenile survival (meaning that juveniles have

relatively high survival rate, probably because of parental care). Winemiller [65] classified *P. fasciatum* as periodic because it has high absolute fecundity and intermediate size-at-maturity. The catfish has intermediate juvenile survival as it has planktonic eggs, and as soon as the yolk sac is reabsorbed, the larvae prey on items, including cannibalizing other larvae. *P. fasciatum* has a smaller size-at-maturity currently, compared to 20 to 30 years ago, mainly due to fishing which selectively removes the largest individuals from the populations, resulting in artificial selection for genotypes maturing at smaller sizes [68]. As periodic strategists, small differences in mortality at early life stages may have a huge influence on stock abundance [65].

Pseudoplatystoma species could be considered vulnerable to fishing pressures, as shown by fisheries stock assessments done for *P. tigrinum* and *P. corruscans*, which showed signs of growth of overfishing. Ruffino et al. [68] concluded that the stock of *P. tigrinum* was exploited very closely to maximum sustainable yields. Doria [67] showed that the fisheries landings of *P. tigrinum* are fewer and individual sizes are smaller than previously. Godinho [69] pointed out that some *P. corruscans* populations have been overfished to the point where they have disappeared.

5. What Is the Geographic Distribution of Genetic Variation within *Pseudoplatystoma* Species?

Maintaining the viability of valued populations is fundamental to fisheries management and conservation. Understanding of population's genetic structure would inform the management and conservation of fishes of the genus *Pseudoplatystoma*. Studies identifying genetically distinct populations are needed to determine appropriate spatial units for managing demographically sustainable fisheries. In cases where genetically distinct gene pools could mix, as perhaps in large rivers, population genetic studies are needed to recognize that mixing and estimate the relative abundances of the respective stocks contributing to mixed-stock fisheries to protect the demographically less-robust populations. Genetic baseline information also is needed to design any hatchery-based programs that might be considered for supplementing wild fish populations [70]. A table of genetic concepts helpful for understanding key concepts of population genetics is presented in Table 3. While population genetic data are lacking for some species of this genus, a review of the existing literature shows that population genetic patterning varies among *Pseudoplatystoma* species.

Table 3. Definitions of key genetic concepts.

Concepts	Ecological or Genetic Meaning
Analysis of Molecular Variance (AMOVA)	An analytical algorithm that partitions genetic variation into within- and between-population components.
Bayesian methods	Methods of statistical inference in which Bayes' theorem is used to update the probability for a hypothesis as more evidence or information becomes available. Bayesian approaches underlie some clustering and assignment tests and phylogenetic inference algorithms in population genetic analyses.
Evolutionary Significant Units (ESU)	A population or a group of populations that merits priority for conservation and separate management because of high genetic and ecological distinctiveness from other such units.
F_{ST}	The coefficient of departure of genotype frequencies from Hardy-Weinberg equilibrium due to differentiation among subpopulations within a larger population.
Fu's F_s	A population genetics statistic helpful in assessing historical population dynamics.
Genetic differentiation	The condition of populations having contrasting genotype frequencies resulting from the dynamic interplay among mutation, gene flow, selection, and random genetic drift over space and time.
Management Unit (MU)	A population that is demographically independent from others and hence should be managed separately.
Maximum parsimony	In the context of phylogenetic inference, a method for evaluating relationships between lineages in which the evolutionary tree with the fewest common ancestors is regarded as the most likely.

Table 3. Cont.

Concepts	Ecological or Genetic Meaning
Microsatellite	A genomic sequence with repeats of 1–6 nucleotide motifs, e.g., GT, CAC, or GACA. There is variation in the repeat number at a given locus among members of a chromosome pair in an individual, among individuals within a population, and often among populations. Such genetic markers are highly useful for population genetic studies.
Mitochondrial DNA COI region	Mitochondrial cytochrome oxidase subunit 3 (COI) gene. This genetic marker is often used for DNA barcoding to distinguish species.
Neighbor-likelihood joining	An agglomerative clustering method for the construction of phylogenetic trees.
Panmictic population (panmixia)	A collection of fish with the absence of genetic structure (the condition of being well mixed, as in a population where all individuals could interbreed).
Phylogenetic tree	A representation of the inferred evolutionary relationships among individuals, populations, or species that shows the branching from a known or hypothesized ancestor to its derived lineages, which outwardly resembles a tree and hence is referred to as this.
R_{ST}	A metric of genetic differentiation that incorporates the differences in the size of microsatellite alleles
Tajima's D	The difference between two measures of genetic diversity: the mean number of pairwise differences and the number of segregating sites, each scaled so that they are expected to be the same in a neutrally evolving population of constant size.

Pereira et al. [71] investigated whether populations of *P. corruscans* were panmictic in the Paraná-Paraguay basin. They found highly significant population genetic differentiation among samples ($F_{ST} = 0.034$ – 0.163 , AMOVA $F_{ST} = 0.082\%$, and AMOVA $R_{ST} = 0.097\%$). The patterning of individuals' multilocus genotypes into inferred clusters using cluster analysis and Bayesian genotypic assignment was largely congruent with the branching topology of a population-level neighbor-joining phylogenetic tree. The results thus demonstrated genetic differentiation among populations. The documented long-distance movements of *P. corruscans* and the geographical scale of genetic differentiation found by Pereira et al. [71] result from a strong tendency for homing to natal nursery areas for reproduction [12]. This result supports the need for separate management of each spawning assemblage as an independent management unit, or MU. That is, fishery management must set sustainable exploitation rates for each MU, as each is demographically independent. We have no indication that these management strategies are being implemented for the fisheries.

Carvalho-Costa et al. [28] sampled *P. corruscans* at two sites in the São Francisco and the Paraná-Paraguay River basins in Brazil. They assessed the DNA sequence variation of a segment of the mitochondrial COI region and repeat-number variation at eight nuclear microsatellite DNA loci. Two mitochondrial DNA sequence haplotypes were detected in the São Francisco River basin and seven in the Paraná-Paraguay River basin. They found identical population tree topologies by neighbor-joining, maximum parsimony, and Bayesian analyses. They obtained high fixation index values between the São Francisco River basin and the Paraguay River basin for both nuclear and mitochondrial markers, i.e., F_{ST} of 0.18 ($p = 0.01$) and ϕ_{ST} of 0.89 ($p = 0.001$). Several private microsatellite alleles were observed for each river basin. Bayesian cluster analysis of the entire dataset indicated the most likely number of genetic clusters to be $K = 2$, corresponding to river basins. Tajima's D and Fu's F_s indices both suggested population expansion of *P. corruscans* in the Paraguay River basin, the geologically recent river system. At the same time, no such indication was found for the São Francisco basin, the geologically older basin. Nuclear and matrilineal DNA divergence, combined with their historical separation into different hydrographical systems, strongly suggested that the two population groups evolved independently, perhaps warranting their recognition as distinct Evolutionary Significant Units, or ESUs. *P. corruscans* is considered abundant in the Pantanal wetlands region within the Paraguay River basin. Populations from the São Francisco River basin belong to a different ESU and hence should be managed as a separate unit. Some of these populations are critically affected by habitat fragmentation from several hydroelectric dams and overexploitation [13].

Hybrid *P. fasciatum* × *P. corruscans* are produced in aquaculture, and hybrids have been collected from the wild, presumably after escape from confinement. Dantas et al. [12] observed variation at five microsatellite DNA loci in three wild populations, and a captive group of *P. corruscans* was considered a potential source of broodstock for an augmentation program in the São Francisco River. F_{ST} and assignment test results showed low differentiation among three wild populations and the captive broodstock. The authors recommended that *P. corruscans* broodstock used in stocking-based augmentation programs for severely impacted river basins be genetically characterized for species purity before possible use as broodstock. Their results suggested that the captive population should not be used to stock areas where wild populations remain extant.

Telles et al. [72] used detailed spatial analyses to investigate the genetic variation of *P. punctifer* (*P. fasciatum*), which is widely distributed and commercially important in the Amazon River basin. They screened samples from fifteen localities along the Madeira and Solimoes rivers at seven microsatellite DNA loci. High genetic diversity was observed. Overall, F_{ST} was relatively low (0.057; $p < 0.001$), although pairwise F_{ST} values ranged from 0 to 0.21 among some pairs of populations. A Mantel correlogram of genetic distance as a function of geographic distance showed that populations up to 80 km apart tended to be more similar than expected by chance. A patch size of around 200 km is compatible with genetic isolation-by-distance and local constraints upon individual dispersal, resulting in spatially structured levels of gene flow. This pattern of genetic variation will inform strategies for maintaining genetic diversity in the species, especially considering threats due to the anthropogenic impacts of large dams constructed in this river system.

P. corruscans is the most-studied *Pseudoplatystoma* species in terms of population genetic structure. However, current knowledge of population genetic structure for catfishes of genus *Pseudoplatystoma* still needs to be more robust to inform spatially explicit fishery and conservation management. Hence, further studies are needed to understand the patterns of population genetic structuring of all *Pseudoplatystoma* species in their respective basins to delineate Management Units and possible Evolutionary Significant Units to manage fisheries and conserve these species properly. Over the longer term, the development of a large collection of single nucleotide polymorphism (SNP) markers could support the execution of genome-wide association studies to identify adaptive genetic variation. This knowledge would inform the conservation of the adaptive potential of the respective populations and species.

6. What Are the Threats to the Conservation of These Species?

The main threats to *Pseudoplatystoma* species are (1) overfishing and (2) alterations in and obstruction of river flow due to the construction of hydropower dams [73]. Other threats—such as industrial, domestic, and agricultural pollution, deforestation, introduced species, hybridization with farmed fish, and genetic erosion—may also affect populations of *Pseudoplatystoma* species, but in our view, they are not less pressing.

Dams interrupt streamflow and generate longitudinal and lateral hydrological changes in river ecosystems [74–76] that can be reflected subsequently in decreased fisheries yields. The most apparent effects of placing dams on rivers are the formation of a new lentic environment upstream from the dam and a tailwater environment downstream from the dam [75]. In general, six effects of dams on fisheries are (1) alteration of flood regime; (2) change in nutrient flow; (3) change in water temperature; (4) disruption of fish migration; (5) change in fish community composition; and (6) change of water chemistry [76]. For *Pseudoplatystoma* species, the alteration of the flood regime and disruption of migration are particularly important [32].

Alteration of the flood regime disrupts lateral connectivity, as dams cause the permanent inundation of upstream floodplains and restrict the seasonal movement of littoral zones that are part of the flood pulse [75]. Further, downstream of the dam, floodplains are not sufficiently inundated in terms of the depth, duration, and seasonality of flooding, which could result in a significant decline in *Pseudoplatystoma* populations and fisheries.

That is, disruption of floodplain inundation is likely to affect the life cycle of *Pseudoplatystoma*, including disruption of migration, recruitment, and survival of cohorts. Dams blocking upstream and downstream migration can cause the decline and even extirpation of species that depend on longitudinal movements along the stream during certain phases of their life cycle [74,75]. Migratory fishes require different environments for the main stages of their life cycle: reproduction, juvenile production, growth, and sexual maturation (review in [73]). As a barrier to upstream migration, a dam prevents adults from reaching spawning grounds during the breeding season, resulting in recruitment failure and eventual extirpation of the population above the dam. Downstream migration past the dam may also be difficult or impossible for many fish species. Fish migrating into the reservoir from tributary streams may be unable to find their way to the dam and subsequently pass downstream through discharge structures. In particular, the modification of the downstream river-flow regime by an impoundment can have various adverse effects on *Pseudoplatystoma* fish species, including loss of stimuli for migration, loss of migration routes and spawning grounds, decreased survival of eggs and juveniles, decreased recruitment to the mature life stage and diminished fisheries production [76].

In addition to obstruction of river flow due to dams, overfishing is especially evident in parts of the São Francisco and Paraná rivers [32], particularly regarding *P. corruscans* stocks [32,77–79]. This species is subject to overfishing in Minas Gerais State, Brazil. *P. corruscans* harvest in the São Francisco River has manifested indications of collapse [79,80]. In the 1950s, the capture of thousands of *P. corruscans* with low fishery effort was the norm [81]. More recently, however, the yield of *P. corruscans* caught in a vital fishing area has declined from 10.3 kg fish/day in 1987 to 0.8 kg fish/day in 1999 [40].

In the Amazon basin, some authors have suggested that *P. tigrinum* and *P. fasciatum* are declining in mean catches and captured at small sizes [68,82–84]. Published landing data are low. *Pseudoplatystoma* species are essential catfishes in the landings of Amazonas State, Brazil. There were landings of 700 tons/y of *P. fasciatum* in seven fish-packing plants near Manaus in 1995 and 1996 [85]. In Tefe, Brazil, *P. fasciatum* landings averaged 18 tons/y between 1991–1994 [86]. In the Magdalena basin, the main threat to *P. magdaleniatum* is also overfishing. Estimates from landing indicate that the population there experienced a reduction of 72.7% between 1995 and 2007 [19]. The reasons for the decline are that the established minimum capture size and the ban on commercialization during the reproductive periods are not respected [87]. The species is not considered to reach maturity until sizes of 65 and 89 cm (total length) for males and females, respectively. Still, the average size-at-capture has declined from 92 cm in 1973 for the entire Magdalena basin to 42 cm in 2010 [88].

7. Conclusions

Although many essential studies have been made to understand the biology of *Pseudoplatystoma* species, many aspects require further investigation. In the absence of information, we have synthesized currently available knowledge to tentatively fill knowledge gaps for some species and to identify priority research topics to inform the sustainable fisheries management and conservation of *Pseudoplatystoma* species (Table 4).

To effectively manage *Pseudoplatystoma* species, knowledge of several key ecological aspects is still lacking (Table 4). The best-studied aspect of the ecology of all *Pseudoplatystoma* species regards the migration of all eight species. However, information on migration timing and distance, reproduction, and adult and juvenile growth is still missing for most species, which impedes fisheries management, including the delimiting of management units and fisheries areas, as well as the planning of dam construction. Based on the migratory life histories of *P. fasciatum*, *P. tigrinum*, *P. punctifer*, and *P. magdaleniatum*, we recommend avoiding the construction of dams, and when unavoidable, planning should include spatially explicit prioritization methods that trade-off electric power production and biodiversity loss under different scenarios in order to lower environmental costs [73].

Table 4. Summary of information available and knowledge gaps for eight species of genus *Pseudoplatystoma*.

Species	Genetics	Fisheries Status	Growth	Reproduction	Movement Ecology
<i>P. fasciatum</i>	Microsatellite DNA showed high genetic diversity with 200 km of genetic isolation by distance	No data	Validation, growth curves	Total spawning in the rising and high-water seasons 31, 52, 43	Adults migrate, juveniles are nonmigratory 31~164 km, bidirectional movement during the dry season and the rising water period 39
<i>P. tigrinum</i>	No data	No data; exploited very close to maximum sustainable 54	Validation, growth curves	Total spawning in the rising water season 44, 52	Adults migrate, juveniles are nonmigratory 31
<i>P. punctifer</i>	No data	No data	Validation, growth curves	No data	No data
<i>P. reticulatum</i>	No data	No data	No validation data, growth curves	Total spawning in the rising water season 46	Believed to be migratory
<i>P. mataense</i>	No data	No data	Validation, growth curves	No data	Believed to be migratory
<i>P. orinocense</i>	No data	No data	No data	No data	Believed to be migratory
<i>P. magdaleniatum</i>	No data	No data	No data	Spawning in the rising water season 45	Believed to be migratory
<i>P. corruscans</i>	Mitochondrial COI region, microsatellite DNA analysis to delineate 2 ESUs	No data; strongly overfished 71	No validation data, growth curves	Total spawning in the rising water season 32, 46	Partial migration of females; homing migration 40

Reproduction data is unavailable for *P. punctifer*, *P. mataense*, and *P. orinocense*, which challenges the development of effective management strategies for these species, including the delimitation of the period when fishing could be prohibited. In the absence of information on the reproduction of the species, we recommend that fishing be prohibited during the flood season for all species within their respective distributions.

Regarding growth, data is totally absent for *P. orinocense* and *P. magdaleniatum*. Moreover, validation of growth rings is missing for *P. reticulatum*, *P. mataense*, and *P. corruscans*. Growth is the main indicator of change in biomass which is essential to determine population production strategies for stock assessment and science-based management. Based on the growth information available for *P. fasciatum*, *P. tigrinum*, and *P. punctifer*, management strategies addressing the minimum size-at-capture should be developed and implemented.

Temporal data on changes in biomass and studies of the population dynamics of all *Pseudoplatystoma* species are few. This is the main ecological aspect impeding the management of the eight species of the genus. However, based on the current knowledge of general patterns of population dynamics of tropical species and the life-history traits of *Pseudoplatystoma* species, we suggest that recruitment of these species be classified as periodic. The biomass of tropical fishes can decrease by around 50% from the flood season to the dry season [63,64]. These considerations are such that harvest should be conservative, allowing populations to have a demographic buffer.

Finally, genetic data is missing for *P. tigrinum*, *P. mataense*, and *P. orinocense*. Therefore, without more studies on population genetics, the management of these species will be not well supported with data informing the delineation of management units. Until data are amassed and analyzed, we suggest that the management of *Pseudoplatystoma* species be done according to the basin in which the respective species are distributed. For instance,

the management of *P. corruscans* in the Paraná-Uruguay basins should be done within the respective MUs. Fishery management must set sustainable exploitation rates for each MU, as each is demographically independent. Management of *P. reticulatum* and *P. corruscans* in the São Francisco and Paraná basins, respectively, should be done independently; these populations putatively belong to different MUs or even ESUs. Populations of *P. corruscans* in the Paraguay River basin are currently expanding, in contrast with those of *P. reticulatum* in the São Francisco River basin. Finally, in the Amazon basin, the management of *P. fasciatum* should be done within distributional patches that are separated from each other by at least 200 km. However, more studies are necessary to guide the management of *P. fasciatum* in the Amazon basin.

8. Future Directions: Knowledge Gaps

We have synthesized current understanding and identified the key knowledge gaps in interconnected areas of study of *Pseudoplatystoma* species. This body of information, complemented with future studies, would help amass the information needed for effective fisheries management and conservation of these species. Our understanding of the systematics and phylogeny of the genus *Pseudoplatystoma* is not yet settled. Further studies are needed to clarify the systematics, taxonomy, and distributions of the respective lineages in the genus. These studies will need suitably broad collections of study material from across the range of the species and well-chosen phylogenetic markers to address subtle patterns of evolutionary change. Historical interbreeding of lineages may complicate the inference of evolutionary history. In particular, the distinctions between *P. fasciatum* and *P. punctifer* and the introgression among *P. mataense* and *P. mataense* are of interest for both basic understanding and practical application in conservation and fishery management.

The growth of *Pseudoplatystoma* species has been better studied than other biological aspects. In general, previous studies indicate that the annulus formation in the hard parts (otoliths and vertebrae) of *Pseudoplatystoma* occurs during the dry season, with slower growth during the low-water season and faster growth during the high-water season. Secondly, we conclude that *Pseudoplatystoma* species have relatively slow growth rates and high longevity compared to many other Neotropical fish species. However, more studies about somatic growth plasticity and validation of annulus formation for all species are needed to understand patterns of growth of *Pseudoplatystoma* species throughout the distribution of the respective species.

The population dynamics of *Pseudoplatystoma* species have not yet been adequately described. Practical knowledge gaps regarding the population dynamics of the *Pseudoplatystoma* species still need to be filled. Population dynamics studies are missing for *P. fasciatum*, *P. punctifer*, *P. reticulatum*, *P. magdaleniatum*, and *P. orinocense*. However, available studies on sustainable fisheries landings suggest that most *Pseudoplatystoma* populations and species are overexploited. Some *Pseudoplatystoma* species seem to be imperiled, and more studies are necessary to understand the population dynamics and guide fisheries management actions to conserve these species.

Finally, regarding the population genetics of species within the genus *Pseudoplatystoma*, more studies of all eight species of the genus are needed. *P. corruscans* is the best-studied species of the genus. However, the same level of investigation should be applied to the other seven species. Ideally, the next steps in the study of molecular genetics of the genus should apply the same molecular markers so that results within and among species can be compared. The investigation of possible Management Units (MUs) and possible Evolutionary Significant Units (ESUs) is crucial for understanding the drivers shaping the population structure of these species and, thus, the appropriate planning for the fisheries management and conservation of the species.

Clearly, challenges in research of the biology of *Pseudoplatystoma* species persist. With continued research and collaboration among research groups, understanding the biology and ecology of this genus would fill these knowledge gaps and contribute to fisheries management and conservation of the eight species of the genus *Pseudoplatystoma*.

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