

UNIVERSIDAD DEL ZULIA

Publicación del Museo de Biología de la Universidad del Zulia ISSN 1315-642X (impresa) / ISSN 2665-0347 (digital)

https://doi.org/10.5281/zenodo.14583578 / Anartia, 39 (diciembre 2024): 9-21

Serbiluz

Biblioteca Digita

positorio Académico

# Population dynamics of *Pseudoplatystoma metaense* Buitrago-Suárez & Burr, 2007 (Pisces, Siluriformes: Pimelodidae) from the Northwestern Orinoco River Basin

Dinámica poblacional de *Pseudoplatystoma metaense* Buitrago-Suárez & Burr, 2007 (Pisces, Siluriformes: Pimelodidae) en la cuenca noroccidental del río Orinoco

Alfredo Pérez<sup>1</sup> & Donald C. Taphorn<sup>2</sup>

<sup>1</sup>Universidade Federal do Amazonas, Instituto de Ciência e Tecnologia (ICET), Programa de Pós-graduação de Ciência e Tecnologia dos Recursos Amazônicos. Campus I, Tiradentes, Itacoatiara, AM. Brasil <sup>2</sup>BioCentro, Universidad Nacional Experimental de los Llanos Occidentales Ezequiel Zamora (UNELLEZ), Guanare, Portuguesa, Venezuela

Correspondence: alfredo.perez@ufam.edu.br

(Received: 24-10-2024 / Accepted: 01-11-2024 / On line: 31-12-2024)

# ABSTRACT

The Matafraile catfish (*Pseudoplatystoma metaense* Buitrago-Suárez & Burr, 2007) is the second most important commercial species in the Apure River region. This species, besides being one of the most abundant, is under strong fishing pressure, and despite its commercial importance, there is no information on its population dynamics and exploitation patterns, which is crucial to guide its sustainable management. The objective of the present study was to generate essential biological parameters to determine the status of the *P. metaense* stock in the Apure River basin, based on size frequency data, collected monthly from commercial landings during the period 1996 - 2003. Some of the population parameters of the species were estimated through empirical relationships and analyzed using fishery stock assessment models (Beverton & Holt 1957). The Yield per Recruit (Y/R) and Biomass per Recruit (B/R) model analyses showed that *P. metaense* is overexploited, as shown by these growth and recruitment descriptors. The current fishing exploitation rate of 0.86 exceeds the Biological Reference Points estimated in 1996 (*E*max = 0.58), confirming that the stock of *P. metaense* in the Apure River is being over-exploited above sustainable levels. The mean size of fish landed in 2003 (*L*mean= 64.90 cm TL) shows that fish are being caught below the mean length of sexual maturity (Lm= 62.88 cm TL). Likewise, the fishing mortality rate ( $F_{2003}$  = 0.95) was higher than the optimal reference point (Fmsy= 0.95). Actions must be taken to monitor the resource to allow its recovery and the size of the fish at first capture to reach acceptable levels (Lc= 54 cm TL).

Keywords: Apure River, Matafraile catfish, overfishing, population dynamics, Venezuela.

## RESUMEN

El bagre Matafraile (*Pseudoplatystoma metaense* Buitrago-Suárez & Burr, 2007) es la segunda especie comercial dominante en la región del río Apure. Esta especie, además de ser una de las más abundantes, se encuentra bajo una fuerte presión pesquera, y a pesar de su importancia comercial, no existe información sobre su dinámica poblacional y patrones de explotación, lo cual es crucial para orientar su manejo sostenible. El objetivo del presente estudio fue generar parámetros biológicos esenciales para determinar el estado del stock de *P. metaense* en la cuenca del río Apure, con base en datos de frecuencia de tallas, recolectados mensualmente de los desembarques comerciales durante el período 1996 - 2003. Los parámetros poblacionales de la especie fueron estimados a través de relaciones empíricas y analizados usando modelos de evaluación de stocks pesqueros (Beverton & Holt 1957). Los análisis del modelo de Rendimiento por Recluta (Y/R), y Biomasa por Recluta

## Pérez & Taphorn

(B/R), mostraron que *P. metaense* está sobreexplotado, evidenciando sobrepesca de crecimiento y de reclutamiento. La tasa de explotación pesquera actual de 0,61 superando los puntos de referencia biológicos estimados en 1996 (Emax = 0,50), lo que confirma que el stock de *P. metaense* en el río Apure está siendo sobreexplotado por encima de los niveles sostenibles. La talla media de primera captura desembarcados en 2003 (Lc= 54,00 cm LT), muestra que los peces están siendo capturados por debajo de la talla media de madurez sexual (Lm= 62,88cm LT). Igualmente, la tasa de mortalidad por pesca ( $F_{2003}$ = 0,95) fue superior al punto de referencia óptimo (Fmsy= 0,40). Se requiere gestionar acciones de fiscalización del recurso, para su recuperación y manejo sustentable. En ese sentido se propone un conjunto de medidas drásticas de ordenación pesquera, como aumentar la talla mínima legal a 76 cm TL).

Palabras clave: bagre Matafraile, dinámica poblacional, río Apure, sobrepesca, Venezuela.

## INTRODUCTION

Venezuela's inland fisheries are comprised of approximately 60 species. These species support traditional or historical fishing in the country's main watersheds, contributing to an annual production of around 50,000 tons (Novoa & Ramos 1978, Novoa 1982, 2002, Machado-Allison & Bottini 2010, Baigún & Valbo-Jørgensen 2023).

In the Apure River system, fishing is carried out from the border with Colombia to its mouth in the Orinoco River. Species such as cachama (*Colossoma macropomum* Cuvier, 1816), palometa (*Mylossoma albiscopum* Cope, 1872), morocoto (*Piaractus orinoquensis* Escobar-Lizarazo et al., 2019) and coporo (*Prochilodus mariae* Eigenmann, 1922) represent approximately 49% of historical catches (Machado-Allison & Bottini 2010, Baigún & Valbo-Jørgensen 2023), while large pimelodids catfish constitute 21%. However, a downward trend in catches of these species and in totals is observed (Baigun & Valbo-Jørgensen 2023).

Populations of large pimelodid catfishes are a crucial component of freshwater fisheries in South America, which has increased their study in the last 30 years (Barthem & Goulding, 1997, Novoa 2002, Petrere *et al.* 2004, Alonso & Pirker 2005, García *et al.* 2009, 2017). Using age-structure-based models, stock assessments began with *Brachyplatystoma vaillantii* (Valenciennes, 1840) in the Amazon River estuary (Barthem 1990). Similar studies include species such as *Hemisorubim platyrhynchos* (Valenciennes, 1840) and *Sorubim lima* (Bloch & Schneider, 1801) in the Cuiabá River (Penha & Matheus 2007), and *B. rousseauxii*(Castelnau, 1855) in the Caquetá River, Colombia (Agudelo-Cordoba *et al.* 2013), among others (Santana *et al.* 2014, González *et al.* 2017).

However, population dynamics studies in species of the genus *Pseudoplatystoma* are limited. Ruffino & Isaac (1999) evaluated *P. tigrinum* (Valenciennes, 1840) in the lower Amazon (Pará, Brazil), while Matheus & Petrere (2004) investigated *P. corruscans* (Spix & Agassiz, 1829) in the Cuiabá River (Brazil) and González *et al.* (2012) studied *P. orinocoense* Buitrago-Suárez & Burr, 2007, in the Orinoco River (Venezuela).

The striped catfish (*Pseudoplatystoma metaense*, Buitrago-Suárez & Burr, 2007) is one of the most important fish species in the Apure River basin (Reid 1983, Novoa 2002). This species, one of the most abundant among the large Venezuelan catfish, is subject to strong fishing pressure due to the capture of juveniles and pre-adults with small gillnets used for prochilodontids (Barbarino 2002, Novoa 2002).

Historical data on the size of *P. metaense* in the lower Apure (Reid 1983) indicate that, in the 1980s, this species reached capture lengths between 60 and 170 cm TL, with a mean length (*L*mean) of approximately 110 cm TL. After 18 years, Barbarino (2005) observed a reduction in the length range from 148 to 120 cm TL, with a mean *L*mean= 75.5 cm TL. This progressive decrease in mean size suggests an unfavorable scenario. Furthermore, the current regulation that allows the artificial selection of large individuals could alter the genetic structure of its populations (Conover & Munch 2002).

This scenario not only reduces stock abundance but also increases the risk of annual recruitment failures and decreases reproductive success by eliminating the longestlived and most fertile individuals ("mega-spawners" according to Froese 2004) in conventional fisheries management (Restrepo 2009). The lack of knowledge about the population structure and the intense, unregulated exploitation put the sustainability of *P. metaense* at risk. We do not know whether the species is being over-exploited or if it is in a situation of overfishing for growth or recruitment; neither what the optimal first-capture size would be to recover the stock, nor whether the minimum legal capture size is adequate. Given this situation, it is essential to carry out studies to evaluate the situation of this species and obtain information that allows the preservation of its populations (FAO 1988). This knowledge is even more relevant in species such as *P. metaense*. With these questions, we set out to evaluate the status of the *Pseudoplatystoma metaense* stock to offer recommendations to improve the management of this resource in the Apure River basin.

## MATERIALS AND METHODS

#### Hydrological system of the Apure River

Commercial artisanal fishing is carried out along the Apure River, which is approximately 600 km long; as well as along the Arauca River, from the border with Colombia to its mouth in the Orinoco along 710 km; the Meta River with 230 km in length and some other smaller rivers such as Payara, Apure Viejo, Apurito, Ruende, Uribante, Caparo, Portuguesa, Paguey, among others (FAO 2005). According to what is reported in official statistics, the base ports that stand out with the highest volume of landings for the year 2000 were: San Fernando (36%), San Juan de Payara (22%) Achaguas (16%), Arichuna (11%) and Guasdualito (5%), although the precision of the data is subject to variable margins of error (FAO 2005).

#### Data collection

From the commercial catches landed by the artisanal commercial fleet of San Fernando de Apure, from the hydrographic system of the Apure River, in the Northwest region of the Orinoco River basin, a sampling program was carried out in collaboration between the Instituto Nacional de Investigaciones Agropecuarias (INIA) in the period 1996-2000, and continued by the Universidad Nacional Experimental de Los Llanos Occidentales "Ezequiel Zamora" (UNELLEZ) in 2003. During the execution of this sampling program, data on the lengths of *P. metaense* were collected, corresponding to an area of approximately 111,800 km<sup>2</sup> (Fig. 1).

#### Data analysis

Fish samples were obtained monthly from local fishermen, selecting a minimum of 30 specimens obtained at random, in situ. The specimens were weighed with a 1 g precision scale, and measured with an ichthyometer of 0-150 cm with 0.1 cm precision. During the monitoring program (INIA-UNELLEZ) from 1996 to 2000, length data for *P. metaense* were obtained from 2,634 specimens.

The length data expressed in Total Length (TL) of the specimens were grouped into 4 cm size classes to build a length frequency distribution.

## Estimation of population parameters

The growth parameters of *P. metaense* (*L*inf, K, to) of the von Bertalanffy equation (VBGF), calculated using the size distribution frequency for the empirical equations

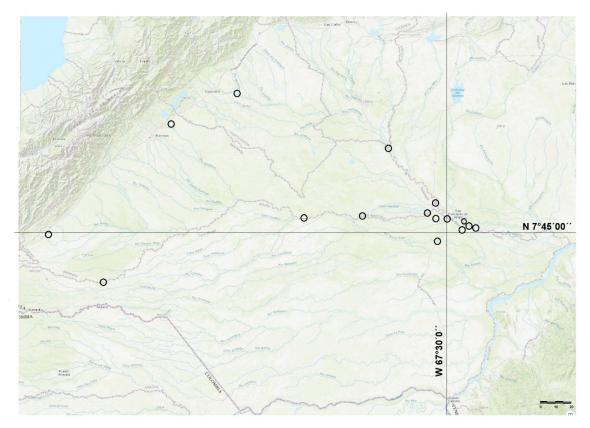


Figure 1. Hydrographic system of the Apure River, in the northwest part of the Orinoco River basin (Venezuela), showing the collection points of *P. metaense*.

of Froese & Binohlan (2003) and Froese (2022), are both shown in Table 2. Several methods for estimating total mortality (Z) were applied, such as the Baranov method (1918), using the linearized catch curve, using the frequency distribution data by size class, prior to transforming the data from length to age using the Pauly equation (1983), assuming that the stock density decreases at a rate proportional to the abundance of each age group, in which the specimens are vulnerable to fishing. Other methods such as those of Beverton (1992) and Ssentongo & Larkin (1973), were also used.

For the estimation of natural mortality (M), the methods of Taylor (1958), Pauly (1980), Hoening (1983), Griffiths & Harrod (2007), Gislason 2010, and Charnov 2012, were used. Fishing mortality (F) was estimated as the difference between the instantaneous rate of total mortality (Z) and the instantaneous rate of natural mortality (M). The exploitation rate (E), which identifies the situation of over-exploitation of the resource, was calculated through the relationship: E= F/(F+M) (Ricker 1975, Sparre & Venema 1997).

The length at first catch (Lc) was estimated as the size class fully represented in the length composition of the catch. The length at first sexual maturity (Lm) was calculated using the empirical equation of Froese & Binohlan (2003). The mean length at catch (Lmean) and the optimal length at catch (Lopt) were estimated using the empirical equations of Froese (2004) and Froese & Binohlan (2003). The age at first sexual maturity (tm) was also calculated using the Beverton & Holt (1957) equation estimated from the length at sexual maturity (Lm).

## Stock assessment models

To estimate the state of exploitation of the resource, the Beverton & Holt (1957) model was used as an age structure model to estimate the yield per recruit (Y/R), as well as the biomass per recruit (B/R), which expresses the mean annual biomass of survivors as a function of fishing mortality (Sparre & Venema 1997). The biomass per recruit (B/R) was calculated from the equation of Beverton & Holt (1957). The relative yield per recruit (U'/R) was also estimated as an approximation of the verification of the equation (E= F/Z) of Ricker (1975).

In order to estimate the variation in stock performance and possible performance scenarios with different lengths at first capture (Lc), several simulations were performed with the Beverton & Holt model (1957), using different values of Lc (40, 50, 65 and 70 cm TL), as an indicator of fishing pressure to facilitate the comparison of the resource performance response.

## Biological Reference Points (BRP)

As the BRP, the maximum fishing mortality (*F*max) was considered, defined as the fishing mortality rate that maximizes the yield per recruit without considering whether the spawning stock biomass (SSB) is conserved to maintain recruitment in the future. Fishing mortality referring to 10% of its maximum yield capacity ( $F_{0.1}$ ) was also considered, which is calculated from *F*max, considered as the rate at which the slope of the yield per recruit curve falls to 10% of its original value. As well as the ratio of biomass per recruit (B/R) between 30-40% of the spawning stock biomass (SSB<sub>30-40%</sub>). As PRBLimite, the ratio (F/M <1) was considered, considering that F=M, is based on the assumption that *F*msy is approximately equal to natural mortality (Caddy & Mahón 1995), and the ratio (SSB/Bo <0.5).

#### Management scenarios

The optimal length at first capture (*Lc\_opt*), was estimated using the empirical equation of Froese *et al.* (2016), *Lc\_opt* (*Linf*\*(2+3\*F/M)/(1+F/M)\*(3+M/K), in order to make management recommendations for this species.

## RESULTS

## Length frequency distribution

In the period 1996-2000, a total of 2,056 specimens of *P. metaense* were randomly measured during this study. At the beginning of this study in 1996, total lengths and body weights ranged from 42 to 122 cm TL, and from 1,100 to 24,700 g, respectively. The length at first capture was Lc=78 cm TL, and the length mean capture was Lmean=83.01 cm TL. A detailed analysis of the lengths by year showed a tendency for the mean capture length to decrease (Table 1, Fig. 2).

A progressive reduction in the length at first capture (Lc), as well as the mean capture length (Lmean), was also observed during the same period (1996-2000). Until 1997, both Lc and Lmean had not crossed the threshold of optimal capture length (Lopt). However, in 1998, Lc crossed the threshold of Lopt and in 2000, it also crossed the threshold of the mean length at sexual maturity (Lm). In the case of the mean capture length (Lmean) in 2000 it crossed the threshold of Lopt.

An analysis of the data corresponding to the last year of available data (2003; n= 578), showed that total lengths and body weights varied from 34 to 117 cm TL and from 755.7 to 33,814 g, respectively. The length at first capture (*Lc*) was estimated at 54.00 cm TL and *L*mean at 64.90 cm TL (Fig. 2).

**Table 1**. Variation in the length distribution (cm TL) of *P. metaense* exploited by the artisanal commercial fleet of the lower Apure in the northwest of the Orinoco River (1996-2000), compared to 2003. Showing the mean catch length (mean); length interval (range: max-min); Mode (mo); Standard Deviation (sd); Coefficient of Variation (CV) and Number of observations (n).

	/						
Years	mean	max	min	mo	sd	CV	n
1996	83.01	117.00	47.00	78.00	14.15	17.04	225
1997	74.15	122.00	43.00	82.00	14.63	19.73	929
1998	70.23	106.00	41.00	71.00	12.53	17.85	301
1999	71.14	103.00	45.00	76.00	10.46	14.70	176
2000	72.58	117.00	42.10	54.00	8.07	24.90	425
2003	64.90	120.00	34.00	54.00	17.30	26.66	578

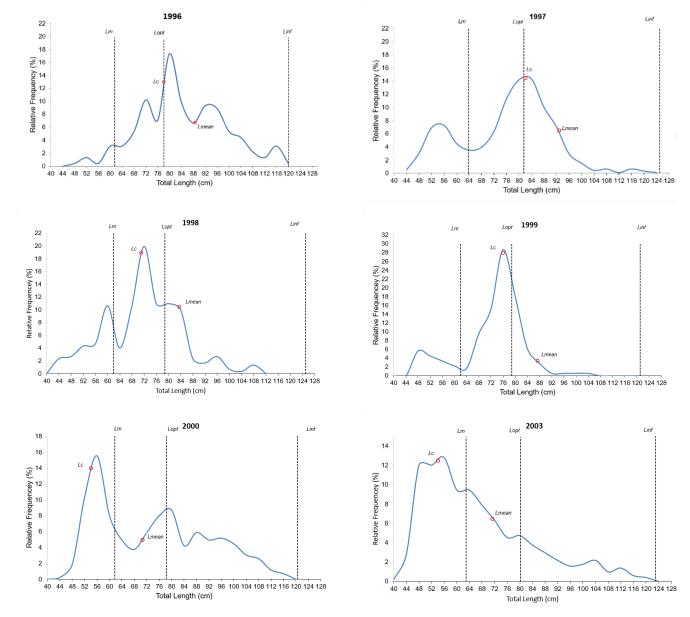


Figure 2. Percentage length composition of *P. metaense*, in the period 1996-2003. Indicating the length at first capture (Lc) and mean length at capture (Lmean), in relation to the length at first sexual maturity (Lm), optimal length at capture (Lopt), and maximum length observed (Lmax).

# Pérez & Taphorn

## Estimation of population parameters

The estimates of population parameters of *P. metaense* are summarized in Table 2. The comparison of population parameters in the periods 1996-2000 with 2003 showed a decrease in the values of Lm, Lopt and Lmean, as well as in Tmax, tm and All natural mortality values were higher in 2003. Total mortality (Z), as well as exploitation rate (E), were also higher in 2003.

## Stock assessment models (Y/R; B/R; U/R)

The yield per recruit curve (Y/R) for the beginning of the 1996-2000 period indicates that sustainable fishing mortality, *i.e.*, as PRB (Fmax= Fmsy) was reached at F=

0.60, and the Biomass per recruit (B/R), for that value of F, was estimated at F= 0.15. For that year, fishing mortality was at a level below Fmax (PRB Limit), practically at (PRB Target)  $F_{0.1} = F_{1996} = 0.20$  (Fig. 3).

## Biological Reference Point

For the year 2003 the value of F was higher ( $F_{2003} = 0.95$ ), showing a situation of overfishing of growth in *P. metaense* (Fig. 4a). Considering the level of F and the length at first capture (*Lc*), the yield curve was not stabilized, therefore, it was impossible to estimate the maximum point of the curve, a similar situation observed for the analysis of biomass per recruit (B/R).

Table 2. Mean values of population parameters of *P. metaense*, in the period 1996-2000, derived from empirical relationships and compared with 2003. Where: *L*inf= maximum asymptotic length; *L*mean= mean length at capture; *L*m= length at first sexual maturity; *L*opt= length at capture optimal; K= constant of VBGF; Tmax= longevity; to= constant of VBGF; M= Natural mortality; Z= Total mortality; Tm= Age of sexual maturity; E= Population exploitation rate.

D (			1996-2000	2003
References	Indicator	Unit.	Value	Value
Froese & Binohlan (2003) Log(Linf) =0.044 + 0.9841*log(Lmax)	Linf=	cm	119.02	120.06
Beverton & Holt (1992) Lmean= $(3^{*}Lc + Linf)/4$	Lmean=	cm	81.96	71.27
Froese & Binohlan (2000) Log( <i>L</i> m) = 0.8979 * Log( <i>L</i> inf) - 0.0782	Lm =	cm	61.03	62.88
Froese (2004) Lopt= $Linf^{*}(3/3 + M/K)$	Lopt =	cm	94.55	97.06
De Merona (1983) K = $5.4^*$ Linf <sup>-0.6811</sup>	K =	1/y	0.21	0.20
Froese (2022) K = $((3/Tmax)-(Ln(1-0.95^{*}(Lm/Linf))/tm)/2$	K=	1/y	0.12	0.11
	Kmean	1/y	0.21	0.20
Beverton & Holt (1992) Tmax = 3/K	Tmax=	yrs	14.38	14.71
Froese & Binohlan (2003) Log(-to)= 0.3922 - 0.2752*Log( <i>L</i> inf) -1.038*Log(K)	to =	1/y	- 0.53	- 0.53
Hoening (1983) $M = Ln(M) = 1.46 - 1.01 Ln(Tmax)$	M =	1/y	0.29	0.28
Griffiths & Harrold (2007) M=1.406*Winf <sup>(-0.096)</sup> *K <sup>(0.78</sup>	M =	1/y	0.10	0.10
Pauly (1980) M=-0.006-0.279*Log( <i>L</i> inf)+Log(K)+0.4634*Log(T°C)	Log(M) =	1/y	0.22	0.21
Taylor (1958) M=-Ln (1- 0.95)/ A <sub>0.95</sub>	M =	1/y	0.22	0.21
Gislason (2010) M= 0.55-1.61*Ln( <i>L</i> mean) +1.44*Ln( <i>L</i> inf)+Ln(K)	M =	1/y	1.81	1.57
Charnov (2012) $M = K^*(Lmean/Linf)^{-1.5}$	M =	1/y	0.20	0.26
	Mmean	1/y	0.16	0.20
Beverton & Holt (1957) Z= K*(Linf – Lmean)/(Lmean-Lc)	Z =	1/y	0.62	0.61
Ssentongo & Larkin (1971) Z=N*K/(N+1)*(Ln ( <i>L</i> inf- <i>L</i> c)/( <i>L</i> inf- <i>L</i> `))-1)	Z =	1/y	1.97	2.49
Baranov (1918) Curve catch = Z	Z =	1/y	0.14	0.36
	Zmean	1/y	0.38	1.16
Beverton & Holt (1957) Tm= to - $(Ln(1-Lm)/Linf/K)$	tm =	yrs	3.80	3.88
Ricker (1975) $E = F/Z$	E=	1/y	0.58	0.86

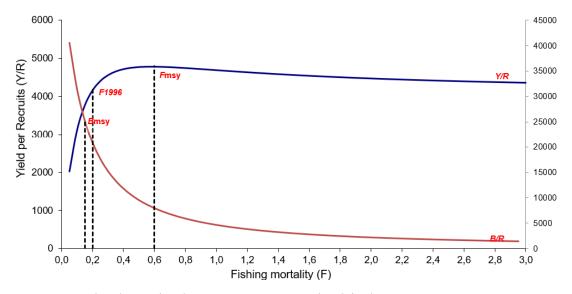


Figure 3. Yield per Recruit (Y/R) curve (blue) and Biomass per Recruit (B/R) (red); of *P. metaense*, in the year 1996.

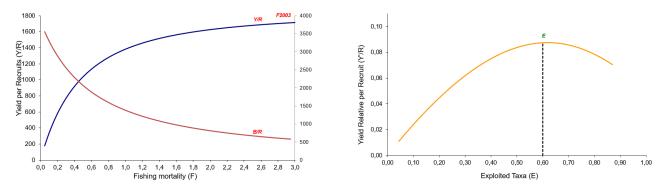


Figure 4. a) Relative Yield (Y/R) curve in blue and Biomass per Recruit (B/R) curve in red for *P. metaense* in 2003; b) Relative Yield per Recruit (U'/R).

This situation occurs because in a scenario without a limit on the length of the capture, the biomass falls below 20% of the level of unexploited biomass (*B*o), where recruitment is affected and the absolute biomass and yield are reduced to extreme levels. This can be better observed in figure 5b. On the other hand, the maximum value at Emax= 0.61 (Fig. 4b), shows the current exploitation level (E), which is higher than the recommended optimal exploitation rate (E= 0.5).

In order to better assess the impact of fishing on *P. me*taense in 2003, we calculated the relative yield based on the F/M ratio, including also the relative biomass. In figures 5a and 5b, we observe that  $F_{0.1}$  (a Target BRP), marks a widely used precautionary level of fishing mortality, where the long-dashed curve represents the yield or biomass per recruit for *P. metaense*, caught length at a firstcapture Lc = 54 cm TL, at which point fishing mortality represents more than four times the natural mortality (F= 4.5\*M). The lowest yields and biomass are obtained when fishing without size limits, as indicated by the dash-dot line, which assumes a start of fishing at 5% of the asymptotic length.

In this case, we observe more clearly the magnitude of the intensity of fishing mortality, to determine the maximum point of the curve (F/M $\approx$  2.8) and the reference value for *P. metaense* in 2003 (F/M $\approx$  4.7), whose values are biologically impossible to reach (Fig. 5a). On the other hand, the analysis of the relative biomass shows that the spawning stock biomass (SSB), without fishing of *P. metaense* should present values greater than 0.5 (PRB Objective). With fishing, the exploitation tolerance of SSB would be 0.4 or 0.3, which represents 40 or 30% of the spawning stock biomass (SSB). Thus, when the values exceed the maximum limit (PRB Limit= SSB<sub>30%</sub>), we are in a situation of overfishing, with the values for 2003 being much lower B<sub>2003</sub> $\approx$  0.18 (Fig. 5b).

Therefore, the graphs in figures 5a and 5b indicate that the reference point F=M would be exceeded, indicating that *P. metaense* is over-exploited. Likewise, the limit of the biomass of the reproductive stock shows values lower than the corresponding ideal reference value for fishing mortality ( $F_{2003}$ ), this represents a reduction in the biomass of the reproductive stock in relation to the virgin biomass close to 82%; evidencing the existence of a severely exploited resource.

#### Management scenarios

The calculation of the optimal length at first capture (Lc\_opt.) of *P. metaense* showed that the Lc/Linf ratio was 0.45, indicating that this proportion is below the expected reference value (Lc/Linf = 0.64) for this species (Fig. 6).

With the start of fishing at  $Lc_{opt} = 76$  cm TL and setting the fishing mortality at a relatively low level (F= 0.5\*M= 0.11), it would allow to locate the mean total mortality rate Zmean = 0.38 and a mean duration of

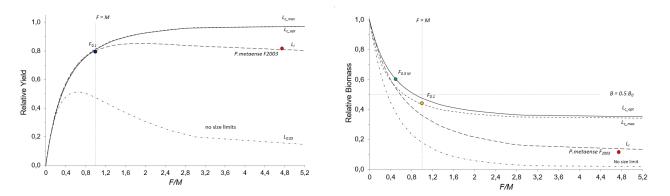
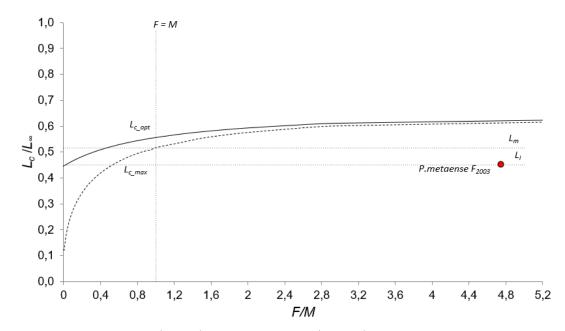


Figure 5. a) Yield per recruit relative to the theoretical maximum yield, and b) Biomass per recruit relative to unexploited biomass, both plotted as a function of the F/M ratio. Where: The optimal length at first capture  $Lc_opt$  (solid line) indicates the length that results in the optimal length at capture (Lopt) relative to the maximum length at first capture  $Lc_max$  (short dashed line). The lowest yields and biomass are obtained by fishing without lower size limits (dotted line), which assumes a start of fishing at 5% of the asymptotic length. The long-dashed line represents the yield or biomass per recruit for *P. metaense*, caught from the length at first capture in 2003 (Lc = 54 cm TL).



**Figure 6.** Optimal length at first capture ( $Lc_{opt}$ ), considering the ratio (Lc/Linf) as a function of the F/M ratio of *P. metaense*. The dashed line ( $Lc_{max}$ ) represents the maximum yield per recruit and the solid line ( $Lc_{opt}$ ) represents the optimal length at first capture. *Lm* represents the length at which 90% of the individuals reached sexual maturity. *Li* indicates the length at which the fish are fully recruited to the fishing gear (Li=Lr=Lc) and F2003 estimates the fishing mortality for that year.

the reproductive phase of 3.04 years or 40% of the natural duration, causing a slight reduction in the impact of commercial fishing.

In simulations with different scenarios of fishing pressure, using the stock assessment model (Beverton & Holt 1957), and considering different values of Lc (70, 65, 50 and 40 cm TL), in a hypothetical case that it were possible to set Lc=70 cm TL, but leaving the fishing effort (f) unregulated (assuming that f = F), it was observed that it would be a biologically nonviable situation (Table 3. Scenario 1). On the other hand, when we regulate or set fishing mortality at a certain point (F= 0.40), and leaving Lcunregulated, it would be a good option, but economically nonviable, due to the level of control to be applied (Table 3. Scenario 2). Therefore, it would be advisable to apply a mixed strategy in which both the effort (f) and the length at first capture are regulated in such a way that it is economically viable and biologically feasible (Table 3. Scenario 3).

These results show that a progressive reduction in Lc is accompanied by a significant reduction in yield, inducing in parallel an increase in fishing mortality. In other words, when we set the values of the length at first capture at acceptable levels (Lc=65 cm LT), the species' resilience capacity is reduced, but the variation in fishing mortality is maintained. According to the Venezuelan fisheries legislation, the minimum legal length (MLL) for landing *P. metaense* is 65 cm TL, this value would maximize yield only when fishing mortality is close to F = 0.40 - 0.60. However, for the period 1996 - 2000, fishing mortality for this species was estimated at F = 0.20, which implies that fish were being caught at a length greater than 78 cm TL.

# DISCUSSION

## Length catch reduction and effects of fishing

The results on *P. metaense* confirm that the predominance of young fish in commercial catches reduces the yield per recruit. This is because the length at first capture (Lc) in 2003 was smaller than that legally permitted (República de Venezuela 1991: MAC Resolution No. 140, March 9, 1991), that is, fish are caught with less than 65 cm TL. Consequently, larger catch volumes would be required to achieve profitable production.

The index E= F/Z, with values close to 0.5, has been considered to indicate a sustainable yield of the resource (Gulland 1983). However, Rochet & Trenkel (2003) maintain that this value could represent in itself a limit of over-exploitation and that any value of E> 0.5 would reflect over-exploitation. The results of this study (E= 0.61)

<i>Scenario 1</i> Fixed <i>L</i> c, as F increases	<i>Lc</i> (cm)	Z	F	<b>Y/R</b> (g)
	70	0.40	0.60	4.781
	70	0.60	3.00	4.074
Biologically unviable	70	0.80	20.00	4.037
	70	1.00	$\infty$	?
<i>Scenario 2</i> Progressive reduction of <i>L</i> c, with a fixed value of F	Lc (cm)	Z	F	<b>Y/R</b> (g)
Economically unviable	70	0.40	0.60	4.781
	65	0.40	0.45	4.182
	50	0.40	0.30	2.885
	40	0.40	0.25	2.307
<i>Scenario 3</i> Progressive reduction of <i>L</i> c, as F increases. F	Lc (cm)	Z	F	<b>Y/R</b> (g)
	70	0.40	0.60	4.781
Maata and a since a lastice	65	0.60	2.20	3.055
Most parsimonious solution	50	0.80	2.00	1.401
	40	1.00	2.55	816

**Table 3.** Simulation of the response of Yield per Recruit (Y/R) and Fishing Mortality (F) for *P. metaense* in the lower Apure, in three management scenarios, manipulating the length at first capture (Lc) and total mortality (Z).

indicate that in terms of fishing effort and biomass for the species, *P. metaense* clearly shows the symptoms of a resource in a state of over-exploitation.

## Length composition and fishing effects

The length composition of the catch in 2003 shows a notable difference from previous studies (Reid 1983, Barbarino 2005), reflecting the accumulated effect of fishing pressure over five decades. The decrease in the mean length of the catch is worrying, since 50% of the individuals caught are below the mean length of maturity.

Thus, the over-exploitation of *Pseudoplatystoma metaense* could trigger multiple ecological effects that affect the stability and structure of aquatic ecosystems. The main implications are grouped into changes in the trophic net, such as a reduction in the number of connections between trophic levels, which makes the network less complex and more vulnerable to additional disturbances. As the number of interactions is reduced, the ecosystem loses resilience and adaptive capacity, which increases the possibility of ecological collapse (Bascompte 2009). On the other hand, without adequate control, the species that constitute the main food of *P. metaense* can increase their population in an uncontrolled manner, which might increase intraspecific competition and depletes food resources for other consumers.

Alterations in species diversity, and when an apex predator disappears or is reduced, other lower-ranking predator species can increase their population density, negatively affecting prey species and those that occupy similar niches. It could increase competition between secondary predators that would partially occupy their role, which could decrease functional diversity and alter established ecological balances (Duffy 2003).

On the other hand, decades of exploitation generate a tendency towards the capture of younger and smaller individuals, which implies a reduction in reproductive success and in the capacity of the ecosystem to replenish the stock. This is particularly problematic in slow-growing species with long reproductive cycles, considering the resilience of the *P. metaense* population is reduced, which makes its recovery difficult and, in the long term, compromises ecological stability.

## Fishing management and recommendations

Selective harvesting by length, where large individuals are preferred, is common in tropical fisheries (Stergiou 2002). The preferential elimination of these individuals negatively affects the demographics, life history, and ecology of the species (Conover & Munch 2002).

To minimize the impact, regulations should be established that allow the reproduction and spawning of a greater number of individuals. This also includes the promotion of optimal capture lengths, where the growth rate is more effective.

To minimize the impact of fishing on *P. metaense* populations, a greater number of individuals should participate in the reproductive events of the species. Therefore, a set of rules must be established to ensure that individuals can reproduce and eventually spawn. Another important characteristic to be taken into account is the mean duration of the reproductive phase. If total mortality (Z = M + F) is reasonably constant after the age at which fish reach sexual maturity (tm), the mean duration of the reproductive phase is simply the inverse relationship of Z (Charnov 1993). Therefore, an increase in the length at first capture of *P. metaense* would translate into higher yields and would enhance the recovery of the stock.

In the 1980s, the first signs of over-exploitation appeared (Castillo 1988), and fishing pressure was already considered a problem. 40 years later, several commercial species have been found to have a length at first capture below the length at first maturity (INSOPESCA 2012). The situation is made even more difficult by the lack of a reliable record of official fishery statistics. Venezuela stopped making fishery statistics available to the public in 2007, and data were only available to the FAO until 2016 when it also suspended sending information to the FAO (Baigún & Valbo-Jørgensen 2023). Currently, the Venezuelan State does not have the technical and legal capabilities, nor the physical infrastructure to support logistics for inland fishing activity (Baigún & Valbo-Jørgensen 2023), and the overfishing of P. metaense clearly shows this situation.

It will inevitably be necessary to take some management actions to avoid irreversible damage to the stock and promote the recovery of the resource. In the current scenario, three main actions could be used in the management of the species:

- 1. A STRICT limitation of the capture for six months, coinciding with the reproductive season of the species.
- 2. A STRICT monitoring of a new minimum legal capture length (76.00 cm LT).
- 3. An EXTENSIVE program to inform and educate fishermen about the reasons for the regulations, and what will happen if they continue fishing without controls.

## Challenges in management

Management in tropical basins, such as the Orinoco and Amazon, presents unique challenges due to the characteristics of small-scale fisheries, which complicates the implementation of length limits (Isaac & Ruffino 1996, Novoa 2002). In this regard, it is suggested to incorporate complementary measures: catch quotas based on scientific data, seasonal closures in key tributaries, and strengthening of surveillance. Also considering the geopolitical context between Venezuela and Colombia in the Orinoquia. In this way, the biological consequences of selective capture by length would be avoided and the negative biological impacts of the artificial selection of capture lengths would be mitigated (Feneberg & Roy 2008).

## General conclusion

Despite the lack of recent data (2016-2024), it is estimated that the population of *P. metaense* has crossed the threshold towards recruitment over-exploitation, evidenced by records of low length in the main landing areas, due to the large number of fish caught with low first-capture length (Lc= 48.5 cm TL; personal observation by the first author in March 2022), in the main regional fairs and markets of the lower Apure. The current situation requires consideration of the implementation of:

- Strict seasonal bans, aligned with the reproductive cycle.
- New minimum legal catch length (76 cm TL).
- Training and awareness of fishermen on the risks of uncontrolled fishing.

## ACKNOWLEDGEMENTS

The authors would like to thank the Fondo Nacional de Ciencia, Tecnología e Innovación (FONACIT) (Project S1-99000994) and the support of the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) of Brazil for conducting research; Aniello Barbarino from the Instituto Nacional de Investigaciones Agropecuarias (INIA) of Venezuela, who kindly provided part of the biofishery data on P. metaense; the fishermen of the Apure River, Pedro Carrillo and Daniel Carrillo for providing samples and the fish wholesalers of the Municipal Market of San Fernando de Apure; Hender Castillo and Rafael for collecting and recording the ichthyological information, as well as for their invaluable support during all field visits. This work was carried out with the logistical and infrastructure support of the Universidad Nacional Experimental de los Llanos Occidentales "Ezequiel" Zamora (UNELLEZ) and the Instituto de Ciencias Exactas e Tecnología da Universidade Federal do Amazonas (UFAM/ICET), Brazil. We acknowledge the critical reading and kind suggestions of Á. L. Viloria and another (anonymous) reviewer.

## REFERENCES

- Agudelo-Córdoba, E., Á. V. J. León, C. A. Bonilla-Castillo, M. Petrere Jr., M. Peláez & F. Duponchelle. 2013. Breeding, growth and exploitation of *Brachyplatystoma rousseauxii* Castelnau, 1855 in the Caqueta River, Colombia. *Neotropical Ichthyology* 11:(3) 637–647.
- Aguilera, N. E. & A. Pérez. 2009. Análisis de la producción pesquera en los cuerpos de agua temporales del bajo llano, Venezuela. *Acta Apuroquia* 1: 32–43.
- Alonso, J. C. & L. E. M. Pirker, 2005. Dinâmica populacional e estado atual da exploração de dourada e de piramutaba. pp. 21–28. *In*: Barthem, R. B. & N. N. Fabré (eds.). *O Manejo da* pesca dos grandes bagres migradores: Piramutaba e Dourada no eixo Solimões-Amazonas. Manaus: Provárzea/IBAMA.
- Anderson, C.N.K., C. Hsieh, S. A. Sandin, R. Hewitt, A. Hollowed, J. Beddington, R. M. May, G. Sugihara. 2008. Why fishing magnifies fluctuations in fish abundance. *Nature* 452(17): 835–839.
- Baigún, C. R. M. & J. Valbo-Jørgensen. 2023. La situación y tendencia de las pesquerías continentales artesanales de América Latina y el Caribe. FAO Documento Técnico de Pesca y Acuicultura N.º 677. Roma, FAO. doi.org/10.4060/cc3839es.
- Bascompte, J. 2009. Disentangling the Web of Life. *Science* 325: 416–419.
- Baranov, T.I. 1918. On the question of the biological basis of fisheries. *Nauchn Issledov. Ikhtiologicheskii Inst. Izv.* 1: 81–128.
- Barbarino, A., D. C. Taphorn, K. O. Winemiller. 1998. Ecology of the coporo, *Prochilodus mariae* (Characiformes, Prochilodontidae), and status of annual migrations in western Venezuela. *Environmental Biology of Fishes* 53: 33–46.
- Barletta, M., V. Cussac, A. A. Agostinho, C. Baigún, E. K. Okada, A. C. Catella, N. F. Fontoura, P. S. Pompeu, L. F. Jimenez-Segura, V. S. Batista, C. A. Lasso, D. C. Taphorn, N. N. Fabre. 2016. Fisheries ecology in South American river basins. pp. 311–348. *In*: Craig, J. F. (dir.). *Freshwater fisheries ecology*. Oxford: John Wiley & Sons.
- Barthem, R. B. 1990. *Ecologia e pesca da Piramutava* (Brachyplatystoma vaillantii). Campinas, Brasil: Universidade Estadual de Campinas, 286 pp. [Tese Doutoral]
- Barthem, R. B. & M. Goulding. 1997. Os bagres balizadores: ecologia, migração e conservação de peixes amazônicos. Brasília:Sociedade Civil Mamirauá/MCT/CNPQ, 130 pp.
- Barthem, R. B. & M. Jr. Petrere. 1996. Fisheries and population dynamics of *Brachyplatystoma vaillantii* (Pimelodidae). pp. 329-340. In: Armantrout, N. B. & R. Wolotira (Eds.). Proceedings of the World Fisheries Congress, Theme 1. Condition of the World's Aquatic Habitats. New Delhi, India: Oxford and IBH Publishing Co. Pvt. Ltd.
- Beddington, J. R. & J. Cooke, 1983. The potential yield of previously unexploited stocks. FAO *Fisheries Technical Paper* 424. Roma: FAO, 47 pp.

- Beverton, R. J. H. 1992. Patterns of reproductive strategy parameters in some marine teleost fishes. *Journal of Fish Biology* 41: 137–160.
- Beverton, R. J. H. & S. J. Holt. 1956. A review of the life spans and mortality rates in nature, and their relation to growth and other physiological characteristics. *Ciba Foundation Colloquia on Ageing*. 5: 142–177.
- Beverton, R.J.H. & S. J Holt. 1957. On the dynamics of exploited fish populations. London: Chapman & Hall, 533 pp.
- Buitrago–Suárez, U. A. & B. M. Burr. 2007. Taxonomy of the catfish genus *Pseudoplatystoma* Bleeker (Siluriformes: Pimelodidae) with recognition of eight species *Zootaxa* 1512: 1–38.
- Caddy, J. F. & R. Mahon. 1995. Reference points for fishery management. FAO *Fisheries Technical Paper* 347: 1–82.
- Castillo, O. 1988. Aspectos biológicos y pesqueros sobre los peces comerciales del bajo llano con enfasis en los bagres (Orden Siluriformes). Caracas: Universidad Central de Venezuela, 114 pp. [Tesis de MSc]
- Charnov, E. L. 1993. *Life history invariants: Some explorations of symmetry in evolutionary ecology*. Oxford: Oxford University Press, xv + 167 pp.
- Charnov, E. L., H. Gislason & J. G. Pope. 2012. Evolutionary assembly rules for fish life histories. *Fish and Fisheries* 14: 213–224.
- Conover, D. A. & S. B. Munch. 2002. Sustaining fisheries yields over evolutionary time scales. *Science* 297: 94–96.
- De Merona, B. 1983. Modele d'estimation rapide de la croissance des poissons. Application aux poissons d'eau douce d'Afrique. *Revue d'Hydrobiologie Tropicale* 16(1): 103-113.
- Duffy, J.E. 2003. Biodiversity loss, trophic skew, and ecosystem functioning. *Ecology Letters* 6: 680–687.
- FAO. 2005. Resumen informativo sobre la pesca por países. Organización de las Naciones Unidas para la Agricultura y la Alimentación. https://www.fao.org/fi/oldsite/FCP/es/ven/ profile.htm
- Fenberg, P. B. & K. Roy. 2008. Ecological and evolutionary consequences of size-selective harvesting: how much do we know? *Molecular Ecology* 17: 209–220.
- Froese, R., H. Winker, D. Gascuel, U.R. Sumaila & D. Pauly. 2016. Minimizing the impact of fishing. *Fish and Fisheries* 17(3): 785–802.
- Froese, R. & C. Binohlan. 2000. Empirical relationship to estimate asymptotic length at first maturity and length at maximum yield per recruit in fishes with a simple method to evaluate length frequency data. *Journal of Fish Biology* 56: 758–773.
- Froese, R. & C. Binohlan. 2003. Simple methods to obtain preliminary growth estimates for fishes. *Journal Applied Ichthy*ology 19:(6) 376–379.
- Froese, R. 2004. Keep it simple: Three indicators to deal with overfishing. *Fish and Fisheries* 5: 86-91.
- Froese, R. 2022. Estimating somatic growth of fishes from maximum age or maturity. *Acta Ichthyologica et Piscatoria* 52(2): 125–133.

- García-Vásquez, A., J.C. Alonso, F. Carvajal, J. Moreau, J. Núñez, J. F. Renno, S. Tello, V. Montreuil & F. Duponchelle. 2009. Life-history characteristics of the large Amazonian migratory catfish *Brachyplatystoma rousseauxii* in the Iquitos region, Peru. *Journal of Fish Biology* 75: 2527–2551.
- Gislason, H., N. Daan, J. C. Rice & J. G. Pope. 2010. Size, growth, temperature and the natural mortality of marine fish. *Fish and Fisheries* 11:149–158.
- González, A., J. Mendoza, F. Arocha & A. Márquez. 2012. Tasa de explotación y rendimiento sostenible de *Pseudoplatystoma fasciatum* en el eje Caicara-Cabruta del Orinoco. *Zootecnia Tropical* 30(2): 155–169.
- González, A., J. Mendoza, F. Arocha & A. Márquez. 2017. Estado de explotación del bagre Dorado *Brachyplatystoma rousseauxii* en el Orinoco medio (Caicara-Cabruta), Venezuela. *Zootecnia Tropical* 35(3-4): 101–110.
- Griffiths, D. & C. Harrod. 2007. Natural mortality, growth parameters, and environmental temperature in fishes revisited. *Canadian Journal of Fisheries and Aquatic Sciences* 64: 249–255.
- Gulland, J. A.1983. Fish stock assessment: A manual of basic methods. New York: John Wiley & Sons, 223 pp.
- Hoenig, J. M. 1983. Empirical use of longevity data to estimate mortality rates. *Fisheries Bulletin* 82: 898–903.
- INSOPESCA. 2012. Informe final del programa integral para el ordenamiento de la actividad pesquera en las comunidades de pescadores artesanales, en el eje Orinoco – Apure. Caracas: IN-SOPESCA, 265 pp.
- Isaac, V. J. & M. L. Ruffino. 1996. Population dynamics of tambaqui, *Colossoma macropomum* Cuvier, in the lower Amazon, Brazil. *Fisheries Management and Ecology* 3: 315–333.
- Machado-Allison, A. & B. Bottini. 2023. Venezuela, República Bolivariana de. pp. 297–340. In: Baigún, C. R. M. & J. Valbo-Jørgensen (eds.). La situación y tendencia de las pesquerías continentales artesanales de América Latina y el Caribe. FAO Documento Técnico de Pesca y Acuicultura N.º 677. Roma: FAO. doi.org/10.4060/cc3839es
- Mateus, L. A. F. & M. F. Penha. 2007a. Dinâmica populacional de quatro especies de grandes bagres na bacia do rio Cuiabá, Pantanal Norte, Brasil (Siluriforme, Pimelodidae). *Revista Brasileira de Zoologia* 24(1): 87–98.
- Mateus, L. A. F. & Penha J. M. F. 2007b. Avaliação dos estoques pesqueiros de quatro espécies de grandes bagres (Siluriformes, Pimelodidae) na bacia do rio Cuiabá, Pantanal Norte, Brasil, utilizando alguns Pontos de Referência Biológicos. *Revista Brasileira de Zoologia* 24(1): 144–150.
- Mateus, L. A. F. & M. Petrere, Jr. 2004. Age, growth and yield per recruit analysis of the pintado *Pseudoplatystoma corruscans* (Agassiz, 1829) na bacia do rio Cuibá, Pantanal de Mato Grosso, Brasil. *Brazilian Journal Biology* 64(2): 257–264.
- Novoa, D. 2002. Los recursos pesqueros del eje fluvial Orinoco--Apure: presente y futuro. Caracas: INAPESCA, 148 pp.
- Novoa, D., F. Cervigón & F. Ramos. 1982. Catálogo de los recursos pesqueros del Delta del Orinoco. pp. 263-386. In:

Novoa, D. (comp.). *Los recursos pesqueros del río Orinoco y su explotación*. Caracas: CVG.

- Pauly, D. 1979. Theory and management of Tropical multispecies stocks. A review, with emphasis on the Southeast Asian demersal fisheries. Manila: ICLARM Studies and Reviews, 35 pp.
- Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters and mean environmental temperature in 175 fish stocks. *Journal du Conseil CIEM* 39(3):195– 212.
- Pauly, D. 1983. Algunos métodos simples para la evaluación de recursos pesqueros tropicales. Documento Técnico de Pesca 234. Roma: FAO, 49 pp.
- Pauly, D. & J. Munro. 1984. Once more on growth comparisons in fish and invertebrates. *Fishbyte* 2: 21.
- Peixer, J., A. C. Catella & M. Petrere, Jr. 2007. Yield per recruit of the pacu *Piaractus mesopotamicus* (Holmberg, 1887) in the pantanal of Mato Grosso do Sul, Brazil. *Brazilian Journal* of *Biology* 67(3): 561–567.
- Penha, J. & L. A. F. Mateus. 2007. Sustainable harvest of two large predatory catfish in the Cuiabá River basin, northern Pantanal, Brazil. *Brazilian Journal Biology* 67(1): 81–89.
- Pérez, A. & A. Barbarino. 2013. Parámetros poblacionales de los principales recursos pesqueros de la cuenca del río Apure, Venezuela (2000-2003). *Latin American Journal Aquatic Research* 41(3): 447–458.
- Petrere, M. Jr., R. B. Barthem, E. A. Córdoba & B. C. Gómez. 2004. Review of the large catfish fisheries in the upper Amazon and the stock depletion of piraiba (*Brachyplatystoma filamentosum* Lichtenstein). *Reviews in Fish Biology and Fisheries* 14: 403–414.
- Reid, S. 1983. La biología de los bagres rayados *Pseudoplatystoma fasciatum* y *P. tigrinum*en la cuenca del río Apure, Venezuela. *Revista UNELLEZ de Ciencia y Tecnología* 1(1): 13–41.
- República de Venezuela. 1991. Ministerio de Agricultura y Cría. Resolución MAC Nº 140 del 9 de marzo de 1991. *Gaceta Oficial* (Caracas) 34710.

- Restrepo, V. R. 2009. Red, green and yellow: Thoughts on stock status and the ICCAT Convention objectives. ICCAT Collective Volume of Scientific Papers 64: 2663–73.
- Ricker, W. E.1975. Computation and interpretation of biological statistics of fish populations. *Bulletin Fisheries Research Board Canadian* 191:1–382.
- Rochet, M. J.& V. M. Trenkel. 2003. Which community indicators can measure the impact of fishing? A review and proposals. *Canadian Journal Fisheries Aquatic Sciences* 60(14): 89–90.
- Rothschild, B. J. & Y. Jiao. 2013. Comparison between Maximum Sustained Yield Proxies and Maximum Sustained Yield. *The Open Fish Science Journal* 6:1–9.
- Ruffino, M. L. & V. J. Isaac. 1999. Dinâmica populacional do Surubim-Tigre, *Pseudoplatystoma tigrinum* (Valenciennes, 1840) no médio Amazonas (Siluriformes, Pimelodidae). *Acta Amazonica* 29(3): 463–476.
- Santanna, I. R. A, C. R. C. Doria & C. E. C. Freitas. 2014. Preimpoundment stock assessment of two Pimelodidae species caught by small-scale fisheries in the Madeira River (Amazon Basin–Brazil). *Fisheries Management and Ecology* 21(4): 322–329.
- SARPA. 1996. Estadísticas del subsector pesquero y acuícola de Venezuela.1990-1995 1(1): 1–40.
- Sparre, P. & S. C. Venema. 1995. Introducción a la evaluación de recursos pesqueros tropicales. Parte 1 - Manual. FAO, Documento Técnico de Pesca 306/1. Rev. 1. Roma: FAO, 417 pp.
- Ssentongo, G. W. & P. A. Larkin. 1973. Some simple methods of estimating mortality rates of exploited fish populations. *Journal Fisheries Research Board Canadian* 30(1): 695–698.
- Stergiou, K. I. 2002. Overfishing, tropicalization of fish stocks, uncertainty and ecosystem management: resharpening Ockham's razor. *Fisheries Research* 55:1–9.
- Taylor, C. C. 1958. Cod growth and temperature. *Journal du Conseil CIEM* 23(3): 366–370.
- Winemiller, K. O. 1989. Pattern of variation in life history among south American fishes in seasonal, environments. *Oecologia* 81:225–241.