

# Sexual maturity ( $L_m$ ) and maximum size ( $L_{max}$ ) ratio: A useful metric for sustainable fisheries management in the Amazon with poor fisheries statistics

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## ABSTRACT

Effective management of tropical multispecies fisheries requires biologically grounded indicators that remain robust under data-limited conditions. This study evaluates the ratio between length at first sexual maturity ( $L_m$ ) and maximum length ( $L_{max}$ ) as a comparative life-history metric for Amazonian fishes. Reproductive and biometric data from 123 commercially important species were compiled to assess variation in the  $L_m/L_{max}$  ratio across geographic regions, habitat types, and life-history strategies. Although statistically significant regional differences were detected, values consistently clustered within a relatively narrow range, indicating functional convergence with bounded variability rather than strict invariance. This convergent pattern supports the use of the  $L_m/L_{max}$  ratio as a heuristic reference for defining biologically meaningful size-based management thresholds for fisheries. By combining a lower limit based on maturity ( $L_m$ ) with an upper limit for megaspawner protection ( $2/3 \times L_{max} + 10\%$ ), we propose the Target Capture Length (TCL) as an intermediate and operational reference point. The TCL framework translates life-history information into practical guidance for fisheries regulation, offering a simple and adaptable tool for improving sustainability in Amazonian fisheries under conditions of limited data availability.

**KEYWORDS:** megaspawner protection, reproductive load, ecological resilience, length-based management, Amazon Basin

## Razão entre maturidade sexual ( $L_m$ ) e tamanho máximo ( $L_{max}$ ): Uma métrica útil para o manejo sustentável da pesca na Amazônia com estatísticas de pesca limitadas

### RESUMO

A gestão eficaz da pesca multiespecífica tropical requer indicadores biologicamente fundamentados que se mantenham robustos mesmo em condições de dados limitados. Este estudo avalia a razão entre o comprimento na primeira maturação sexual ( $L_m$ ) e o comprimento máximo ( $L_{max}$ ) como uma métrica comparativa do ciclo de vida de peixes amazônicos. Dados reprodutivos e biométricos de 123 espécies de importância comercial foram compilados para avaliar a variação na razão  $L_m/L_{max}$  entre regiões geográficas, tipos de habitat e estratégias de ciclo de vida. Embora diferenças regionais estatisticamente significativas tenham sido detectadas, os valores se agruparam consistentemente dentro de uma faixa relativamente estreita, indicando convergência funcional com variabilidade limitada, em vez de invariância estrita. Esse padrão convergente apoia o uso da razão  $L_m/L_{max}$  como uma referência heurística para definir limiares de gestão baseados no tamanho e biologicamente relevantes. Combinando um limite inferior baseado na maturidade ( $L_m$ ) com um limite superior para a proteção de mega-reprodutores ( $2/3 \times L_{max} + 10\%$ ), propomos o Comprimento Alvo de Captura (TCL) como um ponto de referência intermediário e operacional. A estrutura TCL traduz informações sobre o ciclo de vida em orientações práticas para a regulamentação da pesca, oferecendo uma ferramenta simples e adaptável para melhorar a sustentabilidade da pesca na Amazônia em condições de disponibilidade limitada de dados.

**PALAVRAS-CHAVE:** proteção de megadesovadores, carga reprodutiva, resiliência ecológica, gestão baseada no comprimento, bacia Amazônica**CITE AS:** Lozano, A.P.; Kuradomi, R.Y. 2026. Sexual maturity ( $L_m$ ) and maximum size ( $L_{max}$ ) ratio: A useful metric for sustainable fisheries management in the Amazon with poor fisheries statistics. *Acta Amazonica* 56: e56af25178.

## INTRODUCTION

Global inland fisheries face significant challenges related to overexploitation and the lack of robust biological data, compromising the sustainability of fish stocks across multiple systems (FAO 2022). It is estimated that approximately 11.5 million tonnes of fish are harvested annually from inland waters, much of it occurring in contexts characterized by weak governance and limited monitoring (Dudgeon et al. 2006). Effective fisheries management requires regulating key components of the fishing process, including fishing effort and power, catch quotas, gear selectivity, and size limits (Bayley and Petrere 1989; Ruffino 2005). Unregulated harvest—especially in the absence of defined minimum and maximum size limits—can induce demographic and evolutionary changes, including reductions in genetic variability, fisheries-induced dwarfism, and earlier maturation (Olsen et al. 2004; Green 2008).

In the Brazilian Amazon, despite high ichthyofaunal diversity, commercial fishing is largely concentrated on a few high-value species, particularly large catfishes from the family Pimelodidae. Intensive exploitation of these species has led to population declines and a shift toward smaller, less commercially valuable species (Barthem and Goulding 1997; Petrere et al. 2004; Ruffino 2004). While national regulations do establish minimum size limits for certain species (MAPA 2021), technical criteria for defining maximum size limits remain incipient and rarely incorporate biological parameters such as size at sexual maturity (Chaves 2012).

The definition of sustainable size ranges—including both lower and upper limits—is critical to protect juveniles as well as large and highly fecund individuals (“megaspawners”), which can contribute disproportionately to spawning biomass and recruitment (Froese 2004; Birkeland and Dayton 2005; Green 2008; FAO 2022). In data-poor fisheries, however, it becomes necessary to adopt cross-species metrics. Beverton–Holt life-history invariants, particularly the ratio of length at maturity ( $L_m$ ) to maximum observed length ( $L_{max}$ ), have gained recognition as functional indicators of energy allocation between somatic growth and reproduction (Charnov 1993; Jennings et al. 1998; Prince et al. 2015).

In this study, biometric and reproductive data were compiled for 123 commercially important Amazonian fish species, with the objective of analyzing variability in the  $L_m/L_{max}$  ratio as a function of geographic distribution, life-history strategies and habitats types, to propose biologically grounded size limits for adaptive fisheries management in the Amazon Basin.

## MATERIALS AND METHODS

All available information on the reproductive biology of Amazonian fish species was extracted from peer-reviewed sources and gray literature, including books, technical reports from governmental and non-governmental agencies, and repositories of theses and dissertations from Latin American

universities, covering the period from 1984 to 2024 (Table S1). The data extracted included year of data collection, sex, sample size, and size ranges of the analyzed individuals.

Studies that did not define sexual maturity or failed to describe the method used to estimate it were excluded from the review. In most cases, sexual maturity was reported as the median or mean length at which 50% of individuals reach first maturity (Vazzoler 1996). The size-related parameters extracted for each species included: minimum capture length ( $L_{min}$ ), mean length at first maturity ( $L_m$ ), and maximum observed length ( $L_{max}$ ). The list of commercially important Amazonian fish species analyzed in this study was based on Ferreira et al. (1998), which describes the main fish resources of the middle Amazon.

Reproductive data for the main commercial fish species of the Amazon region ( $n = 123$  spp.) were obtained through the literature review (Table S1). To analyze variability in the  $L_m/L_{max}$  ratio, species were grouped according to: (i) geographic regions—Western Amazon (Ucayali–Tefé), Central Amazon (Tefé–Santarém), and Eastern Amazon (Santarém–Belém); (ii) ecological strategies (following the life-history classification proposed by Winemiller and Taphorn 1989; Winemiller 1989); and (iii) habitat types—benthic (B), pelagic (P), and benthopelagic (BP)—based on FishBase classifications (Froese and Pauly 2000).

To establish lower capture limits, we used the reproductive load ( $L_m/L_{max}$  ratio) as a geometric proxy of the proportion of growth allocated up to the size at first maturity ( $L_m$ ). This ratio was calculated for each species (Table S2). The original Beverton (1963) invariant,  $L_m/L_{inf}$  (where  $L_{inf}$  is the asymptotic maximum length), was not used in this study. Instead, we adopted the  $L_m/L_{max}$  ratio, which expresses the proportion of the *observed* maximum length attained before maturity. This approach was justified because  $L_{max}$  values are more consistently reported in reproductive studies, and because  $L_m/L_{max}$  and  $L_m/L_{inf}$  are strongly correlated (Froese and Binohlan 2000; Tsikliras and Stergiou 2014).

Species were also classified according to their vulnerability to fishing (Froese 2004) based on life history strategies and body size. Body size was categorized as small, medium, or large based on the percentage distribution of  $L_{max}$  values (Table 1), using the quartile method to divide the data set (Table S3). The characteristics of life strategies (r-K continuum) for the different species were also described (Table 2).

In cases where  $L_m$  values were unavailable or appeared unreliable, we applied the empirical equation from Binohlan and Froese (2009):  $(L_m) = -0.1189 + 0.9157 * \log_{10}(L_{max})$ . All length measurements were recorded in centimeters (cm) as total length (TL). When total length values were not available, conversions were made using length–length relationships from the FishBase morphometric table (Froese and Pauly 2023).

The  $L_m/L_{max}$  ratio was used as a sustainability indicator for defining size-based management thresholds, aiming to

**Table 1.** Classification of fishing vulnerability, based on the life-history strategy and body size of the Amazonian fish species.

Category	Characteristics	Observations	Vulnerability
K Strategy (Equilibrium)	Late reproduction, Low fertility	Species of large size (> 80 TL cm), protection of mega-spawners.	High
(r-K) Strategy Intermediate	Intermediate fertility	Species of medium size (41-79 TL cm), Balance between growth and reproduction.	Moderate
r Strategy (seasonal)	Early reproduction, High fertility	Species of small size (< 40 cm TL), Accelerated growth lower risk of overfishing.	Low

**Table 2.** Classification of the life strategies considering taxonomic categories; key traits and principal references, for some Amazonian fish species.

Species	Strategy	Key traits	Reference
<i>A. gigas</i>	K	Very large, late maturity, parental care	Castello et al. (2011)
<i>O. bicirrhosum</i>	K	Very large, late maturity, parental care	Winemiller (1989)
<i>C. monocus</i>	K	Late maturity, parental care	Winemiller (1989)
<i>A. ocellatus</i>	K	Late maturity, parental care	Winemiller (1989)
<i>H. malabaricus</i>	K	Late maturity, parental care	Winemiller (1989)
<i>B. filamentosum</i>	r2	Migratory, delayed maturity, high fecundity	Barthem and Goulding (1997)
<i>P. hemiliopterus</i>	r2	Migratory, delayed maturity, high fecundity	Barthem and Goulding (1997)
<i>P. tigrinum</i>	r2	Migratory, delayed maturity, high fecundity	Barthem and Goulding (1997)
<i>P. pirinampu</i>	r2	Migratory, delayed maturity, high fecundity	Winemiller (1989)
<i>P. brachypomus</i>	r2	Migratory, early maturity, multiple spawning	Winemiller (1989)
<i>L. marmoratus</i>	r2	Migratory, early maturity, multiple spawning	Winemiller (1989)
<i>B. amazonicus</i>	r2	Migratory, early maturity, multiple spawning	Winemiller (1989)
<i>H. marginatus</i>	r2	Migratory, early maturity, multiple spawning	Winemiller (1989)
<i>C. macropterus</i>	r2	Migratory, early maturity, multiple spawning	Winemiller (1989)
<i>P. nigricans</i>	r2	Migratory, early maturity, multiple spawning	Winemiller (1989)
<i>S. fasciatus</i>	r2	Early maturity, multiple spawning	Winemiller (1989)
<i>M. albiscopum</i>	r2	Small-bodied, fast growth, short lifespan	Winemiller (1989)
<i>P. altamazonica</i>	r2	Small-bodied, fast growth, short lifespan	Winemiller (1989)

minimize the harvest of immature individuals. The lower threshold was defined as  $L_m/L_{max} * L_{max}$ , which by definition equals  $L_m$ . To define the upper threshold, we used Froese's (2004) reference point for the protection of megaspawners:  $P_{mega} = (2/3 * L_{max}) + 10%$ , which aims to avoid the removal of the largest and most fecund individuals.

Additional upper limits were also explored, following recommendations by Tsikliras et al. (2007) and Tsikliras and Stergiou (2014), who propose setting capture sizes above  $L_m$  (e.g.,  $1.2 * L_m$  or  $1.5 * L_m$ ) to enhance reproductive output. Based on the lower and upper thresholds, we defined a "Target Capture Length" (TCL), calculated as the arithmetic mean of the two limits:  $TCL = (Lower\ Limit + Upper\ Limit) / 2$ .

The variation in the  $L_m/L_{max}$  ratio was analyzed using one-way analysis of variance (ANOVA), considering geographic regions, life strategies, and habitat types as factors, following confirmation of normality and homoscedasticity of residuals. Boxplot visualizations were employed to depict the distribution of  $L_m/L_{max}$  ratio values across factor levels.

To evaluate potential sex-based differences, we applied an analysis of covariance (ANCOVA), assessing the interaction between sex and  $L_m/L_{max}$ . Simple linear regressions of  $L_m$  versus  $L_{max}$  were conducted separately by sex to explore potential patterns in reproductive investment. All statistical analyses were performed at a reference significance level of  $\alpha = 0.05$ , following conventional standards in biological studies. The statistical analyses were performed using PAST software, version 4.17 (Hammer 2001), available at: <https://www.nhm.uio.no/english/research/resources/past/>.

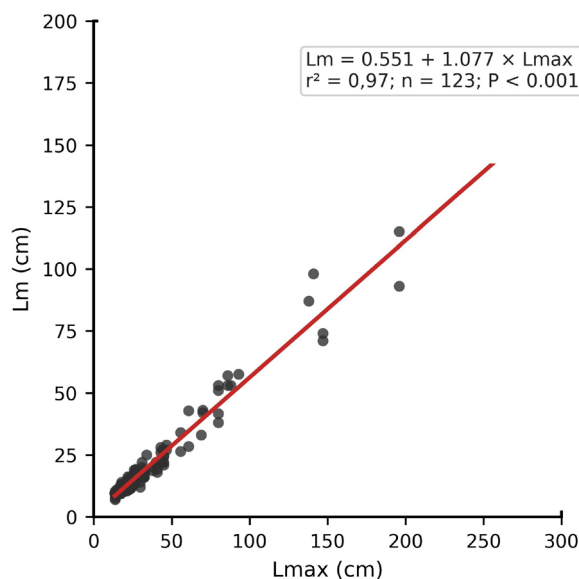
## RESULTS

Length at first maturity ( $L_m$ ) and maximum total length ( $L_{max}$ ) were compiled for 123 species, representing 23 families and 5 orders. Reported maximum lengths ( $L_{max}$ ) ranged from 8 cm in *Hypancistrus zebra* to 450 cm in *Arapaima gigas*. Correspondingly,  $L_m$  ranged from 5.85 cm in male *H. zebra* to 180 cm in male *A. gigas*. Across all species, length at first maturity ( $L_m$ ) exhibited a strong positive linear relationship

with maximum length ( $L_{max}$ ) for both females and males (Figure 1). Differences between sexes were not statistically significant (ANCOVA interaction term:  $F = 1.183$ ,  $p = 0.288$ ).

Across all 123 species analyzed, the  $L_m/L_{max}$  ratio ranged from 0.40 to 0.78, with a global mean of approximately 0.62 (SD = 0.07). This overall distribution indicates that, despite substantial interspecific variability, most species converge toward a similar proportional allocation between somatic growth and reproduction. This general pattern provides the baseline against which variation among geographic regions, life-history strategies, and habitat types is evaluated below.

Analysis of reproductive load patterns, measured as the  $L_m/L_{max}$  ratio, showed regional variation across the Amazon Basin (ANOVA:  $F=22.44$ ,  $p < 0.05$ , Table S4; Figure 2a). Mean values ( $\pm$  SD) increased from the Western to the Eastern Amazon (Table 3), despite the uneven sampling between geographic regions (114 species in western Amazonia and 12 species in eastern Amazonia).



**Figure 1.** Regression between length at first sexual maturity ( $L_m$ ) and maximum total length ( $L_{max}$ ), for 123 Amazonian fish species. Solid lines represent fitted linear regressions ( $p < 0.001$  for both sexes). Individuals of indeterminate sex were excluded.

Regarding life-history strategies,  $L_m/L_{max}$  ratio ranged from 0.52 to 0.76 in K-strategist species and from 0.40 to 0.78 in r-strategists (Table 3), however, the difference in the between these groups was not statistically significant (ANOVA:  $F = 1.784$ ,  $p = 0.178$ ). Reproductive load tends to remain stable among species with contrasting ecological traits (Figure 2b, Table S4). These differences, although statistically significant, remain within a narrow functional range.

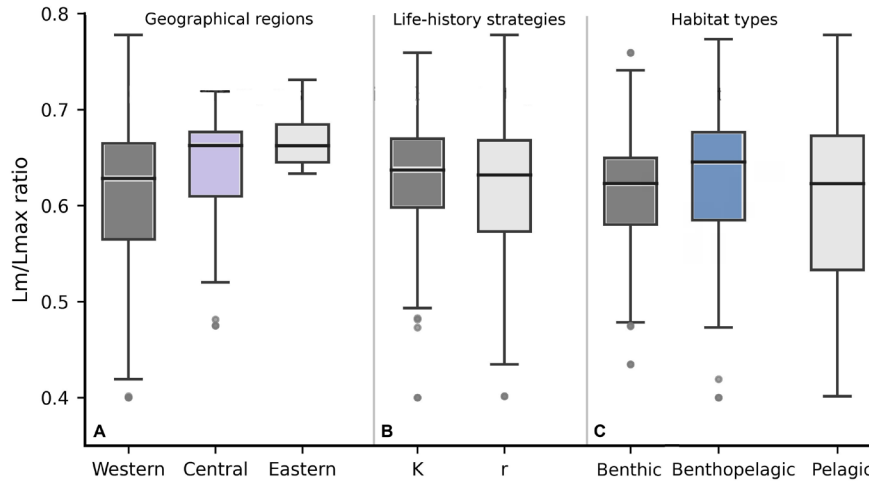
When species were grouped by habitat type (Figure 2c; Table S4), the  $L_m/L_{max}$  ratio ranged from 0.40 to 0.77 (mean  $\pm$  SD =  $0.627 \pm 0.070$ ) in benthopelagic species, 0.40 to 0.77 (mean  $\pm$  SD =  $0.608 \pm 0.083$ ) in pelagic species, and 0.43 to 0.75 (mean  $\pm$  SD =  $0.610 \pm 0.067$ ) in benthic species, but the mean values of  $L_m/L_{max}$  ratio did not differ significantly among groups (ANOVA:  $F = 2.631$ ,  $p = 0.07$ ). Mean values ( $\pm$  SD) by habitat type are presented in Table 3.

Body size mediated the practical implications of reproductive load. Small-bodied species (e.g., *Semaprochilodus insignis*;  $L_m/L_{max} = 0.65$ ) tend to reach maturity near their maximum size, resulting in narrow sustainable exploitation windows. In contrast, large-bodied species (e.g., *Brachyplatystoma rousseauxii*;  $L_m/L_{max} = 0.59$ ) begin reproducing at a lower proportion of their maximum size, which generally produces broader capture windows. Medium-sized species (e.g., *Cichla monoculus*;  $L_m/L_{max} = 0.61$ ) show intermediate values, consistent with the overall mean of  $\sim 0.62$  observed across Amazonian species. Examples of sustainable capture windows derived from different indicators illustrate how body size mediates management flexibility (Figure 3). Despite interspecific variation in  $L_m/L_{max}$ , the Target Capture Length (TCL) consistently identifies an intermediate size range that balances the protection of juveniles and megaspawners, providing a transparent and operational reference for data-poor fisheries.

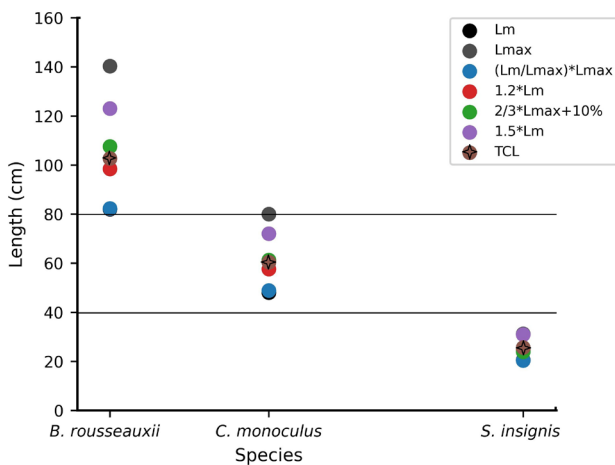
A subset of 29 Amazonian species was selected based on commercial relevance, abundance, economic value, and representation of different life-history strategies (r-K) to compare alternative size-based indicators (Figure 4). The comparison shows that the TCL consistently occupies an intermediate position between the lower limit based on maturity ( $L_m$ ) and the upper limit for megaspawner protection

**Table 3.** Variation in the  $L_m/L_{max}$  ratio (mean), with standard deviation, across Geographic Regions, Life Strategies, and Habitat Types, for Amazonian fish species

Category	Groups	mean $L_m/L_{max} \pm$ SD
Geographic region	Western Amazon	$0.614 \pm 0.074$
	Central Amazon	$0.636 \pm 0.061$
	Eastern Amazon	$0.668 \pm 0.027$
Life-history strategy	K	$0.624 \pm 0.076$
	r	$0.617 \pm 0.071$
Habitat type	Benthic	$0.627 \pm 0.070$
	Benthopelagic	$0.610 \pm 0.067$
	Pelagic	$0.608 \pm 0.083$



**Figure 2.** Variability of the  $L_m/L_{max}$  ratio by geographic region, life-history strategy, and habitat type. The horizontal line inside each box indicates the median; box limits represent the interquartile range (IQR); whiskers indicate the minimum and maximum values within  $1.5 \times IQR$ ; and circles denote outliers.



**Figure 3.** Examples of sustainable capture windows for Amazonian fish species of different body sizes: small species (*Semaprochilodus* spp.), intermediate species (*Cichla monoculus*), and large species (*Brachyplatystoma rousseauxii*). For each species, the figure shows the lower threshold based on  $L_m/L_{max} \times L_{max}$  (equivalent to  $L_m$ ), alternative conservative thresholds above maturity ( $1.2 \times L_m$  and  $1.5 \times L_m$ ), the upper threshold for megaspawner protection ( $2/3 \times L_{max} + 10\%$ ), and the resulting Target Capture Length (TCL). The figure illustrates how capture windows become narrower in small-bodied species and broader in large-bodied species, while the TCL consistently identifies an intermediate and operational harvest range.

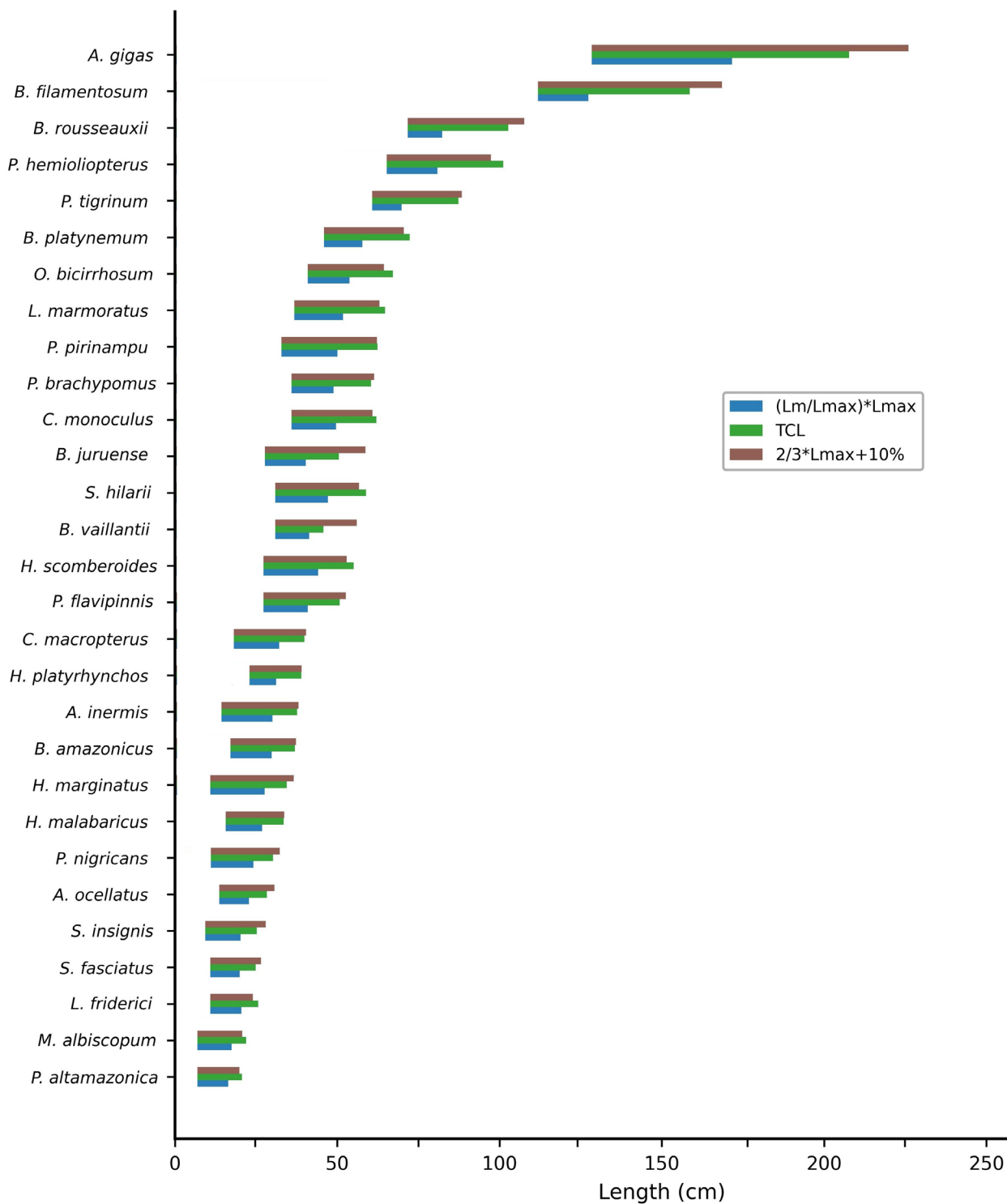
( $2/3 \times L_{max} + 10\%$ ). Because the indicators  $1.2 \times L_m$  and  $1.5 \times L_m$  were very close to  $L_m$  for most species and added limited practical value for management decision-making, the final framework emphasizes three indicators:  $L_m/L_{max} * L_{max}$ , TCL, and ( $2/3 \times L_{max} + 10\%$ ).

Based on the 29-species subset,  $L_m$  was used as a lower limit,  $L_m/L_{max} * L_{max}$  as minimum size limit to protect immature individuals, TCL as an intermediate operational reference, and ( $2/3 \times L_{max} + 10\%$ ) as the maximum size limit for megaspawner protection. These thresholds define biologically grounded capture ranges that can support adaptive regulation of key commercial fisheries (Table 4).

**Table 4.** Proposed lower and upper capture limits (in cm) for several Amazonian fish species of commercial interest. Where: Lower limit of the reproductive load length ( $L_m/L_{max} * L_{max}$ ); TCL= Target Capture Length; Upper limit of optimal capture length ( $2/3 * L_{max} + 10\%$ ).

Species	Lower Limit ( $L_m/L_{max} * L_{max}$ )	TCL	Upper Limit ( $2/3 * L_{max} + 10\%$ )
<i>Arapaima gigas</i>	171.64	184.12	196.60
<i>Brachyplatystoma filamentosum</i>	127.36	137.01	146.66
<i>Brachyplatystoma rousseauxii</i>	82.30	87.98	93.66
<i>Phractocephalus hemiliopterus</i>	80.88	82.82	84.77
<i>Pseudoplatystoma tigrinum</i>	69.79	73.35	76.91
<i>Brachyplatystoma platynemum</i>	57.75	59.59	61.43
<i>Osteoglossum bicirrhosum</i> (50 cm)*	53.76	54.93	56.10
<i>Leiarius marmoratus</i>	51.81	53.33	54.85
<i>Pinirampus pirinampu</i>	50.09	52.16	54.23
<i>Cichla monoculus</i> (25 cm)*	48.88	51.16	52.99
<i>Piaractus brachypomus</i>	40.29	51.31	53.43
<i>Brachyplatystoma vaillantii</i>	46.40	45.69	51.10
<i>Brachyplatystoma juruense</i>	47.16	48.30	49.43
<i>Pellona flavipinnis</i>	48.88	45.04	48.77
<i>Salminus hilarii</i>	40.93	45.11	46.10
<i>Hydrolycus scomberoides</i>	41.31	43.41	45.89
<i>Calophrys macropterus</i>	32.08	33.64	35.19
<i>Hemisorubim platyrhynchos</i>	31.18	32.59	33.99
<i>Ageneiosus inermis</i>	30.00	31.58	33.17
<i>Brycon amazonicus</i>	29.80	30.16	30.77
<i>Hypopthalmus marginatus</i>	27.60	29.76	31.93
<i>Hoplias malabaricus</i>	26.82	28.10	29.38
<i>Astronotus ocellatus</i>	22.80	24.78	26.77
<i>Prochilodus nigricans</i> (25 cm)*	20.17	No limit	No limit
<i>Leporinus friderici</i>	19.93	No limit	No limit
<i>Schizodon fasciatus</i>	20.47	No limit	No limit
<i>Mylossoma albiscopum</i> (15 cm)*	20.43	No limit	No limit
<i>Semaprochilodus insignis</i> (20 cm)*	17.44	No limit	No limit
<i>Potamorhina altamazonica</i>	16.42	No limit	No limit

\* Species listed in the Ordinance SAP/MAPA N° 509- 31/12/2021 (MAPA, 2021).



**Figure 4.** Comparison of size-based indicators used to define minimum and maximum capture limits in Amazonian fish species. The figure highlights the position of the Target Capture Length (TCL) relative to the lower limit based on length at first maturity ( $L_m/L_{max} * L_{max}$ ) and the upper limit for megaspawner protection ( $2/3 * L_{max} + 10%$ ), illustrating the role of the TCL as an intermediate and operational management reference point.

## DISCUSSION

The present study demonstrates that the ratio between length at first maturity ( $L_m$ ) and maximum length ( $L_{max}$ ) in Amazonian fishes follows a convergent life-history pattern, with values clustering around a relatively narrow functional range. Across 123 species representing a broad taxonomic, ecological, and geographic spectrum, the mean  $L_m/L_{max}$  ratio was approximately 0.62 ( $\pm 0.07$ ). This convergent pattern is supported by the mean and variance estimates summarized in Table 3, which show that average  $L_m/L_{max}$  values across regions, life-history strategies and habitat types cluster around  $\sim 0.62$  despite statistically significant differences. Similar mean values of the  $L_m/L_{max}$  ratio have been reported for marine systems and freshwater teleosts worldwide ( $\sim 0.65$ – $0.67$ ), suggesting that this metric reflects a general biological rule rather than a context-specific property of Amazonian fishes (Hordyk et al. 2014; Hordyk et al. 2015; Chen et al. 2022; Froese and Pauly 2023). Such convergence supports life-history theory predictions that proportional allocation to reproduction tends to remain bounded across taxa, even in highly diverse and environmentally heterogeneous systems such as the Amazon Basin (Charnov 1993; Froese 2004; Prince et al. 2015).

However, convergence does not imply strict invariance. Statistically significant differences in the  $L_m/L_{max}$  ratio were detected among Amazonian regions, with mean values ranging approximately from 0.60 to 0.67. These differences, however, occurred within a limited interval, indicating bounded variability rather than unrestricted divergence. Such patterns are consistent with theoretical expectations that life-history traits are shaped by the interaction between universal constraints and local ecological conditions (Charnov 1993; Dmitriew 2011; Chu and Pauly 2024).

In the Amazon Basin, longitudinal gradients in hydrology, sediment load, and habitat stability may partially explain regional differences. Western Amazonian tributaries draining the Andes are characterized by high turbidity, dynamic channel morphology, and strong seasonal variability, conditions often associated with faster growth and earlier maturation in migratory species such as *Prochilodus nigricans* (Barthem and Goulding, 1997; Batista and Petrere 2003). In contrast, the floodplains of the Central and Eastern Amazon provide more stable habitats that may favor prolonged growth and delayed maturity in large-bodied species such as *Arapaima gigas* (Castello et al. 2011; Isaac et al. 2016). Nevertheless, uneven sampling effort among regions—particularly the lower number of species represented in the Eastern Amazon—may influence regional means, and these results should therefore be interpreted with caution.

Regarding life-history strategies, mean  $L_m/L_{max}$  values did not differ significantly between r- and K-strategists, reinforcing the idea that reproductive allocation follows a

conservative functional rule largely independent of strategy classification (Winemiller and Rose 1992; Hordyk et al. 2015; Prince et al. 2015). The absence of statistical differences does not imply ecological equivalence, however. Small-bodied r-strategists typically reach maturity close to their maximum size, resulting in narrow sustainable exploitation windows but allowing rapid population turnover and resilience under fishing pressure (Batista and Petrere 2003). In contrast, large-bodied K-strategists mature at a lower proportion of their maximum size, generating broader capture windows but increasing vulnerability to overfishing due to delayed reproduction and, in many cases, parental care (Winemiller 2005; Hixon et al. 2014). Medium-sized species tend to occupy intermediate positions, combining moderate resilience with greater management flexibility.

It is also essential to distinguish between absolute growth rate and proportional reproductive allocation. Species may reach first maturity rapidly in chronological or absolute size terms due to high growth rates, yet still allocate a similar fraction of total growth to reproduction as slower-growing species. The  $L_m/L_{max}$  ratio captures this proportional allocation rather than growth velocity per se, explaining why convergent values can emerge across species with contrasting growth dynamics (Dmitriew 2011; Chen et al. 2022; Chu and Pauly 2024). Considerable intra- and interspecific variability observed in the compiled data reflects biological diversity, environmental heterogeneity, and methodological differences among studies, including sampling design and maturity estimation methods (Vazzoler 1996; Dmitriew 2011). Such variability should be interpreted as an inherent property of large comparative datasets rather than as methodological noise.

The applied significance of these findings lies in their translation into size-based management guidance. Rather than emphasizing the  $L_m/L_{max}$  ratio as a strict invariant, its primary value resides in providing a biologically grounded reference for defining harvest thresholds (Froese 2004; Prince et al. 2015). By integrating a lower limit based on length at first maturity ( $L_m$ ) with an upper limit aimed at protecting highly fecund individuals ( $2/3 \times L_{max} + 10\%$ ), the proposed Target Capture Length (TCL) operationalizes life-history information into a practical management tool. This dual-threshold framework accommodates species-specific differences in body size and life-history strategy while maintaining conceptual simplicity—an essential feature in data-poor, multispecies fisheries such as those of the Amazon (McGrath et al. 2008; Pereira et al. 2020).

Implementation of this framework must nonetheless be adaptive and context-sensitive. Uniform application of capture limits across species would be inappropriate, particularly for small-bodied species with extremely narrow sustainable windows. In addition, the ecological roles of large-bodied predators and long-lived species warrant special consideration, as their removal can trigger trophic cascades and compromise

ecosystem resilience (Lowe-McConnell 1987; Winemiller 1990; Jepsen and Winemiller 2002). From a governance perspective, effective adoption of size-based rules depends on participatory approaches, co-management arrangements, and communication tools that translate biological concepts into accessible guidance for fishing communities (McGrath et al. 2008; Pereira et al. 2020).

## CONCLUSIONS

The  $L_m/L_{max}$  ratio should be interpreted as a convergent life-history metric with bounded variability, rather than as a strict biological invariant. This conceptual refinement aligns with the significant but limited regional differences, and it avoids overgeneralization when translating the metric into management advice. Despite regional and species-level variability, the constrained distribution of  $L_m/L_{max}$  values provides a biologically meaningful basis for size-based management in data-poor contexts. By combining a lower limit based on maturity ( $L_m$ ) with an upper limit for megaspawner protection ( $2/3 \times L_{max} + 10\%$ ), the Target Capture Length (TCL) offers an intermediate and operational reference that can support the refinement of existing minimum-size regulations and the development of species-specific capture ranges. When coupled with participatory governance, adaptive monitoring, and protection of key reproductive habitats, this framework provides a feasible pathway for improving sustainability in Amazonian fisheries where conventional stock-assessment data are unavailable.

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## SUPPLEMENTARY MATERIAL

### Lozáno & Kuradomi. Sexual maturity ( $L_m$ ) and maximum size ( $L_{max}$ ) ratio: A useful metric for sustainable fisheries management in the Amazon with poor fisheries statistics

**Table S1.** Bibliographic sources used for the extraction of  $L_m/L_{max}$  ratios.

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**Table S1.** Continued

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**Table S2.** Summary of the reproductive load ( $L_m/L_{max}$  ratio) as a geometric proxy of the proportion of growth allocated up to the size at first maturity ( $L_m$ ), for each species.

Species	Geographical Regions			Life Strategies			Habitats Types		
	Western	Middle	East	K	r1	r2	Benthic	Benthopelagic	pelagic
<i>Acestrorhynchus cf. pantaneiro</i>	0.68					0.68			0.68
<i>Acestrorhynchus heterolepis</i>	0.46					0.46			0.46
<i>Acestrorhynchus microlepis</i>	0.63					0.63			0.63
<i>Acestrorhynchus falcirostris</i>	0.53					0.53		0.65	0.48
<i>Ageneiosus inermis</i>	0.60					0.60	0.65	0.54	
<i>Ageneiosus lineatus</i>		0.65				0.65		0.65	
<i>Ageneiosus ucayalensis</i>	0.51					0.51		0.51	
<i>Anodus elongatus</i>	0.64					0.64			0.64
<i>Anodus orinocensis</i>	0.60					0.60			0.60
<i>Anostomoides laticeps</i>			0.67			0.67		0.67	
<i>Arapaima gigas</i>	0.57	0.63		0.58				0.58	
<i>Astronotus crassipinnis</i>	0.71			0.71				0.71	
<i>Astronotus ocellatus</i>	0.67	0.48		0.61				0.61	
<i>Auchenipterus ambyiacus</i>	0.69					0.69		0.69	
<i>Auchenipterus nuchalis</i>	0.67					0.67		0.67	
<i>Auchenipterychthys thoracatus</i>	0.53					0.53		0.53	
<i>Boulengerella cuvieri</i>	0.65					0.65			0.65
<i>Boulengerella maculata</i>	0.43					0.43			0.43
<i>Brachyplatystoma filamentosum</i>	0.56	0.67				0.58	0.58		
<i>Brachyplatystoma juruense</i>	0.63	0.65				0.64	0.64		
<i>Brachyplatystoma platynemum</i>	0.62	0.66				0.63	0.63		
<i>Brachyplatystoma rousseauxii</i>	0.55	0.66				0.59	0.59		
<i>Brachyplatystoma tigrinum</i>	0.63					0.63	0.63		
<i>Brachyplatystoma vaillantii</i>	0.54	0.50				0.53	0.53		
<i>Brycon cephalus</i>	0.61					0.61		0.61	
<i>Brycon melanopterus</i>	0.66					0.66		0.66	
<i>Brycon amazonicus</i>	0.59	0.65				0.61		0.61	
<i>Brycon cephalus</i>	0.66					0.66		0.66	
<i>Bryconops alburnoides</i>	0.67				0.67			0.67	
<i>Calophysus macropterus</i>	0.61					0.61	0.61		
<i>Centromochlus heckelii</i>	0.68					0.68			0.68
<i>Chalceus guaporensis</i>	0.68					0.68			0.68
<i>Chalceus erythrus</i>		0.69				0.69			0.69
<i>Cichla monoculus</i>	0.61			0.61				0.61	
<i>Cichla pleiozona</i>	0.63			0.63				0.63	
<i>Cichla temensis</i>	0.63			0.63				0.63	
<i>Colossoma macropomum</i>	0.63	0.61				0.62		0.62	
<i>Curimata roseni</i>	0.62					0.62		0.62	
<i>Curimata vittata</i>	0.68					0.68		0.68	
<i>Curimata inornata</i>			0.68			0.68		0.68	
<i>Curimatella albuna</i>	0.59					0.59		0.59	
<i>Curimatella dorsalis</i>	0.71		0.71			0.71		0.71	

Table S2. Continued

Species	Geographical Regions			Life Strategies			Habitats Types		
	Western	Middle	East	K	r1	r2	Benthic	Benthopelagic	pelagic
<i>Curimatella meyeri</i>	0.74	0.70				0.72		0.72	
<i>Cynodon gibbus</i>	0.54					0.54			0.54
<i>Geophagus megasema</i>	0.66			0.66				0.66	
<i>Hemiodus immaculatus</i>	0.70					0.70		0.70	
<i>Hemiodus microlepis</i>	0.60					0.60		0.60	
<i>Hemiodus unimaculatus</i>	0.57					0.57		0.57	
<i>Hemisorubim platyrhynchos</i>	0.61					0.61	0.61		
<i>Heros spurius</i>	0.65			0.65				0.65	
<i>Hoplerthrinus unitaeniatus</i>	0.65	0.68				0.65		0.65	
<i>Hoplias malabaricus</i>	0.61			0.61				0.61	
<i>Hoplosternum littorale</i>	0.68			0.68			0.68		
<i>Hydrolycus scomberoides</i>	0.60					0.60			0.60
<i>Hypancistrus zebra</i>			0.73	0.73			0.73		
<i>Hypophthalmus edentatus</i>	0.61					0.61			0.61
<i>Hypophthalmus marginatus</i>	0.55					0.55	0.48		0.57
<i>Hypoptopoma incognitum</i>	0.75			0.75			0.75		
<i>Ilisha amazonica</i>	0.66					0.66			0.66
<i>Laemolyta proxima</i>	0.61					0.61		0.61	
<i>Leiarius marmoratus</i>	0.63					0.63	0.63		
<i>Leporinus agassizi</i>	0.66					0.66		0.66	
<i>Leporinus fasciatus</i>	0.66					0.66		0.66	
<i>Leporinus friderici</i>	0.58	0.54				0.58		0.58	
<i>Lycengraulis batesii</i>	0.75					0.75			0.75
<i>Megaleporinus trifasciatus</i>	0.66	0.67				0.66		0.66	
<i>Megalodoras uranoscopus</i>	0.64		0.64			0.64	0.64		
<i>Metynnis guaporensis</i>	0.63					0.63		0.63	
<i>Metynnis lippincottianus</i>	0.70	0.72				0.70		0.70	0.72
<i>Myloplus schomburgkii</i>	0.66		0.66			0.66		0.66	
<i>Myloplus rubripinnis</i>	0.71		0.65			0.67		0.67	
<i>Mylossoma aureum</i>	0.63					0.63		0.63	
<i>Mylossoma albiscopum</i>	0.65					0.65		0.65	
<i>Nemadoras humeralis</i>	0.71					0.71	0.71		
<i>Ossubtus xinguense</i>			0.68			0.68		0.68	
<i>Osteoglossum bicirrhosum</i>	0.64	0.64		0.64					0.64
<i>Oxydoras niger</i>	0.58					0.58	0.58		
<i>Pellona flavipinnis</i>	0.58					0.58			0.58
<i>Pellona castelnaeana</i>	0.58					0.58			0.58
<i>Phractocephalus hemiliopterus</i>	0.64					0.64	0.64		
<i>Piaractus brachypomus</i>	0.63					0.63		0.63	
<i>Pimelodina flavipinnis</i>	0.66					0.66	0.66		
<i>Pimelodus blochii</i>	0.57					0.57	0.57		
<i>Pinirampus pirinampu</i>	0.62					0.62	0.62		

Table S2. Continued

Species	Geographical Regions			Life Strategies			Habitats Types		
	Western	Middle	East	K	r1	r2	Benthic	Benthopelagic	pelagic
<i>Plagioscion squamosissimus</i>	0.58	0.64	0.64	0.60				0.60	
<i>Platynemichthys notatus</i>	0.66					0.66	0.66		
<i>Platystomichthys sturio</i>	0.66					0.66	0.66		
<i>Potamorhina altamazonica</i>	0.63					0.63		0.63	
<i>Potamorhina latior</i>	0.61	0.67				0.62		0.62	
<i>Potamorhina pristigaster</i>		0.68				0.68		0.68	
<i>Pristobrycon striolatus</i>			0.68			0.68		0.68	
<i>Prochilodus nigricans</i>	0.57					0.57		0.57	
<i>Psectrogaster amazonica</i>	0.64					0.64		0.64	
<i>Psectrogaster rutiloides</i>	0.62					0.62		0.62	
<i>Psectrogaster amazonica</i>			0.69			0.69		0.69	
<i>Pseudoplatystoma punctifer</i>	0.60	0.56				0.59	0.59		
<i>Pseudoplatystoma tigrinum</i>	0.63	0.61				0.62	0.62		
<i>Pterodoras granulosus</i>	0.59					0.59	0.59		
<i>Pterygoplichthys pardalis</i>	0.65			0.65			0.65		
<i>Pygocentrus nattereri</i>	0.56					0.56		0.56	
<i>Rhaphiodon vulpinus</i>	0.61					0.61			0.61
<i>Rhytiodus argenteofuscus</i>	0.69					0.69		0.69	
<i>Rhytiodus microlepis</i>	0.68					0.68		0.68	
<i>Roeboides myersii</i>	0.57				0.57			0.57	
<i>Salminus hilarii</i>	0.64					0.64		0.64	
<i>Satanoperca jurupari</i>	0.59			0.59				0.59	
<i>Schizodon fasciatus</i>	0.55					0.55		0.55	
<i>Semaprochilodus insignis</i>	0.65					0.65		0.65	
<i>Serrasalmus compressus</i>	0.69					0.69		0.69	
<i>Serrasalmus elongatus</i>	0.68					0.68		0.68	
<i>Serrasalmus gouldingi</i>		0.67				0.67		0.67	
<i>Serrasalmus rhombeus</i>	0.64		0.65			0.64		0.64	
<i>Serrasalmus spilopleura</i>		0.67				0.67		0.67	
<i>Sorubim lima</i>	0.62					0.62	0.62		
<i>Sorubimichthys planiceps</i>	0.63	0.57				0.61	0.61		
<i>Squaliforma cf. emarginata</i>	0.51			0.51			0.51		
<i>Steindachnerina bimaculata</i>	0.54					0.54		0.54	
<i>Triportheus auritus</i>	0.50	0.67				0.56			0.56
<i>Triportheus albus</i>	0.62	0.68				0.64			0.64
<i>Triportheus angulatus</i>	0.63	0.68				0.64			0.64
<i>Triportheus elongatus</i>	0.68	0.68				0.68		0.68	0.68
<i>Tympanopleura atronasus</i>	0.66					0.66		0.66	
<i>Zungaro zungaro</i>	0.57	0.61				0.58	0.58		
<b>Total mean</b>	<b>0.61</b>	<b>0.64</b>	<b>0.67</b>	<b>0.62</b>	<b>0.62</b>	<b>0.62</b>	<b>0.61</b>	<b>0.63</b>	<b>0.61</b>

**Table S3.** Body size category (small, medium, e large), based on the percentage distribution of  $L_{max}$  values, using the quartile method, for 29 fish species.

Species	Size class	Quartile %
<i>Arapaima gigas</i> (Schinz, 1822)	Large	100.00
<i>Brachyplatystoma filamentosum</i> (Lichtenstein, 1819)	Large	96.40
<i>Brachyplatystoma rousseauxii</i> (Castelnau, 1855)	Large	92.80
<i>Phractocephalus hemiliopterus</i> (Bloch & Schneider, 1801)	Large	89.20
<i>Pseudoplatystoma tigrinum</i> (Valenciennes, 1840)	Large	85.70
<i>Brachyplatystoma platynemum</i> Boulenger, 1898	Large	82.10
<i>Osteoglossum bicirrhosum</i> (Cuvier, 1829)	Large	78.50
<i>Leiarius marmoratus</i> (Gill, 1870)	Large	75.00
<i>Pinirampus pirinampu</i> (Spix & Agassiz, 1829)	Medium	71.40
<i>Cichla monoculus</i> (Spix & Agassiz, 1831)	Medium	67.80
<i>Piaractus brachypomus</i> (Cuvier, 1818)	Medium	64.20
<i>Brachyplatystoma vaillantii</i> (Valenciennes, 1840)	Medium	60.70
<i>Brachyplatystoma juruense</i> (Boulenger, 1898)	Medium	57.10
<i>Pellona flavipinnis</i> (Valenciennes, 1837)	Medium	53.50
<i>Salminus hilarii</i> Valenciennes, 1850	Medium	50.00
<i>Hydrolycus scomberoides</i> (Cuvier, 1819)	Medium	46.40
<i>Calophysus macropterus</i> (Lichtenstein, 1819)	Medium	42.80
<i>Hemisorubim platyrhynchos</i> (Valenciennes, 1840)	Medium	39.20
<i>Ageneiosus inermis</i> (Linnaeus, 1766)	Medium	35.70
<i>Brycon amazonicus</i> (Spix & Agassiz, 1829)	Medium	32.10
<i>Hypophthalmus marginatus</i> Valenciennes, 1840	Medium	28.50
<i>Hoplias malabaricus</i> (Bloch, 1794)	Small	25.00
<i>Astronotus ocellatus</i> (Agassiz, 1831)	Small	21.40
<i>Prochilodus nigricans</i> (Spix & Agassiz, 1829)	Small	17.80
<i>Schizodon fasciatus</i> (Spix & Agassiz, 1829)	Small	14.20
<i>Leporinus friderici</i> (Bloch, 1794)	Small	10.70
<i>Semaprochilodus insignis</i> (Jardine, 1841)	Small	7.10
<i>Mylossoma albiscopum</i> (Cope, 1872)	Small	3.50
<i>Potamorhina altamazonica</i> (Cope, 1878)	Small	0.00

**Table S4.** Variation of the  $L_m/L_{max}$  ratio, analyzed using ANOVA, considering geographic regions, habitat types and life strategies as factors.

GEOGRAPHICAL REGION	F	df	p
	5.260	2	<b>0.006</b>
<b>Tukey's pairwise comparisons: p(same)</b>	Lower	Middle	Upper
	2.462	0.190	0.009
HABITAT TYPE			
	2.653	2	0.072
<b>Tukey's pairwise comparisons: p(same)</b>	Bentic	Benthopelagic	Pelagic
	2.342	0.222	0.979
LIFE STRATEGY			
	2.570	2	0.078
<b>Tukey's pairwise comparisons: p(same)</b>	K	r1	r2
	1.207	0.670	0.454