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Bite force mechanics and allometry of piranha (Serrasalmidae)

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ABSTRACT

The bite force of the piranha (Serrasalmidae) has drawn considerable attention due to its ability to effectively capture and masticate prey. Herein, we analyze theoretical anterior bite forces using a lever approach and compare them to *in-vivo* maximum bite forces. We provide a mechanics analysis that explains the scaling allometry of the bite force (F_{output}) with the length of the fish (l), $F_{output} \propto l^2$.

1. Introduction

The Serrasalmidae are a family of specialized biters known to be composed of three major subclades: (1) the piranha-clade (carnivorous), (2) the pacu-clade (herbivorous), and (3) the *Myleus*-clade (omnivorous) (Ortí et al., 2008). This family has been traditionally distinguished by their distinct feeding habits and notable dentition (Prance and Goulding, 1981). Piranha usually have triangular-shaped, tricuspid, and serrated teeth found within a single row. The teeth interlock with their adjacent neighbors' lateral cusps creating a unified unit that regenerates as a row simultaneously (Kolmann et al., 2019). *Serrasalmus rhombeus*, commonly known as the Black piranha, have been shown to have the most powerful bite force relative to its size with a maximum recorded bite of 320 N for a 1.1 kg specimen (Grubich et al., 2012). This is primarily attributed to its large adductor mandibulae complex which makes up over 2% of its total body mass (Grubich et al., 2012). While there are studies that successfully compare theoretical bite forces to *in-vivo* anterior bite forces, there has yet to be a mechanics-based analysis which explains the scaling allometry (Grubich et al., 2012; Huby et al., 2019).

2. Results

The theoretical bite force of the piranha can be estimated from the geometry of the maxilla and the size of the adductor mandibulae muscles using an approach developed by Westneat (2003) and adapted by Meyers et al. (2012) In this adaptation, the closing of the lower jaw can be modeled as a third-order lever (Fig. 1A). Three major subdivisions of

the adductor mandibular muscle are responsible for closing, referred to as A1, A2, and A3 (Fig. 1B). The major force generators in the jaw are the A2 and A3 subdivisions. Measured values of the angles (α_1, α_2, and α_3) with respect to the vertical direction, segment lengths ($d_1, d_2, d_3,$ and d_o), and maximum cross sections of the three-muscle groups are measured from piranha specimens. The equation of equilibrium for the moments is:

$$\sum ME = F_{A1}\sin(\alpha_1)d_1 + F_{A2}\sin(\alpha_2)d_2 + F_{A3}\sin(\alpha_3)d_3 - F_{output}d_o = 0 \qquad (1)$$

The force of the muscles (F_{A1} F_{A2}, and F_{A3}) can be approximated knowing the cross-sectional area of the muscle group and the maximum stress produced by muscle (σ_{max}); a value of 0.2 MPa is used, which is the highest range for red muscles as indicated by Westneat (2003). The maximum isometric stress in muscle has been shown to vary from 0.1 to 0.2 MPa depending on muscle location and fiber type (Rome et al., 1992; James et al., 1998). The segments (d_1, d_2, d_3) are the lengths between the fulcrum and the attachment point for each muscle and d_o is the length from the fulcrum to the most anterior tooth tip. Assuming that the jaw length and mandibular muscles scale isometrically with the size of the fish (which has been supported by Richard and Wainright (Richard and Wainright, 1995)) a direct self-similar scaling constant (k) can be found when Equation (1) is divided by d_o:

$$F_{output} = \frac{d_1}{d_o}F_{A1}\,\sin(\alpha_1) + \frac{d_2}{d_o}F_{A2}\,\sin(\alpha_2) + \frac{d_3}{d_o}F_{A3}\,\sin(\alpha_3) \qquad (2)$$

Therefore d_1/d_o, d_2/d_o, and d_3/d_o are fixed and independent of the size. Thus,

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$$k_1 = d_1/d_o, \ k_2 = d_2/d_o, \ and \ k_3 = d_3/d_o \qquad (3)$$

The geometric and angular parameters are assumed, to a first approximation, to be constant. The maximum force that the muscles can impart is proportional to the cross-sectional area (A) of the muscle. Assuming a constant maximum muscle stress of σ_{max},

$$F_{A1} = \sigma_{max}A_1, \ F_{A2} = \sigma_{max}A_2, \ and \ F_{A3} = \sigma_{max}A_3 \qquad (4)$$

Additionally, assuming that the area of the muscle can be represented as proportionality constant (k') multiplied by the length of the fish squared (l^2),

$$A = k' l^2 \qquad (5)$$

When substituting Equations (3)–(5) into (2) we obtain,

$$F_{output} = l^2 * \left[k_1 k_1' \sin(\alpha_1) + k_2 k_2' \sin(\alpha_2) + k_3 k_3' \sin(\alpha_3) \right] * \sigma_{max} \qquad (6)$$

This provides a direct proportionality between F_{output} and l^2. This allometry is indeed closely obtained from the measurements, shown in Fig. 1C. This is a classical expression of non-isometric allometry: the bite force scales as the square of the standard length (SL), where the standard length of the fish is measured from the tip of the nose to its last vertebrae. The maximum stress that the teeth can impart can be assumed to be limited by the compressive strength of the dentine-enameloid complex. The mechanical properties of enamel and dentine are a function of structure and composition and are, to a first approximation, independent of size. Therefore the maximum stress that the teeth can undergo is dependent on the strength of the enamel-dentine composite. This is equal to, to a first approximation, to F_{output}/t^2, where t is a characteristic tooth dimension, which scales isometrically with l. This is the same allometry.

Here, we record a scaling constant of 1.842 for the calculated bite force which includes the average data from Huby et al. (2019) on their calculated bite forces for *Pygocentrus nattereri* (Fig. 1C). This scaling constant is equivalent to the allometry parameter. We also conducted *in-vivo* measurements on three piranha whose values, along with the average of Huby et al. (2019) for *in-vivo Pygocentrus nattereri,* are presented in Fig. 1C. The scaling constant for the *in-vivo* bite force is 1.985 which is very close to the expected allometry from Equation (6). Additionally, we transformed the average *in-vivo* bite forces with respect to standard length obtained by Huby et al. (2019) for nine different piranha species to $\log_{10}$ and when fit to a linear regression we produce an allometric scaling constant of 2.014 (Fig. S1). While our reported values, along with Huby et al. (2019), are in agreement with the proposed allometric scaling, they are slightly lower than Grubich et al. (2012) who record a scaling constant of 2.30 for *in-vivo* bite forces of *Serrasalmus rhombeus.*

Possible sources of error can be attributed to the dissimilarity in bite force performance of the piranha under natural conditions and the use of the bite force tester. The piranhas may underperform when tested with the apparatus. During bite-force testing the piranha exhibits multiple

Table 1
In-vivo piranha bite force (BF) measurements taken along the Paraguay river. Standard length (SL).

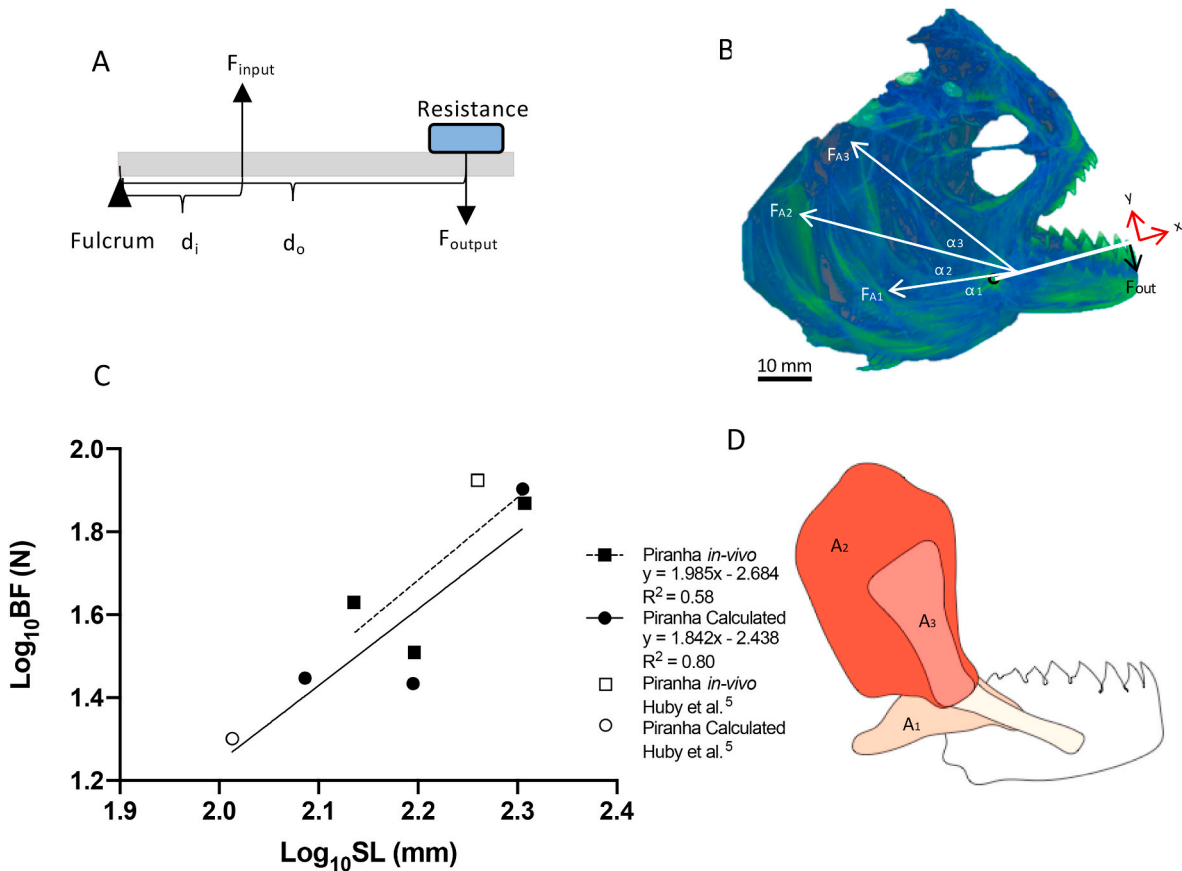| Specimen	Mass (kg)	SL (mm)	Maximum BF (N)	Average BF (N)	Standard Deviation BF
1	0.75	203	73.85	33.40	20.7
2	0.64	157	32.31	26.31	5.7
3	0.50	136	42.37	25.12	12.8

Fig. 1. Jaw mechanics and bite forces of the piranha. A) Simplified third-order lever. B) Relative muscle positions within the skull of a piranha. C) Calculated and *in-vivo* piranha bite forces including findings from Huby et al. (Huby et al., 2019) transformed to $\log_{10}$ and fitted to a simple linear regression against standard length of the fish (SL). D) Schematic of the subunits of the mandibular muscle (A_1, A_2, and A_3) with respective size and orientation.

rapid bites at various force levels (Table 1).

3. Conclusion

The impressive biting capabilities of the piranha have sparked considerable investigation into *in-vivo* and calculated anterior bite forces which have extensively shown a positive allometric relationship. Here, we contribute to the growing literature by providing a mechanics based understanding of this allometric relationship. We propose that $F_{output} \, \alpha \, l^2$ which is in agreement with our *in-vivo* and calculated lever approach which includes data from Huby et al. (2019) on *Pygocentrus nattereri*.

4. Methods

4.1. Specimens

Three adult piranha (*Pygocentrus nattereri*) specimens were purchased from local fish markets in Brazil already deceased. Specimens were transported overnight packed in ice. Upon retrieval specimens standard lengths were recorded and their in-tact skulls preserved and placed in a $-20\,^{\circ}$C freezer until use. Specimens were hydrated in Hank's balanced salt solution (Thermo Fisher Scientific) before jaw muscle dissection. Muscle area, jaw length, lever length of muscle attachment, and angle of attachment were recorded for bite force calculations.

4.2. Bite force analysis

The measurement on live piranhas was made on specimens caught along the Paraguay river and their bite forces were measured using a force gauge assembled with a Flexiforce**TM** A401 sensor (Tekscan). Two force gauges were constructed (Gauge 1 and Gauge 2). The sensor was placed between two wood strips and the assembly was inserted into the piranha's mouth as indicated in Fig. 2. The change in resistance was recorded and converted into a force through the following equations dependent on which gauge was used. Each piranha recorded 5–10 bites (Table 1). These values are consistent with the measurements from Huby et al. (2019) The maximum bite force for each fish was plotted in Fig. 1C. Their mass and length were recorded and they were released back into the river. The measurements on piranha were accomplished during the Roosevelt-Rondon Centennial Expedition, from 2014 to 2016.

Gauge 1: $y = 16.158x^{-0.66}$
Gauge 2: $y = 12.41x^{-0.69}$

Author contributions

Conceptualization, A.V. and M.A.M.; Methodology, A.V.; Formal Analysis A.V; Investigation A.V.; Resources, M.A.M.; Writing – Original Draft, A.V.; Writing – Review & Editing, A.V. and M.A.M.; Visualization, A.V. and M.A.M.; Supervision, M.A.M.; Funding Acquisition, A.V. and M.A.M.

Competing financial interests

The authors declare no competing financial interests.

Data and materials availability

All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials. Additional data related to this paper may be requested from the authors.

Fig. 2. Image depicting set up of *in-vivo* bite force measurements. This was taken along the Roosevelt river with a black piranha (*Serrasalmus rhombeus*). This fish and their respective bite forces were not included in this study and the photograph only illustrates the testing procedure.

CRediT authorship contribution statement

Audrey Velasco-Hogan: Formal analysis, Methodology, Investigation, Writing - original draft, Visualization. **Marc A. Meyers:** Conceptualization, Methodology, Investigation, Supervision, Writing - review & editing, Resources, Project administration, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported i.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jmbbm.2020.104296.

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