SHORT REPORT

Allometric Parameters of *Pterodoras granulosus* (Valenciennes 1833) and Its Application to Fossil Assemblages

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ABSTRACT By means of the analysis of 28 modern individuals of *Pterodoras granulosus*, a silurid of great importance in the archaeological assemblages of the Amazonas and Paraná basins, allometric equations based on the size of the spines have been derived, allowing the reconstruction of size profile and weight of the individuals recovered in fossil assemblages. These equations have been obtained from four different measures, three of them related to different sections of the spine articulation with the cleithrum, an area that usually has an excellent preservation in the archaeological and palaeontological records. This study allows observation of remarkable individual variability of the captured specimens regarding its total weight, mainly due to the weight variability of viscera, and also probably with other metabolic situations, episodic intakes and/or reproductive aspects, among others. Hence, allometric equations determine more accurately length than weight, resulting in proxy data for the reconstruction of different size profiles of archaeological assemblages. Copyright © 2010 John Wiley & Sons, Ltd.

Introduction

Allometric studies on different fish species are frequent in worldwide biological and archaeological literature (Appelget & Smith, 1951; Wit, 1960; Casteel, 1976; Reitz & Cordier, 1983; Bisbal & Gómez, 1986; Desse and Desse-Berset, 1996a, 1996b; Leach et al., 1997; Soupir et al., 1997; Gisbert, 1999; Béarez, 2000; Leach & Davidson, 2001; Brodeur, 2002a, 2002b; Feitoza et al., 2004; Acosta et al., 2007; Carder et al., 2007, among others). The importance of this study and its development are concomitant with the need to state human behaviour in the past. To determine the size of captured fish can offer evidence of the fishing settings, seasonality of captures, the degree of pressure on fishing resources and technology associated to its capture and processing. In the archaeological sites of the Paraná basin (Figure 1) fish remains are abundant (Cione & Tonni, 1978; Caggiano, 1984; Acosta, 2005; Musali, 2005; Pérez Jimeno, 2007; Loponte, 2008; Pérez Jimeno & Musali, 2008; Arrizurieta et al., 2009;

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Escudero & Loponte, in press). However, few advances have been made regarding the size of the captured individuals, except in nominal terms. An exception is a preliminary study performed on the spines of *Pterodoras* granulosus recovered from archaeological assemblages (Acosta et al., 2004; Musali, 2005; Loponte, 2008). This work represents an advance on such studies, seeking to set different allometric equations for *P.* granulosus, a silurid of great importance in archaeological contexts in two of the main hydrographic basins in the world, the Amazonas and Paraná.

Some characteristics of P. granulosus and its archaeological representation

The armado (*P. granulosus;* its common name in English is granulated or armoured catfish) belongs to the Class Actinopterygii, Order Siluriformes, Family Doradidae. It is widespread through the whole Amazonas and Paraná basins (Eigenmann, 1925). Even though generally assumed to be omnivorous, results of isotopic analysis of archaeological specimens from lower Paraná river have shown a predominantly herbivorous C_3 diet (Loponte, 2008), coinciding with current feeding habits in this sector of the basin (Ferriz *et al.*, 2000).



Figure 1. Paraná basin.

The cranium of *P. granulosus* is composed of a series of bones, highly dense and compact, and some rounded bones of high mineral density such as the antorbital (Musali et al., 2003). Unlike other species, P. granulosus has a very small and irregular otolith, unsuitable for allometric studies due to its small size and difficult to be recognised among the hundred thousands of fragments recovered from sieving. Each *P. granulosus* specimen has two pectoral spines and a dorsal one, both very ossified, with an irregular serrated pattern typical of this species. Spines also have a high mineral bone density (Musali et al., 2003). In the lateral and external line, a series of dermal plates is developed (Figure 2). This species does not present a significant sexual dimorphism regarding size variables (Eigenmann, 1925). Not only the appendicular skeleton but also the axial, including vertebrae and lateral dermal plates, have an excellent preservation in the late Holocene record of the lower Paraná, although complete elements are rarely recovered.

Thus, even though it is possible to take hundreds of measures of different bones in order to develop



Figure 2. Pterodoras granulosus (Valenciennes, 1833).

allometric equations on current individuals (see an example of allometric studies of vertebrae in *P. granulosus* in Feitoza *et al.*, 2004), these rarely could be useful to determine the size variation of individuals recovered in the archaeological sites of Paraná basin, because of fragmentation. Therefore, pectoral spines have been selected, in spite of the fact that they are recovered almost invariably fractured in the medial area, because the articular ends are found in excellent integrity and they usually have values of 100% MAU (Musali, 2005), making them highly required elements for the development of allometric equations applicable to archaeofaunal assemblages in the area.

Materials and methods

The setting of allometric equations that has been implemented here, assumed the existence of a relationship between the state of growth of the animal and the general size of spines, an assumption that will be examined with the obtained data. The advantage of relating the somatic state with some dimension properties empirically obtained is related to the inclusion of the variations of each specimen (*cf.* Carlander, 1981; Ricker, 1992; Secor & Dean, 1992). The disadvantage is that a unique curve and its derived equation are obtained, being only applicable to the somatic interval of individuals included in this study, due to a close relation between the state of growth and the individual dimension variables (Hare & Cowen, 1995).

The sample consists of 28 specimens of *P. granulosus* obtained in Paraná Delta, most of them captured in March 2003. These individuals were weighted complete (W_1) and measured (standard size SL and total size TL). Later, viscera were extracted and the weights were recalculated (W_2) . Finally, heads were sectioned and specimens were weighted again, this time without viscera neither skulls (W_3) (Table 1).

Sample	Standard longitude (SL) (cm)	Total longitude (TL) (cm)	Total weight (P1) (gr)	Eviscerated weight (P2) (gr)	headless weight (P3) (gr)
A	49	58	3000	2168	1468
В	32	37	760	625.5	423.5
С	31	38	710	549	372
A1	32	37	1029	833.5	540
A2	33	37	769	612	377.5
A3	36	42	1435	1008	613
A4	37	46	1182	938	576.5
A5	35	40	1174	915.5	613.5
A6	35	43	1103	871	584.5
A7	37	43	1399	1057.5	700
A8	48	54	2384	1769.5	1200
A9	45	52	2729.5	2226	1637.5
A10	41	50	2341.5	1950	1484
A11	35	39	1202.5	1022	770
A12	41	48	1940	1582.5	1150.5
A13	36.5	41	1606	1139	853
A14	42	50	1893.5	1576	1081
A15	35	42	1112.5	883.5	580
A16	38	45	1402.5	1014.5	678
A17	34	40	953	754.5	479.5
A18	37	44	1112.5	928	604.5
A19	40	45	1363.5	1075.5	693.5
A20	36	42	1267.5	1018	667.5
A21	36	42	1323	978	679.5
A22	38	44	1078	828.5	523.5
A23	40	46	1721	1351	957.5
A24	39	43	1460	1129.5	780
A25	49	56	2990	2387.5	1694

Table 1. Dimension Variables of P. Granulosus. Weights were rounded off in intervals of 0.5 g and lengths in intervals of 5 mm

After data (shown in Table 1) were obtained, soft tissue was removed mechanically from every captured individual, and pectoral spines were selected in order to obtain the corresponding measures. Four different measures of dorsal spines (M_1 , M_2 , M_3 and M_4) were taken from the modern samples. The two first ones are referred to the spine's articular sizes (total width of articulation and maximum length from the ventrolateral to dorso-lateral process), M_3 belongs to the distance between medial fossa of the articulation height and its epiphysis end, whereas M_4 belongs to the spine total length (Figure 3). Two digital calliper readings of each spine measure (left and right) of each specimen were taken by two different expert operators and the obtained values were averaged.

The observed weights $(W_1, W_2 \text{ and } W_3)$ were independently correlated with the length of captured individuals (SL and TL) and respective spines measures $(M_1, M_2, M_3 \text{ and } M_4)$.

Results

In modern individuals, captured in Paraná River, the relation between length (Total and Standard) and

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weight revealed an isometric growth that is described by the equations (Figure 4)

$$y = 105.64x - 3177.8$$
 ($r^2 = 0.8648, p < 0.00$)
 $y = 123.75x - 3202.1$ ($r^2 = 0.8902, p < 0.00$)



Figure 3. Size variables of spines of *P. granulosus*. This figure is available in colour at wileyonlinelibrary.com.



Figure 4. Association of variables of P. granulosus (Total weight versus. Total and Standard length).

Although the dimensional variables addressed here have significant relationships, the obtained values show that *P. granulosus* has an important individual variability in weight. In effect, as shown in Figure 4, individuals of the same SL have weight variations up to 35% (individuals B and A1), a situation that is verified in other body sizes (i.e. individuals A16 and A22 with a weight variation of 30%; see Figure 5).

These variations draw the attention to the fact that allometric constructions constitute in general proxy values, in particular for total weights, as they are usually influenced by particular metabolic states in each individual, and that in an archaeofaunal level are regularly invisible for the zoo-archaeologist. Regarding the reference sample, weight variability is noticeable for the same body size. It is also interesting to observe the percentage leaps in weight, up to 26%, in individuals with differences of 0.5 cm of SL (individuals A13 and A21), as well as inverse relationships in adjacent interval individuals (higher SL but less total weight, as it happens with individuals A1 and A2 and between A8 and A9). The variability in total weight



Figure 5. Maximum variations and average weight of individuals of *P. granulosus* included in this study.

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probably reflects episodic intakes, changes in hydrologic conditions and/or nutrients in fluvial system and/ or reproduction-related situations. Even though, the latter is less probable as the reproductive cycle of *P. granulosus* develops in the upper Paraná basin, after the migration of this species during southern hemisphere's autumn (Amestoy & Fabiano, 1992). It is clear that the most influential parameter in total weight variations is the weight of viscera. In the reference sample, the weight of viscera has an average variation of 44% for the same body size listed in Figure 6, and a maximum weight variation of up to 85% (individuals A18 and A4). On the contrary, at equal body size, the non-viscera weight variation averaged only 18%.

Values of M_1 obtained in the spines of modern individuals have scarce inter-individual variability (average 1.48% ± 1.48; maximum 6.74%). This, in addition to the fact that in the archaeological contexts, specimens allow the measurement of this magnitude accurately, makes M_1 one of the most interesting integrated parameters, because its value predicts with significant precision (through relevant equations) the size and weight of the fishes (Figure 6).

Given the fact that the individuals obtained for this study do not have M_1 values lower than 14 mm, the arising equations that use this variable can only be applied when values are equal to 14 mm or higher. In fact, we tried to apply these equations to smaller individuals, recovered after this study, but results were either below actual values, or even negative. With the aim of diminishing the quantity of graphics, only the ones that have higher and more significant correlation values were included, in addition to a table that summarises all the obtained equations (Table 2).

Measure M_2 that does not represent an important inter-individual variability either (average $1.4\% \pm 1.25$;



Figure 6. Association of variables of P. granulosus (M1 facet width versus total weight and standard length).

Table 2. Allometric coefficients of P. granulosus

X measure	Total weight	Eviscerated weight	Eviscerated and headless	Standard longitude
M ₁ M ₂ M ₃ M ₄	y=241.62x-3197.9; $r^{2}=0.77, p<0.01$ y=272.47x-2568.8; $r^{2}=0.79, p<0.01$ y=286.96x-2221.4; $r^{2}=0.74, p<0.1$ y=58.939x-3588.8; $r^{2}=0.66, p<0.5$	y=185.47x-2432.9; $r^{2}=0.74, p<0.01$ y=209.62x-1957; $r^{2}=0.76, p<0.01$ y=223.43x-1719; $r^{2}=0.74, p<0.05$ y=37.684x-2104.9; $r^{2}=0.58, p<0.5$	y=133.18x-1784.5; $r^{2}=0.67, p<0.01$ y=151.26x-1454; $r^{2}=0.70, p<0.05$ y=161.63x-1287.4; $r^{2}=0.68, p<0.5$ y=26.62x-1509.9; $r^{2}=0.51, p<0.5$	y=1.9086x+0.8899; $r^{2}=0.83, p<0.001$ y=2.1148x+6.4214; $r^{2}=0.83, p<0.001$ y=18.295 e 0.0558x; $r^{2}=0.76, p<0.05$ y=0.4601x-1.6781; $r^{2}=0.73, p<0.01$

maximum 5.65%), can also be taken as a descriptive measure for the dimension parameters investigated. Due to the size of used individuals, M_2 can only be used with derived equations of values equal to 11 mm or higher. The relation between M_2 and size is described by equations y = 2.1148x + 6.4214; y = 272.47x - 2568.8, respectively (Figure 7).

The measure M_{3} , which quantifies distance between proximal spine foramen and the extreme articular

facet, is the one that shows higher inter-individual variability between left and right spines (average $5.7\% \pm 5.19$; maximum 15%). Hence, it is less reliable than the previous measures. Its value also predicts the individual standard size and length through these equations:

$$y = 18.295 e^{0.0559x}$$

 $y = 286.96x - 2221.4$



Figure 7. Correlation between M_2 , total weight and standard length (SL).

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Figure 8. Correlation between M_3 , total weight and standard length (SL).

The best usage of M_3 is related to its utility as an alternative measure when damage in proximal area of the spine does not allow us to take values of M_1 and M_2 . The equation derived here for variable M_3 can only be used for values equal to 9 mm or higher (Figure 8).

Finally, the measure M_4 , which refers to the spine total length, has little average inter-individual variation (average $2\% \pm 2.33$; maximum 10%). It predicts standard length and total weight through these equations:

$$y = 0.4601x - 1.6781$$

 $y = 58.939x - 3588.8$

This latter equation shows higher dispersal (see Figure 9), and it can rarely be taken in archaeological contexts, as spines are usually fragmented in its medial area, preventing to obtain its value. Given the size of individuals included in this study, M_4 can only be applied when equal to 74 mm or higher.

By the coordinates of weight and M_4 in Figure 9, a broader dispersion is observed in smaller individuals,

suggesting different behaviour related to the state of maturity of individuals under 95 mm. For individuals over this threshold and 2000 g, it is convenient to use M_4 and the following equation:

y = 67.253x - 4095.7 ($r^2 = 0,75 p < 0.1$)

For calculating eviscerated weight in individuals recovered from the archaeological record, M_1 through the equation y = 185.47x - 2432.9 ($r^2 = 0.7458 \ p < 0.05$) can be used. It can also be measured with other parameters (see Table 2)

Other data, archaeologically useful, obtained in this experiment are that viscera represents on average $22\% \pm 4$ (± 1 standard deviation) of the individuals' total weight (maximum 30%, minimum 15%), in addition to $10\% \pm 2$ of skeleton weight. These values show that nearly 68% of the total weight of *P. granulosus* is useful for human intake.

In zooarchaeological studies in the Paraná basin, MNI values of *P. granulosus* are commonly obtained by pectoral spines, as they are the best preserved elements.



Figure 9. Association of standard length and weight with M_4 .

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Spine #	Lateral.	Measures (mm)		Ratio	Total we	Total weight (g)		Eviscerated weight (g)		
			M ₁	M ₂	M_{1}/M_{2}	<i>M</i> ₁	M ₂	<i>M</i> ₁	M ₂	(%)
1	Left	25.3	19.3	1.31	2915.1	2689.9	2259.5	2088.7	7.6	
3	Right	22.9	18.3	1.25	2335.2	2417.4	1814.4	1879.0	3.4	
4	Right	24.2 17	13.7	1.24	2649.3 909.6	1164.0	2055.5 720.1	914.8	21.2	
6	Left	27.4	21.6	1.27	3422.5	3316.6	2649.0	2570.8	3.0	
7	Right	21.3	18.5	1.15	1948.6	2471.9	1517.6	1921.0	21.0	
8	Right	22.1	16.5	1.34	2141.9	1927.0	1666.0	1501.7	9.9	
10	Left	20	15.8	1.27	1634.5	1736.2	1276.5	1355.0	5.8	
11	Right	20.2	17.1	1.18	1682.8	2090.4	1313.6	1627.5	19.2	
12	Left	18	13	1.38	1151.3	973.3	905.6	768.1	15.2	
13	Right	20.8	16.1	1.29	1827.8	1818.0	1424.9	1417.9	0.5	
14	Left	24.2	19.5	1.24	2649.3	2744.4	2055.5	2130.6	3.5	
15	Left	21.5	17.4	1.24	1996.9	2172.2	1554.7	1690.4	8.0	
20	Right	25.2	19.4	1.30	2890.9	2717.1	2240.9	2109.6	5.9	
21	Right	19.8	15	1.32	1586.2	1518.3	1239.4	1187.3	4.2	
22	Left	22.2	18.2	1.22	2166.1	2390.2	1684.5	1858.1	9.3	
				1.27	34745.2	35401.2	27042.0	27562.7	1.9	

Table 3. Total and eviscerated weight obtained through the application of allometric equations, based on a sample of spines of *P. granulosus* recovered in LV site

Operators usually separate left and right spines, and the higher counting is from which arises the respective MNI. Differences in size of spines are not considered for the MNI, except if it is very noticeable, due to the lack of a database that allows the researcher to know their size variation ranges. Maximum variation percentages of M_1 , M_2 , M_3 and M_4 addressed in this study offer new possibilities for calculating MNI in recovered faunal assemblages. It is particularly useful in small collections where size values of left and right spines may present discontinuous measures over two standard deviations (95% of inter-individual size variables of the measured population crowded here). Consequently, a more accurate MNI could be obtained.

Archaeological application examples

Las Vizcacheras (LV) is an archaeological site located in the Paraná wetland, generated by hunter–gatherer groups during the Late Holocene (1090 ± 40 ¹⁴C BP, Beta 148237; 1060 ± 70 ¹⁴C BP, LP-1401). The depth of the archaeological deposit is 40 cm (Loponte, 2008). The first excavation of this site was carried out by the authors several years ago, where thousand of fragmented bones and several spines of *P. granulosus* were recovered. Due to the fragmentation of the spines, where M_4 was impossible to obtain and M_3 only could be measured in a fraction of the collection, allometric coefficients were applied using M_1 and M_2 in order to establish prehistoric fishing parameters (Table 3). In Table 3, is clear that the average of value differences calculated with M_1 and M_2 measures are small (~2%). The variability of the results between M_1 and M_2 is lower than 10% in most of the spines which ratio M_1/M_2 is between 1.35 and 1.24 (~73% of the spine collection).

The current method to calculate MNI of *P. granulosus* is by separating left and right spines (see above). Taken into account the information listed in Table 3, there are nine left spines and eight right spines. So, nine individuals of *P. granulosus* are present in the sample if we use the traditional analysis. But if we compare M_1 values, we find that some of them match between right and left spines (taken into account the maximum variability measured until today), and another is unpaired. The new MNI is 12 individuals (see Table 4).

Table 4. MNI values reconstructed with paired and unpaired M1 measures of *P. granulosus* recovered in LV site

Spine	Left	Right Exceeds	Max. variation?	MNI
2-5 12-21 10-11 13 15-7 22-8 4-3 14	16.7 18 20 21.5 22.2 24.2 24.2 24.2	17 19.8 20.2 20.8 21.3 22.1 22.9 1 22.9	No Yes No Unpaired No Yes Unpaired	1 2 1 1 1 2 2
1–20 6 Total	25.3 27.4	25.2 1	No Unpaired	1 12

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Concluding remarks

For zooarchaeological studies, to obtain several allometric equations for any species is not as important as to obtain just a few that are reliable, easy to measure and identify, and likely to be obtained with average archaeological record of a region.

Having allometric equations implies a meaningful advance for the discussion of pre-hispanic economies in Amazonas and Paraná basins, as it is currently possible to obtain a dimensional profile of captured individuals.

Equations aimed at obtaining standard length and non-viscera weights describe the real values of such magnitudes more accurately than those of total weight, as the latter is biased mainly by the variability related to viscera weight.

The aim of this study is to create an additional body of information, easy to use and contrast by any operator. It is expectable that new data also allow us to include another ones not represented in this study.

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