Trophic ecomorphology of *Potamotrygon falkneri* and *Potamotrygon motoro* (Chondrichthyes - Potamotrygonidae) on the upper Paraná river floodplain, Brazil

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Abstract. In this paper the the null hypothesis of absence of ecomorphological diversification was tested between *Potamotrygon falkneri* and *Potamotrygon motoro* (Chondrichthyes, Potamotrygonidae) on the upper Paraná river floodplain, Brazil. In the Principal Components Analysis, the five ecomorphological indices were positively correlated with axis 1. Their most relevant contributions were relative width of the mouth and relative opening of the spiracle. The Discriminant Canonical Analysis indicated that the width of the spiracles, followed by the width of the mouth, are the linear measurements that contributed the most to the morphological segregation between the two species. The Mantel test revealed that there is a significant correlation ($Z = 0.27$; $p = 0.0002$) between the ecomorphological distance matrix and the feeding habit model matrix, indicating dependence of the feeding habitats of species in relation the body shape of stingrays. *P. falkneri* presented comparatively larger spiracles, mouth, and pelvic and pectoral fins than *P. motoro*, which may influence in the capture of mobile prey (fishes), while *P. motoro* can use of the suction mechanism, favoring the consumption of prey with little evasive capacity. Ecomorphological diversification culminated in the exploitation of different food resources and provided the coexistence of *P. falkneri* and *P. motoro* in Parana river.

Key words: Ecomorphological diversity, feeding, potamotrygonid, Paraná basin, freshwater stingrays.

Resumo. Ecomorfologia trófica de *Potamotrygon falkneri* e *Potamotrygon motoro* (Chondrichthyes-Potamotrygonidae) na planície alagável do alto rio Paraná, Brasil. Neste trabalho objetivou-se testar a hipótese nula de ausência de diversificação ecomorfológica entre *Potamotrygon falkneri* e *Potamotrygon motoro* (Chondrichthyes, Potamotrygonidae) na planície alagável do alto rio Paraná, Brasil. Na Análise de Componentes Principais os cinco índices ecomorfológicos mostraram-se correlacionados positivamente com o eixo 1, sendo que suas contribuições mais relevantes foram: largura relativa da boca e a abertura relativa do espiráculo. A Análise Discriminante Canônica indicou a largura dos espiráculos, seguido da largura da boca como as medidas lineares que mais contribuíram para a segregação morfológica entre as duas espécies. O teste de Mantel revelou que há correlação significativa ($Z= 0,27$; $p=0,0002$) entre a matriz de distância ecomorfológica e a matriz modelo de hábito alimentar, indicando dependência da forma do corpo das raias em relação aos seus hábitos alimentares. *P. falkneri* apresentou-se com espiráculos, boca e nadadeiras pélvicas e peitorais maiores, comparativamente a *P. motoro*, o que pode interferir na captura de presas móveis (peixes), enquanto *P. motoro*, por sua vez, pode fazer uso do mecanismo de sucção, propiciando o consumo de presas com pouca capacidade evasiva, como os insetos aquáticos. A diversificação ecomorfológica entre *P. falkneri* e *P. motoro* no rio Paraná culminou na exploração diferenciada dos recursos alimentares e proporcionou a coexistência de ambas as espécies.

Palavras-chave: Diversidade ecomorfológica, alimentação, potamotrygonídeos, rio Paraná, raias-de-água-doce.

Introduction

Ecomorphology is the study of the interactions between the morphological and ecological diversities of the organisms in the present and over evolutionary time. These interactions can be studied at various levels: among individuals, species, guilds and communities (Motta *et al.* 1995), analyzing the correlations between the body shape of the organisms and the environmental factors (Oliveira 2005).

Ecomorphological studies are currently based on the argument that adaptive variations in the phenotype of the species may promote differences in their performance, and thus produce variations in the use of the available resources (Wainwright 1994). In this context, there are indications of strong relationships between body shape and the ecological function of morphological structures in fishes, allowing several comparative studies (Winemiller 1992), as related in Gatz Jr. (1979), Wikramanayake (1990), Fugi & Hahn (1991), Delariva & Agostinho (2001) and Oliveira (2005). Ecomorphological analyses are commonly evaluated using indices, which express the shape of the morphological structures and consequently reveal their ecological roles (Gatz Jr. 1979, Winemiller 1991). This procedure allows the evaluation of information restricted to the differences between shapes, since the indices, representing proportions, reduce the dependence of the analyses as regards the size of the individuals.

After the formation of Itaipu reservoir in 1982 (in the upper Paraná river region), three species of Potamotrygonidae Garman, 1877 began to be recorded (Agostinho *et al.* 1997). It is the only family among the Chondrichthyes that includes representatives restricted to freshwater (Rosa, 1985). The group is widely distributed in South American rivers that drain toward Atlantic and presents great diversity, having about 19 to 21 valid species, distributed in three genera: *Plesiotrygon*, *Paratrygon* and *Potamotrygon* (Rosa 1985, Carvalho *et al.* 2003).

The group is derived from marine ancestors that colonized freshwater through sea forays during the Miocene Epoch (5 to 23 million years ago) in South America. This had profound effects on the diversification and structuration of the Neotropical communities, mainly the Amazonian (Lovejoy *et al.* 1998), where the greatest diversity of potamotrygonids is found. One of the first studies about the freshwater stingrays was in the middle Paraná river (Santa Fé, Argentina), with Achenbach & Achenbach (1976), which characterized the species of potamotrygonids of the region and supplied preliminary biological information.

Lonardoni *et al.* (2006) verified differences in the feeding habit and low trophic overlap between *Potamotrygon falkneri* and *Potamotrygon motoro* in the upper Paraná river. They present segregation in the use of food resources, despite of being phylogenetically very close, the former piscivorous and the latter insectivorous. The diet composition was different in drought and flood seasons possibly because of availability variation of food resources in the floodplain. This features trophic flexibility these species. As *P. fakneri* and *P. motoro* live in simpatry in the Paraná river, is believed they have access to same type of prey. Thus diet differences of species in drought season can be result of differences strategies in food exploration in order to avoid competitive interactions.

Considering, therefore, the premise that changes in the exploitation of food resources may be the result of the morphological diversification among species, this study tested the null hypothesis of absence of ecomorphological diversification between *Potamotrygon falkneri* Castex & Maciel, 1963 and *Potamotrygon motoro* (Natterer in Müeller & Henle, 1841) (Chondrichthyes, Potamotrygonidae) on the upper Paraná river floodplain (Brazil).

Material and methods

Study area. The Paraná river is the second largest in South America (4,695 km long, drainage area of 3.1×10^6 km² and flow peaks of 65×10^3 m³.s⁻¹) (Bonetto 1986). The Paraná river basin in Brazil covers a vast area of 891,150 km² or 10.5% of the total area (Agostinho *et al.* 2007). The studied area is in the last undammed stretch of the Paraná River in Brazil. The samplings were carried out by Long-Term Ecological Research (LTER-site 6) Program developed by Núcleo de Pesquisa em Limnologia, Ictiologia e Aquicultura (Universidade Estadual de Maringá) in the upper Paraná River floodplain, between the States of Paraná and Mato Grosso do Sul.

Sampling. Stingrays were collected at three stations in the Paraná River (Fig. 1). Station 1 (22°46'53.59"S / 53°21'19.97"W) was sampled in August/2004 (in the dry period), in a channel formed at the edge of Mutum Island. Stations 2 (22°45'02.27"S / 53°18'00.09"W) and 3 (22°44'57.10"S / 53°16'37.69"W) were sampled in January/2005 (in the rainy period), on the right bank of the Paraná River (Mato Grosso do Sul State) and in a channel between the islands of Porto Rico and Mutum, respectively.
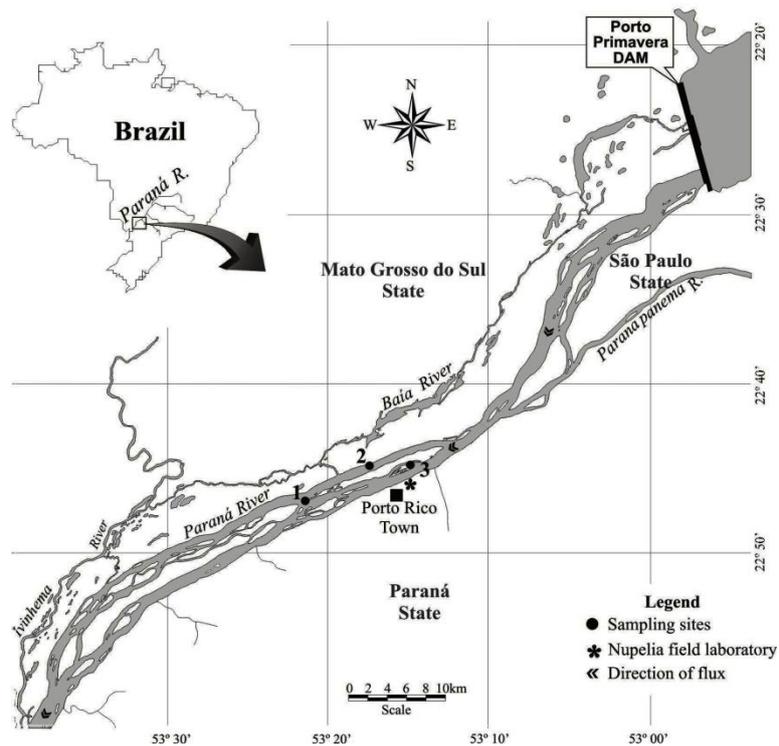
Figure 1. Study area with sampling stations (1,2 and 3) in the upper Paraná river floodplain.

Hook and line, rod and reel, harpoons and long lines were used to capture the stingrays (effort of five hours per day). The baits for the hooks and long lines were specimens of *Astyanax spp.* and fragments of Oligochaeta (earthworms). Species identification and the taking of morphometric measurements were carried out according to Rosa (1985). An analogical caliper (0.1 mm precision) was used to measure recently caught specimens, always by the same researcher. The estimated linear morphometric measurements were: total length (TL), pectoral fin length (PecL), disk width (DiW), tail length (TaL), length and width of the spiracles (SpL and SpW), mouth width (MoW) and pelvic fin length (PelL) (Fig. 2).
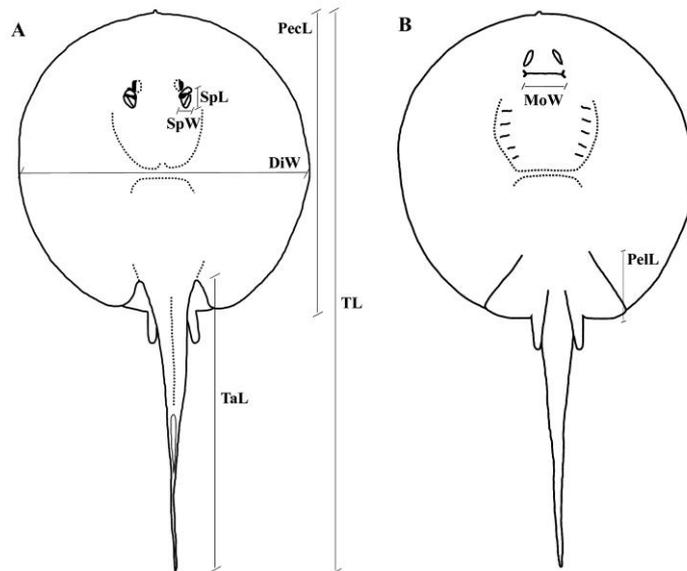
Figure 2. Schematic representation of the linear morphometric measurements. Dorsal measurements (A): TL = total length, PecL = pectoral fin length, DiW = disk width, TaL = tail length, SpL = spiracle length, SpW = spiracle width. Ventral measurements (B): MoW = mouth width, PelL = pelvic fin length.

The linear measurements were transformed ($\log x + 1$), and five ecomorphological indices were calculated from them (Table I). The ecological interpretations of indices were based on the literature about the functional morphology of fish (Alexander 1967, Harder 1975, Lagler 1977, Bond 1979, Gatz Jr. 1979, Compagno 1990, Winemiller 1991, Hahn *et al.* 1997).

Table I. Ecomorphological indices developed for potamotrygonids and their respective ecological interpretations.

Ecomorphological Indices		
Indices	**Formulas**	**Ecological interpretations**
1. Relative length of the pectoral fin	RLPec = PecL/TL	The pectoral fins are the main structures responsible for locomotion (Alexander 1967, Lagler *et al.* 1977, Compagno 1990, Dorit *et al.* 1991, Breda *et al.* 2005) and promote propulsion. The longer the relative length of the pectoral fin, the longer the propulsion will tend to be.
2. Relative length of the pelvic fin	RLPel = PelL/PecL	The pelvic fins in Chondrichthyes offer stability, and guide and break movements (Harder 1975). In addition, the stingrays can use the pelvic fins to create friction and to help stabilize themselves in the substrate (Bond 1979).
3. Relative length of the tail	RLTa = TaL/TL	The tail acts in swimming balance, providing stability in movement (Patrícia Charvet-Almeida, personal communication).
4. Relative width of the mouth	RWMo = MoW/DiW	The mouth is located ventrally and its size is directly related to the potential amplitude of prey size. In this way, larger values of relative width of the mouth indicate larger prey (Gatz Jr. 1979, Balon *et al.* 1986, Winemiller 1991, Hahn *et al.* 1997).
5. Relative opening of the spiracle	ROSp = SpL*SpW	Relatively larger spiracles can indicate greater capacity for the entrance of water in the gill chamber, suggesting greater resistance to low oxygen concentration. The communication of the spiracles with the mouth may help process to increase efficiency in the exploitation of food resources (Rand, 1907).

Principal Components Analysis (PCA) was applied to the correlation matrix (Pearson) formed by the five ecomorphological indices for the both species, using PC-ORD v.4.01 (McCune & Mefford 1999). This ordination is used to summarize a collection of data with wide variability and to reduce their dimensionality. The selection of the axes for interpretation was carried out according to the broken stick model (Jackson 1993), which recommends that only the axes with eigenvalues greater than those expected by chance should be retained. Analysis of Variance was applied to verify if there were significant differences between the species scores produced by the PCA.

Canonical Discriminant Analysis (CDA) with the residuals standardized from the linear measurements by disk width was carried out later to identify the morphological variables that most contributed to the segregation of the two species. In addition, the CDA model reclassified the individuals that compose the observed groups based on the distances between each observation and the centroids of each group (Gotelli & Ellison 2004). In this case, the percentage of correct reclassification is an indication of correct identification of the species. This analysis was carried out using Statistica 7.0.

A Mantel test (Legendre & Legendre 1998) was carried out with the objective of to test the null hypothesis of independence between body shape and feeding habit (Legendre & Legendre 1998). It calculated the correlation between the ecomorphological distance of the individuals and the feeding resources used. The morphological distance was obtained from the Euclidian distances among the canonical scores derived from partial CDAs. These analyses were carried out with two groups of ecomorphological indices that represent distinct ecological roles. The first group was formed by RLPel (relative length of the pelvic fin) and RLTa (relative length of the tail) due to the large contribution these indices to the stabilization of swimming, while the second group was composed of RLPec (relative length of the pectoral fin), RWMo (relative width of the mouth) and ROSp (relative opening of the spiracle) because it is more related to the potential use of different food resources.

Euclidian distance was calculated using Statistica 7.0 and is given by the expression (Gotelli & Ellison 2004):

$$\text{Euclidian distance} = \left[\sum_{i=1}^{n} \left(x_{ij} - x_{ik} \right)^2 \right]^{\frac{1}{2}}$$

In which: n = number of ecomorphological indices; x_{ij} and x_{ik} = values of the ecomorphological index i for the pair of scores produced by partial CDAs for the first and second groups.

The diet model matrix for the Mantel test was constructed from the stomach contents information (Lonardoni *et al.* 2006) from the same individuals analyzed in this study. The value 1 (one) was attributed to a pair of species constituted by the same species, i.e. individuals that possess the same feeding habit, while the value 0 (zero) was attributed to a pair formed by different species, in which individuals presented different feeding habits. This analysis was carried out using NTSYS-pc (Rohlf 1988) and the statistical significance was estimated using 20,000 model matrix permutations.

Results

Forty-eight specimens of *Potamotrygon falkneri* and thirteen of *Potamotrygon motoro* were collected (Table II).

Only the first PCA axis was retained for interpretation because it presented an eigenvalue greater than that expected by chance by the broken stick model (explained variability = 66.42%). ANOVA revealed segregation between *P. falkneri* and *P. motoro* in the first principal component (PC 1), based on the five proposed ecomorphological indices (F = 6.88; p = 0.011) (Fig. 3).

Table II. Total number of individual collected (N), males and females numbers, average and standard deviation for total length (TL), and variation coefficient (VC).

	N Total	Males	Females	TL	VC
P. falkneri	48	24	24	56,7 ± 14,62	25,78%
P. motoro	13	8	5	41,33 ± 14,44	34,94%
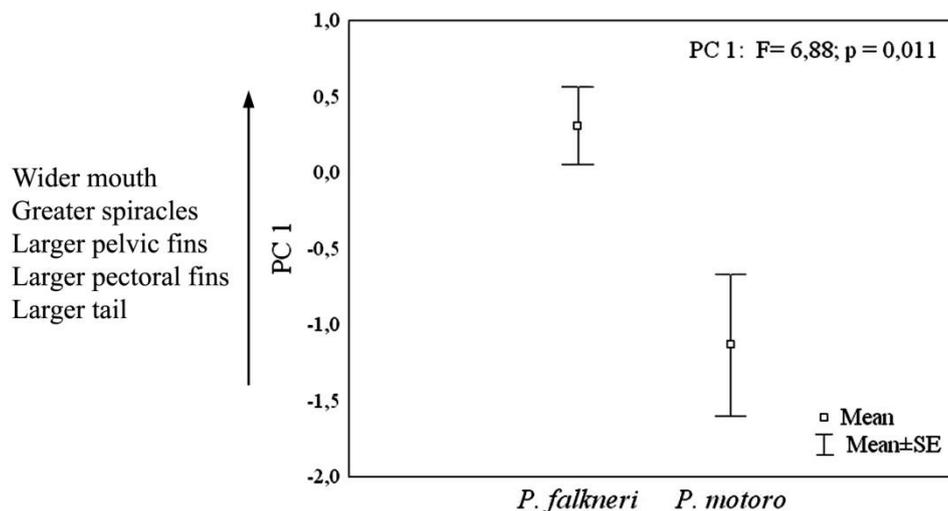
Figure 3. Mean and standard error of the scores of the individuals of *P. falkneri* and *P. motoro* in the first principal component of the PCA (PC1), calculated on the correlation matrix of five ecomorphological indices.

The five ecomorphological indices were positively correlated with PC 1. Their contributions were: relative width of the mouth (RWMo = 0.51), relative opening of the spiracle (ROSp = 0.49), relative length of the pelvic fin (RLPel = 0.48), relative length of the pectoral fin (RLPec = 0.47) and relative length of the tail (RLTa = 0.16). *Potamotrygon motoro* was more related to the negative scores of the PC1 and its distribution differed significantly from *P. falkneri* (Figure 3). The great variation around the mean, in relation to the scores of *P. motoro*, indicates great intraspecific

morphological variation.

The PCA indicated that the individuals of *P. falkneri* presented wider mouths, which shows the potential as regards prey size, i.e. the efficient consumption of relatively larger prey. The relatively greater spiracles may help process taking of food and increase respiratory capacity. In addition, the larger pelvic and pectoral fins may indicate their greater swimming potential in the execution of certain swimming strategies (e.g. rapid movements in short distance to capture prey).

Therefore, this group of characteristics may promote better efficiency in the exploitation of food resources.

Pearson correlation values (r) (p < 0.01) from the canonical variables (residuals standardized from the linear morphometric measurements) with the first canonical axis of the CDA indicate the spiracles (SpW = 0.70) and mouth width (MoW = 0.63) as the measurements that most contributed to the segregation between the two species, following SpL= 0.53 and PelL= 0.37.
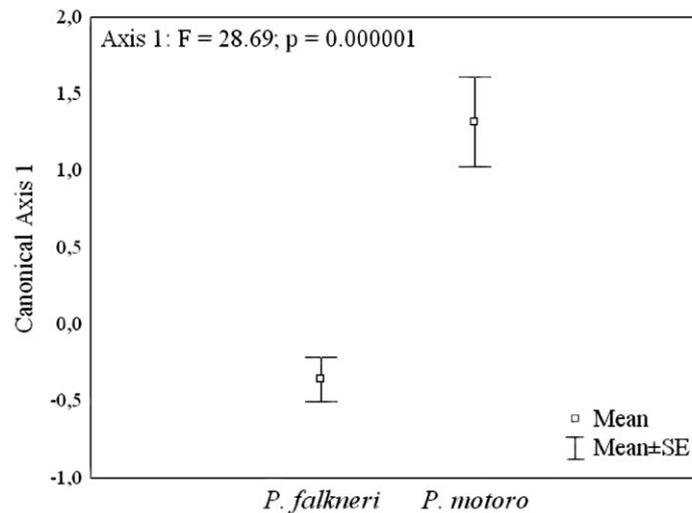
Figure 4. Mean and standard error of the scores of the first canonical axis of the CDA calculated on the correlation matrix of the standardized residuals from the linear morphological measurements by disk width.

The results of CDA (Fig. 4) indicating significant differences in the species take into account the linear measurements. Despite the inverted order of the parameters that most contributed to the formation of the axes in the two multivariate analyses (measurements related to the mouth and the spiracle), the results of the CDA corroborate those observed in the PCA.

According to the CDA (Table III), there was a 93.75% correct classification of *P. falkneri*, while

P. motoro revealed a low percentage of correct classification (38.46%). This is probably due to the great intraspecific ecomorphological variability observed for *P. motoro* in the PCA and CDA.

The Mantel test revealed that there is a significant correlation (Z = 0.27; p = 0.0002) between the ecomorphological distance matrix (Euclidian distance between the partial CDAs scores) and the trophic model matrix, which indicates that the feeding habits of the species depend on the body shape of the stingrays

Table III. Classification matrix predicted by CDA model for the species *P. falkneri* and *P. motoro* in the upper Paraná river.

		Predict Groups			
		P. falkneri	*P. motoro*	Observed Total	Correct Classification (%)
Observed groups	*P. falkneri*	45	3	48	93.75
	P. motoro	8	5	13	38.46
	Predict Total	53	8	61	81.96

Discussion

In this study, the null hypothesis of absence of ecomorphological variation between *P. falkneri* and *P. motoro* was rejected indicating interspecific ecomorphological structuration, which may directly interfere in the efficiency of the natural resource exploitation by these species. The morphological characteristics that most differentiated the two species were width of the spiracles and mouth, followed by the length pelvic and pectoral fins.

The spiracles consist of the first modified gill slit (Rand 1907). These dorsal openings of the oropharyngeal cavity are widely variable characteristics in elasmobranchs. Many families of shark have lost them completely; others possess them, but not have valves to close them. Other groups still possess large spiracles with valves, which are important to the respiratory flow (Summers & Ferry-Graham 2001).

Among the various forms of water flow for respiration, the stingrays employ the two most common: (i) the water enters only through the spiracle when they are buried on the bottom or; (ii) the water enters through the mouth and through the spiracle simultaneously when these fishes swim actively during foraging and migration (Summers & Ferry-Graham 2001). Low oxygen concentration on the bottom is common in the region of study, mainly in the lentic environments. Among the specimens analyzed, *P. falkneri* presented larger spiracles in relation to *P. motoro*, which may indicate a modification in response to hypoxia or better relative respiratory performance. This may be related to the fact that this species has successfully colonized lotic and lentic environments of the upper Paraná River floodplain. More efficient respiratory performance also promotes better physiological conditions that are reflected in the exploitation of food resources, taking into account the communication of the spiracles with the oropharyngeal cavity.

Stingrays present the mouth located ventrally and, as in teleosts, their size is directly related to the potential amplitude of prey size (Gatz Jr. 1979, Balon *et al.* 1986, Winemiller 1991). Prey capture in Elasmobranchii is a process that involves various mechanisms: (i) blowing/suction to reposition the prey; (ii) crushing; (iii) removal of pieces; (iv) biting, which can be employed with movements of the head to reduce prey size (Wilga *et al.* 2007).

The musculature that controls the anatomic system, responsible for feeding is highly conservative in the Chondrichthyes and relatively simple when compared to the Actinopterygii (Wilga *et al.* 2007). Some stingrays protract their jaws during the expansive phase of feeding. This because of the greater mechanical connection that they possess in their jaws and the loss of skull-palate articulation that occurs in function of the dorso-ventral flattening of the body (Rand 1907). Thus, protrusion in elasmobranchs is important because it allows the rapid closing of the jaws, combined with the tearing and swallowing of small pieces of prey or even entire prey (Wilga *et al.* 2001).

Most species of sharks and stingrays are feeders that use suction and can separate and remove material through the manipulation in the oral cavity and reingestion of the food, although stingrays possess more precise control of the lower jaw due to the large number of muscular insertions (Dean *et al.* 2005).

Functional anatomy analyses carried out with *P. motoro* revealed that this species presents spiracular muscles and hypertrophied hyomandibular depressor muscles, which reinforces the use of the suction mechanism in feeding and, in this way, the consumption of benthic invertebrates (Pantano-Neto & Souza 2002). When *Dasyatis americana*, a marine stingray, feeds in sandy bottoms using suction, which consists in the contraction and expansion of the oropharyngeal canal, a jet of sand is frequently observed coming out of the spiracles during the sequence of movements (Aguiar 2005).

The pelvic fins in Chondrichthyes generally offer stability, and brake movements (Harder 1975). In addition, benthic species like stingrays use pelvic fins to create friction and to help stabilize themselves in the substrate (Bond 1979). Their contribution to locomotion was considered minimal (Lindsey 1978), and in males are modified with the presence of copulatory organs.

The pectoral fins are very developed and promote propulsion and direction in swimming (Compagno 1990, Rosenberg & Westneat 1999) and are therefore considered the main structures responsible for locomotion (Alexander 1967, Lagler *et al.* 1977, Compagno 1990, Dorit *et al.* 1991, Breda *et al.* 2005).

The type of swimming used by these fishes is the so-called undulatory locomotion and consists of waves that are produced in the pectoral fins from the anterior part to the posterior. Even the most of the stingrays with spines (Dasyatidae) present this type of locomotion (Rosenberg & Westneat 1999).

The undulation of the pectoral fins allows smooth forward or backward movements (helping in rapid inversion in the direction), making the exploitation of structured habitats possible (e.g. vegetation or rock crevices). Location of the

environment occurs using an electro-sensory system (Lindsey 1978).

The greater relative length of the pectoral fins of *P. falkneri* (piscivorous) may indicate greater propulsion potential during rapid moviments in short distances, when high acceleration is used at the beginning of the movement (interfering directly in the capture of prey). On the other hand, *P. motoro* (considered an insectivorous species in this ecosystem; Lonardoni *et al.* 2006), presents mouth, spiracles and pectoral fins smaller in relation to *P. falkneri*. These morphological characteristics are compatible with its feeding behavior, potentially favoring the efficient consumption of prey with little evasive capacity (e.g. aquatic insects). In addition, the large variation around the mean verified in the analyses suggests greater intraspecific ecomorphological variation, which explains the questionable taxonomic fit of these individuals, with some researchers believing in the existence of a complex of *P. motoro* species, like found by Toffoli (2006) in the Amazon basin collections.

There is a tendency for competitive pressures to cause ecological segregation between species, mainly in those philogenetically related or morphologically similar. This argument has been presented as a natural alternative to the principle of competitive exclusion proposed by Georgii Gause in "The struggle for existence" (Gause 1934). Simultaneously, over evolutionary history, competition tends to stimulate selective adaptations that make possible the coexistence of a diversity of organisms in a given area, promoting specializations in narrower niches (Pianka 2000). Such specializations in the use of resources (especially food) may be expressed by the ecomorphological diversifications presented by *P. falkneri* and *P. motoro* in this study.

Ours results suggest that the significant ecomorphological differences detected between these two species probably allows distinct functional performances of the morphological structures, indicating differential use of resources. The coexistence between these two species in the Paraná river reinforces the thesis that phylogenetically close species can exploit the natural resources in simpatry, because of the differentiated exploitation of the food resources in the environment.

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