

# Community ecology of the metazoan parasites of red porgy, *Pagrus pagrus* (L., 1758) (Osteichthyes, Sparidae), from the coastal zone, state of Rio de Janeiro, Brazil

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**ABSTRACT.** Ninety specimens of red porgy, *Pagrus pagrus* (Linnaeus, 1758) (Osteichthyes: Sparidae) collected from the coastal zone of the State of Rio de Janeiro, Brazil (21–23° S, 41–45°W), from October 1998 to March 2000, were necropsied for parasite studying. All fish were parasitized by metazoan. Twenty-two species of parasites were collected. The nematodes were 59% of the total parasitic specimens number. *Contraeacum* sp. larvae were the dominant species with highest prevalence and abundance. Abundance and prevalence of cymothoid isopod were positively correlated with host total length, while the prevalence of *Parahemiurus merus* (Linton) and *Polymorphus* sp. were negatively correlated with host total length. The host gender did not influence any parasite species prevalence or abundance. The mean diversity in the *P. pagrus* infracommunities was  $H=0.306\pm0.119$ , with no correlation with the host's total length and no significant difference between male and female fish. Three pairs of species shared a significant positive covariation, and two pairs shared significant positive association between their abundances and prevalences, respectively. Negative parasite species association or covariation were not found. Qualitative similarity was observed between the ectoparasite infracommunities of *P. pagrus*, at the genus level, with other sparid fishes of the world.

**Key words:** parasite ecology, community structure, marine fish, Sparidae, *Pagrus pagrus*, Brazil.

**RESUMO.** Ecologia da comunidade de metazoários parasitos do pargo, *Pagrus pagrus* (L., 1758) (Osteichthyes, Sparidae) do litoral do Estado do Rio de Janeiro, Brasil. Foram examinados 90 espécimes de *Pagrus pagrus* (Linnaeus, 1758) (Osteichthyes, Sparidae), provenientes do litoral do estado do Rio de Janeiro, Brasil (21–23° S, 41–45°W), no período de outubro de 1998 a março de 2000, sendo necropsiados para estudo da comunidade de metazoários parasitos. Todos os peixes examinados estavam parasitados. Vinte e duas espécies de parasitos foram coletadas. Os nematóides corresponderam a 59% do total de espécimes de parasitos coletados. *Contraeacum* sp. foi a espécie dominante, com os maiores índices de prevalência e abundância parasitária. A abundância e a prevalência do isópode cimothoídeo apresentou correlação positiva com o comprimento total do hospedeiro, enquanto a prevalência de *Parahemiurus merus* (Linton) e *Polymorphus* sp. apresentaram correlação negativa. O sexo do hospedeiro não influenciou na prevalência e abundância das espécies de parasitos. A diversidade média das infracommunidades de *P. pagrus* foi  $H=0,306\pm0,119$  e não apresentou correlação com o sexo e o comprimento total do hospedeiro. Três pares de espécies apresentaram covarição positiva significativa e dois pares de espécies apresentaram associação positiva significativa entre suas abundâncias e prevalências, respectivamente. Associações e covariações negativas não foram observadas. No presente trabalho foi observada similaridade qualitativa das infracommunidades de ectoparasitos de *P. pagrus*, a nível de gênero, com outros peixes esparídeos.

**Palavras-chave:** ecologia parasitária, estrutura da comunidade, peixes marinhos, Sparidae, *Pagrus pagrus*, Brasil.

## Introduction

The red porgy *Pagrus pagrus* (Linnaeus, 1758) is a benthopelagic sparid fish with widely known

distribution, including Eastern and Western Atlantic Ocean, Mediterranean Sea and northward of the British Isles (Manooch and Hassler, 1978; Menezes and Figueiredo, 1980). This fish migrates to

southern Brazil in winter, together with cold water on the mid-shelf. *Pagrus pagrus* feeds on a wide variety of benthic and demersal fish and invertebrates (Haimovici *et al.*, 1994). The red porgy is very common in the southern Brazilian coastal zone and has a significant commercial importance.

Taxonomic papers about the parasites of *P. pagrus* from Brazil were published by Vicente *et al.* (1985), Barros (1994), São Clemente *et al.* (1994) on anisakid nematodes; Fabio (1998, 1999) and Paraguassú *et al.* (2002) on monogeneans. Another record of digenetic parasites of *P. pagrus* was made by Schulze (1970), from Argentina. Ecological aspects of infection by anisakid larvae were studied by Paraguassú *et al.* (2000) and the pathology caused by these nematodes in *P. pagrus* was described by Rego *et al.* (1985), and Eiras and Rego (1987).

In this report, we analyzed the metazoan parasite community of *P. pagrus* from the coastal zone of the state of Rio de Janeiro, at component and infracommunity levels, and compared our results with those on the parasite communities of other marine sparid fishes.

## Material and methods

From October 1998 to March 2000, 90 specimens of *Pagrus pagrus* were examined. Local fishermen collected fish from coastal zone of Rio de Janeiro (21-23°S, 41-45°W), Brazil. Fishes were identified according to Menezes and Figueiredo (1980) and showed 16-50 cm (mean=29.5±7.2 cm) total length. The average total length for male (30±7.8 cm, n=44) and female (29±6.5 cm, n=46) fishes in the sample were not significantly different ( $t= 0.698$ ,  $P= 0.486$ ). The analysis included only parasite species with prevalence higher than 10% (Bush *et al.*, 1990). The quotient between variance and mean of parasite abundance (dispersion index) was used to determine distribution patterns. Significance of the dispersion index values were tested with  $d$  statistic (Ludwig and Reynolds, 1988). The dominance frequency and the relative dominance (specimens number from one species/total specimens number of all species in the infracommunity) of each parasite species were calculated according to Rohde *et al.* (1995). Spearman's rank correlation coefficient  $rs$  was calculated to determine possible correlations between total host length and parasites abundance. Pearson's correlation coefficient  $r$  was used as an indication of the relationship between the host's total length and the prevalence of parasites, with previous arcsine transformation of the prevalence

data (Zar, 1996) and host samples partitioning into five 7 cm (total length) intervals. The effect of host gender on parasites abundance and prevalence was tested using the  $Zc$  normal approximation to the Mann-Whitney test and the chi-square test, respectively. Parasite species diversity was calculated using the Brillouin index ( $H$ ), because each fish analyzed corresponded to a fully censused community (Zar, 1996). The probable diversity variation related to host gender (Mann-Whitney test) and host total length (Spearman's rank correlation coefficient) was tested., The evenness (Brillouin-based evenness index) was calculated for each infracommunity. The possible interspecific association between concurrent species was determined using the chi-square test. Possible covariation among the abundance of concurrent species was analyzed using the Spearman rank correlation coefficient. Ecological terminology follows Bush *et al.* (1997). Statistical significance level was evaluated at  $P \leq 0.05$ .

Helminths voucher specimens were deposited in the Coleção Helmintológica do Instituto Oswaldo Cruz (Chioc), RJ, Brazil; copepods were deposited in the Coleção de Crustacea do Museu Nacional (MNRJ), Quinta da Boa Vista, Rio de Janeiro, state of Rio de Janeiro, Brazil.

## Results

**Component community** - Twenty-two species of metazoan parasites were collected (Table 1). Nematodes were the most abundant with four species and they accounted for 59% of the total parasites collected. *Contracaecum* sp. was the dominant species, with 1075 specimens collected (56.5% of all parasites); and showed the highest values of mean relative dominance and dominance frequency (Table 2). The *P. pagrus* parasites had the typical overdispersed distribution pattern observed in many parasite systems. *Contracaecum* sp. larvae showed the highest dispersion index values. The lowest dispersion index value obtained for *Polyabroides multispinosus* is originated by the low parasite prevalence values (Table 3). Cymothoid isopod abundance and prevalence were positively correlated with host total length, while the prevalence of *Parahemiurus merus* (Linton) and *Polymorphus* sp. were negatively correlated with host total length (Table 4). The host gender did not influence parasite prevalence or abundance of any species.

**Table 1.** Prevalence, intensity, mean intensity, mean abundance, and site infection of *Pagrus pagrus* metazoan parasites, from the state of Rio de Janeiro coastal zone, Brazil

Parasites	Prevalence (%)	Intensity	Mean intensity	Mean abundance	Site of infection
Digenea					
<i>Lecithochirium</i> sp. (CHIOC 34.523)	5.5	1-6	2.8 ± 2.2	0.1 ± 0.8	Stomach
<i>Parahemiuirus merus</i> (CHIOC 34.524)	34.4	1-29	4.5 ± 6	1.5 ± 4.1	Intestine
Monogenea					
<i>Anoplodiscus longivaginatus</i> (CHIOC 34906a-d)	16.6	1-5	2.3 ± 1.1	0.4 ± 0.9	Gills
<i>Benedenia</i> sp. (CHIOC 34.529)	2.2	1-4	2.5 ± 2.1	0.05 ± 0.4	Gills
<i>Echinopelma brasiliensis</i> (CHIOC 34.530)	18.8	1-5	1.3 ± 1	0.2 ± 0.7	Gills
<i>Encyrtolabre spari</i> (CHIOC 34.531)	57.7	1-23	4.3 ± 4.3	2.4 ± 3.9	Gills
<i>Lamellodiscus</i> sp. (CHIOC 34.532)	12.2	1-14	3 ± 3.8	0.3 ± 1.6	Gills
<i>Polyabroides multispinosus</i> (CHIOC 34.533)	10.1	1-2	1.1 ± 0.3	0.1 ± 0.3	Gills
Cestoidea					
<i>Scolex pleuronectis</i> (CHIOC 34.525)	5.5	1-6	2.6 ± 2.3	0.1 ± 0.8	Mesenteries
Acanthocephala					
<i>Corynosoma</i> sp. (cystacanth) (CHIOC 34.526)	4.4	1-15	8 ± 5.9	0.3 ± 1.9	Mesenteries
<i>Polymorphus</i> sp. (cystacanth) (CHIOC 34.527)	10	1-3	1.3 ± 0.7	0.1 ± 0.4	Mesenteries
Nematoda					
<i>Anisakis</i> sp. (larval) (CHIOC 34.436)	7.7	1-7	2.9 ± 1.9	0.2 ± 0.9	Mesenteries and liver
<i>Contraaceum</i> sp. (larval) (CHIOC 34.437)	93.3	1-100	12.8 ± 14	11.9 ± 14	Mesenteries and liver
<i>Pseudoterranova</i> sp. (larval) (CHIOC 34.438)	6.6	1-5	2.5 ± 1.5	0.1 ± 0.7	Mesenteries
<i>Raphidascaris</i> sp. (larval) (CHIOC 34.439)	8.8	1-3	1.6 ± 0.7	0.1 ± 0.5	Mesenteries and liver
Copepoda					
<i>Caligus haemulonis</i> (MNRJ 15.331)	1.1	-	1	<0.01	Gills
<i>Caligus sepetibensis</i> (MNRJ 15.332)	1.1	-	1	<0.01	Gills
<i>Clavellotis dilatata</i> (MNRJ 15.333)	1.1	-	2	<0.01	Gill rakers
<i>Ergasilus</i> sp. (MNRJ 15.334)	2.2	1-3	2 ± 1.4	0.04 ± 0.3	Gills
<i>Lernanthropus caudatus</i> (MNRJ 14.014)	21.1	1-7	2.5 ± 1.9	0.5 ± 1.3	Gills
<i>Lernocera</i> sp. (MNRJ 15.335)	1.1	-	1	<0.01	Gills
Isopoda					
Cymothoid not identified (MNRJ 15.336)	28.8	1-31	6.9 ± 7.9	1.9 ± 5.3	Gills

**Infracommunities** - All fishes were parasitized by at least one parasite species. A total of 1,902 individual parasites was collected, with a mean abundance of  $21.1 \pm 17.4$ . The value of the dispersion index for the total individual parasites was 14.364. Relationships between the total parasite abundance and the total body length ( $r_s = 0.235, P = 0.025$ ) of fish were observed. The mean parasite species richness,  $3.5 \pm 1.2$  (1-8), was not correlated with total body length ( $r_s = 0.102, P = 0.335$ ) and sex ( $Z_c = -0.217, P = 0.827$ ) of fishes. One

host (1.1%) showed infection with one parasite species and 19 (21.2%), 25 (27.7%), 30 (33.4%), 9 (10%), 4 (4.4%), 1 (1.1%) and 1 (1.1%) had multiple infections with 2, 3, 4, 5, 6, 7, and 8 parasite species respectively. The mean parasite species diversity ( $H$ ) was  $0.306 \pm 0.119$  and the maximum diversity value was 0.644. Parasite diversity was not correlated to host total length ( $r_s = 0.120; P = 0.260$ ) and no significant differences ( $t = 0.873, P = 0.384$ ) in parasite diversity were observed between male ( $H = 0.318 \pm 0.110$ ) and female ( $H =$

$0.295 \pm 0.873$ ). Parasite infracommunities were separated into two groups - ectoparasites (monogeneans and copepods) and larval stages (acanthocephalans and nematodes) to determine possible interspecific associations. Adult endoparasites (digeneans) were not included in this analysis because only one species (*P. merus*) showed prevalence higher than 10%. Among the ectoparasites, three species pairs shared significant positive covariation and two species pairs shared significant positive association (Table 5). The infracommunities of larval stages did not show significant association and covariation.

**Table 2.** Dominance and mean relative dominance frequency of *Pagrus pagrus* metazoan parasites, from the state of Rio de Janeiro coastal zone, Brazil

Parasites	Frequency of dominance	Frequency of dominance shared with one or more species	Mean relative dominance
<i>Parahemiuirus merus</i>	4	3	$0.082 \pm 0.163$
<i>Anoplodiscus longivaginatus</i>	0	1	$0.024 \pm 0.077$
<i>Echinopelma brasiliensis</i>	0	0	$0.018 \pm 0.057$
<i>Encyophylabe spari</i>	9	5	$0.144 \pm 0.178$
<i>Lamellodiscus</i> sp.	1	0	$0.021 \pm 0.088$
<i>Polyabroides multispinosus</i>	0	0	$0.017 \pm 0.107$
<i>Polymorphus</i> sp.	0	1	$0.010 \pm 0.042$
<i>Contracaecum</i> sp.	59	7	$0.539 \pm 0.318$
<i>Lernanthropus caudatus</i>	1	0	$0.026 \pm 0.064$
Cymothoideo no identified	6	1	$0.074 \pm 0.168$

**Table 3.** Dispersion index (DI) and statistic *d* values of *Pagrus pagrus* metazoan parasites, from the state of Rio de Janeiro coastal zone, Brazil

Parasites	DI	<i>d</i>
<i>Parahemiuirus merus</i>	10.894	30.73*
<i>Anoplodiscus longivaginatus</i>	2.467	7.65*
<i>Echinopelma brasiliensis</i>	1.807	4.63*
<i>Encyophylabe spari</i>	6.078	19.59*
<i>Lamellodiscus</i> sp.	7.198	22.49*
<i>Polyabroides multispinosus</i>	1.101	0.69
<i>Polymorphus</i> sp.	1.550	3.31*
<i>Contracaecum</i> sp.	16.150	40.31*
<i>Lernanthropus caudatus</i>	3.349	11.12*
Cymothoideo no identified	13.767	36.20*

(\*) significant values

**Table 4.** Spearman's rank correlation coefficient (*rs*) and Pearson's correlation coefficient (*r*) values used to evaluate possible relationships among the total length of *Pagrus pagrus*, and its parasite community components abundance and prevalence, from the state of Rio de Janeiro coastal zone, Brazil

Parasites	<i>rs</i>	<i>P</i>	<i>r</i>	<i>P</i>
<i>Parahemiuirus merus</i>	-0.051	0.633	-0.899*	0.038
<i>Anoplodiscus longivaginatus</i>	-0.121	0.258	-0.579	0.306
<i>Echinopelma brasiliensis</i>	-0.105	0.321	-0.592	0.292
<i>Encyophylabe spari</i>	-0.062	0.561	-0.877	0.051
<i>Lamellodiscus</i> sp.	-0.005	0.962	-0.389	0.517
<i>Polyabroides multispinosus</i>	0.122	0.251	0.301	0.623
<i>Polymorphus</i> sp.	0.041	0.703	-0.895*	0.040
<i>Contracaecum</i> sp.	0.093	0.379	0.149	0.811
<i>Lernanthropus caudatus</i>	0.120	0.257	0.269	0.661
Cymothoideo no identified	0.431*	<0.001	0.903*	0.035

(\*) significant values; *P* = significance level

**Table 5.** *Pagrus pagrus* ectoparasites concurrent species pairs, from the State of Rio de Janeiro coastal zone, Brazil

Species pairs	<i>rs</i>	<i>P</i>	$\chi^2$	<i>P</i>
<i>Anoplodiscus longivaginatus</i> - <i>Echinopelma brasiliensis</i>	0.233*	0.026	5.240*	0.022
<i>A. longivaginatus</i> - <i>Encyophylabe spari</i>	-0.202	0.055	2.330	0.127
<i>A. longivaginatus</i> - <i>Lamellodiscus</i> sp.	0.191	0.070	3.501	0.061
<i>A. longivaginatus</i> - <i>Polyabroides multispinosus</i>	0.137	0.196	2.013	0.157
<i>A. longivaginatus</i> - <i>Lernanthropus caudatus</i>	0.002	0.981	0.050	0.921
<i>A. longivaginatus</i> - Cymothoid not identified	-0.096	0.364	0.690	0.405
<i>E. brasiliensis</i> - <i>E. spari</i>	-0.126	0.235	0.201	0.654
<i>E. brasiliensis</i> - <i>Lamellodiscus</i> sp.	0.277*	0.008	5.770*	0.016
<i>E. brasiliensis</i> - <i>P. multispinosus</i>	0.029	0.785	0.070	0.788
<i>E. brasiliensis</i> - <i>L. caudatus</i>	0.022	0.832	0.020	0.885
<i>E. brasiliensis</i> - Cymothoid not identified	0.048	0.649	0.420	0.518
<i>Encyophylabe spari</i> - <i>Lamellodiscus</i> sp.	-0.065	0.542	0.780	0.377
<i>E. spari</i> - <i>P. multispinosus</i>	-0.041	0.698	0.220	0.641
<i>E. spari</i> - <i>L. caudatus</i>	0.239*	0.022	1.120	0.291
<i>E. spari</i> - Cymothoid no identified	0.019	0.855	0.031	0.852
<i>Lamellodiscus</i> sp. - <i>P. multispinosus</i>	-0.124	0.244	1.391	0.238
<i>Lamellodiscus</i> sp. - <i>L. caudatus</i>	-0.130	0.220	1.250	0.263
<i>Lamellodiscus</i> sp. - Cymothoid no identified	0.079	0.455	0.340	0.559
<i>P. multispinosus</i> - <i>L. caudatus</i>	0.119	0.261	0.710	0.398
<i>P. multispinosus</i> - Cymothoid no identified	-0.147	0.164	1.540	0.215
<i>L. caudatus</i> - Cymothoid no identified	0.023	0.823	0.020	0.901

(*rs*) Spearman rank correlation coefficient; ( $\chi^2$ ) Chi-square test; (\*) significant values; *P*: significance level

## Discussion

Some composition and structure patterns were detected in the metazoan parasite community of *P. pagrus* from the Brazilian coastal zone: (1) the dominance of anisakid nematodes larval stages; (2) the correlation between parasite abundance and total body length of the hosts, at the infracommunity level; (3) absence of correlations between parasite infrapopulations size and host gender; and (4) scarcity of interspecific associations in the parasite infracommunities.

The literature regarding *P. pagrus* feeding habits is very poor. No researches are known about the diet of *P. pagrus* from Brazilian coastal zone. Manooch and Hassler (1978) and Karagitson *et al.* (1986) classified the red-porgy as a benthic, opportunistic predator, with high ability to switch feeding on the second (various invertebrates) and third trophic level (various fishes). In addition, the *P. pagrus* diet predominant item are crustaceans and fishes. This condition might be explained the dominance of nematode larval stages. High values of *Contracaecum* larvae prevalence and abundance were recently recorded by Paraguassú *et al.* (2000) in red porgy from Rio de Janeiro state coastal zone, suggesting the presence of free-living copepods, *Contracaecum* sp. intermediate host (Huiizinga, 1967), as a *P. pagrus*. diet important component.

Another characteristic of the *P. pagrus* parasite community was the presence of larval platyhelminthes, and acanthocephalans, which are generally common in marine teleost fishes (George-Nascimento, 1987). This could suggest that the *P. pagrus*.

*pagrus* diet does favor its participation as intermediate or transport host in these parasites life cycle. This situation was also recorded in the parasite infracommunities of some benthic marine fishes from Rio de Janeiro (Silva *et al.*, 2000; Alves and Luque, 2001). As mentioned by Cezar and Luque (1999), the presence or absence of these parasite larval stages will be fully explained only by additional information on the population features of the potential intermediate and definitive hosts.

Some benthic fishes of Rio de Janeiro coastal zone, whose parasite communities were studied, showed heterogeneous patterns in relation to possible positive correlation, at the infracommunity level, between parasite abundance and the host total body length (Luque *et al.*, 1996; Knoff *et al.*, 1997; Cezar and Luque, 1999; Silva *et al.*, 2000; Alves and Luque, 2001). A positive correlation between parasite abundance and host size was detected in the red porgy. As pointed out in the classic study by Polyanski (1961), quantitative and qualitative changes in parasitism are expected with the fish growth. According to Saad-Fares and Combes (1992), in the case of the digenleans this correlation might be influenced by changes in the fish diet. In addition, as mentioned by Cezar and Luque (1999), regarding ectoparasites, changes in parasitism levels with ranging host size are expected, because the infection site surface area increases with growth and this provides more space to monogeneans and copepods larvae (Fernando and Hanek, 1976). However, two *P. pagrus* parasites, *Parahemiurus merus* (Linton) and *Polymorphus* sp. showed negative correlation between parasite abundance and host body size. This situation suggests a heterogeneity of diet components or feeding behavior between *P. pagrus* diverse age classes. Better explanations for these patterns will be possible only when the parasites life cycles and their relationship with red porgy feeding patterns and population dynamics becomes known.

Absence of correlation between host gender and the prevalence and abundance of marine fishes parasite community components is common. In *P. pagrus*, the lack of such correlation might be attributed to similarity in ecological relationships (behavior, habitat, and diet) of males and females, as stated by Luque *et al.* (1996). According to Poulin (1996) the host gender influence on parasite prevalence and abundance is a topic hardly touched upon in community analysis discussions, and it is necessary to conduct experiments which show the influence of other factors, mainly the fish physiology and behavior.

Other sparid fishes were studied to determine their parasite fauna qualitative and quantitative aspects. Roubal (1981, 1990), Roubal *et al.* (1983), Byrnes (1985, 1986a, b, 1987), Byrnes and Cressey (1986); Byrnes and Rohde (1992), and Roubal and Diggles (1993) studied the ectoparasites from *Chrysophrys auratus* (Bloch and Schneider) and *Acanthopagrus australis* (Gunther) from Australia; Ogawa and Egusa (1978a, b, 1980, 1981) studied the ectoparasites from *Acanthopagrus schlegili* (Bleeker) from Japanese Sea; and Sasal *et al.* (1999) studied ecological aspects of trematodes parasitic in several sparid species from the Mediterranean Sea. The ectoparasite infracommunities of *P. pagrus* from Rio de Janeiro showed qualitative similarity to genus level with Australian and Japanese sparid species parasite fauna. This first approximation must be observed with caution, because of the high number of biogeographic factors which may have influence on marine fishes parasite communities composition (Holmes, 1990; Poulin and Rohde, 1997). However, this situation might suggest that a complex of ectoparasite species (diplectanids, microcotylids, anoplodiscids, lernanthropids, caligids) is characteristic in sparid fishes. Oliver (1982) showed the high specificity of diplectanids monogeneans on sparid fishes from Mediterranean Sea. A similar situation was observed in mugilid, sciaenids, and carangid fishes from South America by Fernandez (1987), Luque (1996), Takemoto *et al.* (1996) and Knoff *et al.* (1997). A different picture (low similarity) can be observed regarding sparids trematodes endoparasitic infracommunities, which had their compositions strongly influenced by regional differences in diet composition (Sasal *et al.*, 1999).

As stated by Rohde *et al.* (1995), most marine fish metazoan ectoparasite communities live in non-saturated, little ordered assemblages. The results obtained in the present study indicate that this hypothesis is also true for parasite infracommunities in red porgy. The pairwise associated species low number is another characteristic of *P. pagrus* parasite community. According to Rohde *et al.* (1994), although positive associations do no rule out interspecific competition occurrence, and negative associations do no confirm such competition, the associations presence makes less likely that interspecific competition may be of great significance. The interspecific association low number, and the generalist species dominance were also observed in the parasite communities of some marine fishes from Rio de Janeiro, as mentioned by Cezar and Luque (1999) and Alves and Luque

(2001), reinforcing the generalization of Rohde *et al.* (1995).

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