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Experimental analysis testing resource use competition between native and
invasive species of omnivorous fish

Rio de Janeiro

2020

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Dissertação apresentada, como requisito parcial para
obtenção do título de Mestre, ao Programa de Pós-
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do Estado do Rio de Janeiro. Área de concentração:
Ecologia de Rios e Córregos.

Orientadora: Prof.^a Dra. Eugenia Zandonà

Coorientadora: Prof.^a Dra. Rosana Mazzoni

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Jeferson Ribeiro Amaral

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Dissertação apresentada, como requisito parcial para obtenção do título de Mestre, ao Programa de Pós-Graduação em Ecologia e Evolução da Universidade do Estado do Rio de Janeiro. Área de concentração: Ecologia de Rios e Córregos.

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DEDICATÓRIA

À minha família, amigos e todos que estiveram presentes de alguma forma nesta jornada.

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As coisas são boas porque elas são únicas.

Karnal, Leandro

RESUMO

AMARAL, J. R. *Análise experimental da competição pelo uso de recursos entre espécies nativas e invasoras de peixes onívoros*. 2020. 44f. Dissertação (Mestrado em Ecologia e Evolução) – Instituto de Biologia Roberto Alcântara Gomes, Universidade do Estado do Rio de Janeiro, Rio de Janeiro, 2020.

As invasões biológicas são uma grande ameaça à biodiversidade. Suas implicações nos ecossistemas de água doce estão ligadas a mudanças na biodiversidade, problemas econômicos, degradação de ecossistemas, predação e competição com espécies nativas. As espécies exóticas da família Poeciliidae são conhecidas como excelentes invasores ao redor do mundo graças a uma variedade de características que permitem seus estabelecimentos em novos ambientes. Guppies (*Poeciliareticulata*), peixes generalistas e onívoros, tornaram-se difundidos em todo o mundo devido à sua implantação no controle de larvas de mosquitos ou como peixes ornamentais. Esses podem atingir altas densidades em habitats invadidos, mas seu impacto em espécies filogeneticamente semelhantes (por exemplo, poecilídeos nativos) ainda é desconhecido. Nosso objetivo neste estudo foi entender, a partir de experimentos de laboratório e mesocosmos, se os guppies competem por recursos tróficos com uma espécie nativa de poecilídeo (*Phallocerosharpagos*). Para comparar a eficiência no uso desses recursos, testamos as taxas de consumo e taxas de ataque de ambas as espécies em experimentos de laboratório. Experimentos de mesocosmos - longa e curta duração - mantendo as duas espécies separadas ou em conjunto foram realizados para testar a competição por recursos entre elas através de análise de conteúdo estomacal. Nossos resultados mostraram que a espécie nativa apresentou taxas de ataque semelhantes e maiores taxas de consumo quando comparadas às espécies invasoras, sugerindo, contrário ao esperado, que a espécie nativa é mais eficiente em capturar os recursos. No entanto, nos experimentos de mesocosmo, os padrões de competição não foram claros. No experimento de longo prazo, a espécie nativa consumiu menos invertebrados quando estava junto com os invasores e, no experimento de curto prazo, não houve diferenças significativas no consumo de invertebrados entre espécies nos diferentes tratamentos. A análise de variação individual na dieta mostrou uma pequena variabilidade entre as espécies, enquanto as duas espécies em ambos os tratamentos mostraram alta variabilidade individual. Com estes resultados não podemos afirmar que os guppies são competidores superiores quando co-ocorrem com as espécies nativas, nem sua alta eficiência no consumo de invertebrados como espécie invasora.

Palavras-chave: Guppies. *Phallocerosharpagos*. Espécies invasoras. Competição interespecífica. Peixes de água-doce. Livebearing.

ABSTRACT

AMARAL, J.R. Experimental analysis of resource use competition between native and invasive species of omnivorous fish. 2020. 44f. Dissertação (Mestrado em Ecologia e Evolução) – Instituto de Biologia Roberto Alcântara Gomes, Universidade do Estado do Rio de Janeiro, Rio de Janeiro, 2020.

Biological invasions are a major threat to biodiversity. Their implications in freshwater ecosystems are linked to reductions in biodiversity, economic problems, ecosystem degradation, predation and competition with native species. Invasive species of poeciliid fishes are known as good invaders due to a variety of characteristics which allow their establishment in new environments. Guppies (*Poecilia reticulata*), generalist and omnivorous fishes from Central America, became widespread around the world due to their use for mosquito control and the aquarium trade. They can sometimes reach very high densities in the invaded habitat, but their impact on phylogenetically close species (e.g. native poeciliids) is unknown. Our aim in this study is to understand, using laboratory and mesocosm experiments if guppies and a native species of poeciliid in Brazil (*Phallocerosharpagos*) compete for resources. To compare the efficiency in resource use, we tested the consumption and attack rates of both species in aquarium experiments. Mesocosms experiments - long and short duration - with species alone and together were performed to analyze the resource competition between them by gut content analysis. Our results showed that the native species had similar attack rates and higher consumption rates when compared to the invasive species. In the long-term experiment, the native species consumed fewer larvae when were together with the invasive. When we lived fishes for a shorter time in the experiment, there were no significant differences between species and treatments. The individual variation analysis shows us a small variability between species, while species in both treatments show high variability within them. With these results we cannot observe robust evidence that guppies are superior competitors for diet resources when they co-occur with native species, nor their high efficiency in the consumption of invertebrates as an invasive species.

Keywords: Guppies. *Phallocerosharpagos*. Non-native species. Interspecific competition. Freshwater fishes. Livebearing.

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LISTA DE ABREVIATURAS E SIGLAS

| | |
|----------|---------------------------------------------------|
| LMEM | Linear Mixed-EffectModel |
| ANOVA | Analysisofvariance |
| PCoA | Principal CoordinateAnalysis |
| PERMDISP | Permutational analysis of multivariate dispersion |

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INTRODUCTION

Biological invasions represent a threat to ecosystems around the globe (Lodge, 1993; Latombe et al., 2017). The growing and the undetermined dispersal of invasive species are the major factors related to changes in invaded environments with impacts on ecosystem functioning and biodiversity (Mcneely, 2001; Simberloff et al., 2013; Courchamp et al., 2017). The implications of invasive species are observed in different systems and in different ecological levels, ranging from individuals and populations to ecosystem processes (Baxter et al., 2004; Khuroo et al., 2011; Capps & Flecker, 2013; Simberloff et al., 2013; David et al., 2017).

Freshwater environments tend to be especially susceptible to invasions due to water flow and basin connections (Strayer, 2010). In these systems, the impacts of invasive organisms range from a reduction in biodiversity, to even economic consequences (Strayer & Dudgeon, 2010). Empirically, it has been shown that the strong influence of invading organisms via predation, system degradation, and competition for resources can affect the distribution of native organisms (Kloskowski, 2014; Eloranta et al., 2018; Nagelkerke et al., 2018).

In rivers and lakes, most cases of invasive species reported in the literature are represented by top predators (Lowe-McConnell, 1993; Nicholson et al., 2015) or organisms that are generalists (van Kessel et al., 2016; Nagelkerke et al., 2018). The impacts generated by invasive top predators can cause total extirpation or a reduction in the abundance of populations of native prey (Eby et al., 2006; Weyl et al., 2016). Generalist organisms, usually omnivorous, opportunistically use and exploit different resources, being able to modify their diets according to new environmental conditions (Romanuk et al., 2009; de Carvalho et al., 2019a). Also, high degrees of trophic plasticity increase their potential for invasion, facilitating their establishment in new systems where different resources are present (Cathcart et al., 2019).

Invasive species can directly affect native species resource acquisition by interference competition via aggressive encounters (Hart & Marshall, 2012; Jorgensen & Fath, 2014; David et al., 2017; Britton et al., 2018; Culbertson & Herrmann, 2019) or even indirectly through their

shared use of a limited resource depleting resources available for the native species by exploitative competition (Eriksson, 1979; Petren & Case, 1996, 1998; Bøhn et al., 2008; Fletcher et al., 2019). When invasive and native species have similar trophic niches, competition for resources is usually asymmetric (one species outcompeting other creating negative impacts in its fitness; Culbertson & Herrmann, 2019) with invasive species often being the superior competitors (Gozlan et al., 2010; Alexander et al., 2014). As a result of competition, native species can undergo niche shift, its fitness can be negatively impacted by a reduction in their food consumption or they can even suffer competitive exclusion (Elton, 1958; Hardin, 1960; Gause, 1971; Tilman, 1982; Underwood, 1997; Bøhn et al., 2008; Tran et al., 2015; Britton et al., 2018).

In order to minimize competition effects, individuals present differences in functional traits related to the use of available resources, following the resource partitioning theory which assumes that the niche overlap can be mitigated by different uses in available resources (Schoener, 1974; Barros et al., 2017). Here we consider functional trait as any feature measurable at the individual level which causes indirectly effects on its fitness components in an environmental context (Violle et al., 2007). Phylogenetically close species often present similar ecological niches and these organisms tend to be overdispersed in natural communities due to mechanisms such as interspecific competition (Violle et al., 2011). Also, the niche of a species can be expanded if its individuals often present generalist habits by increasing within-individual niche variation or even if individuals of populations diverge in their diet by increasing between-individual variation (Costa-Pereira et al., 2019). The intra and interspecific variability then allow species populations to avoid their similarities in the niche (Jung et al., 2010) and phenotypic plasticity could reduce competition, especially when organisms are generalists in their diets (Begon & Wall, 1987; Gibert & DeLong, 2015).

Worldwide fishes from the Poeciliidae family are invading new ecosystems and characteristics such as eco-physiological tolerance to new environmental conditions (as low oxygen levels, salinity, especially anthropogenically-modified habitats), high fecundity, high growth rates, and opportunistic diets increase their chances of successful establishment (Deacon & Magurran, 2016; Troendle, 2016; Magalhães & Jacobi, 2017). For example, dietary analyses and functional response experiments with fish from the genus *Gambusia* showed that, where they are invasive, they have a high impact on native species (even species of the same

genus) by reducing their growth rates through competition for resource or space (Clem & Whitaker, 1995; Thompson et al., 2012; Mofu et al., 2019; Schopt Rehage et al., 2019). Another common poeciliid invader is the guppy (*Poecilia reticulata*, Peters 1859).

Guppies are native from the northeast tip of South America (Magurran, 2005) but have been introduced to all continents, except Antarctica (Greg Sherley, 2000). They are commercialized in the aquarium trade and used in many countries as a biocontrol of mosquito larvae, especially in tropical and subtropical areas (Deacon et al., 2011). Guppies present a subset of characteristics that allow their invasion and establishment in new systems (Deacon & Magurran, 2016). They are an omnivorous species that eats small insects, algae, and detritus (Zandonà et al., 2011, 2015), and tolerate to live in environments with low oxygen levels (Poulin et al., 1987). As all viviparous fish, it develops its offspring inside the body (Pollux et al., 2009) and a single female is capable to save sperm and re-establish a new population in a new system (Winge, 1937; Deacon et al., 2011; López-Sepulcre et al., 2013).

Studies show that guppies can impact ecologically similar species in their native and non-native environment. In Trinidad, where guppies are native, they act as both competitors and predators of Trinidadian killifishes (*Anablepsoides hartii*), as they feed on similar food sources and consume killifish juveniles, positively affecting their growth rates through an indirect effect on their densities (Walsh et al., 2011). In invaded environments, guppies often show explosive growth, as shown in Hawaii, where guppies were introduced to control mosquito larvae and they became much more abundant than native fish species (Holitzki et al., 2013). As a consequence, guppies are affecting ecosystem processes such as nutrient cycling by increasing levels of nitrogen and carbon. Their high abundance is correlated with increases in benthic biofilm, decreases on densities of aquatic invertebrates, and native species abundance by resource competition. Guppies also act as predators of Trinidadian killifishes juveniles during their migration from the ocean (Holitzki et al., 2013).

However, the effect of guppies to co-occurring fish species is unclear. In Brazilian streams, guppies show high abundance in impacted streams but it is still unknown if guppies are better competitors or if guppies simply thrive better in impacted streams, where other species cannot (Casatti et al., 2009). Thus, it becomes important to understand which is the mechanism that allows guppies to be successful invaders and if they are indeed detrimental to other species.

Guppies are considered excellent invaders around the world and we can assume that they have traits that improve and promote their establishment in new places (El-Sabaawi et al., 2016; Marques et al., 2019). Invasive guppies often coexist with other species (e.g. other poeciliids) that have very similar ecological requirements (Mazzoni & Lobón-Cerviá, 2008; Gorini-Pacheco et al., 2018), thus potentially leading to competitive interactions. However, it is not clear how widespread this phenomenon is and which is the mechanism behind this effect. Questions that arise are: are guppies competing with phylogenetically and ecologically similar native species? Are they better consumers of high-quality resources? Do they have a detrimental effect on native species' acquisition of resources?

Our aim in this study is to understand, using laboratory tests and mesocosm experiments, if invasive species, negatively affect the resource use of native species by competing with them for food. We used a widespread invasive species, the Trinidadian guppy, and common native species, *Phallocerosharpagos* (Lucinda, 2008), which co-occur with guppies in streams in the Rio de Janeiro state, Brazil. These two species occupy a very similar niche, especially having a very similar diet (Neves et al., 2015; Teresa et al., 2015). We performed laboratory experiments to test the efficiency of the two species in catching invertebrates. We hypothesize that guppies, being successful invaders (Deacon & Magurran, 2016), are better competitors and will thus show higher consumption and attack rates. We also ran mesocosm experiments to evaluate resource use when species were alone and when they co-occur. In mesocosm experiments, we analyzed their gut contents, ambient macroinvertebrate abundance and intraspecific variability. We then expect them to negatively affect resource use/consumption of the native species reducing the native species trophic niche. We also hypothesize a high overlap in dietary between both species due to their similarities in trophic resource use when they are together. Still in this treatment, as we are predicting that the invasive species are superior competitor, we expected a high intraspecific variability within the native species due to competition between species, and also a low intraspecific variability within the invasive species due to their faster and higher consumption of better resources such as macroinvertebrates.

1 MATERIAL AND METHODS

Individuals of *P. harpagos* were collected in the Tijuca stream located in the Tijuca National Forest (22° 57' 23.9" S 43° 16 '48.9" W) and guppies in the Carioca stream (22° 56' 21.46" S 43° 12' 04.97" W). All individuals were kept for three weeks in the lab upon collection before starting the experimental trials.

1.1 Ethics

This study was conducted in strict accordance with the recommendations of the Ethics Committee of the State University of Rio de Janeiro (CEUA / 012/2013). All sampling processes complied with current Brazilian laws and IBAMA SISBIO authorized the fish capturing through special license 1916854 (issued to RM) and 31170 (issued to EZ).

1.2 Consumption rate experiment

We performed experiments in fish tanks to measure consumption rates of guppies and *P. harpagos*. Feeding trials were performed with 12 females for each species in 17 L tanks. As prey, we used frozen Chironomidae larvae. These macroinvertebrate taxa were chosen due their common presence in fish guts and due to its easy commercialization in pet shops as frozen fish food. To ensure larvae size was similar to those naturally consumed by guppies in the wild, we separated larvae equal or smaller than 0.5mm using a fine mesh (must have a reference about the size of chironomids consumed by guppies). Fish were starved for 24 hours before the experiments. After that, we placed 20 larvae in the fish tank through a 15 cm long plastic tube with the aid of a pipette filled with 3 mL of water. We released the larvae in the

middle of the water column to homogeneously distribute them inside the aquarium where the focal fish was kept alone.

The experimental trials lasted 10 minutes each and were recorded with a digital camera (Nikon d800). The consumption rate was calculated as the number of larvae consumed per 10 min of trials (Palkovacs et al., 2011). The attack rate was the number of all attacks (successful and unsuccessful) per 10 min of trials. We run two *t*-tests to evaluate the differences in consumption rates and attack rates between the two species.

1.3 Mesocosm experiments

We performed mesocosm experiments, to analyze resource use of the two species in treatments with just conspecifics or together with the other species. Our mesocosms were water storage containers filled with 7L of water. We used 500g of river gravel, bought in a pet shop, with particle sizes between 1cm - 10cm, to allow better colonization of invertebrates and algae (Warbanski et al., 2017) (Fig. 1A). All mesocosms were allocated in a 10 m² area covered with a greenhouse mesh to reduce the light incidence, thus temperature. The mesocosms were located on the campus of the State University of Rio de Janeiro, Rio de Janeiro, Brazil (Fig. 1B).

Prior to the experiment, aquatic insects were allowed to colonize the water storage containers for 45 days before fish introduction. After that, fish were acclimated to the water temperature and released into the water storage containers. As treatments, we had mesocosms with four individuals of each species alone (*P. harpagos* alone and guppies alone), the two species together with two individuals from each species (*P. harpagos* together and guppies together), and mesocosms without fish as our control. We covered the water storage containers with nets (with a 10mm mesh) to prevent fish from jump out.

We adjusted the duration of the experiments to 24h (long-term experiment) and 3h (short-term experiment) based on pilot trials: when we ran the mesocosm experiment for 4 days, the fish did not have any invertebrates in their guts, which is unusual as invertebrates represent a preferred diet item for both species (Dussault & Kramer, 1981; Zandonà et al.,

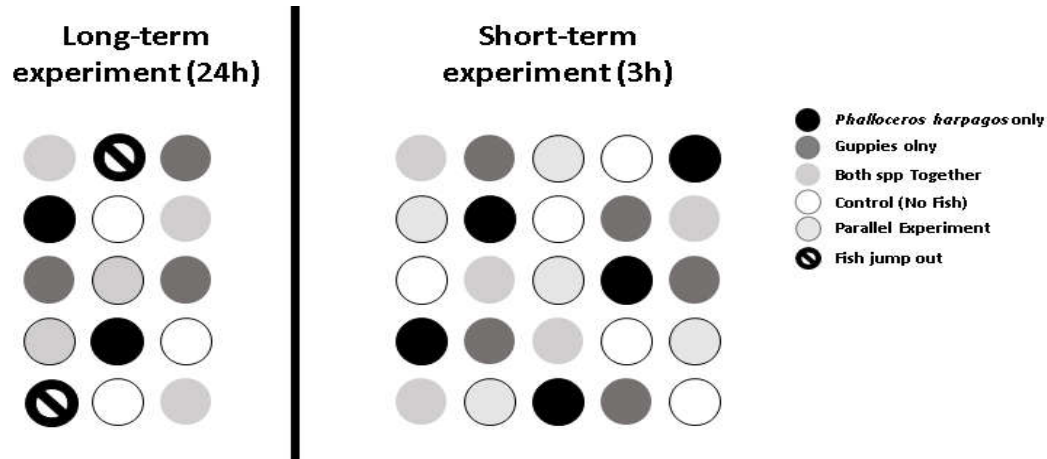
2011, 2015, 2017; Teresa et al., 2015; de Carvalho et al., 2019b). Considering that invertebrates are a very nutritious food item (Zandonà et al., 2011) for which the two species could be competing for, we adjusted the time of the experiment to make sure that the fish did not deplete all invertebrates available in the mesocosms and that we could find them in their guts prior to its full digestion. We thus ran 2 separate mesocosm experiments with different durations: the first with 24h of duration (long-term experiment), we had 3 replicates for each treatment (12 containers in total; Fig.2A); the second we decreased the time of the experiment to 3h (short-term experiment) and we increased the number of replicates (5 for each treatment; Fig.2B). On the long-term experiment, fish from one mesocosm were lost (“*Phallocerosharpagos* only” treatment) as they jump out of water.

Figure 1(A) - The experiment filled with water and substrate and (B) the structure prepared for mesocosms allocation during the experiment



At the end of the experiment, we euthanized all the fish with an overdose of MS-222 and fixed them in formaldehyde for subsequent analysis. For each individual the total weight and standard length were measured. After that, the guts were removed for stomach content analysis. Only the first third of the guts were analyzed. In this portion, that included the stomach and a small part of the intestine, diet items are not completely digested. The content was analyzed onto a gridded slide that had 64 quadrants (2mm each; Zandonà et al., 2011).

Figure 2 - Mesocosms' scheme for long-term and short-term experiments.



Legenda: Black circles represent the water storage containers with the native species alone treatments, dark grey the invasive alone treatments, light grey both species together. White circles outlined in black represent the control treatments, and the light grey outlined black were water storage containers used in parallel experiments. Circles with dash represent lost mesocosm due to fish escape (one from *P. harpagos* only and another one from Parallel experiment). All mesocosms were randomly distributed to avoid bias on invertebrate colonization

The proportion of invertebrates was estimated for the entire slide. Invertebrates' taxa were identified to the lowest taxonomic level, generally the Family (Mugnai et al., 2010). We also estimated the proportion occupied by detritus and filamentous algae inside ten randomly chosen quadrants, while diatoms were counted. As it is difficult to estimate the area occupied by diatoms due to their small size, the diatoms were separated into size classes of known average size, so that we could estimate the area they occupied in each quadrat. We did not use the volumetric methodology for gut content analysis in this study because fish guts were too small to calculate the volume of each consumed item and because the volumetric analysis is not suitable for detritus and algae. Our methodology was the same used in Zandonà et al. (2011).

To test the differences in diet between the two species and treatments, we performed a Linear Mixed Effect model (LMEM) for each food item using their abundances (expressed in the area of the microscope slide) as our dependent variables, treatments and species as fixed

factors and mesocosms as a random factor. We analyzed data using R software (Core & Team, 2014) and the R *lme4* package (Bates et al., 2015) to perform LMEM we used.

1.3.1 Macroinvertebrate abundance

After removing all fish from the mesocosms, water and substrate of each of them were filtered through a Surber sampler (with a 250 μ mesh) and samples were processed to identify macroinvertebrates and estimate their abundance. Only the macroinvertebrates that are reported in the literature as being potential food items (Chironomidae, Culicidae and Odonata larvae; Zandonà et al., 2011) were considered in the analyses. We used an ANOVA to compare the abundance of invertebrates in the mesocosms (dependent variables) between treatments where species were alone, together and the control treatments (independent variable). This analysis was performed only for the short-term experiment, as we did not estimate ambient invertebrates' abundance in the long-term experiment. The analysis was conducted in R (Core & Team, 2014) and boxplots were produced using the package *ggplot2* (Schrepp, 2010).

1.3.2 Intra and Interspecific variability analysis

To access the Intra and Interspecific variability in diet between and within species populations, we calculated the variability as the average distance-to-centroid (represented by the average values of objects in a particular cluster), measured as the average distance from an individual to the centroid of each species. We perform these tests separately for treatments where species were alone and together in the short-term experiment.

To measure distance-to-centroids, we performed a dissimilarity matrix using Bray–Curtis dissimilarity index with proportions of diatoms, filamentous algae, Culicidae, Chironomidae and Odonata larvae. Detritus was not included in this analysis. Then, a

multivariate homogeneity test PERMDISP (Permutational Analysis of Multivariate Dispersion) was performed with the data matrix as our response variable and grouped by "alone" and "together" treatments to observe data dispersion in relation to the centroid.

The differences in intraspecific diet variability between species in each treatment were tested with an analysis of variance (ANOVA) using the average distances to centroid from each species (obtained from PERMDISP analysis) as our dependent variable and species as our independent factor. Also, based on the decomposition of the mean sum of squares we calculated the percentage of variability between and within species (Manna et al., 2019). We used the 'betadisper' function in the R vegan package (Oksanen et al., 2007) for the test of homogeneity of dispersion from the group centroids into PERMDISP. We use Principal Coordinate Analysis (PCoA) as an analysis of agroupment to reduce diet data multidimensionality and give us plots with the distribution of individuals of both species in two dimensions.

2 RESULTS

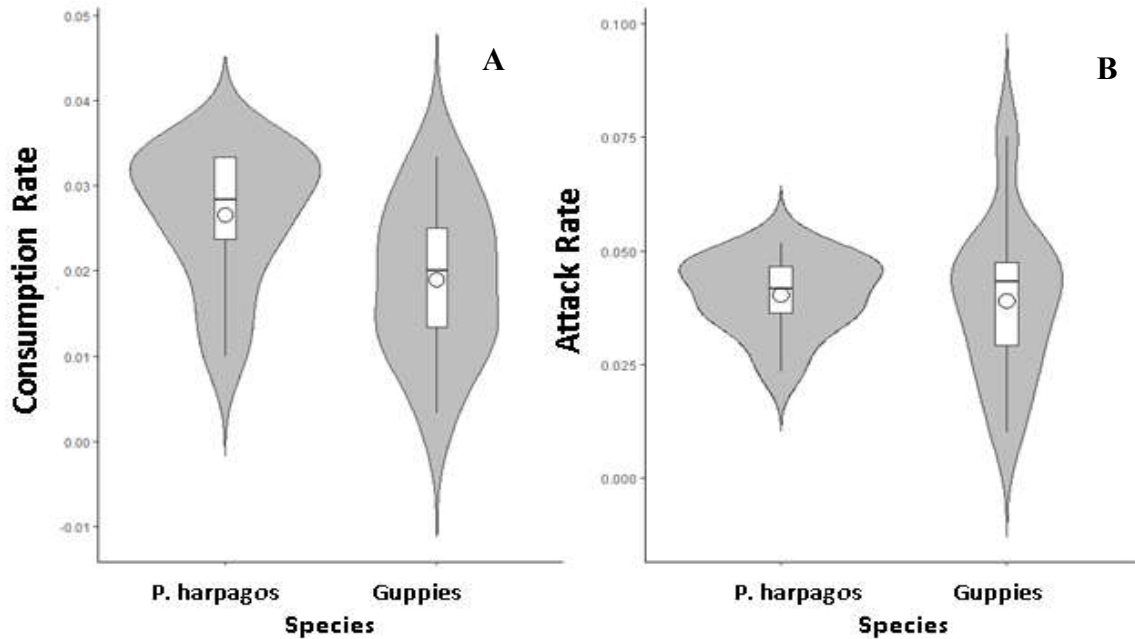
2.1 Consumption rate experiments

The consumption and attack rates show contradictory results. There were significantly different in consumption rates (t -test, $t = 2.11$, $p < 0.05$), with *P. harpagos* presenting a higher consumption rate than guppies (Fig.3A). On the other hand, analysis of the attack rate showed no significant difference between species (t -test, $t = 0.22$, $p < 0.82$) (Fig.3B).

2.2 Mesocosm experiments

In both mesocosm experiments (long-term and short-term experiments), we found macroinvertebrates in the guts of the two species. In the long-term experiment, we only recorded Chironomidae and Culicidae larvae in the guts of both species. The interaction between species and treatments had a significant effect ($F_{(1,19)} = 4.86$, $p < 0.05$) in the quantity of invertebrates in the fish guts. In this case, in treatments where the two species were alone, *P. harpagos* feed more on invertebrates (comprehended by the total area occupied by all macroinvertebrates taxa) than guppies but, in the treatment with the two species together, the opposite happened and the guppies have a higher consumption of invertebrates (Fig.4A).

Figure 3 - Box plot showing the consumption rate (A) and the attack Rate (B) for both species.



Legenda: Circles represent mean values. Error bars represent standard deviation. The width of the shaded area from the violin plot shows the distribution of the data

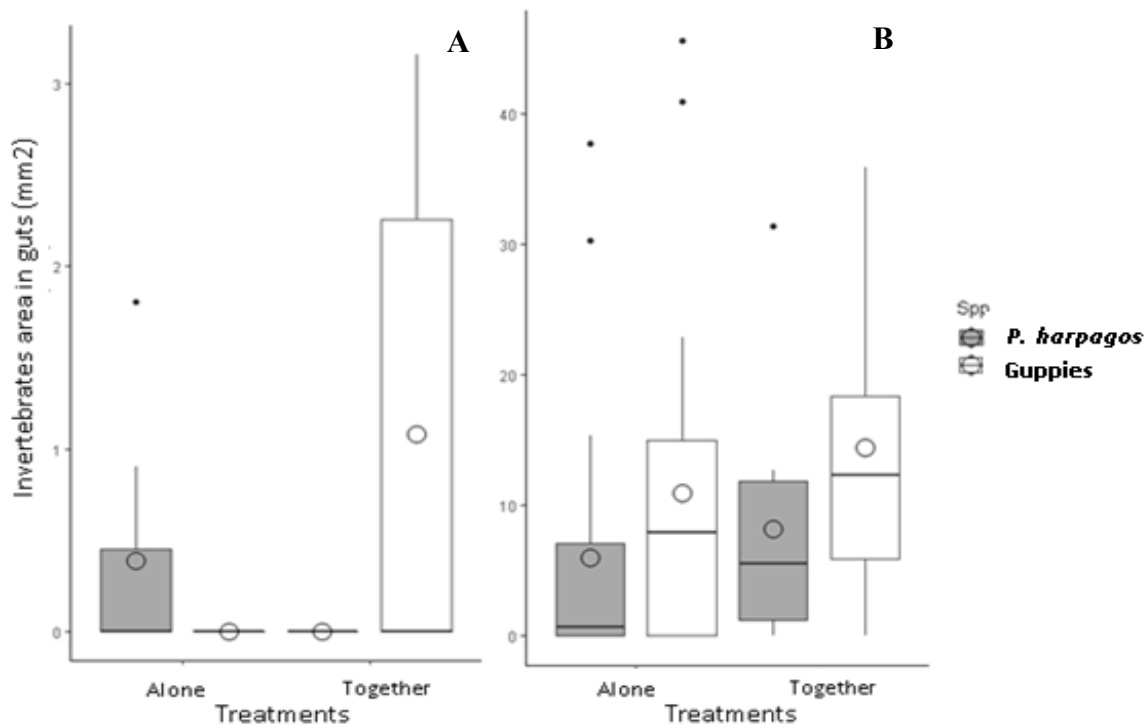
However, in the short-term experiment, there was no significant difference in the amount of invertebrates in the guts of the two species ($F_{(1, 53.54)} = 0.45, p = 0.5$), nor between treatments ($F_{(1, 12.98)} = 0.95, p = 0.34$), nor of the interaction between species and treatments ($F_{(1, 15.16)} = 0.05, p = 0.81$) (Fig.4B). We recorded larvae of Chironomidae, Culicidae and Odonata in guts for both species. In long and short-term mesocosm experiments we found a significant difference between species for diatoms consumption (long-term experiment $F_{(1, 17.93)} = 6.71, p < 0.05$, Fig.5A; short-term experiment $F_{(1, 51.33)} = 13.59, p < 0.001$, Fig.5B), where *P. harpagos* had more diatoms in its gut.

The two experiments showed similar patterns for detritus: there was no significant difference between species (long term exp: $F_{(1, 19.34)} = 0.34, p = 0.56$; short term exp: $F_{(1, 57)} = 1.68, p = 0.19$), no significant effects of treatments (long term: $F_{(1, 5.52)} = 0.34, p = 0.58$; short term: $F_{(1, 6.71)} = 0.03, p = 0.31$), nor for the interaction between species and treatments (long term: $F_{(1, 12)} = 0.01, p = 0.91$; $F_{(1, 56)} = 0.35, p = 0.55$).

We also analyzed the total food content present in the guts, which represents the total amount of food consumed. For both experiments no significant differences between species were

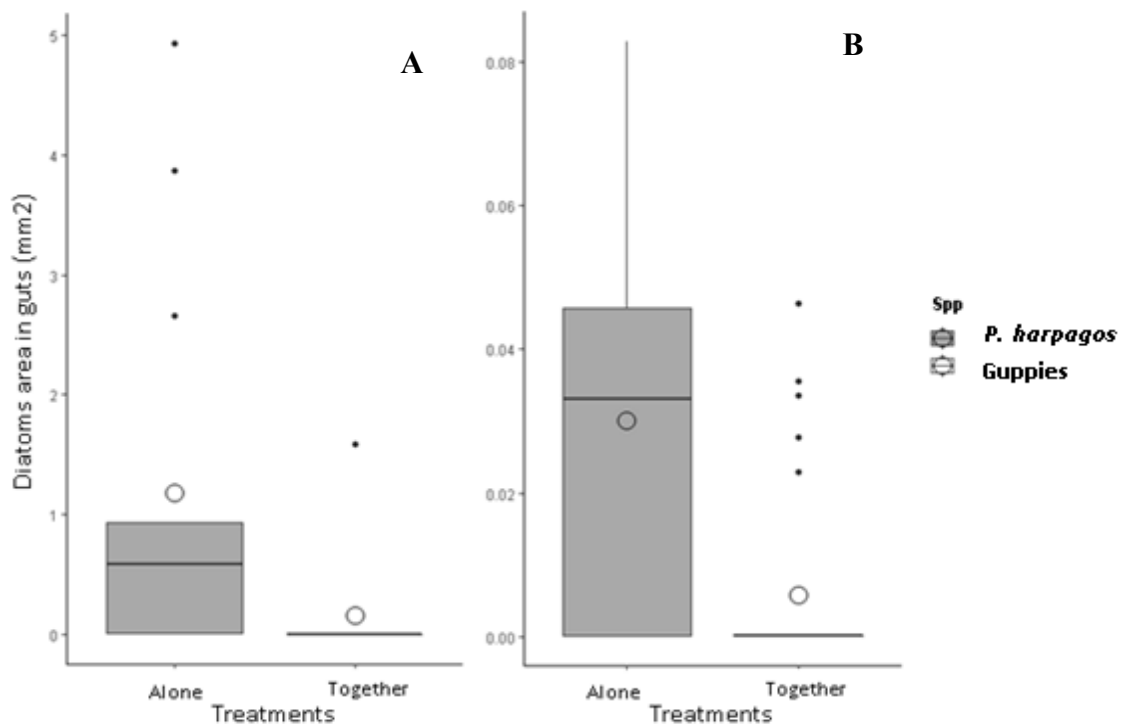
observed (long term: $F_{(1, 19.36)} = 0.46, p = 0.5$, short term: $F_{(1, 57)} = 0.78, p = 0.37$), nor between treatments (long term: $F_{(1, 5.41)} = 0.32, p = 0.5$, short term: $F_{(1, 57)} = 0.63, p = 0.42$) and nor for the interaction between species and treatments (long term: $F_{(1, 11.77)} = 0.04, p = 0.83$, short term: $F_{(1, 56)} = 0.35, p = 0.55$) (Fig.6).

Figure 4 - Invertebrates area in guts (mm²) in the fish guts occupied by invertebrates for the different treatments and species (*P. harpagos* in dark grey and guppies in white) in the long-term experiment (A) and short-term experiment (B).



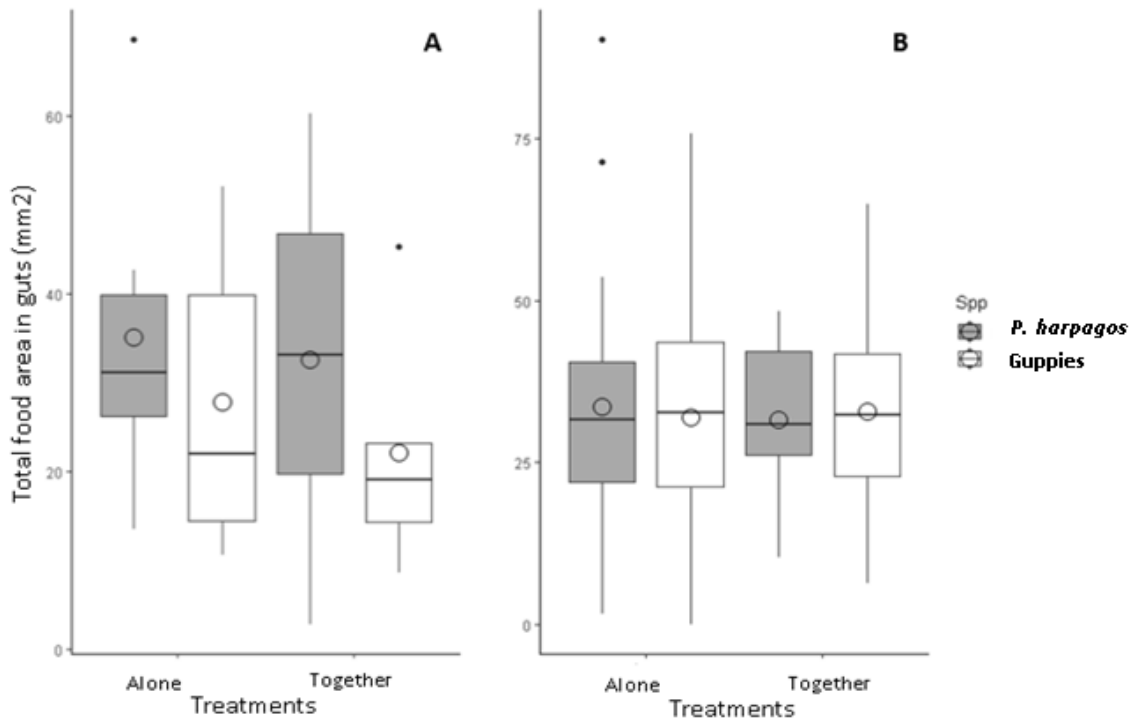
Legenda: Alone treatments are represented by mesocosms with fishes from the same species. Together treatments are represented by mesocosms with fish from both species. Empty circles represent mean values. The line inside the boxes is the median, the box indicates the first and third quartiles and error bars represent standard deviation.

Figure 5- Diatoms area in guts (mm²) for species in the different treatments (*P. harpagos* in dark grey and guppies in white) in the long-term experiment (A) and short-term experiment (B).



Legenda: Alone treatments are represented by mesocosms with fishes from the same species. Together treatments are represented by mesocosms with fish from both species. Empty circles represent mean values. The line inside the boxes is the median, the box indicates the first and third quartiles and error bars represent standard deviation.

Figure 6 - Total food area in guts (mm²) occupied by food items for the different treatments and species (*P. harpagos* in dark grey and guppies in white) in the long-term experiment (A) and short-term experiment (B).

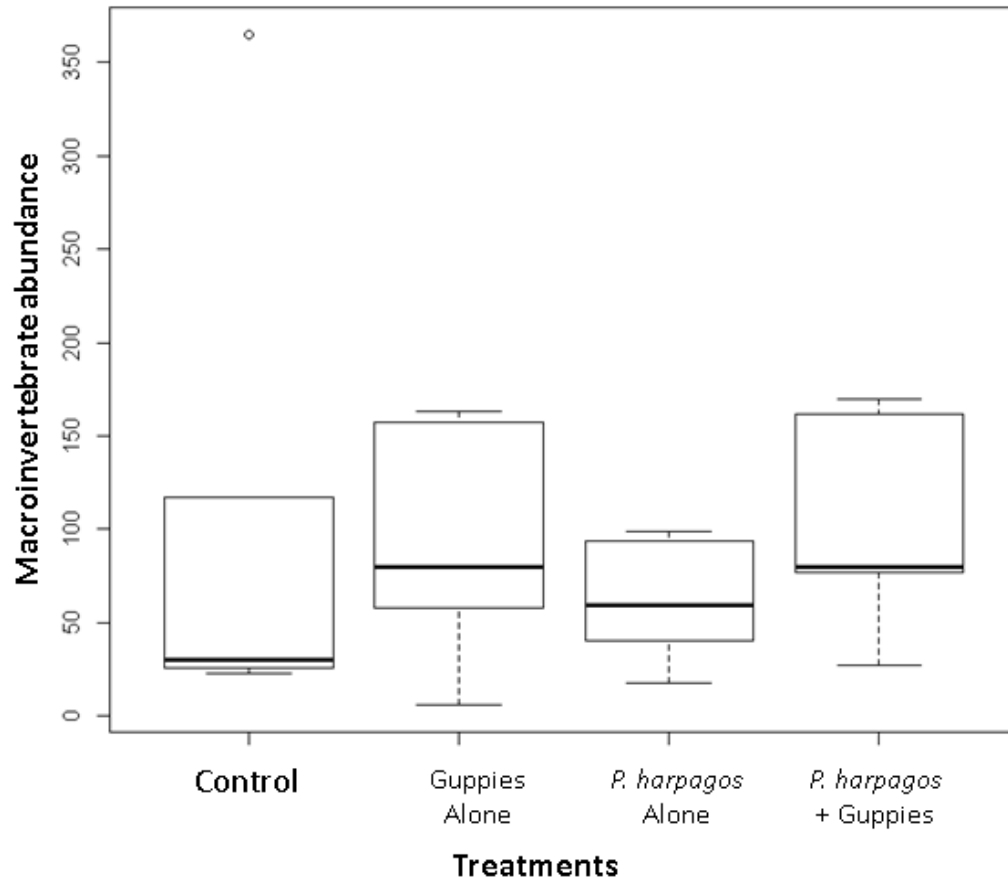


Legenda: Alone treatments are represented by mesocosms with fishes from the same species. Together treatments are represented by mesocosms with fish from both species. Empty circles represent mean values. The line inside the boxes is the median, the box indicates the first and third quartiles and error bars represent standard deviation.

2.2.1 Macroinvertebrate abundance

In relation to the total abundance of invertebrates inside water storage containers after the short-term experiment, there was no significant effect of treatment with or without fishes ($F_{(3,16)} = 0.22, p = 0.87$) (Fig. 7).

Figure 7 - Macroinvertebrates total abundance for the different experimental treatments.

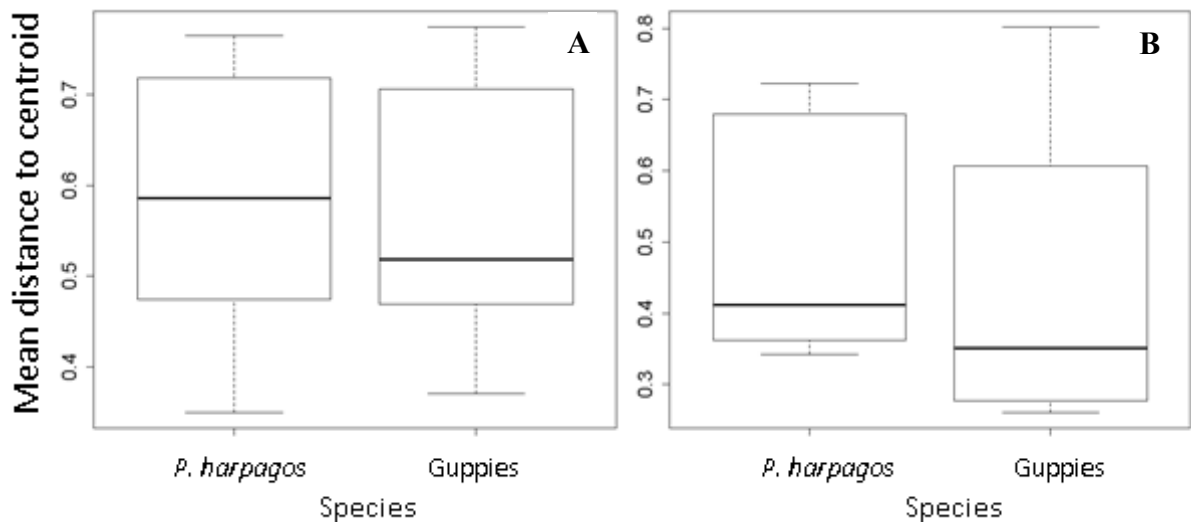


Lgenda: Control treatment without fish; Guppies Alone with individuals of *P. reticulata* only; *P. harpagos* Alone with individuals of *P. harpagos* only; *P. harpagos* + Guppies with individuals from both species together. The line inside the boxes is the median, the box indicates the first and third quartiles and error bars represent standard deviation.

2.2.2 Intra and Interspecific variability analysis

Results from the analysis of variance for diet variability performed for treatments when species were alone and together showed us that there is no significant differences in the mean distance to centroid between species (Alone treatment $F_{(1, 34)} = 0.05$, $p = 0.81$; Fig. 8A; Together treatment $F_{(1, 15)} = 0.23$, $p = 0.63$; Fig. 8B).

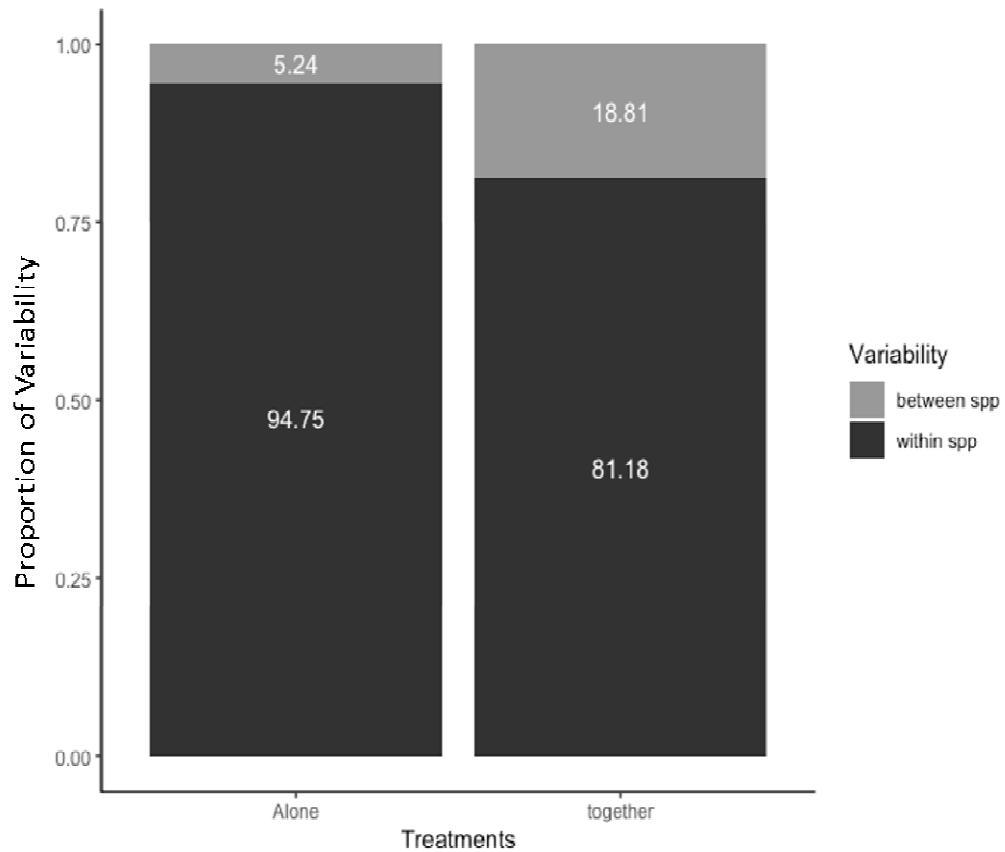
Figure 8 - Distance to the centroid for *P. harpagos* and Guppies in (A) Alone treatments and (B) Together treatments.



Legenda: The line inside the boxes is the median, the box indicates the first and third quartiles and error bars represent standard deviation.

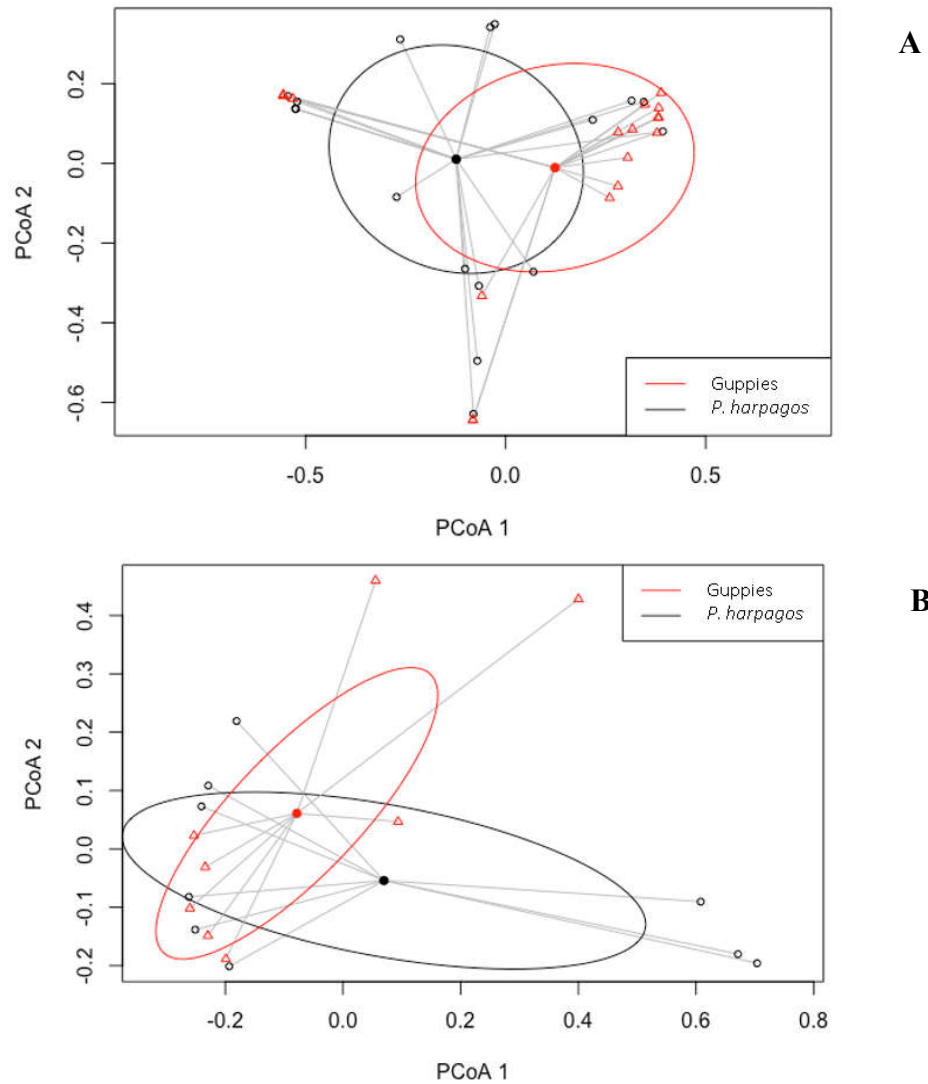
Trait variance analysis for treatments where species were alone, based on the decomposition of the mean sum of squares, revealed that proportional intraspecific variability (within species variability) contributed to 94.75% and interspecific variability (between species variability) contributed to 5.24% of fish's diet (Fig.9). In treatments where species were together, trait variance analysis revealed that intraspecific variability contributed to 81.18% and interspecific variability contributed to 18.81% in fish's diet (Fig.9). The distribution of individuals related to the PCoA (Fig. 10) axis of diet showed us that, different from what we expected, both species within the different treatments had overlapping diets.

Figure 9 - Partitioning of intra- and interspecific variability (light gray and dark gray elements, respectively) on diet in the two different treatments.



Legenda: The values are expressed as a mean proportion of trait variance of the first four PCoA axes computed on diet dissimilarity. Numbers inside bars represent the values of proportions for between and within species variability

Figure 10 - Biplot with the first and second PCoA axis from PCoA with diet data. Groups of species and their distances to centroids from (A) Alone and (B) Together treatments.



Legenda: Red triangles represent guppies individuals, Black empty circles *P. harpagos* individuals. Filled circles represent group centroids. Ellipses represent the average dispersion of those individual data points around their center.

3 DISCUSSION

Forecasting the impact of invasive species on ecosystems has challenged biologists for many decades (Parker et al., 1999; Esler et al., 2010). Our major objective in this work was to identify if guppies affect resource use of a native species, *P. harpagos*, commonly found in sympatry with the invasive species. We were expecting guppies to be superior competitors, out-competing native poeciliids for high energetic resources and reducing their use/consumption of these items. However, our results suggest guppies are not superior competitors in resource use.

Comparisons of foraging metrics such as consumption and attack rates between invasive and native species, allow us to evaluate species performance in resource acquisition (Dick et al., 2017; Britton et al., 2019). Studies analyzing functional responses from invasive and native species using different densities of a single prey have shown that invasive organisms have higher maximum feeding rates due to differences in the way that they capture prey with more consumption and lower handling times (Alexander et al., 2014; Britton et al., 2019; Mofu et al., 2019). However, the results of our experiment suggest that this pattern might not be clear for omnivorous fish that feed on many different types of prey. In our study, similar attack rates were observed for both species, which means that the rate of encounters of prey is similar between them and they have the same potential chances in foraging. Despite that, the native species showed higher consumption rates in comparison to the invasive, which would give advantages to the native species in prey consumption and energy uptake (Guo et al., 2017). This result is different from other traditional studies about invasive and native species' functional responses which have shown that invasive species often show higher consumption rates (Bollache et al., 2008; Britton et al., 2019).

Experiments using single prey could lead to misinterpretation of feeding efficiency. Some studies suggest that when different resources are available, with one abundant and easily accessed prey, the results could be more realistic due to the complexity of resources (Médoc et al., 2018). When we analyze the results from mesocosm experiments, where a variety of resources was available for fish, such as Chironomidae, Culicidae, Odonata larvae, diatoms and detritus, in the long-term mesocosm experiment, in treatments when species were together,

individuals of *P. harpagos* did not feed on invertebrates, differently from guppies which feed on high values of invertebrates. At this point, we can see a strong difference in invertebrate consumption by the invasive species. This pattern can indicate an exploitative competition between the two species once guppies consumed all available invertebrates before *P. harpagos*, depleting the resources for the native species which did not present invertebrates inside their guts.

However, in the short-term mesocosm experiment, there were no differences between species in invertebrate consumption inside the treatments. The high number of available larvae in the mesocosms (observed inside guts and before the experiment) and its high energetic value should make competitors choose the abundant and energetic prey first, increasing population and individual niche size in the same way (Bolnick et al., 2010). In fact, some studies have demonstrated that guppies reduce native species' foraging efficiency and fitness by resource competition (Holitzki et al., 2013; Camacho-Cervantes et al., 2019) but the patterns observed with our two mesocosm experiment are not similar, suggesting that the pattern of resource competition may be dependent of other factors such as time of interactions and amount of resource available (Sale, 1974).

On the other hand, the patterns observed in gut contents showed that independent of the treatments, the amount of area occupied by diatoms in both mesocosms experiments for *P. harpagos* is higher than the observed for guppies' diet. With this result, we can suggest that the native species has a potential preference for diatoms. In literature, some authors characterize *P. harpagos* as omnivorous but its preference for diatoms was observed before in different studies and for other species from this genus (Sabino & Castro, 1989; Aranha & Caramaschi, 1999; Mazzoni et al., 2010). Another potential cause for this pattern could be associated with their foraging habits linked to the search of invertebrates buried in sediments or even the option to eat what is highly abundant inside the mesocosm such as detritus and diatoms (Cruz-Rivera & Hay, 2000; Stevens & Carson, 2002). Isotope analysis has shown that guppies preferentially assimilated C and N from invertebrates. However, in some points where their population density was low due to high predation, the contribution of algae and detritus was relatively high (Zandonà et al., 2017) the same can happen with *P. harpagos* individuals.

As ecological niche theory predicts, when individuals are inhabiting stable environments, they find ways to minimize resource competition (Hutchinson, 1959). The PERMDISP results from the short-term experiment suggest that there are no differences in individual variability between species for both treatments, different from what we expected. With these results we can suggest that to reduce their competition in both treatments, species increase their within-individual variability in the diet. Individual diet specialization occurs in a vast range of taxa (Bolnick et al., 2003) however it is commonly associated with intraspecific competition forces (Svanbäck & Bolnick, 2007) and prey densities (Estes et al., 2003). The lack of resource partitioning in our short-term experiments can be a result of the short timescale, fish could be stressed by their introduction in the mesocosms or their resource use even could be impacted by the high resource availability which in a short time could not be depleted (Colwell & Futuyma, 1971; Evangelista et al., 2014; Manna et al., 2019; Bolnick & Ballare, 2020).

3.1 Perspectives

Although the present study has focused on resource use competition between guppies and *P. harpagos*, around the world many others species are introduced by humans as biocontrol, especially in the zones where arboviruses are carried by mosquitoes (Griffin & Knight, 2012; Azevedo-Santos et al., 2017). The lack of knowledge around the impacts made by a highly abundant and persistent invasive species, such as species of Poeciliids, its strategies to persist in new environments and its impacts on native species need to be better comprehended (Magellan et al., 2019). Our results help us to understand how one invasive omnivorous organism can impact the resource use of native species and even how plasticity in resource use will lead these organisms to overdisperse their diet to avoid competition.

The use of functional responses could be important in this aspect because the results obtained by this type of analysis explain the relationship between resource density and predator consumption rate (Dick et al., 2013), which is important once trophic relationships are key for structuring diversity (Stevens & Carson, 2002; Maron & Marler, 2008; Ptacnik et al.,

2008; Bolnick & Ballare, 2020). However, competition between organisms modulate niche width in many ways. The release of competitors can lead the population and individuals' niche to increase or decrease depending on the situation (Bolnick et al., 2010). The utilization of individual metrics could give us access to results that the population metrics do not. As evolution acts at the level of organisms, intraspecific trait variability analysis could help us understand better how individuals and population niche are shaped by invasion and how patterns associated with these problems could change niche in a finer scale (Bolnick et al., 2003; Chavarie et al., 2019; Marques et al., 2019). Approaches like functional responses analysis allied with intraspecific trait variation could help us to better understand the patterns of invasiveness of determined organisms.

CONCLUSION

In conclusion, this study helps us understand guppies' impacts on native species resource use, and more in general, the patterns of resource use associated with the introduction of a generalist omnivorous organism and how native and invasive species avoid interspecific competition by an increase in intraspecific variability. Although the native species had the highest consumption rate in macroinvertebrates larvae, when both species had a variety of resources, they showed no differences in resource use, a high overlap in species diet and a high individual variability within species. Lastly, studies that aim to find other patterns associated with guppies' invasion should incorporate long term experiments to analyze their impacts in native species fitness.

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