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# Influence of cage fish farming on diet composition of Sardela (*Triportheus nematurus* (Kner, 1858)) in a Neotropical reservoir

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**Abstract:** Cage fish farming promotes the input of organic matter into the surrounding aquatic environment, which can alter the availability of food resources and consequently change the diet of wild fish. Thus, gathering information about cage fish farming influences on the aquatic environment is important. We aimed to evaluate the effects of cage fish farming on the trophic ecology of the omnivorous and non-native fish *Triportheus nematurus*. We collected individuals in areas with (CF) and without (CT) the influence of cage fish farms in April and July 2019, to analyze the stomach contents to determine the diet composition of the individuals. The diet composition and the trophic guild were different between the CT and CF groups. However, the average trophic niche breadth did not differ between groups. *Triportheus nematurus* did not directly consume the organic matter coming from the cages, such as feed. Still, we suggest that the differences occurred due to changes in the availability of food resources promoted by cage fish farms and the attractive potential of the cultivation cages. In short, these results can help understand the implications of this cultivation system in the aquatic environment, contributing with new information and expanding already described data.

**Key words:** aquaculture impacts, diet, freshwater, sardela, trophic guild, wild fish.

## INTRODUCTION

Cage fish farming is one of Brazil's zootechnical activities of great economic relevance, responsible for producing 665 thousand tons in 2023 (IBGE 2024). However, this kind of activity is potentially harmful to the surrounding aquatic environment (Barrett et al. 2018, Nobile et al. 2020). A load of organic matter lost to the aquatic environment, approximately 7.7 mg/cm$^2$ per day (Cacho et al. 2020), promotes changes in the availability of food resources. This organic matter made up of waste feed, fish feces and scales, and dead fish remains can be directly consumed by fish or serve as an attractant for other aquatic organisms, thus altering the variety of food resources available (Nobile et al. 2020, Kliemann et al. 2018, 2022). Consequently, the trophic niche breadth and trophic guild of wild fish can be altered (Gerking 1994, Dias et al. 2020). Therefore, considering the potential impacts of cage fish farming (Nobile et al. 2020), gathering information about their influences on wild fish is essential.

Cage fish farming mainly influences generalist and opportunistic fish species (Kliemann et al. 2018, Nobile et al. 2020, Parra et al. 2023). The opportunistic habit and trophic plasticity (usual behavior in neotropical fish) allow the consumption of food items from different sources available in the environment

(Gerking 1994, Abelha & Goulart 2001). Because of this, fish with generalist and opportunistic habits tend to consume directly the organic matter released from cages once it's easily available with greater abundance (Nobile et al. 2020). As the contraction and expansion of the trophic niche are related to the availability of food resources (Schoener 1974, Perry & Pianka 1997, Chase & Leibold 2003), generalist and opportunistic fish can contract the trophic niche by concentrating their diet on a few items, such as feed, which is abundant near the cages as observed by Kliemann et al. (2022).

*Triportheus nematurus* (Kner, 1858), popularly known as sardela in the Upper Paraná River basin (Pavanelli et al. 2007), is a species that has been reported as omnivorous, insectivorous and frugivorous (Vidotto-Magnoni & Carvalho 2009, Lopes et al. 2017, Araujo et al. 2021) for which the consumption of microcrustaceans, insects and plant material was reported (Galina & Hahn 2008, Novakowski et al. 2008). This species has an opportunistic and generalist characteristic, with the ability to adjust its diet to environmental changes (Lopes et al. 2017) and low dispersion capacity (Rauber et al. 2021). The species is native to the Paraguay River and Lower Paraná River (Malabarba 2004) but non-native to the Upper Paraná River (Júlio Jr et al. 2009, Lima et al. 2020). Kliemann et al. (2022), evaluating the influences of cage fish farms, observed the effects on the feeding of this species, thus being a good model for the work proposed here. In addition, due to the potential impacts of non-native species on native species (Daga et al. 2016) and the favoring of non-native species by cage fish farms (Orlandi-Neto et al. 2022), it is relevant to know the biology of introduced species under the influence of these cultivation systems. Likewise, as *T. nematurus* can be prey for other non-native carnivorous species (Petesse & Petrere Jr 2012), Invasional Meltdown can occur. In this process, the interaction between non-native species facilitates the invasion of each other (Simberloff & Von Holle 1999). As a result, the ecological impacts of non-native species can be magnified (Simberloff & Von Holle 1999).

Through analysis of the food consumed by the fish, it is possible to observe how environmental variations interfere with the feeding of wild ichthyofauna (Schoener 1974, Chase & Leibold 2003, Fonseca et al. 2022, Kliemann et al. 2024). Thus, one way of estimating the influences of cage fish farming is by evaluating the trophic ecology of wild fishes. In this sense, we aimed to assess the influences of cage fish farming on the feeding aspects of *T. nematurus* in a Neotropical reservoir. We hypothesized that the feeding of *T. nematurus* alters due to the organic matter available from the cages. Thus, the following predictions were tested: i) the diet composition of *T. nematurus* differs between the area without an influence of fish farming and the area with influence; ii) there is the consumption of feed from the cultivation cages; iii) there is a contraction of the trophic niche in the area under the influence of cage fish farms and; iv) the trophic guild differs between areas due to the influence of cage fish farms. Based on the predictions, we expect that, as a result of feed consumption, there will be changes in the diet and trophic guild of the species. We also expect a contraction of the species' trophic niche due to the concentration of its diet in a few consumption items, such as feed.

## MATERIALS AND METHODS

### Study area

We performed this study in five sampling sites in the Ilha Solteira Reservoir, between the states of São Paulo, Minas Gerais, and Mato Grosso do Sul, at São Paulo northwest (Figure 1). The reservoir was formed in 1978 to generate electricity (CTG

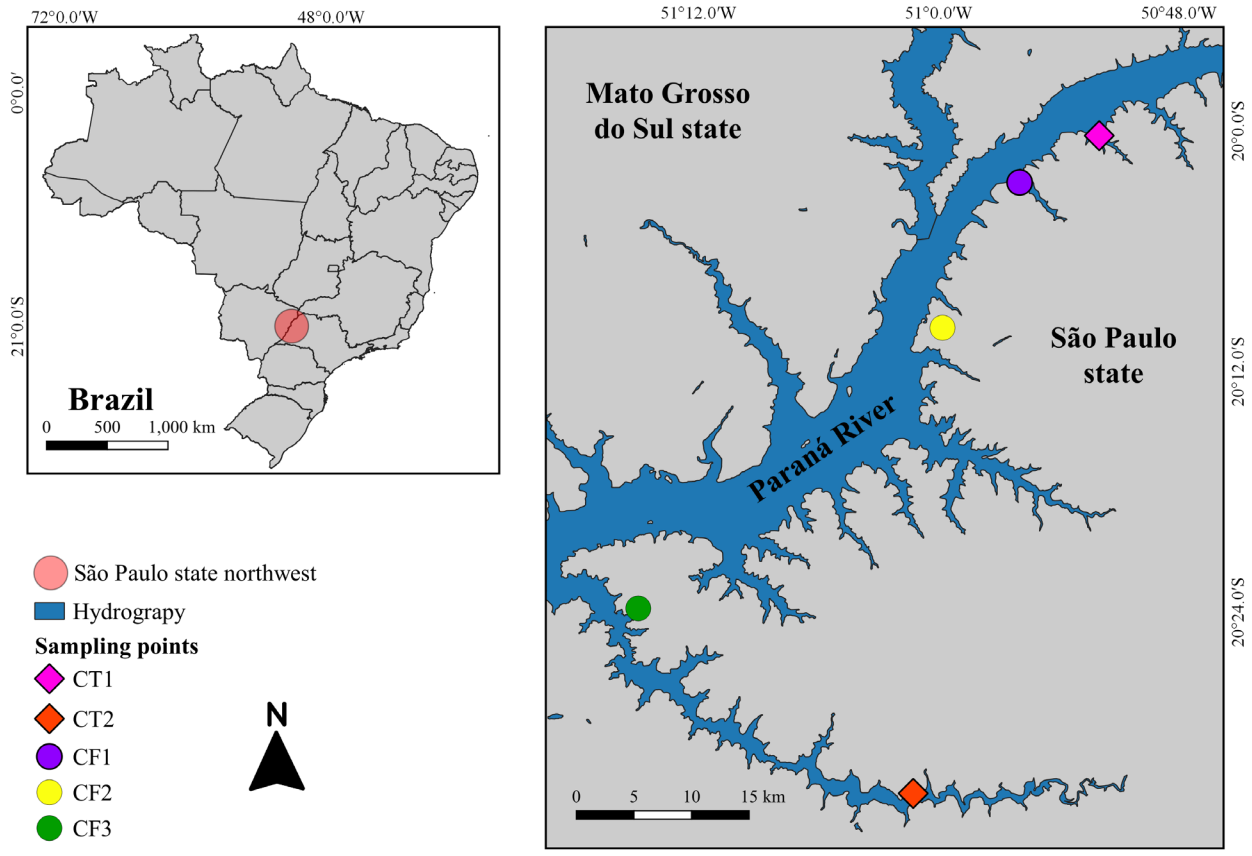


**Figure 1. Study area: sampling sites in the Ilha Solteira Reservoir, Upper Paraná River basin, São Paulo, Brazil. CT1 and CT2 = Control group and CF1, CF2, CF3 = Cage Farm group.**

Br 2020) and has an extension of 1,195 km$^2$ and a volume of 21.06 x 10$^6$ m$^3$ (David et al. 2015, CTG Br 2020). Ilha Solteira Reservoir operates with an accumulation regime, contributing to the regularization of the flow of the Paraná River downstream (David et al. 2015, CTG Br 2020). In this reservoir, 72 cage fish farms were operating, producing approximately 23.407 tons/year of fish, the highest production under the cage system in São Paulo state (CDRS 2021).

## Fish sampling

We sampled fish in April and July 2019 in two sites without influences from cage fish farms (CT1 - 11 km upstream of CF1 and 24.73 km upstream of CF2; and CT2 - 29.15 km upstream of CF3. Approximate measurements obtained from Google Earth) and three sites surrounding the culture cages (CF1, CF2, and CF3) with similar physiographic characteristics (see Kliemann et al. 2022; SISBio License nº 64763-2, Registration SisGen A908D5F). There is no information available on other effects of the surroundings; however, in both sample areas, the land use was for sugarcane cultivation.

The samples were conducted using gillnets (3 to 18 cm between non-adjacent nodes) fixed on the riverbanks and towards the river channel in CT sites and were attached to the first line of cages approximately 150 m from the riverbanks in the CF sites. We euthanized all collected specimens in a 5% benzocaine solution. After euthanasia, we measured the standard length (cm) and total mass (g) of the animals. We

removed the stomachs, fixed them in a 4% formaldehyde solution, and preserved them in 70% alcohol for later laboratory analysis. The animals were euthanized according to the Ethics Committee on Animal Experimentation of the School of Engineering, São Paulo State University (UNESP), Brazil (authorization number 006/2019).

### Laboratory procedures

We analyzed the stomach contents under the optical stereomicroscope, and we identify food items to the lowest possible taxonomic level (Bicudo & Bicudo 1970, Mugnai et al. 2010). In addition, we quantify the food items according to the volumetric method (Hyslop 1980), using the volume of each food item obtained by displacing liquid in a graduated cylinder or a millimeter Petri dish. In the Petri dish, we compress the food items with glass slides up to 1 mm in height, and the number of quadrants occupied by each food item was multiplied by 0.001 to obtain volumes in milliliters (Hellawell & Abel 1971).

### Data analysis

To group the sampling sites into Cage Farm (CF) and Control (CT), we tested the composition of the diet between the sampling sites CT1 and CT2, and CF1, CF2, and CF3 using the Multivariate Analysis of Permutation Variance (PERMANOVA one-way; Anderson 2001). This nonparametric test evaluates significant differences between groups, based on the measured distance, in this case the Bray-Curtis distance, with 999 random permutations (Anderson 2001). Subsequently, we did paired comparisons using the PERMANOVA multilevel post-test. We group the sampling sites into two groups, CF and CT, since we didn't observe significative differences in the diet between the CT1 and CT2 sampling sites and between CF1, CF2 and CF3 (Table SI - Supplementary Material). Thus, the CF group comprised three sites occupied by cage fish farms (CF1, CF2, and CF3) and the CT group, two sites upstream of the fish farms without influence (CT1 and CT2).

To verify the sampling sufficiency (number of individuals suitable for analysis) in each group, we calculated the accumulation curve of food items (Figure S1). Then, considering the food items consumed by individuals in each sampling group (Cage Farm and Control), in addition to the collection curve (observed accumulated richness), we generated the mean curve and its standard deviation from the random exchange of data (i.e., subsampling without replacement, repeated 100 times) (Gotelli & Colwell 2001). The "random" method was applied to eliminate the influence of temporal bias in the samples (Moreno & Halffter 2000).

To test the differences between standard length and total mass between CT and CF groups we apply the T-test for parametric data and the Wilcoxon test for non-parametric data.

To test possible differences in the feeding of the specimens between the CF and CT groups, we used PERMANOVA and the Bray-Curtis distance, with 999 random permutations (PERMANOVA one-way, Anderson 2001). In the case of observed differences using PERMANOVA, we applied a permutation analysis of multivariate dispersions (PERMDISP) to the same dataset and design. This analysis can demonstrate whether the differences found were related to the analyzed factors (PERMDISP $p>0.05$) or just related to the dispersion or heterogeneity of the samples (PERMDISP $p<0.05$) (Anderson et al. 2006). To reduce the dimensionality and demonstrate the relationship between food item consumption and the sampling areas, we applied the Non-Metric Multidimensional Scaling (NMDS) (Kruskal 1964) with the same array of data and Bray-Curtis distance. The food items related to sampling

areas were indicated considering the strong correlation (square root of the column $r^2$) and the significant values tested in permutational analysis (999 permutations using *envfit* function in software R).

To verify differences in the trophic niche breadth between groups, we also used PERMDISP. We measure the trophic niche breadth through diet dispersion in space, assuming that differences in distance between individuals indicate that a population has a more restricted or broader diet than the other (Correa & Winemiller 2014). PERMDISP measures the distance from the multivariate median of the group (similar to the centroid), in this case, the population in each location, through a principal coordinate analysis (PCoA) (Silva et al. 2017). The group median can be calculated using the Bray-Curtis dissimilarity measure, which allows the comparison of the mean dissimilarity in *n* individual observations within the group. To test the null hypothesis that there is no sample dispersion and that the trophic niche breadth did not differ between groups (CF and CT), we calculate a permutation test to compare the average distance of each sample to the group median. The p-value was obtained through 999 permutations of the least squares residues (Anderson et al. 2006).

To classify the trophic guild of *T. nematurus* in the CT and CF groups and verify if the trophic guild differs between the groups, we calculate the percentage of consumption of the food items. For this, we group food items into crustaceans (Decapoda), insects (Hymenoptera, Hemiptera, Odonata, Coleoptera, and Diptera), microcrustaceans (Copepoda and Cladocera), mollusks (Bivalve and Gastropoda), fish (scale and muscle) and terrestrial vegetable (seed and fruit). We carry out the classification considering the predominance of more than 50% of a class of food items in the diet of each group, for example: > 50% of stomach items recorded as insects: insectivore; > 50% detritus/sediment: detritivore; > 50% zooplankton: zooplanktophagous; more than 50% or various invertebrates and fish in stomachs: carnivore; if none of the above statements are valid and the content includes items from different sources (vegetables and animals): omnivore (Neves et al. 2015 adapted from Mérona et al. 2001).

We perform all analyses in the RStudio (RStudio Team 2021). For PERMANOVA, NMDS, PERMDISP, a permutation test, and cumulative curve, we use the 'vegan' package (Oksanen et al. 2020) and the *adonis*, *envfit*, *betadisper*, *permutest.betadisper* and *specaccum* functions, respectively. In addition, we apply a multilevel post-test using the 'pairwise.Adonis' package and the *pairwise.adonis* function. For all analyses we adopted a significance level of $p<0.05$.

## RESULTS

The 57 individuals (40-CT and 17-CF) of *T. nematurus* were analyzed. These individuals showed no differences in standard length (t=-0.94941, p=0.3518) and total mass (W=335.5, p=0.9007) between the CT and CF areas, with an average length of 19.48 cm and a mass of 90.01 g (Table I).

In general, 11 food items were identified. In the CT group, Cladocera, Copepoda and terrestrial plants were the main food items consumed. In the CF group, terrestrial insects, fish fragments and Cladocera were predominant (Table II).

There was a significant difference in diet between CT and CF groups (PERMANOVA, Df=1, F=5.89, p=0.001). The difference in diet between CT and CF was related to the diet composition once there was no difference in dispersion or heterogeneity of the samples between the two groups (PERMDISP, Df=1, F=1.94, p=0.16).

**Table I. Standard length and total mass data of individuals of *Triportheus nematurus* in Ilha Solteira Reservoir, Upper Paraná River basin, São Paulo, Brazil.**

| | Standard length (cm) | | Total weight (g) | |
|---|---|---|---|---|
| | **Control** | **Cage farm** | **Control** | **Cage farm** |
| Mean±Standard deviation | 19.41±3.01 | 19.69±3.27 | 87.54±39.73 | 99.94±45.99 |
| Min - Max | 14.0 - 23.5 | 15.0 - 24.4 | 27.71 - 175.42 | 28.53 - 168.63 |
| t (T-test) / W (Wilcoxon) | t= -0.94941 | | W= 335.5 | |
| p | p= 0.3518 | | p= 0.9007 | |

**Table II. Percentage by volume (%) of each food item consumed by *Triportheus nematurus* in the Control and Cage farm groups in the Ilha Solteira Reservoir, São Paulo, Upper Paraná river basin, Brazil. Values in bold represented the most contributed to the diet in each sample group.**

| **Group** | **Control** | **Cage farm** |
|---|---|---|
| **Food item** | **Percentage by volume (%)** | |
| Copepoda | **30.11** | 9.18 |
| Cladocera | **36.91** | **13.36** |
| Decapoda | | 0.10 |
| Bivalvia | | 1.34 |
| Gastropoda | | 6.68 |
| Invertebrate egg | 0.59 | |
| Aquatic insect | 8.32 | 0.42 |
| Fish fragments | | **20.70** |
| Scale | 0.83 | 2.62 |
| Terrestrial vegetable | **19.94** | 0.33 |
| Terrestrial insect | 3.31 | **45.02** |

The distribution of specimens in two-dimensional space (NMDS-2D/stress-0.12) was related to the feeding in each sampling area. We observed that Copepoda and terrestrial insects were the main items that segregated the sampling areas, with Copepoda mainly related to CT ($r^2$=0.18, p=0.01) and terrestrial insects ($r^2$=0.35, p=0.001) to CF (Figure 2, Table SII). The average trophic niche breadth (CT=0.54 and CF=0.59), in turn, did not differ between groups (PERMDISP, Df=1, F=1.94, p=0.15).

The trophic guild also differed between the groups. In the CT group, the species was classified as zooplanktophagous due to the higher consumption of microcrustaceans (67%) (Figure 3). In contrast, the CF group was classified as carnivorous with insectivorous tendency due to the consumption of insects (45.69%) and consumption in a similar proportion of other items of animal origin (53.88%) (Figure 3).

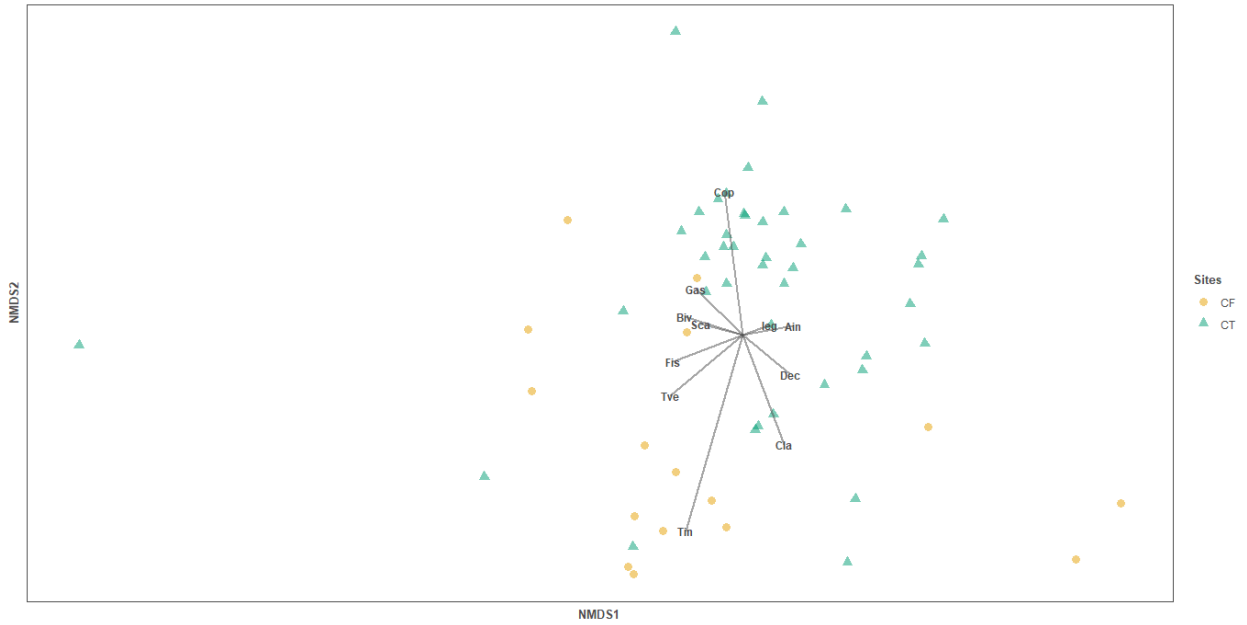


**Figure 2. Differences in diet composition of *Triportheus nematurus* between sites CT and CF (NMDS-2D/stress-0.12), in Ilha Solteira Reservoir, Upper Paraná river basin, São Paulo, Brazil. Cop: Copepoda; Gas: Gastropoda; Biv: Bivalvia; Sca: Scale; Tve: Terrestrial vegetable; Fis: Fish; Cla: Cladocera; Ain: Aquatic insect; Tin: Terrestrial insect; Ieg: Invertebrate egg; Dec: Decapoda. CT = control area and CF = cage farm area.**

## DISCUSSION

Our results confirmed the hypothesis that cage fish farms influenced the diet of *T. nematurus*, providing important insights into the behavioral and dietary changes of fish in response to anthropic influence. Differences were observed in diet composition (prediction i) and trophic guilds between groups (prediction iv), but there was no contraction of the trophic niche in CF group (refuting prediction iii). The species showed higher consumption of microcrustaceans in the CT group and insects in the CF group. Due to the trophic opportunism observed for the species (Lopes et al. 2017) and the input of organic matter from the cages (Montanhini Neto & Ostrensky 2015, Cacho et al. 2020), we expected that there would be direct feed intake. However, such was no observed consumption. Therefore, we infer that the influences of cage fish farms can be observed by the consumption of organisms attracted by fish farms in the CF group. Although the diet was different, the trophic niche breadth remains high and without differences between groups, indicating the trophic plasticity of the species.

Studies showed that the entry of organic matter and the structures of the cages promotes the attraction/proliferation of organisms used as food items by *T. nematurus*, such as insects, Gastropoda, and microcrustaceans (Ramos et al. 2013, Izquierdo-Gómez et al. 2015, Ayroza et al. 2019, Kliemann et al. 2022). This input of organic matter increases the availability and decreases the diversity of food resources (Cacho et al. 2020, Kliemann et al. 2022). As a result, the CF group would have easily accessible food items, allowing *T. nematurus* to alter its diet and maintaining a cost-benefit ratio of energy expenditure between capture and digestion, as predicted by the optimal foraging theory (Schoener 1974). As there were no significant differences in standard length and total weight between the areas, the diet was possibly not influenced by these factors.

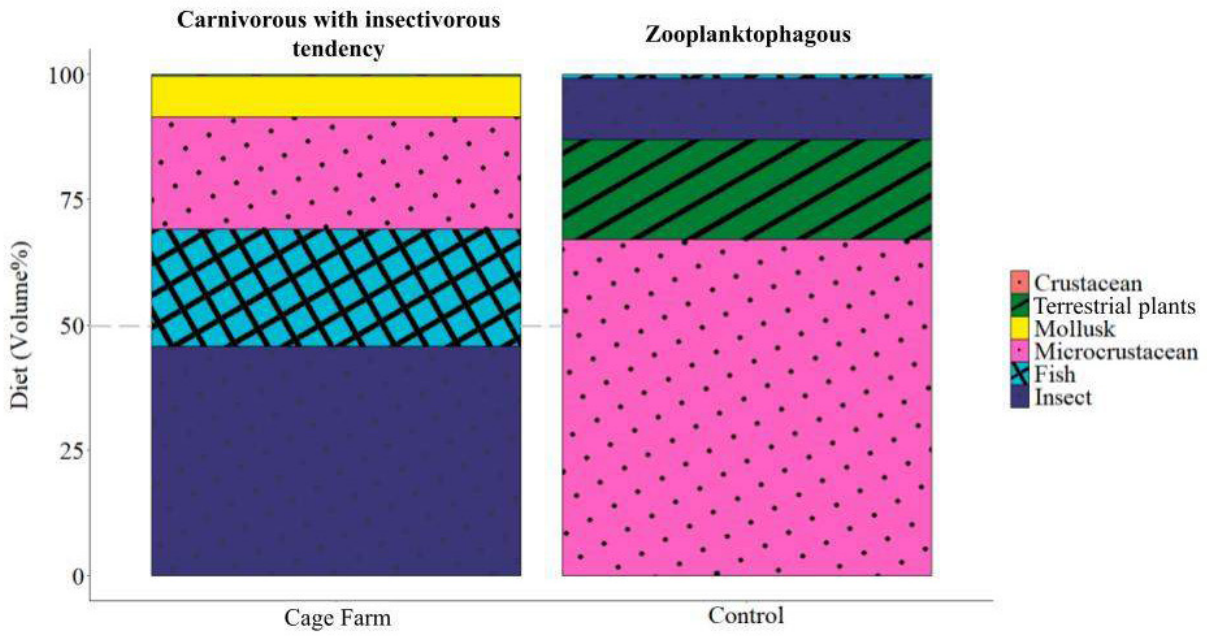


**Figure 3. Composition diet (based on percentage volume (%) of food items consumed) of *Triportheus nematurus* indicating the trophic guild in each sample group CT and CF, in Ilha Solteira Reservoir, Upper Paraná river basin, São Paulo, Brazil. "CT" por "Control" e "CF" por "Cage Farm".**

Although feeding differs between groups, the trophic niche breadth did not differ. Therefore, the CF group had no trophic niche contraction, as predicted iii. We expected that there would be niche contraction due to the high abundance of few resources close to the cages, such as feed (Cacho et al. 2020, Kliemann et al. 2022), resulting in a smaller variety of resources consumed and thus a smaller trophic niche breadth. However, the population of *T. nematurus* presented homogeneity of diet dispersion between groups CF and CT, based on the PERMDISP result (non-significative difference indicated a homogeneous diet dispersion between individuals). In this way, each group consumed predominant food items, i.e., Cladocera, Copepoda, and terrestrial plants in the CT group, and terrestrial insects, fish fragments, and Cladocera in the CF groups, suggesting the high availability of these items in the sampling sites. Thus, individuals could share the most available resources without causing depletion to groups of individuals (Schoener 1974, Chase & Leibold 2003, Neves et al. 2018), once resource sharing may favor long-term intraspecific coexistence, which is essential for population stability (Chase & Leibold 2003, Kliemann et al. 2021).

Changes in diet composition driven by the influence of cage fish farms resulted in differences in trophic guilds between groups. In the CT group, *T. nematurus* was classified as zooplanktophagous, while in the CF group, it presented a carnivorous habit with an insectivorous tendency. Previous studies classified it as insectivorous (Vidotto-Magnoni & Carvalho 2009, Corrêa et al. 2011) and omnivorous (Wantzen et al. 2002, Lopes et al. 2017). Differences in trophic guilds under the influence of cage fish farms were also observed in other species, like *Metynnis lippincottianus* (Cope, 1870) in the Ilha Solteira Reservoir (Ramos et al. 2022). Given these differences in trophic guilds, our results and other studies confirmed plasticity and trophic opportunism for *T.*

*nematurus*, demonstrating the consumption of available food resources in each area. The consumption of Decapoda, Bivalvia, Gastropoda, and Fish fragments exclusively in CF reinforces the interference of cage fish farms in the availability of environmental resources. Studies demonstrated that these organisms are attracted to cages due to the organic matter (Nobile et al. 2020, Kliemann et al. 2022).

A change in the availability of food resources promoted by cage fish farms may favor *T. nematurus*, a non-native species to the upper Paraná River basin (Júlio Jr et al. 2009, Lima et al. 2020). Due to the plasticity and opportunistic behavior of neotropical fish (Abelha & Goulart 2001), the availability of food promoted by cage fish farms favors the maintenance and domination of non-native species (Orlandi-Neto et al. 2022). This process leads to functional impoverishment and homogenization of the biota in areas adjacent to cage fish farms (Orlandi-Neto et al. 2022, Parra et al. 2023). In addition, impacts associated with non-native species can occur in native species, such as the suppression of vital rates (as reproduction and growth), alterations in behavior, loss of functional richness and even the local extinction of species (Ellender & Weyl 2014, Daga et al. 2016, Souza et al. 2021). Further, the competitive exclusion of natives can occur through trophic niche overlaps between native and non-native species, leading to an energy-poor diet and possible local extinction of species (Collier et al. 2018) such as *Hoplosternum littorale* (Hancock, 1828), *Leporinus lacustris* Amaral Campos, 1945 and *Pimelodus platicirris* Borodin, 1927.

In short, the results corroborate the hypothesis that the feeding of *T. nematurus* alters due to the organic matter available from the cages. Furthermore, predictions that diet composition and trophic guild would change between sample groups were also supported. Given this, we inferred that cage fish farming could indirectly modify their diet and other feeding aspects of the surrounding ichthyofauna. Although Kliemann et al. (2022) have analysed the diet and the omnivorous habit of *T. nematurus*, our study complements the existing information indicating that this species uses fish farm resources indirectly, consuming aquatic organisms attracted by the cages. In addition, introduced fish can be favored by the input of food promoted by fish farms, allowing their population to increase, which can magnify the impacts on native species. Given this, the importance of this and similar studies in detail and understanding the trophic ecology of aquatic ecosystems, mainly associated with cage fish farming, is reinforced. In addition, the results presented here may help understand the implications of this cultivation system in the aquatic environment, contributing with new information and expanding already described data.

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## SUPPLEMENTARY MATERIAL

**Figure S1.**
**Tables SI, SII.**

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Conceived and designed the experiments: IPR, RLD, BCKK; Collected specimens: BCKK, JDSG, IPR; Laboratory analysis: VCB; Data analysis: VCB, BCKK; Wrote the paper: VCB, BCKK, NLS, JKKR, JDSG, RLD, IPR.