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Diet and trophic niche of common carp *Cyprinus carpio* in the Lower Santa Lucía River, Uruguay

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Abstract. Common carp (*Cyprinus carpio*) is a highly invasive fish that causes adverse ecological effects worldwide. Taking into account *C. carpio* biological traits, it can potentially exploit different environments by feeding from the benthic zone and affect native fish trophic structure. While extensive research exists for several invaded areas, the ecological aspects and the natural history of this invasion are almost unknown in the southern Neotropics. In this work we analyzed gut contents of this species to unveil aspects of the feeding strategy and trophic niche breadth in one of the oldest locations of invasion in Uruguay, the lower Santa Lucía River (La Plata basin). The results showed that *C. carpio* consumed detritus, native benthic macroinvertebrates, as well as the exotics invasive golden mussel *Limnoperna fortunei* and Asian clam *Corbicula fluminea*. In this scenario, there could be a benefit between *C. carpio* and the invasive bivalves through the biotic melting model or "Meltdown". Also, the common carp fed on native invertebrates that are listed as priority species for conservation. The common carp's feeding strategy was considered omnivorous generalist and its trophic position in the food web was multitrophic. The potential trophic niche overlap with native fish species is discussed based on a bibliographic review.

Keywords: Invasive species, food strategy, La Plata basin.

Dieta y nicho trófico de la carpa común *Cyprinus carpio* en el Río Santa Lucía bajo, Uruguay. Resumen: La carpa común (*Cyprinus carpio*) es una especie de pez altamente invasiva que causa efectos adversos en ambientes naturales alrededor del mundo. Considerando los rasgos biológicos de *C. carpio*, puede potencialmente explotar diferentes ambientes al alimentarse de la zona bentónica, afectando la estructura trófica de los peces nativos. Aunque existe una extensa investigación sobre varias áreas invadidas, los aspectos ecológicos y la historia natural de esta invasión son casi desconocidos en el sur del Neotrópico. En este trabajo analizamos el contenido del tracto digestivo de esta especie para develar aspectos de la estrategia de alimentación y la amplitud del nicho trófico en uno de los lugares de invasión más antiguos de Uruguay, la parte baja del río Santa Lucía (cuenca del Plata). Los resultados mostraron que *C. carpio* consumió detritus, macroinvertebrados bentónicos nativos, así como el mejillón dorado invasor *Limnoperna fortunei* y la almeja asiática invasora *Corbicula fluminea*. En ese escenario, podría haber un beneficio entre *C. carpio* y los bivalvos invasores a través del modelo de derretimiento biótico o "Meltdown". Además, la carpa se alimentó de invertebrados nativos que están catalogados como especies prioritarias para la conservación. La estrategia de alimentación de la carpa común fué considerada generalista omnívora y su posición trófica en la red trófica fue multitrófica. El potencial solapamiento de nicho trófico de *C. carpio* con peces nativos se discute en base a una revisión bibliográfica.

Palabras clave: Especie invasora, estrategia alimenticia, cuenca del Plata.

Introduction

Common carp *Cyprinus carpio* Linnaeus 1758 is the third most frequently exotic species introduced for commercial aquaculture purposes in many countries around the world (Zambrano *et al.* 2006, Gubiani *et al.* 2018). It has become a cosmopolitan species as a result of incidental and intentional dispersion by humans since it has been successfully introduced in freshwater basins around the globe (Casal 2006). Its high tolerance to wide environmental variability makes the species suitable to be used in aquaculture, and together with its feeding behavior has allowed it to cause adverse ecological effects in natural environments in various regions around the world (Sidorkewicj *et al.* 1998, Casal, 2006, Matsuzaki *et al.* 2009, Weber *et al.* 2010, Kloskowski 2011, Vilizzi *et al.* 2015). In this context, the common carp is listed amongst the world's worst 100 invasive alien species (Lowe *et al.* 2000). It has caused adverse ecological impacts in at least 15 countries (Casal 2006, Matsuzaki *et al.* 2009, Weber *et al.* 2010, Kloskowski 2011, Vilizzi *et al.* 2015). It is a species that migrates up to 500 kilometers during its reproductive period, or for favorable food environments (Maiztegui *et al.* 2016, Maiztegui *et al.* 2019). Its trophic niche is broad, allowing it to compete for the resources available with biologically similar native fish species, potentially causing their gradual disappearance (Moyle 1976). Furthermore, during feeding, *C. carpio* generates adverse ecological effects via bioturbation of benthic habitats (Kloskowski 2011).

In the La Plata basin, the introduction of *C. carpio* dates back to the middle nineteenth century in Argentina (Baigun & Quiroz 1985). It is presumed that this exotic species found in Uruguay comes from inland waters of the Province of Buenos Aires (Argentina), introduced in the early twentieth century for commercial purposes (Mac Donagh 1948). From there, it began to colonize other environments of Buenos Aires such as the Salado River basin (Colautti 1997) and the Colorado, Serrano, and Mar Chiquita systems (Maiztegui *et al.* 2016). In Uruguay, *C. carpio* was first reported in 1987 by artisanal fishermen from the Río de la Plata estuary coast, in the town of Juan Lacaze, Department of Colonia (Ares *et al.* 1991). Posteriorly, the species dispersed in a staggered manner throughout the eastern part of the Uruguayan territory (Baigun & Quiros 1985, Fabiano *et al.* 2011). In addition, its cultivation in the 1960s in Brazil and from 1974 in Uruguay, with subsequent escapes from aquaculture stations and by intentional introductions, allowed the invasion into natural environments of Uruguay (Amestoy *et al.* 1998). Currently, the species is distributed in almost the entire La Plata basin (Colautti, 1997, Fabiano *et al.* 2011, Maiztegui *et al.* 2016, Zarucki *et al.* 2021), including the lower Santa Lucia River basin, as well as the Uruguay and Negro rivers basins (Ares *et al.* 1991; Zarucki *et al*. 2020) and in tributaries of the Atlantic Ocean (Fabiano *et al.* 2011, Zarucki *et al.* 2021).

Common carp feeding habits have been studied in Pampean Environments, connected to La Plata basin (Colautti 1997, Colautti & Remes Lenicov 2001, Maiztegui 2016, Maiztegui *et al.* 2019). However, the information about its trophic role and potential trophic impacts is still scarce and fragmented, hampering the understanding of its ecosystem impacts in the La Plata basin. In this context, it is essential to determine the feeding habit of *C. carpio* to predict the potential trophic impact generated over the native community.

In this investigation we focused on the wildlife protected area "Área Protegida con Recursos Manejados Humedales de Santa Lucía" (HDSL, Achkar *et al.* 2012), located in the south of Uruguay, where common carp has been particularly abundant for at least the last three decades (Amestoy *et al.* 1998). The objective of this work was to characterize the diet of *Cyprinus carpio* by analyzing its gut content, its trophic position, and to determine its feeding strategy and niche breadth.

Materials and methods

This work was carried out in the protected area HDSL, where the Santa Lucia River flows into the estuary of the Río de la Plata (Fig. 1A), forming an important saline-coastal wetland system (Achkar *et al.* 2012), where the annual salinity range is between 0.5 and 20.0 g/L (Guerrero *et al.* 2010). Currently, several species of fish and mollusks present in the area are considered priorities for conservation in Uruguay (Loureiro *et al.* 2013, Clavijo & Scarabino 2013). On a broader scale, the Santa Lucía River basin makes up one of the most important wa-

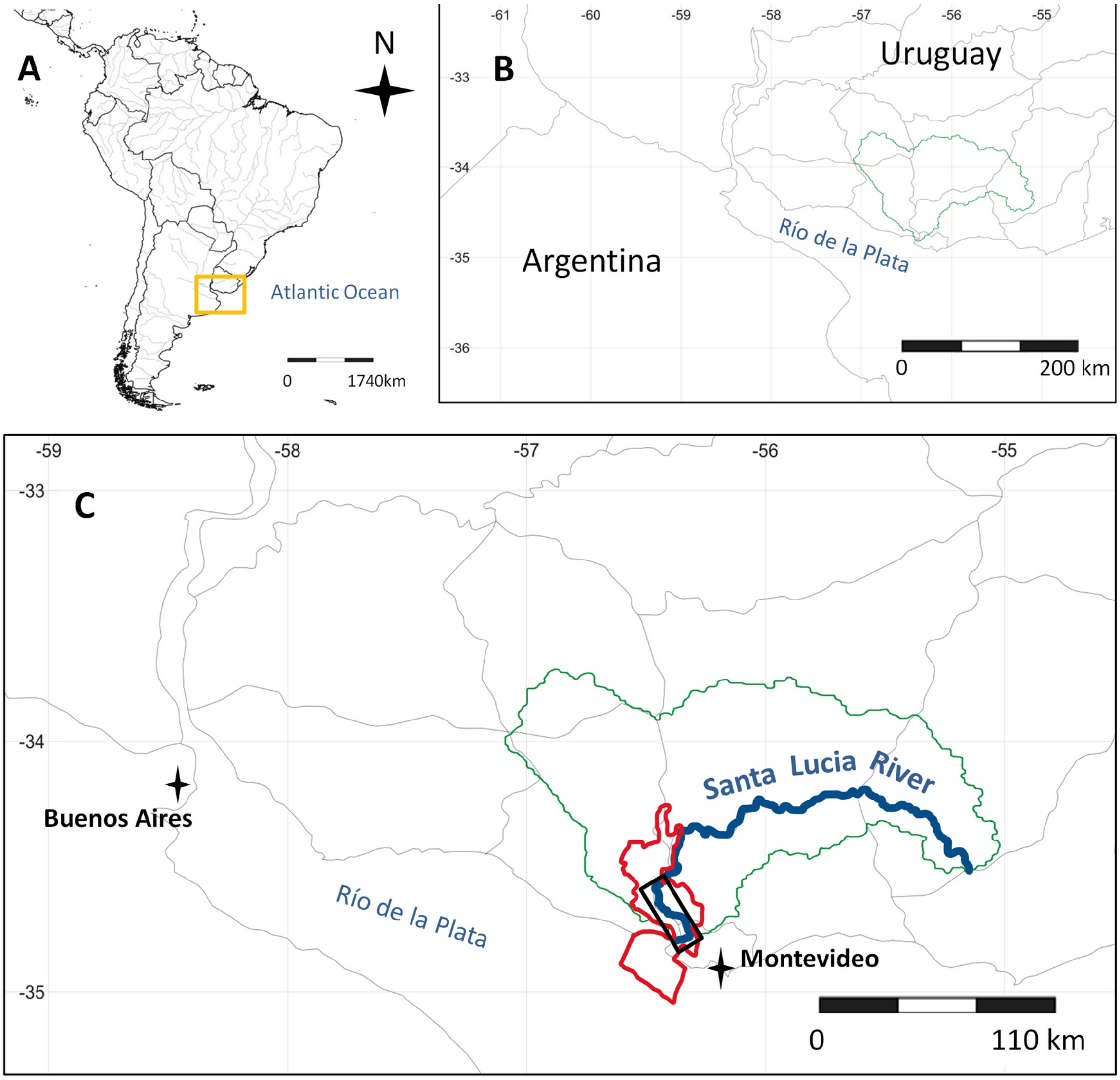

Figure 1. Location where specimens of the invasive common carp *Cyprinus carpio* were captured to perform the gut content analysis. **A**: Rio de la Plata estuary (orange rectangle); **B**: Santa Lucía River basin (green perimeter); **C**: protected area HDSL (red perimeter) within Santa Lucía River basin (green perimeter). Carp sampling area within a 25-kilometer stretch (black rectangle).

ter resources, supplying drinking water to 60% of Uruguay's population (Achkar *et al.* 2012).

Samplings were carried out from March 2018 through February 2019 in different points within the protected area, along 25 kilometers of the lower section of the river. Sampling was carried out every 1 or 2 weeks on average, accounting for a total of 33 sample days (6 in autumn, 5 in winter, 12 in spring and 10 in summer). Samplings were not standardized because they were obtained by surveying catches from recreational and subsistence fishermen, who did not have a regular presence nor in time neither in space along the sampling period (surveying catches of up to 20 fishermen in each sampling day). Usually, we sampled on warmer days or without rain (depending on the season), as we were more likely to encounter more fishermen in good weather conditions. We asked for permission to each fisherman to measure and weight their catch and to extract the whole gut from each carp obtained. We collected 32 individuals from fishermen who were using a fishing rod as catching method. We treated the gut content analysis of all the individuals as one group, and we did not test for differences in diet between sexes because the low number of fish obtained (18 female and 14 males) would bias such results.

Fish collected were euthanized using an overdose of Clove oil before the gut extraction, measured (TL, mm), weighted (g), sexed and their guts were preserved in 4% formalin.

In the laboratory we performed a diet analysis considering the content of the whole digestive tract.

We used Petri plates to carry out the separation of items by taxa. The relative volume (*Rv*) of each dietary item in each digestive tract was estimated using a Petri plate with a millimeter grid at the base, following standardized methods as described in Hyslop (1980). We measured the maximum and minimum length (mm) of each item ingested by the common carp. The items were classified into taxonomic groups at the lowest possible level using taxonomic keys (Scarabino *et al.* 2006, Domínguez & Fernández 2009). From the volume occupied on the grid by each item type, the percentage of each item within all tracts was calculated (termed onwards as "relative volume" or "*Rv*") (Colautti & Remes Lenicov 2001).

We calculated the index of relative importance (I_{RI} *%*) (Pinkas *et al.* 1972) to estimate the importance of the items ingested. The trophic position of *C. carpio* was calculated by adding one to the average of the trophic positions of each item ingested by each specimen (Beckerman *et al.* 2006). The trophic position (*Tp*) of the food items consumed were reviewed using published biological data, assigning value one (1) to primary producers, two (2) to primary consumers, and three (3) to secondary consumers according to Cohen *et al.* (2003), Scarabino *et al.* (2006), and Domínguez & Fernández (2009).

The niche breadth index (*Bi*) was calculated as the number of prey taxa identified as part of the diet of each studied specimen (Beckerman *et al.* 2006) and the fish omnivory index (*Oi*) was estimated as the standard deviation of the trophic positions of its preys (Lazzaro *et al.* 2009). The trophic spectrum and the appearance of the items in the dietary composition were determined by calculating the Frequency of Occurrence (*FO*) (Hyslop 1980, Colautti & Remes Lenicov 2001).

The feeding strategy and the importance of the items ingested was determined with FO data of each food item and with the calculation of the Prey-specific abundance Pi, with the formula: $Pi=\left(\sum Si/\sum Sti\right)100$, where Si is the relative volume of item i, and S_{ti} is the total volume of each stomach with the presence of that item (Amundsen *et al.* 1996). The importance of the items ingested by the common carp was displayed on the chart of Amundsen *et al.* (1996), increasing from the lower left corner to the upper right being nonlinear.

Results

We obtained a total of 32 *C. carpio* specimens in the estuarine protected area HDSL, 18 of which were captured in the spring, 12 in the summer, 1 in autumn, and 1 in the winter. The $TL = 643 \pm 12$ mm with a range between 470 mm and 680 mm; and a mean of Total Weight $TW = 3990 \pm 220$ g. Two of the individuals had empty guts and were thus removed from further analysis.

The diet of *C. carpio* was composed of 16 items, 40.2% of the *Rv* consisted of detritus (e.g., fine particulate organic matter) (Table I). The benthic macroinvertebrates consumed were Ostracoda (19.3%), the native clam *Erodona mactroides* (18.9%), the invasive golden mussel *Limnoperna fortunei* (11.7%), the balanid *Chthamalus sp*. (3.2%), the mollusk gastropod *Heleobia australis* (2.6%), and the mud crab *Neohelice granulata* (1.5%). The *Rv* of the remaining items was lower than 1% and consisted of Chironomidae, the invasive Asian clam *Corbicula fluminea*, Tabanidae, Ephemeridae, Trichoptera and the shrimp *Neomysis americana* (Fig. 2 and Table I). Another item identified in a low proportion (<1%) was microplastic fibers (Fig. 2 and Table I). The presence of gravel (1.9%) was also recorded, varying in rock size (between 0.25 and 8.0 mm long). The largest item ingested by the common carp was a *N. granulata* leg portion with a maximum length of 23.0 mm, followed by a shell portion of *L. fortunei* with 21.0 mm and a shell portion of *E. mactroides* with 14.0 mm (Table 1). The smaller invertebrates consumed were Ostracoda (1 mm), *H. australis* (1 mm) and *N. americana* (1.5 mm; Table I).

The FO of the detritus was 100%, followed by that of Ostracoda, *E. mactroides*, *L. fortunei*, *Chthamalus sp*. and *H. australis* (Table I). In this sense, the trophic spectrum was broad, as *C. carpio* ingested sixteen items. This signifies that the common carp can be considered as an omnivorous-detritivorous species. The detritus was the item with the highest I_{RI} % with a ratio of 40.22%, followed by Ostracoda (Table 1). In this sense, detritus was the dominant item followed by macroinvertebrates such as Ostracoda and *E. mactroides*.

The carp´s trophic niche can be classified as broad by predating up to 13 taxa of aquatic invertebrates such as Crustaceans, Insects, and Mollusks. The omnivory index *Oi* was 0.189 and the common carp's trophic position range was 2.773 ± 0.189 (~3), acting as a secondary consumer. However, the common carp was found to be a multitrophic omnivorous predator simultaneously predating over more than one trophic level.

Table I. Relative volume (*Rv*) of items consumed by *Cyprinus carpio*, the Frequency of Occurrence (%) and the I_{RI} % they occupy, sorted from dominant to occasional items, from top to bottom. æ: Invasive species; §: priority native species for conservation.

FOOD ITEMS	Item length max - min (mm)	Relative volume	*FO* (%)	I_{RI} (%)
Detritus	-	40.2197	100	40.2197
Ostracoda	1.0 - 2.0	19.248	70	13.47
Erodona mactroides §	5.0 – 14.0	18.92	66.7	12.62
Limnoperna fortunei æ	2.0 – 21.0	11.74	53.3	6.26
Chthamalus sp.	3.0 – 6.0	3.19	46.7	1.49
Heleobia australis §	1.0 – 6.0	2.565	33.3	0.85
Gravel	0.5 – 12.0	1.9	30	0.57
Neohelice granulata §	10.0 – 23.0	1.458	20	0.29
Chironomidae	2.0 – 5.5	0.717	13.3	0.095
Corbicula fluminea æ	4.0 – 5.0	0.03	10	0.003
Microplastic fibers	1.0 – 10.0	0.0062	6.7	0.0004
Tabanidae	2.5 – 3.5	0.0033	3.3	0.0001
Ephemeridae	4.0 – 5.0	0.00136	3.3	0.000045
Insect wings	2.0 – 3.0	0.0012	3.3	0.000040
Trichoptera	3.0 – 4.0	0.0002	3.3	0.000006
Neomysis americana	1.5 – 3.5	0.00004	3.3	0.000001

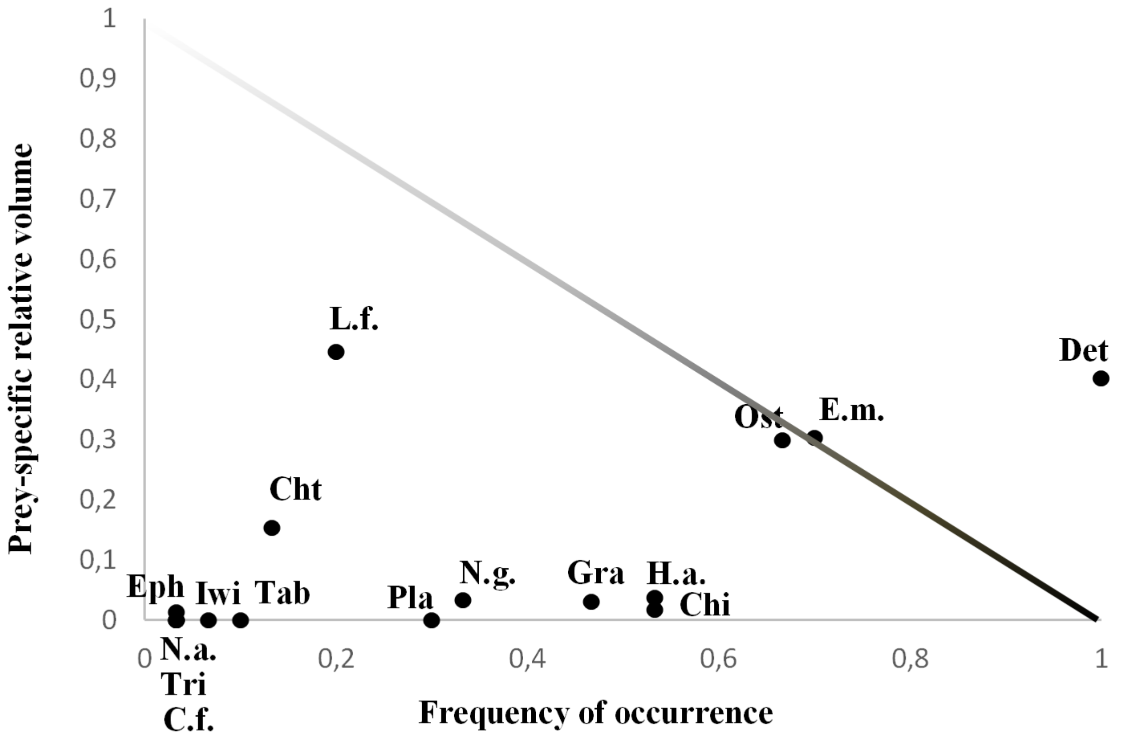

Figure 2. Feeding behavior diagram of *Cyprinus carpio* (Amundsen *et al.* 1996), showing the prey-specific abundance (%) vs. the *FO* of each item present in the diet. L.f.: *Limnoperna fortunei*; Ost: Ostracoda; E.m.: *Erodona mactroides*; Det: Detritus; Cht: *Chthamalus sp.*; Chi: Chironomidae; H.a.: *Heleobia australis*; Gra: Gravel; N.g: *Neohelice granulata*; MPl: Microplastic; Eph: Ephemeridae; Tri: Trichoptera; C.f.: *Corbicula fluminea*; N.a.: *Neomysis americana*.; Iwi: Insect wings; Tab: Tabanidae. The items in or above the line indicate a general preference of the species for that item, while for the items located below the trend line might represent certain specialization of fewer individuals. Items with the highest percentage of *Pi* are located at the top of the chart, indicating a certain degree of preference by the carp while those close to the horizontal axis are ingested occasionally and indicate generalism. Prey items located in the upper left zone of the chart represent the individual specialization, and those of the upper right represent the specialization of the population (Amundsen *et al.* 1996).

Amundsen's chart shows detritus as the main dietary item, being consumed by all individuals and representing more than 40% of the Pi. However, *L. fortunei* as the item with the higher *Pi* = 45% of the dietary in specimens that fed on this item (Fig 2), although it is only predated by 20 % of the individuals. Items located on the lower right margin of Amundsen`s chart (Fig. 2) were ingested by more than half of the specimens, presenting a high *FO* with a low *Pi*, such as Chironomidae and *H. australis*. The secondary items were Chironomidae, Gravel and *N. granulata* while the occasional or "rare" items were Microplastic fibers, *N. americana*, Trichoptera, Ephemeridae, Insect Wings, Tabanidae and *C. fluminea* presenting low *Pi* and low *FO* (Fig. 2). We observed in the graph of Amundsen *et al.* (1996) that *C. carpio* presents a generalist feeding behavior with omnivorous and detritivorous feeding habits, presenting a wide trophic niche.

Discussion

We characterized the diet and trophic niche of the adult stage (Tessema *et al.* 2020) of the invasive fish *Cyprinus carpio* in a freshwater-estuarine protected area in Uruguay. In this context, the species had omnivorous and detritivorous feeding habits, and could be considered generalist. Similar results were obtained in other diet analyses of this species in other regions of La Plata basin (Sidorkewicj *et al.* 1998, Colautti & Remes Lenicov 2001, Maiztegui *et al.* 2019). Detritivorous fish have often been found to act as ecosystem engineers (e.g., Flecker 1996), modifying the accrual of organic matter in the benthic environment, which in turn may affect algal growth and habitat for macroinvertebrates (e.g. Flecker 1996, Hall *et al.* 2002, Taylor *et al.* 2006), therefore affecting the base of the food webs used for other species. Thus, the inclusion of this new detritivore species is not to be neglected, potentially bearing strong consequences in some of the new ecosystems to invade. Our results also suggest that the trophic position of the common carp is multitrophic within the food web, predating on more than one trophic level at a time, which emphasizes its influence over many components of the ecosystem.

Our analyses showed that the common carp fed upon the mud crab *N. granulata*, which is endemic to the Southwest Atlantic Ocean and was listed as a priority species for conservation by the National System of Protected Areas (Sotullo *et al.* 2005). This crab is a bioengineering species, which takes refuge digging holes in the mud where it removes large amounts of sediment, allowing the increase in moisture, organic matter, and substrate penetrability (Escapa *et al.* 2008). This activity affects the structure of benthic communities, and additionally its caves passively retain sediment, detritus, and pesticides during the periods of flooding (Escapa *et al.* 2008). This result opens the possibility of an influence of the common carp over the conservation of this species, and highlights the need to develop further research to evaluate the actual importance of the common carp over its populations. The mollusks *E. mactroides* and *H. australis* are also species listed as priorities for conservation by Clavijo & Scarabino (2013). The native clam *E. mactroides* is used as an economic resource by artisanal fishermen from the Uruguayan coast, an important activity which supports the sustainable development of the mollusk conservation (Beovide *et al.* 2014). The macroinvertebrates ingested by the common carp were generally associated with detritus, as it is a detritivore species that feeds on this resource.

Although the golden mussel *L. fortunei* is a common item in native species diet (González-Bergonzoni *et al.* 2020). The presence of both invasive bivalves *L. fortunei* and *C. fluminea* in the Santa Lucia basin would benefit the invasion of *C. carpio* through the biotic melting model or "Meltdown" (Simberloff & Von Holle 1999). This theory indicates that, as the number of introductions of alien species increases, native species are increasingly affected. This results in the ecosystem subsequently becoming more susceptible to introductions of invasive species, decreasing the resistance of the community's food web. In this sense, invasive species alter the habitat favoring other invasive species, generating a positive feedback system resulting in accelerated accumulation of alien species with their respective ecological impacts (Simberloff & Von Holle 1999). Both invasive mollusks, *L. fortunei* and *C. fluminea*, are grouped into dense patches and could invade different environments and displace benthic macroinvertebrates. The populations of *L. fortunei* are in abundance in several basins of Uruguay, where it has colonized different substrates, including hydroelectric dam turbines and the filtration and water intake systems of the public water treatment plant, generating high economic losses (Brugnoli *et al.* 2006).

Cyprinus carpio and the native species such as the catfish *Iheringichthys labrosus*, the boga *Megaleporinus obtusidens,* and the yellow catfish

Pimelodus maculatus are species with similar feeding behaviors based on the consumption of benthic macroinvertebrates and detritus (Kuczynski *et al.* 2015, López-Rodríguez *et al.* 2019, González-Bergonzoni *et al.* 2020). In this sense, niche overlap between the native species and the common carp should be taken in consideration in further research to have a more complete picture of the effects of this invasive species over local freshwater communities and ecosystems.

In summary, the adverse ecological effects generated by *C. carpio* would modify the food web by altering the trophic interactions of the community above and below its trophic position. The bioturbation generated by foraging common carp could incorporate huge amounts of nutrients into the water column. In addition, it could compete for the resources available with omnivorous or detritivorous native fish, and even introduce exotic pathogens (Gozlan *et al.* 2010). *C. carpio* is considered a species with active foraging throughout the year since food items were analyzed in all the seasons. Conducting a similar analysis of the diet and feeding behaviors of *C. carpio* in other basins of Uruguay could help provide more information on the adverse effects on ecosystems.

The interaction with the recreational and subsistence fishermen was fundamental to carrying out the analysis of the diet of *C. carpio*. Their collaboration demonstrates the scientific support to the fishermen as well, as they showed interest in the study by asking questions about the common carp. In this context, an attempt should be made to implement a *C. carpio* management plan in conjunction with the government, the academy, and sport fishermen in the area.

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Ethics statement

Collection of fish and other biological samples were conducted following all applicable ethical regulations regarding the use and experimentation with animals.

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