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## ORIGINAL PAPER

# The effects of trophic interaction between the Patagonian native *Percichthys trucha* and the invasive *Oncorhynchus mykiss* during the juvenile period

María Gabriela Otturi · Pablo Ezequiel Reggi · Miguel Ángel Battini · Juan Pablo Barriga

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**Abstract** Introduced salmonids have invaded almost all Patagonian freshwater environments, and yet the effect they have had on native fish populations is difficult to evaluate due to a lack of data prior to their introduction. In this study we focused on evaluating trophic interactions during the juvenile period of *Oncorhynchus mykiss*, and the ecologically similar native *Percichthys trucha*. For this purpose, we evaluated the diet and size range of juveniles of both species in the Calefú River over one yearly cycle. The functional response (FR: the relationship between prey density and consumption rate) and functional response ratio (FRR = attack rate/handling time) were estimated for each species, in mono-specific and

multi-specific trials. Comparison of the diet of these species by season showed high similarity for spring and summer. It was also found that juvenile sizes of these species overlap during early ontogeny. Additionally, both species presented a type II FR in mono-specific trials, with similar functional curves. In multi-specific experiments *O. mykiss* juveniles were dominant, leading to a reduction in *P. trucha* food intake. FRR was higher for *O. mykiss* than for *P. trucha* in mono-specific experiments, a difference which increased in multi-specific experiments, indicating the high potential ecological impact of *O. mykiss*. Our results show it is very likely that *O. mykiss* and native *P. trucha* compete in lotic environments, *O. mykiss* being competitively superior, highlighting the potential detrimental effect they may have during the juvenile period, especially in habitats and seasons where food resources are scarce.

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**Keywords** Trophic competition · Functional response · *Oncorhynchus mykiss* · *Percichthys trucha* · Salmonid invasion · Native–exotic interaction

## Introduction

Southern South America has been identified as one of the six global hotspots for fish invasions in freshwater environments, where exotic species represent more

than a quarter of the total number of species (Leprieur et al. 2008). In Argentina, salmonids were frequently introduced from 1904 (Marini 1936) until the present time; mainly because of their sport value. Nowadays, salmonids dominate many freshwater communities (Arismendi et al. 2019), *Oncorhynchus mykiss* (Walbaum, 1792), *Salmo trutta* Linnaeus, 1758 and *Salvelinus fontinalis* (Mitchill, 1814) being the most successfully established species in Patagonia (Pascual et al. 2002). Specifically, *O. mykiss* and *S. trutta* are on the list of the 100 most invasive species worldwide (ISSG 2019), but the impact they have had on fish communities in Patagonia is unknown.

Invasive species generally use resources more efficiently and rapidly than native ones, so comparison of their functional response (FR), i.e. the relationship between prey density and consumption rate of a predator (Holling 1959), can be used to predict the existing, emerging or future effect of an invader competing for a certain resource with a native (Dick et al. 2014; Cuthbert et al. 2019). It has been observed that the greater the difference between the FR of competitors, the higher the expected invader impact on the native community (Dick et al. 2013, 2014; Alexander et al. 2014). Also, FR trials combining several species allow evaluation of behavioural interactions (Nilsson et al. 2004), since results are not always just the simple additive effect of prey consumption by predators. These interactions can provoke any of the following outcomes: (1) a risk-neutral situation for prey when predator effects simply combine additively, (2) risk enhancement as a result of synergism among predators, or (3) risk reduction for prey as a result of antagonism among predators. For this reason, mono and multispecific FR experiments increase the understanding of invasive/native predator interactions when species used in the trials are ecologically similar (Wasserman et al. 2016), and can also be used as a rough predictor of the effect of the exotic predator on the native prey.

In Patagonia, where freshwater fish biodiversity is naturally very low (Ringuelet 1975), the native *Percichthys trucha* (Valenciennes, 1833) is the most ecologically similar fish to the introduced *O. mykiss*, and it is very likely that they might compete for habitat or food. For example, *P. trucha* lives in lentic but also lotic environments, as does *O. mykiss* (Barriga et al. 2007). In lentic environments, these species share similar habitats at different ontogenetic stages

(Macchi et al. 1999; Barriga et al. 2013; Juncos et al. 2013, 2015). During the breeding season, *P. trucha* spawn in the shallow basin of the lake system. These breeding areas, characterized by abundant macrophytes and higher zooplankton density, provide shelter and food for their offspring (Buria et al. 2007). Lattuca et al. (2008) showed that the diet of juveniles of *O. mykiss* and *P. trucha* overlapped in these habitats. In lotic environments, juveniles of both species use sheltering habitats during daytime, such as macrophyte patches (Barriga et al. 2013) or the interstitial spaces of coarse substrate (Otturi et al. 2016). Sharing the same habitat increases the chance of trophic competition between *P. trucha* and *O. mykiss* juveniles in lotic environments, potentially affecting the growth of the native species.

In this research we focused on characterizing trophic interaction during the juvenile period of two fish species of Patagonia: the native *P. trucha*, and the introduced *O. mykiss*. To this end, we carried out a field study and two series of experiments to assess the FR of each species. We also estimated the Functional Response Ratio (FRR) as proposed by Cuthbert et al. (2019). First, we evaluated diet and the size ranges of juveniles of both species in the Calefú River over a yearly cycle. Second, we estimated the FR and FRR of each species individually, using one of the most frequent diet items as prey, the Ephemeroptera nymph, *Meridialaris chiloeensis* (Demoulin, 1955). Following this, we performed multi-specific trials to determine the interaction between predators. Our hypotheses were: (1) *O. mykiss* has a higher FR than *P. trucha*, and (2) the interaction between these species leads to a reduction in *P. trucha* food intake.

## Materials and methods

Field study: fish collection, diet, and length frequencies

We captured juveniles of *P. trucha* and *O. mykiss* during fourteen sampling sessions from September 2002 to August 2003, in the Calefú river (40° 20' × 10'' S, 70° 45' × 12'' W; 595 m above sea level), Neuquén province, Argentina. The Calefú river belongs to the Limay river basin and its ichthyofauna includes native species: *Galaxias maculatus* (Jenyns 1842), *G. platei* Steindachner, 1898, *P.*

*trucha*, *Hatcheria macraei* (Girard 1855), *Trichomycterus areolatus* Valenciennes, 1846, *Olivaichthys viedmensis* (MacDonagh, 1931) and *Odontesthes hatcheri* (Eigenmann, 1909), and introduced salmonids: *O. mykiss*, *S. trutta* and *S. fontinalis*. Fish were caught using a 24 V DC backpack electrofishing unit model 12-B (Smith-Root Inc., Vancouver, WA, USA), during daytime, from 11:00 to 15:00 h. Fishing was performed in an upstream direction along ca. 150 m in riffles and ca. 80 m in runs and pools. The sampling was designed as part of another study to capture all fish present in these specific areas (see details in Barriga et al. 2007). Carbon dioxide-saturated water solution was used to sacrifice captured fish, which were then stored in 4% formaldehyde in the laboratory. Fish standard length (SL) was measured with a digital calliper ( $\pm 0.1$  mm), and stomach contents were examined under a binocular stereomicroscope. Undigested food items were identified following Fernández and Domínguez (2001) to the lowest possible taxonomic level, and counted for each prey category (Wallace 1981). The taxonomic resolution was not homogeneous because some prey items could not be identified further than Order, whereas others could be identified to Family level. The volume of each prey item was measured by water displacement in a graduated cylinder. Three diet measurements were registered for each species. The percentage by number (%N) and percentage by volume (%V) contribution of each prey category ( $i$ ) were calculated as  $\%Ni = 100 Ni Nt^{-1}$ , where  $Ni$  is the total number of items of prey category  $i$  and  $Nt$  is the total number of items of all prey categories;  $\%Vi = 100 Vi Vt^{-1}$ , where  $Vi$  is the total volume of items of prey category  $i$  and  $Vt$  is the total volume of items of all prey categories. Both %N and %V make reference to the relative abundance in percentage of a specific prey category. Also, the frequency of occurrence (%F), the percentage of fish that ate a specific prey category, was determined as  $\%Fi = 100 ni nt^{-1}$ , where  $ni$  is the number of fishes containing prey category  $i$  in the stomach and  $nt$  is the total number of fishes containing food in the stomach. Finally, the importance of the different prey categories to the diet was identified using the compound index of relative importance (IRI) (Pinkas et al. 1971), as modified by Hacunda (1981), which is essentially a mean of the three diet measurements previously estimated:  $IRIi = (\%Ni + \%Vi) \%Fi$ . This index has been expressed as  $\% IRIi = 100 IRIi (\sum IRIi)^{-1}$ .

Similarity in diet composition between species was estimated by season using Schoener's index:  $SI = 1 - 0.5[\sum (\%IRLxi - \%IRLyi)]$ , where  $\%IRLxi$  is the index of relative importance of prey category  $i$  in the *P. trucha* ( $x$ ) diet and  $\%IRLyi$  is the index of relative importance of prey category  $i$  in the *O. mykiss* ( $y$ ) diet (Schoener 1970). The Shannon-Weaver diversity Index (Townsend et al. 2003) was calculated for each species by season, as  $H' = -\sum pi \ln(pi)$ , where  $pi$  is the relative abundance of each prey category.

In order to test differences in diet composition between species, we generated a dissimilarity matrix based on the Bray-Curtis dissimilarity index. For this analysis we transformed the diet data by using the fourth root of percentages of the number and the volume of prey items for each fish (i.e. the percentage corresponding to each prey category over the total prey consumed by one fish). We then performed a non-metric multidimensional scaling (NMDS) to visualize diet variation among individuals. We applied two approaches: first we performed an overall analysis including all the seasons, and second, we performed a seasonal analysis. In the latter we analysed only spring and summer data because of the unbalanced number of individuals captured (*Pt*  $N = 96$  vs. *Om*  $N = 17$ ) for diet analysis. Autumn data did not meet statistical assumptions (*Om*  $N = 02$ ) and during winter we did not capture *O. mykiss*.

For the two approaches we tested diet differences through a multivariate permutation analysis of variance (PERMANOVA) using the vegan package (Oksanen et al. 2019) in R. For the seasonal analysis we also performed 'a posteriori' pairwise comparisons between groups with Bonferroni's correction for multiple testing, using the RVAideMemoire package (Hervé 2020) in R.

Length-frequency analysis was performed throughout the year in order to compare growth rate and fish size range at any particular date for both fish species. The relationship between SL and date was assessed separately for *P. trucha* and *O. mykiss* using linear regression analysis. Date data were changed to numbers, where January first corresponded to 1, and so on. The data were then log<sub>10</sub>-transformed to yield a linear relationship and meet statistical assumptions. The difference between the linear regression slopes, as a proxy for the growth rates of the two species, was tested by an analysis of covariance (ANCOVA) where SL was the dependent variable, species was the

categorical factor and date was the co-variable. As growth rate should be calculated for each cohort found, for this analysis only the most informative *P. trucha* cohort (i.e. the first cohort with the largest number of individuals) was analysed.

### Functional response experiments

We collected fish for the experiments in lotic environments of the Limay river basin. We used a 24 V DC backpack electrofishing unit, model 12-B (Smith-Root, Inc., Vancouver, WA, USA) to capture an average of 80 *P. trucha* juveniles and 80 *O. mykiss* juveniles. We transported the fish in heat-insulated containers to the Centro de Salmonicultura Bariloche of Universidad Nacional del Comahue in the city of San Carlos de Bariloche, Río Negro province, Argentina. Each species was housed separately in circular tanks of 473 l with a permanent water flow supplied from Gutiérrez stream (mean values: temperature 11.2 °C; pH 7.43; O<sub>2</sub> 5.9 mg/l and conductivity 70.5 µS/cm). The tanks were covered to protect fish from birds and prevent disturbance. The acclimatization period lasted for at least 1 week until the FR trials began. During that time, fish were fed with live *Tubifex* sp.

We performed FR experiments from August to November 2015 and during April and July 2017, using 5 aquariums of 10 l each, connected to a recirculation system with a biological filter and a constant water flow that emulated the current of a lotic environment. The aquarium system was placed inside an Incubator (Ingelab, Model I-501 PF) that ensured a constant temperature of 14 ± 0.2 °C. Photoperiod was set at 12 l/12D, alternating 190 and 0 lx every 12 h. The incubator was fitted with an inner black opaque plastic sheet in order to isolate fish visually from the operator when the door was opened to introduce prey. Fish were size matched with respect to standard length (SL ± SE, 5.32 ± 0.40 cm for *P. trucha* and 5.55 ± 0.53 cm for *O. mykiss*, Table S1 of the Supplementary Material).

*Meridialaris chiloeensis* nymphs (Ephemeroptera) were collected manually from the Gutiérrez stream, and used as prey. These nymphs are very abundant in lotic environments (Albariño and Buria 2011) and fish species consumed them readily (present study; Di Prinzio et al. 2015; Navone 2006). Prey size did not differ significantly between fish species trials (*Mann-*

*Whitney*,  $P > 0.05$ ). Individual fish were randomly selected 24 h prior to the trials, allocated to experimental aquariums and held without food to allow for standardization of hunger levels. Each fish was used once in the series of trials.

To analyse the relationship between the proportion of prey eaten and prey density, we determined FR type using logistic regression. Type II function is characterised by a negative first-order term, i.e. the proportion of prey consumption decreases as prey density increases. In contrast, type III function shows a positive first-order term, the consumption of prey increasing and then decreasing (Juliano 2001).

We performed two types of trial: the first with a single individual of one of the two species (i.e. monospecific) per aquarium to obtain the species FR for this specific prey. In this experiment we emphasized observation at low densities, since differences in predatory behaviour that differentiate types II and III FR appear at low densities. For this reason, we used eight prey densities (2, 4, 6, 10, 15, 20, 30 and 60), with five replicates per density.

As a specific amount of prey was provided just once at the beginning of the experiment and not replaced during trials, we used the 'random predator equation' (Rogers 1972) as suggested by Juliano (2001):

$$N_e = N_0(1 - \exp(-a(N_e h - T)))$$

where  $N_e$  is the number of prey items eaten,  $N_0$  is the initial density of prey,  $a$  is the attack rate,  $h$  is the handling time and  $T$  is the total time available. Owing to the implicit nature of the random predator equation, since  $N_e$  appears on both sides of the equation, the Lambert W function was implemented to fit the model to the data (Bolker 2008). Model optimisation was performed using maximum likelihood estimation. To compare functional responses, for each case we constructed 95% confidence intervals around the function using a nonparametric bootstrapping method. We also calculated the functional response ratio ( $FRR = a h^{-1}$ ) as a predictive metric for the potential ecological impact of the invasive predator compared to the native species (Cuthbert et al. 2019).

The experiments were performed after acclimatization, and the specific number of prey items for each trial was introduced into the aquarium through a flexible polymer tube. We determined prey consumption after 20 min by counting the uneaten prey and

subtracting this number from the total number of prey items offered.

The second series of experiments combined a pair of individuals (one of each species, i.e. multi-specific) to evaluate how prey consumption was affected by the presence of the other species. In this case, we presented the pairing of *P. trucha* - *O. mykiss* with 6 prey densities (2, 4, 8, 16, 32 and 64), with four replicates per density, and evaluated prey consumption after 20 min. We sacrificed the fish immediately after each trial with an overdose of benzocaine, and examined their stomach contents to count the prey items eaten by each fish. To analyse predatory performance in multi-specific experiments we calculated the expected combined prey consumption of the two fish species by applying the following model (Soluk 1993):

$$C_{com} = N_0(P_{Pt} + P_{Om} - P_{Pt}P_{Om})$$

where  $C_{com}$  is the predicted combined consumption for *P. trucha* and *O. mykiss* for an initial prey density ( $N_0$ ).  $P_{Pt}$  and  $P_{Om}$  are the probabilities of being preyed on by *P. trucha* and *O. mykiss*, respectively. Data for both predator species were generated from mono-specific experiments. Thus, we compared two models, the expected FR model and the observed FR model estimated from multi-specific experiments.

All functional response estimations were performed using the Frair package (Pritchard et al. 2017) in R (R Development Core Team 2019). In addition, between-species differences in the percentage of consumed prey with regard to total prey offered were tested using a Wilcoxon test, since normality of the data failed.

## Results

### Diet and fish length frequencies

The diet of juvenile fish in Caleufu River was based on aquatic invertebrates, mostly in larval stages. The main prey items of *P. trucha* were Ephemeroptera nymphs and Chironomidae larvae throughout the entire year, while *O. mykiss* ate mainly Ephemeroptera nymphs during spring and summer, shifting to Trichoptera larvae and Notonectidae in autumn. Comparison of the diets of these species by season showed high similarity for spring (SI = 0.64) and

summer (SI = 0.69); however, in autumn similarity was low (SI = 0.07). Diet diversity was highest during summer for both species (Table 1).

The overall analysis of diet showed no significant differences between *P. trucha* and *O. mykiss*, whether using number (PERMANOVA, Pseudo-F = 1.674,  $p = 0.145$ ) or volume (PERMANOVA, Pseudo-F = 1.859,  $p = 0.105$ ) of prey consumed (Fig. 1). In the seasonal analysis we found significant differences in diet in both number (PERMANOVA, Pseudo-F = 5.874,  $p < 0.001$ ) and volume (PERMANOVA, Pseudo-F = 3.710,  $p < 0.001$ ) between species and seasons (i.e. four groups). However, no differences were found between species when comparing number or volume of prey within the same season (Pairwise PERMANOVA,  $p > 0.05$ , Fig. 1).

The progression of fish size cohorts throughout the year in Caleufu river showed that *P. trucha* had two distinctive cohorts while *O. mykiss* showed only one (Fig. 2). This progression also indicates that *O. mykiss* cohort size was situated between the two *P. trucha* cohort sizes, which means that *O. mykiss* individuals overlapped in size with some individuals from the first *P. trucha* cohort (larger individuals), but also overlapped in part with individuals belonging to the second *P. trucha* cohort (smaller size). In addition, the juvenile fish size of both species analysed throughout the year indicates that *O. mykiss* grew faster than *P. trucha* (Fig. 2; Table 2). The linear regression model slope was significantly higher for *O. mykiss* than for *P. trucha* (ANCOVA;  $F_{1, 109} = 138.562$ ;  $P < 0.001$ , Table S2).

### Functional response trials

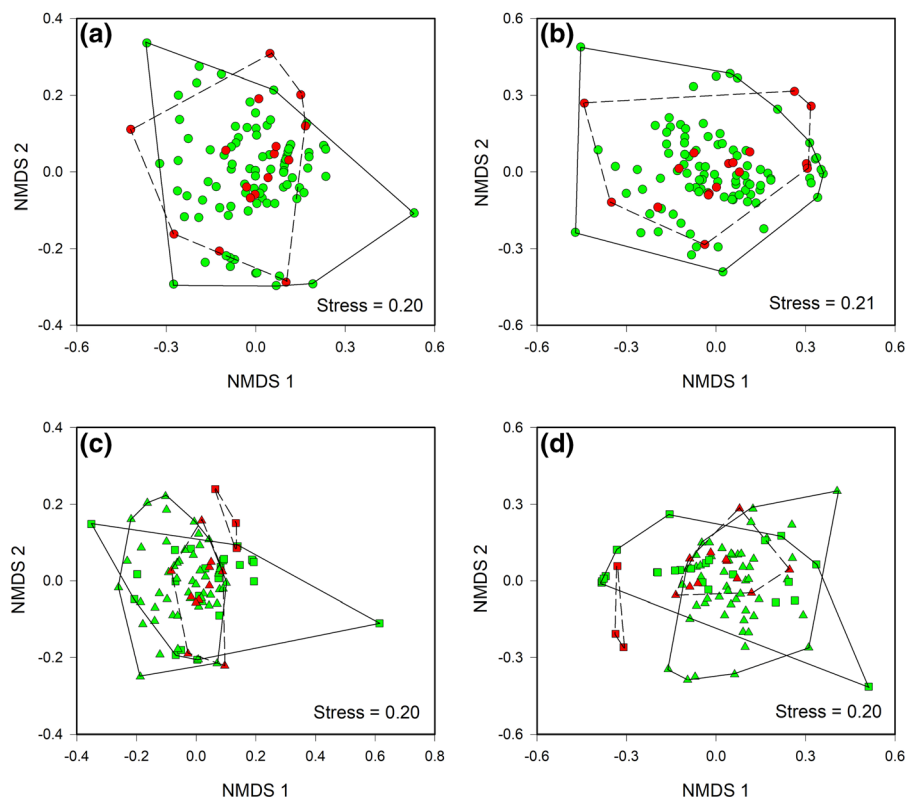
*Percichthys trucha* and *O. mykiss* presented a type II FR in mono-specific trials, since the first order terms of logistic regressions were significantly negative ( $-0.027$  and  $-0.060$  respectively,  $P < 0.001$ ). The parameters  $a$  (attack rate) and  $h$  (handling time) of both FR models were significant ( $P < 0.001$ ). The two species had similar functional curves because 95% confidence intervals overlapped (Fig. 3).

Observed and expected FR models of multi-specific experiments were also of Type II ( $P < 0.001$ ). Both FR models had significant ( $P < 0.001$ )  $a$  and  $h$  parameters and were significantly different based on their 95% confidence intervals, which did not overlap (Fig. 4; Table 3). The two curves were similar up to a

**Table 1** Seasonal diet composition in percentage of relative importance index (%IRI) of *P. trucha* and *O. mykiss* juveniles in Calefufu River, Argentina. Shannon–Weaver diversity index ( $H'$ ) is also indicated

Diet item	<i>P. trucha</i> (n = 96)				<i>O. mykiss</i> (n = 17)			
	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter
Ephemeroptera (N)	64	24	53	100	77	52	0	–
Chironomidae (L)	24	55	36	0	0	38	2	–
Trichoptera (L)	3	7	4	0	0	4	51	–
Plecoptera (N)	5	0	6	0	0	0	0	–
Chironomidae (P)	0	5	0	0	0	1	0	–
Dytiscidae (L)	0	5	0	0	18	0	0	–
Amphipoda	3	2	0	0	0	0	0	–
Notonectidae	0	2	0	0	1	1	33	–
Anisoptera (L)	0	0	0	0	4	0	14	–
Simuliidae (L)	0	0	0	0	0	3	0	–
$H'$	2.75	3.65	2.76	1.00	1.99	2.90	2.85	–

*N* nymphs, *L* larvae, *P* pupae



**Fig. 1** Non-metric multidimensional scaling (NMDS) biplots displaying the food resource used by juveniles of *P. trucha* (green) and *O. mykiss* (red). Analyses were computed using the Bray–Curtis dissimilarity distances based on volume **a**, **c** or number **b**, **d** of prey consumed. NMDS was performed for the

whole year (circles, **a** and **b**) and only for spring (squares) and summer (triangles) seasons (**c**, **d**). Lines (solid for *P. trucha* and dashed for *O. mykiss*) limit the resource area used by each species to show the overlap between them



prey density of 10, after which the curves diverged, the expected model being higher than the observed model (Fig. 4).

*Oncorhynchus mykiss* juveniles were the dominant individuals in multi-specific experiments in terms of consumptive ability. At all experimental densities the percentage of prey consumed was higher for *O. mykiss* than *P. trucha* (Wilcoxon,  $P < 0.001$ ; Fig. 5). In addition, the differences in FR parameters between mono and multispecific trials were lower for *O. mykiss* than for *P. trucha*, and the attack rate parameter overlapped only for *O. mykiss* (Table 3). The change in the curve was therefore stronger for *P. trucha* than for *O. mykiss* when the species were evaluated jointly.

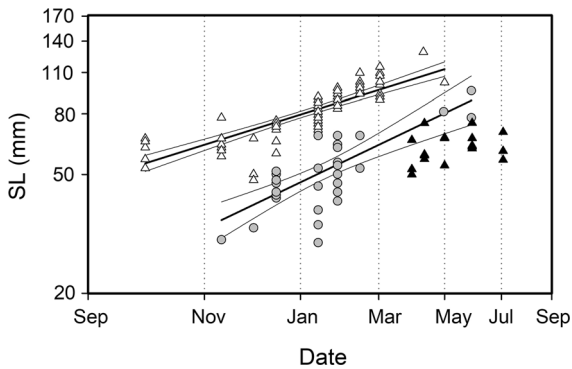
The FRR in the mono-specific trials was 79.913 for *O. mykiss* and 60.758 for *P. trucha*, indicating the higher potential ecological impact of the invader compared to the native. In the multi-specific

experiments, the FRR was lower for both predators, a reduction of around 52% for *O. mykiss*, but 98% for *P. trucha* (Table 3).

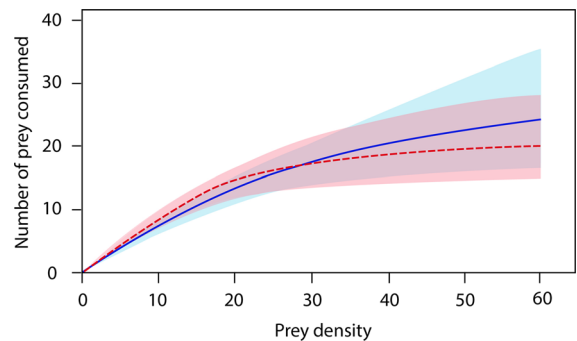
### Discussion

Our results show that introduced *O. mykiss* and native *P. trucha* are very likely to compete in lotic environments, *O. mykiss* being competitively superior. First, we found that the diets of these species overlap during their early life stages, especially during spring and summer. Second, we found that *O. mykiss* presence reduces *P. trucha* food intake in multi-specific FR trials. Together, these results could help to explain why *P. trucha* is almost absent from Patagonian streams and rivers where salmonids are very abundant.

In Caleufu river, *P. trucha* and *O. mykiss* juveniles prey on aquatic macroinvertebrate resources. The diversity of diet items of both species is narrow, with the maximum value in summer. During spring the diets of these species overlap, mainly owing to



**Fig. 2** Size variation in juvenile fish throughout the year for *P. trucha* (triangles) and *O. mykiss* (circles) in Caleufu River, Argentina. Lines indicate linear regression models and their 95% CI for *P. trucha* first cohort (white) and *O. mykiss*. The second cohort of *P. trucha* is also indicated (black). The date was numerically coded, the first of January corresponding to 1. Fish standard length (SL in mm) and date were Log-transformed. Axes are in Logarithmic scale



**Fig. 3** Type II functional responses with 95% confidence intervals (shaded areas) for *P. trucha* (solid line) and *O. mykiss* (dashed line), derived from the nonparametric bootstrapping method, in mono-specific experiments. Nymphs of the Ephemeroptera *M. chiloensis* were used as prey

**Table 2** Linear regression model estimates ( $\pm$  95% CI) between fish size (SL in mm) and date for native and exotic fish from Caleufu River, Argentina., Sampling size, model adjustment and  $P$  value are also shown

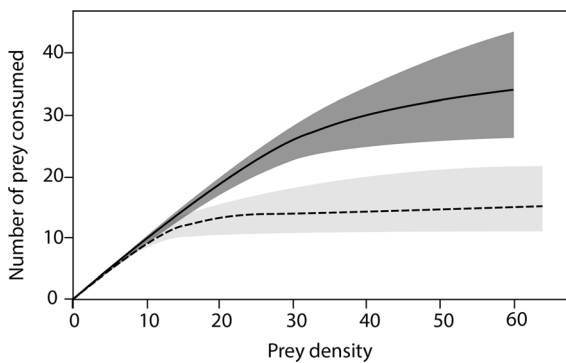
	Slope	Intercept <sup>a</sup>	n	r <sup>2</sup>	p value
<i>P. trucha</i>	1.254 $\pm$ 0.220	- 1.306 $\pm$ 0.533	76	0.71	0.0001
<i>O. mykiss</i>	1.782 $\pm$ 0.497	- 2.884 $\pm$ 0.988	37	0.52	0.0001

<sup>a</sup>Date data were transformed to numbers, January first corresponds to 1

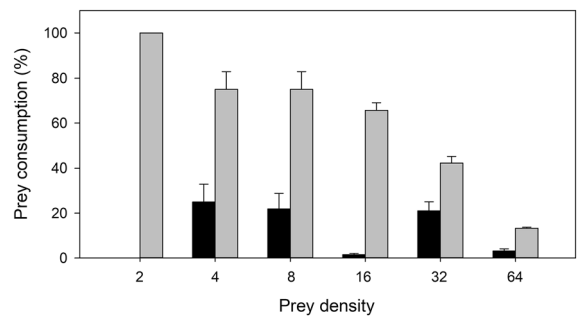
Ephemeroptera nymph consumption, while in summer the presence of Chironomidae larvae is another important overlapping component. As indicated by the PERMANOVA, the native and exotic fish used the same food resource in this period of year. Ephemeroptera nymphs and Chironomidae larvae represent a significant part of the total biomass of macroinvertebrates found in Andean Patagonian rivers (Misereudino 2001), and are commonly eaten by fishes in rivers. It is known that *O. mykiss* juveniles have a generalist feeding strategy, and are capable of feeding on any peak of prey (Arismendi et al. 2011; Di Prinzio et al. 2015). In the same way, *P. trucha* juveniles in

lentic environments have been described as generalized benthic invertebrate predators (Lattuca et al. 2008). In this sense, it is very likely that during spring and summer, the most abundant food period (Navove 2006), *P. trucha* and *O. mykiss* simply use the most abundant prey resource present in the river. In addition, considering that these fish are gape-limited predators, their overlapping size means they are likely to prey on the same aquatic invertebrates.

The juvenile sizes of these species overlap during early ontogeny. The spawning season of *P. trucha* begins at the end of spring (López-Cazorla and Sidorkewicz 2011), and assuming a hatching size of approx. 5 mm (Battini unpublished data), the first cohort individuals from Calefú river correspond to one-year-old fish. In contrast, landlocked *O. mykiss* in northern Patagonia spawn between May and



**Fig. 4** Type II functional responses with 95% confidence intervals (shaded areas) for both species together (*P. trucha* and *O. mykiss*) in the multi-specific experiments, derived from the nonparametric bootstrapping method. Dark grey represents expected functional response based on mono-specific trials, whereas light grey indicates FR based on observed data (multi-specific experiment). Nymphs of the Ephemeroptera *M. chiloeensis* were used as prey



**Fig. 5** Consumption as percentage of total prey offered in the multi-specific experiment. Mean and standard error (SE) is shown for *P. trucha* (black) and *O. mykiss* (grey)

**Table 3** Type II functional response parameters ( $\pm$  SE) estimated for native and exotic fish in mono-specific and multi-specific experiments. Models were calculated for each species (mono and multi-specific) or combining both species (multi-specific)

	<i>O. mykiss</i> (obs)	<i>P. trucha</i> (obs)	<i>O. mykiss</i> + <i>P. trucha</i> (obs)	<i>O. mykiss</i> + <i>P. trucha</i> (exp)
<i>Mono-specific</i>				
<i>a</i>	3.485 $\pm$ 0.418	1.754 $\pm$ 0.200	–	–
<i>h</i>	0.044 $\pm$ 0.003	0.029 $\pm$ 0.004	–	–
$(h T)^{-1}$	22.932 $\pm$ 1.691	34.632 $\pm$ 4.437	–	–
FRR	79.913 $\pm$ 3.748	60.758 $\pm$ 0.758	–	–
<i>Multi-specific</i>				
<i>a</i>	2.860 $\pm$ 0.579	0.243 $\pm$ 0.084	6.288 $\pm$ 1.781	5.518 $\pm$ 0.674
<i>h</i>	0.076 $\pm$ 0.008	0.185 $\pm$ 0.060	0.063 $\pm$ 0.006	0.025 $\pm$ 0.002
$(h T)^{-1}$	13.131 $\pm$ 1.341	5.402 $\pm$ 1.970	15.867 $\pm$ 1.414	40.050 $\pm$ 2.794
FRR	37.556 $\pm$ 3.839	1.315 $\pm$ 0.027	–	–

*a* attack rate; *h* handling time;  $(h T)^{-1}$  maximum feeding; FRR functional response ratio ( $a h^{-1}$ ); *obs* observed; and *exp* expected

September (Arismendi et al. 2011), and a hatching size of 13 mm (Woodworth and Pascoe 1982) would indicate that the first cohort in Calefú river is composed of individuals younger than one-year-old. At the beginning of autumn (i.e. end of March), the second cohort of *P. trucha* appears in the river when the SL of *O. mykiss* juveniles is around 70 mm. At this point, two different native–exotic situations emerge, depending on fish size and time of year. During spring and summer, *P. trucha* juveniles are larger in size than those of *O. mykiss*, which could confer a competitive advantage on the native species during this period. In contrast, during autumn and winter the opposite situation is observed, since *P. trucha* individuals belonging to the second cohort are smaller than those of *O. mykiss*, shifting the competitive advantage in favour of the exotic *O. mykiss*.

Mono-specific FR for *P. trucha* and *O. mykiss* correspond to a Type II function. Contrary to our first hypothesis, the curves were very similar, with considerable overlapping between them. This type of FR is characterized by a hyperbolic curve where consumption rate decelerates as density increases (Real 1977), because more time is spent handling or processing prey and less time is spent searching for it, until prey saturation is reached, when all time is spent handling prey (Koski and Johnson 2002). Fish that forage in environments where prey is patchy typically show this kind of response (Smith 1998). Also, Type II FR is often observed in predators that can destabilize prey populations (Dick et al. 2014). However, at this point we should note that the trials were performed without shelter for prey. As the magnitude and shape of FR are prey-refuge dependent (Barrios-O'Neill et al. 2016; Alexander et al. 2015) the curve could vary, since in nature *M. chiloeensis* inhabits rocky substrates where it can find refuge from predators.

In agreement with our second hypothesis, the observed FR was lower than the expected one in multi-specific trials. This was mainly due to the lower feeding performance of *P. trucha*, indicated by the lower attack rate ( $a$ ) and higher handling time ( $h$ ), while FR parameters varied less for *O. mykiss*. This evidenced a process of interference on the part of *O. mykiss*, negatively affecting *P. trucha* and reducing the food intake principally of the native species.

There are three possible outcomes of interactions between predators in terms of the risk for prey: a

neutral situation where predator effects simply combine additively, enhancement as a result of synergism, or reduction as a result of antagonism among predators (Wasserman et al. 2016). The interaction between *P. trucha* and *O. mykiss* in the multi-specific FR experiments correspond to the last of these. This interaction could be direct aggression, where the subordinate species spend a lot of time retreating or just slowly following the dominant species and not feeding (Wasserman et al. 2016). The reduction in consumption rate—mainly in *P. trucha* but also in *O. mykiss*—when these species interact resulted in a net reduction in the effect on prey populations. The reduced food intake in *P. trucha* is probably the outcome of dominant behaviour on the part of *O. mykiss*. Otturi et al. (2016) found in diel locomotor activity experiments that in the presence of *O. mykiss*, *P. trucha* showed defensive behaviour consisting in erection of the dorsal fin spines and an unusual opening of the operculum. Time spent in this defensive reaction probably interferes with feeding efficiency, evidenced by the higher handling time and lower attack rate of *P. trucha*. The same trend was found when using the functional response ratio, which was higher for *O. mykiss* than *P. trucha* in both mono and multi-specific experiments. In the latter case the difference even increased, indicating the high potential ecological impact of the exotic *O. mykiss* (Cuthbert et al. 2019).

The agonistic interaction between *P. trucha* and *O. mykiss* in the multi-specific FR experiments leads to a reduction in risk for *M. chiloeensis*. The experiments indicate that at low prey densities the difference in prey consumption between species is enhanced in favour of *O. mykiss*. At the same time, salmonids have a strong negative effect on the invertebrate biomass in Patagonian streams (Buria et al. 2007; Albariño and Buria 2011). In this way, *O. mykiss* probably exerts a strong effect on *P. trucha* feeding in lotic environments, first decreasing the invertebrate biomass and then being competitively superior at these low prey densities.

Based only on FR experiments we cannot use direct extrapolation to predict what happens in nature, due to the complex characteristics of natural environments. However, considering the available information, a possible scenario could emerge. During spring and summer, the abundance of macroinvertebrates used as a prey resource for juvenile fish is at a maximum (Navone 2006) and the two species overlap in their

diets. In this situation, *P. trucha* would consume fewer prey number as a result of the negative interference of *O. mykiss*, if both species were of equivalent sizes. However, the question of whether the difference in size observed in favour of *P. trucha* is sufficient to lessen this negative impact remains to be answered. If the densities of *M. chiloeensis* are low, which seems not to be the case in these seasons, *P. trucha* would be negatively affected by *O. mykiss* and it would be expected that *P. trucha*—rather than *O. mykiss*—would switch to other prey. In turn, this shift would indirectly cause increased predation pressure from *P. trucha* on other members of the invertebrate community. This situation could occur during autumn and/or winter when decreasing *M. chiloeensis* abundance would act jointly with fish size difference, favouring *O. mykiss*.

The population dynamics of these two species play an important role in the native–exotic interaction. As we registered in Caleufu river, larger juveniles of *P. trucha* could have the potential to attenuate the detrimental effect of the smaller *O. mykiss* during spring and summer. Therefore, the precise spawning date of *P. trucha* would have substantial implications for offspring survival of this species in lotic environments where *O. mykiss* is present.

Environmental variables greatly influence inter-specific interactions (Dunson and Travis 1991). Temperature affects competition (Warren et al. 2016); for example, Watz et al. (2019) reported the effect of temperature on the FR of two salmonid species. In the present study the experiments were run at 14 °C. Considering that the preferred temperature of *P. trucha* is higher than that of *O. mykiss* (Aigo et al. 2014), it is possible that interspecific interaction will change in favour of *P. trucha* at higher temperatures, in a context of global change (Vigliano et al. 2018). In line with this, Aigo et al. (2008) found an abundance shift in the littoral zone of lakes; i.e., increasing abundance of *P. trucha* in relation to *O. mykiss* with an increment in water temperature. However, *O. mykiss* populations can develop tolerance to high temperatures, mainly in environments where the species has been frequently stocked to maintain the fishery industry. Physiological evidence that *O. mykiss* can undergo a certain level of selection and has the ability to survive hot climates has been obtained from different strains in Japan (Ineno et al. 2005), Australia (Chen et al. 2015) and Argentina (Crichigno and

Cussac 2019). Faced with this dilemma, it would be interesting to perform *P. trucha* and *O. mykiss* FR comparisons at higher temperatures, in order to understand the effect of temperature on prey capture performance.

The abundance of native and exotic species differs between steppe and mountain environments (Aigo et al. 2008). Specifically, *P. trucha* is more abundant in warm steppe waters, with slow flow, fine substrate deposits and submerged vegetation (Barriga et al. 2007, 2013) and is absent in mountain streams. These environments, where only salmonids are found, are characterized by colder, fast-flowing water and substrate of a large size (e.g. Lallement et al. 2016).

Several studies have evidenced the negative effects of salmonids on native populations in the Southern hemisphere (e.g. McDowall 2006, Young et al. 2010, Habit et al. 2010). However, in Patagonian lotic environments, the lack of information on the composition of fish assemblages prior to salmonid introductions (Macchi et al. 2007, Pascual et al. 2007) makes quantification of the effect of salmonid invasion on native fish populations difficult. Our study highlights the potentially detrimental effect of *O. mykiss* on *P. trucha* through negative trophic interference during the juvenile period, especially in those habitats and seasons where food resources are scarce.

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