



Niche overlap in sympatric introduced trout from a southern Patagonian river: evidence from stomach contents and stable isotope analysis

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Abstract: We used a combination of stomach content and stable isotope analyses to assess the trophic interactions and feeding habits of two different salmonid species, brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*) in the Serrano River (Magellan and the Chilean Antarctic Region). We found a high dietary niche overlap, which was supported by Schoener's index and stable isotopes Bayesian ellipses. The diet was dominated by the amphipod *Hyaella* spp. in both species. Nonetheless, evidence suggests that *O. mykiss* has a more generalist feeding strategy than *S. trutta*. The dietary breadth indices and the isotopic niche area, which were broader for *O. mykiss* than *S. trutta*, supported this scenario. This study increases our understanding on the trophic relationships among these introduced trout cohabiting the river and their possible effects in freshwater ecosystems from southern Chile.

Key words: Trophic ecology, exotic species, *Oncorhynchus mykiss*, *Salmo trutta*, Magellan region, Diet.

Sobreposición de nicho en truchas simpátricas introducidas en un río en la Patagonia austral: evidencia mediante análisis de contenido estomacal e isótopos estables. Resumen:

Utilizamos una combinación de análisis de contenido estomacal e isótopos estables para evaluar las interacciones tróficas y los hábitos alimentarios de la trucha marrón (*Salmo trutta*) y la trucha arcoíris (*Oncorhynchus mykiss*) en el río Serrano (Región de Magallanes y de la Antártica Chilena). Encontramos una alta sobreposición de nicho en la dieta, que fue respaldada por el índice de Schoener y las elipses Bayesianas. Para ambas especies la dieta estuvo dominada por el anfípodo *Hyaella* spp. No obstante, la evidencia sugiere que *O. mykiss* tiene una estrategia de alimentación más generalista que *S. trutta*. Los índices de amplitud dietaria y el área del nicho isotópico, que fueron más amplios en *O. mykiss* que en *S. trutta*, respaldan este escenario. Este estudio aumenta nuestra comprensión sobre las relaciones tróficas entre estas truchas introducidas y los efectos en los ecosistemas de agua dulce del sur de Chile.

Palabras clave: Ecología trófica, especies exóticas, *Oncorhynchus mykiss*, *Salmo trutta*, región de Magallanes, Dieta.

Introduction

Introducing exotic species is one of the main causes of biodiversity loss in freshwater ecosystems (Dudgeon *et al.* 2006). Many authors outlined the impact of exotic fishes through predation and competition with native fishes, changing the behavior and abundance of prey and affecting entire food web dynamics (Vander Zanden *et al.* 1999, Nyström *et al.* 2003, Baxter *et al.* 2004). In particular, brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*) are considered two of the most broadly distributed and harmful exotic fish in the world, including even in remote places like southern Patagonia (Cambrey 2003, Crawford & Muir 2008). Indeed, the freshwater fish communities in the Chilean portion of Patagonia are dominated by brown and rainbow trout (Soto *et al.* 2006). Today's assemblage, however, is in part the result of a naturally species-poor native fish community that is the legacy of the region's evolutionary and biogeographic isolation from the rest of South America, given barriers like the Andes Mountains to the east, the Pacific Ocean to the west and the Atacama Desert to the north and recurrent Quaternary glaciations that repeatedly eradicated most suitable freshwater habitats (Cussac *et al.* 2004, González-Wevar *et al.* 2015).

Since their introduction in Chile at the beginning of the 1900s for recreational fishing purposes, both trout species have become widely distributed, established populations and invaded extensive areas as the largest and most abundant freshwater fishes in southern Chilean Patagonia (Campos 1985, Soto *et al.* 2006, Arismendi *et al.* 2009). According to Soto *et al.* (2006), together brown and rainbow trout constitute over 95% of the total fish biomass found in rivers from southern Chile (between 39° and 52°S). However, despite their high abundance and co-occurrence patterns, there is still a need for more information about the trophic interactions among these sympatric species (Lattuca *et al.* 2008, Penaluna *et al.* 2009, Arismendi *et al.* 2012). In addition, the impact of brown and rainbow trout as biological invasions in southern Patagonia is not fully explored, mostly due to the lack of available data on native species abundance and their trophic interactions before trout introductions. Nonetheless, they are known to affect ecosystem processes principally by their predatory

and competitive interactions in food webs and their potential role in facilitating other invasive species via “invasional meltdown” (Valenzuela *et al.* 2014, Ortiz-Sandoval *et al.* 2017).

This study aims to compare the feeding habits and trophic interactions between two sympatric introduced trout (*S. trutta* and *O. mykiss*) in a southern Patagonian river and quantify dietary overlap through the combined approach of stomach content and stable isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) analyses. In particular, the degree of overlap in food resources was expected to reflect the amount of interspecific feeding competition between these sympatric introduced species.

Materials and Methods

This study was carried out in the Serrano River basin (51°14'S, 72°58'W, Fig. 1), half of which lies within the boundaries of the Torres del Paine National Park (UNESCO Biosphere Reserve). This basin is characterized by waters of glacial, pluvial and nival origin and a rainfall regimen of 790 mm year⁻¹ (Rivera *et al.* 2017). It is a major sportfishing destination in the austral summer (from October to April), where anglers catch brown and rainbow trout and Chinook salmon. We used the platform of the recreational fisheries to collect the specimens for this study. All fish caught by anglers during January 2017 were measured and weighed to obtain the size range (total length = TL in cm) and total weight (TW in g). For stomach content analysis, the entire digestive tract was removed and conserved in 80% ethanol. In the laboratory, these contents were identified to the lowest possible prey taxon under a stereoscopic microscope. Every prey item was counted and weighed. In order to assess sample sufficiency, randomized cumulative prey diversity curves with standard deviation, measured with the Shannon-Wiener index, were constructed for each species using EstimateS v.9.1 (Colwell 2019). The percentage of occurrence (%O) of each prey item, the percentage of the total number (%N) of diet items and the percentage of weight (%W) of each item were estimated. The index of relative importance (%IRI) was calculated following Hyslop (1980). The feeding strategy of *S. trutta* and *O. mykiss* was assessed with the graphical method proposed by Amundsen *et al.* (1996). In the graphical method, prey-specific abundance (%P) is

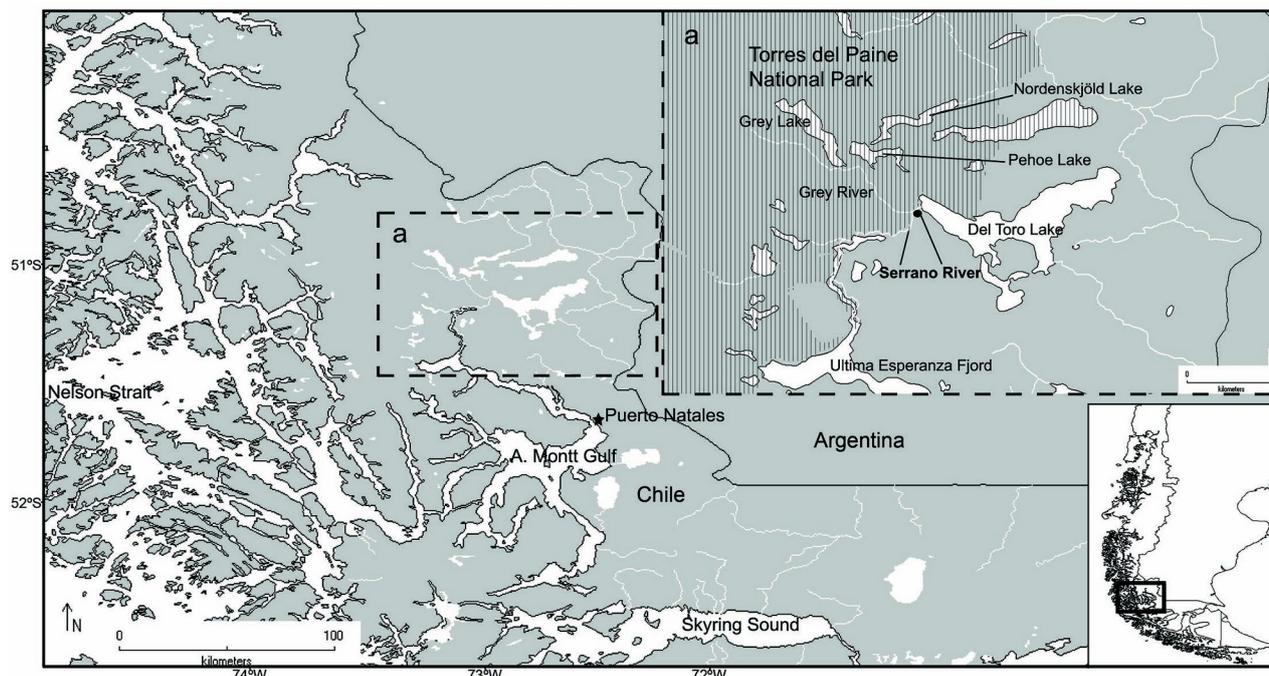


Figure 1. Map of the study area in the Chilean portion of southern Patagonia. (a) Shown in the inset is Torres del Paine National Park and the sampling sites where *Salmo trutta* and *Oncorhynchus mykiss* were collected in January 2017 from the Serrano River.

plotted against the frequency of occurrence (%O), providing a two-dimensional diagram. The number of each prey taxon was used to calculate %P as: $\%P = (\sum A_i / \sum A_t) \times 100$, where P is the prey-specific abundance, A_i is the abundance of prey i in stomach contents and A_t is the total prey abundance, considering only those predators in which the prey i occurs. To estimate trophic niche breadth, we calculated the Levins (1968) index, $B = (\sum p_i^2)^{-1}$, where p_i is the proportion of each item in the diet. Trophic overlap among species was measured using proportional similarity or Schoener's index, $D = 1 - 0.5 \sum_i (|p_i - q_i|)$, where p_i is the proportion of prey item i used by species p , and q_i is the proportion of prey item i used by species q . This index varies between 0 (no trophic overlap) and 1 (complete overlap) (Schoener 1974). We used a threshold of $D \geq 0.6$ to represent biologically significant overlap following Wallace (1981). The proportion was calculated for the percentage of the total numbers of prey items, as well as for the index of relative importance.

To perform stable isotope analysis (SIA), a sample (about 2 cm³) of dorsal muscle tissue from each fish was frozen at -80°C . In the laboratory, samples were dried for 72 h at 60°C , homogenized and underwent a process of lipid extraction with petroleum ether for four h in a Soxhlet extractor. The isotopic composition of carbon and nitrogen was

analyzed at the Laboratory of Biogeochemistry and Applied Stable Isotopes (LABASI) of the Pontificia Universidad Católica de Chile in an isotope-ratio mass spectrometer (Thermo Delta Advantage), coupled with a Flash 2000 Elemental Analyzer by Thermo Scientific (Michener & Lajtha 2007). The results were expressed in δ notation according to the following equation: $\delta X = [(R_{\text{sample}} / R_{\text{standard}}) - 1]$, where X is ^{13}C or ^{15}N and R is the ratio of heavy:light stable isotopes (Unkovich *et al.* 2001, Bond & Hobson 2012). Vienna Pee Dee Belemnite (VPDB) was used as a reference standard for comparison with $\delta^{13}\text{C}$, and atmospheric nitrogen was used for comparison with $\delta^{15}\text{N}$. After checking for assumptions (Shapiro-Wilk and Levene tests), a multivariate analysis of variance (MANOVA) was used to compare isotope values between the species. Univariate analysis of variance (ANOVA) was conducted separately for each isotope value. Least-square regression analyzes were employed to determine relationships between fish length (cm) and $\delta^{15}\text{N}$, and fish weight (g) and $\delta^{15}\text{N}$ for both species. A probability value <0.05 was considered to indicate statistical significance in this study. To characterize the trophic niche of both species, we estimate the isotopic niche width (see Newsome *et al.* 2007) by calculating the Standard Ellipse Area corrected for small sample sizes (SEAc) and dietary niche overlap (% area) using Stable Isotope

Bayesian Ellipses (SIBER) with a statistical software package in R (Jackson *et al.* 2011). These probabilities were derived by Bayesian inference where the posterior probability of the model M, given the data D, i.e Pr(M|D), was based on 100,000 MCMC draws (Jackson *et al.* 2011).

Results

Fish length varied between 33 and 63 cm TL (mean ±SD, 47.9 ± 7.1 cm) for *S. trutta* (n = 19) and from 34 to 58 cm TL (mean ±SD, 42.2 ± 6.9 cm) for *O. mykiss* (n = 15) (Fig. 2). Fish weigh varied from 700 to 2,800 g TW (1,210.5 ± 546.7 g) for *S. trutta* and from 368 to 2,200 g TW (822.8 ± 458 g) for *O. mykiss*.

The cumulative trophic diversity curves seemed to reach an asymptote, suggesting that a sufficient number of stomachs were used to describe and compare the diet composition of the species (Fig. 3). The main diet item for both species was the amphipod *Hyaella* sp. (*S. trutta*: IRI = 46.6%; *O. mykiss*: IRI = 47.6%). For *O. mykiss* unidentified

trichopterans were an important secondary prey (IRI = 40.8%; Table I). Feeding strategy plots (Fig. 4) showed that *S. trutta* and *O. mykiss* both appeared to be generalists (see prey positioned in the lower part of the diagram). These plots also position prey type, indicating some moderate population specialization (e.g., Trichoptera) in both species. Niche breadth was slightly wider for *O. mykiss* (B = 2.73) than for *S. trutta* (B = 2.49). Using the %N and the %IRI, the trophic overlap between both trout was high (D = 1.00).

Stable isotopic values were highly variable for δ¹⁵N among the sampled individuals but similar between species. *Salmo trutta* ranged from -23.5‰ to -20.3‰ (mean ±SD, -21.8 ± 0.9) for δ¹³C and 6.4‰ to 13.7‰ (8.5 ± 2.5) for δ¹⁵N; and *O. mykiss* ranged from -23.7‰ to -19.2‰ (-21.6 ± 1.3) for δ¹³C and 6.4‰ to 13.4‰ (9.1 ± 2.6) for δ¹⁵N. In the multivariate test, no significant differences were found between the species for both isotopes (MANOVA, Wilks λ : 0.98, P = 0.78). In addition,

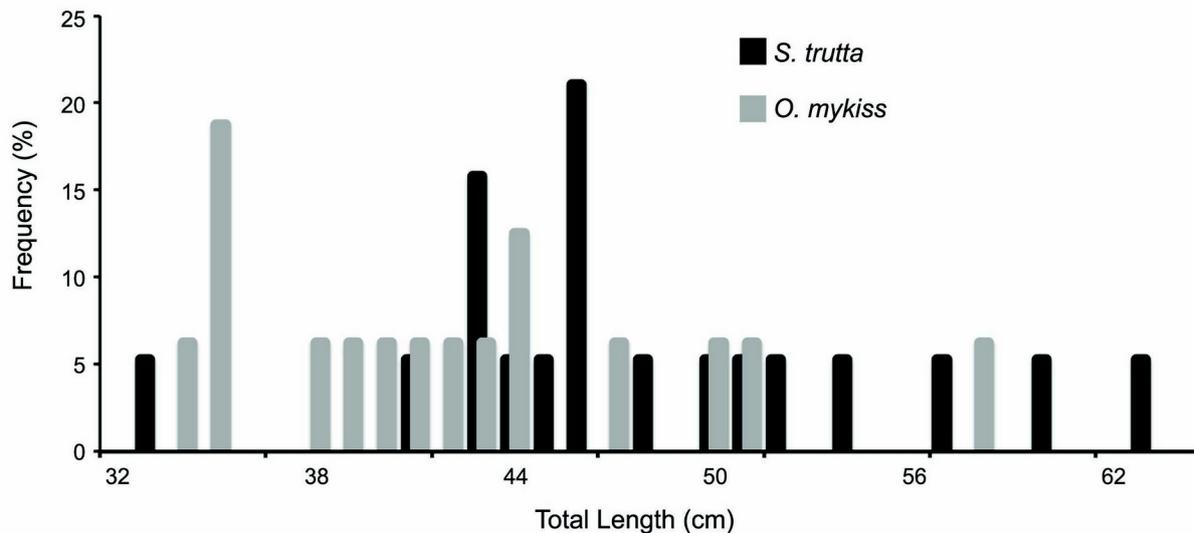


Figure 2. Total length-frequency distributions for *Salmo trutta* and *Oncorhynchus mykiss* from Serrano River basin, in Chile, during January 2017.

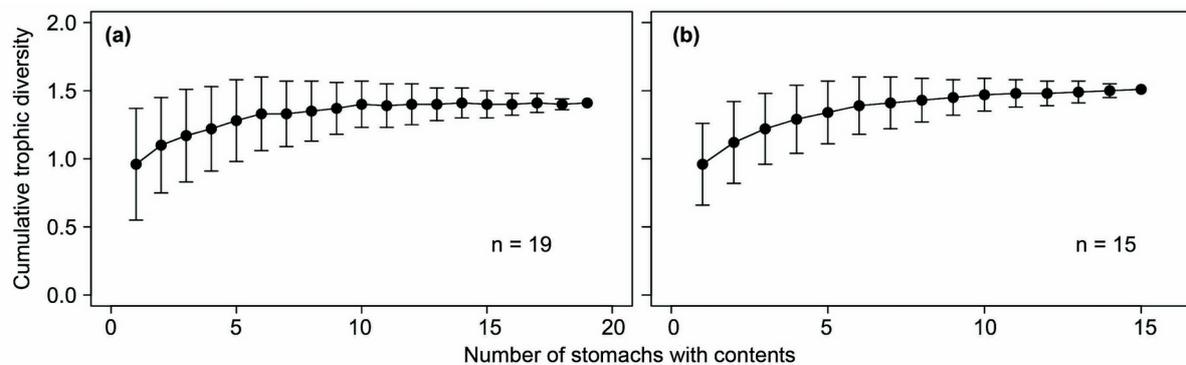


Figure 3. Randomized cumulative trophic diversity curves (Shannon-Wiener index) with standard deviation (bars) for *Salmo trutta* (a) and *Oncorhynchus mykiss* (b) sampled in Serrano River basin, in Chile, during January 2017.

Table I. Summary of results from stomach content analyses. Shown is the index of relative importance (IRI) as a percentage of diet, calculated from percentage by number (%N), percentage by weight (%W) and percentage of occurrence (%O) of the prey items in the stomachs of *Salmo trutta* (n = 19) and *Oncorhynchus mykiss* (n = 15).

Prey	<i>S. trutta</i>				<i>O. mykiss</i>			
	%N	%W	%O	%IRI	%N	%W	%O	%IRI
CRUSTACEA								
<i>Hyalella</i> sp.	61.15	15.04	14.74	46.59	57.02	12.43	18.57	47.61
Unidentified Amphipoda	2.95	4.39	11.58	3.53	5.22	1.40	8.57	2.10
Unidentified Crustacea	0.21	0.02	1.05	0.01	–	–	–	–
MOLLUSCA								
<i>Chilina</i> sp.	0.21	1.46	2.11	0.15	1.97	11.46	4.29	2.12
Lymnaeidae	3.02	3.65	3.16	0.87	4.20	10.06	2.86	1.50
Hidrobiidae	–	–	–	–	0.09	0.04	1.43	0.01
Unidentified Gastropoda	11.81	22.32	9.47	13.42	3.17	9.61	5.71	2.70
INSECTA								
Simulidae	5.63	2.25	8.42	2.75	0.51	0.17	7.14	0.18
Trichoptera	8.51	43.03	13.68	29.27	17.98	52.28	15.71	40.76
Plecoptera	1.03	2.07	5.26	0.68	0.26	0.21	2.86	0.05
Ephemeroptera	2.54	0.45	9.47	1.18	3.17	0.51	10.00	1.36
Chironomidae	0.62	0.01	4.21	0.11	0.86	0.01	5.71	0.18
Leptophlebiidae	0.41	1.49	1.05	0.08	0.77	0.23	1.43	0.05
Ephydriidae	–	–	–	–	0.09	0.07	1.43	0.01
Diptera	0.21	0.05	3.16	0.03	0.09	0.00	1.43	0.00
Odonata	0.07	0.00	1.05	0.00	0.17	0.00	1.43	0.01
Coleoptera	–	–	–	–	0.17	0.11	1.43	0.01
Unidentified Insecta	1.51	1.30	2.47	1.11	4.11	0.57	7.14	1.23
FISH								
Unidentified fish	0.14	2.45	2.11	0.23	0.17	0.83	2.86	0.11

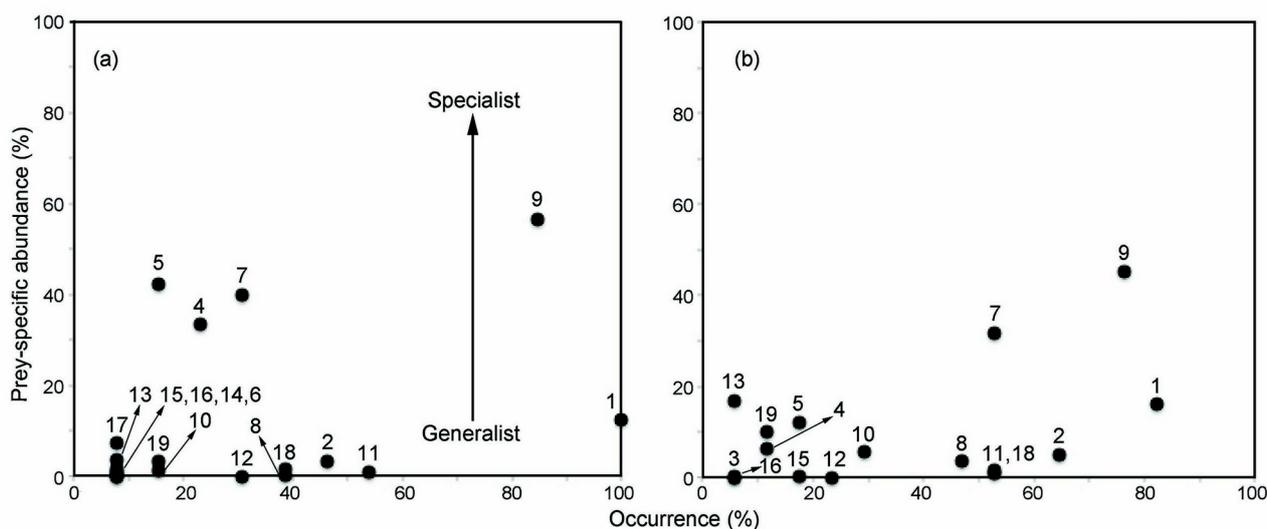


Figure 4. Feeding strategy plots for (a) *Oncorhynchus mykiss* and (b) *Salmo trutta* with stomach content sampled in in Serrano River basin, in Chile, during January 2017. Prey types are numbered as follows: 1. *Hyalella* sp.; 2. unidentified Amphipoda; 3. unidentified Crustacea; 4. *Chilina* sp.; 5. Lymnaeidae; 6. Hidrobiidae; 7. unidentified Gastropoda; 8. Simulidae; 9. Trichoptera; 10. Plecoptera; 11. Ephemeroptera; 12. Chironomidae; 13. Leptophlebiidae; 14. Ephydriidae; 15. Diptera; 16. Odonata; 17. Coleoptera; 18. unidentified Insecta; 19. Unidentified fish. (a) has been labeled to indicate the feeding strategies associated with different areas of the plot, adapted from (Amundsen *et al.* 1996).

there were no significant differences between the species in $\delta^{13}\text{C}$ (ANOVA, $F = 0.30$, $P = 0.58$) and $\delta^{15}\text{N}$ (ANOVA, $F = 0.45$, $P = 0.51$). Significant, positive relationships exist between $\delta^{15}\text{N}$ values and body size ($R^2 = 0.22$, $P = 0.047$) and body mass ($R^2 = 0.35$, $P = 0.009$) for *S. trutta* (Fig. 5a and b). Positive but no significant relationships were found between $\delta^{15}\text{N}$ values and size and mass with for *O. mykiss* (Fig. 5c and d). The isotopic niche width (SEA_c) of both species was larger in *O. mykiss* (9.21‰ , 95% credible interval [CI] = 4.87 – 15.08) than in *S. trutta* (7.04‰ , CI = 4.01 – 10.45, Fig. 6), with a probability of the posterior distribution of the model M given the data D (i.e. $\text{Pr}(M|D) = 0.79$). The niche overlap of *O. mykiss* and *S. trutta* corresponded to 65.9% and 86.2% of their SEA_c , respectively.

Discussion

The application of stomach content analyses provide a ‘snapshot’ of dietary habits, while the use of stable-isotope values reflects biologically integrated nutrients in diet of several months for muscle tissue, however it does not provide direct

evidence of prey items (Hyslop 1980, Peterson & Fry 1987). Therefore, the combination of these two methods provides a more complete understanding of an organism’s feeding habits. Considering the integration of both stomach analyses and stable isotopes, our results provide support for substantial dietary and isotopic niche overlap between *S. trutta* and *O. mykiss* and suggest the existence of potential interspecific competition for food resources among species, indicating similar trophic ecology during the austral summer in the Serrano River. According to Vander Zanden *et al.* (1999), trophic niche overlap between species can be interpreted as shared food sources, and therefore is a potential indicator of competitive interactions. Our results are in accordance with those shown for these same species in streams of northwestern Patagonia (Arismendi *et al.* 2012).

Stomach analyses indicated that the dominant prey items in the diet of *S. trutta* and *O. mykiss* were the crustacean amphipod *Hyalella* sp., followed by unidentified aquatic insects from the order Trichoptera (caddisflies). Benthic Hyalellid amphipods are widely distributed and highly

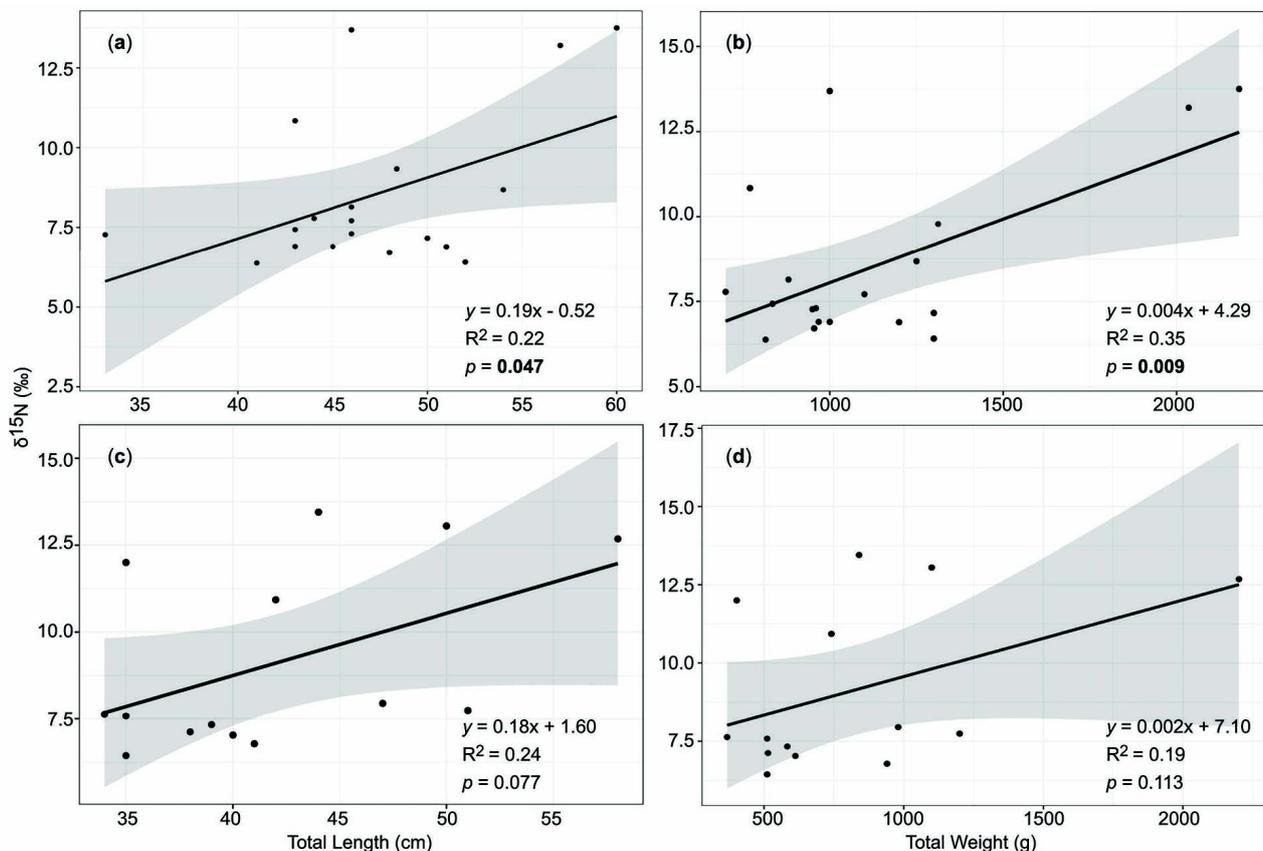


Figure 5. Relationships between $\delta^{15}\text{N}$ values and both fish length and body weight for (a - b) *Salmo trutta* ($n = 19$) and (c - d) *Oncorhynchus mykiss* ($n = 14$) from Serrano River basin, in Chile, during January 2017.

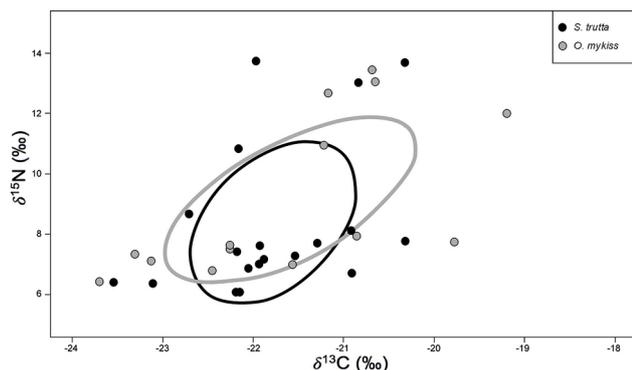


Figure 6. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of *Salmo trutta* (n =19, black circles) and *Oncorhynchus mykiss* (n =14, grey circles) sampled in Serrano River basin, Chile, during January 2017. Ellipses represent standard ellipse areas (SEAc) estimated for each species.

abundant in the rivers and lakes of southern Patagonia (Moorman *et al.* 2006, De los Ríos *et al.* 2007, 2011, Vega *et al.* 2010; Anderson *et al.* 2018). For example, surveys conducted in small streams at Navarino Island (54°S) in southern Patagonia recorded three autochthonous species of Hyalellid amphipods (*H. franciscae*, *H. patagonica* and *H. simplex*) with densities among 2.9 and 4.6 individuals L^{-1} (De los Ríos *et al.* 2011). In this regard, the absence of a physical barrier such as the Andes has favored the dispersion of Hyalellid species between Chile and Argentina (De los Ríos *et al.* 2012). Amphipods were also found to be the main prey for *S. trutta*, as a percentage by occurrence and number, in a river of Tierra del Fuego, but when considering percentage by weight, gastropods followed by amphipods and Trichoptera were the top three prey items (Traba & Ríos 1985). According to Lattuca *et al.* (2008), chironomid larvae and calanoid copepods were the main prey items for *O. mykiss* in a lake from northern Patagonia. In rivers of northwest Patagonia with high density of native fish, larger trout showed piscivorous diet, feeding primarily on native fish from the family Galaxiidae, whereas smaller trout consumed mostly invertebrates (Arismendi *et al.* 2012, Ortiz-Sandoval *et al.* 2017). Our results showed a low %IRI of unidentified fish in both species (IRI = 0.23% in *S. trutta* and IRI = 0.11% in *O. mykiss*) that could be related to low native fish densities in the Serrano River. However, both species showed high variability in the isotopic values (more than 3‰ in $\delta^{13}\text{C}$ and > 7‰ in $\delta^{15}\text{N}$). These values suggest that *S. trutta* and *O. mykiss* could feed on several prey items from different trophic levels. In this regard, the relationships between body size and body mass with $\delta^{15}\text{N}$ suggest

that trophic level influence $\delta^{15}\text{N}$ values (Jennings *et al.* 2008). These differences in $\delta^{15}\text{N}$ values among different sizes probably reflect changes in feeding strategy of larger individuals compared with smaller ones, suggesting that larger individuals of both species could be consuming fishes. However, these results should be further validated with a larger sample size of both species using different sampling techniques such as gillnets and electrofishing to have a wider size range.

A total of four native species corresponding to the family Galaxiidae have been found in the Serrano River basin (González 2012). According to this author, *Galaxias maculatus* was the most abundant native fish in the Serrano River during the austral summer, and often coexisted with *S. trutta*. A plausible explanation for the absence of fish prey items in the diet of *S. trutta* and *O. mykiss* could be the relatively low number of stomachs analyzed in this study. Considering the suggestion of Cowl *et al.* (1992), it is often more common that native fishes in lakes are more susceptible to trout predation than are native fishes in rivers. However, we could not discard an overall decrease in the abundance of *G. maculatus* in the Serrano River since their invasion by trout.

Amundsen *et al.* (1996) suggested that a generalist diet would be indicated by all prey types having low prey-specific abundance and moderate-to-high percentage of occurrence (i.e. most individuals utilize many prey types simultaneously). In this regard, our results suggest that *S. trutta* and *O. mykiss* hold a generalist niche when considering the variability in relative abundances of prey types. A population of a species with a generalist niche will consist of individuals with either many narrow but different dietary niches or a few shared broader niches (Pianka 1994). These populations of *S. trutta* and *O. mykiss* displayed only moderate levels of individual specialization, which means that although the population holds a broad niche, individuals could have narrower niches. We also proposed that *O. mykiss* has a more generalist feeding than *S. trutta*. Both dietary breadth and isotopic metrics (SEAc) support this finding. The foraging ranges of rainbow trout could cover a wide geographical area, which would influence its broad isotopic niche and the wider variation of the isotopic composition of carbon and nitrogen. Further sampling efforts and analyses of more specimens and prey items will enhance our knowledge on the trophic interactions among these introduced trout species and the ecological impact in invaded freshwater ecosystems

from southern Patagonia.

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Ethical statement

The present investigation did not involve the use of regulated animals and did not require approval by an ethical Committee. The Chilean National Forest Corporation granted fieldwork permit under a Technical Memorandum (N° 31/2016 CONAF).

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