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Piscivory and diet overlap between two non-native fishes in southern Chilean streams

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Abstract Trophic relations among introduced species may induce highly variable and complex effects in communities and ecosystems. However, studies that identify the potential impacts for invaded systems and illuminate mechanisms of coexistence with native species are scarce. Here, we examined trophic relations between two introduced fishes in streams of NW Patagonia, rainbow trout (*Oncorhynchus mykiss*) and brown trout (*Salmo trutta*). These species originate from different regions of the Northern Hemisphere but they now coexist as invading species over the world. We used gastric contents and stable isotopes analysis to compare the diets of two size-classes of these two invaders in three localities of southern Chile. Both species displayed similar ontogenic diet shifts with smaller trout consuming mostly invertebrates and larger trout being more piscivorous and epibenthic feeders. However, piscivory was more prevalent in brown trout than in rainbow trout and highest at the site with the greatest density of native fishes suggesting that the availability of native fishes as trout prey may limit the occurrence of trout piscivory. We found an elevated dietary overlap between the two trout species at larger sizes while at smaller size a higher intraspecific dietary overlap occurred suggesting a potential interference competition among the two fish invaders especially at larger sizes. Our results highlight that the impacts of invading species on non-native fishes are context specific (i.e. species and ontogenic stages) and thus, difficult to generalize.

Key words: alien species, native species, predation, South America, stable isotope.

INTRODUCTION

Trophic relations among several invading species can induce complex effects in communities and ecosystems (Crowder *et al.* 1997; Shurin 2001; Best & Arcese 2009), most of which are negative (Ross *et al.* 2004; Johnson *et al.* 2009). In particular, multiple top predator invaders may alter the composition, diversity and population dynamics of lower trophic levels through cascading effects (see review by Bruno & Cardinale 2008). However, the magnitude and direction of those cascading effects can be highly variable because factors can be indirect, non-additive and interact with one another (Bruno & Cardinale 2008). Thus, research on the interactions among multiple top invaders is important to identify potential threats in invaded systems.

The invasion and introduction of top predator fishes can affect profoundly freshwater ecosystems in many ways, including local extinction of native fishes (e.g. Kaufman 1992) and changes in their trophic position due to competition (Vander Zanden *et al.* 1999; Simon & Townsend 2003). For instance, rainbow trout (*Oncorhynchus mykiss* Walbaum) and brown trout (*Salmo trutta* L.) are top predators that have been widely introduced to cool-water environments around the world (Elliott 1994; Crawford & Muir 2008), with initial introductions outside of their native range occurring over a century ago (Crawford & Muir 2008), and both species successfully established in lakes (Soto *et al.* 2006; Lattuca *et al.* 2008; Arismendi *et al.* 2009) and streams (Crowl *et al.* 1992; Simon & Townsend 2003; Soto *et al.* 2006). The two species now often coexist (Cada *et al.* 1987; Crowl *et al.* 1992; Soto *et al.* 2006) although they originate from different regions of the Northern Hemisphere; with rainbow trout being native to Pacific Northeastern Asia and the Pacific Northwest of North America and brown trout from the Palearctic. Despite their common coexistence outside their native range, their trophic relationships in sympatry have received little attention in Patagonia or elsewhere (Elliott 1973; Gatz *et al.* 1987; Simon & Townsend 2003; Penaluna *et al.* 2009).

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In the Southern Hemisphere, invasive rainbow and brown trout have been responsible for the decline of native galaxiid fishes, because of direct predation and food competition (see reviews concerning native galaxiids in Australasia by Crowl *et al.* 1992 and McDowall 2006; additional examples of native galaxiids from Patagonia are provided by Soto *et al.* 2006 and Arismendi *et al.* 2009). However, in situations where non-native top predators have occurred for extensive periods, the effects may not be apparent or obvious because native fishes may have been absent or scarce for a long time. Furthermore, trout tend to become piscivorous as they grow so it is important to consider ontogenetic diet shifts when evaluating trout predation (Mittelbach & Persson 1998; Jonsson *et al.* 1999; Macchi *et al.* 1999; McIntosh 2000; Lattuca *et al.* 2008; Arismendi *et al.* 2009).

Here, we contribute to understanding the trophic relationships between the two fish predators rainbow trout and brown trout in sympatry outside of their native range. We study differences in piscivory and feeding habits between the two trout species and their potential ontogenic diet shifts in streams of southern Chile. We use a combination of stomach contents and nitrogen stable isotope analyses, which together provide the ability to identify trophic relationships among consumers (e.g. Cucherousset *et al.* 2007; Rybczynski *et al.* 2008) and thus, evidence of piscivory. We hypothesize that the availability of native fishes as trout prey may limit the occurrence of trout piscivory especially as many recent studies do not recognize the presence of piscivory (Palma *et al.* 2002; Buria *et al.* 2007, 2009), which may be a result of the legacy of past predation. We also hypothesize that large brown trout will not have an overlapping diet with large rainbow trout because brown trout will be more piscivorous (e.g. Crowl *et al.* 1992; Ebner *et al.* 2007; McHugh *et al.* 2007; Sepulveda *et al.* 2009) suggesting little to no competition among invaders when adults. However, if brown and rainbow trout show diet overlap that may indicate potential interference competition among invaders (e.g. Elliott 1973; McLennan & MacMillan 1984; Cada *et al.* 1987).

METHODS

Study area and fish sampling

We conducted this study in the Lakes District of southern Chile, NW Patagonia (40–42°S, Fig. 1). The climate is temperate with a west-coast maritime influence and annual range of precipitation from 1300 to 2200 mm occurring mostly between April and September (Miller 1976). Since their introduction at the beginning of the 1900s rainbow and brown trout have become widely established and represent the largest and most abundant freshwater fishes in southern Chile (Campos 1985; Soto *et al.* 2006; Arismendi *et al.* 2009). We selected three neighbouring second order stream tributaries from each of the Rio Bueno, Rio Llico and Rio Pescado catchments (i.e. nine streams in total). Even though all three areas shared similar physical and chemical water characteristics (Appendix S1) differences in densities of native fishes among these areas have previously been reported with Rio Bueno supporting the highest densities (Soto *et al.* 2006) a relationship we also found in our study areas (Appendix S1; see more details in Soto *et al.* 2006).

We sampled in each stream four times during the dry season (October–March) from 2002 to 2004 under similar streamflow conditions to avoid sampling difficulties related

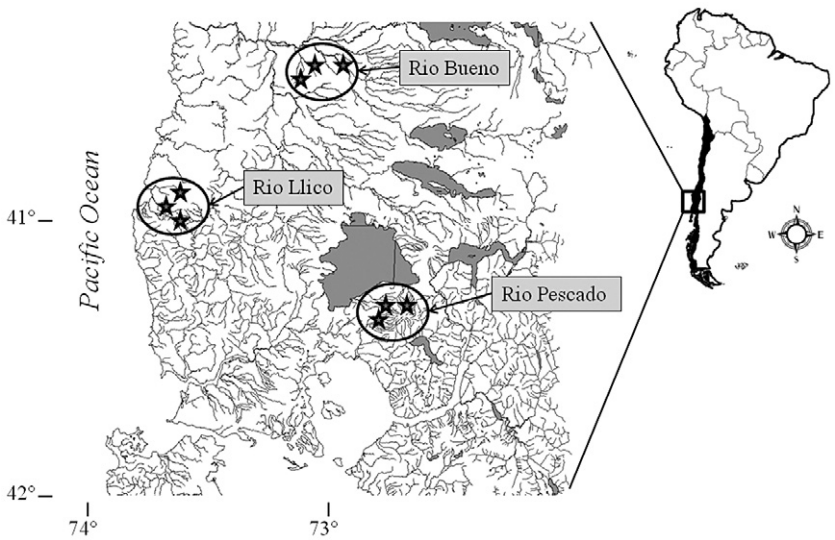

Fig. 1. Map of the study area in NW Patagonia (southern Chile) indicating each stream sampled at each area (Bueno, Llico and Pescado).

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to increasing streamflows and water turbidity during the wet season. At each stream, we captured fish from a 400-m reach using two-pass backpack electrofishing with a uniform total time effort of 1.5 h during daylight hours (10.00–16.00 hours). We sampled all available habitats (pool-run-riffle) to account for different-sized fish. We estimate a catch per unit effort (CPUE; fish m^{-2} electrofished) as an index of relative fish abundance using the same operator during the study to ensure consistency. Additionally, we collected macroinvertebrates from five to six Surber samples before electrofishing (Appendix S1).

Stomach contents and stable isotope analysis

We collected and stored a random subsample of trout stomachs in 70% ethanol (Appendix S1). The sample was completed by picking a trout at random from the first 10 captured, and thereafter we chose every fifth trout captured until we finished sampling the stream reach. To describe the dietary composition of trout we classified stomach contents into 26 categories of aquatic and terrestrial prey (see Appendix S2). We estimated the frequency of occurrence (*%O*) for each prey category by determining the occurrence of a particular prey category as a percentage of the number of stomachs analysed; and the prey percentage of volume (*%V*), determined by the total volume of a certain prey category as a percentage of the total volume of all prey (Hyslop 1980).

We collected tissue from the dorsal muscle of a portion of trout samples for the stable isotope analysis (Appendix S1). Tissues were stored and frozen, then dried at 60°C for 48 h before being ground into a fine powder. We analysed all samples in the Stable Isotope Lab, University of Utah (Salt Lake City) and the isotope ratio was expressed in parts per thousand (‰) according to the equation:

$$\delta^{15}\mathrm{N} = [(R_{\mathrm{sample}} - R_{\mathrm{standard}}) / R_{\mathrm{standard}}] \times 10^3$$

where R corresponded to ^{15}N:^{14}N ratio and the standard used was N_2. An enrichment of the isotopic signature of N indicated a higher trophic level (Peterson & Fry 1987).

Data analysis

We used a Kruskal–Wallis non-parametric median (H) to test for potential differences in the total length of trout sampled by species or area and, thus, validate appropriate diet comparisons (Appendix S1). Trout stomachs were grouped by area (Bueno, Llico and Pescado), species (rainbow trout; brown trout) and size (<13 cm, non-piscivorous or small; ≥13 cm potentially piscivorous or large), which is consistent with previous literature (see L'Abée-Lund *et al.* 1992; Mittelbach & Persson 1998).

We examined potential differences in the frequency of occurrence (*%O*) of fish in the diet between large (≥13 cm total length) rainbow trout and large brown trout using a chi-squared goodness of fit test. As piscivory increases $\delta^{15}N$ values (Peterson & Fry 1987) we used a Mann–Whitney non-parametric test (U) to assess potential differences in $\delta^{15}N$ between large rainbow trout and large brown trout (≥13 cm total length).

At the individual level, we examined potential diet overlap between trout species and among size-classes using a Bray–Curtis ordination (Clarke 1993; Marshall & Elliott 1997). Using the software PRIMER v6.1.5 (Clarke & Gorley 2006), we produced a similarity resemblance matrix using the Bray–Curtis similarity coefficient of square root transformed *%V* (Clarke & Warwick 2001). We examined potential differences of diets among trout groups (species and sizes) by performing a one-way analysis of similarities ANOSIM R statistic test (alpha set at 0.05) using 99 999 permutations (more detailed procedures are provided by Clarke 1993). To establish potential differences among trout groups we made *post-hoc* ANOSIM pairwise comparisons by calculating similarity percentages (SIMPER), which allowed us to determine which prey categories represented the greatest contributions to the total similarities between pairs (>90%; see details in Clarke & Warwick 2001). We also ranked the similarity within trout groups by estimating the index of multivariate dispersion (MVDISP; Warwick & Clarke 1993).

At the population level, we estimated diet diversity using Levin's standardized index, B_a (Hulbert 1978; Krebs 1989). Levin's index ranges from 0 to 1 with low values indicating food dominated by few prey. We also used a modification of the index of preponderance (IP_i) to rank prey items according to their relative contribution to total dietary composition (Marshall & Elliott 1997). *IP* values compare and rank the prey in order of importance reducing discrepancies caused by prey occurring in a high percentage of stomachs, but having a low point score (Marshall & Elliott 1997). We estimated the Vanderploeg and Scavia's relativized electivity ($E_i^\star$) index (Chesson 1978; Vanderploeg & Scavia 1979) to measure the use of aquatic prey (excluding fish) in relation to their abundance in the environment. Only preys that were observed were included in our analysis because the index is sensitive to the occurrence of rare prey items (Lechowicz 1982). This index ranges from −1 to 1 and we defined arbitrarily an $E_i^\star$ above 0.5 to indicate high electivity.

RESULTS

Differences in piscivory between trout species

Both rainbow and brown trout exhibited evidence of piscivory in Rio Bueno and Pescado areas (Fig. 2). At Bueno, where we found the highest density of native fishes, brown trout showed a higher *%O* of fish ($\chi^2 = 4.88$; d.f. = 1; $P < 0.027$) and higher $\delta^{15}N$ signature ($U = 32$, $Z = -1.98$, $P = 0.04$) than rainbow trout. At Pescado, although the trout density was the highest, there were no differences between trout species in either *%O* of fish ($\chi^2 = 0.01$; d.f. = 1; $P = 0.91$) or $\delta^{15}N$ signature ($U = 19$, $Z = 0.96$, $P = 0.34$). Where native fish densities were lowest (Llico) we did not find any fish in the stomach contents, nor were there differences in $\delta^{15}N$ between trout species ($U = 7$, $Z = 0.26$,

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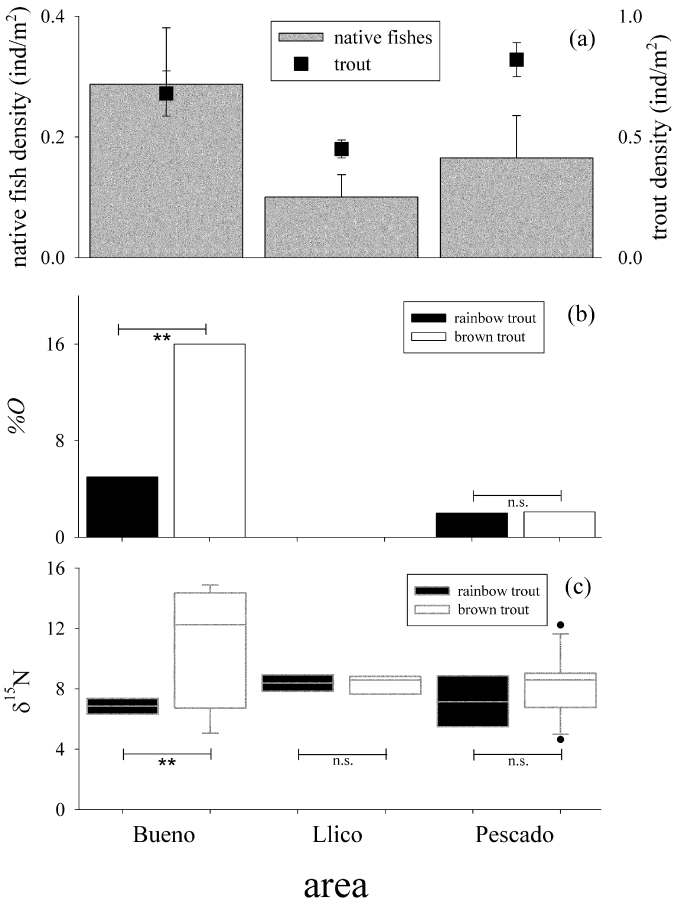

Fig. 2. (a) Mean of density ± SE of native fish and trout by area. (b) Frequency of occurrence (*%O*) of fish in trout stomachs by trout species and area. (c) $\delta^{15}N$ (median ± 5% and 95% percentile) of potentially piscivorous (large) trout by trout species and area. $\delta^{15}N$ on the *y*-axis can be interpreted as being proportional to trophic level.

$P = 0.79$). Overall, we were able to identify 35% of the fish in the stomach samples and all were from the family Galaxiidae (i.e. *Galaxias platei* Steindachner, *G. maculatus* Jenyns and *Brachygalaxias bullocki* Regan). The remaining 65% of the fish in the stomach samples were partly digested and unidentifiable.

Dietary overlap among trout groups

There was a diet overlap among trout species and sizes (R statistic = –0.018, $P = 0.92$). In particular, pairwise ANOSIM results (Table 1) indicated that the diet of large trout overlapped between the two species. The diet of small rainbow and brown trout overlapped at Bueno and Llico. In contrast, the diets of large rainbow and small brown trout differed in all areas. The SIMPER analysis indicated that these significant differences in diet composition were related to the frequency of Ephemeroptera, Plecoptera, Diptera and Decapoda prey categories (Fig. 3).

Intraspecific and population variation of trout diets

The diets of small trout had a higher intraspecific similarity and a lower dispersion than those from large trout at all areas (Fig. 4). Furthermore, the diet of small trout consisted largely of three prey categories (Ephemeroptera, Diptera and Plecoptera) that accounted for most of their intraspecific similarity (Table 2). At the population level, small trout also had a narrower diet breadth (B_a) than large trout, with a higher preponderance of the same aquatic prey (Ephemeroptera, Diptera and Plecoptera; Tables 2,3).

Among species and size-groups, large brown trout had the lowest intraspecific similarity and the highest variability in their diets (Fig. 4). Moreover, four to seven prey categories accounted for most of the intraspecific similarity in large trout (Table 2). At the population level, large trout also relied heavily on both aquatic and terrestrial prey (Table 3). In particular,

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Table 1. Pairwise ANOSIM results by trout group and area

Trout species pairs	Size of pairs	*R* statistic	*P*-value	Area
Rainbow trout – brown trout	Large *vs.* large	–0.12	1	Bueno
		–0.10	0.806	Llico
		0.04	0.061	Pescado
	Small *vs.* small	0.22	0.054	Bueno
		–0.14	0.901	Llico
		0.17	0.000***	Pescado
	Small *vs.* large	0.13	0.083	Bueno
		–0.13	0.963	Llico
		0.19	0.000***	Pescado
	Large *vs.* small	0.23	0.000***	Bueno
		0.49	0.013**	Llico
		0.22	0.000***	Pescado
Rainbow trout – rainbow trout	Small *vs.* large	0.47	0.000***	Bueno
		0.65	0.018**	Llico
		0.01	0.272	Pescado
Brown trout – brown trout	Small *vs.* large	0.02	0.324	Bueno
		0.27	0.000***	Llico
		0.28	0.000***	Pescado

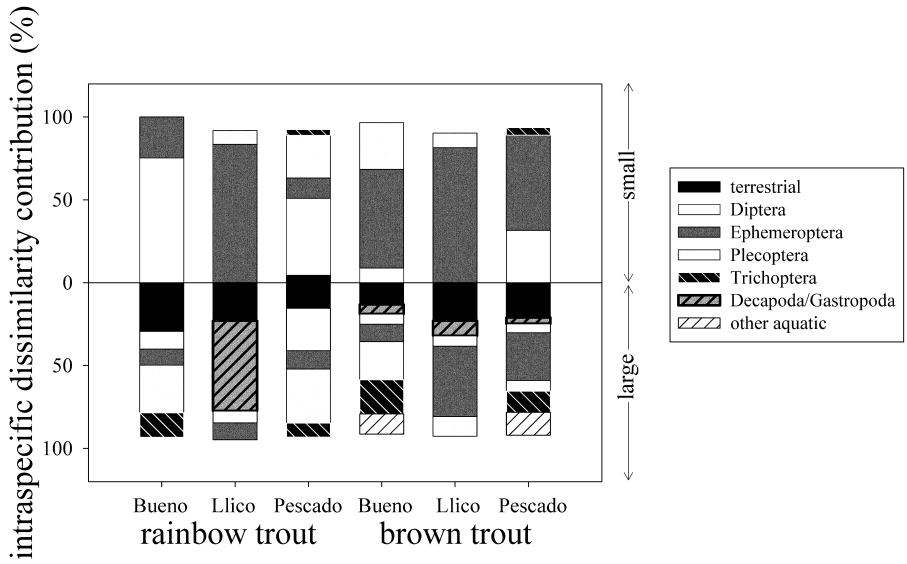

Fig. 3. Similarity percentage analysis (SIMPER) expressed as intraspecific dissimilarity contribution (%) of each prey category by species, size and area.

large rainbow trout had a high preponderance of Diptera (aquatic) and large brown trout a high preponderance of Hymenoptera (terrestrial), fish and Coleoptera (aquatic). Small trout (mainly rainbow trout) also showed a high electivity for Decapoda, Ephemeroptera, Plecoptera and Gastropoda whereas large trout focused more on large prey (Decapoda and Gastropoda). A detailed description of diets (the appendix provides descriptive data rather than analysis) by trout species, sizes and areas is provided in Appendix S2.

DISCUSSION

Our results support the hypothesis of an ontogenic shift in the non-native trout diet from small invertebrate feeders towards piscivory and larger prey (e.g. Decapoda and Gastropoda) as they increase in body size. However, in streams of Australasia where non-native trout similarly exist, published evidence of piscivory is scarce (e.g. Kusabs & Swales 1991; McIntosh 2000) with some evidence from the 1960s (Crowl *et al.* 1992; McDowall 2003). Moreover, previous

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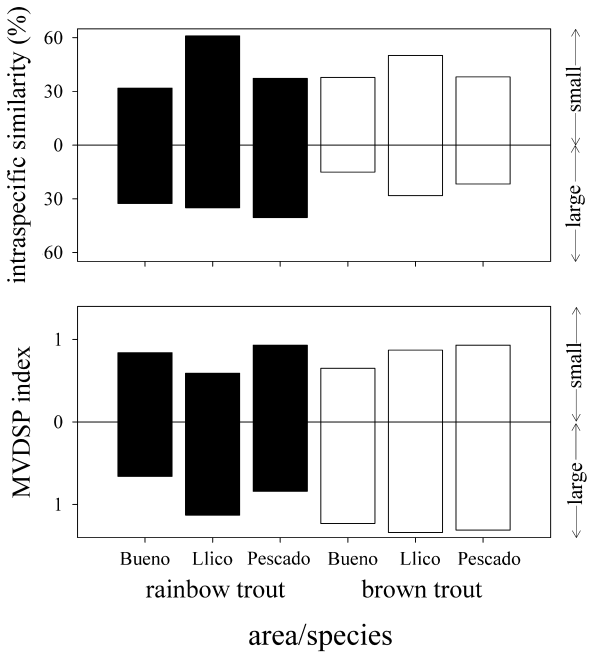

Fig. 4. Mean of intraspecific similarity percentage (above) and multivariate dispersion index MVDISP (below) for small and large trout species and area.

studies conducted in streams of southern Chile and Argentina have found minimal evidence (Arenas 1978; Campos 1985) or no occurrence of trout piscivory on native fishes (Palma *et al.* 2002; Buria *et al.* 2007, 2009). As almost all evidence of non-native trout piscivory originates from studies conducted in lakes (e.g. Burns 1972; Crowl *et al.* 1992) it is often suggested that native fishes in lakes are more susceptible to trout predation than are native fishes in streams (Crowl *et al.* 1992). But, it is possible that piscivory was not previously detected in streams because past predation by non-native trout could have largely eliminated native fishes. In our study, the highest occurrence of piscivory occurred in the area that has both the greatest density of native fishes and large trout. Thus, this raises the hypothesis that trout piscivory could also be influenced by prey availability (density of fishes) and size of trout. This idea is partially supported by our data because there is a higher level of piscivory in brown trout than in rainbow trout based on both the typical piscivory $\delta^{15}N$ signature and stomach analysis for large brown trout in the area with the greatest density of native fishes.

The higher frequency of piscivory found in brown trout compared with other salmonids has also been recorded in North America (e.g. McHugh *et al.* 2007; Sepulveda *et al.* 2009) and in invaded ecosystems of Australasia (Crowl *et al.* 1992; Ebner *et al.* 2007) where predation on native fishes has also been associated more commonly with brown trout than with rainbow trout. Brown trout may be more piscivorous because they are capable of foraging for longer periods in low-light conditions and at night because of their higher scotopic sensitivity (Rader *et al.* 2007). Many streams in southern Chile have high levels of tannins and lower transparency, including those that we sampled in the Central Valley (e.g. Bueno area). As a result there may be a higher threat of piscivory by brown trout because these low-visibility streams also support the highest density of native fishes (Soto *et al.* 2006). Importantly, all of the identifiable fish found in trout stomachs here were native galaxiids, species that are often negatively impacted by predation via non-native trout. For example, Kusabs and Swales (1991) report juvenile trout feeding extensively upon small galaxiids in New Zealand. Additionally, McIntosh (2000) suggests that prior predation by non-native trout is the reason that galaxiids are currently absent from streams containing large trout. In our study area, native galaxiids and both trout species use similar mesohabitat types in Southern Chile (Penaluna *et al.* 2009). This suggests that as they share the same mesohabitat, there is a heightened threat of predation and an additional mechanism of interactive segregation between introduced trout and native fishes. Furthermore, as the majority of fish in the stomach were unidentified we cannot rule out that juvenile trout may be also present in stomachs of large brown trout.

Contrary to our initial hypothesis, we found strong evidence of diet overlap between rainbow trout and brown trout, especially between large individuals. This result suggests the potential for interspecific exploitation competition for food, although additional evidence would be required to confirm this (see Crowder 1990). However, there is evidence of diet overlap between these species in other invaded streams, which supports this hypothesis (see McLennan & MacMillan 1984 for New Zealand and Cada *et al.* 1987 for the Appalachian Mountains in North America). The diet of brown trout and rainbow trout is also known to overlap in Europe where rainbow trout are non-native (Elliott 1973), and there is evidence of interspecific competition for habitat between both trout species in North America (Gatz *et al.* 1987; Vincent 1987).

Our results indicate that trout are generalist predators with broad diet niches. Diet composition can vary qualitatively between areas depending on the availability of larger prey, trout ontogenic stage and species, and the individual behaviour of trout. The higher electivity of large trout on larger preys like Decapoda, especially in brown trout, may be related to high densities of freshwater crabs, *Aegla* spp. (Burns 1972) and their wide distribution in southern South America (Bond-Buckup *et al.* 2008). These crabs are an important dietary source for rainbow and brown trout in Chile (Burns 1972; Arenas 1978), and for rainbow trout in Southern Brazil (Bond-Buckup *et al.* 2008).

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Table 2. Intraspecific similarity contribution (%) of prey categories contributing up to 90% of their total similarity (SIMPER) by trout group and area

			Similarity contribution by prey category (%)						
Size	Trout species	Area	Total terrestrial	Decapoda and Gastropoda	Diptera	Ephemeroptera	Plecoptera	Trichoptera	Other aquatic
Small	Brown trout	Bueno			8.8	59.5	28.2		
		Llico				81.4	8.8		
		Pescado			31.6	57.4		4.5	
	Rainbow trout	Bueno			75.2	24.8			
		Llico				83.4	8.3		
		Pescado	4.5		46.4	12.2	25.8	3.5	
Large	Brown trout	Bueno	13.1	5.8	6.2	10.5	23.0	20.6	12.1
		Llico	22.9	9.2	6.3	42.4	11.9		
		Pescado	21.0	3.8	5.4	28.8	6.4	12.9	13.7
	Rainbow trout	Bueno	29.4		10.7	9.7	28.7	14.8	
		Llico	22.9	54.5	7.2	10.2			
		Pescado	15.5		25.5	11.1	32.6	8.5	

Table 3. Levin's standardized index of niche breadth (B_a), index of preponderance ($IP > 20\%$) and relativized electivity index ($E_i^\star > 0.5$) results of prey categories by trout group and area

Trout species	Piscivory condition	Area	Niche breath (B_a)	Preponderance ($IP > 20\%$)	Electivity ($E_i^\star > 0.5$)
Rainbow trout	Small	Bueno	0.04	Diptera, Ephemeroptera	Decapoda
		Llico	0.03	Ephemeroptera	Ephemeroptera, Plecoptera
		Pescado	0.20	Diptera, Plecoptera	Gastropoda
	Large	Bueno	0.29	Plecoptera, Diptera†	Decapoda
		Llico	0.06	Decapoda	Decapoda
		Pescado	0.29	Plecoptera	Gastropoda
Brown trout	Small	Bueno	0.10	Ephemeroptera, Plecoptera	Plecoptera
		Llico	0.04	Ephemeroptera	
		Pescado	0.13	Diptera, Ephemeroptera	
	Large	Bueno	0.24	Fish	Decapoda
		Llico	0.12	Decapoda, Hymenoptera†	Decapoda
		Pescado	0.34	Coleoptera	Gastropoda

†Terrestrial source.

We found a higher intraspecific diet overlap for small trout than for large trout, especially in brown trout. Large trout may displace and restrict the foraging behaviour and/or habitat use of small trout provoking habitat partitioning among trout by size-class (e.g. Greenberg *et al.* 1997; Spina 2000). Small trout show a narrower diet range compared with large trout mainly because of the higher presence of allochthonous sources in large trout. Small trout have less variability of prey categories and restrict their diets to autochthonous sources indicating that they have more similar diets than large trout.

We provide new information about the role of introduced trout species in invaded stream food webs. Further studies of specific watersheds should enable predictions to be made about the factors influencing the impacts of non-native fishes and may eventually lead to more robust general predictions (McIntosh 2000). Differences among areas and size-classes of trout appeared to be important, suggesting that impacts of invaders can be context specific and difficult to generalize, which appears consistent with previous case studies (see review by Dunham *et al.* 2002).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Main chemical, physical and biological characteristics of streams sampled from Bueno, Llico, and Pescado areas in southern Chile. Numbers represent mean, min and max values obtained from 2002 to 2004.

Appendix S2. Frequency of occurrence (*%O*) and percentage by volume (*%V*) of prey categories grouped as aquatic and terrestrial sources, trout species and size-group in the Bueno, Llico and Pescado areas.

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