Feeding strategy of the non-native rainbow trout, *Oncorhynchus mykiss*, in low-order Patagonian streams

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Abstract The dietary composition and feeding strategy of rainbow trout, *Oncorhynchus mykiss* (Walbaum), in two low-order Patagonian streams were studied. Benthic macroinvertebrate availability was estimated in both riffles and pools. Fish stomach contents were examined to determine prey richness and diversity, prey electivity, food-niche width, and the feeding strategy employed by trout throughout the year. Availability of benthos varied seasonally with Ephemeroptera, Trichoptera, Plecoptera and Diptera species dominating. Rainbow trout diet was composed mainly of benthic macroinvertebrates, followed by terrestrial insects, fish, algae and plants. Different trout size classes segregated the use of food resources to reduce predation pressure. Elected prey included organisms displaying no to high mobility. A high feeding plasticity allows trout to buffer changes in food availability by switching from a specialised to a generalised feeding behaviour. Consequently, trout may exploit abundant but temporary food resources opportunistically, which would explain their marked expansion in Patagonian environments.

KEYWORDS: benthos availability, diet composition, exotic trout, feeding strategy, Patagonia, stream.

Introduction

Non-native fish introductions into freshwater ecosystems is a common practice that often depends on decisions taken by management agencies aimed at developing sport fishing and aquaculture (Soto *et al.* 2001). The negative impact of introduced fish on native fish faunas is well established, although concrete evidence is often lacking, particularly regarding invasion mechanisms (Kolar & Lodge 2000; Gozlan *et al.* 2010). However, it is well known that fish predation alters ecosystem processes by top-down effects, which in turn affect vulnerable or functional components of the community (Nakano *et al.* 1999; Greig & McIntosh 2006). Salmonids are aggressive predators that are visually size-selective and that feed mainly on drifting invertebrates

(Newman & Waters 1984). Consequently, trout are known to have negative effects at the individual, population, community and ecosystem levels in invaded systems (McIntosh & Townsend 1996; Nyström *et al.* 2001; Townsend 2003).

Invertebrate availability in a particular stream may determine fish diet – thus for a determined species, diets are likely to be quite variable among streams. Moreover, it has been suggested that predators frequently feed in particular habitats and preferentially consume certain prey types (Zaret 1980; Reznick 1983; Sih 1987). Thus, research on fish diet and prey availability at a microhabitat scale is important to understand trout feeding strategy.

In Patagonia, the native freshwater fish fauna (Ringuelet 1975; Arratia *et al.* 1983) comprises only 15 species (Baigún & Ferríz 2003). Currently, Patagonian

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freshwater fish communities are largely dominated by the salmonids introduced in the early 20th Century (Dyer 2000; Pascual *et al.* 2002; Soto *et al.* 2006). Prior to the salmonid introductions, most native species were much more widespread and abundant than nowadays (Wegrzyn & Ortubay 1991). Rainbow trout, *Oncorhynchus mykiss* (Walbaum), is the most widely distributed non-native species in the region (Pascual *et al.* 2002; Di Prinzio *et al.* 2009). Few studies in the Patagonian region have focused on the relationship between its diet and macroinvertebrate availability in the environment (Buria *et al.* 2007; Albariño & Buria 2011), compared with elsewhere (e.g. McIntosh & Townsend 1996; Bridcut 2000; McIntosh 2000; Ulrike & Armin 2002; Kawaguchi *et al.* 2003; Penaluna *et al.* 2009; Arismendi *et al.* 2011). The aim of this study is, therefore, to examine diet and feeding strategy of rainbow trout in relation to macroinvertebrate availability at two typical low-order Patagonian streams.

Methods

Study area description

The study was conducted in two-second-order watercourses: the Chiquito Stream (CH) (71°30′ 22″W, 43°21′43″S) in the Frío Basin and Las Minas Stream (LM) (42°31′03″W, 71°25′13″S) in the Carrileufú basin. These permanent streams are located in the mountains in the north-west of Chubut Province in Patagonia (Argentina) in the transition between the Sub-Antarctic forest and the Patagonian steppe. The discharge pattern is bimodal, with one peak coincident with winter rains and a second with snowmelt in spring (Coronato & Del Valle 1988; Paruelo *et al.* 1998). More than 90% of the catchments are covered by native forest. Riparian forest provides shade for a long period of the year. The riparian corridor at CH is the deciduous tree ñire, *Nothofagus Antarctica* (Forest. F.) Oerst., and dense shrub cover of native *Ribes cucullatum* Hook & Arn., *Berberis buxifolia* Lam. and *Berberis heterophylla* Juss., *Maytenus chubutensis* (Speg.) Lourt., Odon. et Sleum., *Schinus patagonica* (Phil.), whereas at LM 'coihues' *Nothofagus dombeyi* (Mirb.) Blume, willow *Salix fragilis* L., and several mixed shrubs species (*Rosa rubiginosa* L., *Fabiana imbricata* Ruiz et Pav., *Discaria chacaye* (G. Don) Tortosa, *Discaria trinervis* (Gillies ex Hook. & Arn.) Reiche and *Discaria articulate* (Phil, sub Colletid) Miers, *Schinus patagonica* (Phil.) I.M. Johnst. ex Cabrera) are present (Kutskcher *et al.* 2009).

Environment characterisation

Sampling sites were visited in May (early autumn), September (late winter) and December (late spring) 2005, and March (late summer) 2006. Samples were taken under stable environmental conditions avoiding periods during and after rainstorms or extremely high discharge events. Substrate composition at each sampling site was estimated visually, and percentages of boulders, cobbles, gravel, pebbles and sand were recorded (as defined by Cummins in Ward 1992). Current speed was measured in mid-channel on three occasions by timing a float as it moved over a distance of 10 m (Gordon *et al.* 1994). Average depth was estimated from five measurements on transects across the channel with a calibrated stick. Wet width of the channel was also determined. Discharge was obtained by combining depth, wet width and current velocity according to Gordon *et al.* (1994). Water temperature was measured at each site on each occasion with a mercury thermometer.

On each sampling occasion, specific conductance (μS_{20} cm^{-1}), pH, turbidity (NTU) and dissolved oxygen (mg O$_2$ L^{-1}) were measured with a Horiba U2-probe. For nutrient analyses, water samples were collected below the water surface and kept at 4 °C prior to analysis. Nitrate plus nitrite nitrogen (μg L^{-1}), ammonia (μg L^{-1}), soluble reactive phosphate (μg L^{-1}) and total suspended solids (mg L^{-1}) were analysed in the laboratory following APHA (1994).

Fish sampling

Fish were sampled seasonally using portable backpack electric fishing gear (Coffelt Manufacturing Inc.-Mark-10 CPS, output 350 V) along 100m reaches. The sampled area was estimated from the length and width of the surveyed reach. All fish caught were frozen and returned to the laboratory where they were later counted, measured (total length, cm), weighed (g) and the stomachs removed for diet analysis.

Diet analysis

Stomach fullness was assessed using a five-point percentage scale ranging from empty (0%) to full (100%) (Amundsen *et al.* 1996). Food items were removed and identified to the lowest taxonomic level possible using specific identification keys (Fernández & Domínguez 2001). The composition of the diet was calculated in terms of relative abundance ($A_i = (\Sigma S_i/\Sigma S_t) \times 100$), frequency of occurrence ($F_i = N_i/N$) and prey-specific abundance ($P_i = (\Sigma S_i/\Sigma St_i) \times 100$) following Hyslop (1980), where S_i is the contribution of prey i to stomach fullness, S_t total stomach fullness of the fish, St_i total

stomach fullness of fish with prey i in its stomach, N_i the number of fish with prey i in their stomach and N the total number of fish with stomach contents.

Stomach contents were examined according to the mixed method of Hureau (1970). Data are expressed in terms of the dietary coefficient (Q), which is the product of the percentage by number and percentage by mass of each prey type. This method reduces the biases due to the use of numeric or weight methods. According to this index, the prey items were separated into the following categories: $Q > 200$ main preys, $200 < Q > 20$ secondary prey and $20 < Q$ occasional prey.

Feeding strategy and food-niche width

Food-niche characteristics were analysed by the graphical method of Amundsen *et al.* (1996). For each prey ($A_i > 5\%$), the prey-specific abundance (P_i) was plotted against the frequency of occurrence (F_i) in a two-dimensional graph. Information on feeding strategy was obtained by examining the distribution of prey along the axes of the graph (see for example Fig. 4). The diagonal from the lower left to the upper right corner provides a measure of prey importance for the whole populations, with dominant prey at the upper right corner and rare and unimportant prey at the lower end. The vertical axis represents the feeding strategy: specialists have prey points positioned in the upper part of the graph, and generalists have all prey points in the lower part. Points located in the upper left indicate specialisation on a given prey by subgroups of the predator population, whereas points in the upper right indicate specialisation by the whole predator population. Hence, if one or a few points are located in the upper right, this reflects a predator population with a narrow niche width, whereas lack of prey points in this part of the diagram reflects a predator population with a broader niche width. Prey points in the upper left and lower right corner represent the same per cent abundance in the diet of the populations as a whole, but illustrate totally different feeding strategies among the individual predators. These differences are related to the between- and within-phenotype contributions to niche width, respectively. In a population with a high between-phenotype component, individuals specialise on different prey categories, whereas in populations with a high within-phenotype component, individuals use many common preys none of which dominate the diet (Roughgarden 1974).

Benthos

Quantitative macroinvertebrate samples were taken with a Surber sampler (0.09 m²; 250 μm pore size). Three samples were taken from riffles and three from pools on each sampling occasion. Samples were fixed *in situ* with 4% formaldehyde, and at the laboratory were sorted under at least 5× magnification. Macroinvertebrate species were identified using available identification keys (Fernández & Domínguez 2001) and counted. Level of taxonomic resolution of benthos specimens and stomach items was the same.

Data analysis; trophic niche width; prey electivity index; diet diversity and richness

Niche width (B) was calculated using Levins (1968) index with 95% confidence limits: $B = 1/\Sigma p_i^2$ $i = 1…n$, where p_i is the fraction of items in the diet that are of

Table 1. Physicochemical characteristics of two low-order Patagonian streams

	Early autumn		Late winter		Late spring		Late summer	
	CH	LM	CH	LM	CH	LM	CH	LM
Current speed (m s^{-1})	0.60	0.86	1.07	1.36	1.00	0.74	0.33	0.33
Depth (m)	0.16	0.20	0.25	0.30	0.17	0.20	0.10	0.20
Wet width (m)	1.50	4.00	2.10	2.00	1.50	6.50	2.40	3.30
Water temperature (°C)	6.60	9.00	2.60	8.20	5.80	9.50	6.80	10.20
Discharge (m^3 s^{-1})	0.02	0.59	0.54	0.96	0.26	0.93	0.08	0.19
Conductivity (μS$_{20}$ cm^{-1})	92.00	186.0	33.00	54.00	66.00	76.00	9.00	164.00
pH	7.00	7.40	7.40	7.50	7.30	7.40	7.30	7.60
Turbidity (NTU)	2.00	0.00	192.00	158.00	3.00	5.00	2.00	4.00
Dissolved oxygen (mg O$_2$ L^{-1})	14.00	14.00	13.70	10.30	12.00	9.60	11.30	9.20
Nitrate plus nitrite nitrogen (μg L^{-1})	0.07	0.02	17.44	0.23	6.48	0.15	nd	0.15
Ammonia (μg L^{-1})	3.89	nd	3.26	1.95	1.46	1.06	0.75	0.49
Soluble reactive phosphate (μg L^{-1})	1.88	0.57	1.17	0.52	0.48	0.57	0.37	0.92
Total suspended solids (mg L^{-1})	2.90	0.27	6.10	52.30	2.00	8.80	5.20	0.80

CH, Chiquito; LM, Las Minas; nd, not determined.

Table 2. Number, length (mean and standard deviation in cm) and mass (mean and standard deviation in g) of the *Oncorhynchus mykiss* (Walbaum) individuals caught, food-niche features and food availability in the Chiquito (CH) and Las Minas (LM) streams. *H*: Shannon–Weaver diversity index

Biological data	Early autumn		Late winter		Late spring		Late summer	
	CH	LM	CH	LM	CH	LM	CH	LM
Fish parameters								
Number	31	30	5	16	28	29	30	30
Length (cm) ± SD	12.00 ± 4.4	7.30 ± 2.9	9.62 ± 2.5	7.29 ± 3.6	13.45 ± 4.4	10.80 ± 2.2	10.60 ± 4.7	11.71 ± 3.4
Weight (g) ± SD	25.53 ± 29.8	5.34 ± 6.9	9.45 ± 6.3	7.51 ± 16.2	35.82 ± 38.7	16.26 ± 10.8	21.58 ± 25.9	19.65 ± 13.7
Food-niche parameters								
Food-niche width	0.075	0.154	0.113	0.085	0.055	0.127	0.082	0.418
Prey diversity (*H*)	2.71	2.89	2.81	2.10	2.47	2.90	2.31	3.79
Population prey richness	39	23	15	18	42	39	22	22
Mean individual prey abundance	33.35	10.5	61.20	17.9	28.25	53.1	4.70	2.73
Food availability								
Benthos richness	38.5	26.0	34.5	22.5	39.5	27.5	42.5	30.0
Benthos density (ind m^{-2})	6951.2 ± 5278.48	3542.2 ± 2563.5	3073.8 ± 2577.7	4336.6 ± 1577.8	3449.7 ± 2628.5	6088.3 ± 2104.3	2510.9 ± 994.5	6230.9 ± 4285.6
Benthos diversity (*H*)	2.38	2.46	2.63	2.00	2.96	2.27	2.49	2.59

category *i*, expressed as Levin's standardised niche breadth from 0 to 1.

Ivlev's (1961) electivity index was used to estimate the degree of prey electivity as $I = (E_i - B_i)/(E_i + B_i)$, where E_i is the percentage by number of taxon *i* in the stomach contents and B_i is the percentage by number of taxon *i* in the benthos. Positive values indicate that the fish select the relevant prey.

Prey diversity was assessed using the Shannon–Wiener index of diversity (Krebs 1989):

$$H = - \sum_{i=1}^{S} (p_i \ln p_i),$$

where *pi* is the fraction of items in the benthos sample that are of category i.

Estimates of prey richness were further obtained by counting the numbers of different prey categories eaten by the whole population (population prey richness) and on average by each individual fish (individual prey richness). Additionally, differences in benthos density per habitat (riffle/pool) in each river were tested using a nonparametric Mann–Whitney test.
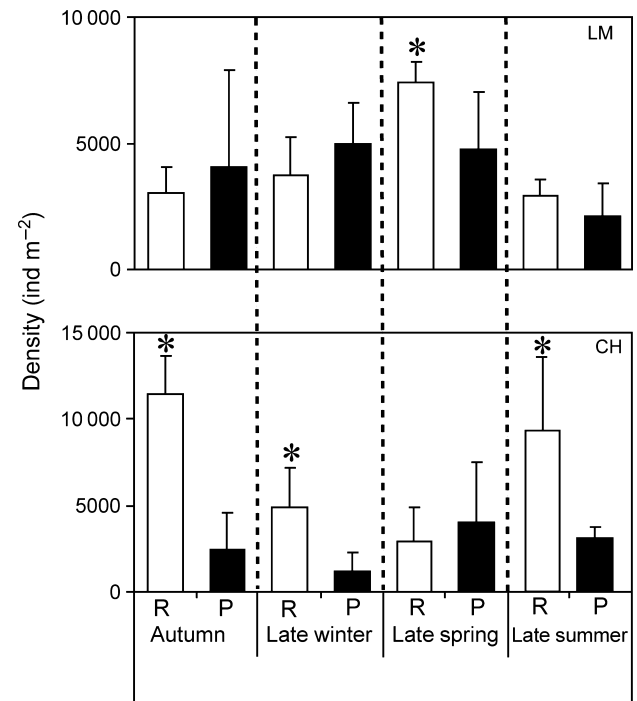

Figure 1. Mean invertebrate density (ind m^{-2}) by season at riffles (R) and pools (P) (*n* = 3) at Las Minas (LM) and Chiquito (CH) streams (Patagonia, Argentina) during the study period (May 2005 – March 2006). Significant differences on density values are marked (*) (Mann Whitney test $P > 0.05$).

Results

Environmental characterisation of sampling sites

Streams were located between 573 (LM) and 670 m.a.s.l. (CH). The substratum at LM was mainly cobbles (35%) and boulders (25%), while at CH, it was cobble (25%) and pebbles (25%); the remaining proportion was spread among the different substrate types. Current speed was between 0.33 m s^{-1} in late summer (both streams) and 1.36 m s^{-1} in late winter (LM)
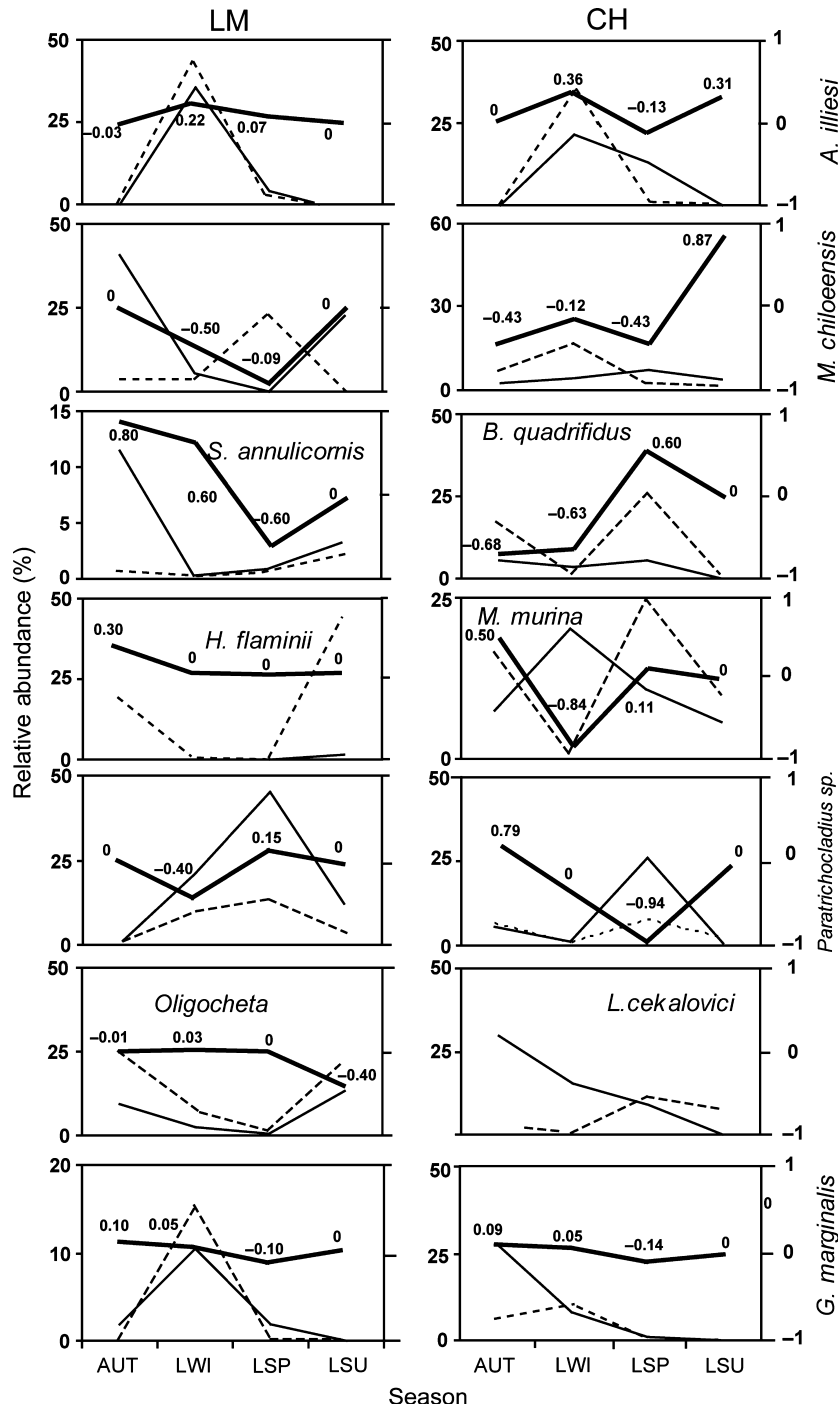
Figure 2. Relative abundance (percent) of the most relevant macroinvertebrates per habitat at Las Minas (LM) and Chiquito (CH) streams (May 2005 – March 2006). Straight lines are riffles and dotted lines are pools (*n* = 3). Electivity index is showed in the right axis with a straight black line. AUT: autumn; LWI: late winter; LSP: late spring; LSU: late summer.

(Table 1). The average depth was 0.17 m at CH and 0.22 m at LM. The main discharge was observed in late winter for both streams (LM 0.96 m^3 s^{-1} and CH 0.54 m^3 s^{-1}). CH (mean: 5.45 °C) was cooler than LM (mean: 9.22 °C). LM presented the highest conductivity (186.0 μS$_{20}$ cm^{-1}) and total suspended solids (52.3 mg L^{-1}). On the other hand, CH exhibited the highest turbidity (192.0 NTU) and had slightly higher values of nitrate plus nitrite nitrogen (17.44 μg L^{-1}), ammonia (3.89 μg L^{-1}) and soluble reactive phosphate contents (1.88 μg L^{-1}).

Benthos

Density of potential prey in benthos samples increased and decreased from early autumn to late summer at LM and CH, respectively (Table 2). In both streams, densities of benthic macroinvertebrates were higher in riffles than in pools (Fig. 1); the differences were significant during early autumn, late winter and late summer at CH and in late spring at LM (Mann–Whitney test, $P < 0.05$). Invertebrate diversity and richness were higher in late spring and late summer at CH and LM, respectively (Table 2). No species was dominant in the benthic community throughout the year (Fig. 2). In both streams, *Aubertoperla illiesi* (Illies) was the most abundant plecopteran and peaked during late winter mostly at pool habitat (Fig. 2). Overall, *Meridialaris chiloeensis* (Demoulin) was the most abundant ephemeropteran, and its highest abundance was observed in pools at LM in early autumn. The most abundant trichopterans at LM were *Smicridea annulicornis* (Blanchard) and *Hudsonema flaminii* (Navás), and their highest abundance was observed in early autumn in riffles and in late summer in pools, respectively. *Brachysetodes quadrifidus* (Schmid) and *Myotrichia murina* (Schmid) were the most abundant trichopteran at CH, and their highest abundance was observed in pools during late spring (Fig. 2). In both streams, *Paratrichocladius* sp. was the most abundant dipterans at riffles in late spring.

Fish data, diet composition and prey electivity

A total of 199 rainbow trout were caught throughout the study period. Individual sizes ranged between 7.29 (LM) and 13.45 cm (CH), whereas their weight ranged from 5.34 (LM) to 35.82 g (CH) (Table 2). The dietary diversity was higher in late summer at LM and in early autumn at CH (Table 2). Rainbow trout diet width was generally higher at LM than at CH. At LM, the niche width was lower during late winter and late spring and peaked in late summer (Table 2), but at CH, the highest niche width was observed in late winter and the lowest in late spring.

Table 3. Dietary coefficient (Q) observed in different size classes of *Oncorhynchus mykiss* (Walbaum) from Las Minas (LM) and Chiquito (CH) streams

	LM			CH		
	Length (cm)	Range (cm)	Q	Length (cm)	Range (cm)	Q
Early autumn						
Small	<10	3.9–6.9	*Brachysetodes* sp. Diptera (A)	<14	4.4–11.0	nr
Large	>10	7.9–13.7	Athericidae (L)	>14	11.6–22.8	*Myotrichia murina* (Schmid)
Late winter						
Small	<10	5.1–7.9	*Aubertoperla illiesi* (Illies) Simuliidae (L)	<14	3.5–5.6	*A. illiesi M. chiloeensis* Simuliidae (L)
Large	>10	14.3–18.7	Oligochaeta	>14	9.4–12.5	*A. illiesi* Simuliidae (L)
Late spring						
Small	<10	7.4–10.0	*Paratrichocladius* sp. *Thienemanniella* sp.	<14	5.5–12.6	*Brachysetodes quadrifidus* (Schmid)
Large	>10	11.3–16.4	*Brachysetodes* sp. Aphididae (A)	>14	13.6–25.1	*B. quadrifidus*
Late summer						
Small	<10	5.5–8.6	Chironomidae fragment	<14	3.4–11.0	*M. murina*
Large	>10	10.8–17.2	nr	>14	11.1–21.0	*M. murina*

nr, no prey recorded; A, adult; L, larvae.

The diet was composed of 89 different prey types (Fig. 3). Benthic and terrestrial invertebrates, fish and vegetal fragments were found in the samples. The main prey ($Q > 200$) also varied throughout the study period. Interestingly, at LM, small (TL < 10 cm) and large individuals (TL > 10 cm) foraged predominantly on different

Table 4. Ivlev electivity indices of prey in the diet of *Oncorhynchus mykiss* (Walbaum) in two low-order Patagonian streams

	Early autumn		Late winter		Late spring		Late summer	
	LM	CH	LM	CH	LM	CH	LM	CH
Lumbriculus variegatus Muller	−1.00	−0.71	0.03	0.05		−0.35	−0.40	
Diplodon chilensis d'Orbigny		+1				−0.06		
Hyalella araucana Grosso & Peralta		−0.45				−0.75		
Chilina patagonica Sowerby	0.82						0.99	
Lymnaea sp.					+1			0.66
Aubertoperla illiesi (Illies)	−0.03		0.22	0.36	0.07	−0.13		0.31
Antarctoperla michaelseni Klapálek	0.36	−0.73	0.40			−0.16	0.45	
Pelurgoperla personata Illies		−0.60		+1				−0.30
Pictetoperla gayi Pictet		0.33						
Notoperlopsis femina Illies	0.31							0.18
Nousia delicata Navás	−0.07	−0.57	+1		+1	−0.77	−0.36	
Nousia crena Pescador & Peters						+1		
Meridialaris chiloeensis Demoulin		−0.43	−0.46	−0.12	−0.93	−0.43		0.87
Dactylophlebia carnulenta Pescador & Peters					−0.50			
Andesiops torrens (Lugo-ortíz & McCafferty)		0.53			+1	−0.39		−0.60
Andesiops sp.					0.23			
Myotrichia murina Schmid		0.50		−0.84		0.11		
Hudsonema flaminii Navás	0.30	+1				0.07		0.92
Brachysetodes sp.	0.85	−0.68	0.06	−0.63	0.56	0.60	0.94	
Neoatopsyche unispina Flint				+1				
Neoatopsyche brevispina Schmid		−0.72						
Cailloma sp.								
Oxyethira bidentata Mosely	+1							
Glossosomatidae sp.		0.41		−0.34		+1		
Mastigoptila longicornuta (Schmid)						+1		
Eosericostoma sp.		0.33				0.83		+1
Austrocentrus valgiformis (Flint)		0.60						
Metrichia patagonica Flint	+1				0.82			
Metrichia neotropicalis Schmid					+1	−0.66		
Smicridea annulicornis Blanchard	0.84	−0.57	0.60		−0.60			
Philorheithridae		+1						0.92
Limnephilidae		0.82	+1			+1		
Elmidae sp. (L)						+1		
Stethelmis kaszabi (L) Hinton	+1	−0.41				0.68		0.97
Dysticidae (A)					+1			
Austrolimnius sp. (A)						−0.26		
Hydrochus stolpi (A) Germain						+1		−0.82
Edwardsina (Edwardsina) sp.				0.17				
Dasyoma sp.	0.36	0.64	−0.38		−0.75			0.42
Muscidae (L)		+1		+1		0.36		
Simuliidae (L)	0.09	−0.15	0.05	0.53	−0.14	−0.2		
Empididae (L)		−0.52			0.46		0.66	
Ablabesmyia sp.				+1				
Ceratopogonidae sp.		0.33			0.88		0.59	
Paratrichocladius sp.	0.03	0.79	−0.40		0.15	−0.94		
Thienemanniella sp.			−0.46		0.74			
Chironomidae sp.			0.09					
Pseudochironomus sp.						+1		
Telmatogeninae sp.						0.12		

CH, Chiquito; LM, Las Minas.

prey (Table 3). Depending on the season, *Brachysetodes* sp., *A. illiesi* and *Paratrichocladius* sp. were the most abundant prey at LM, whereas *Paratrichocladius* sp. *A. illiesi*, *B. quadrifidus* and *M. murina* predominated at CH (Fig. 4). Fish were only represented in the trout diet at LM during late summer (Fig. 4).

Trout selected species of Oligochaeta, Gasteropoda, Plecoptera, Ephemeroptera, Trichoptera, Coleoptera and Diptera (Table 4). The prey selected at both study sites varied throughout the study period. At LM, rainbow trout positively selected the trichopteran *S. annulicornis* during early autumn ($I = 0.80$) and late winter ($I = 0.60$), shifting to the dipteran *Paratrichocladius* sp. in late spring and no prey were positively selected in late summer (Fig. 2). At CH, rainbow trout positively selected *Paratrichocladius* sp. ($I = 0.79$) in early autumn, the plecopteran *A. illiesi* ($I = 0.36$) in late winter, the trichopteran *B. quadrifidus* ($I = 0.60$) in late spring and the ephemeropteran *M. chiloeensis* ($I = 0.87$) in late summer (Fig. 2).

Feeding strategy and food-niche features

The feeding strategy (Fig. 4) reflected that although some prey were positively selected for (Table 4), all the prey were eaten in small proportions by most individuals in

early autumn, late winter and late spring in both streams, suggesting a generalised feeding strategy with a high within-phenotype component to the niche width (Fig. 4a, c,f). During early autumn in LM, rainbow trout fed particularly on *Brachysetodes* sp. and *Paratrichocladius* sp., *Thienemanniella* sp., *A. illiesi* and Diptera pupae in late spring (Fig. 4a,c), whereas in CH, in late winter, they mostly foraged on *A. illiesi* and Simuliidae larvae (Fig. 4f). During late winter in LM (Fig. 4b) and during late spring and late summer at CH (Fig. 4g,h), however, fish displayed a specialised feeding strategy in that all individuals fed on the dominant prey *A. illiesi*, *B. quadrifidus* and *M. murina*, and there were neither high within-phenotype nor between-phenotype contributions to the narrow niche width value (Table 2). Individuals specialised on different prey types by subgroups of the fish population during late summer in LM (mainly on terrestrial preys and fish, Fig. 4d) and early autumn at CH (*M. murina*, *Paratrichocladius* sp., Simuliidae larvae, Fig. 4e). There was a high between-phenotype contributions, coinciding with the broad niche width value (Table 2).
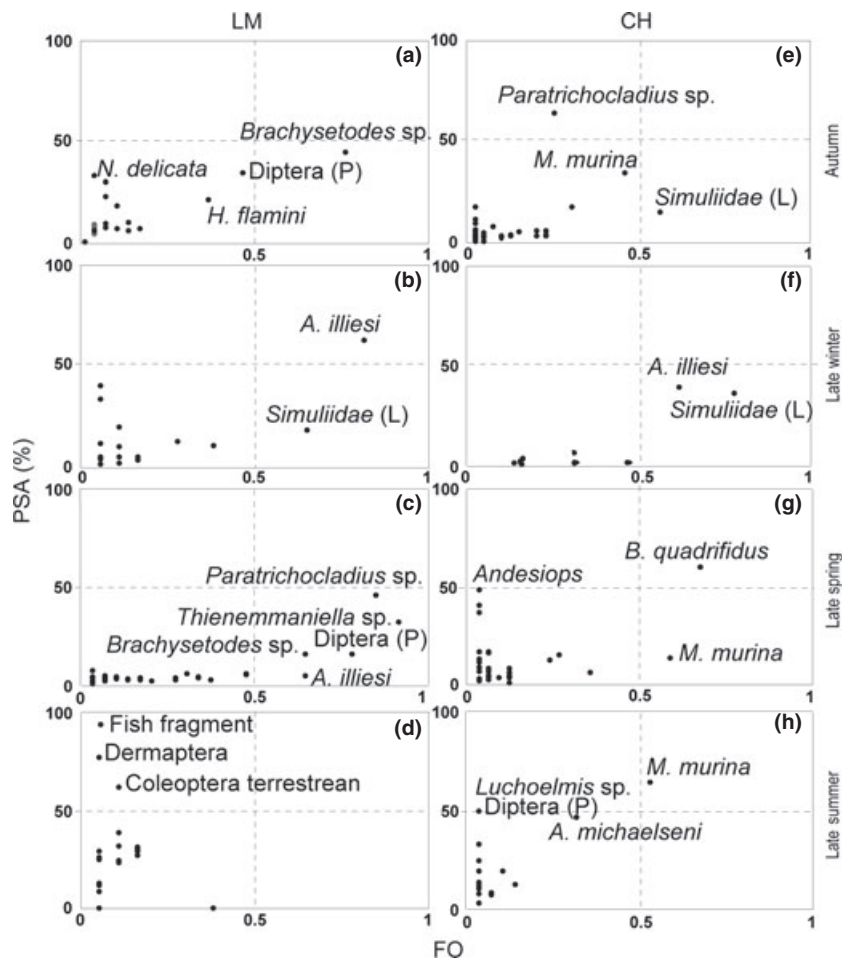
Discussion

The physicochemical values recorded in the streams under study are in general agreement with those from
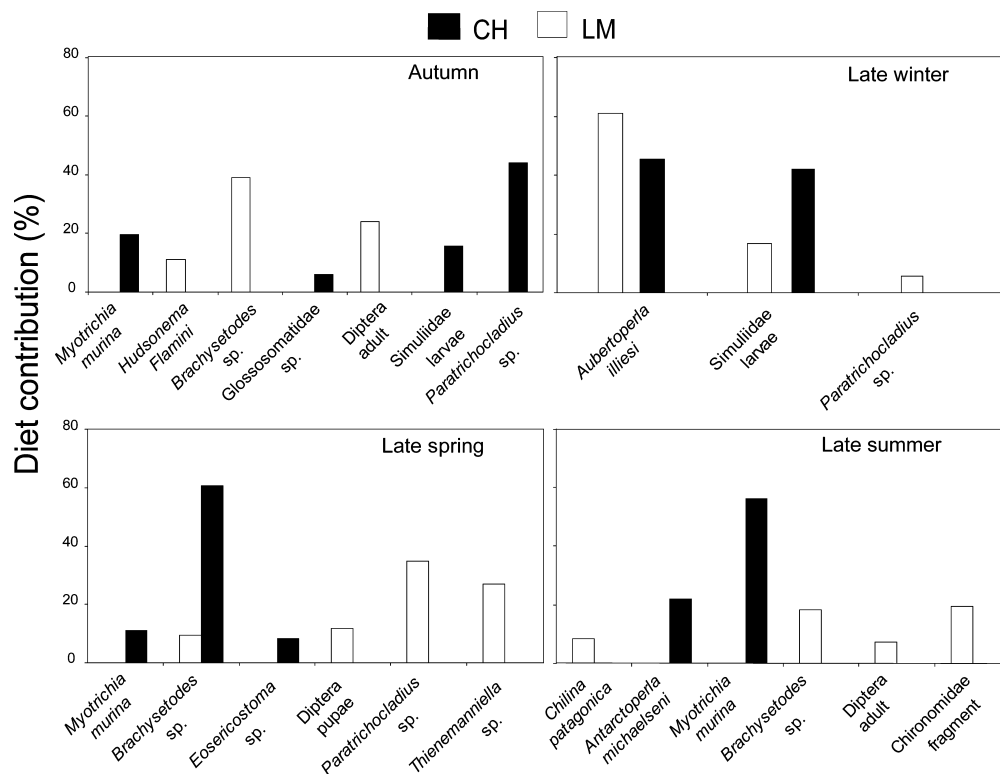
Figure 3. Seasonal changes in the diet (contribution by number percent) of *Oncorhynchus mykiss* at Las Minas (LM) and Chiquito (CH) streams (May 2005 – March 2006). Only those preys that contributed to the diet with more than 5% by number were plotted.

Figure 4. Feeding strategy graph of *Oncorhynchus mykiss* through the year at two low order Patagonian streams (May 2005 – March 2006). CH: Chiquito, LM: Las Minas. PSA (%): prey-specific abundance percentage; FO: frequency of occurence. Only the most important preys are highlighted in the figure.

other streams in the region (Miserendino & Masi 2010; Brand & Miserendino 2011). The structure of the benthic community was similar to those of other streams at Chubut (Velásquez & Miserendino 2003; Miserendino & Pizzolón 2004). As observed in other studies (Miserendino 2001), the most abundant macroinvertebrates at the studied streams varied throughout the study period and belonged to Ephemeroptera, Trichoptera, Plecoptera and Diptera. The abundance of benthic organisms varied according to season and was always higher in riffles than in pools. Species diversity and richness peaked during late spring and late summer, which probably reflects the recruitment period of certain Ephemeroptera, Plecoptera and Trichoptera species (Epele *et al.* 2011; Brand & Miserendino 2012).

As observed in other studies carried out in Patagonia (Buria *et al.* 2009; Arismendi *et al.* 2011; Di Prinzio & Casaux 2012), as well as in Scotland, Japan and New Zealand (Bridcut 2000; McIntosh 2000; Kawaguchi

et al. 2003), benthic macroinvertebrates, terrestrial insects, fish and vegetable matter were represented in the diet of rainbow trout. Except for adult dipterans, benthic macroinvertebrates predominated in the diet of trout from both streams. However, the main prey differed at each sampling site (Table 3). The trophic spectrum was wider at LM than at CH. This is mainly because small and large individuals segregated the use of food resources at LM. Fish were only represented in the diet at LM. It is probable that because of the lower availability of food at this locality (Fig. 1), larger trout are forced to forage on smaller individuals. Consequently, to reduce predation pressure, smaller individuals avoid larger ones by exploiting alternative microhabitats, thus explaining the ontogenetic differences in the composition of the diet observed in this stream. Arismendi *et al.* (2011) also reported an ontogenetic shift in the rainbow trout diet from small invertebrate feeding towards piscivory and larger prey with increase in body size.

Prey positively selected by trout varied seasonally in both streams and included organisms with little (e.g. *Diplodon chilensis* d 'Orbigny, *Lymnaea* sp.) to high mobility (mainly Ephemeroptera, Trichoptera, Plecoptera and Coleoptera), as well as some infaunal species (e.g. sedentary Chironomidae) (Table 4). Electivity of the different preys was not related either to their availability in the environment or to the habitat type (riffles/pools) exploited (Fig. 2). This suggests that the electivity of a specific prey depends not only on their mobility or conspicuousness but also on their body size, activity pattern, digestibility, mode of fixing to substratum and camouflage. Terrestrial prey items contributed little to the diet of trout except during late summer in LM (32.9% by number). Unfortunately, information on their availability in the environment was not available, which prevented estimates of the degree of electivity of those prey items. Buria *et al.* (2009) also observed low contribution of terrestrial prey to the diet of trout in northern Patagonian low-order streams.

At the population level in low-order streams, rainbow trout display different feeding strategies throughout the year, being highly flexible and shifting their niche width. This feeding plasticity was also observed in Chilean Patagonian streams (Arismendi *et al.* 2011) and North American lakes (Hubert & Gipson 1994). According to Amunsden (1995), this feeding flexibility depends on different factors such as prey type characteristics, seasonal changes in resource supply, availability and abundance of prey and food–habitat utilisation. According to their feeding plasticity, trout may opportunistically exploit temporarily abundant food resources, as observed in LM during late winter when individuals foraged intensively on the abundant *A. illiesi* and in CH during late spring and late summer when the main prey were also the abundant *B. quadrifidus* and *M. murina*. This observation supports the proposal by Amundsen *et al.* (1996) that intensive feeding on some prey is related to their high availability in the environment (see also Grimås 1961). However, as indicated previously and according to the Ivlev index, individual trout also positively selected relatively scarce prey. This information is in line with the mixed feeding strategy derived from the graphical method of Amundsen *et al.* (1996) for individuals from both streams.

Rainbow trout showed high feeding plasticity and is capable of buffering changes in food availability by switching between specialised and generalised feeding strategies. This capability, together with a reduced abundance of predators, the absence of rational stock assessment and the continuous stocking of hatchery fish to supplement wild populations, explains the marked expansion of this species in Patagonia (Pascual *et al.* 2002).

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