

The diet of introduced brook trout (*Salvelinus fontinalis*; Mitchill, 1814) in an alpine area and a literature review on its feeding ecology

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ABSTRACT

Introduced fish are a major threat for high altitude aquatic habitats and *Salvelinus fontinalis* have been widely used throughout the Alps for stocking lakes and rivers. Understanding its feeding ecology is a basic, but essential tool for interpreting its impact. To assess which factors determine the diet of *S. fontinalis* we analyzed more than 500 stomachs from several introduced populations from the Gran Paradiso National Park (GPNP, Western Italian Alps) and we measured the availability of several prey groups (zooplankton, aquatic invertebrates, terrestrial invertebrates). We complemented the study with a short, but exhaustive literature review on the *S. fontinalis* feeding ecology. In general the food composition reflected the availability of prey -confirming that *S. fontinalis* is an opportunistic predator- and was influenced by habitat type (stream vs lake), fish size, and seasonality. The obtained results were discussed in the light of the existing literature on the feeding ecology and ecological impact of *S. fontinalis*. Large benthonic insects account for a substantial part of the diet of stream dwelling brook trout, while they are almost absent both in the diet and in the prey species pool of lake-dwelling brook trout, probably reflecting a stronger ecological impact in the lakes.

Key words: Stomach content; alpine rivers; alpine lakes; prey availability; Gran Paradiso National Park; LIFE+ Bioaquae.

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INTRODUCTION

In mountain regions, a substantial part of river basins lies upstream of natural barriers to fish colonization and was thus naturally fishless (Bahls, 1992; Adams, 2001). All habitats upstream of these barriers provide refugia for peculiar aquatic species and communities, often lacking anti-predatory adaptations and thus vulnerable to fish invasions (Bellati *et al.*, 2014). Unlike other clades, where introduction pathways are often unintentional, the widespread presence of fish in mountain regions is commonly linked to deliberate manipulations for recreational angling (García-Berthou *et al.*, 2005), producing an artificial range expansion of native species, or the establishment of new species from different eco-regions. Fish stocking in headwater basins provides source populations facilitating the invasion of downstream habitats, including otherwise inaccessible refugia (Adams, 2001). Introduced fish have profoundly altered the ecology of high altitude aquatic habitats such as streams (Bechara *et al.*, 1993) and lakes (Knapp *et al.*, 2001) and are considered a major threat for their conservation.

The Gran Paradiso National Park (GPNP) is a large protected area of the western Italian Alps and one of the few

Alpine protected areas where fishing is largely prohibited, in accordance with the most recent scientific findings, that clearly show that fishing bans are the most effective measure to stem the spread of invasive fish in mountain areas (Mirò and Ventura, 2013; Mirò and Ventura, 2015). Nevertheless, in the 1960s, before fishing ban was established in the 1970s, some populations of *Salvelinus fontinalis* have been introduced in a number of naturally headwater lakes, which served as a source for the colonization of the downstream habitats. *S. fontinalis* established many reproductive populations in some large portions of the GPNP hydrographic system. This salmonid, native of North America, is considered one of the most impacting fish in alpine aquatic habitats and, unfortunately, it has been one of the most utilized alien species for stocking alpine lakes and rivers (Savini *et al.*, 2010).

To understand the ecological consequences of *S. fontinalis* introduction and to try to recover the invaded ecosystems, the GPNP started a long term research campaign (since 2006) and an eradication project from four headwater lakes (LIFE+ Bioaquae, Biodiversity Improvement of Aquatic Alpine Ecosystems, www.bioaquae.eu).

In this context the understanding of the feeding ecology of *S. fontinalis* is a basic, essential tool to interpret its impact in alpine areas. This study aims at understanding which are the factors determining the diet of lake and stream dwelling *S. fontinalis* from the populations of the GPNP. Our results will be discussed in the light of the existing literature on the feeding behavior of *S. fontinalis* and in relation to its ecological impact in the study area (Tiberti and von Hardenberg, 2012; Magnea *et al.*, 2013; Tiberti *et al.*, 2014a) and may be useful to anyone interested in the invasion ecology of this species in the alpine environment. To this purpose we complemented our study with a short review of the existing literature on the feeding ecology of *S. fontinalis*. Specific aims of the study are: i) to understand how the diet of *S. fontinalis* changes depending on the habitat (lakes vs streams), the fish size, and seasonality; ii) to compare the diet of *Salvelinus fontinalis*

with the availability of prey measured in the different studied habitats; and iii) to review the existing literature on the feeding ecology of *S. fontinalis*.

METHODS

Study area and period

The Gran Paradiso National Park is a protected area in the western Italian Alps (Fig. 1), showing a large altitudinal extension (between 800 and 4061 m) and a typical alpine climate. The sampling sites for *S. fontinalis* stomach contents (Fig. 1) and prey availability are comprised between 1875 and 2757 m asl, above or at the local timberline. A short description of each sampling site is provided in Tab. 1. *S. fontinalis* was the only fish species in all the sampling sites, with the exception of a single site (Orco-3; Tab. 1), where brown trout *Salmo trutta* and rainbow trout *O-*

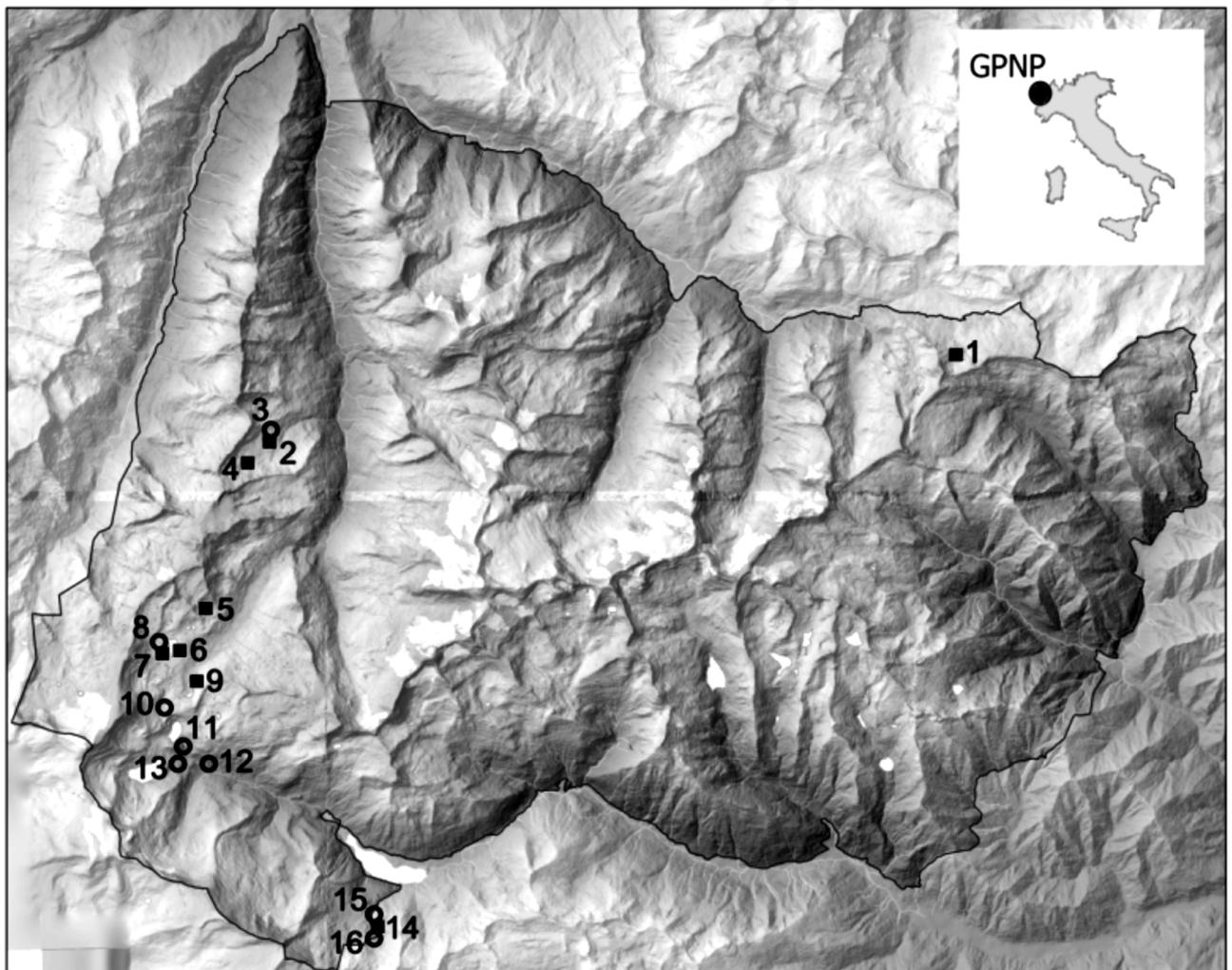


Fig. 1. Map of the Gran Paradiso National Park (GPNP), its position in Italy, and samplings sites (from 1 to 16, see Tab. 1) for *Salvelinus fontinalis* stomach contents. Black line, Gran Paradiso National Park border; black squares, lacustrine sampling sites; empty circles, riverine sampling sites.

corhynchus mykiss were also present. Field work was carried out between 2006 and 2014 from June to November.

Literature review

Web of Science (by Thomson Reuters) and Google Scholar databases searches were conducted to retrieve articles, technical and scientific reports, and theses related to the feeding ecology of *S. fontinalis*. Search terms included all the possible combinations among the terms 'brook trout/*Salvelinus fontinalis*' and the terms 'diet/feeding ecology/food/impact'. The reference lists of each document were reviewed in detail to find additional useful references.

Fish capture and permissions

Between 2006 and 2014 we captured more than 20,000 *S. fontinalis* using a variety of systems including

nets (gillnets, trammel nets, and multimesh gillnets), electrofishing (with a ELT62 II 160 GI backpack equipment) and fishing ropes. A total of 821 captures were made in 2006-2012 during a long term monitoring program (Tiberti *et al.*, 2014c), while the remaining captures were made in 2013-2014 within the fish eradication project LIFE+ Bioaquae. Permissions for fishing activities have been issued by the GPNP (protocol number 1798/1013/BB) with the favorable opinion of ISPRA (Istituto Superiore per la Protezione e Ricerca Ambientale, protocol number 0017655 - 29/04/2013).

Stomach contents analysis

A total of 506 stomachs were dissected for prey presence/absence analysis, a subsample of 232 for prey items counting, and a subsample of 304 (from fish larger than 15 cm) for the analysis of prey biovolumes (Tab. 2). The fish maximum length was converted into seven size classes en-

Tab. 1. Sampling sites of *Salvelinus fontinalis* stomach contents in the Gran Paradiso National Park (data from Tiberti *et al.*, 2010). Coordinates of stream sampling sites refer to their start point, at the lower altitude.

Sampling site	Watershed	Habitat type	UTM 32T coordinates	Altitude	N	Short description
1 Miserino	Ourtier	Lake	380686 – 5048871	2666	1	Area: 4.22 ha. Maximum depth: 9.9 m
2 Djouan	Savaranche	Lake	357850 – 5046521	2515	96	Area: 1.83 ha. Maximum depth: 3.0 m
3 Djouan outlet	Savaranche	Stream	357910 – 5046598	2511	1	Length of the sampled stream stretch: 40 m
4 Nero	Savaranche	Lake	357071 – 5045892	2671	25	Area: 1.71. Maximum depth: 6.0 m
5 Leynir	Savaranche	Lake	355624 – 5041016	2747	96	Area: 4.47 ha. Maximum depth: 22.1 m
6 Rosset	Orco	Lake	354540 – 5039773	2703	19	Area: 16.86 ha. Maximum depth: 46.9 m
7 Leità	Orco	Lake	354052 – 5039506	2701	29	Area: 6.22 ha. Maximum depth: 11.0 m
8 Leità inlet	Orco	Stream	354087 – 5039747	2701	2	Length of the sampled stream stretch: 50 m
9 Nivolet inferiore	Savaranche	Lake	355120 – 5038595	2526	15	Area: 8.24 ha. Maximum depth: 14 m
10 Orco-1	Orco	Stream	354137 – 5037693	2504	5	Length of the sampled stream stretch: 125 m
11 Orco-2	Orco	Stream	354885 – 5036331	2150	1	Length of the sampled stream stretch: 105 m
12 Orco-3	Orco	Stream	355637 – 5035584	1875	4	Length of the sampled stream stretch: 75 m
13 Orco-4	Orco	Stream	354528 – 5035937	2160	7	Length of the sampled stream stretch: 70 m
14 Dres	Orco	Lake	361018 – 5030347	2087	143	Area: 2.71 ha. Maximum depth: 7.4 m
15 Dres outlet	Orco	Stream	360907 – 5030392	2057	5	Length of the sampled stream stretch: 279 m
16 Dres inlet	Orco	Stream	360999 – 5030268	2087	58	Length of the sampled stream stretch: 120 m

N, number of analyzed stomachs.

Tab. 2. Number of specimens of *Salvelinus fontinalis* examined for stomach content analysis divided by sampling habitat, type of analysis, and total length (size classes). Data from 506 specimens sampled in lacustrine and riverine habitats in the Gran Paradiso National Park.

Habitat	Analysis	Class 1	Class 2	Class 3	Class 4	Class 5	Class 6	Class 7	N
		0-5 cm	5-10 cm	10-15 cm	15-20 cm	20-25 cm	25-30 cm	>30 cm	
Lake	Presence/absence analysis	49	42	30	34	167	78	23	423
Lake	Prey counts	44	23	25	27	35	19	9	182
Lake	Biovolume measurements	-	-	-	23	157	69	18	267
Stream	Presence/absence analysis	4	34	5	15	9	16	1	83
Stream	Prey counts	4	5	5	13	9	14	0	50
Stream	Biovolume measurements	-	-	-	14	8	15	0	37

compassing the values from 0 to ≥ 30 cm at five centimeters intervals. Analyzed stomachs belong to all the present size classes. Stomachs were preserved in 70% ethanol.

Stomachs from larger fish were dissected in a Petri dish under a stereomicroscope. Larger prey were sorted until all the prey items identifiable under the stereoscope maximum magnification had been recorded or separated for prey counting and biovolume measurement. What remained in the dish was checked for the presence of microscopic preys (*e.g.*, zooplankton), and, if necessary, we proceeded with a microscopic analysis using a closed counting chamber for zooplankton under a binocular dissecting microscope at 40X (Olympus CH-BI45-3). Stomachs from smaller fish (approximately < 10 cm) were dissected under the stereomicroscope and directly analyzed using the closed counting chamber. Biovolumes were measured by gently pressing the prey items belonging to each prey group in a graduated cylinder. Prey groups with very small biovolumes (< 0.05 mL) were approximated to zero in the subsequent data analyses.

Prey were divided into six macro-groups based on their ecological niche (Tab. 3), so that several prey taxa with complex life history were separated in different groups (*i.e.*, terrestrial vs aquatic life stages). Within macro-groups we used different taxonomic levels (Tab. 3). Fragmented or partially digested items were recognized using body parts resistant to digestion (*e.g.*, cephalic capsule) or recorded as non-identified prey and grouped in a separate category.

Prey availability

Prey availability was determined using different sampling methods depending on the sampled habitat and taxa. All the results concerning prey availability have been qualitatively presented as frequency of occurrence in the samples.

Pelagic zooplankton: 146 samples were collected at all the lacustrine sampling sites (Fig. 1) in June-October 2006-2014. Samples were collected at the deepest point of each lake by taking vertical tows from the bottom to the surface with a conical plankton net (40 cm diameter, 48 μ m mesh). Samples were preserved in 70% ethanol and sorted to species/genus.

Lacustrine macroinvertebrates: 64 samples were collected at sampling sites 2, 4, 5, 6, 7, 9, and 14 (Fig. 1) in June-September 2006-2014. Samples were collected from the littoral zone by conducting 30 standard sweeps with a rectangular dip net (25 cm width, 20 cm height; mesh 0.5 mm). A standard sweep consisted of a 1-m sweep in one direction followed immediately by a 1-m sweep across the same area in the opposite direction (Knapp *et al.*, 2001). Samples were preserved in 70% ethanol and sorted to class/order.

Riverine macroinvertebrates: Twelve samples were collected at sampling sites 3, 15, and 16 (Fig. 1) between

2013 and 2014. Samples were collected with a standard Surber sampler (mouth width 32 cm; mesh 0.5 mm), sampling a total surface of 1 m² including all the available aquatic habitats following Buffagnini and Erba (2007). Samples were preserved in 70% ethanol and sorted to class/order.

Terrestrial invertebrates around the lakes: Pitfall traps (50 mm inner diameter, 70 mm deep, 1/3 filled with a 1:1 solution of water and vinegar) were used to sample ground-dwelling arthropods (Cole *et al.*, 1992) around the lacustrine sampling sites 2, 4, 5, 6, 7, 9, and 14 (Fig. 1) in August-September 2009. The traps were protected with flat stones and were placed at 1, 10 and 50 meters from the coastline, along four transects placed at the four cardinal points (12 traps per lake). Each set of pitfall was left for 9-13 days. 68 samples were obtained (16 traps were flooded or disturbed by cattle). Samples were preserved in 70% ethanol and sorted to class/order.

Terrestrial arthropods falling into the lake: 65 non-empty samples of sinking terrestrial invertebrates were collected at sampling sites 2, 4, 5, 6, 7, 9, and 14 (Fig. 1) in June-September 2013-2014 using sinking traps. Sinking traps consist of a cone of fine plastic mesh (diameter 56 cm; mesh size 1 mm) with their mouth facing upwards. Eight traps per lake were repeatedly placed below the water surface and were left for 5-14 days in correspondence with randomly generated points along the 2 m isobaths. Random points were obtained using the *runifpointOnLines* function of the *spatstat* package implemented in the R 3.1.1 statistical software (R Core Team, 2011). Samples were preserved in 70% ethanol and sorted to class/order.

Data presentation and analysis

For the description of the diet, data are offered on frequency of occurrence of the prey groups ($F_i = N_i/N \times 100$, where N_i is the number of fish with prey i in their stomach and N is the total number of analyzed stomachs), relative abundance ($A_i = S_i/S_t \times 100$, where S_i is the sum of the counts of prey i in all the stomachs and S_t is the total sum of all the prey items counted), and relative biovolume ($B_i = V_i/V_t \times 100$, where V_i is the sum of the biovolumes of prey i in all the stomachs and V_t is the total sum of all the measured biovolumes). Sampling adequacy for diet composition was determined by visual inspection of the cumulative prey curves and using Lehner's formula $Q = 1 - (N_1/I)$ (Lehner, 1996), rising from 0 to 1, where Q is sampling adequacy, N_1 is the number of the food components occurring only once, and I is the total number of the food components. The order of the stomach content analysis was randomized and the cumulative prey curves were represented plotting the cumulative number of prey groups against the cumulative number of stomachs analyzed.

To determine which factors influence the diet of the

studied *S. fontinalis* populations and to avoid pseudoreplications due to repeated and unbalanced samplings at the same sites, we used some generalized mixed effects mod-

els. An exhaustive summary of how the models were fitted is provided in Tab. 4. When modeling the presence/absence of each prey group, we added the remaining prey

Tab. 3. Diet of *Salvelinus fontinalis* from alpine lakes and rivers in Gran Paradiso National Park in relation to prey availability.

Prey groups	Lakes			Streams			Total			Prey availability
	F % N=423	A % N=182	B % N=267	F % N=83	A % N=50	B % N=37	F % N=506	A % N=232	B % N=304	F %
Zooplankton	17.73	21.55	0.77	3.61	0.31	0.00	15.42	20.12	0.63	
Copepoda - <i>Eucyclops surrullatus</i>	1.42	0.27	0.00	-	-	-	1.19	0.25	0.00	41.10 ^f
Copepoda - <i>Cyclops</i> gr. <i>abyssorum</i>	8.75	1.88	0.00	-	-	-	7.31	1.75	0.00	70.55 ^f
Copepoda - <i>Arctodiaptomus alpinus</i>	0.71	1.80	0.07	-	-	-	0.59	1.68	0.06	69.86 ^f
Cladocera - <i>Chydorus</i> sp.	2.36	0.12	0.00	-	-	-	1.98	0.11	0.00	26.71 ^f
Cladocera - <i>Alona</i> sp.	3.55	1.44	0.00	-	-	-	2.96	1.35	0.00	13.70 ^f
Cladocera - <i>Acropoerua harpae</i>	2.36	0.11	0.00	-	-	-	1.98	0.10	0.00	14.38 ^f
Cladocera - <i>Scapholeberis mucronata</i>	0.47	0.13	0.00	-	-	-	0.40	0.12	0.00	0.68 ^f
Cladocera - <i>Daphnia</i> gr. <i>longispina</i>	7.09	15.74	0.70	1.20	0.00	0.00	6.13	14.69	0.57	52.1 ^f
Ostracoda	1.18	0.06	0.00	2.41	0.31	0.00	1.38	0.07	0.00	1.37 ^f
Rotifera	-	-	-	-	-	-	-	-	-	99.31 ^f
Nectonic invertebrates	45.39	42.88	27.23	27.71	1.76	0.32	42.49	40.06	22.99	
Nectonic Coleoptera, i	0.95	0.10	0.04	1.20	0.10	-	0.99	0.03	0.03	14.7 ^g – 18.8 ^h
Nectonic Diptera, p ^a	40.66	42.63	26.00	26.51	1.61	0.16	38.34	39.89	21.17	15.6 ^g – 0.0 ^h
Aquatic Heteroptera	5.44	0.10	1.19	2.41	0.05	0.16	4.94	0.10	0.99	4.7 ^g – 8.3 ^h
Isopoda	0.24	0.05	0.00	-	-	-	0.20	0.04	0.00	0.0 ^g – 0.0 ^h
Benthonic invertebrates	19.62	1.07	4.96	81.93	38.28	45.97	29.84	3.6	12.61	
Benthonic Coleoptera, l and i	0.71	0.00	0.00	2.40	0.05	0.16	0.99	0.01	0.03	8.8 ^g – 56.3 ^h
Plecoptera, l	7.57	0.14	0.04	63.86	8.42	4.03	16.80	0.68	0.78	21.9 ^g – 83.2 ^h
Ephemeroptera, l	0.47	0.02	0.00	32.53	2.51	0.97	5.73	0.17	0.18	4.7 ^g – 91.7 ^h
Tricoptera, l	13.48	0.82	3.07	50.60	26.78	40.81	19.57	2.58	10.12	25.0 ^g – 100.0 ^h
Benthonic Diptera, l ^b	0.47	0.01	0.00	9.64	0.52	0.00	1.98	0.04	0.00	0.0 ^g – 83.3 ^h
Odonata, l	0.95	0.02	1.85	-	-	-	0.79	0.02	1.50	1.6 ^g – 0.0 ^h
Hydracarina	2.13	0.06	0.00	3.61	0.73	0.00	2.37	0.10	0.00	9.5 ^g – 25.0 ^h
Aquatic fossorial invertebrates	40.43	23.15	9.22	44.58	39.74	1.45	41.11	24.04	8.77	
Mollusca - <i>Pisidium</i> sp.	6.15	0.13	0.22	-	-	-	5.14	0.12	1.18	53.1 ^g – 25.0 ^h
Fossorial Diptera, l ^c	36.64	22.87	9.00	43.37	38.49	1.29	37.75	23.70	7.56	100.0 ^g – 100.0 ^h
Oligochaeta	0.47	0.01	0.00	1.20	0.10	0.00	0.59	0.02	0.00	98.4 ^g – 91.7 ^h
Nematomorpha	0.95	0.02	0.00	3.61	0.42	0.16	1.38	0.04	0.03	0.0 ^g – 0.0 ^h
Copepoda – Harpacticoida	2.60	0.12	0.00	3.61	0.73	0.00	2.77	0.16	0.00	Not sorted
Terrestrial invertebrates	74.00	8.87	34.41	65.06	14.95	15.62	72.53	9.44	31.89	
Coleoptera, i	55.08	2.07	10.48	31.32	6.69	3.22	51.19	2.36	9.12	62.8 ^k – 29.2 ^l
Diptera/Imenoptera, i	60.76	6.66	22.93	63.86	7.27	9.67	61.26	6.65	20.45	88.5 ^k – 70.8 ^l
Orthoptera	1.18	0.01	0.22	-	0.10	0.00	1.38	0.01	1.18	10.9 ^k – 0.0 ^l
Lepidoptera, i and l	0.47	0.00	0.11	1.20	0.00	0.32	0.59	0.00	0.15	9.0 ^k – 0.0 ^l
Plecoptera, i	0.95	0.01	0.30	3.61	0.31	0.48	1.38	0.03	0.33	0.0 ^k – 0.0 ^l
Tricoptera, i	0.24	0.02	0.00	8.43	0.16	1.45	1.58	0.06	0.27	0.0 ^k – 1.5 ^l
Hemiptera	4.26	0.09	0.30	3.61	0.16	0.16	4.15	0.09	0.27	0.0 ^k – 0.0 ^l
Collembola	0.24	0.00	0.00	-	-	-	0.20	0.00	0.00	16.7 ^k – 0.0 ^l
Aranea	1.42	0.01	0.07	4.82	0.26	0.32	1.98	0.03	0.12	70.5 ^k – 4.6 ^l
Miriapoda	0.24	0.00	0.00	0.00	0.00	0.00	0.20	0.00	0.00	6.4 ^k – 0.0 ^l
Terrestrial Acarina	-	-	-	-	-	-	-	-	-	32.1 ^k – 0.0 ^l
Vertebrates	2.36	0.03	22.03	10.84	0.83	36.35	3.76	0.07	24.73	
<i>Salvelinus fontinalis</i> ^d	1.89	0.02	7.96	2.41	0.10	0.71	1.98	0.02	6.63	-
<i>Rana temporaria</i> ^e	0.47	0.01	14.07	8.43	0.73	35.64	1.79	0.05	18.10	-
Undetermined rests	14.66	2.52	1.37	6.02	3.40	0.16	13.24	2.56	1.14	

F %, frequency of occurrence of the group in the analyzed stomachs or samples; A %, percent abundance of prey group compared to the sum of all the counted prey items; B %, percent biovolume of prey group compared to the sum of all the measured biovolumes; l, imaginal stage; i, larvae; p, pupae. ^aChironomid pupae; ^bSimuliid larvae; ^calmost exclusively Chironomid larvae; ^dincluding well recognizable fish, fish remains (bones) and, just in one case, eggs; ^eincluding adult and juvenile frogs and frogs remains (bones); ^fbased on 146 zooplankton samples collected in lacustrine sampling sites 1, 2, 4, 5, 6, 7, 9, and 14 between 2006 and 2014; ^gbased on 64 samples for benthic invertebrates collected in lacustrine sampling sites 2, 4, 5, 6, 7, 9, and 14 between 2006 and 2014; ^hbased on 12 samples for benthic invertebrates collected in riverine sampling sites 3, 15, and 16 between 2013 and 2014; ⁱbased on 68 samples for terrestrial invertebrates collected around the lacustrine sampling sites 2, 4, 5, 6, 7, 9, and 14 in 2009; ^jbased on 65 non-empty samples for terrestrial invertebrates falling into the water collected in lacustrine sampling sites 2, 4, 5, 6, 7, 9, and 14 between 2013 and 2014.

groups as covariates (to test for the presence of associations/exclusions between prey groups) and we used the MuMIn package (Bartoń, 2011; Grueber *et al.*, 2011) to select the best fitting models ($\Delta AICc < 4$) among the models including all possible combinations of the fixed covariates. For the *Prey groups* models we report the 95% confidence intervals of the averaged parameter estimates and the relative importance of the covariates provided by the function *model.avg* of MuMIn.

RESULTS

Literature review

Our literature review include 126 publications (articles, theses and reports) from different areas of North America (102 documents), Europe (5 documents), South America (4 documents) and New Zeland (1 document), encompassing more than one century of research (1903-2015). A large part of the studies were carried out in the wild, in riverine, lacustrine, and estuarine habitats, within (75) or outside (34) the native range of *S. fontinalis*. Only a few studies include mesocosm or laboratory experiments (13). In Tab. 5 we provide all the references and we summarize the main objectives of the reviewed literature.

Description of the diet and prey availability

A descriptive summary of the diet of *S. fontinalis* in lakes and streams is provided in Tab. 3. We identified 36 prey groups in the diet of *S. fontinalis* (36 in lakes and 25 in streams) that were clumped into six macro-groups according to their ecology. Sampling adequacy index (Q) was satisfactory for both lacustrine samples (Q=0.94) and riverine samples (Q=0.84), as also demonstrated by the asymptotic

behavior of the prey cumulative curves (Fig. 2). The mean number \pm SD of prey belonging to different prey groups in the stomach contents was 2.59 ± 2.12 (range 0-13; N=423) in lakes and 3.84 ± 2.10 (range 0-10; N=83) in rivers; the mean number of prey items per stomach was 160.37 ± 364.95 (range 0-3223; N=183) and 41.68 ± 66.00 in rivers (range 0-

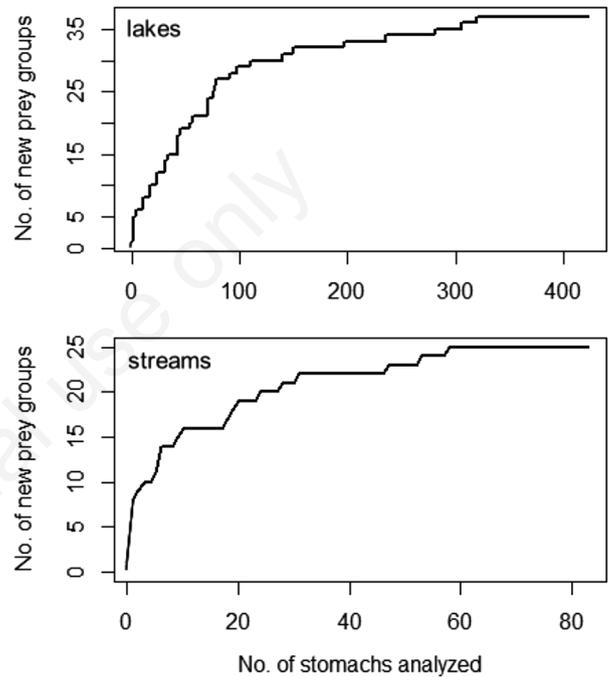


Fig. 2. Diet of *Salvelinus fontinalis* from alpine lakes and rivers: cumulative prey curves.

Tab. 4. Generalized linear mixed models to determine the factors influencing the diet of *S. fontinalis* from alpine lakes and rivers in the Gran Paradiso National Park: summary of their structures.

Models	Models features	
Prey number	Dependent variables	Prey richness (number of prey groups per stomach) and abundance (total number of prey items per stomach)
	Fixed effects	Habitat + size + day
	Random effects	Sampling site + year
	Error distribution	Poisson
Biovolume	Dependent variable	Log transformed of the total biovolume of stomach contents + 1
	Fixed effects	Habitat + size + day
	Random effects	Sampling site + year
	Error distribution	Gaussian
Prey groups	Dependent variables	Presence/absence of each prey group
	Fixed effects	Habitat + size + day + remaining prey groups presence/absence
	Random effects	Sampling site + year
	Error distribution	Binomial

Habitat, stream vs lake; day, standardized Julian date as days gone by June 15 of the year of sampling; size, fish size classes from 1 to 7; prey groups, binomial covariates indicating the presence/absence of each prey group (zooplankton, nektonic invertebrates, benthonic invertebrates, aquatic fossorial invertebrates, terrestrial insects, and vertebrates); year, year of sampling; sampling site, random factor including eight riverine and eight lacustrine sampling sites.

Tab. 5. List of the reviewed literature on *S. fontinalis* feeding behavior with details on the habitat type (including experimental laboratory and mesocosm artificial habitats). Literature is offered in chronological order.

Reference	Habitat	Region	Diet	Native	Objectives
Needham, 1903	River	Pennsylvania, USA	Y	Y	Describing the diet of <i>S. fontinalis</i>
Juday, 1907a, 1907b	Lake	Colorado, USA	Y	N	Describing the diet of <i>S. fontinalis</i>
Morgulis, 1918	Laboratory	-	-	-	Determining the food consumption of <i>S. fontinalis</i>
Clemens <i>et al.</i> , 1924	Lake	Ontario, CA	Y	Y	Describing the diet of the fish inhabiting lake Nipigon
Embody and Gordon, 1924	River	USA	Y	Y	Comparing the diet of wild and captive <i>S. fontinalis</i> to enhance food quality in captivity
Greeley, 1927	-	Massachusetts, USA	Y	Y	Describing the diet of several fish species including <i>S. fontinalis</i>
Greeley, 1928	-	New York State, USA	Y	Y	Describing the diet of several fish species including <i>S. fontinalis</i>
Hildebrand and Towers, 1927	Lake	Utah, USA	Y	N	Describing the diet of several fish species including <i>S. fontinalis</i>
Leonard, 1927	Lake	Québec, CA	Y	Y	Describing the diet of several fish species including <i>S. fontinalis</i>
Clemens, 1928	River	New York State, USA	Y	Y	Describing the diet of <i>S. fontinalis</i>
Needham, 1928	River	-	Y	Y	Determining the food consumption of <i>S. fontinalis</i>
Titcomb <i>et al.</i> , 1928	Laboratory	-	-	-	Assessing the nutritional requirements and grow rates in <i>S. fontinalis</i>
Metzelaar, 1929	Lake and river	Michigan USA	Y	Y	Describing the diet of the salmonids in Michigan
Harkness and Ricker, 1929	Lake and River	Ontario, CA	Y	Y	Describing the diet of <i>S. fontinalis</i>
Detwiler, 1930	Laboratory	-	-	-	Testing <i>S. fontinalis</i> optimal feeding in captivity
Needham, 1930	River	New York State, USA	Y	Y	Describing the seasonal variation in the diet of <i>S. fontinalis</i>
Rimsky-Korsakoff, 1930	-	Vermont, USA	Y	Y	Describing the diet of several fish species including <i>S. fontinalis</i>
White, 1930	River	Prince Edward Is., CA	Y	Y	Describing the diet of <i>S. fontinalis</i>
Ricker, 1930,	Lake and River	Ontario, CA	Y	Y	Describing the diet of <i>S. fontinalis</i>
Sibley and Rimsky, 1931	River	Québec, CA	Y	Y	Describing the biology and diet of <i>S. fontinalis</i>
Ricker, 1932	Lake and River	Ontario, CA	Y	Y	Describing the biology of <i>S. fontinalis</i>
Lord, 1933	River	Vermont, USA	Y	Y	Describing the winter diet of <i>S. fontinalis</i>
White, 1940	Sea	Nova Scotia, CA	Y	Y	Describing the biology of anadromous <i>S. fontinalis</i>
Leonard, 1941, 1942	River	Michigan, USA	Y	Y	Describing the winter diet of <i>S. fontinalis</i>
White, 1940	Sea	Nova Scotia, CA	Y	Y	Describing the biology of anadromous <i>S. fontinalis</i>
Wiseman, 1951	-	-	-	-	Describing the diet of <i>S. fontinalis</i>
Benson, 1954	River	Michigan, USA	Y	Y	Describing the seasonal variation in the diet of <i>S. fontinalis</i>
Baldwin, 1957	Laboratory	-	-	-	Temperature effects on <i>S. fontinalis</i> food consumption
Allen and Claussen, 1960	Beaver pond	Wyoming, USA	Y	N	Describing the diet of <i>S. fontinalis</i>
Tebo and Hassler, 1963	River	North Carolina, USA	Y	Y	Describing the diet of <i>S. fontinalis</i>
Reed and Bear, 1966	River	Colorado, USA	Y	N	Describing the diet of <i>S. fontinalis</i>
Lackey, 1969	Lake	Maine, USA	Y	Y	Describing the diet of several fish species including <i>S. fontinalis</i>
Nyman, 1970	River	Newfoundland, CA	Y	Y	Describing the ecological interaction between <i>Salmo trutta</i> and <i>S. fontinalis</i>
Swift, 1970	Lake	California, USA	Y	N	Describing the diet of <i>S. fontinalis</i> and the calorimetric content of each prey group
Bryan and Larkin, 1972	River, pond	CA	Y	N	Studying the food specialization at an individual level
Griffith, 1974	River	Idaho, USA	Y	N	Comparing resource partitioning between <i>S. fontinalis</i> and <i>Salmo trutta</i>

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Tab. 5. Continued from previous page.

Reference	Habitat	Region	Diet	Native	Objectives
Miller, 1974	River	Wisconsin, USA	Y	Y	Describing the diet of <i>S. fontinalis</i> fry
Wurtsbaugh <i>et al.</i> , 1975	Lake	California, USA	Y	N	Describing the differences in the diet and distribution of young <i>S. fontinalis</i> and <i>Oncorhynchus mykiss</i>
Flick, 1977	Lake	CA	Y	Y	Describing the ecology of <i>S. fontinalis</i> in some Canadian Lakes
Allan, 1978a	River	Colorado, USA	Y	N	Comparing the diet of <i>S. fontinalis</i> and <i>Salmo trutta</i> in relation to prey availability and daytime
Allan, 1978b	River	Colorado, USA	Y	N	Testing the existence of antipredatory defenses in drifting macroinvertebrates
Strogen, 1979	River	Michigan, USA	Y	Y	Describing the diet of <i>S. fontinalis</i>
Johnston, 1980	River	Prince Edward Is., CA	Y	Y	Describing the diet of <i>S. fontinalis</i>
Dutil and Power, 1980	Estuarine areas, Sea	Québek, CA	Y	Y	Describing the biology of anadromous <i>S. fontinalis</i>
Allan, 1981	River	Colorado, USA	Y	N	Assessing the determinants (daytime, fish size, prey availability) of <i>S. fontinalis</i> diet
Williams, 1981	River	Québek, CA	Y	Y	Determining the diet of <i>S. fontinalis</i> fry
Helfrich <i>et al.</i> , 1982	River	North Carolina, USA	N	Y	Studying the agonistic interaction of <i>S. fontinalis</i> with <i>Oncorhynchus mykiss</i>
Magnan and FitzGerald, 1982	Lake	Québek, CA	Y	Y	Describing the diet of <i>S. fontinalis</i> in sympatry with <i>Semotilus atromaculatus</i>
Gaudreault <i>et al.</i> , 1982	Estuarine areas, sea	Cnada	Y	Y	Describing the diet of anadromous <i>S. fontinalis</i>
O'Connell, 1982	River	Canada	Y	Y	Describing the biology of anadromous <i>S. fontinalis</i>
Dawidowicz and Gliwicz, 1983	Lake	Tatra Mts., Poland	Y	N	Describing the diet of <i>S. fontinalis</i>
Magnan and FitzGerald, 1984	Laboratory	-	-	-	Describing the dietary shift in <i>S. fontinalis</i> in the presence of competitors
Fausch, 1984	Laboratory	-	-	-	Relating specific growth rate to net energy gain
McNicol <i>et al.</i> , 1985	River	Manitoba, CA	Y	N	Investigating the feeding and territorial behavior of <i>S. fontinalis</i> fry
Grant and Noakes, 1986	River	Ontario, CA	N	Y	Comparing the size composition of drifting invertebrates and those in the stomachs of <i>S. fontinalis</i>
Cunjak and Power, 1987	River	Québek, CA	Y	Y	Studying the winter feeding of stream dwelling <i>S. fontinalis</i>
Grant and Noakes, 1987	River	Ontario, CA	N	Y	Studying alternative feeding tactics in <i>S. fontinalis</i> fry
Fechney, 1988	River	New Zeland	Y	N	Describing the diet of <i>S. fontinalis</i>
Grant and Noakes, 1988	River	Ontario, CA	N	Y	Studying the aggressive behavior of <i>S. fontinalis</i> fry with different foraging tactics
Walsh <i>et al.</i> , 1988	River	Québek, CA	Y	Y	Describing the daily variations in the diet of <i>S. fontinalis</i> fry
Grant <i>et al.</i> , 1989	River	Ontario, CA	N	Y	Studying the territorial behavior and size of foraging areas in <i>S. fontinalis</i> fry
Hubert and Rodhes, 1989	River	Wyoming, USA	Y	N	Describing the diet of <i>S. fontinalis</i>
Ensign, 1990	River	Appalachi, USA	Y	Y	Effects of the summer food limitation on the <i>S. fontinalis</i> biomass
Bussieres, 1991	River	Québek, CA	Y	Y	Assessing the daily consumption of invertebrates in <i>S. fontinalis</i>
East and Magnan, 1991	Lake	Canada	Y	Y	Assessing the factors regulating piscivory in <i>S. fontinalis</i>
Dewald and Wilzbach, 1992	Mesocosm	-	-	-	Studying the competition between native <i>S. fontinalis</i> and introduces <i>Salmo trutta</i>
Lacasse and Magnan, 1992	Lake	Québek, CA	Y	Y	Determining the abiotic and biotic factors affecting the diet of <i>S. fontinalis</i>
McLaughlin <i>et al.</i> , 1992	River	Ontario, CA	N	Y	Studying the foraging movements in <i>S. fontinalis</i> fry

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Tab. 5. Continued from previous page.

Reference	Habitat	Region	Diet	Native	Objectives
Bechara <i>et al.</i> , 1993	Mesocosm	Québec, CA	Y	Y	Determining the impact of <i>S. fontinalis</i> on the macroinvertebrate fauna
Curry <i>et al.</i> , 1993	Lake and river	Ontario, CA	Y	Y	Describing the diet and growth of <i>S. fontinalis</i> fry
Forrester <i>et al.</i> , 1994	River	New Hampshire, USA	Y	Y	Studying the determinants of the diet of <i>S. fontinalis</i>
Sirois and Boisclair, 1995	Mesocosm	-	-	-	Determining the importance of zooplankton for <i>S. fontinalis</i> fry
Biro <i>et al.</i> , 1995	River	Ontario, CA	N	Y	Determining if the feeding attempts are good indicators of the ingestion rates in <i>S. fontinalis</i> as a species model
Elser <i>et al.</i> , 1995	Lake	California, USA	Y	N	Food web effects of rainbow trout density manipulation
Bourke <i>et al.</i> , 1997	Lake				Studying the polymorphism in <i>S. fontinalis</i> in relation to their foraging habitats
Cavalli <i>et al.</i> , 1997	Lake	Alps, France	Y	N	Describing the diet and growth rates of <i>S. fontinalis</i>
Duffield and Nelson, 1998	River	Wyoming, USA	Y	Y	Determining the stonefly component in the diet of <i>S. fontinalis</i>
Macchi <i>et al.</i> , 1999	Lake	Patagonia, Argentina	Y	N	Describing the predation between introduced and native fish
Dunham <i>et al.</i> , 2000	River	Nevada, USA	Y	N	Describing the diet of introduced <i>S. fontinalis</i> and its daily variation
Gunckel, 2000	River	Oregon, USA	Y	N	Comparing the diet of native <i>S. confluentus</i> and introduced <i>S. fontinalis</i>
McLaughlin <i>et al.</i> , 2000	River	Ontario, CA	N	Y	Assessing the predation success of recently emerged <i>S. fontinalis</i>
Sweka and Hartman, 2001a	River	Appalachi, USA	Y	Y	Describing the fall and winter prey selection in <i>S. fontinalis</i>
Sweka and Hartman, 2001b	River	Appalachi, USA	Y	Y	Assessing the effects of water turbidity on prey consumption
Sweka and Hartman, 2001c	River	Appalachi, USA	Y	Y	Assessing the effects of turbidity reactive distance and foraging success
Hartman and Sweka, 2001	Laboratory	-	-	-	Developing a bioenergetics model for <i>S. fontinalis</i>
Milano <i>et al.</i> , 2002	Lake	Patagonia, Argentina	Y	N	Assessing the impact of piscivorous <i>S. fontinalis</i> on native fish fauna
Power <i>et al.</i> , 2002	Lake	Québec, CA	N	Y	Using stable isotope to assess the trophic niche of <i>S. alpinus</i> and <i>S. fontinalis</i>
Gowan and Fausch, 2002	Stream	Rocky mts., USA	N	N	Studying the movements of foraging <i>S. fontinalis</i>
Gunckel <i>et al.</i> , 2002	Stream, mesocosm	Oregon, USA	N	N	Comparing resource partitioning between <i>S. fontinalis</i> and native salmonids
Sweka, 2003	River	Appalachi, USA	Y	Y	Assessing the aquatic-terrestrial linkages in streams
Hilderbrand and Kershner, 2004	River	Idaho, USA	Y	N	Assessing how introduced <i>S. fontinalis</i> compete with native fish species
Mookerji <i>et al.</i> , 2004	River	Québec, CA	Y	Y	Describing the interaction between <i>S. fontinalis</i> and <i>Salmo salar</i>
Sweka, 2004	Laboratory	-	-	-	Assessing the gastric evacuation rates of <i>S. fontinalis</i>
Thorne, 2004	River	Appalachi, USA	Y	Y	Spatial and seasonal variation in <i>S. fontinalis</i> diet
Webster and Hartman, 2005	River	West Virginia, USA	Y	Y	Assessing the role of terrestrial insects for the diet of <i>S. fontinalis</i>
Morinville, 2005	Estuarine areas	Québec, CA	Y	Y	The bioenergetic basis of anadromy in <i>S. fontinalis</i>
Sotiropoulos <i>et al.</i> , 2006	River	Massachusetts, USA	Y	Y	Studying habitat selection and diet of <i>S. fontinalis</i> fry under low stream flows
Morinville and Rasmussen, 2006	Estuarine areas	Québec, CA	Y	Y	Marine feeding patterns of anadromous <i>S. fontinalis</i>

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Tab. 5. Continued from previous page.

Reference	Habitat	Region	Diet	Native	Objectives
Vander Zanden <i>et al.</i> , 2006	Lake	California, USA	Y	N	Fish production related to benthic vs. pelagic trophic pathways
Utz and Hartman, 2006	River	Appalachi, USA	Y	Y	Temporal and spatial variation in the energy intake of <i>S. fontinalis</i>
Barr, 2007	River	New Hampshire, USA	Y	Y/N	Manipulating habitats (by <i>S. fontinalis</i> introduction) to assess the impact on invertebrates and amphibians
Cucherousset <i>et al.</i> , 2007	River	Pyrenees, France	N	N	Using stable isotope to assess the trophic interaction between <i>S. fontinalis</i> and <i>Salmo trutta</i>
Macchi <i>et al.</i> , 2007	Mesocosm	-	-	-	Assessing the impact of piscivorous <i>S. fontinalis</i> on native fish fauna
McGrath and Lewis, 2007	River	Colorado, USA	Y	N	Assessing how introduced <i>S. fontinalis</i> compete with native fish species
Sánchez <i>et al.</i> , 2007	Lake	Sierra de Gredos, Spain	Y	N	Describing the diet of <i>S. fontinalis</i> and determining the nutritional quality of different preys
Utz and Hartman, 2007	River	Appalachi, USA	Y	Y	Determining which prey organisms sustain <i>S. fontinalis</i> in different seasons
Utz <i>et al.</i> , 2007	River	Appalachi, USA	Y	Y	Assessing the role of terrestrial beetles in the diet of <i>S. fontinalis</i>
Bertrand <i>et al.</i> , 2008	Lake	Québec, CA	Y	Y	Describing the trophic polymorphism in <i>S. fontinalis</i>
Ojala, 2008	River	Massachusetts, USA	Y	Y	Studying the feeding interaction between different fish species
Sweka and Hartman, 2008	River	Appalachi, USA	Y	Y	Investigating the role of terrestrial insects for <i>S. fontinalis</i>
Hartman and Cox, 2008	-	-	-	-	Developing a bioenergetics model for <i>S. fontinalis</i>
Browne and Rasmussen, 2009	Lake	Ontario, CA	Y	Y	Studying the feeding interaction between different fish species
Farwell and McLaughlin, 2009	River	Ontario, CA	N	Y	Studying alternative feeding tactics <i>S. fontinalis</i>
Ferriz <i>et al.</i> , 2010	River	Pampa de Achala, Argentina	Y	N	Describing the distribution and diet of introduced salmonids
Wilson and McLaughlin, 2010	River	Ontario, CA	N	Y	Studying the relationship between brain morphology and foraging strategies in <i>S. fontinalis</i> fry
Courtwright and May, 2013	River	Appalachi, USA	Y	Y	Determining the effects of reductions in terrestrial invertebrate subsidies on <i>S. fontinalis</i> diet
Juncos <i>et al.</i> , 2013	Lake	Patagonia, Argentina	Y	N	Modeling prey consumption of nonnative fish
Farwell <i>et al.</i> , 2014	River	Ontario, CA	N	Y	Studying alternative feeding tactics <i>S. fontinalis</i>
Skinner <i>et al.</i> , 2014	Lake	Michigan, USA	Y	Y	Studying the effects of hypolimnetic oxygenation on the feeding ecology of several fish species
Spares <i>et al.</i> , 2014	Estuarine areas, sea	Nova Scotia, Canada	Y	Y	Describing the diet of anadromous <i>S. fontinalis</i>
Tiberti <i>et al.</i> , 2014b	Lake and river	Alps, Italy	Y	N	Describing the zooplanktonic fraction of the diet in adult and young <i>S. fontinalis</i>
White and Gowan, 2014		Appalachi, USA	N	Y	Studying the foraging behavior of <i>S. fontinalis</i>
Wilson <i>et al.</i> , 2014	River	New Hampshire, USA	Y	Y	Investigating the role of terrestrial insects for the diet of <i>S. fontinalis</i>
Juncos <i>et al.</i> , 2015	Lakes	Patagonia, Argentina	Y	N	Studying the trophic interactions between native and alien fish species
Kraus <i>et al.</i> , 2016	River	Colorado, USA	Y	N	Studying the effects of river pollution on the diet of <i>S. fontinalis</i>

Diet, food composition data are provided (Y) or not (N); native, study from native (Y) or non-native populations (N), but note that we did not check for possible range expansion within the native range of *S. fontinalis*.

366; N=50); the mean biovolume of measured stomach contents was 1.60 ± 2.70 mL (range 0.0-35.0; N=267) in lakes and 1.68 ± 2.26 mL (range 0.0-11.8 mL; N=37) in rivers. Twenty specimens had empty stomachs.

Factors influencing the diet

The diversity of ingested preys (number of prey groups found in each stomach) was higher in rivers than in lakes (Beta=0.20; df=1; F=8.70; P<0.01) and positively affected by the date of sampling (Beta=0.24; df=1; F=36.29; P<0.001), while the effect of fish size was not significant (Beta=0.03; df=1; F=0.93; P=0.11). The abundance of prey items in each stomach depended on the habitat type (rivers vs. lakes: Beta=-1.51; df=1; F=17.90; P<0.001), fish size (Beta=0.44; df=1; F=7202.64; P<0.001) and date of sampling (Beta=0.75; df=1; F=714.33; P<0.001). The biovolume of the stomach contents depended only on the fish size (Beta=0.31; df=1; F=40.74; P<0.001), while the effects of the habitat type and of the date of sampling were not significant.

The GLMs results for the occurrence of each prey group show that habitat type, fish size and date of sampling can have significant effects on different prey groups (Tab. 6). The occurrence of certain prey groups was a significant predictor of the presence of others groups. The occurrence of zooplankton and nektonic invertebrates is higher in the diet of lake dwelling *S. fontinalis* while benthic invertebrates are more related to the riverine diet. Zooplankton, nektonic invertebrates and fossorial invertebrates are negatively influenced by fish size, while the occurrence of terrestrial insects and vertebrates is higher in larger size classes. The presence of benthic and fossorial invertebrates is also influenced by the date of sampling suggesting the existence of some seasonality in *S. fontinalis* food composition. There is a mutual negative effect between the presence of terrestrial invertebrates and zooplankton, and a positive one between benthic and fossorial invertebrates (Tab. 6).

DISCUSSION

A short review on the feeding ecology of *Salvelinus fontinalis*

The feeding ecology of native and introduced *S. fontinalis* populations has been extensively studied and was partially reviewed in Ricker (1932) and Balon (1980). In general, the feeding ecology of *S. fontinalis* is characterized as opportunistic. Prey belong to many taxonomic and functional groups, often representing the most abundant/accessible prey in the studied habitats. This general pattern is accurate throughout the existing literature, but prey composition can vary a lot depending on several abiotic and biotic factors and prey specialization can sometimes occur.

Most of the studies on the feeding ecology of *S. fontinalis* include some direct description of the diet obtained by dissecting or flushing their stomachs. Due to its opportunistic behavior, prey availability is probably the most important factor determining the food composition in *S. fontinalis* (Lacasse and Magnan, 1992). The literature reflects this general finding providing many examples of measurements of prey availability (lists or quantitative measures of benthic and drifting invertebrates, zooplankton, and sympatric fish and amphibians). More recently the importance of terrestrial insect subsidies in aquatic environments has become evident and measures or manipulations of terrestrial prey have been included in the studies concerning the feeding ecology of *S. fontinalis* (Webster and Hartman, 2005; Utz and Hartman, 2007; Sweka and Hartman, 2008; Courtwright and May, 2013; Wilson *et al.*, 2014).

Also the habitat is very important in determining the availability of prey and the diet of *S. fontinalis*. There are several studies from lotic, lentic, and estuarine habitats (Tab. 5). In lotic systems, drifting prey from upstream river course are usually the most important food resource; in lakes, or under reduced levels of water discharge, non-drifting invertebrates and terrestrial prey become dominant (Dawidowicz and Gliwicz, 1983; Sotiropoulos *et al.*, 2006); in estuarine habitats, adult anadromous fish are mainly piscivorous (Spares *et al.*, 2014). The presence of ecological refuges (*e.g.*, aquatic vegetation, aphotic zone, rock interstices) is a recognized factor enhancing the resistance of prey communities (Bechara *et al.*, 1993; Williamson *et al.*, 2011), but its influence on the diet of *S. fontinalis* is little documented (Bechara *et al.*, 1993).

S. fontinalis usually lives in climates with strong seasonal patterns (*e.g.*, alpine and circumpolar climates) and temporal (both daily and seasonal) variations in prey availability affect its diet (Benson, 1954; Allan, 1981; Dawidowicz and Gliwicz, 1983; Cunjak and Power, 1987; Utz and Hartman, 2007). In the complex, the studies on the diet of *S. fontinalis* are biased towards the description of the summer diet. The few studies including winter sampling provide important insight into the overwintering strategies of *S. fontinalis*, which continue to feed mostly/exclusively on the aquatic prey (Benson, 1954; Dawidowicz and Gliwicz, 1983; Utz and Hartman, 2007; Spares *et al.*, 2014). The diet of *S. fontinalis* varies with the age and the size, shifting from small invertebrates to large invertebrates and vertebrates (Allan, 1981; Lacasse and Magnan, 1992), but adult fish maintain the ability to feed on relatively small prey items (*e.g.*, zooplankton larger than ≈ 1.2 mm; Tiberti *et al.*, 2014b) which can become dominant food resource in the absence of large prey. The diet of young *S. fontinalis* is the specific objective of several articles (Tab. 5). Dietary data have been used also to describe interaction between native or introduced *S.*

fontinalis with other fish species. The impact can be mediated by predation on both juvenile and adult sympatric species, or by competition (Dewald and Wilzbach, 1992; Macchi *et al.*, 1999). Dietary analyses are often used to get information on the direct predation on sympatric fish populations (East and Magnan, 1991; Milano *et al.*, 2002) or to determine if there is a segregation of the dietary niche between native and introduced species, potentially favoring their coexistence (Dewald and Wilzbach, 1992). Outside its native range, *S. fontinalis* can have very strong impacts on the native population of small-size fish (Macchi *et al.*, 1999; Milano *et al.*, 2002) and displace native species (McGrath and Lewis, 2007). Within its native range *S. fontinalis* is threatened by the introduction of non-native Salmonids such as *Salmo trutta* and *Oncorhynchus mykiss*, which are seriously shrinking its original range (Dewald and Wilzbach, 1992). However *S. fontinalis* can coexist in competition with several fish species. In these cases there is usually a large dietary niche overlap between the competing species (Griffith, 1974), and it is probable that food resource segregation is not the best factor explaining the ability of *S. fontinalis* to survive

in sympatry.

There are some studies addressing the existence of different feeding strategies and specializations in *S. fontinalis* (Grant and Noakes, 1986; Grant and Noakes, 1987; Bourke *et al.*, 1997; Bertrand *et al.*, 2008; Wilson and McLaughlin, 2010). These studies are individual-based ethological studies and, in the complex, they combine diet, behavioral, genetic, and morphological data to show the ethological, anatomical, and evolutionary consequences of food segregation. The existence of different foraging strategies and of trophic polymorphism in *S. fontinalis* is often documented recording the movements, successful and unsuccessful predation attempts, and territorial behavior in *S. fontinalis* (McNicol *et al.*, 1985; Grant and Noakes, 1988; Grant *et al.*, 1989; McLaughlin *et al.*, 1992; Farwell and McLaughlin, 2009) or relating the feeding behavior with morphological traits (Bourke *et al.*, 1997; Bertrand *et al.*, 2008; Wilson and McLaughlin, 2010). These ethological studies often used young *S. fontinalis* as model species, while similar studies on adults are absent. In the complex individual feeding specialization is little studied even if it is believed to be at the basis

Tab. 6. Fixed effect results from generalized mixed effects models testing the effects of habitat (stream vs lake), fish size classes, sampling date and presence/absence of other prey groups on the presence of each prey group identified in the diet of *Salvelinus fontinalis*. The year and the sampling site identity were added as random effects. All the observations (N=507) have been collected over nine years (2006-2014) at 16 sampling sites (8 streams and 8 lakes) in the Gran Paradiso National Park.

Model	Fixed term	Beta	95% CI	RVI	Model	Fixed term	Beta	95% CI	RVI
Zooplankton (Group-1)	Intercept	1.86	-0.11 3.81	-	Nektonic invertebrates (Group-2)	Intercept	0.48	-0.58 1.55	-
	Habitat	-3.08	-5.67 -0.49	1.00		Habitat	-1.32	-2.55 -0.05	0.87
	Size	-0.89	-1.18 -0.60	1.00		Size	-0.16	-0.31 -0.02	0.98
	Date	-0.05	-0.91 0.47	0.23		Date	0.05	-0.16 0.47	0.31
	Group-2	0.09	-0.43 1.07	0.30		Group-1	0.01	-0.64 0.73	0.15
	Group-3	-0.12	-1.39 0.55	0.28		Group-3	0.05	-0.34 0.76	0.24
	Group-4	-0.14	-1.21 0.38	0.34		Group-4	0.03	-0.31 0.58	0.20
Group-5	-1.27	-2.02 -0.53	1.00	Group-5	0.13	-0.16 0.77	0.41		
Group-6	0.50	-0.98 3.78	0.36	Group-6	-0.01	-1.20 1.11	0.15		
Benthonic invertebrates (Group-3)	Intercept	-4.01	-5.85 -2.17	-	Aquatic fossorial invertebrates (Group-4)	Intercept	0.51	-0.92 1.93	-
	Habitat	3.51	1.81 5.21	1.00		Habitat	-0.11	-1.39 0.54	0.27
	Size	0.16	0.00 0.41	0.76		Size	-0.23	-0.40 -0.06	1.00
	Date	2.58	1.49 3.68	1.00		Date	0.36	0.01 0.81	0.87
	Group-1	-0.42	-1.67 0.20	0.58		Group-1	-0.47	-1.41 0.06	0.70
	Group-2	0.00	-0.60 0.60	0.18		Group-2	0.01	-0.40 0.51	0.16
	Group-4	0.69	0.12 1.29	0.98		Group-3	0.69	0.15 1.27	0.98
Group-5	0.11	-0.34 0.99	0.35	Group-5	0.15	-0.16 0.83	0.44		
Group-6	0.07	-1.43 2.07	0.22	Group-6	-0.01	-1.20 1.05	0.16		
Terrestrial insects (Group-5)	Intercept	0.34	-0.65 1.33	-	Vertebrates (fish and frogs) (Group-6)	Intercept	-12.13	-16.83 -7.42	-
	Habitat	-0.39	-1.32 0.11	0.64		Habitat	1.35	-0.09 4.34	0.64
	Size	0.21	0.04 0.39	0.97		Size	1.47	0.73 2.21	1.00
	Date	0.08	-0.11 0.51	0.42		Date	0.17	-0.36 1.36	0.34
	Group-1	-1.26	-1.94 -0.58	1.00		Group-1	0.25	-1.49 3.66	0.24
	Group-2	0.15	-0.13 0.76	0.48		Group-2	0.02	-1.17 1.43	0.13
	Group-3	0.05	-0.45 0.82	0.29		Group-3	0.07	-1.64 2.39	0.18
Group-4	0.15	-0.14 0.80	0.48	Group-4	0.02	-1.12 1.38	0.13		
Group-6	-0.59	-2.04 0.10	0.61	Group-5	-0.31	-1.98 0.43	0.41		

Beta, averaged parameter estimate; CI, confidence intervals; RVI, Relative Variable Importance (from 0 to 1).

of the existence of different morphotypes in many *S. fontinalis* populations. On the contrary, this issue demonstrated to be a fertile research field in the congeneric species *S. alpinus*, which is considered a classic model for studies of trophic specialization (Jonsson and Jonsson, 2001). Laboratory and mesocosm studies were used to measure several metabolic parameters (optimal feeding, energy requirements, rates of food consumption, and evacuation rates; Morgulis, 1918; Titcomb *et al.*, 1928; Detwiler, 1930; Sweka, 2004), to study competition between native and introduced fish (Magnan and FitzGerald, 1984; Dewald and Wilzbach, 1992), or to understand the predatory impact of *S. fontinalis* (Bechara *et al.*, 1993; Sirois and Boisclair, 1995; Macchi *et al.*, 2007). The latter studies are particularly interesting to understand the invasion ecology of *S. fontinalis*.

Without the intent to review all the existing literature on the ecological impact of introduced *S. fontinalis*, the most common experimental approach to assess its impact is to compare the native communities of invaded and non-invaded habitats (Tiberti *et al.*, 2014a) or before and after fish introductions (Schabetsberger *et al.*, 2009) and eradications (Knapp *et al.*, 2001). In many cases dietary data are not provided, but the pervasive impact of introduced *S. fontinalis* is ascribed to the selective predation on more visible preys and ultimately on its feeding ecology.

Factors influencing the diet

Our results confirm that *S. fontinalis* is an opportunistic predator (Lacasse and Magnan, 1992). However prey composition varied a lot between and within the populations depending on several abiotic and biotic factors influencing prey availability. Habitat type and fish size played an important role in determining the food composition in *S. fontinalis*, and there are some evidences of the seasonal variation in food composition. These results are similar to what described in literature, confirming many of the current knowledge on the feeding ecology of *S. fontinalis*.

Prey availability

Prey availability is probably the most important factor determining the food composition of generalist predators, such as *S. fontinalis* (Allan, 1981; Lacasse and Magnan, 1992; Cavalli *et al.*, 1997). Virtually all the available preys are present in the diet of *S. fontinalis*, with the exception of some very small aquatic and terrestrial taxa (*e.g.*, Rotifera and terrestrial Acarina; Tab. 5), which are probably invisible to *S. fontinalis*. There is a general consistency between the frequencies of occurrence of prey taxa in the stomachs and in the samples for prey availability. Nevertheless some clear discordances between prey availability and prey consumption have been observed. *Arctodiaptomus alpinus* is the second most common crustacean in-

habiting the studied lakes (F%=70%) and is a large zooplankton species (up to 2 mm); therefore, it should be a rather common prey for *S. fontinalis*, but it is only the 9th zooplankton prey in order of frequency of occurrence in the stomach contents. A rapid digestion (but all the other zooplankton species were usually well recognizable) or the existence of effective anti-predator adaptations are possible explanations. Oligochaeta are underrepresented in the diet of *S. fontinalis*, perhaps due to their poor resistance to digestion which can hamper their observation (Hyslop, 1980). Some aquatic macroinvertebrate taxa are also underrepresented in the diet of stream dwelling *S. fontinalis* (*e.g.*, Simuliid larvae and bivalves) while Chironomid pupae are clearly overrepresented in the diet of both stream and lake dwelling *S. fontinalis*. As a matter of facts, stream dwelling *S. fontinalis* feed mainly of drifting macroinvertebrates (Allan, 1981), suggesting that drift, rather than benthic samples, would return a better quantification of prey availability. Underrepresented taxa would belong to non-drifting macroinvertebrates, while Chironomid pupae are usually a significant part of the drift (Fechney, 1988). Diptera pupae are also overrepresented in the diet of lake dwelling *S. fontinalis* possibly indicating that this prey item is actively searched and positively selected by *S. fontinalis*. Concerning terrestrial insects, the presence of terrestrial prey in the stomachs reflect the measures of prey availability, in particular those related to the invertebrates falling into the lakes which are nearly all winged insects (Diptera and Coleoptera). Non-winged invertebrates (*e.g.*, Aranea and Miriapoda) are usually underrepresented in the diet of *S. fontinalis*, even if they could be abundant around the lakes. The measures of prey availability around the lakes do not take into account that some taxa (*e.g.*, winged insects) are more likely to fall into the water.

Habitat: streams vs lakes

Most of the differences between the diet of stream and lake dwelling *S. fontinalis* (Tabs. 3 and 4) should be ascribed to the different prey availability in lakes and streams. For example zooplankton can be found only in lakes and many aquatic invertebrates (*e.g.*, Tricoptera, Ephemeroptera, and Plecoptera) are much more common in rivers. The food composition of *S. fontinalis* clearly reflects these differences.

The abundance of ingested prey items was higher in lakes than in streams, but the biovolumes were not influenced by habitat type, indicating that lake dwelling *S. fontinalis* have to catch a greater number of smaller prey to achieve their energy requirements. According to its size selective predation strategy (Allan, 1981), *S. fontinalis* can shift towards suboptimal smaller prey when large prey are absent. Drifting insects from non-invaded upstream stretch probably supply *S. fontinalis* with large invertebrates from

non-impacted habitats, while large aquatic prey are strongly impacted and therefore unavailable in lakes (Tiberti *et al.*, 2014a), forcing *S. fontinalis* to feed on smaller prey.

Fish size

Fish size is an important factor determining the diet of *S. fontinalis* (Allan, 1981). It negatively influences the consumption of zooplankton, and of fossorial and nektonic aquatic invertebrates, and positively influences the consumption of vertebrates and terrestrial insects (Tab. 3). In the complex we observed a shift from a diet based on zooplankton and aquatic invertebrates (mostly small invertebrates such as chironomid diptera), typical of small fish, to a diet including increasing quantities of larger preys such as terrestrial insects and vertebrates, typical of adult fish. This is consistent with a size selective predation strategy, which optimizes feeding behavior by increasing the energy content per prey and reducing the number of predation attempts (Griffiths, 1980). This strategy is a common feeding strategy of aquatic visual predators, such as salmonids, in general, and *S. fontinalis*, in particular (Allan, 1981). However the size range of the ingested preys is constrained by the predator visual capacity (O'Brien, 1979) and mouth size (Wankowski, 1979). Small fish can see smaller prey, which are invisible/unavailable to larger fish (O'Brien, 1979). For example zooplankton have been regularly found in the diet of young fish, and smaller species (*e.g.*, chydorid cladocerans) can be found only in smaller fish. However adults maintain the ability to feed on larger crustaceans which represent just a marginal fraction of their diet (Tiberti *et al.*, 2014b).

A strong selective predation can wipe out large preys (Tiberti *et al.*, 2014a), in these cases *S. fontinalis* can opportunistically shift its diet towards sub-optimal prey and this could explain the relatively frequent presence of small prey in the stomachs of adult fish (*e.g.*, zooplankton, chironomid larvae and pupae). Cannibalism and predation over large vertebrates has been observed only in adult fish feeding on *S. fontinalis* (up to 21.5 cm) and *R. temporaria* (including large adult specimens) and is the clearest expression of the size selective strategy of *S. fontinalis*. Sometimes ingested prey were so large that they could not be ingested entirely. Cannibalism was observed in 1.89% of the analyzed stomachs, but it probably plays a very important role in regulating the population structure of *S. fontinalis* (Frenette and Dodson, 1984) and the distribution and behavior of small and medium size fish.

Seasonality

Prey availability is often dominated by seasonal cycles, especially in the alpine environment, which is subject to extreme seasonal changes. Our study is limited to the ice free season and the most important seasonal factors

(ice cover and overwintering phenology of prey taxa) (Leonard, 1941; Benson, 1954; Dawidowicz and Gliwicz, 1983; Cunjak and Power, 1987; Utz and Hartman, 2007) are therefore excluded from our study period. However some increasing seasonal trends have been observed for fossorial and benthonic aquatic invertebrates probably reflecting a greater availability of these prey groups. Aquatic invertebrates are by far the most important food resource during the winter (Benson, 1954; Dawidowicz and Gliwicz, 1983) and, at the beginning of summer, they could be still affected by winter predation. Aquatic invertebrates communities could progressively expand during the summer, thanks to a lighter predation pressure determined by a dietary shift towards terrestrial prey. Terrestrial insects are indeed a very important summer temporary resource (Dawidowicz and Gliwicz, 1983; Webster and Hartman, 2005; Sweka and Hartman, 2008; Wilson *et al.*, 2014) and they are a strategic resource to enable *S. fontinalis* to accumulate sufficient energy resources to overcome the winter poor feeding conditions (Utz and Hartman, 2007).

Feeding specialization

Putting the presence/absence of the alternative prey groups as covariates in the models enabled us to check if the presence of a certain prey group was a good predictor of the presence of the other ones, indicating possible associations or mechanisms of exclusion between prey groups. We found that benthic and fossorial invertebrates are positively associated, indicating that *S. fontinalis* feeding in the benthic area are able to find both the prey types, probably stirring up the sediment. Moreover we found that zooplankton and terrestrial insects are negatively associated. This could be due to the different habitat where zooplankton and terrestrial insects can be found (pelagic vs. water surface and littoral areas), to the fact that zooplankton prey selection is different in small and large *S. fontinalis*, or to a specialized feeding strategy in *S. fontinalis*. Zooplanktivorous morphotypes have been indeed described for adult *S. fontinalis*, however zooplankton was just a marginal resource in the studied populations (at least during the ice-free season) and occurred mixed with other prey groups in the stomachs, suggesting that zooplanktivory is an opportunistic rather than a specialized behavior. In the absence of individual-based studies (Wilson *et al.*, 2010) it is impossible to disentangle between feeding specialization and opportunistic feeding on a locally/temporally abundant prey. However feeding specialization has been observed several times in *S. fontinalis* (Bryan and Larkin, 1972; Grant and Noakes, 1986; Grant and Noakes, 1987; Bourke *et al.*, 1997; Bertrandt *et al.*, 2008; Wilson *et al.*, 2010) and occurs when prey availability ceases to be the most important factor determining the diet and different feeding strategies are put into practice. Feed-

ing specialization can last for a limited period -for example different feeding strategies (leading to different food composition) have been described in *S. fontinalis* fry (Grant and Noakes, 1987) - or occur at a certain time of the life of *S. fontinalis* - as in the case of *S. fontinalis* which feed exclusively on vertebrate prey. This kind of specialization has probably been observed just once, in lake Djouan, where two very large fish (>35 cm) were found with adult frogs and fish in their stomachs and no other prey items. Instead the other cases of cannibalism or predation over vertebrates seem to fall within the usual opportunistic behavior of *S. fontinalis*, since other prey items occurred at the same time in the stomachs, and the analyzed fish were within the usual size range of the studied populations of *S. fontinalis*. For the congeneric species *S. alpinus*, a shift to a cannibalistic specialized diet is believed to occur when a certain critic size is reached (Mittelbach and Persson, 1998; Jonsson and Jonsson, 2001).

***S. fontinalis* diet and its ecological impact**

Introduced fish can affect native prey species (Knapp *et al.*, 2001) and produce indirect cascading effects both in high altitude/latitude lakes and rivers ((Sarnelle and Knapp, 2005; Reissing *et al.*, 2006; Buria *et al.*, 2007). In particular *S. fontinalis* is one of the most used fish for stocking programs and is a size-selective generalist predators which can rely on a large number of prey and usually prefer larger ones. However the food composition of *S. fontinalis* reflects the availability of prey and many highly impacted potential prey cannot be found in its diet if they were already brought to extinction. Therefore the diet is often dominated by the less impacted survival organisms, with an higher resistance to fish introduction. The impact of *S. fontinalis* in the lakes of the GPNP have been recently quantified (Tiberti and von Hardenberg, 2012; Magnea *et al.*, 2013; Tiberti *et al.*, 2014a, 2014b) and the diet of lake dwelling *S. fontinalis* accurately attain this general role. The most impacted aquatic organisms, such as large zooplankton species (*Daphnia* sp. and *Cyclops* gr. *abyssorum*) and many nektonic and benthonic invertebrates (Tricoptera, Coleoptera, Plecoptera, Acarina) (Tiberti *et al.*, 2014a), are indeed secondary food resources, while fossorial invertebrates, which are not impacted or even favored by introduced fish (Tiberti *et al.*, 2014a), and small sized diptera pupae represent a substantial part of its diet. It is likely that after leading to local extinction or collapse many of its favorite prey, *S. fontinalis* finally established an equilibrium with some of its sub-optimal prey, such as chironomids. This is also confirmed by Dawidowicz and Gliwicz (1983), who found that chironomids (larvae and pupae) dominate the diet of *S. fontinalis* in an oligotrophic lake.

During the eradication actions provided within the BIOAQUAE project we manipulated the density of *S.*

fontinalis in four lakes and we had the opportunity to observe how the diet of *S. fontinalis* changed while the ecosystems were recovering to their previous fishless state. Already during the eradication, many previously absent taxa rapidly colonized the lakes and were found not only in the samples for prey availability, but also in the diet of *S. fontinalis*. This confirms that the potential/optimal diet of *S. fontinalis* could be quite different from what can be observed in already strongly impacted habitats (Tiberti *et al.*, 2014c). Diet data also allow a better understanding of certain unclear aspects concerning the impact of *S. fontinalis* in the alpine lakes of the GPNP. *Arctodiaptomus alpinus* is weakly or not impacted by *S. fontinalis* (Tiberti *et al.*, 2014a), which is a very uncommon finding since large calanoid copepods are considered very sensitive to introduced fish (Brancelj, 1999). The scarce presence of *Arctodiaptomus alpinus* in the diet of *S. fontinalis* could provide an explanation of the low ecological impact, and it rises some interrogatives about the reasons and the possible adaptations enabling the relatively undisturbed survival of *Arctodiaptomus alpinus*. Some behavioral aspects concerning the vertical migrations of *Arctodiaptomus alpinus* have been explored (Tiberti and Iacobuzio, 2013) but this issue would deserve an in-depth study.

Situation is different for stocked streams, where many sensitive taxa -which are strongly impacted in lakes (*e.g.*, nektonic and benthonic invertebrates; Tiberti *et al.*, 2014a)- are abundant and represent the most important food resource for stream dwelling *S. fontinalis* (Tab. 5). A weaker impact of fish predation is frequently reported in streams (Bechara *et al.*, 1993 and contained references) and, also in our study area, the impact of *S. fontinalis* seems to be less dramatic than in lakes. Among all the possible explanations, streams could have an higher habitat diversity providing many refugia against predation (*e.g.*, rock interstices), drifting insects could be a source of immigrant invertebrates masking the effects of predation, or drifting insects -from upstream non-invaded areas- and terrestrial insects could supply *S. fontinalis* with a sufficient quantity of food to ease the predatory pressure on the benthic community (Bechara *et al.*, 1993).

Terrestrial invertebrates are exogenous prey which represent a substantial fraction of the diet of both lake and stream dwelling *S. fontinalis* (present study; Dawidowicz and Gliwicz, 1983; Wilson *et al.*, 2014). Fish predation does not affect the magnitude of terrestrial insects subsidies -even if the density of some riparian species could hypothetically be affected- but it can affect the nutrient balance of stocked lakes and rivers, metabolizing (by bioaccumulation or excretion) and transferring to the water column the nutrients contained in terrestrial invertebrates (Eby *et al.*, 2006). Indeed fish are believed to serve as a net source of nutrients, potentially affecting the trophic state of the lakes and altering the equilibria be-

tween benthic and pelagic primary production (Vander Zanden and Vadeboncoeur, 2002). Even if they are rarely found in the diet of *S. fontinalis*, also frogs -amphibians in general- could provide a disproportionate additional input of nutrients from the terrestrial area into the aquatic ecosystems. Due to the substantial contribution of *Rana temporaria* to the total prey biovolume (Tab. 5), nutrients from amphibians could influence the nutrient balance. However, unlike terrestrial insects, amphibians are highly impacted by introduced fish and they are usually absent from the prey pool available for *S. fontinalis* (Bradford *et al.*, 1994; Tiberti and von Hardenberg, 2012).

CONCLUSIONS

S. fontinalis is one of the most problematic introduced fish predator in the Alps and in Europe. Dietary data are a basic tool for the understanding of its ecological impact and our study provides an extensive investigation on its diet from the Alpine region. Our results were very useful for the interpretation of some of the impacts observed in our study area (Gran Paradiso National Park) and could be useful to anyone interested in the invasion ecology of this species in the alpine environment. We complemented our study with an exhaustive literature review on the feeding ecology of native and introduced *S. fontinalis*, providing a comprehensive view on the current and past research areas.

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