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SHORT COMMUNICATION

Behind the impact of introduced trout in high altitude lakes: adult, not juvenile fish are responsible of the selective predation on crustacean zooplankton

Rocco TIBERTI,[1,2*] Stefano BRIGHENTI,[1] Rocco IACOBUZIO,[1] Giulia PASQUINI,[2] Matteo ROLLA[2]

[1]Alpine Wildlife Research Centre, Gran Paradiso National Park, Degioz 11, 11010 Valsavarenche; [2]Department of Earth and Environmental Sciences, University of Pavia, Via Ferrata 9, 27100 Pavia, Italy
*Corresponding author: rocco.tiberti@gmail.com

ABSTRACT

*Introduced fish seriously affect zooplankton communities in mountain lakes, often leading to the loss of large species. Selective predation is recognized to be the ultimate cause of such a strong impact. Here we describe the selection of zooplankton prey by analyzing the stomach contents of more than 300 brook trout (*Salvelinus fontinalis*) inhabiting seven alpine lakes in the Gran Paradiso National Park (western Italian Alps). Our results show that planktivory is much more common in young fish, which feed on a larger number of taxa, but also adult fish maintain the ability to feed on zooplankton. There is a direct dependence between the length of zooplankton prey and the length of their fish predators, and adult, not juvenile fish are responsible of the selective predation on large crustacean zooplankton, which drive the impact of introduced fish throughout the entire zooplankton community. In some rare cases, large zooplankton populations develop in the presence of brook trout, and planktivory can become an important temporary resource for adult fish during the ice-free season. Thus, in the early stages of the establishment of non-native trout in alpine lakes, large-bodied zooplankton may represent an important food resource.*

Key words: Planktivory, Salvelinus fontinalis*, stomach content, zooplankton size, Gran Paradiso National Park.*

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INTRODUCTION

Introduced fish are a major threat to once fishless mountain lake ecosystems (Knapp *et al.*, 2001; Eby *et al.*, 2006). Selective predation on more visible prey taxa, such as large zooplankton species, is the ecological mechanism driving the impact. The response of zooplankton communities to fish predation include the decrease or even the loss of large taxa (*e.g.*, large copepods and daphnidae) favoring their smaller competitors (*e.g.*, rotifers and chydoridae) (Schabetsberger *et al.*, 2009; Tiberti *et al.*, 2014). This is a well known ecological process, which has been usually studied comparing the zooplankton communities of naturally fishless and stocked lakes (Knapp *et al.*, 2001; Tiberti *et al.*, 2014) or before-after fish stocking or eradication (Brancelj, 1999; Knapp *et al.*, 2001; Parker *et al.*, 2001; Knapp *et al.*, 2005; Schabetsberger *et al.*, 2009). Zooplankton selective predation in alpine lakes was rarely studied directly (exceptions are Dawidowicz and Gliwicz, 1983; Gliwicz and Rowan, 1984; Tatra Mountains, Poland), but it has always been the theoretical frame within which to interpret the results. As a result little is known about planktivory by introduced salmonids, in particular it is not clear how much fish rely on planktivory in alpine lakes and how prey selectivity change depending on the fish size.

Brook trout (*Salvelinus fontinalis*; Mitchill, 1814) have been largely used by anglers for stocking mountain lakes throughout the Alps, because of its ability to survive in extreme thermal and trophic conditions. In the 1960s, some naturally fishless alpine lakes in the Gran Paradiso National Park (GPNP, western Italian Alps) were stocked with brook trout, which established some reproductive populations, exacting a heavy toll on these fragile ecosystems (Tiberti *et al.*, 2014). This study is based on the data collected in seven of these lakes (Tab. 1). The lakes are oligotrophic, non-dammed, larger than 10^4 m^2, located above the local tree line (higher than 2000 m asl) with their watershed belonging to the alpine and nival belts. Due to the severity of alpine climate the winter ice cover last for 7-9 months per year.

The objective of the present note is to study the selective predation on large zooplankton directly, by analyzing the stomach contents of introduced brook trout in a set of alpine lakes in GPNP. In particular we were interested in understanding i) how common is planktivory in introduced brook trout, ii) if planktivory depends on the size of brook trout, iii) if selective predation is directly observable in the diet of brook trout, and iv) if prey selection changes with fish size.

Planktivory in introduced brook trout

Between 2006 and 2013 we captured more than 8000 brook trout in seven alpine lakes by using fishing nets, electrofishing and an hand net; 821 captures were made in 2006-2012 during a long term monitoring program (Tiberti *et al.*, 2014), while the remaining captures were made in 2013 within the fish eradication project LIFE+ BIOAQUAE (Biodiversity Improvement of Aquatic Alpine Ecosystems, www.bioaquae.eu). We removed the stomach from a representative number of fish belonging to all the present size classes. The fish size was converted into seven size classes based on the fish maximum length and encompassing the values from 0 to ≥30 cm at five centimeters intervals. Stomachs were preserved in 70% ethanol and dissected at the zoology laboratory of the DSTA [Dipartimento di Scienze della Terra e dell'Ambiente (Department of Earth and Environmental Sciences) University of Pavia].

We check 309 stomach contents for the presence of zooplankton, which was found in 60 stomachs (19.4%). The probability of detecting zooplankton considerably changed depending on the fish size (Tab. 2). Planktivory is much more common in young fish (size classes 0-5 and 5-10 cm), but also adult fish maintain the ability to feed on zooplankton (Tab. 2). Planktivory is probably also regulated by the strong seasonal dynamics of alpine lakes: for example Dawidowicz and Gliwicz (1983) show that brook trout largely rely on zooplankton to survive under the ice. Considering also the ice-covered periods in the analysis of the diet of brook trout could probably enhance our understanding about planktivory in introduced fish in alpine lakes.

Zooplankton selective predation

When zooplankton was present, we roughly separated the non-planktonic prey (mainly terrestrial insect, chironomid pupae and larvae) and we identified and enumerated each zooplankton taxon using a closed counting chamber under a binocular dissecting microscope at 40X (Olympus CH-BI45-3). Cladocera, cyclopoid and diaptomid copepods were identified at the species/genus level, while in the case of Ostracoda and Harpacticoida copepods we did not refine the identification. When possible, depending on the conservation status of the specimens, we measured the size of the zooplankton prey with a calibrated eye-piece micrometer. In the case of fish belonging to the adult size classes (total length ≥20 cm) we also measured the biovolumes of the zooplanktonic and non-zooplanktonic fractions of the diet by gently pressing the stomach content in a graduated cylinder.

In the stomachs we found *Arctodiaptomus alpinus* (Imhof 1885), *Cyclops* gr. *abyssorum* (Sars 1863), *Daphnia* gr. *longispina* (Leydig 1860), *Scapholeberis mucronata* (Müller 1776), *Eucyclops serrulatus* (Fisher 1851), *Chydorus* sp., *Acroperus harpae* (Baird 1835), *Alona* sp., some copepod Harpacticoidea and some Ostracoda. This list include all the crustacean zooplankton found in GPNP alpine lakes during an extensive sampling campaign (2006-2013) (Tiberti *et al.*, 2014), excepting *Scapholeberis mucronata* which was never found in the free living zooplankton. Rotifers were not included in the brook trout diets even though they often dominated zooplankton numbers (Tiberti *et al.*, 2014). Many taxa were

Tab. 1. Main characteristics of the Gran Paradiso National Park's studied lakes. Chemical variables are expressed as average values of a series of repeated measures taken from 2008 to 2013. The number of repetition is reported in brackets.

	LEI	LEY	NDJ	DJO	DRE	ROS	NII
Latitude N	45°29'37"	45°30'28"	45°33'06"	45°33'27"	45°24'45"	45°28'49"	45°29'10"
Longitude E	07°07'55"	07°09'08"	07°10'07"	07°10'43"	07°13'25"	07°08'17"	07°08'45"
Altitude (m asl)	2701	2747	2671	2515	2087	2703	2526
Depth (m)	11.0	22.1	6.0	3.0	7.4	46.9	14.0
Area (10^3 m^2)	62.2	44.7	17.1	13.3	26.1	168.6	82.4
Catchment area (10^6 m^2)	3.16	1.57	0.87	0.31	2.92	1.33	1.11
Geology	CS	CS	CS	CS	AG	CS	AG-CS
pH	8.14 (12)	8.02 (18)	8.02 (14)	8.69 (14)	6.99 (14)	7.76 (12)	7.65 (10)
TP (μg L^{-1})	1.75 (12)	2.83 (18)	2.43 (14)	3.50 (14)	4.50 (14)	3.75 (12)	9.00 (10)
k (m^{-1})	0.19 (4)	0.21 (6)	0.20 (6)	0.36 (6)	0.32 (10)	0.21 (5)	0.48 (6)

LEI, Lake Leità; LEY, Lake Nero in the Leynir Valley; NDJ, Lake Nero in the Djouan area; DJO, Lake Djouan; DRE, Lake Dres; ROS, Lake Rosset; NII, Lake Nivolet Inferiore; CS, catchment dominated by thick covering of calcareous schists; AG, catchment entirely composed by acidic gneiss; TP, total phosphorus; k, photosynthetic active radiation extinction coefficient.

just found in the smaller size classes (Tab. 2). In larger fish (total length ≥20 cm) we just found large *Arctodiaptomus alpinus*, *Cyclops* gr. *abyssorum* and *Daphnia* gr. *longispina* (Tab. 2), which are the most common large zooplankton species (length of adults >1 mm; Knapp *et al.*, 2001) in GPNP alpine lakes (Tiberti *et al.*, 2014). The taxonomic differences in the zooplankton stomach contents among the size classes can be sometimes attributable to the different spatial distribution of adult fish (occupying all the lakes' habitats, including the pelagic area) and juvenile fish (confined to the littoral areas) (*unpublished data*). For example *Daphnia* gr. *longispina* is mainly a pelagic species, and was never found in the stomach of the smallest fish, even if its size range (approximately 0.5-2.5 mm) largely overlaps the prey size spectrum of juvenile fish and is therefore a suitable prey for young salmonids (Galbraith, 1967).

To compare the size of the zooplankton prey in relation to the fish size we ran a simple linear mixed effect model (implemented in the lme function of the package nlme of the R statistical software, version 3.0.2; R Development Core Team, 2010) with the log transformed of the zooplankton measures (to approximate normality) as dependent variable and the size classes of brook trout as integer covariate. To take into account the repeated measures from the same stomachs we add to the model as a random term a variable encompassing all the measures from the same stomachs (the model was based on 481 zooplankton measure, from 39 stomachs, from 6 lakes). The model output show that there is a direct dependence between the length of zooplankton prey and the length of their fish predators (Beta=0.182, SE=0.021, P<0.001). Smaller fish predated smaller zooplankton species (*e.g.*, *Chydorus sphaericus*, the smallest crustacean species in GPNP lakes) and individuals (*e.g.*, Cyclopoid copepodites), often less than one mm long. On the other hand, the planktonic fraction of the larger fish (≥20 cm) diet is exclusively composed by adult, larger (>1 mm) individuals of the large zooplankton species (Fig. 1).

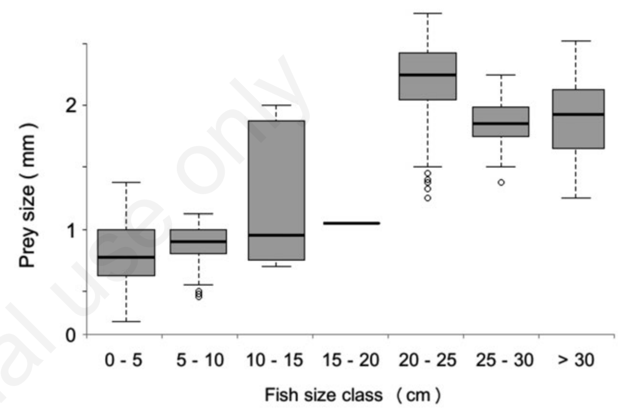

Fig. 1. Size of the zooplankton prey in relation to brook trout size classes. The median, upper and lower quartiles are represented; whiskers, $\pm 1.58 \cdot (IQR)/(n)^{-2}$; IQR, inter-quartile range; n, sample size.

Tab. 2. Zooplankton in the diet of brook trout. The numbers associated to each prey indicate the number of stomachs where the taxon was found. Data from seven alpine lakes of the Gran Paradiso National Park.

Size class (cm)	0-5	5-10	10-15	15-20	20-25	25-30	>30	Tot
Number of analyzed stomachs	39	21	12	27	124	67	19	309
Number of stomachs containing zooplankton	32	13	2	1	4	5	3	60
Stomachs containing zooplankton (%)	82.1	61.9	16.7	3.7	3.2	7.5	15.8	19.4
Number of preyed taxa	9	4	3	1	3	2	2	10
Prey taxa:								
Acropaerus harpae	10	-	-	-	2	-	-	12
Alona sp.	7	3	2	1	-	-	-	13
Arctodiaptomus alpinus	1	-	-	-	-	-	-	1
Chydorus sp.	7	-	-	-	-	-	-	7
Cyclops gr. *abyssorum*	25	4	-	-	1	1	1	32
Daphnia gr. *longispina*	-	-	1	-	2	4	2	9
Eucyclops serrulatus	5	1	-	-	-	-	-	6
Harpacticoida (copepoda)	9	6	-	-	-	-	-	15
Ostracoda	3	-	1	-	-	-	-	4
Scapholeberis mucronata	3	-	-	-	-	-	-	3

Zooplanktivory in the whole brook trout populations is little selective. Indeed the size range of the zooplankton prey largely overlaps the size range of the free living crustaceans sampled in the GPNP alpine lakes during the course of an extensive monitoring campaign (Tiberti *et al.*, 2014) (Fig. 2). The largest zooplankter, *Daphnia pulicaria*, was never found in lakes stocked with fish. Also some very small crustacean (<0.25 mm; naupliar stages of copepods and some juvenile chydorid) are outside of the prey size spectrum of brook trout, maybe because they are below the prey detection capacity of brook trout. Similarly, the absence of rotifers from the fish diet, can be due to their very small size (range 0.1-0.2 mm). Selective predation is clear only in adult fish (Fig. 2) which predate just the largest individuals of the largest zooplankton species. Thus adults, not juveniles brook trout are responsible for the selective predation of more visible zooplankton taxa, which drives the direct and indirect ecological impacts of introduced fish in alpine lakes (Knapp *et al.*, 2001; Eby *et al.*, 2006). In the studied lakes, brook trout selective predation produced a decrease of the densities and size of large zooplankton species, and an indirect advantage for small zooplankton species such as rotifers and *Chydorus sphaericus* (Tiberti *et al.*, 2014; Magnea *et al.*, 2013). The analysis of the stomach contents enabled us to directly describe the selection of prey by brook trout which depends both on the prey and fish sizes. Adult fish exert the selective predation on large zooplankton predating only large (>1.25 mm) individuals while rotifers and *Chydorus* sp., which are outside, or partially outside the size spectrum of brook trout plankton prey, were released from competition from large zooplankton species. These results can likely be extended to a large number of studies concerning the impact of introduced fish in mountain lakes (Brancelj, 1999; Knapp *et al.*, 2001; Parker *et al.*, 2001; Schabetsberger *et al.*, 2009), due to the strong ecological resemblance between limnetic ecosystems from world wide spread mountain ranges.

There is an apparent paradox in our results: very few (5.7%) adult fish eat zooplankton, nevertheless they deeply modify the zooplankton communities. On the other hand, most juvenile fish feed on zooplankton with apparently little effects for the zooplankton community. As a matter of fact it is very rare to find planktivorous fish not because adult fish rarely feed on zooplankton, but just because large zooplankton species are usually absent in stocked lakes (Tiberti *et al.*, 2014). In the rare cases when large zooplankton populations develop in the presence of brook trout, planktivory can become an important temporary resource also for adult fish, which can predate a large number of planktonic crustaceans and they can also become an important, if not dominant, fraction of the diet of brook trout. About 3100 large *Daphnia* gr. *longispina* were found in a single stomach belonging to a 32.7 cm

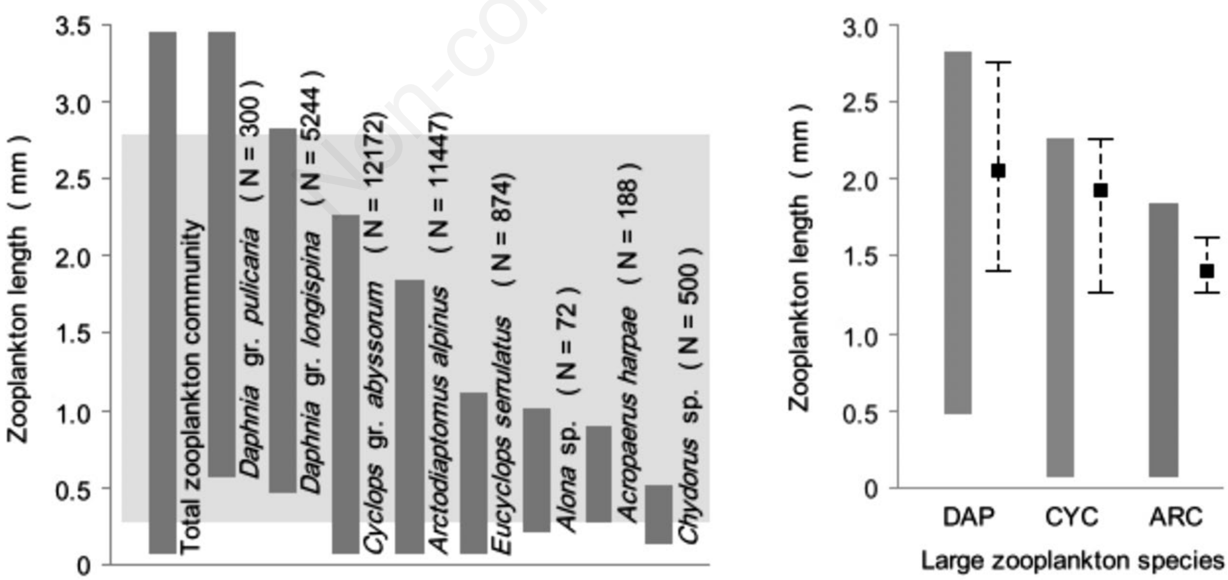

Fig. 2. Left panel: size range (grey bars) of the zooplankton species found between 2006 and 2013 in the pelagic area of the GPNP lakes (from Tiberti *et al.*, 2014) and the size range of zooplankton prey found in the brook trout stomachs (shaded area, N=479). Right panel: size range (grey bars) of the free living large zooplankton species (from Tiberti *et al.*, 2014) and size range (black square, mean; buffers, minimum and maximum) of the same species in the stomach content of adult brook trout (total length ≥20 cm). DAP, *Daphnia* gr. *longispina*; CYC, *Cyclops* gr. *abyssorum*; ARC, *Arctodiaptomus alpinus.*

long brook trout (Lake Dres, September 23, 2013) and when zooplankton was present in the stomach content of adult fish, it represented the 38.9% (mean value based on eight observations) of the total prey biovolume. This allows one to imagine what might be the trophic relationships between introduced fish and zooplankton in the early stages of the establishment of non-native trout populations, when the pristine zooplankton communities provided an abundance of large prey. Juvenile brook trout have a larger prey size spectrum than adults, but also juveniles exert a prey selection, in particular they do not feed on very small zooplankton (<0.25 mm) including naupliar stages of copepods and some juvenile chydorids, but especially rotifers. Thus, also juvenile predation could contribute to enforce the indirect increase of rotifers, which compete both with large and medium-to-small size crustaceans.

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