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**Predation by introduced fish can magnify the terrestrial
arthropod subsidies in mountain lakes**

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Complete List of Authors:	Rolla, Matteo; Swansea University, Department of BioSciences Biffoni, Geordie; University of Genova Brighenti, Stefano; University of Trento Iacobuzio, Rocco; Università Statale di Milano, Dipartimento di Bioscienze Liautaud, Kevin; Ente Parco Nazionale Gran Paradiso Pasquaretta, Cristian; Toulouse University Tiberti, Rocco; Università degli Studi di Pavia, DSTA
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1 **Title page:**

2 **Predation by introduced fish can magnify the terrestrial arthropod subsidies in mountain**
3 **lakes**

4

5 Matteo Rolla^{1,2}, Geordie Biffoni³, Stefano Brighenti^{2,4,5}, Rocco Iacobuzio^{2,6}, Kevin Liautaud²,
6 Cristian Pasquaretta⁷, Rocco Tiberti^{2,8,*}

7

8 ¹*Department of BioSciences, Swansea University, Singleton Park, SA2 8PP, Swansea, UK*

9 ²*Alpine Wildlife Research Centre, Parco Nazionale Gran Paradiso, Degioz 11, 11010*
10 *Valsavarenche, Aosta, Italy*

11 ³*DISTAV, Dipartimento di Scienze della Terra, dell'Ambiente e della Vita, Università di*
12 *Genova, Corso Europa 26, 16132 Genova, Italy*

13 ⁴*Dipartimento di Ingegneria Civile, Ambientale e Meccanica, Università degli studi di*
14 *Trento, via Mesiano 77, 38123 Trento, Italy*

15 ⁵*Sustainable Ecosystems and Bioresources Department, Fondazione E. Mach, IASMA*
16 *Research and Innovation Centre, Via E. Mach 1, 38010 San Michele all'Adige, Trento, Italy*

17 ⁶*DBS, Dipartimento di Bioscienze, Università degli Studi di Milano, Via Celoria 26, 20133*
18 *Milano, Italy*

19 ⁷*Centre de Recherches sur la Cognision Animale (CRCA), Centre de Biologie Intégrative*
20 *(CBI), Université de Toulouse, CNRS, UPS, Bât 4R3, 118 Route de Narbonne, 31062 Cedex*
21 *9, Toulouse, France*

22 ⁸*DSTA, Dipartimento di Scienze della Terra e dell'Ambiente, Università di Pavia, Via*
23 *Ferrata 9, 27100 Pavia, Italy*

24 * **Correspondence:** Rocco Tiberti, DSTA, Dipartimento di Scienze della Terra e
25 dell'Ambiente, Università di Pavia, Via Ferrata 9, 27100 Pavia, Italy. Mobile: 0039 340
26 4717352 e-mail: rocco.tiberti@gmail.com

27

28 **Abstract.**

29 A portion of the terrestrial subsidies to lentic habitats consists of arthropods. In high
30 mountain, originally fishless lakes, terrestrial arthropods are an important seasonal food
31 resource for introduced fish. Here we investigate how brook trout *Salvelinus fontinalis* can
32 alter the input of terrestrial arthropods in ten high mountain lakes contrasting for their
33 stocking history (with and without fish, or manipulated for fish eradication). We used a food
34 consumption model to calculate the minimum and maximum number/biomass of arthropods
35 consumed by fish and we found that they can exceed several folds the number/biomass of
36 arthropods sinking into the lakes, at least under the metabolic rates expected for fish for most
37 of the summer. We interpret this result as an indirect indication that arthropods usually
38 cannot overcome the surface tension at the lake surface and that fish can work as a vector
39 across the water-air interface. We infer that pathways for dead and alive arthropods to leave
40 the lakes do exist and fish can transfer into the water column many arthropods whose fate
41 was leaving the lakes, which may have overlooked ecological and conservation implications.

42

43 **Keywords.** Brook trout, ecological linkages, Gran Paradiso National Park, LIFE+ Project
44 BIOAQUAE, fish eradication

45 **Introduction**

46 Terrestrial subsidies to aquatic habitats include all nutrients of terrestrial origin which
47 are incorporated into the aquatic food web, becoming available in the form of
48 dissolved/particulate organic carbon and terrestrial prey (e.g. terrestrial organisms consumed
49 by aquatic predators) for aquatic biota (Vander Zanden and Gratton 2011). Land-to-lake
50 linkage pathways are largely governed by physical vectors such as gravity, run-off,
51 precipitation, wind. However, they may also be mediated by biotic vectors including
52 dispersal events of terrestrial prey organisms, which may fall into the water (Mehner et al.
53 2005; Bartels et al. 2012).

54 Terrestrial subsidies can fuel the metabolism of aquatic habitats to a variable extent,
55 with the impact on nutrient balance of lakes depending on a number of local factors (Vander
56 Zanden and Gratton 2011). In general, they represent a more significant fraction of the
57 nutrient balance in small oligotrophic lakes (Mehner et al. 2005; Vander Zanden and Gratton
58 2011), such as most small lakes of glacial origin. These are the most common type of lake
59 found globally, and are usually unproductive lakes located in polar and mountain regions.
60 They possess a net heterotrophic metabolism, meaning that bacterial respiration is greater
61 than primary production and that the local food webs rely on external/terrestrial nutrient
62 sources (del Giorgio et al 1997; Cole et al 2006).

63 Due to their biogeographic history and when downstream physical barriers are present
64 (i.e. cascades), mountain lakes are originally fishless. In recent decades, predatory fish (e.g.
65 Salmonidae and Cyprinidae minnows of the genus *Phoxinus*) have been introduced to many
66 formerly fishless lakes for recreational angling (Miró and Ventura 2013, 2015; Ventura et al.
67 2017). Fish introduction usually causes the loss of native species (amphibians,
68 macroinvertebrates and large zooplankton; Knapp et al. 2001; Tiberti et al. 2014a), and
69 results in other indirect ecological impacts (e.g. affecting the nutrient cycles and the trophic

70 state of invaded ecosystems; Schindler et al. 2001; Eby et al. 2006). For example, by feeding
71 on large planktonic herbivores fish can benefit pelagic primary production by decreasing
72 grazing pressure. Besides, by feeding on aquatic and terrestrial prey and excreting wastes in
73 the pelagic zone, fish transfer a small amount of nutrients to the water column of high altitude
74 lakes (Schindler et al. 2001; Milardi et al. 2017) and other lentic habitats (Pace et al. 2004;
75 Persson and Svensson 2006; Carpenter et al. 2011). Incidentally, fish introductions provide
76 an interesting opportunity to compare stocked and natural fishless lakes. Since fish
77 eradications are a realistic conservation measure in high altitude lakes (Knapp and Matthews
78 1998), they also provide the rare opportunity to manipulate the presence of introduced
79 predators in the wild. These characteristics made high altitude lakes ideal model ecosystems
80 to study the ecological role of introduced fish.

81 The role and the magnitude of arthropod input is an overlooked issue in lake ecology
82 (Wurtsbaugh 2007; Piovia-scott et al., 2016), probably because terrestrial arthropods and
83 arthropod fragments account for a small fraction of the total terrestrial subsidies and nutrient
84 budget into lakes (Cole et al. 1990; Cole et al. 2006; Mehner et al. 2005; Wurtsbaugh 2007;
85 but see Carlton and Goldman 1984; Nowlin et al. 2007 for massive arthropods fallouts and
86 their ecological consequences). However, terrestrial arthropods represent a notable fraction of
87 airborne inputs of organic matter (Vander Zanden and Gratton 2011), and a very important
88 food resource during the ice-free season for introduced fish populations in small oligotrophic
89 glacial lakes (e.g. Mehner et al. 2005; Milardi et al. 2015; Tiberti et al. 2016). Here terrestrial
90 arthropods may have a stabilizing role in fish energetics and contribute to the maintenance of
91 fish abundances (Piovia-Scott et al., 2016). Since these fish are introduced species, their
92 impact on the reciprocal subsidies between lakes and surrounding terrestrial habitats is also a
93 conservation issue needing to be thoroughly understood.

94 In the present study, we take advantage of the features which make high altitude lakes
95 good model ecosystems and of a recently completed fish eradication campaign, with the aim
96 of understanding whether the terrestrial arthropod subsidy (arthropods input into the lakes) is
97 influenced by introduced fish. The present study was carried out in ten high altitude lakes
98 contrasting in stocking history: 3 naturally fishless lakes, 3 lakes with brook trout *Salvelinus*
99 *fontinalis* Mitchell 1814, and 4 lakes treated for brook trout eradication. We therefore
100 measured the number of sinking arthropods at different depths in the three lake categories to
101 test our first study hypothesis: (H1) a proportion of terrestrial arthropods falling into the
102 lakes, which would have formerly sunk to lake bottom, is diverted to fish. However, the
103 number of sinking arthropods was so much lower than our naïve expectations, that our test of
104 H1 did not provide a clear indication about its validity. We therefore formulated a further
105 study hypothesis concerning the low number of sinking arthropods. We compared the
106 number/biomass of sinking arthropods and the number/biomass of terrestrial arthropods
107 consumed by the populations of brook trout (as an indirect, minimum estimate of the number
108 of arthropods falling onto the lakes' surface), to indirectly test our second hypothesis: (H2) a
109 proportion of the terrestrial arthropods falling onto the lake surface do not overcome the
110 surface tension of the water, and fish predation works as a vector across the water-air
111 interface, i.e. between the lake surface and the water column. The number/biomass of
112 consumed arthropods in the lakes treated for fish eradication was estimated with a food
113 consumption model. Both H1 and H2 predict that fish can divert (in the form of metabolic
114 wastes, rich in nutrients) some terrestrial arthropods into the water column, changing their
115 final (benthic habitats for H1) or temporary (lakes' surface for H2) destinations. H1 is
116 verified if the proportion of sinking arthropods reaching the bottom is larger in fishless lakes
117 than in the presence of introduced fish. H2 is verified if the number/biomass of terrestrial

arthropods consumed by fish is larger than the number/biomass of terrestrial arthropods sinking into the lakes.

We complemented the study with two field tests concerning the time of underwater arthropod decomposition, and the relationship between number of sinking arthropods and distance from the shoreline. These tests were performed to ensure that the used methods were suitable to quantify the number of terrestrial arthropods sinking into lakes and to discuss some overlooked aspects of the sampling design.

Methods

Study lakes

All the study lakes are included in the Gran Paradiso National Park (GPNP), a large protected area located between 45° 25' and 45°45' N and between 7° and 7°30' W in the Western Italian Alps (Fig. 1). The GPNP shows a large altitudinal extension (between 800 and 4,061 m) and a typical alpine climate. Toponyms of the lakes will be replaced by abbreviations: Nivolet superiore-NIS; Trebecchi superiore-TRS; Losere-LOS; Leità-LEI; Rosset-ROS; Nivolet inferiore-NII; Leynir-LEY; Nero-NER; Djouan-DJO; Dres-DRE. The main geographical, morphological and chemical features of the study lakes are reported in Table 1. The lakes are natural (non-dammed) and they are all located above or at the local tree line with their watersheds belonging to the alpine and nival belts. Thermal stratification occurs only late in the summer in the deepest lakes and the ice-covered season lasts for 7-9 months per year (Tiberti et al. 2010). Based on nutrient content, the studied lakes are oligotrophic or ultraoligotrophic. The presence of brook trout dates back to the 1960s.

143 Sampling and analytical methods

144

145 *Funnel traps for sinking arthropods*

146 To sample the sinking arthropods, we used submerged funnel-traps (inverted cones)
147 constructed with a plastic net (1 mm mesh-size) with their mouth facing upwards (Fig. 2A),
148 which are a variant of the sedimentation traps (Bloesch and Burns 1980), but suitable to
149 retain only larger particles, i.e. arthropods.

150

151 *Proportion of sinking arthropods reaching the lake bottom*

152 We used a paired benthic and surface funnel trap design (Fig. 2B) to test whether fish
153 presence affects the proportion of terrestrial arthropods reaching the bottom (H1). The
154 surface trap should give an estimate of the number of sinking arthropods before being preyed
155 upon by fish feeding above the bottom trap (a ≈ 1.5 m section of water column). During the
156 2013 ice-free season, between June 25th and September 7th, we repeated 2-3 sampling
157 sessions in all the study lakes (obtaining 8-14 replicates of paired benthic and surface samples
158 of terrestrial arthropods for each lake; Table 2). During each sampling session, four plots of
159 traps were placed along the two-meter isobaths and left in the lakes for 4-12 days. Each plot
160 consists of one pair of traps. One trap was placed approximately five cm below the water
161 surface and the other was suspended above the lake bottom. There was approximately 1.5 m
162 between the mouths of the two traps. Each trap pair was suspended from a floating rope
163 anchored to the lake shore and intersecting the two-meter isobath at the sampling point. The
164 sampling points along the 2 m isobaths was randomly generated in the R environment (R
165 3.1.1) using the function “readshapeSpatial” (package “maptools”) to import the shape file of
166 the 2 m isobaths and the function “runifpointOnLines” (package “spatstat”) to generate four
167 random points (R Development Core Team 2013). The point generation was repeated three

times in each lake to generate a sufficient number of random points to change the position of the trap pairs at each sampling session. The water level of most of the lakes was constant, but NER and NII can undergo a water level reduction (approximately 1 m in NER, and 1.5 m in NII) during the summer. However, the water level fluctuation was not detectable over a daily or weekly period and did not affect the vertical displacement of the traps. The sampled insects were removed from the traps and fixed in 70% ethanol directly in the field. The samples were sorted under a stereomicroscope at a magnification of 10x, classified at the order level, enumerated, and their maximum body length was measured.

Number and biomass of terrestrial arthropods sinking into the lakes

The captures of terrestrial arthropods from funnel traps were used to estimate the number ($\text{No.} \times \text{m}^{-2} \times \text{day}^{-1} \pm 95\% \text{ Confidence Intervals}$) and dry biomass ($\text{mg} \times \text{m}^{-2} \times \text{day}^{-1} \pm 95\% \text{ Confidence Intervals}$) of terrestrial arthropods sinking into the lakes. Arthropod dry biomass was calculated from order-specific length-biomass relationships (Sabo et al. 2002). These estimates were also multiplied by the lake surface area to obtain a gross daily estimate of the arthropods falling into each lake ($\times \text{lake}^{-1} \times \text{day}^{-1}$), despite being aware that input of airborne particles could depend on the distance from the shoreline (Psenner 1984; Cole et al. 1990; but see Norlin 1964, 1967 and Cole et al. 1990 showing that this relation is weak or inexistent for terrestrial arthropods and the next paragraph for the description of a dedicated field test).

Number of sinking arthropods and distance from the shoreline

The number of sinking arthropods could vary on the lake surface: intuitively, compared to the pelagic area the littoral area should be the recipient of a larger number of falling arthropods. To check how the measures from the sublittoral zone (at the 2 m isobaths) compare with the measures from the littoral and pelagic zone, we designed a specific field test. Between June

193 26th and August 31st, 2016, we performed 7 repeated sampling in lake DRE to understand if
194 the distance from the shoreline influence the number of arthropods ($\text{No.} \times \text{m}^{-2} \times \text{day}^{-1}$)
195 sinking into the lake. DRE is one of the “eradication” lakes and in 2016 was already fishless.
196 This lake was chosen because of its lower altitude and warmer microclimate, potentially
197 favoring insect production. During each sampling session, two plots of traps were suspended
198 along two transects (floating ropes) perpendicular to the lake shore, one in N-S direction and
199 the other one in E-W direction. Each plot had four traps placed approximately five cm below
200 the water surface at 0 (with the border of the trap in contact with the shoreline), 1, 10, 20 m
201 from the shoreline. Each sampling session lasted for 3-5 days. The sampled arthropods were
202 removed from the traps and fixed in 70% ethanol directly in the field. The samples were
203 sorted under a stereomicroscope at a magnification of 10x, classified at the order level, and
204 enumerated.

206 *Timing of underwater disappearance of terrestrial arthropods*

207 The decomposition timing of the terrestrial arthropods captured in the funnel traps may be too
208 rapid and affect the validity of the sampling results. We therefore performed a field test to
209 assess the decomposition time in four insect categories: small (total length <5 mm) and large
210 (> 5 mm) highly chitinized insects (adult terrestrial Coleoptera and Heteroptera), and small
211 (<5 mm) and large (> 5 mm) poorly chitinized insects (adult terrestrial Diptera). While we
212 are aware that decomposition process could quickly affect soft tissues and arthropods
213 biomass, the specific objective of this field test was understanding if all the arthropods could
214 be easily recognized as such at the end of each sampling session. The insects used in the test
215 were captured in the field using a hand-net, euthanized with low temperature, and preserved
216 at -18°C until the beginning of the test on the 28th June, 2016. We submerged 5 insects per
217 category into transparent plastic boxes closed with a net (1 mm mesh-size) together with two

temperature loggers (measuring interval: 1 hour) at 0 and 6 m depth (using the vertical temperature gradient to simulate two temperature treatments) into Lake DRE. We checked the box content every 4-5 days for the first 15 days and then two weeks later (at day 28) and we took note of the state of decomposition of the different insect categories. Lake DRE was chosen because, compared to the other study lakes, it presents relatively high water temperatures and bacterial load (Tiberti et al. 2014b), therefore providing cautionary short times of degradation of the organic matter.

Statistical analyses

To test H1 we used the counts of terrestrial arthropods (response variables) collected in 2013 with the paired benthic and surface funnel traps. We applied a Bayesian generalized mixed model for count data (GLMM) with Markov-chain Monte-Carlo (MCMC) estimation, using package ‘MCMCglmm’ (Hadfield, 2010) in the statistical environment R v.3.1.1 (R Development Core Team 2013). We included two additive random effects: the lake (to account for the variation attributable to the sampling site) and a grouping variable distinguishing all the counts pairs coming from each plot of paired traps. The lakes’ stocking history (Treatment: Fish-N: naturally fishless lakes; Fish-Y: lakes with fish; Fish-E: Eradication lakes), the sampling depth (Depth: surface vs. bottom), their interaction (Treatment-by-Depth), and the sampling effort (Days: duration of the sampling in days) were added as fixed factors. The Posterior Marginal R^2_{GLMM} and 95% Credibility Intervals were calculated following Nakagawa and Schielzeth (2013) to measure the goodness of fit of the model. H1 is verified when the posterior mean estimates of Treatment-by-Depth are significantly lower in the presence of fish than in the eradication and fishless lakes (meaning that the fish presence is reducing the proportion of terrestrial arthropods reaching the benthic traps). Because most funnel traps in our study (nearly 71%) had no arthropods, and because

these zero values cannot be clearly ascribed to absence data, we used a zero-altered Poisson (ZAP) GLMM (Hadfield, 2015). ZAP models contain two sub-models: one related to the zeroes and one related to counts greater than zero. Therefore, the model results depend on two latent variables: (i) the probability (in logit scale) of the response variable being non-zero, which is here interpreted as the probability of sampling at least one arthropod in the traps, and (ii) the mean parameter of a zero-truncated Poisson distribution, which in this case corresponds to the estimated arthropod count in non-empty traps.

Since data did not meet the assumption for parametric tests, we performed a non-parametric Kruskal–Wallis test to determine if the distance from the shoreline influences the number of terrestrial arthropods sinking into the lakes ($N \times \text{trap}^{-1} \times \text{day}^{-1}$) with the distance from the coast (0,1,10,20 m) as grouping factor.

Daily consumption of terrestrial insects

For each lake treated for fish eradication we estimated absolute fish abundance, and built a simple terrestrial arthropod consumption model. The model parameters were estimated from original data on the brook trout abundance, size structure, and diet and from literature data on the brook trout Gastric Evacuation Rates (GER, the speed with which food leave the stomach after ingestion). Since GER for brook trout is dependent on water temperature (Sweka et al. 2004) we respectively used its minimum and maximum values to account for the uncertainty of this parameter (GER values from literature data; Sweka et al. 2004; Forester et al. 1994; Boisclair and Sirois 1993) to obtain a raw but realistic range of variation of arthropod consumption under different temperature regimes. The models output are four ranges of variation (one per lake) of terrestrial arthropod consumption (both in terms of abundance and biomass), and were compared with the measured numbers and calculated biomasses of sinking arthropods to test H2.

Model formulation

Daily Consumption of Terrestrial Arthropods (CTA) by the fish population has been calculated separately for each lake DJO, DRE, LEY, and NER and is described by:

$$CTA = 24 \times GER \times \sum_{c=1}^4 NF_c \times TA_c \quad [1]$$

Where NF_c denotes the number of fishes belonging to size class c , with c varying from 1 to 4 (from < 15 to ≥ 25 cm at 5 cm intervals). GER denotes the Gastric Evacuation Rate, considered as constant whatever the size class. We used the minimum and maximum GERs measured for brook trout in laboratory (0.005-0.080 h^{-1} ; Boisclair and Sirois 1993; Forester et al. 1994; Sweka et al. 2004) to obtain a reliable CTA range. TA_c denotes the average number of terrestrial arthropods in the stomach contents of a fish belonging to size class c . To estimate TA we had to take into account that the consumed terrestrial arthropods could also be emerging insects with aquatic pre-imaginal stages, captured at their emergence. It was therefore inappropriate to consider all of them as terrestrial prey falling into the water. Conservatively, we decided to exclude all the potentially emerging insects from the CTA estimates. We divided the consumed terrestrial arthropods into three groups. Group 1 includes the arthropod orders without aquatic stages (e.g. Araneae, Opiliones, Lepidoptera, Orthoptera, terrestrial Coleoptera, terrestrial Hemiptera); they were included in the TA estimate. Group 2 includes the insect orders with terrestrial imaginal stages, but aquatic pre-imaginal stages (Trichoptera, Plecoptera, Ephemeroptera, Odonata); they were excluded from the TA estimate. Group 3 includes terrestrial Diptera and Hymenoptera, which, due to the close resemblance of many of their families (e.g. Syrphidae closely resemble Hymenoptera),

were clumped into a single prey-group during most of the diet analyses. However, Diptera comprise some families with terrestrial pre-imaginal stages (e.g. Muscidae, Bombyliidae, Drosophilidae) and some others with aquatic or potentially aquatic pre-imaginal stages (e.g. Chironomidae, Tabanidae, Limoniidae, Tipulidae). For each size class c , TA is described by:

$$TA = \frac{1}{n} \times \sum_{k=1}^n [Ngroup1_k + (a \times Ngroup3_k)] \quad [2]$$

Where n is the total number of fishes belonging to a size class, and k an individual. $Ngroup1_k$ and $Ngroup3_k$ are the number of arthropods belonging to the corresponding groups found in the stomach content of one individual k , and a denotes the estimated proportion of insects belonging to the prey group 3 (adult Diptera/Hymenoptera) with terrestrial pre-imaginal stages (including part of the Diptera and all the Hymenoptera). We therefore performed 40 additive stomach contents analysis, with the specific aim of estimating a :

$$a = \frac{Ngroup3'_{sub}}{Ngroup3_{sub}} \quad [3]$$

Where $Ngroup3'_{sub}$ represents the cumulative number of Diptera/Hymenoptera with terrestrial pre-imaginal stages found in the subsample of stomach contents, and $Ngroup3_{sub}$ represents the total number of Diptera/Hymenoptera found in the same stomach contents subsample.

Contrary to the insects belonging to group 2, which are an occasional trophic resource for brook trout, Diptera/Hymenoptera are a very common prey item (Tiberti et al. 2016). Therefore, a correct estimate of coefficient a is likely to appreciably influence the CTA estimates. Coefficient a is considered constant whatever the size class.

Prey biovolume measurements were used to convert CTA ranges into biomass values (BCTA, daily Biomass of Consumed Terrestrial Arthropods), replacing TA_c in Eq. [1] with VTA_c :

$$BCTA = 24 \times GER \times \sum_{c=1}^7 NF_c \times VTA_c \quad [4]$$

Where VTA_c denotes the average biovolume of terrestrial arthropods in the stomach contents of a fish belonging to size class c and is described by:

$$VTA = \frac{b}{n} \times \sum_{k=1}^n [Vgroup1_k + (a \times Vgroup3_k)] \quad [5]$$

For the same reasons explained for Eq. [2], only the biovolumes (V) of the terrestrial arthropods without preimaginal aquatic stages -those belonging to group 1 ($Vgroup1$) and a fraction of those belonging to group 3 ($Vgroup3$)- were included in Eq. [5]. Biovolumes were converted to dry weight by multiplying by a constant value (b) equal to 0.35 according to Studier and Seveck (1992), who assessed that the water content of a wide range of terrestrial arthropods is approximatively the 65% of their live weight.

Fish abundance and size-structure: parameter estimates

To estimate NF_c we used the fish abundance and total length measures obtained at the end of the eradication campaign in Lakes DJO, DRE, LEY, and NER. Fish abundance was accurately measured along the eradication campaign. Intensive gill-netting was used as eradication method in the sub-littoral and pelagic area, while electrofishing (with a ELT62 II 160 GI backpack equipment) was used to remove the fish from the littoral area and tributaries (Knapp and Matthews 1998). In addition, two days of experimental intensive angling had

342 already substantially contributed to the decline of the population in Lake DRE, just before the
343 start of the eradication campaign (Tiberti et al. 2017). The length of the brook trout removed
344 from the lakes was usually recorded, but not for fish in advanced state of decomposition (e.g.
345 many fish removed at the end of the ice-cover seasons). We therefore assigned those fish to
346 one of four size classes encompassing the values from <15 cm to > 25 cm at 5 cm intervals.
347 For a few fish it was not even possible to assign a size class and they were therefore assigned
348 to the different classes proportionally to the relative abundance of each size class.

349 Fish growth from one season to the next is relevant for the model parameterization since the
350 allocation of one fish to its size class would require a back-calculation of the fish size at a
351 reference date. However, due to the presence of missing data in the length measurements, a
352 precise back-calculation (based on age-length literature data or scalimetric/otolith ring
353 measures; Panfili et al. 2002) was not feasible. We therefore decided to account for fish
354 growth reducing by one unit the size class of those fish captured during the second field
355 season (2014, including the 2014-2015 ice cover season), and by two units the size class of
356 those fish captured during the third field season (2015, including the 2015-2016 ice cover
357 season). This seems a fair realistic adjustment of the data. Indeed, the very large majority of
358 fish captured during the second and third field seasons were young fish, hatched from their
359 nests the previous year, while the large majority of >15 cm fish (100.0 % in DJO; 99.6% in
360 DRE; 97% in LEY; 98.9% in NER) were captured during the first field season. As a result,
361 only the densities of size class 1 (<15 cm) are substantially affected (reduced) by this kind of
362 data adjustment; in particular those fish <15 cm captured during the second field season and
363 those fish <20 cm captured during the third field season have been removed from the total
364 count of captured fish, because they probably were not present (not born) during the first
365 year. On the other hand, the densities of larger size classes, which were redly removed from
366 the lakes during the first field season, are almost unaffected.

367

368 *Fish diet: parameters estimates*

369 To estimate TA_c , between 2006 and 2016 we collected 306 stomach contents (from both
370 daytime and nighttime sampling sessions; 61 in June, 74 in July, 121 in August, 50 in
371 September) from 9 lakes with brook trout (Fig. 1). Stomachs were preserved in 70% ethanol
372 (see Tiberti et al. 2016 for detailed analytical methods). Ingested items were divided into
373 aquatic and terrestrial prey, classified in the different ecological groups 1-3 and sub-groups
374 (see , and enumerated. In addition, the biovolume of each different prey item was measured
375 from a subsample of 236 stomachs to estimate VTA_c by gently pressing the prey items
376 belonging to each prey group in a graduated cylinder. Prey groups with very small
377 biovolumes (<0.05 mL) were approximated to zero.

378

379 **Results**

380

381 **Sinking arthropods**

382

383 *Proportion of arthropods reaching the bottom: paired traps experiment*

384 To test H1, we collected 232 samples (116 trap pairs) for sinking arthropods from 10 lakes.
385 Three traps pairs were discarded because the content of at least one of the two traps was
386 totally or partially lost during the collection. After 4-12 days of sampling, 160 out of 226
387 traps did not contain terrestrial arthropods. During the whole sampling campaign, a total of
388 106 terrestrial arthropods (mean $\pm$ SD per trap: 0.47 ± 0.95 ; 74 Diptera, 27 Coleoptera, 3
389 Araneae, 1 Hymenoptera, 1 Tricoptera) were collected.

390 MCMCglmm results showed that the number of terrestrial arthropods directly depends on the
391 duration of the sampling, while it is not significantly different in the traps placed at different

depths, and among the lakes with different stocking histories (Table 3). The interactive effect of Treatment-by-Depth showed very limited evidence in favor of H1, i.e. we found a significantly higher proportion of terrestrial arthropods reaching the bottom in eradication lakes than in the lakes with fish, but the same proportion was not significantly different between lakes without fish and lakes with fish or treated for fish eradication (Table 3). In spite of the relatively large number of samples, the statistical model showed a low goodness of fit [Posterior Marginal R^2_{GLMM} (95% Credibility Intervals)=0.17 (0.03-0.54)], probably due to the small number of sinking arthropods.

Since the difference between the number of sinking arthropods captured at the lake surface and bottom was not significant, we used the data from both the surface and bottom traps to estimate the flux of sinking arthropods in each lake (Table 2). We found that the number and biomass of sinking arthropods was highly variable among lakes with a range of 0.02 to 1.40 invertebrates $\text{m}^{-2} \times \text{day}^{-1}$ and 0.0 to 4.3 $\text{mg} \times \text{m}^{-2} \times \text{day}^{-1}$ (ANOVA results for arthropod abundance: $F_{9,216}=10.6$, $p<0.0001$; ANOVA results for arthropod biomass: $F_{9,216}=5.0$, $p<0.0001$; Table 2).

Sinking arthropods and distance from the shore

Of the 56 traps surveys (8 traps $\times$ 7 replicates), only 9 traps contained terrestrial arthropods. In total, 16 insects (8 Hymenoptera, 5 Diptera, and 3 Coleoptera) were collected in Lake DRE, corresponding to a mean $\pm$ SD capture rate of 0.34 ± 0.85 sinking arthropods $\times \text{m}^{-2} \times \text{day}^{-1}$. The capture rates were 0.66 ± 1.19 sinking arthropods $\times \text{m}^{-2} \times \text{day}^{-1}$ at 0 m from the shoreline; 0.60 ± 1.08 sinking arthropods $\times \text{m}^{-2} \times \text{day}^{-1}$ at 1 m, 0.00 ± 0.00 sinking arthropods $\times \text{m}^{-2} \times \text{day}^{-1}$ at 10 m; 0.07 ± 0.27 sinking arthropods $\times \text{m}^{-2} \times \text{day}^{-1}$ at 20 m. These results suggest a negative relationship between the distance from the shoreline and the number of sinking arthropods, but the relationship was not significant (Kruskal–Wallis test = 6.91, df =

3, $p=0.07$) and the number of sinking arthropods remained very low even close, or in contact, with the shoreline. The measures recorded during this field test were also comparable with those recorded during the 2013 sampling campaign in the sublittoral area (Table 2).

Time of arthropods degradation

Insects from all four categories were exposed for 28 days (28th June – 26th July, 2016) at a mean water temperature of 10.5 °C (range: 6.7-16.3 °C; 0 m depth) and 8.6 °C (range: 6.2-11.5 °C; 6 m depth; Fig. 3). After the settlement of the cages containing the insects, the state of decay of the insects was repeatedly checked. Until day 15 (which exceed by 3 days the maximum sampling time of the funnel traps) all the insects were still perfectly recognizable; by day 28 some insects showed clear signs of decay (loss of wings or elytra), but all large insects and the majority of small insects were still well recognizable in both temperature treatments.

CTA models: parameters and outputs

Fish abundance and size-structure

The density, abundance and size class distribution of the fish removed from the four lakes treated for fish eradication were highly variable (Table 4). Since fish eradication was completed in all the lakes, the estimates of fish population parameters are precise. In all the lakes more than 1 year have passed without any fish capture: DJO (last fish removed on 14/06/2014), DRE (last fish removed on 11/08/2015), LEY (last fish removed on 05/06/2016) and NER (last fish removed on 07/06/2015).

Terrestrial arthropods in the fish diet and coefficient “a”

Terrestrial arthropods are commonly preyed upon by lake dwelling brook trout. In terms of relative abundance, terrestrial arthropods were moderately important diet items for the brook trout, ranging from 4-8% of the relative abundance of prey in size classes 1-3, but reaching 45% for size class 4 (Table 5). In terms of ingested biovolumes, terrestrial arthropods represented a substantial part of the diet of all the size classes and they are by far the dominant component of the diet of larger brook trout (Table 4). The analysis of 40 additive stomach contents showed that the proportion of terrestrial Diptera/Hymenoptera (group 3) with terrestrial pre-imaginal stages is 0.61 (coefficient “a”).

CTA Models outputs

The model parameters are summarized in Table S1 of the online supplementary material S1. For the calculation of the daily consumption of terrestrial arthropods, the relevant fish frequencies are those obtained accounting for annual growth: the differences between the observed frequencies of Table 4 and the estimated frequencies used to parametrize the model and reported in Table S1 have to be ascribed to the data adjustment.

CTA model outputs returned a range of daily Consumption of Terrestrial Arthropods for each lake which was divided by the lake surface to obtain the consumption $\times \text{m}^{-2}$ (Fig. 4). In Lake DJO the brook trout population consumed 2435 – 38955 terrestrial arthropods $\times \text{day}^{-1}$ corresponding to 0.2 – 2.9 arthropods $\times \text{day}^{-1} \times \text{m}^{-2}$ equal to a dry biomass of 1.8 – 28.4 mg $\times \text{day}^{-1} \times \text{m}^{-2}$; in Lake DRE the brook trout population consumed 8685 – 138960 terrestrial arthropods $\times \text{day}^{-1}$ corresponding to 0.3 – 5.3 arthropods $\times \text{day}^{-1} \times \text{m}^{-2}$ equal to a dry biomass of 6.3 – 101.0 mg $\times \text{day}^{-1} \times \text{m}^{-2}$; in Lake LEY the brook trout population consumed 3921 – 62744 terrestrial arthropods $\times \text{day}^{-1}$ corresponding to 0.1 – 1.4 arthropods $\times \text{day}^{-1} \times \text{m}^{-2}$ equal to a dry biomass of 2.7 – 43.8 mg $\times \text{day}^{-1} \times \text{m}^{-2}$; in Lake NER the brook trout population consumed 881 – 14094 equal to terrestrial arthropods $\times \text{day}^{-1}$ corresponding to 0.1 – 0.8

arthropods $\times \text{day}^{-1} \times \text{m}^{-2}$ equal to a dry biomass of $0.7 - 11.5 \text{ mg} \times \text{day}^{-1} \times \text{m}^{-2}$. The very high variability of the arthropods consumption estimates among the “eradication lakes” mainly depends on the total abundance of fish inhabiting the lakes, which can vary from a few hundred in Lake NER to several thousands in Lake DRE.

Comparison between sinking arthropods and consumption by fish

The number/biomass of sinking and consumed arthropods $\times \text{m}^{-2}$ can overlap when the GER is low, while arthropods consumption can exceed several folds the Upper 95% CI of the number/biomass of sinking arthropods when the GER is kept high (Fig. 4). The gap between sinking and consumed arthropods is comparatively larger in terms of biomass than in terms of abundance (Fig. 4).

Discussion

Number of sinking arthropods and their proportion reaching the bottom

While terrestrial arthropod deposition in lotic ecosystems is well documented (e.g. Mason and MacDonald 1982; Bartels et al. 2012) there are considerably fewer studies from lentic ecosystems, and the deposition of arthropods onto lake surfaces remains relatively unknown (Wurtsbaugh 2007). The few existing data describe occurrence on the lake surfaces (Norlin 1964, 1967; Childress et al. 1981; Bowman 1988), or have to be extrapolated from studies dealing with the deposition of terrestrial particles -including arthropods- over the lakes (e.g. Cole et al. 1990). To the best of our knowledge, the present study is the first attempt to measure the quantity of arthropods sinking into lacustrine ecosystems. Therefore, we do not

491 have any reference to understand how the measured numbers of sinking arthropods compare
492 with those from other lakes.

493 In the present study, the sedimentation traps operated near their detection limit and the
494 estimates they provided (in the order of $0\text{--}2 \text{ organisms} \times \text{m}^{-2} \times \text{day}^{-1}$) were far lower than our
495 initial expectations founded on the observation that terrestrial arthropods drifting on the lake
496 surface can appear very abundant. However, repeated sampling in several lakes seems
497 appropriate for estimating the number of sinking arthropods. The only factor which could
498 affect the validity of these measures is the removal/disappearance of arthropods from the
499 traps, which can be determined either by decay -though we demonstrated that their
500 disappearance requires more time than the sampling periods- or by their mechanic removal
501 from the traps, i.e. by predation. However, the number of sinking arthropods remained low in
502 all lake categories, particularly in fishless lakes and in “eradication lakes” (where fish
503 densities had strongly decreased and invertebrate predators, e.g. aquatic Coleoptera, had not
504 yet recovered), suggesting that fish and invertebrates feeding inside the traps is not of major
505 significance.

506 Therefore, we tested how the estimated numbers of sinking arthropods in the sublittoral zone
507 compare with the corresponding numbers in the littoral and pelagic zone, by placing the traps
508 at different distances from the shoreline. The underlying idea was that many arthropods
509 trapped at the lake surface are transported by wind to the shoreline (Norlin 1967), where they
510 end up sinking and where we were expecting a disproportionate higher number of sinking
511 arthropods. However, in Lake DRE we found marginally significant higher number of
512 sinking arthropods close to the shoreline compared to the pelagic zone, and the recorded
513 measures overlapped the measures in the sublittoral zone. This result is similar to that
514 reported by Norlin (1964, 1967) and Cole et al. (1990), who did not find a correlation
515 between insects falling onto a lake surface and distance from shore. Overall, the number of

sinking arthropods remain low, even close or very close to the shoreline, and the idea of a massive sink of arthropods along the shore is not supported by our data. Even if there is not much known about the magnitude and spatial patterns of insect deposition to lakes, a few studies suggest that the origin of insect fallouts to lakes is mainly the surrounding shoreline (Norlin 1967; Mehner et al. 2005) and the low number of sinking arthropods could be explained by the absence of shoreline vegetation, which enhance the fallout of terrestrial particulate matter and arthropods (e.g. Nakano and Murakami 2001; Piovia-Scott et al. 2016). However, arthropod falling onto lake surface could also derive from the aerial plankton that can drift considerable distances (Cusimano et al. 2016) and which fall or sink all over lakes, not just near the shoreline (Norlin 1967; Wurtsbaugh 2007). Concerning H1, we did not find any significant effect of the presence of fish on the abundance of sinking insects, nor a clear effect on the proportion reaching the lake bottom. This result is very counterintuitive, because of the large number of insects consumed by the fish populations (Table 5; Tiberti et al. 2016). Even if we collected a large number of samples from several lakes, we attribute this result to a weakness of our sampling design: the low number of sinking arthropods produced a large number of empty traps, affecting the power of the statistical models. The very low proportion of variance explained by the model is indicative of an inadequate sampling and suggests that H1 should not be rejected despite these results.

Sinking arthropods, fish consumption and water surface tension

The finding that, compared to the values recorded in the sublittoral zone, the number of sinking arthropods is low also along the shoreline, encouraged us to tentatively use the estimates from the sublittoral zone as a reasonably realistic estimate of the number of sinking arthropods into the lake as a whole. This number probably represents an intermediate value

541 between the lower values of the pelagic zone and the slightly higher values of the littoral
542 zone. The entire lake estimates can be compared with the consumption rates by the
543 introduced fish populations from the lakes treated for fish eradication (for which absolute
544 abundance, size structure, and dietary data were available) to test H2.

545 Before proceeding to the discussion of the comparison between sinking and consumed
546 arthropods, it should be emphasized that the output of the food consumption models likely
547 provides an underestimate of the number/biomass of arthropods falling onto the lakes'
548 surface because: i) the consumption rates depend on the maximum consumption capacity of
549 the fish populations (which strongly vary with water temperature) and are a measure of the
550 minimum availability of terrestrial arthropods, and ii) the consumption rates were cautiously
551 calculated keeping some parameters low (e.g. excluding the insect belonging to the prey
552 group 2 and part of the insects of group 3; Table 4).

553 Considering the abundance of sinking arthropods, the output of the consumption models
554 supported H2 under high GERs. Indeed, the number of sinking arthropods can overlap the
555 number of consumed arthropods when the GER is kept low, but arthropods consumption can
556 largely exceed the number of sinking arthropods when the GER is kept high (Fig. 4). On the
557 other hand, fish usually consume a much larger biomass of arthropods than that of sinking
558 arthropods (Fig. 4), likely due to the size selective behavior of introduced brook trout (Tiberti
559 et al., 2014a) and the model output generally support H2 independently by the GERs values.

560 The lower values of the abundance/biomass ranges are representative of the consumption
561 rates under low water temperatures (minimum GER value was calculated at 2°C; Sweka et al.
562 2004), while the higher values are representative of the consumption rates under warmer
563 conditions (the GER reach an asymptotic maximum at $\approx 12^{\circ}\text{C}$; Sweka et al. 2004). Both the
564 temperatures fall into the range of surface temperatures commonly registered during the ice-
565 free period in the study lakes (Tiberti et al. 2010). Larger consumption estimates are expected

to be representative of the central part of the ice-free season (temperatures $>12^{\circ}\text{C}$ are commonly registered at the lakes' surface in July-September), while lower consumption estimates are expected to occur at thaw and before freezing (October). Arthropod consumption depends also on the fish population abundance and size structure, and the lower range of arthropod consumption was found in Lake NER, where the fish population has a very low abundance (≈ 200 fish).

The arthropods consumed by fish can exceed the number of sinking arthropods and they can have different origins: i) they can be predated by brook trout before falling into the water: brook trout can capture some groups of slow insects when they are near the lakes surface, i.e. butterflies (authors personal observations), but this kind of predation is certainly exceptional; ii) they can be floating arthropods fallen onto the lake surface and drifting on the lakes surface; iii) they can come from the tributaries: in Lakes NER and DJO, tributaries are absent or very short (≈ 100 m) and it seems very unlikely that a significant number of insects could come from inflowing streams. By the way this source could be more important in Lake LEY and in Lake DRE, presenting permanent tributaries extending for >1000 m. However, according to Clifford (1972), more than the 90% of the terrestrial invertebrates drift at the stream surface. Therefore, even assuming that drift from the tributaries represents a substantial part of the terrestrial prey consumed by lake dwelling brook trout, most of the insects carried by the rivers are intended to float over the lakes' surface, apparently without sinking.

Owing to the disproportion between the few sinking arthropods and the many terrestrial arthropods consumed by fish, we concluded that the fate of most of the arthropods falling into the water is not to sink. Our results suggest that when terrestrial arthropods are not eaten by aquatic predators, they often leave the aquatic environment: they can be washed on to the land (depending on the configuration of the shore), drift downstream on the outflowing river

591 surface, or survive and fly away. The ability of terrestrial arthropods to survive a period in the
592 water has been documented and most species may resist floating for several days or weeks
593 (Norlin 1967; Coulson et al. 2002). Contrary to our finding, it is commonly assumed that
594 nearly all terrestrial insects fallen into the lakes become part of the nutrient budget of the lake
595 (Mehner et al. 2005; Mehner et al. 2007; Wurtsbaugh 2007). The results of the present study
596 demonstrate that this assumption is unfounded and that many insects that fall into the lake, if
597 they are not preyed upon by fish, would ultimately leave the lakes and return to the terrestrial
598 environment. For example, Menher et al. (2007), in accordance with Wurtsbaugh (2007),
599 state that fish are not irreplaceable agents in making external nutrients bound in terrestrial
600 insects available to the lake and that lakes are sinks for these nutrients even if they do not
601 harbor insectivorous fishes. In the light of our results we believe that many terrestrial
602 arthropods falling into the lakes would not contribute to the nutrient budget of the lakes if fish
603 predation does not allow them to cross the water-air interface, preventing them from leaving
604 the lakes. Consistent with our findings, the few times that number of arthropods falling upon
605 the surface of lentic habitats have been estimated their abundance/biomass was dramatically
606 larger than what we observed with the sinking traps ($16\text{-}126 \text{ arthropods} \times \text{m}^{-2} \times \text{day}^{-1}$; $16\text{-}93$
607 $\text{mg} \times \text{m}^{-2} \times \text{day}^{-1}$; Bowman 1988). Childress et al. (1981) found similar arthropods biomass
608 values of Bowman (1988), without providing the number of arthropods (but note that both the
609 study sites are not high mountain lakes).

610 Although terrestrial arthropods are not likely to be an important subsidy to nutrient budgets of
611 lakes (Childress et al. 1981; Vander Zanden and Gratton 2011), the idea that surface tension
612 is a major barrier and that -depending on the presence of predatory fish- incoming arthropods
613 might be pushed back to the lake edges or drawn into the water column by fish, could have
614 interesting consequences for understanding the nutrient supply to lakes provided by terrestrial
615 arthropods. In this context fish can also assume the role of a net source of terrestrial

subsidies, diverting to the water column the nutrients contained in many arthropods whose fate was not entering into the lakes. For example, Mehner et al. (2005, 2007) reported that the diet of a lake dwelling population of bleak (*Alburnus alburnus*) was dominated by terrestrial insects (~84%), with potential impacts on the nutrient budget of the lake.

We summarized the possibility for many arthropods to leave (dead or alive) the aquatic habitat into the conceptual scheme of Fig. 5, where the role of fish as vector for terrestrial arthropods across habitat boundaries is highlighted. Fig.5 also shows that there are several pathways through which arthropods can enter and leave lakes and that further studies need to include these pathways.

From a conservation point of view, our results imply that, if fish introduced in mountain lakes consume the arthropods drifting on the lakes surface, their abundance in the benthic zone and in the littoral area (when they are washed out from the lakes) decreases. The floating insects which are diverted to introduced fish and cannot leave the aquatic habitat are subtracted to the terrestrial habitat and terrestrial consumers (e.g. terrestrial insectivores), possibly exacerbating the competition between terrestrial insectivores and introduced fish for aquatic subsidies (emerging insects; Finlay and Vredenburg 2007; Epanchin et al. 2010; Joseph et al. 2011; Piovia-Scott et al., 2016) and representing a further overlooked component of the reciprocal resource subsidies between mountain lakes and terrestrial habitats (see the conceptual model of reciprocal resource subsidies in Piovia-Scott et al., 2016).

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802 **Tables**

803 **Table 1** Main geographic, morphometric and chemical data of GPNP studied lakes; $D_{\max}$:
 804 maximum depth; A: area; Geology - AG: catchment entirely composed by acidic gneiss;
 805 Geology - CS: catchment dominated by thick covering of calcareous schists. Chemical
 806 variables are expressed as mean $\pm$ SD from 14-28 repeated sampling (between 2008 and
 807 2015). TP: total phosphorus; Fish-N: naturally fishless lakes; Fish-Y: stocked lakes; Fish-E:
 808 lakes under fish eradication.

	LOS	NIS	TRS	LEI	ROS	NII	DJO	DRE	NER	LEY
Latitude N	45°28'32"	45°28'41"	45°30'07"	45°29'37"	45°28'49"	45°29'10"	45°33'27"	45°24'45"	45°33'06"	45°30'28"
Longitude E	07°09'25"	07°08'55"	07°08'40"	07°07'55"	07°08'17"	07°08'45"	07°10'43"	07°13'25"	07°10'07"	07°09'08"
Altitude (m)	2568	2538	2729	2701	2703	2526	2515	2087	2671	2747
$D_{\max}$ (m)	7.2	17.1	7.5	11.0	46.9	14	3.0	7.4	6.0	22.1
A (ha)	2.1	3.4	1.4	6.2	16.9	8.2	1.3	2.6	1.7	4.5
Geology	AG	AG	CS	CS	CS	CS	CS	AG	CS	CS
pH	7.0 $\pm$ 0.2	7.1 $\pm$ 0.3	8.0 $\pm$ 0.3	8.1 $\pm$ 0.2	7.8 $\pm$ 0.2	7.7 $\pm$ 0.4	8.7 $\pm$ 0.4	7.0 $\pm$ 0.5	8.0 $\pm$ 0.3	8.0 $\pm$ 0.3
TP ($\mu\text{g L}^{-1}$)	4.0 $\pm$ 2.1	5.7 $\pm$ 3.6	3.2 $\pm$ 1.9	1.8 $\pm$ 0.8	3.9 $\pm$ 1.0	8.1 $\pm$ 3.0	3.5 $\pm$ 1.3	4.3 $\pm$ 2.5	2.3 $\pm$ 1.6	3.0 $\pm$ 0.9
Fish	N	N	N	Y	Y	Y	E	E	E	E

809

810 **Table 2** Sampling of sinking arthropods and estimated number and biomass (in mg) of
811 sinking arthropods in 10 high altitude lakes contrasting for their stocking history (Fish-N:
812 fishless; Fish-Y: stocked; Fish-E: lakes treated for fish eradication). Sampling effort (start
813 and end dates of sampling, number of elapsed days) and the number of active traps (in
814 brackets) are provided for each sampling session. Sampling took place in 2013 in the Gran
815 Paradiso National Park, Western Italian Alps.

Lake Fish Sampling sessions		Number of sinking arthropods $\pm$ 95%CI		Biomass of sinking arthropods $\pm$ 95%CI	
		trap ⁻¹ $\times$ day ⁻¹	m ⁻² $\times$ day ⁻¹	mg $\times$ trap ⁻¹ $\times$ day ⁻¹	mg $\times$ m ⁻² $\times$ day ⁻¹
LOS	N 26/07 – 31/07, 5 (6)	0.35 $\pm$ 0.25	1.40 $\pm$ 0.49	1.06 $\pm$ 0.43	4.29 $\pm$ 0.87
	01/08 – 06/08, 5 (8)				
	09/08 – 14/08, 5 (8)				
NIS	N 15/08 – 20/08, 5 (8)	0.06 $\pm$ 0.10	0.24 $\pm$ 0.19	0.06 $\pm$ 0.10	0.24 $\pm$ 0.19
	20/08 – 25/08, 5 (8)				
	25/08 – 30/08, 5 (8)				
TRS	N 26/08 – 31/08, 5 (8)	0.01 $\pm$ 0.03	0.02 $\pm$ 0.06	0.00 $\pm$ 0.01	0.00 $\pm$ 0.03
	31/08 – 07/09, 7 (8)				
	07/09 – 12/09, 5 (8)				
LEI	Y 27/08 – 01/09, 5 (8)	0.09 $\pm$ 0.11	0.36 $\pm$ 0.24	0.38 $\pm$ 0.25	1.53 $\pm$ 0.50
	01/09 – 08/09, 7 (8)				
	09/09 – 13/09, 4 (8)				
ROS	Y 05/08 – 10/08, 5 (8)	0.04 $\pm$ 0.08	0.17 $\pm$ 0.15	0.04 $\pm$ 0.08	0.18 $\pm$ 0.16
	10/08 – 16/08, 6 (8)				
	16/08 – 21/08, 5 (4)				
	21/08 – 26/08, 5 (8)				
NII	Y 30/08 – 06/09, 7 (8)	0.02 $\pm$ 0.06	0.08 $\pm$ 0.12	0.05 $\pm$ 0.09	0.18 $\pm$ 0.17
	07/09 – 11/09, 4 (8)				
	11/09 – 15/09, 4 (8)				
DJO	E 06/07 – 11/07, 5 (8)	0.26 $\pm$ 0.25	1.04 $\pm$ 0.50	1.03 $\pm$ 0.50	4.20 $\pm$ 1.00
	12/07 – 19/07, 7 (8)				
DRE	E 25/06 – 30/06, 5 (8)	0.04 $\pm$ 0.08	0.17 $\pm$ 0.16	0.11 $\pm$ 0.13	0.43 $\pm$ 0.26
	02/07 – 07/07, 5 (8)				
	07/07 – 15/07, 8 (8)				
NER	E 11/07 – 16/07, 5 (8)	0.11 $\pm$ 0.16	0.46 $\pm$ 0.33	0.13 $\pm$ 0.18	0.53 $\pm$ 0.36
	20/07 – 25/07, 5 (8)				
LEY	E 01/08 – 13/08, 12 (8)	0.02 $\pm$ 0.05	0.07 $\pm$ 0.11	0.03 $\pm$ 0.07	0.12 $\pm$ 0.14
	13/08 – 18/08, 5 (8)				
	18/08 – 25/08, 7 (8)				

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817

Table 3. Posterior density mean estimates $\pm$ 95% Credibility Intervals (from Bayesian generalized mixed model with Markov-chain Monte-Carlo estimate) of the number of sinking arthropods (response variables) in high mountain lakes contrasting fort their stocking history (Treatment – Y: lake with fish; Treatment – N: lake without fish; Treatment – E: lake treated for fish eradication), sampled at different depths (Depth - surface = 0.05 m; Depth - bottom = 1.5 m), and for a variable number of days (Day). Samples were collected in 2013 from 113 surface vs. benthic pairs of traps in 10 lakes of the Gran Paradiso National Park (Italy). Significant p-values (pMCMC) are presented in bold.

Factor		Post-mean	95%CI	pMCMC
Day		0.13	0.05 - 0.25	< 0.05
Depth	(bottom vs. surface)	0.28	-0.27 - 0.77	0.1
Treatment	E vs. N	-1.67	-5.04 - 0.86	0.2
	E vs. Y	-0.33	-3.88 - 2.11	0.8
	N vs. Y	0.48	-3.22 4.93	0.8
Treatment:Depth	E vs. N	0.66	0.21 - 1.56	< 0.05
	E vs. Y	-0.21	-1.94 - 0.41	0.9
	N vs. Y	-0.41	-1.17 - 0.43	0.8

828 **Table 4** Number of lake-dwelling brook trout belonging to different size classes removed at
829 the end of an eradication campaign in four alpine lakes of the Gran Paradiso National Park.
830 1693 and 9 additional brook trout were removed by electrofishing from the tributaries of
831 Lakes DRE and DJO.

Lake	DJO	DRE	LEY	NER
Lake dwelling brook trout				
Class 1 (< 15 cm)	447	10739	898	18
Class 2 (≥ 15 cm and < 20 cm)	113	738	434	1
Class 3 (≥ 20 cm and < 25 cm)	683	1213	1781	14
Class 4 (≥ 25 cm)	159	802	69	167
Not available	3	36	261	1
TOTAL	1396	13528	3444	201
TOTAL × m⁻²	0.108	0.585	0.077	0.012

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Draft

Table 5 Diet of *Salvelinus fontinalis* belonging to size classes 1-4 (from <15 cm to ≥ 25 cm at 5 cm intervals) from alpine lakes in Gran Paradiso National Park. N: number of analyzed stomachs; $\bar{N}$: mean prey number per stomach; F%: frequency of occurrence of the prey groups; A%: percent relative abundance of the prey groups; $\bar{V}$: mean biovolume per stomach.

	Class 1				Class 2				Class 3				Class 4			
	$\bar{N}$	F	A %	$\bar{V}$	$\bar{N}$	F	A	$\bar{V}$	$\bar{N}$	F	A	$\bar{V}$	$\bar{N}$	F	A	$\bar{V}$
	N=	122	122	22	44	44	44	54	68	68	68	75	72	72	72	85
Prey groups																
1. AQUATIC MICROCRUSTACEANS	26.9	45.1	34.8	0.0	-	-	-	-	40.7	7.4	14.6	0.04	43.5	1.4	34.4	0.0
2. AQUATIC INVERTEBRATES	49.4	88.5	63.8	0.1	86.5	88.6	95.7	0.3	216.7	83.8	77.7	0.5	26.3	68.1	20.8	0.2
3. TERRESTRIAL ARTHROPODS	6.1	53.3	7.92	0.1	3.9	59.1	4.2	0.1	21.7	82.4	7.8	0.5	56.6	87.5	44.7	1.7
3.1 Group 1	1.0	27.8	1.3	0.1	2.0	47.7	2.2	0.1	7.9	72.1	2.8	0.3	25.2	84.7	19.9	0.9
Terrestrial Coleoptera	0.9	27.0	1.1	0.0	1.9	43.1	2.1	0.1	7.5	69.1	2.7	0.3	21.2	77.8	16.8	0.8
Orthoptera	-	-	-	-	-	-	-	-	0.0	1.4	0.0	0.0	0.0	2.8	0.0	0.0
Lepidoptera	-	-	-	-	-	-	-	-	0.1	1.4	0.0	0.0	-	-	-	0.0
Terrestrial Hemiptera	0.1	4.1	0.2	0.0	0.0	2.3	0.0	0.0	0.2	5.9	0.1	0.0	3.2	16.7	2.55	0.0
Collembola	0.0	0.8	0.0	0.0	-	-	-	-	-	-	-	-	-	-	-	-
Aranea	0.0	0.8	0.0	0.0	0.0	2.3	0.0	0.0	0.0	1.4	0.0	0.0	0.1	5.6	0.0	0.0
Miriapoda	-	-	-	-	-	-	-	-	-	-	-	-	0.0	1.4	0.0	0.0
3.2 Group 2	0.0	2.4	0.0	0.0	0.0	2.3	0.0	0.0	0.2	11.8	0.1	0.0	0.4	13.9	0.32	0.0
Plecoptera, i	0.0	1.6	0.0	0.0	0.0	2.3	0.0	0.0	0.2	7.4	0.1	0.0	0.3	6.9	0.3	0.0
Tricoptera, i	0.0	0.8	0.0	0.0	-	-	-	-	0.1	4.4	0.0	0.0	0.1	6.9	0.1	0.0
3.3 Group 3 (Diptera/Hymenoptera)	5.1	44.3	6.5	0.1	1.9	34.1	2.1	0.0	13.6	61.8	4.9	0.2	31.0	77.8	24.5	0.8
4. VERTEBRATES	-	-	-	-	-	-	-	-	0.0	2.9	0.0	0.0	0.1	9.7	0.1	0.9

838 **Figure legends**

839 **Fig. 1** Map of the Gran Paradiso National Park - GPNP (A), its location on the Alps (B), and
 840 location of the study lakes. Triangles: “eradication lakes”; dark circles: lakes containing
 841 brook trout (*Salvelinus fontinalis*); pale circles: naturally fishless lakes; small circles: additive
 842 lakes for the sampling of brook trout diet analysis.

843 **Fig. 2 A:** Plan and side elevation view of a funnel trap consisting of an inverted cone made of
 844 plastic net (1 mm mesh size) and ending in a bottle, dotted lines indicate alignment; B: paired
 845 benthic and surface funnel traps (traps plot; B) used to estimate the number of sinking
 846 arthropods and the proportion of terrestrial arthropods reaching the lake bottom.

847 **Fig. 3** Water temperatures and insect categories used to test the underwater timing of
 848 decomposition of terrestrial arthropods in Lake DRE.

849 **Fig. 4** Comparison between number/biomass of sinking arthropods and daily CTA
 850 (Consumption of Terrestrial Arthropods) and BCTA (daily Biomass of Consumed Terrestrial
 851 Arthropods) ranges in four populations of brook trout inhabiting high altitude lakes. Solid
 852 lines: mean $\pm$ 95% CI number/biomass of sinking arthropods; grey bars: CTA/ BCTA ranges.

853 **Fig. 5** Example of arthropods subsidy mediated by a fish predator (black arrows) or not (grey
 854 arrows). Input and output pathways for terrestrial arthropods include: arthropods falling from
 855 the littoral area (Input1), drifting on the tributaries surface (Input2), or in their water column
 856 (Input 3), aerial plankton falling into the lakes (Input4), alive arthropods leaving the lakes
 857 from the surface (Output1) or when reaching the shore (Output2), dead arthropods washed
 858 out to the land (Output3), and drifting arthropods leaving the lakes from the outflowing rivers
 859 (Output 4). Arthropods from Input3 and a fraction of those from 1,2, and 4 sinks to the lakes
 860 bottom (S1 and S2) or is consumed by fish (F2 and F3), together with some arthropods
 861 drifting on the lakes surface (F1). Metabolic wastes include a fraction of particulate matter
 862 which sink to the bottom (S3) and soluble excretes (E) which dissolve in the water column.

Map of the Gran Paradiso National Park - GNP (A), its location on the Alps (B), and location of the study lakes. Triangles: "eradication lakes"; dark circles: lakes containing brook trout (*Salvelinus fontinalis*); pale circles: naturally fishless lakes; small circles: additive lakes for the sampling of brook trout diet analysis.

300x237mm (300 x 300 DPI)

Fig. 2 A: Plan and side elevation view of a funnel trap consisting of an inverted cone made of plastic net (1 mm mesh size) and ending in a bottle, dotted lines indicate alignment; B: paired benthic and surface funnel traps (traps plot; B) used to estimate the number of sinking arthropods and the proportion of terrestrial arthropods reaching the lake bottom.

254x243mm (300 x 300 DPI)

Water temperatures and insect categories used to test the underwater timing of decomposition of terrestrial arthropods in Lake DRE.

146x47mm (300 x 300 DPI)

Fig. 4 Comparison between number/biomass of sinking arthropods and daily CTA (Consumption of Terrestrial Arthropods) and BCTA (daily Biomass of Consumed Terrestrial Arthropods) ranges in four populations of brook trout inhabiting high altitude lakes. Solid lines: mean ± 95% CI number/biomass of sinking arthropods; grey bars: CTA/ BCTA ranges.

89x73mm (300 x 300 DPI)

Fig. 5 Example of arthropods subsidy mediated by a fish predator (black arrows) or not (grey arrows). Input and output pathways for terrestrial arthropods include: arthropods falling from the littoral area (Input1), drifting on the tributaries surface (Input2), or in their water column (Input 3), aerial plankton falling into the lakes (Input4), alive arthropods leaving the lakes from the surface (Output1) or when reaching the shore (Output2), dead arthropods washed out to the land (Output3), and drifting arthropods leaving the lakes from the outflowing rivers (Output 4). Arthropods from Input3 and a fraction of those from 1,2, and 4 sinks to the lakes bottom (S1 and S2) or is consumed by fish (F2 and F3), together with some arthropods drifting on the lakes surface (F1). Metabolic wastes include a fraction of particulate matter which sink to the bottom (S3) and soluble excretes (E) which dissolve in the water column.

438x251mm (300 x 300 DPI)