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Spatial distribution of introduced brook trout *Salvelinus fontinalis* (Salmonidae) within alpine lakes: evidences from a fish eradication campaign

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Abstract
Brook trout *Salvelinus fontinalis* have been used worldwide to stock fishless alpine lakes, negatively affecting native biota. Understanding its spatial ecology in invaded ecosystems can provide information to interpret and contrast its ecological impact. We opportunistically used capture points of brook trout gillnetted during an eradication campaign to assess the distribution patterns of four unexploited populations inhabiting high-altitude lakes. The main eradication method implies the use of many gillnets with several mesh sizes, which are selective for different fish sizes. For each lake we drew six capture maps associated with as many different mesh sizes, and we tested whether the distance from the coastline (which in alpine lakes is a reliable proxy of the most important spatial gradients, e.g. depth, temperature, prey availability, lighting conditions) influences the proportion of captured fish belonging to different size classes and the number of fish captured by the nets with different mesh sizes. To interpret the results, we also provide a cartographic description of the lakes' bathymetry and littoral microhabitats. We found (1) a negative relationship between brook trout distribution and the distance from the coastline in all of the size classes, lakes and mesh sizes; (2) that large brook trout can thrive in the lakes' center, while small ones are limited to the littoral areas; and (3) that the distance from the coastline alone cannot explain all the differences in the catch densities in different parts of the lakes. As in their native range, introduced brook trout populations also have littoral habits. Microhabitats, prey availability and distance from the spawning ground are other likely factors determining the distribution patterns of brook trout populations introduced in alpine lakes. The obtained results also provide useful information on how to plan new eradication campaigns.

Keywords: *Intensive gillnetting, kernel density estimation, Gran Paradiso National Park, Bioaquae LIFE+ project*

Introduction

Brook trout (*Salvelinus fontinalis* Mitchill, 1814) is native to Eastern North America (Behnke 2010). However, its historical native range has been drastically reduced due to habitat loss and introduction of alien species (EBTJV 2006). On the other hand, as early as 1850, brook trout spread outside its native range through both institutional and illegal introductions, under the rising demand of recreational anglers (García-Berthou et al. 2005). Many stocked populations became viable and self-sustaining. Currently brook trout has been introduced worldwide in many alpine, boreal and austral aquatic habitats (FishBase 2016), where it can exert a negative ecological impact on the native vertebrate and invertebrate communities (Knapp et al. 2001). On the whole, within its native range brook trout suffers the problem of non-native species introduction (EBTJV 2006), while out of its range it is considered one of the most impacting alien fish (Savini et al. 2010).

Brook trout inhabit a wide variety of waters. They thrive in lakes, streams, large rivers and estuarine areas (FishBase 2016) and they flourish in alpine

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waters, where they can reach high densities, even if often stunted in size (Hall 1991).

From a conservation point of view, a better understanding of the spatial ecology of brook trout within lakes is an important achievement in the case of both native and introduced populations. In the former case, understanding the habitat use of residual populations is important to address their conservation (Mucha & Mackereth 2008); in the latter, better knowledge of how they thrive in invaded habitats can provide information to interpret and contrast their ecological impact.

In general, studies on the spatial ecology of brook trout are biased toward habitat use of stream-dwelling brook trout in their native range (e.g. Chisholm et al. 1987; Baird & Krueger 2003). Similar studies, focusing on brook trout dwelling either in lakes or outside its native range, are rare or lacking. There are some studies on the distribution of adult brook trout in large and small lakes within its native range (e.g. Lackey 1970; Bourke et al. 1997; Newman et al. 1999; Moore 2008; Mucha & Mackereth 2008; Robillard et al. 2011); some others are limited to the young-of-the-year (YOY) habitat use (e.g. Snucins et al. 1992; Biro 1998; Borwick et al. 2006; Biro et al. 2008) or to the reproductive habitat requirements (e.g. Blanchfield & Ridgway 1997; Armstrong & Knapp 2004).

Our meager understanding of the spatial ecology of brook trout in invaded ecosystems represents a relevant gap of knowledge when the aim is understanding and contrasting the many ecological impacts produced by this species. In particular, a substantial number – the majority, in many regions – of the high-altitude and boreal lakes have been stocked with non-native fish (Bahls 1992; Knapp et al. 2001; Miró & Ventura 2013, 2015), which are likely to be the major direct anthropogenic stressor in these habitats (Pister 2001). Here, a substantial portion of river basins lie upstream of natural barriers to fish colonization, where many peculiar aquatic species and communities can find a fishless refuge (Adams et al. 2001). These species evolved in the absence of fish predation and have a low resistance to introduced fish (Knapp et al. 2001), therefore deserving special attention from a conservation point of view (Kernan et al. 2009). Brook trout is known to be a particularly aggressive invader, producing dramatic ecological consequences in invaded headwater habitats where it serves as a top predator (Knapp et al. 2001). Its introduction in fishless lakes is commonly associated with extirpation or reduction of native species (e.g. invertebrates and amphibians) and can have indirect effects on the whole ecosystem, on its linkage with the surrounding terrestrial habitats (Eby et al. 2006 and references therein), and on the downstream aquatic habitats (Adams et al. 2001). Fishing and stocking bans are the most effective measures to stem the spread of non-native fish in mountain areas (Wiley 2003; Miró & Ventura 2013, 2015). Moreover, in the last 20 years, several eradication attempts using gillnetting and electrofishing have been successfully carried out both in lakes and rivers in mountain protected areas to reverse the effects of introduced fish (Knapp & Matthews 1998; Knapp et al. 2001; Parker et al. 2001; Hoffman et al. 2004; Granados et al. 2006; Pacas & Taylor 2015). Detailed knowledge of the brook trout distribution patterns could simplify future eradication attempts (e.g. focusing the gill-netting efforts in the most densely populated areas) and extend their applicability to a greater variety of ecosystems (e.g. increasingly larger lakes and longer river stretches).

The Gran Paradiso National Park (GPNP, Western Italian Alps) recently undertook an eradication campaign of brook trout from four high-altitude lakes, within the LIFE+ Project Bioaquae (Biodiversity Improvement of Alpine Aquatic Ecosystems, www.bioaquae.eu), aiming at reducing the negative ecological effects of introduced fish. Indeed, almost all of the post-invasion impacts mentioned above have been recorded also in the GPNP lakes (Tiberti & Von Hardenberg 2012; Magnea et al. 2013; Tiberti et al. 2014, 2016c). Brook trout was introduced in the 1960s in several high-altitude lakes of the GPNP. Even if only a few years later a strict fishing regulation was adopted and angling and fish stocking were banned from almost all of the GPNP territory, many of the introduced populations had already been established in several lakes. Considering that brook trout reach sexual maturity at 1–4 years (FishBase 2016), some tens of generations have succeeded one another since fish introduction, suggesting that the studied populations are well naturalized. The eradication methods used in the Bioaquae project (intensive gillnetting and electrofishing) are non-invasive, to minimize the effects on non-target species (aquatic invertebrates and semiaquatic vertebrates). These eradication methods enabled the authors to record the capture point of the fish with a good approximation, thus obtaining a picture of their distribution patterns in the invaded lakes. Moreover, the remoteness of the study lakes (at least a 1-hour walk from the nearest road), the GPNP fishing ban and an efficient surveillance service mean that the studied fish populations can realistically be considered unexploited (also considering unlikely or, in any case, very rare poaching episodes and the sampling mortality of the 2006–2012

monitoring campaign that preceded the eradication project; Tiberti et al. 2013) and therefore increase the interest in the studied brook trout populations. Indeed, studies on the ecology of unexploited fish populations are rare in the fisheries literature (Toetz et al. 1991).

Within this framework, the present study aims at describing the spatial distribution of introduced brook trout in four lakes treated for fish eradication, using both qualitative and quantitative data. In particular, gillnetting capture data are used to assess whether the proportion and the number of fish belonging to different size classes or captured in the nets with different mesh sizes are related to the distance from the coastline, which, in these relatively homogeneous habitats, is strongly related to the most important spatial/environmental gradients (e.g. depth, water temperature, light reaching the bottom) and to the availability of the potential prey. To support the interpretation of the obtained results, we also provide a cartographic description of the lakes' bathymetry and littoral microhabitats. Moreover, the present study aims to explain how the spatial ecology and abundance/biomass of introduced brook trout populations can affect the capture efforts that are needed to complete an eradication campaign, highlighting some potential factors strengthening/weakening the eradication strategy. This latter represents a topic of growing interest in the field of biological conservation (Drolet et al. 2014).

Methods

Assessment of study lakes and littoral microhabitats

The study lakes (Figure 1; Table I) are included in the GPNP, a protected area located between 45°25′

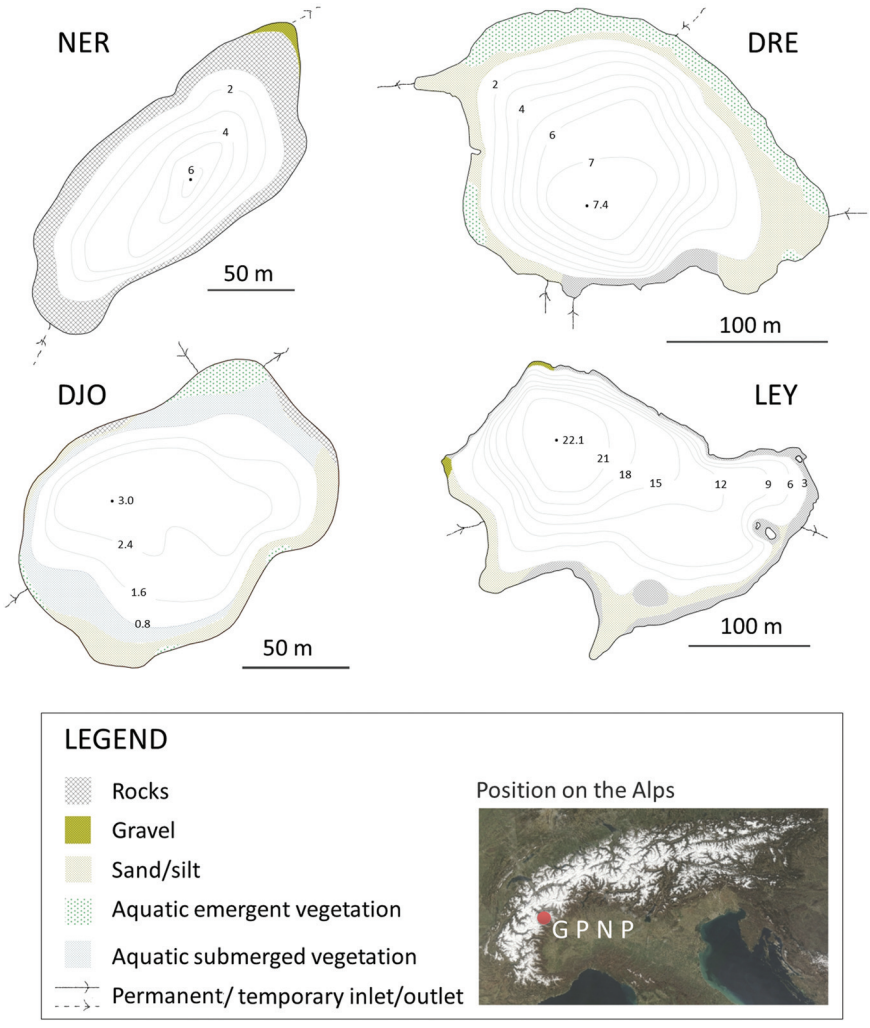

Figure 1. Bathymetries of the study lakes (from Tiberti et al. 2010), littoral microhabitats, and position of the Gran Paradiso National Park (GPNP) on the Alps.

Table I. Main geographic, morphometric and chemical data of the Gran Paradiso National Park studied lakes. Geology – AG: catchment entirely composed by acidic gneiss; CS: catchment dominated by thick covering of calcareous schists. TP: total phosphorus; *k*: photosynthetic active radiation (PAR) attenuation coefficient; DJO: Lake Djouan; DRE: Lake Dres; LEY: Lake Leynir; NER: Lake Nero. Averaged variables are expressed as mean ± standard deviation (SD).

	DJO	DRE	LEY	NER
Latitude N	45°33′27”	45°24′45”	45°30′28”	45°33′06”
Longitude E	07°10′43”	07°13′25”	07°09′08”	07°10′07”
Altitude (m)	2515	2087	2747	2671
Maximum depth (m)	3.0	7.4	22.1	6.0
Area (ha)	1.3	2.6	4.5	1.7
Catchment area (ha)	31	292	157	87
Geology	CS	AG	CS	CS
Maximum surface temperature (°C) [a]	19.0	16.0	12.5	15.0
k [b]	0.35 ± 0.08	0.29 ± 0.07	0.18 ± 0.04	0.20 ± 0.02
pH [c]	8.7 ± 0.4	7.0 ± 0.5	8.0 ± 0.3	8.0 ± 0.3
Total phosphorus – TP [c] (μg L^{-1})	3.5 ± 1.3	4.3 ± 2.5	3.0 ± 0.9	2.3 ± 1.6

[a] measured between 2006 and 2015, 1–4 measurements per ice-free season; [b] averaged over 11–18 measures between 2010 and 2015; [c] averaged over 22–25 measures between 2008 and 2015.

and 45°45′ N and between 7° and 7°30′ E in the Western Italian Alps. In this paper, toponyms of the lakes will be replaced by abbreviations: Djouan – DJO; Dres – DRE; Leynir – LEY; Nero – NER. The lakes are natural (non-dammed) and located above (DJO, LEY and NER) or across (DRE) the timberline. Thermal stratification occurs only in late summer in the deepest lake, LEY, whereas the other lakes are all polymictic. The lakes are well oxygenated throughout the water column during the whole ice-free season (Tiberti et al. 2010). The ice-cover period lasts for 7–9 months, usually, from October to June–July. All the lakes are fed by snowmelt and rainfall; they are oligotrophic and the water transparency is usually high (Tiberti et al. 2010). The GPNP has strictly prohibited recreational angling and fish stocking since the 1970s. However, fish introductions occurred before the fishing ban. With the exception of lake DRE, which was included in the GPNP only in 1979, all of the brook trout populations derived from a single stocking campaign in the 1960s. In lake DRE it is likely that legal and unauthorized fish stocking occurred also later.

Littoral microhabitats were assessed by visual inspection while walking/rowing along the lakes' perimeter. Five microhabitats were identified based on the dominant substrate: (1) rocks (clast diameter > 60 mm), (2) gravel (clast diameter ≤ 60 mm and > 4 mm), (3) sand/silt (clast diameter ≤ 4 mm), (4) areas covered by emergent (e.g. *Carex* sp. and *Eriophorum* sp.) and (5) submerged aquatic vegetation (even if a certain overlap between the last two categories could sometimes occur). Very small microhabitat patches were not mapped, even though the survival of entire brook trout populations can depend on very small (≈2 m^2) patches of suitable reproductive grounds (Armstrong & Knapp 2004).

Fish abundance and estimation of biomass

The number of fish captures was accurately recorded during the eradication process in all of the lakes (Table II). However, due to the poor conservation status of many captured fish and to the very large number of small fish captured during some capture sessions, it was sometimes impossible/impracticable to measure all of the fish with the same precision. Based on the quality of the measurements we distinguish the fish into:

- Group 1: 4762 brook trout (23.5% of the total number of fish captures) for which both the total length (accuracy ± 1 mm) and the body weight (accuracy ± 1 g) were recorded.
- Group 2: 9267 brook trout (45.8%) for which only the total length was recorded.
- Group 3: 5940 brook trout (29.3%) which were not accurately measured, but which were assigned to a size class (four classes from < 15 cm to ≥ 25 cm, at 5 cm intervals, Table II), e.g. when all the non-measured fish were YOY, they were assigned with certainty to size class 1.
- Group 4: 301 brook trout (1.5%) in very bad conservation status, for which there was no information about their size.

Due to these missing data, both measured and estimated weights were used to obtain a realistic estimate of the fish biomass removed from each lake. The length–weight relationships (data from Group 1) were estimated separately for each lake,

Table II. Number and estimated biomass (in brackets in kg) of brook trout belonging to different size classes caught with the fixed capture devices or with other methods. Data from four alpine lakes of the Gran Paradiso National Park. DJO: Lake Djouan; DRE: Lake Dres; LEY: Lake Leynir; NER: Lake Nero.

Lake	DJO	DRE	LEY	NER
Fixed capture devices				
Class 1 (< 15 cm)	206 (3.2)	4362 (57.4)	426 (6.8)	18 (0.2)
Class 2 (≥ 15 cm and < 20 cm)	112 (6.5)	593 (27.9)	425 (22.1)	1 (0.0)
Class 3 (≥ 20 cm and < 25 cm)	655 (65.2)	320 (33.9)	1744 (161.2)	14 (1.2)
Class 4 (≥ 25 cm)	149 (19.4)	114 (19.7)	68 (9.2)	161 (31.8)
Not available	2 (0.1)	31 (1.3)	261 (17.2)	1 (0.2)
Subtotal:	**1124 (94)**	**5420 (140)**	**2924 (217)**	**195 (33)**
Electrofishing, angling[a] and movable nets				
Class 1 (< 15 cm)	241 (1.3)	7809 (89.6)	472 (4.8)	0
Class 2 (≥ 15 cm and < 20 cm)	1 (0.1)	263 (13.7)	9 (0.5)	0
Class 3 (≥ 20 cm and < 25 cm)	28 (2.9)	997 (98.2)	37 (3.2)	0
Class 4 (≥ 25 cm)	10 (1.3)	727 (133.9)	1 (0.1)	6 (1.4)
Not available	1 (0.1)	5 (0.2)	0 (0)	0
Subtotal:	**281 (6)**	**9801 (335)**	**519 (9)**	**6 (1)**
TOTAL	**1405 (100)**	**15221 (476)**	**3443 (225)**	**201 (35)**
TOTAL × m^{-2}	**0.108 (0.008)**	**0.585 (0.018)**	**0.077 (0.005)**	**0.012 (0.002)**

[a] Two angling sessions were organized at lake DRE on 22 and 23 June 2015 to start the eradication (see Tiberti et al. 2016c).

fitting an exponential curve. For all the fish belonging to Group 2, the parameters of the equation of the curves were used to calculate their expected weights. These measured and estimated weights were subsequently used to calculate the mean weight of the fish belonging to each size class in each lake, and these means were used as an estimate of the weight of all the fish of Group 3. Finally, we used all the previous measured/estimated weights to calculate the mean fish weight in each lake, and these means were used as an estimate of the weight of all the fish of Group 4. This procedure enabled the direct measurement or estimation of the weights of all the captured fish, which were summed up to obtain an estimate of the total fish biomass removed from each lake.

Eradication methods and field-data collection

Intensive gill-netting and electrofishing were used as eradication methods (Knapp & Matthews 1998). In addition, 2 days of experimental intensive angling had already substantially contributed to the decline of the population in lake DRE just before the start of the eradication campaign (Tiberti et al. 2016b). Depending on the lake, the eradication actions started in June to August 2013. According to Knapp and Matthews (1998), the eradications can be considered concluded after 1 year without fish captures. At the present time (autumn 2016) this time has expired in lakes DJO (date of removal of the last fish: 14 June 2014 after 245 days from the settlement of the first net; date of removal of the nets: 17 June 2016), DRE (date of removal of the last fish: 11 August 2015, after 781 days from the settlement of the first net; nets will be removed in June 2017), and NER (date of removal of the last fish: 7 June 2015 after 696 days from the settlement of the first net; date of removal of the nets: 3 July 2016). While in Lake LEY this time has not yet expired, just one fish was captured during the 2015–2016 ice-cover season (fish removed on 5 June 2016, after 1095 days from the settlement of the first net). It would be necessary to wait for the 2017 ice-free season to confirm the completion of the eradication also in lake LEY. Two types of nets were used: (1) multi-mesh gillnets (36 × 1.8 m), divided into six panels (6 × 1.8 m) with increasing mesh sizes (10.0, 12.5, 18.5, 25.0, 33.0, 38.0 mm; with smallest mesh size panels placed close to shore); and (2) pelagic gillnets (from 36 × 1.8 m to 50 × 10 m) with a fixed mesh size = 25 mm, placed in the central part of the lakes. The nets were held vertically and fixed to the shore with ropes along several fixed transects, each bearing 1–6 nets. Their vertical displacement was regulated using floaters, but colonization by algae – making the nets heavier – sometimes changed their vertical displacement in an unpredictable way. Since their positioning, the nets were left in the lakes for the whole duration of the project, including the ice-cover season: during the summer they were usually positioned close to the surface, while just before the onset of the winter ice-cover they were moved deeper, to avoid them potentially being trapped in the ice. All these nets represent the fixed capture devices. Their position in the lakes was accurately mapped, and an individual

alphanumeric code (net ID) was assigned to each of them. During the 2013–2016 ice-free seasons, the fish were regularly removed from the nets from a dinghy rowing along the fixed transects. At the same time, electrofishing (with an ELT62 II 160 GI backpack equipment) and some additional movable multi-mesh gillnets were used – with different intensity depending on the lake features – in the littoral area (e.g. among littoral vegetation) or along the tributaries to support the eradication efforts.

The capture effort associated with each net belonging to the fixed capture devices varied in relation to their surface (each panel of the multi-mesh gillnets measures 10.8 m^2, but the surface of the pelagic gillnets ranged between 64.8 and 500.0 m^2) and to the fishing time. Indeed, settling the fixed capture devices in the lakes took 8–45 days (depending on the lake size: 8 days in lake NER, 15 in lake DJO, 41 in lake DRE, 45 in lake LEY). Therefore, the nets which were first settled had the chance to capture a larger number of brook trout, due to the longer fishing effort and to the high initial densities of the fish populations. On the contrary, the nets were or will be removed from each lake all at the same time. In the following analyses and in the preparation of the capture maps, these issues are fully taken into consideration (see below).

For each brook trout caught in the fixed capture devices, we recorded its length, the capture mode (wedged: held by the mesh around the body; gilled: held by the mesh slipping behind the operculum; tangled: held by teeth, maxillaries or other protrusions without the body penetrating the mesh), and the net ID, so that we were able to track a proxy of the location of the capture in the lake.

Limitations of an opportunistic sampling design

The capture data were opportunistically collected during an eradication campaign using a non-random sampling design. The nets were settled to maximize the capture efficiency and the majority of the nets with the smallest mesh size were placed near the shore, based on the eradication methodologies elaborated by Knapp and Matthews (1998) and on a preliminary study carried out in the GPNP (Tiberti et al. 2013). The interpretation of the results should therefore take into account this limitation. In particular, in smaller lakes DJO and NER, due to their geometry and size, the nets with the same mesh size are all settled at similar and short distances from the coastline. Therefore in DJO and NER the capture points with the same mesh size are distributed over a restricted gradient of distance from the coastline. When the aim is to test if there is a relationship between the distance from the coastline and the number of captured fish, such a small distance gradient increases the risk of type II errors (false negative). However, in the larger lakes DRE and LEY, this gradient is fairly large and the differences in the number of captured fish clearly reflect the brook trout distribution.

Due to the non-random distribution of the capture devices, we can provide capture maps (and not distribution maps). Moreover, the distribution analyses are based on gillnetting data from the fixed capture devices only, but a part of the fish populations was removed with alternative methods (electrofishing, angling from the shore, movable gillnets). However, all these methods can be used only in the littoral area and – since the results indicate that brook trout live mainly in the littoral area independent of their size – we concluded that removing part of the littoral fish populations with alternative methods can only weaken this general finding, which, however, remains rather clear alongside our study.

Fish capture mapping

Using the software QGIS 2.12 (QGIS Development Team 2015) and high-resolution satellite photos of the lakes, all fixed capture devices were accurately mapped. The photos were used to identify the exact position of the end of the nets–transects along the shoreline, while the position of the nets along the transects was identified measuring their distance from the end of the transects. This method demonstrated to be more accurate than the use of our GPS (Global Positioning System) device. The capture point of each fish was approximated to be the net/panel center. To highlight the relative density of fishes captured by the different mesh sizes, a density map was built, separately for each mesh size. In particular we used a kernel density estimation (KDE) method, starting from the fish capture points. In its raw definition, a KDE is a non-parametric estimate of the probability density function of a random variable (Silverman 1986). In ecology it can be used to define the home range of species (Fieberg 2007), or in general to identify areas where a punctiform phenomenon occurs with a higher probability. Here this method was used to obtain relative density maps, as a tool for graphically representing the zones within each single lake in which the nets had a higher capture efficiency. The functional shape and width of the kernel is determined by the smoothing parameter, or bandwidth, denoted generally by h (Kie 2013), and its choice is often a crucial point in home range analyses. To date many method have been proposed; KDEs can be adaptive (in which the

kernel bandwidth varies according to density) or fixed (same smoothing), and many statistical methods have been suggested to find the optimal bandwidth (Silverman 1986; Worton 1989; Gitzen & Millspaugh 2003). The present study is based on an objective approach, choosing a fixed KDE and a bandwidth that minimize the least-squares cross validation score (h_{lscv}) (Gitzen & Millspaugh 2003). This method frequently results in undersmoothing, i.e. it gives a KDE estimation, for example of home ranges, that consists of multiple and separate polygons (Kie 2013), so it was selected to highlight and emphasize the differences among mesh sizes. Since the nets were placed on different days and each panel had a different size, a weighting value for each capture point was added and calculated as follows:

$$1/\left(h \times s \times 10^{-6}\right),$$

where h is the number of hours that the net remained in place through the whole study period and s is the panel/net size, expressed in m^2. The density estimates were then standardized by dividing by the sum of the weight values. The analyses were performed using R v. 3.1.1 (R Development Core Team 2013) and the "ks" package (Duong 2016). A KDE was produced for each lake and for each mesh size as raster images that we used in QGIS to produce the relative density maps, scaled from 0 to 1.

Statistical methods

A series of linear regressions were used to test if the fish biomass per m^2 is related to the fish abundance per m^2 and to some important environmental variables (altitude, light attenuation coefficient – k, pH, and total phosphorus concentration – TP; Table I).

A simple size selectivity analysis was performed using a Kruskal–Wallis test to compare the length distributions of the fish captured with the different mesh sizes.

To describe the relationship between the brook trout distribution and the distance from the coastline we used both generalized linear mixed models (GLMMs) and general linear models (GLMs) in the statistical environment R v. 3.1.1 (R Development Core Team 2013): the former were implemented to provide an overview of the general distribution patterns of the brook trout belonging to the different size classes; the latter to provide details about their distribution within each lake.

We follow the indications of Crawley (2012) for GLMMs with proportion data to run four mixed models to test – separately for each size class – whether the distance from the coastline and the mesh size (fixed effects) affect the ratio between the number of brook trout captured in each net and the total number of brook trout (dependent variable) captured in each lake (random effect). To account for some differences related to the fishing effort we normalized the proportion data from each net using two offsets (multiplied together and log transformed): the surface of each net and a temporal factor equal to $(t_1 - t_2)/t_1$ ranging from 0 to 1, where t_1 is the number of days elapsed between the starting date of the eradication (first net settled) and the date of removal of the last fish, and t_2 is the number of days elapsed between the starting date of the eradication (first net settled) and the settlement of each net.

To provide more details about the previous models, 24 GLMs (one model per used mesh-size in four lakes) with a Poisson error distribution were used to test whether the number of fish captured in each panel/net depends on the distance of the nets from the coastline. The dependent variables were the cumulative numbers of fish removed between 2013 and 2016 from each net, while the distance of the net from the coastline (Distance) was added as covariate. To account for the same differences of fishing effort described above we normalized the count data using the same offsets.

Results

Microhabitat assessment

Littoral microhabitats are shown in Figure 1. Lakes DJO, DRE and LEY have permanent tributaries, while the tributaries of Lake NER are visible only during the thaw. Lakes DRE and DJO are characterized by the presence of abundant aquatic vegetation, which is absent in Lakes NER and LEY. Very small microhabitat patches were not mapped, but some very small patches of gravel and fine sediment can be found among the coarser sediments and rocks.

Brook trout abundance, biomass and length–weight relationship

Length–weight relationship and equations for brook trout in each lake are provided in Figure 2. The number and estimated biomass of brook trout captured in each lake were highly variable among lakes (Table II). Despite of the small sample size, the results of the linear regressions (equations and graphs reported in Figure 3) suggest a positive relationship between biomass per m^2 of captured fish, their abundance per m^2 ($F_{1,2} = 21.3$, $P < 0.05$), the

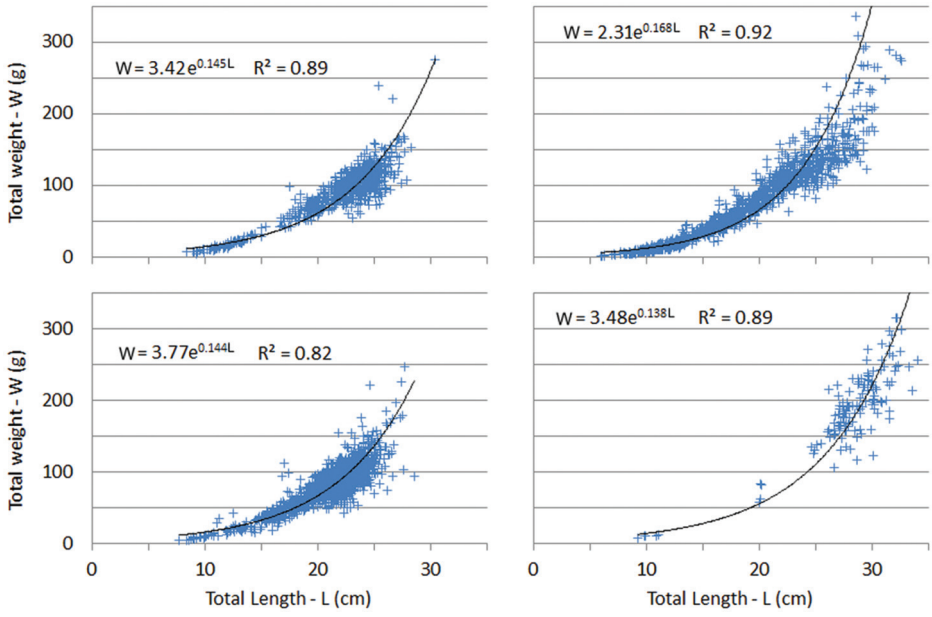

Figure 2. Length–weight relationship for brook trout in four alpine lakes of the Gran Paradiso National Park.

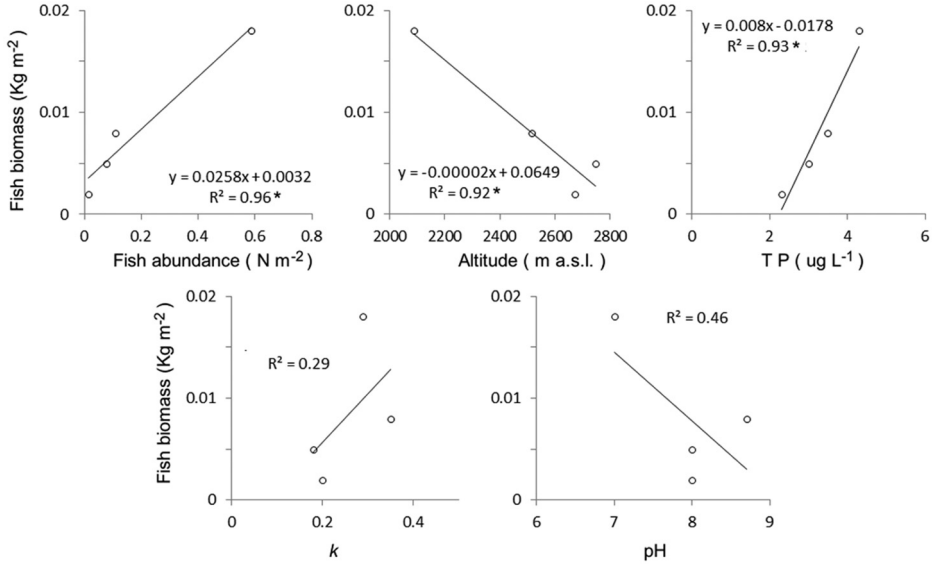

Figure 3. Linear regressions between brook trout biomass per m^2, fish abundance per m^2 and the main environmental variables (altitude, light attenuation coefficient – *k*, pH, and total phosphorus – TP). Equations are reported for significant linear relationships (*: $p < 0.05$).

lakes' altitude ($F_{1,2}$ = 12.5, P = 0.07) and the TP concentration ($F_{1,2}$ = 63.3, P < 0.05). In Lake NER the population was rather rarefied and strongly dominated by large fish, while in the remaining lakes the brook trout populations were clearly size structured. In lake DRE we captured a very large number of small brook trout and also four marble trout *Salmo marmoratus* Cuvier, 1829, one brown trout *Salmo trutta* L., 1758, and one minnow *Phoxinus* sp.

Size selectivity of the capture devices

In general, larger mesh sizes (33 and 38 mm) were inefficient and not very size selective. Notably, the few fish found in the larger mesh sizes were frequently

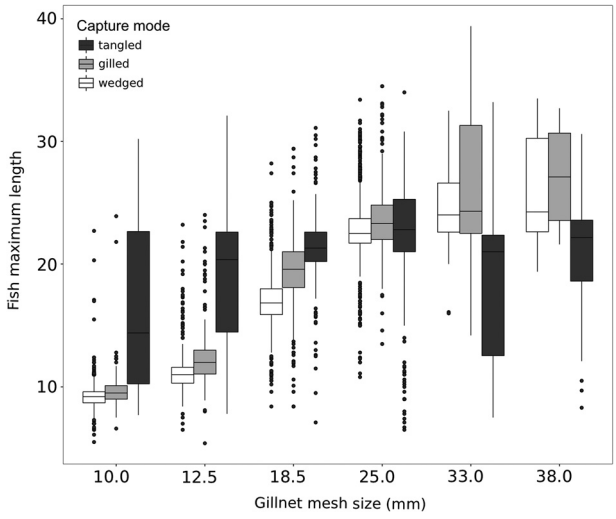

Figure 4. Length distribution of brook trout in relation to different gillnet mesh sizes and capture modes; data from four alpine lakes in the Gran Paradiso National Park.

tangled by the nets. The fish length distribution changed across nets/panels with different mesh sizes (Kruskal–Wallis test = 6.271, df = 5, $P < 0.001$; Figure 4), but pairwise comparisons showed non-significant differences in the length distribution in the larger mesh sizes (25, 33 and 38 mm). Also, the capture mode influenced the fish size distribution: Figure 4 shows that wedged fish are smaller than gilled fish and that both of these capture modes are strongly size selective, whereas the different mesh sizes are not very selective for tangled fish which shows a much larger size variability. A lake-by-lake breakdown of the capture frequency, size distribution and capture mode in each mesh size is also provided in the histograms of Figures 5 and 6. The fixed capture devices were unable to capture or inefficient in capturing the brook trout recently emerging in June–July from their redds (a spawning nest that is built by brook trout in the gravel of streams and lakes in autumn), whose size starts from 1.9 cm and which have been captured in large numbers with the electrofishing equipment (Table II).

Brook trout distribution

In Figures 5 and 6 we provide the capture maps. Since the nets (capture points) are usually spread all over the lakes (in particular in the larger lakes DRE and LEY), the capture maps can provide useful information on the distribution of brook trout populations. The areas with the highest capture densities are usually located around the capture points in the nearshore areas.

GLMM results (Table III) show that the proportion of captured fish belonging to all size classes is higher close to the coastline, and – as clearly shown in the histograms of Figures 5 and 6 – strongly depends on the mesh size. GLM results show that also the frequency of fish captures with all of the mesh sizes was negatively associated with the distance from the coastline, indicating that the catches were more likely near the shore (Table IV). However, this relation was not significant for the largest mesh sizes (18.5–38 mm) in lakes DJO, or for the smallest (10–12.5 mm) and larger (33–38 mm) in lake NER. Consistent with the model results and with the capture densities in Figures 5 and 6, small fish were only captured close to the coastline (authors' personal observation), while adult fish were also captured in the lakes' center, although they remain more abundant in the nearshore habitats.

On the basis of the observations performed during the electrofishing sessions, the distribution of the YOY brook trout was very localized in some very shallow littoral areas of lakes DJO, DRE and LEY (the northwestern rocks in lake DJO, all the permanent triburaries and the southern rocks of lake DRE, the two gravel areas in lake LEY; Figure 1), while in lake NER the brook trout population was skewed toward the larger size classes, and small brook trout and YOY were almost absent.

Discussion

There is a negative relationship between brook trout distribution and the distance from the coastline in all size classes (see GLMM results, Table III), lakes and mesh sizes (see GLM results, Table IV). Gillnets with mesh sizes from 10 to 25 mm were highly size selective (Figures 4–6). Therefore, the capture data from the nets bearing these mesh sizes provide a good approximation of the spatial distribution of the size classes that they preferentially capture. On the contrary, larger mesh sizes (33 and 38 mm) were too large to efficiently capture the relatively small brook trout belonging to the studied populations, resulting in a scattered size distribution of captured fish and providing distribution data which cannot be ascribed to any particular size class. These findings are consistent with those of studies of habitat use by lake-dwelling brook trout from their native range, which indicate that although this species may inhabit a range of depths, it is generally located in nearshore areas (Flick & Webster 1962; Lackey 1970; Newman et al. 1999; Mucha & Mackereth 2008). Curiously, because of this predilection, brook trout native to large North American lakes (e.g. Lake Superior, USA) were given the name "coasters" (Newman & DuBois 1997).

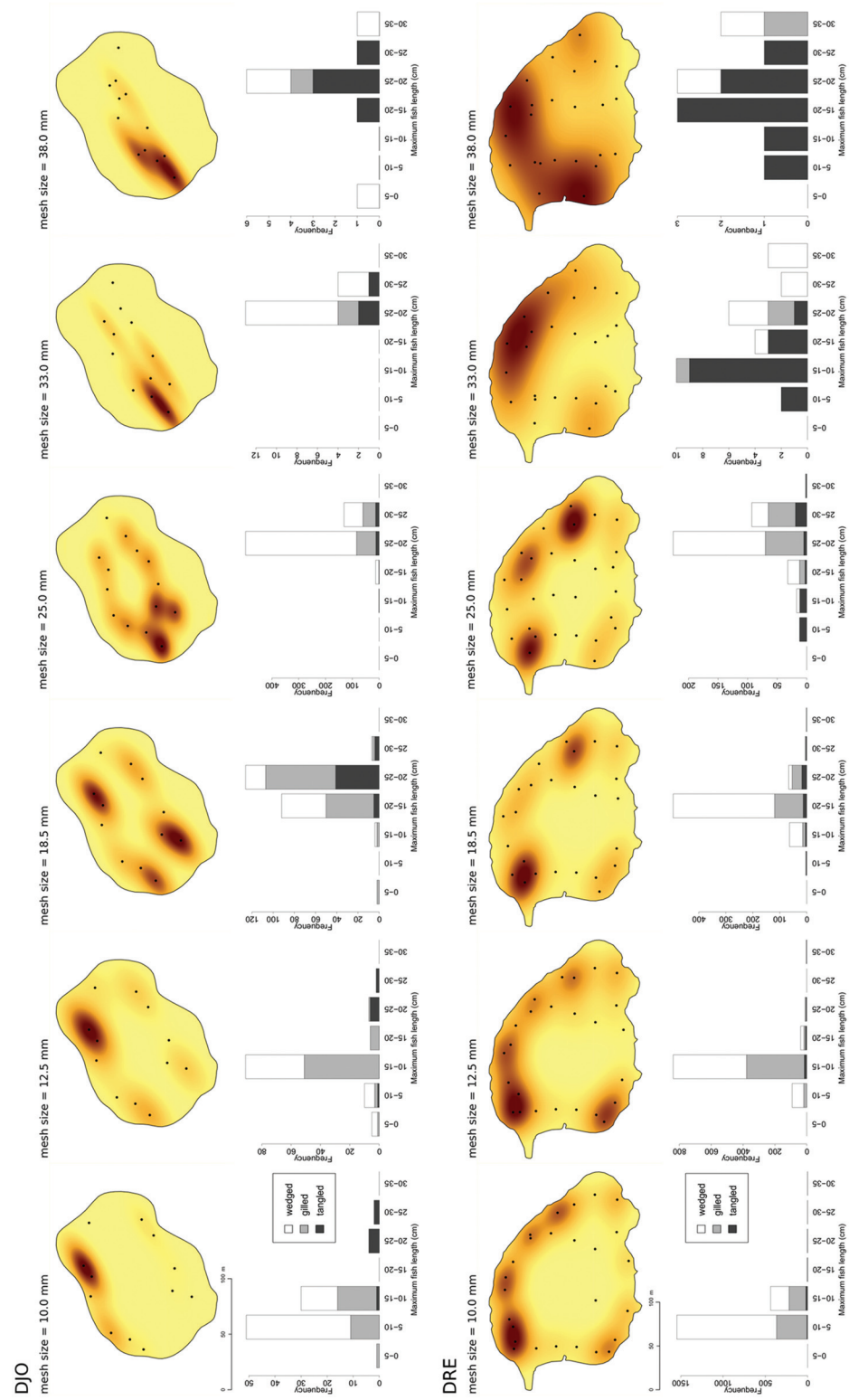

Figure 5. Lakes Djouan - DJO and Dres - DRE: capture maps and length structure of brook trout captured in each mesh size. Black dots indicate the capture points; high capture densities are indicated by darker tonalities.

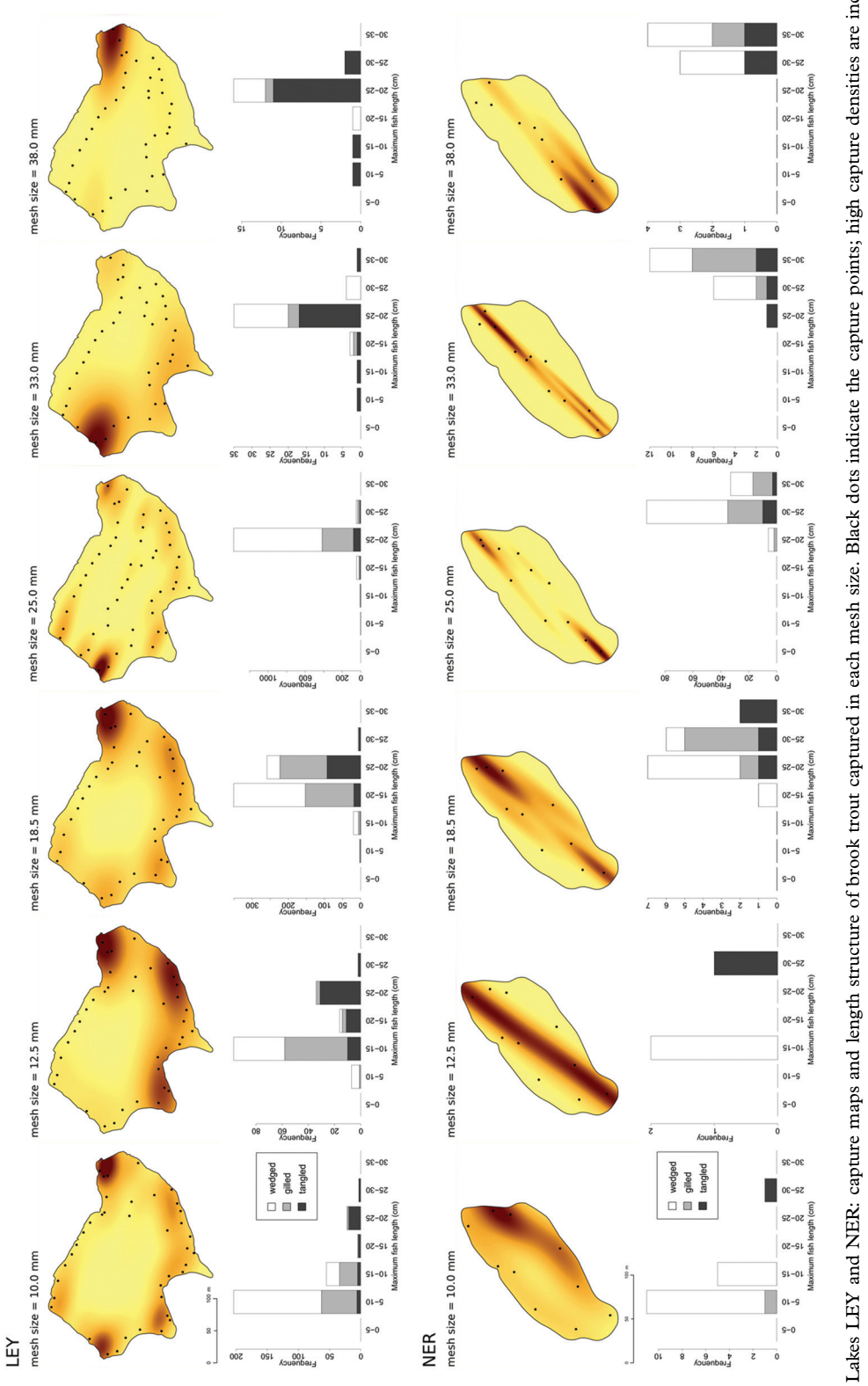

Figure 6. Lakes LEY and NER: capture maps and length structure of brook trout captured in each mesh size. Black dots indicate the capture points; high capture densities are indicated by darker tonalities.

Table III. GLMM results summary: influence of the distance from the coastline and mesh size on the proportion of fish belonging to size classes 1–4 captured in the nets settled for the eradication of brook trout in lakes Djouan - DJO, Dres - DRE, Leynir - LEY and Nero - NER (Gran Paradiso National Park); F value and significance level *p* are reported; Wald *Z*-score [=β/SE(β)] is provided only for continuous variables (distance from the coastline).

	Size class 1 (< 15 cm)			Size class 2 (≥ 15, < 20 cm)			Size class 3 (≥ 20, < 25 cm)			Size class 4 (≥ 25 cm)		
	Z	F	*p*	Z	F	*p*	Z	F	*p*	Z	F	*p*
Intercept	−16.1	-	< 0.001	−13.9	-	< 0.001	−14.8	-	< 0.001	−12.9	-	< 0.001
Distance	−24.1	758.8	< 0.001	−14.8	193.1	< 0.001	−37.7	1421.3	< 0.001	−15.5	239.0	< 0.001
Mesh-size	-	715.5	< 0.001	-	460.7	< 0.001	-	176.3	< 0.001		49.3	< 0.001

Table IV. GLM results summary: influence of the distance from the coastline on the number of fish captured in the nets with different mesh sizes settled for the eradication of brook trout in lakes Djouan - DJO, Dres - DRE, Leynir - LEY and Nero - NER (Gran Paradiso National Park); Wald *Z*-score [=β/SE(β)] and significance level *p* are reported.

	Mesh size											
	10 mm		12.5 mm		18 mm		24 mm		33 mm		38 mm	
	Z	*p*	*Z*	*p*	*Z*	*P*	*Z*	*p*	*Z*	*p*	*Z*	*p*
DJO	−2.60	< 0.01	−2.79	< 0.01	0.88	NS	−1.46	NS	−0.89	NS	−1.70	NS
DRE	−17.51	< 0.001	−9.37	< 0.001	−3.31	< 0.001	−16.03	< 0.001	−3.78	< 0.001	−2.67	< 0.01
LEY	−6.99	< 0.001	−6.64	< 0.001	−14.30	< 0.001	−33.68	< 0.001	−7.86	< 0.001	−5.30	< 0.001
NER	−0.81	NS	−0.99	NS	−2.84	< 0.01	−8.44	< 0.001	−1.47	NS	−1.74	NS

The study lakes are inhabited almost exclusively by brook trout. The origin of the few fish belonging to other species captured in DRE is probably related to illegal introduction and to the use of live baits by poachers. However, such a small number of fish cannot compete with the large *S. fontinalis* population inhabiting DRE and cannot alter its distribution patterns. Therefore all the observed distribution patterns are a typical feature of this species and are not attributable to the spatial competition with sympatric species, which is a potential factor influencing the habitat use of brook trout (Dewald & Wilzbach 1992; McGrath & Lewis 2007).

In these relatively small and homogeneous habitats, the distance from the coastline is strictly related to other important abiotic variables (e.g. depth, temperature, light reaching the bottom) and to the availability of the potential prey and refugia (e.g. littoral vegetation and shelters, or "dark", deep-water refugia). The preference of brook trout for littoral areas could be related to one or more of these gradients and – limited to smaller size classes captured with smallest mesh sizes – to the availability of spatial refugia against cannibalistic fish.

Temperatures are known to influence the habitat use of brook trout (Baird & Krueger 2003): for example, after ice-out brook trout tend to gather in very shallow nearshore areas, where they seek out the warmest conditions (Biro 1998), while as summer progresses brook trout are more concentrated in deeper areas, where they can avoid temperatures above their tolerance limits (Olson et al. 1988). For the same reason, brook trout can also use groundwater upwelling areas and the areas near the tributaries as midsummer thermal refugia (Biro 1998). However, the lakes under study are relatively cold ecosystems and the surface temperatures (Table I) never exceed the maximum thermal tolerance limit for brook trout (≈24°C; Wehrly et al. 2007). Only the shallow lake DJO, characterized by little thermal inertia, could approach this temperature limit during a limited time period. Therefore, temperature is likely just a secondary or very temporary factor influencing the distribution of brook trout in the study lakes.

A factor potentially explaining the observed distribution patterns is related to the feeding behavior of brook trout. The depth and depth-related lighting conditions depend on the distance from the coastline and are important factors influencing the ability of visual predators, such as brook trout, to locate their prey (Sweka & Hartman 2001; Marchand et al. 2002). All of the study lakes are very clear and the photic zone usually extends to the lakes' maximum depth (Tiberti et al. 2010). Whereas brook trout is able to maintain its prey-locating ability also at very

low light levels and can feed also during the nighttime (Forrester et al. 1994), it is likely that the lakes are largely devoid of "dark refugia" against fish predation. On the contrary, in cloudy lakes, the foraging areas can be limited to the surface and littoral waters (Sweka & Hartman 2003), therefore affecting the distribution of predatory fish.

On the other hand, food resources are known to be higher in the littoral zone than farther away from the coastline (in terms of diversity of benthonic macroinvertebrates, magnitude of terrestrial prey subsidy, and abundance of some aquatic or semi-aquatic vertebrate preys, i.e. both juvenile fish and common frog *Rana temporaria*; Vadeboncoeur et al. 2011). Prey availability and the generalist foraging strategy dominating in the study lakes (Tiberti et al. 2016a) could together explain the observed preference of brook trout for nearshore habitats. However, feeding specialization can occur in brook trout (Bourke et al. 1997). Due to their feeding specialization for pelagic prey groups, a fraction of the brook trout populations could show radically different distribution patterns. For example, some large pelagic zooplankton species (e.g. *Daphnia* sp., and *Cyclops* sp.) can provide important food resources (Dawidowicz & Gliwicz 1983) and the existence of zooplanktivorous brook trout morphs is well documented in the literature (Bertrand et al. 2008). These morphs thrive in the pelagic area but, since the brook trout populations are usually dominated by generalist individuals, the habitat use of specialized morphs can be highlighted only with individual-based studies (e.g. radiotracking; Mucha & Mackereth 2008) or with appropriate analyses to distinguish the fish morphs (morphological, dietary, parasitological and isotope analyses; Bertrand et al. 2008; Zimmerman et al. 2009). Our results are strongly influenced by the distribution of dominant, generalist individuals, and they probably miss highlighting possible deviations from the usual brook trout distribution patterns derived from the feeding specialization of some individuals.

A second major finding of the present study is that smaller fish are limited to the littoral areas while large brook trout can also thrive in the lakes' center. The multimesh gillnets of the fixed capture devices were little selective, but very small brook trout (approx. < 6 cm) were too small to be wedged/gilled in the nets. For these very small individuals there are just observational data, derived from the electrofishing sessions, which do, however, provide a fairly clear picture of their distribution. In general, (1) the YOY are confined in small and shallow areas or in the tributaries, probably very close to the spawning grounds (Biro et al. 2008); (2) small brook trout (approx. < 15 cm) are strictly littoral (with very few or no catches in the offshore capture points) as inferred by Tiberti et al. (2013); (3) larger fish can also thrive in pelagic areas, although they remain more abundant in the nearshore habitats. The distribution of YOY and small brook trout can be influenced by their little dispersion from the spawning ground, or by the predation risk confining small fish in littoral antipredatory refugia (e.g. rock shelters and aquatic vegetation). The distribution patterns of large fish could be a consequence of the displacement of brook trout [e.g. Mucha and Mackereth (2008) describe some offshore movements in otherwise littoral individuals] or of their feeding specialization (see Bertrand et al. 2008 and previous paragraph). The capture maps and the GLM results (Figures 5 and 6; Table IV) indicate that the lakes' geometry can influence the strength of these general rules, which are clearer in larger lakes (DRE and LEY) ideally partitioned into littoral and pelagic areas, while in smaller lakes the edge effect associated with the coastline probably affects the entire lake surface. Overall, it is clear that the fish size is a very important predictor of the habitat use and spatial ecology of lake-dwelling introduced brook trout.

The capture maps (Figures 5 and 6) indicate that the distance from the coastline is not the only factor influencing the catch densities in different parts of the lakes, and therefore the distribution of brook trout. Indeed, the capture densities around the capture points at similar distances from the coastline can be very different. This could be due to the effects – or interacting effects – of microhabitats, temperature, availability of antipredatory refugia, prey availability or proximity to the spawning ground. For example, the capture maps (Figures 5 and 6) strongly suggest that the distribution of brook trout in lake DRE is influenced by the littoral emergent vegetation (in the northern and south-western part of the lake's perimeter, Figure 1), probably providing an attractive shelter for small brook trout and a good feeding ground for both small and large fish.

Besides providing spatial distribution data, the eradication actions also provided an estimation of the total biomass and abundance of the brook trout populations, which are interesting parameters that have rarely been quantified with precision. The biomass of the brook trout populations is related to their abundance and to the TP concentration and altitude, which are related to the trophic and thermal state of alpine lakes. It is likely that, among the study lakes, the ones at lower altitudes and with higher nutrient availability levels

provide better physical conditions and more abundant trophic resources, which enable brook trout to reach considerable densities and biomasses. Overall, these distribution and biomass data provide basic autoecological information about one of the most harmful species used for stocking fishless alpine lakes and can be useful for everyone interested in the invasion and restoration ecology of these habitats, in particular when an eradication campaign is projected. Describing the distribution patterns of brook trout and quantifying their abundance and biomass enabled us to make some considerations which could simplify future eradication attempts in similar habitats. When deciding which lakes should be conveniently targeted for similar eradication actions, we suggest choosing small, oligotrophic, cold lakes, without aquatic vegetation, where the fish population is likely to be less abundant and the probability of a successful eradication is likely higher. Although very abundant populations (e.g. lake DRE) from relatively large lakes (e.g. lake LEY) can be successfully eradicated as well, in these cases it is necessary to put in place remarkable capture efforts; the data provided in the present study can help conservation authorities to intervene in the most cost-effective manner and to better predict the efforts needed to recover high-altitude lakes. When deciding where and how to place the capture devices in a particular lake, or where it is convenient to concentrate the eradication efforts, we suggest taking into account that: (1) as suggested by Knapp and Matthews (1998), when using multimesh gillnets, smaller mesh sizes should be placed nearshore; (2) the littoral area should be more intensively fished; (3) the use of large gillnets with an appropriate mesh size is an efficient alternative to the use of multi-mesh gillnets in the pelagic area; (4) the use of low gillnets with small mesh sizes along the nearshore habitats could control the density of young fish and avoid undesirable recruitment spikes; (5) concentrating the capture devices and efforts in the spawning areas could prevent reproduction; (6) concentrating the capture devices and efforts in proximity to or within particular microhabitats and shelters (e.g. aquatic vegetation) could be highly efficient.

This is the first time that an eradication campaign has been used to describe the distribution of lake-dwelling introduced fish. Compared to other methods for studying the distribution of fish, this method, which could be considered an exhaustive sampling of the entire fish population using gillnetting techniques (see CEN 2005), is particularly expensive (in terms of time, personnel and money). However, the issue of a rational use of resources does not arise in this case, since the eradication campaign was used as an opportunistic method to gather ecological data while pursuing a clear conservation goal, i.e. the lakes' restoration. This method has the same application limits as the eradication campaigns using gillnetting as the principal eradication technique. In particular, it can be used only when the entire fish community can be eradicated without concern for native fish. Compared to radiotracking (e.g. Mucha & Mackereth 2008), the present study does not provide an individual description of brook trout movements, habitat use and habitat specialization, but it has the merit to provide a unique picture of the brook trout distribution, comprising all the population, including juveniles, which cannot be tagged. Compared to hydroacoustic methods (e.g. Lucas & Baras 2000), the present study failed to describe brook trout vertical distribution (although this type of data could be achieved with an appropriate field data collection), but it overcomes some of the limits of these methods (e.g. difficulties in the location of the fish close to the lakes' surface and bottom, or in small water bodies such as high-altitude lakes; Lucas & Baras 2000).

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