

Review

The Italian Alpine and Subalpine Trouts. Taxonomy, Evolution, and Conservation

Gianluca Polgar ^{1,*}, Mattia Iaia ², Tommaso Righi ³, and Pietro Volta ⁴

Water Research Institute (IRSA)—CNR, Largo Tonolli 50, 28922 Verbania Pallanza, VB, Italy; mattia.iaia@cnr.it (M.I.); tommaso.righi@cnr.it (T.R.); pietro.volta@cnr.it (P.V.)

* Correspondence: gianluca.polgar@cnr.it or gianluca.polgar@gmail.com

Simple Summary: In a great part of the world, trout fishing has long inspired human spiritual ideals of immersion into nature and recreation, far removed from the fast-encroaching urbanization. Concurrently, these values and emotions fueled a white-heat business, establishing a florid market of outdoor recreation. Since the 20th century, the trout-culture industry strived to provide anglers with fishing entertainment by stocking massive amounts of non-native trouts in dozens of countries, irrespective of the lakes' and rivers' carrying capacity. This had dire consequences on the structural and functional diversity of these ecosystems. 'Trout wars' sparked throughout the world between the promoters of stocking activities and the promoters of 'wild trout management' and ethics. The 'Italian trout war' has been fought on the harsh battleground of trout taxonomy, ecology, distribution, and native vs. non-native interfertile species. Northern Italy, home to the Italian Alpine and subalpine trouts and economic center of the national trout-culture and stocking industry, was particularly affected by this clash. We review here the state of art of this ongoing debate, outlining our scientific view of the taxonomy, evolution, distribution, and sustainable management of the native Italian trouts of northern Italy.

Abstract: During the last 150 years, the trout-culture industry focused on enhancing trout populations by stocking, in response to the growing anglers' demand and the habitat degradation associated to the rapid urbanization and hydropower development. The industrialized north of Italy, home to the Italian Alpine and subalpine trout populations, is the source of most of the revenues of the national trout-culture industry. Its rapid growth and the massive introduction of non-native interfertile trouts eroded the genetic diversity of native lineages, leading to harsh confrontations between scientists, institutions, and sportfishing associations. We review here the state of art of the taxonomy and distribution of the northern Italian native trouts, presenting both scientific results and historical documentation. We think the only native trouts in this region are *Salmo marmoratus*, widespread in this region, plus small and fragmented populations of *S. ghigii*, present only in the Southwestern Alps. We strongly recommend the interruption of stocking of domesticated interfertile non-native trouts in this area, and recommend the adoption of Evolutionary Significant Units for salmonid fishery management. We further propose future research directions for a sustainable approach to the conservation and ecosystem management of the fishery resources and inland waters of northern Italy.

Keywords: Recreational fisheries fishery management; introgressive hybridization; stocking; non-native species; allochthonous species; trout fishing; trout taxonomy

1. Introduction: the global cultural value of trout and the 'trout wars'

In Europe, freshwater angling originated as subsistence and small-scale artisanal fisheries serving local markets, growing alongside sportfishing as early as in the Late Middle Ages, virtually becoming a synonym of trout fishing [1–3]. Analogous subsistence trout-fishing cultures also developed in hunting and gatherer societies, such as the Native American cultures [4].

Sportfishing and trout fly fishing greatly expanded during the 19th century, spreading throughout the world through European colonialism (America, Asia, Africa, Australia, New Zealand) and the rise of the nation-states, associating with cultural, economic, spiritual, and recreational values [3]. Artificial propagation was scientifically described and popularized in France in the 1840s–1850s. In the European imperialistic societies, highly interconnected by steamships and railroads, these propagation methods fueled a burgeoning outdoor recreation industry, i.e. the consumption of nature for leisure-class consumers [5]. This sporting culture gave rise to present-day fishery management and angling, making trout a globalized commodity through the introduction, acclimatization, and naturalization of non-native trout species provided by private and governmental associations. The European diaspora to other continents following World War I further accelerated this process. 'Salmonizing' became a synonym of acclimatization [6]. The first Italian hatchery was established in Piedmont in 1859 [7], and experiments of artificial propagation and acclimatization of non-native fishes, namely *Coregonus* and *Salvelinus* species from Switzerland and Germany, were conducted in several subalpine lakes during the 1860s–1890s [8]. Introductions and translocations accelerated with the establishment of the two Italian fishery centers in Brescia and Rome, in 1893–1895, with jurisdiction over the Padano-Venetian ichthyographic district and the rest of peninsular plus insular Italy, respectively [9,10]. Massive acclimatization and translocation activities (~12 billion fishes of different species, including 16 non-native species) were rapidly implemented in the following 50 years, slowing down after 1945 [10].

During the 20th century, the synergistic effects of the growing anglers' demand for more fish and the habitat degradation associated with urbanization increasingly impacted recreational fisheries. As a result, the goal of the fish-culture industry shifted from essentially seeding new self-sustaining non-native populations to enhancing the fish populations by stocking. This subsequently triggered dramatic conservation and management issues. Artificially stocking more manufactured fish than the ecosystems' carrying capacity and redefining nature as a play garden temporarily allowed to ignore the ongoing environmental damage [11]. Further, massive stocking of non-native trouts started to severely impact native assemblages, both ecologically and genetically, due to the widespread interfertility among salmonid taxa, e.g. [12].

In the 1960s, after World War II, alongside put-and-take fishery practices, the modern ecological movement and the concepts of wild trout management and ethics gradually developed in the USA, initially focusing on pollution, habitat degradation and fragmentation, and then extending to fishing regulations and restoration of wild native populations. Harsh confrontations between conservationists and advocates of stocking sparked everywhere, from USA to South Africa, being described as the 'trout wars' [3].

In Italy, stocking activities dramatically increased in 1970s, after the management of inland waters passed to the provinces in 1974 [9,10]. For at least the subsequent 25 years, stocking was conducted by few large aquaculture facilities. The largest one, located in the Veneto region, was widely used by several northern and central Italian provinces to stock massive amounts of several poorly-determined fish species from the Padano-Venetian province, vaguely defined "pesce bianco" (literally: "white fish" [9]). More recently, government compliance with European legislation [13] confirmed the prohibition to stock non-native fish species and populations into Italian waters, unless a site-specific environmental impact assessment demonstrates the lack of negative impacts on native species and environment [14,15]. The government proposed a reference list of Italian native and non-native species of interest in the fisheries sector. Among the non-native fishes there is

one of the world's worst invasive species, the Atlantic brown trout *S. trutta* Linnaeus 1758 [16], which has been the backbone of the stocking and sportfishing Italian industries for almost two centuries. Even more recently, an amendment to the national Budget law [17] has been proposed [18] to suspend the application of these laws [14,15] until 2023. A harsh conflict is taking place between stakeholders prioritizing the genetic and ecological diversity of native populations, mainly including fishery scientists plus some anglers and managers, and those prioritizing the exploitation of inland fisheries, mainly including fish culturist, anglers, sportfishing associations, the hydropower private sector, and the majority of province and regional administrations. This clash was particularly dramatic in the industrialized north of Italy, home to the Italian Alpine and subalpine trout populations, and source of most of the revenues of the national stocking and angling industries. This 'Italian trout war' also provoked heated debates on the taxonomic and genetic identity of the stocked trouts, e.g. [19], and on the native status of trout species, e.g. [20,21,22,23]. Since 5–10 years, several Italian fish-culture companies started to introduce massive amounts of non-native stocks of peninsular trout (section 2) in this and other regions. Such stocks are collected from several locations in peninsular and insular Italy, including domesticated progeny often hybridized with non-native Atlantic stocks [19]. These were sold as 'Mediterranean trout', e.g. [24], and currently advertised as a conservation-friendly alternative to the non-native Atlantic brown trout. Some authors also hypothesized the presence of viable native populations of a peninsular trout lineage (i.e., *S. cenerinus*; sections 2, 4).

On the other hand, the current global interest in trouts initiated environmental ethics and angler-driven conservation initiatives (e.g., Trout Unlimited in USA; Balkan Trout Restoration Group in Slovenia; numerous European LIFE projects). Shared attachment to place, characterizing a wide range of fish enthusiasts, from anglers to fishery scientists [3], could raise scientific awareness and foster collaboration among different stakeholders. This could develop global networks of multiple parties addressing issues such as sustainability, wild management, and transboundary conservation issues, such as climate change, pollution, and obstacles to fish movements (e.g., dams).

We review here the state of art of the taxonomy and evolution of the Italian trouts, clarifying our scientific view of these topics, and proposing future directions for a scientific approach to the conservation and ecosystem management of the fishery resources and inland waters of northern Italy.

2. Native Italian trouts and the taxonomy of the 'peninsular trout'

Among the valid nominal taxa [25] of the native trouts described in the Italian peninsula and the major Italian islands, *Salmo cettii* Rafinesque-Schmaltz 1810 was described from Sicily; type locality: Val Demone in northeastern Sicily and Val di Noto in southeastern Sicily, no types known [26]. *S. marmoratus* (Cuvier 1829) is a subendemism of northern Italy described from the "lacs de Lombardie"; syntypes not available [25,27] (section 3). *S. cenerinus* Nardo 1847 was described from northeastern Italy; type locality: not far from the sea, in rivers draining to the Venetian lagoon; no types known. The original description of *S. cenerinus* was provided in the early 1800s by S. Chiereghin, and published posthumously [28]; a summary of this description was first published by Nardo [29]. Several authors considered *S. macrostigma* (Duméril 1858) as an Italian trout; however, it was described from North Africa (type locality: Oued-el-Abaïch, Kabylie, Algeria [30]). *S. ghigii* Pomini 1941 was described from central Italy (type locality: Sagittario River; no types known [31]). *S. fibreni* Zerunian & Gandolfi 1990, described from the Lake Posta Fibreno in central Italy, and *S. carpio* Linnaeus 1758, described from Lake Garda, are restricted endemisms defined by ecomorphological and genetic traits [32]. The island of Sardinia might host an undescribed *Salmo* species [12].

The short description and illustration of *S. cenerinus* [29] may correspond to the pelagic morph of several anadromous *Salmo* species ([33,34], pers. obs). Nardo [35] modified his previous view [29], raising doubts on the original description of *S. cenerinus*, accepting

the view of [36] (cited as 1858 by [35]), and eventually considering this taxon as a synonym of *Trutta fario* L. (= *S. trutta*). Heckel and Kner [36] reported only two trout species from the Venetian Provinces: *Salar Ausonii* Valenciennes 1848 [37] (= *Trutta fario* L. sensu [35]) and *Fario carpio* (= *Trutta carpio* sensu [35]= *S. carpio*) from the Garda Lake. While *Salar genivittatus* Heckel and Kner 1858 was subsequently recognized as a morph of *S. marmoratus* [38], Heckel and Kner [36] considered *S. marmoratus* as a color morph of *Salar Ausonii*. Therefore, Nardo [35] likely considered the marble trout of this region as color morphs of *Trutta fario*.

Kottelat [38] assigned *S. cettii* to the native peninsular Tyrrhenian and southern Italian trout, including islands, and “tentatively” assigned *S. cenerinus* to the native north-Italian (Adriatic) peninsular trout. Consistently, he did not consider *S. cenerinus* as jun. syn. of *S. marmoratus*, since “there would be no available name for the present species and it should be either listed as *Salmo* sp. or a new name should be created for it”. Kottelat [38] also synonymized *S. ghigii* with *S. cettii* apparently only because Pomini [31] was unable to discriminate the trouts of the Sagittario River from the Sardinian trouts. Kottelat & Freyhof [39] accepted the point of view of Kottelat [38], while noting that “recent studies (...) suggest that the trouts of Sicily (...) belong to a distinct molecular lineage (...). If confirmed, this lineage should retain the name *S. cettii*; the name *S. ghigii* would probably be the valid name of the others”.

Using combined mitochondrial (mtDNA) and nuclear (nDNA) markers, Segherloo et al. [12] found a close relationship between the Sicilian trout of Val di Noto and Atlantic *S. trutta*. A consistent result was found by another nuclear phylogenetic study of the Moroccan trouts, which included the Sicilian trout of Val di Noto in a robust ‘Afro-Atlantic clade’, likely originated from a colonization wave of an Atlantic lineage from Iberia (Duero; [40]). The only North-African sample analyzed by Segherloo et al. [12], that these authors tentatively assigned to *Salmo pellegrini* Werner 1931, is closely related to Mediterranean and Adriatic brown trouts, thus clearly belonging to a different lineage; this sample comes from the Oum er-Rbia River, where Snoj et al. [40] identified trouts of an ‘Atlas clade’. Several studies showed that the Sicilian trout are morphologically distinct from other Italian trouts [30,41,42,43,44]. Mitochondrial phylogenies also show that the Sicilian trout is included in a clade of North-African trouts, also including the sequenced types of *S. macrostigma* [45] and the Atlantic lineage, called the “Southern Atlantic clade” [46,22]. However, no nuclear or combined mitochondrial and nuclear phylogenies were ever constructed including the types of *S. macrostigma*.

Rafinesque-Schmaltz [26] described *S. cettii* from two trout populations: Val di Noto and Val Demone. The molecular phylogeny of *S. cettii* has been investigated only using the former population, since no genetic samples have ever been collected and analyzed from the Val Demone, which has likely been extirpated [47]. The recovery and analysis of any such molecular sample (e.g. from a museum lot) would have important consequences on the scientific names of Italian trout lineages. There are 3 possible scenarios: (i) the Val Demone population belongs to an undescribed endemic trout lineage; (ii) the Val Demone population is conspecific with the peninsular trout; and (iii) the Val Demone and Val di Noto populations are conspecific (Figure 1).

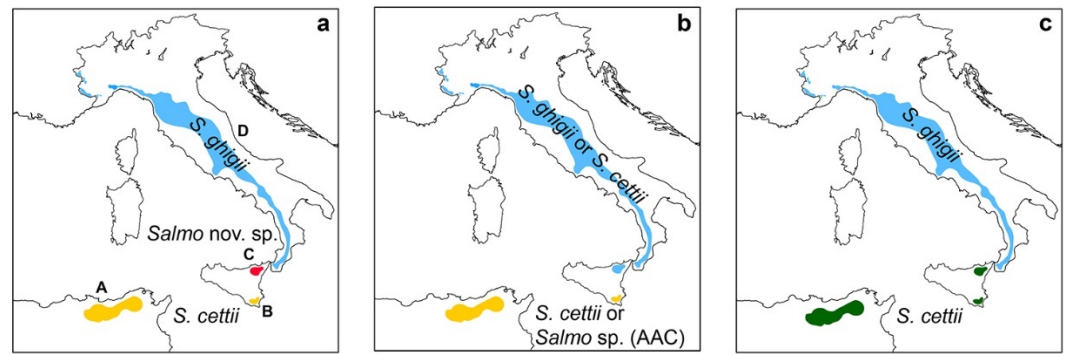


Figure 1. Three possible taxonomic scenarios (peninsular and Sicilian trouts, plus a North-African trout) if native trout samples are collected and analyzed from the Val Demone (no material presently available); **(a)** The native Val Demone population belongs to an undescribed and endemic lineage; **(b)** The native Val Demone population is conspecific with the peninsular trout; **(c)** The Val Demone and Val di Noto populations are conspecific. **A:** hypothetical distribution of a trout taxon of the 'Afro-Atlantic clade' (AAC), conspecific with the Val di Noto trout population [40]; **B** and **C:** Val di Noto and Val Demone populations, respectively, both described as *S. cettii* by Rafinesque-Schmalz [26]; the latter has likely been extirpated; **D:** peninsular trout, distribution range modified from [48]. No types are known for both *S. ghigii* and *S. cettii*. The taxon *S. cettii* is older than all North-African trout taxa [48].

In the first scenario (Figure 1a), the Val di Noto and the North-African Afro-Atlantic clade (sensu [40]) would be classified as *S. cettii* (older than any North-African trout taxon so far described [48]), the peninsular populations as *S. ghigii*, and the Val Demone population would belong to a new species that would require formal description. In the second scenario (Figure 1b), the collection of Rafinesque-Schmalz [26] contained 2 distinct taxa. In the absence of type material, it is arbitrary whether to assign either of the two sampled populations to *S. cettii*. Therefore, there are two possibilities: either (a) Val di Noto plus the North-African populations could be classified as *S. cettii*, and Val Demone plus peninsular populations as *S. ghigii*, or (b) Val Demone plus peninsular populations could be classified as *S. cettii*, and Val di Noto plus the North-African population (Afro-Atlantic clade, AAC [40]) as one of the four North-African *Salmo* species (including *S. macrostigma* [48]), or as a new and yet undescribed species. In the third scenario (Figure 1c), the Sicilian trout plus AAC would be *S. cettii*, and the peninsular populations would be *S. ghigii*. In the absence of material from the Val Demone, we adopt a classification consistent with the third and most parsimonious scenario.

With the limitation of substantial sample biases, several studies did not find genetic or ecological discontinuities between native northern (southwestern Alps [49]) and central-southern peninsular trout lineages that would justify the designation of different taxa, except *S. carpio* and *S. fibreni* [20,32,50,51,52,53,54]. Segherloo et al. [12] assigned trout samples of the Po and Isonzo basins (northern slope of the Italian Apennine range) to *S. cf. cenerinus*, and samples of the Zrmanja to Mornos basins (Balkan peninsula) to *Salmo farioides* Karaman 1938, in the same region of its type locality (Krka River, Croatia; no types available [55]; neotype designated by Bianco [56]). *S. cenerinus* was found in brackish conditions [28]; however, the only native Italian trout recorded in the sea is *S. marmoratus* [57]. Further, there presently are no known native populations (nor genetic signatures of past populations) of peninsular trout in the area where *S. cenerinus* was described. On the other hand, anadromous non-native populations of *S. trutta*, including hybrids, are known to occur in the Adriatic region, including Italian waters [58,59]. Consequently, the hypothesis that the trout described by Chiereghin was a pelagic morph of *S. trutta* cannot be ruled out, since several fish-culture projects were active in this region in the second half of the 19th century [35]. Borroni and Grimaldi [8] just reported that introductions of non-native *S. trutta* had been occurring "for decades" in Italy in the '70s. Bianco and Delmastro [60] and Bianco [56] synonymized *S. marmoratus* and *S. cenerinus* based on the illustration of *S.*

cenerinus, its anadromous habits [28,29], and information gleaned from Gridelli [61], who reported only the presence of the marble trout in the Venezia Giulia region, previous to stocking activities of non-native brown trouts. Gridelli [61] who reported the presence of the marble trout as the only trout species in the Venezia Giulia region, previous to stocking activities of non-native brown trouts, which started in 1934. However, Nardo's [29] Venetian Provinces of the 1850s (type locality of *S. cenerinus*) are geographically distinct from the Venezia Giulia region of the 1930s [62]. Bianco [56] synonymized *S. ghigii* with *S. farioides*, however: (i) no neotype of *S. ghigii* was designated, likely due to the difficulty of finding 'purebred' individuals in the type locality; (ii) no molecular analyses were conducted; and (iii) the synonymy was essentially based on coloration patterns and biogeographical reconstructions. Therefore, we choose not to consider *S. ghigii* as a junior synonym of *S. farioides*. As a result, until further genetic and ecological data are made available on Tyrrhenian and Adriatic native Italian trouts, we choose to consider *S. cenerinus* as jun. syn. of *S. marmoratus* sensu Bianco [56] and *S. ghigii* as a valid name for all the populations of Italian peninsular trout, sensu Zanetti et al. [63] and Lorenzoni et al. [64].

3. Phylogeny and phylogeography of *S. marmoratus*

Nuclear phylogenetic reconstructions and molecular clocks defined a robust *S. marmoratus* clade, including two distinct northern and southern Adriatic clades that diverged $\sim 0.84 \pm 0.4$ million years ago (mya) [65,66], and whose taxonomic status has not yet been evaluated. *S. marmoratus* is closely related to a '*S. trutta* complex' lineage, including several clades associated with different brown-trout taxa [66]. These latter authors estimated the divergence between these two lineages at 1.4 ± 0.8 mya ($2.2\text{--}0.6$ mya). A fossil-calibrated nDNA phylogeny estimated an earlier divergence, at $\sim 4\text{--}5$ mya [67]. An extensive molecular phylogeny combining nDNA and mtDNA sequences rooted with *S. salar*, essentially consistent with previous nDNA phylogenetic reconstructions, supported *S. marmoratus* as a phylogenetic species of possibly hybrid origins, sister to a clade including >20 *Salmo* species [12].

Northern Adriatic *S. marmoratus* populations are strongly associated with the 'Marmoratus' (MA) haplogroup of the mtDNA control region (D-loop) [22,68,69,70,71]. However, MA haplotypes have also been found in several brown trout taxa and populations of Greece, Albania, Croatia, Italy, and Corsica, e.g. [23,48,65,70] (section 4). Like several other brown trout taxa and populations, Southern Adriatic *S. marmoratus* populations are associated with the Adriatic (AD) mtDNA haplogroup [71].

Mitochondrial molecular clocks estimated much more recent origins of the MA and AD haplogroups ($0.21\text{--}0.05$ mya and $0.39\text{--}0.13$ mya, respectively, considering the 95% highest probability density intervals estimated using two different substitution rates [23]) than the time of divergence between *S. marmoratus* and the *S. trutta* complex. It was suggested that the observed mitochondrial-nuclear phylogenetic discordance might be the effect of incomplete lineage sorting or asymmetric introgressive hybridization (mtDNA capture; e.g. [72]). The much older time of divergence between these lineages relative to the time of haplogroup differentiation strongly supports the latter mechanism. Paleointrogressive hybridization between the marble trout and the Apennine Mediterranean trout could have occurred during several secondary contacts as a consequence of the expansion of the Po paleo-basin during glacial maxima, as it occurred in other *Salmo* species [22,32,53,59,65,73]. Mosaic distributions of mtDNA haplogroups among different taxa are common also in areas without a history of non-native trout's stocking (e.g., Albania [74]), and similar distributional and diversity patterns might have occurred in Italy after the Last Glacial Maximum (LGM $\sim 18,000$ years ago).

Phylogenetic patterns, molecular clocks and the zoogeography of congeners suggest that *S. marmoratus* is one of the *Salmo* lineages that diverged in the palaeo-Adriatic drainage, in freshwater refuges formed during the preceding Lago Mare phase (~ 5 mya). During the Pleistocene, reduced salinity, cooler sea temperatures, and extensive palaeo-river basins would have facilitated the westward dispersal of these freshwater lineages across

the region through multiple waves of colonization, bottlenecks, and secondary contacts [32,71,74], allowing *S. marmoratus* to colonize the orographic left tributaries of the palaeo-Po basin [56,75,76]. After the LGM, increased salinity levels and sea-level rise disconnected these populations, facilitating allopatric fragmentation and differentiation of mtDNA lineages, resulting in the present geographic distribution [32].

In the northern Adriatic basin, *S. marmoratus* exhibit a west-to-east geographic gradient in MA-s1 and MA-s2 haplotype distribution, consistent with the described stepwise westward migration and phylogeographic scenario [77]. Significant microgeographic genetic differentiation was also measured within basins, e.g. between rivers and their tributaries, suggesting the presence of limited gene flow among different populations [78,79]. A contact zone between *S. marmoratus* and *S. ghigii* was found in the Southwestern Alps (section 4).

4. Presence of *S. ghigii* in the Italian Alpine and subalpine region

Within the Italian Alpine region [80], viable native populations of *S. ghigii* (section 3) have only been found in the Southwestern Alps (Cottian and Maritime Alps, upper Chisone, Pellice, Po, Stura Demonte, Gesso, and Tanaro basins), where a contact zone with *S. marmoratus* was described [20,21,23,34,48,50,76,79,81,82]. The MA, AD and 'Mediterranean' (ME) haplotype probability densities relative to elevation show an altitudinal zonation suggesting local habitat differentiation between the two sympatric species, with *S. marmoratus* being dominant at 0–1000 m above sea level (asl) and *S. ghigii* at 1000–2000 m asl [23]. These findings are consistent with historical accounts [83,84,85]. The Southwestern Alps are a known glacial refuge, where native populations of *S. marmoratus* and *S. ghigii* could have survived the LGM [81]. Introgression rates of alien Atlantic genes into native trout populations are here highly variable (0–70%; [20]).

In contrast, in most of the Northwestern and Eastern Alps only the lower tracts of the rivers were unaffected by the ice cap during the LGM. Assuming that *S. ghigii* and *S. marmoratus* exhibited a habitat segregation pattern analogous to that presently observed in the Southwestern Alps, the LGM likely allowed the survival of *S. marmoratus* at lower altitudes, while *S. ghigii* might have been pushed into the marble trout habitat and out-competed [81]. Similarly, *S. marmoratus* can rapidly displace brown trout (*S. trutta fario* = *S. ghigii* or *S. trutta*) when restocking practices are interrupted [86]. After the glaciation, upper isolated habitats and headwaters may have only marginally been colonized by *S. marmoratus* and likely remained “fishless” (i.e., troutless), until being stocked with translocated trout by anthropogenic activities, e.g. [87–89]. Introductions and stocking dramatically increased in the 19th century, flooding these systems with non-native Atlantic *S. trutta*, e.g. [81]. Consistently, introgression rates of Atlantic *S. trutta* into *S. marmoratus* are consistently higher in this region, and only traces of the haplotypes associated with native *S. ghigii* were found [21,81].

In the Eastern Alps, mitochondrial variants typically associated with *S. ghigii* (AD and ME haplotypes [50,70]) have been found in the Lake Garda basin, a known glacial refugial area [90], where the past presence of native *S. ghigii* was also supported using a probabilistic approach [91]. These findings are also consistent with the presence of AD and ME haplotypes of *S. carpio*, a possible signature of a paleohybridization event that occurred in Lake Garda [20,23,50,53]. Also the analysis of several museum specimens collected in the second half of the 19th century revealed the presence of AD haplotypes, typically associated with *S. ghigii* in Lake Garda and Lake Maggiore (1877 and 1879, respectively), in specimens with a typical lacustrine phenotype [82]. Lake Maggiore is also known as a glacial refugium [90,92].

The allozymic variants LDH-C1*100 and TF*102 are considered diagnostic of Adriatic and other Mediterranean populations, being fixed in purebred trout populations native in France and northern Italy (*S. ghigii*: contact zone in the Southwestern Alps), and found at high frequency in Danubian native populations [49,93,94]. Largiadèr & Scholl [95] assumed the native status of an “Adriatic fario” in the Po basin, based on molecular

studies conducted in the contact zone [49] and on phenotypic studies that were however unable to discriminate between Atlantic (*S. trutta*) and Adriatic (*S. ghigii*) phenotypes [96]. These authors found these two allozymic variants at high frequency (~20%–30%) in Engadin (Danubian basin), in the Müstair, tributary of the Adige River, and in the Poschiavo valley (Po basin, Poschiavino Torrent, tributary of the Adda River); and at low frequency (~0%–10%) in the Ticino and Valais basins, including a tributary of the Diveria Torrent (Chrummbach); no ‘purebred’ individual were found. In fact, all these populations had been directly or indirectly (via Poschiavo hatcheries) either entirely replaced or heavily stocked with trout lineages of the Danubian basin for at least one century before the study collection [95]. This might explain the genetic similarities between the trouts of the Poschiavino and Ticino valleys, detected using microsatellite and AFLP markers to investigate the adaptive divergence and phylogeographic patterns of trout populations of the Rhine, Rhone, and Po basins [97,98]. Both these studies assumed the presence of Adriatic trout (*S. cenerinus*, sensu [39]) in the Poschiavino and Ticino valleys, based on the literature [39,95,96]. Given the lack of Danubian genetic references (allele size range), it is not possible to know whether the observed “Adriatic” signatures in the Poschiavino and Ticino valleys were originally present in this region, or were left by introduced Danubian stocks [97], as also suggested by the presence of Danubian haplotypes in the Ticino basin [77]. Both these studies also found evidence of introgression of the Poschiavo population into one Rhine population (SE). SE is the closest Rhine population to the Danubian drainage, suggesting the presence of stocking activities and translocations between SE, Poschiavo, and Danubian systems.

There are several descriptive accounts (cuisine recipes, anecdotes, poetry, and even paintings; e.g. [99]) of trouts in the Northwestern and Eastern Alps (e.g., Lakes Como and Garda basins) before the dramatic expansion of the stocking of northern European Atlantic *S. trutta* in the early 19th century (1850–1893, [10]), e.g. [100,101,102,103,104,105,106,107]. Several ones depict or describe trouts without a marbled coloration pattern and with either red and black dots phenotypically compatible with several trout taxa, or with speckled dark patterns on a silvery background, compatible with a generalized pelagic morph of anadromous trout. Adult *S. marmoratus* living in rivers typically exhibit a marbled coloration pattern [108]; however, anadromous individuals in pelagic conditions can exhibit a silvery and dark-speckled coloration pattern, even leading to taxonomic confusion, e.g. [109].

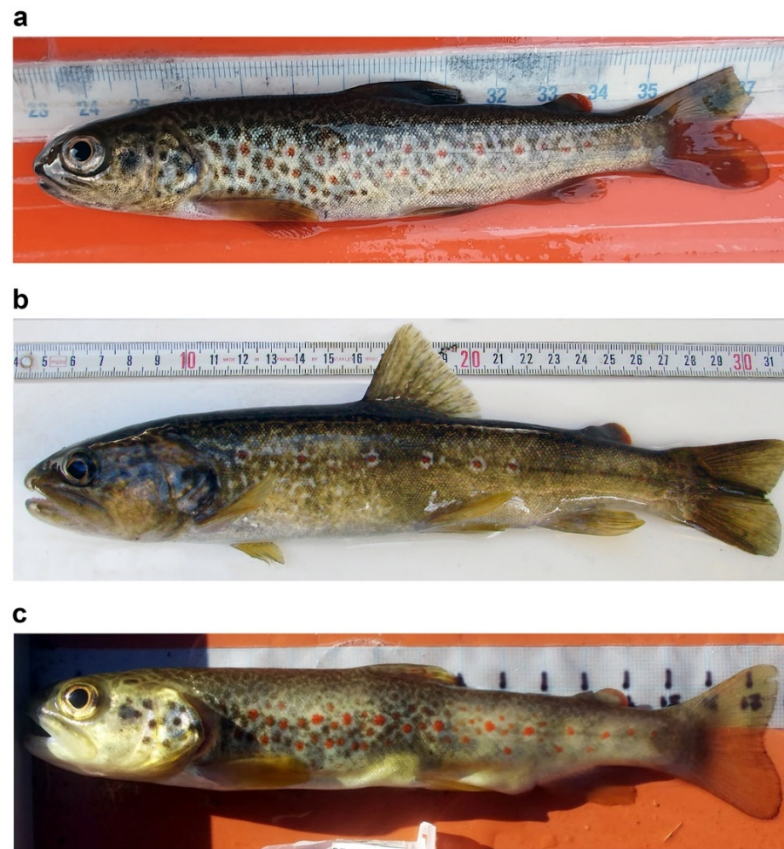


Figure 2. Examples of dotted coloration patterns in *S. marmoratus*: juvenile coloration pattern (a), and adults living in small and fast-flowing streams (b, c); **(a)** Juvenile from Roledo (Piedmont, Verbano-Cusio-Ossola: VCO; 46°10'16.7"N 8°18'49.7"E), 15.5 cm total length – TL, 29.0 g wet mass, 22 months of age, black-and-red dotted pattern, MA haplogroup, q_{Ma} 0.995 (admixture proportion of a cluster including purebred *S. marmoratus* references), 90% BCI 0.966–1.000; **(b)** Adult (reproductive) specimen from Rio Ischielle, tributary of the Avisio Torrent (Province of Trento); the specimen was collected from a population which resided for 2 generations in this small stream, and descended from hatchery-reared *S. marmoratus* collected from the Adige River [110]; 26.9 cm TL, courtesy of Leonardo Pontalti; **(c)** adult (reproductive) specimen from Rio della Balma, tributary of the Sangone River (Province of Torino), 18.5 cm TL, MA haplogroup, q_{Ma} 0.996, 90% BCI 0.978–1.000, courtesy of Paolo Lo Conte.

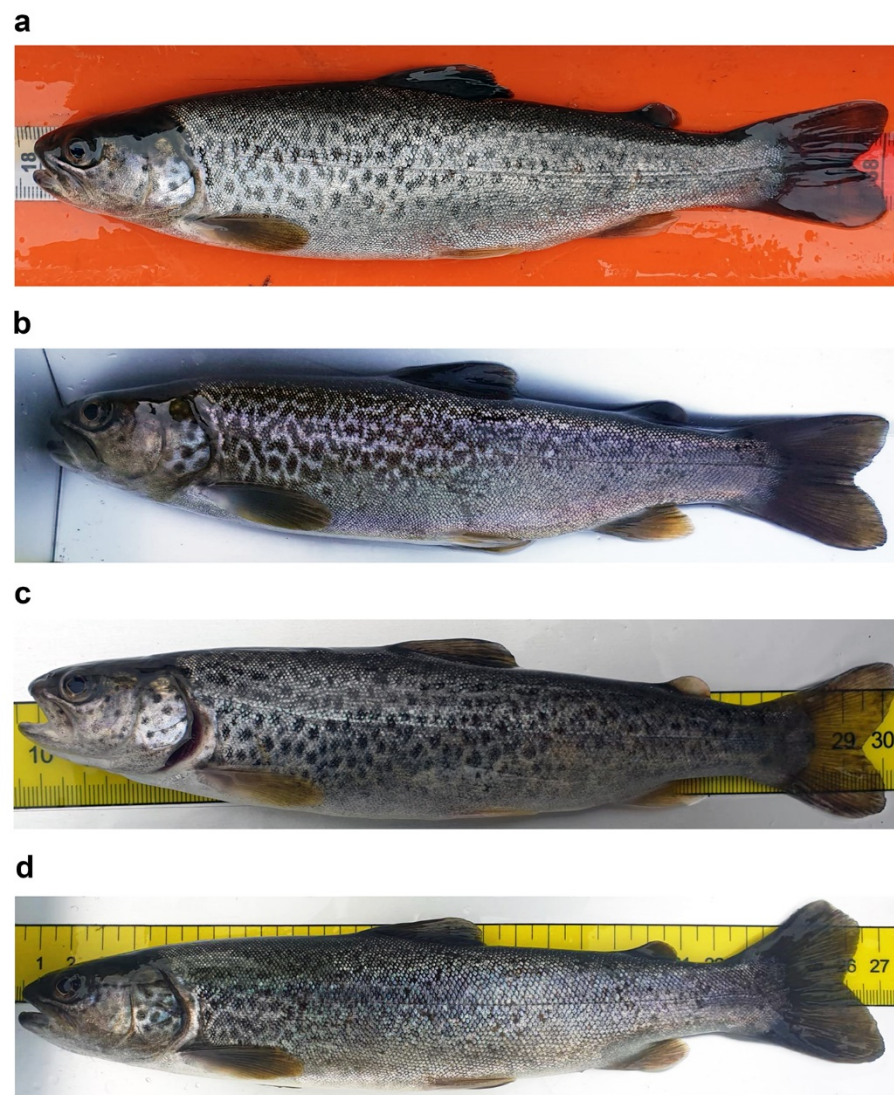


Figure 3. Examples of dotted coloration patterns in *S. marmoratus*: conspicuous ontogenetic chromatic variation in pit-tagged individuals which were recaptured at different times; **(a)** and **(b)** Subadult specimen sampled in Roledo (Piedmont, Verbano-Cusio-Ossola: VCO; 46°10'16.7"N 8°18'49.7"E), age and genetic data unavailable; **(a)** Sampled on 28 April 2021, 20.0 cm TL, 86 g, dotted pattern; **(b)** Recaptured in the same site on 28 October 2021, 23.4 cm TL, 122 g, marbled pattern; **(c)** and **(d)** Subadult specimen sampled in Prata di Vogogna (Piedmont, VCO; 46°1'40.8"N 8°17'2.2"E), age and genetic data unavailable; **(c)** Sampled on 26 April 2021, 20.6 cm TL, weight not available, dotted pattern; **(d)** Recaptured in the same site on 19 October 2021, 26.4 cm TL, 166.0 g, marbled pattern.

Young marble trout typically exhibit an irregular black or black-and-red dotted pattern, with a large black preopercular blotch [108] (Figure 2a); the dark dotted pattern can change to a marbled pattern in a few months in subadults (Figure 3a–d); and adults living in small and fast-flow streams can mature at half the typical length at maturity, while retaining a red-dotted pattern [110] (Figure 2b,c). On the other hand, there is ample evidence of salmonid introductions in old historical times from outside Italy. Translocations and domestication practices of freshwater fishes, even across mountain ranges, go back to the Middle Ages and possibly to the Neolithic, seamlessly continuing through to the 18th and 19th century, before the onset of the fish-culture industry [10,111,112,113,114]. Non-native trouts could have been introduced in northern Italy from adjacent regions, north of the Alpine Divide (e.g., from the Danube basin), just like the common carp *Cyprinus carpio*

L. in the Roman Period [10,115], or from the orographic right tributaries of the Po River (section 5).

Historical local extinctions of *S. ghigii* in the Northwestern and Eastern Alps might also have occurred in historical times, through hybridization and demographic swamping [116], caused by the massive stocking of Atlantic *S. trutta* over the last two centuries. This type of scenario was tested for trout populations of the Lake Garda basin, using a probabilistic approach [91]. Such dramatic effects could have been facilitated by strong numerical differences between native populations and introductions, low hybrid fitness, and very weak reproductive barriers. The presence of partial reproductive barriers between non-native *S. trutta* and *S. marmoratus* [79,117], and marble-trout stocking could have prevented the lineage or local genomic extinction of *S. marmoratus*. On the other hand, in spite of the presence of high introgression rates [81], neither demographic swamping nor local genomic extinctions of native Apennine *S. ghigii* have ever been described in the Tuscano-Latium Italian ichthyogeographic region, where non-native *S. trutta* have been and are being introduced.

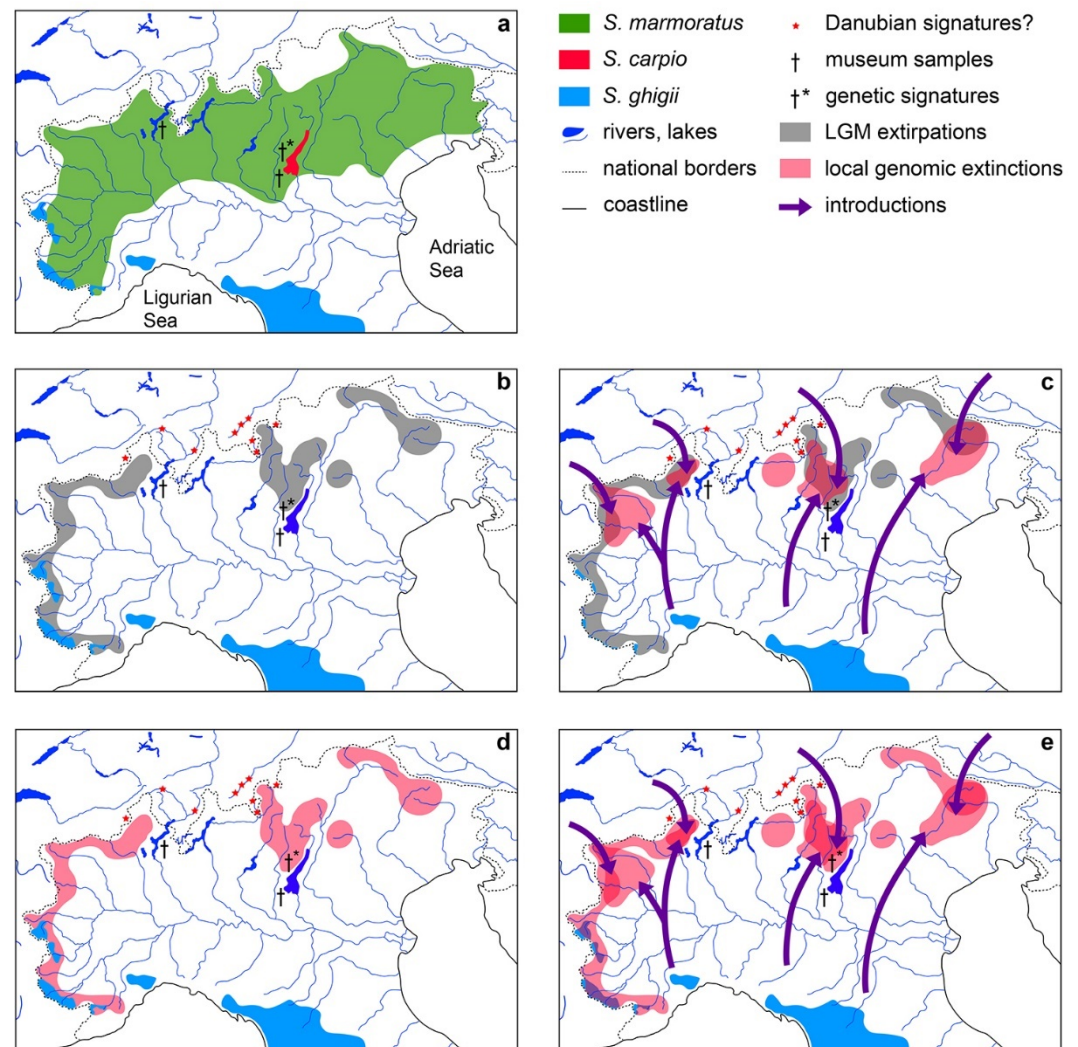


Figure 4. Present distribution of the north-Italian trouts and hypothetical reconstructions of the demographic history of *S. ghigii* in this region; (a) Alpine and subalpine trouts on the Italian territory, modified from [23,48,118], and presence of genetic signatures of extirpated populations of *S. ghigii*; (b) Hypothetical distribution of *S. ghigii* before LGM, and subsequent extinction during LGM, without subsequent introductions of this species in historical times; (c) As in (b), but with subsequent introductions from areas outside the original distribution; (d) Hypothetical distribution of *S. ghigii* after the LGM, assuming no extinction occurred during LGM, without subsequent introductions in

historical times, and subsequent genomic extirpation caused by massive introductions of non-native Atlantic *S. trutta*; (e) As in (d), but with subsequent introductions of *S. ghigii* from areas outside its original distribution. In legend, *Danubian signatures?* refers to the possible presence of genetic variants introduced from the Danube basin (see text); *museum samples*: preserved records of the Adriatic lineage's haplotypes [82]; *genetic signatures*: traces of extirpated populations of *S. ghigii* [91].

Considering (i) the evidence of past widespread presence of *S. ghigii* in this region (before LGM), due to the estimated gene flow between the marble and peninsular lineages (section 5); (ii) the absence of viable populations in this region (with the described exception of Southwestern Alps), and the presence of genetic signatures of extirpated populations (Figure 4a); (iii) the hypothetical extirpation of native populations of *S. ghigii* in this region during LGM; (iv) the anecdotal historical accounts potentially reporting the presence of *S. ghigii* in this region in historical times; and (v) the possibility of recent extirpations of populations of *S. ghigii* due to local genomic extinction caused by massive introductions of non-native *S. trutta*; four potentially falsifiable scenarios can be hypothesized (Figure 4):

1. *S. ghigii* populations were extirpated in most of their range in this region during LGM (except the Southwestern Alps), and were never subsequently introduced from non-native populations (Figure 4b).
2. *S. ghigii* populations were extirpated in most of their range in this region during LGM, and were subsequently introduced from non-native populations (Figure 4c).
3. *S. ghigii* populations survived in this region during LGM, were extirpated by local genomic extinction due to the subsequent introductions of *S. trutta*, and were never subsequently introduced from non-native populations (Figure 4d).
4. *S. ghigii* populations survived in this region during LGM, were extirpated by local genomic extinction due to the subsequent introductions of *S. trutta*, and were subsequently introduced from non-native populations (Figure 4e).

In every scenario, *S. ghigii* has been extirpated in this region, and no native and viable populations are left, except in the Southwestern Alps. Therefore, any introduction from *S. ghigii* populations outside these sites should be considered an introduction of non-native (allochthonous) populations.

Notwithstanding, non-native populations of *S. ghigii* sourced from outside this region have been and are being regularly and massively introduced in the last decade. Such stocking activities will obviously hamper any future investigation attempting to assess the status of populations that may be found in the region. In fact, any new biological variant found in the region that is not present in any of the non-native source populations may still be non-native, i.e., being still undescribed in the source population. Therefore, if the societal priority and management goal is conservation, a precautionary principle should be applied, avoiding any introductions of *S. ghigii* in this region.

5. Current risks of stocking non-native *S. ghigii* in northern Italy

The risk of introgressive hybridization between native *S. marmoratus* and non-native stocks of *S. ghigii* is not only suggested by the widespread interfertility between *Salmo* species. The same presence of gene-flow signatures between these lineages during past secondary contacts before LGM [53] clearly demonstrates the potential for such events. This is particularly the case when native small and fragmented populations are flooded by large amounts of stocked non-native fish [81], in the same ecological conditions that caused the ongoing introgression between *S. marmoratus* and Atlantic *S. trutta* in this region [119].

The ongoing stocking of individuals of *S. ghigii* obtained from non-native populations is also associated with other risks. While hatchery managers introducing *S. ghigii* in this region typically do not publish any genetic screening of the stocks, an independent investigation in a different region showed that a hatchery stock of "Mediterranean trouts" actually contained a mix of both Atlantic haplotypes (44%) and Mediterranean haplotypes

(66%), being characterized by a q_{AT} value (admixture proportion of the cluster characterizing two hatchery stocks of non-native Atlantic *S. trutta*) of 0.42–1.00 [19]. Given the exceptional rarity of such independent investigations, such cases are more likely the rule rather than the exception. Introductions of such hybrid stocks pose an even greater risk than introductions of purebred non-native *S. ghigii*, since hybrids can effectively act as a bridge, facilitating hybridization and introgression between reproductively isolated species [120].

The dispute revolving around *S. ghigii* and the “Mediterranean trout” in northern Italy is also related to another hot and current topic, i.e. the management of stream headwaters. Stocking of native *S. marmoratus* generally occurs in what is considered to be its putative vocational habitat, i.e. in middle and lower river reaches (<1500 m asl [86]). On the other hand, current regulations often prohibit the introduction of non-native species, such as the Atlantic brown trout (section 1). This caused a heated debate, fueled by anglers and sportfishing associations, who advocate the use of non-native stocks of *S. ghigii* to exploit stream headwaters. Most headwater streams in this region were likely troutless, prior to human settlement or stocking (section 4). While this hypothesis still lacks experimental support, the idea of stocking non-native *S. ghigii* in these environments is at odds with conservation principles (section 1). Headwater streams could also be stocked with non-native sterilized fishes, e.g. by a process of triploidisation, thus preventing hybridization with native species downstream. However, massive fish introductions can significantly impact the structure and functioning of freshwater ecosystems, due to interactions with the native communities and recipient environments, including increased competition, predation, biogenic modification of the environment, and potential spreading of diseases [121,122,123,124,125,126]. Therefore, the sustainability of this management strategy must be considered with extreme caution, carefully assessed, and regularly monitored after implementation.

6. Conclusions and future directions

At present, robust scientific evidence identifies *S. marmoratus* as the only native and distinct *Salmo* lineage and taxon in northern Italy except a contact zone in the Southwestern Alps, also inhabited by *S. ghigii*. Introgressive hybridization from non-native *Salmo trutta* into *S. marmoratus* in this region has been repeatedly demonstrated. Given the evidence of past introgression from the peninsular lineage into the marble lineage, genetic introgression from non-native stocks of *S. ghigii* into native *S. marmoratus* is a reasonable possibility.

Genetic signatures of *S. ghigii* outside the contact zone are fragmentary, and strongly suggest past extirpations. It is presently impossible to determine whether viable populations of this species were present in historical times, or most of the native populations were extirpated during the LGM.

Regardless of the academic value of taxonomic debates and the chronic state of flux of the taxonomic consensus, the high interfertility among many salmonid taxa makes a rational approach to the ecosystem management of salmonid populations extremely challenging. Any introduction of trout individuals originating from a non-native population defined by phylogeographic and genetic criteria, even if conspecific with the recipient population, poses the risk of generating hybrid swarms between non-native stocks and native trout lineages. For this reason, translocations, reintroductions, and supportive breeding of salmonid populations should always be managed as Evolutionary Significant Units (ESUs; [32,127,128]). Considering the genetic structure of populations at the microgeographic scale makes conservation actions taxonomy-independent, gaining the sorely needed stability for conservation purposes. In the specific case of reintroductions, using the closest available ESU as a source to rebuild an extirpated population poses the risk of introducing individuals with different life-history traits than those of the original population. For this reason, the potential impacts of reintroductions should always be carefully evaluated, in case prevented, and then monitored, e.g. [129] (sections 3, 4).

Future research could (i) further our knowledge of the genetic structure and micro-geographic patterns of *S. marmoratus* populations within the region, thus identifying ESUs for science-based conservation and management; (ii) investigate the past presence of *S. ghigii* populations in the Italian Alpine and subalpine region using ancient DNA, e.g. in archaeological sites [130] (e.g.,) or in ancient lake sediments [131]; (iii) investigate the past presence of salmonids in hypothetically fishless headwater streams prior to stocking, e.g. using museum records; (iv) investigate the presence of species of evolutionary and conservation interest evolved in hypothetically troutless headwater streams, and their potential interactions with non-native fish candidates for stocking; (v) monitor spatiotemporal dynamics of genetic diversity of trout lineages, both native and non-native, with special attention to the potential onset and development of new hybrid swarms originating from the recent introductions from *S. ghigii* non-native populations; (vi) investigate the genetic structure, ecology and conservation status of *S. ghigii* native populations in the Southwestern Alps, and design and implement dedicated conservation programs, if needed; and (vii) evaluate and implement supporting breeding programs for threatened and heavily fished ESUs of *S. marmoratus*, using state-of-the-art methods to genetically select breeders and minimize domestication effects.

Research efforts will however be insufficient to meet the common goal of sustainable ecosystem management [132], if all the stakeholders are not involved in a durable, empathetic, and collective effort. From anglers to sportfishing associations, hydropower sectors, researchers, conservationists, and governmental institutions, everyone is called to protect, conserve, and promote the native north-Italian trouts, hence preserving the natural heritage of our inland waters.

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