ORIGINAL ARTICLE

Gross mismatches between salmonid stocking and capture record data in a large Alpine lake basin in Northern Italy suggest a low stocking effectiveness for an endangered native trout

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ABSTRACT

Stocking of native and non-native fish species is a widespread practice commonly used to enhance inland recreational fisheries, appropriate when intense harvesting and the degradation or lack of suitable habitat decrease the abundance of the managed species below carrying capacity. In spite of its popularity, this practice is often poorly informed by scientific information. Salmonids are arguably the most popular and commercially valuable freshwater fishes being managed for recreational fisheries. Stocking of both native and non-native taxa has been practiced for almost two centuries in Europe, dramatically altering the structure and function of riverine and lacustrine ecosystems. In the Verbano-Cusio Ossola Province, northern Italy, within the Lake Maggiore catchment, we measured large numerical mismatches between stocking of cultured native (*Salmo marmoratus*) plus non-native trout taxa (*S. trutta*, *S. ghigii*, *Oncorhynchus mykiss*) and the number of fishes captured by local anglers. These observations highlight the need for future studies to estimate the stocking effectiveness of *S. marmoratus*, a critically endangered species of significant cultural and economic value.

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INTRODUCTION

Stocking is a common management strategy to enhance inland recreational fisheries in many industrialized countries, mainly in North America and Europe (Arlinghaus *et al.*, 2015). It should be implemented with the objective to increase the size and abundance of a target species within the system's ecological limits, when the adult stock is not at carrying capacity, *e.g.*, due to intense harvesting or anthropogenic habitat bottlenecks limiting the productivity (Arlinghaus *et al.*, 2015). Stocking is economically and ecologically feasible in cases of i) high fishing mortality, low natural mortality, high growth rate and low recruitment, in combination with the implementation of other regulations, such as length-based harvest limits; and ii) low fishing mortality, low natural mortality, low growth rate and low recruitment, when harvest limits are not useful (Arlinghaus *et al.*, 2015). When stocking volitionally or accidentally causes the introduction of non-native species, it can lead to irreversible and long-lasting effects, affecting the structure, function, biodiversity and evolutionary pathways of the recipient communities (Dudgeon *et al.*, 2006; Gherardi *et al.*, 2008; Wainright *et al.*, 2021). Even when native species are used, inappropriate hatchery management can lead to inadvertent selective breeding and inheritable domesticated traits (Fleming and Peterson, 2001; Tymchuk *et al.*, 2009; Unfer and Pinter, 2018) that can spread through the wild population, significantly reducing reproductive fitness, eroding genetic diversity, disrupting the adaptive spatial population structure (Araki *et al.*, 2008), and even increasing the fishing mortality of wild hybrid stocks (Mezzera and Largiadèr, 2001).

Stocking also implies a considerable investment of economic resources, and large disproportions between the number of stocked and captured individuals are a major concern. Causes include fishing and natural mortality, food availability, and predation (Naish *et al.*, 2007; Mäntyniemi *et al.*, 2012). In order to estimate stocking effectiveness, it is necessary to identify stocked individuals within the catch, which can be accomplished with methods such as tagging and marking (ICES, 2021) or parentage analyses (Wąs-Barcz and Bernaś, 2023). However, such studies need a considerable investment of time and resources and are infrequently conducted. Therefore, it is advisable to gather preliminary information that can provide evidence of their necessity, and to develop hypotheses accordingly.

In Italy, investments, resources, and satellite activities revolving around recreational inland fishing include the building and maintenance of the hatcheries, the commerce of hatchery stocks, issuing of fishing licenses and collection of membership fees for angling associations, angling competitions, and tourism (FIPSAS, 2021). The main stakeholders are the angling associations, typically delegated by province and region administrations to manage inland fisheries.

In the Toce River basin within the Lake Maggiore catchment -Verbano-Cusio Ossola Province (VCO), Northern Italy- (Fig. 1), angling is deeply rooted in the local culture. From 2014 to 2018, a yearly average of ~3,600 resident and non-resident anglers bought a fishing license to fish in these waters. The most important fisheries include the only native species *Salmo marmoratus* Cuvier 1829 (Meraner and Gandolfi, 2018), and three non-native salmonids (Polgar *et al.*, 2022a, 2022b), namely *S. trutta* Linnaeus 1758, *S. ghigii* Pomini 1941 (Meraner *et al.*, 2013; Splendiani *et al.*, 2019, 2020; Lorenzoni *et al.*, 2019;=*S.* cf. *cenerinus* Nardo 1847, sensu Segherloo *et al.*, 2021), and *Oncorhynchus mykiss* Walbaum 1792 (Kottelat and Freyhof 2007). *S. marmoratus* is 'Critically Endangered' in Italy (Bianco *et al.*, 2013), being threatened by habitat destruction, habitat degradation, and genetic introgressive hybridization with introduced stocks of Atlantic *S. trutta* (Meraner and Gandolfi, 2018; Polgar *et al.*, 2022a), as also preliminarily observed in the Toce River (Gibertoni *et al.*, 2014).

Fish habitats are subjected to several anthropogenic impacts in this system, including damming, channelization, water withdrawal, hydropeaking events, extraction of riverbed materials, artificial embankments, degradation or destruction of the riparian vegetation, and climate change (Dresti *et al.*, 2016; Saidi *et al.*, 2014, 2018). Environmental rehabilitation actions targeted fish habitats, mainly including river connectivity restoration, *i.e.*, fish bypass channels (projects IdroLIFE, LIFE CONFLUPO, and LIFE EEL; European Commission, 2021). Other management activities include both input (*i.e.*, closed areas, closed fishing seasons, gear restrictions, licensing), and output (*i.e.*, length-based harvest limits, daily and annual bag limits; FIPSAS, 2021) control regulations.

Trout stocking has been implemented for two centuries in Northern Italy (Sommani, 1948). Two types of stock-enhancement (Lorenzen *et al.*, 2012) are practiced in the VCO Province: i) culture-based fisheries of non-native species (production-oriented), namely put-grow-and-take fisheries of *S. ghigii* (Mediterranean brown trout) and *S. trutta* (Atlantic brown trout), both released as alevins and young, plus a put-and-take fishery of *O. mykiss* (rainbow trout), mainly released as young, but

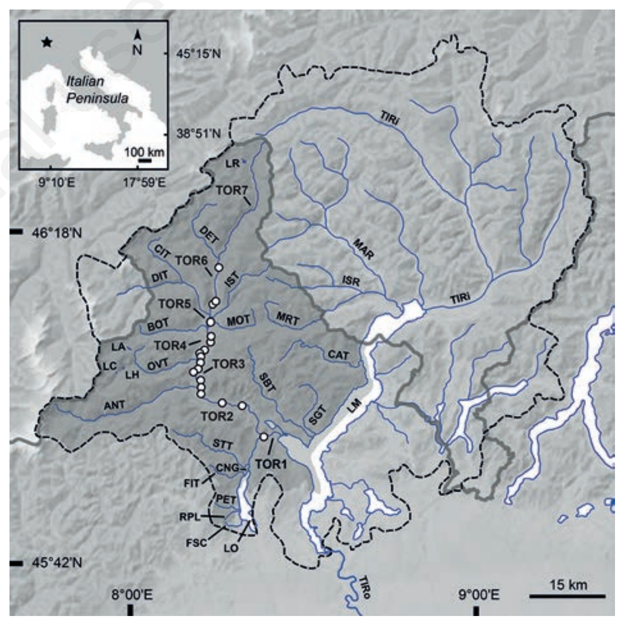

Fig. 1. Lake Maggiore's hydrogeographic basin (dashed black line) and its main river systems (Barbanti, 1994; Galassi *et al.*, 2006). Inset: position of the Lake Maggiore (black star symbol) in the Italian Peninsula; the only outlet from the basin is the Ticino River outlet (TIRo). ANT, Anza Torrent (T.); BOT, Bogna T.; CAT, Cannobino T.; CIT, Cairasca T.; CNG, Nigoglia Channel; DET, Devero T.; DIT, Diveria T.; FIT, Fiumetta T.; FSC, Scarpia Stream; ISR, Isorno River (R.); IST, Isorno T.; LA, Lake Antrona; LC, Lake Camplicciolì; LH, Lake Cheggio (Alpe dei Cavalli); LM, Lake Maggiore; LO, Lake Orta; LR, Lake Morasco; MAR, Maggia R.; MOT, Melezzo Occidentale T.; MRT, Melezzo Orientale T.; OVT, Ovesca T.; PET, Pellino T.; RPL, Plesina Brook (Pellesina B.); SBT, San Bernardino T.; SGT, San Giovanni di Intra T.; STT, Strona T.; Toce R. (TOR); TIRi, Ticino R. inlet; TOR1 to TOR7, seven tracts of the Toce R., defined by confluences with its main tributaries and L. Maggiore; white dots, rod-and-line sample (*Tab. S1*).

including subadults and adults; and ii) a stock-enhancement fishery of the native *S. marmoratus*, released as alevins and young. In Italian inland waters, the introduction of non-native species requires approval from the Ministry of the Environment, pending demonstration that the introduction poses no risks to the environment or native species (European Union, 1992; Italian Regulation, 1997). However, stocking of *S. trutta*, *S. ghigii*, and *O. mykiss* is still allowed in northern Italy without ministerial authorization, due to the lack of an official list of native and non-native freshwater fish species (Polgar *et al.*, 2022b).

Spatiotemporal stocking patterns of native and non-native trout taxa in northern Italy are highly consistent, but potentially based on misconceptions about the habitat distribution of native populations of *S. marmoratus*. Phylogeographic reconstructions suggest that *S. marmoratus* was the only trout species that survived the Last Glacial Maximum (LGM) throughout the Northern Adriatic and Alpine region. After the LGM, only scattered and fragmented remnant populations of the peninsular trout *S. ghigii* survived in glacial refugia, and a contact zone between these species in the Cottian and Maritime Alps, where the species live in sympatry and show habitat segregation (Splendiani *et al.*, 2020; Polgar *et al.*, 2022a). Outside this contact zone, in the North-western and Eastern Alps (Marazzi, 2005), widespread hybridization between non-native *S. trutta* and *S. marmoratus* was recognized (Giuffra *et al.*, 1996; Meraner *et al.*, 2010, 2013; Meraner and Gandolfi, 2018). Numerous genetic studies subsequently demonstrated, with support from historical evidence, that early stocking practices mainly introduced allochthonous Atlantic *S. trutta* in river upper tracts and high altitude basins in this region, many of which likely remained fishless since the LGM (von Siebold, 1863; Fatio, 1890). However, in the '80s-'90s, Italian ichthyologists considered the allochthonous Atlantic *S. trutta* as 'native Alpine trout' populations throughout the Italian Alpine region (*S.* [*trutta*] *trutta*, Gandolfi and Zerunian, 1987), thus describing the observed altitudinal pattern as the natural habitat segregation of 'native brown trout' and marble trout taxa. This model disregarded the findings of Sommani (1960), who documented the presence of *S. marmoratus* at high altitudes in the Eastern Alps, *e.g.*, at 1,500 m above sea level (asl) in the Adige River. Sommani's study employed hydrogeological characteristics of the habitat to model the geographical distribution of this species. A similar approach was also adopted by Splendiani *et al.* (2013) for the native Apennine populations of *S. ghigii* in Central Italy.

Consequently, this concept of an altitudinal zonation of 'native brown' and marble trout in the North-western and Eastern Alps instructed subsequent stocking practices, which likely reinforced it. Even after the widespread introgression of non-native Atlantic trout into native *S. marmoratus* in this region was acknowledged, the notion that the habitat of *S. marmoratus* is limited to lower altitudes and larger water bodies continued to instruct stocking practices ('marble trout zone'), assuming that introducing stocks of non-native brown trout at higher altitudes and smaller water bodies could significantly limit hybridization (GRAIA, 1999).

Within the VCO Province, stocking is managed by the Provincial Fishing Office in public waters; by private individuals in private waters, being outsourced to private contractors and local fishing associations; and by hydroelectric companies, that are contractually obligated to stock trout for environmental compensation and buy live fish from private local hatcheries (P.V., *personal observation*). Fish stocking in protected areas (Natura 2000 network; MTE, 2000) is regulated by national laws (MATTM, 2020) compelling the managers of protected areas to follow strict assessment procedures called VINCA (Valutazione di Incidenza) for the assessment of the potential impact of stocked fish on native biodiversity and habitats of high naturalistic value. Finally, genetic analyses of the domesticated stocks, typically using only the mitochondrial D-loop and nuclear LDH-C1 genes, are seldom conducted and identification of trout breeders is routinely based on phenotypes.

Stocking in Italian is called 'semine' (sowing), exemplifying a vision of lentic and lotic ecosystems being managed as agricultural systems. Although not supported by published scientific studies, the common belief among anglers, politicians, and consultant ichthyologists is that the degradation of fish habitats imposes bottlenecks to natural recruitment and productivity, making stocking practices necessary to sustain the angling pressure and support fish populations.

Salmonids' stocking effectiveness has never been quantified or evaluated in the VCO Province. In order to estimate the stocking effectiveness of a fish species, it is essential to differentiate between stocked and wild individuals. However, if it is assumed that the stocking effectiveness of syntopic and biologically similar species is comparable, the relative abundance of stocked individuals of each species should be consistent with the relative abundance of captured individuals of the same species. Therefore, large mismatches in the relative abundance of stocked and captured individuals among species could suggest different stocking effectiveness of the different species. Within the framework of a set of working hypotheses, we assessed the relative abundance of stocked and captured *O. mykiss*, *S. trutta*, *S. ghigii*, and *S. marmoratus* across 11 water bodies, including the Toce River, its main tributaries, Lake Maggiore, and Lake Orta, using recorded stocking data and anglers' catch records.

METHODS

Study site

The Toce River is located in the Italian North-western Alps (Pennine and Lepontine Alps; Marazzi, 2005), in the Padano-Venetian ichthyogeographic region (Bianco, 1998). This river is one of the main tributaries of Lake Maggiore; it originates from glacier valleys (Lake Morasco dam) at ~1720 m asl (Regione Piemonte, 2021). The river is 83.6 km long, its catchment area is ~1780 km^2, its average slope is 2.4%, its average water discharge a few km before its confluence with Lake Maggiore is ~70 m^3 s^{-1} (daily measurements; Regione Piemonte, 2004), and its average water temperature is ~9.5°C (2001–2019, monthly measurements; Candoglia weather station, Laboratorio di Idrochimica, CNR-IRSA Verbania, CIPAIS). The Toce River catchment has a temperate climate (latitudinal range: 45°55' N–46°28' N) and is characterized by an average rainfall of ~1400 mm yr^{-1} (ADBPO, 2018). The typical north-Italian rainfall regime is characterized by two maxima during spring and autumn, and two minima during summer and winter (Saidi *et al.*, 2014). Consistent with the 'Habitat Directive' and within the Natura 2000 European network for biodiversity protection (European Union, 1992; MTE, 2020; Fig. 2), ~40 km of this river are included in the following protected areas (SAC, Special Area of Conservation; SPA, Special Protected Area): 'Fondo Toce' (SAC, SPA, IT1140001; ~3.6 km^2), 'Fiume Toce' (SPA, code IT1140017; ~26.6 km^2), and 'Greto Torrente Toce fra Domodossola e Villadossola' (SAC, IT1140006; ~7.5 km^2).

Stocking records and catch record cards

Stocking records of 2019 and 2020, including sites (municipalities, fractions, names of water bodies), dates, numbers, and life stages of introduced trout within VCO were obtained from the VCO Province and analyzed. Stocking records prior to 2019 were unavailable. Fish size ranges and ontogenetic life stages were inferred from local common names and denominations, and geographic coordinates from toponyms. All stocked and released fishes were phenotypically determined. Stocking records only used Italian vernacular names. We inferred the corresponding taxonomic species based on our extensive field experience and years of interactions with fishermen and hatchery managers. In particular, i) records of 'trota marmorata lacustre' (lacustrine marble trout), 'trota marmorata' (marble trout), and 'trota marmorata nostrana' (local native marble trout) were determined as *S. marmoratus* (MARM; likely including *S. marmoratus* x *S. trutta* hybrids; Gibertoni *et al.*, 2014); ii) records of 'trota fario' (resident brown trout), 'trota fario lacustre' (migratory brown trout), and 'trota lacustre' (lake trout) as Atlantic *S. trutta* (TRUT); iii) records of 'trota fario mediterranea' (Mediterranean brown trout) and 'trota fario nostrana' (native brown trout) as *S. ghigii* (GHIG; likely including *S. trutta* x *S. ghigii* hybrids); and iv) records of 'trota iridea' as *O. mykiss* (OMMY). For practical reasons dictated by the source of information, life stages for all the species were categorized as alevins or fry (<3 cm total length: TL), young (3-18 cm TL), subadults (19-30 cm TL), and adults (>30 cm TL).

In VCO waters subject to specific constraints managed by FIPSAS ('SPV' areas in Fig. 3), annual fish captures and licensed recreational anglers' presence (number of fishing sessions) were obtained from the catch records and membership cards of 2014-2018, made available by the FIPSAS. Catch record and membership cards from more recent years were unavailable. No-kill fishing grounds or periods were not included. Except no-fishing zones (Fig. 3, yellow stars), angling can be practiced in Piedmont with a fishing license in VCO free waters (Regional Law n. 37, 2006), and with specific permissions in waters with different fishing rights (Fig. 3). Therefore, this dataset

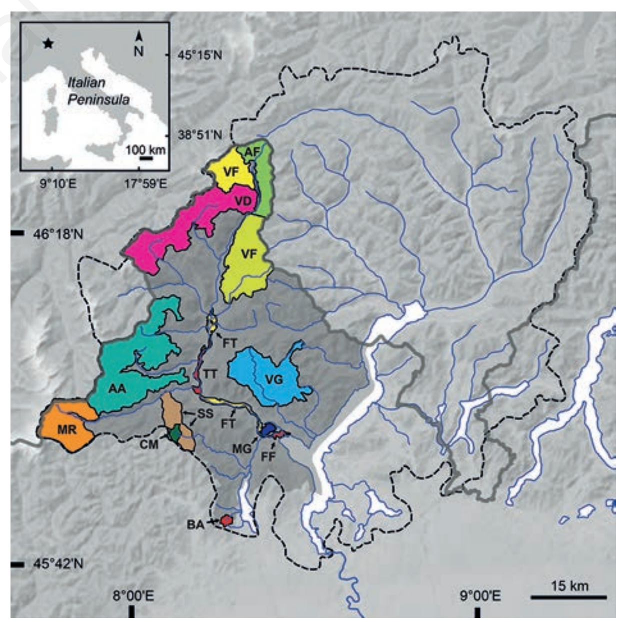

Fig. 2. Protected areas (SAC, Special Area of Conservation; SPA, Special Protected Area) in the Verbano-Cusio Ossola Province. AA, IT1140018, Alte Valli Anzasca, Antrona e Bognanco (SPA); AF, IT1140004, Alta Val Formazza (SAC); BA, IT1140007, Boleto Monte Avigno (SAC); CM, IT1140003, Campello Monti (SAC); FF, IT1140001, Fondo Toce (SAC, SPA); FT, IT1140017, Fiume Toce (SPA); MG, IT1140013, Lago di Mergozzo e Mont'Orfano (SPA); MR, IT1140019, Monte Rosa (SPA); SS, IT1140020, Alta Val Strona e Val Segnara (SPA); TT, IT1140006, Greto Torrente Toce fra Domodossola e Villadossola (SAC); VD, IT1140016, Alpi Veglia e Devero - Monte Giove (SAC, SPA); VF, IT1140021, Val Formazza (SPA); VG, IT1140011, Val Grande (SAC, SPA).

provides an overview of the relative annual catch of the different taxa within the VCO Province. The potential number of fishing sessions per year in these areas was estimated using the proportions of returned catch record cards (in percentage, 63.2%–67.1%; average ± SD 64.9%±1.5%). According to the current regulations, caught fish can be retained only above taxon-specific minimum length limits (MLL; MARM: 40 cm TL, TRUT+GHIG: cm TL, OMMY: 20 cm TL; FIPSAS, 2021; VCO Province, 2021). Therefore, we assumed that anglers' catch records included only fishes that were retained. In order to estimate the total number of both retained and released fishes in the anglers' catch records (captured fishes), we used the proportion of fishes smaller than MLL collected during several rod-and-line field surveys conducted in 2020 (n=153; *Tab. S1*). In these field surveys, we used 3 fishing methods commonly used by local anglers. Comparable amounts of fishing surveys (different sites or days) were made using each method (nymph-fly: n=25, dry-fly: n=20, spinning: n=27; *Tab. S1*).

Irrespective of the origin of individual fishes in each study site, the proportions of the three trout taxa can be described as *MARM:TRUT+GHIG:OMMY* (total number of fishes=*N*). In order to compare the mean proportions of captured and stocked trout taxa per year, we defined a simplified model supported by a set of five assumptions. Namely, i) the annual natural mortality (*M*) and annual natural productivity (*P*) of each trout taxon *x* are equal and constant (M_x=P_x=k); ii) the total annual fishing pressure (total number of captured fishes, irrespective of taxon, *F*) is constant; iii) the total annual stocking (total number of trout stocked per year, *S*) and the proportions of the stocked trout taxa (S_{MARM}:$S_{TRUT+GHIG}$:S_{OMMY}) are constant; iv) the proportions of the captured taxa each year (F_{MARM}:$F_{TRUT+GHIG}$:F_{OMMY}) are equal to the relative abundance of the three taxa in the system (capture equiprobability); and v) the proportions of the stocked trout taxa are equal to their proportions reaching the minimum size length for capture, *i.e.*, the proportions of taxa do not change from stocking to capture. If these assumptions are not violated and *F*=*S*, *N* is constant and the study sites' communities would eventually reach a composition of the three taxa equal to the proportions of the stocked taxa (*MARM:TRUT+GHIG:OMMY*=S_{MARM}:$S_{TRUT+GHIG}$:S_{OMMY}). The rate of attaining equilibrium in such system is contingent upon the disparity between *N* prior to the initiation of both stocking and fishing activities (N_0), and the amount of fishes stocked in one year (S_0). We assume the presence of a sufficiently extensive time period since the commencement of stocking and of a sufficiently large value of N_0–S_0, thereby allowing the system to have reached equilibrium. Therefore, a mismatch in the mean proportions of captured and stocked trout taxa per year in each site would indicate a violation of one or more of the stipulated assumptions. Such observations would offer valuable insights into the relative stocking effectiveness of the examined taxa, without necessitating discrimination between domesticated and wild stocks.

To this aim, a ternary diagram was constructed, using these proportions (section 2.6). In order to quantify the mismatches, pairwise half-Manhattan distances (Miller, 2002) between mean proportions of captured (*x*) and introduced (*y*) trouts per year in each fishing area were computed as:

$$d(x,y)=\tfrac{1}{2}\,(|x_1-y_1|+|x_2-y_2|+|x_3-y_3|) \qquad \text{(eq. 1)}$$

where the subscripts index the three trout taxa, and 0 $\leq d(x,y) \leq 1$.

We used the 'ternary' R package (Smith, 2017) to construct a ternary diagram, which served two purposes: i) comparing the average proportions of trout taxa captured and introduced per year, and ii) calculating half-Manhattan distances between different sites.

RESULTS

In 2019, 267 stocking events were documented, for a total of 2,092,909 salmoniforms, including ~580,000 domesticated *S. marmoratus* (MARM; 34.4%), ~770,000 non-native Atlantic *S. trutta* (TRUT; 45.4%), ~300,000 non-native *S. ghigii* (GHIG; 17.8%), and 39,500 non-native *O. mykiss* (OMMY; 2.3%) (Figs. 3 and 4a; Tab. 1). The rest (n=402,950) were *Thymallus* species. This account does not include 37 stocking records in which release sites could not be georeferenced using location toponyms ('NA'; n=119,382; Fig. 4a; Tab. 1) and other 7 introduction records that lack information about the number, location, or taxa of the released fishes. Domesticated MARM and TRUT were essentially released as young (100.0% and 99.9%, respectively); GHIG were released as both alevins (22.3%) and young (77.7%); and OMMY as young (91.7%), subadults (5.4%) and adults (2.8%). The size difference of the stocked taxa should mirror different management objectives, although no clear and consistent difference in the size-class composition of the stocked taxa was apparent.

In 2020, 231 stocking events were documented, for a total of 2,377,333 salmoniforms, including 799,500 domesticated MARM (39.1%), 1,202,155 individuals of non-native TRUT+GHIG (not discriminated in the original dataset; 58.9%), and 40,678 non-native OMMY (2.0%) (Figs. 3 and 4b; Tab. 1). The rest were represented by *Thymallus* (n=175,000) and *Coregonus* species (Lake Mergozzo, n=160,000). This account does not include 38 stocking events, in which release sites could not be georeferenced using location toponyms (Fig. 4b, 'NA'; n=89,920). Domesticated MARM were mostly released as alevins (98.8%); TRUT+GHIG were mostly released as alevins (63.5%) and young (36.3%); and OMMY as young (89.8%) and adults (10.2%).

Geographic patterns of stocking in 2019 and 2020 are remarkably consistent (Fig. 4). Most MARM were consistently released in Lake Maggiore (LM), S. Bernardino Torrent (SBT), the lower and middle tract of the Toce River (TOR1 to TOR4), and Lake Orta (LO). Most TRUT+GHIG were released in LM, SBT, San Giovanni di Intra Torrent (SGT), Cannobino T. (CAT), Anza T. (ANT), Ovesca T. (OVT), and the upper tract of the Toce River (TOR6, TOR7). OMMY were mainly released in SBT, OVT, and TOR7. Stocking was also conducted within protected areas (Val Grande, Val Formazza, Alpi Veglia e Devero, Alta Val Strona e Val Segnara), and in water bodies draining into protected areas (Figs. 1,3, and 4).

Licensed anglers' catch record cards of 2014-2018 show an average of ~20,123 fishing sessions per year (18,274-21,595) in SPV areas subject to specific constraints, during the fishing season (241 days per year, ~94 anglers per day; Fig. 3; Fig. 5a). This presence did not significantly differ from year to year (Wald-Wolfowitz runs test for 20 sites; p=0.1 to 1.0, using the DescTools R package; Signorell *et al.*, 2021). Considering that the returned cards are only a fraction of the granted licenses, ~132-155 anglers per day likely visited the area during each fishing season (Fig. 5b). An average ±SD of 25,341±3,940 trout per year were retained: 228±65 MARM (0.9±0.1%), 8,969±1,574 TRUT+GHIG (35.3±1.6%), and 16,144±2,355 OMMY (63.8±1.7%). In our 2020 rod-and-line sample (n=153; *Tab. S1*), the

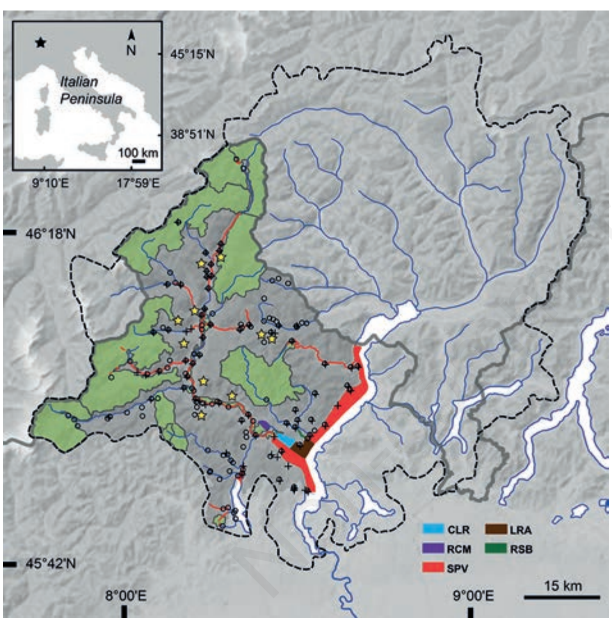

Fig. 3. Trout stocking sites in the Verbano-Cusio Ossola (VCO) Province, during 2019 (black circles) and 2020 (black crosses); the position of these sites was inferred from the names of the waterbodies and municipalities provided by the VCO Province. Thick dark-grey line, national border between Italy and Switzerland; shaded area, VCO Province; areas in pale green, protected areas (Fig. 2). Waters where fishing is regulated by private, leased and public fishing rights are illustrated by different colors. In legend: CLR, exclusive rights 'ex Cuzzi Lamberti'; LRA, rights of the Anglers' Association 'La Riva'; RCM, regulation of the Mergozzo municipality; RSB, fishing reserve of San Bernardino; SPV, FIPSAS section of the provincial anglers of the VCO. All 'free waters' (blue, rivers, white, lakes) are only regulated by fish-specific size limits, and scheduled times and periods. Yellow stars, no-fishing zones associated with fish bypass channels, 100 m up- and downriver of weirs and dams. Other details as in Fig. 1.

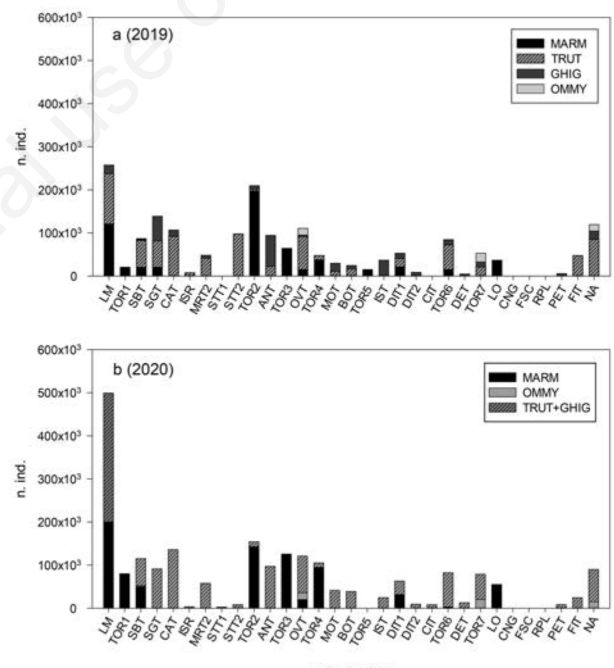

Fig. 4. Stocking of domesticated *S. marmoratus* including hybrids with Atlantic *S. trutta* (MARM), non-native Atlantic *S. trutta* (TRUT), non-native *S. ghigii*, possibly including hybrids with Atlantic *S. trutta* (GHIG), and non-native *O. mykiss* (OMMY) recorded in 2019 (a) and 2020 (b). n. ind., number of individuals; water bodies, basins and river tracts including the georeferenced sites inferred from the available data; MRT2, Melezzo Orientale Torrent, after the confluence with the Isorno R.; STT1 and STT2, Strona T., before and after the confluence with the Nigoglia Channel, respectively; DIT1 and DIT2, Diveria T., before and after the confluence with the Cairasca T., respectively (Fig. 1); NA, records lacking georeferenced release sites. From left to right on the x axis, water bodies are ordered following their confluence sequence, from Lake Maggiore (LM) and Lake Orta (LO), and proceeding upstream. Other abbreviations as in Fig. 1.

proportions of captures of these 3 species that were larger than the minimum size limits (in percentage) were 19%, 76%, and 100%, respectively. Using these figures, and assuming a fishing pressure proportional to the number of both returned and non-returned catch record cards, the adjusted average total catches per year of these 3 species are: 1,847±509 (4.1±0.5%), 18,174±3,044 (40.4±1.7%), and 24,853±3,307 (55.5±1.8%), respectively (Fig. 5b). Despite the fact that fishes were introduced over a larger area than where they were captured, the overall geographic pattern revealed by the distribution of stocked fishes does not align with the observed distribution in both the anglers' catches and our sample. Approximately 13% (n=237) of MARM were captured in the upper Toce River (TOR6 and TOR7, Fig. 5b; ~22% in our sample, *Tab. S2*), and 13% (n=2,816) of TRUT+GHIG were captured in the middle and lower Toce River (TOR1 to TOR5, Fig. 5b; ~63% in our sample, *Tab. S2*).

Mismatches of up to two orders of magnitude were found by comparing the mean proportions of trout taxa captured per year (2014-2018) and the mean proportions of the same trout taxa introduced per year (2019, 2020) in the same areas. The largest half-Manhattan distance (HMD) is between introductions and captures made in LO+CNG (HMD=0.94); very large distances in OVT, TOR1 to TOR3, and TOR4 to TOR5 (0.60≤HMD<0.80); and moderately large distances in LM, DIT-1, and TOR6 (0.40≤HMD<0.60). These mismatches are mainly due to

Tab. 1. Stocking activity in the study area during 2019 and 2020.

	2019 stocking				2020 stocking			2019-2020 means		
	MARM	TRUT	GHIG	OMMY	MARM	TRUT+GHIG	OMMY	MARM	TRUT+GHIG	OMMY
TOR1	20,333	0	0	0	80,000	0	0	50,166.7	0.0	0.0
TOR2	197,333	4133	8000	130	142,500	11,467	40	169,916.7	11,800.0	85.0
TOR3	64,333	0	0	0	125,500	0	0	94,916.7	0.0	0.0
TOR4	37,552	10,000	0	0	95,000	10,000	0	66,276.0	10,000.0	0.0
TOR5	15,052	0	0	0	0	0	0	7,526.0	0.0	0.0
TOR6	15,000	57,420	11,750	380	2500	79,451	460	8,750.0	74,310.5	420.0
TOR7	0	21,000	11,700	20,220	0	58,510	20,340	0.0	45,605.0	20,280.0
STT	0	97,933	0	0	0	10,600	0	0.0	54,266.7	0.0
ANT	0	22,340	71,804	160	0	96,852	160	0.0	95,498.0	160.0
OVT	15,000	76,590	3380	15,580	20,000	85,380	15,660	17,500.0	82,675.0	15,620.0
MOT	0	11,100	18,256	180	500	41,042	100	250.0	35,199.0	140.0
BOT	0	16,720	7800	0	0	38,670	0	0.0	31,595.0	0.0
IST	0	0	36,640	0	0	24,420	0	0.0	30,530.0	0.0
DIT	20,950	20,000	20,360	240	31,500	40,360	180	26,225.0	40,360.0	210.0
CIT	0	0	0	0	0	8000	0	0.0	4000.0	0.0
DET	0	0	4700	0	0	12,850	0	0.0	8775.0	0.0
LM	120,800	116,667	19,880	0	200,000	299,136	0	160,400.0	217,841.2	0.0
SBT	20,000	62,317	2900	1,550	50,000	62,567	2450	35,000.0	63,891.7	2,000.0
SGT	20,000	61,667	56,992	0	0	91,159	0	10,000.0	104,908.7	0.0
CAT	0	92,000	14,640	140	0	135,740	140	0.0	121,190.0	140.0
MRT	0	41,600	6600	0	0	57,699	0	0.0	52,949.3	0.0
ISR	0	7467	0	0	0	3333	0	0.0	5400.0	0.0
LO	35,750	0	0	860	52,000	2070	1088	43,875.0	1035.0	974.0
CNG	0	0	0	60	0	0	60	0.0	0.0	60.0
FIT	0	47,300	0	0	0	24,350	0	0.0	35,825.0	0.0
PET	0	500	5200	0	0	8500	0	0.0	7100.0	0.0
FSS	0	500	0	0	0	0	0	0.0	250.0	0.0
RPL	0	500	0	0	0	0	0	0.0	250.0	0.0
Total	582,104	767,753	300,602	39,500	799,500	1,202,155	40,678	690,802.1	1,135,255.1	40,089.0
NA	0	84,857	19,525	15,000	0	74,920	15,000			

NA, stocking records whose release sites could not be georeferenced using location toponyms; means' totals (2019-2020 means) provide a rough figure of the total number of fishes per year used to stock all the sites; other abbreviations as in Figs. 1 and 4.

the much smaller proportions of captured MARM (in percentage, 0.2%–36.2%, mean 10.5%) relative to introduced MARM (1.5-96.4%, mean 56.2%), and the much larger proportions of captured OMMY (in percentage, 10.1-79.3%, mean 36.5%) relative to introduced OMMY (0.0-13.5%, mean 2.4%) (Fig. 6).

DISCUSSION

Stocking records of 2019 and 2020 clearly follow highly consistent spatial patterns, mirroring a long-established paradigm of the assumed habitat segregation among different trout taxa in the Italian Alpine region (Sommani, 1948, 1960; Gandolfi and Zerunian, 1987; GRAIA, 1999). However, both the anglers' catch record cards and our rod-and-line sampling survey demonstrate the presence of *S. marmoratus* in the upper Toce River, and of *S. trutta* and *S. ghigii* in the middle and lower Toce River. This latter observation clearly indicates that hydrological barriers or habitat segregation do not prevent downward migration of non-native introduced stocks to the middle and lower tracts of the Toce River. On the other hand, upward migration may also occur, being likely influenced by the interaction between natural and artificial barriers with variable permeability, and seasonal high-flow conditions. The co-occurrence of these taxa in the Toce River is also consistent with some preliminary genetic analyses, which demonstrated hybridization and introgression events between *S. trutta* and *S. marmoratus* in this system (Gibertoni *et al.*, 2014; Polgar *et al.*, 2022a). Further studies

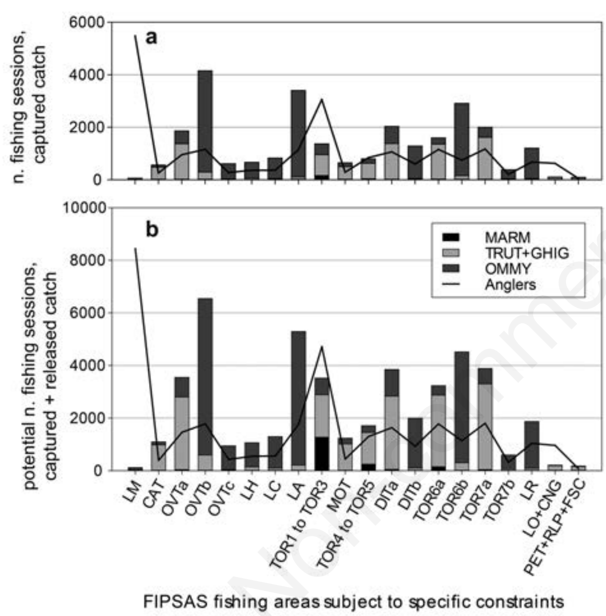

Fig. 5. Mean number of anglers and captured fishes per year. a) Mean number of anglers (n. fishing sessions) and captured fishes per year (captured catch) of the studied fish taxa in fishing areas subject to specific constraints and managed by the FIPSAS ('SPV'; Fig. 3) during 2014-2018, obtained from returned catch record cards. b) Mean potential number of both retained and released captured fishes per year, and potential number of anglers per year (potential n. fishing sessions, captured + released catch), estimated from minimum size limits and proportions of fished size classes in our sample (*Tabs. S1* and *S2*), and from the proportion of returned catch record cards, respectively; the scale on the y axis is the same for both variables (counts). OVTa, Ovesca T.; OVTb, Ovesca T. facilitated zone; OVTc, Ovesca T. winter tourism; DITa, Diveria T.; DITb, Diveria T. touristic zone; TOR6a: Toce River Crodo; TOR6b, Toce River Crodo facilitated zone (only from 2014 to 2016); TOR7a, Toce River Premia; TOR7b, Toce River Piedilago touristic zone. Other abbreviations as in Fig. 1.

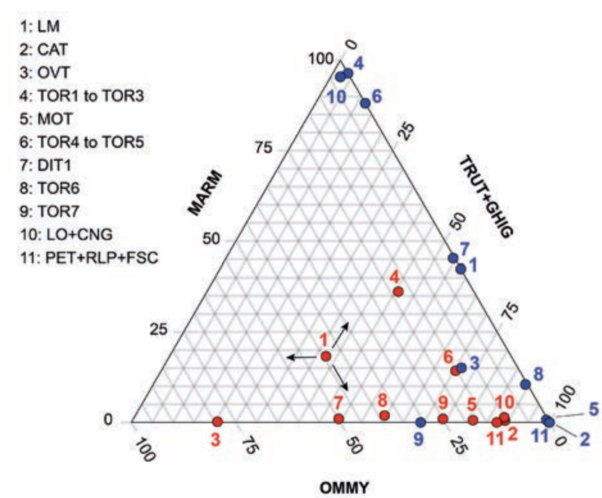

Fig. 6. Ternary diagram mapping the composition (in percentage) of three trout taxa in eleven fishing areas subject to specific constraints, being managed by the FIPSAS (1-11). Two types of compositional data are compared. Red dots indicate the mean percentage of trout taxa captured per year (2014-2018), estimated from both the potential number of anglers present in these areas per year and the percentage of captured fishes (OVT, OVTa+OVTb+OVTc; DIT, DITa+DITb; TOR6, TOR6a+ TOR6b; TOR7, TOR7a+TOR7b in Fig. 5). Blue dots indicate the mean percentage of the same trout taxa introduced per year (2019, 2020) in the same areas; black arrows indicate how to read the three values on each axis of the ternary diagram. Abbreviations as in Figs. 1 and 4.

should clarify the spatial distribution and movements of salmonids within the Toce River basin.

The observed mismatches between the mean proportions of stocked and captured salmonids in the study sites suggest a remarkably lower stocking effectiveness of MARM, compared to the other non-native taxa. However, other non-mutually exclusive factors violating one or more of our assumptions might have contributed to the observed mismatches. Firstly, capture records of marble trout in the catch record cards may be biased, as anglers might not faithfully report their catch, due to the stricter rules for capturing this species, and the scarce regulation enforcement in the Toce River (*personal observation*). The daily bag limits in the VCO Province are 10 individuals (no limits per year) for rainbow trout; 7-8 individuals (no limits per year) for brown and peninsular trout; and 2 individuals (10 individuals per year) for marble trout, including hybrids (FIPSAS, 2021).

The first assumption, which states that the mortality and productivity of each taxon in each sampled system are equal and constant for both stocked and wild individuals, might not hold, as often observed in salmonids (Fleming and Petersson, 2001; Araki *et al.*, 2008). Stocked and domesticated marble trout could be more poorly adapted to wild conditions than the other trout taxa, thus a large amount of the released individuals might die shortly after stocking. This domestication effect might even be stronger if a large proportion of the stocked marble trouts are *S. marmoratus* x *S. trutta* hybrids. Local adaptation to environmental and ecological variation of native stocks (Hendry and Stearns, 2008) can be strongly reduced in hybrids, due to the breakdown of coadapted gene complexes and outbreeding depression (Muhlfeld *et al.*, 2009).

The second (constant fishing pressure) and third (constant stocking rate and proportions of stocked taxa) assumptions are supported by the observed consistency throughout years and sites of the fishing and stocking patterns, respectively. Such consistency reduces the limitations posed by the lack of available stocking data in the capture records' preceding years, and the impossibility to georeference some of the stocking sites.

The fourth assumption (capture equiprobability) might be violated by a differential susceptibility to fishing. A greater susceptibility to fishing of domesticated trout has been repeatedly observed (Mezzera and Largiadèr, 2001; García-Marín *et al.*, 2008). In our case, domestication effects may make rainbow and non-native brown trouts more susceptible to fishing than marble trout, possibly due to a potential adaptive advantage contributed by the native marble genotype in variably introgressed individuals (García-Marín *et al.*, 2008).

The fifth assumption, namely that the proportions of the stocked taxa are equal to their proportions reaching the catchable size, might be severely violated if the different size classes of the different taxa have different survival rates before reaching MLL. The combined effect of different species-specific ecological traits and different proportions of stocked size classes might be that a larger proportion of the stocked marble trout dies before reaching 40 cm MLL, than those of stocked brown and rainbow trout before reaching 22 cm MLL and 20 cm MLL, respectively.

CONCLUSIONS

The gross mismatch observed between the proportion of stocked and captured salmonids in the study area suggests the presence of a lower stocking effectiveness of *S. marmoratus* relative to the other non-native trout taxa. A plausible working hypothesis to explain this observation is that stocked individuals of *S. marmoratus* have lower survival rates.

Future quantitative studies should quantitatively evaluate the effectiveness of salmonid stocking practices in this system (Wąs-Barcz and Bernaś, 2023), with the overarching goal to implement modern adaptive management and structured decision-making in recreational fisheries (Arlinghaus *et al.*, 2015). Several methods can be employed to discriminate between wild and hatchery-bred individuals, such as alizarin-marked otoliths (Caudron and Champigneulle, 2009) and Visible Implant Elastomers (Sánchez-González and Nicieza, 2021), or genetic parentage analysis (Wąs-Barcz and Bernaś, 2023). If future estimates of stocking effectiveness confirm the low success of mass stocking efforts aimed at enhancing *S. marmoratus* populations, as suggested by this study, further research should focus on identifying the factors contributing to the observed mismatch. Namely, i) estimates of the effects of domestication and introgressive hybridization on survival rates, fishing, and stocking activities; ii) estimates of the annual survival rates of the stocked size classes to catchable size; and iii) estimates of the proportions of different stocked size classes for each salmonid taxon, to facilitate the differential management of culture-based and stock-enhancement fisheries.

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Online supplementary material:
Tab. S1. Rod-and-line surveys conducted in 2020.
Tab. S2. Salmonid taxa collected in rod-and-line surveys conducted in 2020.