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LARGE AND DEEP PERIALPINE LAKES

Fish assemblages in deep Italian subalpine lakes: history and present status with an emphasis on non-native species

Pietro Volta · Erik Jeppesen · Paolo Sala · Silvia Galafassi · Claudio Foglini · Cesare Puzzi · Ian J. Winfield

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Abstract We provide a comprehensive overview of the status of fish assemblages in eight Italian subalpine lakes using multiple data sources: historical records, standardised sampling and fishery catch statistics. Thirty-four fish species were recorded, twenty of which are native, seven introduced historically and another seven introduced recently. The number of fish species in individual lakes has increased by between 25 and 65% from 1855 to the present, with the increase being higher in the larger lakes. Non-native species contributed between 4.0 and 71.5% to standardised catches by numbers and between 4.8 and 65.1% by biomass. Roach *Rutilus rutilus* and pumpkinseed *Lepomis gibbosus* dominated electrofishing and benthic catches by number, while open-water catches were dominated by the coregonids European whitefish *Coregonus lavaretus* and gangfish *Coregonus macrophthalmus*. In terms of biomass, electrofishing catches were dominated by crucian carp *Carassius carassius*, largemouth bass *Micropterus salmoides* and wels catfish *Silurus glanis*, benthic catches were dominated by roach, European whitefish and crucian carp, and open-water catches by coregonids. Commercial fisheries are important ecosystem services provided by subalpine lakes, with their harvests now dominated by non-native species. To deliver effective biodiversity conservation and ecosystem services provision, the prioritisation of targets and interventions of management of non-native species is needed.

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P. Volta (✉) · P. Sala · S. Galafassi · C. Foglini
CNR-Institute of Ecosystem Study, L.go Tonolli 50, 28922 Verbania Pallanza, Italy
e-mail: p.volta@ise.cnr.it

E. Jeppesen
Department of Bioscience, Aarhus University, Vejlsøvej 25, 8600 Silkeborg, Denmark

E. Jeppesen
Sino Danish Centre for Education and Research, Beijing, China

C. Puzzi
GRAIA srl – Gestione e Ricerca Ambientale Ittica Acque, Via Repubblica, 1, 21020 Varano Borghi, Varese, Italy

I. J. Winfield
Lake Ecosystems Group, Centre for Ecology & Hydrology, Lancaster Environment Centre, Library Avenue, Bailrigg, Lancaster, Lancashire LA1 4AP, UK

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Introduction

Large and deep subalpine lakes support unique biodiversity and provide important ecosystem services such as tourism, water supply for agriculture, drinking and power production, and fisheries. In Italy, they constitute more than 80% of the total volume of the country's lakes. Furthermore, they are located in one of the most populated and industrialised areas in Europe which contains approximately 16 million inhabitants and a population density of ca. 300 inhabitants km^{-2} (Premazzi et al., 2003).

Subalpine lakes have been under significant pressure since the first decades of the 20th century. Cultural eutrophication (e.g. Guilizzoni et al., 1982; Marchetto et al., 2004; Salmaso et al., 2007) and chemical pollution of industrial origin (e.g. Binelli & Provini, 2003; Galassi et al., 2006; Poma et al., 2014; Rogora et al., 2016) have impacted and are still impacting lakes and their catchments. Additionally, hydromorphological pressures such as dam construction and the abstraction of water for agriculture, drinking water and power production have significantly affected lake tributaries and outlets, with cascading effects on lacustrine biological communities including fish (e.g. Volta et al., 2016). Recently, climate change has added to this array of changes to the physical, chemical and biological environments of subalpine lakes (e.g. Bettinetti et al., 2008; Jeppesen et al., 2012; Gallina et al., 2013; Callieri et al., 2014) and their catchments (e.g. Saidi et al., 2013, 2015). Finally, the spread of non-native species in these habitats (e.g. Volta & Jepsen, 2008; Ciutti et al., 2011; Volta et al., 2013b, c) has recently become a significant concern in relation to biodiversity conservation.

With their large water volume, diversity of habitats and wide catchment areas, subalpine lakes support diverse fish communities that include species of conservation, recreational and commercial interest (e.g. Volta et al., 2011). Due to the relative isolation of subalpine lakes, the fish communities of these water bodies were comparatively sheltered from species invasions and consequent homogenization until the mid-1850s. These conditions resulted in the development of a significant number of endemic species such as the Italian nase *Chondrostoma soetta* (Bonaparte, 1840), south-Alpine pike *Esox cisalpinus* (Bianco & Delmastro, 2011) and pigo *Rutilus pigus* (Lacepède, 1803). Since the end of the 19th century, introductions of non-native species for both commercial and angling interests have led to a homogenization of fish communities in lakes and rivers across the region (e.g. Gandolfi, 2010; Bianco, 2014). Despite the importance of fish in subalpine lakes, information on species composition is only available for selected periods since the 19th century (e.g. Volta et al., 2011 and references therein), and no comparisons of relative abundances among lakes have been conducted. In addition, an absence of standardised fish sampling protocols has prevented the collection of robustly comparable data. Furthermore, despite concerns raised about invasions by non-native fish species, little is known concerning their quantitative importance (i.e. Castaldelli et al., 2013; Trochine et al., 2017) and their effects on native species, ecosystem functioning and food web interactions (Visconti et al., 2013, 2014; Nõges et al., 2018).

In 2000, the European Union implemented the Water Framework Directive 2000/60/EC (WFD, European Parliament, 2000) that encouraged EU member states to adopt standardised, CEN (European Committee for Standardization)-approved fish sampling methods for the assessment of the ecological status of water bodies. Consequently, many member states, including Italy, have adopted CEN standards (e.g. EN 14011, 2003 ; EN 14757, 2005) which have enabled the undertaking of previously impossible analyses of fish assemblages in European lakes over wide geographical scales and anthropogenic pressure gradients (see Brucet et al., 2013; Arranz et al., 2016; Trochine et al., 2017).

With regard to Italy, implementation of the WFD has enabled the first extensive gathering of information on fish communities by means of standardised sampling and, in particular, lakes in the Alpine ecoregion have been sampled intensively. From 2010 to 2016, the CNR-Institute of Ecosystem Study carried out the first standardised fish sampling campaign in most Italian subalpine lakes. We analysed the data collected by this standardised sampling and combined it with information collected from published and grey literature, as well as from commercial fisheries catch statistics and historic records. The aim

of this paper is to provide a comprehensive overview of the status of fish assemblages in Italian subalpine lakes with a special emphasis on the present relative abundance of non-native species. Observed changes are interpreted in the context of anthropogenic and climatic pressures.

Materials and methods

Study area

The lakes included in the present study are located south of the Alps barrier in the Po river basin (Fig. 1) and all have a fluvio-glacial origin (Bini et al., 1978). Lakes Maggiore, Como, Iseo, Idro and Garda flow directly into the Po river basin, while Lake Orta and Lake Mergozzo are connected with the Lake Maggiore catchment and Lake Mezzola is connected to Lake Como. The maximum depth of the studied lakes ranges from 69 m in Lake Mezzola to 410 m in Lake Como, and their surface areas range from 1.83 km^2 of Lake Mergozzo to 368 km^2 of Lake Garda. All lakes are naturally oligomictic and turnover generally takes place in late February–early March. Lake Iseo and Lake Idro are meromictic. All lakes have experienced warming in recent decades due to ongoing climatic changes (Rogora et al., submitted, this volume). Mixing depth is very variable from lake to lake and in the last three decades the number of complete overturns and the thickness of the mixing layer at winter overturn have decreased markedly (Mosello et al., 2010). The trophic status of the lakes ranges from ultraoligotrophic to eutrophic and their main morphometric and limnological characteristics are shown in the Supplementary Material (Table 1S). We excluded Lake Lugano because data from standardised sampling were not fully available.

Data collection and handling

Historical data

We analysed available literature data extracted from the historical library of the Italian Institute of Hydrobiology (presently CNR-Institute of Ecosystem Study) which holds documents dating from 1750 to 1950, supplemented by further investigations of the

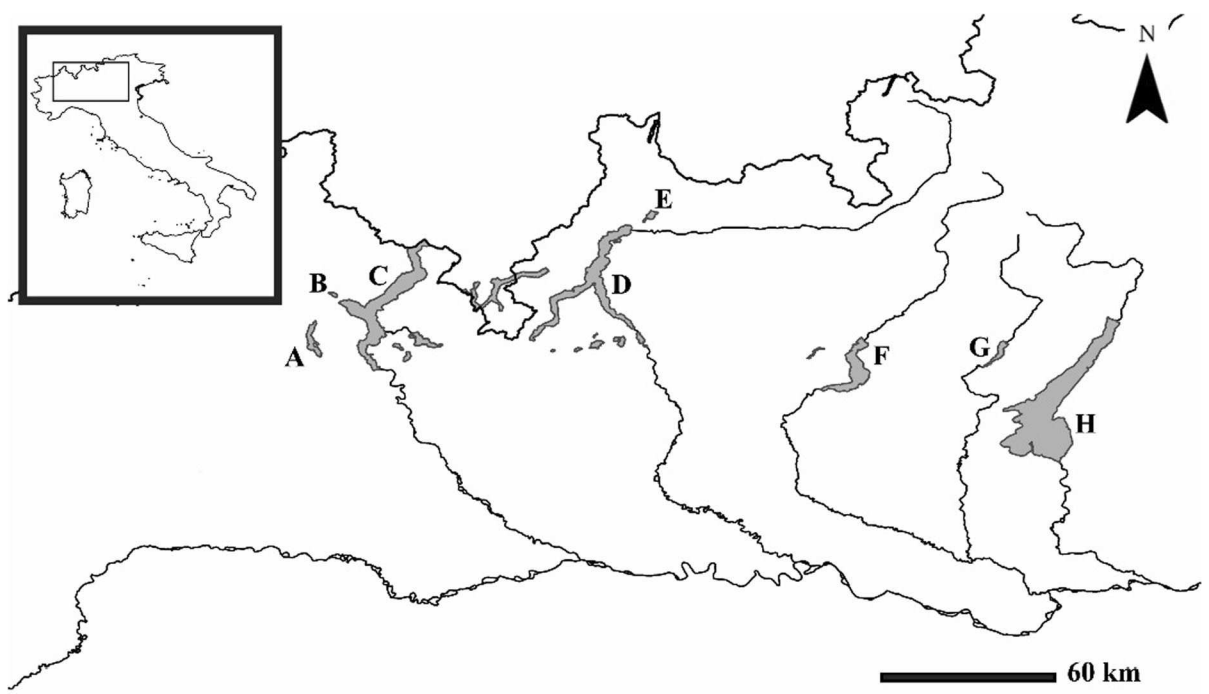

Fig. 1 Geographical distribution of the lakes studied. A = Lake Orta, B = Lake Mergozzo; C = Lake Maggiore; D = Lake Lake Como; E = Lake Mezzola; F = Lake Iseo; G = Lake Idro; H = Lake Garda

published and grey literature (see Online Appendix). Most of the resulting documents are from the period 1860–1940 and include scientific reports from universities and research institutions, together with notes in technical reports of the Ministry of Agriculture and regional authorities on regional economy and commercial trade.

Fisheries catch statistics

Additional recent information was derived on the composition of fish assemblages, commercial harvests (total and species specific) and the number of commercial fishers for each lake from the fishing authorities of Regione Lombardia and the Italian-Swiss Committee for Fisheries, which are responsible of the management of fishing in the study lakes. These historical data were checked against those contained in more recent publications which function as the official reference publications on fish fauna for the Italian Ministry of the Environment (Zerunian, 2004).

Standardised sampling

Fish sampling was carried out between 2010 and 2015 from July to October using benthic and pelagic multimesh gill nets according to a national sampling protocol for fish sampling in lakes, which is based on the CEN gillnet standard (see details of the sampling design in ISPRA (2014); see also Supplementary Material). From 40 to 160 benthic nets were used in each lake depending on area and depth (Supplementary Material, Table 2S). Each benthic net was 40 m long and 1.5 m high and was composed of 16 panels (each 2.5 m long) with mesh sizes ranging from 5.5 to 135 mm. The benthic nets were set from the surface down to 100 m depth and were supplemented with pelagic sampling using 3–12 gill nets linked together, each being 27.5 m long and 6 m high and having 11 panels (with a mesh size ranging from 8 to 55 mm, knot to knot). Four additional nets (40 m long, 6 m high, 4 panels (75, 95, 115 and 135 mm)) were attached to the end of each pelagic net set. In total, each pelagic net set was thus from 242.5 to 435 m long. The nets were set at 10-m intervals from the surface down to 50 m depth. The number of pelagic nets ranged from 14 in Lake Mergozzo to 120 in Lake Garda. Nets were set at dusk between 16.00 and 20.00 h and lifted the following morning between 06.00 and 08.00 h. All fish sampled were sacrificed and subsequently identified to species, measured and weighed.

The littoral area was further evaluated by daytime electrofishing from a boat. The electrofishing device was a built-in-frame EL64GII (Scubla Aquaculture, 7,000 W, 600 V, DC current) with a copper cathode (width 2.5 cm, length 300 cm) and a steel ring anode (thickness 0.8 cm, diameter 50 cm). The Point Abundance Sampling Electrofishing (PASE) method (Copp & Garner, 1995) was used in which the anode is dipped for 20 s at each sampling point. The number of points depended on lake size and habitat complexity and ranged from a minimum of 80 in Lake Mergozzo to a maximum of 154 in Lake Garda (Supplementary Material Table 2S).

Catch Per Unit Effort (CPUE) was calculated as Number Per Unit Effort (NPUE, individuals m^{-2} net or individuals dip^{-1}) and Biomass Per Unit Effort (BPUE, g m^{-2} net or g dip^{-1}). All fish sampled were identified to species, measured (nearest 0.1 cm) and weighed (nearest 0.1 g), before being returned alive to the water.

Typical riverine species, such as lamprey *Lethenteron zanandreai* (Vladykov 1955) and barbel *Barbus plebejus* (Bonaparte 1839) which were sampled in only very small numbers, were excluded from our analyses.

Statistics

Regression analysis was used to test the effects of lake characteristics on fish assemblages. Surface area, maximum depth, total phosphorus and oxygen concentration at winter mixing were used as explanatory variables because they are usually strong predictors of fish species richness, abundance and biomass (e.g. Amarasinghe & Welcomme, 2002; Volta et al., 2011; Brucet et al., 2013). Mean BPUE and NPUE for each sampling gear and the percentage increase of the number of species from 1855 to the present were used as dependent variables.

Results

Fisheries catch statistics

Historically, lake fishing with professional gear (including gill nets, seine nets and traps) was

undertaken by local communities in the near shore for subsistence, whereas fishing in open waters was not a common practice until the end of the 1800 s (e.g. Vagliano, 1710; Cetti, 1862; Pavesi, 1871; Zacchera, 1948). Primarily littoral species such as perch *Perca fluviatilis* (Linnaeus 1758), south-Alpine pike, tench *Tinca tinca* (Linnaeus 1758) and common carp *Cyprinus carpio* (Linnaeus 1758) were the preferred target species. Pelagic fish such as shad *Alosa agone* (Scopoli 1786), bleak *Alburnus arborella* (Bonaparte 1841) and trouts *Salmo* spp. were taken less frequently, usually when they approached the shore or river mouths when spawning, migrating or feeding (e.g. Vagliano, 1710; Pavesi, 1871).

Information on past commercial harvests in Italian subalpine lakes is only intermittent and no reliable time series dating back to 1800 are available. Despite this lack of information, it is still possible to identify important changes in lake fisheries that have occurred during the last two centuries. The historical records indicate significant changes in the composition of catches after the introduction of coregonids and Alpine charr *Salvelinus umbla* (Linnaeus 1758) (from 1880 onwards) and later (from the 1960s) after the adoption of gill nets made of nylon which significantly modified the manner, approach and targeted species of fishing (Zacchera, 1948; Grimaldi, 1972). Moreover, changes in fish harvests have occurred following eutrophication in all lakes, starting after the early 1940s and peaking between the late 1970s and 1990s. For instance, in Lake Maggiore the total annual harvest increased from ca. 300 tons in the late 1800 s as reported by Pavesi (1871) to around 400 tons between the 1910s and 1940s (Zacchera, 1948), and to well in excess of 1,000 tons in the 1980s when eutrophication was at its highest (Volta et al., 2013a, b). Changes in Lake Garda were also noted; the annual harvest increasing from ca. 2,000 tons in the 1950s to 3,000 tons in the 1980s and 1990s (Confortini, 2005). These changes in total harvest were also accompanied by variations in species composition and proportions in the catches. For instance in Lake Maggiore, Vagliano (1710) and later Pavesi (1871) reported shad and bleak to be the most frequently captured species, but after the introduction of European whitefish *Coregonus lavaretus* (Linnaeus 1758) and gangfisch *Coregonus macrophthalmus* (Nüsslin 1882) these two non-native coregonids joined bleak among the most important species in the commercial harvest until the 1980s (Zacchera, 1948; Grimaldi, 1972). The second most notable change is that bleak has been lost from the catches of all lakes in recent years (Regione Lombardia, 2017). The number of commercial fishers has also declined markedly due to changes in local industrial development, temporary fishing bans and changes in the profitability of the catches related to market needs. For instance in Lake Maggiore, after the introduction of fishing bans for shad, bleak, Alpine charr and coregonids from 1996 to 2003 due to DDT (Dichlorodiphenyltrichloroethane) pollution (e.g. Bettinetti et al., 2006; Volta et al., 2009), the number of commercial fishers decreased from around 150 to only 30 individuals.

At present, commercial fishing is only undertaken in 6 of the 8 study lakes: Maggiore, Como, Mezzola, Iseo, Idro and Garda. The total annual harvests, recorded in the statistics of regional fishery offices, range from approximately 2 tons in Lake Idro to 260 tons in Lake Garda (Fig. 2A). The yield per unit lake area ranges from 1.8 kg ha^{-1} $year^{-1}$ in Lake Idro to 10.6 kg ha^{-1} $year^{-1}$ in Lake Mezzola (Fig. 2B), and the annual yield per fisher varies from 536 kg $year^{-1}$ in Lake Iseo to 3901 kg $year^{-1}$ in Lake Maggiore (Fig. 2C).

At present, the most commonly targeted fish species are coregonids (with a dominance of the small-growing gangfisch in the lakes to which it has been introduced), shad and perch, which together contribute between 37.5% in Lake Idro and 92.0% in Lake Como of the total harvest in terms of biomass (Fig. 2D). In some lakes, other species contribute significantly to catches such as tench in Lake Idro (55%) and Lake Iseo (24.6%), roach *Rutilus rutilus* (Linnaeus 1758) in Lake Maggiore (19.6%) and burbot *Lota lota* (Linnaeus 1758) in Lake Mezzola (37.8%).

The contribution (biomass) of non-native species to the commercial harvest ranged from 2.0% in Lake Idro to 75.6% in Lake Maggiore (Fig. 2E). The coregonids dominated the catches of non-native species in all lakes (Fig. 2F), ranging from 68.0% in Lake Maggiore to 100% in Lake Idro. Other species also contributed to the catches, such as roach and wels catfish *Silurus glanis* (Linnaeus 1758) in Lake Maggiore (23.0 and 5.6% by biomass, respectively), Alpine charr in Lake Como (9.9%) and wels catfish (11.8%) in Lake Iseo.

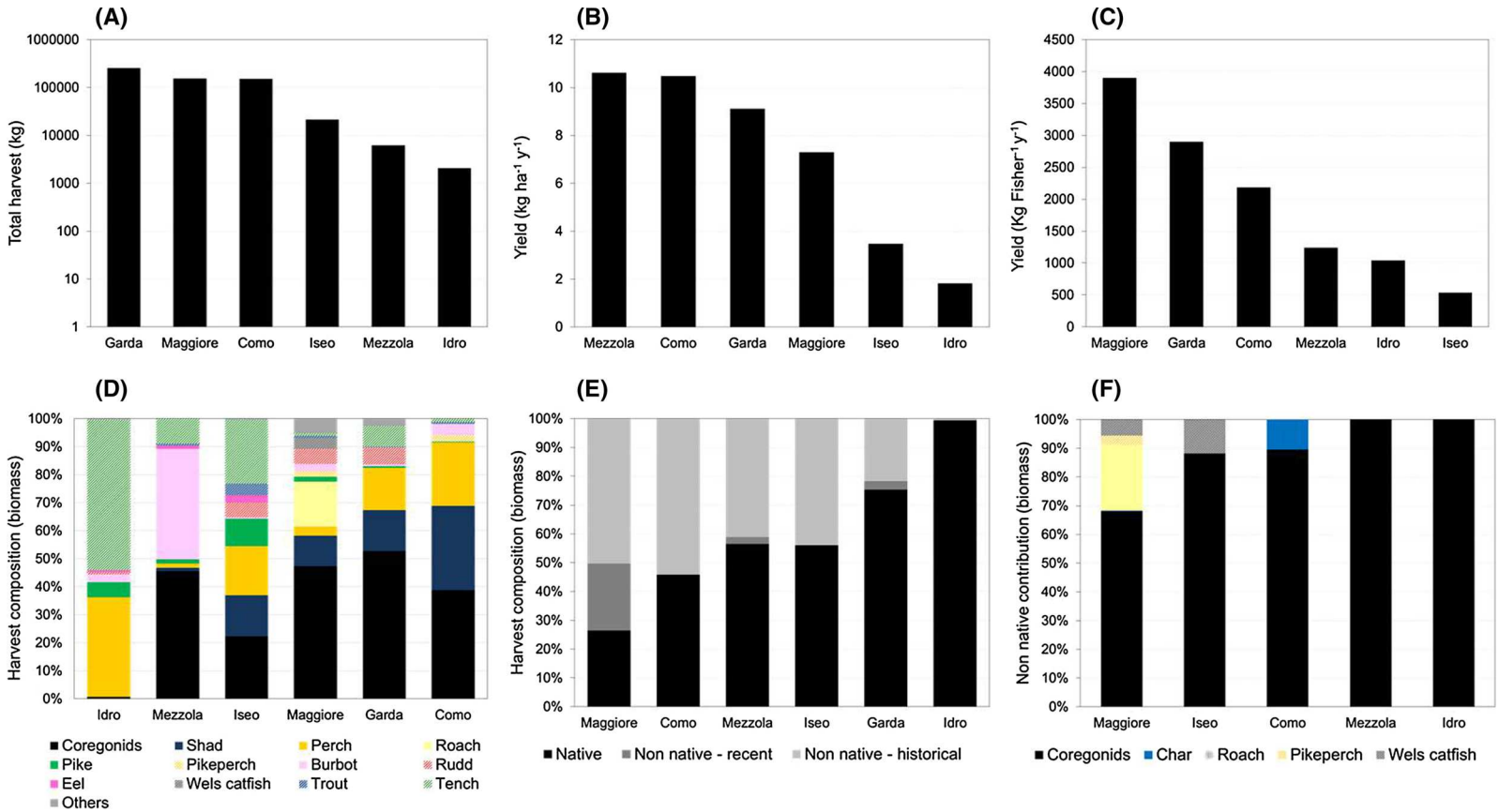

Fig. 2 Commercial fisheries statistics: total annual harvest (**A**); yield per unit area (kg ha^{-1} year^{-1}) (**B**); Catch Per Unit Effort (kg fisher^{-1} year^{-1}) (**C**); harvest species composition (% biomass) (**D**); contribution (% biomass) of native, historical and recent non-native species to the commercial harvest (**E**); species contribution (% biomass) of the non-native component of the harvest (**F**). Commercial fishing is absent in Lakes Orta and Mergozzo

Standardised sampling

A total of 21,771 individuals were sampled, belonging to 33 species (Supplementary Material Table 3S). The highest number of species was recorded in Lake Maggiore and Lake Como (26 species) and the lowest in Lake Orta (13 species). Of the 33 sampled species, 209 were native and 14 were non-native. When considering only information from fishing statistics of the last 10 years, the number of fish species in the study lakes ranged from 16 in Lake Idro to 33 in Lake Maggiore and Lake Garda (Supplementary Material Table 3S).

The NPUE and BPUE of fish catches using electrofishing and benthic and pelagic gill nets are shown in Table 1. Average NPUE from electrofishing ranged from a minimum of 1.1 (± 1.5 s.d.) ind. dip^{-1} in Lake Mezzola to a maximum of 23.1 (± 63.7 s.d.) ind. dip^{-1} in Lake Como. Benthic net NPUE ranged from 0.13 (± 0.13 s.d.) ind. m^{-2} in Lake Mezzola to 1.68 (± 3.33 s.d.) ind m^{-2} in Lake Orta. The NPUE from pelagic nets was two to three orders of magnitude lower than from benthic nets, ranging from 0.0006 (± 0.0014 s.d.) ind. m^{-2} in Lake Idro to 0.033 (± 0.032 s.d.) ind. m^{-2} in Lake Garda. Benthic net BPUE was lowest in Lake Mezzola (9.8 ± 16.7 g m^{-2}) and highest in Lake Orta (26.5 ± 47.5 g m^{-2}), while the BPUE from the pelagic nets ranged from 0.11 (± 0.24 s.d.) g m^{-2} in Lake Idro to 1.83 (± 1.79 s.d.) g m^{-2} in Lake Garda (Table 1).

We tested for statistically significant relationships between NPUE and BPUE, for each of the three types of fishing gears, and total phosphorus, oxygen, lake area and maximum depth. Only BPUE from electrofishing was found to be positively related to total phosphorus ($p = 0.034$, $F = 7.422$, $R^2 = 0.553$). All other relationships were not significant ($p > 0.05$).

Perch, South-alpine pike, pumpkinseed *Lepomis gibbosus* (Linnaeus 1758) and Italian rudd *Scardinius hesperidicus* (Bonaparte 1845) were sampled in all lakes. Perch, italian rudd and roach were recorded with all types of sampling gears, but the other species were only captured by specific gears (Supplementary Material Table 4S). Perch was the overall most abundant species in catches (53.1% by number), but perch and shad were the dominant species by number and biomass in the benthic and pelagic net catches, respectively. Perch contribution to the benthic catches ranged by number from 11.8% in Lake Mergozzo to

Table 1 Number Per Unit Effort (NPUE) and Biomass Per Unit Effort (BPUE) of catches using electrofishing and benthic and pelagic nets

Lake	Electric fishing		Benthic nets		Pelagic nets	
	NPUE (n ind. dip^{-1})	BPUE (g dip^{-1})	NPUE (n ind. m^{-2})	BPUE (g m^{-2})	NPUE (n ind. m^{-2})	BPUE (g m^{-2})
Orta	21.0 (± 42.1)	73.2 (± 181.2)	1.68 (± 3.33)	26.5 (± 47.55)	0.003 (± 0.006)	0.944 (± 1.092)
Mergozzo	2.0 (± 3.5)	75.9 (± 510.9)	0.20 (± 0.31)	15.26 (± 28.15)	0.017 (± 0.040)	0.565 (± 0.902)
Maggiore	1.4 (± 3.0)	24.2 (± 184.9)	0.52 (± 0.94)	13.11 (± 18.37)	0.013 (± 0.014)	1.513 (± 1.163)
Mezzola	1.1 (± 1.5)	115.3 (± 350.5)	0.13 (± 0.13)	9.85 (± 16.71)	0.028 (± 0.017)	1.130 (± 0.974)
Como	23.1 (± 63.1)	612.3 (± 3519.5)	0.48 (± 0.63)	12.63 (± 20.54)	0.014 (± 0.023)	0.641 (± 0.488)
Iseo	12.2 (± 40.7)	339.4 (± 693.5)	0.69 (± 0.87)	24.03 (± 36.02)	0.031 (± 0.044)	1.145 (± 1.473)
Idro	1.7 (± 2.6)	111.0 (± 270.5)	0.16 (± 0.32)	13.35 (± 42.84)	0.0006 (± 0.0014)	0.107 (± 0.238)
Garda	1.5 (± 3.8)	29.8 (± 137.9)	0.33 (± 0.35)	22.24 (± 25.71)	0.033 (± 0.032)	1.834 (± 1.789)

Errors are standard deviations

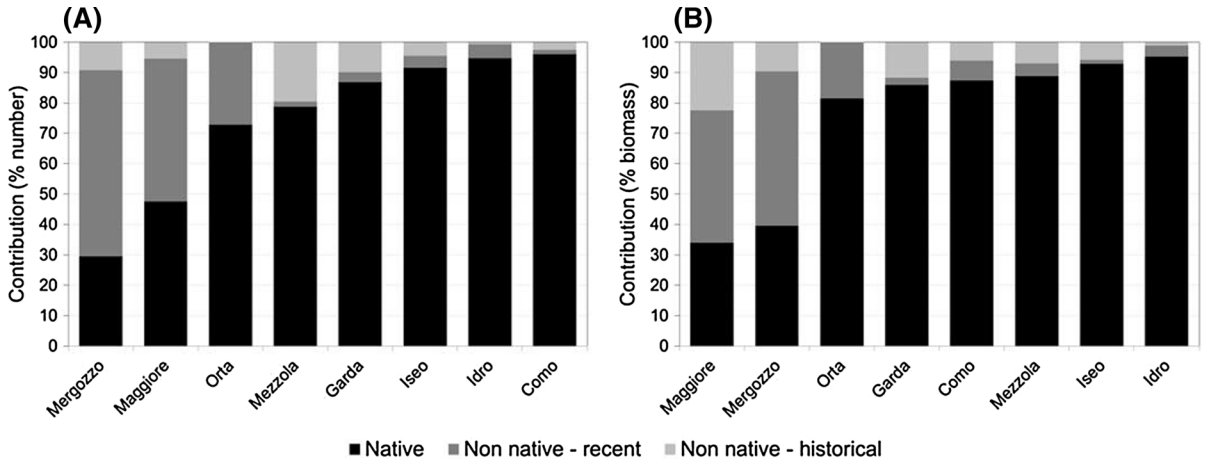

Fig. 3 Commercial fisheries statistics: percentage contribution in terms of number (**A**) and biomass (**B**) to the catches of native, non-native historically and recently introduced species in the eight study lakes

93.1% in Lake Orta (average 58.4%) and by biomass from 6.4% in Lake Idro to 62.1% in Lake Como (average 29.0%). Shad ranged by number and by biomass from 0% in Lakes Orta, Mezzola and Idro to 89.4% by number (average 36.3%) and 88.3% by biomass in Lake Iseo (average 34.9%).

Non-native species contributed (by number) from 4.0% in Lake Como to 71.5% in Lake Mergozzo (Fig. 3A) and in terms of biomass from 4.8% in Lake Idro to 65.1% in Lake Maggiore (Fig. 3B). Pumpkinseed was captured in all lakes, followed by European whitefish and crucian carp *Carassius carassius* (Linnaeus 1758) (6 out of 8 lakes) and pikeperch *Sander lucioperca* (Linnaeus 1758) (5 out of 8 lakes). Other non-native species were captured in 4 or fewer lakes. Roach and pumpkinseed dominated by number the electrofishing catches (Fig. 4A), but in terms of biomass the contributions of crucian carp, largemouth bass *Micropterus salmoides* (Lacepède 1802) and wels catfish were higher (Fig. 4B). Nevertheless, roach, bitterling *Rhodeus amarus* (Bloch 1782) and pumpkinseed dominated by number the benthic nets catches (Fig. 4C), while roach, coregonids, crucian carp and pikeperch constituted the greatest part of the biomass (Fig. 4D). The mesopelagic net catches were dominated by coregonids, both by number (Fig. 4E) and by biomass (Fig. 4F). No non-native species were captured in the pelagic nets in Lake Orta and Lake Idro.

In all lakes, the number of fish species has increased from an average of 19.3 (± 0.8) in year 1850 to 26.7 (± 5.0) in year 2015 (Fig. 5A). The percentage increase in species number ranges from about 28–65% (Fig. 5B). Also, we found that the percentage of non-native species increased with lake volume and area (linear regression, $R^2 = 0.571$, $F = 6.646$, $p = 0.050$ regarding volume and $R^2 = 0.463$, $F = 4.307$, $p = 0.093$, regarding area).

Discussion

This work attempts to provide an overview of the status of the fish assemblages of most of the large and deep Italian subalpine lakes using multiple data sources, including information from historical records, commercial fishing harvests and standardised contemporary fish sampling.

Even though the use of historical data inevitably involves some degree of uncertainty, they provide valuable information on the composition of fish assemblages (Steedman et al., 1996). We found major changes in the richness of the fish communities of the studied lakes during the last two centuries. Our results are consistent with national patterns for Italy revealed by Bianco (2014), who found an overall increase in fish species richness in fresh waters of about 100% from 1866 to 2013. In our study, the highest increase was recorded for Lake Maggiore and the lowest for Lake Iseo. An exception to this pattern of increasing richness is Lake Orta, where a history of pollution has been described in detail in many publications (e.g. Calderoni & Mosello, 1992; Bonacina, 2001). Indeed,

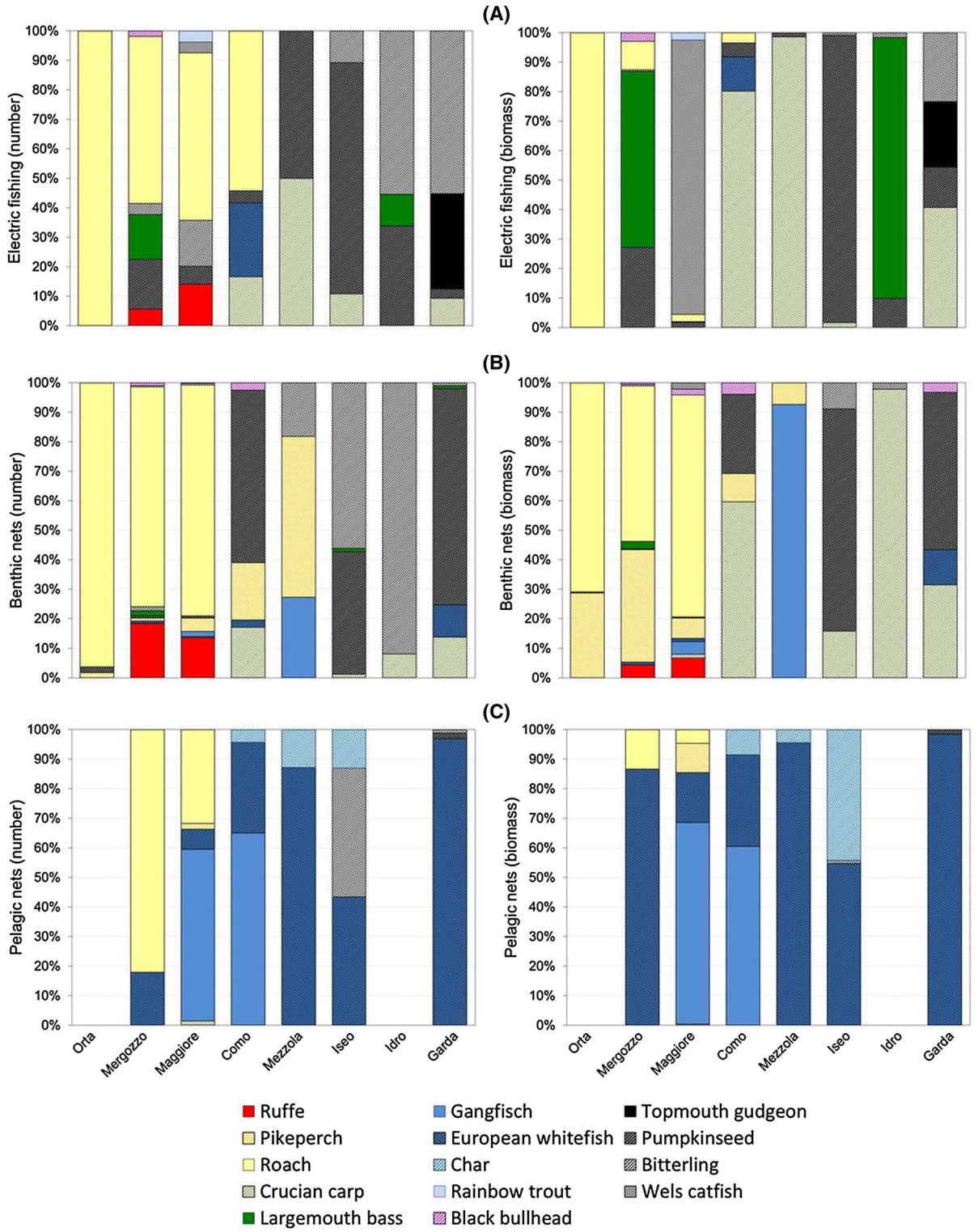

Fig. 4 Percentage contribution in terms of number (left plots) and biomass (right plots) of non-native species to electrofishing (**A**), benthic (**B**) and pelagic (**C**) net catches in the eight study lakes

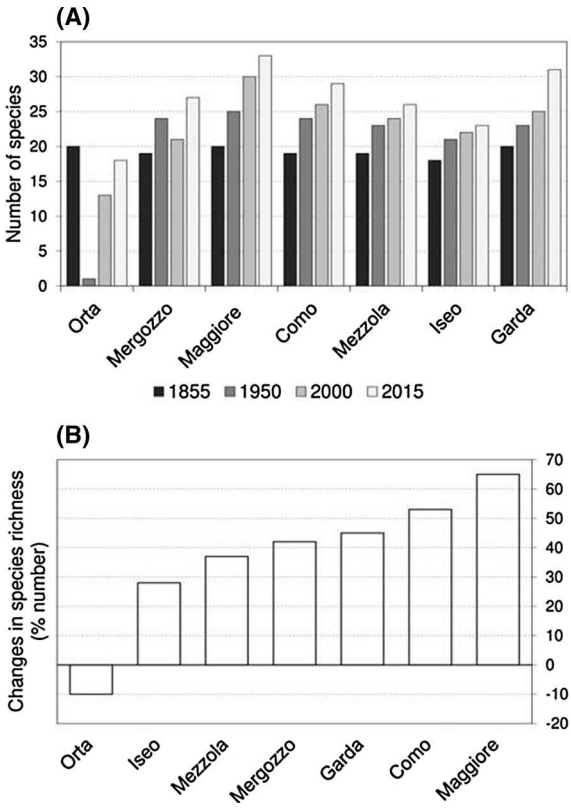

Fig. 5 Fish species richness in the study lakes based on historical and recent data (**A**). Changes in fish species richness (% number) from 1855 to present (**B**)

the number of species inhabiting this lake is still lower than the historical number because not all species have been re-introduced after the recent physico-chemical restoration of the lake (Volta et al., 2016). Our results suggest that large systems have been most capable of accommodating new species. This is not surprising as large and deep lakes offer more habitats and niches to be exploited by introduced species than do smaller ones (Mehner et al., 2005; Juncos et al., 2015).

Changes in fish species richness and composition in subalpine lakes have occurred following the introduction of non-native species of European and American origins in different time periods since the middle 19th century, with the notable exception of common carp which was introduced likely in medieval times (Gherardi et al., 2008) and therefore not classified as non-native in the present analyses. Non-native species were introduced for multiple reasons: to increase the number of species to be exploited by commercial fishers, such as coregonids and Arctic charr (late 19th century and onwards), or by recreational fishers such as pumpkinseed, largemouth bass and black bullhead *Ameiurus melas* from USA in the 1920s; unintentional introductions, probably as live bait (roach) or escapee from put-and-take fisheries (wels catfish) after the 1960s (Volta pers. observations). Up to the 1980s, fishing regulations controlling the use of live bait and fish translocations from different catchments were inadequate and did not consider the seriousness of the potential threat posed by non-native species.

The majority of the introduced species successfully established in a few years without any continuous stocking. The non-native coregonid species *Coregonus lavaretus* and *Coregonus macrophthalmus* became very important in the commercial catches only a decade after their introduction (Grimaldi, 1972). More recently, the same holds true for the less sought after roach, which was recorded for the first time in Lake Maggiore in 1993 as young-of-the-year individuals (Volta, unpubl. data) but had become one of the most abundant species in the lake by the beginning of the 2000s (Volta & Jepsen, 2008). In addition, crucian carp became abundant in many of the study lakes as judged from commercial harvest information, while other introduced non-native species only reached relatively high abundances after some time; for instance pikeperch and, more recently, wels catfish in Lake Maggiore and ruffe *Gymnocephalus cernua* (Linnaeus 1758) in Lake Mergozzo and Lake Maggiore. Pikeperch has been present in Lake Maggiore since at least 1977 when it appeared in the commercial fishery statistics for the first time (Volta et al., 2013a). However, despite its high commercial value, its contribution to the catches was insignificant until the middle of 1990s. Wels catfish was first recorded at the beginning of the 1990s (Volta & Jepsen, 2008) but has only become more frequent in recent commercial catches, with individuals of up to 50 kg being caught. The same holds true for ruffe, being recorded for the first time in Lake Maggiore in the middle of 1990s (Volta & Jepsen, 2008) and now showing a high abundance in standardised sampling catches.

The spread of non-native species in the Italian subalpine lakes in recent decades is not a unique phenomenon within Europe. At the species level, it shows the same pattern as in other physically isolated European countries, such as UK and Ireland. For instance, Winfield et al. (2010, 2011) reported the

invasion of roach and ruffe in Bassenthwaite Lake and Derwent Water in England, in Loch Lomond in Scotland, in Llyn Tegis in Wales and in Lough Neagh in Northern Ireland. The same authors also reported introductions of other typical eurythermal species such as crucian carp and common bream *Abramis brama* (Linnaeus 1758) in some of these lakes. For all these species, the common and most probable pathway of introduction was intentional release or escape of live bait used by anglers fishing for piscivorous fishes (Winfield et al., 2010). The same important pathways of introductions were identified also for other circum-mediterranean countries (Tricarico, 2012).

Finally, it is evident that some of the species intentionally introduced to Italian subalpine lakes did not find suitable environments for completing their life cycles. This is the case for coho salmon *Oncorhynchus kisutch* (Walbaum 1792), which was introduced to Lake Garda in the late 1960s (Amori et al., 1993; Confortini, 2005). The rainbow trout *Oncorhynchus mykiss* (Walbaum 1792) has also been introduced in high numbers to all deep subalpine lakes, and to almost all rivers, for fishing purposes on multiple occasions since the middle of the 19th century. No self-sustaining populations of these Pacific salmonids have been established. The same seems true for some other species recently recorded, such as Asian carp *Hypophthalmichthys nobilis* (Richardson 1845) in Lake Maggiore (Volta, unpubl. data) and common bream in Lake Garda (Confortini, 2005). In the case of the latter, however, there are cases of successful establishment in other water bodies in the Po River Basin (River Po Authority-Autorità di Bacino del Fiume Po, 2008; Volta et al., 2013c).

Our results show that the abundance and biomass of recently introduced non-native species including roach and ruffe are high in some lakes such as Lakes Maggiore, Mergozzo and Orta, but not in all of the study lakes. This establishment holds true for all the habitats investigated (littoral, benthic and, for roach, pelagic), indicating that the changes in the fish assemblages of these lakes have been particularly dramatic. At least for the roach, data on commercial fishing harvests corroborate our findings. Roach and ruffe are omnivorous species (Volta & Jepsen, 2008; Volta et al., 2013b) and so may have an advantage in oligotrophic environments, where they can exploit a large variety of food resources in contrast to some of the native species. Furthermore, their population dynamics may have been accelerated and strengthened by climate change via water warming, as already reported for the same species in other European water bodies (Jeppesen et al., 2012, 2014) and for similar tolerant species elsewhere (Casselman, 2002).

Roach in particular is among the most abundant non-native species in the present surveys. It was recently introduced in the Po River basin (Delmastro & Balma, 1991) and has become one of the most abundant species in many, but not all, of the studied lakes (Volta & Jepsen, 2008; Volta et al., 2013c, 2016). Our data indicate high abundances of roach in oligotrophic environments (Lakes Orta, Mergozzo, Maggiore) but low or negligible abundances in meso-eutrophic lakes, such as Lakes Como and Garda. At the time of the roach appearance in Lakes Garda, Como and Maggiore in the late 1990s, the local trophic status differed significantly among those lakes. Lakes Como and Garda were meso-eutrophic while Lake Maggiore was oligotrophic (Mosello et al., 2010). It is possible that the population of perch in the meso-eutrophic Lakes Como and Garda was dominated by large and so piscivorous individuals, as is usually the case in meso-eutrophic cold lakes (Persson et al., 1991; Olin et al., 2002), potentially preventing the invasion of roach by a stronger predation pressure on roach juveniles. While the perch population in Lake Maggiore and likely then predation on roach had declined following oligotrophication (Volta et al., 2013a, b). As pointed out by Van de Woolfshaar et al. (2006) oligotrophic environments seem to be more beneficial for roach than perch in intraguild predation systems where perch is the top predator and roach is an intermediate consumer. Interestingly in such oligotrophic systems, small-sized predators may compete with their prey, whereby the latter may limit the extent to which potentially piscivorous individuals reach a larger piscivorous stage, inducing an interspecific juvenile bottleneck in the predator population (Byström et al., 1998).

The extent to which the presence of non-native fish species impacts native fish biodiversity and ecosystem functioning in large subalpine lakes is not clear and many confounding factors can obscure direct cause–effect relationships. Our data indicate that no truly lacustrine native species have been lost during the last two centuries in Italian subalpine lakes, with the exception of the recent loss in the 1990s in Lake Garda of two small-bodied species, stone loach *Barbatula*

barbatula (Linnaeus 1758) and three-spined stickleback *Gasterosteus aculeatus* (Linnaeus 1758) (Confortini, 2005). The reasons for the disappearances of these species are unknown, but long-term limnological information (see Mosello et al., 2010) suggests that their extinction might be related to peaking eutrophication and concurrent water warming (see also Salmaso & Mosello, 2010) as both are sensitive and coolwater species. For instance, Moran et al. (2010) showed experimentally that warming reduced three-spined stickleback population biomass by 60% (population size 76%) and nutrient-addition reduced biomass by about 80% (population size 95%).

While the impact of non-native species on native species richness seems negligible at present, impacts on native species population dynamics and abundances have probably occurred as suggested by variations in the composition of commercial harvests over the last two centuries. The extents to which these changes depend on species interactions or to co-occurring environmental changes are very difficult to disentangle. For instance, for the majority of lakes, little is known about the ecological interactions among native and non-native species, such as food niche overlap, predation and habitat competition (but see e.g. Visconti et al., 2013, 2014). However, our data and previous analyses (e.g. Jeppesen et al., 2012; Nõges et al., 2018) suggest that climatic changes, trophic evolution of lakes (both oligotrophication and eutrophication) and fishing pressure may play significant roles in shaping food web interactions and fish population dynamics. However, in order to determine the precise mechanisms involved more detailed investigations are needed.

Among the most recent non-native species introduced to subalpine lakes, wels catfish is probably the one giving rise to most concern. Our data show that this species is present in four out of the eight investigated lakes. Again, Lake Maggiore has the highest density of this species. Although it was recorded only sporadically by commercial fishers up to 2010, it now constitutes an important proportion of the commercial harvest indicating that its population has grown significantly. Our sampling data and commercial harvest information, corroborated by personal communications (Volta data unpublished results.) indicate that wels catfish is caught both in the littoral and in open waters, reflecting its ability to exploit very diverse environments. This species is the largest freshwater fish in Europe and is known to exploit a wide range of food resources, such that it is considered an invasive fish species that presents a considerable risk to native species and ecosystems. Copp et al. (2009), however, have argued that wels catfish is unlikely to exert a trophic pressure on native fishes except under circumstances where other human impacts are already present. Examples of invasions by this species have been reported for rivers or reservoirs in Mediterranean countries (e.g. Carol et al., 2007, 2009), but no significant examples are available for large, deep and oligotrophic lakes at the same latitudes. As a result, its impact on native species and food web structure is unpredictable.

Although currently limited to Lake Garda, the occurrence of topmouth gudgeon *Pseudorasbora parva* (Nichols 1925) is also worth noting. This small-bodied fish is considered among the top worst invasive non-native species in Europe (EU 1141, 2016). Due to its biology and ecology, including aggressive behaviour, fecund reproductive traits and high capacity of dispersal, it must be considered a new potential threat to local fish species. The introduction of topmouth gudgeon in Lake Garda dates back to 1995 (Confortini, 2005), but at present its ecological impact, if any, on local fish species is unknown. However, the potential impacts of this species are numerous as the species is a known facultative parasite (Trombitskiy & Kakhovskiy, 1987; Libosvàrský et al., 1990) and a host of the Rosette Agent (Gozlan et al., 2005).

Subtle but persistent effects of invasions on native biodiversity, such as genetic introgression and hybridization, may also occur. For instance, by using molecular genetics techniques, several cases of genetic introgression have been demonstrated in the wild between the non-native brown trout *Salmo trutta* (Linnaeus 1758) (Atlantic haplotype) and the native endemic marble trout *Salmo marmoratus* (Cuvier 1829) (e.g. Meraner et al., 2013), pike *Esox lucius* (Linnaeus 1758) and endemic south-Alpine pike (e.g. Gandolfi et al., 2017), and pigo and roach (Kottelat & Freyhof, 2007). Our species identification was based only on phenotypic discrimination and our data thus unfortunately lack such genetic details. However, due to massive stocking for fishing purposes in many subalpine water bodies, species-specific genetic introgressions of pike, marble trout, native brown trout and pigo are very likely to have occurred.

Fisheries play an important role among the services provided by subalpine lakes. Two hundred and thirteen fishermen are involved in this sector with a total economic return of about 4.5 million Euro per year, calculated as total revenues from fish sold at the market at an average species price of 7 Euro per kg (Regione Lombardia, 2017). The harvest is significantly higher in the most touristic locations such as Lakes Maggiore, Como and Garda compared to other lakes. Interestingly, the harvest per-capita is highest in the more oligotrophic Lake Maggiore indicating a very high fishing pressure (Nõges et al., 2018) compared to the other more eutrophic lakes. Species composition and proportions in the harvest are quite different from lake to lake, but, in general, catches from small lakes, such as Lakes Idro and Mezzola, rely more on littoral species such as perch and burbot while in larger water bodies such as Lakes Garda, Maggiore and Como they rely more on pelagic species such as coregonids and shad. Differences in catches are due both to differences in species abundances in each lake arising from lake characteristics (Persson et al., 1991; Mehner et al., 2005; Volta et al., 2011), but also to differences in local market preferences. Indeed, while fish caught in small lakes are usually sold as raw fillets or smoked directly by fishers in their villages, the large amounts of fish caught in large lakes are often sold at a central fish market in Milan. It is also worth mentioning that some, but not all, of the established non-native species provide an important ecosystem service by supporting commercial fisheries and thus constitute an important factor in local economies. For instance, coregonids, pikeperch and roach constituted up to 90% of the total commercial harvest in subalpine lakes and directly strongly support the local economy as well as, more indirectly, the wider tourism economy.

The management of coregonids in subalpine lakes is a good example of the difficulties involved in combining legislation and management of non-native species with social and economic interests. According to present Italian law (based on the Habitat Directive 92/43/EC), the non-native coregonids must be excluded from all supportive captive breeding activities and/or further introductions. On the other hand, because coregonids constitute a considerable income to fishermen but are threatened by lake water level fluctuations, their stocking is not only permitted according to regional laws but, in some cases, even financially supported by municipal or regional fishing authorities which build hatcheries and facilities for their rearing. For instance, in Lake Garda at least 40 million larvae of European whitefish derived from eggs taken from local spawners are stocked every year. The same holds true for Lakes Iseo and Como and other lakes such as the large and deep volcanic lakes located in central Italy. This is probably one of the most evident critical points of the Italian approach to the problem of non-native fish species management in fresh waters.

The management of non-native species living established for many years in well-connected freshwater systems is not simple. Removal and density control would require an enormous effort and the impact of any such intervention would probably be weak and short-lived. Prevention, public awareness and education are probably the most preferred management tools for avoiding the spread of non-native species (Brenmer & Park, 2007; Gozlan, 2008), and for fish in large lakes and rivers they are the only feasible options (Boon & Bean, 2011). However, how to manage the species already present is also a key point. We suggest that non-native species already established or at least recorded should be categorised according to different criteria, such as proven harmfulness to native biodiversity and ecosystem functioning, social and economic value as well as the feasibility of density control or removal and invasiveness. After arriving at such a typology, the priorities for their management should be elaborated (Gozlan, 2008). A similar approach has been used in the recent "Three-Year Program for the Fishery and Aquaculture of Regione Lombardia" (Regione Lombardia, 2017), in which non-native species were categorised based on the aforementioned criteria in order to provide priorities for their management and control. Although potentially controversial, this approach ensures that the efforts and resources required for the most achievable and concrete targets are estimated. We admit that this is a difficult task and that quantification of the amount of ecosystem services provided by a non-native species is open to debate. In addition, the categorisation of species based on such characteristics may prove difficult as these may change from site to site depending on morphometry and limnology, biological interactions, climatic variables and local market preferences. However, in the light of an adaptive management of fish communities to obtain effective biodiversity conservation, the need for

prioritisation of targets and interventions is urgent and more collaboration among fishing authorities and freshwater conservation managers is urgently needed (Winfield, 2016).

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