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RESEARCH ARTICLE OPEN ACCESS

Rehabilitation of whitefish fisheries in lakes Geneva and Bourget during the eutrophication period: assessing socio-economic impacts through large collaborative research

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Abstract – Lakes provide ecosystem services such as water resources, tourism, biodiversity, and fishing, and therefore their management represents important societal challenges. Since the early 1960s, significant anthropogenic pressures (human population growth and industrial and agricultural development) have accelerated the degradation of lake ecosystems, leading to eutrophication and subsequent increased sedimentation on fish spawning grounds and decreased dissolved oxygen concentrations. This negatively affects the natural recruitment of whitefish (*Coregonus lavaretus*), an emblematic species of peri-alpine lakes. Over the years, such processes have resulted in a decline in the whitefish population stock, thereby leading to a drastic drop in catch and causing major economic losses. From the beginning of the 1980s, alongside the restoration of water quality, professional fishers, recreational anglers, state services, and researchers from INRA worked together to develop an applied research program called 'Pacage Lacustre' to improve and optimise salmonid stocking. The goal was to counterbalance the low juvenile natural recruitment and maintain whitefish populations. Here, we retrospectively retrace the key stages of this research program and its main impacts on society. Collaborative efforts played a key role in rehabilitating whitefish populations in lakes Geneva and Bourget, particularly when their abundances were the lowest. Therefore, these efforts had a substantial impact on preserving commercial and recreational fishery activities, in addition to favorable societal impacts, highlighting the importance of such collaborative work.

Keywords: Research impact / fishery management / stocking / salmonids / citizen science

1 Introduction

Lakes provide numerous ecosystem services worldwide, such as water resources, tourism, biodiversity, and fisheries; therefore, their preservation presents a major societal challenge (Reynaud and Lanzanova, 2017; Sterner *et al.,* 2020; Inácio *et al*., 2022). In France, the management of peri-alpine lakes is not only a regional challenge, but also a national and international one. Peri-alpine lakes are the largest bodies of freshwater in France; moreover, water from Lake Geneva is shared with Switzerland (Bravard and Clémens, 2008; Pflieger and Bréthaut, 2012). These lakes have substantial fishing potential and represent a renewable resource that has long been used by professional fishers and recreational anglers (Loup, 1950; Bardel, 1956). Similar fish communities are found in these lakes and mainly comprise cyprinids, esocids, and the heavily fished percids and salmonids (Gerdeaux *et al*., 2006).

Since the 1950s, lake ecosystem degradation has intensified due to an increase in anthropogenic pressure due to population growth, expanded tourism, and industrial and agricultural development (Jenny *et al.,* 2020). Between the early 1950s and late 1970s, lakes Geneva and Bourget underwent a period of pronounced eutrophication (Baulaz *et al*., 2021) which considerably affected water quality and associated lake ecosystem services, similar to many lakes around the world at that time (Carpenter, 2005; Schindler, 2012, Schindler, 2016). The desirable threshold of total phosphorous is 15 µg/L to limit excessive algal production and impacts on ecosystem services (OCDE, 1982; Baulaz *et al*., 2021). In 1979, total phosphorus values reached peak values of 90 µg/L in Lake Geneva and 172 µg/L in Lake Bourget (Rimet et al., 2020).

Salmonids, especially whitefish (*Coregonus lavaretus),* receive special attention and undergo extensive scientific monitoring in these two lakes because they are heritage species with high economic value (Gerdeaux *et al.,* 2006*;* Anneville *et al.,* 2015). However, they are highly sensitive to environmental deterioration (Alexander *et al*., 2017). During whitefish reproduction, eggs are deposited on lake substrates at

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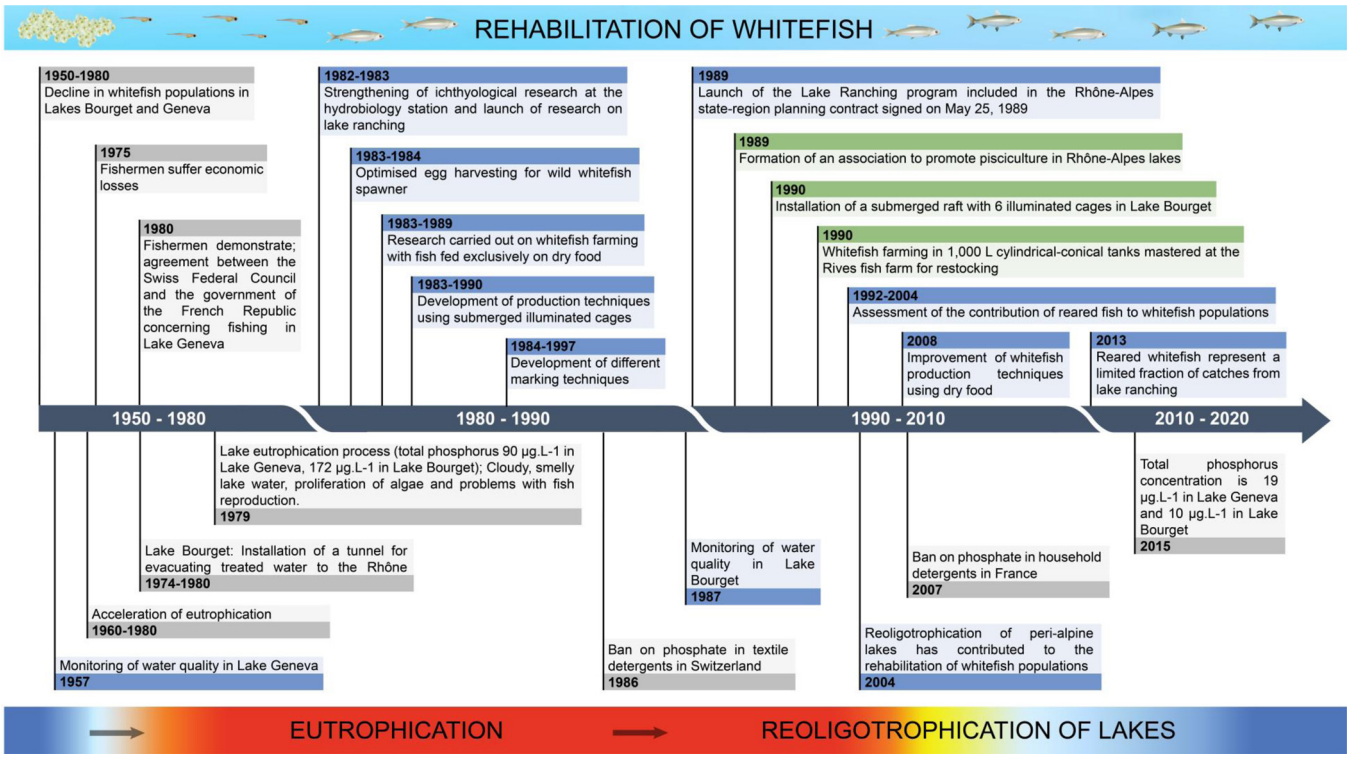

Fig. 1. Chronology of the key phases in the research program of whitefish rehabilitation and reoligotrophication in lakes Bourget and Geneva (1950–2015; adapted from Rogissart *et al*., 2023).

specific temperatures and oxygen levels (Eckmann, 2013). Thus, eutrophication affects the survival of eggs and juveniles due to increased sedimentation rates on spawning grounds and decreased oxygen availability, particularly at the water-sediment interface (Muller and Stadelmann, 2004; Eckmann, 2013). Therefore, during the eutrophication period, recruitment was negatively affected and led to sharp declines in whitefish populations (Gerdeaux *et al*., 2004) and, consequently, major economic losses for fishing companies and related professions such as fishers, fishmongers, and catering (Gagnaire, 1988). In addition, perch (*Perca fluviatilis*) recruitment in Lake Geneva was extremely poor in the early 1980s due to very poor weather conditions (Dubois *et al*., 2008). During these years, perch catches were notably low and led to a social crisis because they represented another crucial source of income for professional fishers.

Supported by anglers and environmental organisations, professional fishers raised these issues with public authorities and elected officials. These protests led to the strengthening of the local fish research group at the Institut National de la Recherche Agronomique (INRA) laboratory in Thonon-les-bains, France, in 1983 (Olive, 1986). The group aimed to intensify research efforts on fish ecology and fishery management in lakes Geneva and Bourget. The works mainly focused on understanding fish reproduction (Gillet, 1989) and the effects of environmental factors on fish dynamics (Gerdeaux, 2004). Moreover, a fish stocking program called 'Pacage lacustre' ('Lake Ranching'; Champigneulle, 1996) was developed to restore lake salmonid populations (Champigneulle, 1989). The goal was to evaluate and refine methods for stocking whitefish populations across peri-alpine lakes using native breeding stock to rehabilitate populations (Aronson *et al*., 1993) and prevent the disappearance of professional fishing, a vital component of local and regional economies (Champigneulle *et al*., 2001). The purpose of this study was to retrospectively outline the key phases of the research program (Fig. 1) and examine its diverse impacts on society (Rogissart *et al.,* 2023), and was inspired by the research impact analysis method (Analyse de l'Impact Sociétal de la Recherche: ASIRPA; see Supplementary Information) developed by the National Research Institute for Agriculture, Food, and the Environment (INRAE), previously called INRA (Joly *et al*., 2015; Smit and Hessels, 2021).

We organized the manuscript into five sections. The first section describes the study sites, whitefish catch, and main research actions conducted by the researchers in this project. The second section highlights the stocking techniques and key outcomes of the whitefish population rehabilitation in lakes Geneva and Bourget. The third section describes and highlights the numerous and important impacts on society of the 'Pacage lacustre' program, including the knowledge acquired through collaborative research among fishers, anglers, stakeholders, authorities, and scientists. The fourth section presents the limitations and threats of stocking practices on fish communities and ecosystems, and the fifth details future challenges of whitefish rehabilitation in lakes.

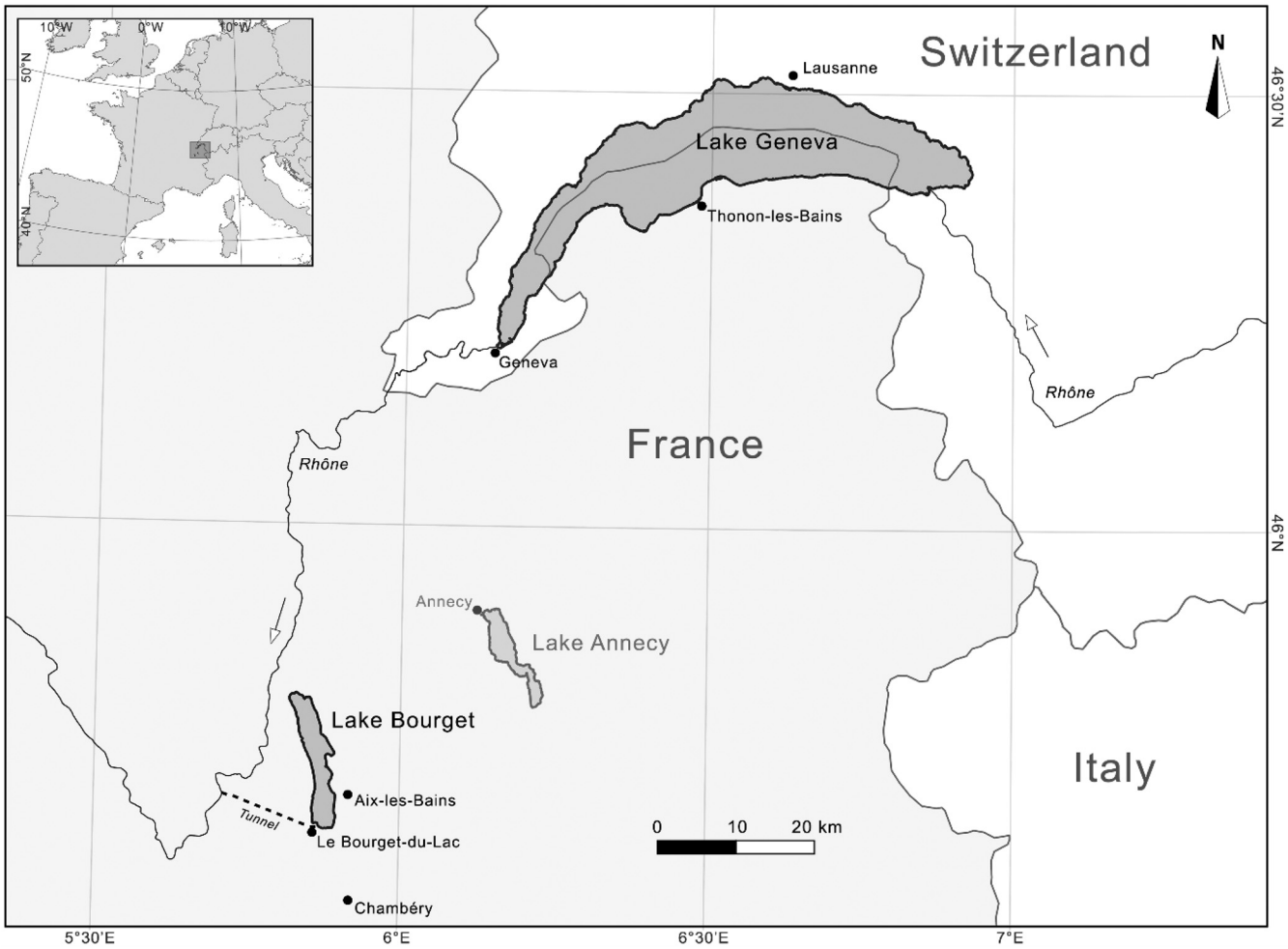

Fig. 2. Location of the two peri-Alpine lakes studied (lakes Bourget and Geneva). Dashed lines indicate the tunnel excavated through the Chat Mountain range to divert the treated sewage from the Chambery, Aix-les-Bains, and le Bourget-du-Lac drainage stations into the river Rhône.

2 Study sites, whitefish catch data, and key research activities

2.1 Study sites

Lake Geneva is the largest natural alpine lake of Western Europe (surface area = 582 km^2 46°27′N – 6°32′E), located on the border between France and Switzerland (Fig. 2), with a maximum depth of up to 309 meters (mean depth = 157 m; Rimet *et al.*, 2020) and is considered as a warm monomictic lake (Anneville *et al.*, 2017). Lake Bourget is the largest natural French lake entirely within France (Fig. 2), located on the western edge of the Alps (surface area = 44.5 km^2; 45°44′N – 5°52′E) and is a deep monomictic lake (maximum depth = 145 m; mean depth = 85 m).

In the context of pronounced eutrophication (Anneville *et al.*, 2017; Baulaz *et al.*, 2021), measures were implemented in Lake Geneva in the early 1970s to decrease phosphorus levels and preserve the water quality (Fig. 3). These measures involved constructing sewage plants on the whole watershed, reducing external phosphorus loading via improving water treatment, and reducing the use of phosphorus to fertilize soils. Furthermore, in 1986, Switzerland prohibited polyphosphates in laundry detergent (Rapin and Gerdeaux, 2013). In France, phosphates have only been banned in domestic laundry detergents since 2007 (National Decree no. 2007-491).

In the same period, between 1974 and 1980, sewage plants around Lake Bourget (Chambéry, Aix-les-Bains and Bourget-du-Lac; France) were also improved to reduce eutrophication. To reduce the discharge of wastewater into the lake (Fig. 3), a tunnel of 12.2 km was dug in a nearby mountain (Massif de l'Epine) to transport it toward the river Rhône. This system is more adequately equipped to sustain the discharge levels evaluated at 40 g/m^2/year of total inorganic nitrogen and 6.72 g/m^2/year of total phosphorus. These levels represent respectively four and nearly ten times the dangerous load (Balland *et al.*, 1977). This engineering action significantly reduced eutrophication in Lake Bourget and helped improve the poor water quality (Jacquet *et al.*, 2014).

The fight against phosphorus inputs included reducing polluting discharges from anthropogenic activities and appropriate management of each lake and its watershed (Loizeau and Dominik, 2005). Physicochemical and biological data (phosphorus, phyto- and zooplankton levels, water

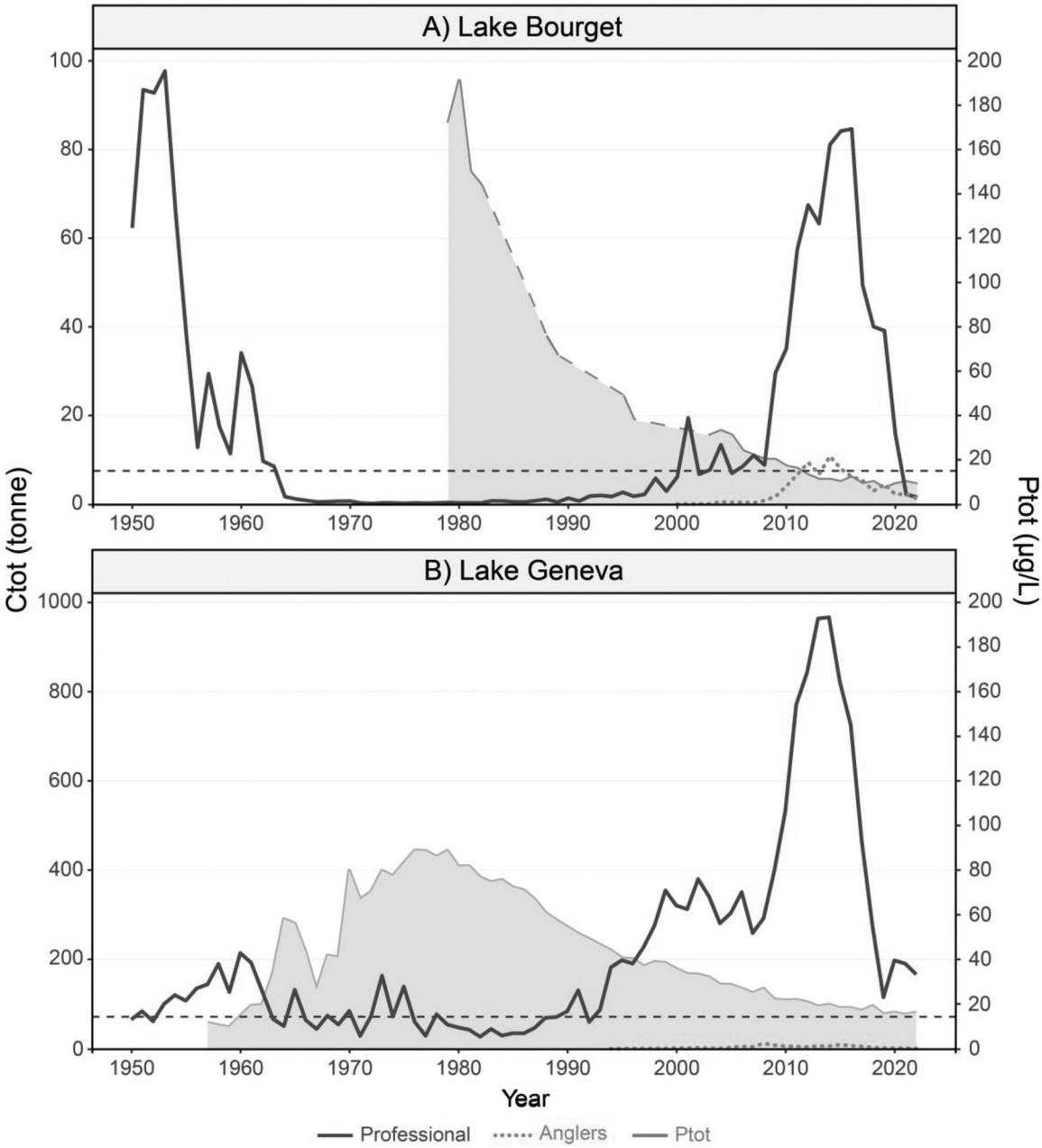

Fig. 3. Change in total whitefish (*Coregonus spp.*) catches (Ctot) by professional fishers (solid blue curve) and recreational anglers (dotted orange curve) in tons (Jacquet *et al.*, 2022; Goulon *et al.*, 2023), along with weighted mean annual concentrations of total phosphorus (Ptot; data from SOERE SI-OLA; Rimet *et al.*, 2020) from 1950 to 2022 in Lake Bourget (A) and Lake Geneva (B). The dashed grey line indicates extrapolated data. The dashed horizontal black line highlights the 15 µg/L Ptot threshold recommended by OCDE (1982).

transparency, oxygen, *etc.*) have been collected since 1957 and 1987 from lakes Geneva and Bourget, respectively (Rimet *et al.*, 2020). The phosphorus concentrations decreased in both lakes beginning in the 1980s, initiating a process of reoligotrophication, leading to the status of Lake Geneva as a meso-eutrophic lake. While phosphorous levels dropped below 20 µg/L in 2013, the current level remains above the 15 µg/L threshold (Fig. 3). Lake Bourget is much smaller than Lake Geneva, with a volume about 30 times smaller and a mean depth 2 times shallower. Lake Bourget became oligotrophic in 2012, with phosphorus concentrations falling below the 15 µg/L threshold. In 2021, total phosphorus concentrations were 16 µg/L in Lake Geneva and 9.5 µg/L in Lake Bourget (Fig. 3). Natural recruitment of whitefish was enhanced by improving water quality (Gerdeaux, 2004).

2.2 Whitefish catches in the two lakes

The European whitefish is a mainly lake-dwelling stenothermic fish belonging to the Salmonidae family and Coregoninae (Bonaparte, 1845) subfamily. Genetic studies (Bernatchez and Dodson, 1994) proposed that populations in

the alpine region should be considered as a single species complex, defined as the *C. lavaretus* (L.) species complex (Østbye *et al*., 2005). This species is mainly found in cold environments such as lakes, reservoirs, and ponds, and has a zooplanktivorous diet (Anneville and Hamelet, 2018). Whitefish fisheries have a high socioeconomic value in peri-alpine lakes (Gagnaire, 1988). In Lake Geneva, whitefish catches fell from 100–200 t/year in the 1950s to 30–50 t/year from 1974 to 1984 (Fig. 3) and in Lake Bourget, whitefish catches collapsed from 100 t/year before 1950 to approximately 0.1 t/year from 1970 to 1980 (Fig. 3; Jacquet *et al*., 2022; Goulon *et al*., 2023).

2.3 Important research actions conducted by the scientific team

Scientific collaborations, bibliographic syntheses and numerous missions to countries such as Czechoslovakia, Poland, East Germany, and Finland have been undertaken to examine the different methodologies applied to whitefish population rehabilitation and to better understand whitefish ecology (Champigneulle, 1983, 1985; Gillet, 1989). The factors limiting the natural reproduction of whitefish were thoroughly analysed, focusing on their habitats, bioecological requirements, and stock dynamics. Eutrophication has emerged as the main force influencing trophic resources, while hindering natural recruitment (Champigneulle, 1985; Champigneulle *et al.,* 2001). Significant changes in whitefish growth have been observed in Lake Geneva, where a sharp increase in size-at-age between 1953 and 1982 (Fig. S3 A) meant whitefish reached 30 cm during the third year compared their fifth year in the 1950s (Champigneulle *et al*., 1983). This change was attributed to the ~4X increase in zooplankton biomass between the early 1960s and early 1980s (Fig. S3 B). Consequently, fish reached the legal capture size (30 cm) prematurely, potentially before they reproduced, thereby affecting the number of spawners and recruitment. These conclusions, supported by a bibliographical synthesis (Champigneulle, 1985), confirm that the release of whitefish juveniles in peri-alpine lakes could help rehabilitate and/or sustain whitefish populations. Therefore, the 'Pacage Lacustre' strategy was implemented to optimise the rearing production of juvenile fish in terms of quantity and quality. This strategy was also cost-effective because it controlled the supply of fish eggs to the natural environment.

Monitoring whitefish release and assessing the relevance of this stocking strategy was essential throughout this process. Assessing the effectiveness of whitefish stockings was challenging, particularly because of extremely low recruitment. Therefore, marking and control surveys on captured whitefish were essential to accurately determine the proportion of fish originating from supportive breeding versus those originating from natural recruitment (Champigneulle and Escomel, 1984; Rojas-Beltran *et al*., 1995). This integrated approach, which combines in-depth knowledge of whitefish ecology, monitoring of releases, well-defined management objectives, and rigorous evaluation of stocking, has been key to the rehabilitation and sustainable management of whitefish populations in lakes Geneva and Bourget.

3 Stocking techniques, methodology development, and results

3.1 Controlling the supply of eggs from wild spawners

From 1983 onwards, stocking was carried out in lakes Geneva and Bourget using only eggs collected from their respective wild spawners, to avoid the introduction of non-native stocks as was previously done using juveniles from different countries (Büttiker, 2005). Professional fishers catch spawners during the reproductive period (from November to January). Prior to 1983, during spawner harvests, a large percentage of gillnet catch was males (>60%) and a majority of captured females were non-ovulated (>55%). These catches resulted in a substantial loss of potential eggs (Champigneulle *et al*., 1983) and a poor balance between the number of females and males. To optimise egg harvesting while reducing costs, the usual practices were changed. First, gillnet meshes were optimised (square or diamond-shaped, 40 mm at Bourget and 44 mm at Lake Geneva) to catch spawners and limit the capture of younger males, who tend to mature earlier than females (Champigneulle *et al*., 2001). Non-ovulated females were kept on fish farms until ovulation, contributing to improved egg harvests (Champigneulle *et al*., 1983). Experimental studies assessed variations in the rate of ovulation in females over time and space to identify the most favourable time and location for spawning (Champigneulle *et al*., 1994, 2001). Second, to ensure the survival of fertilised eggs, artificial fertilisation was conducted promptly, as the proportion of fertilisable eggs declined rapidly beyond a 2 h window following death (Champigneulle *et al*., 1983). Furthermore, fertilisation was carried out using milts from a larger number of males to promote spawner diversity (C. Gillet, pers. com.). Subsequently, the eggs were rinsed several times with clean water to mitigate aggregation before being transported to fish farms for incubation (Champigneulle *et al*., 2001). The survival rate during the first week post-hatching exceeded 70% compared to that in the natural environment, where, according to Viljanen (1988), survival rates could drop below 10% (Champigneulle, 1996).

3.2 Fish rearing production techniques

From the beginning of the 1980s, whitefish production was solely based on living plankton, which had a highly limited production capacity. The goal of the project was to develop techniques for the mass production of juveniles and reduce costs. The Rives fish farm in Thonon-les-Bains (France) was renovated and expanded between 1990 and 1993 thanks to the commitment of the partners (Champigneulle et al., 1991, 2001). Furthermore, because whitefish larvae are vulnerable when released into the natural environment (Eckmann, 2013), research focused on production techniques to pre-grow fish to the fingerling stage. A nutritional program was developed that included physiological research. In 1983, tests were conducted using live and frozen zooplankton and pellets typically used for trout. Zooplankton (mainly *Bosmina spp., Daphnia spp.*, and Cyclops) were collected once a day from a boat on Lake Geneva using a net (300-µm mesh) and then either used

directly or frozen (Dewaele, 1983; Champigneulle *et al.*, 1986). Live zooplankton appeared optimal, providing a better larval survival rate (approximately 20% at two months) and growth comparable to that in the natural environment. Frozen plankton also showed good results, but with lower survival rates (6.5% at 2 months) (Champigneulle *et al*., 1986).

However, zooplankton supply was difficult, uncertain, and expensive. The annual cost of stocking 100,000 fingerlings was estimated at 69,100 francs (€10,519), a significant proportion of which was related to labour costs for harvesting zooplankton (Dewaele, 1983). Trout pellets proved to be unsuitable, resulting in a high percentage of malformed fingerlings (Champigneulle *et al.,* 1986). Therefore, to reduce costs and overcome these problems, a major research effort was made to design dry food to facilitate mass fish farming in tanks (Bergot *et al*., 1986). Meanwhile, pending the development of exclusively dry food, illuminated cages inspired by Polish cages (Boutry, 1983) were used to directly rear juveniles in the lake. This method involved placing whitefish larvae within a cage with a fine mesh (0.5–5 mm depending on the size of the fry) to prevent predation (Champigneulle *et al*., 2001). A nocturnal lighting system in the centre of the cage attracted zooplankton through phototaxis (Champigneulle *et al*., 1986).

In Lake Bourget, this method improved the acclimatisation of fry in the lake and increased their survival when stocked in March and early April under optimal temperature and zooplankton density conditions (40–56% survival rate; Champigneulle and Rojas-Beltran, 1996). Rafts of lighted cages, mainly managed by professional fishers, helped sustain wild whitefish populations at critical times when the stock was at its lowest (approximately 100 kg/year from 1966 to 1990). However, since 2004, the cage technique has been gradually abandoned, not only because of the excessive workload in conducting maintenance operations, but also because of the effectiveness of lower-cost mass rearing techniques using dry feed (0,006 € to 0,05 €/unit compared to 0,06 €/unit in cages).

Substantial progress has been made in the composition and size of low-cost dry food using yeast and/or freeze-dried beef or pork liver (Champigneulle *et al*., 1994) leading to successful whitefish raising in fish farm tanks (50-200 francs/kg, around current 8-30 €/kg). Dabrowski *et al*. (1984), Bergot *et al*. (1986), and Champigneulle (1988) have defined the optimal parameters for rearing: temperature (14−15°C), light (09 am to 5 pm), density (100–200 larvae/L), and feeding rate (every 5 min, 2–4 g/tank/8 h by automatic feeders). Specific cylindrical-conical tanks (5, 60, and 250 L), have been tested (Champigneulle *et al.,* 1989) and later modified into 1,000 L adapted to mass rearing (200-400 larvae/L at 6−11°C; Champigneulle *et al*., 1994) to reduce global costs. This study focusing on egg and larval production allowed better management of the entire fish rearing cycle in large-scale production (Rojas Beltran and Champigneulle, 1991; Rojas Beltran *et al*., 1991, 1992).

3.3 Development of fish marking techniques

To assess stocking efficiency, fish-marking techniques must be developed. Indeed, interannual fluctuations in population dynamics can be caused by various factors such as fishing, environmental conditions, and stock-recruitment relationships, which can completely mask the fish contribution from supportive breeding to those from natural recruitment. External techniques (Sandford *et al.,* 2019) were developed for the fingerlings by cauterising the adipose fin or removing the pelvic fin on individuals with an overall length of 28 mm or more (Champigneulle and Escomel, 1984). Based on a study by Meng *et al*. (1986), marking techniques using the injection of encoded magnetised micromarks into the nasal cartilage were conducted. Champigneulle *et al*. (1987) successfully tested the possibility of using these marks in smaller individuals (30–50 mm in whitefish, Champigneulle and Rojas Beltran, 2001). The application of these techniques has allowed for an operator to mark approximately 1,500–2,000 fish per day. However, given the size of the lakes and the large number of fish to be raised, this marking technique has not facilitated marking on a larger scale, as the stocking of the two peri-alpine lakes requires the release of millions of fish annually.

Therefore, research has focused on mass techniques for internal marking using fluoro-marking which binds to calcified structures, such as bones and otoliths. The first marking technique on the otolith involved the rapid bathing of individuals at the egg or larval stage in a hyperosmotic solution of sodium chloride with tetracycline (Rojas-Beltran *et al.,* 1995a, 1995b). These methods facilitated the identification and quantification of fingerlings released during fishery rehabilitation. Since the late 1990s, the use of tetracycline hydrochloride as a marker has been regulated in many countries due to its antibiotic potency (Wright *et al*., 2002). Therefore, alternatives are required. Alizarin Red S (ARS) was tested as a new marker and then selected (Cachera, 1997; Caudron and Champigneulle, 2006, 2009). The adaptation of mark, release, and recapture techniques allowed for accurate quantification of the effects of releases on the scale of lakes Geneva and Bourget (Tab. S2).

3.4 Efficacy of rearing and quantification of catches

To recapture whitefish, compulsory fishing logbooks were set up for recreational anglers and professional fishers targeting whitefish in Lake Geneva in 1986 and Lake Bourget in 1988. This data collection included recording details of the fishing techniques employed, duration of the fishing trip, fish size, and the number of fish with external marks. The efficacy of stocking was evaluated based on the total catch and results from the recapture logbooks. Catch data over the periods of potentially marked cohorts helped assess the performance of mark, release, and recapture by extrapolation (the weight of the catches of marked fish in catch samples representative of the main fishing periods). Marking experiments demonstrated that the 'Pacage Lacustre' Project played a major role in the rehabilitation and maintenance of whitefish populations in lakes Geneva (Champigneulle and Gerdeaux, 1992) and Bourget (Champigneulle and Cachera, 2003). Indeed, at the end of the 1980s, recaptured fish were estimated to weigh 20–27 kg per 1,000 fingerlings in Lake Geneva (3–4.5 cm; Champigneulle and Gerdeaux, 1992). In the early 2010s, total phosphorus dropped below 20 μg/L in Lake Geneva and 15 μg/L in Lake Bourget, thereby improving the ecological

quality of the water (Jacquet *et al.*, 2014) via a reduction in nutrient inputs; whitefish catches were primarily from natural fish recruitment (Gerdeaux, 2004; Champigneulle and Caudron, 2013). In Lake Bourget, the efficacy of stocking was 10.8%, 9.1%, and 7.1% for the 2004, 2005, and 2006 cohorts, respectively (Champigneulle and Cachera, 2008). The stocking yield was evaluated at 2.3 and 7.8 kg/1000 fingerlings, for the 2004 and 2003 cohorts respectively (Tab. S2). Based on the literature and data from other lakes, the fishing tonnage from stocking in 2010 was estimated to be between 1% and 4% of whitefish catches, with the remainder originating from natural reproduction (Champigneulle and Caudron, 2013).

4 Global impacts on society

These management practices had major impacts at different scales and on different targets. They influenced not only the local and regional economy, but also the environment, regulation laws, lake management, human health, and local political actions with social and territorial consequences, as defined in the ASIRPA method (see supplementary; Joly *et al.*, 2015; Smit and Hessels, 2021).

Supportive breeding enabled the rehabilitation and maintenance of the whitefish populations in lakes Geneva and Bourget (Gerdeaux, 2004; Fig. 3). In supportive breeding, eggs from spawners in the same lakes should be preserved, at least in part, by the genetic heritage of the populations. This approach was based on significant differentiation in the enzyme genes of whitefish in Lake Bourget (Vuorinen *et al.*, 1986). The use of eggs from Bourget spawners could potentially improve the conservation of this population, which is probably better adapted to the environmental conditions of Lake Bourget, especially given its location at the southern limit of its original range in Europe. The rehabilitation of whitefish was the combined effect of reoligotrophication, reinforced by supportive breeding and appropriate environmental conditions (Anneville *et al.*, 2009). Increased temperatures had a positive effect as higher water temperatures in spring improved larval survival by better matching the hatching date of the larvae with the appearance of prey resulting in favorable larval growth. Consequently, whitefish catches rapidly increased for both professional fishers and recreational anglers (Fig. 3). Improvements in water quality have led to drinking water at a lower cost, and the absence of olfactory disturbances and better lake transparency have improved the living environment, reduced stress, and boosted human well-being (Baulaz *et al.*, 2021).

4.1 Socio-economic impact

Since the 1990s, the success of supportive breeding programs in the two peri-alpine lakes, in parallel with the restoration of the aquatic environment, has stabilised the incomes of professional fishers and maintained their livelihood. During the eutrophication period, concerns were prevalent over the potential disappearance of the fishing profession, which could have direct repercussions on catering, tourism, and the overall quality of the area (Gagnaire, 1995). Developing and optimising large-scale production techniques and reducing costs have lowered the total cost of fish stocking. An economic assessment of the program estimated that in 1993, due to dry feed production techniques, pre-summer whitefish production in a tank cost of 10 francs (around current 2.53 €) could generate 70–75 francs in predictable recapture, as opposed to 29–36 francs in a lighted cage in 1990 (based on the purchase price from the fishers, *i.e.*, 30 francs per kg in 1989; Gagnaire, 1995). For anglers, the number of licences has sharply increased over the years and spending is higher on supplies and services (boat rental, purchase of fishing equipment, boat maintenance, hotels, and catering). The economic benefits linked to recreational angling in France's Lake Geneva are were estimated around 12 M€ annually (Mauger, 2016). The benefits for Lake Bourget were estimated around 2 M€ annually, excluding boats, purchases, maintenance, mooring, and launching (Versant Sud Développement, 2014). In peri-alpine lakes, salmonid fishing represents an important interest and attracts a large number of anglers compared to other fish families (Cachera and Hofmann, 2015).

4.2 Political impacts

The management of these two peri-alpine lakes involves two major institutions that played key roles in coordinating policies, communicating results to the public, and addressing key political implications. These management institutions had direct political impacts, particularly through cross-border agreements, fishing commissions, and regulatory adjustments, which affected various stakeholders, including fishers.

For Lake Geneva, a Franco-Swiss cross-border commission, the Commission Internationale pour la Protection des Eaux du Léman (CIPEL), has coordinated the water policy between the two countries since 1962. Furthermore, an international agreement between the Swiss Federal Council and the Government of the French Republic created a Fishery Commission to regulate fishing in Lake Geneva, which came into force in 1982 to harmonise fishing regulations and ensure the protection of fish resources and their environments. The key aspects of this agreement focused on stocking measures including the operation of incubation and breeding establishments in both countries. For Lake Bourget, since 1974, the management is carried out by Comité Intercommunautaire pour l'Assainissement du Lac du Bourget (CISALB), an intercommunity committee. The results of studies on the quality of aquatic environments and biological resources were presented to the working group of the advisory commission, and the synthesised findings were disseminated to the public. For both lakes, the scientific committee provided advice on water quality management, and scientists from the same research group are still part of these commissions. Moreover, scientific studies related to fish ecology, physiology of reproduction, and population dynamics have been crucial for drawing up fishing regulations.

For Lake Geneva, the Fishery Commission still exists today and serves the dual purpose of ensuring the exchange of knowledge between the two countries, addressing challenges and regulatory amendments to protect fish resources and their habitats, and harmonising fishing regulations. Members of the fishing services of Swiss cantons, professional and recreational fishers from both countries, and scientists, including those from INRAE, engaged in discussions on fishery regulations,

which are then proposed to the Fishery Commission. A scientific research group was established to advise the working group based on scientific findings. The 1982 Lake Geneva Agreement specifies the number of fish to be released for the stocking program and maintains whitefish fry production knowledge mainly at the Rives Fish Farm. This development has triggered a series of substantial implications, particularly regarding the organisation of fishing for harvesting whitefish broodstock eggs. On 29 March 1990 a senator from Haute-Savoie drew the attention of the French government, proposing a change in regulations to authorise the sale of spawners caught during egg harvesting fisheries. After several attempts to call this into question, in 2002, the government modified the environmental code and authorised the sale of spawners by professional fishers, ensuring a source of income for fishers during the closure period and their involvement.

4.3 Social and territorial outcomes

The 'Pacage lacustre' project led to the creation of the 'Association pour la mise en valeur Piscicole des Plans d'Eau en Rhône-Alpes' (APERA), which structures and strengthens the collaboration between professional fisher and angler associations. The creation of this association resulted from a partnership among all local stakeholders and was made possible only through the strong involvement of INRA scientists (Champigneulle *et al*., 1991). Today, APERA continues to spearhead stocking operations under the 'Pacage lacustre' program, producing several million of whitefish larvae (Richard *et al.,* 2023).

Support for fish populations has facilitated the preservation of fishing heritage activities in lakes Geneva and Bourget, especially for professional fishers.

An increase in salmonid catches has boosted local economies. Owing to the quality of fishing, recreational fishing has become an important tourist activity, with 5,000 anglers from France and abroad visiting lake Bourget every year for fishing or holidays. The direct economic spin-off for the region was estimated to be more than €1.56 million in 2012. In 2010, nine local jobs depended on recreational fishing (Versant Sud Développement, 2014). Thonon's Fishing and Lake Ecomuseum (Eco-musée de la pêche et du lac at Thonon-les-Bains, France) was built in 1987 and hosts > 5,000 visitors on average each year (Fig. S4, data from 1997 to 2023 from the Thonon-les-Bains town hall), helping preserve the memory and historical heritage of fishing.

The promotion of locally produced fish has given an additional advantage to regional gastronomy, with the development of different preparations that have established themselves on restaurant menus for more than 20 yr (Montuelle and Clemens, 2015), including raw or smoked fish. This last preparation enables fishers to sell their produce over longer periods with a high labour cost to resale the price ratio.

4.4 Scientific and management impacts

4.4.1 Collaboration of scientists, managers, and fishers

Significant scientific and management progress resulted from the 'Pacage lacustre' project, thanks to a collaborative and multidisciplinary approach. This endeavour, initiated in the early 1980s, marked a pivotal moment with the increased involvement of ichthyologists, fostering partnerships with administrations and fishers, both professional and recreational, and the formation of APERA. Sustained exchanges between scientists and managers on experimental techniques and protocols have enabled the implementation of optimised stocking, moving from laboratory experimentation to large-scale production for peri-alpine lakes. One main impact was the renovation of the state-owned fish farm at Rives in Thonon-les-Bains, due to the France's Ministry of Agriculture and the Rhône-Alpes regional council. This facility is one of the most prominent European fish farms for producing juvenile lake salmonids for stocking (Guillard, 1988; Champigneulle *et al*., 1991), today managed by APERA. The Institute's scientific expertise in fishing commissions and its participation in formulating fishery management plans for lakes Geneva and Bourget exemplify the integration of research into fishery regulations. Scientific engagement extends beyond traditional actions, with INRA scientists actively participating in symposiums, national meetings with professional fishers, and international conferences. This collaborative exchange facilitated discussions about the management and development of fish resources, thereby reinforcing the broader impact of the project. This knowledge has been disseminated through various channels, including press releases, weekly reviews, books, and scientific articles; over 72 articles in the general press, specialised journals, and books attest to the widespread awareness generated by the project (Rogissart *et al.*, 2023). Furthermore, fishery data have been used in schoolbooks to explain the link between biodiversity and human activities (Bordi *et al*., 2019; Boucher *et al*., 2021). The first European Congress on whitefish management was organized in Thonon in 1984 by A. Champigneulle (Dabrowski and Champigneulle, 1986). In 2023, INRAE scientists organised the 15th congress (https://coregonid2023.symposium.inrae.fr/).

4.4.2 Successes of cooperation between scientists, managers, and fishers

Collaboration between scientists, managers, and fishers in the whitefish rehabilitation project demonstrated the power of participatory research. The exchange of traditional knowledge and scientific expertise created a synergy in which the real-life experiences of managers and fishers complement the rigorous data-driven approaches of scientists. Environmental restoration was prioritised, which is essential for conserving natural fishery resources. Extensive research was conducted to optimise breeding and develop marking techniques. Managers implemented restocking measures, fishing regulations, and water quality improvements. Fishers actively contributed to the data collection and monitoring of fish populations while supporting the project. Collaboration has been a great success, directly benefiting fishers through significant increases in catch (Fig. 3; Gerdeaux, 2004), preservation of traditional fishing activities, and provision of ecosystem services to local communities (Baulaz *et al*., 2021).

Learning from this experience, other fishery management initiatives can benefit from community involvement, stakeholder participation, and the application of appropriate regulations to ensure the sustainability of fishery resources and protection of the ecosystem. To make a rehabilitation

program more effective, the dialogue among stakeholders must be strengthened. Managers must be informed about what science can and cannot offer to address the problems they face, whereas scientists must work together to provide the necessary information and tools.

5 Limitations and threats

Supportive breeding helped support whitefish populations when their abundances were at their lowest and in parallel with the reoligotrophication of the lakes, facilitating their rehabilitation (Gerdeaux, 2004; Anneville *et al*., 2009). Restoration of water quality has significantly reduced sedimentation on spawning grounds, improving oxygenation and promoting natural reproductive success (Gerdeaux, 2004). However, many questions remain regarding intra- and inter-specific relationships (*e.g.*, competition, predation, habitat, and genetics), carrying capacity, spawning habitat quality and long-term management methods.

5.1 Potential negative impacts of stocking

5.1.1 Inter-specific relationships

Whitefish population dynamic and the reoligotrophication of the environment have led to changes in interspecific fish relationships and the entire food web. The increase in whitefish population have led to stronger trophic competition for zooplankton with species such as roach (*Rutilus rutilus*, Anneville *et al*., 2017). It could have also amplified their competition with larval and young-of-the-year perch in the pelagic zone (Gerdeaux *et al*., 2006; Anneville *et al*., 2017). In addition, reoligotrophication has benefitted macrophyte areas favourable for the natural spawning of pike (*Esox lucius*; Gillet, 1989; Lods-Crozet *et al*., 2013), allowing for the development of their populations and, ultimately, increasing predation on salmonids.

5.1.2 Selectivity from fish sampling

Stocking methods, even those using native broodstock, could potentially induce artificial selection: indeed, the methodology for harvesting whitefish eggs increases this risk by using nets with a specific mesh size, which influences the selection of spawner size and therefore, selects neither the largest nor the smallest individuals. Fishing was conducted over short periods, and thus selected only a small part of the broodstock. Early (mid-November) or late (mid-January) spawners were under-selected. Late spawners are potentially more important for adaptation to changing climatic conditions and, ultimately, for the survival of populations (Stewart *et al.,* 2021).

5.1.3 Fish farm domestication

The effects of domesticated whitefish, particularly when fish are kept for long periods on fish farms, could lead to the selection of individuals which are not necessarily those best able to survive in the natural environment (Eckmann, 2012). In addition, the mixing of gametes during artificial fertilisation, with competition between spermatozoa from different genitors (Wedekind *et al*., 2007; Perroud *et al*., 2021), and the absence of choice of partner (Auld *et al*., 2019), can lead to artificial selection which is not necessarily in favour of the individuals most suitable for survival in the natural environment. This could result in a significant decrease in genetic variability, compromising the adaptive capacity of populations in response to environmental changes. Furthermore, the early life stages of fish farms (incubation, resorption, and first feeding) are not subject to the natural selection that occurs in the lake environment (temperature, pressure, light, feeding, olfactory memorisation, *etc.*).

5.1.4 Genetic diversity

Management practices and fishing contribute to the decline in the genetic diversity of salmonids (McMillan *et al*., 2023), including whitefish (Anneville *et al*., 2015) and genetic diversity remains an important driver for ensuring evolutionary changes and the adaptation of species to environmental changes, such as global warming (Meffe, 1995). Therefore, scientific studies on stocking methods and species ecology must continue to ensure the conservation of heritage fish populations.

5.1.5 Habitat and carrying capacity

Stocking can alter habitat by influencing the use of lacustrine zones and modifying ecological interactions among sympatric forms of whitefish (Heikineheimo *et al*., 2000). In addition, stocking can affect carrying capacity and, therefore, have negative impacts on wild populations and stocked individuals, including increased dispersal, predation and reduced growth and survival rates (Cox, 1994). Assessing the effects of stocking on habitat and carrying capacity is essential for mitigating ecosystem disturbance and effectively improving stocking practices (Taylor *et al*., 2013; Wang *et al*., 2022).

5.2 Spawning habitat and natural recruitment

Spawning habitats, crucial to natural recruitment, can be affected by several anthropogenic stressors, which could compromise rehabilitation efforts. For example, shoreline development can lead to hydrological changes and increased sedimentation, causing the degradation of spawning habitats (Meadows *et al*., 2005; Sundblad and Bergström, 2014). In addition, pollutants and contaminants can negatively affect phenotype, metabolism, and embryonic and larval development (Wedekind *et al*., 2010; Yaripour *et al*., 2021, 2022). Elevated water temperatures can disrupt embryo development and survival (Eckmann, 2013; Stewart *et al*., 2021), which poses an increasing threat, especially in the context of climate change (Desgué-Itier *et al*., 2023). The restoration, protection and monitoring of these spawning habitats are essential to ensure long-term rehabilitation success and hence, the resilience and sustainability of whitefish populations.

5.3 Long-term horizon for stocking as a management method

Whitefish populations in lakes Geneva and Bourget are at the southern limit of their range, and in the context of climate change, these populations are threatened (Stewart *et al*., 2021; Eckmann, 2013). Notably, the contribution of supportive whitefish breeding represented a limited fraction of catches

over the 2003-2013 decade (Champigneulle and Caudron, 2013), during lake reoligotrophication. Stocking success depends on environmental conditions and lake status (Baer *et al*., 2023). New marking surveys in lakes Bourget (2018-2020) and Geneva (2023) will update the estimates of the current contribution of stocking to whitefish populations, especially in the context of climate change. Supportive breeding can be an option to support future whitefish populations if natural recruitment returns close to zero, which is linked to reproductive issues. This remains an open question, requiring a better understanding of the impacts on the diversity of stocking and the way in which the exploitation of this species should be approached, going beyond simple scientific work but becoming a societal question of lake use.

6 Conclusion and future challenges

Collaboration among scientists, managers, and fishers led to whitefish population rehabilitation in lakes Geneva and Bourget, safeguarding professional fishing companies and their sectors, and also created a model for inclusive, participatory research. The project achieved its primary objective and also generated substantial scientific, economic, and managerial impacts. The circulation of knowledge, facilitated by collaborative efforts and multidisciplinary approaches, has become integral to the sustained success of the project in parallel with similar approaches in other peri-alpine lakes. The lessons learned and established practices serve as a model for future endeavours in the ecological restoration and sustainable management of fish resources. However, project limitations highlight the need for ongoing scientific enquiry, adaptive management, and a holistic approach to preserve the delicate balance of peri-alpine lake ecosystems. Threats and limitations (especially harm to intraspecific diversity) are not fully absent from this project, and as these lakes face potential new threats from global change. Further research is required on the adaptive potential of whitefish and the ecophysiology of their reproduction.

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Conflicts of interest

The authors have not disclosed any competing interests.

Supplementary material

Figure S1. Impact pathway adapted from Rogissart et al. (2023).

Figure S2. Radar of impacts adapted from Rogissart et al. (2023).

Figure S3. A) Total size-at-age (cm; year) of whitefish from Lake Geneva in 1950 and 1982 (Dottrens, 1950; Champigneulle et al., 1983). B) Evolution of zooplankton biovolume (ml/m²) in Lake Geneva (adapted from Champigneulle and Caudron, 2013; data from SOERE SI-OLA; Rimet et al., 2020).

Figure S4. A) Number of annual and monthly visitors to Thonon's Fishing and Lake Ecomuseum (Eco-musée de la pêche et du lac) in Thonon-les-Bains, France, dedicated to preserving the memory and historical heritage of fishing. The dashed line represents the annual average from 1997 to 2023. B) Boxplot shows the number of visitors from 1997 to 2023 (data from Thonon-les-Bains, France, town hall). The museum welcomes both individual visitors and groups with limited individual access during the summer season, from June to the end of September.

Table S1. Vector of impacts adapted from Rogissart et al. (2023).

Table S2. Whitefish stocking and assessment of 'Pacage lacustre' contributions in Lake Geneva and Lake Bourget using marking methods by cauterising the adipose fin (ad. fin.) and fluoromarking with Alizarin Red S (ARS) (Champigneulle and Gerdeaux, 1992; Champigneulle and Cachera, 2003, 2008).

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