Fisheries Research 154 (2014) 165–171

Contents lists available at ScienceDirect

Fisheries Research

journal homepage: www.elsevier.com/locate/fishres

Thirty years of reoligotrophication do not contribute to restore self-sustaining fisheries of Arctic charr, *Salvelinus alpinus*, in Lake Geneva

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ARTICLE INFO

Article history:
Received 10 September 2013
Received in revised form
19 December 2013
Accepted 30 January 2014

Keywords:
Alizarine red S
Salmonid
Deep lake
Eutrophication
Otolith marking

ABSTRACT

Eutrophication has been a major stressor in lakes during the last century, with important implications for fish populations and thus fisheries. We summarised the Arctic charr (*Salvelinus alpinus*) fishery data available in Lake Geneva between 1887 and 2011 to describe contemporary catches in a broad perspective in relationship to the trophic status and the stocking history. Actual catches are low, but such levels had already been reached before the period of eutrophication. In addition, the high catch levels during the 1990s appeared to be artificially boosted by intense stocking and therefore cannot be used as a reference point. Thus, fishery data only do not allow for population functionality inference. Subsequently, we evaluated the contemporary contribution of stocking to catches and to the spawners by marking all of the fingerlings stocked in 2007 ($n = 993{,}300$ individuals) with a mass marking otolith technique using alizarine Red S. Multiple markings allowed us to distinguish between three stocking practices and to compare their relative efficiency. From 2009 to 2011, 1929 charr were sampled in recreational catches, commercial catches, and in spawners. More than 51% (980) of the total sample set corresponded to the 2007 cohort. The total contribution of stocked fish was 84% at stage 2+, 72% at stage 3+, and 44% at stage 4+. The results were similar to prior values obtained during the 1980s. Differences in the contributions between the types of samples (commercial catches, recreational catches, and spawners) were found. The results highlighted the fact that the current stocking effectiveness was 4 to 5 times lower compared to the effectiveness during the 1980s. Consequently, the current concern about the Arctic charr population, and the fishery in Lake Geneva, is two-fold: first, the long process of reoligotrophication does not allow for the restoration of self-sustaining Arctic charr populations; second, the stocking effectiveness decreased strongly over the last 30 years. Even if stocking greatly contributes to catches, it still does not ensure a sustainable fishery at a high level.

1. Introduction

Eutrophication has long been identified as one of the major stressors in aquatic ecosystems in both marine and freshwater environments (Smith 2003; Levin et al., 2009; Smith and Schindler 2009). In large and deep lakes, eutrophication is assumed to be a major driver of biodiversity loss, and many fish populations have been adversely impacted during the 20th century. Eutrophication creates deoxygenated hypolimnetic habitats, and as a result, stenoxic and deep water species such as salmonids or coregonids could be threatened, mainly due to adverse effects on reproductive success (Evans et al., 1996; Jones et al., 2008; Vonlanthen et al., 2012). Because these particular species typically spawn on coarse mineral substrate, eggs cannot develop due to low oxygen levels on the bottom (Müller 1992). Fish assemblages have therefore shifted from salmonids to coregonids, from coregonids to percids, and finally from percids to cyprinids, the latter being more tolerant to low oxygen levels (Jeppesen et al., 2000, 2005; Gerdeaux et al., 2006).

In Lake Geneva, total phosphorus concentrations were approximately 10–15 μg/L in the early 1950s and peaked at values close to 100 μg/L in the 1970s, leading to dramatic changes in fish communities. In particular, Arctic charr (*Salvelinus alpinus*) have been severely impacted (Rubin 1990). The major hypothesis surrounding the impact on Arctic charr was that oxygen concentrations in spawning grounds were too low, which severely compromised

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http://dx.doi.org/10.1016/j.fishres.2014.01.023

reproductive success (Rubin 1990). Policy response to the eutrophication included drastic legislation on wastewaters, resulting in a recovery of water quality (Anneville et al., 2005; Jacquet et al., 2012). Today, total phosphorous concentrations are close to 20 μg/L. Therefore, the Arctic charr population was expected to recover to a functional reproductive status and abundance. Based on fishery data, landings effectively increased from 1980 to the end of the 1990s, but this improvement was concurrently supported by an increasing stocking policy. Catches were highly related to the stocking intensity 3 years prior (Champigneulle and Gerdeaux 1995). Recent studies (Rubin 2005; Gerdeaux 2011) indicate a strong population decrease, and therefore, it is challenging to determine the underlying processes for increased catches, as numerous factors – namely natural recruitment, stocking and fishing intensity, and global changes – could be involved.

The first objective of this study was to provide an overview of the fishery data evolution in Lake Geneva along a time series covering pre- and post-eutrophication periods. The second objective was to study the contribution of stocking to catches and to standing population of spawners to assess if reoligotrophication induced restoration of natural reproduction. The assumption was that reoligotrophication allowed for spawning habitat quality recovery, which should then translate into higher contributions of wild-born individuals compared to stocked ones. Therefore, using a mass marking technique, the project evaluated the contemporary (2007 cohort) contribution of stocked *vs* 'wild' fish to professional and recreational catches and to the spawning population, compared to contributions obtained in the early 1980s during the eutrophication period (Champigneulle et al., 1988; Rubin and Büttiker 1993). In addition, the multiple marking techniques allowed us to evaluate the relative contribution and efficiency of three different stocking practices used by resource managers.

2. Materials and methods

2.1. Study site

Lake Geneva is the largest peri-alpine lake in Western Europe and is located on the border between Switzerland and France, between Jura and Northern French Alps (46827°N, 6832°E). Lake Geneva is located at an altitude of 372 m and is 72.3 km in length, with an area of 580.1 km^2, a mean depth of 153 m, and a maximum depth of 310 m. Lake Geneva is a monomictic lake with infrequent holomixis. In fact, during the last 60 years, only 10 complete overturns occurred.

Arctic charr are indigenous in Lake Geneva (Dussart 1955) here, the species is at the meridional limit of its European distribution area. Today, in addition to Arctic charr, the main exploited fish species in Lake Geneva are whitefish (*Coregonus lavaretus*), perch (*Perca fluviatilis*), pike (*Esox lucius*), brown lake-dwelling trout (*Salmo trutta*), roach (*Rutilus rutilus*), and burbot (*Lota lota*) (later being non-native in the lake) (Schlumberger and Élie 2008). Moreover, two non-native crayfish species, *Orconectes limosus* and *Pacifastacus leniusculus*, were artificially introduced into the lake in the 1970s and have subsequently extended their range (Laurent 1983; Dubois et al., 2006). The Arctic charr population in Lake Geneva supports both professional and recreational fisheries. Professional fishermen use gillnets, and anglers use long-lines with lures from moving boats.

2.2. Historical stocking practices

To sustain the fishery, Arctic charr stocking has occurred in Lake Geneva; however, practices have changed through time. In the 1960s and 1970s, the stocking was performed mostly with early stage fry (100,000–400,000 yolk-sac fry per year) (Champigneulle, unpublished data). The yolk sac fry contribution is supposed to have a negligible contribution to Arctic charr populations due to poor results of such practices in the past (Champigneulle 1985). The practices changed in 1977 when an intense stocking program was implemented to try to restore the population and fishery that was threatened by eutrophication. Thus, stocking with summerlings (4–9 cm) was carried out first in addition to the yolk-sac fry and then exclusively since 1988. The yearly number of stocked summerlings increased from 144,000 (2.5 ha^{-1}) in 1977 to 1,600,000 (27.5 ha^{-1}) in 1997. During this period, a positive relationship between catches and stocking 3 years prior has been shown (Champigneulle and Gerdeaux 1995; Gerdeaux 2011). Then, between 1997 and 2006, the quantity of yearly summerlings remained high and stable, with an average of 1,500,000 individuals. Since 2007, stocking has decreased progressively to 500,000 individuals in 2011 in relation to lower spawner catches, a decrease of production objectives, and pathological problems in the hatchery (C. Chataignier, com. pers.).

2.3. Arctic charr catches

Both professional and recreational catches have been recorded by the cantonal fisheries agencies in Switzerland and the Agriculture Department Direction in France. In Lake Geneva, different recording processes have been used over time between country agencies and between Swiss counties, resulting in disjoined fishery data from 1887 to present. Thus, commercial catch data are available since 1887 for the French region of the lake, since 1921 for the Canton de Vaud, and since 1950 for the entire lake. Since 1986, recreational catch data were available from both French and Swiss parts of the lake, when regulations required catch reporting. Some of these data have been partially published for different time periods (Villaume 1936; Rubin 1990; Caranhac and Gerdeaux 1998; Gerdeaux et al., 2006; Gerdeaux 2011; Massol et al., 2007). We summarised all of the published and unpublished data available between 1887 and 2011 to create an overview of the Arctic charr catches in Lake Geneva. Data were also analysed for different time periods in relation to the trophic status of the lake and the stocking practices.

2.4. Relative contribution of stocking and natural recruitment of the 2007 cohort

2.4.1. Stocking practices in 2007

The main stocking practice in 2007 was supportive breeding: wild spawners were caught in Lake Geneva with nets in the main spawning areas in France and Switzerland from mid-November to the end of December 2006. The ripe spawners caught were fecundated (a pool of ova mixed with a pool of milt), and then fertilised eggs were transported into a French (Rives = RH) or Swiss (Lausanne = LH) hatchery. Females that had not ovulated, along with several males, were transported, contained until ovulation, and then artificially fecundated. In France, eggs were incubated, and alevins were reared in the same hatchery (RH). In Switzerland, eggs were first incubated in the LH and the alevins were then transported into the VH (Vouvry Hatchery, Switzerland) for rearing until the summerling stage.

A captive brood stock (CBS) was also used to produce summerlings. The CBS was created in 1977 from wild charr spawners caught in Lake Geneva. It was mostly renewed in 1983, and new gametes from wild spawners caught in Lake Geneva were introduced into the stock in the late 1990s. Subsequently, CBS was not renewed for 15 years, representing approximately 4 generations. The alevins produced from the CBS eggs were reared in the RH until the summerling stage.

Rearing conditions between the RH and VH revealed several differences. The RH used water pumped at a 25 m depth in Lake Geneva, while the VH used spring and river water. In addition to the dry food distributed by automatic feeders, the RH juveniles were fed naturally by a small amount of zooplankton coming from the lake rearing water. The VH rearing density in tanks was higher than for the RH, and the water level in the tanks was higher for the RH (50–60 cm) than for the VH (20–30 cm).

2.4.2. Multiple mass marking of the stocked Arctic charr

All of the summerlings released in Lake Geneva in 2007 were marked by a process consisting of a 3 h bath immersion containing 100 mg/L of Alizarin reds (ARS) (Caudron and Champigneulle 2006). According to the method proposed by Caudron and Champigneulle (2009) on brown trout, three types of marking were used to distinguish the three Arctic charr stocking practices without any ambiguity (Fig. 1):

i. Rives hatchery (RH) - a single ARS marking at the beginning of the reabsorption period at 10 degree-days (°days), at the beginning of the yolk sac reabsorption (after hatching).
ii. Vouvry hatchery (VH) - a single ARS marking at the end of the reabsorption period at 220°days after hatching.
iii. The captive breeding stock (CBS) - two ARS markings, the first carried out at the beginning of the reabsorption phase and the second at the end of this phase at 10 and 220°days, respectively, after hatching.

In total, 993,300 marked summerlings were released in the summer of 2007. A wide spatial distribution release was performed as follows: the entire CBS (127,900) and 392,700 RH individuals were stocked in the French part of Lake Geneva, and the entire VH (282,700) and 190,000 RH individuals were stocked in the Swiss part of Lake Geneva.

The mean body length at the release of the three different stocking origins is not known. However, samples carried out in the hatcheries between the 13th and 26th of July 2007 reported mean lengths of 53.9, 45.9, and 60.0 mm for CBS, VH, and RH, respectively.

2.4.3. Sampling and data collection

Sampling of the 2007 cohort was carried out in 2009, 2010, and 2011 in both recreational and commercial fisheries by volunteer fishermen and in spawners caught on the spawning grounds between mid-November and mid-December. In these three samples, Arctic charr specimens were randomly collected within the size ranges likely to include the marked 2007 cohort.

The age of each individual was evaluated from scales, so that only individuals from the 2007 cohort were included in the analysis. Then, the head of each individual was dissected to remove the otoliths (sagittae). These otoliths were fixed onto a glass slide using a thermo-adhesive (Crystalbond Arenco Adhesive number 509) and polished to expose the core. To find out whether otoliths were marked, each slide was viewed under an epifluorescence microscope (Zeiss Axioskop 40) fitted with a mercury vapour lamp (HBO50) and an Alizarin filter (Zeiss no. 15: BP546/12, FT 580, LP 590). The otoliths were classified as belonging to one of four categories: no ARS marking (indicating individuals derived from natural recruitment, scored O), or marking patterns corresponding to the three stocking practices (RH, VH, and CMS).

2.4.4. Data analysis

The contribution of the marked individuals was expressed as a percentage. The 95% confidence intervals of these marking levels were calculated using Beyer's tables (1986) (Beyer 1986). Chi-squared tests were used to determine differences between samples and years.

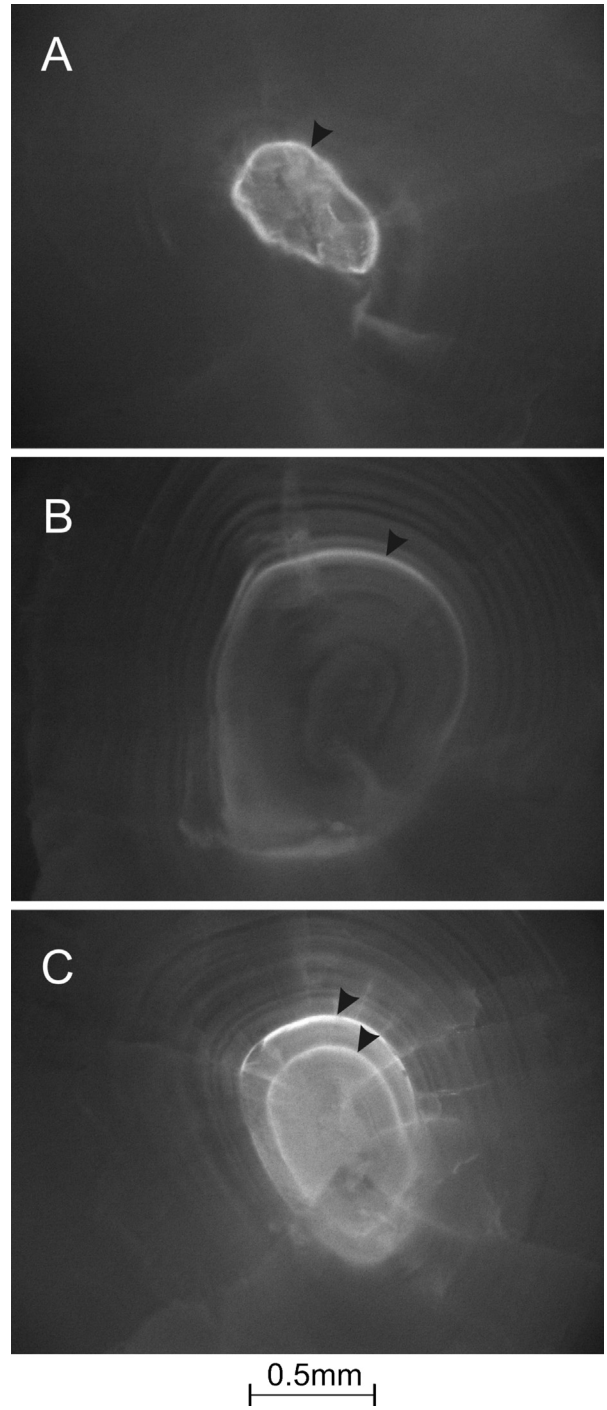

Fig. 1. Photographs of labelled otoliths (sagittae) of adult Arctic charr marked through a 3 h immersion bath containing 100 mg/L of alizarin red S at the beginning of yolk sac reabsorption (A), at the end of reabsorption (B), and at the beginning and at the end of reabsorption (C). Black arrows indicate marking rings.

For each of the three stocking practices, an Index of Relative Efficiency (IRE) was calculated as follows to compare the relative contribution of the three stocking practices (Caudron and Champigneulle 2009):

$$\mathrm{IRE}i = \left(\frac{N_{\mathrm{M}}i}{N_{\mathrm{M}}t}\right) \times \left(\frac{Q_{\mathrm{R}}t}{Q_{\mathrm{R}}i}\right),$$

where IREi is the Index of Relative Efficiency of the stocking origin i, $N_{\mathrm{M}}i$ is the number of marked fish of the stocking origin i in the sample, $N_{\mathrm{M}}t$ is the total number of marked fish in the sample (issued from the three stocking origins), Q_Rt is the total quantity of Arctic charr summerlings released in Lake Geneva in 2007, and Q_Ri is the quantity of Arctic charr summerlings issued from the stocking practice i released in Lake Geneva in 2007.

3. Results

3.1. Overview of Arctic charr catches

On a long timescale, i.e., from 1887 to 2011, catches exhibit important variations (Fig. 2a). In the early 1900s, catches were variable but high. In France, catches decreased in the 1910s, and reached low levels (<10 tons) until 1950. In contrast, in the Swiss part of the lake, collapse occurred later (in the early 1920s).

On an intermediate timescale, i.e., from the pre-eutrophic period to 2011, professional catches were plotted against phosphorous concentrations (Fig. 2b). The catches drastically decreased during the eutrophication period from an average of 16.7 tons (range 13.8–23.5) between 1950 and 1959 when the phosphorous concentration was <10 μg/L (step 1, Fig. 2b) to 3.7 tons on average (1.8–6.1) between 1970 and 1980. Catch levels increased when water quality recovered, with a stronger slope compared to that of the collapse during eutrophication (step 2, Fig. 2b). At the end of the century (1992–2000), catches were 34.2 tons on average (28.6–47.5). In 1997, maximum catches were obtained averaging 47.5 tons, but they decreased thereafter until recent years (step 3, Fig. 2b). Current levels are 9.1 tons on average (6.1–13.2), i.e., between pre-eutrophic and eutrophic period levels.

On a short timescale, i.e., from 1975 to 2011, the relationship between both professional and angler catches and stocking revealed a three-step pattern (Fig. 2c). First, from 1981 to 1999, the relationship between total catches increased linearly according to quantities of summerlings stocked 3 years prior (step 1, Fig. 2c). Between 2000 and 2006, when stocking was maintained at a high level, catches dramatically decreased and reached levels close to those observed before the stocking program used summerlings (step 2, Fig. 2c). Thereafter, stocking intensity decreased and catches remained low and constant (step 3, Fig. 2c).

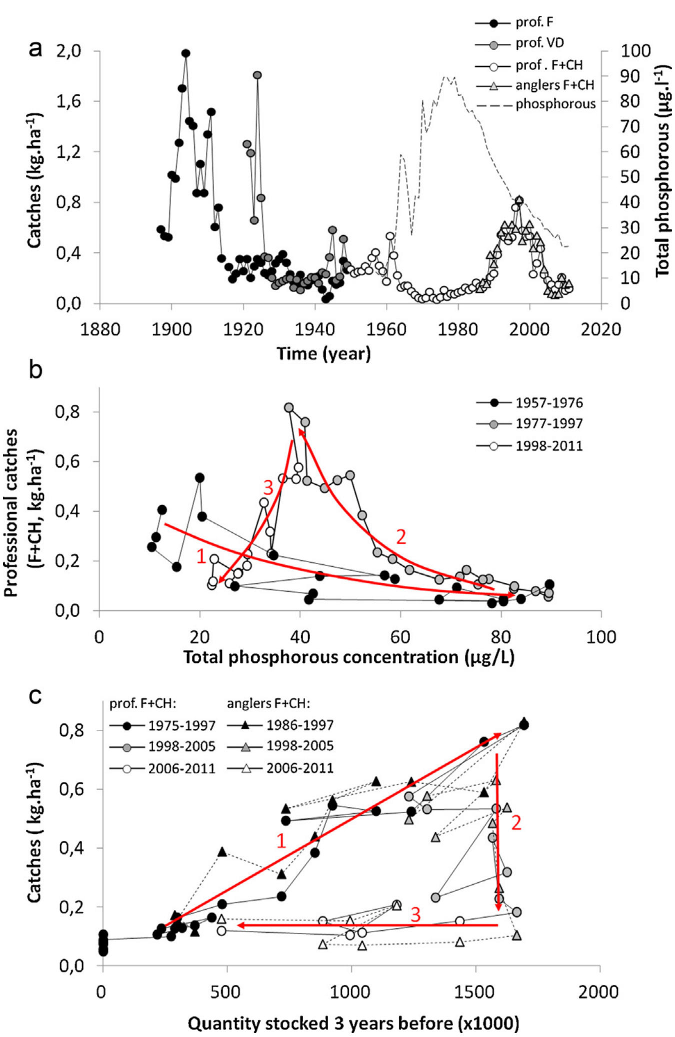

Fig. 2. The dynamic nature of Arctic charr catches in commercial and recreational fisheries in Lake Geneva at different time-scales and in relation to the trophic status and the stocking practice. (a): Overview of the catches between 1897 and 2011 and total phosphorus concentration since 1957. (b): Commercial catches in relation to the total phosphorous concentrations before and after eutrophication between 1957 and 2011. Arrows indicate the three steps of the patterns (see text for details). (c): Commercial and recreational catches in relation to stocking intensity 3 years prior since 1975 and 1986 for commercial and recreational catches, respectively, to 2011. Arrows indicate the three steps of the patterns (see text for details).

Table 1
Repartition by age-classes and for each sampling of the 1929 collected Arctic charr, of which 980 (in grey) correspond to the 2007 cohort between 2009 and 2011.

Years	Sampling	1+	2+	3+	4+	5+	6+
2009	Recreational fishing	0	64	100	5	1	1
	Commercial fishing	4	49	29	2	0	0
	Spawners	0	176	150	0	0	1
2010	Recreational fishing	0	57	90	27	4	0
	Commercial fishing	0	1	57	20	2	0
	Spawners	0	32	138	71	3	0
2011	Commercial fishing	0	0	0	0	0	0
	Recreational fishing	0	56	225	229	15	3
	Spawners	0	12	118	177	10	0

3.2. Contribution of the stocked fish to catches and to the spawning population

A total of 1929 Arctic charr individuals were sampled from 2009 to 2011. After scale reading, 980 of the total sample size (51%), ranging from age-2+ to age-4+, were attributed to the 2007 cohort (Table 1). The error in aging calculated as the percentage of incorrectly aged tagged fish was 2.1%.

Globally, the contribution values of stocked fish to commercial fisheries, recreational fisheries, and spawners is relatively high with a decrease between age-classes; approximately 84% at stage 2+, 72%

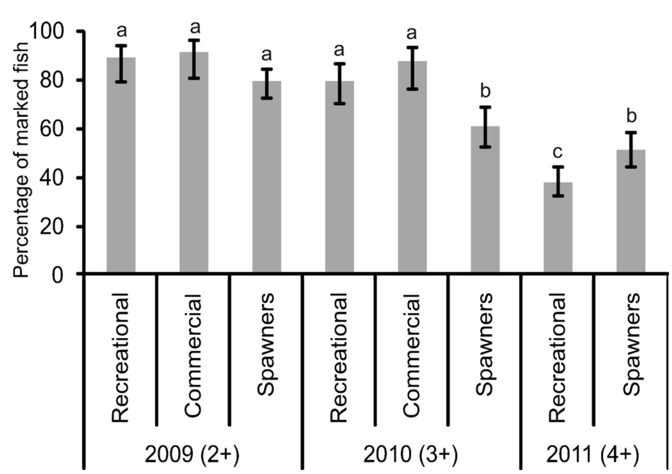

Fig. 3. Contribution of stocked Arctic charr with 95% confidence limits for the three age-classes (2+, 3+, and 4+) in recreational, commercial, and spawner catches for the 2007 cohort in Lake Geneva. Values with no letters in common are significantly different ($P < 0.01$).

at stage 3+, and 44% at stage 4+ (Fig. 3). At stage 2+ (2009 sample), the contributions of stocked fish are high and statistically similar in the three stock components sampled with values between 80 and 92%. At stage 3+ (2010 sample), the contribution of stocked fish in both recreational and commercial fisheries, 80 and 88%, respectively, remained stable and statistically similar. In contrast, in the spawners sample, the stocked fish show a contribution value of 61%; this value is significantly ($P < 0.01$) lower than in the two fisheries and lower than in 2009 at stage 2+. At stage 4+ (2011 sample), the contribution of stocked fish in recreational fisheries (38%) is significantly ($P < 0.01$) lower than at stages 3+ and 2+. In the spawners sample, the stocked fish show a contribution of 51%, statistically similar to stage 3+ and significantly ($P < 0.01$) lower than at stage 2+ (Fig. 3).

For each sample (recreational fishery, commercial fishery, and spawners) and for each age-class (2+, 3+, and 4+), the IRE is always higher for the RH practice than for the two others practices (VH and CBS). The CBS practice shows null or very low IRE and is always lower than RH and VH, except in recreational fisheries at the 2+ stage, where CBS is higher than VH, and in commercial fisheries at the 3+ stage, where VH and CBS show similar IRE. The VH practice shows higher relative contributions compared to the CBS practice with the exception of the 2+ stage in the recreational fishery (Fig. 4). In the spawner samples, the IRE decreased regularly from the 2+ to 4+ stages for the RH practice, whereas it increased for the VH practice.

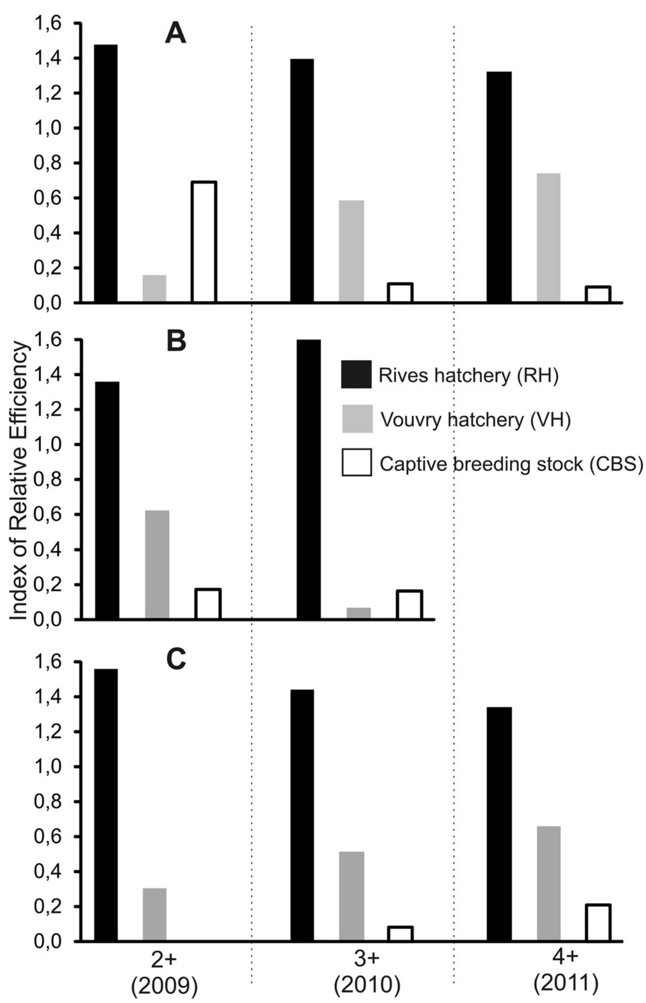

Fig. 4. Index of relative efficiency of the three stocking practices for the three age-classes (2+, 3+, and 4+) in recreational (A), commercial (B), and spawner catches (C) for the 2007 cohort in Lake Geneva.

4. Discussion

It is impossible to know true Arctic charr abundance patterns over the entire period of 1887–2011, as catch per unit effort (CPUE) are not available. Nevertheless, as assumed by various authors, fishing effort can be considered as relatively constant over a recent period (i.e., 1970s to present) (Caranhac and Gerdeaux 1998; Gerdeaux et al., 2006; Massol et al., 2007). More specifically, because catch data from professional and recreational fisheries from 1986–2011 are consistent, they likely provide a good proxy of abundance fluctuation (Pauly et al., 2013). Older data are more obscure, as strong modifications of legislation and fishing practices occurred over time. In 1894, new fishing gear appeared (120 m long, 20 m height) and likely contributed to higher catches (Villaume 1936). Furthermore, between 1894 and 1905, fishing was not restricted during reproduction periods, and fishermen established intense fishing quotas during reproduction periods on spawning grounds, leading to very important catches. Thus, it is not possible to consider the exceptionally high catch levels of the early 1900s as reference levels for the stock. Finally, during the 1990s, the high abundance levels cannot represent a reference level for the natural production of charr because stocking was intense at the time. During the 1990s, catches were closely related to stocking intensity and stocked fish contributed to approximately 80% of the stock, while wild-born individuals lowly contributed to global recruitment (Champigneulle et al., 1988). Therefore, although it is clear that Arctic charr populations declined in the last decade, as suggested by Gerdeaux (2011), this decline is relative to levels that were artificially sustained by intense stocking in the 1990s. In addition, present catch levels are close to the lowest ever registered (between 1970 and 1980, i.e., in the eutrophic period), but such levels were already attained prior to the eutrophication period (during the 1930s) when water quality was good but fishing effort unknown. Finally, fishery data allow the conclusion that the level of the Arctic charr population is low today, but the data do not support a conclusion that the population declined over the last two decades.

Investigations into the contribution of stocked fish to the charr population provided precious complementary information on the population status. In the 1970s, the low level of Arctic charr catches in Lake Geneva were mainly attributed to the eutrophication that led to low egg quantities and a decrease in the natural survival of juveniles (Rubin 1990). The two main findings of the present mass marking study are that a long process of reoligotrophication of the deep Lake Geneva does not allow for the restoration of self-sustaining Arctic charr fisheries and that a strong decrease of the stocking effectiveness (expressed as the kg of fish caught for 1000 fingerlings introduced 3 years prior) occurred between the 1980s and the present time. In fact, the high contributions of stocking obtained for the 2007 Arctic charr cohort (with approximately 1 million summerlings released) are similar to prior results obtained in the 1980s by Rubin and Büttiker (1993), who found stocking contributions ranging from 65 to 92% (for a stocking of approximately 300,000 summerlings). Whereas the improved water quality over the past 30 years was expected to favour a stock recovery, our results indicate that the natural recruitment of Arctic charr still remains very low in Lake Geneva. Similar results have been observed in Lake Bourget, where stocking contributed 80–90% to catches and spawning for the 1990 cohort during the eutrophication period, and 85–93% for the 2004–2005 cohorts after 20 years of reoligotrophication and enhancement of water quality (Champigneulle et al., 2001; Cachera and Champigneulle, unpublished data). Restoration of the pelagic water quality alone is insufficient to restore a functional Arctic charr population. The recovery of favourable oxygen levels in the water column may not be sufficient to allow for egg development, particularly if fine sediment covers the spawning substrate, resulting in local low oxygen concentrations (Müller 1992; Müller et al., 2012).

In addition, whereas the stocking effectiveness of the 1984–1985 cohorts have been estimated from 40 to 50 kg/1000 fingerlings (Champigneulle and Gerdeaux 1993, 1995), the same calculation for the 2007 cohort highlights a value estimated to be 11 kg/1000 fingerlings released (i.e., 4–5 times less than in the 1980s). Similar results were obtained in Lake Bourget, where stocking yielded 56, 30, and 12 kg/1000 fingerlings in the 1985, 1990, and 2005 cohorts, respectively (Champigneulle and Rojas Beltran 2001; Cachera and Champigneulle, unpublished data).

Thus, our results show that the reproductive phase can still be considered a critical phase of the Arctic charr lifecycle despite reoligotrophication. However, major changes in the Lake Geneva ecosystem occurred during the last few decades, and many other factors could have threatened the sustainability of the Arctic charr population and fishery. Rubin (2005) and Gerdeaux (2011) previously discussed 10 hypotheses to explain the decrease of catches since 1997: (1) a natural regulation of the Arctic charr population caused by intra-specific interactions such as cannibalism or limitation of food resources; (2) genetic effects of long-term stocking; (3) a decrease in the success of natural spawning; (4) an increase in the interspecific competition with perch (*Perca fluviatilis*), whitefish (*Coregonus lavaretus*), and/or pike (*Esox lucius*); (5) infection by bacterial kidney disease; (6) a decrease in the trophic resources due to reoligotrophication; (7) predation by piscivorous birds; (8) an unadapted stock management; (9) overfishing of wild spawners to produce eggs for stocking; and (10) indirect effects of global warming on the epilimnion, increasing interspecific competition in the deepest layers. The present study indicates that the hypothesis (3) cannot be excluded as an explanation for the decrease in catches since 1997. In fact, in contrast with the expectation suggested by Gerdeaux (2011), the success of the natural reproduction does not increase with improved water quality. Other recent studies provide also new interesting findings to improve the discussion on the factors threatening the sustainability of the Arctic charr population and fishery. Regarding hypothesis (2), recent analyses of past and contemporary samples suggest that multiple generations of supportive breeding over 30 years did not cause inbreeding effects or genetic drift and therefore cannot explain the recent collapse of the population (Savary 2011). However, this study showed that stocking practices likely led to a more genetically uniform charr population in the lake by melting the gametes coming from the different spawning sites. Supplementing hypothesis (4), the interspecific interactions, other than the competition with fish species such as brown trout, pike, and whitefish, can be proposed as predation by burbot (*Lota lota)* on eggs and juveniles (Knudsen et al., 2010), or by invasive crayfish such as *Orconectes limosus* and *Pacifastacus leniusculus* (Setzer et al., 2011). Finally, two additional hypotheses, not discussed by Rubin (2005) and Gerdeaux (2011), could also be considered. First to consider are the indirect effects of environmental pollutants (hypothesis 11) as reviewed by Scott and Slowman (2004) and Tierney et al. (2010). According to the values published by the International Commission for the Protection of Lake Geneva Waters and/or some tributaries (http://www.cipel.org), some aquatic pollutants such as PCBs, copper, and pesticides show concentrations that could potentially cause physiological, olfactory, and auditory perturbations. The latter two can affect predator avoidance, feeding success, reproductive success, and homing (Scott and Slowman 2004; Tierney et al., 2010). Second, several changes in practices could affect stocking efficiencies (hypothesis 12). In fact, our results indicated large differences in efficiency between different stocking practices (see below). Stocking practices include several parameters such as egg origin, mating plan, hatching and rearing conditions, stage and period of introduction, location, and quantity released. Therefore, we cannot exclude the fact that different parameters changed since 1997, decreasing the stocking efficiency and thus, the Arctic charr yield. Clearly, a multi-disciplinary research approach needs to be developed to study these pluri-hypotheses issues. Finally, our results reveal a very high variability of the relative efficiency of the three stocking practices tested. Summerlings from CBS show poor contributions with relative efficiencies that are either null or very low in most samples. The low survival rate of cultured fish in the wild caused by the negative effects of domestication was widely admitted on salmonids (Huntingford 2004; Ruzzante 1994). However, the higher relative efficiency of this origin in the age-2+ catches in the recreational fishery suggests a higher growth rate and/or a higher catchability of fish from domesticated spawners than fish from wild spawners.

The relative efficiency of the two mains stocking practices (RH and VH) varies greatly with a higher contribution, in general, for the RH practice. RH and VH used wild spawners collected from different spawning grounds in France and Switzerland, respectively. However, the origin of spawners could be considered similar between both stocking practices. In fact, a recent study found no spatial genetic structural differences between the different spawning grounds in Lake Geneva (Savary 2011). The method of fish release into the lake is consistent between both stocking practices. In contrast, the rearing conditions between RH and VH show differences regarding the temperature, feeding, and density, and could thus, partly explain the observed differences. For instance, increased rearing density in VH could lead to increased stress (Fagerlund et al., 1981) and maladaptive behaviour (Brockmark and Johnsson 2010). According to Kolbeinshavn and Wallace (1985), the 30 cm water level used in tanks in VH is classically considered as a minimum to rear Arctic charr to avoid a water height syndrome. Additional experiments and tests are needed to know which factor(s) in rearing conditions allowed for an improvement in the relative efficiency of the RH practices.

5. Conclusion

Our study revealed that a long reoligotrophication period of 30 years in a deep lake such as Lake Geneva does not allow to restore in 30 years a self-sustained Arctic charr fisheries at a high level. The Arctic charr population and fisheries in Lake Geneva are still highly sustained by stocking, with a higher contribution of the practice involving the French Rives hatchery. However, the stocking effectiveness obtained between the early 1980s and now has strongly decreased. Because our study indicated that wild-born Arctic charr are still present in Lake Geneva, research programs need to focus on the natural part of the recruitment process. A multi-disciplinary approach is needed to better understand these underlying phenomena in the deep lakes throughout Europe.

Acknowledgements

This work was supported by funds from the Federal Office for the Environment (FOEN), the French Ministry for Ecology, Energy, Sustainable Development and Sea (MEEDDM), and the Haute-Savoie Departmental Federation of Fisheries. We also thank the technical teams of the Rive and Vouvry hatcheries, the French National Agency for Water and Aquatic Environments, the fishing guards, and the commercial and recreational fishermen for their contribution to the work.

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