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The recent restoration of the whitefish fisheries in Lake Geneva: the roles of stocking, reoligotrophication, and climate change

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The recent history of the whitefish fishery in Lake Geneva has been very positive. Yields over the last seven years have not been attained for 50 years. Stocking has been increased for 10 years. Stocking was first done with larvae, but now with larvae and also juveniles and fingerlings. Stocking could explain the beginning of the increases in whitefish stocks but cannot completely explain the present level of the stock. Other causes are necessary to explain the situation. Lake Geneva sustained a stage of eutrophication (total phosphorus increasing from 20 μg l^{-1} to 90 μg l^{-1}) from 1960 to the mid-1970s. Phosphorus levels have been decreasing since then. Improved water quality has contributed to the restoration of the whitefish population. Climate change has also contributed to better recruitment of whitefish. Stocking seems now to be superfluous and will be restricted in the future to fingerlings.

Introduction

Stocking with larvae and fingerlings of whitefish, *Coregonus lavaretus* (L.), has long been used in the management of fish stocks in European lakes (Meng *et al*. 1986, Salojärvi 1986, Salojärvi 1988, Jokikokko 2002). Before the 1970s, stocking was done with larvae, rarely with fingerlings. During the 1970s, stocking was performed with fingerlings reared in natural ponds with a natural food supply, in illuminated net cages submerged in lakes, or in tanks with live or deep-frozen zooplankton. The perfecting of rearing with dry food allowed the expansion of fingerling production since the end of the 1980s (Champigneulle 1986, Rojas-Beltran & Champigneulle 1991, Rojas-Beltran *et al*. 1991, Champigneulle *et al*. 1994, Enz 2000, Enz *et al*. 2001).

The efficiency of whitefish stocking was evaluated in numerous locations (Salojärvi 1986, Müller 1990, Champigneulle & Gerdeaux 1992, EIFAC 1994, Heikinheimo *et al*. 2000, Lasenby *et al*. 2001). The results published in the literature were summarized in two recent reports. The calculated yields per thousand stocked whitefish are between 0 and 7.3 kg for yolk-sac larvae and between 2 and 250 kg (mean 55.6 kg) for autumn released fingerlings in oligotrophic waters (EIFAC 1994, Lasenby *et al*. 2001). In eutrophied waters, the results are between 0.9 and 38.5 kg (mean 3.1) per thousand stocked larvae and between 8.5 and 83.3 kg (mean 26.3)

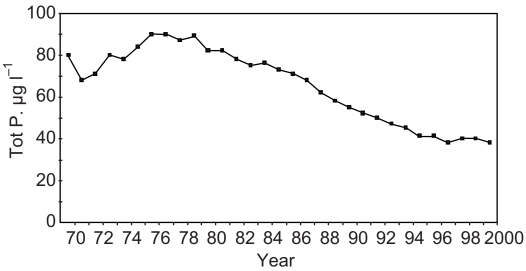

Fig. 1. Total phosphorus concentrations in Lake Geneva, 1970–2000.

per thousand summer released juveniles.

Progress in rearing techniques and results on the efficiency of fingerling stocking encouraged fishery managers to develop the use of fingerlings. In Lake Geneva, the use of juveniles was increased during the 1990s while the traditional stocking with yolk-sac fry was carried on. The yield of the whitefish fishery has been constantly increasing during the last ten years of juvenile stocking in Lake Geneva. The change in stocking strategy could be the cause of the flourishing dynamics of the whitefish population. But other causes could be cited as contributing to this increase, especially the reoligotrophication of the lake and climate change. A relationship between the trophic state of 15 Swiss lakes and the proportion of viable whitefish eggs found prior to hatching was clearly demonstrated by Müller (1992). The effect of climate should also be taken into account (Eckmann *et al.* 1988). The aim of this paper is thus to elucidate the causes of the whitefish population dynamics in Lake Geneva during the last decades and to interpret the findings in relation to current objectives and practices of whitefish fishery management.

Material and methods

Lake Geneva, water quality and climate

Lake Geneva forms the border between France and Switzerland at the North of the French Alps. The lake is characterized by a length of 72.3 km, a surface area of 58 200 ha, an altitude of 372 m, and a mean depth of 153 m (maximum depth 309 m).

An International Commission for the Protection of Lake Geneva Waters (CIPEL in French abbreviation) has been managing surveys of the lake since 1962, and publishes a report annually. A standard survey is made fortnightly in a middle point on the lake. All the classical physicochemical parameters are measured on a vertical profile: temperature, oxygen, and phosphorus and nitrogen concentrations. Daily surface temperatures have been recorded in a littoral location of the lake since 1951.

Lake Geneva fishery

In Lake Geneva, the fishery traditionally uses gill nets for whitefish, arctic char, trout, perch, burbot, pike and roach, the seven most important species in the fishery. Anglers do not catch whitefish in this large lake. Since 1986, fishers have been declaring the daily weight of their catches (Gerdeaux 1988). Before, they declared catches on a monthly basis. It was demonstrated that the total catches are a good estimate of stock abundance (Caranhac & Gerdeaux 1998). During the last 30 years, fishing legislation has remained unchanged. The fishing pressure of anglers has been increasing during the last 20 years. The number of permits has doubled. The number of commercial fishers has remained the same and their fishing pressure is almost constant. As the anglers do not catch whitefish, we consider the fishing pressure stable on this species.

Stocking

Each year during the spawning period, adults are captured. The eggs collected are incubated in hatcheries around the lake. Until the end of the 1970s, only yolk-sac larvae were released. During the 1980s, experimental rearing produced fingerlings (Champigneulle *et al.* 1986). From 1990, the French hatchery has been building new tanks and releasing juveniles as fast as they were growing and exceeding the capacity of the tanks. These fish are classified into two categories, the first one is fish smaller than 3 cm released in April and May (called in this paper juveniles) and the second is fish 5–6 cm long released in July and August (called fingerlings).

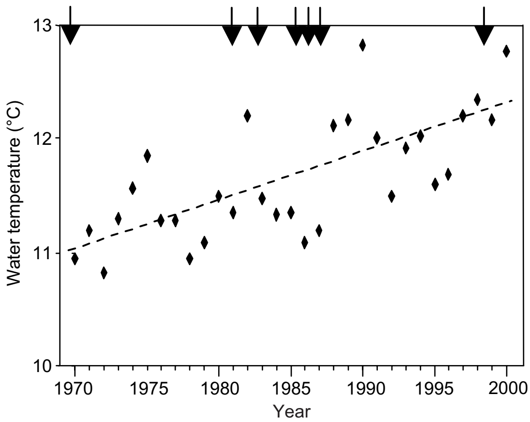

Fig. 2. Mean annual temperature at 5-m depth in Lake Geneva. Arrows indicate the years with a winter overturn.

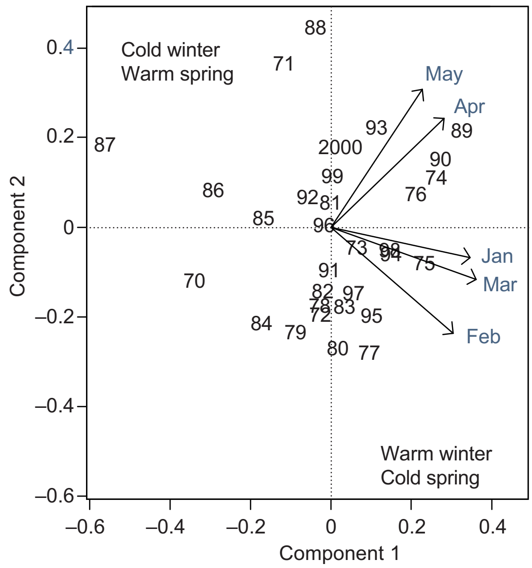

Fig. 3. Results of a Principal Component Analysis on the monthly mean temperature of the surface water in Lake Geneva.

Results

Changes in water quality

The eutrophication of Lake Geneva was at its maximum around 90 μg l^{-1} of total phosphorus in the mid 1970s (Fig. 1). A steady decline in P concentrations started at the beginning of the 1980s. The concentration is now just below 40 μg l^{-1}.

During the last 30 years, mean annual water temperature gradually increased (Fig. 2). This increase was not regular, cold windy winters with over-turn broke the trend. Over the 30 years between 1970 and 2000, winter over-turn occurred in only seven years. Over-turn occurred in 1970, 1979, 1981, 1984, 1985, 1986 and 1999.

In a previous analysis of the influence of climate on whitefish, we found that the best thermal conditions for whitefish recruitment was cold during January and February and warm during March, April and May (Gerdeaux & Deawaele 1986). Surface water temperature increases to 8 °C at the beginning of April. In the last decade, this temperature threshold occurred earlier than in previous years. The April mean temperature was also higher in all of the last 12 years than before. A Principal Component Analysis on the monthly means of daily surface temperatures during the first 5 months of the year separated the years with the best thermal scenarios (1971, 1985, 1986, 1987, and 1988) in the left upper part of the figure (Fig. 3). Statistical analyses were performed on S-PLUS 6.0 (Mathsoft). Note that all the years of the 1990s were in the right side of the figure or near the origin because winter or spring or both were warmer than before. The climate of the four consecutive years 1985–1988 was very favourable for recruitment and the climate of the following years was never unfavourable.

Therefore, the trophic state and the water temperature were generally more favourable for whitefish population dynamics during the second half of the 30 years 1970–1999.

Changes in catches and stocking

Annual catches rose very rapidly and regularly from 1990 to the present, following 20 years of low catches that were usually approximately 60 tonnes per year. Catches in 1994 and later years all exceeded the high catch years of 1973 and 1975 (150 tonnes) (Fig. 4). During the period of eutrophication, catches of perch and roach were higher than during the period of reoligotrophication (Table 1). Catches of arctic char were higher in the 1990s than previously but this increase was due to stocking. More than 80% of arctic char catches are provided by stocking (Champigneulle & Gerdeaux 1995) (Table 1).

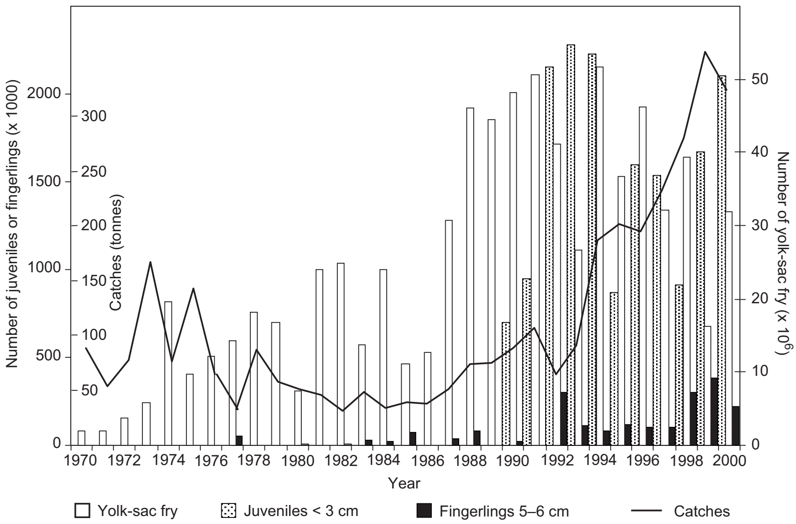

Fig. 4. Stocking rates of fry, juveniles and fingerlings and annual catches of whitefish, Lake Geneva, 1970–2000.

The increase in catches of whitefish in Lake Geneva occurred after a significant change to the practice of stocking in the lake. Significant releases of juveniles started in 1990 after some low releases during an experimental period of rearing. From 1990, between 700 000 and 2.2 million juveniles less than 3 cm total length were released each year. The goal of the hatchery is to release fingerlings in August as much as possible. The success of fingerling rearing was not constant and varied between 80 000 and 381 000 from 1992 to 2000. The release of yolk-sac fry also increased after 1987, and continued to be higher than before.

The French hatchery pumps water from the littoral zone of the lake. Whitefish spawn in this zone in Lake Geneva. Therefore, the thermal conditions of incubation are the same in the lake as in the hatchery. Thus, the hatching date in the hatchery is a good indication of hatching in the lake. This date has advanced slightly during the last decade, but the change has been less than 5 days. This stable hatching date is correlated with the date of spawning which has been almost the same during the last 30 years, i.e. between 15 and 20 December.

Statistical analysis

Whitefish are caught first at the end of their second year but the catch is composed predominantly of three year old fish. However some fish survive until their fourth year of life. The effect of stocking on catches would therefore be expected to be seen primarily 3 years after stocking (Caranhac & Gerdeaux 1998). Thus, we first examined the statistical relationship between stocking in the year n and captures in the year $n + 3$. To mitigate year to year variation, we used two-year moving averages.

Stocking is done at different life stages: yolk-sac fry, juveniles and fingerlings. We utilized the conversion factors used generally in similar studies (1 fingerling = 10 juveniles = 100 larvae) to calculate the number of fish stocked as fingerling equivalents (Müller 1990). The general trend of the number of fingerling equivalents stocked was increasing, but the increase was not regular (Fig. 5). Stocking was very low for the first 5 years of the record, then it was slightly higher during the 13 following years, but fewer than 200 000 fingerling equivalents (3.5 fingerlings per hectare). A significant increase took place during the first years of the 1990s, following which stocking fluctuated above 600 000 fingerling equivalents (> 10 fingerlings per hectare).

The relation between stocking and catches three years later was generally positive but not linear over the 30 years of records (Fig. 6). When stocking was low, during the years 1970–1986, there was no clear relationship between stocking and catches. From 1986 on, a positive relationship was evident. The correlation was positive and significant (Pearson correlation = 0. 62, $P = 0.02$), but the dispersion of the points was high.

A closer examination of the relationship between stocking and catches (Fig. 3) provided an indication that the time-lag between stocking and catches was greater than 3 years. Therefore, the rates of stocking were compared with catches 7 years later. The two curves were very similar (Fig. 7). The correlation between these two variables was 0.94 ($P < 0.001$).

Assuming that a favourable effect of stocking is 100 kg of fish per 1000 fingerlings, we can calculate the optimal yield to be expected from stocking (Fig. 7). The proportion of the yield potentially resulting from stocking varied between 1% and 80% before 1993, and this fraction decreased regularly after 1993. Thus, yields during recent years cannot be explained only by stocking.

Discussion

The increases in the catches of whitefish in Lake Geneva are due to an increase in the stock. Fishing pressure is due only to the commercial fishery. The number of fishermen and the number of drift nets used remained constant. Thus, fishing pressure did not increase significantly during the last 15 years. Furthermore, during the 7 last years, the whitefish market has been saturated sometimes when catches were high and fishers stopped fishing for several days each week. Also, proliferation of filamentous algae also caused halts to fishing sometimes during the last five summers. The increase in the stock is dzemonstrated by the increase in CPUE during the fishing to collect eggs for the hatchery (Fig. 5).

The rate and practice of stocking of whitefish

Table 1. Catch statistics (tonnes) for Lake Geneva, 1970–2001.

Year	Whitefish	Trout	Arctic char	Perch	Pike	Burbot	Roach
1970	88	11	2	519	13		157
1971	54	8	3	1152	10		121
1972	77	8	5	1110	6		256
1973	167	11	3	708	7		163
1974	76	8	2	1091	7		199
1975	143	12	3	1228	3	23	67
1976	64	17	6	580	5	33	207
1977	33	19	3	512	6	40	242
1978	87	27	5	224	6	27	240
1979	58	23	4	54	5	24	231
1980	51	16	5	49	5	30	148
1981	46	12	6	26	3	39	292
1982	30	15	7	95	2	37	350
1983	48	18	6	444	3	25	251
1984	33	25	7	784	3	9	91
1985	38	32	10	342	3	24	178
1986	38	24	8	141	4	29	337
1987	50	9	7	390	2	14	338
1988	73	14	10	299	3	22	442
1989	74	47	35	257	4	39	237
1990	88	25	32	414	4	19	191
1991	106	16	32	697	4	11	137
1992	63	36	64	623	5	12	106
1993	91	32	67	346	6	23	95
1994	186	22	60	254	8	29	75
1995	202	16	67	280	5	17	41
1996	195	17	78	281	5	14	27
1997	232	27	96	222	14	23	42
1998	280	15	62	385	14	14	60
1999	359	16	64	473	20	8	66
2000	326	14	81	377	32	15	54
2001	317	12	39	233	41	15	91

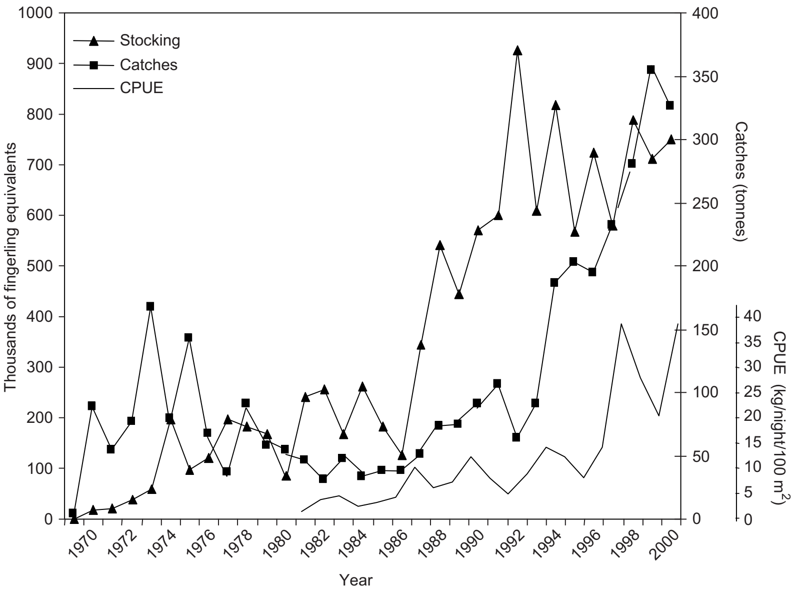

Fig. 5. Total annual stocking as fingerling equivalents, total annual catches and CPUE during spawning of whitefish in Lake Geneva, 1970–2000.

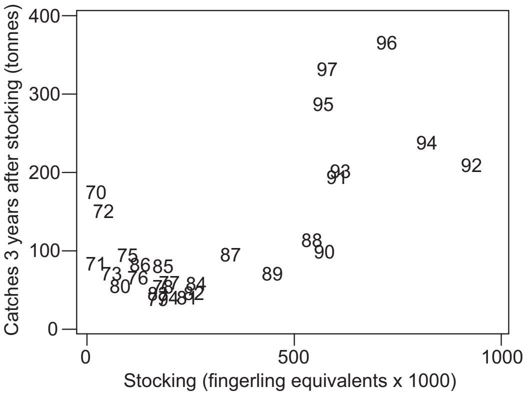

Fig. 6. Relation between stocking and catches 3 years after stocking in Lake Geneva.

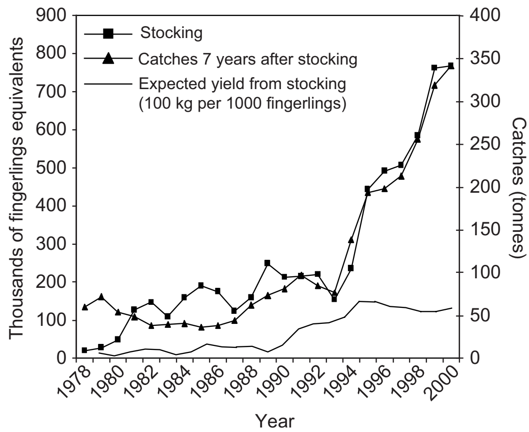

Fig. 7. Total stocking in fingerling equivalents and catches 7 years after stocking using two year moving averages. The expected yield from stocking is given with an estimated efficiency of 100 kg per 1000 fingerlings.

has changed significantly over the last 15 years in Lake Geneva. A substantial effort toward the rearing and stocking of juveniles and fingerlings was undertaken after the results of the first studies on stocking with juveniles and fingerlings became available. These studies demonstrated the efficiency of stocking with larger fish. Although different life stages of whitefish were released, it is impossible to separate the influence of each kind of stocking due to a lack of studies that tagged fish stocked at different stages.

The interpretation of the changes in the whitefish fishery is also complicated by ecological changes in the lake. The effects of climate and trophic state are well demonstrated in the literature. Müller (1992) found during a survey conducted in early 1990 with a sled dredge that the percentage of viable eggs collected on spawning grounds just before hatching is more than 80% in Lake Geneva. This high survival was confirmed by a recent survey (R. Müller pers. comm.). Gillet (1987) also found high viability (> 80%) of experimentally incubated whitefish eggs in Lake Geneva in January 1983, 1984 and 1985. We have no information for the earlier years in

Lake Geneva when the total Phosphorus concentration was higher than 60 μg l^{-1}. According to Müller's (1992) study, it seems likely that the survival of eggs was lower during the 1970s. The trophic state of Lake Geneva could have a weak negative impact on eggs but the impact may not be significant. We can only suppose that the survival of eggs was lower during the 1970s and that it has increased with the reoligotrophication of the lake.

Climate change is probably a more important cause of variation. The warming of the water has been more than 1 °C during the last 30 years in Lake Geneva (Fig. 2). Previous studies emphasized the importance of climate on whitefish dynamics. A cold winter and warm spring are the best conditions. The 4 years from 1985 to 1988 were extremely favourable for whitefish recruitment and the next 10 years were also good for whitefish dynamics. A 1 °C increase in water temperature is large enough to increase survival of whitefish larvae in Lake Geneva. A study on phytoplankton demonstrated that primary production has been starting a month earlier during the last 10 years as compared with previous time periods (Anneville 2001, Anneville *et al.* 2001, Anneville & Leboulanger 2001). This change in the dynamics of primary production means that food for whitefish is supplied earlier in the year. As the hatching of eggs always occurs at the same time in February, larvae can take advantage of this earlier food production. This situation is analogous to the recommended procedure of incubating eggs in cooled water to delay the release of larvae until trophic resources are better in the lake (Klein 1988). The warming of the lake is thus favourable for whitefish recruitment (Eckmann *et al.* 1988, Gerdeaux 1998).

Simultaneously, stocking practices have changed. We found some relationships between stocking and yield, demonstrating as published before, a contribution to the total yield (EIFAC 1994, Champigneulle & Gerdeaux 1992). The best relation was found with a 7 year lag between the stocking rate and catches. This delay could be explained if we suppose that stocking impact is as efficient on the spawning stock as on catches. In fact, the ecological conditions in Lake Geneva have been much better during the last 10 years than before, and stocking contributes also to the increase of the eggs stock, through the reproduction of stocked females. Whitefish are caught in the Lake Geneva fishery after the first reproduction of females (Caranhac & Gerdeaux 1998). The mean weight of a female during spawning is 600 g and the number of eggs laid is about 30 000. The role of the stocked females is potentially sizeable when the survival of eggs and larvae is high. Thus the influence of stocking is postponed to the next generation.

In Lake Geneva, we can conclude that the stocking practices developed at the end of the 1980s were useful and improved the whitefish yield. The impact of stocking is not only an impact in terms of yield but also in terms of reproduction. The stocked fish spawn in the lake and the favourable ecological conditions during the last years have been intensifying the benefit of stocking.

The effect of stocking on the dynamics of the whitefish population is now decreasing and it is possible that stocking is no longer necessary to maintain the fishery. Stocking could even become a negative impact on stock size if the recruitment is density-dependent, as has been demonstrated in many works on whitefish population dynamics. Today, looking at this relationship in Lake Geneva, the top of the curve has not been attained and the effects of stocking are probably not negative. The annual yield is only around 6 kg per hectare. In other similar lakes, the yield is higher. In Lake Annecy, which is oligotrophic and without stocking, the yield is more than 10 kg ha^{-1} (Gerdeaux *et al.* 2001). In oligo or oligomesotrophic lakes, whitefish population dynamics are healthy and the populations can support fisheries (Wanzenboeck 1998). Probably, stocking speeded up the restoration of the whitefish population in Lake Geneva.

Stocking may no longer be necessary, but management habits are difficult to change. The managers decided to stop stocking with yolk-sac fry and to continue with juveniles and fingerlings. The most important question is the future of the dynamics. The sustainability of high yields depends on the management of the fishery. Examples of dramatic drops in the catches from whitefish fisheries in alpine lakes are unfortunately not rare! The numerous compensatory processes that affect whitefish population dynamics require that adequate surveys of the biological parameters of the population are needed to adjust management practices to maintain or even increase yields without stocking (Salojärvi 1992).

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