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Global Ecology and Conservation

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

Persistent high hatchery recruitment despite advanced reoligotrophication and significant natural spawning in a whitefish

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ARTICLE INFO

Keywords:

Eutrophication
Supplementary breeding
Salmonid
Fish growth
Density dependence
Sediment memory effect
Trophic interactions
Artificial selection

ABSTRACT

Many lakes of the pre-Alpine region suffered from severe eutrophication that affected the natural reproduction of whitefish (*Coregonus* spp.) and necessitated large-scale supportive breeding programs. With the advanced reoligotrophication, it is now important to evaluate the relevance of continued artificial breeding for population dynamics. We focused on a whitefish population of a lake that has reached phase III of the reoligotrophication, i.e., lake biomass production is declining since 2012 in response to low phosphorus concentrations. We show that most eggs are naturally spawned, the observed oxygen concentrations would again support embryo development at all depths, and ready-to-hatch embryos can indeed be found on spawning grounds. We marked all hatchery-produced eggs of the 2014 cohort with Alizarin red, stocked them as usual (at larval or early juvenile stages), and recaptured them over a period of five years. Fish were aged from yearly growth rings on scales, and otoliths were checked for marks. We found 90.3 % of the 2014 cohort to be hatchery-born. This ratio did not decline with fish age. We also determined juvenile growth of the cohorts 2012–2020 (based on the first annual ring on scales) and found that stocking intensity predicted juvenile growth ($r^2 = 0.67$). This strong density dependence of individual growth suggests that stocking has largely determined cohort size over the first nine years of reoligotrophication phase III. We conclude that large areas of spawning grounds allow again for successful embryogenesis, that large quantities of eggs are naturally spawned, but that natural recruitment is significantly reduced by ecological or evolutionary factors, e.g., competition with hatchery-born fish, desynchronization of trophic interactions, or long-term effects of fishing- or hatchery-induced evolution.

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<https://doi.org/10.1016/j.gecco.2022.e02219>

Received 6 March 2022; Received in revised form 29 June 2022; Accepted 4 July 2022

Available online 5 July 2022

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1. Introduction

Whitefish (*Coregonus* spp.) are keystone species of pre-Alpine lakes because of their large abundance and their ability to use most of the lacustrine habitats. Large and deep pre-Alpine lakes north of the Alps are therefore commonly referred to a “whitefish lakes”, and they often harbor several whitefish species (Vonlanthen et al., 2012). Most whitefish species present in this region have been managed by supportive breeding to compensate for the loss of functional spawning grounds and to support commercial fishery. The loss of functional spawning grounds was especially pronounced for whitefish in lakes that suffered from eutrophication and corresponding low deep-water oxygen levels (Vonlanthen et al., 2012; Alexander et al., 2017). With the ongoing reoligotrophication and restoration of the limnological state of lakes it is now important to understand whether supportive breeding is still relevant and necessary to avoid population bottlenecks.

Supplementary breeding in hatcheries followed by stocking of larvae or early juveniles into the natural habitat have played an important role in maintaining various whitefish populations during the eutrophication crisis (Müller and Stadelmann, 2004). However, this management tool also comes with several risks (Koch and Narum, 2021). For example, (i) the spawning fishery changes demography and adult sex ratio and thereby affects natural spawning (Székely et al., 2014). (ii) A lack of appropriate genetic management can increase inbreeding coefficients within populations (Fisch et al., 2015; Gossieaux et al., 2019) or (iii) lead to species loss through hybridization (Vonlanthen et al., 2012). (iv) Rearing conditions can relax selection against, for example, genetic load while (v) inducing new types of selection that may lead to adaptations to the artificial environment, potentially on the cost of adaptation to natural spawning grounds (Heath et al., 2003; Hagen et al., 2019). The mostly haphazard mixing of gamete in hatcheries has various consequences, for example, (vi) it circumvents many aspects of intra- and inter-sexual selection and thereby important evolutionary forces that shape genetics and phenotypes (Wedekind, 2002; Chargé et al., 2014), or (vii) it provides a selective advantage to subdominant males that produce more sperm of high velocity than dominant males whose sperm are less competitive (Wedekind et al., 2007; Beirao et al., 2019). (viii) Stocking of large quantities of hatchery-born fish can then induce density-dependent mortality and induce competition with wild-born fish (Satake and Araki, 2012). There are further potential problems linked to supportive breeding, and it cannot be excluded that supportive breeding reduces population fitness over time (Araki et al., 2007; Koch and Narum, 2021). As a consequence, population managers often aim at using supplementary breeding “... as much as necessary and as little as possible”. It is therefore important to understand the significance of hatchery recruitment to a natural population in a lake that is recovering from eutrophication.

Lake Hallwil is among the lakes of the Swiss Plateau that suffered much from anthropogenic eutrophication especially during the second half of the 20th century (Vonlanthen et al., 2012; Steinsberger et al., 2020). As a consequence of this ecological crisis, a lack of oxygen prevented embryogenesis in most, if not all, natural spawning grounds of whitefish and arguably made the population dependent on the supportive breeding that has been performed in three independent hatcheries with gametes collected from adults caught from Lake Hallwil during the spawning season (Enz et al., 2002; Müller and Stadelmann, 2004). Several decades ago, this hatchery program was even supplemented with eggs from other lakes. As a consequence, the current whitefish population of Lake Hallwil shows signs of human-mediated gene flow (Kottelat and Freyhof, 2007; Hudson et al., 2011).

Various measures have been implemented to reduce nutrient loading of Lake Hallwil, and artificial aeration has started in 1986 to reduce hypolimnetic hypoxia and support mineralization of organic material (Müller et al., 2021). The recovery of this lake has been monitored since 1985, with steadily declining total phosphorus concentrations (as determined after winter turnover) from about 200 mg/m³ to concentrations of an average 15.8 mg/m³ in the past 10 years (Steinsberger et al., 2020). Müller et al. (2021) focused on carbon-to-phosphorus ratios of suspended particles in the epilimnion (C:P)_{epi} to describe this recovery in three distinct phases. In phase I (from the start of the monitoring to 2005), total phosphorus concentrations did not limit phytoplankton production and natural reproduction of whitefish appeared impossible despite continuous artificial aeration (Müller and Stadelmann, 2004). In phase II (2005–2012), (C:P)_{epi} increased continuously, phytoplankton began optimizing the declining phosphorus concentrations, and biomass of phytoplankton remained about stable. Similar dynamics that started some years earlier could be observed in the nearby Lake Constance (Jochimsen et al., 2013; Jacobs et al., 2019). Phase III started around 2012 in Lake Hallwil and is characterized by high (C:P)_{epi} and declining biomass of phytoplankton in response to low phosphorus concentrations. The present study started in winter 2013/14 and focuses on the importance of supportive breeding and stocking of the whitefish *Coregonus* cf. *süidteri* during this early stage of lake recovery in phase III, based on a large-scale mark-recapture study design.

Whitefish are typically stocked shortly after hatching or after only few weeks of feeding with zooplankton, but still too early for most marking techniques (von Siebenthal et al., 2017). We therefore used chemical labelling of otoliths (ear stone) with the fluorescent dye Alizarin red S that has successfully been used in whitefish (Eckmann, 2003; Eckmann et al., 2006; Martyniak et al., 2011; Baer et al., 2021) and more than 200 other fishes (Lu et al., 2020). This marking method is generally assumed to be benign to fish and has a high retention rate (Lu et al., 2020), but negative effects on growth and survival have been reported (Meyer et al., 2012) and would potentially bias estimates of stocking success if only a subsample of hatchery-born fish would be marked. We therefore marked all hatchery-produced fish of one cohort and continuously sampled this cohort over a period of 5 years to estimate the contribution of stocked fish on population demography. When sampling fish in the context of this marking experiment and parallel studies (de Guttry et al., unpublished results), we could use the yearly increments on scales to identify fish from the cohorts 2012–2020 and to reconstruct their growth during their first year of life. This allowed us to test for links between average growth and stocking intensity.

Here we quantify the contribution of hatchery-born fish (cohort 2014, i.e., from the 2013/14 spawning season) to the natural population, test whether the rate of hatchery-born fish changes with increasing age of the fish, and compare the size of hatchery- and wild-born fish over time. We also describe the current thermal and oxygen conditions at depths where whitefish would naturally spawn, use mean egg numbers of females that were either caught at the beginning of the spawning season and at later times during the

spawning season to estimate the prevalence of naturally spawned eggs in the wild, and test whether ready-to-hatch embryos can be found at natural spawning sites. We then test whether variance in stocking intensity creates density-dependent growth and hence predicts population size during the first year of life. We discuss our observations in the context of the ongoing reoligotrophication and other ecological and evolutionary factors that could be relevant for fish populations in their transition to a population management that is more closely aligned to natural processes.

2. Methods

2.1. Marking

In the course of the routine hatchery program that involves three independent hatcheries around Lake Hallwil, males and females of that lake were caught in gill nets during the spawning season in winter 2013/14. Their gametes were stripped into beakers, water was added to activate the sperm, and freshly fertilized eggs were incubated in Zuger jars for several weeks until a late eyed stage. Otoliths of these well-developed embryos were then marked with Alizarin red S as in [Eckmann \(2003\)](#). Briefly, batches of up to 50 L eggs (corresponding to about 4.25 million embryos) were exposed in 8 L Zuger jars during 24 h to a concentration of 1 g/L TRIS and Alizarin red S in demineralized water that was pumped in a recirculating system through the Zuger jars and a cooling tank (at 2.6 °C) while temperature, oxygen concentration, pH, and conductivity of the solution were monitored. In total 309 L eggs (ca 26 million individuals) were marked during 9 days. This includes all hatchery-produced embryos of the 2014 cohort of Lake Hallwil whitefish. Embryo mortality after marking was < 1 % in 7 of these 9 days, but 14 % and 21 %, respectively, during the last 2 days of marking. The mortality in these oldest embryos seemed linked to high rates of precocious hatching that was induced by the marking.

After marking, the embryos were returned to the respective hatcheries for further incubation and stocking into the lake following the yearly routine of the involved hatcheries. Ten yolk-sac larvae were euthanized, squeezed on a microscope slide, and examined for markings under a fluorescence microscope. An additional sample of marked embryos were raised in captivity for 2 years to verify the success and the longevity of the marking.

2.2. Recapture

Gill net of increasing mesh sizes were used to sample the 2014 cohort over a period of 5 years: 10–13 mm and 20 mm mesh size in 2014, 20 mm in 2015, 30 mm in 2016, and 36–38 mm in 2017, and 36 mm in 2018 (knot-to-knot mesh sizes). Total lengths of most fish were determined (length measurements are missing for 28 fish in 2015 and all fish in 2016 as only fish heads were available). A few

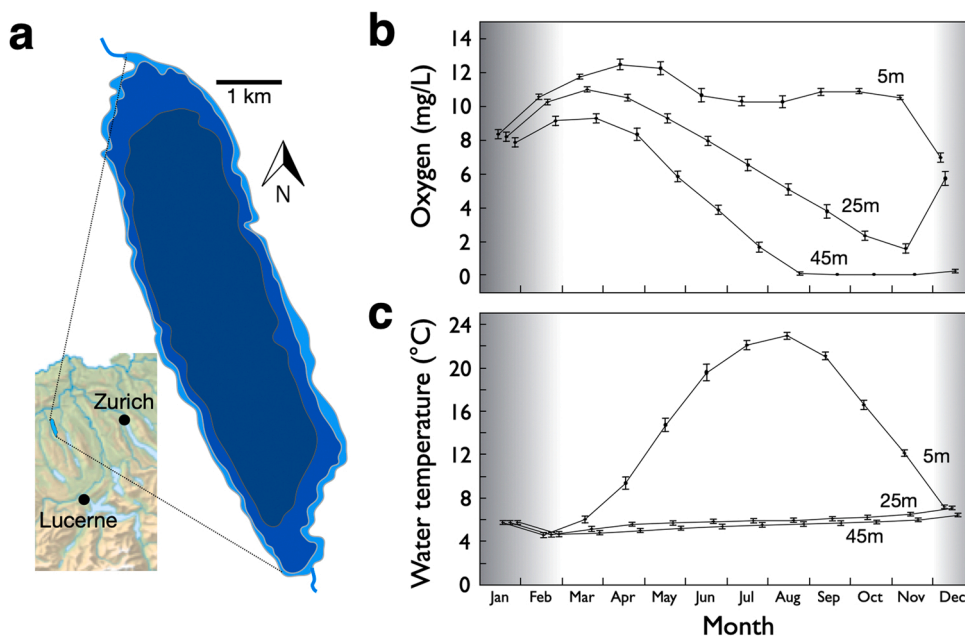


Fig. 1. Characteristics of Lake Hallwil and potential whitefish spawning locations. (A) Contours at 10 m and 25 m depths (redrawn from [Bierlein et al., 2017](#)) and location of the lake relative to the cities Zurich and Lucerne (Switzerland), (B) monthly average oxygen content and (C) average water temperature at 5 m, 25 m, and 45 m depth (mean \pm SE of monthly measurements from 2011 to 2020). The gray background indicates the time when naturally spawned embryos would be developing on the lake ground. The spawning season starts in the second half of December (around the start of lake turnover) and lasts for several weeks. Freshly fertilized eggs fall on the ground. Hatching is expected about 300 day-degrees after zygote formation ([von Siebenthal et al., 2009](#)), i.e., mostly in February.

scales were taken from all fish above the lateral line at the level of the dorsal fin or near the head for later age determination. These scales were cleaned and fixed on a microscope slide. Fish age was examined at 20–40 X magnification using a binocular lens. The annual rings on the scales (Supplementary Fig. S1A) were used to estimate the age of each individual. Otoliths were cleaned, dried, and grinded until a mark or the nucleus were visible under a fluorescence microscope (BP 546 nm/FT 580 nm/LP 590 nm) at a magnification of up to 70x (Fig. S1B).

In order to compare individual growth rates of different cohorts, the distance between the center of a scale to the first annual ring was determined (in mm, at 40X magnification) and used as measure of growth during the first year of life. These estimates were also taken from scales of whitefish caught from 2016 to 2021 in gillnets of various mesh sizes in the context of a Ph.D. thesis (de Guttry, 2021), a cantonal monitoring program that started in 2018, and additional samples taken in January 2022. First-year growth was determined from in total 746 whitefish of 9 different cohorts. Row measurements on scales were used here instead of back-calculations of body length because the latter can be done with various types of formulas (Vigliola and Meekan, 2009) based on assumptions that could not be sufficiently verified for the study population.

2.3. Natural spawning

Whitefish were caught during the spawning season with gillnets (minimal legal mesh sizes in 2012–2017: 38 mm, in 2018: 36 mm, in 2019–2022: 32 mm) that are set on the bottom of the lake and stand vertically 4–6 m high. The fishermen regularly set these nets in different places and depths and then fish the most productive places which are mostly in between 5 and 25 m depth largely all around the lake (Fig. 1A), but fish ready to spawn can also be caught in shallower and deeper water (de Guttry et al., unpublished results).

Oxygen concentration and water temperature have been determined once per month for various depths levels in the context of an ongoing monitoring program and have been provided to us by the canton of Aargau (methodology described in Bierlein et al., 2017; Donis et al., 2017). On February 6th and 19th 2020, i.e. towards the expected end of embryogenesis of naturally spawned eggs, a dredge (Fig. S1C) was dragged along the bottom at about 5 m depth and for about 15 m each to collect naturally spawned eggs and to examine whether they contain well-developed embryos as in Müller (1992). On February 6th, 2022, the dredge was dragged along the bottom at about 15 m depth for about 40 m to test again whether well-developed embryos could be found.

Females spawn their eggs in batches over some time (Esteve, 2005; Auld et al., 2019). In order to estimate the number of eggs that females may be able to spawn naturally before being captured during the spawning season, we counted all eggs that could be stripped from 18 ripe females caught on Dec 20th, 2016 (first day of spawning fishery on the 2016/17 season) and from 30 ripe females caught 20 days later, i.e., towards the end of the spawning season. These fish were haphazardly taken from a large catch (caught in 38 mm gillnets in the context of parallel studies; de Guttry et al. unpublished results). After 2 h of hardening, the eggs from each female were distributed to as many large Petri dishes as necessary to ensure not more than one layer of eggs. These Petri dishes were then photographed on a light table so that egg number could be determined from photos in ImageJ (Schneider et al., 2012). Other samples taken in the course of another study (Perroud et al., unpublished results) were used to test whether the egg mass per female that is available for hatchery breeding declines over a period of 15 days: In total 871 ripe females were sampled from larger catches (in 36 mm gillnets) over 7 days during the second half of the spawning season 2018/19. The sampling in 2018/19 was slightly biased towards females with as many eggs as possible, i.e., the recorded ratios of egg mass per fish weight are not fully representative of females caught during these days but still allow for testing whether this upper range of available egg masses changes over time.

An additional sample was taken on the first day of the spawning fishery on the 2020/21 season (Dec 18th, 2020) in gillnets of 25, 27, 30, and 32 mm mesh sizes to sample different size classes and explore the link between body size and egg number at the beginning of the spawning season. In total 118 females of this sample were ripe and could be stripped. Egg numbers were determined with the same procedure as for the 2017 cohort. In all sampling days that involved egg counting, female body size was determined as standard length (from the tip of the snout to the posterior end of the last vertebra) while size of all other fish was determined as total length that included the caudal fin. In order to convert standard length to total length, both measures were taken on a sample of 43 fish caught on January 10th, 2022. The resulting conversion factor ($r^2 = 0.97$; Fig. S2) was then used to standardize all size measurements to total lengths.

Statistical analyses were done in JMP 15.2.1. Regression analyses and ANOVAs were used if graphical representation of the data suggested that the model assumptions were not significantly violated. Otherwise, Levene's F tests were used to test whether variances differ between groups and Welch's F tests were used to compare means. Directed testing (indicated with p_{dir}) was used when predictions had a clear direction (Rice and Gaines, 1994b), otherwise two-tailed testing was used (p ; α always > 0.05).

3. Results

Fig. 1A shows the depth contours of the lake. By the start of the spawning season in the second half of December, oxygen concentrations are around 5–7 mg/L at depths up to 25 m but still close to 0 mg/L at 45 m. Oxygen concentrations recover at all depths to around 8–10 mg/L in January and February due to vertical mixing of the whole water body, i.e., during the time naturally spawned embryos develop (Fig. 1B). Fig. 1C illustrates how lake turnover has largely homogenized the temperatures at these various depths from December until February.

All 10 yolk-sac larvae and all 18 juveniles that were raised in captivity for 2 years turned out to be successfully marked. The mark was easily recognized two years after staining. In total 523 wild fish were sampled and assigned to their cohorts during the 5 years of monitoring (range: 77–134 per year). Of these fish, 269 (51.4 %) could be assigned to the 2014 cohort, the others belonged to other cohorts. Marks were found in 243 of these 269 fish which corresponds to a 90.3 % rate of hatchery-born fish in the 2014 cohort. Of the

254 fish that were assigned to other cohorts, 144 were checked for marks on the otoliths, and 2 fish (1.4 %) turned out to be marked, i. e., were wrongly assigned to their cohort (one fish in 2016 and one in 2017).

The rates of marked fish did not significantly decline over the years (Fig. 2a; directed heterogeneity test (Rice and Gaines, 1994a): $r_s P_c = 0.29$, $k = 5$, $p_{dir} > 0.15$). Because only few unmarked fish were found, and because not all body lengths were available, fish were grouped to “juveniles” (fish caught in 2014 and 2015) and “adults” (fish caught in 2017 and 2018) to test for differences in size between hatchery-born and wild-born relative to age. It turned out that wild-born fish were on average larger than hatchery-born fish when tested relative to age class, and that this difference in size did not significantly change over time (Fig. 2b; multiple regression of fish length, effect of age: $t = -21.4$, $p < 0.001$, origin: $t = -2.9$, $p = 0.005$, age x origin: $t = -1.7$, $p = 0.09$; see also Fig. S3).

Fig. 2c gives the mean growth during the first year of life of the cohorts 2012–2020 relative to the number of eggs that had been incubated in the three hatcheries and used for stocking to support the respective cohort. This mean growth rates declined with increasing number of eggs (Pearson’s $r = -0.82$, $n = 9$, $p = 0.007$).

When sampling from the natural spawning grounds at 5 m depth, 28 eggs were found on the 1st sampling day of which 7 contained well-developed embryos that seemed ready to hatch. On the 2nd sampling day, 18 ready-to-hatch embryos or egg skins that are typical for recent hatching (Wedekind and Müller, 2005) could be collected. On the 3rd day of sampling at 15 m depth, 4 egg skins that suggested successful hatching and 9 eggs were collected of which 2 contained well-developed embryos.

In order to estimate the prevalence of naturally spawned eggs from the fecundity of the females, egg numbers were determined for females caught at the beginning of the spawning season and 20 days later (2016/17 season). Fig. 3a shows the distribution of egg numbers of these two groups of females that were all caught in the same gillnet (38 mm) and were hence of similar length (ANOVA, $F = 0.09$, $n = 73$, $p = 0.77$) but differed in the variance of recorded egg numbers (Levene’s $F = 13.0$, $p < 0.001$) and in mean egg number: Mean (\pm SE) number of eggs per female was 5833 (\pm 391) at the beginning of the spawning period and 2296 (\pm 257) 20 days later. No link between female size and egg numbers could be found in these two samples (Fig. 3b), but the further sample taken at the beginning of the 2020/21 spawning season in gillnets of various mesh sizes (between 25 and 32 mm) revealed a strong link between female size and egg number. Fig. 3b gives the regression of the combined samples that can be used to predict egg number from fish size at the first day of spawning fishery with an $r^2 = 24.6\%$ ($p < 0.001$). Fig. 3c plots the weights of the freshly stripped egg mass (relative total body weight) over a period of 16 days during the second half of the spawning season 2018/19. These relative weights of stripped egg masses vary over time (ANOVA: $F = 4.0$, $n = 852$, $p < 0.001$) but do not decline towards the end of the spawning season (Spearman rank order correlation coefficient over 7 daily means: $r_s = 0.54$, $p_{dir} > 0.5$).

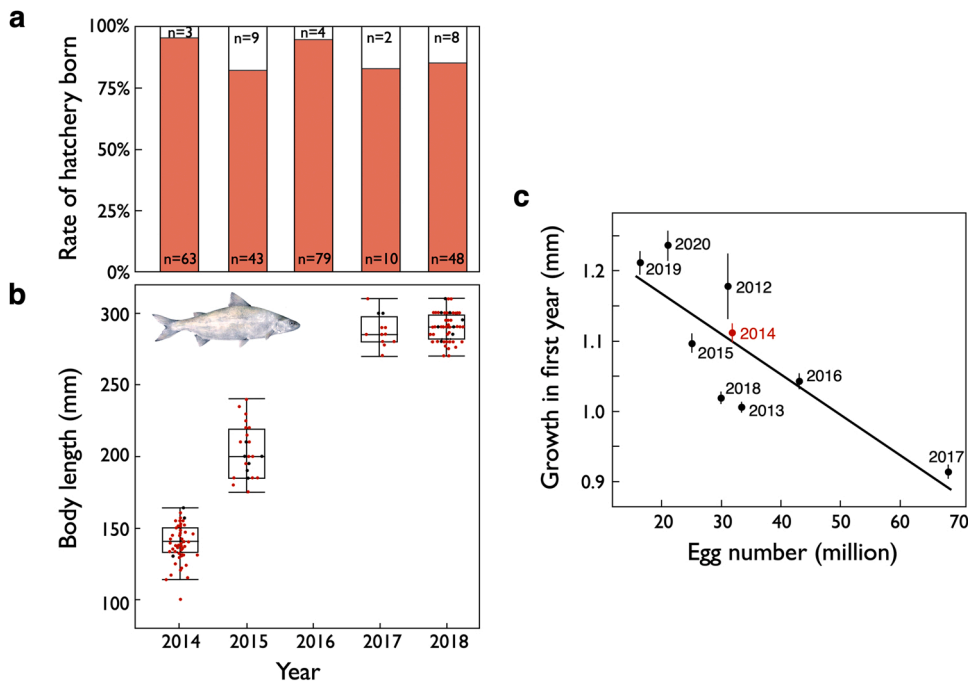


Fig. 2. Performance of hatchery-born fish. (a) Rate of marked (i.e., hatchery-born) whitefish of the 2014 cohort (red bars, the numbers give the counts of marked and unmarked fish). (b) Total body lengths of marked (red) and unmarked (black) whitefish of the 2014 cohort in the year of recapture (Tukey box plots with quartiles, whiskers, and jittered observations; body lengths are missing for 28 fish in 2015 and all fish in 2016). (c) Mean distance (\pm S.E.) between the center of a scale and the first yearly ring (in mm) as a measure of fish growth during the first year of life, given for the cohorts 2012–2020 and relative to the number of eggs that were incubated in the three hatcheries to support the respective cohort (e.g. eggs incubated in winter 2011/12 contributed to the 2012 cohort). The line gives the regression that explains 67.1 % of the variance in growth. See chapter 3 for statistics. Drawing by L. Wedekind.

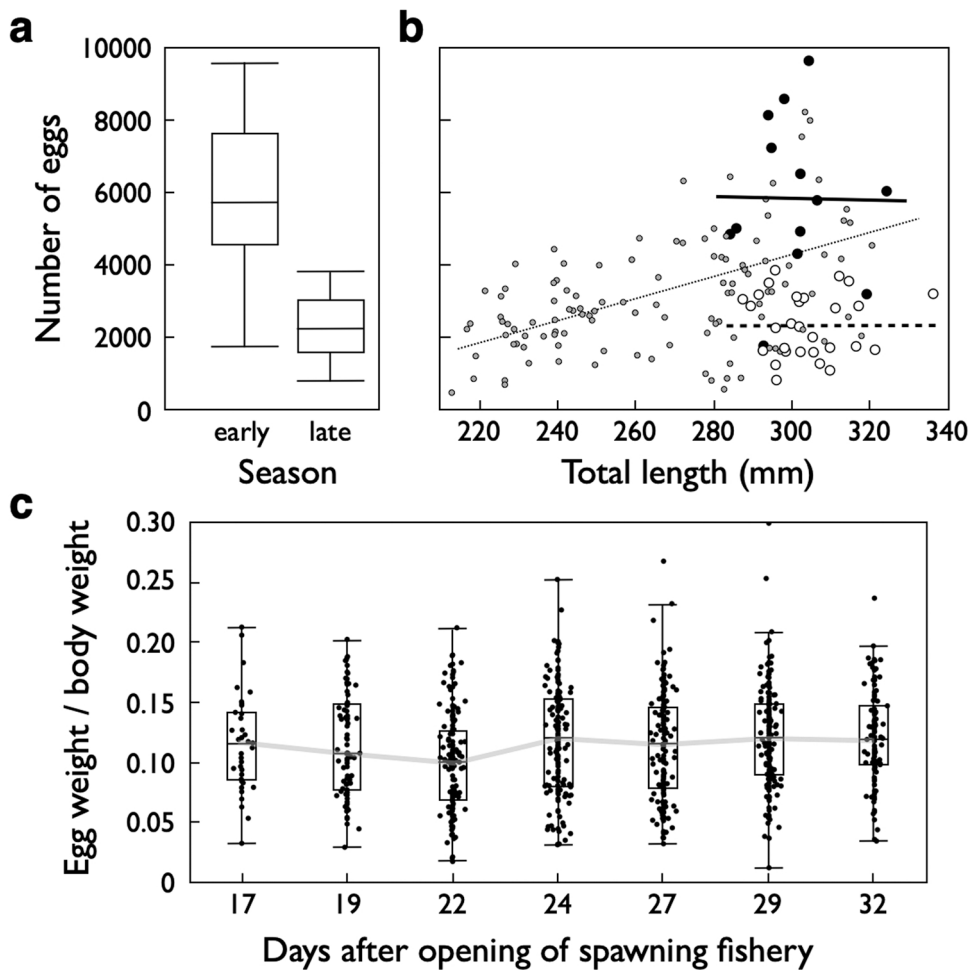


Fig. 3. Egg mass per female caught at the spawning site relative to season and female size. (a) Egg numbers at the beginning of the spawning season in 2016/17 (“early”) and 20 days later (“late”; Welch’s $F = 31.2$, $p < 0.001$). (b) Egg numbers relative to size for females caught early (black symbols and unhatched regression line) and late in the 2016/17 season (open symbols and hatched regression line). Egg numbers of females caught at the beginning of the spawning season 2020/21 and in gillnets of various smaller mesh sizes (small grey symbols) were added to test for the effects of female size on egg number. The dotted regression line gives the regression over both early samples ($F = 41.4$, $n = 129$, $p < 0.001$) that allows predicting egg number from fish size at the first day of spawning fishery (egg number = $-4974.6 + 31.0 \cdot \text{total length}$). (c) Weights of the freshly stripped egg masses relative to total body weight for females caught during the second half of the spawning season 2018/19 (see chapter 3 for statistics). Panels a and c show Tukey box plots with quartiles and whiskers.

4. Discussion

An important question of the present study was whether significant numbers of eggs are naturally spawned. Our observations suggest that the number of naturally spawned eggs exceeds the number of hatchery-reared eggs: Assuming that all females start the spawning season with similar numbers of eggs per body size (Wedekind et al., 2008), regardless of whether they are caught early or late in the season, and assuming that females caught at the first day of spawning fishery have not yet started to spawn, then the difference in mean number between the first and any other day of the spawning season provides an estimate of the number of eggs that were naturally spawned before the female was caught. Females caught on the 20th day of the spawning season have then already spawned at least 60.1 % of their eggs before capture. The fact that relative egg mass did not decline over a period of 16 days during the spawning season suggest that our estimate represents the loss of eggs at various timepoints. However, these 60.1 % may underestimate the number of naturally spawned eggs for several reasons: (i) The variance in egg number was significantly higher at the beginning of the spawning season than later, suggesting that some females of the first day had already spawned some of their eggs. (ii) Our statistics ignores the females that were caught after having spawned all their eggs (because their number was not recorded). (iii) Females of our study population start spawning at the age of 2 + or 3 + (de Guttry et al., unpublished results), and many survive their first spawning season. De Guttry et al. (unpublished results) found that about a third of all females caught by fishermen during the spawning season are 4 + and 5 + old, (>5 + and 2 + females with ripe eggs are rare), i.e. a significant number of females survive one to even two complete spawning seasons and spawn all their eggs naturally during these seasons. Even if this observation does not yet allow for

reliable estimates of the female standing stock (e.g. because minimal legal mesh sizes, fish growth rates, and possibly even mean age at maturation vary from year to year (de Guttry et al., unpublished results), natural spawning is likely to be significant, with the number of naturally spawned eggs most likely exceeding the number of embryos raised in hatcheries. This is also illustrated by the spawn predators that were caught as a bycatch at spawning places and that are typically found to have whitefish eggs in their digestive tracts. These spawn predators are mainly roach (*Rutilus rutilus*) and ruffe (*Gymnocephalus cernua*).

Our sampling with the dredge demonstrated that embryogenesis can be completed in naturally spawned eggs, but the limited sampling did not provide reliable estimates of hatching rates in the wild. We are also unable to provide useful estimates of the significance of egg predation at the natural spawning place. However, our marking experiment revealed that the contribution of naturally spawned eggs to the recruitment of the 2014 cohort does not exceed 10 % despite the advanced reoligotrophication. The rate of hatchery-born fish could even be underestimated if the marking with Alizarin red reduced growth and viability of larvae and early juveniles as it does in Baltic cod (*Gadus morhua*) (Meyer et al., 2012). We found indeed marked fish to be on average smaller than wild-born of the 2014 cohort. The unchanged rate of hatchery-born over different age classes suggest that the marking does not reduce viability at later stages, but this comparison would need to be confirmed on a larger sample of unmarked fish.

When comparing average growth rates of the 9 cohorts since 2012 we found that stocking intensity was a predictor of fish growth during their first year of life (until the first annual ring was built on scales). The link to stocking intensity explained 67 % of the variance in individual growth during this period, which suggests that (i) growth during the first year of life is density dependent, (ii) the number of larvae stocked into the lake largely determines the size of the whitefish population, especially at juvenile stages, and (iii) the link between stocking intensity and population size has not significantly changed over the years. This suggests that natural spawning does still not play a significant role for population growth, 6 years after our marking experiment and 8 years after the start of phase III of reoligotrophication (Müller et al., 2021). The observed variation in stocking intensity remains unexplained but is likely a function of finishing effort, minimal legal mesh size (that ranged from 32 to 38 mm mesh size during the observational period), and number and size of mature females that could be caught during a spawning season.

There are several possible explanations for why hatchery recruitment is so important for our study population. Some of these explanations could be directly linked to the preceding eutrophic conditions of the lake, but there are other potential ecological problems linked, for example, to climate change. It is also possible that stocked fish immediately outcompete many wild-born ones, for example, because of differences in mean size and/or health and vigor if embryogenesis is less stressful in hatcheries than in the wild (von Siebenthal et al., 2009). Moreover, gill net fishing and the long period of supplementary breeding could have induced evolutionary processes that may be maladaptive under more natural conditions. All these potential explanations are non-exclusive.

The recovery from the eutrophication may not be advanced enough to support natural spawning at all depths, even if there are strong signs of lake recovery. Secchi depths have, for example, increased for all seasons by about a factor 2 over the last 15 years, i.e. the water has become significantly more transparent (Müller et al., 2021). Continuous monitoring has also revealed significant declines in phytoplankton biomass and other indicators of ecosystem production, including a > 50 % decline of the amount of organic carbon exported from the productive zone to the hypolimnion (the “net ecosystem production”) (Müller et al., 2021). The corresponding decrease in sedimentation rates of organic carbon can be expected to create conditions at the spawning grounds that allow for embryogenesis at all depths, especially during lake turnover. However, mineralization of organic matter (that is relevant for whitefish embryos because it consumes oxygen) happens in three domains: in the water column, in the sediment surface, and in underlying deeper sediments. While the mineralization in the first two domains seems not to cause oxygen problems during spawning and embryo development (that coincides with lake turnover), the latter can create a so-called “sediment memory effect” or “sediment legacy” that is a typical problem of shallow lakes (< 100 m deep) with a history of eutrophication (Steinsberger et al., 2020). This “memory effect” is caused by continued mineralization in deeper sediments that can cause anaerobic degradation and the production of reduced substances (CH_4 and NH_4^+) (Steinsberger et al., 2020). These reduced substances are likely to diffuse up and affect embryo and larval viability (Müller, 1992), e.g., because lowered pH can reduce mean embryo viability as experimentally demonstrated by de Guttry (2021). It would therefore be interesting to study in more detail the micro-ecological conditions that embryos are exposed on the sediment surface at different depths.

Among the ecological factors that may not be directly linked to the eutrophication crisis but can nevertheless affect growth and survival of wild-born whitefish are changes in the timing of trophic interactions. A desynchronization of functionally connected life stages of different species is now a common problem in various ecosystems and seems often linked to climate change (Visser and Gienapp, 2019). In whitefish, the very early life stages are particularly vulnerable to a temporary lack of suitable food particles. Yolk-sac larvae can only swallow food particles of a narrow size range (e.g. copepod nauplii) and only during the latest stages when the yolk sac no more blocks the esophagus (Lucke et al., 2020). If the yolk sac is used up, the larvae are likely to starve to death if sufficient amounts of suitable food particles are not available.

The synchronization of larval developmental stage and the availability of food particles may mainly be affected by the timing of spawning and by determinants of embryo developmental rate that are not temperature dependent, because we observed that the temperatures at the different spawning depths are about equal. Both parameters vary in the study population: Even if the main spawning season lasts only few weeks from around December 20th to mid-January, first ripe males and females can already be caught in early December and the last ones around mid-February (R. Stadelmann, personal observations), and whitefish often show significant variance in embryo development (Clark et al., 2016). Natural spawning will therefore create some variability in the time when larvae reach the vulnerable stages, and some larvae may happen to be sufficiently synchronized with their prey to survive these critical periods. However, the three hatcheries of Lake Hallwil use various procedures to artificially increase the time span and the developmental stages at which larvae are stocked. Some eggs are incubated in water that is pumped directly from the lake and may well simulate the thermal conditions of the natural spawning place, while others are incubated in lake water that is cooled down by some

degrees Celsius to artificially delay hatching. And while most hatchlings are released into the wild as yolk-sac larvae, some are fed for some days or weeks with zooplankton before release. This variation in procedures artificially increases the probability of releasing larvae at the optimal time point with regard to the availability of their prey. It is therefore possible that this type of risk management contributes to the overall high recruitment rate of hatchery-born fish that we observed. We have recently started another large-scale experiment to test, among others, the relative contribution of the different hatchery protocols to the recruitment. If it turns out that, for example, cooling during incubation increases recruitment rates significantly, then a current desynchronization of the appearance of late yolk sac larvae and their zooplankton prey could significantly reduce the success of natural reproduction. In order to avoid population bottlenecks or even extinction, the potential of the population to evolve rapidly in response to this type of selection would then have to be established before stocking could be ceased. One important question would then be whether the timing of spawning has a genetic basis (Abadia-Cardoso et al., 2013) and whether decades of hatchery breeding has led to maladapted spawning times.

Supportive breeding could have induced further genomic changes that are maladaptive in the wild (Brady et al., 2019). We estimate, for example, that embryo survival rates in the hatcheries of Lake Hallwil vary around 80 % and are significantly lower on the natural spawning grounds. As a consequence, the benign conditions during embryogenesis in hatcheries can lead to an increased mutation load in the population (Araki et al., 2007; van Oosterhout, 2020). Such an effect could be amplified by the fertilization protocols that circumvent most aspects of sexual selection, as long as sexual selection has indeed the expected positive effects on the genetic quality of the next generations (Neff and Pitcher, 2005; Koch and Narum, 2021). The fertilization protocols may also artificially maintain variance in traits like gillraker numbers and thereby prevent much of the phenotypic specialization that would be adaptive in different habitats and that has been observed in other pre-Alpine lakes (Hirsch et al., 2013; Hudson et al., 2017; Jacobs et al., 2019).

The phase III of reoligotrophication that, in the case of Lake Hallwil, started in 2012 (Müller et al., 2021) seems to have started around 10–15 years earlier in the nearby Lake Constance (Jochimsen et al., 2013). Jacobs et al. (2019) concluded from their analyses that the advanced reoligotrophication in Lake Constance has already led to a re-emergence of some of the original ecological whitefish diversity of that lake. It seems that, despite the species collapse that was linked to eutrophication and hybridization (Vonlanthen et al., 2012), remaining alleles with effects on functional traits, morphology, and reproductive behavior (e.g. timing of spawning and depth at spawning) helped to re-establish some of the whitefish diversity within only about 10 generations (Jacobs et al., 2019). However, Lake Constance suffered less from eutrophication and is also deeper than Lake Hallwil and hence predicted to recover faster from eutrophication (Steinsberger et al., 2020).

The whitefish population of Lake Hallwil is of mixed genetic origin (Hudson et al., 2011) and does not seem to suffer from a general lack of genetic diversity. Binz et al. (2001) found 11–20 different alleles on three different loci of the MHC in only 15 individuals, Wedekind et al. (2001) found significant additive genetic variance for stress tolerance, and de Guttery et al. (unpublished results) genotyped about 200 whitefish on about 18k SNP and concluded that the genetically effective population size (N_e) was well above 1000.

There seem to be no distinct ecotypes among the whitefish of Lake Hallwil, and the distribution of gillraker numbers has only one peak (G. Perroud & C. Wedekind, personal observations). However, Perroud et al. (2021) found that males of same age and size but caught at different depths differed in their sexual ornamentation, i.e. there is at least one phenotypic difference between whitefish spawning at different depths. It remains to be tested whether the present genomic variation allows for rapid niche expansion during the continued recovery of Lake Hallwil.

In conclusion, when studying reproduction and recruitment of whitefish in a lake that has reached an advanced stage of reoligotrophication, our observations suggest that the number of naturally spawned eggs exceeds the number of eggs incubated in the hatcheries of Lake Hallwil. We marked the 2014 cohort and found that hatchery-produced fish dominate the cohort in all age classes. Other cohorts were not marked, but the observed link between stocking intensity and first-year growth over a period of 9 years and up to the 2020 cohort suggest that hatchery-born fish still dominate the population in all age classes. The low success of naturally spawned eggs could be due to various ecological and evolutionary factors, including “sediment memory effects” that can be relevant for some time after eutrophication in shallow lakes, desynchronization of functionally connected life stages (e.g. availability of right-sized zooplankton at the various developmental stages), competition between hatchery- and wild-born fish at critical life stages, or changed phenotypes in response to the various types of artificial selection linked to fishing and supplementary breeding. Ceasing supportive breeding of whitefish in a lake that is recovering from a eutrophication crisis could therefore induce population bottlenecks that may threaten the long-term survival of natural populations, even if reoligotrophication is at an advanced stage. However, spawning fishery, artificial fertilization, and rearing embryos and larvae in hatcheries changes the selection regime and are likely to induce evolutionary processes that can also threaten the long-term survival of a natural population. We now need a better understanding of (i) what causes the low success of wild-born fish, and (ii) what is the evolutionary potential of populations to quickly adapt to the new ecological situation that has arisen after the eutrophication crisis and with climate change.

Author contributions

CW, PV, CdG, RS, and NS designed the research; CW, PV, CdG, RS, NS, AP, and GP performed the research; CW analyzed the data and wrote the paper with input from all authors.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data can be downloaded from the Dryad repository (doi: [10.5061/dryad.3r2280gfv](https://doi.org/10.5061/dryad.3r2280gfv)).

Acknowledgements

We thank J. Beninde, J. Bylemans, M. Fischer, L. Garaud, M. Manenti, L. Marquez da Cunha, D. Nusbaumer, T. Kreienbühl, L. Liechti, E. Schäffer, T. Polli, D. Schlunke, K. Schlunke, F. Stettler, A. Stöckli, A. Taverna, P. Truttman, H. Weber, and L. Wedekind for assistance, and D. Bittner, C. Schmid, and L. de Ventura for sharing cantonal monitoring data, permissions, and comments on the manuscript. We also thank K. McConkey and two reviewers for helpful comments. The Aargau Lottery Fond and the Swiss National Science Foundation (31003A_182265) provided financial support.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2022.e02219](https://doi.org/10.1016/j.gecco.2022.e02219).

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