

Human-induced changes in the reproductive traits of Lake Constance common whitefish (*Coregonus lavaretus*)

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Abstract

Size-selective fishery harvest leads to phenotypic changes in fish reproductive traits. When these changes represent an evolutionary response of a stock, they may have severe consequences for future stock dynamics and yields. In freshwater ecosystems, reproductive traits may also be affected by other human impacts such as changes in system productivity. The present study uses regression analysis to evaluate the impacts of changes in lake trophy and of an intensive size-selective harvest over several decades on the reproductive traits of common whitefish in Lake Constance between 1963 and 1999. Fecundity was strongly linked to lake trophy but was also related to the calendar year, suggesting an evolutionary response to size-selective harvest and to massive stocking of the lake with hatchery-reared larvae. The present study is an example of how fish reproductive traits are influenced by the combined action of various human impacts: changes in system productivity, size-selective harvest and massive stocking.

Introduction

The potential for fishery practice to induce phenotypic changes in fish stocks has received increasing attention in recent years. Of particular concern is the possibility of rapid genetic selection for certain traits, which might be difficult or impossible to reverse (Jørgensen *et al.*, 2007; Kuparinen & Merilä, 2007). Evidence is accumulating that size-selective harvesting of stocks may lead to adaptive changes in characteristics such as growth rate. A trend towards slower growth has already been reported for several marine fish stocks in response to heavy exploitation (Hanson & Chouinard, 1992; Conover & Munch, 2002; Swain *et al.*, 2007).

An intensive fishery may also affect reproductive traits such as fecundity and age and size at maturity (Law, 2000; Heino *et al.*, 2002; Walsh *et al.*, 2006). Rijnsdorp *et al.* (2005) recorded a shift towards higher fecundity in North Sea plaice, most probably as a response to size-selective bottom trawling. In a review of fishery-induced

evolution, Jørgensen *et al.* (2007) highlighted three studies documenting increased fecundity as a result of fishery harvest (Yoneda & Wright, 2004; Rijnsdorp *et al.*, 2005; Wright, 2005). To our knowledge, only one study has thus far reported the opposite, that fishery harvest might lead to a decrease in fecundity (Walsh *et al.*, 2006). Age structure and female fecundity are important factors determining the reproductive potential of fish stocks (Scott *et al.*, 2006); so, evolutionary changes in such reproductive traits might be expected to carry potentially severe consequences for future stock dynamics and yields.

Most studies on fishery-induced evolutionary changes have focussed on highly commercial marine species. Other human impacts that might cause phenotypic changes have received less attention, presumably because of their limited relevance in large oceanic systems. In freshwater systems, however, human-induced environmental changes may have profound effects on ecosystem structure and function over very short timescales. Dominant among such changes in recent decades has been the anthropogenic eutrophication of temperate freshwater lakes during the latter half of the 20th century (Smith *et al.*, 1999; van Raaphorst & de Jonge, 2004). Changes in trophic conditions may affect

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fish populations in a variety of ways (Colby *et al.*, 1972; Nümann, 1972; Downing *et al.*, 1990); so, it is imperative that any study of potential fishery-induced evolutionary responses in freshwater lake stocks also takes trophic trends into account (Wright, 2007).

Lake Constance, a pre-alpine lake in central Europe, provides the opportunity to study the combined effects of changes in lake trophic state and of an intensive fishery on the life-history traits of the common whitefish, *Coregonus lavaretus*. The lake was subject to anthropogenic eutrophication followed by re-oligotrophication during the second half of the last century, and the whitefish stock has been intensively fished in a strictly size-selective way in recent decades. A recently published study demonstrated the combined effect of human interventions on the whitefish stocks in Lake Constance, documenting growth over a period of 43 years (Thomas & Eckmann, 2007) and showing that growth during the second year of life significantly correlated with lake trophy, standing stock biomass and calendar year ($R^2_{\text{adj}} = 0.84$). Growth and reproductive investment both depend on per capita food supply, a parameter that is in turn influenced by lake trophy and standing stock biomass (the latter representing a measure of intraspecific competition for food). It is tempting to hypothesize that reproductive traits, such as fecundity or egg weight, may also have been affected by changes in these resource-controlling factors over recent decades. To elucidate the relative contributions of per capita food supply and fishery management (exploitation and stocking) to changes in the reproductive traits of common whitefish, we analysed data on fecundity, egg weight and gonadosomatic index. Unlike other studies, which have compared life-history traits between two discrete time periods of short duration, the present study is based on data from 37 consecutive years.

Methods

Lake Constance whitefish

Lake Constance is a large, warm monomictic pre-alpine lake in central Europe. The lake's main basin, Upper Lake Constance (ULC), has a surface area of 472 km², a maximum depth of 254 m and a mean depth of 101 m. The lake changed from oligotrophic to mesotrophic conditions due to anthropogenic eutrophication in the 1960s and 1970s (PO₄-P concentration during spring turnover: 7 µg L⁻¹ in 1951, 87 µg L⁻¹ in 1979), but phosphorous concentrations decreased steadily since 1980 due to efficient water protection measures. This process of re-oligotrophication proceeded very quickly and by 2004 the phosphorus concentration had fallen below 10 µg L⁻¹ (IGKB 2004).

Common whitefish (*Coregonus lavaretus*) is economically the most important fish species in ULC. The lake stock comprises two ecotypes, the pelagic-spawning

'Blaufelchen' and the inshore-spawning 'Gangfisch'. The fishery is regulated by restrictions on capture effort (number of licences, nets per licence, fishing days per week, net dimensions and mesh size), which are adjusted according to actual harvests by a joint commission of all bordering countries (Austria, Germany and Switzerland). The 'Blaufelchen' ecotype was harvested by about 150 professional fishermen towards the end of the investigation period, each using four monofilament floating gill nets (120 × 7 m each, of 44 mm bar mesh size), 4 days week⁻¹. This corresponds to a fishing effort of only 17% when compared with the beginning of the study period (R. Rösch, personal communication). The legal mesh size, however, remained unchanged during the entire study period, except for the initial 2 years. The mean annual harvest during the last 50 years for Blaufelchen and Gangfisch (1957–2006) was 559 metric tons, but weighted towards the last 10 years (1995–2006) in which the average take increased to 755 tons. This current high level of exploitation represents around half the average standing stock biomass (age classes 1 and older) of about 1500 tons during the late 1980s and early 1990s annually.

For more than a century, the lake has been regularly stocked with hatchery-bred whitefish larvae. During the closed season, which starts on 15 October and lasts until early January, fishermen are allowed to fish for pelagic-spawning Blaufelchen only during the short spawning period, which usually lasts between 3 and 5 days. On board the fishing boats, the fish are immediately stripped of eggs, and these are fertilized and delivered to one of the five hatcheries based around ULC. Beginning in 1964, the hatcheries were successively equipped with cooling units, and since the early 1980s, hatching of most of the eggs incubated in hatcheries is delayed until late March/early April. Larvae held back in this way are supposed to benefit from relatively warm conditions and more abundant zooplankton in their early days and to fare better than naturally spawned counterparts which face a much tougher start when they hatch in February (Flüchter 1980).

Data sampling

We reanalysed the data of Hartmann & Quoß (1993) pertaining to the fecundity of pelagic-spawning whitefish for the years 1963–1991, along with data from eight additional years (1992–1999). During all these years, fish were sampled from the test harvest carried out by fishery managers each year in order to determine the time of spawning as precisely as possible. The test catches generally begin in November and take place at successively shorter intervals (from several days to daily) as spawning time approaches. Spawning of whitefish usually starts between early and mid-December (Rösch, 2007). Fish were sampled with gill nets of legal mesh size (38 and 40 mm bar in the years 1963–1965 and 44 mm

from 1965 onwards). Because the two ecotypes of whitefish clearly segregate by spawning habitat (Eckmann, 1995), the samples were all of the pelagic-spawning Blauefelnchen type.

Fish were measured and weighed, and scales were taken for age determination. From 20 female fish, the total gonad fresh weight was recorded. A subsample of approximately one-eighth of the gonads of each female was weighed and preserved in 3% formalin. Eggs were later counted in the laboratory with the aid of a dissection microscope. Fecundity was expressed as the number of eggs per 100 g fish body weight (gonad weight excluded) and averaged over all females in each spawning season.

Egg weight was calculated for each female from egg number and fresh weight of the gonad subsample. The test samples were obtained on dates that varied between late October and early December from year to year. Previous work has shown that eggs increase in weight in the days prior to spawning (Rösch, 2000); so, variability in sampling dates was an important consideration in the statistical analysis. The beginning of the spawning fishery corresponds closely to the time when the majority of the population is ready to spawn (mass spawning). The interval between the collection of gonad samples from the test harvest and the onset of mass spawning was calculated for each year and termed 'days between sampling and spawning' (DSS). The variable DSS, which ranged between 35 days (1991) and 3 days (1988), was used as a linear factor in regression analysis to account for the continuous increase in egg weight prior to spawning. In some years, when fish from different sampling dates were pooled for analysis, a mean DSS was calculated (normally the different sampling dates

were in quick succession). To visualize the effects of female age and length on egg weight, we fitted a linear regression of median egg weight per year on DSS ($r_{\text{adj}}^2 = 0.42$) and plotted the residuals versus the independent variables.

The gonadosomatic index at the time of sampling (measured GSI) is the fresh weight of gonads represented as a percentage of total fish body weight (including gonads). As with egg weight, measured GSI values were not readily comparable between years. Therefore, using the result from the linear regression analysis of egg weight (cf. Table 1), we estimated egg weight at the time of spawning and calculated the gonadosomatic index each female would have attained at the time of spawning (calculated GSI).

Statistical analysis

Multiple linear regression models were fitted in JMP 7.0 (SAS Institute, Cary, NC, USA) for the dependent variables relative fecundity and egg weight, using mean age and median length of females together with calendar year, phosphorus concentration during spring turnover and yearly averages of whitefish standing stock biomass as independent variables. Values for the latter two variables were taken from Thomas & Eckmann (2007). Factors which were not significant were omitted in the final analysis. The data on whitefish fecundity temporally autocorrelated with a time lag of 1 year (other time lags are not significant). By including fecundity (lagged by 1 year) as an independent variable into the model, the effect of phosphorus concentration is no longer significant. This means that the most plausible mechanistic explanation for the change in

	Term	d.f.	MS	<i>F</i>	r_{adj}^2
Fecundity (mean)	Model	2	4 462 083	34.50	65.0
	Error	34	129 340		
Egg weight (median)	Model	3	4.26314	60.97	83.3
	Error	33	0.06992		
GSI (median)	Model	2	171.798	271.14	93.8
	Error	34	0.634		

	Term	Estimate	<i>F</i>	<i>P</i>
Fecundity (mean)	Intercept	-50 806		0.0001
	Year	28.086	23.29	< 0.0001
	PO ₄ -P	21.087	62.68	< 0.0001
Egg weight (median)	Intercept	3.136		< 0.0001
	DSS	-0.057	71.93	< 0.0001
	Age (mean)	0.7086	82.12	< 0.0001
	PO ₄ -P	0.0049	5.21	0.029
GSI (median)	Intercept	-9.152		< 0.0001
	Fecundity (mean)	0.002	86.51	< 0.0001
	Egg weight (median)	3.837	325.11	< 0.0001

Table 1 Results of multiple linear regression analyses of egg weight, relative fecundity and gonadosomatic index (GSI) of pelagic-spawning whitefish from Upper Lake Constance for the years 1963–1999.

MS, mean squares; *P*, error probability; r_{adj}^2 , adjusted coefficient of determination; DSS, days between sampling and spawning.

whitefish fecundity during the last decades is lost and replaced by a formal autocorrelation which has no explanatory power. The residuals of our model are not autocorrelated.

When the variable “phosphorus concentration” was lagged up to 4 years, we did not see any indication for delayed effects. Measured GSI was regressed on fecundity and on egg weight at the time of sampling.

Results

Fresh egg weight correlated significantly with DSS ($F_{1,34} = 71.9$; $P < 0.0001$), fish age ($F_{1,34} = 82.1$; $P < 0.0001$) and phosphorus concentration ($F_{1,34} = 5.2$; $P = 0.029$). The variables fish age and phosphorus concentration accounted for 70.5% of the residual variance from the egg weight vs. DSS regression (Fig. 1a,b). Other factors, such as standing stock biomass or calendar year had no significant effect on egg weight.

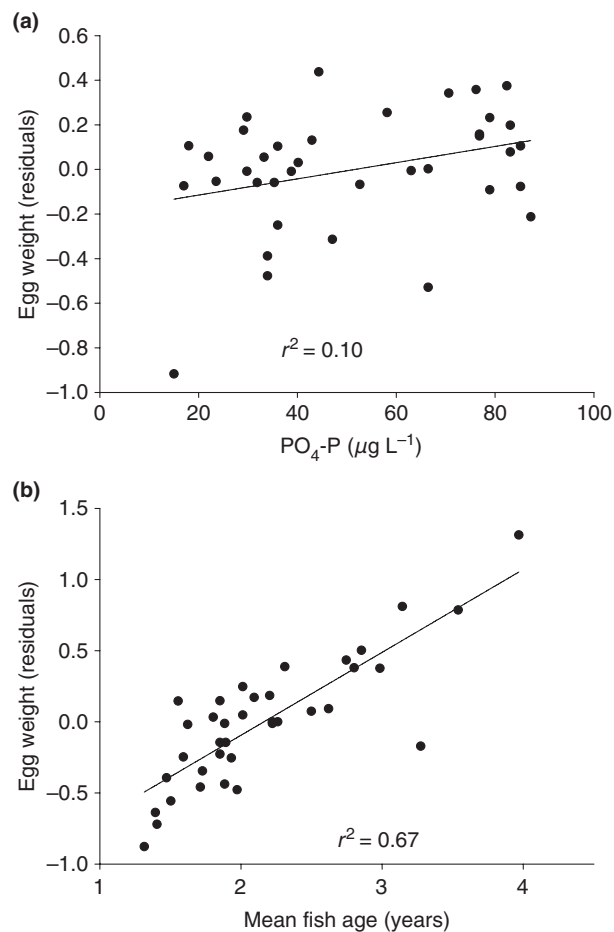


Fig. 1 Residuals of the linear regression between egg weight and the number of days between sampling the fish and mass spawning (DSS) versus phosphorus concentration (a) and mean age (b) of pelagic-spawning whitefish for the years 1963–1999.

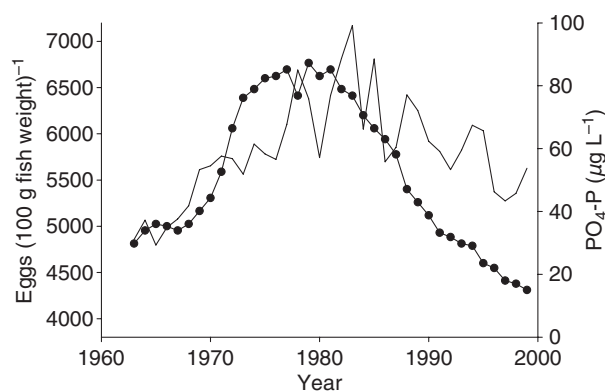


Fig. 2 Relative fecundity of pelagic-spawning whitefish (solid line) and phosphorus concentration during spring holomixis in Upper Lake Constance (black dots) from 1963 to 1999.

Fecundity ranged between 4796 (1965) and 7172 eggs (1983) per 100 g fish weight and was significantly related to phosphorus concentration ($F_{1,34} = 62.7$; $P < 0.0001$). This result, which is based on data collected over 37 years, confirms the earlier results of Hartmann & Quoß (1993), who had analysed a 29-year data set. The new treatment goes further, however, in identifying the second variable, calendar year, as significant with regard to fecundity ($F_{1,34} = 23.3$; $P < 0.0001$). The combined effects of phosphorus concentration and calendar year accounted for 65.0% of variance in fecundity. Standing stock biomass, fish age and fish length had no significant effect on fecundity. The day of sampling did not affect fecundity either, even though somatic weight probably decreased slightly prior to spawning. Figure 2 shows the strong linkage between fecundity and phosphorus concentration. It should be noted that whitefish fecundity at a given lake phosphorus concentration was higher during the re-oligotrophication period of ULC than during the preceding eutrophication. Residual fecundity corrected for phosphorus concentration and for calendar year is displayed in Fig. 3, demonstrating the strong influence of these two variables on fecundity. To assess the relative importance of both variables, scaled estimates centred by their means were used. These estimates indicate how much the dependent variable varies, when one independent variable ranges from the lowest to the highest value while the other independent variable is fixed at its mean value. These estimates revealed that fecundity rose from 5414 eggs per 100 g fish in 1963 up to 6426 eggs in 1999, an increase of 18.7%. For the variable phosphorus concentration, scaled estimates demonstrated that fecundity varied between 6672 eggs per 100 g at 87 $\mu\text{g PO}_4\text{-P L}^{-1}$ in 1979 and 5149 at 15 $\mu\text{g PO}_4\text{-P L}^{-1}$ in 1999, which corresponds to a decrease of 22.8%.

The (calculated) gonadosomatic index increased from the early 1960s until the early 1980s, showing a slightly decreasing trend thereafter (Fig. 4). Measured GSI values, which were determined at different time intervals

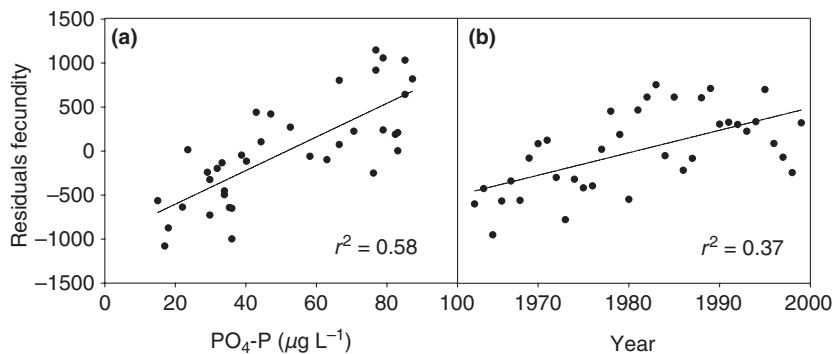


Fig. 3 Residuals of the model testing effects on fecundity: (a) showing residuals with factor 'year' as single independent variable and (b) showing residuals with factor 'phosphorus concentration' as single independent variable.

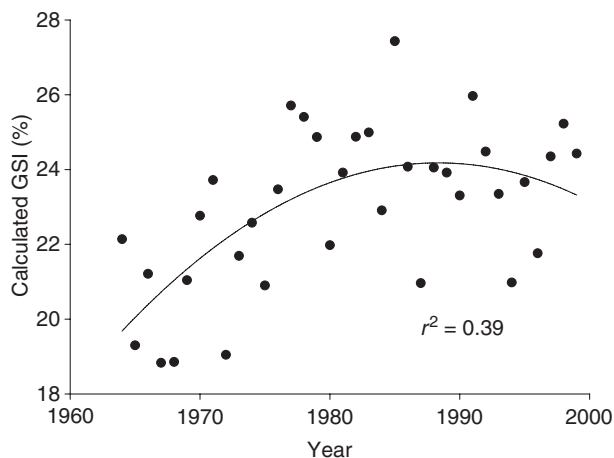


Fig. 4 Calculated gonadosomatic index (GSI) of female common whitefish from Upper Lake Constance for the years 1963–1999. Egg weight of each female was corrected for the time interval between sampling the fish and mass spawning, and multiplied by egg number to estimate the GSI that would have been attained prior to spawning (cf. Methods section). The line is a second-degree polynomial fit to the data.

before peak spawning in different years, corresponded closely ($r^2 = 0.94$) to fecundity and to egg weight at the time of sampling. The effect of egg weight was stronger ($F_{1,34} = 325.1$; $P < 0.0001$) than that of fecundity ($F_{1,34} = 86.5$; $P \leq 0.0001$).

Discussion

Changes in the reproductive traits of female pelagic-spawning whitefish in Upper Lake Constance during recent decades correlate significantly with trends in fish age and size and with lake phosphorus concentration. During these decades, the lake's trophic level has varied as a result of anthropogenic eutrophication and re-oligotrophication. The age and size composition of the female standing stock has also been influenced by the pressures of an intensive, highly size-selective fishery. The rate of exploitation, i.e. the fraction of a population at a given time that is harvested during the time

immediately following (Ricker 1975), was extremely high during at least four decades. Average values for the decades 1947–1956 to 1977–1986 were 0.70, 0.88, 0.84 and 0.80 year⁻¹, and the average rate declined to 0.58 only by the end of the 20th century (R. Eckman, unpublished data). Changes in the reproductive traits of pelagic-spawning whitefish in ULC can, therefore, be taken as an example of how fish stocks attempt to adapt to human impacts on a lake ecosystem, including intensive fishery exploitation. This study is based on a largely unique long-term data set for a lake whitefish population. More data sets on reproductive traits of whitefish covering similar timescales were unfortunately not available; so, our analysis is based on an unreplicated design.

Egg weight

Egg weight was strongly related to female age and to much less degree to phosphorus concentration, whereas standing stock biomass (cf. Thomas & Eckmann, 2007) and time apparently have no effect. The strong influence of female age on egg weight is consistent with conventional life-history theory, which predicts that young fish invest most of their available energy into somatic growth in order to escape from gape-limited predators (Pedersen, 1997). As predation risk decreases with increasing body size, an increasing fraction of the available energy can then be invested in reproduction, through higher fecundity and/or increased egg weight. Young fish generally produce smaller eggs than older individuals (Hislop, 1988). First-time coregonid spawners usually produce eggs of poorer quality than repeat spawners (Kamler *et al.*, 1982). Berkeley *et al.* (2004) showed that older female black rockfish (*Sebastes melanops*) invest their eggs with greater reserves of energy-rich triacylglycerol than younger females, and that larvae hatching from energy-rich eggs grew better and had higher survival rates than larvae from energy-poor eggs. The results of the present study concerning egg weight do not agree with those obtained by a previous study of 38 individual Lake Constance whitefish in 1984 (Rösch, 1987), in which the correlation between egg dry weight and body length

appeared to be independent of fish age. The 1984 data represented a limited subset (38 individuals) of that presented here (more than 600 individuals), which paint a rather more complex picture in which egg weight increases with the age of the female.

Another insight gained from the present analysis that quantitative changes in the food base of whitefish affect egg weight to a minor degree was unexpected and deserves further consideration. The growth rate of pelagic-spawning whitefish during the last decades has responded markedly to changes in phosphorus concentration and even more strongly to changes in standing stock biomass (Thomas & Eckmann, 2007). It was therefore tempting to suppose that egg weight might respond in a similar way to changes in the food base of whitefish, increasing during the 1970s and 1980s, and decreasing thereafter. This expectation is based upon the widely accepted concept that larvae hatching from big eggs are larger than those originating from small eggs (Springate & Bromage, 1985; Elpers, 1988). Large size and rapid growth during larval life confer a variety of advantages that enhance the probability of survival (Hare & Cowen, 1997). For example, larger larvae are able to feed earlier (Gisbert *et al.*, 2000), they can search a larger volume of water for prey (Webb & Weihs, 1986), they are able to ingest larger items and thus target a broader prey spectrum (Hunter, 1981) and they face a reduced predation risk as a result of a more favourable predator-prey size ratio (Fuiman *et al.*, 2006). In the case of ULC pelagic whitefish, egg quality (i.e. egg weight) correlated with maternal age/size but not with the proxy variables used to represent per capita food supply. This result agrees with the observations of Zijlstra (1973), who compared herring eggs produced in years with varying food availability and did not find any influence of food supply on egg weight.

One possible explanation as to why Blaufelchen egg weights have not responded to the pronounced changes in food supply observed over the last four decades is based upon the particular life history of pelagic-spawning whitefish in ULC. Larvae hatch during the second half of February after an incubation time of around 70 days, which is among the shortest embryogenesis periods in the genus (Eckmann, 1987). When larvae arrive at the surface after their ascent from the lake bottom, the temperature is generally low and food is scarce as spring turnover does not usually take place until late February. The larvae's ability to resist starvation, however, is among the highest ever reported for coregonids (Eckmann & Pusch, 1991), permitting them to bridge the gap between hatching and improved feeding conditions in April or early May. These peculiar limnological conditions of ULC have probably prevailed during most of the time since whitefish first colonized the lake after the last glaciation, and they undoubtedly impose a strong selective pressure. It is reasonable to assume that these harsh conditions favour investment in egg weight over egg

number in order to increase the starvation resistance and thus the survival chances of newly hatched larvae. A reduced food supply for adult female whitefish is thereby translated into reduced fecundity rather than lower egg weight, whereas an improved food supply results in increased fecundity with egg weights remaining largely unchanged for females of similar age.

When the majority of fish in a population derive from hatchery-incubated eggs, the evolutionary force towards higher starvation resistance and therefore the maintenance of large egg size might be weakened. Heath *et al.* (2003), for example, found decreasing egg size in salmon populations that face a high degree of stocking with larvae originating from hatcheries. We did not find any comparable trend in our data. The recently obtained (unreplicated) estimate that around 60% of adult whitefish might originate from hatcheries applies only to the later years of the study period when all hatcheries had changed over to delayed hatching. Even when this estimate was true, the remaining 40% of fish would still face natural selective pressures favouring a high egg weight. Additionally, delayed hatching does not guarantee sufficient prey abundance when larvae are released into the lake. A late beginning of spring in some years will still select for larvae with a higher starvation resistance. We might, however, expect a relaxation of the selection for a high egg weight in the long run, if global climate change leads to an earlier onset of spring, and if the intensive stocking programme is continued.

Fecundity

The result of our extended analysis of whitefish fecundity supports the earlier conclusions of Hartmann & Quoß (1993) that relative fecundity is strongly linked to lake phosphorus content. Anthropogenic eutrophication in the 1960s and 1970s led to a controlled, bottom-up biomass increase at all trophic levels, including pelagic zooplankton. The increased food supply for zooplanktivorous whitefish resulted in accelerated somatic growth. The effect was enhanced by low-standing stock biomass during these years (Thomas & Eckmann, 2007). In addition to somatic growth, whitefish were also able to invest more energy in reproduction, in the form of higher fecundity. The reason why standing stock biomass, which influences per capita food supply via intraspecific competition, was significantly related to somatic growth (Thomas & Eckmann, 2007) but not to fecundity remains unclear. A study of vendace, *Coregonus albula*, by contrast showed that standing stock biomass had an effect on fecundity (Sarvala *et al.*, 1992).

The most remarkable result of this study is that the overall increase in fecundity over time is greater than can be accounted for by lake trophy alone. This result suggests an evolutionary response of the Blaufelchen stock in ULC to decades of size-selective fishery. Although fishing effort clearly declined during the study

period (with legal mesh size remaining unchanged), the selection for size is most probably as strong today as it was in earlier years. This notion is supported by results from the monthly test fishery, which hardly catches any fish at all in nets of mesh sizes larger than the legal size. The still strong size selection despite lower fishing effort is probably due to the reduced growth rate of whitefish. Slower growth keeps the window of catchability open for longer time, which cancels out the higher probability of escaping from the size-selective fishery at lower fishing intensities.

An intensive size-selective fishery will harvest predominantly those females that allocate energy to reproduction late in life, thus favouring females that mature younger and smaller. Unfortunately, this hypothesis cannot be tested from the ULC whitefish study, in which age-at-maturity data was not sampled regularly.

The second possible effect of intensive size-selective harvesting is an increase in fecundity (Rijnsdorp *et al.*, 2005), an effect that should be most pronounced in stocks that are targeted shortly after reaching maturity. This is the case in ULC whitefish, where females generally mature at the end of their third year of life, and most fish are harvested before the end of their sixth year of life (Thomas & Eckmann, 2007). Under these conditions, females which allocate a greater fraction of available energy into reproduction early in life produce more eggs overall and enhance their reproductive success. The advantage of the alternative tactic, allocating all available energy into somatic growth and only investing in reproduction when a certain body size has been reached, is effectively cancelled out by the size-selective harvest. Selection for higher fecundity takes place on the phenotypic level, but fecundity can be assumed to have a genetic basis. Several decades of size-selective harvest may well have resulted in selection for high fecundity.

In addition to intensive fishery exploitation, there is probably a second mechanism driving selection for higher fecundity, namely the progressive intensification of stocking. Stocking with hatchery-reared whitefish larvae started more than a century ago in ULC (Rösch, 1993), and the number of larvae stocked per year has increased steadily to its current level of around 400×10^6 individuals per annum (Straile *et al.*, 2007) (Fig. 5). Eggs are obtained from spawners, which are caught with gill nets of legal mesh size, in which females with a larger body girth have a higher catch probability. Higher fecundity (probably, but not necessarily, in combination with larger egg size) results in larger body girth, so that females with higher fecundity are more likely to be caught and to contribute offspring to the stocking cohort for the following spring. This concept is supported by a study of Hay *et al.* (1986), who reported that mature herring with higher GSI are more likely to be caught in gill nets than fish with lower GSI. Eggs obtained in the spawning fishery are incubated in hatcheries under

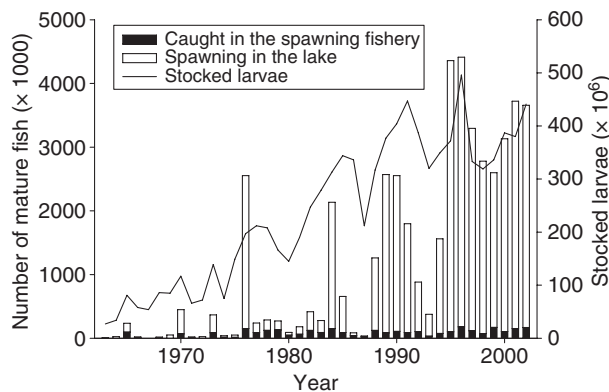


Fig. 5 The reproductive stock (aged 2+ and older) of pelagic-spawning whitefish in Upper Lake Constance, separated into two groups: group 1 (black bars), mature fish which were caught in the spawning fishery and whose offspring were incubated in hatcheries. Group 2 (white bars), mature fish, which remained in the lake and reproduced naturally. The solid line indicates the amount of larvae stocked into the lake from hatcheries.

optimized conditions. Prehatching mortality is typically around 30%, and significantly lower than that of naturally spawned eggs that develop on the lake bottom (Nümann and Quoß 1972; Straile *et al.*, 2007). A recent study using alizarin marking of hatchery larvae suggested that more than 60% of the 2003 Blaufelchen cohort originated from hatcheries (Eckmann *et al.*, 2006). The ratio between the number of spawners which reproduce naturally and the number of spawners caught in the spawning fishery ranged from 1 : 0.85 (1996) to 1 : 23.5 (1967) during the investigation period (Fig. 5). Our analysis showed that in recent years only around 6% of the reproductive ULC whitefish stock (i.e. between 75 000 and 180 000 individuals) are caught in the spawning fishery, but their offspring probably contribute at least 60% to recruitment (Eckmann *et al.*, 2006). Taking into account that these 6% of spawners are not a random assortment of phenotypes (genotypes) but selected according to size/body girth by the gill net fishery, an effect on the gene pool composition is certainly likely. Stocking policy could be a powerful mechanism for a sustained genetic selection towards high fecundity, achieved at the cost of somatic growth.

In a previous study on whitefish growth over the last five decades (Thomas & Eckmann, 2007), evidence was provided for an evolutionary response of ULC whitefish to the size-selective gill net fishery. Similar responses have already been demonstrated for several heavily exploited marine fish species, for example cod (Hanson & Chouinard, 1992; Swain *et al.*, 2007). The previous results concerning whitefish growth can now be complemented with those from the present study to form an extended hypothesis about possible evolutionary responses of the ULC whitefish stock to size-selective harvest. The gill net fishery represents a selective force

towards slower growth, earlier maturation (not previously verified for ULC whitefish so far), and increased fecundity. As higher fecundity can only be obtained at the cost of reduced somatic growth (with egg weight remaining unchanged), there is a twofold selective pressure towards slower growth. Furthermore, in the spawning fishery, which is conducted to obtain eggs for incubation in the hatcheries, females with the largest body girth, i.e. those with the highest fecundity are harvested disproportionately and, therefore, the intensive stocking program at ULC tends to drive evolution towards higher fecundity and slower growth.

There has been only one previous attempt to quantify the contribution of stocking to whitefish year-class strength in ULC (Straile *et al.*, 2007); so, the importance of actual stocking policy for evolutionary changes in the whitefish stock cannot be analysed in great detail. A recent study of whitefish year-class strength in ULC revealed that year-class strength was influenced significantly by both stocking density and the North Atlantic Oscillation index (Straile *et al.*, 2007). A high NAO index during holomixis in late winter leads to higher hypolimnetic temperature, which shortens the development time of whitefish eggs spawned in the next winter, and consequently the loss of eggs to infection and predation. Hence, the NAO influences naturally spawned whitefish eggs with a time lag of 1 year. This suggests that natural reproduction is still highly relevant despite intensive stocking. Consequently, the impact of stocking on the evolution of reproductive traits in ULC whitefish remains ambiguous, but the fishery-induced selection towards slower growth and higher fecundity affects both hatchery-reared and naturally spawning fish.

Gonadosomatic index

The gonadosomatic index increased until the early 1980s in parallel with fecundity. However when fecundity began to decrease during the 1980s and 1990s, GSI did not decrease accordingly but remained relatively constant at around 22–24% (Fig. 4). This effect can be attributed to changes in the age structure of whitefish stock during these decades. Growth rate decreased as a consequence of lake re-oligotrophication and stronger intraspecific competition for food due to higher standing stock biomass (Thomas & Eckmann, 2007), so that age of recruitment into the fishery gradually increased. As egg weight increases with female age, heavier eggs produced by older females largely compensated for reduced fecundity, and GSI, which is strongly related to egg weight and fecundity, decreased only marginally.

Sustained changes in life-history traits of fish caused by human impacts are not limited to exploited marine fish stocks. Our study provides evidence that changes in lake trophy and fishery management at Upper Lake Constance have influenced whitefish fecundity during the last decades, and that evolutionary change towards

higher fecundity is being driven by size-selective fishery and stocking practices. The finding that the majority of whitefish offspring are derived from rather few individuals should be the reason for concern. Genetic diversity will probably be impoverished, and this might have consequences for population structure and production, the extent of which are not yet fully conceivable. Taking these likelihoods into account is a challenge for the future development of fisheries management at Upper Lake Constance and elsewhere, where similar, as yet undetected problems may exist.

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