

Long term anthropogenic impacts on the whitefish (*Coregous
lavaretus* L.) stock of Lake Constance

Dissertation

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1. General Introduction

Human impact on the environment is ubiquitous in most parts of the world. No other species has changed the appearance of this planet in such a short time scale thus far. The effects are diverse, ranging from invisible global climate changes to the radically modified landscapes, which are even visible from space.

Aquatic ecosystems, to be focused on freshwater systems in the following, are a good example to summarize the manifoldness of human actions and their consequences. The beginning of human impact on aquatic systems already started many centuries ago: the first artificial water channel in China, for example was constructed in the 6th century B.C.. Industrialization, which took place at the same time as the explosion of world population, magnified the global human pressure on natural ecosystems. (Sondergaard and Jeppesen 2007) summarized the rising impact of various human impacts on aquatic ecosystem along a time axis.

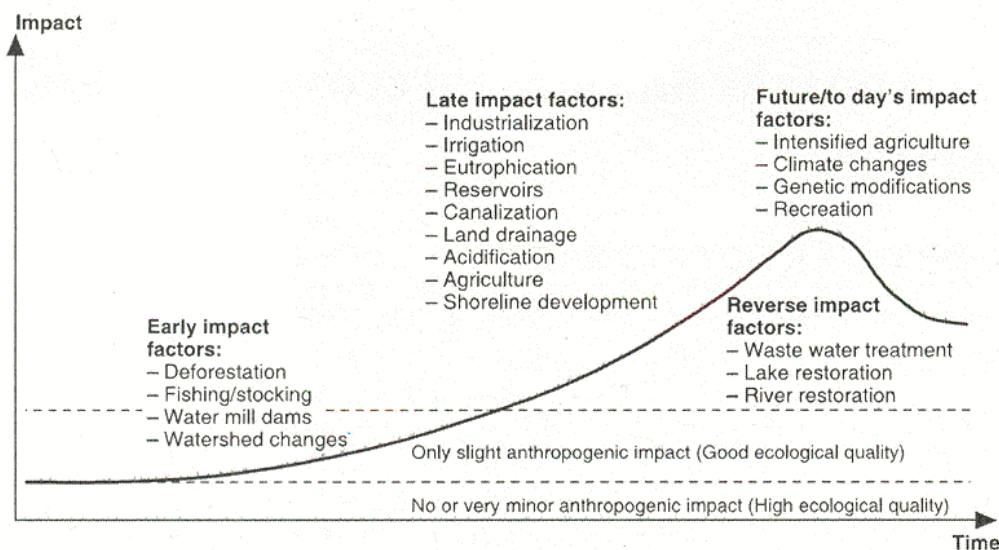


Fig. 1.1: Generalized scheme on human impacts on freshwater ecosystems in industrialized countries and their effects on ecological quality from (Sondergaard and Jeppesen 2007)

We can differ between chemical, physical and biological anthropogenic impacts.

On the chemical side, the altered energy and nutrient fluxes in aquatic ecosystems led to an eutrophication of many freshwater systems in the 2nd part of the 20th century (Colby et al. 1972, Smith et al. 1999, van Raaphorst and de Jonge 2004). Another chemical problem has arisen from the contamination of water with endocrine active matters, as well

as pharmaceutical residues of waste water (Halling-Sorensen et al. 1998, Jones et al. 2002, Bögi et al. 2003). Furthermore, acidification is an issue with regional importance.

The straightening and fitment of streaming water (Kingsford 2000, Tockner and Stanford 2002) is one example how human “physical” activity works. Also in standing waters the morphology and the nativeness of shorelines (Brauns et al. 2007) had been altered in many systems.

Thermal alterations of natural temperature regimes in rivers and lakes as a result of the inflow from cooling water from the industry and power plants and the segregation of river systems with dams are of higher ecological relevance (Pawson and Eaton 1999, Val et al. 2006). A keystone issue of future research is the diverse impacts of global warming on aquatic ecosystems (Covich et al. 1997, Mooij et al. 2005). Large scale meteorological changes will affect water temperature (Cane et al. 1997) and precipitation patterns. Other topics of minor importance in the current discussions of physical aspects in aquatic ecosystems are the pollution with light (Longcore and Rich 2004, Navara and Nelson 2007) and noise (Wysocki et al. 2006).

The introduction of new species (Dukes and Mooney 1999, Sakai et al. 2001) is a biological problem in aquatic ecosystems caused by human activities (conjunction of before water systems, which were separated beforehand; dispersal with boats or ballast water; release of animals/plants kept in private aquaria before).

Another less visible effect with a high relevance to the present study is the sustainable role of humans in evolution. Natural selection is the driving force in evolution. The speed of evolution can be fast even in intact ecosystems (Thompson 1998), for example when a new invader enters an enclosed ecosystem (e.g. an island or lake), and interacts with the existing food web. Other examples are attack and defence mechanisms in predator prey systems which evolve quickly. Nowadays, in many fields human activity displaces natural selection as the driving force of evolution (Palumbi 2001). This is particular apparent in the medical and the agricultural sector, where the massive use of antibiotics and herbicides lead to fast evolution and development of resistance and adaptations in bacteria and plants.

All these anthropogenic impacts, whether chemical, physical or biological, change the ecological niches of species and therefore the fragile interplay of the sensitive ecosystems.

Against this background the present thesis should elucidate the role of human activity on the whitefish (*Coregonus lavaretus* L.) stock of Lake Constance. Several previous studies have already dealt with some aspects of humans on the whitefish stock of Lake Constance. Especially the process of eutrophication has been in the focus of applied fishery science for many years. Whitefish have a special commercial and ecological relevance for Lake Constance. Coregonids characterise oligotrophic, prealpine lakes like no other fish species. Approx. 80% of fish harvested in Lake Constance are whitefish. There are 3 different ecotypes in Lake Constance: Sandfelchen, Gangfisch and Blaufelchen. The differentiation between them is rather difficult. The only time a clear differentiation can be made between the species is during spawning: Gangfisch spawn close to the shore in shallower depth, Sandfelchen close to the shore but in deeper water while Blaufelchen spawn in the middle of the lake in the deepest part.

My motivation to reanalyze effects of anthropogenic activities on the whitefish population was the following:

- The process of reoligotrophication has been completed by now, which offers a good opportunity to examine the entire process of eutrophication & reoligotrophication and its effect on fishery
- Fishermen still report large fluctuations in the annual fishing yield, as well as differences in the distribution patterns of fish
- Global warming is expected to have an effect on recruitment. What will be the consequences for population dynamics?

Due to the commercial interest, data on whitefish have been well documented over the last decades. The analysis has been limited to a time-frame beginning in the 1950s, as documentation before this time is incomplete. Anthropogenic impact has increased in the observed previous 50 years.

In 1944 whitefish were already subject to a broad analysis of its ecology and life history (Elster 1944). A high degree of documentation has been of applied interest for fishermen, fisheries managers and scientists. The good documentation on whitefish fishery enabled me to assess different aspects of whitefish ecology with regard to human influence retroactively.

This thesis cannot consider all possible anthropogenic effects, listed above, on Lake Constance whitefish stock, but focuses on the, in my opinion, most dominant factors.

I name the following four points as the accentuated anthropogenic controlling factors, acting directly or indirectly:

- 1) the changed nutrient content leading to a phase of eutrophication and oligotrophication (indirect)
- 2) global warming (indirect)
- 3) stocking practice, affecting fluctuations in standing stock biomass (direct)
- 4) size-selective fishery as a selective force (direct)

Oligotrophic Lake Constance experienced a rapid increase of nutrient inflow in the middle of the last century. Phosphorus concentration, measured during spring turnover, increased from originally $7 \mu\text{g L}^{-1}$ (1951) to $87 \mu\text{g L}^{-1}$ in 1979 (Fig. 1.2). This dramatic increase in nutrient inflow had severe consequences on the ecosystem (Bäuerle and Gaedke 1998). In consequence algae blooms occurred regularly with negative effects on tourism and fishery.

Fishery was affected in several ways. In the moderate phase of eutrophication fishermen seemed to benefit, though whitefish, as the most important commercial fish species, grew faster and fishery yields increased. In the more pronounced phase of eutrophication the effects towards fishery tipped toward the negative, though fisheries yield remained on a high level. Filamentous algae attached to nylon gill nets in the mid of summer, which made them visible to the fish, which now avoided them. Cyprinid fishes such as carp, bream and roach benefited from the eutrophication and were found in the pelagic zone in huge numbers. In consequence, only a minor fraction of the catches of a few months consisted of marketable common whitefish. Another negative effect was the reduced oxygen saturation of the hypolimnion during eutrophication. This led to a reduced success in egg development of whitefish eggs at the lakes bottom.

Pressure from the public to change the uncontrolled nutrient input was high. A huge amount of money was spent to redevelop the watershed in the 70s. Sewage treatment plants with phosphorus elimination were constructed and the invention of phosphorus free washing detergents in the late 70's, helped achieve the designated aim. The chosen sanctions quickly proved to be successful and the phosphorus concentration began a steady decline returning to $7 \mu\text{g L}^{-1}$ (2008). With the ongoing reoligotrophication fisheries yield has decreased again. Nowadays fishermen state their opinion, claiming that lakes' trophy is too low to sustain an economical fishery.

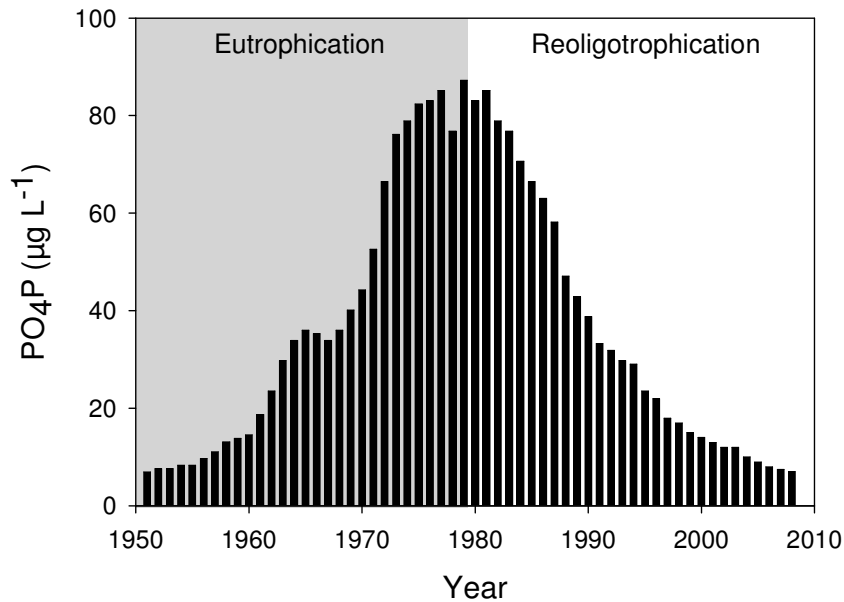


Fig. 1.2: Phosphorus concentration of Lake Constance during spring turnover (1951-2008). Grey background indicating the phase of eutrophication, white background indicating the phase of reoligotrophication.

Global warming will demand increasing attention in the future. Especially in the prealpine region effects will be pronounced. Future winters are expected to be warmer and more humid, precipitation in the summer is expected to drop accompanied with an increase in temperature. We therefore expect a faster and more intense warming of the surface layer. In a first phase of global warming we might expect a positive outcome on whitefish recruitment. Beneath the warming of the surface layer, we expect a slight increase in hypolimnion water temperature as well, which will reduce egg development time and therefore benefits egg survival (Straile 2000). In a later phase of global warming, mixing in autumn might be incomplete, as stratification is more stable. An incomplete mixing will carry less oxygen saturated water into the hypolimnion, in consequence oxygen concentration might decrease over the long run. This again might affect egg development of whitefish negatively. Since our data sets merely give slight indications for climate change effects so far, we discuss this aspect in conjunction with other human induced effects.

Fishery is a field in which human-induced evolution has become strongly visible in recent years. From marine fisheries science we know, that fishery is able to act as an evolutionary selecting force. Next to mortality, reproductive success is the major driving force of evolution. The basic assumption of the fisheries induced evolution theory is that, because of fishing mortality, not all individuals of the same species have the same

probability to die because of fishing mortality. Fishing gear (e.g. gill-nets, trawl nets, fish traps) catches some individuals better than others. The reason for this is that two individuals of the same species differ slightly in a variety of traits, e.g. morphology, growth history, colour, behaviour, distribution. Some of those traits lead to a better catchability than others, for example if a fish grows quickly it reaches legal mesh size earlier in life. If those traits have a genetic base and decide whether an individual faces a higher risk of fishing mortality, fishery is a strong selective factor. If a fish dies earlier it has less opportunities to reproduce and therefore less offspring who can pass genes on to the next generation. In marine fish stocks, fishery is the most important mortality factor for many species, in contrast natural mortality reasons (e.g. predation, parasites, starvation) becoming less important. Size-selective fishery is suspected to change a variety of traits. In literature we found a documented selection for slow growth, increased fecundity, depletion in genetic diversity and earlier maturation at smaller size (Jørgensen et al. 2007). These evolutionary changes are contrary to established life history theories under natural evolution (Edeline et al. 2007), which predicts a development towards an accelerated growth and a gain in genetic diversity. Sustainable effects can be manifold and the full bandwidth is not yet conceivable. The theoretical mechanisms for the fisheries induced evolution theory seem obvious, and yet it is difficult to find evidence for it. So far only the laboratory experiment of Conover and Munch (2002) has given strong indications that the mechanisms work as predicted. Studying fisheries-induced evolution, effects are not always easy to identify, since many environmental factors might lead to the same effects observed (Wright 2007).

Up until the 1950's the fishing gear of choice in Lake Constance was "Klusgarn", a kind of purse seine, and cotton gill nets. The "industrialization" of fishery at Lake Constance started with the invention of nylon gill nets. This material proved to be very efficient and the fisheries yield increased. A fraction of fish harvested, were immature thus a collapse of the stock was feared. Legal mesh size as well as other fishing regulations (number of used nets, fishing days per weeks, licenses), needed several revaluations in the 1960's in order to guarantee a sustainable fishery. Fishing effort has been reduced in the last decades by reducing the number of nets per fishermen, the number of licenses and the number of fishing days per week. Next to the increase in fishing efficiency, the amount of stocked whitefish larvae increased steadily over the years from approx. 27 (1963) to 441 (2002) million larvae per year. The direct whitefish management effort through fishery and stocking increased steadily over time.

Those managing measures do not solely affect the number of fish in the lake and thus the standing stock biomass, but also has the ability to act evolutionary. Gill net fishery is size-selective. In a system with high fishing pressure, as Lake Constance still is, large and deep bodied fish will have a far higher risk of facing fishing mortality early. As growth patterns as well as body shape are an expression of the genetic background of each fish, fishery and stocking have the ability to magnify possible evolutionary responses.

In the first study (chapter 2) we analyzed whitefish somatic growth over an investigation period of 46 years (1955-2000). In contrast to former studies regarding growth performance we included intraspecific competition, next to changes in lake trophy, as a second important environmental factor. We reconstructed standing stock biomass of whitefish for the years 1954-2000 from fisheries-yield data on a monthly scale. Based on these data we calculated the 50 % harvest point of each cohort, considering these fish to grow at medium speed (fast growing fish are caught earlier, the slow growing ones later). Using archived scales from the Institute for Lake Research we were able to back-calculate length-at-age from scales from those medium fast growing fish. This enabled us to compare growth increment of the different cohorts with each other. Multiple linear regression analysis was used to enlighten what controls whitefish growth.

The findings from our growth analysis were the motivation for a laboratory experiment (chapter 3) to test for heritability of growth rate. During spawning fishery we caught fish of same length but different age, therefore showing different growth rates. Next to environmental conditions, changes in the rate of growth might be genetically controlled. Eggs gained from these parental fish were incubated in a Zugjar facility with a capacity to test 24 different batches. Larvae hatched from the different batches were kept at the same conditions with an *ad libitum* feeding. Initial growth performance of larvae was monitored over 40 days, with a sampling interval of 10 days. Next to the length increment the increase in dry weight was documented.

Our second long term study, (chapter 4) investigated changes in reproductive traits, over a period of 37 years (1963-1999). Our results on somatic growth revealed that next to lake trophy, intraspecific competition as well as fishery, as an evolutionary acting selective force, affected growth. This led to the idea, that reproductive traits could be affected in the same way. Somatic growth and reproduction are two competing pathways of energy allocation. Changes in lake trophy and standing stock biomass affect the energy budget a fish has to its disposal. Our hypothesis was, that fecundity (as an important reproductive trait) decreases with sinking lake trophy (this was already shown by (Hartmann and Quoss

1993)), as well as, with increasing standing stock biomass. The question arose as to whether additionally, there is an evolutionary response visible in the reproductive traits as suggested for other fish stocks in literature. We reanalyzed the Hartmann & Quoß data set, which has been extended by 8 additional years. Beside fecundity we were also able to derive data on egg weight and gonadosomatic index from the analysis and test those traits against environmental conditions as well.

Chapter 5 deals with a long term analysis, as well. This study targets the changes in whitefish vertical distribution patterns. Whitefish are caught at different depths throughout the year. In general, fish stay in deep waters early in the year and ascend to the surface in late spring. In the course of summer, fish start descending to greater depth again. Observations of commercial fishermen in recent years suggest that vertical distribution patterns have altered with ongoing reoligotrophication. Nets have been set greater fishing depth in the latest years. We extracted the data regarding fishing depth from monthly reports of fishery wardens. The first documentations reach back to 1958 and have been continuously documented until today. We interpret fishing-depth as an indirect measure for whitefish vertical distribution. The question was, whether we could confirm the trend of altered fishing depth over time and if so, whether such a change in distribution patterns is coherent with environmental changes.

2. The influence of eutrophication and population biomass on whitefish growth – the Lake Constance example revisited

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(Modified by supplementing the years 1998-2000 into analysis)

Gregor Thomas and Reiner Eckmann

2.1 Abstract

Accelerated growth of freshwater fish during anthropogenic eutrophication has been attributed almost exclusively to the increased nutrient content, while density-dependent effects have been largely neglected. We evaluated the relative importance of these factors by studying the growth of 46 consecutive year-classes of whitefish (*Coregonus lavaretus* L.) from Upper Lake Constance. This prealpine lake underwent eutrophication from the 1950s to 1970s, followed by re-oligotrophication. Because whitefish are harvested with gill nets in a strongly size-selective way, we used back-calculated lengths of average fast growing fish to compare growth among cohorts. Standing stock biomass was estimated based upon virtual year-class strengths. Multiple linear regression analysis revealed that growth of whitefish during their 2nd year was most strongly related to standing stock biomass followed by PO₄-P content during spring turnover, and by calendar year, which was incorporated as a third independent variable (adjusted R²=0.87). The negative correlation between whitefish growth rate and calendar year is interpreted as evidence of an evolutionary response to the highly size-selective fishery during at least four decades. We conclude that density-dependent effects on whitefish growth are more important than had been realized previously, and that the impact of eutrophication on growth of whitefish needs to be reconsidered.

2.2 Introduction

Understanding the effects of abiotic and biotic factors on fish growth is of both scientific and commercial interest. Among the abiotic factors, water temperature and a water body's trophic state, are generally considered to be most important, while competition for food, either inter- or intraspecific, is probably the most relevant biotic factor. The trophic state of a water body and the intensity of competition for food can be modified intentionally or unintentionally by human activities over short time scales. A better understanding of human impacts on fish growth, through changes to a waterbody's trophic state or in competitor density, is therefore a prerequisite for the successful management of exploited fish populations.

Lake whitefish (*Coregonus lavaretus* L.) is a species of great commercial importance in many prealpine lakes in central Europe (Nümann 1972, Gerdeaux 2004), as are other species of the genus *Coregonus* in lakes, rivers and estuaries of northern Eurasia and North America (Price et al. 2003, Gassner et al. 2004, Hoff and Todd 2004, Salonen and Mutenia 2004). Any major changes in coregonid yields therefore attract the immediate attention of fishermen and managers and challenge fishery scientists to explore the likely reasons, and eventually to recommend appropriate measures to stabilize yields.

The most dramatic changes in coregonid growth in central European lakes occurred during the 1960s and 1970s, when fish of consecutively younger age were caught (Nümann 1962). Most of the studies of coregonid population dynamics claimed that anthropogenic eutrophication was the main cause of the acceleration in whitefish growth (Nümann 1962, Grimås et al. 1972). The decrease in whitefish growth from many European lakes towards the end of the 20th century was generally attributed to re-oligotrophication (Kirchhofer 1995, Müller and Mbwenembo Bia 1998). Thus, it was an accepted hypothesis that changes of a lake's trophic state, through changes of primary and secondary production, was the main, if not the only, mechanism that controlled fish growth (Downing et al. 1990).

In addition to lake trophic state, however, density-dependence is another key factor influencing fish growth (Walters and Post 1993, Post et al. 1999, Lorenzen and Enberg 2002). With higher population density, intraspecific competition for food can become more intense, resulting in slower individual growth. Several studies on density-dependent growth in coregonid populations have confirmed this general concept. These studies have either compared whitefish growth rates among lakes with different whitefish densities (Bidgood 1973, Lehtonen and Niemelä 1998, Mayr 2001), compared growth rates before and after

stock size reduction through intensive fishing (Healey 1980, Amundsen 1988, Klein 1992, Valkeajärvi 1992, Mills et al. 1995), or monitored whitefish stock oscillations over longer time periods (Helminen et al. 1993, Salonen et al. 1998, Viljanen et al. 2004). Most of the published studies on whitefish growth have, however, focussed either on lake trophic state or on population density.

The earlier studies on whitefish growth in European prealpine lakes were all done during the time of rapid anthropogenic eutrophication, whereby the obvious parallelism between nutrient content and whitefish growth was considered to be evidence for a monocausal relationship. As a much more extensive set of data on whitefish population dynamics, covering 46 year-classes, is now available for Upper Lake Constance, we took advantage of this unique opportunity to reanalyse the earlier concepts about the influence of eutrophication on lake whitefish growth. The first aim of our study was to disentangle the effects of density-dependence and lake trophic state on the growth of lake whitefish using multiple linear regression analysis.

Size-selective harvesting by a commercial fishery can change life-history traits such as size-at-age or age-at-maturity of the fish (Rijnsdorp 1993, Sinclair et al. 2002). If some of the phenotypic variation in these traits is genetic, then fishing may cause evolutionary changes in the life-history (Law 2000, Conover et al. 2005). In an experimental study with *Menidia menidia*, size-dependent mortality did indeed select for the evolution of genotypes with growth rates that were in directions counter to the size-selective harvest within only four generations (Conover and Munch 2002). Additionally, a gillnet fishery for lake whitefish in Lesser Slave Lake evoked changes in growth rate, condition, and mean age, and it was suggested that the highly selective harvest of large, fast-growing fish might provoke an evolutionary response in this stock (Handford et al. 1977). As the fishery for whitefish in Lake Constance has been highly size-selective, at least since the mid-1960s, when monofilament gill nets of a fixed mesh size replaced all formerly used fishing gears, evolutionary changes in the whitefish stock may have occurred during the past four decades. It was, therefore, the second aim of our study to screen the available data for indications of evolutionary responses to this size-selective harvesting.

2.3 Material and Methods

Study site

Upper Lake Constance (ULC) is a large (472 km²), deep ($z_{\max} = 254$ m, $z_{\text{mean}} = 101$ m), warm-monomictic prealpine lake situated at the northern fringe of the European Alps (9°18'E, 47°39'N), shared by Austria, Germany and Switzerland. The lake underwent

pronounced eutrophication during the 20th century, whereby total phosphorus concentrations during winter mixing in February/March (TP_{mix}) increased from $7 \mu\text{g}\cdot\text{L}^{-1}$ in 1951 to $>80 \mu\text{g}\cdot\text{L}^{-1}$ around 1980 (Bäuerle and Gaedke 1998). As a result of drastically reduced P inputs, including the banning of phosphate-containing detergents, sewage collection, and the inclusion of phosphorus stripping in sewage treatment, the lake had returned to oligotrophy by the beginning of the 21st century (TP_{mix} in 2004: $9 \mu\text{g}\cdot\text{L}^{-1}$) (cf. Fig. 2.1).

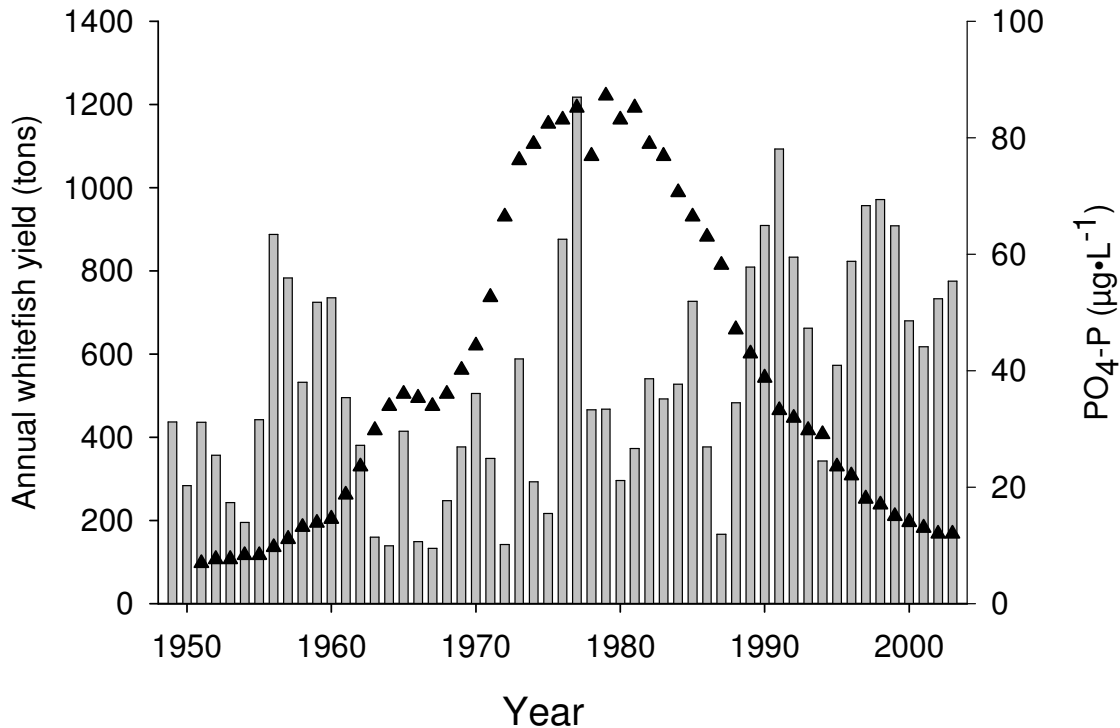


Fig. 2.1: Phosphorus concentration during spring turnover (triangles) and total whitefish (*Coregonus lavaretus* L.) yield (bars) in Upper Lake Constance.

Twenty-nine fish species presently occur in the lake (Eckmann and Rösch 1998) among which lake whitefish is commercially the most important. An uninterrupted record of commercial catches from ULC is available since 1910. Regular surveys of the whitefish stock have been carried out monthly since the beginning of the 1960s, while less regular surveys were conducted in the 1930s, the late 1940s and during the 1950s. These surveys showed that whitefish growth had accelerated to such a degree by the beginning of the 1960s that whitefish reached the legal minimum size to be taken of 30 cm (legal gill net mesh size 38/40 mm) about two years earlier than during the 1930s (Nümann 1966). As a consequence, an increasing fraction of the commercial yields consisted of age-1 fish that had not yet reproduced. The obvious risk of recruitment overfishing was counteracted in

1965 by increasing the minimum mesh size to 44 mm and the legal minimum size to 35 cm (Nümann 1967).

The whitefish fishery at Lake Constance

At the beginning of the 20th century, about 460 professional fishermen were licensed to fish at Lake Constance using drifting cotton gill nets and “Klusgarn”, a seine operated in the pelagic zone. By the mid-1960s, both gears had been replaced almost completely by more efficient monofilament nylon gill nets. During the following decades, the number of nets per licence was successively reduced from 10 to 3, only 4 fishing days per week are allowed instead of 5, and the number of commercial fishing licences was cut by 30%. These measures were taken, firstly to allow for a reasonable income to the commercial fishermen, and secondly to avoid overharvesting the stock as in the 1960s and early 1970s. Altogether, fishing intensity in 2005 had dropped to 17% of what it was in 1961 (Rösch, R., Fischereiforschungsstelle, Langenargen, Germany, pers.comm.).

Virtual year-class strength

Virtual year-class strength (YCS) was calculated for the annual cohorts of 1947 to 2000. These estimates are based upon biweekly to monthly test catches using gill nets of legal mesh size. Samples are analyzed with regard to age and body weight, which provides an estimate of catch composition by age-classes. Using the monthly fishermen’s catch data, the number of individuals of a certain year-class harvested from the lake can then be calculated month by month. Integrating all monthly harvests from year-class *i* across time yields an estimate of the virtual size of this year-class (cf. Eckmann et al. 1988). To account for natural mortality, an instantaneous mortality rate of 0.2 per year was incorporated (Eckmann et al. 2002). The estimates of whitefish YCS at Lake Constance, thus, are not based on estimates of fishing mortality but on the well documented monthly catch reports of all fishermen. These reports are made anonymous during compilation, and they are not supplied to revenue authorities to avoid bias towards low yields. Subtracting the monthly harvests from year-class *i* successively from the initial size of this cohort provides an estimate of the number of fish of year-class *i* that were present in the population in each month, from its recruitment into the fishery until the cohort was fished out. By adding up these numbers across year-classes for each month, the numerical age composition of the whitefish standing stock was obtained.

Size-selective harvest

(Nümann 1959) was the first to point out that whitefish are harvested in a size-selective fashion from Lake Constance using gill nets of a legally fixed mesh size, the faster growing fish being harvested earlier than the slower growing members of the same cohort. In this situation, growth of fish from different year-classes cannot be compared by determining size-at-age, because this measure depends on the time of harvest of the fish from which size-at-age is determined. We assessed this potential bias by back-calculating length at the end of the second year for all whitefish from the cohorts of 1991 and 1992, which had been collected with legal size (44 mm) gill nets in the regular monthly test fishery. For both year-classes, size-at-age was significantly related to the year of harvest (ANOVA, $F_{2,157}=22.09$, $P<0.0001$; $F_{3,210}=35.22$, $P<0.0001$, for the year-classes 1991 and 1992, respectively). The mean length after two years of whitefish sampled in their 3rd, 4th, and 5th years of life decreased from 25.4 cm through 23.2 to 20.7 cm for the 1991 cohort, and from 25.3 through 23.2 to 22.1 cm for the 1992 cohort. Thus, considerable bias may arise when length-at-age is determined without taking into account the age at which the fish are harvested. We therefore decided to compare growth of whitefish from different cohorts by using those fish that were harvested around the time when 50% of the total harvest from a cohort was being obtained (termed average fast growing fish hereafter).

Back-calculation of growth

Scales were generally sampled from the left body side between the dorsal fin and the lateral line. Three scales from each of about 50 average fast growing fish per year-class were used for growth analysis. The widths of annual growth increments and total scale radius were measured on each scale. Length-at-age was back-calculated according to Lee (Ricker 1968) using a y-intercept of 2 cm, which had been established in a previous regression analysis of fish length on scale radius. The results from three scales were averaged, and the mean back-calculated lengths-at-age were calculated for each cohort. In total, 2 385 fish were used in this growth analysis.

Biomass

The standing stock biomass of whitefish was estimated based upon the monthly numerical age-class compositions. For fish in their first and second years of life, growth in length was linearly interpolated between the initial and final lengths. The initial length for age-0 fish was set at 12 mm, i.e. their length at hatching, while lengths after one and two years were those that had been back-calculated from the scales. The growing season of whitefish in Lake Constance lasts from April to October. Therefore growth was interpolated only for

these months, while it was assumed to be zero in the other months. For the year-classes 1947-1954, 1982-1984, and 1986-2000, length at the end of the third year could be back-calculated from scales, and the same procedure was applied for these cohorts. For fish older than two or three years, whose length-at-age could not be back-calculated from scales, von Bertalanffy growth curves were constructed. We used the available back-calculated lengths, including length at hatching (12 mm) and a generalized asymptotic length of 73 cm (www.fishbase.com) to construct Ford-Walford plots, from which the growth parameter k was estimated for each cohort. From the von Bertalanffy growth model, the lengths-at-ages for fish older than two or three years were calculated. As for the younger fish, growth was linearly interpolated for the months April to October.

Length was converted into weight using separate length-weight regressions for each decade. These were constructed from the length-weight data of around 100 fish sampled during the growing seasons in each decade. As these data covered a size range from 25 to 40 cm only, we also incorporated length-weight data for fish from 2 to 8 cm length which were obtained during a standardised beach seine fishery from 1997 to 2004 (Reyjol et al. 2005). All decadal length-weight regressions had R^2 -values of 0.995 and above. For each month the average length per age-class was converted into weight, multiplied by the number of fish per age-class, and then summed across age-classes. Finally, to obtain an estimate of standing stock biomass for each year, we averaged monthly biomass values per year.

Statistical analysis

Multiple linear regression analysis was performed using JMP Version 4.0.4 (SASTM). The length increment of the whitefish during their second year was used as the dependent variable. We considered two independent variables, PO₄-P concentration during spring turnover and the natural logarithm of standing stock biomass, and also incorporated the calendar year as an independent variable at a later stage in the analysis. As the standing stock biomass could be reconstructed only from the years from 1954 onwards, i.e. when the 1947 cohort was fished out, we based our analysis on 46 years of data.

2.4 Results

YCS of the whitefish for the years 1947 to 2000 ranged between 94 000 (year-classes 1964 and 1965) and 4 460 000 (year-class 1974), with a median value of 950 000 individuals. In the 1950s and from the late 1980s until present, the standing stock comprised five to six age-classes, and biomass ranged from 500 tons (9.3 kg•ha⁻¹) to 2000 tons (37.3 kg•ha⁻¹) (Fig. 2.2). During the 1960s and early 1970s, biomass never exceeded 500 tons and even

fell below 30 tons in the spring of 1967. This stock comprised only young fish up to three years of age. Exceptionally strong year-classes dominated the standing stock biomass during 2-3 years, most notably the year-classes of 1974 and 1982. Biomass increased steadily from the early 1980s, except for the years 1986/87 and 1992-1994. During the 1990s, standing stock biomass reached the highest values on record, being about twice as high as in the 1950s. Age-classes 3 and 4 dominated the stock during the most recent years.

Length of whitefish after their first year did not vary much, i.e. by a factor of 1.5, during the study period (Fig. 2.3) but, by contrast, length increment during the second year differed by a factor of 1.9. The fish grew nearly 10 cm more during their second year in the 1970s, when compared to the 1950s and 1990s. Although the length after three years could not be back-calculated from scales for the entire study period, it showed a similar trend.

Linear regression analysis revealed that length after the first year was only weakly correlated with standing stock biomass ($R^2=0.24$, $P=0.0003$, $n=46$) and no correlation existed with PO_4 -P concentration ($R^2=0.05$, $P=0.058$) or calendar year ($R^2=-0.019$, $P=0.867$). The length increments of the whitefish during their second year, however, were significantly correlated with the natural logarithm of standing stock biomass (metric tons) ($P<0.0001$) and with the PO_4 -P concentration ($\mu\text{g}\cdot\text{L}^{-1}$) during spring mixing ($P<0.0001$) with an adjusted R^2 -value of 0.81 (Table 2.1). The year 1954, the first year in our analysis, was excluded because it was considered to be an outlier. When the calendar year was included as the third independent variable, the model fit improved (adjusted $R^2=0.87$). The first two independent variables were still significant at $P<0.0001$, and the variable “calendar year” was significant at $P<0.0001$ with a negative influence on length increment during the second year (Table 2.1). In both models, the residuals were normally distributed and not autocorrelated.

To assess the relative importance of the three independent variables, scaled estimates centered by their means were used. These estimates indicate how much the length increment during the second year changes when one variable ranges from its lowest to its highest value while the other two variables are set to their mean value. Length increment changes due to standing stock biomass (range: 55.1 – 2060 metric tons) are 6.0 cm, they are 3.6 cm due to PO_4 -P concentration (range: 8.3 – 87.2 $\mu\text{g}\cdot\text{L}^{-1}$), and 2.9 cm due to the variable “calendar year” (range 1955 – 2000). This analysis indicates that standing stock biomass had the strongest influence on the growth of whitefish during their second year, followed by PO_4 -P concentration and the variable “calendar year”.

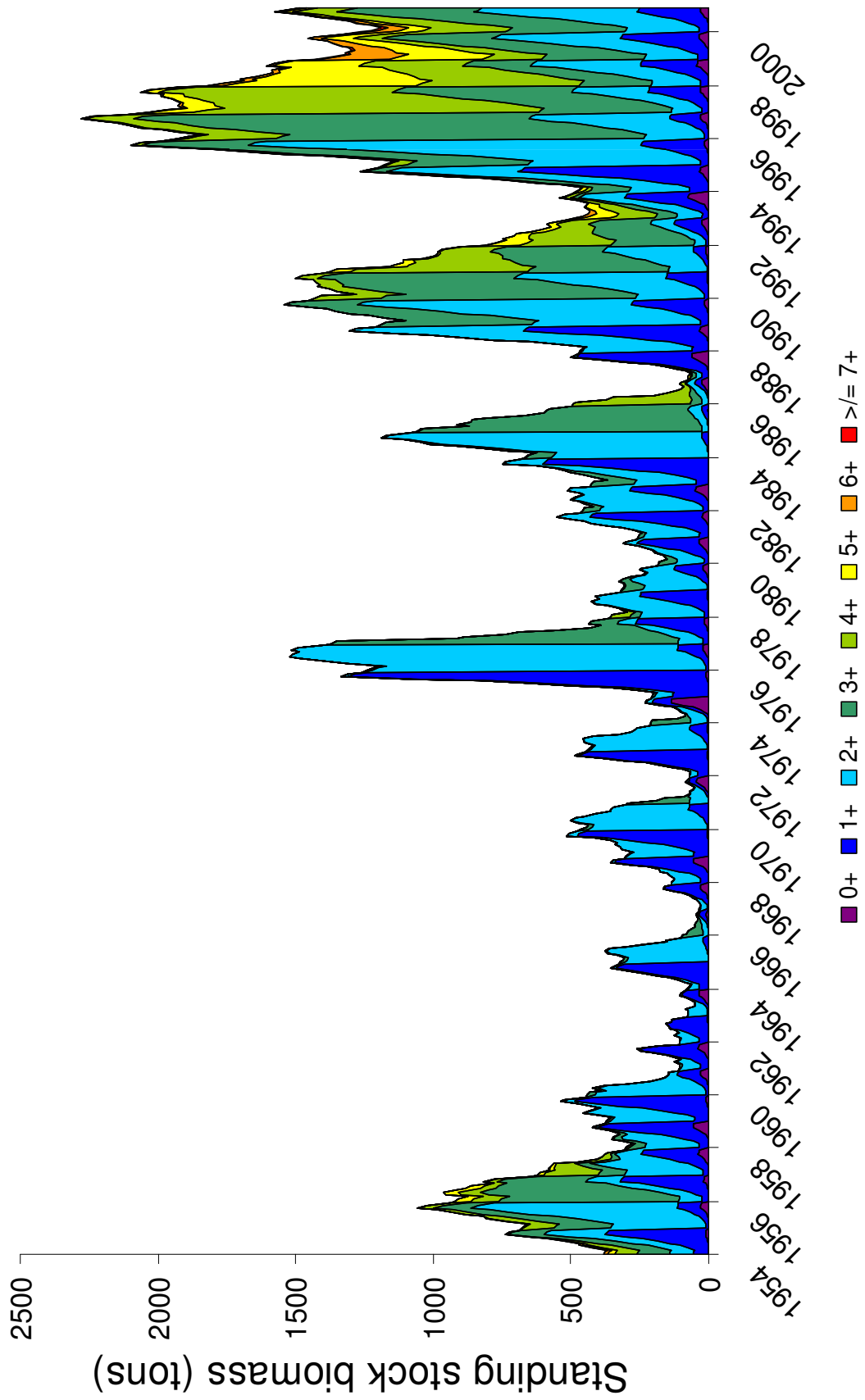


Fig. 2.2: Standing stock biomass by age-class of whitefish in Upper Lake Constance based upon virtual year-class strength.

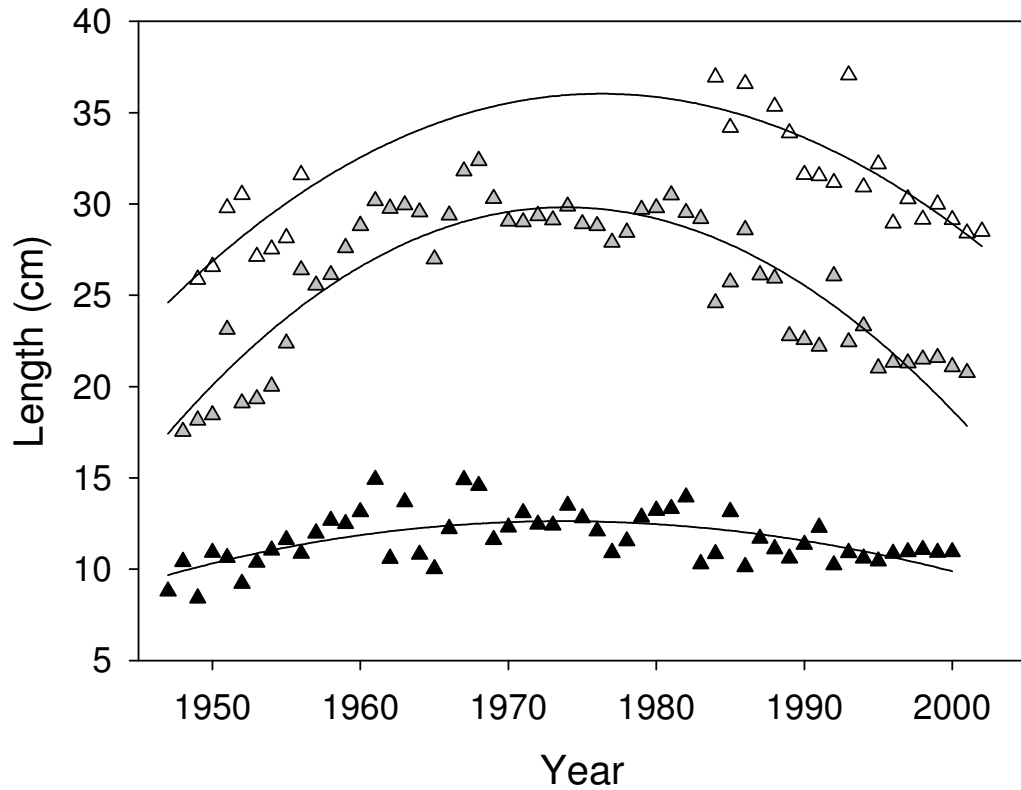


Fig. 2.3: Back-calculated lengths for the 1947-1997 cohorts of lake whitefish from Upper Lake Constance at the end of their 1st (black), 2nd (grey) and 3rd (white) year of life. Second degree polynomials were fit to the data to show trends. Standard error bars are not shown, because they are similar in size to the symbols used.

Table 2.1: Results of 2- and 3-factor multiple regression analyses of whitefish growth in Upper Lake Constance from 1955 to 1997. Length increment in the 2nd year is the dependent variable. The natural logarithm of standing stock biomass (ln biomass), PO₄-P concentration during spring mixing and calendar year were used as independent variables.

Term	Model 1		Model 2	
	Estimate	p	Estimate	p
Intercept	26.969	< 0.0001	149.091	< 0.0001
Ln biomass	-2.255	< 0.0001	-1.662	< 0.0001
PO ₄ -P	0.038	< 0.0001	0.045	< 0.0001
Calendar year			-0.064	< 0.0001
Adjusted R ²	0.81		0.87	

2.5 Discussion

Our results support, and at the same time extend, the earlier concept about the influence of eutrophication on the growth of whitefish. The earlier studies focussed exclusively on lake nutrient content and considered increasing lake phosphorus loads and their bottom-up effects on the pelagic food chain to be the ultimate, and only, cause of faster fish growth (Downing et al. 1990). Growth deceleration towards the end of the 20th century was attributed exclusively to lake reoligotrophication (Eckmann and Rösch 1998). The similar time course of phosphorus concentration and whitefish growth e.g. in ULC (Fig. 2.4) lends supports to this general concept. Our analysis, by contrast, demonstrates that standing stock biomass has an even stronger effect on whitefish growth.

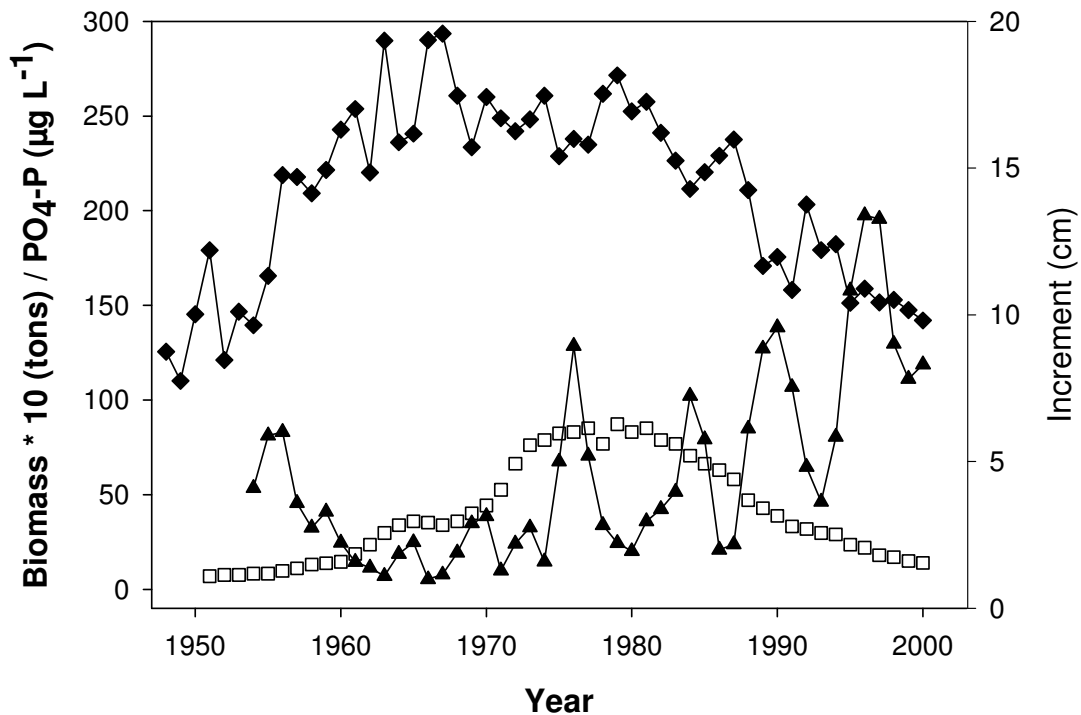


Fig. 2.4: Length increment of lake whitefish in their 2nd year (blank diamonds), phosphorus concentration (blank squares), and yearly averages of standing stock biomass of lake whitefish (black triangles) in Lake Constance.

Standing stock biomass of whitefish showed an opposite trend as compared to phosphorus concentration during the study period, decreasing to consistently low levels in the 1960s and early 1970s, and increasing towards the 1990s, suggesting an influence of stock biomass on whitefish growth in parallel to that of eutrophication. The evolution of standing stock biomass over time was, however, more irregular than the regular increase and then decrease of phosphorus concentration. Particularly weak or strong year-classes resulted in

low or high levels of whitefish biomass, respectively, which were observed at similar levels of phosphorus concentration. This allowed disentangling the effects of both factors on whitefish growth using data from 46 consecutive years. The decrease in the standing stock biomass of whitefish during the late 1950s/early 1960s was most likely caused by greater fishing intensity due to the increased use of efficient nylon gill nets. The subsequent increase in the standing stock biomass of whitefish can be attributed in part to the global reduction of fishing intensity down to 17% from 1961 to 2005 and to the slower growth of whitefish, which results in higher age-at-capture.

Lake trophic state is supposed to influence whitefish growth because of bottom-up enhancement of secondary production. The yearly average crustacean zooplankton density in ULC, integrated over the entire water column, increased from 4×10^5 individuals \cdot m⁻² to above 10^6 during the 1960s and 1970s, and has dropped back in recent years to values between 4 and 6×10^5 individuals \cdot m⁻² (IGKB 2004). Whitefish stock biomass on the other hand most probably affects growth because of intraspecific competition for food, because lake whitefish are by far the dominant consumers of zooplankton in ULC. Potential heterospecific competitors are either not very abundant (lake trout (*Salmo trutta*)), or they use the pelagic zone only sporadically (Eurasian perch (*Perca fluviatilis*)). Intraspecific competition for food is, therefore much more crucial than interspecific competition.

Density-dependent growth of fish, mediated through intraspecific resource competition, can be an important controlling factor of fish population dynamics (Lehtonen and Niemelä 1998, Wootton 1998, Mayr 2001, Lorenzen and Enberg 2002), and it has already been demonstrated for several whitefish stocks (Bidgood, 1973 #285). Food limitation is of course a prerequisite for density-dependent effects on growth. A comparison between whitefish and zooplankton biomasses in ULC during the past decades highlights the potential for intraspecific competition for food in this lake. During the year 1989, an average whitefish standing stock of 1 270 tons consumed roughly 13 000 tons of zooplankton during the growing season (Eckmann et al. 2002). When we assume a similar consumption of zooplankton for the entire study period, the demand for zooplankton would range from 730 to 20 200 tons, i.e. more than a 27-fold difference. The yearly average crustacean zooplankton density in ULC, however, ranged from 4×10^5 to 1.4×10^6 individuals \cdot m⁻² (IGKB 2004), i.e. only a 3.5-fold difference.

The influence of both phosphorus concentration and standing stock biomass on whitefish growth is much less pronounced in the first year than in the second year of their life. This can be attributed to the different temperatures experienced, and to the different food sources utilized by young-of-the-year and older whitefish. During their first months

of life, whitefish live in the epilimnion where their growth is mainly controlled by temperature rather than zooplankton concentration (Eckmann and Pusch 1989). Only later in summer do young whitefish avoid the warm epilimnion and move to deeper layers, where they eventually join their older conspecifics. Nevertheless, they utilise different food resources, preying mainly on daphnids whereas larger whitefish select large carnivorous crustaceans, such as *Bythotrephes longimanus* and *Leptodora kindtii* in addition to daphnids (Eckmann et al. 2002). Juvenile and adult whitefish stay within or slightly below the thermocline during the growing season (Ptak and Appenzeller 1998) at temperatures below 14°C. Their growth, therefore, depends much less on temperature when compared to the very young whitefish, and the influence of food concentration, which depends on lake trophic state and competitor biomass, on their growth is more pronounced.

Including the calendar year as the third independent variable in the regression model improved the model fit, suggesting that whitefish growth rate declined with time, independent of lake trophic state and intensity of competition. The scaled estimate for the variable “calendar year” suggests that growth of two year-old fish declined by almost 0.63 cm every ten years. We consider this result to be circumstantial evidence that the highly size-selective fishery during at least four decades provoked an evolutionary response in the stock by selecting for genotypes with lower growth potential. A similar conclusion was reached by (Handford et al. 1977), who studied growth rates, condition and mean ages of a lake whitefish stock over 34 years.

The potential for an evolutionary change in the growth rate of ULC whitefish is supported by the differences in growth rates of fish from the 1991 and 1992 cohorts, which were harvested from the lake in consecutive years. The selection differential, in this case the difference in length after two growing seasons between the fish harvested at the end of their second year and the population mean, was 1.7 cm for the 1991 cohort and 1.6 cm for the 1992 cohort. Assuming a heritability of 0.2, which is typical for life history traits (Conover and Munch 2002), these data demonstrate the potential for an evolutionary response to size-selective harvest. This estimate of the selection differential is, however, conservative, because it is based upon cohorts which were fished out during 68 and 71 months, respectively. During the 1960s and early 1970s whitefish grew so fast that cohorts were fished out during 17 to 44 months. Up to 60% of these cohorts were even fished at age 1+, i.e. before the fish had reproduced, whereby the fastest growing fish were effectively excluded from contributing genes to the next generation.

We decided to compare growth between cohorts by using the length after two years of the average fast growing fish, because we have shown that whitefish are harvested in a

highly size-selective way from ULC. The definition of the point in time when 50% of a cohort was fished out was possible with high accuracy, based upon monthly catch records and on the monthly age composition of catches derived from the test fishery. As whitefish yields are not evenly distributed across months within a fishing year, this approach is more accurate compared with traditional virtual population analysis using a constant instantaneous rate of fishing mortality. In the case of natural mortality, however, we have incorporated a constant instantaneous rate of 0.2 year^{-1} . Without considering natural mortality, the biomass of those cohorts that were fished out over a longer time (in some cases more than five years) would have been systematically underestimated as compared to cohorts fished out more quickly (during less than two years).

The highly significant influence of stock biomass on whitefish growth needs to be carefully considered in the future management of the whitefish fishery in ULC and elsewhere. An earlier analysis of the factors that influence whitefish year-class strength in ULC has demonstrated that stronger year-classes are produced when lake surface temperature increases earlier in spring (Eckmann et al. 1988). This hypothesis has recently been supported by a reanalysis of an extended data set covering 52 years (Straile et al. in press). Based upon the earlier analysis, (Trippel et al. 1991) have predicted that whitefish year-class strength will likely increase as a result of global climate change. This would probably result in larger stock size, which might translate into enhanced intraspecific competition for food and ultimately into a further reduction of growth rate. Under this scenario, the present stocking practice will need reconsideration. The high standing stock biomass of whitefish in Lake Geneva for example is attributed among other factors to an intensive stocking program (Gerdeaux 2004). Even if the precise contribution of stocking to the whitefish population size in ULC were unknown so far, any reduction of stock biomass would contribute to alleviating intraspecific competition for food. This might be even more necessary in the future, as phosphorus concentrations in ULC are continuing to decrease and a further reduction of zooplankton biomass can be expected.

The present results apply not only to ULC but probably to many other coregonid lakes in Europe and elsewhere. Anthropogenic eutrophication was a worldwide problem during the second half of the 20th century, and it affected many lakes dominated by coregonids (Christie 1972, Colby et al. 1972, Grimås et al. 1972, Wells and McLain 1972). In many of these lakes, eutrophication has been successfully abated in the meantime, and the lakes have returned, or are returning, to pre-eutrophication levels (Eckmann et al. 2006). Additionally, fishing intensity has probably changed in many of these lakes in a way similar to that in ULC, as monofilament gill nets became widely used during the

1950s and early-1960s. It can therefore be speculated that stock size might have decreased in parallel to eutrophication in several other lakes as well, so that the former concepts about the sole dependence of whitefish growth on nutrient concentration deserve to be reconsidered.

2.6 Acknowledgements

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3. Reproduction vs. growth: indications for altered energy fluxes in Lake Constance whitefish through size-selective fishery

Gregor Thomas and Reiner Eckmann

3.1 Abstract

Fisheries-induced evolution (FIE) has been reported for several intensively exploited fish stocks worldwide. Most studies focused on marine populations of high commercial interest, but FIE may also occur in intensively harvested freshwater fish stocks e.g. the whitefish stock of Lake Constance. We have provided evidence for FIE in this stock through the analysis of long-term data sets, which revealed that time had an effect on growth and reproductive traits in addition to the effects of environmental factors. The final proof that the observed changes represent an evolutionary response has not been obtain so far, as laboratory experiments simulating size-selective harvest are difficult to perform with this species due to its large size and high age at maturity. We devised a different approach and tested the growth performance of whitefish larvae produced by females with a different growth history. Our experimental setup allowed rearing 24 different batches of larvae over 40 days. Growth of larvae was inversely correlated to their weight-at-hatch, and larvae with larger yolk sac volume grew more slowly. We attribute this result to the intensive size-selective harvest over several decades, because fish that allocate more energy to reproduction at the expense of growth have an advantage under the present harvest regime over fish that follow the opposite allocation strategy. Our results are in line with FIE theory and suggest a genetic component to life-history traits of Lake Constance whitefish, whereby slow growing females tend to produce larvae of a lower growth performance.

3.2 Introduction

In recent years, fisheries-induced evolution has become a topic of prime importance. Many high-rated studies reported changes of life-history traits in intensively exploited marine and freshwater fish stocks (Jørgensen et al. 2007, Kuparinen and Merila 2007, Mollet et al. 2007, Wright 2007, Hutchings and Fraser 2008). These studies indicate, that size-selective fishery may select for slow growth (Hanson and Chouinard 1992, Swain et al. 2007, Thomas and Eckmann 2007), a decrease in age and size at maturity (Law 2000, Heino et al. 2002, Reznick and Ghalambor 2005), an increase in fecundity (Rijnsdorp et al. 2005) and a decline in genetic diversity (Hauser et al. 2002). Most studies found evidence for fisheries-induced evolution by analyzing long-term data sets, which may include, in addition to the effects of fishery harvest, the effects of changing environmental conditions on fish life-history traits.

Unequivocal proof that selective harvest leads to rapid evolution uncoupled from natural selection mechanisms is difficult to obtain from field studies. Genes coding for the life-history traits in question have not been identified so far. Growth for example is a complex interplay interaction of a variety of metabolic processes, unlikely to be encoded by a few genes only. The laboratory experiment conducted by Conover and Munch (2002) with *Menidia menidia* is the only study providing strong evidence for a genetic shift in response to selective harvest. Harvesting 90 % of either the largest or the smallest individuals resulted in significantly different growth rates after only four generations. Despite the selective pressure being unrealistically strong in this experiment (Brown et al. 2008), the mechanism of selection the study population was submitted to, presumably applies to other intensively fished species as well.

In a previous study we analyzed the growth of whitefish (*Coregonus lavaretus*) in Lake Constance over a period of 43 years from 1954-97 (Thomas and Eckmann 2007). This time period was characterized by profound changes in the lake's environmental conditions. Anthropogenic eutrophication which reached its culmination in 1979, and reoligotrophication in the following years, have had far reaching consequences on the entire ecosystem (Bäuerle and Gaedke 1998). During the study period, whitefish growth was strongly influenced by whitefish standing stock biomass, whereas the trophic state of the lake ranked second. Further analysis revealed that a third factor was significantly correlated to whitefish growth, time. We attributed this effect, which amounts to a growth depletion of 6 mm per ten years during the second year of life, to decades of an intensive size-selective gill net fishery. The exploitation rate of Lake Constance whitefish is likely to

exceed that of heavily exploited marine fish stocks, since Lake Constance is an enclosed system of manageable size. Apart from the fishery, management and stocking policies are potential drivers of rapid evolution of life-history traits. Although the evidence for an evolutionary change in the growth performance in the lake's whitefish stock is rather convincing, we cannot exclude that the observed findings result in part, or entirely from phenotypic plasticity.

Conover and Munch (2002) chose *Menidia menidia* as a model species because of its small size and short generation time. A similar laboratory experiment with whitefish is difficult to perform because of the fish's size and higher age at maturity. For this reason we selected whitefish whose growth history differed from each other and conducted growth experiments with their offspring. We focused primarily on maternal effects and chose female fish which, despite their differences in age, had a similar size. On the other hand, we intended to use males of similar size and age, i.e. having experienced a similar growth history. We wanted to explore whether growth rate of whitefish is partially hereditary, and whether the results of this experiment support the fisheries-induced evolution scenario for Lake Constance whitefish. We hypothesized that slow growing females produced slow growing offspring.

3.3 Materials & Methods

Fertilization & egg incubation

Ready to spawn whitefish were caught overnight in the central part of Upper Lake Constance in early December 2007 with monofilament nylon gill nets of 40 and 44 mm mesh size (knot-to-knot). Since only nine "running" females were caught during the first night, the nets were set again the following night. A total of 75 fish of similar length (around 35 cm total length) were selected for further processing. All fish were measured (standard and total length to 0.5 cm) and weighed (to 1 g), and scales for age determination were taken from the ventral side caudal to the base of the pectoral fins. Age was determined on site and re-checked by 3 independent readers at the laboratory several days later after the scales had dried.

The fish were preserved on crushed ice until the on-site age determination was had been completed. Our final sample contained 24 females of different age classes and 11 males, which were classified as age-3 (cf. Tab. 3.1). The eggs of each female were stripped into a separate dry plastic bowl. All males were stripped into a single dry cup, and the milt was carefully stirred. With a pipette, the milt was equally distributed among the bowls containing eggs. Milt and eggs were mixed and water added. As the females were obtained

on two different days, we had two groups of fathers. Fertilized eggs were transported to the laboratory on ice and incubated in a facility consisting of 24 mini Zug jars. The incubation system of approx. 300 L volume was run as a recirculation system. Tap water was cooled to 4-5 °C in a reservoir and fed into the jars from below, which evoked a continuous gentle circulation of the eggs. Every three to four days approx. 10-20% of the water was exchanged. Each Zug jar was housed in a small aquarium, separated from the others by 500 µm gauze. Dead eggs were regularly sorted out. A subsample of eggs was taken from each egg batch after water hardening to measure egg diameter and dry weight.

Tab 3.1: Age of parental fish used in the experiment according to the age validation in the laboratory. All fish were about the same length (~35 cm).

Age class	♀	♂
2	1	1
3	14	9
4	8	1
5	1	0

Rearing of larvae

Hatched larvae were regularly removed from the Zug jars and the surrounding aquaria where larvae were trapped after being washed out of the jars. The number of larvae hatched within 24 hours was documented at 4:00 p.m. each day. Since only a small amount of larvae from each batch (on average 3 350 eggs per batch) was needed for the rearing experiment, larvae were transferred to the aquaria when the hatch rate exceeded 170 larvae (i.e. about 5%) per day. In order to check for possible differences in length at hatching during the course of the hatching process, the newly hatched larvae from one batch were measured regularly every second day. The length of the hatching process varied over several days for each batch.

The rearing aquaria of 13 L volume were continuously supplied with tap water at the temperature of 11.5°C and aerated. The artificial light climate was adjusted to the natural light regime in March, i.e. light from 6:30 a.m. to 6:30 p.m., with dusk and dawn lasting for 30 minutes each.

Feeding of larvae started 4 days post hatch (dph). Each day, the larvae were fed with *Artemia* nauplii beginning at 8:30 a.m. As the age and size of larvae differed between aquaria, the daily food demand of each batch was different. Therefore, aquaria were checked regularly between 8:30 a.m. 4:30 p.m., and nauplii were added when their concentration was low. In this way we provided an ad libitum food supply for a minimum of 8.5 hours per day. Each morning prior to feeding, the aquaria were cleaned.

When larvae had to be sampled, they were removed prior to the first feeding to keep stomachs empty for dry weight measurement. Sampled larvae were killed with an overdose of TCMP (1.1.1-Trichlor-2-methyl-2-propanol-Hemihydrate) immediately before measuring. Standard length was measured under a dissection microscope linked to a computer with image analysis software. Additionally, yolk sac size was measured and yolk sac volume calculated according to (Blaxter and Hempel 1963). All sampled larvae from one batch were pooled and dried at 60 °C for 24 hours (larvae 0, 10 and 20 days old) or for 48 hours (larvae 30 and 40 days old) and weighed.

The mother's growth was determined by back-calculation of their length at the end of each growing season from scales (cf. Thomas & Eckmann 2007).

Statistical analysis

Mean dry weight per larva was calculated for each batch on each of the five sampling dates (0, 10, 20, 30 and 40 dph). An exponential regression $y = a * e^{b * x}$ (with y =dry weight; x =time in dph; a , b =constants) was fitted to the five values of each batch. With r^2 -values ranging from 0.987 to 0.995, the regression coefficient b of the exponential growth curve was chosen as a measure of larval growth. The values of b were tested by multivariate statistics against several factors characterizing the different batches (egg size, egg dry weight, dry weight of larvae at hatching, length of newly hatched larvae, yolk sac volume, growth rate and age of mothers).

3.4 Results

Larvae started hatching February 12th and ended March 27th. The mean time of reaching the point at which 50% of larvae per batch had hatched was 86 days post fertilization (minimum 75, maximum 94 days). The average duration from the point at which hatching started until 90% of larvae per batch had hatched was 17.8 days (minimum 10, maximum 30 days).

Larvae grew from a mean length-at-hatching of 10.8 mm to a mean length of 27.5 mm in 40 days (mean values: 10d = 13.4 mm; 20d = 18.3 mm and 30d = 22.4 mm)

(Fig 3.1). Differences in dry weight between batches became apparent after 30 and 40 dph (Fig. 3.2). Final dry weight ranged between 29.2 and 43.5 mg between batches. Growth in terms of weight was well described by an exponential model, whereas growth in terms of length was almost linear during the 40 days experiment,

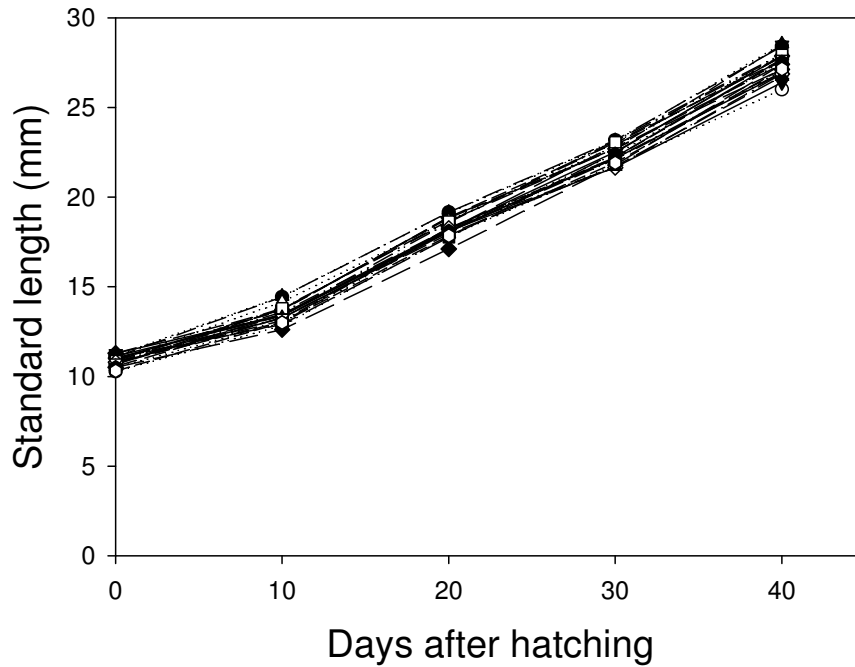


Fig. 3.1: Standard-length of larvae from all 24 batches measured in 10-day time intervals.

Early hatched larvae were around 10% smaller than late hatched larvae from the same batch of eggs (Fig. 3.3), suggesting that larvae continue to grow until hatching. For this reason it was of particular importance to control in which phase of the hatching process larvae were taken for stocking into the aquaria. We determined the point in time at which 50 % of larvae per batch had hatched and plotted these data against the date when larvae were stocked into the aquaria (Fig. 3.4). The length in time between the date of 50% hatch and the stocking of larvae into the aquaria was similar for all batches. The multivariate analysis identified a strong inverse correlation between the larvae's weight-at-hatch and their growth in terms of weight (Fig. 3.5). Larvae of higher weight-at-hatch grew slower than larvae of lower weight-at-hatch ($r^2 = 0.43$; $p = 0.0003$). There were also inverse

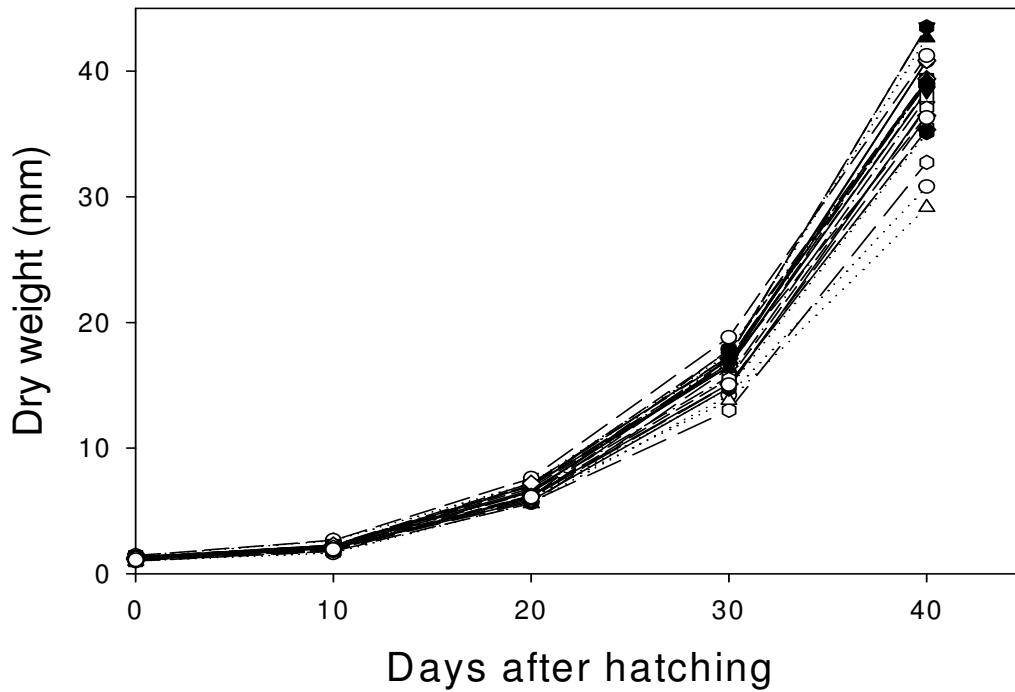


Fig. 3.2: Dry weight of larvae from all 24 batches measured in 10-day time intervals.

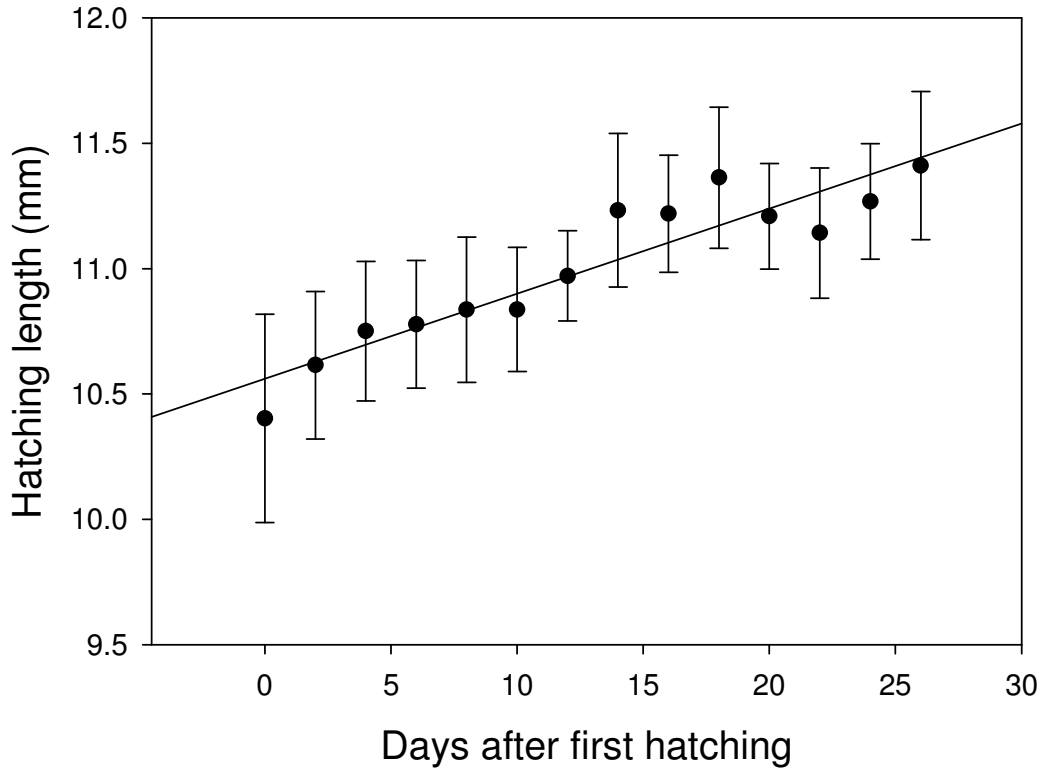


Fig. 3.3: Hatching length of larvae originating from the same batch. Larvae continued growing inside the eggs and successively hatched at larger size.

correlations between growth in terms of weight and yolk sac volume ($r^2 = 0.40$; $p = 0.0006$), egg dry weight ($r^2 = 0.36$; $p = 0.0012$) and egg diameter ($r^2 = 0.14$; $p = 0.038$), whereas the time of hatching was not related to egg dry weight ($r^2 = 0.05$; $p = 0.14$). The negative correlation between growth and larval weight-at-hatch can be attributed mainly to differences in yolk sac volume between larvae from different batches, since weight-at-hatch and yolk sac volume were strongly correlated ($r^2 = 0.63$; $p < 0.0001$). Furthermore, growth of larvae was positively correlated with the time between fertilization and the mid-point of hatching, i.e. larvae from batches that hatched later grew better ($r^2 = 0.30$; $p = 0.0032$). Yolk sac volume declined with increasing time from fertilization to hatching ($r^2 = 0.50$, $p < 0.0001$).

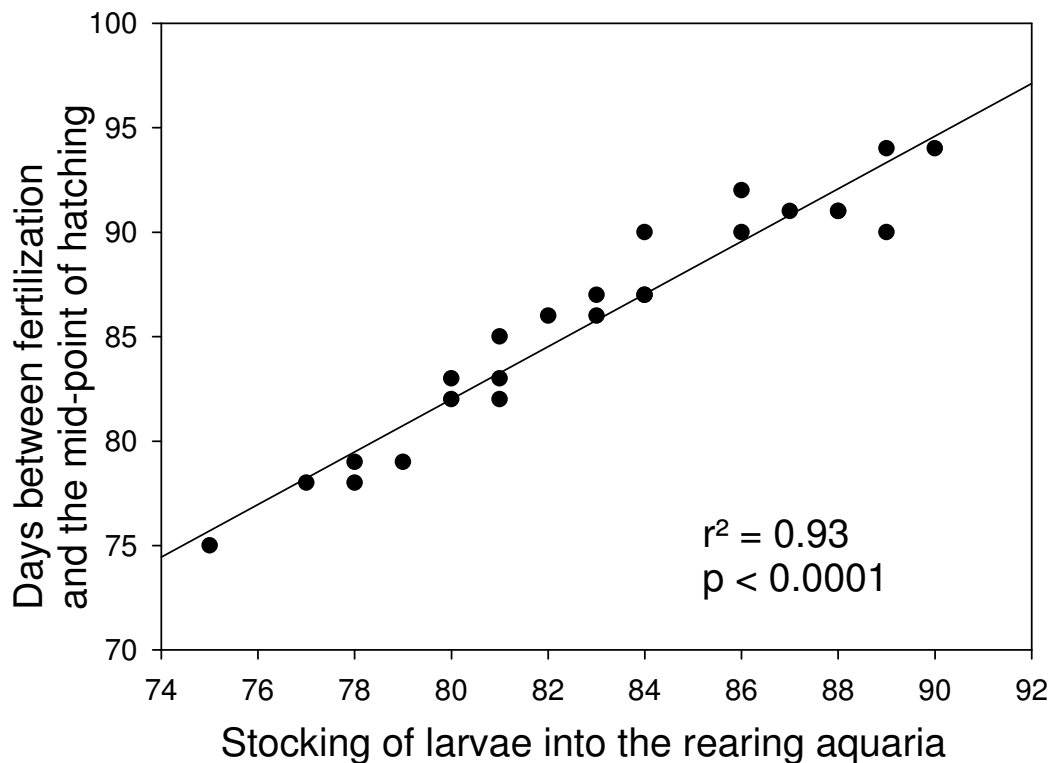


Fig. 3.4: Days until the mid-point of hatching (50% of larvae hatched) versus the time from fertilization until larvae were stocked into the rearing aquaria.

Combining both results, the variability in larval growth can be attributed to 56 % to egg dry weight ($F = 12.6$; $p = 0.0019$) and to the number of days between fertilization and the mid-point of hatching, i.e. when larvae were stocked into the rearing aquaria ($F = 11.1$; $p = 0.0032$). We chose egg dry weight as a measure for larval quality in this final analysis, since yolk sac volume decreases as larvae continue to grow until hatching. This is justified

as yolk sac volume is strongly correlated ($R^2=0.77$) with egg dry weight ($F = 32.2$; $p < 0.0001$) and with the number of days between fertilization and stocking ($F = 27.0$; $p < 0.0001$). Larvae hatching from heavier eggs grew slower, whereas larvae from batches with longer embryonic development had smaller yolk sacs at hatching but grew better. Furthermore, growth rate of females was inversely related to weight-at-hatching of their progeny ($r^2=0.19$, $p=0.035$) i.e. slow growing females produced slow growing larvae.

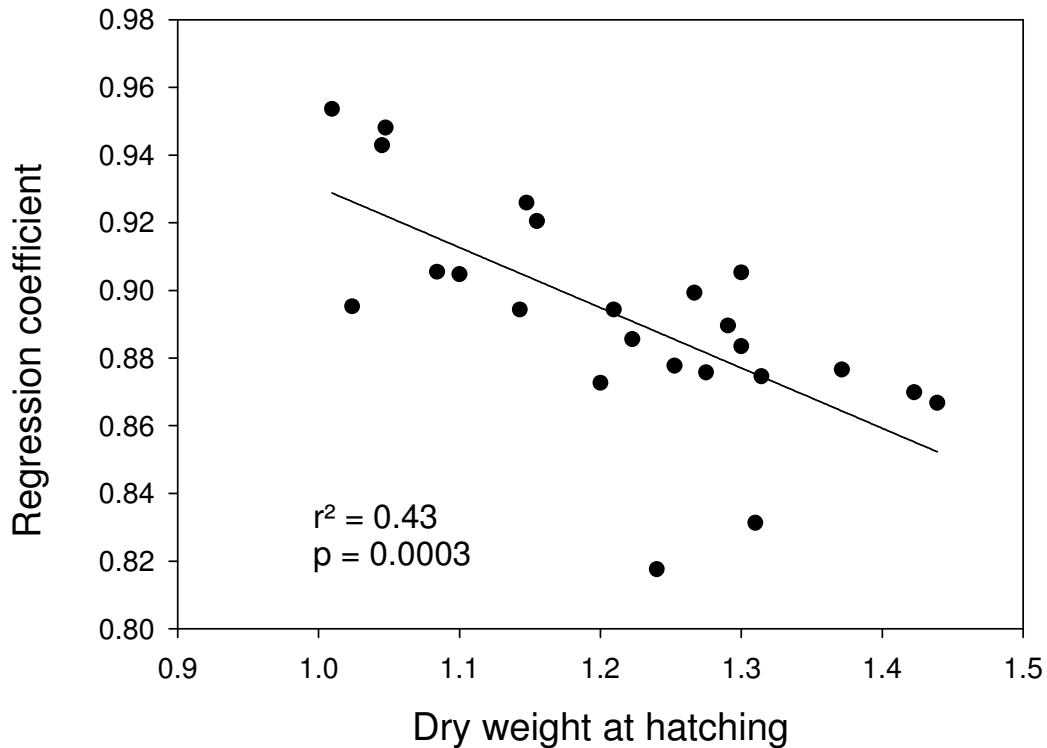


Fig. 3.5: Regression coefficients of the exponential growth curves for all 24 batches of larvae versus dry weight of larvae at hatching.

3.5 Discussion

Our analysis showed that larvae with lower weight-at-hatching showed better growth performance compared to larvae with higher weight-at-hatching, while length-at-hatching was not correlated with growth. Since weight-at-hatching and yolk sac volume are strongly related we conclude that larvae equipped more energy reserves have lower growth rate.

On first glance, this result is rather surprising, as it is commonly accepted that larvae with larger energy stores have better starting conditions and grow faster. Older females of *Sebastes melanops* produce eggs with higher lipid content, and larvae originating from these eggs grow up to 3 times faster than offspring from younger females (Berkeley et al. 2004). (Rana 1985) showed that larvae hatching from larger eggs have

higher starvation resistance. For North Sea plaice (Heath et al. 1999, Kennedy et al. 2007) found higher growth rates of larvae with larger yolk sacs but smaller size-at-hatching.

For populations evolving in the absence of or under low fishing pressure, the positive correlation between energy reserves and growth of larvae is easily understood, but in populations facing intense, size-selective exploitation, this trend can be reversed. This seems to be the case with Lake Constance whitefish, and we will discuss our results in the light of FIE theory. Fish have to change their energy allocation continuously in order to adapt to changing environmental conditions. Basically, surplus energy can be invested either into reproduction or into somatic growth (Schultz and Warner 1991, Jennings and Philipp 1992). Thus, we can distinguish between a “growth” and a “reproductive” strategy of energy allocation, which is probably genetically determined, at least in part. The “growth” life history strategy implies that fish invest a larger proportion of surplus energy into somatic growth. They benefit from growing fast by escaping early in life from gape-limited predators. They can use a wider prey spectrum due to their larger gape (Timmerman et al. 2000), and swimming speed and performance improves with increasing body size (Leis et al. 2007).

In contrast, the “reproductive” strategy favors energy allocation to reproductive traits at the expense of somatic growth. The impacts this strategy has on the fish's reproductive traits include younger age at maturity, higher fecundity, as well as better egg and larval quality. The advantage of this strategy is that more larvae with higher energy content are produced. In an environment with a distinctly higher mortality risk above a critical size, the “reproductive” strategy is likely to be more successful in the long run, because fish produce more offspring before their mortality risk increases. (Rijnsdorp et al. 2005) pointed out that the fishery can affect these general allocation strategies significantly in terms of evolution.

For many fish species, fishery became the dominant cause of mortality, whereas natural mortality became less relevant. In this situation, a shift towards the “reproductive” strategy will occur. Besides environmental factors, however, the genetic background influences the development of reproductive traits as well as early larval performance (Heath et al. 1999, Perry et al. 2004). Size-selective fishery may modify reproductive traits, such as a shift towards younger age and smaller size at maturity (Law 2000, Heino et al. 2002), and towards higher fecundity (Rijnsdorp et al. 2005). Along with an increase in reproductive effort, growth rate will decline. Under strong fishing pressure, growing slow

confers an advantage considering that growing fast means dying early. Hence, a size-selective fishery of high intensity will favor the “reproductive” strategy.

The results of our experiment are in line with this concept. Slow growing females have a higher reproductive investment. This is reflected in the production of large and energy rich eggs. Larvae hatching from larger eggs are heavier because they have larger yolk sacs.

As paternal effects on the performance of early larval stages are considered to be insignificant (Heath et al. 1999), we assume that the growth rate of larvae in our experiment is mainly due to maternal effects. The offspring of slow-growing mothers grew slow as well, suggesting a genetic component to growth performance in Lake Constance whitefish. Slow growth may carry a great deal of disadvantages, but these can be compensated by higher starvation resistance (Rana 1985, Heath et al. 1999), a hypothesis which was not tested in the present experiment.

The correlation between maternal growth and the performance of their offspring in our experiment was not very strong ($r^2=0.19$), albeit significant. The factors controlling the growth rate of female whitefish, however, are manifold and cannot be confined to a genetic component alone. Hence, the main uncertainty in this analysis is that we do not know to which degree the growth of female whitefish is controlled genetically and to which degree environmentally. As each fish has its own individual growth history, experiencing slightly different environmental conditions during its ontogeny, genetic effects on growth rate can become blurred.

The second observed effect, that later hatched larvae grew faster, might be adaptive via a different mechanism. Since the duration of embryogenesis until hatching was unrelated to egg dry weight and to size-at-hatching, the hypothesis that larger larvae need more time until hatching can be discarded. Larvae hatching later in spring may be at a disadvantage as compared to earlier larvae. The former appear in the epilimnion at a time when the latter have already started to improve their prey capture success (Braum 1964) and to exploit the limited zooplankton resources. Late larvae can only compete successfully with their counterparts when they are able to utilize the available resources more efficiently, thereby compensating their initial disadvantages. In summary, hatching late and growing fast are life-history traits that seem to be linked to each other, and this combination of traits is more likely to be expressed in larvae originating from fast growing mothers.

The conclusions drawn from the present results, however, should be treated with caution considering the small number of egg batches (24) studied in this experiment. The

observed findings, however, are in line with FIE theory and support the formerly developed FIE scenario for Lake Constance whitefish.

3.6 Acknowledgements

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

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4.1 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 trophicity and of an intensive size-selective harvest over several decades, on reproductive traits of common whitefish in Lake Constance between 1963 and 1999.

Fecundity was strongly linked to lake trophicity 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.

4.2 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 and Merila 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 and Chouinard 1992, Conover and 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 and Wright 2004, Rijnsdorp et al. 2005, Wright 2005). To our knowledge only one study thus far has 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 and de Jonge 2004). Changes in trophic conditions may affect 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 an intensive fishery on life-history traits of the common whitefish, *Coregonus lavaretus*. The lake was subject to

anthropogenic eutrophication followed by reoligotrophication during the second half of the last century, and the whitefish stock has been intensively fished in a strictly size-selective way throughout 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 and Eckmann 2007) and showing that growth during the second year of life was significantly correlated with lake trophy, standing stock biomass, and calendar year ($R^2 = 0.84$). 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 reproductive traits of common whitefish, we analyzed 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.

4.3 Methods

Lake Constance whitefish

Lake Constance is a large, warm-monomictic prealpine 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 70s (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 reoligotrophication 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, 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 (100x7 m each, of 44

mm bar mesh size), four days per week. This corresponds to a fishing effort of only 17% as compared to the beginning of the study period (R.Rösch, Fisheries Research Station Langenargen, pers. comm.). The legal mesh size, however, remained unchanged during the entire study period, except for the initial two 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 1 500 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 reanalyzed the data of Hartmann and Quoß (1993) pertaining to the fecundity of pelagic spawning whitefish for the years 1963-91, along with data from eight additional years (1992-99). 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 1963-65 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 Blaufelchen 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 1/8th 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 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 ($R^2_{\text{adj}} = 0.42$) 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. Tab. 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 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 and Eckmann (2007). Factors which were not significant were omitted in the final analysis. The data on whitefish fecundity are temporally autocorrelated with a time lag of one year (other time lags are not significant).

By including fecundity (lagged by one 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 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.

4.4 Results

Fresh egg weight was 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. 4.1 a & b). Other factors, such as standing stock biomass or calendar year had no significant effect on egg weight..

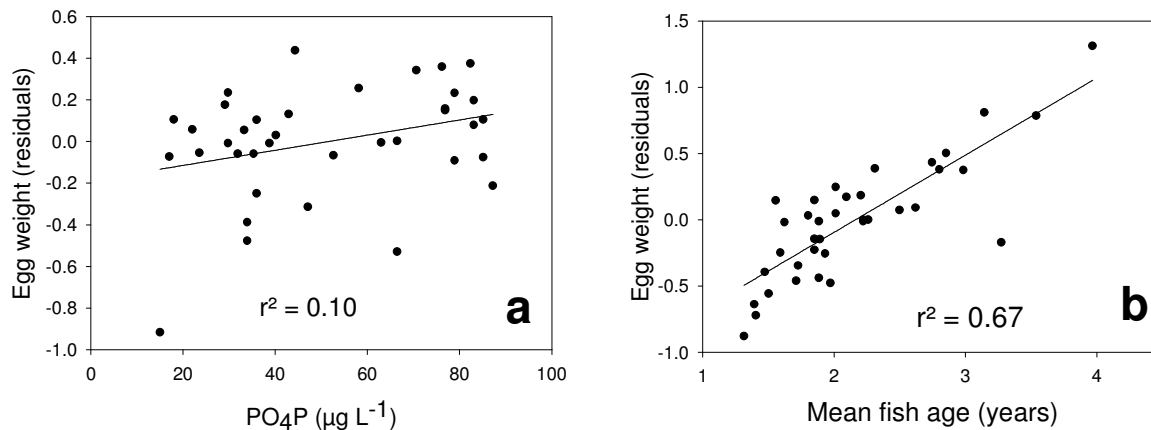


Fig. 4.1: Residuals of the linear regression between egg weight and the number of days between sampling the fish and mass spawning (DSS) versus phosphorus concentration (a) and mean age (b) of pelagic spawning whitefish for the years 1963 to 1999.

Fecundity ranged between 4 796 (1965) and 7 172 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 dataset. 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 phosphorous

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 4.2 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 figure 4.3, demonstrating the strong influence of these two variables on fecundity. To assess the relative importance of both variables, scaled estimates centered 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 5 414 eggs per 100g fish in 1963 up to 6 426 eggs in 1999, an increase of 18.7 %. For the variable phosphorus concentration, scaled estimates demonstrated that fecundity varied between 6 672 eggs per 100 g at $87 \mu\text{g PO}_4\text{-P}\cdot\text{L}^{-1}$ in 1979 and 5 149 at $15 \mu\text{g PO}_4\text{-P}\cdot\text{L}^{-1}$ in 1999, which corresponds to a decrease of 22.8 %.

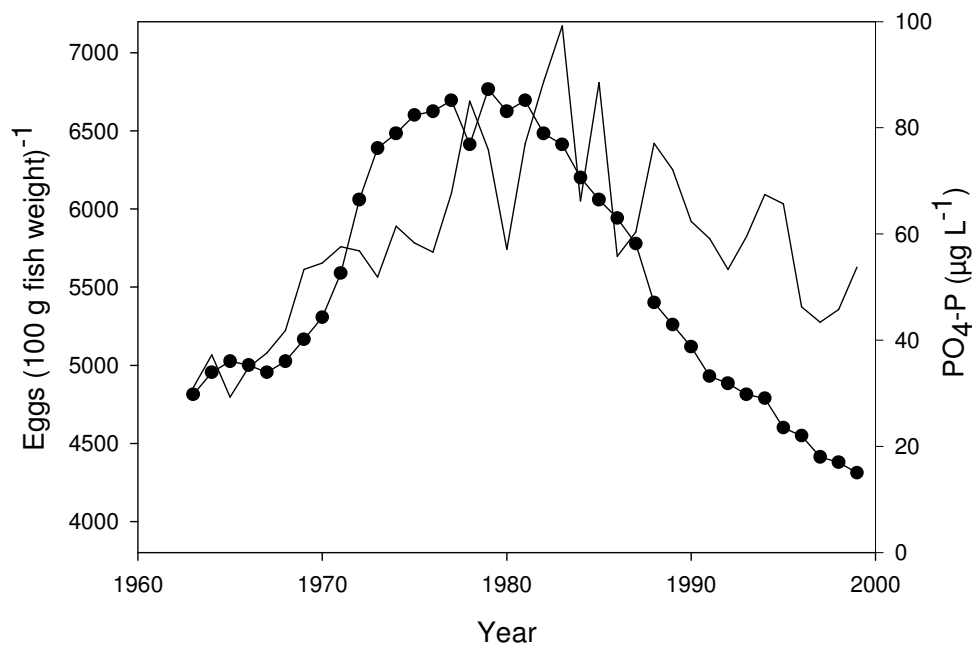


Fig. 4.2: Relative fecundity of pelagic spawning whitefish (solid line) and phosphorus concentration during spring holomixis in Upper Lake Constance (black dots) from 1963 to 1999.

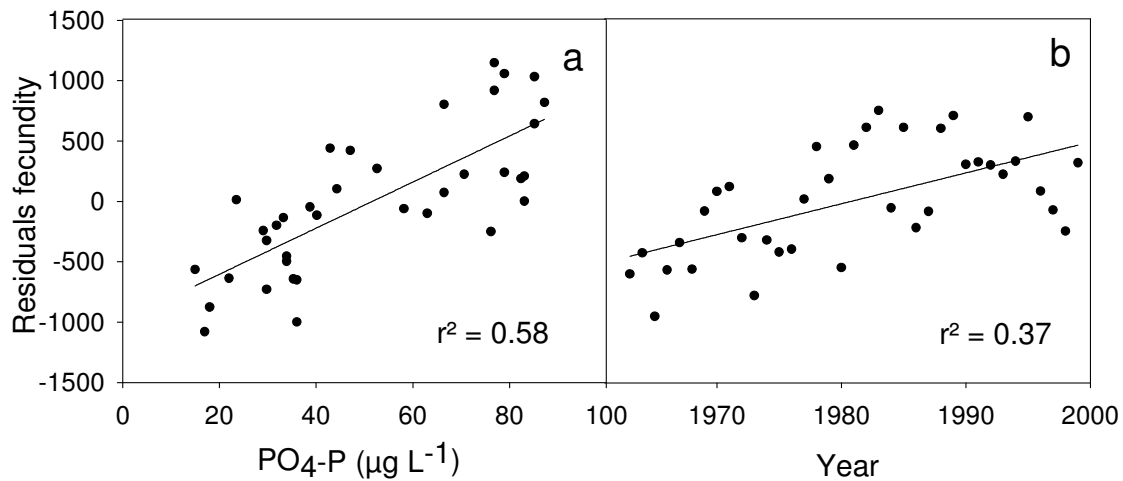


Fig. 4.3: Residuals of the model testing effects on fecundity: a) showing residuals with factor “year” as single independent variable and b) showing residuals with factor “phosphorus concentration” as single independent variable.

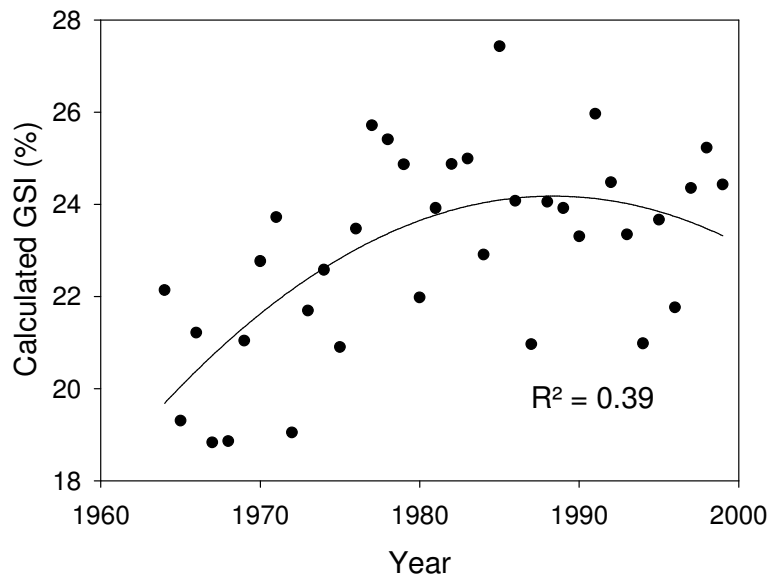


Fig. 4.4: Calculated gonadosomatic index (GSI) of female common whitefish from Upper Lake Constance for the years 1963 to 1999. Egg weight of each female was corrected for the time interval between sampling the fish and mass spawning, and multiplied by egg number to estimate the GSI that would have been attained prior to spawning (cf. Material and methods). The line is a second degree polynomial fit to the data.

The (calculated) gonadosomatic index increased from the early 1960s until the early 1980s, showing a slightly decreasing trend thereafter (Fig. 4.4). Measured GSI values, which were determined at different time intervals before peak spawning in different years, corresponded closely ($R^2 = 0.94$) with fecundity and with 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 ($F_{1,34} = 86.5$; $P < 0.0001$).

4.5 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 (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 time scales were unfortunately not available, so that 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 and 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 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 and 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 and Bromage 1985, Elpers 1988). Large size and rapid growth during larval life confer a variety of advantages that enhance the probability of survival (Hare and 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 and 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) was 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 since 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 and 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, while 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 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 high egg weight in the long run, if global climate change leads to an earlier onset of spring, and if the intensive stocking program is continued.

Fecundity

The result of our extended analysis of whitefish fecundity supports the earlier conclusions of Hartmann & Quöß (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 and 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 and 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 through 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 likely 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 intensity.

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 6th year of life (Thomas and 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 $400 \cdot 10^6$ individuals per annum (Straile et al. 2007) (Fig.4.5). 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 optimized conditions. Pre-hatching 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 number of spawners which reproduce naturally and numbers of spawners caught in the spawning fishery ranged from 1:0.85 (1996) to 1:23.5 (1967) during the investigation period (Fig. 4.5). 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.

In a previous study on whitefish growth over the last five decades (Thomas and 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 and 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. Since 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.

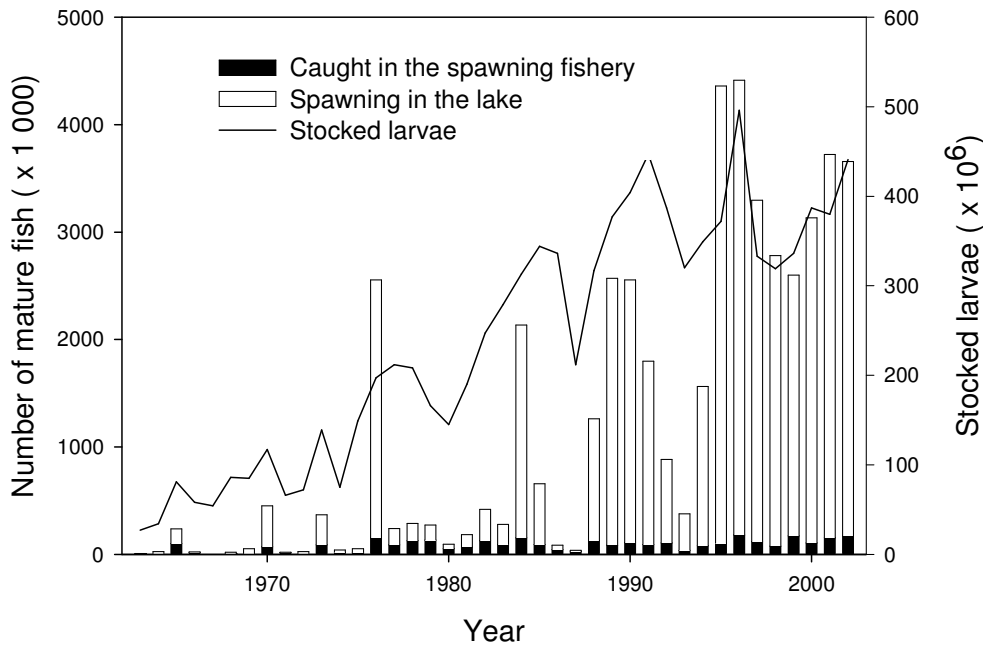


Fig. 4.5: The reproductive stock (aged 2+ and older) of pelagic spawning whitefish in Upper Lake Constance, separated into two groups: Group 1 (black bars), mature fish which were caught in the spawning fishery and whose offspring were incubated in hatcheries. Group 2 (white bars), mature fish, which remained in the lake and reproduced naturally. The solid line indicates the amount of larvae stocked into the lake from hatcheries. Stocking policy could be a powerful mechanism for a sustained genetic selection towards high fecundity, achieved at the cost of somatic 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 analyzed 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 one 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. 4.4). 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 reoligotrophication and stronger intraspecific competition for food due to higher standing stock biomass (Thomas and Eckmann 2007), so that age of recruitment into the fishery gradually increased. Since 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 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.

4.6 Acknowledgements

We are grateful to Dr. Herbert Löffler and Brigitte Engesser (Institute for Lake Research, Langenargen) who relinquished the dataset to us. We thank Amy-Jane Beer for helpful comments and language proof of this manuscript. Sampling and processing of material for this analysis comply with the current law in the EU. The project was supported by the German Research Foundation (DFD) within the priority programme AQUASHIFT (AZ EC 146/3-1.2).

5. Seasonal and long-term changes in fishing depth of Lake Constance whitefish

Gregor Thomas, Roland Rösch and Reiner Eckmann

5.1 Abstract

The pelagic zone of lakes is structured by abiotic and biotic gradients, and these gradients are generally more pronounced in the vertical plane than in the horizontal. Changes in the vertical distribution of pelagic fish, both over seasons and between years, may therefore be caused by changes in environmental conditions. The ecosystem of Lake Constance in central Europe has undergone profound modifications during the last decades due to anthropogenic eutrophication and subsequent reoligotrophication. In this study we focussed on seasonal and interannual changes in the vertical distribution patterns of whitefish and related these to changes in biotic and abiotic gradients. Information on fish vertical distribution, i.e. depths of the float line of gill nets used by professional fishermen, were obtained from the monthly reports of fishery wardens. In late spring/early summer, whitefish congregate close to the surface in all years, but in late summer and fall fishing depth varied significantly as the season progressed and between the five decades from 1958-2007. Multiple linear regression analysis revealed that the average fishing depth in late summer and fall was significantly related to two factors influencing per-capita food supply: lake trophy and whitefish standing stock biomass. In years with low per-capita food supply, whitefish were harvested from greater depths, where temperatures were up to 4°C lower. This may represent a bioenergetic optimization behaviour whereby fish reduce metabolic losses at lower temperatures, or it may result from a reassessment of habitat preference under conditions of limited food supply, according to the ideal free distribution theory. As whitefish are cold-adapted species, their upper distribution limit is set by the temperature vertical gradient, so that enhanced intraspecific competition can only lead to a dispersion to greater depths.

5.2 Introduction

The horizontal and vertical distribution patterns of pelagic fish are shaped by abiotic and biotic environmental gradients. In small- and medium-sized lakes (unlike large lakes and marine systems), these gradients tend to be more pronounced in the vertical plane than in the horizontal. Abiotic factors influencing the vertical distribution of fish include temperature, oxygen concentration and light (Rudstam and Magnuson 1985, Fernöa et al. 1995, Aksnes et al. 2004), while the main biotic factors are the distributions of predators and prey organisms (Mittelbach 1981, Werner et al. 1983, Werner and Hall 1988). The ideal free distribution theory (Fretwell 1972) predicts that individuals of an animal population should distribute along a resource gradient in proportion to availability of the resource. If the animals' distribution is indeed free, then the other factors such as predation risk can be expected to vary predictably with changes in the spatio-temporal patterns of resource availability.

By comparing repeated changes and/or long-term trends in the distribution of an animal population with variations in resource availability, it is possible to analyse the relative importance of individual environmental factors influencing the distribution and migration patterns of a population. The present study used this approach to examine the influence of abiotic and biotic factors on the vertical distribution of pelagic coregonids in Lake Constance over a 50 year period.

The past 50 years have seen considerable changes in environmental conditions in Lake Constance (Bäuerle and Gaedke 1998). Anthropogenic eutrophication began in the 1950s and had profound effects on both abiotic and biotic aspects of the lake's ecology. Increased nutrient input promoted algal growth, which in turn influenced other characteristics, including the subsurface light climate and the structure and function of the lake food webs. These changes, and the subsequent period of re-oligotrophication make the last few decades particularly suitable for studying the influence of resource availability on the vertical distribution of fish.

Excluding water birds, which may link aquatic and terrestrial trophic systems, fish are the top consumers in lake pelagic food webs. Variations in fish community composition, or in the abundance, growth, or distribution patterns of particular species seldom pass unnoticed, particularly in lakes where professional fisheries and angling play an important role, as is the case in Lake Constance.

The ecological knowledge of fishermen has thus far been a largely neglected resource, whose potential usefulness to scientific research has only recently received formal recognition (Haggan et al. 2007). Mackinson (2001) highlighted the advantages of

combining such local information with scientific data. Firstly, in contrast to research surveys, the efforts of fishermen are continuous and long-term. Secondly there are more fishermen than scientists in the field, and data quality increases with the number of informants. Thus the experience of fishermen is a valuable source of information for scientists. Falling back on fishers' knowledge is often the only way of gaining information from the past. Inevitably the reliability and accuracy with which such information is documented varies, and may limit its usefulness. At Lake Constance however, data regarding the practices of the professional fishermen are summarized in monthly reports produced by fishery wardens. These reports are an invaluable resource extending back over several decades, and complementing long-term fisheries statistics and monitoring data.

The present study focuses on observed seasonal and long-term changes of the vertical distribution of whitefish (*Coregonus lavaretus*) in Lake Constance. Information documented by fishery wardens regarding the pelagic gill net fishing depth can be taken as a measure of fish vertical distribution (Horak and Tanner 1964), and shows that fishing depth in summer and fall increased year on year between 1990 and 2003 (Rösch 2003). We have taken the opportunity to expand this study to incorporate the years 1958 to 2007, and to analyse the relationship between changing in fishing depth and various environmental factors both within and between years.

5.3 Material & methods

Lake Constance

Lake Constance is a large prealpine lake in Europe, second in area only to Lake Geneva. Lake Constance is situated at the southern boarder of Germany and is a condominium of Germany, Switzerland and Austria. The lake was formed naturally during the last ice age. The river "Rhine" runs through Lake Constance. The lake comprises two basins with differing morphology. Lower Lake Constance has a surface area of 63 km² and a mean depth of 13 m, while Upper Lake Constance (ULC) has a surface area of 473 km² and a maximum depth of 254 m. ULC is managed jointly by Austria, Germany and Switzerland (Internationale Gewässerschutzkommission für den Bodensee (IGKB) 2004).

Fishery practice

About 150 professional fishermen operate the commercial gill net fishery in ULC. In recent years, whitefish have contributed up to 80% of total fish harvest and are therefore of surpassing economic interest. Perch (*Perca fluviatilis*) ranks second in the commercial fishery, representing 14.5 % of the total harvest in 2003. The whitefish fishery has always

played an important role at ULC. From 1954, drifting nylon gill nets began to replace all previous gear used for catching whitefish in the pelagic zone and by the end of the 1950s became the sole means of harvesting this species. The efficiency of nylon gill nets led to an intensification of the fishing effort, and soon it became apparent that whitefish stocks were being overharvested (Nümann 1964). Consequently, in 1963, the minimum mesh-size was raised from 38/40 to 44 mm. In addition to fixed mesh-size, strict fishing regulations (number of nets per licence and of fishing days per week, overall size of gill nets, closed season) now provide the basis for a sustainable fishery. Compliance with these regulations has been enforced by fishery wardens since the 1950s. Among the six wardens working at ULC, two are employed by the federal state of Baden-Württemberg, one for the eastern and one for the western part of the lake. Both wardens compile monthly reports on fishery-relevant data, such as the location of the core fishing area, average monthly harvests, average fishing depth, as well as additional information on special circumstances, e.g. meteorological events. Fishing depth is recorded as the length of the droplines by which the float lines of pelagic gill nets are attached to surface floats. As gill nets are seven meters high, fishing depth indicates the upper limit of the 7 m deep zone in which fish will be caught.

Data collection

Reports for the western part of ULC date back to 1975, and for the eastern part back to 1956. The possibility that seasonal variations in zooplankton abundance or temperature may differ between the two parts of the lake cannot be excluded. This likelihood is supported by the fact that the fishery is not spread evenly across the lake during the year. For this reason data from just one area, the eastern part of ULC, was used to analyze changes in fishing depth over time. Given the 50 year timescale of the study, responsibility for control of the fishery, and thus for documenting the associated data, has passed from person to person, and there is variation in the quality of data over time. Data pertaining to parameters such as location of the core fishing zone, net depth and average yield per fisherman were recorded regularly but not necessarily documented for every month of every year. Data for the 1950s is often lacking, while in subsequent decades information on fishing depth is rather well documented although the nature of the records varies. Sometimes net depth was given in metres, sometimes in “Klafter”, an approximate local unit of measurement equivalent to the distance between both hands with outstretched arms. For our analysis one “Klafter” was converted to 1.7 metric meters. Not all fishermen fish with the same dropline length on the same day. The way in which this variability is

documented differs between reports. In some reports both minimum and maximum fishing depths are given, while in others the mean depth is reported without any information regarding spread. Whenever fishing depths reported for a particular month varied, a mean depth was calculated for the purpose of the current analyses.

Raw data were extracted from the wardens' reports. As fishing depth can change considerably within a month, average values were calculated for the first and second half of each month. When only one depth was reported for the entire month, this value was used for both data points. The resulting data set covered the years 1958-2007.

Surface temperature data for the years 1961-2006 and Secchi depth data from 1974 to 2005 for the central part of ULC were obtained from the Institute for Lake Research and assigned to the same time grid as the fishing depth data. Volume-weighted averages for phosphorous concentration during spring turnover were obtained from the IGKB report 2004 and supplemented by unpublished data for the most recent years. Values for average annual standing stock biomass of whitefish were taken from (Thomas and Eckmann 2007).

To study the influence of temperature on the vertical distribution of lake whitefish, September fishing depths and vertical temperature profiles were plotted for the years 1961-2006. Since only one temperature profile and two data points for fishing depth were available per month, months in which temperature gradients change continuously are not suitable for this kind of analysis. The month of September was chosen because it represents a relatively stable period for both fish and temperature profiles.

Statistical analysis

For the analysis of long-term trends in fishing depth, data were merged into five decades. Each decade comprised 18 data points, two data points for each month of the fishing season (from the 2nd half of January until the 1st half of October). Because the fishery is constrained during April and May by the minimum allowable fishing depth of two metres, only data from the 1st of June onwards was used in this analysis. Fishing depth was correlated with the factors "decade" and "seasonal course" using a general linear model. In a second step, differences in fishing depth between decades were tested with a post-hoc Student's t-test. The influence of environmental factors on fishing depth was analyzed using multiple linear regression models. For each of the 18 time bins, data for the study period (1958-2000) were used, since independent variables were limited to this time interval. Fishing depth was regressed against phosphorus concentration during spring turnover, the natural logarithm of whitefish standing stock biomass and Secchi depth. The

additional variable “year” was included to account for possible trends in fishing depth across time not accounted for by the aforementioned variables.

5.4 Results

Fishing depth shows a consistent pattern across all years of the study period (Fig. 5.1). From the beginning of the year until the end of February, whitefish are fished from depths of 20 to 35 metres. During the course of March, whitefish ascend to the surface, and by early April fish are caught close to the surface. The most effective fishing depth would immediately below the surface, but because of ship traffic, a minimum net depth of two metres is imposed. Gill nets are set close to this upper limit during April and up until the end of May, when the whitefish begin to descend once again to greater depths. The downward shift is normally completed by the beginning of September when dropline length varies between 9 and 17 meters. Allowing for 7 m net height, this indicates the densest aggregations of fish between 9 and 16 m, and 17 and 24 m.

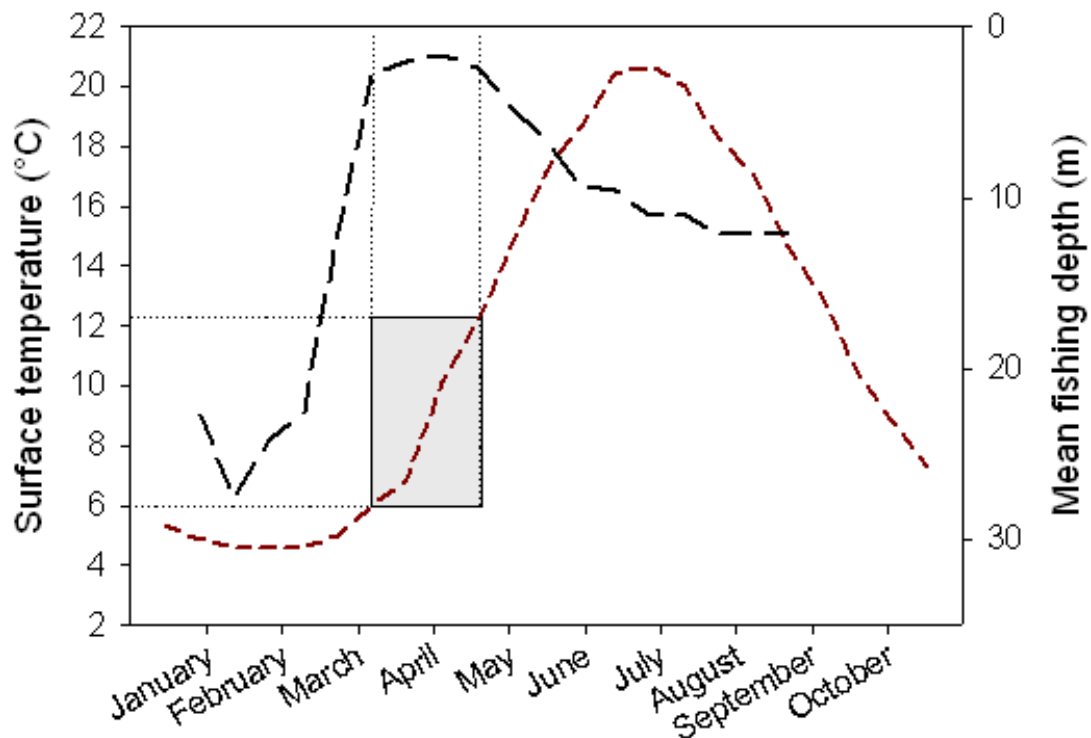


Fig. 5.1: Seasonal changes in average fishing depth (float line of gill nets) for the years 1958-2007 (long dashed line). Surface water temperature in ULC (short dashed line) over the seasons averaged over the years 1963-2007. The grey box displays the temperature range to which whitefish are exposed when they are close to the surface in April/May.

The progress of the gradual downward shift of fishing depth during summer varies between years and shows clear differences between decades (Fig. 5.2). The general linear model employed in this study reveals that fishing depth is related significantly ($p < 0.0001$) to both decade ($F = 24.8$) and seasonal course ($F = 135.8$), while the interaction between the latter two factors is not significant ($p = 0.827$). Student's *t*-test showed that, with the exception of the decade 1968-77, fishing depth differed significantly between all decades.

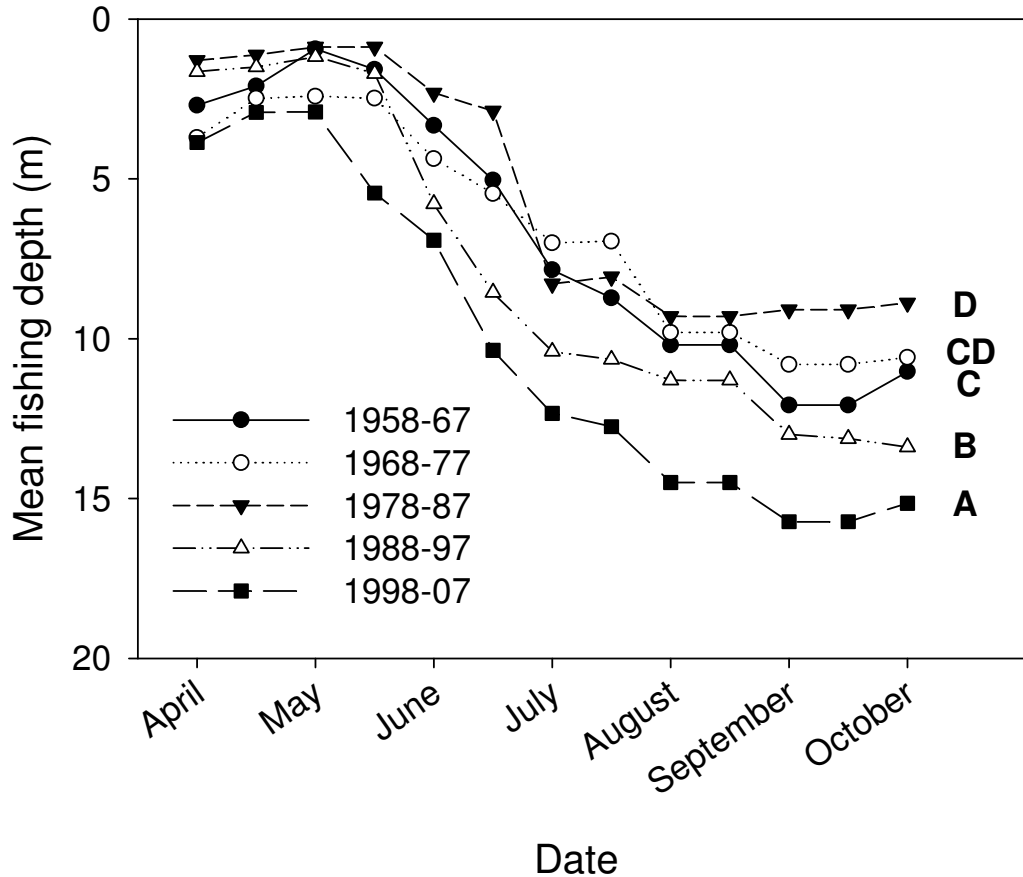


Fig. 5.2: Changes in mean fishing depth (float line of gill nets) from April until the beginning of the closed season. The five decades, comprising the years 1958-07, differ in the amplitude of the seasonal downward migration. Capital letters indicate decades that differ significantly (post-hoc test, $p < 0.05$).

By the end of the fishing season in early October, fish were distributed between 8.9 and 15.9 m on average in the decade 1978-87, but between 15.2 and 22.2 m in the decade 1998-2007. With regard to a single year, the shallowest fishing depth in October was 3.8-10.8 m in 1967, and the deepest was 19.5-26.5 m in 1959. Even though the nets are set overnight, when whitefish may range widely the vertical plane, fishing depth data is most likely correspond to the dusk/dawn distribution of whitefish, since capture probability is

highest in the crepuscular hours when fish foraging activity is highest (Becker and Eckmann 1992).

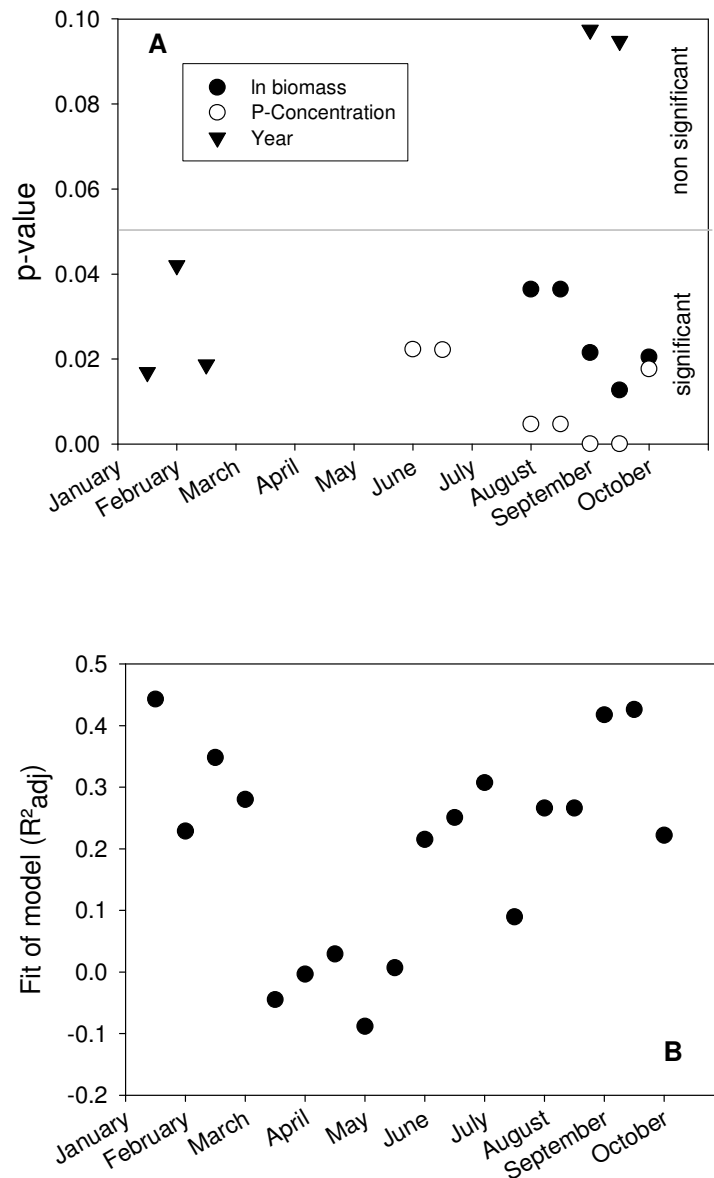


Fig. 5.3: Model output from multiple linear regression analyses of fishing depth versus phosphorus concentration, standing stock biomass, and year. **A:** P-values for the independent factors are indicated when they are lower than 0.1. **B:** The overall model fit (R^2_{adj}) is around zero when fish stay close to the surface but increases continuously towards fall.

In April and May, fishing depth was not correlated to the factor year, nor to any of the environmental variables considered.

Fishing depth was significantly correlated with the factor year in the 1st and 2nd half of February (Fig. 5.3 A). This result should be treated with caution, since fishing depth

might be uncoupled from the fish's vertical distribution during this time of the year. Fishery harvests during late winter and early spring are minimal (approx. 5-10 % of total annual harvest is obtained from January to March). These low capture rate provide insufficient feedback for accurate gauging of the vertical fish density gradient and the gains to be made by altering fishing depth are slight. Furthermore between January 10th and March 31st gill nets are anchored, making any adjustment very laborious. Therefore, nets are checked less often (every second day), and moved to a different depth even less frequently.

During the second half of the fishing season, lake productivity (represented by phosphorous concentration during holomixis) showed a significant correlation with fishing depth except for two time series in July. Fishing depth decreased with increasing lake trophy from the late 1950s to the late 1980s, and vice versa until the most recent years. Fishing depth was related significantly to standing stock biomass from August onwards up to the end of the fishing season in October. The fit (R^2_{adj}) of these multiple linear regression models varied between 0.2 and 0.4 (Fig. 5.3 B). The best fit was found in September, when the partial effects of phosphorus concentration and standing stock biomass were greatest.

The temperature regime whitefish face at the depth fished by gill nets (from the float line to the lead line) during September ranged from 10 to 16°C in most years. In recent years (approx. since 1995) the float lines are set well below the 16°C isotherm, and the temperature in the layer fished by the gill net ranged from 8 to 12°C most of the time (Fig. 5.4).

5.5 Discussion

Whitefish showed a consistent seasonal pattern in their vertical distribution throughout the study period 1958-2007. However the rate and the extent of downward movement in summer and fall differed substantially between decades. These differences were correlated with two factors that influence per-capita food supply of whitefish: lake trophy and whitefish standing stock biomass. In years with high per-capita food supply, resulting from low standing stock biomass and/or high lake productivity, the fish gathered at shallower depths than in years with low per-capita food supply. By the end of the 1990s, whitefish standing stock biomass in ULC was consistently higher than at any other time during the study period (Thomas and Eckmann 2007). Data on standing stock for the most recent years is not yet available, but with phosphorous concentration in ULC returning to

oligotrophic levels, whitefish distribution during the last decade has been the deepest of all five decades considered in our study.

During winter, when water temperatures drop to around 4°C and the abundance of large zooplankton species is low, fish are rather lethargic and foraging activity is minimal. In April, fish ascend towards the surface and start feeding. They benefit from high zooplankton abundance during the spring plankton bloom, and from mild water temperatures. Whitefish stomach fullness is greater at this time than any other period in entire growing season (Eckmann et al. 2002). The gradual return to greater depths starts when surface temperature exceeds approx. 12 °C. As a cold-adapted species, whitefish avoid high water temperatures, preferring temperatures between 8 and 15 °C (Alabaster and Lloyd 1980). (Hamrin 1986) reported that adult vendace (*Coregonus albula*) avoid temperatures in excess of 18 °C, and were therefore distributed in the meta- and hypolimnion of stratified lakes. (Dembinski 1971) found a similar pattern for *Coregonus albula* in Polish lakes, where vendace were distributed at shallow depths from April to July but retreated to the hypolimnion during the summer months. The vertical distribution of lake whitefish in September corresponded to a 10-16°C temperature zone, decreasing in the most recent years to 8-12°C.

(Ptak and Appenzeller 1998) conducted hydroacoustic surveys in Upper Lake Constance in the years 1994-96. The seasonal pattern of whitefish vertical distribution recorded corresponds to that observed in the present study, although data for March until June, were lacking most probably because the aggregation of fish close to the surface made reliable mapping with the echosounder impossible. The daytime distribution of whitefish recorded was similar to the dusk / dawn distribution described here. High amplitude diel vertical migrations, as reported for several other *Coregonus* spp. populations (Hrabik et al. 2006, Mehner et al. 2007), are therefore unlikely for ULC whitefish. Hydroacoustic surveys in 2006 and 2007 support this conclusion (Thomas, unpubl. data).

From the above observations we conclude that with ongoing warming of the epilimnion whitefish evade unsuitable high temperatures by distributing within or below the thermocline. The thermocline thus becomes the upper limit of whitefish habitat in summer, inhibiting distribution towards shallower depths. The timing of the formation and the rate of the vertical expansion of the thermocline is a result of meteorological conditions. Global warming might therefore be expected to influence vertical distribution of whitefish by changing the depth of the thermocline and thus the upper limit of whitefish distribution in summer. No evidence for this scenario has been recorded so far, because the

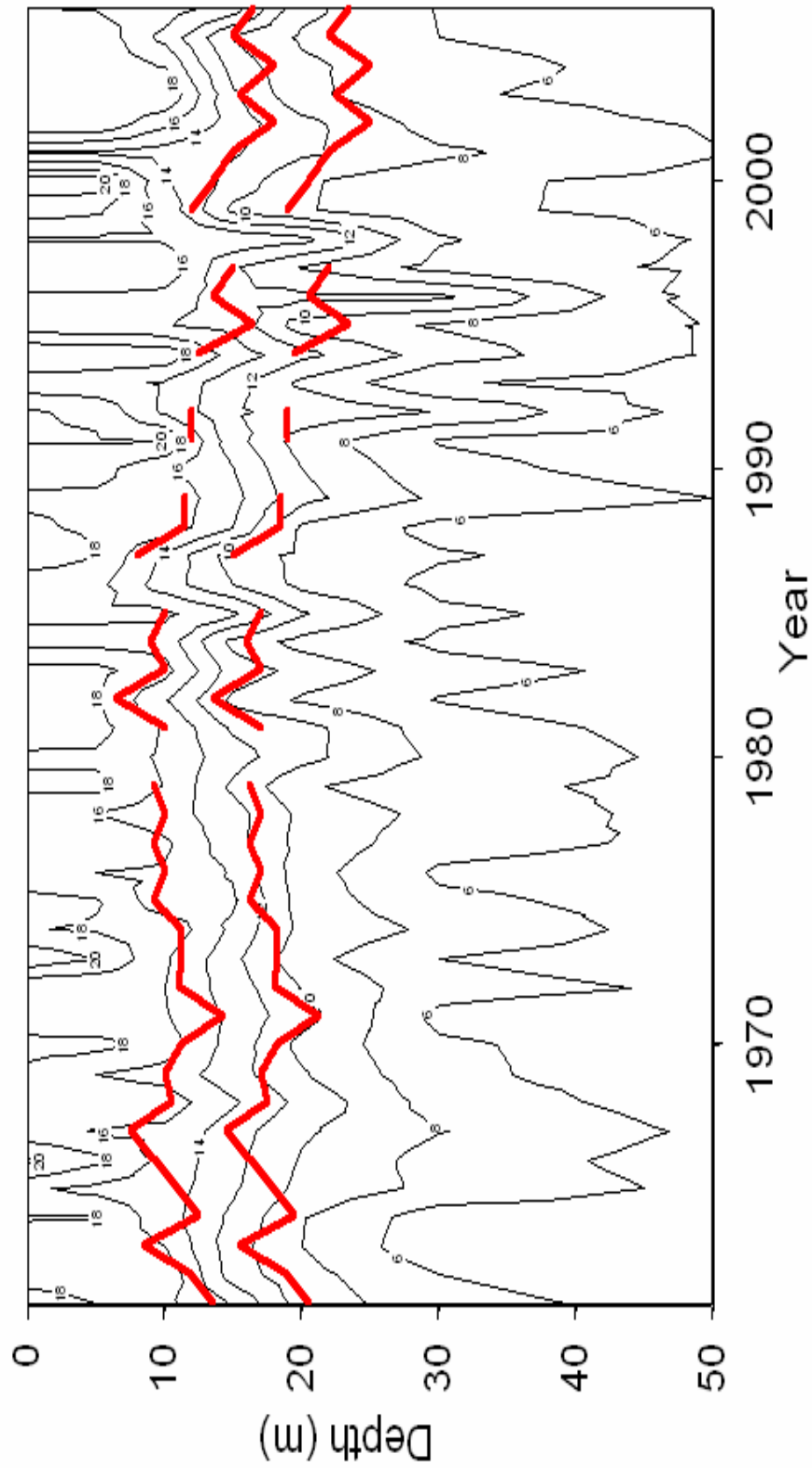


Fig. 5.4: Temperature in the depth layer from which whitefish were harvested in September for the years 1961-2006. Isotherms are shown as grey lines. Fishing depth layer is delimited by dashed black lines (upper line is float line depth, lower line is lead line depth, i.e. gill nets are 7 m high).

variable “time” was significantly correlated to whitefish depth only during months when the thermocline was yet to form (cf. Fig. 5.3 A).

Our study demonstrates a clear correlation between lake productivity and whitefish vertical distribution, assessed in terms of fishing depth. This correlation might be a direct effect of lake trophic status on fish distribution, mediated by prey abundance. Alternatively, the influence might be indirect, via changes in the light climate as a result of changes in lake productivity. However there are indications that light is not the main factor influencing whitefish distribution. At first glance, changes in Secchi depth across the year show a pattern similar to that of the whitefish’s vertical distribution (Fig. 5.5). During the summer months, Secchi depth is the shallowest in August and increases towards the end of the year. Whitefish, however, start to descend earlier in the year and end their downward movement by the beginning of September, before Secchi depth reaches its maximum. Furthermore, a linear regression of fishing depth on Secchi depth for the summer months reveals no significant correlation. This is in line with findings for Lake Stechlin vendace, whose distribution was not correlated with Secchi depth either (Mehner et al. 2007). In contrast, (Bohl 1980) found a positive correlation between the vertical distribution of planktivorous cyprinids and light climate, irrespective of temperature and vertical prey gradients. But cyprinids, unlike salmonid species, have a relatively high tolerance for warm temperatures. The most plausible explanation for the observed vertical distribution patterns of whitefish in summer and fall is lake productivity, which influences whitefish via zooplankton abundance, together with standing stock biomass. In years with low per-capita supply of zooplankton, whitefish seem to be distributed within or directly below the thermocline, where they benefit from low water temperatures and the best of the light during the gloomy hours of the day, when feeding activity is greatest (Eckmann, 2002). When fish abundance is high and/or zooplankton abundance low, competition for food increases at the preferred depth and fish are obliged to reassess their habitat choice (Kacelnik et al. 1992). A proportion of the population will probably move to greater depth, distributing along the resource gradient in proportion to the actual pattern of resource availability, thereby reducing the overall pressure of intraspecific competition (Ward et al. 2006).

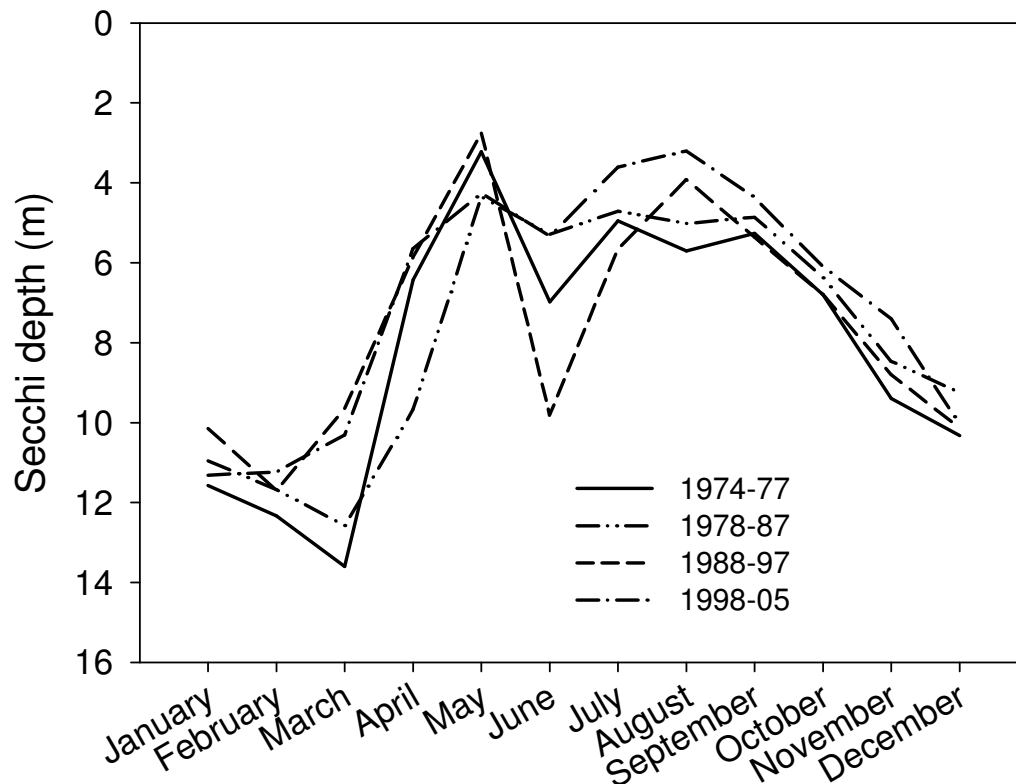


Fig. 5.5: Seasonal course of Secchi depth in ULC for the years 1974-2005, averaged over four time intervals. Note different lengths of time intervals due to limited data availability.

The move to greater depth might imply lower foraging efficiency because of reduced light intensity (Robinson and Tash 1979). The trade-off between intraspecific competition pressure and light-dependent foraging efficiency is likely to be the principle factor controlling the vertical distribution pattern of pelagic zooplanktivorous whitefish in ULC., in line with the ideal free distribution theory. The increase of mean fishing depth, in parallel with decreasing lake productivity and/or increasing standing stock biomass, may not necessarily represent a shift of the entire population to greater depth but rather a wider spread of the fish towards the hypolimnion.

An alternative explanation is based on a study on salmon, which revealed that starving individuals seek cooler (deeper) waters in order to reduce metabolic costs (Javaid and Anderson 1967). In this scenario, mean fishing depth would be greater in years of low per-capita food supply, while the vertical spread of the fish distribution might remain the same. The September fishing depth distribution observed in the current study (Fig. 5.4) indicates that in the most recent years, whitefish are harvested from greater depths, where

temperature is about 4°C lower, than in the period before 1990. As they stand, the results do not allow us to judge which of the two alternative explanations for a deeper distribution of whitefish is more plausible. In both scenarios fish are located deeper and consequently at lower water temperatures.

Our study reveals that changes in the vertical distribution of whitefish in ULC can be linked to changes in environmental conditions that control fish per-capita food supply. Even though the ultimate mechanism(s) remain unresolved, the results might be useful for the future management of the whitefish fishery. Phosphorus concentration has decreased to such a low levels in recent years, from which a further decrease is unlikely, that changes in fishing depth during late summer may be taken as a proxy for whitefish standing stock biomass. This possibility will be tested in the near future.

5.6 Acknowledgements

Thanks to the Regierungspräsidium Tübingen and the Institute for Lake Research, Langenargen for providing us the monthly reports of fishery wardens. Temperature and Secchi depth data are from the International Commission for the Protection of Lake Constance (IGKB) and were provided by Robert Obad (Institute for Lake Research, Langenargen). Amy-Jane Beer corrected the English. We are grateful to the German Research Foundation (DFG) which sponsored this project within its priority programme AQUASHIFT.

6. General Discussion

The results derived from this thesis document serious impacts of human activity on the whitefish stock of Lake Constance in the previous 50 years. Both direct and indirect anthropogenic effects are responsible for changes in growth performance, reproductive traits and vertical distribution of the fish. Most studies on whitefish ecology in Lake Constance so far, have been dominated by a mono-explanatory background of altered lake trophy. In contrast in all our studies (chapter 2-5) we found, combinations of different variables that explain a high degree of variation of the observed traits.

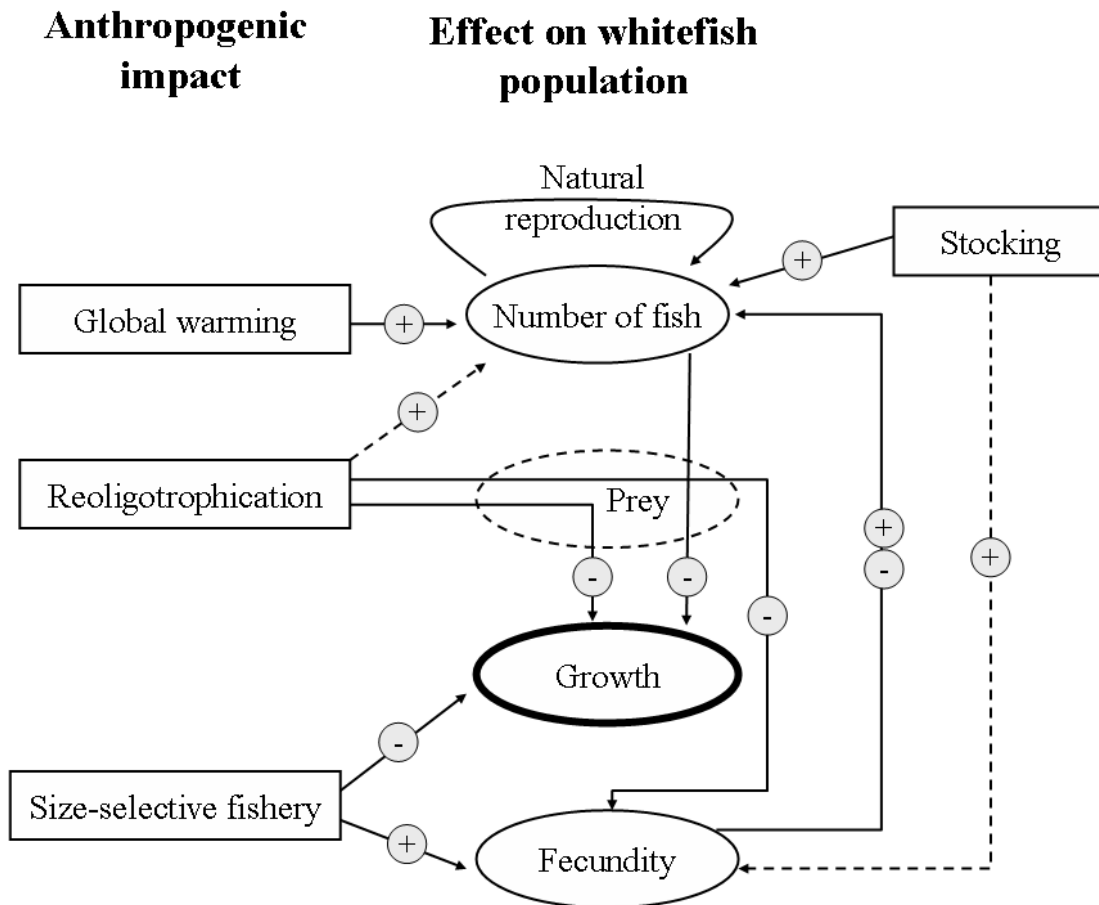


Fig. 6.1: Overview of anthropogenic impacts (squares) and expected effects (ellipse) on the whitefish population of Lake Constance. “Prey” is indicated in dashed line, since being just an intermediate step in the mechanistic explanation to effects on whitefish. Solid lines indicate interactions of high relevance. Dashed interaction lines show linkages of minor or rather speculative relevance. The “+” represents expected amplification of the observed effect, the “-“ stands for a weakening effect.

Figure 6.1 summarizes the newly gained insights of the interplay between the different human impacts and the response of the whitefish stock, gained from this thesis. Some conclusions and outlooks discussed below need further investigation in order to obtain final proof.

Eutrophication, and since 1980 reoligotrophication, were processes of dominating ecological relevance for the entire ecosystem of Lake Constance. Many studies have analyzed the diverse role of eutrophication on the whitefish population. Changes in growth rate for example were almost solely related to eutrophication and reoligotrophication so far (Nümann 1962, 1972). Also fecundity has been solely linked to the lakes phosphorus concentration (Hartmann and Quoss 1993).

In this study, however, I was able to show that intraspecific competition rather than lake trophy is the driving factor for differences in whitefish growth over the last 50 years. Merely regarding the changes in trophy, will not be suffice to explain the observed variation. The magnitude of stock fluctuations varied 37-fold in the investigation period, compared to the 11-fold difference in phosphorus concentration. This explains the much stronger effect of intraspecific competition compared to changes in trophy on food availability and therefore on growth.

The factor climate change is incorporated in the mechanistic model (Fig. 6.1) though this aspect itself was not directly investigated in the studies described in chapters 2-5. However it can interact with the aspects considered in this study and magnifies or compensates projected effects. Furthermore its relevance will rise in future decades. The expected effects of climate change were derived from other publications (Trippel et al. 1991, Straile et al. 2007, Ostendorp et al. 2007).

Global warming in it's first stage is expected to have positive consequences for whitefish recruitment. The North Atlantic Oscillation Index (NAOI) which characterizes large scale meteorological patterns in Europe also shows to have an impact on whitefish recruitment. Hatching will be more successful in years with a high NAOI. With continuing global warming we expect more years with a high NAOI. In those years the hypolimnion water temperature after mixing in fall is slightly warmer (up to 1.3 °C), which leads to a reduction of egg development time (Straile et al. 2007). Due to reduced time between spawning and hatching the loss of eggs to predation or fungal infection is reduced. Therefore, the amount of successfully hatched larvae in the following spring is expected to be higher. An earlier onset of spring due to global warming and in consequence an earlier succession in phyto- and zooplankton dynamics will be positively related to larval survival (Trippel et al. 1991). Both described effects, warmer hypolimnion water during winter and

higher epilimnion temperature in the following spring will therefore lead to better recruitment during a moderate state of global warming. In an onward proceeding of global warming, the effects might turn into a negative development. Referring to Ostendorp et al. (2007) a more stable stratification due to higher water temperatures until fall, will lead to an incomplete mixing. Oxygen saturation of deep water in this scenario will decrease, especially when mixing fails to appear in consecutive years. Eggs at the lake bottom, and therefore recruitment, might suffer from this.

In the initial global warming scenario, when we expect better recruitment and therefore larger standing stocks, intraspecific competition will consequently be more pronounced and growth rate will decrease further. Cumulative the ongoing intensification of stocking will keep fish abundance on a high level. A large whitefish stock might also have a back coupling effect: a large spawning stock produces a larger amount of eggs and therefore high numbers of offspring. This effect is compensated to some extent by reduced fecundity, which decreased with ongoing reoligotrophication. In a later stage of global warming, a possible incomplete mixing might negatively affect natural recruitment, due to insufficient oxygen saturation at the sediment-water interface. This effect had already been a problem in the times of eutrophic conditions, when oxygen consumption due to degradation of organic matter was pronounced. Reoligotrophication improved oxygen saturation at the lakes bottom and therefore egg loss was reduced compared to the 1980s. Natural recruitment might decrease in the long run, due to incomplete mixing. Depending on the amount of stocking, stock size might decrease again and the tightened degree of competition might be more relaxed again.

Aside from trophy, the density-dependent aspect also affects vertical distribution. With increasing fish abundance a shift to greater depth is to be expected. In consequence fishermen have to set their nets deeper in the course of summer. An altered vertical distribution of whitefish is expected to be a result of low individual prey abundance of fish without any consequences itself. Climate change in a more pronounced phase might act on vertical distribution of fish itself. Cold adapted whitefish avoid high temperatures. When epilimnion warms up faster during the year, fish might descend into cooler water depth earlier. Due to the fact, that spring is expected to start earlier as well, it is hard to adjudicate, if whitefish are affected in a positive or negative direction by possibly altered match-mismatch scenarios.

The most remarkable and new insight from this thesis is the indication for fisheries-induced evolution of the whitefish stock of Lake Constance. Though a final evidence of fisheries induced evolution is difficult to adduce so far, the diverse indications support the

theoretical and convincing concept. The practice of size-selective gill-netting and stocking are a basis for an evolutionary change of Lake Constance's common whitefish however.

In heavily exploited stocks, fishery replaces natural mortality factors. This has also proved itself to be true for Lake Constance whitefish following the introduction of nylon gill nets in the 1960s, though the fishing effort has been continuously reduced over the last decades again. The majority of whitefish in Lake Constance is still likely to face fishing mortality. Because fish grow more slowly the window of catchability stays open longer and thereby the individual risk of fishing mortality increases. A large fish stock increases intraspecific competition and the growth rate of fish will decline. In such a system it takes much more time until a fish reaches a size safe from fishery. If fishing pressure is high and fish are catchable over a long period it is unlikely that many fish reach such a large size. In a lake with lower fish abundance, fish will grow faster and the period in which they are vulnerable to size-selective harvest will be shorter. In this system a higher number, but still a minority, of fish will reach a size where they cannot be caught with the used mesh-size. Those few "survivors" would be able to reproduce until dieing of natural causes and therefore produce a high number of offspring with a genetic ability for faster growth. Meanwhile the fishery-induced evolution has also become the most likely explanation for the growth rate decline of Lake Joux's whitefish (*Coregonus palaea*), which faces high fishing pressure as well (Nusslé et al. 2009).

Though fecundity is decreasing with reoligotrophication a selection towards higher fecundity combined with a large spawning stock will increase stock size further. Therefore intraspecific competition stays on a high level, leading to poorer growth. The general path of energy allocation seems to be altered by fishery, shifting from investment into somatic growth towards a more pronounced reproductive investment. If a fish naturally spends more energy for reproduction than somatic growth it matures earlier and produces more offspring. On the other hand those fish grow more slowly, therefore surviving longer in a system with high size-selective fishery harvest. If this energy allocation towards reproduction or growth is determined genetically, those genes accumulate over years, determining a high reproductive investment and poor investment into somatic growth. In contrast, fish with a high investment into somatic growth have less energy available to invest into reproduction. Consequently, they have fewer offspring and due to their fast growth they are caught early while fishing pressure is high. Genes coding fast growth become rare over the years. This insight is supported by our laboratory experiment. Larvae hatching with larger yolk sacs grew more slowly. The increased reproductive investment might be reflected, in addition to a higher fecundity also by larger yolk-sacs. Therefore,

these larvae might be the offspring of the „reproductive“-type of whitefish, which grow slowly.

Selection for slow growth (Chapter 2) and increased relative fecundity (Chapter 4) will intensify the observed trends of the most recent investigated years (1990-2000) towards higher fish numbers and slow growth. Absolute fecundity decreases with reoligotrophication but remains on a higher level compared to conditions prior to eutrophication. Under natural selective forces whitefish should grow more quickly and invest into reproduction later in life, since mortality is more pronounced in early ontogeny. In the fishery mortality scenario those genotypes are most successful which invest the most energy in the reproductive path of energy allocation early in life, at the expense of slow growth.

Stocking is likely to be another major anthropogenic impact. A study of Eckmann et al. (2006) indicates that the majority of caught fish in the lake originate from hatcheries. Taking this into account, the risk of depletion in genetic diversity is high – a minority of fish produce the majority of offspring of tomorrow’s spawners. Fish whose offspring is incubated in hatcheries are caught during spawning-fishery with size-selective mesh sizes as well. Considering that catchability depends on fish morphology and behaviour (size, body girth, size of gonads) the selection is not arbitrary but already might select for certain phenotypes and their genotypes. Fecundity is one trait that seems to be amplified by stocking, as females with many and possibly bigger eggs have a bigger body girth and will be caught more frequently.

The observed indications for an evolutionary change of the whitefish stock in Lake Constance are not a dramatic cause for concern as consequences have been on a moderate level thus far. Nevertheless the results gained from this thesis could be a basis to adapt future stock management to the current situation.

All observed anthropogenic impacts of the current trend (high standing stock biomass, decreasing trophy and size-selective fishery) will culminate in slow growth. Decreasing nutrient input will lead to slower growth compared to eutrophic conditions. It is in the interest of fishermen and managers to keep fish growth at a high level. Fish can only use spare energy for somatic growth or reproduction beyond their metabolic costs. If the standing stock is large, a large proportion of energy will be “wasted” for metabolism for the maintenance of a large stock size. A fixed portion of the ingested food is invested for metabolism and activity. All energy, not used for their metabolism, can be invested into somatic growth or reproduction. For a given food amount, a higher fraction of energy is used for metabolism when stock size is large, because many fish must maintain their

metabolism / activity. When stock-size is small, supplying the same given food amount, more energy is left over for somatic growth or reproduction. A smaller fish stock means that a higher amount of available energy will be spent into somatic growth or reproduction, which would be beneficial for fishery. It is tempting to believe, that high numbers of fish in the lake are supporting satisfactory fishery yields, and yet sometimes “less is more”. In the times when Lake Constance had its original trophy and other human impacts were at a reduced level, Elster (1944) gave a mean standing stock biomass of whitefish for the years 1925-41 with 385 tons (without natural mortality). For the period of 1991-2000 we found a mean biomass of 1,228 tons (including natural mortality with 0.2 per years). In both time intervals trophic conditions were at a similar level. This indicates, that compared to the reference time period of the 1930’s, during which human impact on population management was low the stock size was far too high by the end of the 1990s. Unfortunately estimations are off by several years, as current data on stock size could not be obtained. For an applied reasonable fisheries management an *in situ* estimation of stock size is essential.

The majority of today’s fishermen have carried out fishery in a more productive Lake Constance, when whitefish growth and fisheries yield were higher. They see the main reason for reduced fishery yields in the restoration process of Lake Constance. The uncontrolled nutrient input is the only large scale human impact (of the listed 4 points in the introduction) on Lake Constance, which has been reversed successfully with time, so far. Though reoligotrophication limits the carrying capacity, it is merely the restoration of the original status and only has a partial influence on slow growth.

It will be a far bigger challenge to reverse the evolutionary response of size-selective harvest or the effects of global warming. A changed management policy might be a powerful tool towards optimizing the system to the current situation. Fishermen and fish will benefit from a moderate standing stock size.

7. Summary

This thesis deals with the effects of long-term anthropogenic influences on the whitefish stock of Lake Constance. In the focus of my interest was how changing lake trophy and fisheries management, which is characterized through stocking and fishery, affect whitefish over the years. The results are discussed with the background of global warming, which is an issue of high relevance in future management perspectives.

The results from this study are of applied interest, since whitefish are of super ordinate economical importance for commercial fishermen and characterize the lake like no other fish species.

In the first study (chapter 2.), we analyzed growth performance of whitefish in the investigation period lasting from 1954-2000. This phase includes the time of increasing as well as decreasing phosphorus content. On the basis of fishery statistics we reconstructed standing stock biomass of whitefish on a monthly scale from 1954 to 2000. With archived scales from the Institute for Lake Research we were able to back-calculate length-at-age from medium fast growing whitefish. Length increment in the second year in life differed between 8.5 and 19.6 cm. We tested growth increment against environmental conditions such as phosphorus concentration during spring turnover and standing-stock biomass. Variance in growth was explained to a degree of 80.8 % by changes in phosphorus concentration and standing stock biomass. The influence of standing stock biomass had a stronger effect (expressed by F-value) on growth decline than lake trophy. In a second step of analysis calendar year was additionally incorporated into the model and led to an overall improvement of the model fit to $R^2_{adj} = 0.87$. This means fish growth declines over with time. We attribute this finding to an evolutionary answer to size-selective fishery. By catching the fast growing fish early, the slow growing genotypes have an advantage of reproducing more often. Over many decades the genotype coding slow growth but high reproductive effort will be more successful.

The factor of heredity of growing speed was substance of a laboratory experiment, presented in chapter 3. Since whitefish are unsuitable for laboratory experiments lasting over several generations (too large, mature too late), we had to get fish with differences in growth history from the lake. Growth performance of offspring gained from those parents, were monitored over 40 days post hatching. Parents (24 females) were of same size but differed in age which means they showed different growth rates. Beside the genetic background, growth of parents depends on environmental conditions. The experiment showed that larvae hatching with the highest weight and largest yolk sacs had the lowest

increment in body weight. In contrast larvae with the lowest energy reservoirs at hatching grew better. The growth rate of females and yolk sac size of larvae is correlated inversely with each other. We attribute this finding to altered energy allocation resulting from fishery. Fast somatic growth increases the likeliness of individuals to face fishing mortality, which acts size-selectively. In contrast to this, fishes which spend more energy into reproduction, at the expense of somatic growth, have a longer lifespan and can reproduce more often. The production of larvae with greater yolk sacs could be an indication for such a shift in energy allocation.

Reproductive investment is also the topic of the study presented in chapter 4. A data set on whitefish fecundity comprising the years 1963-99 was reanalyzed and new insights were gained. We could approve the strong linkage between lake trophy and fecundity. Additionally we found other correlations in the investigation period: fecundity remained on a higher level after lake trophy went back to oligotrophic levels. This again is most likely founded in altered energy allocation between somatic growth and reproductive investment. The selective pressure shifts the gene pool towards slow growth and increased reproductive investment (more eggs, larvae with higher energy reservoirs). Beneath fishery, fecundity is likely to be amplified by the practice of spawning fishery and cold breeding in hatcheries. Females with a large number of eggs and therefore having a bigger body girth are more likely to get caught by spawning fishery than females with fewer eggs. Considering that the rather few individuals caught during spawning fishery, contribute a large portion of offspring to the next generation, genes coding for high fecundity will be bequeathed more often.

We were able to extract data on egg weight and gonadosomatic index from the data set and test those data against environmental conditions as well. Egg weight was correlated with fish age and to a lower degree with lakes phosphorus concentration. The gonadosomatic index was well described by combining egg weight and fecundity as independent variables.

The last study (chapter 5) deals with the vertical fish distribution of pelagic whitefish in the long-term trend. The analysis is based on the monthly reports of fishery wardens of the years 1958-2007. Fish are distributed surface close in April and May. With the warming of surface waters in the course of summer, fish start to descend to greater water depth up to 25 meters. Fishes seem to avoid temperatures exceeding 16°C. The degree of downwards movement varies in the investigation period. Depth distribution was correlated with lake trophy and standing stock biomass but seems to be independent from light intensity (measured by Secchi depth). In years with low trophy and high fish density

fish were distributed deeper. When individual prey availability was considered to be higher (high trophy, low intraspecific competition) fish were distributed more shallow. It remains unclear if fish migrate to deeper and colder waters to save metabolic costs or if fish are distributed over a wider vertical layer to reduce intraspecific competition for food. High epilimnion water temperatures impede fish to distribute more shallow.

Against the background of global warming, we expect in the initial phase of warming better recruitment. High fish abundance is likely, when cold breeding of larvae will be further intensified or held on a high level. This will result in increased intraspecific competition which will affect growth rate negatively. In a later phase of global warming an incomplete circulation in consecutive years might affect oxygen saturation on the sediment-water interface negatively. Egg development and with this, natural recruitment, might suffer from insufficient oxygen supply.

Size-selective harvest, causing an evolutionary change selecting for slow growth and increased reproductive investment instead, calls for an aligned fisheries management. A solution of striking simplicity is not found for that issue yet. Effect strength so far is no cause for concern. Spawning fishery and the practice of stocking gives the theoretical foundation for depletion in genetic diversity. Larvae stocked from hatcheries, originate from rather few individuals but do contribute above-average to the next generation. Therefore the question arises if stocking is necessary on a high level in times of presumably high fish abundance?

Future fisheries management should aim on a reasonable stock size. Studies from the 1930s, where human impact on the whitefish stock was lower and lake trophy comparable, could be a good reference to the natural status.

8. Zusammenfassung

Diese Dissertation befasst sich mit dem anthropogenen Einfluss auf die Felchenpopulation des Bodensees im Zeitraum von 1950 bis heute. In dieser Zeit haben wesentliche Veränderungen des Bodensees sowie des Fischereimanagements stattgefunden. Seit den 50er Jahren stieg der Nährstoffgehalt des Bodensees rasant an und bis zum Ende der 70er Jahre war eine deutliche Verschlechterung der Wasserqualität, mit negativen Folgen für Tourismus und Fischerei, zu verzeichnen. Erfolgreiche Sanierungsmassnahmen führten ab 1980 zu einer Umkehr dieses Prozesses und mittlerweile hat der Bodensee seine ursprüngliche Oligotrophie wiedererlangt. Die Fischerei wurde in den 50er Jahren von Klusgarn und Baumwollnetzen auf Nylonkiemennetze als Hauptfanginstrument der Felchenfischerei umgestellt. Da sich das neue Material als sehr effizient erwiesen hat, ist diese Neuerung mit einer starken Intensivierung der Fischerei verbunden gewesen. Die Effizienz dieser Fischerei bedrohte zu Beginn der 60er Jahre den Bestand, da mitunter unreife Felchen gefangen wurden. Ein Zusammenbruch konnte nur durch Beschränkungen der Fischerei und Erhöhung der Maschenweite verhindert werden. Generell stieg mit der Einführung und dem Ausbau der Kalterbrütung und ihrer Kapazitäten in den 60er Jahren der Besatz und damit das Fischereimanagement stark an. Der Anteil an besetzten Larven hat sich in den letzten 40 Jahren mehr als verzehnfacht. .

Die grundlegenden Fragen, die dieser Arbeit zugrunde liegen sind, wie sich Fischerei und Besatz, Eutrophierung und Reoligotrophierung auf die Felchenpopulation ausgewirkt haben und künftig weiter auswirken. Die Ergebnisse werden vor dem Hintergrund der drohenden Klimaerwärmung diskutiert.

Die erste Studie (Kapitel 2) handelt von den Änderungen der Wachstumsgeschwindigkeit der Felchen im Langzeittrend und deren Ursachen. Mit Hilfe von archiviertem Schuppenmaterial konnte das Wachstum der Felchen für den Zeitraum 1954-2000 rückberechnet werden. Die bisherige Einschätzung, dass allein die wechselnde Trophie für Änderungen in der Wachstumsrate der Felchen verantwortlich ist, musste anhand der Ergebnisse erweitert werden. Anhand von Fangstatistiken waren wir in der Lage, die Bestandsbiomasse der Felchen auf einer monatlichen Basis für den oben genannten Zeitraum zu rekonstruieren. Die Bestandsbiomasse, als Maß für die intraspezifische Konkurrenz, war in dieser Zeit sehr variabel und konnte einen großen Anteil an Schwankungen in der Wachstumsrate der Felchen im zweiten Lebensjahr erklären. Der Einfluss der Bestandsdichte auf das Wachstum überstieg dabei den Einfluss

der wechselnden Trophie. Ein dritter Faktor zeigte in der linearen Regressionsanalyse ebenfalls einen signifikanten Einfluss auf das Wachstum: die Zeit. Die Fische wachsen mit der Zeit zunehmend langsamer. Diesen zeitlichen Aspekt schreiben wir einer genetischen Selektion auf Langsamwüchsigkeit zu. Dieser Effekt bewegt sich auf einem geringen Niveau von 0,6 cm alle 10 Jahre für den Zuwachs im zweiten Lebensjahr.

Ein evolutionärer Wandel durch Fischerei ist bereits für mehrere intensiv befischte Meeresfischarten und -bestände dokumentiert. Größenselektiver Fang entzieht dem See die schnellwüchsigen Fische zuerst, da diese die Fanggröße der verwendeten Machennweiten zuerst erreichen. Folglich werden diese Fische dem System eher entzogen als langsamwüchsige Fische. Diese bleiben länger im See, nehmen an mehr Laichzeiten teil und haben daher einen höheren Reproduktionserfolg mit mehr Nachkommen. Als Konsequenz werden Gene, die ein langsames Wachstum kodieren, häufiger in die nächste Generation vererbt als Gene für Schnellwüchsigkeit. Diese Interpretation der Ergebnisse ist aufgrund aktueller Literaturhinweise auch für die Felchen im Bodensee als die wahrscheinlichste anzusehen.

Der Faktor der Vererbbarkeit von Wachstumsgeschwindigkeit wurde in einem Laborversuch (Kapitel 3) näher untersucht. Da Felchen aufgrund ihrer Größe und späten Geschlechtsreife nicht über mehrere Generationen unter Laborbedingungen gehalten werden können, mussten wir Fische mit unterschiedlichem Wachstumshintergrund aus dem See heranziehen. Das Wachstum der Nachkommen von diesen im See gefangenen Elterntieren (24 Weibchen) wurde über einen Zeitraum von 40 Tagen nach Schlupf verfolgt. Die Elterntiere waren gleicher Länge, aber unterschiedlich alt, was auf eine unterschiedliche Wachstumsrate schließen lässt. Neben den Genen ist das Wachstum der Eltern natürlich auch von Umwelteinflüssen abhängig. Der Versuch hat ergeben, dass die Larven mit dem größten Schlupfgewicht und größtem Dottersack die langsamste Wachstumsrate (auf Gewicht bezogen) gezeigt haben. Larven mit weniger Energiereserven zum Schlupfzeitpunkt wuchsen dagegen besser. Dabei gab es einen signifikanten Zusammenhang zwischen der Wachstumsrate der Mutter und der Dottersackgröße der Larven: langsam wachsende Mütter produzierten Larven mit größeren Dottersäcken. Wir führen diese Beobachtung auf durch Fischerei veränderte Energieallokation zurück. Da schnelles somatisches Wachstum die Mortalität durch größenselektive Fischerei stark erhöht, haben diejenigen Fische eine höhere Lebenserwartung, welche die Energie statt in Körperwachstum vermehrt in Reproduktion investieren. Die Produktion von Larven mit größeren Energiereserven könnte daher ein Anzeichen für eine Verlagerung zu Fischen mit

gesteigertem Reproduktionsaufwand sein. Aufgrund des geringen Stichprobenumfangs sind die Ergebnisse dieses Versuchs eine Ausgangssituation für weitere Analysen.

Um die Reproduktionscharakteristika der Blaufelchen geht es auch in Kapitel 4. Ein neu ausgewerteter Datensatz über die Fekundität der Blaufelchen im Untersuchungszeitraum 1963-1999 brachte neue Erkenntnisse. Wir konnten die bisherige Erkenntnis bestätigen, dass die Anzahl an Eiern der Weibchen stark an die Trophie gekoppelt ist. Zusätzlich ließen sich weitere Trends im Untersuchungszeitraum beobachten: die Fekundität der Felchen ist trotz gesunkener Trophie in den letzten Jahren des Untersuchungszeitraums bei vergleichbarer P-Konzentration höher als vor der Eutrophierung. Dies hängt vermutlich mit der bereits oben erwähnten geänderten Energieallokation zwischen somatischem Wachstum und Reproduktion zusammen. Der Selektionsdruck verschiebt den Genpool hin zu langsamerem Wachstum aber gesteigertem Reproduktionsaufwand (mehr Eier, Larven mit mehr Speicherstoffen). Neben der Fischerei verstärkt wohl auch die Praxis der Laichfischerei mit Kalterbrütung die Steigerung der Fekundität. Weibchen mit vielen Eiern haben einen größeren Körperumfang und werden während der Laichfischerei häufiger mit den gröbenselektiv fangenden Kiemennetzen gefangen als Weibchen mit wenig Eiern. Da die vergleichbar wenigen Individuen, die während der Laichfischerei gefangen werden, wohl zu einem großen Teil des Bestandes beitragen, werden Gene, die eine hohe Fekundität codieren stärker in die nächste Generation vererbt.

Neben der Fekundität konnten erstmalig auch das Eigewicht und der gonadosomatische Index aus dem Datensatz berechnet und gegen Umweltfaktoren getestet werden. Das Eigewicht zeigte eine starke Abhängigkeit von dem Alter der Fische und zu einem geringeren Maß von der Phosphorkonzentration. Der gonadosomatische Index konnte zu einem sehr hohen Grad durch Eigewicht und Fekundität erklärt werden.

Die letzte Studie (Kapitel 5) behandelt die vertikale Fischverteilung der pelagischen Felchen im Langzeittrend. Grundlage der Analyse waren Monatsberichte der Fischereiaufseher im Zeitraum 1958-2007. Im April und Mai jedes Jahres sind die Fische dicht an der Oberfläche verteilt. Mit Erwärmung des Oberflächenwassers, wobei 16 °C als Obergrenze angesehen werden kann, wandern die Fische im Verlauf des Sommers in Tiefen bis zu 25 m ab. Dabei gibt es im Untersuchungszeitraum Unterschiede in der Ausprägung der Tiefenverteilung. Diese waren mit den Umweltbedingungen Bestandsbiomasse und Trophie korreliert, zeigten aber keinen Zusammenhang mit dem Lichteinfall (als Maß Secchi-Tiefe). In Jahren mit geringer Trophie und hoher Bestandsdichte waren die Fische im Mittel tiefer verteilt, flacher hingegen, wenn die

individuelle Nahrungsverfügbarkeit (höhere Trophie, geringere intraspezifische Konkurrenz) als höher bewertet wird. Ob die Fische das tiefere, kältere Wasser aufsuchen, um Kosten für den Metabolismus zu senken oder ob die größere Fangtiefe auf eine breitere vertikale Verteilung zur Minimierung der intraspezifischen Konkurrenz um Futter dient, bleibt unklar.

Vor dem Hintergrund der Klimaerwärmung ist zu Beginn der Erwärmung mit einer besseren Rekrutierung der Felchen zu rechnen. Wird die Kalterbrütung von Larven weiter intensiviert oder auf hohem Niveau gehalten, ist daher auch zukünftig mit einer hohen Fischdichte zu rechnen. Die daraus resultierende hohe intraspezifische Konkurrenz wird sich weiter negativ auf die Wachstumsrate auswirken. Ein hoher Bestand hat einen großen Bedarf an Energie zur Aufrechterhaltung des Grundmetabolismus, in einem kleinen Bestand könnte diese Energie zu einem größeren Anteil in somatisches Wachstum fließen. Demnach ist eine zu hohe Fischdichte aus Sicht der Fischerei nicht erstrebenswert. Ein weiterer Wachstumsrückgang durch sinkende Trophie ist indes nicht zu befürchten, da der ursprüngliche Nährstoffgehalt wieder erreicht wurde und eine weitere Reduzierung kaum möglich ist. In einer späteren Phase der Klimaerwärmung besteht die Gefahr, dass sich durch eine Aneinanderreihung von Jahren mit unvollständiger Vollzirkulation die reduzierte Sauerstoffversorgung am Seegrund negativ auf die Eientwicklung auswirken könnte. Somit wäre mit einem Rückgang der natürlichen Rekrutierung zu rechnen.

Zwar ist ein evolutionärer Wandel durch Fischerei derzeit nur sehr schwer zu beweisen, dennoch weisen die Anzeichen deutlich in diese Richtung. Der mögliche evolutionäre Wandel durch größenselektive Fischerei, der auf langsameres Wachstum und stattdessen höheren Reproduktionsaufwand hin selektiert, stellt die Frage nach einem angepassten Fischereimanagement. Eine einfache Lösung für dieses Problem ist allerdings nicht in Sicht, wobei die bisherige Effektstärke noch kein Anlass zur akuten Sorge darstellt. Allerdings ist durch die Praxis der Laichfischerei und Kalterbrütung eine genetische Verarmung zu befürchten. Larven aus Brutanstalten, die von vergleichsweise wenigen Elterntieren abstammen, tragen vermutlich überdurchschnittlich zur nächsten Generation bei. Die Frage nach dem Sinn der Kalterbrütung in Zeiten hoher Fischdichte bleibt offen. Zwar scheint ein Großteil der Fische auf Brutanstalten zurückzugehen, dennoch ist dies nicht gleichzusetzen mit der Annahme, dass bei Nichtbesatz der Bestand zu gering ausfallen würde. Möglicherweise verdrängen Larven aus Brutanstalten die natürlich reproduzierten Larven.

Zukünftiges Fischereimanagement sollte auf eine sinnvolle Bestandsgröße abzielen, Studien aus der Zeit vor der Eutrophierung könnten hierfür eine Referenz des natürlichen und daher sinnvollen Zustandes geben.

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11. Appendix

11.1 Eidesstattliche Erklärung

Ich erkläre hiermit, dass ich die vorliegende Arbeit ohne unzulässige Hilfe Dritter und ohne Benutzung anderer als der angegebenen Hilfsmittel angefertigt habe. Die aus anderen Quellen direkt oder indirekt übernommenen Daten oder Konzepte sind unter der Angabe der Quelle gekennzeichnet. Weitere Personen, insbesondere Promotionsberater, waren an der inhaltlich materiellen Erstellung dieser Arbeit nicht beteiligt. Die Arbeit wurde bisher weder im In- noch im Ausland in gleicher oder in ähnlicher Form einer anderen Prüfungsbehörde vorgelegt.

Konstanz, den 11. Februar 2009



11.2 Abgrenzung der Eigenleistung (Record of achievement)

Der Text dieser Arbeit wurde von mir geschrieben, die Co-Autoren haben basierend auf diesem Text geringfügige Änderungen für die Studien, an denen sie beteiligt waren, angemerkt. Der Text wurde von Muttersprachlerinnen sprachkorrigiert.

Kapitel 2: Die Rückberechnung der Jahrgangsstärke wurde, basierend auf bestehenden Fangzahlen, von mir allein durchgeführt. Den Grossteil der Schuppen, der für die Wachstumsrückberechnung notwendig war, wurde ebenfalls von mir vermessen. Die statistischen Analysen wurden von mir durchgeführt.

Kapitel 3: Die Idee zu diesem Experiment ist von mir, basierend auf den Ergebnissen von Kapitel 2 entstanden. Da diese Versuche sehr arbeitsintensiv waren, war die praktische Arbeit nicht ohne Unterstützung zweiter zu schaffen. Routinearbeiten wurden daher zum Teil von Myriam Schmidt mit übernommen. Auch in diesem Versuch habe ich den größten Anteil an Messungen selbst übernommen. Die Auswertung wurde von mir allein durchgeführt.

Kapitel 4: Die Idee zur Bearbeitung des Datensatzes und die statistischen Analysen und Auswertungen wurden von mir durchgeführt. Der Datensatz wurde vom Institut für Seenforschung zur Verfügung gestellt.

Kapitel 5: Wwie in Kapitel 4 habe ich den Datensatz zur Verfügung gestellt bekommen. Die Eingabe der Daten sowie die Durchführung der Analysen habe ich eigenständig durchgeführt.

11.3 Curriculum vitae

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2003-2004	Diplomarbeit in der Arbeitsgruppe „Gewässerökologie“ (Prof. Benndorf) über den „Prädationsdruck von Cypriniden auf Barschlarven in der Talsperre Saidenbach“ betreut von Dr. Robert Radke
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