

# Influence of climate variability on whitefish (*Coregonus lavaretus*) year-class strength in a deep, warm monomictic lake

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**Abstract** The year-class strength (YCS) of Blaufelchen (*Coregonus lavaretus*) in deep Upper Lake Constance was analysed for a 52-year period, from 1947 to 1998. Despite strong anthropogenic influences on the species' population dynamics due to cultural eutrophication and oligotrophication, intense fishing, and large-scale stocking, the influence of climate variability associated with the North Atlantic Oscillation (NAO) is apparent in the data set. This influence is significant although large-scale stocking of cold-bred larvae was performed to avoid a mismatch of larvae with their food. The importance of stocking on YCS, however, is unclear and was only detectable when analysing a subset of the data. In addition to climate variability a yet unidentified factor related to zooplankton suitability as food for fish larvae, and density-dependent mortality probably related to cannibalism do significantly influence YCS. The NAO seemed to influence YCS twofold, through temperature effects on egg development time and on larval growth rate. The first of these two mechanisms is related to the NAO via a time lag of 1 year due to the specific mixing dynamics of warm monomictic Lake Constance. Hence, a warm

winter in the year before spawning results in earlier hatching of larvae, that is, hatching is decoupled from the actual meteorological conditions. This should make the larvae very prone to mismatch the dynamics of their food. However, we found no evidence for such a mismatch in this 52-year data set.

**Keywords** North Atlantic Oscillation · Egg mortality · Match–mismatch · Time-lagged effects · Stocking

## Introduction

Long-term changes in the size of fish populations or in fish harvests provide classic examples for climate-driven fluctuations of animal populations (Cushing 1982; Alheit and Hagen 1997; Drinkwater et al. 2003; Ottersen et al. 2004). Climate variability and, e.g. recruitment of fish populations, may be linked via a large number of mechanisms (Ottersen et al. 2004) including water temperature effects on fish larvae growth (Eckmann et al. 1988; Ottersen and Loeng 2000; Schindler et al. 2005), effects of mixing on encounter rates between fish larvae and prey (Sundby et al. 1994), horizontal transport of larvae (Köster et al. 2001) and temporal synchronisation, i.e. match or mismatch between larval feeding and prey abundance (Cushing 1969, 1990). Especially, the synchronization of predator–prey dynamics is thought to be disrupted by global warming in aquatic (Edwards and Richardson 2004), but also in terrestrial ecosystems (Dewar and Watt 1992; Visser et al. 1998; Visser and Both 2005).

The pelagic spawning whitefish of Lake Constance, *Coregonus lavaretus* (local name: Blaufelchen) can be

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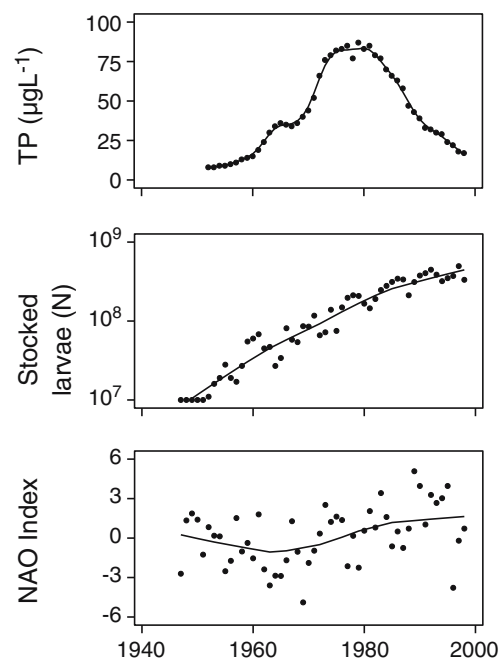
considered especially vulnerable to a potential disruption of its dynamics with its prey due to its specific biology and the mixing regime of the lake. The Blaufelchen of Lake Constance is the only known coregonid population performing pelagic spawning (Eckmann and Rösch 1998). The fish aggregate in the central part of Upper Lake Constance where spawning takes place within a short period of 3–5 days in late November/early December. Eggs sink to the lake bottom at approximately  $1 \text{ m min}^{-1}$ . Most eggs are found at depths  $\geq 200 \text{ m}$ . (Braum and Quoß 1981), where they develop depending on water temperatures (Eckmann 1987) within approximately 2 months (Eckmann and Rösch 1998). After hatching, which takes place around February, larvae ascend to the surface within 1–2 days and stay in the littoral or in the upper water layers of the pelagic zone. Spring growth of larvae has been shown to be strongly temperature controlled (Eckmann and Pusch 1989). Warmer springs will lead to faster growth of larvae. As predatory mortality of fish larvae is strongly size dependent, warmer springs should result in lower predation losses, and hence higher year-class strength (YCS) (Miller et al. 1988; Bailey and Houde 1989). This hypothesis was supported by an analysis of whitefish YCS in 1962–1982 which showed that spring meteorological conditions did best predict YCS (Eckmann et al. 1988).

Upper Lake Constance is a warm monomictic lake with a mixing period in February/March. Winter meteorological conditions determine the lake's cooling during winter, the strength of mixing and consequently the deep-water temperatures of the lake (Straile et al. 2003). After the onset of stratification around April, hypolimnetic water layers are separated from further meteorological forcing until the next mixing period. Hence, deep-water temperatures prevailing during whitefish egg development in December/January are mostly determined by the meteorological conditions of the previous winter. However, after hatching and ascent to the surface, larvae are exposed to the actual winter and spring meteorological conditions. That is, with emergence from the lake bottom larvae can be considered to travel from the previous to the actual winter. This time travel after hatching may result in a mismatch between the larvae and their prey, especially when a warm winter (resulting in early hatching) is followed by a cold winter and early spring (resulting in a delayed spring bloom). In this study we analyse the effect of meteorological forcing on Blaufelchen YCS in the light of the lake's complex hydrodynamics.

## Materials and methods

### Study site

Upper Lake Constance is a large ( $472 \text{ km}^2$ ) and deep ( $z_{\text{max}} = 254 \text{ m}$ ) perialpine lake at the frontier between Austria, Germany, and Switzerland. During the study period, Lake Constance experienced eutrophication and oligotrophication with total phosphorus concentrations increasing from  $<10 \mu\text{g l}^{-1}$  in the 1950s to almost  $90 \mu\text{g l}^{-1}$  in the late 1970s and decreasing again down to  $<10 \mu\text{g l}^{-1}$  in recent years (Fig. 1). The consequences for the lake's ecology have been studied intensively (Walz et al. 1987; Straile and Geller 1998; Eckmann and Rösch 1998; Gaedke 1998; Bäuerle and Gaedke 1998), and the growth of whitefish, but not its YCS was affected (Eckmann et al. 1988; Eckmann and Rösch 1998). The whitefish population in Lake Constance is additionally strongly influenced by humans. Fishing has taken place since mediaeval times, and even stocking has been performed for more than a century (Grim 1983). During the study period stocking of larvae increased strongly in recent years (Fig. 1). More recently, climate variability associated with the North



**Fig. 1** Long-term development of environmental variables suggested to be important for whitefish year-class strength (YCS). Total phosphorus (TP) concentrations during winter mixing; the number of stocked larvae; and the index of the North Atlantic Oscillation (NAO). All trend lines were computed using a LOESS fit

Atlantic Oscillation (NAO) (Fig. 1; Hurrell 1995) has been shown to influence e.g. the strength of winter mixing, spring nutrient concentrations, temperatures (Straile et al. 2003), and *Daphnia* population dynamics during spring (Straile 2000). The spatio-temporal extent of the NAO–temperature relationship in warm monomictic Lake Constance is complex. The NAO was related significantly to water temperatures at all depths during the mixing period (February, March), to surface water temperatures in spring (until May), and to bottom water temperatures until the next mixing period, i.e. until February of the following year (Straile et al. 2003). That is, because of the large depth and warm monomictic character of the lake, deep-water temperatures during a specific winter are not related to the actual NAO, but to the NAO from the previous year, i.e. there is a time lag of 1 year. As a consequence, the incubation temperature of whitefish eggs in December and January is not determined by the actual NAO, but by the NAO of the previous year.

Lake Constance fishermen have reported monthly catches of Blaufelchen from Upper Lake Constance since 1914. In addition regular catches are performed by the Institut für Seenforschung and the Fischereiforschungsstelle des Landes Baden-Württemberg in Langenargen/Germany in order to provide an estimate of the age composition of the fish in each month. Combining this information allows calculation of the number of fish of a certain age class which is harvested from the lake in each month. Summing the catches of a distinct cohort across months gives an estimate of the virtual YCS of this cohort. The 1998 cohort is actually the last one that is fished completely. Hence, 1998 is the most recent year considered in this study. Virtual population analysis also allows us to estimate the numbers of Blaufelchen of age-1 and older present in the lake during spawning. Using these numbers we test for the effect of density dependence (DD) on YCS.

The number of stocked larvae is recorded every year. A small percentage of larvae is pre-fed with lake zooplankton in the hatcheries before stocking. During 6 years (1983–1985, 1990, 1991 and 1995) within our study period, feeding larvae with zooplankton sampled in the lake resulted in histological damage and massive losses, whereas using *Artemia* nauplii as a food did not increase mortality (Eckmann and Rösch 1998). This suggests that the lake's zooplankton during these years was in some form unsuitable for the fish larvae. While several factors could be excluded as a cause for mortality (toxicity due to heavy metals or pesticides, virus or bacterial infections, parasites; Eckmann et al. 1986), it is still not known why the zooplankton was unsuitable

in these years. However, analysis of the RNA/DNA ratios of larvae caught in the lake suggest that the problem of “unsuitable zooplankton” (Eckmann and Rösch 1998) is not restricted to the hatcheries. Hence, in our statistical analysis we include a categorical variable “unsuitable zooplankton” (UZ).

Egg abundances on the sediment were estimated from dredge samples on 11 sampling dates during the winter 2000/2001. Eggs were sampled with a conical net (50 × 30-cm<sup>2</sup> opening, 2-mm-mesh width) mounted on a sledge (Elster 1933). On each sampling date, the sledge was towed along five transects at depths between 170 and 254 m (Jüngling 2001). The area sampled per transect varied between 70 and 140 m<sup>2</sup>. Eggs were analysed microscopically and classified into five categories: healthy, unfertilised, dead, infected with fungi, and empty egg shells. For this study we consider only the number of healthy eggs.

The egg dynamics on the sediment was modelled with an individual-based model which has the following components: eggs were spawned on the 6th of December (median day of spawning in this winter) ± 2 days SD, and will be found at the same day at the bottom of the sediment. From then on each egg has a daily probability of survival. For all eggs, survival was recorded and their accumulated degree-days (number of days survived × temperature at 200 m depth) were calculated. Hatching occurred when an egg reached 330 ± 2 degree-days (Eckmann 1987). The model was fit to the data by adjusting the total number of eggs spawned and the daily survival rate.

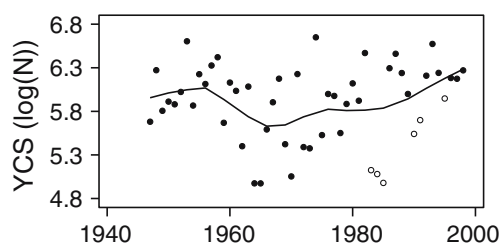
Total phosphorus concentrations were measured monthly during the study period (Rossknecht 1998). We used the total phosphorus concentration during winter (February, March) mixing (TP) as a proxy variable for the trophic status of the lake in a specific year. The index of the NAO (NAO-I) was used as a measure of climate variability and was obtained from the National Center for Atmospheric Research Climate Analysis Section home page (<http://www.cgd.ucar.edu:80/cas/catalog/climind/>) (Hurrell 1995). We used the winter index (average value from December to March) of the NAO in all analyses. We expect the NAO to influence YCS via its effect on water temperatures (Straile et al. 2003). Hence, water temperatures should also be related to YCS. Water temperatures were measured monthly at the central part of the lake at distinct depths, but only from 1962 onwards (Straile et al. 2003). To better compare the statistical relationships between YCS and water temperatures with those between YCS and NAO indices, we computed the latter ones also for the reduced time period from 1962 to 1998. This can be considered also

as a test of the robustness of the results. Within this shorter time series we test also for the effects of DD and trophic changes (TP) as these two variables were not available for the whole study period. YCS, the number of stocked larvae (S), as well as the numbers of large Blaufelchen (DD) were log-transformed prior to analyses. Models were compared using Akaike's Information Criterion (AIC). AIC rewards better model fit while penalizing for the number of parameters. Smaller AIC values indicate better models (Burnham and Anderson 1998). Data analysis was performed using SAS (SAS Institute 1988).

## Results and discussion

Whitefish YCS declined from the mid-1950s to a low in the mid-1960s and since then increased towards recent years (Fig. 2). Considering the years from 1947 to 1998 YCS did not show any significant trend ( $r = 0.05$ , n.s.). YCS in UZ years was significantly lower than in normal years ( $n = 52$ ,  $r^2 = 0.17$ ,  $P < 0.005$ ). This suggests that zooplankton unsuitability was not only a problem in the hatcheries, but resulted also in larval mortality in situ, thereby resulting into a lower YCS. Besides UZ no environmental factor is significantly related to YCS on its own. The best two-factor model according to AIC is with the lagged NAO-I (NAO<sub>-1</sub>-I) and UZ, explaining 32% of the variability in YCS (Table 1; Fig. 3). Variability in NAO<sub>-1</sub>-I did explain variability in YCS in both normal and UZ years. In addition to NAO<sub>-1</sub>-I, also the NAO-I, but not the number of stocked larvae contributed significantly to YCS when the effect of UZ was also considered. The best model included UZ, and both the NAO<sub>-1</sub> and the NAO indices (Table 1)

$$\text{YCS} = 2.98 - 0.9 \times \text{UZ} + 0.08 \\ \times \text{NAO}_{-1} - \text{I} + 0.05 \times \text{NAO} - \text{I}$$



**Fig. 2** Long-term development of whitefish YCS. The trend line is given by a LOESS fit. *Open circles* indicate years with unsuitable zooplankton (UZ)

Using the shorter time scale, i.e. 1962–1998, UZ and the number of stocked larvae alone were significantly related to YCS. However, all other factors contributed significantly to explain YCS variability when UZ was considered. The best model according to AIC explained 70% of the variability in YCS and included UZ, NAO<sub>-1</sub>-I, the number of stocked larvae, and the Blaufelchen stock during spawning (DD), but not TP and the NAO-I (Table 1)

$$\text{YCS} = 0.89 - 0.93 \times \text{UZ} + 1.1 \times \text{S} + 0.07 \\ \times \text{NAO}_{-1} - \text{I} - 0.2 \times \text{DD}$$

During the shorter time period the number of stocked larvae was the best predictor of YCS when considering UZ (Table 1). Both, YCS and the number of stocked larvae increased from the early 1960s onward. However, high levels of stocking did not prevent strong fluctuations in YCS during the last 20 years. Furthermore, YCS was high for the first 10 years of the study period when stocking was still low. Consequently, stocking was not successful in explaining YCS when considering the period 1947–1998. This shows that strong year classes were formed without the high levels of stocking that occurred during recent years. However, it does not exclude the possibility that stocking helped to prevent low YCS in the most eutrophic years, i.e. the 1970s, when O<sub>2</sub> concentrations at the bottom were low (Straile et al. 2003) and may have reduced survival of whitefish eggs. In contrast to the number of stocked larvae, the NAO and more strongly the NAO<sub>-1</sub> indices did contribute significantly to YCS during the entire but also during the shorter time period. For the latter time period the number of Blaufelchen present in the lake at the time of spawning also contributed significantly to the model whereby a higher number of whitefish resulted in a lower YCS. This was already observed by Eckmann et al. (1988) and attributed either to competitive interactions or to adult cannibalism on larvae. Especially the latter mechanism is regarded to be an important density-dependent regulator of YCS in fish populations (Bailey and Houde 1989).

The relationship between YCS and water temperatures was analysed while controlling for the effects of UZ, i.e. using UZ as a partial variable in correlation analyses. As water temperatures in different depths and months were strongly inter-related, YCS was strongly related to water temperatures during different months and depths (Fig. 4). Highest correlation coefficients were observed between YCS and deep-water temperatures during winter, i.e. during egg develop-

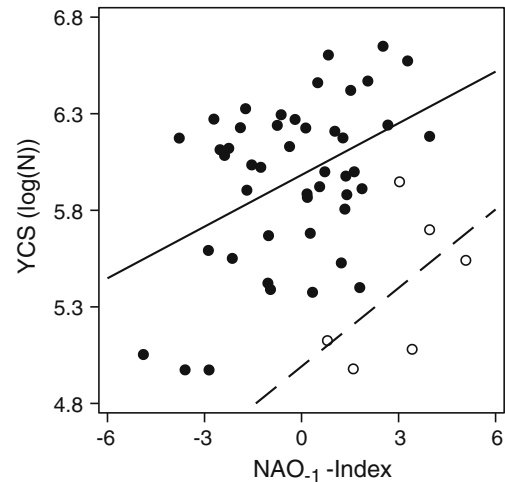
**Table 1** Regression models relating year-class strength (YCS) to the environmental variables NAO index (NAO-I), the lagged NAO-I (NAO<sub>-1</sub>-I), presence of unsuitable zooplankton (UZ), the number of stocked larvae (S), number of adult whitefish during spawning (DD)<sup>a</sup> and the total phosphorus concentration during winter mixing (TP)<sup>a</sup>. For all models Akaike’s information criterion (AIC) is computed to compare model performance. Smaller values of AIC indicate more parsimonious and better models

Variables	n	R <sup>2</sup>	AIC
<b>Complete time series (1947–1998)</b>			
NAO-I	52	0.026	65.8
NAO <sub>-1</sub> -I	52	0.026	65.8
UZ (***)	52	0.17	57.6
S	52	0	67
UZ (***) NAO-I (*)	52	0.27	53
UZ (****) NAO <sub>-1</sub> -I (***)	52	0.32	48.7
UZ (****) S	52	0.21	56.8
<b>UZ (****) NAO<sub>-1</sub>-I (**) NAO-I (P &lt; 0.06)</b>	<b>52</b>	<b>0.37</b>	<b>46.8</b>
UZ (****) NAO <sub>-1</sub> -I (**) NAO-I S	52	0.38	47.7
<b>Reduced time series (1962–1998)</b>			
NAO-I	37	0.04	53.6
NAO <sub>-1</sub> -I	37	0.05	53.1
UZ (*)	37	0.16	48.8
S (**)	37	0.18	47.7
TP	37	0	54.9
DD	37	0	55.1
UZ (***) NAO-I (*)	37	0.29	44.4
UZ (****) NAO <sub>-1</sub> -I (***)	37	0.40	38.2
UZ (****) S (****)	37	0.54	27.7
UZ (*) TP	37	0.16	50.6
UZ (**) DD (****)	37	0.18	49.5
UZ (****) S (****) NAO-I	37	0.56	28.5
UZ (****) S (****) TP (*)	37	0.55	29.3
UZ (****) S (****) NAO <sub>-1</sub> -I (*)	37	0.62	23.0
UZ (****) S (****) DD (*)	37	0.63	22.4
<b>UZ (****) S (****) NAO<sub>-1</sub>-I (**) DD (**)</b>	<b>37</b>	<b>0.7</b>	<b>16.1</b>
UZ (****) S (****) NAO <sub>-1</sub> -I (*) NAO-I DD (***) TP	37	0.73	17.1

\*P < 0.05, \*\* P < 0.01, \*\*\*P < 0.005, \*\*\*\*P < 0.001, \*\*\*\*\*P < 0.0001 (significance levels for the individual variables)

<sup>a</sup> DD and TP were not available for the time series from 1947 to 1998, and hence were only considered for the period from 1962 to 1998

ment at the bottom. This would be expected if the lagged NAO exerts a significant influence on YCS, i.e. if the duration of embryogenesis is important for YCS. Correlations with surface temperatures were also high during spring, i.e. during the larval phase of whitefish. A significant relationship between April temperatures and YCS had also been observed by Eckmann et al. (1988) who suggested that the temperature influence on growth rate affects larval survival and finally YCS. But upper water column temperatures of the winter preceding spawning were also significantly related to YCS. This is due to the fact that during this time mixing takes place and the deep-water temperature is determined (Straile et al. 2003). These correlations



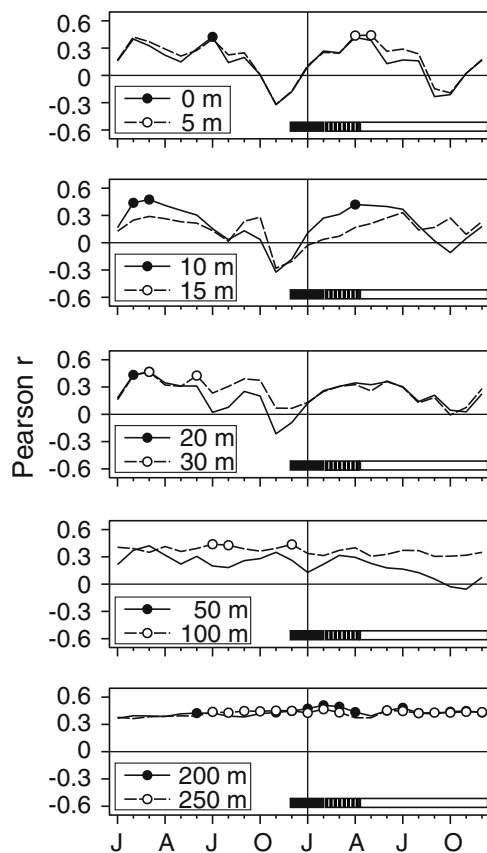
**Fig. 3** Relationship between Blauefchen YCS and the NAO index lagged 1 year (NAO<sub>-1</sub>Index). Open circles represent years with UZ. For abbreviations, see Figs. 1 and 2

again support the link between YCS and the NAO of the previous year.

Hence, the present regression analyses largely confirmed the results regarding the effects of spring meteorology, stocking and DD observed for the time period from 1962 to 1981 (Eckmann et al. 1988). However, Eckmann et al. (1988) did not analyse a possible effect of deep-water temperature variability on YCS as they considered deep-water temperatures to be constant (Eckmann and Rösch 1998). But, deep-water temperatures were not constant, instead they varied during the study period by >1°C (Straile et al. 2003), and consequently may have ecological effects.

When considering the influence of climate variability on YCS, it should be kept in mind that stocking at least in recent years was intense. While the NAO, i.e. spring surface temperatures, might influence both naturally recruited and stocked larvae, the lagged effect of the NAO via bottom temperatures cannot act on stocked larvae. Therefore, with the increasing importance of larval stocking for YCS, i.e. with an increasing contribution of stocked larvae to YCS, the importance of lagged NAO should decrease as stocked larvae never experienced deep-water temperatures. Hence, larval stocking and its possible influence on YCS needs to be discussed thoroughly.

Larval stocking has been performed at Lake Constance for more than a century (Grim 1983). During the study period the number of larvae stocked per year increased approximately 40-fold. In addition, hatcheries around the lake switched from incubation of eggs at 4°C to cold incubation at around 1°C during the 1980s. While before cold incubation was implemented, the



**Fig. 4** Partial Pearson correlation coefficients between the YCS and water temperatures measured at different months and depths in Lake Constance when controlling for the effect of larval mortality. Symbols indicate correlation coefficients with  $P < 0.01$ . Bars show the timing and duration of egg (black), larval (hatched) and juvenile (white) periods

lake was stocked with larvae at approximately the same time when larvae hatched in situ, with cold incubation, larvae are stocked up to 2 months after hatching occurs in situ. The main argument for cold incubation is that later stocking improves the match between the larvae and their plankton food. However, these efforts neither increased YCS significantly, nor did they prevent strong variability in YCS during the study period. Several studies tried to analyse the success of the stocking programme and estimated that 17% (Nümann 1967), 53% (Hartmann and Brenner 1983), 72% (Hartmann and Quoß 1989) of whitefish larvae in the lake derived from stocking. A recent study analysing the recaptures of Alizarin-stained larvae suggested that stocked larvae contributed approximately 60% to the abundance of age-0 fish caught in autumn 2003 (Eckmann et al. 2006). While, the relative success of larvae from the lake versus those from hatcheries likely varies from year to year, these numbers suggest that at least in some years a considerable

percentage of YCS stems from the hatcheries. However, even if 60% originate from hatcheries, the remaining 40% of the YCS are produced in situ and the interannual variability in survival of these fish might be influenced by interannual variability in deep-water temperatures.

A hidden assumption of cold incubation is that whitefish are maladapted to their environment, that is, larval hatching mismatches plankton succession. Clearly, evolution is not expected to result in perfect adaptation; however, it is hard to see why selection would not, e.g. result in later spawning of whitefish, if larvae do predictably hatch too early. However, if we assume that the time of hatching in situ is not a maladaptation, this might imply that delayed hatching reduces survival probabilities of stocked larvae. At least during years with an early start of stratification, in situ hatched larvae might have already increased in size when cold-bred larvae are stocked into the lake. Being larger is often considered to be an important survival advantage for fish larvae (Miller et al. 1988) and delayed hatching of larvae would be even more of a disadvantage if early hatching is an adaptation to avoid predators which will become more numerous as the season progresses. Also a calanoid copepod uses this niche of low predation during late winter/early spring successfully in Lake Constance: late winter offspring of *Eudiaptomus* do have much higher survival probabilities than offspring born during the rest of the year (Seebens et al., in review).

To deepen our understanding of the possible role of egg mortality for YCS, we analysed egg mortality in situ. The fate of whitefish eggs in the lake was examined in the winter 2000/2001. Spawning in this year took place around 6th of December. The first sampling was done on 12th of December and yielded an abundance of  $18.3 \pm 2.4$  healthy eggs  $m^{-2}$  (Fig. 5). Egg density declined continuously towards the last sampling (2nd of March), when only  $0.2 \pm 0.2$  healthy eggs  $m^{-2}$  were found. The data were reasonably fit with an egg mortality rate of  $0.02 \text{ day}^{-1}$  and a total number of 20 spawned eggs  $m^{-2}$  when using a development time of 330 degree-days (Eckmann 1987). These rates suggest an overall egg mortality of 75% during the winter 2000/2001.

Mean winter deep-water temperatures at 200-m depth varied during the study period from 3.8 to 5.1°C. Assuming hatching takes place after 330 degree-days (Eckmann 1987), this range in deep-water temperatures translates into egg developmental times between 65 and 87 days. Hence, deep-water warming during the recent decades (Straile et al. 2003) reduced egg developmental time by about 3 weeks. This has two

implications: first, the period of potential egg mortality is shortened, and second, larvae appear earlier in the plankton.

Egg mortality due to predation has been considered a major loss for the Blaufelchen. Up to now, burbot and planarians have been identified to prey on whitefish eggs (Nümann and Quöß 1972). The Lake Constance whitefish do have short egg development times compared to other whitefish species (Eckmann 1987) which has been interpreted as an adaptation to reduce egg mortality (Eckmann and Rösch 1998). Assuming a mortality rate of  $0.02 \text{ day}^{-1}$  as in 2000/2001 and—all other things being equal—a decrease in developmental time from 87 to 65 days, the simulation model predicts an increase in total egg survival from 22 to 30%. Hence, warming could increase the survival of naturally spawned whitefish eggs considerably.

On the other hand, high deep-water temperatures will result in hatching of larvae already in early February, definitely well before the onset of the phytoplankton bloom and the subsequent increase in zooplankton which may be delayed even until April in some years (Weisse et al. 1990; Gaedke et al. 1998; Straile 2000). Starvation resistance of Blaufelchen larvae is rather high and at the low temperatures after hatching larvae are able to starve for up to 50 days until the point of no return is reached (Eckmann and Pusch 1991). This would allow larvae hatched in February to wait until even a late onset of the phytoplankton bloom. However, several copepod species are present in the plankton also during winter and, e.g. the calanoid *Eudiaptomus gracilis* reproduces also during February (Seebens et al., in review), which will provide nauplii for whitefish larvae. Therefore, larvae present in the lake in February and March do have the chance to feed and may gain some advantage over cold-bred larvae in, e.g. an increased ability to capture evasive

prey like copepods, earlier onset of growth and probably finally in survival (Miller et al. 1988). As a consequence, the YCS time series does not provide any evidence for a mismatch of whitefish larvae with their food despite the time travel of larvae after they emerge from the bottom. Winters with high bottom temperatures or a high  $\text{NAO}_{-1}$ -I which were followed by low spring temperatures or a low  $\text{NAO}$ -I did not show reduced YCS. In contrast, highest YCS were observed in years with high  $\text{NAO}_{-1}$  and  $\text{NAO}$  indices

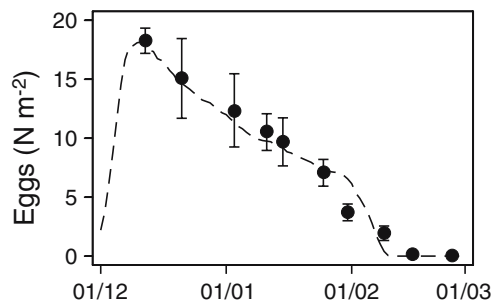
## Conclusions

Climate variability associated with the NAO did influence YCS of Blaufelchen in Lake Constance. Our time series analyses suggest that the influence of the NAO on Blaufelchen ecology is twofold, i.e. affecting the growth of larvae during spring, and with a time lag of 1 year, the egg development time. The influence of climate variability can be detected in the time series despite the fact that the population dynamics are severely modified anthropogenically due to strong fishing pressure, intensive stocking, and changes in the trophic status of the lake. This suggests that with conditions unmodified by humans, the effects of climate variability on the YCS of this population may be very strong. However we are unsure about the relative importance of the two effects on YCS as water temperatures in the lake during different months and depths were strongly interrelated. Nevertheless, our results show that the warm monomictic stratification regime of Lake Constance (Straile et al. 2003) results in a 1-year time lag of an ecological response, i.e. the developmental time of fish eggs, to meteorological forcing. Our results do further suggest that for a better understanding of YCS the fate of naturally spawned eggs and of both naturally and artificially produced larvae should be studied more intensively.

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**Fig. 5** Seasonal course of egg abundances in the winter 2000/2001 in the Blaufelchen spawning area at depths between 170 and 254 m. Model results with a spawning density of  $20 \text{ eggs m}^{-2}$ , a mortality rate of 2% per day and hatching after 330 degree-days are shown as a dotted line

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