Ann. Zool. Fennici 41: 281–290 ISSN 0003-455X
Helsinki 26 February 2004

Population regulation in coregonids: the significance of zooplankton concentration for larval mortality

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Received 26 Aug. 2002, revised version received 23 June 2003, accepted 7 July 2003

Rellstab, C., Bürgi, H. R. & Müller, R. 2004: Population regulation in coregonids: the significance of zooplankton concentration for larval mortality. — *Ann. Zool. Fennici* 41: 281–290.

Population size and fishing yield of coregonids has considerably diminished in many central European lakes where nutrient concentration, in particular phosphorus, has fallen to oligotrophic levels. In re-oligotrophicated Lake Lucerne, apart from slower growth, reduction in year class strength of the slow growing form of lake whitefish was identified as the major cause for decreasing yield. Stocking of lake whitefish larvae could not counteract this process. It was, therefore, hypothesised that larval mortality of lake whitefish, both from stocking and natural reproduction, had increased during re-oligotrophication because of food shortage during the early larval phase. Feeding experiments in aquaria with newly hatched lake whitefish larvae from Lake Lucerne, and using various concentrations of *Artemia salina* and zooplankton, showed a clear relationship between food concentration and mortality over the first 34 days. Elevated mortality of 40% or more resulted from food concentration of 20 zooplankton organisms per litre or fewer. Analysis of zooplankton data from Lake Lucerne indicated that concentration of zooplankton organisms usable by the whitefish larvae in late winter and spring was much lower in the years after 1984 than before. This might explain, at least in part, why year class strength and yield of the slow growing form of lake whitefish has decreased during re-oligotrophication of Lake Lucerne.

Introduction

The size of fish populations is the result of the regulative effect of density-dependent and density-independent processes (Goodyear 1980). Density-dependent processes, such as competition, act according to the density of the fish population, while density-independent processes are controlled by factors external to the populations, like temperature or light. Food concentration is a key factor for larval survival (Hoagman 1973, May 1974). Food concentration depends on the primary productivity of the system and may be influenced by fish and invertebrate predation and other factors such as temperature, patchiness and vertical migration of the zooplankton.

Until the middle of the 20th century, all European pre-alpine lakes were more or less oligotrophic, with clear water during most of the year, and with a diverse fish fauna (Müller 1993). After 1950, the concentration of total phosphorus in Lake Lucerne, an 11 380 ha lake situated in the centre of Switzerland, increased rapidly due to the loadings from agriculture and

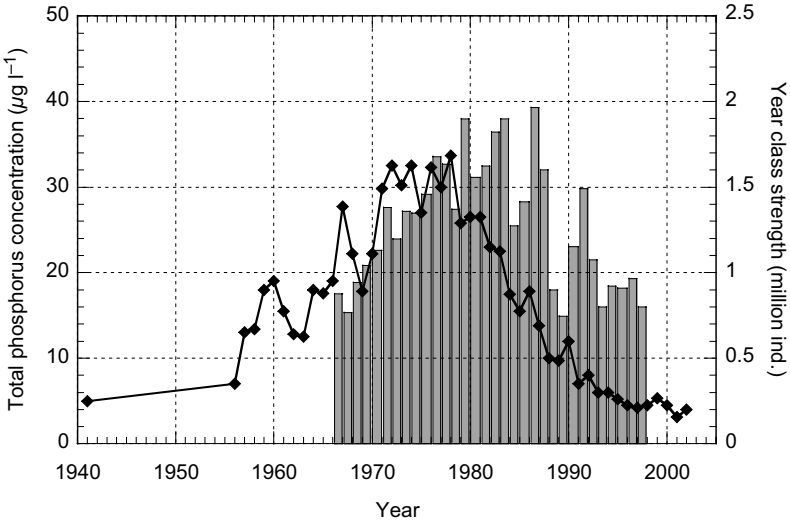

Fig. 1. Phosphorus concentration (spring circulation value) of Lake Lucerne (line), and virtual year class strength of slow growing form of lake whitefish (columns) (Data: Müller & Bia 1998 and EAWAG unpubl. data).

settlements. Maximum phosphorus concentration (spring circulation value) was 33.7 μg l^{-1} in 1978. Thereafter, water protection measures led to a rapid decline of total P concentration to a steady value of about 5 μg l^{-1} since 1995 (Fig. 1; Bührer & Ambühl 1996).

The slow growing form of lake whitefish (*Coregonus zugensis* Nüsslin, nomenclature according to Kottelat (1997), local name "Albeli"), a pelagic species that feeds on zooplankton, is economically the most important fish in Lake Lucerne. It spawns in November and December, and the larvae hatch between mid-January and mid-February (Birrer & Schweizer 1935), i.e. at a time when zooplankton concentration is very low. Larvae live close to the surface and are distributed over the whole lake area (R. Müller unpubl. data). At the age of two to three weeks, their yolk sack is used up, but like many other coregonid species (e.g. Hoagman 1973), the larvae already start feeding on zooplankton during the yolk sack period. As in other fishes, the larval phase is the most critical period (Hoagman 1973, May 1974). Food shortage is considered the major cause of elevated larval mortality in many coregonid species (Taylor & Freeberg 1984, Naesje *et al.* 1986, Ponton & Müller 1989).

Concomitant with the decrease of nutrient concentration, growth, yield and virtual year class strength of the slow growing form of lake whitefish decreased significantly after about 1987 (Fig. 1; Müller & Bia 1998). Between 1978 and 1998, total P concentration accounted for 47% of variation in year class strength (linear regression). Natural reproduction was estimated to contribute more than 70% to the stock (Müller & Bia 1998). It was therefore hypothesised that larval mortality of lake whitefish, originating from stocking (newly hatched larvae) and from natural reproduction, had increased during re-oligotrophication because of food shortage during the early larval phase. To test this hypothesis, feeding experiments in aquaria with newly hatched lake whitefish larvae from Lake Lucerne, and using various concentrations of *Artemia salina* nauplii and zooplankton, were conducted to elucidate the relationship between food concentration, growth and mortality. The experiments carried out by Taylor and Freeberg (1984) using food rations indicated that a ration of 32 *Artemia salina* nauplii per day are sufficient for *Coregonus clupeaformis* larvae to survive. In our experiments, food concentration (number of edible organisms per litre) was chosen as the test criterion. We further aimed at testing the suitability of *Artemia salina* nauplii and live zooplankton for these kinds of feeding experiments.

In order to put the results from the feeding experiments into perspective, long-time series of quantitative and qualitative zooplankton data from Lake Lucerne from 1976 to 1999 were analysed and interpreted, to characterize the feeding conditions for the whitefish larvae in Lake

Lucerne during the last 20 to 25 years and to identify their effect on year class strength. Furthermore, zooplankton was sampled and water temperature was measured in detail during the feeding experiments in early spring of 1999.

Material and methods

Feeding experiments

The basic idea of the feeding experiments was to offer zooplankton not in rations, like Taylor and Freeberg (1984) did, but in concentrations, measured as the number of edible food organisms per litre. Since the density of lake whitefish larvae in Lake Lucerne had been found to be very low (R. Müller unpubl. data), we assumed that predation by the larvae has no significant effect on the concentration of zooplankton in the lake. Therefore, in the experiments, prey concentration was kept as constant as possible. For technical reasons, this is difficult to attain because tanks cannot be very large to accommodate the number of fish larvae required. By keeping the density of larvae in the tanks relatively low, and by regularly measuring and adjusting food concentration, a workable compromise was achieved.

Fertilised eggs of the slow growing form of lake whitefish were obtained from the commercial fisherman A. Hofer, Meggen. The eggs were incubated either at 6 °C ("normal") or at 2 °C ("cold"), in order to obtain larvae for the two consecutive experiments.

The experiments were carried out in grey polyethylene water tanks holding 24.4 litres each. Water flow was adjusted to 0.2 l min^{-1}, so that the water would be replaced every two hours. The water used was sand filtered water taken from Lake Lucerne at 40 m depth. Water temperature was between 6.3 and 7.2 °C, i.e. 1–2 °C higher than the temperature to which the whitefish larvae were exposed in the lake. Light intensity was 136.5 ± 26.6 lux, with light from 08:00 to 18:00. All other parameters that could influence mortality and growth of the larvae were eliminated (weather, waves, etc.) or kept constant (temperature, light, day length, etc.). If larvae died or were taken out for measurements, they were not replaced, because the number of larvae should have no influence on the food density. Forty whitefish larvae were placed into each tank at the beginning of the experiments that lasted for 34 days. Tanks were cleaned daily before the first feeding in the morning. Food density was adjusted three times a day. The density of prey organisms in the tanks was determined by taking a sample of 0.24 l with a plastic tube and counting under a binocular microscope. The difference to the targeted density was added from a tank with prey organisms at a known concentration. The two types of food organisms used were nauplii of *Artemia salina* (Flüchter 1980, Rösch 1995), bred for 48 hours in 2% saltwater at 28 °C, and live zooplankton from Lake Lucerne, graded to a size between 95 and 500 μm by nets. Hartmann and Klein (1993) measured the mouth gape of the slow growing form of lake whitefish and found 0.64 to 0.71 mm for larvae of 9–10 mm length.

Two feeding experiments were conducted. In experiment 1, starting in mid-February, water temperature in the tanks ranged from 6.3 ± 0.2 °C on day 1 to 6.8 ± 0.3 °C on day 34. Five food concentrations in three replicates were tested: 10, 25, 50, 80 and 150 *Artemia* nauplii per litre. In experiment 2, starting at the beginning of April, concentrations were lower because they had evidently been too high in experiment 1. Food concentrations of 2, 5, 10, 20 and 150 *Artemia* or zooplankton organisms per litre were tested in two to four replicates. Water temperature ranged from 6.8 ± 0.5 °C on day 1 to 7.2 ± 0.2 °C on day 34. On days 8, 16 and 22 (experiment 1), and on days 15, 22 and 28 (experiment 2), five larvae were sampled each for measurements. At the end of the experiments, ten larvae, or less if fewer survived, were sampled. Larvae were measured for length, and their wet and dry weight was determined. Larvae were dried for 24 hours at a temperature of 105 °C. At the start of both experiments, length and weight of 40 one-day-old larvae were measured. Mortality in the feeding trials was monitored daily.

Cumulative mortality was calculated according to Weinhart (1992). Because some larvae were removed from the tanks during the experiments, the theoretical number of surviving larvae had to be corrected (Ortlepp 1984). Condition factor was determined according to Fulton (1904):

$$C = (W/L^3)100 \quad (1)$$

where: C = condition factor, W = wet weight (mg) and L = total length (mm)

Results were tested for significance at $p = 0.05$ using two-sided t-test with normal distribution.

Zooplankton data of Lake Lucerne

Zooplankton data for the years 1976 to 1999 had been collected by the Department of Limnology of EAWAG using a twin net with a mesh size of 95 μm. Per sampling day, three vertical tows were taken at the same location and pooled in one bottle. Thus, results are the mean of three samples, but without any error measurements. Unfortunately, sampling methods had changed during this time: until 1986, samples were taken from 0–110 m. After 1986, samples were taken from two depth ranges: 20–110 m, and 0–20 m. Bürgi *et al*. (1999) found 54% of the total zooplankton biomass between 0 and 20 m, and 46% deeper than 20 m. Because larvae of the slow growing form of lake whitefish feed near the lake surface, only the upper range was used. Older samples from the whole water column were corrected using the factors above. Weekly samples of zooplankton density (using the same method as mentioned above, except for the depth range) and water temperature were also taken from January to April 1999 in the depth range of 0–10 m.

Whitefish larvae are highly selective with respect to zooplankton organisms, preferring nauplii and small instars of copepods (Einsele 1941, 1965, Hoagman 1973, Hartmann & Klein 1993, Ponton & Müller 1988). Thus, only these smaller organisms were considered in the analysis of the zooplankton data: nauplii of copepods and juvenile forms of *Mesocyclops*, *Cyclops*, *Eudiaptomus*, *Bosmina* and *Daphnia*.

Results

The duration of the incubation period had a significant impact on length (t-test: $t = -6.9502$, df = 78, $p < 0.001$), wet weight (t-test: $t = 9.5472$, df = 78, $p < 0.001$) and dry weight (t-test: $t = 8.2876$, df = 65, $p < 0.001$) of the newly hatched larvae on day 1. Larvae originating from cold incubation for 102 days (experiment 2) were longer (total length: 10.1 ± 0.7 mm) and lighter (wet weight: 2.4 ± 0.6 mg) than larvae of experiment 1 (cold incubation for 24 days

Table 1. Mortality, total length, dry and wet weights and condition factor of the whitefish larvae after 34 days of experimental feeding (mean ± standard deviation).

Food concentration (ind. l^{-1})	No. of tanks	Mortality (%)	No. of larvae	Total length (mm)	Dry weight (mg)	Wet weight (mg)	Condition factor
Experiment 1 (*Artemia*)							
10	3	37.7 ± 7.0	30	12.0 ± 0.8	0.7 ± 0.2	4.3 ± 0.9	0.24 ± 0.00
25	3	15.8 ± 12.7	29	12.3 ± 1.0	0.7 ± 0.2	4.6 ± 1.1	0.24 ± 0.00
50	3	18.9 ± 12.9	30	12.5 ± 0.7	0.9 ± 0.2	5.5 ± 1.0	0.28 ± 0.00
80	3	17.7 ± 3.3	30	13.3 ± 0.6	1.2 ± 0.4	6.2 ± 1.0	0.27 ± 0.01
150	3	15.3 ± 6.5	30	13.5 ± 0.8	1.1 ± 0.3	6.4 ± 1.3	0.26 ± 0.02
Experiment 2 (*Artemia*)							
2	4	41.0 ± 16.4	39	11.4 ± 0.7	0.5 ± 0.2	3.7 ± 0.8	0.25 ± 0.02
5	4	12.0 ± 6.7	39	12.1 ± 0.6	0.6 ± 0.2	4.8 ± 1.0	0.27 ± 0.01
10	2	13.8 ± 4.3	20	13.2 ± 0.8	0.9 ± 0.2	6.6 ± 1.4	0.29 ± 0.01
20	2	2.8 ± 4.0	20	13.8 ± 0.9	1.2 ± 0.2	8.1 ± 1.2	0.31 ± 0.01
150	2	1.4 ± 2.0	20	16.4 ± 1.4	2.3 ± 0.6	14.6 ± 3.1	0.33 ± 0.00
Experiment 2 (Zooplankton)							
2	4	73.8 ± 19.0	24	11.3 ± 1.2	0.4 ± 0.4	4.1 ± 1.9	0.28 ± 0.03
5	4	49.9 ± 24.6	33	12.2 ± 1.3	0.7 ± 0.5	5.5 ± 2.4	0.31 ± 0.01
10	4	52.6 ± 10.0	24	13.4 ± 1.5	1.2 ± 0.5	8.0 ± 3.0	0.34 ± 0.02
20	2	38.0 ± 0.3	20	13.4 ± 1.4	1.4 ± 0.5	8.1 ± 2.8	0.33 ± 0.03
150	2	8.0 ± 2.1	20	14.9 ± 1.6	2.0 ± 0.6	11.8 ± 3.4	0.36 ± 0.00

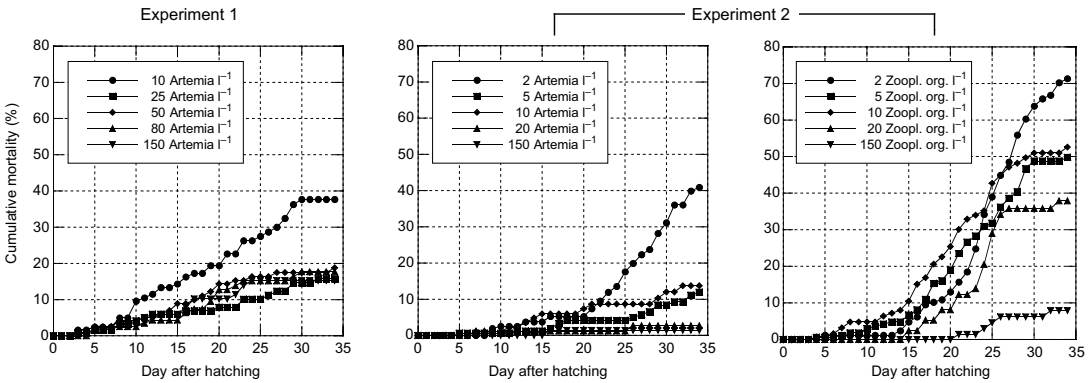

Fig. 2. Cumulative mortality of whitefish larvae of all experimental series as a function of time. Boxes indicate the nominal food concentration in the tanks.

only) (total length and wet weight: 8.9 ± 0.8 mm respectively 3.7 ± 0.6 mg). Mortality on day two (all tanks) was slightly higher in experiment 1 (4%) than in experiment 2 (0.5%). The sum of day-degrees from fertilization to hatching was almost identical in the two experimental groups (288 and 286, respectively).

Food concentration had an impact on survival, length, weight and growth after 34 days (Table 1). At the same concentration level, mortality of larvae fed zooplankton was significantly higher than that of larvae fed *Artemia* (*t*-test: $p < 0.05$, experiment 2). Furthermore, mortality after 34 days of larvae subjected to 102 days of cold incubation (experiment 2) was significantly or almost significantly lower than that of larvae subjected to only 24 days of cold incubation in experiment 1 (*t*-test: $t = 4.216$, df = 3, $p < 0.05$ when comparing larvae with a prey density of 10 *Artemia* per litre; $t = 2.7675$, df = 3, $p = 0.07$ when comparing larvae with a prey density of 150 *Artemia* per litre).

In experiment 1, only larvae exposed to a food concentration of 10 *Artemia* per litre showed elevated mortality (37.7 ± 7.0%) after 34 days (*t*-test: $t = 2.6228$, df = 4, $p = 0.06$, when comparing with larvae reared at 25 *Artemia* per litre). Mortality of larvae reared at 25 *Artemia* per litre was not different from that at 150 *Artemia* per litre (*t*-test: $t = 0.0608$, df = 4, $p = 0.95$). This lower level of mortality (15%–19%) represents the part of mortality not influenced by food concentration. In contrast to mortality, length, dry weight and wet weight were different between all different food concentrations (*t*-test: $p < 0.05$). Cumulative mortality as an effect of time is shown in Fig. 2.

In experiment 2, after 34 days, larvae fed *Artemia* or zooplankton again showed increased survival, length and weight with increased food concentration (Table 1). A prey density of 2 *Artemia* per litre resulted in significantly higher mortality than 5 per litre (*t*-test: $t = 3.2702$, df = 6, $p < 0.05$). At 10 *Artemia* per litre, mortality was not different from that at 5 per litre (*t*-test: $t = -0.3269$, df = 4, $p = 0.76$). Prey densities of 20 and more *Artemia* per litre had almost no effect on mortality. Larvae fed zooplankton experienced much higher mortality than those fed *Artemia* (*t*-tests: $p < 0.05$), when comparing the same food concentration levels. A food concentration of 2 zooplankton organisms per litre resulted in 73.8 ± 19.0% mortality, while at 5 and 10 per litre it was still 50% or slightly more. Prey density of 150 zooplankton organisms per litre had almost no effect on mortality. Cumulative mortality as an effect of time is shown in Fig. 2.

Comparing the condition factor of all larvae tested at a food concentration of 10 organisms per litre shows that larvae fed zooplankton had the best condition, followed by those fed *Artemia* in experiment 2 (longer hatching) and those from experiment 1 (Table 1). All differences are significant (*t*-tests: $p < 0.05$).

The approximate rate of food depletion in the tanks, calculated from the actual prey density before every food density adjustment, was highly variable. In experiment 1, until day 18, larvae at all food concentrations consumed 0%–40% of *Artemia* between two feedings. After day 18,

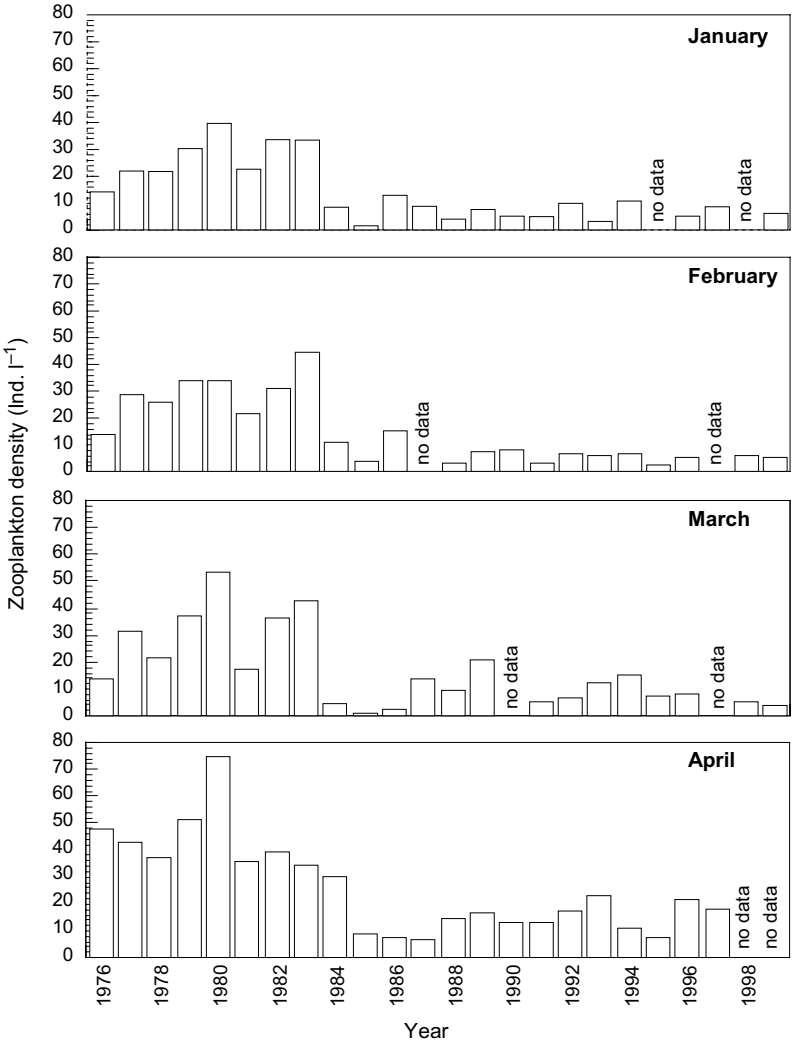

Fig. 3. Spring plankton concentration in Lake Lucerne from January to April, years 1976 till 1999 in a depth range of 0–20 m, considering only organisms edible by the whitefish larvae (nauplii of copepods and juvenile forms of *Mesocyclops*, *Cyclops*, *Eudiaptomus*, *Bosmina* and *Daphnia*).

food depletion was 50%–80% for larvae fed 10 *Artemia* per litre, 30%–80% for larvae fed 25 and 15%–55% for larvae fed 50 or more *Artemia* per litre. In experiment 2, larvae fed 2–10 *Artemia* per litre consumed 100% of the food between most feedings after day 11. During the same time period, at 20 or 150 *Artemia* per litre, food depletion was 10%–60% and 15%–45%, respectively. At 2 or 5 zooplankton organisms per litre, depletion was 50%–100% and 20%–100% respectively after day 13. Larvae fed zooplankton at a concentration of 10–150 organisms per litre consumed 0%–10% until day 20. Thereafter, larvae fed at 10 and 20 organisms per litre ate 20%–80% of the food between two feedings.

The spring concentration (January to April) of zooplankton edible by the larvae of the slow growing form of lake whitefish decreased markedly during re-oligotrophication (Fig. 3). The turning point appears to be around 1984, with a drastic decrease in January, February and March. Before this time, a zooplankton concentration of 20 or more organisms per litre was common in January and February. Thereafter, concentration decreased to about 5 to 10 organisms per litre, or even less. March had slightly higher concentrations, but shows the strongest decline in 1984. A similar decrease occurred in April in 1985 and concentrations level out at 10 to 20 organisms per litre after 1988.

Linear regressions of edible plankton density

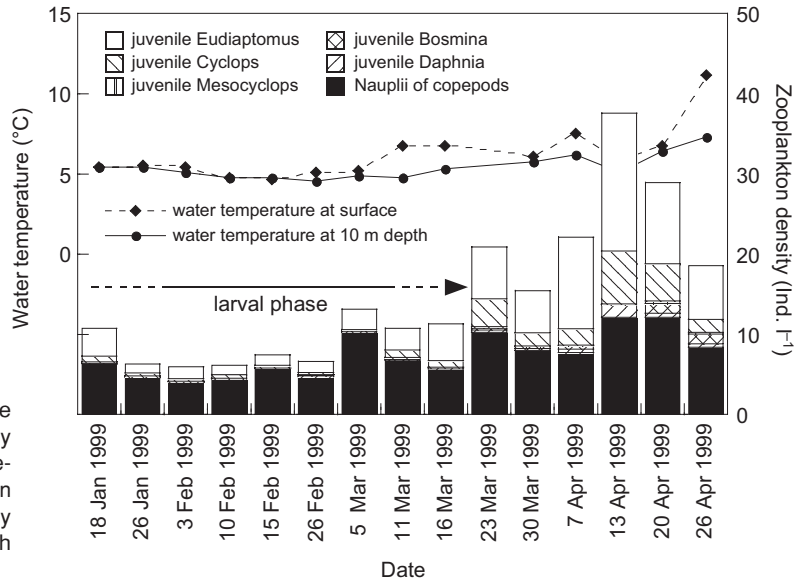

Fig. 4. Water temperature and zooplankton density (only organisms edible by the whitefish larvae) and composition in Lake Lucerne during early spring of 1999 in a depth range of 0–10 m.

versus total phosphorus (P) concentration for the years 1978 (highest P concentration) to 1998 indicate that the P concentration has an impact on zooplankton (R^2 = 0.64 in January, R^2 = 0.69 in February, R^2 = 0.41 in March, R^2 = 0.49 in April). Likewise, comparing zooplankton density and whitefish year class strength, a similar correlation becomes evident, at least in January and February (R^2 = 0.28 in January, R^2 = 0.40 in February, R^2 = 0.14 in March, R^2 = 0.23 in April).

Spring zooplankton in 1999 showed a clear seasonal succession (Fig. 4). Until the end of February, zooplankton density was around 6 organisms per litre. From the beginning of March on, density increased to a maximum of 38 organisms per litre on 13 April. Surface water temperature stayed at 5 to 5.5 °C until early March, then gradually increased to 11 °C at the end of April. The most abundant organisms were nauplii of copepods, followed by juvenile *Eudiaptomus* and juvenile *Cyclops*. Juvenile *Bosmina*, *Daphnia* and *Mesocyclops* were less important. This agrees with zooplankton data of 1976 to 1999, covering a depth range of 0–20 m.

Discussion

Our experiments showed that the higher the food concentration, the better survival after 34 days. This basically corroborates results published by Taylor and Freeberg (1984), and Steinhart and Eckmann (1992), both using rations. There appears to be a threshold prey density above which mortality is not influenced by the food concentration. In experiment 1, the threshold prey density was 25 *Artemia* per litre resulting in 15%–19% residual mortality. In experiment 2, the threshold prey density was 20 *Artemia* and 1%–3% mortality, and somewhere between 20 and 150 zooplankton organisms per litre and 8% residual mortality. The results from our experiment indicate that a zooplankton density of 20 organisms per litre or less is clearly insufficient and leads to a markedly elevated mortality. Rösch (1988) described a mortality of 20% over 45 days as normal when rearing conditions are at optimum.

We found that *Artemia* nauplii are excellent food organisms for larvae of the slow growing form of lake whitefish, inducing lower mortality and better growth than zooplankton, which is in agreement with Eckmann (1985). In experiments 1 and 2, a concentration of 10 *Artemia* per litre or less led to a mortality of 15% to 40%, while with zooplankton, the same food concentration resulted in more than 50% mortality (Table 1). Obviously, zooplankton organisms are more difficult to capture and ingest by the larvae than *Artemia*, at least in the first two to three weeks of

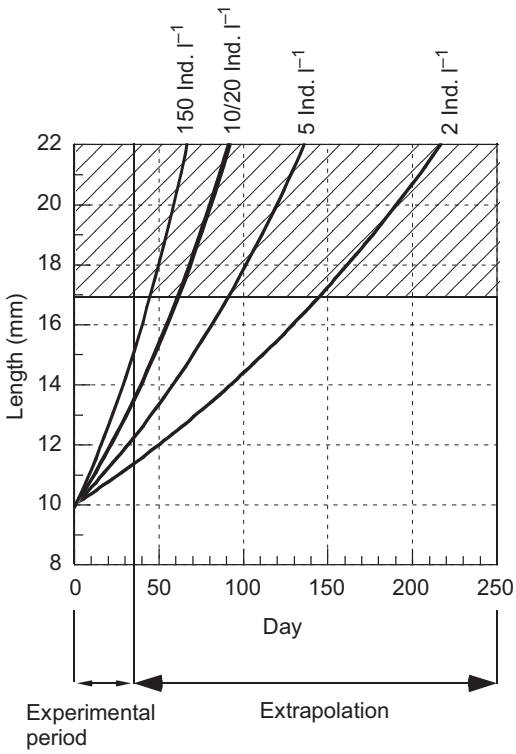

Fig. 5. Representation of exponential growth of larvae reared on different concentrations of zooplankton in experiment 2, extrapolated with regard to the "safe zone" (hatched area, Hoagman 1973) assuming constant temperature and prey concentration.

life. Hartmann and Klein (1993) observed that in the beginning of their experiment, larvae do not eat all the available zooplankton. We conclude that *Artemia* nauplii are very suitable for rearing experiments, but because they are particularly easy to capture, results cannot be directly compared with the conditions in a lake.

Food concentration also influences growth (Table 1). Still, in 34 days, none of the larvae reached the length of 17 mm which Hoagman (1973) defined as "safe zone", i.e. the size at which the larvae in nature would be exposed to a much lower predation pressure. So, at very high food concentrations, mortality can also be reduced indirectly through better growth. Fig. 5 shows an extrapolation of the growth of larvae used in experiment 2, reared on zooplankton. Assuming that all factors like food concentration and temperature remain stable (Fig. 4 shows the typical succession of food concentration and temperature at the beginning of the year), larvae living in an environment with 10–20 food organisms per litre would reach the safe zone in about 60 days.

Our results confirm earlier findings (Rösch 1995) that the duration of the incubation period affects length and weight of the newly hatched larvae, which, however, contradicts Łuczyński and Kolmann's (1985) results. On comparing mortality and growth in our experiments, we conclude that larvae originating from prolonged cold incubation have better survival and growth, and therefore better chances for survival in general, although the number of day-degrees is practically the same as in the "normal" group.

The rate of food depletion in the tanks between two food additions again points to a difference between larvae experiencing different incubation times. Results indicate that the effective average prey concentration in the tanks was generally lower than the targeted concentration. Food depletion was particularly strong in the experiments with *Artemia* and at the lowest targeted food concentrations. Therefore, interpretation of mortality and growth with respect to food concentration in both experiments holds some uncertainty, and extrapolation of growth and mortality from the experiments to the feeding conditions in the lake has to be done cautiously.

The zooplankton data from Lake Lucerne, analysed for their suitability as food for larval lake whitefish, present several uncertainties. One bias may arise from the conversion of the whole-depth data before 1986 to the two depth strata 0–20 m and 20–110 m. Furthermore, zooplankton organisms are not evenly distributed over the entire 0–20 m stratum. Also, whitefish larvae tend to feed close to the surface and not at 20 m depth (Ponton & Müller 1989). Thus, the effective prey density at the feeding depth of the whitefish larvae in Lake Lucerne may well have been higher than shown in Fig. 3. Comparing the long-term zooplankton data (0–20 m, Fig. 3) and the data of the samples taken during the experimental period (0–10 m, Fig. 4) at the same time (thus from January to April 1999) indicates that the zooplankton density in the depth range of 0–20 m is 35%–70% of the density in the depth range of 0–100 m. A further uncertainty results from plankton patchiness (Bürgi *et al.* 1999), because since 1976, only one location per date was sampled in Lake Lucerne.

Zooplankton density in Lake Lucerne for the months of January to April shows considerable but similar variation with time. As a food base for lake whitefish larvae, zooplankton in February and March, but less so in January, is most important, because larvae hatch between mid-January and mid-February (Birrer & Schweizer 1935). In experiment 1, the yolk sacks of the larvae were used up after 13–14 days. Because water temperature was on average 1–2 °C higher in the tanks than in the lake (*see* Fig. 4), yolk should even last longer under natural conditions and thus, the need of external food and the threat of starvation is lower. There has been an obvious and marked decline of zooplankton density after 1983 in January to March, and after 1984 in April (Fig. 3). The particularly poor food conditions for larvae in 1985 could have been responsible for the drop in year class strength that occurred in 1985 (Fig. 1). After 1986, zooplankton density in February never exceeded 8 organisms per litre in the upper 20 meters, presumably causing 50% larval mortality in 34 days according to experiment 2. In March, values vary a lot, with a maximum of 21 organisms per litre in 1989 and a minimum of almost 2 in 1986. This large variation can be explained, at least in part, by the fact that plankton was sampled only once a month, while temperature starts to increase in March (Fig. 4), so the exact sampling time is decisive. Assuming that a food density of 20 zooplankton organisms per litre is critical for larvae, this value has not been reached in January and February after 1984, just once in March (1989) and twice in April (1993, 1996).

Detailed weekly measurements from January to April 1999 provide a more reliable picture on the food conditions for larvae in Lake Lucerne than the monthly samples in Fig. 3, because measurements were taken in the 0 to 10 m depth range (*see* Fig. 4). Until the end of February, zooplankton density shows a maximum of 7.4 organisms per litre. Considering that the rearing experiments exclude other detrimental factors like predators and waves, mortality in the lake must have been even higher than the 50% found for similar prey density after 34 days of experiment.

The regulation of lake whitefish populations in lakes that change trophic state is complex and not completely understood. High larval mortality as a consequence of lower zooplankton density is certainly important but not the only mechanism influencing year class strength in re-oligotrophicating lakes. Slower growth of larvae and juveniles, resulting from lower prey density, may lead to higher age at sexual maturity. Smaller body size at maturity, coupled with lower condition, reduces absolute fertility and thus the number of potential offspring.

The presently very low nutrient concentration of Lake Lucerne will not endanger the population of the slow growing form of lake whitefish, although year class strength has decreased. Re-oligotrophication over the last 25 years is a lead back to the conditions before eutrophication, which was the main aim of lake restoration. Before that time period, coregonid year class strength must have been low but sufficient to sustain the population. As our experiments have shown, delayed hatching for stocking larvae later in spring, a procedure which was introduced in Lake Lucerne in 2001, could possibly help to increase yield. However, management of lake whitefish has its limits as year class strength cannot be augmented at will. Those interested in exploiting the fish stocks will therefore have to adjust to the lake situation, and not vice versa. Raising the nutrient concentration of Lake Lucerne to a more productive level in order to increase fishing yield is at present not possible for political and legal reasons: it would jeopardize the aims of lake restoration. A “healthy”, i.e. oligotrophic lake in central Europe typically holds a diverse fish fauna but does not provide the basis for high fishing yields. The question why the spawning time of lake whitefish and thus hatching of the larvae was not shifted to a later, more propitious period in spring in the course of evolution may represent a topic for future research.

Acknowledgements

We thank Alois Hofer, Meggen, for supplying the whitefish eggs. Technical support for the rearing experiments and with zooplankton sampling was provided by Carole Enz, Erwin Schäffer, Mampasi Mwembeno Bia and Andreas Steffen. Esther Keller analysed the zooplankton samples of early spring 1999. Claus Wedekind, Carole Enz, Susanne Fischer and two anonymous referees contributed constructive com-

ments to earlier versions of the manuscript. We thank all for their help.

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