

## Growth and size-selective mortality of vendace (*Coregonus albula* (L.)) and whitefish (*C. lavaretus* L.) larvae

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Vendace (*Coregonus albula* (L.)) and whitefish (*C. lavaretus* L.) larvae were sampled by stratified random sampling design in four Finnish lakes. Otolith microstructure analysis was used to investigate individual age, hatching time and growth rate of newly hatched larvae to reveal possible size-selective mortality during early life. The majority of the larvae hatched during a short period after the ice-off. Significant differences in hatching length between the lakes were found. Growth rate decreased when larvae became larger and the growth rate was slowest in the lake with the highest density of larvae. However, larger larvae were not relatively more abundant after first weeks and thus, size-dependent mortality was not evident. Hence, we observed that mortality of these two coregonid species during the first weeks was rather random in relation to size of the larvae. Overall, the mortality of vendace larvae with smaller hatching length was higher than that of larger whitefish larvae.

### Introduction

The early life stages of fish play an important role in determining the abundance of a year class. Generally, predation and starvation are the major reasons for mortality in fish larvae (Economou 1991, Letcher *et al.* 1996, Hutchings 1997). Mortality is high in larval phase and size-selective mortality can be remarkable (Houde 1989, Letcher *et al.* 1996, Houde 1997). It is generally recognised that larger larvae have lower mortality as compared with that of the smaller larvae because of decreased predation risk and better foraging success (e.g. Miller *et al.* 1988, Pepin 1993). On the other hand, under

certain conditions larger larvae may be more sensitive to predation than smaller ones (Litvak and Leggett 1992, Pepin *et al.* 1992). This may happen especially when encounter rates between larvae and predators increase more than larval susceptibility declines. Encounter rates may increase by increased swimming speed of larvae and/or increase in predator growth rates, sizes and changes in behaviour. The growth rate and size of larvae are affected by predation as well as water temperature, amount of suitable food and density of newly hatched larvae (Koho *et al.* 1991, Luczynski 1991, Karjalainen 1992, Helminen and Sarvala 1994, Helminen *et al.* 1997). According to Miller *et al.* (1988), mortal-

ity of fish larvae increases with decreased growth rate because larvae are vulnerable to predation and starvation for a longer time.

Vendace and whitefish are widely distributed in Finnish lakes and both are important targets for commercial and subsistence fisheries. Large variation in year-class strength is typical for short-lived species like vendace (Viljanen 1986) and it affects considerably the stock size available for the fishery. Since even small-scale differences in daily growth rate and mortality may notably affect year-class strength (Houde 1989), detailed information on the age, growth and mortality would be valuable in understanding the population dynamics of these coregonids. Otolith microstructure analysis provides a method to obtain individual information on age and growth of larval fish (e.g. Campana and Neilson 1985). In coregonids, age and growth analyses based on otolith microstructure have been performed in larvae reared under experimental conditions (Rice *et al.* 1985, Eckmann and Rey 1987, Huuskonen and Karjalainen 1993, 1995, 1998, Huuskonen *et al.* 1997, Huuskonen 1997) as well as in natural environments (e.g. Rice *et al.* 1987, Rey and Eckmann 1989). The aim of this study was to estimate the individual growth rate and mortality of vendace and whitefish larvae under field conditions by otolith microstructure analysis. The main objectives were: (1) to estimate daily growth rate and size-selective mortality of larvae during the first weeks; (2) to back-calculate hatching length and time of larvae and evaluate their implications to mortality; (3) to assess if the population size estimation method of larval coregonids is sensitive to the hatching time of coregonids.

## Material and methods

### Study areas

Vendace and whitefish larvae were sampled in four Finnish lakes: SW Pyhäjärvi 60°54'–61°06'N/22°09'–22°22'E, S Konnevesi 62°30'–62°40'N/26°20'–26°44'E, Paasivesi 62°06'–62°13'N/29°17'–29°31'E and Harvanselkä 61°47'–61°56'N/29°17'–29°38'E. According to the total phosphorus level the lakes are cat-

egorized as meso-oligotrophic. All lakes support productive vendace fisheries. Range of annual vendace catches have been 6.4–24.0 kg ha<sup>-1</sup> in SW Pyhäjärvi, 0.1–3.4 kg ha<sup>-1</sup> in Paasivesi and 0.2–16.0 kg ha<sup>-1</sup> in Harvanselkä (Karjalainen *et al.* 2000).

### Larval sampling

Larvae were sampled in 2001 immediately after ice-off (1st survey) as well as 1–3 weeks later (2nd survey: in lakes Paasivesi and Harvanselkä 2 weeks later, in S Konnevesi 3 weeks later and in SW Pyhäjärvi 1 week later) using a stratified random sampling. Sampling in each lake consisted of 10–21 sampling areas of which 7–10 areas were in the littoral zone (water depth 0–2 m) and 3–11 areas in the pelagic zone (water depth > 2 m) except in SW Pyhäjärvi where pelagic zone was considered to be water depth more than four meters because of the shallowness of the lake (94% of the lake area is less than 7 m deep) (Sarvala *et al.* 1988).

The samples were collected using a 5-meter vessel equipped with a jet engine. Two bongo nets were fitted in front of the vessel. The length of the nets was 2.5 m with a mesh size of 0.50 mm which is most suitable for the newly hatched vendace larvae (Viljanen and Karjalainen 1992). One of the nets caught larvae from the surface to 0.3 m and the other from 0.3 m to 0.6 m. One haul was taken in every sampling area using a sampling time of 4 minutes and towing speed of 4–6 km h<sup>-1</sup>. In Harvanselkä samples in pelagic zone were gathered using a 27-meter research vessel (r/v *Muikku*) equipped with bongo nets. The towing time was approximately 18 minutes at speed 7–9 km h<sup>-1</sup>. In addition, we used information on yolk reserves of coregonid larvae collected in 1989–2002 using similar sampling procedures and equipment.

All samples gathered were preserved in the field with a 1:1 mixture of 70% ethanol and 1% formalin. Water temperature, direction and strength of wind and other weather parameters were recorded during the sampling. The mean water temperature differed between the surveys in Paasivesi (6.2 °C/7.6 °C) (*t*-test: *p* < 0.01) and in S Konnevesi (7.5 °C/10.7 °C) (*t*-test: *p*

< 0.001) but did not differ in SW Pyhäjärvi (8.8 °C/10.0 °C) ( $t$ -test:  $p > 0.05$ ) and in Harvanselkä (9.7 °C/9.5 °C) ( $t$ -test:  $p > 0.05$ ).

### Otolith analysis

The samples were analysed in the laboratory after 3 to 8 months. From all 149 samples, random samples of vendace and whitefish larvae were taken for the measurements. The larvae were identified on the basis of pigmentation and counts of myomeres (Karjalainen *et al.* 1992). Total length and fresh mass of larvae from each sample were measured. Before measurements larvae were kept in distilled water for 15 minutes to minimize changes in length and fresh mass caused by preservation (Radtke and Dean 1982, Huuskonen and Karjalainen 1995). The developmental state of larvae was estimated visually according to the yolk resources on range 0 (no yolk), 1 (< 33% yolk left), 2 (33%–66% yolk left) and 3 (> 66% yolk left) (Karjalainen and Viljanen 1994). The number of measured larvae in each lake and year varied from 199 to 396 in vendace and from 36 to 270 in whitefish.

From each sample, one vendace larva and one whitefish larva were randomly taken for the otolith analysis. Total numbers of larvae from each lake used in the otolith analysis were 39–40 and 27–33, vendace and whitefish, respectively. The sagittae were dissected from the larvae using fine forceps, insect needles mounted in dowels and a dissecting microscope (48–320× magnification). Otoliths were mounted on a microscope slide with a drop of glycerol and covered with a cover slip. Otolith length, width, radius and maximum diameter of hatch check were measured and the number of daily growth increments was calculated using a compound microscope (125–1250× magnification).

### Calculations

The precision of daily increment counts was assessed by comparing the results of two persons. One of the investigators was a novice in otolith analysis while the other had long-term experience. Linear regression of daily increment

counts by one person against daily increment counts by the other person was performed. We used  $t$ -test to determine if the slope of the regression differed from 1 and the intercept differed from 0. Mean absolute percent error between daily increment counts by two persons was calculated (Mayer and Butler 1993):

$$E\% = 100[\sum(|y_1 - y_2|/y_1)]/n \quad (1)$$

where  $y_1$  = number of daily growth increments counted by one person,  $y_2$  = number of daily growth increments counted by the second person and  $n$  = number of pairs.

The mean number of daily growth increments was used in the otolith analysis. These mean values were then corrected with experimentally determined increment–fish age regressions (Huuskonen and Karjalainen 1995). These equations were  $y = 1.23x - 3.33$  for vendace and  $y = 1.16x - 2.10$  for whitefish, where  $y$  = number of daily growth increment and  $x$  = age of larvae (days).

The back-calculation of fish length is a technique based on the relationship between fish length and otolith radius (Francis 1990, Horppila 2000). The relationship between larval length (TL) and otolith radius ( $S$ ) was calculated as

$$TL = aS^b \quad (2)$$

where  $b$  = slope in equation:

$$\ln(TL) = \ln(a) + b\ln(S). \quad (3)$$

The back-calculation of individual length was performed by Monastyrsky's equation (Raitaniemi *et al.* 2000). It is the most generally used non-linear method taking into account allometric growth of fish (Francis 1990, Smedstad and Holm 1996, Raitaniemi *et al.* 2000). The larval length at age  $i$  was calculated as

$$TL_i = (S_i/S)^b \times TL \quad (4)$$

where  $S_i$  = otolith radius at age  $i$ ,  $S$  = otolith radius and TL = larval length.

The daily instantaneous growth rates of individual larvae based on otolith analysis were calculated as

$$G_{t_0-t_j} = \frac{\ln(TL_i) - \ln(TL_{i,0})}{(t_j - t_0)} \quad (5)$$

where  $TL_i$  = individual larval length at time of survey,  $TL_{i,0}$  = individual larval length at hatching,  $t_j$  = time of survey and  $t_0$  = time of hatching.

The average daily growth rates from hatching to survey were calculated as

$$G_{t_0-t_j} = \frac{\ln(TL_j) - \ln(TL_0)}{(t_j - t_0)} \quad (6)$$

where  $TL_j$  = mean larvae length at time of survey,  $TL_0$  = mean larvae length at hatching,  $t_j$  = time of survey and  $t_0$  = time of hatching.

The mean growth rates of larvae determined from population data were calculated as

$$G_{t_0-t_j} = \frac{\ln(TL_j) - \ln(TL_0)}{t} \quad (7)$$

where  $TL_j$  = mean length of larvae at time of survey determined from population data,  $TL_0$  = mean hatching length of larvae at survey determined from otolith data and  $t$  = mean age of larvae at survey determined from mean individual hatching date in otolith data.

The mortality of fish larvae in relation to predation efficiency of different-size predators was described with the model of Miller *et al.* (1988). Capture success of predators was calculated as

$$C\% = 100 - [(predator\ size/prey\ size + 3.37)/44.76]^{-2.28} \quad (8)$$

Predicted length distributions of the second survey were generated from the distributions

**Table 1.** Density of newly hatched vendace and whitefish larvae (ind. ha<sup>-1</sup> (95% confidence limits)) in study lakes during first survey in 2001.

Lake	Density, ind. ha <sup>-1</sup> (95% c.l.)	
	Vendace	Whitefish
SW Pyhäjärvi	15280 (9310–25078)	279 (257–300)
S Konnevesi	5039 (3725–6816)	20 (18–22)
Paasivesi	2740 (2505–2997)	578 (569–587)
Harvanselkä	856 (707–1037)	6 (5–7)

of the first survey assuming that all larvae had grown at the same mean growth rate as back-calculated from otolith data. It was also assumed that there was no size-selective mortality among the larvae between surveys. The larvae hatched after the first survey were removed from all distributions of the second survey based on yolk classification.

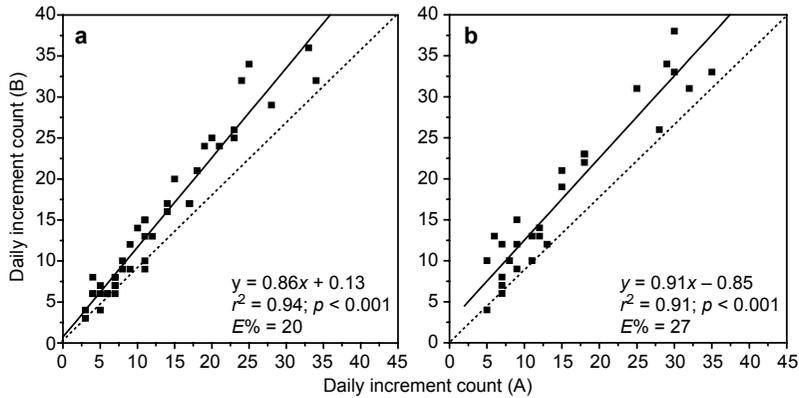
## Statistical analysis

The differences in length distribution and standardised length distributions were tested with the Kolmogorov-Smirnov test. The length distributions were standardised ( $x'i = (xi - x)/s$ , where  $x$  = mean length of larvae and  $s$  = standard deviation of length) to give a mean value of zero and standard deviation of one (Zar 1996). Standardisation of length distributions is a way to observe whether there is any skewness i.e. possible size-selective process acting between the surveys. The means of different parameters between the lakes were compared with ANOVA or non-parametric Mann-Whitney *U*-test when data were not normally distributed. Further, *t*-test was used when comparing individual growth rates and growth rates calculated from population data. Spearman's correlation coefficient with a correction of  $\alpha$  with the Bonferroni method ( $\alpha 1 = 0.05/n$ ) was used to test association between the larval density and growth rate. In addition, combined *p* values of Spearman's correlation coefficient were tested with Fisher's method (Tweedie 2001) ( $-2\sum_1^n \log p_i$  has a  $X_{2n}^2$  distribution under the null hypothesis, where  $p = p$  value of *i*th test and  $n =$  number of test).

## Results

### Densities of larvae

Densities of newly hatched vendace larvae were low in three study lakes in spring 2001 (Table 1) as compared with those of the previous years. Only in SW Pyhäjärvi were larval densities high. Abundance of whitefish larvae was highest in Paasivesi and lowest in Harvanselkä although the densities were generally low.



**Fig. 1.** Relationship between daily growth increment counts counted by two persons (A and B) in (a) vendace ( $E\% = 20$ ,  $a = 0$ ,  $b = 1$ ,  $n = 43$ ) and (b) whitefish ( $E\% = 27$ ,  $a = 0$ ,  $b = 1$ ,  $n = 28$ ) larvae. The 1:1 line is shown by a dotted line.

## Otolith analysis

The Monastyrsky power function relating the larval length (TL) to otolith radius (S) was

$$TL = 2.55S^{0.40}$$

with S.E. 0.22, 0.02, respectively  
( $r^2 = 0.69$ ,  $n = 159$ ,  $p < 0.001$ )

for vendace, and

$$TL = 2.56S^{0.42}$$

with S.E. 0.22, 0.02, respectively  
( $r^2 = 0.79$ ,  $n = 125$ ,  $p < 0.001$ )

for whitefish.

At hatching, the mean length of a vendace otolith was  $38.0 \mu\text{m}$  (S.D. = 11.9,  $n = 159$ ) and that of whitefish otolith  $54.7 \mu\text{m}$  (S.D. = 21.1,  $n = 125$ ).

The relationship between daily growth increments in otoliths counted by two persons was described by a linear equation (Fig. 1). The slopes and intercepts of the equations did not differ from 1 and 0, respectively ( $p > 0.05$ ). The mean percent error of increment counts by two persons was 20% for vendace and 27% for whitefish.

## Back-calculated hatching length and time

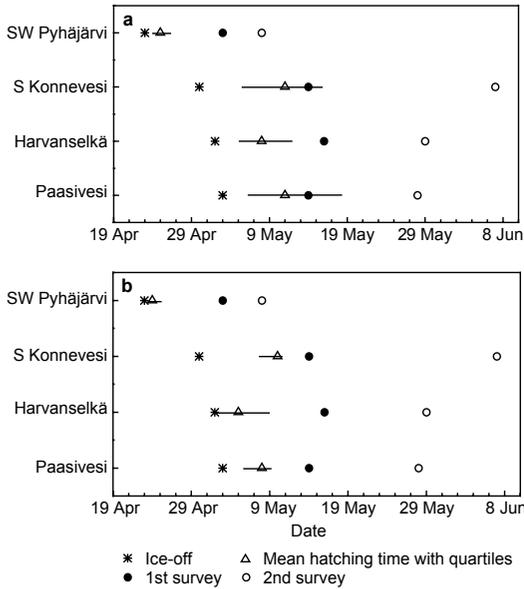
The mean hatching length of the vendace larvae differed significantly among the lakes in both

surveys (ANOVA:  $F = 6.105$ ,  $df = 3$ ,  $p < 0.001$ ). The larvae caught in the second survey had greater hatching length as compared with that of the larvae caught in the first survey except those from SW Pyhäjärvi (Table 2). The mean hatching length differed significantly among the lakes in both surveys also in the whitefish larvae (ANOVA:  $F = 11.889$ ,  $df = 3$ ,  $p < 0.001$ ). The hatching length of the whitefish larvae differed between surveys only in Paasivesi.

The majority of the larvae had hatched by the first survey (Fig. 2). Although the duration of the entire hatching period was 2–3 weeks, the hatching occurred mainly within a few days after the ice-off. During the second survey, most of the larvae had used their yolk resources almost completely except in SW Pyhäjärvi (Fig. 3). The hatching time of the larvae differed neither between littoral and pelagic zones (Mann-Whitney:  $Z = -0.613$ ,  $p > 0.05$ ) nor between species (Mann-Whitney:  $Z = -0.145$ ,  $p > 0.05$ ).

## Growth rate

The back-calculated growth rates based on otolith data were significantly different between lakes and surveys in both vendace (ANOVA:  $F = 8.571$ ,  $df = 1$ ,  $p < 0.01$ ) and whitefish (ANOVA:  $F = 5.639$ ,  $df = 1$ ,  $p < 0.05$ ) (Fig. 4). The larvae caught in the first survey had grown faster as compared with the larvae of the second survey. In S Konnevesi, the mean individual growth rate of the vendace larvae was significantly higher



**Fig. 2.** Mean hatching time with quartiles of vendace (a) and whitefish (b) larvae in the study lakes in 2001. Times of surveys and ice-off are also shown.

than that calculated from the population data ( $t$ -test:  $p < 0.01$ ). In the other lakes, there were no differences in growth rates calculated from otolith and population data ( $t$ -test:  $p > 0.05$ ). No differences in mean length of the larvae included in the population and otolith data were found ( $t$ -test:  $p > 0.05$ ) in lakes Harvanselkä and S Konnevesi i.e. random samples of larvae for the

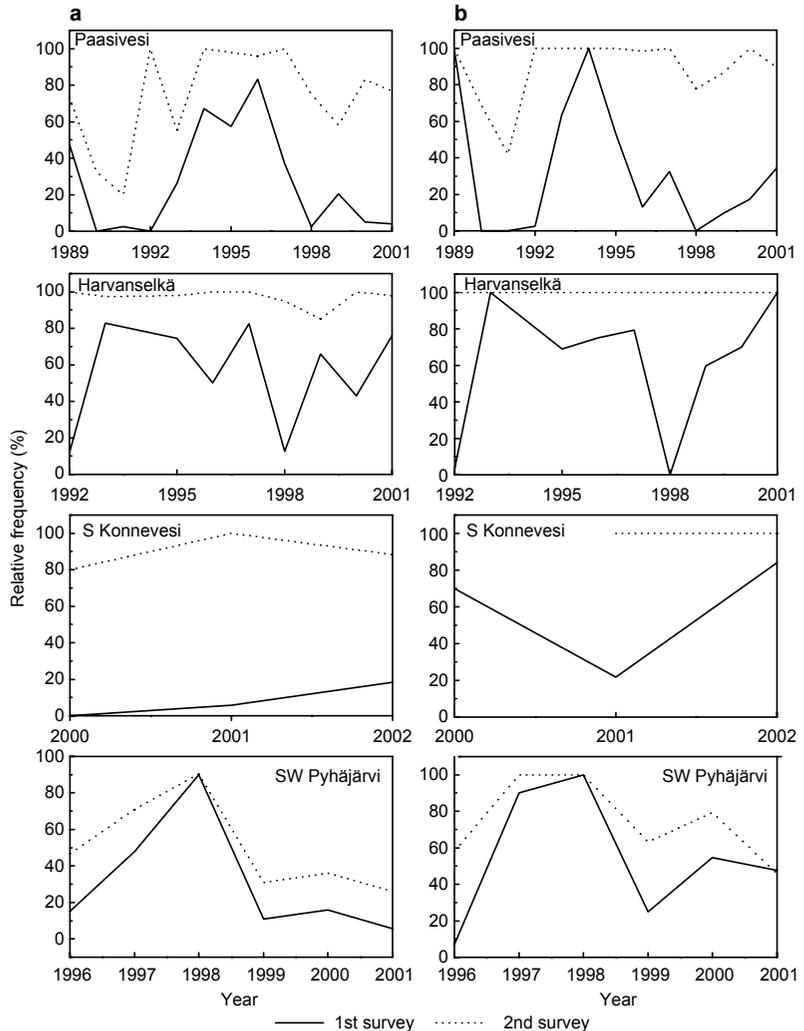
otolith analysis represent whole population data correctly. In other lakes such differences were found ( $t$ -test:  $p < 0.05$ ) so that the mean lengths of the larvae included in the otolith data were significantly higher than those in the population data. The growth rates of the larvae in littoral and pelagic zones did not differ (ANOVA:  $p > 0.05$ ).

The vendace larvae had grown faster than the whitefish larvae (Mann-Whitney:  $Z = -3.344$ ,  $p < 0.001$ ). Highest mean growth rate of vendace larvae was observed in S Konnevesi in both surveys, whereas slowest growth took place in Harvanselkä in the first survey and in SW Pyhäjärvi in the second survey. At the first sampling the mean growth rate of the whitefish larvae was highest in SW Pyhäjärvi and slowest in Paasivesi whereas it was conversely during the second survey. The average daily growth rate ( $\text{mm d}^{-1}$ ) from hatching to second survey was 0.06, 0.03, 0.06 and 0.03 in Paasivesi, Harvanselkä, S Konnevesi and SW Pyhäjärvi, respectively for vendace and 0.04, 0.03, 0.05 and 0.03 in Paasivesi, Harvanselkä, S Konnevesi and SW Pyhäjärvi, respectively for whitefish.

Significant negative correlation was found between the density and growth rate of the vendace larvae in Paasivesi and the whitefish larvae in Harvanselkä (Table 3). Overall, larval density and growth rate showed significant negative correlation when  $p$  values of different correlations were pooled.

**Table 2.** Back-calculated hatching length (mm) of vendace and whitefish larvae in two surveys in study lakes in 2001. Statistical significance of differences between two surveys tested by Mann-Whitney  $U$ -test are shown (– = data not available).

Lake	Vendace				Whitefish			
	Mean	S.D.	$n$	$p$	Mean	S.D.	$n$	$p$
Paasivesi								
1st survey	7.47	0.77	20	< 0.05	10.08	1.32	17	< 0.05
2nd survey	7.88	1.09	14		10.57	1.40	9	
Harvanselkä								
1st survey	7.67	0.73	19	< 0.05	9.14	1.49	21	> 0.05
2nd survey	7.75	0.81	11		8.76	1.01	12	
S Konnevesi								
1st survey	6.80	0.76	20	< 0.001	–	–	–	–
2nd survey	7.97	0.69	18		11.00	1.12	16	
SW Pyhäjärvi								
1st survey	7.30	0.80	20	> 0.05	9.77	1.07	12	> 0.05
2nd survey	7.41	1.29	20		9.16	2.06	20	



**Fig. 3.** Relative abundances of (a) vendace and (b) whitefish larvae with empty yolk sacs in the study lakes during 1989–2002 at the first and second surveys. Data of years 1989–2000 and 2002 from CORNET (Finnish Coregonid Stock Research and Fisheries Network) research project (unpublished). Note that the time between the two surveys is different in the study lakes (two weeks in Paasivesi and Harvanselkä, three weeks in S Konnevesi and one week in SW Pyhäjärvi).

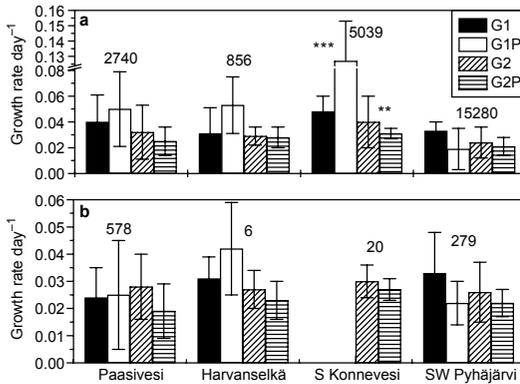
### Length distributions and mortality

The observed length distributions of the vendace larvae differed significantly between the two surveys (Kolmogorov-Smirnov:  $p < 0.05$ ) (Fig. 5). The length distributions of the second surveys were wider as compared with those of the first survey, especially in vendace in S Konnevesi and Paasivesi. The observed length distributions of the second survey differed from the simulated distributions in Paasivesi and S Konnevesi (Kolmogorov-Smirnov:  $p < 0.001$  and  $p < 0.05$ , respectively). Also in whitefish, observed length distributions differed significantly between the two surveys (Kolmogorov-Smirnov:  $p < 0.001$ ), except in Harvanselkä. In whitefish, the observed

length distributions of the second survey differed from the simulated ones in all lakes (Kolmogorov-Smirnov:  $p < 0.001$ ,  $p < 0.001$ ,  $p < 0.001$  and  $p < 0.01$ , in Paasivesi, Harvanselkä, S Konnevesi and SW Pyhäjärvi, respectively; Fig. 5). Standardised length distributions were not significantly skewed. They differed significantly between the two surveys only in the vendace and whitefish larvae of Paasivesi (Kolmogorov-Smirnov:  $p < 0.01$  and  $p < 0.001$ , respectively) but not in other lakes (Kolmogorov-Smirnov:  $p > 0.05$ ).

### Discussion

Variability in growth rates is a prerequisite for



**Fig. 4.** Mean growth rates and standard deviations of (a) vendace and (b) whitefish larvae in the study lakes in 2001. The growth rates calculated from different data indicated as follows: G1 = growth rate between hatching and first survey back-calculated from otolith data, G1P = growth rate between hatching and first survey calculated from mean lengths of population data, G2 = growth rate between hatching and second survey back-calculated from otolith data, G2P = growth rate between hatching and second survey calculated from mean lengths of population data. Statistical differences between growth rates based on different data tested with *t*-test are indicated as follows: \*\* =  $p < 0.01$ , \*\*\* =  $p < 0.001$ . The mean density of the larvae (ind. ha<sup>-1</sup>) for the study lakes is also given.

size-selective processes to operate (Ricker 1969). Unfortunately, there is also variability among the individuals in the relationship between somatic growth and otolith deposition i.e. slow-growing fish tend to have larger otoliths than their fast-growing conspecifics of the same size (e.g. Mosegaard *et al.* 1988, Campana 1992, Huuskonen and Karjalainen 1993). In this study, the  $r^2$  values (0.69 for vendace, 0.76 for whitefish)

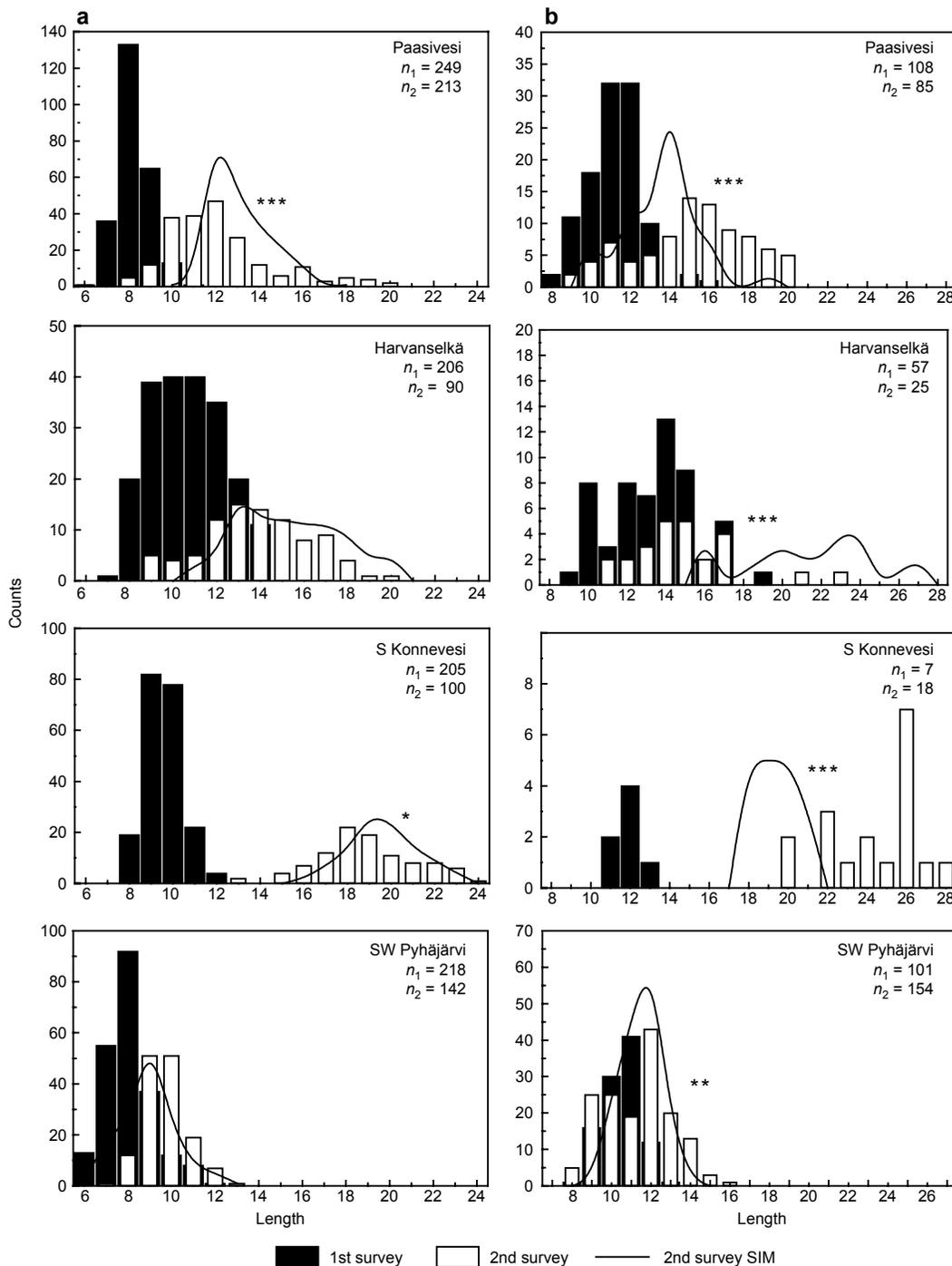
in the otolith growth–somatic growth relationship were not very high indicating uncoupling of otolith and somatic growth rates as well. The accuracy of back-calculated hatching length is dependent on how well the hatch check is located and its diameter measured as well as how it reflects the length at hatching (Pepin *et al.* 2001).

Estimation of a daily growth rate of fish larvae requires accurate age information obtained by counting daily growth increments. Otolith microstructure of Finnish coregonids has been studied quite intensively (e.g. Huuskonen and Karjalainen 1993, 1995, Huuskonen 1997, 1999). These experimental studies have demonstrated that the use of the otolith analysis in reconstructing the history of an individual larva is problematic and much more open to interpretation than the reconstructions in many other fishes. This is also illustrated by the relatively large mean percent errors of increment counts between the readers in the present study. At low temperatures the resolution of daily increments is poor and in fast-growing fish multiple sub-daily increments may exist (Huuskonen 1997). Although the problems were here taken into account by the use of experimentally determined correction equation (Huuskonen and Karjalainen 1995), caution has to be exercised in drawing the conclusions. However, the use of otolith analysis is justified by the fact that it is the only technique available to find out individual growth rate of wild fish larvae.

The majority of larvae hatched during a quite short period around the ice-off. This has been observed indirectly also by Sarvala *et al.* (1988) and Karjalainen *et al.* (2000). The short hatch-

**Table 3.** Correlation between density of larvae (ind. ha<sup>-1</sup>) and growth rate of larvae (d<sup>-1</sup>, both surveys combined) calculated individually by sampling areas. Statistical significance of Spearman's correlation coefficient (1-tailed) with a correction of  $\alpha$  by the Bonferroni method and significance of combined  $p$  values (Fisher's method) for both species is shown.

Lake	Vendace			Whitefish		
	Spearman	$p$ (1-tailed)	$n$	Spearman	$p$ (1-tailed)	$n$
Paasivesi	-0.544	0.001	32	-0.192	0.196	22
Harvanselkä	-0.075	0.347	30	-0.606	0.001	27
S Konnevesi	0.052	0.375	40	-0.044	0.438	15
SW Pyhäjärvi	-0.031	0.428	37	0.192	0.147	32
	Fisher's method: < 0.05			Fisher's method: < 0.05		



**Fig. 5.** Length distributions for (a) vendace and (b) whitefish larvae in the study lakes in 2001. The observed distributions in the first survey are indicated as 1st survey, observed distributions in the second survey as 2nd survey and the simulated distributions of the second survey as 2nd survey SIM. Statistical differences between shapes of observed and simulated length distributions in the second survey tested with Kolmogorov-Smirnov test are indicated as follows: \* =  $p < 0.05$ , \*\* =  $p < 0.01$ , \*\*\* =  $p < 0.001$ . From the distributions of the second survey, the larvae hatched after the first survey based on yolk classification have been removed. The larvae were categorized as follows: 6 = 5.5–6.4 mm, 7 = 6.5–7.4 mm, etc.

ing period supports spatial synchronisation of vendace stocks which is affected by environmental factors (probably meteorological) found by Marjomäki *et al.* (2004). Further, they suggested that synchrony in the variation of the density of newly hatched larvae was higher than in other population indices. Scale of correlation of environmental factors (e.g. ice-off) may be quite small because the most important period for determination of recruitment and temporal difference in the occurrence of this period is typically only a few weeks (Marjomäki *et al.* 2004). Due to short hatching period, environmental factors (especially water temperature) may have a remarkable effect on larval densities. The zooplankton densities are usually low in early spring but the availability of plankton increases rapidly with increase in water temperature (Lehtonen *et al.* 1995). Koho *et al.* (1991) found that the larvae hatching earlier have higher survival rates at all plankton densities. On the other hand, the larvae hatching earlier and at smaller size have a longer period of exposure to predation and also the potential size range of suitable food for them is narrower. Based on our otolith analysis, in most lakes only a small proportion of the larvae hatched between the two surveys. Yolk resources data of several years also support this. Therefore sampling design concerning population size estimation method of coregonids would be practicable. Generally, the first sampling has been done in Finnish lakes immediately after ice-off and it seems to give a reliable estimate of larval abundance hatched in that year.

Generally, larval densities were low in 2001 as compared with densities in other years (Valkeajärvi and Bagge 1995, Helminen *et al.* 1997, Karjalainen *et al.* 2000, Valkeajärvi and Marjomäki 2004). Densities of vendace larvae were especially low in Harvanselkä (856 ind. ha<sup>-1</sup>) and S Konnevesi (5039 ind. ha<sup>-1</sup>) when compared with mean densities of these lakes during 1992–2000 (3250 ind. ha<sup>-1</sup> and 29 619 ind. ha<sup>-1</sup>, respectively). The density of whitefish larvae was low, e.g. in S Konnevesi only 20 ind. ha<sup>-1</sup> whereas the mean densities during 1984–1993 were 2200 ind. ha<sup>-1</sup> (Valkeajärvi and Bagge 1995).

The growth rate of larvae varied between lakes and individuals and the differences in individual size increased in larger larvae. Growth

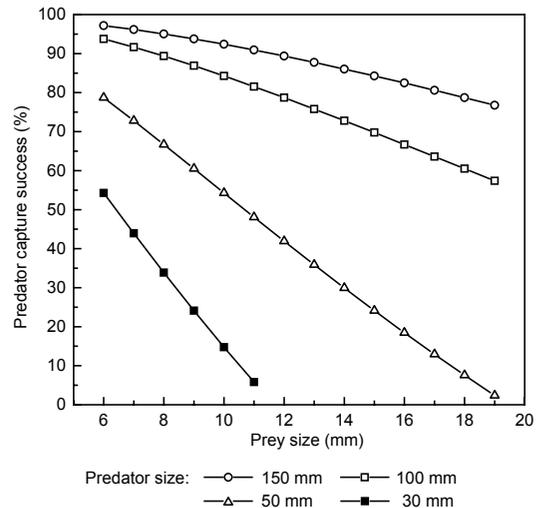
rates decreased when larvae became larger and the growth rates were lower in the lake with the highest larval density. However, the larger larvae did not seem to become relatively more abundant when spring progressed and thus, size-dependent mortality was not observed. Instead, mortality seemed to be rather random in relation to size of the larvae. This should not, however, be taken as an evidence of general non-existence of size selectivity in larval coregonids since under conditions which create larger variation in growth rates than in this study the selectivity may be different. For example, higher density of newly hatched larvae may induce selective forces because large relative size differences are more likely to be present in a large group of fish than in a small group (Folkvord 1997). On the other hand, Miller (1997) and Paradis *et al.* (1999) concluded that size-selective mortality may be difficult to evaluate in the field if predation is not restricted to the earliest period of larval development. It has also been reported that the size-selective mortality may become detectable only after a significant number (50%–70% of original abundance) of larvae died (Cowan *et al.* 1996, Paradis *et al.* 1999). Helminen and Sarvala (1994) suggested that larvae with low myomere counts have lower survival which results in the observed shifts in myomere counts and in apparently high growth rates.

During their first weeks of life the growth rate of coregonid as well as other fish larvae is mostly dependent on water temperature and the availability of zooplankton (Helminen and Sarvala 1994, Lehtonen *et al.* 1995) of which water temperature in early spring can affect survival even more than availability of food (Rey and Eckmann 1989). In our study lakes, the growth rate of larvae caught immediately after ice-off was higher than in the larvae caught later. One explanation for this would be that earlier hatched larvae have advantage in competition with larvae hatched later. However, later hatched larvae may have lower mortality rates with their longer hatching lengths despite their lower growth rates. The average growth rates (mm d<sup>-1</sup>) during 13–29 days after hatching range from 0.03 to 0.06 for vendace and from 0.03 to 0.05 for whitefish. These are slightly higher than in experimentally reared vendace (0.03–0.04) and whitefish (0.01–

0.02) larvae in earlier studies by Huuskonen and Karjalainen (1995) and Huuskonen *et al.* (1997) which however were observed rates of older (37–71 days) larvae. The daily instantaneous growth rates of body fresh mass were 0.07, 0.13, 0.14 and 0.07 in Paasivesi, SW Pyhäjärvi, S Konnevesi and Harvanselkä, respectively. They were higher than mean daily instantaneous growth rate in some Finnish coregonid lakes (0.04) during 1989–1997 (Karjalainen *et al.* 2000). The growth rate was similar in larvae hatched both in littoral and pelagic zones which was also found by Karjalainen *et al.* (2002). Amount of food in gut of vendace larvae is also found to be similar among littoral and pelagic larvae (Sutela *et al.* 2002).

Vendace and whitefish larvae spend their first weeks in the same nursery areas (Karjalainen and Viljanen 1994). The hatching is mainly affected by water temperature but also oxygen content of water has been shown to have an effect on hatching time of vendace larvae (Viljanen and Koho 1991). Therefore input of thawing water to a lake and the weather conditions of spring can affect both timing and length of hatching period. In our study, no differences were found in hatching time between the vendace and whitefish larvae and hence both intra- and interspecific food competition exists. Differences in length at hatching between lakes probably indicate regional differences in water temperature during the spring although there may also be population-specific size differences. The later larvae hatched the larger they were due to longer development time during incubation. The larvae caught during the second survey had been longer at hatching as compared with larvae caught in the first survey which may imply that the larvae with smaller hatching size may have died by the second survey. Hence, larvae with greater hatching length seemed to have slightly lower mortality rates. Also Meekan and Fortier (1996) suggested that the potential for faster growth and thereby for lower mortality expressed by the survivors may have been present at hatching. On the other hand, hatching times of larvae caught in different surveys were the same only in SW Pyhäjärvi.

The mortality among the vendace larvae may be remarkable (64%–95%) during the first three weeks of life while in whitefish the vulnerability to predation is lower due to longer hatching



**Fig. 6.** Effects of a predator size on the mortality of the fish larvae modelled with the method of Miller *et al.* (1988). Prey size-scale corresponds to the sizes of coregonids larvae in first weeks of their life history.

length and shorter “risk” period (Karjalainen and Viljanen 1994, Karjalainen *et al.* 2000). The effects of predation can be both direct and indirect. The predator avoidance may decrease feeding time and thus growth rate of larvae. On the other hand, mortality caused by predation may increase survival rate of the remaining larvae due to higher food availability in lower larval density (Karjalainen 1992). Our results show also that the mortality of the vendace larvae with smaller hatching length was higher than of larger whitefish larvae. The risk of predation decreases with increase in larval size because of e.g. better swimming ability of larvae. Therefore we suggest that size-dependent mortality may play a more significant role in the early life of vendace than of whitefish larvae. This reflects different life-history strategies of these coregonids with trade-off between offspring size and number. Size of offspring is usually clearly linked to their chances of survival (Wootton 1990, Rose *et al.* 2001).

The predator size has an effect on mortality of fish larvae (Fig. 6). The theoretical capture success of the largest fish predator examined (150 mm) was fairly independent of the prey size. Capture success of a 100-mm fish predator decreases by 35% during the increase of prey larvae size from 6 mm to 19 mm while the respective decrease is 75% in a 50-mm preda-

tor. Small-size predators (30 mm) are practically incapable of capturing larvae larger than 10 mm. Predation may be a significant cause of mortality also among coregonids. Minnow (*Phoxinus phoxinus* L.) and perch (*Perca fluviatilis* L.) are the potential fish predators for vendace larvae (Huusko and Sutela 1992, 1997). Mortality caused by the minnow is highest during the yolk sac period of vendace larvae with size under 12 mm. The significance of perch as a predator increases when vendace larvae reach the size of 12–14 mm (Huusko and Sutela 1992, 1997). However, capability of fish larvae to escape predators increases remarkably with increase in the larval size. Vulnerability of fish larvae to predation has been observed to decrease when prey was 10% or more of the predators' size (Paradis *et al.* 1996). In aquatic ecosystems, most outcomes of interactions between individuals, species and populations are determined by the body size (Werner and Gilliam 1984, Fuiman 1994). The shortage and/or quality of food available can result in higher mortality than predation. Rice *et al.* (1985) concluded that larvae of *Coregonus hoyi* did not die only due to a lack of food in field conditions, but starvation could increase their vulnerability to predation. Whether fish larvae died from predation or starvation depended much more on the intrinsic variables related to metabolism and starvation resistance (Letcher *et al.* 1996). We suggest that 50–150 mm fish predators (e.g. smelt, minnow and perch) can cause notable mortality of coregonid larvae, especially in the early life of vendace. One-year-old vendace may also be potential predators via intercohort cannibalism because they live partly in the same areas in the littoral zone as newly hatched larvae. It may also be one explanation to annual oscillations of a vendace stock via delayed density-dependent processes (Marjomäki 2003). Intercohort cannibalism has been documented in marine fishes (e.g. Valdés Szeinfeld 1991, Folkvord 1997) but in vendace only some individuals seem to have cannibalistic features (Huusko and Sutela 1992). However, it would be enough to have a remarkable effect on recruitment in lakes where most of the larvae are concentrated in the pelagic zone, e.g. in Harvanselkä (86%) and Paasivesi (72%) (Karjalainen *et al.* 2002) and larval densities are low (Folkvord

1997). In addition, in spring when the density of zooplankton is low, predators may shift to feeding on larvae (Huusko and Sutela 1992). Large-size (> 150 mm) fish predators (mainly perch), in turn, may not be very important predators of coregonids larvae despite their high foraging efficiency. The relatively small vendace and whitefish larvae may be energetically unfavourable prey items for the larger fish predators.

In conclusion we support the concept of early life stages of coregonids playing an important role in determining year-class strength. The majority of the larvae hatched during a short period after the ice-off. Differences in hatching length between the lakes were found. Growth rate was slowest in the highest larval densities and it decreased when larvae growth progressed. However, larger larvae were not relatively more abundant after first weeks. We agree that the larval mortality is high but the size-selective mortality was not so evident as we expected.

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